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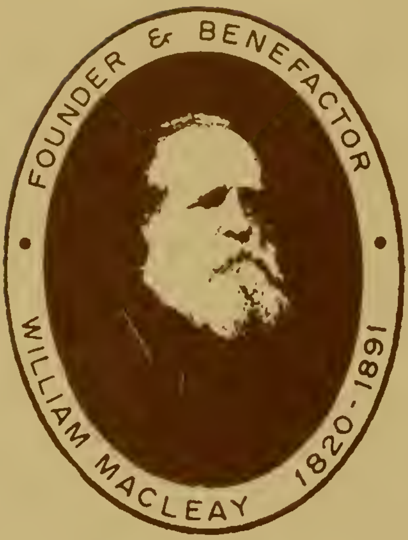

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Cover motif: The fossil *Nymbiella lacerata*, Fig. 15 from the paper by Holmes, this volume. Drawn by Heidi Anderson.

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VOLUME 124
January 2003

EDITORIAL

This is the first volume to be produced entirely by electronic means and in then new A4 format. The process has taken a great deal more time and effort than anticipated, resulting in the publication of Volume 124 being held over until January 2003. Therefore no volume is dated 2002 (Volume 123 was published in Dec 2001). Volume 124 is covered by 2002 subscriptions and memberships.

Volume 125 is expected in the second half of 2003 and will contain a section with papers arising from Monotreme III, a symposium being held 10-11 July 2003 by the Linnean Society of New South Wales and the Australian Mammal Society. Details of that symposium can be obtained from the Secretary of the Linnean Society.

In an attempt to contain the increasing costs of producing this journal, the Linnean Society now uses desk-top publishing to provide Southwood Press with printer-ready copy. At the final stage the journal is in PDF. Therefore any subscriber or member who would prefer to receive the journal in this format on Compact Disc should contact the Secretary. Since postage costs are becoming a major financial burden to the Society, the savings resulting from sending a CD rather than a printed journal are important. It is very likely that in the near future the journal may be available on-line, but at present the files are simply too large to allow transmission of the entire journal volume.

In-house production puts a considerable workload onto voluntary staff and therefore the cooperation of authors in submitting manuscripts in the correct format is essential. It will be necessary to return manuscripts submitted that are not in accordance with the 'Instructions for Authors' as summarized at the back of this volume and as available at the Society's web site or from the Secretary.

This volume is a first step into a new era of publication. It is certainly not perfect, and any comments or suggestions would be warmly welcomed by the editor. This first step has been difficult, and would have been impossible without the technical support of Bruce Welch from Southwood Press and the services of the Dubbo Secretariat in transferring author's artwork and photographs to electronic files.

M.L. Augee
Editor

Larval Distributions of Some Commercially Valuable Fish Species Over the Sydney Continental Shelf

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Smith, K.A. (2003). Larval distributions of some commercially valuable fish species over the Sydney continental shelf. *Proceedings of the Linnean Society of New South Wales* **124**, 1-11.

The cross-shelf and vertical distributions of larvae of 12 species of commercially valuable marine fish are described from continental shelf waters off Sydney, south-eastern Australia. Depth stratified sampling was conducted along a shore-normal transect on 3 and 4 consecutive nights in January and April, respectively, 1994. Larvae of the commercially valuable species *Hyperlophus vittatus, Sardinops sagax, Engraulis australis, Argyrosomus japonicus, Pseudocaranx dentex, Trachurus novaezelandiae, Liza argentea, Sillago flindersi, Acanthopagrus australis, Pagrus auratus, Rhabdosargus sarba* and *Gerres subfasciatus* together represented 11947 of the 50781 total fish larvae in samples. Species distributions extended to the outer shelf or slope, although the majority of larvae occurred in subsurface waters of the nearshore mixed layer. The majority of larvae were at a preflexion stage of development. Where present, later stage larvae tended to exhibit a different distribution to that of earlier stage larvae, although trends were variable among species. Results are discussed in relation to existing information on the larval distributions and spawning times of each species.

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KEYWORDS: ichthyoplankton, fisheries, flexion.

INTRODUCTION

Studies of early life history can provide valuable information to managers of fisheries resources. The spatio-temporal distribution of planktonic larvae, at various developmental stages, can help to infer the timing and location of spawning, and may assist in the interpretation of juvenile recruitment variability. Such information is most useful when coupled with oceanographic data (e.g. Caputi et al. 1996).

Australian marine ichthyoplankton communities are typically diverse but numerically dominated by species of low fisheries value (Leis 1991; Gray 1993; Smith and Suthers 1999). The low abundances of species of higher value often preclude their individual attention in final analyses and published reports, contributing to a dearth of information on the early life history of many of Australia's commercially valuable fish species (hereafter 'commercial species'). The limited number of continental shelf ichthyoplankton studies, compared with those conducted within estuaries, is also a contributing factor.

Several ichthyoplankton studies have been conducted in south-eastern Australian shelf waters (Miskiewicz 1987; Gray et al. 1992; Gray 1993, 1996, 1998; Dempster et al. 1997; Smith and Suthers 1999; Smith et al. 1999; Smith 2000). Although generally not targeted, larvae of numerous commercial species have been encountered in these studies. However, only some of the larval distributions and developmental stages of commercial species captured in shelf waters during previous studies have been described (Gray 1993, 1998; Smith 2000).

Some commercial species occurring off south-eastern Australia are also distributed in other shelf regions, suggesting inferences about early life history may be drawn in the absence of local information. However, widespread intra-specific differences in spawning patterns and modes of larval dispersal among geographic regions and oceanographic regimes demonstrate the importance of local observations (e.g. Juanes et al. 1996). The aim of this paper is to provide local observations on the cross-shelf distributions and larval developmental stages of 12 species of commercial fish found in shelf waters off Sydney during two surveys in 1994. The outer shelf occurrence of larvae of these species has not been previously described off Sydney. Samples described in this paper constitute a valuable contribution to the limited body of knowledge concerning the early life history of commercial fish in Australian marine waters.

MATERIALS AND METHODS

Location and time of study

Data were collected in continental shelf waters adjacent to Sydney, on the south-eastern coast of Australia (Fig. 1). Currents over the shelf are predominantly southward, due to the influence of the East Australian Current (EAC) and associated eddies (Nilsson and Cresswell 1981). Compared to along-shore currents, cross-shelf currents are small, usually <10cm/s (Middleton 1987). Density variability in the Sydney coastal ocean is primarily the result of changes in temperature (Griffin and Middleton 1992). During the summer months, shelf waters generally exhibit strong temperature stratification (White and Church 1986).

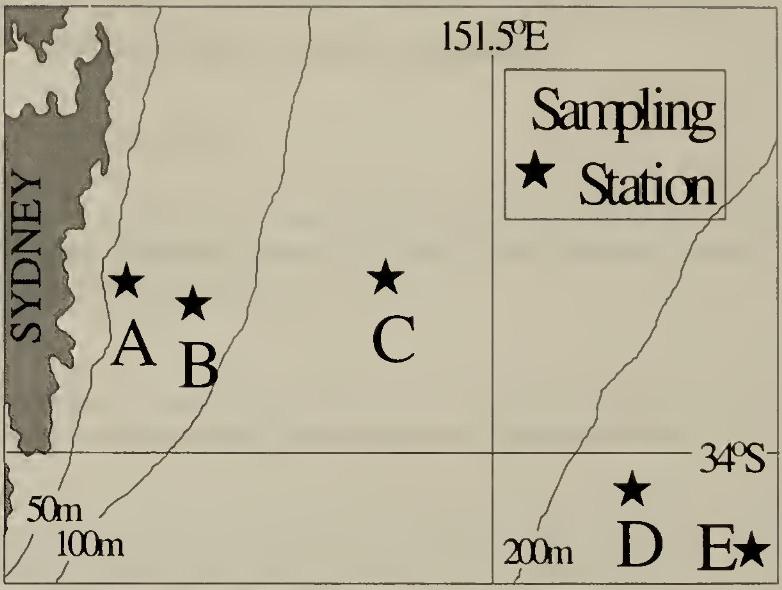

Figure 1. Location of sampling transect across Sydney continental shelf. 200 m isobath denotes shelf break.

Data were collected during two 10 d cruises, in January and April, 1994, aboard the research vessel, R. V. Franklin. On both cruises, data were collected from 5 stations along a cross-shelf transect. The transect began 2.7 km offshore and ended 40 km from the coast. Plankton sampling stations A, B and C were within shelf waters (bottom depths less than 150 m). Station D was at the shelf break, (bottom depth 250m), and station E occurred over the continental slope (bottom depth 600 m) (Fig. 1, Table 1). Plankton was collected on 22, 23 and 25 January and on 5, 6, 7 and 8 April. Some locations were not sampled on 7 April due to bad weather. Plankton was collected at night between 2030 and 0500 hours in January, and 1900 and 0600 hours in April. Sunrise and sunset were at approximately 0600 and 2000 hours in January, and 0600 and 1745 hours in April, respectively.

TABLE 1.
Details of location, bathymetry and sampling depth intervals for ichthyoplankton sampling stations.

Station	Distance offshore (km)	Bottom depth (m)	Depth of sampling intervals (m) Surface	Shallow	Middle	Deep
A	3	67	0-1	15-30	30-40	40-50
B	7	83	0-1	15-40	40-60	60-70
C	16	130	0-1	15-40	40-80	80-120
D	33	250	0-1	15-40	40-80	80-120
E	40	600	0-1	15-40	40-80	80-120

Collection and processing of samples

Surface plankton was collected by a 75 x 75 cm square mouth net (330 μm mesh), fitted with a General Oceanics flow meter. Two surface hauls, each of 6 minutes duration, were conducted at each station per night. Average volume of water filtered by the surface net was 291 m^3.

Subsurface plankton was collected by a multiple, opening and closing net with a square mouth of 1 m^2 and mesh size of 330 μm. The net was fitted with temperature, conductivity and depth sensors and two General Oceanics flow meters - one inside and one outside the net mouth. Real time data were communicated to an operator onboard ship who electronically triggered each net release. At each station, three subsurface depth strata were sampled. Strata were designed to sample above (shallow), within (middle) and below (deep) the thermocline where possible at each station. Actual sampling depths varied according to hydrography and water depth at each station (Table 1). Subsurface haul durations were 10 minutes and each depth stratum was obliquely sampled once per station per night. Average volume of water filtered by the subsurface net was 429 m^3.

Plankton samples were immediately placed into seawater and 5-10% formalin. Fish were removed from samples between 1 and 24 months after collection, counted, identified and then stored in 95% ethanol. Larvae were assigned a developmental stage of preflexion, flexion, or postflexion. Flexion is the stage during which the notochord tip turns upward (Neira et al. 1998). Fin development is largely completed at the end of flexion.

Larvae of twelve commercially valuable fish species were identified by descriptions in Leis and Trnski (1989) and Neira et al. (1998). Some other commercially valuable species, which were present in samples, were excluded due to very low abundance or difficulty in identification to species level. A summary of the Australian distribution and seasonality of each larval species can be found in Neira et al. (1998).

Raw abundances per sample were standardised to density of larvae 100 m^{-3} of water filtered. Mean density of each stage of each species was calculated for each sampling location (i.e. depth within station) during each sampling period.

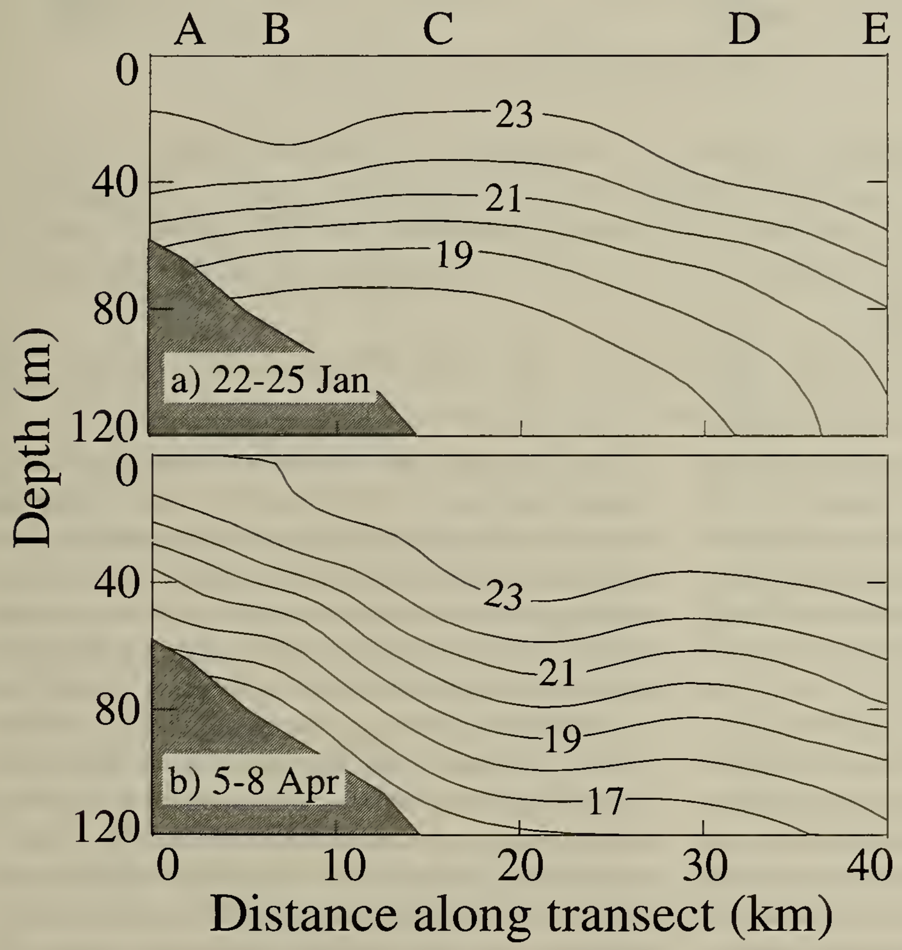

Figure 2. Average temperature (°C) profile across Sydney continental shelf during sampling on a) 22-25 January, and b) 5-8 April, 1994. Sampling stations A-E shown along top of profile.

RESULTS AND DISCUSSION

During both sampling periods, a mixed layer of 23 °C and 20-50 m depth, overlay the shelf. The mixed layer extended over the entire shelf region during January but, during April, was displaced from the nearshore region by cooler, upwelled water (Fig. 2). There was a tendency for the distributions of some species to extend further from the coast in April compared with distributions in January. This tendency was most pronounced in the carangids, *Pseudocaranx dentex* (silver trevally) and *Trachurus novaezelandiae* (yellowtail scad), and coincided with the offshore displacement of the nearshore mixed layer (Fig. 2). For a full description of this coastal upwelling event see Smith and Suthers (1999).

A high density (298 larvae 100 m^{-3}) of *Hyperlophus vittatus* (sandy sprat) occurred in a single deep sample taken at station A on 22 January (Fig. 3a, Table 2). Densities in other January samples were relatively low. Few individuals were taken in April and these mostly occurred at shallow depths over the inner shelf. Flexion and postflexion *H. vittatus* were rare during both sampling periods and no trends were apparent in the vertical distribution of these stages.

The occurrence of *Hyperlophus vittatus* off Sydney in January is consistent with spawning by this species during late summer and early autumn off eastern Australia (Ramm 1986; Miskiewicz 1987). The occurrence of preflexion *H. vitattus* off Sydney (this study) and to the north of Sydney (Miskiewicz 1987), suggest a large potential spawning area. Off Western Australia, spawning also occurs over a long length of coastline (Gaughan et al. 1996). The extremely patchy, coastal distribution of *H. vittatus* larvae observed off Sydney may be typical for this species (Gaughan et al. 1996).

Engraulis australis (anchovy) were less abundant in April than in January. Spawning peaks between spring and autumn throughout the species distribution, and a decline in larval density off Sydney between January and April is consistent with decreasing

TABLE 2.
Range of non-zero densities (larvae 100 m^{-3}) per sample [first line] and percentage of samples containing larvae [second line] per month. (n/a = no larvae; * = larvae in one sample only)

	January			April		
Species	Pre-flexion	Flexion	Post-flexion	Pre-flexion	Flexion	Post-flexion
Hyperlophus vittatus	0.41 - 298.28 14	0.30 - 0.70 3	n/a	0.02 - 0.18 6	n/a	0.02* 1
Engraulis australis	0.24 - 78.33 31	0.42 - 16.67 15	0.31 - 2.00 11	0.01 - 0.83 10	0.01 - 0.02 2	0.01 - 0.74 6
Sardinops sagax	0.41 - 40.00 25	0.30 - 2.00 7	n/a	0.01 - 0.16 8	n/a	n/a
Gerres subfasciatus	0.24 - 25.00 19	0.61 - 1.33 3	n/a	0.02 - 0.09 2	0.02* 1	n/a
Liza argentea	0.24 - 6.67 29	0.30* 1		0.02 - 0.89 18	0.02 - 0.35 7	0.12 - 0.33 2
Agyrosomus japonicus	0.32 - 5.00 19	n/a	n/a	0.01 - 0.62 14	n/a	0.02 - 0.03 2
Sillago flindersi	0.28 - 81.67 42	0.30 - 13.33 31	0.35 - 4.00 14	0.01 - 5.08 31	0.02 - 0.23 16	0.02 - 0.33 10
Acanthopagrus australis	0.35* 1	n/a	0.32* 1	0.01 - 0.15 7	0.02 - 0.04 4	n/a
Pagrus auratus	0.35 - 0.67 6	0.83* 1	n/a	0.02 - 0.42 9	0.02 - 0.15 2	n/a
Rhabdosargus sarba	0.83* 139	n/a	n/a	0.02 - 0.17 8	0.02 - 0.16 3	0.02 - 0.31 3
Pseudocaranx dentex	0.63 - 251.67 43	0.30 - 28.33 28	0.30 - 24.16 13	0.01 - 1.69 22	0.02 - 0.46 4	0.02 - 0.37 2
Trachurus novaezelandiae	0.31 - 1001.91 50	0.31 - 32.00 22	0.40 - 4.00 10	0.01 - 20.62 53	0.01 - 6.00 21	0.01 - 2.62 10

spawning activity between these times. Spawning occurs in estuaries and shelf waters of temperate and sub-tropical Australia (Miskiewicz and Neira 1998). Low densities of larvae over the outer shelf off Sydney (this study, Fig 3b) and elsewhere (Hoedt and Dimmlich 1995) suggests that spawning is restricted to the inner shelf.

Densities of preflexion and flexion stage *Engraulis australis* larvae were highest in shallow and middle depths, and low at the surface (Fig. 3b). The highest density of preflexion *E. australis* was 78 larvae 100 m^{-3}, occurring at shallow depth at station A in January (Table 2). Postflexion larvae occurred at similar densities in surface and subsurface waters in January, but mainly at the surface in April. Previously, Gray (1993, 1996) found *E. australis* larvae most abundant in subsurface waters in November, but equally abundant in surface and subsurface waters in April/May and August/September. Given the tendency of older larvae to dominate surface samples in the present study, previously noted variability may reflect ontogenetic changes in vertical distribution.

Sparids were rare in shelf waters during January and April, 1994 (Fig. 3c). *Acanthopagrus australis* (yellowfin bream) spawns throughout the year along the eastern Australian coast, although there are regional peaks in activity, including a local peak in autumn. This is consistent with a slight increase in larval abundance between January and April. *A. australis* observed during this study were caught within 7 km of the coast. Spawning occurs at the mouths of estuaries and most previous observations of *A. australis* larvae within eastern Australian shelf waters have been within 1 km of the coast (Gray 1993; Miskiewicz and Neira 1998). Additional larvae may have been present in coastal waters in 1994 but distributed inshore of station A.

Preflexion and flexion *Acanthopagrus australis* larvae occurred in subsurface samples but were absent at the surface. Densities of *A. australis* were < 1 larvae 100 m^{-3} in all samples (Table 2). A single postflexion larva, which appeared competent to settle, was taken at the surface at station A in January. This is consistent with observations of settlement stage

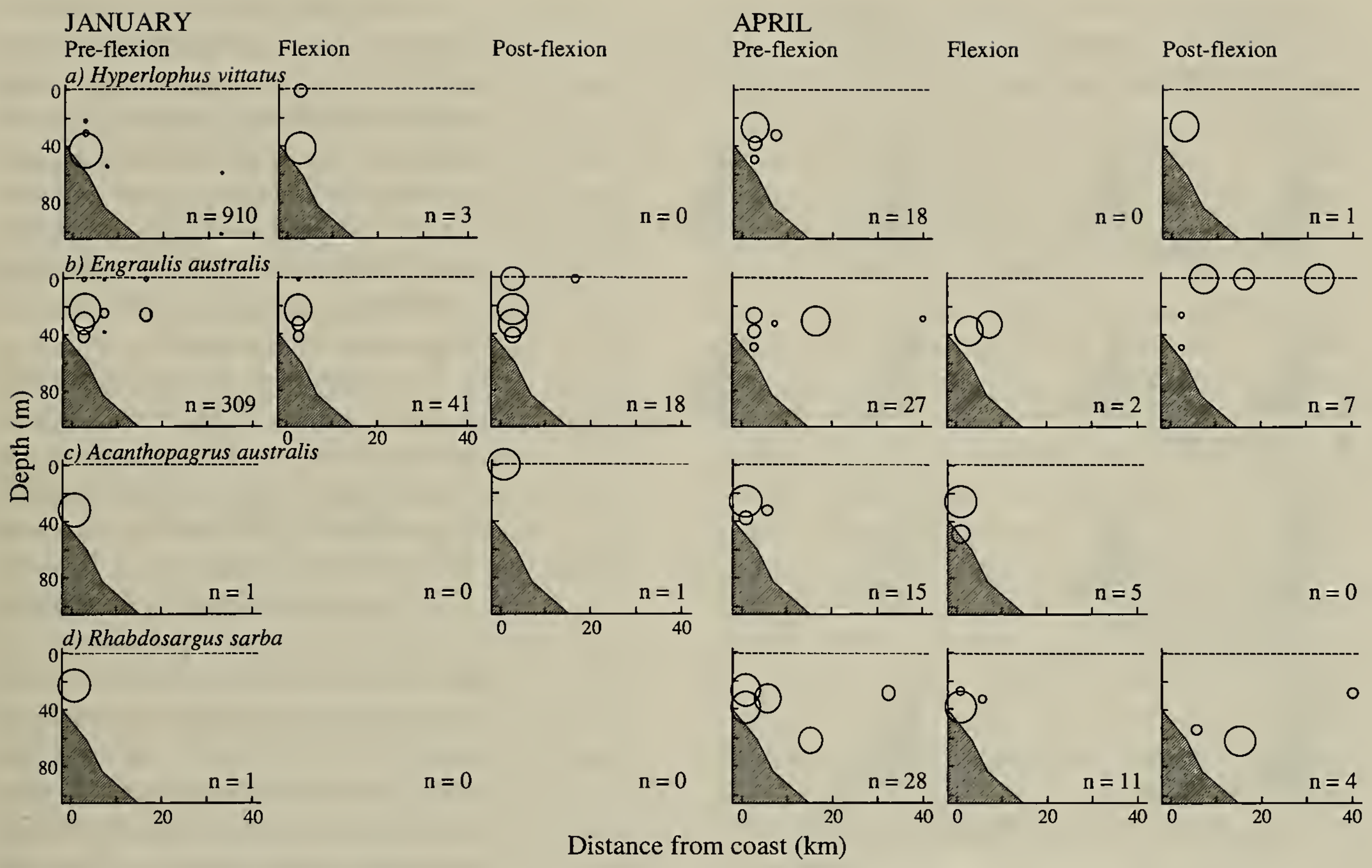

Figure 3. Mean density of preflexion, flexion and postflexion stage larvae of a) *Hyperlophus vittatus,* b) *Engraulis australis* c) *Acanthopagrus australis*, and d) *Rhabdosargus sarba* at sampling locations in January and April, 1994. Circle size is proportional to density of each stage within a month. Circle size is not comparable among stages or months (n = total number of larvae during sampling period)

larvae at the surface in estuarine waters (T. Trnski, pers. comm.).

In January, a single preflexion stage *Rhabdosargus sarba* (tarwhine) was taken, at shallow depth over the inner shelf (Fig. 3d). In April, *R. sarba* was more abundant in samples. Spawning by *R. sarba* occurs during most months of the year off eastern Australia, but local larval abundance and recruitment rates peak in autumn/winter (Miskiewicz and Neira 1998; Smith and Suthers 2000). The increase in larval abundance between January and April, 1994, was consistent with these patterns. A single larva in January, and the presence of early and late stage larvae in April, 1994, suggested that some spawning activity occurred prior to April. Densities of *R. sarba* were < 1 larvae 100 m^{-3} in all samples (Table 2).

In April, preflexion, flexion and postflexion *Rhabdosargus sarba* occurred mainly over the inner and mid shelf, which is consistent with an inner shelf spawning location for this species (Wallace 1975; Miskiewicz 1986). Some preflexion and postflexion larvae also occurred over the outer shelf. The occurrence of postflexion larvae up to 40 km offshore of Sydney contrasts with the estuarine distribution of juveniles. Postflexion larvae, with some swimming ability, are less likely to have been passively advected away from the inner shelf than the less developed preflexion larvae. The outer shelf may be within the typical distributional range of older larvae.

During night-time sampling in 1994, all developmental stages of *Rhabdosargus sarba* occurred in subsurface samples and were absent in surface samples. *R. sarba* larvae are also in subsurface waters off Sydney during the day (Gray 1998), suggesting that larvae do not undertake daily vertical migrations.

Pagrus auratus (snapper) occurred at low densities in January and April (Fig. 4a). Spawning by *P. auratus* occurs throughout the year along the south-eastern coast, with a local peak in spawning activity in autumn (Miskiewicz and Neira 1998). Relatively low densities of larvae off Sydney, particularly in January, may reflect limited spawning at this time. Densities of *P. auratus* were < 1 larvae 100 m^{-3} in all samples (Table 2).

Preflexion and flexion *Pagrus auratus* mainly occurred in subsurface waters of the inner and mid-shelf, although preflexion larvae also occurred at the surface and at shallow depths over the outer shelf in April. Spawning occurs in waters of < 50 m depth (Kailola et al. 1993), and so the presence of preflexion

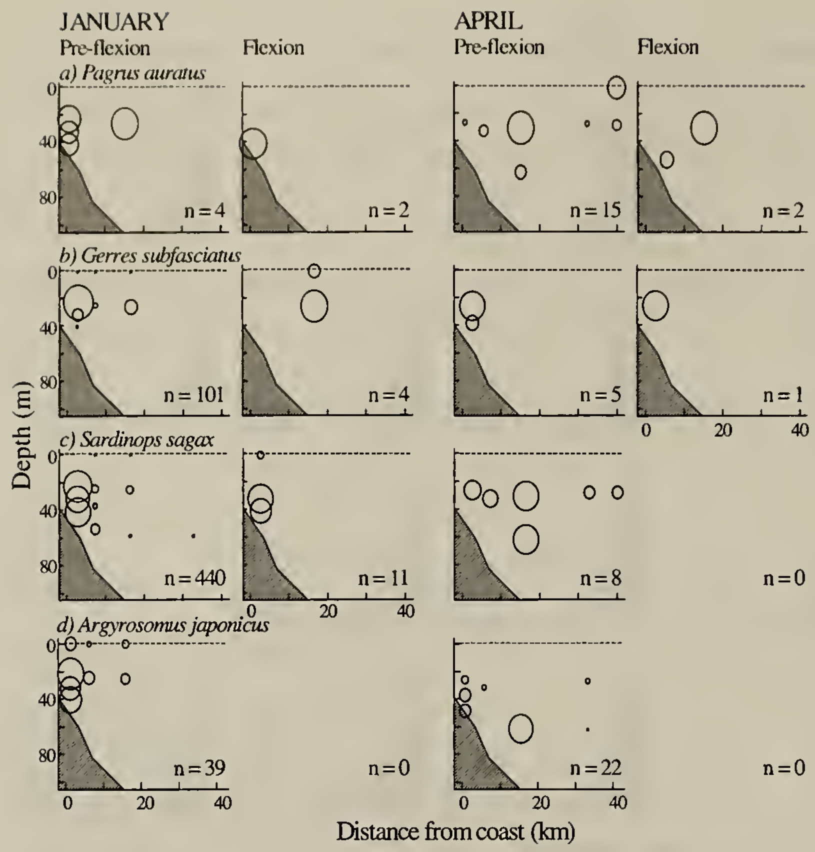

Figure 4. Mean density of preflexion and flexion stage larvae of a) *Pagrus auratus,* b) *Gerres subfasciatus,* c) *Sardinops sagax* and d) *Argyrosomus japonicus* at sampling locations in January and April, 1994. No postflexion larvae of these species in samples. Circle size is proportional to density of each stage within a month. Circle size is not comparable among stages or months (n = total number of larvae during sampling period)

larvae over the continental slope (i.e. 40 km offshore) off Sydney during April may not reflect spawning location. Larvae may have been advected offshore during coastal upwelling at this time (Smith and Suthers 1999). No postflexion *P. auratus* were taken in either month.

In January, preflexion stage larvae of *Gerres subfasciatus* (silver biddy) occurred over the inner and mid-shelf, and flexion stage larvae over the mid-shelf (Fig. 4b). In April, the distribution of both stages was restricted to the inner shelf and densities were very low. No postflexion *G. subfasciatus* were taken in either month. Spawning by *G. subfasciatus* peaks in summer along the south-eastern Australian coast (Miskiewicz and Bruce 1998) and declines in larval density between January and April may reflect a decline in spawning activity between these times. The occurrence of preflexion larvae over the inner shelf suggests a coastal spawning location.

Densities of both preflexion and flexion *Gerres subfasciatus* were greatest at shallow depths. Maximum observed density of preflexion larvae was 25 larvae 100 m^{-3}, at shallow depth at station A in January (Table 2). Larvae occur at the surface during the day (Gray et al. 1992) and at depth during the night (this study), suggesting diel vertical migration by this species.

Sardinops sagax (pilchard) probably spawns off NSW during most months of the year although the timing of peak activity may vary among years (Miskiewicz 1987). Preflexion larvae were relatively abundant in January, 1994, suggesting significant spawning activity in the Sydney region at this time. *S. sagax* was largely restricted to the inner shelf in January (Fig. 4c). Larvae were more evenly distributed across the shelf in April, although densities were very low. An inshore larval distribution is consistent with spawning in estuaries and inner shelf waters throughout temperate Australia (Blackburn 1949; Jenkins 1986; Fletcher and Tregonning 1992; Hoedt and Dimmlich 1995). A small number of early stage larvae were found 30-40 km offshore, which is more likely to reflect larval advection than an offshore spawning location (Smith and Suthers 1999).

In January and April, the densities of preflexion and flexion *Sardinops sagax* were similar at shallow, middle and deep depths, but low at the surface (Fig. 4c). Maximum density of preflexion *S. sagax* was 40 larvae 100 m^{-3}, which occurred within shallow and deep samples at station A in January (Table 2). Flexion stage larvae were absent from samples in April and post-flexion stage larvae were absent from all samples.

The vertical distribution of *Sardinops sagax* is spatially and temporally variable. Off Sydney, *S. sagax* has been observed below the surface during the day (Gray 1996) and night (this study). However, in south-western Australia, *S. sagax* has been observed at the surface during the day but dispersed throughout surface and subsurface waters at night (Fletcher 1999). Hydrology may have influenced these vertical distributions. The water column was stratified during sampling off Sydney, and most larvae occurred just below the thermocline. There was no thermocline during sampling off western Australia.

Similar numbers of preflexion *Argyrosomus japonicus* (mulloway) were caught in January and April, suggesting similar levels of spawning activity at these times (Fig. 4d). The occurrence of larvae in south-eastern Australian coastal waters during January is one month earlier than previous observations, between February and May (Steffe and Neira 1998). However, juveniles are known to enter local estuaries as early as February (Gray and McDonall 1993), and so the presence of larvae in coastal waters during January is possible. In January and April, densities were highest over the inner and mid-shelf. Larvae of this species also occur in nearshore areas and estuaries of South Africa (Beckley 1990). An inshore larval distribution is consistent with spawning by this species along ocean beaches in temperate and subtropical Australia (Kailola et al. 1993).

Preflexion *Argyrosomus japonicus* larvae occurred at all sampling depths, although surface densities were low. Maximum observed density of *A. japonicus* was 5 larvae 100 m^{-3}, at shallow depth at station A in January (Table 2). In April, larvae occurred mainly in middle and deep samples. This distribution may reflect an increasingly demersal habit with increasing size (A. Miskiewicz pers. comm.). This may also explain the rarity of later stage larvae in samples, if later stages typically occurred below the deepest sampling strata. Flexion and postflexion stages of *A. japonicus* were absent from samples in both months.

Liza argentea (flat-tail mullet) was more abundant in April than in January, 1994, suggesting an increase in spawning activity between these months (Fig. 5a). *L. argentea* spawn between December and June (Kailola et al. 1993). *L. argentea* larvae occurred over the inner and mid-shelf in January, and also occurred over the outer shelf in April. Maximum observed density of preflexion *L. argentea* was 7 larvae 100 m^{-3}, at shallow depth at station A (Table 2). The abundance of preflexion larvae over the inner shelf suggested a nearshore spawning location. Larvae tended to occur further from shore with increasing stage.

Flexion and postflexion *Liza argentea* were most abundant at the surface. Later stage *L. argentea* also occur at the surface during the day (Gray 1993), suggesting that older larvae do not undertake daily vertical migrations.

Sillago flindersi (eastern school whiting) was relatively abundant in January and April, 1994, suggesting that the level of spawning activity was similar at these times. The timing of spawning by *S. flindersi* peaks in spring/summer off south-eastern Australia (Kailola et al. 1993). Relatively high densities of later stage larvae in January, 1994, suggest that spawning activity had commenced at least several weeks prior to sampling. Larval of all developmental stages occurred mainly over the inner and mid-shelf regions each month (Fig. 5b). The distribution of preflexion larvae suggested a nearshore spawning location. Maximum observed density of preflexion *S. flindersi* was 82 larvae 100 m^{-3}, at shallow depth at station A in January (Table 2).

Each larval stage of *Sillago flindersi* was present at the surface and at all subsurface sampling depths. However, the vertical distribution of larvae changed between months. Preflexion larvae were most abundant in shallow samples in January but most abundant at the surface in April. Postflexion larvae occurred in shallow samples and at the surface in January, but in mid and deep samples in April. Preflexion and flexion *S. flindersi* larvae have previously been observed mainly in subsurface waters during the day (Gray 1996). The shift by postflexion larvae from warm, surface water in January to cool, deep water in April suggests that vertical distribution is not strongly influenced by hydrography. Postflexion *S. flindersi* may be patchily distributed throughout the water column.

The carangids, *Pseudocaranx dentex* (silver trevally) and *Trachurus novaezelandiae* (yellowtail scad) were considerably more abundant in January than in April. Larvae of these species have been collected off eastern Australian at most times of the year, although spawning probably peaks in summer (Kailola et al. 1993; Trnski 1998) which is consistent with very high densities of larvae in January. The cross-shelf distributions of preflexion and flexion carangid larvae were similar between species (Fig. 5c). Larvae occurred over the inner and mid-shelf in January, and extended to the outer shelf in April. High densities of preflexion larvae over the inner shelf in January suggested spawning by both species over the inner shelf. The occurrence of larvae over the outer shelf in April resulted from the offshore displacement of larvae by a coastal upwelling event (Smith and Suthers 1999).

Preflexion and flexion carangids occurred in subsurface samples in January, but also occurred at the surface in April. Maximum observed density of preflexion *Pseudocaranx dentex* was 252 larvae 100 m^{-3}, at shallow depth at station A in January (Table 2). Maximum observed density of preflexion *Trachurus novaezelandiae* was 1002 larvae 100 m^{-3}, at shallow depth at station A in January (Table 2).

Larvae of both carangids displayed an ontogentic shift in distribution although trends differed between species (Fig. 5d). Larvae of *Trachurus novaezelandiae* occurred further offshore with increasing stage. Larvae of *Pseudocaranx dentex* were

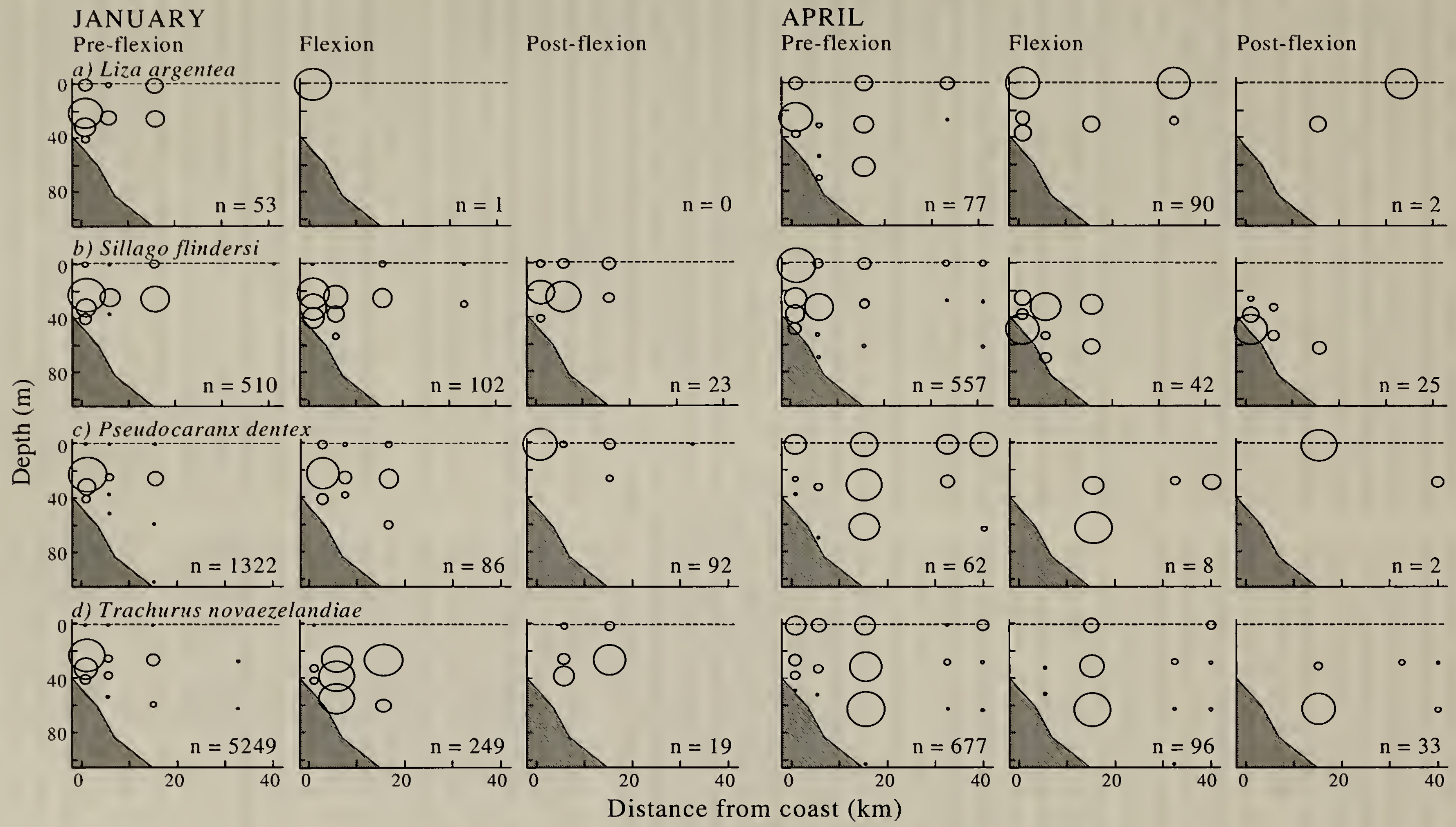

Figure 5. Mean density of preflexion, flexion and postflexion stage larvae of a) *Liza argentea,* b) *Sillago flindersi,* c) *Pseudocaranx dentex* and d) *Trachurus novaezelandiae* at sampling locations in January and April, 1994. Circle size is proportional to density of each stage within a month. Circle size is not comparable among stages or months (n = total number of larvae during sampling period)

more abundant at the surface with increasing stage. During the day, the average size of *Pseudocaranx dentex* larvae is greater in subsurface waters (Gray 1993), which suggests diel vertical migration by this species. However, differences in observations between studies may also reflect differences in hydrography (i.e. lack of water column stratification during sampling by Gray). The shift in cross-shelf distribution between January and April during coastal upwelling indicates that carangid larvae are indeed subject to hydrodynamic influences.

Conclusions

Approximately 90% of larvae of each species occurred at stations A, B or C (i.e. within 17 km of the Sydney coast) during January and April, 1994 (Fig. 6). The highest densities of each species generally occurred at 'shallow' or 'middle' sampling depths, which corresponded to water within the mixed layer or upper thermocline (Fig. 2). No species was most abundant at the surface. These results highlight the importance of the nearshore mixed layer to many commercially significant fish larvae off south-eastern Australia.

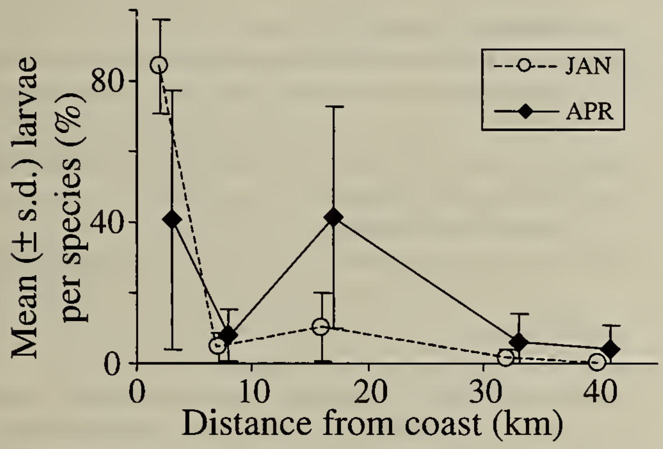

Figure 6. Mean (± standard deviation) percentage of larvae of each species at sampling stations in January and April, 1994.

The vast majority of individuals of all species observed in this study were at a preflexion stage of development. This is not unexpected and is likely to reflect the combined effects of high larval mortality and increasing net avoidance with increasing larval size. In some species, lower catchability of older larvae may also result from a movement away from the marine, pelagic environment towards the end of the larval phase. For example, older *Argyrosomus japonicus* larvae are believed to adopt a benthic habit prior to settlement in estuaries (A. Miskiewicz pers. comm.). Many coastal species have a coastal or estuarine juvenile phase and marine larvae must eventually migrate towards the coast. Postflexion larvae, nearing settlement, could have been present < 2 km from the coast, inshore of station A during this study. This relatively shallow region was not accessible to the sampling gear employed by this study.

Limitations on sampling location imposed by the use of a particular gear type confound many plankton studies, and contribute to an incomplete understanding of the life history of many fish species. In particular, no sampling of the extreme nearshore zone (i.e. m's from shore) or absolute bottom (< 1 m from bottom) is reported for the south-eastern Australian coast. Such regions have been sampled elsewhere by use of light-traps or diver-operated nets and often host settlement stage larvae (e.g. Hickford and Shiel 1999). Off south-eastern Australia, these regions may host late-stage larvae of numerous commercial species, especially sparids, that are highly abundant as juveniles within coastal waters but relatively infrequently observed as larvae.

All species encountered during this study are coastally distributed as juveniles and adults (Kailola et al. 1993), and the nearshore distribution of most larvae suggests that the life cycle of each species is typically completed close to the coast. However, observations of some larvae over the outer shelf and slope during this study provide an insight into the extent of distributional variability that larvae may experience. Larvae of five species (*Sardinops sagax, Hyperlophus vittatus, Pseudocaranx dentex, Trachurus novaezelandiae, Sillago flindersii*) were found > 30 km offshore in January. Larvae of nine species (*Sardinops sagax, Engraulis australis, Pagrus auratus, Rhabdosargus sarba, Pseudocaranx dentex, Trachurus novaezelandiae, Liza argentea, Agyrosomus japonicus, Sillago flindersii*) were found > 30 km offshore in April. The increased incidence of larvae in offshore waters in April, compared with January, is unlikely to have arisen by chance, considering the lower abundances of larvae in April. Passive larval advection during coastal upwelling in April is the most likely cause of these offshore distributions. The frequency of such offshore excursions by coastally-spawned larvae is unknown. Anomalous episodes of offshore advection may contribute to spatial and temporal variability of coastal recruitment by these species. Similarly, downwelling events may enhance the coastal recruitment of surface-orientated larvae.

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New Distribution and Biological Records for Native Dung Beetles, in the Tribe Scarabaeini, from Northern New South Wales

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Williams, G. (2003). New distribution and biological records for native dung beetles, in the tribe Scarabaeini, from northern New South Wales. *Proceedings of the Linnean Society of New South Wales* **124**, 13-16.

New coastal and inland distribution records, and behavioural observations, are given for Scarabaeini dung beetles collected from northern New South Wales.

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KEYWORDS: Coleoptera, Scarabaeidae, Scarabaeini, dung beetles, perching, cave fauna, subtropical rainforest

INTRODUCTION

Northern New South Wales is a centre of diversity for dung beetles in the tribe Scarabaeini (Matthews 1974). Numerous species are restricted to wet forest types along the Great Dividing Range (Williams 2002), but the maritime fauna, and that of isolated forest outliers east and west of the main mountain range complex, has been poorly documented.

This paper gives additional scarabaeine distribution and behavioural records. Unless otherwise stated all beetles were collected at excrement-baited pit-fall traps. Voucher specimens have been deposited in the Queensland Department of Primary Industries Collection, Mareeba, Lorien Wildlife Refuge field reference collection, Lansdowne, and the Australian Museum, Sydney.

NEW RECORDS

Amphistomus speculifer Matthews

New western distribution record

Cedar Brush Nature Reserve, Liverpool Range, NW of Scone, 12-13.ii.1999, G. Williams, subtropical rainforest.

Aptenocanthon hopsoni (Carter)

New northern and eastern distribution records

Dooragan National Park, North Brother Mtn (~480 m.a.s.l.), Laurieton, 30.xii.1998, G. Williams, subtropical rainforest; same locality except, 25-27.xi.1999, G. and T. Williams; Hueys Corner, Fitzroy Creek, Carrai State Forest, WNW of Kempsey, 8-9.ii.1997, G. and B. Williams, warm temperate rainforest; Banda Banda Beech Reserve, NW of Wauchope, 10-11.i.1984, G. Williams and C. Cross, cool temperate rainforest; Cockerawombeeba Flora Reserve, NW of Wauchope, 14-15.i.1988, G. and B. Williams, rainforest; Wilson River Flora Reserve, NW of Wauchope, 5-6.xii.1988, G. Williams, subtropical rainforest; vicinity Mt Seaview-Oxley Highway turnoff, W of Wauchope, 28-29.xii. 1988, G. Williams, warm temperate rainforest.

Aulacopris maximus Matthews

New eastern distribution and behaviour records

Approximately 4.5 km N of Lansdowne, Coorabakh National Park, 19.i.1996, G. and B. Williams, in bat cave, at bat guano; Dooragan National Park, North Brother Mtn (~480 m.a.s.l.), Laurieton, 30.xii.1998, G. Williams, subtropical rainforest; Banda Banda Beech Reserve, NW of Wauchope, 28.i.1985, G. Williams, perching at night on tree trunk (~4m above ground), warm temperate rainforest; 'The Pines', Way Way State Forest, SW of Scotts Head, 20-21.i.1999, G. and T. Williams, subtropical rainforest.

Diorygopyx asciculifer Matthews

New northern and western distribution, and habitat records

Cedar Brush Nature Reserve, Liverpool Range, NW of Scone, 12-13.ii.1999, G. Williams, dry sclerophyll forest, at macropod dung; Camden Head, 25-27.xi.1999, G. and T. Williams, littoral rainforest; Lake Cathie, 26.ii.1999, G. and T. Williams, vine thicket.

Diorygopyx incomptus Matthews

New southern distribution, and habitat records

Glenugie Peak, Glenugie State Forest, SE of Grafton, 16.xii.1998, G. and B. Williams, dry rainforest - vine thicket complex.

Diorygopyx incrassatus Matthews

New northern and eastern distribution, habitat and behaviour records

Dooragan National Park, North Brother Mtn (~480 m.a.s.l.), Laurieton, 30.xii.1998, G. Williams, subtropical rainforest; same locality except, 25-27.xi.1999, G. and T. Williams; Sea Acres Nature Reserve, Port Macquarie, 25-27.xi.1999, G. and T. Williams, subtropical rainforest; Wilson River Flora Reserve, NW of Wauchope, 5-6.xii.1988, G. Williams, subtropical rainforest, perching at night on low foliage; Cockerawombeeba Flora Reserve, NW of Wauchope, 14-15.i.1988, G. and B. Williams, rainforest; same locality except, 25-27.xi.1999, G. and T. Williams; Racecourse Headland, S of Crescent Head, 20.i.1999, G. and T. Williams, littoral rainforest; vicinity 'The Blowhole' Boonanghi State Forest, 24 km W of Kempsey, 8.x.1993, G. Williams, riparian dry rainforest; 'The Pines', Way Way State Forest, SW of Scotts Head, 20-21.i.1999, G. and T. Williams, subtropical rainforest.

Diorygopyx niger Matthews

New southern distribution and behaviour records

Mt Killiekrankie, New England National Park, 12.i.2001, G. and B. Williams, wet sclerophyll forest, at bird carrion; Coachwood Creek, vicinity of 'Kookaburra', Carrai State Forest, WNW of Kempsey, 8-9.ii.1997, G. and B. Williams, wet sclerophyll forest - warm temperate rainforest complex; vicinity 'The Natural Arch', Carrai State Forest, WNW of Kempsey, 8-9.ii. 1997, G. and B. Williams, wet sclerophyll forest.

DISCUSSION

Species of the flightless endemic genus *Diorygopyx* exhibit restricted distribution patterns along the New South Wales north coast (Matthews 1974). *Diorygopyx incrassatus* was previously recorded from the Hastings Valley and the northern rim of the Manning Valley (Matthews 1974, Willams and Williams 1983b). It is replaced to the immediate north by *D. niger* and to the south by *D. asciculifer* (Matthews 1974). In the Carrai Plateau region, west of Kempsey, *D. niger* occurs at higher elevations (e.g., < 1000 m.a.s.l.) and *D. incrassatus* is found in submontane forest (ie. Boonanghi State Forest). The maritime distribution of *D. incrassatus*, however, is skewed northwards into latitudes occupied by *D. niger* and reaches to at least Way Way State Forest, near Macksville. The maritime distribution of *Diorygopyx asciculifer* is similarly skewed northwards. In littoral rainforest south of Port Macquarie *D. incrassatus* is displaced by *D. asciculifer* (Williams 1979, Williams and Williams 1984). At Laurieton *D. incrassatus* occurs in mountainous (~480 m.a.s.l.) subtropical rainforest of Dooragan National Park approximately 3 kilometres inland from the coastline, but *D. asciculifer* occurs in adjacent littoral rainforest remnants at Camden Head, Lake Cathie and Crowdy Bay National Park, to the east, north, and south respectively.

Diorygopyx asciculifer is the southern-most member of the genus, and is widely distributed in rainforests of the Manning catchment (Matthews 1974, Williams and Williams 1983a). In addition, it penetrates to the isolated Liverpool Ranges, west of Barrington Tops, where it has been collected in dry sclerophyll forest. At least one further species of *Diorygopyx, D. duplodentatus* Matthews, originally recorded only from rainforest, also occurs in drier forest types at the western extremity of its known range (C. Reid pers. comm.).

Diorygopyx incomptus was originally described from the Macpherson Ranges (Matthews 1974) but is more widely distributed in rainforests of far northern New South Wales (Williams 2002). It was collected in large numbers in low dry rainforest and associated vine thickets on scree slopes at Glenugie Peak, southeast of Grafton. This is a small area of isolated rainforest occurring within an extensive landscape matrix of dry forest and woodland.

Matthews (1974) cited two specimens of *D. niger* found under old wallaby bones (an association which he considered possibly fortuitous). Numerous adult *D. niger* were collected in and under bird carrion at Mt Killiekrankie in January 2001 possibly confirming necrophagous habits in the species.

The genus *Aptenocanthon* comprises two species from New South Wales (*A. hopsoni*, *A. rossi* Matthews) and a further six species from northern Queensland (Storey 1984, Storey and Monteith 2000). *Aptenocanthon rossi* is known only from the Mt Wilson-Mt Irvine area west of Sydney (Matthews

1974, Williams and Williams 1982) and *A. hopsoni* was previously recorded from montane wet forests in Barrington Tops, Dingo Tops and the Comboyne Plateau (Matthews 1974, Williams and Williams 1983a). However, the distribution of *A. hopsoni* reaches montane rainforests in the Carrai Plateau, and its near-maritime occurrence in submontane rainforest at Dooragan National Park is exceptional.

Aulacopris maximus was recorded by Waite (1898) from the Yessabah bat caves, in the Macleay Valley, northern New South Wales. Fricke (1964) recorded the related southern species *A. reichei* White "densely populating" a small cave sheltering bandicoots in a suburban garden at Mosman, Sydney. *Aulacopris maximus* is possibly a specialist on bat guano (G. Monteith pers. comm.). However, no further records of association with bat caves have been published. *Aulacopris maximus* was collected on a guano heap in a small cave in Coorabakh National Park (formerly part Lansdowne State Forest), near Taree, in January 1996. This is a roost cave seasonally occupied by *Miniopterus* spp., and dissected by an intermittent stream. Bat guano deposits are regularly flushed from the cave during heavy rain, which presumably would limit occupation of the cave and utilisation of guano deposits by invertebrate fauna.

Scarabaeine dung beetles have been recorded from the Americas, and tropical Australia, perching near the ground on plant leaves (Howden, Howden and Storey 1991, Howden and Nealis 1978, Young 1982). This may be a predator avoidance strategy (Young 1982) or related directly to foraging (Howden *et al.* 1991). Howden *et al.* (1991) record the dung beetle genera *Monoplistes, Temnoplectron* (Scarabaeini) and *Onthophagus* (Onthophagini) perching on foliage in tropical Queensland rainforest, but no other Australian records are known. Two subtropical species, *Diorygopyx incrassatus* and *Aulacopris maximus*, were observed nocturnally perching in montane rainforests of the Upper Hastings Valley; several *D. incrassatus* on low foliage in subtropical rainforest, and a single *A. maximus* approximately 4 m above ground on a tree trunk in warm temperate rainforest. *Aulacopris maximus* has previously been collected from inside possum nest boxes placed on tree trunks (Williams 1993). The large numbers of some species recorded by Howden *et al.* (1991) from tropical Queensland suggested 'perching' may be a common, albiet localised, strategy. There are no similar abundance records for Australian subtropical dung beetles, and extensive spot-lighting in New South Wales north coast rainforests indicates that perching may be rare.

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Host-plant Disjunction in a New Species of *Neohoodiella* (Insecta, Thysanoptera, Phlaeothripinae),with Notes on Leaf-Frequenting Thrips in New South Wales Subtropical Rainforests

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Neohoodiella jennibeardae sp.n. is described breeding on the leaves of two unrelated plants in the rainforests of eastern Australia, the dicotyledonous tree *Ficus coronata* (Moraceae) and the monocotyledonous vine *Ripogonum elseyanum* (Smilacaceae). To confirm this remarkably disparate pair of host associations many other plants in these rainforests were examined. This new species was not found on any other plant, although about 40 thrips species were taken from the leaves of 40 plant species in 22 families, and these records are tabulated. *Neohoodiella* is known previously only from a single species in New Caledonia. The genus is characterised by the two character states: abdominal tube one third of body length; dorsal setae elongate but broadly capitate. The head of *N. jennibeardae* bears a bifurcate tubercle that is unique amongst Phlaeothripidae.

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KEYWORDS: Leeuweniini, *Neohoodiella jennibeardae*, host plant associations, subtropical rainforest.

INTRODUCTION

Despite the acknowledged diversity of the insect fauna in Australia's eastern rainforests (Monteith and Davies 1991), our knowledge of many groups is remarkably poor. For the order Thysanoptera, over most of the past 100 years, taxonomic descriptive work far outstripped any real understanding of the fauna. Most of these descriptions were by A. A. Girault, who published more than 130 species group names for thrips between 1924 and 1934 (Mound 1996), based mainly on single, often damaged, specimens, with no information about biology. Recent studies have been directed toward recognising the species described by Girault, establishing their structural variation and hence synonymies, and discovering their host plants (Mound 2002a). This report is part of broader project to understand the biology of a larger proportion of the Australian thrips fauna. Plant names are used as in Mabberley (1997).

Thrips species are proving to exhibit a wide diversity of interesting biological relationships. The apparent lack of natural enemies in *Thrips imaginis* Bagnall, the plague thrips that occurs in such vast numbers during early summer in southern Australia, has long been commented on (Andrewartha and Birch 1954). However, other endemic thrips species also produce huge and apparently unconstrained populations. One was reported recently as invading a school in vast numbers in Queensland (Mound et al. 2002). Moreover, this species has switched from breeding on its native host, *Araucaria*, to breeding on introduced northern hemisphere species of *Pinus*. Very large populations are reported also for thrips species that pollinate certain *Macrozamia* cycads in Australia, with up to 20 000 individuals occurring on a single male cone (Mound and Terry 2001; Terry 2001).

Many thrips species feed on fungi on dead branches or in leaf litter (Mound 2002b), whereas others are phytophagous either in flowers or on leaves, some on single plant species but with a few polyphagous (Mound 2002a). Thrips are increasingly being recognised as plant pollinators, some as generalists (Williams et al. 2001) but others highly specific (Mound and Terry 2001). Similarly, behaviour patterns shown by particular thrips species are increasingly being investigated, such as lekking by males as is now known in two species of Australian Thripidae (Gillespie et al. 2002). Domicile creation, with adults securing leaves together with silk or glue, is described for several species of Phlaeothripidae (Mound and Morris 2001). This behaviour is often accompanied by deliberate female (but not male) dealation, although the significance of such wing removal remains unexplored. Structural polymorphisms, within or between sexes, can be so great that isolated individuals of the same species would not be considered congeneric (Mound et al. 1998), but behaviour patterns associated with such intra-specific variation have been studied in few species.

Most recent research effort on thrips has been directed toward the arid zone of Australia (Crespi and Mound 1997). In this paper, a particularly bizarre new species is described from the eastern rainforests and observations recorded of its biology, this being the second member of a genus known previously only from New Caledonia. This new species was found breeding on the leaves of two very distantly related plants. To examine this disjunct host relationship, a survey was made of thrips associated with the leaves of many different plants in eastern rainforests around Taree, these records being tabulated and discussed below.

Neohoodiella Bournier

Neohoodiella Bournier 1997: 143. Type-species *N. grandisetis* Bournier.

The only previous species in this genus was described from a total of eight females and two males collected by a canopy fogging technique from unidentified forest trees in the Rivière Bleu region of New Caledonia. The genus is a member of the tribe Leeuweniini, in which the adults are distinguished from other leaf-feeding Phlaeothripinae by their elongate tenth abdominal segment, the tube (Ananthakrishnan 1970). In most Phlaeothripidae, the tube is little more than twice as long as the ninth abdominal segment, whereas in Leeuweniini the tube is usually more than four times as long as the preceding segment. *Neohoodiella* differs from the other genera currently recognised in this group in having extraordinarily long setae on the head and pronotum, and the tube 10 times as long as the ninth tergite.

Key to species of *Neohoodiella*

1. Body and legs mainly light brown; antennal segment III with 1 sense cone, IV with 2 sense cones; major setae of head and body with margins smooth; ocellar region not produced over bases of antennae; median pair of major setae on vertex arising anterior to postocular setae; pronotal anteromarginal setae minute; pronotal notopleura each with 2 major setae; pronotal posteroangular setae minute; mesonotal lateral setae minute; abdominal tergite IX setae B2 setaceous in contrast to capitate setae B1; New Caledonia ....*grandisetis* Bournier

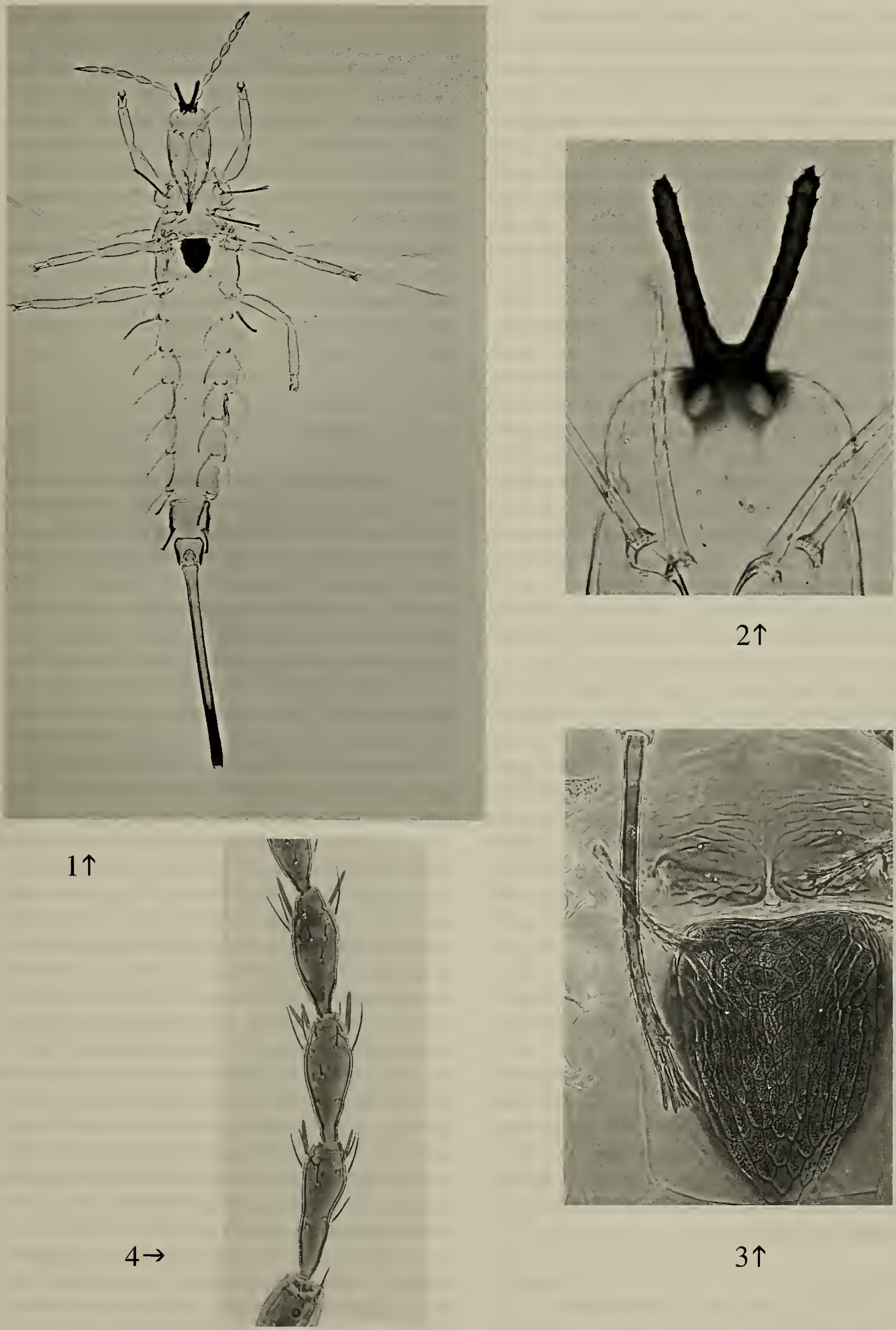
-. Body and legs mainly clear yellow, dark brown on metascutum, tube apex and frontal margin of head (Fig. 1); antennal segment III with 2 sense cones, IV with 3 sense cones (Fig. 4); major setae of head and body with margins coarsely spiculate (Fig. 3); ocellar region with black, V-shaped tubercle projecting over front ocellus and extending beyond apex of antennal II (Fig. 2); median pair of major setae on vertex arising posterior to postocular setae; pronotal anteromarginal setae elongate; pronotal notopleura each with one large and one minute seta; pronotal posteroangular setae elongate; mesonotal lateral setae capitate with shaft spiculate; abdominal tergite IX setae B1 and B2 similar in structure but B2 shorter; eastern Australia ....*jennibeardae* sp.n.

Neohoodiella jennibeardae sp.n.

Holotype ♀, **New South Wales**, Lorien Wildlife Refuge, 3km N of Lansdowne near Taree, from *Ficus coronata* leaf, 27.xii.2000 (LAM 3991), in ANIC, CSIRO Canberra.

Paratypes: 10♀ 6♂ taken with larvae; 1♀ 5♂ at same site, 11.i.2001 (G. Williams); 19km NW of Bellbrook, Nulla Nulla Creek, 1♀ 1♂ from *F. coronata* leaf, 11.i.2001 (G. Williams); NW of Wingham, Dingo State Forest, 4♀ 2♂ from *F. coronata* leaf, 16.xii.2001 (G. Williams); **Queensland**, 100km NW of Brisbane, Conondale N.P., from *Ripogonum elseyanum* leaves, 1♀, 10.x.2000, 3♀ 3♂ taken with larvae 18.iii.2001 (Dr Jenny Beard). Paratypes will be deposited in the US National Museum, Washington, Natural History Museum, London, and the Senckenberg Museum, Frankfurt.

Female macroptera. *Colour*: Body pale yellow; metanotum with dark brown area; head with ocellar area dark brown and bearing black forked tubercle; tube golden with distal quarter brown; forewings pale with short darker line in basal third; antennal segment I dark brown, II yellow, III – IV light brown, V – VIII yellow with apex light brown; major setae mainly yellow but tergites III – VII each with 2 setae pale brown, pronotum with midlateral and posteroangular setae dark brown, mesonotal lateral pair light brown, tergites II and VIII each with 2 setae dark brown. *Structure*: Body elongate (Fig. 1), all major setae unusually long with shafts spiculate and apices with crown-like fringe of stout spicules. Head longer than wide, cheeks convex; eyes slightly smaller dorsally than ventrally; ocellar region produced into pair of long



Figures 1-4. ***Neohoodiella jennibeardae*****. 1, Male; 2, Cephalic tubercles; 3, Meso and metanota overlayed by the left pronotal posteroangular seta; 4, antennal segments II – VI.**

tubercles overlaying front ocellus and extending to apex of antennal segment II, these tubercles with margins spiculate and bearing about 12 small setae; two pairs of postocular setae extending beyond apex of antennal segment II; maxillary stylets retracted to postocular setae, close together medially; mouth cone extending across prosternum. Antennae 8-segmented; III with 2 sense cones, IV with 3 sense cones; VIII slender. Pronotum with 5 pairs of major setae, am shortest, pa and epim arising from pronounced tubercles that obscure the notopleural sutures; prosternal basantra not developed, ferna large, mesopraesternum reduced to paired lateral triangles; metathoracic sternopleural sutures not developed. Mesonotal lateral setae well developed; metanotum reticulate with markings internal to reticles, paired median setae minute (Fig. 3). Legs slender, fore tarsus with no tooth; all femora with one large capitate seta on external margin medially. Forewing slender without duplicated cilia; 3 sub-basal setae long and capitate. Pelta triangular, tergite I with one pair of major setae near spiracle; tergites II – VIII each with 2 pairs of major setae laterally arising from tubercles, II – VII each with 2 pairs of strongly sigmoid wing-retaining setae; tergite IX setae B1 and B2 capitate and spiculate, B3 setaceous; tube exceptionally elongate (Fig. 1).

Measurements (holotype ♀ in micrometres). Body length 3150. Head, length 250; width 200; midvertex setae 230; postocular setae 240; inner margin of ocellar tubercles 130. Pronotum, length 130; width 280; major setae – am 140, aa 200, ml 220, epim 240, pa 230. Forewing, length 1000; distal width 50; sub-basal setae 100, 110, 110. Tergite II lateral setae 190, 210. Tergite VIII lateral setae 180, 170. Tergite IX, length 100; setae B1 180, B2 90, B3 80. Tube, length 960; anal setae 450. Antennal segments I – VIII length, 40, 60, 90, 80, 70, 70, 60, 50.

Male macroptera. Indistinguishable from female in colour and structure but considerably smaller; sternite VIII with broad transverse glandular area on posterior half.

Larvae and pupae. Colour yellow, apex of tube and antennae light brown. All major setae unusually long with broadly capitate apices but shafts not spiculate; head with 2 pairs of setae on vertex; pronotum with 6 pairs; meso and metanota each with 5 pairs; tergites I – VIII each with 2 pairs arising from tubercles; tube three times as long as head.

SYSTEMATIC RELATIONSHIPS

Members of the Leeuweniini are recorded from various countries between India, New Caledonia and Australia (Ananthakrishnan 1970), but only two other species have been described with long setae on the head and pronotum. These are the Indian species, *Kochumania excelsa* Ananthakrishnan (1969), which has the tube little more than twice as long the ninth tergite, and *Neohoodiella grandisetis* in which the tube is 10 times as long as the ninth tergite. Systematic relationships between the genera in the Leeuweniini require further study. The new species is remarkable for the pale yellow colour of the adults as well as the larvae, because adults of almost all large thrips species are brown to black. This pale colour, in combination with the long dorsal setae, results in the individuals being well camouflaged on the leaf surface.

OBSERVATIONS ON BIOLOGY

In common with other members of the Phlaeothripidae, the life history of *N. jennibeardae* involves two larval instars and three pupal instars. All of these life stages, from egg to adult, have been found on the leaves of *Ficus coronata* (Moraceae), a sandpaper fig, at a number of rainforest sites in the region of Taree (NSW), and it has been taken from this plant at sites between northwest of Kempsey and southeast of Gloucester. Moreover, larvae and pupae have been found on the leaves of *Ripogonum elseyanum* (Ripogoneaceae) at Conondale National Park just north of Brisbane (Qld). Although unrelated, the leaves of these two plant species are similar in texture, with prominent hairy veins on the lower surfaces.

Despite the wide separation between the two collection areas, the distribution of *N. jennibeardae* appears patchy and unpredictable. The population on one particular tree at Lorien Wildlife Refuge, Lansdowne, was observed regularly over a period of 18 months. In December, 2000, the thrips could be found on many leaves of this tree, all life stages being present. However, this population progressively declined, until by April 2002 only a single adult could be found. If this fluctuation in population size is normal, then our failure to find the thrips on the majority of *F. coronata* trees that have been examined gives no information about its real distribution. The leaves of this tree species are particularly long-lived, and populations of this thrips presumably prosper only in years when fresh growth is abundant.

Eggs of this thrips are deposited on the lower surface of leaves, but in contrast to many other leaf-feeding Phlaeothripinae the eggs are scattered rather than in groups. This is possibly an adaptation to avoid predation by other insects, because this thrips apparently overwinters primarily as these isolated eggs, not as adults. Adults and larvae commonly position themselves close to prominent veins of a *Ficus* leaf and, because of the large number of setae on their dorsal surfaces, they blend into the hairy under-surface of the leaf lamina. When illuminated artificially, thrips move to the shaded side of a leaf, although in lower light intensities they remain on the hairy lower surfaces, even when a leaf is deliberately inverted. Individuals have also been observed to be active on the leaves of *Ficus* trees during the night. Pupae were present on leaves, but were particularly difficult to find beneath the curve of hairy major leaf veins. No evidence could be found of larvae falling to the ground to pupate.

The behaviour of adults and larvae was observed on detached leaves of *F. coronata* in petri dishes. The thrips are noticeably sluggish in their behaviour, quite unlike common flower-living species of Phlaeothripidae. When disturbed with a brush, they often sat lower onto the leaf surface, usually close to a vein, without being stimulated to walk or run. At other times when molested they waved the tube from side to side, often quite briskly, and sometimes raised it over the head. No aggression was observed between adults and larvae, but adults clearly explore the possibilities of mating. When a male first encountered a prospective mate he sometimes arched the tube over the female, although during copulation the tube was lowered horizontally. Copulation in one pair was observed to take about 1.5 minutes, but the male continued to straddle the female for a further half minute after copulating. During copulation, the male constantly stroked the female with his antennae, and appeared to stroke her abdomen with his mid and hind legs.

Because the two recorded host plants of this thrips belong to such widely unrelated plant families, and considering the geographical range noted above between Taree and Conondale, we attempted to discover the insect on other host plants. To this end, we examined the leaves of numerous tree, shrub, vine and fern species in subtropical rainforests at various sites of the mid-north coastal region of New South Wales. Collecting methods were either by examining leaf surfaces with the aid of a head-mounted magnifier, specimens being removed with a small artist's brush, or by beating fresh foliage of individual plant species onto a sheet or net. This yielded a considerable number of foliage associated thrips species, as listed in Table 1 (located at the end of the paper, p. 25), but produced no evidence for a more extensive host range for *N. jennibeardae*. In particular, this thrips was not found on the other common, but relatively smooth-leaved, species of either *Ficus* or *Ripogonum*.

N. jennibeardae thus appears to be restricted to just two unrelated plants. The first of these, *Ficus coronata* (Moraceae), is a small tree that is distributed widely from the Northern Territory, through Queensland to Victoria (Harden 1990). The second is a vine, *Ripogonum elseyanum* (Ripogoniaceae), that occurs in northern NSW north from Dorrigo to Queensland (Harden 1993). The distribution of these two plants overlaps in the rainforest of northern New South Wales.

NOTES ON LEAF-ASSOCIATED THRIPS

During the survey for alternative host plants for *N. jennibeardae*, various thrips species were taken around Taree from numerous unrelated plant taxa. Thrips are generally perceived as flower-living, but a considerable number of species rarely, if ever, visit flowers. Some species feed only on fungi, whereas others feed only on leaves. Because some of these small insects disperse on the wind, determining their precise biology from casual observations is fraught with difficulties. Adult thrips can be found, sometimes in considerable numbers, on plants to which they have no biological association. Moreover, adults sometimes feed on a plant species on which they do not breed. Thus recognition of true host plant associations amongst Thysanoptera is particularly difficult. The plants listed in Table I cannot be interpreted as the hosts of the thrips found on their leaves without further field studies, but these records provide a starting point for future studies. Many plant species examined in the field did not support thrips but, as indicated above for *Neohoodiella jennibeardae*, this could equally well reflect seasonal or spatial patterns of presence and abundance rather than patterns of non-exploitation by thrips.

One of the most commonly encountered species in this survey was the greenhouse thrips, *Heliothrips haemorrhoidalis* (Bouché), a member of the Thripidae sub-family Panchaetothripinae in which all species breed only on leaves (Mound et al. 2001). This thrips breeds on the leaves of a wide range of plants, particularly introduced species. Damage to native plants by introduced insects is not well documented, but this thrips was observed causing damage to leaves of *Tetrastigma nitens* (Vitaceae) and *Palmeria scandens* (Monimiaceae) near Taree, and large populations have been observed damaging the leaves of *Doryanthes excelsa* (Doryanthaceae) near Sydney. Adults of a related endemic species, *Helionothrips spinosus* Wilson, were found on many plant species, but there is currently no evidence that it breeds anywhere other than on the leaves of *Smilax australis* (Smilacaceae). A third species of Panchaetothripinae, *Anisopilothrips venustulus* (Priesner), is known only from isolated adult females with no reliable host data, taken in many tropical countries and in Australia at scattered localities between Taree and Cape Tribulation in north Queensland. Another introduced panchaetothripine, *Parthenothrips dracaenae* (Heeger), is well known as a pest under domestic situations, damaging the Parlour Palm (*Chamaedorea elegans* - Palmae), but is not commonly taken in the field. In contrast, *Bhattithrips* Mound is an endemic panchaetothripine genus, with three described species and at least two more undescribed, but with no precise information on the biology of any of them.

The sub-family Dendrothripinae (Mound 1999b) appears to be better represented in rainforest than in the more arid parts of Australia. In a small floodplain rainforest remnant at Anthoneys Brush near Taree (see Williams 1993), females of *Ensiferothrips primus* Bianchi were found commonly on five plant species in five families. Females were also taken at other sites on the leaves of two further plant species. However, females together with males and larvae have been taken so far only from the vine *Trophis scandens scandens* (Moraceae) Curiously, this plant is absent from Anthoneys Brush, so the thrips is either highly dispersive or polyphagous. The only other member of this thrips genus, *E. secundus* Mound, is known only from Lord Howe Island, and during a recent visit to that island the host plant of this thrips was found to be the endemic sub-species, *T. scandens megacarpa*, rather than the plants mentioned with the original description (Mound 1999a).

Pseudodendrothrips gillespiei Mound was also described from Lord Howe Island, and several teneral adults were taken recently on that island from the leaves of *T. scandens megacarpa*. The record of one female of this species given here, from subtropical rainforest at Lorien Wildlife Refuge near Taree, represents the first record from the Australian mainland. The species listed as *Pseudodendrothrips* sp.n. was found in large numbers breeding on the leaves of *Ficus fraseri*, and was also taken in considerable numbers on *Ficus coronata* and *F. rubiginosa*. The colour of the forewings, however, varies among the samples taken, from mainly dark to banded. One female of *Dendrothrips glynn* Mound was taken, but the true host of this species is not known as it was based only on three females collected near Cairns. Similarly, the host plant of the widespread *Dendrothrips diaspora* Mound remains unknown, although collecting records suggest that this thrips is possibly polyphagous. In contrast, the species listed as *Dendrothrips* sp.n. was found breeding on the young leaves of the tree *Scolopia braunii* (Flacourtiaceae) at two widely separated sites.

The third sub-family of the Thripidae, the Sericothripinae, includes species that breed in flowers as well as species that breed on leaves. The female listed in Table I as *Neohydatothrips poeta* (Girault) is the third known specimen of this species, and the host plant remains unknown. In contrast, *N. haydni* (Girault) appears to be common on the young leaves of some species of *Indigofera* (Fabaceae), and possibly also on some species of *Swainsonia* (Fabaceae). The largest of the four sub-families of Thripidae, the Thripinae, includes many flower-living species. Williams, et al. (2001) recorded numerous Thripinae from the flowers of rainforest trees and shrubs in this study area, but in the present study, no attempt was made to sample thrips from flowers. Despite this, small numbers of the abundant flower-living species, *Thrips setipennis* (Bagnall), were taken on the leaves of *Claoxylon australe* (Euphorbiaceae), *Acradenia euodiiformis* (Rutaceae) and *Gmelina leichhardtii* (Labiatae), and a few specimens of *Anaphothrips* and *Bregmatothrips* that are possibly associated with grasses were also taken. Of the three leaf-feeding Thripinae in Table I, *Chaetanaphothrips orchidii* (Moulton) is introduced from southeast Asia, and was abundant on the leaves of an orchard tree, *Annona cherimola* (Annonaceae). *Scirtothrips dobroskyi* Moulton was described from the Philippines but is common in northeast Australia, and was found in large numbers on the terminal red leaves of another orchard tree, *Mangifera indica* (Anacardiaceae). The Oriental genus *Rhamphothrips* has only recently been recorded from Australia (Mound 2002a), based on a single female taken on the Cobourg Peninsula (Northern Territory), but an undescribed species of this genus seems to be widespread and abundant on the youngest leaves of *Cissus antarctica* (Vitaceae) in eastern NSW.

Amongst the Phlaeothripidae that were found, some host associations in the list can be dismissed; for example *Nesothrips* and *Hoplandrothrips* species are known to feed on fungi not on green leaves. However, the presence of large numbers of adult *Herathrips nativus* (Girault) on the leaves of *Drypetes deplanchei* (Euphorbiaceae) in dry rainforest at Kiwarrack State Forest south of Taree, is more difficult to understand. The structure of the mouthparts of this species, previously known only from the type series of eight specimens, indicates that it feeds on fungal spores. Single specimens of this species were also collected on leaves of *Baloghia inophylla* (Euphorbiaceae) and *Planchonella australis* (Sapotaceae) at the same site. It seems likely that a large population had built up locally on dead leaves or branches, possibly on the lichens that are abundant at this site, and the individuals on leaves were part of a dispersing population.

The single specimen of *Hoodiella convergens* (Hood) from *Archontophoenix cunninghamiana* (Arecaceae) was presumably a stray, but adults and many larvae of this thrips were found in distorted and partially rolled leaves of the vine, *Tetrastigma nitens* (Vitaceae). One species, *Euoplothrips bagnalli* Hood, was taken in rolled leaf galls on several plants, sometimes in large numbers, but is considered more likely to be a kleptoparasite than a gall-inducing species (Marullo 2001). The rolled-leaf galls on *Smilax* are probably due to *Tolmetothrips smilacis* (Priesner), a species that is widespread northward into the tropics. Foliage beating produced two species of *Teuchothrips*, a genus of leaf-feeding thrips that currently includes 20 named species in Australia and at least as many un-named. The one from *Tetrastigma* has the antennae largely yellow, unlike any other member of the genus, and the one from *Citriobatus pauciflorus* (Pittosporaceae) is unusually small with both winged and wingless adults. The undescribed species of *Haplothrips* from *Austrosteenisia* (Fabaceae) is particularly interesting, because it was taken in large numbers, although without larvae, from the terminal leaflets of this plant, whereas *Haplothrips* species are usually flower-living. Similar in general appearance to this species were two that are presumed to be predatory, *Haplothrips bituberculatus* (Girault) and *Xylaplothrips clavipes* (Karny). The first is usually found on dead twigs, but the second is associated with the galls of other thrips.

Finally, four Phlaeothripidae are listed that were taken in rolled-leaf galls, three apparently representing new genera. The leaf galls on *Drypetes deplanchei* were unusual, involving the margin of each leaf folding in for a distance of about 2 mm, enclosing a narrow tubular space but with the actual margin flattened and closely adpressed to the upper surface of the leaf. Two very different species of thrips were involved; a small but abundant, micropterous species, similar in appearance to certain gall-inducing *Oncothrips* species, presumably induces the galls, but with a second and much larger species that is probably a kleptoparasite. The leaf rolls on *Acronychia oblongifolia* (Rutaceae) were more open and irregular, as is common amongst many members of *Teuchothrips*. These galls also contained two species; a large but short-winged species of *Teuchothrips* presumably induced the galls; the second species is apparently congeneric with an undescribed genus and species that commonly co-exists within the rolled-leaf galls of *Gynaikothrips australis* Bagnall on Moreton Bay fig trees (*Ficus macrophylla*).

These records, from a relatively small area but involving several undescribed taxa, indicate that the diversity of Thysanoptera in Australia's eastern rainforests is considerably higher than published records suggest.

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Table 1.
Thysanoptera from leaves of subtropical rainforest plants near Taree, NSW. ('V' vine, 'S' shrub, 'T' tree, 'SF' State Forest, 'NR' Nature Reserve, 'NP' National Park)

Plant species		Thysanoptera species	Location	Plant community
Anacardiaceae				
Mangifera indica	T	*Scirtothrips dobroskyi*	Lorien Wildlife Refuge, 3 km N Lansdowne	wet sclerophyll forest
Annonaceae				
Annona cherimola	T	*Chaetanaphothrips orchidii*	Lorien Wildlife Refuge, 3 km N Lansdowne	wet sclerophyll forest
Arecaceae				
Archontophoenix cunninghamiana	T	*Hoodiella convergens*	Lorien Wildlife Refuge, 3 km N Lansdowne	riparian rainforest
		Liothrips sp.	Lorien Wildlife Refuge, 3 km N Lansdowne	riparian rainforest
Euphorbiaceae				
Baloghia inophylla	T	*Herathrips nativus*	Kiwarrak SF, S of Taree	dry rainforest
Breynia oblongifolia	S	*Anaphothrips sp.*	Lorien Wildlife Refuge, 3 km N Lansdowne	wet sclerophyll forest
		?*Bregmatothrips sp.*	Lorien Wildlife Refuge, 3 km N Lansdowne	wet sclerophyll forest
		Dendrothrips diaspora	Lorien Wildlife Refuge, 3 km N Lansdowne	wet sclerophyll forest
Bridelia exaltata	T	*Ensiferothrips primus*	Anthoneys Brush, NE of Taree	floodplain rainforest
Claoxylon australe	T/S	*Bhattithrips* sp. n.	Saltwater Reserve, SE Taree	littoral rainforest
		Thrips setipennis	Saltwater Reserve, SE Taree	littoral rainforest
Drypetes deplanchei	T	*Herathrips nativus*	Kiwarrak SF, S of Taree	dry rainforest
		Phlaeothripinae gen.n.2 & 3	Black Head 20km S Taree	littoral rainforest
Eupomatiaceae				
Eupomatia laurina	S/T	*Heliothrips haemorrhoidalis*	Saltwater Reserve, SE Taree	littoral rainforest
		Neohydatothrips poeta	Saltwater Reserve, SE Taree	littoral rainforest
Fabaceae				
Austrosteenisia blackii	V	*Haplothrips* sp.n.	Kiwarrak SF, S of Taree	dry rainforest
Indigofera sp.	S	*Neohydatothrips haydni*	Kiwarrak SF, S of Taree	dry rainforest
		Dendrothrips glynn	Kiwarrak SF, S of Taree	dry rainforest
Flacourtiaceae				
Scolopia braunii	T	*Dendrothrips* sp. n.	Lorien Wildlife Refuge, 3 km N Lansdowne	wet sclerophyll forest
		Dendrothrips sp. n.	Black Head 20km S Taree	littoral rainforest
Malvaceae				
Hibiscus heterophyllus	S	*Ensiferothrips primus*	Kiwarrak SF, S of Taree	wet sclerophyll forest

Plant species		Thysanoptera species	Location	Plant community
Monimiaceae				
Daphnandra micrantha	T	*Anisopilothrips venustulus*	Lorien Wildlife Refuge, 3 km N Lansdowne	subtropical rainforest
Palmeria scandens	V	*Heliothrips haemorrhoidalis*	Tapin Tops NP, NW Wingham	mixed subtropical rainforest – wet sclerophyll forest
		Heliothrips haemorrhoidalis	Upsalls Ck, Kerewong SF, WNW of Kendall	riparian subtropical rainforest
Moraceae				
Ficus coronata	T	*Pseudodendrothrips* sp.n.	Lorien Wildlife Refuge, 3 km N Lansdowne	wet sclerophyll forest
Ficus fraseri	T	*Pseudodendrothrips* sp. n.	Red Head, SE of Taree	headland littoral rainforest
		Thrips setipennis	Harrington	littoral rainforest
Ficus rubiginosa	T	*Ensiferothrips primus*	Anthoneys Brush, NE of Taree	floodplain rainforest
		Ensiferothrips primus	Kiwarrak SF, S of Taree	dry rainforest
		Pseudodendrothrips sp.n.	Kiwarrak SF, S of Taree	wet sclerophyll forest
Trophis scandens	V	*Ensiferothrips primus*	Lorien Wildlife Refuge, 3 km N Lansdowne	subtropical rainforest
		Ensiferothrips primus	Lansdowne Brush, 0.5 km SE Lansdowne	floodplain rainforest
		Ensiferothrips primus	Red Head, SE of Taree	headland littoral rainforest
		Pseudodendrothrips gillespiei	Lorien Wildlife Refuge, 3 km N Lansdowne	subtropical rainforest
Streblus brunonianus	T	*Ensiferothrips primus*	Anthoneys Brush, NE of Taree; Wingham Brush NR	floodplain rainforest
		Heliothrips haemorrhoidalis	Kiwarrak SF, S of Taree	dry rainforest
		Ensiferothrips primus	Kiwarrak SF, S of Taree	dry rainforest
		Xylaplothrips clavipes	Kiwarrak SF, S of Taree	dry rainforest
Myrtaceae				
Backhousia sciadophora	T	*Heliothrips haemorrhoidalis*	Woko NP, ~24 km NNW of Gloucester	dry rainforest
Rhodomyrtus psidioides	T	*Heliothrips haemorrhoidalis*	Lorien Wildlife Refuge, 3 km N Lansdowne	mixed rainforest – wet sclerophyll forest
		Heliothrips haemorrhoidalis	Lansdowne Brush, 0.5 km SE Lansdowne	floodplain rainforest
		Nesothrips propinquus	Lansdowne Brush, 0.5 km SE Lansdowne	floodplain rainforest
Waterhousea floribunda	T	*Liothrips* sp.	Lorien Wildlife Refuge, 3 km N Lansdowne	riparian rainforest
Oleaceae				
Notelaea longifolia	S/T	*Ensiferothrips primus*	Anthoneys Brush, NE of Taree	floodplain rainforest

Plant species		Thysanoptera species	Location	Plant community
Pittosporaceae				
Citriobatus pauciflorus	T	*Heliothrips haemorrhoidalis*	Kiwarrak SF, S of Taree	dry rainforest
		Parthenothrips dracaenae	Kiwarrak SF, S of Taree	dry rainforest
		Ensiferothrips primus	Kiwarrak SF, S of Taree	dry rainforest
		Euoplothrips bagnalli	Kiwarrak SF, S of Taree	dry rainforest
		Haplothrips bituberculatus	Kiwarrak SF, S of Taree	dry rainforest
		Xylaplothrips clavipes	Kiwarrak SF, S of Taree	dry rainforest
		Teuchothrips sp.n.	Kiwarrak SF, S of Taree	dry rainforest
Ripogonaceae				
Ripogonum album	V	*Heliothrips haemorrhoidalis*	Wingham Brush NR	floodplain rainforest
		Helionothrips spinosus	Wingham Brush NR	floodplain rainforest
Ripogonum discolor	V	*Helionothrips spinosus*	Lorien Wildlife Refuge, 3 km N Lansdowne	subtropical rainforest
Ripogonum fawcettianum	V	*Helionothrips spinosus*	Camden Head	headland littoral rainforest
Rubiaceae				
Morinda jasminoides	V	*Neohydatothrips* ?sp. n.	Lorien Wildlife Refuge 3 km N Lansdowne	subtropical rainforest
Rutaceae				
Acradenia euodiiformis	T	*Thrips setipennis*	Lorien Wildlife Refuge, 3 km N Lansdowne	subtropical rainforest
Acronychia oblongifolia	S	*Phlaeothripinae* gen.n. 1	Lorien Wildlife Refuge, 3 km N Lansdowne	Wet sclerophyll forest
		Teuchothrips sp.n.		
Sapindaceae				
Mischocarpus pyriformis	T	*Heliothrips haemorrhoidalis*	Lansdowne Brush, 0.5 km SE Lansdowne	floodplain rainforest
		Haplothrips sp.	Lansdowne Brush, 0.5 km SE Lansdowne	floodplain rainforest
Sapotaceae				
Planchonella australis	T	*Heliothrips haemorrhoidalis*	Lansdowne Brush, 0.5 km SE Lansdowne	floodplain rainforest
		Hoplandrothrips sp.	Lansdowne Brush, 0.5 km SE Lansdowne	floodplain rainforest
		Herathrips nativus	Kiwarrak SF, S of Taree	dry rainforest
Smilacaceae				
Smilax australis	V	*Helionothrips spinosus*	Kiwarrak SF, S of Taree	dry rainforest
		Helionothrips spinosus	Red Head, SE of Taree	headland littoral rainforest
		Tolmetothrips smilacis	Black Head 20km S Taree	littoral rainforest
		Euoplothrips bagnalli	Black Head 20km S Taree	littoral rainforest
Smilax glyciphylla	V	*Helionothrips spinosus*	Saltwater Reserve, SE Taree	littoral rainforest
Ulmaceae				
Aphananthe philippinensis	T	*Ensiferothrips primus*	Anthoneys Brush, NE Taree	floodplain rainforest
Celtis paniculata	T	*Anisopilothrips venustulus*	Camden Head	headland littoral rainforest
		Helionothrips spinosus	Camden Head	headland littoral rainforest

Plant species		Thysanoptera species	Location	Plant community
Verbenaceae				
Gmelina leichhardtii	T	*Thrips setipennis*	Saltwater Reserve, SE Taree	littoral rainforest
Vitaceae				
Cissus antarctica	V	*Rhamphothrips* sp.n.	Lorien Wildlife Refuge, 3 km N Lansdowne	wet sclerophyll forest
Tetrastigma nitens	V	*Heliothrips haemorrhoidalis*	Woko NP, ~24 km NNW of Gloucester	dry rainforest
		Heliothrips haemorrhoidalis	Kiwarrak SF, S of Taree	dry rainforest
		Hoodiella convergens	Kiwarrak SF, S of Taree	dry rainforest
		Euoplothrips bagnalli	Kiwarrak SF, S of Taree	dry rainforest
		Teuchothrips sp.n.	Kiwarrak SF, S of Taree	dry rainforest

Late Ordovician Allochthonous Limestones in Late Silurian Barnby Hills Shale, Central Western New South Wales

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Allochthonous limestone blocks exposed in the Eurimbla area, west of the Mitchell Highway between Molong and Wellington, are substantially older than the enclosing Barnby Hills Shale of Late Silurian age. Nine of the blocks yielded a diverse Late Ordovician conodont fauna, dominated by *Panderodus gracilis*, *Belodina confluens*, *Periodon grandis*, *Paroistodus*? *nowlani* and *Yaoxianognathus*? *tunguskaensis*. Occurrence of *Taoqupognathus blandus* in seven sampled blocks indicates an early Eastonian (Ea2) age, although rare *Taoqupognathus tumidus* in one suggests an extension into the late Eastonian (Ea3). These age determinations are confirmed by the presence of a silicified brachiopod fauna with typical elements (predominantly *Mabella halis* and *Doleroides mixticius*) of the previously defined fauna B of Eastonian 2 age. The conodont and articulate brachiopod faunas from the Eurimbla blocks are comparable with those from autochthonous limestones of Eastonian age elsewhere in the Molong Volcanic Belt, in particular the Bowan Park Group, except for occurrence of the conodont *Webbygnathus munusculum* and brachiopod *Sowerbyella billabongensis* which, in the Lachlan Orogen, are otherwise known only from the Junee-Narromine Volcanic Belt to the west. The allochthonous blocks may have been subject to one or more episodes of erosion and redeposition, prior to final emplacement in the Barnby Hills Shale.

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KEYWORDS: allochthonous limestones, Barnby Hills Shale, brachiopods, conodonts, Late Ordovician, Late Silurian.

INTRODUCTION

Regional mapping recently conducted by the Geological Survey of New South Wales in the central Lachlan Orogen has revealed that allochthonous limestones within the Late Silurian Barnby Hills Shale were derived from two major sources with substantial age differences. Morgan (1999: 92) determined that the Narragal Limestone, of early to middle Ludlow age (Percival 1998), provided the source of the Late Silurian limestone blocks and calcareous debris within the Barnby Hills Shale, based on faunal similarities and regional contact relationships. However, this is only the case within the belt of Barnby Hills Shale situated east of the Mitchell Highway (Fig. 1), for which Meakin and Morgan (1999) provided an extensive list of fossils from both the Silurian limestone blocks and the enclosing siliceous sediments.

Other allochthonous limestones emplaced within the Barnby Hills Shale in the Eurimbla district, west of the Mitchell Highway between Molong and Wellington, were first recognised as Late Ordovician in age by Webby (1969) who identified in them the stromatoporoids *Ecclimadictyon amzassensis* and *E. nestori*, indicative of his early Eastonian coral-stromatoporoid Fauna II. Locations of the larger of these blocks were shown on a regional map by Byrnes (*in* Pickett 1982; reprinted *in* Lishmund et al. 1986), but only relatively recently (Farrell *in* Talent 1995) was detailed mapping of the area undertaken. Percival, Engelbretsen and Brock (1999) noted the occurrence and Eastonian age of a diverse lingulate brachiopod fauna (12 species) from one of the blocks; systematic description of this fauna is underway. Documentation herein of the remainder of the fauna, including

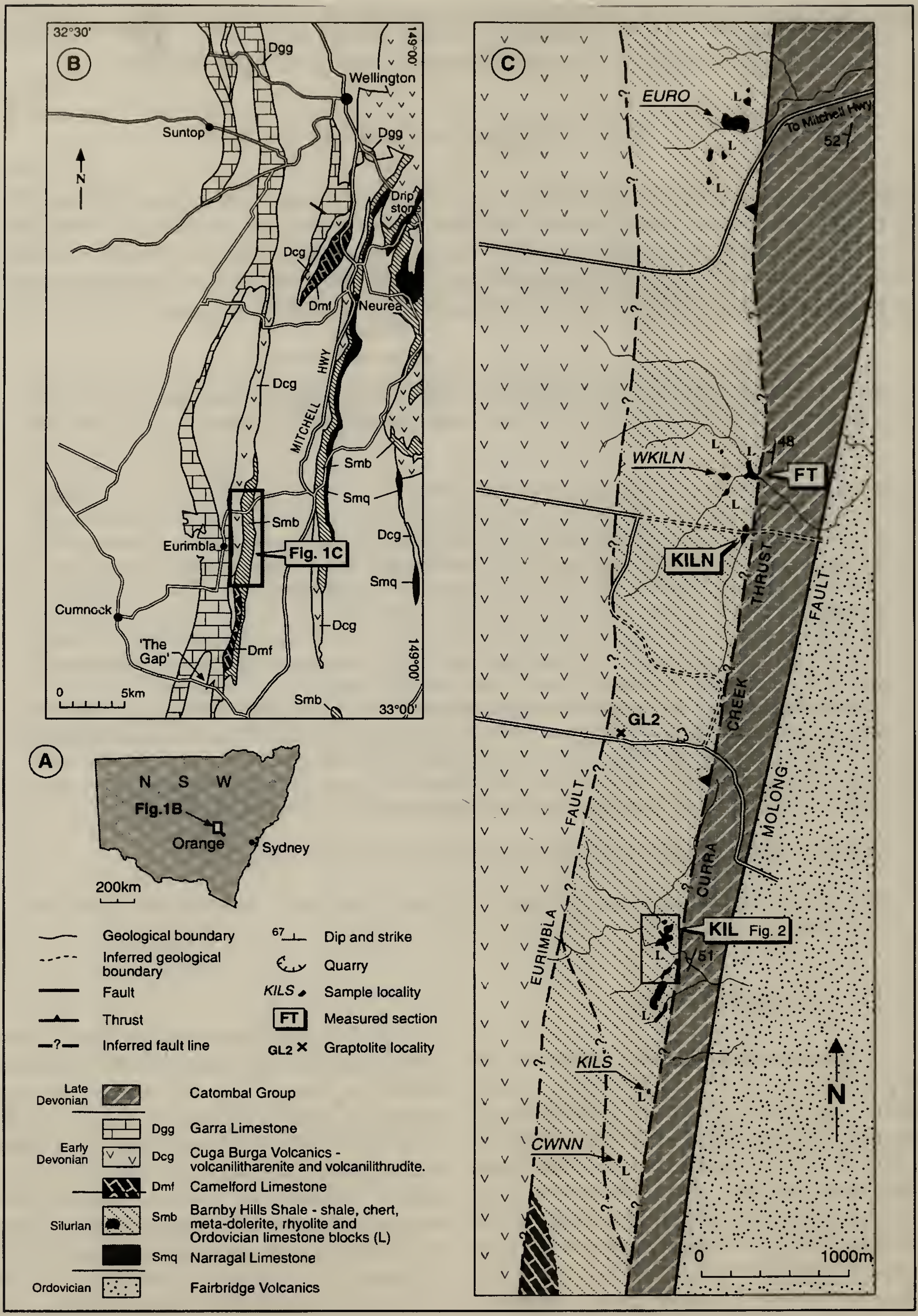

Figure 1. Locality maps. A. New South Wales showing location of figure 1B; B. simplified geological map of the area between Wellington and Cumnock, central New South Wales, showing position of figure 1C; C. geological map of the area to the east of Eurimbla, showing locations of sampled limestone blocks within the Barnby Hills Shale. Position of Figure 2, 'KIL' blocks, is also indicated.

conodonts and articulate brachiopods, provides confirmation of the Eastonian age of this suite of allochthonous blocks, and further enables informed speculation as to their origin.

GEOLOGICAL SETTING

The Barnby Hills Shale was initially proposed by Strusz (1960) for shales, siltstones and a few small limestone lenses comprising the upper member of the Mumbil Formation. He also identified *Monograptus bohemicus* in a siliceous siltstone bed within the unit, supporting a mid to late Ludlow age. The unit was subsequently raised to formation status by Vandyke and Byrnes (1976). Byrnes (*in* Pickett 1982: 146) regarded the section near the old "Mumbil" homestead, which was originally investigated by Strusz (1960), as the type section. However, due to faulting at the top and some internal folding at this locality, Morgan (1999: 90, photo 19 and fig. 21) more recently nominated the section exposed along a railway cutting on "Narrellen" property near Dripstone as the type section. At this locality, the formation is estimated to be 290 m thick, but it reaches a maximum thickness (over 700 m) in the Eurimbla area.

Strusz (1960) stated that the Barnby Hills Shale was in conformable contact with the Early Devonian Cuga Burga Volcanics, but Chatterton et al. (1979) showed that the Camelford Limestone was intercalated between these two units, and that it had a conformable contact with both the Cuga Burga Volcanics and the Barnby Hills Shale. At Neurea, the Barnby Hills Shale conformably overlies the Narragal Limestone, the upper layers of which have been dated, using conodont data, as mid Ludlow *siluricus* Zone (Percival 1998). Graptolites from the Barnby Hills Shale at Neurea include *Bohemograptus bohemicus tenuis* Boucek, *Pristiograptus dubius* cf. *frequens* Jaekel and *Egregiograptus egregius byrnesianum* Rickards and Wright, indicative of a late Ludlow age (Rickards and Wright 1997). Hence in this eastern belt of outcrop of the Barnby Hills Shale, the age of allochthonous limestone blocks derived from the Narragal Limestone (Morgan 1997, 1999) is only slightly older than that of the clastic sediments into which they were redeposited.

This is not the case, however, in the belt of Barnby Hills Shale situated west of the Mitchell Highway, and east of Eurimbla (Fig. 1). In the mapped area (Fig. 1B), the Barnby Hills Shale is fault-bounded, having over-ridden the Late Devonian Catombal Group to the east along the Curra Creek Thrust, and being bounded by the Cuga Burga Volcanics along the Eurimbla Fault to the west. Graptolites recovered from locality 'GL2' (GR 672700E 6352100N, Cumnock 1:50,000 8632-S), within the upper horizons of the siltstone sequence, have been identified as *Monograptus ludensis* (Murchison), indicating a latest Wenlock age (R.B. Rickards pers. comm.). From near the 'KIL' section at GR 673850E 6359110N, Sherwin (1997) reported the occurrence of *Monograptus (Saetograptus) colonus*, indicative of an early Ludlow age (*Neodiversograptus nilssoni* to early *Lobograptus scanicus* zones). North-east of 'The Gap' (Fig. 1), several graptolite species including *Bohemograptus praecornutus* Urbanek (*praecornutus* Biozone, ie middle Ludlow) were discovered in the uppermost horizons of the Barnby Hills Shale (R.B. Rickards pers. comm.). Given the evidence in this area of a latest Wenlock to mid Ludlow age for the upper part of the Barnby Hills Shale, that name is retained despite arguments (Talent and Mawson 1999; Cockle 1999) for its suppression in favour of the more restricted, in both location and depositional time frame, late Ludlow (and younger) Wallace Shale (Sherwin and Rickards 2002) – these two formations being demonstrably non-contemporaneous.

DISTRIBUTION OF ALLOCHTHONOUS LIMESTONES

Eighteen allochthonous limestone bodies of various sizes, ranging from less than a few metres to nearly 200 m in length, are emplaced at or near the faulted base of the Barnby Hills Shale, along the western side of the Curra Creek Thrust, and extend laterally for approximately 7 km on a NS trend (Fig. 2). The limestone outcrops occur in three major groupings. One group is situated in close proximity to the 'KIL' locality; another incorporates the outcrops at 'KILN', 'WKILN' and 'FT' localities, while the third is grouped around a large outcrop at 'EURO'. In addition, two very small isolated outcrops occur at 'CWNN' and 'KILS'.

The limestones are predominantly fine-grained and light to dark grey in colour with some isolated light fawn beds. Muddy intervals and rubbly beds are confined to a single block at the 'KIL' locality. Calcite veining is extensive at locality 'FT' and sets this outcrop at variance to all the others. Apart from a large syncline towards the top of block 'KIL-C', no other folding or faulting is apparent within the allochthonous blocks. Bedding is clearly evident in all blocks and varies from a few centimetres to 1 m in thickness. Apart from the silicified section in block 'KIL-B' (which yielded the abundant brachiopod fauna documented herein) and a coarsely silicified interval around sample number 78 in the same block, macro-fossils are

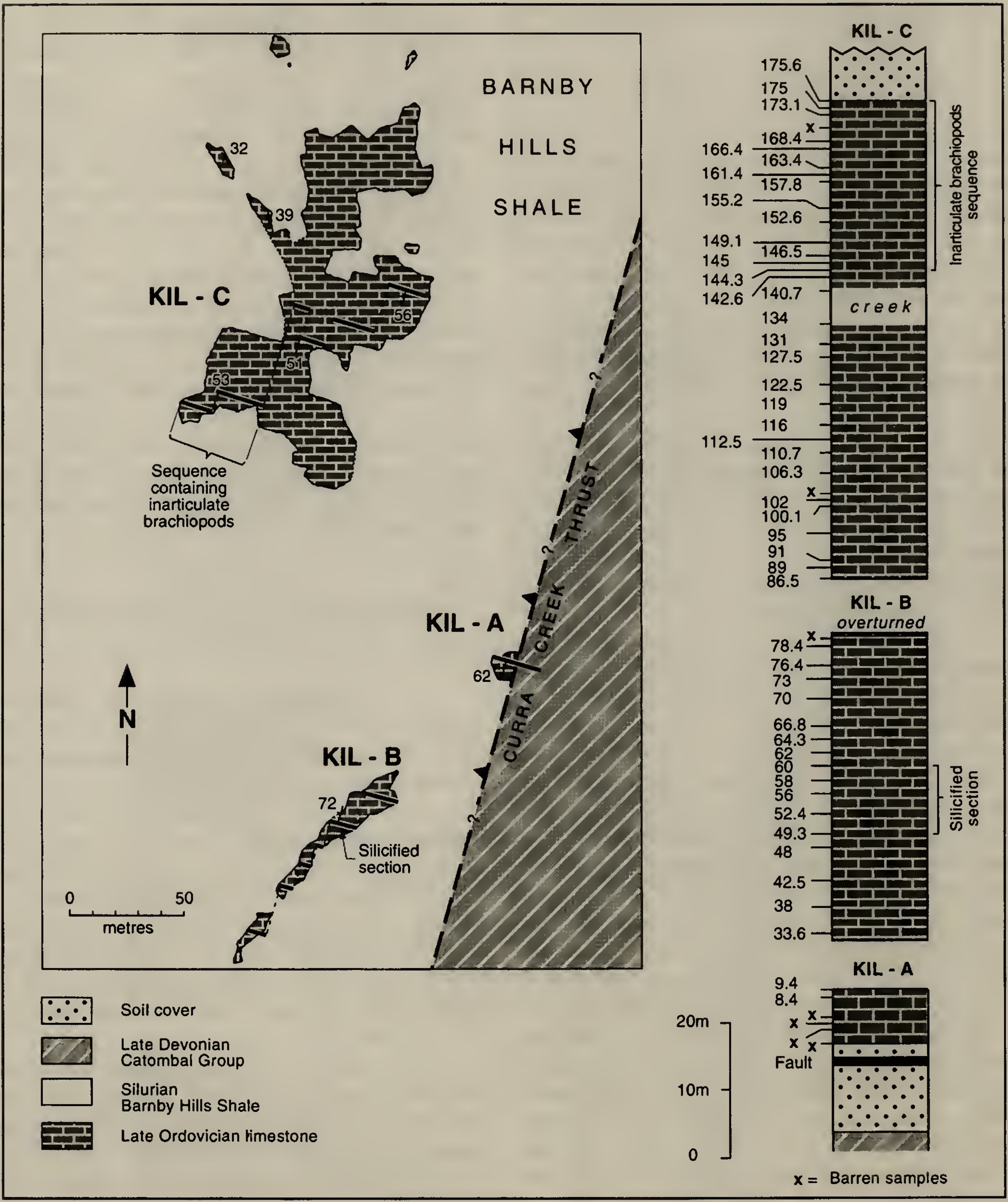

Figure 2. Detailed outcrop map of, and stratigraphic sections measured through, three limestone blocks 'KIL-A', 'KIL-B' and 'KIL-C'; samples producing conodonts are listed to the left of the columns.

extremely rare. Only a few tabulate corals, some stromatoporoids, several brachiopods and one gastropod were recorded from other horizons in the allochthonous blocks.

COMPOSITION AND AGE SIGNIFICANCE OF CONODONT FAUNA

Conodonts recovered from nine individual limestone blocks are represented by 28 species (Fig. 3), and show that these blocks are more or less similar in age (early Eastonian). Twenty-six of these species were previously recorded from the Cliefden Caves Limestone Group (Zhen and Webby 1995), Bowan Park Group (Zhen et al. 1999), Reedy Creek Limestone (Percival, Morgan and Scott 1999), and various other Eastonian successions in central New South Wales (Percival 1999; Packham et al. 1999; Pickett and Furey-Greig 2000; Pickett and Percival 2001), the New England Fold Belt (Furey-Greig 1999, 2000a, 2000b), and eastern Queensland (Palmieri 1978; Simpson 1997). *Coelocerodontus trigonius* Ethington, 1959 and *Panderodus serratus* Rexroad, 1967 are recorded from the Ordovician of eastern Australia for the first time; both are relatively rare, but had a long biostratigraphical range, and are widely distributed.

The six most common species in the fauna - *Panderodus gracilis* (37% of elements), *Belodina confluens* (14%), *Periodon grandis* (12%), *Panderodus* sp. (7%), *Paroistodus*? *nowlani* (6%), and *Yaoxianognathus*? *tunguskaensis* (5%) - are all cosmopolitan or widely distributed geographically. Biostratigraphically significant species present include *Y.*? *tunguskaensis*, which seems to be confined to Eastonian strata of central New South Wales (Trotter and Webby 1995, Zhen and Webby 1995, Zhen et al. 1999), or time equivalents in North China (Wang and Luo 1984; An and Zheng 1990), northwestern China (Wang and Qi 2001), Siberian Platform (Moskalenko 1973), and Canada (McCracken 2000). *Chirognathus cliefdenensis* has previously been reported only from Eastonian rocks of eastern Australia, apart from a recent record from the early Eastonian equivalent *confluens* Zone of southern Baffin Island, Canada (McCracken 2000). Typical species of the *Aphelognathus webbyi* biofacies, which characterises the early Eastonian Fossil Hill Limestone of the Cliefden Caves area, are extremely rare in the present collection, with only two specimens of the Pa element referrable to *A. webbyi* Savage, 1990. *Webbygnathus munusculum* was probably endemic to eastern Australia, with an age range from Ea2 in central New South Wales to Ea3 in the New England Fold Belt (Pickett and Furey-Greig 2000).

Of particular note is the recovery of three species of the Eastonian genus *Taoqupognathus* (*T. philipi*, *T. blandus* and *T. tumidus*) from the 'KIL' locality, where three outcrops were mapped (Fig. 2) and sampled for conodonts (Figs 2 and 3). Zhen and Webby (1995) proposed a lineage for this genus from *T. philipi* to *T. blandus* to *T. tumidus*, which are now recognised as three succeeding conodont zones in the Eastonian (Zhen 2001). *Taoqupognathus blandus* is much more common than the other two species, and indicates an early Eastonian age for these allochthonous limestone blocks in the Barnby Hills Shale. *Taoqupognathus tumidus* is very rare and is only represented by one specimen referable to the P element, which was recovered from the basal part of limestone block 'KIL-B'. However, geopetal structures observed in thin sections prepared from samples taken from the silicified section (Fig. 2) indicate that this outcrop is overturned. Therefore, stratigraphically this late Eastonian (Ea3) species occurs in the highest level of this limestone block. Specimens referrable to *T. philipi* have been recovered from the lower part of limestone block 'KIL-C', and two more specimens doubtfully referred to *T. philipi* are recognised in the two samples of limestone block 'KIL-B'. Occurrence of *T. blandus* and *W. munusculum* in other samples from the same stratigraphic horizon or below suggest that *T. philipi* might well extend upwards into the *T. blandus* Zone or even *T. tumidus* Zone as a relic species (Zhen 2001). Therefore, despite the occurrence of *T. philipi* in some samples, a mid Eastonian (Ea2) age (*T. blandus* Zone) is postulated for the majority of the allochthonous limestone blocks.

BRACHIOPOD FAUNA OF THE ALLOCHTHONOUS BLOCKS

Brachiopods recovered from the silicified portion of the 'KIL-B' section (Fig. 2) include: *Mabella halis*, *Doleroides mixticius*, *Rhynchotrema oepiki*, *Australispira disticha*, *Sowerbyella billabongensis*, with rare *Sowerbyites isotes*, *Zygospira carinata*, *Protozyga definitiva*, *Skenidioides quondongensis*? and *Chaganella speciosa*, together with an indeterminate form provisionally identified as a craniid. All named species recorded here had previously been described (Percival 1991) from *in situ* Eastonian limestones in the Molong Volcanic Belt, such as the Cliefden Caves Limestone Subgroup and the Bowan Park Group, and the Billabong Creek Limestone in the Junee-Narromine Volcanic Belt to the west. Closest correlation is with Brachiopod Fauna B of Ea2 age (Percival 1992), as indicated by the presence of *D. mixticius* and *Sowerbyella billabongensis* which make their first appearances at this level.

Mabella halis and *D. mixticius* overwhelmingly dominate the brachiopod fauna. While *M. halis* is ubiquitous throughout the Eastonian of the central Lachlan Orogen, *D. mixticius* is common only in the Billabong Creek Limestone. Another significant species, previously believed to be restricted to this latter formation, is *S. billabongensis*. On the other hand, two of the rare species in the allochthonous block fauna – *Skenidioides quondongensis*? and *C. speciosa* (represented by a solitary fragmentary specimen) – are otherwise known only from the Molong Volcanic Belt. However, given the location of the Eurimbla area in this Belt, this is not unexpected. The occurrence of *S. billabongensis* in the Eurimbla allochthonous blocks is unusual; seen in the context of the presence of the conodont *Webbygnathus munusculum*, which also is unknown in any other Molong Volcanic Belt limestone, this suggests the possibility of a linkage between the Junee-Narromine Volcanic Belt and the western flank of the northern Molong Volcanic Belt. However, affinities of the majority of the conodont fauna, discussed below, indicate likely derivation of the limestone blocks from a more proximal source area.

STRUCTURAL AND DEPOSITIONAL SETTINGS

To determine the most likely potential source of the allochthonous blocks, an analysis was undertaken of contemporaneous conodont faunas known from Eastonian limestones of the Molong Volcanic Belt. Many species are common to these *in situ* limestones and the allochthonous blocks, but it is the presence or absence of certain restricted species which is critical to revealing closest affinities. The nearest known *in situ* carbonate of Late Ordovician age, which might have provided a potential source area for the Eurimbla blocks, is the Reedy Creek Limestone, exposed near Molong about 20 kms to the south (Percival, Morgan and Scott 1999). The Reedy Creek conodont fauna is almost an exact duplicate of the more fully documented fauna from the Cliefden Caves Limestone Group, described by Zhen and Webby (1995). The latter shares 18 of the 28 species in the allochthonous assemblages, but significantly lacks *Paroistodus*? *nowlani* and *Protopanderodus liripipus*. Both of these species are present in allochthonous limestones near the base of the overlying Malongulli Formation (Trotter and Webby 1995), which is of slightly younger Ea3 age. However, the basal Malongulli Formation fauna is apparently devoid of *Chirognathus cliefdenensis*, *Taoqupognathus blandus*, *T. philipi* and *Yaoxianognathus wrighti*, which are regarded as biostratigraphically important species. The Bowan Park Group fauna (Zhen et al. 1999), particularly that of the Quondong Limestone (Eastonian 2 age), has more species in common with the Eurimbla allochthonous blocks than do the previously mentioned faunas. Thus the affinities of the Eurimbla faunas are closer to *in situ* carbonates on the western flank of the Molong Volcanic Belt, rather than with the Reedy Creek Limestone, contrary to what might have been expected from the latter's geographical proximity.

The presence of *Webbygnathus munusculum*, although extremely rare in the Eurimbla allochthonous blocks (a single specimen recovered from 'KIL-C'), is of some importance in being the first record of the taxon from the Molong Volcanic Belt. Pickett and Furey-Greig (2000), who described this species from Eastonian 2 horizons in the Billabong Creek Limestone of the Junee-Narromine Volcanic Belt, and Ea3 strata in the New England Orogen, commented that "curiously" their new monotypic genus had not been reported from any of the extensive assemblages (discussed above) described from the Molong Volcanic Belt. Hence it is worthwhile investigating other affinities between the conodont faunas from allochthonous limestones at Eurimbla with those from the upper Billabong Creek Limestone (itself in part an allochthonous horizon, although this was deposited penecontemporaneously with the surrounding sediments). A number of significant species found in the Eurimbla allochthonous blocks were not recorded from the Gunningbland area by Pickett and Percival (2001), particularly *Paroistodus*? *nowlani*, *Protopanderodus liripipus*, *Pseudobelodina dispansa*, *Taoqupognathus philipi* and *Yaoxianognathus wrighti*. Thus we conclude that the Billabong Creek Limestone is perhaps not as strong a contender as is the Bowan Park area for a potential source of the Eurimbla allochthonous blocks, and the presence of *Webbygnathus munusculum* in the latter remains enigmatic.

Other erosional remnants in the nearby region are represented by Late Ordovician limestones in the Sourges Shale (Percival, Morgan and Scott 1999), especially the limestone containing conodont sample C1547 that is interpreted as having a middle Eastonian (Ea2-3) age. This outcrop is located about 3 km northeast of Cumnock, and is approximately 6 km west of the Eurimbla allochthonous blocks. Almost due north of the Eurimbla area, along regional strike, further evidence of Late Ordovician allochthonous limestones is found at "Narrawa" in the Wellington district (Percival, Morgan and Scott 1999). This particular occurrence yields corals of coral-stromatoporoid Fauna III age, together with an undescribed inarticulate (lingulate and acrotretid) brachiopod fauna containing several elements in common with the fauna found at 'KIL-C' at Eurimbla. The associated conodont fauna at "Narrawa" is sparse, but includes *Periodon grandis* and *Protopanderodus liripipus*, both of which are represented at Eurimbla. These allochthonous blocks appear to have been emplaced into the Oakdale Formation, here of similar Late Ordovician (late Eastonian to early Bolindian) age.

Allochthonous limestones of Late Ordovician age have also been reported from the Apsley and Bodangora areas, approximately 5 kms SSE and 15 kms NNE, respectively, from Wellington. The Apsley block, located about 400 m E of the railway crossing, is apparently surrounded by Early Devonian Cuga Burga Volcanics. Conodonts recovered from this limestone (collection of the late G.C.O. Bischoff) included *Yaoxianognathus*, *Periodon grandis*, *Panderodus*, and *Taoqupognathus blandus*, indicative of an Eastonian 2 age – identical to that interpreted for the Eurimbla blocks. The Bodangora occurrence is shown on the most recent mapping by the Geological Survey of N.S.W. as an elongate limestone block within the Oakdale Formation at GR 685800E 6409500N (Dubbo 1:100,000 mapsheet). Geological Survey microfossil sample C 061 yielded a small assemblage including the following conodonts: *Belodina confluens*, *Panderodus gracilis*, *Protopanderodus liripipus* and *Taoqupognathus* sp., which can be dated no more accurately than Eastonian.

Having established the age of the Eurimbla allochthonous blocks as early Eastonian (Ea2), and their most likely source as the Bowan Park Group, based on overall similarities in conodont faunas, the mechanism of their emplacement in the Barnby Hills Shale remains to be determined. Clumping of the limestone blocks in three separate groups, two to three kilometres apart, may reflect the presence of discrete channels or submarine valleys. The blocks are also emplaced at various stratigraphic levels within the Barnby Hills Shale, indicating that erosion and redeposition of material was not confined to a single episode. Timing of this series of events is constrained only by the age of the enclosing sediments, ie middle? to late Wenlock to mid Ludlow.

In one possible scenario, the former Molong Volcanic Belt (in which the Bowan Park Group was deposited in the Late Ordovician) subsided in the Early Silurian, becoming the site for further shallow water sedimentation along the Molong High. Uplift of this area, concurrent with deposition of the Barnby Hills Shale in late Wenlock to mid Ludlow time, would have led to erosion of the Molong High succession and emplacement of allochthonous blocks in the deeper water sediments flanking that tectonic feature. The lack of carbonate debris forming breccia deposits within the Barnby Hills Shale in the study area suggests that the limestone blocks either slid down slope individually, or else were associated with a mass flow deposit but, due to their momentum, travelled further into deeper water after the bulk of finer-grained debris had settled. This model pre-supposes that only Eastonian limestone was available at the source site and that any carbonate material aged between Eastonian and the onset of deposition of the Barnby Hills Shale was either not present or had previously been eroded away.

However, elsewhere in central New South Wales, Sherwin (1971) reported allochthonous blocks of Late Ordovician Malongulli Formation and Reedy Creek Limestone redeposited in the Wallace Shale of Late Silurian age, at "Mirrabooka" near Molong. In this instance, blocks with intervening ages are known to have been reworked into the succession, with detritus (including boulder beds) eroded from progressively older deposits. Thus clasts derived from the early Ludlow Molong Limestone appear lower in the Wallace Shale, to be succeeded by the Late Ordovician olistoliths as the Mirrabooka submarine valley (Byrnes 1976; Byrnes *in* Pickett 1982: 159, figs 19, 20) excavated through the western shelf edge of the northern Molong Rise.

Along the eastern margin of the Molong Rise, allochthonous block deposition in Late Silurian to Early Devonian fill of the Hill End Trough (Talent and Mawson 1999) derived from erosion of rocks forming the platform margin to the Mumbil Shelf. This was exposed during the Late Silurian, allowing limestone blocks of various sizes to detach and redeposit in the mud and silt matrix of a lower slope to basinal setting. Again, in this well-documented example, a considerable variety of ages of redeposited blocks, from late Wenlock to Emsian, are evident (Talent and Mawson 1999: text-fig. 7), which is at variance with the Eurimbla situation.

An alternative model to account for the lack of any allochthonous Early Silurian carbonate material, involves tectonic uplift with multiple episodes of redeposition – the first concurrent with limestone breccias emplaced into the basal Malongulli Formation in the Cliefden Caves area (Rigby and Webby 1988). The source of these limestones is interpreted as the Ballingoole Limestone (Eastonian 3 age) in the upper Bowan Park Group. In the northern Molong Volcanic Belt, the Eurimbla blocks appear to have been derived from the slightly older Quondong Limestone, with initial emplacement in the deeper water Oakdale Formation flanking the volcanic belt. Subsequent tectonic uplift of this unit would lead to a second erosional episode in which only the more competent limestones were redeposited as recognisable clasts into the Barnby Hills Shale. This may explain removal of associated finer-grained carbonate debris to leave only the larger blocks in the final depositional episode.

Large-scale faulting on the Curra Creek Thrust and related structures to the west (Scott and Glen 1999; Glen 1999: fig. 95) provides a possible mechanism to explain the occurrence of allochthonous blocks in the Barnby Hills Shale, by bringing Late Ordovician sediments to sufficiently shallow depths to expose them directly to subaerial or submarine erosion without having to wear through Early Silurian cover. In the extensional tectonic regime prevailing in the region during the Silurian, it is probable that some rotational component was involved in such faulting (R.A. Glen, pers. comm.). Further south on the Bathurst 1:250 000 sheet, the Columbine Mountain Fault (Glen 1998: 302) defines the present-day crest of the preserved Molong Volcanic Belt, separating its western side (where the Bowan Park Group was deposited) from the eastern flank, site of the Cliefden Caves Limestone Subgroup and Reedy Creek Limestone. Webby (1992: 56) invoked early movement on the Columbine Mountain Fault as responsible for subsidence of the eastern flank while shallow water carbonate deposition continued in the Bowan Park area, the latter shedding debris into the deep water Malongulli Formation. Timing of this tectonic activity coincides with emplacement of shallow water carbonate blocks into the Oakdale Formation in the Wellington region, and quite feasibly caused displacement of Quondong Limestone equivalents into deeper water sediments.

MATERIAL AND METHODS

Five larger limestone bodies were measured and sampled, and a further four limestone bodies were also spot-sampled (Figs 1 and 2). The majority of conodont samples came from two measured sections through limestone blocks 'KIL-B' (16 samples) and 'KIL-C' (28 samples) (Figs 2 and 3). These samples, each weighing approximately 6 kg, were collected at regular intervals along the measured sections. Conodonts were extracted by completely dissolving the samples in dilute (10%) acetic acid; the residues were separated using the Sodium polytungstate technique outlined in Anderson et al. (1995). Sixty-five samples yielded a total of 1884 conodont elements (Fig. 3), which are relatively well preserved with a CAI of 4. Photographs of the conodonts are SEM photomicrographs captured digitally. Figured conodont specimens bearing the prefix AMF are deposited in the Australian Museum, Sydney. The majority of the conodont species identified are documented by illustration only, as comparable material has been adequately described in recent publications on Late Ordovician conodont faunas of central-western NSW. Only those species providing new or comparative taxonomic information are discussed in detail in the following section.

Brachiopods were obtained by acid dissolution of silicified horizons from limestone block 'KIL'. Illustrated brachiopods are housed in the Palaeontological Collections of the Geological Survey of New South Wales at Lidcombe, and have the prefix MMF. Silicified specimens were not whitened prior to being photographed digitally. As all taxa recognised, with the exception of a possible craniid, were comprehensively described by Percival (1991), only brief remarks are made on significant species.

Grid references of the sampled localities (all on Cumnock 8632-S 1:50,000 sheet, using AMG66 co-ordinates) are as follows: 'KIL-A': 674000E 6358850N, 'KIL-B': 673950E 6358800N, 'KIL-C': 673900E 6358950N, 'KILS': 673850E 6357900N, 'CWNN': 673600E 6357400N, 'KILN': 674350E 6361700N, 'WKILN' (top): 674350E 6362000N, 'FT': 674500E 6362100N, and 'EURO': 674350E 6364650N.

SYSTEMATIC PALAEONTOLOGY

[Conodont taxonomy by Zhen; brachiopod taxonomy by Percival]

Phylum CHORDATA Bateson, 1886
Class CONODONTATA Pander, 1856
Genus CHIROGNATHUS Branson and Mehl, 1933

Type species

Chirognathus duodactylus Branson and Mehl, 1933.

Chirognathus? *cliefdenensis* Zhen and Webby, 1995
Fig. 5A-C

Synonymy

?*Oulodus* cf. *oregonia* (Branson, Mehl and Branson): Trotter and Webby, 1995, p. 483, pl. 4, figs 16-17.

Chirognathus cliefdenensis Zhen and Webby, 1995, p. 281, *partim*, pl. 2, figs 13-22, pl. 3, figs 2-4; non pl. 3, fig. 1; Zhen et al., 1999, p. 86, Fig. 6.13-17.

Yaoxianognathus? *tunguskaensis* (Moskalenko): McCracken, 2000, *partim*, only pl. 3, figs ?26, 28-30.

limestone bodies	KIL-A		KIL-B															
Samples / Conodont taxa	KIL8.4	KIL9.4	KIL33.6	KIL38	KIL42.5	KIL48	KIL49.3	KIL52.4	KIL56	KIL58	KIL60	KIL62	KIL64.3	KIL66.8	KIL70	KIL73	KIL76.4	KIL78.4
Ansella sp.		1			1													2
Aphelognathus webbyi																		
Belodina baiyanhuaensis						4		2						2				
Belodina confluens	2	7	2		5	5	1	3	1	2	2	6	2	2	9	4	4	7
Belodina sp.						4	1		1					2				
Besselodus sp.																		
Chirognathus? cliefdenensis					1										1			2
Coelocerodontus trigonius		2											1					
Drepanoistodus suberectus		1				1						2			3			
"*Oistodus*" sp. cf. *venustus*					1	1		1										1
Panderodus gracilis	2	2	7	1	12	8	3	7	2	5	3	2	2	6	7	4	3	7
Panderodus panderi					1													
Panderodus serratus															1			
Panderodus sp.		7		2	3	7	2			1	4		2	2	3			
Paroistodus? nowlani	1															2		
Periodon grandis																		
Phragmodus undatus											2				1	1		
Protopanderodus liripipus																1		
Pseudobelodina dispansa														1	1			
Pseudobelodina sp.																		
Pseudooneotodus mitratus									1									
Taoqupognathus blandus	2				1						3							1
Taoqupognathus philipi			1?												1?			
Taoqupognathus tumidus				1														
Webbygnathus munusculum																		
Yaoxianognathus wrighti						1												
Y.? tunguskaensis	1	2			2	4	1		1			1	3		2	2		4
Yaoxianognathus sp.						1												
TOTAL	9	22	10	4	27	36	8	13	6	8	14	11	10	15	29	14	7	24

limestone bodies	KIL-C													
Samples / Conodont taxa	KIL86.5	KIL89	KIL91	KIL95	KIL95.7	KIL97.5	KIL100.1	KIL102	KIL106.3	KIL110.7	KIL112.5	KIL116	KIL119.5	KIL134
Ansella sp.		1												
Aphelognathus webbyi														
Belodina baiyanhuaensis			1		2						1			
Belodina confluens	10	26	4	27	8	3		5	6	3	3		2	
Belodina sp.				2										
Besselodus sp.														
Chirognathus? cliefdenensis		1		2			1					2		
Coelocerodontus trigonius									1					
Drepanoistodus suberectus	1	1		1	1									
"*Oistodus*" sp. cf. *venustus*	2									1				
Panderodus gracilis	8	26	1	16	4	7	28	2	11	4	2	5	11	20
Panderodus panderi														
Panderodus serratus														
Panderodus sp.	2	2	7				4		6	2	2		5	1
Paroistodus? nowlani	1													
Periodon grandis														
Phragmodus undatus				2	1		2	3						
Protopanderodus liripipus													1	
Pseudobelodina dispansa	2	4		2			3		1			1		
Pseudobelodina sp.														
Pseudooneotodus mitratus														
Taoqupognathus blandus			1		2									
Taoqupognathus philipi						2	16		2				2	
Taoqupognathus tumidus														
Webbygnathus munusculum				1										
Yaoxianognathus wrighti														
Y.? tunguskaensis	5	10	1	7			9			1			2	
Yaoxianognathus sp.							1	1						
TOTAL	31	71	15	60	18	12	64	11	27	11	8	8	23	21

limestone bodies	KIL-C													
Samples / Conodont taxa	KIL142.6	KIL144.3	KIL145	KIL146.5	KIL149.1	KIL152.6	KIL155.2	KIL157.8	KIL161.4	KIL166.4	KIL168.4	KIL173.1	KIL175	KIL175.6
Ansella sp.							1	1			2	1		1
Aphelognathus webbyi										1				
Belodina baiyanhuaensis			1											
Belodina confluens		1	8	1	1	4	3	5	2	12	9	13		6
Belodina sp.									1					
Besselodus sp.									2	2				1
Chirognathus? cliefdenensis			2									1		
Coelocerodontus trigonius												4		
Drepanoistodus suberectus	1		1	1	1	5	2	9	7	9	7	6		2
"*Oistodus*" sp. cf. *venustus*	2		2			4			1			13		5
Panderodus gracilis	6	12	37	11	17	28	31	17	35	38	54	34	1	48
Panderodus panderi										2				2
Panderodus serratus									1			3		1
Panderodus sp.		3	7	1	4	6	3		4	4	9			2
Paroistodus? nowlani	2	1	9	1	3	15	12	8	3	17	17	17		6
Periodon grandis			2			1	2	9	3	54	11	93		35
Phragmodus undatus												1		
Protopanderodus liripipus							1			2		7		5
Pseudobelodina dispansa			1			3								
Pseudobelodina sp.														
Pseudooneotodus mitratus												5		2
Taoqupognathus blandus	2	1	6	1	2	2	2			2	2	4		
Taoqupognathus philipi														
Taoqupognathus tumidus														
Webbygnathus munusculum														
Yaoxianognathus wrighti						2		7			2			
Y.? tunguskaensis	4				1	1			2	9	6	4		4
Yaoxianognathus sp.														
TOTAL	17	18	76	16	29	71	57	56	61	150	119	206	1	119

limestone bodies	FT						KILN				CWNN	KILS	WKILN				EURO			TOTAL
Samples / Conodont taxa	FT40	FT45	FT51	FT68	FT73	FT84	KILN10	KILN17	KILN40	KILN52			WKILN-A	WKILN-B	WKILN-C	WKILN-D	EURO (top)	EURO (mid)	EURO (base)	
Ansella sp.															1					12
Aphelognathus webbyi												1								2
Belodina baiyanhuaensis										3										16
Belodina confluens	1			2		3	3		3		1	5	5		6		8		1	264
Belodina sp.																				11
Besselodus sp.										1								2		8
Chirognathus? cliefdenensis			1					1												15
Coelocerodontus trigonius																				8
Drepanoistodus suberectus			1								1		9		1	1		1		76
"*Oistodus*" sp. cf. *venustus*														1						35
Panderodus gracilis		1	7	6	3	5	2		8	12	20	2	23	1	10	9	5	1	1	703
Panderodus panderi																				5
Panderodus serratus																				6
Panderodus sp.	1		2							1	6		2		5	2	1			127
Paroistodus? nowlani										1			6		1			2	1?	120
Periodon grandis													18		2					230
Phragmodus undatus				1																14
Protopanderodus liripipus																				17
Pseudobelodina dispansa		1																		20
Pseudobelodina sp.															1					1
Pseudooneotodus mitratus																				8
Taoqupognathus blandus	1			1		1				1				1	1			1		41
Taoqupognathus philipi																				24
Taoqupognathus tumidus																				1
Webbygnathus munusculum																				1
Yaoxianognathus wrighti										1								1		14
Y.? tunguskaensis										2	1		3		1	2		2		100
Yaoxianognathus sp.				1									1							5
TOTAL	3	2	11	11	3	9	5	1	11	21	29	8	67	3	29	14	14	8	3	1884

Figure 3. Distribution chart of conodont species from nine individually sampled allochthonous limestone blocks.

Figure 4. SEM photographs of Late Ordovician conodonts from allochthonous limestones within the Barnby Hills Shale. **A, B,** *Ansella* sp., asymmetrical nondenticulated element; A, AMF121400, 'KIL' 9.4; B, AMF121401, 'KIL' 95. **C**, *Aphelognathus webbyi* Savage, 1990, Pa element, AMF121402, 'KILS'. **D**, *Belodina baiyanhuanensis* Qiu *in* Lin et al., 1984, compressiform element, AMF121403, 'KILN' 52. **E-G**, *Belodina confluens* Sweet, 1979, E, eobelodiniform element, AMF121404, 'KIL' 97.5; F, grandiform element, AMF121405, 'KIL' 70; G, compressiform element, AMF121406, 'KIL' 173.1. **H-K**, *Belodina* sp., grandiform element; H, AMF121407, 'KIL' 56; I, J, AMF121408, 'KIL' 48; K, enlargement of surficial ornament, AMF121409, 'KIL' 49.3. **L-O**, *Besselodus* sp., short-based distacodiform element; L, M, AMF121410, 'KIL' 161.4; N, AMF121411, 'KILN' 52; O, AMF121412, 'KIL' 161.4. **P-X**, *Coelocerodontus trigonius* Ethington, 1959; P, Q, symmetrical trigoniform element, P, AMF121413, 'KIL' 173.1; Q, AMF121414, 'KIL' 9.4; R, S, asymmetrical trigoniform element, AMF121415, 'KIL' 173.1; T, U, asymmetrical tetragoniform element, AMF121416, 'KIL' 173.1; V-X, symmetrical tetragoniform element (W: basal view), AMF121417, 'KIL' 173.1; scale bars 100 μm, except as indicated for K.

Material

Fifteen specimens (6 Pa, 4 Pb, 5 S) from limestone blocks 'KIL-B', 'KIL-C', 'FT' and 'KILN'.

Discussion

All elements, except for the symmetrical Sa, have been recovered from various limestone blocks within the Barnby Hills Shale, and they are identical with the type material from the Cliefden Caves Limestone Group (Zhen and Webby 1995).

McCracken (2000) proposed a septimembrate apparatus for *Yaoxianognathus*? *tunguskaensis* (Moskalenko). This reconstruction is rather different from that recognised by Zhen et al. (1999) on the basis of homologic characters, such as widely spaced, robust denticles on all elements of *Y.*? *tunguskaensis*. McCracken's illustrated Sc and M elements of *Y.*? *tunguskaensis* are typical for *Yaoxianognathus*, especially the Sc (McCracken 2000: pl. 3, fig. 25) which is referable to *Y. tunguskaensis*. However, P (Pa, Pb, Pc) and Sa elements figured by McCracken (2000: pl. 3, figs 26, 28-30) are at least congeneric if not conspecific with *C. cliefdenensis*.

Genus COELOCERODONTUS Ethington, 1959

Type species

Coelocerodontus trigonius Ethington, 1959.

Coelocerodontus trigonius Ethington, 1959
Fig.4P-X

Synonymy

Coelocerodontus trigonius Ethington, 1959, p. 273, pl. 39, fig. 14; Webers, 1966, p. 25, pl. 2, figs 12-14; ?Orchard, 1980, p. 19, pl. 2, figs 17, 22, 23, 29; Nowlan et al., 1988, p. 14, pl. 3, figs 1-5, 8-10 (cum. syn.); McCracken and Nowlan, 1989, p. 1888, pl. 2, fig. 18; Nowlan et al., 1997, pl. 1, fig. 4; Zhang, 1998, p. 56, pl. 5, figs 1-4.

Coelocerodontus tetragonius Ethington, 1959, p. 273, pl. 39, fig. 15.

Coelocerodontus digonius Sweet and Bergström, 1962, p. 1224, pl. 168, fig. 1, Text-fig. 1F.

Material

Eight specimens (6 trigoniform, 2 tetragoniform) from limestone blocks 'KIL-A', 'KIL-B' and 'KIL-C'.

Discussion

Webers' (1966) initial species concept of a bimembrate (trigoniform and tetragoniform) apparatus was revised by Nowlan et al. (1988) as a trimembrate apparatus including a symmetrical trigoniform, a slightly asymmetrical trigoniform and a nearly symmetrical tetragoniform element. All three elements have been recognised in the central New South Wales material, together with an additional slightly asymmetrical tetragoniform specimen. All these elements are characterised by having thin walls and a very deep basal cavity, with the apex nearly reaching the tip of the cusp. The trigoniform elements, with a broad anterior face, a sharp costa on each antero-lateral corner, and a costa along the posterior margin, are either symmetrical (Fig. 4P, Q) or slightly asymmetrical (Fig._4R, S), with a triangular opening of the basal cavity. The latter is identical with the holotype of the form species *C. trigonius*, except for its more antero-posteriorly compressed cusp. The tetragoniform element is quadrate in cross section with four prominent costae, situated on the antero-lateral and postero-lateral corners of each side. Our specimens are identical with the holotype of the form species *C. tetragonius* Ethington, 1959, except that the latter (Ethington 1959: pl. 39, fig. 15) is more laterally compressed.

Zhang (1998) illustrated (but neither defined nor described) laterally compressed, non-costate P elements, and costate Sb, Sc and Sd elements from the Middle Ordovician of South China. Of the two specimens (Zhang 1998: pl. 5, figs 1, 2) referred to as P elements, the more slender is identical with the holotype of the form species *C. digonius* Sweet and Bergström, 1962. The other specimen (Zhang 1998: pl. 5, fig. 1) is a wider conical unit with a more posteriorly extended base. These elements may be differentiated as Pa and Pb, respectively. The specimen designated as the Sd element (Zhang 1998: pl. 5, fig. 4) seems identical with one illustrated as *Coelocerodontus*? sp. from the Middle Ordovician (Darriwilian) of northern Sweden (Löfgren 1978: pl. 1, fig. 40). Neither the P elements, nor the Sd element with a mid-costa on each side, have been recognised in the central New South Wales material.

Coelocerodontus trigonius ranged through the Middle and Upper Ordovician. The type specimen (Ethington 1959: pl. 39, fig. 14) from the upper Galena Formation (*confluens* Zone) of Iowa is associated with a rich conodont fauna including *Belodina confluens*, *Phragmodus undatus*, *Periodon grandis*, and *Drepanoistodus suberectus*. Zhang (1998) reported this species from the Middle Ordovician Guniutan Formation (Darriwilian) of South China. It was also identified from the Upper Ordovician of North America (Winder 1966; Webers 1966; Nowlan et al. 1988, 1997; McCracken and Nowlan 1989), Scandinavia (Hamer 1964) and north England (Orchard 1980). This is the first record of this species in the Ordovician of eastern Australia.

Figure 5. SEM photographs of Late Ordovician conodonts from allochthonous limestones within the Barnby Hills Shale. **A-C**, *Chirognathus*? *cliefdenensis* Zhen and Webby, 1995; A, Pa element, AMF121418, 'CWNN'; B, Sd element, AMF121419, 'KIL' 78.4; C, Sc element, AMF121420, 'KIL' 78.4. **D-I**, *Drepanoistodus suberectus* (Branson and Mehl, 1933); D, M element, AMF121421, 'KIL' 86.5; E, Sb element, AMF121422, 'KIL' 62; F, Sa element, AMF121423, 'KIL' 157.8; G, P element, AMF121424, 'KIL' 155.2; H, Sc element, AMF121425, 'KIL' 157.8; I, Sa element, AMF121426, 'KIL' 95.7. **J**, "*Oistodus*" sp. cf. *venustus* Stauffer, 1935 s.f., M element, AMF121427, 'KIL' 110.7. **K-M**, *Panderodus gracilis* (Branson and Mehl, 1933); K, falciform element, AMF121428, 'KIL' 175.6; L, M, asymmetrical graciliform element, L, AMF121429, 'KIL' 175.6, M, AMF121430, 'CWNN'. **N, O**, *Panderodus panderi* (Stauffer, 1940); N, short-based element, AMF121431, 'KIL' 175.6; O, long-based element, AMF121432, 'KIL' 175.6. **P-T**, *Panderodus serratus* Rexroad, 1967; P, S, T, serrated arcuatiform element, P, AMF121433, 'KIL' 173.1, S, AMF121435, 'KIL' 175.6, T, AMF121436, 'KIL' 173.1; Q, R, non-serrated falciform element, AMF121434, 'KIL' 173.1. **U-W**, *Panderodus* sp.; falciform element, U, AMF121437, 'KIL' 175.6; V, AMF121438, 'KIL' 175.6; W, AMF121439, 'CWNN'; scale bars 100 µm.

Genus DREPANOISTODUS Lindström, 1971

Type species

Oistodus forceps Lindström, 1955.

Drepanoistodus suberectus (Branson and Mehl, 1933)

Fig. 5D-I

Synonymy

Oistodus suberectus Branson and Mehl, 1933, p. 111, pl. 35, figs 22-27.

Drepanoistodus suberectus (Branson and Mehl); Nowlan and McCracken *in* Nowlan et al., 1988, p. 16, pl. 3, figs 19-22 (*cum syn.*); Dzik, 1994, p. 78, pl. 17, figs 2-6, text-fig. 12b; Zhen and Webby, 1995, p. 282, pl. 3, figs 8-10 (*cum syn.*); Nowlan et al., 1997, pl. 1, figs 7-9; Zhen et al., 1999, p. 88, Fig. 6.1-7; Furey-Greig, 1999, p. 310, pl. 2, figs1-3; Furey-Greig, 2000b, p. 137, Fig. 5.8; McCracken, 2000, pl. 1, fig. 12, pl. 2, figs 20, 21; Leslie, 2000, Fig. 5.16-19; Sweet, 2000, Fig. 9.23-25.

Material

Seventy-six specimens (9 P, 6 M, 5 Sa, 12 Sb, 10 Sc and 34 undifferentiated elements) from limestone blocks 'KIL-A', 'KIL-B', 'KIL-C', 'FT', 'CWNN', 'WKILN' and 'EURO'.

Discussion

Elements forming the quinquimembrate apparatus of this species are laterally compressed, with sharp posterior and anterior margins and smooth lateral faces. The P element is weakly asymmetrical with a convex outer lateral face and an inner-laterally curved cusp, and is characterised by having a triangular, anticusp-like extension at the antero-basal corner. The M element is geniculate with a robust cusp. The nearly symmetrical Sa element has a sub-erect cusp, an antero-posteriorly extended base, and a shallow, but open inflated basal cavity. The Sb element is asymmetrical, with a suberect to slightly reclined cusp, a strongly curved basal margin, and the base extended only posteriorly. The Sc element somewhat resembles the P element, but is strongly asymmetrical with a posteriorly reclined cusp, and apparently lacks the prominent antero-basal extension of the latter. The present material is identical with that from the Bowan Park Group and basal Malachi's Hill Beds (Zhen et al., 1999), except that the P element from the limestones within Barnby Hill Shale shows a more strongly extended antero-basal corner.

Genus PANDERODUS Ethington, 1959

Type species

Paltodus unicostatus Branson and Mehl, 1933.

Panderodus serratus Rexroad, 1967
Fig. 5P-T

Synonymy

Panderodus unicostatus serratus Rexroad, 1967, p. 47, pl. 4, figs 3, 4.

Panderodus serratus Rexroad; Cooper, 1975, p. 993, pl. 1, figs 3-5, 7-9, 13, 14, 23; Nowlan et al., 1988, p. 23, pl. 8, figs 5-7; Miller, 1995, pl. 1, figs 15, 16; Jeppsson, 1997, p.107, Fig. 7.4.

Material

Six specimens (4 serrated arcuatiform, 2 falciform elements) from limestone blocks 'KIL-B' and 'KIL-C'.

Discussion

Panderodus serratus ranges from the Upper Ordovician (Ethington and Schumacher 1969; McCracken and Barnes 1981; Nowlan and Barnes 1981; Nowlan et al. 1988) where it is relatively rare, through the Lower and Middle Silurian (Miller 1995; Jeppsson 1997), where it is widely distributed although by no means common. The distribution patterns of *Panderodus serratus* and its abundant ubiquitous associate *P. unicostatus* in the Silurian suggested to Jeppsson (1997) that they represented two distinct species (rather than morphotypes of a single species), distinguishable on presence or absence of the serrated element. In our collections, the serrated element is only represented by four specimens, which are comparable with those recorded from the Upper Ordovician of Canada (Nowlan et al. 1988), except for their smaller denticles and more prominently inner laterally curved cusp. Two additional specimens, which are recognised as the nonserrated falciform element of this species, are laterally compressed with sharp anterior and posterior margins.

Genus PERIODON Hadding, 1913

Type species

Periodon aculeatus Hadding, 1913.

Periodon grandis (Ethington, 1959)
Fig. 6D-L

Synonymy

Loxognathus grandis Ethington, 1959, p. 281, pl. 40, fig. 6.

Periodon grandis (Ethington); Bergström and Sweet, 1966, p. 363-5, pl. 30, figs 1-8 (*cum syn.*); Lindström *in* Ziegler, 1981, p. 243-244, *Periodon*-pl. 1, figs 13-18; Zhang and Chen, 1992, pl. 1, figs 13-16; Ding et al., *in* Wang, 1993, p. 190, pl. 35, figs 18-21; Zhen and Webby, 1995, p. 284, pl. 4, figs 3, 4 (*cum syn.*); Zhen et al., 1999, p. 90, fig. 8.19-8.21; Furey-Greig, 1999, p. 310, pl. 2, figs 21, 22, pl. 3, figs 1, 2.

Material

Two hundred and thirty specimens (36 Pa, 8 Pb, 123 M, 63 S elements) from limestone blocks 'KIL-C' and 'WKILN'.

Figure 6. SEM photographs of Late Ordovician conodonts from allochthonous limestones within the Barnby Hills Shale. **A-C**, *Paroistodus*? *nowlani* Zhen et al., 1999; distacodiform (b) element, A, AMF121440, 'KIL' 73; B, AMF121441, 'KIL' 145; C, AMF121442, 'KIL' 149.1. **D-L**, *Periodon grandis* (Ethington, 1959); D, M element, AMF121443, 'KIL' 152.6; E, Sc element, AMF121444, 'KIL' 166.4; F, Pa element AMF121445, 'KIL' 155.2; G, Sb element, AMF121446, 'KIL' 157.8; H, Pb element, AMF121447, 'KIL' 173.1; I, Sc element, AMF121448, 'KIL' 166.4; J, Pa element, AMF121449, 'KIL' 157.8; K, ?Sd element, AMF121450, 'KIL' 173.1; L, Sa element, AMF121451, 'KIL' 173.1. **M**, *Pseudobelodina dispansa* (Glenister, 1957); AMF121452, 'KIL' 70. **N, O**, *Phragmodus undatus* Branson and Mehl, 1933; N, Pa element, AMF121453, 'KIL' 70; O, Sc element, AMF121454, 'KIL' 60; **P**, *Yaoxiangnathus wrighti* Savage, 1990; Pa element, AMF121455, 'KIL' 48. **Q**, *Pseudooneotodus mitratus* (Moskalenko, 1973); AMF121456, 'KIL' 173.1; scale bars 100 µm.

Discussion

Bergström and Sweet (1966) reconstructed the species as having a seximembrate apparatus, and this concept has been accepted since then by most conodont workers. The holotype of the species is a ramiform specimen referred to as the Sb element (previously the form species *Loxognathus grandis* Ethington, 1959). The Sa position is taken by the form species *Trichonodella insolita* Ethington, 1959, the Sc element is the form species *Eoligonodina magna* Ethington, 1959 (see Bergström and Sweet 1966; and Sweet 1988), while the form species *Prioniodina araea* Webers, 1966 and *Ligonodina tortilis* Sweet and Bergström 1962 were assigned to the Pa and Pb positions respectively. As admitted by Bergström and Sweet (1966: 364), *P. grandis* and *P. aculeatus* Hadding, 1913, the likely direct ancestor of the former, are "similar in overall shape and in most morphologic features." These authors suggested that the geniculate M element of *P. grandis*, as the most characteristic form, could be differentiated from the same element of *P. aculeatus* by having a large, subtriangular base with essentially straight basal margin, and by having denticles on the anterior margin closely appressed to it rather than developed into an anterior process. Lindström (*in* Ziegler 1981) suggested distinguishing these two species by the denticles along the anterior margin of the M element reaching higher towards the tip of the cusp, and by the greater number (about 6 or more) of denticles between the cusp and the biggest denticle on the posterior process of the S elements in *P. grandis*. However, the present central NSW material exhibit a rather centrally, downwardly arched basal margin, and typically more than six smaller denticles between the cusp and the largest denticles on the posterior process. Specimens referred as *P. grandis* showing similar arched basal margin of the M element were also recorded previously from North America (Webers 1966).

Genus TAOQUPOGNATHUS An *in* An et al., 1985

Type species

Taoqupognathus blandus An *in* An et al., 1985.

Taoqupognathus blandus An *in* An et al., 1985

Fig. 7E-H

Synonymy

1985 *Taoqupognathus blandus* An *in* An et al., p. 104, pl. 2, figs 18, 19; An, 1987, p. 192, pl. 30, fig. 20; An and Zheng, 1990, pl. 7, figs 5, 6, 20; Zhen and Webby, 1995, p. 287, pl. 6, figs 1-13; Zhen et al., 1999, p.94-96, Fig. 14.10-16; Wang and Qi, 2001, pl. 2, fig. 15.

Material

Forty-one specimens (11 M, 3 Sb2, 1 Sc2, 6 Sc3, 16 Sc5, 4 undifferentiated S elements) from limestone blocks 'KIL-A', 'KIL-B', 'KIL-C', 'FT', 'KILN', 'WKILN', and 'EURO'.

Discussion

In the lower part of limestone block KIL-C, *T. philipi* and *T. blandus* co-occur. One specimen, from sample 'KIL' 95.7 (Fig. 7E), shows features transitional between typical Sc5 elements of *T. philipi* and *T. blandus*. Considering its rather prominent posterior bulging, we regard this element as an early representative of the Sc5 element of *T. blandus*. A specimen of the Sb2 element of *T. blandus* is also recovered from a slightly lower level (Fig. 7F). Specimens from the upper part of limestone block 'KIL-C' with more prominent and stronger posterior bulging (Fig. 7G), are identical with those illustrated from the upper Belubula Limestone and Vandon Limestone (Zhen and Webby 1995).

Taoqupognathus philipi Savage, 1990

Fig. 7I, J

Synonymy

Taoqupognathus philipi Savage, 1990, p. 828, fig. 8.1-8.12; Zhen and Webby, 1995, p. 287, pl., 5, figs 7-22; non McCracken, 2000, p. 194, pl. 1, fig. 28.

Taoqupognathus tumidus Trotter and Webby, 1995; Furey-Greig, 1999, p. 312, *partim*, only pl. 4, figs 2, 9.

Material

Twenty-two specimens (5 M1, 8 M2, 1 Sc3, 8 Sc5 elements) from the lower part of the limestone block 'KIL-C', and two doubtful specimens from limestone block 'KIL-B'.

Discussion

Taoqupognathus philipi, the oldest species of the genus, is characterized by having slender, elongated elements, with only weakly developed posterior bulging on the S elements. It has been recorded from the Fossil Hill Limestone of the Cliefden Caves Limestone Group (Savage 1990; Zhen and Webby 1995), and the lower Reedy Creek Limestone (Percival, Morgan and Scott 1999) of central New South Wales. Several Sc5 specimens showing the characteristic features of the species (Fig. 7H, I, J) were recovered from block 'KIL-C'. In comparison with the holotype of *T. philipi* from the Fossil Hill Limestone (Savage 1990: fig. 8.11, 8.12), these specimens exhibit a weaker development of posterior bulging and a gently curved anterior margin. No P elements have been recovered from any of our samples.

So far *Taoqupognathus* has only been recorded from Australia and China (Zhen 2001). McCracken (2000) reported the occurrence of *T. philipi* from the Frobisher Bay and Amadjuak formations of southern Baffin Island. McCracken's identification was based on two specimens, one from each formation, but only one supposed Sc5 element was illustrated (McCracken 2000: pl. 1, fig. 28). In our opinion, this specimen cannot even be assigned with any certainty to the Panderodontidae. It lacks any distinctive characters of *Taoqupognathus*, except for a superficially similar outline, especially the tip of the cusp. Similar shape outlines are also seen in some Early Ordovician taxa, like *Macerodus* Fåhraeus and Nowlan, 1978 (also see Ji and Barnes, 1994).

Taoqupognathus tumidus Trotter and Webby, 1995

Fig. 7K

Synonymy

Drepanodus? *altipes*? Palmieri, 1978, pl. 2, figs 24, 25.

gen. unident. Pickett, 1978, fig. 4.

Belodina cf. *B. blandus* (An); Duan, 1990, p. 31, pl. 5, fig.7.

Taoqupognathus tumidus Trotter and Webby, 1995, p. 487, pl. 7, figs 10-24; Zhen et al., 1999,

Figure 7. SEM photographs of Late Ordovician conodonts from allochthonous limestones within the Barnby Hills Shale. **A,** *Pseudobelodina* sp. Zhen et al., 1999; AMF121457, 'WKILN-C'. **B-D,** *Protopanderodus liripipus* Kennedy, Barnes and Uyeno, 1979; B, symmetrical element, AMF121458, 'KIL' 119.5; C, asymmetrical element, AMF121459, 'KIL' 173.1; D, weakly asymmetrical element, AMF121460, 'KIL' 173.1. **E-H,** *Taoqupognathus blandus* An *in* An et al., 1985; E, ?Sc5 element, AMF121765, 'KIL' 95.7; F, Sb2 element, AMF121766, 'KIL' 91; G, Sc5 element, AMF121463, 'WKILN-C'; H, Sc5 element, AMF121464, 'WKILN-B'. **I, J,** *Taoqupognathus philipi* Savage, 1990; Sc5 element, I, AMF121465, 'KIL' 97.5, J, AMF121466, 'KIL' 100.1. **K,** *Taoqupognathus tumidus* Trotter and Webby, 1995; P element, AMF121467, 'KIL' 38. **L-N,** *Webbygnathus munusculum* Pickett and Furey-Greig, 2000; Pa element, AMF121468, 'KIL' 95. **O, P,** *Yaoxianognathus* sp.; O, Pa element, AMF121470, 'KIL '100.1; P, Pb element, AMF121469, 'KIL' 48; **Q, R,** *Yaoxianognathus? tunguskaensis* (Moskalenko, 1973); Q, Sc element, AMF121461, 'KIL' 95; R, Sd element, AMF121462, 'KIL' 89; scale bars 100 μm.

p. 96, fig. 14.1-14.9; Percival, 1999, fig. 3.1, 3.2, 3.5; Packham et al., 1999, fig. 3.14-3.16; Furey-Greig, 1999, p. 312, *partim* only, pl. 4, figs 1, 3-8.
Taoqupognathus ani Wang and Zhou, 1998, p. 190, pl. 3, fig. 4.

Material

A single P element from the lower part of limestone block 'KIL-B'.

Discussion

This species seems much wider in distribution than the other two stratigraphically older species in eastern

Australia and China. After the submission of a review paper on the genus (Zhen 2001), YYZ had the opportunity to examine the late Professor An's conodont collection from the Taoqupo section near Yaoxian (An and Zheng 1990: 81-87), housed at the Department of Geology, Beijing University. Four specimens referable to P, Sb1, and Sb2 elements of *T. tumidus* were recognised in the sample TP34Y-5, which was taken about 30 m below the occurrence of *Favisitina* sp. at the top of the Taoqupo Formation.

T. ani Wang and Zhou, 1998 from the Upper Ordovician of the Tarim Basin is a form species based only on a single element, which is identical to the P element of *T. tumidus* from eastern Australia.

Phylum BRACHIOPODA Duméril, 1806
?Subphylum CRANIIFORMEA Popov et al., 1993
?Class CRANIATA Williams et al., 1996
?Order CRANIIDA Waagen, 1885
?Family CRANIIDAE Menke, 1828

unnamed ?craniid
Fig. 8 ff-kk

Material.
Five ventral? valves from 'KIL' section at 53.5, 58, and 59 m.

Discussion.
Classification of these specimens is problematic, as – if in fact they are craniids – they are atypical of this group. The valves are assumed to be ventral in position because of the apparent and consistent presence of a pedicle foramen. If so, this would be the first recognition of this feature in the remarkably long history of the craniids, which have displayed morphological conservatism from their appearance in the Ordovician to the present day. Most representatives of the group (including all living forms) are cemented to the substrate by their ventral valves. Two genera (*Orthisocrania* and *Pseudocrania*) interpreted as free-living are known from the Ordovician, but neither possesses a foramen.

The specimens from the Eurimbla block are subconical in profile, and circular to ovate in outline (although incompletely preserved, so that orientation is uncertain). There is a suggestion that growth may have been mixoperipheral, as there appears to be a straight hingeline in the largest valve (Fig. 8 kk). Ornament comprises coarse radial costae of irregular size; that extending from the pedicle foramen is often (but not always) the most pronounced. Internal musculature is not preserved, and the dorsal valve is unknown. For these reasons, the taxon is not formally named. No other craniids have been described from Lachlan Orogen strata of Late Ordovician age. However, their recognition may have been impeded by the fact that fragmentary remains would appear indistinguishable from other silicified debris retrieved from acid dissolution of limestones; it is only when the valves are reasonably intact that their affinities can be determined.

Subphylum RHYNCHONELLIFORMEA Williams et al., 1996
Class STROPHOMENATA Williams et al., 1996
Order STROPHOMENIDA Opik, 1934
Superfamily PLECTAMBONITOIDEA Jones, 1928
Family LEPTELLINIDAE Ulrich and Cooper, 1936
Subfamily LEPTELLININAE Ulrich and Cooper, 1936
Genus MABELLA Klenina *in* Klenina, Nikitin and Popov, 1984

Mabella halis (Percival, 1991)
Fig. 8 o-t

Wiradjuriella halis Percival, 1991, p. 138-141, fig. 12: 1-38; Percival 1992, fig. 4: 10, fig. 5: 37-38.
Mabella halis (Percival, 1991), Cocks and Rong Jia-yu 2000, p. 322-323, fig. 208: 2f-i.

Material.
Six valves figured from 'KIL' section, plus several hundred additional specimens.

Discussion.
These specimens conform in all regards to the description given by Percival (1991). *Mabella* sp. is also known from younger (late Eastonian) strata at Gunningbland in the Junee-Narromine Volcanic Belt, where it was first described as aff. *Leptellina* sp. by Percival (1979) and subsequently illustrated as *Wiradjuriella* sp. in Percival (1992: fig. 6, 31). A potential ancestor of *M. halis* may be *Leptellina*? sp. from the Wahringa Limestone Member of the Fairbridge Volcanics, which is exposed at Bakers Swamp, less than 15 kms north of Eurimbla; this occurrence is of earliest Gisbornian (basal Late Ordovician) age (Percival et al. 2001). Other species referred to *Mabella* (according to Percival et al. 2001: 228) include *M. solida* (Nikitin and Popov, 1984) and *M. namasensis* (Klenina, 1984), as well as *M. conferta* (Popov, 1985); all three are from Kazakhstan.

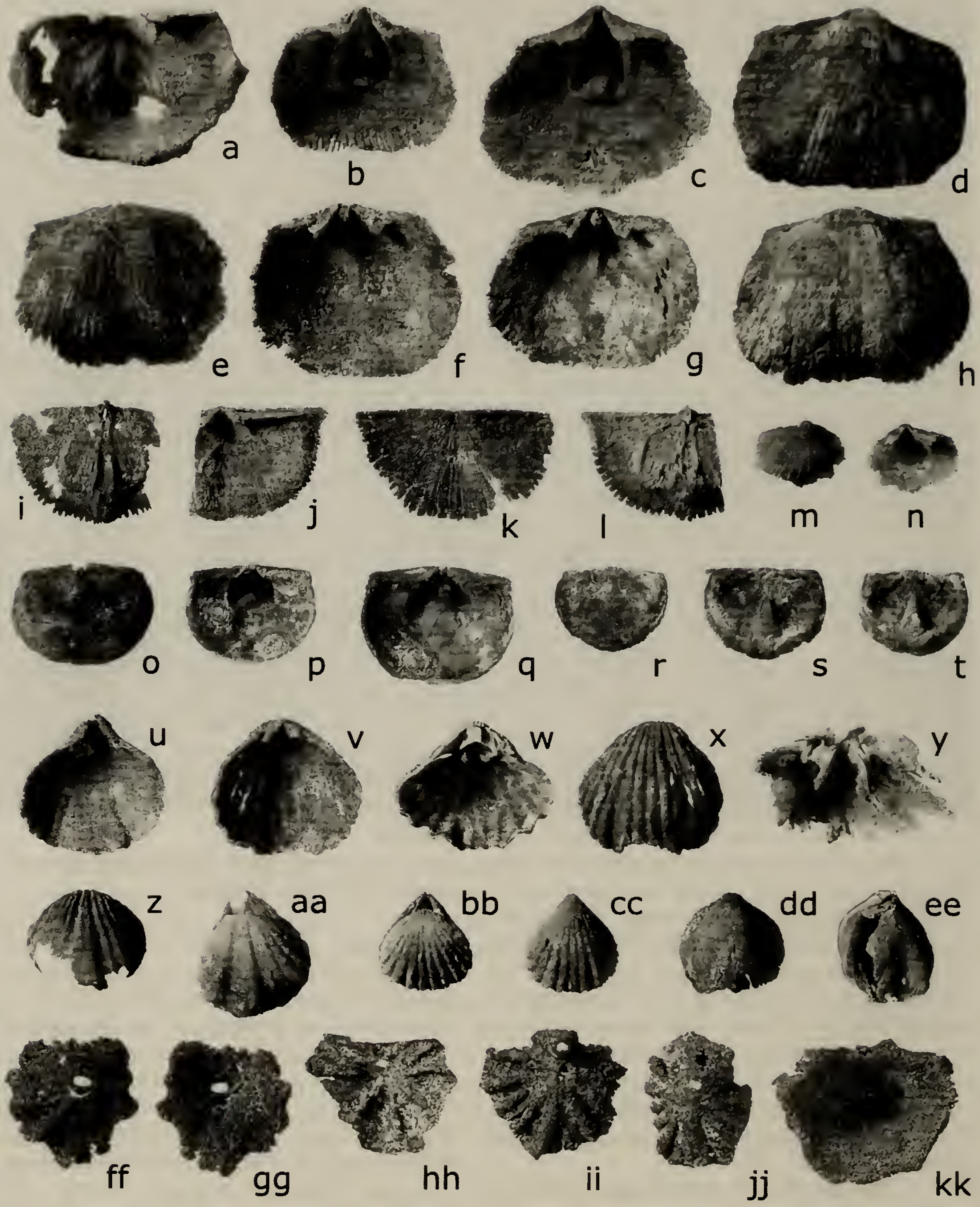

Figure 8. Silicified brachiopods of Late Ordovician age from allochthonous limestone block 'KIL' within the Barnby Hills Shale; all photographs taken by digital camera of unwhitened specimens. All specimens from horizon 'KIL' 53.5 unless otherwise stated. Magnifications all x2 unless otherwise stated. **a**, *Chaganella speciosa* (Percival, 1991), ventral valve interior, MMF36922. **b-h**, *Doleroides mixticius* Percival, 1991; b, ventral valve interior, MMF36923; c, ventral valve interior, MMF36924; d, ventral valve exterior, MMF36925; e, ventral valve exterior, MMF36926; f, dorsal valve interior, MMF36927; g, dorsal valve interior, MMF36928; h, dorsal valve exterior, MMF36929. **i-l**, *Sowerbyella billabongensis* Percival, 1991; i, dorsal valve interior, MMF36930; j, ventral valve interior, MMF36931; k, dorsal valve exterior, MMF 36932; l., dorsal valve interior, MMF36933. **m**, **n**, *Skenidioides quondongensis*? Percival, 1991; exterior and interior views

(Figure 8 continued) (both x3) of incomplete ventral valve, MMF36934, from 'KIL' 59. **o-t**, *Mabella halis* (Percival, 1991); o, ventral valve exterior, MMF36935; p, ventral valve interior, MMF36936; q, ventral valve interior, MMF36937; r, dorsal valve exterior, MMF36938; s, dorsal valve interior, MMF36939; t, dorsal valve interior, MMF36940. **u-y**, *Rhynchotrema oepiki* Percival, 1991; u, ventral valve interior, MMF36941; v, x, dorsal valve interior and exterior, MMF36942; w, dorsal valve interior with interlocked posterior fragment of ventral valve; y, enlargement (x3) of posterior fragment of dorsal valve interior, showing crura, MMF36943. **z, aa**, *Australispira disticha* Percival, 1991; z, incomplete dorsal valve exterior, MMF36944; aa, dorsal view (x3) of juvenile conjoined valves, MMF36945. **bb, cc**, *Zygospira carinata* Percival, 1991; dorsal and ventral views of conjoined valves, MMF36946, x4. **dd, ee**, *Protozyga definitiva* Percival, 1991; ventral valve exterior, and oblique lateral view of conjoined valves, dorsal valve to right, MMF36947, x4. **ff-kk**, unnamed craniid?, all x3; ff, gg, exterior and interior views of presumed ventral valve, MMF36948, from 'KIL' 58; hh, exterior view of presumed ventral valve, MMF36949, from 'KIL' 59; ii, exterior view of presumed ventral valve, MMF36950, from 'KIL' 58; jj, exterior view of presumed ventral valve, MMF36951, from 'KIL' 59; kk, interior view of ?ventral valve, MMF36952.

Family HESPEROMENIDAE Cooper, 1956
Genus CHAGANELLA Nikitin, 1974

Chaganella speciosa (Percival, 1991)
Fig. 8a

Tylambonites speciosa Percival 1991, p. 143-144, fig. 13: 14-35; Percival 1992, fig 4: 11-3, fig. 5: 46-47.

Chaganella speciosa (Percival, 1991) Cocks and Rong Jia-yu 2000, p. 339, fig. 222: 2e-h.

Material.

One specimen, a fragmentary ventral valve from 'KIL' section at 53.5 m.

Discussion.

Percival (1991: 143) noted substantial similarities between *Tylambonites* and *Chaganella*, but differentiated these genera on lack of a pedicle callist in *Chaganella* and chilidial plates being partially fused in the latter rather than discrete as in *Tylambonites*. Such distinctions are now regarded as of specific rather than generic significance.

Class RHYNCHONELLATA Williams et al., 1996
Order ORTHIDA Schuchert and Cooper, 1932
Superfamily PLECTORTHOIDEA Schuchert and LeVene, 1929
Family PLECTORTHIDAE Schuchert and LeVene, 1929
Genus DOLEROIDES Cooper, 1930

Doleroides mixticius Percival, 1991
Fig. 8b-h

Doleroides mixticius Percival 1991, p. 127, 129, fig. 8: 17-39; Percival 1992, fig. 5: 19-21.

Material.

Abundant valves from 'KIL' section at 53.5 m.

Discussion.

The characteristic *Mimella*-like appearance of the ventral muscle field, previously noted by Percival (1991) when establishing the species, is well in evidence in some specimens (eg, Fig. 8b) from the Eurimbla allochthonous block, where *D. mixticius* is one of the most dominant forms. In all other morphological aspects, this species conforms to the generic concept of *Doleroides* as summarised in the recently revised brachiopod Treatise (Williams and Harper 2000: 759).

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The Middle Triassic Megafossil Flora of the Basin Creek Formation, Nymboida Coal Measures, New South Wales, Australia. Part 3. Fern-like Foliage.

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Two quarries in the Basin Creek Formation of the Middle Triassic Nymboida Coal Measures have yielded numerous examples of fern-like foliage. No affiliated fertile material is available to place the fronds in a natural classification. Twenty three species in twelve genera are described as morpho-taxa in Order and Family Incertae Sedis. Plants described in this paper are:- *Cladophlebis conferta* sp. nov., *C. octonerva* sp. nov., *C. paucinerva* sp. nov., *C. retallackii* sp. nov., *C. sinuata* sp. nov., *C. tenuipinnula* sp. nov., *Dictyonymba sparnosa* gen. et sp. nov., *Gouldianum alethopteroides* gen. et sp. nov., *Leconama stachyophylla* gen. et sp. nov., *Micronymbopteris repens* gen. et sp. nov., *Nymbiella lacerata* gen. et sp. nov., *Nymboidiantum glossophyllum* (Tenison-Woods) gen. et comb. nov., *N. multilobatum* gen. et sp. nov., *N. elegans* gen. et sp. nov., *N. fractiflexum* gen. et sp. nov., *N. robustum* gen. et sp. nov., *Nymbophlebis polymorpha* gen. et sp. nov., *Nymbopteron dejerseyi* (Retallack) gen. et comb. nov., *N. foleyi* gen. et sp. nov., *N. uncinatum* gen. et sp. nov., *Nymborhipteris radiata* gen. et sp. nov., *Ptilotonymba curvinervia* gen. et sp. nov. and *Sphenopteris speciosa* sp. nov. The diversity of this new material demonstrates the remarkable recovery of Gondwana vegetation following the end-Permian extinction event.

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KEYWORDS: Gondwana Middle Triassic, megafossil fern-like foliage, Nymboida Coal Measures, palaeobotany.

INTRODUCTION

This paper is the third in a series describing the rich and diverse megafossil flora from two quarries near the village of Nymboida in north eastern New South Wales. A locality map and details of the geology of the Nymboida area were provided in Part 1 of this series (Holmes 2000) which dealt with the Thallophyta and Sphenophyta. Part 2 (Holmes 2001b) included descriptions of 14 taxa of the Filicophyta representing true ferns preserved in a fertile state or remains of sterile material with known fern relationships.

This paper describes fern-like foliage of uncertain systematic position due to the lack of fertile material. It is acknowledged that some at least of these fossil plants are not true ferns. They may be new forms of pteridosperms or even belong to plant groups that are presently unknown. Twenty four species are placed in twelve genera. The names published below are defined as morpho-taxa under the provisions of the International Code of Botanical Nomenclature (ICBN 2000).

The diversity of plants with fern-like foliage that are described below is a remarkable demonstration of the recovery of the world's vegetation following the end-Permian extinction event. That catastrophic and devastating event caused the disappearance of the Gondwana *Glossopteris* Flora and up to 90% of the world's living organisms. It brought about the cessation of all coal formation throughout the world. The "Coal Gap" (Retallack 1996) persisted until early Middle Triassic time. Some of the earliest coal seams following the "Coal Gap" are preserved in the Basin Creek Formation.

Included in this Middle Triassic coal flora are some specimens which in gross morphology are closely similar to ferns. Although some are common and widespread, none have been found with associated or identifiable fertile remains. Most of the morpho-taxa are rare and in some cases are based on a single specimen or just a few individuals. Even though specimens may be rare and fragmentary, provided there are significant diagnostic features for differentiation, they are illustrated and described in order to make known their presence in the Nymboida Flora. The minimum criteria for formal naming are that the specimens demonstrate the attachment of pinnae to a main rachis and preferably with pinnules showing a reasonable state of preservation of the venation. Lebedev (1974) believed that through the use of good descriptions, accurate drawings and adequate photographs, sterile fern fronds could be confidently identified and even placed in natural groupings. In this paper I have attempted as far as possible to follow the guidelines of Lebedev. However, the novelty of most specimens, the lack of associated fertile material and the state of preservation precludes the placement of this material in a natural classification.

A tectonic heating event during the Cretaceous (Russell 1994) has destroyed the cuticle of otherwise often exquisitely preserved leaves and fruits of the entire flora at the two Nymboida localities. There is great scope for further investigations from localities where cuticle and fine cell structure may be preserved.

As in extant floras, the assemblages of fossil plants are directly related to their habitats. Several species of one genus may co-exist in a limited area but each within its own habitat. The presence of several species in the *Cladophlebis*, *Nymbopteron* and *Nymboidiantum* genera may relate to the taxa being derived from differing facies.

The sediments included in the 20 metres depth exposed in the working faces of the Nymboida quarries range from coarse conglomerates to fine shales and coal bands. Each horizon represents a flood event and a particular facies that existed through a short period of geological time (Holmes 2000) on an alluvial floodplain. Fossil soils formed during pauses in the deposition of sediments are also present The reconstruction of the Middle Triassic Nymboida floodplain by Retallack (1977) demonstrates the range of habitats that existed simultaneously. The fossil assemblages, supported by facies evidence, range from in-situ accumulations and fossil soils (autochthonous) to partially dispersed (semi-authochthonous) to long distance transport dispersal and fragmentation (allochthonous).

The origins and relationships of the majority of plants in the Early to Middle Triassic Gondwana floras are problematical. Due to the virtual spatial and climatic isolation of Gondwana and especially eastern Australia from the Northern Hemisphere following the end-Permian extinction event, I believe there is dubious value in attempting to determine close relationships between plants from those two macro-regions based only on gross morphology. This problem, relevant to sphenophytes, was discussed by Holmes (2001a). In this paper, with a few exceptions, I have compared the Nymboida fern-like foliage only with previously described Gondwana material. Where there is no published description matching my material I have erected new species and in some cases, new genera. These new taxa will provide a reference for comparisons with other Gondwana assemblages and, hopefully, will be the foundation for future studies based on better preserved and more complete material that will allow the fossil plants to be placed in a natural classification system. At that stage, more meaningful comparisons may be made with fossils from Triassic northern floras.

Most specimens are illustrated at both natural size and enlarged. The size of reproduction is indicated in the Figure legends and by a bar measure representing one centimetre on each photograph.

All the described, illustrated and mentioned specimens in this paper have been lodged with the Australian Museum, Sydney and have been catalogued with AMF numbers.

SYSTEMATIC PALAEOBOTANY

Order Incertae sedis
Family Incertae sedis
Genus *Cladophlebis* Brongniart 1849
Type species *Cladophlebis albertsii* (Dunker)
Brongniart 1849

The genus *Cladophlebis* was erected by Brongniart (1849) for sterile fern fronds from both the Late Palaeozoic and Mesozoic. It was generally regarded as a form genus. Fertile material has been placed variously in a number of natural genera. In an attempt to define *Cladophlebis* in a strict sense as a natural genus, Frenguelli (1947) carried out an extensive review of over 150 species and forms that had been attributed to *Cladophlebis*. On his restricted definition he recognised 28 Mesozoic species worldwide, including 14 species from the Triassic to Cretaceous in Argentina. Later Herbst (1971, 1978) revised both the Argentinean and Australasian species of *Cladophlebis*. For Australasia he retained as valid species the variable and long-ranging *Cladophlebis australis* with a synonymy list of 26 entries, and *C. mendozaensis*. *C. patagonica* and *C. gondwanica* were regarded as doubtful. However, the Nymboida Flora is rich in ferns and fern-like foliage and contains at least six species described below which are referable to this genus. In Part 2 of this series, fertile ferns were placed in *Asterotheca, Rhinipteris, Todites, Herbstopteris, Osmundopsis* and *Nymbofelicia* (Holmes 2001b). In most cases the associated sterile fronds would have fitted broadly in *Cladophlebis*.

Sterile fronds with no associated fertile material are here placed in the morpho-genus *Cladophlebis* which includes bipinnate fronds, pinnules separated to the base, broadly attached to pinna rachis and variously decurrent, base occasionally slightly lobed either basiscopically or acroscopically, entire to slightly lobed or serrate, parallel-sided to slightly tapering, straight or variously falcate; midvein prominent and usually persistent almost to the apex, lateral veins alternate, forking once, twice or rarely three times, often simple distally. It must be understood that this is an artificial classification based merely on gross form and the individual morpho-taxa may belong in a range of natural genera.

Cladophlebis conferta Holmes sp. nov.

Figures 1A–C

Diagnosis

Medium sized bipinnate frond; pinnae closely spaced at high angle to main rachis; pinnules opposite to subopposite, broadly falcate, midvein fine, four pairs of lateral veins, proximal two pairs twice forked, second pair once forked, distal pair unforked or once forked close to margin.

Description

This taxon is based on two specimens each showing a midportion of bipinnate fronds that may have possibly reached one metre long in life. AMF121014 shows a main rachis tapering from 8 mm to 6 mm over a length of 300 mm. The holotype frond fragment (Fig. 1A) has a smooth main rachis 5 mm in width with seven pairs of overlapping opposite pinnae attached at c. 80° to main rachis at intervals of c. 10 mm. Pinnae linear, tapering in distal half to acute apex, to 100 mm long, 15 mm wide. Pinnules opposite to alternate, closely spaced to overlapping, to 8 mm long, 5 mm wide; length to width ratio of c. 1.6:1; attached at c. 45° at midpinna and at a higher angle closer to the main rachis; basiscopic margin decurrent, slightly contracted above base, margin broadly convex, acroscopic margin straight to slightly convex, apex obtuse; midvein fine, once forked before the pinnule apex; with four pairs of alternate lateral veins at c. 35° to midvein; first two pairs twice forked, second pair once forked and distal pair usually simple; forking very acute with c. 20 vein endings around pinnule margin (Fig. 1C).

Holotype

AMF120987, and portion of the counterpart as isotype AMF121015. Australian Museum, Sydney.

Type locality

Reserve Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF121014, Reserve Quarry, Nymboida.

Name derivation

conferta – *confertus*, (Lat.), *dense, crowded*, referring to the closely spaced pinnae and pinnules.

Discussion

Although known from only two specimens, the preservation is sufficient to provide diagnostic characters. *C. conferta* pinnules have a similar number of lateral veins as *C. octonervia* (described below), but differ by the shorter broader pinnules, the more acute and radiating form of the forking veins and by the fewer vein endings around the pinnule margin. By the closely spaced, long, opposite pinnae and by the form of the sparse and fine venation, *C. conferta* differs from all other Gondwana *Cladophlebis* spp.

Cladophlebis octonerva Holmes sp. nov.

Figures 2 A–C

1921 – *Cladophlebis mesozoica* var *typica* Kurtz pl. 30, Fig. 6.

Diagnosis

Medium sized bipinnate frond, pinnae opposite to alternate, pinnules thick-textured, alternate, oblong to triangular, entire or occasionally lobed, apex obtuse, median vein weak, continuing to apex, four pairs of lateral veins once forked close to midvein then diverging to margin.

Description

Complete fronds not available. The holotype (Fig. 2A), a 180 mm long midportion of a narrow elliptic bipinnate frond, suggests a total frond length of c. 400 mm. The main and pinna rachises are strongly ribbed and grooved. Pinnae opposite to alternate, attached basally at right angles or obtuse, in the middle of the frond at c. 80° to 90°, distally more acute; linear, longest in midportion of frond, to 60 mm long and 14 mm wide, tapering from midway to the acute apex. Pinnules alternate, oblong to triangular or straight to slightly falcate, attached at 90° to 60° to pinna rachis, basiscopic margin slightly contracted, acroscopic base slightly decurrent upwards, margin more convex on proximal side, entire to slightly lobed, apex obtuse, length to width ratio, c. 2–2.5:1. Midvein continuing to the apex, four pairs of lateral veins each once broadly forked close to the midvein; venules continuing to diverge straight or slightly arching to the margin; number of lateral veins decreasing on smaller pinnules distally and apically. First lateral veins occasionally forking again near the margin (Fig. 2C). Number of vein endings around margin c. 16.

Holotype

AMF113484, Australian Museum, Sydney.

Type locality

Reserve Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF113485-86. Coal Mine Quarry, Nymboida.

Name derivation

octonerva – octo, (Lat.), *eight; nerva, (*Lat.*) veins*; referring to the usually four pairs of arching lateral veins in each pinnule.

Discussion

C. octonerva differs from other Nymboida *Cladophlebis* spp. by the shorter broader pinnules with four pairs of once-forking lateral veins in the pinnules. A frond fragment illustrated in Kurtz (1921, pl. 30, Fig. 6) from the Triassic of Argentina, as *C. mesozoica* var. *typica* has pinnule form and once-forking lateral venation closely similar to *C. octonerva.* Stipanicic et al. (1995), in a revision of the material figured in Kurtz (1921), followed both Frenguelli (1947, pl. 7, Figs 2,5) and Herbst (1971, Figs 17, 19), who defined *C. mesozoica* as having twice forked lateral veins. The *C. mesozoica* var *typica* specimen was not accepted as *C. mesozoica* and was merely identified as *C.* sp. By restricting *C. mesozoica* to leaves with twice forked lateral veins, forms such as *C. octonerva* and *C. sinuata* (described below), which are only partially twice forked, are excluded from that taxon.

Cladophlebis paucinerva Holmes sp. nov.
Figures 3A-G

Diagnosis

A small bipinnate frond with short narrow-ovate, opposite to alternate pinnae; pinnules alternate, broad-ovate, apex obtuse, length to width ratio of c. 2:1; midvein straight, dividing well before the apex, with two pairs of alternate lateral veins once-forking halfway to margin.

Description

This taxon is based on a number of small midportions of incomplete fronds to 35 mm long, which bear to five pairs of sub-opposite short pinnae; estimated total length of frond in life c. 50 mm. Rachis 1 mm wide, strongly ribbed and grooved; pinnae well-spaced, attached at c. 45°, narrow ovate to 15 mm long and 6 mm wide, tapering from halfway to the acute apex with c. 6 pairs of alternate pinnules. Pinnules broadly attached at c. 45°, decurrent basiscopically, slightly contracted acroscopically, broad-ovate, 3–4 mm long, 1.5–2 mm wide, becoming more triangular in midportion of pinna then coalescing apically; length to width ratio of c. 2:1; pinnule margin entire or slightly serrate; midvein straight or faintly undulate, forking well before the apex; two pairs of alternate lateral veins attached at a very acute angle, first pair once-forked halfway or closer to the margin, distal lateral veins simple (Fig.3A,D); six to eight vein endings around margin.

Holotype

AMF120979; isotype AMF120980, Australian Museum, Sydney.

Type locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF120981-120984.

Name derivation

paucinerva – paucus, (Lat.), *few; nervus* (Lat.), *nerve*, referring to the small number of lateral veins.

Discussion

Portions of two fronds are preserved on one small slab (Fig. 3C) but their appearance does not suggest that they are detached pinnae of a tripinnate frond. A pinna fragment from Argentina which was illustrated by Kurtz (1921, pl. 32, Fig. 11) as *Asplenium whitbyense* has small pinnules and venation similar to *Cladophlebis paucinerva.* Stipanicic et al. (1995) have reclassified that specimen as *Cladophlebis (Todites?) ugartei* Herbst 1964. As fertile fronds of *C. paucinerva* are not known, it is difficult to make a closer comparison with *C. ugartei. C. paucinerva* differs from all other known Gondwana Triassic *Cladophlebis* spp by its small size and the few lateral veins. The small creeping fern *Micronymbopteris repens* described below differs by the elongated pinnae and much smaller pinnules with no obvious venation. *C. parva* (Fontaine) Bell (1956), a Cretaceous fern from North America, has pinnules similar in size to *C. paucinerva* but differs by the tripinnate form and by the sometimes trilobed first basiscopic pinnules.

Cladophlebis retallackii Holmes sp. nov.

Figures 4A,B; 5A,B

1977 – *Cladophlebis gondwanica* non Frenguelli, Retallack in Retallack et al. p.86, Figs D-F.

Diagnosis

Medium to large bipinnate frond with robust primary rachis and opposite pinnae rachises. Pinnules opposite, straight to slightly falcate, slightly constricted above the basiscopically and acroscopically decurrent base, margins entire, parallel for c. half length then basiscopic margin curves apically to form acute to obtuse rounded apex. Median vein strongly decurrent, basal lateral veins attached to the primary rachis at the base of the midvein and thrice forked. Distally, lateral veins arch away from midvein, forking up to three times proximally, thence twice in mid-region and once apically.

Description

A robust bipinnate lanceolate frond with stout rounded primary rachis and pinnae rachises. In life possibly to one metre in length. Figure 4A is a portion of a large frond, primary rachis to c. 8 mm wide near broken lower section, base missing; pinnae opposite on lower portion of the frond, upwards becoming subopposite and then alternate apically, linear to 100 mm long and 20 mm wide, basal pinnae attached at right angles, becoming more acute, to 45° apically. Pinnules opposite to sub-opposite (Figs 4B, 5B), overlapping to well-separated, mostly oblong, straight to slightly falcate, slightly contracted in width above the decurrent base, attached at right angles close to primary rachis, becoming more acute distally, to 14 mm long and 5 mm wide, with length to width ratio of c. 2.5 (2–3.4):1. Midvein strongly decurrent on pinna rachis then decurving into pinnule and continuing almost to pinnule apex where it divides into two short veinlets. First basiscopic and acroscopic lateral veins attached at or just below the base of the median vein, basiscopic vein arching and forking three times to meet margin at a high angle, first acroscopic vein also branching three times with the adaxial vein running parallel to the pinna rachis. The subsequent five to seven pairs of lateral veins attached at c. 30° to midvein and arching to meet the pinnule margin at c. 45° to 60°, mostly twice forked then once forked near the pinnule apex, with c. 40–50 vein endings around the pinnule margin.

Holotype

AMF120959, Australian Museum, Sydney.

Type locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures. Middle Triassic.

Other material

UNEF133363-4, AMF120954-120959, 120993 and 121167, Coal Mine Quarry. The material from the Cloughers Creek Formation of the Nymboida Sub-Basin referred by Retallack (in Retallack et al. 1977), (see below), to *Cladophlebis gondwanica* and included here in *Cladophlebis retallackii* is also housed in the Australian Museum collections.

Name derivation

retallackii – for Dr G.J. Retallack who carried out research on the Nymboida Flora; pioneer investigator of fossil soils.

Discussion

Retallack (in Retallack et al. 1977) illustrated and briefly described fronds from the Cloughers Creek Formation of the Nymboida Coal Measures which he assigned to *Cladophlebis gondwanica* Frenguelli. Herbst (1978), with reservations, also included this material in *C. gondwanica.* Retallack noted that similar fronds also occurred in the Basin Creek Formation. This is confirmed by my collections, some of which are here illustrated and form the basis for the new taxon *C. retallackii.* The material selected by Frenguelli (1947) as the type for *C. gondwanica* was based on material from Tonkin in Vietnam that had earlier been identified by Zeiller (1903) with the European species *C. roessertii* (Presl) Krystofovich. The Tonkin material illustrated by Frenguelli (1947, Fig.19) has a similar length to width ratio as *C. retallackii* but differs by the more slender, canaliculated primary and pinnae rachises, by the alternate pinnules with straight lateral veins and fewer vein endings around the pinnule margins. Frenguelli included in *C. gondwanica* a frond from the Carnian Molteno Formation of South Africa which had been briefly described by Seward (1908, p.98, pl.8) and assigned to *C. (Todites) roessertii.* Seward's description and one illustration are lacking in details and I have not examined the specimen. From the illustration, the length to width ratio is lower and the pinnae are more acutely attached to the main rachis, so its affinity with *C. retallackii* is doubtful. With the exception of the material described by Retallack (in Retallack et al. 1977), there are no other records of fronds similar to *C. retallackii* in Triassic Gondwana floras.

Cladophlebis sinuata Holmes sp. nov.

Figures 6A-C

1921 – *Cladophlebis mesozoica* forma *typica* Kurtz pl. 32, Fig. 13

1921 – *Cladophlebis mesozoica* forma *crenulata*

Kurtz pl. 32, Fig. 14
?1982- *Cladophlebis mesozoica* Holmes p. 5, Fig. 3A

Diagnosis

Medium sized bipinnate frond; pinnae opposite, well-spaced, attached at a high angle. Pinnules alternate, elongate-triangular, closely spaced, margin irregularly dentate or lobed. Midvein fine, sinuate, forking near the apex, c. five pairs of lateral veins attached to median vein at c. 45°. First two pairs of veins twice forked, following veins once forked.

Description

Cladophlebis sinuata is based on seven specimens. The holotype (Fig. 6A) is a portion of a bipinnate frond showing three pairs of pinnae attached opposite at c. 90° to a conspicuously ribbed and grooved primary rachis 4.5 mm wide. The complete frond is estimated to have been c. 400 mm long. The pinnae are well separated, 45 mm and 35 mm apart, with a length perhaps of 150 mm. Pinnules sub-opposite to alternate, closely spaced to overlapping, broadly attached at c. 80° to ribbed pinna rachis, basiscopic margin contracted and acroscopic base expanded, elongate-triangular to slightly falcate, to 15 mm long and to 10 mm wide just above the base; length to width ratio of c. 1.6:1, becoming smaller and more acutely attached towards the pinna apex, margin broadly lobed or dentate, apex broadly acute to obtuse. Midvein fine, slightly undulate to sinuate, forking close to apex; four to five pairs of alternate secondary veins leave midvein at c. 45°; the proximal two pairs of veins fork twice, the distal two pairs fork once with the last one or two veins unforked (Fig. 6C); 18-24 vein endings around pinnule margin.

Holotype

AMF113512, Australian Museum, Sydney.

Type locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF113513-113518, AMF113541, Coalmine Quarry.

Name derivation

sinuata – *sinuatus*, (Lat.), *wavy* – referring to the course of the fine median vein.

Discussion

Cladophlebis sinuata is close to *C. wielandii* Jain and Delevoryas (1967) from the Carnian Cacheuta Formation of Argentina, but differs by the typically twice forked lateral veins in the basal portion of the pinnule lamina. Material from the Carnian Ipswich Basin, referred to *C. concinna* by Jones and de Jersey (1947, text Figs 4 and 5) has closely spaced pinnules with sinuous midveins. Their text fig. 4 differs from *C. sinuata* by the lateral veins which all fork twice, and text fig. 5 differs by the lateral veins which are all once forked in a manner similar to those referred to *C. concinna* by DuToit (1927) from the Carnian Molteno Formation of South Africa. *C. sinuata* is similar to some forms of the variable *C. mendozaensis* (Geinitz) Frenguelli 1947, Herbst (1971, Figs 13, 14 and 21) from the Upper Triassic of South America, but differs by the finer sinuous midrib, by the more closely spaced to overlapping pinnules and by the generally lower length to width ratio of the pinnules. The Upper Triassic Queensland material which was identified by Herbst as *C. mendozaensis* (Herbst 1978, pl 1, Figs 4 and 5, pl. 3, Figs 16-18) has alternate pinnae and a significantly higher length to width ratio. Specimens illustrated in Kurtz (1921, pl. 32, Figs 13, 14) as *C. mesozoica* forma *typica* and *C. mesozoica* forma *crenulata* have a sinuous midvein and similar lateral venation to *C. sinuata.* These two Carnian Cacheuta Formation specimens of Kurtz were placed by Stipanicic et al. (1995) in *C. mesozoica*, a taxon defined by its twice forking lateral veins, as discussed under *C. octonerva.* Frond fragments from the Middle Triassic Benolong Flora of central-western New South Wales which were placed in *C. mesozoica* by Holmes (1982) are similar in venation pattern and length to width ratio, but are of smaller size and have less vein endings around the pinnule margin. Another sterile pinna fragment from the same assemblage attributed to *Todites pattinsoniorum* Holmes (1982, Fig. 2D) also has similar venation to *C. sinuata*, thus suggesting that the latter could be the foliage of an osmundaceous fern.

Cladophlebis tenuipinnula Holmes sp. nov.
Figures 7A, 8 A-C

Diagnosis

Large tripinnate frond, tertiary pinnae alternate, linear; pinnules alternate, small, straight, closely spaced; lateral veins well-spaced and once forked.

Description

Large tripinnate frond (Fig.8A), primary rachis 35 mm wide near base which suggests a total frond length of from two to three metres. Secondary rachises (Fig. 7A) well separated, to 5 mm wide, straight, to 200 mm long. Secondary rachises in basal region obtuse, changing to right angles in mid-frond then slightly acute apically. Tertiary rachises at high angle to secondary rachis, c. 10 mm apart, linear to 50 mm long, c. 10 mm wide. Pinnules alternate, attached by whole base, linear, straight to slightly curved, 4-5 mm long, 1-1.5 mm wide, length to width ratio of c. 4:1, closely spaced, free to base, margin entire, apex obtuse. Pinnule lamina apparently thick textured which obscures the venation. On some pinnules on AMF113526, which are preserved at an angle to the bedding plane (Fig. 8B), the venation is faintly evident and shows a fine midvein with c. 8 pairs of lateral veins attached at a high angle and once-forked close to the midvein; c. 30 vein endings around the margin. Fragmentary fertile pinnules appear to bear five or six pairs of *Asterotheca*-like synangia but the preservation is too poor to determine the structure.

Holotype

AMF113523; isotypes AMF113524-27, AMF113406, Australian Museum, Sydney.

Type locality

Reserve Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF121016-121018, Reserve Quarry.

Name derivation

tenuipinnula – *tenuis*, (Lat.), *long and slender*, referring to the attenuated pinnules.

Discussion

This is one of the largest fern fronds in the Nymboida Flora, but is known only from dispersed fronds on a single horizon. Some very fragmentary fertile material is available and while the preservation is very poor, the distribution and size of the sori on the pinnules appear to differ from all *Asterotheca* fronds previously described from Nymboida (Holmes 2001b). By the large frond size, by the very stout secondary rachises and by the very small densely spaced attenuated pecopteroid-like pinnules, *C. tenuipinnula* differs from all other Gondwana Triassic ferns.

? *Cladophlebis* sp. A

Figures 9 A-C

Description

Several frond fragments with characteristic narrow-elliptic pinnae with the first pinnules well detached from the main rachis, are here placed doubtfully in *Cladophlebis* due to lack of preserved venation. The available specimens indicate living fronds were from 80 mm to 150 mm long. The pinnae are opposite to sub-opposite, attached in lower portion of frond at c. 90° and becoming more acute (to 60°) apically. Pinnae elliptic to 35 mm long, with four to twelve opposite triangular to rhombic pinnules attached at c. 45° to 80°; pinnules separated proximally but soon coalescing and decreasing in size towards the acute apex; venation obscured by the obviously thick texture of the pinnules.

Material

AMF113508-113510, Coal Mine Quarry, Nymboida.

Discussion

The three specimens illustrated (Figs 9 A-C) show a range of variation but appear to represent intergrading forms. There are some similarities with foliage fragments of the seed ferns *Dicroidium* and *Lepidopteris*. However there is no indication that the fronds may have been forked as in *Dicroidium*, and the lack of pinnules on the main rachis precludes affinities with *Lepidopteris*.

?*Cladophlebis* sp. B

Figures 9 D, E

Description

An apical portion of a tiny bipinnate fern, 30 mm long, pinnae opposite, pinnules broadly attached and well-spaced, rounded, c. 2 mm in diameter. The venation is poorly preserved.

Material

AMF120978, Coal Mine Quarry, Nymboida.

Discussion

Only a single specimen of this tiny sterile fern frond has been collected. It is illustrated to draw attention to its presence. From the matching size and form, this could be a sterile frond affiliated with fertile *Todites parvum* described previously from Nymboida in Holmes (2001b).

? *Cladophlebis* sp. C

?1883 *Alethopteris currani* Tenison-Woods 1883 p. 77, pl. 6, Fig. 4

Figures 10A, B

Description

A small fragment of a pinnate (? bipinnate) frond shows eight pairs of well-spaced opposite decurrent elongate, slightly falcate pinnules with serrate margins, attached at c. 60° to a slender ribbed rachis; midvein decurrent, with four pairs of once-forked lateral veins attached at an acute angle to the midvein. Length to width ratio of c. 4:1.

Material

AMF120994, Coal Mine Quarry, Nymboida.

Discussion

? *Cladophlebis* sp. C has (?pinnae) pinnules somewhat similar in shape and venation to those of *Alethopteris currani* Tenison-Woods (1883) from the Middle Triassic Napperby Formation at Ballimore near Dubbo in central-western New South Wales, but differs by the wider spacing of the pinnules. The Ballimore and Nymboida specimens are too incomplete to warrant formal naming.

Dictyonymba Holmes gen. nov.
Dictyonymba sparnosa Holmes gen. et sp. nov.
Figures 10 C, D

Combined diagnosis

Bipinnate frond; pinnules broad ovate, conjoining, tapering to obtuse apex; lateral veins forking and occasionally joining to form coarse irregular reticulations in the conjoined area between the pinnules and towards the distal margin of each pinnule.

Description

D. sparnosa is described from a single fragmentary specimen showing portions of two parallel pinnae which bear partially conjoined pinnules with well-preserved venation (Fig. 10C). The size and form of the complete frond is not known. The larger pinna fragment is c. 39 mm long, bearing nine pairs of opposite pinnules attached at c. 60° to the pinna rachis, which tapers from 1 mm wide at the broken base. Pinnules broadly ovate but somewhat variable in shape, with convex entire margins, apices rounded, 5–6.5 mm long, 3.3–4.6 mm wide (Fig. 10D). Adjacent pinnules are conjoined for one third to one half of their length. Three to four pairs of once to three times forked lateral veins are attached at c. 45° to 60° to a slightly sinuous midvein. A separate vein enters the basiscopic portion of each pinnule lamina directly from the pinna rachis, forks three times and then meets in the conjoined region with some of the lateral veins from the adjacent pinnule to form an irregular mesh. In the distal free region of each pinnule where the lateral veins fork once or twice and sometimes anastomose, there are c. 18 vein endings around the margin.

Holotype

AMF113507. Australian Museum, Sydney.

Type locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Name derivation

Dictyonymba - *dictyos*, (Gr.) *net*; referring to the net venation and the Nymboida locality.

sparnos - (Gr.*) scarce, rare*; recognising that one fragment only has been collected.

Discussion

Dictyonymba is a monotypic genus represented only by the type species *D. sparnosa.*

Dunedoonia reticulata Holmes (1977) is a pinnate fern-like frond with reticulate venation from the Late Permian of eastern Australia. *Dunedoonia reticulata* differs from *Dictyonymba sparnosa* by the basally contracted and much larger, broader pinnae and by the form of the anastomoses.

Lonchopteris and *Lonchopteridium* spp from the Carboniferous of Europe (Boureau 1975) and *Emplectopteris* Halle (1927) from the Permian of China are fern-like bipinnate fronds with varying forms of anastomosing venation. The form of the pinnules and venation pattern of *Dictyonymba sparnosa* differs in detail from any species described in the above genera. The differences in geographical distribution and time also strongly suggest that this Nymboida form is at least generically distinct. *Dictyonymba sparnosa* is unique in Gondwana Triassic floras.

Gouldiopteris Holmes gen. nov.
Gouldiopteris alethopteroides Holmes gen. et sp. nov.
Figures 11A-D

Combined diagnosis

An alethopteroid pinnatifid frond; pinna lobes with a distinct midrib, opposite, broad-linear, margin entire or slightly undulate, well-spaced, conjoined by a broad wing along primary rachis. Secondary veins closely spaced, arising directly from the main rachis and from the midvein in each pinna lobe at an acute angle (c. 45°), forking once, arching slightly then running parallel to wing and pinna lobe margins.

Description

This is a rare element in the Nymboida Flora. Only three specimens and their counterparts have been collected. The form and dimensions of complete fronds are not known. The holotype (Figs 11A, B) is a mid-section 55 mm long of a pinnatifid frond. Four pairs of opposite lobes are attached to the 3 mm wide primary rachis at c. 70° to 85°. The lobes are well-separated, c. 15 mm apart, broad-linear, 45 mm long and 10 mm wide, bases strongly decurrent to form a conjoining wing c. 2–3 mm wide along the main rachis, lobe margins straight or slightly undulate, apex broadly acute. A broad tapering midvein runs the length of each lobe and forks close to the apex. Lateral veins from both the main rachis and midvein are attached at c. 45°, forking once, usually near the base, then arching slightly and running parallel to each other, reaching the wing or pinna margin at c. 45° to 80°. The density of veins along the pinna lobe margin is c. 20 per 10 mm.

AMF113563 (Fig.11D) is a 100 mm long section of a frond which in life may have reached 200 mm in length. The lobes, to 35 mm long and 6 to 8 mm wide, are attached at c. 40° to 50° to the primary rachis at a spacing closer than those of the holotype.

Holotype

AMF113561, Australian Museum, Sydney.

Type locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF113562, AMF112563, Coal Mine Quarry.

Name derivation

Gouldiopteris – Gould, for Dr R.E.Gould, former palaeobotanist at the University of New England, who encouraged my collecting and research of the Nymboida Flora; *pteris*, (Lat.), *fern.*

alethopteroides – Alethopteris, a Palaeozoic morpho-genus of fern-like fronds similar in gross morphology to the Nymboida material.

Discussion

Gouldiopteris, a monotypic genus with *G. alethopteroides* as the type species, is erected for foliage fragments that conform with the diagnosis of the Palaeozoic form genus *Alethopteris* Sternberg (Wagner 1968). *Alethopteris* is not a natural genus and includes both ferns and pteridosperms. Plants placed in the genus are common and widespread in the Carboniferous of the Northern Hemisphere, the Permo-Carboniferous of China and the Permian of Thailand. Boureau (1975) listed 96 species, varieties and synonyms. Because of the vast time and geographical differences between Northern Hemisphere plants that have been placed in *Alethopteris* and the Nymboida material, it is highly improbable that there is any close relationship. I have erected the new morpho-genus *Gouldiopteris* to avoid suggestions that *Alethopteris* had Mesozoic representatives and a cosmopolitan distribution.

Most early records of *Alethopteris* species in Australia have subsequently been revised or were based on unidentifiable material. *Alethopteris australis* (Morris) Johnston (1888), Feistmantel (1890) and *Alethopteris serratifolia* Johnston (1887) from Tasmania in which the pinnules are separated to the base, were placed in *Cladophlebis australis* (Morris) by Walkom (1926). Specimens from the Upper Triassic of Queensland, originally placed in *Alethopteris lindleyana* (Etheridge Jnr 1892) and ?*Alethopteris lindleyana* (Shirley 1898), were removed by Walkom (1917) to *Cladophlebis royalei*, a species which was described from the Permian of India (Arber 1905). All the above specimens previously placed in *Alethopteris* are bipinnate and do not conform with the diagnoses of *Alethopteris* or *Gouldiopteris.*

Dejerseyia lobata (Jones and de Jersey) Herbst 1977 has simple to pinnatifid leaves with elongate lobes as in *Gouldiopteris alethopteroides* (see also *Dejerseyia lobata* 'forma D' of Anderson and Anderson 1983), but differs from *G. alethopteroides* by the lateral venation of well spaced decurrent secondary veins which arch and divide several times. *Dejerseyia lobata* is now considered to be a gymnosperm (Anderson and Anderson, in press). The form of *Gouldiopteris alethopteroides* is unique in Gondwana Triassic floras.

Leconama Holmes gen. nov.
Leconama stachyphylla Holmes gen. et sp. nov.
Figures 12A-C

1975 *Cladophlebis lobifolia* non (Phillips) Seward, Flint and Gould, pl.1, Fig. 6 only
1977 *Lobifolia dejerseyi* Retallack (in Retallack et al.) pp 88-89

Combined diagnosis

Medium sized bipinnate frond; pinnae opposite, pinnules broad falcate, basiscopic margin sub-circular, acroscopic margin straight to slightly concave; midvein decurrent, weak, soon dissolving into several radiating and forking venules.

Description

This taxon is based on single pinnae (Fig. 12B, C and Flint and Gould 1975, pl.1, fig 6) and a frond fragment showing linear opposite pinnae attached acutely to a slender main rachis (Fig. 12A). Pinnae opposite, linear to 100 mm long; pinnules opposite, closely spaced to overlapping, free to the base, attached at c. 60°, broad falcate, entire, c. 6 mm long and wide; basiscopic margin sub-circular convex through c. 90°; acroscopic margin decurrent upwards at base then straight or slightly concave at an obtuse angle to the rachis; apex rounded-acute. A decurrent weak midvein arches into each pinnule from near the basiscopic margin, giving off two pairs of closely spaced lateral veins then dissolving into forking and radiating venules. First one or two basiscopic lateral veins forking twice to three times; first acroscopic lateral vein forking three times with the near venule running parallel to the pinna rachis; following lateral veins once forked or simple, radiating, c. 24 to 28 vein endings around margin.

Holotype

AMF121183, Australiam Museum, Sydney. (Formerly UNEF14124).

Type locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF121160 formerly UNEF 14104, AMF113544 and its counterpart.

Name derivation

Leconama – lekos, (Gr.*), basin*; *nama*, (Gr.), *stream*; referring to the type locality in the Basin Creek Formation.

stachyophylla – stachys, (Gr.), *ear of grain; phyllon*, (Gr.), *leaf*; referring to the leaf outline resembling an ear of wheat.

Discussion

Leconama is a monotypic genus with *L. stachyophylla* as the type species. A pinna fragment of *L. stachyophylla*, previously illustrated by Flint and Gould 1975, pl. 1, fig. 6, and referred to *Cladophlebis lobifolia*, was included by Retallack (in Retallack et al. 1977) in *Lobifolia dejerseyi*, now *Nymbopteron dejerseyi* Holmes (see below). *Leconama stachyophylla* differs from *Nymbopteron* species by the absence of the conjoining of the first acroscopic pinnule to the main rachis. The pinnule shape and venation pattern distinguishes *L. stachyophylla* from all other described Gondwana Triassic fronds.

Micronymbopteris Holmes gen. nov.
Micronymbopteris repens Holmes gen. et sp. nov.
Figures 13, 14A-D

Combined diagnosis

A small procumbent or climbing plant with elliptic to lanceolate bipinnate fronds to 70 mm long, irregularly spaced along a curved tapering rhizotomous stem. Pinnae alternate, linear, bearing oblong, thick-textured pecopteroid pinnules.

Description

The holotype (Figs 13A, 14A) shows portions of five elliptic bipinnate fronds attached spirally and irregularly to an elongated tapering stem or rhizome. At the broken base the width is 5 mm and tapers through a length of 85 mm to 2 mm wide. Another specimen (Fig. 14B) was retrieved from the same fractured block. I believe that it is the lower portion of the holotype but the section of the stem that would join the two is missing. The lower stem fragment is 12 mm wide with one frond attached at right angles then decurving vertically. The holotype shows an almost complete frond and another four acutely attached incomplete fronds as well as detached fragments nearby. The complete frond is acutely decurrent, bipinnate, elliptic to 70 mm long, c. 35 mm wide; main rachis robust, tapering from 25 mm wide at base; pinnae c. 4 mm apart, with thick rachises, opposite, becoming subopposite to alternate apically, to 30 mm long and 3 mm wide, mostly linear but tapering close to the base and towards apex; pinnules alternate, closely spaced, free to the base, attached at c. 80° to 60°, oblong with rounded apex, c. 1–1.5 mm long, c. 0.5–0.75 mm wide, length to width ratio of c. 2:1; venation obscured by the apparent very thick texture of the pinnule lamina.

Holotype

AMF120962, isotype AMF120963, Australian Museum, Sydney.

Type locality

Reserve Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF120964–120966.

Name derivation

Micronymbopteris – contrived, for *small Nymboida fern.*

repens – (Lat.), *creeping*, for the inferred growth form.

Discussion

Micronymbopteris is a monotypic genus with the type species *M. repens*. Most ferns and fern-like taxa in the fossil record are known only from detached fronds, many of which are incomplete or even fragmentary. The holotype of *M. repens* is a rare and important find as it demonstrates the elongated stem and probable creeping or climbing growth form of the once living plant.

M. repens is unlike any other described fern-like material and its fronds are perhaps the smallest in the Gondwana Triassic fossil record.

Nymbiella Holmes gen. nov.
Nymbiella lacerata Holmes gen. et sp. nov.
Figures 15A, 16A, B

Combined diagnosis

Medium to large bipinnate-bipinnatifid frond; pinnae opposite to subopposite, broad linear; pinnules irregular in width and shape, separated to base or conjoined; apices obtuse, lobed or irregularly lacerated. First basiscopic pinnules sometimes attached to the main rachis. Venation odontopteroid, from one to three or more veins arching from pinna rachis into each pinnule, dividing once, occasionally twice and running parallel to each other to the distal margin.

Description

Medium to large bipinnate-bipinnatifid fronds estimated to reach 600 mm in length and 220 mm in width. No fronds are complete and no bases are present. The holotype (Fig. 15A) is an apical portion of a frond 220 mm long with another frond adjacent and slightly diverging. There is no evidence that the two fragments may be pinnae of a tripinnate fern. The main rachis in the base of this specimen is 3 mm wide and tapers gradually apically. In the length preserved there are 13 pairs of opposite to subopposite pinnae attached at 12–15 mm apart. The pinnae have a decurrent base then continue straight for their whole length at an angle of 60° to 75° to the main rachis. Pinnae broad-linear to 120 mm long and 20 mm wide, tapering in distal quarter to an acute apex. Pinnules of irregular shape and width, 8–10 mm long, attached from 60° to 80°, usually parallel-sided, sometimes contracted at the base (Fig.16A), sometimes several pinnules conjoined (Fig. 16B), apices obtuse, flattened or variously lobed or lacerated. Basal basiscopic pinnules attached around the junction of the pinna rachis with the main rachis and sometimes directly to the main rachis. The pinnule lamina is apparently thin with the venation clearly defined. Venation odontopteroid; one to three or more veins arching into each pinnule, forking once or occasionally twice and running straight and parallel to each other to the distal margin.

Holotype

AMF113530, Australian Museum, Sydney.

Type locality

Reserve Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF113531, 113536, 121174 from Reserve Quarry. AMF113532, 113535, 113537, 121173 from Coal Mine Quarry.

Name derivation

Nymbiella – contrived from *Nymboida*, the source of the material.

lacerata – (Lat.) *lacerated, irregularly torn*, referring to the apical margin of many pinnules.

Discussion

Nymbiella is a monotypic genus with *N. lacerata* as the type species. Over forty specimens are in the collections, all are incomplete and none show the basal region. The extreme variability of pinnule shape and form of *N. lacerata* is unique in Gondwana fern-like fronds. The two frond fragments on the holotype slab appear to be arising from a common base, and suggest a growth form perhaps similar to that of *Osmundopsis scalaris* (Holmes 2001b).

Odontopteris? (Callipteris) laceratifolia from the Upper Palaeozoic of China, illustrated by Halle (1927 pl. 32, figs 1, 2) has bipinnatifid leaves with lacerated margins and odontopteroid venation. However Halle's material differs from *Nymbiella lacerata* by the less divided pinnae and by the veins at a more acute angle. Because of the geographic and time differences I believe that *N. lacerata* should be regarded as generically distinct.

Nymboidiantum Holmes gen. nov.
Type species *Sphenopteris (?)glossophylla* Tenison-Woods 1883 p. 58, pl. 4, fig. 4

Diagnosis

Fern-like foliage; fronds bipinnate or rarely pinnate; pinnules attached at c. 45°, contracted at the base, sessile, lamina elliptic, margin entire, lobed or divided into segments. Three veins enter pinnule base, each forking one or more times as they pass into the lobes or distal portion of the entire lamina.

Discussion

From the gross morphology of pinnules with contracted bases and radiating venation, *Nymboidiantum* resembles the sterile fronds of some extant species of the fern genus *Adiantum* but no close relationship is inferred. Fossil leaves of Palaeozoic age with somewhat similar morphology have been placed variously in the genera *Triphyllopteris* (Boureau 1975; Morris 1975), *Adiantites* (Boureau 1975), *Genselia* (Knaus and Gillespie 2001), *Palmatopteris* (Boureau 1975) and *Archaeopteris* (Feistmantel 1890; Boureau 1970). Others of Late Jurassic to Tertiary age from the Northern Hemisphere have been placed in *Adiantopteris* (Boureau 1975). Because of the vast differences in time and distance, the new genus *Nymboidiantum* is erected to separate the Nymboida material from the genera listed above. Undescribed *Nymboidiantum* foliage from the Carnian Molteno Formation of South Africa has been figured by Anderson and Anderson (1983, pl. 9; Figs 1a, 1b) as 'Incertae sedis gen. A, sp. A'. All the specimens from Nymboida here placed in *Nymboidiantum* are known only from sterile fronds, so their natural affinities are not known. With the exception of *Nymboidiantum glossophyllum* which is known from c. 40 specimens, the other taxa are very rare. I have distinguished five species mainly on the size, form and placement of the pinnules, and there appear to be no intergrading forms. The different fossil species are each preserved in sediments representing specific facies and it may be reasonable to assume that in life they grew in different habitats.

Nymboidiantum glossophyllum (Tenison-Woods 1883) Holmes gen. et comb. nov.
Figures 17A-E, 18C, D

1883 *Sphenopteris (?) glossophylla* Tennison-Woods p.58, pl.4, Fig.4

1983 Incertae sedis foliage gen. A, sp. A Anderson and Anderson, pl.9, Figs 1a and 1b.

Diagnosis emended

Medium sized bipinnate frond; pinnules well-spaced, alternate, elliptic with contracted decurrent base; proximal pinnules sometimes tri-lobed to deeply incised; venation sparse, forking and radiating to apical margin.

Description

The type specimen of Tenison-Woods (1883) is a small fragment showing three pairs of incomplete pinnae attached alternately to a main rachis that is mostly missing in the coarse siltstone matrix (refigured here, Fig. 17A). The elliptic pinnules are closely similar to those on many specimens in the Nymboida collections. However the Nymboida material exhibits a range of variation amongst specimens that I include in this species, especially in the lobing of the proximal pinnules. AMF120946 is a siltstone slab with some almost complete ovate fronds to c. 250 mm long (Fig. 17C), with alternate pinnae bearing to eight pairs of sub-opposite to alternate elliptic pinnules. The pinnules are from 5-10 mm long and 3-5 mm wide, attached at c. 45°-60° to the pinna rachis. Basally the shorter pinnae are at right angles to the main rachis becoming acute apically. Proximal pinnules are sometimes partially divided into two or three lobes (Figs 17B, D, E). On some specimens (Figs 18C, D) the pinnules are divided to the base into three linear lobes. The texture of the pinnule laminae appears to be thick and the venation is rarely observed, except in some rare types of preservation where sparse radiating veins may be faintly visible.

Lectotype

AMF68449, Australian Museum, Sydney. Formerly catalogued as SUF35 in the fossil collections of Sydney University.

Type locality

"Talbragar Mines" of Tenison-Woods (1883). Probably north-east of the present day village of Ballimore on the Talbragar River east of Dubbo, in the Napperby Formation, Middle Triassic.

Other material

AMF121158–121149, 121152, Coal Mine Quarry, AMF121150, 121153, Reserve Quarry.

Discussion

I have examined the specimen of *Sphenopteris (?) glossophylla* Tenison-Woods which is now housed in the Australian Museum, Sydney. It is a small fragment of a pinna rachis with ?alternate ovate pinnules with contracted bases and no visible venation. It agrees well with much of the Nymboida material, which, however, demonstrates a wide range of variation. The emended diagnosis reflects the diversity present in the Nymboida specimens which I now include in this taxon. The type locality, 'Talbragar Mines' near Ballimore on the Talbragar River, is in a very poorly collected area of the Middle Triassic Napperby Formation (previously included in the Wallangarra Formation, Cameron et al. 1999), which outcrops along the south-eastern margin of the Great Artesian Basin in central-western New South Wales. An assemblage of fossil plants from the same formation at Benolong, south west of Dubbo, has been described by Holmes (1982, 2001a).

In gross morphology *N. glossophyllum* is closely similar to some forms of *Triphyllopteris* known from the Carboniferous of Peru and the Northern Hemisphere (Boureau 1975, Figs 557, 558), but these forms are regarded as distinct due to the geographic and time differences.

Comparisons between *Nymboidiantum glossophyllum* and those species described below are given under the respective species.

Nymboidiantum multilobatum Holmes gen. et sp. nov.
Figures 18A, B

Diagnosis

Medium sized bipinnate frond, pinnae sub-opposite; pinnules broad-flabellate, divided into several more or less deeply incised lobes.

Description

Frond bipinnate, estimated length to c. 250 mm; main rachis 4 mm wide near base, tapering gradually, apical portion of frond not preserved. Pinnae sub-opposite, 30 mm wide, length not known. Pinnules alternate attached by contracted base at c. 45° to pinna rachis, rhombic to sub-circular, 15 mm long and wide near main rachis, decreasing in size distally. Pinnules deeply divided into three to five segments, each segment with two or three elongated, obtuse lobes. A single vein enters each pinnule, soon forking into each segment and again into each lobe.

Holotype

AMF113558; isotypes AMF113559, 113560, Australian Museum, Sydney.

Type locality

Reserve Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Name derivation

multi, (Lat.) *many*; *lobata*, (Lat.) *lobed*; referring to the much dissected pinnules

Discussion

This morphotaxon is known only from a single incomplete specimen that is associated with large *Sphenobaiera* leaves. It differs from all other species of *Nymboidiantum* by the larger flabellate pinnules which are divided into several segments, each segment with apical lobes.

Nymboidiantum elegans Holmes gen. et sp. nov.
Figures 19A, B

Diagnosis

Pinnae alternate, linear; pinnules well-spaced, opposite, elliptic, not lobed. First basiscopic pinnule attached in angle between the main and pinna rachis or directly on the main rachis.

Description

The holotype (Fig.19A) is an apical fragment, 130 mm long, of a frond which in life was probably twice that length. Width of the main rachis at the base of the portion preserved is 2.5 mm, tapering gradually to the apex. Main rachis longitudinally striated but not conspicuously ribbed or grooved. Pinnae alternate, decurrently attached at c. 45° to the main rachis, linear, 15 mm wide, to 65 mm long, tapering in the distal portion to an acute apex. Pinnules opposite, evenly spaced, symmetrically elliptical, entire, apex acute, c. 8 mm long and 3 mm wide, well separated, decreasing in size distally and apically, 12 pinnules in a pinna length of 60 mm. The first basiscopic pinnule on each pinna is attached at the base of the pinna rachis or directly to the main rachis. Towards the frond apex the pinnules coalesce to form lobed or entire pinnae. Venation not preserved.

Holotype

AMF113504; isotype AMF113505.

Type locality

Reserve Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF113506, Coal Mine Quarry.

Name derivation

elegans – (Lat.), *elegant*; referring to the neat and even spacing of the pinnules.

Discussion

N. elegans differs from *N. glossophyllum*, *N. robustum* and *N. multilobatum* by the opposite, elliptic, well-spaced pinnules and by the absence of lobing of the proximal pinnules.

Nymboidiantum fractiflexum Holmes gen. et sp. nov.
Figures 19C, D

Diagnosis

Planate, pinnate frond; rachis flattened, grooved, changing direction slightly at each pair of opposite pinnae. Pinnae sessile, rhombic, venation fine, forking and radiating from a short midvein.

Description

This taxon is based on a single specimen which consists of five pairs of opposite pinnae on a slightly zigzag rachis in which the rachis and pinnae appear to be flattened in one plane (Fig. 19C). The rachis as preserved is 50 mm long, with a conspicuous medial groove and longitudinal striations, 2 mm in width near base and not visibly decreasing to the tip, where it forms a short broken projection beyond the last pair of pinnae. Pinnae well-spaced c. 12 mm apart, decurrent on rachis, sessile, attached at c. 45°, c. 35 mm long and 10 mm wide, obtrullate to rhombic, entire with acute apex. Fine lateral veins diverge from a midvein or groove in the proximal one third of the pinna and fork several times distally. In the proximal half of the pinna, the radiating veins run parallel to the margin. In the distal half, the veins terminate along the margin with a density of c. 12 per 10 mm (Fig. 19D).

Holotype

AMF113502, Australian Museum, Sydney.

Type locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Name derivation

fractiflexus – (Lat.) – *deviating from side to side, zigzag,* as in the rachis of this taxon.

Discussion

By its pinnule shape and venation this leaf fragment is placed in the morpho-genus *Nymboidiantum,* but by the flattened zigzag rachis and pinnate form it differs from all other described species. The type specimen of *N. fractiflexus* may be a pinna of a large bipinnate frond as in other *Nymboidiantum* species.

Nymboidiantum robustum Holmes gen. et sp. nov.
Figures 20A-C

Diagnosis

Pinnules broad, ovate, opposite, well-separated proximally, coalescing distally; first acroscopic pinnule broadly but shallowly lobed.

Description

Medium to large bipinnate frond; midportions only of fronds preserved. Complete fronds estimated to exceed 300 mm long. The main rachis of the holotype (Fig. 20B) decreases in width from 2.5 mm to 2 mm over a length of 125 mm. Pinnae opposite to subopposite, broad-linear, 15 mm wide, 40-50 mm long. Pinnules opposite, attached at c. 45°, base slightly contracted, strongly decurrent, well separated proximally, coalescing distally, 4-8 mm wide, 5-12 mm long, margins entire, apex obtuse. First acroscopic pinnule shallowly lobed. The venation is not clear but three veins appear to enter base with each vein forking once.

Holotype

AMF113496, Australian Museum, Sydney.

Type locality

Reserve Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF113495, 113497, 121164, 121166, all Reserve Quarry.

Name derivation

robusta – (Lat.), *robust,* referring to the broad compact pinnules.

Discussion

N. robustum differs from all other *Nymboidiantum* species by the larger pinnules with broadly decurrent bases.

Nymbophlebis Holmes gen. nov.

Nymbophlebis polymorpha Holmes gen. et sp. nov.
Figures 21A, 22A-C, 23A-C

Combined diagnosis

Large polymorphic frond with long opposite linear, slightly arching primary pinnae distally bearing cladophleboid pinnules; in basal and proximal portions of fronds, primary pinnae tripinnate with fine pinnules; distally pinnae becoming bipinnate to pinnate as ultimate segments coalesce and conjoin to form large linear entire pinnules.

Description

This taxon is based on large bi-tri-quadripinnate sterile fronds in which the polymorphic characters may occur on a single primary rachis. Figure 20 is a basal portion of a frond estimated to have reached 1 m long. Secondary rachises opposite, slightly arching or straight, to 150 mm long, 20–30 mm wide with 20 to 30 alternate pinnae-pinnules; proximal portions of the lower rachises often tripinnate to bipinnate but pinnules distally conjoining to progressively coalesce until the primary rachis is simply pinnate (Figs 22. A, B; Figs 23A-C). The cladophleboid distal and apical pinnules are attached by a wide base, slightly contracted basiscopically and enlarged or decurrent upwards on the acroscopic side; broad-linear or slightly tapering, margin entire or slightly lobed close to the tripinnate segments of the frond, 12–18 mm long, 3-5 mm wide, with length to width ratio of c. 3.5–4:1; midvein decurrent, strong, persisting almost to pinnule apex; 8–10 pairs of lateral veins; first basiscopic lateral vein attached in angle between the pinna rachis and midvein, forking twice with proximal venule forking again; other lateral veins decurrent, all twice forked; first dichotomy close to the midvein then again at 1/3 the distance to the margin; venules travelling straight, close and parallel to meet margin at c. 45° to 70°.

Holotype

AMF120995, Australian Museum, Sydney.

Type locality

Reserve Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF120988, 120996-121007, 121009-121013, Reserve Quarry; AMF121008, Coal Mine Quarry.

Name derivation

Nymbophlebis contrived, for *Cladophlebis*-like plant from Nymboida.

polymorpha – (Gr.) *many forms*, referring to the diversity of pinnule shapes within a single frond.

Discussion

Nymbophlebis is a monotypic genus with *N. polymorpha* as the type species. Almost complete fronds of *Nymbophlebis polymorpha* occur at the Reserve Quarry in a bed of olive-grey mudstone. Reliable identification can only be achieved from substantially complete fronds. Retallack (1977) listed frond fragments from the Coal Mine Quarry at Nymboida which agreed well with the the bipinnate portions of *Nymbophlebis polymorpha* as '*C. australis* sensu stricta Morris with twice forked lateral veins'.

The interpretation of *Pecopteris australis* Morris (1845) [= *Cladophlebis australis* (Morris) Walkom (1917)] from the Triassic Newtown Beds of Tasmania has had a long and confused history. The pinnules in the bipinnate portions of *Nymbophlebis polymorpha* are similar in shape to those of Morris's fronds and the lateral veins are twice forking. However, *N. polymorpha* differs in that the primary and secondary forking of the lateral veins occurs close to the midvein and the veins then proceed close and parallel to each other to the margin, in contrast to those of Morris's illustration which fork midway to the margin and then widely diverge.

The polymorphic nature of the complete fronds of *Nymbophlebis polymorpha* argues for their placement in a genus separate to *Cladophlebis*. Isolated bipinnate fragments may be best placed in *Cladophlebis* sp. indet.

The diverse form of the pinnules of *N. polymorpha* is reflected in some forms of the extant genera *Pteris* and *Pteridium*, but no relationship is inferred.

Nymbopteron Holmes gen. nov.
Type species *Lobifolia dejerseyi* Retallack (in Retallack et al. 1977)

Diagnosis

Small to large bipinnate-bipinnatifid fronds, the first acroscopic pinnule of each pinna always confluent between the pinna and main rachises to form a triangular wing. First basiscopic pinnule sometimes enlarged, triangular, rectangular, rounded or variously lobed, often attached between pinna and main rachis or directly to the main rachis; subsequent cladophleboid pinnules of even size and shape for most of the pinna length but decreasing in size and conjoining distally and apically.

Name derivation

Nymbopteron – nymbo; referring to Nymboida, the source of the material; *pteron*, (Gr.), *wing*; referring to the winged shape of the first acroscopic pinnules.

Discussion

The genus *Nymbopteron* is erected to include Australian material formerly placed in *Cladophlebis lobifolia* (Flint and Gould 1975), *Lobifolia dejerseyi* Retallack (in Retallack et al. 1977) and possibly *Cladophlebis lobifolia* (Walkom 1924, 1928). *Cladophlebis lobifolia* sensu stricta is a Northern Hemisphere species, having been recorded from the Middle Jurassic to Early Cretaceous of Europe, Russia and China. Fertile specimens are placed in *Eboracea lobifolia* Thomas (Harris 1961). *Lobifolia,* a genus with a new type, *Lobifolia novopokrovskii* was erected by Lebedev and Rasskazova (1968) who also included the combination *Lobifolia lobifolia*, contrary to ICBN rules (as discussed by Rigby 1977). Retallack (in Retallack et al. 1977) described the new species *Lobifolia dejerseyi* and illustrated a small fragment from the Cloughers Creek Formation (Retallack et al. 1977, Fig.5A). He selected as the holotype a specimen from the Basin Creek Formation that had been assigned to *Cladophlebis lobifolia* by Flint and Gould (1975 Pl.1, fig.4). That specimen is reillustrated here as Fig. 25A. Apart from the geographical and time differences, the Nymboida material described by Retallack and the additional new species described below differ significantly from both the Northern Hemisphere *Lobifolia* species and *Cladophlebis* sensu Frenguelli (1947) by the placement and form of the first basiscopic and acroscopic pinnules. It is essential when identifying fossils as *Nymbopteron* that the material includes the portions of the pinnae attached to the main rachis. Isolated distal pinna fragments may be confused with *Cladophlebis* or *Dicroidium* species.

Four species of *Nymbopteron* are described below. They are distinguished by the frond size, shape and venation of the pinnules and particularly by the shape and position of the first basiscopic pinnules.

While the collected material of some of these species is limited, each species occurs in a sediment type representing a different facies similarly to that noted for *Nymboidiantum* spp. above, and it is most probable that each species grew in a different vegetation type. In the present collection there are no intergrading forms between the species.

Nymbopteron dejerseyi (Retallack, in Retallack et al. 1977) Holmes gen. et comb. nov.
Figures 24A–E and 25A

1975 *Cladophlebis lobifolia* non (Phillips) Seward, Flint and Gould, pl.1, Fig.4 only
1977 *Lobifolia dejerseyi* Retallack in Retallack et al., p.88

Emended diagnosis

Medium sized ovate fronds; first basiscopic pinnule enlarged and of irregular shape, attached in angle between pinna rachis and main rachis or directly on main rachis; venation radiating and forking; following pinnules with midvein persisting almost to apex, first basiscopic vein attached at base of midvein or directly to pinna rachis, lateral veins twice or once broadly forked.

Description

Retallack's holotype, reillustrated here as Fig. 25A, is a midportion of a broad ovate frond estimated to have been up to c. 200 mm long. No complete fronds are available. The main rachis is deeply grooved and ridged (Figs 24A-D), 2–3 mm wide near base. Pinnae well separated, sub-opposite to alternate, basal pinnae short and obtuse with conjoined pinnules (Fig. 24B); in mid-frond, pinnae attached at a right angles and pinnules separated to the base, apically the pinnae becoming moderately acute and pinnules again coalescing (Fig. 24C). First basiscopic pinnule enlarged and of irregular shape, attached in angle between pinna and main rachis or directly to main rachis (Figs 24D, E) in the manner of zwischenfiedern as in *Lepidopteris* species (Anderson and Anderson 1989); with strong midvein at centre base of pinnule, forking into three major lateral veins with each vein again forking once to three times, 8 to 28 vein endings around the margin. The venation in the triangular first acroscopic pinnule bifurcates three times, distal veins almost parallel. The succeding pinnules opposite to alternate, free to the base but closely spaced, ovate to broad-falcate, 4–10 mm long and 2–4 mm wide, length to width ratio of c. 1.6–2:1; midvein slightly sinuous, persistent almost to apex, three to four pairs of alternate lateral veins broadly forking once or twice, first lateral vein sometimes arising directly from the pinna rachis.

Holotype

AMF121158 (formerly UNEF14102), Australian Museum, Sydney.

Type locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF113543-113557, 120972, 120974, 120975, Coal Mine Quarry; AMF120973, 120977, Reserve Quarry.

Discussion

The holotype of this species was placed by Retallack (in Retallack et al. 1977) in the genus *Lobifolia,* which is essentially a Northern Hemisphere genus of Jurassic to Cretaceous age (Lebedev and Rasskazova 1968; Boureau 1975) as discussed above. The conjoining of the first acroscopic pinnules to form a decurrent triangular membrane between the base of the pinna rachis and the main rachis does not occur in *Lobifolia* but is diagnostic for *Nymbopteron.*

N. dejerseyi differs from the other *Nymbopteron* species by the broadly enlarged basal basiscopic pinnules with radiating venation and by the persistent midvein with broadly forking lateral veins in the following pinnules.

Nymbopteron foleyi Holmes gen. et sp. nov.
Figure 25B, C; 26A

Diagnosis

Small to medium sized fronds, first basiscopic pinnules rounded, attached along base of pinna rachis; following pinnules triangular-falcate; midvein weak, forking four or five times into fine radiating venules.

Description

Several almost complete broad elliptic to ovate fronds on AMF113538 (Fig. 26A) are up to 150 mm long and 65 mm wide; main rachis 2 mm wide near base. Pinnae opposite to alternate, basal pinnae short, with decurved attachment, at high angles in mid frond and becoming more acute apically. First basiscopic pinnules attached near the base of the pinnae, semicircular; first acroscopic pinnule enlarged, triangular and conjoined in the angle between the main rachis and the pinna rachis and reaching almost to the next pinna rachis; following pinnules opposite, closely spaced to overlapping (Figs 25B, C), short, broad, rhombic to slightly falcate, apex obtuse; length to width ratio of c. 1.5:1. Venation usually obscure; midvein arising close to the basiscopic margin at c. 45°, then dividing four to five times into venules which radiate evenly at an acute angle to each other to the pinnule margin; c. 16–22 vein endings around margin.

Holotype

AMF113538, part and counterpart, Australian Museum, Sydney.

Type locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF113522, 113539, 113540, 120972, 120985, all from Coal Mine Quarry.

Name derivation

foleyi – for Mr Brian Foley, Nymboida Quarries operator, in recognition of his valuable on-site assistance over a period exceeding 30 years.

Discussion

N. foleyi differs from the other *Nymbopteron* species by the first basiscopic pinnules which are mostly rounded and attached only to the pinna rachis, and by details of the venation pattern in the pinnules.

Nymbopteron rhomboidale Holmes gen. et sp. nov.
Figures 27A-D

Diagnosis

Medium sized bipinnate frond, pinnae subopposite, closely spaced, first basiscopic pinnules large, square to rounded, attached mostly to the main rachis from which a single vein enters the pinnule, forking four times, ultimate veinlets meeting margin at 90° to main rachis; first acroscopic pinnules forming equilateral triangles between the upper side of the pinna rachis and main rachis, proceeding pinnules rhomboidal, overlapping; midvein short, with several radiating and forking lateral veins.

Description

The only specimen (Fig. 27A) is an upper mid portion of a frond with the base and apex missing; estimated length of c. 150 mm; main rachis at broken base 2.5 mm wide, tapering apically to 1.5 mm wide, longitudinally grooved, with six pairs of subopposite broad linear pinnae attached at c. 45° and c. 11 mm apart. First basiscopic pinnules (Fig. 27B) c. 5 mm wide and 5 mm long, attached to basal 3 mm of pinna rachis and 5 mm along the main rachis, distal margin square to rounded, a single vein enters the base of the pinnule from the main rachis, forking four times, the ultimate venules are parallel and pass into the pinnule margin at 90° to the main rachis. First acroscopic pinnules equilateral triangular in shape with proximal margin conjoined to the main rachis; a single vein enters the pinnule from the junction of the pinna rachis with the main rachis, forking three times, with ultimate veinlets parallel to each other and at right angles to the sloping pinnule margin. Succeeding pinnules along the pinnae (Fig. 27D) alternate, overlapping, c. 5 mm wide and 5 mm long hence a length to width ratio of 1:1, rhomboidal, proximal margin curving through 90°, distal margin at right angles to pinna rachis, straight to slightly convex, apex acute, a single vein enters the pinnule at a very acute angle, forking four to six times, with adaxial branches running parallel to the pinna rachis and the other veins radiating evenly to the pinnule margin where there are 16–22 vein endings, distal pinnules decreasing in size and becoming rounded.

Holotype

AMF113556, Australian Museum, Sydney.

Type locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Name derivation

rhomboidale – *rhombus*, (Lat.), an equilateral parallelogram with unequal pairs of opposite angles; referring to the shape of the pinnules.

Discussion

N. rhomboidale differs from all other *Nymbopteron* species by the closely spaced pinnae, by the shorter broader overlapping pinnules and by the distinctive radiating venation. The lateral venation in the proximal portions of the broad overlapping pinnules may be confused as conjoining with the veins of adjacent pinnules as described for *Merianopteris major* Feistmantel (Boureau 1975).

Nymbopteron uncinatum Holmes gen. et sp. nov.
Figure 28A

Diagnosis

A large bipinnate frond with broad uncinate basal basiscopic pinnules.

Description

N. uncinatum is based on two incomplete specimens of large bipinnate fronds, both over 200 mm long and with bases and apices missing. On the portion preserved of the holotype (Fig. 28A) the main rachis is smooth, 4 mm wide at the broken base, tapering gradually upwards, with 15 pairs of opposite, straight pinnae to 80 mm long attached at c. 45°. The specimen AMF120969 has 10 pairs of opposite pinnae to 60 mm long attached at c. 60° to 80°. First basiscopic pinnules attached in the angle between the main and pinna rachises, triangular to 10 mm long, with recurving tip which forms a broad hook-like outline; first acroscopic pinnule vertically elongate and conjoined to the main rachis. Succeeding pinnules opposite to subopposite, separated to the base except at the distal extremity of the pinnae where they coalesce, broadly triangular to slightly falcate with proximal margin broadly convex, the distal margin straight or slightly convex, c. 8 mm long and c. 4 mm wide with a length to width ratio of 2:1. Venation not preserved.

Holotype

AMF120968, Australian Museum, Sydney.

Type locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF120969, Coal Mine Quarry.

Name derivation

uncinatum – (Lat.), *hooked*, referring to the hook-shaped outline of the first basiscopic pinnules.

Discussion

N. uncinatum differs from all other *Nymbopteron* species by its larger and more robust frond size and by the hook-shaped outline of the first basiscopic pinnules. The main and pinna rachises of *N. uncinatum* appear to be rounded and smooth in contrast to the ribbed and grooved rachises of *N. dejerseyi* and *N. foleyi*. This feature may be real or perhaps it is an artifact dependent upon the orientation or deterioration of the frond in the sediment at the time of fossilisation (see comments on *Osmundopsis scalaris* in Holmes 2001b).

Nymborhipteris Holmes gen. nov.

Nymborhipteris radiata Holmes gen. et sp. nov.
Figures 29A, B

Combined diagnosis

Medium sized bipinnate frond, stout main rachis, pinnae alternate, bearing opposite sub-circular pinnules with radiating and forking venation.

Description

A fragment of a mid-portion of a bipinnate frond; main rachis on portion preserved longitudinally wrinkled, 7 mm wide, tapering to 6 mm over length of 90 mm; total length of frond estimated to reach 300 mm. Pinnae sub-opposite to alternate, 11–15 mm apart, attached at c. 60°, straight, length unknown. Pinnules opposite, sub-circular, base broadly attached but slightly constricted basiscopically, margin entire, apex rounded; a single decurrent vein enters the base, soon dividing four times into finer veins which again fork two or three times to radiate throughout the lamina with c. 24 vein endings around the margin.

Holotype

AMF113489, Australian Museum, Sydney.

Type locality

Reserve Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Name derivation

nymborhipteris – contrived; from *Nymboida,* the source of the material; *rhipis,* (Gr.) *fan*; *pteris*, (Gr.) *fern*; referring to the fan-shaped appearance of the pinnules.

radiata (Lat.), *radiating*, referring to the venation pattern in the pinnules.

Discussion

N. radiata, the type species of the monotypic genus *Nymborhipteris,* is based on a single fragmentary specimen (Fig. 29A). The stout striated main rachis and the venation pattern distinguishes *N. radiata* from the forked bipinnate fronds of the corystosperm *Dicroidium zuberii* (Retallack 1977; Anderson and Anderson 1983). In gross morphology this frond differs from all known Gondwana material.

Ptilotonymba Holmes gen. nov.

Ptilotonymba curvinervia Holmes gen. et sp. nov.
Figures 30A-C, 31

1977 *Arctopteris* sp? Retallack in Retallack et al. p. 86, Fig. 5C

1977 *Cladophlebis* sp. cf *C. oblonga*, Bourke et al. Fig. 3.2

Combined diagnosis

Medium to large bipinnate frond; pinnae broad-linear; pinnules strongly decurrent, rhombic; venation asymmetrical; two lateral veins attached to pinna rachis; 4–6 basiscopic lateral veins once forked or simple, slightly recurved; 3–4 acroscopic lateral veins mainly unforked, arching to follow parallel to pinnule margin.

Description

This morpho-taxon is based on five fragments of bipinnate fronds. The holotype (Figs 30B, C) shows incomplete pinnae to 80 mm long in two parallel lots of four apparently attached to separate main rachises. Fig. 31 is a portion of a large frond with the main rachis 18 mm wide near base, decreasing to 12 mm over the 300 mm length preserved, which suggests a total length in excess of 1 metre. Pinnae opposite, to >80 mm long, 20–30 mm apart. Pinnules rhomboidal to rectangular, alternate overlapping, c. 7–10 mm long and 5–6 mm wide, base broad, decurrent on basiscopic side, contracted on acroscopic side, length to width ratio of proximal pinnules c. 1.6:1, margin entire, apex acute to obtuse. Pinnule midvein entering pinnule at c. 30°, arching to c. 45°, at 2/3 of way through lamina to fork and continue as two parallel veins to the apex. Four pairs of asymmetrical lateral veins attached at c. 45°. First one or two lateral veins on basiscopic side of the pinnule fork twice, subsequent veins forking once or unforked near apex, running straight or slightly recurved and parallel to each other to the pinnule margin. On the acroscopic side of the midvein four lateral veins are attached at c. 30°, once forked, the proximal one or two recurving strongly to follow parallel to the pinnule margin for half its length; subsequent veins leaving the midvein at c. 30° and running parallel to each other round distal portion of pinnule margin. Two veins enter the decurrent portion of each pinnule at 45° directly from the main rachis, first vein simple, second vein once forked; 14-18 or more vein endings around pinnule margin with twice as many endings on the basiscopic margin as on the acroscopic margin. Distally the pinnules coalesce and the pinna becomes lobed to entire.

Holotype

AMF113479, Australian Museum, Sydney.

Type locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF11380-83, Coal Mine Quarry.

Name derivation

Ptilotonymba – ptilotos, (Gr.) *feathered*, referring to the feather-like appearance of the pinnules; *nymba,* for Nymboida, the source of the material.

curvinervia – contrived, for the strongly arching lateral veins.

Discussion

Ptilotonymba is a monotypic genus with *P. curvinervia* as the type species. *Arctopteris* sp? of Retallack (in Retallack et al. 1977) and *Cladophlebis* sp. cf *C. oblonga* (Bourke et al. 1977) are frond fragments that agree with *P. curvinervia. Arctopteris* spp from the Lower Cretaceous of Siberia (Samalyna 1964; Boureau 1975) have similar curving lateral venation and coalescing pinnules, but differ by the unforked lateral veins and by the presence of pinnules decurrent on, or attached directly to, the main rachis between the pinnae. *Pecopteris arcuata* Halle (1927 pl. 19, Figs 1-7; pl.20, Figs 1-13) from the Palaeozoic of China has closely spaced to coalescing pinnules with curving venation similar to *P. curvinervia,* but differs by the opposite arrangement of the pinnules and by the unforked lateral veins.

Genus *Sphenopteris* (Brongniart) Sternberg, 1825
Type species *Sphenopteris elegans* (Brongn.)
Sternberg 1825, see Boureau 1975 pp 427-429

Sphenopteris speciosa Holmes sp. nov.
Figures 32A-D

Diagnosis

Medium sized bipinnate frond. Pinnae opposite. Pinnules elongate triangular with deeply incised lobes on proximal pinnae, decreasing in size, number of lobes and degree of lobation distally and apically. Midvein straight and strong in proximal half of pinnule, decreasing in width and forking in the apical lobe. Lateral veins arching and forking into each lobe.

Description

This leaf form is known only from incomplete fronds; the largest being a midportion 150 mm long suggesting a total length of c. 300 mm. Pinnae opposite, recurving, slightly overlapping close to the main rachis; attached at c. 60° to 70°, to c. 100 mm long, 45 mm wide near the base, with up to 10 pairs of pinnules. Pinnules alternate, base contracted, to 25 mm long x 15 mm wide across proximal portion of pinnule, elongate triangular, with to five pairs of deeply incised semicircular lobes, becoming less lobate to entire distally and apically. A single straight midvein traverses each pinnule, decreasing in width and forking in terminal lobe. Lateral veins arch into each lobe, forking to three times into the proximal lobes then decreasingly forked to simple distally.

Holotype

AMF113520 and counterpart, Australian Museum, Sydney.

Type locality

Coal Mine Quarry, Nymboida. Basin Creek

Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF113521, UNEF13557, 13558, Coal Mine Quarry.

Name derivation

speciosa - (Lat.) *showy, beautiful*, for a fossil that I regard as aesthetically pleasing.

Discussion

A number of Australian Triassic fronds have been placed in the form genus *Sphenopteris* (Tenison-Woods 1883; Shirley 1898; Walkom 1917, 1928; Jones and de Jersey 1947). However they all differ significantly from *S. speciosa*, which appears to be unique in Gondwana Triassic floras.

Fern bases with radiating fronds
Figures 33A-C, 34A-C

Description

Eight specimens in the collection are of rhizomes or stems with closely spaced, spirally attached fronds. Figure 33A shows a number of short, straight and parallel-sided rachises radiating from a common rhizome or stem. One rachis (Fig. 33B) bears four pairs of opposite rounded pinnules 12 mm apart arranged pinnately and apparently attached in a plane at right angles to the main rachis. The size of the three lower pairs of pinnules (pinnae?) is not known as they are compressed at an angle to the bedding plane. The uppermost preserved pinnule is 9 mm long and 7 mm wide. It is ovoid in outline with a contracted base, margin slightly lobed, apex obtuse. The venation is not clear but appears to be an indistinct short median vein that forks repeatedly to form fine lateral veins radiating throughout the lamina. The specimens illustrated in Figs 34A, B have c. 12 frond rachises radiating from a central axis c. 10 mm in diameter. They are all incomplete. From an expanded base, the rachises are smooth, straight, to 4 mm in width and to an incomplete length of 80 mm without pinnae or pinnules. Figure 33C is a vertical section of a rhizome with persistent frond rachises radiating three dimensionally into the matrix.

Material

AMF113498-113503, Coal Mine Quarry, Nymboida.

Discussion

The growth form and foliage pattern of the specimen with the pinnate rachis can not be related to any other fern or fern-like plant at Nymboida or other Gondwana localities. All these specimens were at first mistaken for isoetalean plants until AMF113498 (Figs 33A, B) demonstrated their fern-like nature. However the poor preservation of the present material does not warrant the erection of a new taxon.

Circinate frond
Figure 33D

Despite the abundance of fern fossils at the Nymboida quarries, the specimen illustrated (AMF113519) is the only example in the collections of a circinate frond. As the specimen is detached and incomplete it cannot be affiliated with any known taxon.

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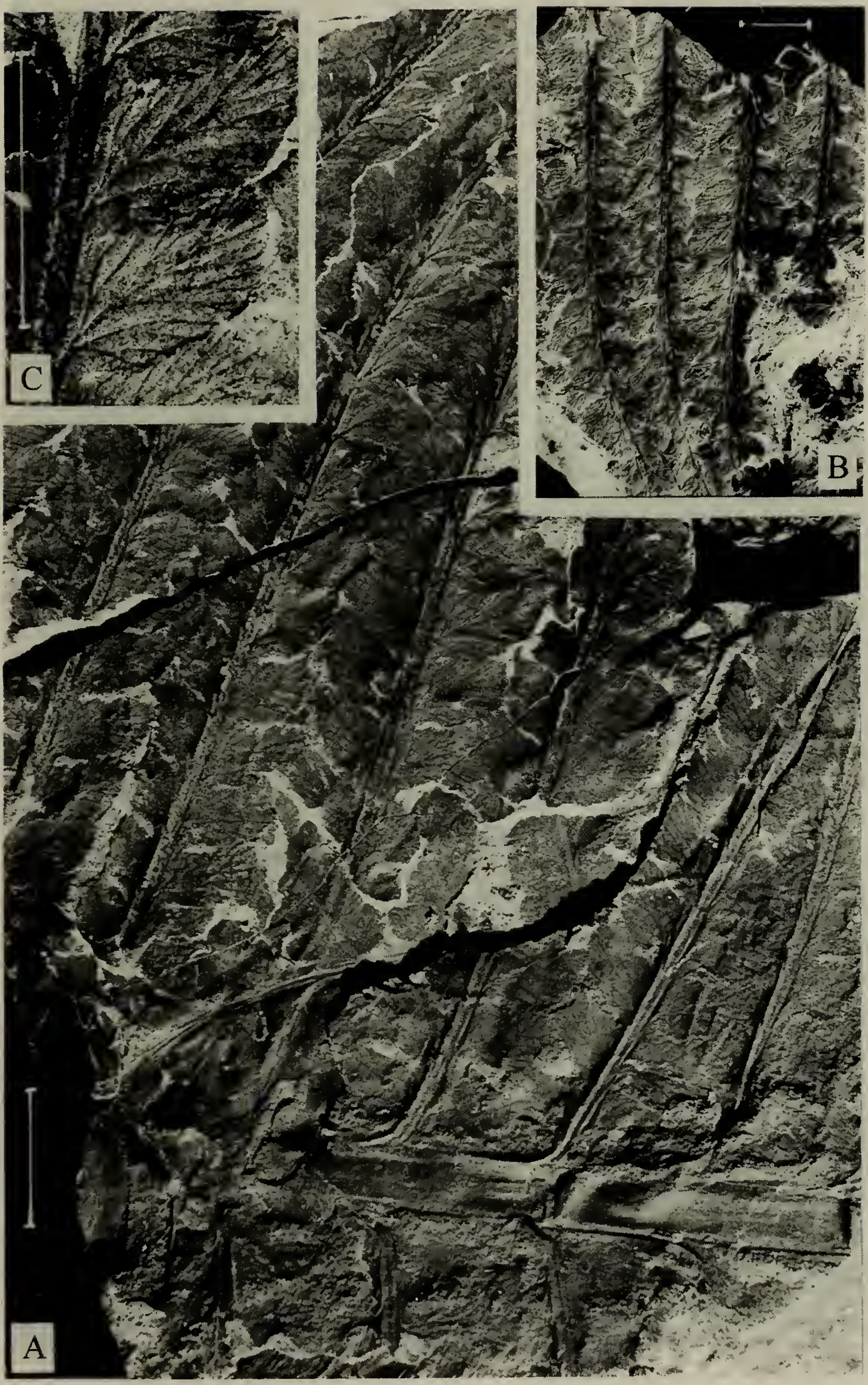

Figure 1. A–C. *Cladophlebis conferta* Holmes sp. nov. A. AMF120987, holotype X2; B. AMF121015; C. AMF120987, X4. Scale bar = 1 cm.

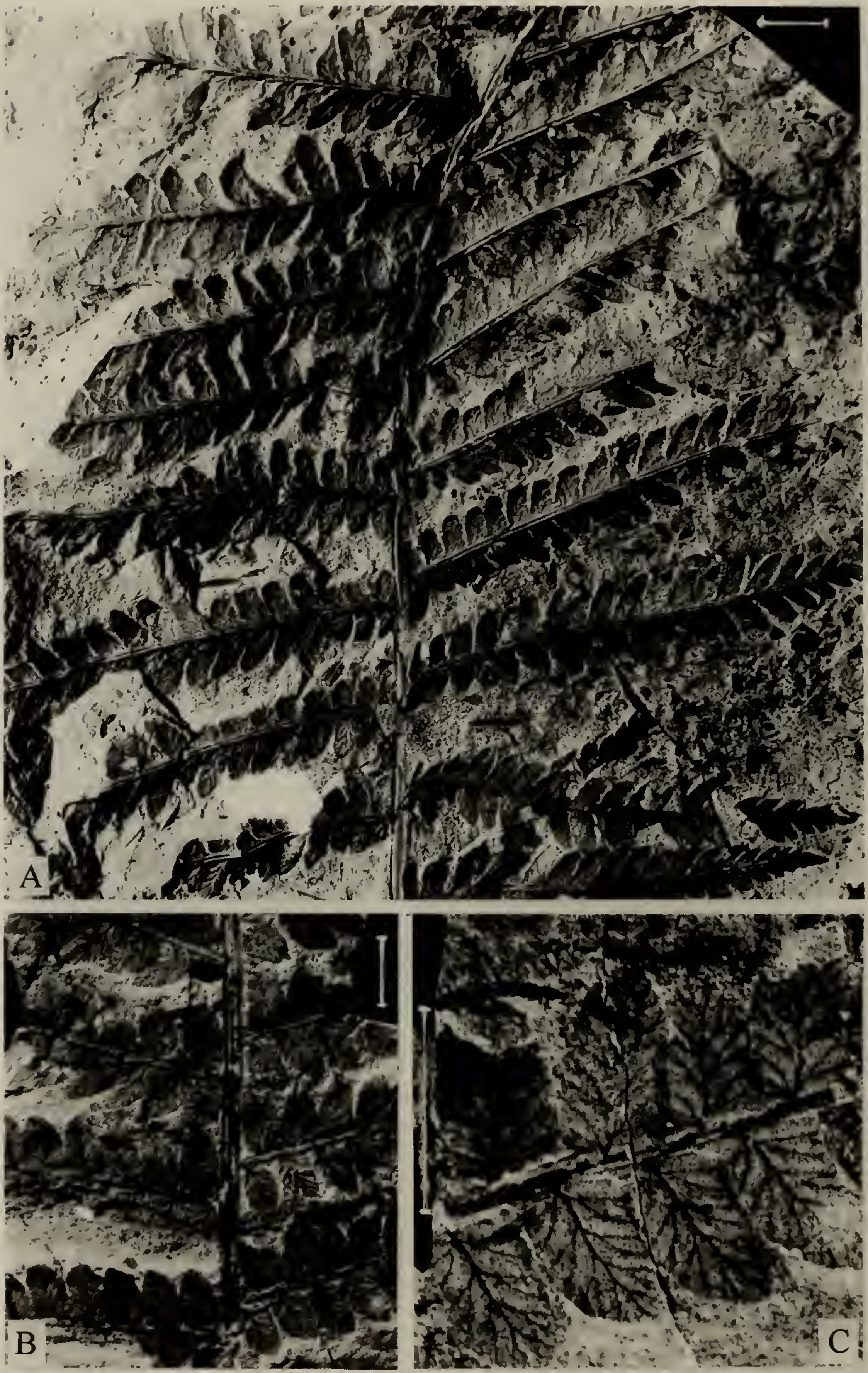

Figure 2. A–C. *Cladophlebis octonerva* Holmes sp. nov. A. AMF113484, holotype; B. AMF113485; C. AMF113485, X3. Scale bar = 1 cm.

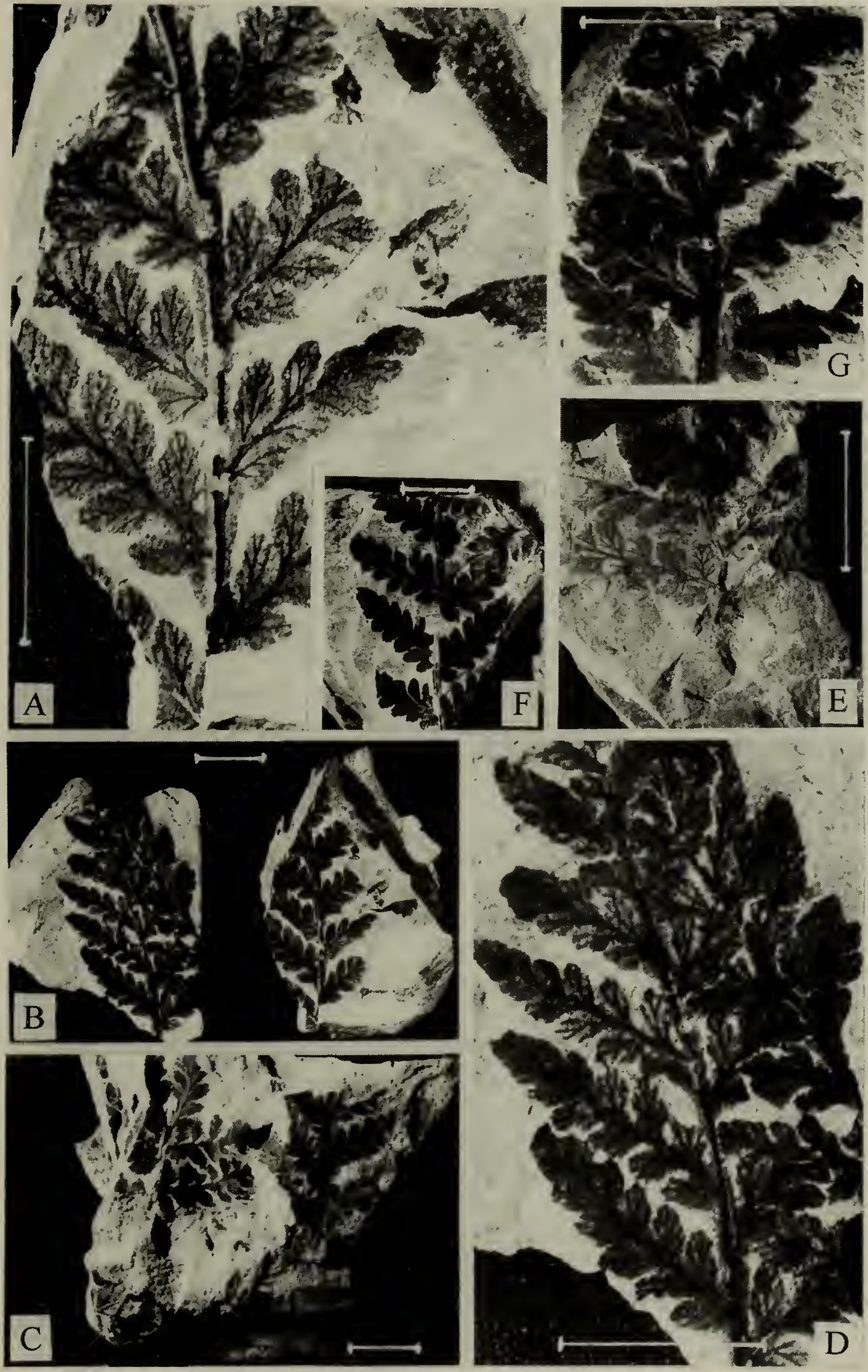

Figure 3. A-G. *Cladophlebis paucinerva* Holmes sp. nov. A. AMF120980, X3; B. AMF120979 and AMF120980 part and counterpart, holotype and isotype; C. AMF120981; D. AMF120979, X3; E. AMF120984, X2; F. AMF120982; G. AMF120983, X2. Scale bar = 1 cm.

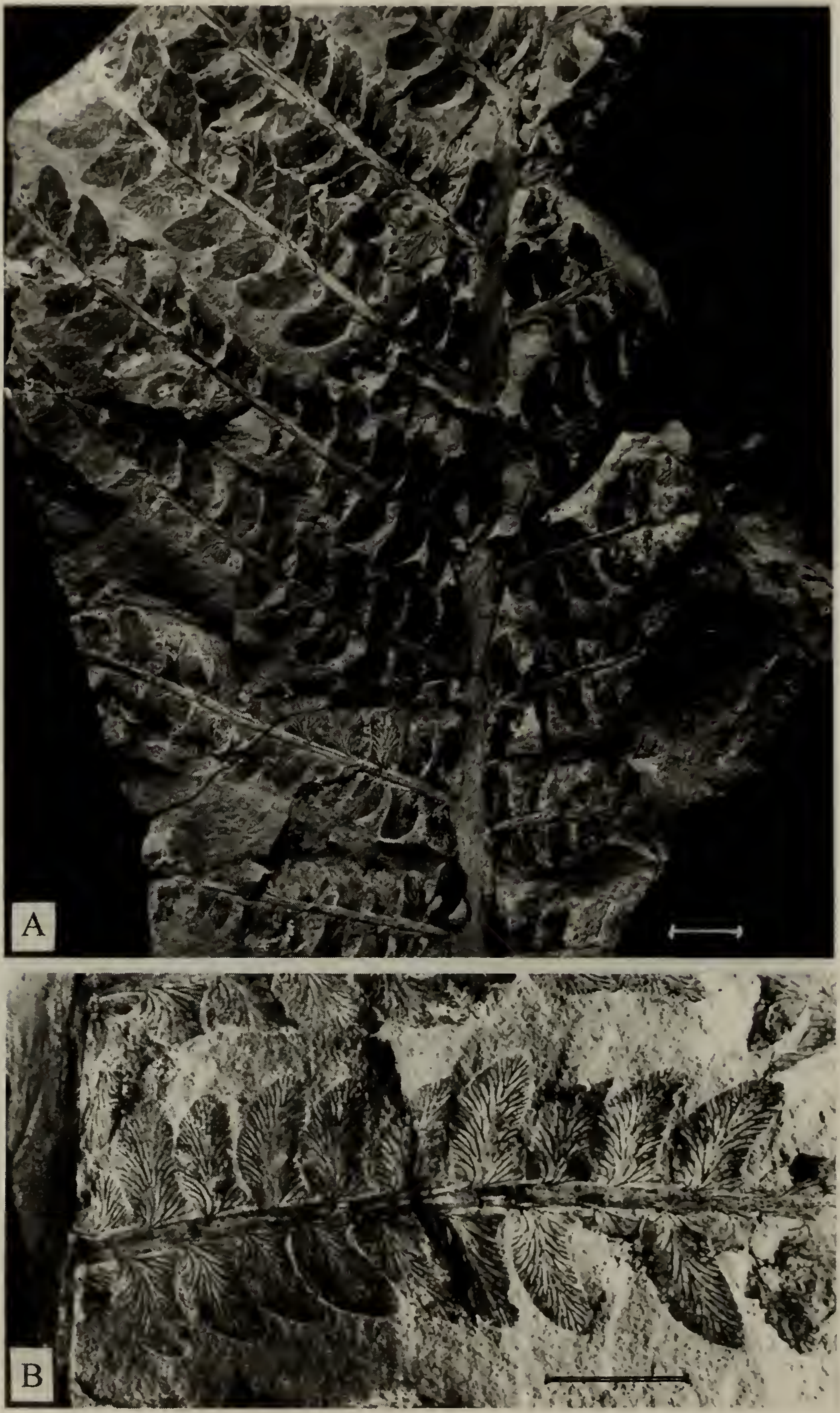

Figure 4. A, B. *Cladophlebis retallackii* Holmes sp. nov. A. AMF120954; B. AMF120958, X2. Scale bar = 1 cm.

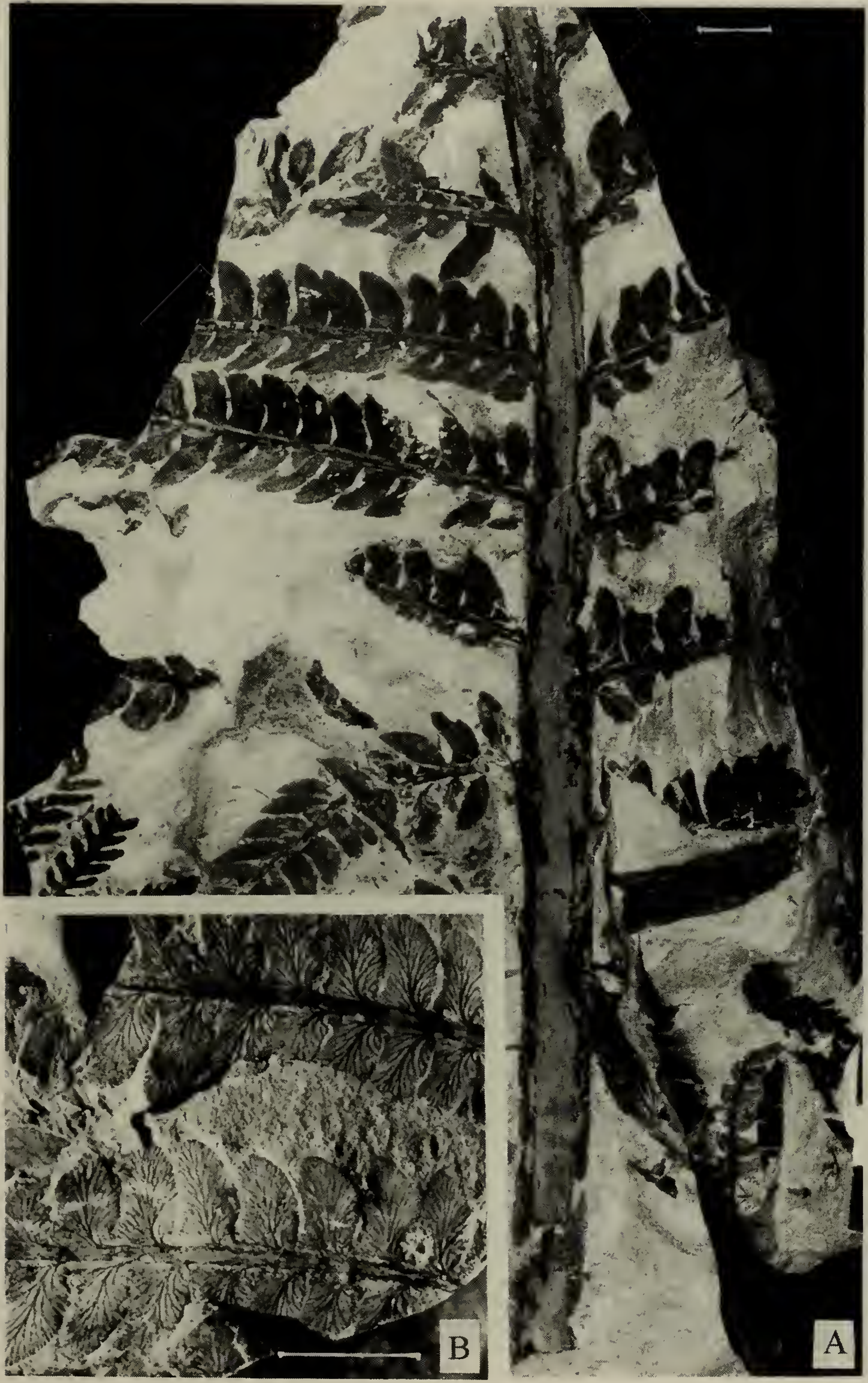

Figure 5. A, B. *Cladophlebis retallackii* Holmes sp. nov. A. AMF120959, holotype; B. AMF120958, X2. Scale bar = 1 cm.

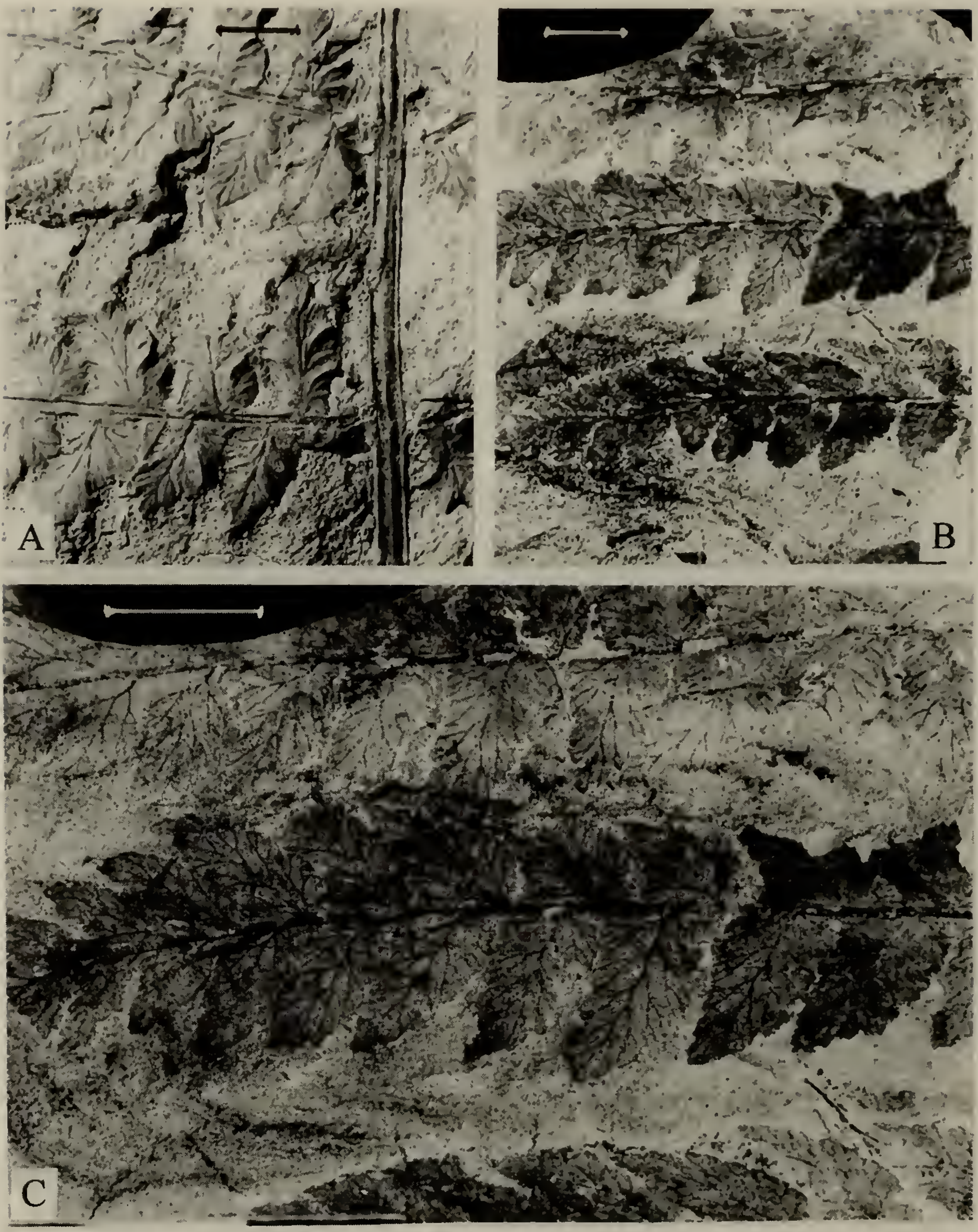

Figure 6. A–C. *Cladophlebis sinuata* Holmes sp. nov. A. AMF113512, holotype; B. AMF113518; C. AMF113518, X2. Scale bar = 1 cm.

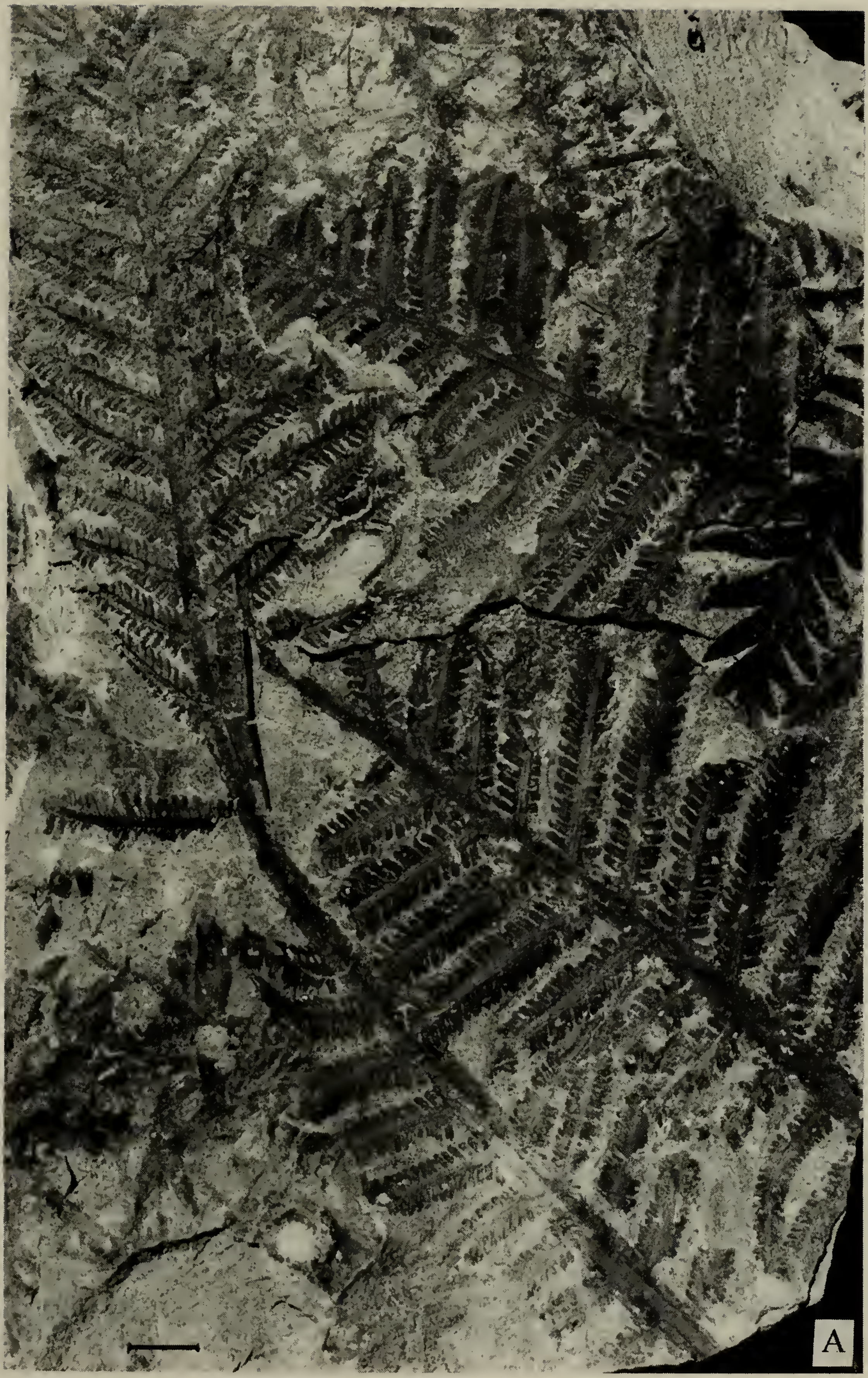

Figure 7. A. *Cladophlebis tenuipinnula* Holmes sp. nov. AMF113523, holotype. Scale bar = 1 cm.

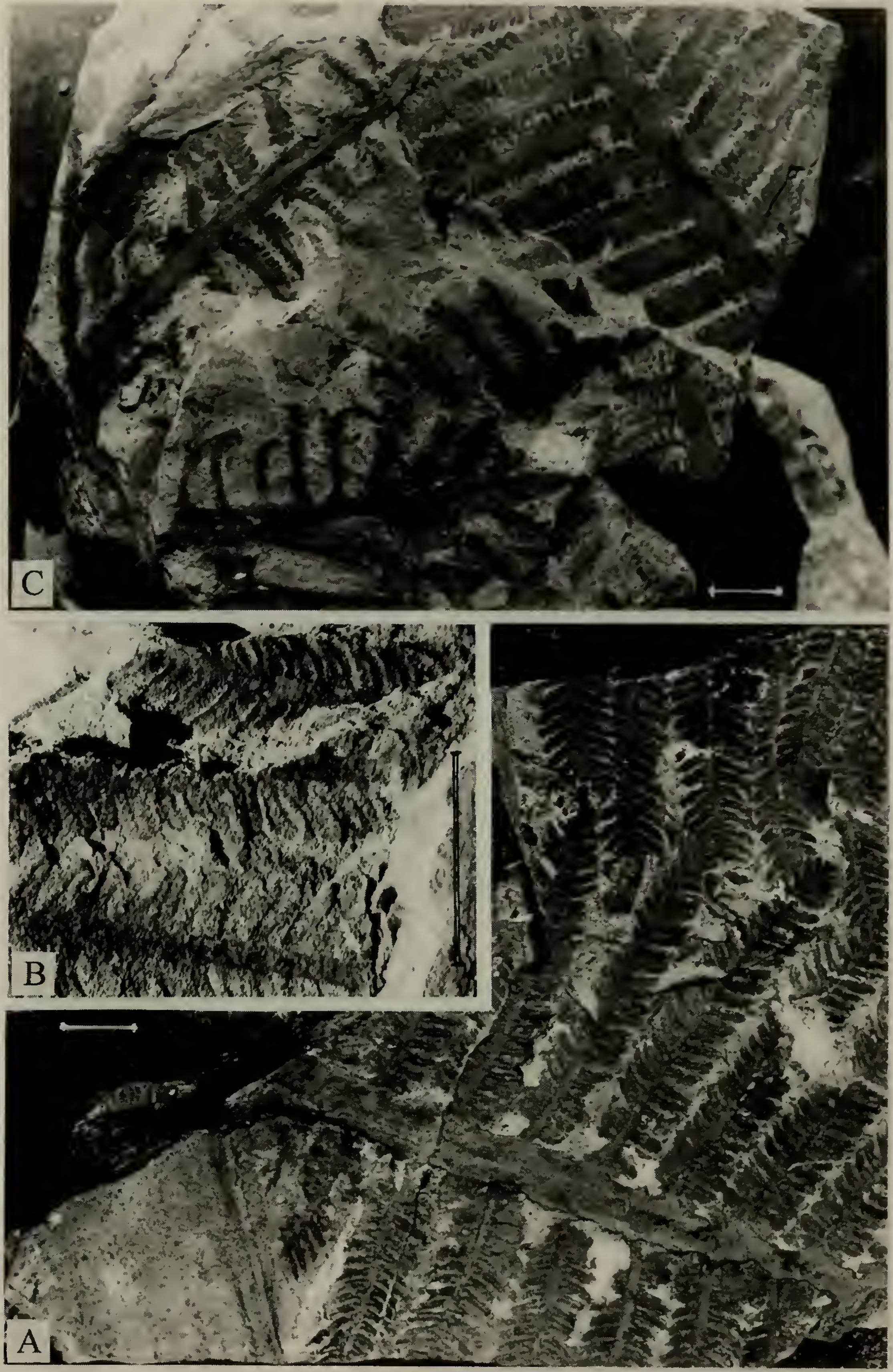

Figure 8. A–C. *Cladophlebis tenuipinnula* Holmes sp. nov. A. AMF113406; B. AMF113526, X3; C. AMF113524. Scale bar = 1 cm.

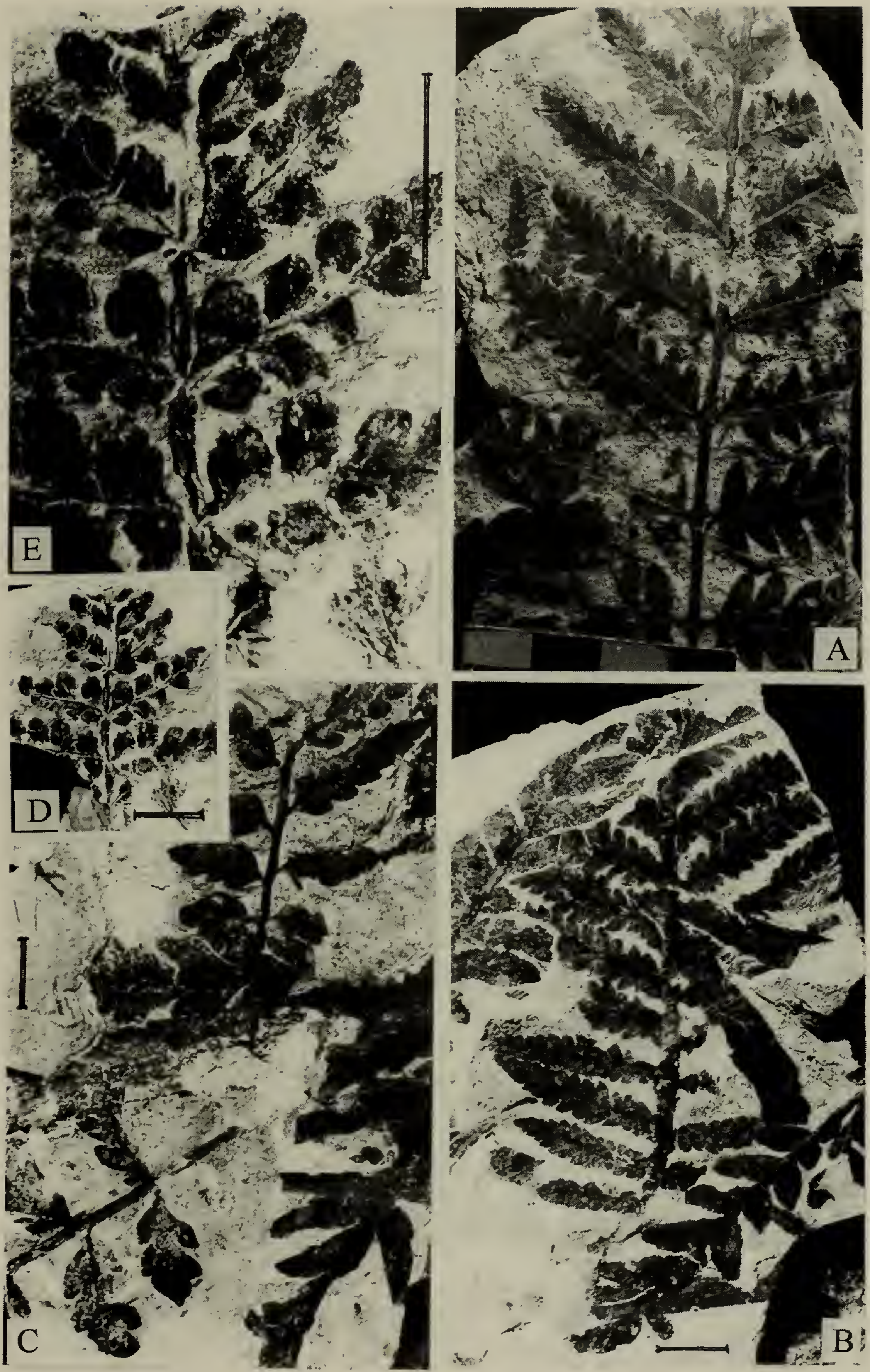

Figure 9. A–C. ?*Cladophlebis* sp.A. A. AMF113508; B. AMF113510; C. AMF113509. D, E. ?*Cladophlebis* sp.B. D. AMF120978; E. AMF120978, X3. Scale bar = 1 cm.

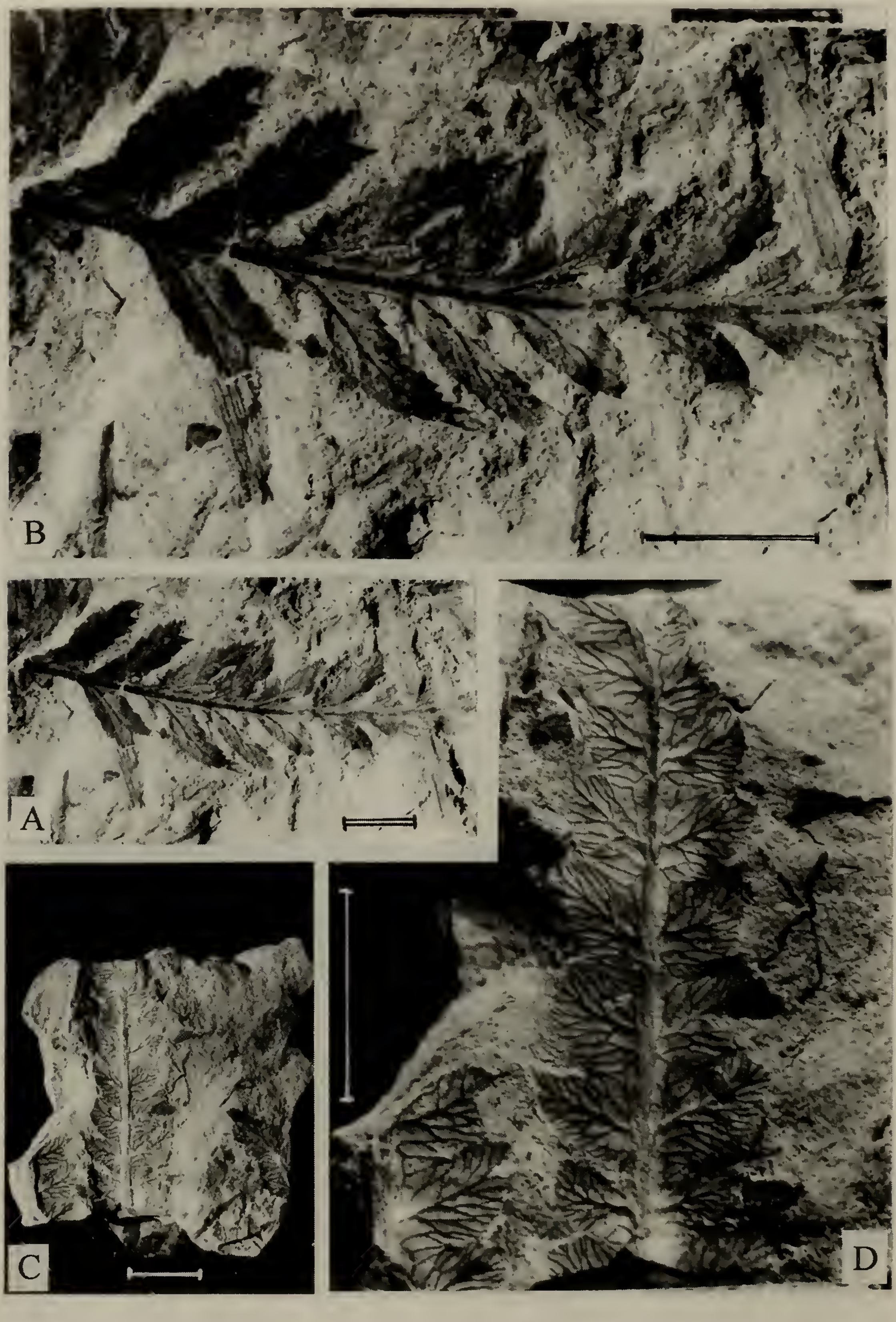

Figure 10. A, B. ?*Cladophlebis* sp.C. A. AMF120994; B. AMF120994, X2.5; C. D. *Dictyonymba sparnosa* Holmes gen. et sp. nov.; C. AMF113507, holotype; D. AMF113507, X3. Scale bar = 1 cm.

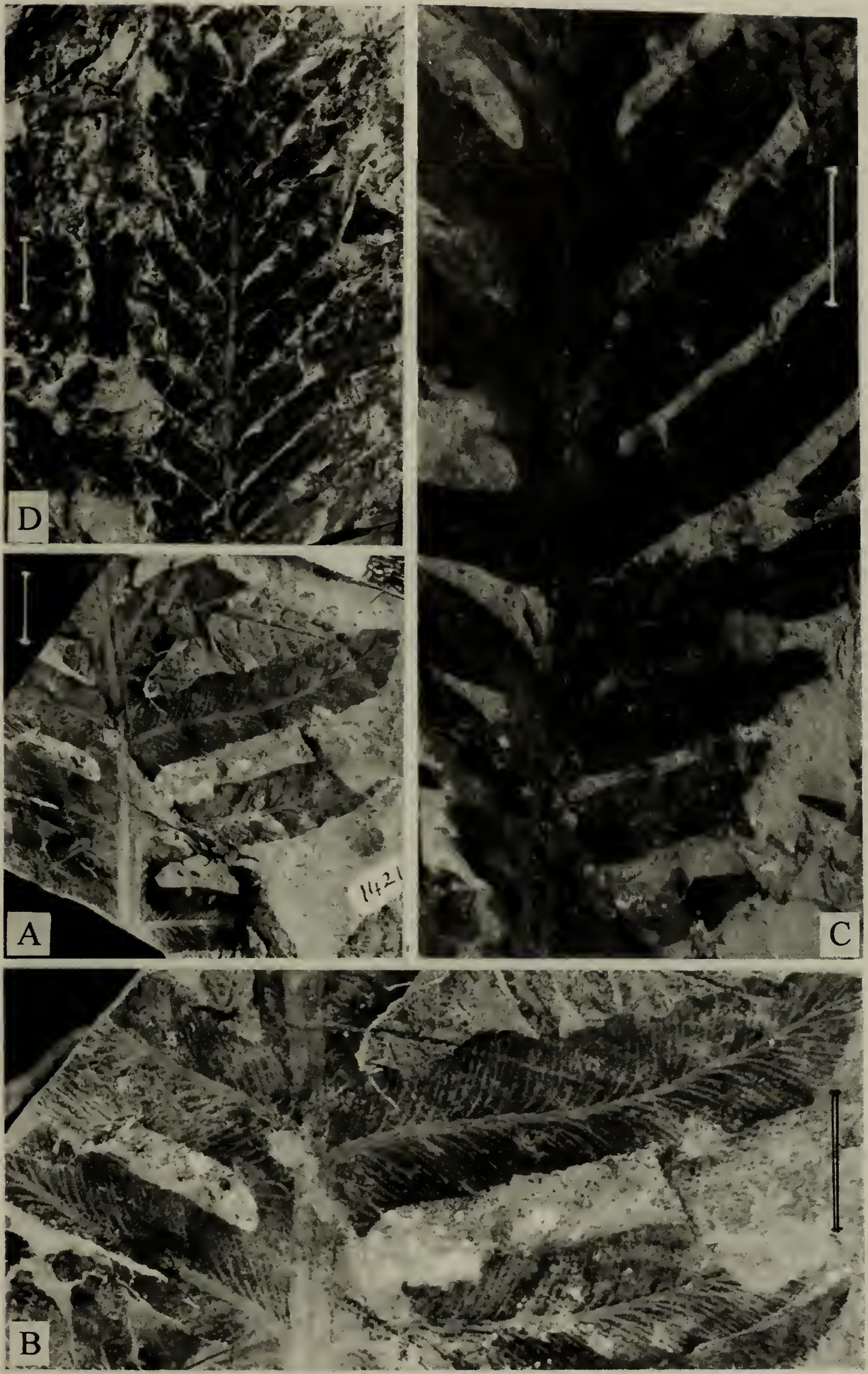

Figure 11. A–D. *Gouldiopteris alethopteroides* Holmes gen. et sp. nov. A. AMF113561, holotype; B. AMF113561, X2; C. AMF113562, X2; D. AMF113563. Scale bar = 1 cm.

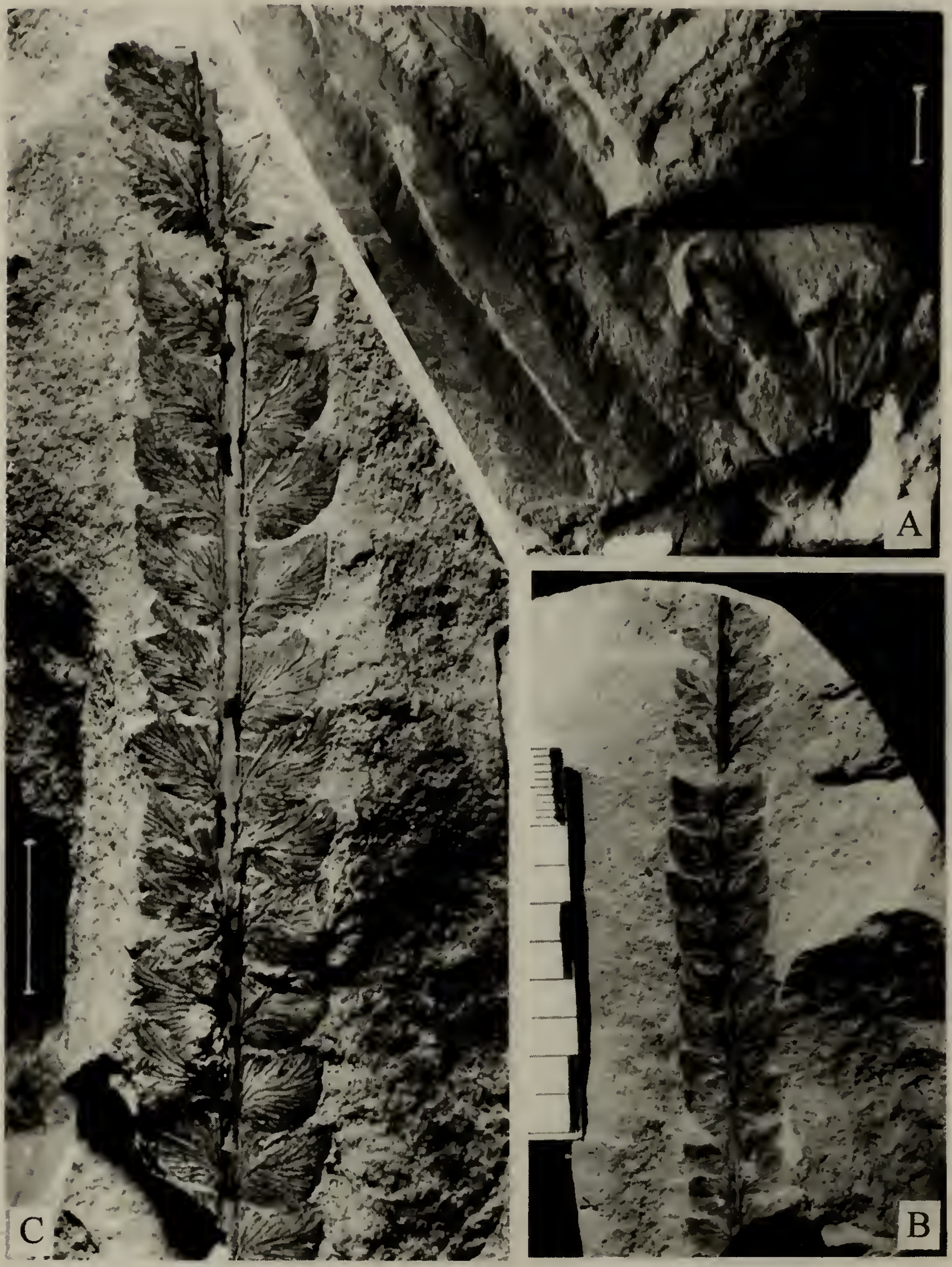

Figure 12. A–C. *Leconama stachyophylla* Holmes gen. et sp. nov. A. AMF121183, holotype; B. AMF121160; C. AMF113544, X2. Scale bar = 1 cm.

Figure 13. A. *Micronymba repens* Holmes gen. et sp. nov. AMF120962, holotype, X2. Scale bar = 1 cm.

Figure 14. A–D *Micronymba repens* Holmes gen. et sp. nov. A. AMF120962, holotype; B. AMF120963, isotype; C. AMF120962, X3; D. AMF120965. Scale bar = 1 cm.

Figure 15. A. *Nymbiella lacerata* Holmes gen. et sp. nov. AMF113530, holotype. Scale bar = 1 cm.

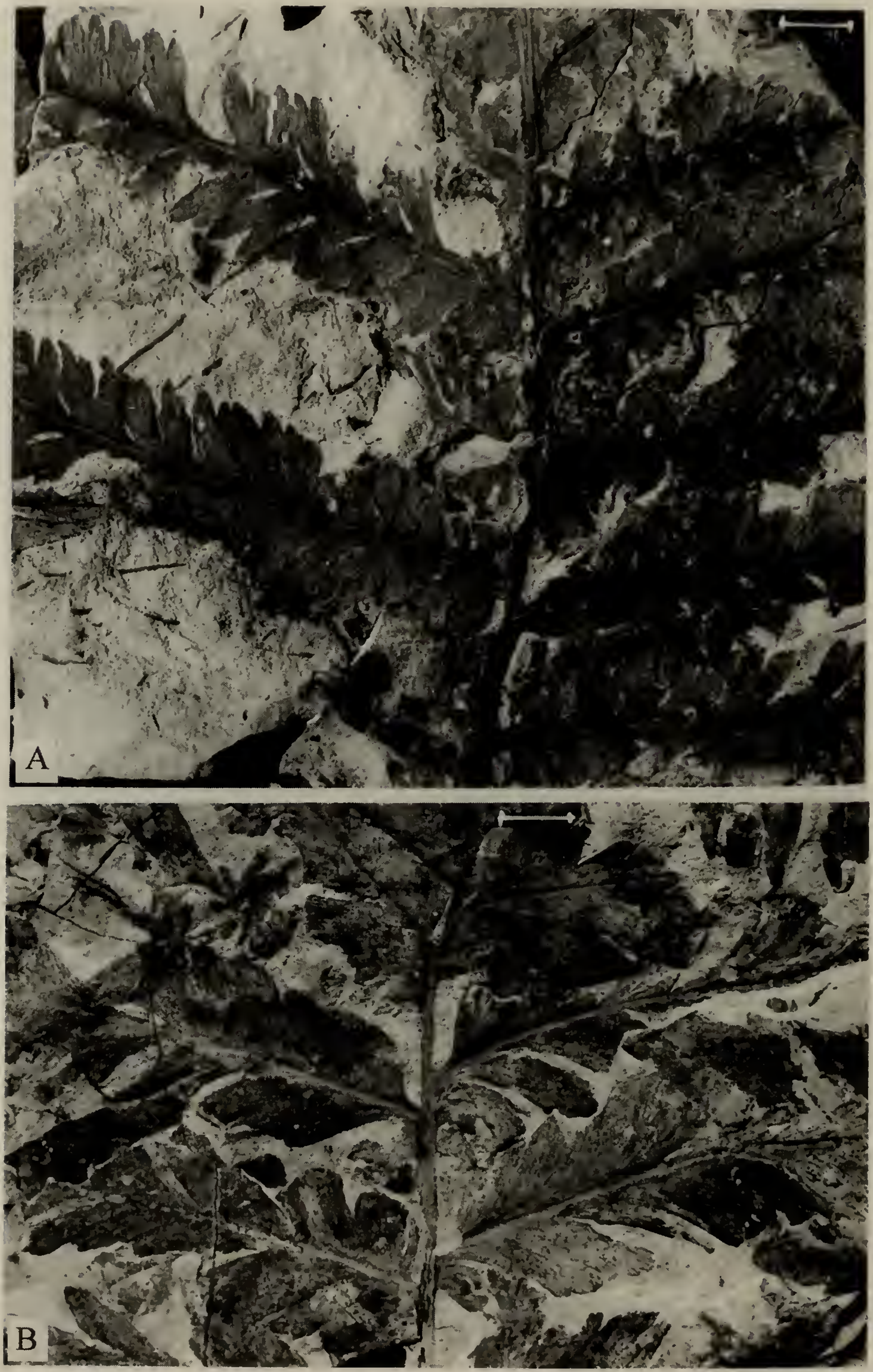

Figure 16. A, B. *Nymbiella lacerata* Holmes gen. et sp. nov. A. AMF113532; B. AMF113533. Scale bar = 1 cm.

Figure 17. A–E. *Nymboidiantum glossophyllum* (Tenison-Woods) Holmes gen. et comb. nov. A. AMF68449, lectotype; B. AMF120945; C. AMF120946; D. AMF120949; E. AMF120948. Scale bar = 1 cm.

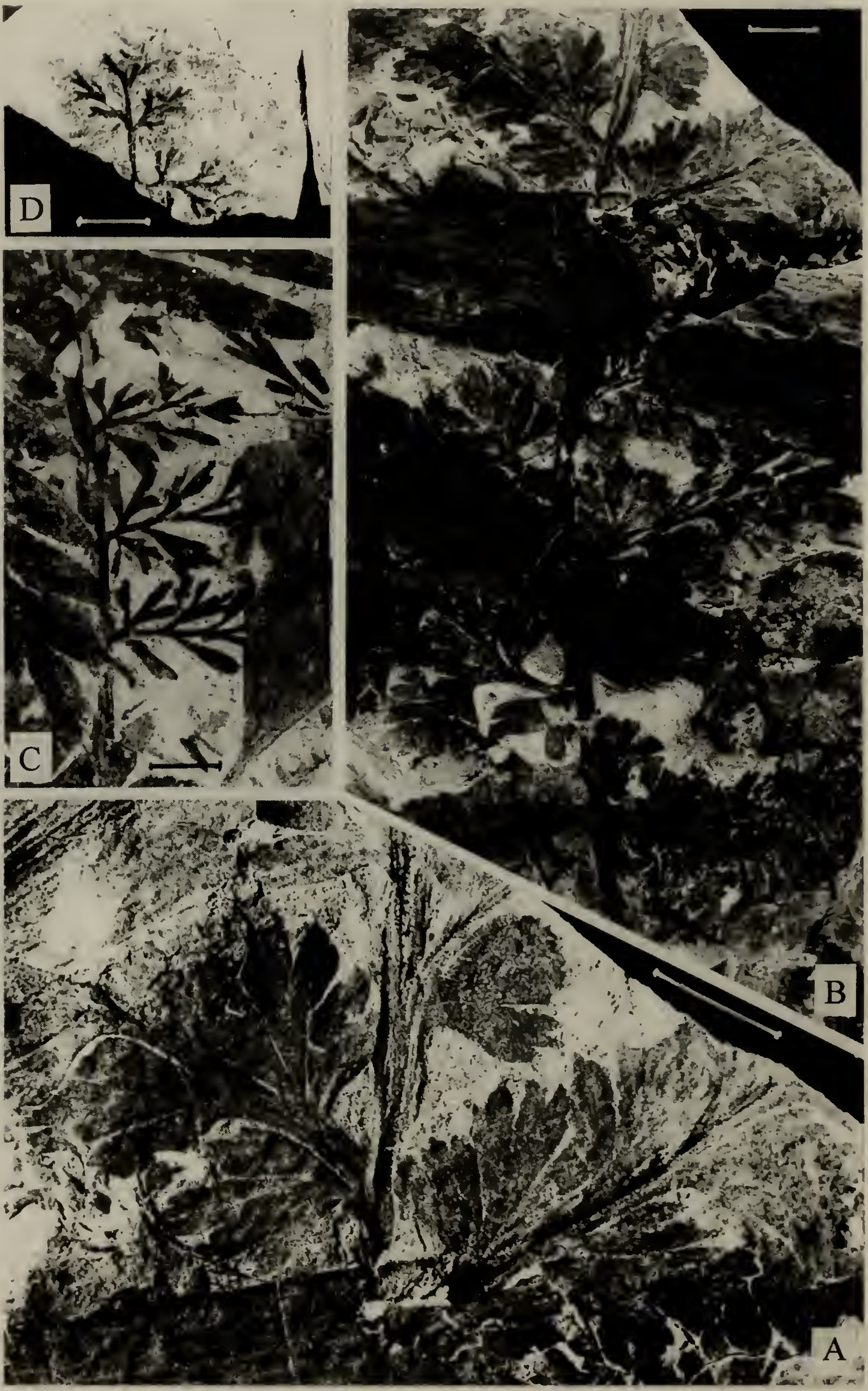

Figure 18. A, B. *Nymboidiantum multilobatum* Holmes gen. et sp. nov. A, B, AMF113558, holotype; B. X2 C, D. *Nymboidiantum glossophyllum* (Tenison-Woods) Holmes gen. et comb. nov.; C. AMF120947; D. AMF12950. Scale bar = 1 cm.

Figure 19. A, B. *Nymboidiantum elegans* Holmes gen. et sp. nov. A. AMF113504, holotype; B. AMF113506 C, D. *Nymboidiantum fractiflexus* Holmes gen. et sp. nov. C. AMF113502, holotype; D. AMF113502, X3. Scale bar = 1 cm.

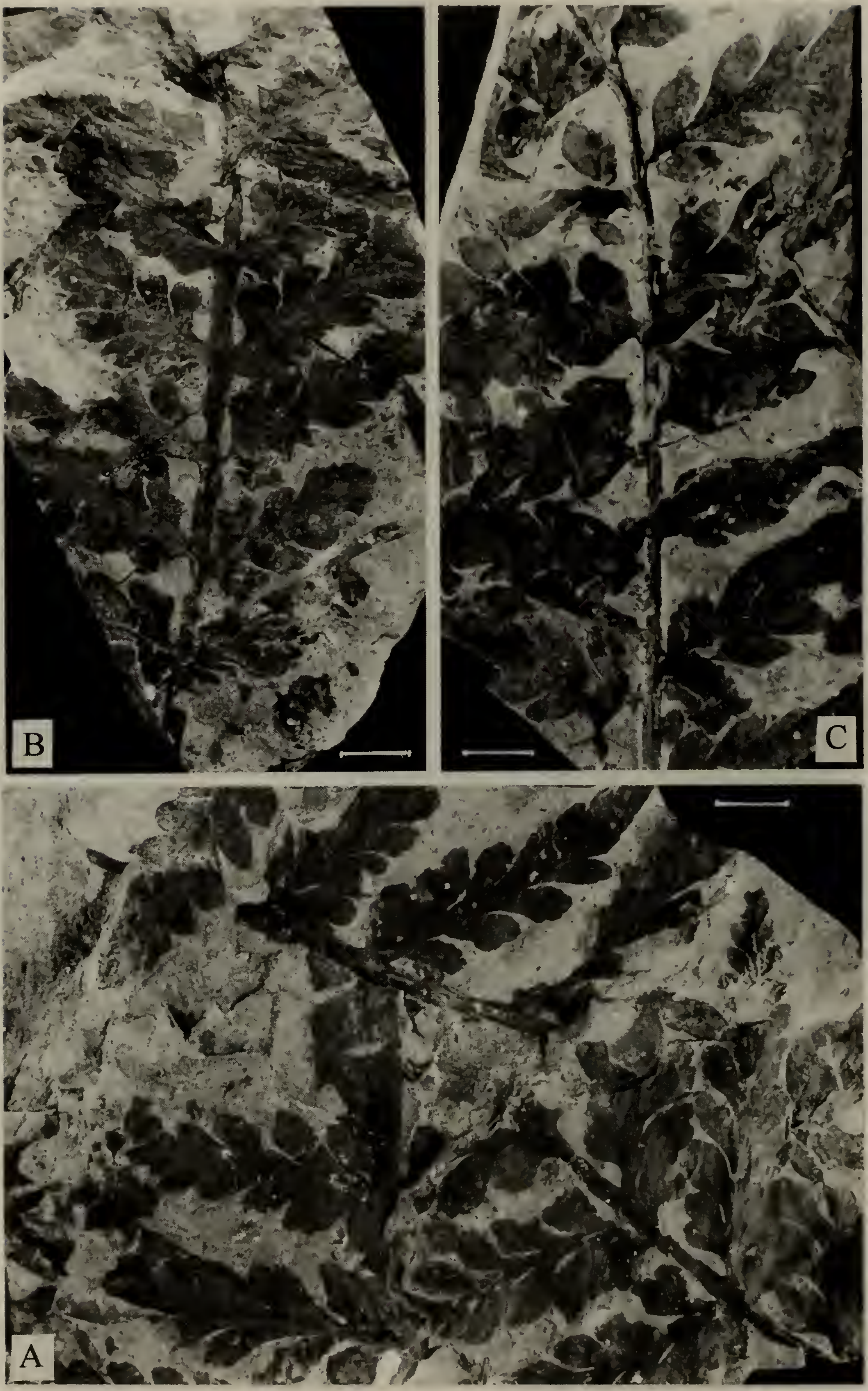

Figure 20. A–C. *Nymboidiantum robustum* Holmes gen. et sp. nov. A. AMF113495; B. AMF113497; C. AMF113496, holotype. Scale bar = 1 cm.

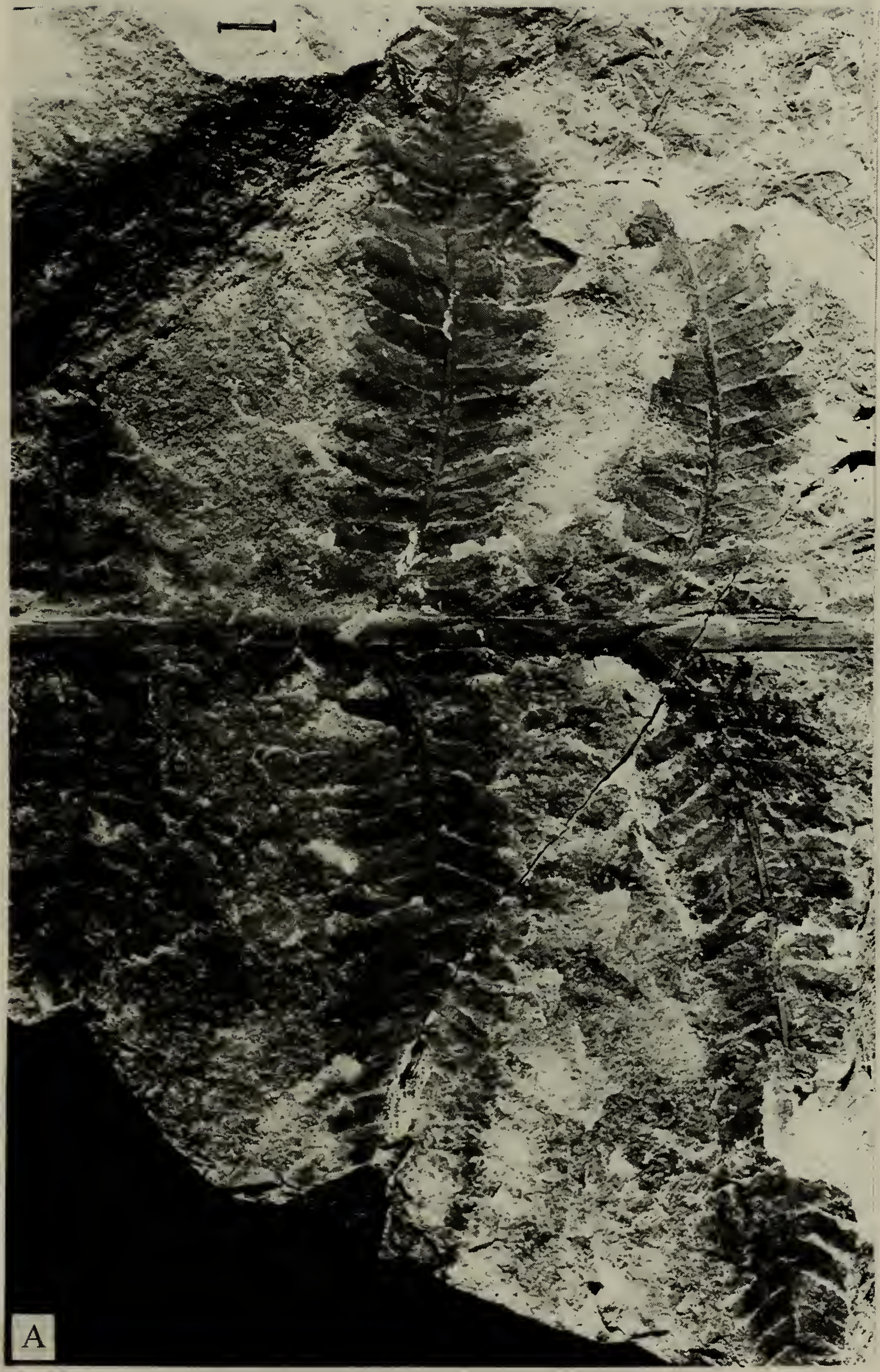

Figure 21. A. *Nymbophlebis polymorpha* Holmes gen. et sp. nov. AMF121010, X0.75. Scale bar = 1 cm.

Figure 22. A–C. *Nymbophlebis polymorpha* Holmes gen. et sp. nov. A. AMF120996; B. AMF121000, X2; C. AMF121001, X2. Scale bar = 1 cm.

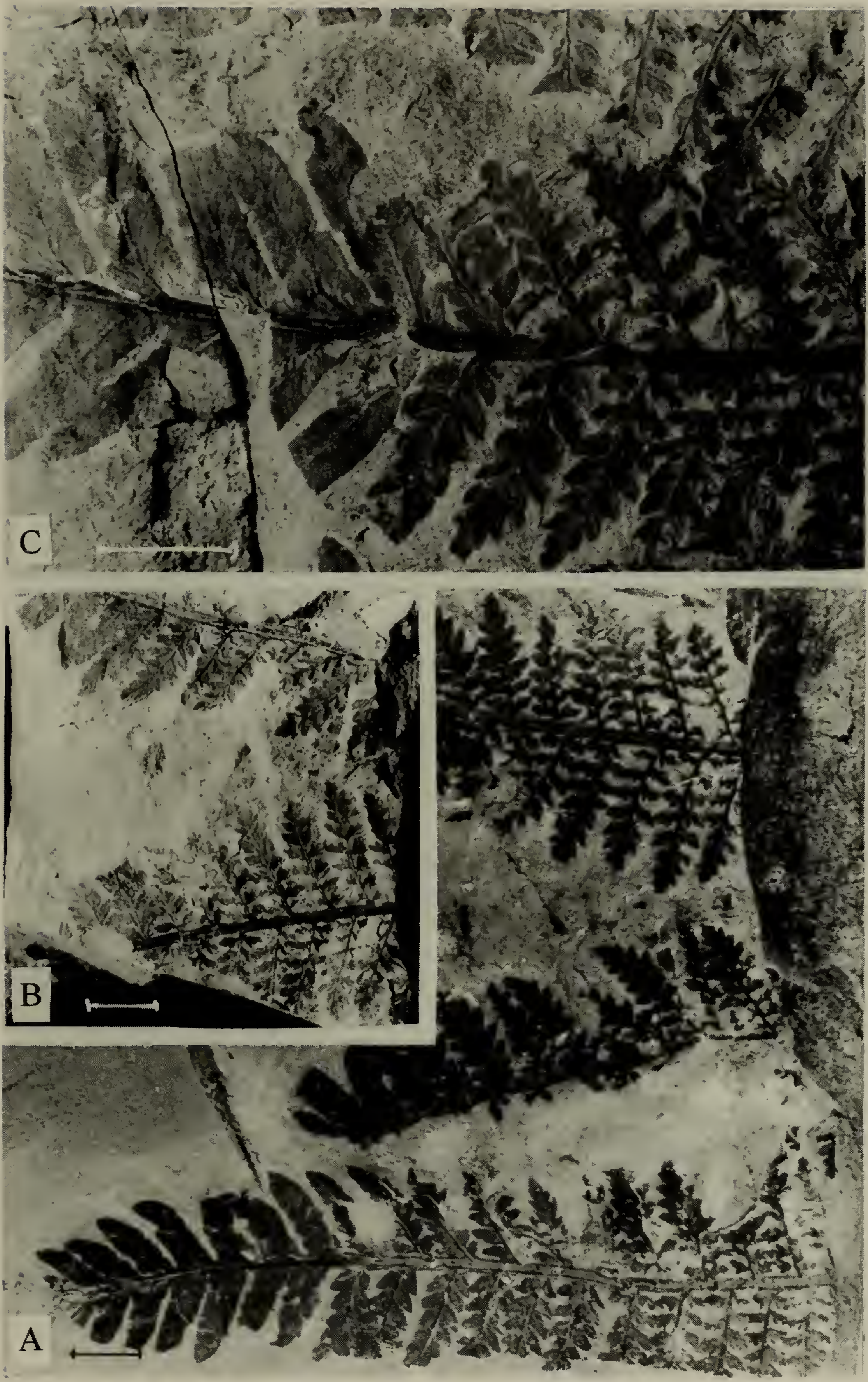

Figure 23. A–C. *Nymbophlebis polymorpha* Holmes gen. et sp. nov. A. AMF120998; B. AMF120999; C. AMF120997, X2. Scale bar = 1 cm.

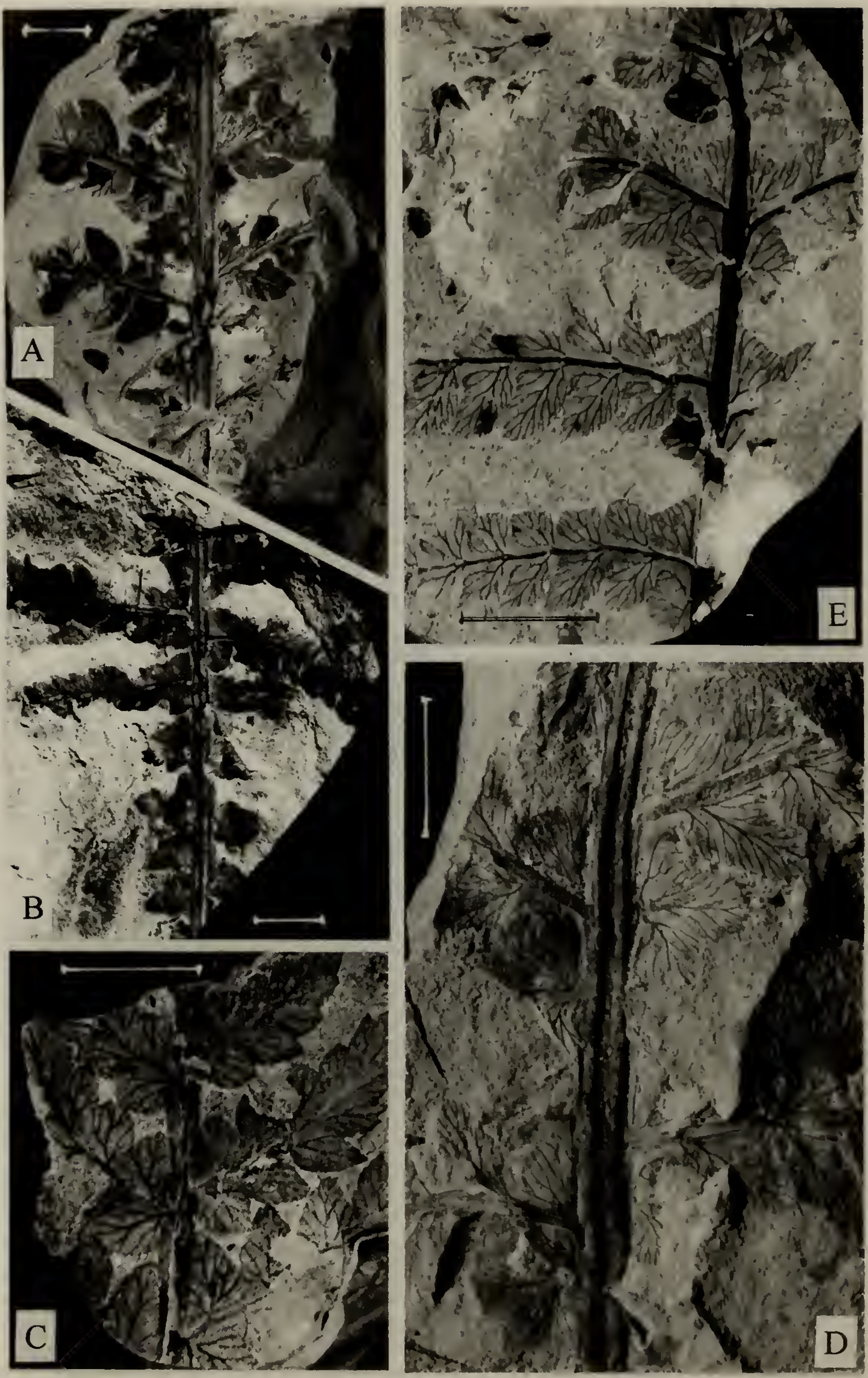

Figure 24. A–E. *Nymbopteron dejerseyi* (Retallack) Holmes gen. et comb. nov. A. AMF113549; B. AMF113548; C. AMF113549, X2; D. AMF113545, X2; E. AMF113547, X2. Scale bar = 1 cm.

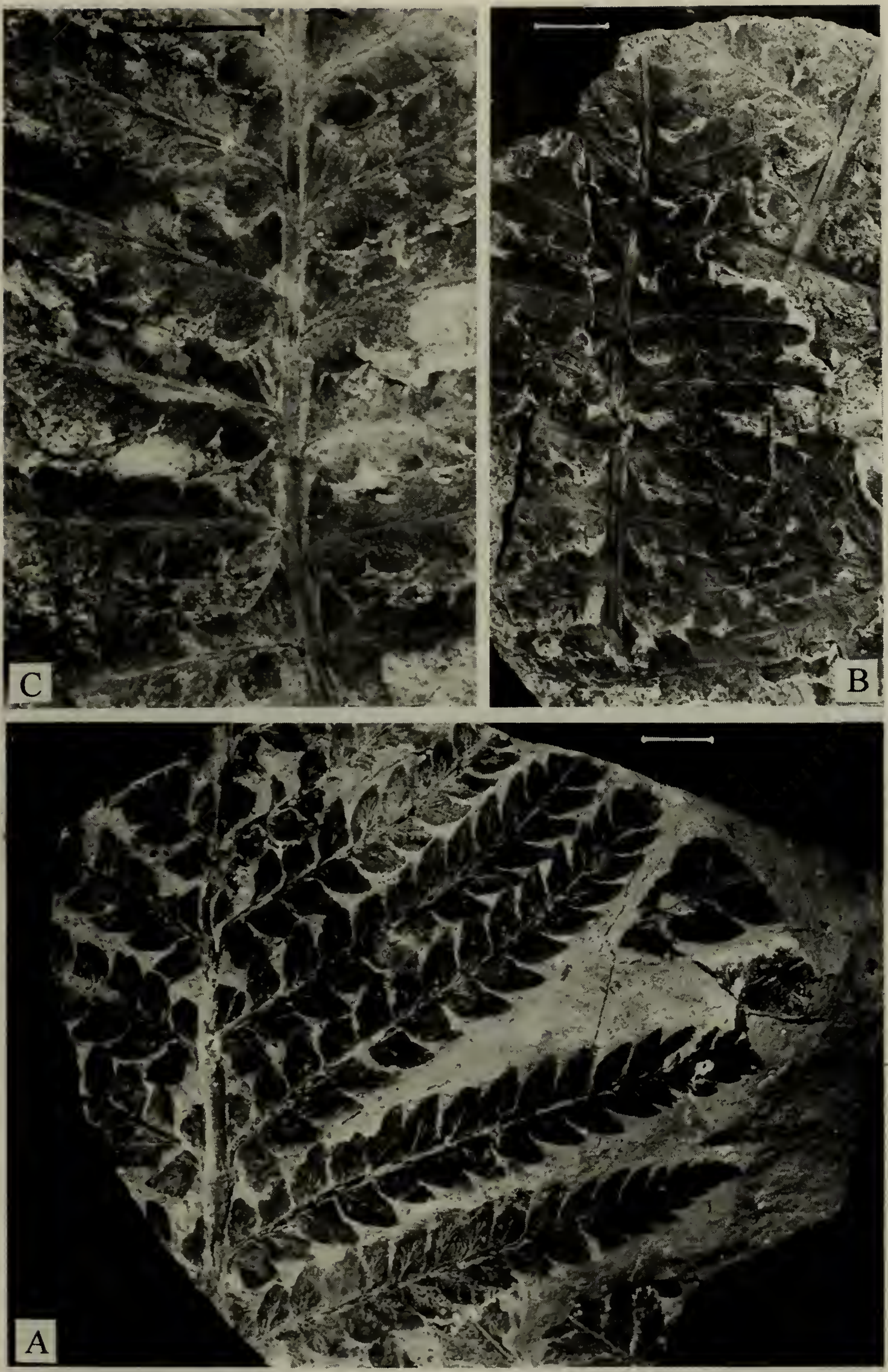

Figure 25. A. *Nymbopteron dejerseyi* (Retallack) Holmes gen. et comb. nov. AMF121158, holotype. B, C. *Nymbopteron foleyi* Holmes gen. et sp. nov. B. AMF113540; C. AMF113522, X2. Scale bar = 1 cm

Figure 26. A. *Nymbopteron foleyi* Holmes gen. et sp. nov. AMF113538, holotype. Scale bar = 1 cm.

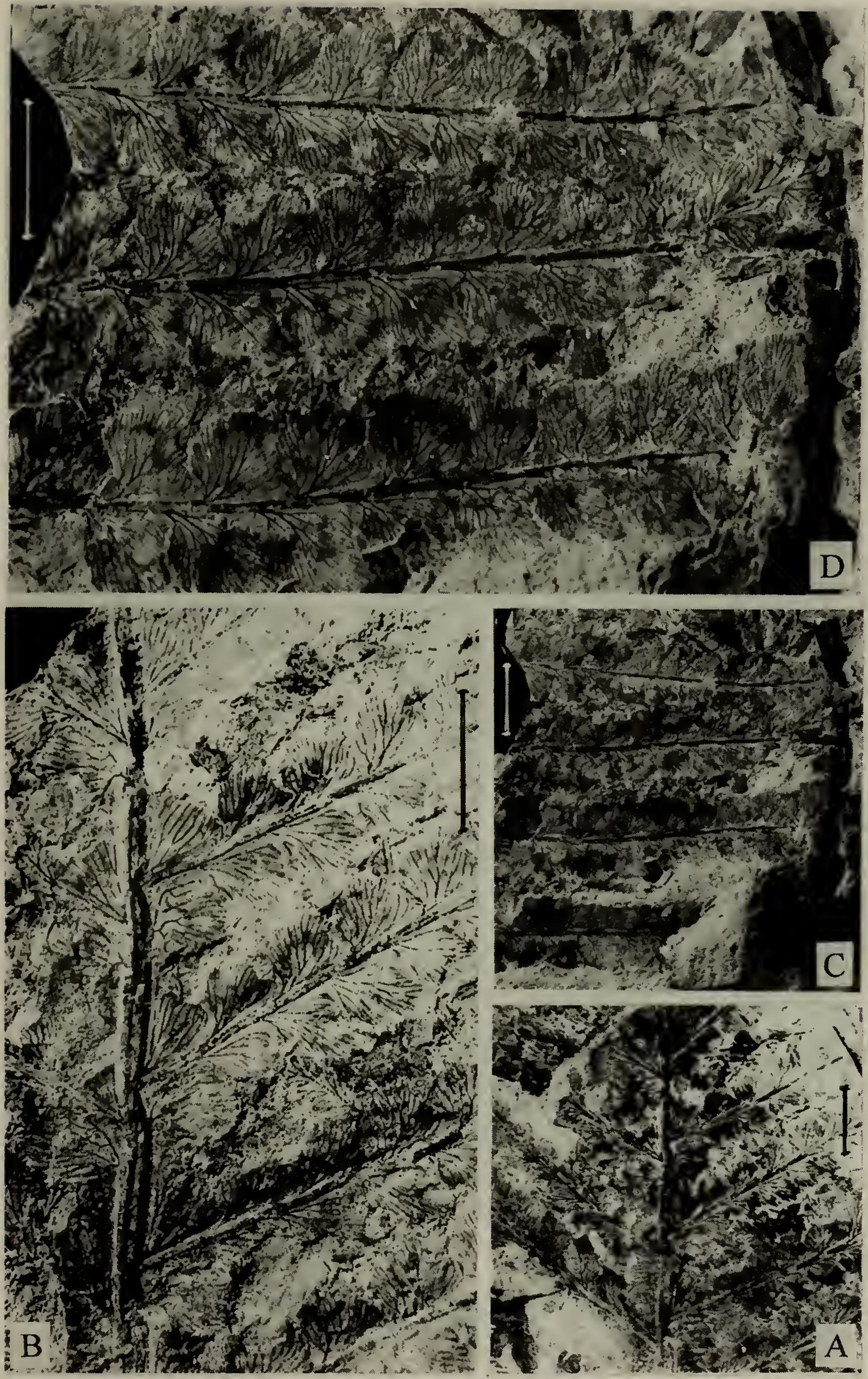

Figure 27. A–D. *Nymbopteron rhomboidale* Holmes gen. et sp. nov. All AMF113556; A. holotype, X1; B. X2; C. X1; D. X2. Scale bar = 1 cm.

Figure 28. A. *Nymbopteron uncinatum* Holmes gen. et sp. nov. AMF120968, holotype. Scale bar = 1 cm.

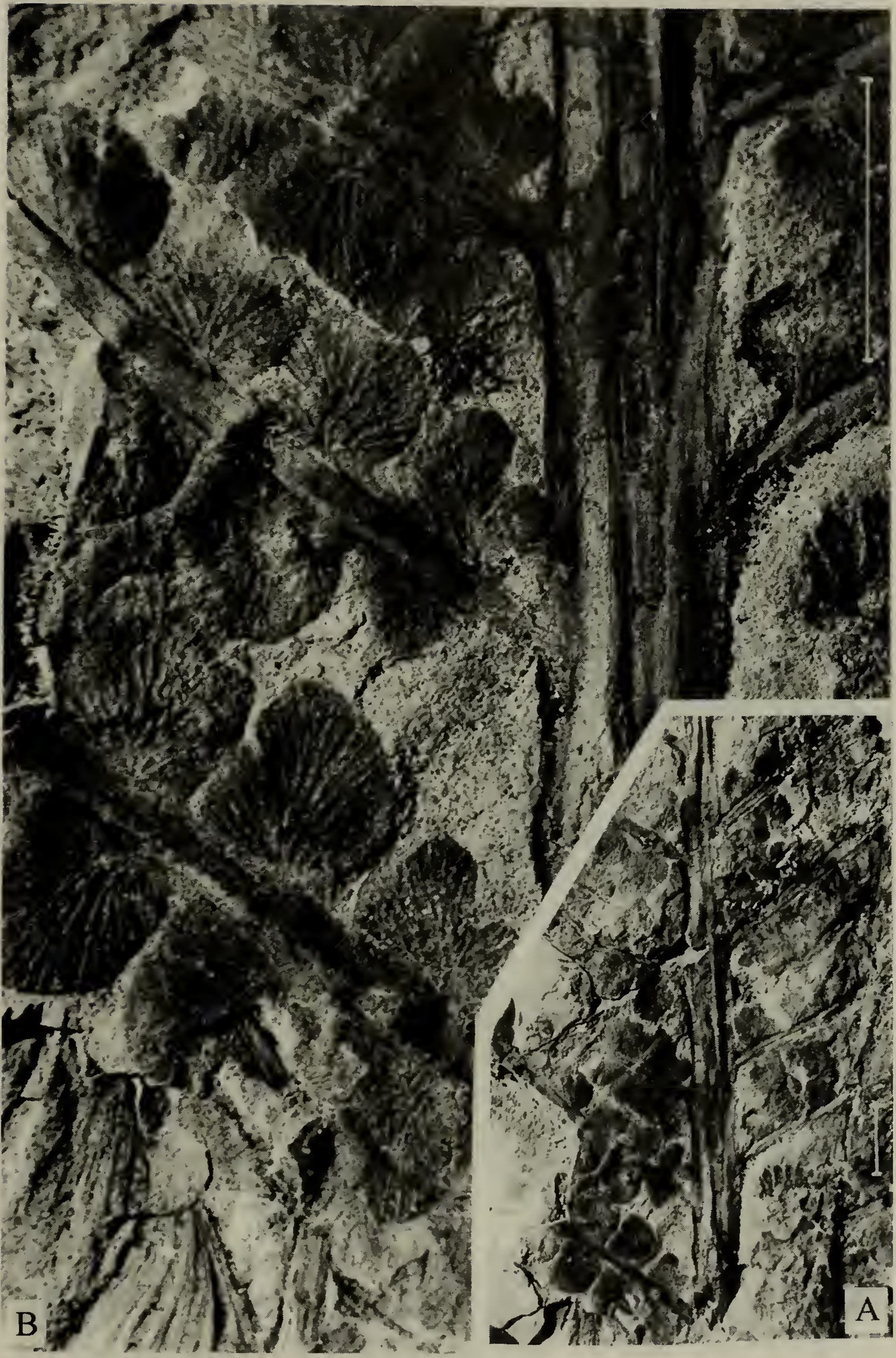

Figure 29. A, B. *Nymborhipteris radiata* Holmes gen. et sp. nov. A. AMF113489, holotype; B. AMF113489, X4. Scale bar = 1 cm.

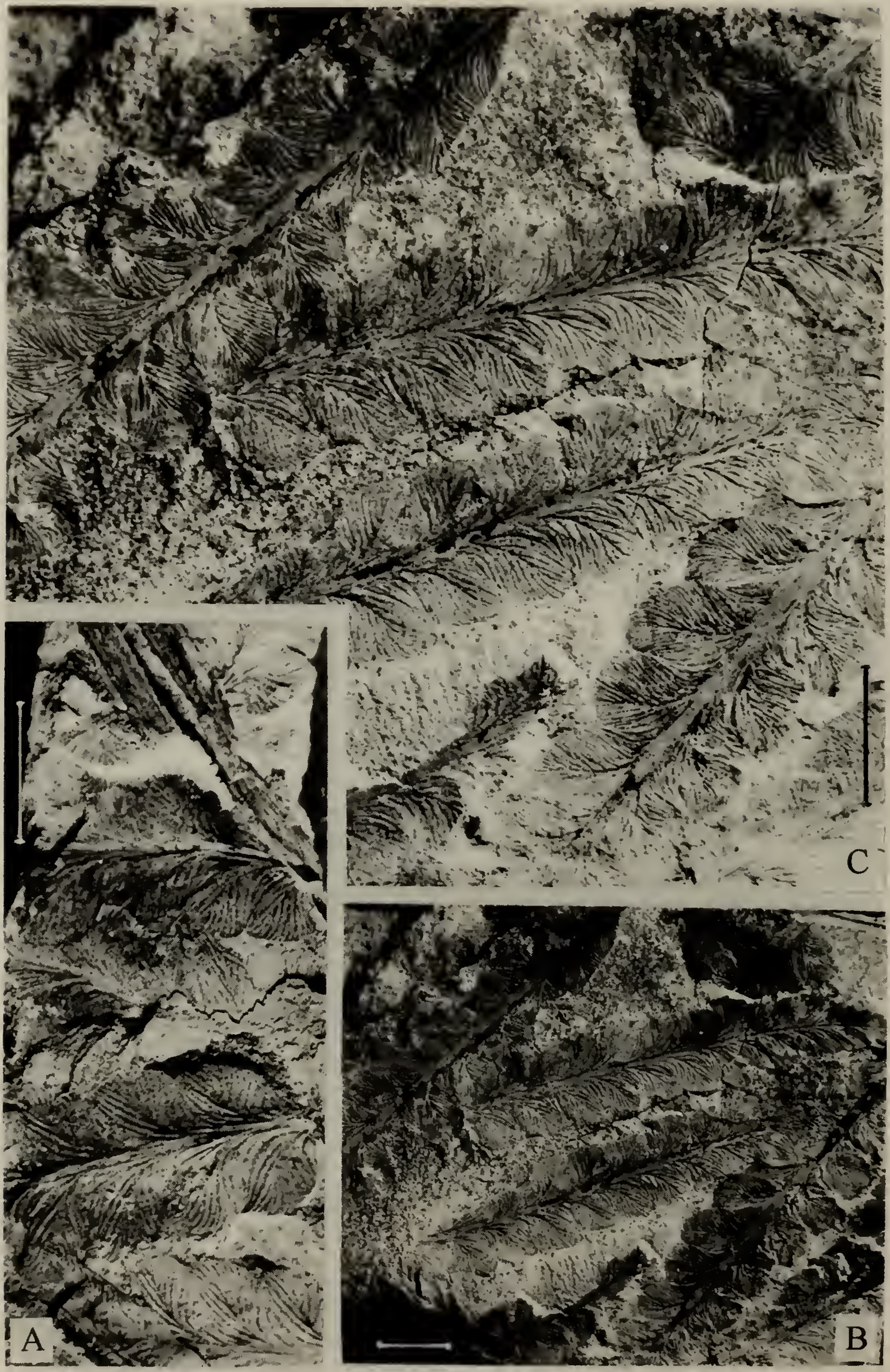

Figure 30. A–C. *Ptilotonymba curvinervia* Holmes gen. et sp. nov. A. AMF113480, holotype, X2; B. AMF113479; C. AMF113479, X2. Scale bar = 1 cm.

Figure 31. A. *Ptilotonymba curvinervia* Holmes gen. et sp. nov. AMF113483. Scale bar = 1 cm.

Figure 32. A–D. *Sphenopteris speciosa* Holmes sp. nov. A. AMF113520, holotype; B. AMF113520, X2; C. UNEF13557; D. AMF113521. Scale bar = 1 cm.

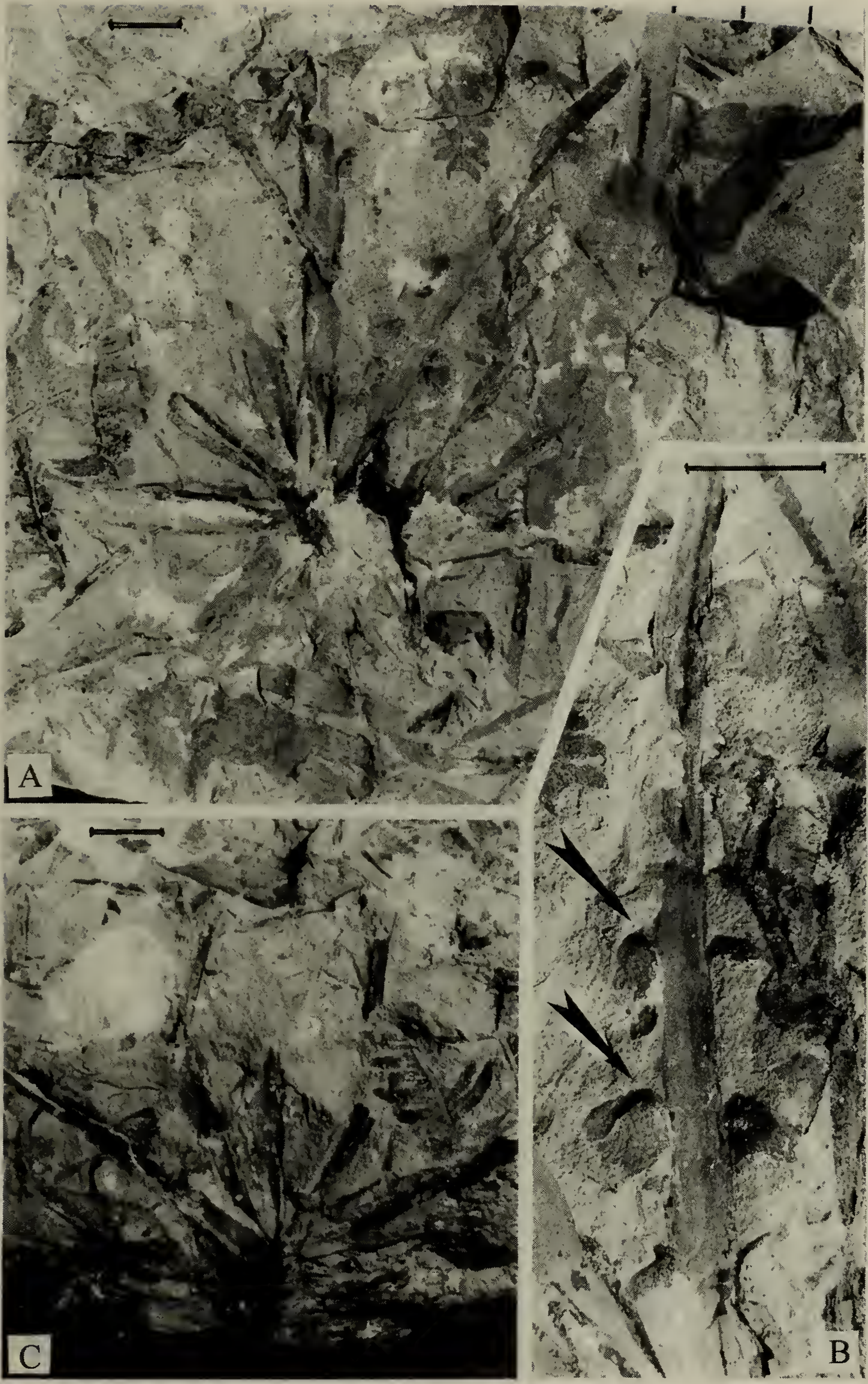

Figure 33. A–C. Fern bases. A. AMF113498; B. X2, pinnae arrowed; C. AMF113501, longitudinal section. Scale bar = 1 cm.

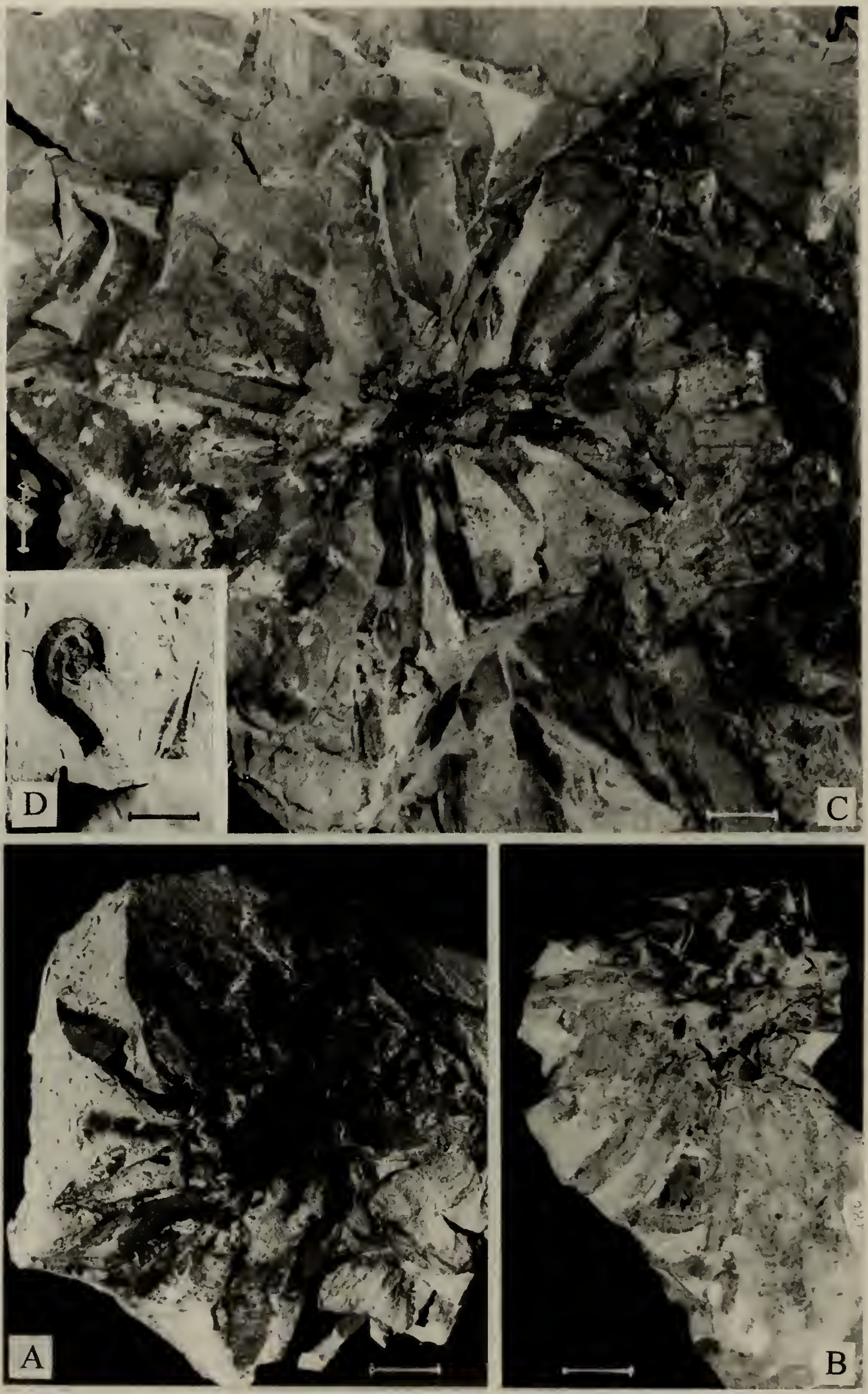

Figure 34. A–C. Fern bases. A. AMF113499; B. AMF113503; C. AMF113500; D. Circinate frond. AMF113519. Scale bar = 1 cm.

First Australian Records of Three Species and Two Genera of Aquatic Oligochaetes (Clitellata: Annelida)

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Pinder, A.M. (2003). First Australian records of three species and two genera of aquatic Oligochaetes (Clitellata: Annelida). *Proceedings of the Linnean Society of New South Wales* **124**, 109-114.

Recent collections of aquatic oligochaetes in New South Wales and South Australia included three species not previously reported from Australia. These are *Nais barbata* Müller 1774 and *Haemonais waldvogeli* Bretscher, 1900 (Naididae) and *Monopylephorus limosus* (Hatai, 1898) (Tubificidae). The last two of these represent the first Australian records of their genera. Brief descriptions and locality details of Australian specimens are provided.

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KEYWORDS: Naididae, Annelida, *Monopylephorus limosus*, *Haemonais waldvogeli*, *Nais barbata*, Australia.

INTRODUCTION

Although knowledge of the Australian aquatic oligochaete fauna has improved significantly in recent years, there are still large areas of the country (including much of south-eastern Australia) for which few records exist. This paper presents the first Australian records of three species from New South Wales and South Australia. These are the tubificid *Monopylephorus limosus* (Hatai, 1898) and the naidids *Haemonais waldvogeli* Bretscher, 1900 and *Nais barbata* Müller, 1774. Neither the genus *Monopylephorus*, which is represented by several species in the northern hemisphere, nor the monospecific *Haemonais* have been reported from Australia until now. The occurrence of *Nais barbata* brings the number of species of this genus in Australia to six. Almost all of the naidids that occur in Australia are cosmopolitan or at least circumtropical (Pinder 2001) and cosmopolitan species constitute about a third of the Australian tubificid fauna (Pinder and Brinkhurst 2000). The species reported below add to this non-endemic component of these families in Australia.

MATERIALS AND METHODS

Serially sectioned specimens were cut at 6 µm, stained with haematoxylin and eosin and mounted in DePeX. Dissected specimens were stained in Grenacher's Borax Carmine and mounted in Permount. Body measurements are of preserved and slide mounted specimens. Specimens are held by the author (AP colln), returned to the New South Wales Department of Land and Water Conservation (DLWC) in Sydney or the Australian Water Quality Centre (AWQC), Salisbury, South Australia or deposited with the Australian Museum in Sydney (AMS). Collection localities are in New South Wales (NSW) or South Australia (SA).

DESCRIPTIONS AND RECORDS

Tubificidae

Monopylephorus limosus (Hatai)

(Figs 1a, 2)

Synonymy

Vermiculus limosus Hatai, 1898, 103-111, Figs 1-5.

Rhizodrilus limosus (Hatai): Michaelsen, 1900, 41; Yamaguchi, 1953, 297.

Monopylephorus limosus (Hatai): Nomura, 1915, 1, Figs 1-30; Brinkhurst, 1971, 558, Fig. 8.34H.

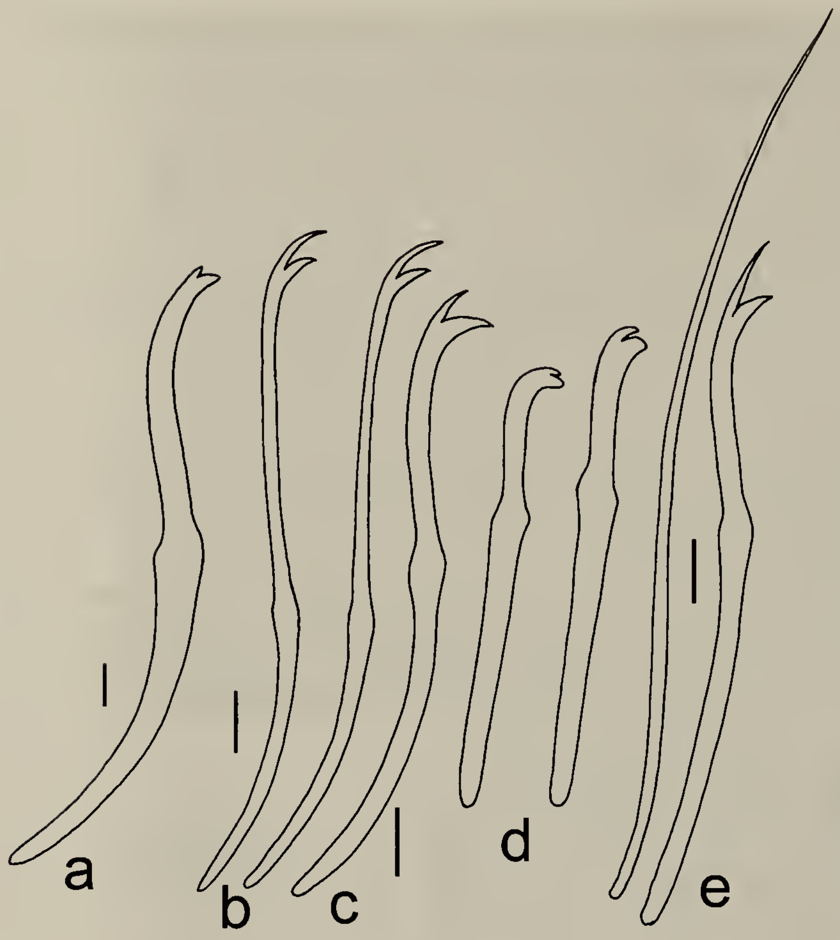

Figure 1. Chaetae of *Monopylephorus limosus* and *Haemonais waldvogeli*. a, bifid chaeta of *M. limosus*. b-f, *H. waldvogeli*: b, two anterior ventral chaetae; c, posterior ventral chaeta; d. penial chaetae; e. a pair of dorsal chaetae (one hair and one bifid chaeta). Scales 10 µm.

Material examined.

Two serially sectioned (AMS W28529 and W28530), 4 dissected (W28528 and AP collection), sludge in pipe from sewage treatment plant to abandoned ocean outfall between North Head (33°48'S 151°18'E) and Malabar (33°57'S 151°15'E) sewage treatment plants, NSW, 1 May 1995. Collection by staff of Sydney Water.

Description of preserved Australian material.

Worms off-white when preserved. Length of body 14 – 26 mm, up to 125 segments. Prostomium rounded conical, anal end bluntly tapered. Coelomocytes abundant throughout body, circular (most 8 – 10 µm) to elongate oval (up to 5 x 15 µm) with large nucleus. Ventral and dorsal chaetae similar in size (125 - 165 µm) and form (all crotchets, hairs absent), starting on II, 4 - 5/bundle in pre-clitellar segments, mostly 3/bundle after clitellum and 2 - 3/bundle in posterior-most part of body. Chaetae of II and rarely those of other segments simple-pointed, most chaetae bifid with rudimentary upper tooth (Fig. 1a). Chaetae present but not modified on X, absent on XI.

Clitellum indistinct due to pale nature of body, but well developed on entire circumference of X and XI, starting after the spermathecal pores ventrally. Male and spermathecal ducts (Fig. 2a, b) paired but terminating in unpaired spermathecal and male bursae. Testes antero-ventral on IX. Ovaries antero-ventral on X. Male funnels ventro-lateral on 10/11, asymmetrical, usually folded, feeding long ciliated vasa deferentia. Vasa deferentia with 3 parts: a short naked section entally, a much longer and broader (up to 350 µm long and 100 µm wide) middle section covered with diffuse prostate tissue and then a narrow ectal portion without prostates. Vasa deferentia enter protrusible pseudopenes apically. Pseudopenes broad medially, narrower at either end, with thick muscle layers (longitudinal over circular), thin lining tissue and with a broad lumen with cilia on ental two-fifths. Pseudopenes terminating on papillae on lateral walls of voluminous left or right lobes of common median bursa. Bursa muscular, with thin uneven lining tissue, opening to the exterior as a small medial pore on XI half-way between 10/11 and 11/12 beneath ventral nerve cord. Each lobe of bursa with a blind sac entad of the pseudopenis/bursa union. Spermathecal ducts each connected apically to bi-lobed common median bursa. Latter with lobed lining tissue and thick muscle layer leading to a single pore behind 9/10. Spermathecal ducts consisting of an ectal section with narrow lining and thick muscle tissue, a middle section, with thinner muscle tissue and broad, deeply lobed lining tissue and an ental section which has a broad lumen (sperm filled in mated specimens) and thin lining and muscle layers.

Remarks

The terminology used for the male genitalia is based on the revelation (Gustavsson and Erséus 1999) that the ciliated ducts partially covered by prostate tissue are modified vasa deferentia in *Monopylephorus*, rather than atria as previously assumed. The Australian specimens mostly match the descriptions of *M. limosus* provided by Nomura (1915) and Erséus and Paoletti

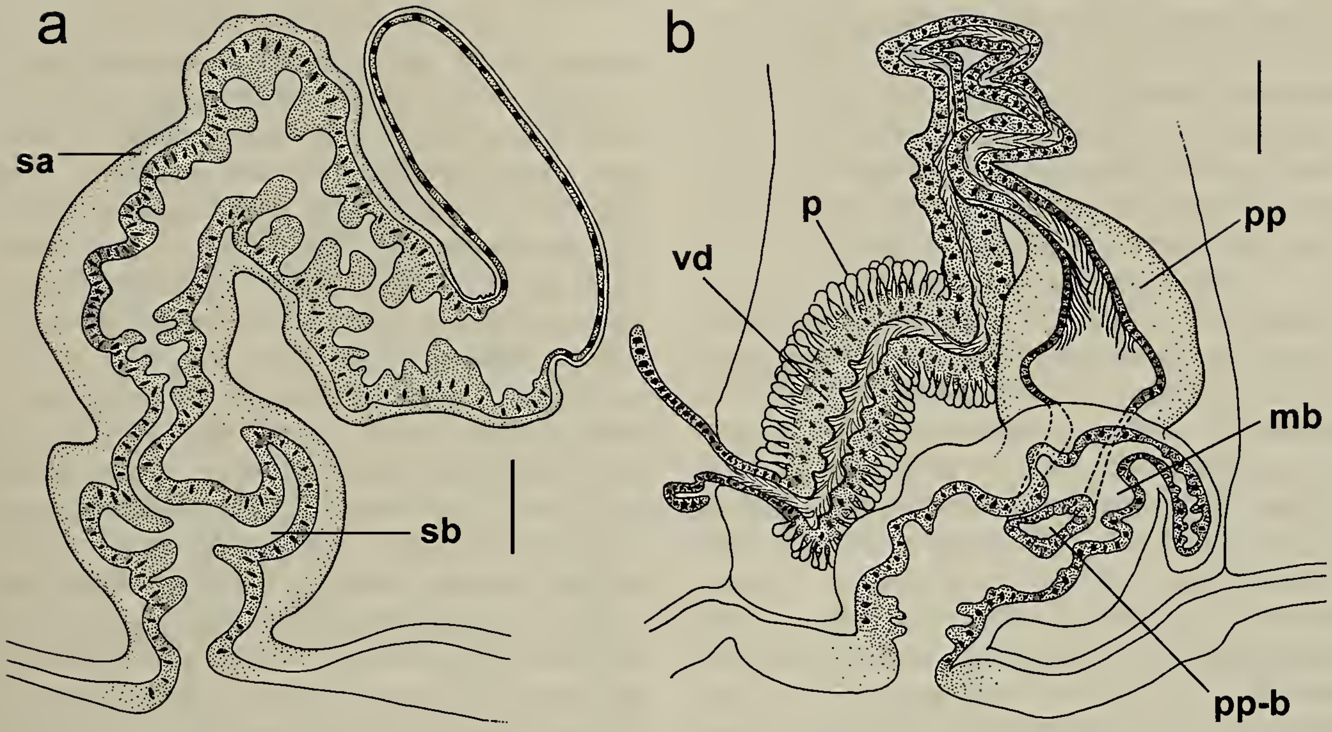

Figure 2. Genital anatomy of *Monopylephorus limosus*. a, spermathecal ducts entering corresponding lobe of median bursa. b, male ducts with pseudopenis shown passing behind (dotted lines) the corresponding lobe of median bursa and entering it laterally. Abbreviations: mb, male bursa; p, prostate; pp, pseudopenis; pp-b, union of pseudopenis with male bursa; sa, spermathecal ampulla; sb, spermathecal bursa; vd, vas deferens. Scale 100 µm.

(1986), which expand on the account of the original Japanese specimens by Hatai (1898). The new specimens differ from previous descriptions in that they have pseudopenes which are ciliated on their ental two-fifths. However, for the present, the Australian specimens are seen as being variants of *M. limosus*. Other *Monopylephorus* species, which are mostly marine, have less complex male bursae (where present at all), and some have eversible rather than protrusible pseudopenes (Baker and Brinkhurst 1981; Brinkhurst and Marchese 1987; Rodriguez 1999). *Monopylephorus limosus* is the only oligochaete known from Australian inland waters that has almost all chaetae bifid with minute upper teeth and with unpaired spermathecal and male pores.

The tolerance of *M. limosus* to a range of salinities and to organic pollution (Chen 1940; Nomura 1915) as well as its apparent introduction to Europe from Asia, suggests this is an opportunistic species (Erséus and Paoletti 1986). It is not clear whether the Australian records are part of a natural distribution, or whether they represent an introduction. In either case, *M. limosus* can be expected to occur at other localities in Australia, at least near coastal population centres but possibly further inland where suitable conditions occur, as in China (Wang Hongzhu pers. comm.). *Embolocephalus yamaguchii* (Brinkhurst 1971), known from Japan and Australia (Pinder and McEvoy 2002), is the only other non-marine tubificid to have an Australasian distribution. Other freshwater species are either cosmopolitan or are known only from Australia (Pinder and Brinkhurst 2000).

Naididae

Haemonais waldvogeli Bretscher

(Figs 1b-e)

Synonymy

Haemonais waldvogeli Brestcher, 1900, 16, Pl. I, Figs 11-14.

Haemonais waldvogeli Brestcher: Sperber, 1948, 154, Fig. 18C; Brinkhurst, 1971, 356, Fig. 7.11M-P.

Haemonais laurentii Stephenson, 1915, 769, Figs 1-5, Pl. LXXIX.

Material examined

Material identified by A. Pinder (on which the following description is based): 1 immature in alcohol (in 2 parts) (AMS W28531), Namoi River at Duncans Junction, 30°18'16"S 149°05'58"E, 30 Mar 2000; 2 immature in alcohol and 2 mature mounted whole on slides (AMS W28532, W28533 and W28534), Macquarie Marsh (North) Third Crossing

Lagoon, 30°44’33"S 147°34’27"E, 12 Apr 2000; Gingham Channel (Gwydir catchment) at Crinolyn, 29°12’37"S 149°08’49"E, 10 Jan 2001; Murrumbidgee River at McKennas Lagoon, 34°25’53"S 145°30’32"E, 8 Feb 2001; 1 immature, Murrumbidgee River at Ganmain Station 1 Storage, 35°00’40"S 147°01’58"E, 22 Nov 2000; Murrumbidgee River at Iris Park Swamp, 35°05’16"S 147°13’30"E, 20 Nov 2000.

Additional material identified by WSL Consultants: Gingham Channel at Rookery, 29°14’51"S 149°19’52"E, 11 Jan 2001; Murrumbidgee River at Coldene Lagoon Storage Gauge, 35°04’26"S 147°45’32"E, 18 Dec 2000;Murrumbidgee River at Ganmain Station 1 Storage, 35°00’40"S 147°01’58"E, 17 Jan 2001; Murrumbidgee River at McKennas Lagoon, 34°25’53"S 145°30’32"E, 29 Nov 2000; Murrumbidgee River at Sunshower Lagoon, 34°36’28"S 146°01’06"E, 27 Nov 2000; Murrumbidgee River at Yarradda Lagoon, 34°35’10"S 145°49’21"E, 28 Nov 2000 and 23 Jan 2001. Collection by Chris Burton, Sean Grimes, Lorraine Hardwick, David Hohnberg, James Maguire, Warwick Mawhinney and Sue Powell (DLWC).

Description of Australian Material

Most specimens incomplete, 2 complete specimens 6.5 mm long, width at VI up to 0.55 mm, number of segments up to 55. Gut containing a variety of diatoms and other algae. Dorsal chaetae (Fig. 1e) starting in XVI to XXI, each bundle with 1 - 2 short (130-150 μm long by 2.5 μm wide), curved hairs with a blunt tip and an equal number of crotchet chaetae. The latter are 100 – 120 μm long by 4.5 – 5 μm wide at the distal (1/3 - 2/5 from the distal end) nodulus with long slightly curved teeth, the upper tooth 1.5 – 2 times longer than the lower. Ventral chaetae all bifid (Fig. 1b-d), normally 3 per bundle (rarely 2), those of first 15 - 19 segments longer, thinner and straighter (105-120 μm long by 3-3.5 μm wide at the nodulus) than those of posterior segments, and with upper teeth slightly longer than the lower. Posterior ventral chaetae 85 – 100 μm long by 4-4.5 μm wide at the nodulus and with upper tooth shorter than the lower. Ventral chaetae with nodulus slightly ental in first few segments, thereafter becoming medial and then slightly ectal. Ventral chaetae of VI (penial chaetae) (Fig. 1d) possibly shorter (laying at awkward angle for measurement) but definitely broader (5-6 μm at the nodulus) than adjacent somatic chaetae with more curved tips and shorter teeth than other ventral chaetae.

Mature specimens too flattened under coverslips to make out much detail of the genitalia, but spermathecae in V and atria in VI, both small and globose with short ducts.

Remarks

The combination of similarly sized dorsal and ventral crotchet chaetae and the position and form of the dorsal chaetae are unique to *Haemonais* and the Australian specimens conform to descriptions of the type and only species, *Haemonais waldvogeli*, given in the literature (e.g. Sperber 1948; Harman and Harrel 1975 and Ohtaka and Nishino 1999). Dorsal chaetae are known to be present in newly developed anterior segments (Sperber 1948) but are gradually shed, so may be found more anteriorly than XVI in some specimens. Outside of Australia, *H. waldvogeli* is widespread, with reports from Europe, Africa, Asia and North and South America. A variant of this species, not recorded from Australia but known from India and North America, lacks teeth on the dorsal crotchet chaetae. *Haemonais waldvogeli* is known from a wide variety of lentic and lotic habitats overseas, particularly where submerged plants are present. Australian specimens have been collected from a variety of wetland habitats, including snags, detritus and from samples taken amongst a wide variety of aquatic plants, including *Azolla*, water ribbon, water hyacinth, *Typha*, water couch and lignum. This species is currently known only from the Murray-Darling catchment of New South Wales, but is probably more widespread, at least in south-eastern Australia.

Nais barbata Müller

(Figs 3a-d)

Synonymy

Nais barbata Müller, 1774, 23.

Nais barbata Müller: Sperber, 1948, 116, Pl. VIII, Fig. 4; Brinkhurst, 1971, 338, Fig. 7.7F-I.

(?) *Opsonais obtusa* Gervais, 1838, 17.

Nais obtusa (Gervais): Michaelsen, 1900, 25.

Material examined

1 immature on slide (AMS W28535), Nattai River at The Crags, NSW, 34°23’21.7”S 150°25’31.6”E, 10 Dec 2001; 2 immature on slide (AMS W28536), Wingecarribee River at Berrima, NSW, 34°29’26.3”S 150°19’57.7”E, 10 Dec 2001; 1 immature in alcohol, Mongarlowe River at Monga Bridge, NSW, 35°32’34.6”S 149°55’47.5”E, 5 Dec 2001; 1 immature in alcohol, Mongarlowe River at Charleyong Bridge, NSW, 35°15’02.8”S 149°55’13.5”E, 5 Dec 2001. 2 immature in alcohol (AP colln), 2 immature in alcohol (AMS W28537) and several returned to AWQC, Murray River at Craignook Landing, SA, 34°53’S 139°39’E, 28 May 2002; 3 immature in alcohol (AMS W28538) and several returned to AWQC, Murray River downstream of Lock

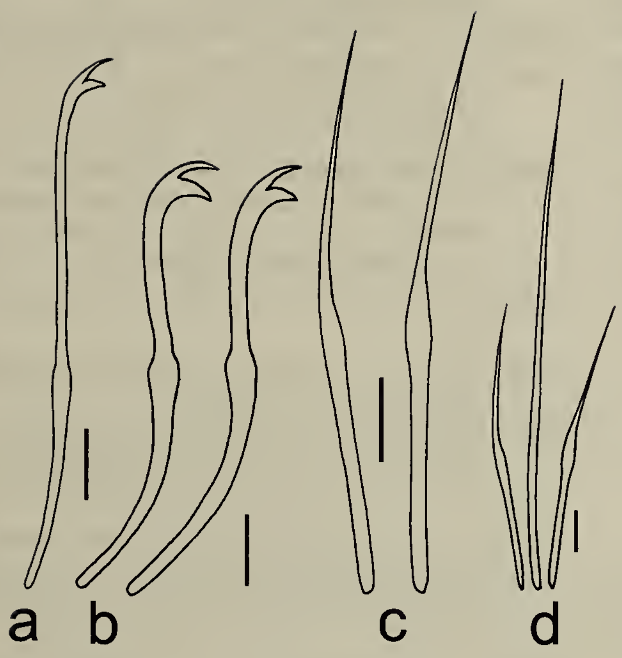

Figure 3. Chaetae of *Nais barbata*. a, ventral chaeta of II; b, ventral chaetae of posterior segment; c, dorsal needle chaetae; d, dorsal needle and hair chaetae. Scales 10 µm.

3, 5km upstream of Overland Corner, 34°11'S 140°21'E, 11 Jun 2002. Collection by Kim Clarke (Ecowise Environmental, Melbourne) or by Vlad Tsymbal, Chris Madden and D. Hicks (AWQC).

Description of Australian Material

Length 1.0 - 2.9 mm long and width at VI 0.15 – 0.2 mm. Gut contents fine detritus and various diatoms. Dorsal chaetae (Fig. 3c, d) from VI, each bundle with 1 - 3 hair chaetae (150 - 200 µm long by 2 µm wide at level of body wall) with an equivalent number of simple-pointed needle chaetae. The latter 58 - 82 um long by 2 µm wide at the slightly distal nodulus, bent slightly at the nodulus, with a parallel sided shaft ental to the nodulus and an ectal end that tapers evenly to a fine point. Ventral chaetae all bifid (Fig. 3a, b), 3 - 4 per bundle, anteriorly with ental nodulus and with upper teeth longer than and slightly thinner than the lower, posteriorly with slightly distal nodulus and teeth about equal in length but the upper slightly thinner. Ventral chaetae of anterior bundles longer and thinner (69 - 78 µm long and 2.5 µm wide at the nodulus) than those of posterior bundles (53 - 74 µm long by 4 µm wide).

Remarks

These specimens match descriptions of *N. barbata* (the type species of *Nais*) provided in the literature (e.g. Sperber 1948). Although these accounts usually state 1-5 hairs and 1-5 crotchet chaetae per dorsal bundle, this refers to ranges for the species and individuals with a maximum of 2 or 3 hairs per bundle and an equivalent number of crotchets (like the Australian specimens) are not uncommon elsewhere (Tarmo Timm, Estonia, pers. comm.). *Nais pseudobtusa* Piguet, 1906 is the only other *Nais* with simple-pointed needles known from Australia (Naidu and Naidu 1980), but in that species the upper teeth of the posterior ventral chaetae are longer than the lower and the nodulus on the needle is located closer to the distal end than in *N. barbata*.

Nais barbata has previously been collected from North America, Europe, the near-east, north-east Asia (Japan and Kamchatka) and northern India (Brinkhurst 1971; Brinkhurst et al. 1990; Liang 1964; Ohtaka and Nishino 1995; Stephenson 1923; Timm 1999). Thus, while other Australian non-endemic naidids are part of more continuous cosmopolitan or circum-tropical distributions, the Australian records of *Nais barbata* are the first for the southern hemisphere and represent more of an outlier. The sites listed above are all from the Murray Darling Basin, ranging from upper tributaries to the main channel of the lower Murray, but the species is likely to be more widespread, at least in the south-east. Specimens from the upper tributaries were collected from fresh, neutral to moderately alkaline waters in riffles and stream edge/backwater samples with sediments dominated by coarse material (gravel to cobble) and often with significant algal growth but no macrophytes. Specimens from the lower Murray were collected from reaches with macrophytes and filamentous algae and fresh moderately alkaline water with high turbidity. Learner et al. (1978) found this species to be most abundant amongst filamentous algae in British streams and noted its abundance in organically polluted European rivers.

ACKNOWLEDGEMENTS

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Behavioural Responses of Two Native Australian Fish Species (*Melanotaenia duboulayi* and *Pseudomugil signifer*) to Introduced Poeciliids (*Gambusia holbrooki* and *Xiphophorus helleri*) in Controlled Conditions

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Experimental treatments to compare behavioural responses included native fish species only, natives plus one exotic species and natives plus both exotic species. The mosquitofish, *Gambusia holbrooki* frequently attacked both native species, but tended to nip *Melanotaenia duboulayi* (especially small individuals) and chase *Pseudomugil signifer.* The frequency of attacks by *G. holbrooki* on *M. duboulayi* rose when all four fish species were present. When food was added, all four species showed a strong increase in aggression, especially in the four-species treatment, where there were significant increases in the frequency of attacks by the swordtail *Xiphophorus helleri* on *M. duboulay* and by *M. duboulayi* on *G. holbrooki*, and of conspecific attacks by *M. duboulayi.* Increased attack frequency was associated with aggregation closer to the water's surface, regardless of the presence of food. The results support the hypothesis that introduced poeciliids can have deleterious competitive effects on native species. However, while juvenile *M. duboulayi* were particularly vulnerable to the secondary effects of fin-nipping, *P. signifer* appeared to be more susceptible to physical displacement and reduced food capture success.

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KEYWORDS: rainbowfish, blue-eye, poeciliids, mosquitofish, aggression, displacement

INTRODUCTION

Prominent among the species of freshwater fish that have been introduced to Australia are the poeciliids *Gambusia holbrooki* (mosquitofish) and *Xiphophorus helleri* (swordtail). *Gambusia holbrooki* is widespread and prolific throughout much of Australia (Arthington 1991). *Xiphophorus helleri* is locally abundant in south-eastern Queensland (Arthington et al. 1983, McKay 1989, McDowall 1996), and there is a strong chance of further spread of this species in tropical and subtropical Australia (Arthington 1991).

Expanding ranges of introduced fishes and widespread declines of native populations have heightened interest in interactions between non-indigenous and resident species. Although the underlying mechanisms have been poorly documented, it is likely that *Gambusia* species exert diverse effects on other fish through interference competition, resource competition and predation (Lloyd 1990). *Gambusia holbrooki* are aggressive towards other species, and damage to fins and scales resulting from nipping by *G. holbrooki* (Lloyd 1987; Howe et al. 1997), coupled with secondary infection, can prove fatal. Such aggressive behaviour by *Gambusia* may cause physiological stress, and in topminnows (*Poeciliopsis occidentalis*) it leads to reduced rates of feeding, fecundity and survival (Schoenherr 1981). *Gambusia holbrooki* may also consume the larvae of *Pseudomugil signifer*, melanotaeniids (rainbowfishes) and other Australian native fish species (Aarn & Ivantsoff 2001).

The ecological impacts of *X. helleri* are poorly understood (Arthington 1991). *Xiphophorus helleri* is primarily herbivorous (Arthington et al. 1983; Arthington 1989) and its diet is likely to overlap more with small omnivores (e.g. *Melanotaenia duboulayi,* Arthington 1992) than insectivorous carnivores (e.g. *P. signifer*). *Xiphophorus helleri* can occur at very high densities in shallow Australian creeks (pers. obs.), and it is possible that this may lead to enhanced interspecific resource competition through the local depletion of invertebrate prey. *Xiphophorus helleri* and *G. holbrooki* often co-occur (Arthington et al. 1983), and the pressure of high numbers of these two species together could subject native species to significant stress (McKay 1978, cited by Arthington 1991; Howe et al. 1997).

Several groups of Australian native fish tend to occur in much lower numbers in the presence of *G. holbrooki* (Arthington et al. 1983; Lloyd 1990), but further work is necessary to disentangle the impacts of introduced species from the effects of habitat modification (Arthington 1991). To this end, there is a clear need for behavioural analyses of interspecific interactions (Lloyd 1990), which are likely to vary with the species involved (Arthington & Lloyd 1989). In particular, because the impact of such interactions tends to be more severe in confined or still water environments (Pen and Potter 1991) and when the native fish are relatively small, it is important to gather comparative information on the effects of density and body size (Howe et al. 1997).

The present study investigated the behavioural responses of *Melanotaenia duboulayi* (Family Melanotaeniidae) and *Pseudomugil signifer* (Family Pseudomugilidae) to *Gambusia holbrooki* and *Xiphophorus helleri* (Family Poeciliidae). Melanotaeniids and pseudomugilids are speciose and abundant in tropical inland waters in the Australia / Papua New Guinea region (McDowall 1996). However, although *M. duboulayi* and *P. signifer* are the commonest representatives of these groups in south-eastern Queensland streams, they have been driven to very low densities in disturbed habitats that support large populations of introduced poeciliids (Arthington et al. 1983). To assess the relative competitive potential of *M. duboulayi* and *P. signifer* in the presence of *G. holbrooki* and/or *X. helleri*, we tested the prediction that the frequency of chasing, fin nipping and displacement of the native species would increase in the presence of the exotics - especially when food was available, when both exotic species were present, and when the body size of the native individuals was relatively small.

MATERIALS AND METHODS

On several occasions in winter (May-September) 1998, fish were collected from a site in Moggill Creek, Brisbane, using bait traps and a seine net. Individuals of these four species were transferred to a laboratory at the University of Queensland, where they were maintained in filtered, single-species aquaria (tank volume 0.05 m^3; c. 50 fish per tank) for 1-3 weeks prior to experimentation. During this time they were fed on a commercial fish flake diet, which was the food used in the experiments. The tanks were filled with aged tapwater and maintained under artificial light (L:D 12:12) at a constant temperature of 23 °C

Experiment 1. : Effects of species composition on behavioural interactions.

Experimental trials were conducted in May and September 1998 in a 90 litre tank (1.5 x 0.5 x 0.35m) maintained under the same conditions as the holding tanks. Grid markings on the tank allowed the vertical height in the water column of the fish to be estimated. The tank was screened by black plastic sheeting to avoid external visual bias and an eye slit was cut into the sheet to allow observations.

In these trials, mixed species groups totalling 20 fish were used and individuals were used only once. The ratio of mean catch rates from repeated sampling at the field site (7:3:6:4 for *M. duboulayi*, *P. signifer*, *G. holbrooki* and *X. helleri* respectively) was used as a guide when determining the relative numbers of fish in the four treatments (Table 1). The treatments were as follows: Treatment 1, native species; Treatment 2, native species plus *X. helleri;* Treatment 3, native species plus *G. holbrooki;* Treatment 4, native species plus both exotic species.

Attempts were also made to equalise sex ratios and to ensure that the fish used in each trial were of a representative range of sizes. Fish biomass was not measured directly but on average the aggregate total length of the fish used (all species combined) was 55.6 cm, 58.4 cm, 50.0 cm and 53.4 cm for Treatments 1 to 4, respectively. The order of trials was randomised with respect to treatment, and ten replicate trials were performed for each treatment.

In each trial, the fish were placed in the tank and left to settle for 15 minutes. This was followed by a period of focal sampling (Martin and Bateson 1990) to record the behaviour of individual fish: a randomly selected fish of each species was watched for two minutes, during which time its depth was recorded every 20 seconds by reference to the markings on the tank. This was followed by a five-minute sampling period in which the occurrence and direction of all agonistic interactions (chases, nips) involving a randomly chosen focal individual were recorded. A single fish flake was then placed on the water's surface in the central, intermediate depth section of the tank and the above procedure, involving both periods of focal sampling, was repeated. Pilot studies indicated

Table 1. Summary of experiments and treatments with mean (±SE) total length (excluding tail sword of *X.helleri*) and numbers of individuals.

				Treatment					
Species / size group	Mean length (cm)	SE	Expt	1	2	3	4	5	6
X. helleri									
Mixed	3.39	0.25	1		6		4		
Small	2.50	0.13	2	8					12
Large	4.50	0.11	2		8			12	
M. duboulayi									
Mixed	3.07	0.15	1	14	9	9	7		
Small	2.61	0.11	2		12		11		
Large	3.89	0.20	2	12		11			
P. signifer	2.10	0.07	1	6	5	4	3		
	2.10	0.07	2					8	8
G. holbrooki	2.00	0.05	1			7	6		
	2.00	0.05	2			9	9		

that a single food source was sufficient to elicit behavioural responses in all fish, while promoting competition. Each trial therefore yielded data on aggressive encounters and the depth of the species concerned, both in the absence and presence of food. Treatment differences in mean chasing frequency, mean nipping frequency and mean depth were examined using analysis of variance and multiple range (Tukey) tests, separate analyses being carried out on the "food absent" and "food present" data. Primary data (numbers of nips and chases) were standardised by dividing the number of attacks received by focal fish per trial by the number of potential aggressors. For interspecific attacks the number of aggressors was n, where n = group size for the attacking species. For conspecific attacks the number of aggressors was n-1. Data were log-transformed prior to analysis since means and standard deviations were linearly related.

Experiment 2. Effects of fish size on interspecific interactions.

This experiment was designed to investigate the impact of relative body size on interspecific interactions. *Melanotaenia duboulayi* and *X. helleri* were each divided on the basis of body size into two groups (large and small) (Table 1). Because *P. signifer* and *G. holbrooki* are relatively small species, only one size class (adult fish, which were similar in size to small *M. duboulayi* and *X. helleri*) were used.

There were six mixed-species treatments, as follows: Treatment 1, large *M. duboulayi*, small *X. heller;* Treatment 2, small *M. duboulayi*, large *X. helleri;* Treatment 3, large *M. duboulayi*, *G. holbrooki;* Treatment 4, small *M. duboulayi*, *G. holbrooki;* Treatment 5, *P.signifer*, large *X. helleri;* Treatment 6, *P. signifer*, small *X. helleri.* Table 1 gives numbers of fish used in the different treatments.

There were seven replicate trials for each treatment. The focal sampling and data analysis procedures were as described for Experiment 1. Separate analyses were carried out to compare the *M. duboulayi* treatments (1-4) and the *P. signifer* treatments (5-6).

RESULTS

Experiment 1

Aggressive encounters

There were several statistically significant between-treatment differences in attack frequency (Fig.1; Table 2). Two main trends were apparent, namely:

(a) Attack levels were significantly higher with the combined treatment (Treatment 4) than the other treatments. A notable exception to this trend occurred in the case of chasing of *G. holbrooki* by *P. signifer*, where the mean frequency for Treatment 3 was marginally significantly higher than that for Treatment 4 ($F_{1,18} = 3.99$; $p = 0.061$).

(b) Significant treatment differences occurred in the presence of food. The only exception here involved attacks by *G. holbrooki* on *M. duboulayi*, where although the difference

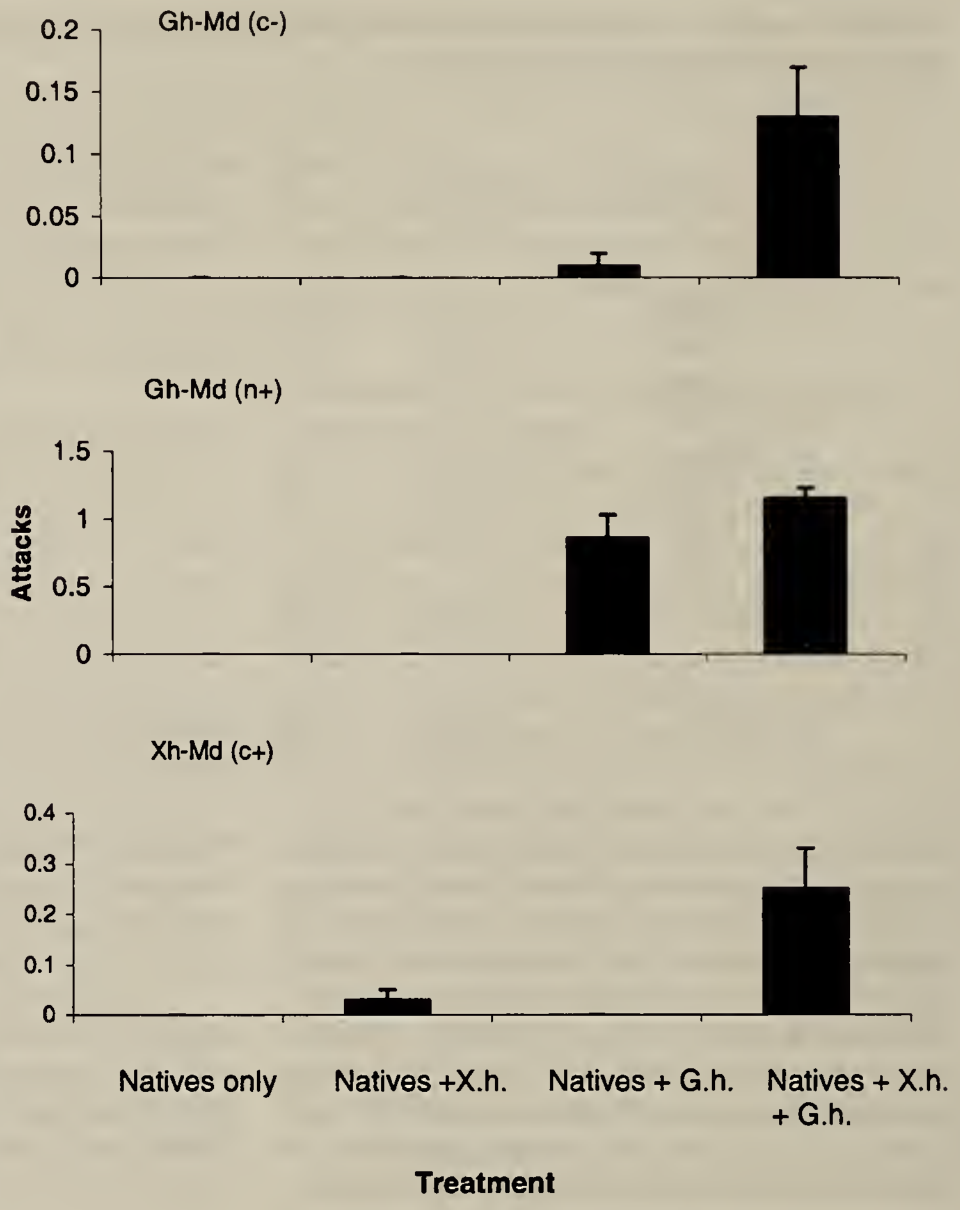

Figure 1a. Standardised (per capita) attack frequencies per trial. Bars represent means and standard errors. c, chases; n, nips; - no food; + food added. Species names are abbreviated (see caption for Table 2) ; the first-named of each pair is the attacking species. Attacks by exotic and native species are shown in Fig. 1(a), above, and Fig. 1(b), facing page, respectively.

between treatment means for nipping was only marginally significant in the presence of food ($F_{1,18}$ = 4,12; p=0.057), treatment means for chasing varied significantly in the absence of food (Table 2).

Table 3 summarises total attack frequency, the frequency of nips relative to chases, and total attack frequency in the presence of food relative to that in the absence of food. The following trends were clear:

(a) On a standardised per capita basis, *M. duboulayi* received more attacks than the other species. Most of these came from *G. holbrooki* but conspecific attacks by *M. duboulayi* were also relatively common. In contrast, attacks on *P. signifer* were less frequent and were mainly conspecific in nature.

(b) Attacks by *G. holbrooki* on *M. duboulayi* mainly involved nipping. Other interspecific and conspecific attacks were dominated by chasing.

(c) The addition of food increased attack frequency. Food addition had a greater relative impact on attacks by *X. helleri* than on attacks by the other species, but absolute levels of aggression by *X.helleri* were very low. Observations indicated that *X. helleri* were territorial and defended localised areas of the tank. Attacks by *M. duboulayi* on conspecifics and on *P.signifer* also increased markedly in relative terms.

Depth preferences

The four species tended to swim at different depths, with *P. signifer* nearest the surface, followed by *G. holbrooki*, *M. duboulayi* and *X. helleri* in order of increasing depth (Fig. 2). However, in the presence of food, *P. signifer* moved deeper while *G. holbrooki* moved closest to the surface. The addition of food had little impact on the preferred depth of *M. duboulayi*, but it affected *X. helleri* differently depending on treatment: when *X. helleri* was alone with the native species, its mean depth increased, but when *G. holbrooki* was also present, the mean depth of *X. helleri* decreased (Fig. 2).

For *P. signifer*, *G. holbrooki* and *M. duboulayi* there was a consistent effect of treatment, individuals of all these species moving closer to the surface in

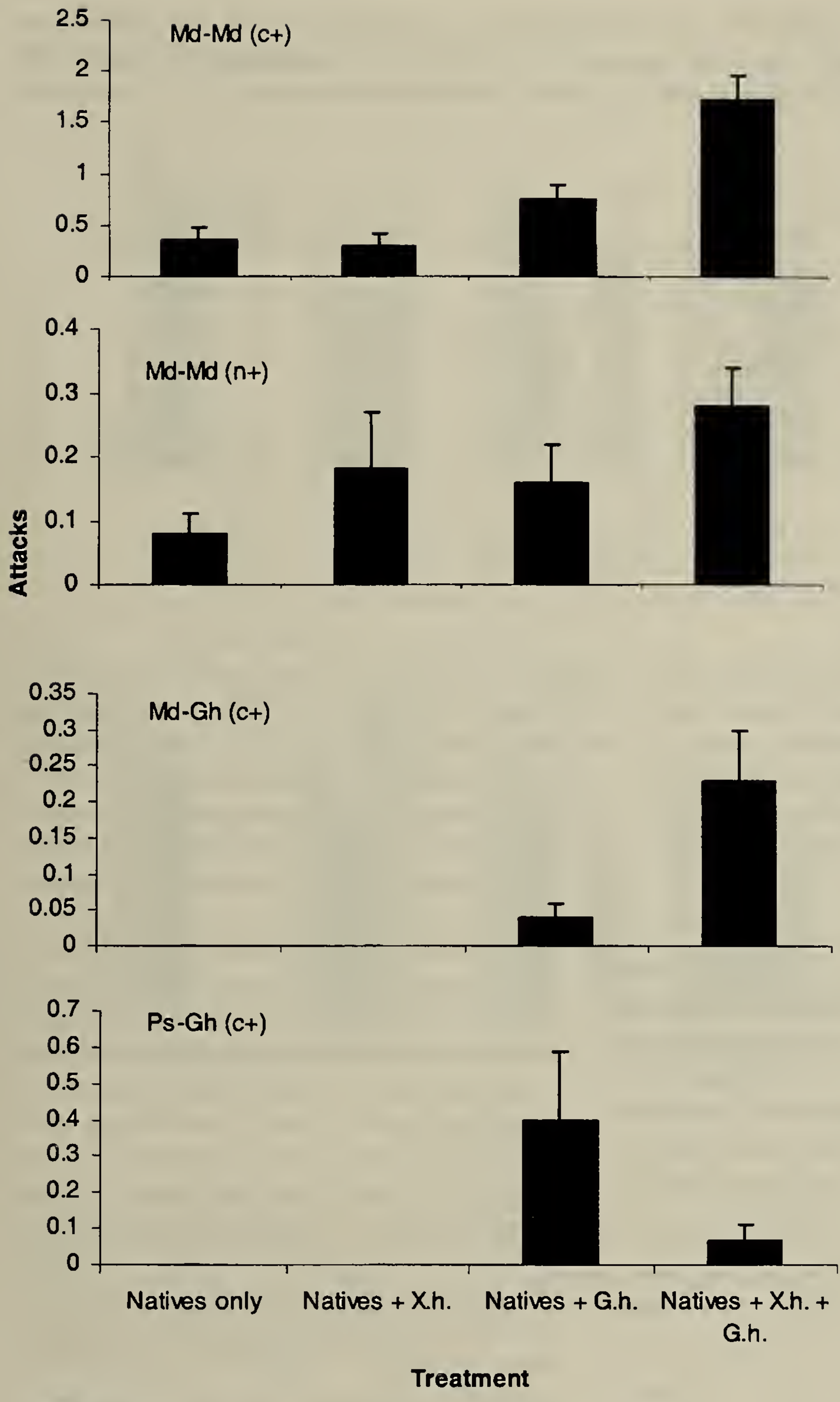

Figure 1b.

Treatment 4 (i.e., when both *G. holbrooki* and *X. helleri* were present; Fig. 2). However, between-trial variation was high and these trends were only marginally significant ($F_{1,18}$ = 4.51, p = 0.048 for *M. duboulayi*; $F_{1,18}$= 4.11, p = 0.058 for *P. signifer;* comparisons of Treatments 1 and 4 in the absence of food).

Feeding success

Individual *M. duboulayi* tended to take food before individuals of the other species (Table 4). Overall, *X. helleri* had a lower per capita feeding success than the other species.

Experiment 2

Larger individuals of *M. duboulayi* were significantly less susceptible to attack by *G. holbrooki*. In the presence of food, *G. holbrooki* chased small *M. duboulayi* approximately six times more often than large *M. duboulayi*, and *G. holbrooki*-small *M. duboulayi* chases were significantly more frequent than those for the other three combinations of *M. duboulayi* and exotic species ($F_{3,24}$= 6.74; p = 0.0019). Similarly, there were significant differences between treatments in terms of the frequency of nips on *M. duboulayi* ($F_{3,24}$= 34.75, p=0.0001), with small *M. duboulayi* being nipped by *G. holbrooki* about eight times more frequently than were large *M. duboulayi*. Attacks by *X. helleri* on *P. signifer* and *M. duboulayi* were infrequent and not significantly affected by the relative size of *X. helleri*.

When offered food and mixed with *G. holbrooki*, large *M. duboulayi* spent significantly more time in the deep section of the tank than did smaller individuals ($F_{3,24}$= 4.54, p = 0.012). There were no significant differences in tank usage with respect to depth between the treatments with natives plus *X. helleri*.

DISCUSSION

The results supported the prediction that the addition of food and the number of exotic species present would positively influence the frequency of attacks on the native species. In most cases, the highest attack rates were recorded when all four species were present, and most significant treatment differences occurred in the presence of food. Food has been shown to increase rates of aggression in other fish species (Syarifuddin & Kramer 1996). It is noteworthy that, although *G. holbrooki* was responsible for most interspecific attacks, chasing and nipping of *M. duboulayi* by *X. helleri* also increased to relatively high levels in the four-species treatment. The species enhancement

Table 2. Main between-treatment differences in attack frequency. Species names have been abbreviated (see key); the first-named of each pair is the attacking species. Underlined treatments are not significantly different. Key to abbreviations: Gh = *Gambusia holbrooki*; Md = *Melanotaenia duboulayi*; Ps = *Pseudomugil signifer*; Xh = *Xiphophorus helleri*

Interaction	Type of attack	Food / no food	F	df	p	Treatment differences
Gh - Md	chases	No food	7.46	1,18	0.014	T4 > T3
Gh - Md	nips	Food	4.12	1,18	0.057	T4 > T3
Xh - Md	chases	Food	5.10	1,18	0.037	T4 > T2
Md - Md	chases	Food	11.57	3,36	0.0001	T4>T3>T1>T2
Md - Md	nips	Food	2.90	3,36	0.048	T4>T2>T3>T1
Md - Gh	chases	Food	5.26	1,18	0.034	T4 > T3
Ps - Gh	chases	Food	3.99	1,18	0.061	T3 > T4

effect was associated with aggregation involving vertical movement toward the surface. When all four species were present in low numbers there was a general tendency (for all species except *X. helleri* in the absence of food) to move closer to the surface. By increasing the local density of fish, such aggregation appeared to promote elevated levels of activity and more aggressive interactions. The broader diversity of species-specific behaviours and salient stimuli may also have encouraged heightened levels of activity. In a study of conspecific and interspecific interactions between brook trout, *Salvelinus fontinalis,* and rainbow trout, *Salmo gairdneri (=Oncorhynchus mykiss),* Newman (1956) postulated that the presence of food increased feeding activity, which in turn increased aggressive activity as the focus of attacks was displaced from food to fellow fish of both species. He noted that feeding fish displayed some movements that are associated with aggression, such as body undulations, swift darting and biting, and suggested that such movements constituted sign stimuli eliciting attacks from other fish. The increased excitement associated with the four-species treatment (Treatment 4) could not be explained in terms of the total number of fish, which remained constant across treatments. Treatment 4 had the lowest numbers of individuals of each of the four species studied. Working with gouramis (*Trichogaster trichopterus*), Syarifuddin & Kramer (1996) found that fish were more aggressive in smaller groups and attributed this to greater costs of contest competition with increasing group size. In the present study it is possible that fish were responding more to the numbers of individuals belonging to each species than to the size of the group as a whole, but testing this hypothesis would require more work.

Table 3. Frequency of attacks (summary table). 'Total attacks' refers to nips plus chases. For each species combination, the ratio of nips to chases and the ratio of total attacks during all food trials to total attacks during all non-food trials are also shown. (+) indicates an increase in the presence of food, but where a ratio cannot be calculated due to a zero "no food" value. Species names have been abbreviated (see caption for Table 2).

Interaction	Total attacks/ trial	Nips : chases	Food : no food
Gh → Md	1.57	2.73	6.45
Gh → Ps	0.60	0.86	4.41
Xh → Md	0.26	0.82	24.50
Xh → Ps	0.08	1.00	(+)
Md → Md	1.06	0.24	9.34
Md → Ps	0.08	0.23	9.67
Ps → Md	0.14	0.46	(+)
Ps → Ps	0.79	0.16	3.59
Md → Gh	0.21	0.52	(+)
Md → Xh	0.05	1.00	1.33
Ps → Gh	0.49	0.56	3.41
Ps → Xh	0.04	(+)	(+)

The four species exhibited considerable variation in the extent and type of aggression displayed. Although *M. duboulayi* were often attacked by *G. holbrooki*, they concentrated

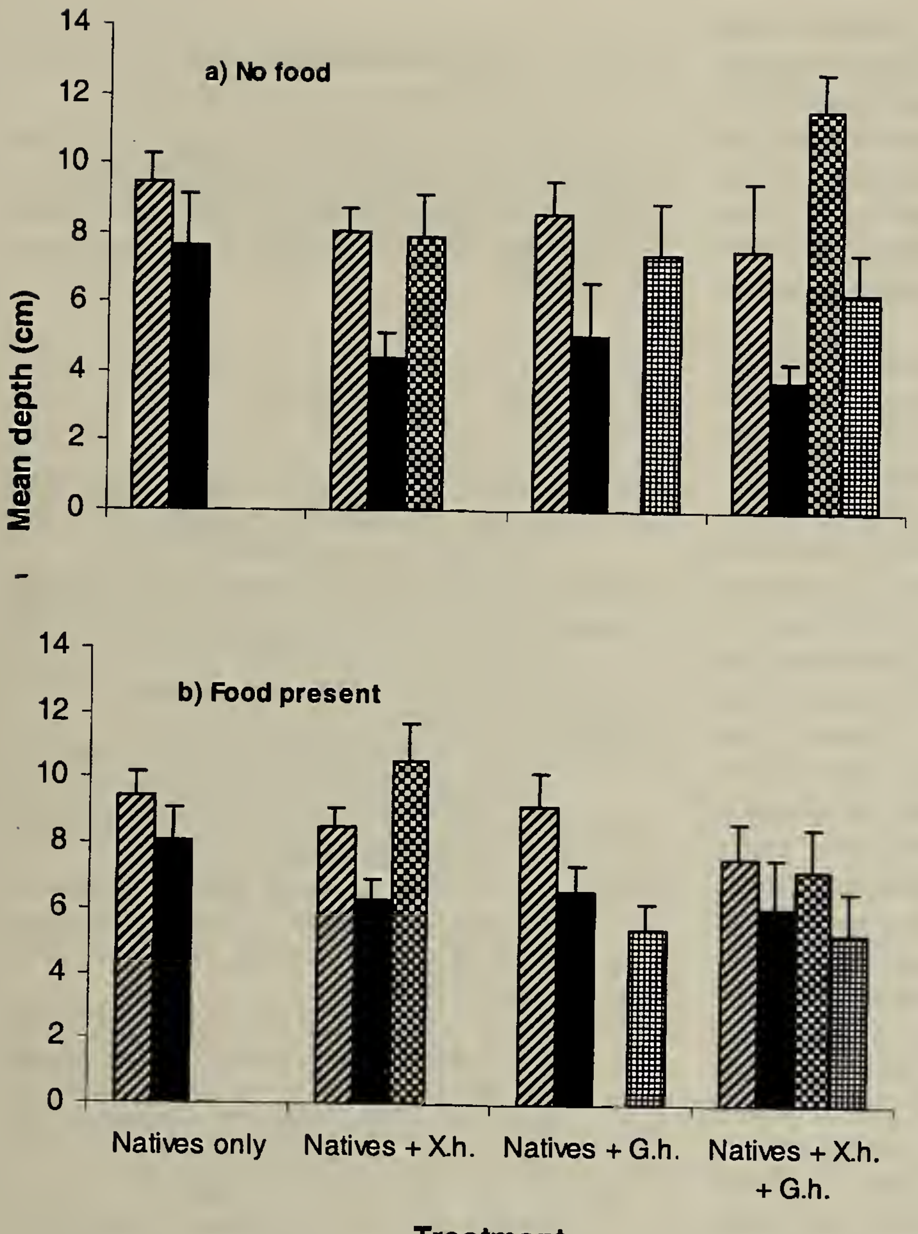

Figure 2. Mean (± SE) swimming depths (in cm) by fish species, treatment and the absence or presence of food.. *M. duboulayi*, oblique bars; *P. signifer*, black bars; *X. helleri*, crossed oblique bars; *G. holbrooki*, crossed vertical/horizontal bars. Exotic species names are abbreviated (see caption for Table 2).

mainly on conspecific rather than interspecific exchanges. In Experiment 1, attacks by *G. holbrooki* on *M. duboulayi* were over 2.5 times more frequent than attacks by *G. holbrooki* on *P. signifer*. Further, *G. holbrooki* tended to nip *M. duboulayi* but chase *P. signifer*. However, these differences were not due simply to the difference in body size between the two native species, since in Experiment 2 *G. holbrooki* attacked small *M. duboulayi* more readily than large *M. duboulayi*. Juvenile *M. duboulayi* therefore appear to be particularly susceptible to nipping.

The depths occupied by the four species examined were a function of (a) species- and size-specific differences in mean depth preference, (b) an increased tendency to aggregate near the surface as species diversity increased, and (c) species-specific changes in depth in response to the addition of food. In the absence of food, *P. signifer* occurred closest to the surface. However, when food was present, *G. holbrooki* moved closest to the surface while *P. signifer* retreated toward the deeper regions of the tank. These results suggest that *P. signifer* is a relatively poor competitor for food at the surface, as does the fact that for *P. signifer* (unlike *M. duboulayi, X. helleri* and *G. holbrooki*) feeding success was lowest when all four species were present.

Table 4. Per capita feeding success of the four species. In this table the percentage of trials when any member of a given species took the offered food before members of any other species has been divided by the number of individuals of the focal species. Species names have been abbreviated (see caption for Table 2).

	Treatment			
	1	2	3	4
Species	Natives only	Natives + X.h.	Natives + G.h.	Natives + X.h. +G.h.
Md	6.6	8.9	6.4	8.7
Ps	1.2	4.0	4.5	1.0
Xh	-	0	-	2.8
Gh	-	-	3.4	4.2

In Experiment 2, larger *M. duboulayi* were less attracted to the shallow part of the tank than were smaller *M. duboulayi*. In the wild, adult *M. duboulayi* tend to occur at greater depths than juveniles and are less inclined to feed at the surface (Hattori and Warburton, in press). These observations may reflect the general tendency for small fish species, and small individuals within species, to occur closer to the surface (Helfman et al. 1997).

There are substantial overlaps among the four focal species in terms of habitat use and diets (Arthington et al. 1983; Arthington 1992), so that the potential exists for interspecific competition. Further, in disturbed urban streams invaded by exotic semiaquatic grasses the extent of open flowing water habitats preferred by *M. duboulayi* and *P.signifer* is typically reduced (Arthington et al. 1983), and the success of these species will depend more heavily on their ability to utilise the low velocity grassy edge habitats favoured by poeciliids. Similarly, the prerequisites for competition exist when mixed populations of native and exotic species are trapped in shrinking ponds during droughts (Howe et al. 1997). Although the present laboratory-based findings should not be applied in a precise predictive way to wild populations, they do illustrate behavioural mechanisms by which exotic fish species may negatively impact on natives under confined conditions in streams and ponds. Where exotic species occur at high density, and especially where *G. holbrooki* and *X. helleri* coexist, associated increases in activity and aggression are likely to lead to elevated stress levels, increased energy expenditure, reduced attentiveness to foraging and anti-predator vigilance, and reduced per capita feeding success in the native species. More research is required on how dynamic behavioural interactions between shoaling fish species affect the composition of local stream assemblages. There is also a need for allied work on the effects of variation in abundance ratios, food availability, temperature and cover on behaviour.

In summary, in laboratory experiments the behaviour of *G. holbrooki* had clear, species-specific impacts on *M. duboulayi* and *P. signifer*. *Gambusia holbrooki* was responsible for both direct aggression and displacement, but it also encouraged increased activity and aggression by other species, including *X. helleri*. The presence of multiple exotic species may therefore exacerbate the negative impact of high poeciliid densities on native species such as *M. duboulayi* and *P. signifer*.

ACKNOWLEDGMENTS

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Echinoids of the Kairuku Formation (Lower Pliocene), Yule Island, Papua New Guinea: Clypeasteroida

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The Kairuku Formation (Lower Pliocene), Yule Island, Papua New Guinea, contains a rich and diverse echinoid fauna. Clypeasteroid (sand dollar) echinoids are an important component of this fauna and seven taxa are recognised. A seagrass community included the clypeasterids *Clypeaster reticulatus* (Linné), *Clypeaster latissimus* (Lamarck) and *Clypeaster humilis* (Leske) and the laganid *Laganum depressum* Lesson in L. Agassiz, 1841. A current-swept, shallow water, sand-dwelling community included *Laganum decagonale* (de Blainville, 1827), *Laganum depressum delicatum* Mazzetti, 1894 and *Laganum depressum sinaiticum* Fraas, 1867. Bathymetric ranges of extant forms of these clypeasteroids suggest water depths from littoral to about 40 m. This diverse fauna has much in common with modern communities of the tropical Indo-Pacific, as well as fossil Plio-Pleistocene faunas of the Indonesian archipelago and the western Indian Ocean region.

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KEYWORDS: Echinoidea, Clypeasteroida, *Laganum*, *Clypeaster*, Tertiary, Lower Pliocene, Faunal Affinities, Papua New Guinea.

INTRODUCTION

The Lower Pliocene Kairuku Formation, Yule Island, Papua New Guinea (PNG) contains a rich and diverse assemblage of regular and irregular echinoids typical of faunas from the tropical Indo-Pacific. The fauna remains poorly understood, with only Tenison-Woods (1878) providing an early note on two species, and Lindley (2001) describing several species. Several faunal lists have also been compiled (F. Chapman in Mayo et al. 1930; F. Chapman and I. Crespin in Montgomery 1930). The fauna is geographically remote from other Tertiary echinoid faunas described in the literature. These include faunas from the Indonesian archipelago (Jeannet and R. Martin 1937) and at Barrow Island off the NW coast of Australia (McNamara and Kendrick 1994).

The present paper is the second in a series describing the echinoid faunas of the Kairuku Formation. It is based on collections made by the writer during fieldwork completed in January 2002. Collection details are provided in the Appendix. Echinoid terminology used herein follows that of Durham (1966). For a map of the Indo-Pacific realm as used herein, the reader is referred to Hemminga and Duarte (2000: fig. 1.1). Specimens have been temporarily allocated Department of Geology, Australian National University (ANU) repository numbers, pending their repatriation to Papua New Guinea at the conclusion of studies, where they will be housed in the Department of Geology, University of Papua New Guinea, Port Moresby.

KAIRUKU FORMATION AND ITS ECHINOID FAUNA

Stratigraphy

The Kairuku Formation was defined by Francis et al. (1982) as a 250 m thick sequence of gently easterly dipping limestone outcropping in a NW trending belt along the eastern coastline of Yule Island (Fig. 1). The formation is dominated by massive, variably lithified biosparite with interbedded cream-coloured micrite and biomicrite. The sequence can be traced SE from Yule Island, across Hall Sound to Poukama and Delena on the mainland. The formation contains a diverse assemblage of marine invertebrates including corals, gastropods, echinoids, larger foraminifera and pelecypods with rare vertebrate remains (shark teeth). Prominent bright yellow-brown coloured bluffs, consisting of massive, poorly lithified, medium-coarse grained biosparite, typically forming

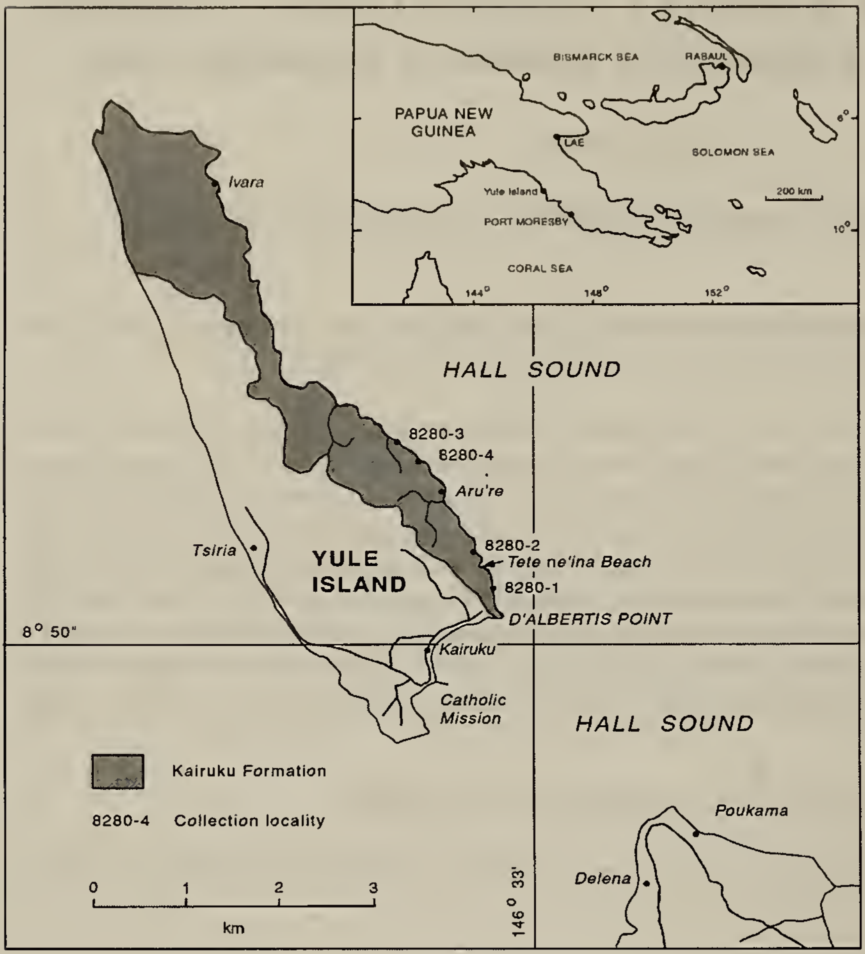

Figure 1. Yule Island, Central Province, Papua New Guinea showing distribution of Kairuku Formation (after Francis et al. 1982) and collection localities. Base from Kairuku 1: 50 000 Sheet 8280-III (Edition 1).

recessive sections of the eastern coastline of the island, were found to be richly fossiliferous for echinoids. The sequences examined during fieldwork represent the lower to mid-levels of the formation. Foraminifera from the unit indicate a Lower Pliocene age – zones N18-N19/20 (Haig et al. 1993).

The Kairuku Formation was deposited during a period of rapid shallowing from mid-neritic in the lower part of the formation to innermost neritic higher in the formation (Francis et al. 1982; Haig et al. 1993). Haig et al. (1993) interpreted the carbonate sand facies, with coral-rich beds and *Marginopora*-rich sands, as a deposit of seagrass meadows. However, Lindley (2001) noted that the echinoid faunas of the formation also included robust, highly turbulent, shallow-water dwelling forms such as the temnopleurid *Temnotrema macleayana* (Tenison-Woods). The limestone-dominated Kairuku Formation, is thus interpreted to have accumulated on a rimmed tropical carbonate shelf with actively growing seaward patch reefs, seagrass covered banks, carbonate sand shoals and elongate depressions. The entire area was subject to wholesale disruption during storm surges or as a result of wind action. These turbulent events helped spread skeletal sands and coral rubble derived from patch reefs.

Echinoid faunas

The Kairuku Formation contains contrasting echinoid faunas: an infaunal seagrass meadow community dominated by clypeasteroids with locally abundant burrowing spatangoids confined to coarse-grained carbonate sands in shallow water, and an epifaunal community from a highly turbulent niche of reef and creviced reef rock, with pockets of current-swept sand, consisting of temnopleuroids and other regular echinoids (Lindley 2001). The seagrass community included the clypeasterids *Clypeaster reticulatus* (Linné), *C. latissimus* (Lamarck) and *C. humilis* (Leske) and the laganid *Laganum depressum* Lesson in L. Agassiz, 1841. A current-swept, shallow water community was dominated by the laganids *L. decagonale* (de Blainville, 1827), *L. depressum delicatum* Mazzetti, 1894 and *L. depressum sinaiticum* Fraas, 1867. Bathymetric ranges of extant forms of these clypeasteroids suggest water depths from littoral to about 40 m.

Clypeasteroid-dominant seagrass meadow dwelling echinoid faunas predominate in the lower Kairuku Formation, south of Tete ne'ina Beach. Modern species of *Clypeaster* are shallow burrowers confined to medium-coarse sand, with their elevated respiratory petaloids serving as 'snorkel' structures (Seilacher 1979). The laganids are also shallow burrowers, only sieving the uppermost sand layer (Seilacher 1979). Burrowing heart urchins are very common and/or dominant in the mid-levels, north of Aru're village. Of the regular echinoids, the compact, robust *Temnotrema macleayana* (Tenison-Woods), an uncommon echinoid observed only in the lower levels of the fomation, was a highly turbulent, shallow-water dwelling form, confined to patch reef habitats. A toxopneustid echinoid, a common component of the fauna at locality 8280-3, about mid-level in the formation, inhabited a current-swept, shallow water habitat.

Despite their fine preservation, some of the echinoid faunas of the Kairuku Formation represent death assemblages. At locality 8280-4, north of Aru're village, high bluffs of massive yellow-brown biosparite are crowded with an infauna of burrowing spatangoids, whose tests are preserved in a range of orientations, and numerous small laganid tests, many resting on their edges or inverted (Fig. 1). This fauna is indicative of the effects of the wholesale disruption and redistribution of sediment resulting from a succession of large storm events. A thin interbed of coarse, chaotic limestone breccia, containing a fauna dominated by *Pecten* sp. and the large clam *Tridacna* sp. with broken tests of heart urchins and laganids, is probably the shallow water deposit derived from a storm related redistribution of coral and skeletal debris from seaward patch reefs.

Faunal affinities

The tropical Indo-Pacific affinity of the Tertiary echinoid faunas of PNG was noted by Lindley (2001). The diverse clypeasteroid fauna of the Kairuku Formation has much in common with modern communities and Plio-Pleistocene faunas. The formation contains three *Clypeaster* species, all found in waters of the Indo-Pacific. Only *C. humilis* is found as fossil, in Java (Miocene), Taiwan (Pliocene) and the Red Sea (Pleistocene). The diversity of the Yule Island clypeasterids contrasts with the impoverished faunas in Australia where just two species are known. *Clypeaster gippslandicus* McCoy from the Middle to Upper Miocene of southern Australia is a member of an echinoid fauna distinct from those of the tropical Indo-Pacific (McNamara and Kendrick 1994). *Clypeaster butleri* McNamara and Kendrick, 1994 is a Middle Miocene species from the Barrow Island fauna, regarded as having stronger affinities with tropical northern, rather than southern, faunas (McNamara and Kendrick 1994).

Four laganids are present in the Kairuku Formation and reflect not only the strong Indo-West Pacific affinity, but interestingly, close relationships with Plio-Pleistocene faunas of the western Indian Ocean region (Red Sea, Persian Gulf and Zanzibar). Only *Laganum depressum sinaiticum* is not present in modern communities. *Laganum decagonale* and *L. depressum* are common Indo-Pacific species, known from fossils in Java (Mio-Pliocene), and Fiji (?Miocene) and Java (Pliocene), respectively. Fossil *Laganum depressum delicatum* is found in the Pliocene of Zanzibar and var. *sinaiticum* is known only from fossils in the Persian Gulf region and the Pleistocene of the Red Sea.

SYSTEMATIC PALAEONTOLOGY

Class ECHINOIDEA Leske, 1778
Subclass EUECHINOIDEA Bronn, 1860
Superorder GNATHOSTOMATA Zittel, 1879
Order CLYPEASTEROIDA A. Agassiz, 1872
Suborder CLYPEASTERINA A. Agassiz, 1872
Family CLYPEASTERIDAE L. Agassiz, 1835
Genus CLYPEASTER Lamarck, 1801

Type species

Clypeaster rosaceus (Linné), by subsequent designation of Desmoulins, 1835; Recent, Caribbean.

Remarks

The literature contains a great number of nominal species (more than 400) of *Clypeaster* (Durham 1966). Mortensen (1948a) in his monograph on the Clypeasteroida added to the earlier attempts of A. Pomel, J. Lambert and other workers in identifying groupings using sections or subgenera and, at the same time, recognised difficulties and limitations because of the great variation in most species of *Clypeaster*. Mortensen's (1948a) classification emphasised internal test structure, ahead of test shape, nature of petals, nature of peristome, situation of periproct, genital pores, the spines etc. Although Durham (1966: U463) argued there is no systematic basis for the recognition of subgeneric groupings, Mortensen's (1948a) key to the clypeasterids, based on Recent species, is useful for the description of the Yule Island fossils.

F. Chapman in 1920 (in Mayo *et al.* 1930) first noted the occurrence of *Clypeaster* sp. in the Kairuku Formation. However, his subsequent detailed echinoid faunal list (F. Chapman and I. Crespin in Montgomery 1930) did not include the genus.

Clypeaster reticulatus (Linné)

Figs 2a-c

Synonymy

Echinus reticulatus Linné 1758, p. 666.

Clypeaster reticulatus (Linné), Jeannet and R. Martin 1937, p. 244; A.M. Clark and Rowe 1971, p. 144, 160.

T. Mortensen (1948a), A Monograph of the Echinoidea 4(2), Clypeasteroida, p. 71-73, lists the previous synonymies.

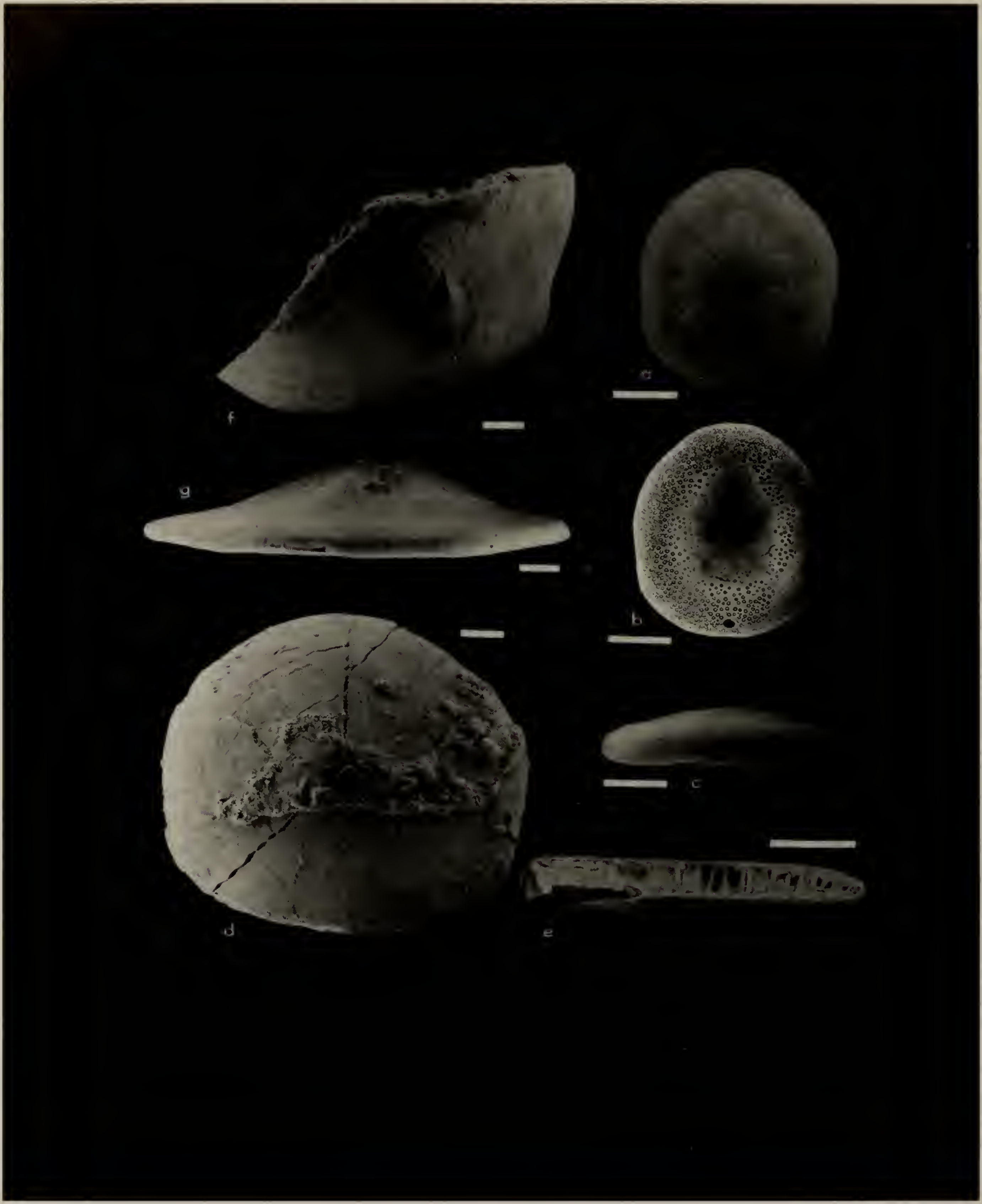

Figure 2. Clypeasterid echinoids. *Clypeaster reticulatus* (Linné). Lower Pliocene, Yule Island, Central Province. 2a-c, ANU 60557, aboral, oral and lateral views. Bar scale = 1.0 cm. *Clypeaster latissimus* (Lamarck). Lower Pliocene, Yule Island, Central Province. 2d, ANU 60558, aboral view; 2e, ANU 60571, sectional view showing marginal internal skeleton of isolated pillars. Bar scale = 1.0 cm. *Clypeaster humilis* (Leske). Lower Pliocene, Yule Island, Central Province. 2f-g, ANU 60561, aboral and posterolateral views. Bar scale = 1.0 cm.

Description

Test of medium size 41 mm x 32 mm, low with elongate pentagonal outline, with more or less concave sides and rounded corners. Margin of test is rounded. Aboral side is slightly raised towards the centre with a shallow depression between the petaloid region and the edge. The oral side is distinctly concave, with the distal part gently rounded and only the proximal part sinking steeply towards a deeply sunken peristome. The test is fairly strong.

Petals are broad and petaloid area about 1/2 to 2/3 test length. The anterior petal is the longest, with the antero-lateral petals slightly shorter than the other petals. With the exception of the anterior petal, all petals are closed distally. Petals are broadest distally, because of the greater width of pore zone in this region. Pore zones along petals are about 2/3 width of interporiferous zones; pores are small and circular. The ridges between pore-pairs carry 1-3 primary tubercles, amongst miliary tubercles. The interporifeous zone is distinctly raised with numerous scattered primary and miliary tubercles. Ambulacral furrows on oral side are weak and very little sunken.

The interambulacral areas on the aboral side of juvenile specimens of this species have a distinctive sculpturing of sutural pits, recalling that of the temnopleurids (Mortensen 1948a: 74). This sculpturing disappears totally with age, with no trace in adult specimens, as is the case with ANU 60557. Interambulacral areas carry scattered primary tubercles set amongst a close covering of miliary tubercles. On the oral side there is a belt of closely spaced primary tubercles and miliary tubercles on the gently rounded distal region. Primary tubercles are weakly scattered on the steeply dipping region towards the peristome.

Apical system is very small, 2 mm in diameter. Genital pores are small. The periproct is close to the posterior edge of the test; it is subrounded and distinctly smaller than the peristome. The peristome appears to be subpentagonal, about 2 mm diameter, and is surrounded by numerous primary tubercles.

Remarks

Clypeaster reticulatus (Linné), a characteristically small species with great variation in form, is type of the *Rhaphidoclypus* Section (Mortensen 1948a). This section is characterised by the complete absence of marginal internal laminae and a conspicuously concave oral side. The species was previously known only from extant forms found in the tropical waters of the Indo-Pacific, from the Red Sea through to the Indonesian Archipelago, to the Hawaiian Islands (Mortensen 1948a). The species is also noted from Barrow Island, NW Australia (McNamara and Kendrick 1994). Mortensen (1948a) recognised a subspecies, *Clypeaster reticulatus sundaicus* Mortensen 1948, distinguished by its possession of thin edged test. The subspecies is widely distributed throughout the tropical Indo-West Pacific, and is also known as fossil from the Lower Miocene of Java and the Plio-Pleistocene of East Africa and the New Hebrides (Jeannet and R. Martin 1937; Mortensen 1948a).

Material

ANU 60557, a complete test from locality 8280-4, northwest of Aru're village, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Clypeaster latissimus (Lamarck)

Figs 2d-e

Synonymy

Scutella latissima Lamarck 1816, p. 286.

T. Mortensen (1948a), A Monograph of the Echinoidea 4(2), Clypeasteroida, p. 63, lists the previous synonymies.

Description

Test of small size 86 mm x 48 mm by comparison with measurements provided by Mortensen (1948a) for this largest of the Clypeasters. Test very low, very gradually rising towards the centre, with an ovoid-subpentagonal outline, distinctly truncated at posterior end. Edge of test is very thin. Oral side flattened.

Petals are elongate-ovoid shape, broadest in the middle. Anterior petal slightly longer than others. Petals closed distally. Petals area slightly more than half test-length. Pore zones are wide, 2-2.5 mm, with the interporiferous area just over three times the width of a pore zone. Inner pores are small, circular; outer pores may be elongate as in ANU 60559. There are 2-5 primary tubercles on ridges between pore pairs. Mortensen (1948a) noted for young specimens there are only 3-5 tubercles on the ridge and for mid-sized specimens, c. 100 mm length, 8-10 primary tubercles. The interporiferous zone is flush with the test. Ambulacral furrows shallow.

Interambulacra are in contact with the apical system. Tuberculation on aboral and oral surfaces is uniformly fine and dense, in excess of 300 per cm^2.

The apical system is very small, only c. 2 mm diameter. Details of genital pores, peristome and periproct unknown.

Remarks

The large flat, thin edged test of ANU 60558, with broad, ovoid and closed petals indicates placement in the *Coronanthus* Section (Lambert 1910; Mortensen 1948a). Mortensen (1948a) described this section as including forms with a large flat test and thin edge. The largest specimen noted by Mortensen (1948a) has a length x width of 235 mm x 190 mm; the smallest 33 mm x 31 mm, with many greater than 102 mm x 87 mm. The oral side is flat and periproct near the edge, circular about the size of the peristome. Petals are broad, ovoid and nearly closed. In addition to *C. latissimus* (Lamarck), the section also includes *C. amplificatus* Koehler, 1922, *C. pateriformis* Mortensen (1948b) and *C. telurus* H.L. Clark, 1914. *Clypeaster latissimus* is a Recent species known from the tropical waters of the Indonesian Archipelago (Sunda Strait, Celebes and Java Sea) and the coast of Indo-China (Mortensen 1948a). The Sunda Strait specimens were collected at water depths of 25-45 m (Mortensen 1948a).

Material

ANU 60558, a complete test; ANU 60559, 60560 and 60571 fragmentary tests from locality 8280-1, immediately south of Tete ne'ina Beach, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Clypeaster humilis (Leske)

Figs 2f-g

Synonymy

Echinanthus humilis Leske 1778, p. 185.

Clypeaster rosaceus (Linné), Gerth 1922, p. 504: Miocene, Java.

Clypeaster humilis Jeannet and R. Martin 1937, p. 242: Upper Miocene, Java; H.L. Clark 1946, p. 337; A.M. Clark and Rowe 1971, p. 144, 161.

T. Mortensen (1948a), A Monograph of the Echinoidea 4(2), Clypeasteroida, p. 88-90, lists the previous synonymies.

Description

Test of moderate size, distinctly longer than broad; estimated at 113 mm x 90 mm, at the upper end of test sizes noted by Mortensen (1948a). Greatest breadth at the antero-lateral petals. Edge is concave in the lateral ambulacra, while the posterior end is rounded. The edge is rather thin, the distal part of the test gently rising from the ambitus to the petaloid region, from where it steepens towards the apex. Marginal internal skeleton consists of isolated pillars.

Petaloid region is a little more than 1/2 of test length. The posterior and antero-lateral petals are closed distally, details of anterior petal not known. Petals are of narrow, elongate ovoid shape, distinctly broadest at the distal end. The interporiferous zone is slightly elevated in this large specimen. Pore zones along petals are about 1/2 width of interporiferous zone; inner pores are small and circular, outer pores elongate. The ridges between pore pairs carry a regular series of 7-9 primary tubercles. Oral ambulacral furrows distinct and extend nearly to edge of test.

Interambulacral areas are in contact with the apical system because of narrow petals. Tuberculation on both aboral and oral surface is uniformly dense, with a close covering of primary tubercles set amongst miliary tubercles.

Apical system is poorly preserved, c. 3 mm diameter; details of genital pores unknown. The periproct small, situated about its own diameter from the edge of the test. Details of peristome unknown.

Remarks

The Indo-Pacific *Clypeaster humilis* (Leske) and the closely allied *C. subdepressus* (Gray) from the West Indies, belong to the *Stolonoclypus* Section. These clypeasterids possess a test with flattened margin and raised central part; a flat or concave oral side; petals more or less distinctly closed; and a well developed marginal internal skeleton (Mortensen 1948a). *Clypeaster humilis* and *C. subdepressus* are distinguished using petaloid characters, including the degree of elevation of the interporiferous zone and the relative number of tubercles on ridges between pore pairs (Mortensen 1948a). Specimen ANU 60561 is readily referred to *C. humilis* using these characters. The species exhibits considerable variation in test outline, profile of the oral surface and size of the petaloid region (Mortensen 1948a). Although the Yule Island specimen appears to possess a distinctly elongated pentagonal test outline, with a gently sloping aboral margin, this variation falls within the limits described for the species by Mortensen (1948a).

Extant forms of *C. humilis* are distributed throughout tropical waters of the Indo-Pacific, with a water depth range from littoral to 216 m. The species is well represented in the fossil record. Gerth (1922) and Jeannet and R. Martin (1937) described the species from the Miocene of Java and fossils have also been recorded from the Pleistocene of the Red Sea and a form with affinities to the species, is noted from the Lower Pliocene of Taiwan (Mortensen 1948a).

Material

ANU 60561, an incomplete test from locality 8280-4, northwest of Aru're village, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Suborder LAGANINA Mortensen, 1948
Family LAGANIDAE A. Agassiz, 1873

Remarks

Mortensen (1948a) and Durham (1966) disagree on the systematic position of several laganids which are represented in the Yule Island fauna. This confusion arises from the great variation within species and particularly applies to the relationships between *Peronella* Gray, 1855, *Hupea* Pomel, 1883 and *Laganum* Link, 1807, and *Jacksonaster* Lambert and Thiéry, 1914 and *Laganum*, all recognised as valid taxa by Durham (1966).

Both workers disagree on the status of *Hupea*. The number of genital pores is fundamental in separating *Laganum* (five genital pores) from *Peronella* (four genital pores) and accordingly Mortensen (1948a) regarded *Hupea* as a synonym of *Peronella*. However, Durham (1966) reinstated *Hupea* as a taxon with five genital pores. The test of *Hupea*, a Pliocene-Recent form from the tropical Indo-Pacific, is described and figured by Durham (1966), and especially resembles that of *Laganum decagonale* (de Blainville, 1827). Both *L. decagonale* and the type species *Hupea decagonale* (Lesson) have small petals about 0.5 length of radius, raised apical area, a distinctly polygonal test outline, with submarginal periproct.

Durham's (1966) diagnoses for *Laganum* and *Jacksonaster* provide very little distinction between these taxa. Only the shape of the periproct, elongate in the case of *Laganum*, round or transversely elliptical for *Jacksonaster*, separates them. They are identical in many respects, including petaloid area, genital pores and test size and shape. That this single character is used for generic distinction is, in the words of Mortensen (1948a: 302) 'rather ridiculous'. Mortensen (1948a) regarded *Jacksonaster* as a synonym of *Laganum*. The writer follows Mortensen's (1948a) scheme.

The faunal list of Chapman and Crespin (in Montgomery 1930) included four laganids: *Laganum* sp., *L. bonani* Klein, 1734, *L. depressum* Lesson in L. Agassiz, 1841 and *Peronella* sp. *Laganum laganum* (Leske) (= *L. bonani*) is noteworthy for its oblong periproct, situated midway between the mouth and the edge of the test (Mortensen 1948a), and was not observed during the present fieldwork. Similarly, *Peronella* sp., characterised by an apical system with four genital pores, is not recorded.

Genus LAGANUM Klein, 1734

Type species

Laganum laganum (Leske), by subsequent designation.

Remarks

The laganid *Laganum depressum* Lesson in L. Agassiz, 1841, present in the Kairuku Formation on Yule Island, was described by Lindley (2001).

Laganum decagonale (de Blainville, 1827)

Figs 3a-b

Synonymy

Scutella decagonalis de Blainville 1827, p. 229.
Scutella decagona Herklots 1854, p. 9: Miocene, Java.
Peronella decagonalis Lesson in A. Agassiz, 1872-74; Tenison-Woods 1878, p. 126; Etheridge 1889, p. 173, 178; Etheridge 1892, p. 209, 215; Jack and Etheridge 1892, p. 692; Tate 1894, p. 213, 214; Carne 1913, p. 17.
Peronella sp., F. Chapman and I. Crespin in Montgomery 1930, p. 57.
Echinodiscus lesueuri Jeannet and R. Martin 1937, p. 254 [*non Peronella lesueuri* Valenciennes in L. Agassiz, 1841].
Jacksonaster decagonus (de Blainville), Jeannet and R. Martin 1937, p. 206: Pliocene, Java
Laganum decagonale (de Blainville, 1827), A.M. Clark and Rowe 1971, p. 144, 162; Gibbs, A.M. Clark and C.M. Clark 1976, p. 133.
Fibulariid (?), Lindley 2001, p. 130.
T. Mortensen (1948a), A Monograph of the Echinoidea 4(2), Clypeasteroida, p. 331, 332, lists previous synonymies.

Description

Test markedly flattened, with rounded decagonal outline; interambulacral edges are distinctly convex and broader than the linear ambulacral edges. In young specimens the test outline is elliptical. ANU 60562, the largest specimen has a test length x width of 52 mm x 45 mm; ANU 60564, the smallest is 28 mm x 22.5 mm. Test is thin with a weakly inflated edge forming a narrow margin. Oral surface shallowly concave.

Petaloid area is small, about 1/2 test length and slightly anterior. Petals are relatively narrow and closed distally; the anterior petal is distinctly longer than the others. Plates of petals apparently simple, running across half the width of the petal. Pores small, about equal sized, conjugate. Interporiferous area is fairly narrow, covered by scattered primary tubercles and numerous miliary tubercles. Ambulacral furrows shallow and rapidly disappearing distally.

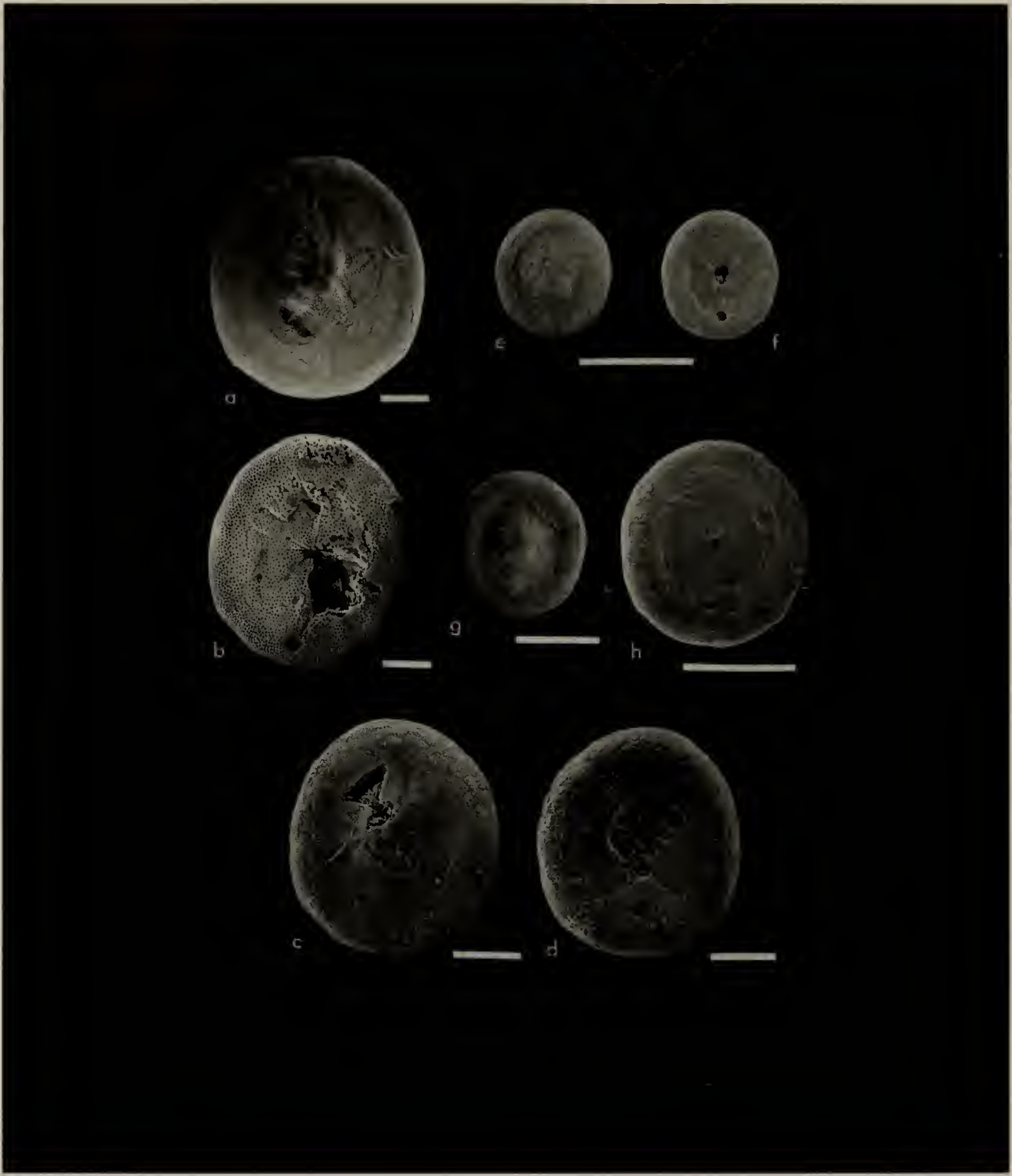

Figure 3. Laganid echinoids. *Laganum decagonale* (de Blainville, 1827). Lower Pliocene, Yule Island, Central Province. 3a-b, ANU 60562, aboral and oral views. Bar scale = 1.0 cm. *Laganum depressum sinaiticum* Fraas, 1867. Lower Pliocene, Yule Island, Central Province. 3c-d, ANU 60565, aboral and oral views. Bar scale = 1.0 cm. *Laganum depressum delicatum* Mazzetti, 1894. Lower Pliocene, Yule Island, Central Province. 3e-f, ANU 60567, aboral and oral views; 3g-h, ANU 60566, aboral and oral views. Bar scale = 1.0 cm.

Interambulacra covered by scattered coarse primary tubercles and fine miliary tubercles; densely spaced primary tubercles are present around edge of test on the weakly inflated margin. Tuberculation on the oral surface is similar to that of the aboral surface.

Apical system raised; composed of single large madreporite plate; stellate with apices opposite interambulacra. Genital pores five, tightly grouped and located in adapical interambulacral position. UPNG F1183 presents an anomaly with genital pores located midway along sides of central plate, at adapical end of ambulacra (Lindley 2001: fig. 7c). Peristome is round. Periproct transversely elongate, near the posterior end, about its own diameter from the edge of the test. It is small, c. 3 mm transverse diameter in ANU 60562, about the same size as peristome.

Remarks

A single small specimen of this species, lacking well-defined food grooves, was tentatively assigned to Family Fibulariidae by Lindley (2001). However, the collection of additional material has permitted referral to *Laganum decagonale* (de Blainville, 1827). Tenison-Woods (1878) originally assigned the Yule Island species to *Peronella decagonalis* Lesson in A. Agassiz, 1872-74. *Peronella* and *Laganum* are similar in many respects, but are separated by the former having only four, rather than five, genital pores (Mortensen 1948a; Durham 1966).

Laganum decagonale is noteworthy for its ten-sided and very thin test. It is a very common extant species in the tropical seas of the Indo-Pacific, particularly the Java and Philippine Seas (Mortensen 1948a). The species has also been recorded from the Admiralty Islands, PNG, and the northern Great Barrier Reef (H.L. Clark 1925; Gibbs et al. 1976). The species is found in water depths ranging from c. 5 to 275 m (Mortensen 1948a). Fossil species synonymous with *L. decagonale* (*Scutella decagonus* Herklots 1854 and *Jacksonaster decagonus* Jeannet and R. Martin 1937) have been described from the Miocene and Pliocene of Java (Mortensen 1948a).

The Yule Island species, with its densely spaced tubercles around the edge, bearing frill spines, was interpreted by Lindley (2001) to have inhabited a current-swept sandy substrate. The frill spines were used for burrowing and, by bending down, to reduce dislocation by currents.

Material

Four complete tests: ANU 60562 from locality 8280-4, northwest of Aru're village; ANU 60563 from locality 8280-1, south of Tete ne'ina Beach; ANU 60564 from locality 8280-2, immediately north of Tete ne'ina Beach; and UPNG F1183 collected by R. Perembo from locality 24 of Francis et al. (1982) = locality 8280-3, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Laganum depressum sinaiticum Fraas, 1867

Figs 3c-d

Synonymy

Laganum attenuatum L. Agassiz and Desor 1847, p. 132: Red Sea and Persian Gulf.

Laganum sinaiticum Fraas 1867, p. 333: Pleistocene, Red Sea region.

Laganum tumidum Duncan and Sladen 1886, p. 379.

Description

Test of medium size, 37 mm x 33 mm, with subrounded outline. Edge of test is thick and rounded. Test margin is broadly inflated, the width of margin extending about 1/3 of distance to apex. Inside this inflated margin the test is moderately sunken, width of sunken region about 1/3 of distance from ambitus to apex. Test then rises gradually to apical system, with a height just above that of inflated margin. Oral surface is shallowly concave. Test is fairly strong.

Petaloid region is about 0.7 of test length. Petals are relatively narrow, distinctly broadest adapically, extend to the inflated margin and are open distally. Pore zones are narrow, about 1/3 width of interporiferous zone, with small circular pores. Interporiferous zone is flush with the test. Tuberculation of interporiferous zones is distinct with a covering of numerous primary and miliary tubercles, separated by a narrow, central corridor with only miliary tubercles. Ambulacral furrows are shallowly sunken and extend 1/2 distance to edge of test.

Interambulacra in contact with apical system; covered by a uniformly scattered covering of primary and miliary tubercles to the mid-region of the inflated margin. The remainder of the inflated margin, the ambitus and the margin of the oral surface has a dense covering of primary tubercles with scattered miliary tubercles. The anterior section of this densely tuberculated margin, level with the anterolateral petals on both the aboral and oral surfaces, contains scattered, very coarse noncrenulate tubercles.

Apical system low, stellate with apices opposite interambulacra. Genital pores five, tightly grouped and located in apical disc. Details of peristome unknown. Periproct is transversely elongate, located closer to posterior edge, about 2/3 of distance from mouth to ambitus. Periproct is surrounded by a narrow rim of primary tubercles.

Remarks

Laganum depressum sinaiticum Fraas, 1867 is a subrounded, thick-edged, heavy form of *L. depressum* found in abundance in the raised Pleistocene deposits of the coastal plains of the Red Sea and also the Persian Gulf (Mortensen 1948a). The writer has not read Fraas' (1867) description of var. *sinaiticum*. However, Mortensen (1948a: Plate LIII, figs 14, 26-27) figured three fossil specimens collected from these beds. The figured specimens range in length x width from the smallest 28 mm x 19 mm to the largest 56 mm x 48 mm. Test size and shape, petaloid area and shape, genital pores, ambulacral furrows and periproct details indicate ANU 60565 is a closely allied form, reinforcing the strong Indo-Pacific affinities of the Yule Island fauna. There are no Recent occurrences of var. *sinaiticum* Fraas.

The distinctive marginal tuberculation, indicative of the possession of robust frill spines, and the thick, strong test of ANU 60565 suggests this species inhabited a sandy substrate constantly swept by currents. Robust frill spines borne by scattered, large antero-marginal tubercles, by bending down, served to reduce shifting and maintain test orientation.

Material

ANU 60565, a complete test from locality 8280-1, south of Tete ne'ina Beach, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Laganum depressum delicatum Mazzetti, 1894
Figs 3e-h

Synonymy

- *Laganum fragile* Mazzetti 1894, p. 217.
- *Laganum delicatum* Mazzetti 1894, p. 241.
- *Laganum depressum* Lesson in L. Agassiz 1841, Stockley 1927, p. 115: Pliocene, Zanzibar.
- *Laganum depressum*, var. *delicatum* Mortensen 1948a, p. 318.

Description

Test very small, length x width ranging from 11.5 mm x 11.0 mm in ANU 60567 to 19.5 x 17.0 mm in ANU 60568. Outline distinctly more rounded than that typical of *L. depressum* and even quite circular in the tests of ANU 60566 and 60567. Test is low with thickened edges; oral side is distinctly concave. Test is fairly strong.

Petaloid region about 0.7 of test length. Petals are relatively narrow, broadest adapically, open distally. Interporiferous zone is flush with test, with even covering of fine tubercles. Ambulacral furrows are shallow and extend 2/3 distance to edge of test.

Interambulacra in contact with apical system; covered by an even scattering of primary and miliary tubercles. Rounded ambital region with dense covering of primary tubercles. Density of primary tubercles on marginal oral surface rapidly diminishes towards the peristome, with primary tubercles confined to interambulacral regions adjacent to the peristome. Remainder of oral surface is covered by fine miliary tubercles.

Apical system typically low, although it may be distinctly raised in some specimens (ANU 60568, 60569). Genital pores five, visible in the smallest specimen, ANU 60567, with a test length of 11.5 mm. Mortensen (1948a) made a similar observation, noting their presence in tests of 9-10 mm length. Peristome round. Periproct is transversely elliptical to rounded, located closer to posterior edge, varying from two to four times its own diameter from the edge.

Remarks

Laganum depressum delicatum Mazzetti, 1894 is a smaller form than the typical *L. depressum*, with none exceeding 30 mm test length (Mortensen 1948a). As such, Mortensen (1948a) was of the opinion that it should not simply be included with *L. depressum*, although he was undecided whether it represented a distinct species or a variety of *L. depressum*. The distinctive development of marginal frill spines on the test of var. *delicatum* from Yule Island also serves to differentiate it from local specimens of *L. depressum*. Fossils figured by Stockley (1927) from the Pliocene of Zanzibar are, in the view of Mortensen (1948a: 319), likely to be var. *delicatum*. Extant var. *delicatum* is only known from the Red Sea (Mortensen 1948a).

The presence of well developed outer marginal frill spines on var. *delicatum* were probably used to sieve sand, burrow and to act as a steering device. It is likely that the laganid was a sand dweller, possibly a seagrass meadow constantly swept by currents.

Material

Ten complete tests including ANU 60566 and 60567 from locality 8280-1, south of Tete ne'ina Beach; ANU 60568 and 60569 from locality 8280-2, immediately north of Tete ne'ina Beach; and ANU 60570 from locality 8280-4, northwest of Aru're village, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

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APPENDIX

Collection details

All collection sites are located along the eastern shoreline of Yule (Rabao) Island, Central Province, PNG (Fig. 1). Grid references are from the Kairuku 1: 50 000 Sheet 8280-III (Edition 1).

8280-1: Collection from a 400 m interval along low coastal cliffs north from D'Albertis Point, near old Kairuku Government Station, to Tete ne'ina Beach (GR 502240 to GR 502244). Interval collected represents the lower levels of the Kairuku Formation.

8280-2: Collection from an approximately 250 m interval of coastline immediately north of Tete ne'ina Beach. Centered on GR 501246. Interval collected is in the mid-levels of the Kairuku Formation, slightly higher level than for locality 8280-1.

8280-3: Collection interval is a 100 m section of shoreline cliffs, extending south from the mouth of a small stream at GR 492260. This sequence probably represents the highest level of the Kairuku Formation collected. Same locality as microfossil locality 24 of Francis et al. (1982). Foraminifera from this site were assigned a N18/19 (Lower Pliocene) age.

8280-4: Lower section of high coastal cliffs behind and to the immediate south of a small beach approximately 500 m north of Aru're village at GR 495259. Stratigraphically equivalent to locality 8280-3.

Echinoids of the Kairuku Formation (Lower Pliocene), Yule Island, Papua New Guinea: Regularia

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Regular sea urchins are an important component of the rich and diverse echinoid fauna of the Lower Pliocene Kairuku Formation, Yule Island, Papua New Guinea. Seven taxa are recognised, including the cidaroids *Phyllacanthus imperialis* var. *javana* K. Martin, 1885, *Phyllacanthus* sp. and *Prionocidaris verticillata* (Lamarck, 1816), the toxopneustids *Cyrtechinus verruculatus* (Lütken) and *Schizechinus* cf. *tuberculatus* (Pomel), a temnopleurid *Temnotrema macleayana* (Tenison-Woods) and a parasaleniid *Parasalenia poehli* Pfeffer, 1887. The cidaroids, parasaleniid and temnopleurid occupied shallow-water reef habitats. The toxopneustids were dominant herbivores in adjacent seagrass meadows. The strong affinities evident between the seagrass meadow- and shallow-water sand-dwelling echinoid faunas of Yule Island and fossil and extant faunas of the Red Sea region, parallel the geographic patterns of species diversity of Indo-Pacific seagrasses, corals and mangroves.

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KEYWORDS: *Cyrtechinus*, Echinoidea, Palaeoecology, Papua New Guinea, *Parasalenia*, *Phyllacanthus*, Pliocene, *Prionocidaris*, Regularia, *Schizechinus*, *Temnotrema*

INTRODUCTION

The Tertiary faunas of Yule Island, and along the south coast of eastern New Guinea (Montgomery 1930), represent the nearest marine fossil occurrences to the Great Barrier Reef (Fig. 1). The Great Barrier Reef's rich and diverse shallow-water echinoderm fauna, in particular, has been intensively documented, including (from north to south) the Murray Islands in Torres Strait (H.L. Clark 1921), Cairns-Pipon Island-Raine Island region (Gibbs et al. 1976), Low Isles (H.L. Clark 1932; Endean 1956), Swain Reefs (A.M. Clark 1975) and the Capricorn-Bunker Groups (Endean 1953). Although it is widely accepted that a significant component of the echinoderm faunas of tropical Australia migrated southward from the East Indies via the Torres Strait or the Arafura Sea (A.H. Clark 1911; H.L. Clark 1946; Endean 1957), with no marine Tertiary record in Queensland, palaeontology has not been of use in determining migrations to this region (Endean 1957). Torres Strait prior to the late Quaternary was emergent (Australasian Petroleum Company 1961; Struckmeyer et al. 1993) and the eastern coast of New Guinea was in closest faunistic contact with the Great Barrier Reef, the coastline at the time (H.L. Clark 1946; Ekman 1953). Accordingly, many of the Lower Pliocene echinoids from Yule Island may be ancestral to those now living on the Great Barrier Reef and elsewhere along tropical northern Australian coasts.

This paper is the third in a series describing the echinoid fauna of the Kairuku Formation, Yule Island, Central Province, Papua New Guinea (Fig. 2). Elements of the Kairuku fauna have been described by Lindley (2001, 2003a). The present descriptions are based on collections made by the writer in January 2002, and the reader is referred to Lindley (2003a) for collection details. Specimens have been temporarily allocated Department of Geology, Australian National University repository numbers, pending their repatriation to Papua New Guinea (PNG) at the conclusion of studies, where they will be housed in the Department of Geology, University of Papua New Guinea, Port Moresby. The classification used herein follows that of Fell and Pawson (1966).

PALAEOECOLOGY

Foraminifera have been used by Haig et al. (1993: Fig. 5) to demonstrate rapid shallowing during the deposition of the Kairuku Formation, from mid-

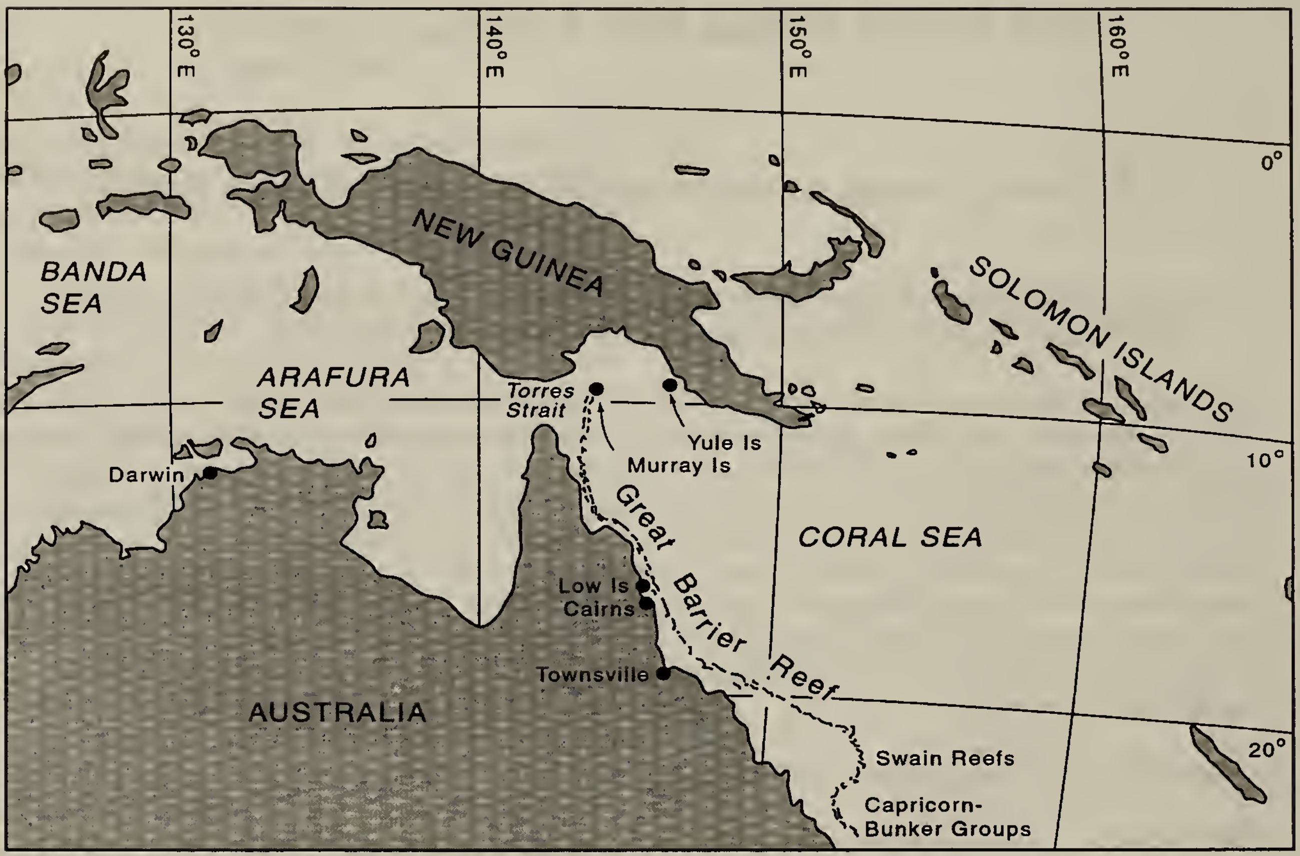

Figure 1. Locality map showing proximity of Yule Island to northern Great Barrier Reef.

neritic in the lower part to innermost neritic carbonate sand facies higher in the formation. The carbonate sand facies, predominant in the sequence collected during the present work, includes coral-rich beds and *Marginopora*-rich sands and has been interpreted by Haig et al. (1993) to have accumulated in seagrass meadows. However, Lindley (2001, 2003a) using the echinoid fauna of the Kairuku Formation, concluded that although some elements of the fauna, including the clypeasterids and laganids, were undoubtedly members of an infaunal seagrass community confined to shallow-water coarse sands, others occupied turbulent-water reef habitats and shallow-water sandy substrates constantly swept by currents. Bathymetric ranges of extant species of Yule Island echinoids indicate water depths during the deposition of the Kairuku Formation from littoral to about 40 m (Lindley 2003a), closely coinciding with Hemminga and Duarte's (2000) observation that the majority of modern seagrasses are confined to depths of less than 20 m.

Tropical echinoids are typically generalist feeders, consuming algae, seagrasses and invertebrates, and considerable data is available on the impacts of their grazing patterns on other coral reef organisms (Hatcher 1983). Echinoids are the dominant invertebrate herbivore in tropical and sub-tropical seagrass communities (McPherson 1965, 1968; Ogden et al. 1973; Hemminga and Duarte 2000). High population densities of the toxopneustid *Lytechinus* A. Agassiz, 1863 commonly leads to overgrazing events in the seagrass beds of the northern Gulf of Mexico (Valentine and Heck 1991). The toxopneustid *Tripneustes* L. Agassiz, 1841 is a dominant consumer of live seagrass leaves in PNG and Philippine seagrass beds (Nojima and Mukai 1985; Klumpp et al. 1993). Therefore, it is likely that *Cyrtechinus verruculatus* (LŸtken) and *Schizechinus* sp., close relatives of *Lytechinus* and *Tripnesutes*, were important herbivores in the seagrass meadow community at the time of deposition of the Kairuku Formation. The relative abundance of *C. verruculatus* as a fossil in the formation is probably related to the enhanced preservation potential associated with this habitat.

Turbulent, shallow-water habitats were developed in and around fringing reef, located seaward of the apparently extensive seagrass meadows. *Parasalenia poehli* Pfeffer, 1887 occupied well concealed habitats, among branches of corals or hidden in crevices beneath coral rock. The small cidaroid *Prionocidaris verticillata* (Lamarck, 1816) was restricted to the reef or lived on adjacent coral sands.

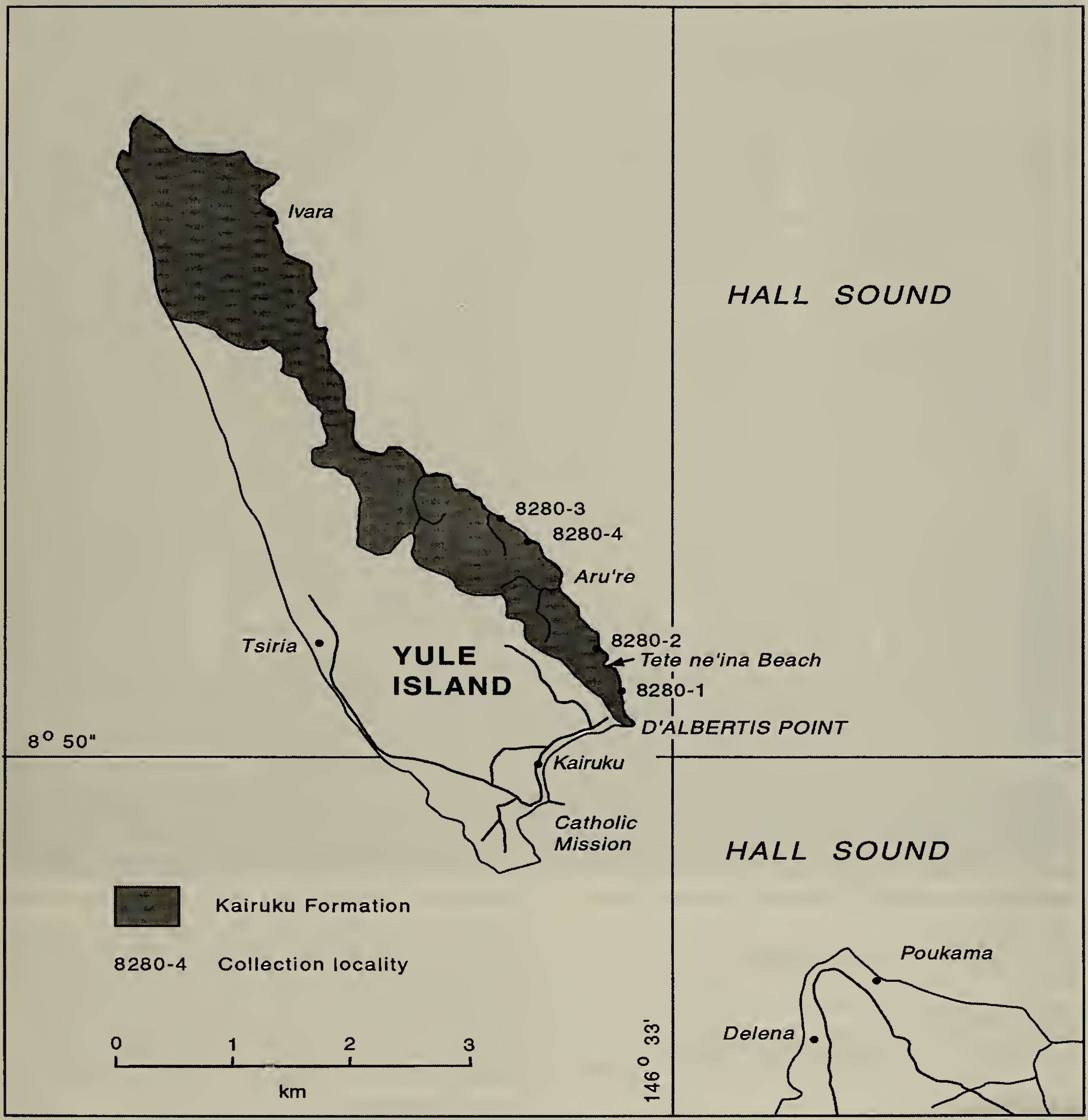

Figure 2. Yule Island, Central Province, Papua New Guinea, showing distribution of Kairuku Formation and collection localities. Base from Kairuku 1:50 000 Sheet 8280-III (Edition 1).

The large cidaroids *Phyllacanthus imperialis* var. *javana* K. Martin, 1885, and *Phyllacanthus* sp. may have favoured the outer side of the reef below low-tide mark, similar to living *P. imperialis* on the nearby Murray Islands (H.L. Clark 1946). The small temnopleuroid *Temnotrema macleayana* (Tenison-Woods) was also an element of the highly turbulent-water habitat (Lindley 2001).

Echinoids play a major role in reef destruction and may be growth limiting (Davies 1983). Glynn et al. (1979) have shown that the cidaroid *Eucidaris* Pomel, 1883, an inhabitant of intertidal reefs, grazes heavily on live corals, estimating an annual rate of bio-erosion of marine limestone attributable to this echinoid in the order of 1.7 kg/m^2. The high rate of marine erosion caused by *Eucidaris* is important in the generation of major reef-flanking sediment accumulations composed of coral and coralline particles excreted by the echinoid (Glynn et al. 1979).

The strong affinities of elements of the Yule Island fauna with both Indo-Pacific and Red Sea echinoid communities have been highlighted in Lindley (2003a) and the present work. These affinities are strongest amongst the species-rich infaunal and epifaunal echinoid communities of the seagrass meadow and the current-swept shallow-water sands. Similar geographic patterns of species richness are evident in corals and mangroves, and parallel seagrass species richness (Heck and McCoy 1979). Seagrass meadows with the richest species diversity are found in the Indo-Pacific and the Red Sea region and the parallelism present between the Yule Island echinoids and seagrasses suggests, in the words of Hemminga and Duarte (2000), that the ‘constraints and processes responsible for the development and maintenance of species diversity of these taxa have been linked throughout their evolutionary history’.

SYSTEMATIC PALAEONTOLOGY

Class ECHINOIDEA Leske, 1778
Subclass PERISCHOECHINOIDEA M’Coy, 1849
Order CIDAROIDA Claus, 1880
Family CIDARIDAE Gray, 1825
Subfamily RHABDOCIDARINAE Lambert, 1900, emended Fell 1966
Genus PHYLLACANTHUS Brandt, 1835

Synonymy

Leiocidaris Desor, 1885, p. 48.

Type species

Cidarites (Phyllacanthus) dubia Brandt, 1835, p. 67, by original designation.

Remarks

Phyllacanthus Brandt, 1835 is a strictly Indo-Pacific and Australasian genus, generally restricted by most workers (Mortensen 1928; Chapman and Cudmore 1934; H.L. Clark 1946; Philip 1963; A.M. Clark and Rowe 1971) to forms having thick, smooth and cylindrical spines. It is on this basis that the Yule Island specimens can clearly be assigned to *Phyllacanthus*. Mortensen (1928) and Philip (1963) provided reviews of extant and fossil species of this genus. Seven living species have been described by Mortensen (1928, 1936), with 4 being confined to the Australian coast (Mortensen 1928; H.L. Clark 1946; Philip 1963). While fossil test fragments are rare, spines of *Phyllacanthus* are well documented in the Tertiary sequences of the Indo-Pacific region and include *Phyllacanthus javana* K. Martin, 1885 and *Phyllacanthus imperalis* var. *javana* K. Martin from the Miocene of Java (Jeannet and R. Martin 1937); *Phyllacanthus imperialis* (Lamarck) from Madagascar, Middle Pliocene of Java, Upper Miocene of Vanuatu, Lower Miocene to Pleistocene of Fiji and the Quaternary of the Suez region (Mortensen 1928; Jeannet and R. Martin 1937; Philip 1963); *Phyllacanthus dubius* Brandt, from the Middle Pliocene of Java (Jeannet and R. Martin 1937); *Phyllacanthus dubius* var. *sundaica* (R. Martin) (*non Phyllacanthus sundaica* K. Martin, 1885) from the Lower Miocene of Java (Jeannet and R. Martin 1937); and *Phyllacanthus* sp. from the Pliocene of Kenya (Philip 1963).

Phyllacanthus is a littoral genus that exhibits a marked preference for seas in which the surface temperature does not fall below the winter isotherm of 15°C (Fell 1966). Like other cidaroids it is a shallow-water dweller, with a preference for hard bottom, such as reefs (Mortensen 1928; Fell 1966). Cidaroids feed upon bottom animals, including molluscs, annelids, bryozoans, foraminifera and sponges (Fell 1966).

F. Chapman and I. Crespin (in Montgomery 1930) recorded the presence of spines of *Phyllacanthus sundaica* K. Martin, 1885 from ‘the limestones of the upper part of e stage’ at Delena, across Hall Sound on the mainland (= Ou Ou Limestone Member of the Middle to Late Miocene Lavao Group, Yule Island: Francis et al. 1982) (Fig. 2). This species is now considered a synonymn of *Chondrocidaris gigantea* (A. Agassiz) (Mortensen (1928: 492). The primary spines of this large species carry very coarse thorns in a random arrangement. Spines of this type were not collected from the Kairuku Formation during the present fieldwork.

Phyllacanthus imperialis var. **javana** K. Martin, 1885

Figs 3a-b

Synonymy

Phyllacanthus javana K. Martin, 1885, p. 289: Mortensen 1928, p. 503; Philip 1963, p. 202; Upper Miocene, Java.

Phyllacanthus cf. *imperialis*, cf. *dubia* Duncan and Sladen, 1885, p. 284; Miocene.

Phyllacanthus javanus: Gerth 1922, p. 517; F. Chapman and I. Crespin in Montgomery 1930, p. 57, 58; Chapman and Cudmore 1934, p. 131; Lindley 2001, p. 119; Upper Miocene, Java; Lower Pliocene, Yule Island.

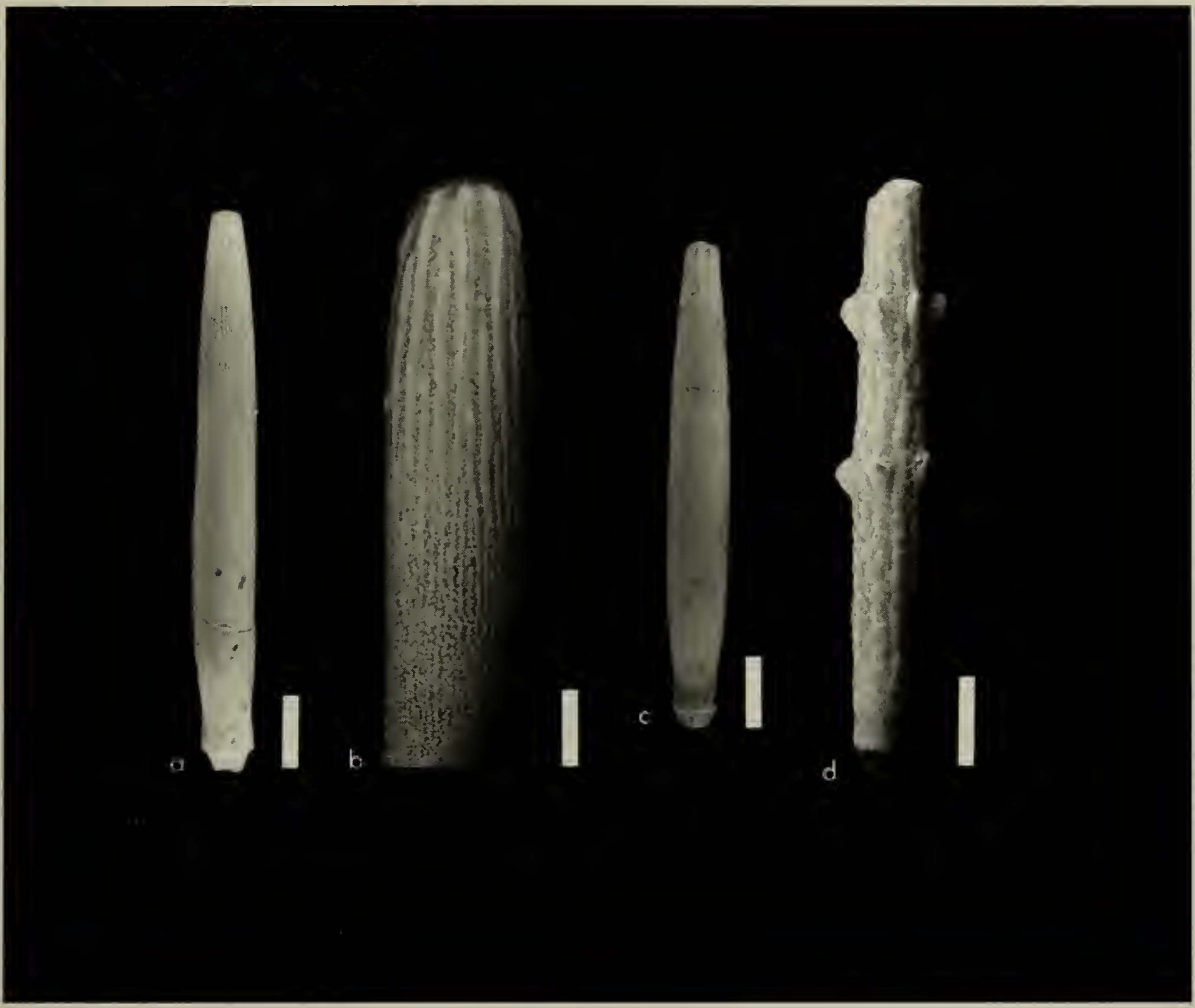

Figure 3. Cidaroid echinoids. *Phyllacanthus imperialis* var. *javana* K. Martin, 1885. Lower Pliocene, Yule Island, Central Province. 3a, ANU 60592, lateral view of spine. Bar scale = 10 mm; 3b, ANU 60598, detail of distal spine end. Bar scale = 2.5 mm. *Phyllacanthus* sp. Lower Pliocene, Yule Island, Central Province. 3c, ANU 60590, lateral view of spine. Bar scale = 10 mm. *Prionocidaris verticillata* (Lamarck). Lower Pliocene, Yule Island, Central Province. 3d, ANU 60589, lateral view of incomplete spine. Bar scale = 2.5 mm.

Leiocidaris imperialis: Jeannet 1928, p. 465.

Leiocidaris (Phyllacanthus) imperialis: Jeannet 1934, p. 13; Miocene, Java.

Phyllacanthus imperialis var. *javana* K. Martin, Jeannet and R. Martin 1937, p. 222, 223; Philip 1963, p. 202; Upper Miocene, Java.

Description

No test fragments which belong to this species have been identified. Primary spines are moderately thick, cylindrical, slightly fusiform. Spine length ranges from 36-80 mm, with a maximum diameter (measured on largest spine) of 9 mm, occurring at 1/3 distance from proximal end; spine gently tapers towards apex. Collar is finely longitudinally striated; collar length between 3.5-5 mm, with an obvious swelling at about 7 mm above collar on spine ANU 60592 of 80 mm length. Surface of shaft with a smooth appearance, but with low magnification a fine ornament is evident, consisting of low, rounded granules forming numerous (> 50) longitudinal ridges. On the distal 1/3 of spine the numerous, occasionally sinuate ridges merge, and interspaces become narrower, to form fewer (15-20), somewhat higher ridges, passing to a fluted spine end.

Remarks

Jeannet and R. Martin (1937) noted that the spines of *Phyllacanthus imperialis* var. *javana* K. Martin, 1885 from the Upper Miocene of Java, are generally slimmer and are often more pointed than those of *Phyllacanthus imperialis* (Lamarck). They also noted that the spine collar length of var. *javana*, ranging from 2.5-4 mm, is distinctly shorter than the 6 mm of *P. imperialis*. The spines of *P. imperialis*, and by association those of *P. javana*, are relatively short, usually equal to test diameter (Mortensen 1928). Mortensen (1928) considered var. *javana* a close relative to *P. imperialis*.

Phyllacanthus imperialis is the only species of *Phyllacanthus* that is widespread throughout the tropical Indo-Pacific (Mortensen 1928; H.L. Clark 1946; A.M. Clark and Rowe 1971). *Phyllacanthus imperialis* from the Murray Islands, Torres Strait, has a distinctive habitat, favouring the outer side of reef below the low-tide mark (H.L. Clark 1946).

Material

Eight isolated primary spines: ANU 60593, ANU 60596-98 from locality 8280-1; ANU 60592 from locality 8280-3; ANU 60594-95, ANU 60599 from locality 8280-4. All localities are from the east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Phyllacanthus sp.
Fig. 3c

Description

No test fragments which belong to this species have been identified. Primary spines are moderately thick, cylindrical, fusiform, with length ranging from 37.5-67.5 mm, with a maximum diameter of 9.5 mm measured at 1/3 distance from proximal end on largest spine. Spine gently tapers to apex. Collar length 3 mm in ANU 60590; details of collar ornament unknown. Surface of shaft is finely and uniformly granulated (not visible to the naked eye), the granules arranged in regular longitudinal series along length of spine. The distal 1/5 length of spine carries nine high ridges passing to a fluted spine end.

Remarks

The primary spines of *Phyllacanthus* sp. in many respects resemble those of var. *javana*, but the presence of notably fewer high ridges on the distal part of the spine is in contrast to the many ridges (15-20) present on spines of the latter form. The Yule Island spine probably represents another variety of *P. imperialis*.

Material

Two isolated primary spines: ANU 60590-91 from locality 8280-1, immediately south of Tete ne'ina Beach, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Genus PRIONOCIDARIS A. Agassiz, 1863

Synonymy

Stephanocidaris A. Agassiz, 1872 (*non* 1863).
Plococidaris Mortensen, 1909, p. 51, 51.

Type species

Cidarites pistillaris Lamarck, 1816, p. 55.

Remarks

The status of the name *Plococidaris* Mortensen, 1909, with *Cidarites bispinosa* Lamarck, 1816 designated as type species, has been the subject of discussion following Mortensen's (1928) referral of *bispinosa* to *Prionocidaris* A. Agassiz, 1863 (H.L. Clark 1946: 287; A.M. Clark and Rowe 1971: 151). These workers considered Mortensen's (1928) retention of the name *Plococidaris*, with *Cidarites verticillata* Lamarck, 1816 redesignated as type species, to be contrary to the Rules of Nomenclature, and it is regarded as a synonym of *Prionocidaris*.

Prionocidaris verticillata (Lamarck, 1816)
Fig. 3d

Synonymy

Cidarites verticillata Lamarck, 1816, p. 56.
Phyllacanthus cf. *verticillata* Duncan and Sladen, 1885, p. 284; Miocene, India.
Cidaris verticillatus: Lemoine, 1906, p. 256; Miocene, Madagascar.
Phyllacanthus verticillatus Cottreau, 1908, p. 38.
Plococidaris verticillata Mortensen, 1909, p. 51, 53; Mortensen 1928, p. 428; Jeannet and R. Martin 1937, p. 220.
Prionocidaris verticillata Döderlein, 1911, p. 242; H.L. Clark 1921, p. 145; H.L. Clark 1932, p. 211; H.L. Clark 1946, p. 287; A.M. Clark and Rowe 1971, p. 151.
Leiocidaris (Plococidaris) verticillata: Jeannet 1934, p. 11; Pliocene, Ceram.
T. Mortensen (1928), A Monograph of the Echinoidea 1, Cidaroidea, p. 428, details the previous synonymies.

Description

No test fragments which belong to this species have been identified. Primary spine small, slim, cylindrical with an incomplete length of 15 mm and a diameter of 1.5 mm. Collar length ca. 0.7 mm; details of collar ornamentation unknown. ANU 60589 with characteristic prominent whorls of blunt thorns, placed one above the other; two are preserved in specimen with three-four usually present in complete primary spines (Mortensen 1928; A.M. Clark and Rowe 1971). Smaller blunt thorns arranged in longitudinal series occur between successive whorls.

Remarks

Prionocidaris verticillata (Lamarck) is a small (30-40 mm diameter) extant species, widely distributed throughout the Indo-Pacific (Mortensen 1928; H.L. Clark 1946; A.M. Clark and Rowe 1971). In particular, the species has been recorded from the Torres Strait by H.L. Clark (1921), with a single specimen collected from Low Isles reef on the Great Barrier Reef, making it ‘one of the rarest of Australian echini’ (H.L. Clark 1946). In spite of the species’ widespread distribution, specimens are not common (H.L. Clark 1946). The species is restricted to coral reefs and many have been found by dredging on coral sand (Mortensen 1928).

P. verticillata, with the ‘very peculiar character of primary spines...may well claim to be the easiest recognizable of all species of Cidarids’ (Mortensen 1928). The species, with its distinct spines, stands alone in genus *Prionocidaris* (see key of A.M. Clark and Rowe 1971), so much so that Mortensen (1928: 428) was adamant that it should represent the type of a separate genus. *Prionocidaris verticillata*, or forms closely related to the species, have been found as fossil from the Miocene of Madagascar and India, Pliocene of Ceram (Indonesia), and the Quaternary of East Africa (Mortensen 1928).

Material

One isolated primary spine ANU 60589 from locality 8280-4, northwest of Aru’re village, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Subclass EUECHINOIDEA Bronn, 1860
Superorder ECHINACEA Claus, 1876
Order TEMNOPLEUROIDA Mortensen, 1942

Remarks

The temnopleuroid *Temnotrema macleayana* (Tenison-Woods) is present in the Kairuku Formation on Yule Island and was redescribed by Lindley (2001).

Family TOXOPNEUSTIDAE Troschel, 1872
Genus CYRTECHINUS Mortensen, 1943

Type species

Psammechinus verruculatus Lütken, 1864, p. 98, by original designation.

Remarks

Cyrtechinus Mortensen, 1943 and the closely related *Nudechinus* H.L. Clark, 1912 and *Gymnechinus* Mortensen, 1903, are distinguished by the number of plates in the buccal membrane. Accordingly, it is very difficult or even impossible to distinguish between naked tests of species of these taxa. All are small forms found in the tropical Indo-Pacific and western Indian Ocean (A.M. Clark and Rowe 1971: 142, 143) and, as with the temnopleurids, appear to be well adapted to life in shallow-water tropical regions, especially in the case of *Nudechinus* which has developed into a considerable number of species (Mortensen 1943). All three taxa have been noted from the Torres Strait and surrounding waters (Mortensen 1943; H.L. Clark 1946; A.M. Clark and Rowe 1971). The Yule Island specimens are assigned to *Cyrtechinus* because of the striking similarity of both ambulacral and interambulacral plating diagrams with those of Hawaiian specimens of the only species, *Cyrtechinus verruculatus* (Lütken) figured by Mortensen (1943: Figs 245a-b).

Cyrtechinus verruculatus (Lütken)

Figs 4a-g, 5a-b

Synonymy

Echinus (Psammechinus) verruculatus Lütken, 1864, p. 98.
Echinus verruculatus Lütken, 1864: Sluiter 1899, p. 110.
Lytechinus verruculatus H.L. Clark, 1912: H.L. Clark 1921, p. 147; H.L. Clark 1946, p. 321.
Cyrtechinus verruculatus (Lütken): Mortensen 1943, p. 393; A.H. Clark 1952, p. 267; A.M. Clark and Rowe 1971, p. 142, 143.
Cyrtacanthus verruculatus (Lütken): A.M. Clark and Rowe 1971, p. 156.
Stomechinid (?), Lindley 2001, p. 126.
T. Mortensen (1943), A Monograph of the Echinoidea 3(2), Camarodonta 1, p. 393, and A.M. Clark and F.W.E. Rowe (1971), Monograph of Shallow-Water Indo-West Pacific Echinoderms, p. 142, 143, details the previous synonymies.

Description

Test small, very regularly hemispherical; distinctly subpentagonal circumference in the largest specimens. Ambitus relatively low; distinctly sunken towards the peristome. It appears not to exceed a size

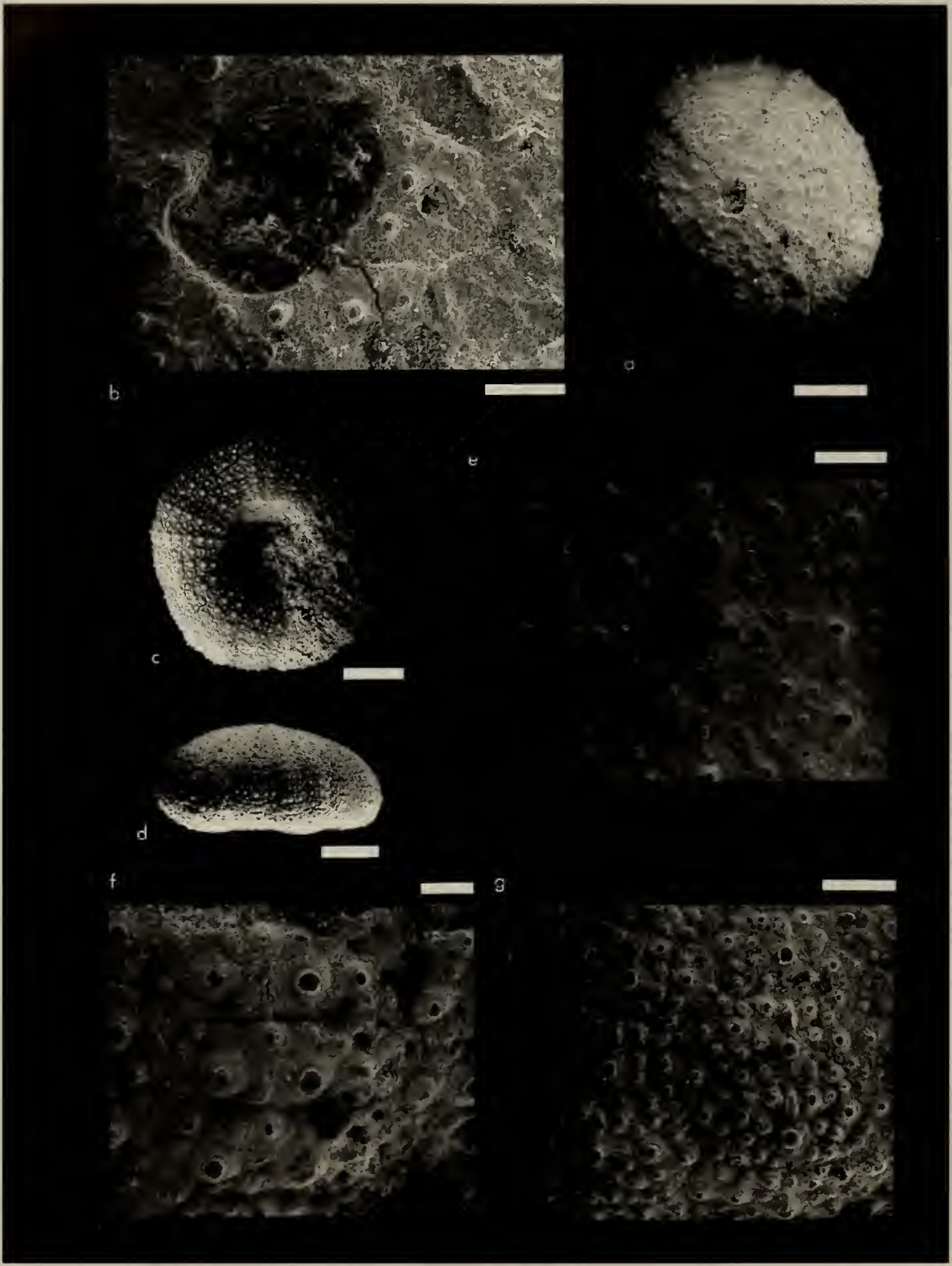

Figure 4. *Cyrtechinus verruculatus* (Lütken). Lower Pliocene, Yule Island, Central Province. 4a-b, ANU 60576, aboral view. Bar scale = 2.5 mm; portion of apical disc, showing periproct and small tubercles adapical to genital pores. Bar scale = 0.5 mm. 4c-f, UPNG F1184, oral, lateral views. Bar scale = 5 mm; apical disc with madreporite top centre, posterior to lower right. Bar scale = 1 mm; ambulacral plating at ambitus (refer to Fig. 5b for plating diagram). Bar scale = 0.5 mm. 4g, ANU 60572, interambulacral plating at ambitus (refer to Fig. 5a for plating diagram). Bar scale = 1 mm.

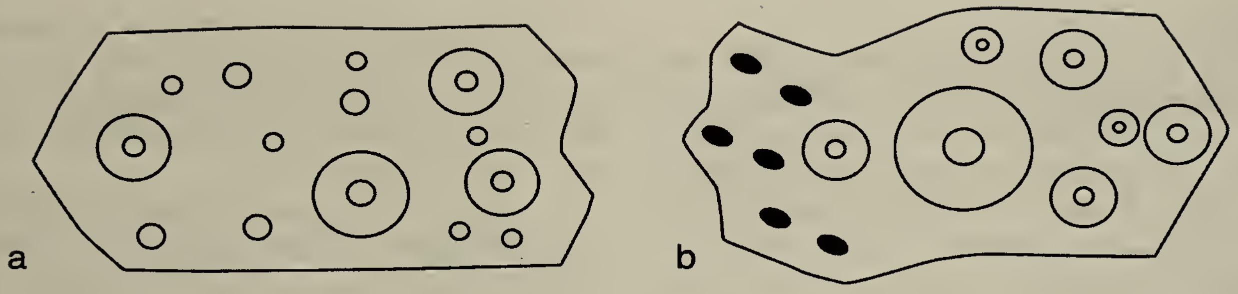

Figure 5. ***Cyrtechinus verruculatus*** **(Lütken). Lower Pliocene, Yule Island, Central Province. 5a-b, plating diagrams at ambitus for interambulacrum, ambulacrum.**

of c. 24 mm horizontal diameter (Table 1). Dimensions are comparable with those presented by Mortensen (1943) for the species, ranging from 10.5 to 24 mm horizontal diameter, with a single specimen of 27 mm considered by him to be very old. Both ambulacra and interambulacra densely covered with tubercles.

Apical system small with a central periproct. In smaller specimens (ANU 60576) Ocular I is insert; in larger specimens (UPNG F1184) both Oculars I and V are narrowly insert. The same relationships were described by Mortensen (1943) in Recent specimens of the species from the central Pacific and East African coast. Tubercles on apical plates increase in size with age, with older specimens having a single large tubercle located adapically to genital pore; young specimens (ANU 60576) have three small, equi-sized tubercles adapical to the genital pore.

Ambulacra at ambitus are about 2/3 width of interambulacra. Ambulacral plates compound, trigeminate, pore pairs in arcs of three. A prominent elevated primary tubercle is present in the middle of each plate, forming a vertical series. Tubercles imperforate, noncrenulate, as large as interambulacral primaries. Large secondary tubercles present admesially to the primary ambulacral tubercles, but do not form prominent vertical series. The number and arrangement of tubercles generally remains the same in various sized specimens. Interambulacral plates are about equal in height to opposite ambulacral plate. Each possesses a sub-central prominent imperforate, noncrenulate primary tubercle; each primary tubercle is surrounded by a semi-circular series of variously sized secondaries. In larger specimens (ANU 60572) there is a tendency for the development of weak ridging radiating from the primary tubercle towards secondaries, forming a sculpturing reminiscent of the temnopleurids.

Peristome large, about 1/3-1/2 horizontal diameter of test; twice size of apical system in larger specimens (Table 1). Gill slits are distinct and small. Tubercles of the oral surface, particularly surrounding the peristome, with a distinctly enlarged, elevated boss compared with those of the apical surface.

TABLE 1. ***Cyrtechinus verruculatus*** **(Lütken): Test dimensions in millimetres.**

Specimen	Diameter	Height	Apical system	Peristome
F1184	24	9	5	10
60578	21.5	7	-	9
60579	21	-	-	-
60577	19	9	4	-
60572	19	8	4	-
60582	18.5	9	-	7
60580	18	6	4	-
60583	17	-	-	-
60581	16.5	-	-	6
60576	16	7	4	6.5
60573	14.5	6	2.5	-
60575	14	6	-	-
60574	11	6	2.5	-

Remarks

Cyrtechinus verruculatus (Lütken) is a Recent species from the tropical Indo-West Pacific (Mortensen 1943; A.M. Clark and Rowe 1971). In particular, it has been recorded from the Java Sea, Sulu Sea and Torres Strait (Mortensen 1943). The fossil record of *C. verruculatus* is problematic given the uncertainty in distinguishing naked tests from those of the closely allied *Nudechinus* H.L. Clark, 1912, and *Gymnechinus* Mortensen, 1903 (Mortensen 1943: 398, 399; A.M. Clark and Rowe 1971). Fossil specimens from the Pleistocene deposits of Egypt have been referred to *Nudechinus scotioprennus* H. L. Clark, 1912, a species common in the Red Sea (Mortensen 1943). Specimens possibly referrable to *C. verruculatus* have been described from the East African coast, from the Pliocene of Mombasa Island and from Mozambique (Mortensen 1943). However, it is suffice to say that forms identical with *C. verruculatus* or an ancestor of the species were present in the western Indian Ocean during the Plio-Pleistocene.

Cyrtechinus is a small form typically restricted to the littoral zone. The low hemispherical test with a low down ambitus, was interpreted by Lindley (2001) as an adaptive strategy, giving stability in currents on either rocky or sandy substrates. Closely allied forms such as *Lytechinus* and *Tripneustes* are dominant consumers of live seagrass leaves in tropical seagrass communities (Nojima and Mukai 1985; Klumpp et al. 1993). *Cyrtechinus verruculatus* is interpreted as a seagrass grazer in meadows constantly swept by currents.

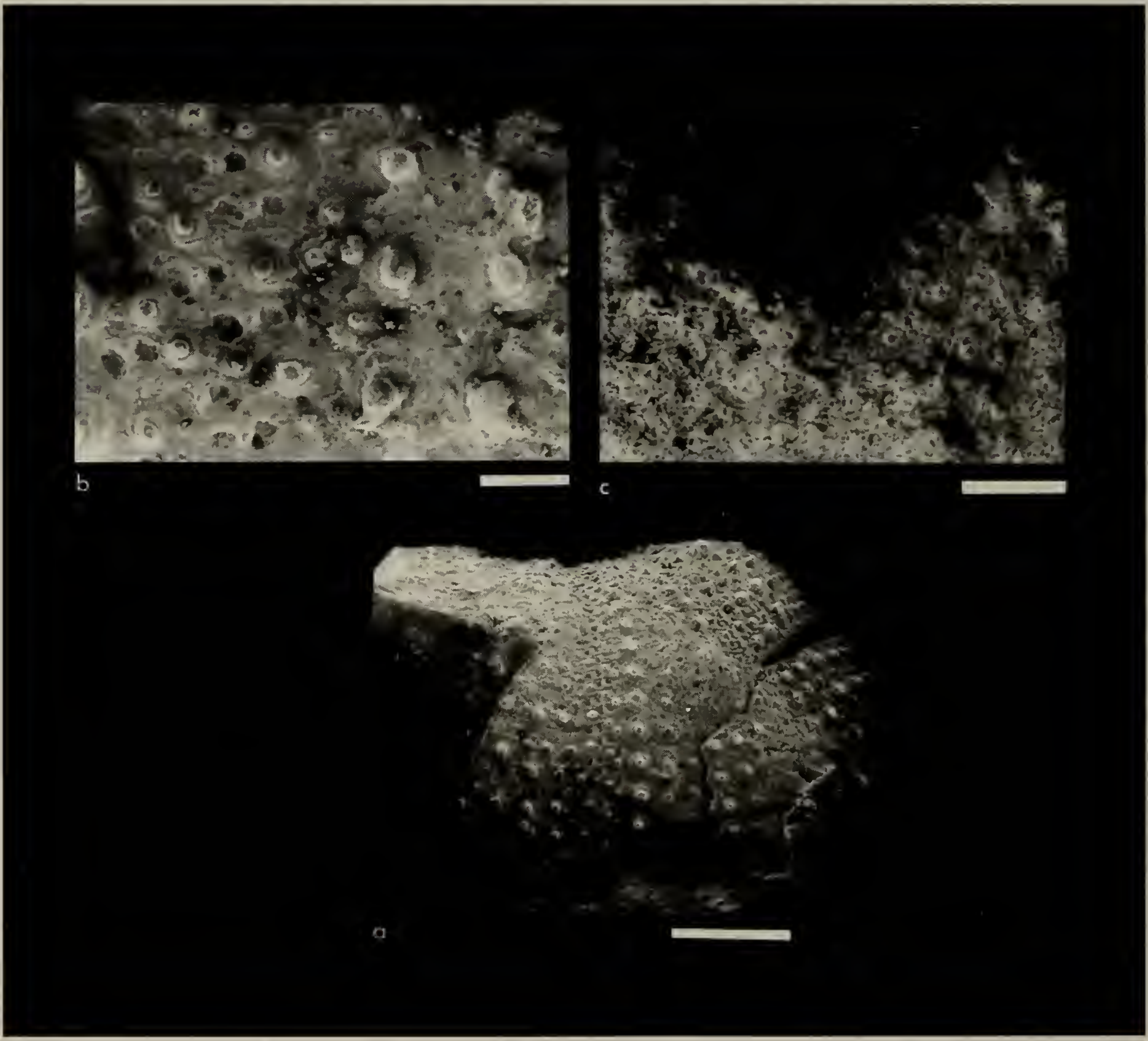

Figure 6. *Schizechinus* cf. *tuberculatus* (Pomel). Lower Pliocene, Yule Island, Central Province. 6a-c, ANU 60600, lateral view with peristome to top. Bar scale = 5 mm; ambulacral plating at ambitus (refer to Fig. 7a for plating diagram). Bar scale = 1 mm; portion of peristome showing deep gill slits. Bar scale = 2 mm.

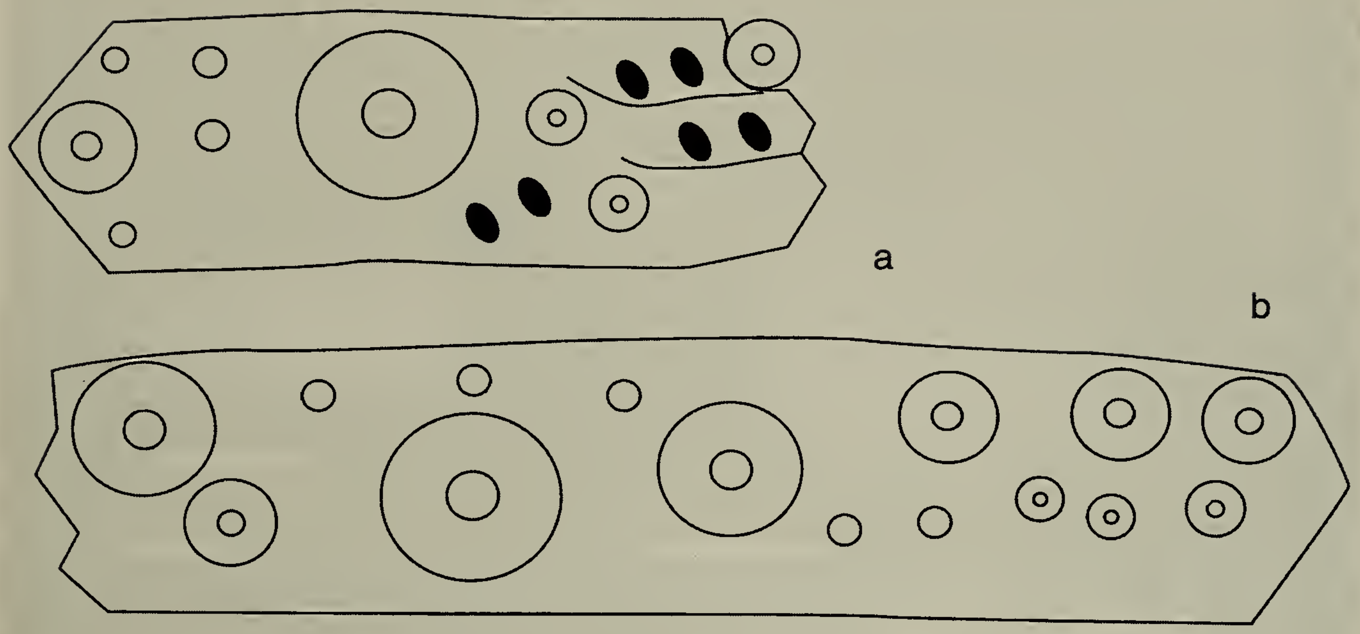

Figure 7. ***Schizechinus* cf. *tuberculatus* (Pomel). Lower Pliocene, Yule Island, Central Province. 7a-b, plating diagrams at ambitus for ambulacrum, interambulacrum.**

Material

Fourteen complete tests: ANU 60572-73, ANU 60575-83 from locality 8280-3; ANU 60574, ANU 60587 from locality 8280-4; and UPNG F1184 collected by R. Perembo from locality 24 of Francis et al. (1982) = locality 8280-3. All localities are northwest of Aru're village, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Genus SCHIZECHINUS Pomel, 1869

Synonymy

Toxophyma Lambert and Thiéry, 1925, p. 280.

Type species

Anapesus tuberculatus Pomel, 1887, p. 298, by original designation.

Remarks

The referral of the Yule Island form to *Echinus* cf. *stracheyi* by F. Chapman and I. Crepsin (in Montgomery 1930) is doubtful. The presence of a primary tubercle on every ambulacral plate clearly distinguishes the Yule Island species from the echinid *Echinus* Linné, 1758, in which primaries are present only on every alternate (or every third) ambulacral plate (Fell and Pawson 1966).

The Yule Island species can be confidently assigned to *Schizechinus* Pomel, 1869 using Mortensen's (1943) key for the Family Toxopneustidae. *Schizechinus* is the only large toxopneustid with trigeminate ambulacral plates each bearing primary and secondary tubercles arranged in regular parallel series (Mortensen 1943; Fell and Pawson 1966). *Lytechinus* A. Agassiz, 1863 is another toxopneustid with a similar test, but differs from *Schizechinus* in that the secondary tubercles do not form a regular series. Mortensen (1943) regards *Schizechinus* a near relation of *Lytechinus*. *Schizechinus* is known only from fossils, from the Mio-Pliocene of North Africa (Malta and Algeria) and Europe.

Schizechinus cf. **tuberculatus** (Pomel)
Figs 6a-c, 7a-b

Synonymy

Schizechinus tuberculatus Pomel, 1869, p. XLII.
Echinus cf. *stracheyi*: F. Chapman and I. Crespin in Montgomery 1930, p. 57; Lower Pliocene, Yule Island.

Description

No complete test is available. However, the portion of test preserved in ANU 60600 suggests a large test, c. 60 mm diameter, comparable with forms figured by Mortensen (1943). Test apparently of high hemispherical shape, inferred from shape of ambital region preserved in ANU 60601. Ambital outline inferred to be circular, relatively low; oral surface

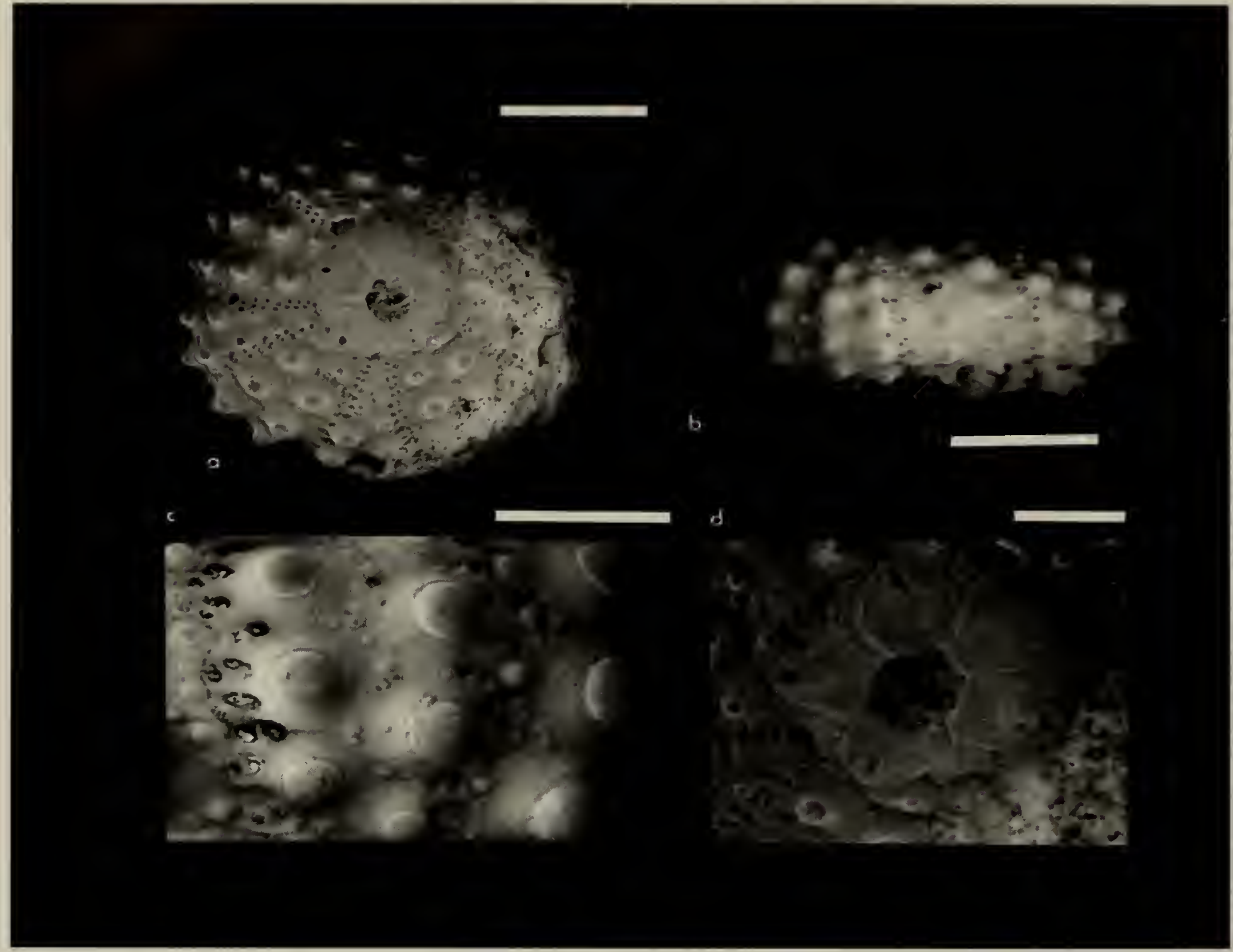

Figure 8. *Parasalenia poehli* Pfeffer, 1887. Lower Pliocene, Yule Island, Central Province. 8a-d, ANU 60584, aboral, lateral views. Bar scale = 5 mm; ambulacral plating at ambitus (refer to Fig. 9a for plating diagram). Bar scale = 2 mm; apical disc, with posterior to lower left. Bar scale = 2 mm.

flattened and distinctly sunken towards peristome (ANU 60600). Details of apical system unknown. Ambulacra at ambitus are about 1/2 width of interambulacra. Ambulacral plates compound, trigeminate pore pairs in arcs of three. A prominent elevated imperforate, noncrenulate primary tubercle, about the same size as interambulacral ones, is present in the middle of each plate, forming a vertical series. Large secondary tubercles are also present on each plate, forming a regular perradial series parallel with the primary series. A varying number of randomly placed small tubercles cover the plates.

Interambulacral plates at ambitus are about equal in height and twice the width of opposite ambulacral plate. Each possesses a sub-central imperforate, noncrenulate primary tubercle, forming a regular vertical series. Each primary is flanked by two secondaries, also forming regular series parallel with the primary series. Varying numbers of randomly placed small tubercles cover the remainder to each plate.

Peristome sunken, c. 10 mm diameter in ANU 60600; gill slits are distinct, deep.

Remarks

This large regular echinoid is represented only by fragmentary material, indicative of the poor preservation potential of such fragile forms (Kier 1977). However, the Yule Island material is tentatively referred to *Schizechinus tuberculatus* (Pomel), figured by Mortensen (1943: Fig. 291a,b) and Fell and Pawson (1966: Fig. 320, 3b,c), on the basis of similarity of (a) ambulacral and interambulacral plating in the ambital region, and (b) inferred test shape. *Schizechinus tuberculatus* (Pomel) is a Miocene echinoid from Algeria. The Yule Island occurrence is the first record of the subtropical *Schizechinus* in the southern hemisphere.

Schizechinus also includes another 12 species, predominantly from the Miocene and Pliocene of the

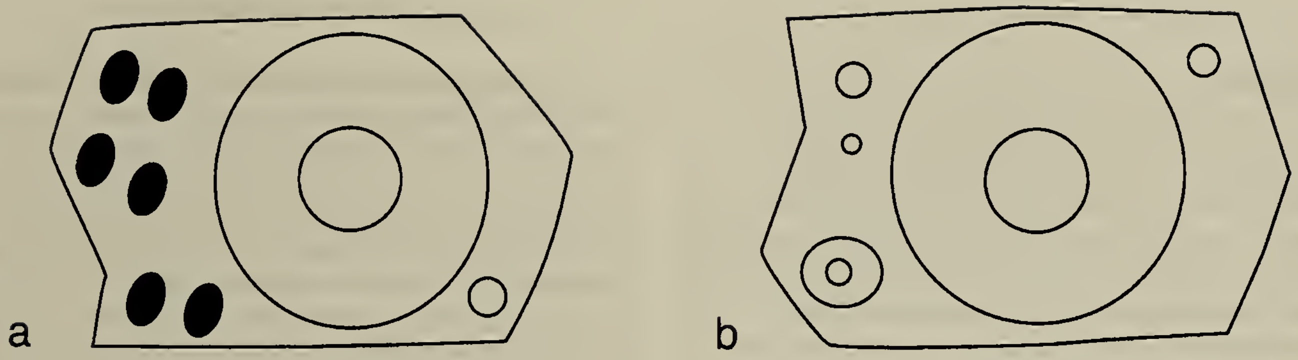

Figure 9. *Parasalenia poehli* Pfeffer, 1887. Lower Pliocene, Yule Island, Central Province. 9a-b, plating diagrams at ambitus for ambulacrum, interambulacrum.

Mediterranean region and Europe (Mortensen 1943). Mortensen (1943) figured two of these species, viz: *Schizechinus angulosus* (Pomel) from the Miocene of Algeria and *Schizechinus duciei* (Wright) from the Miocene of Malta. Test shape is an obvious difference between figured species. Little information on the remaining ten species is presently available to the writer and the Yule Island form may well represent a new species.

Material

Three fragmentary tests: ANU 60600 is a preserved portion of the oral surface, with the margin of the peristome and gill slits; ANU 60601 is a portion of an interambulacrum at the ambitus, with some of the oral surface; ANU 60602 is a portion of the ambital surface. ANU 60600-01 were collected from locality 8280-1; ANU 60602 from locality 8280-3. All localities are from the east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Order ECHINOIDA Claus, 1876
Family PARASALENIIDAE Mortensen, 1903
Genus PARASALENIA A. Agassiz, 1863

Synonymy

Cladosalenia A. Agassiz, 1872, p. 148.

Type species

Parasalenia gratiosa A. Agassiz, 1863, p. 22.

Parasalenia poehli Pfeffer, 1887

Figs 8a-d, 9a-b

Synonymy

Parasalenia pöhlii Pfeffer, 1887, p. 110: H.L. Clark, 1912, p. 369; Lambert and Thiéry, 1914, p. 269; H.L. Clark, 1922, p. 142; H.L. Clark, 1925; H.L. Clark, 1928, p. 469; Mortensen, 1940, p. 49; Mortensen, 1943, p. 272; H.L. Clark, 1946, p. 331.

Parasalenia gratiosa de Meijere, 1904, p. 98.

Parasalenia poehli: A.M. Clark and Spencer Davies, 1966, p. 599, 603; A.M. Clark and Rowe, 1971, p. 142, 157.

Description

Test small, distinctly elongate and low, ANU 60585 measuring 8 x 7.5 x 4.5 mm and ANU 60584 20 x 18 x 9 mm. Dimensions are comparable with those of Mortensen (1943), who noted a range in test length x height from 8 x 3 mm to 17 x 6 mm, and H.L. Clark (1928, 1946), who noted a single specimen from the northern Great Barrier Reef 16 x 13 x 7 mm. Details of oral surface unknown. Mortensen (1943) noted that the test is not very strong, and is easily broken.

Apical system is dicyclic, 8 mm x 6.5 mm, elongate in the plane of long axis of test. Diameter of periproct is about 1/4 of the long diameter of the apical system. The madreporite is limited in size, with pores only occupying about 1/3 of plate. Genital plates are smooth and are without tubercles. Oculars are widely exsert and small.

Ambulacra at ambitus match the width of interambulacra. Ambulacral plates compound, trigeminate, pore pairs in arcs of three. Pore zones very narrow. A large primary tubercle occupies much of plate, leaving little space for development of secondary tubercles and granules. Primary tubercles are imperforate and non-crenulate; the mamelon is relatively large and areole indistinct. Secondary tubercles and granules are either absent or number at most one or two per plate. Primary tubercles on the 2-3 uppermost ambulacral plates are very much diminished in size. Interambulacral plates are about equal in height to opposite ambulacral plate. Primary interambulacral tubercles very large, leaving only a restricted adradial space for 2-3 secondary tubercles. Secondary tubercles do not form regular horizontal or vertical series.

Details of peristome unknown.

Remarks

Parasalenia A. Agassiz, 1863 includes two Recent species, *Parasalenia gratiosa* A. Agassiz, 1863 and *Parasalenia poehli* Pfeffer, 1887, with an Indo-Pacific and Red Sea distribution, and a single fossil species, *Parasalenia fontannesi* Cotteau, 1913, from the Lower Miocene of France (Mortensen 1943; Fell and Pawson 1966). H.L. Clark (1928, 1946) noted a single specimen of *P. poehli* from the northern Great Barrier Reef, representing the only documented occurrence of the species in Australian waters.

There has been considerable discussion regarding the validity of *poehli* as a species (Mortensen 1943; H.L. Clark 1946). *Parasalenia poehli* is a much smaller form, with the largest recorded being 17 mm long, half that of *gratiosa* (Mortensen 1943). Both Mortensen (1943) and H.L. Clark (1946) agree that periproct size is important in distinguishing the two forms. The periproct of *poehli* is relatively smaller, about 1/4 of the long diameter of the apical system; this compares with 1/3-1/2 that length in *gratiosa*. H.L. Clark (1946) regarded the presence or absence of tubercles on genital plates as an important diagnostic character, but Mortensen (1943) believed this character to be 'quite unreliable'. Both Mortensen (1943) and H.L. Clark (1946) observed that the genital plates of *gratiosa* carry tubercles, but not in *poehli*. In addition to periproct size, Mortensen (1943) emphasised the size of primary tubercles, with *poehli* having smaller primary tubercles, with more space for secondary tubercles, than *gratiosa*. A.M. Clark and Rowe (1971) recognised both *poehli* and *gratiosa* as valid species, but using differing characters to those of Mortensen (1943) and H.L. Clark (1946). They distinguished species using, amongst other characters, the length of primary spines relative to test length. In the case of *gratiosa* spines are about equal to test length, whereas for *poehli*, primary spines are only about half as long as test length. Spine length in the parasaleniids is expected to be proportionate to primary tubercle size, and this latter character, as used by Mortensen (1943), is therefore clearly useful in distinguishing naked tests.

Parasalenia occupies generally well concealed habitats, among the branches of corals or hidden in crevices and cavities beneath coral rock (H.L. Clark 1946). Mortensen (1943) noted a bathymetric range extending from littoral to c. 70 m.

Material

Two tests: ANU 60584 from locality 8280-3; ANU 60585 from locality 8280-4. Both localities are northwest of Aru're village, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

ACKNOWLEDGMENTS

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Echinoids of the Kairuku Formation (Lower Pliocene), Yule Island, Papua New Guinea: Spatangoida

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Spatangoid echinoids are well represented in the rich and diverse echinoid fauna of the Lower Plicoene Kairuku Formation, Yule Island, Papua New Guinea. Five taxa are recognised, including the schizasterid *Schizaster (Schizaster) alphonsei* sp. nov., the palaeostomatid *Palaeostoma kairukuensis* sp. nov., the brissid *Eupatagus (Eupatagus) pulchellus* (Herklots) and the spatangids *Maretia planulata* (Lamarck) and *Maretia cordata* Mortensen, 1948. The spatangoids, by comparison with the clypeasteroids and regularia, exhibit a high degree of endemism.

Manuscript received 18 November 2002, accepted for publication 11 December 2002.

KEYWORDS: Echinoidea, Spatangoida, *Schizaster*, *Palaeostoma*, *Eupatagus*, *Maretia*, Lower Pliocene, Papua New Guinea.

INTRODUCTION

This paper, describing spatangoid or burrowing echinoids, is the fourth in a series (Lindley 2001, 2003a, 2003b) on the rich and diverse echinoid fauna of the Kairuku Formation, Yule Island, Central Province, Papua New Guinea (PNG). Two new species are described and the spatangoids, by comparison with the clypeasteroids (Lindley 2003a) and regularia (Lindley 2003b), exhibit a high degree of endemism. The present descriptions are based on collections made by the writer in January 2002, and the reader is referred to Lindley (2003a) for locality details. Some specimens have been temporarily allocated Department of Geology, Australian National University repository numbers, pending their repatriation to PNG at the conclusion of studies, where they will be housed in the Department of Geology, University of Papua New Guinea, Port Moresby. The classification used herein follows that of Fischer (1966) and A.M. Clark and Rowe (1971).

SYSTEMATIC PALAEONTOLOGY

Class ECHINOIDEA Leske, 1778
Subclass EUECHINOIDEA Bronn, 1860
Superorder ATELOSTOMATA Zittel, 1879
Order SPATANGOIDA Claus, 1876
Suborder HEMIASTERINA Fischer, 1966
Family SCHIZASTERIDAE Lambert, 1905
Genus SCHIZASTER L. Agassiz, 1836

Type species

Schizaster studeri Agassiz, 1836, by subsequent designation of ICZN, 1948.

Diagnosis

Test small to large with anterior ambulacrum and frontal notch shallow to deep. Apical system located posterior of centre, with 2-4 genital pores. Anterior ambulacrum shallow to deep with pore pairs oblique or transverse and arranged in single or irregular, double rows. Anterior petals long and almost straight although at times distally flexed; at least twice the length of the posterior petals. Both peripetalous and lateroanal fascioles present and complete (McNamara and Philip 1980a, 1980b).

Subgenus SCHIZASTER L. Agassiz, 1836

Type species

See above.

Diagnosis

Moderate to large species of *Schizaster* with deep anterior notch. Anterior ambulacrum deep and long; pore pairs almost transversely oriented and in single rows. Anterior petals long, deep and flexed; diverging at a low angle usually less than 80° (McNamara and Philip 1980a).

Schizaster (Schizaster) alphonsei sp. nov.
Figs 1a-c

Synonymy

Brisaster latifrons (A. Agassiz, 1898), Lindley 2001, p. 135.

Diagnosis

A small species of *Schizaster* with a relatively low test; apical system is 54 percent of test length from anterior. Anterior ambulacrum broad posteriorly, narrowing anteriorly, very deep, partially overhung by its sides, with the adjoining interambulacra forming narrow vertical keels; anterolateral ambulacra also incised, with sides partially overhung; moderately deep frontal sinus.

Etymology

Named for Alphonse Aisi of Yule Island, Central Province, PNG.

Description

Test of small size, elongate oval, only specimen with length x width x height measuring c. 36.5 x 30 x 17 mm. Test rather low, vertex located 54 percent of test length from anterior; the test slopes very gradually towards the anterior end; details of posterior end unknown. Oral surface gently convex.

Apical system located at vertex, slightly posterior of centre; number of genital pores unknown. Frontal ambulacrum broad posteriorly, but becomes noticeably narrower anteriorly; very deeply sunken, with sides partially overhung. Adjoining interambulacra forming narrow vertical keels. Frontal ambulacrum passes to a moderately deep frontal notch. Pore pairs arranged in a single row. Anterior petals sunken with sides partially overhung; petals are gently curved. Posterior petals short, closed and sunken. Posterior interambulacrum forming a prominent keel. Details of periproct unknown.

Peristome close to anterior end of test, shallowly sunken, with the sunken peristomal region continuing directly to frontal notch. Peripetalous fasciole well developed; a lateral fasciole passes posteriorly to meet with an anal fasciole that is partially preserved in F 1179. Both oral and aboral surfaces with a uniform covering of tubercles.

Remarks

Schizaster (Schizaster) alphonsei sp. nov. can be distingusihed from *Schizaster excavatus* Jeannet and R. Martin, 1937, Middle Pliocene, Java, by its shorter frontal ambulacrum and anteriorly positioned apical system (54 percent of test length from anterior compared with 65 percent, respectively). Jeannet and R. Martin (1937) described two specimens of *S. excavatus*, with length x width x height measuring 47 x 36 x 24 mm and 56 x 45 x 30 mm. This species and *S. (S.) alphonsei* both have low tests and a very deep frontal ambulacrum, wide at its posterior end, narrower anteriorly. *Schizaster (Schizaster) alphonsei* is readily distinguished from *Schizaster (Schizaster)* aff. *compactus* Koehler, 1914, described from the Middle Miocene of Barrow Island, northwestern Australia, by McNamara and Kendrick (1984), by the latter's possession of a smaller (length of 30 mm), globose test and shallow frontal notch. *Schizaster (Schizaster) sphenoides* Hall, 1907, redescribed by McNamara and Philip (1980a) from the Middle Miocene of Victoria, is similar to *S. (S.) alphonsei*, with a very deep frontal ambulacrum with overhung sides. However, this temperate water species can be distinguished from *S. (S.) alphonsei* by its large, subcircular test.

McNamara and Philip (1980a) described the progressive morphological changes in schizasterid echinoids from the Palaeocene to Recent, reflecting adaptation to the occupation of new ecological niches, and noted the following general trends:

(a) the posterior migration of the apex and apical system, allowing more water to flow over the anterior edge of the test toward the peristome;

(b) an increase in declination of the anterior slope, also increasing the flow of water to the anterior;

(c) lengthening of the test, allowing a further posterior migration of the apex and apical system; and

(d) lengthening and deepening of the frontal ambulacrum and the anterior notch, assisting in channelling water to the peristome.

McNamara and Philip (1980a) believed that these morphological adaptations in *Schizaster* were related to the need to enhance the current flow over the aboral surface of the test in a sediment of low permeability. These changes were considered by McNamara and Philip (1980a) to reflect adaptation to deeper burrowing and the occupation of finer sediments and were at their 'extreme' with the *Schizaster* morphotype during the Miocene.

The Lower Pliocene *S.(S.) alphonsei* is an intermediate form transitional between McNamara and Philip's (1980a) *Paraster* form, a sand-dwelling echinoid, and the *Schizaster* form, a mud-dwelling form. The echinoid's small test size, with an apical system slightly posterior of centre, short frontal ambulacrum and gentle anterior slope from the apex are typical of *Paraster* Pomel, 1869. A very deep frontal ambulacrum with a deep frontal notch is typical of the

Figure 1. ***Schizaster (Schizaster) alphonsei*** **sp. nov. Lower Pliocene, Yule Island, Central Province. 1a-c, UPNG F1179, aboral, lateral and oral views. Bar scale = 1.0 cm.** ***Palaeostoma kairukuensis*** **sp. nov. Lower Pliocene, Yule Island, Central Province. 1d-f, UPNG F1186, aboral, lateral and posterior views. Bar scale = 0.5 cm; 1g, UPNG F1186, detail of apical system with elevated processes separating pore pairs, visible along the margins of the frontal ambulacrum (refer to Fig. 2 for an interpretation of frontal ambulacrum). Bar scale = 0.25 cm; 1h, UPNG F1186, view of pentangular peristome. Bar scale = 0.5 cm; 1i, ANU 60635, view of pentangular peristome. Bar scale = 0.5 cm.**

Schizaster morphotype.

Material

Holotype UPNG F1179, a near complete test collected by R. Perembo from locality 24 of Francis et al. (1982) = locality 8280-3. Northwest of Aru're village, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Family PALAEOSTOMATIDAE Lovén, 1867

Remarks

Family Palaeostomatidae differs from the Hemiasteridae in possessing a pentangular, rather than labiate, peristome (Mortensen 1950; Fischer 1966).

Genus PALAEOSTOMA Lovén in A. Agassiz, 1872

Synonymy

Leskia Gray, 1851, p. 134.
Skouraster Lambert, 1937, p. 89.

Type species

Leskia mirabilis Gray, 1851, p. 184.

Emended diagnosis

Test small, ovoid, inflated. Apical system central, or nearly so, 2 genital pores; paired ambulacra broadly petaloid, closed distally; frontal ambulacrum non-petaloid with pores arranged in a single radial row.

Remarks

The emended diagnosis for *Palaeostoma* is broadened from those presented by Mortensen (1950) and Fischer (1966), to include the Lower Pliocene species from Yule Island, strikingly similar in all characters except pore shape and placement in the frontal ambulacrum.

Palaeostoma kairukuensis sp. nov.

Figs 1d-i, 2

Synonymy

Hemiaster sp., F. Chapman in Mayo et al. 1930; F. Chapman and I. Crespin in Montgomery 1930, p. 57; Lower Pliocene, Yule Island.
Ditremaster sp., Lindley 2001, p. 133; Lower Pliocene, Yule Island.

Diagnosis

A relatively large species of *Palaeostoma* with a little marked frontal ambulacrum; pores positioned adapically, arranged in a single radial row, 6-7 pore pairs per row; pores small, circular, each pore pair separated by an elevated process of rectilinear shape.

Etymology

Named after Kairuku, the former Government Station and present village, southeast coast of Yule Island, Central Province, PNG.

Description

Test small, ovoid outline and high vaulted; the largest F1185, a slightly deformed test, with a length x width x height measuring 25 x 20 x c. 11 mm and the smallest ANU 60635 c. 14 x 11 x 8 mm. Vertex subcentral, about 52-60 percent of test length from anterior; test slopes both posteriorly and anteriorly from vertex, with an abrupt steepening near margins. Oral surface is convex.

Apical system located at vertex, ethmophract with madreporite not separating posterior oculars; two genital pores on top of conical elevations. Frontal ambulacrum non-petaloid, sunken posteriorly but flush and little marked anteriorly; frontal sinus very shallow. Pores of frontal ambulacrum are intra-fasciolar, arranged in a single radial row, 6-7 pore pairs per row; pores small, circular. Each pore pair oriented obliquely to line of radial row, pointing perradially distally; separated by an elevated process of rectilinear shape (Fig. 2). Ornament of frontal ambulacrum consists of sparse, irregular granules confined to margins of ambulacrum. Paired ambulacra straight, broad, closed distally, and sunken; posterior petals about 1/3 size of anterior ones. Pores are slit-like, equi-sized; adjacent pore-pairs are separated by 4-5 secondary tubercles. Interporiferous zone, narrow, naked.

Interambulacral areas within the peripetalous fasciole with a covering of fine primary tubercles with prominent bosses, set in a dense covering of granules; a particularly dense clustering of primary tubercles is present in interambulacral areas flanking the pore zone of the frontal ambulacrum. Otherwise, plates of aboral and oral surface with a scattered covering of primary tubercles with prominent bosses and granules, increasing in density towards anterior end of test.

Peristome distinctly pentangular, clearly evident in F1186 and ANU 60635. Periproct circular, located at upper end of curved posterior. Peripetalous fasciole very well marked on F1186; no other fascioles.

Remarks

Palaeostoma Lovén in A. Agassiz, 1872 is a locally common extant genus of the Indo-Pacific (Mortensen 1950; A.M. Clark and Rowe 1971). *Palaeostoma mirabile* (Gray), regarded as a primitive spatangoid, is particularly common in the Java Sea and is known to occur in the Philippine islands, south Japan,

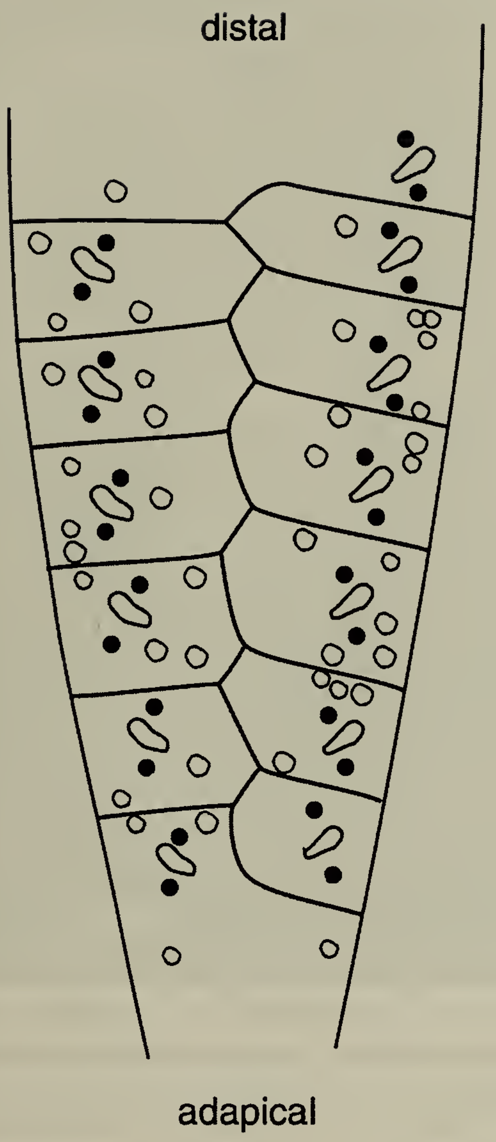

Figure 2. *Palaeostoma kairukuensis* sp. nov. Lower Pliocene, Yule Island, Central Province. Anterior ambulacrum (Amb III) showing pores arranged in a single radial row and pore pairs separated by an elevated process. Plate boundaries are interpretative.

the Indian Ocean, South Pacific islands and the Red Sea (Mortensen 1950; A.M. Clark and Rowe 1971). The maximum test size recorded by Mortensen (1950) was 18 mm length. *Palaeostoma mirabile* lives in mud and has a bathymetric distribution of c. 20-110 m (Mortensen 1950). Only two fossil species have been recorded, *Palaeostoma zitteli* de Loriol, 1881 and *Palaeostoma rochi* Lambert, 1937, from the Eocene of Egypt and Morocco, respectively (Mortensen 1950). Both Eocene forms have distinctive frontal depressions and are clearly not related to the Lower Pliocene species from Yule Island.

Eocene species of *Palaeostoma* and *P. mirabile* are distinguished by their possession of a frontal ambulacrum with pores arranged in a single radial row, the distal one of each pair comma-shaped. In the frontal ambulacrum of *P. kairukuensis* sp. nov. (F1186, measuring 20 mm length), each radial row possesses 6-7 pore pairs, each pore being small and circular. Although Mortensen (1950) and Fischer (1966) did not state the number of pore pairs in the frontal ambulacrum of *P. mirabile*, an illustrated specimen in Mortensen (1950: Plate V, Fig. 4; reproduced in Fischer 1966: Fig. 451) indicates 8-9 pore pairs in each radial row. This specimen measures 15 mm length. The frontal ambulacrum of *P. kairukuensis* is flush at the ambitus, indicating that the entire structure was unlikely to be involved in food gathering and transportation (Smith 1984). The pores of the frontal ambulacrum are all intra-fasciolar, located adapically in a sunken region of the ambulacrum high on the dorsal side of the test. A dense cluster of primary tubercles is present in the flanking interambulacra.

The presence of pore pairs in the adapical region of the frontal ambulacrum, as opposed to the ambital region, indicate that funnel-building tube feet were present (Nichols 1959; Smith 1984). Normally, each pore of a pair gives passage to a tube foot connected internally to its ampulla, and the more perradial pore is grooved to house a branch of the radial nerve (Fischer 1966; Smith 1984). A rimmed area surrounding each pore is an attachment area for the stem retractor muscle, and the width of this area gives a measure of the thickness of the stem retractor muscle and hence an idea of the strength of the tube foot (Smith 1984: 41).These tube feet, typical of the dorsal region of burrowing spatangoids, were primarily engaged in building and maintaining a long open respiratory funnel to the sediment/water interface (Nichols 1959; Durham 1966). The prominent elevated process separating pore pairs in the frontal ambulacrum of *P. kairukuensis* (Fig. 2) may have been an attachment structure for the stem retractor muscle, its small surface area interpreted to indicate tube feet of limited length. Nichols (1959: Figs 41 and 45) figured and described a similar process between pore pairs of ambulacra I and II of *Micraster coranguinum* Leske, 1778, interpreting it as a muscle attachment feature.

Palaeostoma kairukuensis, with its poorly developed frontal ambularcral pore pairs, was probably a shallower burrower than *P. mirabile*. The relatively dense covering of aboral tubercles and the presence of a well developed peripetalous fasciole on the test of the Yule Island species also indicate not only an infaunal mode of life, but also burrowing in fine sands and muds (Smith 1984).

Material

Holotype UPNG F1186, a near complete test;

and paratypes UPNG F1185, a deformed test, collected by R. Perembo from locality 24 of Francis et al. (1982) = locality 8280-3; and ANU 60635-36, two worn specimens, from locality 8280-3. Locality 8280-3 is northwest of Aru're village, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Suborder MICRASTERINA Fischer, 1966
Family BRISSIDAE Gray, 1855
Genus EUPATAGUS L. Agassiz, 1847

Synonymy

Pseudopatagus Pomel, 1885, p. 18.
Melitia Fourtau, 1913, p. 68.
Heterospatangus Fourtau, 1905, p. 606.
Euspatangus Cotteau, 1869, p. 257.
Perispatangus Fourtau, 1905, p. 605.
Koilospatangus Lambert, 1906, p. 185.
Zanolettiaster Sánchez Roig, 1952, p. 14.
Megapatagus Sánchez Roig, 1952, p. 58.

Type species

Eupatagus valenciennesi L. Agassiz, 1847, by subsequent designation of Pomel, 1883, p. 28; Recent, Australia.

Diagnosis

Test ovoid in outline, low, oral side flat; apical system anterior, ethmolytic, with 4 genital pores; paired ambulacra with closed petals; frontal ambulacrum nonpetaloid, pores in single series; primary tubercles on aboral side only within peripetalous fasciole (Fischer 1966).

Subgenus EUPATAGUS L. Agassiz, 1847

Type species

See above

Diagnosis

Ambitus rounded, frontal sinus weak or absent (Fischer 1966).

Eupatagus (Eupatagus) pulchellus (Herklots)
Figs 3a-e

Synonymy

Spatangus pulchellus Herklots, 1854, p. 12; Miocene, Java.
Hemipatagus pulchellus, Desor, 1858, p. 418.
Maretia? pulchella, K. Martin 1880, p. 5; Gerth 1922, p. 512; Miocene, Java.
Brissoides (Brissoides) pulchellus, Lambert and Thiéry 1924, p. 451.
Maretia pulchella, Lambert and Thiéry 1924, p.451
Eupatagus pulchella, F. Chapman and I. Crespin in Montgomery 1930, p. 57; Lower Pliocene, Yule Island.
Eupatagus (Brissoides) pulchellus (Herklots), Jeannet and R. Martin 1937, p. 273; Miocene, Java.
Eupatagus pulchellus (Herklots), Mortensen 1951, p. 472, 473; Miocene, Java.

Description

Test of small size, elongate oval, the largest ANU 60603 measuring 40 x 34.5 x 18 mm, and the smallest, ANU 60616, 27 x 25 x 14 mm. Test low, vertex located centrally; test slopes very gently towards anterior end, with an abrupt steepening near margin; test slopes gently towards posteriorly, to an abrupt vertical termination. Oral surface is gently convex.

Apical system located anteriorly of vertex, at about 37 percent of test length from anterior; four genital pores. Frontal ambulacrum non-petaloid, narrow, not sunken, with a very shallow frontal sinus. Paired ambulacra closed petaloid, weakly sunken. Outer and inner pores of pore pairs are equi-sized; consecutive pore pairs are separated by a rounded transverse ridge and, adapically, a shallow transverse depression. Interporiferous zone covered by randomly arranged secondary tubercles and numerous miliary tubercles.

Posterior interambulacrum V is developed into a prominent keel with irregularly arranged secondary tubercles and numerous miliary tubercles. The paired interambulacra have 4-7 large, perforate, crenulate tubercles within the peripetalous fasciole. Otherwise, the plates of the aboral side with dense covering of secondary and miliary tubercles.

Peristome is large, transversely elliptical, without a prominent lip. Periproct is pear-shaped, situated high up on the vertical posterior end of test, with the point of it just visible in aboral view. Plastron is distinctly inflated particularly in juvenile specimens (ANU 60616), which bear a high, medial keel.

Peripetalous fasciole is difficult to recognise in many specimens; however, in ANU 60608 fasciole is distinct, passing around adoral extremity of petals of paired ambulacra, before disappearing towards frontal ambulacrum. Subanal fasciole present.

Remarks

Eupatagus (Eupatagus) pulchellus (Herklots) is locally very common in the lower to middle Kairuku Kormation. The species appears to be identical in all respects to the specimen figured by Jeannet and R.

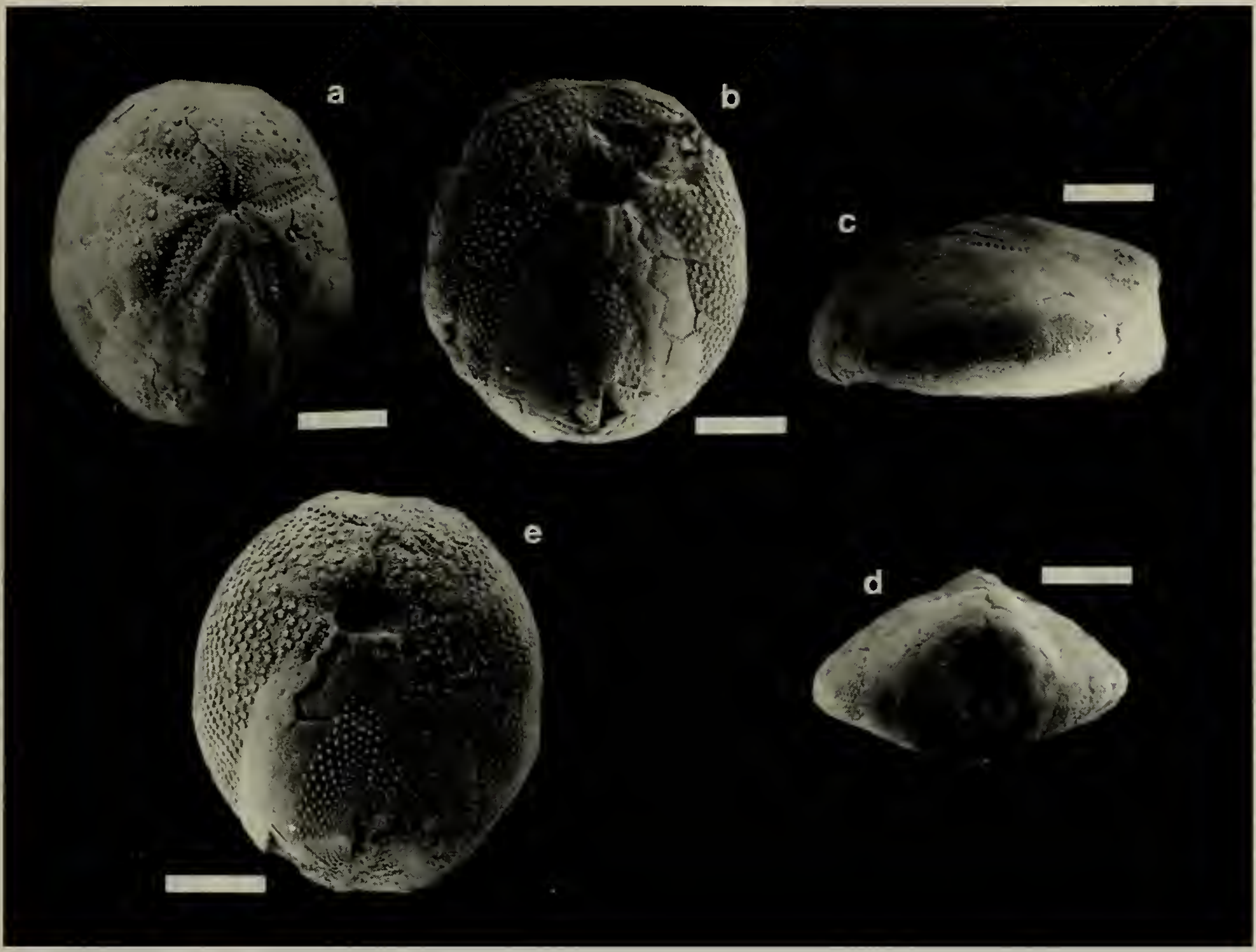

Figure 3. *Eupatagus (Eupatagus) pulchellus* (Herklots). Lower Pliocene, Yule Island, Central Province. 3a-d, ANU 60603, aboral, oral, lateral and posterior views. Bar scale = 1.0 cm; 3e, ANU 60607, oral view. Bar scale = 1.0 cm.

Martin (1937: Figs 50a, b) from the Miocene of Java. The largest of the four specimens described by Jeannet and R. Martin (1937) has dimensions of 40.9 x 35.3 x 23.0 mm and the smallest 33.5 x 29.0 x >20 mm. The difficulty in proving the presence of a peripetalous fasciole in the specimens described and figured by Herklots (1854) led to uncertainty in referral to *Eupatagus* L. Agassiz, 1847 (Mortensen 1951). However, Jeannet and R. Martin (1937) proved the existence of a peripetalous fasciole and Mortensen (1951) believed there was little doubt that the East Indies form is an *Eupatagus*.

Mortensen (1951: 472) considered *E. (E.) pulchellus* to be a near relation of the extant *Eupatagus (Eupatagus) rubellus* Mortensen, 1948. The only known specimen of this species was collected near Tinakta Island of the Tawi Tawi group (5^{o} 12'N; 119^{o} 55'E), Sulu Archipelago, Philippines, at a depth of 24 m (Mortensen 1948b). Many examples of *E. (E.) pulchellus*, preserved in a range of orientations, were collected from the middle Kairuku Formation at locality 8280-4, north of Aru're village on the east coast of Yule Island. This shallow-water sequence was interpreted by Lindley (2003a) to have suffered wholesale disruption and redistribution of sediment resulting from a succession of large storm events.

Material

Twenty-nine complete tests including: ANU 60608, 60611 from locality 8280-2; ANU 60612 from locality 8280-3; and ANU 60603, 60607, 60609-10, 60613-34 from locality 8280-4. All localities are on the east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Family SPATANGIDAE Gray, 1855
Genus MARETIA Gray, 1855

Synonymy

Hemipatagus Desor, 1858, p. 416.
Tuberaster Peron and Gauthier, 1885, p. 46.

Thrichoproctus A. Agassiz (M.S. *nom. nud.*).
Plagiopatagus Lütken (in *litteris, nom. nud.*).

Type species

Spatangus planulatus Lamarck, 1816, p. 326, by original designation; Recent.

Maretia planulata (Lamarck)

Fig. 4d

Synonymy

Spatangus planulatus Lamarck, 1816, p. 326.
Spatangus praelongus Herklots, 1854, p. 11; Miocene, Java.
Spatangus affinis Herklots, 1854, p. 10; Miocene, Java.
Maretia planulata Gray, 1855, p. 48; Tenison-Woods 1878. p. 173: Recent, Australia; Tenison-Woods 1881, p. 204: Recent, Australia; Gerth 1922, p. 512: Pliocene, Java; Jeannet and R. Martin 1937, p. 277: Miocene, Java; Mortensen 1951, p. 21; A.M. Clark and Rowe 1971, p. 146: Recent, northern Australia; Gibbs et al. 1976, p. 135: Recent, Low Isles, northern Great Barrier Reef; De Ridder 1986, p. 48: Recent, New Caledonia.
Maretia ?planulata, K. Martin 1885, p. 286: Miocene, Java.
Maretia ovata, H.L. Clark 1932, p. 277; H.L. Clark 1946, p. 380: Recent, northern Great Barrier Reef.
T. Mortensen (1951), A Monograph of the Echinoidea 5(2), Spatangoida II, p. 27-29, lists the previous synonymies.

Description

Test of moderate size, very low, only specimen measuring 44 x c. 50 x c. 10 mm, length:height in the range of 3-4:1 of A.M. Clark and Rowe (1971); low arched above, with moderately sharp edges; outline elongate oval. Anterior notch apparently lacking, although test is broken in this region. Oral side is gently concave about a medial line passing posterially through frontal ambulacrum.

Details of apical system unknown. Frontal ambulacrum flush and indistinct. Pore pairs are indistinct. Anterior petals flush, straight and closed distally; interporifeous zone is broad, conspicously raised, densly covered with fine miliary tubercles and occasional irregularly placed secondary tubercles. Details of posterior petals unknown.

Details of periproct and peristome unknown. Details of subanal fasciole unknown. The aboral surface between paired petals and frontal ambulacrum with large primary tubercles arranged in horizontal series. Tubercles are perforate, crenulate, with moderately sunken aureoles. Anterolateral margins of test with dense covering of secondary tubercles. Oral surface with uniform covering of distinctively shaped tubercles, best described (and figured) by Mortensen (1951; 33 and Fig. 14), with 'the boss forming a screw, and the aureole unequally deepened, the whole structure almost resembling an ear'.

Remarks

ANU 60606, an incomplete test lacking details of the posterior, peristome and apical system, is assigned to *Maretia planulata* (Lamarck) on the basis of test shape, tubercle arrangement on the aboral surface and the distinctive shape of tubercles on the oral surface. As fossil, *M. planulata* has been recorded from the Pliocene of the Red Sea region and Zanzibar, and the Mio-Pliocene of Java (Mortensen 1951; Jeannet and R. Martin 1937). Extant forms of the species are widely distributed throughout the tropical-subtropical Indo-West Pacific, from East Africa (Mozambique, Madagascar), northern Australia, China and southern Japan, and Fiji and the Gilbert Islands (Mortensen 1951; A.M. Clark and Rowe 1971). On the Australian coast the species occurs from Cooktown southward to Port Jackson, but not from within, or to the west of, the Torres Strait region (H.L. Clark 1946). The spatangoid lives buried in muddy sand within the ebb zone and often comes to the sand surface during exposure on day-time spring tides (Mortensen 1951; Gibbs et al. 1976). Mortensen (1951) records the species to a depth of c. 60m.

Material

ANU 60606, a fragmentary test including left anterior petal and frontal ambulacrum, from locality 8280-1, south of Tete ne'ina Beach, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Maretia cordata Mortensen, 1948

Figs 4a-c

Synonymy

Maretia cordata Mortensen, 1948, p. 132;
Mortensen 1951, p. 41: Recent, East Indies.

Description

Test small, distinctly heart-shaped, aboral side low arched, not flattened. ANU 60604, slightly deformed at its right-anterior end, has a length x width x height of 27 x 26 x 10 mm, similar to the largest of four specimens described by Mortensen (1951),

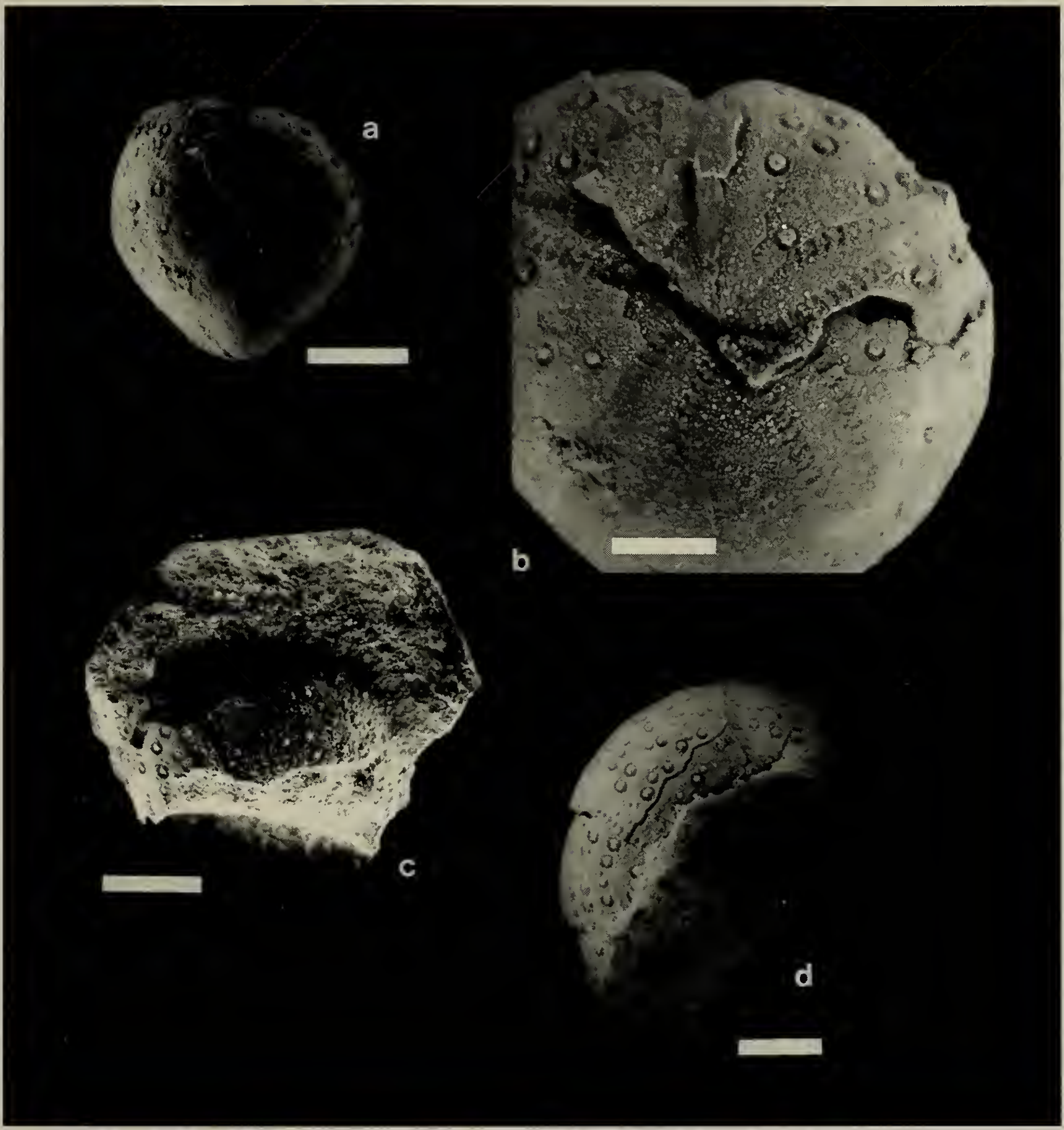

Figure 4. ***Maretia cordata*** **Mortensen, 1948. Lower Pliocene, Yule Island, Central Province. 4a-b, ANU 60604, aboral view and detail of apical system showing anterior series of the right anterior petal (Amb II) with upper 4-5 plates with rudimentary pores or none. Bar scales = 1.0 and 0.5 cm respectively; 4c, ANU 60605, aboral view of incomplete specimen, with left anterior petal (Amb IV) visible. Bar scale = 1.0 cm.** ***Maretia planulata*** **(Lamarck). Lower Pliocene, Yule Island, Central Province. 4d, ANU 60606, aboral view of incomplete test, with left anterior petal (Amb IV) visible. Bar scale = 1.0 cm.**

measuring 28 x 28 x 10 mm; ANU 60605, an incomplete specimen, is slightly larger than Mortensen's (1951) specimens with a width x height of 29 x 14 mm. Test slopes very gently both anteriorly and posteriorly from apical system, with an abrupt steepening near margins. Details of oral surface unknown.

Apical system located at about 44 percent of test length from anterior; number of genital pores unknown. Frontal ambulacrum distinctly sunken, pores pairs indistinct, passing to a conspicuous frontal notch. Petals flush, closed distally. Anterior series of the anterior petals with upper 4-5 plates with rudimentary pores or none. Interporiferous zone is flat, with a sparse covering of miliary and some secondary tubercles. Details of periproct and subanal fasciole unknown.

Posterior interambulacrum V is raised forming a low keel that slightly overhangs the periproct; ornamentation consists of a sparse covering of fine miliary tubercles and some secondary tubercles. The paired interambulacra each with 8-10 perforate, crenulate primary tubercles set amongst a sparse covering of miliary tubercles and occasional secondary tubercles; placement of primary tubercles is random with a tendency toward arrangement in horizontal series near the ambitus.

Details of peristome unknown.

Remarks

Maretia cordata Mortensen, 1948 was erected by Mortensen (1948b) to distinguish tests with a distinctly different shape, deeper frontal depression and broader petals than *M. planulata.* He recorded the species from Palawan Island, Philippines, and the Bali Sea and Flores Sea, Indonesia, at bathymetric ranges of 50-150 m. ANU 60604 and 60605 from the Pliocene of Yule Island, are referable to *M. cordata* on the basis of test size and shape, the presence of a distinct frontal depression and sinus, paired petals distinctly broader than *M. planulata*, and the nature of the anterior series of the anterior petals. Mortensen (1951) noted that large specimens of *M. cordata* carry some large tubercles in the posterior ambulacrum, but the Yule Island specimen ANU 60604, equal in size to the largest described by him, does not have primary tubercles in the posterior ambulacrum.

Mortensen (1951: 44) noted that *Hemipatagus bandaensis* R. Martin (in Jeannet and R. Martin 1937) from the (?) Pliocene of Banda, Indonesia, is a probable ancestor of *M. cordata.* The Pliocene record of *M. cordata* from Yule Island makes this unlikely. *Hemipatagus bandaensis* does not possess a raised keel in the posterior interambulacrum, and the posterior aboral surface curves gradually from the vertex towards margin, contrasting with the flattened-gently sloping surface of *M. cordata.*

Material

Two tests: ANU 60605, an incomplete test lacking posterior details from locality 8280-1, south of Tete ne'ina Beach, and ANU 60604, a complete, though slightly deformed test, from locality 8280-3, northwest of Aru're village, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

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Holocene Foraminifera from Tuross Estuary and Coila Lake, South Coast, New South Wales: A Preliminary Study

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Strotz, L. (2003). Holocene Foraminifera from Tuross Estuary and Coila Lake, south coast, New South Wales: A preliminary study. *Proceedings of the Linnean Society of New South Wales* **124**, 163-182.

Two estuaries on the New South Wales south coast, Tuross Estuary and Coila Lake, were sampled for Foraminifera. Thirty-seven taxa were identified from surface samples but only those requiring extensive taxonomic revision are discussed. The species composition of the total assemblage at each of the sample sites was analysed and the reasons for species distribution explored. A new species, *Fissurina breviductus* sp. nov., is described.

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KEYWORDS: Coastal; Estuary; Foraminifera; Holocene; New South Wales

INTRODUCTION

Tuross Estuary and Coila Lake are adjacent estuaries situated on the New South Wales south coast (Fig. 1). Despite their close proximity to each other, the two estuaries differ markedly in geomorphological character and depositional history. Tuross Estuary is a convoluted, complex estuary, characterised by numerous sandbars, variable depth and is open to the Pacific Ocean via a narrow channel. Coila Lake, in contrast, is a relatively simple, shallow estuary, periodically closed off from the ocean by a large barrier beach and is therefore more correctly defined as a saline coastal lake. Both are drowned river valleys, filled with sediments of Holocene age (Roy and Peat, 1976).

A study of the modern foraminiferal faunas present in the two estuaries was undertaken in an attempt to define the environmental parameters that control the distribution of the assemblages that inhabit the two estuaries and to note differences in assemblage composition in a marine influenced estuarine environment (Tuross Estuary) in comparison to a recently closed lagoonal environment (Coila Lake). Tuross Estuary and Colia Lake were chosen for this study because of their close proximity to each other and the limited amount of anthropogenic activity in the surrounding area.

PHYSICAL CHARACTERISTICS OF STUDY AREA

Tuross Estuary

Tuross Estuary is the larger and more complex of the two estuaries with a total water area of 12.95 km² (Ozestuaries database, 2002). It is classified as a barrier estuary system (Roy, 1984) and a narrow channel at the north end of a large sand spit is the only link between the estuary and the open ocean. The estuary is considered to be one of the least modified estuaries on the New South Wales coastline (Brierley et al., 1995), due mainly to the limited amount of anthropogenic activity in the area.

The sedimentological environments that dominate the estuary have been comprehensively documented by Roy and Peat (1976) and Brierley et al. (1995). According to these two studies, Tuross Estuary can be divided into four major depositional environments with the differences in each of these environments due to differences in the source of the sediment and the energy of the sedimentation processes present in each environment. Deposition in the estuary is attributed to a variety of mechanisms, including tide, wave and fluvial processes (Brierley et al., 1995; Fig. 1).

Coila Lake

Coila Lake is classified as a saline coastal lake, since it is usually cut off from the ocean by a barrier beach (Roy and Peat, 1976). Total water area of the lake is 6.85 km² (Ozestuaries database, 2002), making it one of the largest coastal lakes on the New South Wales coastline (Roy, 1984). Only one major

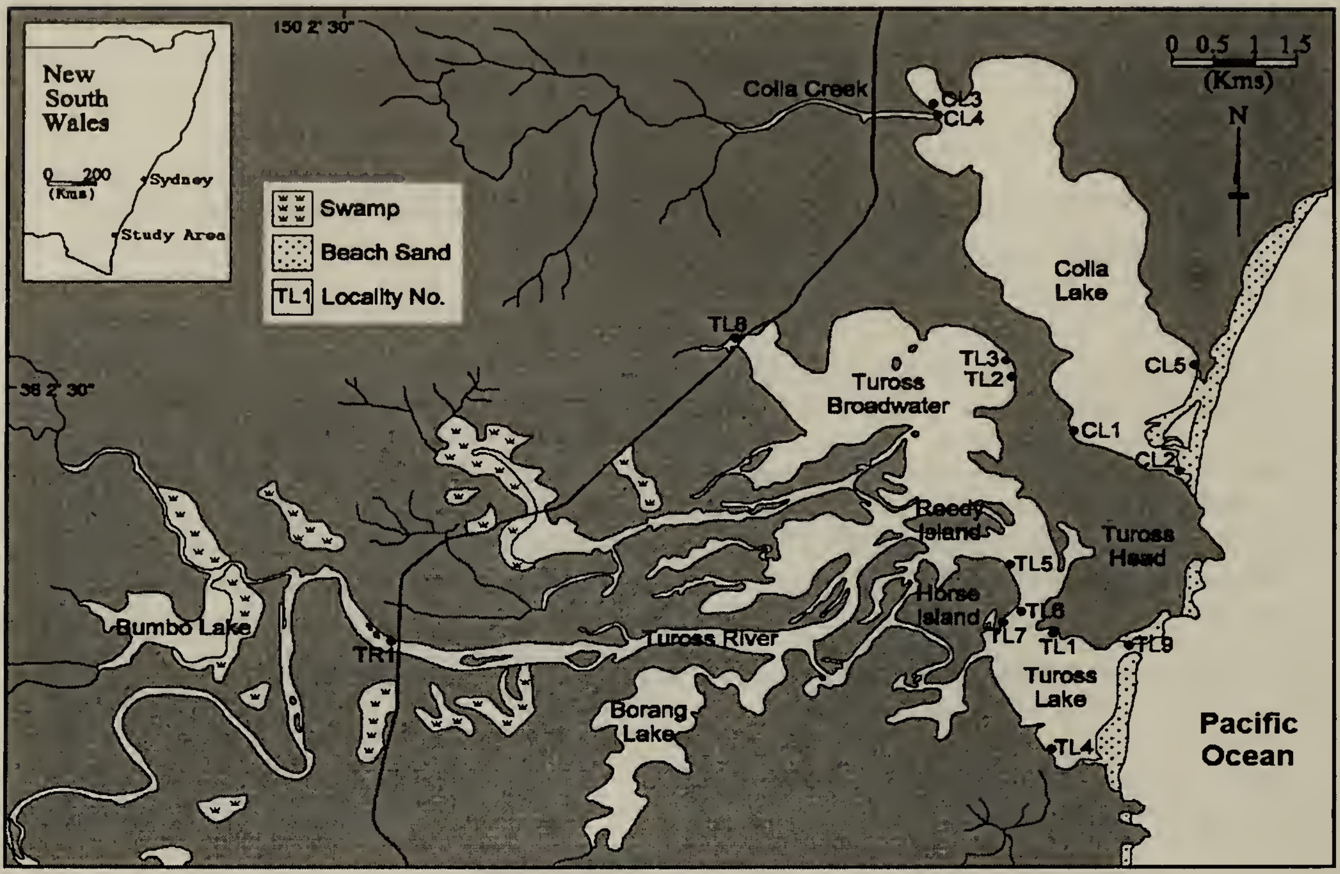


Figure 1. Map of Tuross Estuary and Coila Lake (modified from Tibby, 1996).

tributary, Coila Creek, enters the lake. Freshwater discharge from the creek is low and does not normally possess enough energy to force a channel through the barrier beach located along its southern margin (Roy and Peat, 1976). The lake has however been open to the sea on a number of occasions in recent years. In the period between 1975 and 1999 the barrier beach has been breached four times due to natural events (such as major flooding) and on thirteen occasions by mechanical means in order to lower water levels in the lake (Coila Lake Estuary Management Committee, 2001).

Bathymetrically, Coila Lake is flat bottomed with moderately steep sides. Maximum depth is approximately four metres (Roy and Peat, 1976). Much of the bottom sediment consists of dark coloured sandy muds, deposited by low energy tidal and wind induced currents (Roy and Peat, 1976).

METHODS

Material was described from a total of ten sample sites (see Fig. 1; TL1, TL3, TL4, TL5, TL7 and TL8 in Tuross Estuary and CL1, CL2, CL3, and CL4 in Coila Lake). Each site was examined for foraminifera. The ten sites were chosen because they form a transect across the two estuaries and best exemplify the full gamut of sedimentary environments present in the two estuaries, based upon previous studies of the estuaries by Roy and Peat (1976) and Brierley et al. (1995). Surface sediment was collected at each of the sample sites and was immediately treated with ethanol to perserve any live specimens for later staining. Upon return to the laboratory, each sample was treated with rose Bengal, using the method described by Bell (1996). Samples were then washed through a 1 mm and 63 mm sieve, dried at room temperature and split into 10 gram aliquots for picking.

Water chemistry analysis was undertaken with the use of Hydrolab 4 datasonde. Only the results obtained for conductivity, directly analgous to salinity, obtained at each locality will be discussed herein as the greater portion of this work will form the basis of a later paper (Hostetler et al. in prep).

DISTRIBUTION OF MODERN FORAMINIFERAL FAUNAS

Thirty-seven species of foraminifera were identified from surface samples collected in the two estuaries. In terms of species composition, the foraminiferal fauna present in Tuross Estuary and Coila Lake is similar to other estuaries on the New South Wales south coast (Yassini and Jones, 1989; Yassini and Jones, 1995; Cotter, 1996). Results of staining with rose Bengal revealed only minor variation between live and dead assemblages. Because of this, all analysis is based upon total assemblages, rather than only the live assemblage. Of the 37 species identified, thirty four are benthic species and the remaining three planktonic. All three planktonic species, *Globigerina bulloides* d'Orbigny, *Neogloboquadrina pachyderma* (Ehrenberg) and *Pulleniatina obliquiloculata* (Parker and Jones), are confined to sample site TL1, suggesting that marine influence over sedimentation and water movement in Tuross Estuary does not extend beyond Tuross Lake (Fig. 1).

Three main foraminiferal assemblages were identified in the two estuaries. These are the Lower Estuary Assemblage, the Upper Estuary Assemblage and the Coastal Lake Assemblage. Assemblages were differentiated based upon the faunal composition of the assemblage and the relative abundances of the various taxa that make up the assemblage. Besides a few notable exceptions, dicussed more extensively below, the distribution of these assemblages is unsurprising, with the composition of the foraminiferal faunas at each locality conforming to what would be expected.

The most diverse fauna is the Lower Estuary Assemblage, found at localities TL1 and CL2. The fauna is dominated by rotaliine forms; taxa such as *Rosalina australis* (Parr), *Ammonia aoteana* (Finlay), *E. crispum crispum* (Linne), *E. advenum advenum* (Cushman) and *Parrellina papillosa* (Cushman) having the highest relative abundances. An assemblage of this type is indicative of open estuary conditions where normal marine salinities dominate (Hayward et al., 1999). This assemblage is expected at locality TL1 considering its location (Fig. 1) and the conductivity results obtained for the site, approximately 57 mS/cm. Fully marine conditions return conductivity values around 60 mS/cm. Its presence at CL2 however is surprising as the locality is not currently subject to open estuary conditions, cut off from the open ocean by a barrier beach, and conductivity levels obtained for the site were brackish in nature, around 43 mS/cm. The site has been exposed to fully marine conditions in the past when the barrier beach has been opened by either natural or unnatural causes (Coila Lake estuary management committee, 2001). It is therefore proposed that the assemblage found at this site is a relict fauna associated with a time when the lake was open to the ocean. This assertion is supported by the lack of "live" specimens obtained at the site, determined using rose Bengal stain on the collected samples, suggesting that a living foraminiferal fauna does not currently inhabit the locality and the noticeably abraded nature of the material, suggesting deposition occurred some time ago.

The remaining sample localities in Tuross Estuary, excluding TL4, possess a fauna that is herein designated the Upper Estuary assemblage. This assemblage is characterised by a mixture of agglutinated and calcareous taxa; including *Scherochorella barwonensis* (Collins), *Ammobaculites exiguus* Cushman and Bronniman, *Quinqueloculina oblonga* (Montagu), *Elphidium advenum advenum* (Cushman), *Elphidium excavatum clavatum* Cushman and *Elphidium lene* Cushman and McCulloch. This fauna is indicative of shallow sub-tidal middle estuary conditions, with salinity levels slightly below normal marine conditions (Hayward et al., 1999). This assemblage is found at localities TL3, TL5, TL7 and TL8, sites characterised by either mangroves or reed beds. The conductivity values obtained for these sites were between 53-56 mS/cm, only slightly below normal marine values. The presence of this fauna at locality TL8 indicates that even the extremities of Tuross Estuary are subject to moderately saline conditions (Fig. 1).

The Coastal Lake assemblage dominates at the three remaining sample sites in Coila Lake, CL1, CL3 and CL4 and is also present at locality TL4. This assemblage consists of predominantly agglutinated taxa, in most cases dominated by the species *Ammobaculites exiguus* Cushman and Bronnimann and *Scherochorella barwonensis* (Collins). In areas where high amounts of aqueous vegetation are present, such as marsh settings, *Trochammina inflata* (Montagu) is also a major constituent of the fauna. This fauna is indicative of a shallow sub-tidal situation where brackish conditions dominate (Collins, 1974; Hayward et al., 1999). Conductivity levels for these four sites do not exceed 45 mS/cm. The presence of this assemblage in Coila Lake is unsurprising, considering the lake is cut off from the open ocean but its presence at locality TL4 is unexpected. Located is the eastern part of Tuross Estuary, close to the estuary mouth, the foraminiferal fauna at the site should be comparable to the Lower Estuary Assemblage found nearby at TL1. This is not the case, with the fauna made up mainly of two taxa, *Ammobaculites exiguus* Cushman and Bronnimann and *Scherochorella barwonensis* (Collins), which make up to 91% of the total abundance; the remaining 9% is composed of minor agglutinated forms and rare calcareous species. The difference in the faunal assemblage found at locality TL4 to that found in other parts of Tuross Estuary is related to the presence of a large sandbar, which isolates the site from the main part of the estuary. This isolation has created an environment, which, in terms of both water chemistry and sedimentary environment, is more comparable to a slightly brackish lagoonal situation, and a faunal assemblage that reflects these conditions.

DISCUSSION

Salinity is the main controlling factor on the distribution of foraminiferal species in Tuross Estuary and Coila Lake. Sites that are subject to, or have been subject to, fully marine conditions, such as TL1 and CL2 , possess a fauna that is relatively high in diversity and characterised by numerous calcareous taxa. Hayward et al. (1999) noted that localities of this kind, where normal marine conditions are prevalent and there is little tidal exposure, are generally the most diverse localities in any particular estuary. Conversely, sites in the upper, or northern, part of Coila Lake, where brackish conditions dominate, are characterised by a low diversity fauna that is composed of agglutinated taxa. Those areas in Tuross Estuary where salinity is variable, in the middle and upper parts of the Tuross Estuary, possess a fauna which lies somewhere between the previous two and is a mixture of calcareous and agglutinated taxa.

SYSTEMATIC DESCRIPTIONS

Unless otherwise stated, the higher level classification follows Loeblich and Tappan (1987). Although revised classification schemes have been published (e.g. Loeblich and Tappan, 1992; Sen Gupta, 1999), Loeblich and Tappan's (1987) scheme is considered less controversial and since it is in widespread use, allows comparisons to be made between this study and others. The only departure that has been made from Loeblich and Tappan (1987) is the use of –OIDEA rather than –ACEA as the ending of all superfamily names, following recommendation 29A of the ICZN 4th edition.

No attempt has been made to describe those taxa that have been comprehensively monographed in other systematic studies (Albani, 1968a; Albani 1979; Hayward et al., 1997; Hayward et al., 1999). Only new taxa or those requiring substantial revision are described in detail. A full list of species recovered from the two estuaries can be found in Table 1.

Order FORAMINIFERIDA Eichwald, 1830
Suborder TEXTULARIINA Delage and Herouard, 1896
Superfamily HORMOSINOIDEA Haeckel, 1894
Family HORMOSINIDAE Haeckel, 1894
Subfamily REOPHACINAE Cushman, 1910

Scherochorella Loeblich and Tappan, 1984

Type species:
Reophax minuta Tappan, 1940

Scherochorella barwonensis (Collins), 1974
(Plate 1, Figs. 1-3)

1974 *Reophax barwonensis* Collins, p. 8; Pl. 1, fig 1.
1980 *Reophax barwonensis* Apthorpe, Pl. 29, Fig. 7.
1989 *Protoschista findens* Yassini and Jones, Figs. 10.10, 10.11.
1992 *Reophax barwonensis* Bell and Drury, p. 12; Fig. 4.5.
1995 *Reophax barwonensis* Bell, p. 229; Fig. 2.1.
1995 *Protoschista findens* Yassini and Jones, p. 69; Figs. 39, 43.
1996 *Reophax barwonensis* Bell, p. 5; Pl. 1a.

Description:
see Collins (1974), p. 8.

Remarks:

The designation of this species has been highly contentious. Much of the confusion associated with this taxon has arisen due to its variable morphology. Specimens found in Tuross Estuary and Coila Lake display variability in the total number of chambers present, the coarseness of the test and the size of the proloculus relative to the subsequent chambers (Plate 1, Figs. 1-2). This variation could be explained by the presence of both microspheric and megalospheric forms (Bell, 2002 pers. comm), although this possibility was not mentioned by Collins (1974) in his original description of the species.

I have followed Loeblich and Tappan (1984) in assigning this species to the genus *Scherochorella* based upon its subglobular proloculus, appressed chambers and depressed sutures. This assignment has been previously rejected by Bell and Drury (1992) who state that the specimens illustrated as part of their study (Bell and Drury 1992, Fig 4.5) do not exhibit a flattened test, nor could they be considered tiny; both diagnostic features of the genus *Scherochorella* (Loeblich and Tappan, 1984). However, as test size cannot be considered a good generic character in foraminifera,

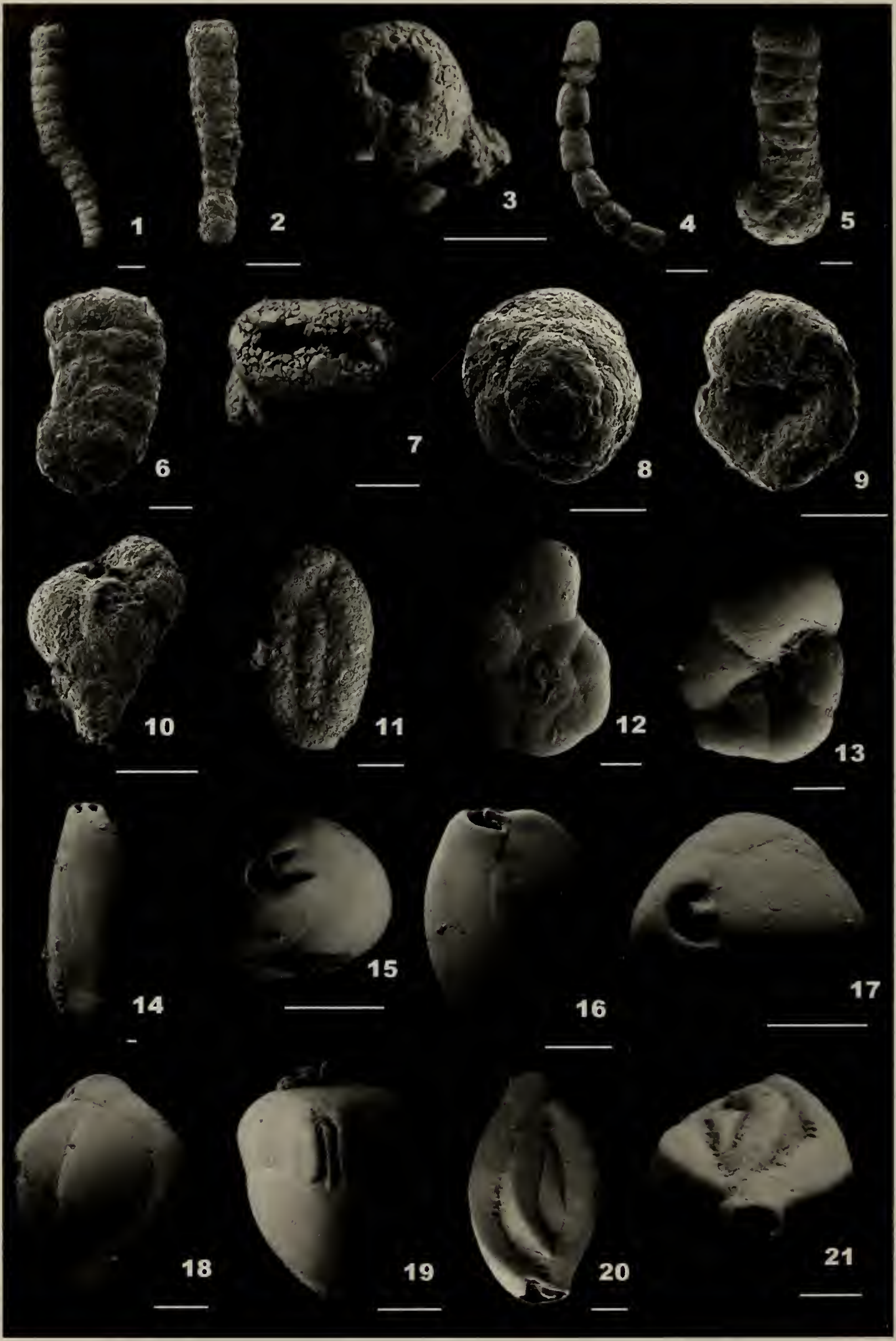
Table 1. Species recovered from Tuross Estuary and Coila Lake. X indicates the localities at which each species occurs.

Species Name	TL1 July	TL1 Jan	TL3 July	TL3 Jan	TL4 July	TL4 Jan	TL5 July	TL5 Jan	TL7 July	TL7 Jan	TL8 July	TL8 Jan	CL1 July	CL1 Jan	CL2 July	CL2 Jan	CL3 July	CL3 Jan	CL4 July	CL4 Jan
Reophax barwonensis		X	X	X	X	X		X				X					X	X	X	
Leptohalysis collinsi					X															
Ammobaculites barownensis					X	X					X	X						X		X
Ammobaculites exiguus			X	X	X	X	X	X			X	X					X	X	X	X
Miliammina fusca			X				X	X			X	X	X							
Portatrochammina sorosa	X	X	X	X	X	X	X	X				X								
Trochammina inflata			X	X			X	X				X							X	X
Eggerella subconica			X								X								X	X
Cornuspira involvens		X	X																	
Spiroloculina carinata	X																			
Quinqueloculina oblonga	X	X	X	X	X		X	X	X	X					X	X				
Quinqueloculina poeyana		X					X													
Quinqueloculina sp.cf. Q. disparilis		X																		
Triloculina gladius sp. nov.	X																			
Lenticulina sp.	X	X																		
Lagena blomaeformis												X								
Fissurina breviductus sp. nov.		X																		
Guttulina irregularis	X	X																		
Bolivina striatula		X	X																	
Bulimina sp.	X	X					X													
Trochulina dimidiatus	X	X																		
Rosalina australis	X	X																		
Pileolina australensis	X																			
Cibicides dispars	X	X														X				
Ammonia aoteana	X	X	X	X	X	X	X					X								
Elphidium advenum advenum	X	X													X	X				
Elphidium advenum macelliforme	X										X									
Elphidium crispum crispum	X	X													X					
Elphidium crispum ssp.	X	X																		
Elphidium excavatum clavatum			X	X			X	X			X									
Elphidium lene	X	X																		
Elphidium macellum	X	X																		
Parrellina papillosa	X	X													X	X				
Parrellina verriculata	X	X																		
Pulleniatina obliquilaculata	X	X																		
Neogloboquadrina pachyderma	X	X																		
Globigerina bulloides	X	X																		

as often it is environmentally controlled, and the flattened nature of the type species could be due to burial distortion (Loeblich and Tappan, 1987), Bell and Drury's (1992) assertion is herein rejected.

Hayward and Hollis (1994), in their assessment of New Zealand brackish water foraminifera, asserted that *S. barwonensis* Collins is a junior synonym of *Reophax moniliforme* Siddall. Bell (1996) indicated this synonymy cannot be justified since *barwonensis* has a more robust test than *moniliforme*, and both taxa have differing habitats: *R. moniliforme* Siddall is associated with inner shelf environments and *S. barwonensis* Collins is found in shallow-water intertidal environments.

This species has only previously been described from Victoria and Tasmania. This may be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due, in part, to misidentification of the species as *Protoschista findens* Parker, particularly in studies conducted on modern material in New South Wales (Yassini and Jones, 1989; Yassini and Jones, 1995). *Protoschista* is characterised by branching at the proloculus and the formation of two or three uniserial series, a feature that none of the specimens illustrated from New South Wales possess (e.g. Yassini and Jones, 1989 Figs 10.10-10.11; Yassini and Jones, 1995 Figs. 39,43). The range of the species can thus be extended to the south coast of New South Wales (Yassini and Jones, 1995; this study).

Specimens of *S. barwonensis* Collins in Tuross Estuary and Coila Lake are generally found in low energy environments, such as localities TL3, TL8 and CL3, where the substrate is composed of predominantly muddy material and where aqueous vegetation, such as reed beds, are absent. The species tolerates a wide range of salinity conditions, from fully marine through to conductivity values below 34 mS/cm.

Superfamily LITUOLOIDEA de Blainville, 1827
Family LITUOLIDAE de Blainville, 1827
Subfamily AMMOMARGINULININAE Podobina, 1978

Ammobaculites Cushman, 1910

Type species:

Spirolina agglutinans d'Orbigny, 1846

Ammobaculites barwonensis Collins, 1974
(Plate 1, Figs. 6-7)

1974 *Ammobaculites*? *barwonensis* Collins, p. 9; Pl. 1, Figs. 3a-b.
1980 *Ammobaculites barwonensis* Apthorpe, p. 225; Pl. 28, figs. 4, 5, 10-13.
1989 *Ammobaculites foliaceus* Yassini and Jones, Fig. 10.4.
1992 *Ammobaculites barwonensis* Bell and Drury, p. 13; Figs. 4.7-4.9.
1995 *Ammobaculites barwonensis* Bell, p. 229; Fig. 2.1.
1995 *Ammobaculites foliaceus* Yassini and Jones, p. 71; Figs. 51-53.

Description:

see Collins (1974), p. 9; Apthorpe (1980), p. 225.

Remarks:

In his original description of *Ammobaculites barwonensis*, Collins (1974) was doubtful of the generic placement of this species because of the absence of a definite terminal aperture and suggested that "it is possible that minute interspaces between grains on the distal face function as such" (Collins, 1974, p. 9). An emended description by Apthorpe (1980) showed that the aperture is terminal and is generally an ellipse or elongate slit.

As noted by Apthorpe (1980) the morphology of this species is variable, particularly the overall shape and degree of compression of the test. Typical specimens, as illustrated by Collins (1974, Pl. 1 Figs. 3a-b) and Apthorpe (1980, Pl. 28 Figs. 4, 5, 10-13), are moderately compressed and rectangular in outline but a highly compressed, flabelliform variant does exist (Apthorpe, 1980, Pl. 28, Fig. 11; Bell and Drury, 1992, Fig. 4.7). There is a morphological continuum between the two forms (Apthorpe, 1980), suggesting that both morphotypes probably belong to *A. barwonensis* Collins. Both variants, as well a number of intermediate forms, were recovered from both surface and core samples collected in Tuross Estuary and Coila Lake, but the majority of specimens tend to be highly compressed and flabelliform in shape. It is unknown whether the morphology of the species is affected by environmental conditions.

Like *Reophax barwonensis* Collins, this species has previously only been described from Victoria. Also like *R. barwonensis* Collins, this is probably due to misidentification of specimens as *Ammobaculites foliaceus* (Brady) (Yassini and Jones, 1989; Yassini and Jones, 1995). *Ammobaculites*

Plate 1 Facing page: (Unless otherwise specified all scale bars = 100 µm) - 1. *Scherochorella barwonensis* (Collins), TL4 July; 2-3. *Scherochorella barwonensis* (Collins), TL4 515-535; 4. *Leptohalysis collinsi* Bell, TL4 140-160; 5. *Ammobaculites exiguus* Cushman and Bronnimann, CL3 July; 6-7. *Ammobaculites barwonensis* Collins, TL4 July; 8-9. *Portatrochammina sorosa* (Parr), TL4 490-510; 10. *Eggerella subconica* Parr, CL3 690-710; 11. *Miliammina fusca* (Brady), TL3 July; 12. *Trochammina inflata* (Montagu), TL3 110-130; 13. *Trochammina inflata* (Montagu), TL3 70-90; 14-15. *Quinqueloculina oblonga* (Montagu), TL4 490-510 (Scale bar for Fig. 15 = 10 µm); 16-17. *Quinqueloculina seminula* (Linne), TL1 560-580; 18-19. *Triloculina tricarinata* d'Orbigny, TL1 July; 20-21. *Spiroloculina carinata* Fornasini, TL1 300-320 *foliaceus* (Brady) differs from *A. barwonensis* Collins by its extremely thin, almost transparent wall, very compressed test and smooth exterior (Brady, 1881; Brady, 1884). The range of *A. barwonensis* Collins can therefore be extended to the south coast of New South Wales (Yassini and Jones, 1989; Yassini and Jones, 1995; This study).

The species is found in both Tuross Estuary and Coila Lake, with highest abundances occurring at shallow intertidal localities, such as CL4 and TL8 (Fig. 1). The species has not been recovered from the eastern, more marine, part of Tuross Estuary, suggesting this species is confined to brackish water conditions.

Superfamily TROCHAMMINOIDEA Schwager, 1877
Family TROCHAMMINIDAE Schwager, 1877
Subfamily TROCHAMMININAE Schwager, 1877

Portatrochammina Echols, 1971

Type species:
Portatrochammina eltaninae Echols, 1971

Portatrochammina sorosa (Parr), 1950
(Plate 1, Figs. 8-9)

1950 *Trochammina sorosa* Parr, p. 278; Pl. 5, Figs. 15-17.
1967 *Trochammina sorosa* Hedley *et al.*, p. 23; Pl. 6, Figs. 4a-c, Text Figs. 11-15.
1992 *Trochammina sorosa* Bell and Drury, p. 13; Fig. 4.12.
1996 *Trochammina sorosa* Bell, Pl. 11.
1996 *Tritaxis conica* Cotter, Figs. 4.10-4.11.
1999 *Trochammina sorosa* Bell and Neil, p. 221; Fig. 3E.
1999 *Portatrochammina sorosa* Hayward et al., p. 87; Pl. 2, Figs. 4-5.

Description:
see Hayward *et al.* (1999), p. 87.

Remarks:
Hayward et al. (1999) placed this species in the genus *Portatrochammina* based on the presence of an umbilical flap, discovered upon re-examination of the topotype material by Hedley et al. (1967). This feature was neither described or illustrated in Parr's (1950) original description of the species but is present on specimens found in Tuross Estuary and Coila Lake. *P. sorosa* (Parr) has a restricted distribution and is currently only known from the south-eastern coastline of Australia and New Zealand (Hayward et al., 1999). Specimens of *P. sorosa* (Parr) found in Tuross Estuary and Coila Lake tend to be variable in the number of whorls and are generally more trochospiral than the specimens illustrated by Parr (1950, Pl. 5 Figs. 15-17) from off the east coast of Tasmania. In the modern setting, the distribution of *P. sorosa* (Parr) is widespread in Tuross Estuary but no specimens were recovered from surface samples collected in Coila Lake. This would suggest that *P. sorosa* (Parr) prefers normal marine salinities.

Suborder MILIOLINA Delage and Herouard, 1896
Superfamily CORNUSPIROIDEA Schultze, 1854
Family CORNUSPIRIDAE Schultze, 1854
Subfamily CORNUSPIRINAE Schultze, 1854

Cornuspira Schultze, 1854

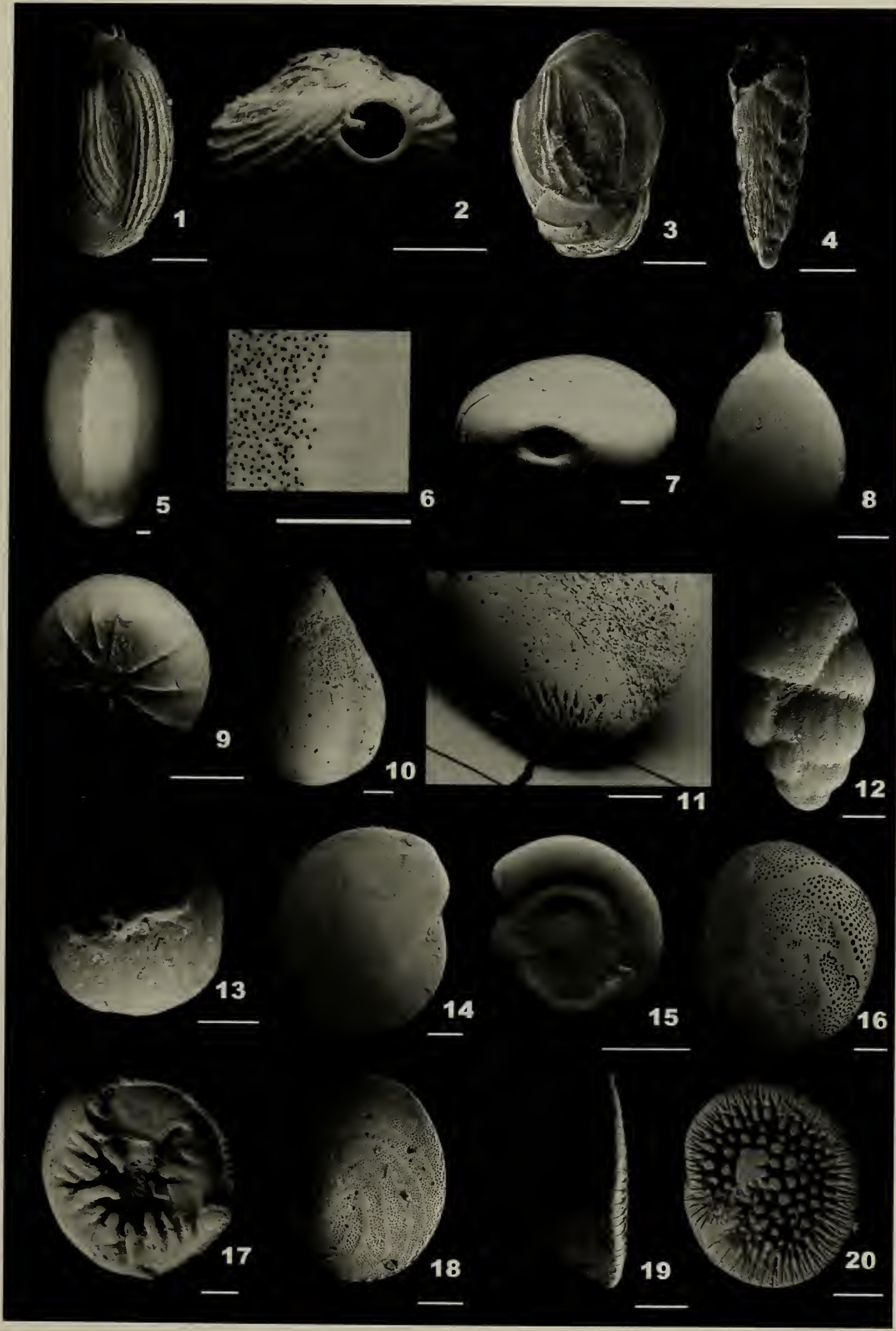
Type species:
Orbis foliaceus Philippi, 1844

Cornuspira involvens (Reuss), 1850
(Plate 2, Fig. 15)

1850 *Operculina involvens* Reuss, p. 370; Pl. 46, Figs. 20a-b.
1884 *Cornuspira involvens* Brady, p. 200; Pl. 11, Figs. 1-3.
1967 *Cyclogyra involvens* Hedley et al., p. 24-25; Text Fig. 16.
1999 *Cornuspira involvens* Hayward et al., p. 94; Pl. 3, Fig. 16.

Description:
see Hayward et al. (1999).

Plate 2 Facing page: (Unless otherwise specified all scale bars = 100 µm) - 1-2. *Quinqueloculina poeyana* d'Orbigny, TL5 July; 3. *Quinqueloculina sp. cf. Q. disparilis* d'Orbigny, TL1 January; 4. *Bolivina striatula* Cushman, TL4 515-535; 5-7. *Fissurina breviductus* sp. nov., TL1 January; 8-9. *Lagena blomaeformis* Yassini and Jones, TL1 410-430; 10-11. *Guttulina irregularis* (d'Orbigny), TL1 July; 10-11. *Bulimina* sp., TL5 July; 12. *Lenticulina* sp., TL1 July; 13. *Cornuspira involvens* (Reuss), TL1 January; 14. *Rosalina australis* (Parr), TL1 January; 15. *Rosalina australis* (Parr), TL1 300-320; 16-18. *Pileolina australensis* (Heron-Allen and Earland), TL1 630-650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Remarks:

This species has a cosmopolitan distribution (Culver and Buzas, 1986; Loeblich and Tappan, 1994) but it has rarely been described from Australia and never from the south-eastern coastline of New South Wales. It is generally found in fully marine conditions, with those specimens found in marsh environments probably carried there by tidal currents (Hayward et al., 1999).

Specimens of *C. involvens* (Reuss) are extremely rare in the study area and are only found in Tuross Estuary, at TL1 and TL3. Although *C. involvens* (Reuss) is generally found inhabiting inner shelf environments (Hayward et al., 1999), one of the tests recovered from TL1 during January collection did stain with rose Bengal. This, along with the pristine nature of the test, suggests that live specimens of this species do inhabit the estuary.

Suborder LAGENINA Delage and Herouard, 1896
Superfamily NODOSARIOIDEA Ehrenberg, 1838
Family LAGENIDAE Reuss, 1862

Fissurina Reuss, 1850

Type species:

Fissurina laevigata Reuss, 1850

Fissurina breviductus sp. nov.
(Plate 2, Figs. 5-7)

Diagnosis:

Differs from other species of *Fissurina* in its small size, short entosolenian tube, perforate flanks with smooth central area and its distinctively depressed simple aperture.

Description:

Test unilocular, tiny, approximately 0.1 mm in length and 0.05 mm in width. Relatively ovate in outline but gently tapering towards apertural end. Test is laterally compressed. Aperture simple, ovate in shape, with area immediately around aperture slightly depressed. Wall glassy, perforate on flanks with central area smooth. Possesses a short entosolenian tube that is free, straight and central.

Type Material:

Holotype: MU59414; Paratype A: MU59379; Paratype B; MU59415; All type specimens collected from locality TL1 in Tuross Estuary.

Etymology:

Latin for "short tube"; in reference to its short entosolenian tube.

Remarks:

Based upon its ovate outline, smooth surface, ovate terminal aperture and entosolenian tube, this species is assigned to genus *Fissurina*. It does not however, accord with any of the described species within this genus, nor does it resemble any species previously described from shallow water environments along the south-eastern Australian coastline. This may in part be due to its small size, generally less than 100 μm in length.

This species does resemble a variant of *Lagena globosa* Montagu, documented by Sidebottom (1912, Pl. 14 Figs. 13-15) from the outer shelf and abyssal plain of the south-west Pacific, *Lagena globosa* var. *emaciata* Reuss. Both the specimens illustrated by Sidebottom (1912) and those found as part of this study are ovoid in shape, smooth walled, possess a free, centralised entosolenian tube, and have a single terminal aperture. It is unclear whether the specimens shown by Sidebottom (1912) are depressed around the aperture.

Sidebottom's (1912) material was collected from depths of below 710 fathoms, whereas the material from the Tuross Estuary is from shallow water. Such extreme bathymetric differentiation make it unlikely that the specimens illustrated by Sidebottom (1912) and the specimens collected from the study area are conspecific. Specimens of *F. breviductus* sp. nov. from the study area are confined to surface and core samples from locality TL1 and all specimens found in surface samples had taken up the rose Bengal stain, suggesting the tests were in-situ and their natural habitat is a shallow water open estuary environment.

Family POLYMORPHINIDAE d'Orbigny, 1839
Subfamily POLYMORPHININAE d'Orbigny, 1839

Guttulina d'Orbigny, 1839

Type species:

Polymorphina (les Guttulines) *communis* d'Orbigny, 1826

Guttulina irregularis (d'Orbigny), 1846
(Plate 2, Figs. 10-11)

1846 *Globulina irregularis* d'Orbigny, p. 226; Pl. 13, Figs. 9-10.
1930 *Guttulina irregularis* Cushman and Ozawa, p. 25; Pl. 3, Figs. 3,4; Pl. 7, Figs. 1,2.
1937 *Guttulina irregularis* Parr and Collins, p. 192; Pl. XII, Fig. 2.
1995 *Nevellina coronota* Yassini and Jones, p. 89; Fig. 244.
1999 *Guttulina irregularis* Hayward et al., p. 117; Pl. 7, Figs. 10-11.

Description:

see Hayward et al. (1999), p. 117.

Remarks:

This species can be distinguished from other species of *Guttulina* by its pyriform test, rounded periphery and non-depressed sutures (Hayward et al., 1999). It has been recorded from a number of localities throughout the west Pacific (Parr and Collins, 1937; Nomura, 1981; Hayward et al., 1999).

In the study area, this taxon was recovered from surface samples as locality TL1. The abraded nature of the tests suggests they have been transported to the site by onshore oceanic currents, since *G. irregularis* (d'Orbigny) is generally found at inner- and mid-shelf depths (Hayward et al., 1999)

Suborder ROTALIINA Delage and Herouard, 1896
Superfamily BOLIVINOIDEA Glaessner, 1937
Family BOLIVINIDAE Glaessner, 1937

Bolivina d'Orbigny, 1839

Type species:

Bolivina plicata d'Orbigny, 1839

Bolivina striatula Cushman, 1922
(Plate 2, Fig. 4)

1922 *Bolivina striatula* Cushman, p. 27; Pl. 3, Fig. 10.
1937 *Bolivina striatula* Cushman, p. 154; Pl. 18, Figs. 30, 31.
1950 *Bolivina striatula* Parr, p. 239.
1974 *Brizalina striatula* Collins, p. 30.
1979 *Brizalina striatula* Albani, p. 33; Fig. 56-6.
1980 *Bolivina striatula* Apthorpe, Pl. 27, Fig. 2.
1989 *Brizalina striatula* Yassini and Jones, Fig. 13.3.
1995 *Brizalina striatula* Yassini and Jones, p. 132; Figs. 526-529, 543-544, 655.
1996 *Bolivina striatula* Bell, Pl. 5d.
2001 *Brizalina striatula* Albani et al.

Description:

see Hayward *et al.* (1999), p. 127.

Remarks:

The amendments made by Sgarrella (1992) to the genus *Bolivina*, with *Brizalina* now a junior synonym of *Bolivina*, are adopted herein. *B. striatula* Cushman is easily distinguished from other species of *Bolivina* by its parallel fine ribs on the lower half of the test. This species is generally found in sheltered, slightly brackish environments (Hayward *et al.*, 1999) and its geographic distribution is extensive (Murray, 1991). This species is extremely rare in Tuross Estuary with only small numbers recovered from localities TL1 and TL3. The species was not recovered from Coila Lake.

Superfamily DISCORBOIDE Ehrenberg, 1838
Family DISCORBIDAE Ehrenberg, 1838

Lamellodiscorbis Bermudez, 1952

Type species:

Discorbina dimidiata Jones and Parker in Carpenter et al., 1862

Lamellodiscorbis dimidiatus (Jones and Parker), 1862
(Plate 3, Figs. 3-4).

1862 *Discorbina dimidiata* Jones and Parker in Carpenter et al., p. 201; Text Fig. 32b.
1945 *Discorbis dimidiatus* Parr, p. 208.
1967 *Discorbina dimidiatus* Hedley et al., p. 33; Text-Figs. 28-43.
1974 *Discorbis dimidiatus* Collins, p. 34.
1989 *Lamellodiscorbis dimidiatus* Yassini and Jones, Figs. 17.9-17.11.
1992 *Lammellodiscorbis dimidiatus* Hansen and Revets, p. 176; Pl. 4, Figs. 1-3, 7-8
1995 *Trochulina dimidiata* Yassini and Jones, p. 158; Figs. 916-917.
1996 *Lamellodiscorbis dimidiatus* Bell, Pl. 5b.
1999 *Trochulina dimidiatus* Hayward et al., p. 139; Pl. 10, Figs. 9-11.

Description:

see Hayward et al. (1999), p. 139.

Remarks:

A number of authors (Loeblich and Tappan 1987, Yassini and Jones 1995, Hayward et al. 1999) have assigned this species to the genus *Trochulina*, suggesting that both *Discorbina* and *Lamellodiscorbis* are junior synonyms of *Trochulina*. However, Hansen and Revets (1992) clearly illustrate the validity of both *Discorbina* and *Lamellodiscorbis* and so herein *dimidiatus* has been assigned to *Lamellodiscorbis*.

This species is distinguished by its characteristic umbilical side, which has short, thickened umbilical plates bordered by deep clefts along the sutures (Hayward et al., 1999). Collins (1974) noted that specimens are sometimes strongly biconvex with secondary thickening on both faces. The geographic distribution of *L. dimidiatus* (Jones and Parker) is confined to coastal waters of Australia and the Pacific (Heldey et al., 1967; Yassini and Jones, 1995; Hayward *et al*, 1999) and it is generally found in stenohaline environments (Cann et al., 2000) with greatest abundance occurring in exposed, shallow, high energy environments.

Specimens from the study area were only recovered from samples collected at locality TL1. The broken and abraded nature of the tests, as well as the lack of any "live" specimens of *L. dimidiatus* (Parker and Jones) in the surface samples from locality TL1, suggests that living examples of this species do not inhabit the estuary but rather are transported in via currents.

Superfamily GLABRATELLIOIDEA Loeblich and Tappan, 1964
Family GLABRATELLIDAE Loeblich and Tappan, 1964

Pileolina Bermudez, 1952

Type species:
Valvulina pileolus d'Orbigny, 1839

Remarks:
Pileolina was recorded as a genus of uncertain status by Loeblich and Tappan (1988), however I follow Hayward et al. (1999). in placing the genus in the family Glabratellidae.

Pileolina australensis (Heron-Allen and Earland), 1932
(Plate 2, Figs. 18-20)

1932 *Discorbis australensis* Heron-Allen and Earland, p. 416.
1995 *Glabratella australensis* Yassini and Jones, p. 160; Figs. 731-734.

Description:
see Heron-Allen and Earland (1932), p. 416.

Remarks:
With the validity of the genus *Pileolina* established by Hayward et al. (1999), the species *australensis* Heron-Allen and Earland is herein reassigned to the genus. The genus *Glabratella*, where *australensis* Heron-Allen and Earland was most recently assigned by Yassini and Jones (1995), is characterised by the presence of globular chambers and a rounded periphery (Loeblich and Tappan, 1988; Hayward et al., 1999) whereas specimens of *australensis* described by Heron-Allen and Earland (1932) and illustrated by Yassini and Jones (1995, Figs. 731-734), as well as those found as part of this study, do not have globular chambers and have an acute periphery. These features, along with the flat, involute umbilical site with radiating striae and papillae clearly place the species in *Pileolina.*

Pileolina australensis (Heron-Allen and Earland) is easily distinguished from most other species of *Pileolina* by the ornament present on its umbilical side, which consists of strong tubercules located centrally and numerous prominent striae around the outer edge (Plate 2, fig. 20). *P. australensis* (Heron-Allen and Earland) does resemble *P. zealandica* Vella, which has a similar ornament on the umbilical side, but can be discriminated by the nature of the chambers on the spiral side, which in *P. australensis* (Heron-Allen and Earland) are much longer than in *P. zealandica* Vella (Hayward et al. 1999).

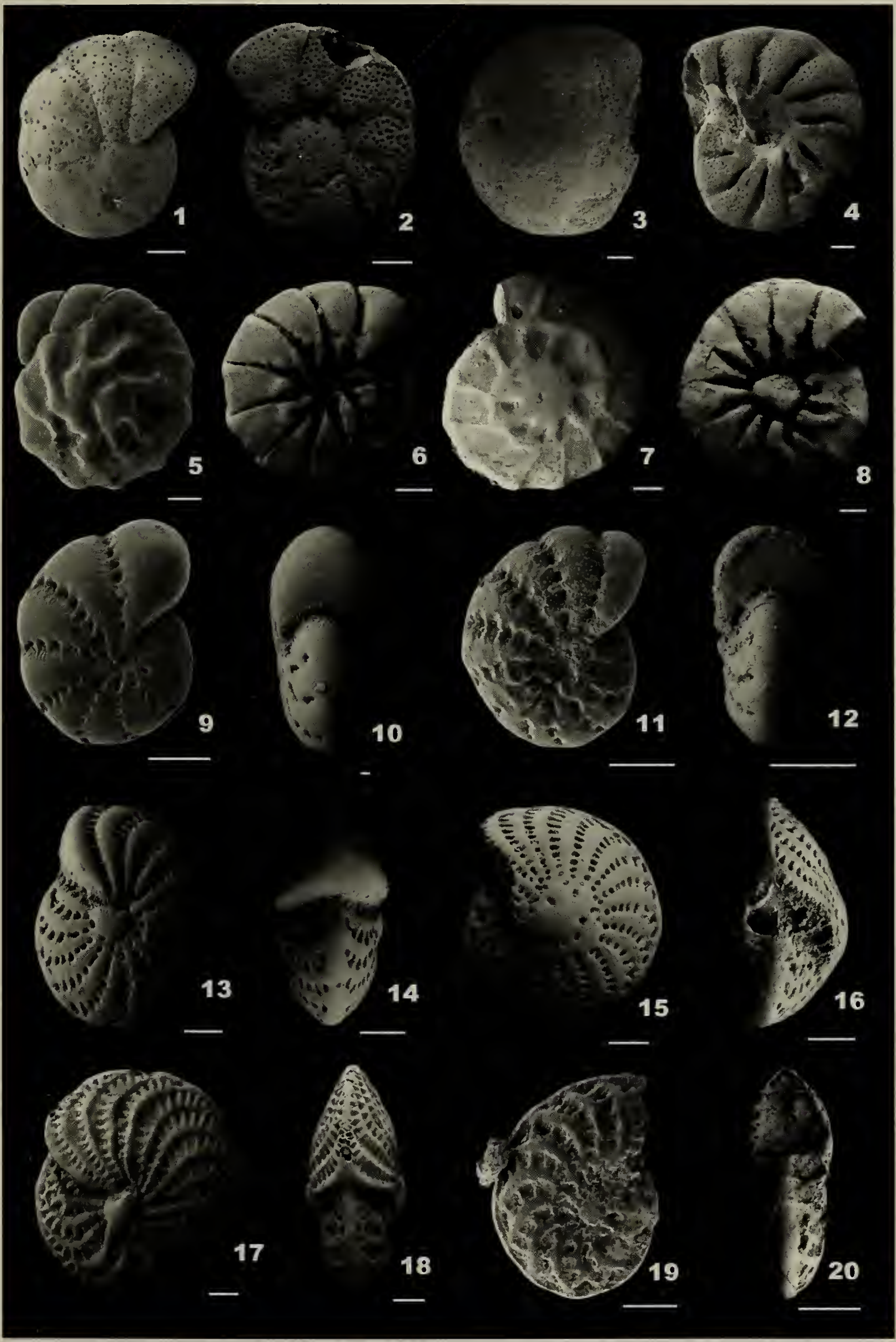
Pileolina australensis (Heron-Allen and Earland) is endemic to Australia and its distribution is confined to a variety of marine dominated environments (Yassini and Jones, 1995). Specimens found in the study area conform to these ecological parameters and tests were only found at locality TL1, where marine conditions dominate.

Superfamily PLANORBULINOIDEA Schwager, 1877
Family CIBICIDIDAE Cushman, 1927
Subfamily CIBICIDINAE Cushman, 1927

Cibicides de Montfort, 1808

Type species:
Cibicides refulgens de Montfort, 1808

Plate 3 Facing page: (Unless otherwise specified all scale bars = 100 µm) - 1-2. *Cibicides dispars* (d'Orbigny), TL1 July; 3. *Lamellodiscorbis dimidiatus* (Jones and Parker) TL1 300-320; 4. *Lamellodiscorbis dimidiatus* (Jones and Parker), TL1 July; 5-6. *Ammonia aoteana* (Finlay), TL4 515-535; 7-8. *Ammonia aoteana* (Finlay) TL4 140-160; 9. *Elphidium lene* Cushman and McCulloch, TL7 July; 10. *Elphidium lene* Cushman and McCulloch, TL7 July (Scale bar for figure 5 = 10µm); 11-12 *Elphidium excavatum clavatum* Cushman, TL4 515-535; 13-14. *Elphidium advenum advenum* (Cushman), TL1 410-430; 15-16. *Elphidium crispum crispum* (Linne), TL1 180-200; 17-18. *Elphidium crispum* (Linne) ssp. TL1 300-320; 19-20. *Elphidium advenum macelliforme* McCulloch, TL1 515-535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Cibicides dispars (d'Orbigny), 1839
(Pl. 3, Figs. 1-2)

1839 *Truncatulina dispars* d'Orbigny, p. 38; Pl. 5, Figs. 25-27.
1980 *Cibicides dispars* Boltovskoy et al., p. 24; Pl. 8, Figs.12-16.
1995 *Cibicidoides floridanus* Yassini and Jones, p. 169, Figs. 889-896.
1999 *Cibicides dispars* Hayward et al., p. 154; Pl. 14, Figs. 22-24.

Description:

see Hayward et al. (1999), p. 154.

Remarks:

There has been a great deal of confusion concerning the taxonomic assignment of planoconvex species of *Cibicides* (Hayward et al., 1999). Because of this, the broad view taken by Hayward et al. (1999) with respect to *C. dispars* (d'Orbigny) is followed herein. Whilst the material found in the study area does not exactly match the specimens of *C. dispars* (d'Orbigny) illustrated by Boltovskoy et al. (1980, Pl. 8 Figs. 12-16) and Hayward et al. (1999, Pl. 14 Figs. 22-24), mainly due to the lack of perforations on much of the involute side in the Tuross Estuary specimens, they match the original description given by d'Orbigny (1839) and have an overall morphology that is otherwise strikingly similar. Therefore specimens from the study area are referred to *C. dispars* (d'Orbigny). Also of note is that the specimens recovered from the study area are clearly conspecific with the material identified by Yassini and Jones (1995) as *Cibicidoides floridanus* (Cushman), a designation that was later recognised as a junior synonym of *C. dispars* (d'Orbigny) by Hayward et al. (1999).

Specimens of *C. dispars* are present in Tuross Estuary and Coila Lake but are confined to localities where marine influences dominate (TL1, CL2). This is not unexpected since the species thrives in fully marine inner- to mid- shelf environments. Some specimens found in surface samples from TL1 did take up the rose Bengal stain, indicating that *C. dispars* (d'Orbigny) can survive in estuarine conditions and is not necessarily washed in from shelf environments.

Superfamily ROTALIOIDEA Ehrenberg, 1839
Family ROTALIIDAE Ehrenberg, 1839
Subfamily AMMONIINAE Saidova, 1981

Ammonia Brünnich, 1772

Type species:

Nautilus becarii Linne, 1758

Ammonia aoteana (Finlay), 1940
(Plate 3, Figs. 5-8)

1940 *Strebulus aoteanus* Finlay, p. 461.
1967 *Ammonia aoteanus* Hedley et al., p. 47; Pl. 11, Figs. 4a-c, Text Figs. 56-60.
1974 *Ammonia aoteanus* Collins, p. 40; Pl. 3, Figs. 30a-c.
1968a *Ammonia beccarii* Albani, p. 30; Fig. 129
1968b *Ammonia beccarii* Albani, p.110; Pl. 9, Figs. 7, 9-10
1979 *Ammonia beccarii* Albani, p. 40; Fig. 88-1
1980 *Ammonia aoteanus* Apthorpe, p. 225; Pl. 27, Figs. 5-6; Pl. 29, Figs. 1-2.
1994 *Ammonia beccarii* (Linne) forma *aoteanus* Hayward and Hollis, p. 213; Pl. 4, Figs. 1-3.
1996 *Ammonia aoteanus* Bell, p. 6.
1996 *Ammonia beccarii* List, p.19; Pl. 1 Figs. G-H

Description:

see Finlay (1940), p. 461; Hayward and Hollis (1994), p. 213.

Remarks:

The problems surrounding the species, subspecies and formae within the genus *Ammonia* have been discussed extensively in the literature (see Bell, 1996 for summary). Due to the large deal of morphological overlap within the genus and subjective recognition of key features by workers (Murray, 1979), it appears that genetic studies will be required to sort out the relationships between the numerous morphological variants.

Because of the uncertainty surrounding the genus, two main approaches have traditionally been used in descriptions of *Ammonia* in estuarine faunas in south-eastern Australia. In New South Wales, specimens falling within the genus *Ammonia* have been referred to as *Ammonia beccarii* (Linne) (Albani, 1968a; Albani, 1978; Albani, 1979; Yassini and Jones, 1989; Yassini and Jones, 1995; Cotter, 1996) whereas in Victoria, specimens have been referred to *Ammonia aoteana* (Finlay) (Collins, 1974; Apthorpe, 1980; Bell, 1996), a species of *Ammonia* described by Finlay (1940) from the south-west Pacific. The lack of strongly beaded sutures on the umbilical side of specimens from Tuross Estuary and Coila Lake, a feature typical of *A. beccarii* (Linne) *sensu stricto* (Hayward and Hollis, 1994, Pl. 4 Figs. 1-3), indicates that the specimens of *Ammonia* from the study area can be assigned to *A. aoteana* (Finlay).

The material from the study area displays a wide variation in morphology that is characteristic of the species and widely distributed throughout the two estuaries. The only discernible trend in morphology is a tendency for specimens recovered from localities where marine conditions dominated, such as TL1, to have an umbilical boss. Specimens from slightly brackish localities such as TL3 and TL8, tend to lack this feature. The correlation between the presence or absence of an umbilical boss with prevailing salinity is also a feature that has been noted in variants of *Ammonia beccarii* (Linne) (Murray, 1979).

Family ELPHIDIIDAE Galloway, 1933

Remarks:

The family Elphidiidae, and in particular the genus *Elphidium*, has undergone a great deal of reassessment since it was first described by Galloway (1933), with a number of genera of doubtful validity erected within the family. In an attempt to gain standardisation in identification of the members of this family, particularly in Australia, all Elphidiidae in this study were identified following the concept of the family presented by Hayward et al. (1997), except where otherwise noted.

Subfamily ELPHIDIINAE Galloway, 1933

Elphidium de Montfort, 1808

Synonymy:

see Loeblich and Tappan (1988), p. 674.

Type species.

Nautilus macellus var.? Fichtel and Moll, 1798

Elphidium advenum (Cushman), 1922

1922 *Polystomella advena* Cushman, p. 56; Pl. 9, Figs. 11-12.

1997 *Elphidium advenum* Hayward et al., p. 64.

Description:

see Hayward *et al.* (1997), p. 64.

Elphidium advenum advenum (Cushman), 1922

(Plate 3, Figs. 13-14)

Synonymy:

see Hayward et al. (1997), p. 65.

Description:

see Hayward et al. (1997), p. 65.

Remarks:

E. advenum advenum (Cushman) is easily distinguished from other species of *E. advenum* by its distinctive umbilical boss, which fills the entire umbilical area. The original material illustrated by Cushman (1922, Pl. 9 Figs. 11-12) did not clearly display the presence of an umbilical boss, however it is described in the text as a feature of the species. In a later publication by Cushman (1939), the boss is clearly illustrated. This species has been recorded from a variety of environments, from brackish water intertidal conditions to exposed inner shelf environments (Hayward et al., 1999). *E. advenum advenum* (Cushman) is found throughout the south-west Pacific (Hayward et al., 1999) as well as the coastline of Australia (Albani and Yassini, 1993).

Specimens of *E. a. advenum* (Cushman) from the study area differ from the material illustrated by Hayward et al., (1997), in that they have a much weaker keel and are slightly less laterally compressed. Tests of this subspecies were recovered from localities TL1, TL8 and CL2 in both surface and core material. The sites represent a range of environmental conditions, particularly TL8 in comparison to TL1 and CL2, supporting the assertion that this species tolerates a wide range of conditions.

Elphidium advenum macelliforme McCulloch, 1981

(Plate 3, figs. 19-20)

1981 *Elphidium macelliforme* McCulloch, p. 119; Pl. 40, Fig. 1

1993 *Elphidium macelliforme* Albani and Yassini, p. 28; Figs. 65-66

1997 *Elphidium advenum macelliforme* Hayward et al., p. 68; Pl. 5, Figs. 6-12

Description:

see Hayward et al. (1999), p. 68

Remarks:

This species is distinguished from most other sub-species of *E. advenum* Cushman by its less inflated chambers and narrower, less incised sutures. It is distinguished from *E. advenum limbatum* (Chapman) by its distinct umbonal boss. This species is found along the coastline of Australia (Albani and Yassini, 1993) as well as in the eastern part of the Pacific Ocean (McCulloch, 1981). In the study area, this species appears to be only tolerant of marine conditions as specimens were confined to site TL1.

Elphidium crispum (Linne), 1758

Synonymy:

see Hayward et al. (1997), p. 74.

Description:

see Hayward et al. (1997), p. 74.

Elphidium crispum crispum (Linne), 1758
(Plate 3, Figs. 15-16)

Synonymy:

see Hayward et al. (1997), p. 74.

Description:

see Hayward et al. (1997), p. 74.

Remarks:

This subspecies is distinguished from other similar species of *Elphidium*, in particular *E. macellum* (Fichtel and Moll) and *E. craticulatum* (Fichtel and Moll), by its distinctive sparsely pitted boss. This subspecies is extremely common along the east coast of Australia and is abundant in shallow subtidal situations where normal marine salinities are present. Specimens of *E. c. crispum* (Linne) are found in material collected at localities TL1 and CL2, the two localities where marine conditions dominate.

Elphidium excavatum (Terquem), 1875

Description:

see Hayward et al. (1997)

Remarks:

As stated by Hayward et al. (1997), this species is distinguished by its broadly rounded unkeeled periphery, low number of chambers in the final whorl (less than 12) and the presence of papillae of the sides of sutural pits, the umbilical area and the base of the apertural face. Its distribution is extensive, recorded from a variety of environments worldwide (Miller et al., 1982).

Elphidium excavatum clavatum Cushman, 1930
(Plate 3, Figs. 11-12)

Synonymy:

see Hayward et al. (1997), p. 76

Description:

see Hayward et al. (1997), p. 76.

Remarks:

E. excavatum clavatum Cushman differs from other subspecies of *E. excavatum* (Terquem) because of the intermediate length of its septal bridges, it umbilical collar and the presence of a small umbonal boss (Hayward et al., 1997).

In the study area, *E. e. clavatum* Cushman is distinguished from specimens of *E. lene* Cushman and McCulloch, also found in Tuross Estuary, by its less numerous septal bridges and more numerous papillae. The highest abundance of this species was recorded from locality TL3, indicating it favours middle estuary, intertidal environments. The species is possibly tolerant of a wide range of conditions however, as rare specimens were also recorded from localities TL1 and CL2.

Elphidium lene Cushman and McCulloch, 1940
(Plate 3, Figs. 9-10)

1940 *Elphidium incertum* (Williamson) var. *lene* Cushman and McCulloch, p. 170; Pl.19, Figs. 2, 4.
1968a *Elphidium poeyanum* Albani, p. 34; Fig. 158.
1979 *Cribroelphidium poeyanum* Albani, p. 47; Fig. 110-1.
1989 *Elphidium depressulum* Yassini and Jones, p. 263; Figs. 16.1-16.3.
1992 *Elphidium poeyanum* Bell and Drury, p. 15; Fig. 4.20.
1993 *Cribroelphidium poeyanum* Albani and Yassini, p. 17; Figs. 10-15.
1995 *Cribroelphidium poeyanum* Yassini and Jones, p. 178; Figs. 1074-1075.
1997 *Elphidium lene* Hayward et al., 1997, p. 84; Pl. 13, Figs. 1-8.

Description:

see Hayward et al. (1997), p. 84

Remarks:

This species resembles *E. excavatum* (Terquem) in overall appearance, but differs in its more compressed test, higher apertural face, more numerous septal bridges, and less papillose ornament (Hayward et al., 1997). *Elphidium lene* Cushman and McCulloch is found along the east coast of Australia, but has generally been referred to either *Cribroelphidium poeyanum* (d'Orbigny) or *E. poeyanum* (d'Orbigny) (Albani, 1968; Bell, 1992; Albani and Yassini, 1993; Yassini and Jones, 1995). *E. poeyanum* (d'Orbigny) is characterised by a coarsely perforate surface (Hayward et al., 1999), a feature not evident on specimens found in Tuross Estuary and Coila Lake, or from other parts of eastern Australia. The specimens are thus referred to *E. lene* Cushman and McCulloch.

In the study area, *E. lene* Cushman and McCulloch is confined to Tuross Estuary. The highest abundance was recorded at locality TL7, a shallow salt marsh environment but it is also recorded from locality

TL1, where fully marine conditions dominate, suggesting that this species tolerates a wide range of conditions.

Elphidium macellum (Fichtell and Moll), 1798
(Plate 4, Figs. 1-2)

Synonymy:
See Hayward et al., 1997, p. 84

Description:
See Hayward et al., 1997, p. 84

Remarks:
This species is distinguished from other species of *Elphidium* by its compressed profile, narrow radial ribs that extend to the peripheral keel and its depressed umbilical area with few irregular papillae (Hayward et al., 1997). Most specimens found in the study area have between 8-10 septal bridges extending across each chamber but rare specimens have less than seven. This species is common of shallow subtidal foraminiferal associations along the eastern Australian coastline. In the study area, specimens are confined to sites were normal marine conditions dominate (TL1, CL2).

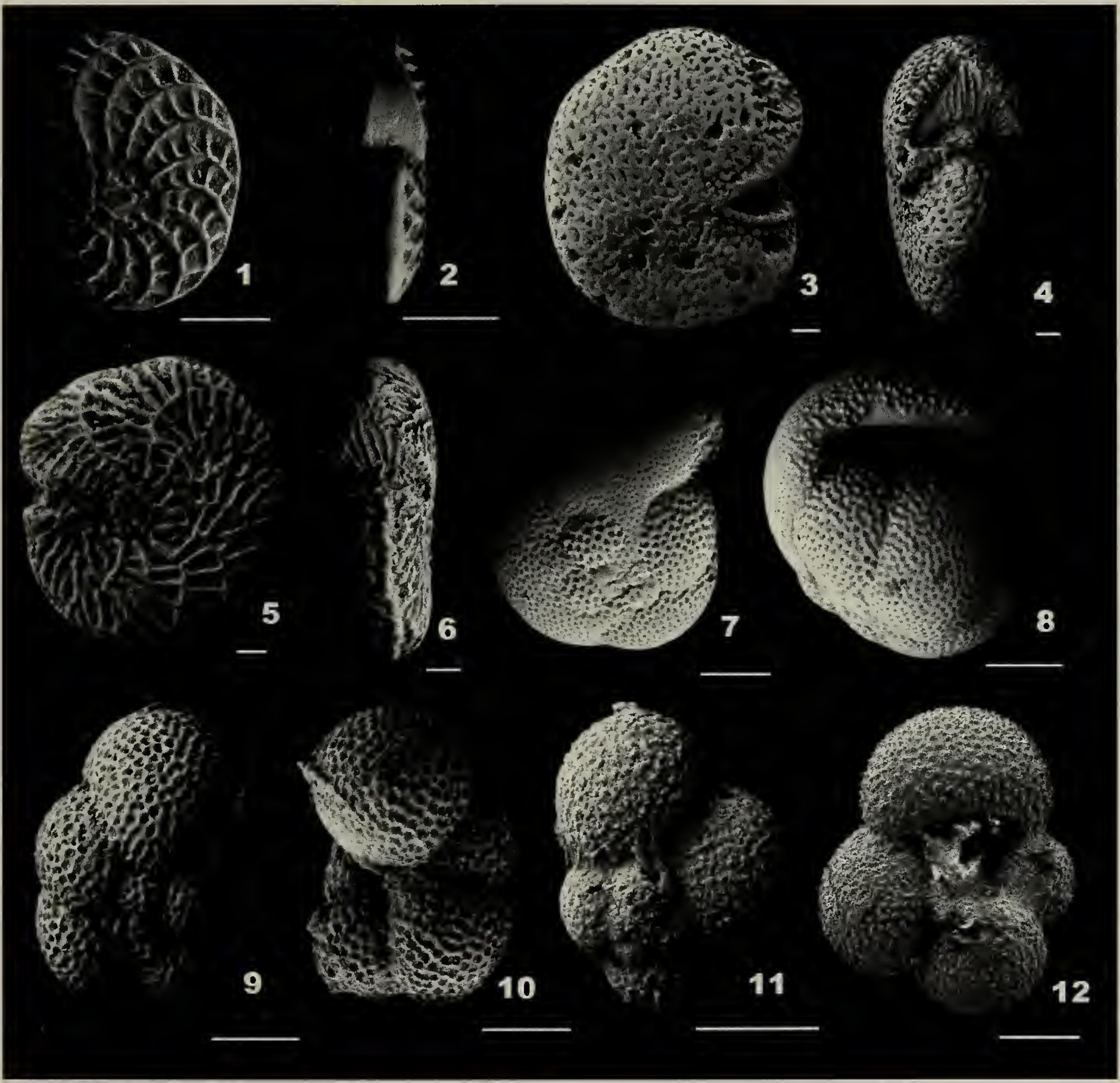

Plate 4 (Unless otherwise specified all scale bars = 100 μm) - 1-2. *Elphidium macellum* (Fichtell and Moll), TL1 300-320; 3. *Parrellina papillosa* (Cushman), TL1 July 4; 4. *Parrellina papillosa* (Cushman), TL1 July; 5-6. *Parrellina verriculata* (Brady), TL1 July; 7-8. *Pulleniatina obliquilculata* (Parker and Jones), TL1 July; 9-10. *Neogloboquarina pachyderma* (Ehrenberg), TL1 515-535; 11-12. *Globigerina bulloides* d'Orbigny, TL1 515-535

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Radio-tracking Studies of Common Ringtail Possums, *Pseudocheirus peregrinus*, in Manly Dam Reserve, Sydney

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In radio-tracking studies in Manly Dam War Memorial Reserve, Common Ringtail Possums were found to survive an average of 319 days, with 80% of known deaths being due to predation by foxes and cats. The study area contained few large trees with hollows and 88% of the nest sites used were dreys. Any drey might be used by several possums, although rarely simultaneously. Ringtails were found to be sedentary, usually occupying dreys and foraging within a *Banksia ericifolia* thicket. Only 37% of the radio-tracked possums moved more than 50 m from their point of capture, and such movements often resulted in the establishment of a new foraging range. Males were more likely to make such shifts than females.

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KEYWORDS: Common Ringtail Possum, drey, home range, *Pseudocheirus peregrinus*, radio-tracking,

INTRODUCTION

This paper reports a long-term study (1994-1999) of Common Ringtail Possums, *Pseudocheirus peregrinus*, in the Manly Dam War Memorial Reserve. It complements and extends an earlier study (Augee et al. 1996) carried out in Ku-ring-gai Chase National Park. The latter study was terminated by fires which burnt the study area in January 1994.

The Ku-ring-gai Chase study found mean survival of Common Ringtail Possums to be 101 days after the commencement of radio-tracking. It provided the first quantitative evidence of high levels of predation on possums by foxes and cats (Rose et al. 1994, Augee et al. 1996), perhaps related to the unexpected finding that up to 10% of the nest sites were on the ground (Augee et al. 1996). Unlike other possums, ringtails are not dependent on tree hollows for nesting sites. They use tree hollows but also construct free-standing nests, known as "dreys", that are often mistaken for birds' nests. Ringtail dreys are larger and more spherical than those of birds except for some babblers, none of which occurred in either study area. Nests on the ground were usually constructed in grass clumps and varied in structure from simple depressions to fully lined shelters similar to arboreal dreys.

Most of the possums radio-tracked in the Ku-ring-gai study were introduced into the area and it is possible that their behaviour was atypical compared to lifetime residents. The Manly Dam Reserve study was based on resident, "wild" ringtails and was designed to determine if the high levels of predation and patterns of nest usage reported by Augee et al. (1996) are a widespread occurrence or simply the result of unusual conditions prevailing in the Ku-ring-gai Chase study.

The Manly Dam Reserve study site was selected because it seemed likely to be less susceptible to bushfire than Ku-ring-gai Chase. That assumption turned out to be incorrect as part of Many Dam Reserve did burn, but only after this study was completed. Both studies areas are Sydney sandstone woodland, although Manly Dam Reserve contains relatively few large trees with hollows compared to Ku-ring-gai Chase.

The Manly Dam Reserve study was designed not only to provide data on survival and nest usage of wild Common Ringtail Possums, but also to run long enough to gather data on long term movements and dispersal of individuals and intraspecific relationships.

In the course of radio-tracking incidental data were obtained, particularly in regard to reproduction.

MATERIALS AND METHODS

The study area

The study area comprised 8 ha in the north-west corner of the Manly Dam War Memorial Reserve as shown in Fig. 1. Its topography was undulating and consisted of moderately sloping hillsides around the headwaters of Curl Curl Creek and tributaries. The vegetation was predominantly dry sclerophyll shrubland and heathland on Hawkesbury Sandstone. Five vegetation communities were identified within the Manly Dam Reserve study area:

Banksia ericifolia Thicket: Scrub to 4 metres height and 60-70% cover. Predominantly *Banksia ericifolia*, with *Kunzea ambigua* and *Hakea teretifolia*.

Low Open Woodland: Low eucalypts to 8 metres at 3 - 4 metre intervals. Dominated by Red Bloodwood *Corymbia gummifera* and stringybarks. Sparse shrub layer and dense sclerophyllous ground layer.

Heathland/Low Open Woodland: Dense low shrubs and grassland to 2 metres, with areas of low, scat-

Figure 1. The study area in Manly Dam War Memorial Reserve.

tered eucalypts to 8 metres.

Open Forest: Trees to 20 metres and 30 - 40% cover. Dominant species include Sydney Peppermint *Eucalyptus piperita*, Smooth-barked Apple *Angophora costata*, Red Bloodwood *Corymbia gummifera*, Silver-top Ash *E. sieberi* and stringybarks.

Riparian Open Forest: Trees to 20 metres height along the bank and floodplain of the creekline. Dominated by Black Wattle *Callicoma serratifolia* and eucalypts with a shrub layer of *Banksia ericifolia* and a ground layer with sedges such as *Gahnia* spp. and Coral Fern *Gleichenia* spp.

Animals

Seventy-nine ringtails were caught in the study area and fitted with radio-collars. They were designated with numbers 242-320. Sex is indicated by the prefix F for females and M for males. Individual details are given in Appendix I. Individuals weighing less than 600 g were classified as juveniles.

For ringtails that had been followed since they were pouch young, their mother was of course known. We were able to identify probable fathers in cases where nest sharing with the mother had been observed at about the right time for conception and where nest sharing between an adult male and the juvenile was observed.

Radio-tracking system

Ringtails were caught by shaking them from low lying trees or bushes, fitted with radio-transmitters built into collars and subsequently located by tracking the radio signal as described in Augee et al. (1996).

The process of capture and collaring usually resulted in the animal moving to a nest other than the one in which it had been captured, but on only one occasion was that nest site out of the foraging range. One individual (F245), after it took several attempts to recapture her and replace a faulty transmitter, dispersed immediately by 110 m to a new foraging range in which she remained for more than two years.

Data collection

The position of each Ringtail was usually determined weekly, although more frequent determinations were often made in the first few weeks after a collar was fitted. The nest site (drey, tree hollow, ground nest or other) was recorded.

When radio collars were replaced in order to change batteries, pouches of females were examined. The presence and estimated weight of any joeys was noted. Approximate date of birth was extrapolated from the growth curve published by Smith (1995, p. 37).

Probable cause of death was determined from corpses using the criteria set out in Augee et al. (1996). Briefly, intact transmitter collars with little distortion found in association with scattered fur but no body parts were scored as fox kills. Cached collars and collars located a considerable distance from the last recorded nest site were also scored as fox kills. However mangled corpses or collars found with body parts (usually heads, paws, intestines and often the caecum) were scored as cat kills.

Foraging and home ranges

In a separate study of ringtails carried out by Newton (1997) at Manly Dam, the areas used by individual ringtails foraging around their nesting sites were found to average 0.020 ha for females and 0.034 ha for males. These foraging ranges had a maximum diameter of about 50 m. In the present, long-term study therefore we considered movements less than 50 m as foraging movements and movements over 50 m as exploratory. These longer movements may or may not have resulted in a shift of foraging range. When ringtails were found to establish a new foraging range, new nest sites more than 50 m from their previous site were considered to be dispersal. We use the term "home range" to refer to the sum of all foraging areas used by an individual throughout the course of the study. Home ranges are illustrated in figures by the smallest convex polygon that can be drawn to connect the outermost recorded nest sites. Only data for those animals (62 out of 79) that were tracked for more than a month were used in determination of home ranges.

Survival statistics

Where mean survival is given it has been calculated only for individuals whose date of death could be determined.

Survival functions for various data subsets were estimated using software provided by K.H. Pollock based on his (Pollock et al. 1989) modification for staggered entry of animals of the Kaplan-Meier product limit estimator (Kaplan and Meier 1958) as detailed in Augee et al. (1996). The survival functions in this study and the previous Ku-ring-gai Chase study (Augee et al. 1996) were based on weekly observations.

RESULTS

Survival

The mean survival of all ringtails was 319 days after commencement of radio-tracking (n = 60, SD = 336, median = 172 days). Mean survival of adults was 465 days (n = 33, SD = 374, median = 371 days). Mean survival of juveniles was 140 days (n = 27, SD = 156, median = 90 days).

The mean survival of all resident ringtails was

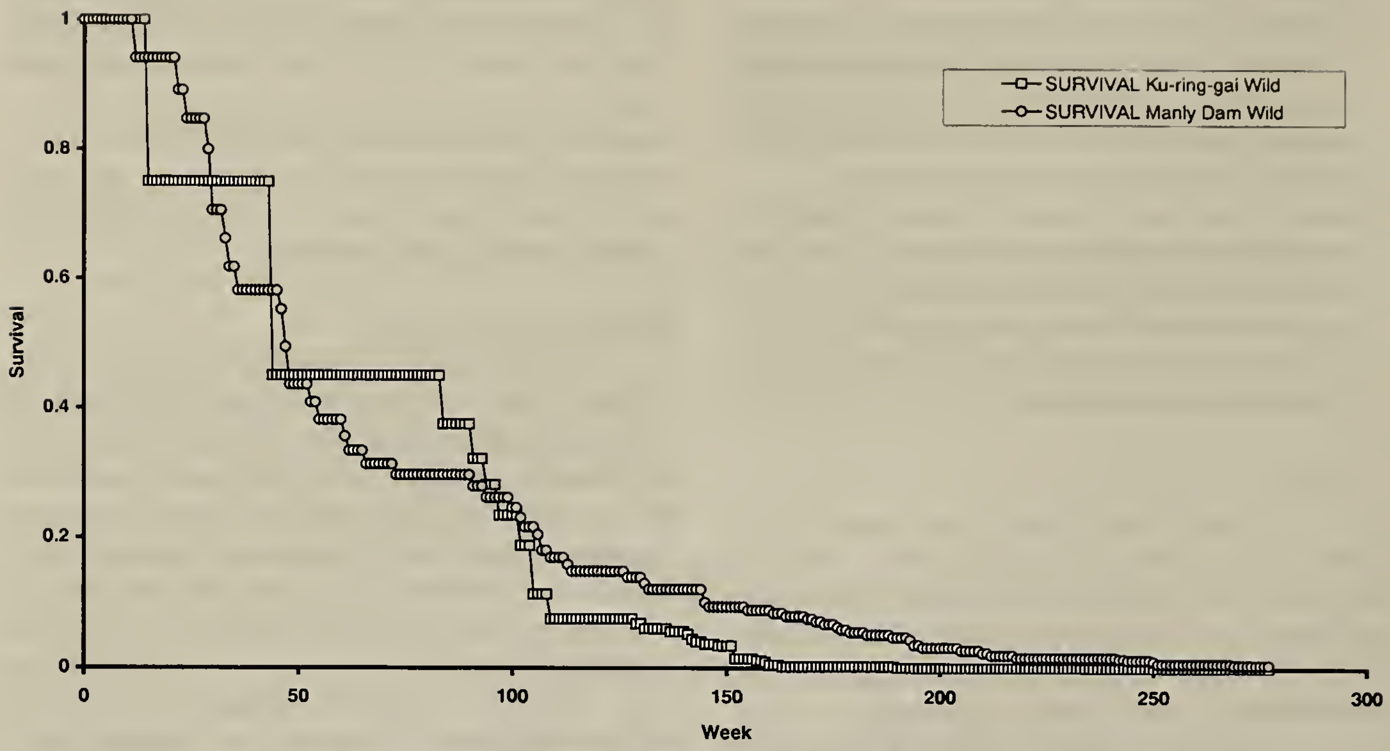

Figure 2. Comparison of Kaplan-Meier survival functions (modified for staggered entry) for all wild ringtails radio-tracked at Manly Dam Reserve (n=78) and Ku-ring-gai Chase (n=41). Chi-squared = 10.227; P<0.01.

much greater at Manly Dam Reserve (319 days) than at Ku-ring-gai Chase (182 days). The Kaplan-Meier survival functions, modified for staggered entry of animals, for all wild possums tracked at Manly Dam Reserve and at Ku-ring-gai Chase are shown in Fig. 2. The survival function for the Manly Dam Reserve population is significantly lower (Chi-squared = 10.227, P<0.01).

Figure 3 compares the survival functions for juvenile and wild ringtails at Many Dam Reserve. The relatively low survival function for juveniles is highly significant (Chi-squared = 13.069, P<0.001).

Predation

The fates of all 79 resident ringtails radio-tracked are shown in Table 1. Predation by introduced

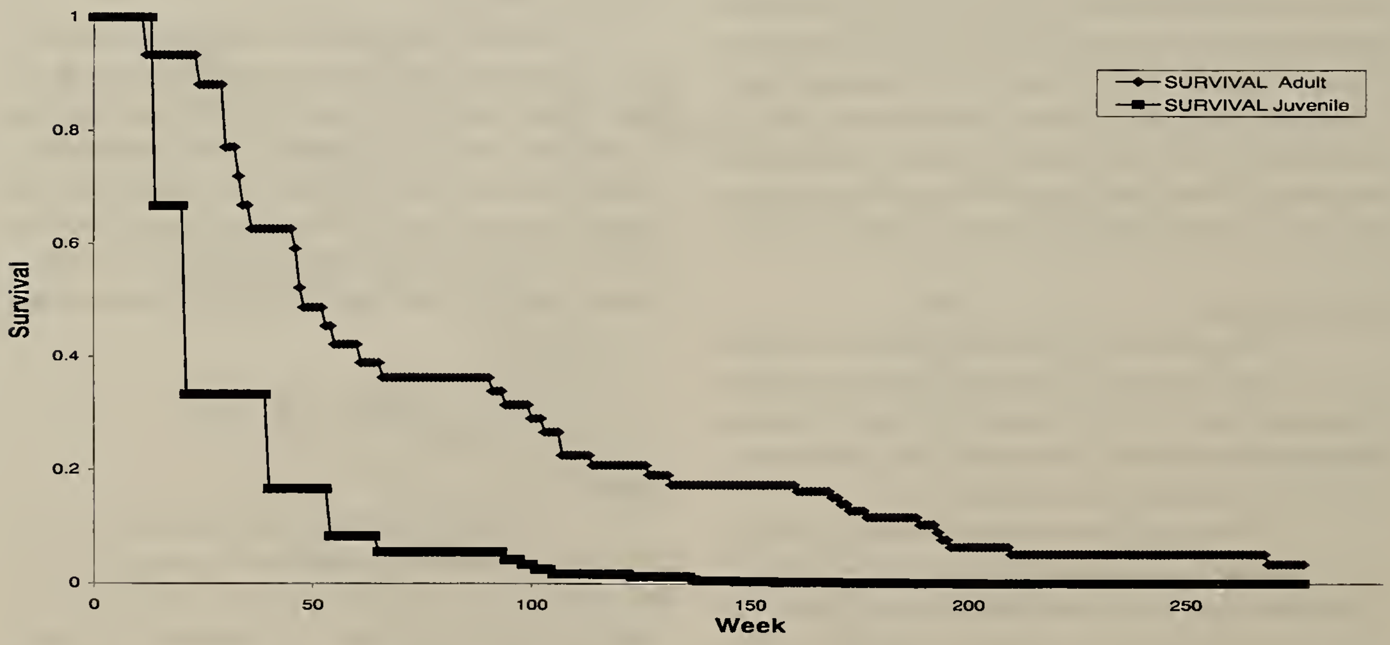

Figure 3. Comparison of Kaplan-Meier survival functions (modified for staggered entry) for adult ringtails (top curve, n=44) and juveniles (n=34) at Manly Dam Reserve. Chi-squared = 13.069, P<0.001.

Table 1. Fate of Common Ringtail Possums tracked in Manly Dam Reserve 1994-1999 and Ku-ring-gai Chase National Park 1990-1994

FATE	Manly Dam	Ku-ring-gai Wild	Ku-ring-gai Introduced
Killed by fox	28	18	39
Killed by cat	20	4	28
Radio-signal lost, reason undetermined	12	8	27
Killed on road	9		1
Still alive at end of study (collar removed)	4		
Transmitter failed, seen but not recaught	3		
Killed by python	1	3	5
Killed by goanna	1		6
Killed by raptor	1		2
Killed by unknown predator		1	4
Killed in bush fire		4	1
Total	79	38	113

carnivores (foxes and cats) was heavy; 80% of known causes of death (Table 1).

Nest sites

During this study a total of 2,907 daytime positions was determined by radio tracking. Of these, 88% were in dreys, 6.1% were on the ground and 3.6% were in tree hollows.

Dreys were constructed in tree/shrub species listed in Table 2 with the majority in *Banksia ericifolia*. On average, individual ringtails at Manly Dam Reserve used seven different dreys during the period they were radio-tracked. The actual number ranged from one to 21 depending mainly on the length of time any one possum was tracked.

The figure for usage of ground positions (6.1%) is skewed by one individual (M275) that was located 70 times on the ground after having dispersed to an area of heathland where there were no shrubs, bushes or small trees sturdy enough to support a drey. If this animal is excluded, only 4% of the locations were on the ground.

Sharing of nest sites

Dreys were used and kept in repair by more than one individual ringtail. Table 3 lists single and multiple occupancies for all known nesting sites in one thicket. The thicket illustrated had the greatest use of any in the study area. Table 3 contains an example of nest sharing within a family, with each parent (F266 and M295) sharing with each other and on separate occasions with offspring (M307 and M308). F266 also shared with her daughter F292, the father of which is unknown.

Competition

There is some evidence for exclusion as a result of competition. In two cases ringtails moved into an area immediately after an occupying ringtail died (M261 replaced M244, and F242 replaced F243). In

Table 2. Characteristics of four thickets in the Many Dam study area. Common Ringtail Possums listed as occupants did not necessarily overlap in time. Area and floristic data from Newton (1997).

OCCUPANTS	THICKET AREA (ha)	SPECIES IN WHICH NESTS OCCURRED
M263, F266, M295, M307, M308	0.165	*Banksia ericifolia, Kunzea ambigua* and *Corymbia gummifera*
F242, M254, M279, M300	0.12	*B. ericifolia, K. ambigua, Hakea teretifolia,* and *E. punctata*
M290, M297, F298, F311	0.18	*B. ericifolia, K. ambigua, H. teretifolia,* and *E. haemastoma*
F136, M246, F248, F249, M282	0.275	*B. ericifolia, K. ambigua, B. serrata, H. teretifolia,* and *E. haemastoma*
F253, M264, M284, F287, M310	0.16	*B. ericifolia, K. ambigua, Callicoma serratifolia, E. punctata* and *Leptospermum trinervium*

Table 3. Occupancy of dreys in a single thicket by Radio-collared ringtails during the period 1994-1999. Cases where occupancy was simultaneous are indicated by / and bold. *M307 and M308 are siblings; M295 is their father; F266 is their mother, ** F266 is the mother of F292

Drey designation	Occupiers
C1a	**M259/F132**
C1	F242, M263, M261, M289
C2	**M259/F266**, M263, F285
C3	**F266/M259**
C4	**M295/F266**, M308, M307
C5	M259, M263
C6	F285, M259, M263
C7	M259
C8	M263, M259
C9	M259, **F266/M295**, M263, M244, M261, F249, **M279/F292, M295/M307/M308***
C10	F266, M259, M263, M244
C11	M295
C11a	**F266/M307***
C12	M263
C13	F289, M263, M279
C14	M263
C15	**M263/F277**
C16	F277
C17	F266, M295, M263, **M307/M308***
C18	F289
C19	M259, **F266/F292****, F289
C20	F266, M295
C21	M295
C22	**M295/F266**, M307
C23	F266, **M307/M308***
C24	M295
C25	**F266/M307**, M295
C26	M295

another case, M275 dispersed from the foraging area he had occupied for four months after another male, M264, incorporated that area into his own. M275 thereafter remained in his new foraging range.

Movements

Table 4 sets out all instances for ten individuals in which exploratory movements from one nest site resulted in the occupation of a new nest site more than 50 m away. The number of these movements for an individual varied from one (F245) to 13 (F296) (Table 4). It is important to note that 39 of the 62 animals tracked for more than one month did not make any exploratory movements and remained within 50 m of the point at which they were initially captured and collared.

Forty-four percent of males tracked made exploratory movements while only 28% of the females did so.

Table 5 shows that some ringtails remain for extended periods, in some cases their entire life, in the same foraging area (thicket) in which they were born.

Distribution of nesting sites and home ranges

Fig. 4 is a plot of all nesting sites on a map of the study area. All nesting sites for any given individual are enclosed in the smallest polygon that can be formed by joining outer sites for that animal to form an estimate of home range. The distribution is patchy across the study area and the overlapping concentrations of home ranges correspond to the distribution of thickets (Fig. 4). The thickets were composed primarily of *Banksia ericifolia* and *Kunzea ambigua*. Details of the floristics (from Newton 1997) of four thickets in the study area are given in Table 2. Nest sites rarely occurred in large trees. Over the entire period of this study only five dreys were found in *Eucalyptus* or *Angophora* spp.

Reproduction

When the pouches of females at the time of radio-collar replacement were examined, almost all were found to contain joeys. Although Pahl (1987) found numerous single births in southern Victoria, in this study all mothers with pouch young were found to be carrying twins; not one instance of single birth was found. Pouch young were attached to the posterior pair of nipples (ringtails have two pairs of nipples in the pouch). The annual distribution is shown in Fig. 5, from which it appears that breeding occurs throughout the year, with a peak of births in May and November, and a trough in January-March.

DISCUSSION

Mean survival of wild possums at Manly Dam Reserve (319 days) was greater than determined for

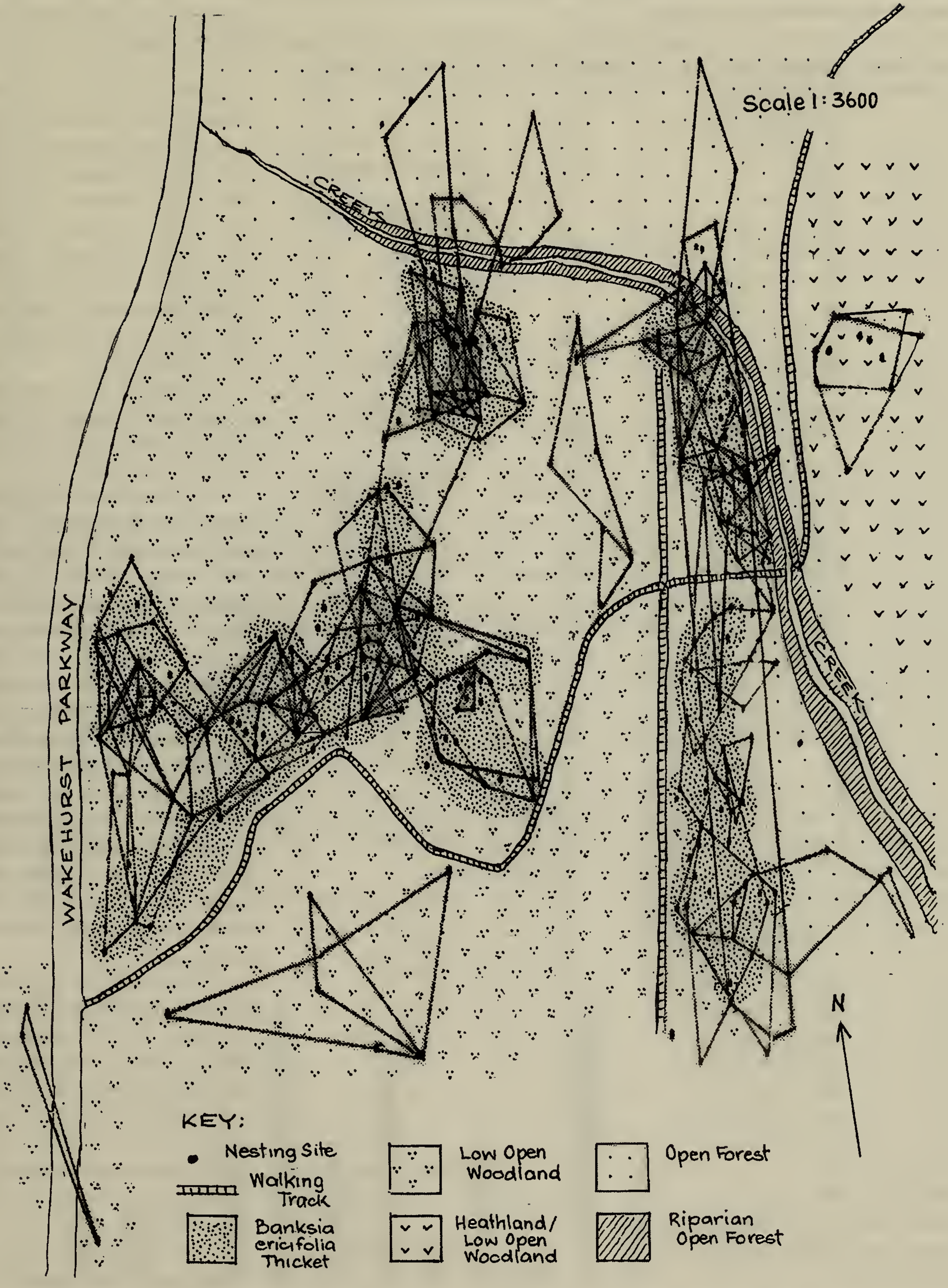

Figure 4. Home ranges (as defined in the text) of all ringtails radio-tracked at Manly Dam Reserve 1994-1999 superimposed on a vegetation map of the study area. Dots = nest sites. Vegetation communities are defined in "Methods" above.

Table 4. Examples of long distance movements by Common Ringtail Possums in Manly Dam Reserve. For each ringtail listed all known movements over 50 m are given.

Animal	Distance (m)	Duration (days)	Terminal event
F242	55 (from a to b)	18	
	55 (return to a)	14	
	55 (return to b)	1140	killed by fox
F245	110	741	killed by goanna
M254	122	7	
	105	14	road kill
M261	50	36	
	68	21	
	53	14	
	65	21	
	64	539	
	56	21	killed by fox
M264	75	28	
	110	764	killed by cat
M275	122	370	
	88	7	
	65	78	transmitter failed
M279	65 (a to b)	7	
	63 (return to a)	7	
	63 (return to b)	266	
	94	21	
	104	14	
	89	1	roadkill
F289	86	14	
	61	7	
	61	27	
	74	39	
	51	17	
	61	42	
	121	43	
	83	293	killed by fox
F296	110	14	
	121	28	
	135 (a to b)	7	
	135(return to a)	34	
	131	7	
	131	21	
	145	7	
	136	28	
	159	21	
	232	14	
	293	7	
	94	30	
	373	1	killed by cat
M317	88	28	
	84 (a to b)	10	
	84 (return to a)	4	killed by fox

wild possums in the previous study at Ku-ring-gai Chase (182 days; Augee et al. 1996). Likewise the survival functions for these two data sets (compared in Fig. 2) indicate a significantly ($p<0.01$, Chi-squared = 10.227) lower survival function for wild possums in the Ku-ring-gai study. The major cause of death is predation by foxes and cats; 80% at Manly Dam Reserve and 76% at Ku-ring-gai Chase. Usage of ground nest sites is also similar in both studies; 6% at Manly Dam Reserve and 7% at Ku-ring-gai Chase. The most likely explanation for the apparently greater life expectancy at manly Dam Reserve is lower numbers of introduced predators, but there is no way to test this hypothesis with available data.

Juveniles are clearly at greater risk than adults, having a significantly lower survival function (Fig. 3).

The vegetation within the Manly Dam Reserve study area consisted mostly of low heath, with taller mature eucalypts and riparian vegetation along a creek line and *Banksia*/*Kunzea* thickets separated by low scrubby heath. Ringtails preferred the thickets, constructing dreys primarily in *Banksia ericifolia* and to a lesser extent in the low trees and sturdy bushes listed in Table 2. Some ringtails utilized hollows in the trees near the creek line and one individual utilized the heath, making several nests on the ground.

In Ku-ring-gai Chase the figure for usage of tree hollows was about 33% (Augee et al. 1996). In Manly Dam Reserve there are few large, mature trees and only 3.6% of daytime positions were in hollows. One animal also nested briefly in an arboreal termite mound about 5 m up a eucalypt tree.

At any given time, a ringtail would use several nest sites, most often within a single thicket. Around these sites the animal would forage over an area usually less than 0.2 ha with a maximum diameter of 50 m. This foraging range was consistent regardless of the habitat,

Table 5. Residency time of progeny that never left their natal sites. All were juveniles (<600 g) at time of collaring. Days are measured from time of collaring.

Subject	Female Parent	Probable Male Parent	Natal Area Days	Killed in natal area or moved
M259	F249	M244	638	K
F274	F248	M246	35	K
F278*	F242	M254	27	M
M279*	F242	M254	519	K
M282	F248	M246	967	K
M284	F245	M280	232	M
F291	F245	M280	37	K
F296	F287	M264	158	M
M297	F298	M290	253	M
M307*	F266	M295	293	K
M308*	F266	M295	166	M
F311	F298	M290	89	M
M318*	Uncollared	Uncollared	211	M
F319*	Uncollared	Uncollared	83	K

being observed for animals living along the creekline amongst large trees as well as in thickets.

Like many arboreal mammals (e.g. squirrels, McDonald 1984), ringtails are sedentary. At Manly Dam Reserve 39 of the 62 animals tracked remained within the foraging range where they were first caught. One female (F273) remained in the same foraging range for 582 days until being killed by a fox.

The sedentary nature of the species is further evidenced by data obtained from 14 individuals for whom their female parent and place of birth were known (Table 5). Of the seven ringtails that were killed within the natal area (i.e. within 50 m of the site of their birth), four had lived there for extended periods from the time of being collared (293, 519, 638 and 967 days).

Some ringtails did move out of their foraging range, occasionally establishing a new nest site more than 50 m from the previous nest site. In a few instances the animal quickly returned (F242, M279, F296 and M317 in Table 4), however most such movements resulted in the establishment of a new foraging range. For example F312 remained in the foraging area where she was first caught for 90 days, then moved about 800 m to a new foraging range, remaining there 174 days. At that time her collar was removed since this unusually large dispersal movement had taken her out of the study area.

Dispersal movements, resulting in the establishment of a new foraging range, were made by both sexes, although more males (15) did so than females (8). However, the animal making the greatest number and longest dispersal moves was a female (F296, Table 4). The animal making the second greatest number of moves was also a female (F289, Table 4). The reasons for such shifts in foraging range are unclear.

In many mammalian species there is a pattern of dispersal by juveniles (McDonald 1984). Some of the ringtail dispersals observed in this study were by juveniles (e.g. M264, M279, F296 and M317 in Table 4). However dispersal of juveniles was not a consistent pattern as only 10 out of 26 (38%) of juveniles tracked for more than a month made dispersal movements. Of the juveniles with known parents (Table 5), three (M282, M279 and M259) remained within the parental foraging range after the death of the parents. As can be seen from Table 3, M307 and M308 remained in association with both parents. One female of known parents (F296) made frequent moves greater than 50 m from the parental foraging area, usually returning, until killed by a cat 280 m from the parental foraging area (at which time

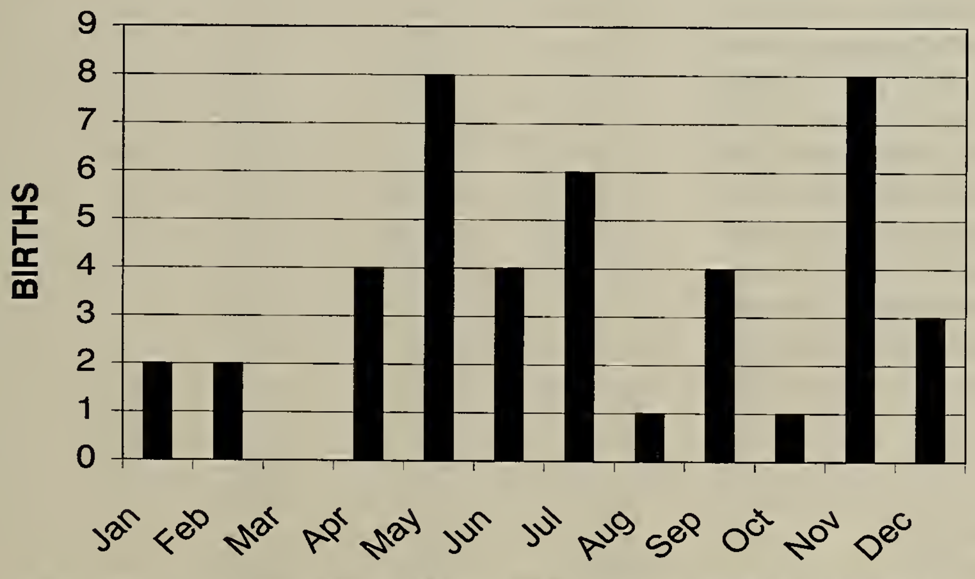

Figure 5. Annual distribution of births of Common Ringtail Possums at Manly Dam Reserve.

both parents were still alive).

On the other hand, most ringtails in this study were mutually tolerant with considerable overlap in home range (Fig. 4) and foraging range (Table 2). Individual dreys were used by as many as 11 different individuals (Table 3). Simultaneous occupancy occurred (Table 3), usually by adult males with adult females and rarely two males. We did not observe simultaneous occupation of a drey by two adult females, although on one occasion the same drey was used by two adult females (F242 and F243) on different nights over a period of 3 weeks . We observed many instances of females sharing with joeys that were too small to radio-collar. In the only instance where we were able to track parents and their offspring simultaneously (F266 and M295, parents of M307 and M308), they were found to frequently share nest sites (see Table 3). The degree to which this familial tolerance continues as the juveniles reach maturity is unknown.

Although there was no evidence that any movements made by the ringtails were related to predation, the majority of ringtails in this study, as in the study carried out earlier in Ku-ring-gai Chase (Augee at al. 1996), were killed by predators, usually foxes or cats (Table 1). While it is possible that deaths due to "unknown predators" in the Ku-ring-gai Chase study might have been due to dogs, we feel it unlikely that any deaths were due to dogs but misidentified at Manly Dam Reserve. Dogs are not allowed in the reserve unless on a lead and this rule is actively policed and well respected by local residents. During the entire course of the study we saw only one dog off the leash.

CONCLUSION

Ringtail possums are usually sedentary, remaining within a foraging range of approximately 50 m diameter in the Manly Dam Reserve study area. They may on occasion move beyond this range, although the reasons for such long distance movements are unknown. They are probably all exploratory, but most result in the establishment of a new foraging range and can be considered dispersal movements. Presumably the new foraging range provides improved feeding or reproductive resources or less competition with conspecifics. Predation by foxes and cats was severe throughout the study area.

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APPENDIX I

Details for all ringtails in the Manly Dam Reserve study

No.	Sex	Weight	Collar attached	Collar retrieved	Survival (days)	Fate
242	F	770g	7/9/94	3/12/97	1181	FOX
243	F	995g	7/9/94	4/5/95	238	CAT
244	M	785g	7/9/94	27/4/95	231	CAT
245	F	800g	7/9/94	17/12/97	1196	GOANNA
246	M	900g	14/9/94	26/9/96	742	FOX
247	F	940g	14/9/94	26/7/95	314	FOX
248	F	750g	21/9/94	29/8/96	708	CAT
249	F	880g	21/9/94	8/8/96	687	FOX
250	F	920g	21/9/94	13/9/95	356	CAT
251	F	950g	21/9/94	27/9/95	370	CAT
252	M	770g	12/10/94	6/4/95	175	CAT
253	F	780g	12/10/94	6/4/95	175	FOX
254	M	810g	7/11/94	10/8/95	275	ROADKILL
255	M	870g	7/11/94	23/3/95	135	TX.Failure
256	F	400g	7/11/94	30/3/95	142	ROADKILL
257	F	930g	7/11/94	30/11/94	22	CAT
258	M	420g	16/11/94	8/2/95	83	CAT
259	M	550g	11/1/95	10/10/96	638	CAT
260	M	800g	11/1/95	22/2/95	41	ROADKILL
261	M	700g	11/1/95	13/11/96	672	FOX
262	M	700g	15/2/95	20/5/95	93	ROADKILL
263	M	675g	15/2/95	26/9/96	588	CAT
264	M	620g	13/4/95	23/4/98	11O6	CAT
265	M	940g	4/5/95	29/6/95	55	SIGNAL LOST
266	F	700g	11/5/95	27/5/98	1112	CAT
267	M	890g	11/5/95	5/6/96	389	CAT
268	M	720g	12/7/95	2/8/95	20	RAPTOR
269	F	940g	12/7/95	2/8/95	20	FOX
270	M	930g	12/7/95	21/5/98	1005	FOX
271	M	995g	19/7/95	11/10/95	83	FOX
272	F	550g	19/7/95	9/8/95	20	CAT
273	F	760g	9/8/95	20/3/97	588	FOX
274	F	595g	11/10/95	15/11/95	35	FOX
275	M	830g	8/11/95	8/10/97	700	TxEXPIRE
276	F	675g	8/11/95	15/5/96	199	SIGNAL LOST
277	F	675g	15/11/95	13/12/95	28	FOX
278	F	550g	3/1/96	31/1/96	28	ROADKILL
279	M	580g	17/1/96	19/6/97	519	R0ADKILL
280	M	970g	17/1/96	26/6/96	159	FOX
281	M	920g	17/1/96	28/2/96	42	SIGNAL LOST
282	M	625g	13/3/96	6/11/98	967	CAT
283	M	460g	26/6/96	22/8/96	57	FOX
284	M	510g	26/6/96	10/3/97	258	FOX
285	F	570g	22/8/96	21/9/96	30	FOX
286	F	860g*	29/8/96	13/2/97	168	PYTHON
287	F	720g	5/9/96	19/2/98	532	SIGNAL LOST

No.	Sex	Weight	Collar attached	Collar retrieved	Survival (days)	Fate
continued						
288	M	560g	12/9/96	7/11/96	56	FOX
289	F	850g	26/9/96	28/1/98	489	FOX
290	M	900g	17/10/96	14/10/98	726	SIGNAL LOST
291	F	455g	29/12/96	5/2/97	37	SIGNAL LOST
292	F	460g	8/1/97	13/2/97	35	SIGNAL LOST
293	M	440g	15/1/97	19/6/97	155	FOX
294	F	490g	26/2/97	26/6/97	120	CAT
295	M	580g	20/3/97	8/12/98	509	SIGNAL LOST
296	F	420g	27/3/97	22/1/98	300	CAT
297	M	300g	24/4/97	12/3/98	352	FOX
298	F	890g	1/5/97	29/12/99	971	RELEASED
299	M	520g	29/5/97	19/6/97	20	FOX
300	F	375g	13/8/97	27/8/97	13	ROADKILL
301	F	725g	20/8/97	3/11/99	804	FOX
302	F	700g	20/8/97	16/9/98	385	CAT
303	F	625g	20/8/97	29/12/99	860	RELEASED
304	M	650g	20/8/97	1/1/98	133	Tx.FAILURE
305	M	850g	27/8/97	10/12/97	118	SIGNAL LOST
306	F	355g	15/10/97	26/10/97	10	FOX
307	M	265g	10/12/97	30/9/98	293	CAT
308	M	255g	10/12/97	27/5/98	167	ROADKILL
309	M	450g	21/1/98	18/11/98	300	SIGNAL LOST
310	M	475g	11/2/98	6/11/98	119	SIGNAL LOST
311	F	340g	30/9/98	30/9/98	90	ROADKILL
312	F	320g	6/11/98	12/2/98	173	RELEASED
313	F	450g	9/2/98	30/9/98	27	SIGNAL LOST
314	F	350g	14/10/98	11/11/98	27	FOX
315	F	245g	13/1/99	28/4/99	104	FOX
316	M	300g	27/1/99	5/12/99	104	FOX
317	M	400g	24/3/99	30/6/99	97	FOX
318	M	310g	4/7/99	29/12/99	265	RELEASED
319	F	300g	4/7/99	30/6/99	83	FOX
320	M	250g	6/2/99	23/6/99	20	CAT

BOOK REVIEW

BIRDS OF AUSTRALIA'S TOP END

Denise Lawungkurr Goodfellow (2001)

Scrubfowl Press, Parap N.T.
RRP $A29.50

I wondered at first if a review of yet another bird guide was appropriate for the *Proceedings*, however it seems to me that all natural scientists have some interest in birds. Even on a geology field trip it is hard to ignore the most obvious and varied daytime fauna. A field guide is a useful part of anyone's field gear. The big three (Pizzey and Knight, Simpson and Day, and Slater and Slater) are of course Australia wide, but there are also a number of local guides and lists of varying quality to supplement them. In some localities the landscape and the avifauna are so unique that a local guide is pretty near essential. The Northern Territory, or more specifically the Top End, is one such place.

This book is primarily aimed at visitors to the top end who come specifically to see birds. Australian and overseas twitchers looking to add to their bird lists will find this book invaluable. Unlike the big three, it provides specific instructions on where to find particular species and the best time and means.

The author has a great interest in birdwatching tourism, which is discussed in the opening pages, and this book does much to encourage and facilitate this. There is a section on safety, which includes some hints for driving safely, most of which are usually ignored by Top Enders themselves.

For the locals there is a section on how to attract birds to your garden.

For the beginner or the student looking for a general reference on bird biology there are sections on bird evolution, physiology, behaviour and sex.

For everyone there is a concise discussion of the problems of conservation in the Top End.

The above features are found in the introduction, but of course the heart of the book is the species descriptions, backed up by watercolour illustrations by the author. For those few species which I have observed myself in the Top End, the colours appear correct. However no bird guide ever written provides colours acceptable to everyone and the user must always be aware that variation is the theme of life.

Besides describing the appearance, of both sexes where necessary, species accounts usually include details of flight, calls, similar species, breeding, habitat, range where found, alternative common names and birdwatching hints. In many cases there is also the Kunwinjku name. This is an Aboriginal language understood widely in the Top End. This of course has nothing to do with species identification but has everything to do with Denise's strong respect for Aboriginal culture and knowledge of the Australian environment. She has included some of this in notes which follow many species accounts. These notes, as well as frequent footnotes and "author's notes" make this book great reading as well as useful. The "author's notes" usually relate Denise's own experiences with the bird in question.

Of great use to the occasional bird watcher is the inclusion of description of higher taxa such as families. This level is usually left out of field guides and may not be essential for identifying species, but it is of great use in understanding relationships and overall characteristics.

With each entry there are references to the matching entries in both Pizzey and Knight ("Field Guide to the Birds of Australia") and Simpson and Day (also titled "Field Guide to the Birds of Australia"); not only a generous feature but a very useful one except for those like me who are loyal to "The Slater Field Guide to Australian Birds".

This is a unique field guide and represents an incredible amount of work by the author, Denise Lawungkurr Goodfellow, who still finds time and enthusiasm to show visitors the avifauna of the Top End. A trip to the Leanyer Sewage Ponds with Denise is an experience, like the book, not to be missed.

M.L. Augee
Sydney
November 2002

INSTRUCTIONS FOR AUTHORS

(this is an abbreviated form - the full instructions can be obtained from our web site or from the Secretary)

1. The *Proceedings of the Linnean Society of New South Wales* publishes original research papers dealing with any topic of natural science, particularly biological and earth sciences.

2. Manuscripts should be submitted to the editor (M.L. Augee, PO Box 82, Kingsford NSW 2032). All manuscripts are sent to at least two referees and in the first instance three hard copies, including all tables and figures, must be supplied. Text must be spaced at one and a half or double line spacing.

3. The final version, incorporating referees' and editor's comments, must be supplied on floppy disc or CD in WORD for PC format (Mac discs will not be accepted). Photographs must be supplied as black & white prints or as .TIF files (JPG is not acceptable). Figures other than photographs must be in hardcopy, XL or WORD files.

4. References are cited in the text by the authors' last names and year of publication (Smith 1987). For three or more authors the citation is (Smith et al. 1988). The format for the reference list is:

Journal articles:

Smith, B.S. (1987). A tale of extinction. *Journal of Comparative Paleontology* **12**, 45-67.

Smith, B.S., Wesson, R.L. and Luger, W.J. (1988). Blood levels of oxygen in Tasmanian Devils during deep sleep. *Australian Journal of Sleep* **356**, 1-45.

Chapters or papers within an edited work:

Ralph, P.H. (2000). The use of ethanol in field studies. In 'Field techniques' (Eds. K. Thurstle and P.J. Green) pp. 34-78. (Northwind Press, Sydney).

Books:

Young, V.H. (1998). 'The story of the wombat'. (Kangaroo Paw Press, Brisbane).

5. An abstract of no more than 200 words is required. Sections in the body of the paper usually include: INTRODUCTION, MATERIALS AND METHODS, RESULTS, DISCUSSION, ACKNOWLEDGEMENTS and REFERENCES. Some topics, especially taxonomic, may require variation.

6. Subheadings within the above sections should be in the form:

Bold heading set against left margin

This is the form for first level subheadings.

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This is the form for the next level. Further use of subheadings should be avoided.

Italics are not to be used for headings but should be reserved for genus and species names.

7. Up to 10 KEYWORDS are required to facilitate computer searches. The more specific the terms the better. Please put in alphabetical order.

8. Paragraphs are to be set off by a tab indentation without skipping a line. Do not autoformat the first line. In fact please do not use ANY autoformatting - this can be fatal when transferring to the publisher platform.

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Use 12 point type - preferably TIMES font.

Do not justify

Margins should be about 3 cm top, 2.5 cm bottom, 3 cm left and 2.5 cm right. This is the area available for text; headers and footers are outside these margins.

10. Figures can be line drawings, photographs or computer-generated graphics. No figures will be accepted larger than 15.5 X 23 cm. Width of lines and sizes of letters in figures must be large enough to allow reduction to half page size.

If a scale is required it must be presented as a bar within the figure. It is the editor's prerogative to reduce or enlarge figures as necessary and statements such as "natural size" or "4X" in the legend are unacceptable.

While there is no objection to full page size figures, it is journal policy to have the legend on the same page whenever possible and figures should not be so large as to exclude the legends. Figure legends should be placed together on a separate page

11. Tables must be on separate pages at the end of the manuscript and NOT placed within the body. Table legends may be above the table or supplied on a separate page but must never be actually part of the table. It may be necessary to reduce tables but the legends will need to remain the size of the text body (10 point in the final form).

While the draft manuscript is expected to be in 12 point type, it may be necessary to use smaller type for large tables. Do not use vertical lines in tables unless absolutely necessary to demark data columns. Keep horizontal lines to a minimum. Do not place the table in a box border.

Tables in WORD or XL are acceptable.

12. Details of punctuation, scientific nomenclature, etc. are to be found in the complete instructions.

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THE LINNEAN SOCIETY OF NEW SOUTH WALES

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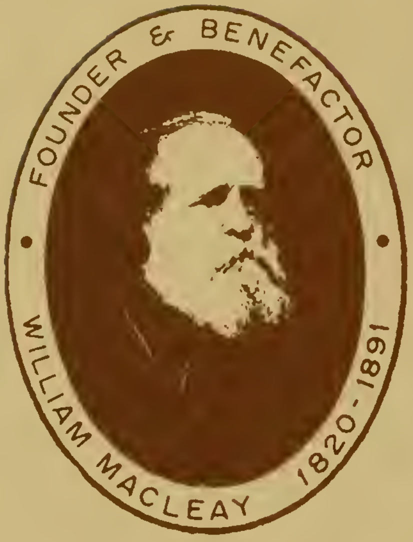

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VOLUME 125
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EDITORIAL

This volume consists of three parts. The first part contains general contributions. The second part contains research papers and review papers arising from the symposium “Monotreme III” held by the Linnean Society of NSW and the Australian Mammal Society at the University of Sydney in July 2003. The third section contains book reviews and an obituary to Merv Griffiths, the pre-eminent monotreme biologist of all time.

The publication of this volume has been delayed by the preparation of the papers from “Monotreme III” and is covered by subscriptions and membership fees for 2003.

Intending authors should read the summary of “Instructions for Authors” at the back of this volume carefully. More details are available in the full version available at the Society’s web site or from the Secretary. The preparation of this volume has been prolonged and made difficult by the failure of some authors to provide figures and tables in the format required. In order to keep the costs at a level which allows our Society to continue publication, we set the journal completely ourselves. Therefore we do not have the flexibility of large commercial publishers. We can only deal with figures as photographs, original line drawings or .TIF files. Jpeg files for example are useless in our system. Auto-formatting and track changes are a disaster, as are tables and/or figures that have been put inside the text. To date we have taken the time to re-set and sometimes re-scan figures, however in future we will apply the policy that final copy not prepared in accordance with the instructions will simply be returned and held over if necessary until the next issue.

M.L. Augee
Editor

Review of Australian Cave Guano Ecosystems with a Checklist of Guano Invertebrates

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This work provides a check-list of all invertebrate species known, or believed to be, associated with cave guano in Australia. A total of 240 species in 121 families, representing 25 orders is listed. These species inhabit 60 karst areas in all mainland states of Australia and Christmas Island (Indian Ocean). Comprehensive assessment of all available records (published and in collections) show that the distribution of several species is more extensive than previously believed. It is unknown whether this is because of inadequate identification of specimens, poorly defined taxonomy or unrecognised intra-species variation due to a lack of specimens. Twenty species from five orders show restricted distributions and guano dependence, although endemic status can not yet be assigned. Amongst these species, eight pseudoscorpions and eight Coleoptera are distributed across several mainland states and Christmas Island.

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Keywords: Arthropoda, Australia, biospeleology, cave, checklist, ecosystem, guano, invertebrate.

INTRODUCTION

Australian cave guano ecosystems are poorly known with only a few communities studied in detail (e.g. Richards 1971; Harris 1973; Bellati et al. 2003). Previous studies concerned with the terrestrial cavernicolous fauna of Australia have mentioned species associated with guano, but have provided little in the way of detail with regard to the ecology of specialised guano communities and species. This paper seeks to synthesise the knowledge of guano ecosystems and communities in Australian caves. A review of guano ecosystems and habitats precedes a checklist of all species known to be associated with Australian cave guano deposits.

Populations of cavernicolous animals are usually small because of limited food supplies. However, caves containing guano differ fundamentally because there is a virtually unlimited food supply, commonly resulting in large animal populations. Guano in caves is deposited by bats, birds, orthopterans (crickets and grasshoppers), and small mammals, with each type of guano sustaining a unique assemblage of taxa. Guano deposits are extremely variable, unlike other cave habitats, and consist of numerous micro-habitats differentiated by fluctuating temperature, moisture, and pH. Guano ecosystems contain obligate guano-dwelling organisms (guanobites), opportunistic guano-dwelling animals (guanophiles), and transient guano-using animals (guanoxenes) (Gnaspini and Trajano 2000). The basis for many guano ecosystems is the numerous species of fungi and bacteria that can grow on guano, even in complete darkness.

Cave food sources

Cavernicolous populations are dependant for their survival upon energy inputs into cave systems. These inputs can vary widely, with availability of food usually being the primary limiting factor (Peck 1976). Inflowing streams and periodic floodwaters introduce significant amounts of zooplankton, accidentals, and organic debris that, for many cave ecosystems, represent the main energy inputs (Peck and Christiansen 1990; Humphreys 1991). Tree roots penetrating the roofs and walls are another important energy source found commonly in tropical caves and lava tubes (Hoch 1988; Hoch and Howarth 1999). Dead animals can be a source of food for scavengers near cave entrances (Richards 1971). Accidentals wandering in from cave entrances also provide a food source, although this is generally periodic in nature and inconsistent in quantity.

For the most part cave environments are generally depaurporate in food and consequently are sparsely populated with cavernicolous animals. However, caves containing guano deposits differ substantially because they have a virtually unlimited food supply. When present, guano from bats, birds, and Orthoptera (crickets and grasshoppers) generally forms the major energy source (Park and Barr 1961; Poulson 1972; Martin 1977), with large, varied and unique ecosystems often revolving around such deposits.

SOURCES AND DIVERSITY OF CAVE GUANO

Cave guano deposits from specific sources can each possess a unique assemblage of taxa (Horst 1972; Poulson 1972). Throughout the world's biogeographic provinces different taxa are responsible for being the most important guano producers. The most widespread and common guano is that produced by bats and these deposits are generally the largest in volume. The spatial and temporal deposition of bat guano differs from tropical to temperate caves. Cave-dwelling bats in temperate regions show an annual cycle of occupancy over summer months when pups are born, before colonies disperse to cooler, wintering caves where they enter torpor. This annual cycle results in large amounts of guano deposited over summer months and then a cessation of guano input for approximately seven months. In contrast, tropical caves generally show constant bat occupancy rather than an annual cycle and less congregation of individuals due to warmer ambient temperatures. Gnaspini and Trajano (2000) note that many bat populations in tropical Brazil are commonly nomadic, resulting in roaming colonies varying their location in an irregular and non-seasonal fashion. This results in non-continuous deposition. The diet of bats (either haematophagous, insectivorous, frugivorous, or nectarivorous) also influences the composition of guano piles and hence the associated guanophilic communities (Gnaspini 1992; Ferreira and Martins 1998, 1999). Large populations of the common vampire bat (*Desmodus rotundus* Geoffroy) predominate in Brazilian karst near inhabited areas, due to large numbers of domestic livestock resulting in haematophagous guano deposits. Guano from non-haematophagous bats is absent, or greatly reduced as vampire bats exclude other bat species, thus changing the guanophilic communities present.

Birds are common guano producers in the northern parts of South America, the Caribbean and tropical caves of south-east Asia. Cave-dwelling birds nest in the dark zone, providing an important energy resource for many cavernicolous animals. Cave-dwelling birds in South American and Caribbean caves include guácharos (*Steatornis caripensis* Humboldt) (Snow 1975; Gnaspini and Trajano 2000). This bird discards palm seeds, sometimes with flesh still attached, and deposit droppings in caves, thus providing a wide range of organic matter for cavernicolous animals. Because of the presence of discarded seeds, some taxa associated with seeds and detritus, such as lygaeid bugs are found only in guano of this type. Swiftlets (*Aerodramus* spp) nest in the entrance and dark zones of tropical caves in south-east Asia, northern Australia and the Pacific and are insectivorous (Medway 1962). These birds also support a range of guanophilic taxa in the caves of Christmas Island (Humphreys and Eberhard 2001). Richards (1971) reported that droppings from several species of birds nesting in the entrance zone of Nullarbor Plain caves support a wide variety of cavernicolous animals.

Rhaphidophorid crickets are often important producers of guano in temperate caves such as those of the Nullarbor Plain (Richards 1971). The sometimes large populations of these crickets can accumulate sizeable guano deposits in caves. These deposits are important as few other food sources exist in areas such as the Nullarbor Plain because the low mean rainfall limits organic flood debris and bat populations are generally small. Rhaphidophorid guano is also utilised in Mammoth Cave, Kentucky, where it is widely dispersed through the cave system (Howarth 1983).

Small mammals are often significant guano producers in temperate zones of North America. The guano of porcupines (*Erethizon dorsatum* L.) is reported by Calder (1965) to support a community of collembolans and mites active throughout the year in Frenchman's Cave (Hants County, Nova Scotia, Canada). Cave rats (*Neotoma* spp), navigate using urine trails (Howarth 1983). Although common in the caves of the Canadian Rockies and Vancouver Island, their faeces are mostly unusable as a food source due to the high ammonia content from systematic urination at these sites (Trapani 1997).

GUANO ECOSYSTEMS AND FOOD WEBS

Guanobites are animals that require the presence of guano for survival. They will only feed on guano and will not use other food sources within caves. Although guanobitic species are occasionally found on other substrates in caves as they move between discontinuous guano deposits, they do not feed or reproduce on these substrates (Gnaspini and Trajano 2000). When guano deposition is seasonal (e.g. bat maternity caves), guanobites will commonly become quiescent until bats return and restore fresh guano input. Other guanobite populations crash when guano input ceases and then quickly reproduce when guano input recommences.

Guanophiles use guano resources opportunistically and are able to complete their entire life cycle using the guano substrate. Guanophiles will however utilise other cave food resources when available and do not have to rely upon guano to feed or reproduce. Abundance of guanophilic animals will decrease if fresh guano is not available, simply due to food limitation, but individuals will attempt to exploit other food resources to survive until fresh guano is available. Troglobites and troglophiles that have a generalist role in epigean ecosystems are classified as guanophiles if they utilise guano when available, even though they are capable of surviving subterranean habitats without this resource.

Guanoxenes will exploit a guano resource for feeding or reproduction but require other substrates within a cave to complete their life cycle (Gnaspini and Trajano 2000). Guanoxenes can be either troglobites, troglophiles or trogloxenes (Gnaspini and Trajano 2000).

The cyclical nature of many guano deposits resulting from the annual breeding cycle of bats, leads to a similar cycle in arthropod abundances. Low population numbers of many species reflect changes in micro-habitat conditions resulting from the cessation of fresh guano deposition and lower air and guano temperatures. Guano communities decrease in numbers as many species stop breeding until the food supply (i.e. fresh guano) is restored. This has been observed in the mite *Uroobovella coprophila* Womersley, which is quiescent during winter months in Carrai Bat Cave, northern New South Wales (Harris 1971).

Arthropods in guano communities feed either directly on guano or fungus growing on guano deposits and these in turn support a number of predators scavengers and omnivores (Gillieson 1997). Generalised guano food webs have a guano source directly supporting a range of guanivores including Phoridae (Diptera), Anobiidae (Coleoptera), Tineidae (Lepidoptera), Collembola and mesostigmatid mites (Acarina). Predators that prey upon these consumers include spiders, pseudoscorpions, beetles and opiliones. Specialised parasites and parasitoids are also active in many guano ecosystems. Braconid wasps (Hymenoptera) are found in many Australian guano caves and parasitise the larvae of *Monopis* spp (Lepidoptera: Tineidae). The larvae of the guanobite *Derolathrus* sp. (Coleoptera: Jacobsoniidae) are parasitised by small myrmarid wasps (Hymenoptera). Parasitic relationships in guano ecosystems are generally poorly understood and further research will undoubtedly reveal many more examples. Some of the most numerous taxa associated with guano deposits are mites (Acarina), particularly from the families Gamasidae, Actinedidae, Oribatidae and Armadillidae (Womersley 1963a, b; Gnaspini and Trajano 2000). Extremely high numbers (>33 million/m^2) have been recorded on fresh guano (Harris 1973; Bellati 2001). Guanivores from all biogeographic regions are taxonomically similar, usually belonging to the same families. Differences, however, are found among the predators of guanivore communities and are often represented by taxa from different families depending on the biogeographical region (Gnaspini and Trajano 2000).

Bat guano micro-habitat variation

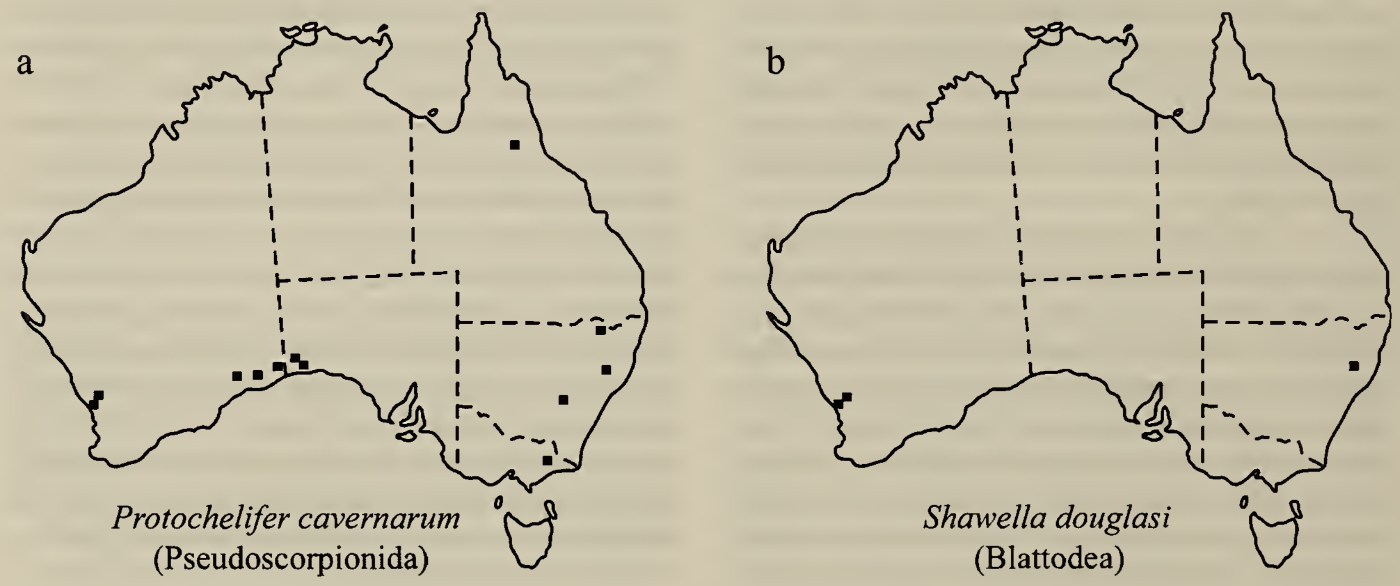
Guano environments are extremely variable, consisting of numerous micro-habitats when compared with the majority of subterranean habitats (Harris 1970). Bat guano deposits have been found to exhibit variable temperature of both the ambient air above deposits and within deposits (Harris 1970). In addition, the relative humidity, CO_2 concentration, and ammonia concentration also change when bats occupy a cave due to their breathing and urine (Decu 1986). Variations in pH can be extreme, resulting in strong differentiation between fresh and old guano deposits. The annual cycle of bat roosting adds a temporal component to many guano deposits and also serves to alter air temperature in roosting chambers. Bat maternal chambers are especially variable when extremely large numbers of bats enter a chamber on an annual basis to birth young (Harris 1970).

Large numbers of bats can raise the air temperature in a chamber by up to 10°C. This effect is most prevalent in high-domed chambers where heated air is trapped, but Harris (1970) also noted small increases in air temperature close to guano piles of up to 1.4°C due to heat released from guano breakdown. Increased air temperature of up to 12°C has also been noted in Cuban caves where large numbers of the leaf-nosed bat, *Phyllonycteris poeyi* Gundlach, roost (Decu 1986). This temperature increase can act as a barrier for colonisation by generalist cavernicolous invertebrate species, but allows guanophilic and guanobitic populations to reach large numbers.

Temperature within a guano pile can increase significantly with depth. Temperatures 5 cm below the surface of guano piles in Carrai Bat Cave, New South Wales are 1.7°C higher compared with surface temperatures, and 15 cm below the surface temperatures are 3.0°C higher (Harris 1970). Surface guano temperatures have also been reported to increase by 9.3°C, and these increases in both surface and subsurface temperatures were attributed by Harris (1970) to the increase in the metabolic rate of the organisms inhabiting the guano pile. The initiation of growth and reproduction of mites in guano may be linked to the increase in temperature associated with bat occupation of a chamber (Harris 1971).

Varying water content of guano due to desiccation with increasing age, results in noticeable micro-habitat differentiation. Fresh guano collected from the tops of piles in Bat Cave (U2), Naracoorte, South Australia, has been measured at up to 85% water by weight (Moulds 2003). Guano from the base of piles is a lighter grey colour due to desiccation and can contain as little as 6% water by weight (Moulds 2003). Guano moisture content increases with the birth of pups as their faecal matter is predominately liquid prior to being weened (approximately 6-8 weeks after birth for the large bent-wing bat *Miniopterus schreibersii bassanii* Cardinal and Christidis) (T. Moulds unpublished data). The surface of guano deposits commonly exhibit a patchwork appearance of dark moist areas and light grey drier areas. Different species within guano ecosystems prefer different micro-habitats. Richards (1971) noted the majority of guanophilic arthropods in Nullarbor Plain caves were only found in completely or partially dry guano.

Guano shows a marked difference in pH between fresh and old deposits. Fresh guano is commonly basic, with the pH varying according to the volume of urine deposited with faeces. Fresh guano commonly has a pH of 8.5-9.0 that rapidly becomes acidic (5.0-5.5) with age and depth, although the centre of guano piles has a stable pH of around 4 (Harris 1971). In bat maternity caves the pH of piles will gradually decrease over winter as no fresh guano is deposited. Data from Bat Cave (U2) (Naracoorte,



Protochelifer cavernarum
(Pseudoscorpionida)

Shawella douglasi
(Blattodea)

Ptinus exulans
(Coleoptera)

Uroobovella coprophila
(Acarina)

Figure 1. Different distribution patterns of guano associated species across Australia.

Table 1. Possibly endemic, guano dependent species in Australia.

State	Order	Genus and Species	Dependance		Cave
			Cave	Guano	
QLD	Pseudoscorpionida	*Sathrochthonius webbi*	Tb	Gp	Holy Jump Lava Cave (BM1)
QLD	Coleoptera	*Choleva australis*	Tp	Gp	Royal Arch Cave (CH9)
QLD	Coleoptera	*Dermestes uter*	Tp	Gp	Royal Arch Cave (CH9)
QLD	Coleoptera	*Alphitobius diaperinus*	Tp?	Gp?	Bat Cleft (E6)
QLD	Coleoptera	*Omorgus costatus*	Tp	Gp?	Johannsens Cave (J1-2)
QLD	Coleoptera	*Anomotarus subterraneus*	Tp	Gp	Riverton Main Cave (RN1)
NSW	Pseudoscorpionida	*Oratemnus cavernicola*	Tp	Gp?	Jump Up Cave, Gray Range
NSW	Pseudoscorpionida	*Sundochernes guanophilus*	Tp2	Gb	Fig Tree Cave (W148)
NSW	Pseudoscorpionida	*Tyrannochthonius cavicola*	Tp2	Gb	Grill Cave (B44)
NSW	Acarina	*Neotrombidium gracilipes*	Tp2	Gb	Fig Tree Cave (W148)
NSW	Acarina	*Hypoaspis annectans*	Tp	Gp	Carrai Bat Cave (SC5)
Nullarbor	Pseudoscorpionida	*Cryptocheiridium australicum*	Tp2	Gp	Murra-El-Elevyn Cave (N47)
Nullarbor	Isopoda	*Abedaioscia troglodytes*	Tb	Gp?	Pannikin Plain Cave (N49)
Nullarbor	Coleoptera	*Quedius luridipennis*	Tp?	Gp	Abrakurrie Cave (N3)
VIC	Pseudoscorpionida	*Pseudotyrannochthonius hamiltonsmithi*	Tp2	Gp	Mount Widderin Cave (H1)
VIC	Coleoptera	*Achosia lanigera*	Tp?	Gp	Wilson Cave (EB4)
SA	Pseudoscorpionida	*Austrochthonicus cavicola*	Tp2	Gp	Cathedral Cave (U12)
SA	Pseudoscorpionida	*Protochelifer naracoortensis*	Tp2	Gp	Bat Cave (U2)
WA	Blattodea	*Paratemnopteryx atra*	Tb	Gp	Mines nr Marble Bar
Christmas I	Coleoptera	*Alphitobius laevigatus*	Unknown	Gp	Upper Daniel Roux Cave (CI56)

South Australia), show that late in spring, before guano deposition recommences, tops of guano piles can become acidic, occasionally as low as pH 5.0 (Moulds 2003). The ever changing pH of guano piles due to age and urine content creates marked micro-habitats used by differing species.

Micro-habitat variation of bat chambers is further complicated by the movement of bat roosts in a chamber within a breeding season. These movements are a response to avoiding unfavourable conditions caused by ammonia concentrations and high local temperatures (Poulson 1972).

DISTRIBUTION, BIOGEOGRAPHY AND ENDEMISM

This is the first checklist for Australian guano-associated invertebrates. The full geographic range of many guanobitic and guanophilic species can now easily be appreciated. Many species have been shown to have unexpectedly wide distributions, sometimes spanning several climatic regions. Several possible explanations exist for these patterns. The lack of systematic searching and collation of published records, and collections has resulted in a poor understanding of many species distribution and degree of endemism. This is commonly combined with a lack of accurate identification by taxonomic experts leading to the lumping of several similar species into one. Inadequate species definitions from groups requiring systematic revision will also result in species being artificially lumped or split (eg Diptera: Phoridae, David McAlpine, pers. comm. 2002). A lack of collections from most karst areas, both above and below ground, is the greatest problem, resulting in large gaps in distributions and a poor knowledge of variation within species. The paucity of records among some taxa also provides a focal point for future collecting priorities.

The collation of this checklist has revealed associations of species across wide geographic regions. Figure 1a shows the extensive range of *Protochelifer cavernarum* Beier (Pseudoscorpionida) from Jurien Bay, Western Australia, across southern Australia and north to Undara Lava Tubes in northern Queensland. The distribution of *Shawella douglasi* Princis (Blattodea: Blattellidae) (Fig. 1b) is disjunct with records from northern New South Wales and Jurien Bay, Western Australia. This may be the result of misidentification, poor taxonomic description or a paucity of collecting between these localities, especially throughout northern Australia. Despite a number of invertebrate collections from the Nullarbor karst no individuals have been recorded, possibly due to extremely small populations of troglobitic species and the extremely large size of the karst area concerned. Several species including *Ptinus exulans* Erichson (Coleoptera: Anobiidae) show very wide distributions from mid-north New South Wales across the Nullarbor Plain to the west coast of Western Australia (Fig. 1c). The distribution of *U. coprophila* (Acarina: Urodinychidae) (Fig. 1d) is directly linked to the distribution of maternal sites for the large bent-wing bat *M. schreibersii*. The single record of this species from Undara (north Queensland) may be spurious, a misidentification or an individual transported via phoresy, especially as no records exist between southern and northern Queensland despite large bat maternity caves around Rockhampton. These data raise further questions regarding the colonisation of guano deposits by invertebrates and the boundaries of possibly ill-defined species concepts.

Endemic status of guano species, has, in the past been assigned without a full understanding of the distribution of Australian guano fauna. This is apparent for the maternal chamber of Bat Cave (U2), Naracoorte, where previous studies (Hamilton-Smith 2000), identified 'several endemic species' to the maternal chamber or Bat Cave as a whole. This checklist has shown that Bat Cave contains only a single endemic species, *Protochelifer naracoortensis* Beier, and this pseudoscorpion may possibly be found in other caves in the continuous karst of the Otway Basin. Bat Cave does, however, form the most diverse guanophilic arthropod community in Australia. This highlights the amount of assumed knowledge concerning guano invertebrates in Australia and their distribution. The number of endemic species to specific bat caves is currently unknown but is almost certainly significantly lower than previously believed. Several species have been identified as possessing restricted distributions and guano dependence, although none can yet be positively identified as endemic (Table 1). The restricted distribution status of all species listed in Table 1 is tentative and more extensive collecting, both above and below ground, must be undertaken before distribution can be confirmed. This is especially true for troglophilic species as epigean occurrence of these species will effect their endemic status. The degree of a species' guano dependence will also affect its endemic status and more ecological knowledge is required to confirm species habits. Species confined to single caves or isolated areas are more likely to be endemic when combined with guano dependence. Only Fig Tree Cave (W148) (Wombeyan, NSW) and Royal Arch Cave (CH9) (Chillagoe, QLD) are found to contain two species showing both restricted distribution and guano dependence (Table 1).

The presence of nematodes is almost a certainty in guano caves as they are almost ubiquitous in every other habitat both above and below ground. Despite this the records of nematodes from guano are extremely limited primarily because the majority of caves and karst areas remain completely unsampled for these invertebrates. Nematodes play a potentially important role in the micro-habitat of guano piles and have been recorded in large numbers from overseas caves (Decu 1986). Nematodes are also believed to be one of the first colonisers of new bat caves, being deposited by in urine and faeces (Decu 1986). Further sampling of Australian cave guano will almost certainly reveal a greater diversity of species. Currently no free living nematodes have been recorded by the author from Bat Cave, Naracoorte despite several collection events.

Currently no guano invertebrates are recorded from Tasmania, primarily due to the absence of cave-dwelling bats. The possibility remains however, that guano communities occur in orthopteran guano or other invertebrate guano deposits or even bird guano. The guanophilic mite *Macrocheles tenuirostris* Krantz and Filipponi was first recorded from mutton bird nests in Tasmania and has since been collected from bat guano in Victorian and New South Wales caves. Further field observations within Tasmanian caves may yet reveal these communities.

Opportunities for future research in this field are vast with only limited knowledge existing for most karst areas. The ecological classification for many species is poorly known and this will only be achieved through increased observations in situ. The microbiology of guano deposits also remain very poorly known in Australian, as well as in overseas caves. Many karst areas remain completely unstudied biologically, especially with regard to the diversity of invertebrate guano communities.

SYSTEMATIC CHECK LIST OF AUSTRALIAN GUANO INVERTEBRATES

This checklist includes all Australian cavernicolous species found in association with guano from both caves and mines. Records have been compiled from the speleological literature (both scientific and amateur), unpublished records, and personal observations. Parasites of cave-dwelling mammals (bats) have been included as they are often found in guano, although their potential roles in guano ecosystems is currently unknown. Taxa are arranged systematically by Phylum, Class and Order then alphabetically by Family. Undetermined taxa have been placed at the end of their respective order or family. Due to changes in taxonomy and higher systematics of many taxa the names and position of species can be uncertain. This checklist has adopted the most recent higher classifications attainable and many old names have been updated to reflect changes in the literature. Many groups in this checklist are in need of revision and so some species concepts may be altered in the future resulting in the splitting of some species and the lumping of others. This will obviously affect the distribution of species as presented in this work.

Cave names and numbers following the Australian Karst Index (Mathews 1985), and are listed for all species' records along with appropriate references. Records from caves in the Nullarbor Plain, southern Australia, have not been divided along state boundaries in order to reflect the extremely large and continuous nature of this karst area. Taxa previously considered to be obvious accidentals to cave environments have been excluded from this checklist.

The following ecological classification is modified from Hamilton-Smith (1967), and Gnaspini and Trajano (2000), and is based on the degree of cave and guano dependence of taxa. Abbreviations are those used in the checklist.

Trogloxene (Tx): an organism that regularly uses the cave environment for part of its lifecycle or as shelter but must leave the cave to feed and or breed.
1st order Troglophile (Tp1): an organism that can complete its entire lifecycle within a cave but possess no specific adaptations to the cave environment and recorded in both epigean and hypogean habitats.
2nd order Troglophile (Tp2): an organism that can complete its entire lifecycle within a cave but possess no specific adaptations to the cave environment and recorded only from hypogean habitats.
Troglobite (Tb): obligate cavernicolous organisms that possess specific adaptations to the cave environment.
Guanoxene (Gx): an organism that may use guano for reproduction and/or feeding but requires other substrates to complete its life cycle.
Guanophile (Gp): an organism that inhabits and reproduces both in guano piles as well as other substrates within a cave.
Guanobite (Gb): an organism that requires guano deposits to complete its entire life cycle.
Bat Parasite (P): an animal that is an obligate bat parasite requiring bats to complete its lifecycle.

Ecological classifications have been assigned to taxa wherever possible. These designations were made using available knowledge concerning behaviour, life history, and distribution within caves. However, information regarding species' ecology was found to be lacking or minimal in most cases. Because of such constraints some taxa have not been assigned a guano classification. Further, information on other taxa was insufficient to confirm their association with guano ecosystems. Thus, taxa previously recorded only from guano caves, but without a confirmed association with guano, have been included for completeness even though some of these species may be unassociated with guano.

Phylum Platyhelminthes

Class Tubellaria

Order undetermined

Undetermined genus and species, Tx, Gx?. VICTORIA: Dickson Cave (M30), Murrindal (Yen and Milledge 1990).

Phylum Nemathelminthes

Class Nematoda

Order Strongyloidea

Trichostrongylidae

Nycteridostrongylus unicollis Baylis, Tx, Gx, P. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith unpublished data).

Molinostrongylus dollfusi Mawson, Tx, Gx, P. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith unpublished data).

Order Undetermined

?Rhabditida

Undetermined genus and species, Gp?. VICTORIA: Starlight Cave (W5), Warrnambool (T. Moulds unpublished data), bacterial feeder (K. Davies pers. comm. 2003).

Undetermined Family

Undetermined genus and species, Gp. NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Harris 1970).

Undetermined genus and species, Gp. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998).

Phylum Mollusca

Class Gastropoda

Order Stylommatophora

Charopidae

Elsothera funera Cox, Gx?. NEW SOUTH WALES: Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); VICTORIA: Wilson Cave (EB4), East Buchan (Yen and Milledge 1990); Shades of Death Cave (M3), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

Undetermined Family

Undetermined genus and species, Tx, Gx?. NORTHERN TERRITORY: Cutta Cutta Cave (K1), Katherine (Hamilton-Smith unpublished data); QUEENSLAND: Carn Dum (E15), Mount Etna (Hamilton-Smith unpublished data).

Phylum Annelida

Class Oligochaeta

Order Haplotaxida

Lumbricidae

Undetermined genus and species, Tp, Gx?. VICTORIA: Wilson Cave (EB4), East Buchan (Yen and Milledge 1990).

Order Undetermined

Undetermined genus and species, Tp?, Gx?. QUEENSLAND: Four Mile Cave (C14), Camooweal (Hamilton-Smith unpublished data).

Phylum Arthropoda

Class Arachnida

Order Scorpionida

Undetermined Family

Undetermined genus and species, Gx?. VICTORIA: Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

Order Araneae

Agelenidae

Undetermined genus and species, Gx?. VICTORIA: Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Dickson Cave (M30), Murrindal (Yen and Milledge 1990).

Amaurobiidae

Undetermined genus and species, Gx?. VICTORIA: Spring Creek Cave (B1), Buchan (Yen and

Milledge 1990); Mabel Cave (EB1), East Buchan (Yen and Milledge 1990); Wilson Cave (EB4), East Buchan (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

Ctenizidae

Misgolas sp., NEW SOUTH WALES: Yessabah Bat Cave (YE1), Yessabah (Gray 1973b).

Cyatholipidae

Undetermined genus and species, Gx?. VICTORIA: Lilly Pilly Cave (M8), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Dickson Cave (M30), Murrindal (Yen and Milledge 1990).

Cycloctenidae

Cyclotenus abyssinus Urquhart, Tp. VICTORIA: Shades of Death Cave (M3), Murrindal (Hamilton-Smith unpublished data).

Toxopsioides sp., Tp. NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Gray 1973b); Yessabah Bat Cave (YE1), Yessabah (Gray 1973b).

Undetermined genus and species, Gx?. VICTORIA: Moon Cave (B2), Buchan (Yen and Milledge 1990); Wilson Cave (EB4), East Buchan (Yen and Milledge 1990); Shades of Death Cave (M3), Murrindal (Yen and Milledge 1990); Lilly Pilly Cave (M8), Murrindal (Yen and Milledge 1990); Dickson Cave (M30), Murrindal (Yen and Milledge 1990).

Desidae

Badumna socialis Rainbow, Tp, Gx?. NEW SOUTH WALES: Chalk Cave (B26), Bungonia (Hamilton-Smith unpublished data).

Colcarteria carrai Gray, Tp?. NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Gray 1992).

Colcarteria yessabah Gray, Tp. NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Gray 1992).

Dictynidae

Undescribed genus and species, Gx?. VICTORIA: Moon Cave (B2), Buchan (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

Filistatidae

Undescribed genus and species, Tp2. WESTERN AUSTRALIA: Cape Range peninsula (Gray 1994).

Gradungulidae

Progradungula carraiensis Forster and Gray, Tp1, Gp . NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Forster et al. 1987).

Linyphiidae

Laetesia weburdi Urquhart, Gx?. NEW SOUTH WALES: Jenolan Caves (Hamilton-Smith unpublished data).

Undetermined genus and species, Gx?. VICTORIA: Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

Lycosidae

Lycosa speciosa Koch, Tp1. NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Gray 1973b).

Mimetidae

Australomimetus maculosus Rainbow, Tp. NEW SOUTH WALES: Yessabah Bat Cave (YE1), Yessabah (Gray 1973b); Colong Main Cave (CG1), Colong (Hamilton-Smith unpublished data); Jenolan Caves (Hamilton-Smith unpublished data).

Undetermined genus and species, Gx?. VICTORIA: Spring Creek Cave (B1), Buchan (Yen and Milledge 1990); Mabel Cave (EB1), East Buchan (Yen and Milledge 1990).

Pholcidae

Physocyclus sp., NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Gray 1973b); Colong Main Cave (CG3), Colong (Gray 1973b).

Psilochorus sp., NEW SOUTH WALES: Yessabah Bat Cave (YE1), Yessabah (Gray 1973b) .

Pisauridae

Undetermined genus and species, NEW SOUTH WALES: Comboyne C4 Cave, Comboyne (Gray 1973b); Carrai Bat Cave (SC5), Stockyard Creek (Gray 1973b).

Salticidae

Undetermined genus and species, Gx?. VICTORIA: Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

Segestriidae

Undetermined genus and species, Gx?. VICTORIA: Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

Stiphidiidae

Stiphidon sp., Gx?. NEW SOUTH WALES: Colong Cave (CG1), Colong (Hamilton-Smith unpublished data).

Theridiidae

Theridon sp., Tp, Gp. NEW SOUTH WALES: Colong Cave (CG1), Colong (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

Steatoda sp., Tp, Gp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

Theridiosomatinae

Undetermined genus and species, Gp?. NEW SOUTH WALES: Colong Cave (CG1), Colong (Hamilton-Smith unpublished data); Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data).

Uloboridae

Philoponella patherinus Keyserling, Tp. NEW SOUTH WALES: Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data).

Undetermined Family

Undetermined genus and species, Gp?. NEW SOUTH WALES: Cave C4, Comboyne (Hamilton-Smith unpublished data); The Drum Cave (B13), Bungonia (Hamilton-Smith unpublished data); Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Colong Cave (CG1), Colong (Hamilton-Smith unpublished data); Gable Cave (CL7), Cliefden (Hamilton-Smith unpublished data); Youndales Cave (Hut Cave) (KB1), Kunderang Brook (Hamilton-Smith unpublished data); Glen Dhu Cave (Allston Cave) (TR15), Timor (Hamilton-Smith unpublished data); Tuglow Cave (T1), Tuglow (Hamilton-Smith unpublished data); Punchbowl Cave (WJ8), Wee Jasper (Hamilton-

Smith unpublished data); Willi Willi Bat Cave (Main Cave) (WW1), Willi Willi (Hamilton-Smith unpublished data); Basin Cave (W4), Wombeyan (Hamilton-Smith unpublished data); Fig Tree Cave (W148), Wombeyan (Hamilton-Smith unpublished data); NORTHERN TERRITORY: Cutta Cutta Cave (K1), Katherine (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Abrakurrie Cave (N3) (Hamilton-Smith unpublished data); Madura Cave (Madura 6 Mile Cave) (N62) (Hamilton-Smith unpublished data); QUEENSLAND: Four Mile Cave (C14), Camooweal (Hamilton-Smith unpublished data); Royal Arch Cave (CH9), Chillagoe (Hamilton-Smith unpublished data); Holy Jump Lava Cave (BM1), Bauer's Mountain (Hamilton-Smith unpublished data); Barker's Cave (U34), Undara (Hamilton-Smith unpublished data); Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); Winding Stairway Cave (E2), Mt Etna (Hamilton-Smith unpublished data); Speaking Tube (E7), Mount Etna (Hamilton-Smith unpublished data); Elephant Hole (E8), Mount Etna (Hamilton-Smith unpublished data); Piglet Help! Help! Cave (E17), Mount Etna (Hamilton-Smith unpublished data); Ilium Cave (E31), Mount Etna (Hamilton-Smith unpublished data); Viator Main Cave (VR1), Viator Hill (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Snowflake Cave (L1), Glenelg River (Hamilton-Smith unpublished data); Cathedral Cave (U12), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Moon Cave (B2), Buchan (Yen and Milledge 1990); Mabel Cave (EB1), East Buchan (Yen and Milledge 1990); Wilson Cave (EB4), East Buchan (Yen and Milledge 1990); Trogdip Cave (EB10), East Buchan (Hamilton-Smith unpublished data); Shades of Death Cave (M3), Murrindal (Yen and Milledge 1990); Lilly Pilly Cave (M8), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990); SSS Cave (M44), Murrindal (Hamilton-Smith unpublished data); Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith unpublished data); Bat Cave (P6), Portland (Hamilton-Smith unpublished data); Mt Widderin Cave (H1), Skipton (Hamilton-Smith unpublished data); Panmure Cave (H5), Mount Napier (Hamilton-Smith unpublished data); Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data); Grassmere Cave (W6), Warrnambool (Hamilton-Smith unpublished data).

Order Opilionida

Triaenoncychidae

Holonuncia cavernicola Forster, Tp2. NEW SOUTH WALES: Basin Cave (W4), Wombeyan (Hamilton-Smith 1967); Punchbowl Cave (WJ8), Wee Jasper (Hamilton-Smith unpublished data).

Holonuncia seriata Roewer, Tp1, Gx. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998).

Undetermined genus and species, Tp, Gp. VICTORIA: Moon Cave (B2), Buchan (Yen and Milledge 1990); Wilson Cave (EB4), East Buchan (Yen and Milledge 1990); Shades of Death Cave (M3), Murrindal (Yen and Milledge 1990); Lilly Pilly Cave (M8), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Dickson Cave (M30), Murrindal (Yen and Milledge 1990).

Undetermined Family

Undetermined genus and species, Tp, Gp? NEW SOUTH WALES: The Drum Cave (B13), Bungonia (Hamilton-Smith unpublished data); Chalk Cave (B26), Bungonia (Hamilton-Smith unpublished data); Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Cliefden Main Cave (CL1), Cliefden (Hamilton-Smith unpublished data); Gable Cave (CL7), Cliefden (Hamilton-Smith unpublished data); Colong Main Cave (CG1), Colong (Hamilton-Smith unpublished data); Youndales Cave (Hut Cave) (KB1), Kunderang Brook (Hamilton-Smith unpublished data); Moparabah Cave (Temagog Cave) (MP1), Moparabah (Hamilton-Smith unpublished data); Glen Dhu Cave (Allston Cave) (TR15), Timor (Hamilton-Smith unpublished data); Tuglow Cave (T1), Tuglow (Hamilton-Smith unpublished data); Fig Tree Cave (W148), Wombeyan (Hamilton-Smith unpublished data); Yessabah Bat Cave (YE1), Yessabah (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Lynch Cave (N60) (Hamilton-Smith unpublished data); QUEENSLAND: Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data);

VICTORIA: Trogdip Cave (EB10), East Buchan (Hamilton-Smith unpublished data); Unnamed Cave (NG1), New Guinea Ridge (Hamilton-Smith unpublished data).

Order Pseudoscorpionida

Atemnidae

Oratemnus cavernicola Beier, Tp, Gp?. NEW SOUTH WALES: Jump Up Cave, Gray Range (Beier 1976).

Cheiridiidae

Cryptocheiridium australicum Beier, Tp2, Gp. NULLARBOR PLAIN: Murra-El-Elevyn Cave (N47) (Richards 1971).

Cheliferidae

Protochelifer naracoortensis Beier, Tp2, Gp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Beier 1968; Bellati et al. 2003).

Protochelifer cavernarum Beier, Tp2, Gb. NEW SOUTH WALES: Murder Cave (CL2), Cliefden (Beier 1967, 1968); Island Cave (CL6), Cliefden (Hamilton-Smith unpublished data); Belfry Cave (TR2), Timor (Beier 1967); Ashford Caves, Ashford (Beier 1968); NULLARBOR PLAIN: Warbla Cave (N1) (Richards 1971); Weebuddie [Weebubbie, sic] Cave (N2) (Beier 1975); Abrakurrie Cave (N3) (Richards 1971); Murrawijinie No.3 Cave (N9) (Richards 1971); Mullamullang Cave (N37) (Richards 1971); Lynch Cave (N60) (Richards 1971); QUEENSLAND: Taylor Cave (4U4), Undara (Howarth 1988); Collins Cave No.1, Undara (Howarth 1988); VICTORIA: Clogg's Cave (EB2), East Buchan (Beier 1968); WESTERN AUSTRALIA: Gooseberry Cave (J1), Jurien Bay (Beier 1968); Eneabba Caves (E1-3), Eneabba (Lowry 1996); Arramall Cave (E22), Eneabba (Lowry 1996); River Cave (E23), Eneabba (Lowry 1996); Weelawadji Cave (E24) Eneabba (Lowry 1996); Super Cave (SH1), South Hill River (Hamilton-Smith unpublished data).

Protochelifer sp. Tp, Gp. SOUTH AUSTRALIA: Cathedral Cave (U12), Naracoorte (Bellati et al. 2003).

Chernetidae

Sundochernes guanophilus Beier, Tp2, Gb. NEW SOUTH WALES: Fig Tree Cave (W148), Wombeyan (Beier 1967).

Troglochernes imitans Beier, Tp, Gp. NULLARBOR PLAIN: Murra-El-Elvyn Cave (N47) (Beier 1975); Cocklebiddy Cave (N48) (Beier 1975); Pannikin Plain Cave (N49) (Beier 1975); Dingo Cave (Dingo-Donga) (N160) (Richards 1971).

Chthoniidae

Austrochthonius cavicola Beier, Tp, Gp. SOUTH AUSTRALIA: Cathedral Cave (U12), Naracoorte (Beier 1968).

Paraliochthonius cavicolus Beier, Tp2, Gp. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998).

Pseudotyrannochthonius hamiltonsmithi Beier, Tp2, Gp. VICTORIA: Mt Widderin Cave (H1), Skipton (Beier 1968).

Sathrochthonius tuena Chamberlin, Tp2, Gp. NEW SOUTH WALES: Basin Cave (W4), Wombeyan (Beier 1967), Deua Cave (DE1), Deua (Eberhard and Spate 1995); Punchbowl Cave (WJ8), Wee Jasper (Beier 1968); Imperial Cave (J4), Jenolan (Hamilton-Smith 1967; Gibian et al. 1988); Southern Limestone, Jenolan (Hamilton-Smith 1967; Beier 1968; Gibian et al. 1988); Paradox Cave (J48), Jenolan (Hamilton-Smith unpublished data).

Sathrochthonius webbi Muchmore, Tb, Gp. QUEENSLAND: Holy Jump Lava Cave (BM1), Bauer's Mountain southern Queensland (Muchmore 1982).

Tyrannochthonius cavicola Beier, Tp2, Gb. NEW SOUTH WALES: Grill Cave (B44), Bungonia (Beier 1967; Harvey 1989).

Undetermined Family

Undetermined genus and species, Tp, Gp?. NEW SOUTH WALES: Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); QUEENSLAND: Royal Arch Cave (CH9), Royal Arch Tower, Chillagoe (Matts 1987).

Undetermined genus and species, Tp?, Gx. VICTORIA: Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

Mites

The mites have been arranged according to the higher classification used by Halliday (1998). Many changes to nomenclature have occurred since previous checklists of cavernicolous fauna have been published so the family placement of some species has been updated to reflect this. Previous family placements have not been recorded but where synonymy has occured the old name (either family or genus) has been included in brackets. Previous generic placements have been recorded in brackets with the prefix "=".

Order Acariformes

Suborder Astigmata

Histiostomatidae

Histiostoma sp. NULLARBOR PLAIN: Mullamullang Cave (N37) (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

Rosensteiniidae

Nycteriglyphus (*Coproglyphus*) *dewae* Zakhvatkin, Tp2, Gb. NEW SOUTH WALES: Basin Cave (W4), Wombeyan (Womersley 1963a; Richards 1967b); Fig Tree Cave (W148), Wombeyan (Womersley 1963a; Richards 1967b); Railway tunnel, North Sydney (Womersley 1963a); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Womersley 1963a).

Nycteriglyphus sp., Tp, Gp. NULLARBOR PLAIN: Murra-El-Elevyn Cave (N47) (Richards 1971); Dingo Cave (160) (Richards 1971).

Glycyphagus sp., Tp, Gp. NULLARBOR PLAIN: Murra-El-Elevyn Cave (N47) (Richards 1971); Dingo Cave (N160) (Richards 1971).

Suborder Prostigmata

Labidostomidae

Undetermined genus and species. NEW SOUTH WALES: Island Cave (CL6), Cliefden (Hamilton-Smith unpublished data).

Neotrombidiidae

Neotrombidium gracilare Womersley, Tp2, Gb. NEW SOUTH WALES: Fig Tree Cave (W148), Wombeyan (Womersley 1963a); Murder Cave (CL2), Cliefden (Womersley 1963a); Punchbowl Cave (WJ8), Wee Jasper (Womersley 1963a); VICTORIA: O'Rourke's Cave (B12), Buchan (Hamilton-Smith 1967); Wilson Cave (EB4), East Buchan (Hamilton-Smith 1967).

Neotrombidium gracilipes Womersley, Tp2, Gb. NEW SOUTH WALES: Fig Tree Cave (W148), Wombeyan (Hamilton-Smith 1967).

Neotrombidium neptunium Southcott, VICTORIA: Clogg's Cave (EB2), East Buchan (Hamilton-Smith unpublished data).

Neotrombidium sp., Tp, Gb. NULLARBOR PLAIN: Firestick Cave (N70) (Richards 1971); Dingo Cave (N160) (Richards 1971).

Trombiculidae

Rudnicula barbarae Domrow (= *Trombicula*), Tx, Gx, P. NORTHERN TERRITORY: Kuhinoor Mine, Pine Creek (Hamilton-Smith unpublished data).

Trombicula thomsoni Womersley, Tx, Gx, P. NEW SOUTH WALES: Bonalbo Colliery (Hamilton-Smith unpublished data); Riverton (Hamilton-Smith unpublished data); NORTHERN TERRITORY: Kuhinoor Mine, Pine Creek (Hamilton-Smith unpublished data).

Trombicula dewae Domrow, Tx, Gx, P. NORTHERN TERRITORY: Kuhinoor Mine, Pine Creek (Hamilton-Smith unpublished data).

Order Parasitiformes

Suborder Ixodida

Argasidae

Argas sp., Tx, Gx, P. QUEENSLAND: Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data).

Ixodidae

Amblyomma moreliae Koch, Gx, P. QUEENSLAND: Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data).

Ixodes simplex simplex Neumann, Gx, P. Bat parasite in eastern Australia (Hamilton-Smith 1966b; Eberhard 1998); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data); Spring Creek Cave (B1), Buchan (Hamilton-Smith unpublished data); Slocombe's Cave (BA1), The Basin (Hamilton-Smith unpublished data); Anticline Cave (M11), Murrindal (Hamilton-Smith unpublished data); Panmure Cave (H5), Mount Napier (Hamilton-Smith unpublished data); Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data); Grassmere Cave (W6), Warrnambool (Hamilton-Smith unpublished data).

Undetermined genus and species, Gx, P. QUEENSLAND: Clam Cavern (CH26), Walkunder Tower, Chillagoe (Matts 1987); Spatial Cavern (CH41), Walkunder Tower, Chillagoe (Matts 1987); Royal Arch Cave (CH9), Royal Arch Tower, Chillagoe (Matts 1987); VICTORIA: Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith unpublished data)

Suborder Mesostigmata

Ameroseiidae

Ameroseius plumosus Oudemans, Tp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

Laelapidae

Cosmolaelaps sp., Tp2, Gb. NEW SOUTH WALES: Church Cave (WJ31), Wee Jasper (Hamilton-Smith 1967); QUEENSLAND: Railway tunnel, Samford (Hamilton-Smith 1967).

Hypoaspis (*Gaeolaelaps*) *annectans* Womersley, Tp, Gp. NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Harris 1971).

Hypoaspis (*Gaeolaelaps*) sp.1, SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

Hypoaspis (*Gaeolaelaps*) sp.2, SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

Hypoaspis (*Gaeolaelaps*) sp., Tp2, Gb. NEW SOUTH WALES: Cave C4, Comboyne (Hamilton-Smith 1967).

Ichoronyssus (*Pleisiolaelaps*) *miniopteri* (Zumpt and Patterson 1952) (= *Neospinolaelaps*, *Spinolaelaps*), Tp, Gx, P. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998); Bonalbo Colliery (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith unpublished data).

Ichoronyssus (*Pleisiolaelaps*) *aristippe* Domrow, NEW SOUTH WALES: Cheitmore Cave, Cheitmore (Hamilton-Smith unpublished data); Wombeyan Caves (Hamilton-Smith unpublished data); Bonalbo Colliery (Hamilton-Smith unpublished data).

Macrochelidae

Macrocheles spatei Halliday, Tp1, Gp. NEW SOUTH WALES: Deua Cave (DE1), Deua National Park (Halliday 2000).

Macrocheles tenuirostris Krantz and Filipponi, Tp1, Gp. NEW SOUTH WALES: Paradox Cave (J48), Jenolan Caves (Halliday 2000); Cleatmore Cave, Deua National Park (Halliday 2000); Colong Cave, Woof's Cavern (CG1), Colong (Halliday 2000); Church Cave (WJ31), Wee Jasper (Halliday 2000); TASMANIA: Fisher Island, in nests and burrows of muttonbird (Krantz and Fillipponi 1964); VICTORIA: Panmure Cave (H5), Warrnambool (Hamilton-Smith 1967).

Macronyssidae

Macronyssus aristippe Domrow (= *Ichoronyssus*), Tp, Gx, P. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998).

Trichonyssus australicus Womersley, Tx, Gx, P. NULLARBOR PLAIN: Warbla Cave (N1) (Hamilton-Smith unpublished data).

Parantennulidae

Micromegistus gourlayi Womersley. NEW SOUTH WALES: Comboyne C4 Cave, Comboyne (Hamilton-Smith unpublished data).

Parasitidae

?*Eugamasus* sp., Tp, Gp. NULLARBOR PLAIN: Dingo Cave (N160) (Richards 1971).

Sejidae (Ichthyostomatogastridae)

Asternolaelaps australis Womersley and Domrow, Tp, Gb. SOUTH AUSTRALIA: Bat Cave (U2) Naracoorte (Womersley and Domrow 1959; Hamilton-Smith 1967); VICTORIA: O'Rourkes Cave (B12), Buchan (Hamilton-Smith 1967).

Spinturnicidae

Spinturnix psi Kolenati, Tp, Gx, P. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998).

Undetermined genus and species, Tp, Gx, P. NEW SOUTH WALES: Colong Main Cave (CG1), Colong (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Weebubbie Cave (N2) (Hamilton-Smith unpublished data); Murra-El-Elevyn Cave (N47) (Hamilton-Smith unpublished data); QUEENSLAND: Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data); Flogged Horse Cave (Cammoo Cave) (J83), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Spring Creek Cave (B1), Buchan (Hamilton-Smith unpublished data); WESTERN AUSTRALIA: Stockyard Cave (E3), Eneabba (Hamilton-Smith unpublished data).

Urodinychidae

Uroobovella (*Austruropoda*) *coprophila* Womersley (= *Cilliba*), Tp2, Gp. NEW SOUTH WALES: Cave C4, Comboyne (Smith 1982b); Carrai Bat Cave (SC5), Stockyard Creek (Harris 1973); Punchbowl Cave (WJ8), Wee Jasper (Hamilton-Smith unpublished data); Church Cave (WJ31), Wee Jasper (Hamilton-Smith 1966b, 1967); Fig Tree Cave (W148), Wombeyan (Hamilton-Smith 1966b, 1967); Cheitmore Cave, Cheitmore (Hamilton-Smith unpublished data); QUEENSLAND: Arch Cave (U22), Undara (Hamilton-Smith unpublished data); Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003); VICTORIA: Anticline Cave (M11), Murrindal (Hamilton-Smith 1967).

Genus and species undetermined, NEW SOUTH WALES: Deua Cave (DE1), Deua (Eberhard and Spate 1995).

Undetermined Family

Undetermined sp. 1, Tp, Gp. NULLARBOR PLAIN: Murra-El-Elevyn Cave (N47) (Richards 1971).

Undetermined sp. 2, Tp, Gp. NULLARBOR PLAIN: Murra-El-Elevyn Cave (N47) (Richards 1971).

Undetermined Acarina

Undetermined Family

Undetermined genus and species, Gp. CHRISTMAS ISLAND (Indian Ocean): Grimes Cave (CI53) (Humphreys and Eberhard 2001).

Undetermined genus and species, Tp, Gp. NEW SOUTH WALES: Gable Cave (CL7), Cliefden (Hamilton-Smith unpublished data); NORTHERN TERRITORY: Kintore Cave (K2), Katherine (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Weebubbie Cave (N2) (Hamilton-Smith unpublished data); Murra-El-Elevyn Cave (N47) (Hamilton-Smith unpublished data); QUEENSLAND: Flogged Horse Cave (Cammoo Cave) (J83), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Asbestos mine near Arkaba, Flinders Ranges (Hamilton-Smith unpublished data); Drop Drop Cave (L29), Lower south east (Hamilton-Smith unpublished data); Joanna Bat Cave (U38), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Spring Creek Cave (B1), Buchan (Yen and Milledge 1990); O'Rourkes Cave (B12), Buchan (Hamilton-Smith unpublished data); Mabel Cave (EB1), East Buchan (Yen and Milledge 1990); Wilson's Cave (EB4), East Buchan (Hamilton-Smith unpublished data); Trogdip Cave (EB10), East Buchan (Hamilton-Smith unpublished data); Lilly Pilly Cave (M8), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Dickson Cave (M30), Murrindal (Yen and Milledge 1990); Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith unpublished data); Bat Cave (P6), Portland (Hamilton-Smith unpublished data); Grassmere Cave (W6), Warrnambool (Hamilton-Smith unpublished data).

Class Crustacea

Order Isopoda

Armadillidae

Merulana sp. nov., Tp. NEW SOUTH WALES: Fig Tree Cave (W148), Wombeyan (Dennis 1986).

Oniscidae

Plymophiloscia sp. Vandel, Tp, Gp. NULLARBOR PLAIN: Pannikin Plain Cave (N49) (Richards 1971; Gray 1973a).

Undetermined genus and species, Tp, Gp. QUEENSLAND: Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); Speaking Tube (E7), Mount Etna (Hamilton-Smith unpublished data); Carn Dum (E15), Mount Etna (Hamilton-Smith unpublished data); VICTORIA: Trogdip Cave (EB10), East Buchan (Hamilton-Smith unpublished data).

Philosciidae

Abebaioscia troglodytes Vandel, Tb, Gp?. NULLARBOR PLAIN: Pannikin Plain Cave (N49) (Vandel 1973).

Eurygastor montanus troglophilus Vandel, Tp?. VICTORIA: Anticline Cave (M11), Murrindal (Vandel 1973).

Laevophiloscia dongarrensis Wahrberg, Tp, Gx?. WESTERN AUSTRALIA: Yanchep Cave (YN16), Yanchep (Vandel 1973); Minnie's Grotto (YN28), Yanchep (Vandel 1973); Gooseberry Cave (J1), Jurien Bay (Vandel 1973).

Laevophiloscia hamiltoni Vandel, Tp, Gx. WESTERN AUSTRALIA: Weelawadji Cave (E24), Eneabba (Vandel 1973); Labyrinth Cave (AU16), Augusta (Vandel 1973)

Laevophiloscia michaelseni Vandel, Tp. NULLARBOR PLAIN: Cocklebiddy Cave (N48) (Vandel 1973).

Porcellionidae

Porcellio scaber Latreille, Tp1. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

Undetermined Family

Undetermined genus and species, Tp, Gx. NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Hamilton-Smith unpublished data); The Drum Cave (B13), Bungonia (Hamilton-Smith unpublished data); Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Cliefden Main Cave (CL1), Cliefden (Hamilton-Smith unpublished data); Cave C4, Comboyne (Hamilton-Smith unpublished data); Youndales Cave (Hut Cave) (KB1), Kunderang Brook (Hamilton-Smith unpublished data); Moparabah Cave (Temagog Cave) (MP1), Moparabah (Hamilton-Smith unpublished data); Main Cave (Ballroom Cave) (TR1), Timor (Hamilton-Smith unpublished data); Glen Dhu Cave (Allston Cave) (TR15), Timor (Hamilton-Smith unpublished data); Tuglow Cave (T1), Tuglow (Hamilton-Smith unpublished data); Piano Cave (Long Cave) (WA12), Walli (Hamilton-Smith unpublished data); Church Cave (WJ31), Wee Jasper (Hamilton-Smith unpublished data); Willi Willi Bat Cave (Main Cave) (WW1), Willi Willi (Hamilton-Smith unpublished data); Yessabah Bat Cave (YE1), Yessabah (Hamilton-Smith unpublished data); NORTHERN TERRITORY: Cutta Cutta Cave (K1), Katherine (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Abrakurrie Cave (N3) (Hamilton-Smith unpublished data); Cocklebiddy Cave (N48) (Hamilton-Smith unpublished data); QUEENSLAND: Barker's Cave (U34), Undara (Hamilton-Smith unpublished data); Elephant Hole (E8), Mount Etna (Hamilton-Smith unpublished data); Viator Main Cave (VR1), Viator Hill (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith unpublished data); Cathedral Cave (U12), Naracoorte (Hamilton-Smith unpublished data); Fox Cave (U22), Naracoorte (Hamilton-Smith unpublished data); Cave Park Cave (U37), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Spring Creek Cave (B1), Buchan (Yen and Milledge 1990); Mabel Cave (EB1), East Buchan (Yen and Milledge 1990); Wilson Cave (EB4), East Buchan (Yen and Milledge 1990); Shades of Death Cave (M3), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data); WESTERN AUSTRALIA: Drovers Cave (J2), Jurien Bay (Hamilton-Smith unpublished data); Stockyard Cave (E3), Eneabba (Hamilton-Smith unpublished data).

Order Amphipoda

Undetermined Family

Undetermined genus and species, Tp, Gx. VICTORIA: Wilson Cave (EB4), East Buchan (Yen and Milledge 1990).

Class Myriapoda

Order Diplopoda

Undetermined Family

Undetermined genus and species, Tp2, Gx. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998).

Undetermined genus and species, Tp?, Gx. NEW SOUTH WALES: Island Cave (CL6), Cliefden (Hamilton-Smith unpublished data); The Drum Cave (B13), Bungonia (Hamilton-Smith unpublished data); Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Paradox Cave (J48), Jenolan (Hamilton-Smith unpublished data); Moparabah Cave (Temagog Cave) (MP1), Moparabah (Hamilton-Smith unpublished data); Carrai Bat Cave (SC5), Stockyard Creek (Hamilton-Smith unpublished data); Belfry Cave (TR2), Timor (Hamilton-Smith unpublished data); Tuglow Cave (T1), Tuglow (Hamilton-Smith unpublished data); Fig Tree Cave (W148), Wombeyan (Hamilton-Smith unpublished data); Punchbowl Cave (WJ8), Wee Jasper (Hamilton-Smith unpublished data); Church Cave (WJ31), Wee Jasper (Hamilton-Smith unpublished data); Willi Willi Bat Cave (Main Cave) (WW1), Willi Willi (Hamilton-Smith unpublished data); Yessabah Bat Cave (YE1), Yessabah (Hamilton-Smith unpublished data); QUEENSLAND: Barker's Cave (U34), Undara (Hamilton-Smith unpublished data); Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); Winding Stairway Cave (E2), Mt Etna (Hamilton-Smith unpublished data); Elephant Hole (E8), Mount Etna (Hamilton-Smith unpublished data); Piglet Help! Help! Cave (E17), Mount Etna (Hamilton-Smith unpublished data); Jolly Roger Cave (E29), Mountt Etna (Hamilton-Smith unpublished data); Glen Lyon River Cave (GL1), Glen Lyon (Hamilton-Smith unpublished data); Viator Main Cave (VR1), Viator Hill (Hamilton-Smith unpublished data); VICTORIA: Spring Creek Cave (B1), Buchan (Yen and Milledge 1990); Mabel Cave (EB1), East Buchan (Yen and Milledge 1990); Wilson Cave (EB4), East Buchan (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith unpublished data).

Order Chilopoda

Scolopendromorpha

Undetermined genus and species. NULLARBOR PLAIN: Mullamullang Cave (N37) (Richards 1971).

Undetermined Family

Undetermined genus and species, Gp?. NEW SOUTH WALES: Cave C4, Comboyne (Hamilton-Smith unpublished data); Youndales Cave (Hut Cave) (KB1), Kunderang Brook (Hamilton-Smith unpublished data); Carrai Bat Cave (SC5), Stockyard Creek (Hamilton-Smith unpublished data); Moparabah Cave (MP1), Moparabah (Hamilton-Smith unpublished data); Belfry Cave (TR2), Timor (Hamilton-Smith unpublished data); NORTHERN TERRITORY: Cutta Cutta Cave (K1), Katherine (Hamilton-Smith unpublished data); Kintore Cave (K2), Katherine (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Cocklebiddy Cave (N48) (Hamilton-Smith unpublished data); QUEENSLAND: Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data); Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Cathedral Cave (U12), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Panmure Cave (H5), Mount Napier (Hamilton-Smith unpublished data).

Superclass Hexapoda
Class Insecta

Order Collembola
Armadillidae

Buddelundia albomarginata Wahrberg, Tp, Gx?. NULLARBOR PLAIN: Murrawyinee [sic] No.1 Cave (N7) (Vandel 1973); Cocklebiddy Cave (N48) (Vandel 1973); Lynch Cave (N60) (Vandel 1973); Madura Cave (N62) (Vandel 1973); Old Homestead Cave (N83) (Vandel 1973); Unnamed cave (N140) (Vandel 1973).

Entomobryidae

Lepidocyrtus sp., Tp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

Lepidosira australica Schött, Tp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

Undetermined genus and species, Gp?. NEW SOUTH WALES: Belfry Cave (TR2), Timor (James et al. 1976); Chalk Cave (B26), Bungonia (Hamilton-Smith unpublished data).

Hypogastruridae

Hypogastrura sp., NEW SOUTH WALES: Grill Cave (B44), Bungonia (Wellings 1977); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

Isotomidae

Folsomia candida Willem, Tp. NEW SOUTH WALES: Paradox Cave (J48), Jenolan (Eberhard 1993); Imperial Cave (J4), Jenolan (Eberhard and Spate 1995); Tuglow Main Cave (T1), Tuglow (Eberhard 1993); Jillebean Cave (Y22), Yarrangobilly (Eberhard 1993).

Paronellidae

Undetermined genus and species, NEW SOUTH WALES: Fig Tree Cave (W148), Wombeyan (Eberhard and Spate 1995).

Undetermined Family

Undetermined genus and species, Tp, Gp. NULLARBOR PLAIN: Cocklebiddy Cave (N48) (Richards 1971); Lynch Cave (N60) (Richards 1971); Dingo Cave (N160) (Richards 1971); VICTORIA: SSS Cave (M44), Murrindal (Hamilton-Smith unpublished data); Mt Widderin Cave (H1), Skipton (Hamilton-Smith unpublished data).

Undetermined genus and species, Tp?, Gp?. NEW SOUTH WALES: Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Colong Main Cave (CG1), Colong (Hamilton-Smith unpublished data); Glen Dhu Cave (Allston Cave) (TR15), Timor (Hamilton-Smith unpublished data); NORTHERN TERRITORY: 16 Mile Cave, Katherine (Hamilton-Smith unpublished data); QUEENSLAND: Speaking Tube (E7), Mount Etna (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Cathedral Cave (U12), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Moon Cave (B2), Buchan (Yen and Milledge 1990); Mabel Cave (EB1), East Buchan (Yen and Milledge 1990); Wilson's Cave (EB4), East Buchan (Hamilton-Smith unpublished data); Trogdip Cave (EB10), East Buchan (Hamilton-Smith unpublished data); Lilly Pilly Cave (M8), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Panmure Cave (H5), Mount Napier (Hamilton-Smith unpublished data).

Order Diplura
Undetermined family

Undetermined genus and species, SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

Order Blattodea

Blattellidae

Neotemnopteryx australis Saussure, Tp, Gp. NEW SOUTH WALES: Moparabah Cave (Temagog Cave) (MP1), Moparabah (Hamilton-Smith 1967); Cave C4, Comboyne (Hamilton-Smith 1967); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

Neotemnopteryx fulva Saussure (= *Gislenia australica* Brunner), Tp, Gb. NEW SOUTH WALES: Glen Dhu Cave (Allston Cave) (TR15), Timor (Richards 1967a); Murder Cave (CL2), Cliefden (Richards 1967a); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Richards 1967a); Haystall Cave (U23), Naracoorte (Richards 1967a); VICTORIA: Mabel Cave (EB1), East Buchan (Richards 1967a).

Neotemnopteryx sp., Tp, Gp?. NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Hamilton-Smith unpublished data); QUEENSLAND: Royal Arch Cave (CH9), Chillagoe (Hamilton-Smith unpublished data); Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data); Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); Winding Stairway Cave (E2), Mt Etna (Hamilton-Smith unpublished data); Elephant Hole (E8), Mount Etna (Hamilton-Smith unpublished data); Viator Main Cave (VR1), Viator Hill (Hamilton-Smith unpublished data).

?*Neotemnopteryx* (?*Gislenia* sp.), Tp, Gp?. NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Richards 1967a); Cave 4, Comboyne (Richards 1967a); Hill Cave (TR7), Timor (Richards 1967a); Moparabah Cave (Temagog Cave) (MP1), Moparabah (Richards 1967a); Swallow Cave (CU1), Cudgegong (Richards 1967a); QUEENSLAND: Royal Arch Cave (CH9), Chillagoe (Richards 1967a); Riverton Main Cave (RN1), Riverton, southern Queensland (Richards 1967a); Viator Cave (VR4), Viator Hill, southern Queensland (Richards 1967a); Johannsen's Cave (J1), Limestone Ridge, Rockhampton (Hamilton-Smith 1967); Winding Stairway Cave (4E2), Mt Etna (Hamilton-Smith 1967); SOUTH AUSTRALIA: Alexandra Cave (5U3), Naracoorte (Richards 1967a); Bat Cave (U2), Naracoorte (Richards 1967a).

Paratemnopteryx atra Princis, Tb, Gp. WESTERN AUSTRALIA: Mines near Marble Bar (Princis 1963; Richards 1967a; Moore et al. 2001).

Paratemnopteryx rufa Tepper, Gb?. NULLARBOR PLAIN: Murrawijinie No.3 Cave (N9) (Richards 1971); Abrakurrie Cave (N3) (Richards 1971).

Paratemnopteryx sp., Tp, Gb?. QUEENSLAND: Pinwill Cave (4U17), Undara (Howarth 1988).

Shawella douglasi Princis, Tp, Gb?. NEW SOUTH WALES: River Cave (SC1), Stockyard Creek (Hamilton-Smith 1967); WESTERN AUSTRALIA: Drovers Cave (J2), Jurien Bay (Hamilton-Smith unpublished data); Jurien Bay caves (Princis 1963; Richards 1967a); Eneabba Caves (E1-3), Eneabba (Lowry 1996); Weelawadji Cave (E24), Eneabba (Lowry 1996).

Trogloblattella nullarborensis Mackerras, Tb, Gp. NULLARBOR PLAIN: Abrakurrie Cave (N3) (Mackerras 1967; Richards 1971); Koonalda Cave (N4) (Mackerras 1967); Mullamullang Cave (N37) (Mackerras 1967); Roaches Rest Cave (N58) (Mackerras 1967); Arubiddy Cave (N81) (Mackerras 1967).

Blattidae

Polyzosteria mitchelli Angas, Tp. NULLARBOR PLAIN: Warbla Cave (N1), (Mackerras 1965); Kestrel Cavern (N40) (Mackerras 1965; Richards 1967a).

Polyzosteria pubescens Tepper, Tp. NULLARBOR PLAIN: Weebubbie Cave (N2) (Hamilton-Smith unpublished data).

Zonioploca medilinea Tepper, Tp?. NULLARBOR PLAIN: Warbla Cave (N1) (Richards 1967a).

Order Orthoptera

Rhaphidophoridae

Australotettix carraiensis Richards, Tp, Gx. NEW SOUTH WALES: Barnett's Cave (SC6), Stockyard Creek (Richards 1964); Carrai Bat Cave (SC5), Stockyard Creek (Richards 1964); Col's Cave, Stockyard Creek (Richards 1964); Lot's Mansion, Stockyard Creek (Richards 1964); River Cave (SC1) Stockyard Creek (Richards 1964).

Cavernotettix buchanensis Richards, Tx, Gx. VICTORIA: Wilson Cave (EB4), East Buchan (Richards 1966; Yen and Milledge 1990); Trogdip Cave (EB10), East Buchan (Hamilton-Smith unpublished data); Spring Creek Cave (B1), Buchan (Richards 1966; Yen and Milledge 1990); Shades of Death Cave (M3), Murrindal (Yen and Milledge 1990); Lilly Pilly Cave (M8), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Dickson Cave (M30), Murrindal (Yen and Milledge 1990); Nargun's Cave (NN1), Nowa Nowa Caves (Richards 1966; Yen and Milledge 1990); Weta Cave (NN2), Nowa Nowa Caves (Richards 1966; Yen and Milledge 1990).

Cavernotettix montanus Richards, Tx, Gx. NEW SOUTH WALES: small cave nr Glory Cave, Yarrangobilly (Richards 1966); Jersey Cave (Y23), Yarrangobilly (Richards 1966); Restoration Cave (Y50), Yarrangobilly (Richards 1966); Unnamed cave, Yarrangobilly (Richards 1966); Cooleman Cave (CP1), Cooleman Plains (Richards 1966); Unnamed cave opp. Blue Waterhole, Cooleman Plains (Richards 1966); Unnamed cave nr Murray Cave, Cooleman Plains (Richards 1966).

Cavernotettix wyanbenensis Richards, Tx, Gx. NEW SOUTH WALES: Wyanbene Cave (WY1), Wyanbene (Richards 1966); Bat Cave, Cheitmore (Richards 1966).

Pallidotettix nullarborensis Richards, Tx, Gx. NULLARBOR PLAIN: Warbla Cave (N1) (Richards 1971); Weebubbie Cave (N2) (Richards 1971); Murra-El-Elevyn Cave (N47) (Richards 1971); Cocklebiddy Cave (N48) (Richards 1971); Pannikin Plain Cave (N49) (Richards 1971); Tommy Grahams Cave (N56) (Richards 1971).

Undetermined genus and species, Tx, Gx. NEW SOUTH WALES: Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Colong Main Cave (CG1), Colong (Hamilton-Smith unpublished data); QUEENSLAND: Danes Four Cave (C4), Camooweal (Hamilton-Smith unpublished data); Kaiser Creek Cave (C12) (Two Mile Cave, Tar Drum Cave), Camooweal (Hamilton-Smith unpublished data); Haunted Cave (CH1), Chillagoe (Hamilton-Smith unpublished data); VICTORIA: Starlight Cave (W5), Warrnambool (T. Moulds unpublished data).

Order Psocoptera

Liposcelidae

Liposcelis corrodens Broadhead, Tp1, Gp. WESTERN AUSTRALIA: Arranmall [sic] Cave (E22), Eneabba (Smithers 1975); undetermined caves (Smithers 1975).

Psyllipsocidae

?*Psyllipsocus ramburi* Selys-Longcamp, Tp1, Gp. NEW SOUTH WALES: Murder Cave (CL2), Cliefden (Hamilton-Smith 1967); Island Cave (CL6), Cliefden (Smithers 1964); Hill Cave (TR7), Timor (James et al. 1976); Basin Cave (W4), Wombeyan (Smithers 1964); Fig Tree Cave (W148), Wombeyan (Smithers 1975); Punchbowl Cave (WJ8), Wee Jasper (Smithers 1964); Church Cave (WJ31), Wee Jasper (Smithers 1964); NULLARBOR PLAIN: Weebubbie Cave (N2) (Richards 1971); Abrakurrie Cave (N3) (Hamilton-Smith 1967; Richards 1971); Koonalda Cave (N4) (Richards 1971); Madura Cave (N62), (Richards 1971); QUEENSLAND: Riverton Main Cave (RN1), Riverton, southern Queensland (Hamilton-Smith 1967); SOUTH AUSTRALIA: Bat Cave

(U2), Naracoorte (Smithers 1964; Bellati et al. 2003); Blackberry Cave, Naracoorte (Smithers 1964); VICTORIA: Clogg's Cave (EB2), East Buchan (Smithers 1964); O'Rourkes Cave (B12), Buchan (Smithers 1964); Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith 1967).

Trogiidae

Lepinotus inquilinus Heyden, Tp1, Gp. WESTERN AUSTRALIA: Arranmall (sic) Cave (E22), Eneabba (Smithers 1975).

?*Lepinotus reticulatus* Enderlein, Tp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Smithers 1964; Bellati et al. 2003)

Undetermined genus and species, NEW SOUTH WALES: Fig Tree Cave (W148), Wombeyan (Dennis and Mayhew 1986).

Undetermined Family

Undetermined genus and species, Tp, Gx. NEW SOUTH WALES: Gable Cave (CL7), Cliefden (Hamilton-Smith unpublished data); QUEENSLAND: Viator Main Cave (VR1), Viator Hill (Hamilton-Smith unpublished data); VICTORIA: Lilly Pilly Cave (M8), Murrindal (Yen and Milledge 1990).

Order Hemiptera

Cixiidae

Undetermined genus and species, Tp. QUEENSLAND: Mount Etna Main Cave (E1), Mount Etna (Hamilton-Smith unpublished data); Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data).

Lygaeoidea

Undetermined family and genus, Gp?. VICTORIA: Starlight Cave (W5), Warrnambool (T. Moulds unpublished data).

Reduviidae

Armstrongula sp. Tp, Gp. SOUTH AUSTRALIA: McKinley's Daughter's Cave (F175), Flinders Ranges (T. Moulds unpublished data); Unnamed mine, Weetootla Gorge, Gammon Ranges (T. Moulds unpublished data).

Centrogonus sp. Tp, Gp. NORTHERN TERRITORY: Kintore Cave (K2), Katherine (Hamilton-Smith unpublished data).

Undetermined Emesinae genus and species, Tp, Gp. QUEENSLAND: Crazy Cracks Cave, Jacks Gorge, Broken River (T. Moulds unpublished data); Not Another Frig Tree Crave, Jacks Gorge, Broken River (T. Moulds unpublished data); Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data).

Undetermined genus and species, Tp, Gp. NORTHERN TERRITORY: Cutta Cutta Cave (K1), Katherine (Hamilton-Smith unpublished data); QUEENSLAND: Queenslander Cave (CH15), Queenslander Tower (CH5246) Chillagoe (T. Moulds unpublished data); Trezkinn Cave (CH14), Chillagoe (T. Moulds unpublished data); Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data).

Undetermined genus and species, Tp, Gp?. QUEENSLAND: Elephant Hole (E8), Mount Etna (Hamilton-Smith unpublished data).

Undetermined Family

Undetermined genus and species, QUEENSLAND: Royal Arch Cave (CH9), Chillagoe (Hamilton-Smith unpublished data).

Order Neuroptera

Myrmeleontidae

Aeropteryx sp., Tp, Gp. SOUTH AUSTRALIA: McKinley's Daughter's Cave (F175), Flinders Ranges (T. Moulds unpublished data); Moro Bat Cave (F47), Flinders Ranges (T. Moulds unpublished data); Unnamed cave, Brachina Gorge, Flinders Ranges (T. Moulds unpublished data); Unnamed bat cave, Chambers Gorge, Flinders Ranges (T. Moulds unpublished data); Unnamed cave, Chambers Gorge, Flinders Ranges (T. Moulds unpublished data); Unnamed mine, Weetootla Gorge, Gammon Ranges (T. Moulds unpublished data).

Myrmeleontinae sp., Tp?. QUEENSLAND: Royal Arch Cave (CH9), Chillagoe (Hamilton-Smith unpublished data).

Undetermined Family

Undetermined genus and species, QUEENSLAND: Holy Jump Lava Cave (BM1), Bauer's Mountain (Hamilton-Smith unpublished data).

Order Coleoptera

Anobiidae (Ptinidae)

Ptinus exulans Erichson, Tp1, Gp. NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Hamilton-Smith 1967); Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Island Cave (CL6), Cliefden (Hamilton-Smith 1967); Jenolan Caves (Hamilton-Smith 1967); Willi Willi Bat Cave (WW1), Willi Willi (Hamilton-Smith 1967); Bungonia various caves (Eberhard 1998); Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Colong Main Cave (CG1), Colong (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Warbla Cave (N1) (Richards 1971); Murrawijinie No. 1 Cave (N7) (Richards 1971); Murra-El-Elevyn Cave (N47) (Hamilton-Smith 1967; Richards 1971); Firestick Cave (N70) (Richards 1971); Dingo Cave (N160) (Richards 1971); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith 1967; Bellati et al. 2003); Blanche Cave (U4), Naracoorte (Hamilton-Smith 1967); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith 1967); Clogg's Cave (EB2), East Buchan (Hamilton-Smith 1967); WESTERN AUSTRALIA: Goosebury Cave (J1), Jurien Bay (Hamilton-Smith 1967).

Carabidae

Anomotarus subterraneus Moore, Tp, Gp. QUEENSLAND: Riverton Main Cave (RN1), Riverton, southern Queensland (Moore 1967).

Cratogaster melus Laporte, Tp?. QUEENSLAND: Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data).

Darodilia sp., Tp?. QUEENSLAND: Winding Stairway Cave (E2), Mt Etna (Hamilton-Smith unpublished data).

Gnathaphanus pulcher Dejean, Tp?. NORTHERN TERRITORY: Cutta Cutta Cave (K1), Katherine (Hamilton-Smith unpublished data); Kintore Cave (K2), Katherine (Hamilton-Smith unpublished data); QUEENSLAND: Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data).

Lecanomerus sp., Gp?. NEW SOUTH WALES: Youndales Cave (Hut Cave) (KB1), Kunderang Brook (Hamilton-Smith unpublished data).

Mecyclothorax ambiguus Erichson, VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data).

Meonis sp., Tp, Gp. QUEENSLAND: Main Mount Etna Cave (E1), Mount Etna (Hamilton-Smith unpublished data).

Mystropomus subcostatus Chaudoir, Tp?. QUEENSLAND: Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); Winding Stairway Cave (E2), Mt Etna (Hamilton-Smith unpublished data); Speaking Tube (E7), Mount Etna (Hamilton-Smith unpublished data); Elephant Hole (E8), Mount Etna (Hamilton-Smith unpublished data); Piglet Help! Help! Cave (E17), Mount Etna (Hamilton-Smith unpublished data).

Notonomus angustibasis Sloane, Tp?, Gx. NEW SOUTH WALES: Comboyne C4 Cave, Comboyne (Hamilton-Smith unpublished data).

Notospeophonus castaneus castaneus Moore, Tp2. SOUTH AUSTRALIA: Blanche Cave (U4), Naracoorte (Hamilton-Smith 1967); Blackberry Cave (U8), Naracoorte (Hamilton-Smith 1967); Stick Cave (U11), Naracoorte (Moore 1964); Cathedral Cave (U12), Naracoorte (Moore 1964); Fox Cave (U22), Naracoorte (Hamilton-Smith 1967); Haystall Cave (U23), Naracoorte (Hamilton-Smith 1967); Cave Park Cave (U37), Naracoorte (Hamilton-Smith unpublished data); Tantanoola Caves (Hamilton-Smith 1967); VICTORIA: Bat Cave (P6), Portland (Moore 1962); Byaduk Caves, Byaduk (Moore 1962); Panmure Cave (H5), Mount Napier (Moore 1964); Mt Widderin Cave (H1), Skipton (Hamilton-Smith 1967); Snowflake Cave (L1), Glenelg River (Hamilton-Smith 1967); Curran's Creek Cave (G4), Glenelg River (Hamilton-Smith 1967).

Notospeophonus castaneus consobrinus Moore, Tp, Gp. VICTORIA: Spring Creek Cave (B1), Buchan (Hamilton-Smith unpublished data); Moon Cave (B2), Buchan (Hamilton-Smith unpublished data); Mabel Cave (EB1), East Buchan (Hamilton-Smith unpublished data); Wilson's Cave (EB4), East Buchan (Hamilton-Smith unpublished data); Trogdip Cave (EB10), East Buchan (Hamilton-Smith unpublished data); Slocombe's Cave (BA1), The Basin (Hamilton-Smith unpublished data); Shades of Death Cave (M3), Murrindal (Hamilton-Smith unpublished data); Anticline Cave (M11), Murrindal (Hamilton-Smith unpublished data); SSS Cave (M44), Murrindal (Hamilton-Smith unpublished data).

Notospeophonus jasperensis jasperensis Moore, Tp2, Gp. NEW SOUTH WALES: Punchbowl Cave (WJ8), Wee Jasper (Moore 1964); Pylon 58 Cave (WJ99), Wee Jasper (Moore 1964); Basin Cave (W4), Wombeyan (Hamilton-Smith unpublished data).

Notospeophonus jasperensis vicinus Moore, Tp2, Gp. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998).

Notospeophonus pallidus Moore, Tp2, Gp?. NEW SOUTH WALES: Childrens Cave (CL12), Cliefden (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Myponga (Moore 1964); NULLARBOR PLAIN: Warbla Cave (N1) (Hamilton-Smith 1967; Richards 1971); Weebubbie Cave (N2) (Richards 1971); Abrakurrie Cave (N3) (Hamilton-Smith 1967; Richards 1971); Koonalda Cave (N4) (Hamilton-Smith 1967; Richards 1971); Koomooloobooka Cave (N6) (Richards 1971); Murrawijinie No.3 Cave (N9) (Richards 1971); Knowles Cave (N22) (Hamilton-Smith 1967; Richards 1971); Mullamullang Cave (N37) (Richards 1971); Joe's Cave (N39) (Hamilton-Smith 1967; Richards 1971); Moonera Tank Cave (N53) (Richards 1971); Madura Cave (Madura 6 Mile South Cave) (N62) (Richards 1971); Lynch Cave (N60) (Richards 1971).

Notospeophonus sp., Tp, Gp?. QUEENSLAND: Viator Main Cave (VR1), Viator Hill (Hamilton-Smith unpublished data).

Phloeocarabus sp. Tp?, Gp?. QUEENSLAND: Haunted Cave (CH1), Chillagoe (Hamilton-Smith unpublished data).

Pogonoglossus sp., Tp, Gp?. NORTHERN TERRITORY: Cutta Cutta Cave (K1), Katherine (Hamilton-Smith unpublished data).

Pseudoceneus sp. Tp, Gp?. WESTERN AUSTRALIA: Stockyard Cave (E3), Eneabba (Hamilton-Smith unpublished data).

Speotarus lucifugus Moore, Tp, Gp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Moore 1964; Bellati et al. 2003); NULLARBOR PLAIN: Warbla Cave (N1) (Richards 1971); Weebubbie Cave (N2) (Richards 1971); Abrakurrie Cave (N3) (Richards 1971); Koonalda Cave (N4) (Richards 1971); Winbirra Cave (N45) (Richards 1971); Murra-El-Elevyn Cave (N47) (Richards 1971); Cocklebiddy Cave (N48) (Richards 1971); Moonera Tank Cave (N53) (Richards 1971); Lynch Cave (N60) (Richards 1971); Unnamed cave (N139) (Richards 1971).

Speotarus princeps Moore, Tp2, Gp. NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Moore 1964); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data).

Speotarus sp., Tp, Gp. NULLARBOR PLAIN: Warbla Cave (N1) (Hamilton-Smith unpublished data); Weebubbie Cave (N2) (Hamilton-Smith unpublished data); Murra-El-Elevyn Cave (N47) (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Mount Sims Cave (F7), Walpunda Creek, Flinders Ranges (Hamilton-Smith unpublished data); WESTERN AUSTRALIA: Gooseberry Cave (J1), Jurien Bay (Hamilton-Smith unpublished data).

Thenarotes speluncarius Moore, Tp, Gp. NULLARBOR PLAIN: Abrakurrie Cave (N3) (Richards 1971); Koonalda Cave (N4) (Richards 1971); New Cave (N11) (Richards 1971); Lynch Cave (N60) (Richards 1971); Decoration Cave (N84) (Richards 1971); SOUTH AUSTRALIA: Cave No. 1, Buckalowie, Flinders Ranges (Hamilton-Smith unpublished data).

Trechimorphus diemenensis Bates, Tp1, Gx. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998); Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Jenolan Caves (Moore 1964); VICTORIA: Dalley's Sinkhole (M35), Murrindal (Hamilton-Smith 1967).

Trichosternus vigorsi Gory, Tp? Gx. NEW SOUTH WALES: Comboyne C4 Cave, Comboyne (Hamilton-Smith unpublished data).

Undetermined genus and species, NEW SOUTH WALES: Grill Cave (B44), Bungonia (Eberhard and Spate 1995); Belfry Cave (TR2), Timor (James et al. 1976); Glen Dhu Cave (Allston Cave) (TR15), Timor (Hamilton-Smith unpublished data); Tuglow Cave (T1), Tuglow (Hamilton-Smith unpublished data); QUEENSLAND: Kaiser Creek Cave (C12) (Two Mile Cave, Tar Drum Cave), Camooweal (Hamilton-Smith unpublished data); Mount Etna Main Cave (E1), Mount Etna (Hamilton-Smith unpublished data); Cave with the thing that went thump! (E5), Mount Etna (Hamilton-Smith unpublished data).

Undetermined genus and species, Tp, Gp. QUEENSLAND: Barker's Cave (U34), Undara (Hamilton-Smith unpublished data); VICTORIA: Spring Creek Cave (B1), Buchan (Yen and Milledge 1990); Mabel Cave (EB1), East Buchan (Yen and Milledge 1990); Wilson's Cave (EB4), East Buchan (Hamilton-Smith unpublished data); Shades of Death Cave (M3), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

Cryptophagidae

Anchicera sp., Tp, Gp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

Atomaria sp., Gp. Southern Australia (Hamilton-Smith 1968).

Undetermined genus and species, Tp, Gp. NEW SOUTH WALES: Basin Cave (W4), Wombeyan (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Fox Cave (U22), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Wilson's Cave (EB4), East Buchan (Hamilton-Smith unpublished data); Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith unpublished data).

Curculionidae

Mandalotus sp. Gp?. NEW SOUTH WALES: Chalk Cave (B26), Bungonia (Hamilton-Smith unpublished data).

Talaurinus sp. Gp?. QUEENSLAND: Johannsen's Cave (J1-2), Mount Etna (Hamilton-Smith unpublished data).

Dermestidae

Dermestes ater DeGeer, Tp, Gp. QUEENSLAND: Royal Arch Cave (CH9), Chillagoe (Hamilton-Smith unpublished data).

Undetermined genus and species, Tp, Gp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003); QUEENSLAND: Holy Jump Lava Cave (BM1), Bauer's Mountain (Hamilton-Smith unpublished data); Unidentified cave in southern Queensland (Hamilton-Smith 1967); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data).

Endomychidae

Undetermined genus and species, Gp. NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Hamilton-Smith unpublished data).

Histeridae

Carcinops sp., Gp. CHRISTMAS ISLAND (Indian Ocean): Upper Daniel Roux Cave (CI56) (Humphreys and Eberhard 2001).

Saprinus sp., Gp. NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Hamilton-Smith unpublished data); QUEENSLAND: Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data); Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith unpublished data); Clogg's Cave (EB2), East Buchan (Hamilton-Smith unpublished data).

Tomogenius ?ripicola Marseul, Tp, Gb. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Lynch Cave (N60) (Richards 1971); Thylacine Hole (N63) (Richards 1971); Dingo Cave (N160) (Richards 1971).

Undetermined genus and species, Tp, Gp. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998); Ashford Main Cave (AS1), Ashford (Hamilton-Smith unpublished data); Carrai Bat Cave (SC5), Stockyard Creek (Hamilton-Smith unpublished data); Willi Willi Bat Cave (Main Cave) (WW1), Willi Willi (Hamilton-Smith unpublished data); QUEENSLAND: Holy Jump Lava Cave (BM1), Bauer's Mountain (Hamilton-Smith unpublished data); Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data); Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); Winding Stairway Cave (E2), Mt Etna (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Sand Cave (Joanna) (U16), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Chimney Cave (BR1), Bat Ridges, Portland (Hamilton-Smith unpublished data); Clogg's Cave (EB2), East Buchan (Hamilton-Smith unpublished data); Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith unpublished data); Bat Cave (P6), Portland (Hamilton-Smith unpublished data); WESTERN AUSTRALIA: Gooseberry Cave (J1), Jurien Bay (Hamilton-Smith unpublished data).

Jacobsoniidae

Derolathrus sp., Tp, Gb. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003); Various caves in southern Australia (Hamilton-Smith 1967).

Undetermined genus and species, Tp, Gb. VICTORIA: Bat Cave (P6), Portland (Hamilton-Smith unpublished data); Panmure Cave (H5), Mount Napier (Hamilton-Smith unpublished data).

Lathridiidae

Corticaria sp., Gp. Southern Australia (Hamilton-Smith 1968); NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Weebubbie Cave (N2) (Hamilton-Smith unpublished data); Abrakurrie Cave (N3) (Hamilton-Smith unpublished data): VICTORIA: Skipton Cave (Mount Widderin Cave) (H1), Mount Napier (Hamilton-Smith unpublished data).

Leiodidae

Choleva australis, Tp, Gp. QUEENSLAND: Royal Arch Cave (CH9), Chillagoe (Hamilton-Smith unpublished data).

Choleva sp., Tp, Gp. NULLARBOR PLAIN: Cocklebiddy Cave (N48) (Richards 1971); Lynch Cave (N60) (Richards 1971).

Nargomorphus minusculus Blackburn, Tp1, Gp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith 1967; Bellati et al. 2003); VICTORIA: Anticline Cave (M11), Murrindal (Hamilton-Smith 1967).

Pseudonemadus adelaidae Blackburn, Tp, Gp. NEW SOUTH WALES: Glen Dhu Cave (Allston Cave) (TR15), Timor (Hamilton-Smith unpublished data); QUEENSLAND: Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data).

Pseudonemadus australis Erichson, Gp. VICTORIA: Chimney Cave (BR1), Bat Ridge, Portland (Hamilton-Smith unpublished data); Bat Cave (P6), Portland (Hamilton-Smith unpublished data); Panmure Cave (H5), Mt Napier (Hamilton-Smith unpublished data).

Pseudonemadus integer Portevin, Gp. NEW SOUTH WALES: Comboyne C4 Cave, Comboyne (Hamilton-Smith unpublished data); QUEENSLAND: Speaking Tube (E7), Mount Etna (Hamilton-Smith unpublished data); Viator Main Cave (VR1), Viator Hill (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Cathedral Cave (U12), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Trogdip Cave (EB10), East Buchan (Hamilton-Smith unpublished data); Mt Widderin Cave (H1), Skipton (Hamilton-Smith unpublished data); Panmure Cave (H5), Mt Napier (Hamilton-Smith unpublished data).

Pseudonemadus sp., Gp. Southern Australia (Hamilton-Smith 1968).

?Leiodidae

Undetermined genus and species, NEW SOUTH WALES: Basin Cave (W4), Wombeyan (Smith 1982a).

Melyridae

Heteromastix sp. Tx?, Gx?. NEW SOUTH WALES: Colong Main Cave (CG1), Colong (Hamilton-Smith unpublished data).

Merophysiidae

Undetermined genus and species, Gp. NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Hamilton-Smith 1967).

Pselaphidae

Rybaxis? sp., Tp, Gp. NEW SOUTH WALES: Basin Cave (W4), Wombeyan (Hamilton-Smith 1966a); Bungonia various caves (Eberhard 1998).

Tyromorphus speciosus King, Tp1. NEW SOUTH WALES: Unidentified cave, Southern Limestone, Jenolan (Hamilton-Smith 1966a); Paradox Cave (J48), Jenolan (Hamilton-Smith unpublished data); QUEENSLAND: Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith 1966a); VICTORIA: Anticline Cave (M11), Murrindal (Hamilton-Smith 1966a).

Undetermined genus and species, Gp. QUEENSLAND: Rope Ladder Cave, Mingella (Weinstein and Slaney 1995).

Undetermined genus and species, Tp, Gp. VICTORIA: Wilson's Cave (EB4), East Buchan (Hamilton-Smith unpublished data).

Ptilidae

Achosia lanigera Deane, Tp?, Gp. VICTORIA: Wilsons Cave (EB4), East Buchan (Hamilton-Smith unpublished data).

Undetermined genus and species, Tp, Gp. NEW SOUTH WALES: Comboyne C4 Cave, Comboyne (Hamilton-Smith unpublished data).

Rhizophagidae

Undetermined genus and species, Gp. QUEENSLAND: Rope Ladder Cave (FR2), Mingella, Fanning River (Weinstein and Slaney 1995).

Scarabaeidae

Aulacopris maximus Matthews, Tp1, Gb. NEW SOUTH WALES: Yessabah Bat Cave (YE1), Yessabah (Waite 1898); Unknown cave in Coorabakh National Park (formerly part Lansdowne State Forest), Taree (Williams 2003).

Aulacopris reichei White, Tp1, Gp. NEW SOUTH WALES: Yessabah Bat Cave (YE1), Yessabah (Lea 1923); Unknown cave, Mosman (Fricke 1964).

Amphistomus accidatus Matthews, Tx, Gp. QUEENSLAND: Elephant Hole (E8), Mount Etna (Hamilton-Smith unpublished data).

Saprosites mendax Blackburn, Gp. SOUTH AUSTRALIA: Cathedral Cave (U12), Naracoorte (Hamilton-Smith unpublished data).

Undetermined genus and species, Gp. NEW SOUTH WALES: Willi Willi Bat Cave (Main Cave) (WW1), Willi Willi (Hamilton-Smith unpublished data).

Silphidae

Ptomaphila lachrymosa Schreibers, VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data).

Staphylinidae

Myotyphlus jansoni Matthews, Tp1, Gp. NEW SOUTH WALES: Unidentified cave, Southern Limestone, Jenolan (Hamilton-Smith and Adams 1966); Paradox Cave (J48), Jenolan (Hamilton-Smith unpublished data); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith and Adams 1966); Bat Cave (P6), Portland (Hamilton-Smith 1967).

Tineidae

Lindera tessellatella Blanchard, Gb?. NEW SOUTH WALES: Humicrib Cave (WJ34), Wee Jasper (Eberhard and Spate 1995).

Monopis crocicapitella Clemens, Tp, Gb. NEW SOUTH WALES: Drum Cave (B13), Bungonia (Eberhard 1998); Grill Cave (B44), Bungonia (Eberhard 1998); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data).

Monopis sp., Gb. NEW SOUTH WALES: Gable Cave (CL7), Cliefden (Eberhard and Spate 1995); Colong Main Cave (CG3), Colong (Eberhard and Spate 1995); Jenolan undetermined cave (Gibian et al. 1988); Basin Cave (W4), Wombeyan (Smith 1982b); Undetermined caves, Wombeyan (Dew 1963); Signature Cave (WJ7), Wee Jasper (Hamilton-Smith unpublished data); Punchbowl Cave (WJ8), Wee Jasper (Hamilton-Smith unpublished data); Dogleg Cave (WJ10), Wee Jasper (Eberhard 1993); Church Cave (WJ31), Wee Jasper (Hamilton-Smith unpublished data); Humicrib Cave (WJ34), (Eberhard 1993); Carey's Cave (WJ100), Wee Jasper (Eberhard 1993); NULLARBOR PLAIN: Abrakurrie Cave (N3) (Richards 1971); Koonalda Cave (N4) (Richards 1971); Mullamullang Cave (N37) (Richards 1971); Cocklebiddy Cave (N48) (Richards 1971); Moonera Tank Cave (N53) (Richards 1971); Thylacine Hole (N63) (Richards 1971); Old Homestead Cave (N83) (Richards 1971); Dingo Cave (N160) (Richards 1971).

Undetermined genus and species, Gb. CHRISTMAS ISLAND (Indian Ocean): Smiths Cave (CI9) (Humphreys and Eberhard 2001); Upper Daniel Roux Cave (CI56) (Humphreys and Eberhard 2001); NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Hamilton-Smith unpublished data); Cliefden Main Cave (CL1), Cliefden (Hamilton-Smith unpublished data); Willi Willi Bat Cave (Main Cave) (WW1), Willi Willi (Hamilton-Smith unpublished data); QUEENSLAND: Rope Ladder Cave (FR2), Mingella, Fanning River (Weinstein and Slaney 1995); Queenslander Tower (CH5246), Chillagoe (Matts 1987); Spring Tower (CH5223-5), Chillagoe (Matts 1987); Donna Tower (CH5155), Chillagoe (Matts 1987); Royal Arch Tower (CH5158-9), Chillagoe (Matts 1987); Tea Tree Tower (CH5137), Chillagoe (Matts 1987); Ryan Imperial Tower (CH5239), Chillagoe (Matts 1987); Wallaroo Tower (CH5201), Chillagoe (Matts 1987); Tower of London Cave (CH5) Chillagoe (Matts 1987); Kaiser Creek Cave (C12) (Two Mile Cave, Tar Drum Cave), Camooweal (Hamilton-Smith unpublished data); Holy Jump Lava Cave (BM1), Bauer's Mountain (Hamilton-Smith unpublished data); VICTORIA: Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Dickson Cave (M30), Murrindal (Yen and Milledge 1990); Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith unpublished data); Grassmere Cave (W6), Warrnambool (Hamilton-Smith unpublished data).

Undetermined Family

Undetermined genus and species, Gp. CHRISTMAS ISLAND (Indian Ocean): Smiths Cave (CI9) (Humphreys and Eberhard 2001); Swiflet Cave (CI30) (Humphreys and Eberhard 2001); Managers Alcove (CI50) (Humphreys and Eberhard 2001); Grimes Cave (CI53) (Humphreys and Eberhard 2001); Upper Daniel Roux Cave (CI56) (Humphreys and Eberhard 2001).

Undetermined genus and species, NULLARBOR PLAIN: Abrakurrie Cave (N3) (Hamilton-Smith unpublished data).

Order Hymenoptera

Braconidae

Apanteles ?carpatus Say, Tp1, Gp. NEW SOUTH WALES: Humidicrib Cave (WJ34), Wee Jasper (Eberhard and Spate 1995); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data).

Apanteles sp., Tp, Gp. NEW SOUTH WALES: Church Cave (W31), Wee Jasper (Hamilton-Smith unpublished data); Willi Willi Bat Cave (Main Cave) (WW1), Willi Willi (Hamilton-Smith unpublished data).

Undetermined genus and species. Tp?. QUEENSLAND: Holy Jump Lava Cave (BM1), Bauer's Mountain (Hamilton-Smith unpublished data).

Formicidae

Amblyopone australis Erichson, VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data).

Iridomyrmex purpureus Smith, Tx, Gx. SOUTH AUSTRALIA: Eregunda Mine near Blinman, Flinders Ranges (T. Moulds unpublished data).

Oligomyrmex sp., Tp?, Gx?. QUEENSLAND: Crazy Cracks Cave, Jacks Gorge, Broken River (T. Moulds unpublished data).

Pachycondyla sp., Gp. CHRISTMAS ISLAND (Indian Ocean): Upper Daniel Roux Cave (CI56) (Humphreys and Eberhard 2001).

Undetermined genus and species, NEW SOUTH WALES: Church Cave (WJ31), Wee Jasper (Hamilton-Smith unpublished data); QUEENSLAND: Royal Arch Cave (CH9), Chillagoe (Hamilton-Smith unpublished data); Spring Cave, Mount Surprise (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

Ichneumonidae

Undetermined Cryptinae genus and species, Gp?. NEW SOUTH WALES: undetermined caves (Hamilton-Smith 1967); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data); Spring Creek Cave (B1), Buchan (Hamilton-Smith unpublished data); Wilson's Cave (EB4), East Buchan (Hamilton-Smith unpublished data).

Myrmaridae

Gonatocerinae sp., Gp?. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

Undetermined Family

Undetermined genus and species, Tp, Gp. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998).

Undetermined genus and species, Gp?. NEW SOUTH WALES: Church Cave (WJ31), Wee Jasper (Hamilton-Smith unpublished data); Willi Willi Bat Cave (WW1), Willi Willi (Hamilton-Smith unpublished data); VICTORIA: Panmure Cave (H5), Mount Napier (Hamilton-Smith unpublished data); Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data).

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A Devonian Brachythoracid Arthrodire Skull (Placoderm Fish) from the Broken River Area, Queensland

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Young, G.C. (2004). A Devonian brachythoracid arthrodire skull (placoderm fish) from the Broken River area, Queensland. *Proceedings of the Linnean Society of New South Wales* **125**, 43-56.

An incomplete brachythoracid arthrodire skull acid-prepared from the Devonian limestones of the Broken River area of Queensland is described as *Doseyosteus talenti* gen. et sp. nov. It supposedly comes from strata dated by conodonts as late Early Devonian in age (Emsian stage), but shows several derived features of the skull, typical of Middle-Late Devonian brachythoracids, and not seen in any arthrodire from the Emsian limestones of the Burrinjuck area of NSW. The alignment with conodont zones of stratigraphic subdivisions of the Burrinjuck sequence is revised. Published information on the provenance and age of all previously described placoderm taxa from Broken River is reviewed and amended. The new taxon may be most closely related to Late Devonian (Frasnian) brachythoracids from Iran and the Gogo Formation of Western Australia.

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KEYWORDS: Placoderm fishes, Arthrodira, Brachythoraci, Broken River, Devonian, new genus *Doseyosteus*, Queensland.

INTRODUCTION

Devonian sedimentary rocks, including many marine limestones, are well exposed in the Broken River area of Queensland (Fig. 1). Conodonts form the basis for dating the sedimentary sequence (Mawson and Talent 1989; Sloan et al. 1995). Vertebrate remains reported from this sequence include microfossils from many horizons (De Pomeroy 1996; Turner, Basden and Burrow 2000), and less well known vertebrate macro-remains. The latter include two genera of antiarch placoderms described by Young (1990), a ptyctodont toothplate ascribed to ?*Ptyctodus* sp. by Turner and Cook (1997), a new species of the brachythoracid arthrodire *Atlantidosteus* Lelièvre 1984 described by Young (2003a), an isolated suborbital plate of another arthrodire illustrated by Turner et al. (2000, fig. 8.7), and jaw remains of an onychodontid (Turner et al. 2000, fig. 5). Undescribed vertebrate macro-remains include various placoderm bones, most of which belong to brachythoracid arthrodires. The Arthrodira is the most diverse order within the class Placodermi, and its major subgroup, the Brachythoraci, comprises nearly 60% of about 170 genera within the Arthrodira (Carr 1995). The brachythoracid arthrodires were one of the most successful groups of early gnathostome fishes (e.g. Young 1986; Janvier 1996). In marine environments of the Late Devonian they included probably the largest predators of their time. The major radiation of brachythoracid subgroups had apparently already occurred by the Middle Devonian, and primitive representatives were already widespread in shallow marine environments of the Early Devonian (e.g. Young et al. 2001; Mark-Kurik and Young 2003), and are important in considering the origins and interrelationships of major brachythoracid subgroups (e.g. Lelièvre 1995).

The stratigraphic occurrence of various placoderm remains in the Broken River sequence were reviewed by Young (1993, 1995, 1996), De Pomeroy (1995, 1996), and Turner et al. (2000), and they have been mentioned in relation to conodont studies by Sloan et al. (1995). There has been conflicting information published about the provenance of some of the described placoderm taxa. These were collected from the Broken River area many years ago by Professor John Jell, University of Queensland, and sent to Canberra for acid preparation and study. In this paper I describe a new arthrodire skull from this collection, and review the locality information and age determinations for previously described placoderm taxa.

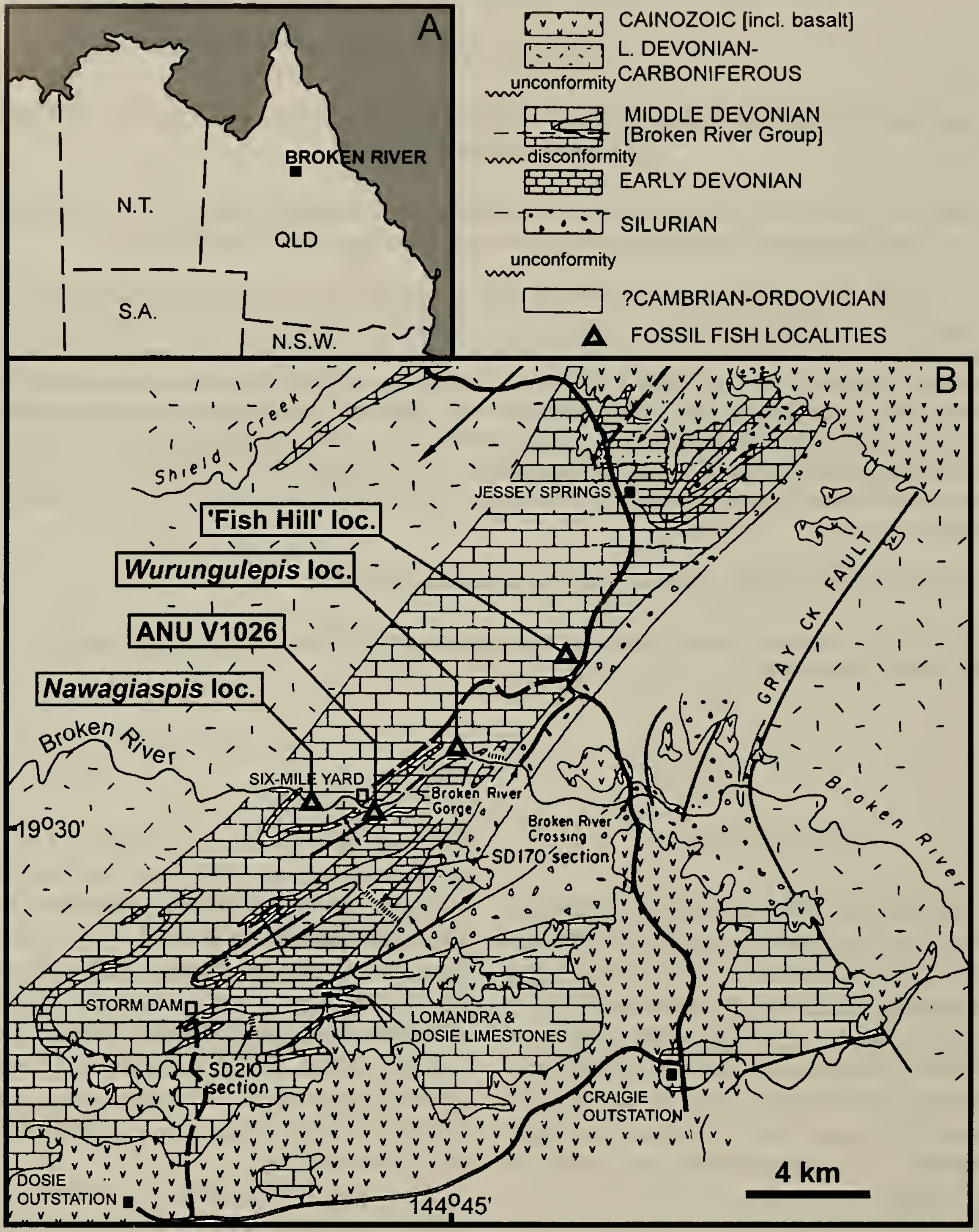

Figure 1. (A) location of the Broken River area in Queensland, Australia; (B) geological map of the collecting area (modified from Turner, Basden and Burrow 2000, fig. 2), showing localities for previously described placoderm taxa, and the specimen described in this paper (ANU V1026).

LOCALITY AND AGE OF DESCRIBED PLACODERM TAXA FROM THE BROKEN RIVER AREA

Wurungulepis denisoni Young 1990

According to information provided with this specimen, it came from University of Queensland locality L4399 (not L4339, given in error by Young 1990: 45), on the north bank of the Broken River, Grid Reference 640 460 on the Burges 1:100 000 sheet, and was assigned a Middle Devonian (?Eifelian) age within the Broken River Formation (J.S. Jell, letter of 17 April 1980). Judging by the map of the area published by Sloan et al. (1995: fig. 2), the locality lies within outcrop referred to as ‘undifferentiated Broken River Group’.

A ‘*Wurungulepis-Atlantidosteus* fauna’, of assumed Eifelian age, was listed in the macrovertebrate zonation of Young (1993, 1995, 1996). However De Pomeroy (1995: 480) assigned *Wurungulepis* to the late Emsian *serotinus* Conodont Zone (CZ), citing a personal communication of J.A. Talent. This information was repeated by Turner et al. (2000: 498). Later (pers. comm. 28/8/95) J.A. Talent had advised A. Basden that this specimen was collected from the grid reference cited above, situated on a bend of the Broken River in an anticline, in strata which were pre-Dosey Limestone in the sequence, and equivalent to the Bracteata Formation and Lomandra Limestone (spanning the Emsian-Eifelian boundary; Sloan *et al.* 1995: fig. 3).

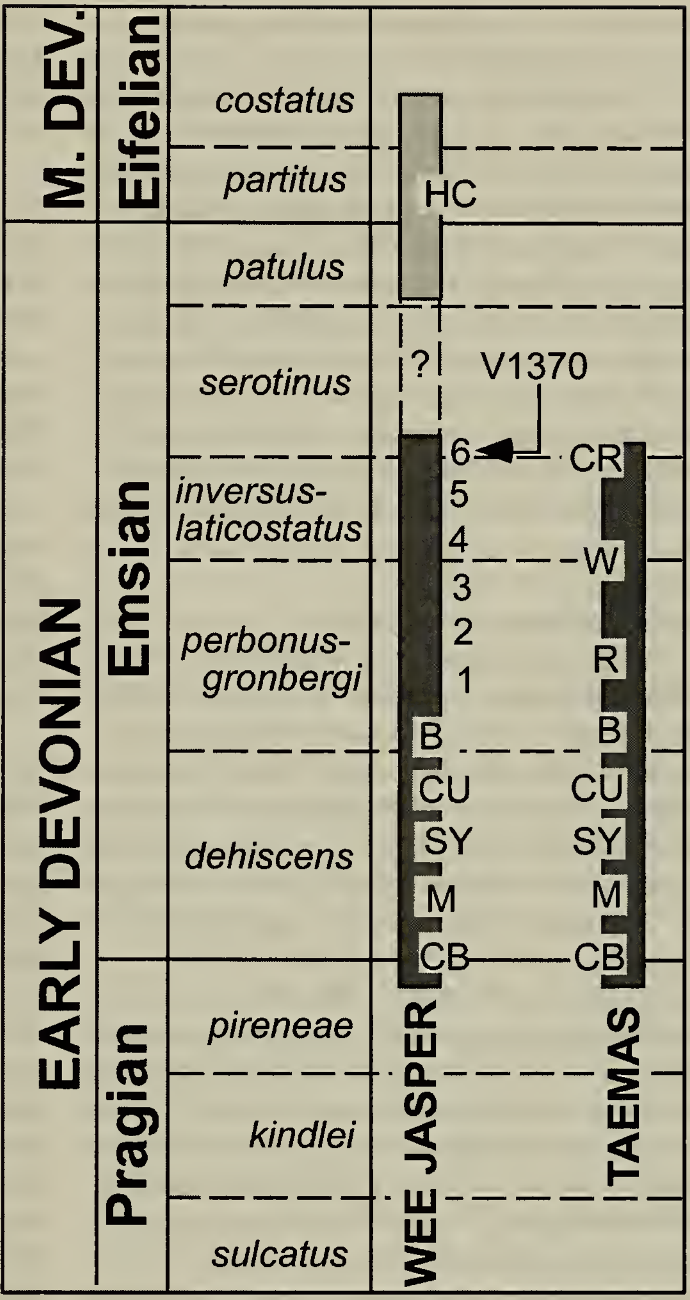

Figure 2. Proposed alignment with conodont zones of subdivisions of the Early Devonian limestone sequence (Murrumbidgee Group) around Burrinjuck Dam, N.S.W., revised from Basden et al. (2000: fig. 2). Abbreviations for stratigraphic subdivisions are: B - Bloomfield Limestone Member; CB - Cavan Formation; CR - Crinoidal Limestone Member; CU - Currajong Limestone Member; HC - Hatchery Creek Formation; M - Majurgong Formation; R - *Receptaculites* Limestone Member; SY - *Spirifer yassensis* Limestone Member; W - Warroo Limestone Member; 1-6 - units of Upper Reef Formation. V1370 – horizon for highest known arthrodire in the sequence.

No conodont data were obtained from the specimen, so its precise position relative to the standard conodont zonation is uncertain. *Wurungulepis* is an early representative of the asterolepidoid antiarchs, with a high short trunk armour (Young 1990), and was placed within the asterolepidoid clade adjacent to *Sherbonaspis*, and as sister group to *Stegolepis*, *Asterolepis*, *Remigolepis* and *Pambulaspis*, by Zhu (1996: fig. 29). As earlier discussed (Young 1990: 48) the initially suggested Eifelian age was consistent with the oldest asterolepid (pterichthyodid) occurrence in Europe, cited as *Gerdalepis* from the Eifelian of Germany by Denison (1978), although this occurrence is slightly younger (early Givetian) according to Otto (1998: 118). However Gardiner (1994) cited Young (1974) for an older record (Emsian) of the asterolepid antiarchs, but the ‘cf. *Pterichthyodes*’ mentioned by Young (1974) was based on an erroneous attribution by Hills (1958: 88) to the Early Devonian limestone sequence of an ‘Antiarchan from Taemas’. In fact, the specimen in question came from the overlying Hatchery Creek Formation, of presumed Eifelian age (Fig. 2). This specimen was assigned to the new genus *Sherbonaspis* by Young and Gorter (1981). Previously, the suggested Emsian age of a pterichthyodid antiarch from the Georgina Basin (Young 1984a) was noted as possibly the oldest occurrence of this group anywhere recorded. New evidence now indicates that two assemblages may have been mixed in this region (Burrow and Young, in press), with the limestone occurrence yielding the antiarch probably younger than the diverse

Wuttagoonaspis fauna from underlying sandstones (Young and Goujet 2003).

The antiarchs are a major subgroup of the class Placodermi, ranging in age from Early Silurian to latest Devonian. In recent years there has been a significant expansion in our knowledge of the group. A cladistic analysis of their distribution in relation to phylogeny by Young (1984b) involved 22 taxa and 40 characters. In a recent review of antiarch phylogeny, Zhu (1996) noted some 45 genera and 154 species, and his data matrix used 66 characters for 40 genera. The original age assessment of Eifelian for *Wurungulepis* from Broken River is most consistent with our current knowledge of this large and diverse group.

Nawagiaspis wadeae Young 1990

This specimen is recorded from locality BRJ68D (University of Queensland locality L4428; 'small limestone outcrop on eastern side of gully 1 km upstream from Six Mile yard'), Grid Reference 596 442 on the Burges 1:100 000 sheet, which was assigned a Middle Devonian (?Givetian) age within the Broken River Formation (J.S. Jell, letter of 17 April 1980). Apparently this specimen was found by Dr Mary Wade.

Again, De Pomeroy (1995: 480) referred this taxon to the significantly older (late Emsian) *serotinus* CZ, based on its assigned position within the Bracteata Formation in section Br4 of Sloan et al. (1995, fig. 6). This information was repeated by Turner et al. (2000: 498, 506). However Prof. J.A. Talent's previous advice to the author (pers. comm. 5/8/92), was that this specimen was considerably younger (*ensensis* – *varcus* Zones; late Eifelian - Givetian). Clearly, there was some confusion about which fish specimen was being referred to. Subsequent advice given to A. Basden (pers. comm. 28/8/95), was that *N. wadeae* came from the bank of Dosey Creek (Grid Reference 616 437), the location of section Br2 within outcrop of the Bracteata Formation (Sloan et al. 1995: fig. 2). The different, and presumably correct, locality information provided with the specimen, as cited above, corresponds to the vicinity of the boundary between the Papilio and Mytton Formations on the map of Sloan et al. (1995: fig. 2). This is consistent with the Givetian age first suggested by J.S. Jell.

Nawagiaspis wadeae is another antiarch, originally interpreted as possibly a primitive bothriolepidoid (Young 1990), although in Zhu's (1996) phylogeny it comes out as a basal asterolepidoid. Apart from primitive Chinese antiarchs, and the erroneous Emsian pterichthyodid occurrence discussed above, the stratigraphic record of this group is Middle-Late Devonian (Gardiner 1994, fig. 32.1). The bothriolepidoid clade had an earlier history in Asia, and apparently expanded its range to most regions of the world in the Givetian (Young 2003b).

The confusion about the provenance of this specimen may have resulted from the misconception that it was a recognisable 'skull' when collected. Turner et al. (2000) used this term to refer to the type, but the specimen as collected was a largely complete trunk armour, and the incomplete skull, missing its central portion, formed a minor part of the specimen. The whole specimen may have appeared to a non-vertebrate worker to represent a 'skull'. Such fish remains, when collected in the field, are generally not determinable until after acid preparation (e.g. the type specimen of *Atlantidosteus pacifica* Young 2003a, before preparation, was assumed to be a ventral plate of the trunk armour, rather than a large suborbital bone from the cheek).

A summary list of prepared fish remains from the original J.S. Jell collection was provided to J.A. Talent in 1995 to check on age and locality data. This list mentioned only one skull, the brachythoracid specimen described below, of which locality data provided by J.S. Jell are almost the same as stated by Sloan et al. (1995) for *N. wadeae*. Thus it seems that the specimen described below, previously listed as a 'skull', has been confused with the type of *N. wadeae*, leading to erroneous locality and age information being given in De Pomeroy (1995), Sloan et al. (1995), and Turner et al. (2000). In the context of the global distribution in time and space of this major placoderm subgroup (see above), it is almost certain that *Nawagiaspis* is Middle Devonian in age, and a Givetian age, as first suggested by J.S. Jell, is most consistent with other information about the stratigraphic distribution of the more derived antiarchs.

Atlantidosteus pacifica Young 2003a

This specimen came from locality BRJ 67B (University of Queensland locality L 4472), Grid Reference 675 485 on the Burges 1:100 000 sheet, described as 'Top of ridge to three-quarters way down western slope, west of road between Six Mile Dam and Diggers Creek' (J.S. Jell, letter of 17 April 1980). This is the locality (with a slightly different grid reference) referred to as 'Fish Hill' by Turner et al. (2000: 507). They assigned it a middle Eifelian age (*costatus* - *australis* conodont zone), but noted that Sloan et al. (1995) gave a slightly longer *partitus* - early *kockelianus* zonal range for the Fish Hill section. This is consistent with the original assignment of a Middle Devonian (?Eifelian) age within the Broken River Formation by Prof. J.S. Jell. This occurrence is part of the evidence for proposing an Eifelian '*Wurungulepis-Atlantidosteus* fauna' in the macrovertebrate zonation of Young (1993, 1995, 1996).

***Doseyosteus talenti* gen. et sp. nov.**

This specimen, described below, was the only one in the J.S. Jell collection lacking a sample number at the time of preparation. It is highly probable that it was a sample collected the year before the other material, and was taken to Canberra separately by Dr P. Jell (J.S. Jell, letter of 17 April 1980). The following locality details, provided by Prof. J.S. Jell (letter of 17 April 1980), indicate that it is the specimen collected from the alternative erroneous locality for *Nawagiaspis* just discussed: 'BRJ34 = L 4054. Grid Reference 616 438 Burges 1:100,000 sheet. Western bank of Dosey Creek, 750 m upstream from its junction with Broken River. Base of thick limestone lens in Broken River Formation, Middle Devonian. ? Eifelian'.

In a published listing of University of Queensland locality numbers (Turner et al. 2000: 506), UQL4054 is assigned to 'basal part of limestone, Lomandra/Dosey Limestone, Broken River Group', with a slightly different grid reference (615 438), but the same locality description as above. However, it is assigned to the Emsian *serotinus* CZ, citing Sloan et al. (1995).

Again, no conodonts were obtained from the sample, and section Br4 through the Bracteata Formation at this locality did not produce identifiable conodonts (Sloan et al. 1995: caption to fig. 6). Nevertheless, these authors (p.5) considered the entire formation to belong to the *serotinus* CZ, making it equivalent to the upper part of the Burrinjuck (NSW) limestone sequence, which extends from the top of the *pirenae* CZ (latest Pragian) into the *serotinus* CZ (the second youngest zone of the late Emsian). It is therefore relevant to make comparisons with the stratigraphic distribution of the diverse arthrodire assemblage described from the Burrinjuck limestone sequence.

The described arthrodire fauna from the Burrinjuck sequence (White 1952, 1978; White and Toombs 1972; Young 1979, 1981, in press a, b; Young et al. 2001; Mark-Kurik and Young 2003) includes 10 genera of brachythoracids, amongst which the most derived taxa (*Cathlesichthys* and *Dhanguura*) come from the upper part of the Wee Jasper limestone sequence. Basden et al. (2000, fig. 2) showed the youngest arthrodire skull from the Wee Jasper section (ANU V1370; the holotype of *Dhanguura*) to come from the uppermost unit 6 of the 'Upper Reef Formation' of Young (1969). This specimen is more advanced than other arthrodires known from the Burrinjuck sequence in possessing several derived characters of the skull, the most obvious being the T-shaped rostral plate, a feature of more derived eubrachythoracids (character 5 of Carr 1991; character 4 of Lelièvre 1995). Eubrachythoracids were the most diverse fish group of the Middle and Late Devonian, and the new Broken River brachythoracid described below clearly belongs to this group, with a skull which is more advanced in several respects than any of the known Burrinjuck arthrodires (see below). Gardiner (1994) lists the first occurrence of this grouping (his family Coccosteidae) as *Coccosteus* Miller 1841 from the Middle Devonian (Eifelian) of Scotland, for which a late Eifelian age is indicated by spores of the *devonicus-naumovae* zone (V.T. Young 1995). The same species (*Coccosteus cuspidatus*) is recorded from the Kernave Member of the Narva Formation in the Baltic sequence, although a related brachythoracid '*Protitanichthys*' occurs a little earlier, and in equivalent strata (*costatus* CZ) in the Rhenish sequence (Mark-Kurik 2000). However Otto (1997: 115) suggested that remains of early eubrachythoracids (coccosteids) first occur in the early Eifelian of Scotland, Germany, and the Baltic sequence.

Dhanguura johnstoni Young (in press a) comes from a horizon about 420 m stratigraphically above the boundary equivalent of the Bloomfield and *Receptaculites* Members of the Taemas Limestone. A similar horizon high in the limestone sequence has produced the large lungfish *Dipnorhynchus cathlesae* Campbell and Barwick 1999. The lungfish locality is close to localities L537 and L538 of Pedder et al. (1970) which yielded tetracorals *Vepresiphyllum dumosum*, *Sulcorphyllum pavimentum*, *Chalcidophyllum vesper* and *C. gigas*. This represents the uppermost 'tetracoral teilzone' of the Murrumbidgee Group (Pedder et al. 1970: fig. 4), and is Coral Fauna F in the scheme of Garratt and Wright (1989). These authors considered the succeeding G and H Coral Faunas to overlap, and belong to the late Emsian, rather than Eifelian as previously assessed. Garratt and Wright (1989) also aligned Coral Fauna F from Wee Jasper (and the Sulcor Limestone of northern NSW) with the mid-Emsian *inversus* CZ (see column 13 of Young 1995, 1996). However Basden et al. (2000: fig. 2) showed the uppermost beds of the limestone sequence at Wee Jasper (containing Coral Fauna F) extending well into the next youngest *serotinus* CZ. Evidence supporting this (summarised by Basden 2001, table 2.1) derives from reassignment of some of the conodonts from the highest productive sample (C62) in Pedder et al.'s (1970) section 2, referred by them to *Polygnathus linguiformis*

linguiformis, but reassigned to *Polygnathus inversus* by Klapper and Johnson (1975), and to *Polygnathus serotinus* (delta morphotype) by Mawson (1987). On the other hand, the age in terms of conodont zone alignment of several constituent members of the Taemas Limestone, as indicated by Basden et al. (2000, fig. 2), seem to be too young, and should be revised downwards on the following evidence. Lindley (2002a: 275) noted that the occurrence of the index species of Coral Fauna D (*Chalcidophyllum recessum*) in the Currajong Limestone Member indicates that it should be aligned with the *dehiscens* rather than the *perbonus* CZ. The overlying Bloomfield Limestone Member may also have lower beds of *dehiscens* rather than the *perbonus* CZ age (Basden 2001: table 2.1). The Warroo Limestone Member contains *perbonus* CZ elements (Nicoll, in Lindley 2002b), and the uppermost Crinoidal Limestone Member in the Taemas sequence may align with both the *inversus* and the *serotinus* CZ (Basden 2001: table 2.1).

These revised alignments are summarised in Fig. 2. Correlation with the upper part of the Wee Jasper sequence is unclear, because the constituent members of the Taemas Limestone are difficult to recognise in the thicker upper part of the sequence, represented by units 1-6 of Young (1969). If the new arthrodire skull described below from Broken River is of *serotinus* CZ age, as proposed by Sloan et al. (1995), it is still considerably more derived (see below) than any arthrodire from the Burrinjuck sequence. If correctly dated, this would indicate that derived features characterising the Middle-Late Devonian eubrachythoracid arthrodires had originated at least by late Emsian time.

To summarise, it is emphasised that there is no overlap in the arthrodire skull characters just discussed between the Burrinjuck and Broken River limestone sequences, even though the youngest occurrences in the former sequence are also the most derived taxa within the better-documented Burrinjuck arthrodire fauna. For the new taxon described below, this evidence would support either a latest Emsian age (but younger than the Burrinjuck sequence), or an Eifelian age as originally suggested by Prof. J.S. Jell.

ABBREVIATIONS

The specimen described below (prefix **ANU V**) is housed in the Earth and Marine Sciences Department, Australian National University, Canberra (GCY Vertebrate Collection). Standard abbreviations for placoderm dermal bones are used in the text and figures, and together with other morphological abbreviations are listed as follows:

anth, anterior nuchal thickening;
Ce, central plate;
cf.Ce, area overlapping Ce plate;
cf.M, area overlapping marginal plate;
cf.PM, area overlapping postmarginal plate;
cf.PtO, area overlapping postorbital plate;
cr.im, inframarginal crista;
csc, central sensory line canal;
d.end, openings of dermal tube for endolymphatic duct;
dep, depression;
gr.M, groove on Ce plate which received the edge of the marginal plate;
ifc.ot, otic branch of infraorbital sensory groove;
if.r, infranuchal ridge;
if.pt, infranuchal pit;
kb, knob-like thickening of inframarginal crista;
lcp, lateral consolidated part of skull roof;
llc, main lateral line sensory canal;
M, marginal plate;
mp, middle pitline;
mppr, posterior median process of nuchal plate;
Nu, nuchal plate;
oa.Ce, area overlapped by Ce plate;
oa.M, area overlapped by M plate;
oa.Nu, area overlapped by Nu plate;
orb, orbital notch;
Pi, pineal plate;
plpr, posterolateral process or lobe on Ce plate;
PM, postmarginal plate;
pmc, postmarginal sensory groove;
pnp, postnuchal process of paranuchal plate;
PNu, paranuchal plate;
pp, posterior pitline;
PrO, preorbital plate;
PtO, postorbital plate;
R, rostral plate;
soa, subobstantic area;
soc, supraorbital sensory canal;
th.end, endolymphatic thickening;
th.pre, pre-endolymphatic thickening;
tnth, transverse nuchal ridge or thickening;
vg, vascular grooves.

SYSTEMATIC PALAEONTOLOGY

Class PLACODERMI McCoy, 1848
Order ARTHRODIRA Woodward, 1891
Suborder BRACHYTHORACI Gross, 1932

Doseyosteus talenti gen. et sp. nov.

Name

From Dosey Creek, the type locality, and the Greek *osteus* (bone). The species name recognises

Professor John A. Talent, Macquarie University, who has had a long and distinguished career in Devonian research, including extensive work in the Broken River area of Queensland.

Diagnosis

A eubrachythoracid arthrodire in which the skull shows an embayed anterior margin of the nuchal plate resulting from overlap by the central plates, the central plates have strong posterolateral lobes separating the nuchal and paranuchal, and a mesial process of the marginal plate extends to the anterior angle of the paranuchal. Subobstantic area of skull extending onto marginal plate. Dermal bones smooth, or ornamented with fine tubercles.

Remarks

Since only the skull is known, and it is incomplete, several features characterising the derived subgroup 'Eubrachythoraci' are for the present inferred for this new taxon. Definition of the eubrachythoracid arthrodires is discussed by Carr (1991: 379-381) and Long (1995: 55). Thus *Doseyosteus talenti* gen. et sp. nov. is assumed to have had a T-shaped rostral plate, a posteriorly placed pineal plate separating the preorbitals, a dermal process of the preorbital plate forming the anterodorsal margin of the orbit, and trilobate central plates. The holotype shows a strongly developed posterior thickening of the skull roof, which in the midline is represented by the anterior nuchal thickening. This is much more prominent than the transverse ridge on the posterior margin of the nuchal plate, and is a derived feature seen in coccosteomorph and pachyosteomorph brachythoracids, but generally lacking in Early Devonian taxa, for example the genus *Cathlesichthys* from Burrinjuck, NSW (Young, in press a). The embayed anterior margin and inferred proportions of the nuchal plate, and the strong posterolateral lobe of the Ce plate, are resemblances to the Late Devonian taxa *Eastmanosteus* and *Golshanichthys*, but the former differs in having the posterior pitline well developed on the posterolateral lobe of the central plate, and both forms lack the mesial process of the marginal plate inferred for this new taxon.

Material

ANU V1026 (holotype), an incomplete skull preserved as two unconnected portions.

Locality and Horizon

Locality BRJ34 (University of Queensland locality L4054), Grid Reference 616 438, Burges 1:100 000 sheet; western bank of Dosey Creek, 750 m upstream from its junction with Broken River (J.S. Jell, letter of 17 April 1980; see discussion above). Horizon was described as the 'base of thick limestone lens in Broken River Formation', assigned to the Bracteata Formation (Sloan *et al.* 1995) or the 'Lomandra/Dosey Limestone, Broken River Group (Turner *et al.* 2000). Age: ?late Emsian - Eifelian (see discussion above).

Description

ANU V1026 represents a large part of the posterolateral region of a brachythoracid skull roof, preserved as two separate portions. The larger portion (Fig. 3A,D) includes parts of the Nu, PNu and Ce plates (Fig. 4A,B), and the right postmarginal corner of the skull is preserved as a separate portion (Figs. 3B,C, 4C,D). The specimen was extracted from the rock in six pieces, but they are well preserved, suggesting that it was broken up before incorporation in the sediment. The nuchal (Nu) plate is represented by most of its right half, including the midline, so its overall shape can be estimated. Midline length of the Nu is about 70 mm. It has an embayed posterior margin, with a prominent posterior median process (mppr, Fig. 4). Except for the posterior lateral corner the right lateral margin of the Nu plate is fairly well displayed on the external surface. The bone is fractured in its middle region, and shows anteriorly that it was both overlapped and underlapped by the central (Ce) plate, a condition also reported in *Holonema* (Miles 1971). Along the anterior margin of the plate a thin overlapping lamina of the Ce plate has broken away to reveal an extensive overlap area (oa.Ce, Fig. 4B). In unbroken condition the anterior margin of the Nu plate would have been deeply embayed (Fig. 5). On its visceral surface extensive contact faces for the central plates are developed in the normal manner (cf.Ce, Fig. 4A). Other features shown are the prominent infranuchal pits (if.pt) and ridge (if.r) and the transverse nuchal thickening or ridge (tnth).

Noteworthy is the strong development of the anterior nuchal thickening (anth), which is relevant to the question of the age of this specimen (see discussion above). This is a derived feature of brachythoracids, and in ANU V1026 is more pronounced than in any Emsian brachythoracid from the Burrinjuck fauna. These have Nu plates which are fairly flat in front of the infranuchal pits. This is the case even in a form like *Cathlesichthys*, which is derived in having a very strong transverse nuchal ridge (Young in press a). In posterior view ANU V1026 shows that the anterior nuchal thickening is more pronounced than the transverse nuchal ridge, the reverse of the condition in *Cathlesichthys*. This advanced character is also seen in most Middle-Late Devonian brachythoracids, such

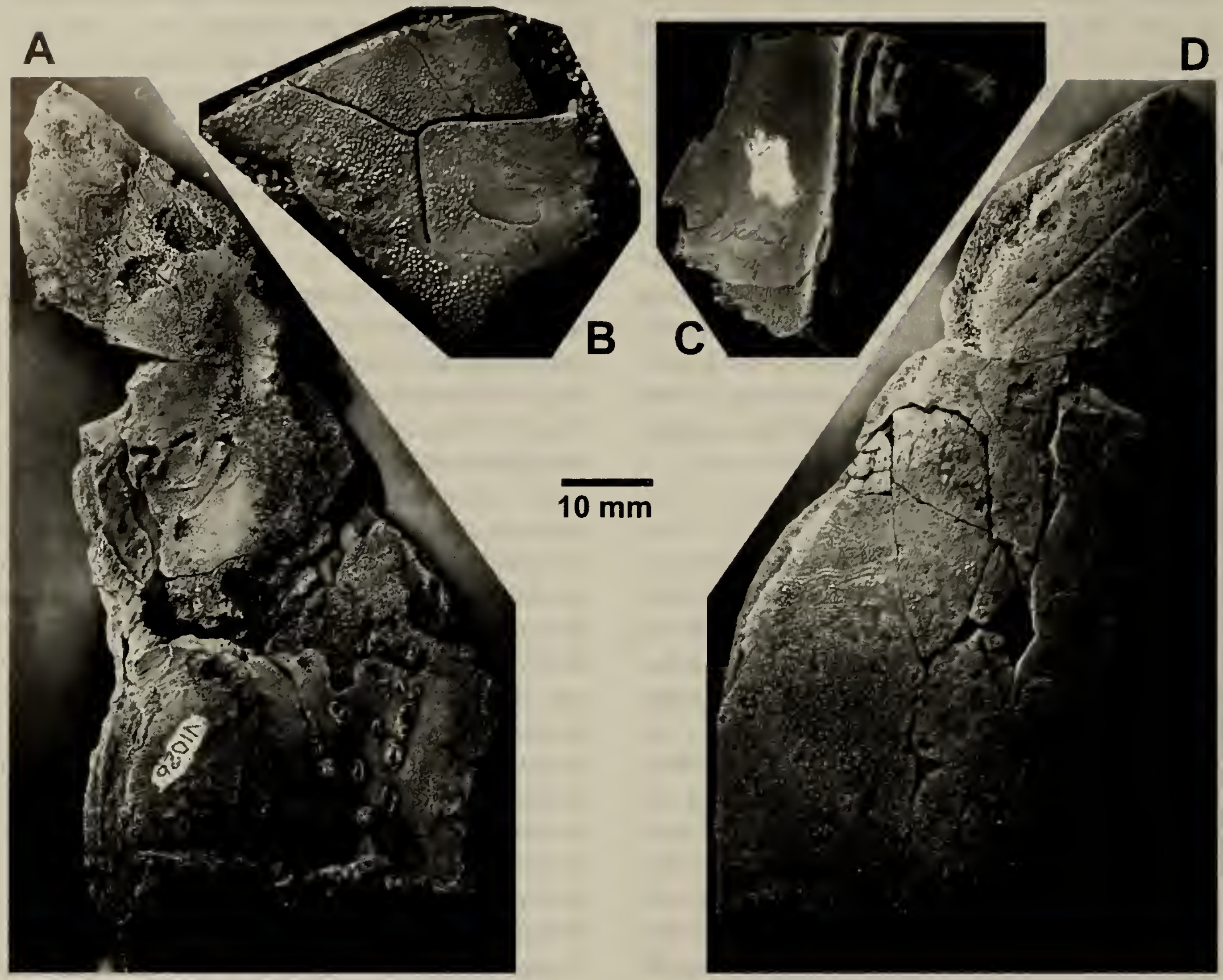

Figure 3. ***Doseyosteus talenti*** **gen. et sp. nov. Holotype (ANU V1026). Larger (A,D) and smaller (B,C) skull portions in external (B,D) and internal (A,C) views.**

as *Golshanichthys*, *Tafilalichthys*, and various Gogo forms (e.g. Lelièvre et al. 1981; Lelièvre 1991; Miles and Dennis 1979; Long 1988, 1995; Dennis-Bryan 1987). These taxa all resemble the giant Famennian form *Dunkleosteus*, where the 'posterior consolidated arch' of the skull roof ('PCA' of Heintz 1932: fig. 13) is a broad thickening running in front of the infranuchal pits, as the main transverse thickening of the skull. In contrast, in the Early Devonian form *Cathlesichthys* from Burrinjuck, the transverse nuchal ridge located behind the infranuchal pits forms the main thickening supporting the posterior skull margin.

The right paranuchal (PNu) plate of *Doseyosteus* gen. nov. is represented externally by an elongate portion including the mesial margin forming sutures with the Nu and Ce plates (PNu, Fig. 4B). There is also a small broken part of the postnuchal process (pnp). The PNu and Ce plates were also connected by a complex interlocking suture; a broken part around the anterior end of the PNu exposes an overlap area (oa.Ce, Fig. 4B), and the edge of a more extensive contact face is shown on the visceral surface (cf.Ce, Fig. 4A). The endolymphatic thickening forms a broad thickened area mesially (th.end), combining with the thickened portion of the Nu plate (anth). This thickened part of the skull is much more prominent than in primitive brachythoracids like *Buchanosteus* or *Taemasosteus* (White 1978; Young 1979). Along the broken edge of the specimen, maximum bone thickness (in the part enclosing the endolymphatic duct) is almost 15 mm, which is three times the bone thickness at the anterior preserved extremity of the Nu. The exoskeletal division of the right endolymphatic duct opens on the visceral skull roof surface at the anterior edge of the area of thickened bone (th.end), and is also visible on the broken margin of the specimen (d.end, Fig.4A).This is also an advanced character of the brachythoracid skull – in large Emsian brachythoracids

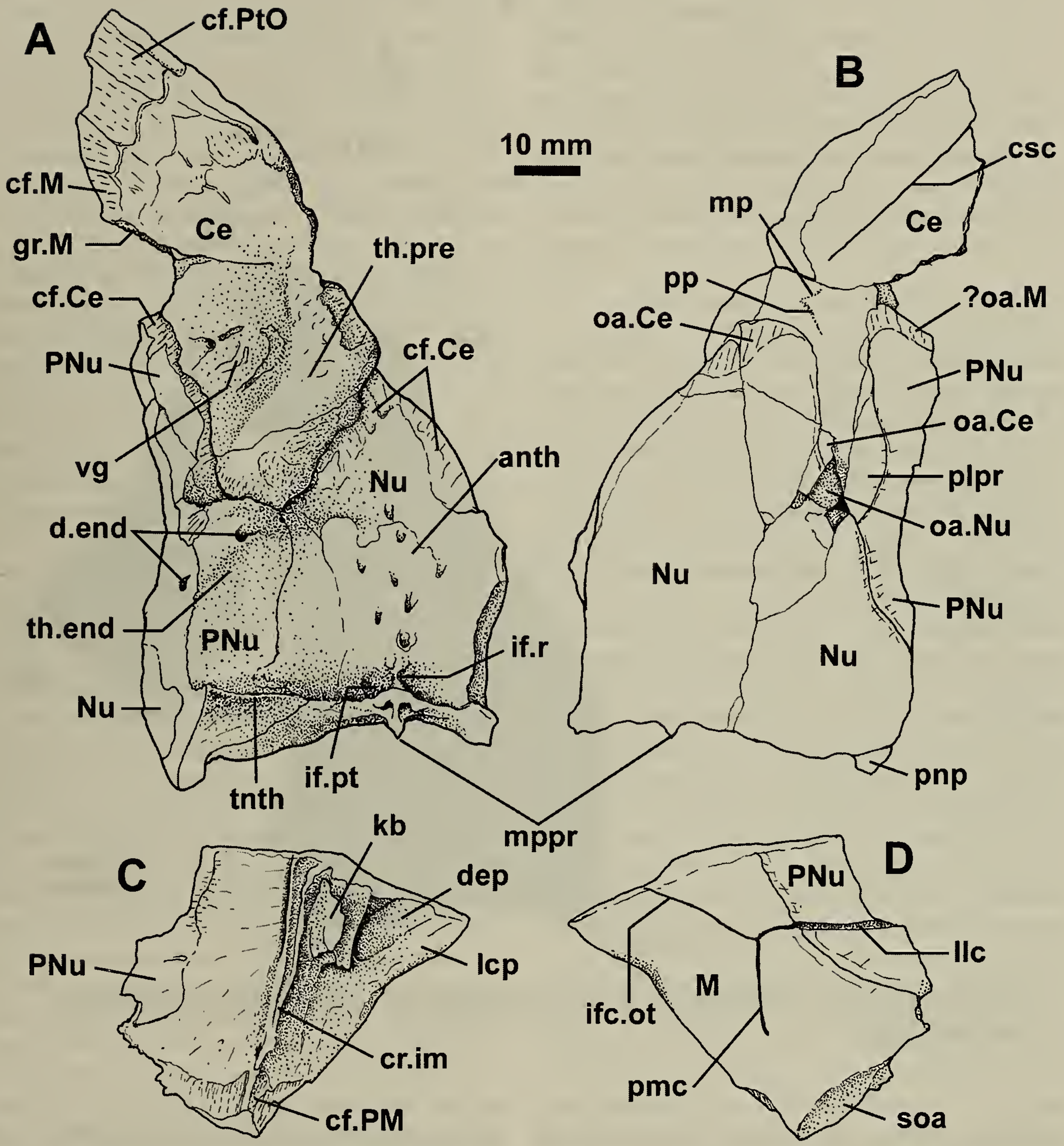

Figure 4. ***Doseyosteus talenti*** **gen. et sp. nov. Holotype (ANU V1026). A,B. Larger portion of skull in internal (A) and external (B) views. C,D. Smaller skull portion in internal (C) and external (D) views.**

from Burrinjuck the endolymphatic duct is not within the bone, but anteriorly forms a bony tube attached to or projecting from the inner surface of a much thinner PNu plate (Young in press a: figs. 3, 4, 7A, 9B). A similar condition occurs in *Holonema* from Gogo (J.A. Long, pers. comm.; Miles 1971: fig. 53).

The preserved part of the right Ce plate is crossed by a prominent sensory groove (csc), which must be the central sensory canal rather than the supraorbital sensory canal, because of its oblique orientation to the midline. Middle and posterior pitlines are represented by faint markings in the region of the ossification centre (mp, pp). Anterolateral and posterolateral margins of the preserved part of the Ce plate are somewhat fractured, but appear to approximate natural margins. The former is bevelled

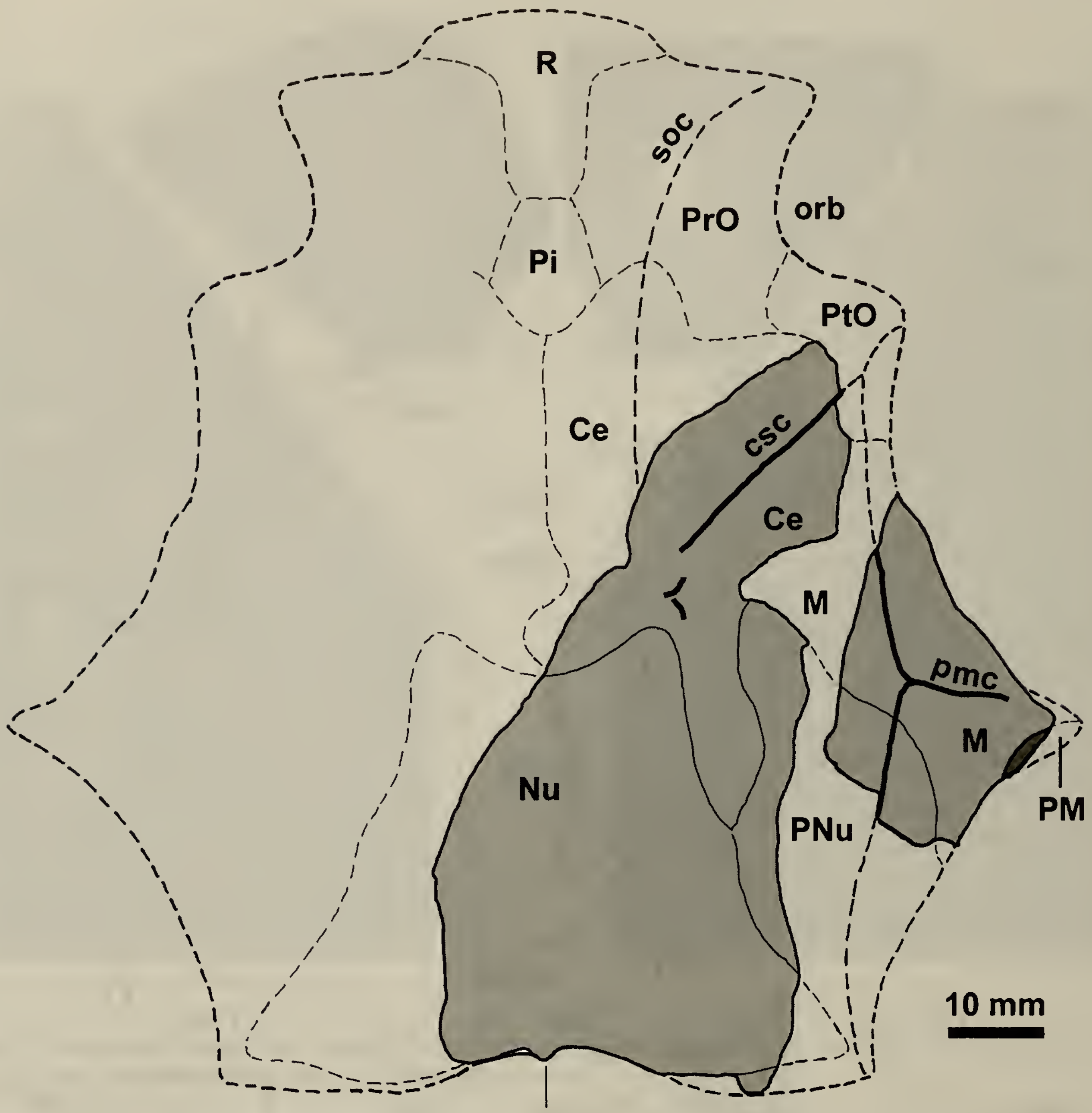

Figure 5. ***Doseyosteus talenti*** **gen. et sp. nov. Attempted skull roof reconstruction, preserved portions shaded.**

externally, and internally shows a contact face for the postorbital plate (cf.PtO), showing that it overlapped the PtO extensively, as in most other brachythoracids (e.g. Miles and Westoll 1968: fig. 2; Young 1979: fig. 1; 1981: fig. 5). *Holonema* is an exception in this respect (Miles 1971: fig. 12). Subdivisions of the posterior part of this contact face suggest that it also overlapped the marginal (M) plate (cf.M, Fig. 4A).

The posterolateral margin of the Ce plate is somewhat thicker, and carries a deep groove (gr.M) for an interlocking suture, the Ce plate providing external and internal laminae to enclose the margin of the contiguous bone. The nature of the preserved margins suggests that they approximate the suture position. Since the anterior end of the PNu is well shown on the specimen, and is most unlikely to have extended to this margin of the Ce plate, it seems that the intervening space must have been occupied by a mesial projection of the M plate (M, Fig. 5). This arrangement has not previously been recorded in brachythoracids. A similar but smaller process of the M intrudes the Ce plate of *Buchanosteus*, but this is some distance in front of the PNu (Young 1979: fig. 1).

There is a long posterolateral projection of the Ce plate partly separating the Nu and PNu plates (plpr, Fig. 4B), a feature seen in various other brachythoracids. An early example with this morphology is *Ulrichosteus* Lelièvre, 1982a from the Givetian of Germany, but this form has the Nu plate extending anteriorly in front of the PNu, whereas in *Doseyosteus* the PNu is slightly longer. *Ardennosteus* Lelièvre, 1982b also has a strong posterolateral lobe of the Ce, but this Famennian form differs in its sinuous interlocking sutures, broader transverse nuchal thickening, and coarse tubercular ornament. Development of a posterolateral lobe of the Ce is one of three features representing the 'trilobate' condition of the Ce plates (characters 13, 14, 21 of Carr 1991), a widespread condition amongst Middle-Late Devonian eubrachythoracids which has proved difficult to define. Internally this part of the Ce is more extensive, the overlapped portion extending back to the endolymphatic thickening, again as in other brachythoracids. The visceral surface of the Ce is gently concave laterally, with several shallow grooves (vg) resembling the vascular grooves described in *Holonema* by Miles (1971: fig.12). This depressed region is flanked mesially by the pre-endolymphatic thickening (th.pre), which forms a low broad ridge with a curved anteromesial orientation. The preserved anteromesial edge of the Ce plate is thickened and abraded (Fig. 3D).

Associated with this skull portion was a smaller part of the left preobstantic corner of the skull roof (Fig. 3B,C), assumed to have belonged to the same individual. The specimen includes part of the PNu and M plates (Fig. 4C,D), and is crossed by a section of the main lateral line (llc), and the infraorbital (ifc.ot) and postmarginal (pmc) sensory canals. Unlike forms such as *Coccosteus*, *Holonema* and *Buchanosteus* (Miles and Westoll 1968; Miles 1971; Young 1979), the M plate carries part of the subobstantic area (soa, Fig. 4D). A subobstantic area of similar extent is seen in the Gogo brachythoracid *Harrytoombsia* Miles and Dennis (1979: fig. 4), and in all plourdosteids *sensu* Long (1995). The PM plate is missing, but on the visceral surface there is a clear contact face for this bone (cf.PM, Fig. 4C). The visceral surface also shows the inframarginal crista to be strongly developed, dorsally as a very prominent irregular knob of bone (kb) separated posteriorly by a deep groove from the ventrally directed crista (cr.im), which itself carries a groove. The free ventral margin of the plate is thickened (lcp), representing the 'lateral consolidated part' of the skull, and a depression between the thickening and the inframarginal crista (dep) may correspond to similar structures in *Coccosteus* and *Buchanosteus* Young (1979: 314).

The external ornament on both specimens comprises fine tubercles in some areas, sometimes only faintly discernible on a generally smooth surface (Fig. 3B,D). The fine ornament is similar to that on the SO plate of *Atlantidosteus pacifica*, but that form displays affinity with the homostiid arthrodires in a range of features (Young 2003a), whereas the skull of *Doseyosteus talenti* gen. et sp. nov. lacks various specialised characters of *Homostius* and related forms (e.g. elongate Nu and PNu plates, small dorsal orbits, etc.). The reduced ornament also distinguishes this new form from various 'coccosteomorph' arthrodire remains known from the early Middle Devonian of northern Germany and the Baltic sequence (Otto 1997, 1999).

An attempted reconstruction of the skull roof of the new taxon based on available information is presented in Fig. 5. The skull could have been broader across the preobstantic corners than shown, since the gap between the two preserved portions is based only on a general alignment of sutures and sensory grooves. The anterior part of the skull is unknown, and restored shape of bones is generally based on various coccosteomorph arthrodires (e.g. Denison 1978: fig. 57). Advanced features depicted (T-shaped R plate, Pi plate separating PrO plates, trilobate Ce plates) are based on their co-occurrence with preserved skull characters in all other known taxa. They need to be confirmed with additional material. On the larger preserved portion, the breadth and anterior embayment of the Nu plate, and the marked posterior lobe of the Ce plate separating the Nu and PNu plates, are general resemblances to *Eastmanosteus* and *Golshanichthys*, as noted above. The M and Ce plates retain extensive contact to separate the PNu from the PtO, the assumed primitive condition for brachythoracids. In contrast, the plourdosteid arthrodires, which were widespread in the Late Devonian, and apparently replaced the largely Middle Devonian coccosteids (Long 1995), have a much enlarged PtO reaching back to contact both the Ce and PNu plates. In consequence the M plate is reduced in size, whereas in *Doseyosteus* gen. nov., although not completely preserved, the M plate was clearly a more extensive bone, which apparently shows a unique feature in the large mesial process embaying the Ce plate in front of the PNu.

In summary, this new but poorly known brachythoracid shows a range of advanced characters otherwise only seen in Middle or Late Devonian taxa, and it resembles the Frasnian taxa *Eastmanosteus* and *Golshanichthys* in several features which might indicate a close relationship. *Eastmanosteus yunnanensis* Wang, 1991 from the Givetian of China would otherwise be the earliest known member of this group (family Dinichthyidae). *Kiangyousteus* Liu, 1955, also from China (Givetian of Szechuan), may be another primitive dinichthyid (Denison 1978). Both taxa differ from the new form described here in their well-developed coarse tubercular ornament, presumably a primitive feature. *Doseyosteus talenti* gen. et sp. nov. displays an unusual shape of the M plate which is apparently unique to this new genus and species. More material, including the unknown trunk armour, which in brachythoracids comprises 17 separate bones, will clarify the affinities of this new taxon.

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Effects of Slashing and Burning on *Thesium australe* R. Brown (Santalaceae) in Coastal Grasslands of NSW

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Two studies examined the effects of burning and cutting on aspects of the population dynamics of a nationally vulnerable herb, *Thesium australe* on the central and north coast of NSW. Study sites were grasslands dominated by *Themeda australis* with scattered native shrubs (*Banksia integrifolia, Acacia sophorae)* and the exotic shrub *Chrysanthemoides monilifera* ssp. *rotundata.* In the first study (May 1995 to December 1996), *Thesium australe* occurred at high density ($1/m^2$) on exposed, long-unburnt headlands. In the second study, (December 1996 to December 1998), *Thesium australe* was at low density ($<1/100m^2$) on more protected and recently burnt hinterland. On the headlands, winter treatments had no significant effect on the survival, density and vigour of *Thesium australe.* In the hinterland, one year after summer treatments, seedling recruitment resulted in a higher density of *Thesium australe* in the cut plots than either the burnt or the control. Flowering and fruiting of *Thesium australe* were not restricted by season. After winter and summer treatments, flowering and fruiting occurred within 6 months and 1 year, respectively. Although exposed coastal headlands may require no management intervention to increase the occurrence of *Thesium australe*, except where the possibility of shrub invasion exists, a regime of slashing on less exposed hinterlands may be needed to reduce competition from *Themeda australis.* Further research is necessary to determine if slashing or burning the more protected hinterland would yield different results if carried out in seasons other than summer.

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KEYWORDS: fire, grasslands, headlands, mowing, slashing, *Thesium australe.*

INTRODUCTION

Although *Thesium australe* is a herb with a wide ecological tolerance, extending from tropical to alpine climates, it is confined to widely scattered locations in open woodlands and grasslands where *Themeda australis/ T. triandra* (Kangaroo Grass) is common in the understorey (Scarlett et al. 1994). On the north coast of NSW, *T. australe* occurs on grassy headlands used predominantly for passive recreation, often adjacent to residential areas (Griffith 1992; Fig. 1).

In south-eastern Australia, open woodland and grassland communities have largely been modified and fragmented by introduced grazers, cultivation and changed fire regimes (Stuwe and Parsons 1977; Scarlett and Parsons 1990; McDougall and Kirkpatrick 1994; Tremont and McIntyre 1994; Prober and Thiele 1995; Lunt 1997). As a consequence *T. australe* is rated as nationally vulnerable (Briggs and Leigh 1996) and vulnerable in NSW under Schedule 2 of the NSW Threatened Species Conservation Act 1995

Non-coastal, long-unburnt grasslands dominated by *Themeda australis / triandra*, have been shown to be species poor (Stuwe and Parsons 1977; Kirkpatrick 1986; McDougall 1989), largely as a result of the high competitive ability of this tussock grass (Groves 1974). With a general recent decline in fire frequency on coastal headlands (Griffith 1992), dominance by *Themeda australis* and the recruitment of native and exotic shrubs are potential threats to the survival of *T. australe* (Griffith 1992), although Cooper (1986) suggested that headlands exposed to salt-laden winds may be an exception. He cites the persistence of *T. australe* at Perpendicular Point, 20 years after fire, as an example.

Research on *Thesium alpinum* in Denmark found that it became extinct as a result of shading from trees (Lojtnant and Worsoe 1980). *Thesium australe* may be similarly sensitive. In coastal Victoria, an increase in native shrub and tree recruitment has been linked to a decline in fire frequency (Bennett 1994; McMahon et al. 1994; Lunt 1998a b). On the north coast of NSW, increased recruitment of native shrubs

Figure 1. Grassland habitat of *Thesium australe* at Look at Me Now Headland on the north coast of NSW.

and trees (*Acacia*, *Banksia, Allocasuarina* spp.) and an invasive exotic shrub, Bitou bush, (*Chrysanthemoides monolifera* ssp. *rotundata* have been observed (Dodkin and Gilmore 1985; Griffith 1987; Griffith 1992).

A number of studies have suggested a regime of regular burning and/or mowing to maintain species richness in grasslands and prevent shrub invasion (Groves 1974; Stuwe and Parsons 1977; Kirkpatrick 1986; McDougall 1989; Lunt 1990a, 1998b). Current information on the response of *T. australe* to fire in the field has been based on observations. While Leigh and Briggs (1989) suggest that survival and recruitment are unaffected by fire, Archer (1984) believed seeds were stimulated to germinate. In laboratory trials, Scarlett (pers. comm.) found that heat did not stimulate seed germination. There have been no studies on the effect of mowing or cutting on *T. australe* (Griffith 1992).

On coastal headlands and conservation reserves where burning or slashing grasslands may be used for conservation or hazard reduction purposes, it is important to establish their effect on native species. Two separate studies examined the effects of a single burning and a single cutting on aspects of the population dynamics of *T. australe*, namely:

1/ its survival, density, vigour and reproductive status where it occurred at relatively high density on long-unburnt, exposed headlands (winter treatments);

2/ its density and reproductive status where it was at very low density in a more protected and recently burnt hinterland (summer treatments).

These were not intended to be comparative studies and indeed the different timing and methods of treatment (see Materials and Methods), driven by the availability of resources, make this not possible anyway.

MATERIALS AND METHODS

The studies were located at several sites on the north and central coast of NSW (Fig. 2): Perpendicular Point (AMGR Easting 485600, Northing 6499200); Look at Me Now Headland (E 518000, N 6661300); and Old Bar Park (E 461300, N 6462800). Perpendicular Point and Look at Me Now Headland are within respectively, Kattang Nature Reserve (NR) and Moonee Beach NR. Both are managed by the New South Wales National Parks and Wildlife Service (NSW NPWS). Old Bar Park is managed by The Greater Taree City Council.

All three sites are used for recreation, predominantly by walkers. Although no motor vehicular access is allowed in the NRs, there was evidence of their past usage at Look at Me Now Headland, where at the time of this study wheel ruts were still very obvious. Vehicles were used on Perpendicular Point as recently as 1986 (Cooper 1986). There is some use of motor vehicles in Old Bar Park, but this is mostly on the pre-existing tracks and the airstrip (author's personal observations).

Perpendicular Point and Look at Me Now Headland are characterised by black headland soils, which are loamy soils high in organic matter (Parbery 1947). Yellow podzolic soils predominate at Old Bar Park (Long 1996). Aspects and slopes of the study sites varied. At Perpendicular Point the site was located on a north-western aspect with a slope of 9°, whilst at Look at Me Now Headland the site was on a more exposed southerly aspect with a slope of 6°. The site at Old Bar Park was flat.

The study sites were in grassland communities dominated by *Themeda australis*. Scattered shrubs at Perpendicular Point included native (e.g. *Acacia sophorae, Banksia integrifolia*) and exotic (e.g. *Chrysanthemoides monilifera* ssp. *rotundata*) taxa. Another nationally endangered herb, *Zieria prostrata* (Briggs and Leigh 1996) also occurred on a number of the headlands with *T. australe* (Griffith 1992; NPWS 1998).

Thesium australe was found at Perpendicular Point in 1957 (Cooper 1986) and at Look at Me Now Headland and Old Bar Park after 1992 (Griffith 1992). Although at relatively high density at Perpendicular Point and Look at Me Now Headland (approximately 1/m^2), at Old Bar Park it occurred mostly as very scattered plants (approximately <1/100 m^2). Thus, the focus at this latter site was more on recruitment

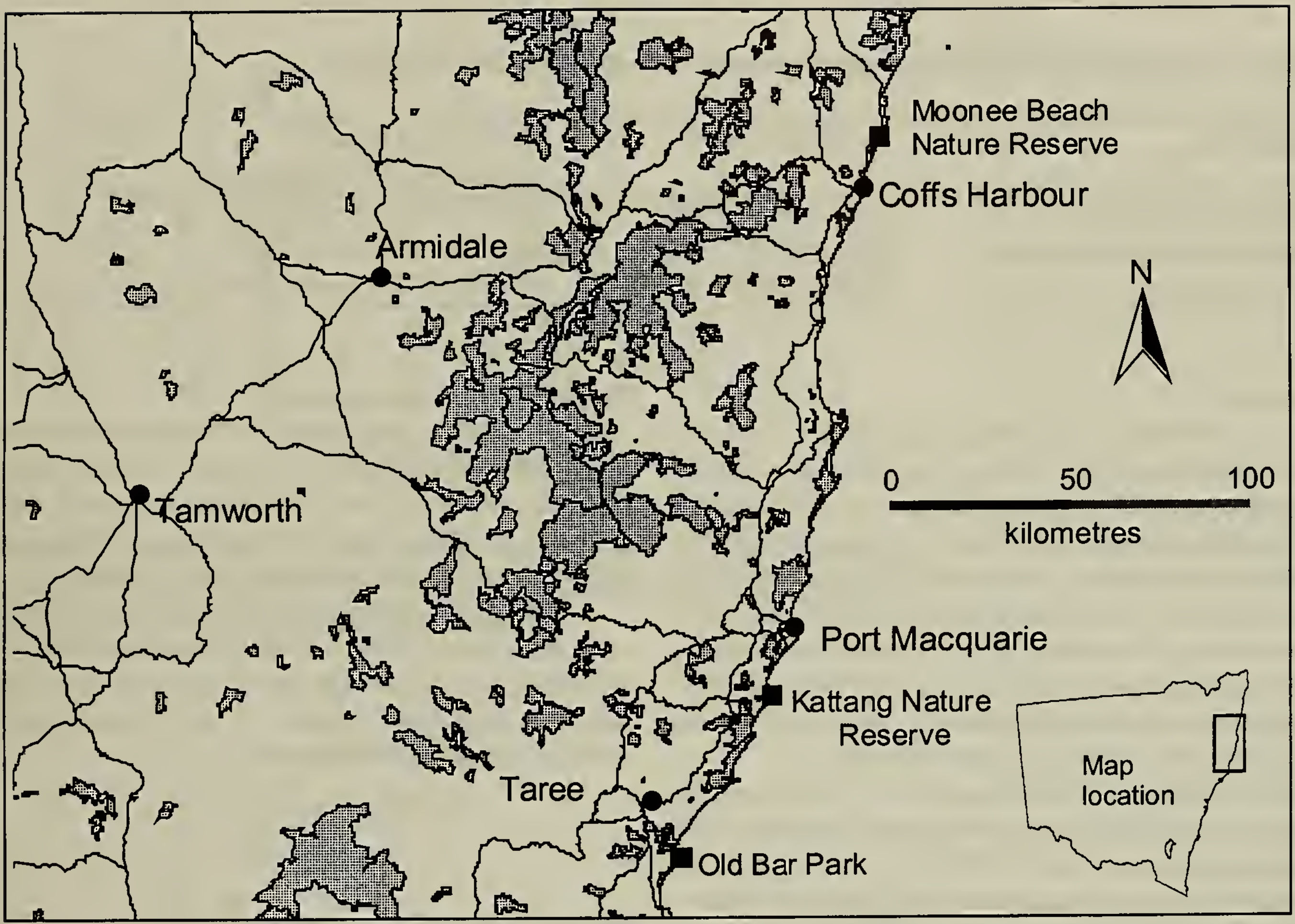

Figure 2. Locality of study sites within Moonee Beach NR (Look at Me Now Headland), Kattang NR (Perpendicular Point) and Old Bar Park on the north and central coast of NSW. Stippled areas represent estate managed by NSW National Parks and Wildlife Service.

responses to treatments.

There was little information on the fire history at the three sites. Griffith (1992) believed that Perpendicular Point may not have burnt for a considerable period of time. In 1985, Cooper (1986) believed that Perpendicular Point had not burnt for at least 20 years. There was no record of the last fire at Look at Me Now Headland. Old Bar Park was last burnt in 1991 by a low intensity fire (T. Cross pers. comm.). Approximately 1 year prior to this study Old Bar Park was slashed (S. Griffith pers. comm.), presumably for hazard reduction purposes.

Headlands (high density plants)

Treatments were applied in winter (July 1995) at Perpendicular Point and Look at Me Now Headland (Table 1). There were 15 replicate plots of each treatment (burnt, cut, control). Each treatment was allocated randomly to a 0.5 m x 0.5 m plot laid out in rows, over a total area of 75 m^2 at Perpendicular Point and 112 m^2 at Look at Me Now Headland. Plots were burnt using a gas burner. Because of the heavy dew, each burnt plot was subjected to heat for 5 minutes, until all of the grasses and herbs had been burnt and the bare ground had been heated and scorched. This simulated a high intensity burn (R. Bradstock pers. comm.). In the cutting treatment all grasses and herbs, including *T. australe* were cut to within 0.5 cm of the ground with shears.

At both sites, in all plots, individual *T. australe* plants were tagged and numbered and the fates of the original and emerged plants were surveyed over 1.5 years (Table 1). Data on plant vigour (number of stems/ plant; Perpendicular Point only) and the incidence of flowering or fruiting were also collected.

Analyses of the proportion of *T. australe* plants surviving 6 and 16 months after treatment, were made using Generalised Linear Modelling (GLIM), with a binomial error structure (Crawley 1993). The effects of the factors, treatment (burnt, cut, control) and site (Perpendicular Point, Look at Me Now Headland) and their interactions were examined using the chi-squared

Table 1. The dates of treatment applications and monitoring at the study sites.

Study Site	Treatment (date)	Monitoring Dates (pre and post treatment)
Perpendicular Point	burn, cut (26/7/95)	12/5/95, 14/2/96, 4/12/96
Look at Me Now Headland	burn, cut (27/7/95)	26/7/95, 11/2/96,18/12/96
Old Bar Reserve	burn, slash (16/12/96)	3/12/96, 2/12/97, 16/12/98

statistic.

The density of *T. australe* plants (0.25 m^{-2}) was examined using fully factorial analyses of variance (ANOVA) and Tukey tests for pairwise comparisons. The effects of treatments (burnt, cut, control) and sites (Perpendicular Point, Look at Me Now Headland) were examined at pre- and post-treatment dates (0, 6 and 16 months). To satisfy Cochran's test of homogeneity of variances, data were square root transformed and if necessary a more conservative level of significance ($p<0.01$) was applied (Underwood 1981).

Analyses of the vigour of *T. australe* plants (number of stems/plant) at Perpendicular Point were made using one-way ANOVAs. The effects of treatments (burnt, cut, control) were examined at pre- and post-treatment dates (0, 6 and 16 months). Data from all plots and cohorts within each treatment were pooled.

Hinterland (low density plants)

At Old Bar Park, where *T. australe* occurred at very low density, large plots were subjected to burning or slashing. Each treatment (burnt, slashed, control) was allocated to a 10 m x 10 m plot within an overall area of 40 m x 50 m. There were 2 replicates of each treatment. Whilst for practical purposes the two burnt plots were placed together, replicates of the cut treatment and control were randomly allocated to the remaining plots. Burning took place in hot conditions during summer (December 1996). Two plots were slashed the next day to within 5 cm of the ground. The resulting cuttings were removed from the plots. Individual *T. australe* plants were tagged, numbered and followed for 2 years (Table 1).

Although not measured quantitatively at Perpendicular Point and Look at Me Now Headland, observations indicated that the measurement of bare ground may be useful in discussing trends in the data. The cover of grasses/herbs and bare ground were measured at each census (≤ 5 replicates) in classes (1=1-10%, 2=11-20%,......,10=91-100%) within randomly allocated quadrats (1 m^2), located within each treatment plot. Rock cover was negligible.

Analysis of the density of *T. australe* plants in each plot (number/100 m^2) was made using fully factorial ANOVAs and Tukey tests for post hoc comparisons. The effects of the treatments (burnt, cut, control) were examined on each day of sampling.

Analyses of the cover classes of bare ground were made using a two-way fully factorial ANOVA. The effects of treatment (burnt, cut, control) and sampling date (pre-treatment, 1 and 2 years post-treatment) were examined.

RESULTS

Headlands (high density plants)

Site, but not treatment, had a significant effect on the proportion of plants surviving 6 and 16 months after the start of the study (Fig. 3). At both times survival was higher at Perpendicular Point than at Look at Me Now Headland (respectively $X^2=10$, df=1, $p<0.005$; $X^2=8.5$ df=1, $p<0.025$). By the end of the study between 80% and 100% of the original plants had suffered mortality.

Six months after the application of treatments there was no significant difference in the density of *T. australe* (0.25 m^{-2}) with respect to treatment and site ($p>0.05$; Fig. 4). Sixteen months after treatment, however, there was a significant effect of site ($F=4.72$, df = 1,84, $p<0.05$). Look at Me Now Headland had a higher density of plants than Perpendicular Point.

At Perpendicular Point there was no significant difference in the vigour of *T. australe* (number of stems/plant) with respect to treatment either prior to treatment, or 6 months and 16 months after treatment ($p>0.05$; Fig. 5). There appeared to be a general increase in plant vigour over this period.

Within 6 months of applying treatments at Perpendicular Point and Look at Me Now Headland, flowering and fruiting of original plants and new recruits of *T. australe* were recorded in summer (11 February 1996).

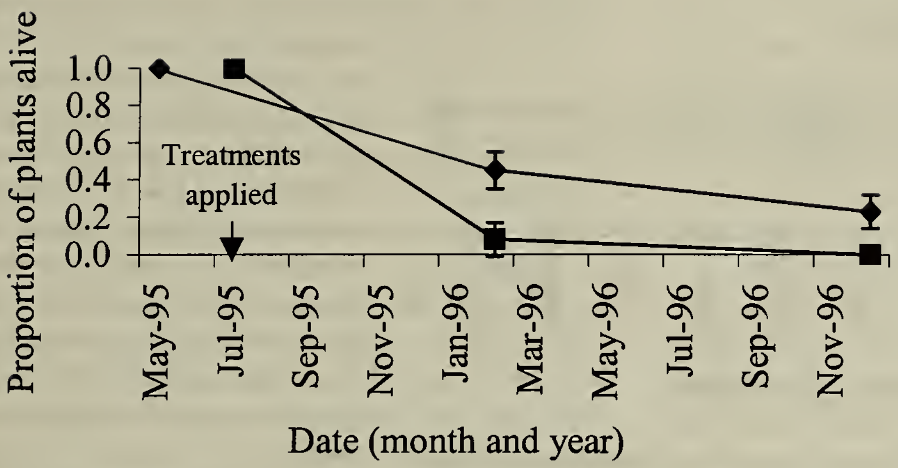

Figure 3. Proportional survival of *T. australe* (mean, se) at Perpendicular Point (◆) and Look at Me Now Headland (■) following treatments (pooled; burnt, cut, control) applied in July 1995.

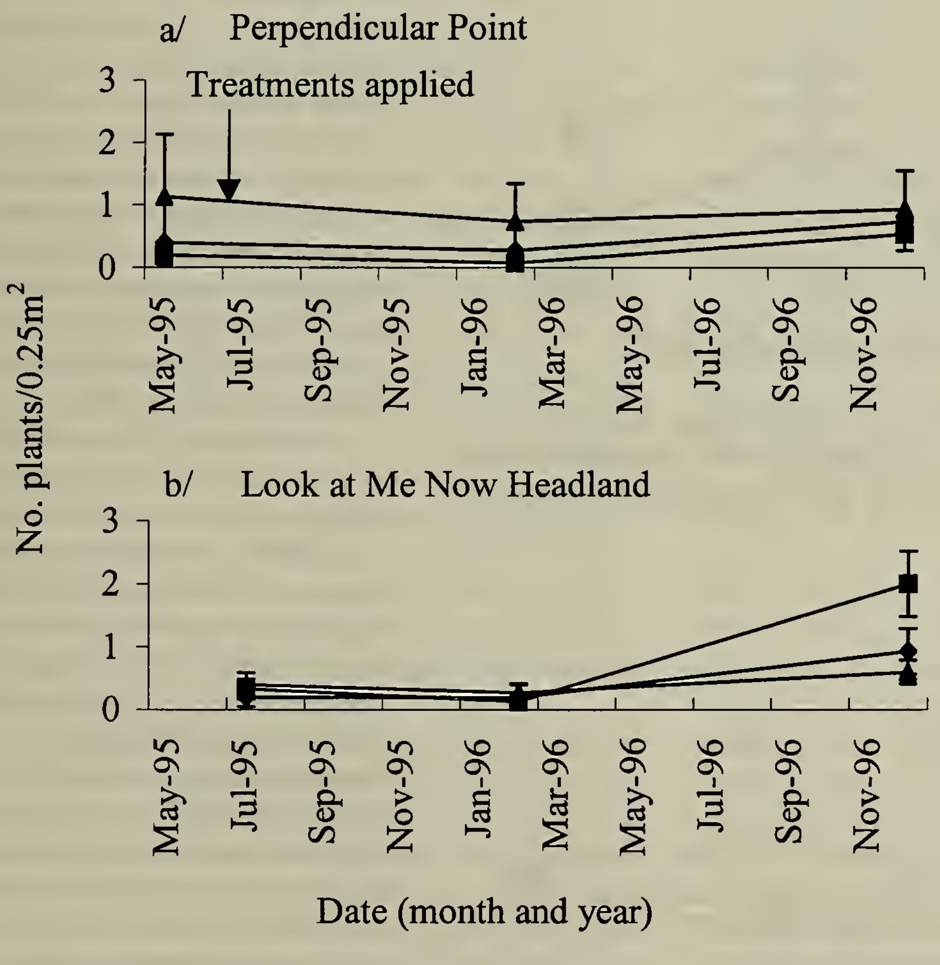

Figure 4. The density (mean, se) of *T. australe* plants (0.25 m^{-2}) before and after treatments at Perpendicular Point and Look at Me Now Headland. Treatments (burnt ◆, cut ■, control ▲) were applied in July 1995.

Hinterland (low density plants)

The density of *T. australe* plants at Old Bar Park was significantly affected by treatment 2 years after application. The slashed areas had a higher density than either the burnt or the control which were not significantly different from one another (F=15.5, df=2,3, $p<0.05$; Fig. 6). Pre-treatment and 1 year after treatment, there was no significant difference in the density of *T. australe* between treatments ($p>0.05$).

There was a significant interactive effect of treatment and time of sampling on the cover of bare ground at Old Bar Park (F=3.12, df=4, 27, $p<0.05$; Fig. 7). Whilst there was no significant difference between the plots prior to the imposition of treatments, 1 and 2 years (no significant difference) after burning, the bare ground was significantly higher than in the slashed or the control at any time (except burn at 2 years = pre-burn and cut at 2 years).

Within 1 year of treatment application, flowering and fruiting of new recruits of *T. australe* were recorded in summer (2 Dec 1998).

DISCUSSION

Headlands (high density plants)

Burning or cutting *T. australe* plants in winter, did not significantly affect their survival. Similarly, Leigh and Briggs (1989) found the survival of a population of *T. australe* near Canberra, was unaffected by a trial burn in autumn. Indeed, the

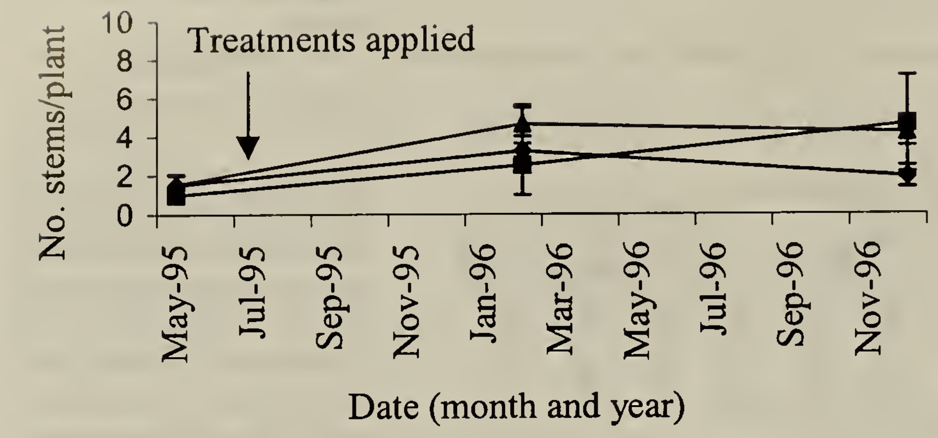

Figure 5. The size of *T. australe* plants before and after treatments at Perpendicular Point. Size was measured as the number of stems per plant (mean, se). Treatments (burnt ◆, cut ■, control ▲) were applied in July 1995.

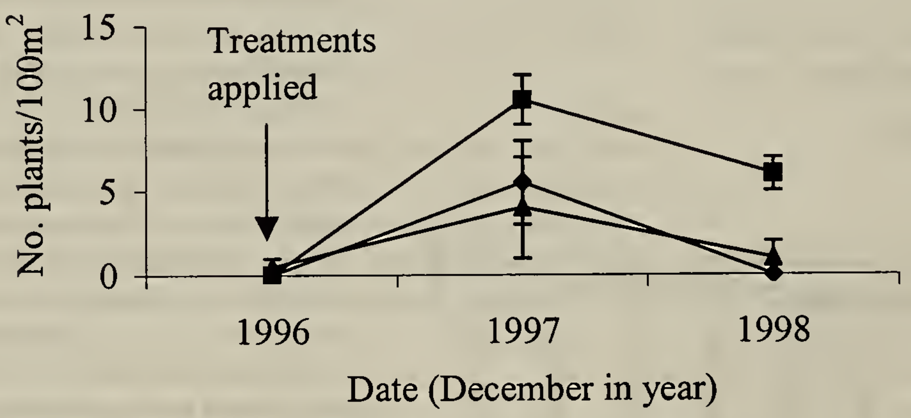

Figure 6. The density (100 m^{-2}) of *T. australe* plants (mean, s.e.) in the hinterland at Old Bar Park before and after treatments were applied (burnt ◆, slashed ■, control ▲). Treatments were applied in December 1996.

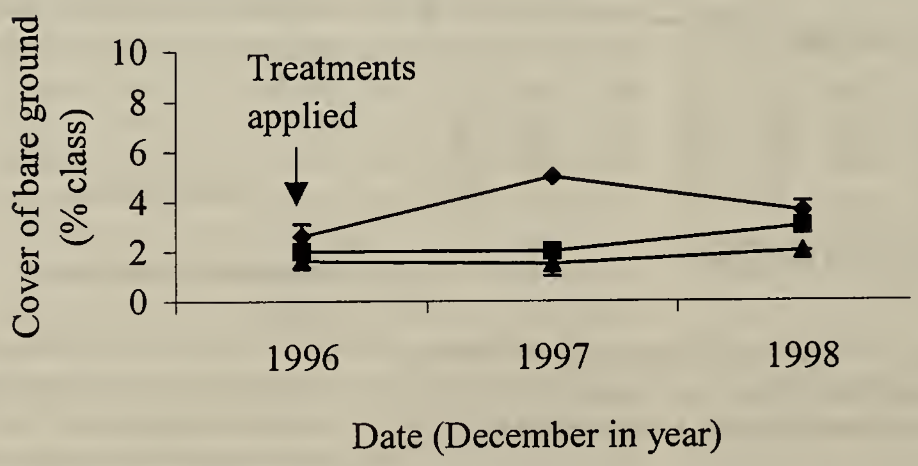

Figure 7. Cover classes (mean, se) of bare ground before and after treatments (burnt ◆, slashed ■, control ▲), in the hinterland at Old Bar Park. Treatments were applied in December 1996. Cover classes:1=0-10%.....10=11-100%.

existence of buds in the immediate vicinity of the soil surface (McIntyre et al. 1995) allows the species to resprout after disturbance. In subalpine and tableland climates, it is the habit of *T. australe* to die back to the rootstock during winter and resprout in spring (Cooper 1986; Archer 1987; Gross et al. 1995; Cohn 1999). This is not the case in coastal areas, where the species persists all year round (Cohn 1999).

Whilst a study on the southern tablelands of NSW (Leigh and Briggs 1989), describes *T. australe* as an annual or a biennial, this study suggests that the species may live longer on the coast. After 6 and 16 months, respectively, approximately 30% and 17% of plants were still alive. Since it is likely that these plants originated at least 9 months previously in spring, their ages were more than likely 15 months and 25 months, respectively. Certainly, Prober and Thiele (1998) believe it possible that *T. australe* lives longer in less severe climates.

Although there was no significant effect of treatment on the density of *T. australe*, there was a higher density at the more exposed Look at Me Now Headland than at Perpendicular Point 2 years after treatments. This agrees with Cooper's (1986) hypothesis that competition from Kangaroo Grass (*T. australis*) on exposed headlands is reduced by salt laden winds. It is also possible that the experimental burn, which was hotter than would be experienced naturally, even in extreme conditions (R. Bradstock pers. comm.), could have led to some mortality of *T. australe* seeds near the soil surface, thus reducing the effectiveness of this treatment. The small size of the plots may also have reduced treatment effectiveness. Finally, more time may have been required for the *T. australe* populations to respond to a reduction in competition brought about by the experimental treatments.

Thesium australe is able to grow and reproduce very quickly following disturbance in winter. In December, 6 months after burning or cutting, there was no significant difference in the vigour of plants in the treated plots and the control. At the same time resprouting plants and new recruits were flowering and beginning to fruit. Indeed, flowering and fruiting of *T. australe* at both Perpendicular Point and Look at Me Now Headland occurred throughout the year (Cohn 1999). By contrast, flowering and fruiting has been found to be seasonal at inland locations, occurring from spring to autumn (Stanley and Ross 1983; Briggs and Leigh 1985; Gross et al. 1995; Cohn 1999).

Hinterland (low density plants)

At the more protected Old Bar Park, where *T. australe* was mostly absent from the plots prior to treatment, summer slashing rather than burning led to significant seedling recruitment of *T. australe*, 2 years after treatment (Fig. 6). Although it is generally recognised that burning provides the bare ground for seedling establishment that slashing does not (Lunt 1990a), other factors seemed to be at play in this study.

The comparable cover of bare ground in all treatments at the time of the high numbers of *T. australe* in the slashed plots (Fig. 7), indicates that a reduction in grass height may have been responsible. In Victoria, Lunt (1990b) believed that selective grazing of tussocks to a height of 5 cm by rabbits and kangaroos may have contributed to the maintenance of species richness by reducing competition from perennial grasses. Thus, it is probable that a reduction in the height of the dominant species *Themeda australis* rather than an increase in bare ground, led to significant recruitment of *T. australe* seedlings in the slashed treatment.

Given that the post-fire conditions reduced competition from *Themeda australis*, it is curious that there was not a significant effect on *T. australe* numbers. In the same summer following burning, seedlings of *T. australe* were observed in these plots (S. Long pers. comm.). Their low numbers throughout the study, however, may have resulted from the more exposed conditions, reflected by higher cover of bare ground, experienced during the first and second summers (Fig. 7). In addition, *T. australe's* hemiparasitic dependence on other herbs and grasses, (Scarlett et al. 1994), may have made it difficult for *T. australe* to survive, given that its hosts were also recovering from the effects of the fire. Indeed summer 'dying back' of *T. australe* in times of water stress has previously been recorded by Leigh and Briggs (1989). Whilst older *T. australe* plants may have the resources to recover, seedlings, such as those observed in this experiment soon after the burning, may not have had that capability.

Management implications

The results from this study, coupled with the long-term persistence of *T. australe* on exposed headlands in the absence of active management (Cooper 1986; Griffith 1992), indicate that there is apparently no need for a change in this regime, except where shrub recruitment (native or exotic), may be competing with the survival of *T. australe*.

By contrast, in the more protected hinterlands, where *T. australe* also occurs, active management may be required to reduce competition from Kangaroo Grass (*T. australis*). Although, results from this study indicate that early summer slashing of a grassland (5 cm height) resulted in recruitment of *T. australe* plants, further research is required to determine if this is the most appropriate time of the year and method. Of particular concern is that disturbance of the summer growing Kangaroo Grass (*T. australis*) at this crucial time could result in the introduction of weed species (Griffith 1992). There is also a need to determine if burning outside summer, especially in autumn or early spring, would yield different results. This is important in the light of other work, which indicates that fire rather than mowing in grasslands is preferable to maintain species richness (Kirkpatrick 1986; Lunt 1991; James 1994).

If shrub encroachment becomes a threat to the survival of *T. australe,* studies have recommended various fire intervals of between 2 and 10 years to reduce dominance of native shrubs (Groves 1974; Lunt 1998b) or a regime of frequent fire and mechanical disturbance to reduce exotic shrub frequency (e.g. *Chrysanthemoides monolifera*; Kirkpatrick 1986). Although this study did not examine an appropriate disturbance interval for *T. australe*, its quick growth and reproductive development and its continued presence at Hat Head (S. Griffith pers. comm.), which has burnt every 2 to 4 years for the past 15 years (NSW NPWS Records), indicates it can apparently cope with a relatively frequent disturbance regime. Studies in Victoria (Scarlett and Parsons 1982, 1993) suggest that the absence of *T. australe* and other late-flowering species along railway lines has resulted from annual, late-season burning. Further research is required in coastal areas to determine an appropriate disturbance interval for the long-term conservation of *T. australe*.

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Trichromothrips veversae sp.n. (Insecta, Thysanoptera), and the Botanical Significance of Insects Host-specific to Austral Bracken Fern (*Pteridium esculentum*)

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Austral bracken fern, *Pteridium esculentum*, differs from its European counterpart in supporting one species of both thrips and aphid. The previously undescribed species of thrips, *Trichromothrips veversae* sp.n. (Thripidae), is widespread and locally abundant in southern Australia breeding on the youngest fronds of bracken but not on other ferns. It is unique among nearly 30 species of this Old World tropical genus in lacking long setae on the pronotum.

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INTRODUCTION

Common bracken fern is often considered to be a single, cosmopolitan species *Pteridium aquilinum* (Dennstaedtiaceae). In retaining this view, the major reference work on botanical nomenclature (Mabberley, 1997) recognised two subspecies, the nominate one from the Northern Hemisphere and Africa, and *P. aquilinum caudatum* from the Southern Hemisphere. In Australia, in contrast, Brownsey (1989) recognised three species of *Pteridium*: *P. aquilinum* introduced to a small area of South Australia in the Adelaide Hills; *P. revolutum* native to north-eastern Queensland but extending widely across New Guinea and South East Asia; and *P. esculentum* native to southern and eastern Australia but extending to South East Asia and the Pacific. More recently, Thomson (2000) has concluded from an extensive study of both structural and molecular characters that several of the *Pteridium* varieties distinguished worldwide, including *esculentum*, "might best be treated as species".

These differences in opinion concerning the botanical status of bracken fern are not without entomological significance. No species either of aphid (Homoptera) or of thrips (Thysanoptera) is known to live on bracken in Europe, where this plant is widespread and abundant and often an invasive weed. In contrast, the aphid species *Shinjia orientalis* (Mordwilko) (= *S. pteridifoliae* Shinji) has been reported widely on *Pteridium* from northern India and Japan to eastern Australia. Moreover, populations of bracken in eastern North America support another aphid species, *Mastopoda pteridis* Oestlund, and in western North America five aphid species in the genus *Macrosiphum* have been reported from *Pteridium* (V. F. Eastop, 2003 pers. comm.). If *Pteridium* were truly monotypic, comprising one worldwide panmictic species, then different populations might be expected to support similar, if not identical insect species. The description here of a new species of Thripidae that is widespread on bracken in Australia would thus appear to provide further support for the recognition of distinct species within this ubiquitous plant genus. Presumably these insects are reflecting diversity within the genus *Pteridium* that botanists have been reluctant to acknowledge.

The existence of this thrips species had been suspected for many years. In 1967, the wife of the eminent Australian insect ecologist H.G. Andrewartha, Hattie Vevers-Steele after whom the new species described below is named, drew the attention of one of us (LAM) to some specimens of a thrips species taken from bracken near Adelaide during her studies on Australian Thysanoptera (see Mound, 1996). The specimens were in poor condition, and efforts at that time to locate the species in the field were not successful. However, during the past 10 years this thrips has been found to be widespread across southern Australia, but breeding only in the curled apices of the youngest fronds of bracken. This species was listed by Shuter and Westoby (1992) from a population of bracken near Sydney as "Anaphothripinae gen. et sp.

indet", but is here recognised as a new species of the widespread Old World genus *Trichromothrips*. However, within that genus it exhibits one remarkably deviant autapomorphy – the absence of any long setae on the pronotum. This thrips has been found only on *Pteridium esculentum*, as defined by Brownsey (1998), even when this has been found growing in association with other ferns that are superficially similar, such as the closely related *Hypolepis muelleri* (Dennstaedtiaceae), or young specimens of the more distantly related tree fern *Dicksonia antarctica* (Dicksoniaceae). No thrips have been found on any species of *Hypolepis*, although *Scirtothrips frondis* Hoddle and Mound breeds abundantly on the youngest fronds of *Dicksonia* and has also been taken on a species of *Cyathea* (Hoddle and Mound, 2003).

Trichromothrips Priesner

Trichromothrips Priesner, 1930: 9. Type species *T. bellus* Priesner.

Bhatti (2000) has fully defined and reviewed this genus, synonymising the genus *Dorcadothrips* Priesner and providing a key to identify the 27 included species. Of these, 24 are from the Old World, between Africa and Queensland but mostly from South East Asia. The other three species, two from Hawaii and one widespread, may also have come originally from the Oriental region. The collection data for most of the species are probably not reliable indicators of the plants on which these thrips breed, but two species (*T. billeni* Strassen and *T. bilongilineatus* Girault) are associated with ferns (Mound, 2002b), and in the region of Japan around Tokyo and Yokahama, *T. alis* Bhatti or a closely related species is found on a species of *Polystichum* (Dryopteridaceae). Finally, three related genera of Thripidae are also associated with ferns, *Laplothrips* Bhatti, *Octothrips* Moulton and *Pteridothrips* Priesner (Mound, 2002b).

Members of these four genera are unusual in bearing a pair of setae on the dorsal apical margin of the first antennal segment. This character state is also shared by species in the following genera of Thripidae, although none involves fern-living species: *Alathrips* Bhatti, *Bregmatothrips* Hood, *Ceratothripoides* Bagnall, *Craspedothrips* Strassen, *Diarthrothrips* Williams, *Furcithrips* Bhatti, *Megalurothrips* Bagnall, *Mycterothrips* Trybom, *Odontothrips* Amyot and Serville, *Odontothripiella* Bagnall, *Pezothrips* Karny, *Sorghothrips* Priesner, *Watanabeothrips* Okajima, *Yoshinothrips* Kudo. Moreover, although the two species comprising the Oriental genus *Bathrips* Bhatti lack this pair of setae on the dorsal apical margin of the first antennal segment, they share many other character states with *Trichromothrips* species, and these two genera are possibly closely related.

Trichromothrips veversae sp.n.

Holotype ♀ macroptera, **Australian Capital Territory**, Woods Reserve, from young fronds of *Pteridium esculentum*, 6.xii.2002 (LAM 4244), in ANIC, CSIRO Entomology, Canberra.

Paratypes: 2 males, 17 females, same host, date and locality as holotype (Masumoto, Mound and Wells); 3 females at same locality but 16.i.1999 (LAM 3664).

Specimens excluded from the type series were collected widely in southern Australia, including Tasmania, Western Australia, New South Wales, and the Australian Capital Territory (see Distribution below).

Female macroptera

Colour: body yellow with orange pterothorax, ocelli bright red, antennae brown, abdomen with transverse light brown markings, wings shaded; colour of cleared and mounted specimens yellow, tergites shaded anteromedially and along antecostal line, IX and X shaded, mesonotum and metanotum weakly shaded; head and antennal segment I pale, segments III to VIII almost uniformly dark brown with extreme base of segments III to V slightly paler, II paler than segment III; all legs greyish brown; fore wing and scale greyish brown, but base of fore wing paler.

Structure: Head slightly wider than long, not prolonged in front of eyes, with a few transverse striae posteriorly on vertex (Fig. 1); ocellar setae I absent, setae III no longer than length of an ocellus and arising between anterior margins of posterior ocelli; three pairs of postocular setae, pairs I and II close together behind ocelli; ventral surface of head with 5 pairs of setae between compound eyes anterior to anterior tentorial pits; mouth-cone rounded, maxillary palpi 3-segmented; compound eyes without pigmented facets. Antenna 8-segmented (Fig. 3); forked sense-cones on III and IV exceptionally stout; segment I with 2 dorsal apical setae; II with weak microtrichia laterally only, III to VI with a few large microtrichia on dorsal and ventral surfaces; III with 2 dorsal and 2 ventral setae.

Pronotum medially with few or no lines of sculpture and 4 to 10 discal setae; posterior margin with five pairs of setae, none of which is longer than the discal setae. Mesonotum with weak transverse lines of sculpture, without campaniform sensilla near anterior margin, median pair of setae far ahead of posterior margin. Metanotum (Fig. 2) medially without sculpture and one pair of small setae far from anterior

Figure 1. *Trichromothrips veversae*, head and pronotum.

margin, without campaniform sensilla. Prosternal ferna not divided; mesothoracic sternopleural suture not developed; meso- and metasternum each with well-developed spinula. All tarsi 2-segmented. Forewing veinal setae short, less than half width of wing in length; first vein with about 8 setae near base and 2 (rarely 3) setae near apex; second vein with about 10 setae; posterior fringe cilia wavy; forewing scale with 4 marginal setae.

Abdominal tergites without posteromarginal craspeda or lateral ctenidia; tergites II to VIII without sculpture medially, lateral to seta S2 with about 7 anastomosing transverse lines bearing tuberculate microtrichia; tergite VIII without posteromarginal comb; tergite IX with paired campaniform sensilla posteromedially; tergite X undivided; pleurotergites without discal seta, sculpture similar to lateral areas of tergites. Sternites without discal setae; sternite II with two pairs of posteromarginal setae, sternites III to VII with three pairs, on VII all three pairs arise in front of sternal posterior margin.

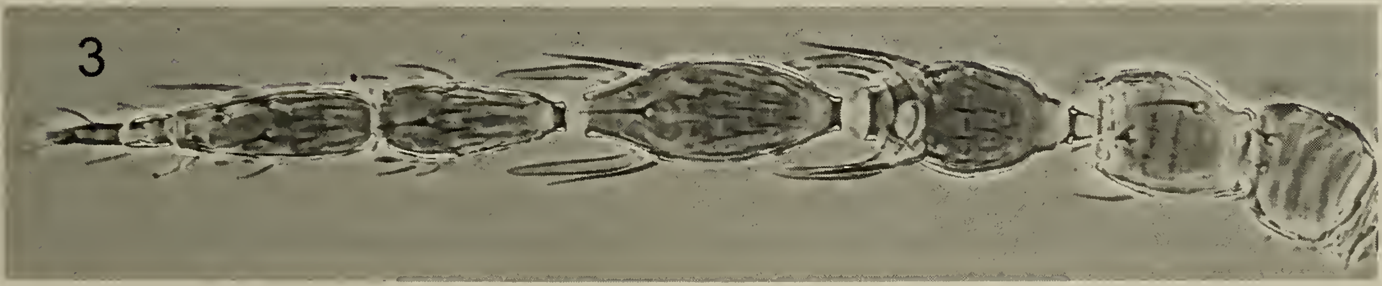
Measurements (holotype female in μm with small paratype female in parentheses): Body length 1400 (1100). Head, length 90 (85); width 125 (105). Pronotum, length 105 (95); width 160 (130); posteromarginal setae 15 (12). Forewing, length 750 (650). Antennal segments 25, 32, 50, 57, 40, 43, 10, 17 (25, 30, 40, 47, 35, 37, 7, 15).

Figure 2. *Trichromothrips veversae*, mesonotum and metanotum.

Male aptera

Colour paler than female. Structure similar to female except: forked sense-cones on antennal segments III and IV small and slender; one of three available males lacks ocellar setae II; mesonotum transverse with 4 or 5 setae near lateral margins; pleurotergal sutures weakly developed; tergite IX

Figure 3. *Trichromothrips veversae*, antenna.



posterior margin with horn-like paired drepanae extending beyond segment X; sternites III to VIII each with about 50 small, irregularly arranged, glandular areas, marginal setae arising at margin on all sternites.

Measurements (paratype male in µm). Body length 1000. Head, length 83; width 100. Pronotum, length 85; width 130; posteromarginal setae 15. Tergite IX drepanae length 60. Antennal segments 25, 30, 37, 40, 32, 37, 7, 15.

Larva II.

Colour pale yellow with red eyes, progressively developing extensive pale red hypodermal pigment in meso- and metathorax and anterior abdominal segments, body usually turning deep yellow progressively; major dorsal setae parallel-sided with bluntly square apices, 3 pairs on head, 6 pairs on pronotum, 3 pairs on abdominal tergites II – VIII, 2 pairs on IX, antennal II with 2 pairs of similar but smaller setae; setae on tergite X and abdominal sternites with apices acute; sternite IX posterior margin with row of about 30 small tooth-like tubercles.

Systematic relationships

Currently, this new species cannot be placed in any of the 10 species-groups distinguished by Bhatti (2000) within *Trichromothrips*, although it shares with the other 27 species the many character states listed by that author in his diagnosis of the genus. In contrast to those species, it lacks any long pronotal setae, the metasternal spinula is well developed not weak, and females have unusually stout antennal sense cones.

In Australia, only one other species of *Trichromothrips* has been collected in good numbers: *T. bilongilineatus* (Girault) from ferns near Gosford (Mound, 2002a). Of the other two members of the genus listed from Australia, the record of *T. xanthius* (Williams) is based on one female taken in quarantine in North America but labelled as coming from Australia (Mound, 1996), and *T. obscuriceps* (Girault) is known from a single sample apparently taken on *Crinum* lilies near Brisbane. The genus is probably well established in northern Australia, but only a few specimens are available, representing two further unidentified species, swept from grasses near Darwin. All of these species have long pronotal posteroangular setae.

The lack of long pronotal setae gives *T. veversae* the superficial appearance of an *Anaphothrips* species. This is another example of the ineffective supra-generic classification within the subfamily Thripinae, in which traditional subtribal names such as Aptinothripina do not refer to definable groups (Mound, 2002c), despite their continued use by various authors (eg. Vasiliu-Oromulu et al. 2001). There are several unrelated Thripinae genera in which species usually have two pairs of long pronotal setae, but in which one or more species have these setae no longer than the discal setae and are thus "Anaphothripine" in appearance, eg. *Dichromothrips* Priesner, *Pseudanaphothrips* Karny and *Thrips* Linnaeus.

The presence or absence of long setae on the pronotum was recognised as a poor indicator of phylogenetic relationships by Mound and Palmer (1981), who proposed a series of informal genus-groups within the Thripinae. These authors included *Scolothrips* Hinds, a genus of predatory thrips, in their *Dorcadothrips* genus-group (Mound and Palmer, 1981). *Scolothrips* species resemble some *Trichromothrips* species in general appearance, for example the pale slender body and bulging compound eyes, but they have very long ocellar setae and the pronotum bears six pairs of elongate setae. Moreover, the dorsal apical margin of the first antennal segment does not bear a pair of setae, and the mesosternal sternopleural sutures are weakly developed. The character state on the first antennal segment discussed above suggests that the genus-groups recognised by Mound and Palmer (1981) require reappraisal.

Distribution and host records

T. veversae has been found to be locally abundant in many parts of southern Australia, including Western Australia near Albany, Tasmania near Hobart, and various sites in South Australia (Adelaide Hills; Cox's Scrub south of Adelaide; and Kangaroo Island). It is abundant in the mountains of the ACT, and is widely distributed in the eastern forests of New South Wales from near Eden to the Blue Mountains. It possibly occurs even further north, but a sample taken from *Pteridium* at Beerwah, north of Brisbane, yielded only *Scirtothrips dobroskyi* Moulton (Hoddle and Mound, 2003). In a survey of the insects associated with bracken in New Guinea, Kirk (1977) does not mention thrips, but since thrips on ferns are associated only with very young fronds, or even with croziers that are not yet fully expanded, these minute insects are often difficult to detect. Similarly, the list given by Balick et al. (1978) of insects taken from ferns worldwide is based on a survey of published records, derived mainly from general collecting, and some of the thrips species listed are fungus-feeders, not fern-feeders. Mound (2002b) emphasised that several published records of thrips on ferns are based on single samples or even single specimens, and thus cannot be relied on to indicate a host relationship.

In Japan, the common species of bracken fern is considered also to represent *Pteridiium esculentum* and, as indicated above, the aphid species *Shinjia orientalis* has been recorded from this plant in Japan as well as Australia. However, searches for thrips on substantial populations of bracken in Japan, particularly near Narita City, have failed to discover *Trichromothrips veversae.*

At Crafers in the Adelaide Hills, South Australia, a substantial population of adults and larvae of *Thrips imaginis* Bagnall was found on bracken fronds in an open field during December 2002, together with a few larvae of *Trichromothrips veversae.* However, this seems to be a rare host association for the highly polyphagous Australian Plague Thrips.

At several sites, near Adelaide and on Kangaroo Island, larvae of *T. veversae* were found bearing up to 12 larval Eucharitidae (Hymenoptera). This is presumably a phoretic association, but no observations were made on associated ants, the probable host of these small wasps.

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Cyst Shell Morphology of the Fairy Shrimps (Crustacea: Anostraca) of Australia

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Timms, B.V., Shepard, W.D. and Hill, R.E. (2004). Cyst shell morphology of the fairy shrimps (Crustacea: Anostraca) of Australia. *Proceedings of the Linnean Society of New South Wales* **125**, 73-95.

Cyst shell morphology is described for 31 species and 4 genera of endemic Australian fairy shrimp. All four genera have distinctive cyst shell structure.

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KEYWORDS: *Branchinella,* branchiopodid, *Parartemia, Streptocephalus.*

INTRODUCTION

Australia has a relatively simple fauna of anostracans, with about 50 species in five genera. The list is currently growing because of recent discoveries, but presently stands at 29 described and one undescribed species of *Branchinella* (Thamnocephalidae), 8 described and 7 undescribed species of *Parartemia* (Parartemidae), two species of *Artemia* (Artemidae), and two described and perhaps many undescribed species of *Streptocephalus* (Streptocephalidae) and a species of an undescribed branchipodid genus (Timms, in press). All species are endemic, except for the two species of *Artemia*, one of which is certainly introduced and the other possibly introduced (see McMasters et al., in press; Timms, in press).

Little is known on the biology of Australian species (Timms, in press) and even less on detailed morphology and of adults and of cysts. Some general observations on cyst morphology of some species have been made by Herbert and Timms (2000), Timms (2002) and Timms and Geddes (2003).

Cyst shell morphology is much better known in fairy shrimp that occur in Europe, Africa and North America, and even the species occurring on some oceanic islands have been described. Political units from which cysts of fairy shrimp have been described include: France (Thiéry and Gasc 1991); Italy (Mura 1986, 1991b); California (Hill and Shepard 1997, Shepard and Hill 2001); Africa (Brendonck and Coomans 1994a, b; Brendonck and Riddoch 1997); and the Galapagos Islands of Ecuador (Brendonck et al. 1990). Some cyst studies have centered on certain families, genera, subgenera or species groups: streptocephalids and thamnocephalids (Mura 1992, DeWalsche et al. 1991); streptocephalids (Hamer et al. 1994a, b); *Branchinecta* (Mura 1991a), *Chirocephalus* (Mura 2001, Mura et al. 2002), *Linderiella* (Thiéry and Chanpeau 1988); *Streptocephalus* (Brendonck et al. 1992; Brendonck and Coomans 1994a, b; *Streptocephalus (Parastreptocephalus)* (Brendonck et al. 1992); the *Streptocephalus sealii* group (Shepard 1999). Cyst descriptions are also now becoming a common part of descriptions of new species. Identification keys based solely on cyst morphology have been produced for some branchiopod groups (Brendonck and Coomans 1994a, b; Shepard and Hill 2001; Thiéry and Gasc 1991). Cyst shell morphology is useful for identifying all genera so far examined, and many, but not all, species. Besides a perceived lack of differences between some related species, intraspecific variation associated with various predation levels (Mura et al. 2002, Dumont et al. 2002) and perhaps incipient speciation (Mura et al. 2002) may lead to confusion in some species.

Cyst morphology includes both external and internal structure (Hill and Shepard 1997). The outermost part of the shell is represented by the cortex surface. This surface often has spines, spinules, ridges of several different forms, buttons and ropey folds. The cortex is generally relatively thin. Below the cortex is the thick alveolar layer, which may be divided into various distinct sublayers. The alveolar layer is usually highly vacuolated with the vacuoles separated by curved or straight, solid struts of varying length. The innermost layer is the tertiary base which is relatively thin, solid and sometimes lamellate throughout. Often the interior surface has an impressed polygonal pattern. An additional cyst shell character is inpocketing of the entire shell. Inpocketing is only typical of cyst shells which have a fairly uniform alveolar layer.

The goal of this paper is to describe the external and internal structure of the cyst shell in as many as possible of the endemic Australian fairy shrimp fauna. This is a prerequisite for understanding differences between genera and species, as a base for understanding any intraspecific differences and for the construction of identification keys. Comparative information on *Artemia* cysts is provided by Shepard and Hill (2001) and is not repeated here. This is of overseas material, but is unlikely to be different from Australian cysts, as all *Artemia* cysts are the same (G. Mura, pers. com.; W. Shepard, pers. com.), except for *A. monica*, which does not occur here.

METHODS

Specimens of fairy shrimps were collected in the field and preserved in 70-80% ethyl alcohol and identified by BVT using Geddes 1981 and Timms in press. Females with the most mature looking cysts (those with a regular pattern all over the surface and which retain their sphericity) present in the brood pouch(es) were selected for dissection of the cysts. Cysts were removed and air-dried on filter paper. Then the cysts were mounted on SEM stubs using double-stick tape and gold-coated. A Zeiss DSM 940 SEM was used for measuring and photographing the cysts. Cyst morphology is described as in Hill and Shepard (1997), Shepard (1999) and Shepard and Hill (2001). Cyst stubbs have been stored in the private collection of REH.

RESULTS

Cysts were obtained for 31 of the 50 or so species of fairy shrimp known to exist in Australia. Those species include: *Branchinella affinis* Linder 1941, *B. arborea* Geddes 1981, *B. australiensis* (Richters 1876), *B. basipina* Geddes 1981, *B. buchananensis* Geddes 1981, *B. budjiti* Timms 2001, *B. campbelli* Timms 2001, *B. complexidigitata* Timms 2002, *B. dubia* (Schwartz 1917), *B. frondosa* Henry 1924, *B. hattahensis* Geddes 1981, *B. kadjikadji* Timms 2002, *B. lamellata* Timms and Geddes 2003, *B. longirostris* Wolf 1911, *B. lyrifera* Linder 1941, *B. nana* Timms 2002, *B. nichollsi* Linder 1941, *B. occidentalis* Dakin 1914, *B. pinnata* Geddes 1981, *B. proboscida* Henry 1924, *B. simplex* Linder 1941, *B. wellardi* Milner 1929, *Parartemia contracta* Linder 1941, *P. cylindrifera* Linder 1941, *P. informis* Linder 1941, *P. minuta* Geddes 1973, *P. zietziana* Sayce 1903, *Streptocephalus queenslandicus* Herbert and Timms 2000, *Streptocephalus n. sp.* a, *Streptocephalus n. sp. b* and an undescribed branchiopodid anostracan (all three from the Paroo, nw NSW-sw Qld - Timms and Sanders 2002 and Timms unpublished data. Two different cyst types were found in *Branchinella occidentalis*. Full descriptions could not be made for *Branchinella affinis, B. nana* and *Parartemia informis* due to the presence of only immature cysts. Locality and collection details for each species are listed in Appendix 1. The described Australian fairy shrimp species for which we did not have cysts include the following: *Branchinella apophystata* Linder 1941, *B. compacta* Linder 1941, *B. denticulata* Linder 1941, *B. halsei* Timms 2002, *B. insularis* Timms and Geddes 2003, *B. latzi* Geddes 1981, *B. tyleri* Timms and Geddes 2003, *Parartemia extracta* Linder 1941, *P. longicaudata* Linder 1941, *P. serventyi* Linder 1941 and *Streptocephalus archeri* Sars 1896.

The cyst characteristics of Australian anostracans are as follows.

Family Parartemidae

Parartemia contracta Linder

Cyst shape spherical (Fig. 1). Cyst size 250-275 µm (mean = 263.3; n = 10). External surface with some inpocketing, adjacent inpockets separated by indistinct ridges; individual cysts with 2-6 inpockets; surface smooth. Alveolar layer (Fig. 2) uniform; short struts; vesicles small rounded and subequal. Tertiary layer thin.

Parartemia cylindrifera Linder

Cyst shape spherical (Fig. 3). Cyst size 204-225 µm (mean = 214.6; n = 10). External surface with some inpocketing; adjacent inpockets separated by ridges; individual cysts with several inpockets each; surface smooth. Alveolar layer uniform, mostly solid (Fig. 4). Tertiary layer thin.

Parartemia informis Linder

Immature cyst shape spherical. Cyst size 162-176 µm (mean = 167.5; n = 10).

Parartemia minuta Geddes

Cyst shape spherical (Fig. 5). Cyst size 180-232 µm (mean = 208.0; n = 30). External surface with inpocketing; adjacent inpockets separated by ridges; individual cysts with several inpockets each; surface smooth. Alveolar layer uniform and solid (Fig. 6). Tertiary layer thin.

Parartemia zietziana Sayce

Cyst shape spherical to hemispherical (Figs. 7-8). Cyst size 180-208 µm (mean = 192.7; n = 11). External surface with inpocketing; inpocketing usually at one end; adjacent inpockets separated by ridges; ridges usually with sloping walls and rounded tops; surface smooth. Alveolar layer uniform and solid (Fig. 9). Tertiary layer thin.

Family Branchiopodidae

undescribed branchiopod genus and species

Cyst shape very irregularly spherical (Fig. 10), with projecting flanges that interlock with those of other cysts binding the cyst mass together (Fig. 11). Cyst diameters 208-250 µm (mean = 229.7; n = 20). External surface with ridges defining irregular polygons; intersecting ridges often extending as flanges; entire surface covered with shallow, rounded to polygonal depressions; polygon size variable and larger on flanges and ridges (Fig. 12). Cortex relatively thick (» 2 µm); one layer of short columns, columns parallel to each other and perpendicular to the surface. Alveolar layer (Fig. 13) thin; with small and uniform vesicles. Tertiary base thin.

Family Streptocephalidae

Streptocephalus queenslandicus Herbert and Timms

Cyst shape tetrahedral (Fig. 14-15); cyst size 169-208 µm (mean = 195; n = 20). External surface with ridges dividing surface into 4 triangular faces; ridges each with 2 longitudinal grooves in middle half producing 3 short ridge crests; intersecting ridges flare outward; triangular faces gently convex with 1 or 2 small bumps midface; surface granular. Alveolar layer (Fig. 16) with 2 sublayers; inner sublayer with short straight struts and medium-sized vesicles and hollows; outer sublayer uniform and solid; vesicular layer extends outward into ridge intersections. Tertiary layer thin.

Streptocephalus n. sp. a (locality: Pine Tree Pool, Budgerie Paddock, Bloodwood Station, 130 km NW of Bourke, NSW)

Cyst shape tetrahedral (Fig. 17); cyst size 254-300 µm (mean = 283.0; n = 20). External surface with ridges dividing surface into 4 triangular faces; ridges with nearly vertical sides, top rounded (Fig. 18), middle half of ridge along each face with a series of large punctae on each side, intersecting ridges flare outward; triangular faces flat to convex; surface bumpy. Cortex thick (2-3 µm). Alveolar layer (Fig. 19) with 2 sublayers; inner sublayer with thin short struts defining variably-sized, interconnecting vesicles; outer sublayer uniform and solid. Tertiary layer thin.

Streptocephalus n. sp. b (locality: Box Hole, on road 3 km south of homestead, Currawinya National Park, SW QLD)

Cyst shape tetrahedral (Fig. 20); cyst size 240-268 µm (mean = 249.3; n = 20). External surface with ridges dividing surface into 4 triangular faces; ridges each with 2 longitudinal grooves in middle producing 3 short ridge crests (Fig. 21); intersecting ridges producing rounded corners; triangular faces depressed, flattened, with small bumps midface; surface mildly bumpy. Alveolar layer (Fig. 22) vesicular; inner vesicles smaller; vesicles under ridges larger. Tertiary layer thin.

Family Thamnocephalidae

Branchinella affinis Linder

Cyst shape spherical (Fig. 23). Cyst diameter 95-134 µm (mean = 113.2; n = 20). External surface with steep-walled, arcuate ridges defining pinched polygons.

Branchinella arborea Geddes

Cyst shape spherical (Fig. 24). Cyst size 183-201 µm (mean = 191.6; n = 10). External surface with ridges defining flat-bottomed polygons; ridges straight-sided, surface covered with small punctae (Fig. 25). Alveolar layer (Fig. 26) with 2 sublayers; inner sublayer with small subequal vesicles; outer sublayer with long struts and large hollows. Tertiary base thin.

Branchinella australiensis (Richters)

Cyst shape spherical (Fig. 27). Cyst size 197-222 µm (mean = 213.5; n = 10). External surface with ridges defining polygons; ridges straight-walled, top pinched into a bead running along ridge, bead with pores (Fig. 28); polygons with flat bottoms. Alveolar layer (Fig. 29) with variably-sized vesicles; inner vesicles usually smaller than outer ones. Tertiary base thin.

Branchinella basipina Geddes

Cyst shape spherical (Fig. 30). Cyst size 225-275 µm (mean = 253.5; n = 10). External surface with ridges defining pinched polygons; ridges with sloping sides, tops evenly rounded; polygons with concave bottoms; surface rugose. Alveolar layer (Fig. 31) with small, subequal vesicles. Tertiary base thin.

Branchinella buchananensis Geddes

Cyst shape spherical (Fig. 32). Cyst size 204-232 µm (mean = 217.9; n = 10). External surface with ridges defining pinched polygons; ridges with sloping sides; polygons with concave bottoms; surface rugose. Alveolar layer (Fig. 33) with 2 sublayers; inner sublayer with small subequal vesicles; outer sublayer with long branching struts and large unequal vesicles. Tertiary base thin.

Branchinella budjiti Timms

Cyst shape spherical (Fig. 34). Cyst size 141-155 µm (mean = 144.7; n = 23). External surface with sinuous ridges defining tightly pinched polygons; ridges steep-sided with rounded tops; polygons with sinuous valley-like bottoms; surface slightly bumpy. Alveolar layer (Fig. 35) with 2 sublayers; inner layer with small vesicles; outer sublayer with long parallel struts and large hollows. Tertiary layer thin.

Branchinella campbelli Timms

Cyst shape spherical (Fig. 36). Cyst size 162-194 µm (mean = 172.3; n = 20). External surface with broad ridges defining pinched polygons; ridges with sides sloped to vertical, ridge tops very broad; surface scaley. Alveolar layer (Fig. 37) thick, with small to moderate sized vesicles. Tertiary layer thin.

Branchinella complexidigitata Timms

Cyst shape spherical (Fig. 38). Cyst size 211-307 µm (mean = 251.0; n = 40). External surface with ridges defining irregular polygons; ridges narrow, steep-sided, midline of ridges with sharp-pointed projections (Figs. 39-40); polygons with bottom flat to concave; surface smooth to scaley and porous. Alveolar layer (Fig. 41) thin; small to medium sized circular vesicles. Tertiary base thin.

Branchinella dubia (Schwartz)

Cyst shape spherical (Fig. 42). Cyst size 187-215 µm (mean = 197.1; n = 32). External surface with ridges defining polygons; ridges straight, steep-walled and narrow; polygons with bottoms flat to slightly concave; surface covered with short wrinkles, pores abundant (Fig. 43). Alveolar layer (Fig. 44) with 2 sublayers; inner sublayer with small rounded subequal vesicles; outer sublayer with long sometimes branching struts and large hollows. Tertiary base thin.

Branchinella frondosa Henry

Cyst shape spherical (Fig. 45). Cyst size 185-211 µm (mean = 196.1; n = 10). External surface with ridges defining polygons; ridges with sloping sides, tops rounded; polygons with bottom flat to slightly concave; surface smooth. Alveolar layer (Fig. 46) with 3 sublayers; inner sublayer with small vesicles; middle sublayer with long sometimes branching struts and large hollows; outer sublayer with medium-sized vesicles. Tertiary base thin.

Branchinella hattahensis Geddes

Cyst shape spherical (Fig. 47). Cyst size 254-289 µm (mean = 268.9; n = 20). External surface with ridges defining polygons; ridges with steep sloping sides, ridge tops with a sinuous bead and sharp-pointed and sometimes recurved projections (projections sometimes with film between) (Figs. 48-49); polygons with bottoms flat to slightly concave; surface strongly rugose or bumpy. Alveolar layer (Fig. 50) with 2 sublayers; inner sublayer with small- to medium-sized rounded vesicles; outer sublayer with narrow curving struts and large hollows. Tertiary base thin.

Branchinella kadjikadji Timms

Cyst shape spherical (Fig. 51). Cyst size 254 µm (n = 2). External surface with ridges defining polygons; ridges steep-sided and sinuous, tops with rounded bead; polygons irregularly shaped, bottoms flat; surface smooth (Fig. 52). Alveolar layer (Figs. 53-54) with at least 2 sublayers; outer sublayer with medium-sized rounded vesicles; next sublayer inside with short struts and large hollows. Tertiary base not visible in available cross-sections.

Branchinella lamellata Timms & Geddes

Cyst shape spherical (Fig. 55). Cyst size 124-180 µm (mean = 147.6; n = 31). External surface with ridges defining polygons; ridges with sloping sides and rounded tops; polygons irregular and highly pinched, bottoms concave; surface bumpy. Alveolar layer (Fig. 56) with narrow struts and very large hollows. Tertiary base thin.

Branchinella longirostris Wolf

Cyst shape spherical (Fig. 57). Cyst size 264-300 -µm (mean = 276.9; n = 29). External surface with ridges defining polygons; ridges very narrow, not always connecting to other ridges, ridge junctions extended into spines with tips that are bifid, trifid or recurved (Fig. 58); polygons with concave bottoms; surface bumpy to scaley. Alveolar layer (Fig. 59) mostly hollow with very narrow struts. Tertiary base thin.

Branchinella lyrifera Linder

Cyst shape spherical; inpocketing common (Figs. 60). Cyst size 158-183 µm (x = 171.5; n = 20). External surface with numerous short flat-topped columns, columns often connected by ridges; ridges of variable widths (Figs. 61-62). Alveolar layer solid (Fig. 63). Tertiary base thin.

Branchinella nana Timms

Immature cyst shape spherical. Cyst size 144-158 µm (mean = 152.3; n = 19).

Branchinella nichollsi Linder

Cyst shape spherical (Fig. 64). Cyst size 187-247 μm (mean = 202.3; n = 30). External surface with ridges defining polygons; ridges narrow, steep-sided, with zig-zag patterns, tops with narrow bead (Fig. 65); polygons tightly pinched, bottoms flat to concave; surface slightly bumpy. Alveolar layer (Fig. 66) mostly hollow, with very thin struts. Tertiary base thin.

Branchinella occidentalis Dakin (two cyst morphs)

Type I cyst: Cyst shape spherical; inpocketing common (Fig. 67). Cyst size 257-328 μm (mean = 283.5; n = 20). External surface with narrow sinuous ridges defining small, irregular, pinched polygons; ridges steep-sided and short. Alveolar layer (Fig. 68) not well developed. Tertiary base not seen.

Type II cyst: Cyst shape spherical (Fig. 69). Cyst size 550-571 μm (mean = 565.3; n = 20). External surface with ridges defining rounded depressions; ridges narrow except where intersecting, sides vertical, tops flat; rounded depressions with bottoms slightly concave and extremely porous (Fig. 70); surface smooth. Alveolar layer (Fig. 71) with 3 sublayers; inner sublayer with small equal rounded vesicles; middle sublayer with few struts, mostly open hollows, pores connecting to outside; outer layer with stringy vermiform struts, connecting to inner side of external surface. Tertiary layer thin.

Branchinella pinnata Geddes

Cyst shape spherical (Fig. 72). Cyst size 173-190 μm (mean = 181.1; n = 10). External surface with ridges defining pinched polygons; ridges with sides nearly vertical, tops rounded; polygons irregular in shape, bottoms flat to concave; surface very bumpy. Alveolar layer (Fig. 73) with 3 sublayers; inner sublayer with small rounded subequal vesicles; middle layer with long branching struts and large hollows; outer sublayer with medium-sized irregularly shaped vessicles. Tertiary layer thin.

Branchinella probiscida Henry

Cyst shape spherical (Fig. 74). Cyst size 158-187 μm (mean = 174.9; n = 19). External surface with ridges defining polygons; ridges vermiform with sides nearly vertical, tops smooth and rounded; polygons irregular in shape, some pinched, bottoms slightly concave and with pores; surface generally smooth (Fig. 75). Alveolar layer (Fig. 76) without distinct sublayers; struts usually short; vesicles irregular in shape and variable in size. Tertiary layer thin.

Branchinella simplex Linder

Cyst shape spherical (Fig. 77). Cyst size 144-201 μm (mean = 176.4; n = 32). External surface with ridges defining polygons; ridges with sides slightly sloping to vertical; polygons pinched, bottoms concave; surface smooth with irregularly spaced punctae. Alveolar layer (Fig. 78) uniform; short branching struts and medium-sized hollows. Tertiary layer thin.

Branchinella wellardi Milner

Cyst shape spherical (Fig. 79). Cyst size 158-176 μm (mean = 168.4; n = 30). External surface with ridges defining polygons; ridges narrow and steep-sided, tops sharp except broader at intersections (Fig. 80); polygons irregular in shape, some pinched, bottoms concave to flat; surface punctate to porous. Alveolar layer (Fig. 81) uniform, thick; short struts with small interconnected vesicles. Tertiary layer thin.

DISCUSSION

Australia is currently experiencing a surge of interest in its fairy shrimps, as indicated by the large percentage of newly described species and species awaiting description (Timms, in press). Species descriptions omit information on cyst shells, but suitable descriptions for many species are provided here. Although about 40% of known species are yet to be studied (and for most of these, data are unlikely to be available in the near future), enough descriptions of cyst shell morphology are available for comparison between Australian and overseas fauna and among the Australian species.

Cysts of the species examined could be easily separated at the genus level, but only with difficulty or not at all at the species level. The most distinctive are those of *Streptocephalus* with their overall tetrahedral shape and distinct facet-edge ridges and convex to concave faces with bumps. This feature places them within the *sudanicus* species group of Maeda-Martínez et al. (1995) and subgenus *Parastreptocephalus* of Brendonck et al. (1992); *Streptocephalus* species with mature spherical cysts have yet to be found in Australia.

Cysts of the new branchiopodid genus are also distinctive because of flanges from ridges defining irregular polygons. Almost all of the species of *Branchinella* have cysts with a polygonal surface largely reminiscent of those of overseas members of the genus (Belk and Sisson 1992, Mura 1992, Brendonck and Riddoch 1997; Sanoamuang et al. 2003). Cysts of *B. lyrifera* are discordant for the genus because they are covered with flat-topped columns with little evidence of polygons, though the columns are connected by uncoordinated ridges.

Cysts of *Parartemia*, an Australian endemic genus, are described for the first time. They are smooth, rather like those of *Artemia* (Hill and Shepard 1997), but with some inpocketing. Given possible undetected variation within species, particularly in those subjected to predation (Mura et al. 2002), it is unwise to compare species within genera.

None of the Australian cysts examined here have extreme anti-predation devices such as honeycombing or long spines (Dumont et al. 2003). Some species have minor protruding structures which may assist against predation. The most developed are the bifid/trifid/recurved spines at ridge junctions in *B. longirostris*. Interestingly this species lives in gnammas (rock pools) in which many potential predators live including flatworms (Pinder et al. 2000). Other species of *Branchinella* with small spines include *B. complexidigitata* in which they are sharp pointed and *B. hattahensis* where the spines are recurved. The flanges on the cysts of the undescribed branchipodid genus could be antipredation devices, but another explanation is that they assist in holding the egg mass together (as observed when trying to separate the cysts). The value of such a strategy is questionable, given the decreased possibly of dispersal of a clumped egg mass, but perhaps it helps to deter egg predators.

The cyst shell structure (especially the cross-sectional structure) in this study ranged from relatively simple (e. g., in *Parartemia*) to complex (e. g., in *Branchinella budjiti* and an undescribed branchipodid genus). During the examination of *Branchinella occidentalis* the first set of cysts appeared to be not completely mature so a second set was examined. This second set was of a very different size and form. Thus, it appears that either the species has two different cyst morphs or there may be a cryptic species in what is now known as *B. occidentalis*. At least other species are known to have two cyst types: *Eubranchipus serratus* (Hill and Shepard 1997) and *Streptocephalus sealii* (R. Hill, pers.com.). During the course of this study the only cyst structure found that has not been seen in any other fairy shrimp before was the external flanges and the parallel columns in the cortex of the undescribed genus of branchipodid fairy shrimp. Therefore, with minor exception, the maximum range of structural diversity in cysts may have been described. Whether or not this is true will be decided by examination of the remaining undescribed cysts of other world genera.

The structure of the cyst shell, especially in the alveolar layer, begs a functional explanation. It is likely that the structure represents a compromise between crush-resistance and rehydration ability. But other functions that have been suggested include: protection from abrasion and ultraviolet light (Belk 1969); a float for cysts (Morris and Afzelius 1967); a barrier against physio-chemical stresses and an aid to gaseous exchange (Tommasini and Sabelli 1989); an anti-predation device (Dumont et al. 2003) and, dispersal aids or inhibitors (Brendonck et al. 1992).

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APPENDIX 1

Locality data for species examined.

Branchinella affinis: Far North Bulla claypan, Rockwell Station, 180 km SW of Cunnamulla, Queensland. 28° 52' S, 144° 56'E, 27-iii-2000.

Branchinella arborea: Marsilea Pool, Bloodwood Station, 130km NW of Bourke, NSW. 29° 33'S, 144° 52'E, 1-vi-1999.

Branchinella australiensis: Lower Crescent Pool, Bloodwood Station, 130 km NW of Bourke, NSW, 29° 33'S, 144° 52'E, 1-vi-1999.

Branchinella basispina: Homestead Dam, Balladonia Station, 220 km E of Norseman, WA. 32° 28'S, 123° 52'E, 3-iii-1975.

Branchinella buchananensis: Gidgee Lake, Bloodwood Station, 130 km NE of Bourke, NSW, 29° 33'S, 144° 50'E, 28-ix-1998.

Branchinella budjiti: a claypan on Muella Station, 128 km NE of Bourke, NSW, 29° 31'S, 144° 56'E, 6-xii-1999.

Branchinella campbelli: Muella Lake, Tredega Station, 140 km NW of Bourke, NSW, 29° 31'S, 144° 53'E, 27-vi-1998.

Branchinella complexidigitata: Lake Arro near Eneabba, 300 km N of Perth, WA, 29° 44'S, 115° 10'E, 2-ix-1999.

Branchinella dubia: pool 89 km from Derby on the Gibb R Road, Kimberley, WA, 17° 26'S, 124° 36'E, 31-i-1985.

Branchinella frondosa: Steves Pool, Muella Station, 128 km NW of Bourke, NSW, 29° 33'S, 144° 55'E, 24-xi-1998.

Branchinella hattahensis: Mid Kaponyee Lake, Currawinya National Park, SW Queensland, 28° 50'S, 144° 19'E, 5-vii-1997.

Branchinella kadjikadji: claypan on Kadji Kadji Station, 35 km ENE of Morewa, WA, 29° 08'S, 116° 24'E, 14-viii-1998.

Branchinella lamellata: a claypan near Warburton Crossing, Clifton Hills Station, NE South Australia, 27° 02'S, 138° 53'E, 5-xii-2000.

Branchinella longirostris: Warrdagga Rock, via Paynes Find, WA, 29° 24'S, 117° 30'E, 26-viii-2001.

Branchinella lyrifera: Turkey claypan, Bloodwood Station, 130 km NE of Bourke, NSW, 29° 34'S, 144° 50'E, 1-iv-1999.

Branchinella nana: Lake Arrow, near Kalgoorlie, WA, 30° 32'S, 121° 24'E, 14-v-1995.

Branchinella nichollsi: Lake Hannan near Kalgoorlie, WA, 30° 40'S, 121° 28'E, 17-iii-1937.

Branchinella occidentalis: Freshwater Lake, Bloodwood Station, 130 km NW of Bourke, 29° 29'S, 144° 50'E, 2-vii-1997 (Type I); Plover claypan, Bloodwood Station, 130 km NW of Bourke, 29° 29'S, 144° 48'E, 29-vi-1998 (Type II).

Branchinella pinnata: a blackbox swamp, Tredega Station, 140 km NW of Bourke, NSW, 29° 29'S, 144° 52'E, 30-vi-1999.

Branchinella probiscida: Darko claypan, Currawinya National Park, SW Queensland, 28° 52'S, 144° 18'E, 4-xii-1999.

Branchinella simplex: Lake Arrow, near Kalgoorlie, WA, 30° 32'S, 121° 24'E, 14-v-1995.

Branchinella wellardi: Marsilea Pool, Bloodwood Station, 130km NW of Bourke, NSW. 29° 33'S, 144° 52'E, 1-vi-1999

Parartemia contracta: small lake adjacent to Lake O'Grady, WA, 30° 25'S, 117° 25'E, ?-viii-1978.

Parartemia cylindrifera: Lake Grace, WA, 33° 06'S, 18° 24'E, 24-viii-1978.

Parartemia informis: Lake Ballard, WA, 29° 37'S, 121° 07'E, 18-viii-1978.

Parartemia minuta: Lower Bell Lake, Bloodwood Station, 130 km NW of Bourke, NSW, 29° 00'S, 144° 48'E, 28-ix-1998.

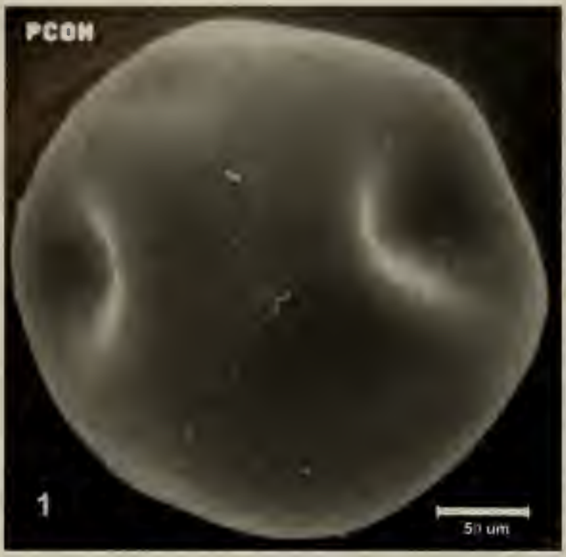
Parartemia zietziana: small lake on 'Flowerfield' via Beeac, Victoria, 38° 10'S, 143° 09'E, 15-viii-1970.

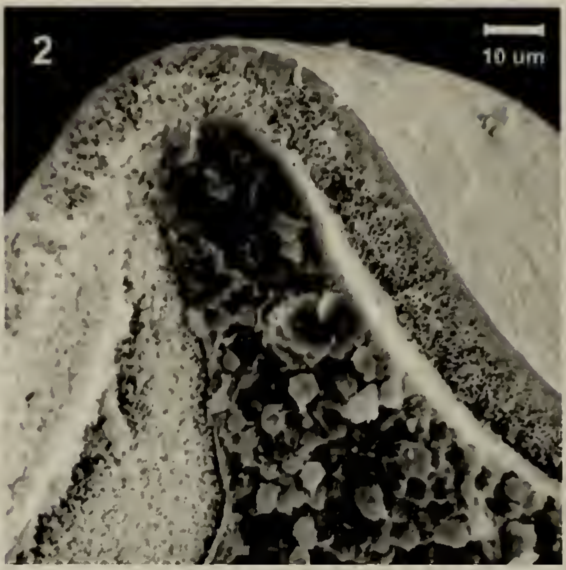
Streptocephalus queenslandicus: fish rearing ponds, Walkamin Research Station, via Atherton, Queensland, 17° 08'S, 145° 26'E, ii-1997.

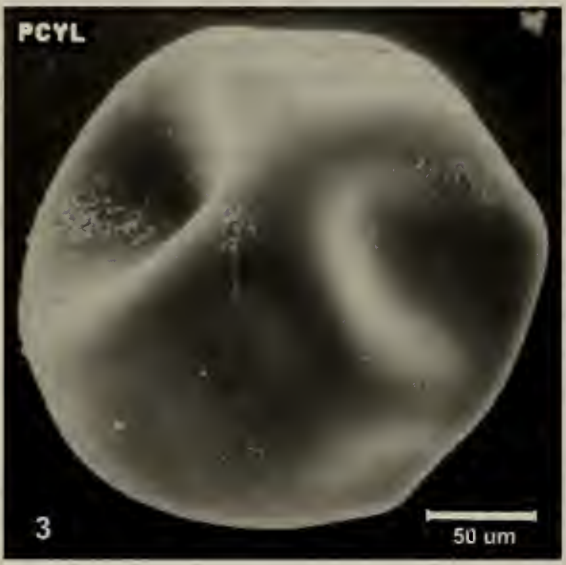
Streptocephalus n.sp. a: Pine Tree Pool, Bloodwood Station, 130 km NE of Bourke, NSW, 29 29'S, 144 49'E, 2-xii-1999.

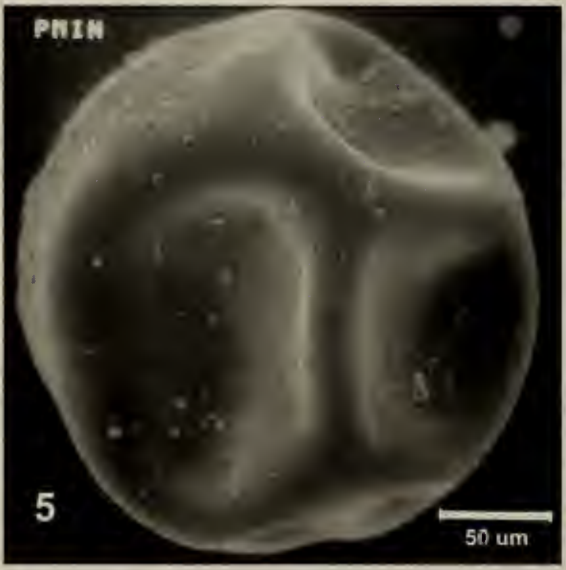
Streptocephalus n.sp.b: Box Hole, 4 km S of Homestead, Currawinya National Park, Qld., 28 51'S, 144 29'E, 1-iv-1999.

Undescribed new branchiopod genus: Marsilea Pool, Bloodwood Station, 130km NW of Bourke, NSW. 29° 33'S, 144° 52'E, 24-viii-1998.









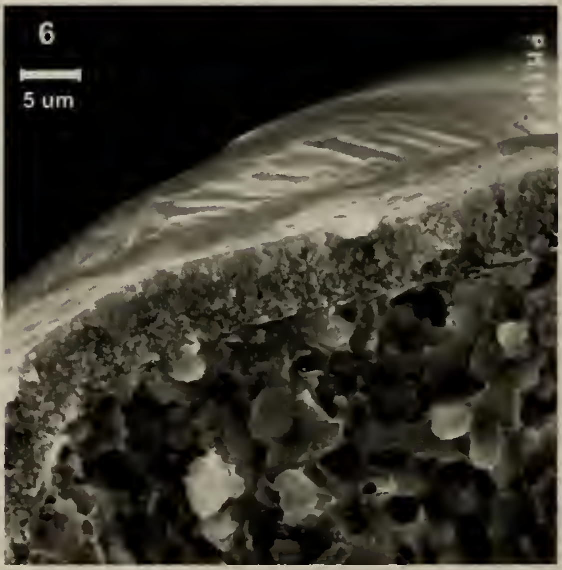
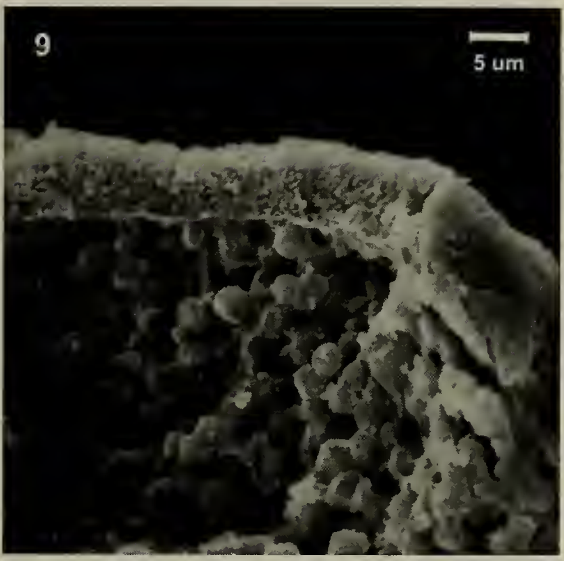
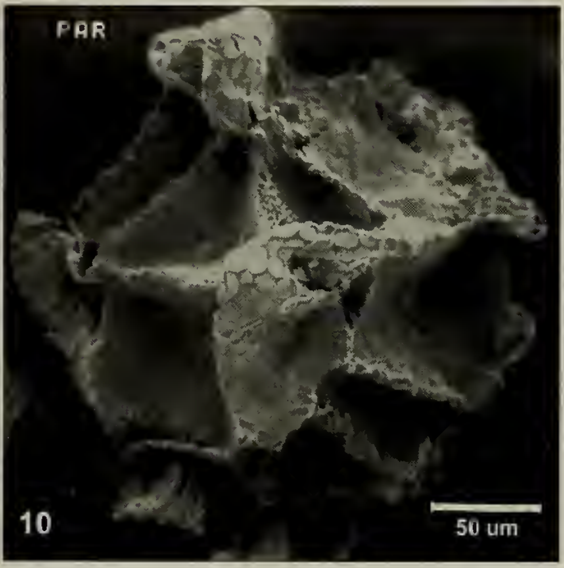
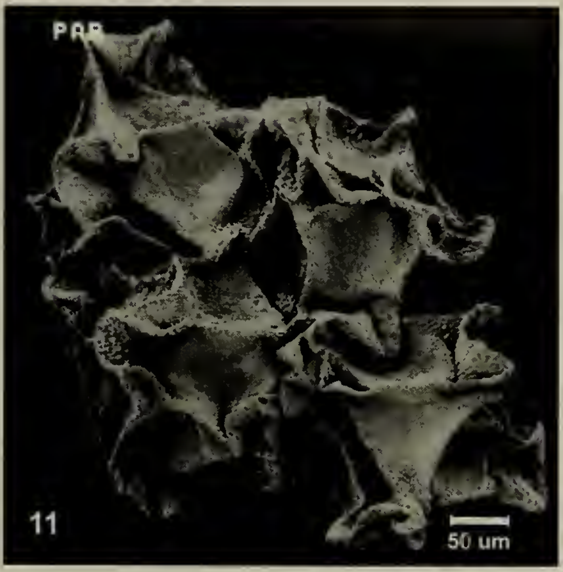


Figure 1. *Parartemia contracta* cyst. Bar = 50 μm.
Figure 2. *Parartemia contracta* cyst shell cross section. Bar = 10 μm.
Figure 3. *Parartemia cylindrifera* cyst. Bar = 50 μm.
Figure 4. *Parartemia cylindrifera* cyst shell cross section. Bar = 10μm.
Figure 5. *Parartemia minuta* cyst. Bar = 50 μm.
Figure 6. *Parartemia minuta* cyst shell cross section. Bar = 5 μm.







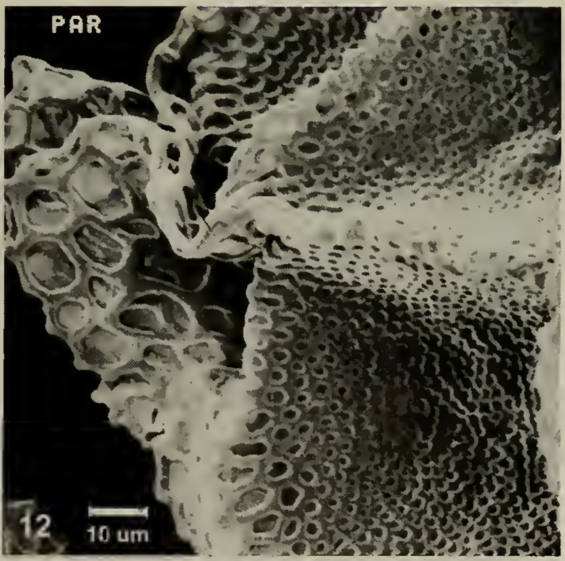
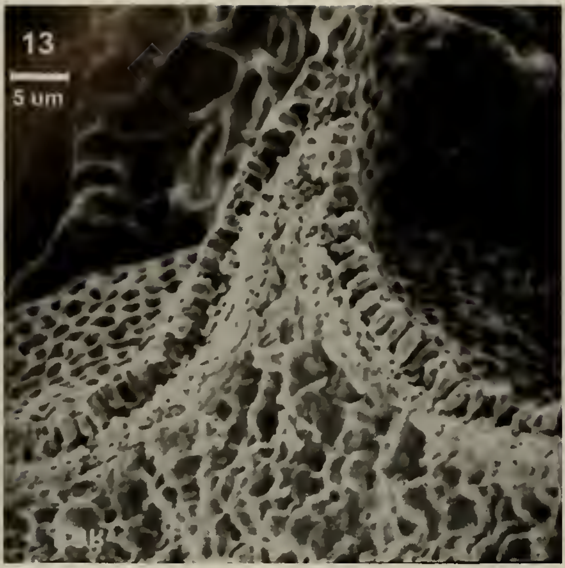
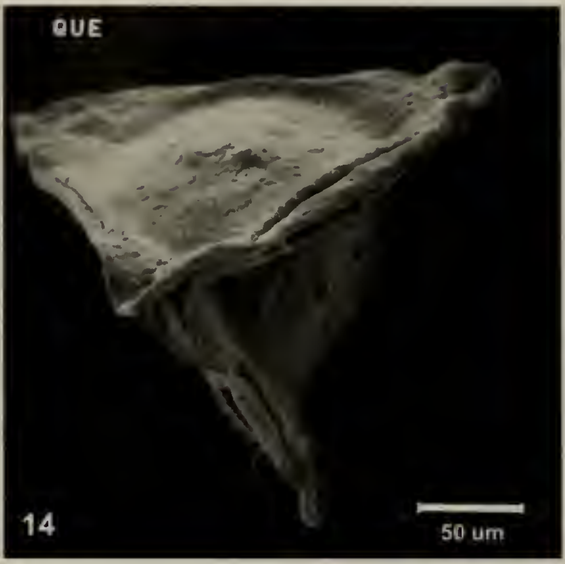
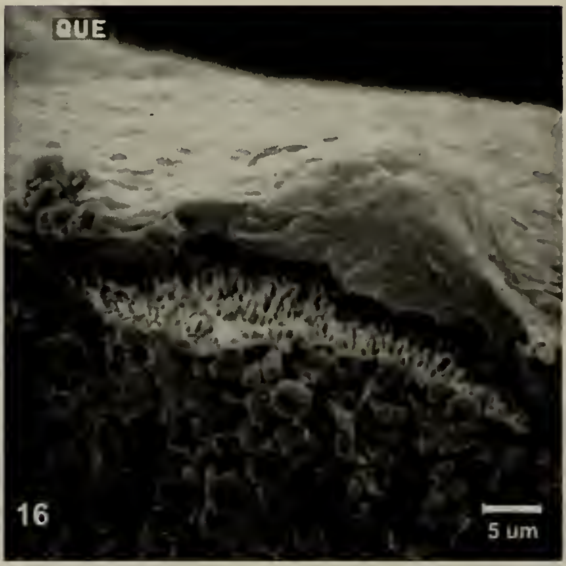
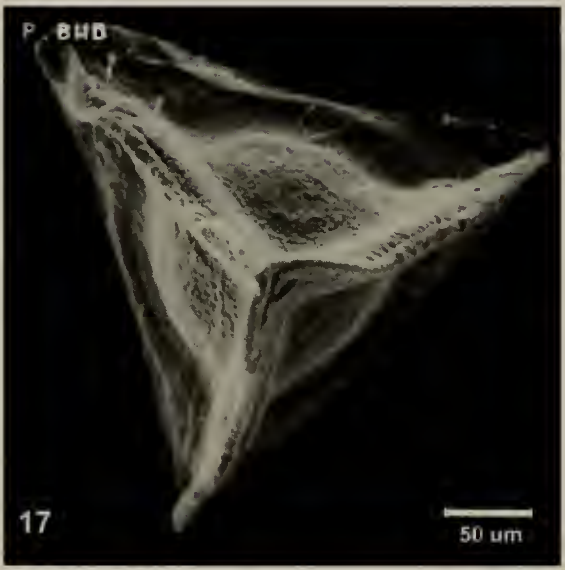


Figure 7. *Parartemia zietziana* cyst. Bar = 50 µm.
Figure 8. *Parartemia zietziana* cyst. Bar = 50 µm.
Figure 9. *Parartemia zietziana* cyst shell cross section. Bar = 5 µm.
Figure 10. Undescribed branchipodid species cyst. Bar = 50 µm.
Figure 11. Undescribed branchipodid species cysts clumped together. Bar = 50 µm.
Figure 12. Undescribed branchipodid species cyst surface. Bar = 10 µm.









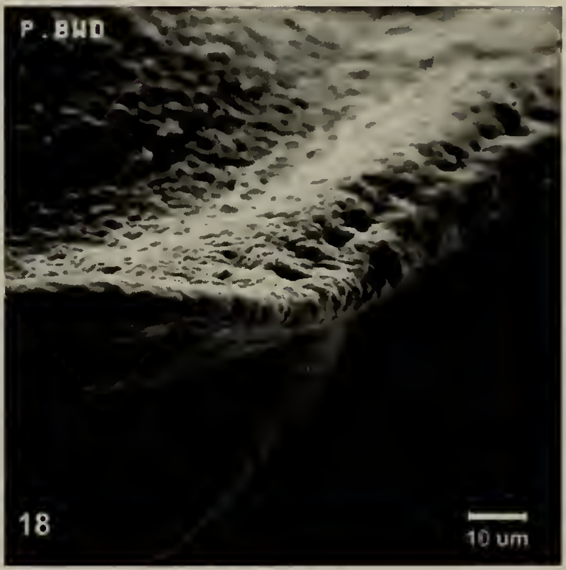
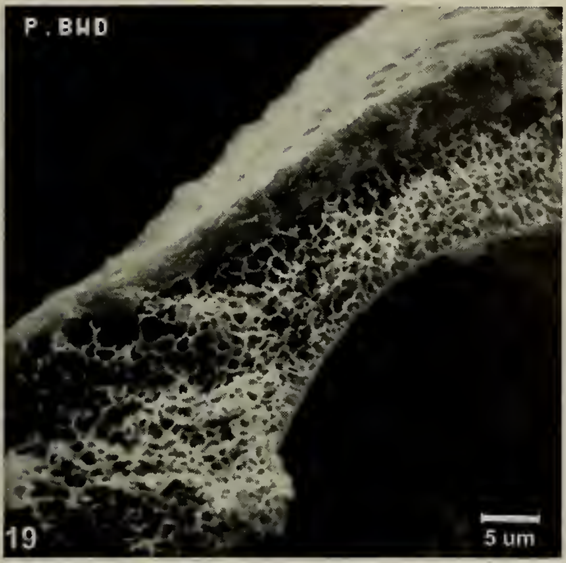
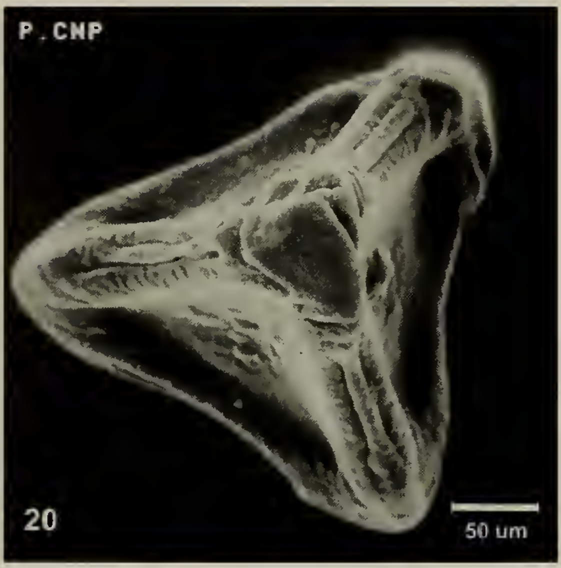
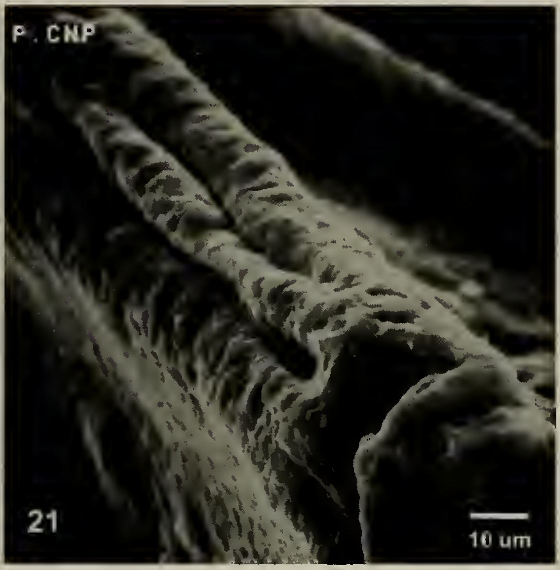
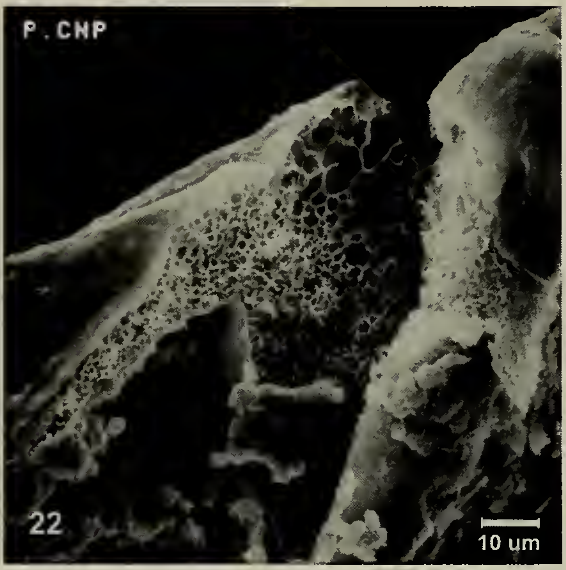


Figure 13. Undescribed branchipodid species cyst shell cross section. Bar = 5 µm.
Figure 14. *Streptocephalus queenslandicus* cyst. Bar = 50 µm.
Figure 15. *Streptocephalus queenslandicus* cyst. Bar = 20 µm.
Figure 16. *Streptocephalus queenslandicus* cyst shell cross section. Bar = 5 µm.
Figure 17. *Streptocephalus* n. sp. a cyst. Bar = 50 µm.
Figure 18. *Streptocephalus* n. sp. a cyst ridges. Bar = 10 µm.









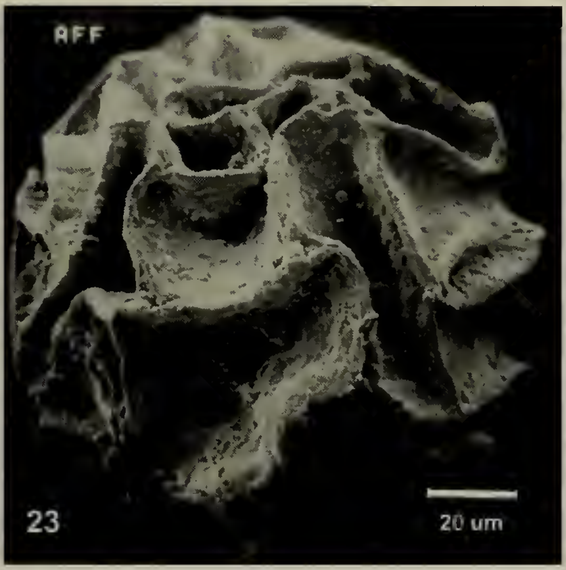
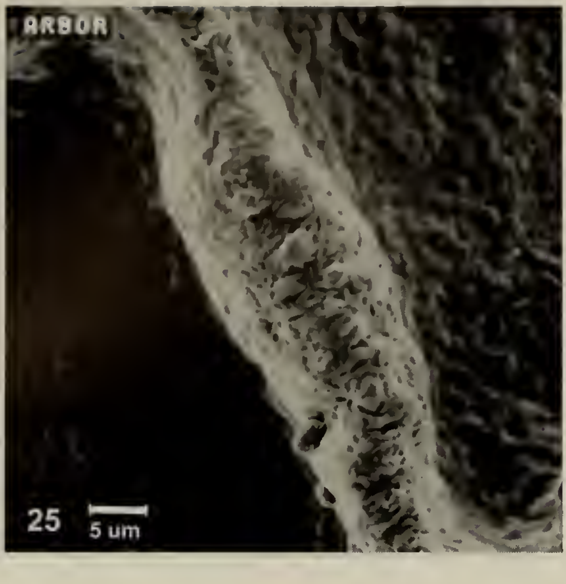
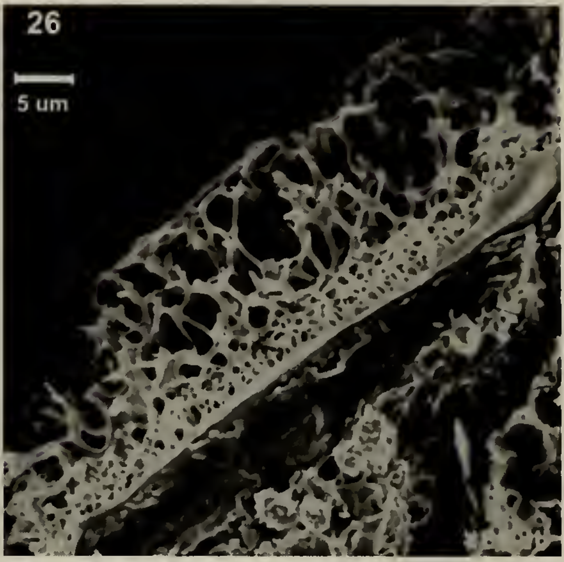
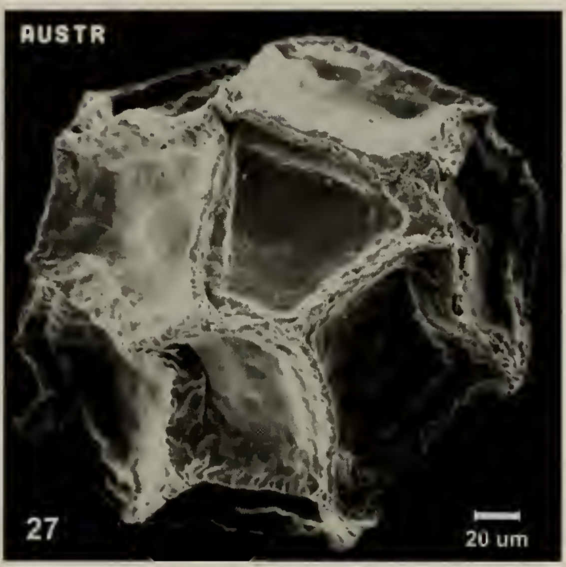
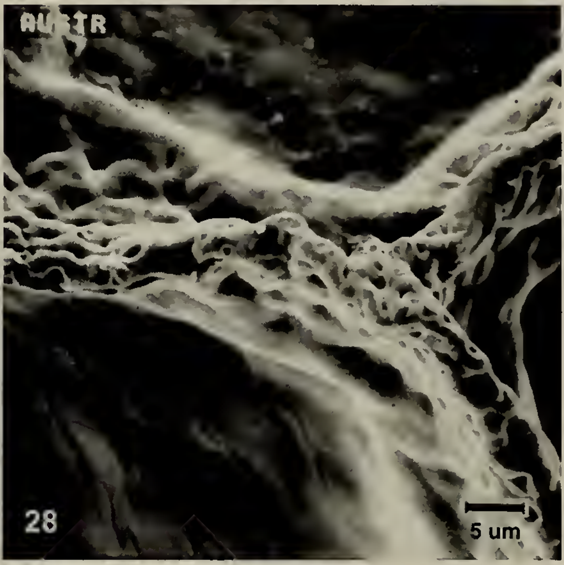


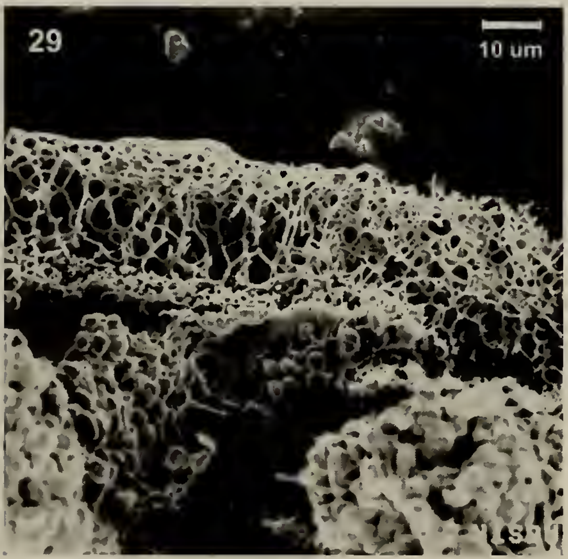
Figure 19. *Streptocephalus* n. sp. a cyst shell cross section. Bar = 5 μm.
Figure 20. *Streptocephalus* n. sp. b cyst. Bar = 50 μm.
Figure 21. *Streptocephalus* n. sp. b cyst ridges. Bar = 10 μm.
Figure 22. *Streptocephalus* n. sp. b cyst shell cross section. Bar = 10 μm.
Figure 23. *Branchinella affinis* cyst (not quite mature). Bar = 20 μm.
Figure 24. *Branchinella arborea* cyst. Bar = 20 μm.











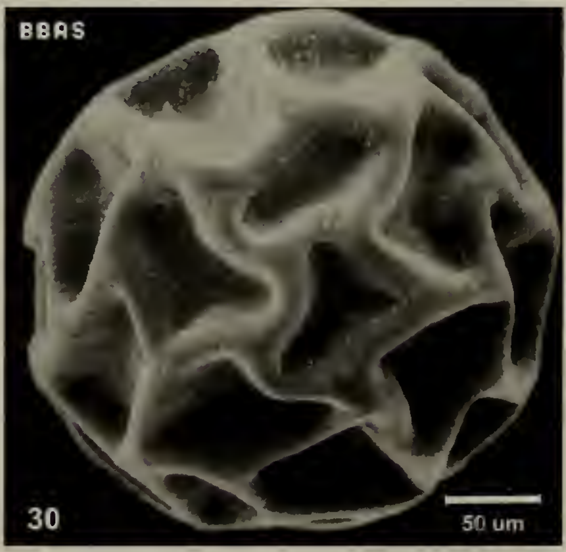
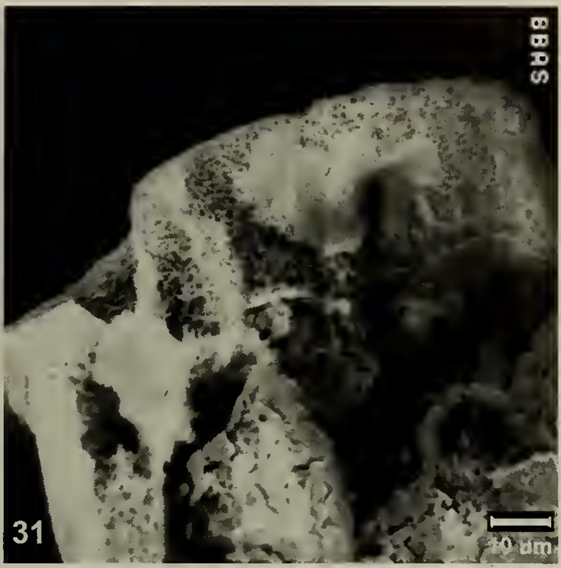
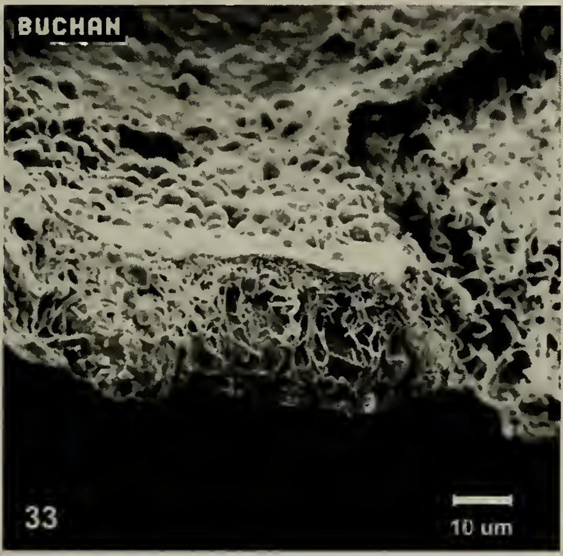


Figure 25. *Branchinella arborea* cyst ridge. Bar = 5 µm.
Figure 26. *Branchinella arborea* cyst shell cross section. Bar = 5 µm.
Figure 27. *Branchinella australiensis* cyst. Bar = 20 µm.
Figure 28. *Branchinella australiensis* cyst ridge structure. Bar = 5 µm.
Figure 29. *Branchinella australiensis* cyst shell cross section. Bar = 10 µm.
Figure 30. *Branchinella basipina* cyst. Bar = 50 µm.





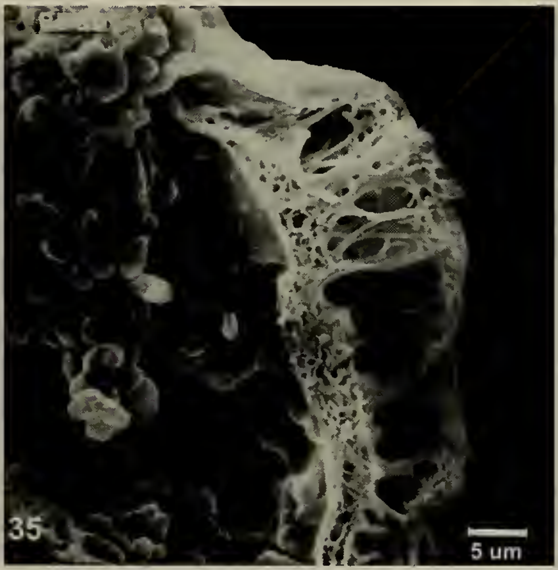
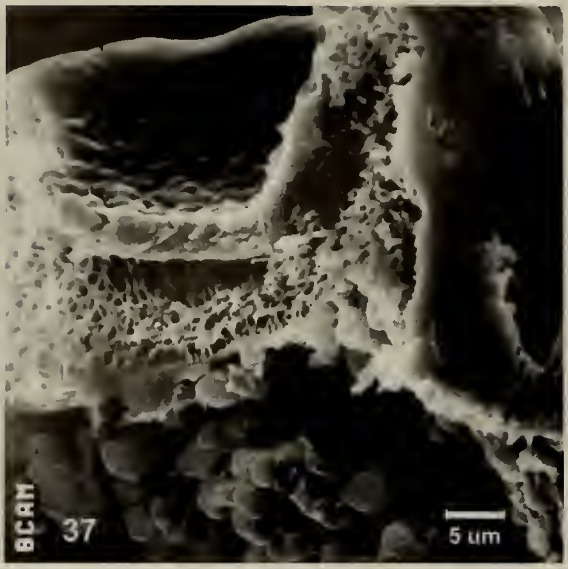
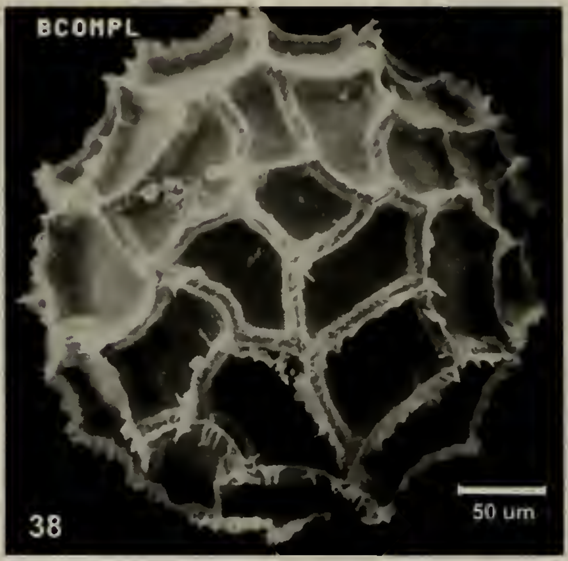
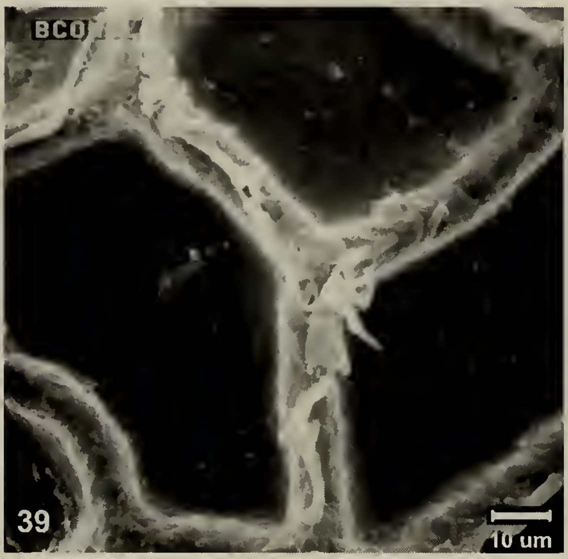
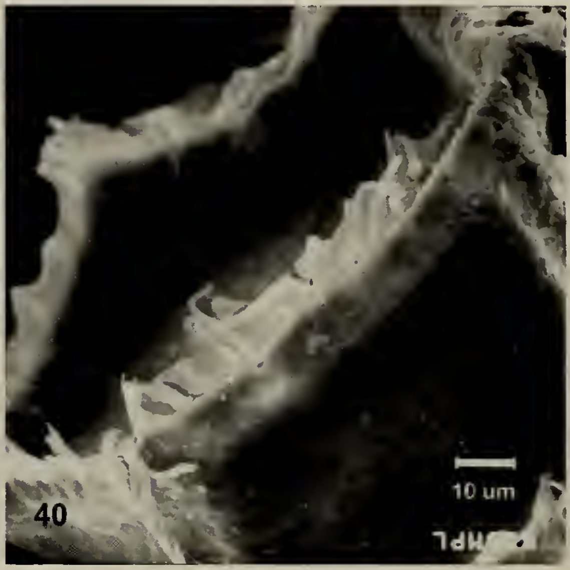


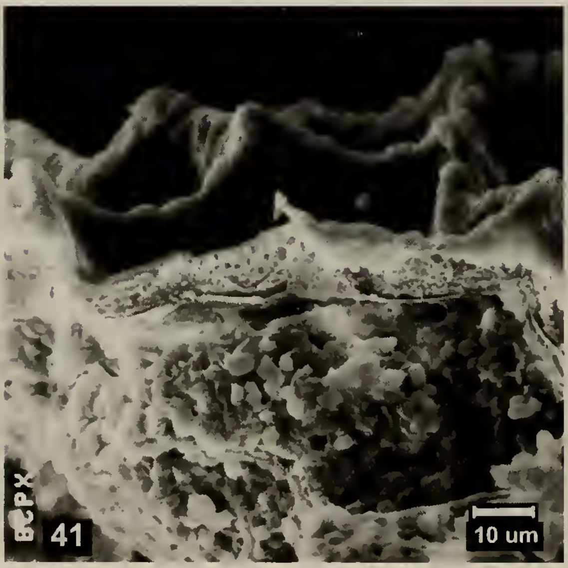
Figure 31. *Branchinella basipina* cyst shell cross section. Bar = 10 µm.
Figure 32. *Branchinella buchananensis* cyst. Bar = 50 µm.
Figure 33. *Branchinella buchananensis* cyst shell cross section. Bar = 10 µm.
Figure 34. *Branchinella budjiti* cyst. Bar = 20 µm.
Figure 35. *Branchinella budjiti* cyst shell cross section. Bar = 5 µm.
Figure 36. *Branchinella campbelli* cyst. Bar = 20 µm.











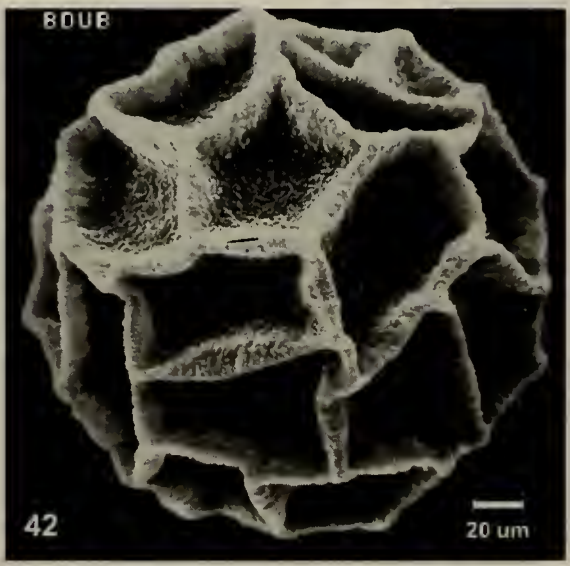
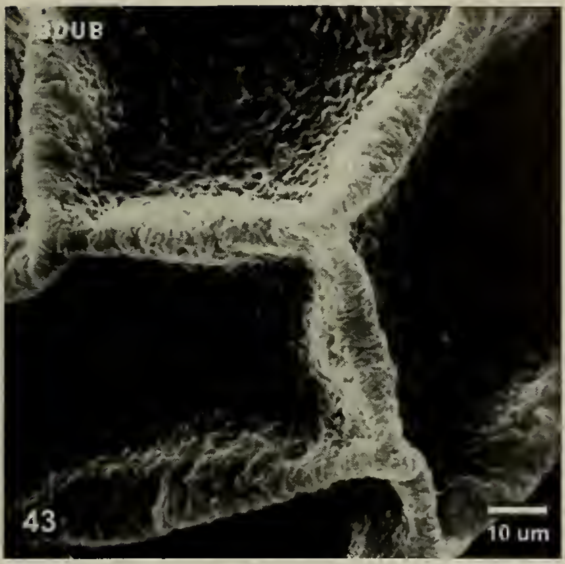
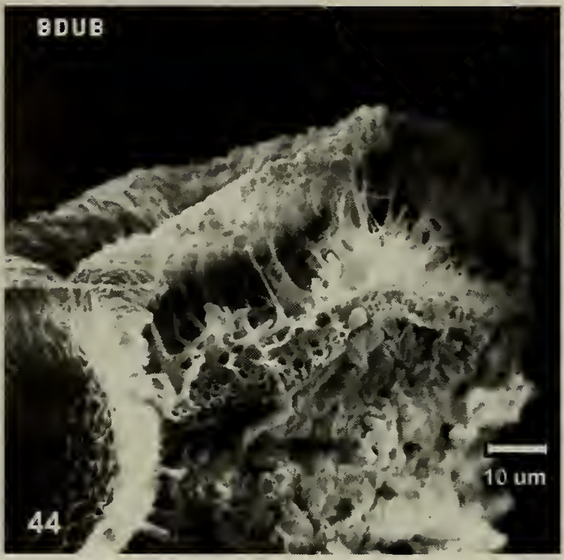
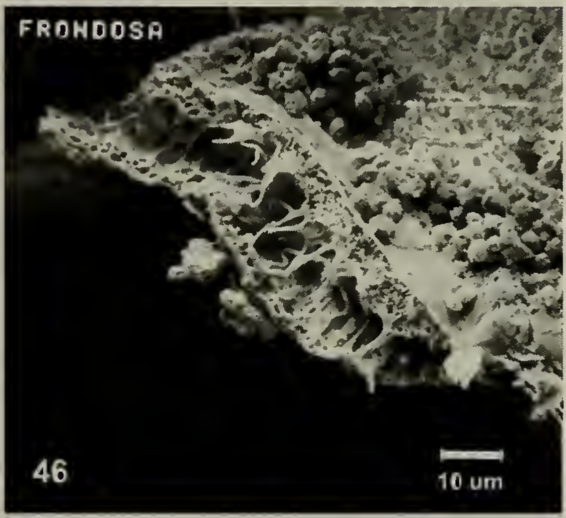
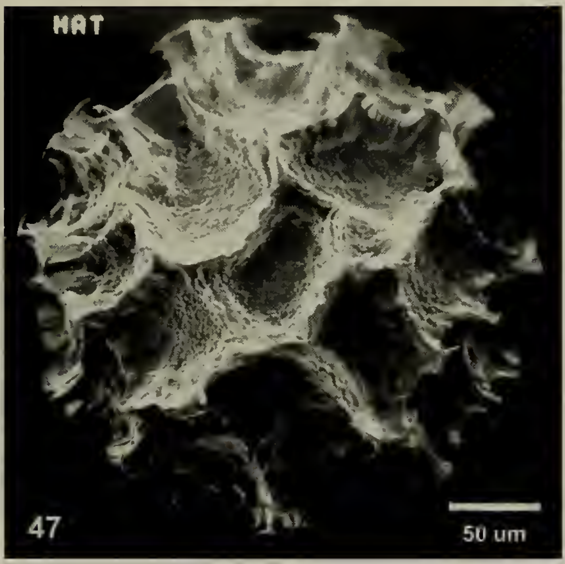


Figure 37. *Branchinella campbelli* cyst shell cross section. Bar = 5 µm.
Figure 38. *Branchinella complexidigitata* cyst. Bar = 50 µm.
Figure 39. *Branchinella complexidigitata* cyst surface structure. Bar = 10 µm.
Figure 40. *Branchinella complexidigitata* cyst surface structure. Bar = 10 µm.
Figure 41. *Branchinella complexidigitata* cyst shell cross section. Bar = 10 µm.
Figure 42. *Branchinella dubia* cyst. Bar = 20 µm.









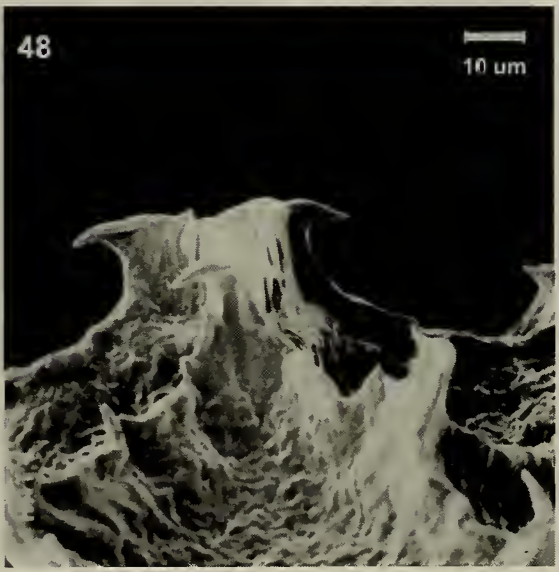
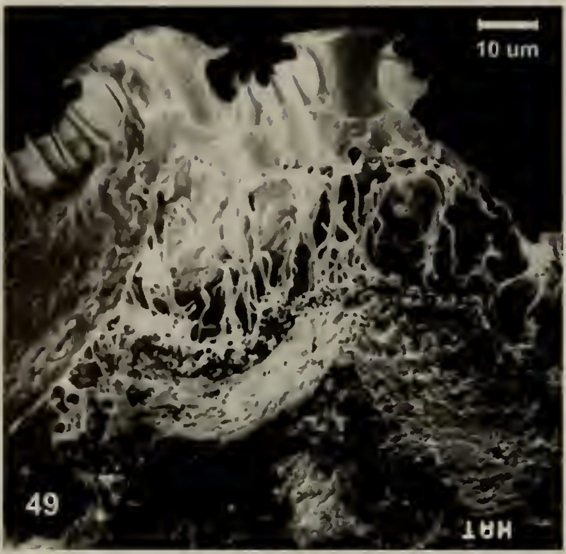
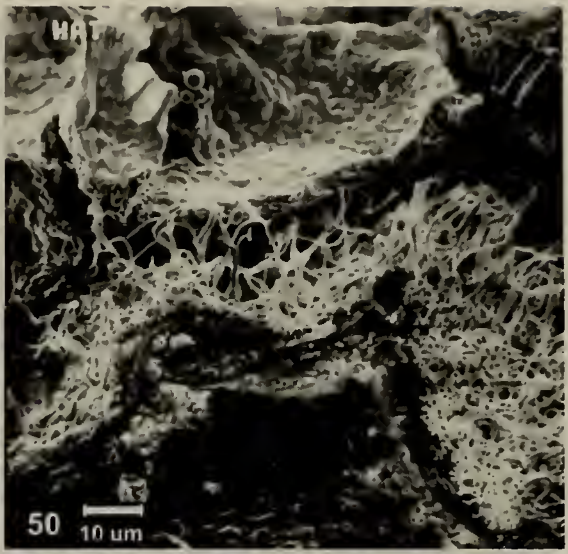
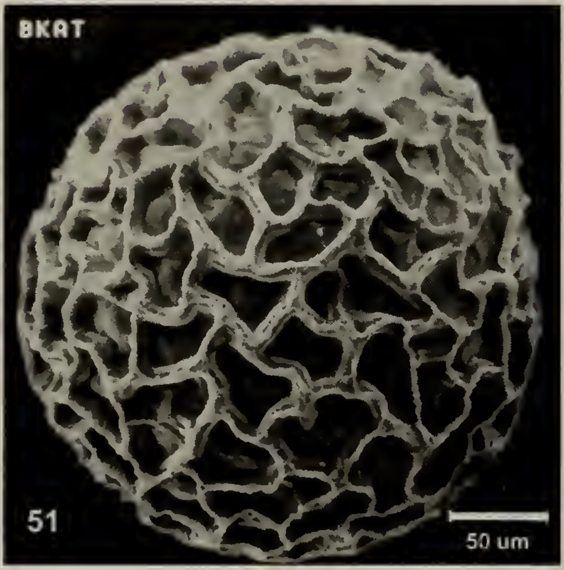
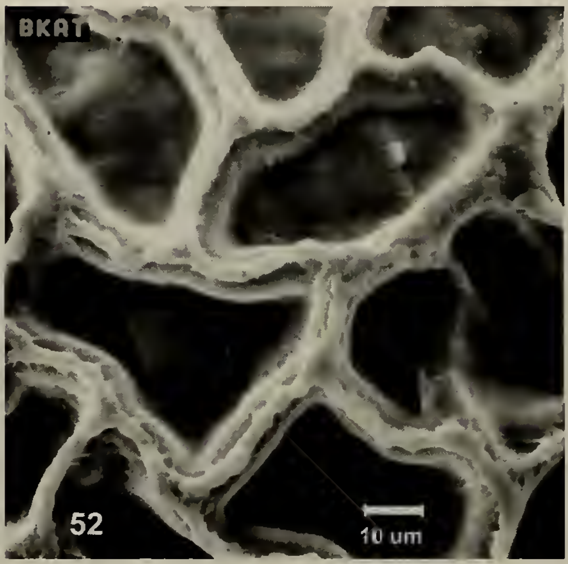


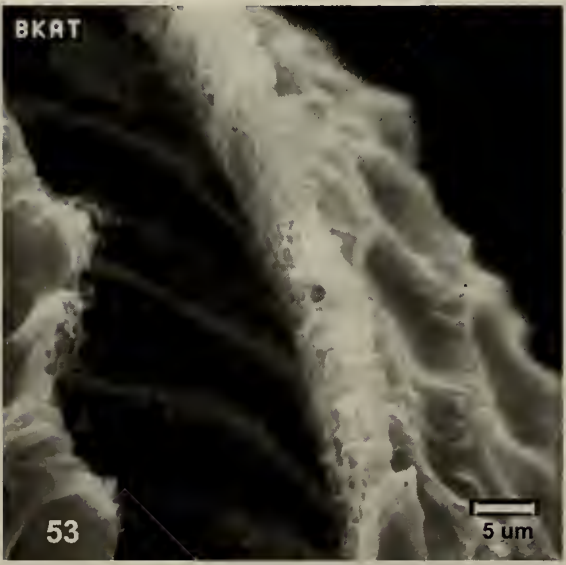
Figure 43. *Branchinella dubia* cyst surface. Bar = 10 µm.
Figure 44. *Branchinella dubia* cyst shell cross section. Bar = 10 µm.
Figure 45. *Branchinella frondosa* cyst. Bar = 20 µm.
Figure 46. *Branchinella frondosa* cyst shell cross section. Bar = 10 µm.
Figure 47. *Branchinella hattahensis* cyst. Bar = 50 µm.
Figure 48. *Branchinella hattahensis* cyst surface structure. Bar = 10 µm.











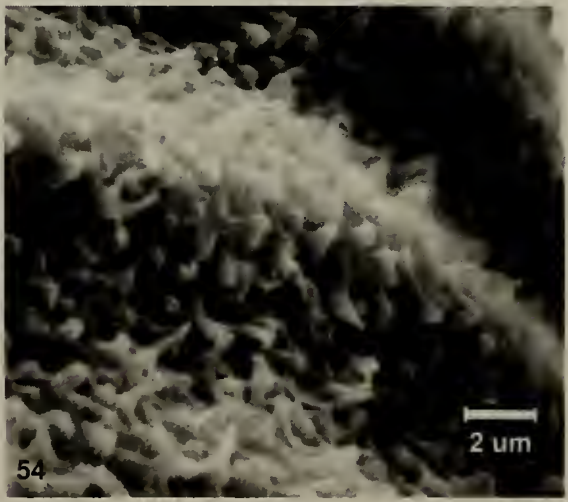
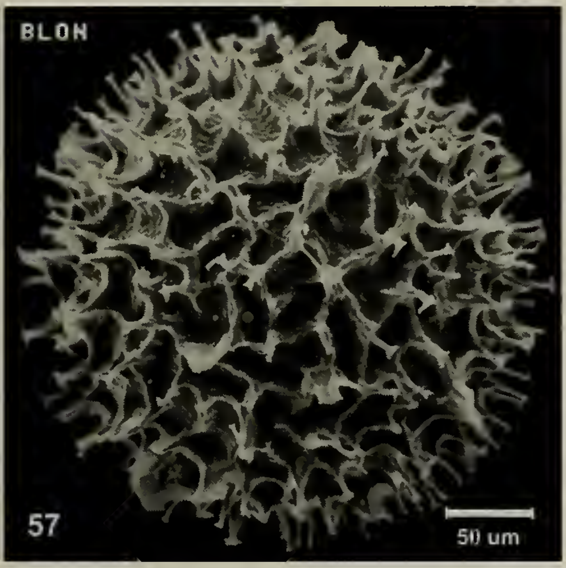
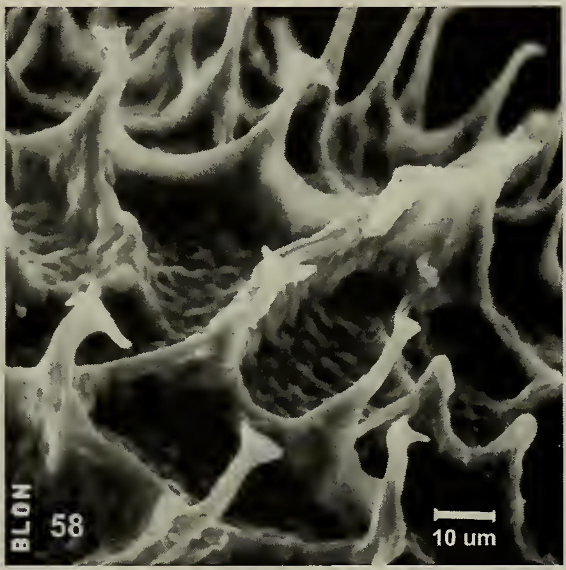
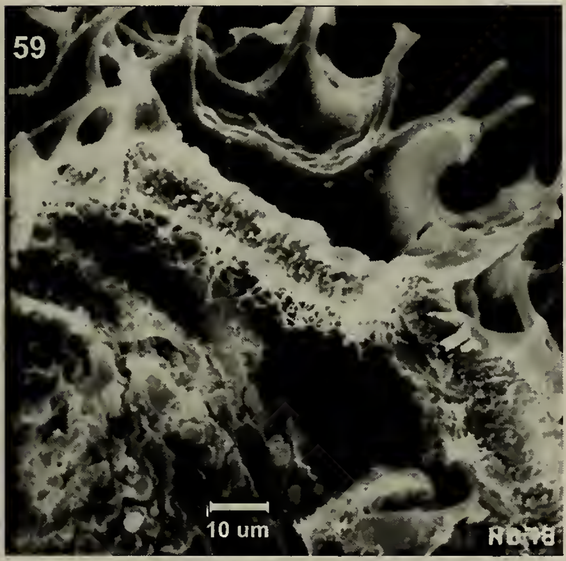


Figure 49. *Branchinella hattahensis* cyst shell cross section with ridge spines. Bar = 10 μm.
Figure 50. *Branchinella hattahensis* cyst shell cross section. Bar = 10 μm.
Figure 51. *Branchinella kadjikadji* cyst. Bar = 50 μm.
Figure 52. *Branchinella kadjikadji* cyst surface. Bar = 10 μm.
Figure 53. *Branchinella kadjikadji* cyst shell cross section showing outer sublayer of alveolar layer pulled away from inner sublayer. Bar = 5 μm.
Figure 54. *Branchinella kadjikadji* cyst shell fracture showing inner sublayer of alveolar layer. Bar = 2 μm.







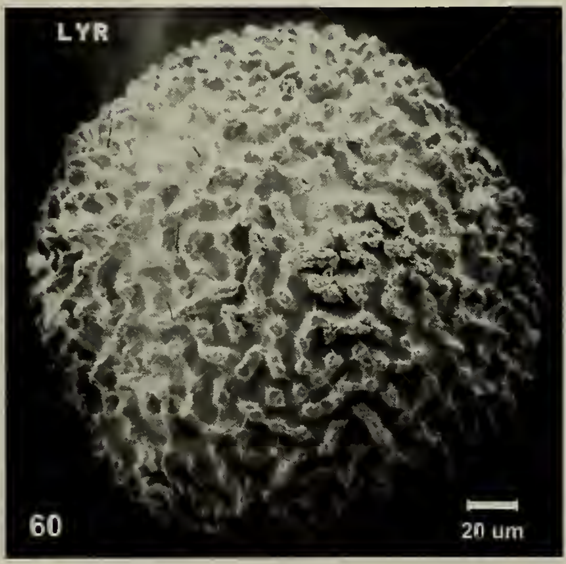
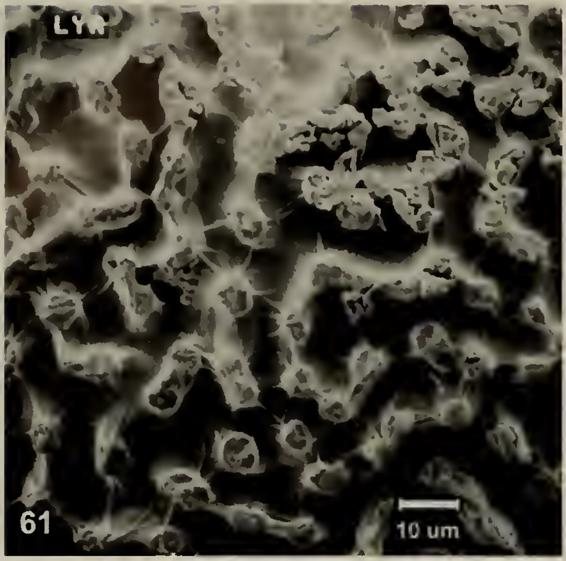
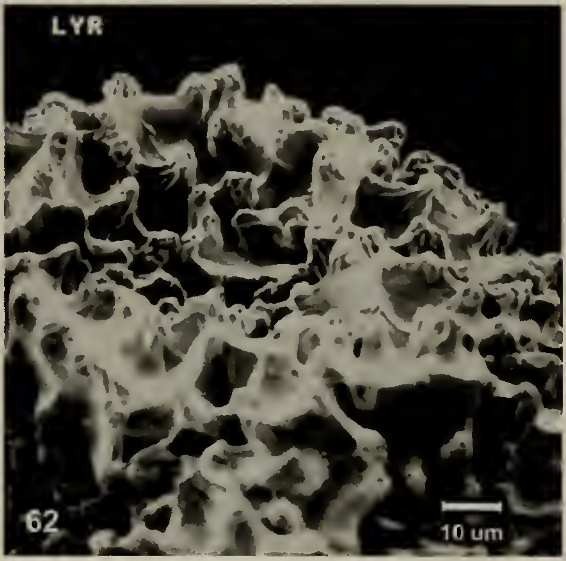
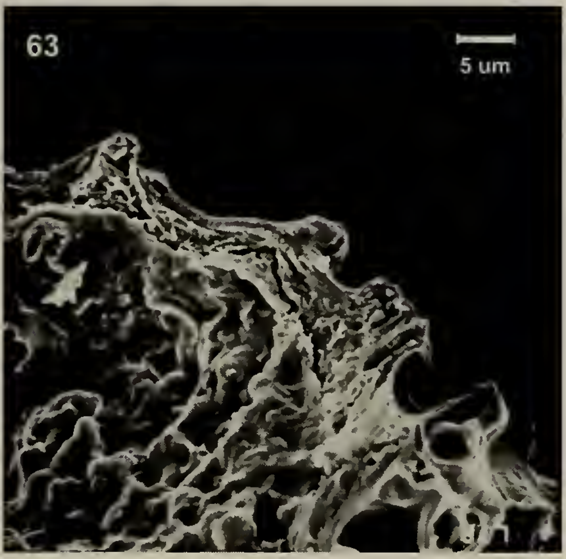
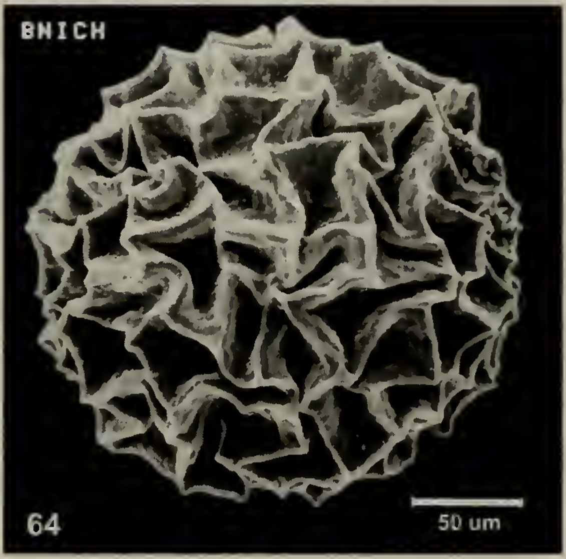


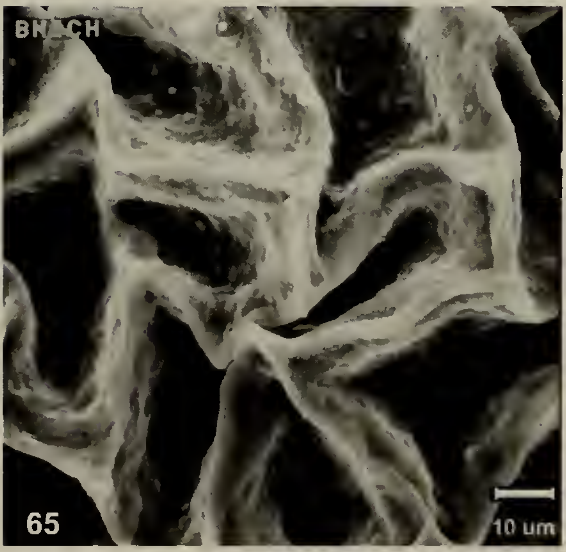
Figure 55. *Branchinella lamellata* cyst. Bar = 20 μm.
Figure 56. *Branchinella lamellata* cyst shell cross section. Bar = 5 μm.
Figure 57. *Branchinella longirostris* cyst. Bar = 50 μm.
Figure 58. *Branchinella longirostris* cyst surface structure. Bar = 10 μm.
Figure 59. *Branchinella longirostris* cyst shell cross section. Bar = 10 μm.
Figure 60. *Branchinella lyrifera* cyst. Bar = 20 μm.











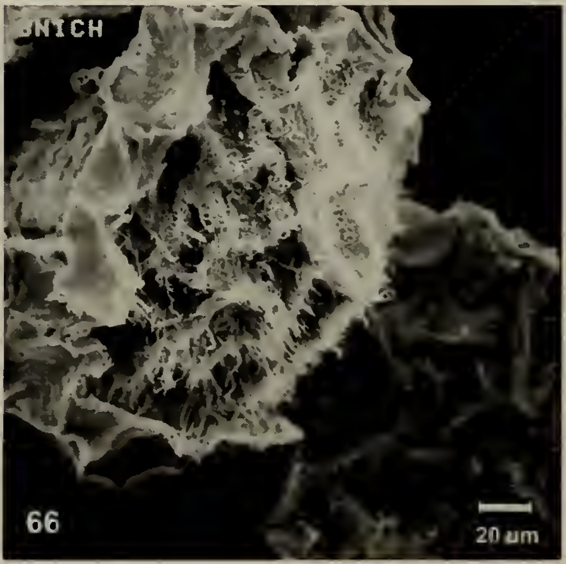
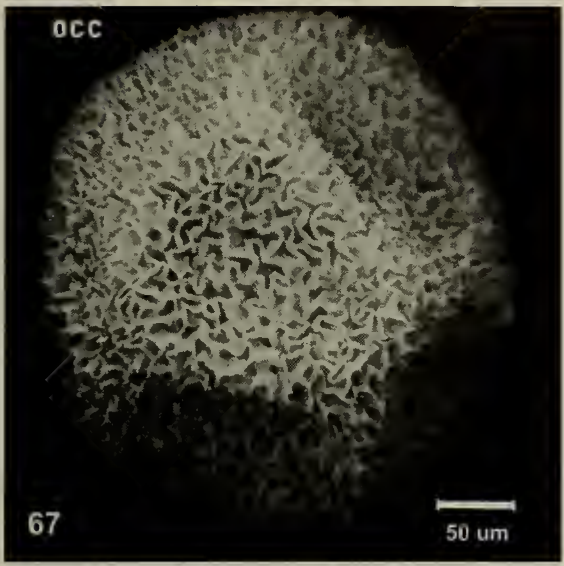
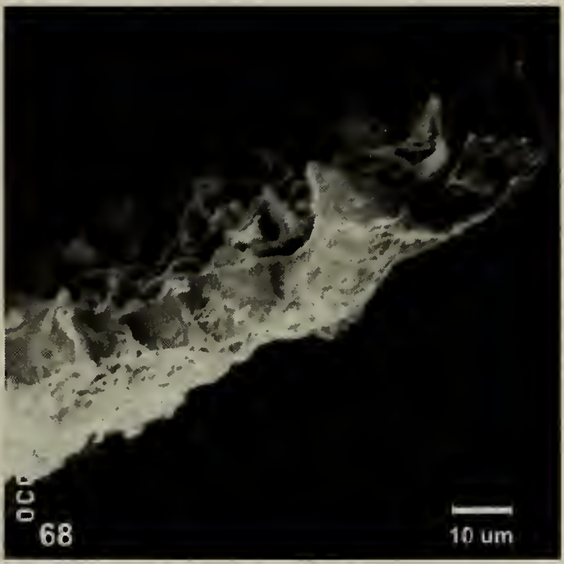
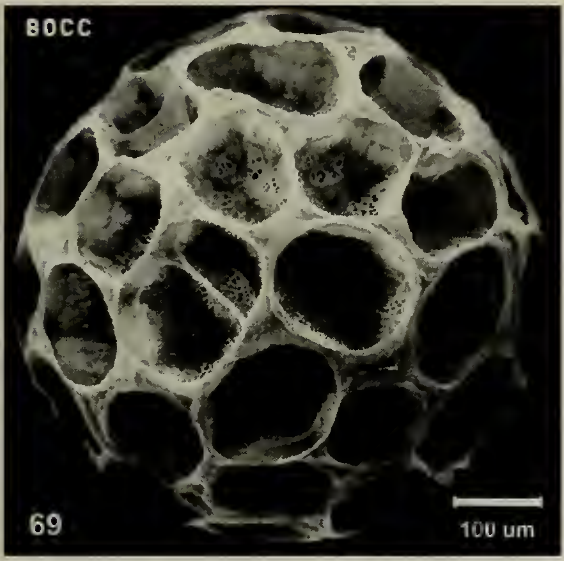
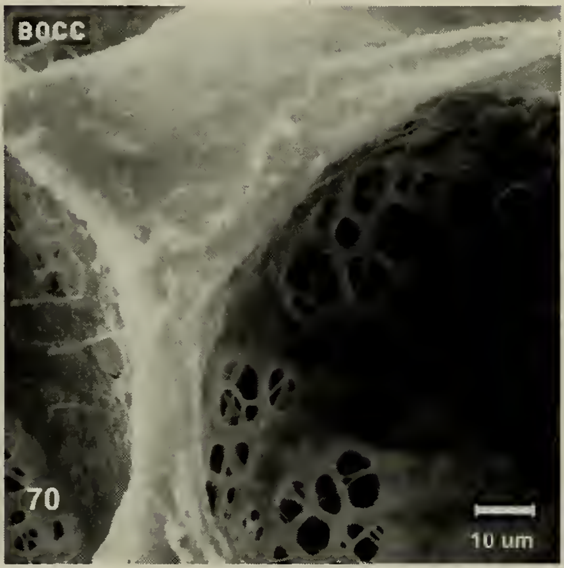


Figure 61. *Branchinella lyrifera* cyst ridges, polar view. Bar = 10 µm.
Figure 62. *Branchinella lyrifera* cyst ridges, side view. Bar = 10 µm.
Figure 63. *Branchinella lyrifera* cyst shell cross section. Bar = 5 µm.
Figure 64. *Branchinella nichollsi* cyst. Bar = 50 µm.
Figure 65. *Branchinella nichollsi* cyst ridge. Bar = 10 µm.
Figure 66. *Branchinella nichollsi* cyst shell cross section. Bar = 20 µm.









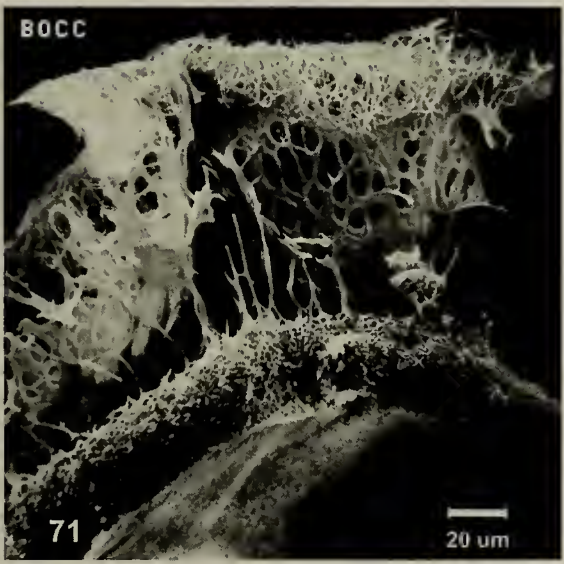
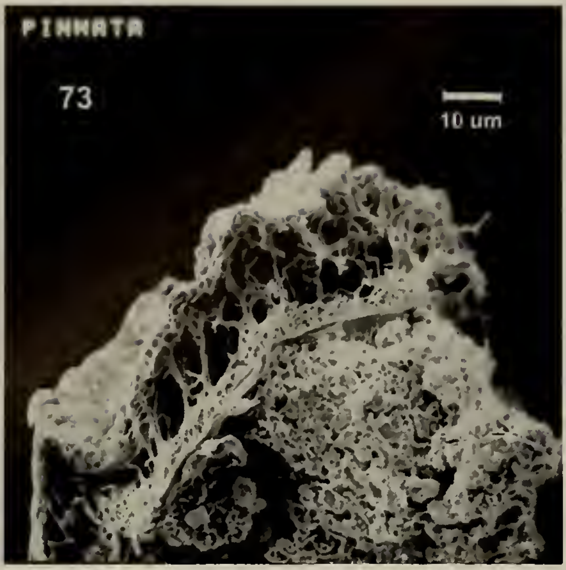
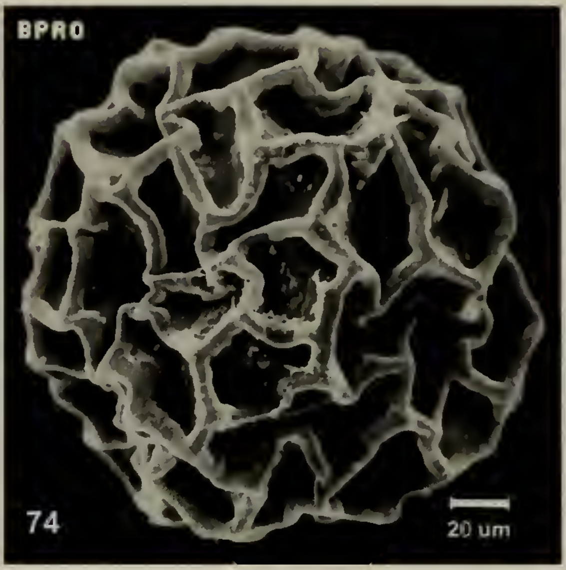
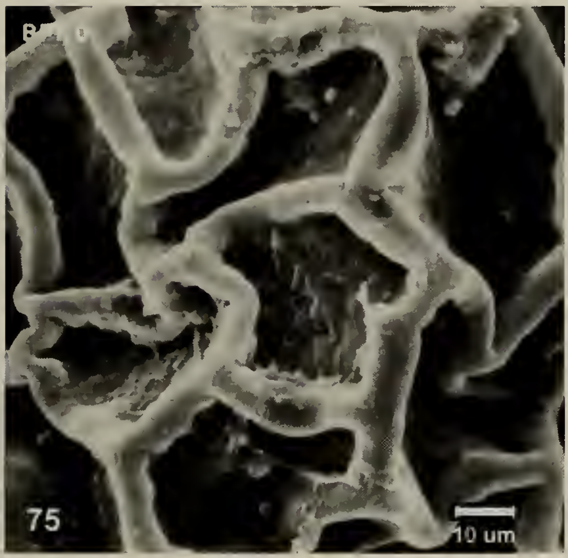
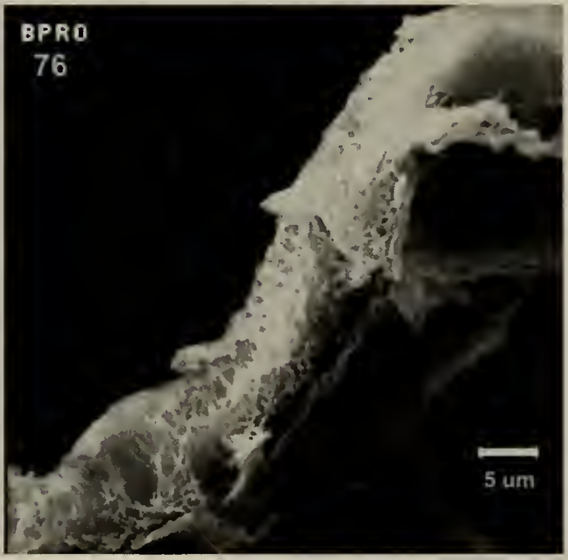


Figure 67. *Branchinella occidentalis* cyst (type I). Bar = 50 μm.
Figure 68. *Branchinella occidentalis* cyst (type I) shell cross section. Bar = 10 μm.
Figure 69. *Branchinella occidentalis* cyst (type II). Bar = 100 μm.
Figure 70. *Branchinella occidentalis* cyst (type II) surface. Bar = 10 μm.
Figure 71. *Branchinella occidentalis* cyst (type II) shell cross section. Bar = 20 μm.
Figure 72. *Branchinella pinnata* cyst. Bar = 20 μm.









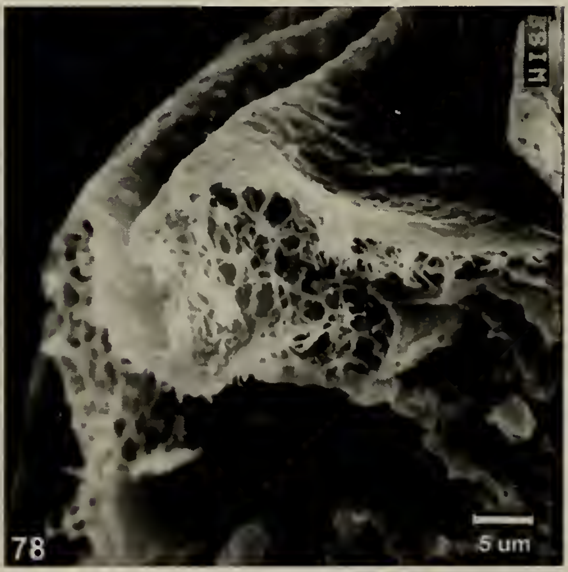
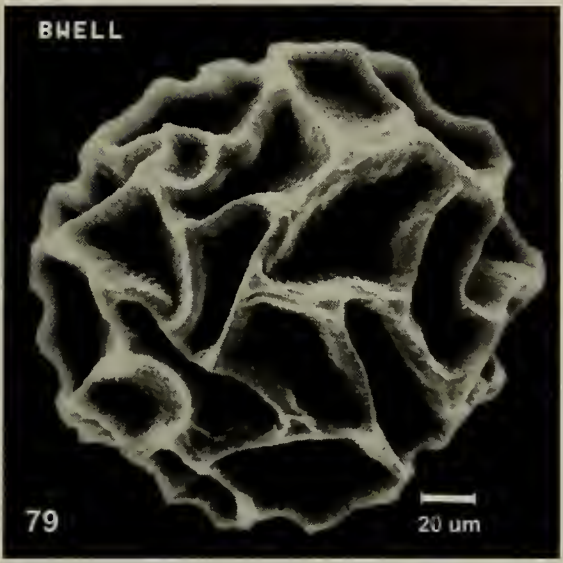
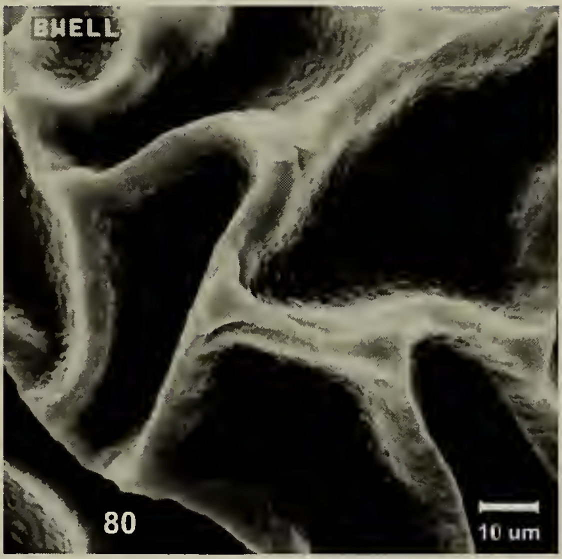


Figure 73. *Branchinella pinnata* cyst shell cross section. Bar = 10 µm.
Figure 74. *Branchinella probiscida* cyst. Bar = 20 µm.
Figure 75. *Branchinella probiscida* cyst surface. Bar = 10 µm.
Figure 76. *Branchinella probiscida* cyst shell cross section. Bar = 5 µm.
Figure 77. *Branchinella simplex* cyst. Bar = 20 µm.
Figure 78. *Branchinella simplex* cyst shell cross section. Bar = 5 µm.





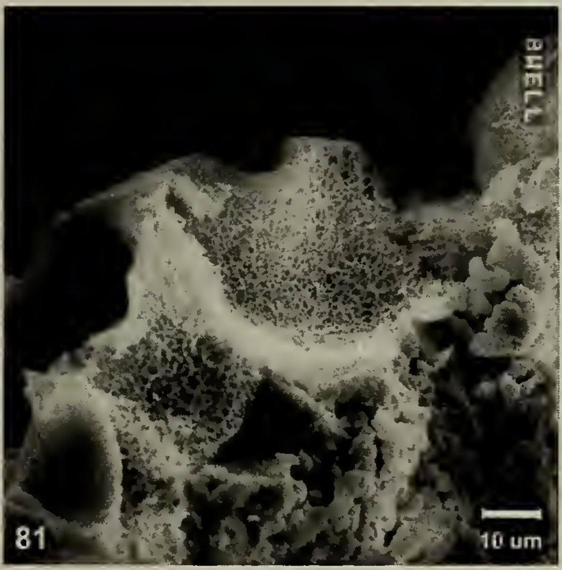


Figure 79. *Branchinella wellardi* cyst. Bar = 20 µm.
Figure 80. *Branchinella wellardi* cyst ridges. Bar = 10 µm.
Figure 81. *Branchinella wellardi* cyst shell cross section. Bar = 10 µm.

The Yule Island Fauna and the Origin of Tropical Northern Australian Echinoid (Echinodermata) Faunas

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Systematic description of the rich Lower Pliocene echinoid fauna from Yule Island, Papua New Guinea, and recently available palaeogeographic data from onshore Papua, the Gulf of Papua and Torres Strait have provided new insights into the origins of the extant tropical northern Australian echinoid fauna. Previous studies of echinoderm origins, hindered by a lack of fossil evidence, concluded that tropical northern Australian echinoderms were derived predominantly by Recent migrations from East Indian and West Pacific stocks. However, 47 per cent of species from the Yule Island fauna are extant in northern Australian waters, indicating that present faunistic patterns were to a large extent, in-place by at least the Lower Pliocene. Palaeogeographic evidence supports the earlier observations of H. Barraclough Fell, that migration of echinoid stock into (and out of) eastern New Guinea and tropical northern Australia probably occurred during the Lower to Middle Miocene, when widespread tropical to sub-tropical reef development occurred across a 5600 km belt from SE Asia through New Guinea and into the SW Pacific as far as Fiji. This favourable pathway for exchange between echinoid stocks disappeared during the Upper Miocene, when the onset of tectonic instability throughout the region, and the establishment of a discontinuous volcanic arc, resulted in influx of terrigenous sediments and may have caused the death of the reef complex. This pattern of sedimentation has persisted to the present.

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KETWORDS: Biogeography, East Indies, Echinoidea, Great Barrier Reef, Palaeogeography, Papua New Guinea, Pliocene, Queensland.

INTRODUCTION

Echinoderms are one of the most intensively studied shallow-water faunas of tropical northern Australia (Endean 1982). Their specific composition and general distribution in the region is well known because of the work of A.H. Clark (1908, 1911a, 1915, 1915-1967), H.L. Clark (1907, 1909, 1915, 1921, 1925, 1926, 1928, 1932, 1938, 1946), Endean (1953, 1956, 1957, 1961, 1965), A.M. Clark (1970), A.M. Clark and Rowe (1971), and Gibbs et al. (1976). However, studies of the origins of these echinoderm faunas have been hindered by the lack of outcropping marine Tertiary sequences with macro-invertebrate faunas (Endean 1957). McNamara and Kendrick (1994) described the Middle Miocene echinoid fauna from the Poivre Formation on Barrow Island, off the Western Australian coast, about 1 500 km WSW of the northern Great Barrier Reef (GBR). The Poivre Formation represents the northern-most exposure of Miocene marine deposits in Australia, and contains the only tropical Miocene macro-invertebrate fauna in Australia (McNamara and Kendrick 1994). The diverse Mio-Pliocene echinoid fauna described by Jeannet and R. Martin (1937) from Java, about 1 000 km WNW of the northern GBR, provides closer (geological) time links with the region than does the Barrow Island fauna. However, caution is necessary in reviewing Jeannet and R. Martin's (1937) fauna, with the validity of some species identifications in need of re-evaluation and name changes required, in accordance with present taxonomic nomenclature. The rich Pliocene Yule Island, Papua New Guinea, echinoid fauna comprising 19 species, is located less than 300 km from the northern end of the GBR, and represents the nearest Tertiary echinoid fauna to the GBR region (Lindley 2003a-c; Fig. 1). This paper examines the importance of the Yule Island fauna with respect to the origins of extant echinoid faunas of tropical northern Australia.

The taxonomic classification used herein follows that of Fell (1966), Fell and Pawson (1966), Durham (1966) and Fischer (1966).

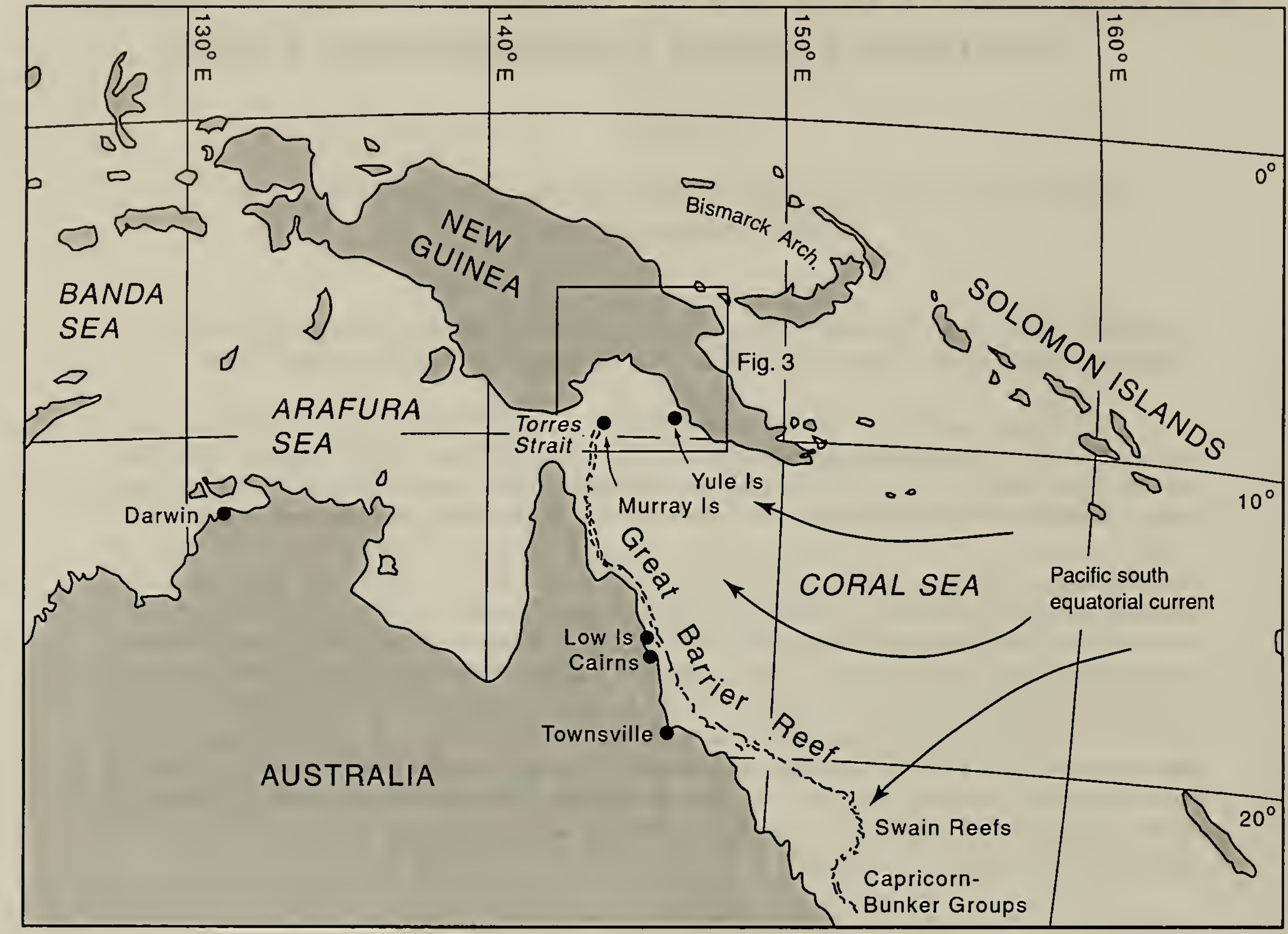

Figure 1. Locality map showing proximity of Yule Island to tropical northern Australia.

FAUNAL PROVINCES AND MAINLAND AND REEF ECHINODERM FAUNAS

Tropical northern Australian seas embrace two faunistic provinces, namely, the Tropical Australian Province and the Solanderian Province (Endean 1957).

The Solanderian Province (Whitley 1932) is restricted to the fauna of the GBR, and includes echinoderms which Endean (1957) designated as 'reef' species (Fig. 2). These echinoderms are considered to have strong affinities with West Pacific stocks, with their pelagic larval stages transported onto the GBR by the Pacific south equatorial current Endean (1957). Endean (1957) considered that the lack of reef structures to the west of Torres Strait has proved a major barrier to the migration of reef stocks into the Solanderian Province.

The Tropical Australian Province of Endean (1957) incorporates the Banksian Province of Whitley (1932) and the Dampierian Province of Hedley (1904, 1926) and extends from Geraldton, on the Western Australian coast, to Wide Bay (26°S) on the southern Queensland coast (Fig. 2). As originally proposed, the Banksian Province included the marine faunas of coastal districts of Queensland, distinct from those of the GBR, and the Dampierian Province along the Western Australian coast. However, Endean (1957) concluded that Torres Strait does not present a major biogeographical boundary separating the Dampierian and Banksian Provinces, and that they should be considered one single faunistic unit. The Tropical Australian Province contains an echinoderm fauna designated by Endean (1957) as 'mainland' species, typically found in habitats dominated by terrigenous sediments. Mainland echinoderms have strong affinities with East Indies stocks, with the principal exchange route being via Torres Strait and the Arafura Sea (Endean 1957). He noted that for Queensland waters, there is little intermingling between reef and mainland stocks.

The East Indies Province lies to the north of Australia (Fig. 2). H.L. Clark (1946) defined the geographic limits of this faunal province, to include the sea and its islands between 90° and 155°E, with a

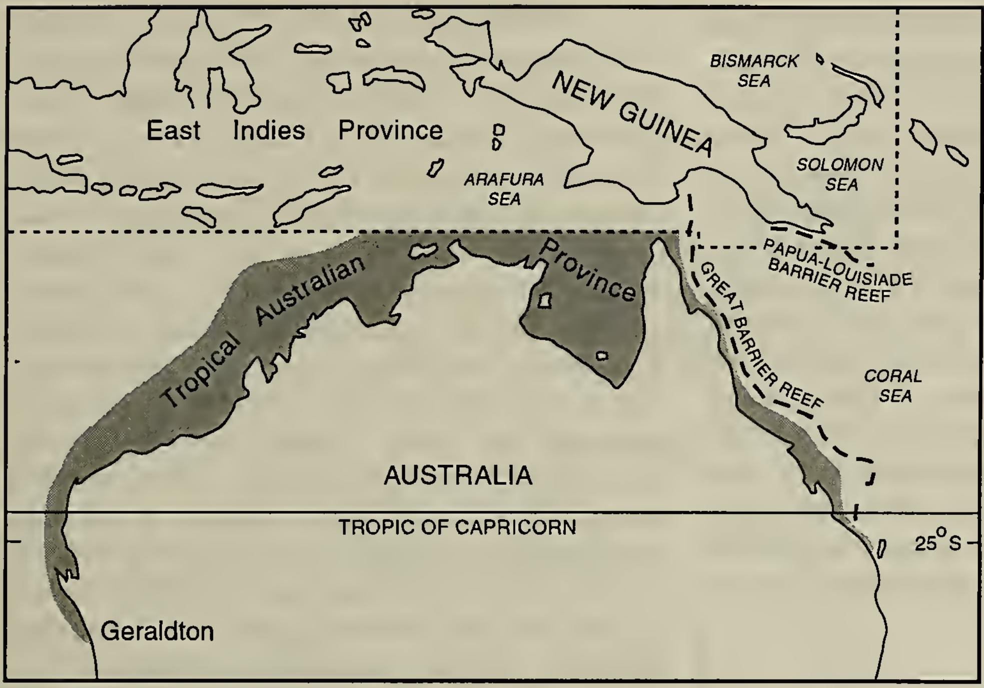

Figure 2. Australia and New Guinea showing the distribution of biogeographical zones mentioned in the text.

southern limit coinciding with the northern limit of what is now know as the Tropical Australian Province. At its eastern extent, it includes the island of New Guinea with the eastern boundary following longitude 155° between the Bismarck Archipelago and the Solomon Islands to 5°N, where it turns west to 130°E.

PREVIOUS BIOGEOGRAPHICAL STUDIES

Austin Hobart Clark and Hubert Lyman Clark

Much of our knowledge of shallow-water Australian echinoderms is based on the intensive work of A.H. Clark and H.L. Clark. A.H. Clark (1911b) concluded that 'The crinoids of Australia have come from the north, from the great East Indian Archipelago'. H.L. Clark (1946) extended A.H. Clark's observations to other echinoderm groups, and concluded that the 'evidence is overwhelming that Australian echinoderms have come southward from the East Indian area, either around the eastern end of New Guinea or across the Timor Sea'. H.L. Clark (1921, 1946) thought that the extant Queensland fauna postdated the 'depression of land areas east of New Guinea which led to the connection of the Coral Sea with the western Pacific and the East Indian region'. The Dampierian fauna had migrated from farther west and was well established when formation of the Torres Strait made mingling of the two faunas possible.

H. Barraclough Fell

Fell (1953) also concluded that there had been a mainly southward migration along the Indo-Malayan archipelago, but noted that northward movements of Australasian echinoderms into the Indo-Pacific could be detected from the Miocene onward. He believed that the archipelago, or its Tertiary equivalents, provided the shallow-water migration route, both into and out of Australia. Fell (1953) noted that profound changes in fossil Australian echinoid faunas occurred during the Upper Miocene, an event he attributed to cooling climate.

Robert Endean

Endean (1957) saw several obstacles to H.L. Clark's (1946) echinoderm migration patterns around New Guinea. Firstly, he believed there was little likelihood of any significant exchange of mainland species via the northern shores of New Guinea. Deep waters are present immediately offshore of the north coast of the island, and the large Sepik and Mamberamo Rivers, by contributing large volumes of freshwater and silt, acted as natural barriers to the spread of littoral echinoderms. He argued that in eastern New Guinea there was a lack of suitable habitats for mainland echinoderms, with the Papua-Louisiade Barrier Reef, extending along the southeastern coast of New Guinea and to the east of the island, representing an additional barrier to the migration of mainland species. Endean (1957) considered that the Fly River, which empties large amounts of silt and freshwater into the Gulf of Papua, acted as an ecological barrier to the spread of reef species to the west of Torres Strait.

Endean (1957) concluded that extant tropical northern Australian echinoderm faunas were derived predominantly from Recent migrations of East Indian and West Pacific stocks. With the Queensland mainland species having strong affinities with those of the East Indies, the principal exchange route of these forms was via the Torres Strait and the Arafura Sea, the deepwater of the Coral Sea serving as a barrier to the spread of mainland species to the West Pacific.

Endean (1957) believed that reef species have strong ties with those of the West Pacific. Given that very few of the reef species which occur outside of Australian waters are present in waters west of Torres Strait, he concluded that there was insignificant exchange of reef species in Queensland waters with those of the East Indies by way of the Torres Strait. Rather, the main route of exchange of Queensland and West Pacific echinoderms must have been by way of either the south coast of eastern New Guinea or the Coral Sea. However, since eastern New Guinea and the GBR are separated by deep water from West Pacific localities, Endean (1957) believed the most likely route of exchange of Queensland's reef species and West Pacific stocks must have been via pelagic larval stages swept into the Coral Sea by the unidirectional Pacific south equatorial current.

ANALYSIS OF THE YULE ISLAND ECHINOID FAUNA

The echinoid faunas from the Lower Pliocene of Yule Island, Middle Miocene of Barrow Island and the Mio-Pliocene of Java each contain mixed assemblages of clypeasteroid, regular and spatangoid echinoids, representative of very different palaeoecologies. Because none of these faunas is dominated by an echinoid group unique to a particular palaeoecology, valid comparisons can be made between these fossil faunas. Using a similar argument, these comparisons are extended to the extant faunas of tropical northern Australia.

Of the 19 echinoid species described from Yule Island, a group of seven species is not recorded from either the Barrow Island and Javanese faunas or the extant echinoid fauna of tropical northern Australia (Table 1 - located after the reference list). These species include *Schizechinus* cf. *tuberculatus* (Pomel), *Phyllacanthus* sp., *Laganum depressum sinaiticum* Fraas 1867, and *L. depressum delicatum* Mazzetti 1894, *Palaeostoma kairukuensis* Lindley 2003c, *Maretia cordata* Mortensen 1948, and *Schizaster (Schizaster) alphonsei* Lindley 2003c. Only two of these echinoids are endemic, viz. *S.(S.) alphonsei* and *P. kairukuensis*. *Laganum depressum sinaiticum*, and *L. depressum delicatum* are notable in that they are otherwise only recorded extant in the western Indian Ocean (Persian Gulf). Similar observations of western Indian Ocean affinities have been made amongst fossil reef corals from the nearby Upper Pliocene-Lower Pleistocene Era Beds, northwest of Yule Island, notably the faviid coral *Parasimplastrea simplicitexta* Umbgrove 1942 (Veron and Kelley 1988).

From an analysis of the remaining 12 species, nine occur in tropical waters of northern Australia either in mainland or reef stocks. These species include *Cyrtechinus verruculatus* (Lütken), *Prionocidaris verticillata* (Lamarck 1816), *Parasalenia poehli* Pfeffer 1887, *Clypeaster humilis* (Leske), *C. latissimus* (Lamarck), *C. reticulatus* (Linnaeus 1758), *Laganum depressum* Lesson in L. Agassiz 1841, *L. decagonale* (de Blainville 1827) and *Maretia planulata* (Lamarck). Nine species are known as fossil in the Mio-Pliocene of Java, viz. *Prionocidaris verticillata*, *Phyllacanthus imperialis* var. *javana* K. Martin 1885, *Temnotrema macleayana* (Tenison-Woods 1878), *L. depressum*, *L. decagonale*, *C. reticulatus*, *C. humilis*, *M. planulata* and *Eupatagus (Eupatagus) pulchellus* (Herklots). The presence of these species as fossil in the Mio-Pliocene of Java, and the observed low levels of species endemism, suggests that the two populations were well-connected prior to and during the Pliocene. By contrast, the Yule Island fauna, as with the Javanese fauna, does not have any species in common with the Middle Miocene fauna of Barrow Island (Table 1).

Significantly, 47 per cent of echinoid taxa (nine species) from the Yule Island fauna, now inhabit northern Australian waters. Clearly, this observation conflicts with Endean's (1957) proposal that tropical Australian echinoderms were derived from Recent migrations from East Indian and West Pacific stocks. Of these nine species, four can be included as mainland stock, viz. *C. verruculatus*, *C. reticulatus*, *C. humilis* and *C. latissimus*; three are of reef stock, viz. *L. decagonale*, *P. verticillata* and *P. poehli*; and two species occur in both reef and mainland waters viz. *L. depressum* and *M. planulata*. Endean (1957) noted a similar, but limited intermingling of echinoderm stock, including the echinoids *M. planulata* and *Salmacis sphaeroides*, in waters surrounding the Low Isles, a coral-dominated locality relatively close to the mainland (about 11 km distant), north of Cairns. He regarded these species as having 'strayed into the coral environment'. Such a near-shore intermingling is envisaged during the Pliocene of Yule Island (Fig. 3).

MIO-PLIOCENE PALAEOGEOGRAPHY OF THE GULF OF PAPUA AND ADJACENT AREAS

Advances in the knowledge of the geological evolution of onshore Papua and the western Coral Sea have emerged with the synthesis of extensive oil well and outcrop data gathered during hydrocarbon exploration of the past 25 years (Home et al. 1990; Carman 1993; Struckmeyer et al. 1993 amongst others). These advances have permitted a detailed

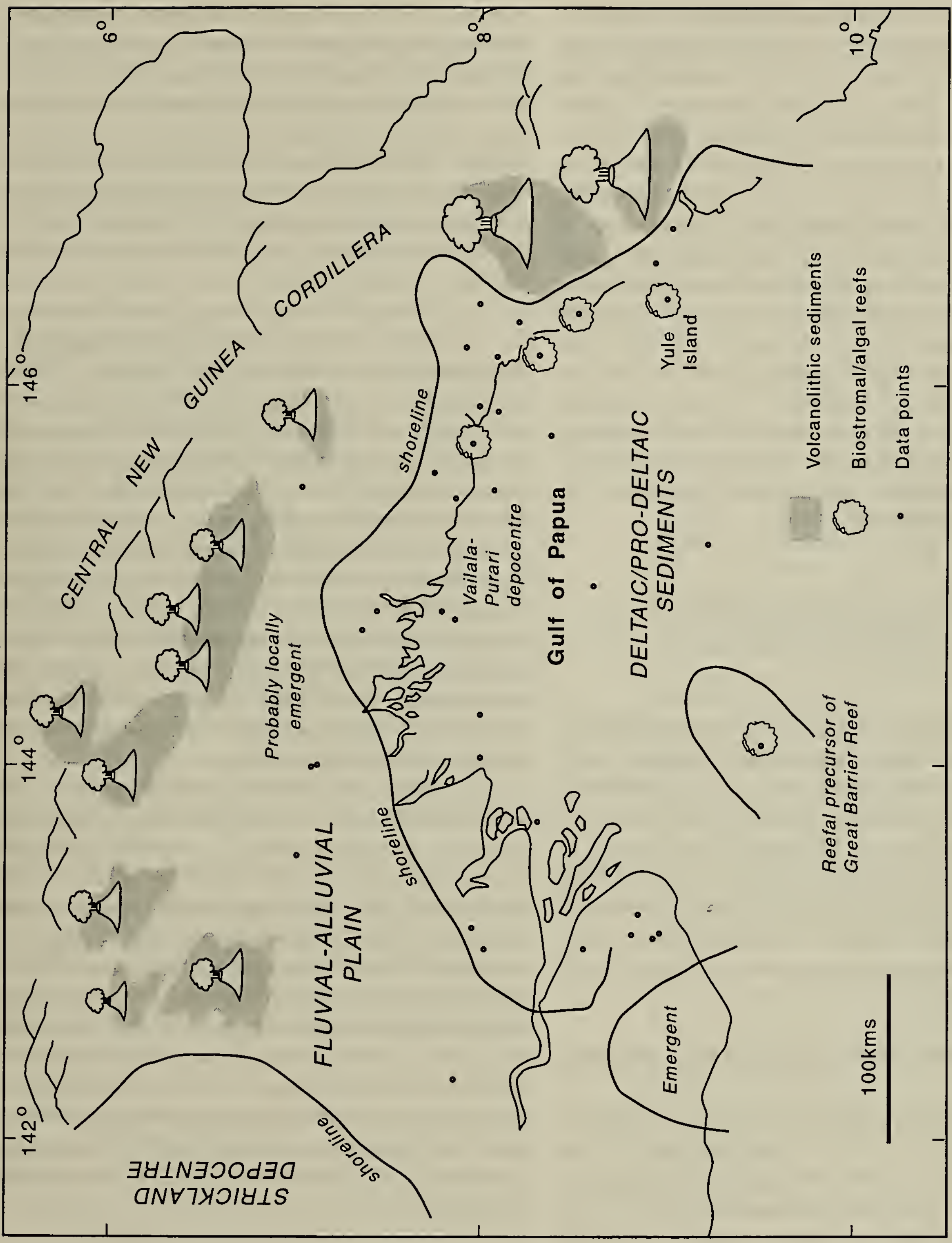

Figure 3. Pliocene (c. N20) palaeogeography of onshore Papua-Gulf of Papua-Torres Strait region showing emergence in Torres Strait, reef development (including the Kairuku Formation at Yule Island) along the northern coastline of the Gulf of Papua and reefal precursors to the Great Barrier Reef. Modified after Carman (1993).

understanding of the development of Mio-Pliocene sedimentary facies and the region's tectonic history.

Tectonic stability during the Lower to Middle Miocene was associated with the development of an extensive tropical to sub-tropical platform carbonate reef complex, not only in the Papuan Basin, but in a region extending from SE Asia to Fiji, a distance of some 5 600 km, and including northern Australia (Coleman and Packham 1976; Home et al. 1990; McNamara and Kendrick 1994). During the late Miocene, the onset of tectonic compression along the edge of the Pacific Plate across much of the region resulted in major uplift and the establishment of a discontinuous volcanic arc. In New Guinea, as elsewhere throughout the region, the influx of terrigenous sediments, to the north and south of an uplifting central cordillera, resulted in the death of the Miocene reef complex (Home et al. 1990; Carman 1993; Struckmeyer et al. 1993). The western end of the Gulf of Papua became emergent during this time and sedimentation was predominantly on a fluvial/ alluvial plain adjacent to a volcanic province (Carman

1993; Fig. 3). South of a fluctuating Pliocene shoreline, poorly sorted deltaic/pro-deltaic sediments were deposited across a greater part of the rapidly subsiding Gulf of Papua (Home et al. 1990; Carman 1993). More than 4 000 m of sediment were deposited in the Vailala-Purari depocentre, near the mouth of the Purari River (Carman 1993), indicative of very rapid subsidence. Subsidence and the large quantities of clastic sediment were deterrents to coral growth across a large part of the region. However, biohermal reef limestone (foraminiferal zone c. N20: Lower Pliocene/Upper Pliocene boundary), surrounded by interpreted argillaceous micritic limestone, penetrated in the Anchor Cay 1 Well, only 250 km WSW of Yule Island, is associated with reefal precursors of the present day GBR which existed farther south (Carman 1993). These patterns of sedimentation have continued to the present day (Home et al. 1990).

ORIGIN OF TROPICAL AUSTRALIAN ECHINOID FAUNAS

Preamble

Migration of adult littoral echinoderms may occur via connected shallow-water, typically near-shore habitats. Deep water, a lack of interconnected reefal structures, and large influxes of freshwater and silt poured out from large coastal rivers, all act as ecological barriers to their spread (Endean 1957). However, for echinoderms possessing prolonged larval stages, transport of pelagic young by currents, may distribute species across deep water (Endean 1957; Nichols 1969).

Lower to Middle Miocene origin of the Yule Island fauna

The Yule Island echinoid fauna comprises representatives of reef and mainland species and species common to both reef and mainland faunas. Comparisons show that, with the relatively low level of species endemism evident in the Yule Island echinoid fauna, prior to the Lower Pliocene the fauna was well-connected with at least the population in Java, having not developed in isolation. Palaeogeographic evidence indicates that an excellent interconnected exchange route for echinoderms existed during the Lower to Middle Miocene when an extensive tropical to sub-tropical reef complex existed across a 5 600 km belt extending from SE Asia through New Guinea to Fiji. Both reef and mainland species migrated along this reef complex.

Endean's (1957) West Pacific influence on extant reef echinoid populations of tropical northern Australia may be more apparent than real. For all echinoids, reef and mainland, only one, *Rhynobrissus hemiasteroides* Agassiz, is endemic to the West Pacific. Eleven species occur in the Indian Ocean and East Indies, and 21 are widely distributed throughout the Indo-Pacific. The origins of the reef stock at Yule Island, with its apparent 'West Pacific affinity', is readily accounted for by the interconnected pathway afforded by the 5 600 km long Lower to Middle Miocene reef complex that extended well into the SW Pacific.

Fell (1953) noted that a great extinction of the Australasian echinoid stocks occurred during the late Miocene, an event he and Fleming (1949) attributed to a cooling climate. The cooling event coincided with the previously noted retreat of widespread platform carbonate deposition from SE Asia and the SW Pacific. However, the demise of the Miocene carbonate platform in the western Coral Sea was accompanied by a resurgence of tectonic instability and associated volcanism. This tectonic instability is evident in the post-Miocene geological record that succeeds carbonate deposition throughout the region (Coleman and Packham 1976) and it is possible that an increase in volcanic activity, and in-turn atmospheric volcanic aerosols, was responsible for the late Miocene cooling climate.

The late Miocene extinction saw the disappearance of, for example, the warm-water echinoid genera *Schizaster* L. Agassiz 1836 and *Phyllacanthus* Brandt 1835 from New Zealand (Fell 1953). Fell (1953) considered that the impact of the extinction event in low latitudes was reduced. A comparison of the Yule Island fossil fauna with low latitude Miocene faunas from India, Java and Fiji supports this view. Eight species from the Yule Island fauna, *P. imperialis* var. *javana*, *P. verticillata*, *T. macleayana*, *L. decagonale*, *L. depressum*, *C. reticulatus*, *C. humilis* and *E.(E.) pulchellus* are known from the Miocene faunas of these regions (Jeannet and R. Martin 1937; Mortensen 1948; Lindley 2001, 2003a-c).

Origin of Tertiary and extant northern Australian echinoid faunas

As previously noted, mainland and reef echinoid populations are believed to have established themselves in the region to the north of Australia and adjacent areas during the Lower to Middle Miocene when platform carbonate sedimentation prevailed throughout much of SE Asia and the SW Pacific. Fell (1953) proposed a broadly similar outline for Australasian echinoid origins.

The Middle Miocene echinoid fauna from the Poivre Formation on Barrow Island is a far from complete representation of the original fauna

(McNamara and Kendrick 1994). The fauna (at a generic level) has much in common with the Miocene faunas of Java and India (McNamara and Kendrick 1994), but its relative geographic isolation during the Miocene, 15-20°S of Yule Island and Java, may explain the faunal mismatch at species level. Barrow Island during the early Miocene was located about 40°S, Yule Island 25°S and eastern Indonesia 20°S (Veevers et al. 1991: Fig. 12). McNamara and Kendrick (1994) noted that, at a generic level, the echinoid fauna has strong affinities with modern communities of the region.

Endean (1957) considered that the extant NW Australian echinoderm fauna, dominated by mainland species, has strong affinities with East Indies stocks, but exhibits a high degree of endemism. The deep water of the Timor and Arafura Seas appears to have served as a barrier to any significant post-Miocene exchange between the East Indies and NW Australian mainland faunas, and exchange with Queensland mainland faunas has only been possible since the opening of Torres Strait. The strait was emergent during at least the late Miocene-early Pliocene (Fig. 3). Ekman (1953) noted that the average age of echinoid species was at most 4-6 million years, and the origin of many endemic species in the NW Australian mainland fauna may have resulted from the long period of geographic isolation following the demise of the Lower to Middle Miocene (10-20 Ma) reef.

The Lower Pliocene coral growth at Yule Island (foraminiferal zones N18/N19-N20: 4-6 Ma) was part of a chain of interconnected reefs extending NW along the northern margin of the Gulf of Papua, remnants of the formerly extensive Miocene reef complex (Fig. 3). Reef species were confined to these coral structures, which were in-turn flanked by terrigenous sediments, a habitat dominated by mainland species. In the southern Gulf of Papua, reef precursors to the GBR did not appear until 3-4 Ma (Lower Pliocene/Upper Pliocene boundary: foraminiferal zone c. N20: Carman 1993; Haig 1996). These precursor reefs were situated only 250 km WSW of Yule Island and extended farther south (Carman 1993), indicating that, although large quantities of terrigenous sediment at this time were deterrents to coral growth, reefs were able to establish themselves in parts of the Gulf of Papua. Of the nine echinoid species (47 per cent) of the Yule Island fauna that are recorded extant in northern Australian waters, five are recorded on the GBR, suggestive of ties between both faunas. With major barriers to echinoderm migration existing to the west (Torres Strait was emergent) and along northern New Guinea (deep waters and terrigenous sedimentation), it is likely that species exchange occurred from existing Pliocene Gulf of Papua echinoid stocks to proto-GBR structures and farther south.

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TABLE 1: Distribution of selected shallow-water tropical echinoid groups in the East Indies and Australia. Compiled from Endean (1957); A.M. Clark and Rowe (1971); Gibbs et al. (1976); Jeannet and R. Martin (1937); Philip (1963); Mortensen (1943); H.L. Clark (1946); Lindley (2001, 2003a,b,c); McNamara and Kendrick (1994); and McNamara and Philip (1980).

Species	**Java, Mio-Pliocene**	**Yule Is, Lower Pliocene**	**Barrow Is, Middle Miocene**	**Australian 'mainland' species**	**Australian 'reef' species**
CIDARIDAE					
Phyllacanthus dubius	x				
Phyllacanthus dubius var. *sundaica*	x				
Phyllacanthus imperialis	x			x	x
Phyllacanthus imperialis var. *javana*	x	x			
Phyllacanthus sp.		x			
Phyllacanthus cf. *clarkeii*			x		
Prionocidaris bispinosa				x	x
Prionocidaris verticillata	x	x			x
Prionocidaris baculosa	x				
Prionocidaris baculosa var. *annulifera*	x				
Stylocidaris reini	x				
Cidaris mertoni	x				
Cidaris aculeata	x				
Cidaris sp.	x				
Chondrocidaris sundaica	x				
Eucidaris sp.			x		
Goniocidaris cf. *murrayensis*			x		
DIADEMATIDAE					
Diadema setosum				x	x
Diadema savignyi					x
Echinothrix calamaris					x
Echinothrix diadema					x
Astropyga radiata				x	
PARASALENIIDAE					
Parasalenia poehli		x			x
Parasalenia gratiosa				x	x
Parasalenia sp.					x
TOXOPNEUSTIDAE					
Schizechinus cf. *tuberculatus*		x			
Cyrtechinus verruculatus		x		x	
Nudechinus darnleyensis				x	
Nudechinus multicolor					x
Tripneustes gratilla				x	x
Tripneustes pregratilla			x		
Gymnechinus epistichus				x	x
Toxopneustes pileolus				x	x

Species	Java, Mio-Pliocene	Yule Is, Lower Pliocene	Barrow Is, Middle Miocene	Australian 'mainland' species	Australian 'reef' species
ECHINOMETRIDAE					
Echinometra mathaei				x	x
Heterocentrotus mammillatus					x
Echinostrephus aciculatus					x
Echinostrephus molaris					x
ECHINONEIDAE					
Echinoneus cyclostomus					x
Echinoneus abnormalis					x
TEMNOPLEURIDAE					
Temnopleurus alexandri				x	x
Temnopleurus toreumaticus	x			x	
Salmacis belli				x	
Salmacis sphaeroides				x	x
Salmacis sphaeroides belli	x				
Salmacis rarispina	x				
Salmacis bicolor	x				
Temnotrema macleayana	x	x			
Temnotrema bothryoides				x	
Temnotrema siamense				x	x
Temnotrema phoenissa					x
Opechinus cf. *collignoni*	x				
Opechinus cf. cheribonensis	x				
Opechinus madurae	x				
Opechinus percultus	x				
Opechinus percultus var. *oligoporus*	x				
Martinechinus molengraaffi	x				
Microcyphus sp.	x				
Desmechinus rembangensis	x				
Desmechinus erbi	x				
Mespilia globulus				x	x
Temnopleurid sp.					x
ARACHNOIDIDAE					
Arachnoides placenta				x	
CLYPEASTERIDAE					
Clypeaster reticulatus	x	x		x	
Clypeaster humilis	x	x		x	
Clypeaster latissimus		x		x	
Clypeaster telurus				x	
Clypeaster blumenthali	x				
Clypeaster brevipetalus	x				
Clypeaster butleri			x		
Clypeaster cf. malumbangensis	x				
Clypeaster sp. A	x				

Species	Java, Mio-Pliocene	Yule Is, Lower Pliocene	Barrow Is, Middle Miocene	Australian 'mainland' species	Australian 'reef' species
CLYPEASTERIDAE (Cont)					
Clypeaster sp. B	x				
LAGANIDAE					
Laganum decagonale	x	x			x
Laganum depressum	x	x		x	x
Laganum depressum var. *sinaiticum*		x			
Laganum depressum var. delicatum		x			
Laganum herklotzi	x				
Peronella lesueuri	x			x	x
Peronella orbicularis				x	x
Sismondia javana	x				
ASTRICLYPEIDAE					
Echinodiscus angulosus	x				
Echinodiscus tenuissimus				x	
Echinodiscus sp.	x				
FIBULARIIDAE					
Fibularia crispa	x				
Fibularia cf. *scabra*	x				
Fibularia rhedeni	x				
Fibularia ovulum					x
Fibularia volva				x	
Fibularid sp.			x		x
Echinocyamus cf. *cribellum*	x				
Echinocyamus sp.	x				
ECHINOLAMPADIDAE					
Echinolampas ovatus	x				
Echinolampas elevatus	x				
Echinolampas depressus	x				
Echinolampas tumulus			x		
PLIOLAMPADIDAE					
Pliolampas minutus	x				
Pliolampas javanus	x				
Pliolampas elevatus	x				
HEMIASTERIDAE					
Hemiaster cf. *eupetalum*	x				
Opissaster sp.	x				
SPATANGIDAE					
Maretia planulata	x	x		x	x
Maretia cordata		x			
Maretia bandaensis	x				
Maretia mojsvari	x				

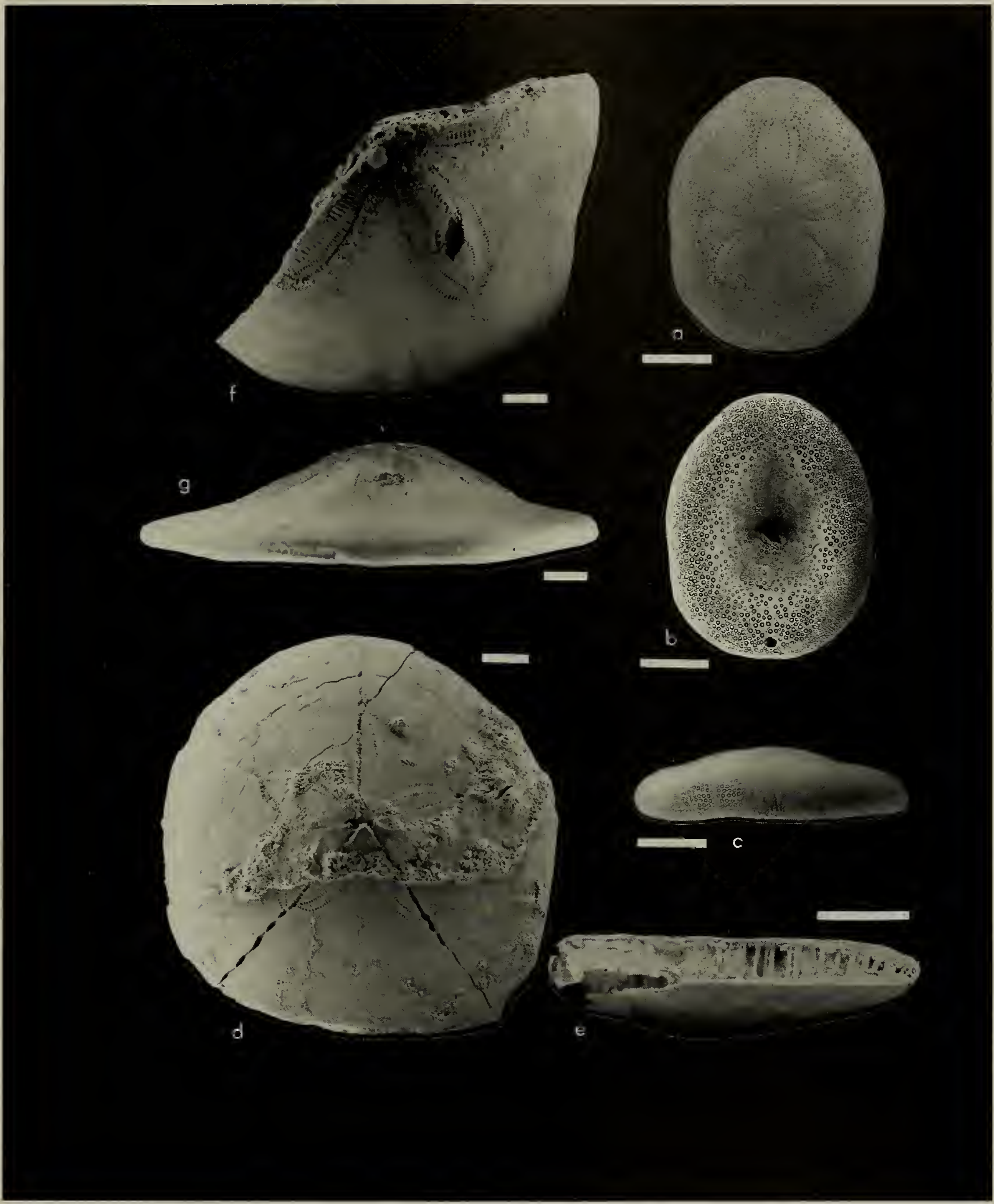
Species	**Java, Mio-Pliocene**	**Yule Is, Lower Pliocene**	**Barrow Is, Middle Miocene**	**Australian 'mainland' species**	**Australian 'reef' species**
PALAEOSTOMATIDAE					
Palaeostoma kairukuensis		x			
BRISSIDAE					
Metalia spatagus				x	x
Metalia sternalis					x
Brissus latecarinatus	x			x	x
Brissus sp.	x				
Rhynobrissus hemiasteroides				x	
Eupatagus (Eupatagus) pulchellus	x	x			
Eupatagus affinis	x				
Eupatagus sp.	x				
LOVENIIDAE					
Breynia aff. *carinata*			x		
Breynia australasiae				x	
Breynia paucituberculata	x				
Breynia sp. a	x				
Breynia sp. b	x				
Lovenia elongata				x	x
SCHIZASTERIDAE					
Schizaster (Schizaster) lacunosus				x	x
Schizaster (Schizaster) alphonsei		x			
Schizaster (Schizaster) compactus				x	
Schizaster (Schizaster) aff. *compactus*			x		
Schizaster (Schizaster) sp. A					x
Schizaster subrhomboidalis	x				
Schizaster progoensis	x				
Schizaster cf. *pratti*	x				
Schizaster excavatus	x				
Schizaster jeanneti	x				
Schizaster sp. 1	x				
Schizaster sp. 2	x				
Schizaster sp. 3.	x				
Schizaster sp.	x				
Proraster jukesii	x				
Moira lethe				x	
Hemifaorina tuber	x				

ERRATA

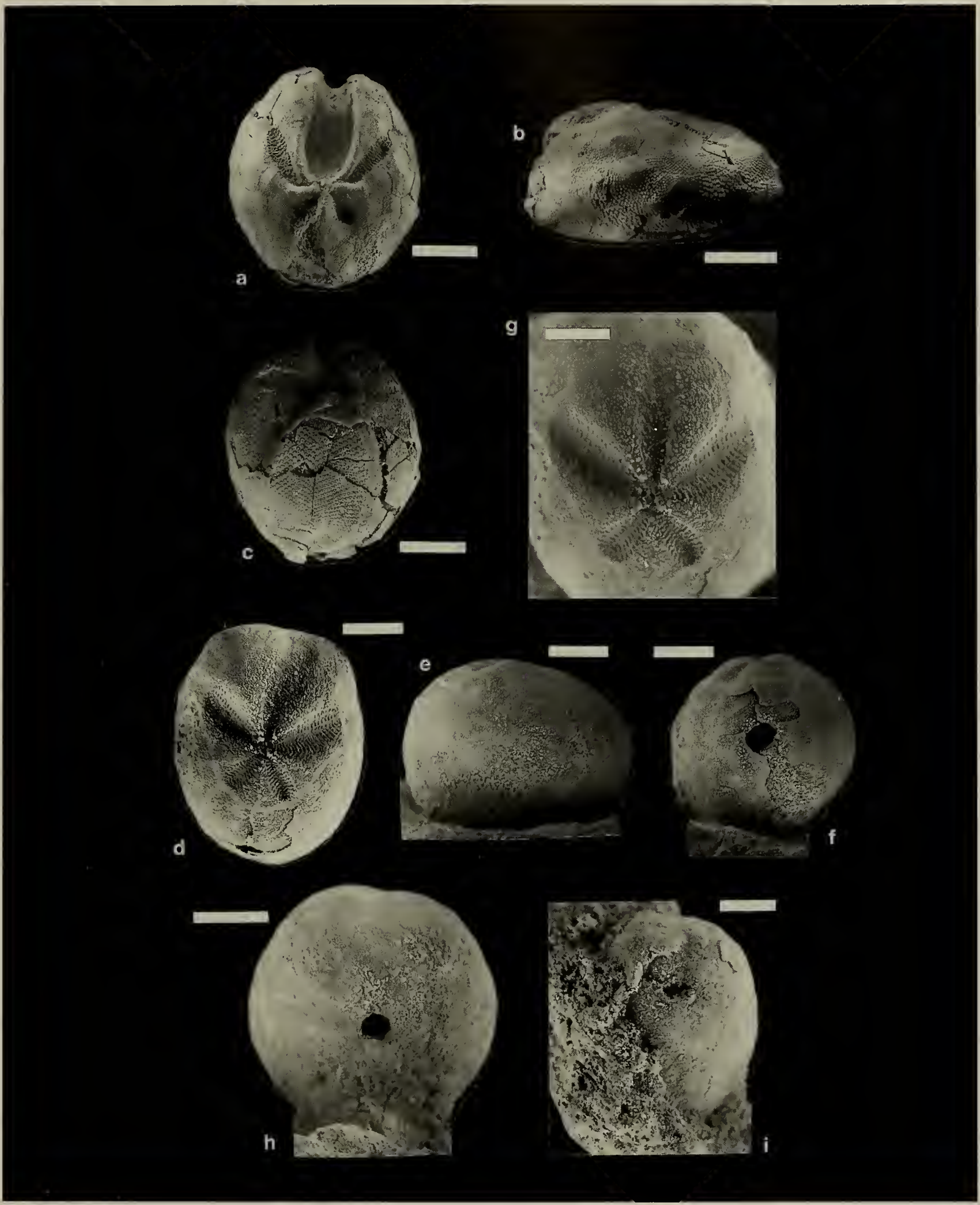
The following figures are replacements for:

Figure 2 (page 128) of Lindley, I.D. (2003). Echinoids of the Kairuku Formation (Lower Pliocene), Yule Island, Papua New Guinea: Clypeasteroida. *Proceedings of the Linnean Society of New South Wales* **124**, 125-136.

Figure 1 (page 155) of Lindley, I.D. (2003). Echinoids of the Kairuku Formation (Lower Pliocene), Yule Island, Papua New Guinea: Spatangoida. *Proceedings of the Linnean Society of New South Wales* **124**, 153-162.



Replacement Figure 2 (page 128) of Lindley, I.D. (2003). Echinoids of the Kairuku Formation (Lower Pliocene), Yule Island, Papua New Guinea: Clypeasteroida. *Proceedings of the Linnean Society of New South Wales* **124**, 125-136.



Replacement Figure 1 (page 155) of Lindley, I.D. (2003). Echinoids of the Kairuku Formation (Lower Pliocene), Yule Island, Papua New Guinea: Spatangoida. *Proceedings of the Linnean Society of New South Wales* **124**, 153-162.

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Some living and fossil echinoderms from the Bismarck Archipelago, Papua New Guinea, and two new echinoid species

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Starfish and sea-urchin records of the Bismarck Archipelago, Papua New Guinea, are scattered throughout the literature of the past 160 years. This paper lists the region's valid starfish and sea-urchin species records contained in the literature. In addition, records of 17 species of starfish and sea-urchins from material in the Department of Geology, Australian National University and the East New Britain Historical and Cultural Centre collections are included, with descriptions of two new sea-urchin species, the schizasterid *Schizaster (Paraster) ovatus* sp. nov. and the echinometrid *Heliocidaris robertsi* sp. nov. Some Tertiary echinoids from the region are described for the first time, namely *Stereocidaris* cf. *squamosa* Mortensen 1928 (Lower-Middle Miocene: Manus Island), *Stereocidaris* sp. (Pliocene: east New Britain), *Phyllacanthus* sp. (Pliocene: east New Britain) and *Echinoneus* sp. (Pleistocene-Holocene: Tanga Group, New Ireland).

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KEYWORDS: Asteroidea, Bismarck Archipelago, East Indies, Echinoidea, Extant, Fossil, Papua New Guinea, West Pacific.

INTRODUCTION

The Bismarck Archipelago, northern Papua New Guinea (PNG), encompasses the islands of New Britain, Bougainville, New Ireland and adjacent groups (Tabar, Lihir, Tanga and Feni), St. Matthias Group, the Admiralty Group, including Manus Island, and the surrounding waters of the Bismarck Sea (Fig. 1). It lies along the easternmost boundary of the East Indian Faunal Province. To the east and southeast lies the West Pacific Ocean or Melanesia faunal province (Endean 1957 and A.M. Clark and Rowe 1971, respectively).

Knowledge of the extant starfishes and sea-urchins (Echinodermata: Asteroidea and Echinoidea, respectively) from the Bismarck Archipelago comprises records scattered throughout a diverse literature of the past 160 years. The earliest described asteroid is *Echinaster eridanella* Müller and Troschel 1842 (= *Echinaster luzonicus* Gray 1840) with a type locality in New Ireland. Sladen (1889) and A. Agassiz (1879 1881) described the asteroids and echinoids, respectively, collected during the 1873-76 voyage of *H.M.S. Challenger*. This expedition passed through the Admiralty Group and retrieved two new deep-water echinoids in the Bismarck Sea (the arbaciid *Pygmaeocidaris prionigera* (A. Agassiz 1879) and the temnopleurid *Prionoechinus sagittiger* A. Agassiz 1879), at a site between the Admiralty Group and New Guinea. Loriol (1891) described additional asteroids from the archipelago, including *Nardoa finschi* de Loriol 1891 (= *Nardoa tuberculata* Gray 1840) and *Nardoa mollis* de Loriol 1891 (= *Nardoa novaecaledoniae* Perrier 1875), both with type localities in New Britain. Bell (1899) described the non-holothurian echinoderms collected by Arthur Willey during his 1895-97 visit to New Britain and the Loyalty Islands (Willey 1902). H.L. Clark (1925) redescribed several of Willey's Bismarck Archipelago echinoids and erected two new species (the arbaciid *Coelopleurus elegans* (Bell 1899) and the diadematid *Micropyga nigra* H.L. Clark 1925) with type localities in New Britain. H.L. Clark (1946) and A.H. Clark (1954) recorded additional asteroids and echinoids from the archipelago. Struder (1876, 1880) and H.L. Clark (1908) provided descriptions of the extant echinoderm fauna of west New Guinea, a region contiguous with the Bismarck Archipelago.

During the past 20 years echinoderm research in the region has concentrated on the biology of asteroids and comatulid crinoids at Hansa Bay and Madang, on the southern shores of the Bismarck Sea

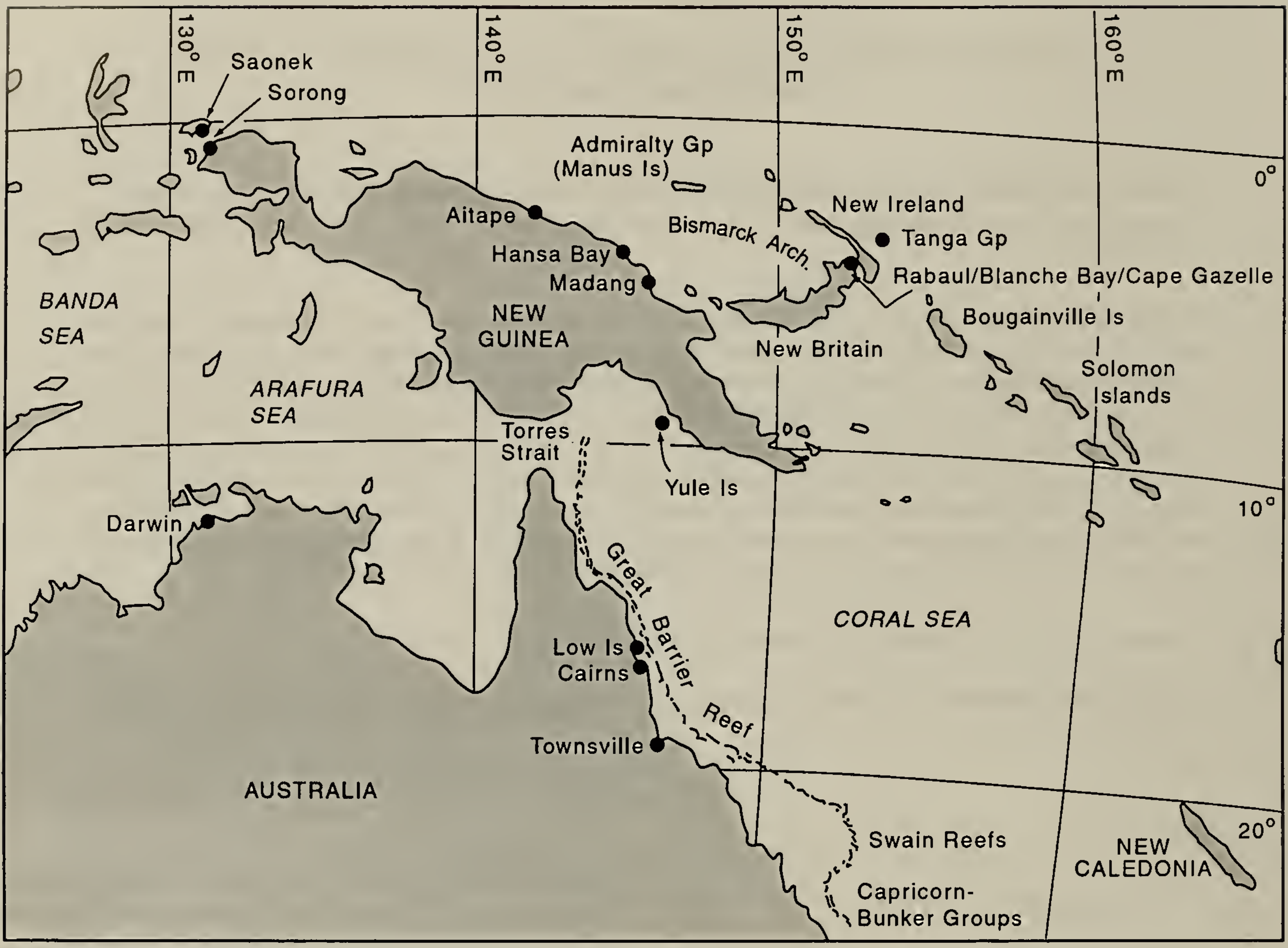

Figure 1. Locality map showing the Bismarck Archipelago, Papua New Guinea, and other localities discussed in text.

(Britayev et al. 1999; Bouillon and Jangoux 1984; Eeckhaut et al. 1996; Messing 1994).

This paper describes some extant asteroids and echinoids from the Bismarck Archipelago. It also provides for the first time, a tabulation of previously reported asteroid and echinoid occurrences (Tables 1 and 2 respectively; tables located after the reference list) in the region. Several Tertiary echinoids from the archipelago are also described. The author is not aware of any previous description of the region's fossil echinoderm fauna.

The specimens described in this paper were collected between 1981-2003, and do not necessarily represent the results of thorough, methodical site collections. The Cape Gazelle, east New Britain, locality encompasses any one of a number of nearby localities, including Tovarur Plantation, Reiven Beach and southeastern Tokua Airport. Full systematic descriptions are provided for all fossil species while in most cases, only brief remarks concerning the significance of occurrences are provided for extant species. Specimens prefixed ANU are housed in the Department of Geology, The Australian National University; specimens prefixed B are housed in the East New Britain Historical and Cultural Centre, Kokopo, East New Britain Province, PNG. Terminology and classification used herein follows that of the *Treatise on Invertebrate Paleontology* and A.M. Clark and Rowe (1971).

SYSTEMATIC DESCRIPTIONS

Class STELLEROIDEA Lamarck 1816
Subclass ASTEROIDEA de Blainville 1830
Order VALVATIDA Perrier 1884
Suborder GRANULOSINA Perrier 1894
Family OPHIDIASTERIDAE Verrill 1867
Genus LINCKIA Nardo 1834

Synonymy

Cribella Agassiz 1835 (*non* Forbes 1841).
Acalia Gray 1840.
Catantes, *Undina* Gistl 1847.

Type species

Linkia typus Nardo 1834 (= *Asterias laevigatus* Linnaeus 1758) by original designation.

Linckia multifora (Lamarck 1816)

Synonymy

Asterias multifora Lamarck 1816, p. 565.
Linckia leachi Gray 1840, p. 285: Mauritius.
Linckia costae Russo 1894, p. 163: Daret Is., Red Sea.

Materials and locality

Two specimens, ANU 60651-2, collected at Ralum, Blanche Bay, East New Britain Province, PNG.

Remarks

Linckia multifora (Lamarck 1816) is widely distributed throughout the Indo-Pacific, from the Red Sea to the Hawaiian Islands (A.M. Clark and Rowe 1971). This record is the first from New Guinea.

Family OREASTERIDAE
Genus PROTOREASTER Döderlein 1916

Type species

Asterias nodosa Linnaeus 1758, p. 420, by subsequent designation.

Protoreaster nodosus (Linnaeus 1758)

Synonymy

Oreaster nodosus, Bell 1884, p. 70; H.L. Clark 1908, p. 280; Fisher 1911, p. 346; H.L. Clark 1921, p. 31.
Pentaceros nodosus, Bell 1899, p. 136.
Protoreaster nodosus, Döderlein 1916, p. 420; H.L. Clark 1946, p. 106; A.M. Clark and Rowe 1971, p. 34, 54; Rowe and Gates 1995, p. 106.

Material and locality

Single beach worn specimen, ANU 60650, collected at Ralum, Blanche Bay, East New Britain Province, PNG.

Remarks

Protoreaster nodosus (Linnaeus 1758) is a common East Indian starfish with a range extending to the West Pacific (Caroline Islands) (H.L. Clark 1946; A.M. Clark and Rowe 1971). Bell (1899) previously described the species from the collections of Arthur Willey in Blanche Bay. H.L. Clark (1908, p. 280) described variations in specimens from several west New Guinea localities (Humboldt Bay, Sorong, Ansus, Jappen Island). Although the present specimen (R/r = 20/9 mm) has lost most of its granules and abactinal plates, it is identified as a juvenile *P. nodosus* (L.M. Marsh, pers. comm.). It is similar to a specimen of *P. nodosus* in the Western Australian Museum (WAM 599-76: R/r = 27/11 mm) collected by L.M. Marsh from Pulau Langkai, off south Sulawesi, Indonesia. Two juvenile specimens (R = 11-12 mm) from the Andaman Islands, figured and described by Koehler (1910: plate XVI, fig. 1) as *Anthenea* sp., are also very similar to ANU 60650. These specimens may also be *P. nodosus* (L.M. Marsh, pers. comm.).

Class ECHINOIDEA Leske 1778
Subclass PERISCHOECHINOIDEA M'Coy 1849
Order CIDAROIDA Claus 1880
Family CIDARIDAE Gray 1825
Subfamily STEREOCIDARINAE Lambert 1900
Genus STEREOCIDARIS Pomel 1883

Synonymy

Typocidaris Pomel 1883
Phalacrocidaris Lambert 1902
Anomocidaris Agassiz and Clark 1907

Type species

Cidaris cretosa Mantell 1835; subsequent designation Lambert and Thiéry 1909 (Feb., p. 31; *non* Mar., where *C. merceyi* was designated, p. 152).

Stereocidaris cf. **squamosa** Mortensen 1928
Figs 2, 3a

Synonymy

Stereocidaris indica Bell 1909, p. 21; H.L. Clark 1925, p. 26.
Stereocidaris squamosa Mortensen 1928b, p. 70; Mortensen 1928a, p. 245.

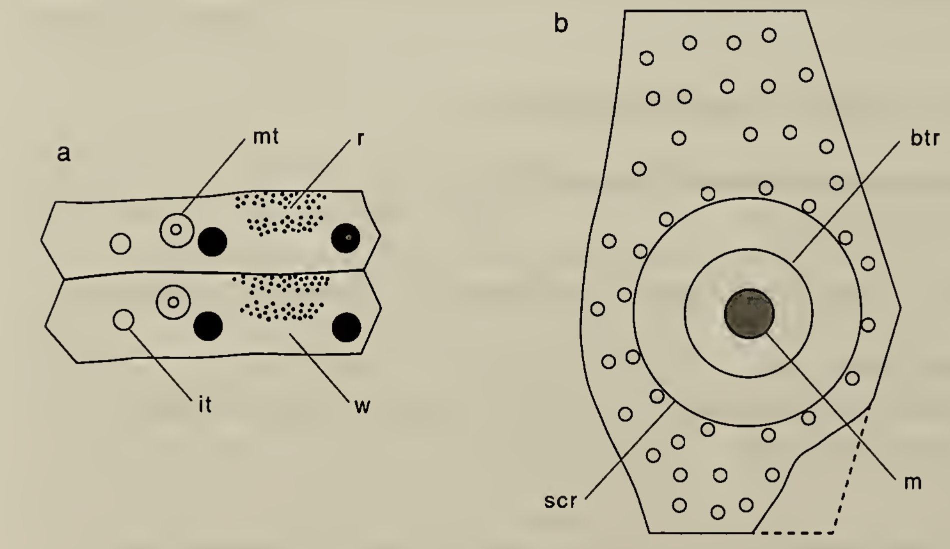

Figure 2. ***Stereocidaris* cf. *squamosa* Mortensen 1928. Lower-Middle Miocene, Manus Island, Manus Province. 2a-b, plating diagrams at ambitus for ambulacrum, interambulacrum. Abbreviations: btr basal terrace; it inner tubercle; m mamelon; mt marginal tubercle; r ridge; scr scrobicular ring; w wall.**

Material

An incomplete specimen ANU 60638, with an interambulacral plate and portion of ambulacral series.

Locality and horizon

Village of Drankei, west bank of Wari River, central southern Manus Island, Manus Province, PNG. Grid reference 060612 Lorengau 1: 100 000 Sheet 8393 (Edition 1). The collection horizon is an outlier of the (lower) Mundrau Limestone. A sample of limestone from a nearby outlier of the Mundrau Limestone at Metawarei village, 0.5 km northwest of Drankei village, contained a foraminiferal assemblage of mid or upper Tf1 age, and suggests a late Lower

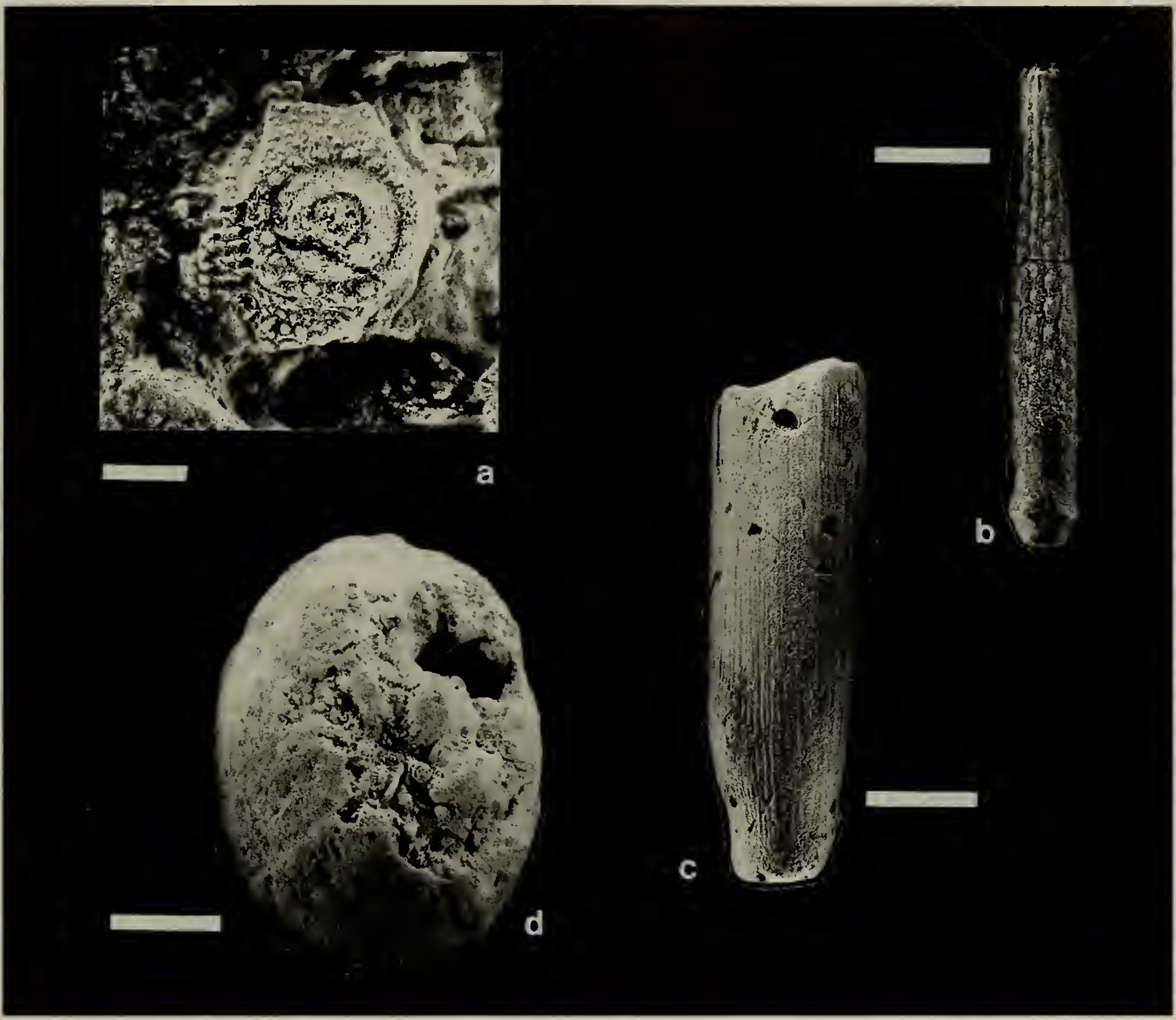

Figure 3. Tertiary echinoids from the Bismarck Archipelago. *Stereocidaris* cf. *squamosa* Mortensen 1928. Lower-Middle Miocene, Manus Island, Manus Province. 3a, ANU 60638, incomplete interambulacral plate with large tubercle and part of adjacent ambulacral plating (refer to Figs 2a, b for plating diagram). Bar scale = 2.5 mm. *Stereocidaris* sp. Pliocene, Sikut River area, East New Britain Province. 3b, ANU 60639, primary spine. Bar scale = 2.5 mm. *Phyllacanthus* sp. Pliocene, Mevelo River area, East New Britain Province. 3c, ANU 60637, proximal portion of primary spine. Bar scale = 5 mm. *Echinoneus* sp. Pleistocene-Holocene, Boang Island, Tanga Group, New Ireland Province. 3d, ANU 60640, aboral view of worn specimen. Bar scale = 5 mm.

Miocene or earliest Middle Miocene age for the unit (Francis 1985).

Description

Test size and shape unknown.

Ambulacra sinuate, rather broad, ca. 39% of width of interambulacra. Interporiferous zone about twice width of a pore-zone. Interporiferous zone with distinctly vertical series of marginal tubercles and inner tubercles; marginal tubercles slightly larger than those of inner series. Pores are rather small, circular, nonconjugate and separated by a broad wall; ridge low and narrow. The arrangement of pores and tubercles in ANU 60638 is strikingly similar to that described for *Stereocidaris squamosa* Mortensen 1928 by Mortensen (1928a: 245 and Plate LXX, fig. 7).

Interambulacral plate higher than broad (height:width = 8.0:5.5) with aureole of moderate size but not very deep, well separated. The very high plate of ANU 60638 exhibits a broad miliary covered space between successive aureoles, one unequal to the other, indicating it to be from an upper interambulacral, or aboral, position on test (Fig. 2). Mamelon apparently large, the part of plate is damaged in ANU 60638. Edge of aureole is not raised, and the scrobicular tubercles are not prominent. Outside the scrobicular ring, the interambulacral plate has a sparse to moderate covering of tubercles of similar size to scrobicular tubercles. On the adradial edge of plate there are a few secondary tubercles outside the scrobicular ring.

Apical and periproctal systems unknown.

Details of primary and secondary spines unknown.

Remarks

Stereocidaris Pomel 1883 is a well characterised genus with both fossil and extant species (Mortensen 1928a; Chapman and Cudmore 1934). The genus is distinctive for its usually very high interambulacral plates, ambulacra that are generally conspicuously sinuate and nonconjugate pores (Mortensen 1928a; Fell 1966). The oldest occurrence of the genus is from the Cretaceous of Europe. In the Tertiary it is known from the Eocene of Europe and Australia, Oligocene of New Zealand, Miocene of Australia and Indonesia, and Pliocene of Australia and New Zealand (Mortensen 1928a; Chapman and Cudmore 1934; Fell 1966). Mortensen (1928a) noted the lack of fossil *Stereocidaris* from the Indo-Pacific, with K. Martin's (1918) record of the occurrence of a spine of *Dorocidaris papillata* (= *Stereocidaris*) from the Miocene of Java the only known fossil. This may well represent a collection bias. Extant species of *Stereocidaris,* numbering 15, with nine subspecies, are distributed throughout the Indo-Pacific, including southeast Africa (Mortensen 1928a). Notably the genus has not been recorded from Australasian seas (H.L. Clark 1925; Fell 1966).

The Manus Island specimen, represented by a small fragment of plating from an adapical position, is tentatively assigned to *Stereocidaris squamosa* Mortensen 1928. As already noted, the striking resemblance of the ambulacral and interambulacral plating of this single specimen to that described by Mortensen (1928a) for *S. squamosa* cannot be ignored. *Stereocidaris squamosa* is an extant species recorded from 270 m depth on the Saya de Malha Bank (10° 30'S), about 800 km southeast of the Seychelles in the Indian Ocean (Mortensen 1928a). The species has a small-moderate sized test that ranges in diameter from 30-47 mm, with height from 18.5-29 mm (Mortensen 1928a). Longest spines range in length from ca. 50-59 mm. The late Lower Miocene/ earliest Middle Miocene Manus Island occurrence represents the first fossil occurrence of test remains of *Stereocidaris* from the Indo-Pacific.

Stereocidaris sp.

Fig. 3b

Material

An isolated fragmentary spine, ANU 60639.

Locality and horizon

Collected '5 km east of the intake structure of the Warangoi hydro-scheme' (Lindley unpubl. field notes), in the headwaters of Matuli Creek, a tributary of the Warangoi River, Sikut area, northeastern Gazelle Peninsula, East New Britain Province, PNG. Grid reference 081961 Merai 1: 100 000 Sheet 9388 (Edition 1). The collection horizon is from the Sinewit Formation, of Mio-Pliocene age (Lindley 1988). However, fossil evidence and a K-Ar radiometric age from the Sikut and adjacent areas, indicates the formation in this area is restricted to the Pliocene (Read 1965; B. McGowran in Lindley 1988; Lindley 1988; Corbett et al. 1991).

Description

No test fragments which belong to this species have been identified.

Primary spine cylindrical, distinctly fusiform, tapering, point not widened. Spine length 15 mm, with maximum diameter of 2 mm occurring about 1/2 distance from proximal end. The shaft with about 16 series of low rounded warts; only towards the point do they assume the shape of low rounded ridges. The collar is only 0.75-1 mm long, slightly increasing in thickness towards inconspicuous milled ring. Neck is equal in length to collar.

Remarks

The primary spines of cidaroids possess a distinctive structure with a compact outer or cortex layer covering all except the collar and enveloping a central core consisting of an irregular calcareous meshwork (Mortensen 1928a). The cortex layer is found only in a few other echinoids, mainly the salenids, and spinule and wart ornament along the shaft is formed by this alone (Mortensen 1928a). Mortensen (1928a: 50) considered that primary spine shape and structure is of considerable use in cidaroid classification, both at specific and generic levels.

The primary spine ANU 60639 is identified as that of a cidaroid by its spine shape and its possession of an outer cortex layering. The nature of the inner central core meshwork is clearly visible on the spine collar. The nature of wart development, the number of longitudinal series, and their distal transition to low rounded ridges, bears a strong resemblance to that seen in the primary spines of some extant species of *Stereocidaris*, including *Stereocidaris grandis* (Döderlein) and *Stereocidaris hawaiiensis* Mortensen 1928b, found only in Japanese seas and Hawaiian seas, respectively (cf. Mortensen 1928a: Plate XIX, fig. 5 and XXI, fig. 5, respectively).

Subfamily RHABDOCIDARINAE Lambert 1900, emended Fell 1966
Genus PHYLLACANTHUS Brandt 1835

Synonymy

Leiocidaris Desor 1885, p. 48.

Type species

Cidarites (Phyllacanthus) dubia Brandt 1835, p. 67, by original designation.

Phyllacanthus sp.

Fig. 3c

Material

One isolated fragmentary spine, ANU 60637.

Locality and horizon

Collected in stream float from an unnamed large western tributary of Mevelo River, Lakit Range, southwestern Gazelle Peninsula, East New Britain Province, PNG. Grid reference 660623 Pondo 1:100 000 Sheet 9288 (Edition 1). Lakit Limestone, Pliocene (Lindley 1988).

Description

No test fragments which belong to this species have been identified.

Proximal portion of primary spine moderately thick, cylindrical, fusiform, with a maximum diameter of 8.0 mm. Details of distal shaft unknown. Details of spine base, milled ring and collar unknown. Spine swells rapidly above the collar. Surface of shaft is finely and uniformly granulated (not visible to the naked eye), the granules forming numerous (> 50) longitudinal series along length of spine.

Remarks

Lindley (2003b) described the spines of *Phyllacanthus imperialis* var. *javana* K. Martin 1885 and *Phyllacanthus* sp. from the Lower Pliocene Kairuku Formation, Yule Island. Unfortunately, the characters diagnostic of these species, including spine collar length and the number of ridges on the distal part of the spine, are not visible on ANU 60637.

Subclass EUECHINOIDEA Bronn 1860
Superorder ECHINACEA Claus 1876
Order TEMNOPLEUROIDA Mortensen 1942
Family TOXOPNEUSTIDAE Troschel 1872
Genus TOXOPNEUSTES A. Agassiz 1841

Synonymy

Boletia Desor 1846, p. 362.

Type species

Echinus pileolus Lamarck 1816, p. 45, by original designation.

Toxopneustes pileolus (Lamarck 1816)

Synonymy

Echinus pileolus Lamarck 1816, p. 45.
Toxopneustes pileolus, A. Agassiz 1841, p. 7; H.L. Clark 1925, p. 123; Mortensen 1943a, p. 472; A.M. Clark and Rowe 1971, p. 156; Rowe and Gates 1995, p. 258.
Mortensen (1943a: 472) lists additional synonymies.

Material and locality

Single naked test, B20022, from the vicinity of Cape Gazelle, New Britain, East New Britain Province, PNG.

Remarks

Toxopneustes pileolus (Lamarck 1816) is widely distributed throughout the Indo-West Pacific (Mortensen 1943a; A.M. Clark and Rowe 1971; Miskelly 2002).

Genus TRIPNEUSTES L. Agassiz 1841

Type species

Echinus granularis Lamarck 1816, p. 44, by original designation.

Tripneustes gratilla (Linnaeus 1758)

Synonymy

Echinus gratilla Linnaeus 1758, p. 664.
Tripneustes gratilla, H.L. Clark 1925, p. 124; Mortensen 1943a, p. 500; A.M. Clark and Rowe 1971, p. 156; Rowe and Gates 1995, p. 259.
Mortensen (1943a: 500) lists additional synonymies.

Material and locality

Single naked test, B20023, from the vicinity of Cape Gazelle, New Britain, East New Britain Province, PNG.

Remarks

Tripneustes gratilla (Linnaeus 1758) is widely distributed throughout the Indo-West Pacific (Mortensen 1943a; A.M. Clark and Rowe 1971). Previous records from the Pacific include the Marshall Islands, Norfolk Island, Hawaiian Islands, Kermadec Islands, Solomon Islands, Fiji and Hood Lagoon, south coast of Papua (H.L. Clark 1925; Mortensen 1943a; A.M. Clark and Rowe 1971; Miskelly 2002).

Order ECHINOIDA Claus 1876
Family ECHINOMETRIDAE Gray 1825
Genus ECHINOMETRA Gray 1825

Synonymy

Ellipsechinus Lütken 1864, p. 165.
Plagiechinus Pomel 1883, p. 78.
Mortensenia Döderlein 1906, p. 233.

Type species

Echinus lucunter Linnaeus 1758, p. 665, by original designation.

Echinometra mathaei (de Blainville 1825)

Synonymy

Echinus lucunter Lamarck 1816, p. 50 (*non E. lucunter* Linnaeus).

Echinometra mathaei, H.L. Clark 1925, p. 143; H.L. Clark 1932, p. 216; Mortensen 1943b, p. 381; H.L. Clark 1946, p. 332; A.M. Clark and Rowe 1971, p. 157; Rowe and Gates 1995, p. 211.

Mortensen (1943b: 381) lists additional synonymies.

Material and localities

Fourteen naked tests from Gargaris village, northern coast of Malendok Island, Tanga Group, New Ireland Province, PNG; one partly naked test from beach at Ralum, Blanche Bay, East New Britain Province, PNG; one naked test from Penlolo village, south coast of New Britain, West New Britain Province, PNG; one naked test, B 20016, from Cape Gazelle, New Britain, East New Britain Province, PNG.

Remarks

Echinometra mathaei (de Blainville 1825) is a long ranging species, recorded from late Lower Miocene-early Middle Miocene rocks in the western and eastern Mediterranean Sea (Negretti et al. 1990). Extant *E. mathaei* is one of the most widely distributed echinoids, occurring throughout tropical-subtropical waters of the Indo-West Pacific (Mortensen 1943b; A.M. Clark and Rowe 1971). H.L. Clark (1908) recorded the species from Sorong, west New Guinea and Miskelly (2002) recorded it from the Solomon Islands. This record indicates a wide distribution throughout the Bismarck Archipelago (Tanga Group, New Ireland; Blanche Bay, New Britain; and south coast New Britain).

Genus HETEROCENTROTUS Brandt 1835

Synonymy

Acroladia L. Agassiz and Desor 1846, p. 373.

Type species

Echinus mamillatus Linnaeus 1758, p. 664, by subsequent designation of Pomel 1883, p. 77.

Heterocentrotus mammillatus (Linnaeus 1758)

Synonymy

Echinus mamillatus Linnaeus 1758, p. 664.

Heterocentrotus mammillatus, H.L. Clark 1925, p. 147; Mortensen 1943b, p. 409; H.L. Clark 1946, p. 333; A.M. Clark and Rowe 1971, p. 158; Rowe and Gates 1995, p. 213.

Mortensen (1943b: 409) lists additional synonymies.

Material and locality

A single naked test, B 20017, and unlabelled isolated spines (housed in the East New Britain Historical and Cultural Centre, Kokopo) from Cape Gazelle, New Britain, East New Britain Province, PNG; an isolated primary spine, ANU 60648, from Nosnos village, Boang Island, Tanga Group, New Ireland Provine, PNG.

Remarks

Heterocentrotus mammillatus (Linnaeus 1758) is widely distributed throughout the Indo-Pacific, from the Gulf of Suez and Madagascar to the Hawaiian Islands and Fiji (Mortensen 1943b). It is recorded from the Solomon Islands by Miskelly (2002). The largest test of *H. mammillatus* noted by Mortensen (1943b) has a long diameter of 82 mm, with most individuals having diameters of 72 mm or less. The long diameter of the Cape Gazelle test is 72 mm. The Tanga spine has a length of 74 mm and, given that the primary spines of *H. mammillatus* usually do not exceed the long diameter of the test (Mortensen 1943b), appears to have come from a relatively large individual.

Genus HELIOCIDARIS L. Agassiz and Desor 1846.

Synonymy

Toxocidaris A. Agassiz 1863, p. 22.

Type species

Echinus tuberculatus Lamarck 1816, p. 50, by original designation.

Diagnosis

Low hemispherical echinoids, widest at circular ambitus. Ambulacral plates with 7 or more pore-pairs to each plate; arcs may be irregularly double; expanded poriferous tracts of the flattened adoral surface are petaloid. Oculars I and IV usually insert. Gill-slits are shallow (Philip 1965; Fell and Pawson 1966).

Remarks

Heliocidaris L. Agassiz and Desor 1846 is distributed along the southern coasts of Australia, northern New Zealand, Kermadec Islands and Lord Howe Island (Mortensen 1943a). Two species are included in the genus by Mortensen (1943a), viz: *Heliocidaris tuberculata* (Lamarck 1816) and *Heliocidaris erythrogramma* (Valenciennes 1846) and, given their similar morphologies, he has questioned whether they are really conspecific. *Anthocidaris* Lütken 1864 is a closely allied genus (only known species *Anthocidaris crassispina* [A. Agassiz 1863]) from the coasts of southern Japan and China, distinguished from *Heliocidaris* by the spicules of the tubefeet (Mortensen 1943a). On the status of *Anthocidaris*, Mortensen (1943a: 328) questioned whether the genus should be merged into *Heliocidaris*. Philip (1965) described the only known fossil representative of the genus, *Heliocidaris ludbrookae* Philip 1965 from the Lower-early Middle Miocene (Longfordian-Batesfordian) of southeastern Australia.

Heliocidaris robertsi sp. nov.

Figs 4, 5a-e

Diagnosis

Test low hemispherical, somewhat inflated above. Ambulacral plates with 12 pore-pairs per plate; ambital and aboral pore-arcs doubled. Ambulacral and interambulacral plates relatively large; each bearing a primary tubercle and numerous secondary tubercles; aureoles of primaries not in contact. Primary tubercles of ambital and aboral ambulacral plates with an aborally positioned secondary tubercle.

Etymology

Named for Mr Michael Roberts, amateur conchologist of Kokopo, East New Britain Province, PNG.

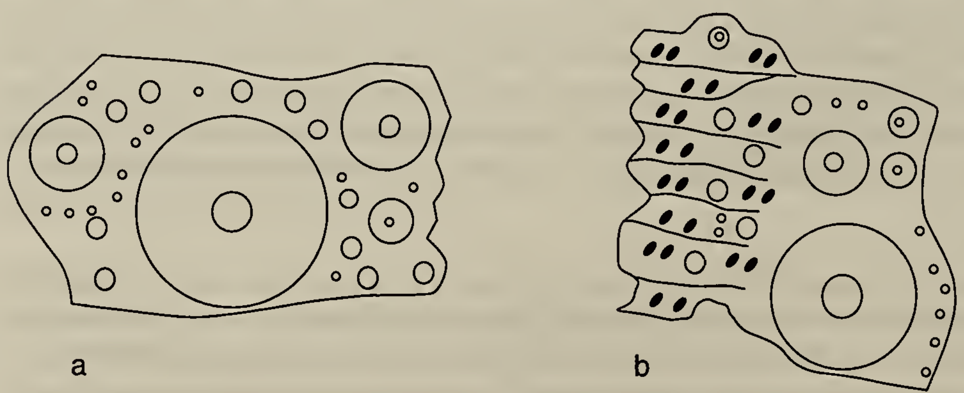

Figure 4. ***Heliocidaris robertsi*** **sp. nov. Cape Gazelle area, East New Britain Province. 4a-b, plating diagrams at ambitus for interambulacrum, ambulacrum.**

Material and locality

Single naked test, ANU 60654, from the vicinity of Cape Gazelle, New Britain, East New Britain Province, PNG.

Description

Test low hemispherical, somewhat inflated above, widest at circular ambitus. The oral side is flattened, scarcely sunken towards the peristome. Only specimen of 38 mm diameter.

The pore zones are conspicuously petaloid on the

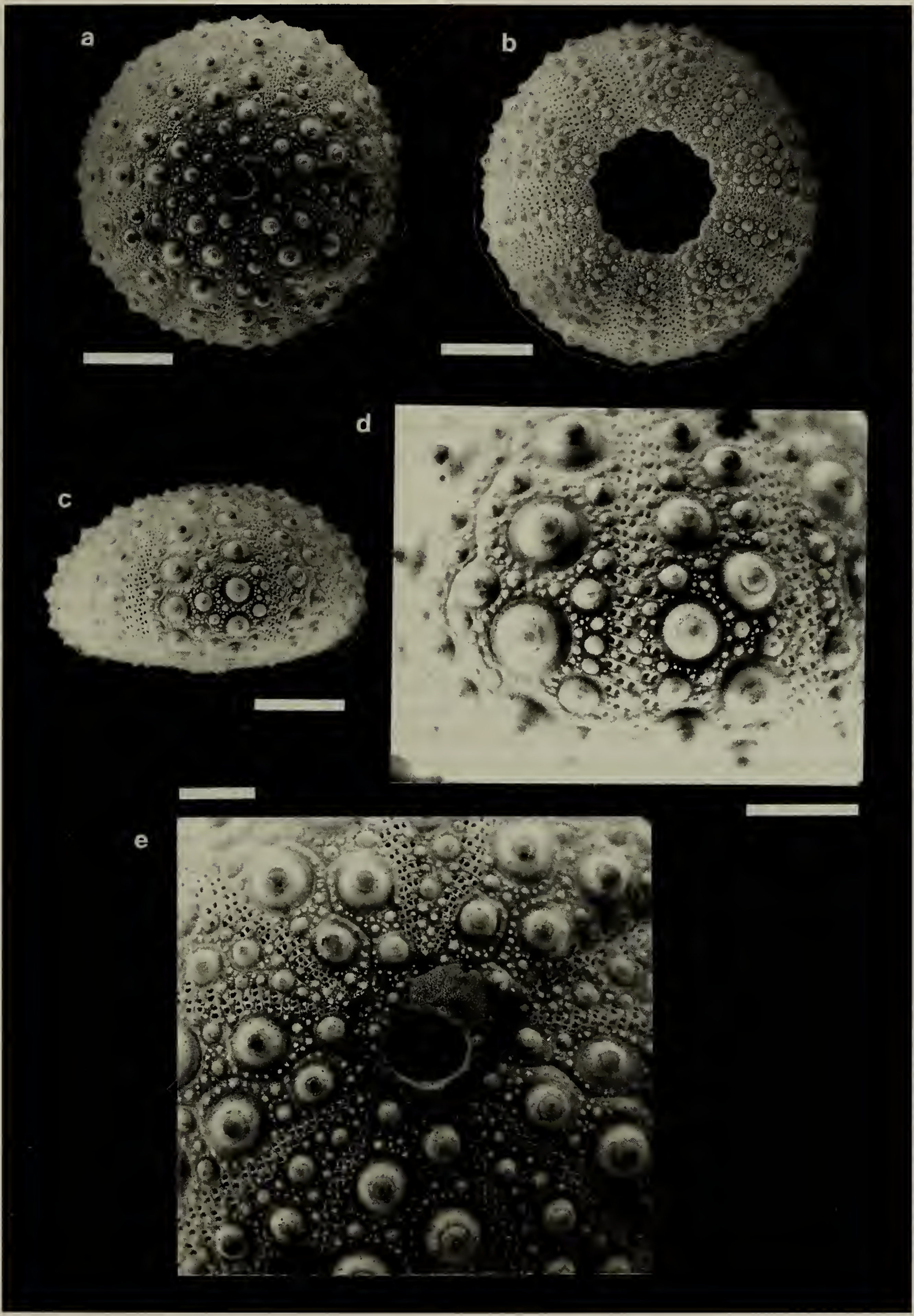

Figure 5. ***Heliocidaris robertsi*** **sp. nov. Cape Gazelle area, East New Britain Province. 5a-e, ANU 60654, aboral, oral, lateral views. Bar scale = 10 mm; ambulacral plating at ambitus (refer to Fig. 4b for plating diagram). Bar scale = 5 mm; apical disc. Bar scale = 2.5 mm.**

oral surface, about 1.5-2 times the width of interporiferous zone. The pore-series in this area are almost horizontal and are separated by secondary tubercles forming a single prominent vertical series; scattered miliary tubercles are also present. In the ambital region there are 12 pore-pairs arranged in double arcs (Fig. 4). Above the ambitus the pore-zones become much narrower. Primary tubercles in the ambital zone are large, almost as large as the interambulacral primaries; aureoles of adjacent primaries in each vertical series widely separated. Sutures between adjacent plates are seen very distinctly on the outer adoral side of the boss. Each ambulacral plate at and above the ambitus has a prominent secondary tubercle positioned aborally to the primary tubercle; 4-5 other secondary tubercles are also present. Miliaries tend to be arranged along the perradial sutures of ambital and superoambital ambulacrals; elsewhere on each plate only a sparse covering of miliaries is present.

The interambulacral primaries are large, forming prominent series aborally; their aureoles are distinctly separated, leaving a broad space at the upper edge of each plate, occupied by several small tubercles and miliaries. Usually sutures between adjacent plates are close to, but do not cross, aureole of successive tubercle. In the median space there is on the oral surface and in the ambital region a conspicuous double series of secondary tubercles about half the size of the ambulacral primaries. Below the ambitus all the tubercles decrease rapidly in size, with the secondaries disappearing, and only the primaries continuing to the peristome.

The apical system is small, only about 18 percent of the test diameter. There is typically one large tubercle on each genital plate, except the very large madreporite, and a scattering of small tubercles over the remainder (Fig. 5e). Ocular I and IV are broadly insert. The peristome is very small, about 29 percent of test diameter. Gill-slits shallow.

Details of spines and pedicellarie unknown.

Remarks

Heliocidaris robertsi sp. nov. is readily distinguished from *H. tuberculata* and *H. erythrogramma* and the closely allied *A. crassispina* by its possession of double pore-arcs on the adoral surface. The double pore-arcs of *H. robertsi* are very similar to those of *Heterocentrotus trigonarius* (Lamarck 1816), figured by Mortensen (1943a: fig. 132c) and Fell and Pawson (1966: fig. 324, 7c). However, any resemblance between the new species and *H. trigonarius* is easily discounted because of the latter's possession of a distinctly elongated test and a significantly larger peristome (51 percent of test diameter).

The biogeographical position of *H. robertsi* is noteworthy in that it is the tropical representative of two closely allied temperate water genera, *Heliocidaris*, a very common form restricted to southern Australia and New Zealand, and *Anthocidaris*, an equally common form restricted to Japan and China.

Pore-arc doubling is almost as strongly developed in other echinometrids including *Colobocentrotus* Brandt 1835 and *Zenocentrotus* A.H. Clark 1931, and incipient development may also been seen in *Echinometra* Gray 1825 (Mortensen 1943a: 281). All three genera possess an elliptical or oblong ambitus. The functional significance of doubling of pore-arcs in compound plates relates to (a) increasing the area over which tube-feet are spread, and thereby increasing respiratory and feeding efficency (Mortensen 1943a; Woods 1958; Durham 1966; A.M. Clark 1968) and (b) strengthening of the test (Durham 1966). The doubling of pore-arcs on the aboral surface of *H. robertsi* greatly increases the number of tube-feet in this area, not only aiding in improved respiration, but allowing it to catch food particles falling onto its upper surface. With such adaptations to its upper surface, the echinoid may have been a reef rock borer, inhabiting a hole perhaps several centimetres deep.

Superorder GNATHOSTOMATA Zittel 1879
Order HOLECTYPOIDA Duncan 1889
Suborder ECHINONEINA H.L. Clark 1925
Family ECHINONEIDAE Agassiz and Desor 1847
Genus ECHINONEUS Leske 1778

Synonymy

Echinanaus Gray 1825, p. 7 (*nom. van.*).
Pseudohaimea Pomel 1885, p. 118.
Koehleraster Lambert and Thiéry 1921, p. 331.

Type species

Echinoneus cyclostomus Leske 1778, by subsequent designation of H.L. Clark 1917, p. 101.

Remarks

Echinoneus Leske 1778 is an Oligocene-Recent form, with some ten fossil species described from the Oligocene and Miocene of Europe (Mortensen 1948a; Wagner and Durham 1966). Two Recent species are known, viz. *Echinoneus cyclostomus* Leske 1778 and *Echinoneus abnormalis* de Loriol 1883, distinguished by the presence or absence of imperforate primary tubercles and well developed glassy tubercles. Recent forms are distributed throughout the West Indies, Indo-Pacific and Australia. Mortensen (1948a) considered that many of the fossil species are very difficult to distinguish and may in fact be Recent *E. cyclostomus.*

Echinoneus sp.

Fig. 3d

Material

One poorly preserved test, ANU 60640.

Locality and horizon

Nosnos village, Boang Island, Tanga Group, New Ireland Province, PNG. Grid reference 296246 Tanga 1:100 000 Sheet 9591 (Edition 1). Unnamed poorly compacted bioclastic limestone, Pleistocene-Holocene (Wallace et al. 1983).

Description

Test ovoid, moderate size, measuring 23 x 17 x 11.5 mm; oral surface weakly concave. Ambulacra narrow, not petaloid. Other details of ambulacra unknown. Details of interambulacra unknown. Details of tubercles unknown. Apical and periproctal systems unknown.

Remarks

The lack of well preserved tubercles on this specimen makes it difficult to assign a species.

Echinoneus cyclostomus Leske 1778

Synonymy

Echinoneus cyclostomus Leske 1778, p. 173; H.L. Clark 1925, p. 177; H.L. Clark 1946, p. 353; Mortensen 1948a, p. 75; A.M. Clark and Rowe 1971, p. 158; Rowe and Gates 1995, p. 215.

Mortensen (1948a: 75) lists additional synonymies.

Material and locality

Twelve naked tests, including ANU 60641, from Gargaris village, northern coast of Malendok Island, Tanga Group, New Ireland Province, PNG; one naked test, B 20021, from Cape Gazelle, New Britain, East New Britain Province, PNG.

Remarks

Echinoneus cyclostomus Leske 1778 is the only known case of a (tropical) cosmopolitan echinoid, having been recorded from the West Indies, Ascension (but not the African west coast) and the Indo-Pacific-East Africa (Zanzibar, Natal), Madagascar to the Pacific islands (Funafuti, Palmyra, Hawaiian Islands), and from Japan to Queensland (Great Barrier Reef) and Lord Howe Island (Mortensen 1948a). Miskelly's (2002) record of *E. cyclostomus* from the Solomon Islands represents the nearest previous record to that from the Tanga Group and Cape Gazelle.

Echinoneus abnormalis de Loriol 1883

Synonymy

Echinoneus abnormalis de Loriol 1883, p. 41; H.L. Clark 1917, p. 102; H.L. Clark 1925, p. 176; Mortensen 1948a, p. 80; A.M. Clark and Rowe 1971, p. 158.

Koehleraster abnormalis Lambert and Thiéry 1921, p. 331.

Material and locality

One naked test, ANU 60641, from Gargaris village, northern coast of Malendok Island, Tanga Group, New Ireland Province, PNG.

Remarks

This species is represented by a single naked test measuring 30 x 22.5 x 15 mm. *Echinoneus abnormalis* de Loriol 1883 is distinguished from *E. cyclostomus* by possessing perforated, non-glassy spine tubercles. The apical system of the Tanga specimen is distinctly anterior to that of co-occurring specimens of the much more common *E. cyclostomus*. *Echinoneus abnormalis* has a restricted distribution, known from Mauritius (type locality), Kei Islands, Palmyra Island, Banda, Ellice Islands and the Hawaiian Islands (Mortensen 1948a; A.M. Clark and Rowe 1971). The recent record of *E. abnormalis* from the vicinity of Raine Island on the northern Great Barrier Reef (Gibbs et al. 1976) represents the first from Australasian waters. The record from the Tanga Group is the second from the East Indies. The species is observed to be sympatric with the much more common *E. cyclostomus* in many localities, a fact Gibbs et al. (1976) suggested may have resulted in it having gone unrecognised in samples. Mortensen (1948a: 81) considered that the two species probably didn't live together at the same localities. Of the 15 specimens of *Echinoneus* collected from the Malendok Island locality, only one was an *E. abnormalis*, suggesting that in this case, the species' apparent rarity may be related to different niches within the same locality.

Order CLYPEASTEROIDA A. Agassiz 1872
Suborder CLYPEASTERINA A. Agassiz 1872
Family CLYPEASTERIDAE L. Agassiz 1835
Genus CLYPEASTER Lamarck 1801

Type species

Clypeaster rosaceus (Linnaeus 1758), by subsequent designation of Desmoulins 1835.

Clypeaster reticulatus (Linnaeus 1758)

Synonymy

Lindley (2003a) lists previous synonymies.

Material

Single naked test, B20020, from the vicinity of Cape Gazelle, New Britain, East New Britain Province, PNG.

Remarks

Clarification of Lindley's (2003a) statement on the distribution of *Clypeaster reticulatus* (Linnaeus 1758) is needed. The species is a very common Indo-West Pacific echinoid, distributed in the western Indian Ocean and the Red Sea, throughout the East Indies and east into the Pacific Ocean to the Hawaiian Islands (A.M. Clark and Rowe 1971). Previous south Pacific records of the species have been made by A. Agassiz (1863), Mortensen (1948b) and A.H. Clark (1954) from the Gilbert Islands, New Caledonia and Marshall Islands, respectively. Mortensen's (1948b) New Caledonian record has not been confirmed by De Ridder (1986: 29). McNamara and Kendrick (1994) have also recorded the species from Barrow Island, northwestern Australia. The species is known from fossil in Java (Lower Miocene), Yule Island, PNG (Lower Pliocene), East Africa (Pliocene-Pleistocene) and the New Hebrides (Pleistocene) (Mortensen 1948b; Lindley 2003a).

Family ARACHNOIDAE Duncan 1889
Subfamily ARACHNOIDINAE Duncan 1889
Genus ARACHNOIDES Leske 1778

Synonymy

Echinarchinus Leske 1778, p. 217.

Type species

Echinus placenta Linnaeus 1758, p. 666, ICZN 1954.

Arachnoides placenta (Linnaeus 1758)

Synonymy

Echinus placenta Linnaeus 1758, p. 666.

Arachnoides placenta (Linnaeus 1758): L. Agassiz 1841, p. 94; Bell 1899, p. 136; H.L. Clark 1925, p. 154; H.L. Clark 1946, p. 340; A.M. Clark and Rowe 1971, p. 161; Rowe and Gates 1995, p. 176.

Mortensen (1948b) lists additional synonymies.

Material and locality

Single naked test, B20018, from the vicinity of Cape Gazelle, New Britain, East New Britain Province, PNG.

Remarks

Arachnoides placenta (Linnaeus 1758) is a common littoral species throughout the East Indies and the south Pacific (Mortensen 1948b; A.M. Clark and Rowe 1971). The first record of the species from the Bismarck Archipelago is that of Bell (1899) from an unspecified locality in New Britain.

Suborder LAGANINA Mortensen 1948
Family LAGANIDAE A. Agassiz 1873
Genus LAGANUM Link 1807

Synonymy

Lagana Gray 1825, p. 427.

Type species

Laganum petalodes (= *Echinodiscus laganum* Leske 1778, p. 204), by original designation.

Laganum laganum (Leske 1778)

Synonymy

Laganum Bonani Klein 1734, p. 25.

Echinodiscus laganum Leske 1778, p. 204.

Laganum laganum, Mortensen 1948b, p. 312.

Laganum depressum, Lindley 2001, p. 130.

Mortensen (1948b: 312) list previous synonymies.

Material and locality

Single test, ANU 60649, from Penlolo village, south coast of New Britain, West New Britain Province, PNG.

Remarks

Laganum laganum (Leske 1778) is distinct with its pentagonal test with thick, swollen edges, and an oblong-elongate periproct situated midway between the mouth and test edge. The species is common in the East Indies, and is also recorded from Port Jackson and Tasmania (Mortensen 1948b). Mortensen (1948b) also recorded it from the Bismarck Archipelago (Table 2). H.L. Clark (1908) recorded the species from Saonek, Waigiou Island, in west New Guinea (Fig. 1)

Suborder SCUTELLINA Haeckel 1896
Family ASTRICLYPEIDAE Stefanini 1911

Genus ECHINODISCUS Leske 1778

Type species

Echinodiscus bisperforatus Leske 1778, p. 196.

Echinodiscus tenuissimus (L. Agassiz in Agassiz and Desor 1847)

Synonymy

Lobophora tenuissima L. Agassiz and Desor 1847, p. 136.

Echinodiscus tenuissimus, Gray 1855, p. 20; H.L. Clark 1914, p. 71; H.L. Clark 1925, p. 171; Mortensen 1948b, p. 411; A.M. Clark and Rowe 1971, p. 144 162; Rowe and Gates 1995, p. 185.

Mortensen (1948b: 411) lists additional synonymies.

Material and locality

Two tests, B 20024 (naked) and B 20025 (with spines), from the vicinity of Cape Gazelle, New Britain, East New Britain Province, PNG.

Remarks

Echinodiscus tenuissimus (L. Agassiz in Agassiz and Desor 1847) is a widely distributed Indo-West Pacific form, occurring throughout the East Indies, northern Australia, southern Japan and the south Pacific (Mortensen 1948b; A.M. Clark and Rowe 1971). In the south Pacific, the species is recorded from Tanna, Vanuatu, (H.L. Clark 1925) and from New Caledonia (A.M. Clark and Rowe 1971). However, De Ridder (1986) only noted the occurrence of *Echinodiscus bisperforatus* Leske 1778 from New Caledonia. H.L. Clark (1925) observed that New Caledonian specimens of *E. tenuissimus* in the British Museum (Natural History) have a form more like *E. bisperforatus*. The Cape Gazelle specimens have very short lunules, about one quarter the length of the radius taken through them, and there is no difference in the tuberculation and spines of the ambulacral and interambulacral areas of the oral surface, both diagnostic characters of *E. tenuissimus* (Mortensen 1948b; A.M. Clark and Rowe 1971).

Superorder ATELOSTOMATA Zittel 1879
Order SPATANGOIDA Claus 1876
Suborder HEMIASTERINA Fischer 1966
Family SCHIZASTERIDAE Lambert 1906
Genus SCHIZASTER L. Agassiz 1836

Type species

Schizaster studeri L. Agassiz 1836, p. 185, by subsequent designation ICZN 1948.

Remarks

McNamara and Philip (1980a, b) questioned the familial classification of the spatangoids used by Mortensen (1951) and Fischer (1966) and, in particular, the Family Schizasteridae. Within the Schizasteridae McNamara and Philip recognized genera sharing the gross morphological test features of *Schizaster*, viz. a posteriorly located apical system, with the apex of the test posterior to this; a long, typically sunken, poriferous frontal ambulacrum; and sunken petals, of which the posterior pair are markedly shorter than the anterior ones. Within this group, McNamara and Philip (1980a, b) included the genus *Schizaster* L. Agassiz 1836 (with its subgenera *Dipneutes* Arnaud 1891; *Paraster* Pomel 1869 and *Ova* Gray 1825 [= *Diploraster* Mortensen 1951]); *Brisaster* Gray 1855; *Kina* Henderson 1975; *Moira* L. Agassiz 1872 (= *Moiropsis* L. Agassiz 1881); and *Proraster* Lambert 1895 (= *Hypselaster* Clark 1917). The author accepts their emended diagnosis for *Schizaster*.

Subgenus PARASTER Pomel 1869

Type species

Schizaster gibberulus L. Agassiz 1847, by original designation of Pomel 1869, p. 14.

Diagnosis

Species of *Schizaster* with a small to moderate sized test, with a shallow frontal sinus. Apical system slightly posterior of centre. Frontal ambulacrum shallow with pore pairs inclined at about 45° and arranged in single rows. Anterior petals almost straight, diverging at an angle up to 110° (McNamara and Philip 1980a).

Remarks

There is difficulty in placing the Cape Gazelle species firmly within McNamara and Philip's (1980a) subgenus *Paraster* Pomel 1869. This is particularly in relation to details of the anterior petals, their flexed nature and 80° angle of divergence, both characters diagnostic of subgenus *Schizaster* L. Agassiz 1836. The frontal ambulacrum does not possess the steeper sided walls typical of species referred to *Schizaster (Schizaster)* (McNamara and Philip 1980a). Furthermore, McNamara and Philip (1980a) noted that species referred to *Schizaster (Schizaster)* possess a more elongate, narrower test than those assigned to *Paraster*. The Cape Gazelle species is assigned to *Schizaster (Paraster)* by its possession of a small test, shallow frontal sinus, apical system slightly posterior of centre and shallow frontal ambulacrum with pore pairs inclined at about 45°. The species is probably morphologically transitional between the *Paraster* and *Schizaster* morphotypes.

Schizaster (Paraster) ovatus sp. nov.

Figs 6a-d

Diagnosis

A small species of *Schizaster (Paraster)* with a moderately depressed, ovoid test; apical system is 55 percent of test length from anterior, with four genital pores. Anterior ambulacrum relatively narrow and shallow; pore pairs inclined at about 45° and arranged in single rows; outer pores elongate, with similarly sized inner pores comma-shaped. Frontal sinus shallow.

Etymology

Ovatus L. egg-shaped, in reference to the form of the test, distinctive amongst the Schizasteridae.

Material and locality

Holotype ANU 60653, a complete naked test from the vicinity of Cape Gazelle, New Britain, East New Britain Province, PNG.

Description

Test of small size, elongate ovoid, with length x width x height measuring 34 x 28 x 18 mm; test length:width = 1.21, width:height = 1.55. Test moderately depressed, with apical system located 55 percent of test length from anterior; test highest posterior to apical system, along keel of ambulacrum V. Oral surface is gently

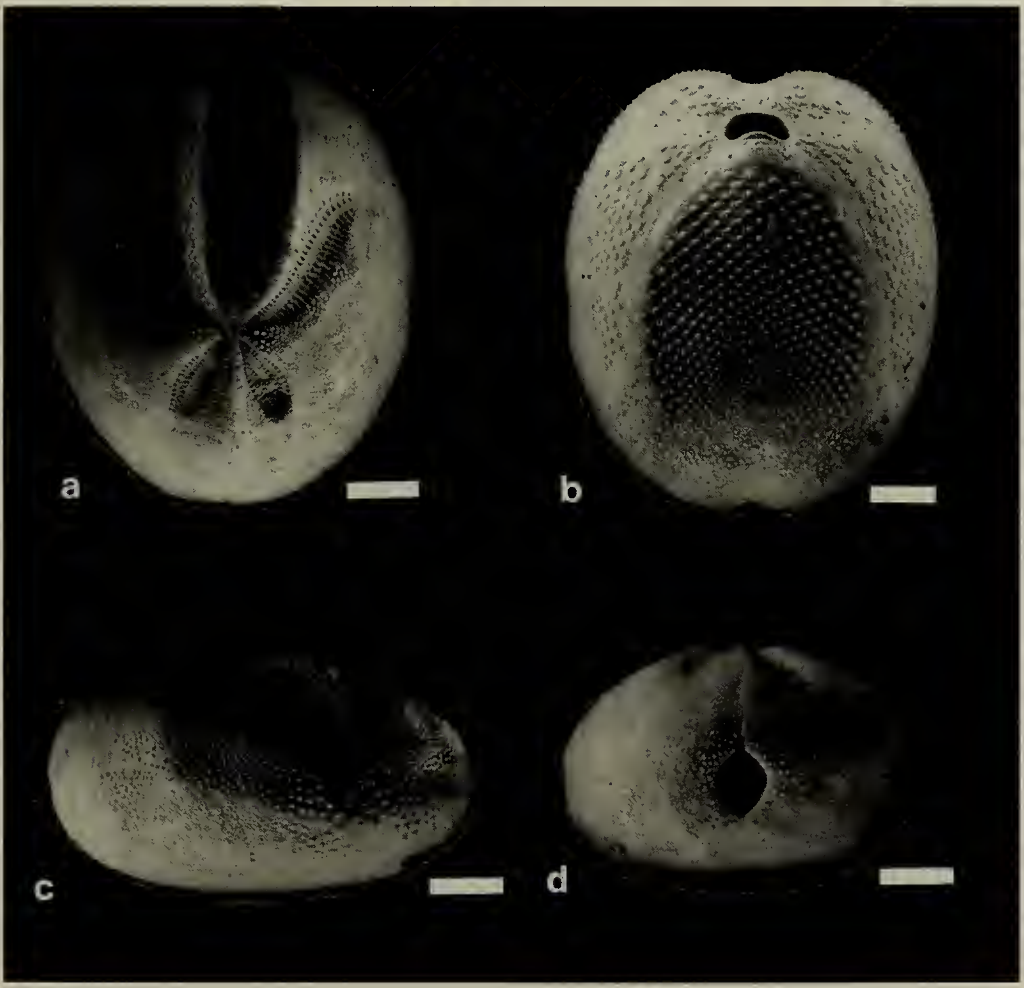

Figure 6. *Schizaster (Paraster) ovatus* sp. nov. Cape Gazelle, East New Britain. 6a-d, ANU 60653, aboral, oral, lateral, posterior views. Bar scale = 2.5 mm.

convex. Apical system ethmolytic, depressed, with four genital pores, posterior pair being larger than anterior pair. Frontal ambulacrum long, shallow and narrow (12 percent of test length); pore pairs inclined at about 45° and arranged in a single row. Outer pores elongate, with similarly sized inner pores comma-shaped. Frontal sinus broad and shallow. Interambulacra II and III form sharp, high keels. Anterior petals diverging at angle of 80°; flexed distally and shallow, bearing pore pairs which are elliptical, widely spaced and conjugate; 26 pairs are present. Posterior petals are moderately long (occupying 21 percent of test length), bearing 18 pore pairs.

Peripetalous fasciole is distinct, passing transversely between posterior petals and thickening at petal ends; the fasciole describes a concave arc between the extremities of the posterior and anterior petals, with an outwards flexure, corresponding with a constriction, forward of the apical system. Fasciole reaches maximum thickness at the extremities of the anterior petals. Peripetalous fasciole passes forward from anterior petals at about 60° before curving strongly to close with frontal ambulacrum; constrictions occur on interambulacral keel and adjacent to the abrupt curvature. Lateroanal fasciole is narrower than peripetalous fasciole and of more constant width. Lateroanal fasciole extends abaxially posteriorly from peripetalous fasciole at constriction between posterior and anterior petals; at ambitus it runs far below periproct, close to adoral surface.

Peristome oval and slightly sunken; situated anteriorly, anterior tip of labrum 15 percent of test length from anterior. Anteriorly labrum is strongly curved; bounded by thick rim that degenerates laterally. Labrum as long as broad; posterior extension triangular, about as long as broad. Labrum carries several small tubercles anteriorly. Plastron is pear-shaped and broad, maximum width being 3/4 length. Plastron tubercles are arranged in curving rows.

Periproct at mid-level on sub-truncate end of test. Periproct longitudinally elliptical, with a prominent narrow slit extending a short distance axially and aborally towards interambulacrum V, nearly reaching apical surface (Fig. 6d).

Remarks

Schizaster (Paraster) ovatus sp. nov. can be distinguished from other *Schizaster*-like heart urchins by its small, distinctively narrower and less inflated test, and long, shallow and narrow frontal ambulacrum. The test L:W and L:H ratios of 1.21 and 1.88 are larger than for most other echinoids of this group. The presence of four genital pores would suggest that the holotype is a mature specimen. McNamara and Philip (1980b) noted that in *Schizaster (Ova) myorensis* McNamara and Philip (1980b) the onset of maturity, occurring at a test length of about 25 mm, followed the sequential opening of the first, second, third and fouth genital pores.

Morphological adaptations in *Schizaster*-like heart urchins are related to a need to produce a more efficient current flow over the aboral surface in sediment of low permeability (McNamara and Philip 1980a). The posterior migration of the apex meant more water would flow over over the frontal sinus to the peristome; the deepening of the frontal ambulacrum and the frontal sinus assisted in channelling water to the peristome; and the deep and long frontal ambulacrum further enabled more-funnel-building tube feet to be accommodated, presumably in response to finer-grained sediment (McNamara and Philip 1980a). The weakly vaulted test of *S.(P.) ovatus* with its shallow, open frontal ambulacrum and shallow frontal sinus suggests the species was a shallow-burrower in coarse (permeable) shell gravel.

Suborder MICRASTERINA Fischer 1966
Family BRISSIDAE Gray 1855
Genus BRISSUS Gray 1825

Synonymy

Bryssus Martens 1869, p. 128 *(nom. van.)*.
Brissus (Allobrissus) Mortensen 1950, p. 162.

Type species

Spatangus brissus unicolour Leske 1778, p. 248 by subsequent designation of ICZN, Op. 290 1948.

Brissus (Brissus) latecarinatus (Leske 1778)

Synonymy

Brissus carinatus Gray 1825, p. 431; A. Agassiz 1872-74, p. 96, 596.
Brissus latecarinatus (Leske 1778): H.L. Clark 1921, p. 153; H.L. Clark 1925, p. 219; H.L. Clark

1946, p. 375; Mortensen 1951, p. 514; A.M. Clark and Rowe 1971, p. 165; Gibbs et al. 1976, p. 135.
Brissus (Brissus) latecarinatus: Rowe and Gates 1995, p. 187.
Spatangus Brissus latecarinatus Leske 1778, p. 249.
Mortensen (1951: 514) lists additional synonymies.

Material and locality

Three naked tests, ANU 60643-5, from Nosnos village, Boang Island, Tanga Group, New Ireland Province, PNG; one naked test, B 20014, from Cape Gazelle, New Britain, East New Britain Province, PNG.

Remarks

Brissus (Brissus) latecarinatus (Leske 1778) is a widely distributed species throughout the Indo-Pacific (Mortensen 1951; A.M. Clark and Rowe 1971). It is present on Australian coasts, from Queensland to Port Jackson, and is also known from Lord Howe Island (H.L. Clark 1946). Miskelly's (2002) record of the species from the Solomon Islands is nearest to the present record in the Tanga Group. The largest specimen, ANU 60644 from the Tanga Group, measures 70 x 60 x 39 mm, considerably smaller than the largest known specimen, from Hawaii, measuring 130 x 108 x 74 mm (H.L. Clark 1946). The shape of the periproct of the Tanga Group and Cape Gazelle specimens, somewhat pointed above and below, differs from the rounded periproct evident in specimens figured by Mortensen (1951: Plate XXXIII, fig. 7) and Miskelly (2002). In this respect, the Bismarck Sea specimens closely resemble *Brissus (Allobrissus) agassizii* Döderlein 1885 (Mortensen 1951: Plate XXXIII, fig. 7). Gibbs et al. (1976) noted the similarity of a Pelican Island, Great Barrier Reef, specimen of *B. (B.) latecarinatus* with *B. (A.) agassizii.* The posterior end of this particular specimen, like that of *B. (A.) agassizii*, is vertically truncated, with the posterior interambulacrum being only slightly carinate aborally (and not prolonged backwards to overhang the periproct and conceal it from dorsal view).

Genus METALIA Gray 1855

Synonymy

Xanthobrissus Agassiz 1863, p. 28.
Prometalia Pomel 1883, p. 34.
Eobrissus Bell 1904, p. 236.
Metaliopsis Fourtau 1913, p. 68.

Type species

Spatangus sternalis Lamarck 1816, p. 326, by original designation.

Metalia spatagus (Linnaeus 1758)

Synonymy

Echinus spatagus Linnaeus 1758, p. 665.
Metalia spatagus (Linnaeus 1758): H.L. Clark 1925, p. 216; H.L. Clark 1932, p. 219; H.L. Clark 1946, p. 372; Mortensen 1951, p. 540; A.M. Clark and Rowe 1971, p. 166; Gibbs et al. 1976, p. 136; Rowe and Gates 1995, p. 190.
Mortensen (1951: 540) lists additional synonymies.

Material and locality

Two naked tests, ANU 60646-7, from Nosnos village, Boang Island, Tanga Group, New Ireland Province, PNG.

Remarks

Metalia spatagus (Linnaeus 1758) is widely distributed through the Indo-Pacific (Mortensen 1951; A.M. Clark and Rowe 1971). H.L. Clark (1932) provided the first record of this species from Australasian waters (Low Isles, Great Barrier Reef), recording the largest known specimen, measuring 110 x 93 x 52 mm. By comparison, the largest Tanga specimen measures 54 x 40 x 29 mm. Miskelly (2002) records the species from the Solomon Islands.

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Table 1. Reported starfishes from the Bismarck Archipelago, Papua New Guinea.

ASTERIINAE
Tarsaster stoichodes Sladen 1889: Fisher 1919, p. 491: north of the Admiralty Group (150 fathoms).

ASTERINIDAE
Asterina cephus (Müller and Troschel 1842): A.H. Clark 1954, p. 258: Seleo Island, Aitape district.
Patiriella exigua (Lamarck 1816): A.H. Clark 1954, p. 258: Admiralty Group; Seleo Island, Aitape district.

ASTEROPSEIDAE
Asteropsis carinifera (Lamarck 1816): A.H. Clark 1954, p. 258: Seleo Island, Aitape district.

ASTROPECTINIIDAE
Astropecten monacanthus Sladen 1883: Bell 1899, p. 136: New Britain.
Astropecten polyacanthus Müller and Troschel 1842: Fisher 1919, p. 64: Admiralty Group.

ECHINASTERIDAE
Echinaster luzonicus (Gray 1840): Rowe and Gates 1995, p. 59. (= *Echinaster eridanella* Müller and Troschel 1842, p. 24; Bell 1899, p. 138): New Ireland; New Britain.

LUIDIIDAE
**Luida aspera* Sladen 1889: Fisher 1919, p. 171: north of Admiralty Group (150 fathoms).

OPHIDIASTERIDAE
Linckia laevigata (Linnaeus 1758): Bouillon and Jangoux 1984, p. 249: Laing Island reef, Hansa Bay.
Nardoa novaecaledoniae (Perrier 1875): Rowe and Gates 1995, p. 88. (= *Nardoa mollis* de Loriol, 1891, H.L. Clark 1946, p. 115; A.H. Clark 1954, p. 255): New Britain; Seleo Island, Aitape district.
Nardoa tuberculata Gray 1840: Rowe and Gates 1995, p. 88. (= *Nardoa finschi* de Loriol 1891; *Nardoa pauciforis* von Martens 1866, H.L. Clark 1946, p. 115): New Britain.
Ophidiaster granifer Lütken 1871: A.H. Clark 1954, p. 256: Seleo Island, Aitape district.

OREASTERIDAE
+*Anthenea sidneyensis* Döderlein 1915: Rowe and Gates 1995, p. 98: Manus Island (Admiralty Group).
Culcita novaeguineae Müller and Troschel 1842: A.H. Clark 1954, p. 254: Seleo Island, Aitape district.
Pentaster obtusatus (Bory de St. Vincent 1827). [= *Pentaceropsis obtusata* (Bory de St. Vincent 1827) Bell 1899, p. 136]: Blanche Bay, New Britain.
Protoreaster lincki (de Blainville 1830): *Oreaster lincki* (= *Pentaceros lincki*, Bell 1899, p. 136): Blanche Bay, New Britain.
Protoreaster nodosus (Linnaeus 1758): H.L. Clark 1946, p. 106; A.H. Clark 1954, p. 254. (= *Pentaceros nodosus*, Bell 1899: p. 136; *Oreaster nodosus* H.L. Clark 1908): Blanche Bay, New Britain; Seleo Island, Aitape district.

PTERASTERIDAE
Hymenaster pullatus Sladen 1889: Fisher 1919, p. 467: southwest of the Admiralty Group (1,070 fathoms).

NOTES
+ the writer follows Spencer and Wright (1966) and Rowe and Gates (1995) in placing *Anthenea* in Family Oreasteridae. H.L. Clark (1946) and A.M. Clark and Rowe (1971) placed the taxon in Family Goniasteridae.

* Denotes type locality in Bismarck Archipelago.

Table 2. Reported shallow and deep-water sea-urchins from the Bismarck Archipelago, Papua New Guinea.

ARACHNOIDIDAE

Arachnoides placenta (Linnaeus 1758): Bell 1899, p. 136; H.L. Clark 1925, p. 154: New Britain.

ARBACIIDAE

**Pygmaeocidaris prionigera* (A. Agassiz 1879): A. Agassiz 1881, pl. XXXIV, figs 14 and 15; H.L. Clark 1925, p. 73 (= *Podocidaris prionigera* A. Agassiz 1879, p. 199): between New Guinea and Admiralty Group (1,070 fathoms).

**Coelopleurus elegans* (Bell 1899): H.L. Clark 1925, p. 73. (= *Salmacis elegans* Bell 1899, p. 135): New Britain.

CIDARIDAE

Eucidaris metularia (Lamarck 1816): H.L. Clark 1925, p. 20. (= *Cidaris metularia* de Blainville, 1830, Bell 1899, p. 134): New Britain.

Prionocidaris baculosa var. *annulifera* (Lamarck): Mortensen 1928a, p. 437, 446. (= *Schleinitzia crenularis* Struder 1876, p. 463; 1880, p. 865): west New Guinea.

Stylocidaris reini (Döderlein): H.L. Clark 1925, p. 24; Mortensen 1928a, p. 342, 347, 474 (= *Phyllacanthus annulifera* Bell 1899, p. 134): New Britain; Milne Bay.

DIADEMATIDAE

Echinothrix calamaris (Pallas 1774): A.H. Clark 1954, p. 250: Bougainville Island.

**Micropyga nigra* H.L. Clark 1925: A. Agassiz 1879, p. 200; H.L. Clark 1925, p. 47. (= *Astropyga elastica* Struder, Bell 1899, p. 135): New Britain.

Micropyga tuberculata A. Agassiz 1879, p. 200: A. Agassiz 1881, pl. VII; H.L. Clark 1925, p. 48: Blanche Bay, New Britain.

ECHINOMETRIDAE

Echinometra mathaei (de Blainville 1825): A.H. Clark 1954, p. 251: Bougainville Island; Seleo Island, Aitape district; Normanby Island. (= *Echinometra lucunter* Bell 1899, p. 136).

ECHINOTHURIIDAE

Araeosoma gracile (A. Agassiz 1881): A. Agassiz 1881, p. 89; H.L. Clark 1925, p. 61: Admiralty Group (150 fathoms).

LAGANIDAE

Laganum decagonale (de Blainville 1827): A. Agassiz 1881; H.L. Clark 1925, p. 156; Mortensen 1948b, p. 332, 336; Lindley 2003a, p. 133: near Admiralty Group (150 fathoms).

Laganum depressum var. *tonganense* (Quoy and Gainard): Mortensen 1948b, p. 324: Admiralty Group.

Laganum laganum (Leske): Mortensen (1948b), p. 312: Bismarck Archipelago.

SPATANGIDAE

Maretia ovata (Leske 1778): A. Agassiz 1881; H.L. Clark 1925, p. 226: Admiralty Group.

TEMNOPLEURIDAE

Prionechinus agassizii Wood-Mason and Alcock 1891: H.L. Clark 1925, p. 78. (= *Echinus elegans*, A. Agassiz 1881): near Admiralty Group.

**Prionechinus sagittiger* A. Agassiz 1879, p. 202: A. Agassiz 1881, pl. IVa, figs 11-14; H.L. Clark 1925, p. 79: between New Guinea and Admiralty Group (1,070 fathoms).

Temnopleurus sp., Bell 1899, p. 135: New Britain.

Temnopleurus reevesii (Gray 1855): A. Agassiz 1881; H.L. Clark 1925, p. 81: near Admiralty Group (150 fathoms).

Temnotrema scillae (Mazetti 1894): Mortensen 1904, p. 86; H.L. Clark 1925, p. 91 (= *Pleurechinus reticulatus* in H.L. Clark 1925, p. 91): New Britain.

TOXOPNEUSTIDAE

Tripneustes gratilla (Linnaeus 1758): A.H. Clark 1954, p. 250: Bougainville Island; Seleo Island, Aitape district.

INVALID RECORDS

Astriclypeus manni Verrill, Sluiter 1895, p. 73, New Ireland; Mortensen 1948b, p. 416, 418.
Colobocentrotus mertensi Brandt 1835, Sluiter 1895, p. 69, New Ireland; Mortensen 1943b, p. 433.
Mellita longifissa Michelin 1858, Sluiter 1895, p. 73, New Ireland; Mortensen 1948b, p. 427, 428.
Taxonomic reason: Erroneous labelling (Mortensen 1948b, p. 418; Mortensen 1943b, p. 433; Mortensen 1948b, p. 428, respectively).

NOTES

* Denotes type localities in Bismarck Archipelago

Conodont Faunas from the Mid to Late Ordovician Boundary Interval of the Wahringa Limestone Member (Fairbridge Volcanics), Central New South Wales

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Zhen, Y.Y., Percival, I.G. and Webby, B.D. (2004). Conodont faunas from the Mid to Late Ordovician boundary interval of the Wahringa Limestone Member (Fairbridge Volcanics), central New South Wales. *Proceedings of the Linnean Society of New South Wales* **125**, 141-164.

Twenty-nine conodont species are documented from the Wahringa Limestone Member and other isolated limestone pods of the Fairbridge Volcanics, in the Bakers Swamp area between Wellington and Orange, central New South Wales. Three conodont assemblages are recognised within the Wahringa Limestone Member. The oldest is characterised by the occurrence of *Pygodus protoanserinus* and *Pygodus serra*, indicative of a late Darriwilian age (Da3 to early Da4). The overlying assemblage B, bearing *Belodina monitorensis*, probably ranges across the Mid to Late Ordovician boundary. Assemblage C with abundant *Belodina compressa* in the upper part of the Wahringa Limestone Member is of late Gisbornian (Gi2) age. The conodont faunas are significant in being the first described from the Lachlan Orogen in New South Wales spanning the Mid to Late Ordovician interval, although resolution of the actual boundary level is limited in the section measured.

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KEYWORDS: Conodonts, Fairbridge Volcanics, Late Ordovician (Gisbornian), Mid Ordovician (Darriwilian), Wahringa Limestone Member.

INTRODUCTION

The Molong Volcanic Belt (MVB) is a meridionally-aligned tectonic feature of Ordovician age within the east Lachlan Orogen in central New South Wales (Glen et al. 1998). Ordovician strata in the northern sector of the MVB near Bakers Swamp between Orange and Wellington (Fig. 1) are represented by the Early Ordovician Mitchell Formation and Hensleigh Siltstone – the latter yielding conodonts of Bendigonian age (upper *Prioniodus elegans* Zone) from allochthonous limestones (Zhen et al. in press) – and the Fairbridge Volcanics of Mid to early Late Ordovician age. Two autochthonous limestone units occur in the Fairbridge Volcanics. The lower one, known as the Wahringa Limestone Member, is the subject of this paper. Representative conodonts were illustrated earlier in a preliminary report defining this unit, and their age connotations discussed (Percival et al. 1999). Subsequent detailed sampling has yielded many more elements and species, enabling broad confirmation of the original age determination and providing increased precision for the upper age limit of the limestone. The faunas are systematically described here for the first time. They are significant in spanning the Mid to Late Ordovician boundary, an interval which is otherwise poorly represented in shallow water settings of eastern parts of the Lachlan Orogen.

STRATIGRAPHY

Much of the Fairbridge Volcanics consists of andesitic lava flows, with subsidiary boulder conglomerates (Morgan, Scott & Percival, in Meakin & Morgan 1999). Allochthonous limestones are

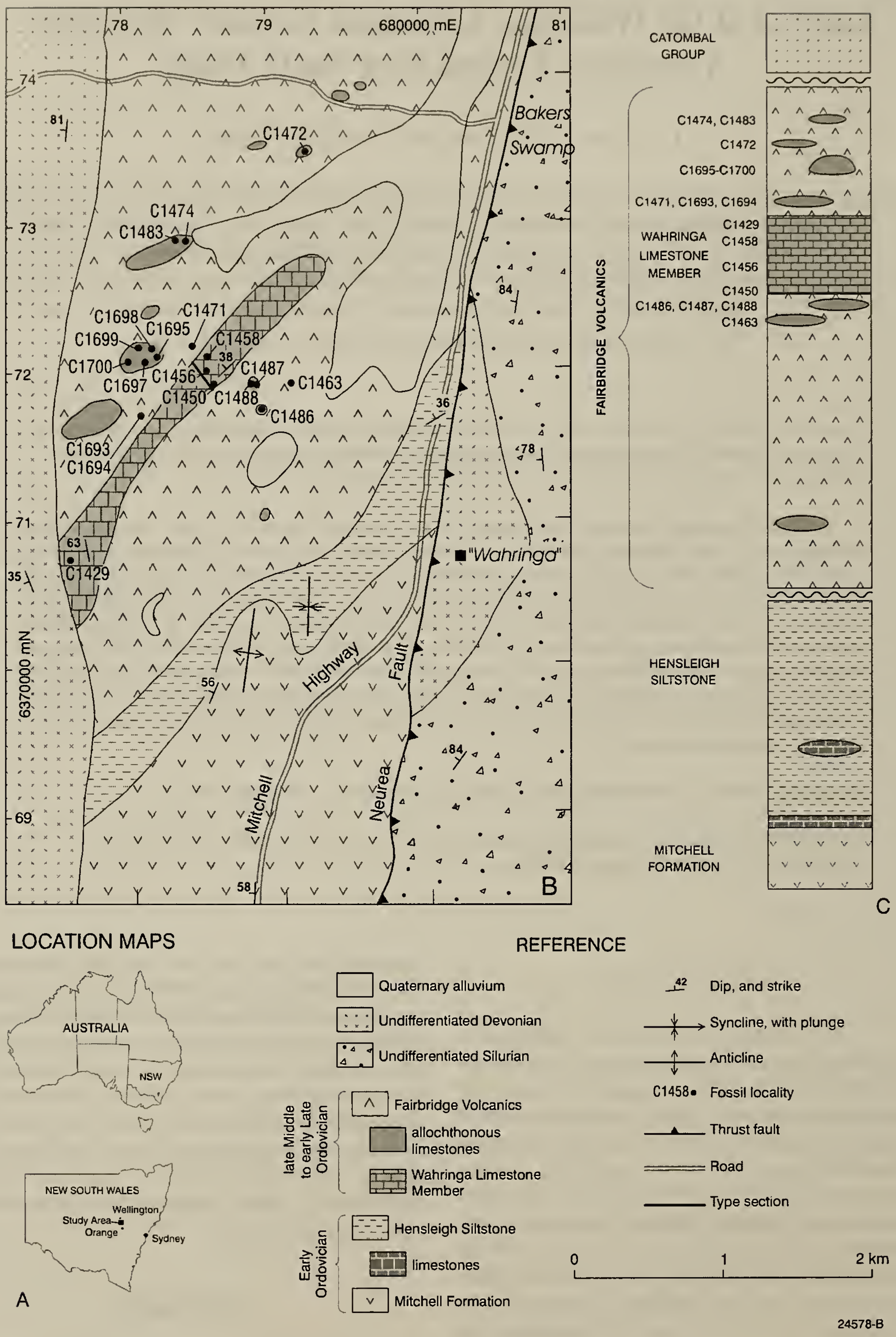

Figure 1. Locality maps. A. location of Wahringa area, between Wellington and Orange, central New South Wales; B. simplified geological map of the Wahringa area; C. generalised stratigraphic column for this area, showing spot sampled horizons within the Wahringa Limestone Member and the allochthonous limestone blocks within the Fairbridge Volcanics. For further details of the sampled section, see Figure 2.

uncommon in the lower Fairbridge Volcanics below the Wahringa Limestone Member and conodont yields are disappointingly low. Numerous allochthonous limestone pods emplaced within the Fairbridge Volcanics, stratigraphically overlying the Wahringa Limestone Member, were also processed for conodonts. With the exception of six samples that contained *Belodina compressa* (indicating an early Late Ordovician or Gisbornian age), these were either barren or yielded only sparse, non-diagnostic elements.

Wahringa Limestone Member of Fairbridge Volcanics (Fig. 2)

The name derives from the "Wahringa" property, located approximately 28 km south of Wellington on the Mitchell Highway. Here the Wahringa Limestone Member is exposed along strike for approximately 400 m and attains a thickness of 88 m in its type section (situated just north of a bend in Bakers Swamp Creek). Invertebrate macrofossils described or illustrated from the Wahringa Limestone Member comprise brachiopods, gastropods, nautiloids, crinoids, demosponges, stromatoporoids, and a species of tabulate coral (Percival et al. 2001). The unit is subdivisible into three parts: lower beds rich in oncolites, ooids and volcaniclastic detritus, a middle part of muddy, thinly bedded limestones rich in brachiopods, and an upper section that is more massive. The variation in lithologies reflects an increase in water depth from shallow subtidal at the base, to below normal wave base in the middle and upper beds. However, this depth increase does not have a controlling influence on the three distinct conodont assemblages recognised, which represent age-significant rather than biofacies-distinct assemblages.

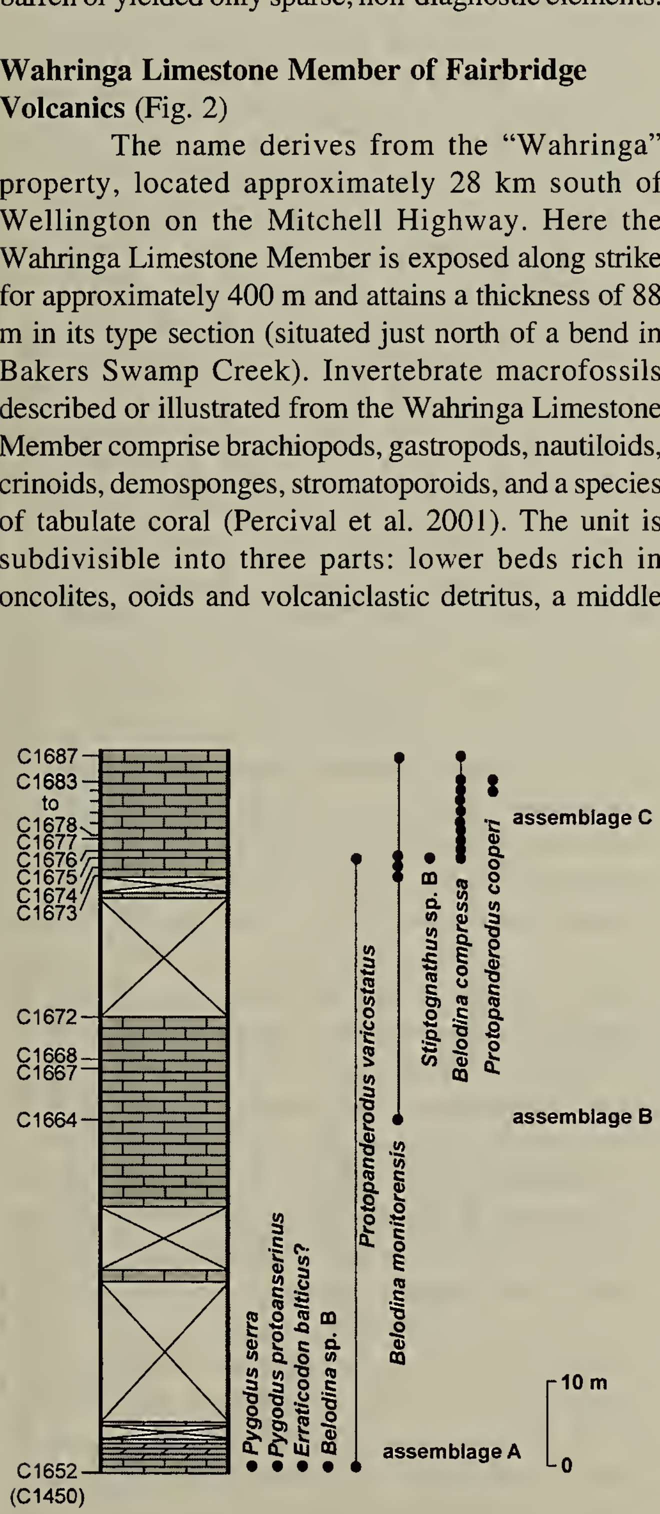

Figure 2. Stratigraphic section measured through the Wahringa Limestone Member showing sampled horizons and ranges of selected, age-significant conodont taxa.

Lithologies in the lower part of the member, which consist mainly of red ooidal grainstones, calcarenites and oncolitic grainstone-packstones, are particularly characteristic of very shallow deposition. Fauna present in these beds (not observed at other levels of the measured section) include the large gastropod *Maclurites* cf. *M. florentinensis*, the siphonotretoidean brachiopod *Multispinula*, and a *Calathium*-like receptaculitid. Demosponges, including *Archaeoscyphia*? sp. B, *Malongullospongia*? sp. and *Hindia* cf. *H. sphaeroidalis*, are more widely distributed but are especially common at this level. Fossil grains are subangular to rounded, frequently algal-coated and include dasycladacean and solenoporid algae. Large oncolites with well-preserved cyanobacterial *Girvanella* filaments and ooids are also abundant.

The middle part of the Wahringa Limestone Member is characterised by fine to coarse grained skeletal grainstone (interbedded with silty layers) that is dominated by remains of echinoderms, brachiopods, dasycladacean algae, molluscs, trilobites, and ostracods. Brachiopods, including *Sowerbyites*?, *Leptellina* and rare *Sowerbyella* are concentrated in thin-bedded packstones in the middle part of the unit. Stromatoporoids (*Labechia*, *Labechiella*), mostly preserved in growth position, occur slightly above this level and range into the uppermost limestone beds of the unit.

The most common lithologies in the upper part of the Wahringa Limestone Member are fine to coarse grained skeletal, oncolitic grainstone and lesser packstone to wackestone lacking internal lamination. Grains include ostracods, dasycladacean algae, rare ooids, and oncolites with associated *Girvanella*.

CONODONT BIOSTRATIGRAPHY

Twenty-nine conodont species based on 897 individual specimens were recovered from 44 samples (Fig. 3), collected from the Wahringa Limestone Member and various limestone pods within the enclosing Fairbridge Volcanics. The faunas range in age from late Darriwilian (Da3, lower *Eoplacognathus suecicus* Zone) to late Gisbornian (Gi2, *Belodina*

Localities	1st pods below Wahringa Lst				Wahringa Limestone Member type section																					Wahringa Lst Mbr NE of type section						*	Isolated limestone pods in Fairbridge Volcs above Wahringa Lst type section												Total
Samples Conodont taxa	C1463	C1486	C1487	C1488	C1450	C1456	C1458	C1464	C1652	C1664	C1667	C1668	C1672	C1673	C1674	C1675	C1676	C1677	C1678	C1679	C1680	C1681	C1682	C1683	C1687	C1707	C1709	C1710	C1711	C1712	C1713	C1429	C1471	C1472	C1474	C1483	C1693	C1694	C1695	C1696	C1697	C1698	C1699	C1700	
Acodus sp.					2				1												1																								4
Ansella nevadensis					4		1					2					1							1	1																				10
Ansella sp.	1	1											1																																3
Ansella biserrata									1																																				1
Appalachignathus delicatulus	1																																												1
Belodina compressa			1	1			32									1	1	2	2	1	1	1	5	5	10					1		144	1	32	8	2	2	2							255
Belodina monitorensis						4	1			1				1	3	3				1?					2									1											17
Belodina sp. A																																1													1
Belodina sp. B					1				2																																				3
Besselodus sp.																4	1						1									2		1	1										10
Dapsilodus variabilis					1				1							1													1																4
Dapsilodus viruensis							4									3																													7
Drepanoistodus sp.					1				1																									1	1										4
Erraticodon balticus?					1																																								1
Erraticodon sp.	1																																												1
Oistodus? sp. cf. *venustus*					2	2		1						1		1																			3										10
Panderodus gracilis		1	4		10	4	63	2	23	3	2			1	10	7	16	1	3	1	3		6	5	6	1		1				42	4	66	96	34			4	2	4	3	1	1	430
Peridon aculeatus	1?				11	3	23		19		1			1		21	3						3	1	3				1		1			2	1	1				1					97
Phragmodus flexuosus					1																																								1
Protopanderodus cooperi							3																2	1			1																		7
Protopanderodus nogamii	2				1																																								3
Protopanderodus robustus							1														1																								2
Protopanderodus varicostatus									1							7																													8
Protopanderodus liripipus							1																																						1
Pseudooneotodus mitratus																																			1										1
Pygodus protoanserinus					1				9																																				10
Pygodus serra									1																																				1
Stiptognathus sp. A	2																																												2
Stiptognathus sp. B																2																													2
TOTAL	8	2	5	1	36	13	129	3	59	4	3	2	1	4	13	50	22	3	5	3	6	1	17	13	22	1	1	1	2	1	1	189	5	103	111	37	2	2	4	3	4	3	1	1	897

Figure 3. Distribution chart of conodont species from 44 samples through the Wahringa Limestone Member, and allochthonous limestone blocks in the Fairbridge Volcanics, from above and below the Wahringa Limestone Member. Column with asterisk depicts occurrence of species in sole sample (C1429: middle or upper beds) from southwestern extremity of outcrop of the Wahringa Limestone Member.

compressa Zone).

The oldest fauna is represented by a small assemblage, including *Appalachignathus delicatulus*, *Protopanderodus nogamii*, ?*Periodon aculeatus*, *Ansella* sp., *Erraticodon* sp., and *Stiptognathus* sp. A from a single sample C1463, which was obtained from several small limestone clasts within the Fairbridge Volcanics at a stratigraphic level some 120 m below the Wahringa Limestone Member (Percival et al. 1999). This fauna is comparable with that recently described from allochthonous limestones of Da3 age in the Oakdale Formation of the Bell River valley (Zhen and Percival in press), situated approximately 23 km southeast of the "Wahringa" area. Of the six species recognised in sample C1463, four also occur in the Bell River valley fauna. *Stiptognathus* sp. A is rare, but the other three species (*Appalachignathus delicatulus*, *Protopanderodus nogamii*, and *Erraticodon* sp.) dominate in all five samples from the Oakdale Formation (Zhen and Percival in press). On this basis, the age of sample C1463 can now be revised downwards to the *E. suecicus* Zone from the previously-interpreted level near the Mid/Late Ordovician boundary (Zhen et al. 2001).

In its type section, the Wahringa Limestone Member consists of three laterally continuous outcrops separated by two intervals of poor or negligible exposure (Fig. 2). Initially, one spot sample was collected from each of these three major outcrops, representing the lower, middle, and upper beds of the unit. Subsequent more intensive collecting during section measuring produced 17 samples that yielded conodonts. Although most of these samples have low yields and diversity, three conodont assemblages (herein referred to as A, B, and C from oldest to youngest) can be distinguished.

Assemblage A was recovered from sample C1652 at the base of the Wahringa Limestone Member and spot sample C1450 within the lower part of this unit (essentially an equivalent stratigraphic level to C1652) in the type section. The fauna consists of 15 species including *Acodus* sp., *Ansella nevadensis*, *Ansella biserrata*, *Belodina* sp. B, *Dapsilodus variabilis*, *Drepanoistodus* sp., *Erraticodon balticus*?, *Oistodus*? sp. cf. *venustus*, *Panderodus gracilis*, *Periodon aculeatus*, *Phragmodus flexuosus*, *Protopanderodus nogamii*, *Protopanderodus varicostatus*, *Pygodus serra*, and *Pygodus protoanserinus*. Most of these species are widely distributed and relatively long ranging, but the two species of *Pygodus* are important biostratigraphically. *Pygodus protoanserinus* has a range from the upper *E. robustus* Subzone to the *E. lindstroemi* Subzone (of the upper *Pygodus serra* Zone). One specimen (see Fig. 9K, L) referrable to the middle form of the Pa element of *Pygodus serra* (Zhang 1998a) was also recovered in the sample C1652. Co-occurrence of *P. serra* and *P. protoanserinus* places the base of the Wahringa Limestone Member precisely within the upper *E. robustus* Subzone (upper Da3 to lowest Da4) of the *P. serra* Zone.

Closest correlations are with successions in China. In the top Guniutan Formation (upper *P. serra* Zone) of Hunan Province, Zhang (1998b) recorded the co-occurrence of *Pygodus protoanserinus* with *Erraticodon balticus*?, *Protopanderodus varicostatus*, and *Periodon aculeatus*. *Pygodus serra*, *Periodon aculeatus*, *Protopanderodus varicostatus*, *Protopanderodus nogamii*, and *Panderodus gracilis* also occur in the lower part (*P. serra* Zone) of the Pingliang Formation of the Ordos Basin (An and Zheng 1990).

Only five samples from the middle section of the Wahringa Limestone Member have yielded conodonts. These faunas are of very low diversity and productivity, and are referred to herein as Assemblage B. They include *Ansella nevadensis*, *Ansella* sp., *Belodina monitorensis*, *Panderodus gracilis*, and *Periodon aculeatus*. Of these, only *B. monitorensis* is significant for age determination, occurring widely within the late Darriwilian to Gisbornian interval (Sweet in Ziegler 1981). Assemblage B is likely very close to the Mid/Late Ordovician boundary, probably within the *Cahabagnathus sweeti* Zone, although the precise recognition of the boundary within the middle Wahringa Limestone Member is not determinable on current evidence.

The upper part of the type section of the Wahringa Limestone Member is relatively more productive, with 12 samples yielding an assemblage (designated as Assemblage C) of 15 species including *Acodus* sp., *Ansella nevadensis*, *Belodina compressa*, *Belodina monitorensis*, *Besselodus* sp., *Dapsilodus variabilis*, *Dapsilodus viruensis*, *Drepanoistodus* sp., *Oistodus*? sp. cf. *venustus*, *Panderodus gracilis*, *Periodon aculeatus*, *Protopanderodus cooperi*, *Protopanderodus varicostatus*, *Protopanderodus liripipus* and *Stiptognathus* sp. B. As a zonal index species of late Gisbornian equivalents in the North American Midcontinent zonal scheme, the occurrence of *Belodina compressa* in the upper part of the Wahringa Limestone Member indicates that top of this unit may be as young as Gi2. This species also occurs in six samples from limestone pods within the Fairbridge Volcanics above the Wahringa Limestone Member. The presence of two elements confidently identified as this species in limestone pods in the Fairbridge Volcanics slightly below the base of the Wahringa Limestone Member (samples C1487 and C1488) cannot be explained at present, as this

Figure 4. A-G, *Acodus* sp.; A, B, P element, MMMC2639, C1450, A, inner lateral view, B, outer lateral view; C, D, P element, MMMC2640, C1652, C, outer lateral view, D, anterior view; E-G, Sa element, MMMC2641, C1680, lateral views. H-P, *Ansella nevadensis* (Ethington and Schumacher 1969); H-J, Pa element, MMMC2642, C1450, H, inner lateral view, I, outer lateral view, J, showing surface striation; K, L, Pb element, MMMC2643, C1450, K, outer lateral view, L, inner lateral view; M, N, Sa element, MMMC2644, C1683, lateral views; O, P, Sc element, MMMC2645, C1450, O, outer lateral view, P, inner lateral view. Q, *Ansella biserrata* Lehnert and Bergström in Lehnert et al. 1999; Pa element, MMMC2646, C1652, outer lateral view. R, S, *Ansella* sp.; R, Pb element, MMMC2647, C1486, inner lateral view; S, Pb element, MMMC2648, C1672, outer lateral view. T, *Appalachignathus delicatulus* Bergström et al. 1974; Pb element, MMMC2649, C1463, inner lateral view. Unless otherwise indicated scale bars are 100 µm.

contradicts the species succession in all known global occurrences.

LOCALITIES AND SAMPLES

Details of the localities and measured section are shown in Figures 1 and 2, and summarised in the Appendix. Distribution of conodont species is presented in Figure 3. All illustrations of conodont elements are presented as SEM photomicrographs (Figs 4-9). Figured specimens bearing the prefix MMMC ("Mining Museum microfossil catalogue") are deposited in the collections of the Geological Survey of New South Wales, Sydney. Individual samples are referred to by the prefix "C". Although all species recorded are documented by illustration, only those where adequate material was recovered, or which are of biostratigraphic significance, are described. Unless otherwise mentioned, all specimens are from the Wahringa Limestone Member.

SYSTEMATIC PALAEONTOLOGY

Class CONODONTATA Pander 1856

Genus ANSELLA Fåhraeus and Hunter 1985a

Type species

Belodella jemtlandica Löfgren 1978.

Ansella nevadensis (Ethington and Schumacher 1969)

Fig. 4H-P

Synonymy

Roundya sp. Sweet and Bergström 1962, p. 1244, 1245, text-fig. 5.

New Genus A Ethington and Schumacher 1969, p. 478, 479, pl. 68, fig. 12, text-fig. 4J.

Oepikodus copenhagenensis Ethington and Schumacher 1969, p. 465, pl.68, figs 5, 9, text-fig. 4L.

Oistodus nevadensis Ethington and Schumacher 1969, p. 467, 468, pl. 68, figs 1-4, text-fig. 5C; Tipnis et al. 1978, pl. 6, fig. 7.

Belodella nevadensis (Ethington and Schumacher); Bergström 1978, pl. 79, figs 9, 10; Bauer 1987, text-fig. 5D.

Ansella nevadensis (Ethington and Schumacher); Fåhraeus and Hunter 1985a, p. 1175, 1176, pl. 1, figs 7, 10, pl. 2, figs 11a, b, 13a, b, 14, text-fig. 2A-C; Bergström 1990, pl. 1, figs 11-14; McCracken 1991, p. 47-49, pl. 3, figs 3, 4, 8, 9, 13, 14, 19-31 (cum syn.); ?Bauer 1990, pl. 1, fig. 1; ?Bauer 1994, fig. 3.4, 3.5.

Material

Ten specimens (1 Pa, 4 Pb, 4 Sa, 1 Sc).

Description

The P elements are characterised by a prominent median costa on each side, and display a sharply inner laterally curved anterior margin. The Pa element has a row of denticles along the posterior edge (Fig. 4H-J). The denticle next to the cusp is the largest, and the others become gradually smaller towards the base. A sharp costa on each side extends from the tip of the cusp and disappears a short distance away from the basal margin. The Pb element has a sharp posterior margin without any denticles, a weaker and broader costa on the inner lateral side, and a sharp, strong costa on the outer lateral side (Fig. 4K, L). The Sa element is symmetrical with a row of closely spaced small denticles along the posterior margin, and bears a sharp antero-lateral costa on each side (Fig. 4M, N). The asymmetrical Sc element has an inner laterally curved anterior margin, and a row of small closely spaced denticles along the posterior margin (Fig. 4O, P). Specimens are ornamented with fine striation.

Discussion

Originally proposed as the form species *Oepikodus copenhagenensis* Ethington and Schumacher 1969 and New Genus A Ethington and Schumacher 1969 (found in association with *Oistodus nevadensis* in the Copenhagen Formation of Nevada), these elements were considered as part of the species apparatus of *A. nevadensis* by Fåhraeus and Hunter (1985a), and are herein assigned to the Pa and Sb positions. Fåhraeus and Hunter (1985a) also illustrated a symmetrical Sa element (Fåhraeus and Hunter 1985a, pl. 2, fig. 14) from the Cobbs Arm Limestone of Newfoundland. Specimens from the Wahringa Limestone Member permit differentiation of denticulate Pa and adenticulate Pb elements. The latter has not been recognised previously, but its assignment to the Pb position is consistent with the apparatus composition of comparable species such as *A. jemtlandica* and *A. crassa* Bauer 1994, from central New South Wales (Zhen and Percival in press).

Ansella biserrata Lehnert and Bergström in Lehnert et al. 1999

Fig. 4Q

Synonymy

Ansella biserrata Lehnert and Bergström in Lehnert et al. 1999, p. 210, 212, pl. 1, figs 4, 7, pl. 3, figs 1-3, 5 (cum syn.).

Material

One specimen (Pa).

Discussion

Lehnert and Bergström in Lehnert et al. (1999) recognised a quadrimembrate apparatus for *A. biserrata* including biserrate, planoconvex, oistodiform, and triangular elements. We refer the biserrate and planoconvex elements to the Pa and Pb positions respectively, whereas the triangular element is regarded as taking either the Sa (symmetrical) or Sb (asymmetrical) position. The sole specimen from the lower Wahringa Limestone Member (C1652), with smooth lateral faces and fine denticles along its anterior and posterior margins, strongly resembles the holotype (a biserrate element) of *A. biserrata* from the basal Lindero Formation (*Pygodus serra* and *P. anserinus* zones) of west central Argentina (Lehnert et al. 1999).

Ansella sp.

Fig. 4R, S

Synonymy

Serraculodus? sp. Zhen and Webby 1995, p. 286, only pl. 5, figs 1, 3, 4.

Ansella sp. Zhen et al. 2003a, p. 38, fig. 4A, 4B.

Material

Three specimens (Pb).

Discussion

These specimens are similar to the Pb element of *A. nevadensis*, but they lack the prominent lateral median costae of that species. They are identical with some specimens from the Fossil Hill Limestone of Eastonian age at Cliefden Caves previously assigned to *Serraculodus*? sp. (Zhen and Webby 1995). They can be distinguished from the Pb elements of both *A. jemtlandica* (Löfgren 1978) and *A. crassa* Bauer 1994 in lacking the posteriorly more expanded base displayed in the latter two species (Zhen and Percival in press).

Genus BELODINA Ethington 1959

Type species

Belodus compressus Branson and Mehl 1933.

Belodina compressa (Branson and Mehl 1933)

Fig. 5A-I

Synonymy

Belodus compressus Branson and Mehl 1933, p. 114, pl. 9, figs 15, 16.

Belodus grandis Stauffer 1935, p. 603-604, pl. 72, figs 46, 47, 49, 53, 54, 57.

Belodus wykoffensis Stauffer 1935, p. 604, pl. 72, figs 51, 52, 55, 58, 59.

Oistodus fornicalus Stauffer 1935, p. 610, pl. 75, figs 3-6.

Belodina dispansa (Glenister); Schopf 1966, p. 43, pl. 1, fig. 7.

Belodina compressa (Branson and Mehl); Bergström and Sweet 1966, p. 321-315, pl. 31, figs 12-19; Webers 1966, p. 24, pl. 1, figs 2, 6, 7, 13, 15; Sweet in Ziegler 1981, p. 65-69, *Belodina* - plate 2, figs 1-4; An et al. 1983, only pl. 25, figs 13, 14; Moskalenko 1983, fig. 3Q-S; Leslie 1997, p. 921-926, figs 2.1-2.20, 3.1-3.4 (cum syn.).

Belodina confluens Sweet; Percival et al. 1999, p. 13, fig. 8.21.

Material

255 specimens, including eobelodiniform, compressiform, grandiform and dispansiform elements, mainly from the upper part of the Wahringa Limestone Member; some specimens from allochthonous limestones in the Fairbridge Volcanics above the Wahringa Limestone Member, and two elements from limestone pods (C1487, C1488) in the Fairbridge Volcanics which apparently underlie the Wahringa Limestone Member.

Discussion

Of the known species of *Belodina*, three including *B. compressa*, *B. confluens* Sweet 1979, and *B. monitorensis* Ethington and Schumacher 1969, are morphologically very similar to each other, reflecting their close phylogenetic relationship. Well-documented successions in the U.S.A. (Sweet 1979) show that the oldest species, *B. monitorensis*, preceded *B. compressa* which was succeeded by *B. confluens*. Sweet (in Ziegler 1981, p. 65) revised all three species as consisting of trimembrate apparatuses, and emphasised that the type species of the genus, *B. compressa*, was characterised by having a distinct flattening (in lateral view) of the anterior margin near the antero-basal corner. This feature is more prominent in the compressiform element, as shown by the types (Branson and Mehl 1933) and also the specimens figured by Webers (1966); also see Sweet in Ziegler (1981). Both *B. confluens* and *B. compressa* are commonly found in association with a more slender, rastrate element bearing smaller denticles. Bergström (1990) suggested that these dispansiform elements might represent juveniles of the rastrate elements. Many other workers included these dispansiform elements in a separate species (*dispansa*) assigned either to *Pseudobelodina* (Sweet in Ziegler,1981, Nowlan and McCracken in Nowlan et al. 1988,

Figure 5. A-I, *Belodina compressa* (Branson and Mehl 1933); A, inner lateral view, B, outer lateral view, grandiform element, MMMC2650, C1472; C, dispansiform element, MMMC2651, C1429, inner lateral view; D, compressiform element, MMMC2652, C1472, inner lateral view; E, compressiform element, MMMC2653, C1458, outer lateral view; F, compressiform element, MMMC2654, C1683, outer lateral view; G, dispansiform element, MMMC2655, C1429, outer lateral view; H, inner lateral view, I, outer lateral view, eobelodiniform element, MMMC2656, C1683. J-N, *Belodina monitorensis* Ethington and Schumacher 1969; J, outer lateral view, K, inner lateral view, grandiform element, MMMC2657, C1687; L, inner lateral view, M, outer lateral view, compressiform element, MMMC2658, C1456; N, eobelodiniform element, MMMC2659, C1456, outer lateral view. O, P, *Belodina* sp. B; O, eobelodiniform element, MMMC2660, C1450, inner lateral view; P, eobelodiniform element, MMMC2661, C1652, outer lateral view. Q, *Belodina* sp. A; grandiform element, MMMC2662, C1429, outer lateral view. R-T, *Besselodus* sp.; R, S, Sa element, MMMC2663, C1676, lateral views; T, M element, MMMC2664, C1675, anterior view. Scale bars are 100 μm.

McCracken and Nowlan 1989, Trotter and Webby 1995, Leslie 1997, McCracken 2000) or to *Belodina* (Schopf 1966, Barnes 1977, Nowlan and Barnes 1981, Sansom et al. 1995). In comparing the apparatus architecture of *Panderodus*, Sansom et al. (1995) suggested that these slender dispansiform elements, which were previously included in *Belodina dispansa* (Glenister 1957) and *Belodina arca* Sweet 1979, might belong to the species apparatus of co-occurring *B. confluens*. Based on twelve well preserved, fused clusters of *B. compressa* recovered from the Plattin Limestone of Missouri and Iowa, Leslie (1997) demonstrated that *B. compressa* consisted of a quadrimembrate apparatus including the M (eobelodiniform), S1 (compressiform), S2 (grandiform) and S2 (dispansiform) elements. He further suggested that the dispansiform element – although superficially similar in morphology to *Pseudobelodina dispansa* – was apparently not conspecific. Leslie also rejected the possibility that such elements represented the juveniles of compressiform and grandiform elements in consideration of the range of sizes and growth series preserved in the dispansiform elements.

The material of *B. compressa* and *B. confluens* from central New South Wales shows recognisable differences between the two species. Compressiform elements of *B. compressa* display in lateral view a straight segment of the anterior margin near the antero-basal corner. In comparison, the anterior margin of the compressiform element of *B. confluens* is regularly curved near the antero-basal corner. Hence specimens of *B. compressa* previously reported from the Fork Lagoons Beds of central Queensland (Palmieri 1978), and from the Trelawney Beds of the New England Fold Belt (Philip 1966) were subsequently reassigned to *B. confluens* (Zhen and Webby 1995). Specimens from the Wahringa Limestone Member and various limestone pods within the Fairbridge Volcanics are the first confirmed records of *B. compressa* from eastern Australia.

Belodina monitorensis Ethington and Schumacher 1969
Fig. 5J-N

Synonymy

Belodina monitorensis monitorensis Ethington and Schumacher 1969, p. 456, pl. 67, figs 3, 5, 8, 9, text-fig. 5D.

Belodina monitorensis marginata Ethington and Schumacher 1969, p. 456, pl. 67, figs 1, 2, 4, 6, text-fig. 5E.

Eobelodina occidentalis Ethington and Schumacher 1969, p. 456, pl. 67, figs 16, 20, text-fig. 5H.

Belodina monitorensis Ethington and Schumacher 1969, p. 455, 456; Sweet in Ziegler 1981, p. 79-81, *Belodina* - plate 1, figs 10, 11; *Belodina* - plate 2, figs 5-7; Bauer 1987, p. 12, pl. 1, figs 10, 13, 14; Bauer 1990, pl. 1, fig. 9; Bauer 1994, fig. 3.16, 3.17, 3.20, 3.21.

Material

17 specimens including eobelodiniform, compressiform and grandiform elements.

Discussion

Belodina monitorensis was originally defined as having prominent antero-lateral costae on either side of the grandiform element and generally four or five denticles on both grandiform and compressiform elements. A similar antero-lateral costa is also commonly found in the grandiform elements of *B. compressa* (Fig. 5B; also see Leslie 1997, fig. 2.3), and in the grandiform elements of *B. confluens* (McCracken 1987, pl. 1, fig. 1; Zhen and Webby 1995, pl. 1, figs 17, 20; Zhen et al. 1999, fig. 5.8). Therefore, this character appears to be unreliable in characterising *B. monitorensis*. Although *B. confluens* and *B. compressa* typically have a greater number of denticles (five to nine), it seems rather arbitrary to split *B. monitorensis* (typically four or five denticles) from *B. confluens* based solely on the former having fewer denticles.

Though the species status of *B. monitorensis* is uncertain in our view, stratigraphically it occurs much earlier than typical *B. confluens*. In the type section of the Wahringa Limestone Member, *B. monitorensis* occurs lower than *B. compressa*, but it is also found in association with the latter species in several samples in the upper part of the type section. The Wahringa Limestone Member specimens are comparable with the type material of *B. monitorensis* in having only three or four denticles, and in having an antero-lateral costa on the furrowed side of the grandiform element (Fig. 5J), also shown by the holotype (Ethington and Schumacher 1969, pl. 67, fig. 5). Therefore, the species is tentatively retained here pending further detailed studies on *B. monitorensis* and other related species.

Belodina sp. A
Fig. 5Q

Material

One specimen from sample C1429 (upper beds of the Wahringa Limestone Member at the southwestern extremity of its outcrop).

Discussion

This compressiform element has a squat cusp and two short and stout denticles along the posterior margin. The specimen is not as strongly compressed laterally as other known species of *Belodina*.

Belodina sp. B
Fig. 5O, P

Material
Three eobelodiniform specimens.

Discussion
From its association with *Pygodus protoanserinus* in two samples (C1450 and C1652) from the lower part of the Wahringa Limestone Member this species has a late Darriwilian age (upper Da3 to lowest Da4, upper *P. serra* Zone), making it one of the earliest representatives of the genus *Belodina*. With a less extended heel it shows some morphological resemblance to the eobelodiniform element of *Belodina beiyanhuaensis* Qiu in Lin, Qiu and Xu 1984, but no rastrate elements have been recovered to confirm such an assignment.

Genus ERRATICODON Dzik 1978

Type species
Erraticodon balticus Dzik 1978.

Erraticodon balticus? Dzik 1978
Fig. 6P, Q

Synonymy
Erraticodon balticus Dzik 1978, p. 66, pl. 15, figs 1-3, 5, 6, text-fig. 6; ?Stouge 1984, p. 84, pl. 17, figs 9-19; Watson 1988, p. 113, pl. 5, figs 2-10, pl. 8, figs 1, 2, 5, 6, 8-13 (cum syn.); Dzik 1991, p. 299, fig. 12A; Ding et al. in Wang 1993, p. 176, pl. 37, only figs 19-28, non fig. 18; ?Pohler 1994, pl. 3, figs 3-5; Lehnert 1995, p. 87, pl. 10, figs 13, 16, pl. 12, figs 3-5; ?Zhang 1998b, p. 71, pl. 9, figs 6-13; ?Albanesi in Albanesi et al. 1998, p. 176, pl. 4, figs 16-18; ?Johnston and Barnes 2000, p. 19, pl. 4, figs 18, 20, 23, 24, 29; Zhao et al. 2000, p. 203, pl. 36, figs 1-16; ?Pyle and Barnes 2002, p. 111, pl.20, figs 8, 9.

Material
One specimen (M).

Discussion
Dzik (1978) originally defined the species as consisting of a seximembrate apparatus, but later (Dzik 1991) determined a septimembrate apparatus with digyrate Pa and Pb elements as typical of the species (Zhen et al. 2003b). *Erraticodon balticus* is characterised by having an accentuated denticle on the posterior process of the Sa, Sb and Sc elements (Dzik 1991, fig. 12A). The specimen from the Wahringa Limestone Member is broadly comparable with the M element of the illustrated type material (Dzik 1978, pl. 15, fig. 5), except that the latter has a reclined cusp; as our specimen has an erect cusp, it is only questionably referred to this species.

Specimens ascribed to *Erraticodon balticus* from the Guniutan Formation of South China (Zhang 1998b), the San Juan Formation of the Precordillera in Argentina (Albanesi in Albanesi et al. 1998), the Ospika Formation of British Columbia (Pyle and Barnes 2001), and the Cow Head Group of western Newfoundland (Johnston and Barnes 2000), all apparently lack the distinctive larger denticle on the posterior process of the S elements, and therefore should only be doubtfully assigned to the species.

Erraticodon sp.
Fig. 6O

Material
One specimen (Sa) from sample C1463, a limestone pod in the Fairbridge Volcanics stratigraphically below the Wahringa Limestone Member.

Discussion
This alate element is identical with the Sa element of a new species of *Erraticodon* under description from allochthonous limestones within the Oakdale Formation of central New South Wales (Zhen and Percival in press). It has a prominent cusp with a flange-like costa on each side, which extends basally to define the upper margin of the lateral processes. The lateral processes bear four widely spaced, peg-like denticles. Comparison with other species of *Erraticodon* are discussed elsewhere (Zhen and Percival in press).

Genus PERIODON Hadding 1913

Type species
Periodon aculeatus Hadding 1913.

Periodon aculeatus Hadding 1913
Figs 6R, S, 7A-K

Synonymy
Periodon aculeatus Hadding 1913, p. 33, pl. 1, fig. 14; Lindström 1955b, p. 110, pl. 22, figs 10, 11, 14-16, 35; Löfgren 1978, p. 74, pl. 10, fig. 1; pl. 11, figs 12-26, Fig. 29 (cum syn.); Sweet in Ziegler 1981, p. 237, *Periodon* - plate 1, figs 1-6; Nowlan 1981, pl. 4, figs 1-9; An 1987, p. 167, pl. 24, figs 7-17; Bergström 1990, pl. 1, figs 15, 16, pl.

Figure 6. A-D, *Dapsilodus variabilis* (Webers 1966); A, B, symmetrical distacodontiform element, MMMC2665, C1675, lateral views; C, symmetrical distacodontiform element, MMMC2666, C1450, lateral view; D, acodontiform element, MMMC2667, C1652, outer lateral view. E-J, *Dapsilodus viruensis* (Fåhraeus 1966). E, F, Sa element, MMMC2668, C1675, lateral views; G, outer lateral view, H, inner lateral view, Sb element, MMMC2669, C1675; I, outer lateral view, J, inner lateral view, Sc element, MMMC2670, C1675. K-M, *Drepanoistodus* sp.; K, outer lateral view, L, inner lateral view, Sc element, MMMC2671, C1652; M, P element, MMMC2672, C1450, inner lateral view. N, *Oistodus*? sp. cf. *venustus* Stauffer 1935; anterior view, MMMC2673, C1450. O, *Erraticodon* sp.; Sa element, MMMC2674, C1463, postero-lateral view. P, Q, *Erraticodon balticus*? Dzik 1978; M element, MMMC2675, C1450, P, posterior view, Q, anterior view. R, S, *Periodon aculeatus* Hadding 1913; Pb element, MMMC2676, C1450, R, inner lateral view, S, outer lateral view. Scale bars are 100 μm.

2, fig. 15; An and Zheng 1990, pl. 12, figs 12-17; McCracken 1991, p. 50, pl. 1, figs 13, 20, 22, 25-28, pl. 2, figs 24-27, 31, 34, 35 (cum syn.); Pohler 1994, pl. 4, figs 30-32; Dzik 1994, p. 111, pl. 24, figs 10-13, text-fig. 31b; Lehnert 1995, p. 110, pl. 10; fig. 2, pl. 11, figs 10, 11, pl. 13, figs 9, 11, 12, pl. 16, figs 8, 9, 11-13; Armstrong 1997, p. 774, pl. 2, figs 13-21; text-fig. 3; Albanesi in Albanesi et al. 1998, p. 170, pl. 15, figs 16-17, pl. 16, figs 19, 20 (cum syn.); Zhang 1998b, p. 80, 81, pl. 14, figs 1-8 (cum syn.); Johnston and Barnes 2000, p. 32-35, pl. 13, figs 12, 13, 17, 18, 20-31, pl. 14, figs 1-7, text-figs 4, 5 (cum syn.); Rasmussen 2001, p. 110, pl. 13, figs 8-11 (cum syn.); Pyle and Barnes 2002, p. 107, pl. 21, figs 7-9.

Material

97 specimens.

Description

Both Pa and Pb elements are angulate with a prominent cusp which is laterally compressed with a median costa on each side. The Pb element differs from the Pa element in having a twisted posterior process and a strongly inner laterally curved and downwardly extended anterior process (Fig. 6R, S). The M element is makellate with an adenticulate outer lateral process, and with 4-6 closely spaced denticles along the inner lateral margin. The alate Sa element has a long posterior process bearing closely spaced denticles. The sixth denticle away from the cusp is much larger and more robust (Fig. 7E, F). The lateral process on each side is blade-like, bearing small closely spaced rudimentary denticles along the edge. The basal cavity is shallow with a recessive basal margin zone. The Sb element is tertiopedate and asymmetrical, and bears a long denticulate posterior process with closely spaced, strongly reclined denticles, a long inner lateral process with more than seven small confluent denticles, and a short outer lateral process with only two small denticles (Fig. 7H, G). The Sc element is bipennate with a long, denticulate posterior process, bearing closely spaced, strongly reclined denticles, and with an inner laterally curved anterior process bearing small confluent denticles (Fig. 7I-K).

Discussion

Following the *Treatise* definition of the genus (Clark et al. 1981, p. W128), Sweet (1988) proposed a seximembrate apparatus for *P. aculeatus*, consisting of angulate Pa and Pb, makellate M, and ramiform alate Sa, tertiopedate Sb and bipennate Sc, elements. Albanesi (in Albanesi et al. 1998, text-fig 31, pl. 9, fig. 10) suggested a septimembrate apparatus for the species by recognizing a lozognathiform Sd element, which bears a long denticulate, twisted posterior process, a short, denticulate outer lateral process and an inner laterally curved, sharp, blade-like anterior costa. Rasmussen (2001, pl.13, fig.11) also recognised a modified tertiopedate Sd element, and described it as characterised by a multidenticulate, twisted, posterior process and weakly denticulated anterior process, and process-like extension of the outer-lateral costa or carina, but only a poorly preserved specimen was illustrated. In the Wahringa collections no Sd elements have been recognised.

Löfgren (1978, p. 75) suggested that the number of small denticles between the cusp and the biggest denticle increases from a mean of 4.7 to 5.6 in successively younger samples. Specimens from the Wahringa Limestone Member may therefore represent more advanced forms of the species within its stratigraphic range, as shown by the M elements, which are strongly geniculate with a sinuous basal margin and bear 4-6 denticles (mean 5.5) along the inner lateral margin.

Genus PHRAGMODUS Branson and Mehl 1933

Type species

Phragmodus primus Branson and Mehl 1933.

Phragmodus flexuosus Moskalenko 1973
Fig. 7L, M

Synonymy

Phragmodus sp. Moskalenko 1972, p. 48-50, text-fig. 1, table 2.

Phragmodus flexuosus Moskalenko 1973, p. 73, 74, pl. 11, figs 4-6; Sweet in Ziegler 1981, p. 255-258, *Phragmodus* - plate 2, figs 1-6 (cum syn.); Bauer 1987, p. 24, 25, pl. 3, figs 10, 14, 15, 17, 18, 20, 24, text-fig. 8; Ethington and Clark 1982, p. 79-82, pl. 9, figs 2-7 (cum syn.); Bauer 1994, p. 367, 368, fig. 5.25, 5.26, 5.28, 5.30-5.33; Percival et al. 1999, fig. 8.15.

Material

One specimen (Sa).

Discussion

This specimen is alate with a suberect cusp, a long denticulated posterior process, and with a flange-like costa on each lateral side. The straight posterior process supports more than seven widely spaced denticles,

Figure 7. A-K, *Periodon aculeatus* Hadding 1913; A, outer lateral view, B, inner lateral view, Pa element, MMMC2677, C1450; C, posterior view, D, anterior view, M element, MMMC2678, C1450; E, F, Sa element, MMMC2679, C1450, lateral views; G, outer lateral view, H, inner lateral view, Sb element, MMMC2680, C1450; I, outer lateral view, J, inner lateral view, Sc element, MMMC2681, C1450; K, Sc element, MMMC2682, C1652, outer lateral view. L, M, *Phragmodus flexuosus* Moskalenko 1973; Sa element, MMMC2683, C1450, lateral views. N-U, *Panderodus gracilis* (Branson and Mehl 1933); N, posterior view, O, inner lateral view, P, outer lateral view, graciliform element, MMMC2684, C1450; Q, posterior view, R, basal view, S, lateral view, aequaliform element, MMMC2685, C1458; T, falciform element, MMMC2686, C1697, outer lateral view; U, falciform element, MMMC2687, C1458, inner lateral view. Scale bars are 100 μm.

which are reclined, similar in size, with V- or U-shaped spaces between. It is comparable to the type material from Siberia, except that the Wahringa specimen exhibits a rather straight posterior process with more or less equal-sized denticles, and a few small, rudimentary denticles on the lower edge of the lateral processes. Although Moskalenko (1972) initially recognised nine morphotypes for the species, she later

(Moskalenko 1973) formally described the species as a form species. Based on a detailed revision, Ethington and Clark (1982) redefined *P. flexuosus* as consisting of a seximembrate apparatus. However, the illustrated S elements from Utah display more pronounced undulations and twisting of the posterior process and size variation of the denticles on the posterior process (Ethington and Clark 1982, pl. 9, figs 3, 6) than the type material from Siberia (Moskalenko 1973).

Genus PROTOPANDERODUS Lindström 1971

Type species
Acontiodus rectus Lindström 1955a.

Protopanderodus cooperi (Sweet and Bergström 1962)

Fig. 8A-E

Synonymy

Scandodus rectus Lindström 1955a, p. 593, only pl. 4, figs 22, 23.

Acontiodus cooperi Sweet and Bergström 1962, p. 1221, pl. 168, figs 2, 3, text-fig. 1G.

Scandodus sp. Sweet and Bergström 1962, p. 1246, pl. 168, figs 13, 16.

Protopanderodus cooperi (Sweet and Bergström); Zhang 1998b, p. 81, 82, pl. 14, figs 13-17 (cum syn.).

Material
Seven specimens (6 Sa, 1 Sb).

Discussion
This species is rare in the Wahringa collections. Two morphotypes are recognised as representing the Sa and Sb elements, all with sharp anterior and posterior margins, and a suberect cusp and one costa on each lateral side. The Sa element is symmetrical with a sharp median costa (Fig. 8A, B). The Sb element resembles the Sa, but is slightly asymmetrical with a more strongly developed costa on the inner side (Fig. 8C-E). No scandodiform P elements and no laterally compressed Sc elements, as characterising *P. cooperi* of previous authors, were recovered. Based on the original definition of the species given by Sweet and Bergström (1962) and more recent revision (Zhang 1998b), elements of *P. cooperi* exhibit sharp anterior and posterior margins, a well developed anticusp-like extension at the antero-basal corner, deep antero-lateral recesses in the basal margin, and no more than one costa on each lateral face. *Protopanderodus cooperi* can be differentiated from *P. rectus* (Lindström) in having an anticusp-like extension at the anterobasal corner, and from *P. varicostatus* in displaying no more than one costa on each lateral side.

Zhang (1998b) provided a comprehensive synonymy list, and illustrated what she recognised as P, M, Sa and other undifferentiated S elements; however, Zhang provided neither diagnosis nor descriptions of the constituent elements of the species apparatus of *P. cooperi*. This species was originally proposed as a form species from the Ferry Formation of Alabama. The holotype (Sweet and Bergström 1962, pl. 168, figs 2, 3) is slightly asymmetrical, defined here as taking the Sb position. Zhang (1998b) included the form species *Scandodus* sp. Sweet and Bergström 1962 in the P position of *P. cooperi*. Based on their illustrations and brief discussion, the P element is inferred to be a scandodiform element with broad costa on the inner lateral face and with a smooth outer lateral face. Zhang (1998b) also included the holotype of *Scandodus rectus* Lindström 1955a as occupying the M position in *P. cooperi*. This scandodiform element is similar to the P element previously defined, except that only a broad carina is developed on the inner lateral face. For consistency, these two scandodiform elements are tentatively taken to represent the Pa and Pb positions in *Protopanderodus*. The symmetrical Sa of *P. cooperi* was illustrated from the Guniutan Formation of South China (Zhang 1998b, pl. 14, fig. 13), and was also recovered from the Wahringa samples (Fig. 8A, B).

Protopanderodus robustus (Hadding 1913)

Fig. 8J-M

Synonymy

Drepanodus robustus Hadding 1913, p. 31, pl. 1, fig.5.

Protopanderodus robustus (Hadding); Löfgren 1978, p. 94, 95, pl. 3, figs 32-35, text-fig. 31G-J (cum syn.); An 1987, p. 173, pl. 11, figs 7-10 (cum syn.); McCracken 1989, p. 20-22, pl. 1, figs 1-10, text-fig. 3E (cum syn.); Albanesi in Albanesi et al. 1998, p. 129, 130, pl. 11, figs 17-20, text-fig. 14A (cum syn.).

Material
Two specimens (Sa, Sc).

Discussion
One specimen in the Wahringa collection (Fig. 8L, M) which has sharp anterior and posterior margins and is laterally compressed with a postero-lateral costa on each side, is regarded as representing the Sa element of *Protopanderodus robustus*. The other specimen with a single costa on the outer lateral face is referred to the

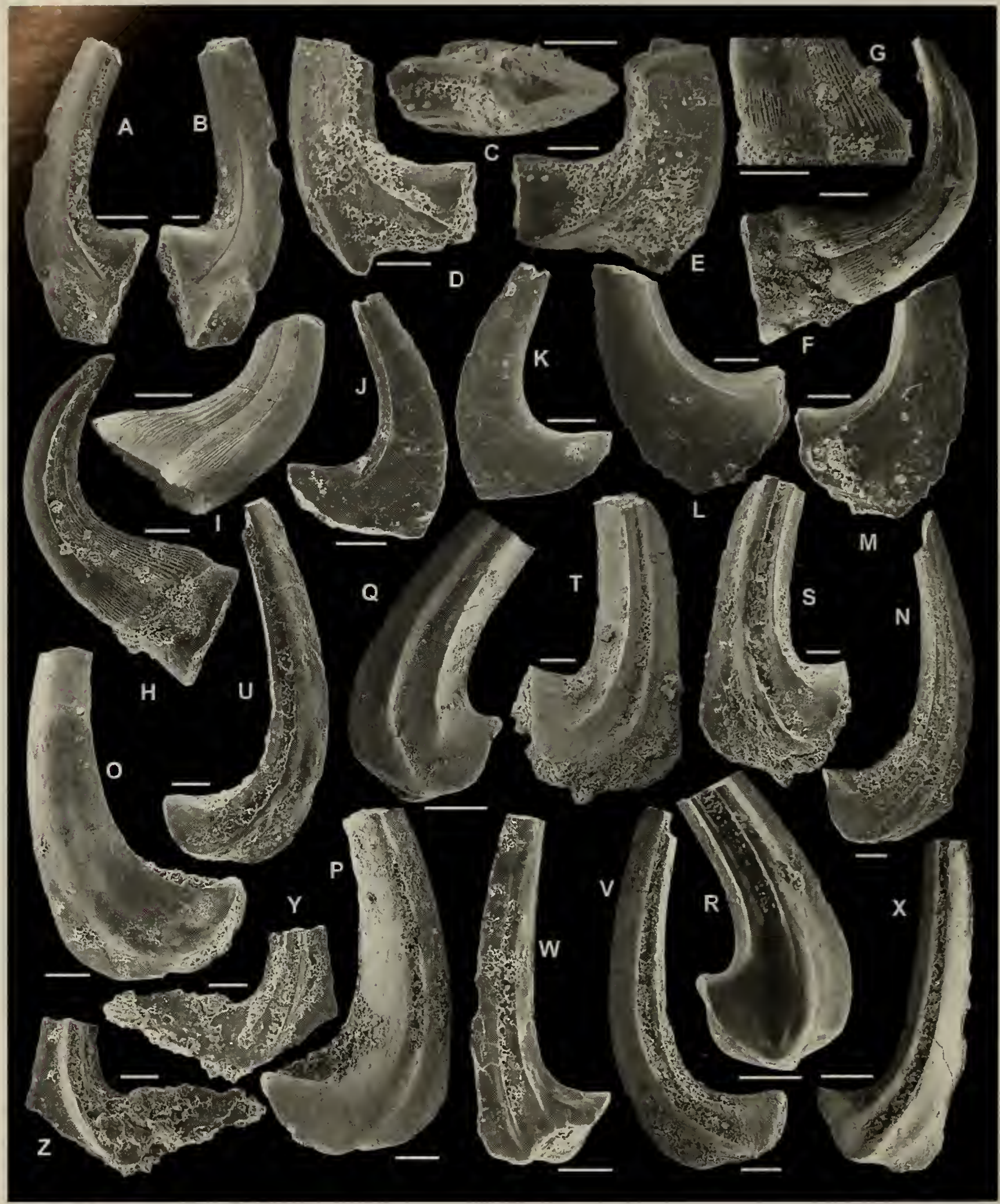

Figure 8. A-E, *Protopanderodus cooperi* (Sweet and Bergström 1962); A, B, Sa element, MMMC2688, C1683; lateral views; C, upper view, D, outer lateral view, E, inner lateral view, Sb element, MMMC2689, C1682. F-I, *Protopanderodus nogamii* (Lee 1975); F-H, Sa element, MMMC2690, C1450, lateral views; I, Sa element, MMMC2691, C1463, lateral view. J-M, *Protopanderodus robustus* (Hadding 1913); J, outer lateral view, K, inner lateral view, Sc element, MMMC2692, C1680; L, M, Sa element, MMMC2693, C1458, lateral views. N-X, *Protopanderodus varicostatus* (Sweet and Bergström 1962); N, Pa element, MMMC2694, C1652, inner lateral view; O, outer lateral view, P, inner lateral view, Pb element, MMMC2695, C1675; Q, R, Sd element, MMMC2696, C1675, lateral views; S, T, Sd element, MMMC2697, C1682, lateral views; U, outer lateral view, V, inner lateral view, Sb element, MMMC2698, C1675; W, inner lateral view, X, outer lateral view, Sc? element, MMMC2699, C1675. Y, Z, *Protopanderodus liripipus* Kennedy et al. 1979; Sa element, MMMC2700, C1458, lateral views. Scale bars are 100 µm.

Sc element of the same species (Fig. 8J, K). Although Lindström (1971), and Johnston and Barnes (2000) maintained the original generic assignment of the form species *Drepanodus robustus* Hadding 1913, most other authors followed the revision of Löfgren (1978) who regarded it as a species of *Protopanderodus*. Löfgren (1978) recognised three morphotypes: symmetrical acontiodiform (an Sa element) with a postero-lateral costa on each side (Fig. 8L, M), asymmetrical acontiodiform (an Sc element) with a strong costa on the outer lateral face and a non costate inner lateral face (Fig. 8J, K), and scandodiform (interpreted here as a P element). Based on this multielement species definition, *P. robustus* is morphologically very close to *P. cooperi*. Specimens referable to *D. robustus* were also recorded from the Pratt Ferry Formation of Alabama, where the type material of *P. cooperi* was described (Sweet and Bergström 1962). Zhang (1998b) suggested that the holotype of *D. robustus* might be an element of an uncertain species of *Protopanderodus*, but she included all the material described from Sweden by Löfgren (1978) as *P. robustus* (Hadding) in her synonymy of *P. cooperi*. This implies that *P. cooperi* may be a junior synonym of *P. robustus*. Given that the base of the holotype of *Drepanodus robustus* is apparently broken (see also Lindström 1955b), it remains difficult to separate these two species.

Protopanderodus varicostatus (Sweet and Bergström 1962)

Fig. 8N-X

Synonymy

Scolopodus varicostatus Sweet and Bergström 1962, p. 1247, pl. 168, figs 4-9, text-fig. 1A, C, K.

Scandodus unistriatus Sweet and Bergström 1962, p. 1245, pl. 168, fig. 12, text-fig. 1E.

Protopanderodus varicostatus (Sweet and Bergström); Dzik 1976, only text-fig. 16f, g; Fåhraeus and Hunter 1985b, p. 183, text-fig. 2; Bauer 1987, p. 27, pl. 3, figs 19, 21-23; An 1987, p. 173, pl. 11, figs 2, 3; Dzik 1994, p. 74, pl. 14, figs 1-5, text-fig. 11b; Zhang 1998b, p. 83, 84, pl. 15, figs 14-19 (cum syn.).

Material

Seven specimens from sample C1675, and one specimen from C1652.

Discussion

Sweet and Bergström (1962) originally recognised three form-groups for the species, namely symmetrical, slightly asymmetrical, and markedly asymmetrical. Fåhraeus and Hunter (1985b) proposed a quinquimembrate apparatus for this species, with elements referred to as groups A to E. Group A is a symmetrical multi-costate element with two costae on each lateral face. Group B is an asymmetrical tri-costate element (= the markedly asymmetrical form group of Sweet and Bergström 1962) with two costae on the inner lateral face and a postero-lateral costa on the outer lateral face. Group C is an asymmetrical multi-costate element (= slightly asymmetrical form group of Sweet and Bergström 1962) with a twisted cusp and two costae on each side. Group D is a tri-costate element, similar to group B but less laterally compressed with costa on the outer lateral face situated more towards the middle. Group E is a scandodiform element represented by the form species *Scandodus unistriatus* Sweet and Bergström 1962 (here assigned to the Pb position).

Zhang (1998b) illustrated one of the multi-costate specimens as the P element, and two morphologically different scandodiform specimens as the M element. One of the latter specimens (Zhang 1998b, pl. 15, fig. 19) is comparable with the form species *S. unistriatus* Sweet and Bergström 1962, and is regarded here as representing the Pb element of *P. varicostatus* (Fig. 8O, P). The other specimen illustrated as the M element (Zhang 1998b, pl. 15, fig. 14), which was recovered from the same sample with other illustrated specimens of *P. varicostatus*, has a multi-costate inner lateral face with three costae bordering two grooves and a few, shorter and weaker secondary costae near the base. It is designated here as occupying the Pa position of the species.

Similar specimens (arcuatiform) referrable to the Pa element of *P. varicostatus* were also reported from allochthonous limestone clasts within the Shinnel Formation of Scotland (Armstrong 1997, pl. 3, figs 3, 4). Morphologically it resembles the Pa element of *Protopanderodus* cf. *calceatus* Bagnoli and Stouge 1996, recovered from the allochthonous limestones in the Oakdale Formation of central New South Wales (Zhen and Percival in press, pl. 17, figs A, C). However, this latter element has one larger, open groove on the inner lateral face, while the Pa element of *P. varicostatus* from South China (Zhang 1998b, pl. 15, fig. 14) and from the Wahringa area (Fig. 8N) has two equally developed, narrower grooves with a sharp costa between them. *Protopanderodus liripipus* Kennedy et al. 1979 is also multi-costate, but with a more posteriorly extended base (Fig. 8Y, Z).

Three morphotypes of multicostate (S) elements with two costae on each side are recognised from sample C1675 and possibly should be assigned to the Sd, Sb and Sc? positions, as no tri-costate elements have been recovered. The Sd element is symmetrical with a reclined cusp and a short base. The Sb element is weakly asymmetrical with suberect cusp and a longer base. The Sc? element is asymmetrical and laterally strongly compressed with a suberect cusp and a short base.

Genus PYGODUS Lamont and Lindström 1957

Type species
Pygodus anserinus Lamont and Lindström 1957.

Pygodus protoanserinus Zhang 1998a
Fig. 9B-J

Synonymy
Pygodus anserinus Lamont and Lindström 1957, p. 68, only fig. 1d.
Pygodus serrus (Hadding); Bergström 1971, p. 149, pl. 2, figs 22, 23; An 1981, pl. 4, figs 1-3; An 1987, pl. 24, fig. 25, pl. 26, figs 3, 6, 13, pl. 29, figs 2, 3; Nicoll 1980, fig. 3H-L; Ding et al. in Wang, 1993, p. 198, pl. 30, figs 10, 13, 15-18, 20-22, 24, pl. 35, 24, 26.
Pygodus protoanserinus Zhang 1998a, p. 96, Fig. 2D, pl. 3, figs 9-18 (cum syn.); Zhang 1998b, p. 86, 87, pl. 16, figs 6-8 (cum syn.).
Pygodus serra (Hadding); Percival et al. 1999, fig. 8.18; Pickett and Percival 2001, fig. 4C.

Material
Four Pa (stelliscaphate), five Pb (pastinate), and one Sb (tertiopedate) elements.

Discussion
Five species were assigned to *Pygodus* in the recent study of the genus by Zhang (1998a). They have short stratigraphic ranges and hence are very useful biostratigraphic index fossils. Sweet and Bergström (1962) and Bergström (1971) initially suggested that the apparatus of *Pygodus anserinus*, the type species of the genus, included elements represented by the form species *Pygodus anserinus* Lamont and Lindström 1957, and *Haddingodus serrus* (Hadding). Bergström (1971) also raised the possibility that the *Pygodus* apparatus might include elements represented by the form species *Tetraprioniodus lindstroemi* Sweet and Bergström 1962 and *Roundya pyramidalis* Sweet and Bergström 1962. This quadrimembrate *Pygodus* apparatus composition has been widely accepted (Löfgren 1978, Clark et al. 1981, Sweet 1988). Subsequently, Armstrong (1997) has implied a septimembrate apparatus for *Pygodus*, but with only confirmed elements occupying the Pa, Pb, Pc, M and Sc positions. By including two pygodiform elements in the apparatus, Armstrong (1997) suggested that the *P. anserinus* apparatus consisted of the stelliscaphate Pa, pastiniscaphate Pb, bipennate Pc (= pastinate Pb of other authors' usage - see Zhang 1998a, b), tertiopedate M (termed an S element by other authors - see Zhang 1998a, b, and herein), and the ramiform Sc element. More recently Zhang (1998a, 1998b) proposed a quinquimembrate apparatus for *Pygodus*, including stelliscaphate Pa, pastinate Pb, and three ramiform S elements (alate, tertiopedate and quadriramate).

Distinctions between *P. serra* and *P. protoanserinus* were discussed in detail by Zhang (1998a). *Pygodus protoanserinus* ranges from the *E. robustus* Subzone to the *E. lindstroemi* Subzone of the upper *serra* Zone in Baltoscandia, Scotland, North America, China, and Australia. The stelliscaphate Pa element from the lower part of the Wahringa Limestone Member is identical with the type material of *P. protoanserinus*, being characterised by having the middle denticle row situated more towards the outer denticle row on the upper surface. Specimens illustrated by Nicoll (1980) as *P. serrus* from the Pittman Formation at Black Mountain, Canberra, ACT, are here reassigned to *P. protoanserinus* on this same basis. A single specimen from the lower part of the Wahringa Limestone Member has the middle row of the denticles positioned centrally, and is therefore referred to *P. serra* (Fig. 9K, L), being more comparable with the middle form of the Pa element of that species as defined by Zhang (1998a).

Genus STIPTOGNATHUS Ethington, Lehnert, and Repetski 2000

Type species
Reutterodus borealis Repetski 1982.

Stiptognathus sp. A
Fig. 9O, P

Synonymy
Stiptognathus sp. Zhen and Percival in press, fig. 21L-O.

Material
Two specimens from sample C1463 from an allochthonous limestone within the Fairbridge Volcanics, stratigraphically below the Wahringa Limestone Member.

Discussion
The symmetrical Sa and geniculate M elements recovered from sample C1463 are identical with those from the allochthonous limestones of the Oakdale Formation (Zhen and Percival in press). Denticles on these specimens are small, closely spaced and blunt.

Figure 9. A, *Pseudooneotodus mitratus* (Moskalenko 1973); upper view, MMMC2701, C1474. B-J, *Pygodus protoanserinus* Zhang 1998a; B, Pa element, upper view, MMMC2702, C1450; C, Pa element, upper view, MMMC2703, C1652; D, upper view, and E, enlargement showing surface structure, Pa element, MMMC2704, C1652; F, inner lateral view, G, outer lateral view, H, anterior view, Pb element, MMMC2705, C1652; I, outer lateral view, J, showing surface structure, Sb element, MMMC2706, C1652. K, L, *Pygodus serra* (Hadding 1913); K, upper view, L, basal view, Pa element, MMMC2707, C1652. M, N, *Stiptognathus* sp. B; M, antero-lateral view, N, posterior view, Sa element, MMMC2708, C1675. O, P, *Stiptognathus* sp. A; O, M element, MMMC2709, C1463, posterior view; P, Sa element MMMC2710, C1463, antero-lateral view. Unless otherwise indicated scale bars are 100 µm.

Stiptognathus sp. B
Fig. 9M, N

Material

Two specimens (Sa) from sample C1675.

Discussion

The cusp of this symmetrical element is triangular in cross section with a gently curved, wide anterior face, posterior costa, and an antero-lateral costa on each side. Three sharp costae extend basally into three blade-like processes, which bear small, upward-pointed denticles along the edges. They are easily distinguishable from the blunt denticles of *Stiptognathus* sp. A.

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APPENDIX
LOCALITY DATA

All grid references are AMG66 co-ordinates and relate to the Cumnock 8632-S 1:50,000 topographic sheet (first ed., 1978).

Allochthonous limestones stratigraphically below Wahringa Limestone Member
C1463: GR 679150 mE 6371900 mN
C1486: GR 678750 mE 6371800 mN
C1487: GR 678720 mE 6371800 mN
C1488: GR 678700 mE 6371800 mN

Wahringa Limestone Member, type section
C1450, C1652 (basal beds): GR 678650 mE 6372000 mN
C1456, C1664, C1667-C1668, C1672 (middle beds): GR 678700 mE 6372050 mN
C1458, C1464, C1673-1683, C1687 (upper beds): GR 678700 mE 6372100 mN

Wahringa Limestone Member, northeast extremity of outcrop
C1707, C1709-1713: centred on GR 679330 mE 6372620 mN

Wahringa Limestone Member, southwest extremity of outcrop (middle or upper beds)
C1429: GR 677570 mE 6370800 mN

Allochthonous limestones stratigraphically above Wahringa Limestone Member
C1693, C1694: GR 678000 mE 6371310 mN
C1695, C1696: GR 678100 mE 6372000 mN
C1697, C1698: GR 678050 mE 6372000 mN
C1699: GR 678025 mE 6372000 mN
C1700: GR 678010 mE 6372000 mN
C1471: GR 678500 mE 6372200 mN
C1472: GR 679250 mE 6373550 mN
C1474: GR 678100 mE 6372600 mN
C1483: GR 678500 mE 6372800 mN

Wenlock (Early Silurian) Brachiopods from the Orange District of New South Wales

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Wright, A.J. and Strusz, D.L. (2003). Wenlock (Early Silurian) brachiopods from the Orange District of New South Wales. *Proceedings of the Linnean Society of New South Wales* **125**, 165-172.

Two late Wenlock (Early Silurian) brachiopod species from the Ulah Formation near Orange, New South Wales, are closely associated with graptolite faunas. *Visbyella cumnockensis* occurs in the *testis* Biozone on Wallace Creek in the Four Mile Creek area, and *Strophochonetes melbournensis* is recorded from the *ludensis* Biozone on Spring Creek. Poorly preserved but similar *Visbyella*? and *Strophochonetes*? From the Prídolí Wallace Shale at Cheesemans Creek are also illustrated. These occurrences provide significant new stratigraphic and distributional data for the species.

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KEYWORDS: Brachiopods, New South Wales, Pøídolí, Silurian, *Strophochonetes melbournensis*, Ulah Formation, *Visbyella cumnockensis,* Wallace Shale, Wenlock.

INTRODUCTION

The Silurian strata of the area west and southwest of Orange, NSW, in the valleys of Spring Creek and Four Mile Creek (Fig. 1), have yielded a diversity of fossils, but very few shelly fossils have ever been described, apart from corals described by authors including Etheridge and McLean (full references to these works can be found in Pickett 1982). The most abundant and important fossils in the region are graptolites, which have been known for more than 50 years and were reported by Packham and Stevens (1955) and Jenkins (1978, 1986).

Jenkins recorded (but did not describe) brachiopod faunas from limestones in the Four Mile Creek area, but few brachiopods have been reported from clastic strata common in the area. Rickards and Wright (1997) described two brachiopod species from late Wenlock strata (*ludensis* Biozone) in Cobblers Creek (Fig. 1), and in the section at 'Mirrabooka Park' brachiopods were noted in Wenlock strata during field work by L. Muir, R.B. Rickards, G.H. Packham and A.J. Wright. A diverse and abundant shelly fauna occurring with the late Wenlock graptolite *Testograptus testis* on the Cadia gold mine access road, several kilometres to the east of Four Mile Creek, was illustrated by Rickards et al. (2001).

The two species described here are recorded for the first time from the region near Orange. One, *Visbyella cumnockensis* Walmsley et al., 1968, was originally described from near Cumnock, 55 km northwest of Orange, where it occurs with *T. testis* (Walmsley et al. 1968:315). *Visbyella* has been reported also, but not illustrated, by Pickett (1982) and Pogson and Watkins (1998). The other species, *Strophochonetes melbournensis* (Chapman 1903), was previously known only from Wenlock and Ludlow strata in the Melbourne Trough, Victoria. Pickett's report was based on the record of *Visbyella* cf. *cumnockensis* by Sherwin (1971). Sherwin's locality is younger, and contains a sparse and poorly preserved fauna including also a chonetoide similar to *Strophochonetes? savagei* Strusz, 2000 from Cumnock. These taxa are illustrated but not described. Documented brachiopod occurrences in the Orange region are still insufficient, however, to permit any notion of a regional brachiopod zonation.

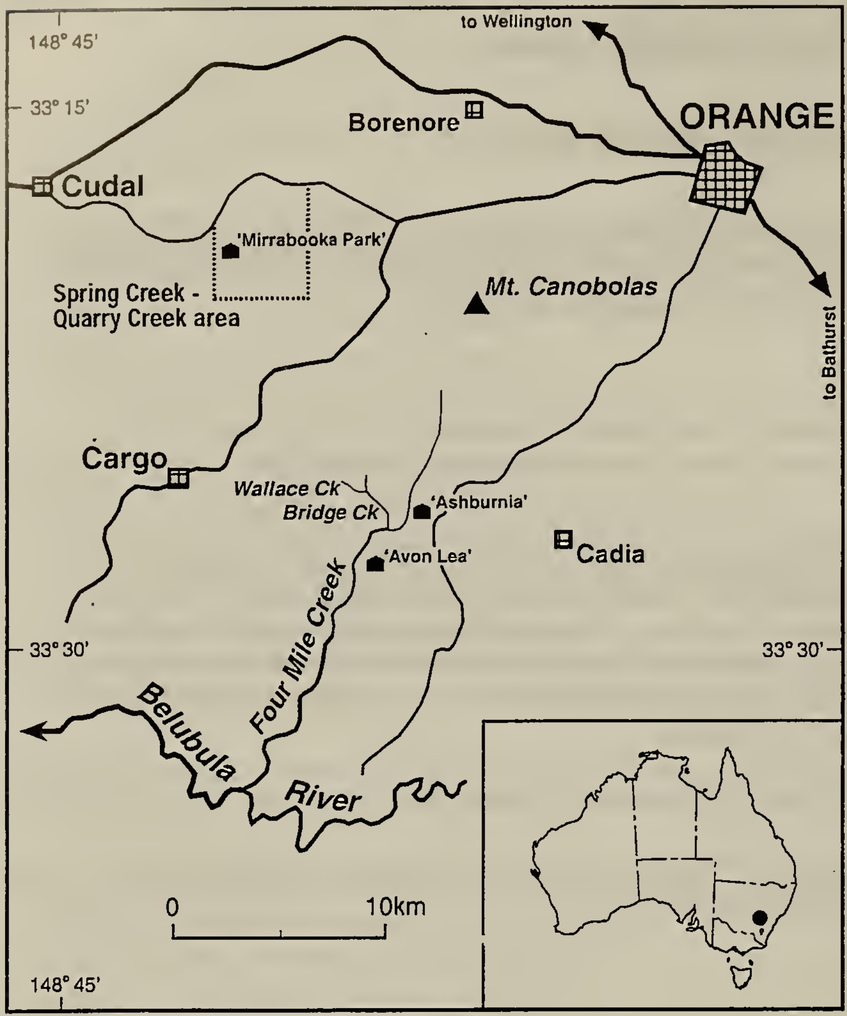


Figure 1. Map of the area southwest to west of Orange, central New South Wales, showing the geographic context of the two localities, LM3 on Wallace Creek east of Cargo and W940 near 'Mirrabooka Park' east-southeast of Cudal. Inset: the location of Orange within Australia.

LOCALITIES

LM3.

Visbyella cumnockensis was collected from Wallace Creek in the Four Mile Creek area, in grey-brown siltstones assigned by Jenkins (1978) to the Wenlock-Ludlow Ulah Formation. These beds have also yielded the graptolites *Cyrtograptus* and a new species of *Monograptus* (L. Muir, pers. comm.), and overlie beds containing *T. testis*. The brachiopod specimens are moulds of a single pedicle and a single brachial valve on the same bedding surface, which could represent the disarticulated valves of a single shell. No other macrofossils have been found at this locality. In contrast, the type material of *V. cumnockensis* is entirely of specimens in the 'butterfly' position, with the shell opened so that the conjoined valves lie on the bedding surface. The age assigned to the Ulah Formation by Chapman et al. (2003) is late Wenlock to Prídolí; the age of the strata at this locality is late Wenlock.

W940.

The somewhat more abundant specimens of *Strophochonetes melbournensis* were collected from dark siltstones of the Ulah Formation on the southern side of Spring Creek at 'Mirrabooka Park', directly opposite One Tree Hill. There are also occasional poorly preserved brachiopods, including pentamerides, in beds at about the same level on One Tree Hill itself. The shells at W940 occur with a graptolite fauna that includes *Monograptus ludensis* (R.B. Rickards, pers. comm.). Only disarticulated valves are known at this locality; small phosphatic brachiopods are quite common, and there are rare specimens of other brachiopods including strophomenides and atrypides. Most specimens of *Strophochonetes melbournensis* at this locality retain shelly material and the spines on the pedicle valve hinge line are often preserved. The environment was most probably a low-energy one.

MO/I/27.

A few poorly preserved orthide and chonetoide specimens have been collected from this outcrop of fine thin-bedded siltstone low in the Wallace Shale, about 600 m east of 'Mirrabooka' homestead. The fauna also includes occasional trilobites. The locality lies within the *Monograptus transgrediens* Biozone.

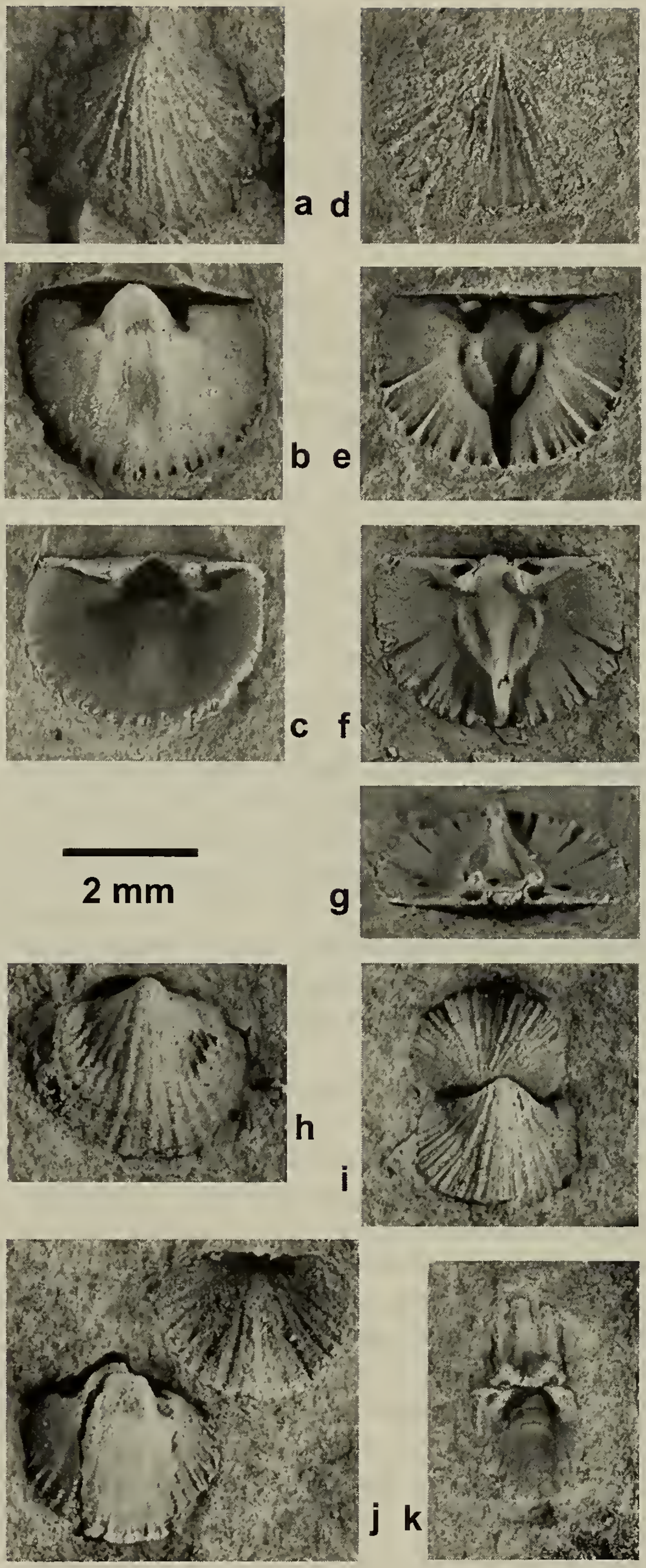
SYSTEMATIC PALAEONTOLOGY

Suprageneric taxonomy follows that in Kaesler (2000); references to authorship of suprageneric taxa are therefore not repeated here. Specific diagnoses have been rephrased to accord with currently accepted terminology (Kaesler 1997). Details of localities are given in the descriptive section below.

Abbreviations.

Ls - shell length
Ld - dorsal valve length.
Ws - shell width
Wh - hinge line width

Figure 2. a-g, *Visbyella cumnockensis* Walmsley et al., 1968. a-c, ventral valve counterparts; a, latex cast of exterior, AM F124331. b-c, internal mould and latex cast, AM F124332. d-g, dorsal valve counterparts; d, latex cast of exterior, AM F124333. e-g, internal mould and latex cast (in ventral and postero-ventral views), AM F124334. h-k, cf. *Visbyella cumnockensis*, Prídolí, Wallace Shale. h, latex cast of ventral valve, MM F37431. i, latex cast of shell in 'butterfly' position, MM F21132. j, external mould of dorsal valve plus internal mould of ventral valve, MM F21125. k, latex cast of incomplete interior of shell in 'butterfly' position, MM F37428. Scale bar 2 mm.



AM - Australian Museum
MM – Mining Museum Collection, Geological Survey of NSW
CPC - Commonwealth Palaeontological Collection
NMV - Museum of Victoria
SU - Sydney University (Geology Department)

Suborder DALMANELLIDINA Moore 1952
Superfamily DALMANELLOIDEA Schuchert 1913
Family DALMANELLIDAE Schuchert 1913
Subfamily RESSERELLINAE Walmsley and Boucot 1971
Genus VISBYELLA Walmsley, Boucot, Harper and Savage 1968

Type species

Orthis visbyensis Lindström 1861, by original designation; late Llandovery, Gotland.

Diagnosis

Subcircular, small valves with apical deltidium and hypercline dorsal interarea; ventral interior with recessive dental plates and cordate muscle scar; dorsal interior with trilobed, dorsally-facing cardinal process and median septum (Harper p. 797 in Kaesler 2000).

Visbyella cumnockensis Walmsley, Boucot, Harper and Savage 1968
Fig. 2 (a-g)

Synonymy

1968 *Visbyella cumnockensis* sp. nov.; Walmsley et al., pp. 313-315, pl. 61 figs 6-12.

Type material

Holotype AM F67781; paratypes AM F67782-67788 (formerly SU P19511, 19512-19518; all renumbered when collections were transferred from the University of Sydney to the Australian Museum).

New material

External and internal moulds of a ventral valve (AM F124331, F124332) and a dorsal valve (AM

F124333, F124334) from one bedding plane at locality LM3 (Grid reference 782 988, Cudal 8631 II and III 50 000 topographic sheet, Wallace Creek, Four Mile Creek area south of Orange, N.S.W.); Ulah Formation, *Testograptus testis* Biozone; late Wenlock (Early Silurian).

Diagnosis

Relatively small, weakly sulcate, coarsely multicostellate *Visbyella* with semicircular outline. Dorsal median ridge broad and low posteriorly, becoming narrower and higher to form an anterior median septum (after Walmsley et al. 1968)

Description

Shell small, almost plano-convex. Ventral valve broadly naviculate, with low suberect beak; dorsal valve weakly convex with shallow but distinct sulcus. Outline suboval, moderately transverse, with straight hinge, obtuse slightly rounded cardinal angles; greatest width at about 0.4Ls. Ventral interarea strongly apsacline, almost flat, apical angle about 120°; delthyrium open, apical angle about 70°, rimmed by narrow crescentic deltidium. Dorsal interarea low, concave, catacline, apical angle about 150°; notothyrium filled by cardinal process, apical angle about 80°. Ribs rather angular, stronger medially than laterally, increasing by bifurcation on the ventral valve, intercalation on the dorsal valve; about 30 counted at ventral valve margin.

Ventral interior with prominent subtriangular muscle field, impressed posteriorly but slightly raised anteriorly, length 1/3Ls and width 1/4Ws. Diductor scars elongate oval, divergent, depressed a little below slightly shorter flat adductor field. Raised anterior margin to adductor field distinctly denticulate, extends forward to about 3/4Ls as low ridge. Vascula media flank this ridge as broad, shallow furrows extending from the diductor scars. Muscle field flanked by stout dental plates, divergent forward at about 100° and slightly divergent ventrally, not extending beyond muscle field. Teeth strong, wide, triangular, with distinct crural fossettes on antero-median faces. Valve floor faintly radially furrowed, marginally strongly crenulated.

Dorsal interior with prominent oval muscle field extending to 2/3Ld, width 1/3Ws, defined by strong ridges arising just in front of brachiophores and increasingly raised anteriorly, which converge to abut on median septum. Diductor scars impressed, elongate oval, subequal, posterior scars subparallel, anterior scars convergent forward; scars separated by tapering ridge from which rises the stout median septum. Septum highest a little in front of muscle field, and extends to valve margin. Cardinal process large, directed posterodorsally, continuous with well developed notothyrial platform; no shaft. Brachiophores stout, blade-like, divergent ventrally, supported by low, thick plates. Sockets oval, diverging from valve axis at about 75°, deeply excavated into thick triangular socket pads. Valve floor radially grooved, marginally strongly crenulated.

Dimensions

	AM F124332	AM F124334
valve	ventral	dorsal
Ls, Ld	est 2.85	2.59
Ws	3.90*	3.73
Wh	3.60*	3.32
Ls/Ws	est. 0.73	0.69
Wh/Ws	est. 0.92	0.89

* values obtained by doubling exposed half-width, assuming a symmetrical shell.

Remarks

The Wallace Creek occurrence of this species is almost exactly the same age as the original occurrence at Cumnock, and our admittedly limited new material corresponds closely in all specific characters to the type material. The specimens are slightly larger than shells of the type series (the maximum length and width of any specimens of the type series are 2.1 mm and 3.1 mm respectively), but the ratio Ls:Ws is close to the 2:3 cited for the type material; while the marginal crenulations in the ventral valve are less extensive. The internal moulds of the disarticulated valves are somewhat better than the types, and features of the hinge line can be seen more clearly.

The species was also tentatively recorded by Sherwin (1971, p. 223) from the Pridolí Wallace Shale at locality MO/I/27 in the Cheesemans Creek area north of Quarry Creek; his report was the basis for subsequent reports by Pickett (1982, pp. 154-155) and Pogson and Watkins (1998, p. 131). This occurrence is in significantly younger strata than the two other occurrences noted herein. Sherwin's report was based on several specimens from one locality; we were recently guided to this locality by Dr Sherwin, and collected a further seven specimens of the 'orthid' species, which is very rare at the locality (also collected were a few poor specimens of a chonetide, identified as *Strophochonetes*? cf. *savagei* Strusz, 2000, and illustrated in Fig. 4 for comparison with *Strophochonetes melbournensis*).

Unfortunately the only internal mould of a dorsal valve of the Wallace Shale orthide (Fig. 2k) is incomplete, and appears to lack a median septum, although its presence anteriorly cannot be completely ruled out. It was initially thought that the absence of a septum would rule out the presence of *Visbyella*. However, one specimen (AM F125552) of *Visbyella cumnockensis* on one of the type slabs is close in size to the Wallace Shale material and, unlike all the other type specimens, lacks a median septum, so this is not an infallible character of this species. Other morphological features of the Wallace Shale material are not well preserved; there appear to be more than 30 costellae, and the internals of both valves, in so far as they are preserved, are similar to those of the Wallace Creek material (compare Figs 2h-i with Fig. 2a, and Fig. 2j with Fig. 2b).

Hence no conclusive argument can be presented to refute the presence of *Visbyella* at this locality, unlikely as it might seem. This opinion is slightly supported by the presence of a similar orthide (probably *Resserella*), but definitely lacking a median septum, in the late Ludlow Cardinal View Shale (Bauer 1994) at Bungonia, NSW. Unfortunately, our experience gives us no reason to expect more definitive material at this very unproductive Wallace Shale locality.

Suborder CHONETIDINA Muir-Wood 1955
Superfamily CHONETOIDEA Bronn 1862
Family STROPHOCHONETIDAE Muir-Wood 1962
Subfamily STROPHOCHONETINAE Muir-Wood 1962
Genus STROPHOCHONETES Muir-Wood 1962

Type species

Chonetes cingulatus Lindström 1861, by original designation; Wenlock, Gotland.

Diagnosis

Shell small, plano- to moderately concavo-convex; well developed median enlarged costa; long, symmetrically arranged high-angled spines varying from intraverse cyrtomorph proximally to orthomorph vertical distally; cardinal process strongly bilobed internally, anteriorly bounded by cardinal process pit; no median septum; anderidia long, narrow, anteriorly divergent at about 60° and isolated on valve floor; inner socket ridges short, thin, as two rounded ridges almost parallel to hinge (after Racheboeuf p. 369 in Kaesler 2000).

Strophochonetes melbournensis (Chapman 1903)

Fig. 3

Synonymy

1903 *Chonetes melbournensis* sp. nov.; Chapman, pp. 74-76, pl. XI, fig. 2 only.
1945 *Chonetes (Chonetes) melbournensis* Chapman; Gill, pp. 132-133.
1953 *Chonetes infantilis* n. sp.; Öpik; p. 15, pl. III, figs 19-22.
2000 *Strophochonetes melbournensis* (Chapman, 1903); Strusz, pp. 249-251, figs 2-3.

Type material

Lectotype NMV P1419, paralectotypes NMV P615-6, 619, 623, 625-7, 630-633, 637-43 designated by Strusz (2000); Melbourne Formation, Melbourne and South Yarra, Victoria; Ludlow (Late Silurian). Type material of *Chonetes infantilis* Öpik, 1953: holotype CPC 661, paratypes CPC 662-663, *Illaenus* Band, Wapentake Formation, Heathcote, Victoria; late Wenlock (Early Silurian).

New material

AM F124306 - 124330, locality W940 (grid reference 743 123, Cudal 8631-II and III 50 000 topographic sheet; south bank of Spring Creek, 'Mirrabooka Park', southwest of Orange, central N.S.W.); Ulah Formation, with *Monograptus ludensis*; Late Wenlock (Early Silurian).

Diagnosis

Small, weakly concavo-convex, subquadrate *Strophochonetes* with up to 5 pairs of gently intraverse-cyrtomorph hinge spines, and finely multicostellate ornament with median rib on ventral valve usually strongly enlarged. Valve floors heavily papillose, ventral muscle field distinct, anderidia short and diverging at 60-80° (after Strusz 2000).

Description

Shell small, plano-convex, ventral valve of very low convexity. Outline subquadrate, lateral margins gently sigmoid, with shallow re-entrants in front of small triangular ears; hinge width usually slightly less than greatest width (mean Wh/Ws 0.93). Ventral protegulum posteromedially furrowed, variably raised above remaining shell surface; distinct protegular lobe, weaker lateral lobes on dorsal valve. Maximum observed width 9.8 mm, length 6.5 mm, most specimens being much smaller; mean Ls/Ws 0.75, ratio decreasing with increasing shell size. Interareas mostly obscure; ventral interarea apparently low, apsacline, flat, delthyrium wide, beak very low; pseudodeltidium not seen; dorsal interarea linear, attitude unclear. Myophore small, projecting posteroventrally, bifid, each lobe less strongly bifid, flanked by small but distinct cardinal crests. Chilidium obscure, might be present as very narrow ridge wrapped around base of myophore. Hinge spines fine, relatively long, upright

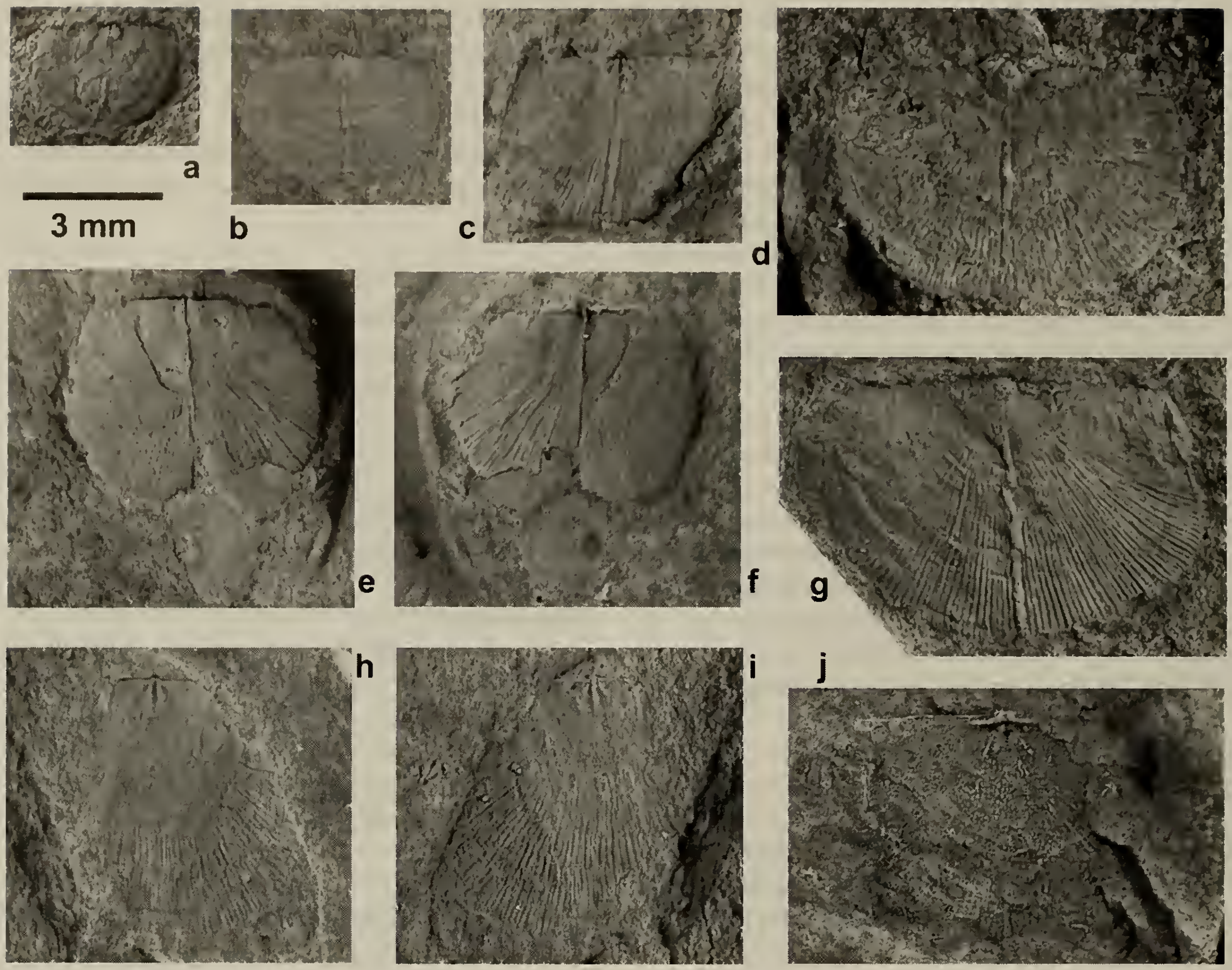


Figure 3. ***Strophochonetes melbournensis*** **(Chapman, 1903). a-g, ventral valves; some hinge spines are visible in b-e, only spine bases in f-g. a, juvenile valve AM F124320. b, juvenile with particularly prominent protegulum, AM F124317. c, juvenile AM F124322. d, AM F124324. e-f, internal mould and latex cast, AM F124312. g, AM F124326. h-j, dorsal valves; h-i, incomplete external mould and latex cast showing well developed protegular and lateral nodes, AM F124318. j, latex cast of incomplete interior, AM F124307. Scale bar 3 mm.**

or nearly so (initial angle with hinge line about 60-80°), straight (particularly in small specimens) to gently cyrtomorph intraverse, symmetrically placed; up to 4 each side of beak (AM F124324). Ornament of fine, rounded radial ribs, 29-34 counted in 5 mm at 5 mm radius, separated by narrower furrows; increase is by bifurcation only. Median rib on ventral valve prominent, arises within protegulum; remaining ribs arise at or in front of margins of concentrically wrinkled protegular regions.

Ventral interior with low, narrow median septum, reaching forward to about 0.2Ls; septum posteriorly raised and slightly widened. Teeth small, widely divergent. Muscle field generally obscure other than for weak or absent endospines; in one specimen (AM F124312) the field is weakly impressed, with small, elongate subtriangular, slightly divergent adductor scars further impressed posteriorly. Remainder of valve floor densely covered by fine endospines radially arranged beneath ribs, weakest towards cardinal margin and ears.

Dorsal interior still not well known. Cardinal process small, internally bifid, fused to short but strong inner socket ridges which are curved parallel to hinge margin. Short, shallow furrow in front of cardinal process, but no median ridge developed. Anderidia visible in only one specimen (AM F124307); they are short (0.2Ld), fine, low, diverging at about 60°. Muscle field obscure. Distal two-thirds of valve floor with numerous small radially arrayed endospines, as in ventral valve.

Dimensions

		valve	Ls, Ld	Ws	Wh	Ls/Ws	Wh/Ws
AM	F124307	dorsal	4.9	–	8.7*	–	–
	F124312	ventral	est. 4.8	5.6*	5.4*	est. 0.86	0.96
	F124318	dorsal	5.5	–	–	–	–
	F124322	ventral	3.6	4.7	4.4	0.77	0.94
	F124324	ventral	5.3	7.2	7.2	0.74	1.00
	F124326	ventral	5.6	8.4	7.2	0.67	0.86

* values obtained by doubling exposed half-width, assuming a symmetrical shell.

Discussion

Although preservation is not particularly good, the Wenlock specimens from Spring Creek conform in all important aspects (very low ventral convexity, rib increase only by bifurcation, and less prominent protegular and lateral lobes on the dorsal valve) with *S. melbournensis* rather than *S. kemezysi* Strusz, 2000. Some of the minor differences could be related to the small size of most of the specimens (several are clearly juvenile, none approaches the maximum size recorded for the Victorian material). Some could be of age significance, but without better and more abundant material from older levels in Victoria this remains unclear. Thus no ventral valves show the anterior sulcus seen in some Victorian Late Silurian shells, and no more than 4 spines have been seen to either side of the ventral beak. The NSW specimens tend also to be more elongate (Ls/Ws very variable, mean 0.76; for Victorian specimens the mean is 0.61). Internally, the ventral muscle field is less obvious, and there are no coarser endospines near the hinge. In this last respect, and in a greater tendency for spines on small specimens to be straight, the Late Wenlock Spring Creek specimens are more like the few poor specimens from the Early Wenlock of Heathcote than the Ludlow material from Melbourne. Dorsal interiors, while still few and inadequate, do add some information, particularly the form of the cardinal process and its flanking cardinal crests. The presence internally of a weak posteromedian dorsal furrow instead of a low ridge places these specimens closer to typical *Strophochonetes* than are the type specimens.

Figure 4. ***Strophochonetes*? cf. *savagei* Strusz, 2000. Latex cast of ventral valve, MM F21133. Scale bar 3 mm.**

Three similar chonetoide specimens (MM F21133, 37435, 37436) are available from the Wallace Shale locality - the best of them is figured (Fig. 4). All are small and weakly convex. In the absence of internal data, particularly of the dorsal valve, generic identity must remain uncertain. The long more or less upright hinge spines, low ventral valve convexity, fine ribbing and accentuated median rib all indicate *Strophochonetes*, however, and of the Australian taxa described by Strusz (2000) the closest is undoubtedly *S? savagei* from the Early Lochkovian of Manildra, northwest of Orange. *S. melbournensis* and *S. kemezysi* Strusz, 2000, while superficially similar, are both larger and more coarsely ribbed; the latter has very prominent protegulae. In only one respect these specimens appear unlike typical *Strophochonetes*, and that is in the alternating pattern of hinge spine insertion described for instance by Strusz (2000, p. 259) for the strongly convex and fairly coarsely ribbed Australian species of *Johnsonetes* Racheboeuf, 1987 (all of which lack spine 1'). However it is not clear that spine 1' is undeveloped in the Wallace Shale specimens. Moreover, the Manildra species show considerable variation in spine form, and some asymmetry cannot be ruled out.

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Early Silurian Graptolites from Cadia, New South Wales

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A low-diversity graptolite fauna is reported from the Ulah Formation at Cadia, central western New South Wales. The assemblage includes *Testograptus testis*, *Monoclimacis flumendosae*, fragments of *Monograptus flemingii*, possible *Cyrtograptus* and unidentifiable retiolitid meshworks, and is correlated with the *lungreni-testis* Biozone, of late Wenlock (Early Silurian) age.

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KEY WORDS: Cadia, graptolites, Lower Silurian, Wenlock.

INTRODUCTION

Three Silurian faunas were documented by Rickards et al. (2000) from the vicinity of Cadia open cut, south of Orange, New South Wales. One of these faunas, of late Wenlock-early Ludlow aspect, consisted of shelly fossils and graptolites collected by Dr Ian Percival from a slumped mudstone at a locality on the access road to the Cadia open cut. This fauna was discussed and illustrated by Rickards et al. (2000), who figured but could not determine the poor graptolite material to genus or species because of the poor preservation of the fragmentary material. The locality (grid reference 687240E, 6295047 N, Canowindra 8360-N 1:50 000 topographic sheet) is on the eastern face of the access road to the Cadia open cut, about 1 km from the entrance gates; a map of the region showing the location of this and other fossil localities was provided by Rickards et al. (2000, Fig. 1). The fossiliferous strata are considered to correlate with the Ulah Formation, at Four Mile Creek west of Cadia (see Rickards et al. 2000, Fig. 1), in which the *Testograptus testis* fauna occurs.

NOTES ON THE GRAPTOLITE FAUNA

Since the publication of Rickards et al. (2000), we have made a further but small graptolite collection from the Cadia mine shelly fossil locality which permits fuller identification of the low-diversity fauna and determination of its age. The Cadia graptolite fauna consists of *Testograptus testis* (Barrande), *Monoclimacis flumendosae* (Gortani), fragments of *Monograptus flemingii* (Salter), fragmentary stipes possibly belonging to *Cyrtograptus*, and fragmentary retiolitid meshworks which cannot be assigned, even approximately, to a genus.

In discussing this as 'the Cadia graptolite fauna' we are mindful of the presence of other graptolites in Silurian strata in the vicinity of the Cadia mine. Full documentation of any such graptolite faunas as that documented here is important as graptolite localities in the vicinity of Cadia mine (such as the Prídolí 'borrow pit' locality, W910 of Rickards et al. 2000) are very much less common than at Four Mile Creek, and are under threat. A brief review of graptolites previously reported from Cadia by Offenberg (1963) was given by Rickards et al. (2000).

We have not provided here any systematic descriptions of the fauna, but limited comments on the morphological detail are included in the explanatory text for Figure 1. The Cadia specimens have undergone soft sediment deformation, with a considerable amount of twisting and breakage, in contrast to the Rodds Creek black shale specimens (Rickards et al. 2000) which were undeformed other than by diagenetic flattening.

AGE OF THE CADIA GRAPTOLITE FAUNA

The dominant species is *Testograptus testis* (Barrande), which normally indicates the late Wenlock (Early Silurian) *lundgreni-testis* Biozone. *Testograptus testis* has been recorded, very rarely, from the *ludensis*

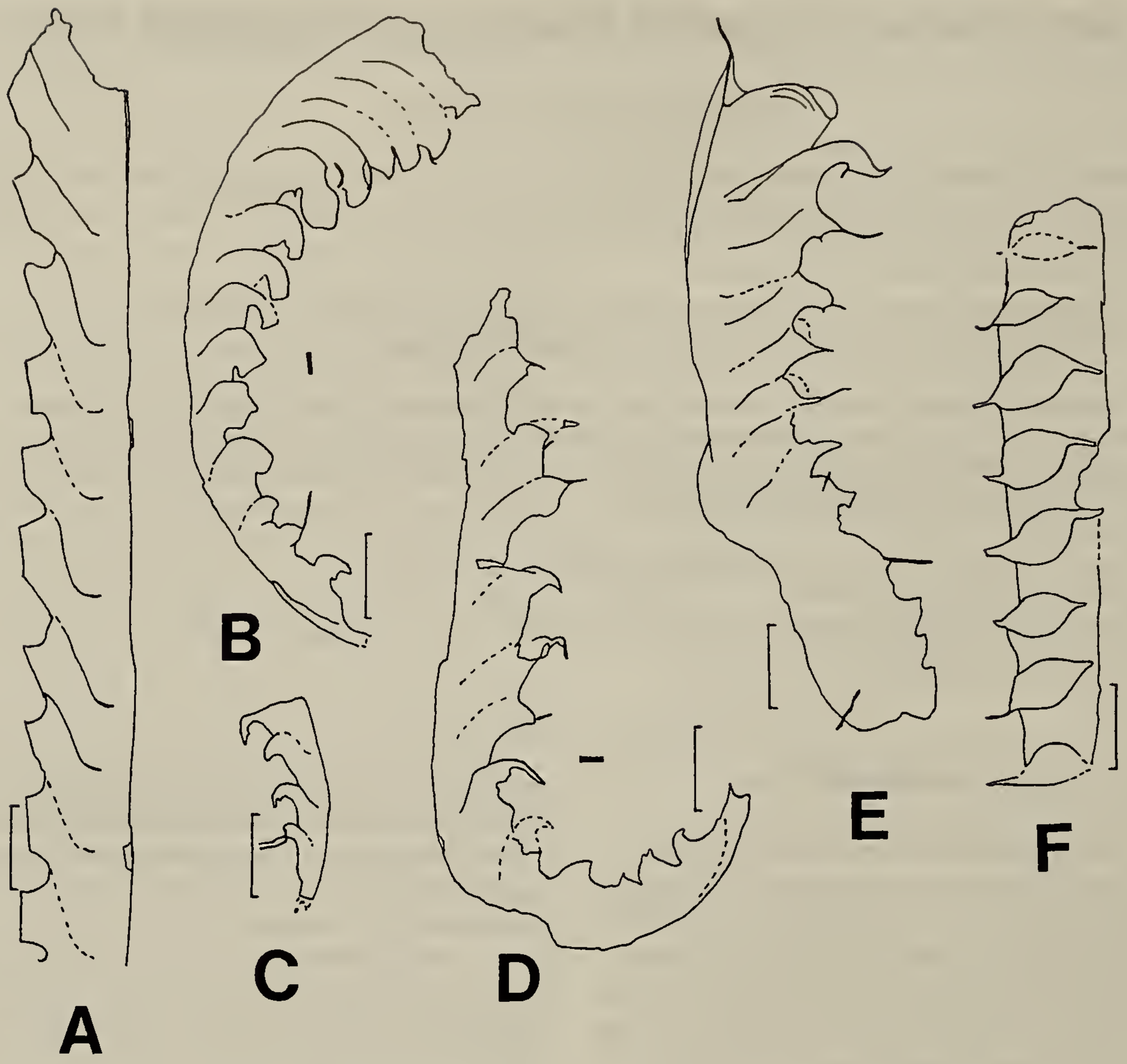

Figure 1. (A) ***Monoclimacis flumendosae*** **(Gortani), AM F114926, distal thecae, undeformed, low relief. (B-E)** ***Testograptus testis*** **(Barrande). (B) proximal end, AM F114928, showing some soft sediment deformation distally; (C) AM F114925, a proximal end with spines visible on th1; (D) AM F114930, spines on several thecae; (E) AM F114929, distal thecae with a growing end visible. (F)** ***Monograptus flemingii*** **(Salter), AM F114927, subscalariform view of mesial thecae.**

All figures x10, scale bar 1mm; heavy bar indicates deformation stretching direction, possibly not tectonic. All specimens from locality W 937, grid reference 687240E, 6295047 N, Canowindra 8360-N 1:50 000 topographic sheet. Unfigured specimens are AMF 114931-940.

Biozone (Rickards et al. 1995) but, as the Cadia specimens are abundant and occur with *Monoclimacis flumendosae* (Gortani), a pre-*ludensis* Biozone is indicated for this fauna.

The Cadia fauna is probably slightly younger than the Rodds Creek fauna (Rickards et al. 2000). Although this latter assemblage included some *lundgreni-testis* Biozone indicators, the presence of *Cyrtograptus* ex gr. *rigidus* Tullberg indicated a probable middle rather than late Wenlock for the Rodds Creek fauna. The Cadia fauna is thus significantly older than the Prídolí fauna from the 'borrow pit' locality (W910) 2 km to the southeast (Rickards et al. 2000).

Correlation with the Four Mile Creek sequence is probably with *testis*-bearing beds of the Ulah Formation in Wallace Creek; in Spring and Quarry Creeks, the *testis*-bearing beds of the same formation are largely green and black mudstones (Packham, Rickards and Wright, unpublished data).

SHELLY FAUNAS

The disarticulated and fragmental shelly fauna in this slump unit is unusually abundant and diverse for the region, in contrast with clastic units of this age in the Four Mile Creek area and the Spring-Quarry Creek areas which are singularly poor in shelly fossils. The faunas at Cadia have undergone soft-sediment deformation and are clearly transported. Described shelly faunas (other than corals) from the Four Mile Creek area and the Spring Creek areas are limited to two species of *ludensis* Biozone brachiopods described by Rickards and Wright (1997) from Cobblers Creek (see Fig. 1 of Rickards et al. 2000) and by Wright and Strusz (2004) from Spring Creek and Wallace Creek (see Fig. 1 of Rickards et al. 2000: *ludensis* Biozone and *lundgreni-testis* Biozone respectively). Other brachiopod faunas from the region were listed by Jenkins (1978, 1986), but the only rich faunas cited by him are from Llandovery (Early Silurian) limestones.

CONCLUSIONS

Graptolites identified from the Cadia Mine access road locality are *Testograptus testis*, *Monoclimacis flumendosae*, fragments of *Monograptus flemingii*, ?*Cyrtograptus* and retiolitids. The fauna is late Wenlock (Early Silurian) and is probably best correlated with a level high in the *lundgreni-testis* Biozone. It appears to be slightly younger than the probably middle Wenlock Rodds Creek black shale fauna (Rickards et al. 2000), and is assumed to correlate with the *testis* fauna of the Ulah Formation in the Four Mile Creek area to the west of Cadia.

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Silicified Early Devonian Trilobites from Brogans Creek, New South Wales

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Trilobites in an Emsian silicified fauna from the Carwell Creek Formation at Brogans Creek SE of Mudgee, NSW, include *Acanthopyge (Jasperia) bifida*, *Dentaloscutellum hudsoni* and *Proetus nemus*, all originally described from the Taemas area of NSW, together with *Sthenarocalymene*. *Proetus nemus* was known from limited material at Taemas, but is the most abundant species at Brogans Creek. Fuller description substantiates membership in *Proetus* (=*Devonoproetus*), rather than *Ryckholtia*, *Longiproetus* or *Rhenocynproetus*. Early ontogenetic stages of the trilobites are lacking at Brogans Creek, in contrast to Taemas. Conodonts co-occurring with the shelly fauna at Brogans Creek and at Taemas include *Polygnathus nothoperbonus*, which indicates the *Polygnathus perbonus* Conodont Zone (medial Emsian).

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Keywords: Trilobita, Devonian, New South Wales, *Acanthopyge* (*Jasperia*), *Dentaloscutellum*, *Proetus*, *Sthenarocalymene*.

INTRODUCTION

The presence of Devonian limestone at Brogans Creek (Fig. 1), located SE of Mudgee in the central tablelands of NSW, was first noted by Carne and Jones (1919) and later by Lishmund et al. (1986). Fossils from the limestone were discussed in detail by Colquhoun (1998) and Colquhoun and Meakin in Colquhoun et al. (in Meakin and Morgan 1999). Colquhoun (1995) illustrated the conodonts *Pandorinellina e. exigua* and *Polygnathus nothoperbonus* from Brogans Creek, the latter species considered (after Mawson 1987) to be characteristic of the medial Emsian (*Polygnathus perbonus* zone).

Here we provide the first descriptions of any of the well-preserved and abundant fossils from the quarry at Brogans Creek. A silicified trilobite fauna is of low diversity, but it provides new data on some taxa described from the Taemas area by Chatterton (1971), in particular the proetid *Proetus nemus*.

Stratigraphic assignment and age

The Devonian strata at Brogans Creek were considered part of the Carwell Creek Formation by Colquhoun et al. (1999). The limestones that have yielded the trilobites and other fossils documented here have also yielded (Colquhoun 1995) the medial Emsian conodont *Polygnathus nothoperbonus*, so this limestone is significantly younger than most limestones occurring in the area between the Mudgee and Brogans Creek, with the principal exception of those reported by Pickett (1972) and Colquhoun (1998) from the Mount Knowles Limestone Member of the Carwell Creek Formation and by Pickett (1978) from the Mount Frome Limestone, both located to the E of Mudgee.

Little is known about the sequence of the Devonian strata in the vicinity of the Brogans Creek quarry, and recent land reclaimation operations have concealed formerly productive parts of the abandoned quarries. Colquhoun (1998) stated that the sequence grades upwards from the fossiliferous limestone through crinoidal sandstone into massive shale and volcarenite. The sequence of beds that yielded silicified fossils is about 10 m in thickness. Beds immediately overlying these strata have yielded the tetracorals *Xystriphyllum mitchelli* and *Embolophyllum*, both also described from the Receptaculites Limestone Member at Taemas and Wee Jasper by Pedder et al. (1970).

The similarity of the macrofauna to that from the Receptaculites and Warroo limestone members of the Taemas Formation in the Burrinjuck Dam area of NSW (see Pedder et al. 1970) necessitates some consideration of the ages of these units. Conodont data summarised by Talent et al. (2000) for the Taemas

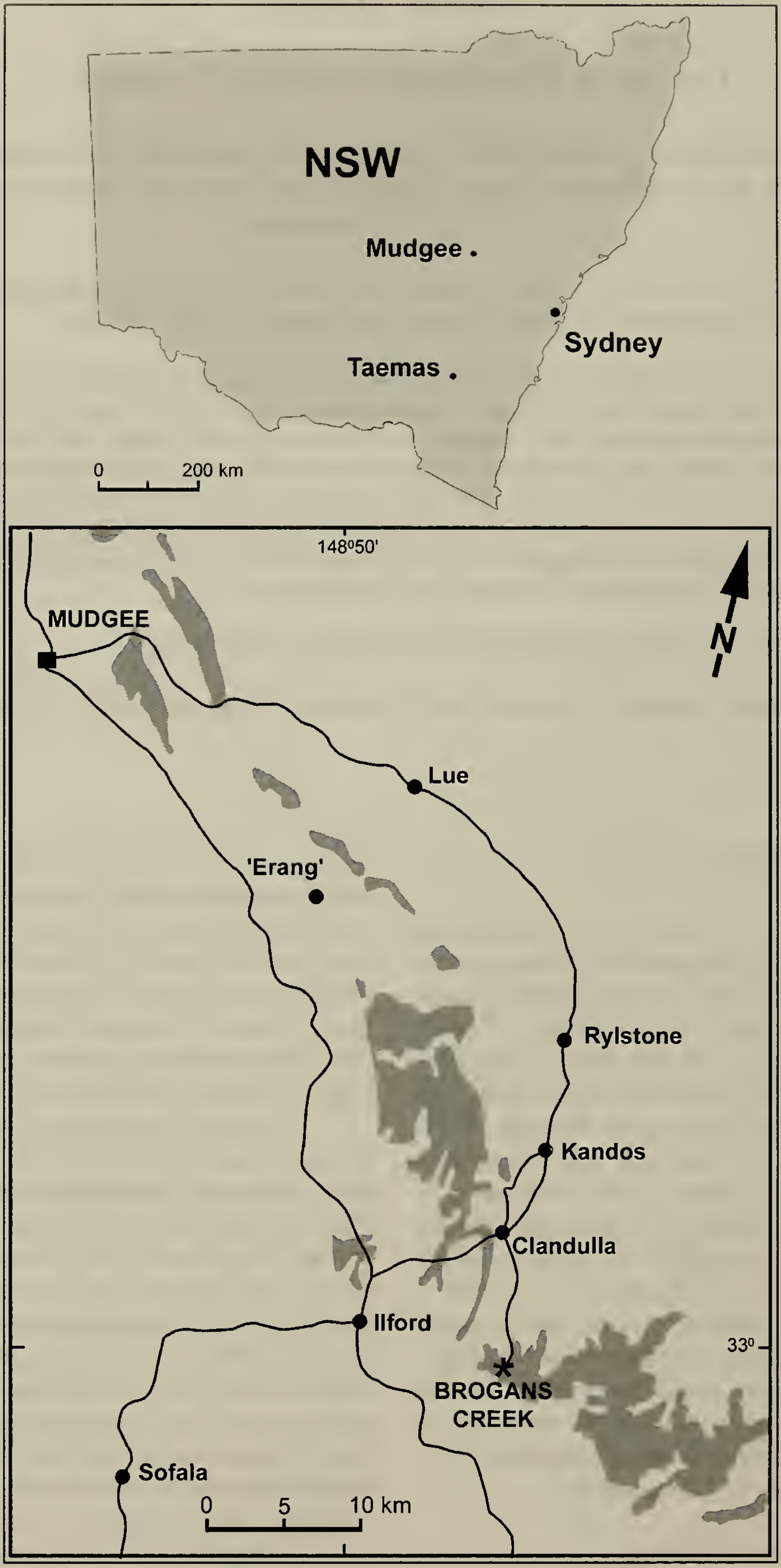

Figure 1. Location of trilobite collection at Brogans Creek. Map of NSW indicates Taemas, where the same species have been described (Chatterton 1971). Shading in inset map (after Colquhoun 1995) shows distribution of Lower Devonian platform sediments.

area of NSW indicate that the Receptaculites and Warroo limestones at Taemas, which overlie the Cavan Formation with its *Polygnathus pireneae* to *P. dehiscens* fauna, are probably early Emsian. Lindley (2002) recorded *Polygnathus nothoperbonus* from the Warroo Limestone Member, further confirming the assignment of this limestone to the medial Emsian *Polygnathus perbonus* Conodont Zone. However, Basden et al. (2002) concluded that the Warroo Limestone should be correlated with the *Polygnathus inversus* to *P. serotinus* Conodont Zones. On balance the co-occurrence of *P. nothoperbonus* in both areas of NSW seems to indicate unequivocally a medial Emsian age for the macrofaunas. This supports the conclusions of Garratt and Wright (1988:Fig. 3), who correlated their *Malurostrophia-Taemostrophia-Howittia* fauna (essentially the shelly fauna discussed here) with the *Polygnathus gronbergi* (=*P. perbonus*) Conodont Zone.

Faunal characters and affinities

The fossiliferous limestones have yielded very rich and well-preserved invertebrate faunas, dominated by brachiopods, tabulate corals and tetracorals, trilobites, gastropods, ostracodes, cephalopods, tentaculitids, crinoid debris and sponges; bivalves are subordinate at this locality. Most of the trilobites and brachiopods at Brogans Creek are conspecific with those described from Emsian limestones in the Lake Burrinjuck sequence at Taemas and 'Bloomfield' by Chatterton (1971, 1973). With respect to the trilobites, the faunal composition of the Brogans Creek assemblage is best matched in the lower half of the Receptaculites Limestone at Locality Γ of Chatterton (1971). The three species identified here, *Proetus nemus*, *Dentaloscutellum hudsoni* and *Acanthopyge bifida*, are represented in the lower Receptaculites Limestone at Locality Γ and at that locality as well as Brogans Creek they occur with *Sthenarocalymene*. Silicified residues from Brogans Creek yield the following for minimal number of individuals per species, based on the most abundant skeletal element: *Proetus nemus* (N=54), *Dentaloscutellum hudsoni* (N=16), *Acanthopyge bifida* (N=7), and *Sthenarocalymene* sp. (N=2). About 120 kilograms of limestone have been etched to produce our fauna.

In terms of diversity, the silicified assemblage consists additionally of more than 15 brachiopod species (*Malurostrophia flabellicauda reverta* Chatterton; *Salopina kemezysi* Chatterton and other dalmanellids; *Schuchertella murphyi* Chatterton; *Coelospira dayi* Chatterton; *Howellella* sp.; *Ambothyris runnegari* Chatterton; *Howittia* sp.; ?*Buchanathyris* sp.; reticulariid indet.; *Cydimia parva* Chatterton; *Parachonetes flemingi* Chatterton; *P.* sp. cf. *P. konincki* Chatterton; rhynchonellids). Some 30 gastropod species are under study by Dr A.G. Cook. Tetracoral species are dominated numerically by an abundant solitary *Plasmophyllum*, as well as other solitary corals (?acanthophyllids) and rare fragments of ?*Calceola*. The sponge *Amphipora* is locally abundant, and presumably represents lagoonal phases of deposition or influx of lagoonal debris; several biofacies are evident. Colquhoun (1998) indicated that the Brogans Creek limestone was deposited in a well-oxygenated, normal salinity environment. The trilobite material is represented by disarticulated sclerites, but many brachiopods shells are articulated. Scolecodonts are at least as common as conodonts in residues; this is also a feature of limestones in the Capertee Valley (S of Brogans Creek) where the strata are highly deformed and preservation is poor. Despite the disarticulated nature of parts of the Brogans Creek shelly fauna, their excellent preservation indicates that postmortem transportation was minimal.

SYSTEMATIC PALAEONTOLOGY

Figured material is in the Palaeontology collection, Australian Museum, Sydney (prefix AMF).

Order PROETIDA Fortey and Owens, 1975
Family PROETIDAE Salter, 1864
Subfamily PROETINAE Salter, 1864
Genus PROETUS Steininger, 1831

Type species

Calymmene concinna Dalman, 1827; by original designation.

Proetus nemus Chatterton, 1971
Fig. 2a-p, Fig. 3a-t

Proetus nemus Chatterton, 1971:65-67, Pl. 16, Figs 18-32.
Ryckholtia? *nemus* (Chatterton). Lütke, 1990:21.

Material

39 cranidia, 103 librigenae, 3 hypostomes, 62 thoracic segments, 50 pygidia.

Diagnosis

Proetus with relatively elongate, tapering glabella, its posterior two thirds with dense, mostly moderate sized tubercles, its anterior third granulate. Facial suture divergent between γ and β. Genal ridge strong along

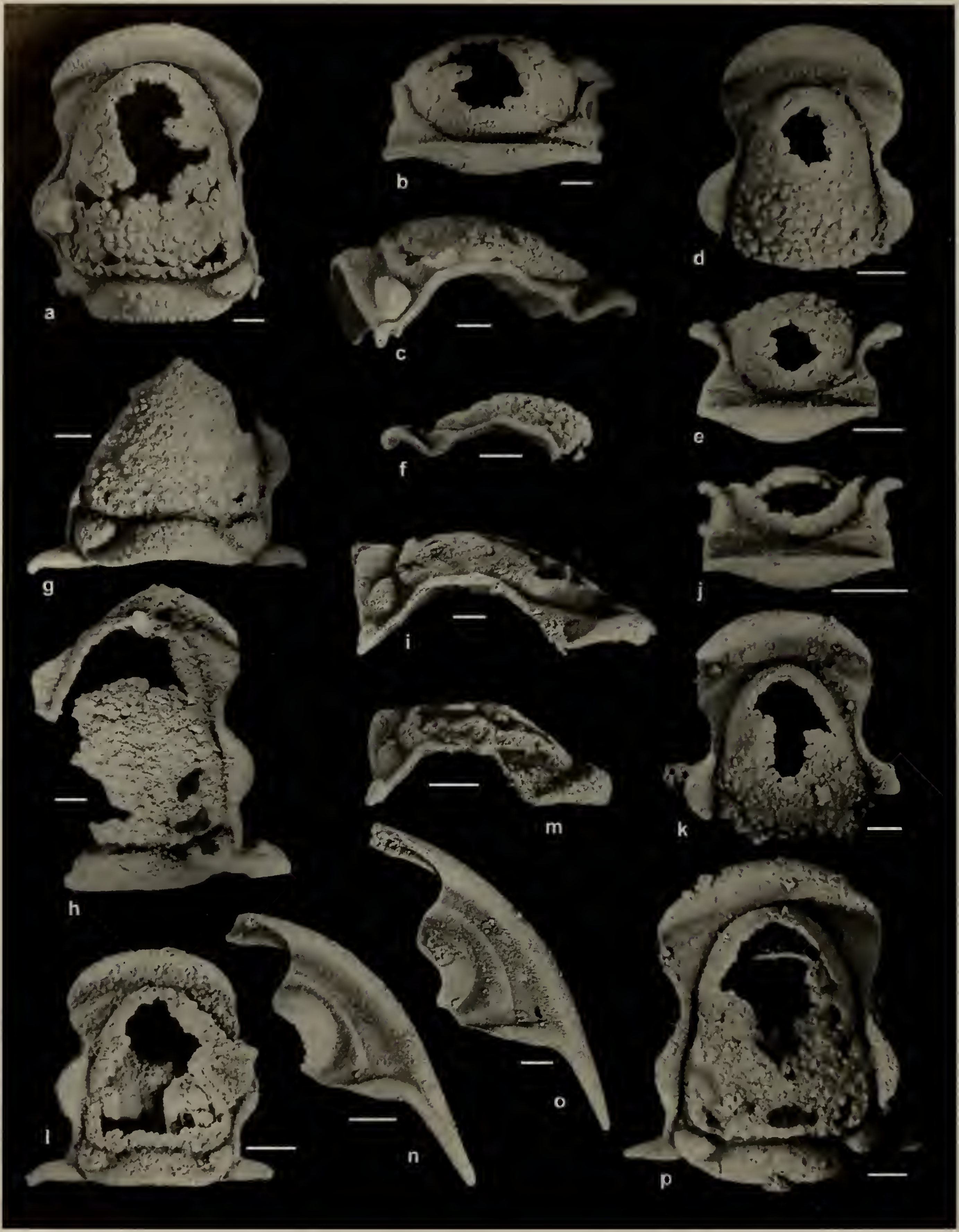

Figure 2. ***Proetus nemus*** **Chatterton, 1971. Carwell Creek Formation (medial Emsian), Brogans Creek, NSW. Scale bars 1 mm. a-c, AMF 124700, cranidium, dorsal, anterior and lateral views; d-f, AMF 124701, cranidium, dorsal, anterior and lateral views; g, AMF 124702, cranidium, dorsal view; h, AMF 124703, cranidium, dorsal view; i, AMF 124704, cranidium, lateral view; j, AMF 124705, cranidium, anterior view; k, AMF 124706, cranidium, dorsal view; l-m, AMF 124707, cranidium, dorsal and lateral views; n, AMF 124708, librigena, dorsal view; o, AMF 124709, librigena, dorsal view; p, AMF 125485, cranidium, dorsal view.**

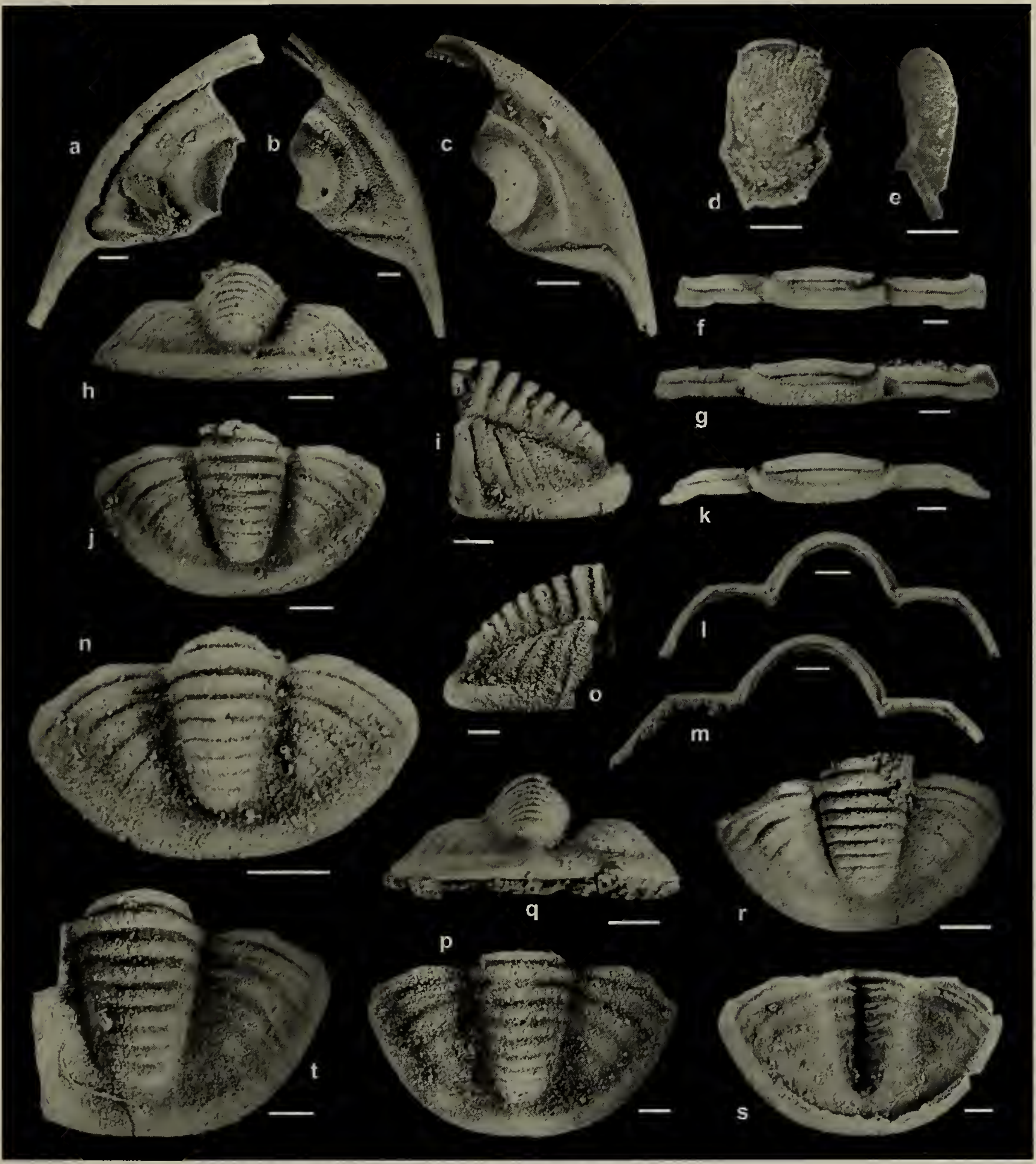

Figure 3. ***Proetus nemus*** **Chatterton, 1971. Carwell Creek Formation (medial Emsian), Brogans Creek, NSW. Scale bars 1 mm. a, AMF 124710, librigena, internal view; b, AMF 124711, librigena, dorsal view; c, AMF 124712, librigena, dorsal view; d-e, AMF 124713, hypostome, ventral and lateral views; f, AMF 124714, thoracic segment, dorsal view; g, AMF 124715, thoracic segment, dorsal view; h-j, AMF 124716, pygidium, posterior, lateral and dorsal views; k, AMF 124717, thoracic segment, dorsal view; l, AMF 124718, thoracic segment, anterior view; m, AMF 124719, thoracic segment, anterior view; n, AMF 124720, pygidium, dorsal view; o-p, AMF 124721, pygidium, lateral and dorsal views; q-r, AMF 124722, pygidium, posterior and dorsal views; s, AMF 124723, pygidium, ventral view; t, AMF 124724, pygidium, dorsal view.**

all but posteriormost part of librigenal field, distinct but less prominent on preocular fixigena; small caecal pits abundant on librigenal field; genal spine relatively long. Pygidium with seven axial rings and lunate terminal piece (7+1); anterior three or four pleural furrows well impressed, fifth and sixth faint.

Description

Cranidial length about equal to maximum width at ω; width at δ slightly more than 80% width at ω; width at β 85-95% width at δ. Axial furrow narrow, moderately, evenly deep. Glabella widest basally, length (excluding L0) 1.1-1.2 times basal width, with moderate taper anteriorly, slightly constricted at S2, gently convex (sag., tr.); frontal lobe rounded; terminating at but not overhanging anterior border furrow. S1 originating opposite midlength of palpebral lobe, shallow, directed posteromedially, distally birfucate, with posterior branch terminating well in front of S0; S2 parallel with S1, more weakly incised, originating just behind anterior edge of palpebral lobe; S3 obscure. Posterior two thirds of glabella with mostly moderate sized tubercles, some small tubercles, densely packed so as to nearly touch; anterior third of glabella granulate, non-tuberculate. S0 transverse medially, narrow (sag., exsag.), deep, flexed forwards abaxially against lateral occipital lobes. L0 distinctly wider than basal part of glabella, length about 20% its width; lateral occipital lobes large, drop-shaped, isolated from remainder of L0 by deep furrows; L0, including lateral lobes, covered with tubercles as on posterior part of glabella, including moderately large median tubercle behind midlength. Preglabellar region 13-15% of cranidial length; in large specimens, composed of an inclined, medially flat posterior half and moderately convex (sag.) anterior half bearing 5-6 terrace lines in dorsal view; in small specimens, posterior half forms a wide (sag., tr.) depressed field with a broad (tr.), gently inflated transverse median swelling. Genal ridge well developed on preocular fixigena, anteromedially directed, terminating at juncture of preglabellar and anterior border furrows, stronger in small specimens. Postocular fixigena 25-35% width (tr.) and about 60% length (exsag.) of L0. Palpebral lobe arcuate, 35-45% length of glabella; palpebral furrow faint or indistinct. Anterior sections of facial suture diverging from each other at 45-62° between γ and β, running subparallel against anterior border furrow, then strongly converging between β and α. Posterior sections of facial suture running subparallel or gently diverging between ε and ξ, close to axial furrow, then sharply turned outwards to ω.

Librigenal field moderately wide, gently convex (tr.); genal ridge strong along all but posteriormost part of field, closer to eye socle than to lateral border furrow; most of field with abundant, small caecal pits, least distinct at posterolateral corner of field. Eye socle narrow, separated from visual surface and librigenal field by shallow furrows. Posterior border furrow narrow, deep; lateral border furrow wider, the two merging at genal angle, extending along a variable extent of the genal spine, usually along about half its length. Lateral border 70-80% as wide as narrowest part of librigenal field in dorsal view, strongly convex (tr.); terrace lines well defined along entire length and width of lateral border and along genal spine. Genal spine relatively long, its inner margin straight or faintly concave. Panderian notch large, semicircular. Connective suture with straight, diagonal course along most of its length, its extent relative to cranidium indicating that rostral plate is trapezoidal or triangular, fairly wide anteriorly (cf. *P. concinnus*: Owens 1973:Text-fig. 1B).

Hypostomal width across shoulders about 65% sagittal length. Anterior margin weakly convex medially, flexed backward abaxially. Anterior lobe of middle body strongly inflated (tr.), anteromedial part raised but not forming discrete rhynchos; middle body gently convex (sag.) along most of length, fairly steeply turned up anteromedially; anterior lobe bearing many sinuous terrace lines. Middle furrow moderately deep, directed posterolaterally across abaxial third of middle body then abruptly effacing. Border furrow narrow, distinctly impressed around entire middle body, shallowest against anterior wing. Anterior border uniformly narrow (sag., exsag.); lateral border gently converging between anterior wing and shoulder; shoulder rounded; posterolateral margin straight between shoulder and pair of blunt spines at lateral edge of posterior border; posterior border narrow (sag., exsag.), about 10% length of hypostome, with gently convex posteromedian margin.

Number of thoracic segments unknown. Axial furrow narrow, shallow. Axis strongly convex (tr.), 32-41% width of thorax. Articulating half ring varying from equal in width (sag.) to 1.6 times as wide as preannulus along length of thorax, 70-90% length of ring; preannular furrow transverse to gently concave medially, sharply impressed but much shallower than articulating furrow; ring covered with small, dense tubercles or coarse granules. Pleural furrow narrow, about as deep as articulating furrow, gently flexed forward at fulcrum, abruptly shallowing then effacing on inner part of articulating facet; anterior and posterior pleural bands equal in width (exsag.) proximal to fulcrum; pleurae moderately declined abaxial to fulcrum, at midwidth (tr.) of rib. Pleural tips with curved anterolateral margin, blunt rounded posterior projection. Panderian notch deep, U-shaped.

Pygidium subsemicircular, length (excluding articulating half ring) 55-60% width. Axial width about 35% pygidial width anteriorly; axial furrows narrow, uniformly impressed along most of length. Seven axial rings and short, lunate terminal piece (7+1); first one or two ring furrows lengthened medially as short preannulus; more posterior ring furrows shallower but with moderately deep incision across axis, posterior few gently convex backwards; axis raised strongly above pleurae, gently convex in sagittal profile, moderately arched (tr.); rings with dense small tubercles or coarse granules. Postaxial region about 20% length of pygidium. Pleural furrows narrow (exsag.), anteriorly convex, anterior three or four well impressed, fifth and variably sixth faintly discernible; first pleural furrow terminates near pygidial lateral margin, others terminate at shallow posterior border furrow; interpleural furrows narrower and shallower than pleural furrows; pleural ribs with sculpture of dense, medium sized granules. Border widening back to its intersection with third pleural furrow, then maintaining even width, occupying most of postaxial region, weakly convex. Doublure extending in nearly as far as border furrow, bearing several terrace lines.

Discussion

The sample from Brogans Creek resembles that from Taemas in that the largest cranidia (Fig. 2a-c, h, i, p; Chatterton 1971:Pl. 16, fig. 28) have the anterior end of the glabella abutting the inclined posterior part of the anterior border, whereas small specimens have a broad depression between the frontal lobe and the convex, terraced part of the anterior border (Fig. 2d-f, j, k; Chatterton 1971:Pl. 16, fig. 25). The latter morphology, associated with a more pronounced fixigenal ridge (Fig. 2d, k versus 2a, h, p) is confined to small specimens. This difference in the preglabellar region is bridged by intermediate sized specimens, and is ascribed to ontogenetic variation. The transverse median swelling in the depression of small specimens (Fig. 2e, j) retains a faint expression in large cranidia. No bimodality can be detected in the strength of the librigenal ridge (Figs. 2n, o, 3b, c), which is consistently pronounced.

In assigning this species to *Proetus*, Chatterton (1971) acknowledged its distance from the type species, the Wenlock *P. concinnus* (Dalman). However, several other Australian Emsian and Eifelian Proetinae are validly assigned to that genus. These include *Proetus talenti* Chatterton, 1971 (type of *Devonoproetus* Lütke, 1990), *P. sparsinodosus* Feist and Talent, 2000, and *P. latimargo* Feist and Talent, 2000, the latter two originally assigned to *Devonoproetus* at the subgeneric level. *Devonoproetus* is a junior synonym of *Proetus* s.s. (Adrain 1997; Zhou et al. 2000).

Proetus nemus was reassigned, with question, to the otherwise Ludlow-Lochkovian *Ryckholtia* Šnajdr, 1980 (type *Proetus ryckholti* Barrande, 1846) by Lütke (1990). The new material described herein conflicts with this reassignment. Membership in *Ryckholtia* is precluded by the pronounced tuberculate sculpture on the glabella and axial rings of *P. nemus*, the strongly defined lateral occipital lobes, and sagittal elimination of the preglabellar field.

This species displays characters that suggest alternative assignments. The elongate, tapering glabella of *Proetus nemus* and its pattern of sculpture (strong tuberculation posteriorly, becoming subdued anteriorly), together with the profile of the preglabellar region, including the wide (sag., exsag.) anterior cranidial border furrow, and the divergence of the facial suture between γ and β resemble *Longiproetus tenuimargo* (Richter, 1909) (type of *Longiproetus* Cavet and Pillet, 1958). *Longiproetus* has been regarded as a synonym of *Gerastos* Goldfuss, 1843 (Owens 1973), a valid subgenus of *Gerastos* (Šnajdr 1980), restricted to its type species on the basis of a distinctive shape of the rostral plate (Lütke 1990), or slightly expanded to include a small group of Rhenohercynian mid Eifelian to early Givetian species (Basse 1996, 2002). Lütke (1990) reassigned the Bohemian species that had been referred to *Longiproetus* (e.g., Šnajdr 1980) to *Coniproetus* Alberti, 1966, and other genera, whilst the inadequately known Emsian species referred to *Longiproetus* by Pillet (1972) defy classification. Despite the similarities in the glabella and preglabellar region, several characters conflict with an alliance between *P. nemus* and *Longiproetus*. Notably, the strong genal ridge of *P. nemus* is lacking in *L. tenuimargo* and other certain congeners (*sensu* Basse 2002), the prominent lateral occipital lobes contrast with the inconspicuous lobes in *Longiproetus* s.s., L0 is wider than the basal part of the glabella, the cephalon is much less vaulted, the palpebral lobe is situated more posteriorly, and the pygidium is relatively paucisegmented (7+1 rings versus 8+1). The course of well preserved connective sutures on librigenae suggests that the rostral plate of *P. nemus* is more regularly trapezoidal or triangular than is that of *L. tenuimargo* (Lütke 1990:Text-fig. 8).

Affinities to species that have been assigned to *Devonoproetus* by recent workers better account for the large occipital lobes, width of L0 relative to the glabella, and 7+1 pygidial segmentation. Among these, *Proetus latimargo* Feist and Talent, 2000 (Eifelian, Queensland) and *P. zhusilengensis* Zhou et al., 2000

(Emsian, Inner Mongolia) resemble *P. nemus* in having a tongue-shaped glabella (narrowest in *P. nemus*) with dense, pronounced tuberculation, and *P. latimargo* shares the divergence of the facial suture between α and β.

Among those species that have been referred to *Devonoproetus*, the strong genal ridge of *Proetus nemus* is developed in a group recognised by Basse (2002) as a separate genus, *Rhenocynproetus*, from which the Australian "*Devonoproetus*" species were explicitly excluded. The presence of a genal ridge in other genera of Proetinae [e.g. *Gerastos*: Šnajdr 1980:Pl. 3, Fig. 13, Pl. 4, Fig. 17; *Coniproetus* (*Bohemiproetus*): Šnajdr 1980:Pl. 6, Figs 5, 6, 14; Lieberman 1994:Fig. 9.3) demonstrates that this feature is not an infallible indicator of relationships. Characters cited by Basse (2002) as excluding Australian species of *Proetus* from *Rhenocynproetus* also distinguish *P. nemus*; these include the large size of the lateral occipital lobes and weaker outer edge of the eye socle. *Proetus nemus* possesses (plesiomorphic) features considered by Basse (2002) to more generally distingish *Proetus* from *Rhenocynproetus*, such as a less inflated glabella, the lateral occipital lobes wider than the base of the glabella, terrace lines developed on the dorsal as well as lateral extent of the cranidial border, and the well developed librigenal spine. The presence of a pair of posterior border spines on the hypostome (Fig. 3d) is shared with *Proetus* (e.g. Whittington and Campbell 1967:Pl. 1, Fig. 17; Schrank 1972:Pl. 4, Fig. 7), including *P. talenti*, but is likely symplesiomorphic (Adrain 1997).

Order CORYNEXOCHIDA Kobayashi, 1935
Suborder SCUTELLUINA Hupé, 1953
Family STYGINIDAE Vogdes, 1890
Genus DENTALOSCUTELLUM Chatterton, 1971

Type species
Dentaloscutellum hudsoni Chatterton, 1971; by original designation.

Dentaloscutellum hudsoni Chatterton, 1971
Fig. 4a-i

Dentaloscutellum hudsoni Chatterton, 1971:12-22, Pl. 1, Figs 1-24, Pl. 2, Figs 1-24, Pl. 3, Figs 1-12, Pl. 24, Fig. 15, Text-figs 4-5.

Material
4 cranidia, 29 librigenae, 1 hypostome, 1 thoracic segment, 5 fragmentary pygidial margins.

Discussion
This species was fully described based on specimens from the Receptaculites Limestone near Taemas (Chatterton 1971). The Brogans Creek material is considered to be conspecific, the only possible difference being slightly more numerous cranidial tubercles (Fig. 4b, c) than in the type material.

Order LICHIDA Moore, 1959
Family LICHIDAE Hawle and Corda, 1847
Subfamily TROCHURINAE Phleger, 1936
Genus ACANTHOPYGE Hawle and Corda, 1847

Type species
Acanthopyge leuchtenbergii Hawle and Corda, 1847; by subsequent designation of Reed (1902).

Subgenus JASPERIA Thomas and Holloway, 1988

Type species
Acanthopyge (Mephiarges) *bifida* Edgell, 1955; by original designation.

Acanthopyge (Jasperia) *bifida* Edgell, 1955
Fig. 4j-t

Acanthopyge (Mephiarges) *bifida* Edgell, 1955:138; Chatterton, 1971:30-41, Pl. 6, Figs 1-24, Pl. 7, Figs 1-27, Pl. 8, Figs 1-17, Text-figs 8-10.

Material
7 cranidia, 1 rostral plate, 7 librigenae, 3 hypostomes, 1 thoracic segment, 2 pygidia.

Discussion
The Brogans Creek specimens are indistinguishable from those described from Wee Jasper (Edgell 1955) and Taemas (Chatterton 1971). The species was fully described by Chatterton (1971), rendering description of the Brogans Creek material unnecessary. A few specimens are illustrated (Fig. 4j-t) in support of the conspecificity of the collections.

Order PHACOPIDA Salter, 1864
Suborder CALYMENINA Swinnerton, 1915
Family CALYMENIDAE Milne Edwards, 1840
Genus STHENAROCALYMENE Siveter, 1977

Type species
Sthenarocalymene lirella Siveter, 1977; by original designation.

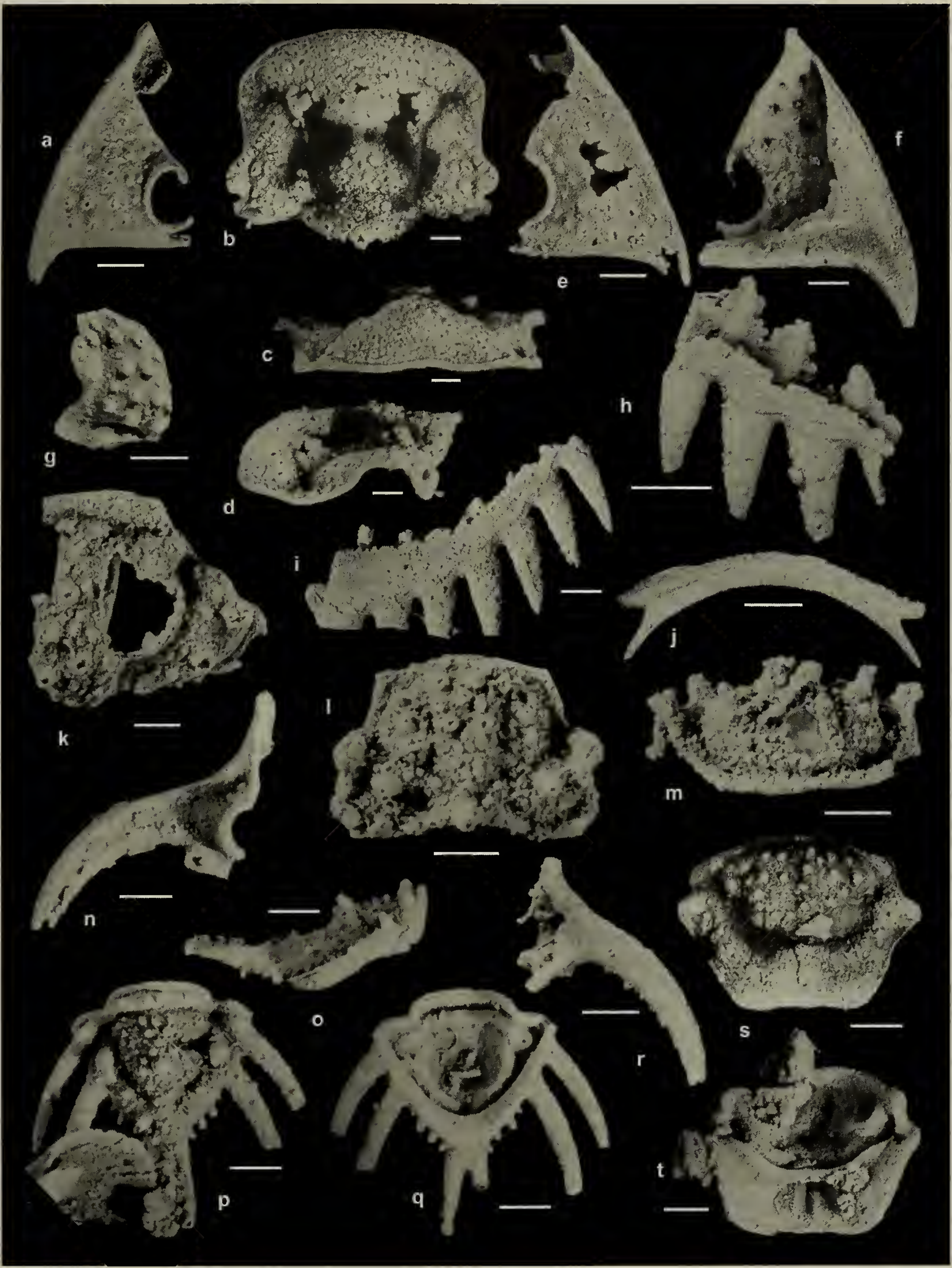

Figure 4. a-i, *Dentaloscutellum hudsoni* Chatterton, 1971. Scale bars 1mm. a, AMF 124725, librigena, dorsal view; b-d, AMF 124726, cranidium, dorsal, anterior and lateral views; e, AMF 124727, librigena, dorsal view; f, AMF 124728, librigena, ventral view; g, AMF 124729, fixigena, dorsal view; h, AMF 124730, incomplete pygidium, ventral view; i, AMF 124731, incomplete pygidium, ventral view. j-t, *Acanthopyge (Jasperia) bifida* Edgell, 1955. Scale bars 1 mm. j, AMF 124732, rostral plate, ventral view; k, AMF 124733, cranidium, dorsal view; l-m, AMF 124734, cranidium, dorsal and anterior views; n, AMF 124735, librigena, dorsal view; o-q, AMF 124736, pygidium, lateral, dorsal and ventral views; r, AMF 124737, librigena, ventral view; s-t, AMF 124738, hypostome, ventral and dorsal views.

Sthenarocalymene sp.

Material

Two cranidial fragments, one fragmentary librigena.

Discussion

A few calymenid cephalic fragments indicate the presence of a species lacking a buttress between the fixigena and L2. On this basis the material is assigned to *Sthenarocalymene*, the non-buttressed calymenid in many Australian Lower Devonian faunas [see Sandford (2000) for discussion of this genus, its synonym *Apocalymene* Chatterton and Campbell, 1980, and *Gravicalymene* Shirley, 1936]. The Brogans Creek material may be identical with *S. quadrilobata* (Chatterton, 1971), which co-occurs with the other taxa described herein in the lower Receptaculites Limestone at Locality Γ of Chatterton (1971), but specific identity requires better specimens.

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A New Species of the Henicopid Centipede *Dichelobius* (Chilopoda: Lithobiomorpha) from Southeastern Australia and Lord Howe Island

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Edgecombe, G.D. (2004) A new species of the henicopid centipede *Dichelobius* (Chilopoda: Lithobiomorpha) from southeastern Australia and Lord Howe Island. *Proceedings of the Linnean Society of New South Wales* **125**, 189-203.

The genus *Dichelobius* Attems, 1911, based on *D. flavens* Attems, 1911, from the southwest of Western Australia, has its only other previously assigned species in New Caledonia and Chile. The Tasmanian type species of the monotypic *Tasmanobius* Chamberlin, 1920, is regarded as a member of *Dichelobius*. *Dichelobius giribeti* n. sp. represents the genus in eastern mainland Australia (southeastern New South Wales, the Australian Capital Territory, and northeastern Victoria) and on Lord Howe Island. *Dichelobius bicuspis* Ribaut, 1923, is widely distributed in New Caledonia.

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KEYWORDS: Anopsobiinae, Chilopoda, *Dichelobius*, Henicopidae, Lithobiomorpha.

INTRODUCTION

The subfamily Anopsobiinae is a group of minute centipedes (Chilopoda) in the predominantly southern temperate family Henicopidae. Anopsobiinae is distributed chiefly in the Southern Hemisphere, with species described from Patagonian Argentina and Chile (Silvestri 1899, 1909a-b; Verhoeff 1939; Chamberlin 1962), the Falkland Islands (Eason 1993), New Zealand (Silvestri 1909a; Archey 1917, 1937), New Caledonia (Ribaut 1923), Tasmania (Chamberlin 1920), New South Wales (Edgecombe 2003), southwest Western Australia (Attems 1911), and the Cape region of South Africa (Attems 1928). Four Gondwanan genera have been named: *Anopsobius* Silvestri, 1899, *Catanopsobius* Silvestri, 1909b, *Dichelobius* Attems, 1911, and *Tasmanobius* Chamberlin, 1920. Four additional anopsobiine genera, all monotypic, occur in the Northern Hemisphere, namely *Anopsobiella* Attems, 1938, *Ghilaroviella* Zalesskaja, 1975, *Shikokuobius* Shinohara, 1982, and *Rhodobius* Silvestri, 1933. In total, 17 species and subspecies of Anopsobiinae have been described.

Silvestri (1909a) cited the occurrence of an anopsobiine from Sydney, but formal descriptions of Anopsobiinae in eastern Australia are limited to *Tasmanobius relictus* Chamberlin, 1920, based upon a single specimen from Tasmania, and *Anopsobius wrighti* Edgecombe, 2003, from northern New South Wales. Mesibov (1986) indicated the presence of two species of Anopsobiinae in Tasmania. The present study continues a systematic treatment of Anopsobiinae of Australia by documenting a new species of *Dichelobius* from New South Wales, the Australian Capital Territory, Victoria, and Lord Howe Island (Fig. 1).

For electron microscopy, specimens were photographed on a Leo 435VP using a Robinson backscatter detector. Digital images were assembled into plates with Photoshop. Morphological terminology is as summarised by Edgecombe (2001:203), with terminology for the mandible as in Edgecombe et al. (2002:40, Fig. 4).

The following abbreviations are used for repositories of specimens examined:

AM - Australian Museum, Sydney
ANIC – Australian National Insect Collection, Canberra
MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, MA
MNHN – Museum National d'Histoire Naturelle, Paris
NMW – Naturhistorisches Museum Wien
QM – Queensland Museum, Brisbane
WAM – Western Australian Museum, Perth.

Other abbreviations: Berl., ANIC Berlesate; CBCR, Australian Museum Centre for Biodiversity and Conservation Research; Ck, Creek; Mt, Mountain; NP, National Park; rf, rainforest; SF, State Forest.

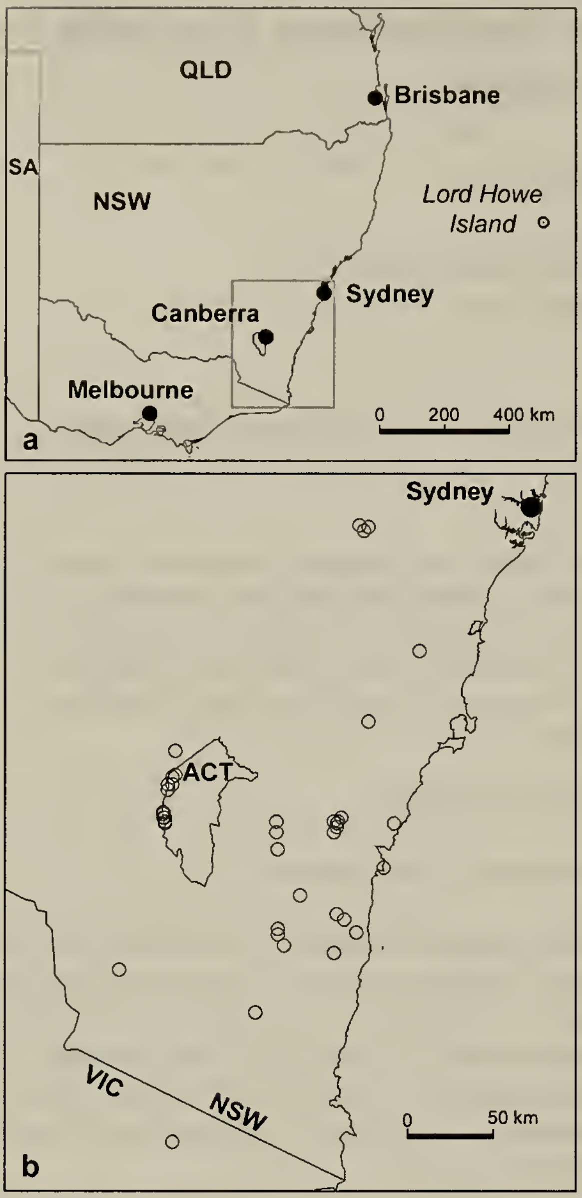

Figure 1. a, southeastern Australia and Lord Howe Island. Inset shows location of map in b, indicating records of *Dichelobius giribeti* n. sp. (open dots) in New South Wales, the Australian Capital Territory, and Victoria.

Collectors: GBM – G.B. Monteith; JFL – J.F. Lawrence; RJB – R.J. Brooks; RWT – R.W. Taylor.

Order LITHOBIOMORPHA Pocock, 1902
Family HENICOPIDAE Pocock, 1901
Subfamily ANOPSOBIINAE Verhoeff, 1907
Genus DICHELOBIUS Attems, 1911

Tasmanobius Chamberlin, 1920 **n. syn.**

Type species

Dichelobius flavens Attems, 1911; by monotypy.

Assigned species

Dichelobius relictus (Chamberlin, 1920) n. comb.; *D. bicuspis* Ribaut, 1923; *D. schwabei* Verhoeff, 1939; *D. giribeti* n. sp.

Diagnosis

Anopsobiinae with spiracle on segments 3, 10 and 12, variably present on segment 14.

Discussion

The Gondwanan genera *Dichelobius*, *Tasmanobius* and *Anopsobius* share several apomorphic characters relative to Northern Hemisphere Anopsobiinae. These include coxal pores confined to legs 14 and 15, a ventrodistal spur on the prefemur of legs 14 and 15, an elongate longitudinal median furrow on the head shield, the basal article of the female gonopod extended as a short process bearing the spurs, and indistinct scutes on the proximodorsal part of the pretarsal claws (Edgecombe and Giribet 2003). Considering previous concepts of *Dichelobius* (Attems 1928; Verhoeff 1939; Shinohara 1982), reduced spiracles are the only morphological character that unites its members to the exclusion of *Anopsobius* as delimited by Chamberlin (1962) and Edgecombe (2003). The *Dichelobius* distribution of spiracles is shared by the eastern Australian species *D. giribeti*. The cladistic reliability of a diminished number of segments with spiracles can be questioned because other genera of Anopsobiinae have been diagnosed based on having spiracles confined to segments 3, 10 and 12 (*Tasmanobius*), 3, 12 and 14 (*Rhodobius*) or 3 and 10 only (*Catanopsobius*). However, molecular sequence data provide independent support for a close relationship between *D. flavens* and *D. giribeti*, with the implication that their shared spiracle distribution can be considered a synapomorphy (Fig. 2a). Parsimony analysis of five molecular loci as well as combination of the molecular data and morphology unite *D. flavens* and *D. giribeti* to the exclusion of *Anopsobius* species under many explored gap costs and transversion:transition ratios (Edgecombe and Giribet 2003) (Fig. 2c). An alternative relationship between *D. giribeti* and *Anopsobius* (Fig. 2b) is discussed below.

Verhoeff (1925) cited the presence of a median suture in the maxillipede pleural band as an additional character by which *Dichelobius* is distinguished from *Anopsobius*. The presence of a median suture (see Fig. 6j) is a plesiomorphic character, shared with Henicopinae, and is thus not useful for defining *Dichelobius* as a clade.

Tasmanobius relictus Chamberlin, 1920, is considered to be a member of *Dichelobius* as grouped

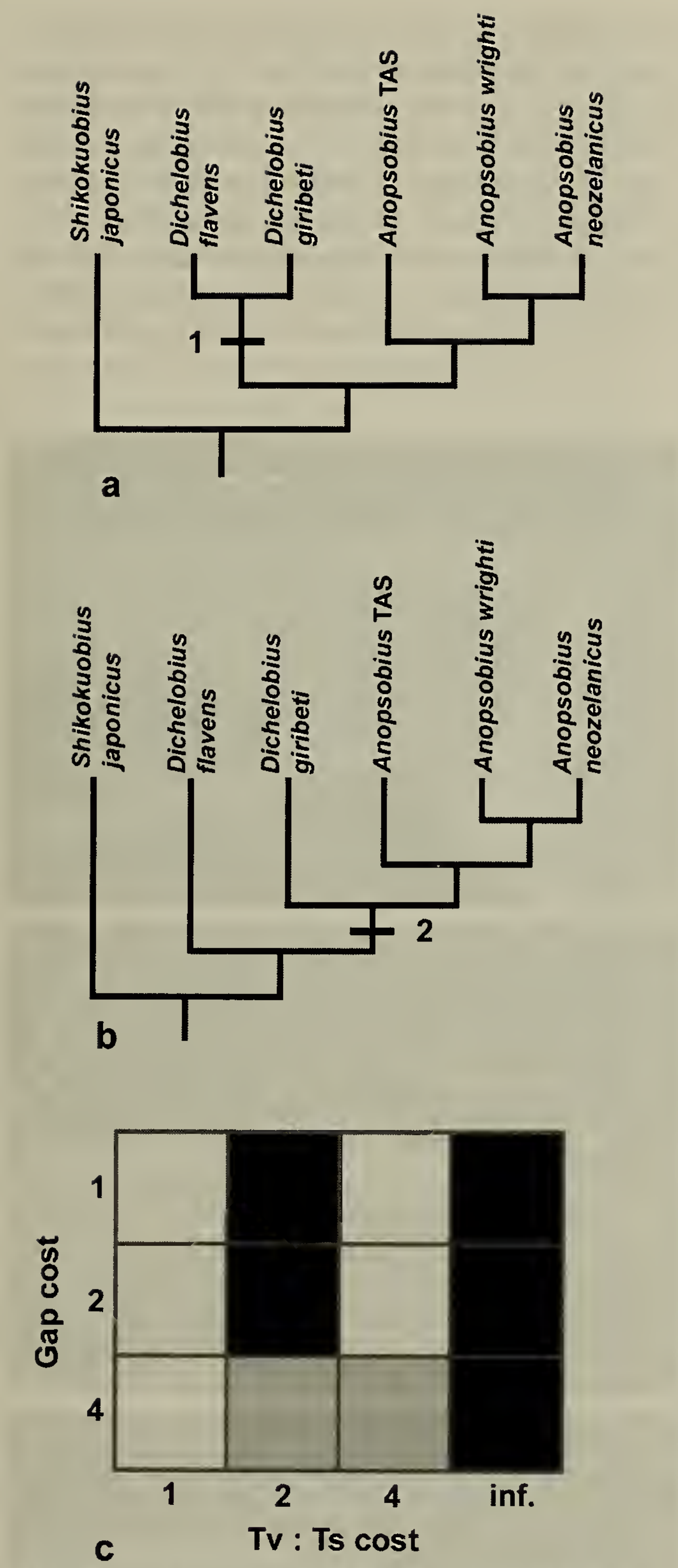

Figure 2. a, b, alternative cladograms for Anopsobiinae based on combined morphological and molecular data (Edgecombe and Giribet 2003). Character 1, absence of spiracles on segment 8; character 2, short posteroventral spine on pretarsal claw; c, summary of 12 analyses for combined morphological and molecular data with different gap costs (gap:substitution = 1:1, 2:1, 4:1) and transversion:transition costs (1:1, 2:1, 4:1, infinity). Black squares, parameters that resolve cladogram a (*Dichelobius* monophyletic); white squares, parameters that resolve cladogram b (*Dichelobius* paraphyletic); grey square, cladograms a and b of equal length.

herein (with *Tasmanobius* consequently being a junior subjective synonym of *Dichelobius*). *Tasmanobius relictus* was described as having spiracles on segments 3, 10, and 12, as in *Dichelobius*. Mesibov (1986) suggested that a widespread Tasmanian anopsobiine species (Anopsobiine sp. 2 of Mesibov 1986) may be *Tasmanobius relictus*, and that species closely resembles *Dichelobius giribeti*. The holotype and sole type specimen of *T. relictus* (MCZ 14533) is in poor condition, and lacks locality data more specific than Tasmania, making the identification of any other specimen as this species problematical. The description by Chamberlin did not note a spiracle on segment 14 which is present in the Tasmanian *Dichelobius*, though this is not obvious in contracted specimens, as noted by Mesibov (1986). A spiracle being absent on segment eight in *T. relictus* and the colour being "nearly chestnut" (Chamberlin 1920) make it probable that this species is identical with the Tasmanian *Dichelobius* (=Anopsobiinae sp. 2 of Mesibov 1986) rather than the northwestern Tasmanian *Anopsobius* (=Anopsobiinae sp. 1 of Mesibov 1986), which has a spiracle on segment 8 and is more orange-yellow than orange-brown. Accordingly, the name *Dichelobius relictus* (Chamberlin, 1920) is applied to Anopsobiinae sp. 2 of Mesibov (1986).

Attems' (1928:74) key to anopsobiine genera followed Chamberlin's (1920) in distinguishing *Dichelobius* and *Tasmanobius* based on the former having a 1-jointed tarsus 13 and the latter a 2-jointed tarsus 13. This distinction is inconsistent with the referral of *D. bicuspis*, which has a 2-jointed tarsus 13 (even *fide* Attems 1928:77). The supposed difference between these species seems to be nothing more than a terminological difference in what constitutes a "joint", since *D. flavens*, *D. bicuspis* and *D. relictus* are, upon direct comparison, identical with respect to the segmentation of leg 13. All have a distinct articulation on the tarsus of leg 13, though it is less flexed than is the articulation on leg 14.

Other ambiguities concerning Attems' description and illustrations of *Dichelobius flavens* have plagued previous interpretations of the genus, and exaggerated differences between *D. flavens* and other species. Interpretation of *D. flavens* is based on examination of syntypes from Lion Mill (WAM), Freemantle and Eradu (NMW), and large new collections from the southwest of Western Australia (AM, ANIC, WAM). *Dichelobius bicuspis* and *D. schwabei* were distinguished from *D. flavens* by the first two species having two coxal pores on legs 14 and 15 in the female, versus a single pore on each of the coxae in *D. flavens*. This cannot be upheld, since large females of *D. flavens* characteristically have two coxal pores on both legs 14 and 15. Attems' (1911:157, Fig. 10) described and figured a single spur on the female gonopod in *D. flavens*, which Ribaut (1923) and Verhoeff (1939) cited as a distinction from the pair of spurs in *D. bicuspis* and *D. schwabei*, respectively. Large specimens of *Dichelobius flavens* resemble congeners (and indeed all other Anopsobiinae) in having a pair of spurs. The specimen drawn by Attems, with a single spur and single coxal pore, is typical of immature stadia of all *Dichelobius* species (see Archey 1937:pl. 23, fig. 6, for a comparable stage in *Anopsobius neozelanicus*). Ribaut (1923:27) distinguished *D. bicuspis* by its plumose setae along the length of the inner margin of the distal article of the telopodite of the first maxilla versus only three plumose setae confined to the distal end of this article in *D. flavens* (Attems 1911:Fig. 3). Either Attems' drawing is erroneous or else the illustrated

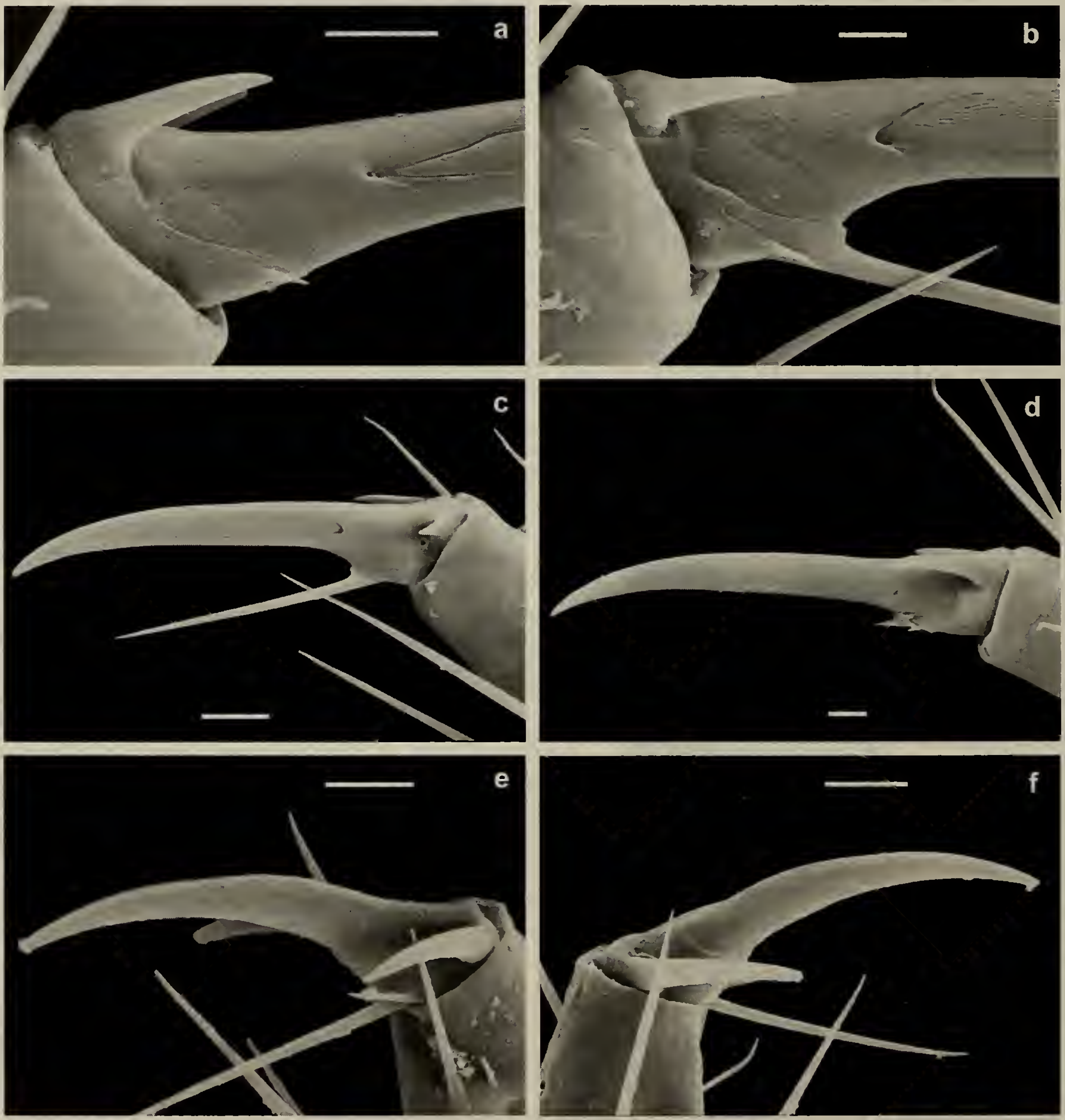

Figure 3. Pretarsal claws in Anopsobiinae. a, *Dichelobius relictus* (Chamberlin, 1920). Leg 14, posterior side. b, c, *Dichelobius flavens* Attems, 1911. Leg 14, posterior and anterior sides. d, *Anopsobius neozelanicus* Silvestri, 1909. Leg 14, posterior side. e, f, *Shikokuobius japonicus* (Murakami, 1967). Leg 13, posterior and anterior sides. Scales 10 µm except b, 5 µm.

specimen is anomalous, because *D. flavens* has plumose setae all along the inner margin of this article, the same as *D. bicuspis* (Ribaut 1923:Figs. 30, 31) and other congeners.

Certain characters of the pretarsus (claws) conflict with the monophyly of *Dichelobius* as grouped herein. *Dichelobius flavens* (Fig. 3b, c) and *D. bicuspis* differ from *D. giribeti* (Fig. 8b) and *D. relictus* (Fig. 3a) in having a long, needle-like spine (="sensory spur" of Eason 1964:Fig.486) originating ventrally on the posterior side of the main claw. In the latter two species, the posteroventral spine is short, and a short spine is shared by species of *Anopsobius*, such as *A. neozelanicus* Silvestri, 1909a (Fig. 3d) and *A. wrighti* (Edgecombe 2003:Figs.30, 31). The short spine appears to be apomorphic within the Gondwanan group of Anopsobiinae (i.e., a clade composed of *Anopsobius* + *Dichelobius*) because the Japanese anopsobiine *Shikokuobius japonicus* resembles *Dichelobius flavens* and *D. bicuspis* in possessing a greatly elongated posteroventral spine (Fig. 3e, f). The cladogram implied by this character, in which *D. giribeti* is more closely related to *Anopsobius* than to *D. flavens* (Fig. 2b), is retrieved under several parameter sets for combined morphological and molecular data (Fig. 2c). This cladogram would favour the assignment of *D. giribeti* to another genus. Should this topology find further support from additional data, *Tasmanobius* Chamberlin, 1920, could be rediagnosed to receive *D. giribeti*. A rediagnosed concept of that genus might emphasise the shared 14-15 antennal articles, short pretarsal posteroventral spine, absence of a distal spinose projection on the tibia of leg 12, and lack of spiracles on segments 5 and 8.

Key to *Dichelobius* species

1a. Dental margin of maxillipede coxosternite lacking median notch .... *schwabei* Verhoeff, 1939 [Chile]
1b. Dental margin of maxillipede coxosternite with median notch...... 2

2a. 14-15 (usually 15) antennal articles; pretarsus with short posteroventral spine, not more than one-eighth length of main claw (Fig. 8b)...... 3
2b. 17 antennal articles; pretarsus with needle-like posteroventral spine nearly as long as main claw (Fig. 3c)..... 4

3a. Spiracle absent on segment 14...... *giribeti* n. sp. [southeastern Australia, Lord Howe Island]
3b. Spiracle present on segment 14...... *relictus* Chamberlin, 1920 [Tasmania]

4a. Tibia of leg 12 with short, blunt distal projection...... *flavens* Attems, 1911 [Western Australia]
4b. Tibia of leg 12 with spinose distal projection...... *bicuspis* Ribaut, 1923 [New Caledonia]

Dichelobius giribeti n. sp.

Dichelobius sp. Edgecombe, 2004:Fig. 38A.
Dichelobius sp. ACT. Edgecombe and Giribet, 2003:Figs. 1-3.

Etymology

For Gonzalo Giribet, my collaborator in henicopid phylogeny, who sequenced DNA from this species.

Diagnosis

Dichelobius usually with 15 antennal articles; head pale orange, tergites orange-yellow; four to six (most commonly five) teeth on each dental margin of maxillipede; spiracle lacking on segment 14; two coxal pores on legs 14 and 15 in females, one or two pores on both legs in males; short posteroventral spine on pretarsus.

Type material

Holotype: AM KS 82628, female (Fig. 4b), Badja SF, NSW, Peters Rd, 36°08'52"S 149°32'09"E, J. Tarnawski and S. Lassau, 13.iii.1999; length of body 5.1 mm. Paratypes, all from type locality, same collection: AM KS 82629, male (Fig. 4c), KS 82630, male (Fig. 5b-e), KS 82631, female (Figs. 6a-g, 7a, b, d, h, j-l, 8k), KS 82632, female (Fig. 8i, j, n), KS 82633, male (Fig. 8l), KS 82634, 10 females, 1 male.

Other material

NSW: AM KS 82635, Kanangra-Boyd NP, Empress Fire Trail turnoff, 33°59'S 150°08'E, M. Gray, G. Hunt and J. McDougall, 27.iii.1976, *Eucalyptus pauciflora*; AM KS 82636, female (Figs 4a, 5a), KS 82637, female (Fig. 8b, e), KS 82638, male (Fig. 6i, j), Monga SF, NSW, Link Rd, 35°34'04"S 149°54'14"E, R. Harris and H. Smith, 16.iii.1999; AM KS 82639, Buckenbowra SF, Macquarie Rd, 70 m S from junction with Milo Rd, 35°38'15"S 149°53'27"E, 1020 m, L. Wilkie and R. Harris, 16.iii.1999; AM KS 82640, Tallaganda SF, South Forest Way, 35°42'50"S 149°32'20"E, J. Tarnawski and S. Lassau, 15.iii.1999; AM KS 82641, Dampier SF, Coomerang Rd, 36°04'01"S 149°54'57"E, R. Harris and H. Smith, 11.iii.1999; AM KS 82642, Badja SF, Wiola Ck Fire Trail, 36°05.56'S 149°35.09'E, J. Tarnawski and S. Lassau, 13.iii.1999; AM KS 82643, Badja SF, Burkes

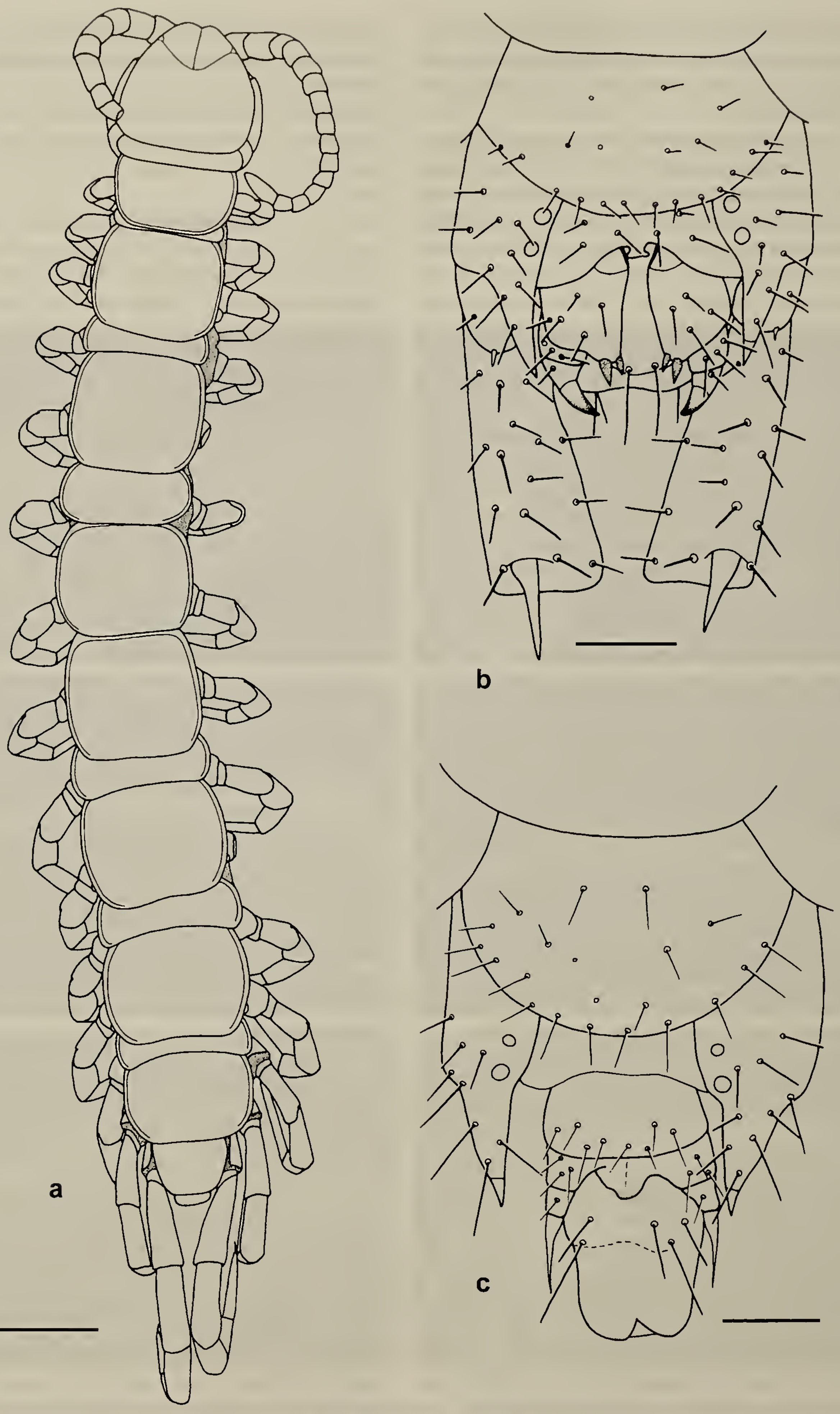

Figure 4. a-c, *Dichelobius giribeti* n. sp. a, AM KS 82636, female, Monga SF, NSW. b, holotype AM KS 82628, female, Badja SF, NSW, terminal segments and gonopods; c, AM KS 82629, male, Badja SF, NSW, terminal segments and gonopods. All scales 100 µm.

Rd, 36°10’33"S 149°31’58"E, J. Tarnawski and S. Lassau, 13.iii.1999; AM KS 82644, Badja SF, Burkes Rd, approx. 1.3 km E from junction with Peters Rd, 36°10.55’S 149°31.97’E, 992 m, J. Tarnawski and S. Lassau, 13.iii.1999; AM KS 82645, Bodalla SF, 300 m along Reservoir Link Rd from junction with Big Rock Rd, 36°07.25’S 150°2.82’E, 121 m, L. Wilkie and R. Harris, 09.iii.1999; AM KS 82646, Bodalla SF, Orange Ridge Rd, 36°16’55"S 149°53’31"E, R. Harris and H. Smith, 12.iii.1999; AM KS 82647, Wadbilliga NP, 9.6 km N on Bumberry Ck Fire Trail, 36°14.33’S 149°33.60’E, 1059 m, L. Wilkie and R. Harris, 13.iii.1999.

ANIC (ex. Berl. 855), Kanangra-Boyd NP, W Morong Creek, 33°58’S 150°04’E, 1200 m, L. Hill, 03.x.1982; ANIC (ex. Berl. 829), Kanangra-Boyd NP, Kanangra Brook and Rocky Spur, 34°00’S 150°06’E, L. Hill, 20.iii.1982, closed forest; ANIC (ex. Berl. 852) Twin Falls, 14 km SE Moss Vale, 34°39’S 150°28’E, 600 m, L. Hill, 11.vii.1982; ANIC (ex. Berl. 663), Pigeon House Range via Nerriga, 35°02’S 150°08’E, J.C. Cardale, 22.xi.1979; ANIC (ex. Berls 2, 18, 34, 78A, 206A, 222, 246, 468, 657, 851), Clyde Mt, 35°33’S 149°57’E, 500-c. 800 m, various collections 1966-1982, dry sclerophyll, wet sclerophyll, rf; ANIC (ex. Berl. 877), 2 km N Monga, 35°34’S 149°56’E, M.S. Harvey, 18.ix.1983, wet sclerophyll; ANIC (ex. Berl. 594), Monga, 35°35’S 149°55’E, JFL and T. Weir, 10.iii.1978, wet sclerophyll; ANIC (ex. Berl. 739), Tallaganda SF, 7 km ENE Captains Flat, 35°34’S 149°31’E, W. Allen, 29.viii.1981; ANIC (ex. Berl. 1069), Kioloa SF, 35°35’S 150°18’E, JFL and N. Lawrence, 4-5.iii.1986; ANIC (ex. Berl. 927), Milo Forest Preserve, 1.6 km S Monga, 35°36’S 149°55’E, L. Hill, 25.xii.1983; ANIC (ex. Berl. 218), 8.8 km ESE Captains Flat, 35°38’S 149°31’E, 940 m, RWT, 10.i.1970, dry sclerophyll; ANIC (ex. Berl. 891), Rosedale, 35°49’S 150°14’E, R.J. Moran, 20.xi.1983, eucalypt litter; ANIC (ex. Berl. 933), Kosciusko NP, 1 km ENE Mt Sunrise, 36°22’S 148°29’E, L. Hill, 4.ii.1984; ANIC (ex. Berl. 935), Kosciusko NP, 4 km NNE Mt Perisher, 36°22’S 148°29’E, L. Hill, 4.ii.1984; ANIC (ex. Berl. 10), Brown Mt, 36°36’S 149°23’E, c. 3000 ft., RWT, 5.i.1967, wet sclerophyll; ANIC (ex. Berl. 20), Brown Mt, c. 2800 ft., RWT and R.J. Bartell, 30.iii.1967, rf; ANIC (ex. Berl. 24), Brown Mt, 2500-3000 ft., RWT and R.J. Bartell, 11.iv.1967; ANIC (ex. Berl. 41), Brown Mt, Rutherford Creek, 2700 ft., RWT and RJB, 9.xii.1967, rf; ANIC (ex. Berl. 42), Brown Mt, c. 3000 ft., RWT and RJB, 9.xii.1967, rf.

ACT: ANIC (ex. Berl. 283), Black Mt, eastern slope, 35°16’S 149°06’E 750 m, J. Simmons, 26.v.1970, dry sclerophyll; ANIC (ex. Berl. 228), Uriarra to Piccadilly Circus, 35°19’S 148°51’E, 700 m, RWT, 27.i.1970, dry sclerophyll; ANIC (ex. Berl. 225), Uriarra to Piccadilly Circus, 35°20’S 148°50’E, 500 m, RWT, 16.i.1970, wet sclerophyll; ANIC (ex. Berl. 231), Uriarra to Piccadilly Circus, 35°20’S 148°50’E, 1000 m, RWT, 16.i.1970, wet sclerophyll; ANIC (ex. Berl. 999), Wombat Creek, 6 km NE Piccadilly Circus, 35°19’S 148°51’E, 750 m, JFL, T. Weir and M.-L. Johnson, 30.vi.1984, open forest; ANIC (ex. Berl. 1001), Piccadilly Circus, 35°22’S 148°48’E, 1240 m, JFL, T. Weir and M.-L. Johnson, 30.vi.1984, subalpine eucalypt litter; ANIC (ex. Berl. 1000), Blundells Creek, 3 km E Piccadilly Circus, 35°22’S 148°50’E, 850 m, JFL, T. Weir and M.-L. Johnson, 30.vi.1984, open forest; ANIC (ex. Berl. 821), Brindabella Range, Franklin Rd, N end Moonlight Hollow, 2 km SW Bulls Head, 35°24’S 148°48’E, M.S. Harvey and R.J. Moran, 3.iv.1983; ANIC (ex. Berl. 926), Ginini Flat, 2 km NE Mt Ginini, 35°31’S 148°46’E, 1580 m, L. Hill, 20.viii.1983; ANIC (ex. Berl. 659), Mt Ginini, 35°32’S 148°46’E, 1660 m, JFL and T. Weir, 16.x.1979; ANIC (ex. Berl. 1068), 1 km S Mt Ginini, 35°33’S 148°46’E, JFL, 11.xi.1986; ANIC (ex. Berl. 704, 705), 1 km N Mt Gingera, 35°33’S 148°47’E, A.A. Calder, 18.ii.1981; ANIC (ex. Berl. 26), Mt Gingera, 35°34’S 148°47’E, c. 5500 ft., E.B. Britton, 13.iv.1967, wet sclerophyll; ANIC (ex. Berl. 50), Mt Gingera, summit, E.B. Britton and Misco, 19.vii.1967; ANIC (ex. Berl. 661), Mt Gingera, E.C. Zimmerman, 20.xi.1979; ANIC (ex. Berl. 830, 831), Mt Gingera, 1620-1700 m, L. Hill, 6.iii.1982; ANIC (ex. Berl. 1084), Snowy Flat Creek, 0.5 km NE Mt Gingera, 35°35’S 148°47’E, A.A. Calder, 28.vi.1988.

VIC: ANIC (ex. Berl. 1045), Cobb Hill, 14 km SE Bonang, Goonmirk Ra, 37°18’S 148°50’E, JFL and N. Lawrence, 24.xi.1985.

LORD HOWE ISLAND: AM KS 35592, NE area of Mt Gower summit, moss forest near campsite, 31°35.2’S 159°04.7’E, 855 m, M.R. Gray, 12-15.ii.1971; AM KS 35589, creek crossing above Boat Harbour, 31°33.5’"S 159°05.5’E, 60 m, M.R. Gray, 8.ii.1971; AM KS 82998, female (Figs. 6h, 8a, d, f, g), KS 82999, male (Figs. 6k, l, o, 7g, m, 8c, h, m), KS 83000, male (Figs. 6m, n, 7c, e, f, i), west end of Mt Gower summit on south edge, 31°35.32’S 159°04.2’E, I. Hutton, 15.v.2001; AM KS 84206-84233, additional localities/samples on Mt Gower, AM KS 84234-84237, four localities on Mt Lidgbird, I. Hutton and CBCR, 2000-2002; AM KS 84238, North Hummock, trail to Intermediate Hill, 31°32’54"S 159°04’58"E, CBCR, 3.xii.2000, mixed rf; AM KS 84239, western slope of Malabar Ridge, 31°30’57"S 159°03’31"E, CBCR, 24.xi.2000, broad megaphyllous closed sclerophyll forest; AM KS 84240, Transit Hill, 31°32’01"S 159°04’40"E, I. Hutton, 14.iv.2002; AM KS 84241, Little Island, below Far Flats, 31°34’08"S 159°04’32"E, I. Hutton, 10.viii.2001, under *Ficus* *columnaris*.

Description

Length (anterior margin of head shield to telson) up to 6.6 mm; length of head shield up to 0.7 mm; leg 15 33-40% length of body. Colour: head shield and maxillipede pale orange; antenna and most tergites orange-yellow, T14 and tergite of intermediate segment deeper orange; legs 1-13 pale yellow to pale orange, legs 14 and 15 may be deeper orange.

Head shield (Fig. 5a) smooth, of equal length and width, slightly wider than T1, median notch contributing to biconvex anterior margin; longitudinal median furrow incised to transverse suture, about one-third length of head shield; posterior two-thirds of region distal to antennocellar suture desclerotised; setae on head shield arranged with bilateral symmetry, four larger pairs anterior to antennocellar suture, ten pairs behind suture, including four evenly spaced submarginal pairs; head shield lacking posterior and lateral borders.

Antenna 27-32% length of body, 2.5-3.3 times length of head shield, composed of 14 or (usually) 15 articles; basal two articles enlarged, most articles in distal half moniliform, sclerotised part generally of subequal length and width; ultimate article about twice length of penultimate. Basal article bearing about a dozen sensilla microtrichoidea proximally on dorsal side (Fig. 6a). Trichoid sensilla arranged in three whorls per article; one or occasionally two curved,

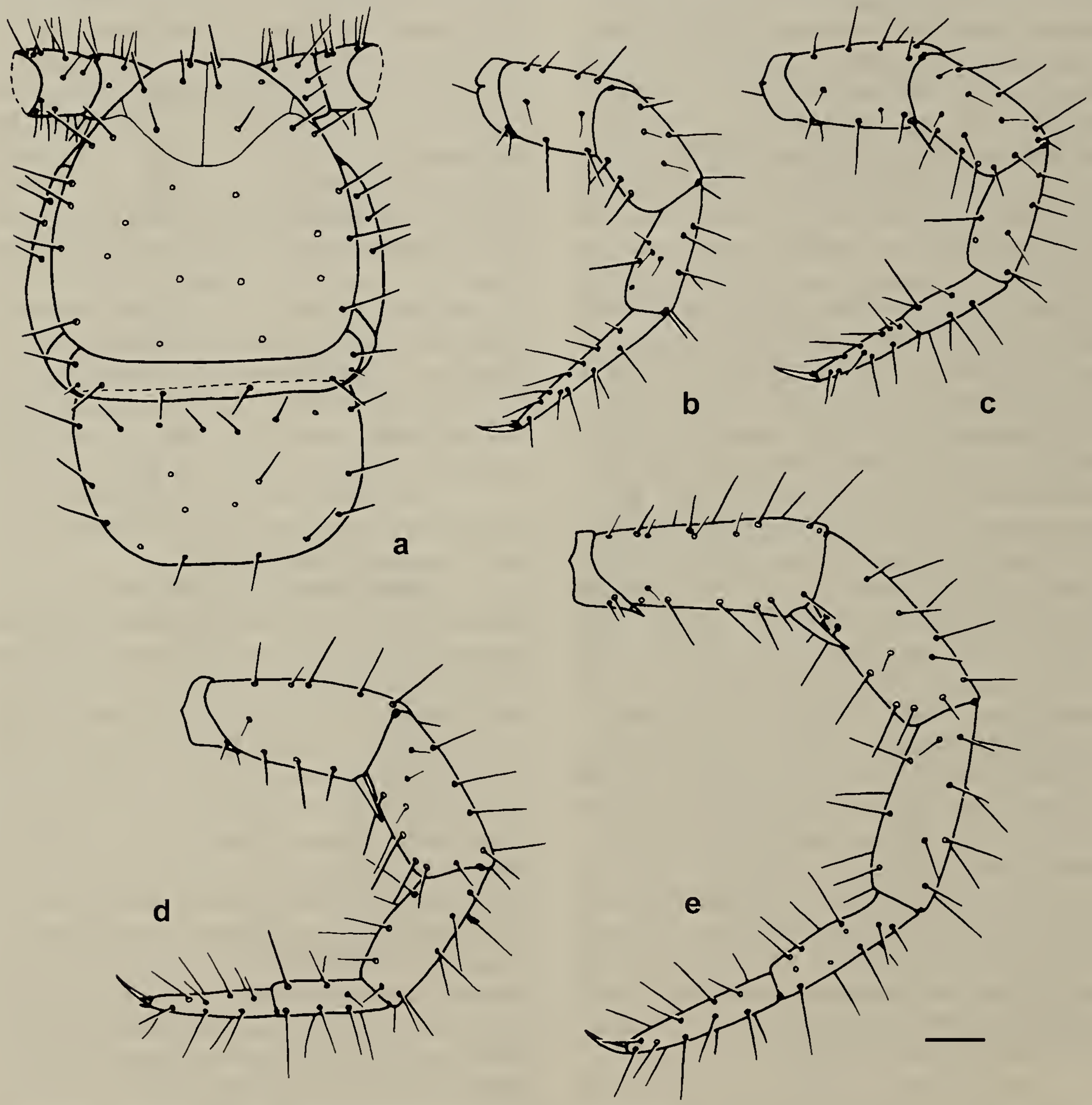

Figure 5. a-e, *Dichelobius giribeti* n. sp. a, AM KS 82636, female, Monga SF, NSW, head shield, maxillipede segment and T1; b-e, AM KS 82630, male, legs 12-15, Badja SF, NSW. All scales 100 µm.

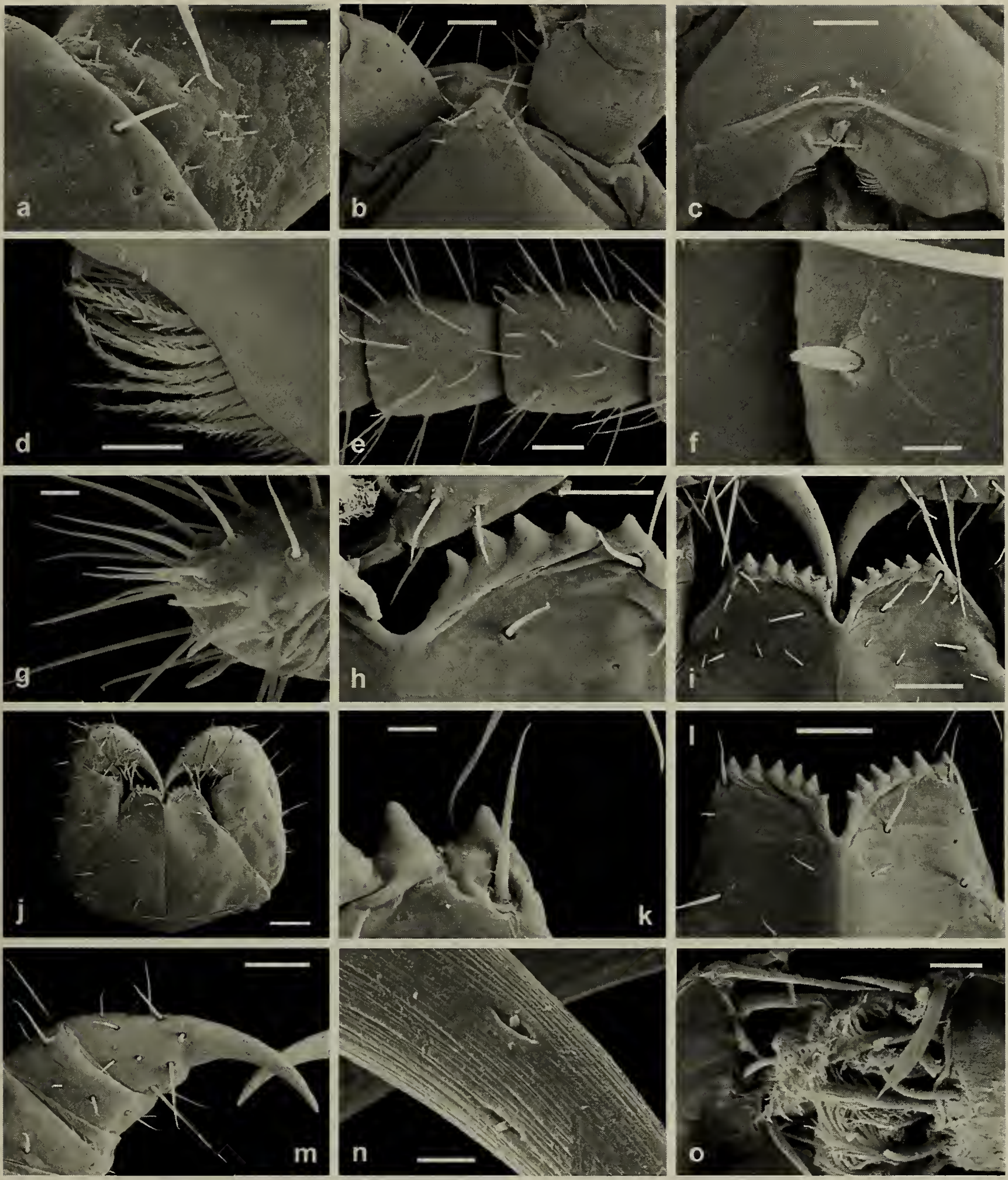

Figure 6. ***Dichelobius giribeti*** **n. sp. Scanning electron micrographs. a-g, Badja SF, NSW; h, k-o, Mt Gower, Lord Howe Island; i, j, Monga SF, NSW. a-g, AM KS 82631, female. a, cluster of sensilla microtrichoidea on proximal part of antenna, dorsal side, scale 10 µm; b, clypeus, scale 50 µm; c, posterior part of clypeus and labrum, scale 50 µm; d, labral margin, scale 10 µm; e, antennal articles 10-13, dorsal side, scale 30 µm; f, basiconic sensillum at anterior edge of antennal article 12, dorsal side, scale 5 µm; g, tip of terminal antennal article, scale 10 µm. h, AM KS 82998, female, dental margin of maxillipede, scales 100 µm, 30 µm. i, j, AM KS 82638, male, dental margin and ventral view of maxillipede, scales 50 µm, 100 µm. k, l, o, AM KS 82999, male. k, porodont, scale 10 µm. l, dental margin of maxillipede, scale 50 µm. o, anterior angle of telopodite of first maxilla, scale 10 µm. m, n, AM KS 83000, male, telopodite of maxillipede and detail of tarsungulum, showing sensilla coeloconica, scales 50 µm, 5 µm.**

digitiform sensilla near anterior edge on dorsomedial side of a few, variable antennal articles (Fig. 6e); four or five articles with a single, short, fusiform sensillum at anterior edge on dorsal side (Fig. 6f), most consistent on articles 11, 12 and 14; digitiform and fusiform sensilla sometimes cooccur on a single article (article 7 or 9); ultimate article with cluster of 8 or 9 trichoid sensilla at apex, one or two curved, digitiform sensilla behind apical cluster (Fig. 6g).

Clypeus with apical cluster of three setae on ventral side near lateral margin, single seta medially (Fig. 6b); transverse band of four setae in front of labrum, outer pair slightly to distinctly smaller than inner (Fig. 6c); transverse seta projecting from sidepiece; labral margin moderately concave where cluster of 7-13 bristles projects; bristles with numerous short, spine-like projections along lateral margins and on ventral surface along their lengths (Fig. 6d). Tömösváry organ large, longitudinally ovate, outer edge at lateral margin of cephalic pleurite (Fig. 8k).

Maxillipede (Figs 6h-n): coxosternal width across dental margin 39-44% maximum width; lateral margin flexed inward at base of dental projections and less convergent than against posterior part; each dental margin convex, usually with 5+5, 4+5 or 5+4 teeth, sometimes 4+4, 6+5, 5+6 or 6+6; inner tooth smaller than others, its apex well posterior to base of outer tooth; median notch varying from broadly V-shaped (Fig. 6h) to deeply parabolic (Fig. 6l); porodont of similar length and thickness to largest coxosternal setae, its socket at posterolateral edge of outermost tooth (Fig. 6k); setae relatively sparsely, fairly evenly scattered on coxosternite; tarsal and pretarsal parts of tarsungulum of about equal length (Fig. 6m). Dorsal and ventral sides of tarsungulum with several sensilla coeloconica (Fig. 6n). Bands of pleural collar separated by longitudinal median suture (Fig. 6j).

Mandible: Six curved aciculae (Fig. 7j), all with many (up to 18) short, blunt denticles along both margins (Fig. 7i) on distal half to two-thirds. Four paired teeth, dorsal three with accessory denticle field delimited by deep groove; dorsalmost tooth and basal part of second and third teeth composed of densely tuberculate rhomboid and polygonal scales (Fig. 7l), becoming denticulate near furry pad (Fig. 7m). Fringe of branching bristles terminates against dorsalmost acicula (Fig. 7f); ventralmost bristles in fringe with flattened bases lacking spines, distal two-thirds with short spines along both margins and on outer face; bristles multifurcating at their distal tips, with three or four spines that are longer and thicker than those more proximally (Figs 7f, k); more dorsal bristles gradually become more uniformly spinose to their broader bases, with more numerous distal spines (Fig. 7k), grading into wide scales that form a nearly continuous double-fringe of hair-like spines, each scale composed of a narrow outer fringe and a wider inner fringe, each with 12-15 spines per scale (Fig. 7l); fringe terminates at edge of dorsalmost tooth, against a large, smooth scale that separates dentate lamina from furry pad (Fig. 7m). Furry pad composed of a few scales with distal spines and cluster of six or seven mostly simple, elongate spines.

First maxilla: sternite indistinctly delimited from coxa (Fig. 7a), short, wide. Coxal projections tapering, with rounded apex bearing four or five simple setae; one small seta along inner margin near base of coxal projection. Telopodite strongly delimited from coxal projection; basal article of telopodite with single marginal seta anterolaterally or lacking setae; distal article with one or two setae near outer margin, anterior angle terminating as a long, stout spine; entire inner margin fringed with row of six or seven plumose setae (Fig. 7b), paired in posterior part of row, with slender branchings along more than half of their length (Fig. 7c); five shorter simple setae inserting near bases of plumose setae on ventral side; anterior plumose setae fringed on dorsal side by a few elongate spines.

Second maxilla: anterior margin of coxa gently concave; band of four or five small setae across anterior part of coxa. Inner edge of tarsus with a row of five or six brush-like setae with abundant, slender branchings nearly to their bases (Fig. 7d, h). Claw composed of up to five digits with concave, scoop-like inner surfaces (Fig. 7g); large, curved medial digit with furrows or sutures running along its length (Fig. 7e); outer digits shorter, separated from medial digit by a slender, spine-like digit.

Tergites smooth, all with rounded posterior angles, lacking projections; T1 about 85% width of widest tergite (TT10 or 12). Posterior margins of TT1, 3, 5 and 7 transverse (Fig. 4a); TT8, 10 and 12 gently concave; TT9, 11, 13 and 14 transverse to weakly concave; tergite of intermediate segment transverse or gently concave, posterior angle rounded. Two or three moderately long setae on lateral margins of long tergites, usually with short setae between these; posterior margins of tergites fringed with four to twelve setae, generally more abundant on more posterior segments (maximal number typically on T13); setae on inner part of long tergites include transverse band of up to six setae across anterior third, two or three pairs in two bands behind this.

Legs 12-15 (Fig. 5b-e) with length ratios 1: 1.1 : 1.3-1.4 : 1.7. Leg 15 basitarsus 85-115% length of distitarsus (Fig. 5e); basitarsus 70-75% length of tibia; tibia 2.9-3.4 times longer than maximal width, basitarsus 3.4-4 times, distitarsus 5.2-5.7 times.

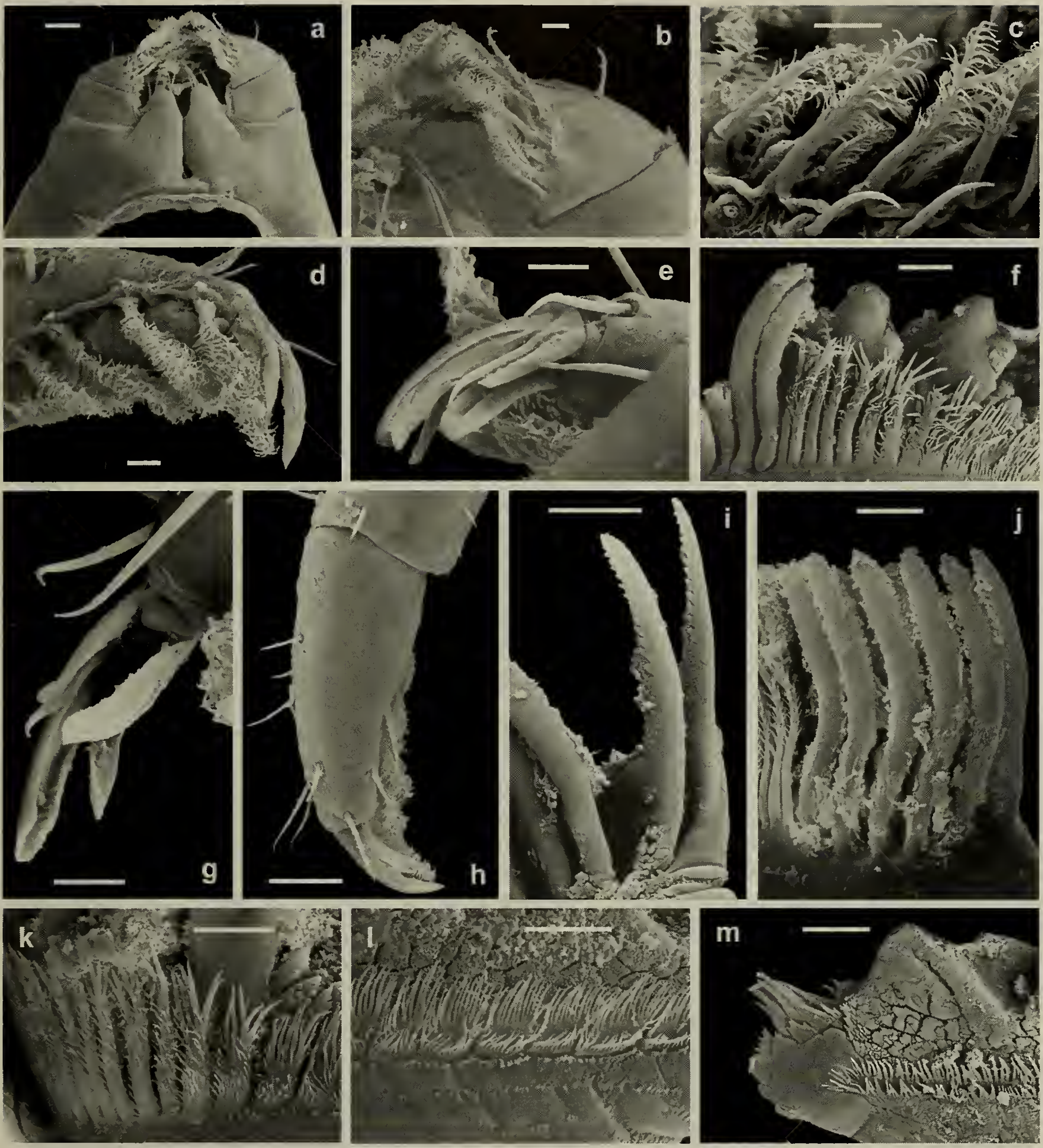

Figure 7. ***Dichelobius giribeti*** **n. sp. Scanning electron micrographs. Scales 10 μm except where indicated. a, b, d, h, j-l, AM KS 82631, female, Badja SF, NSW; c, e-g, i, m, Mt Gower, Lord Howe Island. a, ventral view of first maxillae, scale 50 μm; b, distal article of telopodite of first maxilla; d, h, tarsus and claw of second maxilla, scales 10 μm, 30 μm; j, aciculae; k, l, ventral and dorsal parts of fringe of branching bristles on mandible. c, e, f, i, AM KS 83000, male. c, plumose setae on inner margin of telopodite of first maxilla; e, claw of second maxilla; f, aciculae and fringe of branching bristles on mandible; i, aciculae. g, m, AM KS 82999, male. g, claw of second maxilla, scale 10 μm; m, dorsalmost tooth of mandible and furry pad.**

Basitarsus 90% length of distitarsus on leg 14 (Fig. 5d). Coxal projections on leg 15 tapering (in ventral view) at about 25-30 degrees; terminal spine with distinct (Fig. 8e) or indistinct (Fig. 8i) basal joint, its surface with fine longitudinal grooves and ridges like those on pretarsal claws. Trochanter of leg 15 with small ventrodistal spur (Figs 5e, 8h). Prefemur of legs 14 and 15 with large ventrodistal spur; leg 15 spur with basal width about 25% maximum width of prefemur (Fig. 4b). Sharp distal spinose projections on tibiae of legs 1-11, absent on legs 12-15. Two tarsomeres of leg 13 defined by distinct constriction in width and weak articulation without flexure; articulation between tarsomeres stronger on leg 14. Setae fairly evenly distributed on all podomeres along leg, tarsal setae only slightly more slender than those on prefemur-tibia; proximo-distal gradient in setal thickness enhanced on legs 14 and, especially, 15, with distinctly thickened prefemoral setae, including on dorsal side of leg. Anterior and posterior accessory claws present on all legs, 25-40% length of main claw (Fig. 8a, b); accessory claws with closely-spaced linear ridges on their surface except for pitted proximoventral part separated by a shallow suture (Fig. 8c). Main claw curved, subdivided by sutures; deepest sutures define an elongate scute on both lateral sides of claw, proximal end of this scute at about distal end of shorter accessory claw; large pore or pair of pores at proximal end of scute on both sides of leg (Fig. 8c); strong suture extends from lateral pore across ventral surface of main claw (Fig. 8d), defining proximal end of an elongate, triangular ventral scute (Fig. 8g). Proximal part of main claw densely pitted; on ventral side of claw, ornament changes abruptly at suture delimiting lateral scute, becoming linear grooves and ridges as on accessory claws (Fig. 8d), with these lineations well developed on lateral scute and along length of claw on dorsal side; change from pitted to linear ornament gradual on dorsal side of claw, with pits irregular proximally, becoming aligned as rows of pits, then linear grooves. Pair of distally-directed spines proximoventrally, at distal end of a curved suture (Fig. 8d); larger spine not more than not more than one-eighth length of main claw, with tiny subsidiary spine at its base (Fig. 8b).

Coxal pores: on legs 14 and 15; 2,2/2,2 in females (Fig. 4b), 1,1/1,1 in small males, either 1,1/1,1 or 2,2/2,2 (Fig. 4c) in large males, occasionally one and two pores on opposing sides of either leg or 1,2/1,2; pores round, separated by less than their diameter when paired; inner pore often smaller than outer pore in male, inner pore sometimes larger than outer pore in female.

Female (Fig. 4b): Sternite of segment 15 gently convex posteromedially, fringed by a submarginal setal band that extends along entire posterolateral and posterior margin; several setae scattered on inner part of sternite. Posterior margin of first genital sternite moderately embayed between gonopod articulations, sternite bearing 6-11 setae. Gonopod with pair of spurs at terminus of a short (Fig. 8n) to moderately long (Fig. 8e, f) projection; bases of spurs nearly touching each other; inner spur substantially shorter and narrower than outer spur, both bullet-shaped, pointed (Fig. 8n); four or five setae on basal article of gonopod, three large setae on second article, one large seta on third (Fig. 8j); second and third articles variably with one and two smaller setae, respectively, on ventromedial face (Fig. 8n); claw simple.

Male (Fig. 4c): Posterior margin of sternite 15 evenly convex; 10-13 setae fringing margin of sternite, 10-12 additional setae scattered over its ventral surface; first genital sternite entire medially, bearing 6-12 setae aligned in two imprecisely-defined transverse rows; gonopod bearing two or three setae on first article, two on second article, none or one on third article, which grades into long, flagelliform terminal process, up to 80% length of rest of gonopod (Fig. 8l); terminal process bearing numerous slender spines proximally (Fig. 8m).

Larvae: five larval stadia (ANIC Berl. 18 and 231) identified as L0-LIV by comparison to limb development in other Lithobiomorpha (Table 1). LI with 11 antennal articles; LII-LIV all with 14 articles. LII and LIII with 2+2 teeth on dental margin of maxillipede; LIV with 3+3 teeth.

Discussion

Specimens from Lord Howe Island resemble those from the Australian mainland in all meristic characters and in fine detail. Intrapopulation variation is observed with respect to the number of teeth on the maxillipede coxosternal margin, the depth of the median notch in the maxillipede coxosternite (relatively shallow in Fig. 6h, relatively deep in Fig. 6l), the concavity of the posterior margins of the short tergites, and the length of the spur-bearing process on the female gonopod. Samples vary in the frequency with which large males have either one or two coxal pores on legs 14 and 15 (usually two in Lord Howe specimens versus one in the large sample from Clyde Mountain, NSW, but also two in large specimens from the type locality and in the Brindabella Range, e.g., Piccadilly Circus, Mt Gingera and Mt Ginini).

Distinction from other congeners is indicated in key above. *Dichelobius relictus* and *D. giribeti* are consistently distinguished by the presence of a spiracle on segment 14 in the former, and *D. relictus* is generally a deeper brown colour. The two species share minute details of mandibular and maxillary structure, indeed to the extent that description of the mouthparts for *D. giribeti* serves for *D. relictus* as well.

The early larval stadia of *Dichelobius giribeti* differ in detail from those of Lithobiidae and Henicopinae (see Table 1) with respect to limb development. Segmentation of L0 is matched by

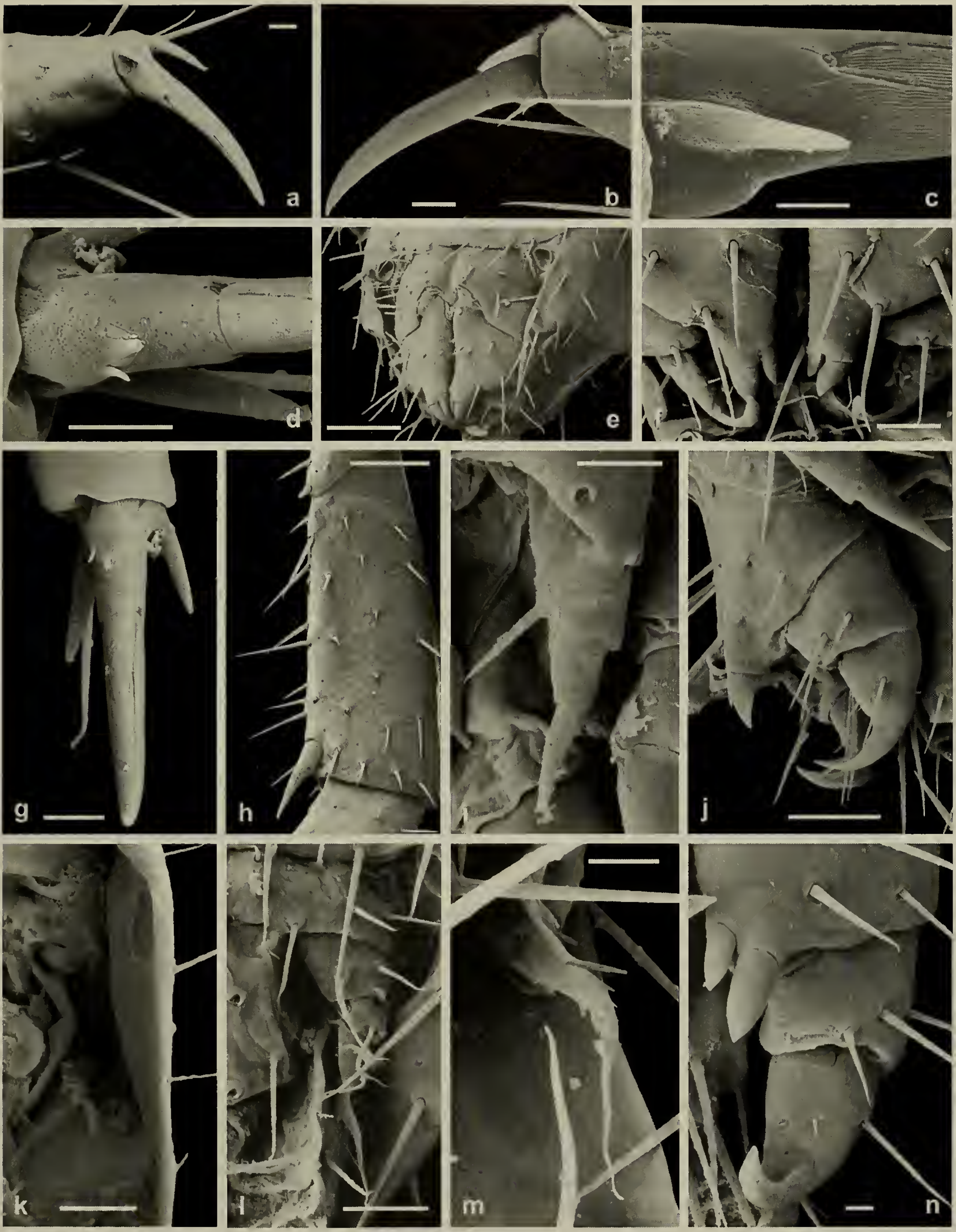

Figure 8. *Dichelobius giribeti* n. sp. Scanning electron micrographs. a, c, d, f-h, m, Mt Gower, Lord Howe Island; b, e, Monga SF, NSW; i-l, n, Badja SF, NSW. a, d, f, g, AM KS 82998, female. a, pretarsus of leg 14, scale 10 μm. d, g, ventral views of pretarsus of leg 14, scales 10 μm; f, gonopods, scale 30 μm. b, e, AM KS 82637, female. b, pretarsus of leg 14, posterior view, scale 10 μm; e, ventrolateral view of first genital sternite and gonopods, scale 100 μm. c, h, m, AM KS 82999, male. c, pretarsus of leg 15, detail of anterior accessory claw, scale 5 μm; h, prefemur of leg 15, anterior side, scale 100 μm; m, terminal process on gonopod, scale 10 μm. i, j, n, AM KS 82632, female. i, leg 15 coxal process, scale 30 μm; j, n, lateral and ventral views of gonopod, scales 50 μm, 10 μm. k, AM KS 82631, female, cephalic pleurite with Tömösváry organ, scale 50 μm. l, AM KS 82633, male, gonopod, scale 30 μm.

Table 1. Comparison of limb development in larval stadia of Lithobiomorpha. Modified from Andersson (1979:Table II), adding data for *Dichelobius giribeti*.

	Lamyctes emarginatus Lithobius 8 spp.			*Lamyctes coeculus*			*Dichelobius giribeti*		
	Pairs of			Pairs of			Pairs of		
Stadium	Legs	half-developed legs	Limb-buds	Legs	half-developed legs	Limb-buds	Legs	half-developed legs	Limb-buds
LO	7	——	1 large	6	——	2 large	6	——	2 large
LI	7	1	2 small	6	2	——	6	2	2
LII	8	——	2	8	——	2	8	——	2
LIII	10	——	2	10	——	2	10	——	2
LIV	12	——	3	12	——	3	12	——	3

Lamyctes coeculus, but larval stadium LI has a unique combination of half-developed legs and limb-buds in *D. giribeti*. Segmentation of stadia LII-IV is as in other lithobiomorphs. Four larval stadia identified by Eason (1993) for *Anopsobius macfaydeni* have seven, eight, ten and twelve pairs of legs, the last three obviously being LII-LIV. The taxonomic significance of the distinction between six- and seven-legged first larval stages in *Dichelobius giribeti* and *Anopsobius macfaydeni* is unclear without additional data for Anopsobiinae.

Dichelobius bicuspis Ribaut, 1923

Dichelobius bicuspis Ribaut, 1923:24, Figs. 27-34.
Dichelobius bicuspis: Würmli, 1974:526.

Material

NEW CALEDONIA: PROV. NORD: AM KS 83001, 1 female, 1 male, Mt Panié, nr summit, 20°34'S 164°46'E, 1500 m, C. Burwell, 9.xi.2001, rf; MNHN, 1 female, 1 larval stadium LIV, Mt Panié, 20°34'53"S 164°45'38"E, 1350 m, J. Chazeau, A. & S. Tillier, 18.xi.1986, wet *Agathis* forest; QM S60653, 1 female, Pic d'Amoa, N slopes, 20°58'S 165°17'E, 500 m, GBM, 10.xi.2001, rf; QM S60654, 1 male, Me Maoya, summit plateau, 21°12'S 165°20'E, 1400 m, GBM, 12.xi.2002, rf. PROV. SUD: MNHN, 3 females, Mt Do, 21°45'37"S 165°59'33"E, 840 m, A. & S. Tillier & Monniot, 2.iv.1987, wet *Araucaria* forest; QM S60655, 1 male, Mt Humboldt refuge, 21°53'S 166°24'E, 1300 m, GBM, 7-8.xi.2002, rf; AM KS 83002, 1 male, R Bleue, Pourina Track, 22°04'S 166°38'E, 900 m, GBM, 18.xi.2001, rf; AM KS 83003, 1 male, Mt Ouin, 22°01'S 166°28'E, 1100 m, GBM, 9.xi.2002, rf; AM KS 83004, 1 female, 1 male, QM S60656, 1 male, Mt Mou base, 22°05'S 166°22'E, 200 m, GBM, 30.x.2001, 15.xi.2001, rf; MNHN, 3 females, 1 juvenile, Rivière Bleue, 22°06'13"S 166°39'16"E, 160 m, A. & S. Tillier, 1.viii.1986-30.iv.1987; QM S60657, 1 male, Mt Koghis, 22°11'S 166°01'E, 750 m, GBM, 29.xi.2000, rf; AM KS 83005, 1 female, Yahoué, 22°12'S 166°30'E, 100 m, GBM, 4.xi.2001, rf.

Remarks

Dichelobius bicuspis was based on a few specimens from Mt Humboldt (the type locality) and Mt Canala, New Caledonia, with Würmli (1974) adding a record at Nékliai. New collections are listed above to indicate that the species has a more widespread distribution.

ACKNOWLEDGEMENTS

I thank Suzanne Bullock (Scientific Interface) and Sue Lindsay and Yongyi Zhen (Australian Museum) for assistance with illustrations and electron microscopy, and the referees for useful suggestions. Geoff Monteith (Queensland Museum) and Jean-Paul Mauriès (Museum National d'Histoire Naturelle, Paris) kindly provided material from New Caledonia. Collection study was hosted and loans were arranged by Matthew Colloff (Australian National Insect Collection), Gonzalo Giribet and Laura Leibensperger (Harvard University), and Mark Harvey and Julianne Waldock (Western Australian Museum). Verena Stagl (Naturhistorisches Museum Wien) is thanked for arranging loan of C. Attems' types.

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A Survey of Ectoparasite Species on Small Mammals During Autumn and Winter at Anglesea, Victoria

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A survey of the ectoparasites of small native mammals was carried out between April and August 2002, in heathlands surrounding Anglesea, Victoria. *Antechinus minimus*, *A. agilis*, *Rattus lutreolus*, *R. fuscipes*, *Sminthopsis leucopus* and *Isoodon obesulus* were the dominant host mammal species examined. A total of 921 ectoparasites were collected and identified as five flea species, seven mite species and two species of tick. *Isoodon obesulus* was found to have the highest ectoparasite species richness, with eleven of the fourteen species present; while *S. leucopus* displayed the lowest ectoparasite species richness with only three species found on the hosts examined. The flea *Pygiopsylla hoplia* was the only ectoparasite species in this study to have a distribution across all host mammal species. A new distribution record was made for a *Haemaphysalis* tick species.

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KEYWORDS: Anglesea, ectoparasites, host specificity, marsupials, rodents, species richness.

INTRODUCTION

The main groups of ectoparasitic arthropods encountered on Australian mammals include fleas (order Siphonaptera), mites (order Acariformes), ticks (order Parasitiformes) and lice (order Phthiraptera). These ectoparasites, as a group, have evolved specialised piercing and sucking mouthparts, designed for the extraction of blood from a host, with the degree of host specificity displayed by ectoparasites varying amongst species (Kemp et al. 1982; Dunnet and Mardon 1991).

Many species of ectoparasites are of considerable medical and veterinary importance. Fleas are capable of transmitting various rickettsial, filarial and protozoan diseases (Dunnet and Mardon 1991), and ticks can transmit pathogenic filariae, bacteria, protozoa, rickettsiae and viruses to wild and domestic animals and humans (Obenchain and Galun 1982; Aeschlimann 1991). Previous research on ectoparasites in the Anglesea region has been limited to flea surveys as a precursor to the introduction of myxomatosis (Dunnet and Mardon 1991) and calicivirus (F. Bartholomaeus pers. comm.), and basic natural history of ticks (Roberts 1970). Ectoparasites also negatively impact on the health of both domestic and wild animals through large infestations, which are of importance in management considerations of rare or endangered small mammal species present at Anglesea as increases in host densities may increase ectoparasite loads.

The objective of this study was to survey ectoparasite species on small native mammals near Anglesea, Victoria because an awareness of the ectoparasites is important for the potential transmission of disease to humans, domestic animals and livestock. It is also of interest to the general ecology of small mammals in the region.

METHODS

Ectoparasites were removed from small mammals trapped at two sites at Anglesea, Victoria (Fig. 1). The sites chosen for study were the Eumeralla Scout camp (38°24'0"S, 144°12'36"E) and Bald Hills Road (38°23'24"S, 144°8'24"E) at the Alcoa Lease. Both sites were selected using knowledge that they contained many host species, and these species were all relatively abundant. The Eumeralla Scout camp consisted of a coastal tea tree, *Leptospermum continentale* shrub layer, with plants varying from 20 centimetres to over two metres in height and *Eucalyptus obliqua* at a height of over two metres

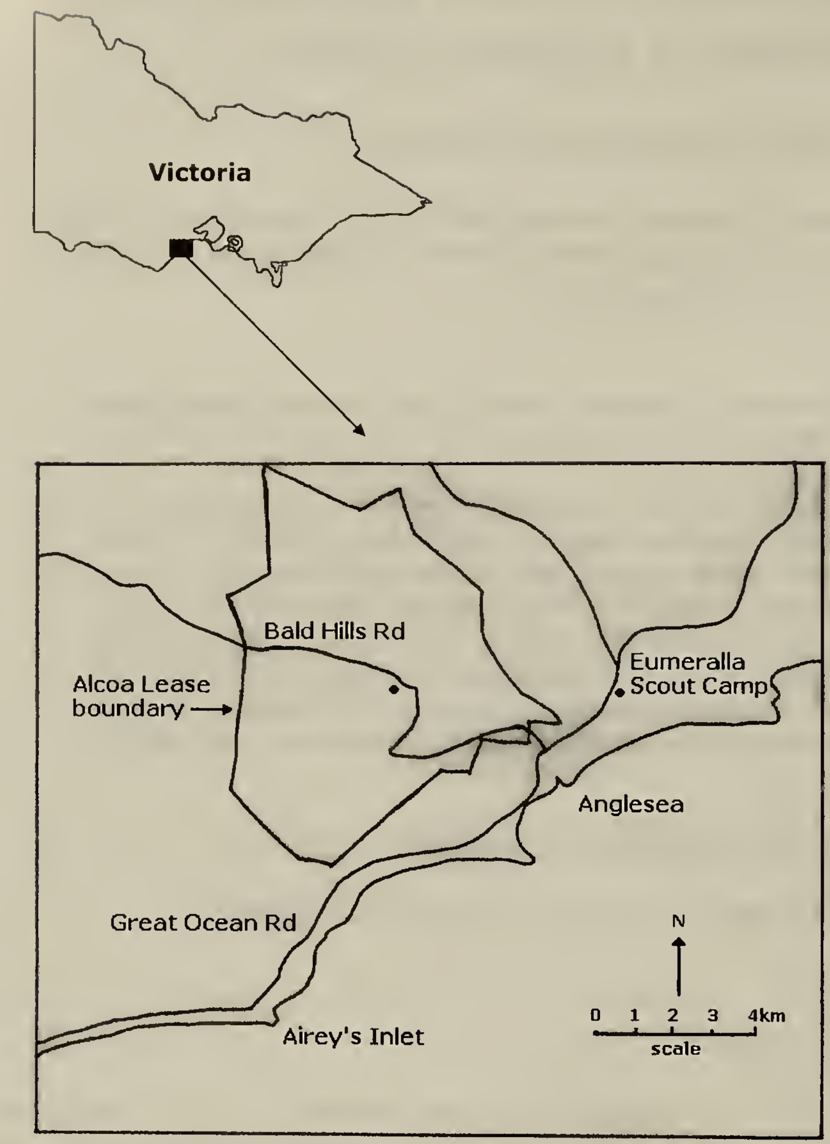

Figure 1. Location map of study area.

forming the canopy. The site was a flat open heathland with woodland dispersed through it, and a swamp consisting mainly of *Gahnia radula* and also *L. continentale*. The Bald Hills Rd site on the Alcoa Lease was situated on a slope of approximately 30° in a southwesterly direction. The heathland was dominated by *L. continentale, Epacris impressa, Conospermum mitchelli, L. myrsinoides, Platylobium obtusangulum* and *G. radula* were the main species present in the understorey. Stands of *Eu. willisi* and *Banksia marginata* were present at the study site.

Trapping of small mammals was carried out during Autumn and Winter 2002, due to the study being an honours project requiring completion during an academic year. Trapping sessions of three nights each were carried out at Eumeralla in June (3-6.6.02), July (8-11.7.02) and August (6-9.8.02), with a total of 131 mammals captured over the three sessions and at the Bald Hills Rd site in April/May (29.4-2.5.02), July (22-25.7.02) and August (19-22.8.02), with 161 captures recorded. Any previously trapped mammals captured again in following sessions were re-examined for ectoparasites and were counted accordingly. Fifty aluminium Elliott traps (32 x 9 x 10 cm) were placed in transects across the Eumeralla site. The site at Bald Hills Rd consisted of 100 traps set in a grid pattern (100 m x 100 m) at ten metre intervals. Traps were baited using a rolled oats, peanut butter and honey mix and were cleared within three hours of sunrise.

Upon capture, mammals were transferred from the trap into a lightweight mesh bag, identified, ear notched for identification purposes, weighed, sexed and inspected for ectoparasites. As ticks were physically attached to the host, they were removed using fine forceps to grip the tick as close to the host's skin as possible and flipping it over to remove the tick while leaving the mouthparts intact. Fleas and mites were removed by ruffling the host's pelage with fingers in order to dislodge the ectoparasites, or the host was combed using Licemeister combs or animal flea combs. Numbers of each ectoparasite taxa were recorded from each mammal and all ectoparasites collected were placed in labelled containers of 70% ethanol.

Identification of fleas, mites and ticks were carried out using descriptions provided by Dunnet and Mardon (1974), Domrow (1987, 1991) and Roberts (1970) respectively.

A linear regression on host mammal body weight and ectoparasite species richness was carried out using log transformed data.

RESULTS AND DISCUSSION

A total of 292 individual mammals were trapped over 1350 trap nights from the two sites. The host mammals trapped included *Antechinus minimus* (74), *A. agilis* (69), *Sminthopsis leucopus* (4) (Dasyuriomorphia: Dasyuridae), *Isoodon obesulus* (10) (Peramelemorphia: Peramelidae), *Rattus fuscipes* (50) and *R. lutreolus* (85) (Rodentia: Muridae).

Examination of 296 host mammals yielded 364 fleas and 557 acari (mites and ticks) in total. From this, five flea species were identified, along with seven mite species and two tick species. Of these, two species of mites were unable to be identified to species level; these were referred to by their family names as unidentified Laelapidae and unidentified Trombiculidae. Table 1 shows the number of examinations of each host mammal species and the species of ectoparasites removed from the host species.

The most common host examined for ectoparasites was *Rattus lutreolus*, with 85 examinations and the host examined least was *Sminthopsis leucopus* with only four examinations. *Sminthopsis leucopus* is an uncommon mammal in the Anglesea area. Lunney (1995) states although it has a wide distribution throughout southern Australia, it prefers sparse ground to forage, whereas the sites in this study had very dense ground cover.

Figure 2 shows *I. obesulus* as having the greatest ectoparasite species richness and *S. leucopus* the smallest. A significant linear association was found between host weight and ectoparasite species richness (MS=0.098, F=7.966, df=1, P=0.048) with 64.32% of the variation in ectoparasite species richness accounted for by mean body weight of the hosts. This is consistent with previous studies showing that host body size determines ectoparasite species richness (Kuris et al. 1980, cited in Stanko et al. 2002). Another factor that can influence ectoparasite species richness is the social behaviour of the host. Stanko et al. (2002) found that higher host densities generally equated to lower species richness on individuals, possibly because of anti-parasitic behaviours such as grooming. As bandicoots have a reputation of 'pugnacious behaviour between conspecifics' (Lobert 1990) and indicate a low social tolerance (Thomas 1990), it could be that the bandicoots examined in this study had a higher species richness of ectoparasites and a higher abundance of each species in part due to a combination of larger body size and lack of social grooming.

The most common ectoparasite collected was the flea *Pygiopsylla hoplia*, which was recorded on every host mammal species. According to Dunnet and Mardon (1974), *P. hoplia* is the most commonly collected Australian species of flea. It has a distribution across Australia, excluding the Northern Territory, and has been recorded on many species of peramelids, dasyurids and rodents (Dunnet and Mardon 1974). In contrast, *Stephanocircus dasyuri* was mostly recorded on *I. obesulus*, and occasionally on *A. minimus*. The similar foraging nature of both these mammal species may be the reason why this species of flea was not recorded on any other hosts. *Macropsylla hercules* was only recorded on *Rattus* spp. and *I. obesulus*, perhaps due to the size of the host animals, as this flea is very large. *Macropsylla hercules* is commonly collected from various native *Rattus* species from southern Australia (Dunnet and Mardon 1974). The other species of flea collected, *Acanthopsylla rothschildi rothschildi* and *Bibikovana rainbowi* appeared to display little host specificity, as they were recorded from the majority of the host species.

Host specificity for acarine ectoparasites collected varied. The highly host specific *Androlaelaps marsupialis* was only found between the groove of the tibia and fibula on the hind legs of *I. obesulus* where grooming is difficult (pers. obs.). Similarly, *Mesolaelaps anomalus* was recorded only on *I. obesulus*. In contrast, the trombiculid mites and the tick *Ixodes tasmani* showed a broad host range, being found on all host species except for *S. leucopus* and *A. minimus* respectively. The trombiculids were found most frequently inside the ears of hosts during this study, but can be found on any exposed skin including legs, feet and tails (pers. obs.). Trombiculid mites are parasitic during their larval stage and later live in the soil as free living adults (Domrow 1962). One small infestation was recorded in the pouch of a female *I. obesulus*, and it has been suggested that larval trombiculids occurring in the pouches of *A. minimus* can directly infest any pouch young present (B. Wilson, Deakin University, pers. comm.). *Ixodes tasmani* is a common species of tick with a distribution widespread across southern Australia with a wide range of hosts (Roberts 1970).

The species of *Haemaphysalis* collected from *I. obesulus* was identified as *H. humerosa*, but differences in the spiracular plate between the Anglesea specimens and specimens from known populations in Queensland have been observed. An alternative identification is *H. ratti*. Further research is being carried to provide a definite identification of the specimens (I. Beveridge, University of Melbourne, pers. comm., D. Kemp, CSIRO, pers. comm).

Other ectoparasitic arthropods were collected from host mammals studied. Lice (Phthiraptera, species unknown) were collected from *R. lutreolus* on three occasions; but were not observed on any other host mammals examined. The rove beetle species *Myotyphlus jansoni* (Coleoptera: Staphylinidae) was collected from *Rattus lutreolus* on five occasions. However, *M. jansoni* is not an obligate ectoparasite. *Myotyphlus jansoni* has only been recorded on a very small number of individual native *Rattus* species previously (Hamilton-Smith and Adams 1966). The beetles are usually collected near the anus or tail (as they were in this study) and have also been recorded in bat guano in a cave near Warrnambool, Victoria; thus it may be assumed that the beetles feed on the excreta of the rats, which is not strictly an ectoparasitic

Host species	No. of mammals examined	Body weight (g) (Mean ± SD)	Siphonaptera	Number	Acari	Number
Antechinus minimus	74	50 ± 13	*Pygiopsylla hoplia*	36	*Andreacarus tauffliebi*	5
(swamp antechinus)			*Acanthopsylla rothschildi*	5	*Mesolaelaps sminthopsis*	1
			Bibikovana rainbowi	1	*Androlaelaps telemachus*	5
			Stephanocircus dasyuri	3	Trombiculidae	17
Antechinus agilis	67	31 ± 9	*Pygiopsylla hoplia*	11	*Mesolaelaps sminthopsis*	4
(agile antechinus)			*Acanthopsylla rothschildi*	39	*Androlaelaps telemachus*	3
					Trombiculidae	8
					Ixodes tasmani	6
Rattus fuscipes	50	106 ± 23	*Pygiopsylla hoplia*	4	*Androlaelaps telemachus*	1
(bush rat)			*Bibikovana rainbowi*	5	Trombiculidae	23
			Macropsylla hercules	7	*Ixodes tasmani*	7
Rattus lutreolus	85	95 ± 21	*Pygiopsylla hoplia*	3	*Andreacarus tauffliebi*	50
(swamp rat)			*Bibikovana rainbowi*	7	*Mesolaelaps sminthopsis*	2
			Macropsylla hercules	6	Trombiculidae	12
					Ixodes tasmani	2
					unidentified Laelapidae	10
Sminthopsis leucopus	4	22 ± 3	*Pygiopsylla hoplia*	1	*Ixodes tasmani*	1
(white footed dunnart)			*Acanthopsylla rothschildi*	1		
Isoodon obesulus	10	400 ± 173	*Pygiopsylla hoplia*	90	*Androlaelaps marsupialis*	10
(southern brown bandicoot)			*Acanthopsylla rothschildi*	2	*Mesolaelaps anomalus*	55
			Bibikovana rainbowi	2	*Mesolaelaps sminthopsis*	317
			Macropsylla hercules	1	Trombiculidae	5
			Stephanocircus dasyuri	140	*Ixodes tasmani*	2
					Haemaphysalis sp.	11

Table 1. Species of ectoparasites collected from host mammals.

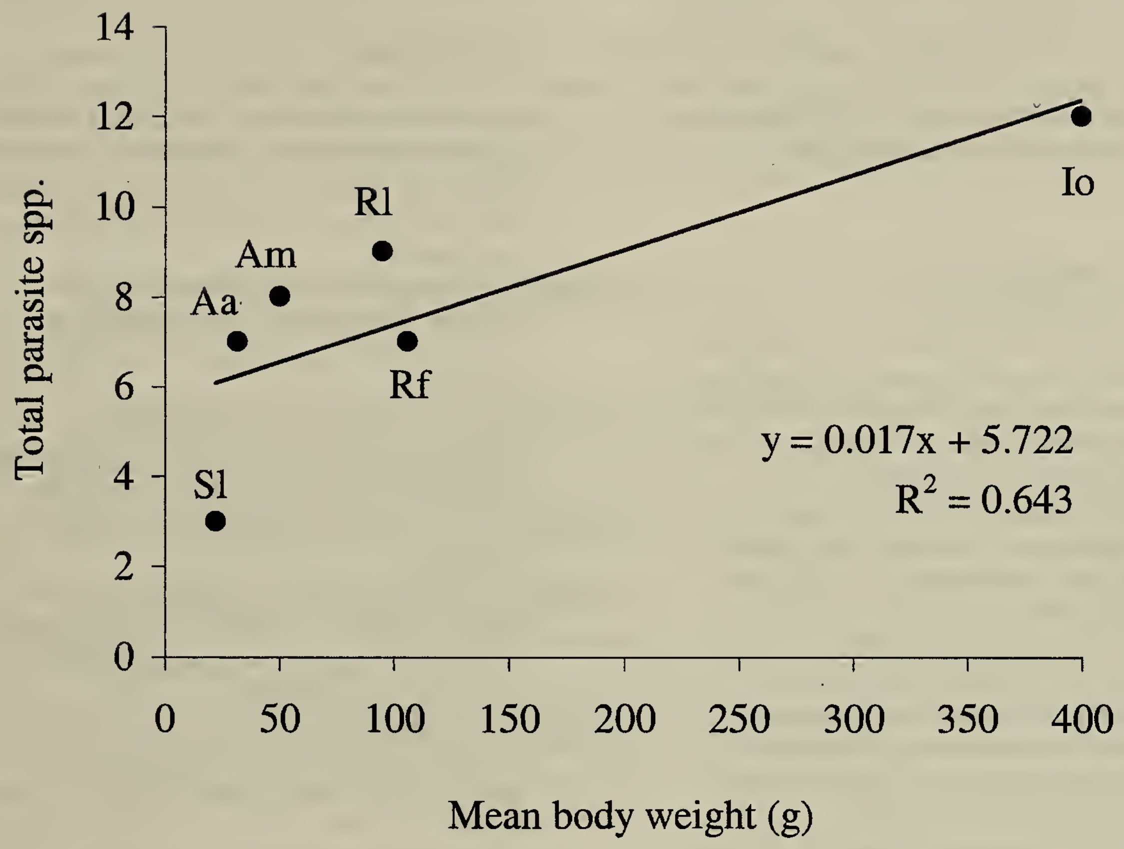

Figure 2. Relationship between ectoparasite species richness and body weight of host mammals. Sl = *Sminthopsis leucopus*, Aa = *Antechinus agilis*, Am = *Antechinus minimus*, Rl = *Rattus lutreolus*, Rf = *Rattus fuscipes*, Io = *Isoodon obesulus*.

relationship (Hamilton-Smith and Adams 1966; Lawrence and Britton 1991).

The ectoparasite species collected during this study were all considered to be common throughout the region (Roberts 1970; Dunnet and Mardon 1974) and all are theoretically able to transmit pathogens to animals or humans. Generally, fleas are known to be intermediate hosts for the cosmopolitan rodent tapeworm, *Hymenolepis diminuta* and the canine tapeworm *Dipylidium canium*, along with being able to transmit various filarial, rickettsial and protozoan pathogens, however native Australian fleas have not been found to contribute epizootics in the field (Dunnet and Mardon 1991). *Ixodes tasmani* has been recorded as an intermediate host of various rickettsiae, including *Rickettsia australis*, the organism which causes Queensland tick typhus (Campbell and Domrow 1974, cited in Cavanagh 1999). *Haemaphysalis* ticks are vectors of *Coxiella burnetii* (Q fever), in bandicoots and macropods and domestic livestock (Kettle 1995). Therefore it is recommended that care be taken when in areas where ticks are present, especially at the Eumeralla Scout Camp where groups of scouts may come into contact with ticks while carrying out activities in the area.

In conclusion, it was found that there was a significant relationship between ectoparasite species richness and body weight of host mammal species. There was no difference in the species of ectoparasites collected from both study sites, except for *M. jansoni*, which was only found on *R. lutreolus* at the Bald Hills Rd site. As there have been no other studies carried out of this type in the region, it is recommended that a study over a longer time frame be carried out in order to accurately assess seasonal variations of ectoparasite numbers.

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Occurrence and Conservation of the Dugong (Sirenia: Dugongidae) in New South Wales

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Recent sightings of dugongs well beyond the southern limit of their accepted range (~27°S) on the Australian east coast prompted a review of past records of dugongs and their current conservation status in New South Wales. While archaeological analyses have identified bones of *Dugong dugon* in Aboriginal middens at Botany Bay (~34°S) and colonial records indicate stranded animals as far south as Tathra (~36.5°S), there were no verified sightings of live individuals in NSW waters for some years; however, five separate sightings of individuals and pairs were documented in the austral summer of 2002/03 in estuaries on the NSW central coast (~32-33.5°S). It is suggested that conditions such as warm sea temperatures and low rainfall (promoting seagrass growth) may be facilitating explorative ranging south by dugongs.

The IUCN lists dugongs as 'vulnerable' at a global scale and they are also classified 'vulnerable' under the Threatened Species Conservation Act NSW 1995, yet they are not routinely considered in risk assessments for inshore development in this State. Threatening processes such as shark meshing persist. The importance of considering dugongs in future impact assessments for inshore marine and estuarine developments is emphasized.

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KEYWORDS: conservation, distribution, dugong, Dugong dugon, risk assessment, sightings, status, vulnerable.

INTRODUCTION

The dugong (*Dugong dugon*), along with all other extant Sirenians, is regarded as a shallow water, tropical and sub-tropical species (Martin and Reeves 2002; Rice 1998). Dugongs are thought to be strictly marine, inhabiting the coasts of some 37 countries and territories (Marsh et al. 2002). Despite their widespread distribution, dugong numbers have declined in most of their known range and they are believed to be represented by fragmented, relic populations in most countries. Likely causes for this decline and continuing threats include: large-scale destruction of seagrass as a result of sedimentation, dredging, mining, trawling, and pollution; incidental take as by-catch in commercial and recreational gill and mesh nets as well as shark nets set for bather protection; direct takes from indigenous hunting, and vessel strikes and disturbance (Marsh et al. 1999, 2002; Hodgson 2003).

Australian waters are the dugong's stronghold, where their distribution is described as extending from Shark Bay in Western Australia (25°S) around northern Australia to Moreton Bay in southern Queensland (27°S) (Marsh et al. 2002). Dugongs are a 'listed marine species' under the Australian *Environment Protection and Biodiversity Conservation Act* 1999 (EPBC Act). The EPBC Act reflects Australia's commitments under various international conventions including the *Bonn Convention on the Conservation of Migratory Species of Wild Animals*, which lists the dugong on Appendix 2. Dugongs are also considered 'vulnerable' under the *Threatened Species Conservation Act* NSW 1995 and under the *Nature Conservation Act* Qld 1992.

Evidence of a decline in dugong numbers along the urban coast of Queensland (Marsh et al. 2001) led to the establishment of a series of dugong protection areas in some key dugong habitats in Queensland (Marsh et al. 1999; Marsh 2000). No similar protection has been afforded dugongs in NSW, presumably on the assumption that only vagrants of the species range into NSW waters. Dugongs have been considered in some impact assessments for aquaculture developments in NSW (e.g. Anon. 2001a), but not others (e.g. Anon. 2001b). These assessments occurred in the same location, suggesting consideration of dugongs and potential impacts thereon is inconsistent in NSW.

In this paper, we highlight past and present evidence that the dugong's range on the east coast of Australia extends into NSW waters, including estuaries, when environmental conditions are suitable. Given their conservation status under both international conventions and national acts, we suggest that occasional visitation warrants adherence to the legal obligation of considering dugongs and their preferred habitats in future impact assessments.

EARLY RECORDS TO RECENT SIGHTINGS

Dugong bones have been found associated with edge-ground hatchet heads in Aboriginal middens near Sydney, indicating that at least small numbers of dugongs have utilized NSW waters for many centuries (Etheridge et al. 1896). In 1799 Flinders described the catching of dugongs by Aborigines in Moreton Bay, southeast Queensland (Mackaness 1979). Aborigines in NSW also caught dugongs in more recent times, with bones having been found in middens as far south as Botany Bay in the late 18th Century (Troughton 1928).

There are currently two sources of dugong sightings in NSW: the Atlas of NSW Wildlife and records of by-catch from shark meshing supervised by NSW Fisheries. The Atlas of NSW Wildlife yields 83 reports of live, stranded and dead animals for the period 1788 to 2003 (Anon. 2003b; Fig. 1).

A significant portion of these reports (63) occurred in late 1992 and throughout 1993. This influx of animals occurred after the loss of 1,000 km^2 of seagrass from Hervey Bay in southeast Queensland following floods (Preen and Marsh 1995). Two dugongs were caught in NSW shark meshing during this time (Swansea in November 1992 and January 1993). Three earlier captures were also made in shark nets (Bronte in July 1951, Bondi in July 1951, Queenscliff in April 1971) (Krogh and Reid 1996).

Only two records of dead and stranded individuals have been reported to the NSW National

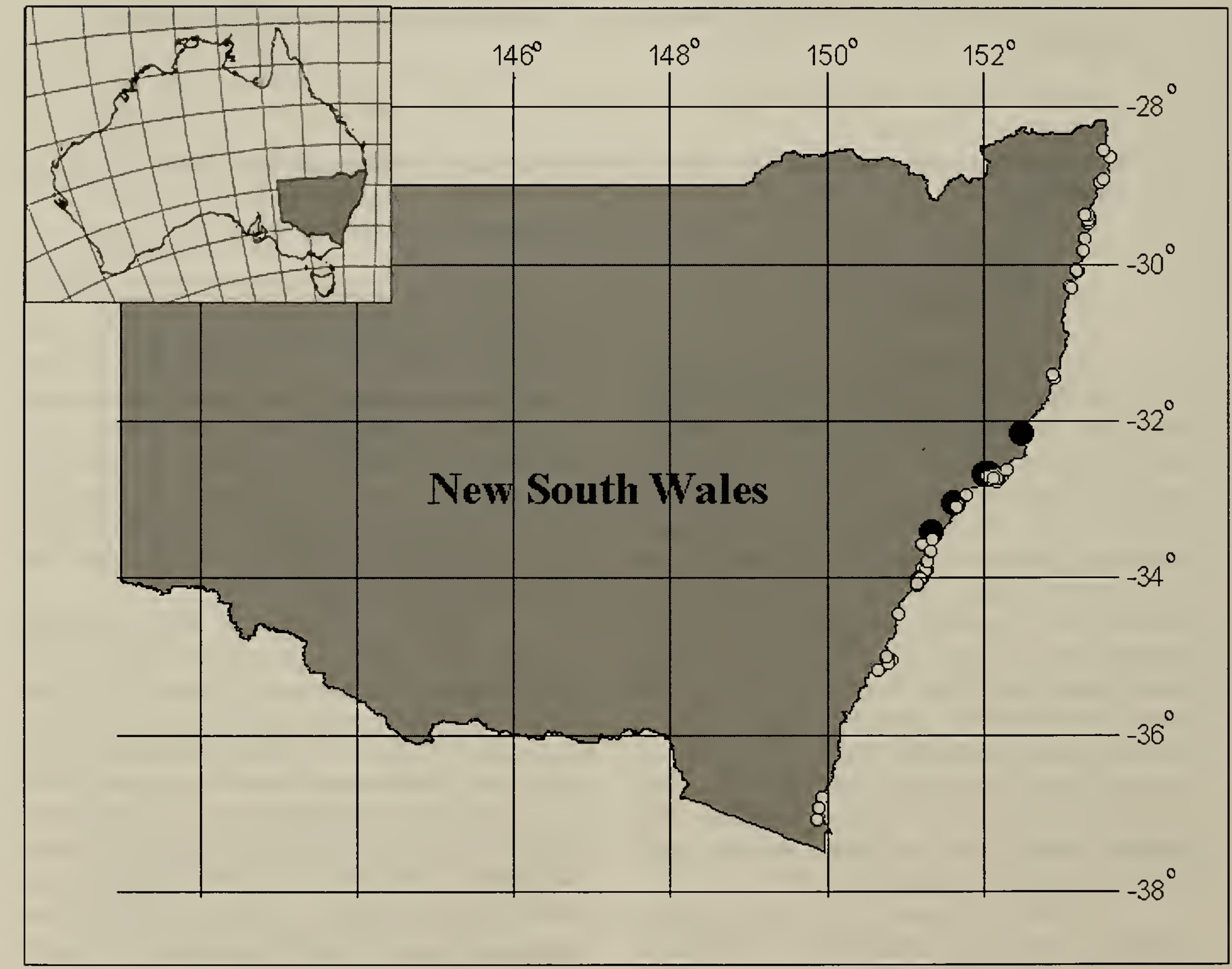

Figure 1. Past records of dugongs on the NSW coast from 1788 to 2003 (open circles; Anon. 2003b) and dugong sightings in central NSW estuaries during summer 2002/03 (filled circles).

Estuary	Date	Lat./Long.	Description	Source
Wallis Lake	Late Oct. 2002	32°11.0′ 152°30.2′	Kayak tour operator reports dugong/s over seagrass beds within Wallis Lake	S. Smith, pers. comm.
Port Stephens	10th Jan. 2003	32°42.8′ 152°06.7′	Dolphin watch operators report two adult dugongs near Manton Bank	D. Aldritch, pers. comm.
Lake Macquarie	24th Jan. 2003	33°20.5′ 150°29.8′	Recreational fishers report cow-calf pair travelling seaward out Swansea Channel	B. Roche, pers. comm.
Port Stephens	1st Feb. 2003	32°41.8′ 152°03.2′	Dolphin watch operator report dugong/s in upper estuary west of Soldiers Point	D. Aldritch, pers. comm.
Brisbane Water	3rd Feb. 2003	33°30.1′ 152°20.3′	Resident reports dugong/s off Orange Grove beach	Anon. 2003b

Table 1. Dugong sightings in central NSW estuaries in the austral summer of 2002/2003.

Parks and Wildlife Service (NPWS) in the last decade, with no live sightings occurring until late 2002/03. Between late October 2002 and early February 2003, five separate sightings of individuals and pairs within (or swimming out of) central coastal estuaries were reported to NPWS and/or the authors (Table 1; Fig. 1). These occurred along a c. 200km stretch of coastline and we do not know if these sightings include repeat sightings of the same individual(s).

SEAGRASS DISTRIBUTION AND WATER TEMPERATURES

All the estuaries in which dugongs were sighted are known to support seagrass meadows (Table 2). Dugongs have been recorded eating the seagrasses listed in Table 2, with the exception of *Ruppia* spp. (Anderson 1986, Marsh et al. 1982, Lanyon et al. 1989). Species of the genus *Halophila* are preferred. The distribution of dugongs has been reported as being constrained to water temperatures >~18°C (Anderson 1986, 1994; Marsh et al. 1994; Preen et al. 1997). However, the water temperatures at the sites in Table 2 were above this thermal threshold in summer 2002/03.

DISCUSSION

The low abundance of dugongs in NSW waters may be the result of a number of factors including limited availability of seagrass in the region, relatively low water temperatures during winter months and in open coastal waters between estuary and bay habitats, and/or human pressures. The entire NSW coast supports only 155 km^2 of seagrass (West et al. 1989), the major portion of which would be *Posidonia australis* and species of the Zosteraceae family, which are not favoured by dugongs. In relative terms, the amount of seagrass in NSW is much less than the total area of seagrass in Moreton Bay alone (250 km^2: Abal et al. 1998) and would contain correspondingly small cover of *Halophila* spp. Troughton (1928) interpreted historical records as suggesting that dugongs may have occurred in greater numbers in NSW prior to European settlement. It has also been suggested (MacMillan 1955) that dugong populations on the tropical east coast were again beginning to expand into the northern rivers region of NSW. Any expansion of the dugong's range into NSW waters further south than this region may have been inhibited by the loss of seagrass beds in areas such as Port Macquarie and Botany Bay to anthropogenic influences (Pointer and Peterkin 1996).

The dugong observations in 2002/03 (Table 1) were in areas of NSW which have some of the largest seagrass beds, at least two of which include *Halophila* species – part of the preferred diet of dugongs (Marsh et al. 1982; Table 2). The increasing evidence that individual dugongs embark on movements over many hundreds of kilometres within tropical waters (N. Gales pers. comm; Marsh and Lawler 2001, 2002; Marsh

Estuary (latitude)	Seagrass species and approximate area coverage	Water temp. (°C)
Wallis Lake (~32.2°S)	Zosteraceae, *Posidonia australis*, *Ruppia* and *Halophila* spp. ~30.785km^2	October mean: 18.9 October 2002: 21.0
Port Stephens (~32.7°S)	Zosteraceae, *Posidonia australis* and *Halophila* spp. ~7.453km^2	January mean: 24.1 February mean: 24.6
Lake Macquarie (~33.1°S)	Zosteraceae, *Posidonia australis*, *Ruppia* and *Halophila* spp. ~13.391km^2	January mean: 21.6
Brisbane Water (~33.4°S)	Zosteraceae, *Posidonia australis* and *Halophila* spp. ~5.490km^2	February mean: 22.1

Table 2. Extent of seagrass meadows and water temperatures at sighting ocations. Sources for seagrass coverage and water temperature data: West et al. (1985) and Anon. (2003a) respectively. Water temperatures are means from 1987-2002, unless otherwise stated.

and Rathbun 1990; Marsh et al. 2002) suggests it is possible that dugongs explore and utilize these southern seagrass beds. Warm water temperatures during the summer months of 2002/03 may have encouraged this behaviour.

Although only five dugongs have been reported drowned in shark nets in NSW over the last c. 50 years (Krogh and Reid 1996), such deaths are not inconsequential since few dugongs are commonly found south of Moreton Bay. Two of these mortalities coincided with a seagrass dieback event (Preen and Marsh 1995) and further impact on Queensland seagrass beds or increase in water temperature in NSW may see an increase in shark net capture of dugongs off NSW beaches. Such events will highlight negative effects on populations of non-target species, and the efficacy of shark control programs for bather protection in NSW and Queensland will again be called into question (Anon. 2002).

The dugong is classified as 'vulnerable' at a global scale on the IUCN Red List of Threatened Species. As the only extant species in the family Dugongidae, the extinction of the dugong will result in biodiversity loss at the family and generic levels as well as at the species level. In the light of inconsistencies evident in risk assessments for inshore development in NSW, we re-iterate that dugongs should be considered occasional visitors to NSW coastal waters. Their limited numbers warrant the dugongs' consideration in future impact assessments for estuarine and inshore marine developments. The estuarine nature of recent sightings suggests that explorative ranging by dugongs is not necessarily limited to strictly marine environments, rather to areas where seagrass beds occur. This also adds weight to the importance of assessing potential impacts on seagrass habitats.

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Captures, Capture Mortality, Age and Sex Ratios of Platypuses, *Ornithorhynchus anatinus*, During Studies Over 30 Years in the Upper Shoalhaven River in New South Wales

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Data collected during a number of studies over a period of 30 years in the upper Shoalhaven River, New South Wales, are presented. A total of 700 individual platypuses (*Ornithorhynchus anatinus*) were captured during the studies, consisting of 137 juvenile females, 94 juvenile males, 292 adult females and 177 adult males. The overall sex ratios of both adults (1.65:1) and juveniles (1.46:1) were significantly biased towards females. Females were found to live up to 21 years. Very few recaptures of juvenile males made estimates of longevity equivocal, but three individuals were at least 7 years old when last captured. Capture and handling mortality during the various studies was low (0.86%). Sixty-two percent of platypuses marked in the study area were never recaptured, fewer adult males were recaptured than females (36% and 51% respectively) and recaptures of juveniles were much lower than for adults (32% females and 14% males). Recapture data suggest considerable mobility by adults and dispersal by juvenile platypuses along the upper Shoalhaven River and its tributaries.

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Keywords: Age, Capture, Marking, Mortality, *Ornithorhynchus anatinus*, Platypus , Sex Ratio

INTRODUCTION

Over the past 30 years a number of research projects has been carried out in a study area in the upper Shoalhaven River in New South Wales. Individual projects have included investigation of temperature physiology (Grant and Dawson 1978a,b; Grant 1983; Hulbert and Grant 1983a,b), diet (Faragher et al. 1979), movements and home ranges (Grant 1983, 1992), haematology and pathology (Munday et al. 1998; Whittington and Grant 1983, 1984, 1995; Whittington et al. 2002), lactation and milk composition (Grant et al. 1983, Gibson et al. 1988; Grant and Griffiths, 1992) and population genetics (Gemmell 1994; Akiyama 1999). During these studies, long-term data have been collected on recaptures, capture mortality, longevity and sex ratios of platypuses (*Ornithorhynchus anatinus*).

During the later studies from 1987, the investigation and use of Passive Integrated Transponder (PIT) tags or "microchips" was begun, probably the first time that this marking method was used on a wild mammalian species in Australia (Grant and Whittington 1991). The long-term success of this method in the mark and recapture studies of the platypus is reported below.

Collins (1973) tabulated the ages of eight platypuses kept in captivity in a variety of locations, including the Bronx and Budapest Zoos. These ranged from four to 17 years, although anecdotal information from zoos and sanctuaries indicates that the species may survive in captivity for up to 21 years (Whittington 1991). Concerning the longevity of platypuses in the wild, the naturalist Harry Burrell (1927) wrote that "the length of life of the platypus is not known. It is my intention to ring-mark some fully furred young as opportunity offers, and it may be that we shall gain some information on this point at a later date, if these marked individuals are captured". Burrell did not later report the ages of platypuses he may have "ring-marked". However, Grant and Griffiths (1992) reported the ages of platypuses marked in the upper Shoalhaven River as being between as much as 4 years for males and 8 for females. Since that report, a further 12 years of research has resulted in the data presented in this paper on the ages and sex ratios in this population of platypuses. Mortality of capture and handling of platypuses in previous studies has not previously been discussed in the literature and this aspect of the studies is presented in the current paper.

METHODS

Between June 1973 and January 2004, platypuses were captured in 16 pools in the upper Shoalhaven River in New South Wales using the unweighted "gill" net methods outlined in Grant and Carrick (1974). Until 1987, individuals were marked using stainless steel leg bands (Grant and Carrick (1974) but these were phased out after trials on the use of Passive Integrated Transponder (PIT) tags proved to be successful (Life Chip tags; Destron Fearing Corporation Scanner; Grant and Whittington 1991).

Sex was determined using the presence or absence of the adult spur or the morphology of juvenile spurs. Absolute ages were determined from individuals initially captured as juveniles and minimum ages for adults were estimated using the time of loss of the female spur, the morphological changes in the males spur (Temple-Smith 1973; Grant 1995), and subsequent recaptures. Females possessing a spur were categorised as being in their first year of life (0 years of age) and males could be assigned to their first or second year of life (0 or 1 year of age). As the females in this area lose the spur between October and December in their first year after emergence from the nesting burrows, any female lacking a spur at first capture was considered to be = 1 year of age (i.e. in their second year of life). It should be noted that two female juvenile platypuses bred in captivity at Taronga Zoo in the 2002/2003 breeding season apparently lost their spurs within only 4 months after emergence from the nesting burrow (Adam Battaglia, Taronga Zoo, pers. comm.). Males with adult spur morphology were considered to be at least in their third year of life, or = 2 years old. Subsequent recaptures permitted minimum ages to be assigned to individuals, beginning with a minimum age at first capture of one year for adult females and two years for adult males (Temple-Smith 1973; Grant and Griffiths 1992; Grant 1995).

Recaptures were recorded for animals in all of the 16 pools of the 12.5 km section of the upper Shoalhaven River and 3.9 km of an adjacent creek. However, by 1987 a number of these pools had filled with sand and were no longer netted. By 1993, the previously largest and deepest pool (1 km long x 2-5 m deep) was completely filled with sand and was no longer sampled, although many of the platypuses originally captured in this pool were captured in the pools downstream. From 1988, when PIT tagging had become the predominant method of marking, sampling was mainly restricted to three pools in the Shoalhaven River itself and one in the adjacent creek. In most years after that time these pools were sampled late in the year (mainly December) when lactating animals were most likely to be caught and at the end of summer (mainly February or March) when juveniles had newly emerged (Grant and Griffiths 1992).

RESULTS

Sex ratios

During the studies from June 1973 to January 2004, 700 individual platypuses were captured. Table 1 shows the numbers in each of four age/sex classes. All sex ratios were significantly biased towards females. The ratio of females to males was 1.58 females:1 male ($Chi^2 = 34.87$; $p < 0.001$) for all animals, 1.46:1 for juveniles ($Chi^2 = 8.00$; $p < 0.01$) and 1.65:1 for adults ($Chi^2 = 27.38$; $p < 0.001$).

Age

Only 45 individuals (41 females and 5 males), first marked as juveniles, were subsequently recaptured. Figure 1 shows the distribution of ages of these individuals at their latest recapture. Two juvenile females were recaptured regularly over periods of 13 and 16 years but were not captured again in 5-6 subsequent years. These animals were assumed to have

	Juvenile	Adult	Total
Males	94	177	271
Females	137	292	429
Total	231	469	700
Sex Ratio (F:M)	1.46:1	1.65:1	1.58:1
Chi^2	8.00	27.38	34.87
p	** < 0.005	** < 0.001	** < 0.001

Table 1. Numbers and sex ratios of platypuses captured in the upper Shoalhaven River study area. ** significant at < 0.01 level.

Year (Actual)	Juvenile Female	Juvenile Male	**Year (Minimum)**	Adult Female	Adult Male
0	96	89	**0**	-	-
1	21	4	**1**	181	28
2	3	1	**2**	33	117
3	3	-	**3**	18	11
4	3	-	**4**	18	9
5	2	-	**5**	10	6
> 5	9	-	**> 5**	32	6
Total	137	94	Total	292	177

Table 2. Numbers of platypuses allocated to actual and estimated minimum age categories in the upper Shoalhaven River study area. Actual = ages of animals initially captured as newly-emerged juveniles; Minimum = minimum ages; calculated from years between initial and last capture of individuals first captured as adults.

died. However, one was again recaptured and lactating at the end of the study, when her age was 21 years. As indicated in the Methods section, females without spurs are at least in their second year of life (>/=1 year old) and it is possible to attribute males to either their first second or third year of life (0, 1 or 2 years old) based on spur morphology changes. Ages of >/= 2 years could be attributed to 111 female adults caught and subsequently recaptured. Similarly 32 adult males were attributed to the >/= 3 year age category. The distribution of these minimum ages are shown in Table 2 and Fig. 1.

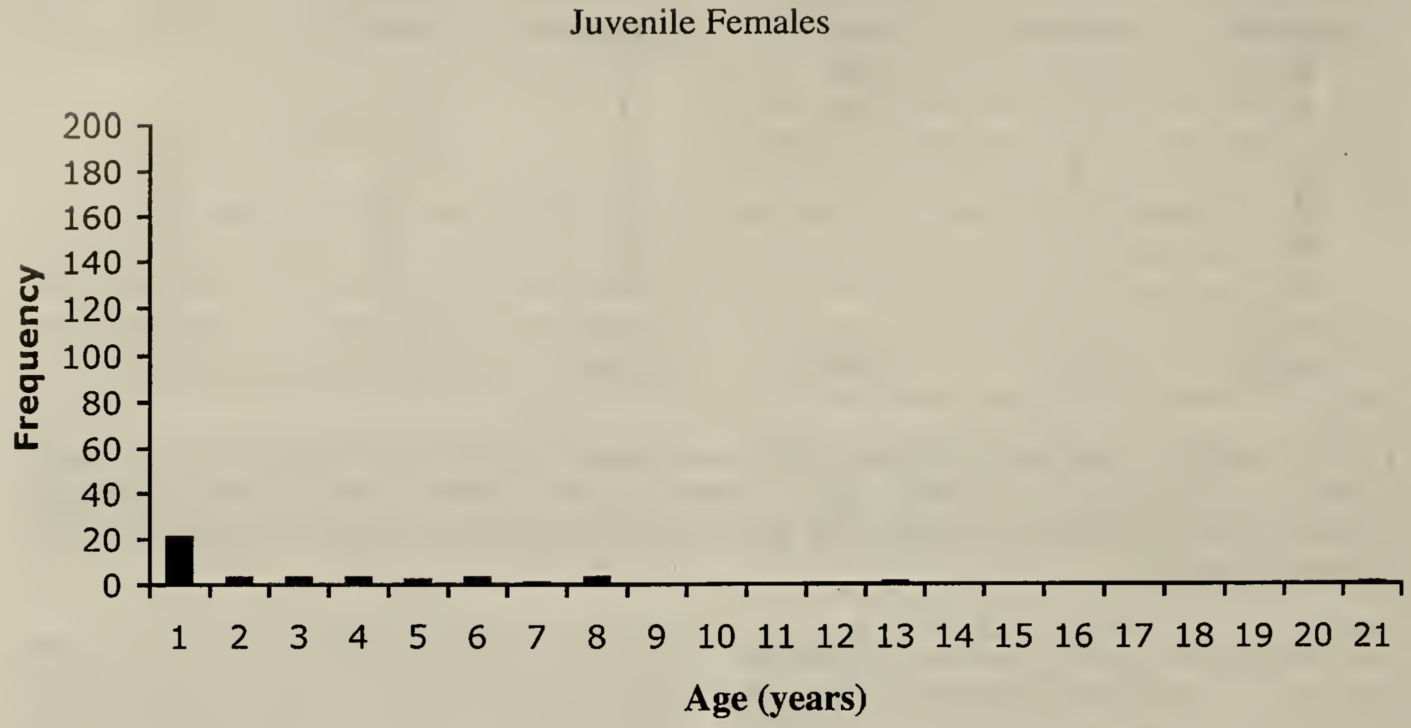
While most platypuses caught in the study could only be attributed to the >/= 1-2 year age category, 9 females first captured as juveniles survived between 5-21 years and 32 of those initially captured as adults survived 5-15 years. One juvenile male was subsequently recaptured at 2 years of age but 32 males, first captured as adults, survived to minimum ages of 3-7 years.

Recaptures

The numbers of juvenile, adult male and adult female platypuses recaptured at least once in the latter 12 years (when most animals were marked with PIT tags) were not significantly different from those of the first 18 years of the study (when the majority were marked with leg-bands)(Table 3). Table 4 presents combined recapture data for both leg-banded and PIT tagged animals for the whole study period.

	Juvenile Female	Juvenile Male	Adult Female	Adult Male
Leg-banded				
Total recaptures (≥ 1 recapture)	33	9	105	53
Total captures	97	69	214	134
% recapture	34.0%	13.0%	49.1%	39.5%
PIT tagged				
Total recaptures (≥ 1 recapture)	24	2	47	15
Total captures	54	32	86	41
% recapture	42.5%	6.3%	54.7%	36.6
Chi^2	1.60	1.04	0.77	0.12
p	NS <0.20	NS <0.31	NS <0.38	NS <0.73

Table 3. Comparison between total number of recaptures (>/= 1) for leg-banded and PIT tagged platypuses in the upper Shoalhaven River study area. Animals marked with both bands and PIT tags between 1987 and 1991 are included in both sets of data. NS = not significant.



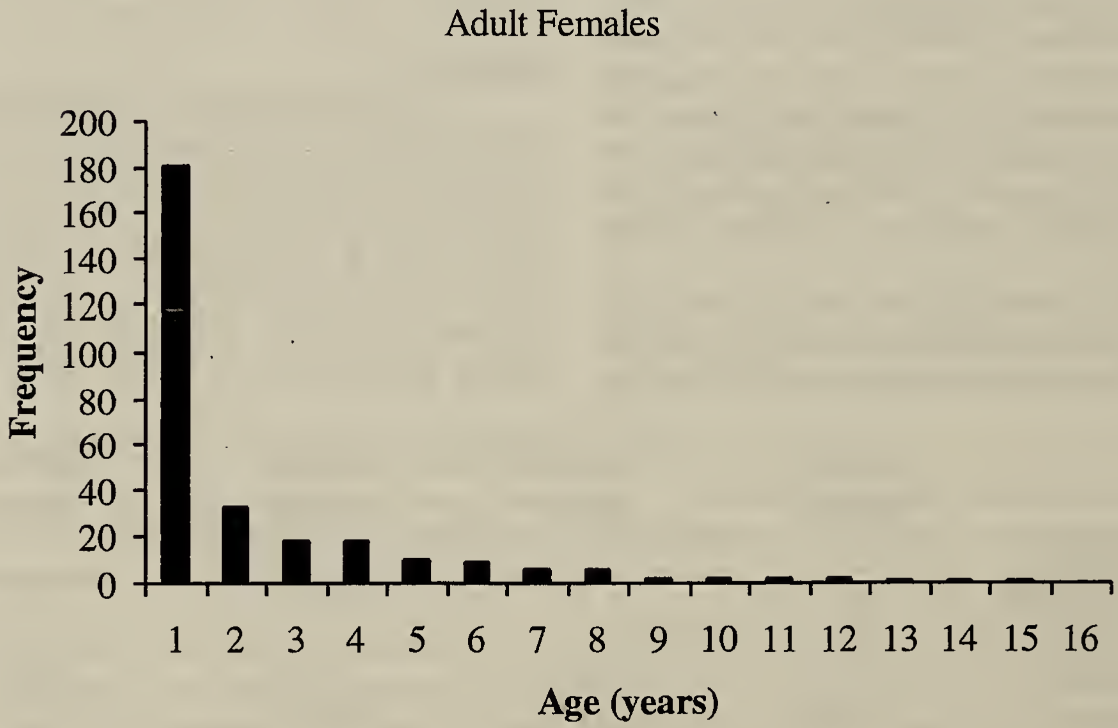


Figure 1. Actual and minimum age frequencies of platypuses in the study. Actual ages are shown for those animals initially caught as juveniles (Juvenile Females and Juvenile Males). Estimated minimum ages shown are for animals caught first as adults (Adult Females and Adult Males).

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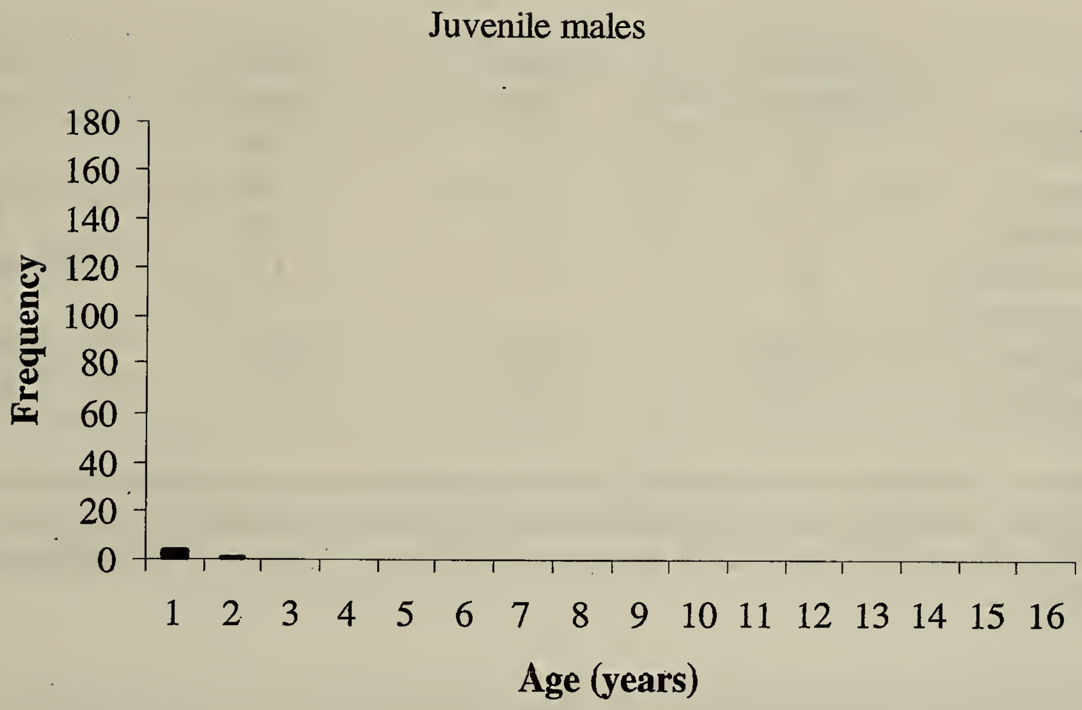
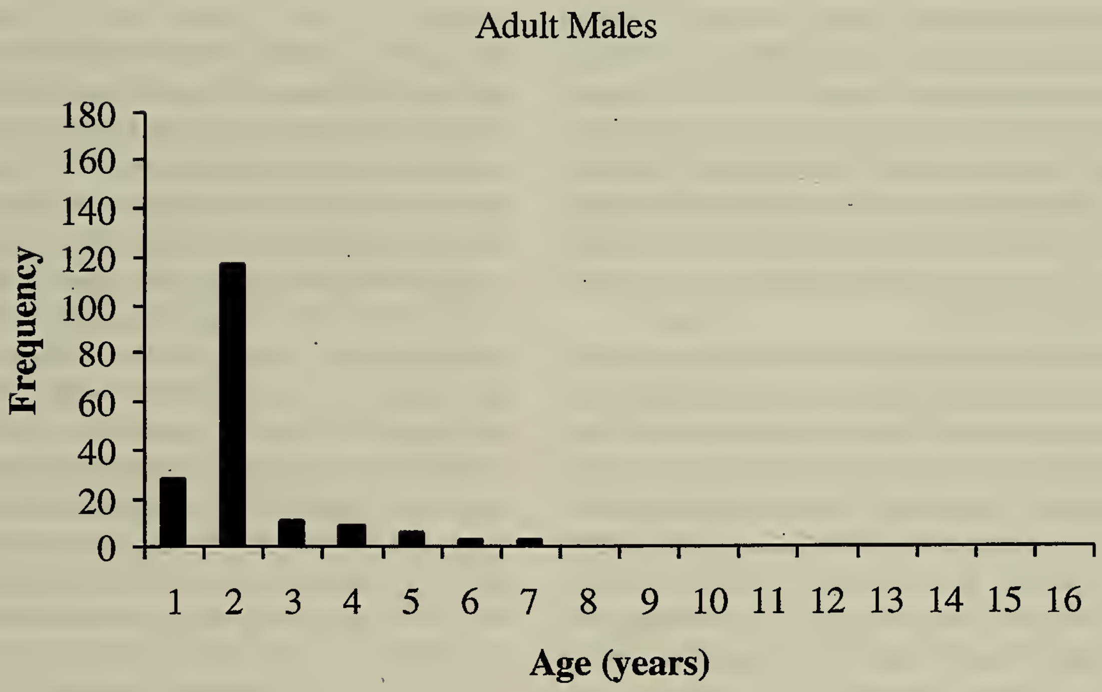
Considerable numbers of both male and female adults and juveniles were captured only once.

Table 4 shows that total recaptures (>/= 1 times) and recaptures in the categories of 1, 2-5 and >5 times were lower for adult males than for females and that total recaptures of juvenile males was less than half (14%) that of juvenile females (32%). The majority of recaptured males were caught within the first months after initially emerging from the nesting burrows (0 years of age), while recaptures of juvenile females were spread across 0-21 years after emergence (Figure 1 and Table 4).





Capture mortality

Of the 700 platypuses captured during the various research projects six died as a result of capture and handling (0.86%). Two drowned as a result of netting, two died suddenly within a few hours of capture (sudden death; animals appeared healthy and no obvious cause of death was identified from post-mortem examination by veterinarians), one succumbed to anaesthesia and one became caught in submerged vegetation by its transmitter attachment and drowned during telemetry work. Details are in Table 5.

DISCUSSION

Sex Ratios

As reported by Grant and Griffiths (1992) for the first 18 years of the study, the sex ratios for both adults and juveniles were significantly biased towards females. Table 6 compares the sex ratios for captured adult platypuses in three other areas (Grant unpublished). Although based on much smaller sample

	Juvenile Female	Juvenile Male	Adult Female	Adult Male
1 recapture	17	10	66	34
2-5 recaptures	19	3	58	20
>5 recaptures	7	0	18	6
Total recaptures (≥ 1 recaptures)	43	13	142	60
% recapture	**32%**	**14%**	**51%**	**36%**
Total captures†	135	94	278	165

Table 4. Total recaptures of male and female juvenile and adults platypuses in the upper Shoalhaven River study area. †Mortalities and some animals which would have been unlikely to have been recaptured after the netting of some pools was discontinued are not included in this total captures figure.

sizes, none of these were significantly different from parity. Grant and Griffiths (1992) also reported no significant difference between males and females in total numbers of platypuses (juvenile and adults not specified) captured in various rivers of New South Wales and the Australian Capital Territory (Table 6). Like the situation in the upper Shoalhaven River, during the earlier years of a study (1986-90) in the Duckmaloi River on the central tablelands of New South Wales, a bias towards females in both adult and juvenile platypuses was found. However, in the later years (1991-2000) more adult males than females were recorded (David Goldney, University of Sydney, Orange, pers. comm.).

The recapture data discussed below seems to indicate that female platypuses in the upper Shoalhaven River survived for significantly longer periods than males. Over time, this longer survival of females would presumably have led to a sex ratio weighted towards females in the population. However, this explanation does not account for the disparity between numbers of male and female juveniles in this population.

Most juvenile male platypuses disappeared from the upper Shoalhaven River population in their first year (86%; Table 4). However, 13% of juvenile females were recaptured in the area up to age one year, 19% were recaptured later than two years after emerging from the nesting burrows and two even remained in the area up to age 13 and 21 years respectively. Twelve juvenile females (9%) bred in the area, eight of these over a number of breeding seasons. Differential dispersal may contribute to the difference in the adult sex ratio, but again this does not explain the significant bias to females in the numbers of juveniles captured at the time they were becoming independent (late January-late March), unless most male juveniles dispersed immediately after independence, with females dispersing later. Unfortunately the data from this study do not permit this hypothesis to be rigorously tested, as most sampling only occurred early and late each year.

The possibility also exists that the uneven sex ratios are determined by differential fertilisation of eggs, development of embryos or pre-emergence survival of young but no explanation arises from the data collected in this study concerning the significant

Cause of Death	Juvenile Female	Juvenile Male	Adult Female	Adult Male	Total
Drowned in net	1	0	1	0	2
Sudden death	0	0	0	2	2
Anaesthesia (ether)	1	0	0	0	1
Snagged transmitter	0	0	1	0	1
Total	2	0	2	2	6

Table 5. Capture and handling mortalities in platypuses during work on various projects in the upper Shoalhaven River study area

Location	Adult Female	Adult Male	Sex Ratio (F:M)	Chi^2 Probability
Various streams NSW/ACT[†]	101	117	1.15:1	1.17 $p \leq 0.28$
Various streams NSW/ACT[‡]	47	47	1:1	-
Barnard River, NSW	24	22	1.10:1	0.09 $p \leq 0.77$
Thredbo River, NSW	14	10	1.4:1	0.67 $p \leq 0.41$
Wingecarribee River, NSW	29	30	1:1.03	0.02 $p \leq 0.90$
Shoalhaven River, NSW	**285**	**173**	**1.85:1**	**27.38**** **$p < 0.001$**

Table 6. Comparison of sex ratios of adult platypuses in various studies in New South Wales and the Australian Capital Territory (ACT). Collected by [†]Temple-Smith and [‡] Griffiths (from Grant and Griffiths 1992); ** significant at < 0.01 level.

bias towards females in the sex ratio of juvenile animals. In the Barnard River study referred to in Table 6, where the adult sex ratio was not different from parity, the sex ratio for juveniles was heavily male-biased (14 males; 3 females) during the single breeding season studied. A similar result was also obtained once during a single breeding season (12 males to 3 females; 1978/79) in the current study, indicating differences between individual years. However, in the 24 years during the study in which juveniles were captured, the numbers of females exceeded males in 87.5% of those years. Considerable annual differences in recorded annual sex ratios were also found in the Duckmaloi River study (David Goldney, University of Sydney, Orange pers. comm.).

Age

The minimum estimated age for male platypuses in this study (7 years) was considerably less than for females (up to 21 years), with nine adult females surviving for a minimum of 10 years. These data suggest that females live longer than males in the wild. However, determination of actual age, or the estimated minimum age, depended on recapture data and, as discussed, recapture of males was much lower (36% recaptured >/= once) than for females (51% recaptured >/= once). After being regularly captured previously, 13 and 21 year old females (first marked as juveniles) had not been recaptured for the last 6 and 5 years respectively of the study. Except for one adult female, which had been captured in December 2002 and was not caught in March 2003, all the other adult females >/= 10 years of age had also not been recaptured in the latter years of the study. These data appeared to indicate a life span of 10-16 years may represent an expected upper range of longevity for female platypuses in the wild. However, the final recapture of one female at the age of 21 years showed a maximum female longevity in the wild comparable to that in captivity. While the data for males in the wild appeared to show shorter life spans (up to 7 years), this could equally represent non-recapture of older males. Reports do not suggest differing longevity between the sexes in captivity (Collins 1973; Whittington 1991).

Recaptures

PIT tags were initially used because of the occurrence of notched and broken male spurs as a result of bands abrading the spur base. However, it was also suspected that the lower capture rates in males, particularly juveniles may have been attributable to band losses. Bands were normally fitted more loosely to males to permit the much greater radial growth of the hind legs in this sex. No significant differences between captures for banded and PIT tagged males (Table 3) indicated that band loss could not fully explain the lack of recaptures, although four female animals, initially marked with bands and PIT tags, were found to have lost their bands during the latter part of the study, indicating some band loss. Only one PIT

Home range(km)	Maximum distance (km)	Source	Location
0.2-2.0	5.6 (24 hr max. = 4.0)	Grant, 1983	Shoalhaven River
0.4-2.3	2.3	Grant, 1983, Grant et al. 1992	Thredbo River
0.3-2.3	2.3	Serena, 1994	Badger Creek
2.9-7.0	15.0	Gardner and Serena, 1995	Watts River and Badger Creek
0.4-2.6	2.6	Gust and Handasyde, 1995	Goulburn River
Adult: 2.9-7.3 Juvenile: 1.4-1.7	24 hr max. = 10.4 (male) 24 hr max. = 4.0 (female)	Serena et al. 1998	Yarra River, Mullum Mullum Creek, Diamond Creek
	40 in 18 months (juvenile)	Australian Platypus Conservancy 1999	Yarra catchment Andersons to Steels Ck
	48 in 7 months (young male)	Australian Platypus Conservancy 2001	Wimmera River

Table 7. Home ranges and maximum distances moved by platypuses in various studies, including the Shoalhaven River (bold).

tag failure or loss was confirmed in 220 tags applied to animals during the studies. The lack of spur damage, some evidence of band loss and no significant differences being found between recaptures of leg-banded and PIT tagged animals confirmed PIT tagging as the preferred method of marking platypuses (Grant and Whittington 1991).

Large numbers of both adult male (64%) and female (49%) platypuses were not recaptured in the study area after being marked either with leg bands, PIT tags or both. This observations suggests one, or a combination of the following:

Loss of marks. Double marking indicated that some band loss did occur during the study but there was little indication that PIT tags were lost or failed.

Mortality. Little is known about the causes and incidence of mortality in platypuses.

Foxes (or dogs) will take platypuses on land, from shallow riffle areas and by digging into burrows (Serena 1994; Grant 1993; Anon. 2002). Large eagles may also be possible natural predators of platypuses (Rakick et al. 2001). The remains of a platypus near a burrow excavated by a fox or dog, an isolated skull in a pool and part of a skull in a pile of other mammalian bones (mainly cattle and sheep) were the only observed evidence of mortality found during the studies in the upper Shoalhaven River.

While 50% of 131 individuals tested positive to leptospirosis antibodies (*Leptospira interogans* serovar *hardjo*)(Munday et al. 1998), no clinical symptoms of the disease were observed and nothing is known of any disease organism, resulting in significant mortality in this population. The *Mucor* fungus, which has caused mortality in Tasmanian populations, has not so far been detected in mainland populations of platypuses, including those in the upper Shoalhaven River (Whittington et al. 2002).

Mobility. Diurnal and longer-term mobility over distances of up to 5.6 kilometres have been previously reported in individuals in the upper Shoalhaven River (Grant 1983, 1992, 1995; unpublished) and in other studies. These data are summarised in Table 7.

After the marking of 700 individual platypuses (including significant numbers of new juveniles) during the 30 years, it was expected that the majority of the population would eventually be marked and that unmarked dispersing juveniles or adults might still enter the area but would be in fairly small numbers. In fact, considerable numbers of new adult animals were captured throughout the study. Some individuals were captured as many as 20 times over periods of up to 21 years and yet the times between recaptures of these individuals was often quite variable. For example, despite the pools being regularly netted during the study, two adult females were only subsequently recaptured nine and 10 years respectively after their initial capture in those pools. Even for females identified as breeding in particular pools during different breeding seasons, periods of time between some recaptures of these animals ranged from 1 to 10 years.

These latter observations suggest that a great deal of mobility probably characterises the platypus populations in the upper Shoalhaven River, although the effects of mortality and/or dispersal cannot be ruled out as reasons for the influx of new animals and the lack of recapture of a significant proportion of the platypuses in the upper Shoalhaven River study area. All of these possibilities need further study.

While there was capture and handling mortality during the studies in the upper Shoalhaven River population, this was quite low (< 1%) due to the utilisation of methods developed through considerable experience by the author and other researchers over the past three decades.

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Breeding in a Free-ranging Population of Platypuses, *Ornithorhynchus anatinus*, in the Upper Shoalhaven River, New South Wales - a 27 Year Study

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A total of 150 captures of lactating platypuses (97 individuals) were made over a period of 27 years in the study area. The proportion of lactating females from December samples ranged from 18 to 80% (mean 43.4±17.7%; n = 21 breeding seasons). The percentage of juveniles in samples taken at the seasons when young were leaving the nesting burrows varied from 0-63% (mean 34.4±17.9%; n = 22 breeding seasons). Only 8.8% percent of captured juvenile females went on to breed in the area; one bred in its second breeding season after emergence but two others did not breed until at least their 4th breeding season. Some females bred during at least 2-3 consecutive breeding seasons but others failed to breed in consecutive years. The percentages of females lactating in the months of September to April indicated a spread in the breeding season. Lactation in the wild was apparently shorter than reported in captivity, lasting more than 3 but less than 4 months. The majority of variation in breeding activity and recruitment could not be explained in terms of drought or observed riverine and riparian changes during the study.

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KEYWORDS: Breeding, Drought, Lactation, New South Wales, *Ornithorhynchus anatinus*, Platypus, Recruitment, Sedimentation

INTRODUCTION

Platypuses (*Ornithorhynchus anatinus*) mate in late winter or early spring. Eggs are laid and the developing young are nourished on milk in the nesting burrows for several months, after which juveniles leave these burrows, become independent and most disperse from natal sites. There is a north-south cline in the timing of the breeding season, which begins earliest in north Queensland and latest in Tasmania (Temple-Smith and Grant 2001). The current study was carried out near the centre of this cline, on the southern tablelands of New South Wales in the upper Shoalhaven River. It began with the investigation of the nature of lactation and the composition of the milk of the platypus (Griffiths et al. 1973; Grant et al. 1983; Messer et al. 1983; Parodi and Griffiths 1983; Griffiths et al. 1984; Griffiths et al. 1985; Gibson et al. 1988; Teahan et al. 1991; Grant and Griffiths 1992; Joseph and Griffiths 1992). However, in the mid-1980s there was considerable change to the habitat of the platypus within the study area, with sand slugs encroaching into many of the pools and considerable bank erosion occurring as a result of poor past and present riparian and catchment land management practices. On completion of the initial studies early in the 1990s, the investigation continued by sampling in December, when females captured would be most likely to be lactating, and in February or March when juveniles had left the nesting burrows but had not yet dispersed (see also Grant, 2004 this volume).

While the study has permitted general aspects of lactation to be further considered since the work of Grant and Griffiths (1992), it has also investigated the effects of stream degradation and drought on the platypus population in the upper Shoalhaven River. With regard to this latter aspect of the study, the hypothesis being tested was that successful breeding, as indicated by females breeding and young being recruited to the population each year, would be adversely affected by stream degradation and/or by droughts.

MATERIALS AND METHODS

Study Site

The study area consisted of a series of 16 pools in agricultural land, separated by riffle areas along 12.5 kilometres of the upper Shoalhaven River and 3.9 kilometres of an adjacent tributary stream, near Braidwood on the southern tablelands of New South Wales. A narrow discontinuous strip of riparian vegetation, consisting of both introduced and indigenous species of trees and shrubs, interrupted by numerous gaps, which were normally eroded as a result of access by sheep and/or cattle from the surrounding pasture land to the river. During the period of the study (late 1977 to early 2004), some of these pools suffered in-filling by sand slugs. For some pools, the effects on the habitat from sand in-filling was so severe that they were deleted from the sampling program. During the study period, three significant droughts occurred.

Sampling Periods

Two to four pools representative of the area (core area) were sampled during December, then again in February and/or March of 21 and 22 breeding seasons respectively over the 27 years of the study. Other pools within and outside these core area pools were sampled intermittently at various times during research in associated projects (Grant, 2004 this volume).

Capture, Marking and Possessing

Animals were captured using the unweighted "gill" net methods outlined in Grant and Carrick (1974). Until 1987, individuals were marked using stainless steel leg bands (Grant and Carrick 1974) but these were phased out after trials on the use of Passive Integrated Transponder (PIT) tags proved to be successful (Life Chip tags; Destron Fearing Corporation Scanner; Grant and Whittington 1991; Grant 2004; this volume). After removal from the nets, animals were weighed, measured and age and sex were determined (Temple-Smith 1973; Grant 2003 this volume). Females were injected intramuscularly with 0.1-0.2 mL of synthetic oxytocin (1-2 International Units; Syntocinon, Novartis) to induce milk "let down" (Griffiths et al. 1972, 1973, 1984; Grant and Griffiths 1992). In females that were lactating, milk could be expressed from the mammary gland, using gentle pressure along the flanks towards the areolae, 5 minutes after injection.

Data Collection

The percentage of lactating females captured in each December sample and the percentage of juveniles caught in relation to the total numbers of animals captured at each sampling in February and/or March were calculated. These provided indices of breeding and recruitment success for each breeding season. The timing and duration of lactation were determined from these data and from the capture and recapture of females in other pools of the study area.

RESULTS

Timing and duration of lactation

During the 27 years of the study, captures of 150 lactating platypuses were made. A total of 97 individuals were lactating at least once during the study (Table 1). Only a single individual was found lactating in late September, with the highest proportions of lactating animals being captured in December and January. Sequential recaptures of three individuals within the same breeding season showed lactation in the field lasted at least 70-98 days (2.3-3.3 months) (Table 2). Other sequential data showed that 97% (30 from 31) of females found lactating in December or January, had ceased lactation when recaptured in March. Of five individuals lactating in December, three were no longer lactating when recaptured in February (Table 2).

Breeding ages of juvenile platypuses

Of 137 female platypuses captured as juveniles, only 12 were later recaptured as breeding females in the study area (8.8%, Table 3). One of these individuals was lactating in its second breeding season after emergence from the nesting burrow, but three others did not breed until at least their 3rd or 4th breeding season. The individual (FJ222) which bred in the second breeding season (1983/84) failed to breed the following year (1984/85). This animal was not captured

	Sept.	Oct.	Nov.	Dec.	Jan	Feb.	Mar.	Apr
Total	26	5	25	256	60	59	179	5
Lact.	1	1	7	106	24	10	1	0
%	3.8	20.0	28.0	41.3	40.0	17.6	0.6	0

Table 1. Numbers and percentages of individual female platypuses lactating in all samples in the upper Shoalhaven River study area

Animal	December	January	February	March	April	Lactation duration
FA015	✓	-	X	-	-	
FA019	✓	-	-	X	-	
FA046	✓	-	X	-	-	
FA126	✓	✓	✓	X	-	>72 days
FA133	✓	-	-	X	-	
FA158	✓	-	-	✓	X	>98 days
FA158	✓	-	-	X	-	
FA161	✓	-	-	-	X	
FA161	✓	-	-	X	-	
FA185	✓	-	-	X	-	
FA185	✓	-	-	X	-	
FA185	✓	-	-	X	-	
FA209	✓	-	-	X	-	
FA212	✓	-	-	X	-	
FA214	✓	-	-	X	-	
FA276	✓	-	-	X	-	
FA335	✓	-	-	X		
FA368	✓	-	-	X	-	
FA368	-	✓	-	X	-	
FA370	✓	-	✓	X	-	>70 days
FA391	✓	-	-	X	-	
FA462	✓	-	-	X	-	
FA514	✓	-	-	X	-	
FA535	✓	-	-	X	-	
FA530	-	✓	-	X	-	
FA547	✓	-	-	X	-	
FJ157	✓	-	X	-	-	
FJ222	✓	-	-	X	-	
FJ248	✓	-	-	X	-	
FJ248	-	✓	-	X	-	
FJ272	✓	-	-	X	-	
FJ272	-	✓	-	X	-	
FJ272	✓	✓	-	X	-	
FJ436	✓	-	-	X	-	
FJ469	✓	-	-	X	-	

Table 2. Recaptures of lactating platypuses within given breeding seasons ✓ Lactating; X Not lactating; - not recaptured.

in the breeding season of the next year (1985/86) but was lactating again in the subsequent breeding season.

Breeding success and recruitment

Twenty-eight females were captured in successive breeding seasons. While some females were captured lactating in up to three consecutive breeding seasons, many failed to breed in consecutive seasons, with 39% not lactating in a season immediately following one in which they did breed. (Table 4).

The mean percentage of lactating (breeding) animals in December of 21 breeding seasons in the core section of the study area was 43.4±17.7% but the numbers and proportions fluctuated considerably between breeding seasons from 80% down to 18% of the numbers of females captured (Figure 1).

The data showed a general relationship between the numbers of juvenile platypuses captured in February and/or March in the core area of the study site and the total numbers of lactating animals captured in each of the breeding seasons sampled (Figure 1). In some years recruitment of juveniles was low after reasonable numbers of lactating females had been captured in December and in other years higher than expected recruitment levels were observed in February/March after relatively low numbers of lactating females had been captured in the previous December. However, in general higher percentages of juveniles were captured at the end of breeding seasons when the percentage of lactating females sampled was also high (Figure 1).

Animal	79/ 80	80/ 81	81/ 82	82/ 83	83/ 84	84/ 85	85/ 86	86/ 87	87/ 88	88/ 89	89/ 90	90/ 91	91/ 92	92/ 93	93/ 94	94/ 95	95/ 96	96/ 97	97/ 98	98/ 99	99/ 00	00/ 01	01/ 02	02/ 03	03/ 04
FJ157	**	-	X^M	✓ X^F	-	-	X^M	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FJ217			**	-	-	✓	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FJ222†			**	X	✓	X	X^M	✓ X^M	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FJ230			**	X^M	-	✓	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FJ235#			**	X	X	-	-	-	✓	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FJ248				**	-	X^M	-	-	X	X	X^F	X	X	✓^{S}	✓ X^M	-	-	X	✓^{J} X^M	✓	-	-	-	-	✓^{J}
FJ272#					**	X	X	X	✓ X^M	- -	✓^{J} X^M	✓ ✓^{J} X^M	✓	-	✓	X^N	-	X^F	-	-	-	-	-	-	-
FJ273					**	-	-	X	-	X^S	-	-	✓	-	-	-	-	-	-	-	-	-	-	-	-
FJ409											**	-	-	-	-	-	-	✓	-	-	-	-	-	-	-
FJ436												**	X	-	✓ X^M	X^N	-	X	-	-	-	-	-	-	-
FJ469#															**	X^N	X	X	✓^{J} X^M	X^M	-	X^M	-	-	-
FJ496																**	-	X X^M	-	-	-	-	-	✓	-

Table 3. Juvenile platypuses originally captured in the study which later bred within the study area. ** emerged; X not lactating; ✓ lactating ^{N} month of capture (eg November); - not captured/sampled; † First breeding in second breeding season after emergence from nesting burrow; # First breeding at 3-4 breeding seasons after emergence.

Animal	77/78	78/79	79/80	80/81	81/82	82/83	83/84	84/85	85/86	86/87	87/88	88/89	89/90	90/91	91/92	92/93	93/94	94/95	95/96	96/97	97/98	98/99	99/00	00/01	01/02	02/03	03/04
FA019	-	-	✓	-	✓	✓	?	✓	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FA124			X	✓	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FA126			X	X	-	-	-	-	-	-	-	✓	X	✓	-	-	-	-	-	-	-	-	-	-	-	-	-
FA133			?	✓	✓	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FA147			?	-	✓	X	-	?	?	?	✓	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FA158			?	X	✓	✓	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FA161				✓	✓	✓	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FA185				X	✓	-	?	✓	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FA188				X	✓	X	✓	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FJ222					**	X	✓	X	?	✓	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FJ235					**	X	X	-	-	-	✓	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FJ248						**	-	X	-	-	X	X	?	X	X	✓	✓	-	-	X	✓	✓	-	-	-	-	✓
FJ272							**	X	X	X	✓	-	✓	✓	✓	-	✓	X	-	-	-	-	-	-	-	-	-
FA280								X	X	?	X	X	X	✓	-	-	-	-	-	-	-	-	-	-	-	-	-
FA282								X	?	X	✓	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FA370											X	?	✓	X	-	-	-	-	-	-	-	-	-	-	-	-	-
FA333										X	-	-	-	✓	-	✓	-	-	-	✓	-	✓	✓	X	-	-	-
FA335										X	-	✓	✓	✓	-	-	-	-	-	-	-	-	-	-	-	-	-
FA370											X	?	✓	X	-	-	-	-	-	-	-	-	-	-	-	-	-
FA391												?	✓	X	-	-	-	-	-	-	-	-	-	-	-	-	-
FA423														✓	-	-	✓	-	-	-	-	-	-	-	-	-	✓
FJ469																	**	X	X	X	✓	?	-	-	-	-	-
FA513																				X	X	X	✓	-	-	-	-
FA514																				X	X	?	?	X	-	✓	✓
FA529																					X	X	✓	-	-	-	-
FA534																					?	-	X	X	-	✓	-
FA535																						X	✓	X	-	?	-
FA559																							X	-	-	-	✓

Table 4. Female platypuses captured in November to January in consecutive breeding seasons in the whole study area during the study. ** newly emerged juveniles; ✓ lactating; X not lactating; ? caught during February, March or April (could have bred but have finished lactating; see Table 2).

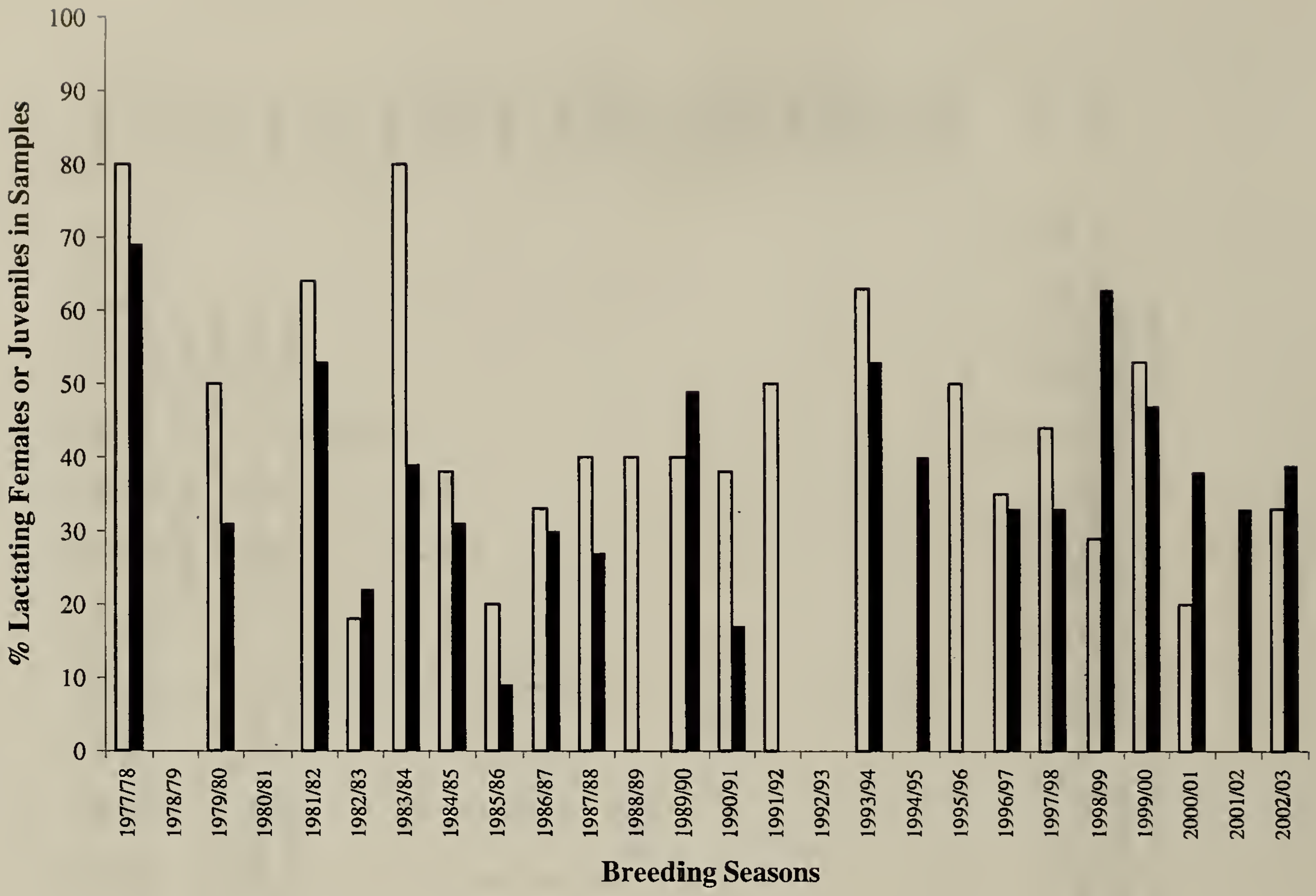

Figure 1. Percentages of lactating females captured in relation to total adult females caught in each December sample (n = 21) and the percentages of juveniles in each February and/or March sample (n = 22) in the core study area. Open bars = lactating females (5 seasons not sampled); solid bars = juveniles (4 seasons not sampled; 1988/89 and 1991/92 seasons no juveniles were caught).

DISCUSSION

The low overall percentages of lactating animals in samples caught in September (3.8%), October (20%), November (28%) and in February (17.6%), March (0.6%), April (0%), contrasted with higher percentages in December (41.3%) and January (40%). This indicated a spread in the breeding season. However, it appears that the majority of animals were breeding around the same time, with a few individuals breeding earlier (eg. one already lactating by the end of September) and a few later (eg. one still lactating in March; Table 1).

The sequential recaptures of lactating females within the same breeding seasons provided evidence that lactation in the wild can last at least 98 days (3.3 months) but is unlikely to exceed four months. This suggestion is supported by the distribution of lactating females in the various months (Table 1), combined with the observation that all but one of 31 females lactating when captured in December or January (97%) had ceased lactation on their subsequent recapture in March (Table 2).

Nestlings in the wild may be weaned more rapidly than those bred in captivity. Lactation in captive animals has been reported to continue as long as 145 days (4.8 months; Holland and Jackson 2002; Healesville Sanctuary and Taronga Zoo, unpublished) and requires lactating females to consume up to 100% of their body weight in food during peak lactation (Holland and Jackson 2002). It may be that the young are weaned more quickly in the wild depending on the local availability of macroinvertebrate food items (Faragher et al. 1979) for the breeding females. Certainly in some years of this study, lactating females were in poorer body condition, based on observations of tail fat reserves (Temple-Smith 1973; Grant and Carrick 1978) and general body condition. Interestingly, both the lactating females and the captured juvenile animals in the 2002/03 breeding season, at the end of a very severe drought, were judged to still be in good body condition. However, four lactating females captured at the beginning of January 2004 appeared to be in poorer condition, despite the river flows being an improvement on those of the previous breeding season, when surface flows in the study area stopped for several weeks (pers. comm. from local residents).

Recapture rates of juvenile platypuses during the various studies in the area was quite low. Thirty-two percent of female platypuses first captured as juveniles were recaptured compared to only 14% for males (Grant 2004; this volume). In spite of this, only 12 female juveniles were recruited into the breeding population.

Although the breeding season was predictable, the breeding of individuals in any one season was much less predictable, with varying numbers of non-breeding females in any sample, individuals not breeding until later in life and breeding animals failing to breed in consecutive seasons (Table 4). Similar observations have been made with platypuses in captive conditions, where no individuals have so far bred in successive breeding seasons (Holland and Jackson 2002; Healesville Sanctuary and Taronga Zoo, unpublished). Temple-Smith and Grant (2001) have speculated whether resource availability, social organisation or genetic factors are involved in this uncertain breeding in the species but little is known of any of these aspects of platypus biology.

A decline was expected in the number of platypuses breeding and/or the number of juveniles recruited to the population after the mid 1980s, when sand slugs began to reduce the pools available for foraging and the provision of refuge areas during drought. Surprisingly, no such overall trend occurred in either numbers breeding or in recruitment data and there is no ready explanation for the considerable variation in the numbers breeding between the seasons covered by the study. Such variations must be attributable to more subtle changes occurring in the environment and/or to unexplained sampling effects.

Both breeding success and recruitment fell sharply in the 1982/83 breeding season, corresponding to the end of a long and severe drought, which lasted from October 1978-February 1983. The effects of the drought provided an explanation for the observation that three females lactating in the 1981/82 season did not breed in the 1982/83 season. However, there were no similar trends recorded in the 1993-95 or 2001-03 droughts, although during the latter, lactation and recruitment percentages were slightly below the mean values for each (Fig. 1). As discussed above, all lactating females and juveniles captured in the 2002/03 sampling were considered to be in good body condition in spite of the severe drought conditions which existed at the time.

During the 1988/89 and 1991/92 breeding seasons no juvenile platypuses were captured. There is no obvious reason for the observed lack of recruitment in 1988/89, but two local over-bank flood events in late December/early January (pers. comm. from local residents) of 1991/92 may have drowned many nestlings confined to burrows during that season. This would explain the failure to capture juveniles in a year when the percentage of lactating females in the previous December had been slightly higher the mean value (Fig. 1).

Prior to enactment of legislation protecting platypuses in all states of Australia (1892 in Victoria to 1912 in South Australia; Grant and Denny 1991), thousands were hunted for their fur. Their numbers are reputed to have declined dramatically, although rebounding since protection has been enforced (Grant and Denny 1991; Grant and Temple-Smith 1978). The species is currently listed as protected, but is either regarded as ‘common’ or not threatened, in all states (except for South Australia, where it is probably now extinct, except for an introduced population on Kangaroo Island). In spite of this, there is concern at the fragmentation of populations in some river systems and in small local populations as a result of habitat degradation, illegal and recreational fishing and encroaching effects of urban and regional development (Grant and Temple-Smith 2003). While this study demonstrates that the species has continued to survive and reproduce in the upper Shoalhaven River in spite of considerable riparian and riverine degradation, the effects of drought and the combination of both of these perturbations, further investigation leading to a complete understanding of the factors determining the uncertain breeding in the species is critical to its conservation. Many questions regarding the population biology and reproduction of *Ornithorhynchus anatinus* still remain unanswered but the long-term studies reported here and in Grant (2004, this volume) have gone some way to providing a greater understanding of some aspects of the species’ field biology, which could not have been achieved by a study of shorter duration.

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Depth and Substrate Selection by Platypuses, *Ornithorhynchus anatinus*, in the Lower Hastings River, New South Wales

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Platypuses were observed foraging most frequently in water >1 metre in depth during normal (91.3%) and drought (82.1%) conditions. Mean water depth in the study pools was 1.08±0.66 and 0.86±0.61 metres during normal and drought conditions respectively. The distribution of depths in the study area was significantly different from the distribution of depths where platypuses were observed during normal ($Chi^2 = 90.2$; $p < 0.01$) and drought conditions ($Chi^2 = 37.35$; $p < 0.01$). Platypuses were apparently not simply utilising depths in relation to their occurrence but preferring to forage in water deeper than 1.5 metres and avoided depths < 1 metre. Overall distribution in numbers of platypuses observed foraging over different benthic substrate types was not significantly different ($Chi^2 = 12.9$; $p > 0.05$) from the distribution of these substrate categories in the study area. However, when the substrates were considered separately, significant preference was shown for cobbled substrate ($Chi^2 = 18.4$; $p < 0.01$) and avoidance of gravel ($Chi^2 = 9.7$; $p < 0.01$). These observations have implications for catchment, stream and riparian management, where activities leading to sedimentation and reduced flushing flows may reduce depths and/or alter the distribution of preferred foraging substrates.

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KEYWORDS: depth, foraging, Hastings River, *Ornithorynchus anatinus*, platypus, substrate.

INTRODUCTION

During foraging in the wild, platypuses dive to feed almost exclusively on small benthic invertebrate animals (Faragher et al. 1979; Grant 1982), which are normally unevenly and often sparsely distributed in a variety of substrates and depth zones (Boulton and Brock 1999; Elliott 1977; Young 2001). The platypus is small, has a high metabolic demand to regulate its body temperature in water and has an estimated maximum aerobic capacity for diving of only 40-60 seconds (Bethge 2002; Bethge et al. 2001; Evans et al. 1994; Grant and Dawson, 1978). Consequently its foraging is restricted to relatively shallow depths and the species is seldom reported occurring in deep lakes or impoundments (Bryant 1993; Grant 1991; McLeod 1993; Ellem et al. 1998; Ellem and McLeod 1998). The current study reports on observations of depths of diving and foraging over different substrates by platypuses in a coastal river in New South Wales during drought and normal flow conditions. Grant and Bishop (1998) discussed the importance of the measurement of physical habitat variables associated with platypus occurrence as a means of assessing possible impacts of stream use and management activities. As part of the monitoring and detection of possible environmental effects of the Hastings District Water Supply Augmentation Scheme, the utilisation of depth and substrate categories by foraging platypuses was investigated.

METHODS

Study area

The study was undertaken in two separate 1.5 kilometre sections of the lower Hastings River near Wauchope in New South Wales. Immediately above a large riffle separating the riverine section from the upper estuary tidal influence, the study area consisted of a series of pools, riffles and runs, with the banks predominantly consisting of earth consolidated by the roots of riparian vegetation, but with a number of gravel/cobble bars and sections of bedrock also present . Predominantly surrounded by agricultural land, especially pastures for dairy cattle, much of the stream bank supported a narrow strip of vegetation consisting of river oaks (*Casuarina* sp), rainforest species (e.g. *Waterhousea floribunda*, *Ficus coronata*) and introduced weed species (e.g. willows, *Salix* sp; *Lantana camara*; privet, *Ligustrum* spp, wild tobacco, *Solanum mauritianum*). A range of macrophyte species also occurred in the stream (especially *Myriophyllum verrucosum*), although these were reduced to low incidences after several flood events. The aquatic grass, *Potamophila parviflora*, was also common along several sections of bank and occurred in island clumps within several sections of the stream.

Sampling

The 3 kilometres of river surveyed consisted of four riffle areas and five pools. Each section was surveyed in both directions during the two hours prior to darkness and immediately after first light in winter (late May to early July) and spring (September to October) over six years from 1998-2003 (88 longitudinal transects x 2 river sections = 176 longitudinal transects; i.e. the whole 3 kilometres was surveyed 88 times). During 1998-2000 the same number of longitudinal transects (16) was surveyed in both winter and spring but from 2001 to July 2003 fewer were surveyed in winter (8) and more in spring (24), as lower numbers of platypuses were normally observed during the winter period. Depth and the predominant substrate type were recorded at the point where each platypus was first seen foraging. It should be noted that visibility, due to turbidity and/or poor light conditions, often meant that a determination of substrate could not be made at all of these points. During the 2001 and 2002 sampling periods, visibility was so low (probably due to the high abundance of phytoplankton) that the substrate could be observed only in few instances where platypuses were foraging.

Physical habitat analysis

The stream was paced out into 60 x 50 metre sections (3 km) and marked at each point with brightly-coloured flagging tape. At each of these points depth measurements were made at both edges (approximately 2 metres from bank) and in the middle of the river (using a weighted line or the kayak paddle graduated in 25 cm units). These depth measurements (n = 174) provided a measure of the distribution of depth categories in the study area (Figs 1 and 2). The occurrence of benthic substrates (mud, sand, gravel, cobble and bedrock) was scored on a scale of 1-5 (using the following estimated percentage cover of each substrate type; 0 = 0%; 1 = 0-5%; 2 = 5-25%; 3 = 25-50%; 4 = 50-75%; 5 = >75%) along three transects parallel to the stream bank between corresponding depth measurement points at the beginning and end of each 50 metre section. Substrates along these transects were not homogeneous, often with some of each type within a single transect. However, the predominant substrate types (score of 4 or 5; i.e. >50% estimated coverage) for each transect (n = 174) were used as a measure of the distribution of the occurrence of substrates (Fig. 3). Data on depths and substrate distribution were collected once during July 2000 but depth measurements were repeated in October 2002 when the river was under severe drought conditions and was barely flowing.

Data analysis

The null hypothesis being tested was that the occurrence of platypuses across depth and substrate categories was the same as the occurrence of these categories in the study area. The overall distribution of numbers of platypuses observed foraging within the various depth and substrate categories and the recorded numbers of occurrence of these physical attributes in the stream (n = 174 samples), were compared using Chi^2 analysis (Statistica, StatSoft Inc.) with expected values calculated using 2 x 5 contingency tables (Bailey 1969). Comparisons between numbers of platypuses observed foraging at specific depths or on specific substrates compared to those not foraging at these specific depths or substrates (i.e. all other depths or substrate categories) were made using Chi^2 for 2 x 2 contingency tables. Comparisons between drought and non-drought measurements of depth were made using Student's t-tests for unpaired samples (Bailey 1969; Statistica; StatSoft Inc). Indices of selection/avoidance (Response Index) of depth or substrate categories by platypuses were calculated as:

$$\text{Response Index} = \frac{\text{\% Occurrence of platypuses in a depth or substrate category}}{\text{\% Occurrence of that depth or substrate category in the stream}}$$

An index of greater than unity suggested a selection response and less than one an avoidance response to a depth or substrate category. All means given are ± Standard Deviation.

RESULTS

Depth selection

The mean depths of the stream during non-drought and drought were significantly different, being 1.08±0.66 and 0.86±0.61 metres respectively ($t = 3.48$; $p < 0.001$). The maximum water depth recorded by these transect-based measurements was 2.75 metres but platypuses were recorded foraging at depths of up to 3.2 metres and the maximum depth recorded opportunistically (not along transects or at foraging sites) was just under 4 metres.

Figure 1 shows the numbers of observations

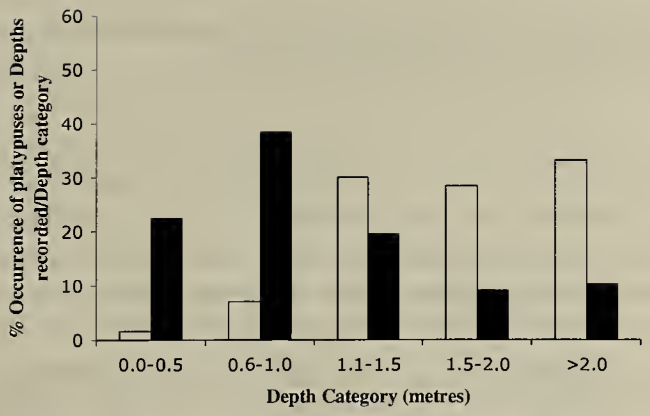

Figure 1. Percent occurrence of platypuses observed foraging in various depth categories (n = 127 observations; white bars) and the percentage of occurrence of these depth categories (n = 174 observations; black bars) in the Hastings River study area during non-drought conditions.

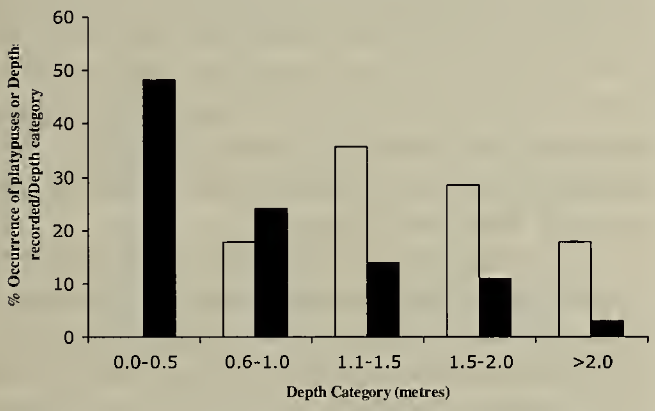

Figure 2. Percent occurrence of platypuses observed foraging in various depth categories (n = 28 observations; white bars) and the percentage of occurrence of these depth categories (n = 174 observations; black bars) in the Hastings River study area during drought conditions.

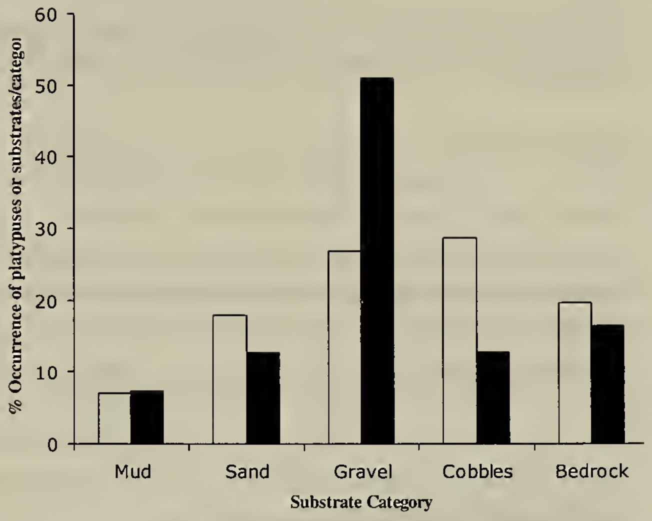

Figure 3. Percent occurrence of platypuses observed foraging in various substrate categories (n = 56 observations; white bars) and the percentage of occurrence of these substrate categories (n = 174 observations; black bars) in the Hastings River study area during non-drought and drought conditions.

of platypuses foraging in the various depth categories during a range of non-drought conditions. These data show that 91.3% of the platypuses (total n = 127) were observed foraging in depths greater than 1 metre, despite this depth category occurring in only 39.1% of the study area. The distribution of numbers of platypuses foraging within the depth categories and the recorded numbers of occurrence of these categories were significantly different ($Chi^2 = 90.2$; $p < 0.01$).

Platypuses showed significant preferences for water deeper than 1.5 metre (Response Indices 3.1-3.2) and avoidance of depths of less than 1 metre (Response Indices 0.2-0.7). Foraging within the 1.1-1.5 metre category showed no significant preference or avoidance by platypuses (Table 1a).

During severe drought conditions (July and October 2002) there was a significant difference between the distribution of foraging platypuses (n = 28) and the distribution of recorded depth categories ($Chi^2 = 37.35$; p = < 0.01; Fig. 2). Response Indices showed a similar, but apparently more marked pattern towards preference for depths > 1 metre (Response Indices 2.6-6.2) and avoidance of shallower depths (Response Indices from 0-0.7). Considering the small sample sizes of platypuses foraging in specific depth categories (n = 0-10) no Chi^2 analyses were attempted on these data collected during the drought.

Substrate selection

The numbers of platypuses observed foraging on particular benthic substrate types (n = 56) are shown in Figure 3. The overall distribution of numbers of platypuses foraging over the various substrates was not significantly different from the distribution of these substrates ($Chi^2 = 12.9$; $p > 0.05$). However, only 26.8% of platypuses were found foraging over gravel substrates, while this substrate type was the most abundant in the study area (50.9%). While cobbles made up only 12.7% of the available substrate, 28.6% of the platypuses observed were foraging over this substrate. Response Indices of 0.5 and 2.3 respectively

Table 1. Chi² and probability values (2x2 contingency tables; Statistica; StatSoft Inc.) for comparisons of:

a. platypuses foraging at specific depths and those not foraging at each of these depths

Depth Category	0.0-0.5 m	0.6-1.0 m	1.1-1.5 m	1.6-2.0 m	> 2 m
Chi ^{2}	27.1	38.8	4.3	18.8	4.3
	< 0.01*	< 0.01*	> 0.05	< 0.01*	< 0.01*

b. platypuses foraging on specific substrates and those not foraging on each of these substrates

Substrate Category	Mud	Sand	Gravel	Cobbles	Rock
Chi ^{2}	0.01	0.96	9.70	18.70	0.26
	> 0.05	> 0.05	< 0.01*	< 0.01*	> 0.05

* indicates statistical significance.

for gravel and cobbles, suggested avoidance of the former and preference for the latter. Individual comparisons between platypuses foraging over specific substrates compared to all other substrates showed significant differences from expected for gravel and cobbles but not for the other substrate types (Table 1b).

DISCUSSION

The study suggested that platypuses observed in the early morning and late afternoon/evening were selecting the deeper sections of their habitat, with 91.3% of the observed individuals foraging in water > 1 metre in depth and 33.1% foraging in water of greater than 2 metres, which constituted only 39.1% and 10.3% of the area respectively during normal flow conditions. Even during the severe drought conditions, 82.1% of platypuses were still observed foraging in water deeper than 1 metre, despite the fact that the proportion of recorded depths > 1 metre had decreased by 11.5%. During the drought observations, 48.3% of the area had a depth of 0.0-0.5 metres but no platypuses were observed forging in this depth category. Thus, platypuses appeared to show preference for foraging in deeper areas and an avoidance of shallower depths within the area during the study in both drought and non-drought conditions.

These observations were similar to those reported for a study in a small alpine lake in Tasmania (Lake Lea). While reporting a maximum dive depth of 8.77 metres, Bethge (2002) and Bethge et al. (2003) found that the majority of dives recorded for platypuses fitted with data loggers were to depths of less than three metres (98% of dives), with a mean diving depth of 1.28 metres. These workers also found a large proportion of the foraging dives were to depths of less than one metre (48%), although, during winter (when the lake level was higher than in summer), most dives were to depths greater than 1 metre. Platypuses were monitored foraging in the same area, rather than moving to the shallower parts of the lake during the winter, suggesting that foraging was determined by factors other than depth preference, possibly including substrate type and/or availability of benthic food species. However, the workers in this study did not report on these possibilities.

Rohweder (1992), Bryant (1993) and McLeod (1993) also reported platypuses foraging in water less than 5 metres in depth. While Ellem et al. (1998) found increasing depth of pools (up to 2 metres) to be positively related to the observed presence of platypuses in 36 pools on the Macquarie River system in the Bathurst area of the central tablelands of New South Wales, Ellem and McLeod (1998) found radio-tacked platypuses using shallower parts of some sections of a weir pool in the Duckmaloi River near Oberon in New South Wales.

Bethge (2002) also reported platypuses foraging in deeper areas and spending less time on the surface of the water in Lake Lea during daylight hours than at night. He speculated that these behavioural changes may have been related to avoidance of predators. Little is known regarding predation by indigenous predators which could take foraging platypuses from the water. Predation by the introduced red fox (*Vulpes vulpes*) on platypuses moving through or foraging in shallow water, such as riffle areas, has been reported (Serena 1994; Grant 1993; Anon. 2002) and the species has been included as a possible food item of wedge-tailed eagles (*Aquila audax*)(Rakick et al. 2001; Marchant and Higgins 1993).

Several white-breasted sea eagles (*Haliaeetus* *leucogaster*) and several ospreys (*Pandion haliaetus*) were observed at the Hastings River study site. Both of these species were seen taking fish from the surface of the water. Although a grey goshawk (*Accipiter novaehollandiae*) has been reported attacking a juvenile platypus on land (Richards 1986), it seems unlikely that either this species or the osprey would be large enough to take even a juvenile platypus (which are around 65-70% adult weight when they first leave the nesting burrows; Grant and Temple-Smith 1998) from the water. It is possible however, that the sea eagle may represent a potential predator of the platypus. During the study a sea eagle was observed retrieving a large dead Australian bass (*Macquaria novemaculeata*) of 485 mm in length, and estimated to weigh 2.5 kg (Harris 1987), from the bottom of a pool. The eagle was unable to fly with the fish and dragged it to a nearby gravel bar, where part of the flesh was eaten before darkness fell. Soon after first light the following morning the eagle was seen carrying off the remaining carcass of the bass. Interestingly, the platypus does not seem to have been recorded as a food item of this species of large eagle (Marchant and Higgins 1993; Olsen 1999).

Substrate selection

Higher invertebrate productivity is often associated with areas where logs, roots and vegetation provide a range of habitats for an array of types of benthic invertebrate species and coarse substrates (gravel, cobbles, rocks) provide fixed habitat, rather than a shifting substrate, such as sand and fine sediment (Young 2001; Boulton and Brock 1999; Smith and Pollard 1998). Data in the study were restricted by a small sample size due to the inability to observe the type of substrate over which platypuses were seen foraging in times of high turbidity and/or poor light conditions. However, there was some indication that platypuses were avoiding sections of the study area which consisted mainly of mud or sand (Fig 3) but this was not statistically significant (Table 1b). There appeared to be marked avoidance of gravel (the most abundant substrate; 50.9% of the area) and preference shown for areas where cobbles were the predominant substrate (12.7% of the area). Both of these trends were statistically significant (Table 1b).

The complexity of benthic habitat has been previously identified as being positively related to the occurrence of platypuses (Rohweder 1992) and Serena et al. (2001) found a positive relationship between numbers of radio-tracked platypuses and the occurrence of coarser substrates, including gravel, pebbles, cobbles, large rocks and coarse particulate organic matter. These observations may be related to the distribution of benthic food organisms but this was not investigated in the present study. No explanation of the apparent avoidance of gravel substrate in the present study is suggested as the species has been observed by the author foraging on gravel substrates in other areas.

Implications for stream management

The development of adaptive management strategies for streams, particularly with regard to water extraction and the operation of impoundments, should consider flows which maintain pool depth and benthic habitat diversity by preventing the accumulation of sand and fine sediments. The removal of riparian vegetation, erosion as a result of unrestricted stock access to stream banks and poor catchment management practices have also resulted in the infilling of pools by sand ‘slugs’ in many streams in eastern Australia (Brooks and Brierley 1996; Boulton and Brock 1999; Brierley et al. 1999; Grant et al. 2003).

Grant and Bishop (1998) encouraged the use of physical habitat analysis, considering broad habitat variables normally associated with platypus occurrence, in any attempts to monitor and/or predict effects of human activities impinging on streams and their catchments. More recently a habitat simulation model was used by Davies and Cook (2001) to generate weighted useable habitat area estimates for the platypus at various proposed discharge regimes in a regulated river in Tasmania. This model used more specific habitat requirements of the species in terms of depth, velocity and substrate, calculating habitat preference curves based on available information from the literature and from experts in the field. These authors observed that: “Platypus[es] are known to feed in very shallow water and up to ca 1-3 m” and “foraging is optimal at depths of < 2 m” and “platypus[es] actively feed in silt, sands, finer gravel substrates, and are known to forage on coarse gravel to smaller cobble substrate. Feeding activity is not deemed to be efficient or to frequently occur on coarse cobble, boulder or bedrock substrates”

While the important modelling work of Davies and Cook (2001) drew upon the information available to the authors at the time, the data from the current study and that from Serena et al. (2001) do not totally support the information used to generate their habitat preference curves for the species in mainland sites. It is vitally important that studies seeking to predict possible impacts of human activities on the platypus (or any other species) must consider the widest range and the most currently available information on which to base assumptions.

Too often, assessment of possible environmental impact is based on ‘conventional wisdom’ which may be enshrined in publications which are either not current or poorly researched. It is not acceptable, for example for one Environmental Impact Statement to become the main reference for statements or predictions made in another such document, without reference to the wider and most current scientific literature. The following example from the assessment of dam development on the Burnett River in Queensland sharply illustrates these concerns.

Arthington (2000) suggested that "platypus[es] feed by scooping prey items and mud into cheek pouches in the mouth and grinding the mixture to a sludge before digesting it". Based on this suggestion, the resultant Environmental Impact Statement concluded that "the deposition of sediments in the shallower areas of the dam would provide extra foraging area for Platypus[es]" as "an increase of available muddy substrate would provide more foraging area. Hard substrates offer less feeding opportunities because prey cannot be as easily scooped and ground up if they are on hard substrates or if the scooped material contains large pebble material" (Anon. 2003). Neither the literature nor the current study support the original suggestion by Arthington (2000) which consequently has led to a very equivocal prediction regarding the possible impact of dams on platypus foraging. It is crucial that such equivocal predictions do not become established in the literature consulted by those carrying out environmental impact assessment studies.

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Distribution of the Platypus in the Bellinger Catchment from Community Knowledge and Field Survey and its Relationship to River Disturbance

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Lunney, D., Grant, T. and Matthews, A. (2004). Distribution of the platypus in the Bellinger catchment from community knowledge and field survey and its relationship to river disturbance, *Proceedings of the Linnean Society of New South Wales* **125**, 243-258.

Platypus distribution in the Bellinger catchment was investigated using a combination of field and community surveys. The field survey in 1996 consisted of netting and observations from the river bank and a canoe. The community-based wildlife survey consisted of a questionnaire and colour maps on which respondents were asked to mark the locations of sightings. Platypuses were observed or caught in 36 locations from all three rivers of the catchment. Two of the three platypuses captured were lactating females. The community recorded 123 locations of platypuses. The fact that the wildlife survey yielded similar results to the field surveys in identifying the location of individuals highlights the value of community records for platypus surveys. There were major floods in 2001, after which we contacted respondents who had reported seeing platypuses three years before. Of the 21 respondents who had been near the river since the flood, 7 had seen platypuses, principally in the tributaries of the Bellinger River. The habitat quality of the rivers was evaluated for platypuses and records were related to disturbance and rehabilitation. The species has survived in this system, but its future can only be assured by strategies which prevent further degradation of its habitat and institute proactive rehabilitation of the damaged sections of these streams.

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KEYWORDS: Catchment management, community wildlife survey, distribution, platypus, river management, wildlife.

INTRODUCTION

Grant (1992) and Grant et al. (2000) reported the distribution of the platypus *Ornithorhynchus anatinus* in New South Wales as having changed very little since the occupation of Australia by Europeans. Platypuses are considered common in the river systems of the coastal, tableland and western slopes (Grant 1991, 1992) and are frequently reported from streams flowing through agricultural land in these areas. In three separate surveys in New South Wales, 52-76% of recorded platypus sightings were from agricultural land (Grant 1991; Lunney et al. 1998; Rohweder and Baverstock 1999). The current study investigated the distribution of the platypus in a typical north coast river system, the Bellinger catchment, where the highland headwater streams arise in forested areas but grade into predominantly agricultural land (especially cattle grazing) towards the coast.

The distribution of platypuses in the Bellinger-Kalang river system was investigated using both field and community surveys. Community surveys have been successful in identifying locations of platypuses (Lunney et al. 1998; Turnbull 1998; Rohweder and Baverstock 1999; Otley 2001). This survey was part of a wider community-based survey of the distribution of a number of key native wildlife species in the Bellinger and Kalang valleys adjacent to Bellinger River National Park. This study sought to assess the co-existence of typical rural community activities and wildlife species, including the platypus. The field observations and capture of platypuses were compared with the questionnaire reports for this and other native species in the catchment with the aim of testing the hypothesis that information gained from survey data provided by the community would be a reliable indicator of the presence of wildlife species in the area.

Since our field and questionnaire study, Cohen et al. (1998) assessed the Bellinger-Kalang catchment using the River Styles framework (Brierley et al. 2002) and assigned conservation and rehabilitation priorities to various stream reaches. Using analysis of aerial photography and field observations, Cohen et al. (1998) assigned various sections of the Bellinger-Kalang catchment to a number of River Styles which have particular geomorphic attributes. The authors of the study stress that these categories are a "record of the character and behaviour of sections of river" and "are not a direct measure of river condition". A separate set of procedures has been developed to appraise geomorphic river condition, building on attributes of river character and behaviour that are pertinent to any given River Style (Fryirs 2003). The attributes used in discerning the River Styles are shown in Table 1 and include channel planform and stability, morphology and geometry (depth and width), as well as descriptions of geomorphic units (e.g. pools, riffles, point bars), bed character (e.g. sand, gravel, cobbles) and vegetation character (including riparian vegetation and woody debris in the stream). Some of these attributes have been identified with the occurrence and foraging activity of platypuses and include:

> Channel geometry: pool depth has been positively related to the occurrence of the species (Ellem et al. 1998; Grant 2004), with platypuses often being observed foraging in water of greater than one metre depth and less than 5 metres. It has been suggested that foraging in shallow water can expose individuals to predation, especially from the introduced fox *Vulpes vulpes* (Grant and Denny 1993; Serena 1994; Anon. 2002).
>
> Geomorphic units: pool/riffle sequences have also been found to be associated with the presence (Rohweder 1992; Bryant 1993) and foraging (Serena et al. 2001) of platypuses, this probably being related to the benthic productivity of such geomorphic units (Hynes 1970; Logan and Brooker 1983; Boulton and Brock 1999).
>
> Bed character: the complexity of the bed substrate, including large particle sizes (rocks, cobbles, pebbles and gravel), has been positively related to both occurrence (Rohweder 1992) and foraging activities (Serena et al. 2001; Grant 2004) of platypuses, again probably resulting from greater benthic productivity (Hynes 1970; Marchant et al. 1984; Boulton and Brock 1999).
>
> Vegetation character: medium-to-large trees, especially indigenous species, are associated with the use of river reaches by foraging platypuses (Serena et al. 2001) and overhanging vegetation has also been identified as a variable found in areas where platypuses are found (Rohweder 1992; Bryant 1993; Serena et al. 1998). This association between riparian vegetation and platypus occurrence is related to a number of important functions of such vegetation, including stabilisation of the bank, provision of cover from predators, supply of organic material to the food chains of the stream and shade moderating temperature variations, especially in summer (Riding and Carter 1992; Boulton and Brock 1999).

The abundance of woody debris, included in the "vegetation character" attribute of Cohen et al. (1998), is also known to be positively associated with platypus occurrence (Rohweder 1992) and foraging (Serena et al. 2001), again probably being related to the complexity of habitats available for macroinvertebrates (Benke et al. 1985; Anon. 1998; Anon. 2000a).

Cohen et al. (1998) also sorted sites in the Bellinger-Kalang catchment, grouping river reaches into five categories based on procedures outlined in Brierley and Fryirs (2000). These are summarised in Table 2 and are generally ranked from the least (conservation) to the most disturbed sites (degraded), although the "strategic" priority #2 sites were identified as being more disturbed than the priority #3 sites and were given a higher priority as they may impact on other sites downstream. This paper analyses these Rivers Styles and conservation/rehabilitation categories in relation to the data on occurrence of the platypus. We propose priorities for conservation and rehabilitation of the river system for the future survival of platypuses in the Bellinger and Kalang river system and in rural areas in general.

Major floods in the Bellinger catchment in early 2001 provided an opportunity to assess the impact of floods on a known population of platypuses. A follow-up community survey was undertaken to determine the survival of platypuses post-flood.

METHODS

Study area

The Bellinger is a fertile river valley on the north coast of New South Wales just south of Coffs Harbour, and includes the main townships of Bellingen and Urunga (Figure 1). The valley extends approximately 50 km inland from the coast at Urunga, and is approximately 20 km wide from Tucker's Nob range in the north to the Bellbucca ridge in the south.

River Style	Channel planform and stability	Channel morphology	Channel geometry	Geomorphic units	Bed character	Vegetation character
Upland stream	Single thread, locally unstable	Irregular	10 m wide 1.5 m deep	Fine grained floodplains, pools, riffles	Sand to gravel	Pasture, weeds and regrowth
Headwater stream	Single thread, stable	Irregular to asymmetrical	10-20 m wide 1-2 m deep	Waterfalls, bedrock steps, bedrock cascades, glides, rapids, pools, riffles, mid-channel islands	Boulders to cobbles	Native forest, high woody debris loading
Gorge	Single thread, stable	Regular to irregular	20-40 m wide 2-3 m deep	Bedrock steps, cascades, rapids, glides, pools, riffles, boulder bars	Boulders to cobbles, minor gravel	Native forest, irregular woody debris loading
Bedrock river discontinuous alluvial floodplains	Single thread, locally unstable	Highly variable, ranging from regular to irregular, asymmetrical to symmetrical	40-100 m wide 5-10 m deep	Pools, riffles, point bars, lateral bars, islands.	Cobbles to gravel, minor sand	Native forest and pasture, low to moderate woody debris loading
Alluvial river meandering gravel-bed	Single thread, generally unstable	Asymmetrical	30-120 m wide, 2-10 m deep	Pools, riffles, point bars, lateral bars	Cobbles to gravel, minor sand	Pasture, native forest, weeds, minor woody debris
wandering gravel -bed	Single thread, naturally unstable	Asymmetrical	20-50 m wide, 1-3 m deep	Pools, riffles, point bars, islands	Cobbles to gravel	Pasture, native forest, weeds, minor woody debris
discontinuous	Single thread, generally stable	Asymmetrical	3-15 m wide, 2-3 m deep	Scour pools, vegetated lateral bars	Sand to silt	Pasture, native forest, weeds, minor woody debris
Tidal	Single thread, generally unstable	Symmetrical	30 - 100 m wide, 2-5 m deep	Pools, point bars, lateral bars	Sand, silt, minor gravel	Pasture, weeds, minor native forest

Table 1. Geomorphic attributes of each River Style in the Bellinger-Kalang catchment (Cohen et al. 1998: Table 4)

Priority	Nature of Sites
1. Conservation sites	least disturbed; river structure and vegetation relatively intact
2. Strategic sites	may be sensitive to disturbance or may affect sites downstream
3. High recovery potential	may show signs of natural recovery
4. Moderate recovery potential	moderately degraded with reasonable potential for recovery
5. Degraded	highly degraded reaches with little natural recovery potential

Table 2. Priority ranking of sites for river rehabilitation in the Bellinger-Kalang catchment (Cohen et al. 1998).

Forested lands rise steeply from the valley, forming the extremely rugged fringe of the New England Plateau. The Bellinger Valley comprises the catchment areas of the Bellinger and Kalang Rivers, referred to in earlier maps as the North and South Arms of the Bellinger River. The third major river of the valley, the Never Never River, is a tributary of the Bellinger River, which it joins near Gordonville, about 10 kilometres upstream of Bellingen township. Tidal influence extends to Bellingen on the Bellinger River and as far as Spicketts Creek on the Kalang River (Cohen et al. 1998). The valley and floodplain was rapidly cleared by the cedar-getters and during settlement in the mid to late 1800s (Anon. 1978; Lunney and Moon 1997). Now, the land is used primarily for dairying and beef cattle grazing, with small areas being planted for crops. The population of the valley was 12,253 in 1996, representing a population growth of 21 per cent over the previous 10 years (Anon. 2001a).

The upper reaches of the streams of the Bellinger and Kalang valleys flow through steep forested areas in their headwaters, but degradation due to human activities, particularly clearing for

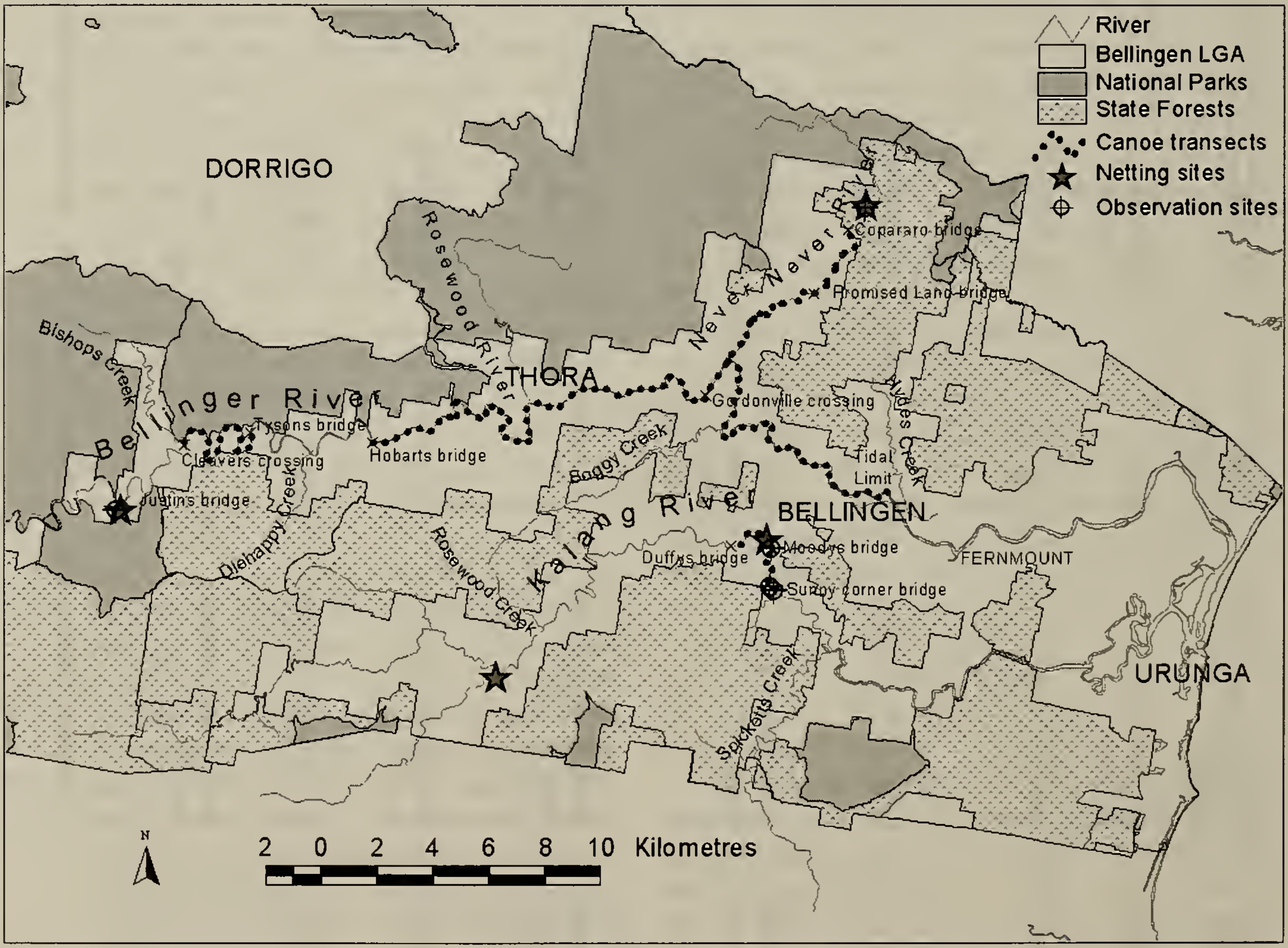


Figure 1. Location map of the Bellinger catchment, showing main features of the study area and the sections surveyed in the field work.

Location	Kalang River Jamisons Creek	Kalang River Jamisons Creek	Bellinger River Justins Bridge
Date	14.12.96	14.12.96	15.12.96
Sex	Female	Female	Female
Age	adult	adult	adult
Length (cm)	39.0	43.5	43.0
Bill length (cm)	4.9	4.9	5.1
Bill width (cm)	4.2	4.4	4.3
Weight (g)	730	905	900
Spur	0	0	0
Milk (oxytocin)	No	Yes	Yes

Table 3. Details of platypuses captured during field survey in December 1996.

agriculture, increases from the middle reaches to lower reaches upstream of the tidal limits at Bellingen and Spicketts Creek (Figure 1). Access of cattle to river banks has resulted in bank damage, especially in the lower Kalang River and the Bellinger River downstream of Thora. Parts of these sections of the rivers and their tributaries have good bank habitat for platypuses, but other sections are of lower quality due to the occurrence of natural gravel bars, to the effects of past gravel extraction, and to earth banks being cleared and/or damaged by cattle. The upper reaches of both these rivers and the Never Never River provide good platypus bank habitat, although some cattle damage to banks in parts of the upper sections of the Bellinger River and lower Never Never River was present at the time of the survey.

Riparian vegetation is generally continuous on both banks of the upper reaches of all the streams in the system but becomes less continuous in the lower reaches of most streams. The Bellinger River between the Never Never River junction and Bellingen was considered to be the most degraded section of the system. River oak *Casuarina cunninghamiana* was the main native riparian species found, while exotic species – willows *Salix* sp., camphor laurel *Cinnamomum camphora*, privet *Ligustrum* sp. and lantana *Lantana camara* – were widely distributed in the riparian zones of most streams at the time of the study.

Field sampling

Field sampling was carried out over 10 days during December 1996. The sections of the system surveyed by canoe, bank observation and netting are shown in Figure 1. The dates of platypus captured are given in Table 3.

Canoe and bank observations were made either in the two hours prior to darkness and/or the two hours after dawn. Most of the Bellinger River from the mid-catchment gorge to Bellingen was surveyed by canoe either in the late afternoon or early morning (Figure 1). The Kalang River was unsuitable for canoe transects along much of its length due to its smaller size and the presence of obstacles in the channel. The section of river downstream from Duffys Bridge was suitable for use of the canoe and was surveyed a number of times.

Live trapping of platypuses was carried out at four sites, one on the Never Never River, one on the upper Bellinger River and two on the Kalang River (Figure 1) using the methods of Grant and Carrick (1974). All captured females were injected with 0.2 ml of synthetic oxytocin (Syntocinon) to indicate the presence of lactation (Grant and Griffiths 1992).

The Kalang River was less intensively sampled than the Bellinger section of the catchment due to its unsuitability for canoe transects and difficulty of access for observation at sites which appeared to represent good platypus habitat. However, netting was carried out at one downstream and one upstream site on the Kalang River to assess the accuracy of reports obtained from local residents during the survey and to compare with community reports from this part of the river system.

Habitat assessment

At a number of accessible sites (mainly at road crossings) on the Bellinger (15), Never Never (8) and Kalang (15) rivers the following data or rank scores were collected to provide an assessment of habitat characteristics known to be associated with the occurrence of platypuses and their use of an area (Rohweder 1992; Bryant 1993; Ellem et al. 1998; Grant and Bishop 1998; Serena et al. 1998, 2001). This scoring procedure was based on both published and unpublished field observations of platypus habitat:

Habitat Category - this was a broad scoring of habitat suitability (1 best to 5 worst). Note: in the following categories, shade/shelter is usually provided by overhanging vegetation, but shade did not have to be present at time of observation as long as vegetation would provide shade/shelter at some times of the day. This is important not only to the platypus itself but to benthic invertebrate prey species:

Category 1. EXCELLENT HABITAT - pools and/or riffle areas with >75% earth banks consolidated by roots of vegetation and providing significant shade/shelter, on both sides of river.

Category 2. GOOD HABITAT - pools and/or riffle areas with 50-75% earth banks consolidated by roots of vegetation and providing significant shade/shelter, on at least one side of river or evenly distributed on both sides.

Category 3. MODERATE HABITAT - pools and/or riffles with 25-50% earth bank consolidated by vegetation and providing a little shade/shelter.

Category 4. POOR HABITAT - pools and/or riffles with 5-25% earth banks consolidated by roots of vegetation and providing little or no shade/shelter.

Category 5. MARGINAL - pools and/or riffles with < 5% earth banks consolidated by roots of vegetation and providing no shade/shelter

Riparian characteristics - these were features of banks that had been associated with platypus occurrence in other studies and were expressed as a percentage of sites at which they were present:

- bank damage attributable to stock access;
- bank damage attributable to floods;
- presence of riparian vegetation;
- presence of *C. cunninghamiana* (the most predominant native riparian tree species);
- presence of introduced plant species in the riparian zone (especially willows, lantana, privet and camphor laurel).

Community-based survey

A community-based wildlife survey, in which the platypus was one of the target species, was posted to residents of the Bellinger-Kalang valley in December 1997. A total of 3000 survey forms was distributed by post to every household. There was a free-post return. The survey consisted of a questionnaire and colour maps on A3 size paper. The first colour map was a user-friendly map of the area where respondents to the survey could mark on it the locations of fauna, including the platypus, they had seen in the area. A grid was included on this map so that grid references could be determined with ease. These locations were then transferred to the geographical information system, ArcView, for analysis. The survey form, including the maps of the catchment, appear in Figure 2A&B.

Relationship to River Styles

To investigate the possibility that analysis of River Styles may be a useful method of predicting platypus occurrence or relative abundance in sections of a river system, platypus records from the field and community surveys were allocated by one of the authors (TRG, who has Provisional River Styler accreditation) to the various River Styles identified in the Bellinger System by Cohen et al. (1998). Stream reaches representing various River Styles from Cohen et al. (1998: Figures 1A and 9) were transposed onto the relevant 1:25000 topographical maps and the distances calculated using a manual map measure (Uchida Curvimeter).

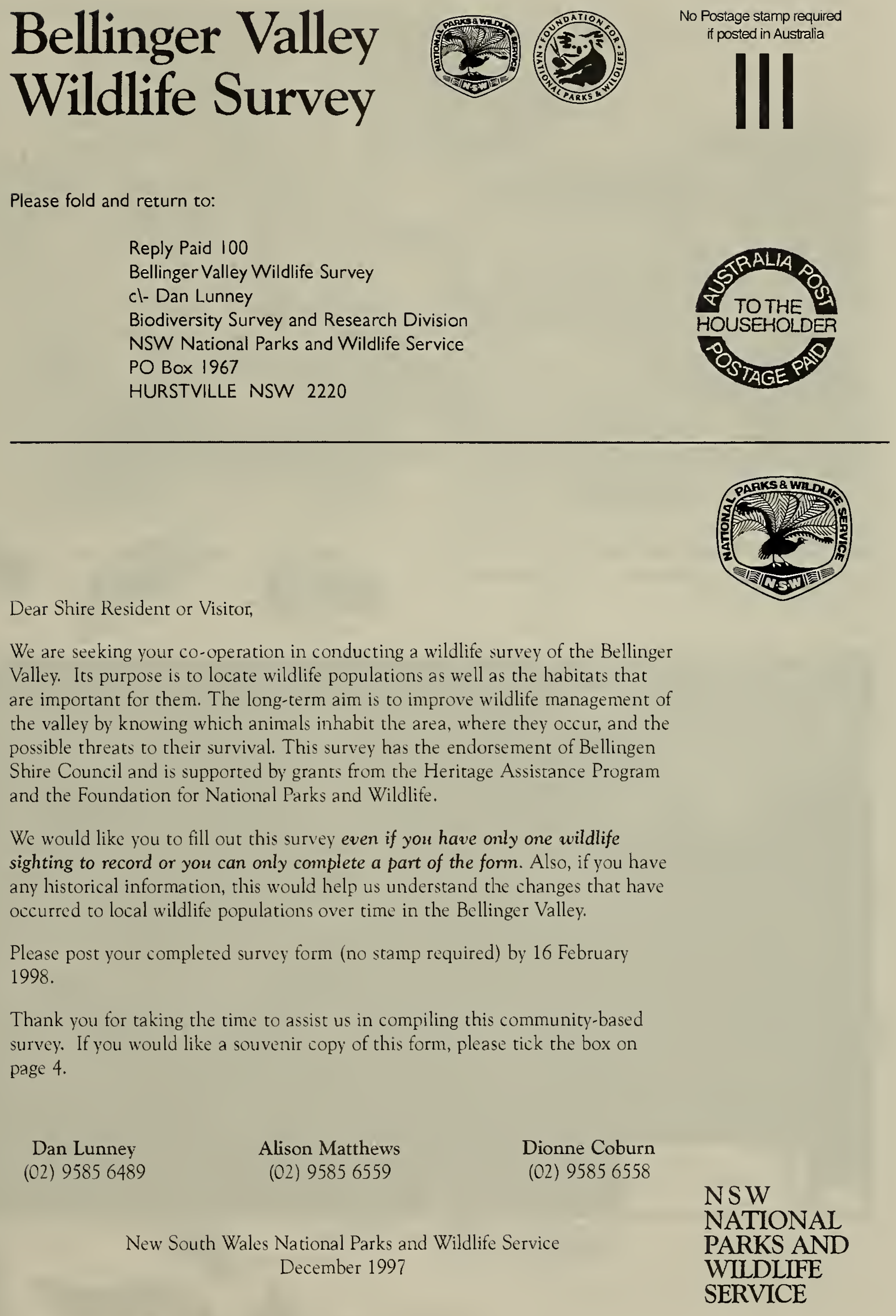
As only two platypus records were obtained from the mountain headwater streams and upland stream River Styles, these stream categories and observations were not included in the analysis. Observations of platypuses in streams which were not classified by Cohen et al. (1998) or were in the tidal sections of the rivers (one observation only) were also not considered.

Relationship to river disturbance

As was carried out for the River Styles categories, conservation/rehabilitation sections from Cohen et al. (1998: Figures 1A and 9) were transposed onto the relevant 1:25000 topographical maps and the distances calculated using a manual map measure (Uchida Curvimeter). Platypus records from the field and community surveys were allocated to the various conservation/rehabilitation categories.

Post-flood survey

In September 2001 we contacted those community members who had reported platypuses in the wildlife survey conducted three years previously. A letter was individually addressed to each respondent and contained a covering note, a questionnaire to gather information on post-flood platypus sightings and a map showing the results of the community and field locations of platypuses on which each respondent could mark recent sightings.



Bellinger Valley Wildlife Survey

No Postage stamp required
if posted in Australia

Please fold and return to:

Reply Paid 100
Bellinger Valley Wildlife Survey
c\- Dan Lunney
Biodiversity Survey and Research Division
NSW National Parks and Wildlife Service
PO Box 1967
HURSTVILLE NSW 2220

AUSTRALIA POST
TO THE HOUSEHOLDER
POSTAGE PAID

Dear Shire Resident or Visitor,

We are seeking your co-operation in conducting a wildlife survey of the Bellinger Valley. Its purpose is to locate wildlife populations as well as the habitats that are important for them. The long-term aim is to improve wildlife management of the valley by knowing which animals inhabit the area, where they occur, and the possible threats to their survival. This survey has the endorsement of Bellingen Shire Council and is supported by grants from the Heritage Assistance Program and the Foundation for National Parks and Wildlife.

We would like you to fill out this survey ***even if you have only one wildlife sighting to record or you can only complete a part of the form.*** Also, if you have any historical information, this would help us understand the changes that have occurred to local wildlife populations over time in the Bellinger Valley.

Please post your completed survey form (no stamp required) by 16 February 1998.

Thank you for taking the time to assist us in compiling this community-based survey. If you would like a souvenir copy of this form, please tick the box on page 4.

Dan Lunney	Alison Matthews	Dionne Coburn
(02) 9585 6489	(02) 9585 6559	(02) 9585 6558

New South Wales National Parks and Wildlife Service
December 1997

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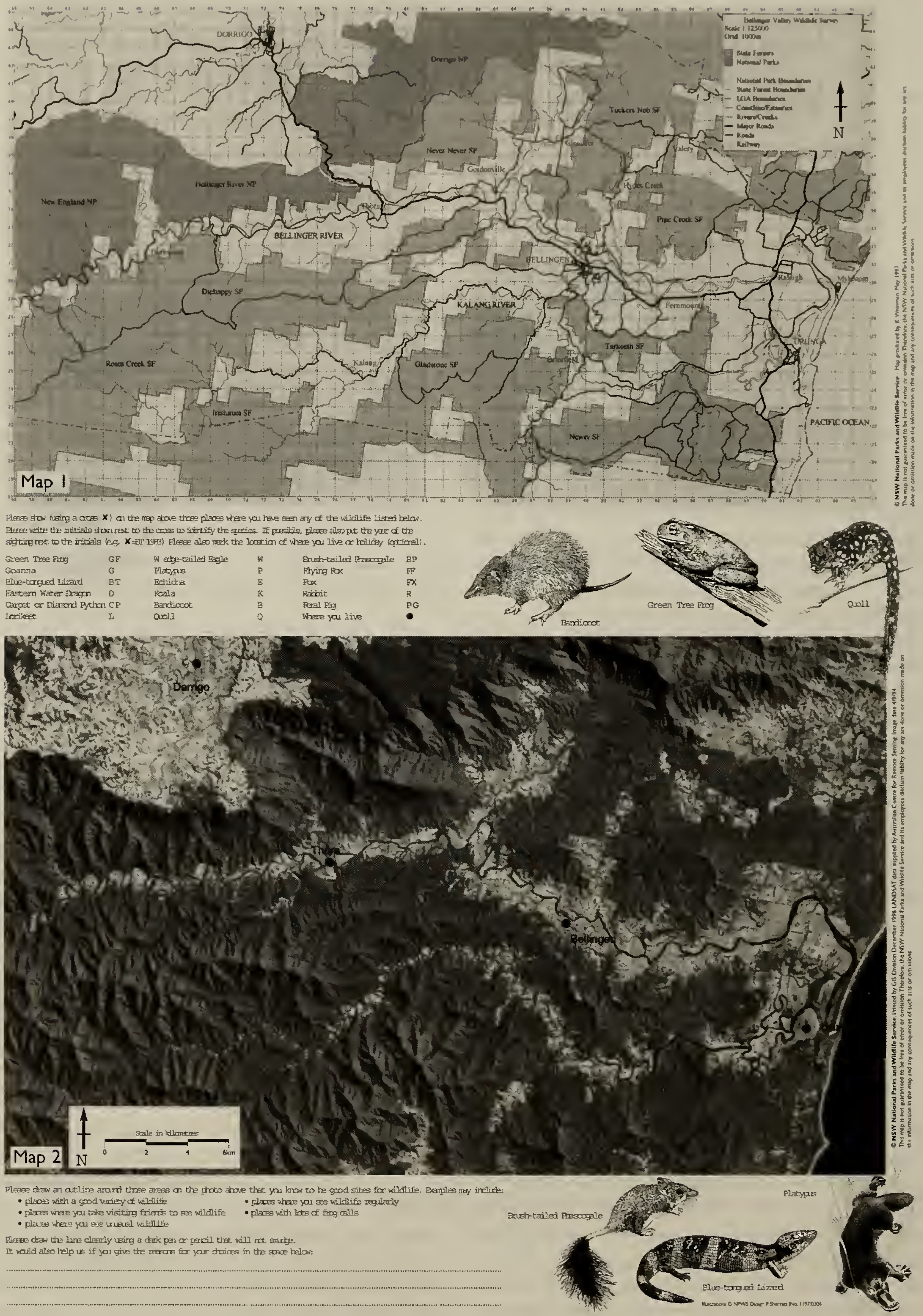
Figure 2A. The Bellinger Wildlife Survey form.



Please show (using a cross ✗) on the map above those places where you have seen any of the wildlife listed below. Please write the initials shown next to the cross to identify the species. If possible, please also put the year of the sighting next to the initials (e.g. ✗=BT 1983) Please also mark the location of where you live or holiday (optional).

Green Tree Frog	GF	Wedge-tailed Eagle	W	Brush-tailed Phascogale	BP
Goanna	G	Platypus	P	Flying Fox	FF
Blue-tongued Lizard	BT	Echidna	E	Fox	FX
Eastern Water Dragon	D	Koala	K	Rabbit	R
Carpet or Diamond Python	CP	Bandicoot	B	Feral Pig	PG
Lorikeet	L	Quoll	Q	Where you live	●

Please draw an outline around those areas on the photo above that you know to be good sites for wildlife. Examples may include:

- places with a good variety of wildlife
- places where you take visiting friends to see wildlife
- places where you see unusual wildlife
- places where you see wildlife regularly
- places with lots of frog calls

Please draw the line clearly using a dark pen or pencil that will not smudge.
It would also help us if you give the reasons for your choices in the space below:

....

....

....

© NSW National Parks and Wildlife Service. Printed by GIS Division December 1998 LANDSAT data supplied by Australian Centre for Remote Sensing Image date 4/9/94
This map is not guaranteed to be free of error or omission Therefore, the NSW National Parks and Wildlife Service and its employees disclaim liability for any act done or omission made on the information in the map and any consequences of such acts or omissions

Illustrations © NPWS Design P Sherratt No. 1197/0306

Figure 2B. The Bellinger catchment map provided with the Wildlife Survey form.

RESULTS

Field survey

Platypuses were observed or caught in all three rivers at a total of 36 locations (Figure 3). Two platypuses were captured at one of the two sites (the upstream site) on the Kalang River but none was observed in the limited sampling of this river by foot or by canoe. None was caught at the Never Never River netting site, but one was captured at the site on the upper Bellinger River. All the individuals captured were female, two of which were lactating, indicating the occurrence of breeding populations in both the Bellinger and Kalang rivers. All animals captured were within expected dimensions and body condition (Table 3). Platypuses were found to be common and continuously distributed along the Bellinger and Never Never Rivers, being captured or observed at 35 sites (Figure 3).

The canoe transect survey method was most successful, yielding 2.2 animals per hour of observation, compared with 0.17 for both netting and observations by foot from river banks (Table 4).

Community reporting of the occurrence of platypuses

A total of 522 replies (17.4% return) was received to the Bellinger valley wildlife survey. Platypuses were recorded at 123 sites by the community-based survey. Only two platypus records were obtained from the headwater streams of the catchment and the field survey did not sample these streams. These data showed a much lower number of sightings (13) in the Kalang River and its tributaries than in the Bellinger River (110) and its tributary streams.

The field and community-based data showed that the platypus is commonly found throughout the Bellinger River catchment, including the Never Never and Rosewood Rivers, and its distribution is probably continuous above the tidal limit at Bellingen to the headwater streams, which were not surveyed in this study. There was one report of a platypus downstream of the tidal limit on the Bellinger River. As well as being reported less often along the Kalang River

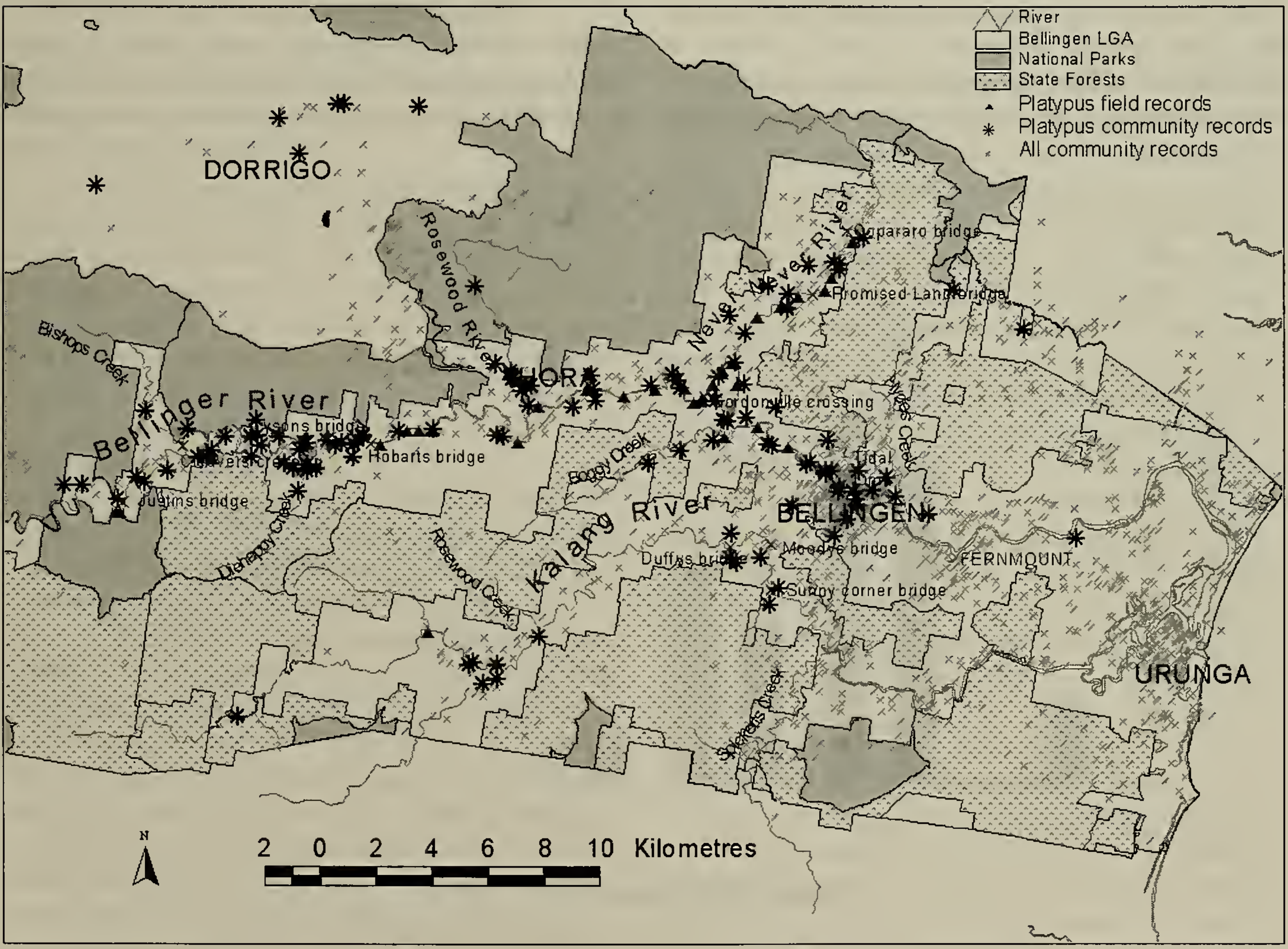


Figure 3. The location of field and community-based records of platypuses in the Bellinger catchment.

Method	Kalang River			Bellinger River			Never Never River			Total
	Hrs	No.	CPU *	Hrs	No.	CPU	Hrs	No.	CPU	CPU
Canoe observations	3.75	0	0	9.5	29	3.05	2.75	6	2.2	2.20
Bank observations	4.0	0	0	0.25	1	4.0	1.5	0	0	0.17
Netting	8.5	2	0.23	4.5	1	0.22	5	0	0	0.17
Total	16.25	2	0.12	14.25	31	2.18	9.25	6	0.65	0.98

*CPU: Catch/Observation per Unit Effort
Canoe = individuals seen/hour observation in each observation period
Observation = individuals seen/hour in each observation period
Netting = individuals captured per net hour (1x50m net in water for 1 hour)
Total = division of total individuals seen/caught by total hours of observation or net hours

Table 4. Success of various field survey methods used for recording platypuses in December 1996.

system, platypuses seemed to be more discontinuous in their distribution in this part of the river system (Figure 3).

Reliability of the community-based data set

The distribution of community-based reports of platypuses in the Kalang and Bellinger components of the river system showed considerable overlap with the field records (Figure 3). There were few observations by the community outside the areas in which the field work identified the occurrence of the species. One exception to this was the section of the Kalang River between Moodys Bridge and Sunny Corner, where no sightings or captures were made during the field work, but where platypuses were reported by the community.

Habitat assessment

There was little difference among the 15 sites sampled on the Bellinger and Kalang rivers in terms of habitat suitability (Figure 4), although on the Kalang River, 13% of the sites sampled were classified as

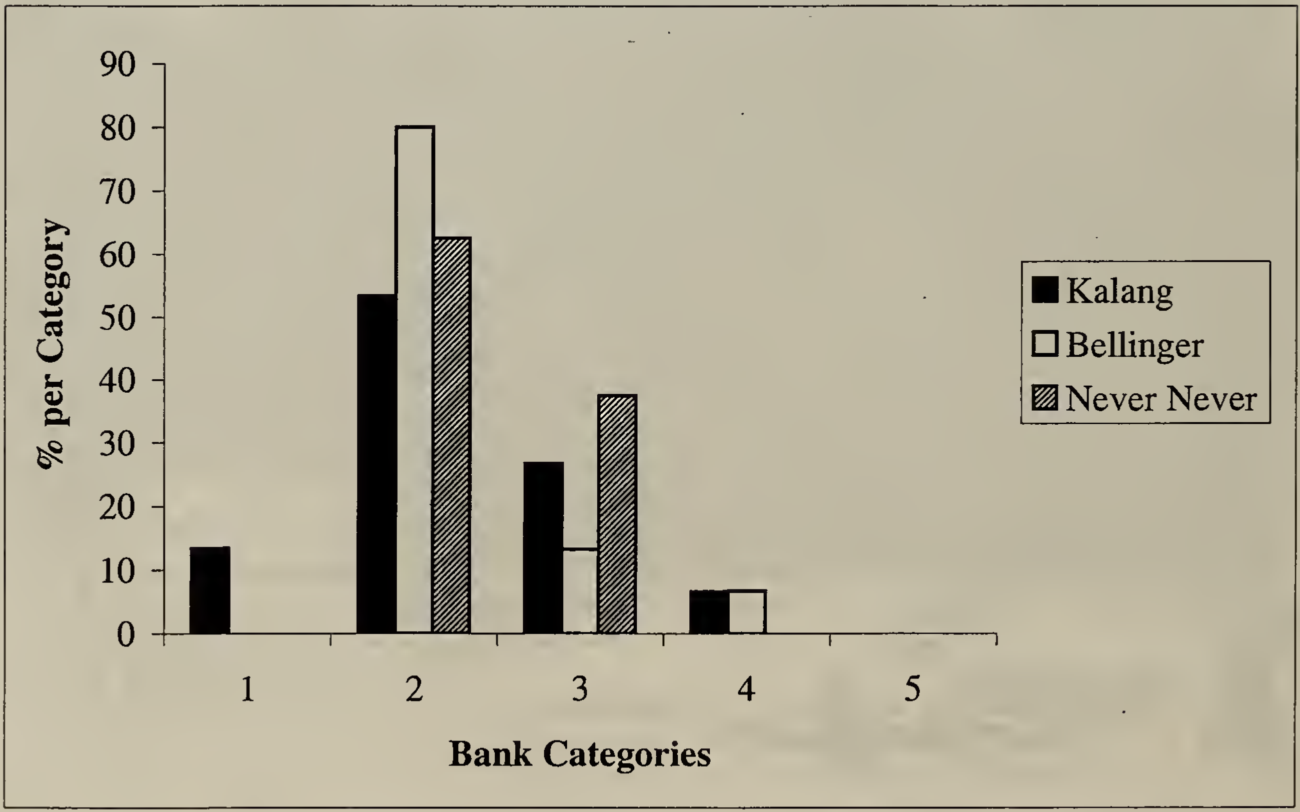


Figure 4. Percentage of sites at which bank suitability categories were recorded on the Kalang, Bellinger and Never Never Rivers.

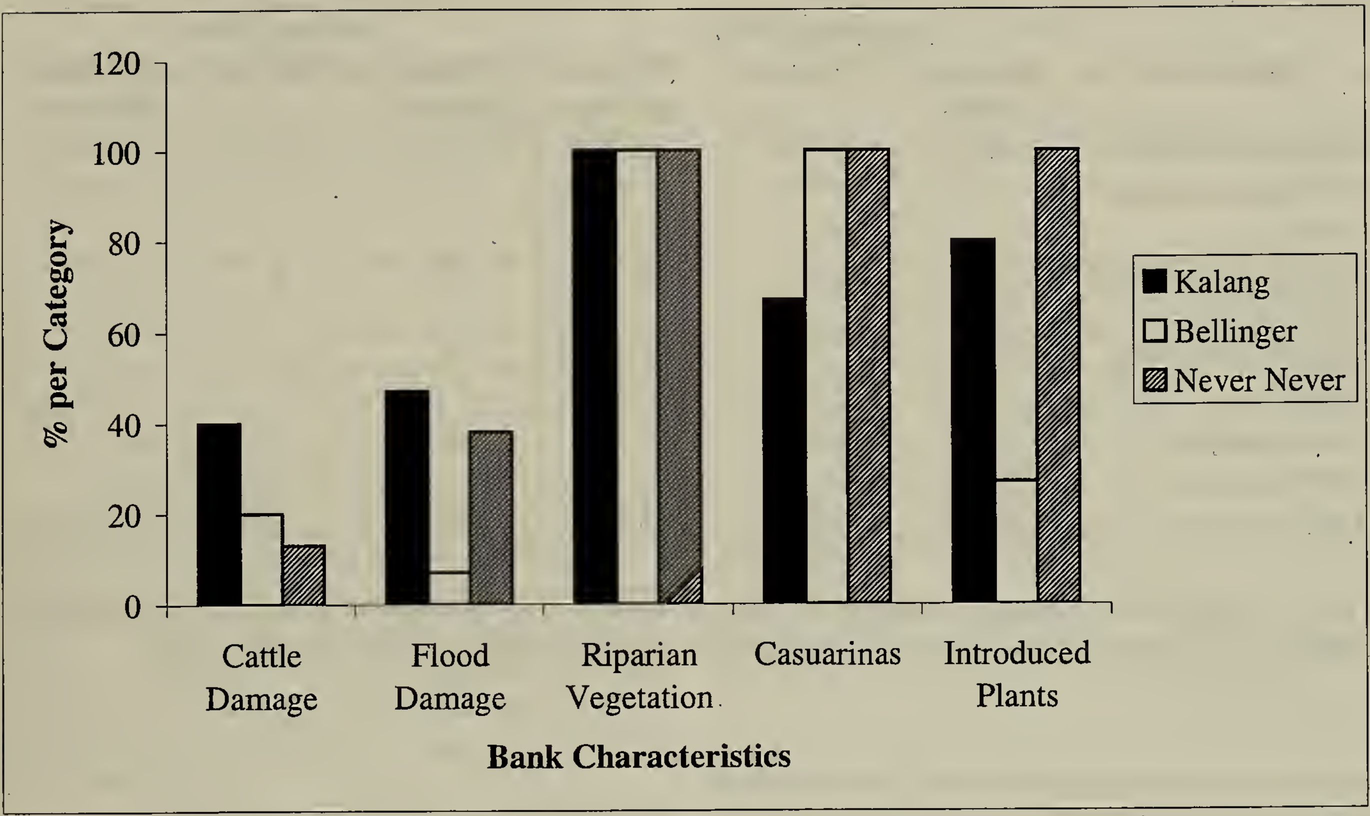


Figure 5. Percentage of sites exhibiting various bank characteristics on the Kalang, Bellinger and Never Never Rivers.

category 1, whereas none of the sites on either the Bellinger River or its major tributary, the Never Never River, fell into this category.

All sites sampled had some riparian vegetation present but fewer sites on the Bellinger River had introduced species of riparian plants and more had *C. cunninghamiana* trees on the riverbank. More sites on the Kalang and Never Never Rivers than on the Bellinger River exhibited cattle and flood damage (Figure 5).

Relationship to River Styles

Table 5 details the lengths of each River Style, the total numbers of platypuses recorded in the field and community surveys and the numbers of platypus records per kilometre of each River Style.

The River Styles of the Bellinger and Kalang sections of the catchment differ, with almost all (97%) of the Kalang River catchment being classified as confined bedrock with discontinuous alluvial floodplains, while the Bellinger River catchment contained a variety of Rivers Styles, ranging from 57% confined bedrock with discontinuous alluvial flood plains, through 24% alluvial with a meandering gravel bed to 10% and 9% of alluvial stream with a wandering gravel or discontinuous bed (Table 5).

In the Bellinger River, there were significantly more platypus records in the alluvial meandering gravel bed sections of river and fewer in the discontinuous alluvial stream than expected if platypuses were distributed uniformly across River Styles (χ^2=26.64, 3d.f., P<0.01). In the Kalang River, platypus records were distributed evenly across River Styles. Expressed on the basis of platypus records per kilometre of river represented by each River Style, the Bellinger River had 0.95 records/km in the confined bedrock with discontinuous flood plains River Style, while the Kalang River (where this River Style made up 97% of the river downstream of the mountainous headwater reaches) had only 0.23 records/km (less than 25% of the value for the Bellinger). In the only other River Style represented in the Kalang River, alluvial river with meandering gravel bed (3% of the river), there were no platypus records and yet this was the River Style on the Bellinger River which had most records (2.1/km).

Relationship to river disturbance

The lengths of each conservation and rehabilitation priority reaches proposed by Cohen et al. (1998), along with the total numbers of platypus records from the field and community-based data, as well as the number of records per kilometre for each priority category in the Bellinger and Kalang

River Style	Bellinger River Distance (km)	Platypus	Platypus per km	Kalang River Distance (km)	Platypus	Platypus per km
Confined bedrock with discontinuous floodplain	58.9	56	0.95	59.9	14	0.23
Alluvial meandering gravel bed river	24.8	53	2.14	2.1	0	0
Alluvial wandering gravel bed	9.8	13	1.33	0	0	0
Discontinuous alluvial stream	9.1	3	0.33	0	0	0
Total	**102.6**	**125**	**1.22**	**62**	**14**	**0.23**

Table 5. River Style distances, numbers of platypus records and numbers of platypuses reported per kilometre of river in the Bellinger and Kalang rivers and their tributaries in December 1996.

catchments, were compared (Table 6). The number of platypus records per kilometre of river in the Bellinger River increased from the "strategic" category (0.74/km) through the "high recovery potential" (0.97/km) and "moderate recovery potential" (1.80/km) categories to be highest in the most "degraded" (2.25/km) section of the river. There were significantly more platypus records than expected in the degraded and moderate recovery potential categories (χ^2=17.99, 3d.f., p<0.01). In addition, the number of records of platypuses in the Bellinger River was much higher (1.22/km) than in the Kalang River (0.23/km), in spite of the fact that the latter system appears to be less disturbed than the Bellinger River.

Post-flood survey

A total of 43 replies was received from respondents who had reported platypuses in the 1997 survey. Twenty-one respondents had been near the river since the 2001 floods and of these, 7 had seen platypuses. Sightings of platypuses post-flood were in Hydes Creek (6 sightings), Boggy Creek (1 sighting), the Never Never River (1 sighting), the Kalang River between Duffys and Moodys bridges (1 sighting) and the upper Bellinger River between Diehappy and Bishops Creeks (2 sightings).

River Style	Bellinger River Distance (km)	Platypus	Platypus per km	Kalang River Distance (km)	Platypus	Platypus per km
Conservation	-	-	-	20.5	5	0.24
Strategic	5.4	4	0.74	13.9	4	0.29
High recovery potential	70.9	69	0.97	21.9	5	0.22
Moderate recovery potential	16.1	29	1.80	5.7	0	0
Degraded	10.2	23	2.25	-	-	-
Total	**102.6**	**125**	**1.22**	**62**	**14**	**0.23**

Table 6. Conservation/rehabilitation priority distances, numbers of platypus records and numbers of platypuses reported per kilometre of river in the Bellinger and Kalang rivers and their tributaries in December 1996.

DISCUSSION

Data from the field and community surveys

The results strongly support the hypothesis that the community-based data from this study are reliable. The field observations and captures of platypuses closely corresponded to community records. As a result of this correspondence, the field and community data were combined in the analysis of platypus occurrence in relation to River Styles and conservation and rehabilitation priorities. Further, a post-flood survey was able to be conducted because of the reliability of community records.

The lack of sightings from the headwater streams of the whole catchment suggest a lack of observation, rather than the species not occurring in them. This is supported by the low reporting of other wildlife species in the community wildlife survey in these areas (Figure 3). It is assumed that platypuses would almost certainly occupy these sections of the catchment streams, although this was not determined by the field survey.

The field and community-based data rank the Bellinger River part of the system as being more suitable for occupation by platypuses than the Never Never and Kalang rivers. The limited habitat data collected during the survey point to the Kalang River having less suitable platypus habitat than either the Never Never or Bellinger Rivers. The discontinuous distribution of the platypus in the Kalang River, especially between Moodys Bridge and Rosewood Creek, almost certainly identified poorer habitat conditions. As community reports of other wildlife species were made along the Kalang River, the lack of platypus records from these sections means that the species is not found or is uncommon in these sections of the river. Further, any temporary loss of individuals from an area, such as from a flood, should not affect an accurate determination of distribution if the community had observed them in these sections of the river at other times. This is one of the values of the community survey, namely it was not restricted to one point in time and it also considered historical records. Qualitative field observations of the Kalang River between Moodys Bridge and Rosewood Creek confirmed that this section had poorer habitat quality than other sections of the river, with considerable disturbance of the river banks due to depletion of the riparian vegetation and cattle access, as well as accumulation of sand in the river bed.

The field survey did not allow an adequate explanation to be made of the differences between the Bellinger and Kalang sections of the river system in terms of the observed platypus distribution. While parts of the Kalang were more degraded than sections of the Bellinger and Never Never rivers, platypus reports and field sightings were common in the Bellinger River between the Never Never River junction and the town of Bellingen, a river section which was also highly altered by bank clearing, stock damage to banks and past gravel extraction.

One report was obtained of a platypus in the tidal section of the Bellinger River, close to the entrance of Connells Creek. Three reports of platypuses in the tidal section of the river were also made to the authors during the field study; one at Fernmount in the 1940s, another at the mouth of Hydes Creek in 1996 and one near the Old Butter Factory in Bellingen (which was said to be "recent"). Platypuses have occasionally been found in the sea (Fleay 1980; Connolly and Obendorf 1998) and in estuarine habitats, but such occurrences are irregularly reported and are considered unusual (Stone 1983; Grant 1991, 1999; Rohweder 1992; Hird 1993; Menkhorst 1995; Connolly and Obendorf 1998; Rakick et al. 2001). It seems unlikely that the species regularly occupies the brackish or saline waters of estuarine environments. Nothing is known of its abilities to osmoregulate under marine or brackish conditions or any need by the species to have access to fresh water to groom salt from the fur, as occurs in several species of otters (Kruuk 1995). Platypuses are known to consume a range of benthic invertebrates as food but insect larvae are the most common prey items (Faragher et al. 1979; Grant 1982). In a number of rivers along the coast of New South Wales, tidal influences and/or saline intrusion into the lower reaches results in the diversity of benthic macroinvertebrates beginning to change at the tidal limit from being numerically dominated by insect fauna to being dominated by Crustacea, including amphipods and isopods, with oligochaetes worms and gastropod molluscs also having greater representation (Anon.1993; Simon Williams, then of Australian Water Technologies, pers. comm.). This could affect platypus distribution in the lower reaches of rivers of coastal New South Wales. It is also known that increased conductivity impairs the ability of the platypus to locate moving prey items, particularly small invertebrates, using the electrosensory mechanisms in its bill (Pettigrew et al. 1998). Competition with benthic-feeding fish species, which do not enter the freshwater sections of rivers, and possible predation by larger fish species, may also be involved in the occurrence of platypuses being unusual in tidal areas.

Relationship to River Styles

The differences in distribution and numbers of platypus records between the two rivers were not found to be related to the differences in River Styles between the two parts of the system. On the basis of our findings in the Bellinger catchment we consider that analyses using the River Styles framework (Brierley et al. 2002) will not successfully predict the occurrence of platypuses. However, methods integrating geomorphic and biological considerations could lead to a framework which may be capable of predicting the suitability of streams for occupation by the platypus. Such integration could also provide a better basis for river management and rehabilitation than arises from the consideration of either geomorphic or biological considerations in isolation. This approach has been called the "landscape ecology approach" by Tockner et al. (2002).

Relationship to river disturbance

This study has shown platypuses to be present in degraded habitat of the Bellinger catchment. However, it would be a mistake to be complacent about these observations and regard disturbances of rivers to be benign with respect to the platypus.

Despite the common occurrence of platypuses in agricultural areas, there are strong indications that platypus distribution has been fragmented and/or their numbers reduced in the streams of the Eden area (Lunney et al. 1998) and in the Bega (Brooks and Brierley 1997), Thredbo (Goldney 1998) and Richmond (Rohweder and Baverstock 1999) rivers of New South Wales and in the Wimmera River system in Victoria (Anon. 1999, 2000b, 2001b). In each of these instances the changes have been mainly attributed to the effects of agricultural practices. Lack of reports of platypuses from the Kalang River in the disturbed section between Moodys Bridge and Rosewood Creek also point to a fragmentation of platypus distribution within this part of the Bellinger catchment.

Lunney et al. (1998) attributed fragmentation of platypus populations in the Eden region (Bega Valley Shire) of New South Wales to the effects of farming, particularly cattle grazing and the clearing of the riparian vegetation since 1830. Brooks and Brierley (1997) and Brierley et al. (1999) have detailed the effects of early agricultural practices in the Bega River valley of New South Wales, confirming that these practices were almost certainly responsible for the irreversible changes to that river system. However, Turnbull (1998) recorded the occurrence of platypuses in most of the rivers around Bombala, in the tableland headwater streams of the Bega and Snowy Rivers in New South Wales, in spite of the area having been utilised for both cattle and sheep grazing for the past 160 years.

Of the 11 platypus sightings made by respondents to the post-flood questionnaire in the Bellinger catchment, 8 were in tributary streams. This suggests that the tributaries act as refuge areas during extreme floods. The tributaries could also be important for this population if the main streams of the Bellinger River system experience further degradation. This latter suggestion is based on our data from the Bega River (Lunney et al. 1998) where historically platypuses were found in the lower reaches, but it is now so degraded, shallow, sandy and exposed, that it no longer supports viable platypus populations. Instead platypuses occur only in the more protected and less developed tributary streams of the Bega River system.

Conservation and rehabilitation

Considering that the distribution of this unique Australian species overlaps extensively with activities of rural communities, its conservation depends on the adaptive management of these activities. The species has survived the current environmental disturbances so far, but its future conservation can only be assured by strategies aimed at preventing any further degradation of its habitat in these areas and by proactive rehabilitation of damaged sections of streams and a recognition of the possible importance of the tributary streams in retaining refuge populations of platypuses.

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Reducing the By-catch of Platypuses (*Ornithorhynchus anatinus*) in Commercial and Recreational Fishing Gear in New South Wales

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Grant, T.R., Lowry, M.B., Pease, B., Walford, T.R. and Graham, K. (2004). Reducing the by-catch of platypuses (*Ornithorhynchus anatinus*) in commercial and recreational fishing gear in New South Wales. *Proceedings of the Linnean Society of New South Wales* **125**, 259-272.

The problem of platypus by-catch mortality in the eel, yabby and carp trap fisheries in New South Wales is reviewed, and the results of several experiments to determine the effectiveness of gear modifications to reduce platypus by-catch are presented. Entrance screens with 50-60 mm openings prevented the entry of platypuses into eel or yabby traps. Larger screens were not effective as a deterrent to platypuses entering traps. By-catch of platypuses in the eel fishery can be minimised by restricting traps to estuarine areas, where platypuses seldom occur, and by providing air spaces in the cod ends of traps used in impoundments and farm dams. Prohibiting the use of yabby traps in areas where platypuses are known to occur provides the most practical protection against by-catch of platypuses in this fishery. Platypuses were unable to exit from prototype carp traps, designed to permit escape of air-breathing species, but the provision of appropriately-sized openings at the base of the entrance funnels in these drum traps permitted platypuses to escape.

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KEYWORDS: by-catch, carp, eel, fishing, *Ornithorhynchus anatinus*, platypus, yabby.

INTRODUCTION

By-catch mortality of air-breathing vertebrates, including several species of freshwater turtles and diving birds, water rats (*Hydromys chrysogaster*) and platypuses (*Ornithorhynchus anatinus*), has been recognised for some time as a significant problem in various inland fisheries in Australia (Jackson 1979; Beumer et al. 1981; Grant 1991, 1993; Grant and Denny 1991; Leadbitter 2001). Such by-catch mortality of platypuses is of particular concern in small streams, where multiple drownings of breeding individuals have the potential to impact severely on small local populations. For example, an abandoned fyke net in a tributary of the Gellibrand River in Victoria was found to contain the skeletons of 17 platypuses (Serena 2003).

There has often been conflict between the desires of fishers to maximise catches of their target species, and the implementation of effective methods to reduce non-target by-catch. This has resulted in a diverse range of regulations enacted by fishery authorities and voluntary gear modifications by fishers aimed at reducing the mortality of non-target species (e.g. Leadbitter 2001). Unfortunately, little research or monitoring has been done to assess the effectiveness of voluntary and regulated gear modifications.

An historical assessment of inland fishing in New South Wales showed that commercial fishing probably resulted in significant platypus mortality when small-mesh nets were used (Grant 1991, 1993; Grant and Denny 1991). No commercial or recreational fishery using nets or traps to capture native fish species or salmonids in freshwater sections of coastal rivers is now permitted in New South Wales (NSW), but there is a commercial eel fishery based on the use of baited traps in estuaries, farm dams and a few large impoundments. West of the Great Dividing Range, the commercial fishery for native fin-fish species was phased out in 2001. Fishers previously involved in that industry have been encouraged to fish for yabbies, mainly (*Cherax destructor*), using "Opera house" traps (Rankin 2000). The introduced carp (*Cyprinus carpio*) is also targeted by commercial fishers using a variety of gear, including traps, mesh and haul nets and electrofishing.

There are a number of options to prevent or minimise mortality of air-breathing wildlife species in traps. The most direct way is to ban fishing in areas where these potentially vulnerable species occur.

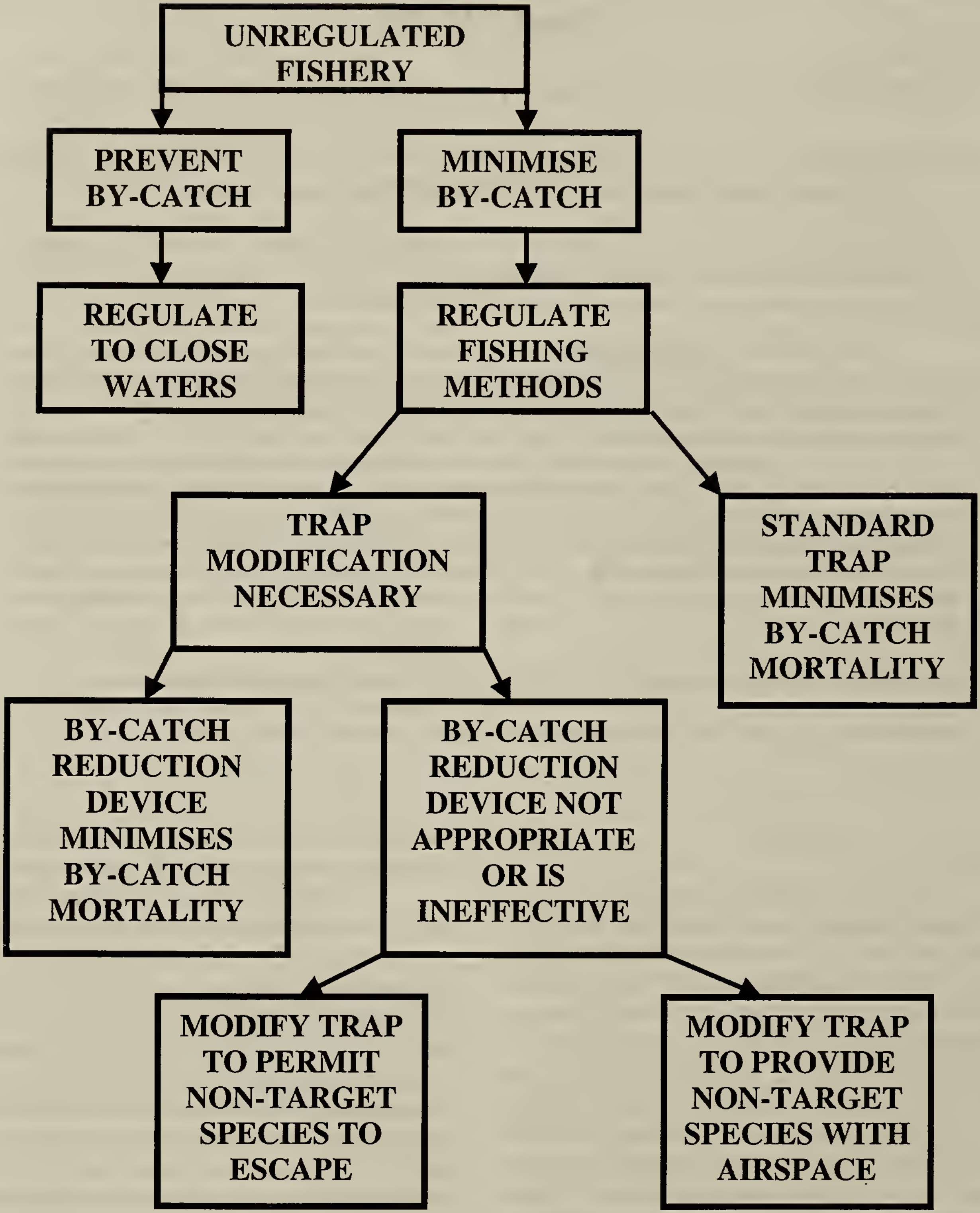

Figure 1. Schematic diagram of possible options available to achieve by-catch reduction of air-breathing species in fisheries operations.

However, maintaining a commercial fishery, while still addressing the issue of by-catch mortality, is to adopt capture methods which minimise by-catch. Mortality of air-breathing non-target species can be reduced or prevented by trap modifications, such as fitting devices to keep non-target species out (By-catch Reduction Device - BRD), providing a route to let them escape or permitting access to an airspace once they have entered a trap. Figure 1 summarises these possible options, which need to be explored in relation to the following issues:

Fishery requirements. The practicalities and economics of the fishery, in terms of trap design and cost, catch per unit effort, size of target species, and even the necessity to hide traps from possible interference and/or vandalism must be considered. For instance, a device which reduces by-catch but unduly restricts the entry of the target species into a trap may be economically unviable.

Behaviour of target species. It is necessary to know the reactions of the target species to trap modifications provided for non-target species. For example, the target species may escape via holes provided for the non-target species, or its behaviour could prevent the non-target species from utilising air spaces or escape routes provided.

Behaviour of non-target species. In fishing areas where a number of potential by-catch species occur, escape holes, BRDs or air spaces in traps may not be suitable for all potential non-target species. For example one species may use an escape hole in a trap which will not be used by another species.

This paper reviews past efforts to reduce the mortality of platypuses in the eel, yabby and carp fisheries and reports on a number of recent studies carried out to assess the effectiveness of trap modifications designed to reduce by-catch mortality of this species in these fisheries. The three fisheries are reviewed in separate sections of the paper and the experiments pertinent to each are discussed within these sections.

THE EEL FISHERY IN NEW SOUTH WALES

Freshwater eels were initially captured in upper estuarine waters of NSW as a by-catch of other fisheries. A fledgling industry targeting eels, based on the use of traps, was established in the early 1980s. At that time prices for eels were low but in the late 1980s and early 1990s a high-value export market to Asia was established. This increased interest in the fishery and the adoption of potentially more productive fishing methods. Requests were made by fishers to extend their operations into freshwaters using fyke nets (Figure 2a), which were known to be involved in the mortality of air-breathing wildlife species in the eel fisheries both in Tasmania and in Victoria (Jackson 1979; Beumer et al. 1981; Grant 1991). The potential fishers drew attention to a brief experiment in Lake Crescent and Dee Lagoon in Tasmania, where two fyke nets screened with 100 mm square mesh grids, and two unscreened control nets, were deployed in those lakes for six days. During that time, two platypuses were captured in the unscreened nets but none were captured in the ones with the screens in place (Grant 1991). While it appeared from this very limited experiment that a 100 mm mesh screen may have been effective in reducing platypus by-catch in Tasmania, an experiment done in the upper Shoalhaven River did not support this contention (Grant, unpublished data). Six platypuses (two female and four male) were placed separately between the river bank and the wing of a fyke net with a 100 mm mesh entrance screen in place. Two of these animals moved off after bumping the mesh and did not enter the fyke net but the other four either passed straight through into the net, or did so after first investigating the screen.

At the time it was also known that elevating the cod end of fyke nets above the surface was effective in permitting platypuses to breathe and survive capture (Jackson 1979; Beumer et al. 1981; Grant 1991; Figure 2b). Unfortunately professional fishers were unprepared to do this, as they feared their catch could be stolen and/or their equipment vandalised if it was visible above the surface.

As a result of the brief experiment with the Shoalhaven River platypuses described above, and advice from experts in the other states regarding the poor compliance of fishers to fit BRDs and/or to raise the cod-ends of their nets above the water level, the request by fishers to use fyke nets for eels, and to extend the fishery to freshwater streams was denied by NSW Fisheries. Instead, the fishery was restricted to estuarine waters, a limited number of impoundments and private farm dams, using baited traps without wings to direct animals into the traps (NSW Fisheries Eel Policy Document, May 1992).

The standard eel traps used in the fishery are shown in Figure 2c. They consist of a metal rod frame 50 cm wide by 40 cm high by 90 cm long covered with 30 mm mesh polyethylene netting. The single entrance funnel (or ‘valve’) is located in one end of the trap. The opening in the funnel consists of a hole in the netting stretched firmly into a 100 mm wide slot, and pulled approximately 20 cm into the trap. The traps used in estuaries have a 1.5 m long cod end (bag with a draw-string) on the opposite end of the trap from the entrance funnel. Those used in freshwater impoundments and farm dams are similar to the estuary trap, but have a 5 m long cod end. A 150-200 mm diameter float is fastened inside the cod end near the draw-string and from one to three 50 cm diameter aluminium hoops are fastened to the inside of the cod end to keep the passage to the surface open. These traps are normally baited with frozen pilchards or mullet to attract eels.

In the late 1990s anecdotal reports to the National Parks and Wildlife Service, NSW Fisheries and one of the authors (TRG) indicated that platypuses

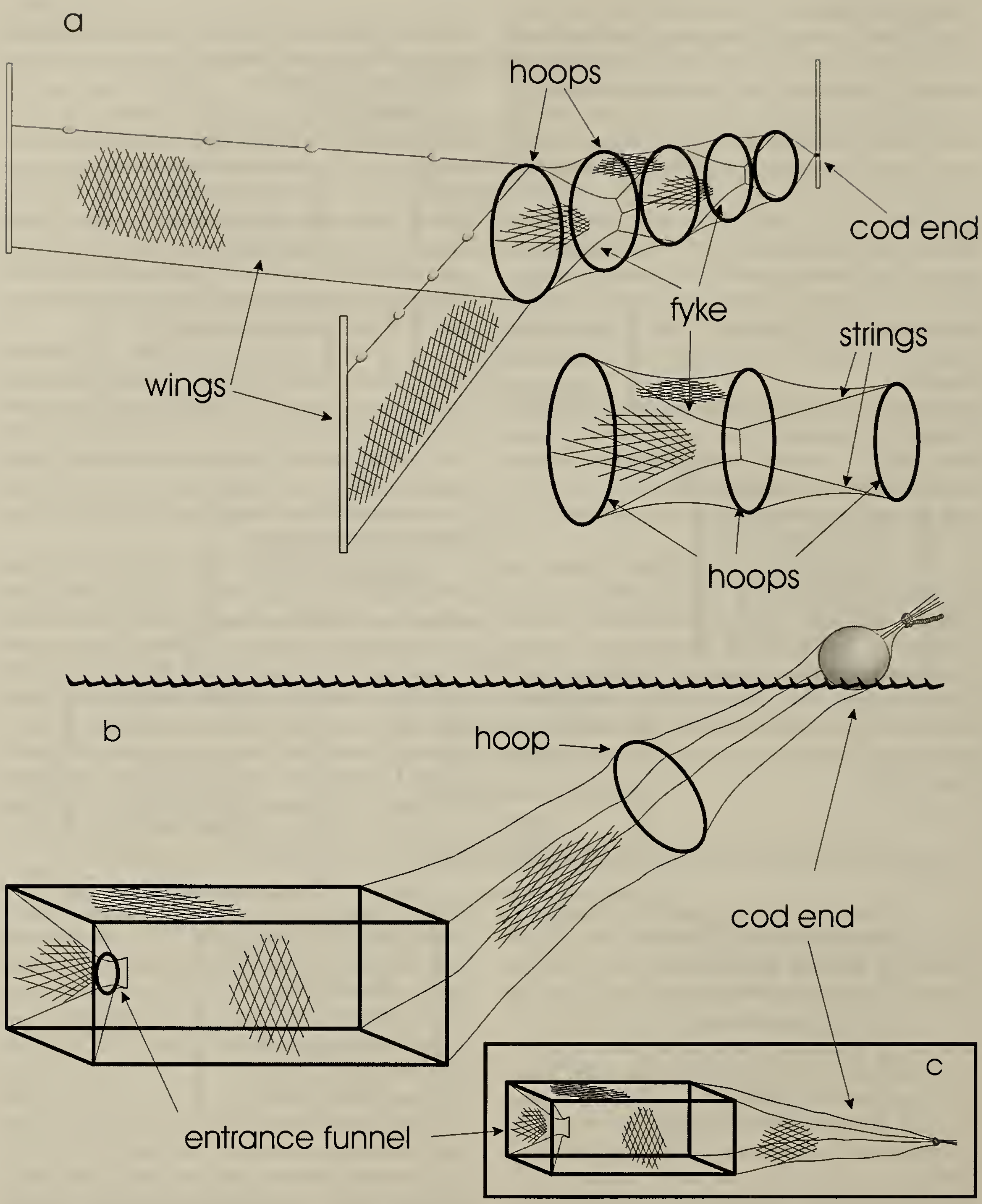

Figure 2. (a) Fyke net used in eel fisheries in Tasmania and Victoria. (b) Commercial eel trap used in the impoundment or farm dam eel fishery, showing the elevated cod-end creating an air space. (c) Typical eel trap used in the tidal estuary fishery in New South Wales. Note the entrance funnel or 'valve' which permits animals to enter the traps in one direction (wide outside to narrow inside). Animals are unable to locate the narrow inside entrance to escape. In Experiment 1 grids were placed at the narrow end of the funnel and in Experiment 2 at the wide end.

were being drowned in eel traps, not only in the upper reaches of some estuaries (where tidal influence changed with river discharges) but also in farm dams and impoundments (where air spaces were not consistently being maintained in the cod ends of traps). As a result, the following experiments were undertaken to determine if it was possible to reduce this mortality of platypuses by trap modification.

EXPERIMENT 1 - Investigation of grid sizes for a platypus exclusion device

The objective of this experiment was to determine the optimum grid size for excluding most platypuses from eel traps. The experiment was conducted in two pools on the Wingecarribee River in New South Wales from 17-19 February 2000.

Methods

The entrance funnels in eight standard eel traps were fitted with grids of different sizes. Each grid was a square divided into four equal openings; the openings in these grids ranged from 55 to 90 mm, in 5 mm increments. The plastic material used to make the grids was reinforced with lengths of 3 mm wire. The traps were fastened end to end (in order of decreasing grid size) and placed on a flat sandy area in the pools where platypuses were to be captured (Figure 3a). Water depth varied between traps but all had an airspace to allow the platypuses to breathe during the experiment.

Trials were done in different pools on two days. Platypuses were captured using unweighted gill nets (Grant and Carrick 1974) during the evening or morning. Once the required numbers of platypuses were captured, each individual was measured and weighed, then tested individually in the experiment. Platypuses were placed through an access door into the first trap leading into an entrance funnel with the 90 mm grid in place (Fig. 3a). Red-filtered lights were used to observe the animals at night, as observations in captivity indicated that platypuses are less responsive to disturbance under red light illumination (Grant, personal observation). The time that animals remained in each trap before passing through each grid was recorded, along with the number of attempts that each animal made to pass through the entrance funnel into the next trap in the series. Animals were removed from the experiment and released immediately if they remained in any trap for more than 15 minutes.

Results

A total of ten platypuses were used in the trials, comprising two adult males (1190 and 1760 g), six adult females (890-1060 g) and two juvenile females (700 and 760 g). Data are summarised in Table 1.

Trial 1: Animals tested at night were reluctant to pass through the 85 mm grid and none passed through the 75 mm grid, while a single female captured in the morning, and tested in daylight readily, passed through all grid sizes, although exhibiting some delay at the 80 and 70 mm grids. However, it was noted that the traps with 85-70 mm grids, which were apparently difficult for the animals to negotiate, were located in slightly shallower water than the rest of the traps. The water level in these traps was located at or just above the top of the grid, whereas the water level in the other traps was well above the top of the entrance grids. It was thought that this difference in water depth may have influenced platypus behaviour. Subsequently, all traps were placed in deeper water (well over the top of the grid) during the second trial.

Trial 2: The largest male (1760 g) could not pass through the 65 mm grid, but the smallest female (700 g) passed through each grid in less than 1 minute. The two slightly larger females did not initially pass through the 55 mm grid. However, it was found that, due to some unevenness on the bottom of the pool, the trap with this grid was in slightly shallower water than the preceding traps in the series. After moving this last trap to a position in slightly deeper water, animals passed through the 55 mm grid almost immediately.

The data from Trial 1 indicated that there was a greater reluctance for platypuses to negotiate the grids when the traps were less submerged. However, Trial 2 confirmed that female platypuses of up to 1 kilogram in weight could pass through a 55 mm grid. Animals smaller than 1 kg passed through easily, while the 1 kg female had a tighter squeeze. Only one male platypus was captured for use in Trial 2. This was the largest animal tested (1760 g) and was stopped by the 65 mm grid. A grid between 55 and 65 mm would apparently be required to exclude most adult male platypuses.

EXPERIMENT 2 - Investigation of possible avoidance of entrance grids by free-swimming platypuses

In Experiment 1, each platypus was closely confined inside the traps so there was an imperative to find an escape route. However, two of the four animals in Trial 2 hesitated, and made more than one attempt to pass through the 70 mm grid, indicating possible deterrent effect of this grid size. Experiment 2 was designed to test whether grids across the outer end of the entrance funnel (Figure 3b) deterred foraging

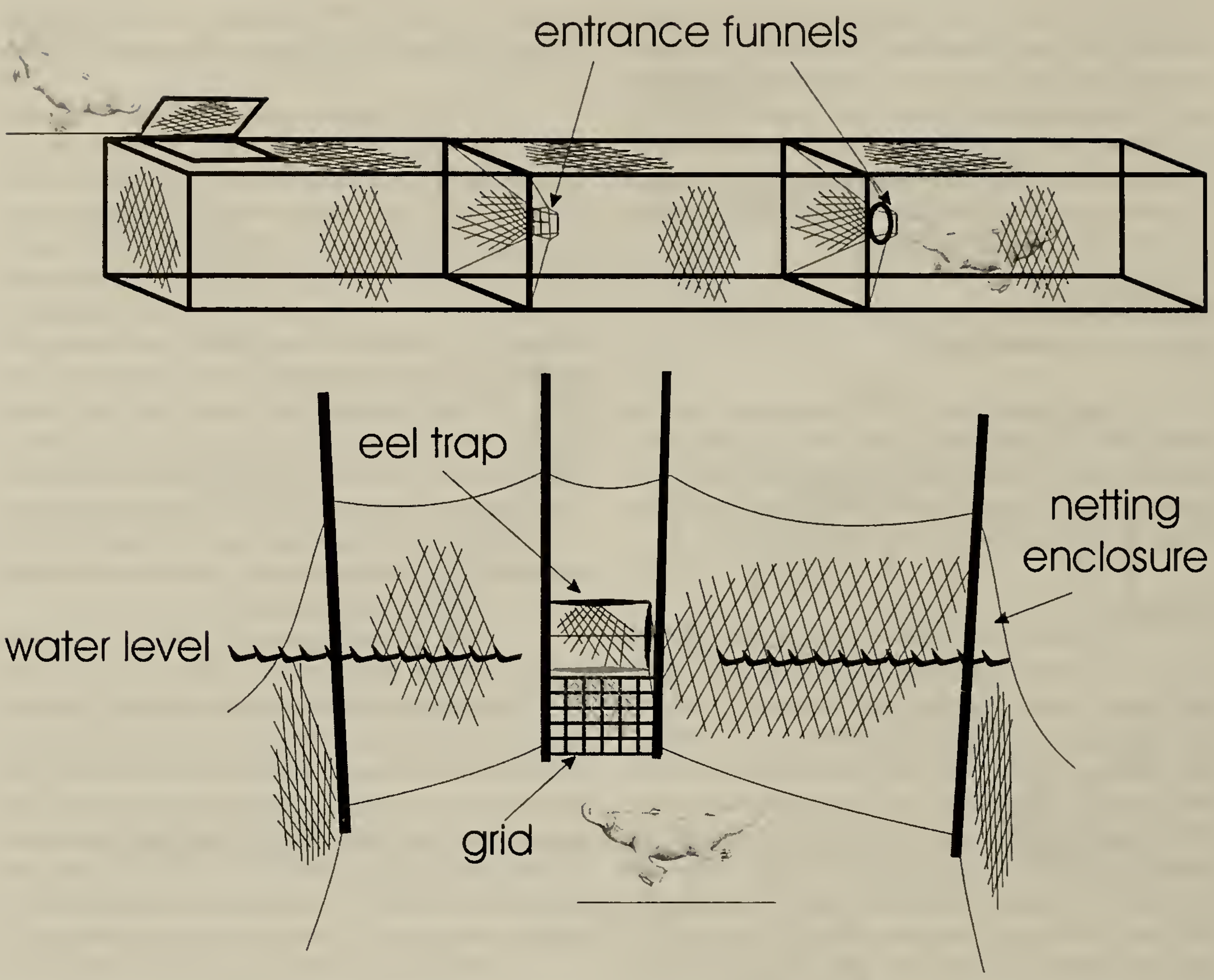

Figure 3. Set up used in Experiments 1 and 2 to test the effectiveness of by-catch reduction devices (BRDs) on entry of platypuses into eel traps. (Top) Experiment 1. Traps were attached together in a line with grids of different sizes at the narrow end of each entrance funnel or 'valve'. (Bottom) Experiment 2. Mesh enclosure in a river pool with trap entrance attached. Note the position of the replaceable rectangular grid across the outer (wide) entrance of the funnel.

platypuses from entering traps. The experiment was done in a pool on the upper Shoalhaven River in the southern tablelands of New South Wales from 17-19 March 2000.

Methods

A circular enclosure, 1.5 m high x 3 m diameter, made from 10 mm mesh monofilament gill net material, was constructed in a pool between the two netting sites where platypuses were captured for the experiment. The enclosure was designed so that the only possible escape for a platypus was through the grid of the entrance funnel of a trap inserted in the enclosure wall. Square grids, made from 4 mm steel rods, with 50, 60, 70 and 80 mm openings were used in this experiment. Each trial was done by attaching a replaceable grid to the entrance funnel of the trap, then placing a platypus into the enclosure (Figure 3b). At night, red-filtered lights were used to observe the animals. The time each animal remained in the enclosure before passing through the grid was recorded, along with the number of attempts that each made to pass through the grid. If an animal did not pass through a particular grid in the test series, this was replaced by the next larger grid in the series and the observations repeated. After the first animal was obviously unable to exit the 50 mm grid, the trials on all others were begun with either the 60 or 70 mm grid.

Results

Eight relatively small platypuses (ranging in

Table 1. Details of platypuses exiting through the various grid sizes within the funnels of eel traps in the two trials of Experiment 1. + = animal exited specific grid size; X = platypus did not exit through specific grid size.

Sex/ age	Weight (g)	90 mm Grid	85 mm Grid	80 mm Grid	75 mm Grid	70 mm Grid	65 mm Grid	60 mm Grid	55 mm Grid
Trial 1									
Male Adult	1190	+	X	X	X	X	X	X	X
Female Adult	1060	+	+	X	X	X	X	X	X
Female Adult	1030	+	X	X	X	X	X	X	X
Female Adult	1020	+	+	+	X	X	X	X	X
Female Adult	920	+	+	+	+	+	+	+	+
Female Adult	890	+	+	+	X	X	X	X	X
Exited		6/6	4/6	3/6	1/6	1/6	1/6	1/6	1/6
Trial 2									
Male Adult	1760	+	+	+	+	+	X	X	X
Female Adult	1000	+	+	+	+	+	+	+	+
Female Juvenile	760	+	+	+	+	+	+	+	X
Female Juvenile	700	+	+	+	+	+	+	+	+
Exited		4/4	4/4	4/4	4/4	4/4	3/4	3/4	2/4

size from 500 to 940 g) were tested in the enclosure at night. Results of the grid-deterrent trials are shown in Table 2.

The first platypus was initially placed in the enclosure with the 50 mm grid. After six attempts to go through the grid it was apparent that the animal would not fit through the spaces. After several tentative attempts at the 60 mm grid it appeared to stop trying to escape through the subsequent grids and remained in the enclosure even after the largest grid was completely removed. The test with the second platypus was started with the 60 mm grid in place, but this platypus was less active than the first animal and made only one tentative attempt to pass through this grid. It then readily passed through the 70 mm grid after only one attempt. Trials with the next three platypuses were all started with the 60 mm grid. All three of these animals swam past the grid at least once before escaping through it. The last three animals were initially trialed with the 70 mm grid, and all passed through it at the first attempt. Overall, two animals out of five appeared to be deterred by a 60 mm grid (40%) and only a single animal was deterred by a 70 mm grid (Table 2).

EXPERIMENT 3 – Platypus behaviour in the elevated cod ends of traps modified for use in farm dams and impoundments

The objective of this experiment was to record the behaviour of platypuses in modified eel traps used in impoundments and farm dams (Figure 2c) and to investigate their ability to negotiate the long cod end extension to the air space. The experiment was done in a pool on the upper Shoalhaven River from 17-19 March 2000.

Method

Two impoundment eel traps, with 5 m cod ends (Figure 2c) were placed in a pool of 0.5 m depth.

Table 2. Details of platypuses deterred from entering the various grid sizes across the entrances of eel traps in Experiment 2. Animals are arranged in the order in which they were used in the experiment. + = animal passed through specific grid size; X = platypus did not pass through specific grid size i.e. deterred; - no data;

Sex/Age	Weight (g)	50 mm Grid	60 mm Grid	70 mm Grid	80 mm Grid
Female Adult	800	X	X	X	X
Female Juvenile	500	-	X	+	-
Male Juvenile	800	-	+	-	-
Male Juvenile	740	-	+	-	-
Male Juvenile	640	-	+	-	-
Female Adult	940	-	-	+	-
Female Adult	900	-	-	+	-
Female Juvenile	690	-	-	+	-

One trap had three evenly spaced hoops in the cod end and the other had only one hoop near the airspace. The cod end of each trap was stretched and tied off above the surface of the water to a star-picket. Three platypuses (one male and two females) were placed consecutively in the trap with three hoops, and one female platypus was placed in the trap with one hoop. Each platypus was observed for 15 to 20 minutes before being released.

Results

In each case the platypus spent several minutes searching the inside of the trap before travelling up the cod end to the airspace. Each took several breaths then travelled to the trap where it again searched around or 'wedged' itself under the entrance funnel. Within five to eight minutes each would again travel up to the airspace for several breaths before returning to the trap. Platypuses travelled back and forth from the trap to the airspace 2-3 times during the 15-20 minutes they were confined in the trap.

DISCUSSION - Eel Trap Experiments

The results of Experiments 1 and 2 indicated that a grid of 50-55 mm would be necessary to exclude platypuses from entry into eel traps. Such a by-catch reduction device (BRD) would almost certainly affect the catch rates and sizes of eels (Koed and Dieperink 1999). This would be unacceptable to commercial fishers, particularly those fishing for adults of the long-finned species (*Anguilla reinhardtii*). Free-ranging platypuses may be deterred from entering traps fitted with external grids of 70 mm or less across the entrance funnels but such screening would be unlikely to significantly reduce platypus by-catch in eel traps.

Raising the cod end to provide an air space would facilitate the survival of platypuses captured in eel traps fitted with elongated cod ends. Platypuses captured in these traps were reluctant to stay at the surface and preferred to remain submerged in the trap between taking breaths. This behaviour, which minimises the time spent at the surface, may be a mechanism to avoid natural predation. Because platypuses must breathe at least every 2-10 minutes (Bethge 2002), captured individuals would need to travel back and forth to the airspace many times during any extended period of confinement after capture. This would be stressful and energetically demanding. It is essential that captured animals be released as soon as possible after capture. Studies using fyke nets (with elevated cod ends) to capture fish have shown that platypuses can survive for periods of up to 24 hours (Grant and NSW Fisheries, unpublished data). However, hypothermia has been reported in platypuses restrained in fyke nets after a few hours in cold conditions (Serena, personal communication). The current regulations in New South Wales demand that eel traps be inspected at least every 24 hours.

The platypus forages aerobically for short periods by holding its breath, following a comparatively large inspiration of air after each dive (Evans et al. 1994; Bethge 2002). The behaviour observed in this study of 'wedging' themselves under an object, and reducing energetic demands by remaining stationary, has been reported in captivity to last up to 11 minutes (Evans et al. 1994; Bethge et al. 2001; Bethge 2002). The function of this behaviour and its occurrence in the wild has not been determined. However, from the perspective of by-catch mortality this behaviour would not prevent platypuses from being drowned in completely submerged traps during normal fishing operations, which demand a period of trap submergence of hours rather than minutes.

Observation of traps with airspaces maintained only by the use of a float has shown that the cod end can easily become twisted or bunched. This situation would undoubtedly prevent a captured air-breathing species from reaching the airspace. This can be avoided by stretching the cod end tightly to a fixed point, either on the bank or a star picket driven into the bottom of the water body. It should be noted however, where traps are set with elevated cod ends attached to a fixed point, allowance needs to be made for anticipated rises in water level as a result of rainfall and/or tidal influences. Attachment of the cod ends of eel traps to a fixed point is mandatory under regulations for the use of eel traps in impoundments and farm dams in NSW.

THE COMMERCIAL AND RECREATIONAL YABBY FISHERY IN NEW SOUTH WALES

The results of the experiments done to evaluate the effectiveness of devices to prevent or deter platypuses from entering eel traps are also directly applicable to both the commercial and recreational 'yabby' [freshwater crayfish] fisheries. Based on the lack of adverse reports and on the assumption that the traps used to capture yabbies were small and did not have mesh wings to direct foraging platypuses into them, Grant (1993) suggested that "yabby fishing poses little threat to platypuses". This conclusion is now thought to be incorrect, as anecdotal reports from a number of states suggest that yabby traps were affecting some local platypus populations. These traps have also been implicated in the mortality of other non-target species, especially freshwater turtles. The drowning of as many as five platypuses in a single yabby trap has been reported, although the species' attraction to these traps is not fully understood. Platypuses are known to locate their prey by sensing the electrical fields generated by muscular activity of the prey species, especially large food items such as yabbies (Pettigrew et al. 1998). A trap containing live yabbies may therefore attract platypuses during their normal foraging activities. Once there is a dead platypus in a trap, more yabbies may feed on the decomposing carcass, which could in turn attract other platypuses into the trap.

Rankin (2000) suggested that a fixed ring 60-70 mm in diameter may prevent platypuses from entering traps and also facilitate their escape. Some commercially available yabby traps are fitted with 90 mm entrance rings, which are effective in excluding larger turtles but which are still reported to have drowned platypuses. The experiments described above for eel traps indicate that a 90 mm diameter ring is too large to exclude platypuses. Similarly, neither the experiments reported here nor anecdotal observations support Rankin's (2000) suggestion that platypuses could escape by returning through a fixed entrance ring.

Allanson and Thurstan (1999) evaluated the effect of entrance rings of different diameters in yabby traps using relatively small captive-bred yabbies (*Cherax destructor*). These trials showed that the smallest ring tested (63 mm) still permitted yabbies of the same size to enter the experimental traps as were entering the control traps with no rings fitted. However, the experimental traps caught substantially fewer yabbies. When the results of Allanson and Thurston's (1999) experiments were discussed with commercial fishers, it was concluded that the use of such a small entrance ring was not a viable option for the commercial yabby fishery.

Current regulations in New South Wales exclude the use of traps in commercial and recreational yabby fishing from known platypus waters and 90 mm rings are required in all yabby traps to exclude most turtles. Closed waters are located east of the Newell Highway, from the Victorian border (Murray River) to the Queensland border (Macintyre River), along with local closures around Deniliquin on the Edward River, Echuca on the Murray River and between Narrandera and Darlington Point on the Murrumbidgee River, where platypuses are also know to occur.

THE CARP FISHERY IN NEW SOUTH WALES

Carp (*Cyprinus carpio*) were probably first introduced into Australia around 1850 but did not spread until the introduction of the 'Boolarra' strain in the 1960s. Ecological effects of high densities of carp are poorly understood, but increased bank damage, disturbance of aquatic macrophytes and turbidity are all possible consequences. The overall disruption of riverine food webs by the large biomass of carp is thought to be detrimental to freshwater ecosystems (Schiller and Harris 2001). Carp are harvested in New South Wales using a variety of gear, including traps, haul and mesh nets, and electrofishing equipment. There is considerable overlap between the distribution of carp and platypuses (Boulton and Brock 1999), making the use of submerged traps a concern in this fishery.

A drum trap was constructed by NSW Fisheries (Fig. 4), which was designed to permit the escape of air-breathing vertebrate species, including

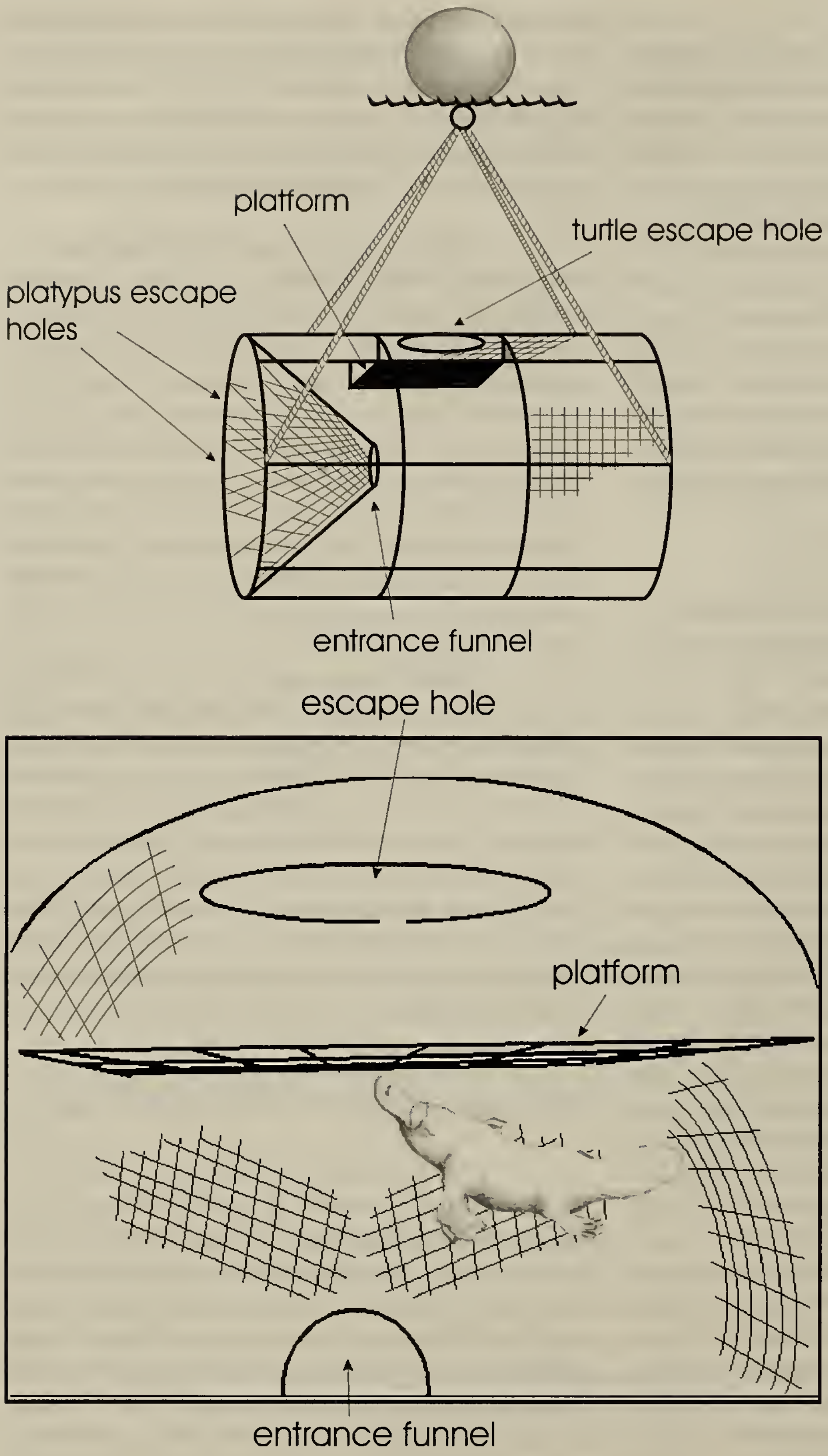

Figure 4. (Top) Modified drum trap showing escape hole in the roof above the mesh platform. Note the entrance funnel (or 'valve') on the left end of the drum. The entrance was sealed in the experiments and the triangular escape holes were made at the base of this funnel. (Bottom) Inside the trap showing the position of the steel mesh platform below the escape opening.

platypuses, water rats, turtles and diving birds, through a hole in the trap's roof. A wire-mesh platform was positioned below the escape hole so that small vertebrate species could pass through the 8 cm gap between it and the roof of the trap and exit through the escape hole, while larger carp would not be able to escape. Carp are also inclined to congregate near the bottom of a trap. The design assumed that air-breathing species would tend to swim towards the surface and search along the roof of the trap for a means of escape (surface/search behaviour). The objective of the following experiment was to test the effectiveness of the escape device for platypuses.

EXPERIMENT 4 - Assessment of escape of platypuses from a prototype carp trap

Platypuses close their eyes, ears and nostrils when under water, using the sensory mechanisms in their bills to find their way around (Pettigrew et al. 1998). It was expected that platypuses in the experiment would exhibit surface/search behaviour and be able to escape from the modified drum trap. The experiment was done in several pools on the Wingecarribee River, New South Wales from 25-27 November 2002 to determine if this expectation was realised.

Method

The trap consisted of a 90 cm diameter x 170 cm long cylinder, covered with black plastic mesh (55 mm x 40 mm), except at the entrance end, where a conical funnel or 'valve' made from 3 mm diameter braided polyethylene trawl netting was strung tightly between the circular steel frame at one end of the trap and an oval ring rigidly suspended inside the trap (Figure 4).

The trap was fully submerged in the pools from which the platypuses were captured. The trap was oriented with the escape hole uppermost. A remote lens for a video camera was

Table 3. Results of Experiment 4. Assessment of escape of platypuses from the carp trap in the Wingecarribee River.

Sex/Age	Weight (g)	Length (cm)	Time in trap (sec)	Approaches to platform	Escape
Female Adult	1080	48.5	150	0	**No**
Male Adult	1880	55.2	165	3	**No**
Male Juvenile	1790	56.5	180	0	**No**
Male Adult	1880	57.5	180	0	**No**
Male Juvenile	1400	53.0	30	0	**Yes**

mounted inside the trap to record the behaviour of the animals and these images were stored for later analysis.

Platypuses were captured using unweighted gill nets (Grant and Carrick 1974). Each animal was weighed and measured, then temporarily marked with a piece of brightly coloured tape attached to the tail, making the platypuses more visible to observers and to the video camera. Based on observations reported above and Bethge (2002), who reported a maximum foraging dive duration of 138 seconds, individuals were immersed for a maximum of 3 minutes before the trap was lifted to permit them to breathe. If they exited the trap prior to lifting, the elapsed time was recorded. The numbers of times each animal approached the platform below the escape hole was recorded. All animals were used only once in the experiment and remained in the trap for no more than 3 minutes.

Results

Table 3 shows the dimensions of the platypuses used, the time in the trap, the number of approaches to the platform below the escape hole, and whether or not individuals escaped. Only one juvenile male platypus managed to find the escape hole (after 30 seconds in the trap), but showed reluctance to leave the steel ring around the hole. It re-entered the body of the trap three more times before finally leaving the trap completely. This animal repeatedly relocated the escape hole after re-entering the trap, taking 30, 50 and 50 seconds respectively, before finally escaping. The other four trial animals failed to find the escape hole and were released after 2-3 minutes.

Contrary to expectation, platypuses (including the one which escaped) spent most of the time investigating the bottom or ends of the trap, rather than exhibiting surface/search behaviour. In fact, they seemed to actively avoid the platform area below the escape hole. All animals searched with their bills around the corners of the trap between the sides and ends. The video showed them frequently investigating the acute angled edge between the base of the entrance funnel and the sides of the trap. When released, all animals were observed to surface and appeared to be breathing heavily.

EXPERIMENT 5. Assessment of escape of platypuses from the modified carp traps

In Experiment 4, platypuses were observed continually searching for an escape hole around the corners of the trap. It was therefore decided to test the effectiveness of escape holes positioned around the base of the entrance funnel. Because the gap between the funnel and the sides of the trap was quite narrow at the base of the funnel, it was considered that most carp would be too large to access openings in this position. Experiment 5 tested the effectiveness of these modifications. The experiment was done in one pool on the Wingecarribee River on 27 November 2002 and then in four pools on the upper Shoalhaven River from 21-23 December 2002.

Methods

Every third mesh attached to the trap frame at the base of the funnel was released and tied back to provide 90 x 90 x 90 mm triangular openings (Fig. 4, top). In the initial trial in the Wingecarribee River these openings were made only in the upper half of the trap, but in the later trials in the upper Shoalhaven River, openings were made in both the upper and lower halves of the trap.

Fourteen platypuses were individually placed in the submerged trap as described in Experiment 4. Again observations were made of the number of times animals approached the platform below the escape

Table 4. Results of Experiment 5. Assessment of escape of platypuses from the modified carp trap. * not observed escaping but were not present in trap when it was lifted after 3 minutes; - escape holes only available in upper part of this trap.

Sex	Weight (g)	Length (cm)	Time in trap (sec)	Approaches to platform	Escape	Escape location
Female	850	43.0	85	1	Yes	-
Female	690	41.0	15	0	Yes	lower
Female	900	46.0	22	0	Yes	lower
Female	940	43.5	15	0	Yes	lower
Female	900	44.0	40	0	Yes	upper
Female	790	41.0	41	0	Yes	upper
Female	870	43.5	140	0	Yes	upper
Female	930	44.0	33	0	Yes	upper
Female	860	44.0	<180*	0	Yes	lower
Female	840	43.5	45	0	Yes	upper
Female	790	43.0	156	0	Yes	upper
Male	1850	55.2	35	1	Yes	-
Male	1740	52.0	<180*	0	Yes	lower

hole. Escapes through the triangular holes at the base of the entrance funnel were partitioned as being from the 'upper' or 'lower' openings in the trap. Some underwater video observations were made but the turbidity of the pools made viewing difficult. However, brightly coloured tape attached to the tails of the animals (see Experiment 4) usually permitted their movements in the trap to be observed. Again, if the platypus was not seen to escape, the trap was lifted from the water after a maximum of 3 minutes.

Results

Thirteen platypuses escaped from the openings around the base of the entrance funnel of the trap within 3 minutes (Table 4). As was observed in Experiment 4, all animals attempted to find an escape route around the bottom or ends of the trap. Another individual used in the initial trial located a hole inadvertently left at the bottom of the trap (which was sealed before subsequent trials). No preference was shown for escape location, with six animals exiting from the 'upper' and 5 from the 'lower' openings, where both were available (Table 4). One individual moved into the space between the platform and the escape hole but did not find the hole, submerging again and leaving the trap by one of the openings at the base of the entrance funnel. Only two individuals approached the platform at any time during their confinement in the trap. In two instances the platypuses could not be seen, but were no longer in the traps when they were lifted after 3 minutes. It was presumed that they had exited the lower holes, as they were not seen leaving the upper ones, which were visible to the observers.

DISCUSSION - Carp trap experiments

Experiment 4 indicated that the unmodified carp trap would probably result in significant mortality of platypuses if deployed in areas where their distribution overlaps that of carp. However, experiment 5 indicated that carp traps with appropriate escape holes could be used to reduce by-catch of platypuses. Platypuses over a size range of 690-1880 grams were able to exit quite quickly (15-156 seconds) through the 90 mm triangular openings in the modified carp trap.

It should be noted that the platypuses used in these experiments were not particularly large. There is considerable sexual dimorphism in the species, with the average male being around 75% heavier and 20% longer than females (Carrick 1995; Grant 1995; Connolly and Obendorf 1998). Individuals of up to twice the size of those used in current experiments are found in some mainland areas (especially west of the Great Dividing Ranges; Carrick 1995; Grant 1995) and in Tasmania males may reach up to three kg (Connolly and Obendorf 1998). Further experiments are required to determine the size of escape holes effective for larger platypuses. In the interim, the authors recommend triangular openings of 100 x 100 mm for east-flowing streams in New South Wales and openings of at least 120 x 120 mm for west-flowing streams in the state. Trials would also need to be carried out to assess the effectiveness of retaining captured carp in the presence larger escape holes.

The unexpected lack of surface/search behaviour in platypuses during Experiments 4 and 5 indicates the importance of field trials of fishing equipment with regard to specific wildlife species. The reason for the unexpected lack of surface/search behaviour in water can only be speculated upon. Platypuses frequently forage among dense woody debris and under submerged overhanging banks (Grant 1995 and personal observation). It may be that a behavioural response of moving down and/or sideways away from an obstruction during foraging may be of greater survival value than attempting to rise directly to the surface when seeking an escape route. No 'wedging' behaviour (Evans et al. 1994; Bethge et al. 2001; Bethge 2002; Experiment 3) was exhibited by animals in the carp traps. Rather, all individuals searched constantly for an escape route.

GENERAL CONCLUSIONS

The results of the literature reviewed and experiments presented in this paper indicate that any fishery in freshwaters of New South Wales based on the use of traps should not be operated as an unregulated fishery (Figure 1) if reducing platypus mortality is a priority. By-catch minimisation has been possible in the eel fishery by a combination of closures of some inland waters and by modifications to provide an airspace in traps used in farm dams and impoundments. Exclusion devices (e.g. grids across the entrance funnels of traps) do not provide a commercially viable option for reducing the by-catch of platypuses in eel or yabby traps. Banning of yabby traps from areas where platypuses occur is currently the only available means of avoiding by-catch mortality in this fishery. The commercial and recreational yabby fisheries in New South Wales are currently restricted to waters where platypuses do not commonly occur or are very uncommonly reported. Trap modifications, which permit the escape of platypuses, appear to be the most feasible means of by-catch minimisation in the use of traps to capture carp.

ACKNOWLEDGMENTS

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Platypus Burrow Temperatures at a Subalpine Tasmanian Lake

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Bethge, P., Munks, S., Otley, H. and Nicol, S. (2004). Platypus burrow temperatures at a subalpine Tasmanian lake. *Proceedings of the Linnean Society of New South Wales* **125**, 273-276.

When platypuses are in their burrows, microhabitat is of great importance for energy conservation, especially where air temperatures frequently fall below freezing in winter. In this study, we investigated burrow temperatures of platypuses (*Ornithorhynchus anatinus*) living at a sub-alpine Tasmanian lake. Nine individual platypuses were equipped with time-depth recorders with integrated temperature sensors measuring ambient temperature. Burrow temperatures were recorded in two minute intervals for a total of 61 resting periods (duration: 5.45 to 27.20 hours) and were averaged over the period of resting. Mean burrow temperatures were 17.5 and 14.2°C (SD=2.76 and 0.89, respectively, n=9) in summer and winter, respectively, and ranged between 12.2 and 22.8°C for individual resting periods. In winter, burrow temperatures were held fairly constant over the resting period while in summer larger variations were observed. Burrow temperature in winter was found to be up to 18°C higher than outside air temperature.

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Key words: Burrow temperature, Energetics, *Ornithorhynchus anatinus*, Platypus, Tasmania

INTRODUCTION

The platypus, *Ornithorhynchus anatinus*, inhabits the lakes, rivers and streams of eastern Australia from the Cooktown area in the north to Tasmania in the south. Over much of its range, the animal is found in alpine and tableland areas where, especially in winter, air temperatues fall well below freezing and water temperatures approach 0°C (Grant 1995). Grant (1983a) suggested that under such conditions, the microhabitat of platypus burrows is of great importance for energy conservation. Even in an unoccupied artificial burrow the insulation of layers of earth was found to provide significant buffering effect against outside ambient temperature changes both in winter and in summer (Grant 1976). (Grant 1983b) suggested a further modifying effect of the animal's presence on the microhabitat temperature, elevating it several degrees above that of an unoccupied burrow.

In this study ambient temperatures in occupied platypus burrows at a sub-alpine Tasmanian lake were investigated. The use of time-depth recorders with integrated temperature sensors made it possible to determine burrow temperatures during naturally occuring resting periods of the equipped animals.

MATERIALS AND METHODS

Field experiments were carried out at Lake Lea (41°30′ S, 146°50′ E), a sub-alpine lake in northwestern Tasmania. Information on burrow temperatures was obtained from nine individual platypuses (4 adult males, mass: 2.27 kg ± 0.26 (SD), 5 adult females, mass 1.48 kg ± 0.07 (SD)) between November 1998 and January 2000. Platypuses were captured and processed following the methods outlined in Otley et al. (2000) and Bethge et al. (2003). Individuals were equipped with combined data logger-transmitter packages (max 62 mm x 28 mm x 18 mm, weight 50 g, Fig. 1) consisting of a specially designed standard transmitter (Faunatech, Eltham, Victoria) and a time-depth recorder (LTD 10, Lotek Inc., Canada). The packages were attached with glue (5 min-Araldite, Selleys Inc., Australia) to the guard fur of the lower back of the animals, just above the tail, following the method outlined in Serena (1994). Animals were released at the site of capture. After approximately two weeks the animals were relocated by radiotracking and recaptured on emergence and the devices were removed.

The data loggers allowed measurement of ambient temperature in the range from 2 to 25°C with

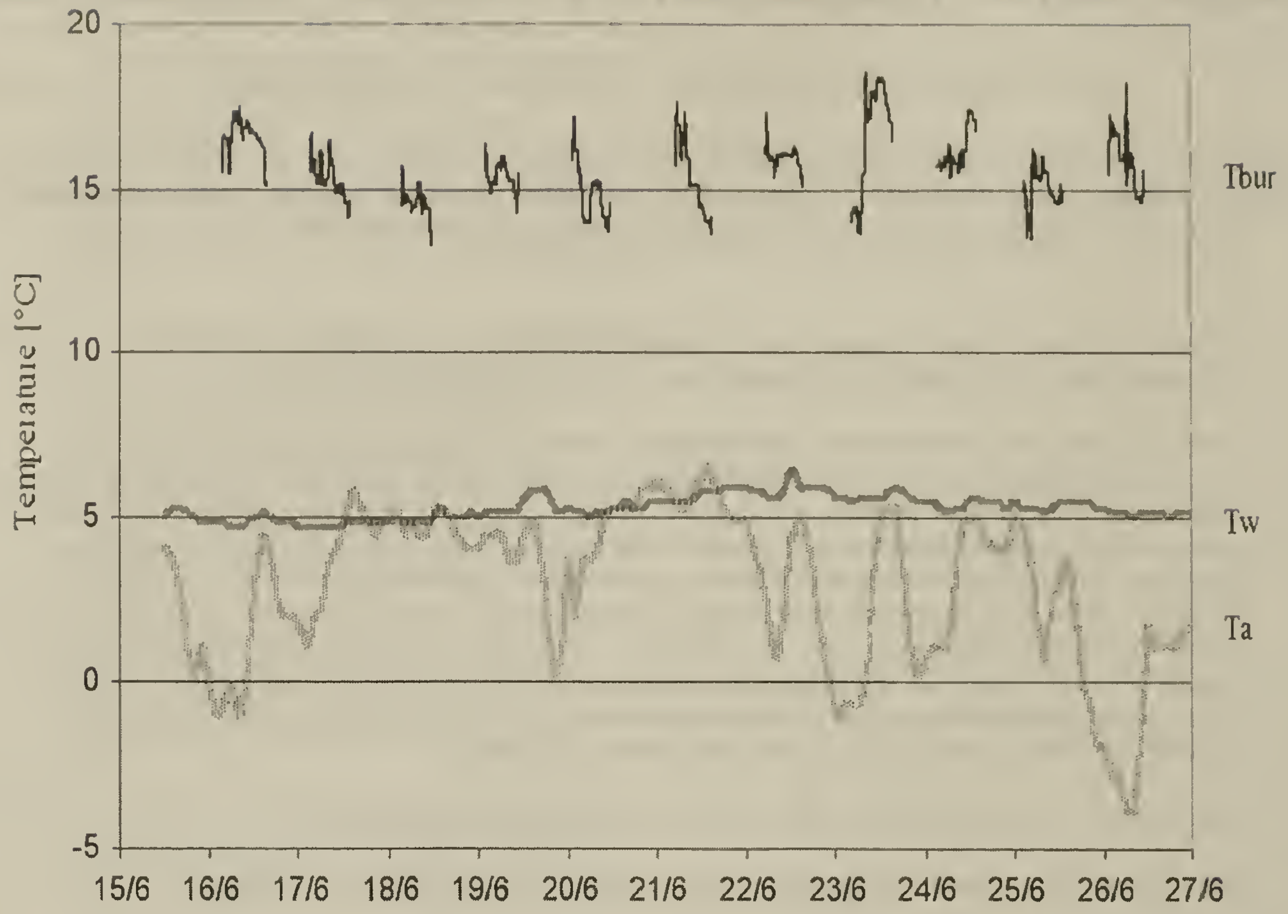

Figure 1: Winter sample data of water (Tw), air (Ta) and burrow temperatures (Tbur, derived from a time-depth recorder with integrated temperature sensor fitted to the back of a platypus; the temperature is only shown at times when the animal was in the burrow).

an accuracy of 0.06°C. The devices were calibrated by the manufacturer (Equipment for temperature-calibration: Neslab RTE-2000 Bath/Circulator and Omega HH40 Thermistor/Thermometer). Temperature sensors were located at the back end of the devices and were facing backwards when the devices were fixed on the platypus's lower backs. Ambient temperature was measured in two-minute intervals for 11 days each. While foraging, the sensors measured water temperatures. In resting platypuses, ambient temperatures close to the animals' bodies (approx. 5 mm from above the fur) were recorded. The resting period was defined as the time span between the end of the last dive of a foraging trip (detected by the depth sensor of the time-depth recorders) and the beginning of the first dive of the following foraging trip. Burrow temperatures, i.e. ambient temperatures during resting periods, were recorded in two minute intervals for a total of 61 resting periods and were averaged over the period of resting. Resting periods ranged from 5.45 to 27.20 hours.

All investigated platypuses occupied burrows in consolidated steep or gently sloping earth banks of the lake or along associated creeks. Water and air temperatures at Lake Lea were recorded in two-hour intervals using archival tags (HOBO Thermocouple logger and Stowaway Temperature Logger, Onset Computer Corp., USA). Water temperature was measured in the lake while air temperature was taken in a wind shaded forest patch nearby.

RESULTS

Mean burrow temperatures were 17.5 and 14.2°C (SD=2.76 and 0.89, respectively, n=9) in summer and winter, respectively, and ranged between 12.2 and 22.8°C for individual resting periods. In winter, burrow temperature was held fairly constant over the resting period while in summer larger variations were observed. A low but significant correlation between air temperature and burrow temperature was found with higher air temperatures resulting in higher burrow temperatures (p=0.003, n=61). Ambient air temperatures ranged between -4°C and 31°C and water temperatures between 0°C and 29°C depending on season. Samples of measured burrow temperatures and corresponding air and water temperatures are shown in Fig. 1 and Fig. 2 for winter and summer, respectively.

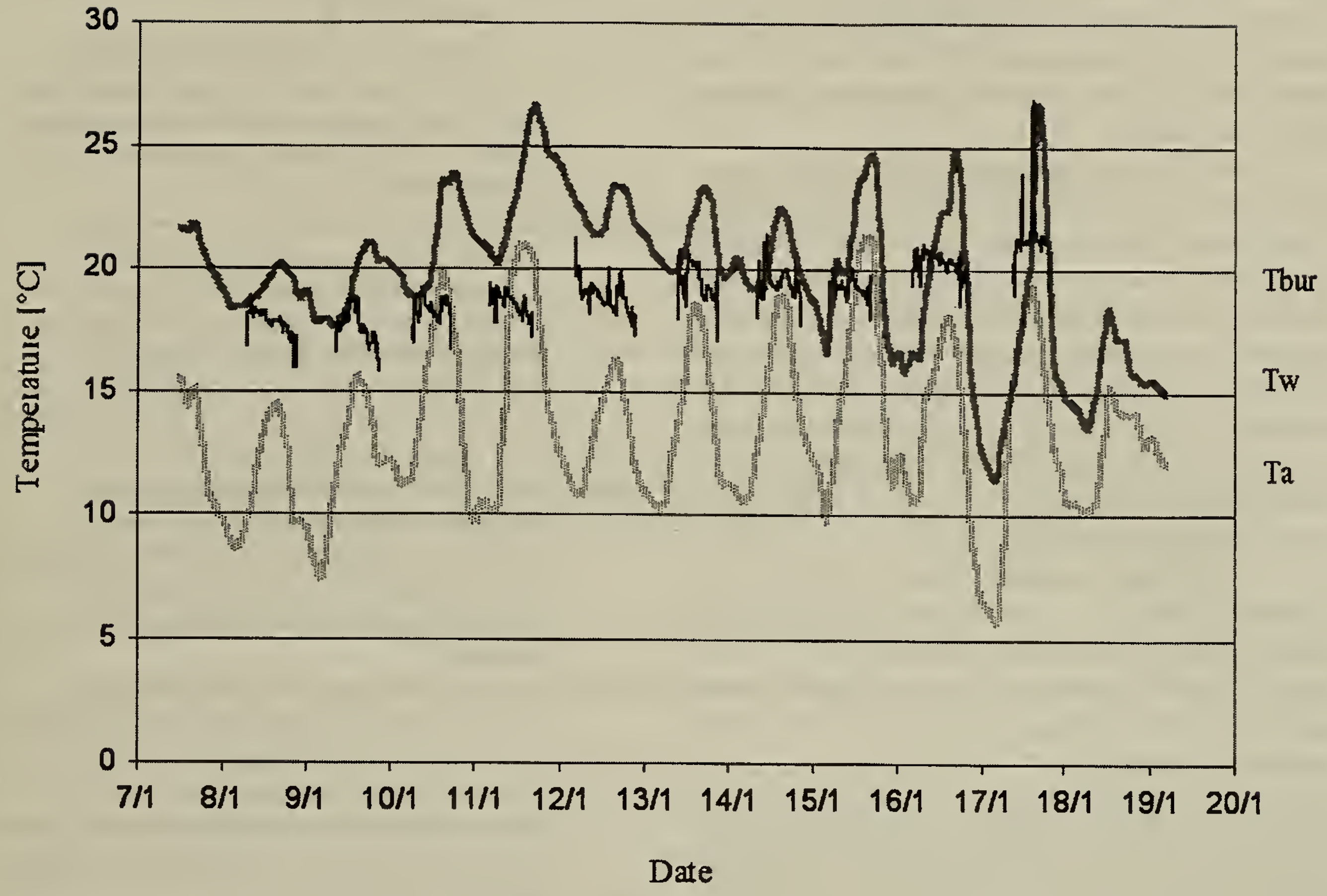

Figure 2: Summer sample data of water (Tw), air (Ta) and burrow temperatures (Tbur, derived from a time-depth recorder with integrated temperature sensor fitted to the back of a platypus; the temperature is only shown at times when the animal was in the burrow).

DISCUSSION

Grant (1983b) suggested that platypus burrows act as microenvironments, buffering the animals against the rigours of below-freezing air temperatures in winter, and modifying the effects of high summer temperatures. Accordingly, we found that in winter, burrow temperatures at Lake Lea were up to 18°C higher than outside air temperatures (Fig. 1). In summer, the burrows at Lake Lea clearly buffered high midday temperatures of over 25°C (Fig. 2). These findings are in line with results by Grant (1976) and Munks (personal communication). In winter, unoccupied artificial burrow temperatures in the upper Shoalhaven River, NSW, averaged around 14°C (this study: 14.2°C) despite the fact that ambient air temperatures dropped as low as -5°C. During summer the temperature of an unoccupied artificial burrow averaged around 18°C (this study: 17.5°C) with air and water temperatures being several degrees higher (Grant 1976, Grant 1995). Munks (personal communication), while monitoring the burrow of a breeding platypus in lowland Tasmania, recorded a mean burrow temperature of 16.5°C (range 12.5 to 20°C) during late summer/early autumn.

The consistency of these data from different sites suggests that platypus burrow temperatures are fairly constant regardless of habitat. Whether this is a consequence of the metabolic heat produced by the animals or mainly of physical characteristics of their burrows, remains unclear. Results of Grant (1976) from unoccupied burrows are in line with findings presented here from occupied burrows. This suggests that - at least in burrows located in consolidated earth banks - physical characteristics of the burrow are more important for burrow temperature than the absence or presence of the animal. This view is supported by the significant correlation between air temperature and burrow temperature found in this study.

However, Munks (personal communication) reported peak burrow temperatures when the mother returned to the nest to suckle her young. Also, Grant (1983b) suggested that the animal's presence further elevates the microhabitat temperature of the burrow. In captivity, Grant (1976) observed, that the temperature in an uninsulated plywood nest box rose around 1 to 2°C above ambient temperature when an animal was inside.

We suggest that these different observation are a consequence of different burrow characteristics. In this study, all investigated platypuses occupied burrows in consolidated earth banks. Under such conditions, the insulation properties of the surrounding earth and of the nesting material inside the burrow are most likely the main factors determining burrow temperature. A fairly constant burrow temperature may of course be more critical during the breeding period (Grant, personal communication), which makes deep earth burrows ideal for nesting.

A different situation, however, might occur in burrows, which are closer to the surface or above ground. Otley et al. (2000) reported that 25 % of burrows at Lake Lea were located within dense vegetation, such as sphagnum and button grass. The insulation properties of such burrows would be expected to be poor compared to underground earth burrows. How animals cope with high thermal stress in vegetation burrows and if they use this sort of burrow site regardless of season or even during nesting requires further investigation.

ACKNOWLEDGMENTS

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Ultrasonography of the Reproductive Tract of the Short-beaked Echidna (*Tachyglossus aculeatus*)

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Higgins, D.P. (2004). Ultrasonography of the reproductive tract of the short-beaked echidna (*Tachyglossus aculeatus*). *Proceedings of the Linnean Society of New South Wales* **125**, 277-278.

We describe a brief investigation of ultrasonography as a tool to monitor reproductive activity and to determine the sex of short- beaked echidnas (*Tachyglossus aculeatus*). We found trans-abdominal ultrasound to be of limited use for monitoring ovum development but it appears to be useful for imaging the uterus. We also found ultrasonography to be a useful tool to confirm the sex of echidnas by visualizing the testis.

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KEYWORDS: abdomen, echidna, monotreme, reproduction, Tachyglossus, testis, ultrasound, uterus.

Here we describe a brief investigation of ultrasonography as a tool to monitor reproductive activity and to determine the sex of short- beaked echidnas (*Tachyglossus aculeatus*). Griffiths (1968) described the gross anatomy of the reproductive tract of the female echidna. An ovum of 3-4 mm diameter is ovulated from one of the two flat, sauropsid-like ovaries, which lie ventrocaudal to the kidneys (Griffiths 1968). Although only one ovum is ovulated in the echidna, Flynn (1930) reported that up to three large ova and several much smaller ova may occur on the ovary. Hughes and Carrick (1978) concluded from Hill and Gatenby (1926), Caldwell (1887) and Flynn and Hill (1939) that the ovum has a vitelline membrane, a zona pellucida and a proalbumen which may be analogous to the liquor folliculi of the graafian follicle, but has no follicular antrum. During its passage down the fallopian tube, the ovum swells to 5 mm diameter. The shell membrane is first laid down in the fallopian tube and later thickens in the uterus. The egg absorbs fluid *in-utero* and expands from 6.5mm diameter to 15 mm x 13 mm.

Ten short- beaked echidna carcasses were placed in dorsal recumbency. A portable ultrasound machine with a 7.5 Mhz linear transducer (SSD- 500, Aloka, Japan) was used to image the abdomen. Results were confirmed by dissection. An additional nine echidnas were then anaesthetized and examined in a similar fashion. Positioning the transducer on the ventral abdominal wall, lateral to the epipubic bones avoided the need to shave the hair of the pseudopouch and minimised interference by intestinal gas. Dissection confirmed that the gonads lie against the dorsal body wall, dorsal to the cranial ends of the epipubic bones. Ovaries of freshly dead echidnas lacked grossly visible developing ova. Of frozen and thawed bodies, which generally had poorer tissue contrast, ovaries and ova were not visible by ultrasonography. A structure in the expected location of the ovaries and comprising several 2- 3 mm diameter, thin walled, echolucent bodies was sometimes visible in living echidnas during the breeding season, however, the scarcity of surrounding interstitium made repeatable identification of individual putative ova very difficult. In addition, the small intestine frequently cast gas shadows over the gonads, reducing their visibility. It is likely that trans-rectal ultrasound would improve visualization of the ovaries but may be of limited use in serial observations, where the extent of manual or chemical restraint required may introduce variations to the reproductive cycle (Clarke and Doughton 1983, River and Rivest 1991). The entire oviducts of reproductively active live and dead animals were clearly visible, especially when adjacent to a full bladder. Ova were not seen in the oviducts of any of our animals. Testes appeared as 15 to 25mm long, ovoid, homogenous, soft tissue structures and, when present, were always visible caudal to the kidney and, on the left side, dorso-caudal to the mobile, spherical portion of the spleen. Due to their similar appearance on ultrasound, both the spleen and testis were sighted on the left before the left testis was identified.

In conclusion, we found trans-abdominal ultrasound to be of limited use for monitoring ovum development but it appears to be useful for imaging the uterus. In sexing echidnas, the inability to extrude or palpate a phallus does not confirm its absence, and other characteristics such as absence of a pseudo-pouch or presence of spurs may not be reliable indicators of sex, therefore the gender of echidnas in captive collections is sometimes mistaken. We found ultrasonography to be a useful tool to confirm the sex of echidnas in these circumstances.

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Excretion Profiles of Some Reproductive Steroids in the Faeces of Captive Female Short-beaked Echidna (*Tachyglossus aculeatus*) And Long-beaked Echidna (*Zaglossus sp.*)

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Higgins, D.P., Tobias, G. and Stone, G.M. (2004). Excretion profiles of some reproductive steroids in the faeces of captive female short-beaked echidna (*Tachyglossus aculeatus*) and long-beaked echidna (*Zaglossus sp.*). *Proceedings of the Linnean Society of NSW* **125**, 279-286.

We evaluated and applied an existing faecal reproductive steroid extraction and radio-immunoassay (RIA) procedure to samples from captive short-beaked (*Tachyglossus aculeatus*) and long- beaked (*Zaglossus sp.*) echidnas. Steroids were extracted from faeces with diethyl ether, resuspended in 80% methanol and lipids removed with petroleum ether. The methanol fraction was purified and assayed for progestins or oestrogens, results corrected for procedural losses and converted to ng/ g dry weight of faeces. One *T. aculeatus* was injected with radiolabelled and natural progesterone and faecal extracts were subjected to high- performance liquid chromatography (HPLC) to allow partial identification of radiolabelled and RIA- reactive metabolites. The major RIA-reactive substance and the major labelled [^{14}C] compound co-eluted with progesterone. An additional RIA-weak compound co-eluted with 20β-dihydroxyprogesterone, and three additional RIA-weak, radio-labelled compounds eluted but were not identified. Increases in faecal progestin of echidnas occurred at 17 ± 3 ($n = 5$), 33 ± 3 ($n = 4$) and 48 ($n = 1$) day intervals, supporting a cycle length of approximately 17 or 33 days. However, further study incorporating more animals, behavioral observations and more frequent sampling of faecal oestrogens is required to produce more definitive results.

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KEYWORDS: Faecal reproductive steroids, HPLC, monotreme, oestrogen, progestin, radioimmunoassay, Tachyglossus aculeatus, Zaglossus.

INTRODUCTION

The short- beaked echidna (*Tachyglossus aculeatus*) is widespread within Australia and New Guinea. The long- beaked echidna (*Zaglossus bruijnii*) is restricted to the highlands of New Guinea where it is endangered by human interference (Flannery 1990). Despite more than 100 years of captive husbandry, it is rare for these animals to breed in captivity (Augee et al. 1978; Boisvert and Grisham 1988) and knowledge of the timing and hormonal control of the reproductive cycles of monotremes is limited. The presence of a luteal phase is generally accepted, based on histological evidence (Hill and Gatenby 1926; Griffiths 1968; Hughes and Carrick 1978; Griffiths 1984) but its role and duration is unknown. In addition, observations of gestation range from greater than 10 days (Carrick 1977) to 28 days (Broom 1895) after mating. Griffiths (1984) speculated that, like some reptiles and bats (Racey and Potts 1970), female echidnas may store sperm, or that torpor may alter gestational length, as in pygmy possums (*Cercartetus* spp), brown antichinus (*Antichinus stuartii*), eastern quolls (*Dasyuris viverrinus*) (Tyndale- Biscoe 1973) and bent-winged bats (*Miniopterus* spp) (Wimsatt 1969).

Longitudinal studies better define reproductive cycles and illustrate inter-individual variation than cross-sectional studies, which are more conveniently applied to wild animals (Lasley 1985). However, even captive echidnas are cryptic and curl into a tight ball when threatened, making difficult the frequent collection of blood, urine or urogenital swabs without anaesthesia or forceful restraint, which may cause variation of reproductive cycles and behaviour (Clarke and Doughton 1983; Rivier and Rivest 1991; Cleva et al 1994). Non- invasive faecal reproductive steroid assays have been used to describe the reproductive cycles of many species. This paper reports the initial assessment and application of a faecal reproductive steroid assay as a non- invasive technique for the first sequential study of female echidna reproductive endocrinology.

MATERIALS AND METHODS

Animals and housing

Study animals were six female *T. aculeatus,* aged between 4 and 7 years and of 3 to 5 kg bodyweight, and three female *Zaglossus bruijnii* (probably *Z. bartoni* of Flannery and Groves 1998), aged between 20 and 32 years and of 6.5 to 14 kg bodyweight, all from the Taronga Zoo collection. The study was conducted in two phases: From May to September 1995, two *T. aculeatus* and all *Zaglossus sp.* were housed in two indoor enclosures with reverse cycle seasonal lighting and in the continual presence of a male of their species. From June to October 1997, four female *T. aculeatus* were housed outdoors, in adjacent 5.1 x 6.3 m enclosures. These females were housed individually to accommodate the solitary nature of the animal (Augee et al. 1975; Abensperg-Traun 1991) and to facilitate identification of the source of faeces. A male *T. aculeatus* had access to all four enclosures through magnetically controlled doors until they failed, after which he was manually rotated, daily, between enclosures. Sixty-centimeter deep woodchip substrate, half pipes, tables, tree branches and logs were provided as shelter.

Feeding and sample collection

Animals were fed daily slurry of minced beef, egg, cereal, vitamin and mineral supplements and sufficient unprocessed bran to produce firm stools. Initially, 1mm x 1mm x 3mm food grade polyethylene pellets (Hoechst Industries, Australia) were added to the food of the indoor groups to identify the source of faeces. It appeared possible that not all pellets were being excreted, therefore the feeding of pellets was discontinued and for the course of the study each animal from the indoor groups was placed in a separate room for 24- 48 h once weekly and faeces were collected. Blue food dye (8 mg/day, Hexacol Brilliant Blue FCF Supra 75328, Pointing Hodgsons Pty Ltd, Australia), was added to the food of the outdoor female animals to make faeces more visible, and all visible faeces were collected daily. Samples were handled using latex gloves and stored in plastic zip- lock bags at -20°C for up to one year.

Extraction and purification

Due to the need to separate echidnas for sample collection in the first phase of the study, the sampling interval for progestin excretion profiles of echidnas housed indoors was 5 to 7 days. Sampling interval for progestin and oestrogen excretion profiles of echidnas housed individually outdoors in the second phase of the study was 1 to 3 days. The steroid extraction technique was based on a procedure used by Hindle and Hodges (1990). Each stool was finely chopped and mixed, then duplicate 0.5g samples were transferred to new glass vials (Econo Glas Vial, Packard, USA). Pieces were broken up using a glass rod, 5 ml diethyl ether (APS, Ajax Finechem, Australia) was added and vials were rotated for 30 min then centrifuged at 1500 G for 15 min at 4°C. The faecal sediment and aqueous portion were frozen in liquid nitrogen. Supernatant was decanted, evaporated at 30°C under nitrogen gas and reconstituted in 5 ml 80%(v/v) methanol (80% MeOH) by rotation for 30 min. Solutes were partitioned by addition of 5ml of petroleum ether (B.P. 40°C to 60°C, APS, Ajax Finechem, Australia), rotation for 20 min, and centrifugation at 1500 G for 15 min. The 80% MeOH fraction was aspirated and then stored at -20°C. Following extraction, faecal residue was dried at 100°C for 4 hours and weighed to determine dry matter content.

Aliquots of 500 μl faecal extract in 80% MeOH were dried at 80°C under vacuum, reconstituted in 1ml 10% MeOH by agitation at 30°C for 30 min, and purified using Sep-Pak C18 Cartridges (Waters Scientific, Milford, USA) according to manufacturers recommendations. Eluants of 25%, 50%, 75%, 90% and 100% MeOH were collected and stored at -20°C.

Radioimmunoassay (RIA)

Duplicate 200 μl aliquots of eluates (unknowns) were dried and reconstituted in 200μl 10% MeOH in 1P buffer (0.031M Na_2HPO_4, 0.019M $NaH_2PO_4.2H_2O$, 0.154M NaCl and 0.1%w/v gelatin, pH 7.4) by agitation at 30°C for 60 min. Radiolabelled steroids ([1,2,6,7-^{3}H] progesterone in toluene ([^{3}H]P, 96 Ci/mmol; Amersham Australia, Sydney, NSW) or [2,4,6,7-^{3}H] oestradiol in toluene ([^{3}H]E, 104 Ci/mmol; Amersham Australia, Sydney NSW)) were dried and reconstituted in 1P buffer to approximately 15000 dpm/ 100 μl. Our ovine antiserum to progesterone-11α-hemisuccinate-BSA conjugate (1:55000 final dilution, #C-9817 Sirosera™, CSIRO Bioquest, Blacktown, Australia), cross-reacted with progesterone (100%), 11β- hydroxyprogesterone (32.5%), corticosterone (18.8%), 20α- hydroxy-4-pregnane-3-one (0.7%), 17α- hydroxyprogesterone (0.2%), 20β- hydroxy-4-pregnane-3-one (0.2%), pregnenolone (0.2%), oestradiol (<0.2%), testosterone (<0.2%), cortisol (<0.2%) (Curlewis, Axelson and Stone, 1985). Our ovine antiserum to 17β- oestradiol-6-carboxymethyloxime-BSA (1:100000, #9757

Sirosera™, CSIRO Bioquest, Blacktown, Australia), cross-reacted with oestradiol (100%), oestrone (10.8%), oestriol (2.3%), oestradiol- 17α (<0.1%), progesterone (<0.1%), testosterone (<0.1%), androstenedione (<0.1%), cortisol (<0.1%), corticosterone (<0.1%) (Curlewis 1983). Standards were generated from two overlapping doubling dilutions of progesterone (BDH Chemicals, Australia) from 500 - 7.84 pg/100 µl or oestradiol (BDH Chemicals, Australia) from 500 - 1.96 pg/100 µl.

Reactions contained 100 µl radiolabelled steroid, 100 µl antiserum and either 200 µl of unknown in 10% MeOH in 1P buffer or 100 µl 20% MeOH in 1P buffer and 100 µl of standard. The resulting 400 µl was vortexed for 30 sec and incubated at 4°C for 18 h. Triplicate "total" (200 µl 1P buffer, 100 µl radiolabelled hormone in 1P buffer, 100 µl 20% MeOH in 1P buffer), "non-specific binding" (200 µl 1P buffer, 100 µl radiolabelled hormone in 1P buffer, 100 µl 20% MeOH in 1P buffer) and "B_0" (100 µl 1P buffer, 100 µl antiserum in 1P buffer, 100 µl radiolabelled hormone in 1P buffer, 100 µl 20% MeOH in 1P buffer) standards were processed simultaneously with unknowns and standards.

Free radiolabelled hormone was removed from all except "total" solutions by incubation for 10 min at 4°C with 500 µl of charcoal/ dextran solution (0.25% w/v Norit-A filtered activated charcoal powder, Matheson, Coleman and Bell, USA) and 0.025% w/v dextran T70 (Pharmacia Fine Chemicals, Sweden) suspended in 1P buffer). In place of the charcoal/ dextran solution, 500 µl of milli Q water was added to "total" solutions. After centrifugation at 1500 G for 10 min at 4°C, the supernatant was decanted and its radioactivity measured as counts per minute (cpm) on a Beckmann LS 6500 Liquid Scintillation Spectrometer (Beckmann Instuments Inc, CA, USA.), which then converted cpm to disintegrations per minute (dpm) using an external standard.

High- performance liquid chromatography (HPLC) of excreted metabolites

One female *T. aculeatus* was injected intraperitoneally with 5 mCi of [4-^{14}C] progesterone ([^{14}C]P, 48.9 mCi/mmol, NEN Dupont, USA) and 2 mg of natural progesterone in 30% (v/v) propylene glycol in isotonic saline. Eight 0.5 g faecal samples were obtained two days after injection. Extracts from these samples were pooled into two samples and subjected to sep-pak chromatography. Eluates of 2252 dpm and 2440 dpm were dried under N_2 gas, reconstituted in 75% acetonitrile, filtered and subjected to HPLC (K65B HPLC system, ETP Kortec, Australia) at a flow rate of 0.5 ml per minute, using 61% acetonitrile at a pressure of 2250 psi at room temperature. Fractions were collected every 30 sec for 22 min, then every minute for 19 min, then every 10 min for 20 min. Absorbance at 240nm was measured, to monitor the separation of steroids with a 4-ene-3-ketone structure. Elution time of progesterone was identified using [^{3}H]P and a progesterone standard and the column was calibrated for testosterone, androstenedione, progesterone and 20α dihydroprogesterone.

Assessment of extraction, purification and RIA procedures

Three different solvents were tested for use in the extraction process. Faeces containing metabolites of injected radiolabelled and natural progesterone were agitated in 90% MeOH, 80% MeOH or diethyl ether, and partitioned with petroleum ether as described above. The three solvents and their petroleum ether portions were assayed for progestins as above.

The Sep-pak chromatography elution profile for oestrogen calculated by Spanner et al. (1997) was assumed for this study. The elution profile for progestin was determined by Sep-pak chromatography of solutions containing 200 fmol [^{3}H]P, using the series of MeOH dilutions described previously or the same series of dilutions of ethanol (EtOH). Co-elution of metabolites of faecal origin with progesterone was determined by adding 25000 dpm [^{3}H]P to duplicate faecal extracts from five female *T. aculeatus* and subjecting these to Sep-pak chromatography.

Sample steroid recovery was estimated by adding 25000 dpm [^{3}H]P or 30000 dpm [^{3}H]E to respective samples and then performing the extraction. Duplicate 50 µl aliquots of purified 80% MeOH extract were combined with 500 µl Milli-Q water and 5 ml of scintillation fluid. Triplicate "total" vials were prepared, each containing 100 µl of radiolabelled hormone solution, 50 µl 80% MeOH, 400 µl Milli-Q water and 5 ml of scintillation fluid. Triplicate "blank" vials were prepared, each containing 50 µl 80% MeOH, 500 µl Milli-Q water and 5 ml of scintillation fluid. Radioactivity was measured and percentage recovery was calculated by the formula:

$$R = [400(d-B)/ (T-B)] \times 100$$

where R = percentage recovery (%), d = sample dpm, B = mean "blank" dpm, T = mean "total" dpm.

To assess parallelism, faecal extracts from three faecal samples were reconstituted and diluted twofold and fourfold in 10% MeOH in 1P buffer. Standards were similarly diluted and all dilutions were assayed for progestins as described above. Spanner et al. (1997) estimated parallelism of the oestradiol assay.

The inter- assay coefficients of variation for progesterone and oestradiol assays were taken as the mean of the coefficients of variation of repeated (n=2), duplicated extraction and assay of 6 and 4 randomly chosen samples, respectively.

The intra- assay coefficient of variation was estimated from the mean of two coefficients of variation, each calculated from five concurrent replicate extractions and assays of two randomly chosen samples. The intra-assay coefficient of variation was estimated for two progesterone extraction methods to determine the homogeneity of steroid in the stool. In the first (unmixed) method, 5 samples were taken from an intact stool. In the second (mixed) method, the stool was finely chopped and mixed and each of the 5 samples consisted of at least 5 randomly chosen pieces from the mix. Spanner et al. (1997) estimated the intra-assay coefficient of variation of the oestradiol assay.

Data analysis

Standard curve generation and conversion of dpm to pg hormone/ scintillation vial were calculated with “Assayzap” (Biosoft, Cambridge). All other calculations and graphs were made using “Excel 5.0” (Microsoft, USA). Mean steroid recovery was calculated from the first 60 samples in each assay. Mean recovery was used to correct results of progestin assays for procedural losses. As steroid recovery was more variable in oestrogen assays, results were corrected using a recovery value calculated for each individual sample. Faecal steroid peaks were defined as those values greater than 1.5 standard deviations from the mean of all values from that animal (Graham et al 1995).

RESULTS

High pressure liquid chromatography

The eluate with the highest RIA activity and moderate radioactivity was collected at 26 min, approximating the progesterone standard, which eluted at 25.5 min. [^{3}H]P eluted at 24 min. A moderately radioactive eluate with poor RIA activity that was collected at 22 min coincided with a 20β-dihydroxyprogesterone standard, which has a low cross reactivity with the antiserum. Other [^{14}C]-labelled, moderately RIA-reactive compounds that eluted at 30, 36 and 38 min and one [^{14}C]-labelled, weakly RIA-reactive compound that eluted at 22 min were not identified. One RIA-reactive compound that eluted at 41 min did not co-elute with a [^{14}C]-labelled metabolite and this substance is yet to be identified.

Assessment of progestin extraction, purification and RIA procedures

As an initial solvent, ether extracted 37.0 ± 4.3% (mean ± S.E.) more [^{14}C] labelled progestin than either 80% MeOH or 90% MeOH and was used in all subsequent extractions. Less than 10% of extracted steroid appeared in the petroleum ether fraction. Mean percentage recovery of [^{3}H]P through extraction and Sep-pak chromatography was 52% ± 7.17 (mean ± SD). Mean percentage recovery of [^{3}H]E was 30% ± 13.7 (mean ± SD).

Almost all [^{3}H]P was recovered during Sep-pak chromatography. MeOH was chosen as the chromatography solvent as EtOH eluted the [^{3}H]P across a greater range of EtOH concentrations. Of recovered [^{3}H]P metabolites, 79.1% eluted in the 90% MeOH fraction and 93% eluted in the 75% MeOH and 90% MeOH fractions combined, with a mean 75% MeOH: 90% MeOH ratio (75:90 ratio) of 1:3.5. Of the progestin RIA- reactive faecal steroids recovered from the column, 85% was measured in the combined 75% MeOH and 90% MeOH fractions with a mean 75:90 ratio of 1:2.5.

Correlation coefficients of parallelism curves for the progestin assay ranged from 0.988 to 1.000. Dose response curves for standards and extracts did not differ significantly (P>0.05) in slope. Sensitivity of the assay, as defined by 10% displacement from the Bo binding was 10 pg/assay tube. The intra- assay coefficients of variation were estimated to be 6.2% (mixed) and 25.7% (unmixed), therefore the mixed method was employed in all further extractions. The inter- assay coefficient of variation was estimated to be 14.9% for progesterone assays and 6.8% for oestradiol assays.

Faecal progestins

Maximum and minimum faecal progestin concentrations from each of the six *T. aculeatus* ranged from 480 to 1800 ng/g dry weight faeces (mean 860 ng/g) and 5 to 100 ng/g dry weight faeces (mean 71 ng/g), respectively. Intervals between samples that contained progestin peaks clustered at 17 ± 3 (n = 5), 33 ± 3 (n = 4) and 48 (n = 1) days. Maximum and minimum faecal progestin concentrations from each of the three *Zaglossus sp.* ranged from 260 to 500 ng/g dry weight faeces (mean 420 ng/g) and 10 to 70 ng/g dry weight faeces (mean 40 ng/g), respectively. Two *Zaglossus sp.* produced two peaks each and the intervals between samples that contained these were 28 and 70 days. The third produced one peak.

Faecal Oestrogens

Maximum and minimum faecal oestrogen concentrations from the four animals ranged from 21 to 45 ng/g dry weight faeces (mean 33 ng/g) and 3 to 14 ng/g dry weight faeces (mean 7 ng/g), respectively. Intervals between adjacent oestrogen peaks were 8, 19, 24 and 30 days apart. Fluctuations approaching 1.5 SD above the mean were common and made difficult the detection of any possible cyclic activity as intervals between these ranged from 4 to 16 days.

Combined profiles

Of the 8 oestrogen peaks, 7 were associated with progestin increases to concentrations less than 1.5 SD above the mean. Combined oestrogen and progestin profiles from two *T. aculeatus* are shown in Figures 1 and 2.

DISCUSSION

Feeding and sample collection

Plastic pellets were less suitable as a faecal marker than the blue food dye. *T. aculeatus* consumed 95% of pellets placed in their food while *Zaglossus sp.* consumed less than 50%. Not all ingested pellets were recovered, indicating that pellets were being retained or faeces were remaining undetected. Food containing the blue dye was readily eaten and faeces containing the dye were considerably more detectable than those without. Passage time of the plastic pellets ranged from 12 hours to greater than 48 hours.

High pressure liquid chromatography

The strong antiserum cross-reactivity of the substance which eluted at 26 min, and its proximity to the elution time of the progesterone standard, makes progesterone its likely identity, however further confirmation of this would be desirable as we are unable to explain the elution of [^{3}H]P 2 min earlier.

The cross-reactive metabolites that were less polar than progesterone were not identified. These substances may contribute to the difference in 75:90 ratio between the Sep-pak elution profiles of [^{3}H]P and progestins of faecal origin as the 75%MeOH, or less polar, component was less in the [^{3}H]P profile. As a priority, future studies should identify the RIA-reactive

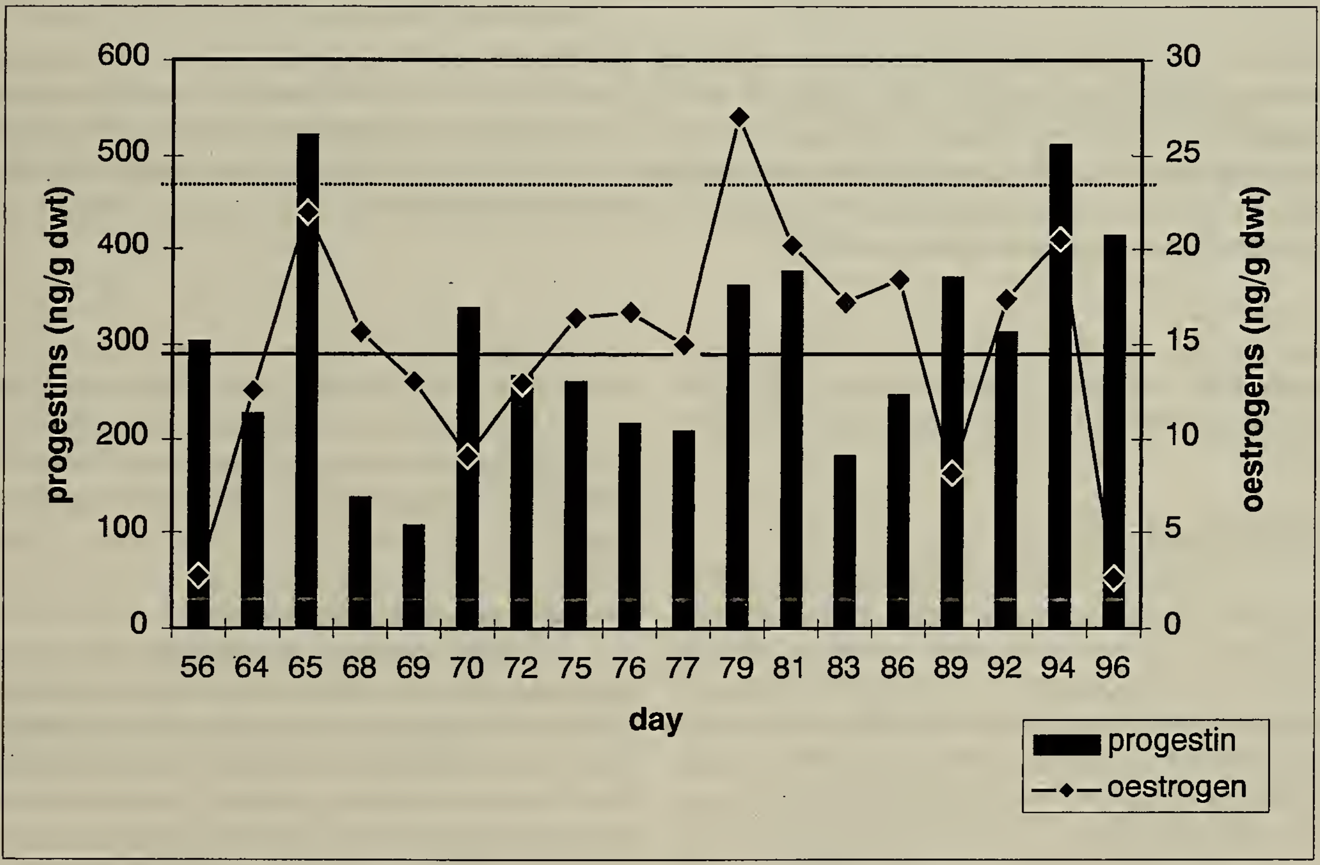

Figure 1. Combined faecal oestrogen and progestin profiles of one *T. aculeatus* over a 40-day period showing alternating progestin and oestrogen peaks greater than 1.5 SD above the mean, suggesting an oestrous cycle of 29 days. Also visible are increases less than 1.5 SD above the mean, suggesting concurrent progestin and oestrogen rises at 65, 79 and 94 days with interceding raised progestin/ lowered oestrogen periods surrounding 70 and 89 days, suggesting two cycles of 15 days. _______ = mean faecal progestin/ oestrogen concentration; .... = mean faecal progestin/ oestrogen concentration + 1.5 SD.

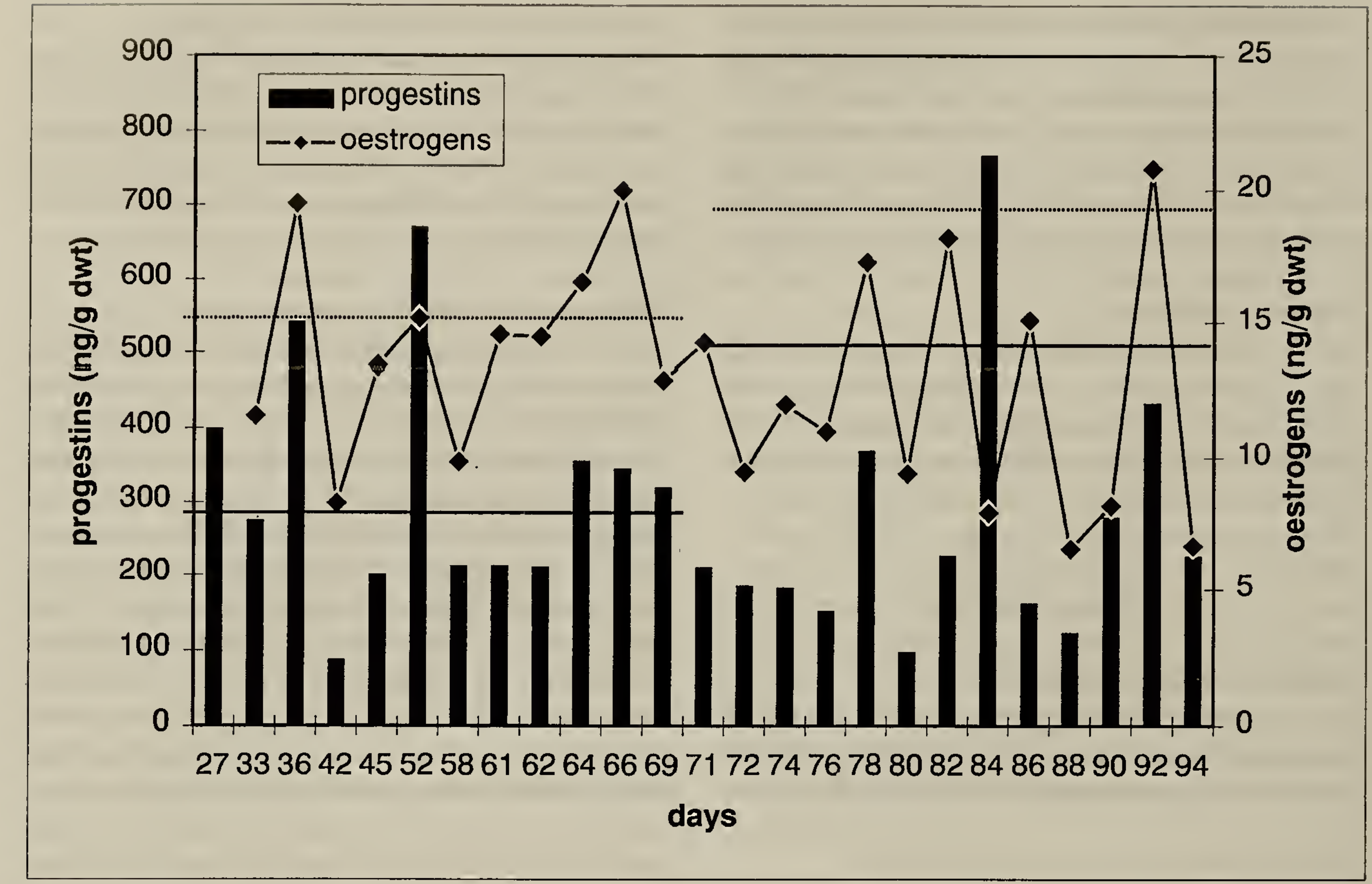

Figure 2. Combined faecal oestrogen and progestin profiles of one *T. aculeatus* over a 67-day period showing alternating progestin and oestrogen peaks greater than 1.5 SD above their respective mean, suggesting an oestrous cycle of approximately 32 days. Also visible are additional fluctuations of oestrogen concentration at 52, 78, 82 and 86 days and progestin at 36 days, which hinder clear interpretation of oestrous cycles. _______ = mean faecal progestin/ oestrogen concentration; .... = mean faecal progestin/ oestrogen concentration + 1.5 SD.

compound that did not correspond to a radiolabelled metabolite. A similar examination of oestrogen metabolites would assist interpretation of oestradiol assays.

Extraction and recovery

As homogeneity of steroid in the faeces was poor, mixing of the stool before sampling was necessary to reduce intra-assay variance. Though diethyl ether extracted the most steroid, recovery through extraction was low and variable in this study, especially in oestradiol assays. We attempted to correct for this by correcting for procedural losses using individual recovery values for each sample in oestrogen assays but progestin assay data were corrected using a mean recovery value. Use of individual recovery values for progestin samples may have improved interpretation of data.

MeOH concentrations exceeding 5% in the RIA incubations considerably reduced steroid-antibody binding. At each corresponding concentration, EtOH had a greater effect on steroid-antibody binding than MeOH. Reconstitution of eluates in 10% MeOH to produce a final concentration of 5% MeOH in the assay provided adequate steroid solubility and minimised interference with steroid-antibody binding.

Progestin and oestradiol profiles

Mean, maximum and minimum progesterone and oestrogen values varied among animals, indicating that this technique may be unsuitable for assessing the status of an animal from a single measurement. The small number of animals available for the study and the need for further work to identify antiserum-reactive metabolites limits the conclusions that can be drawn from the sequential data obtained in this study. However, the lack of knowledge in this area makes some trends worthy of comment for consideration in future work.

The intervals between subsequent progestin peaks in this study suggest a progesterone periodicity of 16-17 days. However, as there was no clear pattern in oestrogen excretion, we could not determine whether this reflects concurrent vitelline progesterone and oestrogen peaks at 32- 34 day intervals with an interspersed luteal peak at 16-17 days (see figs 1 and 2), or concurrent vitelline progesterone and oestrogen peaks at 16-17 day intervals with an interceding luteal phase with progestin increases below our arbitrary significance criterion. We expect that daily sampling and identification of potentially confounding RIA-reactive faecal steroids would be necessary to resolve this question. However, observations of fetal development add some support to the hypothesis of a 17-day progesterone cycle. Decreasing blood progesterone is a precursor to parturition in many species of eutheria (Rowlands and Wier 1984) and metatheria (Tyndall-Biscoe and Renfree 1987), and to oviposition in many reptilia (Licht 1984). At 17 days the tammar wallaby fetus consists of 17- 20 somite pairs (Griffiths 1984), similar to the 19-20 somite pairs possessed by the echidna at oviposition (Hill and Gatenby 1926; Luckett 1976; Hughes and Carrick 1978). Both young also exhibit similar stages of development at parturition or hatching 11 days later (Griffiths 1984). The similar rates of development in the last third of gestation and incubation suggests that the age of the echidna fetus at oviposition is approximately 17 days, consistent with a luteal phase of 16 to 17 days.

The many irregular oestrogen fluctuations we measured could be inherent in the technique or indicative of follicular development and atresia. Hill and Gatenby (1926) described channels, from the vitellus to a well-developed lymphatic sinus in the ovarian medulla and histological features indicative of follicular regression in the platypus.

The authors believe that this study provides a starting point for further work and suggest the further identification of progesterone and oestrogen metabolites and the comparison of faecal steroid concentrations with blood hormone concentrations, urogenital cytology, ultrasonography of the reproductive tract or behaviour in a controlled study accounting for the potential confounding effects of repeated physical or chemical restraint.

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Anatomy of the Central Nervous System of the Australian Echidna

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Even from their gross appearance, the brain and spinal cord of the Australian echidna show unusual features. The spinal cord is one of the shortest ever recorded for any mammal, ending at the mid-thoracic level, a feature which may be related to the defensive posture of the echidna. The pattern of termination of unmyelinated afferents in the spinal cord as revealed by lectin labelling with the B4 isolectin from *Griffonia simplicifolia* is also quite different from that seen in placental mammals, with termination in patches within deeper layers of the dorsal horn. Within the brainstem, specializations of the trigeminal system are apparent with great enlargement of all trigeminal nuclei. The mesencephalic trigeminal nucleus also shows an unusual aggregation of neurons in a central midline position quite unlike therian mammals. While the dorsal thalamus of therian mammals shows compartmentation related to function , the dorsal thalamus of the echidna is remarkable for its lack of cytoarchitectural differentiation. Most of the high encephalization in this mammal is attributable to the highly gyrified cerebral cortex. This cortex is further distinguished by the positioning of the major functional areas (primary motor, somatosensory, visual and auditory areas) towards the caudal pole of the brain.

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KEYWORDS: cerebral cortex, echidna, monotreme, spinal cord, thalamus, trigeminal.

INTRODUCTION

In this paper we will be reviewing what is known about the anatomy of the central nervous system of the Australian echidna (Tachyglossus aculeatus), with special reference to those features with functional relevance. Even at the level of gross inspection, the central nervous system of the echidna is remarkable for the large size of the brain and the short relative length of the spinal cord.

PERIPHERAL RECEPTORS AND ELECTRORECEPTION

One of the most remarkable features of monotreme neurobiology, and one which touches on trigeminal nuclei development and cortical organization, is the reported presence of electroreception in two members of this subclass (short-beaked echidna and platypus) (Iggo et al. 1985; Scheich et al. 1986; Gregory et al. 1987, 1988, 1989; Proske et al. 1998). This sensory modality utilizes the trigeminal system in both monotremes studied.

To date, physiological and anatomical studies of peripheral sensory systems in this animal have concentrated on peripheral receptors of the trigeminal system. The short-beaked echidna is known to use its sensitive snout as its major sensory tool. Anatomical studies of this snout have revealed a rich distribution of unusual receptors on the tip (Andres et al. 1991; Manger and Hughes 1992). One of these, the gland duct receptor system (Andres et al. 1991) or mucous sensory gland (Manger and Hughes 1992), is present in both platypus and echidna and is thought to be involved in electroreception (Iggo et al. 1985; Scheich et al. 1986; Gregory et al. 1987, 1988, 1989). Despite this attention to snout receptors, very little attention has been given to the structure or function of central trigeminal pathways in any monotreme.

SPINAL CORD ANATOMY

The spinal cord of the Australian echidna was examined by Ashwell and Zhang (1997). Even at the gross level, the spinal cord is notable because of its relatively short length, terminating at the level of the seventh thoracic vertebra (Figure 1a)(cf human spinal cord which terminates at the intervertebral disc between lumbar vertebrae 1 and 2). This may represent an adaptation to the pronounced vertebral flexure, which this mammal achieves when it adopts its defensive posture (Figure 1b). Since the spinal cord lies posterior to the vertebral column, extreme flexion would place the neural elements (spinal cord and cauda equina) under considerable tension, amounting to an increase of 15% in length or 6 cm in a large adult. The cauda equina in this animal is collectively as thick as the spinal cord, but consists of multiple nerve bundles

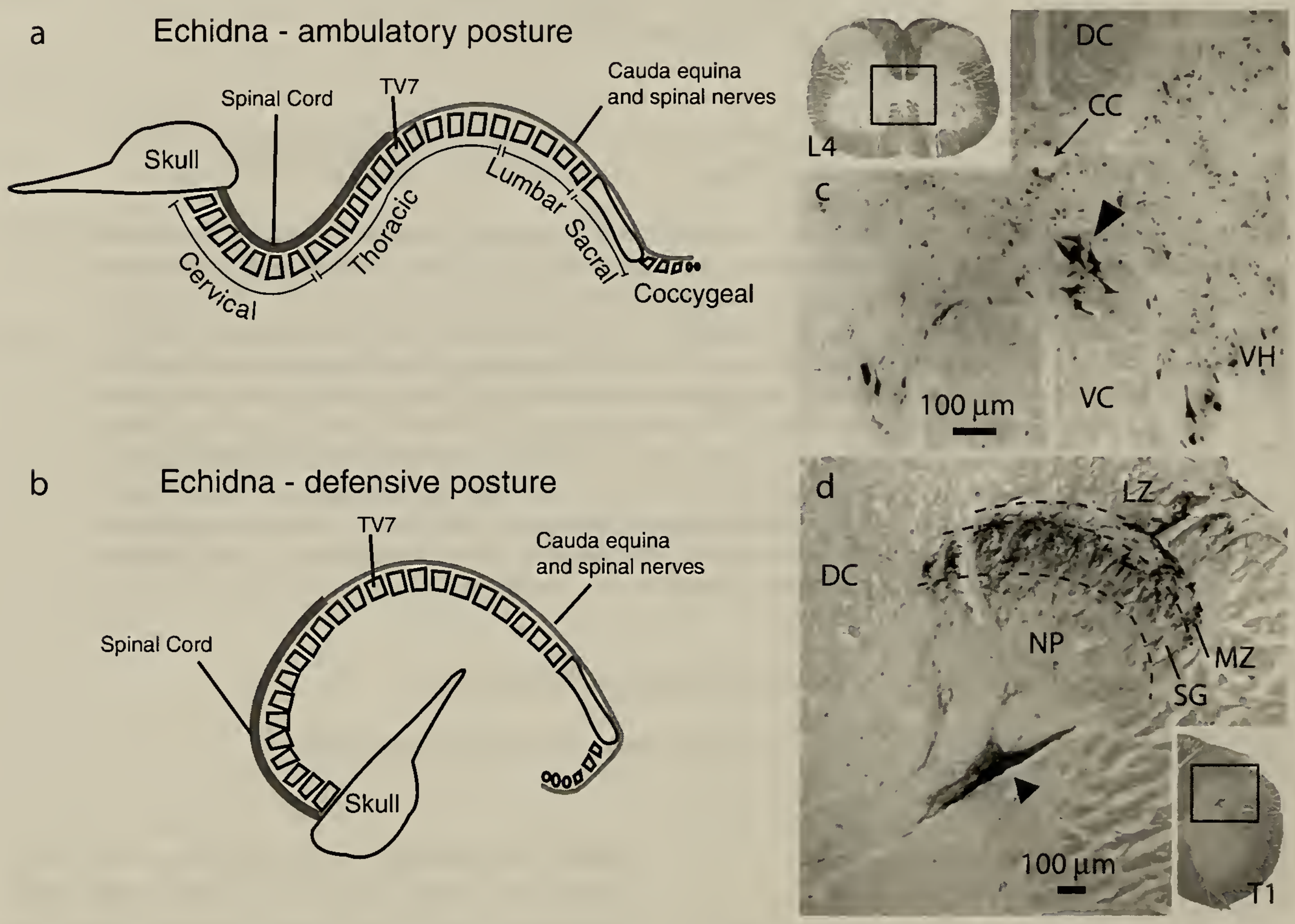

Figure 1. The spinal cord of the Australian echidna is very short, ending opposite the seventh thoracic vertebra when the animal is in the ambulatory posture (a). This may be an adaptation which allows pronounced flexing of the vertebral column in the defensive posture (b), since the spinal nerves of the cauda equina would be more tolerant of the stretching associated with flexing of the vertebral column than the much thicker and more vascular spinal cord. Figures c and d show features of the spinal cord reported in Ashwell and Zhang (1997). Please see that paper for ethical clearance details and tissue preparation methods. Figure 1c shows the large neurons of the median nuclear group (arrowhead) at the lower lumbar level of the spinal cord (L4). The small inset indicates the position of the larger image. CC – central canal of spinal cord: DC – dorsal column; VC – ventral column; VH – ventral horn. Figure 1d shows unmyelinated afferent fibres labelled with a peroxidase conjugated B4 isolectin from *Griffonia simplicifolia*. The small inset indicates the position of the larger image. These afferents enter via Lissauer's zone (LZ) and some descend to deep layers of the dorsal horn (arrowhead) terminating in the nucleus proprius (NP), unlike unmyelinated afferents to therian spinal cord, which are confined to the superficial layers; e.g. marginal zone – MZ; substantia gelatinosa – SG).

which are free to move independently of each other, unlike the spinal cord where individual axons are tightly bound together and are surrounded by delicate capillaries. Therefore the stretching of neural elements associated with extreme vertebral flexure, which is not only large of itself but also affects different segmental nerve roots to a greater or lesser extent, is perhaps more easily accommodated by shifting more of the nerve pathway length into the cauda equina.

At a histological level, the spinal cord was found to have similar cytoarchitectural features characterising the laminar organization to that seen in the spinal cords of eutherian mammals (Ashwell and Zhang 1977). Spinal cord nuclei found in eutherians were also identified in the monotreme, except for the central cervical nucleus. In addition, a distinct group of large neurons, named the median nuclear group, was identified in the ventral part of Rexed's lamina X and extending into the ventral funiculus at the lower lumbar level (Figure 1c). Fibre calibre in the dorsal and ventral roots of the echidna was similar to that reported in eutheria, suggesting similar proportions of afferent fibre classes and α and β motorneurons.

The distribution of unmyelinated primary afferent fibres within the dorsal horn of the echidna spinal cord have been examined using lectin labelling with *Griffonia simplicifolia* isolectin B4. When conjugated with horseradish peroxidase, GSB4 is known to label unmyelinated primary afferents terminating in both the dorsal horn and cranial nerve sensory nuclei (Streit et al. 1985; Plenderleith et al. 1989; Ashwell and Zhang 1997). It was seen that the pattern of labelling with this lectin within the spinal cord differed significantly from that seen in eutheria in several respects. Firstly, while labelling was seen within layers I and II of the echidna dorsal horn (similar to eutheria, Streit et al. 1985; Plenderleith et al. 1989), labelled fibre bundles were also seen coursing around the lateral margin of the dorsal horn as well as through layers I and II to terminate in deeper layers of the echidna dorsal horn (Figure 1d). In eutheria, lectin labelled primary afferents terminate only in the superficial layers of the dorsal horn (Streit et al. 1985; Plenderleith et al. 1989). This deeper labelling in the echidna was found to consist of discrete patches in the central and lateral parts of layers III and V (corresponding to the nucleus proprius). Furthermore, in upper cervical segments of the echidna spinal cord, labelled axons were identified coursing around the margins of the dorsal columns to terminate in the internal basilar nucleus (Ashwell and Zhang 1997). These two aforementioned features reflect unusual primary afferent termination in the echidna, but the elucidation of the functional significance of these would require electrophysiological studies. Generally however, spinal cord cytoarchitectural organization seems to be highly conserved across mammals.

CORTICOSPINAL TRACT

The echidna corticospinal tract (Figure 2a) differs from other mammals (Figure 2b, c, d) in both its position within the brainstem and in the level at which it decussates (Goldby 1939). The tract runs through the cerebral peduncle, decussates in the pons, and continues in the lateral medulla, dorsal to the spinal tract of the trigeminal nerve. At the spinomedullary junction it enters the most posterior part of the lateral column of the spinal cord and has been traced as far caudally as the 24th spinal segment, which corresponds to lower lumbar to upper sacral levels. No evidence has been found for the presence of a pyramidal tract close to the ventral midline of the medulla, nor for a decussation in the usual position at the caudal end of the medulla, as seen in most eutheria. In no other mammal is the pyramidal decussation as high as in the echidna, nor does the tract, after decussation, lie in such an extreme lateral position as in this monotreme. It is of interest to note, however, that a high decussation of the pyramidal tract is particularly characteristic of a small number of highly specialised mammals, which probably developed these corticospinal specialisations at a very early period in mammalian evolution (Goldby 1939). For example, some bats and edentates have a decussation just caudal to the pons and there is a tendency in some of these mammals for fibres from this high decussation to take up a lateral position in the medulla, e.g. in an armadillo, *Lysiurus unicinictus*, and the pangolin, *Manis tricuspis* (Goldby 1939). Since both of these eutherians are capable of pronounced vertebral flexure, as is the echidna, one is tempted to speculate that a high pyramidal tract decussation may be advantageous for mammals which use this type of defensive posture, although the precise nature of the advantage which this may confer is not clear at present.

In polyprotodontid metatheria e.g. the American opossum *Didelphis virginiana*, the corticobulbar and corticospinal tracts have been shown to be small and probably extend no further than the upper cervical segments of the spinal cord (Turner 1924, see also review by Heffner and Masterton 1983) and yet as noted above the pyramidal tract in the echidna is much more extensive. Among eutherians, both hedgehogs and tree shrews (Figure 2c) show termination of the corticospinal tract at higher segmental levels (upper cervical for the hedgehog and midthoracic for the tree shrew, for review see Heffner and Masterton 1983) than that seen in the echidna. These observations have made the extensive and unusual corticospinal pathway of the surviving monotremes of particular interest. Extension of the corticospinal tract down the greater length of the spinal cord is usually regarded as a feature of advanced neurological organization, as seen in primates (Figure 2d) and carnivores, because it allows direct control of the cerebral cortex over motor units within many levels of the spinal cord.

BRAINSTEM AND HYPOTHALAMUS

The gracile and cuneate nuclei are extraordinarily large in the echidna (Figure 3a), reflecting the well-developed somatosensory pathways for the limbs of the echidna. Furthermore, estimates of the proportion of white matter in the dorsal columns to total white matter in the cord gave an average result of 25%, suggesting well-developed trunk and appendicular somatosensory pathways comparable in development to carnivores and primates (Ashwell and Zhang 1997). In absolute terms the dorsal column pathway is as large as that in the domestic cat and *Macaca fuscata* - therians of similar body weight. This degree of development of the dorsal columns ranks the echidna among the most neurologically specialized primates with well-developed discriminative tactile sense. Perhaps the high level of somatosensory development can be attributed to dense innervation of the echidna's forelimb (Mahns et al. 2003)

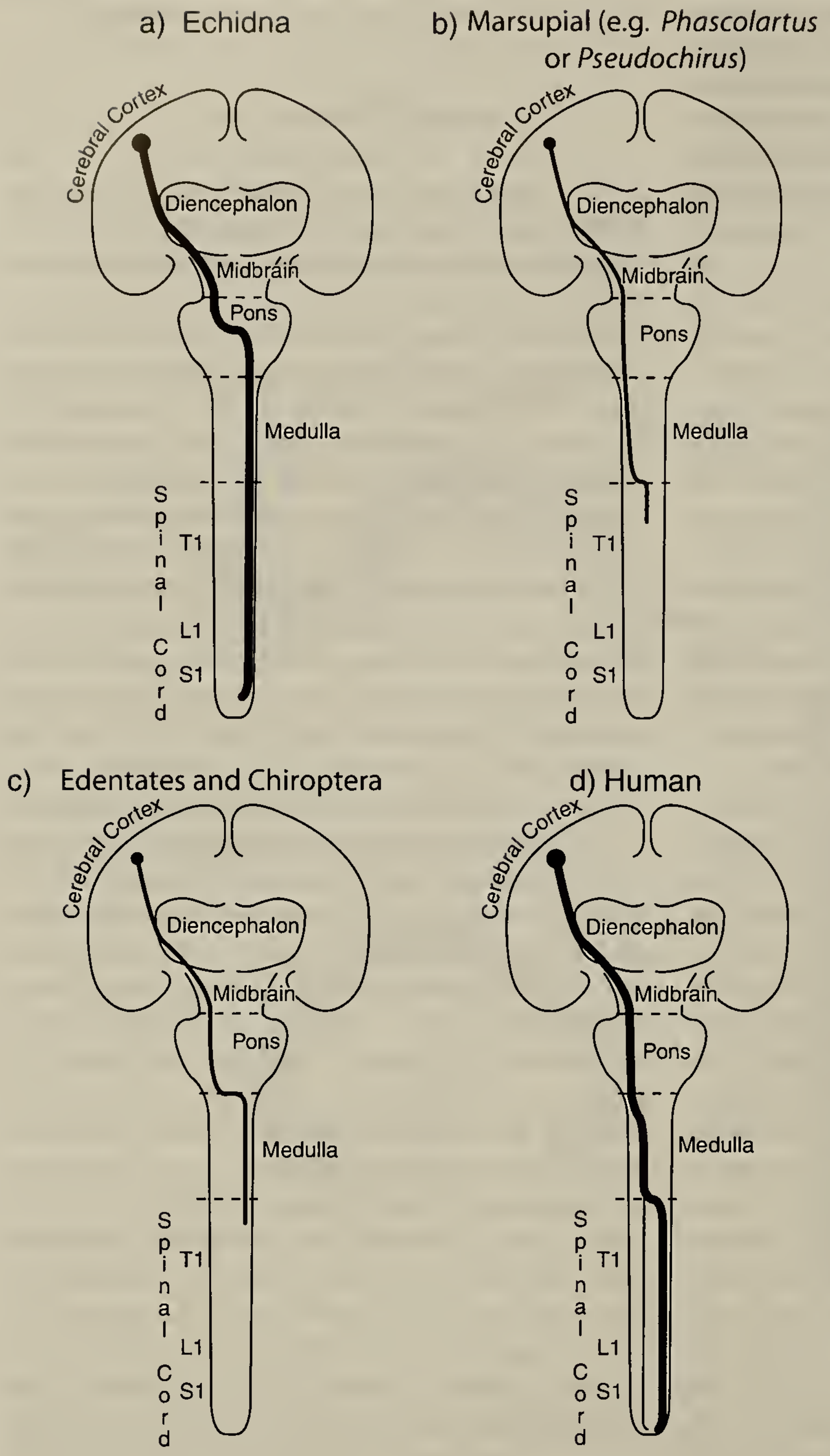

Figure 2 Diagrammatic summary of the course, size and extent of the corticospinal tract (bold) in representative mammals. Note that the corticospinal tract in the echidna is large, has a high decussation and extends to caudal levels of the spinal cord. Contrast this with the small size of the corticospinal tract in marsupials (b) and bats and edentates (c) and restriction of the tract to upper segmental levels of the spinal cord in those mammals. In size and extent, the echidna corticospinal tract is more like that seen in primates (d) and carnivores: mammals in whom a long and large corticospinal tract is believed to confer neurological advantages in the form of direct cortical control of motor units in the spinal cord. The corticospinal tract of the echidna also has a relatively high level of decussation (crossing over) compared to therian mammals, although some mammals (e.g. edentates and chiroptera - c) with the ability to flex their vertebral column also have a high level of decussation. No undecussated ventral corticospinal tract, as seen in primates (d) has been reported in the echidna. Data for the echidna is derived from Goldby (1939), while data for other mammals comes from Kappers, Huber and Crosby (1960).

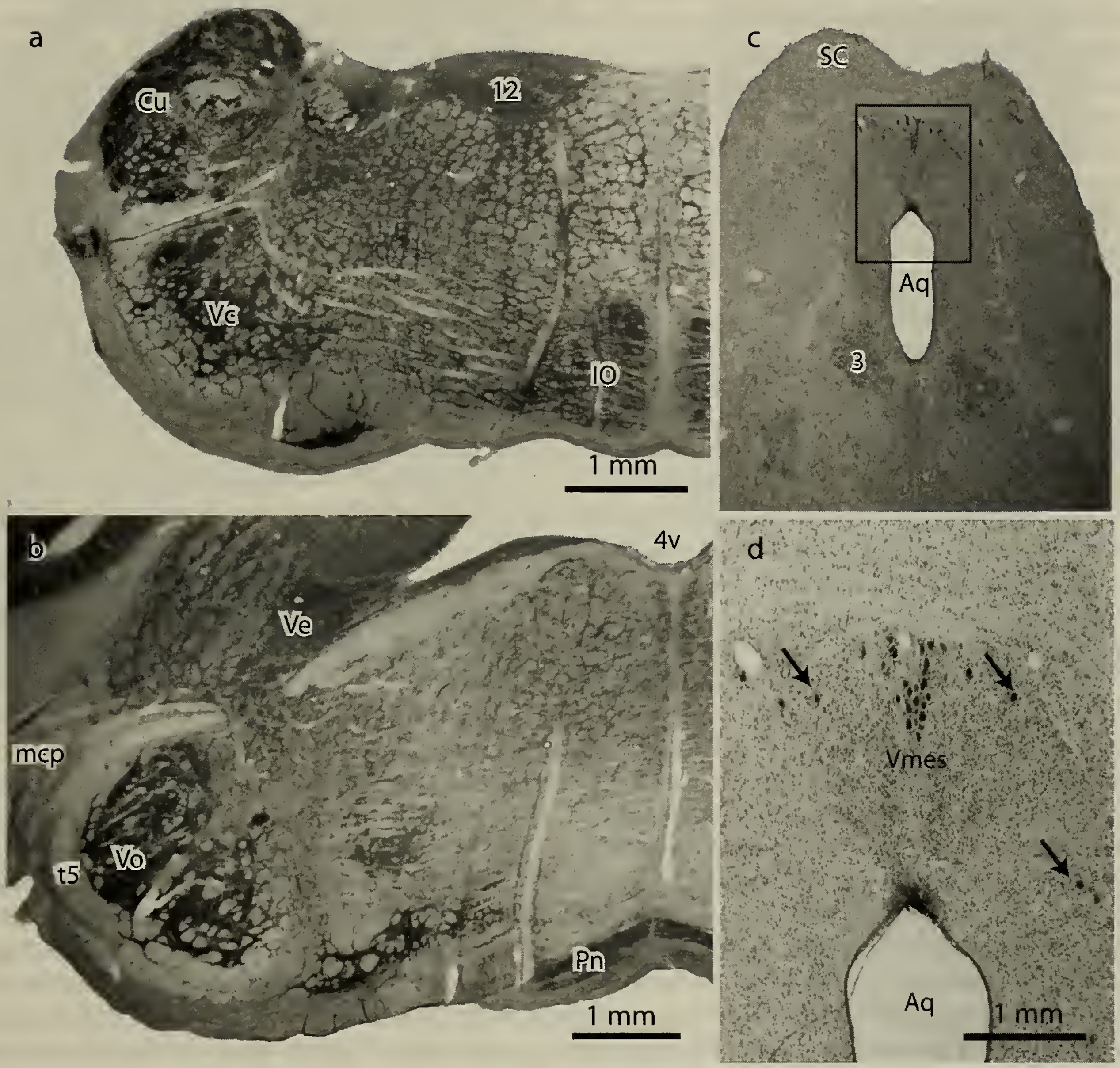

Figure 3. Coronal cryostat section (40 µm thickness) through the brainstem of an echidna stained for cytochrome oxidase by the Wong Riley technique (Wong-Riley 1979)(a, b) and Nissl substance (c, d). Please see Hassiotis and Ashwell (2003) for details of experimental ethics and animal acquisition. Strong cytochrome oxidase reactivity demonstrates the presence of high densities of mitochondria in axon terminals of major sensory pathways for limb and trunk somatosensory pathways (e.g. cuneate nucleus) and cranial somatosensory pathway (e.g. nucleus of the trigeminal spinal tract). The mesencephalic nucleus of the trigeminal nerve occupies a midline position dorsal to the cerebral aqueduct. The inset in c indicates the position of d. 3 – oculomotor nucleus; 4v – fourth ventricle; 12 – hypoglossal nucleus; Aq – cerebral aqueduct; Cu – cuneate nucleus; IO – inferior olivary nuclear complex; mcp- middle cerebral peduncle; Pn – pontine nuclei; SC – superior colliculus; t5 – trigeminal spinal tract; Vc –caudal part of the nucleus of the trigeminal spinal tract ; Ve – vestibular nuclei; Vmes – mesencephalic nucleus of the trigeminal nerve; Vo –oralis part of the nucleus of the trigeminal spinal tract.

or spines, although this has never been studied histologically. Alternatively, this specialization may have arisen because the echidna spends time in subterranean channels, where visual and auditory input are of little benefit, and the sense of smell and touch are of the most value. At present there are no morphological studies of echidna postcranial tactile receptors available to shed light on this.

The trigeminal nerve is also greatly enlarged in the echidna as are the nuclei of the trigeminal spinal tract (Figure 3a, b). This is consistent with the impression from behavioural and electroreception studies that the echidna's snout is extremely sensitive (see above). The trigeminal system in the echidna displays a high degree of specialisation similar in kind to that seen in *Ornithorhynchus*, but not to such a large extent. In other words, it does not appear to be as sensitive an electroreceptive tool as the platypus bill (Proske et al. 1998). Another note-worthy feature is that the motor nucleus of the trigeminal nerve in the echidna brainstem is much larger than would be expected in an animal whose jaw musculature is so poorly developed (Abbie 1934).

The mesencephalic nucleus of the fifth nerve in echidna is very like that seen in reptiles in that it adopts an almost exclusively mid-line distribution (Abbie 1934, Figure 3c, d). Metatheria exhibit a condition intermediate between that of the echidna and eutheria with more extensive development of the lateral mesencephalic V extensions. The mesencephalic nucleus and root of the fifth nerve are generally considered as being concerned with proprioceptive sensibility of jaw musculature. Since the echidna has very poor jaw musculature, such a pronounced development of mesencephalic V is inexplicable.

The echidna auditory and vestibular apparatus are also notable. In *Ornithorhynchus*, the entire labyrinth has been described as being typically avian (Gray 1908). In the echidna, the inner ear shows dissimilarities to therians, in that the echidna cochlea is banana shaped and has only half a turn, hence is partially coiled, whereas in humans the cochlea has two and a half turns, and is fully coiled (Gray 1908). The cochlea also shows maximal response to sound of about 5kHz, substantially lower than in eutheria (Augee and Gooden 1993). It has been proposed that when the cochlea evolved from the primitive labyrinth, it employed the existing vestibular connections within the brain, and that when the cochlear apparatus attained a mammalian level of structural specialization, a trapezoid body appeared in the brainstem. The trapezoid body in the echidna is so rudimentary that it reveals its primitive vestibular and primarily trigeminal origin, because it consists almost entirely of vestibular parts and external arcuate fibres which include a large trigeminal element (Winkler 1921; Abbie 1934). In therians, the pronounced increase in auditory fibres almost completely obscures the original trigeminal and vestibular connection. Winkler (1921) has argued that the poor cochlear development in the echidna renders the vestibular fibres relatively conspicuous. While central auditory pathways have never been closely examined in the echidna, these observations suggest that those pathways are either organized differently or not as extensive as in theria.

The hypothalamus in the echidna has been reported to have few striking features (Abbie 1934). The mammalian hypothalamus is very old phylogenetically (Simerly 1995) and very conservative in structure throughout the vertebrate series. One peculiarity, which links the echidna hypothalamus with that of reptiles, and is in sharp contrast to the majority of mammals, is the extremely poor development or possible absence of the echidna mammillothalamic tract (Abbie 1934). Regidor and Divac (1987) for example found no evidence of the mammillothalamic tract in the echidna on examination of myelin-stained coronal sections. This pathway is a key link in the Papez circuit underlying memory and emotions in eutheria. Its poor development in the echidna may indicate that this mammal has an alternative circuit for these functions.

THE ABSENCE OF A CLAUSTRUM IN THE FOREBRAIN

The absence of a claustrum in the echidna was initially noted by Abbie (1940) and by Divac and co-workers (Divac et al. 1987a) and was further discussed more recently (Butler et al. 2002). Similarly, no claustrum has been identified in the platypus brain (Butler et al. 2002). This structure has been identified in all therian mammals so far examined (Johnson et al. 1994) and is believed to have a structural and chemical affinity with the neocortex, although its precise functional significance is uncertain. It engages in reciprocal connections with neocortex and receives projections from the non-specific intralaminar nuclei of the thalamus (see Butler et al. 2002 for review). The question remains open as to whether the claustrum was present in ancestral mammals and disappeared in the monotremes, or whether its evolution represents an exclusively therian brain development.

THE DISTRIBUTION OF CHEMICALLY IDENTIFIED NEURONS

Manger and co-workers have recently examined the distribution of cholinergic, catecholaminergic and serotonergic neurons in the brains of the platypus and echidna (Manger et al. 2002a, b, c). Those authors showed that while there are many similarities between monotremes and therians in the distribution of these neurons, there were also some evolutionarily and potentially functionally significant differences. For example, cholinergic cells are present in the monotreme brain, but important cells groups identified in theria do not appear to be present in the platypus or echidna. These include cholinergic cells in the cerebral cortex, nuclei of the vertical and

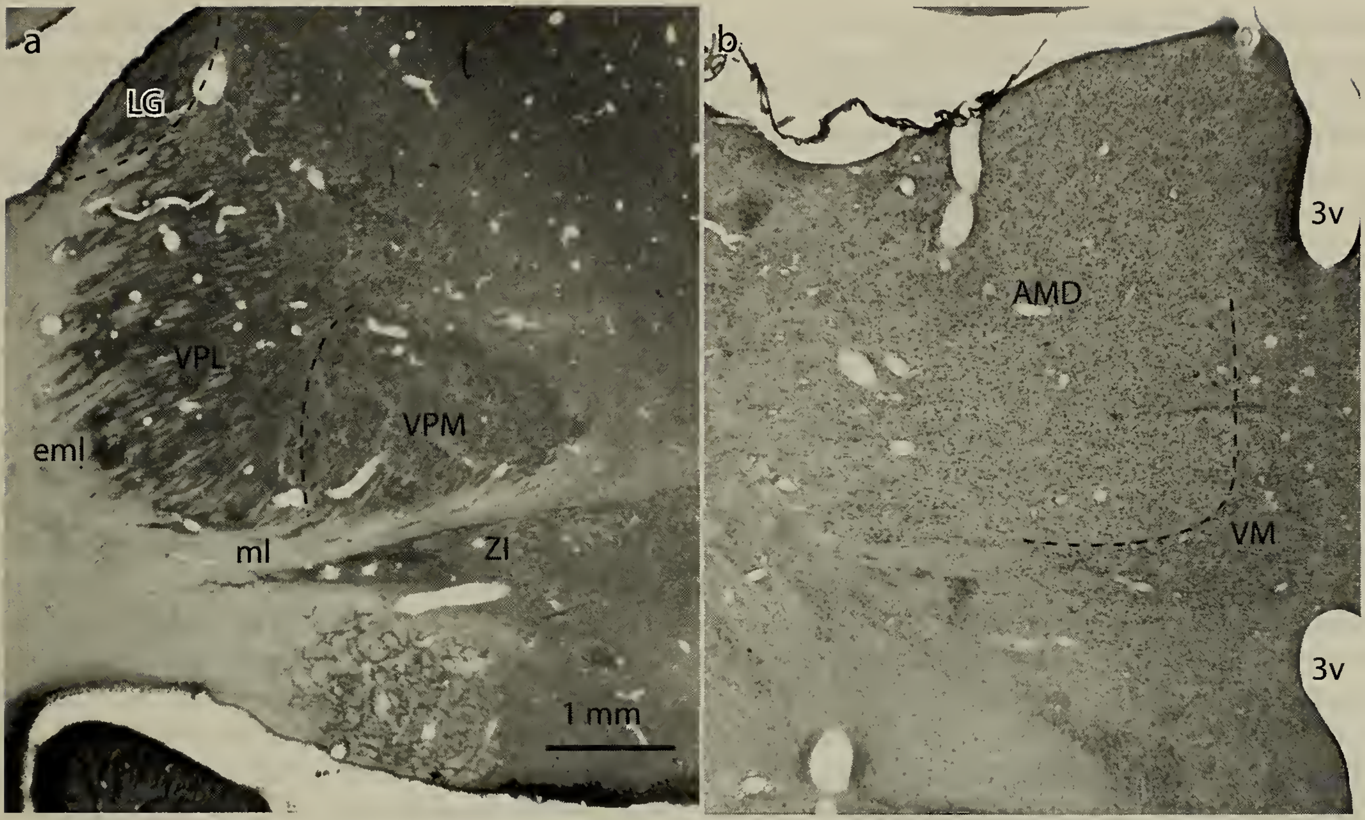

Figure 4. Coronal cryostat sections (40 µm thickness) through the caudal thalamus (a) and rostral thalamus (b) stained for cytochrome oxidase and Nissl substance, respectively. Please see Hassiotis and Ashwell (2003) for details of experimental ethics and animal acquisition. Note the large ventral posterior thalamic nucleus with lateral (VPL) and medial (VPM) compartments. In theria these two regions serve processing of somatosensory (touch) information from the body and head, respectively. Contrast the size of these two nuclei with the lateral geniculate nucleus (LG) processing visual information. The reticular thalamic nucleus, which is found in all therian mammals external to the ventral tier nuclei (i.e. embedded in the external medullary lamina to the left of 4a), appears to be absent from the echidna thalamus. The rostral thalamus (b) contains a large nucleus (anteromediodorsal -AMD) with no clear division into subnuclei. This may correspond to the mediodorsal nucleus of therians. 3v – third ventricle; eml – external medullary lamina; ml – medial lemniscus; ZI – zona incerta.

horizontal limbs of the diagonal band of Broca, the magnocellular preoptic nucleus, the substantia innominata, nucleus of the ansa lenticularis, hypothalamic nuclei and the parabigeminal nucleus (Manger et al. 2002a). They proposed that the absence of cholinergic neurons from the hypothalamus might be related to the unusual features of monotreme sleep (Siegel et al. 1996, 1998).

The catecholaminergic system of the monotreme brain appears to be very similar to that found in theria, but there were some minor differences in the form of the absence of A4, A3 and C3 groups from the locus coeruleus and caudal rhombencephalon. It should be noted however, that these are only small differences and this great similarity demonstrates the high degree of evolutionary conservatism in these neurons across amniote species (Manger et al. 2002b).

Serotonergic neurons in monotremes appear to fall into three groups: hypothalamic, rostral nuclear and caudal nuclear clusters. The rostral and caudal nuclear groups are found consistently across all mammals while the hypothalamic cluster, although not reported in other mammals, is found in most other species of vertebrates (Manger et al. 2002c).

THE THALAMUS AND THALAMOCORTICAL PROJECTIONS

Campbell and Hayhow (1971) identified several thalamic nuclei in echidna, which exhibited cyto- and myeloarchitectonic features resembling those found in other mammals (Figure 4). However, echidna thalamic nuclei are not as easily distinguished as those in opossums (Bodian 1939, 1942; Oswaldo-Cruz and Rocha-Miranda 1968; Benevento and Ebner 1971) or other commonly used laboratory mammals (Rose 1942; Rose and Woolsey 1949). Chemoarchitectural characteristics of the thalamus in echidnas and rats have been compared in sections stained for myelin, acetylcholinesterase (AChE), succinate dehydrogenase (SDH) and cytochrome oxidase (CO) by Regidor and Divac (1987). Numerous species differences were noted, but in general the thalamus is architecturally more homogenous in echidnas than in rats, especially within the anterior portion (Figure 4b). The large structure localized in the anteromediodorsal part of the thalamus of the echidna has been found to contain small amounts of acetylcholinesterase and oxidative enzymes; in this respect resembling the mediodorsal nucleus of rats. Regidor and Divac (1987) concluded that this brain structure of echidnas corresponds to the mediodorsal nucleus in placental species.

Welker and Lende (1980) defined and described the thalamic nuclei that contribute major projections to the isocortex in echidna. Their purpose was to determine whether the echidna thalamus exhibited mammalian thalamocortical relations more similar to those found in metatheria, or to those in eutherian mammals. Welker and Lende also attempted to identify whether an enlarged thalamic nucleus was sending afferents to the enlarged frontal cortex. They performed a series of partial ablations of the somatic sensory, auditory, visual and motor areas, as well as in several different portions of the greatly enlarged frontal neocortex (see below) and demonstrated that the thalamocortical connections in the echidna are similar in most respects to those demonstrated in eutherian mammals. One unusual feature observed by Welker and Lende was a large nuclear mass in the dorso-fronto-medial thalamus (presumptive anteromediodorsal nucleus discussed above), which projects to the enlarged frontal cortex (Divac et al. 1987a, b). It has been hypothesised that this nuclear region is homologous to the eutherian mediodorsal nucleus. Their data also revealed that projections to separate motor and somatic sensory cortical areas from the thalamus were spatially distinct (Welker and Lende 1980).

CORTICAL STRUCTURE AND ORGANIZATION

Until the late 1800's it was generally believed that all mammals possessed a corpus callosum (Turner 1890), a major fibre bundle connecting the neocortex of the two hemispheres of the brain. Elliott Smith (1902, 1903) dispelled this notion in his early studies of comparative cortical organization. He showed that in monotremes and metatheria, the anterior commissure is the major cerebral commissure, being the sole connection between all parts of the neo- and paleocortex, with only a small archicortical commissural connection being present dorsally (the hippocampal commissure).

Several striking aspects of gross cortical anatomy have been noted in *Tachyglossus aculeatus*. The most obvious of these is the high degree of gyrification (36% of isocortex buried in fissures), comparable to that in many eutherian mammals (e.g. cat 40%, squirrel monkey 39%). The second is the large proportion of the brain volume occupied by the cerebral cortex (43%), similar to values in eutheria (prosimians – 54%, Pirlot and Nelson 1978). Among the brains of eutheria, a highly gyrified cerebral cortex is usually considered as an attempt to maximise the number of cortical columns available for the processing of information. Therefore a highly gyrified cortex is considered the hallmark of more neurologically advanced mammals such as carnivores, primates and cetaceans. This raises the question as to why an animal like the echidna, which leads a solitary existence and has no known complex social life, has such a highly gyrified cortex. One principal difference between the brains of the two living Australian monotremes is that the platypus' cortex is quite smooth (lissencephalic), whereas the echidna cortex is complexly folded.

Another most remarkable aspect of echidna neurobiology concerns cortical topography. Ziehen (1897, 1908), Brodmann (1909) and Schuster (1910), all published early observations on the cortex in the Monotremata. Brodmann examined the cortex in echidna and established that there is a typical six-layered distribution. The echidna has been noted to have a thinner cortex, perhaps due to its denser packing of neurons compared to the platypus (Abbie 1940). In both the echidna and the platypus, Ziehen (1897, 1908) showed that there was a change in the type of cortex between the anterior (olfactory) and posterior (sensorimotor) portions of the hemisphere, and Schuster (1910) confirmed his observations. Nevertheless, these early authors concluded that the plan upon which the monotreme brain is constructed conforms in every respect to the basic pattern prevailing among the vast majority of other mammals (Abbie 1940).

To date, the most detailed anatomical study of the echidna cortex was performed in the 1940's by Abbie. Since the 1940's, no further in-depth anatomical studies have been done on the anatomy of the echidna cortex as a whole, although specific systems have been

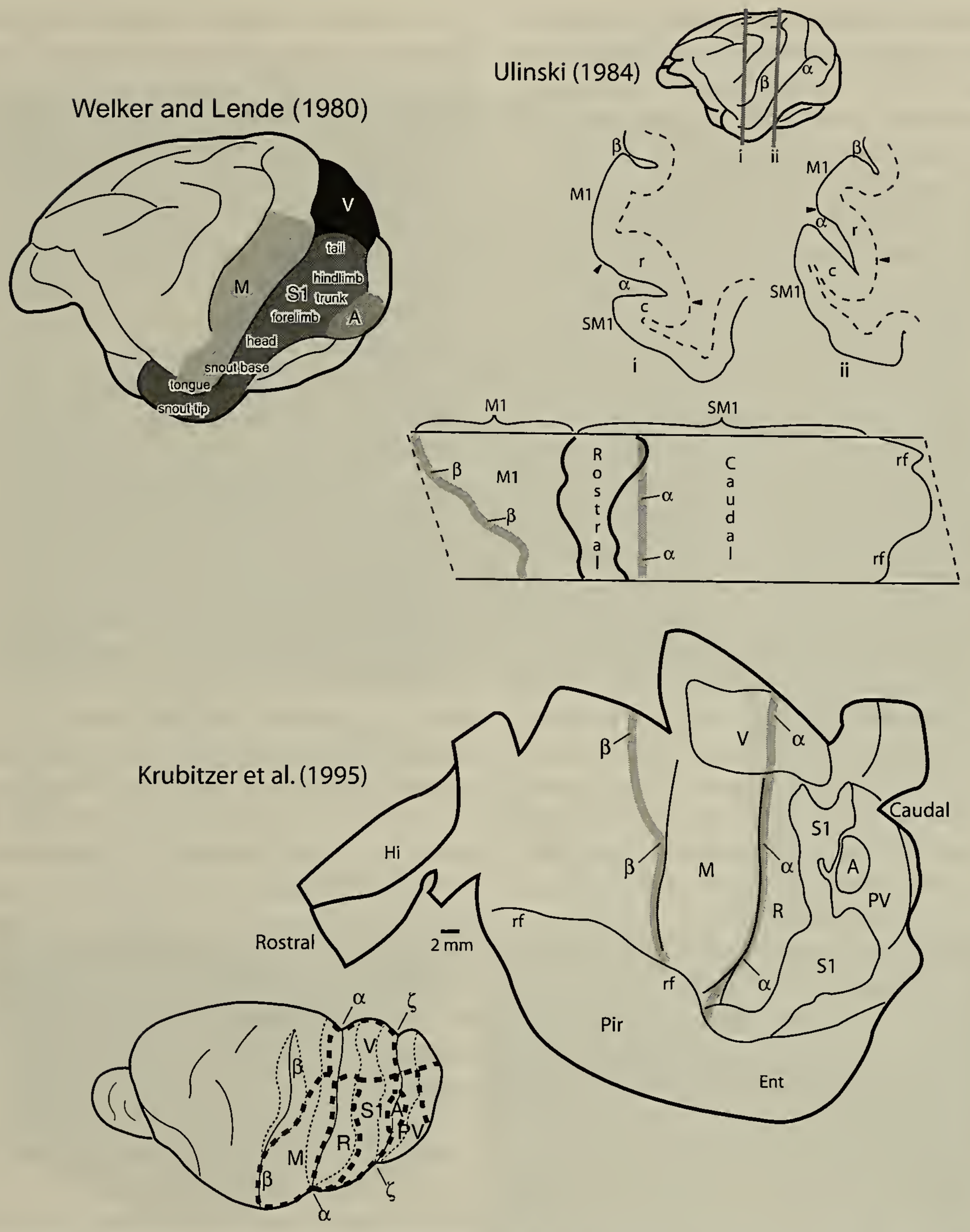

Figure 5. Electrophysiology and cytoarchitecture of the echidna cerebral cortex. The earliest study illustrated is by Lende (1964)(results shown in a summary diagram redrawn from Welker and Lende 1980). Greek letters denote major consistent sulci as delineated by Smith (1902). The Welker and Lende map shows only the externally visible gyral surface and indicates the position of motor (M), somatosensory (S1), visual (V) and auditory (A) cortices. The Ulinski map shows cytoarchitectural fields identified by that author (Ulinski 1984). Two coronal sections (i and ii) are illustrated with the positions of rostral (r) and caudal (c) fields of the somatosensory cortex (SM1) marked. The small lateral view shows the rostrocaudal positions from which these sections were taken. The figure below the two sections shows a flattened representation of cortex. Note that Ulinski's "r" field lies rostral (and superior) to the deepest part of the α sulcus. The lower two illustrations summarize the findings of Krubitzer et al (1995). The smaller diagram shows a representation of the entire flattened cortical surface with the sulcal walls opened. Solid lines in the Krubitzer map indicate the deepest point of the sulci, while dotted lines indicate the sulcal rims at the external cortical surface. The larger illustration shows a drawing of the completely flattened cortical surface with the boundaries of functional areas indicated relative to β and α sulci (thick grey lines). Note that the rostral somatosensory field in Krubitzer's map lies caudal to the α sulcus (cf Ulinski map). Ent – entorhinal cortex; Hi – hippocampus; M – manipulation cortex; Pir – piriform cortex; PV – parietal ventral somatosensory cortex; R –rostral somatosensory cortex; S1 – primary somatosensory cortex.

studied. Abbie described the monotreme neocortex as comprising two broad components; one related to the hippocampus, labelled by him as parahippocampal regions and located in the anterior and medial parts; and the other related to the piriform cortex, labelled as the parapiriform regions, located posteriorly and laterally. He also defined sulcal boundaries to these regions. When labelling the cortex, Abbie adopted the system of Elliot Smith (1902), using Greek letters to name the major and deepest sulci (Figure 5). There are two pronounced sulci in the monotreme cortex, denoted as α and β. These divide the frontal cortex from the posterior motor and sensory cortices.

More recent functional studies of the isocortex of *Tachyglossus aculeatus* have indicated that the primary motor, somatosensory, auditory and visual areas are located in the caudal half of the isocortex (Lende 1964)(Figure 5). Aside from the posterior location of these areas, the following relationships are unlike those described in any other therian mammals: the somatic sensory area is confined to the ventral portion of the lateral surface; the visual area is located dorsal to the somatic sensory area and borders the representation for the tail; the auditory area is located posterior to the visual and somatic sensory areas and borders the latter at the representation of the back. These relationships might be described as rotational dislocation of the areal relations relative to that found in eutherians in that the somatic sensory area has been displaced downward and backward, the auditory area upward, and the visual area upward and forward (Lende 1964).

The somatosensory representation in the echidna is in some respects similar to that of other mammals. The area for the tail is found uppermost and the areas for hind limb, trunk, forelimb, and head are located laterally and ventrally, in that sequence. This is the same as the basic mammalian pattern of somatosensory area 1 (S1) as established by Woolsey (1952). A relatively large portion of somatosensory cortex in the echidna was found by Lende to be devoted to the head, and particularly the snout and tongue, as might be expected from the ant-eating habits of the echidna (Lende 1964).

Physiological studies have indicated that more than 50% of the rostral cortex of the echidna has no attributable primary motor or sensory function and has been considered as an expanded prefrontal cortex (Welker and Lende 1980). If this interpretation is correct, then the proportion of isocortex in *Tachyglossus aculeatus* occupied by the prefrontal area exceeds that in humans (29%) Divac et al. (1987a, b)(see section on thalamus and thalamocortical projection in previous pages).

Ulinski's study (1984) examined the cytoarchitecture and thalamic afferents of the somatosensory area (SMI) in the echidna. His findings indicated that SMI contains two cytoarchitectonic fields. A caudal field with a well-developed layer IV present extends across the post α gyrus and onto the floor of sulcus α The rostral field was reported to extend from the floor of sulcus α onto its rostral bank. It also was reported to have a well-developed layer IV but with a large number of pyramidal neurons in layer V. The remainder of the pre α gyrus was reported to contain a single cytoarchitectonic field with a thin layer IV and layer V heavily populated with larger pyramidal cells. This field corresponded to the physiologically defined motor area M1. Thalamic afferents to somatosensory area were examined by placing pressure injections of horseradish peroxidase into the two architectonic fields. The results indicated that the somatosensory area in *Tachyglossus aculeatus* contains two cytoarchitectonic fields that resemble areas 3a and 3b in some placental mammals, leading Ulinski to the conclusion that the collection of cytoarchitectonic fields corresponding to areas 4, 3a, and 3b is a basic mammalian character which has been modified in metatherian and many eutherian mammals.

In more recent times, Krubitzer et al. (1995) undertook a detailed study of monotreme cortical organization as part of a comparative approach to determining those features of the isocortex which characterise all the major lines of mammalian evolution, More specifically, their investigation was designed to determine the internal organization and number of somatosensory fields in the monotreme isocortex.

The isocortices of both monotremes were found to contain four representations of the body surface. A large area that contained neurons predominantly responsive to cutaneous stimulation of the contralateral body surface was identified as the primary somatosensory area (S1). This was found caudal and ventral to the α sulcus. Another somatosensory field (R) was identified rostral to S1. The topographic organization of R was similar to that found in S1, but neurons in R were responsive most often to light pressure and taps to peripheral body parts. Neurons in cortex located rostral to R were responsive to manipulation of joints and hard taps to the body. This field was termed the manipulation field (M) and occupies the position of the motor cortex identified by Lende. Note that Krubitzer's M field occupies an area which Ulinski denoted as the rostral somatosensory field and Krubutzer's R field occupies at least part of Ulinski's caudal somatosensory field (Ulinski 1984)(Figure 5). Consequently the two studies are not easily reconciled. A parieto-ventral somatosensory field (PV) was also identified by

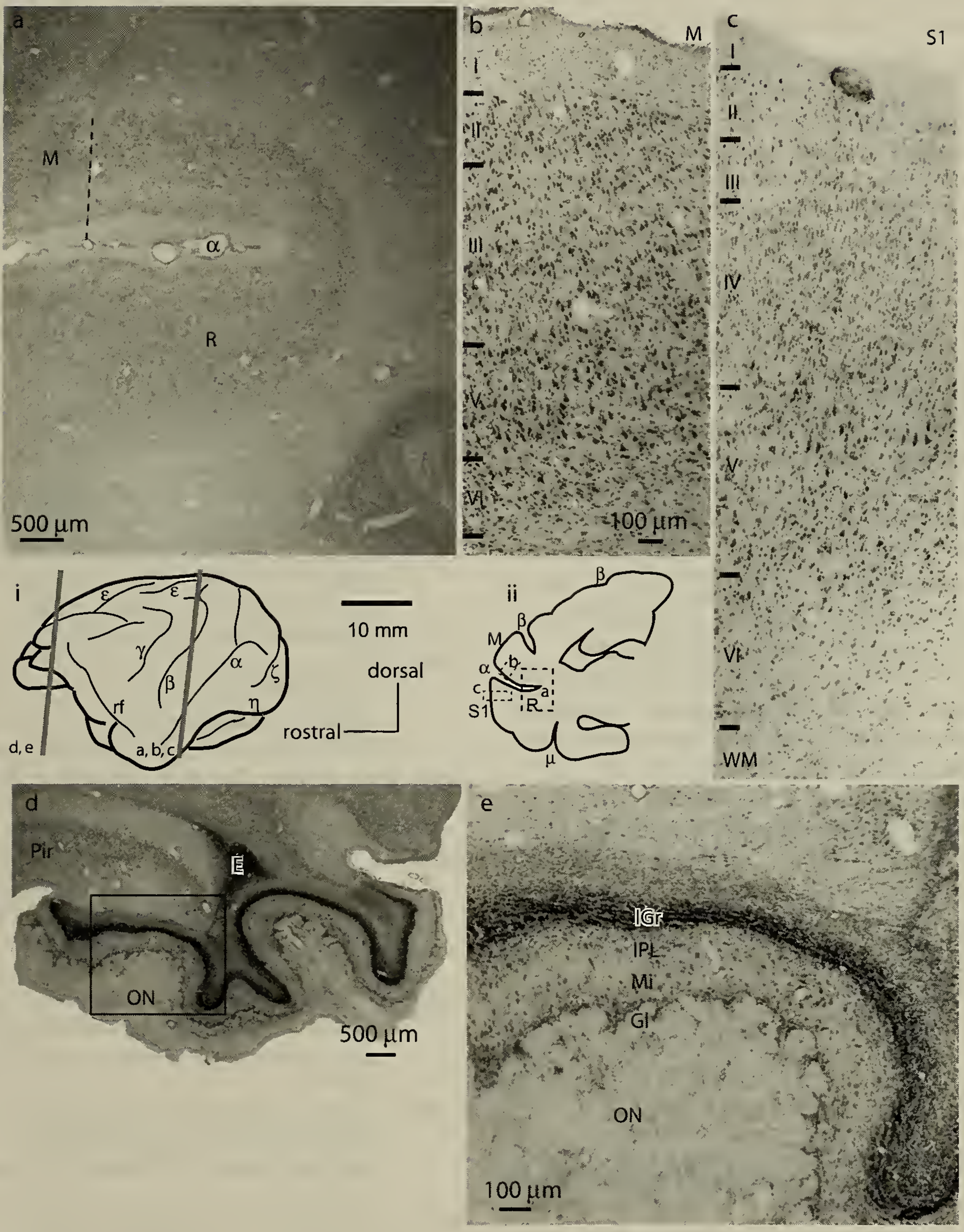

Figure 6. Nissl stained cryostat sections in the coronal plane through the cerebral cortex and olfactory bulb of the echidna. Please see Hassiotis and Ashwell (2003) for details of experimental ethics and animal acquisition. The inset drawings show: i) a lateral view of the echidna cerebral hemisphere indicating the planes of section shown in a, b, c and d, e, respectively; and ii) a line drawing of a coronal section showing the positions from which a, b, and c were taken. Figure 6a shows a lower power view of motor cortex (M) and the rostral field of somatosensory cortex (R). Figures 6b and c show motor cortex and S1 somatosensory cortex, respectively with layers indicated by Roman numerals. WM – subcortical white matter. Figures 6d and e show low and high power views of the olfactory bulb. Rectangle in d indicates the position of e. Note the lack of a clear tightly grouped monolayer of mitral cells (Mi) as is seen in therian mammals (Switzer and Johnson 1977). E – ependyma of lateral ventricle; Gl – glomerular layer; IGr – internal granular layer; IPL – internal plexiform layer; ON – olfactory nerve fibre layer; Pir – piriform cortex.

Krubitzer and was thought to be homologous to its therian counterparts (Krubitzer et al. 1995). The evidence for the existence of four separate somatosensory representations in somatosensory cortex was taken to indicate that cortical organization is more complex in the echidna than had been previously thought. Furthermore, although the two monotreme families have been quite separate for at least 55 million years (Richardson 1987), the similarity of cortical field organization in both monotremes studied suggested either that the original differentiation of sensory fields occurred very early in mammalian evolution, or that the potential for division of somatosensory cortex into numerous fields was highly constrained in evolution, so that both species arrived at the same result independently.

Figure 6 shows the cytoarchitecture of the echidna motor and somatosensory cortices. Nomenclature for cortical areas is adopted from Krubitzer et al (1995). As in eutherian motor cortex (Figure 6b), the echidna M cortex is characterised by large pyramidal neurons in layer V. The S1 part of somatosensory cortex (Figure 6c) is characterised by a layer IV rich in densely packed small neurons.

Several other aspects of cortical function in this species are also of note; particularly the apparent absence of an SII somatosensory representation and the relatively lateral position of the motor representation compared to that in eutheria (Krubitzer et al. 1995). Until recently, functional studies had failed to identify any parietal association cortex, but Krubitzer et al. (1995) was able to identify a topographically discrete, multimodal area between the primary sensory cortical areas, which may represent such an area.

CONCLUDING REMARKS

There are a number of unusual features of the anatomy of the brain and spinal cord of the echidna. Some of these are probably indicative of the early branching of the monotreme lineage from therian mammals (e.g. absence of the claustrum), some have potential functional significance for the unusual physiology of this mammal (e.g. the absence of hypothalamic cholinergic neurons), while some appear to be peculiar adaptations to the niche occupied by this mammal (e.g. trigeminal nuclei development and short spinal cord).

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Monotreme Tactile Mechanisms: From Sensory Nerves To Cerebral Cortex

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Electrophysiological recordings from single tactile sensory nerve fibres supplying the limb extremities in the echidna (*Tachyglossus aculeatus*) reveal a remarkable resemblance between monotreme peripheral tactile mechanisms and those of placental mammals. The similarities apply to a concatenation of attributes, including the classification of sensory fibre types and aspects of functional properties and tactile coding capacities. The analysis demonstrates that high-acuity tactile signalling from the distal forelimb in the monotreme is based upon a triad of major tactile fibre classes as is the case for placental mammals. Furthermore, the functional similarity between corresponding classes in monotreme and placental species suggests that peripheral tactile sensory mechanisms are highly conserved across evolutionarily-divergent mammalian orders.

Evidence for a unique and striking dependence upon tactile sensory mechanisms in monotremes comes from both behavioural observations on the animals and from the exceptional prominence given to the representation of tactile inputs in the cerebral cortex of these species. In the platypus, for example, almost half of its lissencephalic cortex is allocated to the processing of inputs from the bill. Furthermore, within the specialized area of bill representation in the platypus cortex, the receptive fields of individual neurones are amongst the smallest ever recorded within the somatosensory areas of cortex (often <1mm in diameter), presumably conferring great fidelity and precision on the tasks of tactile localization and discrimination involving the bill. However, in both the platypus and the echidna there is a complete and highly ordered somatotopic representation of tactile inputs from the contralateral body surface, conforming with the so-called primary somatosensory cortex (SI) of other mammals. Controversy applies to the issue of whether additional, multiple body representations are present in the monotreme cortex, as neither Lende (1964) nor Bohringer and Rowe (1977) found evidence of this, in contrast to Krubitzer et al. (1995a), who have argued for four body representations in the cortex of *both* the echidna and the platypus.

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EVOLUTIONARY PLACE OF THE MONOTREME BRAIN

The emergence, 100-200 million years ago, of monotremes on a separate evolutionary line from their placental and marsupial mammalian counterparts has contributed, in particular in the 19th century, to the hypothesis that living monotremes are closer to ancestral mammalian forms than their placental and marsupial relatives, and therefore that the monotreme nervous system may provide a window on the status of the ancestral mammalian brain. These notions were implicit in the designation of monotremes as the Prototheria, or first mammals, while the marsupial mammals were designated the Metatheria and were thought to represent the next stage of evolution towards the Eutherian, or complete mammals. This hierarchical concept of the relations between the three great orders of mammals was, in part, influenced by the presence in living monotremes of reptilian or avian-like reproductive mechanisms. This possession of oviparity, or the capacity to lay eggs, set the monotremes aside from mammals of the marsupial and eutherian orders. Furthermore, a concatenation of other anatomical or functional attributes shared with reptilian and avian representatives, but not with other mammals, tended to re-inforce these hierarchical concepts. These attributes have been documented by Augee and Gooden (1993) and include, among others, the arrangement of the shoulder girdle, the less elaborate coiling of the cochlea, and the presence of dwarf nephrons in the kidney. Perhaps surprisingly, the presence of the single opening from the cloaca for both reproductive and excretory activity, which led to their *monotreme* designation, is not entirely diagnostic for this mammalian group as some marsupials and other vertebrates share this feature (Augee and Gooden 1993).

Despite the retention of several plesiomorphic attributes in living monotremes there should be no expectation that such attributes need be a generalized feature of this mammalian order. Thus, in other respects of their anatomy or physiology, monotremes need not have proved any more conservative or constrained in their evolutionary progress than their marsupial or placental relatives with whom they have shared perhaps 200 million years in which to evolve from the ancestral forms of their evolutionary forebears. Indeed, we see some hint of this evolutionary metamorphosis and divergence *within* the monotreme ranks themselves, even in gross features of central nervous system organization. For example, although the divergence of the monotreme line into separate platypus and echidna strands has occurred ~50-80 million years ago (Griffiths 1978; Dawson 1983; Richardson 1987), or even as recently as ~20 million years ago (Belov and Hellman 2003), one encounters striking differences between them in the gross morphology of the cerebral cortex. The echidna has a quite elaborately folded, or gyrencephalic cerebral cortex, whereas, in contrast, the platypus possesses a smooth, essentially unfolded, lissencephalic cortex. The elaborate pattern of the cortical fissures in the echidna was analyzed and classified by Elliot Smith (1899, 1902) according to a scheme of Greek characters. The most consistent fissures form a series of mediolaterally oriented sulci designated α, β and δ, with other less prominent and less consistent sulci being present (Elliot Smith 1899, 1902; Hines 1929; Burkitt 1934; Lende 1964). The only departure from lissencephaly in the platypus cortex is the presence of a slight and shallow rhinal sulcus on the ventral surface of the cerebrum (Elliot Smith 1902).

The divergence within monotreme evolution that has given rise to the lissencephalic and gyrencephalic forms of the cerebral cortex in the platypus and echidna is similar to that seen within both the placental and marsupial orders. Among the placental mammals, lissencephaly is apparent in the cortex of the rat and rabbit and even in some primates, such as the marmoset monkey (*Callithrix jacchus*; Brodmann 1909; Rowe et al.1996; Zhang et al. 1996, 2001), whereas in the cat, the human being, and in a great many other placental mammals the cortex has acquired a prominent gyrencephalic form. However, the fact that the echidna and platypus display such striking differences in cortical folding serves as a clear reminder that the monotremes have had the same opportunity for evolutionary change and adaptation as have the species within the placental or marsupial orders.

Quantitative indices of brain development in monotremes and other mammals

A variety of quantitative measures of brain development also reinforce the conclusion that the brain of living monotremes is no more likely to provide a guide to the status of the ancestral mammalian brain than that of any contemporary placental mammal (for review, Rowe 1990). Furthermore, such measures fail to identify the living monotremes as being systematically less advanced in neurological terms than many of their marsupial and placental relatives. The quantitative measures invoked for these comparisons have been based usually upon indices related to the ratio of brain mass to total body mass and include, for example, the *Encephalization Quotient* (*EQ*) put forward by Jerison (1973) and defined for a given species as the ratio of *actual brain mass* (E_i) divided by the *expected brain mass* (E_e) for a mammalian species of a given body mass (P_i). The *expected brain mass* was obtained from the equation:

$$E_e = kP_i^{2/3}$$

that governs the overall relation between brain mass and body mass for the large range of living mammals for which Jerison gathered data. An *EQ* value of 1 was assigned by Jerison for the *average* living placental mammal with values varying by a factor of approximately 25 times, from a low of ~0.25 for basal insectivores, such as the hedgehog (*Erinaceus europaeus*) and the Madagascan tenrecs, through to values of ~6 - 7 for human beings and cetaceans such as the bottlenose dolphin (*Tursiops truncatus*). Values of ~0.5 - 0.75 along the *EQ* scale were assigned to the echidnas by Jerison (1973) who argued that they "*are well in advance of didelphids like the opossum or insectivores like the hedgehog in relative brain size and differentation*". He argued that the monotremes should be considered, in terms of brain development, to be "*at almost the same level as living progressive mammals*" and speculated that they had reached this level by parallel evolution.

It must be emphasized that comparisons of brain *development* based upon measures such as the *EQ* are somewhat arbitrary and that relativities arrived at across species may change if other measures were to be used. However, a variety of alternative measures, including for example, the relative extent of the neocortex, once again fail to identify monotremes as being distinctly less developed neurologically than eutherian mammals (Pirlot and Nelson 1978; for review Rowe 1990). In addition, behavioural tests of discriminative learning in the echidna reveal an ability in particular, in spatial and positional discrimination tasks, that is not inferior to eutherian or metatherian species (Buchmann and Rhodes 1978).

SENSORY AND PERCEPTUAL MECHANISMS IN MONOTREMES

Behavioural observations from as early as the 19th century have pointed to the pre-eminence of the tactile sense in the perceptual life of both the platypus and the echidna (for review: Rowe 1990; Rowe et al. 2003). In the case of the platypus it was apparent that, for both navigation and feeding, the animal relies, perhaps exclusively, upon sensory information from the bill as its eyes, nose and external auditory canals remain closed in the course of swimming and foraging (Bennett 1877; Burrell 1927; Griffiths 1978; Grant 1984). While vision may be of more importance in the echidna than the platypus (see Gates 1978) it is probable that it assumes a lesser importance than the trigeminal tactile inputs from the snout and tongue which appear to play a similar prominent sensory role to that of the bill in the platypus. However, tactile information from the limb extremities, in particular, from the forelimb, also assumes great importance in the digging and burrowing activities of the echidna (Griffiths 1978; Augee and Gooden 1993). Because of this prominent sensory role for the distal forelimb as a tactile exploratory organ in the echidna we have recently undertaken an analysis of tactile neural mechanisms associated with the forepaw in *Tachyglossus aculeatus* (Mahns et al. 2003; Rowe et al. 2003). As tactile neural mechanisms have been most intensively investigated for the distal glabrous skin of the forelimb in a great variety of species, this analysis permitted a comparison with placental mammals enabling us to establish the extent to which correspondence or divergence had arisen over the separate evolutionary paths taken within the different mammalian orders.

Peripheral tactile neural mechanisms associated with the distal forelimb in the echidna: comparison with placental representatives

Tactile sensory nerve fibres that arise from the distal glabrous skin of the limbs in the cat and in a variety of Old- and New-World monkeys fall into three major functional classes (Lindblom 1965; Lindblom and Lund 1966; Jänig et al. 1968, Talbot et al. 1968, Iggo and Ogawa 1977, Ferrington and Rowe 1980; Ferrington et al. 1984; Coleman et al. 2001). These include one broad class that responds to static skin displacement with a so-called slowly adapting (*SA*) pattern of response that provides the basis for their designation as the *SA* class of fibres which, in both cat and primate species, appears to be associated with Merkel receptor endings (Jänig et al. 1968, Talbot et al. 1968; Iggo and Muir 1969; Jänig 1971; Iggo and Ogawa 1977; Ferrington and Rowe 1980; Coleman et al. 2001).

The remaining tactile sensory nerve fibres supplying the primate hand or cat footpads are sensitive to only the dynamic components of tactile stimuli and can be divided into two distinct classes according to their sensitivity and responsiveness to cutaneous vibration (Jänig et al. 1968; Talbot et al. 1968; Johnson 1974; Iggo and Ogawa 1977; Ferrington and Rowe 1980; Ferrington et al. 1984; Coleman et al. 2001). One class, designated the rapidly adapting (*RA*) or quickly adapting (*QA*) class is most sensitive to vibration at ~20-50Hz, and appears to be associated with intradermal, encapsulated receptors known as Krause corpuscles in the cat (Jänig 1971; Iggo and Ogawa 1977) and as Meissner corpuscles in primates (Talbot et al. 1968; Coleman et al. 2001). The other purely dynamically-sensitive class (the *PC* class) is exquisitely sensitive to vibrotactile stimuli at 200-400Hz and is presumed to be associated with the Pacinian corpuscle (*PC*) class of receptor (Hunt 1960; Hunt and McIntyre 1960; Sato 1961; Jänig et al. 1968; Talbot et al. 1968; Lynn 1969; Ferrington and Rowe 1980; Ferrington et al. 1984; Coleman et al. 2001).

In human subjects where microneurography studies have permitted the recording and characterization of tactile sensory nerve fibres supplying the hand and finger tips, the same broad divisions apply, except that the *SA* group of fibres is reported to fall into two classes, designated the *SAI* fibres that appear to correspond with the single broad *SA* class in both the cat and non-human primates, and an *SAII* class that appears to be associated with Ruffini receptor endings, principally in the regions of skin around nail beds or skin creases near metacarpophalangeal joints (Knibestöl and Vallbo 1970; Johansson and Vallbo 1979). Although the *SAII* class is known to be present in the cat, it appears, in that case, to be confined to the hairy regions of skin, once again in association with Ruffini receptors (Chambers et al. 1972; Gynther et al. 1992).

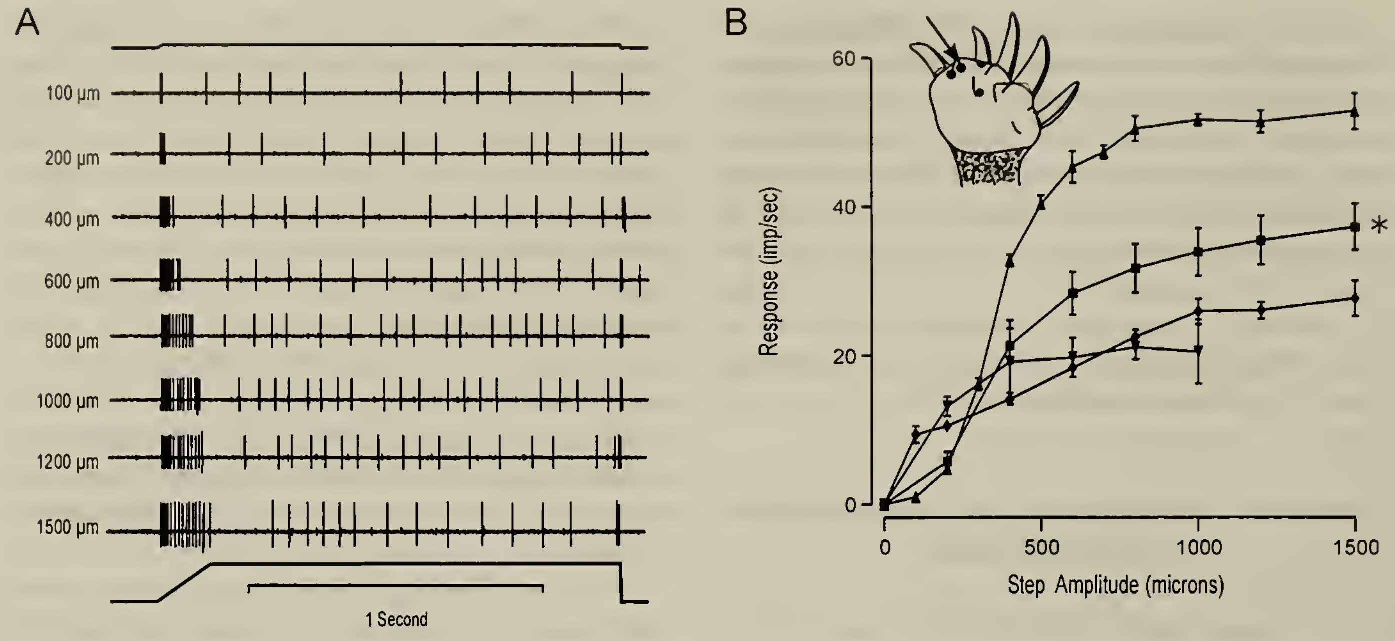


Figure 1. Response traces and stimulus-response relations for representative low-thresholds SA afferent fibers supplying the glabrous skin of the echidna forepaw. (A): response traces to step indentations (lasting 1.5s) at a range of amplitudes (100 to 1,500 µm; represented in the two waveforms above and below the impulse traces). Stimuli were applied to the RF focus (indicated by the arrow in the inset in B) by means of a 2mm diameter stimulus probe. (B): stimulus-response relations for four SA fibers based on the mean response (impulses/sec ± S.D.) over the first one second from the onset of the 1.5s step indentation, plotted as a function of the indentation amplitude (modified from Mahns et al. 2003).

For perhaps most mammalian species the densely innervated glabrous skin of the limb extremities represents the skin area of greatest tactile acuity (Darian-Smith 1984; Coleman et al. 2001; Johnson 2001, 2002) and may be regarded for most species as the tactile equivalent of the visual system's fovea. Some exceptions to this, where the tactile 'foveal' role may be served by other structures, could include the bill in the platypus (Bohringer and Rowe 1977; Rowe 1990; Rowe et al. 2003) and the nasal appendages of the star-nosed mole (Catania and Kaas 1997). Nevertheless, it is probable that in the echidna, the distal forelimb glabrous skin assumes a similar crucial tactile sensory role as the footpads in the cat or the hand and fingers in primates.

Electrophysiological analysis of tactile sensory nerve fibres supplying the echidna forepaw

Microdissection of the ulnar or median nerves in the echidna forelimb permitted electrophysiological recording from almost 30 individual tactile sensory nerve fibres that supplied the glabrous regions of the echidna distal forelimb (Mahns et al. 2003). Once an individual sensory fibre was isolated, its cutaneous receptive field (*RF*) was mapped by means of gentle probing with *von Frey* hairs of known calibrated force. The functional characteristics of the fibre were then characterized by applying precise mechanical stimuli with a probe (usually 1-2 mm diameter) to the centre of the *RF*. The analysis, based upon the use of a feedback-controlled mechanical stimulator, revealed that the echidna tactile afferent fibres could be classified, like their placental counterparts, into two broad groups, one displaying slowly adapting (*SA*) response characteristics to static skin displacement, the other displaying a pure dynamic sensitivity.

Functional characteristics of slowly adapting (SA) tactile afferent fibres supplying the echidna forepaw

Tactile fibres in the *SA* class varied widely in their sensitivity to skin displacement. Those with lowest thresholds displayed small, circumscribed *RFs* and a sensitive grading of their impulse output as a function of skin displacement (Fig. 1A,B) and were therefore presumably well able to signal information about the location and intensity of skin perturbations encountered on the glabrous skin surface. A higher-threshold subclass of the *SA* fibres (Mahns et al. 2003) had larger *RFs* and less-well sustained responses (Fig.2A) and may contribute to the signalling of much more diffuse pressure encountered by the foot in locomotor or digging activity. The lesser sensitivity of this subgroup may be explained by the nature of

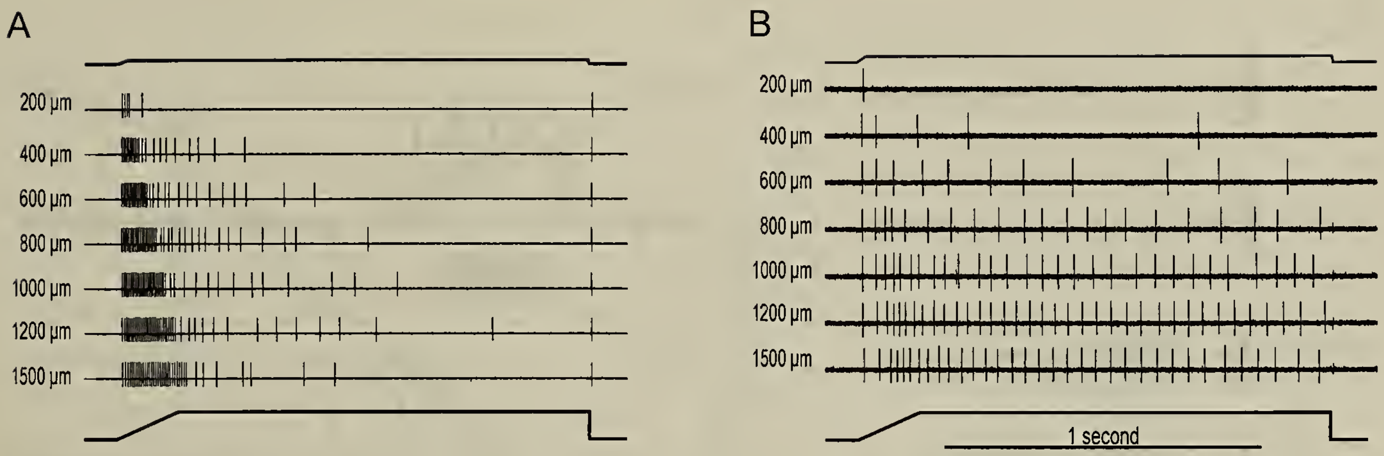


Figure 2. Response traces for a representative of the sensitive SA fibers associated with the echidna forepaw (A) and for claw-associated SA fibers. (B). The impulse traces in A and B show responses to the ramp indentation applied at a range of amplitudes (200-1,500µm) to the glabrous skin (A) or to the base of the claw (B) (modified from Mahns et al. 2003).

the echidna forepaw which is a very much thicker, cushioned structure than the footpad in the cat. This gross anatomical specialization appears to equip the echidna well for its robust digging and burrowing activity but may create, as a consequence of the viscoelastic properties of the footpad, a mechanical housing for many *SA* sensory endings that imposes limitations on the effective mechanical coupling between the skin surface and the receptor endings, and this, in turn, may account for the higher thresholds and more diffuse *RF* boundaries (Mahns et al. 2003).

A further subset of *SA* fibres was associated with the base of the powerful claws and displayed a gradation in impulse output related to displacement at the base of the claw (Fig.2B), attributes that should equip them to subserve a kinaesthetic role in signalling movements of the powerful claws (Mahns et al. 2003).

The low-threshold *SA* fibres appear to conform in properties to the *SAI* class of tactile afferent, already identified in the echidna snout (Iggo et al. 1996) and in the skin of placental species where it is generally thought to be associated with the Merkel receptor endings. Although the less-sensitive and claw-associated *SA* fibres in the echidna (Fig.2A,B) have some attributes resembling the placental *SAII* fibre class, in particular, a rather regular temporal pattern in the impulse activity of the claw-associated *SA* fibres (Mahns et al. 2003), the absence of spontaneous activity in these fibres is more consistent with an *SAI* identification. Thus, despite the rather disparate behaviour of the different subsets of *SA* fibres associated with the echidna forepaw it appears that, as a broad class, they probably conform more closely to the *SAI* class with its implied association with Merkel receptor endings. However, any conclusions about the receptor associations and precise identity if the echidna *SA* fibres must remain tentative until correlative histological data are available for the receptors.

Functional characteristics of dynamically-sensitive tactile afferent fibres supplying the echidna forepaw

Dynamically-sensitive tactile sensory fibres associated with the echidna forepaw could be divided into two classes principally according to their differential sensitivity to vibrotactile stimuli but, in addition, could often be distinguished on account of *RF* characteristics and sensitivity to manual stimuli (Mahns et al. 2003). One class resembled the *rapidly adapting* (*RA*) class of tactile afferent identified in association with the cat and primate glabrous skin in having small, circumscribed *RFs* and displaying maximum vibrotactile sensitivity at frequencies < 50 Hz (Fig.3). The second class had larger *RFs* and a bandwidth of vibrotactile sensitivity that extended up to 300-400 Hz, properties resembling those identified for the *PC* sensory fibres that are associated with Pacinian corpuscle (*PC*) receptors in the glabrous skin of placental species, including the cat, marmoset and macaque monkeys, and human subjects (reviewed above).

Tactile coding capacities of dynamically-sensitive tactile afferent fibres in the echidna

The *RA* class of afferents supplying the echidna footpad had absolute response thresholds of

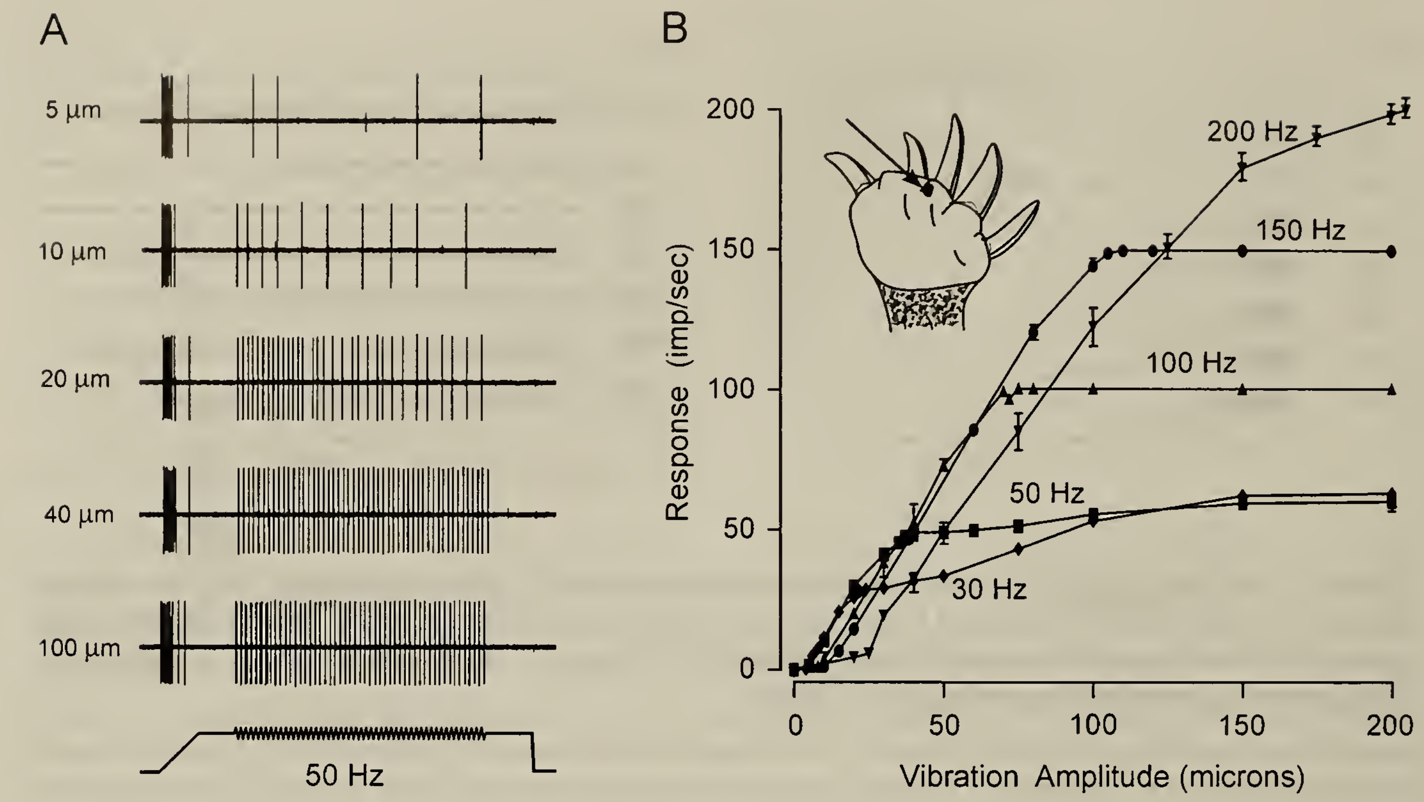


Figure 3. Impulse records and stimulus-response relations for a representative RA afferent fiber supplying the echidna forepaw. A): Activation of the fiber as a function of amplitude increases in the 50Hz vibration train. The response achieves a 1:1 following pattern over the first ~15 cycles at 20 µm, and this response pattern is sustained throughout the 1-second duration of the vibrotactile stimulus at 40 µm. (B): Stimulus-response relations for this RA fiber show 1:1 plateau levels of response at <40 µm at frequencies of 30 and 50 Hz. At 100, 150, and 200 Hz, the 1:1 level was attained only at amplitudes of ~70, 100, and 200 µm, respectively. The RF for the fiber is indicated in the inset in B (modified from Mahns et al. 2003).

<10 µm at frequencies below ~100 Hz. With increases in the intensity of vibrotactile stimuli, their response (in impulses/s) progressively increased until they attained a regular impulse discharge on successive cycles of the vibration stimulus. As the spike discharges in this so-called *one-to-one* pattern of response were tightly phaselocked to the vibration waveform the interspike intervals approximated the vibration cycle period. For example, at 50 Hz the interspike intervals approximated 20 ms and at 100 Hz were ~10ms (Fig. 4). Because of the tight phaselocking, the pattern of discharge displayed a metronomic regularity that reflected very precisely in its temporal pattern the periodicity inherent in the vibrotactile stimuli. The impulse sequence thus provided a reliable signal, in an impulse pattern code, of the frequency, or pitch parameter of the vibrotactile stimuli. The tightness of phaselocking could be quantified by constructing cycle histograms (*CHs;* Fig. 4B) which show the time of occurrence of impulses during each vibration cycle. The *CHs* use a pulse associated with the onset of each vibration cycle as a stimulus marker and have an analysis time that corresponds to the vibration cycle period. Responses that are tightly synchronized, or phaselocked, appear in the *CH* as a narrow peak as seen in Fig. 4B. When impulses occur independently of the phase of the applied vibration waveform the distribution in the histogram appears flat (Coleman et al. 2001; Mahns et al. 2003). The bandwidth of vibrotactile frequencies over which responses in the echidna RA fibres remained phaselocked extended from ~5 Hz up to ~200 Hz, matching the behaviour of their placental counterparts in the cat (Ferrington and Rowe 1980; Ferrington et al. 1984; Rowe and Ferrington 1986) and in the macaque and marmoset monkeys (Talbot et al. 1968; Coleman et al. 2001).

Functional capacities of the presumed-PC class of tactile sensory fibre in the echidna

Controlled vibrotactile stimuli permitted the distinction to be made between the RA afferent fibre

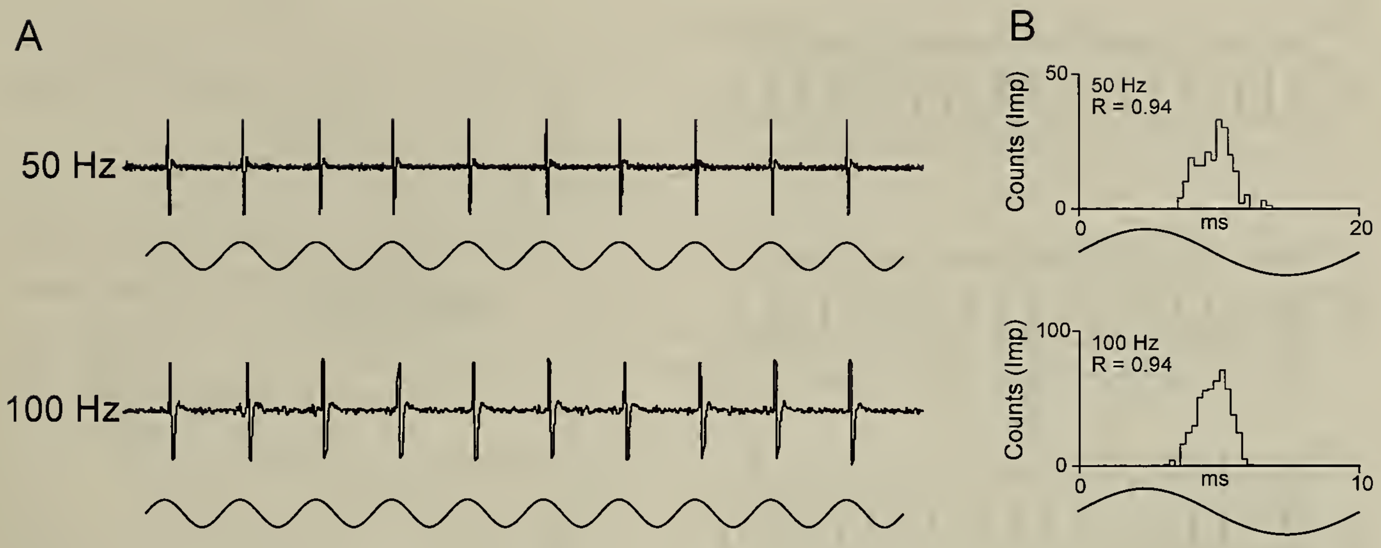


Figure 4. Precision of impulse patterning in the responses of echidna RA afferent fibers to vibrotactile stimuli. (A): Impulse traces show the tightly phase-locked pattern of response reflecting the periodicity of the 50 and 100 Hz vibrotactile stimuli. Quantitative measures of phase locking based on the vector strength or resultant, R (see Materials and Methods), were derived from the cycle histograms in (B), constructed to show the distribution of impulse occurrences throughout successive cycles of the vibration stimulus at the two frequencies. The analysis time in each CH corresponds to the cycle period of the vibration (modified from Mahns et al. 2003).

class and a class of dynamically-sensitive tactile afferents with a distinctly broader bandwidth of sensitivity (Fig.5) reminiscent of placental PC fibres (Mahns et al. 2003). These putative *PC* fibres supplying the echidna forepaw had absolute response thresholds as low as ~5 μm for the broad range of frequencies from ~50 to 300 Hz (Fig.5C) which may equip the animal to detect small vibratory perturbations set up by termites in either the soil or in timber material encountered in the animal's use of the forepaw as an exploratory organ. Furthermore, these broad bandwidth vibrotactile sensors would be well-suited to serve as an early-warning system for the detection of ground-borne vibration signalling the movements of any predators or other animals in the vicinity (McIntyre 1980; Mahns et al. 2003). As the *PC* fibre responses to vibrotactile stimuli remained tightly phaselocked at frequencies up to and beyond 400 Hz, the metronome-like patterning in their discharge (Fig. 5A) would ensure that these fibres retained high acuity for signalling the temporal details of vibrotactile perturbations over a broad bandwidth of frequencies (Mahns et al. 2003). Although the bandwidth of vibrotactile responsiveness in the echidna PC fibres (Fig.5) did not extend to frequencies quite as high as those of placental *PC* fibres (Mahns et al. 2003) the explanation probably lies in the lower body temperature of the echidna (~28-32°C; Grigg et al. 1992) rather than a fundamental difference in the receptors; in particular, as Sato (1961) has demonstrated that *PC* fibres in the cat display a displacement to lower frequencies in both bandwidth and peak sensitivity as temperature is lowered.

The use of controlled sinusoidal vibration as a dynamic form of tactile stimulation in these studies permitted the precise quantification of both the frequency and intensive parameters of the stimuli. However, in addition, it provides a form of dynamic tactile stimulation that mimics in a controlled way the vibrational disturbances set up in the skin in association with relative movement between the skin and any textured surface encountered in the tactile exploratory movements of the forelimb. The properties revealed for echidna *RA* and *PC* fibres indicate that they are well suited to underpin the echidna's capacity to signal and code information about textural changes in the ground surface or in the coarseness or fineness of objects encountered, such as sand, gravel or soil, in the tasks of locomotion, digging and burrowing.

In summary, it appears that for the distal forepaw of the echidna, the tasks of tactile exploration and perception are based upon a triad of major tactile sensory fibre classes, comprising a broad *SA* class and both *RA* and *PC* classes with functional capacities

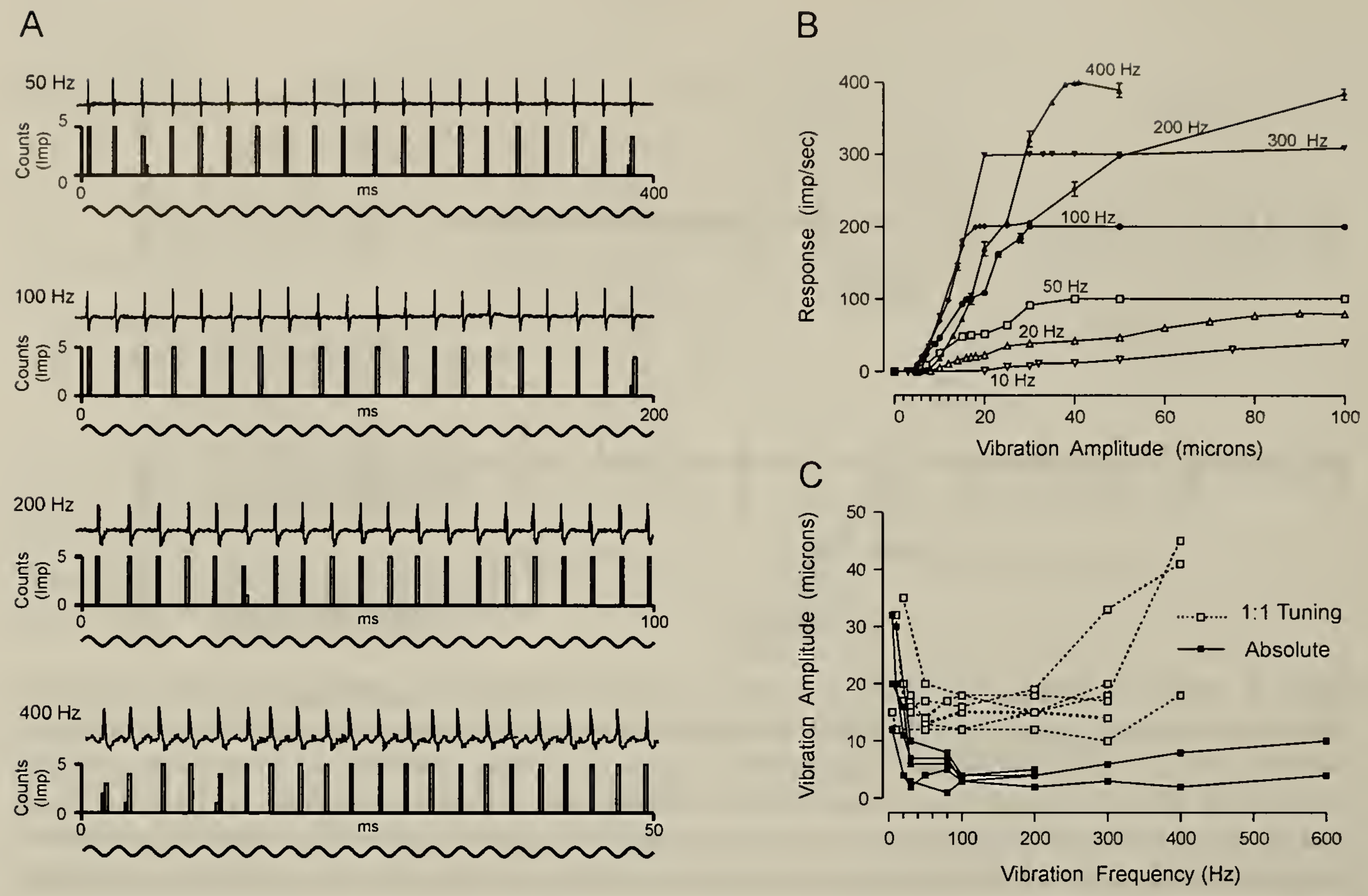


Figure 5. (A): Temporal patterning in the vibrotactile responses of PC-like fibers in the echidna. Impulse traces and peristimulus time histograms (PSTHs) show the metronome-like impulse pattern at the 1:1 response level at vibrotactile frequencies of 50-400 Hz. Each PSTH was constructed from five consecutive responses to 20 cycles of vibration at each of the indicated frequencies. (B and C): Stimulus-response relations and vibrotactile frequency bandwidths for the putative PC class of echidna tactile afferent fiber. (B): Stimulus-response relations for a single PC-like fiber with RF on the lateral aspect of the forepaw glabrous skin, based on plots of the mean response (impulses/second) as a function of vibration amplitude at seven frequencies in the range 10-400 Hz. (C): Plots of absolute (solid lines) and 1:1 tuning thresholds (dashed lines) derived for five PC-like afferent fibers from stimulus-response data of the type shown in (B) (modified from Mahns et al. 2003).

resembling those of the corresponding classes in placental mammals. The issue of whether the broad *SA* class might contain subsets will be resolved only with more detailed morpho-functional correlative analysis on both the receptor endings and the associated sensory nerve fibres. However, the breakdown of the echidna tactile sensory fibres into three broad classes resembling those in placental mammals suggests that peripheral mechanisms for tactile sensation in the distal glabrous skin are highly conserved across different mammalian orders (Mahns et al. 2003).

CEREBRAL CORTICAL ORGANIZATION FOR TACTILE PROCESSING IN MONOTREMES

The behavioural evidence for the pre-eminence of the tactile sense in the platypus, and probably also in the echidna, has been re-inforced by electrophysiological studies on the organization of the cerebral cortex in these two species. In the platypus in particular, the allocation of neocortical space to tactile processing is quite spectacular as was demonstrated with both evoked potential and single-neuron microelectrode recording studies first undertaken in our laboratory in the 1970s (Bohringer and Rowe 1977; Rowe 1990), and more recently by Krubitzer et al. (1995a). With evoked potential mapping, a brief electrical stimulus delivered at a point on the skin surface activates sensory fibres that generate a synchronous input to the areas of cerebral cortex involved in processing information from that source of sensory input. From the cortical surface overlying these areas it is possible to record an *evoked potential* that is usually biphasic, consisting of an initial positive-going deflection followed by a larger negative-going

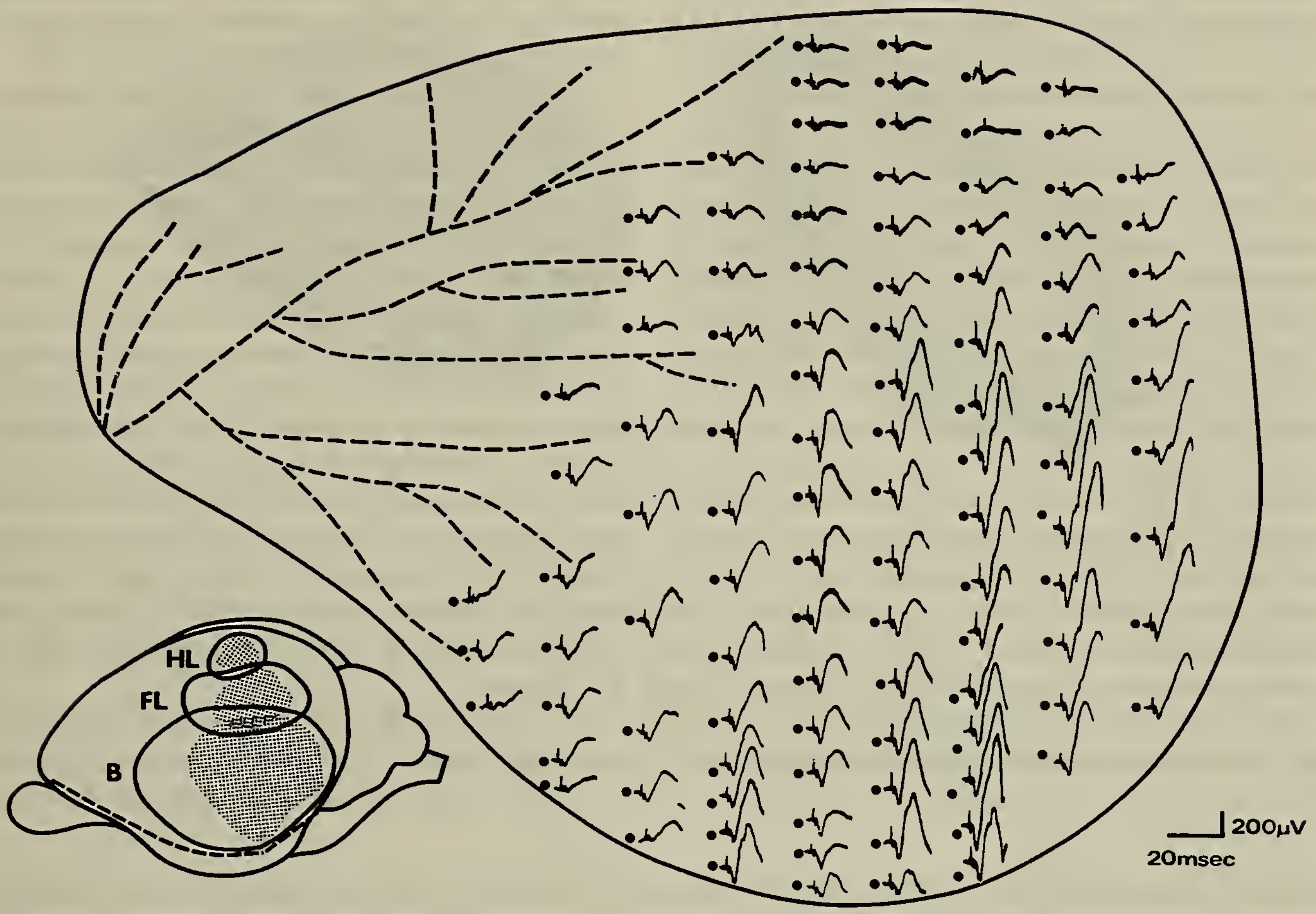


Figure 6. Evoked potentials (positively downwards) recorded from the cortical surface of the platypus following bipolar stimulation of the anterolateral margin of the contralateral bill (1V, 100-microseconds pulse). Each recording was made from the position indicated by the dot at the left of the trace. Dotted lines indicate positions of large blood vessels in frontal region of hemisphere; view of hemisphere and whole brain (inset) from dorsolateral aspect. Stippled areas in inset represent focal projection sites and include sites at which positive-going responses exceed 100μV for bill (B), 30μV for fore limb (FL) and 10μV for hind limb (HL). Zones between stippling and continuous lines include sites from which smaller responses could be recorded (from Bohringer and Rowe 1977).

component (Fig.6, and Bohringer and Rowe 1977). The initial positive-going component is thought to arise from the direct excitatory action of thalamo-cortical afferent input on cortical neurons (Mountcastle and Poggio 1968), and therefore the cortical region from which this component can be recorded is thought to represent the projection focus for that source of input. The evoked potentials illustrated in Fig.6 were recorded in response to stimulation on the anterolateral margin of the bill and reveal that a vast area of the dorsal surface of the contralateral cerebral hemisphere is taken up with the processing of bill inputs. At each recording point indicated by the dots on the main figure, responses were also recorded to forelimb (FL) and hindlimb (HL) stimulation in the platypus allowing the isopotential contour maps for these and the bill (B) inputs to be constructed on the inset figure, with the stippled areas indicating the focal projection sites for the three sources of input, and the zone between the stippling and continuous line a region from which smaller evoked potentials could be recorded.

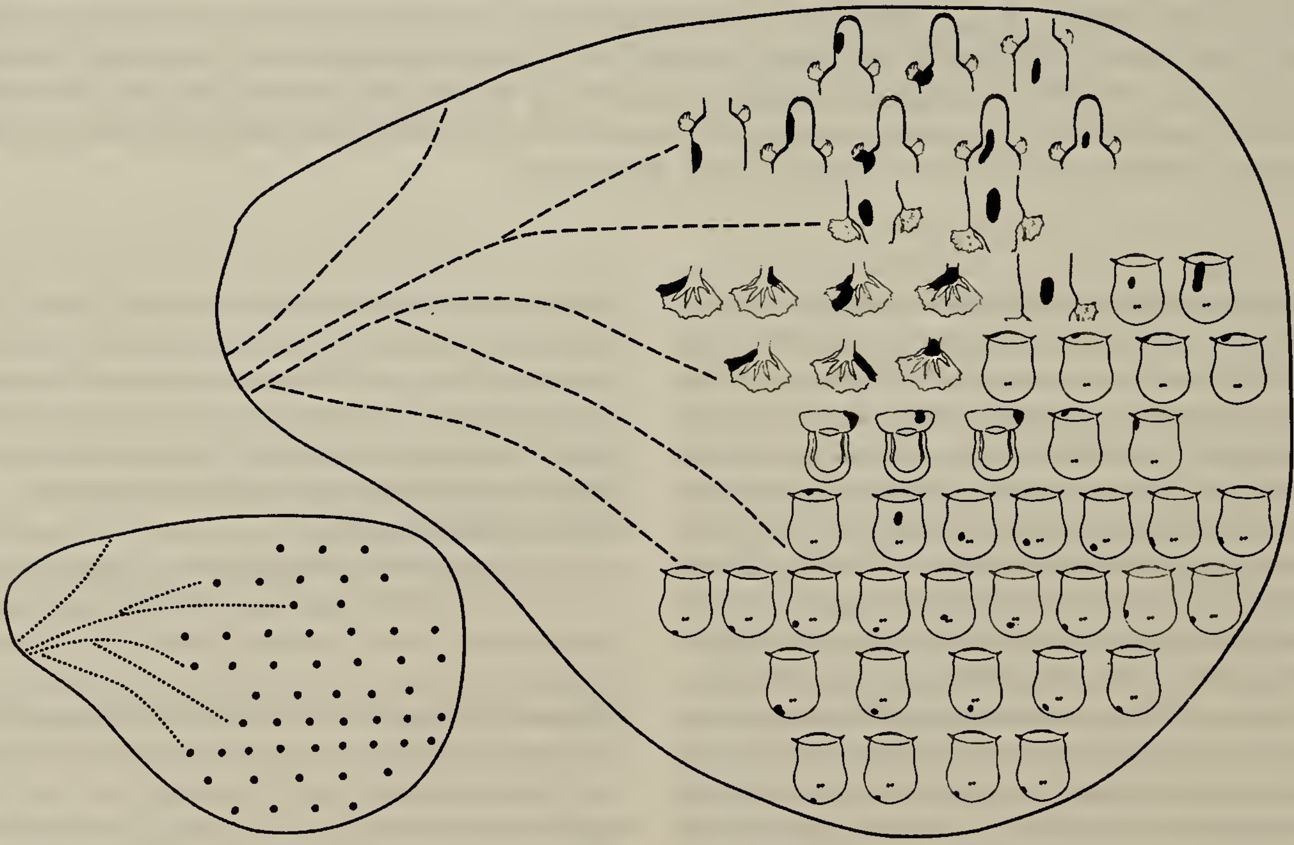
Single neuron mapping of the somatosensory cortex in monotremes

More detailed single-neuron microelectrode recordings from as many as 250 individually-discriminated cortical neurons in up to 67 electrode penetrations in a given experiment on the platypus somatosensory cortex confirmed the highly ordered and complete cortical representation of tactile inputs from the contralateral body, extending from the mid-sagittal region of the hemisphere out to the region of the rhinal sulcus (Figs.7 and 8) on the ventrolateral surface, the one sulcus present as an exception to the lissencephalic state of the platypus cerebral cortex. As the microelectrode mappings were based on inputs generated by light tactile stimulation of the skin surface they confirm the remarkable size of the cortical space devoted to tactile processing, in particular, from the bill. This is important as the electrical stimuli delivered to the skin in evoked potential mappings could have activated a combination of tactile and the putative electroreceptive afferent fibres postulated to be present in the bill of the platypus (see below). The continuity of tactile representation across the somatosensory cortex of the platypus was confirmed in several detailed mappings (Bohringer and Rowe 1977) and is apparent in Fig.8 which shows the tactile receptive fields outlined on the figurines for 60 individual neurons isolated in nine electrode penetrations made in a single anteroposterior plane in the posterior region of the hemisphere. While tactile receptive fields for individual neurons are up to ~15 cm^2 on regions such as the tail and trunk, those on the distal glabrous skin of the limbs were much smaller, while those on the bill, in particular, its anterior and lateral margins, were no more than 1mm in diameter. These represent the smallest tactile receptive fields ever recorded in the cortex and are therefore capable of conferring great precision and fidelity upon the tasks of tactile localization and discrimination involving the bill.

Where the electrode penetration was made normal to the cortical surface, the neurons encountered had very similar receptive field locations (Fig.8) indicative of the *columnar* organization, well described for the cerebral cortex of placental mammals (e.g. Mountcastle 1957), in which neurons of similar functional properties are grouped in columns oriented normal to the surface. In penetrations, such as number eight in Fig.8, that passed obliquely through successive cortical columns in the region of bill representation, there was a remarkably orderly and progressive shift in the representation of the bill surface that is apparent in the enlarged and expanded view of this electrode track in Fig.9, emphasizing once again the striking, fine-grain spatial resolution available within the area of bill representation in the somatosensory cortex of the platypus.

The somatosensory cortex of the echidna, mapped by Lende (1964), also has a striking allocation of space to the tongue and snout representations but,

Figure 7. Inset shows entry points (filled circles) for 54 microelectrode penetrations into the platypus cortex. The black areas on figurines show the combined receptive field areas for all neurons (up to 15) sampled in each of the penetrations. Dotted lines represent positions of large blood vessels in frontal region of hemisphere; view of hemisphere from dorsolateral aspect (from Bohringer and Rowe 1977).



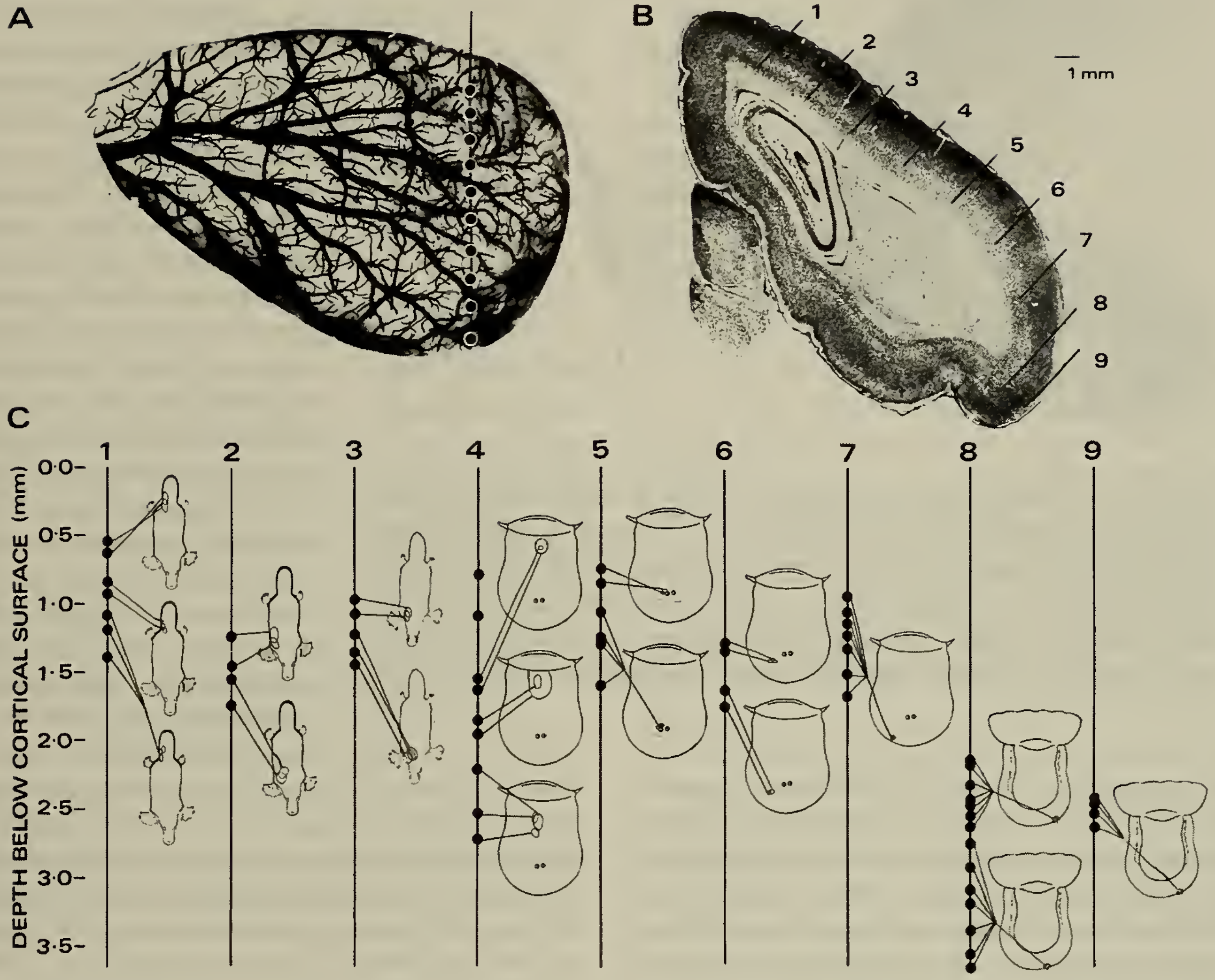


Figure 8. (A): Photograph of cortical surface of the platypus from dorsolateral aspect indicating a plane in which 9 penetrations were made. (B): Coronal section through hemisphere at the plane indicated in A, showing the course of the 9 penetrations. (C): Reconstruction of penetrations 1-9 indicating location of each neuron studied (filled circles) and its peripheral receptive field. No fields could be found for the first two neurons in penetration 4. Receptive fields for all neurons in each of the penetrations 7-9 were confined to the shaded areas on each of the associated figurines (from Bohringer and Rowe 1977).

in addition, a prominent representation of the distal forearm, presumably reflecting its importance in digging and burrowing.

Multiple representation of the body within the monotreme cerebral cortex

For both the platypus and the echidna, the early cortical mapping studies in our laboratory (Bohringer and Rowe 1977; Rowe 1990) and that of Lende (1964), led to the conclusion that there was a single body representation in the contralateral cerebral hemisphere, conforming to the so-called primary somatosensory cortex (*SI*) of other mammals. No evidence was found for a second representation that might correspond to either the SII area that is well recognized in, for example, the cat and primate species (for review, Rowe 1990; Johnson 1990; Rowe et al. 1996; Zhang et al. 1996, 2001) or indeed, to any other areas of somatosensory representation that have been reported in some placental species (Kaas 1982, 1987; Krubitzer and Kaas 1990; Krubitzer et al. 1995b), and now more recently, for both the echidna and platypus (Krubitzer et al. 1995a). Krubitzer et al. (1995a) have proposed that there are four somatosensory representations within the contralateral cerebral cortex of both the platypus and the echidna which they designate the primary somatosensory cortex (*SI*), the *Rostral* deep field (*R*), the *Manipulation* field (*M*) and

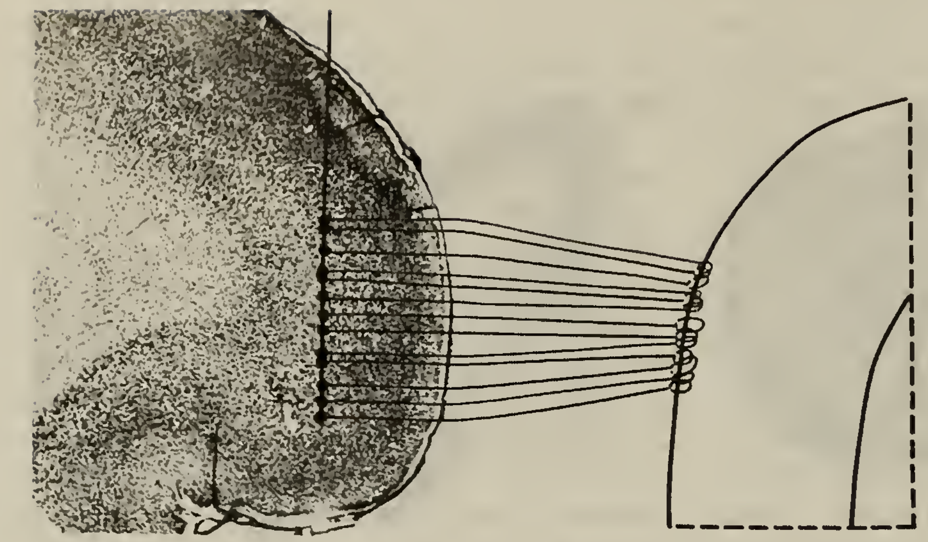


Figure 9. Coronal section of platypus cerebral cortex showing the position of a microelectrode penetration (track 8 in Fig.8) made obliquely to the cortical surface. The filled circles indicate the locations of the 14 neurons studied. The receptive field for each neuron is indicated on the right which is an enlargement of the area on the ventral surface of the bill (modified from Bohringer and Rowe 1977).

the *Parietal Ventral* field (*PV*). Furthermore, each is said to contain "a complete representation of the body surface", a surprising claim to us, considering that the four areas are not all defined as being concerned with the processing of mechanosensory data from the body *surface*. The area given the *SI* designation is concerned principally with *cutaneous* inputs, whereas area *R* immediately rostral to *SI* is said to contain neurons that respond "most often to stimulation of deep receptors" and which required light taps or light pressure to the body surface to elicit a response. However, as the tactile stimuli employed in their study, whether brushing, tapping, or pressure forms of cutaneous stimulation, were neither quantified nor reproducible, it is difficult to see how reliable distinctions were made in terms of neural response thresholds between neurons in the different cortical representation areas.

Topographic organization of the putative multiple areas of somatosensory representation in the monotreme cerebral cortex

As responsiveness criteria may be insufficient to permit an unequivocal division of the monotreme somatosensory cortex into four distinct areas (Krubitzer et al. 1995a), such a differentation must therefore depend upon topographic considerations, in particular upon the extent to which the four putative areas constitute complete and discrete representational maps of the body. In the case of adjacent areas, whether, for example, *SI* and *R*, or *SI* and *PV*, Krubitzer et al. (1995a) state that the boundaries coincide with a *reversal* in the representation of peripheral receptive fields as one progresses across a sequence of cortical recording sites. For example, in both platypus and echidna cortex, the receptive fields on the upper body may shift from proximal body locations, including the face, shoulder and upper limb, to the distal forelimb, and then move back to more proximal parts of the limb and shoulder. Similar *reversals* were seen across sequences of recording sites involving the hindlimb representations, leading to the interpretation by Krubitzer et al. (1995a) that the *separate* representations of proximal limb and associated trunk regions constitute parts of two distinct body representations. However, an alternative interpretation must be considered, which emerges from the detailed studies carried out in the macaque monkey by Werner and Whitsel (1968, 1973) and Whitsel et al. (1969, 1971) for *SI* in the postcentral gyrus, and for the more laterally-placed second somatosensory area, *SII*.

The representation of the body within the cerebral cortex: a reflection of the dermatomal trajectory

The crucial observation emphasized by Werner and Whitsel was that the body maps in both *SI* and *SII* of the cerebral cortex owe their essential topographic properties to the serial and overlapping projection of the dorsal roots. In the case of the macaque postcentral gyrus, the representation of spinal roots, from sacral through to cervical, forms a succession of antero-posteriorly oriented bands progressing from medial to lateral across the cortex (e.g., Figs. 6 and 8 in Werner and Whitsel 1973).

Within the SI area of the macaque monkey, and indeed within the macaque *SII* as well, the representations of the postaxial and preaxial arm and leg areas are separated by the representation of the more distal parts of the limbs, in particular, the digits and toes respectively. This effectively gives rise to a *split* representation of the upper parts of the limbs. In the case of the postcentral gyrus, one component lies medial to the distal limb representation, the other lateral to it, an arrangement represented schematically to illustrate this dermatomal trajectory in Fig.8 of Werner and Whitsel (1973). One may observe how the dermatomal trajectory generates the *split* representation of the upper regions of either forelimb or hindlimb within the cerebral cortex by examining, in a human anatomy text (e.g., Williams and Warwick 1980) the dermatomal boundaries of successive spinal roots associated with either the lower or upper regions of the body. In the case of the upper body, the ventral and dorsal axial lines of the upper limb mark a border between the innervation fields of C5 and T1. Therefore, in any representation of the body surface within the cerebral cortex, one might expect, with the central map being laid down according to the dermatomal trajectory (Werner and Whitsel 1968, 1973; Whitsel et al. 1969, 1971), that the central representation of the upper arm will be split along the axial lines with the input from the distal limb, carried over the C6, 7 and 8 roots, creating a clear separation in the cortical representation of lateral and medial surfaces of the upper arm.

As the same fundamental plan and sequence for tactile dermatomes is also found in both the cat and monkey (Sherrington 1898; Kuhn 1953; Hekmatpanah 1961), one may assume that this organizational plan for spinal segmental innervation is a general one that would operate across mammalian orders, *including* the monotreme representatives.

Is there multiple representation of the body within the platypus and echidna cerebral cortex?

If one examines the receptive fields plotted for the platypus and echidna somatosensory cortex by Krubitzer et al. (1995a) in their Figs. 6 and 16, it might be argued that those fields on the proximal parts of the limb, on either side of the distal limb representation, are not clearly and systematically separated into representations of the medial and the lateral surfaces of the limb as might be expected in a perfect reflection of the dermatomal trajectory. However, this is hardly surprising on several grounds that are outlined in a recent review (Rowe, in press).

The fundamental point to be emphasized is that the *reversals* in receptive field representation described by Krubitzer et al. are consistent with the sequence of representation that might be expected within a *single* body map whose plan is determined by the dermatomal trajectory. In view of these considerations we would re-emphasize our 1977 finding (Bohringer and Rowe 1977; Rowe 1990) of a single large representation of the contralateral body within the platypus cerebral cortex and the similar conclusion reached even earlier by Lende (1964) for the echidna. Furthermore, we wish to emphasize the fundamental importance and significance of Werner and Whitsel's studies (1968, 1973; and Whitsel et al. 1969, 1971) on body representation within the cerebral cortex, and the need that arises from their studies, to take account of the dermatomal trajectory as the crucial determinant of representational topography within central neural systems.

Sensory and perceptual specialization in monotremes: trigeminal electroreceptive mechanisms

As the monotremes emerged in mammalian evolution on a separate line from therian mammals in the early Mesozoic (Dawson 1983; Rowe 1990; Augee and Gooden 1993) the possibility that some qualitatively different apparatus for neural sensing might have emerged was given some credence in the 1980s with both behavioural and electrophysiological studies reporting the presence of electroreception in monotremes (Scheich et al. 1986; Gregory et al. 1987, 1988, 1989a,b). These and subsequent reports suggested that electroreception might be associated with the bill of the platypus and the snout of the echidna, in each case in association with the trigeminal nerve rather than the lateral line system that is the principal basis of electroreception in certain fish (Cahn 1967; Bullock 1999). However, neither behavioural nor electrophysiological data have provided any suggestion of electroreception in association with other skin regions or somatosensory nerves of the monotremes, such as the median or ulnar nerves of the forelimb.

The first behavioural evidence for electroreception in the platypus bill came in a short report from Scheich et al. (1986) that the platypus could detect weak electric fields with threshold strengths as low as 50-200 μV cm^{-1}. Furthermore, they reported that an electroreceptive processing zone was present in the posterolateral region of the contralateral cerebral cortex on the caudal side, but *next to,* the map of bill mechanoreceptive input identified by Bohringer and Rowe (1977). In our view this is a puzzling finding on several grounds (for review, see Rowe 1990). First, in an earlier detailed electrophysiological mapping of the cerebral cortex we found that the cortical region concerned with tactile representation of the bill occupied almost the whole of the posterolateral region of cortex (Bohringer and Rowe 1977; Rowe 1990). Furthermore, we constructed separate cortical maps of bill representation based upon mechanical stimulation which was specific for tactile inputs, and electrical stimulation which would have activated both tactile and the putative electroreceptive afferents.

However, comparison of the two maps (Figs.6 and 7; and Bohringer and Rowe 1977) reveals no evidence of a separate area of bill representation in the map based upon the electrical stimulation, from that obtained with pure tactile stimulation. In contrast to the Scheich et al. (1986) report that electroreceptive-induced cortical evoked potentials were found *next to* the map of bill mechanoreceptor input, those by Iggo et al. (1992) and Krubitzer et al. (1995a) indicated that the electrosensory area of cortical representation lay *entirely within* the border of the tactile representation area defined for the bill in our earlier study (Bohringer and Rowe 1977; Rowe 1990). However, Krubitzer et al. (1995a) have described a "clear functional parcellation" *within* this *SI* region whereby regions responsive to just tactile input were interdigitated with regions responsive to both tactile and electroreceptive inputs (e.g. Fig.10 in Krubitzer et al. 1995a). Furthermore, the regions of pure tactile sensitivity coincided with myelin and cytochrome oxidase-dense regions of SI while the regions of putative bimodal sensitivity coincided with myelin-light regions. What the significance of such differences in myelin density might be in this circumstance remains unclear. However, there may not be universal agreement with this assertion anyway, judging by the allocation of light and dark areas in their Fig.10B; for example, the myelin-dark region drawn to contain four recording sites of pure mechanosensitivity in part B of their figure appears rather paler in the adjacent tangentially-oriented photomicrograph than some areas represented as *myelin-light* in Fig.10B. It is likely to be difficult to make these distinctions reliably, in the tangentially-cut cortical sections, firstly without objective analysis of image density, and secondly, in the absence of systematic control for laminar depth across the extent of the cortical section under study.

Electrosensory field-strength thresholds illustrated for cortical neurons in Fig.10 by Krubitzer et al. (1995a) ranged up to 900 μV cm^{-1}; however, it was not clear what field strength might have activated neurons in the purely tactile-sensitive regions.

Behavioural and afferent fibre thresholds for electroreception

A further concern in relation to claims for electroreception in monotremes arises over the thresholds reported for the phenomenon. At the behavioural level, Scheich et al. (1986) reported field strength values as low ~50-200 μV cm^{-1} for the platypus, and, more recently, values of 20μVcm^{-1} have been reported (Manger and Pettigrew 1996; Pettigrew 1999). However, individual trigeminal afferents, believed to be of the electrosensitive class, had threshold field strengths of ~4mV cm^{-1} (Gregory et al. 1988, 1989b). As these values were based on a substantial fibre sample, and as these values are vastly higher than reported behavioural thresholds for the platypus, one might infer that any putative electroreceptive sense must depend upon some other source of afferent input. Proposals that spatial summation, based upon convergence of a number of trigeminal electroreceptive afferents onto central neurons, may confer the observed behavioural thresholds upon the animal are difficult to accept when none of the sampled afferent fibres has thresholds low enough to account for this.

To the extent that there are contentious issues associated with the claims for electroception within the monotreme order of mammals, it is important that further rigorously controlled investigations be pursued to resolve such issues, in particular, more detailed behavioural studies based upon objective analysis rather than anecdotal accounts of the movement patterns of the platypus and echidna in relation to presumed electrosensory stimuli.

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The Role of Push Rods in Platypus and Echidna – Some Speculations

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Proske, U. and Gregory, J.E. (2004). The role of push rods in platypus and echidna – some speculations. *Proceedings of the Linean Society of New South Wales* **125**, 319-326.

This is a review of the structure and innervation of the mechanosensory organ, the push-rod, in skin of the platypus bill and echidna snout. Four receptor types can be identified in association with push rods in platypus and echidna: (i) central vesicle chain receptors, (ii) peripheral vesicle chain receptors, (iii) Merkel endings and (iv) paciniform corpuscles. Function of the vesicle chain receptors remains unknown. Merkel endings are known to be slowly adapting with irregular discharge (SAI) while paciniform corpuscles are rapidly adapting vibration-sensitive (RA). Recordings made from echidna nose skin have identified both SAIs and RAs. In addition, responses typical of SAII endings (regular discharge) and rapidly adapting, but vibration insensitive, responses were observed. It was concluded that the push rod in monotremes is not associated with mechanoreceptors unique to the group. Skin of the platypus bill and the echidna nose contains erectile tissue. It is conjectured that blood engorgement inflates the skin to facilitate contact between push rods and the external environment. In addition platypus push-rods have a ring of contractile tissue around their tips which, on contracting, restricts mobility of the rod, perhaps when the platypus leaves the water. Possible cooperative roles between electroreceptors and mechanoreceptors are discussed.

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KEYWORDS: Cutaneous receptors; electroreceptors; mechanoreceptors; Merkel receptors; push rod; sensation; slowly adapting; vibration.

INTRODUCTION

In a recent publication we presented some speculations about the role of electroreceptors in the detection of prey items by platypus and echidna (Proske and Gregory 2003). Here we want to extend these speculations to the mechanoreceptors. This, therefore, is a review account of our own work and that of others and speculations based on those observations.

THE PLATYPUS PUSH ROD

The bill of the platypus has two prominent sense organ structures, the electroreceptors associated with sensory-innervated mucous glands, and mechanoreceptors associated with the push rods. They are distributed differently, the electroreceptors being lined up in rostro-caudally directed rows, the push rods distributed more or less uniformly across the bill, with particularly high concentrations on the edge of the bill (Fig. 1). In the platypus, although it has not been stated explicitly, it appears that push rods are absent from skin, including glabrous skin, of other parts of the body. In other words, push-rods seem to be specifically associated with the bill, as are the electroreceptors.

There have been estimated to be 46,500 push rods in the platypus (Manger and Pettigrew 1996), distributed in the skin covering the outside of the upper and lower bill and lining the mouth (Fig. 1a). They are especially numerous around the margins of the upper bill.

The platypus push rods (Fig. 2a) are about 70 μm in diameter and 400 μm long, spanning nearly the full thickness of the epidermis. They consist of a column of flattened spinous cells attached rather loosely to the surrounding epidermis, which allows them relatively free movement in all directions. The rounded tip of the push rod protrudes slightly above the surrounding skin surface. Each push rod is innervated by 25 to 40 myelinated nerve fibres. These terminate in 4 types of sensory ending.

The first type is the central vesicle chain receptor, supplied by 5 to 8 medium sized myelinated axons. The receptor consists of axon terminals running

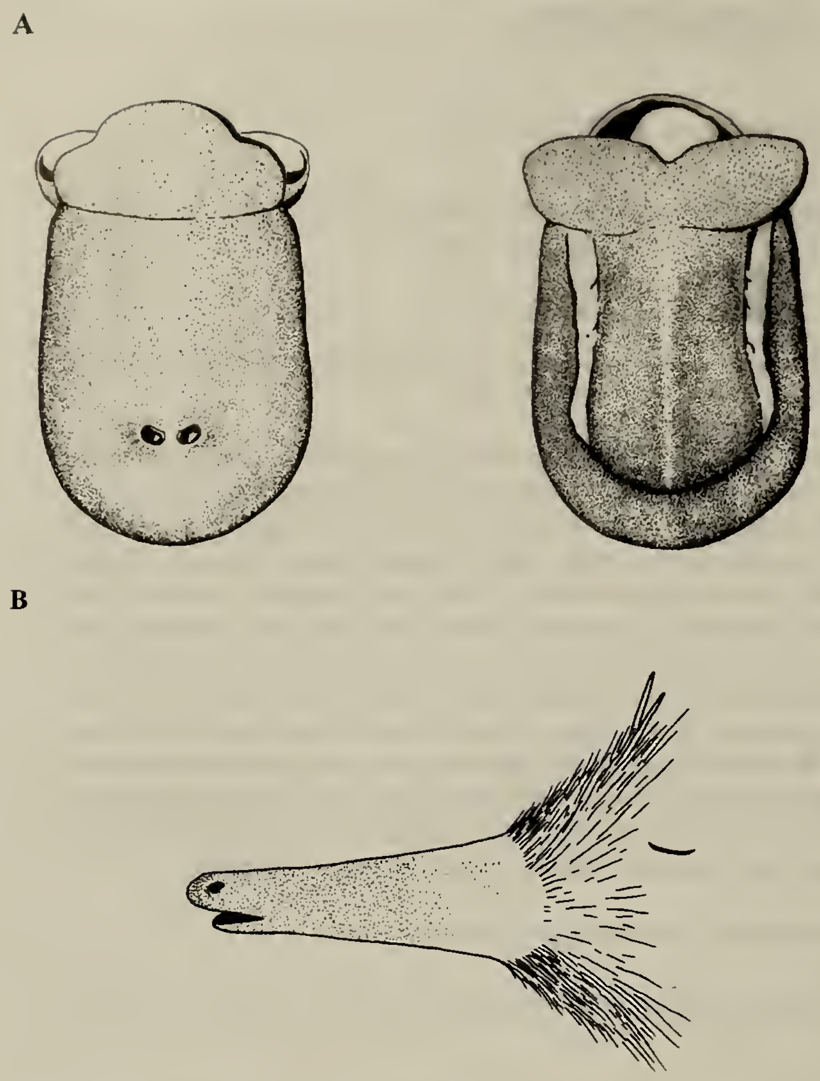

Figure 1. Dorsal and ventral view of the platypus bill *(A)* and lateral view of the echidna snout *(B)*. Dots indicate the distribution pattern of push rods, which are more numerous near the edge of the bill and tip of the snout. (A, rearranged from Andres and von During, 1984; B, from Proske, 1997.)

vertically up the push rod near the centre, with a regular array of vesicle-like protrusions along their length.

The second type, the peripheral vesicle chain receptor, is similar, but the myelinated axons (as many as 18) supplying it are thinner and their terminals are located towards the periphery of the push rod.

The function of the vesicle chain receptors is still unknown. Their structure is somewhat reminiscent of Meissner corpuscles found in the glabrous skin of many mammals. Meissner corpuscles consist of a coiled arrangement of endings from a number of myelinated axons that terminate between layers of flattened Schwann cells, and they are known to be rapidly adapting mechanoreceptors. If, as is likely, vesicle chain receptors are mechanosensitive, their disposition in the centre and around the periphery of the push rod appears favourable for detecting compression or bending of the rod, and perhaps in this way the direction in which a stimulus is acting can be signalled. The receptors extend to within just a few cells of the skin surface, giving rise to the suggestion that they would also be well placed to function as thermoreceptors (Catania 1995).

The third type of receptor in the push rod is the Merkel cell. Up to 12 Merkel cells are located at the base of each push rod, and each myelinated afferent nerve fibre supplying them branches to supply 6 to 8 Merkel cells. The functional properties of Merkel cell receptor complexes have been well documented in other mammalian and avian species, where they are one of the common receptor types found. They are slowly adapting mechanoreceptors, giving rise to what in other mammals are termed Type I responses characterised by a high degree of variability in the train of impulses discharged when stimulated. Figure 3 shows an example, recorded from the echidna.

The fourth type of ending is a group of 3 to 6 paciniform corpuscles, lying in the dermis immediately underneath the column of epidermal cells comprising the push rod. These are one of the most intensively studied types of cutaneous receptor and like the Merkel cell, they are found ubiquitously amongst birds and mammals. They are a rapidly adapting mechanoreceptor giving highly phasic responses to stimulation and able to signal faithfully vibratory stimuli at frequencies up to about 1,000 Hz. Figure 3 shows an example, again recorded from the echidna.

The paciniform corpuscles at the bottom of the platypus push rods have been reported to be arranged with their long axes oriented either strictly parallel or perpendicular to the skin surface, and at right angles to each other, thus building up a three dimensional system for transducing any direction of movement of the push rod (Andres & von During 1984). This further implies that the push rods are free to move and not constrained to displacement in any particular direction.

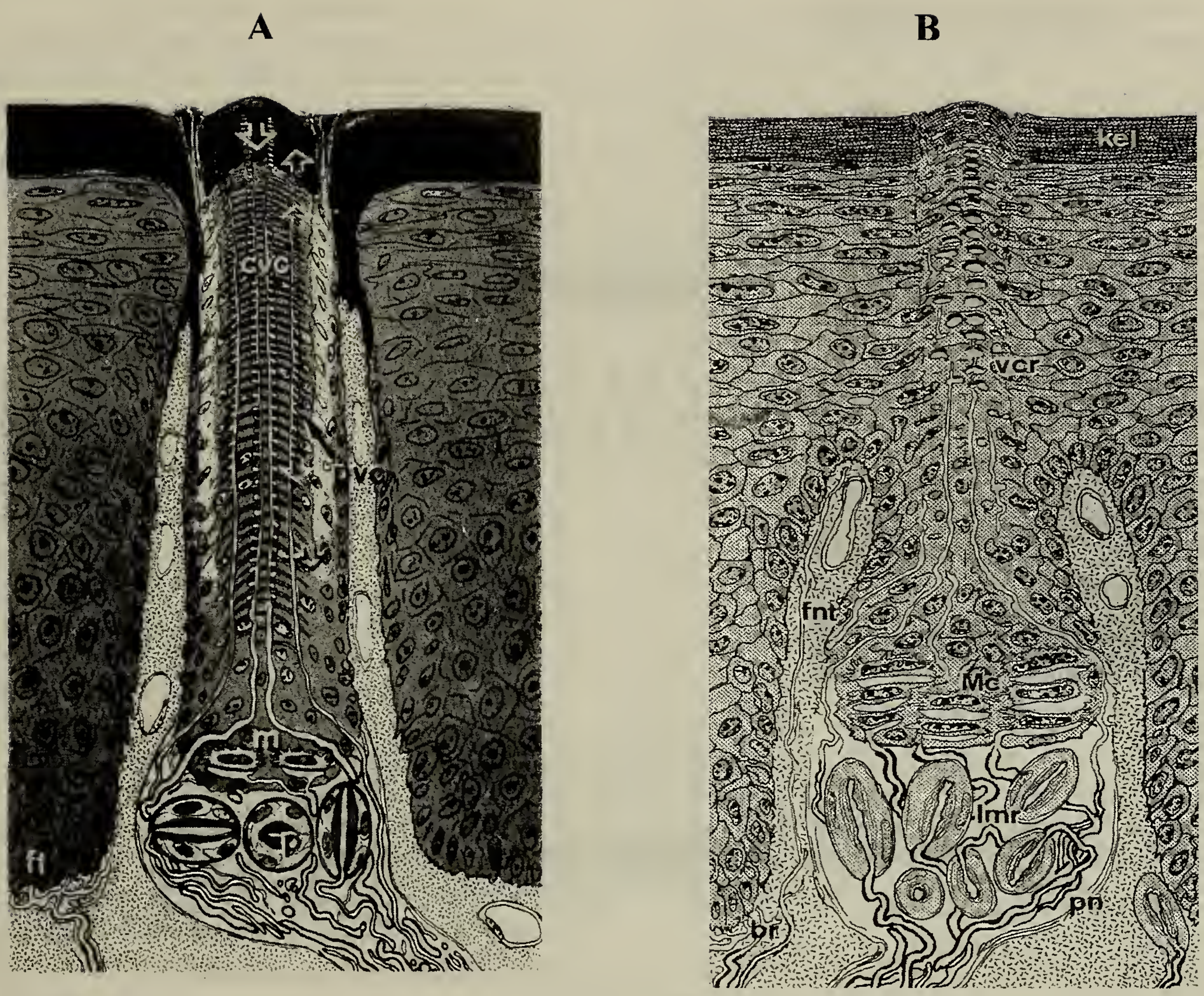

Figure 2. Schematic representations of push rods in the platypus bill *(A)* and echidna snout *(B)*, showing the 4 types of sensory terminals: lamellated, paciniform corpuscles (p, lmr), Merkel cells (m, Mc), central vesicle chain receptors (cvc) and peripheral vesicle chain receptors (pvc), the latter 2 having a single label (vcr) in B. The platypus push rod is attached rather loosely to the surrounding epidermis, allowing relatively independent movement in all directions, while the echidna push rod appears more firmly anchored in the epidermis. (A, modified from Andres and von During, 1984; B, modified from Andres et al, 1991.)

THE ECHIDNA PUSH ROD

In the echidna push rods are scattered across the surface of the snout, becoming fewer at its base, in the region where the hairs begin (Fig. 1b). They are especially dense near the tip of the snout, which is also the region where the electroreceptors are found. As for the platypus, there is no evidence of push rods in skin of other parts of the body.

The structure of the echidna push rod follows the same plan as that in the platypus with two differences. Its nerve supply is less dense and the column of cells comprising the rod is less mobile than in the platypus – there is a less clearly differentiated boundary between the column of spinous cells with tonofibrils and the surrounding epidermis.

The echidna push rods (Fig. 2b) are smaller than those in the platypus and are innervated by only about half as many myelinated nerve fibres. However, they contain larger numbers of Merkel cells and paciniform corpuscles (Andres et al. 1991).

RESPONSE PROPERTIES OF THE RECEPTORS

What emerges is that the push rod is a specialised mechanoreceptor complex, having separate receptor systems for signalling steady stimuli and phasic or vibratory stimuli, and if the speculations

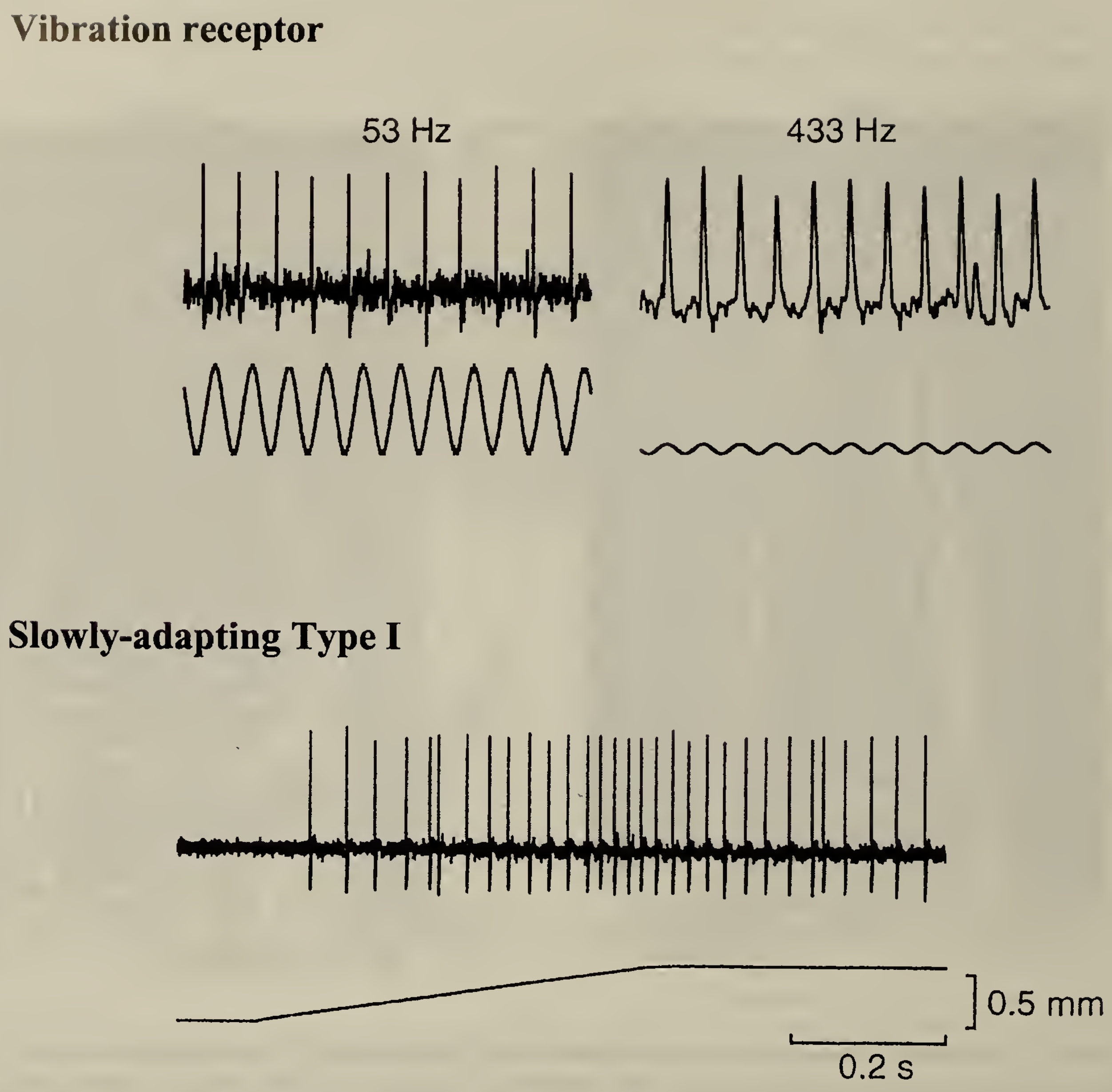

Figure 3. Responses of single receptors in the echidna snout, shown as action potentials recorded in dissected nerve filaments. The vibration sensitive mechanoreceptor is shown responding in a 1:1 entrained fashion to stimulation at just above threshold amplitude and at the frequencies indicated. The stimulus is represented in the traces below the action potentials. This type of response is characteristic of paciniform corpuscles. The slowly adapting Type I response in the lower part of the figure is typical of Merkel cell receptors. It is characterised by an absence of resting or unstimulated discharge, a sensitivity to stimulus velocity and an adapting, irregular discharge during constant skin indentation. The stimulus is shown in the trace below the train of action potentials, and consisted of a linearly increasing skin indentation to an amplitude that was then held constant. (From Iggo et al, 1996.)

about vesicle chain receptors are correct, a third system for signalling the direction in which a mechanical stimulus is acting.

In an electrophysiological study of tactile receptors in the echidna, Iggo et al. (1996) recorded from 44 mechanoreceptor afferents with receptive fields in the skin of the snout. The receptors were not identified morphologically but some attempt was made to associate a response with the site of a push rod. While it could not be ascertained with certainty that particular responses arose from within a push rod, two types of responses observed were typical of endings found at the base of push rods and identified as such in other mammals. In our study we classified responses into 4 types, based on similarities to the 4 main types of response seen in other mammals and for which the morphological identity of the receptors has been established.

The first type of receptor was characterised by a rapidly adapting response to mechanical stimulation of the bill skin and a high sensitivity to vibration at frequencies up to about 800 Hz (Fig. 3). This type of response is characteristic of Pacinian and paciniform corpuscles in other mammals and can confidently be ascribed to the paciniform corpuscles found in the snout skin and especially prominent at the base of pushrods.

The second type of response was an irregular, slowly adapting discharge (Fig. 3). These SAI responses have been known for some time to be generated in other mammals by Merkel cell receptors, the second ending type found prominently at the base of push rods. The examples encountered in the echidna typically had very small receptive fields, with a diameter well below 100 µm and a threshold for a response to skin displacement of 4 µm. Such small, low threshold fields are consistent with their belonging to Merkel receptors at the base of push rods that are somewhat shielded from stimuli not directly applied to the push rod tip.

The most numerous type of response to mechanical stimulation was a slowly adapting, regular discharge, termed a Type II response in other mammals. These have been identified with Ruffini endings in the dermis, signalling preferentially stretch of the skin. A similar morphological type is present in echidna snout skin, but not in direct association with push rods.

The fourth type of response was a rapidly adapting discharge to skin stimulation. These receptors were distinguished from the other rapidly adapting group by not showing a sensitivity to vibration at high frequencies, and they responded well only to frequencies below 300 Hz.

The study shed no light on the function of vesicle chain receptors. Perhaps they are the rapidly adapting receptors unresponsive to high frequencies of vibration, but the number found seemed too few, at only about 15% of the sample studied. It may be that one or both types of vesicle chain receptor are responsible for at least some of the Type II slowly adapting responses, which accounted for nearly half the sample studied. What can be said is that no completely new mechanoreceptive responses, unknown in other species, were seen in the echidna, either in this study or in an earlier one by the same group (Iggo et al. 1985).

There is some evidence that the sensitivity of the push rod complex to external stimuli is not fixed, but can be varied, and in two ways. First, in both echidna and platypus, there is a venous cavernous system in the bill or snout, beneath the skin. It is postulated that engorgement of the venous sinus may change the mechanical properties of the skin, affecting transmission of mechanical stimuli to the receptors at the base of the push rod and effectively changing its sensitivity. It may also lead to protrusion of rod tips beyond the skin surface, to allow them to present more effectively to environmental stimuli.

Secondly, Manger et al. (1998) have described a ring of contractile material around the tip of the platypus push rod. Perhaps this is used to restrict the mobility of the push rod and in this way also change its effective sensitivity. Why might it be desirable to change the sensitivity of the push rod by altering the mechanical coupling between the stimulus and the receptors? Perhaps the answer for the platypus lies in the different environments, air and water, the animal inhabits. An appropriate sensitivity for one medium may not be optimal for the other and the platypus may have evolved a means of adjusting between the two. A similar argument could apply to the echidna, which uses the tactile receptors in the snout both in the ground and above it. However there are no reports of the presence of contractile cells in association with echidna push rods, which, anyway, seem to be much less mechanically independent of the surrounding skin.

COMPARISONS WITH OTHER ANIMALS

The push rod theme reaches its most exuberant expression in the star-nosed mole. Protruding from the snout of this animal is an extraordinary array of 22 radiating fleshy pink fingers entirely covered with thousands of small domes. These domes are the tips of Eimer's organs, which have a remarkable similarity to the push rods in monotremes, except for containing fewer sensory endings and being innervated by fewer sensory nerve fibres than push rods (Fig. 4). There is a single Merkel receptor at the base and a single lamellated receptor immediately underneath in the dermis. A single vesiculated nerve terminal runs up the centre of the Eimer's organ and 5 - 10 at the periphery (Catania 1995).

Eimer's organs are believed to be tactile sense organs, responsive to the onset and offset of depression of the papilla and to sustained compression (Catania & Kaas 1995).

The star-nosed mole is a burrowing insectivore living almost entirely underground in swamps and bogs. As in the monotremes, the function of the vesiculated receptor terminals has not been conclusively established. It is assumed that the star is a sensitive tactile organ used by the mole to explore its environment for prey. Some other members of the family Talpidae, moles, shrew moles and desmans, have Eimer's organs (Catania 2000), but only the star-

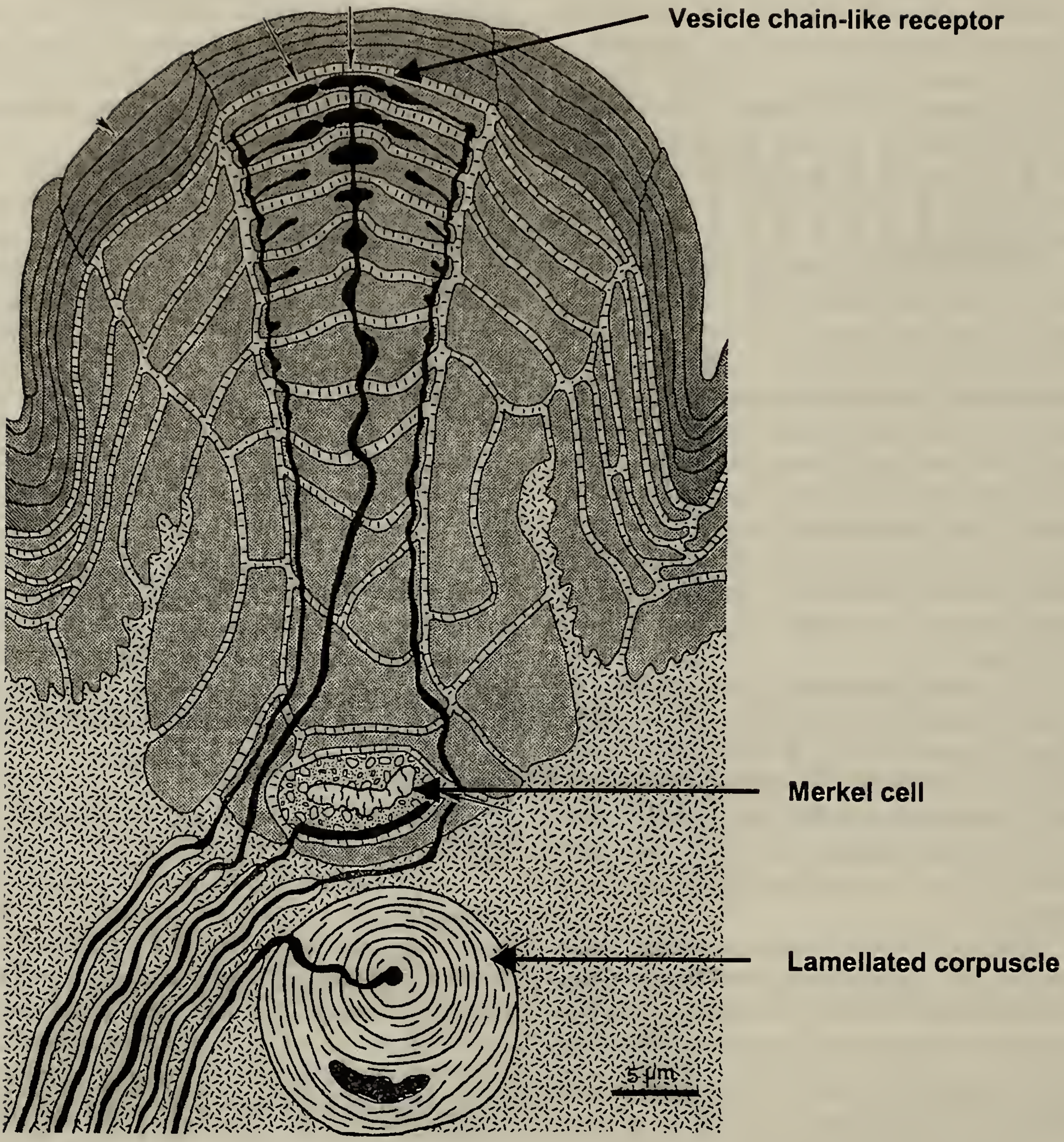

Figure 4. Schematic of an Eimer's organ in the star-nosed mole, showing the single Merkel cell and lamellated corpuscle, as well as the central and peripheral neural processes similar to the central and peripheral vesicle chain receptors of the monotreme push rod. (Modified from Catania, 1995.)

nosed mole has developed such an elaborate structure to deploy them.

FUNCTIONAL CONSIDERATIONS

If it is accepted that push rods subserve a mechanosensory function and are designed to raise fidelity of transmission of static and dynamic stimuli, it poses the question of why such an arrangement is needed. Speculation about the mechanoreceptors in monotremes has focussed on two aspects.

In the platypus, there is a close association between the electrosensory and tactile senses, and cells in the cerebral cortex have been found that receive inputs from both modalities (Iggo et al. 1992; Manger et al. 1996). Pettigrew et al. (1998) have postulated a system for determining the distance and perhaps direction of live objects underwater, based on a cooperation between the two senses. An animal like a shrimp would generate both an electrical pulse and a mechanical pressure wave when it flicked its tail. The electrical pulse would arrive at the platypus first and be detected by the electroreceptors. After a delay depending on the shrimp's distance, the mechanical pressure wave would arrive and the receptors in the pushrods would be stimulated. Suitably tuned cells in the cortex would detect the delay between the two inputs, and thus distance could be computed. Directional information could also be derived if the push rods have a directional sensitivity as speculated, and this would be combined with the hypothesised directional information derived from the electroreceptors (Manger et al. 1996).

A second possible role for push rods concerns our speculation about close-range electrolocation (Proske and Gregory, 2003). As the platypus fossicks about on the bottom of a stream or pond, pushing its bill into the detritus looking for live prey, its electroreceptors will allow it to distinguish animate from inanimate objects. It is conceivable that the alerting signal from the electroreceptors receives confirmation of the presence of a prey item from the detailed mechanosensory signals provided by push rods. Similarly for the echidna, there may be a functional cooperativity between inputs from electroreceptors and mechanoreceptors as the animal pushes its nose into the soil in its search for prey.

Speculating more broadly about push rods as vehicles for mechanoreceptor stimulation, it is of interest that they are located exclusively in bill skin of the platypus and in nose skin of the echidna. Being at the front end of the animal, perhaps they subserve some kind of teletactile function, that is, detection of disturbances in the water or in the soil created by prey at some distance ahead of the animal.

Vertebrates have evolved a number of ways of stimulating, at a point, a population of receptors with both static and dynamic properties. An example that comes to mind is the vibrissae of mammals. Here it is known that the various afferents supplying each vibrissa project to the same area of cerebral cortex to form identifiable 'barrels' (Miller et al. 2001). It suggests that central processing of tactile information coming from these structures requires the presence of both static and dynamic components of the stimulus and the processing is done by neurones lying in close proximity to one another.

For push rods, the presence of a mobile column of epidermal cells that is able to excite paciniform and Merkel cell receptor types at the same time, provides the opportunity for similar central processing of static and dynamic stimuli. It remains to determine why it is necessary to process the information in this way. Presumably the nature of the sensory experience evoked by stimulation of a push rod is dependent on the simultaneous presentation of static and dynamic features of the stimulus.

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Obituary

MERVYN EDWARD GRIFFITHS
1914-2003

Mervyn Griffiths (who always preferred to be called "Merv") was born in Sydney on 8th July 1914, was educated at North Sydney Boys' High School and obtained his Bachelor Degree in Zoology with first Class Honours in 1937, followed by his Master of Science in 1938 at Sydney University

Merv first began publishing in the scientific literature in 1936 with a paper on *The colour changes in batoid fishes* in the Society's *Proceedings* and contributed six further papers to this journal between 1936 and 1942.

After completing his Master studies, Merv was awarded the Travelling Research Scholarship for the 1851 Exhibition, which took him to McGill University in Montreal, Harvard University and the National Institute for Medical Research in London. From this work he produced 10 papers, including research on *diabetes mellitus* and the secretory functions of the pituitary. In 1941 Merv returned to the University of Sydney where he continued his work on diabetes in the Department of Medicine, where he was a Linnean Macleay Fellow in Physiology in 1941. The fellowship was renewed in 1942, but only a few months into his second fellowship year he joined the Royal Australian Air Force.

Merv was in the Empire Air Training Scheme during 1943 in Edmonton, Canada and became a Pilot Officer in 1944. He held the post of Commanding Officer of the 3rd Malaria Control Unit in Darwin from 1944-45 and left the RAAF in February 1946 at the age of 31, continuing his involvement in diabetes research as a Zoologist in the Institute of Anatomy in Canberra. He became the Senior Biochemist at the Institute in 1949, publishing his work on the biochemistry of diabetes through to 1957, when he returned to zoology, joining the C.S.I.R.O. Wildlife Survey Section [which later became the Division of Wildlife Research] as a Senior Research Officer in June 1957.

In 1959 he was awarded his Doctor of Science Degree by Sydney University for his thesis entitled *The Relationship of the Pituitary Gland to Experimental Diabetes and the Action of Insulin.*

Although his initial published works at the C.S.I.R.O. were concerned with rabbits, Merv became interested in the biology of marsupials, particularly macropods. In 1965 he published his first paper on the biology of the group for which his research is best known, and which became his consuming passion - the Monotremes. His monograph on the *Echidnas* was published in 1968. During his time at the Division of Wildlife Research, Merv was the scientific director of two films, *The Echidna* and the *Comparative Biology of Lactation*, both of which won awards.

Merv retired in October 1975 from the C.S.I.R.O. Division of Wildlife Research as Senior Principal Research Officer, but not from the field of wildlife research. His interests broadened, although the monotremes remained his prime focus. His classic work *The Biology of the Monotremes* in 1978 pulled together all of the disparate research carried out on the group to that time.

Merv was variously honoured by scientific societies, including being awarded the Peter Aitken Medal by the South Australian Museum in 1988 and becoming a Fellow of the Royal Zoological Society of N.S.W. in 1991. In his "retirement" Merv researched and published widely in a number of fields, where his own work and collaboration with colleagues and friends resulted in a further 33 publications to add to his pre-retirement total of forty-three.

Merv Griffiths died on 6th May 2003. The above summary of his academic life cannot adequately describe his contribution to biological science in Australia. Throughout his academic career Merv remained a great "generalist" in a world of increasing numbers of scientific "specialists". His encouragement, generous advice, support and sometimes cajoling, are deeply appreciated by many of these specialists.

Tom Grant
Sydney
May 2003

BOOK REVIEW

Admiral Doenitz's Legacy

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Murray, D.R. 2003 Seeds of concern. The genetic manipulation of plants. UNSW Press.156pp. ISBN 0 86840 460 8. $34.95.

Over the last decade there has been increasing public concern about the development and use of genetically modified organisms. This has been manifest in media coverage involving 'shock-horror' headlines such as 'Frankenfoods', litigation, product boycotts, increased sales of 'organic' products, illegal destruction of genetically modified crops and, recently, the rejection by Zambia of food aid which may have contained genetically modified grains. Opposition has been global, but at its most intense in Europe.

What is the basis for the concern and is it justified?

Some of the concerns are clearly unnecessary, reflecting an unfortunate lack of basic scientific knowledge amongst the media and general public. Alarmist stories about how eating genetically modified organisms involves consuming DNA, as if non-modified organisms lack DNA, do not add to the credibility of journalists or their editors. For products which are extracted, highly refined and purified, whether their origin is from modified or unmodified organisms is irrelevant in terms of the end qualities and properties.

Other issues have more substance, but at least in Europe, the GM debate is only a symptom of a much broader concern about the nature of modern agriculture. Public confidence has been disturbed by the outbreaks of both BSE and Foot and Mouth disease, which are seen as components of a broader malaise. Neither disease of course has anything to do with genetic modification, although particularly in the case of BSE, significant portions of the media and the public believe it does.

To understand the origins of the perceived malaise it is necessary to go back to the First World War. For the first time submarines proved to be an important weapon, and convoys of food supplies were disrupted. Between the wars submarine technologies were substantially developed. Agriculture was little changed, indeed for much of the period European agriculture was in decline, as cheap imports from north America and the southern hemisphere satisfied the market. During the Second World War U-boats maintained a blockade which almost brought Britain to defeat.

The post war response was – 'never again', and the still prevailing policy of self sufficiency was developed. Governments plan to win the last war, so the fact that the weapons of mass destruction which brought the Second World War to an end changed the nature of any future global war, did not influence policy development.

From some perspectives the self sufficiency policy could be judged a success. Who in 1945 would have anticipated the vast European Union surpluses, or that in 2003 British livestock-feed grains would be exported to Australia? Nevertheless it is the cost of this success which is now being questioned.

The drive for increased production and efficiency was powered by subsidies, both direct and, indirect, and the developing agribusiness companies. Synthetic pesticides and herbicides (such as DDT and MCPA) were first used on a large scale towards the end of the war, and in the immediate post war years usage burgeoned, being proclaimed as an example of the new scientific approach to farming. There was little external scrutiny of government programs and the administrative bureaucracies were captive to their clients – farmers and agribusiness.

The first expressions of concern surfaced with the publication of Rachel Carson's *Silent Spring* (1962). Both the publication and its author were subject to sustained attack by both government and agribusiness, but the basic thesis was increasingly supported by independent evidence. The publication of *Silent Spring* was one of the key events leading to the modern environmental movement, resulted in the banning in the west, if not globally, of some pesticides and the institution of greater scrutiny of new chemicals. Nevertheless these were only minor hiccups on the way to industrialization of agriculture.

Other changes included, in northern Europe, the decline of mixed farming in favour of specialization, the loss of woodlands, hedgerows and wetlands, the loss of genetic diversity amongst crops as many local varieties were replaced by a few new cultivars, and increased use of nitrogen fertilizers resulting in greener, but floristically simpler, basically *Lolium* monocultures, pastures. New crops came to prominence, most notably oilseed rape (known in more sensitive nations such as Australia as canola) converting the landscapes of Constable to ones more akin to those of van Gogh. Lifestock production was increased through adoption of so-called factory farming techniques, changing, for example, chicken from a luxury to a convenience food but raising widespread community concerns about animal welfare and creating substantial environmental problems associated with effluent management.

The changing face of the countryside, increasing awareness of the impacts on biodiversity, and concerns about potential impacts on human health has led to an upsurge of public disquiet (Shoard 1980, Harvey 1997, 2001, Humphrys 2001, Green 2002), but reform of the European agricultural system, although debated for several decades has been slow to eventuate. The idealized countryside of an urban population is often a bucolic dream, the product of a Romantic imagination, and ignores the earlier extensive changes wrought by the Agricultural Revolution and enclosures (Fox and Butlin 1979), but the issues raised by commentators such as Harvey (1997) are nevertheless well documented and cannot lightly be dismissed.

However, the public concern over the consequences of agricultural policy runs contrary to the public expectation, also developed since 1945, of a never ending supply of cheap food. This expectation is well summarized by Gummer (2001) (John Gummer is a former UK Minister for Agriculture and Secretary of State for the Environment).

"Many in the rich world, who do not blanch at forking out £30,000 for a more fashionable motor car, will refuse to expend threepence more on a fresher lettuce or a tastier loaf of bread. Food, which ought to rank highest among our spending priorities, has been relegated to the rank of necessity, and in this advanced civilization of ours, only luxuries deserve to be prized. We take necessaries as our right and expect them to be delivered at a discount.

So it is that food prices demand a smaller and smaller proportion of a prosperous household's income and take less time than ever for the average worker to earn. What is more, now that packaging, distribution and preparation are necessary on-costs, the basic food content of what we buy represents an even smaller proportion of what we pay. With one in three meals eaten out of the home and most of the rest to a growing extent pre-prepared, that proportion will continue to fall".

In demanding cheap food the public neglects to take into consideration the considerable subsidies paid out of the taxpayers' pocket to farmers by governments.

The trend to cheap food has also been assisted by the growth of supermarket chains. For many foodstuffs, prices to farmers are determined by a global oligopoly of retailers. With the availability of cheap airfreight a further consequence of the growth of the supermarket chains is the abolition of seasons, with the same range of produce being available globally year round. This means that the shelves of European supermarkets may be replete with sugar peas from Zambia, green beans from Kenya, salad greens from Tanzania and southern Africa, even brussel sprouts from Australia. When the costs of freight and packaging are considered the return to farmers must be very small, and does not take into account environmental degradation and disruption of traditional agricultural economies. Additionally agriculture in developing countries is adversely affected by dumping of surpluses from elsewhere – tomato producers in West Africa for example cannot compete even in their local market against heavily subsidized Italian canned tomatoes (Bradshaw 2003).

There is little doubt that if global agriculture had remained as it was in 1945 it would have been impossible to support the current human population of about six billion. Currently global food production is capable of providing adequate nutrition for the world population (Waterlow *et al.* 1998), famine and malnutrition are the consequences of failures of political systems, not of agriculture. What is less certain is whether, without extensive adoption of new molecular techniques, it will be possible to feed the predicted human population in 2050 of eight billion (Waterlow *et al.* 1998), particularly given the added impacts of global warming.

The increased production is due in part to an increase in the land area devoted to agriculture but is largely the consequence of new technologies. The development of agricultural chemicals, mechanization and application of conventional plant and animal breeding can rightly be regarded as scientific and engineering triumphs. Nevertheless broader questions of ecological sustainability were not part of the agenda until recently, and the true costs of food production have rarely been calculated.

How is this discussion relevant to any debate about use of genetically modified organisms in Australia?

Firstly, despite talk about free trade and level playing fields, world agricultural markets are still heavily influenced by government subsidies and policy intervention. Whether the original motivation for these government programs can still be justified (and in the case of the much maligned European Common Agricultural Policy, maintenance of the social structure of rural communities was as important as ensuring self-sufficiency) it is unlikely that there is political will for change. Australia's agricultural future, both in terms of access to overseas markets and ability to control imports, will be very much determined by what happens in Washington and Brussels. The US is currently seeking action by the World Trade Organisation to require the European Union to lift its restrictions on genetically modified food (Sanger 2003). The outcome of these proceedings will have global implications, determining for example whether Australia could similarly impose controls on imports of genetically modified organisms. President Bush has argued that Europe's approach has discouraged use of genetically modified foods in the third World and this contributed to continuing famine in Africa (Sanger 2003). Most would argue that African famines have a number of causes, and that absence of genetically modified crops is not one of them. There will be continuing pressure for increased efficiency (as measured in production of cheap food) and this will have social and economic consequences. Secondly agribusiness is global, and increasingly vertically integrated, so that much plant breeding and development of genetically modified plants will be in the hands of a few multinationals, with the results imported into Australia. The growing hegemony of a few agribusiness company has considerable implications beyond the issue of genetic modification. Any choices that farmers might have in terms of crop varieties or chemicals are becoming increasingly illusory. President Eisenhower famously warned of the influence of the military industrial complex – his words would equally apply to agribusiness.

To date, the introduction of genetically modified crops in Australia has been, as it also has been in Europe, a public relations disaster for agribusiness. However, information about the nature of the genetically modified crops has not been readily accessible to the public.

David Murray's *'Seeds of Concern'* attempts to fill the gap, with the objective of promoting informed debate. The author is a distinguished plant scientist so his critique cannot be dismissed by the more enthusiastic proponents of the technology as well intentional but misinformed. However, while the book is aimed, in part, at the intelligent lay person, the assumed level of chemical/biochemical knowledge is high and may well deter the intended audience.

The technology to achieve genetic manipulation exists, and the genie cannot be put back in the bottle. Murray recognizes this and discusses possibilities for using the technologies which could potentially be of considerable benefit to humankind. Unfortunately the benefits of the majority of genetically modified plants released to date accrue to agribusiness and farmers rather than the consumer. Genetic manipulation is possible in the whole range of organisms. Modification of microorganisms for industrial processes has not attracted much public attention, modification of domestic animals (including farmed fish) is still largely at the trial stage, but genetically modified plants are in the landscape and market place and very much in the public eye.

Murray provides a very succinct introduction to plant cell biology and the techniques of genetic manipulation. In commercially released genetically modified plants the most frequent changes are the introduction of herbicide resistance or of genes which express insecticidal compounds. Murray explains the underlying basis for both changes, but also discusses actual and potential drawbacks with the use of plants modified in these ways in the field. It is far from clear that in the long term these approaches will have benefit. The number of potential applications of genetic modification which have been touted in the media is very large. Murray explains how in some cases, such as lowering caffeine levels in coffee or preventing expression of polyphenol oxidases, the proponents are ignorant of the biological function of these compounds or of consumer requirements. The yield costs of genetic modification are often, as Murray points out, given little consideration. What Murray regards as failings of current patenting regimes and of Australia's Plant Breeders Rights legislation are discussed at some length. I would support the critique although recognizing that commercial interests would be expected to take a different view. These difficulties also arise with conventional plant breeding, but, with the heavy investment in genetic modification are likely to be more apparent as companies seek to protect what they regard as their intellectual property.

The regulatory framework for release of genetically modified organisms currently applying in Australia is discussed in some detail. While this regime is important, Murray does not raise the issue of general lack of regulation of many agricultural activities. Farmers world wide argue that they are over regulated, and arguments in favour of less regulation abound (see Ridley 2001, Pennington 2001, and the continuing opposition by farmers in Eastern Australia to control of land clearing). While it is the case that some aspects of agriculture are heavily regulated, key decisions are left to farmers. The cover of '*Seeds of Concern*' shows a field of canola (rape); the decision of European farmers to adopt broad acre rape cultivation had a profound visual and ecological impact, but was not one in which the broader community participated. The change in the northern hemisphere from spring to winter cereal cultivation has had major effects on many bird species, but again was a decision of farmers and agribusiness. In the Australian context changes from pastoralism to cropping, or the spread of cotton growing (both changes which may be facilitated by the development of genetically modified plants) will have social, ecological and environmental consequences, but the decisions will be made by landholders with few avenues for external scrutiny, let alone any requirement for approval. Even if the specific concerns of the Gene Technology Regulator are met, the broader questions raised by agricultural change will remain unaddressed. These are clearly issues beyond those which Dr. Murray set out to address, but they do need to be placed on the policy agenda.

Dr. Murray also manages within the compass of his admirably concise book to mount a defence of Mendel against claims that his results might have been 'polished', express skepticism about proposals to clone thylacines, and have a few swipes against the pontifications of the great and the good. Despite in a few places being ill served in matters of layout by the publisher, this is an important contribution to the debate about genetically manipulated plants and of the future of agriculture.

There are indeed 'seeds of concern', perhaps leading to seeds of doubt.

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BOOK REVIEW

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Wellington Caves Fossil Studies Center, 89 Caves Road, Wellington NSW 2820

Duyker, Edward. 2003. Citizen Labillardière: a naturalist's life in revolution and exploration (1755-1834)
Edward Duyker. The Miegunyah Press, Melbourne 2003. $59.95

This book is a splendid example of the need for academic presses in Australia; Miegunyah Press is an imprint of Melbourne University Publishing. It is a scholarly, extremely well documented work covering a poorly known but important aspect of Australia's early history. As such it cannot be considered an "easy read" nor a likely undertaking for a commercial publisher. It is however a goldmine of information and will be a valuable reference source for anyone seeking information on the roots of natural history study in Australia or the contributions of French scientists to such study. The use of this book as a reference is greatly facilitated by three complete indexes (botanical, zoological and general) and a fully detailed bibliography. The amount of research into resources in several languages required to produce this book is amazing. Such detail insures its use for many years to come.

"Citizen Labillardière" can be read simply as a biography of a very interesting man who lived through very interesting times. He stands astride the "troubles" in France as the country shifted from the Ancien Régime to the National Assembly and constitutional monarchy; to a republic overtaken by the "Reign of Terror"; to an Empire (Napoleon); to the restoration of the monarchy; and then to the final overthrow of the Bourbons. The "citizen" in the book title indicates Labillardière's general political leaning, but it is also the story of a man of science trying for the middle road in turbulent politics. It is therefore a story of survival and adventure. Much of the adventure comes from travel, often arduous, over much of the globe.

After graduating in medicine (1772), Labillardière immediately begins his life of travel with a journey to England. There he establishes connections with Joseph Banks and other British scientists that will serve him well in the future. He travels through the Alps and Lebanon, always collecting botanical specimens and possessing a remarkable enthusiasm for climbing mountains. Then comes his big break; he is appointed as a naturalist on the expedition to be lead by Bruny d' Entrecasteaux in search of the missing La Perouse (last seen by the British at Botany Bay on 10 March 1788). This small fleet, consisting of the Recherche and the Espérance, left France on 28 September 1791. After stops at Tenerife and the Cape of Good Hope, where Labillardière made many collections, they landed in Van Diemen's Land, at Recherché Bay, on 20 April 1792. There Labillardière collected 5,000 specimens in five weeks. Sailing north in search of La Perouse, the expedition went to New Caledonia, New Guinea and the Solomons before returning to Recherche Bay. At that time Labillardière records positive encounters with the native people; indeed he seems to have been a sympathetic and astute observer of the Tasmanian natives.

Leaving Van Diemen's Land, the expedition went to Tonga, passing close by the tip of New Zealand, and to New Caledonia. A return to Van Diemen's Land, with the great likelihood of discovering that it was not part of the mainland and discovering the strait later to be discovered by Bass, was not to be, and d'Entrecasteaux died at sea on 19 July 1793. Already falling apart with rifts between royalists and republicans, the expedition died when, upon reaching Java, the Dutch were found to be at war with France. The Dutch imprisoned Labillardière and others, although not the royalists who collaborated with them. Labillardière was finally released on 29 March 1795 and, after spending six months at Ile-de-France enroute, was back in Paris in March 1796.

Meanwhile most of his collection of botanical specimens had been taken to England and were claimed by the royalist French court in exile there. Banks however used his strong influence and the collection was returned to Labillardière.

There was an odd interlude in the life of Jacques-Julien Labillardière when, in the summer of 1796, he went to Italy as part of a commission to oversee seizure of Italian art and other treasures taken as tribute after General Napoleon Bonaparte conquered that country. In 1800 Labillardière was made a full member of the Académie des sciences.

Besides the political turmoils of his time, Labillardière also straddled a revolution in biological science, during the change from strict application of Linnean principles (which saw taxonomy as a rigid set of categories, determined in the case of plants by the structure of the sexual parts of flowers) to a more natural approach (systematics including as much evidence as possible, especially physiological and morphological). Labillardière's "Sertum austro-caledonicum" published in 1824 abandoned the strict Linnean approach. It should be noted, however, that well before that time zoologists (such as the towering figure of Baron Cuvier) had widely accepted the natural system. Not unlike today when about the only resistance to modern systematics, such as cladistics, comes from botanical taxonomists, many of whom one suspects strongly regret that upstart Antoine-Laurent de Jussieu who started tinkering with the Linnean system in 1789.

Labillardière died 8 January 1834 aged 79. He had a truly adventurous life and made a significant contribution to the advancement of science, although the claim by Duyker that he was "one of the founders of botany, zoology and ethnography in Australia" is overly generous. Labillardière was basically a collector with a sometimes off-hand approach to record keeping. Nonetheless, he did record many "firsts" and many names he gave to plants are valid today.

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2. Manuscripts should be submitted to the Editor (M.L. Augee, PO Box 82, Kingsford NSW 2032). All manuscripts are sent to at least two referees and in the first instance three hard copies, including all figures and tables, must be supplied. Text must be set at one and a half or double spacing.

3. The final version, incorporating referees' and editor's comments, must be supplied on floppy disc or CD in WORD for PC format (Mac discs will not be accepted). Photographs must be supplied as black and white prints or as .TIF files (Jpeg is not acceptable). Figures other than photographs must be in hardcopy, EXCEL or WORD files. The text file must contain absolutely no auto-formatting or track changes. Tables and/or figures must be separate from the text file.

4. References are cited in the text by the authors' last name and year of publication (Smith 1987). For three of more authors the citation is (Smith et al. 1988; Smith and Jones 2000). Notice that commas are not used between the authors' names and the year. The format for the reference list is:

Journal articles:

Smith, B.S. (1987). A tale of extinction. *Journal of Paleontological Fiction* **23**, 35-78.

Smith, B.S., Wesson, R.I. and Luger, W.K. (1988). Levels of oxygen in the blood of dead Ringtail Possums. *Australian Journal of Sleep* **230**, 23-53.

Chapters or papers within an edited work:

Ralp, P.H. (2001). The use of ethanol in field studies. In 'Field techniques' (Eds. K. Thurstle and P.J. Green) pp. 34-41. (Northwood Press, Sydney).

Books:

Young, V.H. (1998). 'The story of the wombat'. (Wallaby Press, Brisbane).

5. An abstract of no more than 200 words is required. Sections in the body of the paper usually include: INTRODUCTION, MATERIALS AND METHODS, RESULTS, DISCUSSION, ACKNOWLEDGEMENTS and REFERENCES. Some topics, especially taxonomic, may require variation.

6. Subheadings within the above sections should be in the form:

Bold heading set against left margin

This is the form for the first level headings and the first line of text underneath is indented

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This is the next level, and again the first line of text underneath is indented.

Further subheadings should be avoided.

Italics are not to be used for headings but are reserved for genus and species names.

7. Up to 10 KEYWORDS are required. These are often used in computer search engines, so the more specific the terms the better. 'Australian' for example is useless. Please put in alphabetical order.

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If a scale is required it must be presented as a bar within the figure. It is the editor's prerogative to reduce or enlarge figures as necessary and statements such as "natural size" or "4X" in the legend are unacceptable.

While there is no objection to full page size figures, it is journal policy to have the legend on the same page whenever possible and figures should not be so large as to exclude the legend. Figure legends should be placed together on a separate page at the end of the manuscript.

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While the draft manuscript text is expected to be in 12 point type, it may be necessary to use smaller font size for large tables. Do not use vertical lines in tables unless absolutely necessary to demark data columns. Keep horizontal lines to a minimum. Do not place the table in a box border.

WORD or EXCEL tables are acceptable.

12. Details of punctuation, scientific nomenclature, etc. are to be found in the complete instructions.

Part 2 – monotreme papers

Part 3 – obituary, book reviews, instructions to authors

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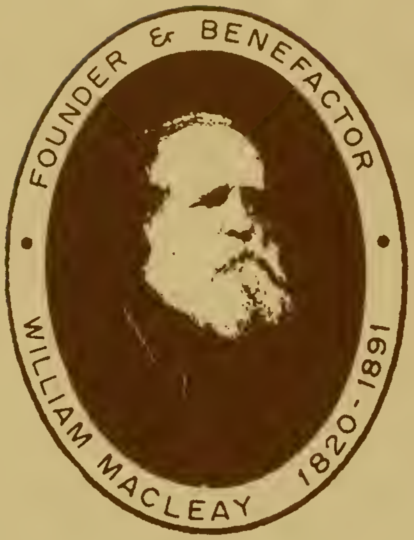

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Cover motif: *Cowralepis mclachlani*, a fossil fish from Cowra (page 215)

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The Middle Triassic Megafossil Flora of the Basin Creek Formation, Nymboida Coal Measures, New South Wales, Australia. Part 4. Umkomasiaceae. *Dicroidium* and Affiliated Fructifications

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Holmes, W.B.K. and Anderson, H.M. (2005). The Middle Triassic megafossil flora of the Basin Creek Formation, Nymboida Coal Measures, New South Wales, Australia. Part 4. Umkomasiaceae. *Dicroidium* and affiliated fructifications. *Proceedings of the Linnean Society of New South Wales* **126**, 1-37.

The forked leaves of the morpho-genus *Dicroidium* are the most commonly occurring foliage in the collections from two quarries in the Middle Triassic Basin Creek Formation at Nymboida, N.S.W. The extensive Nymboida collections include leaves which, in gross morphology, range from simple with entire margins to pinnatifid, pinnate, bipinnatifid and bipinnate forms. The wide range of variation, which includes intergrading forms, creates problems in establishing species boundaries. For comparison with other Gondwanan material, the Nymboida leaves have been placed in five 'species complexes' distinguished as '*Dicroidium coriaceum*', '*D. odontopteroides*', '*D. lineatum*', '*D. dubium*' and '*D. zuberi*'. In each complex there is a continuum of variation of form and there are intergrading forms that link each complex. Illustrations of over eighty leaves demonstrate the range of variation present. A single leaf only of *D. elongatum* has been collected. An unusual leaf is described as ?*D. nymboidense* sp. nov. Fertile material affiliated with *Dicroidium* includes three species of female strobilus, *Umkomasia distans, U. sessilis* and *U.* sp. A. together with dispersed cupules and ovules. Microsporophylls are placed in *Pteruchus* sp. cf. *P. matatamajor* and a single specimen in *P.* sp. A.

Manuscript received 17 February 2004, accepted for publication 18 August 2004.

Keywords: *Dicroidium,* Middle Triassic flora, Nymboida Coal Measures, *Pteruchus, Umkomasia.*

INTRODUCTION

This is the fourth in a series of papers describing the rich and diverse Middle Triassic megafossil floras from two quarries located near the village of Nymboida in north-eastern New South Wales. A locality map showing the Coal Mine and Reserve Quarries and a summary of the geology of the Nymboida Sub-basin was included in Part 1 (Holmes 2000), which also dealt with the Thallophyta and Sphenophyta. Part 2 (Holmes 2001) included descriptions of 14 taxa of the Filicophyta known from material preserved in a fertile state or remains of sterile material with known fern relationships. Twenty four morpho-taxa of fern-like leaves of unknown relationships were described in Part 3 (Holmes 2003).

In this paper abundant material of the leaf morpho-genus *Dicroidium* and its affiliated male and female fructifications, *Pteruchus* and *Umkomasia* respectively, from the two Nymboida localities is described and illustrated.

A history of *Dicroidium*

Dicroidium appeared first in the Middle Early Triassic (Smithian), becoming more numerous and diverse in the Middle and Late Triassic (Ladinian to Carnian) of the Gondwana super-continent (Retallack 1977, Anderson and Anderson 1983). There are no reliable Jurassic records (Anderson and Anderson 2003, p.243) and the genus is presumed to have become extinct at the Triassic-Jurassic boundary. The success and diversification of the genus is recorded in numerous publications since the first description and illustration of three leaf fragments from Tasmania by Morris (1845, as *Pecopteris odontopteroides*). The genus *Dicroidium* was erected by Gothan (1912), who recognised that the forked Gondwanan leaves, usually referred to *Thinnfeldia*, were distinct from the unforked leaves of the Northern Hemisphere. Walkom (1917) retained the name *Thinnfeldia* and later erected the genus *Johnstonia* (Walkom 1925b) for simple forked fronds from Tasmania.

In an overview of genera attributed to the '*Thinnfeldia*' series, in which he accepted *Dicroidium*, Frenguelli (1943) also erected the new genera *Dicroidiopsis*, *Diplasiophyllum*, *Xylopteris* and *Zuberia* for Gondwana forked leaves. Townrow (1957) and Archangelsky (1968) synonymised Frenguelli's new genera with *Dicroidium*. Retallack (1977), in a biostratigraphical review of *Dicroidium* and allied genera, retained *Johnstonia* and *Xylopteris*. Anderson and Anderson (1983), in their extensive study of *Dicroidium* in the Molteno Flora (South Africa), provided a detailed historical review, references and comprehensive lists to 1982 of all the illustrated material from Gondwana that they considered to fall within the genus. They also discussed synonyms and forking fronds distinct from *Dicroidium*.

Gothan (1912) studied the cuticle of *Dicroidium* and showed that it was distinct from *Thinnfeldia*. Jacob and Jacob (1950) and Townrow (1957) added further evidence for the separation. Anderson and Anderson (1983) carried out a comprehensive cuticular study (light and scanning electron microscopy) on *Dicroidium* in the Molteno Formation. Based on permineralised material from Antarctica, Pigg (1990) and Boucher et al. (1993) have described the anatomy of *Dicroidium* leaves. The permineralised fructifications, *Pteruchus* and *Umkomasia*, have been described by Yao et al. (1995) and Slavins et al. (2002) respectively.

While the forked leaves of *Dicroidium* are ubiquitous in Gondwana Triassic floras (Retallack 1977; Anderson and Anderson 1983) their origin is unresolved (Boucher et al. 1993; Axsmith et al. 2000). Archangelsky (1996) suggested that the Carboniferous pteridosperm *Botrychiopsis* may provide a plausible ancestral morphology for the Umkomasiaceae. Retallack (1980) noted that the multi-forked *Lepidopteris callipteroides*, which occurs immediately above the Late Permian coal seams in the Sydney Basin, probably belonged to the pteridosperm stock that gave rise to *Dicroidium*, most likely through intermediate forms similar to '*Dicroidium*' *gopadense* from Nidpur in India (Bose and Srivastava 1971). Palaeozoic pteridosperms from Siberian and Cathaysian sources that survived the end-Permian extinction in refugia as yet unidentified should also be considered. Since Thomas (1933) first suggested *Umkomasia* as a possible early angiosperm this has been much debated and remains unresolved (see Slavins et al. 2002 for a recent discussion).

Thomas (1933) placed *Dicroidium* and its affiliated fertile organs in the Family Corystospermaceae. This family name has been widely used but according to ICBN rules a family must be based on the ovulate genus, in this case *Umkomasia* and therefore Umkomasiaceae. Meyen (1987) placed the Family Umkomasiaceae and the Class Umkomasiales in the gymnosperm Order Ginkgoopsida. Anderson and Anderson (2003), in their recent review of *Umkomasia* and *Pteruchus* from the Molteno Flora, followed this classification.

The question of *Dicroidium* attachment

While the leaves of *Dicroidium* are abundant and widespread throughout Triassic Gondwana, the form of a whole plant is still debated. Various authors have suggested that *Dicroidium* ranged from shrubs to tall trees (Retallack 1980; Anderson et al. 1998; Anderson and Anderson 2003) or was a large tree (Taylor 1996). Petriella (1978) reconstructed *Dicroidium* as a palmiform tree to 10m high. The reconstruction by Retallack and Dilcher (1988, fig.10) showed a tall deciduous forest tree in a seasonally wet lowland.

Despite the large numbers of *Dicroidium* leaves preserved in the Nymboida sediments, no leaves have as yet been found attached to a stem. The only convincing specimen elsewhere of leaves attached to a stem was illustrated by Anderson and Anderson (1983, Pl. 88, fig. 1). Another incomplete specimen (Anderson and Anderson 1983, Pl.88, fig. 2) suggested that the leaves were attached in a fascicled manner to a stem. Anderson and Anderson (2003 p. 257, text fig.5) base their reconstruction on these specimens.

In a paper describing *Umkomasia uniramia*, Axsmith et al. (2000, figs 6 and 8) illustrated a *Dicroidium odontopteroides* leaf apparently contiguous with, or overlain by, a stem of a plant with long and short shoot morphology. By analogy with extant plants bearing long and short shoot morphology (e.g. *Gingko biloba*) it would be unlikely in the extreme for a plant with this growth morphology to bear a leaf on the long shoot section of a stem subsequent to the formation of well-developed short shoots. On the illustrated Antarctic specimen even the short shoots are in a leafless state. The close association of the *Dicroidium* leaf and stems bearing short shoots suggests an affiliation but this is not exclusive as other leaves (e.g. *Heidiphyllum*, *Taeniopteris*) are present in the same deposit. We do not accept the claim of Axsmith et al. (2000) that their specimen "demonstrates unequivocal evidence" of *Dicroidium* attachment.

Archangelsky (1968) argued a case for the affiliation of silicified logs of *Rhexoxylon* and *Dicroidium* leaves. Meyer-Berthaud et al. (1993) described permineralised twigs from Antarctica as *Kykloxylon* and suggested that the stems bore *Dicroidium fremouwensis* Pigg (1990) leaves, but in neither of these cases have the leaves been found in organic connection.

Dicroidium and its fertile organs

Thomas (1933) described the female organ *Umkomasia* and the male *Pteruchus*. Based on close association and similarity of cuticles he regarded them as the fructifications of *Dicroidium*. This affiliation is now generally accepted (Townrow 1962; Holmes 1982; Anderson and Anderson 1983, 2003; Crane 1985; Retallack and Dilcher 1988; Yao et al. 1995 and Slavins et al. 2002).

The fertile genera *Karibacarpon* (Lacey 1976, Holmes and Ash 1979) and *Fanerotheca* (Anderson and Anderson 2003) have also been linked to *Dicroidium*. The species described by Axsmith et al. (2000) as *Umkomasia uniramia* from Antarctica is an ovulate organ with single pedicillate cupules arranged in a terminal radial whorl on a peduncle attached to a leafless short shoot on a mature stem bearing further leafless short shoots. From the significant differences in the architectural arrangement of this fructification we believe it should be placed in a morpho-genus separate from *Umkomasia*.

Problems with *Dicroidium* taxonomy

In many early records (Walkom 1917, Frenguelli 1943) the forked leaves now known as *Dicroidium* (Gothan 1912) were placed in several genera and particularly in *Thinnfeldia*. Walkom (1917) considered his "*Thinnfeldia*" leaves to be ferns as they were closely associated with frond fragments bearing sori. Townrow (1957) separated these fertile fragments from *Dicroidium* as they were indeed ferns which Holmes (2001) has placed in the new genus *Herbstopteris*. Several genera of forked fronds have been described as separate from *Dicroidium* based mainly on morphological differences of pinna or pinnule shape (eg *Johnstonia, Xylopteris*, *Zuberia* and others). Townrow (1957), Archangelsky (1968), Holmes (1982) and Anderson and Anderson (1983, 2003) have regarded most of these additional genera as synonyms of *Dicroidium*. Leaves illustrated by Anderson and Anderson (1983, Pl. 74, figs 1-9) which showed typical *D. elongatum* (= *Xylopteris elongata*) pinnae and typical *D. odontopteroides* pinnae on the same leaf indicate how closely related these 'genera' are. It is far more likely that those leaves are interspecific rather than intergeneric 'hybrids' or even one polymorphic species. Some South American workers continue to use a multiplicity of generic names for *Dicroidium* leaves (Artabe 1990; Artabe et al. 1998; Gnaedinger and Herbst 1998, 2001).

Early authors appear to have worked only on limited museum collections or had very little field experience because they failed to recognise the variability within their 'species' and the intergrading forms that may have linked the 'species'. Holmes (1982) discussed the problems created by the variation and intergrading forms of *Dicroidium* in the Middle Triassic Benolong Flora. He referred to the work of Meyen (1979), who had demonstrated from a large population of Permian pteridosperm leaves previously placed in several genera and many species that they all belonged in the single species *Rhaphidopteris praecursoria*. Rees and Cleal (1993) showed that the leaves of a Jurassic pteridosperm previously placed in six species and four genera all belonged to *Archangelskya furcata*.

The revision by Retallack (1977) of the *Dicroidium* genus (plus *Xylopteris, Johnstonia* and *Tetratilon*, which he retained as allied but distinct) was a significant attempt to provide a taxonomic guide to the genus that would mainly be useful for stratigraphic purposes. However, his descriptions and stylised sketches of the taxa he recognised failed to demonstrate the range of variation within a single population of each taxon. The necessity under the IBCN Code (ICBN 2001) for typification has also exacerbated the problem of dealing with variable fossil populations.

The photographic record by Anderson and Anderson (1983) of 1133 individual *Dicroidium* leaves arranged in 'palaeodemes' was a notable achievement and clearly demonstrated the diversity within single populations of *Dicroidium* leaves. They were the first to use palaeo-gamma taxonomy for *Dicroidium*, i.e. using the data of comprehensive collections from many localities. They defined a 'palaeodeme' as a "collection of specimens representing a single breeding population showing a normal distribution of variation and derived from a single fossil assemblage from a discrete lithological unit". The same authors did not attempt to define precise boundaries between taxa as they considered "it would be unproductive considering the general morphological fluidity within the genus" and they had "little doubt that *Dicroidium* speciation was anything but simple and came closer to the reticulate speciation model of Sylvester-

Bradley (1977)". Based on the palaeodeme approach, Anderson and Anderson (1983, 1989) listed a total of 32 taxa comprising 10 species, 17 subspecies and 15 formae. In their recent revision (Anderson and Anderson 2003) *Dicroidium* now comprises 21 taxa of specific rank plus 15 formae.

The reasons listed by Boucher et al. (1993) provided a good summary of why *Dicroidium* is not a well-understood genus: there is a large amount of morphological variation; there is inconsistency in naming; variations in cuticular features are not well enough known; complete plants are not known; sample sizes are small especially from remote areas; and often only fragments are preserved.

MATERIALS

In the Holmes' catalogued collection of over 2600 slabs of Nymboida material, approximately one third of the slabs bear leaves that can be attributed to *Dicroidium*. The female and male fertile organs *Umkomasia* and *Pteruchus* affiliated with *Dicroidium* are rare and have been found at a ratio of one identifiable specimen to c. 70 leaves. This is closely similar to the ratio observed at the Benolong locality (Holmes 1982). In the Molteno assemblages Anderson and Anderson (2003, p. 240, 250) also noted that the fertile organs were rare and gave the return for each locality only in terms of man-hours spent chipping open fossiliferous slabs.

The Nymboida fossil plant material is preserved mostly as carbonaceous compressions, but a tectonic heating event during the Cretaceous (Russell 1994) has destroyed the cuticle of otherwise beautifully-preserved specimens.

In addition to the material held in the Holmes collection we have examined other Nymboida specimens housed in the University of New England Geology Department and the Australian Museum.

OUR METHOD OF NOMENCLATURE

Earlier attempts to classify Nymboida *Dicroidium* leaves were made from limited and usually fragmentary specimens, i.e. using mainly palaeo-alpha taxonomy (De Jersey 1958, Flint and Gould 1975, Retallack et al. 1977). Retallack (1977 Microfiche Frames G11-G13) listed 12 *Dicroidium* taxa plus one each of *Johnstonia* and *Tetraptilon* (both here included in *Dicroidium*) and two ovulate species from the Coal Mine Quarry.

In this present revision we have used mainly palaeo-beta taxonomy and based our classification on our comprehensive collection of over 2600 selected and catalogued slabs that have been accumulated during many trips to the Nymboida quarries over a period of almost 40 years. The bulk of the collection was made from fallen blocks that had been blasted or bulldozed from the quarry faces. The exact source of the in situ material is mostly unknown. Except in rare cases such as the slabs containing large numbers of similar leaves (e.g. Figs 2 and 6A), we are unable to identify specific populations or palaeodemes as was achieved by Anderson and Anderson (1983, 1989, 2003). Future work involving in situ collecting from specific assemblages (i.e. from discrete lithological units) would allow palaeo-gamma taxonomy and the material to be documented into palaeodemes.

Dicroidium foliage is the most commonly preserved fossil at Nymboida and also in the catalogued collection. The forked leaves occur in a diversity of forms ranging and intergrading from simple leaves with entire margins to pinnate to bipinnate. Faced with this continuum one could place all the leaves in one polymorphic species or, on the other hand, describe numerous species each based on a 'single' type specimen. Due to this range of variation and intergradation we are unable to determine reliable diagnostic features. This makes it difficult to identify the Nymboida *Dicroidium* material to a specific level.

Although the sediments in the Nymboida quarries were deposited over a relatively short period of geological time (Holmes 2000) they do represent many different sedimentary facies, e.g. coal seams, shales, fossil soils, siltstones and sandstones. The enclosed fossils certainly would have been derived from a range of habitats so it is most likely that various species of *Dicroidium* plants had evolved or adapted to occupy particular environmental niches. Only one variable species of *Pteruchus* plus a possible second species are recognised in the Nymboida collections while at least three separate species of the female *Dicroidium* fructification *Umkomasia* are present. It is therefore most likely that several discrete species of plants bearing *Dicroidium* leaves were growing in the region in the Middle Triassic.

For the Nymboida *Dicroidium* leaves to be compared with collections from other geographical and stratigraphical localities we have separated the leaves into informal complexes based on leaf morphology, which range from simple to pinnate, bipinnatifid and bipinnate. Except for the single specimen placed in *D. elongatum* (Figs. 19, 20A) and the few rare and problematic specimens (Figs 20B-E) we have grouped the foliage material into five 'species complexes' each named for a previously-described species that represents the core of the complex. Specimens in the Selected References lists also have a gross morphology identifiable with the core of the complex. Each complex includes a particular section of the range of diversity of the Nymboida *Dicroidium* leaf collections and is linked by intergrading forms with adjacent complexes. We illustrate over 80 reasonably well-preserved leaves (Figs 1-18), that demonstrate the variation within each complex and the obvious forms intergrading between successive complexes. While we acknowledge that our form of classification is subjective, it is based on a large and representative collection of reasonably well-preserved material.

Due to constraints imposed by the lack of storage facilities at the Australian Museum only the specimens illustrated in this paper have been allocated AMF numbers. All other specimens remain in the Holmes Collection.

SYSTEMATIC PALAEOBOTANY

Order	Ginkgoopsida Meyen 1987
Class	Umkomasiales Meyen 1984
Family	Umkomasiaceae Meyen 1984

Genus *Dicroidium* Gothan 1912

Type species

Dicroidium odontopteroides (Morris 1845) Gothan 1912

Synonymy [Synonymised by]:

Johnstonia Walkom 1925b [Townrow 1957]
Dicroidiopsis Frenguelli 1943 [Archangelsky 1968]
Diplasiophyllum Frenguelli 1943 [Archangelsky 1968]
Zuberia Frenguelli 1943 [Townrow 1957]
Xylopteris Frenguelli 1943 [Archangelsky 1968]
Tetraptilon Frenguelli 1950 [Anderson and Anderson 1983]
Hoegia Townrow 1957 [Archangelsky 1968]

'*Dicroidium coriaceum* complex'

Figures 1A-C; 2A-E

Selected References

1925b *Johnstonia coriacea*, Walkom, figs 6,7
1927 *Johnstonia coriacea*, Du Toit, fig. 12D, 13B
1932 *Johnstonia coriacea*, Du Toit, text fig. 2A
1967 *Dicroidium coriacium*, Jain and Delevoryas, Pl. 91, fig. 1
1982 *Dicroidium coriaceum*, Holmes, figs 3C, D
1983 *Dicroidium coriaceum* subsp. *coriaceum*, Anderson and Anderson, Pl. 36, figs 3-6; Pl.76, figs 1-6
1983 *Dicroidium coriaceum* subsp. *dutoitii*, Anderson and Anderson, Pl. 41, figs 1-28; Pl.76, figs 12-17

Description

Forked leaves of variable length and width, usually entire, sometimes lobed and grading to pinnatifid.

Discussion

D. coriaceum was first described from Tasmania by Johnston (1887) as *Rhacophyllum coriaceum*. Walkom (1925b) re-examined Johnston's material and transferred it to the new genus *Johnstonia*. He noted that the margins were entire or slightly lobed. Specimens attained a length up to 100 mm above the dichotomy and the breadth of the larger specimens was 10 mm, though in general they were narrower. Antarctic material with leaves having a broad lamina and the fork closer to the apex were described by Townrow (1967) as *D. dutoitii*. He selected as the holotype a leaf illustrated by DuToit (1927, text fig. 12D) from the Molteno Formation of South Africa, which differed quite significantly from the Antarctic specimens. Retallack (1977) placed the Antarctic material in *Johnstonia coriacea* var *obesa* with the South African material retaining the epithet *dutoitii*. Anderson and Anderson (1983) have separated *D. dutoitii* from *D. coriaceum* on palaeodeme evidence at localities in the Molteno Formation although their illustrations show some overlap in leaf dimensions. From South America, Jain and Delevoryas (1967, Pl. 91, fig. 1) illustrated a single slab that encompasses the size range of both above species. Holmes (1982) also noted a wide variation in size range of *D. coriaceum* in the Benolong flora of NSW. The Nymboida leaves illustrated in Figure 1 are a larger form, ranging from 120-140 mm long and 5-10 mm wide and from entire to lobed, and could be regarded as a form of *D. dutoitii* Townrow (1967). As only three slabs of this larger form are present in the Nymboida collections and their full range of variation is not known we place them in the *D. coriaceum* complex.

The specimens illustrated in Figures 2A-E and Figure 4C were all collected from a single slab of whitish siltstone. We believe that, with the exception only of the pinnate fragment on the lower left of Fig. 2A, all the other leaves represent a single population. They range in length from c. 40-80 mm long and 3-

7 mm wide. The leaf margins are mostly entire but lobed and pinnatifid forms (Fig. 2E and Fig. 4C) are present. The latter forms intergrade with, and are very close to, the pinnatifid and pinnule coalescing forms of the '*D. odontopteroides* complex'.

'*Dicroidium odontopteroides* complex'

Figures 3A-E; 4A-G; 5A-D; 6A; 7A-C; 8A; 9A-C; 10A,D,E

Selected References

1845 *Pecopteris odontopteroides*, Morris, Pl. 6, fig. 3

1890 *Thinnfeldia odontopteroides*, Feistmantel, Pl. 26, figs 2, 2a

1917 *Thinnfeldia lancifolia*, Walkom, Pl. 7, fig. 2; Pl. 3, fig. 1

1975 *Dicroidium odontopteroides*, Flint and Gould, Pl. 3, figs 10, 11

1982 *Dicroidium odontopteroides* var. *moltenense*, Holmes, figs 4A, B

1983 *Dicroidium odontopteroides* subsp. *orbiculoides*, Umk 111 palaeodeme, Anderson and Anderson, Pl. 42

1983 *Dicroidium odontopteroides* forma *odontopteroides*, Umk111 palaeodeme, Anderson and Anderson, Pl. 43

1992 *Dicroidium odontopteroides*, Taylor et al., fig. 1

2000 *Dicroidium odontopteroides*, Axsmith et al., fig. 3, leaf only

2001 *Dicroidium odontopteroides*, Gnaedinger and Herbst, fig. 4E (in gross morphology but with denser venation)

Description

Usually once-forked pinnate frond to 160 mm long; pinnae to 40 mm long and 15 mm wide, not basally contracted, ranging from semi-orbicular to broadly triangular, to elongated rectangular or slightly tapering, with rounded or broadly obtuse apex; the longer pinnae with a midrib and alethopteroid venation; shorter rounded pinnae with odontopteroid venation as in Fig. 7C. The specimens illustrated in Figs 7A and B represent the core of this Nymboida complex. The leaf in Fig. 8A is the largest specimen from this complex in the collection.

Discussion

Taxonomic confusion has arisen since the original description and illustrations of *Dicroidium odontopteroides* (as *Pecopteris odontopteroides*) by Morris (1845). Only three frond fragments were illustrated and Morris noted that the specimen (Pl. 6, fig. 4) with more elongate pinnae was probably a variety of the species. When compared with the range of variation encompassed in our *D. odontopteroides* complex, Morris's three specimens show a very limited range of variation as would be expected for this morpho-species. However, due to the lack of understanding of the range of variation that commonly occurs in a single population, leaves similar to Morris's elongated pinna form were raised to specific rank i.e. *Dicroidium lancifolium* (Gothan 1912; Walkom 1917; Frenguelli 1943; and others, see Hypodigm Lists of Anderson and Anderson 1983). The presence of a midrib (alethopteroid venation) in the more elongated pinnae has been regarded by some authors as a specific or varietal diagnostic feature. The form of venation is usually dependent on the length and shape of the pinnae, which varies according to the position on the frond and whether on the inside or outside of the fork. Both odontopteroid and alethopteroid forms of venation may be observed on a single frond. Leaves placed in *D. lancifolium* by several authors are best regarded as long-pinnaed forms of *D. odontopteroides*.

The range of variation of fronds within this Nymboida complex encompasses forms that accord with several published species, subspecies, varieties or forms. On the classification of Retallack (1977, Microfiche Frames I1 to I7) these varieties include *D. odontopteroides* var. *moltenense*, *D. odontopteroides* var. *obtusifolium* and *D. odontopteroides* var. *odontopteroides*.

Specimens with short broad pinnae (Figs 3A-D; 4C, D, G; 7C) agree with leaves from the *D. odontopteroides* subsp. *orbiculoides* palaeodeme of Anderson and Anderson (1983, Pl. 42), which included *D. crassinervis* forma *obtusifolium*, *D. odontopteroides* subsp. *orbiculoides* and *D. crassinervis* forma *crassinervis*. Boucher et al. (1993) separated compression and impression material from Mt Falla in the Beardmore Glacier area of Antarctica into *D. odontopteroides*, *D. lancifolium* and *D. dubium* based on minor morphological and cuticular features, which may have represented a normal range of variation within a single species complex. Frenguelli (1950) erected the genus *Tetraptilon* for *Dicroidium odontopteroides*-like leaves from Argentina in which the frond had a double fork. This feature has been recorded also in *D. odontopteroides* assemblages from Australia (Flint and Gould 1975, Pl. 3, fig. 10; Retallack 1977) and South Africa (Anderson and Anderson 1983, Pl. 87, figs 1,2,4 and 6, Pl. 88, fig. 1). Anderson and Anderson (1983) synonymised the genus *Tetraptilon* with *Dicroidium*. In our collections these multiple forked fronds comprise c. 1% of the *D. odontopteroides* complex. The forking may result in three, four or five branches, with four branches being the most common (Figs 5A-D and Fig. 6A). On some bedding planes this is the only form of leaf preserved. This suggests that for some trees double-forked leaves were the normal frond and not aberrant as was surmised by Anderson and Anderson (1983, Pls 71, 87) because of their rare occurrence. The slab illustrated in Figure 6A is a good example of the range of variation in a single population of double-forked leaves. A single specimen of a double-forked *D. dubium* (Fig. 6B) has also been collected.

In a recent paper, Gnaedinger and Herbst (2001) recognised the great morphological variability in *Dicroidium* leaves from three Upper Triassic formations in northern Chile. They illustrated a number of examples that indicated an intergrading 'line' from *D. obtusifolium* to *D. odontopteroides* (varieties *moltenense* and *remotum*) to *D. odontopteroides* var. *odontopteroides* to *D. lancifolium* var. *lancifolium*. This range of morphology is here included in our '*D. odontopteroides* complex'.

Leaves illustrated in Figures 9A, B are forms intergrading with extremes from the *D. lineatum* complex.

'*Dicroidium lineatum* complex'

Figures 10B,C; 11A,B,D; 12A-C

Selected References

- 1883 *Gleichenia lineata*, Tenison-Woods, Pl. 3, fig. 6; Pl. 8, fig. 2
- 1898 *Thinnfeldia indica* var. *falcata*, Shirley, Pl. 7, fig. 2
- 1917 *Thinnfeldia acuta*, Walkom, Pl. 3, fig. 4
- 1977 *Dicroidium lancifolium* var. *lineatum*, Retallack, Microfiche Frame H17
- 1983 *Dicroidium odontopteroides* subsp. *lineatum*, Anderson and Anderson, Pl. 64, figs 12-29; Pl. 65, figs 1-3; Pl. 79, figs 4, 6
- 1985 *Dicroidium lancifolium* var. *lineatum*, Artabe, Pl. 3, fig. 5
- 1992 *Dicroidium lancifolium*, Taylor et al., fig. 2
- 2001 *Dicroidium lancifolium* var. *lineatum*, Gnaedinger and Herbst, fig. 2, A-E, fig. 3 L

Description

Forked pinnate leaf to 200 mm long; pinnae elongated-triangular to 35 mm long, tapering to acute apex, broad base, usually decurrent.

Discussion

This complex is closely allied to the *D. odontopteroides* complex but has been separated on the basis of the decurrent pinnae which taper to an acute apex.

Retallack (1977, Microfiche Frames H17, H18) placed leaves of this complex as a variety of *D. lancifolium*, which we regard as belonging in the '*D. odontopteroides* complex'. Leaves comparable to our '*D. lineatum* complex' were described by Anderson and Anderson (1983) from the Molteno Formation of South Africa as *D. odontopteroides* subsp. *lineatum* but were later raised to specific rank (Anderson and Anderson 2003).

In the Nymboida collection, forms with undulate margins or incipient lobes (Figs 11C; 12A,D) are linking forms with the '*D. dubium* complex' below.

'*Dicroidium dubium* complex'

Figures 6B;.13A-C; 14A-E; 15A-D; 16A

Selected References

- 1890 *Gleichenia dubia*, Feistmantel, Pl. 26, fig. 3
- 1908 *Thinnfeldia odontopteroides*, Seward, fig. 4
- 1928 *Thinnfeldia talbragarensis*, Walkom, Pl. 27, fig. 1
- 1947 *Thinnfeldia talbragarensis*, Jones and deJersey, Pl. 1, fig. 5
- 1965 '*Thinnfeldia*' *talbragarensis*, Hill et al., Pl. T4, fig. 6
- 1982 *Dicroidium dubium* var. *dubium*, Holmes, fig. 7D
- 1983 *Dicroidium dubium* subsp. *dubium*, Anderson and Anderson, Pl. 33, figs 21-31
- 1983 *Dicroidium dubium* subsp. *tasmaniense*, Anderson and Anderson, Pl. 44, figs 7-16; Pl. 53, figs 15-20; Pl. 59, figs 1-14; Pl. 60, figs 1-5
- 1983 *Dicroidium dubium* subsp. *switzifolium*, Anderson and Anderson, Pl. 44, figs 17-20

Description

Forked bipinnatifid leaf; pinnae elongate, tapering to acute apex; margin variously lobed, proximal lobes sometimes separated to the pinna rachis but coalescing distally. Leaves variable in size from 70 - 200 mm long; pinnae in mid-portion of leaf from 15 - 90 mm long, 4 - 15mm wide.

Discussion

Fronds of the '*D. dubium* complex' are the most commonly occurring *Dicroidium* fossils at the Nymboida quarries. Leaves that represent the core of this complex (Figs 13C, 14D,E, 15B,C) are bipinnatifid to partially bipinnate and agree well with the Molteno palaeodemes of *D. dubium* subsp. *dubium* as recognised by Anderson and Anderson (1983, p. 106). Pinnae on the same frond may vary from entire to lobed and pinnate. Specimens with narrower pinnae and undulate margins are intergrading forms with the '*D. lineatum* complex' while the bipinnate forms intergrade with those of the '*D. zuberi* complex' (Fig. 15A). The apical leaf fragment showing large bipinnatifid pinnae (Fig. 16A) may be compared with *D. dubium* var. *australe* (sensu Retallack 1977, Microfiche Frame H8).

'*Dicroidium zuberi* complex'

Figures 16B,C; 17A-D; 18A

Selected References

1890 *Thinnfeldia odontopteroides*, Feistmantel, Pl. 24, figs 1,2; Pl. 25, figs 1,2
1917 *Thinnfeldia feistmantelii*, Walkom, Pl. 2, figs 1,2
1944 *Zuberia zuberi*, Frenguelli, Pl. 4
1975 *Hoegia papillata*, Flint and Gould, Pl. 2, figs 4,5
1977 *Dicroidium zuberi*, Retallack et al., Figs A-F
1979 *Dicroidium zuberi*, Petriella, Pl. 2, fig. 5
1983 *Dicroidium zuberi*, Anderson and Anderson, Pl. 61, figs 1-13; Pl. 62, figs 1-4; Pl. 81, figs 1-5
1985 *Dicroidium zuberi* var. *papillatum*, Artabe, Pl. 4, fig. 2

Description

Frond bipinnate, small to large, 150 - 600 mm long; pinnules variable in shape, rounded to blunt rhomboid or falcate, inclined towards pinna apex, coalescing distally and apically. Basiscopic pinnules often decurrent on main rachis.

Discussion

Leaves of this complex are widespread but not common at the Nymboida localities. Solitary large leaves are sometimes preserved intact in beds of sandstone thus indicating they were tough and resistant to damage during transport. *D. zuberi* is differentiated from *D. dubium* by the presence of pinnules divided to the pinna rachis, but there are numerous intergrading forms with deeply bipinnatifid fronds (Fig. 17A,B).

Retallack (1977, Microfiche Frame G12) listed three varieties of *D. zuberi* from Nymboida based on the pinnule shape of mostly fragmentary material. Our extensive collections clearly demonstrate intergrading forms that link the varieties. Indeed pinnules on the same leaf may include different varietal types (Figs 16B, 18A). The range of pinnule shapes in the Nymboida '*D. zuberi* complex' supports the decision of Anderson and Anderson (1983) to recognise the previously described *D. zuberi* varieties *feistmantelii, sahnii, barrealensis* and *papillatum* as normal variations within a single species.

We agree with Archangelsky (1968), Retallack (1977) and Anderson and Anderson (1983, 2003) that the continued placement of these leaves into the separate genus *Zuberia* (Artabe 1990; Gnaedinger and Herbst 2001) is not warranted.

Dicroidium elongatum (Carruthers) Archangelsky 1968

Figures 19, 20A

Holotype

Designated by Retallack (1977) *Sphenopteris elongata* Carruthers 1872, Pl. 27, fig.1

Selected References

1883 *Trichomanides spinifolium,* Tenison-Woods, Pl. 3, fig. 7
1898 *Trichomanides elongata* var. *spinifolia*, Shirley, Pl. 5, fig. 2
1917 *Stenopteris elongata,* Walkom, Pl. 6, figs 1, 3
1965 *Xylopteris spinifolia*, Hill et al., Pl. T5, fig. 7
1977 *Xylopteris spinifolia,* Retallack, Microfiche Frames J13, 14
1982 *Dicroidium spinifolium*, Holmes, Fig. 5B,C
1983 *Dicroidium elongatum* forma *remotifolium,* Anderson and Anderson, p.115, Pl. 48, figs 24-32

Description

Known only from a single incomplete specimen from the Coal Mine Quarry (AMF125082). Frond bipinnate, c. 120 mm long; pinnae linear at c. 45° to main rachis; pinnules well-spaced, elongated triangular to linear.

Discussion

This solitary specimen is preserved in siltstone together with other fragments that appear to have been subjected to long distance transport before burial. In the probable contemporary Benolong Flora (Holmes 1982) leaves of a '*Dicroidium elongatum* complex' comprised 20% of the preserved plant remains. Holmes reconstructed the Benolong environment as a dry sclerophyll woodland on low fertility sandy soils. The presence of a rich fern and fern-like leaf flora at Nymboida (Holmes 2001, 2003) suggests a vegetation growing in a moist environment with rich soils. This solitary specimen of *D. elongatum* together with associated plant fragments was most likely transported from a drier less fertile upstream source.

D. elongatum is a species complex of pinnate to tripinnate intergrading forms. In the past the various forms have been separated into species, subspecies and formae. Jones and de Jersey (1947) considered the pinnate to tripinnate forms to represent an evolutionary series but all forms are now known to occur together. Holmes (1982) noted that leaves with intergrading characters of most forms were present in the Benolong Flora.

? Dicroidium nymboidense Holmes sp. nov.

Figure 20B

Diagnosis

A small pinnate frond; pinnae few, large elongate-ovate, rounded, irregularly lobed; venation odontopteroid, two decurrent veins entering each pinna then dividing acutely up to five times to form parallel venation to the pinna apices.

Description

This new morpho-taxon is based on a single frond impression and counterpart. Frond pinnate, 115 mm long with base missing; curving rachis with five opposite pairs of pinna and a terminal pinna, increasing in size apically; fifth pair of pinnae to 55 mm long, 25 mm wide, elongate-ovate with two or three broad irregular obtuse lobes; texture of pinnae thin, venation conspicuous; two veins enter each decurrent pinna at c. 30°, arch and divide from three to five times then run parallel to each other to pinna apex; the upper of the two primary veins forming a short median vein.

Holotype

AMF125083 Australian Museum, Sydney.

Type Locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Discussion

This rare and problematical frond is placed with reservations in *Dicroidium*. The rachis curves sideways basally but the leaf base is missing and no fork is preserved. However, on the right margin of the specimen there is a pinnule fragment with venation that divides and runs parallel and is aligned at an angle appropriate for a pinna if it were a portion of a forked *Dicroidium* frond. The venation, while essentially odontopteroid, is somewhat similar to that in the decurrent, ovate, sometimes lobate pinnules of *Nymboidiantum* spp (Holmes 2003, Figs17-19). However the size and texture of the pinnae of ?*Dicroidium nymboidense* is unlike that of any *Nymboidiantum* spp. While we are uncertain of its generic placement it is certainly a distinct species and is described and illustrated to draw attention to its presence in the Nymboida Flora.

Dicroidium sp. *A*

Figures 20C,D

Description

Apical portions of two fronds with extremely widely spaced pinnae; Fig. 20C is pinnate, pinnatifid with slightly lobed or entire strongly decurrent pinnae; Fig. 20D is bipinnate with broadly triangular pinnules and basiscopic pinnules decurrent on or attached directly to the main rachis.

Discussion

The wide spacing of the pinnae of these incomplete fronds sets them apart from all other more completely preserved fronds. They may possibly represent aberrant forms of *D. dubium* and *D. zuberi* respectively. *D. pinnis-distantibus* (Kurtz) Frenguelli (Retallack 1977, Microfiche Frame M 8) also has very widely spaced pinnae but with entire pinnae margins.

Dicroidium sp. *B*

Figure 20E

Description

The apical portion of a very large bipinnatifid *Dicroidium*-like frond with deeply dentate pinna margins.

Discussion

This single portion of an obviously very large frond differs by its size and shape from all other bipinnatifid material from Nymboida. *D.* sp. *B* differs from the large *D. dubium* var. *australe* (Retallack 1977, Microfiche Frame H8) and *D. dubium* ssp. *helvetifolium* (Anderson and Anderson 1983, p. 105) by the acute triangular pinna lobes. A distal fragment of a somewhat similar-sized but pinnate frond from the Late Triassic Ipswich Basin was attributed by Walkom (1917) to *Danaeopsis hughesi*, now *Dicroidium hughesi* Lele (1962), a species described from India.

Fertile organs associated with *Dicroidium* leaves

Genus *Umkomasia* Thomas 1933

Type species

Umkomasia macleani Thomas 1933 p.203, figs 1, 2, 56; Pl. 23, figs 1-4

Umkomasia distans Holmes 1987

Figures 21A; 22A

Holotype

AMF 63824, Holmes 1987, fig. 3, fig. 4, A-D

Paratypes

AMF 63825-28

Description

An *Umkomasia* strobilus with widely spaced alternate and spirally arranged branches on an elongate axis; branches with one or two opposite pairs of cupules and a terminal pair or a single cupule; cupules pedicillate, irregularly rounded, 3.5 to 5 mm in diameter.

Discussion

U. distans was described and illustrated by Holmes (1987) based on three specimens of reasonably preserved cupule bearing axes from the Coal Mine Quarry, Nymboida. Additional material has been collected (Fig. 21A) but this is fragmentary. For comparisons with other material see Holmes (1987). This species was regarded as distinct from the Molteno species by Anderson and Anderson (2003, Table 51).

Umkomasia sessilis Holmes 1987

Figures 21B,C; 22B

Holotype

AMF63829 and counterpart AMF63830, Holmes 1987, fig. 5, fig. 6 A-C

Paratype

AMF63831

Description

An elongate *Umkomasia* strobilus with alternate, spirally arranged branches bearing two pairs of opposite, sessile cupules 4 - 5 mm in diameter.

Discussion

U. sessilis differs from *U. distans* by the sessile cupules. *U. decussata* Anderson and Anderson (2003) has sessile cupules but differs by the more numerous pairs of cupules with a decussate arrangement. The partial strobilus located on the lower left hand side of Figure 10A probably belongs here.

Umkomasia sp. *A*

Figure 22C

Description

A portion of a single elongate *Umkomasia* strobilus with well-separated alternate branches, each branch with one or more (?) pairs of cupules borne on long expanding pedicels; cupules strongly decurved, 8-10 mm long.

Discussion

U. sp. *A* differs from *U. distans* and *U. sessilis* by the larger decurved cupules and by the elongated and expanding pedicels. The cupules of *U. gracilliaxis* Anderson and Anderson (2003) from the Molteno Formation are decurved and of a size similar to *U.* sp. *A*. However, their cupules with four lobes each is a feature not preserved on this Nymboida specimen.

Isolated *Umkomasia* cupules

Figures 22D-F

Specimen AMF125092 (Fig. 22D) shows a pair of adjacent and opposite dorsally compressed semicircular cupules each c. 16 mm in diameter, with a 4 mm wide peduncle attached to the proximal margin. These cupules are closely comparable with the cupule shown in a dorsal view of *Karibacarpon (Umkomasia) feistmantelii* (Holmes and Ash 1979, Fig. 6.2) from the Early Triassic Lorne Basin assemblage and with cupules from the Sydney Basin (Walkom 1925a, Pl. 31, fig. 9; Retallack 1980, fig. 21.9E). No additional specimens have been found at Nymboida to show whether these cupules may have split on dehiscence into several lobes as occurs in *U. feistmantelii* fructifications (Holmes and Ash 1979, fig. 6. 3-5; Walkom 1925a, Pl. 29, fig. 9; 1932, Pl. 5, figs 3-5; Retallack 1980, Fig 21.9F).

Specimen AMF125093 (Fig. 22E) is a thick rounded tapering mass, 15 mm wide, of carbonaceous material attached to a stout peduncle 2 mm wide. On opposite sides of the mass are decurved acute projections. This problematic specimen may represent a pair of large fleshy conjoined cupules, perhaps similar to *Umkomasia* sp. of Retallack (1980, Fig.

21.9E).

Specimen AMF125094 (Fig. 22F) is an isolated dehisced cupule c. 7 mm wide, split into ?4 acute lobes. This cupule was thin textured in contrast to the thick fleshy appearance of the previous specimen. Preservation is too poor to allow for comparisons with known fructifications.

Dispersed *Umkomasia* ovules

Figure 21D

Dispersed platyspermic ovules occur frequently on some horizons at both the Coal Mine and Reserve Quarries. The ovules illustrated are c. 5 mm wide and c. 7 mm long, with an acute bifid apex. They are similar in form and shape to the ovules illustrated by Thomas (1933, fig. 33) and Anderson and Anderson (2003, Pl. 82, figs 11-16) and associated with *Dicroidium* leaves at the Umk111 locality of the Molteno Formation. In size they are closest to the ovules associated with *U. quadripartita* from the Mat 111 locality (Anderson and Anderson 2003, Pl. 85, figs 7-10).

Genus *Pteruchus* Thomas 1933

Type species

Pteruchus africanus Thomas 1933, fig. 34, Pl. 24, fig. 71

Pteruchus sp. cf *P. matatimajor* Anderson and Anderson 2003

Figures 23A-E

Selected references

1947 *Pteruchus* cf *africana*, Jones and de Jersey, text fig. 51

2003 *Pteruchus matatimajor*, Anderson and Anderson, p. 254, Pls 92-94

Description

This morpho-taxon is based on the five incomplete strobili illustrated and numerous other detached heads. The main axis is stout, to 2.5 mm wide, length not known; microsporophylls oval to linear-oblong, in pairs on a slender forked peduncle; heads 11-23 mm long, 5-9 mm wide; microsporangia spindle- or cigar-shaped, 2-3 mm long, 0.35-0.5 mm wide, covering whole abaxial surface.

Discussion

None of the Nymboida specimens is complete. Figure 23B clearly shows the paired nature of the microsporophylls. In this feature and size they are closely similar to the *Pteruchus* strobilus illustrated by Jones and deJersey (1947, text fig. 51) from Ipswich, and also with *P. matatimajor* (Anderson and Anderson 2003) from the Matatiele assemblage in the Molteno Formation. We consider the Nymboida material as close to *P. matatimajor* and quite separate from *P. africanus*, which has smaller unpaired microsporophylls. The identification of *P. dubius* and *P. johnstonii* from the Coal Mine Quarry by Retallack (1977, Microfiche Frame G12) is doubtful as it was based on fragmentary material. The microsporophylls placed in *Pteruchus johnstonii* from the middle Triassic Benolong assemblage by Holmes (1982) differ from the Nymboida specimens by their shorter, more rounded unpaired heads. *P. feistmantelii* (Holmes 1987 p.172) from the Lorne Basin (Holmes and Ash 1979) and the Sydney Basin (Walkom 1925a, Pl. 31, fig. 10; Retallack 1980) was very much longer and more gracile.

It is interesting to note that in both the Molteno and Nymboida localities where *P. matatimajor* or a comparable form occurs, the leaves of the *D. dubium* complex are the most common *Dicroidium*.

Pteruchus sp.

Figure 23F

Description

A detached microsporophyll, 40 mm long and 9 mm wide; forking distally.

Discussion

This microsporophyll is larger than all other Nymboida *Pteruchus* heads and the forking structure is unique. In size it approaches the long gracile microsporophyll of *P. feistmantelii* from the Lorne Basin, Australia (Holmes and Ash 1979).

CONCLUSION

Leaves of the *Dicroidium* morpho-genus are the most commonly occurring fossils in the large collections made from the Nymboida quarries. Collections have been made from differing sedimentary facies and may represent vegetation from various habitats depending on the degree of transport or dispersal before burial. The Nymboida leaves ascribed to *Dicroidium* display a wide range of variation and intergrading forms ranging from simple to pinnate to bipinnate.To identify individual leaves with previously described species ignores the presence of the intergrading forms. Therefore we have separated the leaves into five 'species complexes' each centred on a widely distributed and well-recognised morpho-species. The single leaf of *D. elongatum* present in the Nymboida flora is possibly a transported specimen from a source far beyond the Nymboida flood-plain vegetation which comprises the bulk of the preserved material. Future descriptions of all fossil floras should recognise the variability and range of intergrading forms due to ecological factors, the chance factors involved in the fossilisation process and discovery of the fossilised material.

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Figure 1. A–C. *Dicroidium coriaceum* complex. Larger leaves with mainly entire margins. A. AMF125016; B. AMF125017; C. AMF125018. Scale bar = 1 cm.

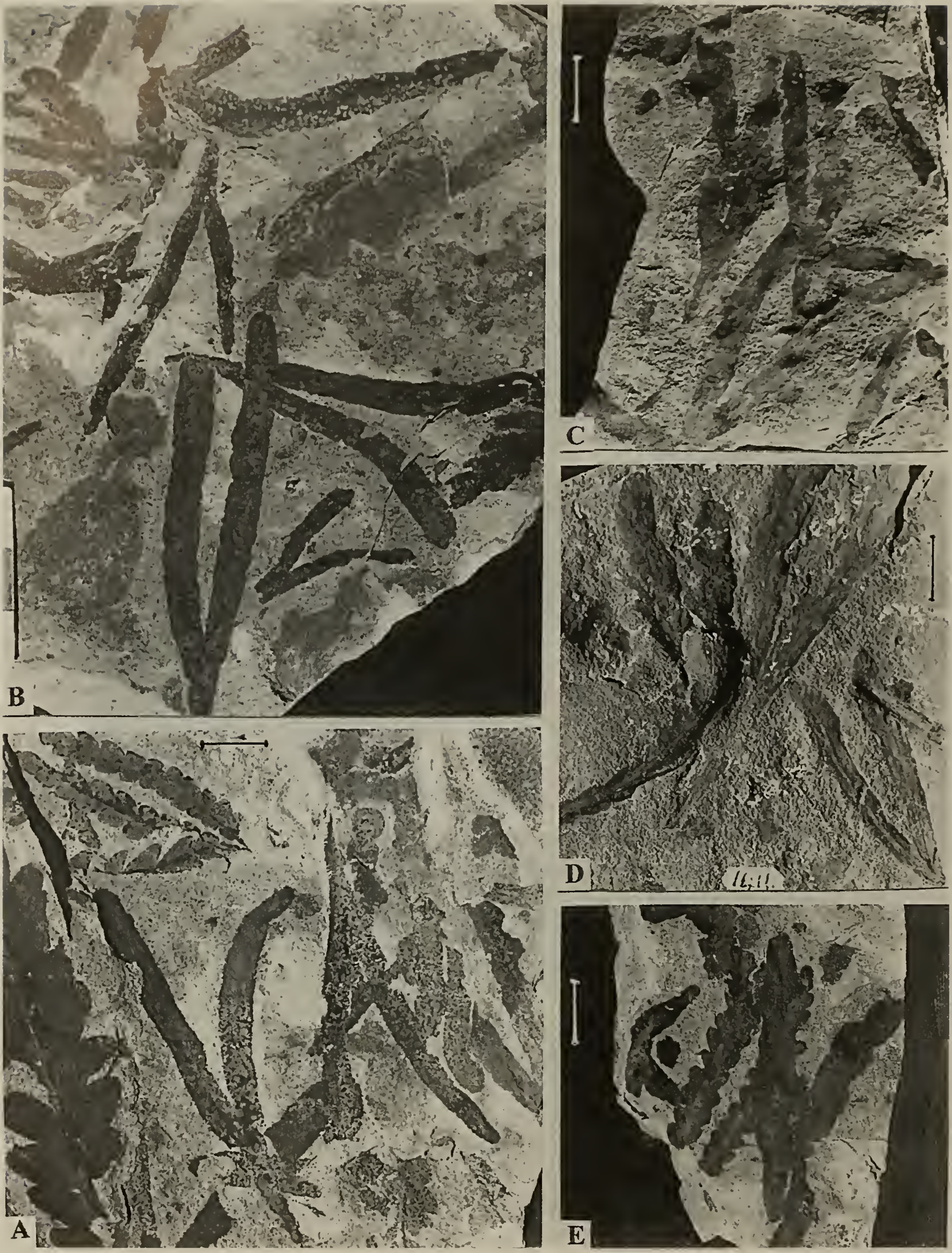

Figure 2. A–E. *Dicroidium coriaceum* complex (excluding the leaf on lower left of Fig. 2A). Smaller leaves with margins ranging from entire to pinnatifid. All specimens from the same slab of siltstone and represent a single population. A. AMF125019; B. AMF125020; C. AMF125021; D. AMF125022; E. AMF125023, pinnatifid leaf on left hand side intergrading with shorter pinnuled forms of the *D. odontopteroides* complex. Scale bar = 1 cm.

Figure 3. A-E. *Dicroidium odontopteroides* complex. Pinnate leaves with short pinnules. A. AMF125024; B. AMF125025; C. AMF125026; D. AMF125027; E. AMF125028. Scale bar = 1 cm.

Figure 4 A-G. *Dicroidium odontopteroides* complex. Pinnate leaves with short, variously rounded and inclined pinnae. A. AMF125029; B. AMF125030; C. AMF125031; D. AMF125032; E. AMF125033; F. AMF125034; G. AMF125035. Scale bar = 1 cm.

Figure 5 A-D. *Dicroidium odontopteroides* complex. Pinnate leaves forking into 3, 4 or 5 branches. A. AMF125036; B. AMF125037; C. AMF125038; D. AMF125039. Scale bar = 1 cm.

Figure 6. A. *Dicroidium odontopteroides* complex – an assemblage of double-forked leaves demonstrating size and shape variation. AMF125040. B. *Dicroidium dubium* complex – a double forked leaf. AMF125041. Scale bar = 1 cm.

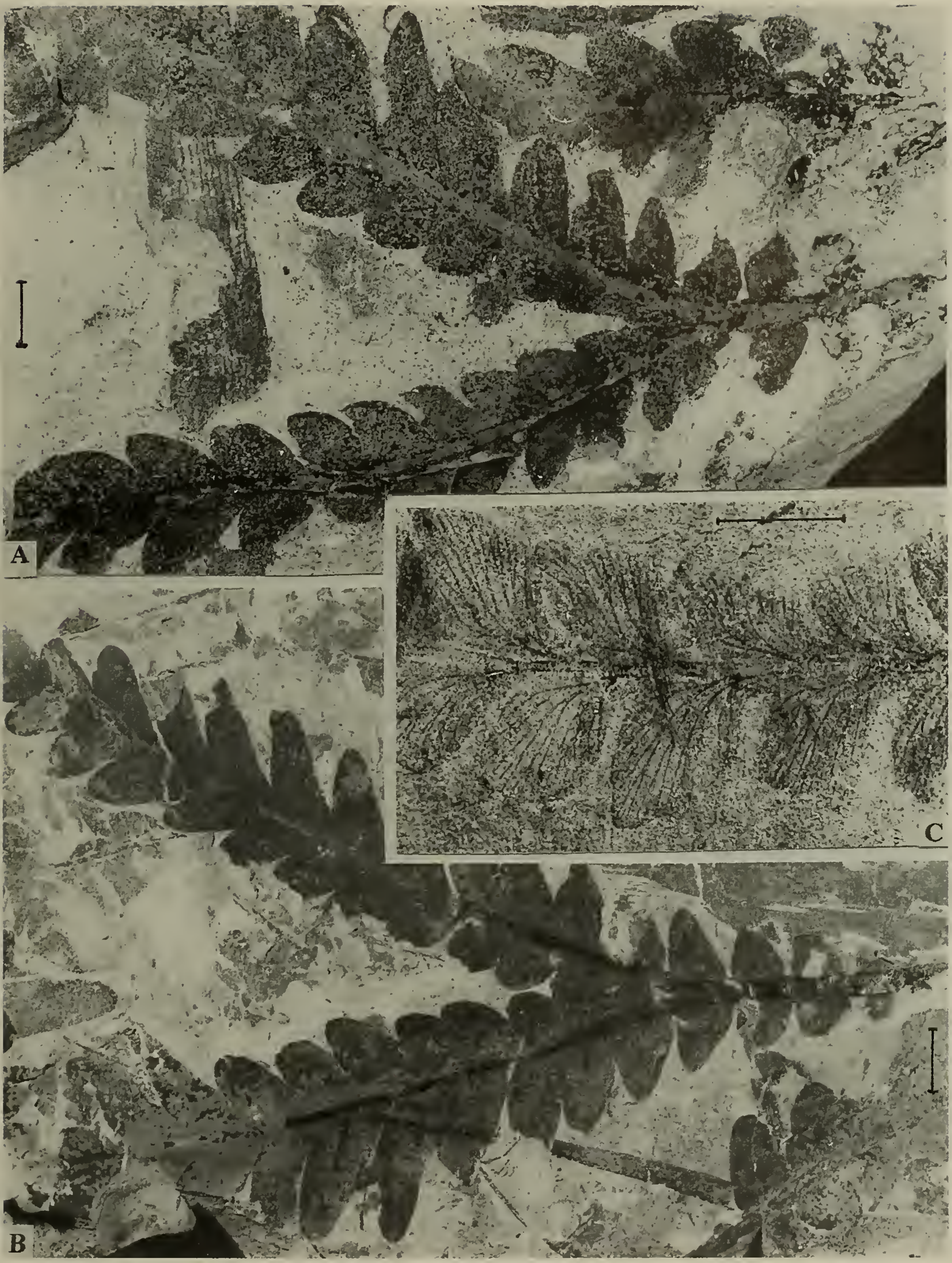

Figure 7. A-C. *Dicroidium odontopteroides* complex. Larger leaves with variously elongated pinnae. A. AMF125042; B. AMF125043. C. AMF125044, leaf showing 'odontopteroid' venation. Scale bar = 1 cm.

Figure 8. A. *Dicroidium odontopteroides* complex. The largest leaf in the complex. AMF125045. Scale bar = 1 cm.

Figure 9. A-C. *Dicroidium odontopteroides* complex. A, B. Forms approaching *Dicroidium lineatum* complex. A. AMF125046; B. AMF125047; C. AMF125048. Scale bar = 1 cm.

Figure 10. A,D,E. *Dicroidium odontopteroides* complex, approaching *Dicroidium lineatum* complex. A. Note portion of *Umkomasia sessilis* strobilus on lower right. AMF125049; D. AMF125050; E. AMF125051. B,C. *Dicroidium lineatum* complex. B. AMF125052; C. AMF125053. Scale bar = 1 cm.

Figure 11. A,B,D. *Dicroidium lineatum* complex. A. AMF125054; B. AMF125055; D. AMF125056. C. Intergrating form between *Dicroidium lineatum* complex and *Dicroidium dubium* complex. AMF125057. Scale bar = 1 cm.

Figure 12. A,D. Forms intergrading between *Dicroidium lineatum* complex and *Dicroidium dubium* complex. A. AMF125058; D. AMF125059. B,C. *Dicroidium lineatum* complex. B. AMF125060; C. AMF125061. Scale bar = 1 cm.

Figure 13. A-C. *Dicroidium dubium* complex showing range of pinna forms. A. AMF125062; B. AMF125063; C. AMF125064. Scale bar = 1 cm.

Figure 14. A-E. *Dicroidium dubium* complex. A. AMF125065; B. AMF125066; C. AMF125067; D. AMF125068; E. AMF125069. Scale bar = 1 cm.

Figure 15. A-D. *Dicroidium dubium* complex. A and D approaching *Dicroidium zuberi* complex. A. AMF125070; B. AMF125071; C. AMF125072; D. AMF125073. Scale bar = 1 cm.

Figure 16. A. *Dicroidium dubium* complex- large bipinnatifid form, AMF125074. B, C. *Dicroidium zuberi* complex. B. AMF125075; C. AMF125076. Scale bar = 1 cm.

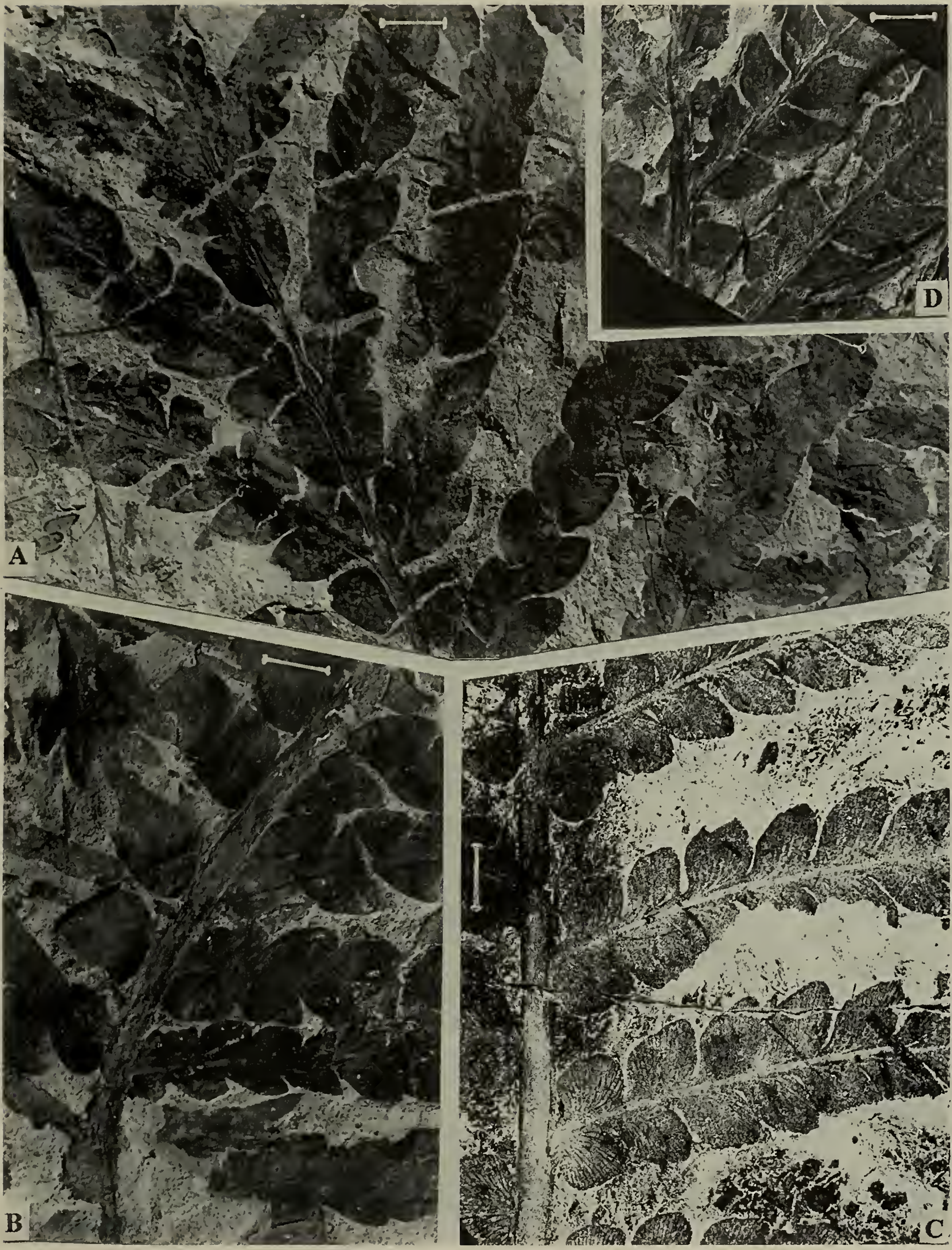

Figure 17. A-D. *Dicroidium zuberi* complex. A. AMF125077; B. AMF125078; C. AMF125079; D. AMF125080. Scale bar = 1 cm.

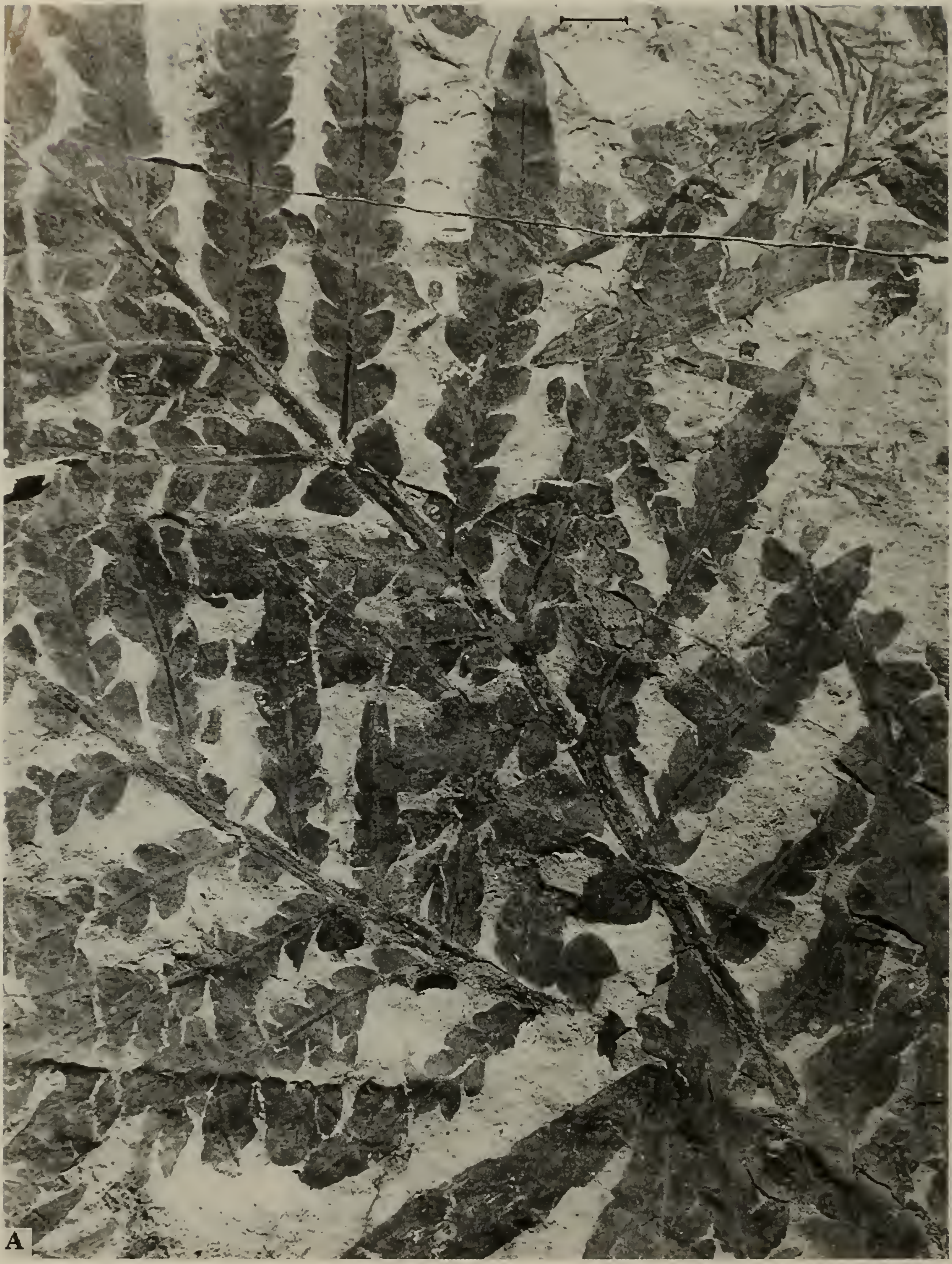

Figure 18. A. *Dicroidium zuberi* complex. AMF125081. Scale bar = 1 cm.

Figure 19. *Dicroidium elongatum* AMF 125082. Scale bar = 1 cm.

Figure 20. A. *Dicroidium elongatum* AMF125082. B. ?*Dicroidium nymboidense* sp. nov. AMF125083. C, D. *Dicroidium* sp. *A*. C. AMF125084; D. AMF125085. E. *Dicroidium* sp. *B*. AMF125086. Scale bar = 1 cm.

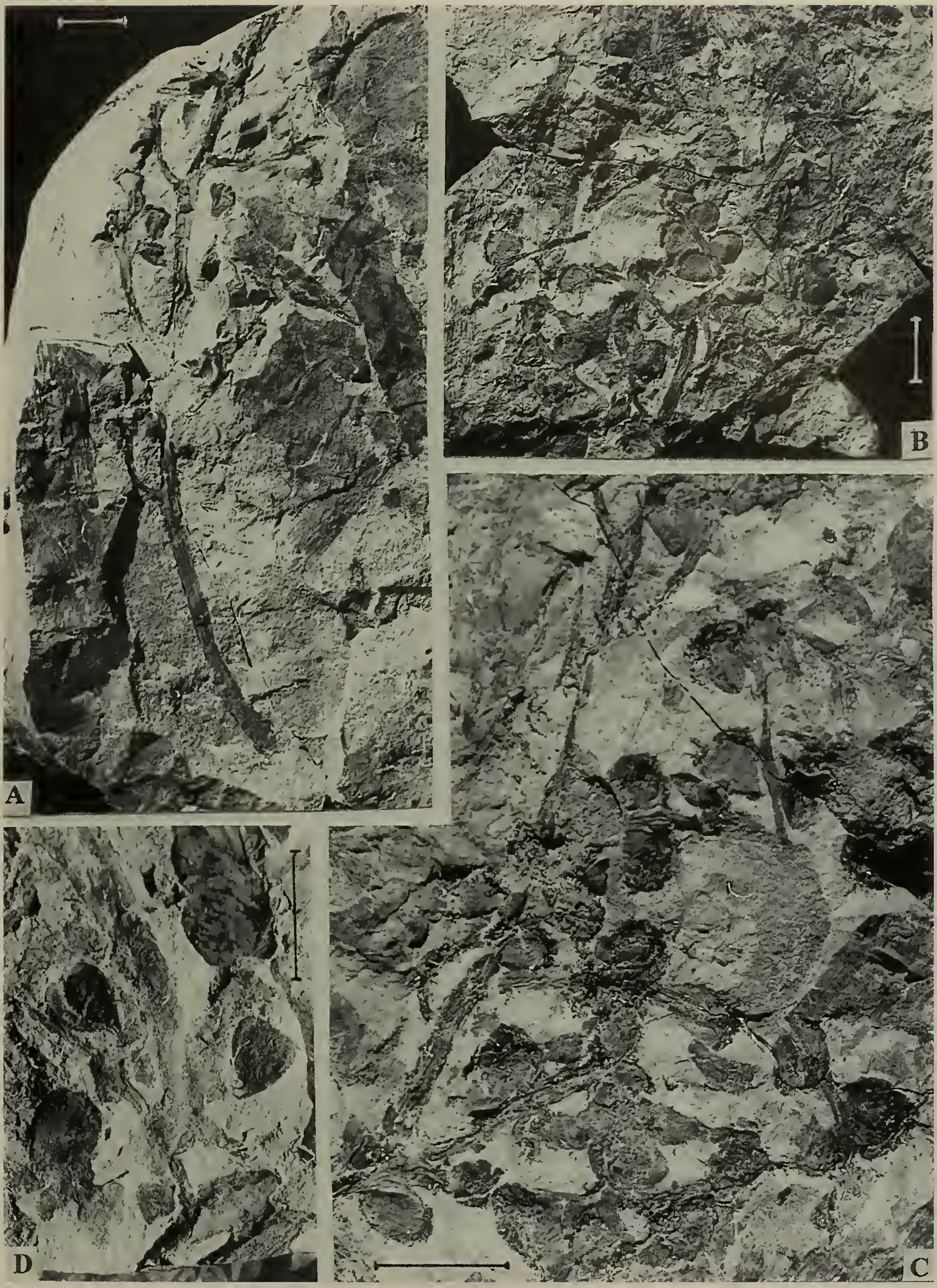

Figure 21. A. *Umkomasia distans.* Holotype. AMF63824. B, C. *Umkomasia sessilis.* B. Holotype AMF63831. C. AMF125087. D. Dispersed *Umkomasia* ovules showing bifid micropyle. AMF125088. Scale bar = 1 cm.

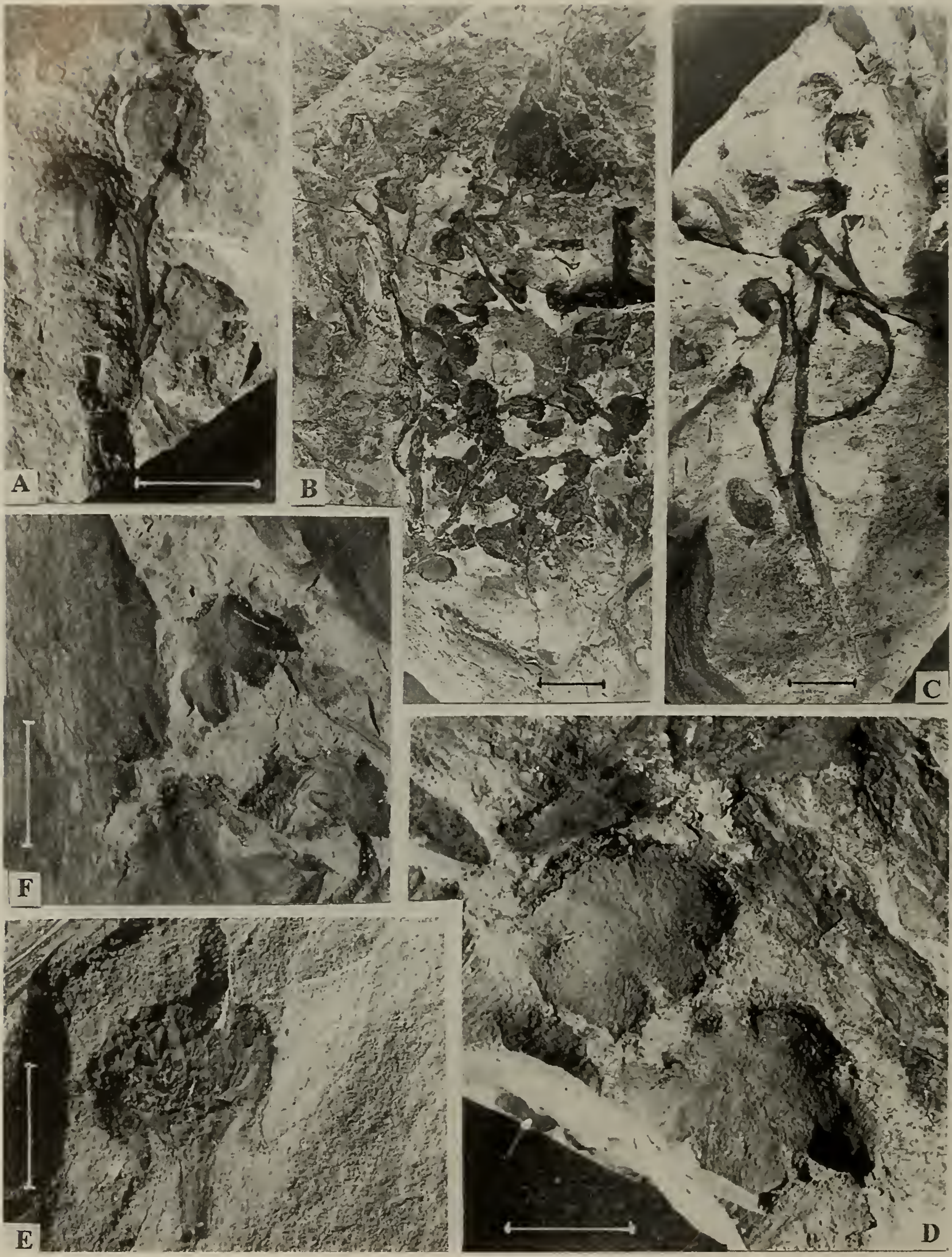

Figure 22. A-C. *Umkomasia* sp. strobili and cupules: A. *Umkomasia distans*. AMF125089. B. *Umkomasia sessilis*. AMF125090. C. *Umkomasia* sp. AMF125091. D-F. *Umkomasia* cupules: D. AMF125092; E. AMF125093; F. AMF125094. Scale bar = 1 cm.

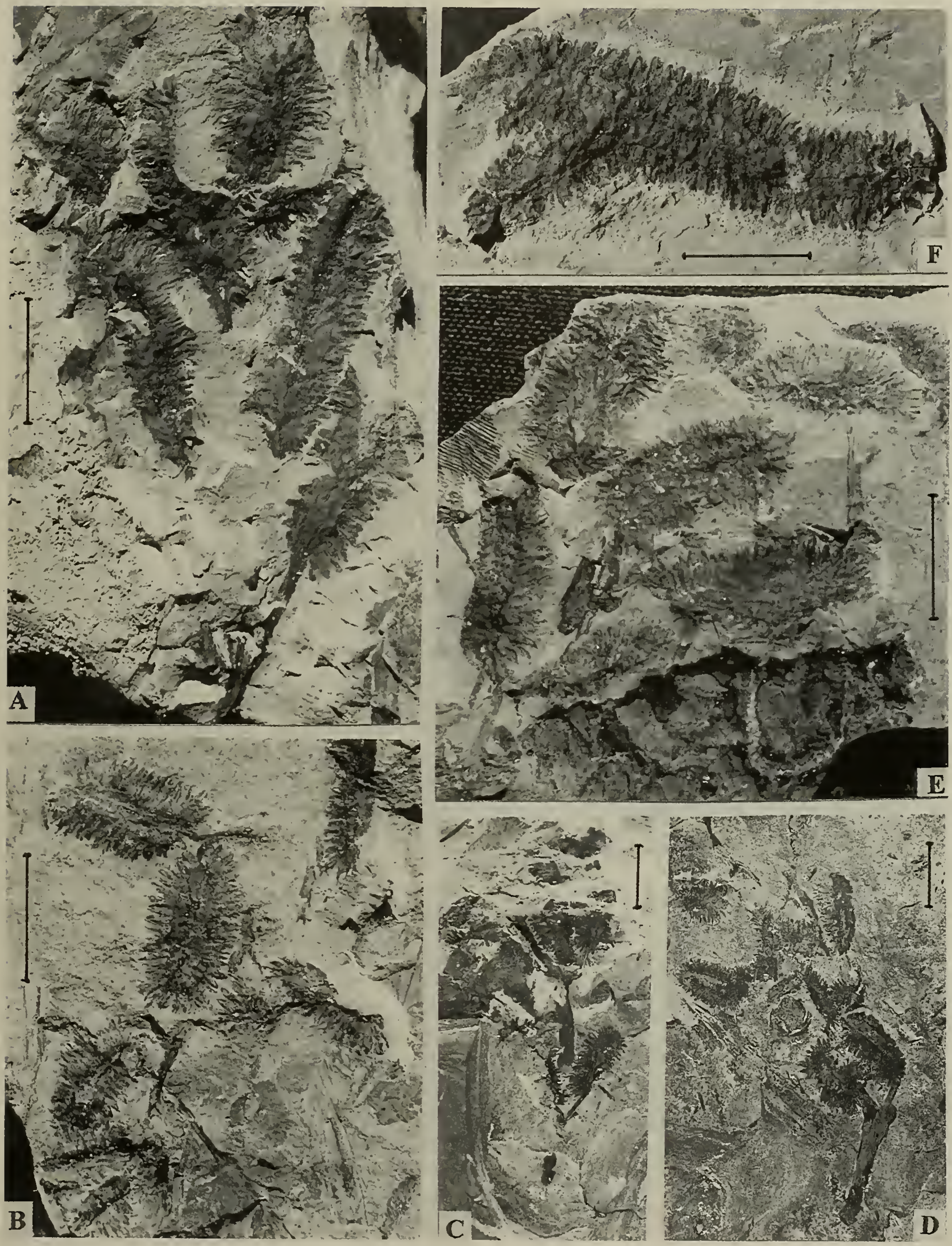

Figure 23. A-E. *Pteruchus* sp.cf. *P. matatimajor* microsporophylls. A. AMF125095; B. AMF125096; C. AMF125097; D. AMF125098; E. AMF125099; F. *Pteruchus* sp. A. AMF125100. Scale bar = 1 cm.

The Middle Triassic Megafossil Flora of the Basin Creek Formation, Nymboida Coal Measures, New South Wales, Australia. Part 5. The Genera *Lepidopteris, Kurtziana, Rochipteris* and *Walkomiopteris.*

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Holmes, W.B.K. and Anderson, H.M. (2005). The Middle Triassic megafossil flora of the Basin Creek Formation, Nymboida Coal Measures, New South Wales, Australia. Part 5. The genera *Lepidopteris, Kurtziana, Rochipteris* and *Walkomiopteris. Proceedings of the Linnean Society of New South Wales* **126**, 39-79.

Leaves attributed to the gymnosperm genera *Lepidopteris, Kurtziana* and *Rochipteris* and the leaf sedis incertae *Walkomiopteris eskensis* (Walkom) Holmes and Anderson gen. et comb. nov. are described from two quarries in the Basin Creek Formation of the Middle Triassic Nymboida Coal Measures. Based on extensive collections of leaves, the morpho-genera *Lepidopteris* and *Kurtziana* each reveal a wide range of variation. *Lepidopteris* is divided into three 'morpho-species complexes' with intergrading forms based on *L. madagascariensis*, *L. africana* and *L. stormbergensis* and a new species *L. dissitipinnula* apparently without links to the three complexes. The *Lepidopteris* fertile organs, *Peltaspermum* and *Antevsia* are present. *Kurtziana* is separated into two 'morpho-species complexes' based on *K. brandmayri* and *K. cacheutensis*. *Rochipteris* is a diverse genus but of very rare occurrence. Six new species are described; *R. obtriangulata* and *R. tubata* display a close-spaced spiral or whorled arrangement. Seven leaves of *R. incisa* have been examined. *R. sinuosa*, *R. pusilla* and *R. nymboidensis* are represented by single dispersed leaves. *Walkomiopteris eskensis* (Walkom) gen. et comb. nov. is redescribed from additional Nymboida material.

KEYWORDS: *Kurtziana*, *Lepidopteris,* Middle Triassic Flora, Nymboida Coal Measures, *Rochipteris*, *Walkomiopteris*.

INTRODUCTION

In this fifth part of a series describing the early middle Triassic Nymboida flora, leaves assigned to three gymnosperm genera: *Lepidodopteris* with some associated fertile organs, *Kurtziana*, *Rochipteris* and the new genus *Walkomiopteris* sedis incertae are illustrated and described.

Part 1 (Holmes 2000) of this series dealt with the Bryophyta and Sphenophyta, Part 2 (Holmes 2001) with the Filicophyta, Part 3 (Holmes 2003) with fern-like foliage and Part 4 (Holmes and Anderson in press) with the genus *Dicroidium* and its fertile organs *Umkomasia* and *Pteruchus*.

The material described below is based mainly on the collections made by the senior author and his family from two Nymboida quarries over a period of almost forty years. Details of the Coal Mine Quarry and the Reserve Quarry together with a summary of the geology of the Basin Creek Formation, the Nymboida Coal Measures and the Nymboida Sub-basin were provided in Holmes (2000).

METHODS

In living populations of extant plants there is often a large range of variation in leaf shape, e.g. juvenile, adult, shade, sun-leaves, etc. A preserved holotype in a herbarium seldom exhibits this range of variation. It is only through wide experience in the field that this variation can be recognised and appreciated. In the fossil record, leaves constitute the vast majority of preserved plant organs. Most early palaeobotanical taxonomy was based on very limited material in the field or a few museum specimens. Original diagnoses rarely acknowledged the variation that could occur in a 'natural' species. To compound the problem of separating fossil leaves into 'natural' species, the assemblages from one locality may represent vegetation from a range of habitats and growing through an unknown period of time. As in Part 4 of this series, which dealt with the highly variable morpho-genus *Dicroidium* (Holmes and Anderson in press), we address the problem of variability observed in the large collections of *Lepidopteris* and *Kurtziana* leaves by creating 'species complexes'. A 'species complex' includes leaves displaying a range of variation centred on a previously-described species. Intergrading forms often link the 'complexes'. The Selected References are of specimens we consider to represent a mid-range for each 'species complex'. Leaves illustrated in the Figures should enable comparisons to be made with material from other locations and horizons. Leaves in the genera *Rochipteris* and *Walkomiopteris* are represented respectively by ten and six specimens only, so are placed in morpho-species based on gross morphology of the material available.

At the Nymboida quarries most specimens are preserved as carbonaceous compressions in which the gross morphology is usually well-preserved. However, spores and cuticles have been destroyed by a tectonic heating event during the Cretaceous Period (Russel 1994).

Type and illustrated material is housed in the Australian Museum, Sydney. Some additional specimens are in the collections of the Geology Department, University of New England, Armidale, NSW, and the type of *Walkomiopteris eskensis* is housed in the collections of the Queensland Museum, Brisbane.

SYSTEMATIC PALAEOBOTANY

Ginkgoopsida S.V.Meyen 1987
Peltaspermales F. Nemejc 1968
Peltaspermaceae H.H. Thomas ex T.M. Harris 1937
Genus *Lepidopteris* Schimper 1869
Type species *Lepidopteris stutgardiensis* Schimper 1869

The proposal by Poort and Kerp (1990) to unite the leaves of *Lepidopteris 'natalensis'* with the ovulate organ *Peltaspermum thomasii*, which occur together at the Waterfall locality in the Molteno Formation (locality Umk111 of Anderson and Anderson 1983), in the 'natural genus' *Meyenopteris* is untenable. The leaf species *Lepidopteris stormbergensis* has priority over *L. natalensis*. An additional leaf and ovulate species have been described from the same Umk111 locality (Anderson and Anderson 2003). Until fruit, leaves and stems are found in organic connection, it is premature to erect a 'natural genus'. In accordance with ICBN (2001) Articles 1.2 the morpho-genus *Lepidopteris* should be retained for dispersed leaves and the morpho-genera *Peltaspermum* and *Antevsia* for the dispersed female and male organs respectively.

Leaves of the *Lepidopteris* genus occur in the Permian of the Northern Hemisphere. The first Gondwanan record is of *L. callipteroides*, a branched leaf form from the basal Narrabeen Group (earliest Triassic), of the Sydney Basin (Retallack 2002). This species apparently did not persist through to the Middle Triassic.For many Gondwanan *Lepidopteris* leaves the application of specific names has at times been questionable. Some species are known only from impressions while some, with better preservation have been described with cuticle information (Carpentier 1935; Townrow 1960, 1966; Baldoni 1972; Baldoni and de Cabrera 1977; Anderson and Anderson 1989). However, as noted by Townrow (1966), there are problems of identification of specimens both with or without cuticle. Rigby (1977) suggested reserving the name *L. stormbergensis* for all leaves lacking cuticle and *L. natalensis* and *L. madagascariensis* for those with preserved cuticle, while Retallack in Retallack et al. (1977) argued that the diverse range of leaves from the Cloughers Creek Formation in the Nymboida Coal Measures was best placed in *L. madagascariensis* on the basis of the thick leaf substance and mostly obtuse pinnules although no cuticle was present. We regard the Cloughers Creek leaves as being best placed in our '*L. stormbergensis*' and '*L. africana*' complexes.

In the Nymboida collections, *Lepidopteris* leaves are preserved on c. 3% of the catalogued slabs. While individual leaves may be identified on gross morphology with the types of *L. madagascariensis*, *L. africana* or *L. stormbergensis*, there are numerous intergrading forms that link these three 'species'. The same problem was noted by Holmes (1982) for the Benolong Flora where leaves of *L. stormbergensis*, *L. africana* and *L. mortonii* formed an intergrading series. Anderson and Anderson (1989) noted that at 11 of their 30 localities where both *L. africana* and *L. stormbergensis* were present, in most cases they formed an unbroken morphological range and were regarded as one palaeodeme. At the remaining 19 localities only one or other of the species was present.

As our collections of *Lepidopteris* have been made from the various sedimentary facies in the two Nymboida quarries they were probably sourced from differing vegetation types (Retallack 1977; Holmes 2000) and the *Lepidopteris* material may indeed belong to several true species each specific to one palaeodeme. However, on our present state of knowledge we must accept the collection as representing a single variable population sample. To enable the Basin Creek material to be compared with that from other localities, we place the *Lepidopteris* leaves in three 'species complexes' while noting the intergrading forms that link the complexes. A distinct leaf-type with widely-spaced pinnules and no intergrading links with the three 'complexes' is erected as a new morpho-species.A notable feature of *Lepidopteris* leaves, with and without preserved cuticle, is the usual presence of 'blisters' or 'lumps' on the main and/or pinna rachis (Townrow 1956, 1960, 1966; Holmes 1982; Anderson and Anderson 1989, 2003) resulting from a proliferation of epidermal cells around trichome bases. Townrow (1960) noted that in a population of leaves attributed to *Lepidopteris stormbergensis* there was a series of leaves with rachises ranging from smooth to markedly blistered. Lumps or blisters are not apparent on the Nymboida *Lepidopteris* leaves but some do have punctate or striate rachises. Townrow (1966) described the main rachis of *Lepidopteris* as having a wing and with dorsally-attached pinnae. A rachis wing is not evident in the Nymboida material and the pinnae appear to be attached laterally.

'Lepidopteris madagascariensis complex', based on *L. madagascariensis* Carpentier 1935

Figures 1A,B; 2A–C

Selected references

1935 *Lepidopteris madagascariensis*, Carpentier, Pl.3, figs 3,4
1936 *Lepidopteris madagascariensis*, Carpentier, Pl.5, fig.4
1966 *Lepidopteris madagascariensis*, Townrow, Text fig. 1E, Pl.1, fig.1
1975 *Lepidopteris madagascariensis*, Flint and Gould, Pl.2, figs 1, 2
1979 *Lepidopteris madagascariensis*, Holmes and Ash, Fig.5.6, 5.7
1983 *Lepidopteris madagascariensis*, Retallack, Fig.5A
1995 *Lepidopteris madagascariensis*, Retallack, Figs 2A, 3A

Description

Small broad-elliptic bipinnate leaves c. 50–150 mm long, c. 40–70 mm wide, leaf base truncate, main rachis 2 mm wide and tapering to apex, sometimes punctate and/or longitudinally striate; c. 20 pairs of well-separated opposite to alternate straight or arching pinnae, decreasing in length basally and apically, are attached at a high angle towards base, at c. 60° in mid-frond and more acute apically; pinnules not conjoined, oblong, truncate to obtusely rounded, attached by whole base to pinna rachis at c. 60°; first basiscopic pinnule decurrent; with one or more pinnules attached laterally on rachis between pinnae. These latter are generally referred to as 'zwischerfiedern'.

Material

AMF126801–3, AMF126805 Coal Mine Quarry; AMF126804 Reserve Quarry

Discussion.

Typical leaves of this complex are not as numerous as those in the '*L. africana* complex'. It is distinguished from the two complexes below by the oblong pinnules with obtuse apices separated to the base on the mid-frond pinnae and by the higher angle of attachment of these pinnules. However, basal and apical pinnae often have coalescing to coherent pinnules. Figure 2A shows, on the same slab, portions of several leaves that obviously represent a single population (palaeodeme). One leaf is typically '*madagascariensis*' while others show pinnules becoming coherent and grading into the form of the '*L. africana* complex'.

'*Lepidopteris africana* complex', based on *L. africana* (Du Toit 1927) Holmes 1982

Figures 2D; 3A,B; 4A,B; 5A,B

Selected references.

1927 *Callipteridium africana*, Du Toit, Pl.27
1944 *Callipteridium argentinum*, Frenguelli, Pl.1, figs 1,2
1965 *Lepidopteris stormbergensis*, Hill et al., Pl.T6, fig.1
1977 *Lepidopteris madagascariensis*, Retallack et al., fig.9D
1982 *Lepidopteris africana*, Holmes, Figs 8C, 8D
1983 *Lepidopteris africana*, Anderson and Anderson, Pl.13, fig.1
1989 *Lepidopteris africana*, Anderson and Anderson, p.92, figs 1–3, Pl.13, figs 1–10, Pl.43, figs 1–16

1998 *Lepidopteris madagascariensis*, Gnaedinger and Herbst, figs 14a–c
2001 *Lepidopteris madagascariensis*, Gnaedinger and Herbst, fig. 11a
2003 *Lepidopteris africana*, Anderson and Anderson, p.157, fig.1

Description

Small to medium-sized bipinnatifid leaves 120–>170 mm long, 25–70 mm wide, with a truncate leaf-base 4 mm wide, tapering gradually to apex; pinnae closely spaced, longest at 2/3 of leaf length where attached at c. 45° to main rachis, apically the pinnae decrease in length and become more acute, basally the pinnae have a higher angle of attachment, become shorter, with rounded apices and entire to undulate margins; pinnae with coherent pinnules forming a serrate margin; the basiscopic base of the pinnae strongly decurrent along the main rachis to the acroscopic base of the pinna below, leaving no space for zwischerfiedern.

Material

AMF126806 Reserve Quarry; AMF126807–12 Coal Mine Quarry

Discussion

The leaves illustrated in Figures 3A,B and 4A were exposed on one bedding plane and surely represent a single population (palaeodeme). Figure 4B shows another bedding plane assemblage showing many '*L. africana*' leaves of varying size together with a fragment of a leaf with larger separated pinnules that approaches '*L. stormbergensis*' but with pinnules coalescing distally and apically. Large leaves with pinnules becoming less coherent form intergrading links between '*L. africana* complex' and '*L. stormbergensis* complex' (Figs 5C; 6A,B; 7A).

'*Lepidopteris stormbergensis* complex', based on *L. stormbergensis* (Seward 1903) Townrow 1956
Figures 6C; 8A,B; 9A,B

Selected references.

1903 *Callipteridium stormbergense*, Seward, Pl.7, fig.5
1927 *Lepidopteris stuttgardensis*, Du Toit, Pl.28
1956 *Lepidopteris stormbergensis*, Townrow, figs 1A, 1B
1960 *Lepidopteris stormbergensis*, Townrow, text figs 5C,F,G
1965 *Lepidopteris stormbergensis*, Hill et al., Pl.T6, fig.2
1975 *Lepidopteris stormbergensis*, Flint and Gould, Pl.2, figs 1,2
1977 *Lepidopteris madagascariensis*, Retallack et al. fig. 9A
1982 *Lepidopteris stormbergensis*, Holmes, fig.8A
1983 *Lepidopteris stormbergensis*, Anderson and Anderson, Pl.13, figs 2,3
1989 *Lepidopteris stormbergensis*, Anderson and Anderson, p.93, figs 1–4, Pl.26, figs 2–5, Pl. 27, figs 1–4
1998 *Lepidopteris madagascariensis*, Gnaedinger and Herbst, Pl.3, fig.h, figs 14a,c
2003 *Lepidopteris stormbergensis*, Anderson and Anderson, p.157, fig.4

Description.

Large bipinnate to tripinnatifid leaves, broad-oblanceolate, to 400 mm long and 180 mm wide. Rachis to 5 mm in mid-frond; pinnae opposite to alternate, longer pinnae at mid-frond attached at c. 80°–45°, closely spaced to overlapping on larger and tripinnatifid fronds; pinnules on mid-portion of mid-pinnae 6–25 mm long, 3–6 mm wide, tapering to acute or narrow obtuse apex, margin entire to serrate. On the largest leaves (Figures 8B, 9B) the pinnules are deeply lobed to pinnatisect. First basiscopic pinnule attached to base of pinna rachis or strongly decurrent on main rachis; nil to three zwischerfiedern between pinnae on main rachis in mid-portion of leaf.

Material

AMF126816–21, AMF126851, all Coal Mine Quarry.

Discussion

The leaf assemblage preserved on AMF126819, AMF126821 and AMF126851 are parts and counterparts from the same bedding plane and show fronds ranging from bipinnatifid to tripinnatifid and include the largest in the collection (Figure 8B). Zwischerfiedern preserved on the tripinnatifid leaf (Figure 9B) are broad-elongate with a lobed margin. This assemblage demonstrates the large range of variation even within a single population.

Lepidopteris dissitipinnula Holmes and Anderson
sp. nov.
Figures 10A–C

Diagnosis

A medium-sized *Lepidopteris* leaf with sub-opposite slightly arching to recurved pinnae; pinnules well-spaced, elongated-linear with obtuse apices, margins parallel, entire to lobate.

Description

Based on two specimens, both with base and apices missing, length preserved to 110 mm; rachis at base of preserved section 2–3 mm wide; pinnae elongate-lanceolate, alternate, c. 12 mm apart, longest pinnae to 65 mm. Specimen AMF113528 (Figures 10A,B) has slightly recurved pinnae attached at c. 60°; AMF126823 (Figure 10C) has lower pinnae attached at right angles and arching slightly and the upper pinnae attached at c. 60°, but this may also be an artifact of preservation. Pinnules opposite, spaced c. one pinnule width apart, decurrent, straight or slightly arched, apex rounded-obtuse, margins parallel, entire to lobate. Pinnules are longest at mid-pinna, to 12 mm long, 1–2 mm wide, decreasing in length basally and apically, basal basiscopic pinnule not decurrent on main rachis; one or two pairs of narrow, elongate zwischerfiedern on main rachis between pinnae.

Holotype

AMF113528 and counterpart AMF113529 Australian Museum, Sydney.

Type Locality

Coal Mine Quarry. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF126823 Coal Mine Quarry.

Name Derivation

dissitus, (Lat.) *well-spaced*; referring to the well-separated pinnules.

Discussion

Lepidopteris dissitipinnula differs from all described *Lepidopteris* morpho-species by the elongated-linear well-spaced pinnules and perhaps is closest to *L. madagascariensis*. However, at Nymboida there are no intergrading forms to link *L. dissitipinnula* with the '*L. madagascariensis* complex'. Both specimens of *L. dissitipinnula* are preserved in a white sandstone matrix in contrast to all other *Lepidopteris*, material which is preserved in black to grey shales and mudstones, thus suggesting they were sourced from ecologically separated populations.

Genus *Peltaspermum* Harris 1937

Type species. *Peltaspermum rotula* Harris 1937

The ovulate organ *Peltaspermum* had a wide Laurasian and Gondwanan distribution. It is generally accepted as the female fructification of the plant that bore *Lepidopteris* leaves (Thomas 1933; Harris 1937, Townrow 1960, Anderson and Anderson 2003). Poort and Kerp (1990) revised the *Peltaspermum* - *Lepidopteris* association based on western and central European material. They proposed the creation of the 'natural genus' *Peltaspermum* by emending the diagnosis of *Peltaspermum* to include *Lepidopteris* leaves. As *Peltaspermum* and *Lepidopteris* are both morpho-taxa under ICBN (2001) Article 1.2 a new name would be required for a 'natural genus'.

Despite the large number of *Lepidopteris* leaves in the Nymboida collection, *Peltaspermum* is known only from two incomplete strobili and two detached peltate discs.

Peltaspermum* cf *monodiscum Anderson and Anderson 2003

Figures 11A–E

Description

Based on two incomplete strobili. Axes as preserved c. 40 mm and 25 mm long, 2 mm wide; six discs c. 4 mm in diameter attached at 8–10 mm intervals singly or opposite each other by a peduncle c. 5 mm long. Each disc is c. 6 mm wide, pendant, showing four decurved, linear lobes 4 mm long, 1 mm wide. As the fossils represent sideways-compressed discs, the number of lobes in life would be eight. A single detached disc and its counterpart (Figures 11D, E) show a radially symmetrical disc c. 9 mm in diameter with ten linear lobes around the circumference, each c. 1 mm wide and 2–3 mm long. A possible peduncle protrudes from one side of the disc but its point of attachment is uncertain.

Material

AMF126824–6 Coal Mine Quarry.

Discussion

Anderson and Anderson (2003 pp. 152, 158, 159) described and illustrated from the Molteno Formation of South Africa some reasonably intact strobili with lobed receptacles attached singly to an axis. They refer to the receptacles as 'discs'. Their specimens have 11 or 12 lobes. The Nymboida material with 8–10 lobes is otherwise closely comparable.

***Peltaspermum* sp A**

Figures 11F,G

Description

One specimen and its counterpart shows a spherical disc 18 mm in diameter with c. 13–14 broad obtuse lobes around the margin, each separated by an incision or ridge reaching from half to two thirds distance to the centre, which is marked with an irregular-shaped abcission scar c.1.8 mm in diameter.

Material

AMF126852 and counterpart AMF126853 Coal Mine Quarry.

Discussion

Peltaspermum sp. A differs from *P. cf. monodiscum* by the larger size and less incised lobes. Similar detached peltoid discs have a wide distribution and are associated in Gondwana deposits with the peltaspermaceous genera *Lepidopteris* (Harris 1937; Holmes and Ash 1979; Holmes 1982, Anderson and Anderson 2003) and *Scytophyllum* (Zamuner et al. 1999) and in the Northern Hemisphere with *Lepidopteris, Tatarina, Comia, Pachydermophyllum* and *Scytophyllum* (Meyen 1987). This isolated Nymboida disc has insufficient diagnostic features to place it in any known species.

Genus *Antevsia* Harris 1937
Type species *Antevsia zeilleri* (Nathorst) Harris 1937

Antevsia strobili have been recorded from Rhaetic localities in Sweden (Antevs 1914), Greenland (Harris 1932) and from the Upper Triassic Molteno Formation of South Africa (Anderson and Anderson 2003). *Antevsia* has been linked at those occurrences with *Lepidopteris* on the basis of similar cuticles (Antevs 1914; Harris 1932) and the same distinctive blistering on the strobilis axes as on the foliar rachises (Anderson and Anderson 2003).

***Antevsia* sp A**
Figures 12A–C

Description

Two fragmentary specimens from Nymboida show clusters of sessile sporangia. AMF 126828 (Figures 12A,B) is a portion of a strobilis overlain by a fragment of a *Sphenobaiera* leaf. The curved axis, which may be an almost complete branch, is c. 60 mm long, 1.4 mm wide at the base and tapering to 0.8 mm distally. Blisters are not apparent. Clusters of up to five irregularly elliptic microsporangia to 2 mm long are scattered along the branch axis. It is not certain whether the sporangial sacs are sessile or shortly pedunculate. The second specimen, AMF126829 (Figure 12C), is of two detached clusters and some scattered sporangial sacs to 5 mm long. Associated with the sporangia is a detached oval-shaped indeterminate ovule.

Material

AMF126828 and AMF126829 Coal Mine Quarry.

Discussion

Antevsia sp. A has some similarities to *Antevsia mazenodensis* Anderson and Anderson (2003) from the Molteno Formation but the preservation is not sufficient for specific determination.

Order Matatiellales Anderson and Anderson 2003
Family Matatiellaceae
Genus *Kurtziana* Frenguelli 1942a
Type species *Kurtziana cacheutensis* (Kurtz) Frenguelli 1942a

In frond morphology and venation pattern *Kurtziana* differs from all other Gondwanan ginkgoopsid leaf genera. Based on mutual occurrence Anderson and Anderson (2003) have given a Grade 2 affiliation of *Kurtziana* leaves with the female strobilis *Matatiella* and placed the leaf genus in the Order Matatiellales.

The genus *Kurtziana* was erected by Frenguelli (1942a) for unforked pinnate leaves with pinnae having contracted pinna bases and attached laterally to the rachis. These leaves from Argentina were first illustrated by Kurtz (1921, Pl. 16, figs 198–199) as *Danea cacheutensis*. A second species, *K. brandmayri* Frenguelli (1944), was erected for leaves in which the pinnae were closely-spaced to imbricate and attached to the dorsal surface of the rachis. A very large leaf from Chile has recently been described as *K. paipotensis* Herbst and Gnaedinger (2002). *Kurtziana* leaves with preserved cuticle have been described by Petriella and Arondo (1982) and Artabe et al. (1991). Herbst and Gnaedinger (2002) have erected the new morpho-genus *Alicurana* for *Kurtziana* leaves with preserved cuticle. To date *Kurtziana* is best known from South American localities.

Kurtziana leaves are also known from South Africa (Du Toit 1927; Anderson and Anderson 1983). In a recent publication, Anderson and Anderson (2003) illustrated five species and noted the presence of 16 species, generally of rare occurrence, from the Molteno Formation of South Africa. From Australia, the leaf '*Thinnfeldia*' *eskensis* Walkom (1928) is here transferred to *Kurtziana cacheutensis*.

Kurtziana leaves are represented on c. 2% of catalogued slabs in the Nymboida collection. They are preserved as impressions and due to their probable coriaceous nature, only rare examples show clear details of the venation. One bedding plane in Coal Mine Quarry was covered with complete *Kurtziana* leaves, perhaps indicating an autumnal deposit of a deciduous plant. The Nymboida specimens exhibit a range of variation in frond and pinna size, in pinna shape and manner of attachment to the rachis. Some agree closely with the types of *K. cacheutensis* and *K. brandmayri*, others with *K. cacheutensis* sensu Herbst and Gnaedinger (2002) from collections that also exhibited a variation in leaf form. We have separated the leaves into two 'species complexes' based essentially on the perceived dorsal or lateral attachment of the pinnae to the rachis, a feature sometimes obscured by the manner of preservation.

'*Kurtziana brandmayri* complex', based on *Kurtziana brandmayri* Frenguelli 1944

Figures 13A,B

Selected references.

1944 *Kurtziana brandmayri*, Frenguelli, text fig. 2, Pl. 4, figs 1,2
1965 "*Thinnfeldia*" *eskensis*, Hill et al., Pl. T5, figs 3,4
1991 *Kurtziana brandmayri*, Artabe et al., Fig. 1
2002 *Kurtziana brandmayri*, Herbst and Gnaedinger, figs 2A–C; Pl. 4, figs D–F

Description.

Kurtziana leaves with elliptic lamina, to c. 240 mm long, 100 mm wide, rachis to 4 mm wide, decreasing in width distally, striate and sometimes punctate, with expanded leaf base. Pinnae opposite to sub-opposite, closely spaced to overlapping, sessile, with contracted auriculate or caudate bases, attached to the dorsal surface of the rachis; oblong to linear-ovate or tapering to rounded-acute apex, 40–50 mm long, 8–18 mm wide; basal pinnae broad-oval, increasing in length to mid-portion of leaf. Angle of attachment of pinnae to rachis, from 80° near base to 75° in mid-leaf and becoming more acute apically.

Material

AMF126830–1 Coal Mine Quarry.

Discussion

The Nymboida specimen on Figure 13A agrees closely with the type of *K. brandmayri* (Frenguelli 1944, Pl. 4, figs 1,2) by the closely-spaced to overlapping oblong pinnae with obtuse apices and constricted auriculate bases attached at a high angle to the rachis. Other specimens with a dorsal attachment of the pinnae and contracted bases differ by the pinnae being not so closely-spaced, with a more acute angle of attachment and by the tapering of the pinnae to a narrower rounded-acute apex.

'*Kurtziana cacheutensis* complex', based on *Kurtziana cacheutensis* (Kurtz) Frenguelli 1942a

Figures 14A–D;15A; 16A,B; 17A

Selected references

1928 '*Thinnfeldia*' *eskensis*, Walkom, Pl.27, fig. 2, Pl.28, fig. 1
1942a *Kurtziana cacheutensis* (Kurtz) Frenguelli, Pl.1
1975 *Dicroidium eskense*, Flint and Gould, Pl. 3, fig. 3
1983 *Kurtziana cacheutensis*, Anderson and Anderson, Pl. 9, fig. 5
2002 *Kurtziana cacheutensis*, Herbst and Gnaedinger, Fig.1A–H

Description

Elliptic-ovate pinnate leaves, 100–200 mm long, 40–100 mm wide, pinnae attached laterally to a striated rachis 2–3 mm wide, opposite to alternate, separated by c. one pinna width, linear-oblong, tapering slightly to acute rounded apex, to 45 mm long, 9 mm wide in midleaf, pinna acroscopic base contracting to midvein, basiscopic base contracted or variously decurrent. Pinnae inserted laterally on rachis at c. 60° becoming more acute apically.

Material

AMF126832–9 Coal Mine Quarry.

Dicussion

This is the most common form of *Kurtziana* at Nymboida, sometimes forming monotypic autumnal deposits on a bedding plane (Figure 15A) or associated with leaves of the conifer *Rissikia* (Figure 16B). This species complex is separated from the *K. brandmayri* complex by the lateral attachment of the pinnae to the rachis. Some specimens (Figures 15A and 16A) are closely comparable with the illustrated type of *K. cacheutensis* (Frenguelli 1942a). However, there is a wide range of variation in leaf size, pinna size and shape, spacing and inclination of pinnae to rachis and the degree of contraction or decurrence of the basiscopic base of the pinna. Figure 17A shows two leaves with extreme decurrent pinnae in the apical half of the leaf and contacted pinnae in the basal half. Some leaves (e.g. Figure 14C) appear to have pinnae with asymmetrical laminae but this is probably an artifact of preservation caused by the inrolling of one edge of the pinna.

Order Petriellales Taylor et al. 1994
Family Kannaskoppiaceae Anderson and Anderson 2003
Genus *Rochipteris* Herbst, Troncoso and Gnaedinger 2001
Type species *Rochipteris lacerata* (Arber) Herbst et al. 2001

Flabellate leaves with anastomosing venation have long been known from the Triassic floras of Gondwana. Early records were from Queensland by Carruthers (1872, as *Cyclopteris cuneata*) and Shirley (1898, as *Sagenopteris cuneata*), from Tasmania by Johnston (1888 as *Cyclopteris australis*), from Victoria by Chapman (1927 as *Psygmophyllum fergusoni*), from New Zealand by Arber (1917 as *Chiropteris lacerata*), from Chile by Solms-Laubach (1899 as *Chiropteris copiapensis*) and South Africa by Seward (1903 as *Chiropteris cuneata*). Other records may be found in Etheridge (1895), Chapman and Cookson (1926), Frenguelli (1942b, 1944) and Menendez (1951). The taxonomy of the group was confused. Retallack (1980) discussed the problems and subsequently recognised six species under an emended diagnosis for *Ginkgophytopsis*. Herbst et al. (2001) made a detailed analysis of the significant differences between the essentially Northern Hemisphere genus *Ginkgophytopsis* and the Gondwanan leaves. For the Gondwanan leaves they erected the new genus *Rochipteris* in which was included five species based mainly on material from Argentina and Chile. Barone-Nugent et al. (2003) redescribed leaves from the Leigh Creek Coal Measures of South Australia and the Ipswich Coal Measures of Queensland as *Rochipteris etheridgei* and *R. ginkgoides* respectively.

In a recent significant publication on Gondwana Triassic gymnosperms, Anderson and Anderson (2003) described some remarkable material from the Molteno Formation of South Africa. Included were specimens of flabellate leaves with anastomosing venation and with either female or male fructifications attached to a stem. The female strobili were described as *Kannaskoppia*, the male strobili as *Kannaskoppianthus* and the attached leaves as *Kannaskoppifolia*. Under ICBN (2001), Article 1.2, detached leaves are regarded as morpho-taxa and thus *Rochipteris* Herbst et al. (2001) has priority over *Kannaskoppifolia*. *Kannaskoppifolia* may be used as a genus for leaves attached to a stem.

Anderson and Anderson (2003) regarded *Kannaskoppiafolia* (= *Rochipteris*) as "ubiquitous, diverse, long-lived, relatively frequent but generally lacking in abundance". Barone-Nugent et al. (2003) noted that their *Rochipteris* species appeared to be distinct between separate basins and showed a strong degree of intra-Gondwanic provincialism in marked contrast to *Dicroidium* species, which are widely distributed throughout Gondwana (Retallack 1977; Anderson and Anderson, 1983; Holmes and Anderson, in press). Forty years of collecting at Nymboida has yielded the six new species described below, but, with the exception of two species, the others are represented by a single specimen only. The species have been distinguished on leaf morphology, venation pattern and vein density. Two of the Nymboida species are important in demonstrating, for some species at least, that *Rochipteris* foliage is inserted on the stem either as a close spiral or a terminal whorl.

Rochipteris obtriangulata Holmes and Anderson sp. nov.
Figures 18A–C; 19A–D

Diagnosis

Obtriangular lamina, lateral and distal margins straight, entire; angle of divergence 20°–30°; veins sub-parallel, dichotomising c. five times and anastomosing twice in distal half of lamina; leaves attached in close spirals or whorls of eight to ten; venation density 20–25 per 10 mm.

Description

Based on a slab bearing impressions of one almost complete whorl and two incomplete whorls plus other isolated single leaves. The leaves are obtriangular, c. 40 mm long and 12 mm wide at the truncate apex. Lamina diverging from the acute sessile base at c. 20°–30°. Lateral margins straight, leaf apex truncate, straight and entire. Veins sub-parallel, dichotomising close to base and then four or five more times to leaf apex; from c. mid-lamina the veins converge and conjoin with adjacent veins, usually twice, to form irregular linear elliptical areoles; venation density at 2/3 leaf length 20–25 per 10 mm. Foliage arranged in a close spiral or a terminal whorl of 8–10 leaves but leaf bases and stem not visible.

Holotype

AMF126840 and counterpart AMF126842;

paratype AMF126841, Australian Museum, Sydney.

Type Locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Name Derivation

obtriangulata (Lat.), *obtriangular*; referring to the reversed triangular leaf form.

Discussion

The straight lateral margins of the expanding laminae and the truncate entire apex differentiates *R. obtriangulata* from all other described *Rochipteris* species. They are close to the leaves from the Molteno Formation locality Umk111 illustrated as *Kannaskoppifolia* sp. C by Anderson and Anderson (2003).

Rochipteris tubata Holmes and Anderson sp. nov.

Figures 20A–C

Diagnosis

Vase-shaped lamina, lateral margins concave, distal margin convex-rounded, entire; angle of divergence at base 15° increasing to 60°–90° apically; veins sub-parallel, dichotomising from near base, anastomosing in distal 2/3 of lamina. Foliage in a close spiral or whorl of c. 7 leaves; vein density 20–25 per 10 mm.

Description

Based on one almost complete whorl of seven leaves. Lamina vase-shaped; leaves to 30 mm long, 19 mm wide, rising from an attenuated base at c. 15° and expanding distally in a curve to 60°–90°. Lateral margins concave, apical margin convex-rounded, slightly undulate. Venation sub-parallel, dichotomising c. five times from near base and anastomosing in distal 1/3 of lamina. Seven leaves apparently attached in a close spiral or terminal whorl but leaf bases and stem not visible. Density of veins c. 20–25 per 10 mm.

Holotype

AMF126843 Australian Museum, Sydney.

Type Locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Name Derivation

tubata (Lat.), *trumpet*; referring to the expanding outline of the leaf lamina.

Discussion

Rochipteris tubata is arranged in a whorl of leaves similar to *R. obtriangularis* but unfortunately in neither species is their attachment to the stem visible. The venation in both species is similar but *R. tubata* is separated on the basis of the expanding lamina and rounded leaf apex. The whorls of leaves in *R. obtriangulata* and *R. tubata* suggest a strong relationship to the stems bearing *Kannaskoppia* fruits (Anderson and Anderson 2003), which have small groups or whorls of leaves attached at intervals along the slender stem.

Rochipteris incisa Holmes and Anderson sp. nov.

Figures 21A–C; 22A

Diagnosis

Medium-sized cuneate leaf with arched apex; one to six deep incisions to below mid-lamina forming sub-parallel lobes; venation parallel, occasionally bifurcating or conjoining to form extremely elongated linear areoles. Venation density c. 18 per 10 mm.

Description

Based on three leaves from the Reserve Quarry and eight from Coal Mine Quarry. Leaf cuneate, to 115 mm long and c. 70 mm wide; lateral margins straight or slightly concave, diverging from base at c. 45°–80°; apex semicircular, deeply incised to form a number of linear segments from 8–10 mm wide, incisions reaching to 1/3 distance from the lamina base, distal ends of segments entire or with a minor incision. Veins fine and parallel, dichotomising and occasionally conjoining to form extremely elongated areoles; density of veins c. 18 per 10 mm.

Holotype

AMF126844 Australian Museum, Sydney.

Type Locality

Reserve Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures.

Other Material

AMF126827, 126862, Reserve Quarry; AMF126863–66, Coal Mine Quarry.

Name Derivation

incisa, (Lat.), *incised*, referring to the regularly incised distal margin.

Discussion

Rochipteris incisa shows some similarities in shape and outline to the attached Molteno leaves *Kannaskoppifolia vincularis* (Anderson and Anderson 2003). It differs from all other Nymboida *Rochipteris* spp in lamina shape and venation details. *Rochipteris etheridgei* (Arber) Barone-Nugent et al. is similar in outline to *R. incisa* but differs by its larger size, the less-deeply incised segments, the sinuate venation and by the presence of a broadly-flared leaf base (Barone-Nugent et al. 2003, fig. 3B, Pl. 1, figs 2–5).

On the same slab and adjacent to the holotype of *R. incisa* is a smaller spathulate leaf with venation similar to that of *R. incisa* (Figure 21B). This spathulate form is similar to leaves from Argentina that have been placed in *Rochipteris cuneata* (Carruthers) Herbst et al. 2001. That species was based on *Cyclopteris cuneata* Carruthers (1872), a poorly preserved leaf fragment with both apex and base missing. We believe that our spathulate leaf may belong to the same population as *R. incisa* and perhaps represents a juvenile or immature stage of development.

Rochipteris sinuosa Holmes and Anderson sp. nov.

Figures 23A–C

Diagnosis

A small flabellate leaf, diverging at c. 45° from short expanded leaf base; divided into two major segments by a deep incision; one segment again divided by a shallower incision; veins radiating from base, sinuous, approaching and diverging from each other, occasionally dichotomising but rarely anastomosing. Vein density c. 18 per 10 mm.

Description

Based on a single leaf with apical margin missing. Leaf as preserved, 42 mm long, 25 mm wide; flabellate, expanding at c. 45° from a short flared leaf base 4 mm wide. Lamina divided into two major segments by a medial incision commencing at c. 12 mm from the leaf base; the left segment is again divided by a narrow incision commencing at 18 mm from the base. The lamina lateral margins are slightly concave, the apical margin is missing. Veins run in a sub-sinuous manner parallel to the lateral margins, dichotomising occasionally, approaching and diverging from each other but rarely forming a true anastomosis. The apparent areoles are elongate-elliptic. Vein density in the upper portion of the lamina c. 18 per 10 mm.

Holotype

AMF126845 Australian Museum, Sydney.

Type Locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Name Derivation

sinuosa (Lat.) *sinuous*; referring to the venation.

Discussion

The gross morphology, sub-sinuous venation and paucity of anastomoses distinguishes this leaf from other Nymboida *Rochipteris* species. *Rochipteris sinuosa* closely resembles the specimens from the Llantenes Formation of Argentina attributed to *Chiropteris copiapensis* Steinmann and Solms by Menendez (1951, Pl.3, figs 1–4). However, those specimens have been synonymised with *Rochipteris lacerata* (Arber) as a new combination by Herbst et al. (2001). *Rochipteris lacerata* was described originally from New Zealand by Arber (1917) as *Chiropteris lacerata* and after detailed discussion by Retallack (1980, 1983) was transferred to the genus *Ginkgophytopsis*. *Rochipteris lacerata* sensu Herbst et al. (2001) is larger than *R. sinuosa*, is deeply incised into several parallel-sided segments and has straight parallel venation that dichotomises and anastomoses to form long areoles. *Rochipteris copiapensis* (Solms-Laubach) sensu Herbst et al. (2001) is a large leaf divided into two equal segments with straight, bifurcating and anastomosing venation. In outline and venation pattern, *R. sinuosa* differs from the ten illustrated but undescribed *Kannaskoppifolia* = *Rochipteris* leaves from the Molteno Formation (Anderson and Anderson 2003).

Rochipteris nymboidensis Holmes and Anderson sp. nov.

Figures 24A–D

Diagnosis

A small cuneate leaf, lateral margins concave, apical margin convex, entire; venation dense, straight and parallel, dichotomising, very rarely anastomosing; vein density c. 30–35 per 10 mm.

Description

Based on a single specimen. A cuneate leaf 63 mm long, with leaf base missing, 50 mm wide at the entire to slightly undulate apex. Angle of divergence from base c. 25°, increasing to 90° at lamina apex. Venation very fine, parallel, straight, dichotomising and very rarely anastomosing. Density of veins across mid-upper portion of lamina c. 30–35 per 10 mm.

Holotype

AMF126846 Australian Museum, Sydney.

Type Locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures.

Name Derivation

nymboidensis, referring to the Type Locality.

Discussion

The entire leaf with very dense venation with only rare cross connections distinguishes this leaf from all other described species of *Rochipteris*. *Rochipteris nymboidensis* is similar in outline but differs by the denser venation and fewer anastomoses from the undescribed *Kannaskoppifolia* sp. *D* of Anderson and Anderson (2003).

Rochipteris pusilla Holmes and Anderson sp. nov.

Figures 25A–C

Diagnosis

A very small cuneate leaf, lateral margins slightly convex, apex entire to undulate; venation dichotomising to five times from base, becoming more dense apically, conjoining to form linear areoles in apical half of lamina; in upper 2/3 of lamina venation density c. 21 per 10 mm.

Description

Based on a single almost complete leaf and its counterpart. Lamina narrow cuneate, 20 mm long, 14 mm wide; leaf base truncate 1.5 mm wide, diverging at ca. 45°, lateral margins entire, slightly convex; apex entire to slightly undulate. Two veins enter the base of the lamina, each bifurcates five or six times to terminate at distal margin. In the distal 1/3 of the lamina adjacent veins sometimes conjoin to form elliptic areoles, which become shorter and narrower towards the leaf apex; vein density across the upper 2/3 of the lamina is c. 21 per 10 mm.

Holotype

AMF126854 and counterpart AMF126855; Australian Museum, Sydney.

Type Locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures.

Name Derivation

pusilla, (Lat.), *very small*; this being the smallest *Rochipteris* species as yet described.

Discussion

The previously-described smallest leaf, *Rochipteris tasmanica* (Walkom) comb. nov., differs from *R. pusillia* by its larger size, the lamina expanding more widely and with a sparser, more open network of veins with a density of c. 10 per 10 mm (Walkom 1925) The venation of *R. pusilla* is somewhat similar to that in the small but less diverging leaves illustrated as *Kannaskoppifolia* sp. A and *K.* sp. B by Anderson and Anderson (2003) from the Molteno Formation of South Africa.

Sedis Incertae

Genus *Walkomiopteris* Holmes and Anderson gen. nov.

Walkomiopteris eskensis (Walkom) gen. et comb. nov.

Figures 26A–F

Type species *Sphenopteris eskensis* Walkom 1928, Pl.16,3; text fig.4

Combined diagnosis

Small wedge-shaped to semi-circular leaves apparently arranged in pairs, axis unknown; proximal portion of lamina contracted to petiole-like base; primary vein thick at base, dichotomising up to three times to form sparse radiating veins to lamina apical margin.

Description

Based on the type specimen of Walkom (1928) and four additional specimens from the Nymboida quarries. The individual leaves are conjoined into pairs; 17–30 mm long, 15–20 mm wide, wedge-shaped to semicircular, margin entire or variously shallowly-lobed; contracted into a petiole-like base to 5 mm long; a stout midvein enters the base of the lamina and soon dichotomises up to three times, with the fine venules radiating distally; c. 16 vein endings around lamina apical margin. Walkom's specimen from the Esk Beds of Queensland (Figure 26A) shows a cluster of eight irregularly-arranged but not connected leaves, the best preserved leaf is c. 20 mm long, 15 mm wide with fine radiating and dichotomising veins. The Nymboida material is larger, to 30 mm x 20 mm. On two specimens

(Figures 26B,C,D) leaves are conjoined into pairs while AMF113490 (Figure 26F) suggests a whorled arrangement but no axis or stem is preserved. While cuticle is not preserved, specimen AMF113492 shows an impression of cellular structure of rounded thick-walled cells and elongated rectangular cells along the veins (Figure 27C).

Material

Type specimen F1729 Queensland Museum, Brisbane, from railway cutting near Ottaba railway station. AMF113440, Coal Mine Quarry; AMF113491–3, AMF126848–9, Reserve Quarry Nymboida.

Name derivation

Walkomiopteris – for the eminent palaeobotanist and mentor to WBKH, Dr A.B. Walkom, who described the type material from the Esk Beds of Queensland.

Discussion

Walkom (1928) noted that this was a unique form of leaf in the Australian Mesozoic. In the mistaken belief that the leaves were pinnately connected to a rachis, he placed them in the genus *Sphenopteris*, a generalised leaf form with similar venation and which ranges from Devonian to Jurassic. *Sphenopteris* probably includes both ferns and pteridosperms (Boureau 1975). Anderson and Anderson (1983 Pl.9 figs 2,3) illustrated as foliage gen. B, sp. A, paired leaves with radiating venation similar to *Walkomiopteris*, but later collected material reveals that they belonged to a pinnate fern (Anderson and Anderson in press).

CONCLUSION

Leaves of the form-genera *Lepidopteris* and *Kurtziana* are preserved on 3% and 2% respectively of catalogued slabs in the Holmes Nymboida Collection. This has provided ample material to appreciate the range of variation existing in the genera. Recognising this variation we have placed the *Lepidopteris* leaves into three 'species complexes', each complex includes a range of variation with intergrading forms linking the complexes. One leaf form without links to the 'species complexes' is described as the new species *Lepidopteris dissitipinnula*. *Kurtziana* leaves are separated into two 'species complexes' based on the dorsal or lateral attachment of the pinnae; each complex includes leaves of variable morphology. Leaves of *Rochipteris* are rare, but on selected diagnostic features we have erected six new morpho-species. Due to the very limited material, the variation that may exist within a 'species' or the possibility of intergrading forms between 'species' is unknown. The leaf morphology of *Walkomiopteris eskensis* is unique among Gondwanan Triassic plants. This morpho-species probably represents the foliage of a gymnospermous plant.

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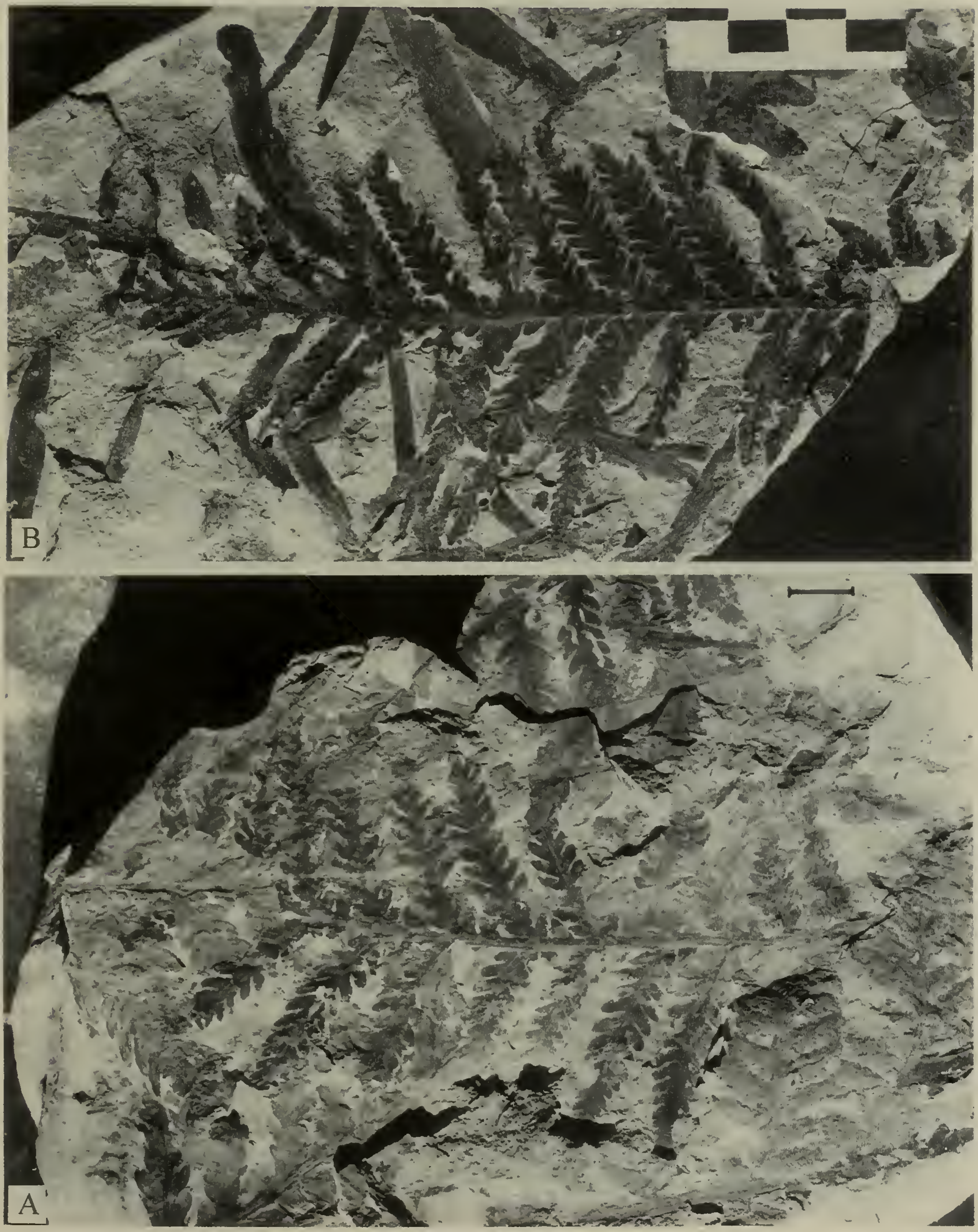

Figure 1, A,B. '*Lepidopteris madagascariensis* complex' A. AMF126801; B. AMF126802. Both Coal Mine Quarry. Scale bar = 1 cm

Figure 2. A. Centre leaf '*Lepidopteris madagascariensis* complex', other leaves intergrading with '*Lepidopteris africana* complex'. AMF126803, Coal Mine Quarry. B,C. '*Lepidopteris madagascariensis* complex'. B. AMF126804, Reserve Quarry. C. AMF126805, Coal Mine Quarry. D. Leaves grading to '*L. africana* complex'. AMF126806, Reserve Quarry. Scale bar = 1 cm.

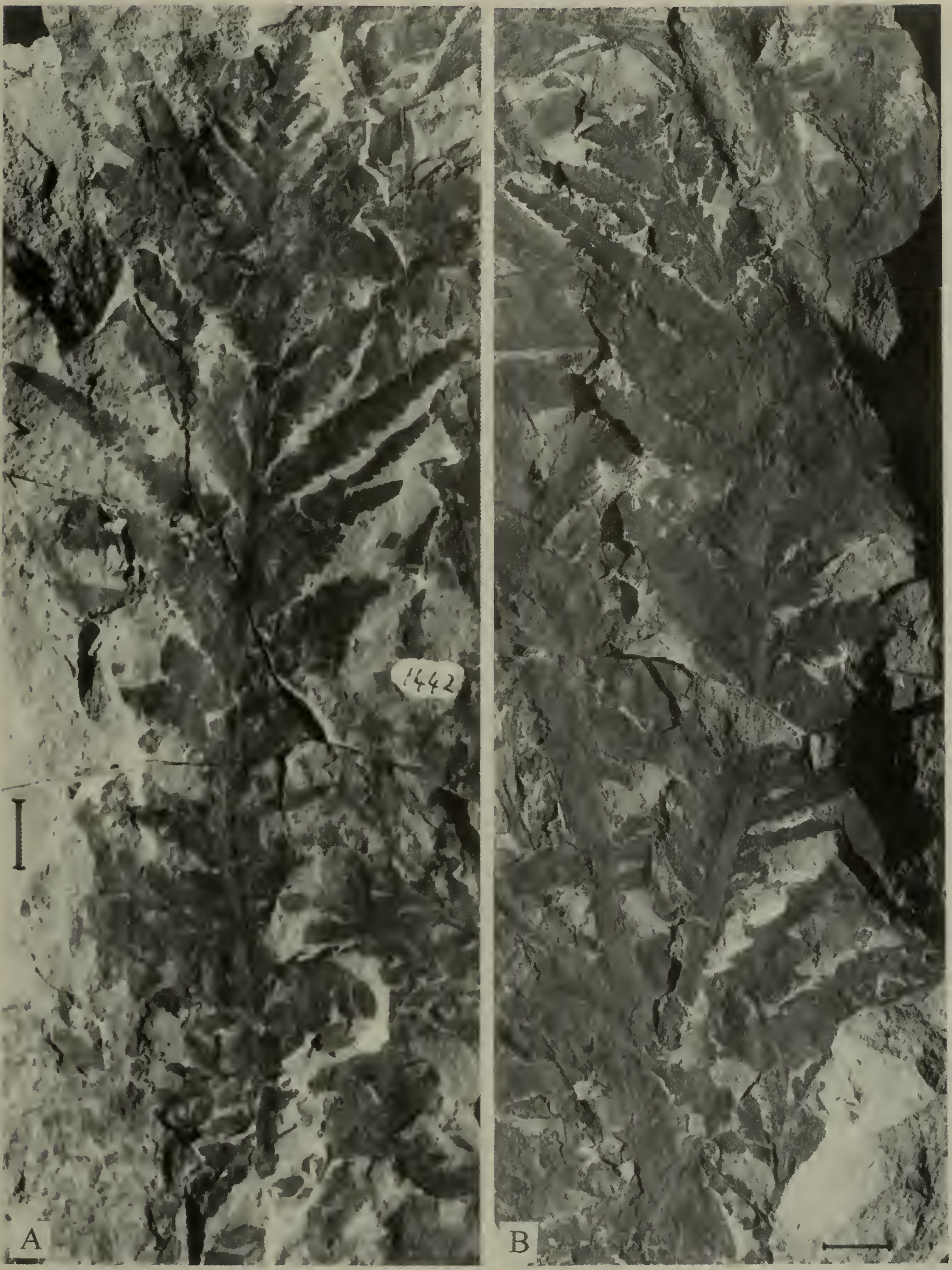

Figure 3. A,B. '*Lepidopteris africana* complex'. A. AMF126807. B. AMF126808. Both Coal Mine Quarry. Scale bar = 1 cm.

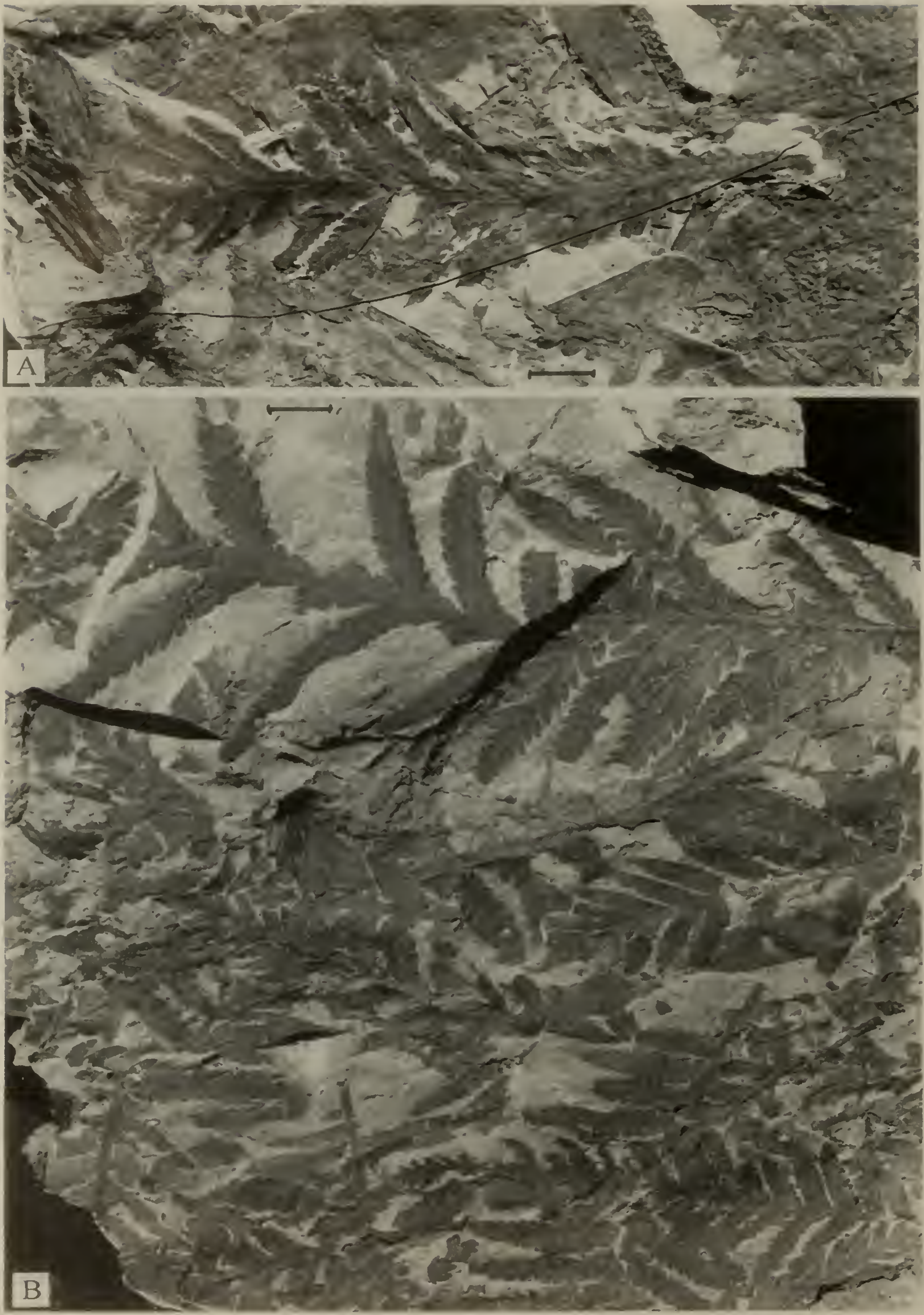

Figure 4. A. '*Lepidopteris africana* complex'. AMF126809. B. '*L. africana* complex', leaf at top right '*L. stormbergensis* complex'. AMF12806810. Both Coal Mine Quarry. Scale bar = 1 cm.

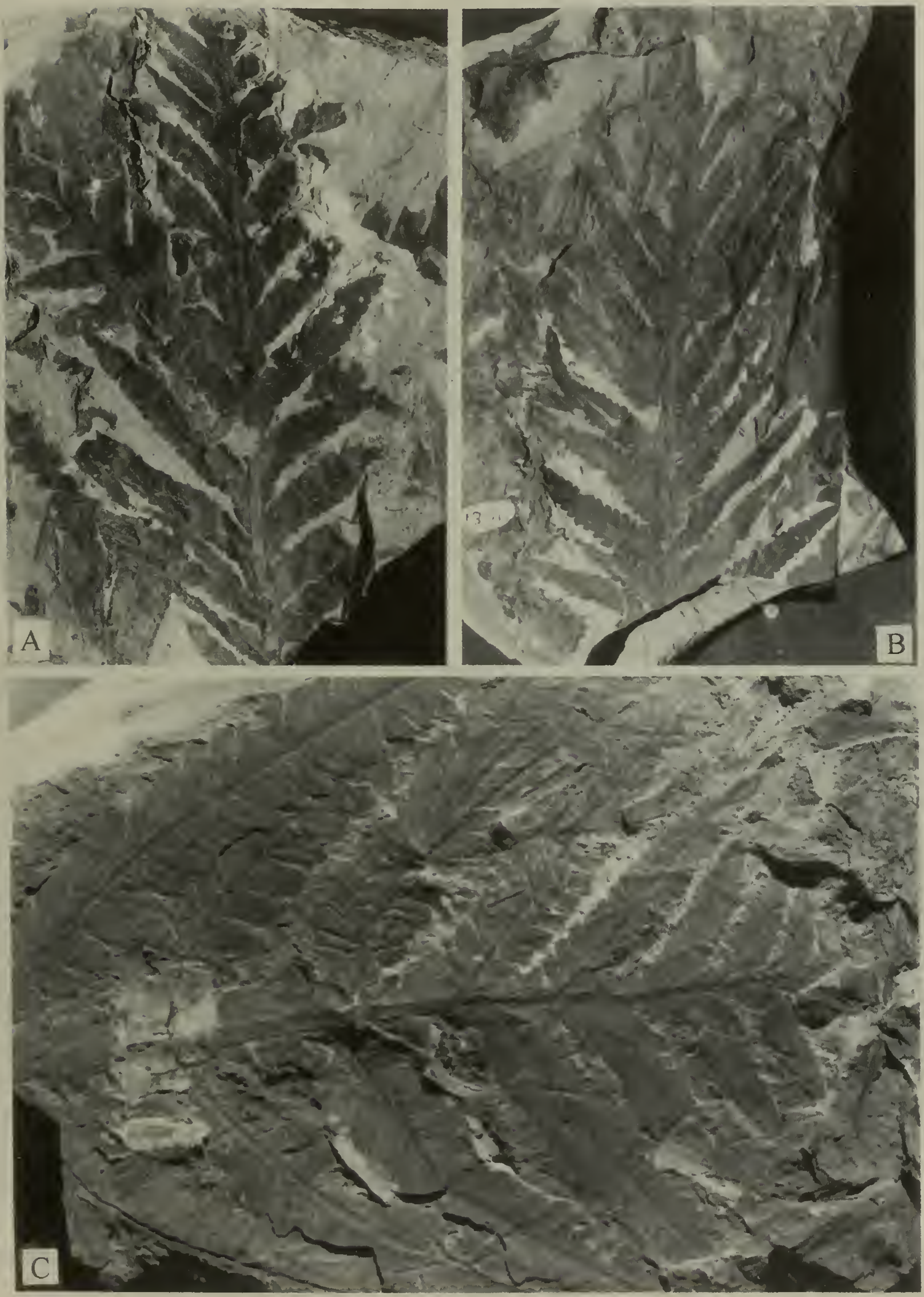

Figure 5. A,B. '*Lepidopteris africana* complex'. A. AMF126811. B. AMF126812. C. '*L. stormbergensis* complex'. AMF126813. All from Coal Mine Quarry. Scale bar = 1 cm.

Figure 6. A,B. '*Lepidopteris africana* complex' intergrading with '*L. stormbergensis* complex'. A. AMF126814, Reserve Quarry. B. AMF126815, Coal Mine Quarry. C. Small complete leaf of '*L. stormbergensis* complex'. AMF126816, Coal Mine Quarry. Scale bar = 1 cm.

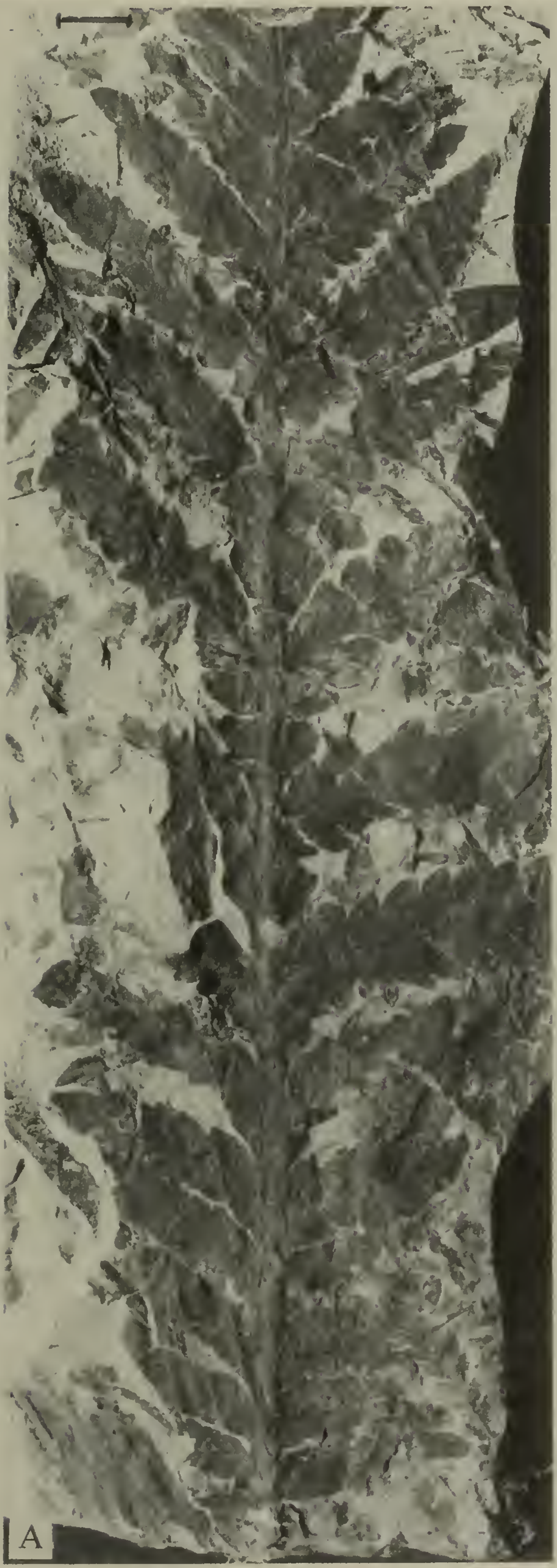

Figure 7. A. Intergrading form between '*L. africana* complex' and '*L. stormbergensis* complex'. AMF126817, Coal Mine Quarry. Scale bar = 1 cm.

Figure 8. A,B. '*Lepidopteris stormbergensis* complex'. A. AMF126818. B. AMF126819. Both from Coal Mine Quarry. Scale bar = 1 cm.

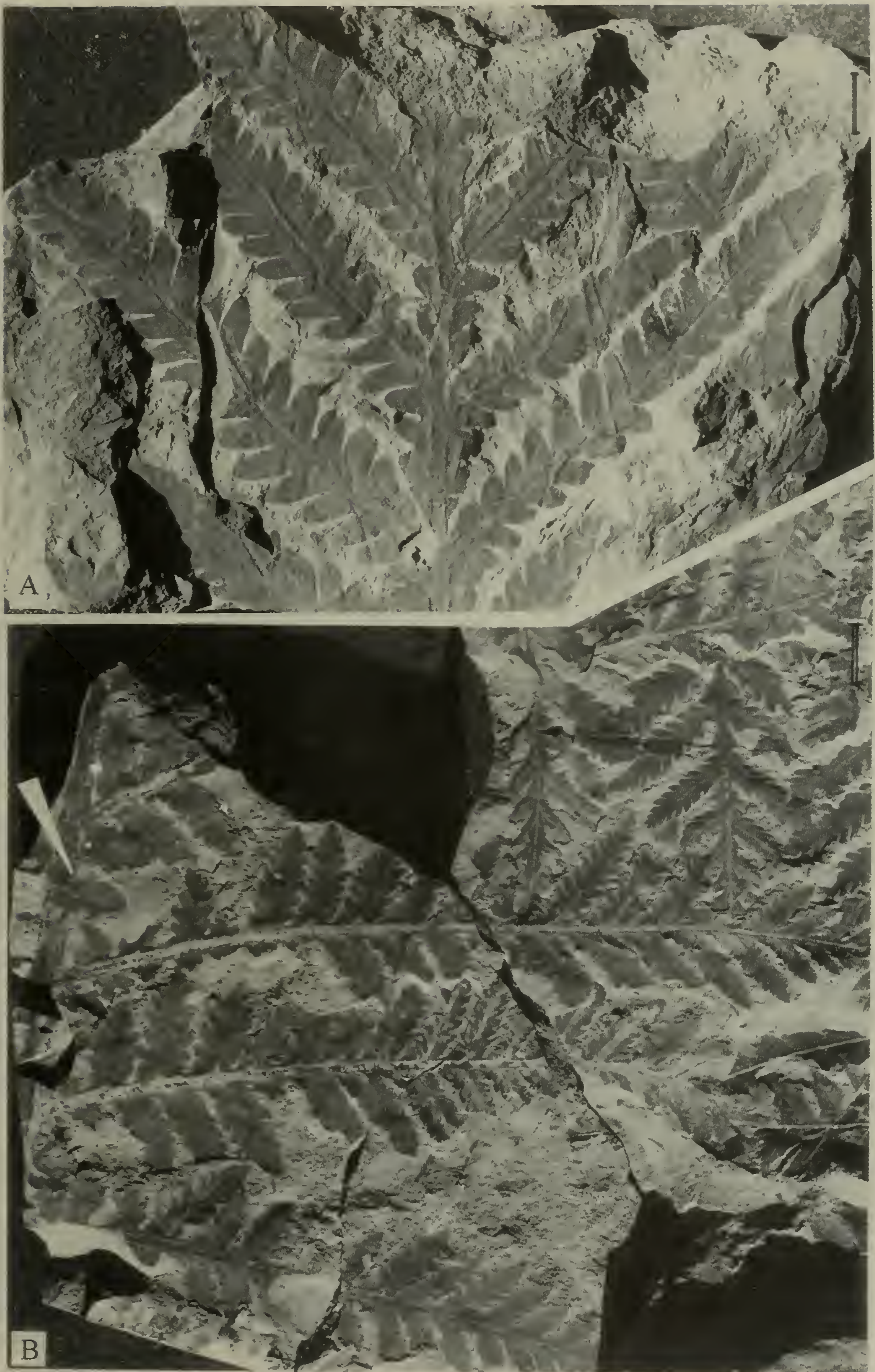

Figure 9. A,B. '*Lepidopteris stormbergensis* complex'. A. AMF126820. B. AMF126851, lobed zwisherfiedern arrowed. Both from Coal Mine Quarry. Scale bar = 1 cm.

Figure 10. A-C. *Lepidopteris dissitipinnula* sp. nov. A, B. AMF113528. Holotype. C. AMF126823. Both from Coal Mine Quarry. Scale bar = 1 cm.

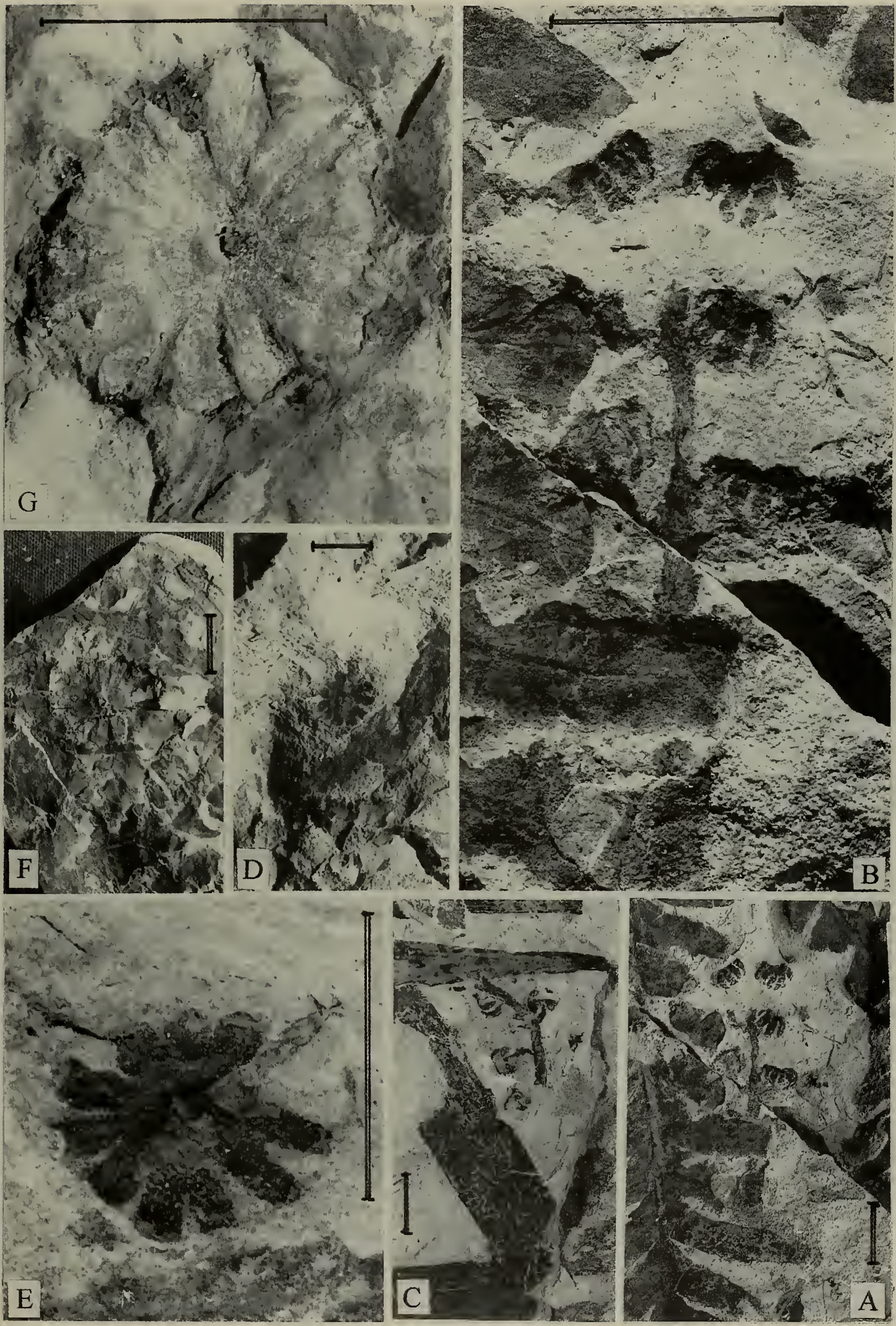

Figure 11. A-E. *Peltaspermum* cf *monodiscum*. A,B. AMF126824. C. AMF126825. D,E. AMF126826. F,G. *Peltaspermum* sp. A. AMF126852. All from Coal Mine Quarry. Scale bar = 1 cm.

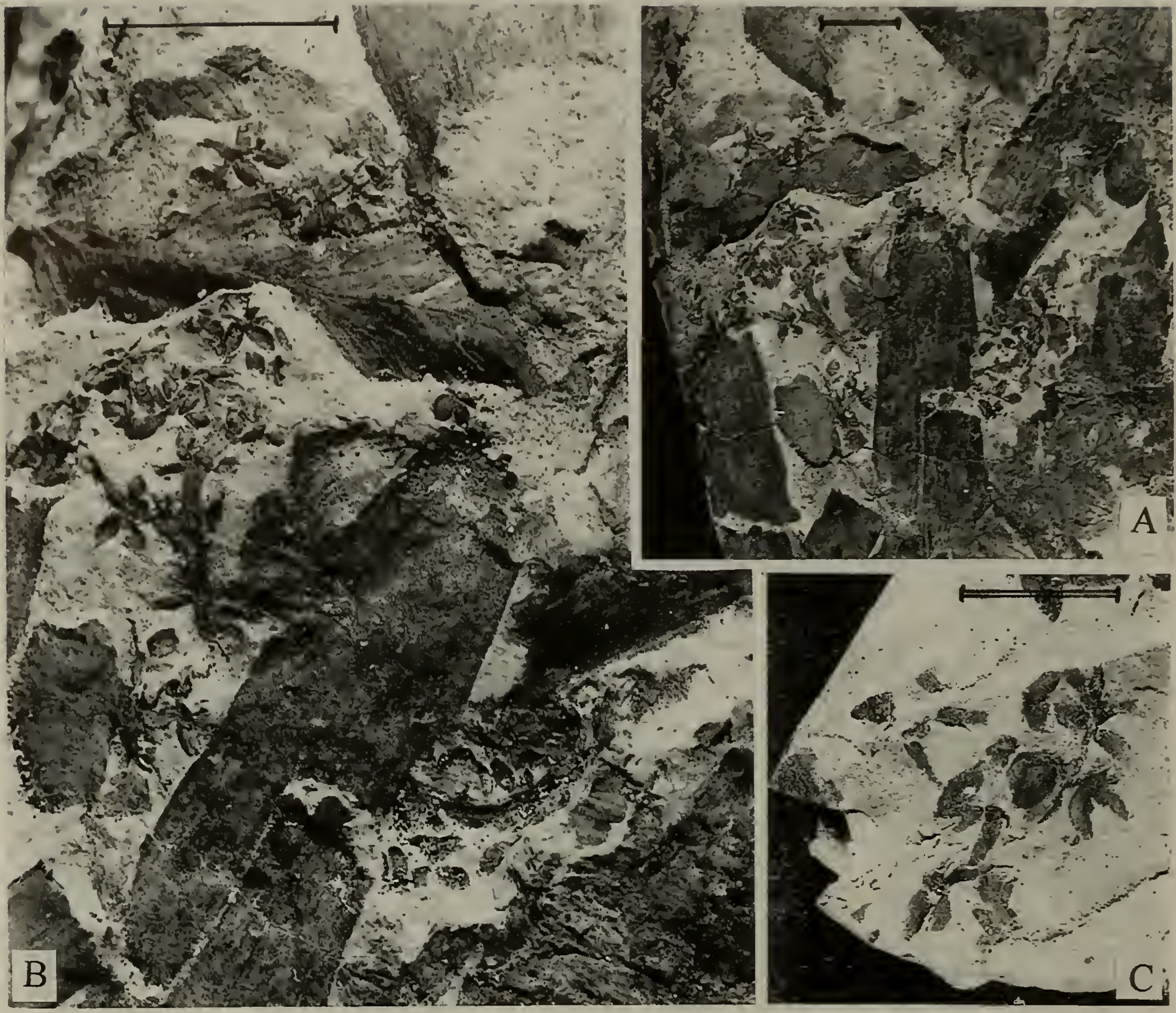

Figure 12. A-C. *Antevsia* sp. A. A,B. AMF126828. C. AMF126829. Both from Coal Mine Quarry. Scale bar = 1 cm.

Figure 13. A,B. '*Kutrziana brandmayri* complex'. A. AMF126830. B. AMF126831. Both from Coal Mine Quarry. Scale bar = 1 cm.

Figure 14. A-D. '*Kurtziana cacheutensis* complex'. A. AMF126832, showing venation. B. AMF126833. C. AMF126834. D. AMF126835. All from Coal Mine Quarry. Scale bar = 1 cm.

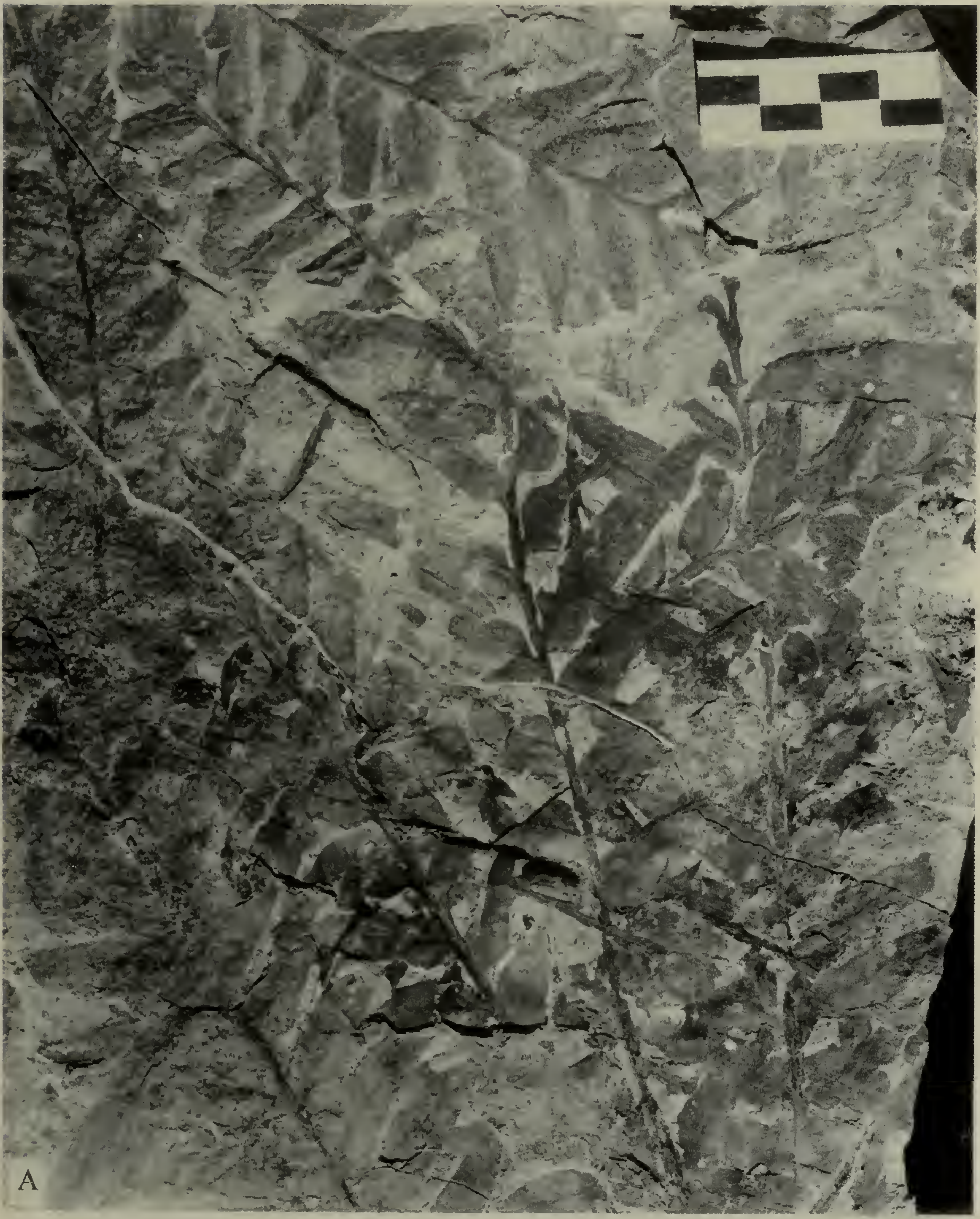

Figure 15. A. Leaf assemblage of '*Kurtziana cacheutensis* complex'. A. AMF126836. Coal Mine Quarry. Scale bar = 1 cm.

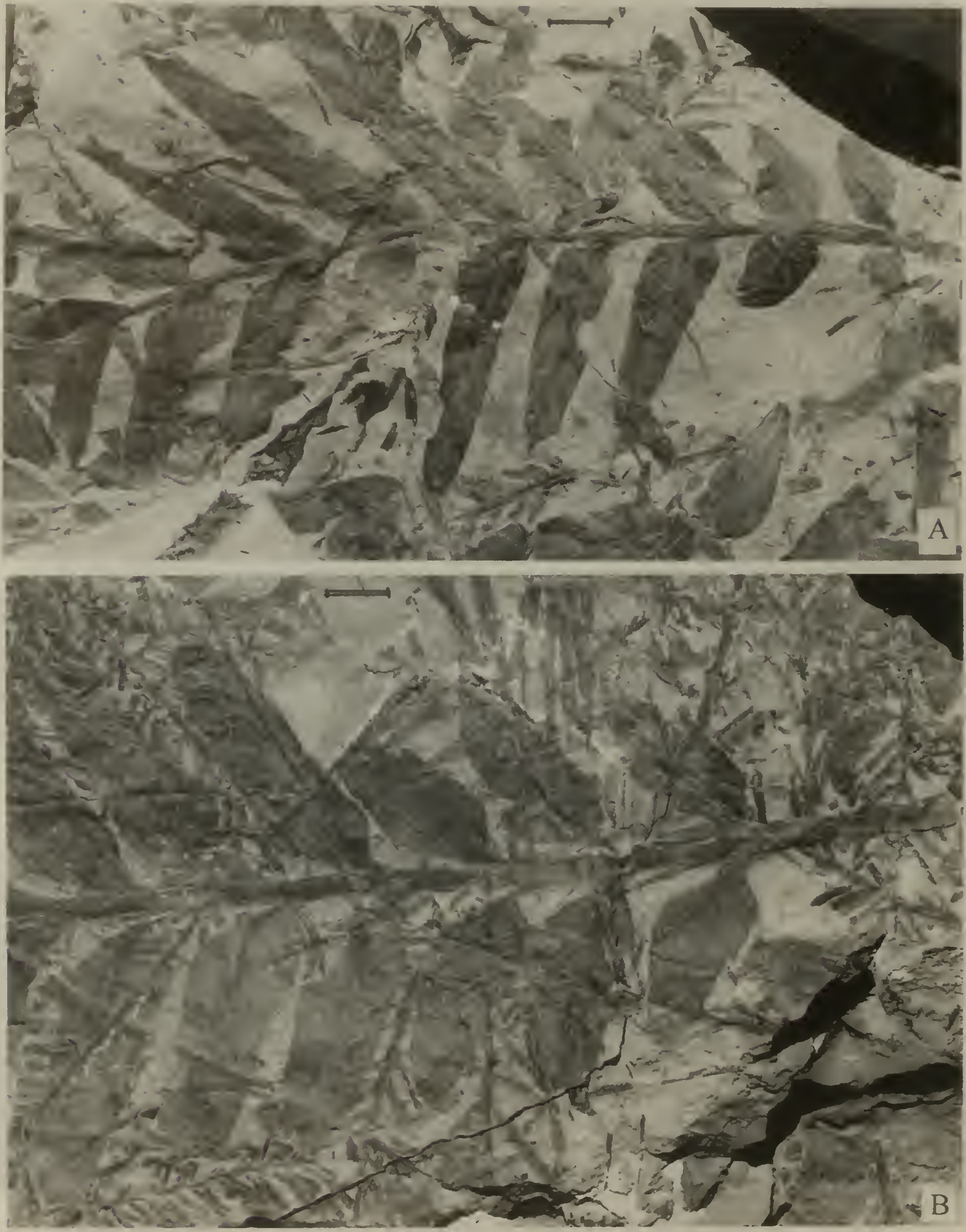

Figure 16. A,B. '*Kurtziana cacheutensis* complex'. A. AMF126837. B. AMF126838, leaf associated with *Rissikia* sp. Both from Coal Mine Quarry. Scale bar = 1 cm.

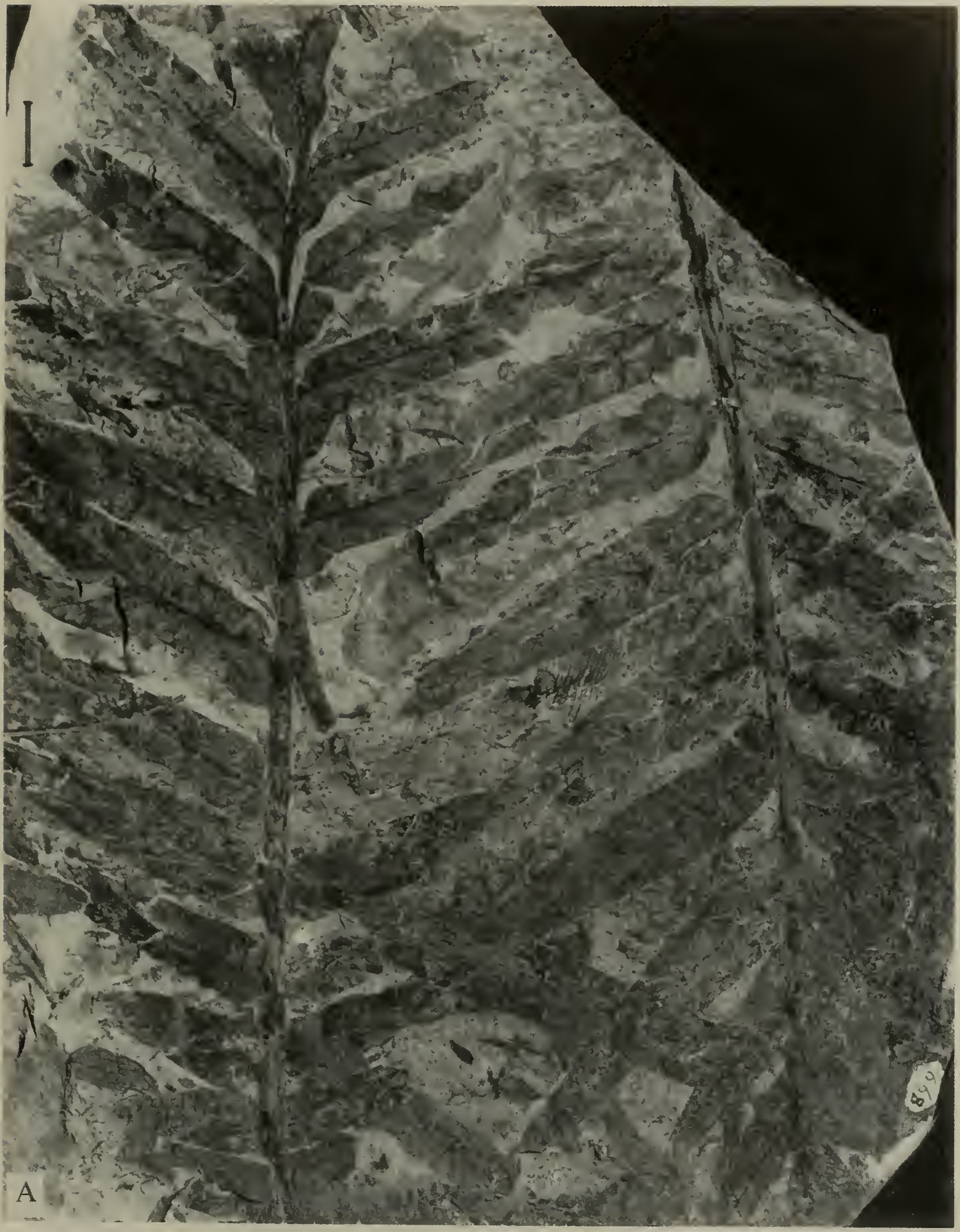

Figure 17. A. '*Kurtziana cacheutensis* complex'. AMF126839. Coal Mine Quarry. Scale bar = 1 cm.

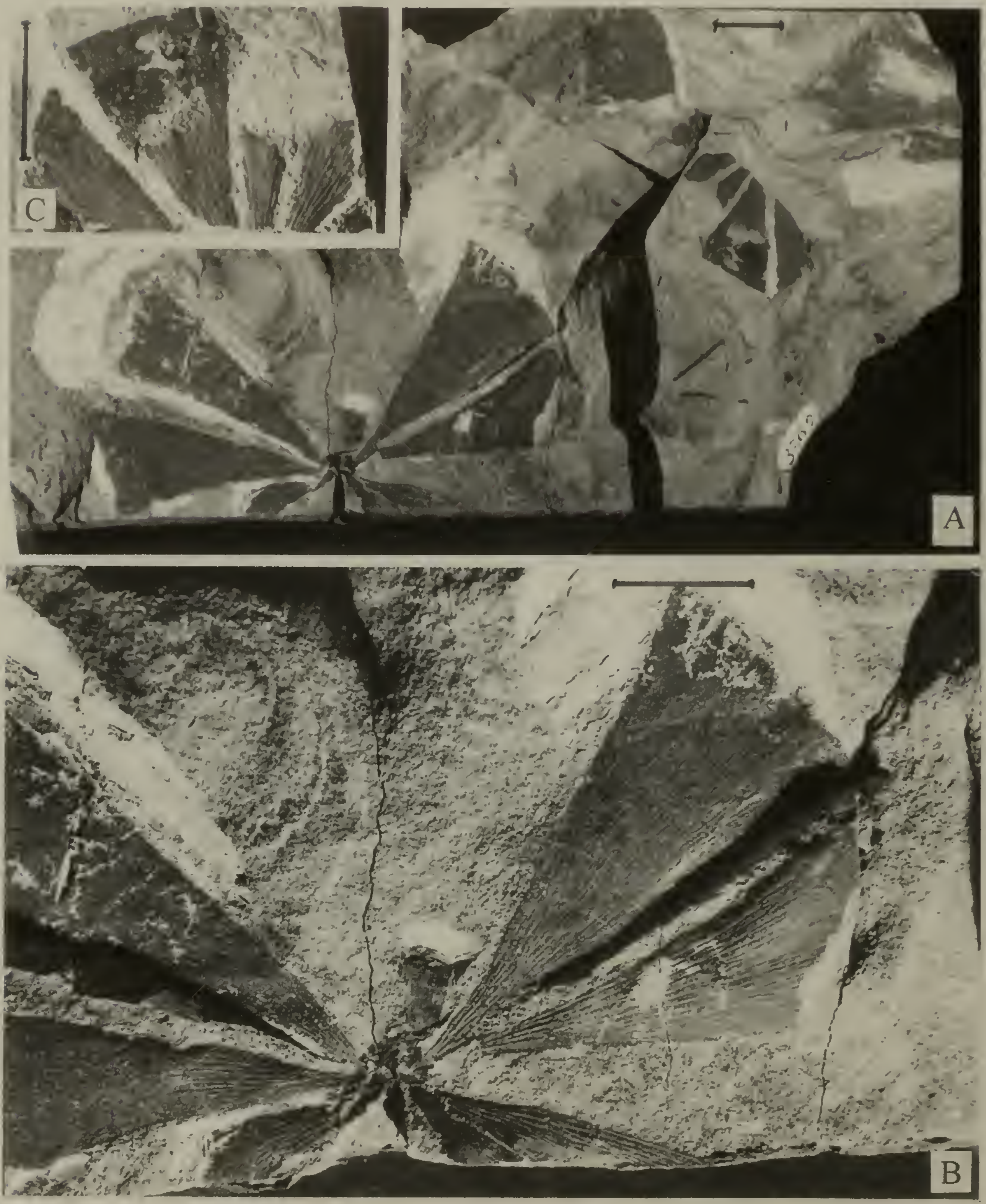

Figure 18. A-C. *Rochipteris obtriangulata* sp. nov. A. Portions of two whorls of leaves, AMF126840 holotype on left and AMF126841. B. AMF126840 and C. AMF126841 enlarged to show venation. Coal Mine Quarry. Scale bar = 1 cm.

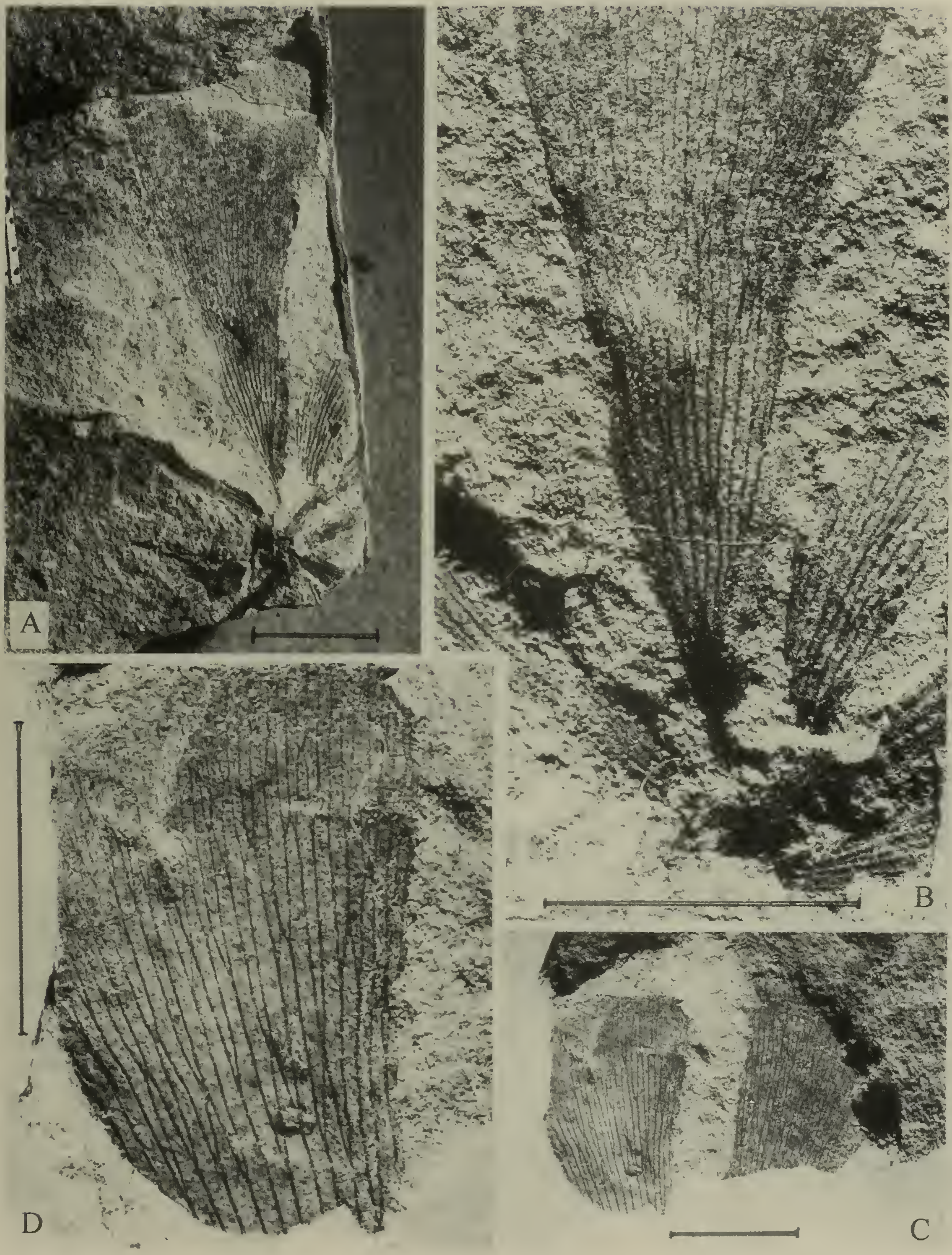

Figure 19. A-D. *Rochipteris obtriangulata* sp. nov., enlarged to show venation. AMF126842, counterpart of holotype. Coal Mine Quarry. Scale bar = 1 cm.

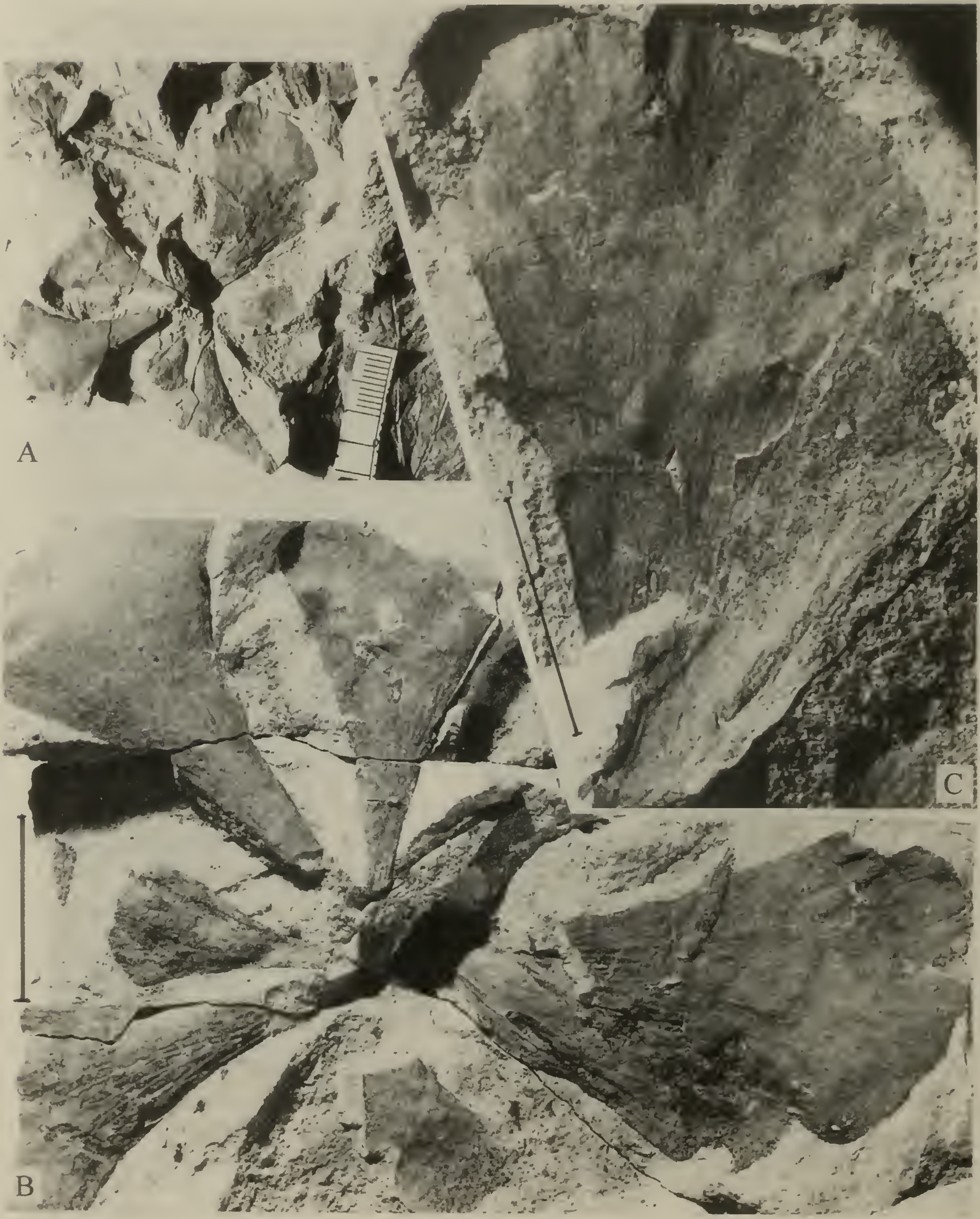

Figure 20. A-C. *Rochipteris tubata* sp. nov. Holotype. AMF126843. Coal Mine Quarry. Scale bar = 1 cm.

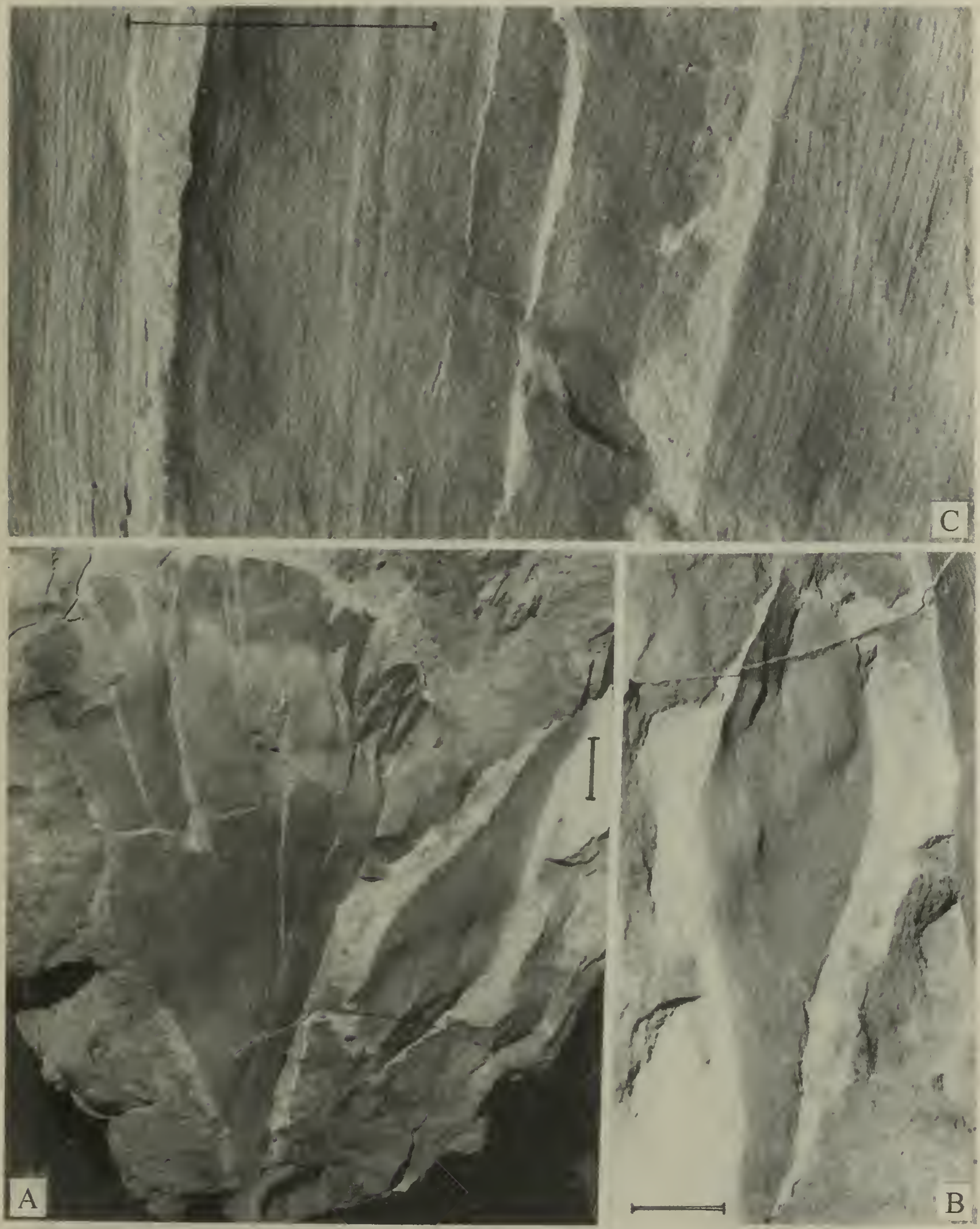

Figure 21. A. *Rochipteris incisa* sp. nov. Holotype on left, AMF126844, on right, AMF126827, juvenile leaf? B. AMF126827. C. AMF126844, to show venation. Reserve Quarry. Scale bar = 1 cm.

Figure 22. A. *Rochipteris incisa* sp. nov. Holotype. AMF126844. Reserve Quarry. Scale bar = 1 cm.

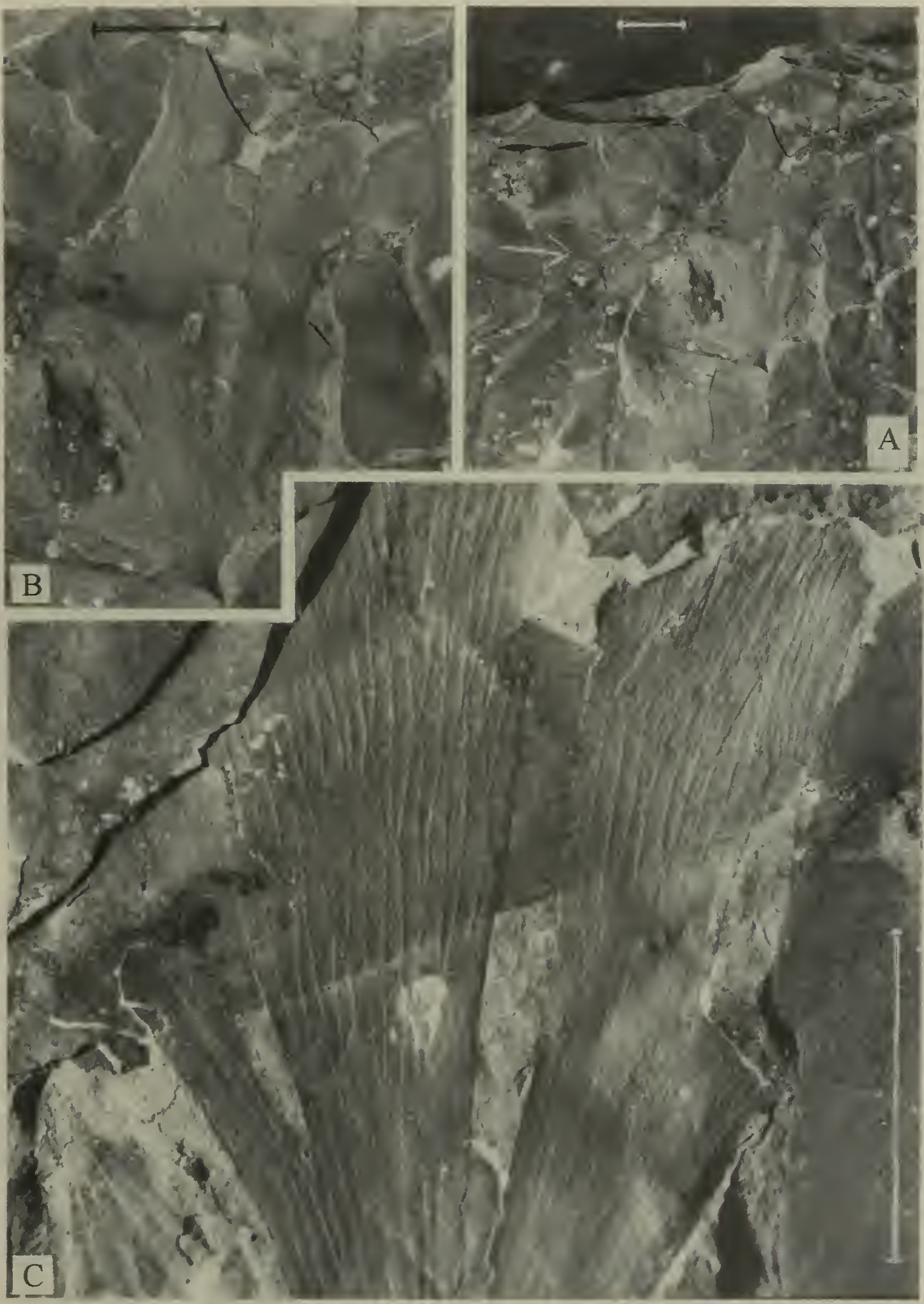

Figure 23. A-C. *Rochipteris sinuosa* sp. nov. Holotype. AMF126845. Coal Mine Quarry. Scale bar = 1 cm.

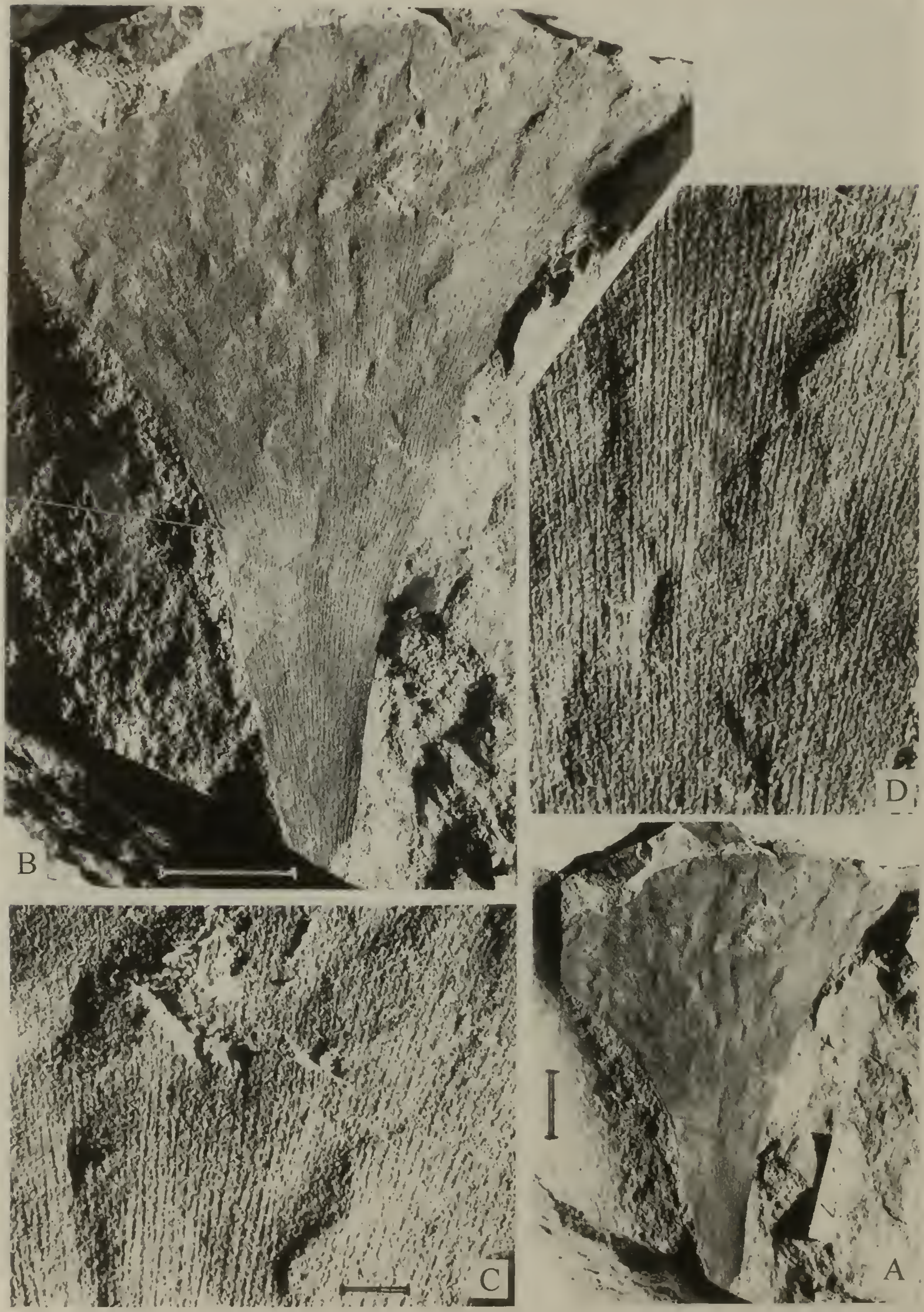

Figure 24. A-D. *Rochipteris nymboidensis* sp. nov. Holotype. AMF126846. Coal Mine Quarry. A and B, scale bar = 1 cm.; C and D, scale bar = 0.2 cm.

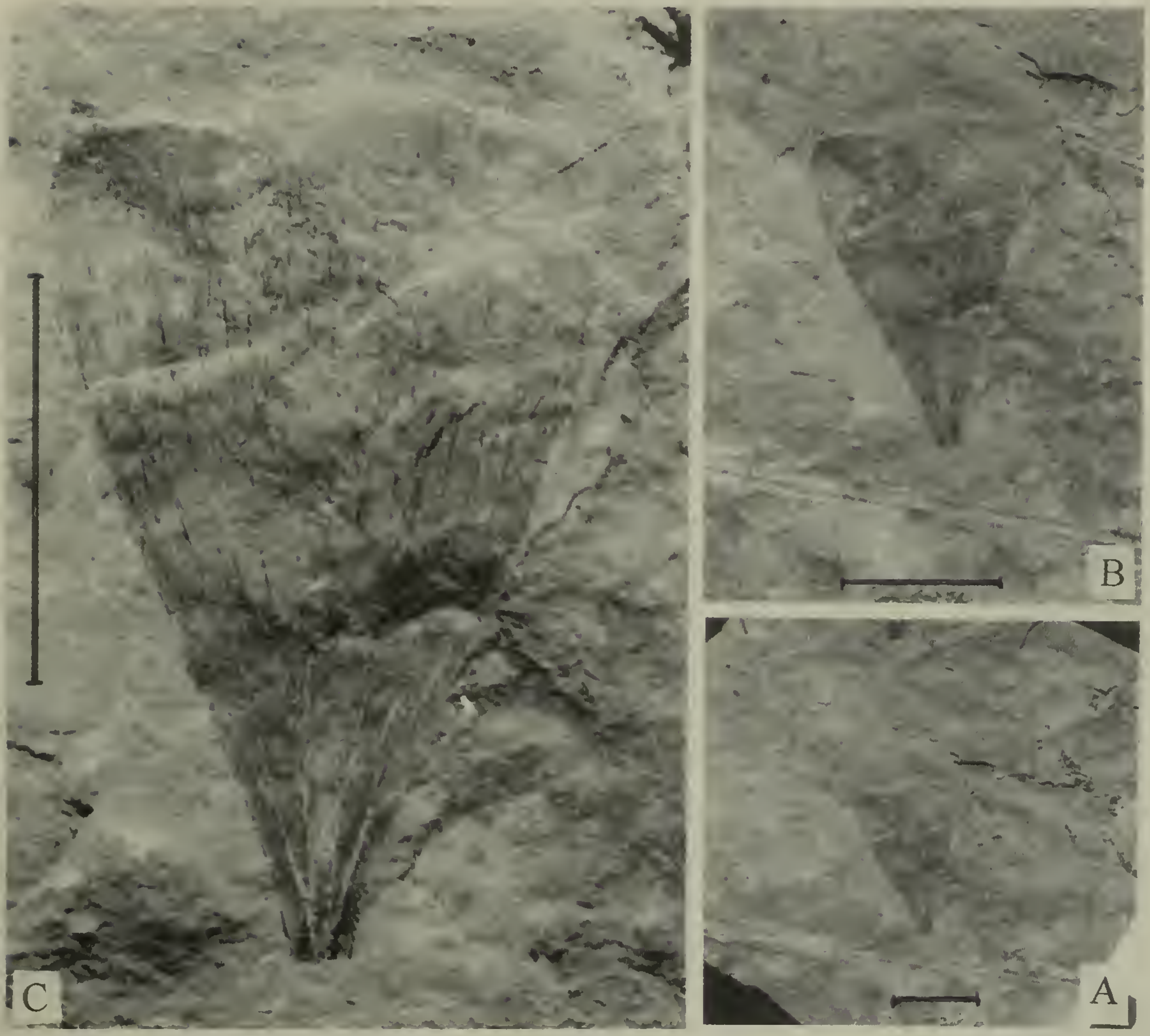

Figure 25. A-C. *Rochipteris pusilla* sp. nov. Holotype. AMF126854. Coal Mine Quarry. Scale bar = 1 cm.

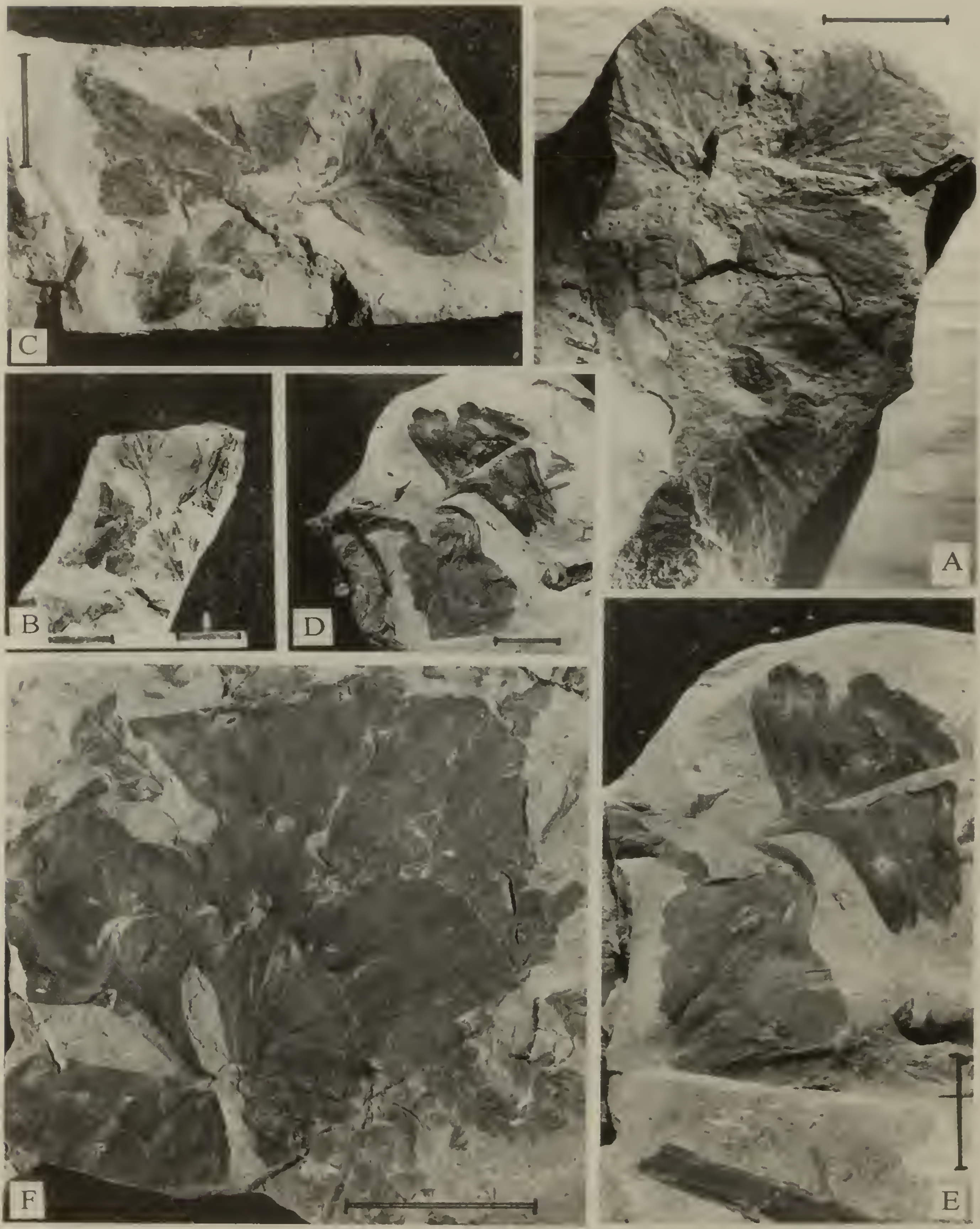

Figure 26. A-F. *Walkomiopteris eskensis* gen. et comb. nov. A. Holotype, QMF1729. Cutting near Ottoba railway station, Queensland. B. AMF113491. C. Counterpart of B. D,E. AMF113493. F. AMF113440. B-E. Reserve Quarry; F. Coal Mine Quarry. Scale bar = 1 cm.

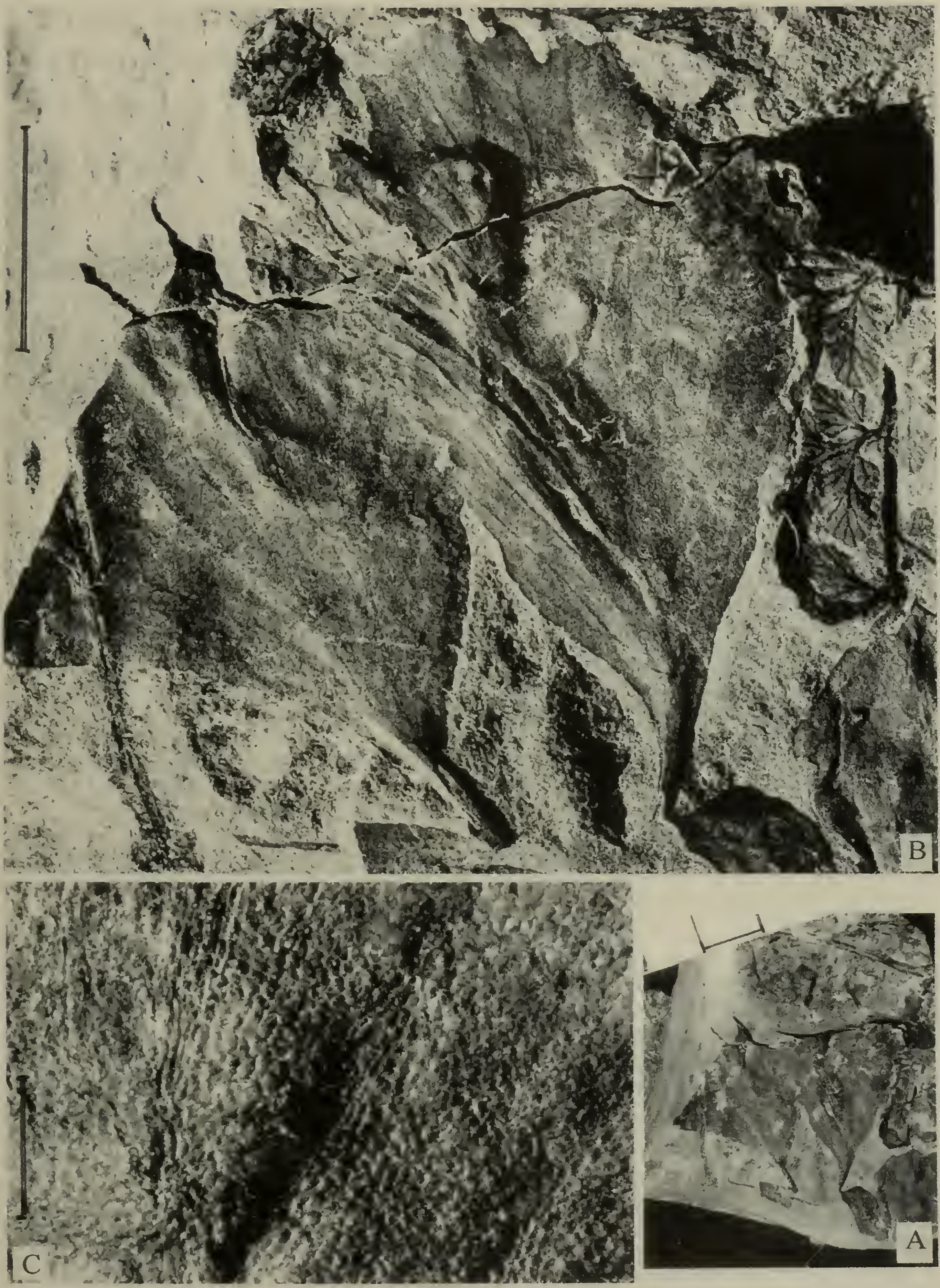

Figure 27. A-C. *Walkomiopteris eskensis* gen. et comb. nov. AMF113492. Reserve Quarry. A,B. Scale bar = 1 cm. C. To show cell structure. Scale bar = 0.1 cm.

Revision of *Discomesites* and *Estaingia* (Trilobita) from the Lower Cambrian Cymbric Vale Formation, Western New South Wales: Taxonomic, Biostratigraphic and Biogeographic Implications

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Paterson, J.R. (2005). Revision of *Discomesites* and *Estaingia* (Trilobita) from the Lower Cambrian Cymbric Vale Formation, western New South Wales: taxonomic, biostratigraphic and biogeographic implications. *Proceedings of the Linnean Society of New South Wales* **126**, 81-93.

The taxonomy of *Discomesites* and *Estaingia* from the Lower Cambrian Cymbric Vale Formation of western New South Wales is revised. *Discomesites* is regarded as a valid subgenus of *Pagetides*. *Pagetides* (*Discomesites*) *fragum* is considered a senior subjective synonym of *P.* (*D.*) *lunatulus*. *Pagetides* (*Discomesites*) *spinosus* from the Shackleton Limestone in the Holyoake Range, Transantarctic Mountains, is considered to be a junior subjective synonym of *P.* (*D.*) *fragum*. *Estaingia cerastes* from the Cymbric Vale Formation is considered to be synonymous with *Hsuaspis* cf. *H. bilobata* from the Shackleton Limestone. The Cymbric Vale Formation trilobite fauna is of late Early Cambrian (late Botoman) age, equivalent to the *Pararaia janeae* Zone of South Australia, based on correlation of the *Syringocnema favus* archaeocyathan fauna. Absolute ages of recently dated tuffs from the Cymbric Vale and Billy Creek Formations are questioned, based on new information regarding the stratigraphic position of the Cymbric Vale Formation tuff in relation to archaeocyathan and trilobite biostratigraphy. The co-occurrence of *Pagetides* (*Discomesites*) *fragum* and *Estaingia cerastes* in the upper part of the Cymbric Vale Formation and in the Shackleton Limestone represents the first species-level correlation between the Lower Cambrian of Australia and Antarctica using trilobites. The distribution of these trilobite species, in association with the *Syringocnema favus* archaeocyathan fauna, provides supporting evidence that Australia and Antarctica were connected by a continuous carbonate-detrital shelf during the late Early Cambrian (mid-late Botoman), allowing faunal exchange between these regions.

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KEYWORDS: Antarctica, Australia, biogeography, biostratigraphy, Botoman, Early Cambrian, geochronology, Gondwana, New South Wales, Trilobita.

INTRODUCTION

Since the publication of Öpik's (1975b) taxonomic study on the trilobites from the Lower Cambrian Cymbric Vale Formation, several important palaeontological and geochronological studies on the Early Cambrian of Australia and Antarctica, relevant to the Cymbric Vale Formation, have been published (Kruse 1978, 1982; Debrenne and Kruse 1986; Bengtson et al. 1990; Zhuravlev and Gravestock 1994; Palmer and Rowell 1995; Jago et al. 1997; Jenkins et al. 2002). The scope of this study is to revise the taxonomy of two key trilobite taxa from the Cymbric Vale Formation, *Discomesites* and *Estaingia*, as well as review the archaeocyathan biostratigraphy of the Cymbric Vale Formation and stratigraphic position of a recently dated tuff within the unit, allowing the Cymbric Vale trilobite fauna to be placed in both a biostratigraphic and biogeographic context.

The Cymbric Vale Formation is part of the Lower to early Middle Cambrian Gnalta Group, which crops out in the Mt Wright area of western New South Wales (Fig. 1). The Gnalta Group comprises (in ascending order): the Mount Wright Volcanics, Cymbric Vale Formation and Coonigan Formation. The Lower Cambrian Mount Wright Volcanics and overlying Cymbric Vale Formation are considered to be conformable, based on common archaeocyathan faunas (Kruse 1982). The uppermost beds of the Cymbric Vale Formation are disconformably overlain by the early Middle Cambrian 'first discovery

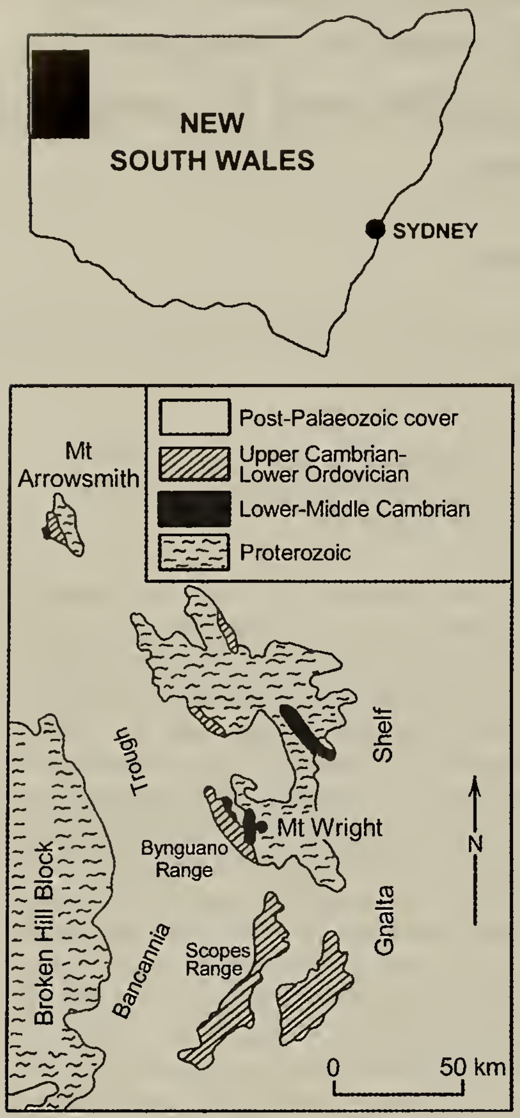

Figure 1. Generalised geological map of northwestern New South Wales, showing location of Mt Wright; modified from Shergold et al. (1982, text-fig. 1D).

limestone' of the Coonigan Formation (Roberts and Jell 1990).

The Cymbric Vale Formation attains a maximum thickness of 1900 m and consists predominantly of interbedded blue, green and grey-white chert and green to brown tuff (Kruse 1982). Archaeocyath-bearing limestone lenses occur throughout the formation and contain two distinct archaeocyathan faunas (Fig. 2): Fauna 1 (L96-L99) occurs in the upper Mount Wright Volcanics and in the lower part of the Cymbric Vale Formation and is assigned an early Botoman age; Fauna 2 (L100-L101) occurs in the upper Cymbric Vale Formation and has been assigned a mid-late Botoman age (Kruse 1978, 1982; Zhuravlev and Gravestock 1994; Kruse and Shi in Brock et al. 2000). The uppermost beds of the Cymbric Vale Formation consist of well-bedded lithic and feldspathic siltstone and sandstone interbedded with impure iron-rich carbonate rocks with abundant trilobites, molluscs, brachiopods, eocrinoids and sponge spicules (Öpik 1975b; Kruse 1982; Jago et al. 1997).

The first formal taxonomic study of the Early Cambrian trilobites from the Cymbric Vale Formation was by Öpik (1975b). He recorded the trilobites *Dinesis* aff. *granulosus* (Lermontova), *Estaingia bilobata* Pocock, *Strenax cerastes* Öpik, *Strenax* (*Sematiscus*) *fletcheri* Öpik, *Serrodiscus daedalus* Öpik, *Meniscuchus menetus* Öpik, *Discomesites fragum* Öpik, *Discomesites lunatulus* Öpik and *Pagetia* sp. nov. Öpik (1975b) correlated the Cymbric Vale fauna with Daily's (1956) South Australian faunal assemblages 9, 11 and 12, equivalent to the *Pararaia janeae* Zone of South Australia (Bengtson et al. 1990), and to the Botoman Sanashtyk'gol Horizon of the Altay-Sayan region of Siberia.

Jago et al. (1997) recorded a trilobite faunule from a new locality within the Cymbric Vale Formation, reassigning the species *Estaingia bilobata* Pocock and *Strenax cerastes* Öpik, originally documented by Öpik (1975b), to a single redefined species, *Hsuaspis cerastes* (Öpik), and also described *Redlichia* cf. *ziguiensis* Lin, a taxon previously unknown from the Cymbric Vale Formation. Jago et al. (1997) also suggested that the Cymbric Vale trilobite fauna is of late Early Cambrian (late Botoman) age.

BIOSTRATIGRAPHIC IMPLICATIONS

The taxonomic revision herein of *Pagetides* (*Discomesites*) *fragum* Öpik, 1975b and *Estaingia cerastes* (Öpik, 1975b) from the Cymbric Vale Formation of western New South Wales is based on reexamination of Öpik's (1975b) type material plus additional collections housed at Geoscience Australia (Canberra) and provides the first direct interregional correlation between the Lower Cambrian of Australia and Antarctica using trilobites. Palmer (in Palmer and Rowell 1995) described a number of Early Cambrian trilobite assemblages, ranging in age from Atdabanian to Toyonian(?), from the Shackleton Limestone in the Holyoake Range of the central Transantarctic Mountains. One of the Botoman assemblages ('Assemblage 3') contains the taxa *Pagetides* (*Discomesites*) *spinosus* Palmer and *Hsuaspis* cf. *H. bilobata* (Pocock). The synonymy herein of *Pagetides* (*Discomesites*) *spinosus* with *P.* (*D.*) *fragum*, and *Hsuaspis* cf. *H. bilobata* with *Estaingia cerastes* permits direct correlation of the trilobite fauna from the uppermost Cymbric Vale Formation with trilobite 'Assemblage 3' from the Shackleton Limestone. Unfortunately, further support for this correlation

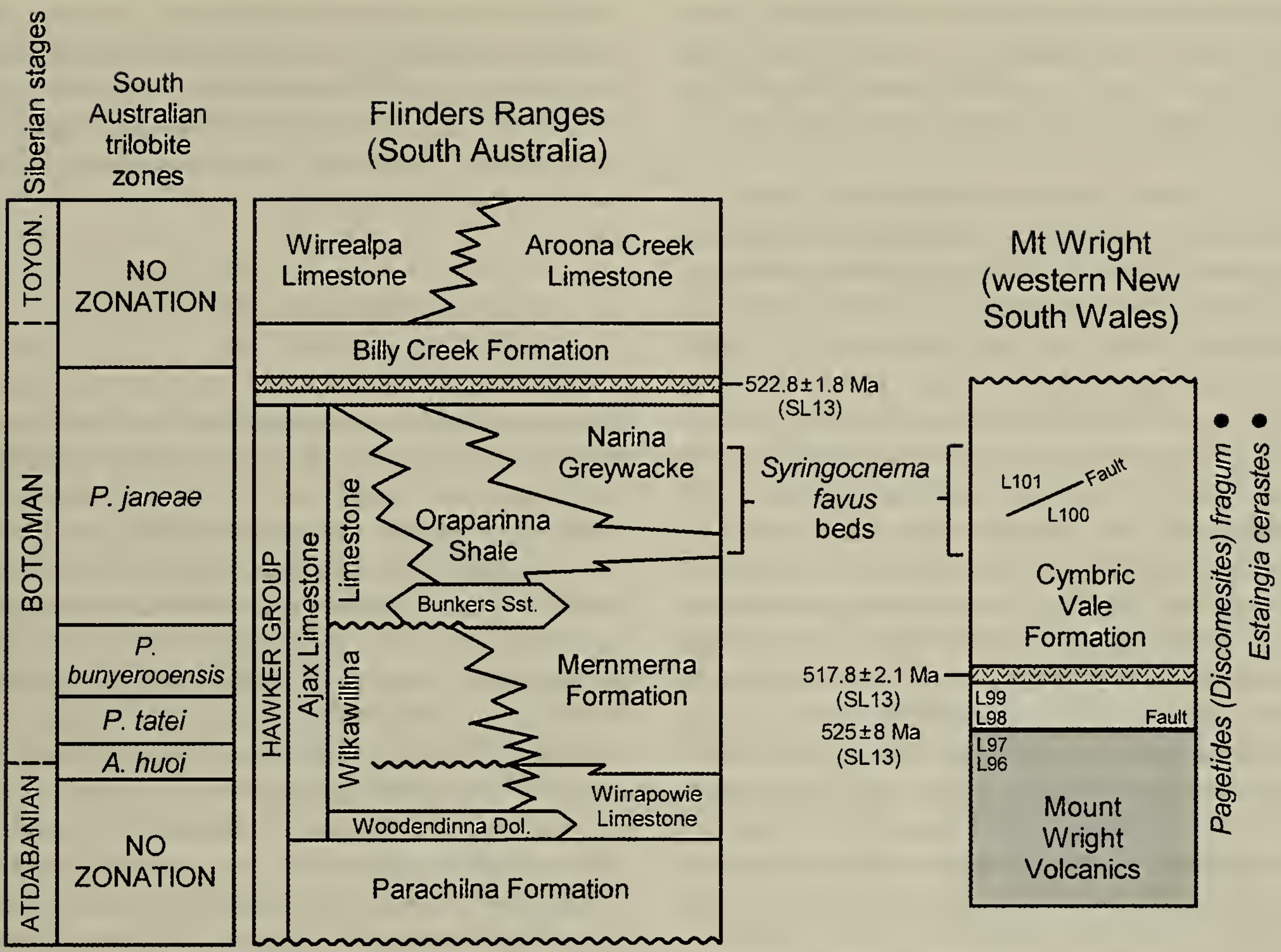

Figure 2. Correlation diagram of the Lower Cambrian successions of Mt Wright (western New South Wales) and the Flinders Ranges (South Australia). L96-L99 represent Fauna 1 and L100-L101 represent Fauna 2 of Kruse (1982). Tuff ages: Billy Creek Formation, 522.8 ± 1.8 Ma (Gravestock and Shergold 2001); Cymbric Vale Formation, 517.8 ± 2.1 Ma (Jenkins et al. 2002) and 525 ± 8 Ma (Zhou and Whitford 1994).

based on similar archaeocyathan faunas from the Cymbric Vale Formation (Kruse 1978, 1982) and the Shackleton Limestone (Debrenne and Kruse 1986) is complicated. Trilobites and archaeocyaths described from the Shackleton Limestone were sampled from different localities in the Holyoake Range; see discussion by Palmer and Rowell (1995:4). Exposed sections of Shackleton Limestone in the Holyoake Range are considerably thick (up to 200 m) and seem to conform to a coherent stratigraphy; however, each section is bounded either by intensely disturbed zones of folding or faulting, or fields of ice or névé (Rowell et al. 1988:399; Rees et al. 1989:343). Sampling of trilobites and archaeocyaths from disparate localities in the Holyoake Range, coupled with the structural complexity of the region, makes correlation between faunas difficult.

Documentation of archaeocyathan faunas from the Cymbric Vale Formation (Kruse 1978, 1982), and the development of a preliminary Early Cambrian archaeocyathan biozonation for Australia (Zhuravlev and Gravestock 1994), has allowed for the correlation of the Cymbric Vale Formation with the Lower Cambrian succession in South Australia. As noted by Kruse and Shi (in Brock et al. 2000), Fauna 2 from the upper Cymbric Vale Formation can be correlated with the mid-late Botoman *Syringocnema favus* beds of the Adelaide Geosyncline (Fig. 2), based on five co-occurring species. Zhuravlev and Gravestock (1994, Table 2) have recorded the *S. favus* beds occurring in the Koolywurtie Member of the Parara Limestone on Yorke Peninsula in the Stansbury Basin, and in the upper Ajax Limestone (Ajax Mine and Mount Scott Range) and upper Wilkawillina Limestone (Wilkawillina Gorge) in the Arrowie Basin. Trilobites from coeval beds in the Flinders Ranges (Arrowie Basin) are representatives of the *Pararaia janeae* Zone (Bengtson et al. 1990). While species-level correlation between the Cymbric Vale and Flinders Ranges trilobites is not possible, generic similarities are evident with the occurrence of *Serrodiscus* and *Estaingia* in both areas (Öpik 1975b; Bengtson et al. 1990). Since the Cymbric Vale trilobite fauna occurs in the uppermost part of the formation, stratigraphically above archaeocyathan Fauna 2 (= *S. favus* beds), it is equivalent to the *Pararaia janeae* Zone (*sensu lato*) or possibly even younger, thus supporting the late Botoman age suggested by Jago et al. (1997).

A dated felsic tuff from the Cymbric Vale Formation was recently re-calculated by Jenkins et al. (2002) using the SL13 U-Pb SHRIMP method. The tuff was originally collected by Zhou (1992) and subsequently dated by Zhou and Whitford (1994), yielding an age of 525 ± 8 Ma (SL13). However, Jenkins et al. (2002) produced an age of 517.8 ± 2.1 Ma. Unfortunately, neither publication citing the age of the Cymbric Vale tuff (Zhou and Whitford 1994; Jenkins et al. 2002) provided information about the stratigraphic position of the tuff horizon, especially in regard to the local biostratigraphy. However, Zhou's (1992) unpublished PhD thesis does provide an Australian standard national grid reference for the dated sample (i.e., 6332E; 65498N). Based on this grid reference and mapping by Zhou (1992, map 7) and Kruse (1982, text-Fig. 2), the dated tuff appears to have been collected in the vicinity of, or possibly stratigraphically above, Kruse's (1982) localities L98 and L99 in the lower Cymbric Vale Formation (Fig. 2).

In light of the known stratigraphic position of the dated Cymbric Vale tuff, there appears to be an age discrepancy of dated tuffs from the Cymbric Vale Formation and the lower Billy Creek Formation (Flinders Ranges), based on the correlation of the *Syringocnema favus* beds. Gravestock and Shergold (2001) reported a SHRIMP age of 522.8 ± 1.8 Ma from a tuff within the lower Billy Creek Formation using the same standard (SL13) used by Jenkins et al. (2002) to re-calculate the Cymbric Vale tuff. This means that the "older" (522.8 Ma) Billy Creek Formation tuff occurs stratigraphically above the *Syringocnema favus* beds in the Flinders Ranges, and the "younger" (517.8 Ma) Cymbric Vale tuff occurs stratigraphically below archaeocyathan Fauna 2 (= *S. favus* beds) in western New South Wales (Fig. 2). This discrepancy implies that the age of the tuff horizon in the Cymbric Vale Formation or Billy Creek Formation is erroneous, or perhaps both ages are incorrect. This age discrepancy may be related to the standard used, since the reliability of the SL13 standard has been questioned in recent years (see Jago and Haines 1998 for detailed discussion). It is interesting to note that the original age of the Cymbric Vale tuff of 525 ± 8 Ma, calculated using the SL13 standard (Zhou and Whitford 1994; Jago and Haines 1998), is more in accord with the archaeocyath and trilobite biostratigraphy and the age of the Billy Creek Formation tuff. Furthermore, ages of the Cymbric Vale and Billy Creek Formation tuffs using the alternative QGNG standard yield dates of 531.8 ± 8 Ma and 529.6 ± 1.8 Ma respectively (Jago and Haines 1998), that better conform to archaeocyath and trilobite biostratigraphy.

BIOGEOGRAPHIC IMPLICATIONS

Jago (in Brock et al. 2000) noted that Early Cambrian trilobites from Australia have close faunal ties with other regions of East Gondwana, such as Antarctica, South and North China, Iran and India. However, Jago also demonstrated that faunal links with distantly separated palaeogeographic regions such as western Gondwana (e.g. Morocco), Laurentia and Siberia are not uncommon. In discussing the biogeographic patterns of Early Cambrian trilobite faunas from Antarctica, Palmer (in Palmer and Rowell 1995:5) observed that 'Antarctic faunas do not show any consistent similarity to faunas from any one geographic region of the rest of Gondwana'. This appears to be true for any palaeogeographic region when treating Early Cambrian trilobite faunas as a whole, although by closely observing faunal assemblages from specific time intervals, whether they be zones or stages, distinct biogeographic patterns often emerge (for example, see Theokritoff 1979, 1985; Burrett and Richardson 1980; Alvaro et al. 2003). Moreover, Alvaro et al. (2003:17) have commented that in the Lower Cambrian 'the ideal of a global biostratigraphy and palaeobiogeography suffers from both a relatively limited diversity of trilobites and their pronounced endemism. Furthermore, the distribution of trilobites is...strongly controlled by facies, so that even a precise interregional correlation is difficult'.

The occurrence of *Pagetides* (*Discomesites*) *fragum* and *Estaingia cerastes*, in addition to the *Syringocnema favus* archaeocyathan fauna, in the Cymbric Vale Formation (Gnalta Shelf) and the Shackleton Limestone (Holyoake Range) provides supporting evidence that a continuous continental shelf connected southeastern Australia and the Transantarctic Mountains during the Early Cambrian (Rowell and Rees 1991; Courjault-Radé et al. 1992; Wrona and Zhuravlev 1996; Veevers et al. 1997; Brock et al. 2000; Veevers 2000). The palaeogeographic distance between the Gnalta Shelf and the Holyoake Range is estimated to be around 2500 km (Brock et al. 2000, Fig. 8), although the shelf may have extended as far as King George Island, implying a length of over 6500 km. Courjault-Radé et al. (1992,

Fig. 2) have suggested that throughout the Early Cambrian, and indeed the Middle and Late Cambrian, a continuous carbonate-detrital shelf connected Australia and Antarctica. The widespread dominance of the *Syringocnema favus* fauna in Australia and Antarctica during the mid-late Botoman coincides with a global high sea level, allowing faunal exchange between these regions (Zhuravlev and Gravestock 1994; Wrona and Zhuravlev 1996; Gravestock and Shergold 2001). This strong faunal link between Australia and Antarctica during the Botoman is also supported by conspecific occurrences of small shelly fossils (SSF), such as *Eiffelia araniformis* (Missarzhevskiy), *Chancelloria racemifundis* Bengtson, *Halkieria parva* Conway Morris, *Dailyatia ajax* Bischoff, *Lapworthella fasciculata* Conway Morris and Bengtson, *Hyolithellus micans* (Billings), *Hyolithellus filiformis* Bengtson, *Byronia*? *bifida* Wrona, and *Aetholicopalla adnata* Conway Morris, from glacial erratics of King George Island, Antarctica (Wrona 2004) and the Parara, Wilkawillina and Ajax Limestones and Kulpara and Mernmerna Formations in South Australia (Bengtson et al. 1990; Gravestock et al. 2001).

The carbonate-detrital shelf connecting Australia and Antarctica may have persisted until at least the early Late Cambrian (Idamean), based on other conspecific occurrences of benthic, shelf-dwelling polymerid trilobites and other biotas. For example, Holmer et al. (1996) described an Early Cambrian lingulate brachiopod faunule, containing *Eoobolus* aff. *E. elatus* (Pelman), *Karathele napuru* (Kruse) and *Vandalotreta djagoran* (Kruse), from the glacial erratics of King George Island, Antarctica. These same brachiopod species have been documented from the Toyonian (latest Early Cambrian) Wirrealpa and Ramsay Limestones in South Australia (Brock and Cooper 1993; Gravestock et al. 2001), and early Middle Cambrian units in the Northern Territory: Tindall Limestone, Daly Basin (Kruse 1990); Montejinni Limestone of the Wiso Basin and Gum Ridge Formation of the western Georgina Basin (Kruse 1998); and the Top Springs Limestone, northern Georgina Basin (Kruse 1991). The latest Middle Cambrian (*Glyptagnostus stolidotus* Zone) trilobite species *Rhodonaspis longula* Whitehouse has been recorded from the Georgina Limestone, Glenormiston, Queensland, Australia (Whitehouse 1939; Öpik 1963) and in the Spurs Formation, Northern Victoria Land, Antarctica (Jago and Cooper 2001). Furthermore, the early Late Cambrian (Idamean) trilobite species *Protemnites magnificans* Shergold and Webers has been recorded from the Dolodrook River limestones, eastern Victoria, Australia (Paterson and Laurie 2004) and from the Minaret Formation, Ellsworth Mountains, West Antarctica (Shergold and Webers 1992).

The position of Australia and Antarctica during the Cambrian, coupled with the persistence of carbonate deposition in Australia and Antarctica throughout the Cambrian, indicates that these regions remained within the tropical Carbonate Development Zone (30 ± 5° north and south latitudes) (McKerrow et al. 1992; Courjault-Radé et al. 1992; Brock et al. 2000; Li and Powell 2001). Hence migration of trilobite species between Australia and Antarctica was not inhibited by a latitudinal thermocline during the Cambrian. However, this does not explain the lack of conspecific occurrences of Early Cambrian trilobites between Australia and Antarctica, although one may argue that a paucity of data from Antarctica could be responsible. Moreover, there is a distinct absence of conspecific occurrences between western New South Wales (Gnalta Shelf) and South Australia (Adelaide Geosyncline). One possible explanation for the absence of conspecific occurrences of Early Cambrian trilobites between South Australia and Antarctica is the presence of a tectonic barrier during this time, i.e., the Kanmantoo Trough (Haines and Flöttmann 1998; Flöttmann et al. 1998). The Early Cambrian palaeogeographic relationship between the eastern Arrowie Basin (eastern South Australia) and the Gnalta Shelf (western New South Wales) is, however, poorly understood. Various studies (e.g., Cook 1988; Gravestock and Hibburt 1991; Scheibner and Basden 1998; Zang 2002) have inferred connection between the eastern Arrowie Basin and the Gnalta Shelf via a common seaway. While correlation of the *Syringocnema favus* beds provides supporting evidence for a connected seaway during the late Early Cambrian (mid-late Botoman), there may have been some form of geographic barrier that inhibited trilobite migration between these regions. Firstly, it is important to note that the Cymbric Vale Formation trilobites occur stratigraphically above the *S. favus* beds and that during their temporal separation the palaeogeography between the eastern Arrowie Basin and the Gnalta Shelf may have altered significantly, severing ties between these regions. There are two possible palaeogeographic barriers that may have hindered migration of Early Cambrian trilobites between the eastern Arrowie Basin and the Gnalta Shelf: (1) the Mount Wright Volcanic Arc situated immediately to the west of the Gnalta Shelf; and (2) an inferred trough situated to the west of the Mount Wright Volcanic Arc (Scheibner and Basden 1998, Fig. 14.6). A small outcrop of the Lower-Middle Cambrian Teltawongee beds, considered by

Mills (1992) to be coeval with the Gnalta Group, occurs at the northern end of the Mount Wright Block at Nundora. The Teltawongee beds are thought to have been deposited as a turbidite slope-trough facies (Mills 1992). Scheibner and Basden (1998) suggested that the Teltawongee beds might extend beneath the large thickness of Devonian sediments within the Bancannia Trough, situated to the west of the Gnalta Shelf. This inferred trough would have created an oceanic barrier between the eastern Arrowie Basin and the Gnalta Shelf.

Wrona (2004) observed that Lower Cambrian horizons in Australia and Antarctica that contain very similar faunas correspond with transgressive episodes that occurred during the early Botoman, late Botoman and middle Toyonian (Gravestock and Shergold 2001; Gravestock et al. 2001). Wrona (2004:52) suggested that several isolated basins might have existed along the East Antarctic craton and that those basins 'connected only during the most prominent transgressions, thus allowing faunal exchange'. Alvaro et al. (2003) suggested that species migration of Cambrian trilobites along the western Gondwanan margin coincides with transgressive episodes and subsequent connection of neighbouring platforms. This also appears to have been the case in influencing trilobite migration patterns along the eastern Gondwanan margin, especially between Australia and Antarctica.

SYSTEMATIC PALAEONTOLOGY

Specimens come from the Commonwealth Palaeontological Collection (prefix CPC) housed at Geoscience Australia, Canberra.

Order AGNOSTIDA Salter, 1864
Suborder EODISCINA Kobayashi, 1939
Family EODISCIDAE Raymond, 1913
Genus PAGETIDES Rasetti, 1945

Type species

Pagetides elegans Rasetti, 1945, Early Cambrian, Sillery Formation, Quebec, Canada.

Subgenus DISCOMESITES Öpik, 1975b

Type species

Discomesites fragum Öpik, 1975b, Early Cambrian, Cymbric Vale Formation, Mt. Wright, western New South Wales, Australia.

Discussion

Palmer's (in Palmer and Rowell 1995) treatment and diagnosis of *Discomesites* as a subgenus of *Pagetides* is supported here.

Pagetides (*Discomesites*) *fragum* Öpik, 1975b
Fig. 3A-K, Fig. 4A-J

Discomesites fragum Öpik, 1975b:32, Pl. 5, Figs 1-8.

Discomesites lunatulus Öpik, 1975b:34, Pl. 6, Figs 1-4.

Neopagetina sp., Rowell et al. 1989, p. 14, Fig. C.

Pagetides (*Discomesites*) *spinosus* Palmer in Palmer and Rowell, 1995:7, Fig. 7.

Material

13 cranidia, 8 pygidia; CPC13176-13179 [Type material of *Discomesites fragum*], CPC13180-13183 [Type material of *Discomesites lunatulus*] and CPC37623-37635 [New topotype material from Site A of Öpik (1975b)].

Discussion

The characters that Öpik (1975b) used to differentiate *Discomesites fragum* from *D. lunatulus* can be explained by ontogenetic variation, deformation, preservation or misinterpretation. Öpik's differential characters include: ornamentation, length of the occipital spine, pygidial shape and number of pygidial axial rings.

Öpik (1975b) distinguished *Discomesites fragum* from *D. lunatulus* by its dense granulose ornament; however, this difference is the result of either ontogenetic variation and/or preservation. Firstly, it is important to note that specimens of *D. lunatulus* are considerably smaller than those of *D. fragum*. The type series cranidia of *D. lunatulus* range between 2.6-2.9 mm (n=2) in length (sag.), whereas the type series cranidia of *D. fragum* range between 3.4-4.1 mm (n=3) in length (sag.). This correlation between size and ornamentation can also be observed in pygidia of *Discomesites*. Smaller pygidia (<2.7 mm in length) appear to lack the granulose ornamentation (Fig. 4C-H, J), whereas larger pygidia clearly show dense granulation (Fig. 4A-B, I). It is also worth mentioning that some specimens of *Discomesites* that lack granulose ornamentation, including those of *D. lunatulus*, have a coating of 'desert varnish' (iron oxide), while others appear to have been indurated or partially silicified. It is therefore possible that the difference in ornamentation may have been caused by weathering or diagenesis.

The differentiation of *Discomesites* species

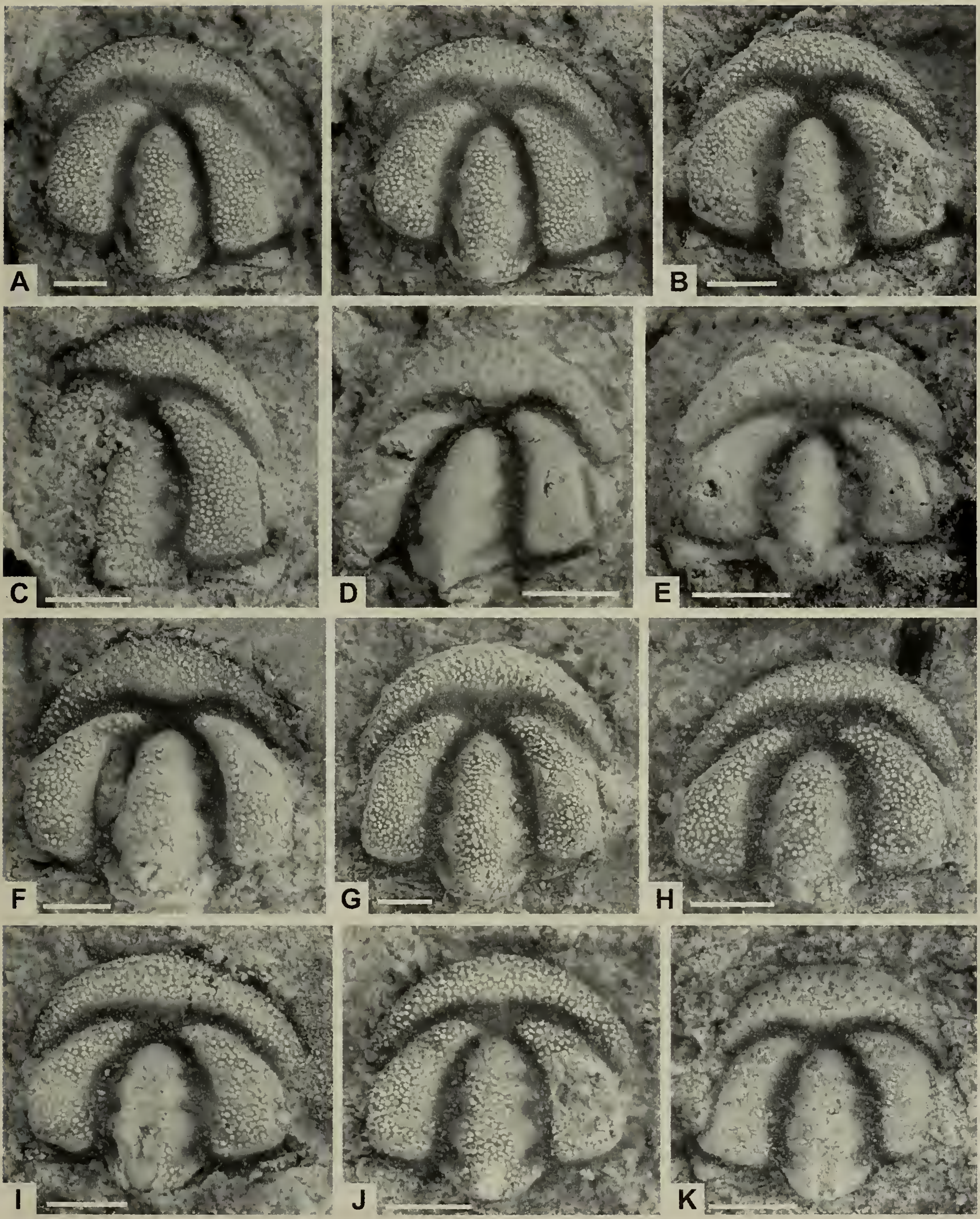

Figure 3. ***Pagetides (Discomesites) fragum*** **Öpik, 1975b. All scale bars = 1 mm. A, CPC13177, holotype cranidium, dorsal view, stereo pair; B, CPC13176, cranidium, dorsal view; C, CPC13178, latex cast of partial cranidium, dorsal view; D, CPC13180, holotype cranidium of** ***Discomesites lunatulus*** **Öpik, 1975b, dorsal view; E, CPC13181, cranidium, dorsal view; F, CPC37623, cranidium, dorsal view; G, CPC37627, cranidium, dorsal view; H, CPC37628, cranidium, dorsal view; I, CPC37632, cranidium, dorsal view; J, CPC37635, cranidium, dorsal view; K, CPC37629, cranidium, dorsal view.**

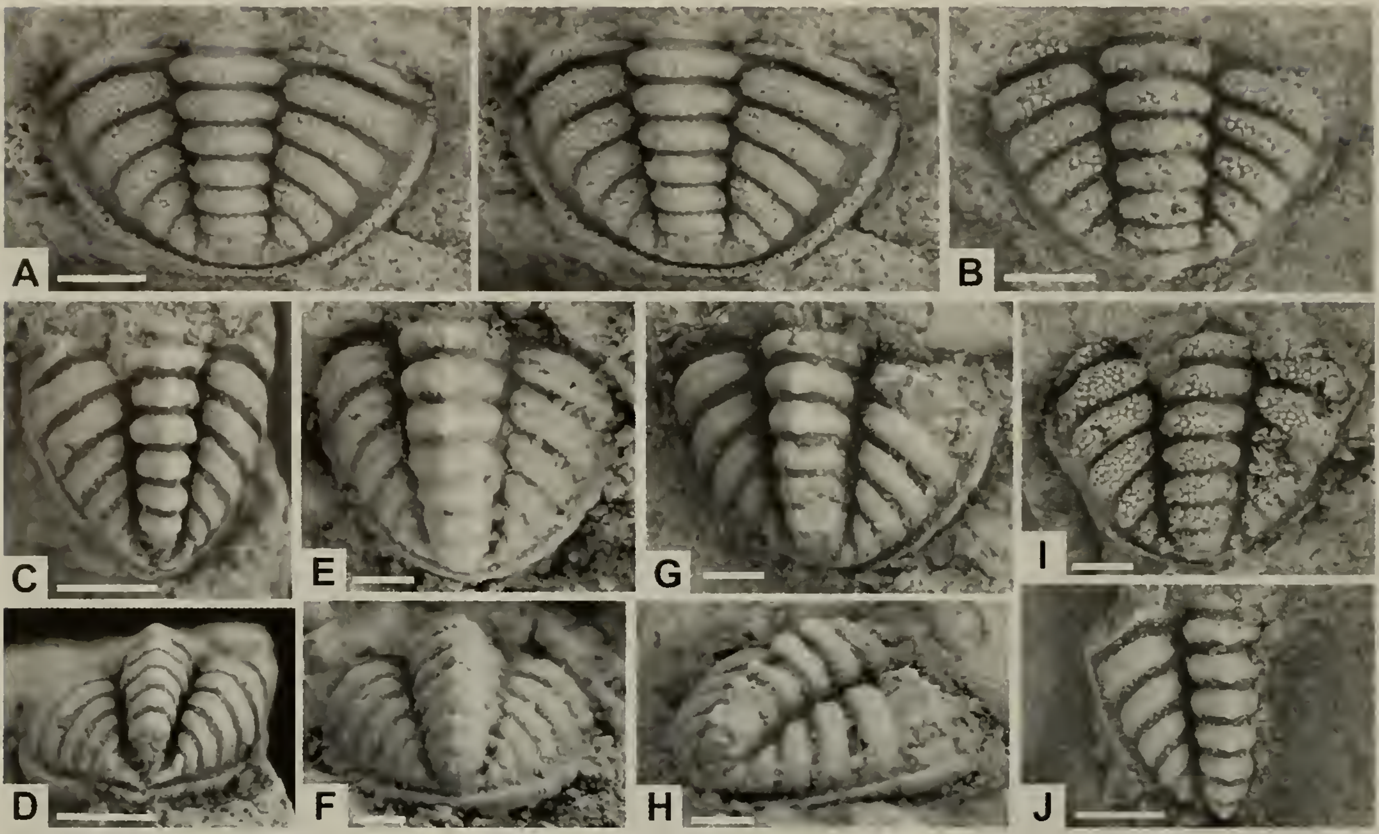

Figure 4. *Pagetides (Discomesites) fragum* Öpik, 1975b. A, CPC13179, latex cast of pygidium, dorsal view, stereo pair, scale bar = 1 mm; B, CPC37631, pygidium, dorsal view, scale bar = 1 mm; C-D, CPC13182, pygidium, dorsal and posterior views, scale bars = 1 mm; E-F, CPC13183, pygidium, dorsal and posterior views, scale bars = 0.5 mm; G-H, CPC37624, pygidium, dorsal and oblique posterolateral views, scale bars = 0.5 mm; I, CPC37630, pygidium, dorsal view, scale bar = 1 mm; J, CPC37626, partial pygidium, dorsal view, scale bar = 1 mm.

based on occipital spine length appears to have been exaggerated by Öpik (1975b). He described the occipital spine of *D. lunatulus* as 'slender and relatively long'. However, specimens of *Discomesites* that have a preserved occipital spine, including the holotype of *D. fragum*, show no significant difference in size and shape to that of the holotype of *D. lunatulus*. Therefore occipital spine length does not appear to be a reliable diagnostic character.

Pygidial characteristics used by Öpik (1975b) to distinguish species of *Discomesites* can be attributed to preservation or misinterpretation. Öpik (1975b:32) differentiated *D. fragum* from *D. lunatulus* by its 'relatively broad pygidium with six axial annulations', and stated that the latter species possesses seven axial rings. Firstly, tectonic deformation of fossils from the Cymbric Vale Formation is relatively common; see for example, specimens illustrated by Öpik (1975b, Pl. 1, Figs 4-5; Pl. 2, Fig. 1). The larger pygidium of *D. lunatulus* illustrated by Öpik (1975b, Pl. 6, Fig. 3) (see Fig. 4C-D for dorsal and posterior views) has clearly been laterally compressed, thus appears to be narrower (tr.). This was, in fact, noticed by Öpik (1975b:35) in his comments on the illustrated specimens. Öpik illustrated only two pygidia of *D. lunatulus*, of which only one (CPC13183) has a complete axis preserved. Examination of pygidium CPC13183 reveals the presence of only six distinct axial rings and a terminal piece. It is likely that Öpik misinterpreted the change in slope at the base of the axial node on the terminal piece as an axial furrow. Therefore, based on the evidence above, *D. lunatulus* is herein considered a junior subjective synonym of *D. fragum*.

Palmer (in Palmer and Rowell 1995:7) distinguished the Antarctic species *Discomesites spinosus* from Australian species of *Discomesites* based on the 'presence of axial spines on the thoracic and pygidial segments and of distinct nodes on the pygidial margin'. Examination of Öpik's (1975b) type material of *Discomesites*, in addition to new topotype material from the Cymbric Vale Formation, reveals that smaller pygidia of *Discomesites* (<2.3 mm sagittal length) have axial rings bearing short, median axial nodes or spines (Fig. 4E-H, J). Larger pygidia have less conspicuous axial nodes; in some cases the nodes appear to be absent (Fig. 4A-D, I), implying that axial nodes vary ontogenetically. The pygidia of *Discomesites spinosus* illustrated by Palmer and Rowell (1995, Fig. 7.2-7.3) conform to this ontogenetic pattern, being less than 2.5 mm in length (sag.).

The presence of marginal nodes opposite the pleural furrows on the pygidium of *Discomesites spinosus* appears to be a rather dubious diagnostic character. Marginal nodes are not clearly delineated on the pygidia illustrated by Palmer and Rowell (1995, Fig. 7.2-7.3). A pygidium of *D. lunatulus* (CPC13183) and an associated unnumbered pygidium display what appear to be faint marginal nodes opposite the pleural furrows. However, this character does not seem to be consistent in all pygidia of *Discomesites* from the Cymbric Vale Formation.

Palmer (in Palmer and Rowell 1995:7) noted that the Australian species of *Discomesites* have 'a slight posterior deflection of the inner margin of the [anterior cranidial] border on the axial line'. This is certainly true for the majority of *Discomesites* cranidia from the Cymbric Vale Formation, although there is a great deal of variation, and some cranidia do not display this deflection at all (Fig. 3E, I, J). Therefore, *D. spinosus* is herein considered a junior subjective synonym of *D. fragum*.

Order REDLICHIIDA Richter, 1932
Suborder REDLICHIINA Richter, 1932
Superfamily ELLIPSOCEPHALOIDEA Matthew, 1887
Family ESTAINGIIDAE Öpik, 1975a
Genus ESTAINGIA Pocock, 1964

Type species

Estaingia bilobata Pocock, 1964, Early Cambrian, Emu Bay Shale, Kangaroo Island, South Australia.

Discussion

Jell (in Bengtson et al. 1990:310) originally regarded *Estaingia* and *Zhuxiella* as junior subjective synonyms of *Hsuaspis*. This synonymy was supported in subsequent studies by Palmer and Rowell (1995), Nedin (1995), Jago et al. (1997) and Nedin and Jenkins (1999). Jell (in Bengtson et al. 1990) also suggested that *Strenax* may be regarded as a junior subjective synonym of *Pseudichangia*. Jago et al. (1997) supported Jell in synonymising *Strenax* with *Pseudichangia*, but considered both genera to be junior synonyms of *Hsuaspis*. Recently, Jell (in Jell and Adrain 2003:334) discovered a nomenclatural error between the synonymous genera *Estaingia* and *Hsuaspis*. Jell noted that *Estaingia* should be considered the senior name because the publications in which the name *Hsuaspis* was first mentioned (Zhang et al. 1957; Zhang 1957) did not satisfy the ICZN criteria for availability, thus *Hsuaspis* must be considered *nomen nudum* in both publications. Therefore *Hsuaspis* became available in Lu et al. (1965), a year after its synonym *Estaingia* was erected by Pocock (1964).

Estaingia cerastes (Öpik, 1975b)
Fig. 5A-K

Strenax cerastes Öpik, 1975b:14, Pl. 2, Figs 1-6.
Strenax (*Sematiscus*) *fletcheri* Öpik, 1975b:16, Pl. 3, Figs 1-2.
Estaingia bilobata Pocock, Öpik 1975b:11, Pl. 1, Figs 1-7.
Bergeroniellus sp., Rowell et al. 1989, p. 14, Fig. A.
Hsuaspis cf. *H. bilobata* Pocock, Palmer in Palmer and Rowell 1995:16, Fig. 12.
Hsuaspis cerastes (Öpik), Jago et al. 1997:71, Fig. 2B-L, Fig. 3.

Material

11 cranidia, 3 librigenae, 5 pygidia; CPC13152-13158 [Öpik's (1975b) illustrated material of *Estaingia bilobata*], CPC13159-13163 [Type material of *Strenax cerastes*], CPC13164 [Holotype cranidium of *Strenax* (*Sematiscus*) *fletcheri*] and CPC37636-37641 [New material from Site A of Öpik (1975b)].

Discussion

The revision of *Estaingia cerastes* from the Cymbric Vale Formation has been previously documented by Jago et al. (1997) and will only be briefly discussed here. Jago et al. (1997) noted that specimens of *E. bilobata* illustrated by Öpik (1975b) do not belong to this species because Öpik's specimens possess a longer (sag.) glabella (relative to cranidial length) and show a marked forward expansion of the glabella, whereas the type cranidia of *E. bilobata* illustrated by Pocock (1964) display a shorter (sag.) glabella that either tapers anteriorly or has a slight waist. Nedin and Jenkins (1999, Fig. 4) have documented the difference in glabella length (or preglabellar field) between specimens of *E. bilobata* and *E. cerastes*. Nedin and Jenkins (1999) have also demonstrated that *E. bilobata* and *E. cerastes* can be differentiated based on cranidial length/width ratios. Jago et al. (1997) also suggested that Öpik's specimens of *E. bilobata* and *Strenax cerastes* are likely to represent the same species based on the variation displayed in Öpik's illustrated specimens and those illustrated by Jago et al. (1997). Therefore, in placing *Strenax* in synonymy with *Hsuaspis*, Jago

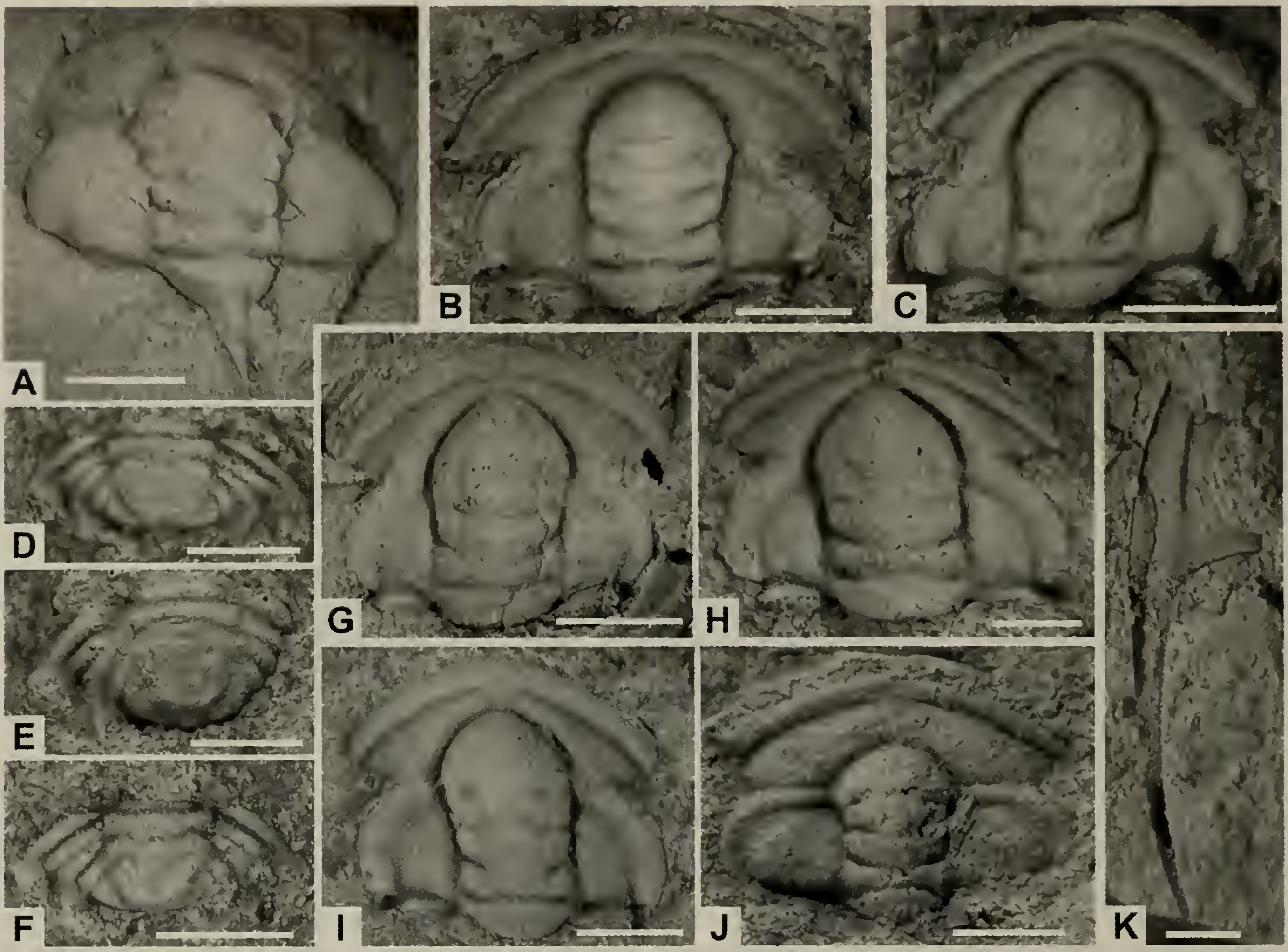

Figure 5. *Estaingia cerastes* (Öpik, 1975b). A, CPC13159, latex cast of holotype cranidium of *Strenax cerastes*, dorsal view, scale bar = 5 mm; B, CPC13152, cranidium, dorsal view, scale bar = 5 mm; C, CPC13156, cranidium, dorsal view, scale bar = 5 mm; D, CPC13157, pygidium, dorsal view, scale bar = 2.5 mm; E, CPC13158, latex cast of pygidium, dorsal view, scale bar = 2.5 mm; F, CPC37638, pygidium, dorsal view, scale bar = 2.5 mm; G, CPC13153, cranidium, dorsal view, scale bar = 5 mm; H, CPC37637, cranidium, dorsal view, scale bar = 2.5 mm; I, CPC37636, cranidium, dorsal view, scale bar = 2.5 mm; J, CPC13164, latex cast of holotype cranidium of *Strenax (Sematiscus) fletcheri*, dorsal view, scale bar = 1 mm; K, CPC37641, librigena, dorsal view, scale bar = 2.5 mm.

et al. (1997) reassigned *E. bilobata* and *S. cerastes* described by Öpik (1975b) from the Cymbric Vale Formation to a single species, *Hsuaspis cerastes*, reassigned herein to *Estaingia cerastes* (Öpik). Jago et al. (1997:71) also noted that the holotype cranidium of *Strenax* (*Sematiscus*) *fletcheri* Öpik, 1975b 'is clearly an immature specimen which should not be the basis of a new taxon'. The holotype of *Strenax* (*Sematiscus*) *fletcheri* is considered herein a juvenile specimen (sagittal length: 3.0 mm) and junior subjective synonym of *Estaingia cerastes*.

Jago et al. (1997) suggested that specimens of *Hsuaspis* cf. *H. bilobata* described by Palmer (in Palmer and Rowell 1995) from the Shackleton Limestone in the Transantarctic Mountains may belong to *Hsuaspis* (=*Estaingia*) *occipitospina*, originally described by Jell (in Bengtson et al. 1990). Jago et al. (1997:71) based this interpretation on the fact that the Antarctic specimens 'have a glabella of similar length to *H. occipitospina* as well as a similar preglabellar median ridge [= plectrum]'. The Antarctic specimens do appear to have a shorter (sag.) glabella, similar to *E. bilobata* and *E. occipitospina*, compared to that of *E. cerastes*. However, it is important to note that the Antarctic cranidia are considerably smaller (sagittal length: 3.8-5.6 mm) than the large holaspid cranidia of *E. cerastes* (sagittal length: 11-18 mm) illustrated by Öpik (1975b) and Jago et al. (1997). Smaller cranidia of *E. cerastes* (Öpik 1975b, Pl. 3, Figs 1-2; Jago et al. 1997, Fig. 2K) of similar size to the Antarctic cranidia show similar glabella lengths. Therefore the glabella of *E. cerastes* appears to become longer (sag.) relative to the cranidial length during ontogeny; a trend also observed by Jago et al.

(1997:73). This trend is reversed in *E. occipitospina* in that the glabella becomes shorter (sag.) relative to cranidial length during ontogeny (Bengtson et al. 1990, Fig. 200). Furthermore, the presence of a plectrum does not appear to be a defining character amongst species of *Estaingia*, since all species possess this feature, including *E. cerastes* (Öpik 1975b, Pl. 1, Fig. 5, Pl. 2, Fig. 5, Pl. 3, Fig. 2; Jago et al. 1997, Figs 2D, E, G, 3B). Jago et al. (1997) also observed that the Antarctic specimens possess an occipital node rather than an occipital spine; however, Jago et al. (1997:71) demonstrated that the occipital spine in *E. cerastes* varies considerably, with some specimens having a small node, while others possess a long, slender spine.

Estaingia occipitospina can be further differentiated from *E. cerastes* in having a longer (sag.) anterior cranidial border that tapers laterally and the palpebral lobe and eye ridge can be clearly distinguished, with the eye ridge being considerably narrower and of low relief in relation to the palpebral lobe. Specimens of *E. cerastes* and *H.* cf. *H. bilobata* have an anterior cranidial border of approximately equal length (sag., exsag.), and display a palpebral lobe that is continuous with the eye ridge.

Further evidence to suggest that *Estaingia cerastes* and *Hsuaspis* cf. *H. bilobata* are synonymous can be seen in the morphology of the glabella and pygidium. Although the anterior part of the glabella in the Antarctic specimens is not greatly expanded, the glabella does show a slight expansion anteriorly. This can also be observed in small cranidia, of similar size to the Antarctic specimens, of *E. cerastes* (Öpik 1975b, Pl. 3, Figs 1-2; Jago et al. 1997, Fig. 2K). Based on the description and illustration of the pygidium of *H.* cf. *H. bilobata* given by Palmer (in Palmer and Rowell 1995:16, Fig. 12.4), there seems to be no apparent difference in the pygidia of *E. cerastes* (Fig. 5D-F; Öpik 1975b, Pl. 1, Figs 6-7). This pygidial similarity was in fact observed by Palmer (in Palmer and Rowell 1995:16), noting that 'all of the pygidial characteristics [of *H.* cf. *H. bilobata*] are shared with specimens from the Cymbric Vale fauna of New South Wales, Australia, assigned by Öpik (1975b) to *Estaingia bilobata* [= *Estaingia cerastes*]'.

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First Record of an Australian Fur Seal (*Arctocephalus pusillus doriferus*) Feeding on a Wobbegong Shark (*Orectolobus ornatus*)

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Allen, S. and Huveneers, C. (2005). First record of an Australian fur seal (*Arctocephalus pusillus doriferus*) feeding on a wobbegong shark (*Orectolobus ornatus*). *Proceedings of the Linnean Society of New South Wales* **126**, 95-97.

The Australian fur seal (*Arctocephalus pusillus doriferus*) is listed as a 'vulnerable' species in New South Wales (NSW) under the Threatened Species Conservation Act, recovering from exploitation by commercial sealing activities around southeastern Australia. Recent dietary studies indicate they are generalist predators that feed on a wide variety of both vertebrates (fish and, occasionally, birds) and invertebrates (cephalopods and, occasionally, crustaceans). While a small number of elasmobranchs have been reported from the diets of a variety of fur seal species, no published evidence exists of either fur seals preying on wobbegongs (*Orectolobus* spp.), or of large wobbegongs as prey items in the diet of any predator. Here we describe an account of an Australian fur seal feeding on a large ornate wobbegong (*Orectolobus ornatus*). Wobbegongs are also listed as 'vulnerable' in NSW by the IUCN, with commercial fishing catch having dropped over 50% from 1990-2000. Knowledge of relationships between high trophic level species is important for assessing interactions between marine mammals and fisheries and also presents interesting challenges for the conservation of commercially targeted species.

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KEYWORDS: *Arctocephalus*, Australian fur seal, diet, *Orectolobus*, threatened, wobbegong.

INTRODUCTION

The diets of Australian and New Zealand fur seals (*Arctocephalus pusillus doriferus* and *A. forsteri*, respectively) have been extensively studied around southeastern Australia and New Zealand in the last decade (e.g. Gales & Pemberton 1994; Fea et al. 1999; Littnan 2004). Diagnostic techniques have primarily involved faecal and regurgitate sampling, while more recent work has also included stable isotope and fatty acid analyses (Littnan 2004). These studies have indicated that fur seals target a large number of prey species, with a relatively limited number of cephalopods and fish species constituting the majority of their diet. There is evidence of some seasonal and spatial variation in Australian fur seal diet (Hume et al. 2004; Littnan 2004) and seasonal variation in New Zealand fur seal diet (Fea et al. 1999). A very small portion of fur seal diet is made up of crustaceans, birds and some small elasmobranchs (Gales & Pemberton 1994; Fea et al. 1999; Hume et al. 2004). Here we describe the first account of an Australian fur seal feeding on a large ornate wobbegong (*Orectolobus ornatus*).

INTERACTION ACCOUNT

During a coastal survey of small cetaceans from Port Stephens to Sydney on December 28th 2003, an Australian fur seal (distinguished from the sympatric New Zealand fur seal by facial profile and fur colouration) was witnessed carrying the body of a large ornate wobbegong (distinguished from the sympatric spotted wobbegong *O. maculatus* by skin pattern and colouration). The interaction occurred approximately 3.2 nautical miles north of Norah Head lighthouse on the central coast of New South Wales (33°13.3′S, 151°35.2′E). Excellent conditions (Sea State 1, no cloud cover, clear water and being able to approach to within 5m of the animals) facilitated reliable identification of both species, with video footage of the event used to confirm identification and behaviour after the voyage. The shark's head had been removed and the fur seal was thrashing the body from side to side in an apparent attempt to separate manageable portions of the shark's flesh. This behaviour is common for pinnipeds feeding on prey too large to swallow (Rand 1959; Reeves et al. 1992).

Female Australian fur seals grow to a maximum length of around 1.5m, while males can reach 2.0-2.25m (Warneke and Shaughnessy 1985). The fur seal was estimated to be approximately 1.5m in length and the presence of a light mane suggested it was a sub-adult male. The ornate wobbegong becomes sexually mature at around 1.8m in length and grows to 2.9m (Last and Stevens 1994). The wobbegong's total body length was estimated to be around 1.4m (sex was not determined).

Only post-capture manipulation was witnessed, with no predation event observed, so we cannot discount the possibility that the shark was found dead or was scavenged from a fishing line by the fur seal. Wobbegongs are, however, commercially targeted using set-lines in NSW; 89% are gut-hooked, 100% remain alive until retrieved and killed by fishermen, and no wobbegong fisherman in NSW have witnessed line depredation by fur seals (C. Huveneers unpub. data). It is unlikely that a carcass would be discarded by a fisherman or that the shark could have been removed from the hook by the fur seal without tearing the shark's body cavity. Predation thus seems to be the most plausible explanation for the above observation of an Australian fur seal carrying the body of an ornate wobbegong.

ELASMOBRANCHS IN FUR SEAL DIET

The remains of two spiny dogfish (*Squalus acanthias*) were found in 357 faecal and regurgitate samples of Australian fur seals hauling out around Tasmania (Gales and Pemberton 1994), while a more recent study of the same colonies found no elasmobranch remains in 1044 samples (Hume et al. 2004). Similarly, no sharks or rays were found in the diet of Australian fur seals around Kanowna or the Skerries, Victoria (n=1008; Littnan 2004). The remains of one dogfish were found in 584 faeces and regurgitates from New Zealand fur seals at the Otago Peninsula (Fea et al. 1999) and elasmobranchs including the puffadder shyshark (*Haploblepharus edwardsii*) have been recorded in the diet of the Cape fur seal (*A. p. pusillus*) off South Africa (Rand 1959; Martin 2004). Adult wobbegongs might be considered potential prey items for numerous pinnipeds, cetaceans and large shark species, but there has been no published account to date.

CONCLUSION

Pinnipeds and elasmobranchs are high-level predators that occupy important niches in marine ecosystems (e.g. Cortes and Gruber 1990; Read and Brownstein 2003). Interactions between them can have both direct and indirect effects on marine mammals, fish and invertebrates at lower trophic levels. Quantifying the diet of high trophic level species is therefore important for modelling of interactions between marine mammals and fisheries and assessing the effects of stock depletion by commercial fishing (see Goldsworthy et al. 2003; Myers and Worm 2003; Hutching and Reynolds 2004; Littnan 2004). It also presents challenges for conservation and fisheries management when predator/prey relationships involve more than one threatened or vulnerable species. This note represents the first record of a large wobbegong being fed upon by a fur seal.

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Effects of Javan Rusa Deer (*Cervus timorensis*) on Native Plant Species in the Jibbon-Bundeena Area, Royal National Park, New South Wales

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A reconnaissance survey and exclosure experiment were carried out to examine the effects of Javan rusa deer on native flora and vegetation in Royal National Park on the southern outskirts of Sydney, Australia. Of 78 native plant species examined during the survey, only nine showed no evidence of vertebrate herbivory or physical damage and the majority of these plants were ferns and sedges. The other 69 species showed effects that included defoliation (young and/or old leaves), removal of shoots, bark-stripping, stem breakages and destruction or consumption of reproductive material. These effects varied in severity between species and from place to place, and were inferred to have been caused by deer based on the local abundance of deer droppings, footprints and the scarcity of other vertebrate herbivores in the area. The survey also revealed localised soil erosion associated with high densities of deer footprints and droppings. An unreplicated exclosure experiment showed that planted saplings of *Syzygium paniculatum*, a threatened rainforest tree, suffered major defoliation, bark stripping, stem breakages and some mortality when exposed to deer for several months. Many of the surviving plants showed signs of recovery when deer were subsequently excluded, although full recovery of their leaf canopies could take several seasons. The observed effects on vegetation and individual plant species are consistent with studies on several other deer species in a range of ecosystems overseas. A model of the effects of deer herbivory based on plant life-history suggests that curtailment of seed production and seedling recruitment are likely to be the major impacts of deer on plant population viability. Reductions in net growth and survival of established plants and possibly post-dispersal predation of seeds are less likely to be significant influences.

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KEYWORDS: browsing, *Cervus timorensis*, deer, endangered ecological communities, feral animals, fire, grazing, herbivory, plant demography, *Syzygium paniculatum,* threatened species, threatening process.

INTRODUCTION

Javan rusa deer (*Cervus timorensis*) is one of six deer species that have established wild populations in Australia (Moriarty 2004a). Rusa deer were introduced into Royal National Park in 1906 by the Park Trust for exhibition purposes (NSW National Parks and Wildlife Service 2002). The seven introduced animals were initially kept within a fenced enclosure at 'Deer`Park' on the Hacking River near Warumbul. The deer soon escaped and established a wild population that has persisted in the Park and adjacent areas to the present day. Hamilton (1981) suggested that rusa deer essentially replaced fallow deer (*Dama dama*), which were introduced some 20 years earlier and likely to be the species reported as widespread in the Park in 1914 (Anon. 1914). High densities of Rusa deer are now regularly observed in the vicinity of Bundeena, Grays Point, Garie-Era and various sites along the Hacking River valley. The deer population is likely to have fluctuated since its introduction, although densities appear to have increased markedly since bushfires in January 1994, which burnt more than 90% of the Royal National Park (pers. obs.). After the fires, the population within Royal National Park was estimated to include less than 500 individuals. Quantitative surveys carried out between 1999 and 2001 indicate that the population increased from 2500 to 2900 individuals during that time (Moriaty unpubl. data, NSW National Parks and Wildlife Service 2002).

Rusa deer grow to 1 m tall at the shoulder and weigh 100-160 kg. Males develop large antlers but females do not. The deer are active nocturnally, resting in dense native vegetation by day. They are dietary opportunists, apparently preferring grass but browsing opportunistically on the buds, shoots and leaves of woody plants and herbs (Bentley 1979). Recent dietary data from Royal National Park indicate that food sources vary with season and location. In native vegetation remote from settled areas, 80% of their average summer diet consists of native browse, with grasses making up the remaining 20% (Moriaty 2004b). In other seasons, the grass component becomes negligible in these areas. However, the grass component varies seasonally from 40% to 70% in animals living close to cleared grassy areas (Moriarty 2004b).

Concerns about impacts on native vegetation have resulted in a recent preliminary determination of feral deer as a Key Threatening Process under the *NSW Threatened Species Conservation Act 1995*. A recent survey of rangers employed by Rural Lands Protection Boards in NSW identified deer as the most important emerging pest animal threat (West and Saunders 2003). More than 40% of respondents indicated that there had been a moderate to high increase in the distribution and abundance of wild deer in their area. In another recent survey more than 80% of land managers reported browsing of native plants and agricultural crops as an impact of feral deer (Moriarty 2004a). Despite numerous detailed studies on the impacts of deer on native vegetation in other countries (e.g. Okuda and Nakane 1990, Veblen et al. 1992, Kay 1993, Jane 1994, Anderson and Katz 1993, Mladenoff and Stearns 1993, Khan et al. 1994, Augustine and Frelich 1998, Akasi and Nakashisuka 1999, McShea and Rappole 2000, Fuller and Gill 2001, Coomes et al. 2003, Rooney et al. 2004), there are relatively few published data from Australia on this subject. In Royal National Park and adjacent urban areas, the high densities of deer, their free movement in open areas and their exclusion from some properties provide opportunities to examine the effects of deer on native vegetation. The aims of this study were to document the various impacts of deer on native vegetation, compile a list of native plant species affected by deer and to quantify the effects of deer on a threatened plant species, *Syzygium paniculatum*.

METHODS

Study area

Jibbon-Bundeena is a 300 ha area located in the far north-east corner of Royal National Park on the shores of Port Hacking on the southern outskirts of Sydney (lat. 34° 06'S, long. 151° 09'E). The bedrock of Hawkesbury sandstone is overlain in some parts by podsolised marine and aeolian sand dunes that may exceed 10 m in depth. The dune crests and slopes are freely drained, although the swales and flats may be periodically waterlogged. The exposed sandstones carry shallow to skeletal yellow earths with variable drainage characteristics.

The area includes a mosaic of rainforests, eucalypt forests, heathlands and wetlands. Littoral rainforest on the hind dunes of Jibbon and Bonnie Vale beaches is dominated by *Cupaniosis anacardioides* with *Acmena smithii, Glochidion ferdinandi* subsp. *ferdinandi* and *Banksia integrifolia* subsp. *integrifolia*. It forms part of an Endangered Ecological Community (Littoral Rainforest in NSW) under the *NSW Threatened Species Conservation Act 1995* and includes *Syzygium paniculatum*, which is currently listed as a Vulnerable species. The eucalypt forests are found principally on deep sands. On dune slopes they are dominated by *Corymbia gummifera* and *Angophora costata* with an understorey of sclerophyllous shrubs and bracken. On sandy flats, *Eucalyptus botryoides* and *A. costata* form a taller forest with an understorey that includes a mixture of mesophyllous and sclerophyllous shrubs and herbaceous plants. Heathlands occur on deep sands and on the exposed sandstone plateau. Floristic composition varies between these substrates, although both communities comprise a dense to open cover of sclerophyll shrubs interspersed with sclerophyll sedges. Wetlands are restricted to lagoons in dune swales and swampy sand flats. They are mainly herbaceous communities dominated by *Baumea juncea* with *B. articulata, Leptocarpus tenax* and other sedges. They are currently listed as an Endangered Ecological Community (Sydney Freshwater Wetlands) under the *NSW Threatened Species Conservation Act 1995*.

The township of Bundeena occupies about 100 ha within the study area, covering sand dunes, sand flats and sandstone ridges. The majority of the town precinct comprises suburban dwellings on blocks <0.1 ha, some of which are fenced to exclude deer from gardens. There are substantial areas planted with exotic grass on road verges and in parks and yards. Native plants, relics of the original vegetation, persist as solitary individuals or in clumps throughout the town. At least some of the deer in the area spend some of their nocturnal foraging time within the suburban limits of Bundeena. They graze on grassy areas and are fed vegetable matter by a few local residents. They also browse on a variety of forbs and woody plants, including various vegetables, exotic ornamental plants and local native plants.

Survey

Extensive reconnaissance was undertaken throughout the native vegetation and the suburban area to observe deer behaviour and movement, record plant species consumed or damaged by deer and effects of deer on the structure of vegetation and soils. Observations were made opportunistically between 1999 and 2003. Observations on native plants were confined to bushland areas within 1 km of Bundeena township, but at least 20 m beyond the suburban/bushland boundary. The effects were classified into the following categories: young foliage and shoots consumed; young and old foliage and shoots consumed; bark stripped; woody stems broken; seedlings uprooted; inflorescences damaged or consumed; and unaffected. Qualitative observations on damage to vegetation structure and soils were also recorded during the reconnaissance of bushland.

To examine the effects on soils where deer activity was concentrated, three sites were identified where deer were fed by local residents. All three sites were on deep, unconsolidated sand dune soils on the interface between eucalypt woodland and the eastern edge of the suburban area. They were separated from one another by distances of 200 metres, and not included in the reconnaissance survey, which sampled bushland away from the suburban interface. Soils and vegetation at these sites were observed between 1999 and 2003, and qualitative descriptions of vegetation cover and soil level were compared to those of equivalent sites on the bushland/suburban interface approximately 50 m distant from each feeding site. The equivalent sites were also on sand and had similar vegetation (disturbed heathy woodland) and a similar management history to the feeding sites.

Exclosure experiment

Ninety-three individuals of *Syzygium paniculatum* were planted in a 0.1 ha yard, grassed with *Pennisetum clandestinum* and enclosed within 1 m high wire fencing. The plants were 1.0 – 1.4 m tall and were watered for three months after planting. After one month, all plants were in a healthy condition and growing new shoots when the yard was opened, allowing deer access. Initially relatively few deer entered the yard, but after several weeks, several animals gained regular access during nights. After three months, the gate was closed. Deer gained intermittent access to the yard after that time until the perimeter fence was raised to a height of 1.5 m. As a qualitative control treatment, five plants were observed in an adjacent yard that was maintained to exclude deer throughout the duration of the experiment. Brush-tailed possums, the only other vertebrate herbivore on the site, were observed in both the treatment and control yards. Effects on *Syzygium paniculatum* were recorded six months after deer initially gained access as follows: >75% foliage and branchlets consumed; ≤75% foliage and branchlets consumed; main stem broken within 30 cm of base; bark removed; or foliage and branches unaffected. One year after deer had been excluded, plants were recorded as either dead, alive and growing new shoots or alive and not growing new shoots.

RESULTS

Vegetation structure and soils

Reconnaissance of bushland suggested that structural irregularities in the vegetation, including tracks and open areas with low densities of woody plants, were associated with deer access and activity. Footprints indicated that a number of tracks in the area were used by both humans and deer. However, numerous tracks in the area showed no evidence of regular human usage and generally dissipated after some distance or terminated in open areas in the forest understorey or heathland. These open areas varied from 2 – 50 m^2 and had conspicuously lower densities of shrubs and groundcover than the surrounding vegetation (Fig 1a). Resting deer were disturbed from some of these sites during reconnaissance and the presence of droppings, footprints and/or dead remains of deer at most sites suggested that they function as deer encampments. There was little evidence of significant surface erosion on the sand dunes within heathlands or woodlands, except along the tracks (Fig. 1b), which were depressed below the general soil surface. However, the wetland soils were exposed, compacted and deformed on the surface by deer footprints. These areas of bare compacted soil were most commonly encountered around the margins of wetlands.

The three sites where deer were fed by local residents on the bushland/suburban interface had a low open cover of grasses, herbs and shrubs when observations began in 1999. By 2003, all three sites were denuded of vegetation cover and had lost up to 0. 6 m of topsoil (Fig. 2). At two of the sites, retaining walls supporting built-up residential yards had been

Figure 1. Changes in the structure of vegetation and soils related to deer activity: a (top) clearing approximately 220 m east of Bundeena within a dry sclerophyll forest from which all woody understorey plants have been eliminated and groundcover plants have been thinned exposing bare soil; b (bottom) an area near the beginning of the coast walk opened up by deer activity approximately 6 months prior to photophraph, showing deer footprints on bared soil surface and lignotubers of *Lambertia formosa* exposed by significant soil erosion.

Figure 2. Site on the bushland/suburban interface at the end of Scarborough Street, Bundeena, where concentrated deer activity resulted in substantial loss of soil. The relic shrub with exposed root burl is *Leucopogon ericoides*. Feeding of deer ceased at this site approximately two years prior to photograph, though the animals continue to pass through the area and maintain an exposed soil surface.

substantially undermined by erosion of the dune. The denuded areas had high densities of deer droppings and footprints, and varied in area from 400 to 1075 m^2. The roots of trees and large shrubs (*Corymbia gummifera*, *Banksia integrifolia* subsp. *integrifolia*) had been exposed and broken in the eroded sites. Substantial volumes of sand had been transported downslope and deposited within the adjacent area of native vegetation. The equivalent sites on the bushland/suburban interface, approximately 50 m from each of the feeding sites, showed lower densities of deer prints and dung, comparatively little evidence of erosion and sedimentation, and retained an open continuous cover of grasses, herbs and scattered shrubs.

Plant survey

Seventy native plant species from 29 families and two introduced species showed evidence of damage by deer (Table 1). Young foliage and shoots were preferentially browsed on most of the plant species recorded. Older and tougher leaves were less affected, although in many species there appeared to be little distinction between consumption of young and old leaves (Fig.3). The effects of browsing were spatially variable because some species that were heavily browsed in some areas appeared to be relatively unaffected in others. The removal of shoots was particularly frequent and conspicuous in many leguminous species (family Fabaceae), with some individuals being completely defoliated. Rainforest species, notably *Acmena smithii, Cissus antarctica, Clerodendrum tomentosum, Rapanea howitteana* and *Syzygium paniculatum,* also suffered high levels of defoliation. The plant families Epacridaceae and Proteaceae also had large numbers of affected species.

Bark was removed or damaged on large woody stems of six species (Table 1). In some cases, scattered remains of bark and the abraided appearance of the stem from which bark was removed suggested that damage was probably caused by antler rutting. In other cases, particularly the rainforest species, bark had been torn off in strips and may have been consumed as food. In several monocotyledonous species, including orchids, *Doryanthes* and *Xanthorrhoea*, inflorescences had been consumed or destroyed. Remains of destroyed *Xanthorrhoea* inflorescences indicated that this occurred during the bud stage.

Only nine species of plant consistently showed no evidence of damage by deer. Three of these were ferns and three were sclerophyllous sedges.

Family	Species	Young foliage and shoots consumed	young and old foliage and shoots consumed	Bark stripped	Woody stems broken	Seedlings uprooted	Inflorescences damaged or consumed	Not affected
Agavaceae	*Doryanthes excelsa*	X					X	
Anacardiaceae	*Euroschinus falcata*	X						
Anthericaceae	*Thysanotus virgatus*		X				X	
Apiaceae	*Platysace linearifolia*		X					
Arecaceae	*Livistona australis*	X				X		
Asparagaceae	**Asparagus densiflorus*		X					
Casuarinaceae	*Allocasuarina distyla*	X						
Casuarinaceae	*Casuarina glauca*	X			X			
Cyperaceae	*Caustis pentandra*	X						
Cyperaceae	*Lepidosperma concava*	X						
Cyperaceae	*Schoenus brevifolius*							X
Dennstadetiaceae	*Pteridium esculentum*							X
Dennstadetiaceae	*Hypolepis muelleri*							X
Dilleniaceae	*Hibbertia scandens*		X					
Elaeocarpaceae	*Elaeocarpus reticulatus*	X						
Epacridaceae	*Astroloma pinifolia*	X?						
Epacridaceae	*Brachyloma daphnoides*		X					
Epacridaceae	*Epacris longiflora*	X						
Epacridaceae	*Leucopogon ericoides*	X						
Epacridaceae	*Leucopogon parviflorus*	X						
Epacridaceae	*Monotoca elliptica*	X?						
Epacridaceae	*Monotoca scoparia*	X						
Epacridaceae	*Styphelia viridis*		X					
Euphorbiaceae	*Phyllanthus gunnii*	X?		X				
Euphorbiaceae	*Ricinocarpos pinifolius*		X					
Fabaceae	*Acacia implexa*	X						
Fabaceae	*Acacia longifolia*		X					
Fabaceae	*Acacia suaveolens*		X					
Fabaceae	*Aotus ericoides*		X					
Fabaceae	*Bossiaea ensata*	X						
Fabaceae	*Bossiaea heterophylla*		X					
Fabaceae	*Dillwynia floribunda*	X						
Fabaceae	*Kennedia rubicunda*		X					
Fabaceae	*Phyllota phyllicoides*		X					
Fabaceae	**Senna pendula* var. *glabrata*		X					
Fabaceae	*Viminaria juncea*		X?					
Iridaceae	*Patersonia glabrata*	X						
Lomandraceae	*Lomandra longifolia*	X						
Luzuriagaceae	*Geitonoplesium cymosum*		X					
Moraceae	*Ficus rubiginosa*		X					
Myrsinaceae	*Rapanea howitteana*		X					
Myrtaceae	*Acmena smithii*		X					
Myrtaceae	*Angophora costata*	X				X		
Myrtaceae	*Corymbia gummifera*	X?		X	X		X	
Myrtaceae	*Leptospermum laevigatum*		X					
Myrtaceae	*Leptospermum polygalifolium*	X						
Myrtaceae	*Leptospermum squarrosum*		X					
Myrtaceae	*Leptospermum trinervium*		X					
Myrtaceae	*Melaleuca nodosa*							X
Myrtaceae	*Syzygium paniculatum*		X	X				

Family	Species	Young foliage and shoots consumed	young and old foliage and shoots consumed	Bark stripped	Woody stems broken	Seedlings uprooted	Inflorescences damaged or consumed	Not affected
Oleaceae	*Notelea longifolia*	X						
Orchidaceae	*Caladenia caerulea*[+]						X	
Orchidaceae	*Cyrtostylis reniformis*[+]						X	
Orchidaceae	*Glossodia minor* X *Caladenia caerulea* hybrids[+]						X	
Orchidaceae	*Pterostylis sp.* [+]						X	
Phormiaceae	*Dianella caerulea*	X						
Poaceae	*Austrostipa pubescens*		X					
Proteaceae	*Banksia ericifolia*							X
Proteaceae	*Banksia integrifolia* subsp. *integrifolia*	X	X					
Proteaceae	*Banksia marginata*		X					
Proteaceae	*Banksia oblongifolia*		X					
Proteaceae	*Banksia serrata*	X		X				
Proteaceae	*Conospermum taxifolium*		X					
Proteaceae	*Hakea laevipes* subsp. *laevipes*		X					
Proteaceae	*Hakea propinqua*				X			
Proteaceae	*Isopogon anemonifolius*	X						
Proteaceae	*Lambertia formosa*							X
Proteaceae	*Persoonia levis*		X					
Proteaceae	*Petrophile pulchella*		X					
Proteaceae	*Telopea speciosissima*	X					X	
Proteaceae	*Xylomelum pyriforme*		X					
Restionaceae	*Hypolaena fastigata*							X
Restionaceae	*Leptocarpus tenax*							X
Rutaceae	*Acronychia oblongifolia*	X		X				
Sapindaceae	*Cupaniopsis anacardioides*	X						
Sinopteridaceae	*Pellaea falcata* var. *falcata*							X
Solanaceae	*Solanum stelligerum*	X?						
Ulmaceae	*Celtis paniculata*			X	X			
Verbenaceae	*Clerodendrum tomentosum*		X					
Vitaceae	*Cissus antarctica*	X						
Vitaceae	*Cissus hypoglauca*	X						
Xanthorrhoeaceae	*Xanthorrhoea resinifera*						X	

* Introduced species
[+] Margaret Bradhurst, unpubl. data.

Table 1. (opposite page and above) List of plant species affected by deer. Nomenclature follows Harden (1990-2002) and recent updates (www.plantnet.rbgsyd.gov.au).

Effects on *Syzygium paniculatum*

All 93 individuals of *Syzygium paniculatum* suffered some loss of foliage when deer gained access to the yard (Table 2). For a large majority of individuals, the level of defoliation was severe, with less than 25% of foliage remaining on the plant. About 15% of plants were severely damaged, having their bark stripped off or their main stem broken near ground level. However, about 90% of plants began to recover when deer were excluded, shooting new foliage in the next growing season. The five plants in the adjacent yard, where deer remained excluded, did not suffer any appreciable loss of foliage. Scats and nocturnal observations indicated that deer regularly gained access to the open yard, but not to the closed control, while common brush-tailed possums gained access to both yards and were the only other vertebrate herbivore observed at the site.

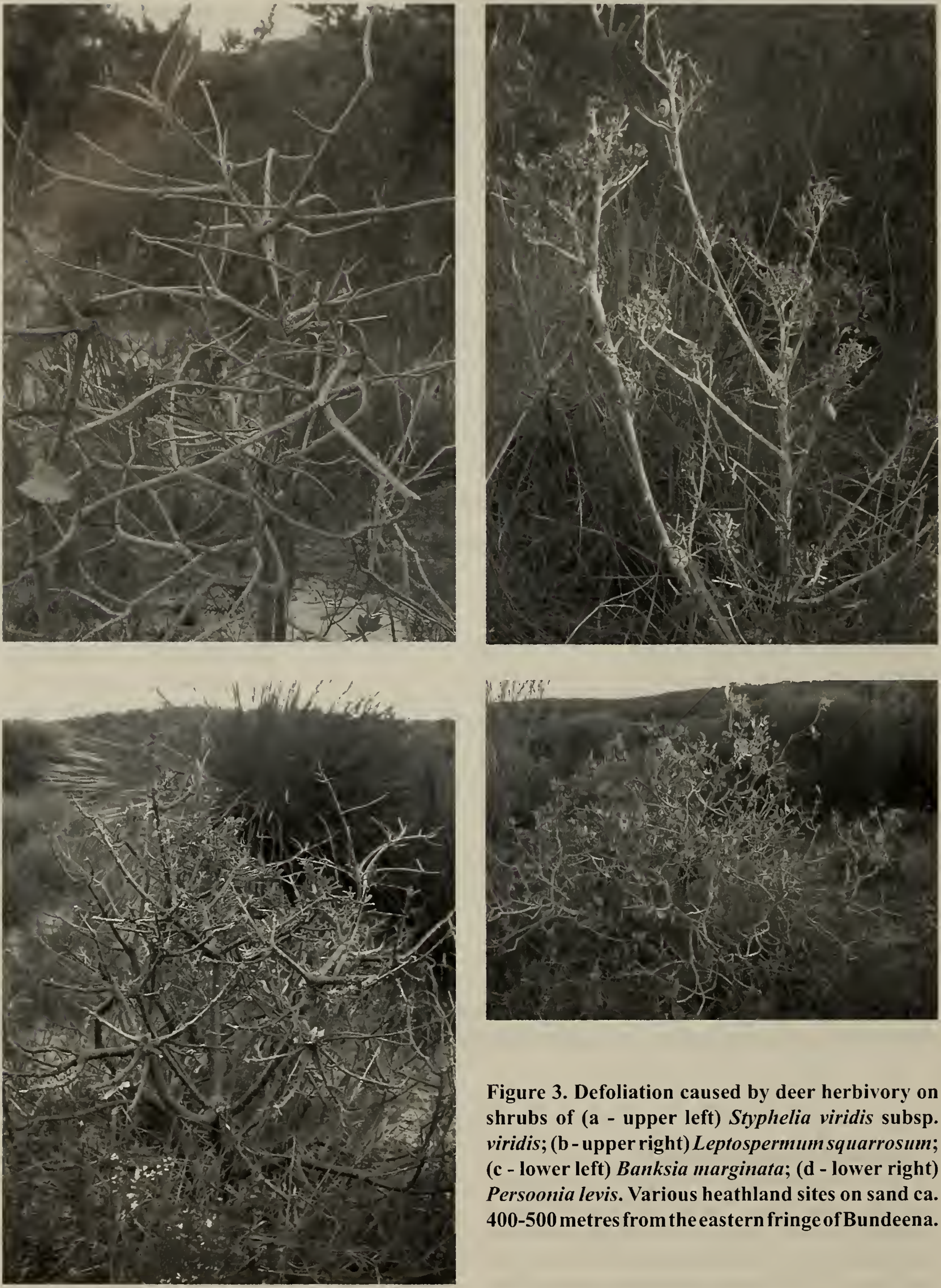

Figure 3. Defoliation caused by deer herbivory on shrubs of (a - upper left) *Styphelia viridis* subsp. *viridis*; (b - upper right) *Leptospermum squarrosum*; (c - lower left) *Banksia marginata*; (d - lower right) *Persoonia levis*. Various heathland sites on sand ca. 400-500 metres from the eastern fringe of Bundeena.

	Control	Treatment 6 months after deer gained access	Treatment one year after deer gained access and were subsequently excluded		
Effect class	Number (%) of plants (N=5)	Number (%) of plants (N=93)	Alive & sprouting new foliage	Alive but with no new foliage	Dead
>75% foliage and branchlets consumed	0	78 (84)	72	5	1
≤75% foliage and branchlets consumed	0	3 (3)	3	0	0
main stem broken within 30 cm of base	0	9 (10)	7	1	1
bark removed	0	3 (3)	2	0	1
foliage and branches unaffected	5 (100)	0 (0)	-	-	-

Table 2. Effects of deer on planted *Syzygium paniculatum* in the exclosure experiment.

DISCUSSION

Deer consumed a wide variety of plant material including young and old foliage, branchlets, bark and reproductive material of a large number of plant species from a broad taxonomic spectrum. The generalisation that deer limit regeneration and reproduction in a wide variety of plant species appears to hold for different species of deer studied across a broad range of ecosystems all over the world, including North America (McShea and Rappole 1999, Opperman and Merenlender 2000, Rooney 2001, Rooney et al. 2004), Europe (Kay 1993, Fuller and Gill 2001, Rackham 2003) and Asia (Okuda and Nakane 1990, Kahn et al. 1994, Akasi and Nakashisuka 1999), where deer are native, and Australia (Moriarty 2004a), New Zealand (Jane 1994, Coomes et al. 2003) and South America (Veblen et al. 1992), where they have been introduced. In both cases, deer populations seem to have increased recently, either as a result of expansion into new habitats at previously uninhabited locations (Forsyth et al. 2004) or as a result of landscape changes within their natural range (Mladenoff and Stearns 1993, Fuller and Gill 2001). The large number and diversity of native plant species affected by deer in the Bundeena-Jibbon area were also consistent with previous studies in Royal National Park that have shown deer to be adaptable dietary generalists. Hamilton (1981), for example, showed that the proportion of food types consumed by deer varied with season and habitat. Deer faeces generally contained higher proportions of shrub and herb fragments in winter and/or spring, and higher proportions of grass fragments in other seasons. Faeces recovered from rainforest had the highest content of shrub and herb material (ca. 80%), while faeces from grassland/wet sclerophyll habitats had the highest content of grasses (70-90%) and faeces from dry sclerophyll forest and heathland had roughly equal proportions of broad-leaf and grass material. Moriarty (2004b) recorded similar dietary variation from rumen analyses, with grasses comprising the majority of food in the vicinity of cleared areas, while native plants other than grasses were the major food source in other areas.

Our list of plant species affected by deer is substantially larger than previously reported lists (Hamilton 1981), but most unlikely to be exhaustive. Uncommon species and herbaceous species, which may be consumed in their entirety, are likely to be under-recorded in reconnaissance surveys such as ours. There is also a risk that signs of browsing could have been overlooked on some plants or that evidence of browsing was erroneously attributed to deer. The latter source of errors is unlikely to be significant because wallaby and possum scats were rarely seen within the study area, whereas deer scats were very common. Alternative techniques entail different sampling errors. Analyses of faeces and rumen samples, for example, face difficulties of identifying plant fragments, high variability between samples and limitations that labour-intensive laboratory analysis impose on sample size. Nevertheless, it would be possible to compile a more comprehensive list of plants consumed by deer with increased sampling effort and a combined sampling approach including exclosure experiments and analyses of faeces and rumen.

In addition to the direct effects of herbivory, deer had substantial, though localised, impacts on soils and vegetation structure. Dune soils were severely eroded at parts of the urban interface where feeding by humans lead to intensive deer activity. The comparison with equivalent sites nearby indicated that the severe impacts diminish rapidly with distance from feeding sites. However, destabilisation of the dune may result in the longer term if the denuded sites become the catalyst for more widespread mobilisation of sand. Within native vegetation, shrub cover was locally reduced along deer tracks and in encampment areas but erosion of sand was generally minimal. Impacts on wetland soils were more marked, with increased exposure, compaction and surface deformation evident in all three wetlands inspected.

The exclosure experiment showed that deer may have very substantial impacts on the populations of at least some plant species over a relatively short time frame. The extent of foliage and shoot removal precluded any chance of reproduction in the plants exposed to browsing by deer. The level of mortality caused by bark stripping and stem breakages, while comparatively small over the duration of the experiment, would account for an appreciable reduction in a cohort of saplings over several years. The combined effects of foliage and shoot removal and cumulative mortality are likely to delay or prevent the growth of individual plant canopies above the browse height. *Syzygium paniculatum* appears to be one of the more palatable native plants in the study area, despite the essential oils in its foliage and the availability of copious grass in the vicinity. The observed effects on *S. paniculatum* probably represent the more severe of those to be observed among wild plant populations although, in bushland, severe defoliation was observed in species from a wide range of plant families including Fabaceae and Epacridaceae (Fig. 2). Effects are likely to be particularly severe in rainforest communities, such as the Littoral Rainforest Endangered Ecological Community. They also have major implications for revegetation projects, which may be prone to major losses if deer gain access to the plantings before they grow beyond browse height (e.g. Opperman and Merenlender 2000).

A number of limitations in the design of the exclosure experiment impose constraints on interpretation of the results. The comparison was based on unreplicated treatments with unbalanced sample sizes. In the field, plants would be exposed to deer browsing at a much younger stage and would not be surrounded by grassy areas as they were in our experiment. Despite these differences between the experimental conditions and those in the field, the symptoms of deer browsing observed in the experimental population were substantial (relative to the control plants) and similar to those observed in other rainforest and sclerophyll forest plant species during reconnaissance of native vegetation. Data from replicated exclosures, which have recently been established in native vegetation (Moriarty 2004b), will help to resolve uncertainties that arise when interpreting our experimental results in the context of wild plant populations.

In Fig. 4, we propose a model of impacts based on plant life histories as a means of structuring future experimental investigations on the medium- to long-term impacts of deer herbivory on native vegetation. The model proposes that deer herbivory has its largest impact on population viability by interrupting two major plant life-cycle processes: seedling establishment and seed production. Compared with established plants, seedlings have less capacity to recover after defoliation and could be more palatable due to the lower content of fibre, tannins and phenolic compounds in their leaves. Bushfires expose more seedlings to browsing by deer because they release seeds of many species from dormancy or canopy storages (Keith 1996). Populations of plant species that only regenerate from seed are exposed to greater risks of decline than those in which a proportion of pre-fire established plants survive. Factors that influence the density of post-fire deer populations, such as fire size and patchiness and deer dispersal patterns, are potentially important in mediating the impact of deer on seedling recruitment.

A second mechanism of deer impact on the viability of plant populations is through the reduction of fruit production (Fig. 4), as the resulting decline in seed banks reduces the capacity for seedling recruitment. These effects are likely to be most significant in species such as terrestrial orchids and lilies, in which all reproductive material may be consumed in a single visit, and those species whose reproductive effort is largely limited to the post-fire period (Keith 1996). While the magnitude of reductions in fecundity remain to be quantified under varying levels of browsing, our qualitative observations during reconnaissance suggest that the current densities of deer populations in the Jibbon/Bundeena area could be causing substantial reductions in seed production in a wide range of plant species.

A third life-cycle process susceptible to interruption by deer herbivory is the survival and growth of established plants. These effects are likely to be less significant in plant species that are capable of growth above the vertical reach of deer (c. 1.5-2.0 m). However, sustained herbivory could slow or block the transition from juvenile to mature growth forms and could also reduce survival in mature individuals if bark stripping occurs at levels observed in the exclosure experiment. These effects have resulted in failure of revegetation projects elsewhere in Royal National Park (e.g. Hacking River Valley) and in other parts of the world (Augustine

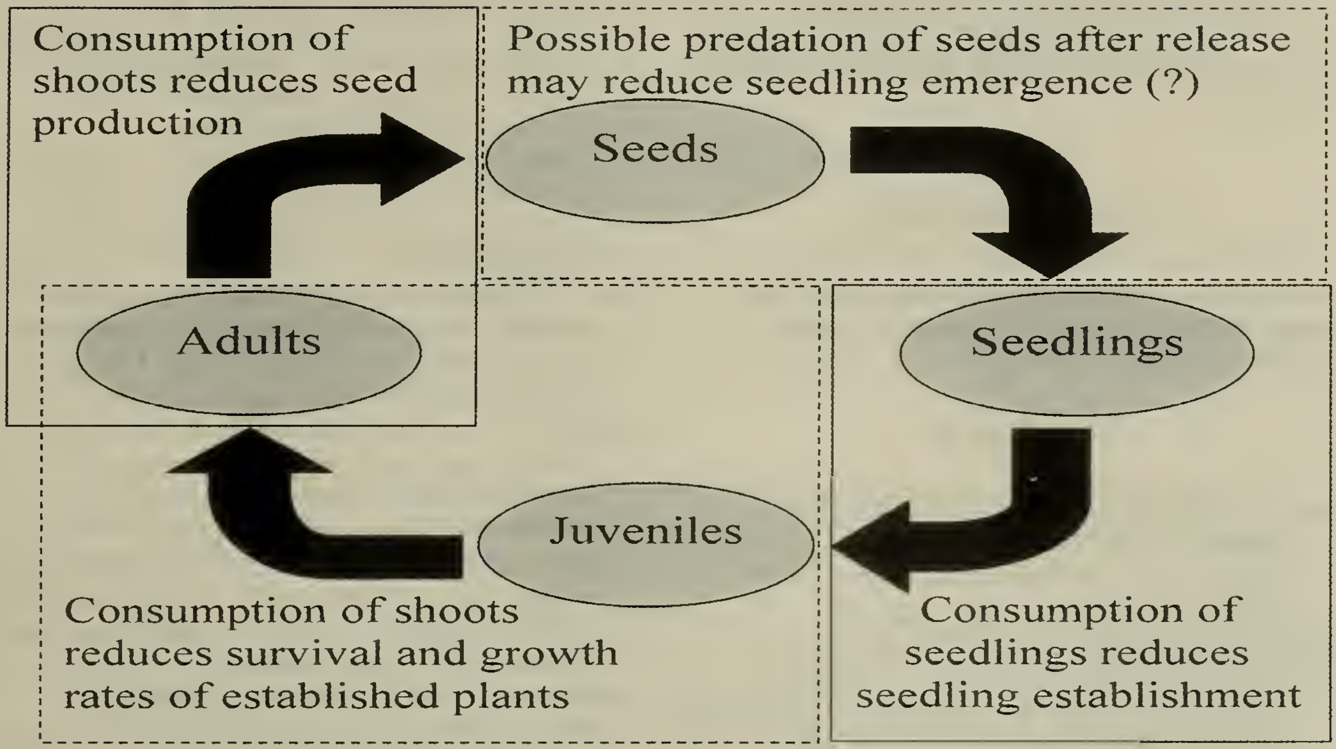

Figure 4. Simplified plant life cycle showing life history processes influenced by deer herbivory. Processes marked by unbroken lines are predicted to exert a greater influence on population viability than those marked by broken lines.

and Frelich 1998, Opperman and Merenlender 2000, Coomes et al. 2003), imposing substantial additional costs on the rehabilitation of degraded areas. Deer are also implicated in the predation of seeds after their release from plants. For example, the removal of *Telopea speciosissima* seeds from experimental caches coincided with deposition of deer faeces at the site (T. D. Auld and A. Denham, unpublished data). However, the magnitude of seed losses is unknown.

In wild populations, the impacts on survival and growth of established plants are likely to be less significant than effects on seedling recruitment and fruit production, but all three processes will have cumulative impacts on the population viability of many plant species. The magnitude of impacts for any given plant species will depend upon its palatability relative to other available forage, density of the deer population, the accessibility of edible plant tissues and the propensity to replace leaf tissue. The model (Fig. 4) nevertheless predicts the decline of many woody plant species and some herbaceous species because the recruitment of new seedlings fails to compensate for the attrition of established plants. This is supported by Moriarty's (2004b) observation that 30-70% fewer plant species occurred in understorey vegetation exposed to high deer densities compared with that exposed to low deer densities. On the other hand, deer herbivory could favour the relatively few unpalatable plant species, particularly those ferns and sedges that may spread vegetatively to occupy space vacated by declines in densities of palatable shrubs and herbs. The abundance of *Pteridium esculentum* and relative scarcity of shrubs in forest understories adjacent to cleared grassy areas would seem consistent with this prediction. The predicted transformation of forest understories from structurally complex, floristically diverse assemblages to simple assemblages dominated by ferns and sedges is likely to reduce the suitability of habitats for a range of vertebrate and invertebrate fauna (Catling 1991, York 1999).

Reducing the density of deer populations may slow or reverse some effects of deer herbivory, as suggested by the observed recovery of surviving individuals of *Syzygium paniculatum* when deer were excluded from the treatment yard. Such effects have also been observed elsewhere (Anderson and Katz 1993, McShea and Rappole 2000). However, it is not known what level of deer control in the wild would produce such a response. Furthermore, the recovery of native vegetation would be impeded by deer-related soil erosion and compaction, or if densities of shrubs or their seed banks had already declined to very low levels. Our model suggests that fire management and the control of deer after fire are likely to be crucial in managing impacts of deer herbivory on native vegetation.

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A New Early Silurian Species of *Trimerella* (Brachiopoda: Craniata) from the Orange District, New South Wales

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Trimerella australis, a new species of craniate brachiopod, is described from silicified material extracted from Early Silurian limestone in the Bowan Park district, 22 km west of Orange in central New South Wales. Accompanying conodonts of the *Distomodus staurognathoides* Zone indicate this unnamed unit is mid Llandovery (latest Aeronian to earliest Telychian) in age, and support correlation with the Cobblers Creek Limestone at the base of the Waugoola Group. As with most other occurrences of trimerellide brachiopods in the Late Ordovician and Early Silurian of the Lachlan Orogen, *T. australis* completely dominates its depauperate faunal associates of corals including *Aphyllum*? sp., cf. *Axolasma* sp. and cf. *Halysites cratus* Etheridge, 1904 , and very rare atrypide brachiopods. Although all specimens of *T. australis* are disarticulated, the community is interpreted as preserved essentially in situ, representing a very shallow water Benthic Assemblage 2 environment.

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KEYWORDS: Benthic Assemblage, biostratigraphy, Brachiopoda, Craniata, early Silurian, halysitid, tetracorals, trimerellide

INTRODUCTION

Silurian trimerellide brachiopods from the Lachlan Orogen of eastern Australia are poorly known compared to their Late Ordovician predecessors. Only *Keteiodoros bellense* from the Dripstone Formation (Early Silurian, Wenlock) of the Oakdale Anticline, southeast of Wellington, NSW (Strusz et al. 1998), has been fully documented. One other trimerellide specimen, identified by Strusz (1982) as *Trimerella* sp. from the Walker Volcanics of the Canberra area, has been illustrated from Silurian strata in NSW; the age of this occurrence is reported as either Wenlock (Strusz 1982) or early Ludlow (Talent et al. 2003). Unidentified trimerellide material, possibly *Trimerella*, is known from the Manildra district (Savage 1968), in limestone (probably allochthonous) of the Greengrove Formation, the age of which has been interpreted as either lower mid Llandovery (Munson et al. 2000) or mid to late Llandovery (Talent et al. 2003). Here we document the new species *Trimerella australis*, from the Bowan Park district west of Orange, in limestone of mid Llandovery age (*Distomodus staurognathoides* Conodont Zone, equated to the upper *convolutus* to lower *crispus* Graptolite Zones). This new species qualifies as the biostratigraphically most precisely constrained Silurian representative of this order presently known from eastern Australia.

STRATIGRAPHIC SETTING AND AGE

Abundant silicified specimens of the new species of *Trimerella* occur in an unnamed limestone, situated at Grid Reference 672400 mE 6315070 mN (GDA94 co-ordinates) in the Quarry Creek area, east of the Bowan Park district, about 22 km west of Orange (Fig. 1). The limestone was first mapped in detail by Packham and Stevens (1955, fig. 1), who depicted it as two outcrops offset by an east-west fault. Immediately west of the Silurian limestone lie Late Ordovician volcanics equated to the Malachis Hill Formation. To the east, the more northerly outcrop of limestone that yielded the abundant trimerellides abuts

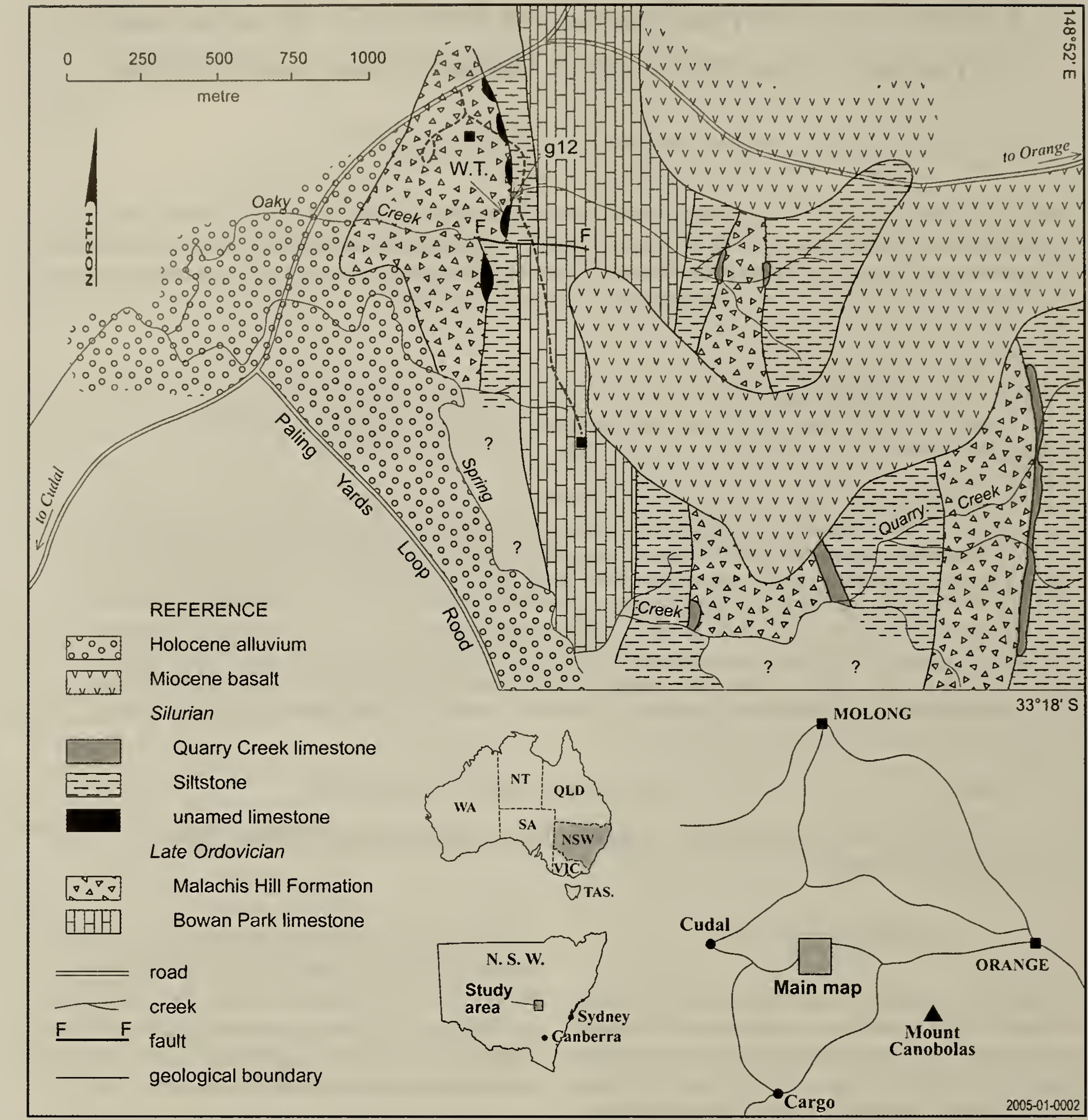

Figure 1. Map of the Quarry Creek area, east of Bowan Park district, 22 km west of Orange, NSW, showing the location of the limestone in the W.T. section of Bischoff (1987) that yielded the trimerellide brachiopods and associated fauna documented in this paper. Geology adapted from Packham and Stevens (1955) and mapping by Packham in Jenkins (1986) and Rickards et al. (1995).

graptolite-bearing beds (g12 locality of Packham and Stevens), considered by those authors to be of late Llandovery age. These graptolitic beds are probably faulted against the limestone. Revised identifications in Rickards et al. (1995, table 1) of many of the late Llandovery graptolite faunas found by Packham and Stevens have indicated that these localities should now be assigned ages in the early to mid Wenlock. R.B. Rickards (pers. comm. 2004) informs us that the graptolite fauna from g12 contains *Testograptus testis* and should be reassigned to the late Wenlock *lundgreni-testis* Biozone. Farther east is limestone of Late Ordovician age, termed the Barton Limestone by Packham and Stevens (1955). Current terminology has seen this name suppressed in favour of the Bowan Park Limestone Subgroup that is extensively developed in the Bowan Park area to the west.

Bischoff (1987) sampled the Silurian limestone (approximately 16 m thick) in his W.T. section, and first recognised its mid Llandovery age, based on conodonts. These were identified by Bischoff as *Aulacognathus angulatus*, *Distomodus staurognathoides* (alpha morphotype), *Oulodus australis*, *O. planus planus*, *Ozarkodina excavata eosilurica* and *Oz. waugoolaensis*; two additional species – *Oulodus panuarensis* and *Pterospathodus cadiaensis* – were very rare in Bischoff's collections. Our sample GSNSW C1892 from the upper part of the limestone, where the trimerellides are particularly abundant, yielded *Oulodus australis*, *O. planus planus*, *Oz. waugoolaensis*, together with *Panderodus* sp. The additional conodont species recorded by Bischoff (1987, table 5), but not identified in our sample, were restricted to the lower part of his W.T. section. Bischoff assigned this conodont fauna to his *Aulocognathus antiquus – Distomodus staurognathoides* alpha Assemblage Zone, which he correlated with the lower *turriculatus* Graptolite Zone, possibly extending into the upper part of the preceding *sedgwickii* Graptolite Zone. Simpson (1995) queried the veracity of *A. antiquus*, and argued that Bischoff's assemblage zone bearing this name should be equated with the *Distomodus staurognathoides* Zone of global usage. Uncertainty in interpretation of the *Aulocognathus* lineage proposed by Bischoff only affects the lower limit of the Zone, and Strusz (1996) (following Simpson) aligned the local conodont zone with the interval represented by the *convolutus* to lower *crispus* graptolite zones. This range encompasses the full extent of the age of the W.T. section as interpreted by Bischoff (1987).

The Quarry Creek Limestone is regarded as either late Llandovery or early Wenlock in age (Bischoff 1987). Rickards et al. (1995) discussed possible problems with the conflict in age between this limestone and the overlying Panuara Formation, but this appears to have been resolved with revision of graptolite identifications from the lower part of the latter unit supporting an early Wenlock age. Munson et al. (2000) placed the Quarry Creek Limestone straddling the Llandovery-Wenlock boundary. Although Talent et al. (2003, figure 6) depicted the Quarry Creek Limestone as occupying a lower Wenlock horizon, they admitted the possibility (p. 200) that this unit is entirely upper Llandovery. Whatever its precise age range, the Quarry Creek Limestone is substantially younger than the unnamed limestone of Bischoff's (1987) W.T. section, and the two horizons cannot be equated as shown in Jenkins (1986, figure 34) and Rickards et al. (1995, figure 2).

The unnamed limestone in the W.T. section is thus the oldest Silurian stratum in the Quarry Creek area, and is correlated using conodonts (Bischoff 1987) with the Cobblers Creek Limestone at the base of the Waugoola Group in the Angullong district, SSW of Orange. Recognition of this relationship is significant in constraining the upper limit of the Panuara Hiatus that separates the Ashburnia and Waugoola groups. Krynen and Pogson (in Pogson and Watkins 1998, p.109) interpreted the base of the Waugoola Group as diachronous, ranging from early late Llandovery in the Angullong Syncline succession, to terminal Llandovery (*P. amorphognathoides* Conodont Zone) in the Quarry Creek area. However, the presence of mid Llandovery strata in the W.T. section indicates that the base of the Waugoola Group in the Quarry Creek area is essentially the same age as elsewhere, and hence is isochronous rather than diachronous.

FAUNAL ASSOCIATES AND DEPOSITIONAL ENVIRONMENT

As with almost all other occurrences of trimerellide brachiopods known from the Late Ordovician and Early Silurian of the Lachlan Orogen, *T. australis* is numerically abundant and completely dominates an otherwise depauperate group of faunal associates. As extraction of fossils was by dissolution of bulk limestone samples in dilute acids, the silicified residues obtained are believed to be fairly representative of the preservable elements of the trimerellide community. In the W.T. section, faunal associates comprise the tetracorals cf. *Axolasma* sp. (Fig. 2a, b) and *Aphyllum*? sp. (Fig. 2d-f), the halysitid tabulate coral cf. *Halysites cratus* Etheridge, 1904 (Fig. 2c), an indeterminate finely-ribbed atrypide brachiopod (Fig. 2g-i) and a smooth atrypide (Fig. 2j). Each of these taxa is represented by at most a few specimens only, compared to many dozens of *T. australis* valves (although a high proportion of the latter are fragmentary, due either to post-mortem breakage or, more likely, incomplete silicification). One example of *Aphyllum*? is preserved on the exterior surface of a dorsal valve of *T. australis*, with the calyx adjacent to the anterior margin (Fig. 3p). Possibly the coral not only employed the trimerellide as a substrate but could also have obtained nutrients from the inhalant or exhalant currents of the living brachiopod. All examples of *T. australis* are disarticulated valves, probably resulting from storm or current activity disturbing in situ specimens or redistributing deceased individuals (cf Webby and Percival 1983). Orientation of shells is generally horizontal, and erratic rather than consistently either convex up or down.

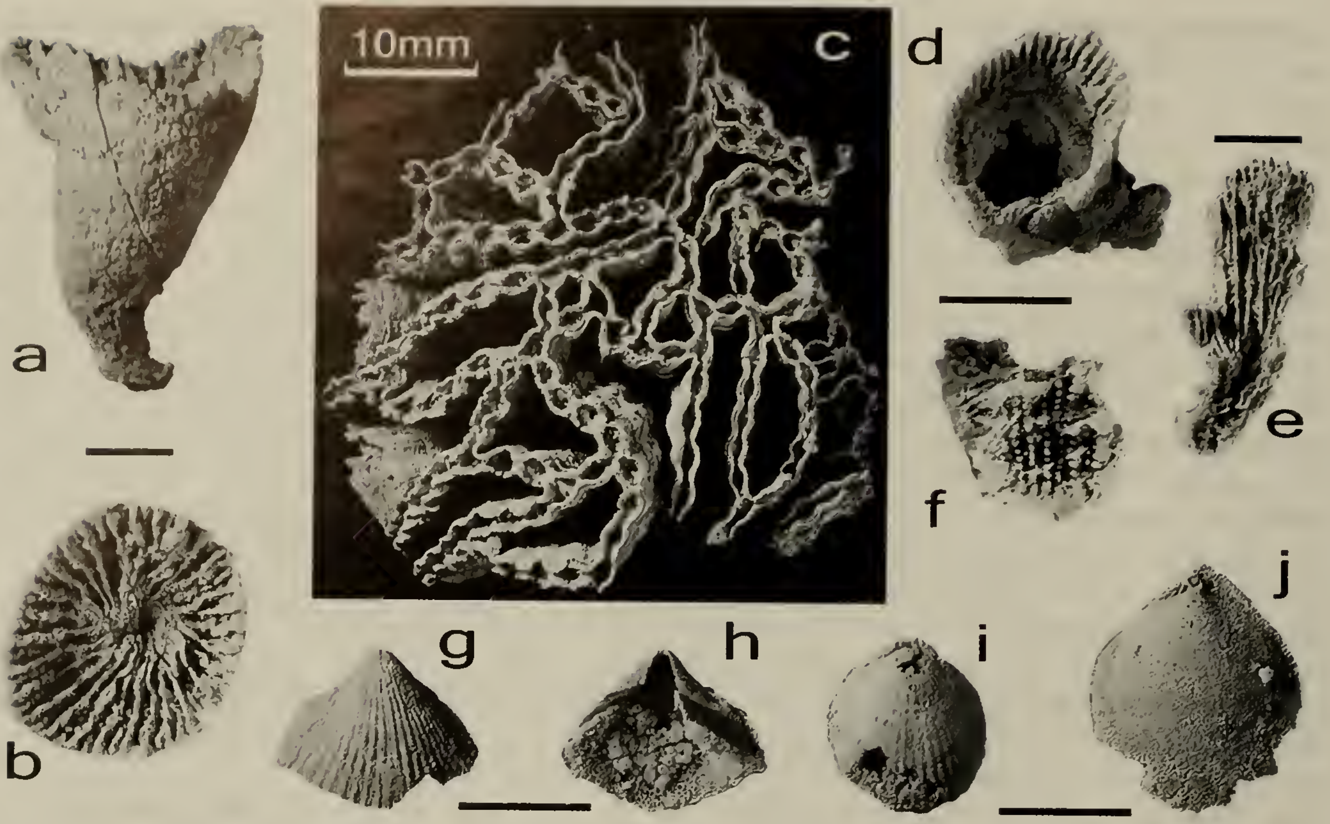

Figure 2. Corals and articulate brachiopods associated with *Trimerella australis*. All specimens silicified; scale bars in black represent 5 mm. (a, b) cf. *Axolasma* sp., MMF 44114, lateral and calical views, displaying axial vortex. (c) cf. *Halysites cratus* Etheridge, 1904, MMF 44115, with calical views of partial colony. (d-f) *Aphyllum*? sp., oblique view of calyx, MMF 44116, longitudinal broken fragment, MMF 44117 showing septa and budding, and fragment of interior of calyx, MMF 44118 displaying acanthine septa. (g, h) indeterminate ribbed atrypide, external and internal views of partial ventral valve and fragment of attached dorsal valve, MMF 44119. (i) external view of dorsal valve of conjoined specimen of ribbed atrypide, MMF 44120. Note circular pitting on surface, possibly caused by predatory sponge. (j) dorsal view of conjoined valves of smooth atrypide, MMF 44121.

Comparable trimerellide communities include Late Ordovician shell beds consisting of *Eodinobolus stevensi* in the lower Fossil Hill Limestone at Cliefden Caves and Daylesford Limestone at Bowan Park (Webby and Percival 1983, Percival 1995), and *Belubula spectacula* in the Belubula Limestone at Cliefden Caves (Percival 1995). *Keteiodoros bellense* from the Dripstone Formation (Wenlock) of the Oakdale Anticline (Strusz et al. 1998) is the only locally-documented Silurian example of an in situ trimerellide community. The Late Ordovician examples from Cliefden Caves and Bowan Park were assigned to a Benthic Assemblage 1 or upper B.A. 2 depositional setting, equivalent to a marine shoreline (intertidal to very shallow subtidal) environment (Percival and Webby 1996). Ordinarily this would be in protected waters such as a lagoon or embayment, as trimerellides – lacking a pedicle attachment – relied on posterior gravity weighting for stability of orientation when alive. Such shallow waters are also highly susceptible to disturbance during storms, accounting for death assemblages and stacked shell beds commonly encountered in trimerellide occurrences. Strusz et al. (1998) attributed to *Keteiodoros bellense* in the Dripstone Formation a B.A. 2 (shallow subtidal) setting, in quiet waters inshore of a protective *Palaeophyllum* wave barrier.

We found no evidence of a protective wave barrier, such as might have been formed by coral thickets or reefs, associated with the *T. australis* shell beds. However, comparable halysitid tabulates and solitary tetracorals associated with this occurrence, and also with *Keteiodoros bellense*, suggest that the depositional environments of these Silurian trimerellides were similar. The stratigraphic position of the *T. australis* shell beds, in limestone deposited following the erosional Panuara Hiatus, also argues for very shallow water, nearshore conditions. Therefore, a quiet water depositional environment no deeper than B.A. 2, and possibly as shallow as B.A. 1, is interpreted for this unit.

SYSTEMATIC PALAEONTOLOGY

Phylum BRACHIOPODA
Class CRANIATA Williams, Carlson, Brunton, Holmer and Popov, 1996
Order TRIMERELLIDA Goryansky and Popov, 1985
Superfamily TRIMERELLOIDEA Davidson and King, 1872
Family TRIMERELLIDAE Davidson and King, 1872
Genus *Trimerella* Billings 1862

Type species

Trimerella grandis Billings, 1862, by subsequent designation of Dall (1870).

Diagnosis

Shell dorsibiconvex, elongate triangular; ventral valve flattened, ventral interarea high, triangular, apsacline, with deep concave homeodeltidium occupying more than half of interarea; dorsal valve strongly convex, beak incurved; ventral umbonal cavities small or vestigial; both valves with distinctly raised visceral platforms, extending anterior of centre; visceral platforms with deep vaults, separated by median partition extending anterior to platform; dorsal hinge plate high, strongly incurved; dorsal *vascula lateralia* broad, slightly divergent, lacking trace of bifurcation (Popov and Holmer 2000, p.185).

Species included:

?*T. asiatica* Li, 1984; *T. jiangshanensis* (Li, 1984) (formerly *Prosoponella*) and *T. zhoujiashanensis* (Li and Han, 1980) (formerly *Machaerocolella*) – both genera synonymised with *Trimerella* by Percival (1995) and Popov et al. (1997); all preceding species from Late Ordovician (early Ashgill) Huangnehkang Formation, Jiangshan county, W. Zhejiang, China (according to Rong and Li 1993).

T. attentuata Goryansky, 1972 from Early Silurian (late Llandovery to early Wenlock) Donenzhal Formation, Kazakhstan (Popov et al. 1997).

T. acuminata Billings, 1862 from Silurian (Wenlock-Ludlow) Guelph Limestone, Ontario (Popov and Holmer 2000, p. 186); Niagara Group, Ohio and Illinois; Gotland and Faro islands, Sweden; Gorno Altay of Russia (Kul'kov 1967).

T. billingsi Dall, 1871 from Silurian (Wenlock-Ludlow) Guelph Limestone, Ontario.

T. grandis Billings, 1862 from Silurian (Wenlock-Ludlow) Guelph Limestone, Ontario; Niagara Group, Ohio.

T. lindstroemi (Dall, 1870) from Silurian (Wenlock) Högklint beds, Gotland (Popov and Holmer 2000, p. 186) and (Ludlow) Klinteberg Limestone, Gotland (Cocks in Murray 1985, p. 55).

T. ohioensis Meek, 1871 from Silurian (Wenlock-Ludlow) Guelph Limestone, Ontario; Niagara Group, Ohio and New York (Popov and Holmer 2000, p. 186).

T. wisbyensis Davidson and King, 1874 from Early Silurian (Wenlock) of Gotland and Estonia.

Trimerella australis sp. nov.
Fig. 3a-q, Fig. 4a-b

Type material

Holotype MMF 44100; paratypes MMF 44101-44113, from unnamed Early Silurian limestone on 'Coorombong' property, east of the Bowan Park district, about 22 km west of Orange, NSW. All specimens curated in the NSW State Palaeontological Reference Collection, held at the Geological Survey of NSW Geoscience Centre, Londonderry.

Diagnosis

Broadly acuminate *Trimerella* with vestigial to shallow ventral umbonal chambers; narrow ventral platform divided medially by parallel-sided furrow, and deeply excavated beneath by twin vaults; dorsal platform supported by median septum longer than rudimentary counterpart in ventral valve but terminating well short of anterior margin.

Description

Dorsibiconvex shell apparently lacking external ornament or pronounced growth lamellae; widest at, or slightly anterior to, midlength. As all specimens are fragmentary, overall dimensions are estimated from reconstructions (Fig. 4); maximum width approximates 45-50 mm, and maximum length is probably at least 60 mm for ventral valves, and about 45 mm for brachial valves. Height of conjoined valves estimated at no more than 20 mm.

Ventral valve broadly acuminate with posterolateral margins forming a right angle at slightly incurved beak; pseudointerarea apsacline to orthocline. Homeodeltidium shallowly depressed, marked by incised flattened chevrons and extending to about one-third width of pseudointerarea at anterior edge (Fig. 3a); homeodeltidium delineated from elongate triangular propareas by incised groove; deltidial ridges lacking, except in one possibly immature individual where the lateral margins of the homeodeltidum are slightly raised (Fig. 3g). A depressed flattened area immediately in front of the

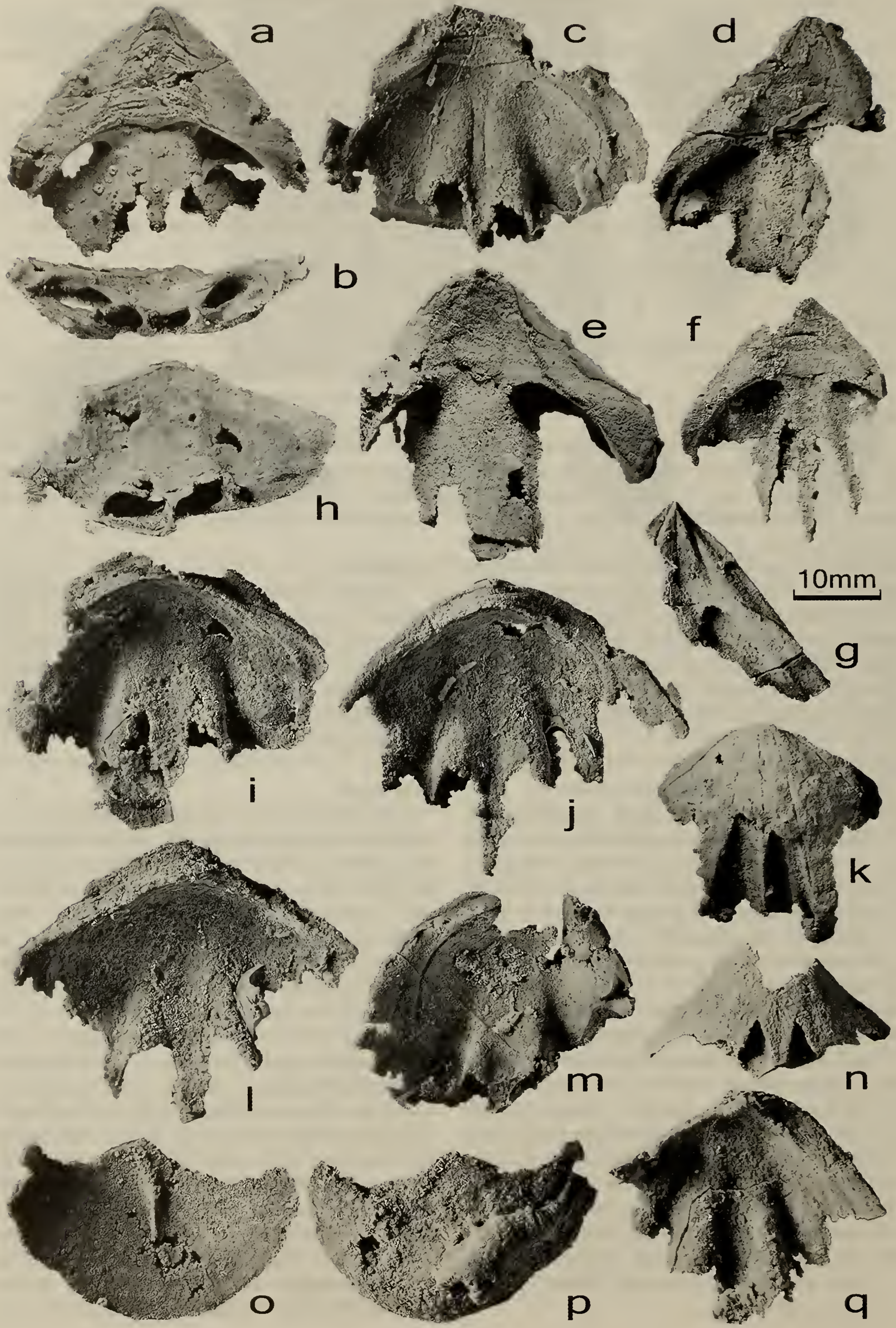
a
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Figure 3. (LEFT) *Trimerella australis* sp. nov. from unnamed Lower Silurian limestone near Quarry Creek. a-b is the holotype, all other figured specimens are paratypes. All specimens 1.5 times natural size. (a, b) internal view of posterior fragment of ventral valve showing pseudointerarea, and oblique view of specimen to display umbonal and platform chambers, MMF 44100. (c) internal view of finely preserved posterior fragment of ventral valve, showing vaulted platform, MMF 44101. (d) internal view of posterior fragment of ventral valve showing pseudointerarea, MMF 44102. (e) internal view of posterior fragment of ventral valve showing pseudointerarea and platform, MMF 44103. (f) internal view of posterior fragment of ventral valve showing pseudointerarea and eroded platform represented by lateral and medial walls of chambers, MMF 44104. (g) internal view of posterior fragment of ventral valve showing partial pseudointerarea, MMF 44105. (h, i) internal view of posterior fragment of dorsal valve, oriented obliquely to show platform chambers, h, and normal view showing platform, i, MMF 44106. (j) internal view of posterior fragment of dorsal valve, showing pseudointerarea and platform, MMF 44107. (k) external view of posterior part of dorsal valve, partially eroded anteriorly revealing interior of platform chambers, MMF 44108. (l) internal view of posterior fragment of dorsal valve, showing pseudointerarea and platform, MMF 44109. (m) internal view of posterior fragment of dorsal valve, showing platform and marginal area, MMF 44110. (n) external view of fragment of ventral? valve, partially eroded anteriorly revealing interior of platform chambers, MMF 44111. (o, p) internal and external views of anterior fragment of dorsal valve showing median septum, o, and tetracoral *Aphyllum*? sp. growing adjacent to valve margin, p, MMF 44112. (q) internal view of posterior fragment of dorsal valve, showing platform, MMF 44113.

anterior edge of the pseudodeltidium may represent the site of a very weakly impressed umbonal muscle scar (Fig. 3a, c, f). Umbonal chambers variably developed even in fully grown specimens, where they may be rudimentary (Fig. 3c) or shallowly excavated (Fig. 3a, b, d, e, f) beneath pseudointerareas, but are always less prominent than visceral platform chambers (Fig. 3b, c, n). Cardinal buttress absent, instead replaced by distinct narrow parallel-sided median furrow slightly depressed below level of adjacent visceral platform (Fig. 3a, c), although this feature is not always apparent (Fig. 3e). Platform surface smooth, lacking traces of muscle scars, and narrowly rounded, reflecting conical vaulted chambers that extend to posterior end of cardinal buttress furrow. V-shaped anterior extremity of platform supported by very short median septum not extending beyond mid-length of valve. Lateral muscle scars, inserted along crescentic

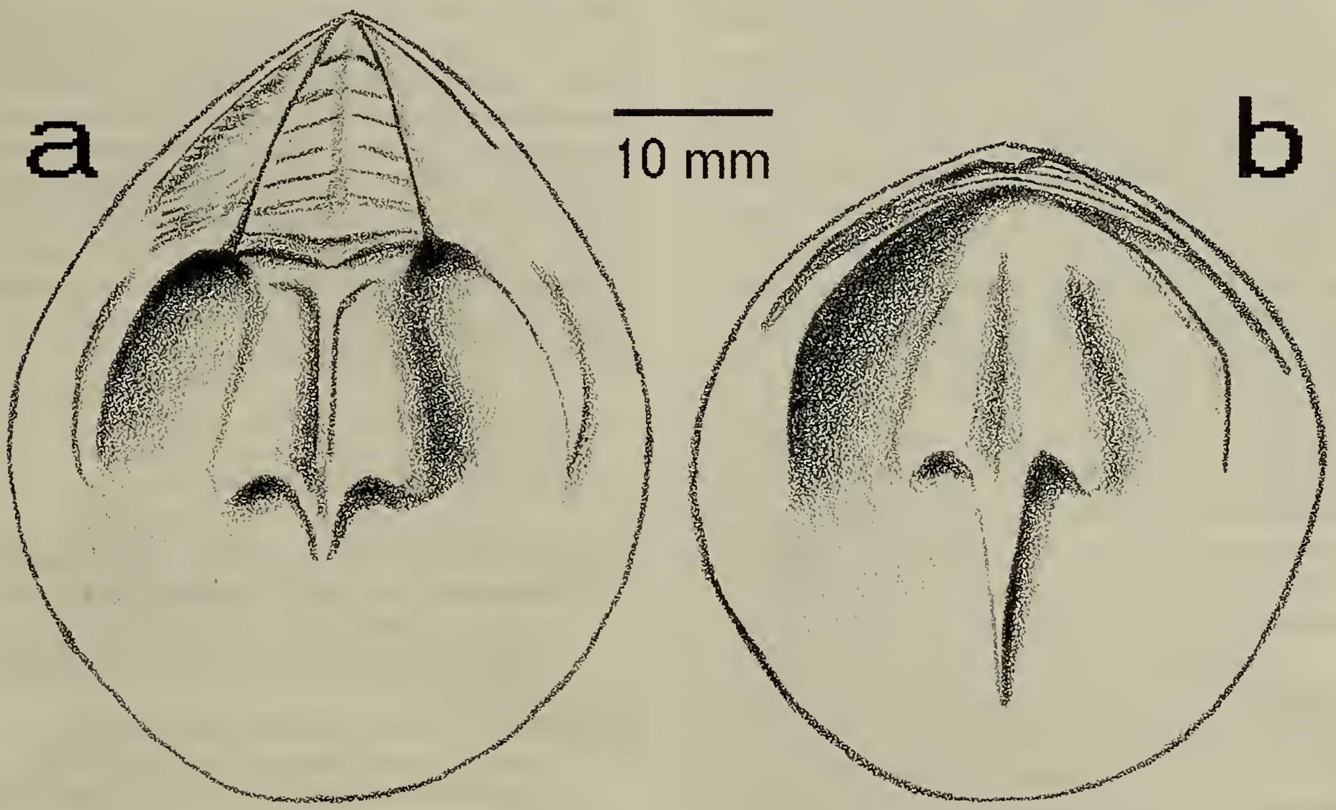

Figure 4. Reconstructions of (a) ventral and (b) dorsal valves of *Trimerella australis*.

furrows parallel to valve margins, prominent in some specimens (Fig. 3c). Pallial canals not visible.

Dorsal valve elongately ovate, with rounded to subangular beak that tends to be slightly to markedly asymmetric, and is gently to moderately incurved (Fig. 3j, l). Brachidial plate curvilinear, prominent but relatively low, occupying all of very low pseudointerarea that expands and merges laterally with broad marginal area raised slightly above valve floor; incised boundary between marginal area and valve floor Fig. 3m) may equate to crescent of previous authors. Marginal area indistinguishable anterior to midlength. Umbonal chambers lacking; umbonal muscle scar not apparent. Visceral platform narrow, distinctly vaulted with long conical chambers beneath (Fig. 3h, i, k); ventral surface strongly convex, bisected longitudinally by broad shallow median depression (Fig. 3j, m, q). No trace of muscle scars on visceral platform, which does not extend into anterior half of valve. Anterior edge of wall separating vaults beneath platform is continuous with thin low median septum, much longer than its counterpart in ventral valve but ending well short of anterior valve margin; the median septum on the one specimen available (Fig. 3o, Fig. 4b) is estimated to terminate between three-quarters and four-fifths valve length. Internal shell surface smooth; no pallial canals discernible.

Remarks

Trimerella attentuata Goryansky, 1972 (revised by Popov et al. 1997), from the late Llandovery to early Wenlock Donenzhal Formation of Kazakhstan, is closest in age and general appearance to the new species. It differs in being much smaller (attaining just half the dimensions of *T. australis*), and in the relatively longer extension of the visceral platform and median septum in the dorsal valve. The ventral platform of *T. attenuata* is relatively wide and in two figured specimens (Popov et al. 1997) bears prominent diagonal growth lines, whereas that of *T. australis* is narrow and smooth. There does, however, appear to be a comparable narrow median furrow developed on the platform of both species, and neither displays any conspicuous extension of a median septum anterior to the ventral platform. All illustrated examples of *T. attenuata* are internal moulds that do not adequately reveal details of the pseudointerareas.

Comparisons with previously established Wenlock to Ludlow species are also hindered by significant differences in preservation. These species of *Trimerella* were originally defined on the basis of natural internal moulds that frequently lacked details of pseudointerareas and visceral platform surfaces. All of the species depicted by Davidson and King (1874) and Hall and Clarke (1892) have been reconstructed with elongate median septa, that in the case of the dorsal valve extend almost to the anterior margin of the valve, unlike *T. australis*. The new species also seems to be compressed dorsoventrally compared with most Wenlock to Ludlow forms. Few of these have been photographically illustrated in the 130 years since Davidson and King's (1874) monograph, but figures in the Treatise (Popov and Holmer 2000, p. 187) confirm the differences discussed above between all these species and *T. australis*.

From species of *Trimerella* described from the Late Ordovician (early Ashgill) Huangnehkang Formation of Jiangshan county, W. Zhejiang, China (Li and Han 1980, Li 1984), *T. australis* is readily distinguished by its relatively deeply excavated ventral platform chambers and absence of a well-developed median septum extending anterior to this platform. Dorsal valves of both ?*T. asiatica* and *T. zhoujiashanensis* are inadequately known and cannot be compared with that of *T. australis*. The new species is furthest removed morphologically from *T. jiangshanensis* (characterised by the presence of stout median septa extending to the margins of both valves).

ACKNOWLEDGMENTS

The presence of trimerellides in the unnamed limestone of Bischoff's W.T. section was discovered during field studies in 1998 by Jonathan Dunningham of Emmanuel College, Cambridge. We are grateful to the owners of 'Coorombong' for access to their property. Preparation of the fragile silicified specimens was skilfully carried out by Gary Dargan, who dissolved the enclosing limestone in dilute hydrochloric acid. David Barnes carefully photographed the specimens and compiled the digital plates. Reviews by two anonymous referees were helpful in improving the final version of this paper. Publication by Percival is authorised by the Director of the Geological Survey of NSW.

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Electrophoretic Evidence for the Presence of *Tandanus tandanus* (Pisces: Plotosidae) Immediately North and South of the Hunter River, New South Wales

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Jerry, D.R. (2005). Electrophoretic evidence for the presence of *Tandanus tandanus* (Pisces: Plotosidae) immediately north and south of the Hunter River, New South Wales. *Proceedings of the Linnean Society of New South Wales* **126**, 121-124.

Eel-tailed catfish from the genus *Tandanus* are morphologically conservative. Previous allozyme electrophoretic surveys have demonstrated that up to three species of *Tandanus* catfish occur in south-eastern Australian freshwater streams. Two of these species are previously undescribed cryptic species. However, the taxonomic status of catfish in many coastal river systems is yet to be examined using allozyme electrophoresis. In this study four diagnostic allozyme markers were used to determine the taxonomic status of eel-tailed catfish in four NSW coastal populations from the Wallamba, Coolongolook, Hawkesbury and Georges River systems. Electrophoretic analyses demonstrated that the species of catfish in these four populations is *T. tandanus*. These results extend the distribution of *T. tandanus* to the coastal rivers immediately north and south of the Hunter River, NSW.

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KEYWORDS: allozymes, catfish, cryptic species, *Tandanus*.

INTRODUCTION

The eel-tailed catfish, *Tandanus tandanus* (Mitchell 1838), had until recently been regarded as a single, broadly distributed species that inhabits freshwater streams throughout the Murray-Darling Basin and coastal drainages of eastern Australia (Allen 1989). However, allozyme electrophoresis studies in the 1990's demonstrated that what was originally thought to be one species of *Tandanus* was in fact a complex assemblage containing up to an additional two undescribed cryptic species (Musyl 1990, Musyl and Keenan 1996, Jerry and Woodland 1997). These studies highlighted that the taxonomy of *T. tandanus* should be revised to recognise the presence of at least three species of *Tandanus* in south-eastern Australia; i) *T. tandanus* which occurs throughout the Murray-Darling River Basin and in the Mary, Brisbane and Hunter coastal rivers; ii) an undescribed species of *Tandanus* within the coastal river systems between and including the Bellinger River and Manning Rivers and; iii) an undescribed species of *Tandanus* restricted to the coastal basin of the Clarence River system (and possibly the Richmond and Tweed River systems) (Fig. 1) (Jerry and Woodland 1997).

The taxonomic status of eel-tailed catfish in many other NSW coastal river systems, however, is unresolved. For example, it is not known what taxonomic variant occurs immediately north and south of the Hunter River population of *T. tandanus*. Of particular interest is whether the distribution of the "Bellinger" variant of *Tandanus* extends south to the Hunter River, or whether *T. tandanus* extends north. The aim of the present study therefore was to use species diagnostic allozyme markers to determine whether *T. tandanus* has a wider distribution in the coastal drainages immediately north and south of the Hunter River (the area designated "taxonomy uncertain" in Fig. 1).

MATERIALS AND METHODS

Catfish were sampled from four coastal river drainages north and south of the Hunter River, NSW. The populations sampled were the Wallamba and Coolongolook Rivers (north of the Hunter River) and the Hawkesbury and Georges Rivers (south of the

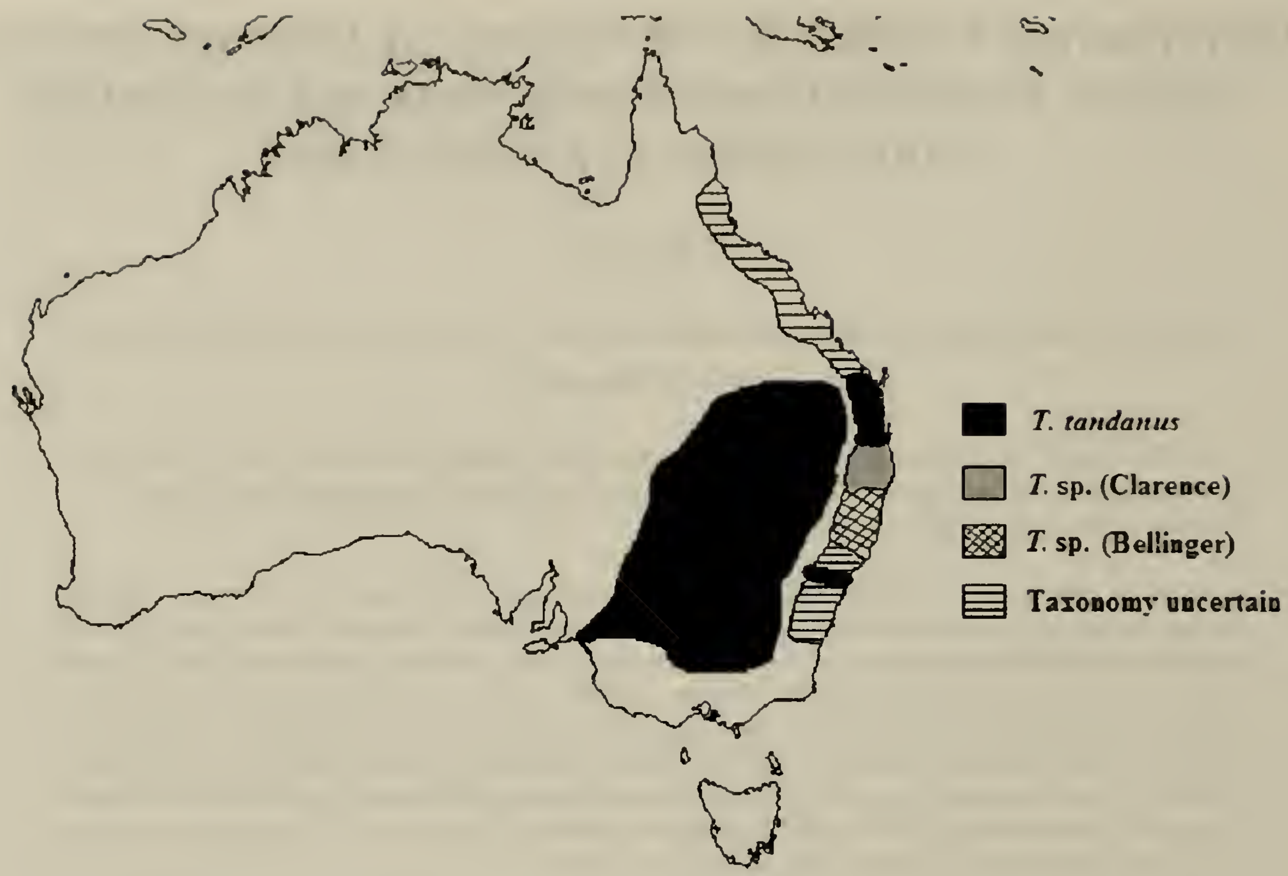

Figure 1. Distribution of Tandanus tandanus, Tandanus sp (Clarence) and Tandanus sp (Bellinger) in eastern Australia. T. tandanus occurs in the Murray-Darling, Brisbane, Mary and Hunter River drainages, T. sp (Clarence) in the Clarence and possibly Richmond and Tweed Rivers, and T. sp (Bellinger) in the Bellinger, Macleay, Hastings and Manning Rivers. Note; Tandanus catfish also inhabit other coastal drainages throughout eastern Australia, however, the taxonomic status of these populations has not been confirmed using diagnostic allozyme markers and it is possible that one or more cryptic species are present. Currently they are considered to be *T. tandanus*.

Hunter River) (Fig. 2). Catfish were opportunistically sampled by gill netting during biological surveys (K. Bishop, personal communication), with two adult specimens collected from each of the river drainages. Upon capture whole specimens were immediately frozen and shipped to the laboratory on dry ice where liver and muscle tissues were excised. Tissue samples were prepared for electrophoresis according to the methods described by Shaklee and Keenan (1986).

Musyl (1990) and Musyl and Keenan (1996) identified four *Tandanus* species diagnostic allozyme markers (International Enzyme Commission Number in parentheses); Glucose-6-phosphate isomerase GPI* (5.3.1.9.), Esterase EST* (3.1.1.-), Umbelliferyl esterases UMB-1* and UMB-2* (3.1.1.-). These markers were used to delineate the taxonomic status of the catfish samples according to the running and scoring conditions described in Jerry and Woodland (1997). To confirm the mobility of diagnostic alleles, the test populations were run against reference specimens of *T. tandanus* (Hunter River) and *T.* sp "Bellinger" (Manning River) in line-up gels for all enzyme systems.

RESULTS

Catfish sampled from the four riverine systems exhibited identical allele motilities at all enzyme loci to those of the *T. tandanus* reference sample from the Hunter River (Table 1). More specifically, test catfish samples exhibited the slower EST*(100) and UMB-2*(100) and the faster GPI*(100) and UMB-1*(100) alleles compared to the mobility of alleles diagnostic to the "Bellinger" variant from the Manning River. Although sample sizes were very small, no genetic variation was observed at any of the allozyme loci. This is consistent with the loci being "fixed" and diagnostic for different alleles among the various species.

DISCUSSION

Figure 2. River populations of Tandanus sampled from coastal drainages of central NSW. Hatched area represents known distribution of Tandanus sp (Bellinger) (ie Bellinger River south to the Manning River).

Fixed alleles at the allozyme markers GPI*, EST*, UMB-1* and UMB-2* have been shown by several authors to be diagnostic in discriminating between the three known species of *Tandanus* inhabiting rivers and streams of south-eastern Australia (Musyl 1990, Musyl and Keenan 1996, Jerry and Woodland 1997). Therefore, based on the electrophoretic evidence presented herein, catfish that inhabit the two major coastal river drainages both north and south of the Hunter River can be considered to be *T. tandanus*.

The known distributional range of *T. tandanus* in coastal drainages of NSW can be extended to include the Wallamba, Coolongolook, Hawkesbury-Nepean and Georges River systems. A variant of *Tandanus* is also found in coastal drainages as far south as the Shoalhaven River in southern NSW and given the close geographical proximity of these drainages, is likely to be *T. tandanus*. However, further studies will be required to verify the taxonomic status of this population.

Table 1. Allele motility at four species diagnostic allozyme loci of Tandanus catfish sampled from four NSW coastal rivers. Allele mobility is calculated as the relative distance moved in the gel of the allele compared to that of the Hunter River population (designated a mobility of 100). The Manning River sample is a representative of the "Bellinger" species of Tandanus (Jerry and Woodland 1997).

Locus	Hunter	Wallamba	Coolongo-look	Hawkesbury	Georges	Manning
EST*	100	100	100	100	100	112
GPI-1*	100	100	100	100	100	84
UMB-1*	100	100	100	100	100	85
UMB-2*	100	100	100	100	100	119

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Diversity and Biogeography of Subterranean Guano Arthropod Communities of the Flinders Ranges, South Australia.

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Moulds, T. (2005). Diversity and biogeography of subterranean guano Arthropod communities of the Flinders Ranges, South Australia. *Proceedings of the Linnean Society of New South Wales* **126**, 125-132.

This study documents the arthropod diversity and ecology of guano-associated species in 12 caves and mines of the Flinders Ranges, South Australia. Twenty two species from 12 orders and two classes are recorded. This represents a five-fold increase in species richness across the region from previously published and unpublished records. Eregunda Mine and Weetootla Gorge Mine 2 were the most diverse with five and six species recorded respectively. Specious groups included the tenebrionid beetle genus *Brises* and the emesine reduviid bug genus *Armstrongula*. Guano communities in the Flinders Ranges contain species in common with the Nullarbor Plain to the west and isolated arid karst areas to the north. There are few affinities with species found in the moist coastal regions of south-eastern Australia.

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KEYWORDS: Arthropoda, biospeleology, cave, food web, guano, invertebrate.

INTRODUCTION

Guano-associated invertebrate communities are poorly known for the vast majority of Australian caves. Animals in these communities are classified according to their ecological dependence on guano as either obligate guano-dwelling animals (guanobites), opportunistic guano-dwelling animals (guanophiles) or transitory guano-dwelling animals (guanoxenes) (Gnaspini and Trajano 2000; Humphreys 2000). The composition and evolution of guanophilic arthropod communities is dramatically different from resource-poor troglobitic (obligate cave-dwelling) communities (Gnaspini 1992; Gnaspini and Trajano 2000). The presence of virtually unlimited food resources enables a wide diversity of normally epigean (surface-dwelling) species to utilise the stable conditions found in caves. This has been previously demonstrated by studies in the south-east and Nullarbor Plain karst areas of South Australia (Richards 1971; Moulds 2004).

Several karst regions containing guano deposits are located in South Australia, ranging from high rainfall coastal areas such as Kangaroo Island and the lower south-east, to dry arid areas such as the Nullarbor Plain, Flinders Ranges and Davenport Ranges. The guanophilic arthropod assemblage in the maternal chamber of Bat Cave, Naracoorte, located in the upper south-east of South Australia, has received the most intensive study for guano invertebrates in Australia (Hamilton-Smith 2000; Sanderson 2001; Bellati et al. 2003; Moulds 2003). A major study of cavernicolous arthropod diversity and ecology on the Nullarbor Plain (Richards 1971) documented the subterranean communities, including those associated with guano. This was the first Australian study to document guanophilic arthropod ecology and provide possible geographic relationships with other Australian guanophilic communities.

The Flinders Ranges, situated between the immense karst area of the Nullarbor Plain to the west, and the karst areas of south-eastern South Australia, contain a number of widely-scattered caves in horizontal or gently dipping Neoproterozoic crystalline limestone (Lewis 1976; Webb et al. 2003). Many of these caves support small (< 50) transient populations of cave-dwelling bats, dominated by the inland cave bat (*Vespadelus findlaysoni* Kitchener, Jones and Caputi), with the chocolate wattled bat (*Chalinolobus morio* Gray) occasionally recorded. The only previously published accounts of guanophilic arthropods for the Flinders Ranges are records of the beetle *Brises acuticornis* Pascoe from three caves

(Hamilton-Smith 1967; Mathews 1986). In addition, several unpublished records of undetermined Acarina, Coleoptera (Carabidae) and Diptera (Nycteriibidae) were recorded by Elery Hamilton-Smith (Moulds 2004).

This study was undertaken due to the paucity of knowledge of cavernicolous invertebrates, specifically guano invertebrates, of this important biogeographic region that links the comparatively well-studied eastern and western karst regions of South Australia. The diversity of guano-associated arthropods in 12 exemplar caves and mines of the Flinders Ranges is documented. Data collected through direct observation and relevant literature are combined to summarise species interactions as a food web. Biogeographic relationships of guanophilic arthropods are believed to be more closely related to nearby arid karst areas than to wetter coastal areas. These relationships are assessed and discussed.

METHODS

Nine caves and three mines were sampled during two field trips in April and September 2003 (Fig. 1). Specimens were primarily collected individually using hand-held forceps due to the extremely localised guano deposits at most sites (Upton 1991). Guano samples were also taken from Weetootla Gorge Mines, Eregunda Mine, and Chambers Gorge caves for extraction of arthropods in Tullgren funnels as described by Upton (1991). Guano was also collected when available in sufficient quantities and measured for pH, allowing micro-habitat conditions

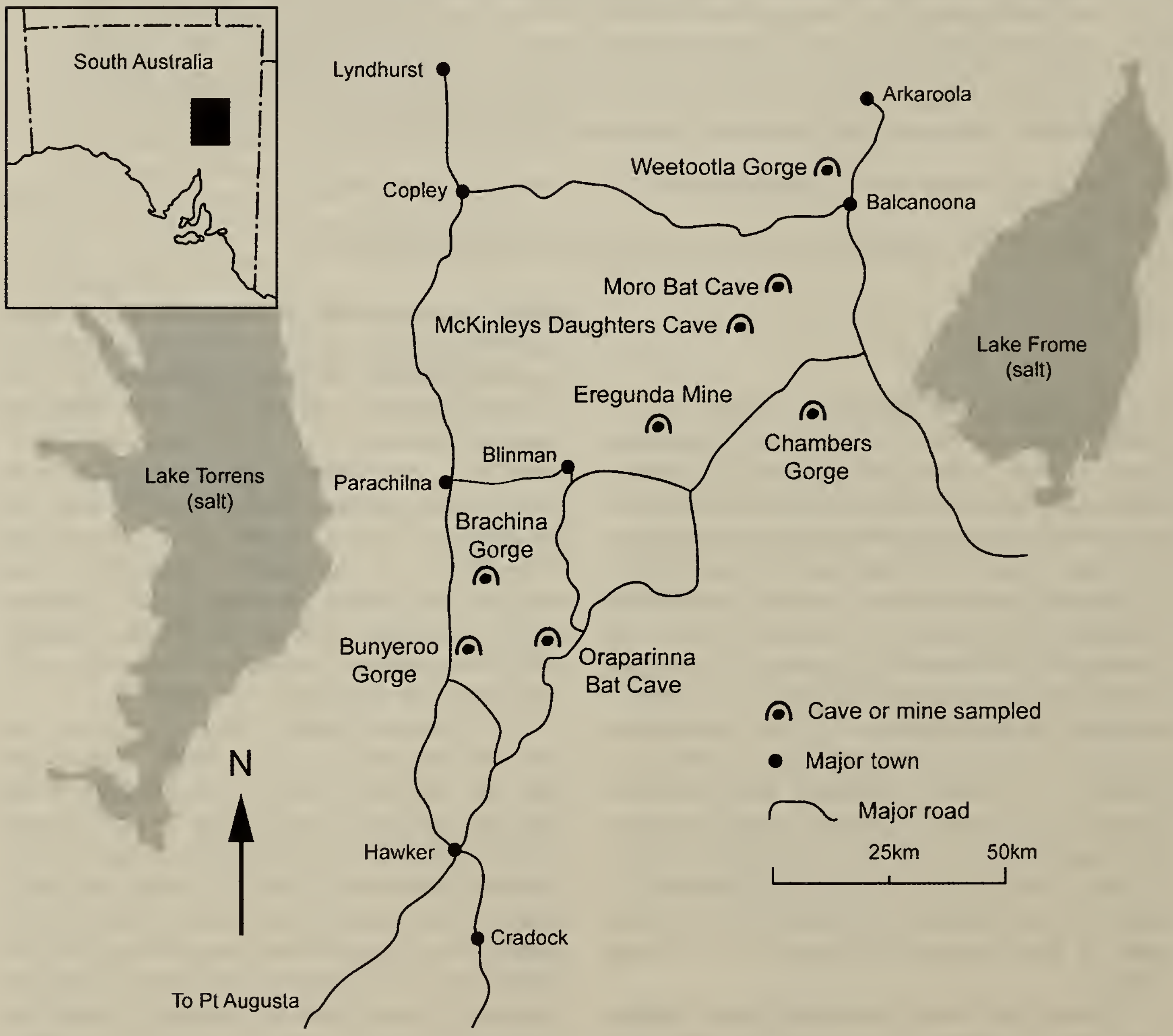

Figure 1. Localities of guano sites visited in the Flinders Ranges. Brachina, Bunyeroo, Chambers, and Weetootla gorges all contain two sites.

to be assessed. The caves examined during this study do not include every guano-bearing cave in the area, but rather represent a cross-section of active bat caves found throughout the Flinders Ranges. A list of all Flinders Ranges caves historically known to contain guano can be found in Hamilton-Smith et al. (1997).

Terminology

Australian caves are referred to by a binomial alpha-numeric system according to Mathews (1985), with those of the Flinders Ranges using the prefix 'F'. Mines are not included in this system and are referred to by name only. The division of caves into four environmental zones (entrance, twilight, transition, and deep zones, according to the amount of light and degree of interaction with surface climatic conditions) follows Humphreys (2000).

Cave and mine site descriptions

The majority of caves examined during this study are small, rarely extending into complete darkness or attaining a deep zone. Weetootla Gorge in the Gammon Ranges was the northern-most area examined. Weetootla Gorge Mines 1 and 2 (Fig. 1) are horizontal magnesite adits excavated prior to the early 1970s. The entrances were gated in the early 1990s with 15 cm grids preventing access by large animals, although inland cave bats are still able to negotiate the entrances. Weetootla Gorge Mine 2 was found to contain 36 inland cave bats, counted using an infrared video of the flyout at dusk (T. Reardon, pers. comm. 2003). The adit is approximately 90 m long and breaks into a natural rift at its termination. Bat roosts are located near the end of the adit, 50-70 m from the entrance. Small guano piles 1 m wide by 1-2 m in length lie directly on the solid magnesite floor. Weetootla Gorge Mine 1, located 200 m downstream of Weetootla Gorge Mine 2, contained only two widely separated guano piles with no evidence of fresh guano. No bats were sighted inside this adit, suggesting the roost is used infrequently.

The remainder of mines and caves examined were situated in the northern and central Flinders Ranges and are described from north to south (Fig. 1). Moro Bat Cave (F47), located in Moro Gorge, is 50 m above a permanent stream and extends into the cliff face terminating in the transition zone. The cave contains several bat guano deposits and dung of the yellow-footed rock wallaby (*Petrogale xanthopus* Gray) which uses the entrance area as a daytime retreat. The vertical slot entrance to McKinleys Daughters Cave (F175) located near stream level leads to a narrow high aven (terminal roof hole). A thin veneer of dry guano and numerous small mammal bones sit on a fine silt floor in the twilight zone. Unidentified bats were present high in the aven. Eregunda Mine, north-east of Blinman, is a 25 m long adit containing several guano deposits under an active roost of inland cave bats (for further details see Moulds, in press). Two unnamed caves, on the southern side of Chambers Gorge in a high valley, contain several inland cave bats and substantial desiccated guano in the transition zone chambers. Two caves near the Teamster's Campsite in Brachina Gorge contain minor guano deposits mixed with fine soil. One of these is located at river level and the other approximately 40 m above the river. Two caves at the western end of Bunyeroo Gorge, near river level, are small with only one reaching the transition zone and the other only containing a twilight zone. Oraparinna Bat Cave, located north of Wilpena Pound, contained extensive amounts of guano within the primarily horizontal joint controlled passages.

Guano microhabitat conditions

Guano caves in the Flinders Ranges often have extremely low relative humidities and are commonly characterised by dry, acidic, pellet-like guano, even under active bat roosting areas that normally have moist, basic conditions (Harris 1970; Decu 1986; Gnaspini and Trajano 2000). Weetootla Gorge Mines 1 and 2 had relative humidities less than 20% during September 2003. This has consequently affected the water content of guano deposits, which have been historically recorded from 3.3% (Arcoota Creek Cave) to 12.7% (Clara St. Dora Cave) (Winton 1922), comparable to the driest guano found in Bat Cave, Naracoorte (Moulds 2003). Several artificial entrances in Oraparinna Bat Cave opened for guano mining have been the cause of desiccated guano piles near these entrances, limiting the distribution of some arthropods. Despite an active bat roost in Weetootla Gorge Mine 2, virtually no fresh guano was found. The guano beneath an active bat roost in Weetootla Gorge Mine 2 had a pH of 5.5.

RESULTS

Species recorded

Twenty two arthropod species were collected from 12 orders and two classes (Table 1). This represents a substantial increase from the single species previously recorded in the literature (*Brises acuticornis*) and the four unpublished species records of Elery Hamilton-Smith. Two sites, Eregunda Mine and Weetootla Gorge Mine 2, were extremely diverse with five and six orders recorded respectively. Active arthropod communities were found at all 12 sites, but not in

Location	Cave	Order	Family	Genus	Species
Brachina Gorge	Unnamed river cave	Coleoptera	Anobiidae		sp 1
		Neuroptera	Myrmeleontidae	*Aeropteryx*	sp 1
	Unnamed hillside cave	Neuroptera	Myrmeleontidae	*Aeropteryx*	sp 1
Bunyeroo Gorge	Unnamed cave no.1	Hemiptera	Reduviidae	*Armstrongula*	sp 1
	Unnamed cave no.2	Hemiptera	Reduviidae	*Armstrongula*	sp 2
Chambers Gorge	Unmaned cave no.1	Neuroptera	Myrmeleontidae	*Aeropteryx*	sp 1
		Zygentoma	Nicoletiidae	*Trinemura*	sp 1
	Unnamed bat cave	Araneae			sp 1
		Neuroptera	Myrmeleontidae	*Aeropteryx*	sp 1
		Orthroptera	Gryllidae		sp 1
Mount McKinley	McKinleys Daughters Cave (F175)	Diptera			sp 1
		Hemiptera	Reduviidae	*Armstrongula*	sp 1
		Neuroptera	Myrmeleontidae	*Aeropteryx*	sp 1
Moro Gorge	Moro Bat Cave (F47)	Lepidoptera	Noctuidae	*Dasypodia*	*selenophora*
		Lepidoptera	Pyralidae		sp 1
		Neuroptera	Myrmeleontidae	*Aeropteryx*	sp 1
Oraparinna	Oraparinna Bat Cave (F8)	Coleoptera	Anobiidae	*Ptinus*	*exulans*?
		Coleoptera	Anobiidae		sp 1
		Coleoptera	Tenebrionidae	*Brises*	*acuticornis*
Point Well	Eregunda Mine	Araneae	Pholcidae		sp 1
		Coleoptera	Tenebrionidae	*Brises*	undetermined
		Hymenoptera	Formicidae	*Iridomyrmex*	*purpureus*
		Pseudo-scorpionida	Cheliferidae	*Protochelifer*	sp 1
		Psocoptera			sp 1
Weetootla Gorge	Mine 1	Araneae	Pholcidae		sp 2
		Coleoptera	?Dermestidae		sp 1
	Mine 2	Araneae	Pholcidae		sp 3
		Blattodea			sp 1
		Coleoptera	Tenebrionidae	*Brises*	*caraboides*
		Hemiptera	Reduviidae	*Armstrongula*	sp 3
		Neuroptera	Myrmeleontidae	*Aeropteryx*	sp 1
		Orthroptera	Gryllidae		sp 1

Table 1. Arthropods collected from guano deposits in the caves and mines of the Flinders Ranges. Caves are listed alphabetically by the area in which they are found. Some specimens could only be identified to subfamily or genus.

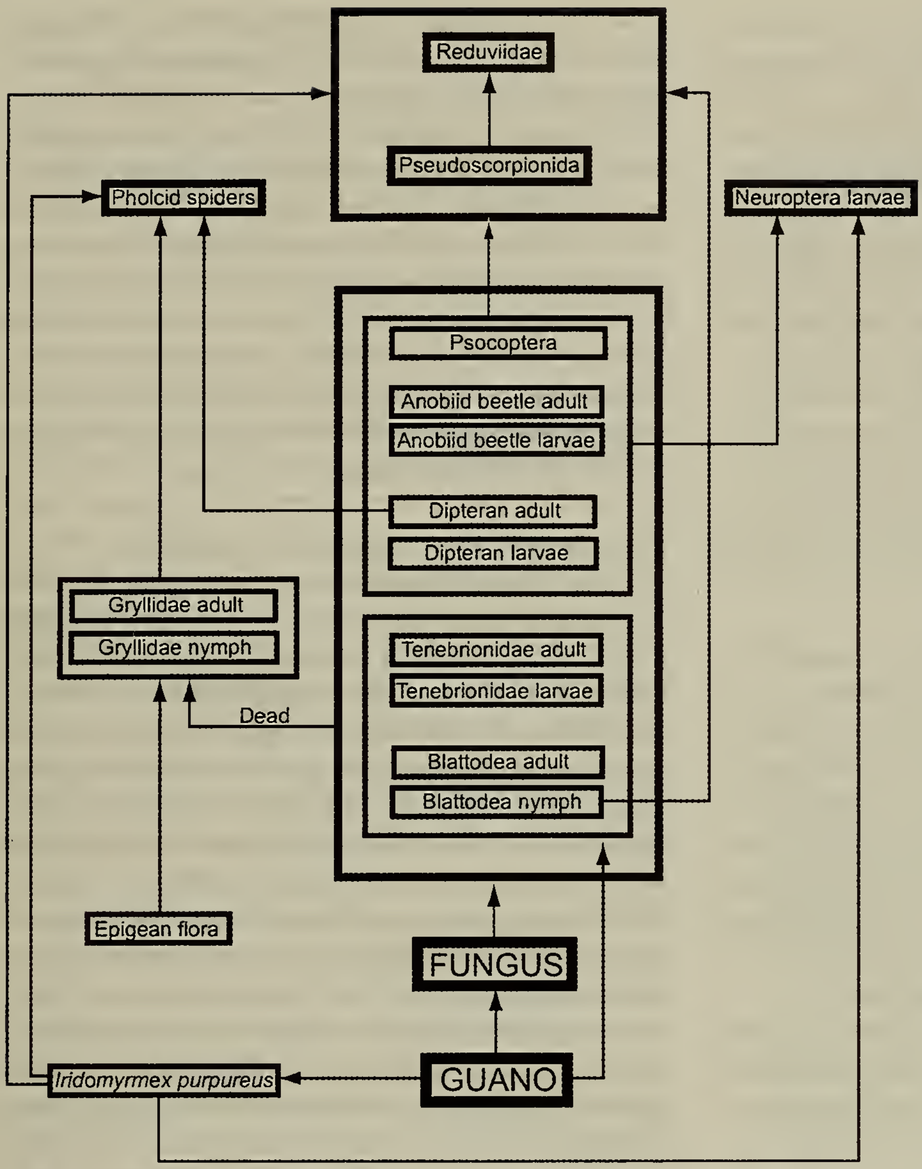

Figure 2. Food web of a Flinders Ranges guano community. Arrows represent the direction of energy flow within the food web. Guano ecosystems are extremely variable, consisting of numerous micro-habitats differentiated by moisture, pH and temperature. Fungi and bacteria are an important basis for guano ecosystems, providing usable nutrients for many species unable to consume guano directly.

very old guano deposits that were extremely dry and powdered. The beetle *B. acuticornis duboulayi* Bates (Tenebrionidae) was found in Oraparinna Bat Cave and an unidentified *Brises* larvae in Eregunda Mine. The second record of *B. caraboides*, from Weetootla Gorge Mine 2, greatly increases the distribution of this species, previously known only from the type locality near Eucla on the Nullarbor Plain. The emesine reduviid genus *Armstrongula* (Hemiptera) (Table 1) has a wide distribution in the Flinders Ranges, with three undescribed species recorded. Previously known species of *Armstrongula* are recorded from under bark near the Bogan River, New South Wales (Wygodzinsky 1950). The presence of an unidentified *Protochelifer* species (Pseudoscorpionida) in Eregunda Mine in the central Flinders Ranges is an important intermediate record for this widespread, and often cavernicolous genus, between the Nullarbor Plain and the south-east of South Australia. The cosmopolitan beetle *Ptinus exulans* Erichson (Anobiidae), and an unidentified anobiid, were also recorded from Oraparinna Bat Cave.

Food web and species interactions

A food web for the Flinders Ranges hypogean guano communities is shown in Figure 2. This was constructed using numerous direct field observations of many taxa combined with previously documented feeding biology of taxa from the literature.

The trophic basis of all the discrete ecosystems examined is bat guano. Tenebrionid beetle adult and larvae (*B. caraboides*) and nymphal cockroaches were observed directly scavenging on guano deposits in Weetootla Gorge Mine 2. Tenebrionid beetles also act as general scavengers of organic material. Meat ants (*Iridomyrmex purpureus* Smith) were observed in the twilight zone of Eregunda Mine removing fresh guano and carrying it to their nest, possibly as a food source (Moulds, in press). The presence of ants adds a unique element to the species interactions at this locality by providing a potentially rich external food source for many of the predatory species such as pholcid spiders, reduviid bugs and neuropteran larvae. More commonly, guano deposits form a direct energy source for a succession of bacteria, yeast and fungi that support the majority of arthropods found in these environments (Fletcher 1975). Anobiid beetles have been recorded feeding on fungi and insect remains in guano deposits and spider webs (Richards 1971; Hickman 1974).

Gryllid crickets shelter in caves during the day and feed on plant material growing near cave entrances when conditions are favourable, similar to rhaphidopohorid cave crickets (Richards 1961, 1965, 1966). An individual was observed in September 2003 feeding upon arthropod remains in an unnamed bat cave in Chambers Gorge.

Myrmeleontid neuropteran larvae are common inhabitants of sandy floors in entrance and twilight zones, capturing small arthropods including ants, small beetles, fly larvae, and Psocoptera that fall into their conical pits. The presence of guano near neuropteran pits attracts additional prey for these sedentary predators, making guano deposits a beneficial habitat. In the larval stage, Neuroptera are part of guano food webs, but the adults play little role other than foraging for both plant and animal food in the epigean environment (New 1991). Adult Neuroptera were, however, commonly found during the day, sheltering in many of the caves examined (Table 1).

Reduviid bugs of the subfamily Emesinae are common predators in many subterranean guano deposits, stalking arthropods in small groups (Moulds, unpublished data). Individuals were observed in September 2003 on the guano surface in McKinleys Daughters Cave and caves in Bunyeroo Gorge. These bugs form the top predator within the Flinders Ranges guano deposits. Prey were generally consumed where captured, although sometimes were dragged away from guano deposits for later consumption.

A single cheliferid pseudoscorpion individual was also found in guano deposits. Pseudoscorpions spend most of the time under rocks, only emerging to hunt micro-arthropods.

DISCUSSION

Environmental limitations of population size

The most limiting factors against the development of large guanophilic arthropod communities in the Flinders Ranges are low humidity and transient bat populations that limit guano sites in volume and continuity. Guanophilic communities commonly inhabit environments of saturated humidity with many species preferring the strongly basic conditions associated with fresh guano (Moulds 2003). Low humidity, common in the Flinders Ranges, severely reduce fungal growth as many of the opportunistic phycomycetes found on fresh guano are susceptible to desiccation (Poulson 1992; Poulson and Lavoie 2000). Reduced growth of fungi, the primary food source of guanophilic communities, results in lower species abundance and diversity when compared with guanophilic communities in more humid locations such as coastal south-eastern Australia (Yen and Milledge 1990; Eberhard and Spate 1995; Bellati et al. 2003). Further, the paucity of moist substrates removes key refugia for the numerous moisture-dependant species commonly found in guano caves. Consequently, families such as Jacobsonidae, Sciaridae and Sphaeroceridae are notably absent from the Flinders Ranges, and have been replaced by arid-adapted species such as tenebrionid beetles. Arid-adapted species comprise a substantial part of the species richness for caves across the entire region. The often stochastic semi-permanent bat colonies in the Flinders Ranges can have catastrophic consequences for guanophilic arthropod communities reliant on fresh moist guano for survival.

Biogeography and dispersal mechanisms

The guanophilic arthropod fauna of the Flinders Ranges shows closest similarity in species diversity to that of the Nullarbor Plain and isolated karst areas to the north and east. The tenebrionid beetles *Brises acuticornis*, *B. caraboides* and the carabid *Thenarotes speluncarius* Moore are found in both regions (Moore 1967; Richards 1971; Mathews 1986). *Brises acuticornis* is recorded from epigean and hypogean habitats and may use rabbit or wombat burrows for shelter during the day, aiding in long range dispersal ability (Mathews 1986). The major extension to the known distribution of *B. caraboides* from near Eucla on the Nullarbor Plain to the Gammon Ranges in the northern Flinders Ranges is significant as it provides additional species similarities between these two regions.

The isolation of three species of *Armstrongula* within the Flinders Ranges suggests that increasing aridity through the region may have prevented the movement of hydrophilic cavernicolous species between karst areas. The disjunct karst formations of the region are also likely to have restricted the dispersal ability of other species. The occurrence and distribution of emesine reduviid bugs in guano caves, including those of the Flinders Ranges, is presently poorly understood but no records are known for this subfamily from the wetter southern karst areas of Australia.

The relationship of the single *Protochelifer* (Pseudoscorpionida) collected from the Flinders Ranges (Eregunda Mine) to *P. naracoortensis* Beier from south-east South Australia and to *P. cavernarum* Beier from the Nullarbor Plain is unknown at present. It is unclear if this single record from the Flinders Ranges is indicative of a paucity of pseudoscorpions in general or simply a result of minimal collecting.

The guano mite *Uroobovella coprophila* Womersley, ubiquitous in southern Australian bat caves, is notably absent from the Flinders Ranges and other arid localities (Moulds 2004). This is probably due to rapid desiccation of fresh guano, even beneath active bat roosts, excluding this mite as it relies upon fresh, moist, highly basic guano and virtually disappears during periods when these conditions are not available (Harris 1973). This species shows a strong association with breeding colonies of the large bent-wing bat, *Miniopterus schreibersii* (Kuhl), which does not occur in the Flinders Ranges or other arid regions (Churchill 1998). The similar distribution pattern of *U. coprophila* and *M. schreibersii* suggest this mite may be phoretic on bats or guano-associated invertebrates such as carabid beetles, although no observations have been reported. Phoresy requires further investigation to determine its importance in the distribution of this, and other, guano-associated species.

The change in fauna composition moving south from the Flinders Ranges into the wetter costal areas of south-eastern Australia is marked, with several taxa such as the guano mite *U. coprophila*, histerid beetles and phorid flies becoming dominant on fresh guano. This study represents only a first step in documenting the diversity of cavernicolous guanophilic arthropods in the Flinders Ranges. Many previously known caves remain to be investigated and new caves are still being discovered. The transient nature of bat colonies and their relatively small numbers make the study of guanophilic fauna difficult. However, the region warrants further attention as it represents an important interface between the cavernicolous fauna of the Nullarbor Plain and the wetter coastal areas of south-eastern Australia.

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Song Analyses of Cicadas of the Genera *Aleeta* Moulds and *Tryella* Moulds (Hemiptera: Cicadidae)

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Moulds, M.S. (2005). Song analyses of cicadas of the genera *Aleeta* Moulds and *Tryella* Moulds (Hemiptera: Cicadidae). *Proceedings of the Linnean Society of New South Wales* **126**, 133-142.

The songs of *Aleeta curvicosta, Tryella castanea, T. crassa, T. kauma* and *T. rubra* are analysed. Differences between the songs of the five species are discussed in addition to differences across the distribution of species and within populations. Timbal action of all four *Tryella* species was found to be similar to that of *Aleeta curvicosta*, that is a single muscle contraction produces multiple sound pulses as each rib of the timbal buckles.

A corrigenda to a recent review of the systematics of these genera (Moulds 2003) is provided.

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KEYWORDS: *Aleeta*, cicada, song, timbal action, *Tryella*.

INTRODUCTION

In a recent review of the genus *Abricta* Stål (Moulds 2003) I showed that the Australian species in that genus are best placed in two new genera, *Abricta curvicosta* (Germar) to *Aleeta* Moulds and the remaining species to *Tryella* Moulds. *Aleeta* and *Tryella* are very distinct from other Australian genera, the nearest being *Chrysocicada* Boulard. Adults characteristically perch head downwards and also call in that position (Fig. 1). They sing both during the heat of the day and at dusk, the dusk call seeming more vigorous. Timbal structure of *Aleeta* and *Tryella* is also very similar, there being many long parallel ribs (9-13 in *Aleeta*, 9-11 in *Tryella*) interspersed by very short ribs (compare figs 20, 22-29 in Moulds 2003).

Below I compare the songs of *Aleeta curvicosta* and four species of *Tryella*. In particular I discuss differences between the five species as well as differences across the distribution of *T. castanea* (Distant) and *T. crassa* Moulds, and differences within a single population of *T. crassa*. I also investigate the timbal contraction mechanisms of the four *Tryella* species and show how these are similar to that of *Aleeta curvicosta*.

Only the song of *Aleeta curvicosta* has been studied previously. Young (1972a) showed that *A. curvicosta* has neurogenic timbal muscles that contract alternately. He also described and illustrated the timbal, which is strongly and evenly ribbed so that during the inward movement each rib buckles separately producing 7-9 separate pulses of sound with each muscle contraction. A similar mechanism has been described for the periodical cicada *Magicicada cassinii* (Fisher) (Young & Josephson 1983b). Young calculated the pulse repetition frequency for the natural song of *A. curvicosta* as 1050/sec and the sound frequency range from 7.5-10.5 kHz. In his second paper concerning sound production in cicadas (Young 1972b), a slow speed oscillogram of the song of *A. curvicosta* was included, which clearly shows the spaced introductory phases characteristic of this species. This paper also included a sonogram of the song not represented in his first paper (Young 1972a).

Young and Josephson (1983a) further investigated timbal muscle contraction and rib buckling in *A. curvicosta* confirming the interpretation of Young (1972a). They calculated the muscle contraction frequency for the timbals as 72 Hz. Some brief additional data concerning the song of *curvicosta* have been provided by Ewart (1995) and Moulds (1990), but no further study of the calling mechanisms has been published.

Figure 1. A male of *Tryella crassa* in full song. The body is raised above the substrate and the wings are held clear to prevent damping. *Tryella* and *Aleeta* species normally sing with the head facing downwards.

MATERIALS AND METHODS

Calling songs were recorded in the field under natural conditions using an Akai X V portable tape recorder at a tape speed of 9.525 cm/sec and an AKG D19C dynamic microphone. Sound analysis data and oscillograms were generated using a Kay DSP Sonagraph Model 5500.

Twenty three recordings were obtained in all, from nine localities, covering a total of four species of *Tryella* across seven localities in addition to a recording from *Aleeta curvicosta* (Table 1).

Acoustic terminology follows that of Greenfield (2002). In particular, a pulse is here defined as ". . a brief packet of sound or vibrational waves that generally corresponds with a single repetitive action". Pulse repetition frequency is defined as the number of pulses produced by the timbals each second and has been calculated from that part of the call containing uninterrupted contractions.

RESULTS

Note: oscillograms and sonograms (Figs 2-27) are at the end of the paper

Song structure by species

Aleeta curvicosta (Germar) recorded at Waverley Creek, Central Queensland (Figs 6, 19), showed song characteristics that agreed closely with data obtained from specimens from New South Wales (Young 1972a, 1972b, and Young & Josephson 1983a, 1983b). Pulse repetition frequency was measured at 1025/s, very close to the 1050/s as measured by Young. Pulses were arranged in syllables as described by Young (1972a), who found that the syllables represented a single buckling of a timbal and each pulse the buckling of a single rib (Fig. 19). In the introductory part of each complete sequence, syllables were grouped into short echemes in which the amplitude rises then suddenly cuts off, with the interval between these echemes gradually decreasing until they merge into the continuous phase; this structure is identical to that described by Young (1972a, 1972b). Young (1972a) also found that within the continuous phase, syllables were grouped into clusters of four, representing four alternating timbal contractions between the right and left timbals. This differs from groupings of three found in an individual from Waverley Creek (Fig. 19). Fig. 19c also shows the coalescence of the syllables produced by the alternate contractions of left and right timbals. Song carrier frequency was 6-12 kHz, also close to the 6.5-11.5 kHz range given by Young. Young (1972b) described the song as having a rasping quality that is clearly more pronounced in this species than in the four *Tryella* species studied.

Tryella castanea (Distant) had a continuous regular call that showed little variation in internal structure. Amplitude modulation was remarkably even overall, but there was strong internal modulation (Figs 3, 7a, 8a, 21a) with the song switching alternately every 0.25 s or so between phrases with syllables compressed and phrases where the syllables were separated by very brief (up to ca. 4 ms) gaps. The syllables are believed to represent single timbal buckles of multiple pulses (see 'Timbal buckling' below). The pulse repetition frequency was measured at approximately 750/s for the dusk call and 1050/s for the day call. The song carrier frequency was

Table 1. Summary of song recordings of *Aleeta curvicosta* and *Tryella* species.

Species	Locality	No. recorded	Date recorded
Aleeta curvicosta (Germar)	QLD: Waverley Ck	1	23-Jan-1992
Tryella castanea (Distant)	NT: Dingo Ck	3	1-Jan-1992
T. crassa Moulds	NT: Adels Grove	3	18-Dec-1991
	NT: Mataranka	5	11-Jan-1992
	QLD: W of Georgetown	3	16-Jan-1992
T. kauma Moulds	QLD: Walkers Ck	1	15-Jan-1992
T. rubra (Goding & Froggatt)	WA: Kununurra	3	1-Jan-1992
	NT: Timber Ck	3	25-Dec-1991
	NT: Top Springs	1	24-Dec-1991

concentrated between 8-13 kHz (Figs 21b, 22b, 23b) with weak side bands extending as low as 2 kHz and as high as 14 kHz (Figs 7b, 8b). To the human ear, the high concentrated frequencies are dominated by the lower side bands which, combined with the rapid but regular pulse repetition frequency, gives the call a vigorous rhythmic buzzing sound.

Tryella crassa Moulds had a continuous, even call that showed little amplitude modulation (Figs 4, 9-14, 20a). Syllables were coalesced into echemes of 14-18 that were interspersed by two, or sometimes three, syllables only slightly separated from each other and the coalesced echemes (Figs 9-14, 25-27). The syllables consisted of a train of pulses inferred to result from a single timbal buckle (see 'Timbal bucking' below) (Fig. 20). The pulse repetition frequency ranged from around 1100/s during the heat of the day to near 850/s during the dusk chorus, but even within single populations noticeable variation was encountered (Figs 12-14). The song carrier frequency was concentrated between 7-12 kHz (Fig. 20b) with an extreme range of approximately 4-15 kHz. This high sound frequency was audible only as a hiss and the ear hears mainly the regular grouped pulse frequencies, which give the song a slight buzzing quality.

Tryella kauma Moulds had a continuous regular song with slight amplitude modulation (Figs 2, 24). Syllables of sound (timbal contractions) were arranged evenly through the call in discrete echemes (approximately 25-70 ms long) with very distinct inter-echeme gaps. The pulse repetition frequency was near 1120/s taken from a recording made during midmorning. The dominant song carrier frequency was concentrated between 8-13 kHz with weak side bands reaching 6 and 14 kHz. These high frequencies and the small size of this species give the song a quiet hiss-like quality.

Tryella rubra Goding & Froggatt had a song distinctly divided into echemes of usually 8-10 syllables (timbal contractions) that were coalesced together, each of similar amplitude (Figs 5, 15-18, 25, 26). The length of these echemes varied within single populations and apparently also between populations (Figs 15-18). Sometimes the interval between echemes contained isolated syllables. The pulse repetition frequency ranged from 1220/s at Kununurra to 1280/s at Top Springs and Kununurra; all specimens were recorded during the heat of the day. The dominant song carrier frequency for all individuals was concentrated between 6-11 kHz (Figs 25b, 26b, 27b) with very weak side bands extending from 1.5 kHz to 12 kHz. These high frequencies and the short repetitive echemes give the song a hiss-like buzzing quality.

Song comparisons

For all five species examined song characteristics clearly differentiate each (Figs 2-6). By far the most distinctive call was that of *Aleeta curvicosta*, primarily because of its unique introductory phrasing of discrete echemes (Fig. 6). In fact, the arrangement of echemes was the main component of song structure to show consistent and easily recognisable differences between all species. While there were some differences in echeme pattern both within and between populations of conspecifics (e.g. in *Tryella crassa*, Figs 9-11 and 12-14), oscillograms clearly showed these differences never approached the degree of difference shown intraspecifically (Figs 2-6).

The characteristic regular pulse pattern of *T. castanea* was identical for two very different phenotypes of this species from Dingo Creek that otherwise were associated only on the basis of male genitalia and allozymes (Moulds 2003) (Figs 7-8). *Tryella castanea* is one of the most variable of *Tryella* species in both pigmentation and size (see Moulds 2003, Figs 54a-e). The song of *T. kauma* (Fig. 2) is similar to that of *T. castanea* but differs in being a more vigorous call and having a much more even amplitude. The songs of *T. crassa* and *T. rubra* are also similar to each other in that each consists of a regular succession of distinct echemes (Figs 4, 5) and, like *Aleeta curvicosta*, the syllables from individual timbal contractions coalesce together; however the echemes differ structurally (*crassa* with 14-18 syllables per echeme, *rubra* with 8-10) and the echemes are separated by different interval structures.

Pulse repetition frequency was remarkably similar for all five species. Day calls fell within the range 1050-1280/s but were probably dependent to some extent upon temperature. Populations of *T. crassa* had pulse repetitions for day calls ranging from 1220-1280/s. Dusk calls, on the other hand, showed much lower pulse repetition frequencies, as low as 850/s. Dusk calling by *T. castanea* showed a similar low pulse repetition frequency rate of 750/s compared with a day call rate of 1050/s. These low pulse repetition rates for dusk calls are almost certainly a consequence of lower temperatures; very hot day temperatures raise the body temperature of day-calling individuals.

Similarly, song frequency showed little intraspecific variation, the ranges concentrated between 6-13 kHz, but with all species individually showing a broad range of at least 5 kHz, thus making species diagnosis by frequency alone unreliable. However, frequency distribution patterns from sonograms did suggest that further investigation may show features characterising species. For example, *T. castanea* was unique in having weak, but nevertheless distinct, side bands extending to as low as 2 kHz (Fig. 8b).

Timbal buckling

Analyses of the calling songs of these species also provided an opportunity to compare timbal buckling actions. The high pulse repetition frequencies of *T. castanea, T. crassa, T. kauma* and *T. rubra* suggest timbal action equivalent to that detailed for *A. curvicosta* by Young (1972a), where each inward buckle of a timbal produced a train of discrete pulses caused by the individual buckling of ribs.

For all five species studied, oscillogram pulses, when aligned against sonograms comprising only the strongest frequency distributions, showed trains of pulses (syllables) corresponding with clusters of descending frequency. Extrapolating from the work of Young (1972a) for *A. curvicosta*, these are interpreted as individual rib buckles from a single inward buckling of the timbal, the frequency of each rib buckle falling progressively as the timbal collapses. *Aleeta curvicosta* from Waverley Creek showed six such pulses for each timbal buckle (Fig. 19), compared with the 7-9 rib pulses range recorded by Young (1972a). *Tryella crassa* showed 7-8 pulses (Fig. 20), *T. castanea* 6-7 (Figs 21-23), *T. kauma* 9 (Fig. 24) and *T. rubra* 6-7 (Figs 26-27).

While it is unlikely that the numbers I have recorded reflect a full range of the number of pulses resulting from single timbal buckles for each species, evidence suggests that multiple pulsing from a single timbal buckle does occur in all these species. In other words, for each of these species a single inward timbal buckle produces a very rapid pulse train that in turn leads to very high pulse repetition frequencies.

DISCUSSION

The male calling songs of the five species recorded, *Aleeta curvicosta, Tryella castanea, T. crassa, T. kauma* and *T. rubra*, each showed unique characteristics enabling clear separation of each species by song alone. This separation held true for the distinct morphs of *T. castanea*: the songs of the two very different morphs proved identical, confirming the association of these morphs previously derived from male genitalia and allozymes.

The arrangement of the introductory phrases in the song of *Aleeta curvicosta* differed significantly from those of the four *Tryella* species examined, reflecting their generic separation. More subtle differences (e.g. a concentration of intense pulse frequency between 6 and 11 kHz) probably account for the small difference in the perception of the call detectable to the human ear when compared to songs of *Tryella* species. However, there is also an overall similarity in song structure between all five species. All have similar high frequency ranges, similar high pulse repetition frequencies and, at least in part, continuous, regular buzzing sequences to their songs. These characteristics appear to characterise the songs of the Australian *Aleeta* and *Tryella* species. Further, a single timbal buckle in each of the five species appears to give rise to a succession of individual pulses as each rib buckles in succession rather than all ribs buckling in unison as in many other cicadas. It is this multiple pulsing from individual rib buckling that produces the very high pulse repetition frequencies for *Aleeta* and *Tryella* species.

Corrigenda to Moulds (2003)
p. 245, column 2, line 1: delete 'be'
p. 272, key to species, couplet 3: '16' should read '6'
p. 272, key to species, couplet 4, 3rd line: 'no' should read 'not'

ACKNOWLEDGEMENTS

Dr A. Ewart and Dr D.C. Marshall provided extensive discussion and comments on the manuscript, my wife Barbara and son Timothy gave assistance with field work and Dr Shane McEvey helped with preparing electronic images; to all I am most grateful.

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2 *Tryella kauma*

3 *Tryella castanea*

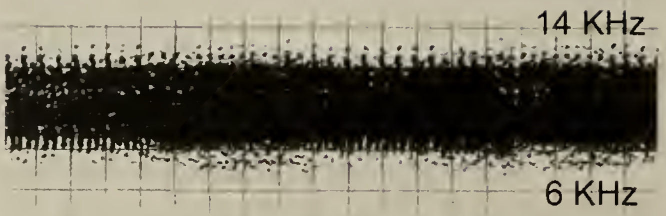
4 *Tryella crassa*

5 *Tryella rubra*

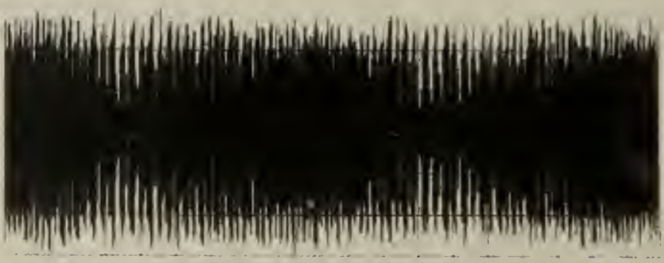
6 *Aleeta curvicosta*

Figs 2-6. Slow oscillograms of the free song (male calling song) of *Aleeta curvicosta* and four *Tryella* species: (2) *T. kauma*, Walkers Creek near Normanton, N. Queensland; (3) *T. castanea*, Dingo Creek, western NT; (4) *T. crassa*, Mataranka, NT; (5) *T. rubra*, Top Springs, NT; (6) *A. curvicosta*, after Young and Josephson, 1983a. Note that figure 6 is at a different time scale.

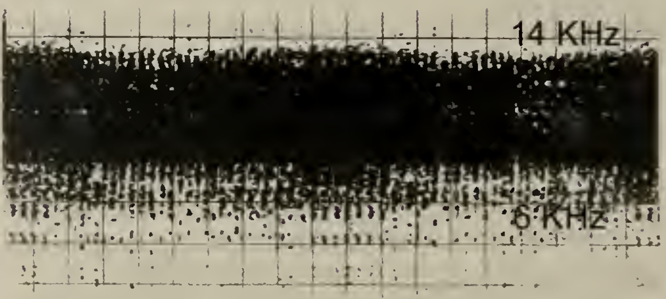
7a



7b

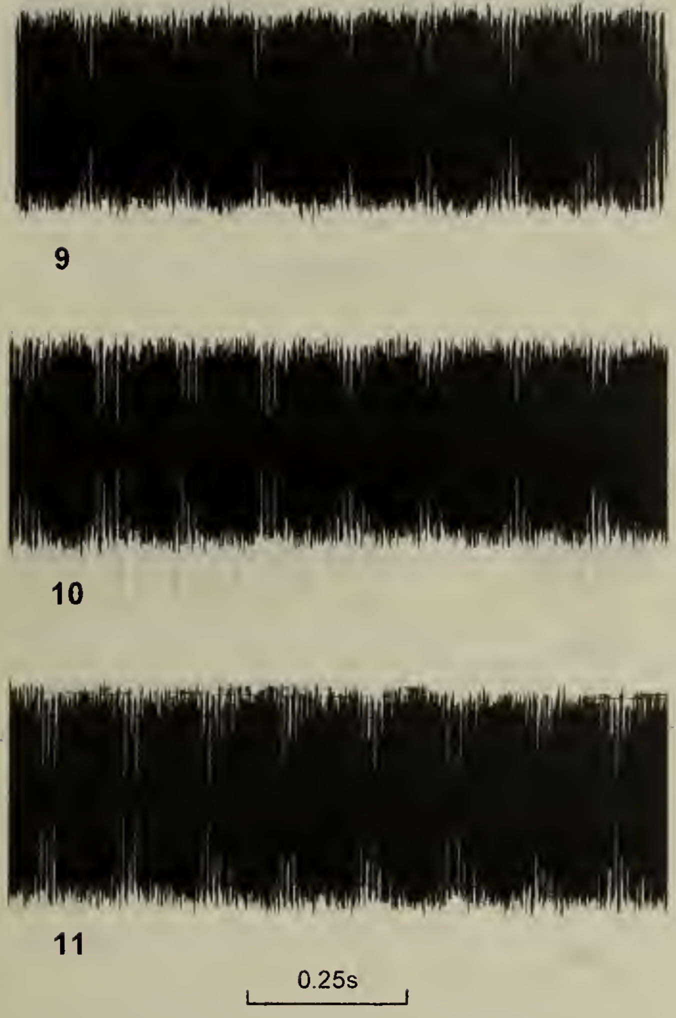


8a

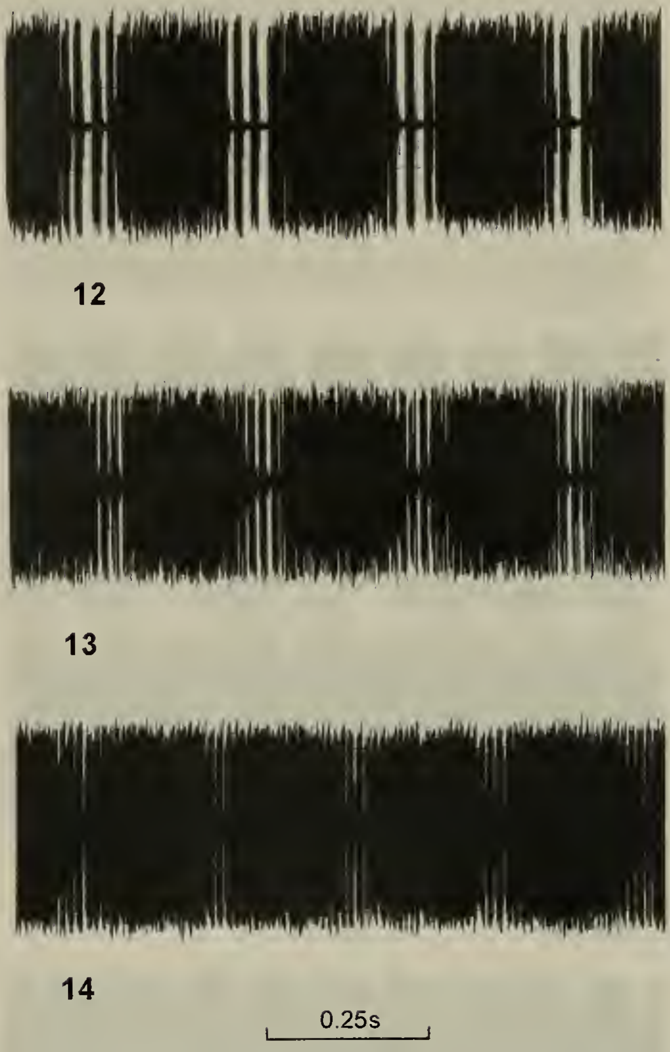


8b

Figs 7-8. *Tryella castanea*; (a) synchronised oscillograms and (b) sonograms for two males from Dingo Creek, NT: (7) dark individual; (8) pale individual. (a) Waveform and (b) spectrographic analyses.



Figs 9-11. *Tryella crassa*; slow speed oscillograms at identical time scale of day call for 3 individuals recorded during a 35-minute interval from 40km W of Georgetown, Qld.

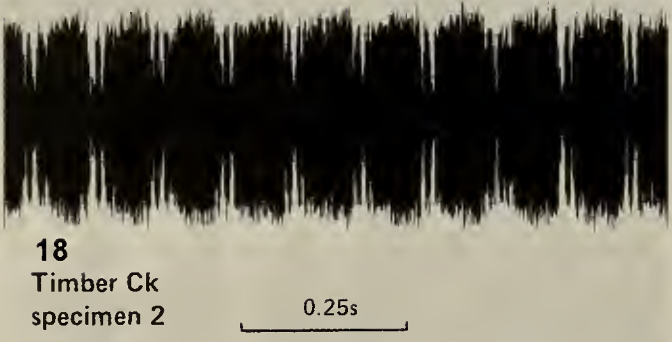


Figs 12-14. *Tryella crassa*; slow speed oscillograms recorded during a 10-minute interval, at identical time scale, of dusk call for 3 individuals from Mataranka, NT: (12) echemes widely separated by intermediate syllables (i.e. single timbal contractions); (13) echemes with moderate separation; (14) echemes with minimum separation.

15
Top Springs

16
Kununurra

17
Timber Ck
specimen 1



18
Timber Ck
specimen 2

Figs 15-18. *Tryella rubra*; oscillograms of day calls at identical time scales for 4 individuals: (15) Top Springs, NT; (16) Kununurra, WA; (17-18) Timber Creek, NT

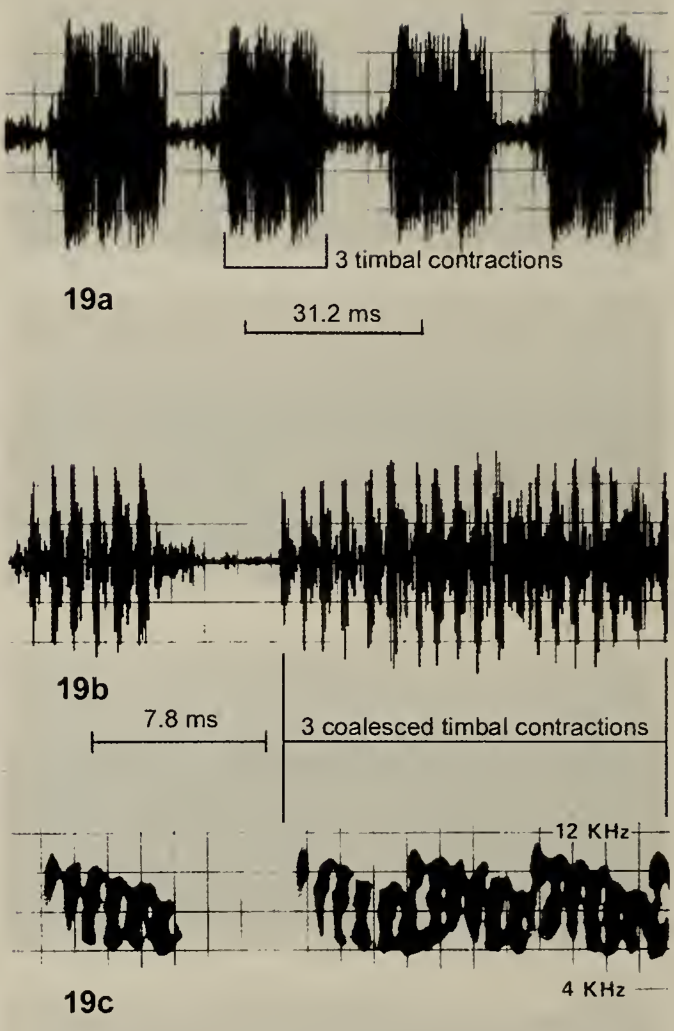


Fig. 19. *Aleeta curvicosta*; slow speed oscillogram of the (a) free song, (b) synchronised high speed oscillograms, and (c) sonogram of day call from an individual from Waverley Creek, Central Queensland. (b) and (c) show a sequence of three timbal contractions showing the coalescence of the syllables from these contractions.

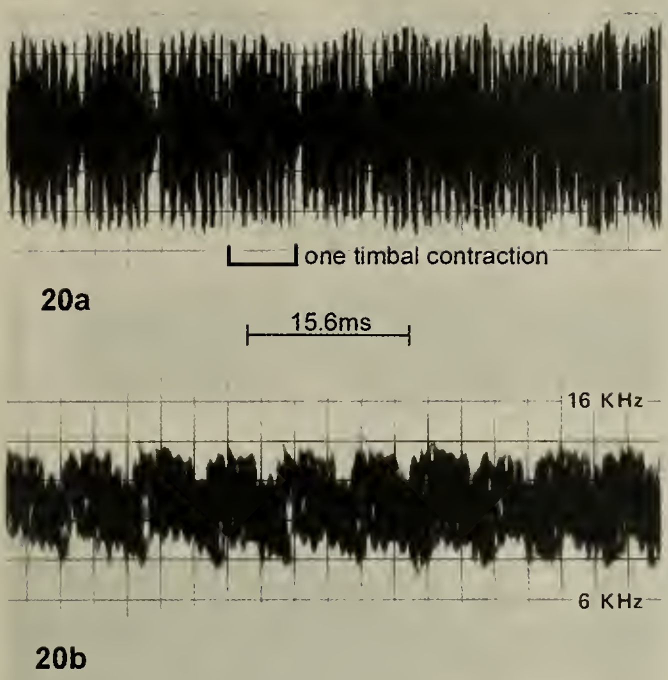
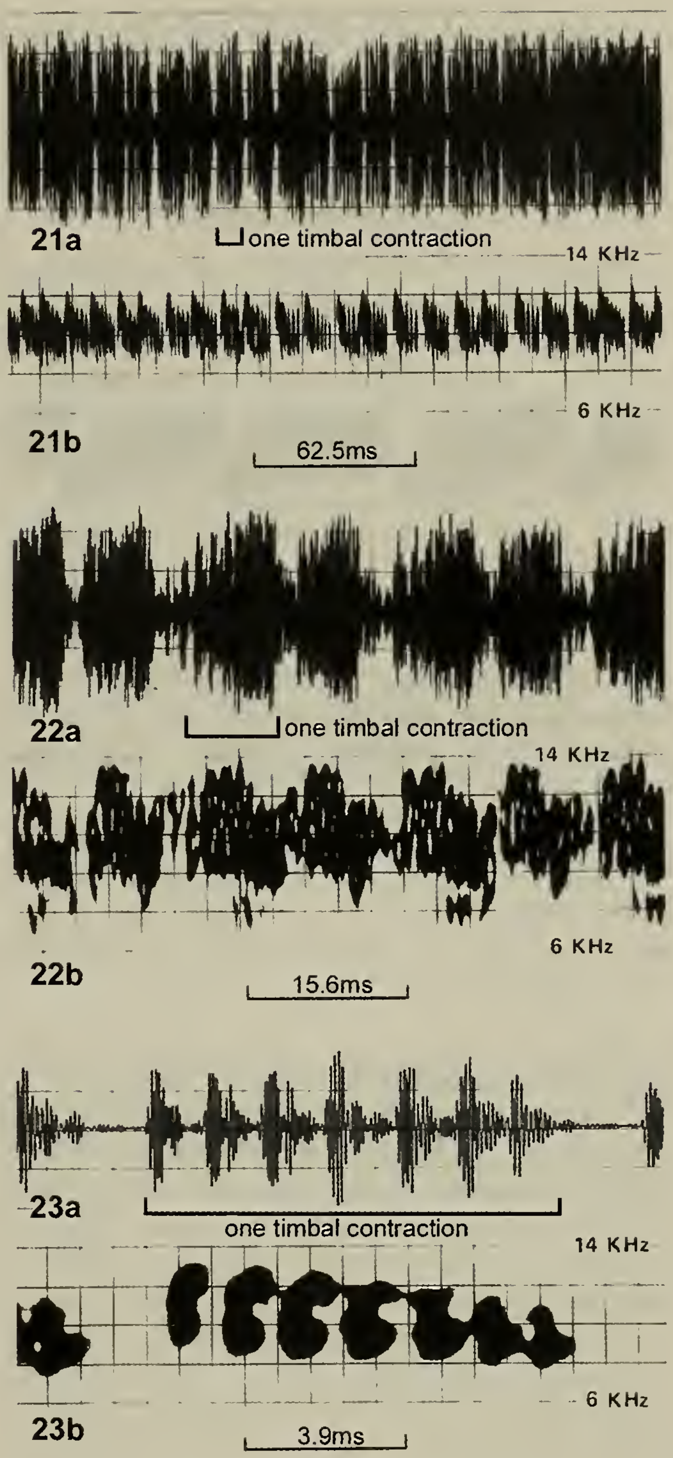


Fig. 20. *Tryella crassa*; (a) synchronised oscillogram and (b) sonogram of dusk call for an individual from Adels Grove, Lawn Hill Stn, Queensland.



Figs 21-23. *Tryella castanea*; (a) synchronised oscillograms and (b) sonograms of day call for a single individual from Dingo Creek, NT: (21) a train of pulses; (22) portion of the same train of pulses at greatly increased time scale showing individual timbal buckles within a series of timbal contractions; (23) a single timbal contraction showing sound pulses generated from the separate buckling of seven ribs.

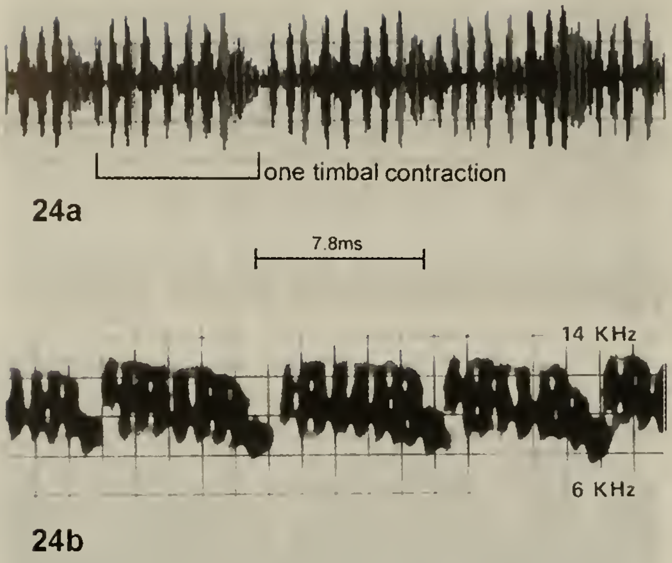
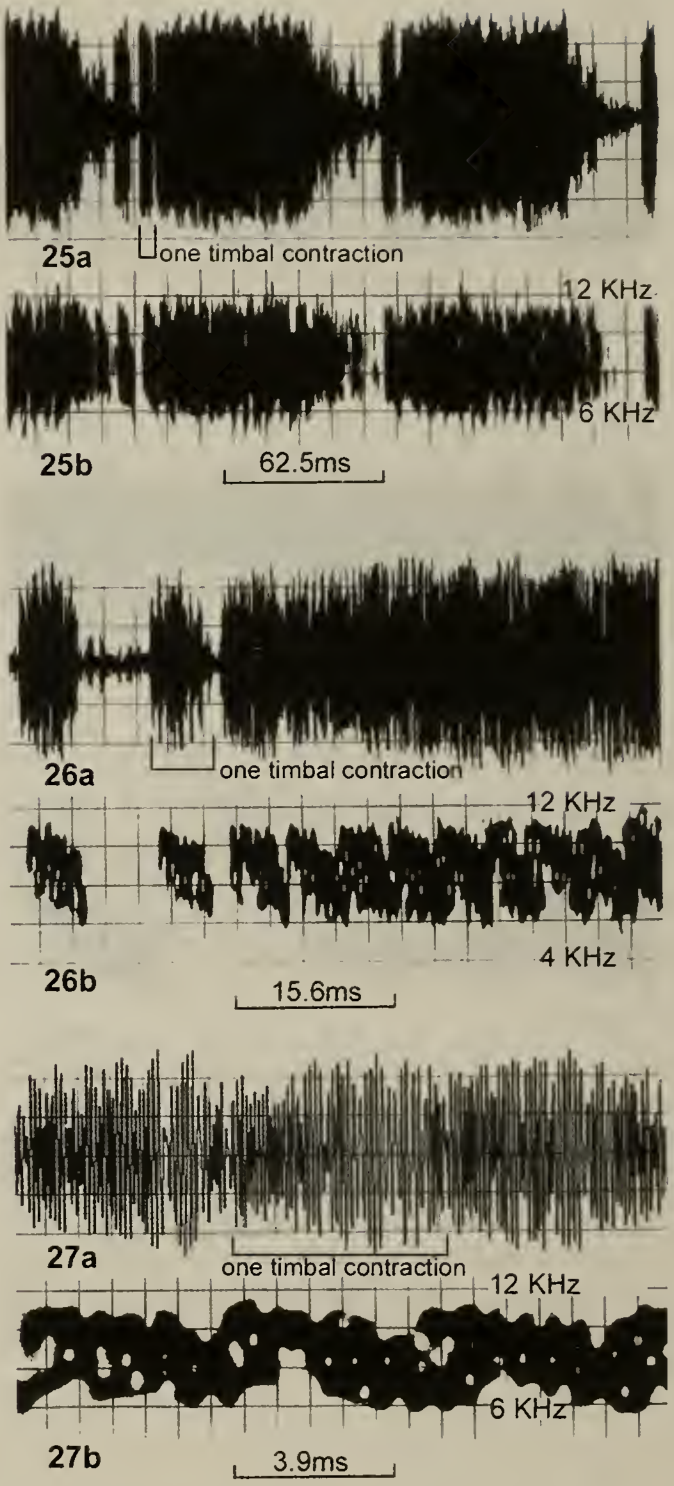


Fig. 24. *Tryella kauma*; (a) synchronised oscillogram and (b) sonogram of day call for an individual from Walkers Creek, Queensland.



Figs 25-27. *Tryella rubra*; (a) synchronised oscillograms and (b) sonograms of a day call for a single individual from Top Springs, Queensland: (25) a train of pulses; (26) portion of the same train of pulses at greatly increased time scale, the sonogram showing positions of individual timbal buckles; (27) a sequence of three timbal contractions showing the coalescence of the syllables from these contractions.

Llandovery (Early Silurian) Graptolites from the Quidong Basin, NSW

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Late Llandovery (Early Silurian) graptolites from several localities in the Merriangaah Siltstone, Quidong Basin, southern NSW, are described as *Monograptus priodon* (Bronn, 1835), *Oktavites falx* (Suess, 1851) and *Oktavites bodentoeriensis* Loydell, 2003. This is the first use of the generic name *Oktavites* in Australia. The firm age for this fauna to the *spiralis* graptolite Biozone and new age data from the Quidong Limestone place a maximum age for the unconformity between the Siltstone and the overlying Quidong Limestone, constraining the Quidongan Orogeny between the latest part of the Llandovery and the late or latest Wenlock.

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KEY WORDS: Early Silurian, graptolites, Llandovery, Merriangaah Siltstone, Quidong.

INTRODUCTION

Graptolites were first reported from the Quidong Basin in southeastern NSW by Crook et al. (1973, p. 116), who listed "*Retiolites geinitzianus angustidens*, *Monograptus* cf. *audumcus* and *Monograptus* of the *priodon* group" from the Merriangaah Siltstone, and inferred an age of "late Llandoverian to early Wenlockian" (middle of the Early Silurian). This material was found at Quidong by M. Tuckson (see Sherwin 1972) and the identifications cited by Crook et al. (1973) were by G.H. Packham. The Quidong Basin, 20 km N of Delegate (Fig. 1), is a farming region, although sulphides (copper–lead–zinc) in the carbonates of the area were mined in the 1860s, and the locality continues to be targeted as a mineral prospect (McQueen 1989).

Here we describe graptolites collected by us in May 2004 from three localities in the Quidong Basin (Fig. 2). Re-collection of the fauna was necessitated by the almost complete disappearance of the original collection; three poorly preserved, indeterminate specimens exist in the Mining Museum collections, presumably representing salvage from the collections of the University of Sydney.

This graptolite fauna is important because Crook et al. (1973) recognised the Quidongan Orogeny to account for what they considered an unconformity between the Merriangaah Siltstone and the overlying Quidong Limestone (Fig. 2). Scheibner (1972) originally introduced the term without definition. Crook et al. (1973, p.116) inferred that the Quidong Limestone was Ludlow in age, based on comparison of brachiopods in the mudstone conformably overlying the Quidong Limestone (the Delegate River Mudstone) to those in the "Ludlovian Silverdale Formation at Yass". This age was consistent with the late Wenlock-early Ludlow age assigned to the limestone by Hill (1943, p. 58) based on the similarity of the Quidong rugose coral fauna to the rugose fauna at Yass from the Bowspring and Hume limestones of the Silverdale Formation. Packham (1969, p. 121) also concluded the Quidong Limestone was "Wenlockian to early Ludlovian", comparing its diverse fauna of brachiopods, trilobites and corals with faunas from Hattons Corner, Yass. On this basis the orogeny was placed by Crook et al. (1973) within the Wenlock. Our studies of the Quidong Basin graptolites allow refinement of the age of this graptolite fauna; along with new data on the age of the Quidong Limestone, the

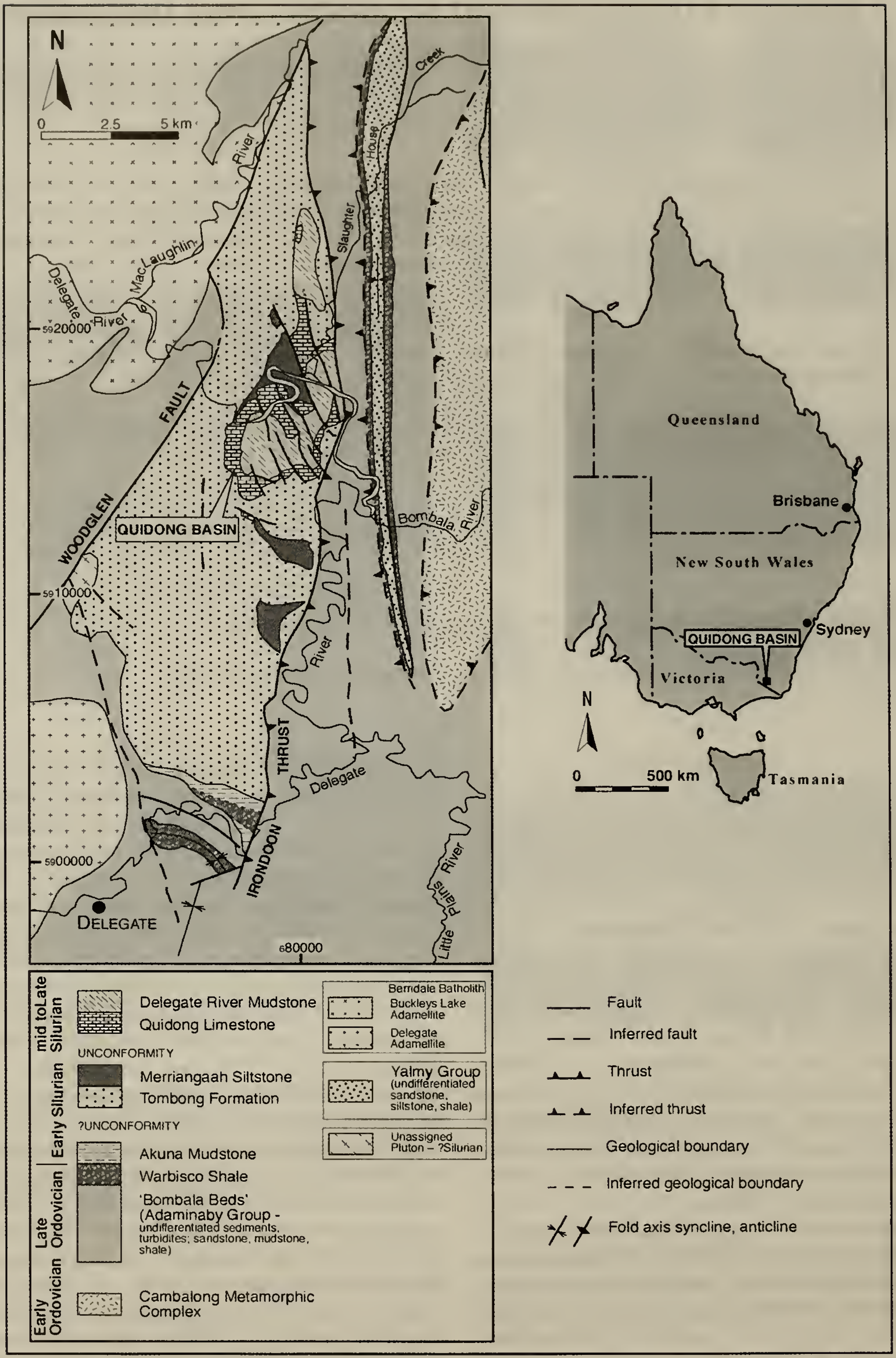

Figure 1. Location and geological setting of the Quidong Basin in the Tombong Block in southeastern New South Wales (modified after Lewis and Glen 1995, and McQueen 1989).

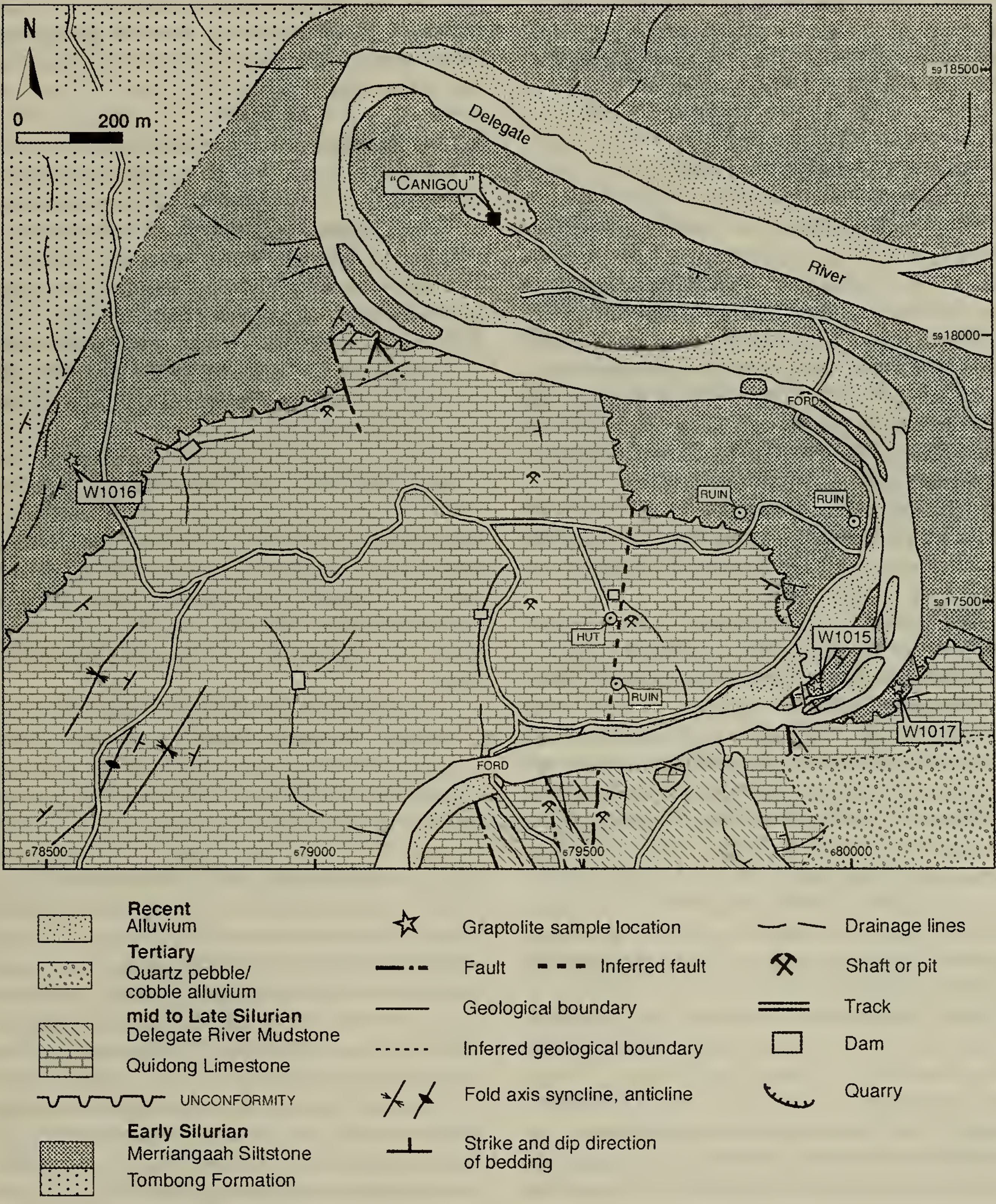

Figure 2. Geology of part of the northern area of the Quidong Basin. Sites sampled for graptolites indicated by W1015, W1016 and W1017.

age of the hiatus can be more closely constrained.

It is not our purpose here to discuss critically the whole matter of Early and Middle Silurian diastrophism in NSW. Crook et al. (1973) discussed the relationship of the tectonic history of the Quidong Basin area in relation to that of the Canberra and Orange districts. As two of us (RBR, AJW) are engaged in studies with Gordon Packham of the graptolite-rich sequences at the Spring-Quarry Creek area, at Four Mile Creek and the Angullong district near Orange, it is premature to comment on the nature of breaks in the sequence that have been recognised there by

Packham (1969) and Jenkins (1978, 1986). Further, the nature of the Merriangaah Siltstone – Quidong Limestone contact is a topic being investigated by RAP, and is only briefly discussed here.

GEOLOGICAL SETTING

The Quidong Basin is a structural entity of approximately 25 sq. km representing the preserved remnants of a sedimentary basin comprising Mid to Late Silurian sediments that unconformably overlie a 500 m–thick Early Silurian quartzose turbidite pile. Collectively, these Silurian sediments occupy a fault-bounded, triangular area defined as the Tombong Block (Lewis and Glen 1995) that sits within Ordovician turbiditic sandstones and shales ('Bombala Beds' – Adaminaby Group) (Fig. 1). The Tombong Block forms part of the southernmost section of the Hill End–Cooma Zone, a meridional structural zone situated in the east of the Lachlan Fold Belt (Lewis and Glen 1995).

The Early Silurian component of the Tombong Block comprises two units: the lower Tombong Formation and the higher Merriangaah Siltstone. The Tombong Formation occupies the bulk of the Tombong Block and consists of approximately 400 m of quartz-rich sandstones and siltstones and interbedded shales. The presence of chert and slate pebbles in the Tombong Formation indicates that it was possibly derived from the Adaminaby Group (Lewis et al. 1994). Beds in the unit are generally 30 cm to 50 cm thick, but range up to 1 m in thickness, and have lateral continuity equivalent to outcrop exposure. No fossils have been recovered from the Tombong Formation.

The relationship between the Tombong Formation and the overlying Merriangaah Siltstone is conformable. The transitional boundary linking these formations is well-exposed on the northwest margin of the Quidong Basin (Fig. 2). Where the Merriangaah Siltstone is absent on the western and southern margins of the Basin (Fig. 1), the contact between the Tombong Formation and the overlying Quidong Limestone is disconformable.

In the north of the Quidong Basin (Fig. 2) are extensive exposures of the Merriangaah Siltstone, which is estimated to be at least 80 m thick (Lewis et al. 1994, p. 35), and is composed of laminated beds of fine to very fine quartz sand intercalated with coarse quartz siltstone. The graptolite specimens in this study were recovered from beds composed of sand-sized grains. Bed thicknesses are mostly between 5 cm and 15 cm; cross-laminations and ripple marks are common. The trace fossils *Paleodictyon* isp. and ?*Gordia* isp. were described from the unit (Webby 1969). Our material was collected at three localities (Fig. 2), as follows:

W1015: the riverside location illustrated by Crook et al. (1973, plate 2, fig. B), approximately 3-4 m below the unconformity. This locality has yielded a monospecific graptolite fauna of *M. priodon*;

W1016: most westerly locality sampled, about 10 m below unconformity. This locality has yielded *Oktavites bodentoeriensis*; and

W1017: 1-2 m below the unconformity first recognised by Herbert (1965) and Woodhill (1965). The fauna from here is *Oktavites falx* and *M. priodon*.

The mid to Late Silurian fill of the Quidong Basin consists of the highly fossiliferous Quidong Limestone and the conformably overlying, erosionally-truncated Delegate River Mudstone. Conodonts recovered from the Quidong Limestone by one of us (RAP) indicate that the unit ranges from the late or latest Wenlock. The unconformity separating the Quidong Limestone from the underlying Merriangaah Siltstone is angular.

During Honours studies at the University of Sydney, Woodhill (1965) and Herbert (1965) described the unconformity based on lithologic relationships and the angular contact between the Merriangaah Siltstone and the Quidong Limestone. The deformation indicated because of the angularity of the unconformity has been attributed to "inferred periods of compression" (Gray 1997, p. 149) that were a feature of the stabilization of the Lachlan Fold Belt between the end of the Ordovician and the Middle Devonian (Collins and Vernon 1992). However, cleavage trends within the Merriangaah Siltstone and the overlying mid to Late Silurian sediments are similar (RAP, unpublished studies), suggesting that, if the cleavage resulted from horizontal shortening, such deformation was subsequent to the termination of the second round of basin fill and was therefore not responsible for the angularity. An alternative hypothesis indicating that extensional rifting produced the angular unconformity has been suggested by Pickett (1982, p. 10) and Glen (1992, p. 373), the angular discordance being a manifestation of block rotation on listric normal faults that formed part of a new, or renewed, round of basin extension.

Significantly, the late Llandovery start of the hiatus in sedimentation represented by the unconformity in the Quidong Basin is approximately coeval with the metamorphism of turbidites forming the Cooma Complex, based on an age for the metamorphism

(433±3 Ma) derived from detrital zircon and monazite by Williams (2001). The Cooma Complex is one of five fault-bound metamorphic complexes in the Eastern Metamorphic Belt (EMB) located in the southeastern part of the Lachlan Fold Belt (Johnson, 1999, fig. 2); the Cambalong Complex, 6 km to the east of the Quidong Basin (Fig. 1), is another in this narrow (<50 km wide), generally meridionally-trending Belt. If the complexes comprising the EMB are similar in age and the metamorphism, at least in part, is due to compressional deformation (Johnson, 1999, p. 440), then the Quidong Basin and Cambalong Complex represent juxtaposed coeval elements with contrasting structural styles separated by a thrust boundary (Fig. 1).

SYSTEMATIC PALAEONTOLOGY

Figured material is lodged in the Australian Museum (AMF). Three specimens from Quidong are held by the Geological Survey of NSW (MMF 18915-7) and are now lodged in the repository at Londonderry, NSW.

Class Graptolithina Bronn 1849
Order Graptoloidea Lapworth, 1875
Family Monograptidae Lapworth, 1873
Genus *Monograptus* Geinitz, 1852

Type species

Lomatoceras priodon Bronn, 1835;
subsequently designated by Bassler (1915).

Monograptus priodon (Bronn, 1835)
Figures 3A-B

1835 *Lomatoceras priodon* Bronn, p. 56, pl. 1, fig. 13.
1842 *Gr. Priodon*; Geinitz, pp. 699-700, pl. 10, figs 16A-B.
1850 Grapt. *priodon*. Bronn; Barrande, pp. 38-40, pl. 1, figs 3-9, 14, (*non* 1-2, 10, 11-13).
1993 *Monograptus priodon* (Bronn, 1835); Loydell, pp. 107-112, pl. 5, figs 2, 12; text-fig. 20, figs 4-5, 11, 26.
1993 *Monograptus priodon* (Bronn, 1835); Štorch & Serpagli, pp. 42-43, pl. 9, figs ?3, 4-5, text-fig. 123A, ?H.

Loydell (1993) synonymised well over one hundred records of *M. priodon*; of these, however, *M. rickardsi* Hutt, 1975 seems to us specifically distinct from *M. priodon*. Loydell demonstrated the very widespread record of *M. priodon* in late Llandovery and Wenlock strata.

Material

Numerous adult rhabdosomes were collected from localities W1015 and W1017. Specimens from W1017 are associated with *Oktavites falx,* are preserved in low relief with minimal pyritisation and are current-aligned. Specimens from locality W1015 are rather weathered, pyritised adult specimens in full relief and are also current-aligned. At locality W1015 no associated species was found.

Description

Monograptus rhabdosome, at least 15 cm long, with a distal dorsoventral width of 2.8-3.0 mm in three-dimensional specimens; proximal observed dorsoventral width of rhabdosome 1.0 mm and observed thecal spacing 11-14 in 10 mm; distal thecal spacing 8-11 in 10 mm; thecal overlap ca ½; thecal hooks strongly retroverted with lateral processes (but not spines); sicula not seen.

Remarks

This material is on slabs covered with current-oriented specimens, but no proximal ends have been found, although some specimens probably end within 10 mm of the sicula. Specimens from W1017 are extremely well-preserved, agree with many other descriptions of the species and are typical of those found in the late Llandovery.

Genus *Oktavites* Levina, 1928

Type species

Graptolithus spiralis Geinitz, 1842, subsequently designated by Obut (1964), from the Llandovery of Germany.

Remarks

Oktavites was not recognised in the 1970 edition of the graptolite Treatise, being considered a junior synonym of *Monograptus* (Bulman 1970, p. V132) for reasons given by Bulman and Rickards (*in* Bulman 1970, p. V132). However, the thecal structure of *Oktavites spiralis* has long been quite well-known; Loydell (1993) effectively redefined *Oktavites* in modern terminology and, at the same time, drew a contrast with species of *Spirograptus,* including the type species *S. turriculatus* (Barrande, 1850). Thus *Oktavites* has broadly triangular thecae with the thecal apertures laterally expanded, whereas *Spirograptus* has 1 or 2 apertural spines, sometimes apertural symmetry, but usually little lateral expansion. The

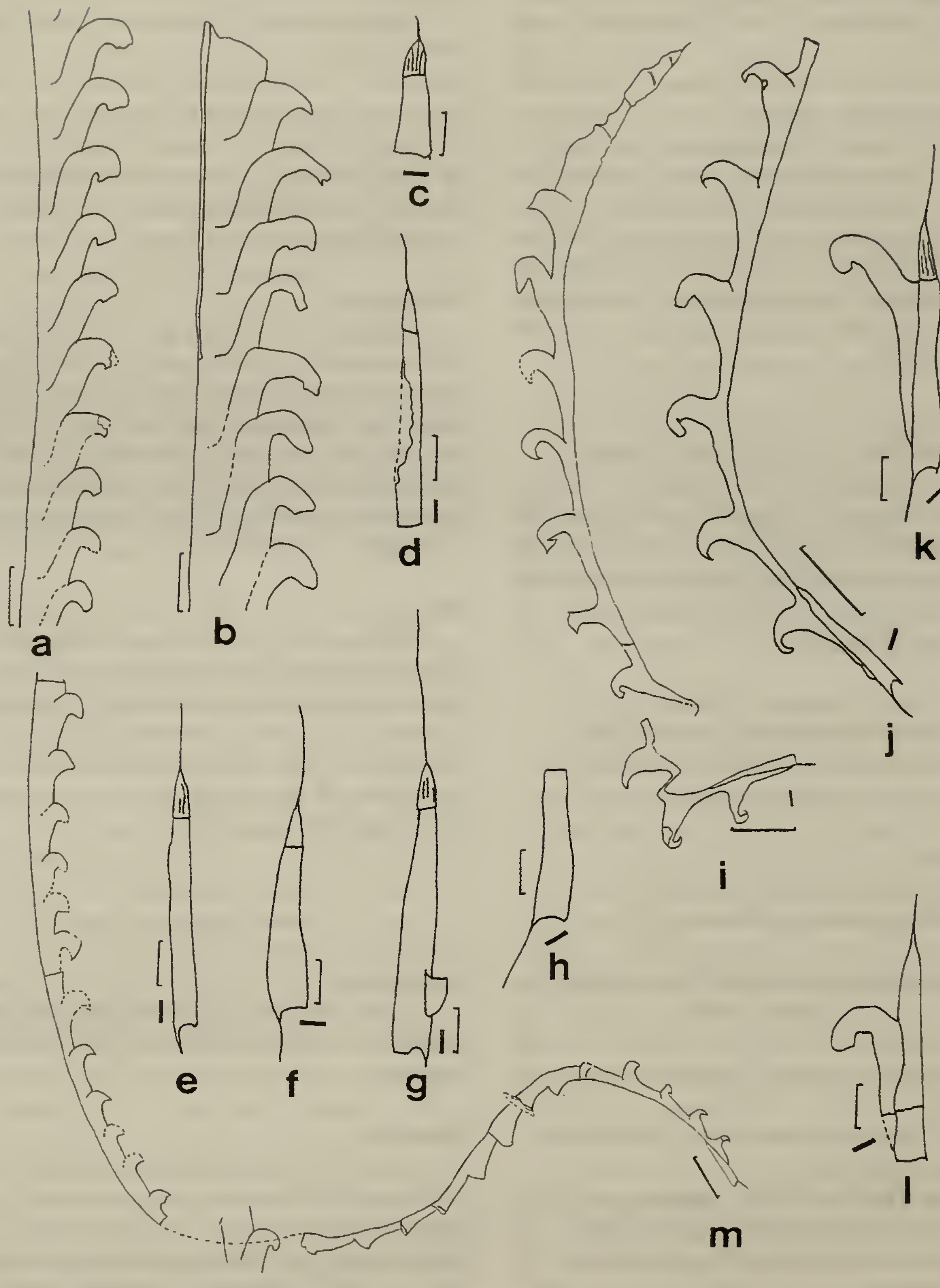

Figure 3. (a-b) *Monograptus priodon* (Bronn), respectively AM F 123128, 123129 from locality W1017, preserved in moderate relief, specimen a being quite close to the proximal end, specimen b of mesial thecae; scale bar 1 mm. (c-l) *Oktavites bodentoeriensis* Loydell, respectively AM F123120, 123114, 123116, 123119, 123121, 123118, 123115, 123113, 123124 and 123117, all from locality W1016; scale bars of c-h, k-l are 0.10 mm; scale bars of i-j are 1 mm. (m) *Oktavites falx* (Suess), AM F123125, from locality W1017; heavy bar indicates a lineation on the bedding plane that may be soft sediment deformation rather than tectonic deformation; scale bar of m is 1 mm.

generic name *Oktavites* has not been previously used for Australian graptolites, although *O. spiralis* was recorded from the Melbourne Trough, Victoria as *Monograptus spiralis* (see Rickards and Sandford 1998). Neither *Oktavites falx* nor *O. bodentoeriensis* (see below) has previously been recorded from Australia.

Oktavites falx (Suess, 1851)

Figure 3m

1851	*Graptolithus falx* n. sp.; Suess, p. 119, figs 10a-b.
1945	*Spirograptus falx* (Suess, 1851); Přibyl, pp. 11-32, pl. 5, figs 1-6.
?1990	*Oktavites falx* (Suess); Ge, pp. 152-153, pl. 64, figs 3, 6, 9.
1993	*Oktavites? falx* (Suess, 1851); Loydell and Cave, figs 8k-n.
?1994	*Monograptus* aff. *falx* (Suess, 1851); Zalasiewicz and Tunnicliffe, text-fig. 8A-B.
1998	*Oktavites? falx* (Suess, 1851); Štorch, pp. 124-5, text-fig. 3, figs 11-13.
2003	*Oktavites falx* (Suess, 1851); Loydell, pp. 59-60, text-fig. 1, figs 11-12.

Lectotype

The specimen figured by Suess (1851, pl. 9, fig. 10a) from the *spiralis* zone of the Litohlavy Formation, Praha-Malá Chuchle, Bohemia, was designated by Přibyl (1945).

Material

Two specimens from locality W1017, AM F123125a-b and AM F123126a-b; the former is on a bedding plane with many well-preserved specimens of *M. priodon*. Specimens are more or less flattened except for the proximal end, which is in low relief and well preserved.

Description

Oktavites with low-angled triangular thecae, reaching 13-9 in 10 mm; proximal dorsoventral width 0.4-0.5 mm, distally about 1 mm; thecal apertures with small lateral expansion and suggestions in places of tiny spines; dorsal wall strongly recurved; thecal height at th1 (hence dorsoventral width at same point) 0.4-0.5 mm; distal thecae inclined at a lower angle and less triangular than proximal ones (20° down to 10°); thecal overlap slight; rhabdosome with some spiral coiling beginning around th7; sicula 1.2 mm long, apex to just above level of hook of th1; origin of th1 halfway from sicular aperture; sicular aperture simple; virgella short, slim spine.

Remarks

The proximal thecae of *O. falx* are similar to those of *O. bodentoeriensis* from Quidong but are essentially smaller, much more closely spaced (13-12 in 10 mm compared with 7½ -8 in 10 mm) and with a lower metathecal height. Štorch's (1998) specimens from Spain are very close to the Quidong specimens, perhaps beginning their spiral coiling a little later (ca th10-15, rather than ca th7), but otherwise having the same dimensions and measurement. The stratigraphically earlier forms illustrated by Loydell (2003) have stronger rhabdosomal coiling but have exactly the same proximal end as the Quidong specimens.

Oktavites bodentoeriensis Loydell, 2003

Figs 3C-L

2003	*Oktavites bodentoeriensis* sp. nov.; Loydell, p. 60, text-fig. 1, figs 14-17; text-fig. 3.

Holotype

Specimen figured by Loydell (2003, text-fig. 1, fig 15) from the lower *spiralis* Biozone of the Rauchkofel Bodentöri section, Carnic Alps, Austria.

Material

Two adult specimens, AM F123113 and 123115, and eight early growth stages, AM F123114, 123116-121, 123124 all from locality 1016. Two further, poorly-preserved possible early growth stages from the same locality, AMF 123122-3.

Diagnosis

Oktavites with some rhabdosomal coiling beginning ca th12; prosicula 0.16-0.28 mm long; sicula 1.2-1.5 mm long; virgella short and fine. Proximal dorsoventral width of rhabdosome 0.6-0.8; distal dorsoventral width 0.75-0.85 mm. Proximal thecal spacing 7 in 10 mm; distal thecal spacing 7.5-8 in 10 mm; thecal overlap very low (diagnosis modified after Loydell on the basis of our new material).

Description

Of the two adult rhabdosomes AM F23113 (Fig. 3J) shows no twisting of the stipe after th7, whereas AM F123115 (Fig. 3I) begins to twist at around th10-11, so an open spiral coiling of rhabdosome can be predicted.

Prosicula well seen on several specimens, occuring as isolated specimens on bedding planes. Several longitudinal spiral strengthening threads visible (Fig. 3C) and these may coalesce to form nema, a fine thread up to 0.7 mm long and commonly seen on early growth stages. There seems to be a slight constriction at the origin of the metasicula (Figs 3d, g, k). When complete, the sicula is 1.2-1.5 mm long and its apex is invariably above the level of the hook of th1.

Origin of th1 very low on metasicula, perhaps 0.1-0.15 mm above sicular aperture, which has a diameter of up to 0.12 mm. Th1 completed before protheca of th2 begins (Figs 3e, k). Protheca of th2 very slim (0.1 mm), and expands only slightly as metatheca is approached. A marked change occurs in angle of free ventral wall with onset of metatheca (a change from 5° to 20-40°) and metatheca is quite high (giving the full dorsoventral width). Thecal hook occupies about 1/3 of metathecal height. Overall thecal profile axially elongate-triangular, with prominent hook showing no sign of torsion; there is some indication of apertural expansion and there are tiny thecal spines (Fig 3l, th5 and th6 of visible thecae). Central part of metathecal hook strongly retroverted, facing dorsal side of rhabdosome.

Remarks

The nature of the thecal hook confirms Loydell's (2003) attribution of this species to *Oktavites* rather than *Spirograptus* (which has less transverse expansion of the thecal aperture) or *Torquigraptus* (which shows thecal torsion of the metathecal axis). The Quidong specimens are very close to Loydell's originals from the Carnic Alps and differ only in having slightly more widely-spaced thecae (7.5-8 in 10 mm compared with 8-10 in 10 mm). The Quidong specimens give a fuller idea of the early development, which is not well known in species of *Oktavites* other than the type species *O. spiralis*. *Oktavites bodentoeriensis* differs from *O. falx* in the same part of the rhabdosome, in having a more robust proximal end and different thecal spacing.

BIOZONAL AGE OF THE QUIDONG BASIN GRAPTOLITES

The age indicated for the assemblage is probably early *spiralis* Biozone (in old terminology early to mid *crenulata* Biozone: Llandovery, Early Silurian). *Monograptus priodon* has a long time range, possibly appearing (Loydell 1993) in the upper part of the *turriculatus* Biozone (earliest Telychian=late Llandovery), but certainly is common from the *griestoniensis* Biozone (Telychian) to the early middle Wenlock. However, both *O. falx* and *O. bodentoeriensis* are restricted to the Llandovery; the former appears in the early *spiralis* Biozone (more coiled forms) and ranges into the upper *spiralis* Biozone (almost uncoiled specimens), whereas the latter was recorded from the early *spiralis* Biozone of the Carnic Alps by Loydell (2003). This seems the most likely level in the *spiralis* Biozone for the Quidong material.

Crook et al. (1973) listed the following graptolites from Quidong: *Retiolites geinitzianus angustidens* Elles and Wood, *Monograptus aduncus* Bouček and *Monograptus* ex gr. *priodon* (Bronn), stating that they were identified by G.H. Packham. It was suggested that the last of these named forms was similar to *M. parapriodon* Bouček because of the narrow rhabdosome and high thecal spacing; if so, it is different from the specimens of *M. priodon* described here but has broadly the same age implication, as *Monograptus parapriodon* occurs in the *crenulata* Biozone. *Retiolites g. angustidens* ranges from the *crispus* Biozone to the early Wenlock. *Monograptus aduncus* is now referred to *Monoclimacis* and is from the early Wenlock rather the late Llandovery; however, we would need to re-examine this material given the improvements in recent years of our understanding of *Monoclimacis*. We have been unable to locate these specimens but the ages indicated are not in dispute with our more precise age of early *spiralis* Biozone, except for the identification of *Monoclimacis aduncus*. With the help of Dr Ian Percival and Dr Lawrence Sherwin we were able to examine three specimens (MMF 18915-7) in the collections of the Geological Survey of NSW (now held in the NSW State Palaeontological Reference Collections at the Geological Survey of NSW Geoscience Centre, Londonderry); as no retiolitids were present, part of the original collection is missing.

We have also been unable to check the Pickett (1982) record of *M. sedgwickii* Portlock but, as we remark in the following description of *M. priodon*, there is a preservational view of *M. priodon* that can appear superficially like *M. sedgwickii*; however, even under these circumstances the two have a quite different thecal overlap.

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Silurian graptolites from the Barnby Hills Shale and Hanover Formation, New South Wales

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Additional collections of graptolites from the Barnby Hills Shale and new collections of graptolites from the Hanover Formation in the Lachlan Fold Belt of central western NSW are documented. The Late Silurian Hanover Formation is shown to range from the *spineus* Biozone (late Ludlow) to the *parultimus* Biozone (Přídolí). A fauna containing *Monograptus ludensis* is recorded from the Barnby Hills Shale, which is now known to range from the *ludensis* Biozone (late Wenlock) to the *inexspectatus* or *kozlowskii* Biozone (late Ludlow). New dendroid graptolite taxa described here include *Dendrograptus typhlops* sp. nov. from the Barnby Hills Shale and *Dictyonema paululum hanoverense* subsp. nov. from the Hanover Formation. *Monograptus spineus*, from the Hanover Formation, is reported for the first time outside Europe. The new data confirm that strata assigned to the *cornutus* and *praecornutus* biozones (late Ludlow) are widely distributed in central NSW, and confirm previous suggestions for a latest Ludlow sea level highstand followed by a shallowing.

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KEY WORDS: Barnby Hill Shale, graptolites, Hanover Formation, Ludlow, Přídolí, Silurian.

INTRODUCTION

A diverse Late Silurian (late Ludlow: *inexspectatus* or *kozlowskii* Biozones) graptolite fauna was described by Rickards and Wright (1997a) from the Barnby Hills Shale at Neurea, NSW (Fig. 1). In this paper we document further biostratigraphic control for this region of NSW by describing additional Silurian graptolites from the Barnby Hills Shale from various localities, and documenting the first Silurian graptolites from the Hanover Formation in the vicinity of Cumnock in central western NSW (Fig. 1). These new collections provide definitive age controls for the latter formation, in particular.

GEOLOGICAL BACKGROUND

The fossils described here are from two largely Late Silurian formations located in the northern part of the Lachlan Fold Belt, New South Wales, in the region from east of Orange to south of Wellington (Fig. 1). The Barnby Hills Shale is part of the Early Silurian to earliest Devonian Mumbil Group, a carbonate - volcanic - fine-grained clastic sequence, which was deposited on the Mumbil Shelf. The Hanover Formation was deposited in the Cowra Trough, a marine basin to the west of the Mumbil Shelf, and forms part of the Early Silurian to earliest Devonian Cudal Group (Meakin and Morgan 1999).

Barnby Hills Shale

Strusz (1960) introduced the term Barnby Hills Shale Member for the upper unit of his 'Mumbil Formation', and Vandyke and Byrnes (1976) subsequently raised the unit to formation status; the Mumbil Group was established by Pickett (1982). Discussions of the formation were given by Morgan

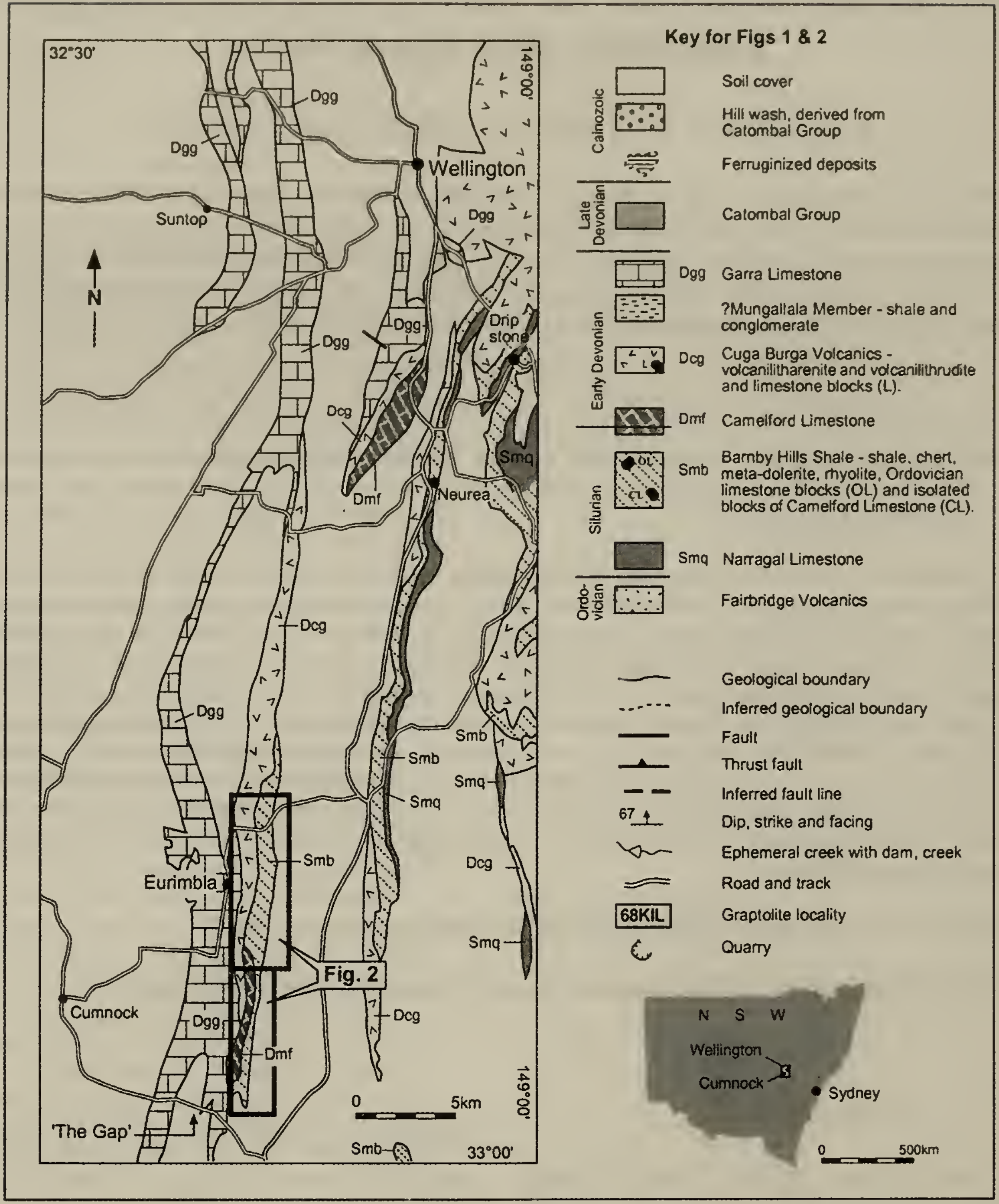

Figure 1. Simplified geology of the area between Wellington and Cumnock (NSW) (modified after Talent and Mawson 1999) showing major Silurian and Early Devonian carbonate units and associated shale sequences along the Mumbil Shelf, and showing location of Fig. 2.

(in Pogson and Wyborn 1994; in Meakin and Morgan 1999).

Talent and Mawson (1999) and Cockle (1999) advocated the relegation of this unit to a junior synonym of the Wallace Shale, a formation erected for strata in the Four Mile Creek area, SSE of Orange (Stevens and Packham 1953) but which also occurs in the Spring-Quarry Creek area (Packham and Stevens 1955) west of Orange. The Wallace Shale exhibits distinctive red, green and yellow banding, and is easily distinguished lithologically from the Barnby Hills Shale. The age of the Barnby Hills Shale is late Wenlock to late Ludlow, based on earlier data (Rickards and Wright 1997a) as well as data presented here. The only age-diagnostic fossils described from the Wallace Shale are the Přídolí graptolites described by Sherwin and Rickards (2002) and, probably, the Přídolí graptolite fauna from near Cadia described by Rickards et al. (2001); the deeply weathered graptolitic strata at the latter locality cannot be assigned with certainty to the Wallace Shale on the basis of their lithology. There is insufficient reason, we believe, to synonymise and discard this very distinctive stratigraphic unit (see also Zhen et al. 2003).

The formation crops out mainly in four meridional fault slices (Morgan et al. 1999) and extends from the town of Molong in the south to north of Wellington in the north, a strike distance of almost 80 km. The bulk of the fauna described here from the Barnby Hills Shale is from the western belt that extends from 'The Gap' to north of Eurimbla (Figs 1-2). Farrell (1992; in Talent 1995) recognised its Late Silurian age in the western belt, and also identified a number of interbedded limestones of Silurian and Ordovician ages, which had been earlier noted by Byrnes (in Pickett 1982, fig. 19). Dating of graptolites from shales enclosing Ordovician limestone outcrops in the northern section by Sherwin (1994a, 1997) as Silurian proved that the limestone is allochthonous and that the shales correlate with the Barnby Hills Shale (Zhen et al. 2003).

The western belt is faulted at its base against the Late Devonian Catombal Group (Fig. 2). In the south, the formation is conformably overlain by the Siluro-Devonian Camelford Limestone but, to the north, it is faulted against the early Devonian Cuga Burga Volcanics. The Silurian limestone outcrops in the southern section are Přídolí and are thought to be remnants of the lower horizons of the Camelford Limestone 'grounded' along the Curra Creek Thrust (Farrell 2001). To the east, the Barnby Hills Shale forms part of a continuous Siluro-Devonian sequence.

In the vicinity of the original road cutting type section just east of the Mitchell Highway at Neurea (see Rickards and Wright 1997a, and Fig. 1 herein) the formation conformably overlies the Narragal Limestone. This road cutting, which yielded the material described by Rickards and Wright (1997a), has been, regrettably, over-collected and the now almost barren exposures have been also severely damaged by large-scale removal of rock for other, non-geological purposes. Morgan (in Meakin and Morgan 1999) nominated a new type section for the formation along a railway cutting at Dripstone (Fig. 1) where exposures are good and formation boundaries are exposed. Unfortunately graptolites are extremely rare in this section: on our first visit we found rare graptolites identified in the field as *Bohemograptus*, *Linograptus* and *Dictyonema*, but these specimens have been mislaid; no more material was collected on a second visit to the section. In this type section the formation is 290 m thick; in the Eurimbla area, the western belt appears to reach a thickness of over 700 m but the unit may be internally folded (Morgan in Meakin and Morgan 1999).

We also describe and illustrate poorly-preserved graptolites from this formation near Lewis Ponds; this locality, 15 km northeast of Orange, was described as the Mullions Reserve by Meakin in Pogson and Wyborn (1994). This material was first reported by Sherwin (1993) as "*Monograptus bohemicus* subsp., with siculae of *hercynicus* type", and the occurrence was further documented by Meakin (in Pogson and Wyborn 1994). All the abundant graptolites (Fig. 5D-E) belong to a monospecific assemblage of *Bohemograptus paracornutus* Rickards and Wright, 1999b, are tectonically deformed, and occur in black cleaved pyritic slates; this is the southernmost known fossiliferous development of the formation.

Hanover Formation

The term Hanover Formation was introduced by Maggs (1963) and first published by Offenberg et al. (1971). Bradley (in Pickett 1982, fig. 14) included the formation in the Cudal Group. Morgan (in Meakin and Morgan 1999) found that the unit was much more widespread than shown by previous workers and provided a thorough discussion of the formation. The Hanover Formation crops out in a number of complex meridional fold and fault repetitions from Cumnock to Geurie (Morgan et al. 1999). The fossils described here were found in the easternmost block of Hanover Formation, in a rail cutting east of Cumnock (Fig. 1). Previous workers considered the rocks in the cutting to be part of a Devonian package (the 'Carinya Shale' of Maggs [1963] and Offenberg et al. [1971]), but Morgan (in Meakin and Morgan 1999) determined a Silurian age and correlated the rocks with the Hanover Formation.

The Hanover Formation has few diagnostic features and closely resembles the Barnby Hills Shale in lithology, as well as a number of other shale-siltstone dominated facies in the area. The formation conformably overlies the Wenlock Canowindra Volcanics and is overlain either by the Early Devonian Cuga Burga Volcanics or their lateral equivalent, the Berkley Formation. In the study area the formation is faulted at its base against the Cudal Fault, and is internally complexly folded and faulted. No one section has yielded both top and base of the Hanover Formation, so its total thickness is not known; Bradley (in Pickett 1982) estimated a thickness of 300 m.

Lithological Description

The Barnby Hills Shale and the Hanover Formation consist dominantly of poorly-outcropping siltstone and shale, with subordinate interbedded fine- to coarse-grained volcaniclastic sandstone, radiolarian chert, marly siltstone and detrital calcareous horizons

Figure 2. Simplified geological map showing graptolite localities in the area between The Gap and Larras Lee.

(Morgan in Meakin and Morgan 1999; Morgan in Meakin and Morgan 1999). The formations are characterised by poorly- to well-bedded and finely-laminated buff siltstone and shale, and vary from brown to grey to green to red. Beds are in the order of 1 mm to 2 cm in thickness. Laminations exhibit slump, scour, grading, flame and other sedimentary structures, and bioturbation is common (Morgan in

Meakin and Morgan 1999; Morgan et al. in Meakin and Morgan 1999).

Numerous detrital limestone beds are present within both formations, including allochthonous limestone blocks up to 180 m long. The beds are commonly highly fossiliferous and are of varying ages. In the Hanover Formation, a massive to well-bedded fossiliferous detrital limestone bed is present 100 m across strike to the west of the graptolite locality, for which Percival (1998) determined a probable late Llandovery age. In the Barnby Hills Shale, large allochthonous limestone blocks containing Late Ordovician fossils (Zhen et al. 2003, Webby 1969) lie adjacent to one of the graptolite localities (68 KIL on Figure 2A). In contrast, a large limestone block at the southern end of the western belt of the Barnby Hills Shale contains Late Silurian fossils (Farrell 2001).

PALAEONTOLOGY AND AGE

Barnby Hills Shale

Graptolites from the Barnby Hills Shale were first recorded by Strusz (1960) as *Monograptus bohemicus*. Sherwin (1993, 1994b) identified the common species in the fauna as an undetermined subspecies of *Bohemograptus bohemicus*, indicating a middle to late Ludlow age; a late Ludlow age was suggested by Sherwin (1997). Sherwin (1994a, 1997) identified *Saetograptus colonus* from shale in the KIL study area in the western belt, indicating an early Ludlow age (basal *nilssoni* Biozone to part way through the *scanicus* Biozone). No graptolites were described or illustrated until Rickards and Wright (1997a) described the substantial late Ludlow (*inexspectatus* or *kozlowskii* Biozones) fauna of dendroids and graptoloids including the age-diagnostic *Bohemograptus bohemicus tenuis* (Bouček 1936) from the belt at Neurea (Fig.1). The Barnby Hills Shale is locally conformably overlain by the Přídolí to Lochkovian Camelford Limestone (Farrell 1992, 2003).

Meakin (in Pogson and Wyborn 1994, p. 105) drew attention to the occurrence of this formation at South Mullion Reserve, ENE of Orange. The occurrence at this locality (W859) of poorly preserved *Bohemograptus paracornutus* (Figs 5D-E) indicates the *cornutus* Biozone.

The graptolite faunas described here from this formation are thus from four localities (Figs 1-2):

68 KIL (Fig. 2): 'Kildara' property; *ludensis* Biozone, late Wenlock, Barnby Hills Shale; *Monograptus ludensis* (Murchison, 1839) and indeterminate retiolitids.

Blind Gully (WEEM 13b: see Fig. 2): *praecornutus* Biozone, late Ludlow, Barnby Hills Shale; *Bohemograptus praecornutus* Urbanek, 1970; *Linograptus posthumus* Richter, 1875; *Dendrograptus* sp. nov.; *Acanthograptus aculeatus aculeatus* (Počta, 1894); *Thallograptus acanthicus vandenbergi* Rickards and Wright, 1997a; and *Dictyonema* sp.

W 825: Dripstone railway cutting, type section of Barnby Hills Shale, late Ludlow; *Bohemograptus*, *Dictyonema* and *Linograptus* (not described or figured); this collection has been mislaid.

W 859: roadside quarry at South Mullion Reserve, lower Lewis Ponds Road (Bathurst 1:250 000 sheet, grid reference 705420E, 6320760N). Poorly-preserved and highly-deformed graptolites occur in cleaved, pyritic black slate. The only species identified is the late Ludlow *Bohemograptus paracornutus* Rickards and Wright, 1999b.

Hanover Formation

The Hanover Formation has yielded graptolites including *Saetograptus chimaera* and brachiopods (Sherwin 1997), and plant fragments (Morgan *in* Meakin and Morgan 1999). Maggs (1963) identified *Monograptus colonus*, *M. salweyi*, *M. bohemicus* and *?Spinograptus spinosus* from a locality 3 km roughly along strike north of the graptolite locality described here; his identifications suggest the *nilssoni* or *scanicus* Biozone, early Ludlow. Sherwin (1996) identified the graptolites *Agastograptus* spp., ?*Paraplectograptus* sp. and *Monograptus ludensis*, indicating a latest Wenlock age (*ludensis* Biozone). The Hanover Formation thus probably extends from late Wenlock throughout the Ludlow and possibly to the end of the Přídolí, considering that the formation appears to be conformably overlain by the early Devonian (Lochkovian) Cuga Burga Volcanics and Berkley Formation (Morgan et al. in Meakin and Morgan 1999). Graptolite data reported here indicate an age range of *spineus* Biozone (late Ludlow) to *parultimus* Biozone (Přídolí).

The fauna described here from this formation is from one locality:

WEEM 409 (a, c): *spineus* (late Ludlow) and *parultimus* (early Přídolí) Biozones, Cumnock railway cutting, Hanover Formation; *Dictyonema elegans* Bulman, 1928; *Dictyonema paululum hanoverense* subsp. nov.; *Pristiograptus shearsbyi* Rickards and Wright, 1999b; *Monograptus spineus* (Tsegelnuk, 1976); *Neocolonograptus* *parultimus* (Jaeger, 1975). Three collections have been made from different levels in this cutting, as follows: WEEM 409 has *Neocolonograptus parultimus* and *Dictyonema elegans* and *D. paululum*; WEEM 409a has ?*Neocolonograptus parultimus*, *Linograptus posthumus*, *P. shearsbyi* and *N? mitchelli*; and WEEM 409c has *Monograptus spineus* and *P. shearsbyi*.

DEPOSITIONAL ENVIRONMENTS

The Barnby Hills Shale and Hanover Formation were deposited in a quiet, deepwater environment, reflecting the progressive subsidence of the Cowra Trough and Mumbil Shelf during the Middle to Late Silurian (Byrnes 1976; Morgan, Colquhoun and Meakin in Meakin and Morgan 1999), which allowed widespread distribution of fine-grained sediments. The time of initiation of subsidence varied, beginning in the Cowra Trough in the Wenlock, and on the western margin of the Mumbil Shelf in the early Ludlow. Ordovician basement rocks were still locally exposed, shedding large limestone blocks downslope into deeper water (Morgan, Colquhoun and Meakin in Meakin and Morgan 1999; Zhen et al. 2003; Zhen and Percival 2004). By middle or late Ludlow the Mumbil Shelf was totally submerged. Fine-grained sedimentation continued in the Cowra Trough and on the margins of the Mumbil Shelf into the earliest Devonian. Parts of the Shelf underwent shallowing during the late Ludlow or early Přídolí, permitting local deposition of the Camelford Limestone. Conditions changed substantially in the early Devonian, with the onset of dominantly mafic to intermediate volcanism in the Cowra Trough and on the Mumbil Shelf (Cuga Burga Volcanics and Berkley Formation), thus terminating quiet mud sedimentation (Morgan, Colquhoun and Meakin in Meakin and Morgan 1999).

The late Ludlow *praecornutus* Biozone, and the slightly younger *cornutus* Biozone characterised by *B. paracornutus* and *B. b. tenuis*, are now known to range widely within central N.S.W. Both characteristic taxa have been recorded from the Yass area by Rickards and Wright (1999b); we have also seen *B. paracornutus* in collections made by G.H. Packham just south of Neurea, and probably the same species collected by him from the Manildra area (Savage 1968). *Bohemograptus b. tenuis* was described from Neurea by Rickards and Wright (1997b).

In both the Yass (Rickards and Wright 1999b) and Neurea (Rickards and Wright 1997a) areas, Ludlow graptolitic beds are succeeded sharply by shallow water strata (the Rainbow Hill Marl at Yass and the Camelford Limestone near Wellington), providing evidence for a sea-level highstand followed by a latest Ludlow shallowing. Various authors have drawn attention to the regression at the end of the Ludlow (Talent 1989, Johnson et al. 1991, Johnson and McKerrow 1991, Kaljo et al. 1995) and Pickett (1982) noted the widespread deposition in NSW during the period dominated by bohemograptid graptolites; the NSW setting appears to conform to the global sea-level pattern at this time.

SYSTEMATIC DESCRIPTIONS

Material described here is deposited in the Australian Museum, Sydney (AM F).

Class Graptolithina Bronn, 1849
Order Dendroidea Nicholson, 1872

Genus *Dendrograptus* J. Hall, 1858

Type species.

Graptolithus hallianus Prout, 1851; subsequently designated by J. Hall (1862).

Dendrograptus typhlos sp. nov.

Fig. 3A-B

?1995 *Dendrograptus* sp.; Rickards et al., p. 18, fig. 12B.
?1997a *Dendrograptus* sp.; Rickards and Wright, p. 214, fig. 6A.
?1999b *Dendrograptus* sp.; Rickards and Wright, p. 191, fig. 3A.

Type Material

Holotype AM F114618; paratypes AM F114620-1; all well-preserved though not showing the autothecae too well; all from Blind Gully, locality WEEM 13B; *praecornutus* Biozone, late Ludlow, Barnby Hills Shale.

Etymology

The species name is the Greek word for blind, after the Blind Gully locality.

Diagnosis

Dendrograptus branching every 1-3 mm, more or less regularly, at angles from 40-90°; younger parts of colony have a lateral stipe width of 0.2-0.4 mm

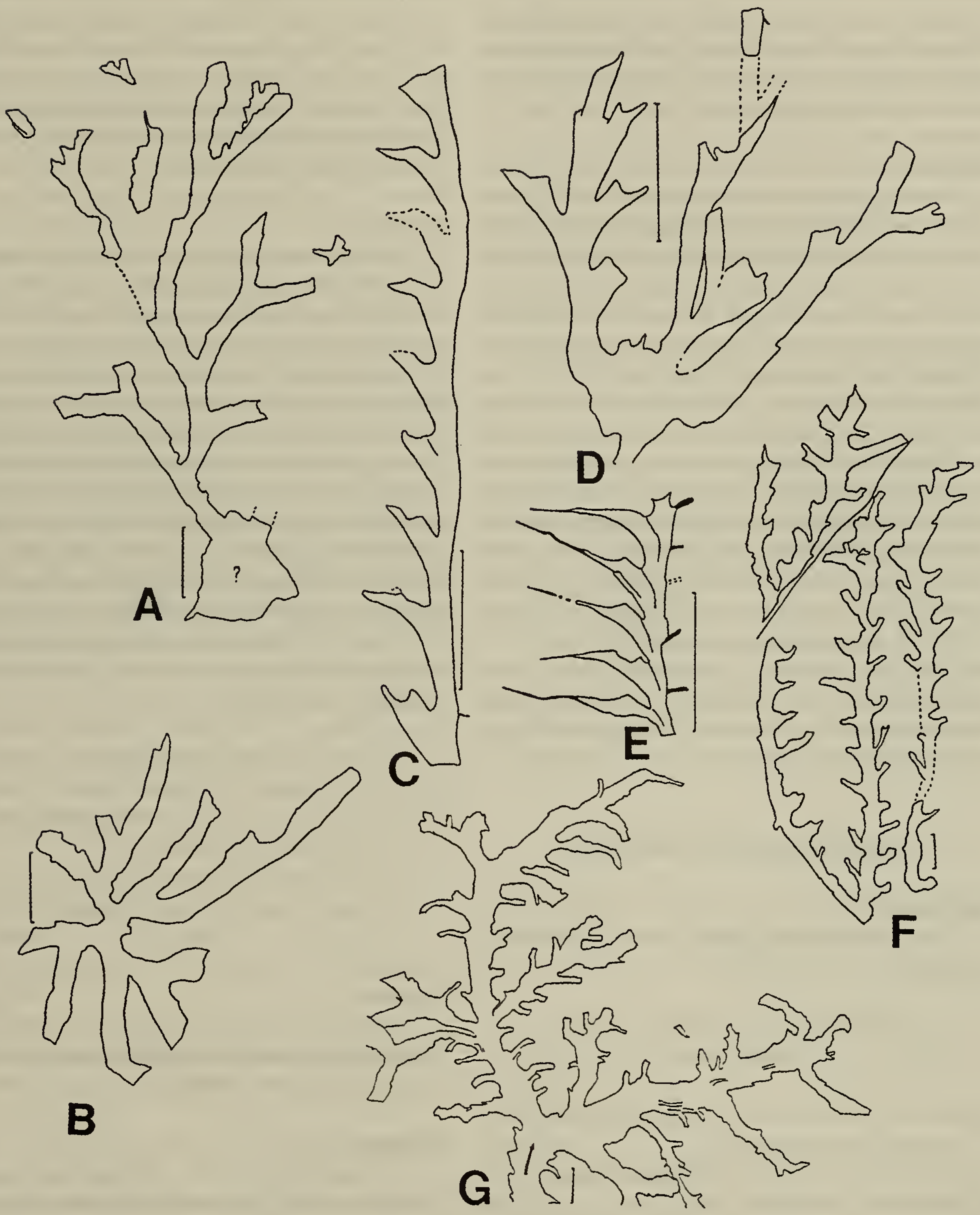

Figure 3A-G. A-B, *Dendrograptus typhlos* sp. nov.; respectively AM F114618 (holotype) and 114620; question mark indicates possible holdfast in holotype. Blind Gully, *praecornutus* Biozone, Ludlow. C-D, *Dictyonema elegans* Bulman, 1928; respectively AM F 92382 and 92381, locality WEEM 409, *parultimus* Biozone, Přídolí; E, *Dictyonema paululum hanoverense* subsp. nov., AM F92380 (holotype), WEEM 409, *parultimus* Biozone, Přídolí. F, *Acanthograptus aculeatus aculeatus* (Pocta, 1894), AM F114616, Blind Gully, *praecornutus* Biozone, Ludlow. G, *Thallograptus acanthicus vandenbergi* Rickards and Wright, 1997a, AM F14619, Blind Gully, *praecornutus* Biozone, Ludlow. Scale bars 1 mm.

but, nearer the proximal end, lateral widths of 0.3-0.5 mm occur. Possible compound stipes proximally but no indication of them distally. Autothecae difficult to see, possibly spaced at ca 30 per 10 mm. Largest specimen 25 mm × 20 mm.

Remarks

Perusal of the studies of Rickards et al. (1995) and Rickards and Wright (1997a, 1999b) demonstrates that identification of *Dendrograptus* specimens is not easy. In Australian rocks the genus seems to be relatively rare, occurring sporadically throughout the Silurian and the earliest Devonian (Rickards and Wright 2001). The specimen figured by Rickards et al. (1995, fig. 12B) as *Dendrograptus* sp. has similar dimensions to *D. typhlos* and may be an earlier occurrence of it: the Quarry Creek specimen is from the *lundgreni/testis* Biozone of the Wenlock. *Dendrograptus* sp. (of Rickards and Wright 1997a, fig. 6A) from the Ludlow Barnby Hills Shale at Neurea has similar dimensions but may have a lower autothecal spacing (15-20 in 10 mm). *Dendrograptus* sp. (of Rickards and Wright 1999b, fig. 3A) from the *praecornutus* Biozone of the Yass district also has an apparently lower thecal spacing (20 in 10 mm), although is otherwise similar and occurs only a little lower stratigraphically than the Blind Gully specimens.

Genus *Dictyonems* J. Hall, 1851

Type species

Gorgonia retiformis J. Hall, 1843; subsequently designated by Miller (1889).

Dictyonema elegans Bulman, 1928
Fig. 3C-D

1928 *Dictyonema elegans* sp. nov; Bulman, p. 52, text-fig. 26; pl. 6, figs 22-3.
1997a *Dictyonema elegans* Bulman; Rickards and Wright, p. 214, figs 5C, 8D.
A fuller synonymy was given by Rickards and Wright (1999b).

Material

Several fragmentary specimens (AM F 92381-2, AM F114613 a-b, AM F114614) from locality WEEM 409, *parultimus* Biozone, Hanover Formation, near Cumnock.

Description

Dorsoventral width (excluding ventral apertural processes) 0.4-0.5 mm. Ventral apertural processes robust and relatively short: however, their distal extremities may be broken. Autothecal spacing 20 in 10 mm. One specimen (Figure 3D) may be close to the holdfast position, or may enclose the holdfast between 3 or 4 diverging stipes; the latter are seen partly in profile and partly in dorsoventral view. No obvious signs of bithecae.

Remarks

Rickards and Wright (1999b) gave a summary of the variation seen in Australian records of the species, which is now known to range through the Ludlow and Přídolí (the type British material being Wenlock). The present specimens agree with previous records (Rickards and Wright 1997a) from the Barnby Hills Shale in having an autothecal spacing of only 20 in 10 mm, which may be contrasted with the types and with Quarry Creek specimens from the Wenlock and Ludlow respectively, which have 25 in 10 mm, and with the Yass Ludlow and Přídolí specimens, which have 30 in 10 mm. Thus, whilst it is certain that these are all very similar forms, it cannot be argued that the range of variation is as yet constrained in any stratigraphic sense. Even so, *D. elegans* has great potential in this regard.

Dictyonema paululum Bulman, 1928

1928 *Dictyonema paululum*, n. sp.; Bulman, p. 58, pl. 5, figs 9-11; ?pl. 4, fig. 13.

Dictyonema paululum hanoverense subsp. nov.
Fig. 3E

Material

Holotype, a single fragment of well-preserved stipe in profile view, AM F 92380, locality WEEM 409, *parultimus* Biozone, Přídolí; Hanover Formation.

Diagnosis

A subspecies of *Dictyonema paululum* characterised by dorsoventral width of 0.50 mm, crowding of autothecae (28-30 in 10 mm) and dissepiments.

Description

Five autothecae seen on the specimen, spaced at ca 28-30 in 10 mm. Autothecal apertures slightly isolated and, whilst there is no dorsal apertural spine, there is a long ventral spine approaching 0.5 mm in length. Fine dissepiments seen at dorsal edge of stipe; spacing rather close at 20-30 per cm, possibly one to each autotheca. One possible bithecal tube visible on free ventral wall of penultimate theca. No indications of internal structure save traces of some autothecal overlap.

Remarks

This specimen differs from Bulman's late Llandovery originals in that the dorsoventral width is greater (0.50 mm compared with 0.15-0.25 mm), as is the crowding of autothecae (28-30 in 10 mm compared with 19-20 in 10 mm in Bulman's originals) and dissepiments. In overall appearance they are very similar, however, and especially resemble Bulman's (1928, pl. 5, fig. 11) specimen. *Dictyonema elegans* Bulman, 1928 (see also Rickards and Wright 1997a) is another similar form, although all the biocharacters have different measurements; clearly they belong to the same dictyonemid group typified by slightly isolated autothecal apertures, ventral spines, no dorsal process, and external bithecae. *Dictyonema paululum australis* Rickards and Jell, 2002, from the *griestoniensis* Biozone of the Graveyard Creek Subprovince of Queensland, has very similar dimensions overall but differs in having a low dissepimental spacing (12-14 in 10 mm) and a higher stipe spacing (20+).

Dictyonema paululum hanoverense subsp. nov. is not associated with dendroids other than *D. elegans,* but the Blind Gully locality has yielded several rhabdosomal fragments we refer to *Dictyonema* spp. indet.; further material is needed for a more satisfactory identification.

Genus *Acanthograptus* Spencer, 1878

Type species

Acanthograptus granti Spencer, 1878; by original designation.

Acanthograptus aculeatus aculeatus (Počta, 1894)
Fig. 3F

1894 *Inocaulis aculeatus* n. sp.; Počta, p. 199, pl. 7, figs 22-25.
1894 *Inocaulis demetosa* n. sp.; Počta, p. 200, pl. 7, figs 7, 8a.
?1909 *Inocaulis diffusus* (Spencer); Gurley *in* Bassler, p. 53, fig. 68.
1957 *Acanthograptus aculeatus* (Počta); Boucek, p. 88, pl. 15, figs 1-9, text-figs 37 a-g.
1995 *Acanthograptus aculeatus* (Počta); Rickards et al., p. 24, figs 11F, 15C-F.

Material

One well-preserved rhabdosome, AM F114616a, b, from Blind Gully locality WEEM 13B, Barnby Hills Shale, *praecornutus* Biozone.

Description

Acanthograptus with a lateral stipe width of 1.5 mm, parallel-sided; 10-12 twigs per 10 mm of stipe, on each side; twigs alternating on opposite sides (in dorsal or ventral view); stipe diversions infrequent and irregular; twigs may have two autothecae in each termination; broad bases to twigs suggest presence of bithecal openings there; stipe may be compound; central part of stipe ca 0.4 mm in diameter.

Remarks

Previous records of *A. a. aculeatus* range from the late Wenlock to early Ludlow, but the Blind Gully specimens are late Ludlow (*praecornutus* Biozone). Thus the species seems to have a long range with little morphological change. However, Rickards and Wright (1997a) described a more slender subspecies, *A. a. neureaensis*, from the *inexspectatus* or *kozlowskii* biozonal level in the Barnby Hills Shale at Neurea.

Genus *Thallograptus* Ruedemann, 1925

Type species

Dendrograptus? succulentus Ruedemann, 1904; by original designation.

Thallograptus acanthicus Bouček, 1957

Thallograptus acanthicus vandenbergi Rickards and Wright, 1997a
Fig. 3G

1997a *Thallograptus acanthicus vandenbergi* subsp. nov.; Rickards and Wright, pp. 219-20, fig. 61.

Material

Four specimens AM F114619, 114622-4, and one possible specimen AM F114617a-b, all from Blind Gully locality WEEM 13B, *praecornutus* Biozone, late Ludlow, Barnby Hills Shale.

Description

Thallograptus reaching 20 mm x 15 mm, with robust, spiky stipes which branch and diverge more or less at right angles; stipes compound, with bundles of long, narrow tubes; main stipe width 1.5 mm proximally, down to 0.5 mm most distally; progressive dichotomies become narrower, and all stipe termination is by single, conspicuous autothecal tubes.

Remarks

No bithecae have been detected and the autothecal spacing cannot be given until more autothecal openings can be seen on the ventral stipe surface. This subspecies resembles *Acanthograptus a. aculeatus* but the latter is more slender and has a very regular association of twigs opening alternately on one side of the stipe and the other. *Thallograptus a. vandenbergi* is a smaller and more slender subspecies than the type subspecies. The species is very rare, with one specimen only recorded from Bohemia (the holotype of Bouček's 1957 nominate subspecies) and five definite Australian specimens.

Order Graptoloidea Lapworth, 1875

Genus *Pristiograptus* Jaekel, 1889

Type species

Pristiograptus frequens Jaekel, 1889, by original designation.

Pristiograptus shearsbyi Rickards and Wright, 1999b

Figs 4D-E

1999b *Pristiograptus shearsbyi* n. sp.; Rickards and Wright, p. 194, figs 3J-P, 11A-B, 13B-E.

Material

AM F 92371, 92376, 114574-81 from localities WEEM 409 and 409c, respectively the *parultimus* and *spineus* biozones, Hanover Formation.

Description

Straight, thin *Pristiograptus* with dorsoventral width proximally 0.5 mm, distally 0.8-1.2 mm; sicula 1.2-2.1 mm long, reaching midway between apertures of th1 and th2 in case of shorter siculae, and up to the level of th2 aperture in rhabdosomes with long siculae; $\sum = 1.2\text{-}1.4$ mm; thecal overlap ca ½; thecal inclination 20-30°; proximal thecal spacing 11 in 10 mm; distal thecal spacing 10 in 10 mm; sicula with short, dorsal tongue.

Remarks

This material is very close to the Yass material; the species ranges from the *praecornutus* Biozone into the Přídolí. Some Hanover specimens have a slightly greater dorsoventral width (up to 1.2 mm compared with 0.85 mm) and some have a longer sicula (up to 2.1 mm compared with 1.65 mm).

Genus *Monograptus* Geinitz, 1852

Type species

Lomatoceras priodon Bronn, 1835; subsequently designated by Bassler (1915).

Monograptus spineus (Tsegelnuk, 1976)

Fig. 4A

1976 *Acanthograptus spineus* sp. n.; Tsegelnuk, p. 113, pl. 34, figs 6-9.

1983 *Bugograptus spineus* (Tsegelnuk); Tsegelnuk, p. 145, fig. 34.

1988 *Monograptus spineus* (Tsegelnuk); Koren' et al., p. 17, fig. 8.

1995 *Monograptus* (*Uncinatograptus*) *spineus* (Tsegelnuk); Urbanek, p. 3, figs 1D, 2, 7C-E.

1997 *Monograptus* (*Uncinatograptus*) *spineus* (Tsegelnuk); Urbanek, pp. 149-154, pl. 11, figs 3-6; pl 12; pl. 13, figs 13, 35-41.

1997 *Monograptus spineus* (Tsegelnuk); Koren' and Sujarkova, p. 80, pl. 6, figs 1-2, text-figs 14A-1.

Material

A single, well-preserved proximal end, AM F 92370, from locality WEEM 409c, Hanover Formation, *spineus* Biozone, Ludlow.

Description

The well-preserved proximal end has 3.5 thecae, the sicula, virgella, virgula and sicula thickening bands all clearly preserved. Thecal overlap low; thecal hooks well-developed, with a pair of lateral spines and a central retroflexed portion showing fuselli on th1. Upper sicular band coincides with base of th2, but it may or may not represent pro-metasicular boundary. Second band halfway along sicula, which is 1.4 mm long, its apex reaching midway between th1 and th2. Thecal spacing 12.5 in 10 mm and dorsoventral width 1.1-1.2 mm. $\sum = 0.9$ mm.

Remarks

This specimen is the first record of the species outside Podolia, Poland, and Russia. Urbanek (1997) considered the species indicative of the late Ludfordian (Ludlow) *spineus* Biozone. It overlaps with the lower (Ludlow) part of the range of the more common species *M. formosus* Bouček, 1931, previously recorded from Yass, N.S.W. by Packham (1968) and Rickards and Wright (1999b).

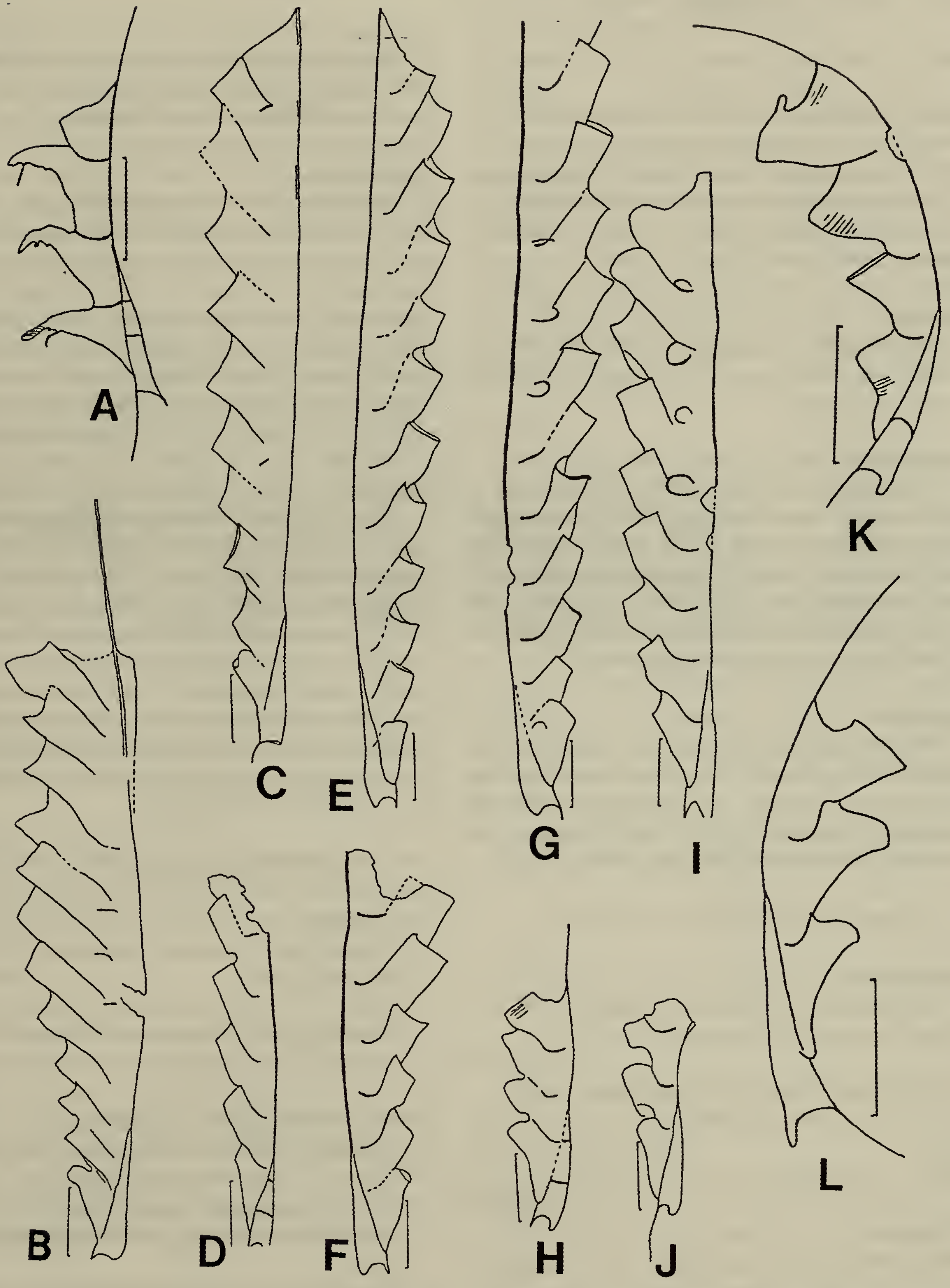

Figure 4A-L. A, *Monograptus spineus* (Tsegelnuk, 1976), AM F92370, WEEM 409c, *spineus* Biozone, Ludlow. B-C, *Monograptus ludensis* (Murchison, 1839), AM F114572-3, 68 KIL, *ludensis* Biozone, Wenlock. D-E, *Pristiograptus shearsbyi* Rickards and Wright, 1999b, AM F92376 and 923371, WEEM 409c, *spineus* Biozone, Ludlow. F-J, *Neocolonograptus parultimus* (Jaeger, 1975), respectively AM F92379, 92377, 92378, 92374 and 92375, WEEM 409, *parultimus* Biozone, Přídolí. K-L, *Bohemograptus praecornutus* Urbanek, 1970, AM F102918 from Blind Gully; and MMF 33611, WEEM 409a, both *praecornutus* Biozone, Ludlow. Scale bars 1 mm.

Monograptus ludensis (Murchison, 1839)
Fig. 4B-C

1839 *Graptolithus ludensis* n. sp.; Murchison, p. 694, pl. 26, fig. 2 (*non* fig. 1).
1996 *Colonograptus ludensis* (Murchison); Lenz et al., p. 1396, figs 3P, D, 4M-R.
1997b *Monograptus ludensis* (Murchison); Rickards and Wright, pp. 236-7, figs 2D-H, 4A-E, 5J.
For further references see Rickards et al. (1995) and Rickards and Wright (1997b).

Material

Well-preserved specimens: AM F114572-3, 114582-600, from locality KIL 68, *ludensis* Biozone, Barnby Hills Shale.

Description

Robust pristiograptid-like rhabdosomes up to 30 mm long and 2 mm broad, but with aperture of th1 clearly rounded; proximal end and sicula often slightly curved ventrally; proximal dorsoventral width 0.8-1.0 mm; proximal thecal spacing 14-10 in 10 mm; sicula 1.8-2.2 mm reaching to level of aperture of th2; thecal overlap ca ½ - ¾; thecal inclination 45-50°.

Remarks

These forms are very close to many previous descriptions and would correspond with the sort of *M. ludensis* that has been sometimes called *M. praedeubeli* Barca and Jaeger, 1990; this matter was discussed by Rickards and Wright (1997b).

Genus *Neocolonograptus* Urbanek, 1997

Type species

Monograptus lochkovensis Přibyl, 1940; by original designation (Urbanek 1997, p. 128).

Neocolonograptus parultimus (Jaeger, 1975)
Fig. 4F-J

1899 *Monograptus ultimus* n. sp.; Perner, p. 13, pl. 10, figs 4, 5 (*non* fig. 14 a, b =*Neocolonograptus ultimus*).
1975 *Monograptus parultimus* n. sp. Jaeger, p. 119, pl. 2, figs 4, 8; text-fig. 4.
1997 *Neocolonograptus parultimus* (Jaeger); Urbanek, pp. 166-7, pl. 21, figs 1-7; fig. 48.
1999b *Monograptus parultimus* Jaeger, 1975; Rickards and Wright, p. 165, figs 3Q-S, U.

More detailed synonymies are given by Urbanek (1997), Koren' and Sujarkova (1997) and Rickards and Wright (1999b).

Material

Well-preserved specimens from localities WEEM 409 and 409a: AM F 92374-5, 92377-9, 114601-11, *parultimus* Biozone, Hanover Formation.

Description

Neocolonograptus rhabdosomes up to 12 mm long with distal dorsoventral width up to 1.6 mm, proximally 0.6-0.8 mm and proximal end often with slight ventral curvature; sicula 1.6-2.0 mm long, with occasionally-preserved thickening bands, apex below level of aperture of th2; dorsal tongue conspicuous; virgella short; slight rounding on first theca or some higher thecae; thecal overlap ca ½; thecal spacing 10.5-13 in 10 mm; $\sum$ = 1.3-1.4, 1.6 in one specimen.

Remarks

This material is close to that described from Yass by Rickards and Wright (1999b), which in turn was shown to be close to Jaeger's types from Kosov Quarry; however, the Barnby Hills Shale specimens have a $\sum$ value closer to that of the material from south Tien Shan described by Koren' and Sujarkova (1997). There is also a suggestion in our present collection that the apertural undulations of the proximal thecae are slightly less than in the specimens from Yass. It is possible that they are slightly earlier, perhaps near the base of the *parultimus* Biozone.

Genus *Bohemograptus* Přibyl, 1967

Type species

Graptolithus bohemicus Barrande, 1850; by original designation.

Bohemograptus praecornutus Urbanek, 1970
Fig. 4K-L

1970 *Bohemograptus praecornutus* n. sp.; Urbanek, pp. 301-10, text-fig. 16, pl. 20C, pls 23, 24
1999b *Bohemograptus praecornutus* Urbanek; Rickards and Wright, pp. 200-202, figs 5C-L, 13K
A full synonymy is given in Rickards and Wright (1999b)

Material

Two specimens, AM F102918, and MMF 33611 from Blind Gully locality WEEM 13B near Cumnock; and a less well-preserved specimen, AM F114612 from the same locality; *praecornutus* Biozone;

Barnby Hills Shale.

Description

Robust *Bohemograptus* with tight ventral curvature. Dorsoventral width at th1 0.6-0.7 mm, distal dorsoventral width not seen; proximal thecal spacing 14 in 10 mm (distal thecal spacing not seen); thecal overlap ca 1/2; thecal inclination 40-50°; Σ 1.0-1.4 mm. Conspicuous sicula with pronounced dorsal tongue, 1.4-1.8 mm long, reaching to a little above aperture of th1.

Remarks

These specimens differ from the Yass material only in having a slightly longer sicula in one specimen: all the other measurements agree closely. They are, therefore, very close indeed to Urbanek's (1970) originals from Poland. As in the Yass district the presence of *B. praecornutus* can be taken as an indicator of the *praecornutus* Biozone.

Bohemograptus paracornutus Rickards and Wright, 1999b
Fig. 5D-E

1999b *Bohemograptus paracornutus* n. sp., Rickards and Wright, p. 202, figs 5M-Q, 6A-N, 7, 9A-B, 10A-E.

Material

AM F 114767-8 and at least 50 other specimens from the Mullions Reserve locality, all highly deformed tectonically, and in a monotypic assemblage.

Remarks

The highly deformed nature of the specimens precludes a useful description. There is, however, no doubt about the nature of the strikingly flared sicula, which is identical to that of the type material from Yass, nor in the nature of the thecae with their slightly raised lateral apertural rim and gently concave free ventral wall. Some specimens (e.g. Fig. 5E) are abnormal in thecal spacing and nature of the sicula, but this may be caused by tectonic deformation.

Genus *Enigmagraptus* Rickards and Wright, 2004

Type species

Neocucullograptus? *yassensis* Rickards and Wright, 1999; by original designation.

Species recognised

Enigmagraptus yassensis (Rickards and Wright, 1999b); *E.* sp. cf. *yassensis* (Rickards and Wright, 1999b); *E. mitchelli* (Rickards and Wright, 1999b); *E. pennyae* Rickards and Wright, 2004.

Diagnosis

One of the tiniest known graptolites, with a dorsoventral width up to 0.25 mm; widely spaced thecae; axially elongate protheca usually developed from thread-like origin; tiny metatheca up to half rhabdosome width, consisting of hood derived from dorsal metathecal wall, and variously enrolled ventrally to enclose simple ventral thecal margin; small sicula with virgella and dorsal apertural process in type species (corrected after Rickards and Wright 2004).

Remarks

Since the description of the Yass material of *E. yassensis* and *E. mitchelli* by Rickards and Wright (1999b), *E. yassensis* has also been found at Cumnock and *E.* sp. cf. *yassensis* has been found at the 'borrow pit locality (W910)' near Cadia mine (Rickards et al. 2001). *Enigmagraptus mitchelli* was, until now, known only from the type locality at Yass. *Enigmagraptus pennyae* was described by Rickards and Wright (2004) from the same locality (W910) as *E.* sp. cf. *yassensis*. All these localities are Přídolí; W910 is probably late Přídolí, whereas the other occurrences are best assigned to the *parultimus* Biozone, early Přídolí.

Enigmagraptus mitchelli (Rickards and Wright, 1999b)
Fig. 5A-C

1999b *Neocucullograptus? mitchelli* n. sp.; Rickards and Wright, p. 200, figs 4S, T.

Material

Three specimens, AM F 92372-3 and 114571, all from locality WEEM 409a; *parultimus* Biozone; Hanover Formation.

Description

There is one proximal end with a partially preserved sicula and 2 ½ thecae, with virgella and virgula also preserved. Sicula may be ca 0.5 mm long, although apex is missing; it reaches only part way along th1. Thecal spacing of this proximal part, and a fragment possibly also close to proximal end (Fig. 5A), ca 7.5-8 in 10 mm but there is some soft sediment deformation along specimen shown in Fig. 5C so thecal spacing of 7 in 10 mm might be more likely in undeformed material. A more distal fragment

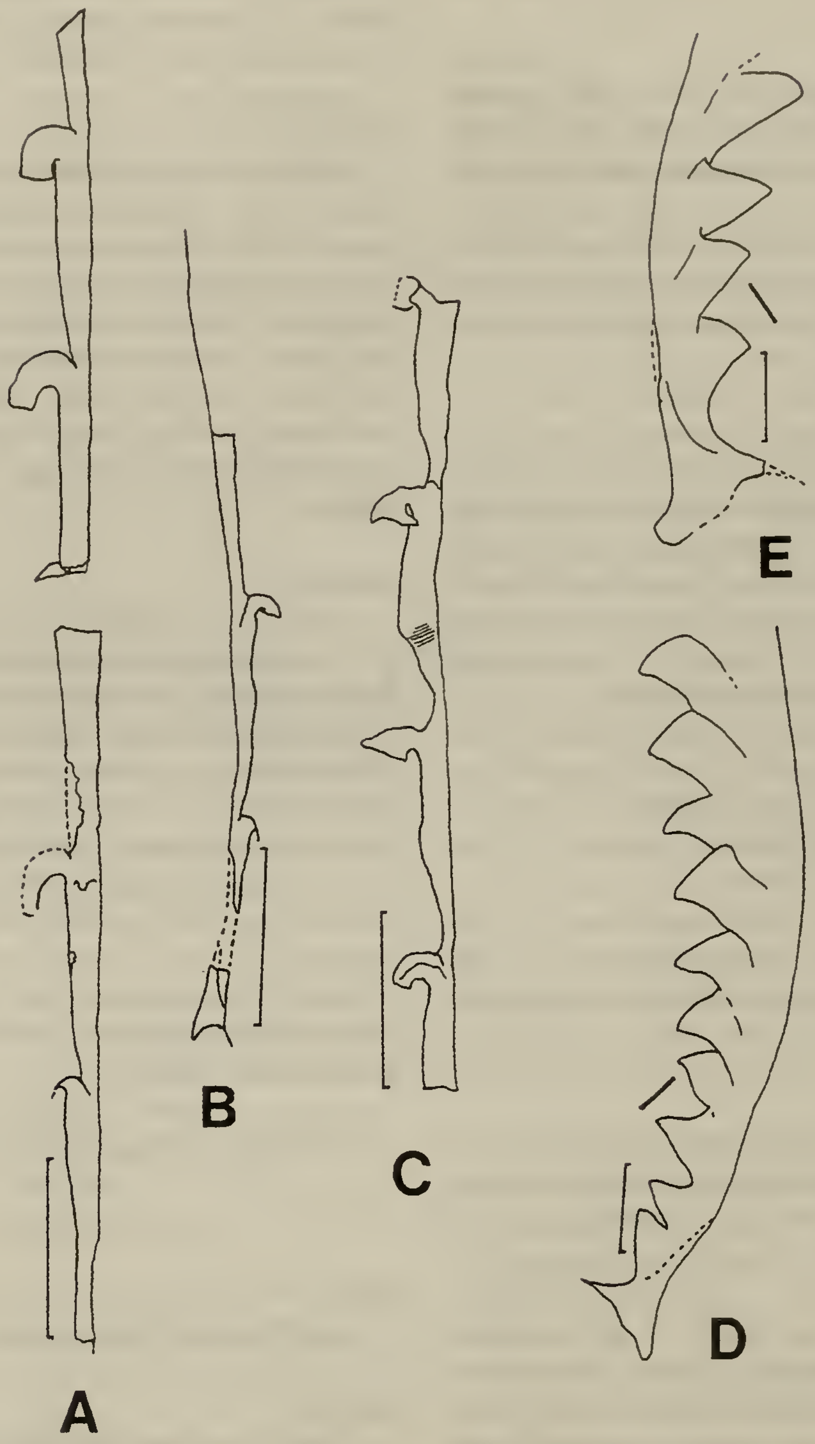

Figure 5A-E. A-C, *Enigmagraptus mitchelli* (Rickards and Wright, 1999b), respectively AM F92373, 92372 and 114571, WEEM 409a, ?*parultimus* Biozone, Přídolí; D-E, *Bohemograptus paracornutus* Rickards and Wright, 1999, AM F114768 and 114767 respectively; approximately *cornutus* Biozone, late Ludlow, W859, Mullions Reserve. AM F114767 appears to have abnormal dimensions: heavy bar = tectonic stretching direction. Scale bars 1 mm.

(Fig. 5A) shows 7 in 10 mm. Maximum dorsoventral width, including hook, of most distal fragment is 0.4 mm, but proximal end is only 0.2 mm at th1. Late metathecal part has a dorsoventral width of 0.15 mm on th2 and 0.2 mm on most distal thecae seen. Thecal overlap low and thecal angle (of free ventral wall) only a few degrees at most.

Remarks

These rare specimens are similar to those described from the same stratigraphic level (*parultimus* Biozone) from Yass by Rickards and Wright (1999b).

They differ in being more slender and in having a higher thecal spacing (7 in 10 mm compared with 4.5 in 10 mm). However, it is possible that these represent the proximal ends of the same species: certainly the profile of the hook is very similar as are most other features such as overlap and inclination. Only four specimens are known (including one from Yass) and the nature of the thecal hook is far from certain.

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Altitude, Frost and the Distribution of White Box (*Eucalyptus albens*) on the Central Tablelands and Adjacent Slopes of NSW

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The apparent rarity of white box (*Eucalyptus albens*) at high altitude has been explained by assuming an intolerance to low temperatures. These propositions were assessed by (a) a field survey of the occurrence of white box at high altitude on part of the NSW Central Tablelands and adjacent slopes and (b) a pot trial study of the response of seedlings of white box and yellow box (*E. melliodora*) to low temperatures during winter 1997. The field survey confirmed that, unlike yellow box, white box was absent from a large part of the Central Tablelands. However, it was recorded at altitudes up to 925 m a.s.l. near Orange but at lower altitudes further south. Aspect was not limiting at high altitude though low slopes appeared to be. Survival and growth of white and yellow box seedlings were low at the high altitude site but there was little difference between species regardless of whether frosted seedlings were subjected to early or delayed exposure to direct morning sunlight. Hence, alternative explanations for the local distribution pattern of white box on the Central Tablelands and adjacent slopes need to be examined.

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KEYWORDS: altitude, aspect, *Eucalyptus albens*, *Eucalyptus melliodora*, frost, lignotuber, photoinhibition.

INTRODUCTION

White box (*Eucalyptus albens* Benth.) extends from south-east Queensland along the slopes of NSW to central Victoria. Disjunct populations occur in eastern Victoria, western Victoria and the Southern Flinders Ranges of SA. The most recent description of the habitat of *E. albens* was prepared by Prober and Thiele (1993) and draws heavily on previous accounts. They reported that it generally occurs on fertile soils derived from a wide variety of parent materials. Within its area of occurrence, mean annual rainfall ranges from 500 - 800 mm, mean maximum temperature in the hottest month 27 - 32 °C, mean minimum temperature in the coldest month -1 - 5 °C and frost frequency 5 - 70 per year.

Cambage (1902) and Beadle (1981) suggested that its absence from higher parts of the tablelands was due to 'coldness' or intolerance of heavy frosts. It has been recorded at high altitude but its upper altitudinal limit is difficult to determine as altitude is rarely recorded on locality details accompanying herbarium specimens. Actual and apparent altitude records in CSIRO's (since discontinued) Eucalist, Victorian Flora Information System and NSW National Herbarium databases (Table 1) indicated a record at ~1060 m above sea level (a.s.l.). Boland et al. (1984), however, reported an occurrence from an unspecified locality, possibly in northern NSW, at 1200 m a.s.l., some 600 m higher than in an earlier edition of this publication (Hall et al. 1970).

Though frosts are common at high altitudes, they are also common in 'frost hollows' produced by cold air drainage at lower altitudes. Hence, if *E. albens* is intolerant of heavy frosts it would not be expected to occur in depressions subject to frequent frosts. The relative occurrence of *E. melliodora* Cunn. ex Schauer (yellow box) and *E. albens* in the Central Western Slopes and Central Tablelands botanic subdivisions of NSW (explained and mapped in various editions of Anderson, e.g. 1968) suggests that this may be the case. For example, around Bathurst ~670 m a.s.l.), which is located in a basin subject to

Table 1. Some high altitude records (metres above sea level) for *E. albens* across its natural range from north to south. Sources: CSIRO's 'Eucalist' (since discontinued), Victorian Flora Information System (VFIS), National Herbarium of NSW (NSW).

Specified altitude	Possible maximum altitude	Location	Source(1997)
900	-	Glenn Innes - Emmaville, NSW	Eucalist
-	850	Top of Mt. Wallaby, Woolomin	NSW
-	1100	Hanging Rock, Nundle, NSW	NSW
780	-	WSW of Quirindi. NSW	Eucalist
-	1060[A]	Pinnacle Lookout [Coolah Tops]	NSW
731	-	Wattle Flat - Sofala	Eucalist
-	960[B]	Mt. Remarkable, S.A.	Eucalist
-	1204[C]	Mt. Mcquarie, Blayney, NSW	NSW
900	-	South of Suggan Buggan, Vic.	VFIS
850	-	Southeast of Suggan Buggan, Vic.	VFIS
-	704[D]	The Paps, Mansfield, Vic.	NSW
-	1167[E]	Mt. William, Grampians, Vic.	Eucalist

[A]. Confirmed by M. Sharp (pers. comm., 2001) who also noted that *E. albens* occurs elsewhere in Coolah Tops National Park at elevations up to ~1090 m a.s.l.

[B]. Occurs on the southern foothills but is unlikely to extend to summit ridge (W. Semple, personal observations).

[C]. Most likely a record from the slopes of Mt. Macquarie, where *E. albens* occurs up to at least 870 m a.s.l. (this paper). A summit location cannot be confirmed due to its conversion to exotic pine forest.

[D]. Not observed above 550 m a.s.l. on this hill (J. Lawrence, pers. comm., 2001).

[E]. Probably a mis-identification as *E. albens* is not mentioned in Elliot et al. (1984).

cold air drainage, *E. melliodora* occurs in both the basin and at higher altitudes, whereas *E. albens* is restricted to the latter (e.g. towards Hill End). Around Orange (800 - 900 m a.s.l.), which is located on a plateau, *E. melliodora* is relatively common up to ~900 m a.s.l. but *E. albens* is rare. However, within the Central Western Slopes, *E. albens* commonly occurs on hills and slopes and *E. melliodora* on flats and lower slopes. These patterns could be explained, at least partially, by assuming that *E. melliodora* has a higher tolerance to frost than does *E. albens*. This explanation is at variance with other authorities and local observations. For example, Bower et al. (2002) reported that *E. melliodora* is more common on more fertile, though perhaps less well-drained, soils than *E. albens*. Though *E. albens* is not typically associated with poor soils, its local distribution pattern is often explained in terms of differences in soil properties (e.g. Prober 1996).

If frost does affect the local distributions of *E. melliodora* and *E. albens*, it would be expected to operate at a sensitive stage of the life cycle, viz. the seedling, especially those that emerged in autumn or winter. According to Cremer (1990), frost can affect young seedlings in three main ways: (a) 'wilting' where leaves become flabby and darkened with a waterlogged appearance, which is followed within days by drying; (b) damage to roots which are more sensitive than shoots; and (c) 'frost heave' where the stem of the seedling is gripped by a frozen soil crust and forced upwards by underlying ice crystals resulting in roots being detached from the soil. A further possibility is that of 'stress-induced photoinhibition' where photosynthetic capacity is reduced in stressed seedlings and that under high light conditions, more light energy is absorbed than can be used or dissipated. The visual effects of this would presumably be leaf death similar to 'wilting'. Based on work by Ball et al. (1991), Egerton (1996) proposed chronic cold-induced photoinhibition as a major reason for the absence of eucalypt seedlings growing to immediate north of *E. pauciflora* Sieber ex Sprengel trees near Canberra. However, earlier work with ~30 cm tall, frost-hardened, subalpine eucalypt seedlings in a radiation frost room by Harwood (1980) indicated no difference in leaf damage between seedlings that were exposed, on one occasion only, to bright sunlight v. darkness following frosting.

As part of research into the factors affecting the recruitment of *E. albens*, its local distribution pattern around Mt. Canobolas on the Central Tablelands of NSW was investigated in the mid 1990s. Preliminary results (Semple 1997) indicated that *E. albens* mainly occurred on slopes with non-easterly aspects at altitudes above 780 m a.s.l. On the basis of these results and Egerton's (1996) hypothesis, the survey was extended to a wider area and the effects of low temperatures on young eucalypt seedlings were investigated in a pot trial during winter 1997. The hypotheses tested in the pot trial were that (1) seedlings of *E. albens* are less frost tolerant (as assessed by survival and indices of growth) than those of *E. melliodora* and (2) frosted seedlings of *E. albens* (and possibly those of *E. melliodora*) are adversely affected by exposure to direct sunlight.

METHODS

Upper altitudinal limits of *E. albens* on the tablelands and adjacent slopes

Over a number of years, roads radiating from two local high points, Mt. Canobolas (1397 m a.s.l.) and Mt. Macquarie (1204 m a.s.l.) were examined for the highest occurrences of *E. albens*. Each location was plotted on a map and altitude and aspect recorded. Trees, which could be confidently identified in adjacent paddocks, were also included in the survey. All 11 sites in Semple's (1997) earlier survey were revisited.

It was appreciated that the reduced likelihood of roads traversing the highest points in the landscape, the absence of public roads in some areas, and selective tree removal on roadsides were potential sources of error in this technique.

Effect of frost ± early morning sunlight on seedlings of *E. melliodora* and *E. albens*

Seedlings were raised in 30 cm diameter x 27 cm deep black plastic pots containing sandy loam topsoil from an *E. albens* site at Cowra overlain by ~2 cm of seed-raising mixture. A slow-release fertiliser was mixed with the soil in all pots in an attempt to overcome any nutritional problems that may have adversely affected *E. melliodora*, which usually occurs on fertile soils. Half of the 16 pots used in the experiment were randomly allocated to seed (collected from around Molong on the upper Central Western Slopes) of *E. albens* and the other half to *E. melliodora* in early March 1997. Seedlings and weeds were progressively removed until 30 similar-sized seedlings of either species were present in each pot. Due to settling of the soil, the rim of each pot was later cut down to ~2½ cm above the soil surface. At the commencement of the experiment on 1 May 1997, seedlings were at the four to six leaf stage with those of *E. albens* generally being more advanced due to earlier emergence.

Two pots of each species were randomly allocated to four treatments, consisting of the factorial combination of light (Delayed or Early Light) and location (Orange, 870 m a.s.l. or Cowra, 380 m a.s.l.). The Delayed Light treatment was realised by placing pots ~1 m to the west of an existing or constructed north-south opaque steel fence, thereby delaying exposure to direct morning sunlight until 1035 hours (early July) at both locations. The Early Light treatment was achieved by placing the pots in an open area exposed to direct sunlight at 0740 hours (early July) at Cowra and 0805 hours at Orange where 'sunrise' was delayed by topography and vegetation. Pots were watered as required, avoiding prolonged waterlogging. At 1 to 2 weekly intervals, the positions of the four pots in each location by light treatment were rotated. Each pot was also rotated through 180° in an attempt to evenly distribute shading from the rim of the pot. At the same time, seedlings were counted, dead plants removed and apparent cause of death noted.

On 15 September 1997, each seedling was assessed for height of main stem (from the cotyledons to the upper-most live leaf) and the number of live pairs (or part pairs) of seedling leaves on the main stem. Pots with high numbers of healthy plants (viz. all those at Cowra) were systematically thinned to about 15 plants per pot. On 13 October when the likelihood of further frosts was low, all pots were relocated to a concrete apron with an automated watering facility at Cowra to evaluate subsequent growth under uniform conditions. Seedling numbers were recounted in early November and, together with measurements of heights, in early January 1998.

Data (survival, mean numbers of leaves and mean heights) were analysed as a 2^3 factorial design of Location (2) x Species (2) x Light treatment (2), replicated twice, using analysis of variance methods. Visual examination of residual diagnostic graphs indicated a non-normal distribution in the September seedling height data and a transformation to natural logarithms was carried out. Treatment means were examined for significant differences ($P = 0.05$) using the least significant difference (lsd) multiple comparison procedure (Steel and Torrie 1960).

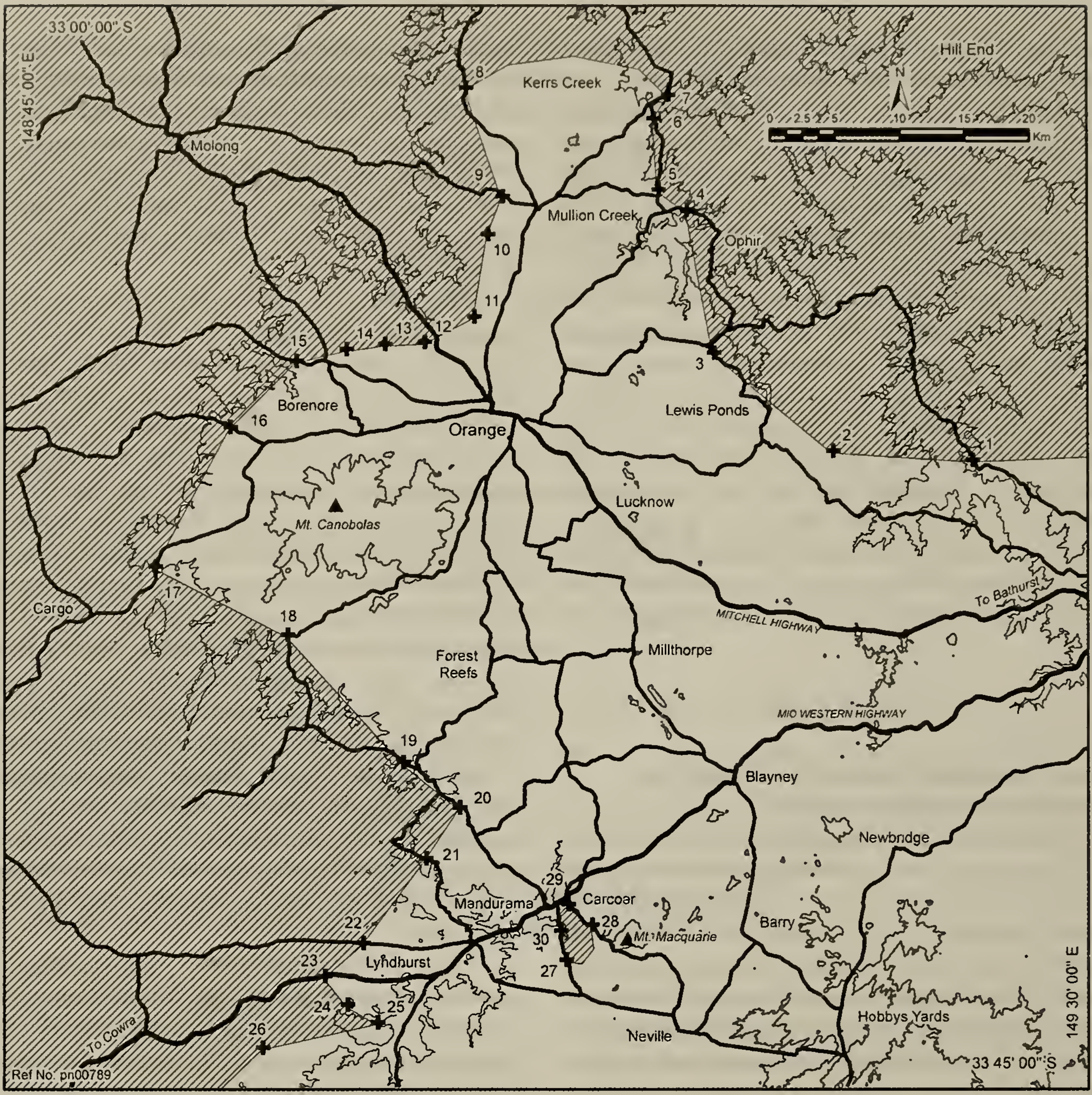

Figure 1. Part of the Central Tablelands and adjacent slopes of NSW showing areas where *Eucalyptus albens* is likely (hatched area, including the small area south of Carcoar) or unlikely (unhatched area) to occur. Numbered +s indicate locations of *E. albens* at the highest elevations on roads (thick lines). Thin lines indicate the 1000 m (near Mts. Canobolas and Macquarie and Hobbys Yards in the south-east) and 700 m contours.

RESULTS

Upper altitudinal limits of *E. albens* on the tablelands and adjacent slopes

Eucalyptus albens was absent from most roadsides above 900 m in the vicinity of Orange but to the south-west, its highest occurrence was rarely above 750 m a.s.l. It was absent from many roadsides, particularly those to the south-east of Orange. The occurrence or non-occurrence of *E. albens*, as determined in the roadside survey, is shown in Fig. 1. All occurrences were of mature trees though regeneration was evident at some sites.

Elevation

Thirty main sites (Fig. 1) and nine nearby subsidiary sites were identified as being the highest elevation occurrences on the roads travelled. The highest elevations were recorded near Orange: to the east on the fall of the Central Tablelands to the Macquarie River valley (925 m a.s.l., site 2) and to the north (890 m a.s.l., site 9a) on the western fall of the tablelands. A disjunct population at high elevation (up to 870 m a.s.l., site 28) was also recorded near Carcoar on the western and north-western slopes of Mt. Macquarie. The site with the lowest elevation (660 m a.s.l., site 23) occurred west of Lyndhurst on the Mid

Table 2. Mean monthly terrestrial minima and frost frequencies at the Orange Agricultural Institute[A] (1975-96) and the Department of Infrastructure, Planning and Natural Resources Research Centre at Cowra[B] (1943-97), together with monthly data for 1997.

	Terrestrial minima (°C)				Frost[C] frequency (days/month)			
	Cowra (mean)	Cowra 1997	Orange (mean)	Orange 1997	Cowra (mean)	Cowra 1997	Orange (mean)	Orange 1997
May	3.3	4.6	2.2	2.1	6.3	3	7.1	8
June	1.3	-1.2	-0.2	-2.5	10.9	19	13.6	24
July	0.1	-1.8	-1.2	-4.1	13.9	20	18.1	28
Aug	0.8	-0.9	-0.8	-2.7	11.2	19	16.3	25
Sept	2.6	3.4	0.8	1.4	6.8	1	11.3	9
Oct	5.5	4.3	3.0	2.1	1.9	4	5.2	9

[A]. 890 m a.s.l and 3.4 km from the Orange experimental site.

[B]. 381 m a.s.l. and c.100 m from the Cowra experimental site.

[C]. A frost was considered to have occurred when a minimum of ≤ -0.9 °C was recorded at 2.5 cm above grass.

Western Highway. Many other sites in the south-west were of relatively low elevation, e.g. sites 17, 19, 21, 22, 24 and 26 were at elevations below 750 m a.s.l. The situation was similar but less marked in the north-east (sites 3, 4, 6, 7 and 8).

Aspect

Approximately 25 % of the 39 occurrences occurred on crests and hence could not be allocated a single aspect though averaging was attempted. Virtually all occurrences, especially at higher altitudes, were on sloping land. No sites occurred in drainage lines but at one relatively low elevation site (720 m a.s.l., site 3a), *E. albens* extended down-slope to a drainage line. When each site was allocated an aspect (N, E, S or W quadrants), the numbers of sites in each quadrant declined from W ≈ N > E > S. Of the 12 highest elevation sites, i.e. ≥800 m ASL, numbers in each quadrant were W = E ≈ N > S.

Effect of frost ± early morning sunlight on seedlings of *E. melliodora* and *E. albens*

Monthly terrestrial minima were lower and frost frequencies were higher than average at both sites from June to August 1997 (Table 2). During the main period of the experiment, 1 May to 12 October, 97 frosts were recorded at Orange and 63 at Cowra. Five or more days of consecutive frosts occurred on six occasions at Orange and seven at Cowra. The lowest terrestrial minima recorded were -8 °C at Cowra and -9 °C at Orange, both on 21 July. Frosts persisted for longer at Orange than at Cowra – particularly in the Delayed Light treatment. The soil in the pots was often frozen at or just below the surface during midwinter in Orange.

Effect of frosts on seedlings

At Orange a progressive decline in numbers of seedlings of both species commenced in June (Fig. 2). Seedlings in the Early Light treatment were adversely affected initially but by mid August, mean numbers of survivors were similar in all treatments. Most deaths at Orange were frost-related, i.e. wilting and/or frost heave with the latter particularly affecting small (≤6 leaves) seedlings, which were more common in *E. melliodora* than in *E. albens* populations. None of the deaths at Cowra (20 by mid October) showed definite frost effects (Table 3).

In July, it was noted that some seedlings of both species had produced shoots in leaf axils as well from the cotyledon area, i.e. the site where the lignotuber would subsequently develop. When assessed in mid September, axillary shoots were present in 95 % of all seedlings and 'lignotuberous shoots' in 78 %. The early development of lignotuberous shoots apparently had no adverse effect on the development of lignotubers, which were present in 89 % of surviving seedlings in early January 1998.

Differences between treatments

Mean seedling survival (in October), main stem height and numbers of leaves (in September) were significantly higher at Cowra than at Orange (Table 4). Apart from mean numbers of leaves on *E. melliodora* seedlings being greater than on *E. albens*,

Table 3. Probable cause of death of seedlings (120 of each species initially) in both Early and Delayed Light treatments at (a) Orange and (b) Cowra between 1 May and 11 October 1997.

	Unknown	Frost heave	'Wilt'	Frost heave and 'wilt'	All causes
(a) Orange					
Eucalyptus albens	2	12	67	6	87
E. melliodora	5	32	31	2	70
(b) Cowra					
Eucalyptus albens	6	0	0	0	6
E. melliodora	14	0	0	0	14

there were no significant differences between the species across the two sites. Significant interactions suggested that mean height and number of leaves were significantly higher for all seedlings in the Delayed than in the Early Light treatment at Cowra but not at Orange; and that across both sites, *E. albens* seedlings were significantly taller in September in the Delayed than the Early Light treatment (Table 4).

Most of the seedlings present in mid October 1997 survived until early January 1998 at which time the mean height of seedlings raised at Cowra was significantly higher than those raised at Orange but the difference was less marked than previously. There were no other differences between species and treatments and their interactions (Table 4).

DISCUSSION

Natural occurrence of *E. albens* at high altitudes

The roadside survey data indicated that *E. albens* did not have a consistent upper altitudinal limit around Mts. Canobolas and Macquarie on the Central Tablelands of NSW. In the south-west of the study area it did not occur above 750 m whereas nearer to Orange it extended to elevations above 800 m. At the latitude of about Millthorpe (~33° 30' S), *E. albens* does not occur further east than is shown in Fig. 1 (apart from a recently-discovered, small disjunct population at 750 m a.s.l. on the northern footslopes of Mt. Panorama at Bathurst) despite the availability of other low elevation sites in the Bathurst Basin. It extends further east to the north of Orange (as shown) and to the south of the study area in the vicinity of Abercrombie, south of Blayney. Clearly, the Central Tablelands represent a barrier to the distribution of *E. albens* but on its own, altitude (and presumably frost severity) does not appear to be a limiting factor except at very high altitudes.

Other potential limiting factors include higher rainfall and waterlogging, which may favour other eucalypt species on the tablelands, and soil differences. High altitude occurrences of *E. albens* were sometimes associated with certain soil landscapes (composites of soils, topography and lithology) as mapped by Kovac et al. (1990). The disjunct population near Carcoar was associated with 'Razorback' soil landscape (steep to rolling topography with shallow well-drained soils derived from the Sofala Volcanics) and occurrences north-east of Orange were loosely associated with 'Panorama' soil landscape (steep to level-crest topgraphy with moderately fertile soils derived from Tertiary basalt) and similar areas too small to be shown on Kovac et al.'s map. A close association with basic igneous material was reported from the Macquarie region north of Dubbo by Biddiscombe (1963, p. 20), who suggested that 'soil nutrient status may be more decisive to *E. albens* than is moisture status'. However, further south in the South-eastern Riverina (Moore 1953) and Monaro (Costin 1954) regions, *E. albens* was reported to occur on a wide variety of soils and parent materials but generally on steep to undulating topography.

The earlier supposition that *E. albens* did not occur on easterly aspects (i.e. those likely to be exposed to early morning sunlight) at high altitude was not supported by the expanded roadside survey. This was clearly indicated by its presence on easterly aspects at the two highest altitude sites. The preponderance of northerly and westerly aspects on the western part of the Central Tablelands was probably responsible for the earlier supposition. As all of the higher altitude occurrences were on slopes, it is likely that low slope rather than aspect may be a factor that limits its occurrence at high altitude.

Differences between seedlings of *E. melliodora* and *E. albens* in the pot trial

Seedlings at Cowra performed significantly 'better' than those at Orange in all attributes measured

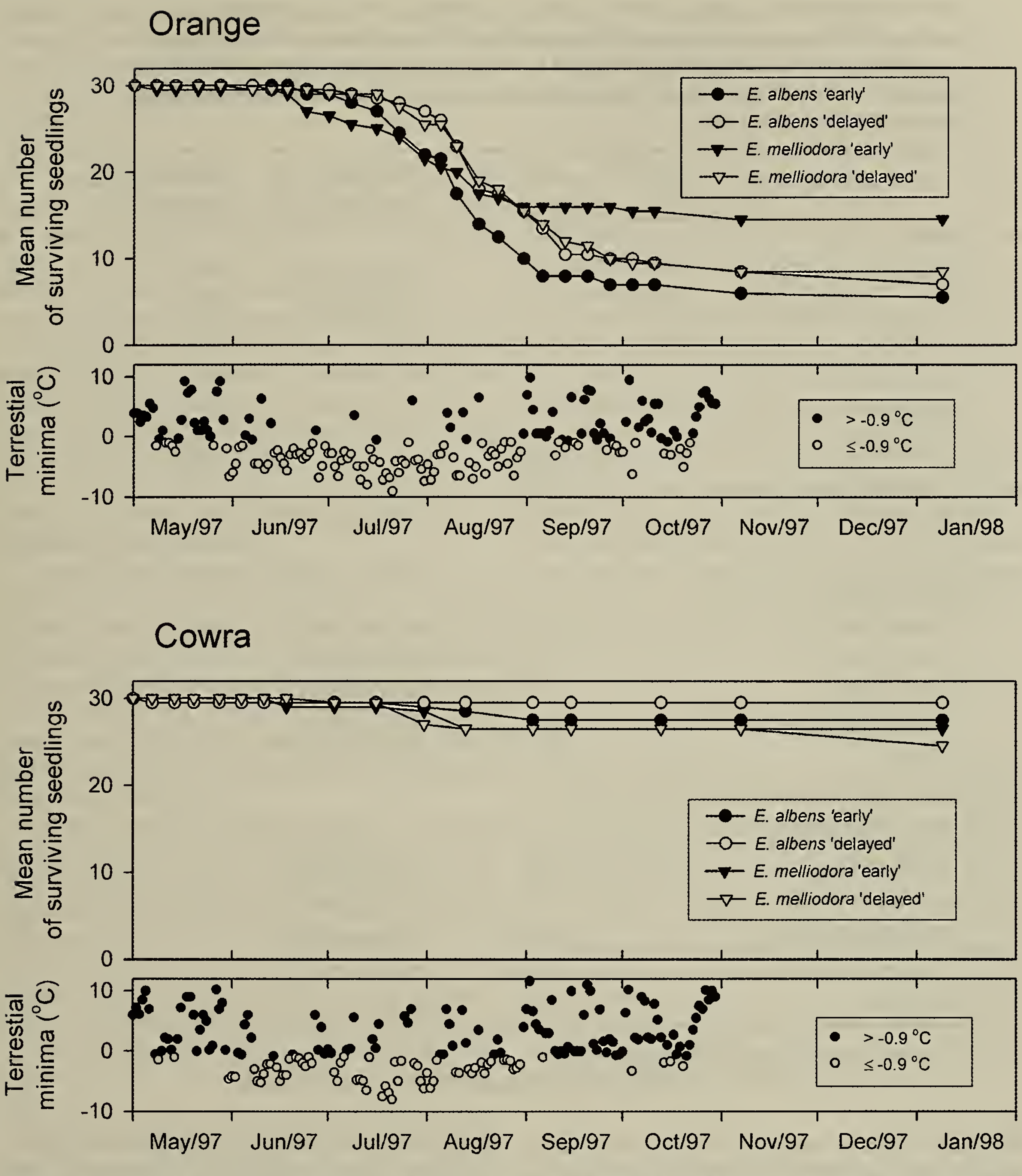

Figure 2. Survival of *E. melliodora* and *E. albens* seedlings under two morning light treatments, 'delayed' and 'early', during winter 1997 at Orange (870 m a.s.l.) and Cowra (380 m a.s.l.). Seedlings at Cowra were thinned on 15 September and numbers presented have been adjusted for this. All seedlings were relocated to an early light area at Cowra on 13 October 1997. Also shown are daily terrestrial minimum temperatures at each site. Open circles indicate frosts.

(Table 4). Conditions at Orange were particularly harsh during the 1997 winter and this was exaggerated by seedlings being in uninsulated above-ground pots where freezing of the topsoil occurred in midwinter. This was probably uncommon under normal conditions at Orange and seedlings may have experienced conditions more typical of an altitude that was well above the site – a suggestion that would also apply to the Cowra seedlings. Seedling deaths at Orange were mainly attributed to frost heave and 'wilt'. Other

Table 4. Differences in mean survival (at October 1997), numbers of leaf-pairs (September 1997) and mean stem height (September 1997 and January 1998) between seedlings of two eucalypt species exposed to two light treatments at two sites. Within columns in each section, values followed by the same lower case letter are not significantly different (*P* = 0.05).

	Survival %	Leaf-pairs per seedling	$\log_e$(Height+1) Sept 1997	Height (mm) Jan 1998
SITE				
Orange (ca 870 m a.s.l.)	34.6 a	3.15 a	2.89 a (17.0) [A]	407 a
Cowra (ca 380 m a.s.l)	91.7 b	7.41 b	4.39 b (80.0)	476 b
lsd (5%)	*19.9*	*0.73*	*0.19*	*61*
SPECIES				
E. albens	- [B]	4.53 a	-	-
E. melliodora	-	6.03 b	-	-
lsd (5%)		*0.73*		
SITE x LIGHT				
Orange Early	-	3.55 a	2.97 a (18.5)	-
Orange Delayed	-	2.75 a	2.81 a (16.7)	-
Cowra Early	-	6.75 b	4.18 b (64.1)	-
Cowra Delayed	-	8.07 c	4.61 c (99.5)	-
lsd (5%)		*1.03*	*0.27*	
SPECIES x LIGHT				
E. albens Early	-	4.08 a	3.50 a (32.0)	-
E. albens Delayed	-	4.97 a	3.82 b (44.8)	-
E. melliodora Early	-	6.22 b	3.65 ab (37.5)	-
E. melliodora Delayed	-	5.85 b	3.60 ab (35.6)	-
lsd (5%)		*1.03*	*0.27*	

[A]. Back transformed means (mm) in parentheses.

[B]. Only statistically significant main order and interaction effects have been tabulated.

presumed effects of frost at both Cowra and Orange were the production of shoots from leaf axils and the cotyledon or 'proto-lignotuber' area.

Though seedling densities in the pots were initially higher than would be expected in cases of natural regeneration, it was unlikely that the results were confounded by the effects of competition, which if operative, would have been more likely to affect growth than survival. At Orange, pots were not crowded due to the many deaths. Also, young woodland eucalypts, including *E. melliodora*, grow little if at all during winters at Orange (Semple and Koen 2001). At Cowra, where seedlings did grow and deaths were few, densities in all pots were similar, including after thinning in September 1997. Competition effects would have been constant across treatments and hence, would not have confounded the relativity of the results.

There was no significant difference between the survival rates of the two species but it was possible that the susceptibility of the smaller *E melliodora* seedlings to the unusual occurrence of frost heave at Orange (Table 3) may have masked differences at that site and possibly across sites in the analysis. The only significant difference detected between the two species was higher numbers of leaves in *E. melliodora*. The results therefore suggest that although *E. melliodora* seedlings may be slightly more frost tolerant than those of *E. albens*, the difference is unlikely to explain the rarity of *E. albens*, relative to *E. melliodora*, at altitudes up to ~900 m a.s.l. or in 'frost hollows' at lower altitudes.

The fact that some *E. albens* seedlings survived in uninsulated pots at an altitude of 870 m a.s.l. at Orange, together with a natural occurrence of mature trees at 925 m a.s.l., is further evidence that alternative explanations need to be sought for the rarity of *E. albens* on the Central Tablelands. Though it is possible that it may have been more common before European settlement in the mid 1800s and since selectively removed, Cambage (1902), who travelled widely in this area, did not record it at any site where it is currently absent.

Differences between delayed and early light treatments in the pot trial

Pots in the Delayed Light treatment were exposed, at least at the colder Orange site, to a longer period of frosting, which may have enhanced the formation of ice crystals in the soil. Hence, seedlings in this treatment had increased likelihood to damage by frost heave but a lower likelihood of cold-induced photoinhibition. As any one or more of these factors may have affected the results, they cannot be considered separately.

Despite deaths being more common at Orange in the Early Light treatment during early winter (Fig. 2), differences in survival rates between the two treatments were not evident by spring. Significant differences in growth indices were evident at Cowra and across sites for *E. albens* such that seedlings in the Delayed Light treatment were taller and/or had more leaves than those exposed to Early Light. However by January, following a period of enhanced growing conditions, these effects were far less pronounced (Table 4).

The pot trial results, together with natural occurrences on high altitude sites with easterly aspects, suggested that early morning sunlight's supposed adverse effect on frosted seedlings (photoinhibition) was not a useful hypothesis for explaining the presence/absence of *E. albens* on the slopes and tablelands.

CONCLUSIONS

It was hypothesised that the local distributions of *E. albens* and *E. melliodora* on the Central Tablelands (where *E. melliodora* is relatively common and *E. albens* is rare) and adjacent Central Western Slopes (where *E. albens* tends to occur on upper slopes and *E. melliodora* on lower slopes) could be explained by different responses to frost. Pot trials at high and low altitude sites during the 1997 winter suggested that seedlings of both species were relatively frost tolerant. Though seedlings exposed to delayed morning sunlight were taller and/or had more leaves than those exposed to early morning sunlight, the differences were marginal and relatively short-lived when conditions for growth improved. Neither light treatment significantly affected seedling survival. Difference in frost tolerance between the two species was therefore an unlikely explanation for their distribution pattern on the slopes and tablelands.

Observations of the occurrence of *E. albens* at high altitude in the field also supported its apparent tolerance to low temperatures (at least up to 925 m a.s.l.) regardless of aspect. Differences in geology, slope, drainage and/or soils are probably more important factors than exposure to frost in explaining the localised occurrence of *E. albens* on the Central Tablelands and adjacent slopes.

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Collections of *Galerina* (Agaricales, Fungi) Made by J.B.Cleland and Housed in the State Herbarium of South Australia

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Twenty-five collections by J.B. Cleland of *Galerina* (or which have been regarded as possibly belonging to *Galerina)* have been studied and their true status has been determined. Details are provided of the size and state of the collections and results are given of microscopic analysis of the material. The results have been evaluated in the light of recent taxonomic studies and suggestions are provided about the taxonomic position of each of the collections, together with discussions of the reasons for the conclusions. Ten of the collections have been shown to belong to genera other than *Galerina*. All the remaining collections have been assigned to previously described species of *Galerina* - *G. lurida, G. marginata, G. muscolignosa, G. unicolor, G. vittiformis.*

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KEYWORDS: Agaricales, Australia, Cleland, *Galerina*, herbarium, mushrooms.

INTRODUCTION

J.B.Cleland (1878-1971) was one of the great collectors of Australian larger fungi over a long period, first in New South Wales and later and particularly in South Australia. His work on fungi was largely summarised in his 'Mushrooms and Toadstools and other Larger Fungi of South Australia' (1934-1935), though he continued collecting until very late in his life. The basic material of his book has been revised by Grgurinovic and published as 'Larger Fungi of South Australia' (1997). The collections of *Galerina* were re-examined as part of the work for a forthcoming volume by Australian Biological Resources Study on some genera of the Family Cortinariaceae in Australia (in press 2005). A summary of these results is published there, but this paper in addition provides a full documentation of the status of each of the collections, notes on the size and state of each collection together with details of the original Cleland collecting notes. Some of these collections were in part discussed by Cleland in his first paper, Australian Fungi: Notes and Descriptions. No. 1 (Cleland and Cheel 1918). Cleland's understanding of concepts of European species was guided particularly by the work of Rea (1922). The earlier work of Massee (1892-1895) was important for Rea and the illustrations of Cooke (1881-1891) were also a major influence. The use of European names should be interpreted in this light, with due consideration for later European use of these same names, particularly by Watling and Gregory (1993).

MATERIALS AND METHODS

Material was examined in 5% KOH and stained with Congo Red. Spores were examined and drawn at x2000. Cystidia were drawn at x1000. Spore shapes were named following the nomenclature of Bas (1969). Spore details are reported as a range of spore sizes, mean length and width ($\bar{X}$) and mean ratio of length:breadth (Q). Ornamentation of the spores was recorded in terms of height (high, medium or low), width (coarse, fine) and shape of the tip of the ornamentation (blunt, pointed).

Cystidia shapes were described following the categories of Vellinga (1988). In many cases cystidia could not be recovered. Measurements of the cystidia, when the form is lageniform, are recorded as length, width of the basal portion, width of the neck and width of the apex if it is inflated. In most cases, the collections were originally described as being species of *Galera*. As it was later determined that this was not a valid generic name, the name *Galerina* became the universally accepted generic name for these species (see Donk 1962).

The species are arranged alphabetically according to the species names on the packets. The collections were first located in the Waite Agricultural Research Institute (ADW) and later the whole of the Cleland material was transferred to the State Herbarium of South Australia (AD). For completeness, both the earlier and the current numbers are cited. However the AD numbers are the current valid numbers.

COLLECTIONS EXAMINED

1. *Galerina (Galera) campanulata* AD-C 42538 (ADW 13793)

Microscopic details: Spores 15.0–18.0 x 9.6–10.5 µm, $\overline{X}$ = 16.3 x 10.3 µm, Q = 1.59, strongly ferruginous, oval to elliptic, wall thick, smooth, with no visible perispore, with broad very evident apical germ-pore. Cystidia sparse, scattered, fusiform to lageniform, never capitate. Basidia clavate to pyriform, two-spored. Pileal surface mostly collapsed, but seems clearly to be a distinct thin layer of thin-walled globose cells.

Packet label:
Galerina (Galera) campanulata
Milson Is. 10/11/14 J.B.Cleland
+Pencil annotation
(= Galerina)
on rich soil Milson Is (Sydney) NSW

Cleland Notes: (sparse)
Gills narrow, ascending, adnate. Cap pallid brown. Stem hollow, almost white (brownish tint).
On rich soil.
Milson Island
10/11/14
Galera
Spores 13.6–15.5 x 8.5 µm.

Collection: The collection consists of six fruit-bodies, each about 1 cm in diameter, cap convex to conical, with a long thin stipe.

Notes: This species was named by Cleland as *Galera campanulata* Massee, a species which in the British Fungus Flora (Dennis, Orton and Hora, 1963) is regarded as a doubtful species, and is not recorded by Watling and Gregory (1993) or Moser (1983). Cleland, in the discussion of this species in the 1918 paper, compares it to *Galera silignea* and also discusses differences between this species and *Galera tener*. Since these are now regarded as *Conocybe* species, this suggests that Cleland regarded this collection as belonging to what can now be regarded as *Conocybe*. The description of this species by Rea (1922) probably represents current interpretation of this species at the time: pileus deep cinnamon, persistently campanulate; stipe pallid, base darker; gills tawny cinnamon; spores 12 x 7 µm; smell strong; by roadsides.

The microscopic features detailed above, smooth spores with germ-pore and cellular cuticle, seem to clearly indicate a species of *Conocybe*. The cystidia of the related species, *C. tener*, are lecythiform with a distinct globular apex. Hence if the rarely found cystidia are representative of the collection, it is not close to *Conocybe tener*, but belongs in a quite different section of the genus.

If the few cystidia found above are regularly present, this collection could still be a *Conocybe* but of a different section. At this stage the identity of the collection remains in doubt, but the genus is clear, the smooth spores with apical germ-pore could not be *Galerina,* particularly with a cellular cuticle. The other less likely possibility would be a species of the genus *Pholiotina* section Piliferae, but this genus is less often found in Australia than *Conocybe.*

2. *Galerina (Galera) campanulata* AD-C 42539 (ADW 13794)
Microscopic details: Spores 10.2–11.1 x 7.2–8.4 µm, $\bar{X}$ = 10.6 x 8.0 µm, Q = 1.34, pallid dull ferruginous, blunt ovoid, apex depressed with fairly indistinct germ-pore, smooth, with no visible perispore, wall visibly thickened. No cystidia could be recovered. Basidia clavate to pyriform, clearly four-spored.

Packet label:
Galera campanulata
Neutral Bay 18/12/14 J.B.Cleland
+ Pencil annotation
Galerina
on wet ground in lawn (Sydney) NSW

Cleland Notes: Collection envelope has note on outside –
Cap conico-campanulate, yellowish brown, darker towards summit, edge slightly striate. Gills pale fawn. Stem white, hollow, brittle, shining.
On wet ground in lawn. Neutral Bay. 18/12/14.
Spores yellow brown, oval, with several small vacuoles, 13–13.8 x 7.7–8.5 µm.
A single paper slip inside the envelope has the same details with the following variation
Cap about 1/2" diameter. Conico-campanulate. Slightly sticky. Tawny brown, darker towards summit. Slightly striate.
Gills pale cream.
Among grass
Neutral bay
19/2/14

Collection: The collection consists of a single fruit-body.

Notes: This collection seems clearly related to the previous collection, though the spores seem different. Possibly they represent two-spored and four-spored variants of the same species. The absence of cystidia makes more certain results almost impossible. See under the previous collection (AD-C 42538) for more discussion of the other possibilities.

3. *Galerina (Galera) lateritia* AD-C 42540 (ADW 13788)
Microscopic details: Spores 10.8–12.9 x 7.5–8.4 µm, $\bar{X}$ = 12.2 x 8.1 µm, Q = 1.51, clear ferruginous, ovoid, wall smooth, apex a little thin, with an indistinct germ-pore, with no visible perispore. Basidia clavate to pyriform. No cystidia could be located. Pileal surface collapsed and difficult to reconstruct, but seems to be a thin complete layer of globose thin-walled cells.

Packet label:
Galera lateritia Adelaide 22/9/13 J.B.Cleland
+ Pencil annotation
Galerina
Amongst grass S. Aust.

Cleland Notes:
Pileus conical 3/4 x 3/4", very pale fawnish white, ? slightly striate. Stem white 2", slightly bulbous, attenuated up, finely striate, no ring, hollow. Gills fairly close, narrow, pale fawn, just adnexed, hymen… free.
Among moss. Adelaide. 22/9/13.

Collection: The collection consisted of three good substantial fruit-bodies, each about 1cm in diameter.

Notes: This, and the next two collections probably should be regarded as the same species as the characters are very similar but this would require cystidia to decide the issue. Clearly they are not *Galerina* as they have a cellular cuticle and smooth spores. Clearly on the characters available, this is a species of *Conocybe*, or possibly a *Pholiotina* Section Piliferae, but cystidia and other features would be needed to decide the issue. *Conocybe* seems to be the most likely genus.

Galerina lateritia is now regarded as being the same as *Conocybe lactea*, which is a very pale species.

4. *Galerina (Galera) lateritia* AD-C 42541 (ADW 13789)
Microscopic details: Spores 13.5–14.1 x 7.5–8.7 µm, $\overline{X}$ = 13.6 x 8.2 µm, Q = 1.70, deep brown to chocolate in mass, ovoid, thick-walled, smooth, with clear narrow apical germ-pore. Basidia pyriform, mostly partly collapsed. No cystidia could be recovered, even though the material appeared to be in good condition.

Packet label:
Galera lateritia
Sydney 20/3/14 J.B.Cleland
+ Pencil annotation
Galerina
Amongst grass, Sydney, NSW (+ formalin specimen)

Cleland Notes:
Pale brownish fawn, apex particularly conical, about 3/8 x 3/8", apex acute to obtuse. Gills reddish brown, narrow, crowded, just free. Stem whitish, silky. Hollow, attenuated up, thin, 1 3/4".
Amongst grass; Sydney 20/3/14
Galera ? *lateritia*. Formalin specimen.
Other collection like this has spores brown, 12.5 x 7–7.6 µm.

Collection: The collection is of 6-7 fruit-bodies which are in good condition; the dried fruit-bodies are up to 1 cm in diameter.

Notes: This is clearly not a *Galerina*. This collection and the next one clearly have a cellular cuticle and either belong to the genus *Conocybe* or to *Pholiotina* Section Piliferae. These three collections may represent variants of the same species or they may represent two close but different species. They clearly do not represent *Conocybe lateritia* as it is now understood, as this is a very pale species. At the moment it seems best to regard all three collections as belonging to the same species.

5. *Galerina (Galera) lateritia* AD-C 42542 (ADW13790)
Microscopic details: Spores 12.0–15.0 x 8.4–9.6 µm, $\overline{X}$ = 12.8 x 8.7 µm, Q = 1.47, deep ferruginous, oval, thick-walled, smooth, with no visible perispore, with distinct apical germ-pore; basidia large, pyriform, often collapsing. No cystidia of any kind could be recovered.

Packet label:
Galera lateritia
Milson Is. 29/11/14 J.B.Cleland
+ Pencil annotation
Galerina
Amongst grass Milson Island, NSW
Kew No 6 see also Formalin Specimen No 27

Cleland Notes:
Conical then expanded to become broadly conical with pointed umbo, umbo dark tan, rest pale tan, densely striate. Gills narrow, very crowded, adnate, yellowish brown. Stem 1 3/4" white, finely streaked, attenuated upwards, hollow, base slightly bulbous.
Amongst grass Milson Island 29/11/14
Spores yellow brown, oval slightly oblique, 12 x 8 µm.

Collection: The collection has two fruit-bodies, together with three fruit-bodies glued to the back of the collecting slip, each about 1 cm diameter.

Notes: This is clearly not a *Galerina* species, because of the smooth spores with germ- pore. Obviously it is close to the previous collections. In the absence of any cystidia, it should be regarded as another collection of the previous species, i.e. a *Conocybe* or *Pholiotina* Section Piliferae species. The former should be regarded as the more probable in terms of the known frequency of the two genera in Eastern Australia.

6. *Galerina mycenoides* AD-C 42543 (ADW 13715)
Microscopic details: Spores 7.5–8.1 x 4.5–5.1 µm, $\bar{X}$ = 7.9 x 4.9 µm, Q = 1.62, pale golden, broadly ovoid, thin-walled, smooth, without apical germ-pore, with no visible perispore. Basidia narrowly clavate, four-spored. Cheilocystidia abundant 60–80 x 3–8 µm, cylindrical to fusiform or narrowly lageniform, apex often slightly enlarged 4–7 µm; no pleurocystidia could be recovered.

Packet label:
Pholiota mycenoides
Orange NSW 10/10/16 J.B.Cleland
+Pencil annotation
Galerina mycenoides
on ground

Cleland Notes:
Pholiota. Cap convex then expanded, centre dimpled when moist, somewhat chestnut and striate, drying to pallid tawny white. Gills adnate, cinnamony brownish, moderately close. Stem 1", often wavy, brownish tan, white down often near base, base a trifle swollen, slightly hollow. Ring as superior whitish fibres, often obscure, sometimes very definite.
On ground. Orange 10/10/16.
Spores 7–8.5 x 4.2–4.5 µm.

Collection: The collection is of numerous fruit bodies singly in granules of clay soil, all dirty and granular.

Notes: This is not a species of *Galerina* as the spores were thin-walled and smooth, without a germ-pore. Nor was this a species of *Pholiota* Section Aporini, as the spores are thin-walled and too pale. The collection probably represents a species of *Tubaria* even though the spores were not easily collapsing, nor were they reniform. It probably comes closest to *Tubaria rufofulva* which also has similar cheilocystidia, though the cap colours seem somewhat different. See Grgurinovic (1997) and Moser (1983) for other related species. *Galerina mycenoides* has larger, finely rough spores, and other different features. See also Rea (1922), who places *Galerina mycenoides* in *Pholiota*, and reports it as growing among moss.

7. *Galera hypnorum* AD-C5506 (ADW 13787)
Microscopic details (from packet a): Spores 12.3–13.2 x 6.6–7.9 µm, $\bar{X}$ = 12.6 x 6.9 µm, Q = 1.80, well coloured, elliptic to amygdaliform, plage usually obvious, flat, smooth and usually with a distinct rim, perispore thin, mostly obvious, not swelling or loosening, ornamentation moderately low to low, coarse, blunt. Cheilocystidia fairly sparse, broadly lageniform; pleurocystidia absent.

Packet label:
Galera hypnorum
Greenhill Rd., 27/6/21 J.B.Cleland
+ Pencil annotation
Holotype *Galerina nyula*
Amongst moss Adelaide

Cleland Notes:
Galera hypnorum
Up to 1/4", campanulate, umbonate, striate, watery cinnamon, paler when dry. Gills tawny cinnamon,

tending to be distant, adnate. Stem up to 1", brownish cinnamon, slender. Amongst moss.
Greenhill Road 27/6/21
Spores oblique, 11 to over 12.8 x 7.5, yellow brown.

Collection: There are two sub-packets –

a. with fragments of 2-3 fruit-bodies, with the label "winged spores".
b. with fragments of 4-5 fruit-bodies, with the label "ellipsoid spores".

There are no separate collecting notes for these individual fruit-bodies.

Packet b. is clearly the collection referred to in Grgurinovic as the other collection. From it the following details were found:

Microscopic details: Spores 11.7–12.6 x 6.0–8.7 µm, $\overline{X}$ = 12.03 x 8.28 µm, Q = 1.45, well coloured, ovoid to slightly elliptic, plage not obvious, a vague flat area above the apiculus, perispore not visible, ornamentation low to moderately low, fairly coarse, blunt. Cystidia could not be recovered.

Notes: Sub packet a. Material clearly corresponds to the description of *Galerina nyula* in all the details published by Grgurinovic (Grgurinovic 1997), and doubtless corresponds to some of the records of *Galerina hypnorum* in Australia. However it is quite distinct from *Galerina muscolignosa* (see Wood 2001), which has distinctly calyptrate spores and which seems to be the common species in much of Eastern Australia. Also *Galerina oreophila* may also be confused with *Galerina nyula*, but *Galerina oreophila* has more distinctly lageniform cystidia, slightly broader spores, a mixture of two-spored and four-spored basidia and an alpine or sub-alpine habitat.

Sub packet b. Material has microscopic features that suggest it may be a collection of a species of *Cortinarius* because of the lack of cystidia and the spores without a plage and without visible perispore. It probably represents a species of the subgenus Telamonia, but further identification will await more work on that sub-genus, and it would be made more difficult by the lack of any macroscopic field details.

8. *Galerina nyula* AD-C5507 _ (ADW 13785)

Microscopic details: Spores 7.8–9.3 x 4.8–5.4 µm, $\overline{X}$ = 8.9 x 5.2 µm, Q = 1.72, fairly well coloured, elliptic to vaguely amygdaliform, plage flat, without rim, not obvious, appears smooth, perispore thin, often not obvious, often somewhat loosening but not fully calyptrate, ornamentation low to very low, somewhat coarse, blunt. The material was too fragmentary for cystidia to be recovered.

Packet label:
Galera hypnorum
Lisarow 5/8/16 J.B.Cleland
+ Pencil annotation
Galerina nyula
Lisarow NSW

Cleland Notes: No field notes were present.

Collection: The collection consists of fragmentary parts of about three fruit-bodies, among moss, with conical mycenoid caps, small and conical to convex with long thin stems. Clearly among moss.

Notes: The distinctive characteristics of the spores indicate that this collection does not represent *Galerina nyula*. Rather it should be regarded as belonging to *Galerina muscolignosa* despite a smaller degree of loosening of the perispore on the spores, because of the spore size and the level of ornamentation on the spores.

9. *Galera hypnorum* AD-C 5508 _ (ADW 137867)

Microscopic details: Spores 7.5–9.6 x 5.4–6.3 µm, $\overline{X}$ = 9.0 x 5.3 µm, Q = 1.69, well coloured, elliptic to slightly amygdaliform, plage slightly flatter, with no distinct rim or smooth patch, perispore thin, often a little loosening or slightly calyptrate, ornamentation low, a little coarse, blunt. No cystidia could be recovered from the limited material.

Packet label:
Galera hypnorum
Mosman 23/7/16 J.B.Cleland
+ Pencil annotation
Galerina nyula
amongst moss Mosman (Sydney) NSW
Miss Clarke (Watercolour) No 133 Formalin specimen 229

Cleland Notes:
Galera. Cap conico-campanulate 1/4", base 5/16" high, ?without definite umbo, dark yellow brown, striate, drying pallid tan. Gills moderately distant, ascending, adnate, yellow brown, not ventricose . Stem up to 1", slender, yellow brown.
Amongst moss. Mosman

Collection: The collection consisted only of fragmentary material.

Notes: Comparisons with Collection AD-C 5507 above seem to indicate that it is the same species, and the same remarks apply. This collection also represents *Galerina muscolignosa.*

10. *Galera hypnorum* AD-C 5509 (ADW 13783)
Microscopic details: Spores 8.4–9.6 x 5.4–6.3 μm, $\bar{X}$ = 9.0 x 5.6 μm, Q = 1.60, well coloured, elliptic, slightly amygdaliform in profile, plage smooth, flat, with a slight rim, ornamentation very low, moderate, rounded, perispore clearly present, thin, regularly loosening, sometimes variously in bubbles. No cystidia could be recovered from the limited material.

Packet label:
Galera hypnorum
J.B.Cleland, no locality; no date
+ Pencil annotation
Galerina nyula

Cleland notes:
Only torn fragments in packet; only a few scraps can be partially reconstructed - *Galera* (new sp. ?)
...apex of stipe mealy...
...moss...

Collection: The collection was very fragmentary, with no intact fruit-bodies remaining; one partial cap remained and produced the spores described above; the material was too fragmentary for cystidia to be recovered.

Notes: Comparison with Collections AD-C 5507 and AD-C 5508 above seems to indicate that they represent the same species. Clearly they do not represent *Galerina nyula* for the reasons given above. It fits best within *Galerina muscolignosa.*

11. *Galera hypnorum* AD-C 5510 (ADW 13784)
Microscopic details: Spores 10.5–12.6 x 6.3–7.5 μm, $\bar{X}$ = 11.7 x 7.1 μm, Q = 1.66, well coloured, ovoid, some slightly pointed at apiculus, only rarely slightly amygdaliform in profile, plage not visible or distinct, without a rim, no visible perispore, ornamentation low to very low, a little coarse, rounded. Basidia often or mostly, two-spored. No cystidia could be recovered.

Packet label:
Galera hypnorum
J.B.Cleland no locality or date

+Pencil annotation
'Galerina nyula'
vide Miss Clarke Watercolour 133
Formalin spec 229
(Perhaps same coll as AD-C 5508 ? G.Bell 02)

Cleland notes

No macroscopic details, a single slip has, in pencil (JBC) - spores 8–8.5 x 6 µm, oval, peculiar double outline, ?wing at one end, yellow brown, edge a little turned in when young, so as to be globular (with a sketch of a globular head and two spores, clearly calyptrate).

And around it, in the same hand (JBC), in fine ink
Galera hypnorum Batsch
Vide Miss Clarke Picture 133 Formalin specimen 229
Rec. in Trans. Roy. Soc. SA XLII, 1918 p 119

Collection: The collection consists of about seven fruit bodies in fair condition. The collection was clearly made from soil with moss.

Notes: Cleland's second set of notes (above) presumably may mean that he thought that it was the same species as the illustration he cited. He does not necessarily mean that this was a comment about this collection or that this one was the one that was painted by Miss Clarke.

As the spores figured in Cleland's notes are clearly calyptrate, and the spores of the current specimen are clearly not calyptrate, one suspects that the written slip in the packet does not correspond with the specimen and has been misplaced from elsewhere. This is confirmed by the spore sizes cited by Cleland (8–8.5 x 6 µm) while the present specimens have much larger spores (10.5–12.6 x 6.3–7.4 µm).

From the details available from the specimens, as the spores are mostly produced on two-spored basidia, the spore size and morphology suggest this represents a collection of *Galerina vittiformis* possibly var. *pachyspora*. Final certainty could not be produced from the details that could be gained from the specimens. However, it is clear that the specimens do not represent *Galerina nyula*.

12. *Pholiota pumila* AD-C 42544 (ADW 13720)

Microscopic details: Spores 7.5–9.0 x 4.2–4.8 µm, $\overline{X}$ = 8.2 x 4.8 µm, Q = 1.71, golden, fairly thin-walled, elliptic to slightly amygdaliform, plage usually not marked, flat, smooth, sometimes with a small rim, perispore thin, sometimes a little swollen and occasionally slightly loosening, ornamentation low, fine, a little blunt. A few narrow lageniform non-capitate cystidia were recovered, both cheilocystidia and pleurocystidia present and of similar morphology.

Packet label :
Pholiota pumila
Spit, Sydney 9/7/16 Amongst moss J.B.Cleland
+Pencil annotation
Galerina
formalin specimen No 216

Cleland notes:

Pholiota. Cap 3/16", broadly conical, faintly striate, apex rather pointed, yellow brown, finely granular, with less hygrophanous appearance. Gills adnate, very pallid brown, rather distant, with short ..! Stem 5/8", attenuating up, moderately stout, pallid brown, somewhat silvery mealy, slightly hollow, ring superior ?definite.

Amongst moss. Spit.

Collection: The collection consists of only a few small fruit-bodies, clearly among moss. Dried fruit-bodies small and mycenoid.

Notes: The finely rough spores clearly indicate a species of *Galerina.* If Cleland's notes are accurately interpreted, with a 'ring', then the specimens almost certainly fit *Galerina lurida.* Though the spores seem more finely rough, all the other features fit *Galerina lurida* well. It was not possible to detect remains of a ring on the stipe of the dried specimens, but this would not be unusual with this species, where the texture of the ring is variable and hence it persists in differing degrees in mature specimens. On balance, this collection should be regarded as being of *Galerina lurida.*

13. *Pholiota pumila* AD-C 42545 (ADW 13721)
Microscopic details: Spores 7.8–9.0 x 4.5–5.4 µm, $\overline{X}$ = 8.4 x 5.0 µm, Q = 1.69, Golden ferruginous, elliptic to amygdaliform, plage large, flat, smooth, sometimes with a distinct rim, perispore thin, obvious, sometimes swelling irregularly and a little loosening, but not calyptrate, ornamentation low, fairly fine, blunt. Cheilocystidia fairly frequent, narrowly lageniform, apex distinctly rounded to slightly capitate, 40–50 x 8–12 x 3–5 x 6–9 µm, pleurocystidia similar, fairly frequent.

Packet label:
Pholiota pumila
Amongst moss Mosman 13/8//16 J.B.Cleland
+Pencil annotation
Galerina

Cleland notes:
Pholiota.....moss
Cap 3/8", convex then nearly plane, trace fibres, dark reddish brown, striate.
Gills reddish brown, adnate, moderately close. Stem 1", dark brown, slightly striate, solid
? Film of rather dirty white ring. 13/8/16

Collection: The collection consists of three fruit-bodies, in good condition. The specimens are clearly more substantial than those for collection 42544.

Notes: Details of this collection are similar to those for collection AD-C 42544. Despite the differences in habit, they both should be regarded as specimens of *Galerina lurida.* Clearly, with rough spores, this is not a *Pholiota.* These collections may indicate that *Galerina lurida* is a somewhat variable species.

14. *Galerina subifinosa* AD-C 42546 (ADW 13792)
Microscopic details: Spores 10.5–12.0 x 7.5–8.7 µm, $\overline{X}$ = 11.4 x 8.2 µm, Q = 1.40, ferruginous, sometimes a little pale, ovoid or slightly elliptic to slightly amygdaliform, plage flat, smooth, with a low rim, not very strongly developed, perispore not visible, ornamentation moderate, coarse, blunt, apex not mucronate. Basidia mostly collapsed, clavate, mostly four-spored, with a few two-spored. Cheilocystidia fairly common, narrowly lageniform, apex rounded, not capitate, 50–75 x 7–14 x 2–7 x 5–7 µm. Similar pleurocystidia also present.

Packet label: *Galerina subifinosa*
Mosman 30/7/16 J.B.Cleland among moss
+Pencil annotation
? *G. rubiginosa*
? misreading of Cleland handwriting (G.Bell 02)

Cleland notes:
Spores 10.5–11 x 7.5 µm, oblique, oval, finely rough, yellow brown.
Cap 3/8", base to high, conico-campanulate, obtuse umbonate, dark chestnut, coarsely ribbed to umbo.
Gills dark reddish brown, adnate, broad, moderately distant.
Stem to 1 1/4", slender, dark brown, slightly, hollow.
Among moss. Mosman 30/7/16

Collection: The collection consists of a single fruit-body only.

Notes: This collection seems clearly to belong to Section Galerina of *Galerina* because of the presence of clear pleurocystidia. In this group it seems to be part of the *Galerina vittiformis* complex. It does not correspond with *Galerina vittiformis* var. *pachyspora* because of the four-spored basidia, darker cap colours and slightly different spore shape. The name *Galerina subifinosa* appears to be an unpublished manuscript name and hence has no status. It seems probable that it represents a misreading of Cleland's label, which was originally intended to be *Galerina rubiginosa*. This is given added support by the fact that apart from these two collections, no *Galerina rubiginosa* collections are found in the Cleland collections, when that species was recorded in the 1918 paper. *Galerina rubiginosa,* as it is now understood, is one of the species within the *Galerina vittiformis* complex, and it has been split between several species. The Cleland collections, with darker cap colours, slightly smaller spores and four-spored basidia do not clearly fit any of the current species or varieties. The nearest would be *Galerina vittiformis*, possibly as a new form or variety. It may represent *Galerina vittiformis* var. *vittiformis* f. *tetraspora* (see Singer and Smith 1964, and Breitenbach and Kränzlin 2000). This collection seems to correspond to the one quoted by Cleland in the 1918 paper, with the note "Miss Clarke Watercolour No. 132".

15. *Galerina subifinosa* AD-C 42547 (ADW 13791)

Microscopic details: Spores 10.5–12.6 x 6.6–7.8 µm, $\overline{X}$ = 11.6 x 7.4 µm, Q = 1.58, ferruginous, sometimes a little pale, ovoid or a little elliptic to slightly amygdaliform in profile, with distinct flat smooth plage, with slight rim, with no visible perispore, ornamentation moderate to low, coarse, blunt. Basidia clavate, much collapsed and reviving poorly, four-spored, with only a few two-spored. Cheilocystidia mostly collapsed, narrow lageniform, longish, not capitate. Similar pleurocystidia also clearly present.

Packet label:
Galerina subifinosa
Mosman NSW amongst moss 30/7/16 J.B.Cleland
+Pencil annotation
(*Galerina rubiginosa*)
(probably a misreading of J .B. Cleland handwriting G. Bell 02)

Cleland notes:
Pileus campanulate, 3/16" high, 3/8" broad, almost chestnut, striate, striae darker, not definitely viscid. Gills adnate, reddish brown, moderately distant.
Stem slender 1", reddish brown, slightly mealy, trace of being hollow.
Amongst moss Mosman 30/7/16

Collection: The collection consists of three fruit-bodies, in fairly good condition, fairly small, with some sandy soil and moss.

Notes: This collection is clearly a *Galerina* species, and probably represents another collection of the species found above in collection AD-C 42546. Its identity is discussed fully there.

16. *Galerina (Pholiota) subpumila* AD-C 11883 (ADW 12930)

Microscopic details: Spores 9.3–10.2 x 6.0–6.6 µm, $\overline{X}$ = 9.5 x 6.4 µm, Q = 1.49, well coloured, golden, wall slightly thick, quite smooth, apical germ-pore small or narrow, but clearly distinctly present. Cheilocystidia narrowly lageniform, not capitate, 30–40 x 4–8 x 10–13 µm, a few similar pleurocystidia also present.

Packet label:
Pholiota subpumila
Greenhill Rd., 12/6/26 J.B.Cleland
+Pencil annotation
Holotype
(Greenhill Rd. runs between SE corner of Adelaide and summit of Mt. Lofty)
Cleland notes:

Pileus up to 5/8” to 1 1/8”, convex then flattened or a little depressed, umbonate when young, sometimes a little wavy, shining waxy looking, dark tan.
Gills rather close, adnate or slightly decurrent, watery brown, rather triangular.
Stem equal or slightly attenuated upwards, 1 1/2”, whitish, fibrillose with a slight tinge ? of cap colour.
Spores yellow brown 8–9.5 x 5.5 µm, oblique.

Collection: The collection consists of five fruit-bodies, in good condition, with moss.

Notes: With smooth spores, which also have a distinct germ-pore, the collection clearly represents a *Pholiota*, not a *Galerina*. It has been well re-described by Grgurinovic (1997) as *Pholiota subpumila* and the current study has confirmed the details given there.

17. *Galerina (Pholiota) subpumila* AD-C 12393 (ADW12931)
Microscopic details: Spores 8.7–9.9 x 6.0–7.2 µm, $\overline{X}$ = 9.09 x 6.45 µm, Q = 1.41, golden, wall distinctly thickened, completely smooth, with narrow apical germ-pore, usually narrow but always distinctly present. Cheilocystidia narrow lageniform to lageniform, clearly present and fairly frequent, less frequent similar pleurocystidia also present.

Packet label:
Pholiota subpumila
Greenhill Rd., 11/6/27 J.B.Cleland
+Pencil annotation
On moss
(Runs between SE corner of Adelaide and summit of Mt. Lofty)

Cleland Notes:
No notes of macroscopic details.
Spores yellow brown, 9 x 6.5–7 µm
On moss

Collection: The collection consists of five fruit-bodies in good condition, with some soil and debris.

Notes: This collection clearly matches all the features of *Pholiota subpumila* - see discussion under the previous collection and Grgurinovic (1997).

18. *Galerina (Pholiota) subpumila*` AD-C 12104 (ADW 12929)
Microscopic details: Spores 7.8–10.5 x 5.7–6.6 µm, $\overline{X}$ = 8.9 x 6.2 µm, Q = 1.44, well coloured, golden, ovoid, wall moderately thickened, smooth, with small distinct apical germ-pore, constantly and clearly present. Cheilocystidia fairly frequent, fusiform to narrowly lageniform, pleurocystidia less common, but clearly present, of similar morphology.

Packet label:
Pholiota subpumila
Waterfall Gully, SA 27/6/21 J.B.Cleland
+Pencil annotation:
amongst moss
Miss Fiveash watercolour 24
(34° 58’ S; 136° 41’ E)

Cleland notes:
Cap 5/8” convex, umbonate (obtuse), pallid yellow brown, edge rather mealy. Gills dingy greyish brown, decurrent (slightly), moderately close, watery cinnamon. Stem up to 1 1/2” pallid whitish, with a superior well-marked whitish ring, solid. Flesh watery. Amongst moss. Waterfall Gully 27/6/21

Base of stem ?occasionally swollen.
Spores rather a dull dark brown, thin-walled, ellipsoid but a little irregular, thick-walled 8 x 6.4 µm.

Collection: The collection consists of numerous fruit-bodies, in good condition, with soil and debris.

Notes: Clearly this collection is *Pholiota subpumila,* as are the previous collections. For a discussion of this species, see there and Grgurinovic (1997).

19. *Galerina (Pholiota) subpumila* AD-C 22424 (ADW 12928)
Microscopic details: Spores 8.4–9.6 x 5.1–6.0 µm, $\overline{X}$ = 9.1 x 5.6 µm, Q = 1.62, strongly and deeply coloured, elliptic, profile distinctly amygdaliform, without apical callus and apex not less ornamented, plage large flat, smooth, obvious, with small rim, ornamentation high, coarse, blunt, perispore obvious, thick, swelling, but only occasionally slightly loosening, never calyptrate. Cheilocystidia and pleurocystidia both clearly present, similar, narrowly lageniform, apex slightly capitate but never abruptly so, 45–50 x 3–7 x 10–13 µm.

Packet label:
Pholiota subpumila
Eagle on the Hill 6/6/32 J.B.Cleland
+Pencil annotation
(34° 59” S ; 138° 40” E) near moss
Galerina

Cleland notes:
Pileus ochraceous tawny XV ½” slightly convex, slightly umbilicate, substriate. Gills ochraceous tawny, adnate to decurrent, rather distant. Stem 3/4”, same colours, slender, slightly fibrillose. Ring indefinite, rather distant, stem cartilaginous. Flesh same colour. Near moss.
Spores golden brown, 8 x 4.5 µm, obliquely elliptic, perhaps slightly rough.

Collection: This collection consists of three small fruit-bodies on a twig of wood, with some soil and debris. No velar remains are now visible on the stipe. Clearly the original fruit bodies were quite small.

Notes: Because of the rough spores, with plage, without germ-pore, this collection is clearly not of *Pholiota subpumila*, but clearly represents a species of *Galerina.* The species that it might represent are *G. marginata* or *G. lurida.* It is probably best regarded as a small specimen of *Galerina marginata*, since *Galerina lurida* is clearly not lignicolous and it has spores and cystidia that are slightly different from the present collection.

20. *Galerina (Pholiota) subpumila* AD-C 22425 (ADW 12932)
Microscopic details: Spores 8.4–9.3 x 5.1–6.0 µm, $\overline{X}$ = 8.9 x 5.6 µm, Q = 1.59, well coloured, ovoid to elliptic, amygdaliform in profile, plage obvious, smooth, mostly with a distinct rim, ornamentation obvious, moderately low, coarse, blunt, perispore marked, swollen, with some slight loosening but never calyptrate. Cheilocystidia and pleurocystidia clearly present, but not abundant, of similar morphology. Narrowly lageniform, apex rounded or sometimes vaguely capitate, 40–50 x 12–16 x 4–7 x 4–9 µm.

Packet label:
Pholiota subpumila
Coromandel Valley 26/6/27 J.B.Cleland
+Pencil annotations
Galerina
amongst moss
Clarendon, Coromandel Valley, SA.

Cleland notes:
Pholiota. Moss. Cap near Sudan Brown III. Stem paler cap, drying to Tawny Olive XXIX. Stem up to 3”, equal, or attenuating up, ring, pallid, subsuperior, not striate. Not hygrophanous. Spores 7.5 x 5.2 µm,

oblique, rather ovate, dark yellow brown.

Collection: This collection consists of three fruit-bodies, each fairly substantial, clearly from among soil and moss and clearly not on wood. One of the dried fruit-bodies shows traces of a fine fibrillose ring.

Notes: Because of the rough spores with a plage and without a germ-pore, this collection is clearly a species of *Galerina* and not of *Pholiota*. Hence the identification as *Pholiota subpumila* is incorrect. The substantial fleshy habit and habitat on soil, not on wood, clearly point to a good collection of *Galerina unicolor* if that species is recognised as being separate from *Galerina marginata* (for discussion of this point, see Wood 2001).

21. ***Galerina unicolor*** AD-C 42548 (ADW 13728)

Microscopic details: Spores 9.3–10.5 x 5.7–6.3 µm, $\overline{X}$ = 10.0 x 6.0 µm, Q = 1.68, elliptic to amygdaliform, plage smooth, often marked with abrupt margin, ornamentation moderately low, coarse, blunt, perispore obvious, thin, not swelling or loosening at all. Cheilocystidia and pleurocystidia not in good condition, sparse but clearly present, similar, narrowly lageniform, clearly not bifurcate.

Packet label:
Pholiota unicolor
Lawn 6/16 J.B.Cleland
+ Pencil annotation:
Galera
(probably Sydney NSW)

Cleland notes:
No macroscopic details
Spores yellow from 8.5 x 5.2 µm ?over 10.5 x 5.2 µm, ?oblique .... swollen hyphae

Collection: The collection consists of numerous fruit-bodies, in good condition, clearly fleshy, with moss and debris, and one fruit-body clearly on heavy bark, but substrate connection not clear for any of the other specimens.

Notes: On balance, this collection should be retained as *Galerina unicolor* since there is no certainty that the substrate was wood. But note that if consensus on species limits changes, this would become *Galerina marginata*.

22. ***Pholiota unicolor*** AD-C 42549 (ADW 13729)

Microscopic details: Spores 8.4–9.6 x 5.4–6.3 µm, $\overline{X}$ = 9.0 x 5.9 µm, Q = 1.54, elliptic to amygdaliform, plage distinct, flat, smooth, with distinct rim, ornamentation low to very low, coarse, blunt, perispore mostly obvious, usually thick and somewhat swollen, some slightly loosening, but never calyptrate. Cheilocystidia and pleurocystidia sparse and difficult to find, but both clearly present and similar, narrowly lageniform, always simple, never bifurcate.

Packet label:
Pholiota unicolor
Mt. Wilson 6/6/15 J.B.Cleland
+Pencil annotation
Galerina
Mt. Wilson (NSW)
Kew No 24 Miss Clarke Watercolor No 85

Cleland notes:
Pholiota. Pileus at first deeply reddish tan, drying to pale brown, smooth, convex, umbonate, 1". Gills adnate, reddish brown, moderately close. Ring ?moderately distant, marked. Stem 1 1/2", slightly

attenuated upwards, base a little swollen, covered with whitish mealy fibrils, brownish below, solid.
On a separate piece of paper: Spores 8.5 to 10.4 x 5.2 μm, oblique. Chrysalis-like. Brown.

Collection: A good collection of five fruit-bodies in good condition, all growing on old wood.

Notes: On balance, because of the substrate, this collection should be regarded as *Galerina marginata,* because the spores have a thick perispore and low wall ornamentation. The wood substrate is quite clear and underlines the species identification.

23. ***Pholiota unicolor*** AD-C 42550 __(ADW 13730)
Microscopic details: Spores 8.7–9.9 x 5.1–6.6 μm, $\overline{X}$ = 9.1 x 5.6 μm, Q = 1.63, ovoid to elliptic or amygdaliform, mostly with clear large smooth flat plage, with distinct rim, ornamentation low, a little narrow, blunt, perispore sometimes not obvious, often fairly thick and swollen and some with a slight degree of loosening. Cheilocystidia and pleurocystidia, sparse and difficult to recover, but both similar and clearly present, narrowly lageniform, always simple and never bifurcate.

Packet label:
Pholiota unicolor
Lisarow 5/8/16 J.B.Cleland
+Pencil annotations
Galerina
on trunks (fallen) Lisarow (NSW)

Cleland notes:
(Pileus) 3/4", nearly plane, dingy darkish brown and finely striate, drying to pallid brownish. Gills adnate, dingy cinnamon. Stipe dirty brown, fibrillose, ?streaked.
On trunks (fallen). Lisarow 5/8/16
Spores dull brown, oblique 8.5–9.0 x 4–5 μm.

Collection: The collection consists of eight small fruit-bodies in good condition, clearly attached to wood fragments. There is no visible annulus on the dried material. Habit naucorioid, but much smaller than the previous collections.

Notes: Since Cleland called this collection *Pholiota unicolor* one assumes the presence of some kind of ring and some degree of robust stature. If this is so, there is no reason for this collection not to be regarded as being *Galerina marginata* since it is clearly on wood.

24. ***Pholiota unicolor*** AD-C 42551 _ (ADW 13731)
Microscopic details: Spores 8.1–9.0 x 4.5–5.1 μm, $\overline{X}$ = 8.4 x 4.8 μm, Q = 1.76, elliptic to amygdaliform, plage large, flat, smooth, mostly without a rim, ornamentation low, fairly fine, blunt, perispore thin, not very obvious, sometimes distinctly swollen and occasionally a little loosened. Cheilocystidia and pleurocystidia sparse, difficult to recover, but both clearly present and with similar morphology, narrowly lageniform, apex simple, never bifurcate.

Packet label:
Pholiota unicolor
Lisarow 5/8/16 J.B.Cleland
+Pencil annotations
Galerina
Scattered on fallen trunks Lisarow NSW

Cleland notes:
Pileus 1 1/4 ", convex acutely umbonate, watery yellow brown and edge finely striate, drying pallid brown, smooth. Gills moderately close, adnate with a decurrent tooth, pale cinnamon, becoming dingy

cinnamon. Stipe up to 1 1/2" ?slender, base somewhat swollen, pallid to brownish, fibrillosely streaked. Ring superior, often slight.

Differs from *P. unicolor* in being larger, umbo marked, gills not triangular.

Collection: The collection consists of six fruit-bodies on wood or heavy bark.

Notes: The collections were made clearly from wood and the specimens are clearly somewhat fleshy. Though they appear larger than the previous collection, they probably are still smaller than many current collections. However, it should be regarded as a good collection of *Galerina marginata.*

25. *Psilocybe foenisecii* AD-C 5608 (ADW 13155)
Microscopic details: Spores 10.5–12.3 x 7.2–8.7 µm, $\overline{X}$ = 11.6 x 7.7 µm, Q = 1.51, ovoid, wall distinctly thick, with small distinct germ-pore, distinctly and clearly smooth. Cheilocystidia present, ventricose, pleurocystidia absent.

Packet label:
Psilocybe foenisecii
Ryde NSW 27/5/16 J.B.Cleland
+Pencil annotations:
Galerina sp.
On roadsides

Cleland notes:
No macroscopic description present.
P. foenisecii ?. Spores dull dark brown not definitely purple, 8.5–10.5 , occasionally 12 x 5.2 to 7 µm
(Cap) brown and striate when moist, pallid white when dry.
On roadsides. Ryde 27/5/16

Collection: The collection consists of several small fruit-bodies in fairly good condition, on soil debris with some small plant material.
Note – AMY 1986 'not *P. foenisecii*, spores smooth, probably a *Galerina.*'

Notes: Clearly this collection matches the description of *Psilocybe korra* Grg. (See Grgurinovic 1997) There this collection is cited as the only other collection in addition to the type (AD-C 5609) from Adelaide. Other collections under the same name are correctly named *Panaeolus foenisecii*, which has verrucose spores, a cellular cap cuticle and different cystidia. That species is now usually regarded as *Panaeolina foenisecii.*

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A Recent Expansion of its Queensland Range by *Eupristina verticillata,* Waterston (Hymenoptera, Agaonidae, Agaoninae), the Pollinator of *Ficus microcarpa* l.f. (Moraceae).

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McPherson, J.R. (2005). A recent expansion of its Queensland range by *Eupristina verticillata,* Waterston (Hymenoptera, Agaonidae, Agaoninae), the pollinator of *ficus microcarpa* l.f. (Moraceae). *Proceedings of the Linnean Society of New South Wales* **126**, 197-201.

In 2004, the first *Ficus microcarpa* seedlings were observed self-establishing in Brisbane, Queensland. Prior to this the only *F. microcarpa* in the city were cultivated specimens. This self-establishment is a certain indicator of the presence of *Eupristina verticillata*, the obligate pollinator wasp of *F. microcarpa.* A *Ficus* species must exceed a critical population size (CPS) for its pollinator, a species of agaonid wasp, and other non-pollinator symbionts to colonize a new area and then maintain their new population. This CPS has often been estimated to be approximately 300 mature trees. The CPS for *F. microcarpa* has been exceeded in Brisbane for some time. Brisbane has been colonized by the wasps *Odontofroggatia galili* (a gall species), since at least 1975, and *E. verticillata*, since at least 2004. Previously, the southern extreme of the range of *E. verticillata* was central Queensland, approximately 600 km north of Brisbane. This was probably achieved through a stationary, inland, trough system drawing tropical air to the southeast over a few days. Brisbane's new *E. verticillata* population may not persist, as it must compete for short-styled *F. microcarpa* flowers with a long established *O. galili* population. Further, it must contend with a winter of greater duration and lower mean temperature than its tropical origins may allow.

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KEYWORDS: dispersal, *Eupristina verticillata, Ficus microcarpa, Odontofroggatia galili,* persistence, population, Queensland.

INTRODUCTION

On March 26, 2004, four *Ficus microcarpa* L.f. seedlings were found growing on a monument and road reserve infrastructure at North Quay, Brisbane, Queensland. The largest of these was approximately 100 mm in height and diameter (Figure 1). Prior to this the only *F. microcarpa* occurring in Brisbane were deliberately cultivated specimens. The Settler's Monument, which identifies the nascent colony of Moreton Bay's first graveyard, is located under the canopy of a *F. microcarpa* (Figure 2) that is part of an ongoing phenology study begun in September 1996. The presence of these seedlings indicates the presence in Brisbane of the obligate pollinator of *F. microcarpa*, identified by Wiebes (1994) as being *Eupristina verticillata* Waterston, whose former southern limits were in central Queensland. No *F. microcarpa* seedlings were noted in Brisbane's CBD prior to March 2004, and none were located in a major 1996 *Ficus* hemi-epiphyte audit of 21 Brisbane parks that involved checking 3,580 trees and palms (McPherson 1999). *Ficus microcarpa* syconia investigated by the author at various times prior to March 2004 contained only the non-pollinator wasp *Odontofroggatia galili* Wiebes, although *E. verticillata* would have arrived prior to then but went undetected.

As a genus *Ficus* has two distinct characteristics: the floral receptacle or syconium (the 'fig') containing large numbers of male and/or female flowers; and apart from rare exceptions (Kendelhue and Hockberg 1997) each *Ficus* spp. being exclusively pollinated by its own unique species of agaonid wasp. Further, a 'typical' individual *Ficus* exhibits strict synchrony of syconial initiation and development, but does so asynchronously relative to local conspecifics. While a *Ficus* population may exhibit seasonal highs and lows in syconial production, at any time in a sufficiently large population some individuals bear syconia at various developmental stages. Departures from this 'typical' pattern occur, as syconia in all stages of development within a single tree have been reported for *Ficus aurea* Nutt. (Bronstein and Patel 1992), *Ficus benjamina* L. (Corlett 1984), *Ficus macrophylla* Desf. *ex* Pers. (Gardner and Early 1996), and *F. microcarpa* (Corlett 1984; Bronstein 1989).

The syconia of monoecious *Ficus* spp. such as *F. microcarpa* are functionally protogynous. Female pollinator wasps depart maturing syconia when male flowers are shedding pollen. Entering a young syconium when female flowers are receptive, they gall the flowers with short styles and pollinate those with long styles. Adult pollinator wasps live only two to three days, so rapid location of receptive 'female phase' syconia year round is critical to their persistence in an area (Ware and Compton 1994; Gardner and Early 1996). Various estimates have been made regarding the Critical Population Size (CPS) of *Ficus* spp. that allows pollinator persistence. There is a degree of 'in principle' consensus that approximately 100 *Ficus* individuals are required for establishment of wasps and approximately 300 individuals needed for long-term wasp persistence (McKey 1989; Thompson, *et al.* 1991). Different *Ficus* spp. seem to exhibit longer or shorter mean periods between crops. This would affect CPS, as would asynchronous intra-tree production of syconia. More study is required to ascertain the CPS for different *Ficus* spp. and even of a single *Ficus* species growing in different climates.

Many non-pollinator agaonid wasp species share syconia with pollinators. In the case of *F. microcarpa*, *O. galili* is a common 'cuckoo' species in syconia of *F. microcarpa*. It has been present in Brisbane since at least 1975 (Boucek 1988) and probably considerably longer. The long-term presence of *O. galili* in Brisbane indicates that *F. microcarpa* exceeds minimum CPS for the wasp population's persistence. Survival of most non-pollinator agaonids depends on cohabitation of syconia with pollinators as unpollinated syconia usually abscise (Ramirez and Montero, 1988). However, abscission can be prevented by the presence of galls resulting from a few non-pollinator agaonids such as *Odontofroggatia* Ishii spp. (Boucek, 1988), allowing development of seedless, mature syconia.

It is likely that most agaonid wasps disperse only short distances. However, reports of wasps covering long distances exist. Several Australian agaonid wasp species have become naturalized in New Zealand, presumably after being caught in a major air current (Gardner and Early 1996). Stowing away in aircraft or vehicles also allows long dispersal distances (McKey 1989).

Ficus microcarpa occurs naturally in suitable habitats throughout the tropics of south and east Asia and Australia, with central Queensland as the 'natural' southern limit for *F. microcarpa* in Australia (Chew 1989). Due to its hardiness, beauty and excellent shade it has been widely planted in the tropics and subtropics of the world. It is a common park and street tree in Brisbane, thriving in the moist-subtropical climate. Huge specimens dating from the 19th and early 20th Centuries can be found in Brisbane's CBD and inner suburbs. Innumerable small to medium sized specimens, planted in the late 20th to early 21st Centuries are growing in parks and along roads throughout the city and frost-free areas of southeast Queensland.

Ficus microcarpa is an invasive urban 'weed' in the Americas, Hawaii and elsewhere, beginning its invasion after the introduction of its pollinator (McKey, 1989). Finding a vacant ecological niche, both plant and pollinator rapidly established and spread. Given its reputation as an invader of urban space, and since it is autochthonous to much of coastal Queensland, the question arises as to why it has not reached and survived in Brisbane prior to this recent occurrence.

MATERIALS AND METHODS

Monthly surveillance of 39 mature *Ficus* of various species, including eight *F. microcarpa*, has been undertaken since September 1996 for Brisbane's

Figure 1. A *Ficus microcarpa* seedling at left and a *Ficus benjamina* seedling at right, growing in the base of the Settler's Monument, North Quay, Brisbane, 26/03/04. The *F. microcarpa* has an erect habit with mostly obovate, flat leaves, while *F. benjamina* has a pendulous habit with mostly ovate, curling leaves.

Figure 2. The Settler's Monument, North Quay, Brisbane, located beneath a medium-sized *Ficus microcarpa*, 26/03/04.

CBD. Data on the phenology of these *Ficus* spp. and any other interesting observations have been recorded. These data included notes on any seedlings appearing near mature trees.

On March 27, 2004 'male phase' syconia that had no wasp exit holes were collected from an immense *F. microcarpa* in the Brisbane City Botanic Gardens and incubated in glass jars covered by paper towels and sealed with rubber bands. After two days, wasps that had emerged were killed and *O. galili* identified by using the key of Boucek (1988) and *E. verticillata* using the Wiebes (1994) key. During each subsequent month, syconia exhibiting exit holes were collected from each of the eight study trees, dissected, and investigated for seeds and galls. Seeds and galls were easily differentiated as galls were either hollow or contained pre-emergent wasps.

Using mean monthly temperature data supplied by the Regional Observations Database (Accessed July 16, 2004) of the Brisbane Office of the Bureau of Meteorology, mean monthly minimum temperatures for Brisbane Aerodrome during the months from May to September during the years in the periods 1950-99 and 2000-03 were compared using Students t test.

RESULTS

The four seedling *F. microcarpa* were noted during the phenology audit for March 26, 2004. Subsequent to the initial discovery, two new *F. microcarpa* seedlings germinated on the Settler's Monument or nearby infrastructure. As yet they have not been found establishing in other areas of the CBD.

Syconia that lacked exit holes released both *E. verticillata* and *O. galili* during incubation. If possible, specimens of both species will be lodged with the Queensland Museum should later verification of either taxon be thought necessary. Syconia from which wasps had departed contained a mix of seeds and galls until August 2004, when only galls could be found. Since germination was occurring naturally in the CBD the viability of the seeds was not tested.

Only July returned a significant difference between monthly mean minimum temperatures in the blocks 1950-99 and 2000-03 (Table 1). The July mean of 7.8°C for 2000-03 was less than the 9.5°C mean of for 1950-99.

Table 1. Comparisons of mean monthly minimum temperatures at Brisbane Aerodrome, Eagle Farm, for the years in the periods 1950-99 and 2000-03.

	May	June	July	August	September
Mean minimum temp. 1950-99	13.8°C	11.0°C	9.5°C	10.1°C	12.5°C
Mean minimum temp. 2000-03	12.6°C	10.2°C	7.8°C	9.3°C	12.4°C
Student's t	1.862	1.219	2.249	1.299	0.346
Significance	P = 0.680	P = 0.228	P = 0.029	P = 0.200	P = 0.731

DISCUSSION

At some time between 1999 and 2004, *E. verticillata* reached Brisbane, found and pollinated a number of *F. microcarpa*. Seed from one of these trees has been germinating in cracks in the mortar of the stone-block Settler's Monument and in the surrounding footpath on North Quay. The precise date of the arrival is unknown but, from the size of the seedlings initially found, it would be closer to five years.

As per the dispersal of Australian agaonids to New Zealand (Gardner and Early 1996) it is probable that *E. verticillata* travelled south in a rapidly moving, surface air mass. If this was the case, it is likely that quite a few *F. microcarpa* were pollinated in subtropical coastal Queensland and as far south into New South Wales as the air mass penetrated.

It would require a northwesterly wind blowing steadily at over 12.5 kmh^{-1} to move wasps the approximately 600 km from the Rockhampton area to Brisbane in less than two days. While unusual, this can happen when trough systems sit for a few days over inland Queensland. Tropical air is pulled southeast, resulting in hot northwesterly winds blowing over southeast Queensland and northeast New South Wales. Clouds of fig wasps emerging from natal syconia could be caught up in this air mass.

Will *E. verticillata* persist in Brisbane? Possibly. A likely pattern is occasional population irruptions followed by local extinction. Wasps were still present in good numbers in June 2004 and successfully dispersing between trees, but seed could not be located during August, indicating a population decline. Hypothetically, if *E. verticillata* had dispersed to Brisbane at some time prior to 1999 it may have failed to establish due to strong competition for short-styled flowers from *O. galili*. Gardner and Early (1996) noted a decline in the numbers of pollinator wasps per syconia after the dispersal of non-pollinator agaonids to New Zealand. Also, Brisbane's winter may be too long and its temperatures too low for the survival of *E. verticillata*.

Ultimately, *E. verticillata* has had over a century in which to establish a permanent population in Brisbane but has yet to succeed. Any earlier failure to establish a permanent population can not be attributed to climatic factors, as Brisbane's winters in the early 21st Century were marginally cooler than winters in the second half of the 20th Century. It may be successful if the steadily expanding *F. microcarpa* population has reached a size where a residue *E. verticillata* population could survive competition and winter in suitable refugia, and then expand rapidly as the season warmed. A suitable refugium would have a warmer microclimate and a large number of *F. microcarpa* growing within it. This would ensure short pollinator dispersal flights, less stress during cold, adverse weather and consistently available 'female' phase syconia.

If *E. verticillata* does become established, then *Ficus microcarpa* would begin to establish itself as a hemi-epiphyte and lithophyte throughout Brisbane. While a boon for local frugivores, this would be a disaster for the local authority and other property managers. *Ficus* spp. have tremendous potential to damage trees and infrastructure. At least six *Ficus* spp. are already establishing in Brisbane as hemi-epiphytes or lithophytes (McPherson 1999), causing various amounts of damage and requiring ongoing attention to minimize their impact. None of these species has a literature reputation for invasiveness to compare with *F. microcarpa* (Starr 2003). Already hard-pressed and under-funded vegetation control services would be presented with yet another problem plant to manage should *F. microcarpa*, the acknowledged 'Big Kahuna' of invasive *Ficus* spp., begin establishing in numbers in Brisbane.

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A New Phyllolepid Placoderm Occurrence (Devonian Fish) from the Dulcie Sandstone, Georgina Basin, Central Australia

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Young, G.C. (2005). A new phyllolepid placoderm occurrence (Devonian fish) from the Dulcie Sandstone, Georgina Basin, central Australia. *Proceedings of the Linnean Society of New South Wales* **126**, 203-213.

A new phyllolepid placoderm occurrence from a low level in the Dulcie Sandstone, Georgina Basin, Northern Territory, lies about 200 metres stratigraphically above an older fish assemblage containing *Wuttagoonaspis*. A new species *Austrophyllolepis dulciensis* is characterised by an unusually broad anterior ventrolateral plate. The stratigraphic range of other species in this genus from southeastern Australia and Antarctica suggest a Givetian-Frasnian age. Early members of the order Phyllolepida are endemic to east Gondwana, and other phyllolepids of similar age occur in Turkey and Venezuela. In the Northern Hemisphere (Europe, Russia, Greenland, North America) phyllolepids are restricted to the latest Devonian stage (Famennian). This disjunct space-time distribution for the group supports a Gondwanan origin for the Phyllolepida, and later access to northern landmasses resulting from closure of the ocean between Gondwana and Laurussia at or near the Frasnian-Famennian boundary.

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KEYWORDS: Devonian, Georgina Basin, Phyllolepida, Placoderm fishes.

INTRODUCTION

Devonian fossil fish remains from central Australia were first documented by Hills (1959), who identified the placoderm genera *Bothriolepis* and *Phyllolepis* and concluded a Late Devonian age for the Dulcie Sandstone in the Dulcie Range, N.T. (Georgina Basin; Fig. 1). An older fish assemblage from the basal part of the Dulcie Sandstone at the northwestern end of the Dulcie Syncline was discovered during geological mapping by the Bureau of Mineral Resources in 1961. Further material was collected by the author from these and many new localities during two field trips to the Georgina Basin (1974, 1977). The entire fauna of the lower assemblage, including a new species of the genus *Wuttagoonaspis* Ritchie (1973), has been described by Young and Goujet (2003). Ten new localities in the lower part of the Dulcie Sandstone were documented, of which six (localities GY74/8-13) were collected in 1974 along the southern flank of the Dulcie Range on the southeastern edge of the Barrow Creek 1:250 000 sheet (Fig. 1B). There were no taxa in common with the earlier descriptions of Hills (1959) and Young (1985, 1988), which dealt with younger fish assemblages from the upper part of the Dulcie Sandstone (localities GY1-7 of Young 1988: fig. 4). A diagnostic group in these younger assemblages are the phyllolepid placoderms.

The specimens described in this paper were collected from one of the localities (GY74/8) documented by Young and Goujet (2003). Initially they were put aside as unidentified smooth mudclast impressions in sandstone. However, the shape of bones now clearly demonstrates that the sample represents impressions of bones belonging to a phyllolepid placoderm. Some 19 genera representing 13 taxa of family or higher rank have been documented by Young and Goujet (2003) in the *Wuttagoonaspis* Assemblage, which is known from localities over about one million square kilometres of the Australian continent. However, phyllolepid placoderm remains have never been confirmed in that assemblage. This

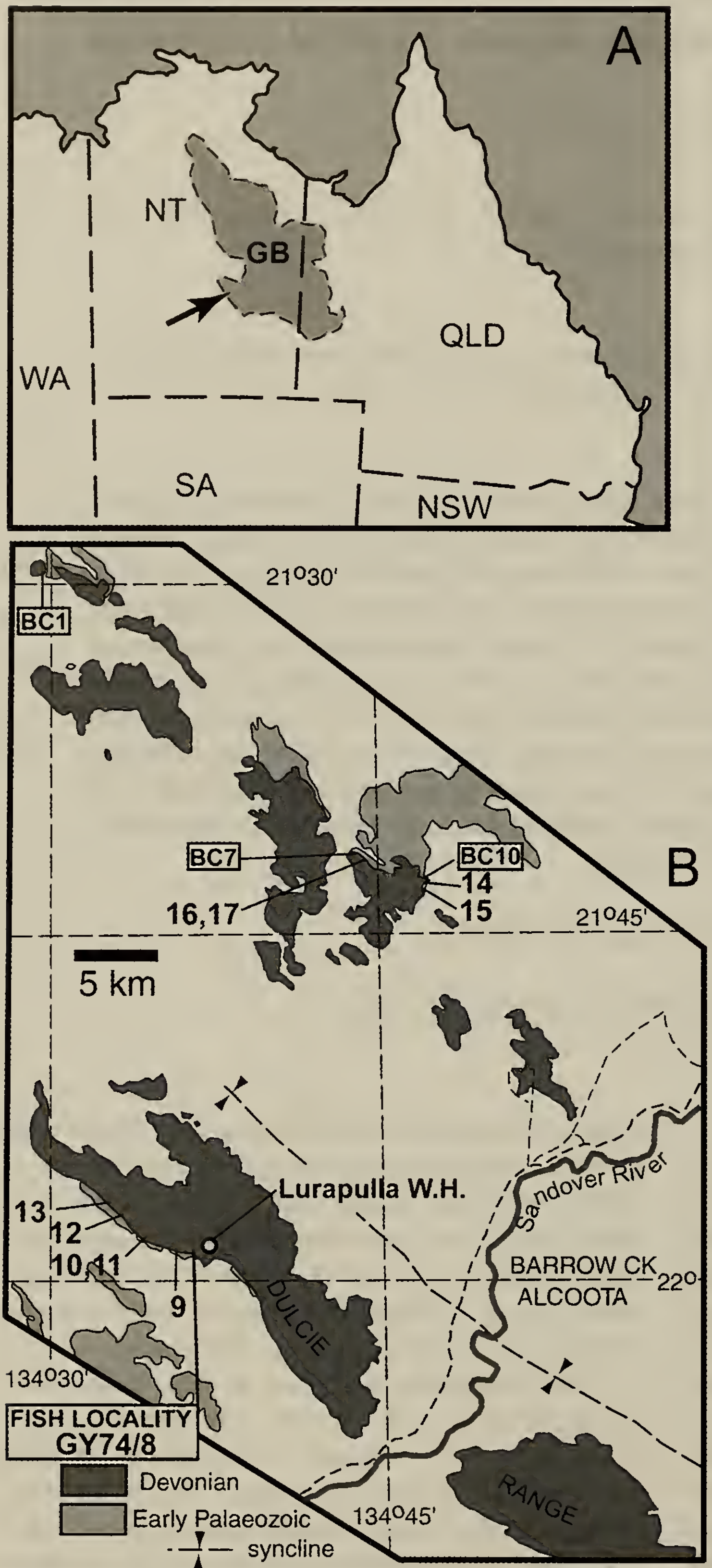

Figure 1. A, location of the Dulcie Range, on the southwestern flank of the Georgina Basin (GB) in northern Australia. B, Fossil fish localities in the northwestern part of the Dulcie Syncline, with geology generalised from the Barrow Creek and Alcoota 1:250 000 sheets (modified from Young and Goujet 2003: fig. 1). The samples described herein come from locality GY74/8.

new phyllolepid occurrence is significant in coming from an intermediate level in the Dulcie Sandstone, all previous examples of phyllolepids (Hills 1959; Young 1988) coming from near the top of the sequence.

Phyllolepids, like *Wuttagoonaspis*, have dermal bones with ridged ornament. Before *Wuttagoonaspis* was described by Ritchie (1973), all fish remains with ridged ornament from the Australian Devonian were referred to *Phyllolepis* without question (e.g. Rade 1964). In Europe *Phyllolepis* is only known from the youngest stage of the Late Devonian (Famennian), and on this basis all such occurrences in Australia were originally assigned to the Famennian (e.g. Hills 1929, 1931). But Hills (1958) also noted that the temporal significance of different placoderm genera in the Upper Devonian of Europe did not apply in Australia, and Young (1974) demonstrated that some phyllolepid occurrences were older (Frasnian) than in Europe. Some authors (e.g. Ritchie 1973) considered the phyllolepids and *Wuttagoonaspis* to be only distantly related, and recently Dupret (2004) has regarded the ridged ornament as a non-homologous character. The alternative hypothesis (e.g. Miles 1971; Young 1980; Long 1984; Young and Goujet 2003) is that ridged ornament is a shared derived feature, which with some others indicates that *Wuttagoonaspis* and phyllolepids are sister groups. Apart from ornament, the shape of bones is quite different in the two taxa, so impressions with ridged ornament can be readily assigned to one or the other group if bone margins are complete. Thus, examination of the ridged fragment called *Phyllolepis* by Gilbert-Tomlinson (1968) showed clearly that it belongs to *Wuttagoonaspis* (Young and Goujet 2003, fig. 3E). Similarly, impressions of the inner unornamented surface described below can unequivocally be assigned to a phyllolepid on the basis of bone shape.

Locality

Fossil fish localities GY74/8-13 along the southern flank of the Dulcie Range (Fig. 1B) supposedly came from the basal 10 m of the Dulcie Sandstone (Haines et al. 1991: 32), but poor outcrop, and some material collected from scree, make the actual interval of occurrence difficult to establish (Young and Goujet 2003). The boundary with the underlying Tomahawk beds (Cambro-Ordovician) is variously interpreted, as a faulted contact on the second edition of the Barrow Creek 1:250 000 geological map (Haines et al. 1991) but as a disconformity on the adjacent Huckitta map sheet (Freeman 1986).

The most easterly of these fish occurrences (GY74/8, Figure 1B) is recorded in field notes as being immediately above the contact with the underlying Tomahawk beds and was the first at which fish remains were discovered by the author in the lower Dulcie (on 7 July 1974). This is the locality yielding the specimen described below. Locality 74/8 was about 800 m west of the field campsite at Lurapulla Waterhole.

Stratigraphic level

The samples were labelled 'top of Dulcie; collected 7/7/74'. According to field diary records only locality 74/8 was visited on that day, when the adjacent section through the Dulcie Sandstone was also examined. Stereo air photos of locality 74/8 (Barrow Creek 17-10-70, run 9, photos 0025, 26) show the highest elevation in the vicinity of two ridges about 1 and 1.8 km to the NW, where beds have a very shallow dip (5° on the Barrow Creek geological sheet, first edition). Lower beds are more inclined, with a dip of 16° marked on the second edition geological map just above Lurapulla Waterhole. Estimates based on air photo interpretation suggest that the samples described below came from an interval about 200+ m above the fish horizon at the base of the sequence. At locality 74/8 the basal level yielded only indeterminate phlyctaenioid arthrodire remains (impressions with tuberculate ornament). However, another locality along strike about 3 km to the NW (74/11) produced some 50 samples belonging to seven taxa, including *Wuttagoonaspis* (Young and Goujet 2003: table 1). At none of the 26 localities covered in that study were phyllolepid remains identified. It was concluded that younger bothriolepid-phyllolepid placoderm assemblages did not occur in the lower part of the Dulcie Sandstone, nor in the Cravens Peak Beds (*contra* Gilbert-Tomlinson 1968, and Draper 1976). However, they are recorded from the upper part of the Dulcie Sandstone at the southeastern end of the Dulcie Range (about 490 and 600 m above base; Young 1988), where the type section records a thickness of 621 m. These horizons occur in sandstone mesas in the core of the syncline, representing the upper subdivision of the formation and are separated by valleys of recessive strata from more prominent outcrops of the lower Dulcie Sandstone (e.g. Freeman 1986, pl. 20).

Freeman (1986) identified the upper and lower facies in the vicinity of the type section but dismissed the suggestion (Gilbert-Tomlinson 1968) of a possible paraconformity within the lower unit. He noted a decrease in thickness to an estimated 250 m in the northwestern exposures on the Huckitta sheet. No sections were measured by Haines et al. (1991) on the Barrow Creek sheet, but the Dulcie Sandstone is much thinner (30-40 m) on the Elkedra sheet to the north-west (Stidolph et al. 1988).

A question arises as to whether the thinning of the Dulcie is general throughout the sequence or whether the lower or upper part is missing from the thinner stratigraphic sections. As first noted by Gilbert-Tomlinson (1968), the lower and upper fish assemblages in the Dulcie generally do not occur together. The occurrence reported here is the only one known so far that represents two distinct fish faunas within the same section. Previously (Young 1985: 251) a stratigraphic thickness of about 430 m was estimated between the lower *Wuttagoonaspis* and upper *Bothriolepis* – *Phyllolepis* fish assemblages, but the new fossil sample described below comes from some 200 m above the lower fish horizon. Decrease in thickness to the north-west from the type section would place this new phyllolepid occurrence near the top of the formation as exposed on the Barrow Creek sheet. If it correlates with those from the SE it could be assumed that the middle recessive part of the Dulcie Sandstone in the type section has been lost, retaining two distinct fish assemblages with no taxa in common within a section some 200-300 m thick. It is considered more likely that it represents a lower phyllolepid assemblage, given that a rather diverse fauna of unknown biostratigraphic relationship is indicated from fragmentary remains already described (Young 1988). Comparison can be made with the Pertnjara Group in the Amadeus Basin, where thickness extrapolations suggest a separation between the assumed level for the *Wuttagoonaspis* fauna in the base of the Deering Siltstone Member and the *Bothriolepis* assemblage within the Harajica Sandstone Member to be about 280 m at Stokes Pass, and possibly as low as 100 m at Dare Plain (Young 1985: 251, 252). A new species of the phyllolepid *Placolepis* has recently been described from the Harajica fish assemblage (Young in press a).

ABBREVIATIONS

Measurements of total length (L), breadth (B), length of the anterior division of the AVL (L_{AD}), and level of the lateral corner (lc) of the PVL (as a percentage of total length) are summarised in Figure 3 (below). Bone proportions are given as a ratio of breadth to length expressed as a percentage (abbreviated as 'B/L index'). Standard abbreviations for placoderm dermal bones and other structures are used in the text and figures as follows:

ADL, anterior dorsolateral plate;
AL, anterior lateral plate;
AMV, anterior median ventral plate;
AVL, anterior ventrolateral plate;
cf.IL, contact face overlapping interolateral plate;
cf.SP, contact face overlapping spinal plate;
IL, interolateral plate;
lc, lateral corner;
m.AMV, margin abutting anterior median ventral plate;
m.PMV, margin abutting posterior median ventral plate;
oa.AVL, area overlapped by AVL plate;
pect, pectoral embayment (margin) of AVL plate;
PMV, posterior median ventral plate;
PNu, paranuchal plate;
PVL, posterior ventrolateral plate;
ppec, prepectoral corner;
ptpec, postpectoral corner;
SP, spinal plate.

SYSTEMATIC PALAEONTOLOGY

Class PLACODERMI McCoy, 1848
Order PHYLLOLEPIDA Stensiö, 1934

Diagnosis

Placoderms in which the nuchal plate is much enlarged, as broad or broader than long, and surrounded by five smaller paired bones including paranuchal, marginal, postorbital and preorbital plates. Paranuchal plate with well-developed postnuchal process, and rostral, pineal, and central plates absent from skull roof. Trunk armour relatively broad; median dorsal plate lacks an inner keel; anterior dorsolateral plate with narrow elongate exposed area; anterior ventral and posterior lateral plates absent; posterior dorsolateral and anterior and posterior median ventral plates reduced or absent. Anterior ventrolateral plates short and broad, and posterior ventrolaterals triangular, with ossification centres near anteromesial corners; both ventrolateral plates relatively flat, lacking a lateral lamina, and meeting in part or all of the midline in non-overlapping sutures. Dermal ornament mainly of smooth concentric ridges, with some tubercles and tubercle rows.

Remarks

The diagnosis provided by Ritchie (1984: 344) was slightly reworded from that of Denison (1978: 41), and included reference to the absence of rostral and pineal plates from the skull, used by Denison to separate his two suborders 'Antarctaspina' and 'Phyllolepina'. *Antarctaspis* is now regarded as an actinolepid related to *Toombalepis* and *Yujiangolepis*, which also have converging sensory grooves on the nuchal plate (Young and Goujet 2003: fig. 16), a primitive feature and not a criterion for indicating close relationship to phyllolepids. Ritchie (1984: 346) gave an additional diagnosis for the family Phyllolepidae that combined features of Denison's subordinal and family diagnoses, but there are no good criteria for grouping genera within the order at this stage.

The above diagnosis excludes characters that are evidently primitive by outgroup comparison (e.g. converging sensory canal grooves on the skull, median dorsal plate short and broad and lacking inner keel, sliding dermal neck-joint). New characters include features of the trunk armour bones typical of the group. The much reduced external part of the anterior dorsolateral (ADL) plate is a condition approached in *Bryantolepis*, *Kujdanowiaspis* (Denison 1958: fig. 108) and *Wuttagoonaspis*. The anterior ventrolateral (AVL) is relatively broad compared to that of other primitive arthrodires, in which the posterior ventrolateral (PVL) has complex midline overlaps, and a prominent lateral lamina (Denison 1958: figs. 112, 114). The ossification centre of the PVL is normally placed laterally near the posterior end of the lateral lamina (e.g. *Actinolepis*; Mark-Kurik 1973: fig. 13), but its anteromesial position in phyllolepids is well shown by the concentric ornament of *Austrophyllolepis* (Long 1984: fig. 11D). New phyllolepids from southeastern Australia show that the posterior dorsolateral (PDL) plate is retained in some members of the order (Young, in press b), although it is lost in *Phyllolepis*, *Austrophyllolepis*, and probably *Placolepis* (Long 1984; Ritchie 1984).

Genera included in the family and order are *Phyllolepis*, *Austrophyllolepis*, and *Placolepis*, plus two new phyllolepid taxa from southeastern Australia (Young in press b). The genus *Pentagonolepis* Lohest, 1888, from the Famennian of Belgium, was synonymised with *Phyllolepis* by Leriche (1931), Stensiö (1939) and Denison (1978). However, the ridged ornament on the nuchal plate from the skull roof, on which the species *Phyllolepis (Pentagonolepis) konincki* is based (Stensiö 1939, fig. 6B), suggests a rounded anterior margin (incomplete), somewhat similar to the corresponding bone of *Placolepis* described by Ritchie (1984). The Belgian specimen differs from *Placolepis* in that the middle pitline is directed towards the lateral corner of the plate, as in *Phyllolepis*, rather than well behind that corner. It seems likely that the paranuchal plate from the same skull had extensive contact with the postorbital plate. Restudy of this material, and any new specimens from Belgium, is needed to confirm the shape of the nuchal, but '*Pentagonolepis' konincki* Loheste, 1888 could be a valid taxon, morphologically intermediate between *Placolepis* and *Phyllolepis* in the configuration of skull bones. It is noted that the first Devonian tetrapods from continental Europe have recently been described from these localities, in the Evieux Formation of Belgium (Clément et al. 2004).

Austrophyllolepis Long, 1984

Diagnosis

Phyllolepids in which the sensory groove passes off the paranuchal plate in the anterior third of plate length, and the external surface of the marginal plate is similar in breadth and length, with the postmarginal sensory canal junction in about the middle of plate length. A small suborbital plate is articulated to an ossified process below the postorbital plate, and the submarginal plate may be ossified. The trunk armour has a posterior median ventral plate that forms a distinct notch in the mesial margins of anterior and posterior ventrolateral plates. The ridged ornament includes extensive areas of tuberculation and some ridge duplication.

Austrophyllolepis dulciensis sp. nov.

Name

Shortened from 'Dulcie', after the type formation and locality (Dulcie Sandstone and Range, Georgina Basin, Northern Territory).

Diagnosis

A species of *Austrophyllolepis* in which the anterior ventrolateral plate is as broad as long (breadth/length index about 100), with anterior and posterior divisions about 20% and 30% of total length and a slightly concave spinal margin; posterior median ventral plate elongate and free part of spinal plate relatively short.

Remarks

The generic diagnosis from Young and Long (in prep.) is updated from Long (1984). Most of the characters are not observable in the material described below, but the evidence of a posterior median ventral (PMV) plate in the trunk armour is the criterion for referring the species to *Austrophyllolepis* (see further comments below). Characters in the specific diagnosis separate the new species from previous species of *Austrophyllolepis*. The unusually broad anterior ventrolateral (AVL) plate distinguishes *A. dulciensis* sp. nov. from all previously described phyllolepids in which this plate is known.

Material

ANU V3064 (holotype; associated AVL, PVL and SP plates); ANU V3065 (incomplete PVL plate), both preserved as impressions in hard sandstone.

Locality and Horizon

Locality GY74/8, southern flank of Dulcie Range (Fig. 1B), from a horizon about 200 m above the exposed base of the Dulcie Sandstone (see Young and Goujet 2003: 5 for locality details).

Description

The impressions of closely associated phyllolepid trunk armour plates comprise an almost complete right AVL plate, overlain by a SP plate and a right PVL plate (Fig. 2A). Another AVL is separated by 45 mm from the first (Fig. 2B), and an incomplete left PVL impression is preserved on the second smaller sandstone sample (ANU V3065). The two AVL plates (termed AVL#1, AVL#2) were first assumed to be internal impressions of left and right plates from one individual, because both appeared to lack ornament. Closer examination showed that both are right plates. The second specimen (AVL#2; Fig. 2B) is slightly convex rostrocaudally, and must have been an external surface impression, even though it is smooth. A new phyllolepid genus with smooth dermal bones has recently been documented from southeastern Australia (Young, in press b). However, in ANU V3065 absence of ornament may be a post-mortem effect due to 'sand-blasting' in a river current removing the ridged ornament from most of the external surface. Short sections of relatively coarse ridges are retained on the downturned posteromesial and spinal margins of the bone (ri, Fig. 2B), presumably protected from abrasion beneath the sediment-water interface. The relatively flat ventral plates of the phyllolepid trunk armour would have made them hydrodynamically stable with either external or internal surfaces uppermost, in contrast to some other common placoderm remains, for example the strongly angled trunk armour bones of the widespread antiarch *Bothriolepis*.

The anterolateral and prepectoral corners of AVL#2 are incomplete, and the posterolateral part is missing off the edge of the sample. This and the first AVL clearly came from two individuals of about the same size, and shape differences are assumed

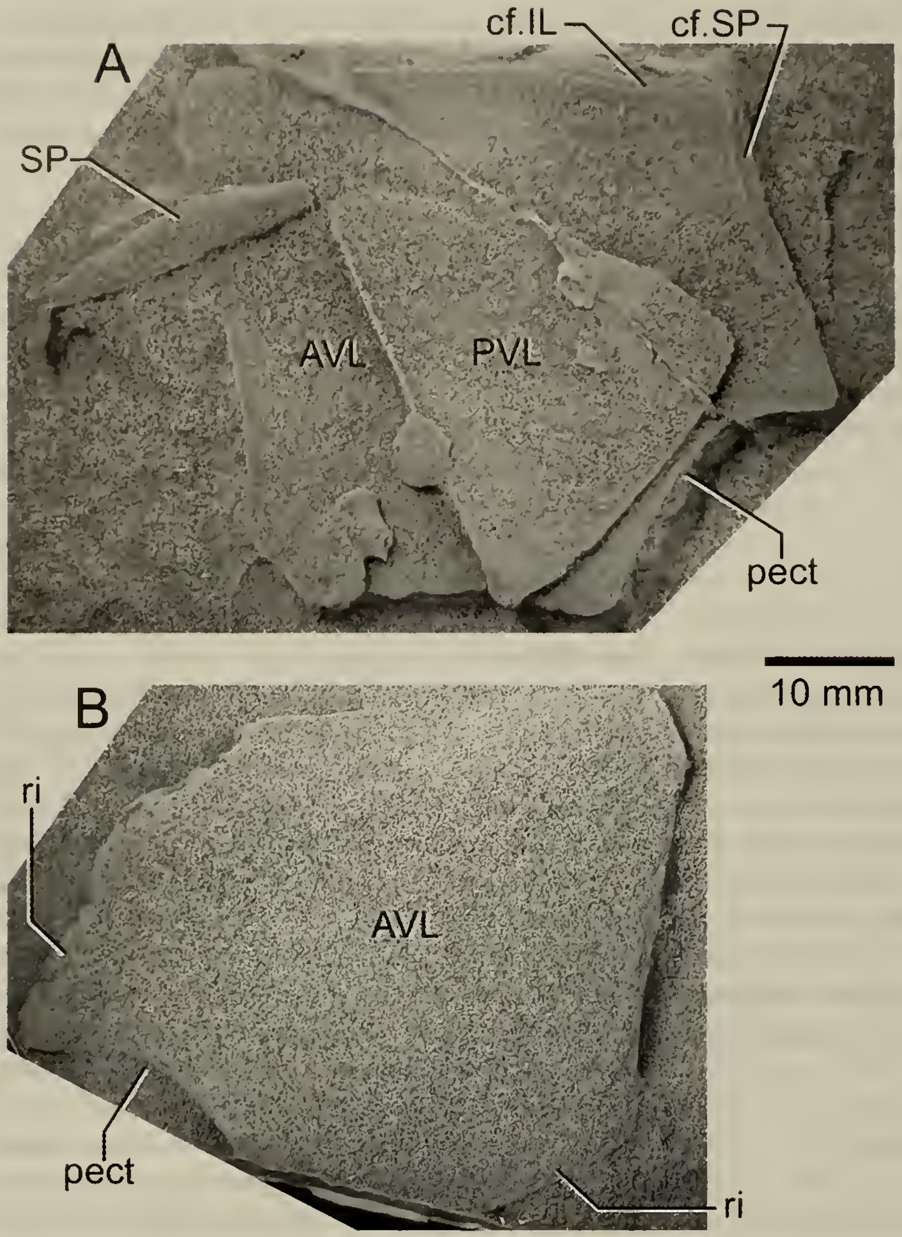

Figure 2. ANU V 3064 showing associated AVL, PVL and SP plates of *Austrophyllolepis dulciensis* sp. nov. (A), and the second AVL plate (B). Both are latex casts of sandstone impressions whitened with ammonium chloride.

to be intraspecific variation, given the very similar proportions of the two restored plates (see below). AVL#1 (Fig. 2A) exposes the visceral surface, which is gently concave rostrocaudally, with the anterior margin curved up, forming a slight rim mesially. Around the anterolateral corner a second ridge inside the margin defines a narrow contact face for the IL and SP plates (cf.IL, cf.SP, Fig. 2A, 3A). A diagonal groove crosses the visceral surface of the AVL in *Placolepis* (Ritchie 1984: fig. 11A-B) and is a distinctive feature of that genus. It is not developed in the Victorian material of *Austrophyllolepis* (Long 1984, 1989) and is absent in this new specimen. The spinal margin, which in all other phyllolepid taxa is convex, in this AVL is gently concave anteriorly and straight posteriorly (Fig. 3A). The mesial margin, normally straight in phyllolepids, is slightly convex anteriorly and concave posteriorly, again showing the raised rim typical of phyllolepid AVL plates where they form a non-overlapping suture in the midline. In that case the margin must be straight, but AVL#1 indicates a gap in the midline for a small PMV plate, as in *Austrophyllolepis* from Victoria (Long 1984: fig. 11D). In AVL#2 the preserved spinal margin and the posterior part of the mesial margin are also gently concave (Fig. 2B), as in AVL#1. Reconstruction (Fig. 4), based on AVL#2, suggests that the Dulcie Range species must have had a larger PMV than in the Victorian species. Of these, *A. ritchiei* had the longer PMV (Long 1984: figs. 7B, 13B) but with a concave external margin (convex in the new specimens). There is a distinct short posteromesial margin on AVL#1 (m.PMV, Fig. 3A), occasionally seen in other species (e.g. interpreted as a broken edge in *Phyllolepis concentrica* by Stensiö 1939: fig. 1).

AVL#2 differs in lacking a posteromesial margin, but has an anteromesial margin defined by distinct corners (m.AMV, Fig. 4). Ritchie (1984: 342-3) assumed the AMV to be absent in European *Phyllolepis* and in *Placolepis*, as did Long (1984) for *Austrophyllolepis*. One specimen assigned to *A. youngi* does suggest an anterior median element (Long 1984: fig. 18C), as in *Phyllolepis woodwardi* from Europe (Stensiö 1939: fig. 2). An AMV plate is also present in a new phyllolepid taxon from Merriganowry, N.S.W. (A. Ritchie, pers. comm.). Since both AMV and PMV plates were primitively present they would be expected to be variably developed in basal phyllolepid taxa (for example the two PMV plates in Victorian material; Long 1984: fig. 6).

Both AVLs as restored are as broad as long (B/L

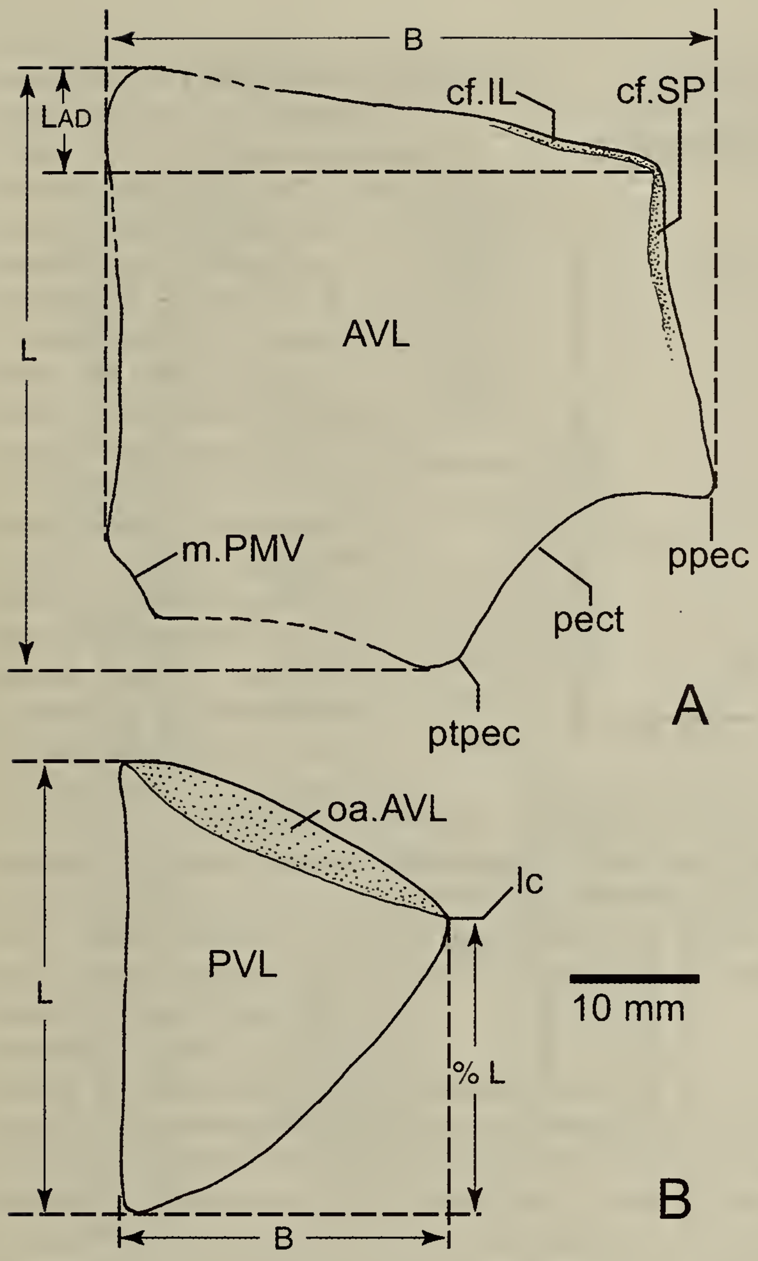

Figure 3. ***Austrophyllolepis dulciensis*** **sp. nov. A, AVL plate of Fig. 2A (AVL#1) slightly restored. B, PVL plate of Fig. 2A, restoration of external surface. ANU V3064.**

index 100), with a similar length of the anterior division (19-20%). In contrast, in both *Austrophyllolepis* and *Placolepis budawangensis* (Long 1984; Ritchie 1984: fig. 11), and all species of *Phyllolepis* from Europe (Stensiö 1939), the AVL is consistently longer than broad. Since the precise measurements for the AVL as summarised in table form by Stensiö (1939: 7) were not clearly defined, measurements used here are indicated in Fig. 3.

The main difference in the two AVLs described here is the orientation of the posterior margin, giving a greater posterior angle (~78°) in AVL#1 than in AVL#2 (~60°), the latter approximating to the anteromesial angle of the PVL (~65°). Distortion in the specimens is discounted because the anteromesial angle of the AVL is much the same in both (75-80°).

The complete PVL impression shows the visceral surface of a left plate (Fig. 2A), with a raised inner rim along its straight mesial margin (L 33 mm) which abutted against the right PVL. A thickened zone inside the anterior margin probably reflects the position of the overlap area for the AVL on the external surface (oa.AVL, Fig. 3B). The B/L index (73) places this PVL at the broader end of the variation for *Placolepis budawangensis*, which is broader than in *Austrophyllolepis edwini*, *A. youngi* and three European species (*Phyllolepis orvini*, *Ph. nielseni*, *Ph. tolli*), but more narrow than in *A. ritchiei* (Young 1988: table 1), with *Austrophyllolepis* differing from the other taxa in the more posterior level of the lateral corner (Long 1984: fig. 7; 1989: fig. 4). The shape and proportions of the PVL described here are also notably different from the two PVLs from the Amadeus Basin (Young 1988: table 1). The second incomplete PVL (ANU V3065) shows the mesial margin of a right plate impression, also 33 mm long, and thus perhaps from the same individual.

The complete PVL of Fig. 2A does not fit properly against the underlying AVL, but makes a good fit with AVL#2, so these were used for the reconstruction (Fig. 4). The associated SP plate impression is missing both ends, but restored length is about 33 mm. The distal 4 mm of the preserved part has a closed posterior margin, with the bases of about 4 denticles preserved on what is assumed to be the ventral margin. This margin shows a slight angle in the middle of the preserved part, assumed to fit into the concave margin on the AVL. The opposite lamina (presumed to be dorsal) is more rounded. This SP plate cannot be restored with the free part of the spine as long as in *Placolepis*, or in the Victorian *Austrophyllolepis* (33% and 25% of total length respectively; Ritchie 1984: 342; Long 1984: 272). However, in *Phyllolepis orvini* the free part of the SP plate is much shorter (Stensiö 1936: fig. 20).

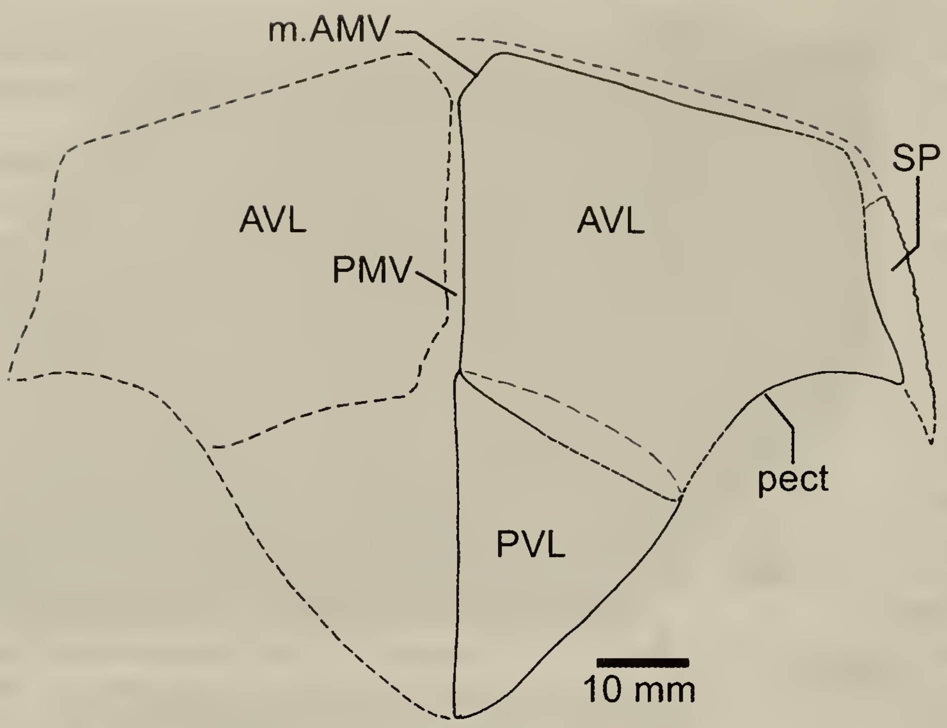

Figure 4. *Austrophyllolepis dulciensis* sp. nov. Attempted restoration of ventral trunk armour; outline shape, and plates of the right side based on the AVL plate of Fig. 2B (AVL#2), and the PVL plate of Fig. 2A; left side indicates the shape of AVL#1 (Fig. 2A); gap left for the PMV plate suggests a variable shape in this species (PMV).

DISCUSSION

These few phyllolepid remains are apparently 'primitive' compared to *Phyllolepis* in Europe by showing evidence of a PMV plate of appreciable size, a character by which they can be referred to *Austrophyllolepis* Long, 1984. However, they differ from all three species of the genus so far described (Long 1984, 1989). It is unclear how reliable the criterion of PMV presence will prove as a generic character, since both AMV and PMV were presumably present in phyllolepid ancestors and their reduction and loss may have occurred independently in different lineages. For the present this criterion is retained to allocate this species to the genus *Austrophyllolepis*. Although the ridged ornament is not preserved, the distinctive triangular PVL plate clearly places these impressions within the Phyllolepida as defined above. In other arthrodires, and in *Wuttagoonaspis* (e.g. Young and Goujet 2003: fig. 8G), the PVL has a distinct lateral lamina, the primitive condition. The loss of this lamina, giving an essentially flat bone, may account for the fact that impressions of the phyllolepid PVL are more commonly found than other bones of the trunk armour, because its hydrodynamic qualities would have resembled those of a flat mud clast.

The fact that this phyllolepid evidently came from a horizon some 200+ m stratigraphically above a completely different fish assemblage, which lacks phyllolepids but contains the possible primitive sister group *Wuttagoonaspis*, might suggest that this is a relatively early phyllolepid occurrence. In a comparison of stratigraphic thicknesses between fish horizons across central Australia, Young (1985: fig. 10) concluded that the previous Dulcie Range phyllolepid occurrences could be somewhat younger than the phyllolepid – bothriolepid occurrences in the Harajica Sandstone of the Pertnjara Group in the Amadeus Basin. This new description of probable *Austrophyllolepis* sp. lower in the Dulcie sequence suggests that the diversity of phyllolepids in central Australia is greater than previously thought, as is now demonstrated in southeastern Australia (Young, in press b) and Antarctica (Young and Long submitted). By comparison with species of both *Austrophyllolepis* and *Placolepis* in southeastern Australia, the age of the lower phyllolepid occurrences in central Australia can be assumed to lie within the Givetian-Frasnian interval. Recent work on the age of the Mount Howitt fish assemblage within the Middle-Late Devonian volcanics of eastern Victoria, the type locality for *Austrophyllolepis*, supports a late Middle Devonian age on both palaeontological and isotopic evidence (Long 1999; Compston 2004).

The diversity of phyllolepid taxa in East Gondwana, and their earlier occurrence than in the Devonian of the Northern Hemisphere, supports the hypothesis of a Gondwanan origin for the group, followed by dispersal into Laurussia in the Famennian resulting from palaeogeographic change at or near the Frasnian-Famennian boundary (Young 1989, 1990, 1993b, 2003). A summary of biostratigraphic ranges (Fig. 5) shows diverse phyllolepids in the Givetian-Frasnian of East Gondwana, with related forms in the largely endemic *Wuttagoonaspis* assemblage (Young

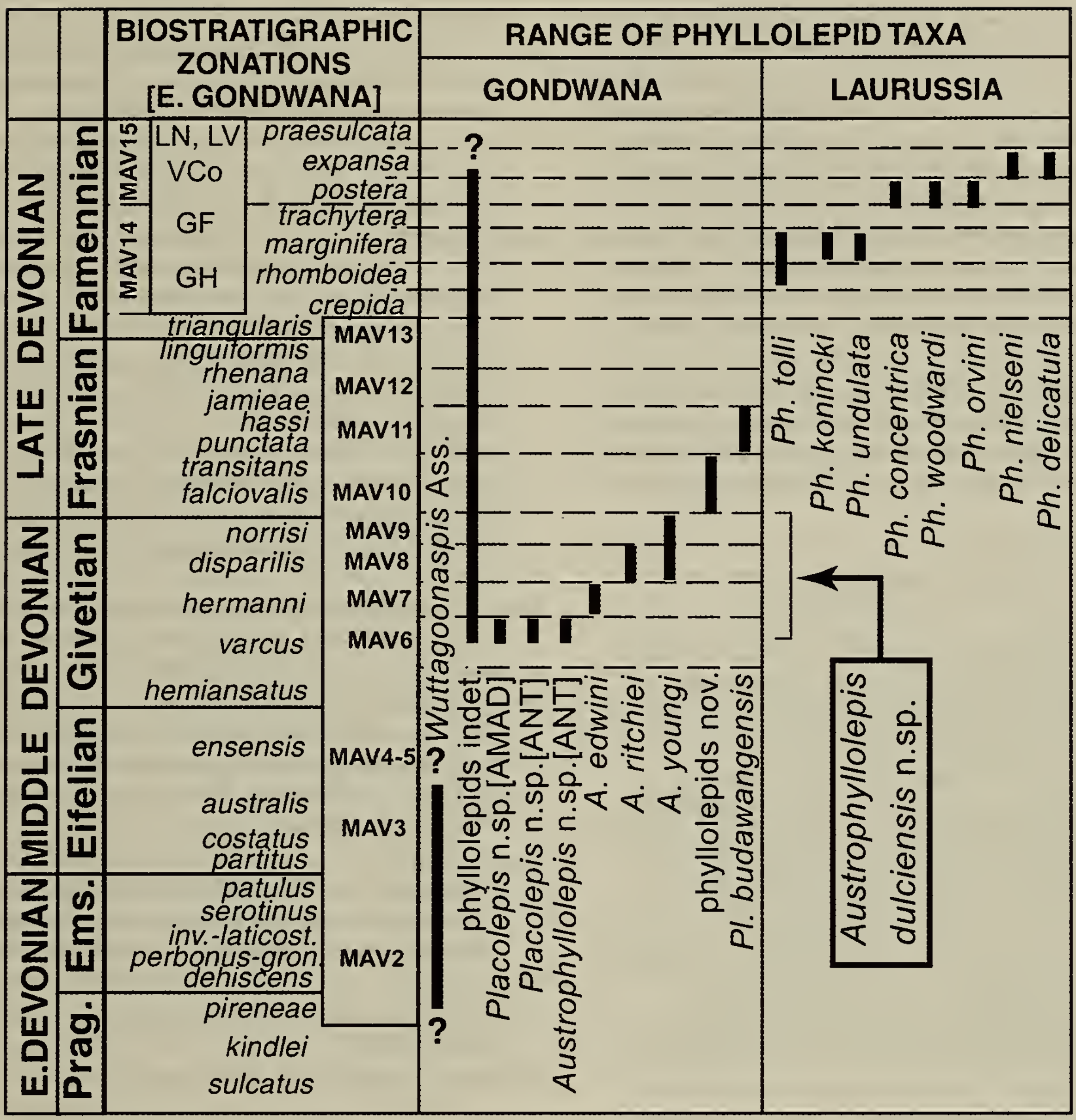

Figure 5. Summary of known stratigraphic ranges (?Pragian-Famennian) for wuttagoonaspids-phyllolepids in East Gondwana (Australia, Antarctica), and the genus *Phyllolepis* in Laurussia (ANT= Antarctica; AMAD= Amadeus Basin). Approximate interval for *Austrophyllolepis dulciensis* sp. nov. from the Dulcie Sandstone indicated, based on the range of other species of the genus. Australian stratigraphic range data updated from Young (1993a: fig. 9.3) and Young (1999: fig. 5). Conodont zonation after Talent et al. (2000). Approximate alignment of macrovertebrate (MAV), miospore (GH, GF, VCo, LN, LV), and conodont zones modified from Young (1996) and Young and Turner (2000).

and Goujet 2003) probably extending down into the Early Devonian, some 22 conodont zones before species of the genus *Phyllolepis* are documented in the Northern Hemisphere (in the Famennian *rhomboidea* conodont zone). This disjunction in time and space is an outstanding feature of global distribution patterns amongst Devonian fishes.

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Cowralepis, a new genus of phyllolepid fish (Pisces, Placodermi) from the Late Middle Devonian of New South Wales, Australia

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Ritchie, A. (2005). *Cowralepis*, a new genus of phyllolepid fish (Pisces, Placodermi) from the Late Middle Devonian of New South Wales, Australia. *Proceedings of the Linnean Society of New South Wales* **126**, 215-259.

Cowralepis mclachlani, a new genus and species of phyllolepid placoderm (Pisces, Placodermi), is described from numerous articulated specimens discovered near Cowra, New South Wales, Australia. *Cowralepis,* represented by a growth series, illustrates ontogenetic changes from juvenile to adult and throws new light on the dermal, endocranial, visceral and axial skeleton of phyllolepids and on placoderm interrelationships. The head shield is longer than the trunk shield, the reverse of the situation in other phyllolepid genera. The presence of two pairs of upper tooth plates, plus a posterior dorsolateral plate, an anterior median ventral plate and one or more posterior median ventral plates in the trunk shield is confirmed. The phyllolepid jaw apparatus and associated structures, first reported in *Austrophyllolepis*, are reinterpreted. The branchial skeleton, an occipital ossification and a fused synarcual, previously unknown in phyllolepids, are described. *Cowralepis* had an ossified vertebral column, a large epicercal caudal fin and small pelvic fins but lacked a dorsal fin. The *Cowralepis* material has suffered regional tectonism and illustrates why tectonic deformation must be taken into account in the interpretation of fossils from ancient fold belts.

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KEYWORDS: *Cowralepis*, Placoderm, phyllolepid, tectonism.

INTRODUCTION

In January1993, during the preliminary excavation of a major Late Devonian fish site near Canowindra, New South Wales (Ritchie in press), the late Mr Reg Dumbrell, a Canowindra resident, showed the writer some Devonian fish specimens he had collected from another site, about 15 km south, in Cowra Shire. Dumbrell's best find, on a piece of black shale 10 cm square, was a small, articulated armoured fish, a phyllolepid, with the tail of a second individual lying beside it. Articulated phyllolepids had previously been recorded from only two sites in the world – Dura Den, Fife, Scotland, and Mt Howitt, Victoria, Australia.

The source of Dumbrell's find was unexpected; the margins of the approach roads to Merriganowry Bridge, a causeway over the Lachlan River, 20 km northwest of Cowra, NSW, and about 2 km from any natural rock outcrop. In March 1993 the writer and colleagues visited the site, located more fish fossils and solved the mystery. The fish-bearing black shale was not *in situ.* It had been quarried elsewhere, trucked in and crushed for road-base material - the local roads were literally paved with fossil fish!

Cowra Shire Council confirmed the source to be a small quarry 2 km from Merriganowry Bridge, just north of Merriganowry Hall and only 50 metres east of the main road from Cowra to Forbes (Young 1999, fig.1B, locality 6). This quarry, on private land, had been worked on and off for 10-15 years, apparently without anyone noticing, or at least reporting, the presence of abundant, well-preserved fossil fishes in the shale.

With permission of the new landowner, Mr Alex McLachlan, the writer first visited Merriganowry in June 1993 and uncovered a fossil treasure trove. Some sixty phyllolepid specimens, large and small, many complete with tails, were recovered by the writer in three days digging! At a conservative estimate, tens or hundreds of thousands of fossil fish specimens had been quarried from this site and crushed for road material before its scientific importance was recognised.

When informed of its unique scientific importance, Mr McLachlan immediately arranged for the quarry to be secured and fenced, at considerable cost, and made it available to the Australian Museum for long-term, systematic investigation under scientific supervision. Since September 1993 the Merriganowry site has been excavated by paying volunteer groups supervised by the writer and Dr Zerina Johanson from the Australian Museum and organised by an eco-tour operator, Monica Yeung, Gondwana Dreaming Inc., of Canberra.

All of the material collected by these groups has been retained for scientific study and deposited with the Australian Museum, providing a unique scientific research resource. Several hundred fish specimens have been recovered from Merriganowry, many of them articulated individuals complete with tails, and they represent a continuous growth series from juveniles 5 cm long to adults over 35 cm long. Strangest of all, after 11 years of supervised group digs, every fish fossil recovered from Merriganowry (with the exception of dissociated scales in associated coprolites) appears to belong to a new genus of phyllolepid placoderm, *Cowralepis*.

Phyllolepids were dorsoventrally flattened placoderms with a distinctive, sub-concentric ridged ornament, hence their name meaning ‘leaf-scale’. Most phyllolepid finds consist of dissociated or fragmentary dermal bony plates; articulated specimens are extremely rare, which is why the Merriganowry site is so important.

Most of our previous knowledge of phyllolepids comes from three genera: *Phyllolepis* from the Late Devonian of the Northern Hemisphere, and *Austrophyllolepis* Long, 1984 and *Placolepis* Ritchie, 1984 from the Middle-Late Devonian of Australia; for reviews of earlier phyllolepid discoveries see Long (1984 263-4) and Ritchie (1984 321-3). Many of the new phyllolepid discoveries since 1984 have come from Gondwanan sites. In Australia these include the Amadeus and Georgina Basins, central Australia (Young 1985, 1988, in press a), southeastern New South Wales (Young in press b), Victoria (Long 1989) and Queensland (Turner et al. 2000). Phyllolepids have also been described from Antarctica (Young 1989, 1991; Young and Long in press), Venezuela, South America (Young et al. 2000; Young and Moody 2002) and Turkey (Janvier 1983). Articulated phyllolepids have also recently been reported from Pennsylvania, U.S.A. (Daeschler et al. 2003).

Phyllolepid fishes have not yet been recorded either from Asia, where diverse fossil fish assemblages of appropriate age are extensively documented, or from Africa.

GEOLOGICAL SETTING

Horizon and age.

The phyllolepids described here all come from the Merriganowry Shale Member that was uncovered by quarrying for road-base material in the 1980’s and early 1990’s. The more resistant outcrops (rhyolitic volcanics) forming the east margin of the quarry had initially been mapped as part of the Canowindra Volcanics, of possible Silurian age. The quarry exposed a conformable relationship between the fish-bearing black shales and underlying volcanics, showing that the latter must also be Devonian in age, not Silurian.

Young (1994, 1999, figs 2, 3) correlated the volcanic sequence at Merriganowry with the much younger Dulladerry Volcanics, which cropout over a large area of NSW between Narromine, Dubbo, Forbes and Bathurst and underly the Late Devonian Hervey Group on the western edge of the Hervey Syncline. The youngest Dulladerry Volcanics are now estimated to be Late Middle Devonian in age (Givetian), which would date the Merriganowry black shales as either Late Givetian or Early Frasnian (Young 1999, fig. 5B). This is consistent with the fish and associated palaeobotanical evidence.

No direct contact has been identified between the west-dipping shale and volcanic sequence at Merriganowry and the overlying Hervey Group, but sandstone ridges 1 km north of Merriganowry quarry, with the same strike and dip, have been mapped as Peaks Sandstone, the basal unit of the thick Hervey Group, suggesting a conformable sequence between them.

Although the very limited exposure of the Merriganowry Shale Member precludes a total thickness estimate, its exposed lower section, directly overlying the volcanics in Merriganowry quarry, dips at 45° to the WSW (245°), and the fish-bearing sequence is estimated to be at least 25 metres thick. Excavations over the past 12 years have confirmed the presence of fish remains on hundreds of different bedding planes throughout the sequence, from just above the underlying volcanics to the top of the section exposed in the quarry.

Environment of Deposition.

Young (1999, 144; P. O'Brien, pers. comm. 1994) reported that "the locality is a black shale deposit closely associated with the underlying volcaniclastics including rhyolite blocks and possible flows. The shale includes slumped beds and graded interbeds of rhyolitic sand up to 30 cm thick, suggesting deposition in a lake of sufficient size and depth for turbidity currents to be generated, with water depths of tens to hundreds of metres, perhaps an elongate deep lake such as are associated with strike slip faulting."

Krynen (in Pogson and Watkins 1998, 224-5), in formally naming the Merriganowry Shale Member, noted "this sequence suggests initial subaerial outwash fan deposition in a volcanic rift setting passing upwards to turbiditic deposition in a deep lake environment following at least local cessation of volcanism. The formation of the lake may have been associated with strike-slip faulting within the volcanic rift."

Associated fauna and flora

The Merriganowry fauna is extremely restricted. The only identifiable fish remains, recovered after 11 years of systematic collecting with the assistance of many hundreds of volunteers, almost all appear to belong to one genus of phyllolepid, *Cowralepis* gen. nov., described here. A few fragments of eurypterid integument have been recovered from one layer high in the section. Apart from these, the only other fossils recovered are fragmentary plant remains including lycopods ('*Protolepidodendron*') and branching stems (cf. *Prearamunculus*) and what appears to be an egg sac (Fig. 18D).

What the abundant phyllolepids ate remains a mystery - probably plant debris and small invertebrates not preserved as fossils. Coprolites up to 20 mm long, presumably derived from the dominant phyllolepids, are common throughout the Merriganowry section but are invariably deeply weathered. When cleaned out, these may reveal traces of their contents, but preserved only as natural moulds. They include comminuted bone fragments, some of which appear to be of phyllolepid origin, and several coprolites contained abundant minute scales, about the size and shape of thelodont denticles, but not well enough preserved to be identifiable.

It appears unlikely that the phyllolepids lived on the bottom of the lake because the shale layers are generally smooth, flat and undisturbed, free of burrowing organisms and with very few trace fossils. The abundance of articulated phyllolepid specimens complete with delicate tails indicates an absence of scavengers and suggests that the bottom conditions were probably anoxic.

The observation that about half of the dorsoventrally flattened phyllolepids found *in situ* at Merriganowry were buried upside down suggests that they probably lived in the upper, better-oxygenated water levels and only after death fell randomly to the bottom where they lay undisturbed until covered. The same conditions must have persisted for many thousands of years as the shale deposit slowly accumulated, during which time the fauna was dominated by phyllolepid fishes to the virtual exclusion of all other groups.

The Merriganowry fauna, and the conditions under which it lived and was buried, thus presents a sharp contrast with the Late Devonian mass-kill fish site discovered only a few kilometres to the north, near Canowindra, New South Wales (Ritchie in press). The Canowindra assemblage of placoderms and sarcopterygians, dominated by two antiarch genera, *Bothriolepis* and *Remigolepis,* comes from a single bedding plane on which many thousands of fishes lie crowded tightly together, almost all of them (about 95%) buried right way up. Canowindra represents a unique time capsule, a sample of a single population killed and buried quickly as the result of a local environmental disaster, probably an extreme drought.

MATERIAL AND METHODS

Note: to facilitate cross-referencing of specimens all figures are located at the end of the paper from page 240

The original bone was often preserved but deeply weathered and was removed by washing, by airbrasives, mechanically or with dilute hydrochloric acid. The resulting detailed natural moulds (negatives) were cast using black-pigmented latex rubber. The latex casts were whitened with ammonium chloride sublimate and photographed with a Nikon Coolpix digital camera. Most of the images used here show the original uncorrected dimensions, with the exception of several specimens (Figs 6a-D, 9F, 10H, 11B, 16A-C) in which these have been digitally modified, as indicated, using Adobe Photoshop LE, to correct for the effects of regional tectonic deformation.

Silicone rubber moulds were prepared from the latex casts (which have a limited shelf life) and most of the figured specimens have been replicated as resin casts (positives) for collection and study purposes and for scientific exchange with other institutions.

Interpreting tectonically deformed fossils – the long and the short of it.

Not only do the Merriganowry phyllolepids represent a very wide growth range, from juveniles to adults, but they also display considerable variation both in relative proportions and in ornament (Fig. 2). Some specimens are deceptively symmetrical (Fig. 5), but most show visible evidence of deformation and/or asymmetry.

They confirm a) that the Merriganowry Shale Member had undergone significant shear strain, b) that the fish fossils provide a means of directly measuring this and c) that much of the morphological variation and deformation at Merriganowry can be attributed to post-mortem tectonic deformation, which must be taken into account in interpreting such material.

Many of the fossils found in areas subjected to major regional tectonism are distorted, a phenomenon documented for many types of fossils since the mid-19th century. Ramsay and Huber (1983, 127-149) illustrated how tectonically deformed fossils (trilobites, brachiopods, corals, graptolites, ammonites etc.) could provide structural geologists with a useful method of strain measurement. Graphical techniques developed for restoring deformed fossils have mostly been used for invertebrates and plants (Cooper 1990) but less often for vertebrates.

Tectonic strain is most readily detected in fossil organisms that were originally bilaterally symmetrical, where the original axis of symmetry can only lie in two directions, at right angles on the bedding plane without any loss of symmetry. Such organisms (the Welsh Ordovician trilobites, *Angelina* and *Bathyuriscus* are classic examples) provide the simplest subjects for study (Ramsay and Huber 1983, figs 8.7, 8.8). Where the original shape of these fossils is already known it can be used to determine the shear strain in deformed specimens and restore them to their original shape. Dorsoventrally flattened (and bilaterally symmetrical) armoured fishes such as phyllolepids provide ideal subjects especially where, as at Merriganowry, innumerable specimens were buried articulated and undisturbed *post mortem*.

Despite the widespread use of length/breadth ratios and angular measurements in the description and classification of fossil vertebrates, such correction techniques have rarely been applied to fossil vertebrates. Failure to recognise, and correct for, tectonic deformation has undoubtedly led to misidentification of fossil species and proliferation of invalid taxa.

Because most of the *Cowralepis* specimens were discovered only **after** blocks had been excavated for splitting by volunteers, their original orientation in the ground had been lost. A small number of *Cowralepis* specimens were found *in situ* (<5%) as the outcrop was excavated and their orientation could be measured before removal.

The extremes of deformation displayed by *Cowralepis* specimens from Merriganowry are illustrated by two types of specimens displaying bilateral symmetry - **broad symmetric** and **narrow symmetric** - depending on whether the broad symmetry axis is parallel to the long or to the short axis of the strain ellipse (Fig. 5A-D). Such specimens cannot be used to determine shear strain. Most of the phyllolepids from Merriganowry are visibly asymmetric, or skewed, to various degrees, and appropriate correction techniques need to be applied.

Digital reconstruction of deformed fossils.

The first step is to determine the direction of **greatest principal extension** (GPE) and **smallest principal extension** (SPE) of the fossil. At Merriganowry the GPE coincides approximately with the strike direction of the steeply dipping shale layers and the SPE lies at right angles to it, up-dip and down-dip. *Cowralepis* specimens discovered *in situ* are marked with strike and dip directions before removal (Fig. 3B).

In specimens where the original orientation of the specimen has been lost the GPE orientation may be determined from prominent directional wrinkling of the smooth bony plate surfaces. This marks the intersection of the axial plane cleavage with the bedding plane (Figs 1A, 4A, 5A-D, 11A, 14A), and its orientation can be estimated to within a few degrees.

Where such surface wrinkling is not well developed, the GPE can be identified using standard techniques used by structural geologists for determining first generation cleavage and incipient cleavage in clastic rocks of low to very low metamorphic grade (Durney and Kisch, 1994). Dr David Durney, Macquarie University, visited Merriganowry with the writer to advise on their use in determining the GPE of *Cowralepis* specimens.

Using graphical methods described by Ramsay and Huber (1983, fig. 8.5, Breddin curve) and Cooper (1990, fig. 5, Wellman's method - deformed right angles) the degree of shear strain at Merriganowry was estimated. It was then tested on several examples in which two *Cowralepis* specimens were recovered lying close together on the same bedding plane but in different orientations. The availability of modern computers and digital image processing programmes makes this process much easier. After trial and error, the approximate degree of correction required to bring both specimens back to symmetry, and to the same proportions, was determined and this has since been applied to many single *Cowralepis* specimens (Figs 6A-D, 9E, F, 10G, H, 11A, B).

When the GPE had been determined, a digital image of the fossil (or cast) was rotated until the GPE was horizontal. Using Adobe Photoshop the image was then reduced by 10% in the direction of GPE and increased by 10% in the direction of SPE. Reducing the GPE and increasing the SPE by the same amount produces a corrected image with approximately the same surface area as the deformed original (Figs 9F, 10H, 11B; strain directions indicated by arrows with percent correction indicated).

How many species?

The remarkable range of morphological variation in phyllolepids from Merriganowry raises the question – how many species are present at this site? If the specimens illustrated here (cf. Figs. 2, 5) had been recovered from several different sites, how many 'species' or even 'genera' of phyllolepid might have been erected?

Many factors are involved: the presence of unique characters and morphological variation (breadth/length and angular measurements); variation in ornament; extent and direction of sensory canal grooves; differential changes during growth (allometry); differential changes through time (heterochrony); differences in preservation (selective diagenesis); sexual dimorphism; sample size, and whether the sample comes from one horizon or from different levels ; and, where relevant, tectonic deformation.

This is illustrated by the problems encountered in interpreting phyllolepid material from three widely separated Devonian sites in southeastern Australia – Mount Howitt, Victoria (Long 1984), Nettleton's Creek, New South Wales (Ritchie 1984) and Merriganowry, New South Wales (this paper).

The Mount Howitt fauna, excavated by Monash University teams in the 1960's and 70's, comprises a diverse assemblage of late Middle Devonian fishes (placoderms, acanthodians, sarcopterygians, actinopterygians) represented by hundreds of articulated specimens in all stages of growth. These include a small number of placoderm specimens described by Long (1984) as a new genus of phyllolepid, *Austrophyllepis,* represented by two species, *A. ritchiei* and *A. youngi.* (1984, figs 8 and 13 respectively)

Long (1984, 274) differentiated *A. ritchiei* (fig. 7) from *A. youngi* (fig 13) "..only by the proportions of the dermal armour (figs 8, 25), specifically the preorbital, paranuchal, nuchal, median dorsal, anterior and posterior ventrolateral plates. Although the ornament appears to be more finely developed in *A. youngi* relative to *A. ritchiei* it is not a distinguishing feature for the species as a whole." *A. ritchiei* was shorter and wider and *A. youngi* was longer and narrower, but otherwise there was very little to separate them.

Long (1984, fig. 8) also analysed proportional differences in the breadth/length index of the nuchal and median dorsal plates of *Austrophyllolepis,* based on a small sample of 23 specimens. These appeared to fall into two distinct clusters for each plate, with no overlap, and were interpreted as support for two species of *Austrophyllolepis* at Mt Howitt.

The writer suspected this interpretation might be incorrect after examining several specimens of *Austrophyllolepis* from Mt Howitt in the Australian Museum collection (not included in Long's sample), some of which, when measured, fell between the ranges shown for *A. ritchiei* and *A. youngi.* Casts of the figured specimens of *A. ritchiei* (Long 1984, figs 3, 4) and *A. youngi* (1984 fig. 9) showed the same signs of deformation as those seen in phyllolepids from Merriganowy (asymmetry, surface wrinkling aligned in the direction of GPE) indicating that the Mt Howitt phyllolepids had also experienced tectonic deformation.

The computer image correction techniques used on Merriganowry phyllolepids were applied to the Mt Howitt specimens with similar results. The *Austrophyllolepis ritchiei* specimens became longer, narrower and symmetrical and the *A. youngi* specimens became shorter, broader and symmetrical.

Long later admitted (1999, 36) ".. that there may only be one species present, as deformation of the strata can account for the distortion of plate measurements that separate the two originally named species." The hypothesis that only one species of *Austrophyllolepis* is present at Mt Howitt can be readily tested by the recovery and analysis of additional *Austrophyllolepis* material from the Mount Howitt site, which is still accessible, and checking whether the deformation present in the fossils is directly related to regional tectonism.

A similar wide range in length/breadth proportions was also observed in the head and trunk plates of another phyllolepid, *Placolepis budawangensis* Ritchie (1984), from Nettleton's Creek, NSW described at the same time as *Austrophyllolepis*. This was especially noticeable in the nuchal plates (1984, figs 4, 5). Several ventral trunk shield plates, found closely associated on the same bedding plane (but lying in different orientations), probably came from one individual. They displayed similar ornament but differed markedly in shape and proportions (1984, fig.

11). This was attributed to post-mortem deformation caused by regional tectonism. All of the material came from one small excavation about two metres square in a creek bank, and from the same siltstone unit. The writer concluded that only one species of *Placolepis* was represented in the Nettleton's Creek fauna.

The same applied to the associated material of *Bothriolepis longi* Johanson and Young (1999, figs 3, 5, 6). The presence of long/narrow and short/broad variants of *Bothriolepis* initially raised the possibility of two species being present (1999, 66) but this was dismissed. The morphological deformation at Nettleton's Creek is largely the result of regional tectonism.

In the analysis of tectonically deformed material, standard length/breadth ratios and angle measurements are of limited value. The writer applied the same length/breadth index method used by Long (1984, fig. 8) to *Cowralepis*, but based on a much larger sample - 143 nuchal plates and 124 median dorsal plates. The length/breadth distribution of both samples (not shown here) were similarly very widely scattered but not meaningfully clustered. It is clear that such graphs cannot be used to demonstrate the presence of one or more species in a fauna, especially where the specimens come from different layers and where tectonic deformation is involved, as at Merriganowry, Mount Howitt and Nettleton's Creek.

The articulated phyllolepid specimens from Merriganowry, covering a wide size range, made possible another approach. Unlike length/breadth ratios, plate ratios along the same axis are not altered by distortion, so the most useful plates for analysis are the large median plates in the head and trunk shield, the nuchal and median dorsal plates.

Eighty specimens (including many of the figured specimens) were selected in which both the nuchal and median dorsal plates remained in close association and lay in the same orientation. The length of each Nu and MD was measured separately along the midline and combined to provide data for the horizontal axis; the vertical axis illustrates the relative lengths of the nuchal and median dorsal plates (Fig. 3A.)

The eighty specimen points (Fig. 3A) are widely scattered, with little obvious clustering (other than an abundance of smaller individuals), and are of little use in determining whether one or more species of phyllolepid are present at Merriganowry. What they do appear to illustrate is a dramatic allometric change in the relative lengths of the *Cowralepis* head and trunk shields during ontogeny. This is discussed more fully in the description of the dermal skeleton.

Based on the material available for study, only one genus of phyllolepid placoderm appears to be present at Merriganowry. *Cowralepis* gen. nov. displays a combination of characters not found in other phyllolepid genera. These include: head shield longer than trunk shield; only one pair of sensory canal grooves (central sensory line) crosses from circumnuchal plates onto the Nu plate; lateral line canal groove passes off PNu onto Mg plate between 78-92% of PNu length (intermediate between *Placolepis* and *Austrophyllolepis*); a fenestra is present between the PtO, Mg and PNu plates and the Nu plates (most noticeably in juvenile specimens); a small posterior dorsolateral plate is present under the lateral margins of the median dorsal plate.

The phyllolepid specimens from Merriganowry cover a wide size range and display a remarkable degree of morphological variation; they also come from many different levels within the Merriganowry Shale Member and thus represent a large and mixed sample covering a wide time span. Most importantly, every phyllolepid specimen from Merriganowry has been deformed, limiting the use of standard proportional length/breadth ratios for taxonomic determination.

While it is certainly possible that the material recovered from Merriganowry may well include more than one species of *Cowralepis,* it is **not** possible to confirm or refute this at present.

The course proposed here is to designate a single species, *Cowralepis mclachlani* sp. nov. to establish the new taxon in the realisation that it may include material from more than one species. It will take many more years of excavation, including the use of heavy equipment, to sample throughout the whole shale section at Merriganowry before the question of how many species are present can be tested. Twelve years of digging using many hundreds of volunteers has barely made a dent in the Merriganowry quarry, but this unique site has the potential for a long-term systematic research program, with educational and eco-tourism benefits as a bonus.

Abbreviations.

ADL, anterior dorsolateral plate; **AL**, anterior lateral plate; **AMV**, anterior median ventral plate; **ant ridge**, inner anterior ridge on AVL plate; **Art**, articular; **AVL**, anterior ventrolateral plate; **Bhy**, basihyal; **buttr AL**, buttress on inner surface of ADL plate, below AL plate; **Chy**, ceratohyal; **csl**, central sensory line; **d.end**, ductus endolymphaticus; **d.pr**, dorsal process; **d.sp**, dorsal spine; **f.bhy**, buccohypophysial foramen on parasphenoid; **fen** fenestra; **GPE**, direction of Greatest Principal Extension; **h.arch**, haemal arch; **h.sp.**, haemal spine; **Ign**, inferognathal;

IL, interolateral plate; **ioc**, infraorbital canal groove; **l.ind**, lateral indentation in parasphenoid; **llc**, main lateral line sensory canal groove; **MD**, median dorsal plate; **Mg**, marginal plate; **mp.PNu**, mesial process on paranuchal plate; **n.arch**, neural arch; **n.can.**, neural canal; **not.**, notochord; **Nu**, nuchal plate; **oa.AVL**, overlap area for AVL plate; **oa.Nu**, overlap area for nuchal plate; **Occ oss**, occipital ossification; **Ot**, otolith; **p.pao**, paraotic plate; **PDL**, posterior dorsolateral plate; **pect**, pectoral embayment (margin) of AVL plate; **pel.b**, basal plate of pelvic fin; **pel.d**, distal element of pelvic fin; **PMg**, posterior marginal plate; **PMV**, posterior median ventral plate; **PN**, postnasal plate; **pnpr**, postnuchal process of paranuchal plate; **PNu**, paranuchal plate; **ppl**, posterior pitline; **PrO**, preorbital plate; **Psp**, parasphenoid; **PtO**, postorbital plate; **Sgn ant**, anterior superognathal; **Sgn post**, posterior superognathal; **SMg**, submarginal; **soc**, supraorbital canal groove; **Sp**, spinal plate; **SPE**, direction of Shortest Principal Extension; **sub-h.sp.**, sub-haemal spine; **Syn**, synarcual; **vpl**, ventral pitline; **zyg.**, zygopophosis.

SYSTEMATIC PALAEONTOLOGY

Class PLACODERMI McCoy, 1848
Order PHYLLOLEPIDA Stensiö, 1934

Diagnosis

Placoderms with greatly enlarged nuchal plate, slightly wider than long, surrounded by five pairs of smaller bones – paranuchals, marginals, postorbitals, post nasals and preorbitals. Paranuchal plate with well-developed postnuchal process. Rostral, pineal and central plates absent from skull roof. Anterior and posterior superognathals; anterior superognathal large and wide, posterior superognathal very small; inferognathal long, narrow anteriorly, wider posteriorly. Trunk armour broad and dorsoventrally flattened; median dorsal plate lacks an inner keel; anterior dorsolateral plate with long, narrow exposed area; posterior dorsolateral plate reduced or absent; anterior lateral plate small, rhomboid; posterior lateral plate absent. Anterior ventrolateral plate short and broad, with ossification centre near posteromesial corner; posterior ventrolateral plate triangular, with ossification centre near anteromesial corner; both plates relatively flat with straight, non-overlapping mesial suture. Interolateral plate long, narrow, with denticulate postbranchial lamina; anterior median ventral plate short, broad, separating interolaterals; posterior median ventral plate(s) small, narrow, variable in number (0-2). Dermal ornament consists of smooth, slightly undulating, subconcentric ridges, locally of rows of tubercles. Pelvic fins small; dorsal fin absent; caudal fin large, epicercal.

COWRALEPIS MCLACHLANI
new genus and species
Figs 1-20

'a new genus and species of phyllolepid': Krynen, 1998, 225.
'a new phyllolepid': Young, 1999, 144.

Name

The **genus** is named after Cowra (Aboriginal for 'place of the rocks'), the nearest town in central west New South Wales; and *lepis* (Gk), ' scale'.

The **species** name acknowledges the contribution of Mr Alex McLachlan, owner of 'Mooroonbin', near Cowra, NSW (which includes Merriganowry), in enclosing the quarry site and making it available to the Australian Museum for scientific investigation; also after the Lachlan River near where the first discoveries were made. Only one species, *Cowralepis mclachlani* sp. nov. is recognized at present from the Merriganowry site.

Repository

All of the described, figured and mentioned specimens in this paper are lodged in the palaeontology collections of the Australian Museum, Sydney, as indicated by the prefix **AMF.**

Holotype

AMF103767a, b, medium sized individual complete with tail, seen in dorsal and ventral view (Fig. 1A-D)

Figured material

AMF90003a (Fig. 4A, 6A); AMF90004 (Fig. 16C); AMF90007b (Figs 12A, 14A); AMF90011a, b (Figs 18E, F; Fig. 19); AMF90012 (Fig. 7H): AMF90018 (Fig. 5D); AMF90027 (Fig. 2C); AMF90029a (Fig. 7G); AMF90034a, b (Fig. 2D); AMF90044b (Fig. 2I); AMF90048a (Fig. 17A, B); AMF90048b (Figs 17C, D); AMF90051 (Fig. 5C); AMF90053 (Fig. 2B); AMF90054a, b (Fig. 7D, E); AMF96747a (Fig. 2G); AMF96750 (Fig. 2E); AMF96751a (Fig. 13A); AMF96755a, b (Fig. 13C); AMF96762 (Figs 4B, 6B, 7C); AMF96764 (Fig. 16A); AMF96765 (Fig. 16B); AMF96779 (Figs 7A, B, 10E, 12E); AMF96780 (Fig. 10F); AMF96781 (Fig. 9A, B); AMF96783 (Figs 9E-G, 12F); AMF96784 (Fig. 7F); AMF96785 (Fig. 13D, E); AMF96786 (Fig. 10G, H); AMF100018 (Fig. 5D); AMF103753a, b (Figs 5A, B, 6C, D); AMF103754 (Fig. 7I); AMF103755 (Fig. 10A); AMF103756 (Fig. 2A); AMF103763 (Fig. 13B); AMF103768 (Fig. 9D); AMF103770 (Fig. 8C, D); AMF103776 (Fig. 14B); AMF103778a (Fig. 2J); AMF103784 (Fig. 2H); AMF103787 (Fig. 10D); AMF104154b (Figs 8A, B, 9C); AMF104155 (Fig. 10C); AMF104157a (Fig. 2F); AMF104160 (Fig. 8F); AMF104164 (Fig. 10B); AMF127151a (Fig. 18D); AMF127152 (Fig. 8E); AMF127154b (Fig. 18B); AMF127156 (Figs 11A, B, 12B-D); AMF127159 (Fig. 18A); AMF127162 (Fig. 8G).

Locality

All of the figured material comes from a small quarry, the type locality (and only known exposure) of the Merriganowry Shale Member. The quarry (GR642750 6373750) is on a small rise on the east side of the Cowra to Forbes road on Mooroonbin property, 1.5 km northwest of Merriganowry homestead and 20 km northwest of Cowra, New South Wales.

Diagnosis

Moderately large phyllolepid, reaching ca. 35 cm in length. Widest part of nuchal plate lies just posterior to centre of ossification; anterior nuchal margin more angular than in *Placolepis*, less angular than in *Austrophyllolepis* and *Phyllolepis*. Nuchal plate same length as or longer than median dorsal plate in juveniles; nuchal plate 20-60% longer than median dorsal plate in adults. Supraorbital canal, infraorbital canal and pit-line grooves not developed on nuchal plate. Lateral line canal groove on paranuchal plate diverges anteriorly from nuchal margin and canal groove crosses anterolateral margin between 78-92% PNu length. Marginal plate separates postorbital and paranuchal plates. Marginal plate and posterior division of postorbital plate lack contact with the nuchal plate in juveniles, leaving fenestra between them; marginal plate and posterior division of postorbital plate meet lateral margin of nuchal in adults, fenestra reduced. Posterior dorsolateral plate present; small, subtriangular, hidden under lateral margin of median dorsal plate; posterior lateral plate absent. Anterior and posterior median ventral plates both present. Occipital region of endocranium ossified; vertebral column fused anteriorly, forming long narrow synarcual under median dorsal plate.

Remarks

In addition to *Cowralepis* gen. nov. described here, there are now five other named genera of phyllolepids - *Phyllolepis*, *Austrophyllolepis*, *Placolepis*, plus two new genera recently described by Young (in press) from the Middle Late Devonian of the Pambula area, southeastern New South Wales. The later are known only from a handful of dissociated, and mostly incomplete, head and trunk plates.

Cowralepis differs from all of these in that the head shield is longer than the trunk shield; it is also the only phyllolepid known in which a fenestra is developed between the nuchal (Nu) and lateral cranial plates (PtO, Mg, PNu). *Cowralepis* differs from *Phyllolepis*, *Austrophyllolepis* and *Placolepis* in the presence of a posterior dorsolateral plate (PDL) in the trunk shield; a feature it apparently shares with the two new genera from near Pambula, NSW (Young, in press) discussed beow.

DESCRIPTION

The three main developmental divisions of the skull and skeleton in vertebrates are

a) dermal skeleton - includes the skull roof, cheek and operculum, denticulated or tooth-bearing bones of the palate and inside and outside of the lower jaw, and small dental plates of the buccal cavity and inside visceral arches.
b) endocranium.
c) visceral skeleton - Meckel's cartilage plus palatoquadrate, forming the core of the upper and lower jaws, plus branchial arches.

Dermal skeleton

The **head shield** of phyllolepids consisted of a very large nuchal plate (Nu) bordered anteriorly and laterally by five pairs of smaller plates, interpreted here as the preorbitals (PrO), postnasals (PN), postorbitals (PtO), marginals (Mg) and paranuchals (PNu), the last of which articulate with the trunk shield. Another pair of small plates, the submarginals (SMg) flanked the Mg plates laterally, but were only loosely associated with them.

Nuchal

In *Cowralepis* the Nu was slightly wider than long and sub-polygonal in shape (Fig. 6A, C, 15A) with the greatest width posterior to the centre of ossification. In this it is closest to *Placolepis* and differs from *Phyllolepis* and *Austrophyllolepis*, in which the Nu is always widest anterior to the centre of ossification (Fig. 20B). The anterior margin of the Nu was more angular than in *Placolepis* and less angular than in *Phyllolepis* and *Austrophyllolepis*.

Cowralepis differs most noticeably from

Placolepis, *Austrophyllolepis* and *Phyllolepis* in the relative lengths of its nuchal and median dorsal plates. In the other three genera the Nu plate is always shorter than the MD. In all but a few *Cowralepis* specimens it is the Nu that is longer, sometimes much longer, than the MD. Eighty *Cowralepis* specimens were selected in which the dorsal shield was well preserved and the Nu and MD plates were closely associated and lying in line. Unlike length/breadth measurements, the relative lengths of such plates should be unaffected by the tectonic deformation.

The results, illustrated graphically in Fig. 3A, show the relative length of the Nu and MD plates in a wide range of growth stages of *Cowralepis* and appear to indicate a dramatic increase in length of the head shield relative to the trunk shield during ontogeny.

Length Nu+MD	**sample number**	**Nu/MD x 100**
30 – 50 mm	20 individuals	av. 110.7%
50 – 70 mm	33 individuals	av. 107.8%
70 – 90 mm	10 individuals	av. 108.8%
90 – 110 mm	11 individuals	av. 123.2
110 – 130 mm	2 individuals	av. 113.5%
130 – 150 mm	2 individuals	av. 134.0%
150 – 170 mm	2 individuals	av. 139.0%

In only a few specimens of *Cowralepis* was the Nu plate slightly shorter than the MD. In sixty- three individuals with a combined Nu + MD length between 30 mm and 90 mm, the Nu plate was on average 8-10% longer than the MD. The main increase in the relative length of the head shield appears to have taken place from 90 mm (Nu + MD) upwards, with many specimens known in which the Nu plate is 20-40% longer than the MD.

In the holotype, AMF103767 (Figs 1A, 3A), the Nu is 32% longer than the MD; in AMF90003A (Figs 4A, 6A) the Nu is 39% longer. The most spectacular example is also the largest known specimen of *Cowralepis*, AMF103754a (Fig. 7I) in which the Nu plate is 60% longer than the MD.

These results indicate that, in at least one phyllolepid, *Cowralepis,* the head shield grew relatively larger than the trunk shield during later stages of growth and the head shield/trunk shield length index was not fixed but varied with age.

Cowralepis differs from all other phyllolepid genera in that only one pair of sensory canal grooves cross onto the Nu plate from the surrounding circum-nuchal plates; this is the central sensory line (Figs 2, 5A, C, 15A; csl) which is also visible on the ventral surface of the Nu (Figs 4B, 9A, 11). In contrast, three pairs of sensory canal grooves cross onto the Nu plate in *Austrophyllolepis* and four pairs in *Placolepis* and *Phyllolepis* (Fig. 20B), as discussed below.

Circum-nuchal plates

The two anterior pairs of plates on the head shield were interpreted differently in *Placolepis* Ritchie (1984, fig. 2) and *Austrophyllolepis* Long (1984, 264, fig. 1). The writer followed Denison (1978, fig. 29) in identifying the median pair as the postnasal plates (PN) flanked by preorbital plates (PrO) plates; Long interpreted the median pair as the PrO plates flanked by the PN plates. The general consensus now is that the latter version is preferred, with the qualification that some uncertainty remains about the homology of the plates identified as the postnasals (Fig. 15A).

Preorbital plate

The PrO plates that form most of the anterior margin of the head shield are subrectangular, wider than long, and meet mesially in a sinuous suture. They are subdivided longitudinally by the supraorbital sensory canal groove (Fig. 15, soc) into a smaller mesial portion and a larger lateral division. The anterior margin of the head shield in *Cowralepis* (Figs 1, 2, 4-6, 13A, 14B) is straighter than in *Placolepis* and *Austrophyllolepis* and was not indented medially as in *Phyllolepis* (Fig. 20B).

In *Cowralepis* the suborbital canal (soc) terminates at the posterior margin of the PrO plate and does not cross onto the nuchal plate as in *Placolepis, Austrophyllolepis*, and *Phyllolepis,* in all of which the soc crosses onto the Nu plate, maintains the same course and converges towards the centre of ossification of the Nu (Fig. 20B).

An unusually preserved specimen of *Cowralepis* (Fig. 14B, soc) reveals why the supraorbital canal grooves appear to terminate suddenly at the posterior dermal margin of the PrO plates. In this specimen, seen in dorsal view, the circum-nuchal plates are in place but the nuchal plate has been lost, exposing the normally hidden overlap areas of the PrO and PN plates. The supraorbital canal grooves on the left and right PrO plates converge posteriorly towards the posterior overlap area where they turn sharply towards the midline. Just before reaching the midline they again turn sharply posteriorly to resume their original course, but would have been hidden under the anterior margin of the Nu plate.

Postnasal plate

The postnasal plates flank the PrO plates laterally to form the anterolateral corners of the head shield. The PN plates are relatively larger in *Cowralepis* than in *Placolepis, Austrophyllolepis* and *Phyllolepis* (Fig. 20B). The V-shaped canal groove on the PN plate is interpreted as a loop of the infraorbital canal (Fig. 15A, ioc). It is also visible as a prominent ridge on the visceral surface of the plate (Figs 1B, 4B, 5B, 9A, E, 10B, C, 11, 13A). In *Cowralepis* and *Austrophyllolepis* the infraorbital canal does not cross onto the nuchal plate, unlike in *Placolepis* and *Phyllolepis* (Fig. 20B).

Postorbital plate

The postorbital plate is relatively larger in *Cowralepis* than in *Placolepis, Austrophyllolepis* and *Phyllolepis*, especially its posterior division. The infraorbital sensory canal groove (Figs 15A, 20B, ioc) continues over the PtO onto the nuchal plate as the central sensory line (csl), as in the other three genera. In small to medium-sized specimens of *Cowralepis* the posterior division of the PtO is separated from the Nu plates by a crescentic fenestra (Fig. 2G, fen). In larger specimens (Figs 1A, 5A, 6A, 11, 15A, B) the posterior division of the PtO contacts the Nu margin along its full length (cf. below).

Marginal plate

The Mg plate in *Cowralepis* is a small, subtriangular plate, longer than wide, tapering posteriorly and with a transverse anterior margin. It was closer in shape to the Mg plate of *Austrophyllolepis* than that of *Placolepis* (Long 1984, fig. 2B). The Mg is often partly obscured by the plates around it (Figs 1A, 2, 5A, B, 6A, B) and its shape is most clearly seen in ventral views of the head shield (Figs 4B, 6B, 14A) or in specimens that are dissociated (Fig. 7F). A small projection on the mesial margin of the Mg fitted into a notch in the PNu plate where the lateral line canal groove crossed over (Fig. 7F).

The Mg separated, and was overlapped anteriorly and posteriorly by, the PtO and PNu plates (as in *Placolepis*). In smaller *Cowralepis* specimens (Fig. 2), the mesial margin of the Mg plate fell far short of the Nu margin, leaving a fenestra (shared with the PtO) between them. In larger individuals, the Mg plate enlarged mesially until it just met the nuchal margin, although it is not clear if an overlap relationship had developed between them.

In *Cowralepis*, the relationship between the Mg plate and the plates surrounding it (PNu, PtO and Nu) changes during growth and appears to represent a morphological condition intermediate between *Placolepis* and *Austrophyllolepis*, as discussed below.

Paranuchal plate

The posterolateral corner of the head shield in phyllolepids was formed by a rather large paranuchal plate with a long, broad lateral division and a narrow, tapering, postnuchal process (pnpr) that extended mesially almost to the midline (Figs 1, 2, 3A, C, 6A, 15A, B). The shape and overlap areas of the PNu in *Cowralepis* are best seen in isolated examples (Fig. 7F, G) or where the nuchal plate has been dislodged (Fig. 14B).

The lateral division of the PNu was traversed by a long curving groove that housed the lateral line sensory canal (llc) and crossed the Mg/PNu boundary at different levels in different phyllolepid taxa. This character, used by Long (1984, fig. 2A, 266) to differentiate *Austrophyllolepis* from *Placolepis* and *Phyllolepis,* is one of the most useful characters in separating and diagnosing phyllolepid taxa.

The length of the PNu, measured from its posterior margin to where the lateral line intersects its lateral margin, is expressed as a percentage of the total PNu length (cf. Young in press b, fig. 2A). Because both of these dimensions lie in the same direction their ratios are not altered by tectonic deformation, unlike breadth/length ratios.

In *Austrophyllolepis* the lateral line canal crossed the lateral margin of the PNu at around 68-72% of total PNu length. It is thus intermediate between *Phyllolepis orvini* Heintz (1930) from Greenland (Stensiö 1934, pl. 5, figs 1, 2) in which the lateral canal crossed at 48-56% PNu length and *Placolepis* (Ritchie 1984, fig.6A-C) where the canal crossed onto the Mg at the apex of the PNu, effectively 100%. In a new genus from southeastern NSW described by Young (in press b, figs 3A, C, 4A) the PNu llc index is 71%, placing it within the *Austrophyllolepis* range.

The same analysis was applied to the Merriganowry phyllolepid material. Thirty-six examples of *Cowralepis* PNu plates were measured, many of them representing left and right PNu plates from the same individual. In *Cowralepis* the lateral line groove crossed the PNu margin at between 78.5% and 92% of the PNu length, with an average of 86%. This range therefore falls intermediate between that of *Placolepis* and *Austrophyllolepis* but does not overlap with either of them.

The lateral line canal groove on the PNu plate of all phyllolepids turns sharply mesially towards the posterolateral corner of the nuchal plate. In *Placolepis*, *Austrophyllolepis* and *Phyllolepis* it continues onto the nuchal surface for a short distance as the posterior pit-line (ppl), but no trace of a pit-line has been detected in *Cowralepis.*

The mesial margin of the PNu plate (Fig. 7F, G) is formed by a well-developed overlap area for the nuchal plate (oa.Nu) and carries a short blunt process that lay under the posterolateral corner of the nuchal plate. On the posterior margin of this process lies a deep groove directed anteromesially. It is suggested here that this groove (Fig. 7F, G, d.end) may have housed the endolymphatic duct that in most placoderms reached the surface via a small foramen on either the nuchal or paranuchal plate. In *Cowralepis* there is no visible surface opening on either plate but it is possible that the endolymphatic duct may have opened on the margin between the plates.

Gavin Young (pers.comm.) has recently described a new phyllolepid from the south coast of New South Wales in which the paranuchal plate bears a strongly developed mesial process on the inner margin of the PNu (Young in press b, figs 3A-C, 4A, B, mp.PNu) that would have projected under the corner of the nuchal plate. This mesial process is clearly comparable to, but much larger than, the small blunt process seen in *Cowralepis* paranuchal plates (Fig. 7F, G, mp.PNu).

Interrelationships of nuchal, paranuchal, postorbital and marginal plates.

The Nu, PNu, PtO and Mg plates in *Cowralepis* illustrate a condition morphologically intermediate between that in *Placolepis* and *Austrophyllolepis* (Figs 15A, 20B). They also document a remarkable change in the relationships of these plates throughout ontogeny.

Placolepis and *Phyllolepis* (Fig. 20B) illustrate the extremes of the range in the known phyllolepid genera. *Placolepis* differed significantly from *Phyllolepis* in the size and shape of its PNu plate (much shorter than in *Phyllolepis*) and in the relationships of the PNu with the Mg, PtO and Nu plates.

In *Placolepis* (Ritchie 1984, fig. 8E) the lateral line canal groove closely followed the PNu/Nu margin to the anterior corner of the PNu where it crossed over the Mg onto the PtO. The Mg plate in *Placolepis* thus separated the PNu and PtO plates and was overlapped mesially by the lateral margin of the Nu.

In *Phyllolepis* (Ritchie 1984, fig.8F) the lateral line canal groove on the PNu plate crossed from the much smaller Mg plate attached about midway along the PNu lateral margin. A large triangular anterior extension of the PNu (mesial to the lateral line canal) separated both the marginal plate and posterior part of the postorbital plate from any contact with the nuchal.

Austrophyllolepis (Long 1984, figs 2, 7, 10, 13, 19B) displayed a condition intermediate between that of *Placolepis* and *Phyllolepis*. The Mg plate was similar in size and shape to that of *Phyllolepis* but was attached more anteriorly to the PNu margin than in *Phyllolepis*. *Austrophyllolepis* also resembles *Phyllolepis*, but differs from *Placolepis*, in its large anterior extension of the PNu (1984, fig. 2A), which separated the Mg and Nu plates and contacted the posterior mesial margin of the PtO (Long 1984, figs 2B, 19B).

The new evidence from *Cowralepis* complements that of *Placolepis*, *Austrophyllolepis* and *Phyllolepis*. *Cowralepis* resembled *Placolepis* in that the Mg plate separated the PtO and PNu plates, and the anterior division of the PNu did not contact the PtO. *Cowralepis* resembled *Austrophyllolepis* and *Phyllolepis* in that neither the Mg plate nor the posterior margin of the PtO plate contact the lateral margin of the Nu (leaving a fenestra between them) – but only in juveniles and smaller individuals (Fig. 2). In adult *Cowralepis* specimens the PtO meets the Nu along its full length while the Mg barely contacts the Nu, or just falls short, but it always separates the Pto and PNu plates (Fig. 15).

The distinctive shape of the nuchal plate in *Phyllolepis* appears to be the derived condition in phyllolepids, compared to that in *Placolepis*. It could have arisen by either:

a) <u>a posterior migration of the lateral line canal groove on the PNu plate</u> - since the angle of the lateral canal on the PNu does not appear to have changed significantly in the different phyllolepid genera, nor have its relationships to the marginal and postorbital plates (Long 1984, fig. 2A; this paper Figs 15, 20B).

b) OR, the alternative, preferred here, <u>progressive enlargement of the anterior division of the PNu plate, mesial to the lateral line, first separating the Mg plate and, later, the posterior part of the PtO, from the Nu</u> - i.e. that the distinctive, parallel-sided shape of the nuchal plate in later phyllolepids (*Phyllolepis*) is largely the result of differential anterior enlargement of the paranuchal plate mesial to the lateral line canal groove (Fig. 20B).

OR by a combination of both processes

Submarginal plate

One more dermal bone in the cheek area remains to be accounted for. Long described a small unornamented bone lying lateral to the marginal plate in *Austrophyllolepis*. It was only seen in two specimens, leaving its nature and identification uncertain. It lacked a laterosensory groove, appeared to be loosely attached to the cheek and was identified as the postmarginal plate (Long 1984, 284, fig.19B, C; PMg).

A similar, but much larger, plate is present in most of the articulated specimens of *Cowralepis* (Figs 1A,

2B, C, E-G, I, J, 4A, B, 5D, 6A, B, 7F, 14A, B, 19). Its size, shape and relationship to the Mg are best seen in AMF96784 (Fig. 7F). The plate was long, narrow and slightly curved, with a shallow convex dermal surface. A low ridge crossed its dermal surface obliquely from the posteromesial corner to the anterolateral corner. It lay against the lateral margin of the Mg, but was only loosely attached to it and easily dislodged. From its position lateral to the Mg this plate appears to have formed part of a moveable cheek or gill cover and must therefore be the submarginal plate (SMg), not the postmarginal.

A submarginal plate is present in many placoderms, loosely attached in the cheek area and usually closely associated with the hyomandibula (Janvier 1996 fig. 4.42.14). The long, narrow submarginal of the dorsoventrally flattened *Cowralepis* resembles that found in deep-bodied ptyctodonts such as *Ctenurella* (Moy-Thomas and Miles 1971, fig. 8.13; Miles and Young 1977, figs 15, 19; Long 1997, figs 25, 28, 29) and *Campbellodus* and *Austroptyctodus*, both from Gogo, W.A. (Long 1997, figs 5, 6 and 28, 29, 35 respectively) and there can be little doubt that they are homologous.

Trunk shield

The dorsal and ventral trunk armour of *Cowralepis* (Fig. 15A-C) is basically similar to that of other phyllolepid genera, with a few differences detailed below. The wide variation in length/breadth proportions of the trunk plates in *Cowralepis* (most of which can be attributed to regional tectonism) precludes the use of such measurements for diagnosis. The trunk (and cranial) plates of *Cowralepis* also display a wide variety of dermal ornament, ranging from almost smooth surfaces to dense subconcentric ridges, but whether this variation is inter-specific or intra-specific remains to be determined.

Dorsal trunk shield

The dorsal trunk shield of *Cowralepis* (Figs 1A, 2, 4A, 5A, C, 6A, D, 15A, B) consisted of a large, subpentagonal median dorsal plate (MD) flanked laterally by an extremely narrow anterior dorsolateral plate (ADL) carrying the lateral line canal groove. A broad anterior flange on the ADL fitted under the posterior margin of the PNu plate on the head shield. Supported laterally by a similar flange, the postbranchial lamina, on the adjacent anterior lateral plate (AL), this provided phyllolepids with a sliding neck joint like that present in actinolepids and wuttagoonaspids. The spinal plate (Sp), linking the dorsal and ventral shields laterally, was relatively small, with a short posterior spine.

The dermal surface of the **anterior dorsolateral plate** (ADL) was long and very narrow and often obscured by the adjacent AL and MD plates (Figs 1A, 5A, C). Much more informative are specimens of the ADL seen in ventral view and showing its full shape, including the extensive mesial and lateral overlap areas that contacted the ventral margins of the MD and AL plates respectively (Figs 7A, B, 13A, D, 15B).

In AMF96779 (Fig. 7A, B) numerous cranial and trunk plates from one individual had become dissociated before burial. They included ventral views of the left (Fig. 7A) and right (Fig. 7B) ADL plates; an otolith from the same individual is figured elsewhere (Fig. 12E). A strongly developed, smoothly rounded ridge (ant ridge) extends the full length of the ventral anterior margin of each ADL plate and presumably supported the anterior flange on the ADL that fitted under the PNu plate in the head shield to form the sliding neck joint.

The inner surface of both ADL plates display an unusual feature not previously recorded in phyllolepids. The course of the lateral line canal is visible as a narrow ridge (llc) on the inner surface, running the length of the plate. Where this meets the anterior margin another, more strongly developed, ridge emerges from the margin ventral to the lateral line canal ridge.

The second ridge diverges posteriorly from the lateral line canal at 20-25°, becomes broader distally and bifurcates near the rear margin. Along most of its length this inner ridge on the ADL plate would have underlain the AL plate, acting as a strengthening buttress (buttr AL) for the latter. The same features are also visible in two figured specimens of *Cowralepis* in which the ADL plate is preserved *in situ* (Fig. 13A, D).

No trace of either **posterior dorsolateral** (PDL) or **posterior lateral** (PL) plates has been reported in the dorsal shields of *Phyllolepis*, *Austrophyllolepis* and *Placolepis*, raising the question whether this was a primary or a secondary condition. Both PDL and PL plates are present in a wide range of arthrodires; separate PL plates are also found in early antiarchs and PDL plates in palaeacanthaspids and petalichthyids. This suggests that PL and PDL plates were primitive components of the placoderm trunk shield.

The presence of a rather large PDL plate has been deduced in two new phyllolepid genera from Pambula, NSW, described by Young (in press b), although the PDL itself has not been recovered in either. In one taxon the median dorsal plate displays a short straight posterolateral margin between the lateral and posterolateral corners (Young, in press b, fig. 5A, B, lc, plc), interpreted as the attachment point for a PDL plate. In the second new taxon, the ventral posterolateral margin of the MD plate displays a long, narrow contact face for a PDL plate (figs 7B, H, 8B, cf. PDL). In both of these new genera the PDL plate probably extended well beyond the lateral margins of the MD.

Cowralepis provides another example of a phyllolepid retaining a PDL plate in its trunk armour and illustrates an interesting intermediate condition in the reduction and secondary loss of PDL plates from the trunk shield. PDL plates are preserved in many *Cowralepis* specimens at all stages of growth, including the holotype (Figs 1A, B, 4B, 5B, 6B, D, 16A, 19), but they are very unusual dermal plates in that they were not visible at the surface (Fig. 15A, B).

The explanation is simple: in *Cowralepis,* the PDL plate was reduced to a mere remnant tucked neatly under, and attached to, the lateral margin of the median dorsal and did not extend beyond it. This is best illustrated in AMF96762 (Figs 4B, 6B, 7C), seen in ventral view, where the right PDL is still in place but the left PDL had become detached and drifted sideways. This exposes a contact area for the PDL on the ventral side of the MD plate consisting of several shallow pits. The PDL was crescentic to sub-triangular, with a rounded and thickened lateral margin. The anterior extension of the PDL was still in contact with the posterior end of the ADL plate (Fig. 16A).

Ventral trunk shield

The ventral trunk shield (Figs 1B, 4B, 5B, D, 6B, D, 8F, 15C, 16A,B, 19) consisted mainly of a pair of large, wide, flat anterior ventrolateral (AVL) plates, bordered anteriorly by long, narrow interolateral (IL) plates, and posteriorly by a pair of smaller, subtriangular posterior ventrolateral (PVL) plates. Whether phyllolepids ever possessed, or have lost, paired anterior ventral (AV) plates, like those present in actinolepids, wuttagoonaspids and the Chinese petalichthyid *Eucaryaspis* (Liu 1991), remains unknown.

The **interolateral (IL)** plate was already known from *Phyllolepis orvini* (Stensiö 1936, fig. 21), *Phyllolepis woodwardi* Stensiö (1939, text-fig.2), *Austrophyllolepis* (Long 1984, figs 18, 20) and *Placolepis* (Ritchie 1984 fig. 11E-D). The IL in *Cowralepis mclachlani* is almost identical (Fig. 8 A-E), a long, narrow, slightly curved plate tapering mesially to a sharp point. The post-branchial lamina was strongly convex and ornamented with 9-10 parallel rows of very fine denticles (Fig. 8D).

Although an **anterior median ventral (AMV)** plate was reconstructed in *Phyllolepis orvini* (Stensiö 1969 figs 199A, B) the best evidence for an AMV in phyllolepids was provided by an articulated specimen of *Phyllolepis woodwardi* from Dura Den, Scotland (Stensiö 1934, text fig. 2D; 1936 text fig. 5; 1939 text fig. 2) in which a reasonably large, well-developed AMV is preserved *in situ,* flanked laterally by the interolateral plates (IL).

Long (1984) was unable to identify an AMV in the *Austrophyllolepis* material from Mt Howitt and omitted it from the reconstructions of *A. ritchiei* and *A. youngi* (1984, figs 7, 13). In several specimens of *Austrophyllolepis* (1984, figs 5, 6, 11D, 18C) the anteriomesial corners of the AVL are distinctly rounded and part of what may be a small AMV is visible in one specimen (fig. 18C). The writer also was unable to locate or identify an AMV plate in the dissociated material of *Placolepis* and omitted it from his reconstruction (Ritchie 1984, figs 2D, 8C), but again the anteromesial corners of the AVL plates are slightly rounded (figs 10J, K, 11F, G, 12A, B).

Cowralepis reveals that the apparent absence of an AMV plate in *Austrophyllolepis* and in *Placolepis* is most probably due to the vagaries of preservation rather than original absence. As noted above, well-developed and robust IL plates are present in several specimens of *Austrophyllolepis,* but all of them were slightly displaced. The AMV was a much smaller plate, easily dislodged and lost *post mortem.*

In many of the apparently complete, articulated specimens of *Cowralepis* from Merriganowry it is not uncommon to find both the AMV and IL plates missing. The explanation appears to be that, during burial and compaction of the wide but slightly convex, ventral trunk shield, the narrow, curved IL plates, which supported and presumably strengthened the anterior margin of the AVL plates, were displaced by flattening and swung forwards, especially in the midline, and were often lost. In the process, the associated AMV was also detached and, being much smaller, is easily overlooked.

Every stage of this process is illustrated by *Cowralepis.* Many specimens show the AMV and IL plates still *in situ* and in association (Figs 1B, 4B, 5B, D, 14A, 15C). In most of the specimens where the IL plates have sprung forward, the AMV is missing. Other specimens show the AMV almost in place but slightly detached (Figs 8A, B, E) and reveal its size, shape and overlap areas. The AMV was three times wider than long. Its anterior margin was slightly concave and the posterior margin was bluntly pointed medially, matching the rounded corners of the AVL plates against which it fitted. In AMF127152 (Fig. 8E) the AMV displays two pairs of overlap areas; laterally to accommodate the sharp pointed mesial ends of the IL plates and posteriorly for the anteromesial corners of the AVL plates.

Rounded anteromesial corners are well displayed in most AVL plates of *Austrophyllolepis* (Long 1984, figs 4-7, 11-13) and are also present in AVL plates of *Placolepis budawangensis* Ritchie (1984, figs 10-12). On the new evidence from *Cowralepis mclachlani*, the writer would now have no hesitation in restoring an AMV plate in *Placolepis* even though none has yet been found. On balance it is suggested that most, if not all, phyllolepids probably retained an AMV plate in their ventral trunk armour.

The first evidence for a **posterior median ventral plate (PMV)** came from a specimen of *Phyllolepis woodwardi* from Dura Den, Scotland (Stensiö 1939, text-fig. 2) in which "fragments of bone, not nearer determinable" were noted and labelled (*px*) in the mid-ventral line at the junction of the AVL and PVL plates. Long (1984, 267) suggested that these may be ". . fragments of the axial skeleton", exposed through a gap in the ventral trunk shield. He figured a rather large, narrow PMV plate in several specimens of *Austrophyllolepis* (1984, figs 7, 9B, 11D, 13, 18C) plus an example of ". . an abnormal development" in a juvenile specimen of *Austrophyllolepis* displaying two PMV plates (figs 4C, 6).

The *Cowralepis* material indicates that this condition may not, in fact, be so abnormal in phyllolepids. In the holotype of *Cowralepis mclachlani* (AMF103767B, Fig. 1B) and in several other specimens (AMF127162, Fig. 8G) a single slender PMV is visible. More commonly two PMV plates are clearly present, the anterior PMV being normally longer than the posterior one (Figs 5D, 16B). But other specimens from Merriganowry with apparently intact ventral shield show no trace of a PMV at the intersection of the AVL and PVL plates (Figs 4B, 6B, 8F).

The new evidence from *Cowralepis* suggests that the number of PMV plates in phyllolepids was not fixed but could vary within a genus and, possibly, even within a species, from none to at least two.

Sensory canals on the trunk shield

The lateral line system continued posteriorly from the head shield over the narrow ADL plate on the dorsal trunk shield. In *Placolepis, Austrophyllolepis* and *Phyllolepis* an anterior mesial branch of this crossed onto the corner of the MD plate as the dorsal sensory canal groove (Long 1984, figs 7, 13; Ritchie 1984 fig. 2A, C) but no trace of this canal groove has been detected in *Cowralepis*.

In the ventral trunk shield, the only trace of sensory canal grooves consists of a short shallow stretch of the ventral pit line (vpl) parallel to the posterior margin of the AVL plate in a few specimens of *Cowralepis* in which the ornament is well developed (Figs 5B, 6D, 8F, vpl). The ventral pit line is also present in *Placolepis*, *Austrophyllolepis* and *Phyllolepis*.

Tooth plates and parasphenoid

Although lying deep inside the head, the tooth plates and parasphenoid originated as part of the dermal skeleton. Amongst the placoderms, only the arthrodires and the acanthothoracids had two pairs of gnathal plates in their upper jaw, the anterior and posterior superognathals (Sgn) that occluded against a single inferognathal plate (Ign) in the lower jaw. Where two pairs of superognathals are present the posterior pair are normally the larger.

The only previous evidence for tooth plates in phyllolepids comes from *Austrophyllolepis,* in which large, broad superognathals and narrower inferognathals were preserved in several specimens (Long 1984, figs 5, 6, 12C, 16, 17, 18B), although usually slightly displaced.

The upper and lower tooth plates are preserved in many specimens of *Cowralepis*, both *in situ* and in association (Figs 9, 10, 11, 14, 19) and have also been found as isolated elements. They confirm the presence of two pairs of supragnathal elements in *Cowralepis*: a large anterior supragnathal, corresponding closely to that of *Austrophyllolepis*, and a very small posterior supragnathal, nestling against its posterolateral margin. The small posterior element has only been identified in about a dozen of the many hundreds of phyllolepid specimens from Merriganowry, and it is not surprising, given its size, that it was not located in the much smaller sample of phyllolepid specimens available from Mt Howitt.

The **anterior superognathals** (Figs 4B, 5B, 6B, D, 9A, E-G, 10A-C, G, H, 15C, D) were long, broad and flat, subtriangular in shape with a concave mesial margin. In the largest individuals of *Cowralepis* the anterior Sgn plates reached over 3 cm in length and 1 cm wide. They were broadest posteriorly and tapered anteromesially to a narrow apex near the anterior margin of the head shield where they met in the midline under the preorbital plates at an angle of 90-100^0 (Figs 14A, 19). The occlusal surface was densely covered with rows of small, sharp conical teeth radiating from the ossification centre of the plate and increasing in size towards the margins, but with a very sharp line of demarcation running up the midline towards the anterior apex (Fig. 10G, H); a similar linear feature can be seen in the superognathals of

Austrophyllolepis (Long 1984, figs 16, 18B).

The anterior Sgn in *Cowralepis* closely resembles the example depicted in *Austrophyllolepis ritchiei* (Long 1984, fig. 17), except that the teeth in the latter did not extend to the margins, leaving an edentulous rim all round the plate. The shape of this plate does not match that in the accompanying reconstruction (Long 1984, fig. 14B) where its posterior margin was shown as sharply truncated, straight and attached to a rounded plate.

In sharp contrast to the anterior plate, the **posterior superognathal** was minute, only 2-4 mm in diameter (Figs 9E-G, 10A, B, C). It was semicircular, with one straight or slightly concave margin. Because of its size it is often obscured by larger ventral plates in the fossil specimens. The original relationships of the three gnathal plates are best demonstrated in AMF96783 (Fig. 9E-G) where the inferognathal is in occlusion against the anterior superognathal and the curved margin of the posterior Sgn neatly fits into the posterior margin of the larger superognathal; its straight margin is therefore the posterior face. In three other examples (Fig. 10A-C) the posterior Sgn is completely exposed but slightly displaced.

Given the small size of this element, and the fact that in placoderms with two pairs of superognathals (arthrodires and acanthothoracids) the posterior element is normally larger than the anterior, Gavin Young (pers. comm.) has suggested another interpretation for this small plate in *Cowralepis*. Young et al. (2001, 673, fig. 5A, sc) noted a third small denticulate plate, also ca. 2mm across, at the posterior end of the posterior superognathal plate in a buchanosteid arthrodire from Taemas, NSW

The **inferognathal** (Ign) comprises two laminae meeting at right angles; a tooth-covered dorsal (horizontal) occlusal lamina and a smooth, vertical anterolateral lamina. In most *Cowralepis* specimens the Ign is preserved in occlusion against the anterior superognathal and shows only the smooth groove that housed Meckel's cartilage (Figs 9A, E-G, 10A, E, 11). The Ign was very narrow anteriorly, broadening out only in the posterior half; its occlusal area (Fig, 10D) was much smaller and narrower than that of the anterior Sgn and a row of larger teeth extended along the outer ridge to the anterior apex (not visible here because of the rotation) as in *Austrophyllolepis* (Long 1984, figs 16, 17). The posterior margin of the inferognathal was smooth, tooth-free and serrated or sharply pointed (Fig. 10D, E).

Parasphenoid

In many placoderms the palate bore a small bone, the parasphenoid, with a median foramen for the buccohypophysial canal; whether this is the homologue of the parasphenoid in osteichthyan fishes is still uncertain.

The parasphenoid is well preserved *in situ* in many specimens of *Cowralepis* and was apparently firmly attached to the palatal surface of the endocranium. It is best displayed in specimens where the branchial ossifications are either not preserved or have been lost (Figs 5B, 6D, 8A, 9A-F, 10G, H, 15C).

Based on the new evidence from *Cowralepis,* the reconstruction of the subcranial ossifications of *Austrophyllolepis* (Long 1984, fig, 14A, B) needs to be modified. The parasphenoid is shown in the correct position but the superognathals lay farther forward, almost meeting under the anterior margin. The otoliths (which would have been covered by the parasphenoid in the position depicted) were situated more posterolaterally, lying between the parasphenoid and the paranuchal.

The *Cowralepis* parasphenoid was very large (up to 1/3 the length of the head shield), flat and thin and was centrally situated under the nuchal plate. Its overall shape is best displayed in AMF96781 (Fig. 9B), and it consisted of a slightly raised, lightly tuberculated central area which was widest posteriorly and tapered anteriorly. A single median buccohyphophysial foramen (f.bhy) is situated level with the widest part of the plate.

The central raised area was surrounded by a wide, thin radiating flange with scalloped edges. It was deeply indented laterally (l.ind) opposite the buccohypophysial foramen as far as the central raised area and continues as a shallow tapering groove onto the central raised area. The *Cowralepis* parasphenoid does not differ significantly from that in *Austrophyllolepis* (Long 1984, fig. 17), known only from a few specimens.

In a review of parasphenoids in the Placodermi, Dennis-Bryan (1995) noted that parasphenoids had been recorded from 36 placoderm genera, of which all but three were arthrodires; one of the three exceptions was *Austrophyllolepis* (Long 1984). It was observed that placoderm parasphenoids appeared to be species specific, but were of limited use at higher taxonomic levels. In overall shape the *Cowralepis* parasphenoid most closely resembles those of the Gogo brachythoracid arthrodires, *Gogetosteus* and *Eastmanosteus* (Dennis-Bryan 1995, fig. 2 B, D), but these were much more robust structures and easily detached from the endocranium.

Placoderm parasphenoids were divided into two main types - 'primitive' and 'advanced'. 'Primitive' parasphenoids were flat, lacked lateral notches or grooves, had a central tuberculated area and a large median buccohypophysial foramen, single or paired. 'Advanced' parasphenoids were thicker, with lateral notches and grooves and buccal foramina reduced; tubercles were reduced or absent, and a well-developed median ventral crest was developed.

In a prescient comment Dennis-Bryan (1995, 136) cited two notable exceptions, *Pholidosteus* and *Austrophyllolepis*; "The former is considered to be an advanced arthrodire but has the so-called primitive parasphenoid, and in the latter case the reverse is true. It is perhaps possible that the dorsoventrally flattened phyllolepids are more advanced among placoderms than was first thought."

Visceral skeleton

In many placoderms both the dermal skeleton and endocranium are known from a wealth of well-preserved material. The visceral skeleton of placoderms, however, is rarely preserved and is poorly known (Denison, 1978, 5-7; Janvier, 1996, 153). In most cases it was probably unossified and, even where perichondral ossification was present, it was often delicate and easily destroyed by taphonomic processes.

In all gnathostomes the principal paired visceral structures are the mandibular and hyoid arches and several branchial arches. The mandibular arch comprises the palatoquadrate and mandibular (Meckel's) cartilages, both of which may be perichondrally ossified and, in the hyoid arch, the main elements (when preserved) are the hyomandibula, ceratohyal and basihyal elements.

Prior to the discovery of *Cowralepis* the only direct evidence on the visceral skeleton in phyllolepids came from several *Austrophyllolepis* specimens in which various paired and unpaired ossifications were preserved lying against the ventral surface of the head shield, but displaced (Long 1984, figs 6, 16, 17, 18B, 20). Long based his interpretation (fig. 17) on the only example in which these ossifications appeared to be in association and reconstructed them as three pairs of bones plus a large median parasphenoid and a pair of otoliths (Long 1984, fig. 14A).

Long interpreted the three pairs of elements as the superognathals, metapterygoids (the middle division of the palatoquadrate) and the quadrates, and he reconstructed them as connected in series (Long 1984, fig. 14B). He also suggested (Long 1984, 281) that this series might only have developed at maturity. Many of the articulated *Cowralepis* specimens, juvenile and adult, show some or all of the same visceral ossifications (and many others) *in situ* and in association and reveal that Long's interpretation is invalid.

Quadrate or articular?

Immediately posterior to the gnathal plates, and in direct line with the inferognathal, lay a robust bone with a narrow posterior stem and a wide anterior margin. This bone was strongly perichondrally ossified but open at both ends (Figs 10F, 11, 12C, D, F). A prominent ventral ridge ran obliquely from its anteromesial to its posterolateral margin. Anterolaterally it flared out into a wide triangular flange, with a rounded anterior margin. Posteriorly, on the mesial side of the ventral ridge, there was a deep smooth-sided pit (Figs 10F, 12F).

Long interpreted this plate as the quadrate and reconstructed it as attached anteromesially to a large, flat plate which he labelled the metapterygoid (Long 1984, figs 14B, 17).

Cowralepis suggests a different interpretation. The same two plates are preserved in a large number of specimens, in place and closely associated (Figs 9A, E, F, 11, 14A). The robust bone (Long's 'quadrate') was not originally attached distally to the rounded plate (Long's 'metapterygoid') but lay lateral to it (Fig. 15C, D). Although they have sometimes drifted slightly apart *post mortem* they appear to have been closely associated throughout growth.

The anterior margins of both the rounded plate, and the robust plate lateral to it, covered (ie. lay below) the posterior ends of both the superognathals and the inferognathal. They therefore lay ventral to Meckel's cartilage. This would suggest that the latter cannot be the quadrate, as originally proposed, and it is interpreted here as the **articular**, the posterior ossification of the lower jaw.

Miles and Dennis (1979, fig.11B-E) illustrated a small perichondrally ossified articular plate attached to the rear of the inferognathal in the brachythoracid *Harrytoombsia* from Gogo, Australia. More recently Johanson (2003, fig. 4) has figured large, well-ossified articular bones attached to the inferognathal in other Gogo brachythoracids (*Eastmanosteus, Gogopiscis* and *Incisoscutum*).

Metapterygoid or ceratohyal?

If the robust bone is the articular this raises the question – what was the rounded plate lying along its mesial margin? This was very thin and flat and normally seen in ventral view (Figs 9A, F, 11, 12C, 14A, 18F, 19, Chy) but occasionally in dorsal view (Fig. 14B, Chy). It consisted of two layers of perichondral bone separated by a thin sheet of cartilage and continued to grow throughout life, as indicated by the prominent semicircular growth lines on the flat plate, which radiate from a centre of ossification midway along the straight margin.

Since it lay ventral to the inferognathal (and to Meckel's cartilage) it cannot be the metapterygoid (a palatoquadrate ossification) as suggested by Long (1984) and it is interpreted here as the **ceratohyal** (Fig. 15C, Chy), a ventral element of the hyoid arch.

In smaller *Cowralepis* individuals (Figs 5B, 6D, 9A, E, F) the ceratohyal was slightly longer than the articular but fell a long way short of the midline. In larger individuals (Figs 11A, B, 14A) the ceratohyal was almost twice as long as the articular and had expanded anteromesially to make contact with, and fit neatly against, the concave lateral margins of a large robust median plate, discussed below.

Basihyal

Almost every *Cowralepis* specimen in which the gnathal, articular and ceratohyal elements are preserved also features a large, robust, median perichondral ossification lying anteromesial to the ceratohyals and a short distance posterior to the symphysis of the upper and lower tooth plates (Figs 1, 4B, 9A, B, E, F, 11, 14A, 18F). The distinctive features of this robust plate are illustrated here by stereopair images (Fig. 12A, B).

The plate is about three times as long as wide, with a flat basal platform, rounded anteriorly and posteriorly and with concave lateral margins. A prominent, narrow ventral keel runs most of the length of the plate. The keel is shallowest anteriorly where it divides over the basal platform into numerous radiating buttresses and rises gradually towards the posterior margin where it terminates in a deep pit that probably housed a ligament operating to lower the jaw. Midway along the basal platform, on either side of the keel, there is a small round pit with a raised rim, most clearly seen in AMF96783 (Fig. 9E,F; cf. also 12A).

In smaller individuals the ceratohyals are well-separated from this median plate (Figs 6D, 9A, F) but, during growth, they gradually increase in size until they meet the lateral margins of the median plate, extending almost to its anterior margin (Figs 11, 14A).

In virtually every specimen of *Cowralepis* in which it is preserved *in situ* this median bone lies posterior to, and is quite separate from, both the gnathal plates and the mandibular arch. The close lateral association with the ceratohyals confirms that it also lies ventral to the inferognathal and it is interpreted here as the anterior ossification of the hyoid arch, a median **basihyal.**

Long (1984, fig. 17) figured a rather shapeless, unnamed median bone in *Austrophyllepis* overlapping the anterior margin of the parasphenoid but this was not identified or included in the reconstruction (fig. 14B). Given its close association with the parasphenoid this plate may be the homologue of the basihyal in *Cowralepis* (Figs 9A, B, 15C), but this can only be settled by the recovery of more phyllolepid material from Mt Howitt.

Basibranchials or hypobranchials?

In several medium-sized to large *Cowralepis* specimens in which the visceral skeleton is preserved, the large median plate interpreted above as the basihyal is closely followed posteriorly by up to four pairs of flat, rounded to irregular bony plates that meet in the midline (Figs 1B, 4B, 6D, 11, 14A, 18F, 19). The anterior pair sometimes even wrap around the rounded posterior margin of the basihyal (Fig. 14A). If the above interpretation of the mandibular and hyoid arch elements is correct, these four pairs of plates must be associated with the third to sixth visceral arches. This is very similar to Ørvig's reconstruction of the visceral skeleton in the ptyctodont, *Ctenurella* (Miles 1971, fig. 8.13).

Ossified basal visceral elements have only been recorded from *Pseudopetalichthys* (Stensiö 1969, Figs 168A, B), *Tapinosteus* and now in *Cowralepis.* Stensiö's reconstruction of the branchial skeleton in *Tapinosteus* (1963, figs 83A, B; 1969, fig. 166A, B), derived from serially sectioning the holotype, shows a median basihyal followed by three pairs of hypobranchials, (each pair subdivided with dotted lines) and depicted as separated by unpaired basibranchials. The reconstruction was based on a chondrichthyan model (e.g. *Chimaera monstrosa*; Stensiö 1969, fig. 169), consistent with Stensiö's proposed grouping of chondrichthyans, placoderms and acanthodians into his Elasmobranchiomorphi, an association no longer considered to be valid.

This raises the question – are the four pairs of visceral elements in *Cowralepis* the homologues of the basibranchials (which are median and unpaired in chondrichthyans) or the hypobranchials (which are paired)? Goodrich (1930) and others have suggested, from embryological evidence, that the basal visceral elements in gnathostomes may have been primitively paired. There is no trace of any median elements between the pairs of basal branchial elements in *Cowralepis* that met in the midline and the paired elements present here are interpreted as **hypobranchials** (Figs 6B, 11B, 14A, B, 15D, Hbr).

The whole complex of basal visceral ossifications under the head of *Cowralepis* (large disc-shaped ceratohyals, a robust basihyal and several pairs of hypobranchials) would appear to have provided a firm floor to the buccal cavity, and the deep pit on the posterior face of the basihyal (Fig. 12B) may have housed a strong ligament that depressed the lower jaw.

There are many more specimens of *Cowralepis* displaying the visceral skeleton than those figured here and a fuller account, tracing its ontogenetic development, will be presented elsewhere.

'Suborbital'

Long (1984, figs 4A, 5, 14A, 16, 19) figured a small curved bone in the cheek area of *Austrophyllolepis* but found it difficult to homologise this with other placoderms because it lacked ornament and was folded into a ". . double lamina with a large valley in between" (Long 1984, 283). The plate was interpreted as a greatly reduced and modified suborbital plate (SO) from its situation below, or lateral to, the PtO plate, just where the infraorbital sensory line of most placoderms divided to send a supraoral line ventrally.

A similar small curved bone is present in several specimens of *Cowralepis* (Figs 5B, 6D, 14B, 15C, hae), but is best preserved in AMF127156 (Fig. 11A, B), details of which are shown as stereopairs (Fig. 12C, D, hae). In this rather large individual of *Cowralepis* the bone is 6 mm long and 3 mm wide, bean-shaped and strongly convex. Its surface is very smooth and deeply creased longitudinally by a curving groove close to, and following, the concave margin.

In most of the *Cowralepis* specimens in which this element is present it does not lie near the lateral margin of the PtO (as depicted in *Austrophyllolepis*) but farther in, under the inner margin of the PtO plate and almost touching the posterior end of the bone interpreted above as the articular. The new evidence from *Cowralepis* does not support the earlier identification of this bone as a suborbital plate.

The very strongly convex shape, complete lack of ornament and its position rule out a dermal origin. Gavin Young (pers.comm.) has suggested it may be a small perichondral ossification of the visceral skeleton and, from its position near the mandibular joint, possibly a hyoid arch element, and this interpretation is provisionally accepted here (Fig. 15C, hae).

Endocranium

In many *Cowralepis* specimens two very robust, median ossifications lying entirely within the trunk armour are often clearly visible through the dorsal and ventral armour, which has been impressed onto them (Figs 4B, 6B). They are most clearly seen in situ in a few specimens where the ventral plates have either been lost, or are preserved as isolated elements (Fig. 13).

The shorter, wider, structure is the **occipital ossification,** the longer, narrower ossification is the **synarcual**, the anterior section of the axial skeleton (discussed below) and the junction between them is the craniothoracic articulation.

The **Occipital ossification** lies anterior to the neck joint and represents the ossified posterior (occipital) part of the endocranium (Fig. 13A, B, D, E; Occ oss). It does not include the otic region and extends from the anterior margin of the ventral trunk shield to the posterior margin of the head shield.

There is a discrepancy in shape between the occipital ossification in small individuals (Fig. 13D, E) and in larger specimens (Fig. 13A, B). In juveniles it is broad and flat, narrowest posteriorly with concave sides and a straight posterior margin (the neck joint). Anteriorly it flares into two round, flat processes meeting mesially, with a median notch on the anterior margin.

In larger individuals (Figs 4B, 6B, 13A, B) the occipital ossification is much longer, like two spools attached side by side. The lateral margins are still concave and the anterior margin is wider than the posterior margin, but the central shaft of each half of the ossification is smoothly rounded with one or more rows of regularly spaced deep pits, separated by narrow ridges, developed around the circumference at either end.

While this may indicate the presence of two species, differential development of the occipital ossification between small and large individuals, as noted here, has been described in pyctodontids by Miles and Young (1977, 166)

Otoliths and paraotic plates

Almost all articulated specimens of *Cowralepis* display two solid, bean-like structures lying against the ventral surface of the nuchal plate midway between the midline and the anterior process of the paranuchal plate (PNu). Long (1984, figs 6, 9, 11, 12, 17, 18C) identified similar structures in *Austrophyllolepis* as otoliths and the *Cowralepis* material supports this.

The otoliths were dense calcareous bodies, oriented anterolaterally (Figs 1B, 4B, 5B, D, 8A, 9A, 11A, B, 13D, 14B). They were very solid bodies, not hollow, as demonstrated by the fact that the nuchal plate has often been moulded over them, and they were proportionally larger in smaller individuals than in more mature ones. One specimen of an isolated otolith displays its aggregate crystalline nature and surface structure in fine detail (Fig. 12E)

In life, the otoliths were internal structures located within the fluid-filled sacculus of the left and right otic labyrinth and were deeply embedded within the endocranium, the anterior part of which, in *Cowralepis*, was apparently cartilaginous. As noted by Long (1984, 281) the position of the otoliths in *Austrophyllolepis* (and now also in *Cowralepis*) corresponds closely to the site of the saccular cavities in *Buchanosteus* (Young 1979), *Kujdanowiaspis* (Stensiö 1963) and other euarthrodires. Calcified otoliths have not been recorded from other placoderms, but their presence in both *Cowralepis* and *Austrophyllollepis* suggests that they were probably present in all phyllolepids. Otoliths were also present in the extinct acanthodians and are found in extant osteichthyans, but in both of these groups there are three separate otoliths in each otic capsule, not one.

The otoliths in *Cowralepis* display an interesting feature not observed in *Austrophyllolepis*. In smaller individuals the posterior half of each otolith is often overlain or, more correctly, underlain by a subcircular to irregular bony disc with concentric growth rings (Fig. 8B). In slightly larger individuals this disc had grown to cover two thirds of the otolith (Fig. 11A, B), and in the largest individuals it was large enough to completely cover the otolith, onto which it was moulded from below (Fig. 14A). Because these sub-otic plates appear to be underlain ventrally by the hypobranchial ossifications, and therefore lay dorsal to them, it is suggested that these plates were attached to the palate immediately under each otic capsule as paraotic plates (Fig. 15D, p.pao).

The nearest equivalent in placoderms appears to be a large pair of denticle-covered paraotic plates developed on the palate in *Nefudina qalibahensis*, a rhenanid placoderm from the Early Devonian of Saudi Arabia (Lelièvre et al. 1995, 111, pl.1, fig.1, p.pao). The paraotics lay immediately under the otic capsules and were attached to the palatal surface of a well-ossified endocranium, just posterior to a large denticulate parasphenoid. Their robust nature and denticulate surface suggests they may have been used in food processing. In contrast, the paraotics in *Cowralepis* were thin, smooth-surfaced discs, lacking ornament and may have served to protect the undersurface of the otic capsules. Gavin Young (pers. comm.) has suggested that they may represent areas of ossification on the floor of the endocranium.

Axial skeleton and fins

In many placoderms the anterior vertebral elements, housed within the trunk shield, were fused into a **synarcual** ossification on which rested the median dorsal plate. Stensiö reconstructed the posterior of the endocranium and a long narrow synarcual in *Paraleiosteus* (1969, fig. 34) in lateral view, and that of *Cowralepis* must have looked rather similar.

The synarcual in *Cowralepis* was long and narrow and its overall shape is displayed in two individuals seen in ventral view, AMF96762 (Figs 4B, 6B) where it is overlain by the ventral trunk plates and AMF96751 (Fig. 13A) where the ventral plates have been lost, fully exposing both the synarcual and occipital ossifications. AMF96753 (Fig. 13C), an isolated synarcual, preserved in counterpart, displays both its dorsal (left) and ventral (right) surfaces revealing that, like the occipital ossification, it was clearly divided into left and right sections. The ventral surface displays a deep longitudinal median groove that widens anteriorly into an elongate diamond-shaped foramen.

Long's reconstruction of the trunk and fins in *Austrophyllolepis* (1984 Fig. 23), based on the few incomplete specimens available at the time (Long 1984, figs 21, 22), can be revised from *Cowralepis*. There is no evidence for the presence of a dorsal fin in *Cowralepis* (or in *Austrophyllolepis*), the pelvic fins were much smaller than shown and were tucked under the body close to the ventral shield, and the caudal fin was epicercal (= heterocercal) with the notochord/vertebral column supporting the upper lobe.

The vertebral column is fully known in only a few placoderm genera, the best examples of which are *Ctenurella* (Stensiö 1969, fig. 178) and *Coccosteus* (Miles and Westoll 1968, text fig. 48) in both of which a persistent unrestricted notochord was enclosed dorsally and ventrally by neural and haemal arches bifurcating around it.

Many specimens of *Cowralepis*, small and large, have the vertebral column and tail fin attached, often almost complete and preserved in part and counterpart in fine detail (Figs 1, 4, 16-18). Even the smallest specimens display the beginnings of a well-ossified backbone (Figs 2D, 18A). The complete exposure of the vertebral elements indicates that *Cowralepis* lacked any scale-covering, a feature also noted in *Austrophyllolepis* by Long (1984, 297).

In *Cowralepis,* the tail was relatively long and powerful, and the relative length of the dermal shield to the body and tail change during growth. In small to medium-sized individuals the body and tail forms 65-70% of the total length; in the largest specimens this drops to just over 50% of the total length (Fig. 16 B, C).

Cowralepis had at least 60 vertebrae posterior to the trunk shield and pelvic fin. Anteriorly these consist only of dorsal (neural) and ventral (haemal) arcualia but posteriorly they deepen to support the caudal fin and were supplemented ventrally by an additional row of sub-haemal elements (Fig. 18C, sub-h.sp) extending to the tip of the sharply pointed tail.

The exquisite preservation of some *Cowralepis* specimens (Fig. 17A-D) allows reconstruction of the vertebral elements (Fig. 18C) and comparison with those of *Coccosteus* and with *Incisoscutum ritchiei* in which uncrushed vertebral elements were recovered by acid preparation (Dennis and Miles, 1981, 248-50, figs 21, 22).

In *Incisoscutum* the neural arch (housing the nerve cord) was separated from an overlying triangular opening (housing the dorsal ligament) by horizontal bony flanges that met mesially. In *Coccosteus* a similar transverse flange carried an anterior median bony projection that Miles and Westoll (1968, text. fig. 46) called the zygopophysis; by contrast, in *Incisoscutum*, the same flange carried a pair of well-developed zygopophyses.

The condition in *Cowralepis* was simpler; the neural arch was an open V-shaped incision with no transverse flange separating the nerve cord and dorsal ligament, and with a single prominent zygopophysis at the apex of the neural arch (Fig. 18C, zyg). The dorsal spines were long, narrow and angled sharply backwards.

Where the neural arch sat on the notochord it broadened out into large curved basal pads, as in *Incisoscutum* (Dennis and Miles 1981, fig 22). In the haemal arches the paired dorsal contact processes were oval with deep pits (Fig. 17D). The haemal spines were much longer than the dorsal spines and strongly sinuous in shape, especially in the caudal fin. An unusual feature in *Cowralepis,* not recorded in any other placoderm, was the development of an extra row of sub-haemal radial elements, considerably deepening the hypochordal lobe of the fin and increasing the propulsive force of the tail.

Pectoral fin

None of the remarkably complete *Cowralepis* specimens from Merriganowry display any trace of the pectoral fin which clearly lacked any scale covering, nor is there any trace of the scapulocoracoid or of fin basals, suggesting that these were probably cartilaginous and not perichondrally ossified. The size and shape of the pectoral fin in *Cowralepis* remains conjectural (Fig. 20A).

Pelvic girdle and fin

The pelvic girdle and fin skeleton is preserved in situ in many specimens of *Cowralepis*, of all sizes, including the holotype, AMF103767 (Figs 1A-D, 4B, 6B, 7H, I, 16A-C, pel.b, pel.d). It lay immediately behind, or slightly overlapped, the posterior margin of the ventral shield but it has also been found detached and isolated (Fig. 7D, E).

The pelvic fin was first identified in *Austrophyllolepis*, based on two specimens (only one of which was figured) where it consisted of two perichondral ossifications, a larger anterior element, and a shorter, narrower, distal element (Long 1984, figs 21, 22, pel.b, pro).

Based on the many well-preserved specimens of the same element in *Cowralepis,* the anterior element (basal pelvic plate) preserved in *Austrophyllolepis* is probably incomplete. In *Cowralepis* the basal pelvic plate was longer and narrower, with slightly concave margins (Fig. 7D, E, H, pel.b). The left and right pelvic plates met in the mid-ventral line and diverged posterolaterally at about 45° to the body axis.

Long noted that part of the lateral margin of the basal plate appeared to bear “short grooves denoting serial divisions for articulation of cartilaginous pelvic fin ray elements” (1984, fig. 20, art; 285). No evidence of such grooves has been detected in *Cowralepis* and I suspect that this feature in *Austrophyllolepis* was probably an artefact of preservation.

The shorter distal element (Figs 4B, 6B, D, 7D, E, H, I, pel.d) was interpreted by Long as a propterygium (1984, figs 21, 22, pro), the anterior of three principal cartilages in the paired fins of elasmobranch fishes, and thus a pre-axial element. In contrast, the smaller bone in the *Cowralepis* pelvic fin is normally attached distally to the basal plate, and in line with it, unlike in *Austrophyllolepis* where it appears to have been displaced. This suggests that it was an axial element.

Janvier (1996, 244) noted that although one group of placoderms (ptyctodonts) may have possessed claspers on the pelvic fin, “. .the problem with pelvic claspers is that they are apparently lacking in all other placoderms, although very few pelvic fins have actually been preserved. Long (1984) has described a peculiar club-shaped endoskeletal (probably metapterygial) element in the pelvic fin of the phyllolepid *Austrophyllolepis*; this may suggest the presence of a pterygopodium that supported the clasper.”

The distal element of the pelvic fin in *Cowralepis* (Figs 1C, D; 6B, D; 7D, E, H, I; 16A, pel.d) is interpreted as the homologue of the metapterygium in the elasmobranch fin.

Sexual dimorphism

Long (1984, 275, 286) discussed the possibility that the ‘propterygial’ element in *Austrophyllolepis* may have been a clasping organ, rather than just an extension of the pelvic fin. Zangerl (1981) pointed out that “. . the pelvic girdle of *Austrophyllolepis* showed some resemblance to the male clasping organs of primitive chondrichthyans, particularly *Cobelodus*". Judgement was suspended because of insufficient material; the only two specimens of the *Austrophyllolepis* pelvic skeleton were similar, with no evidence of dimorphism to indicate male and female versions.

This can now be re-examined using the numerous examples of pelvic fins in *Cowralepis*. Because of the vagaries of preservation, and its relatively small size, the pelvic fin is not always visible even in individuals in which the body and tail is well preserved. However, where it is preserved, the pelvic fin skeleton is always approximately the same length in similar-sized individuals, with no evidence for larger and smaller variants, or for the presence of claspers, that might indicate sexual dimorphism.

Sexual dimorphism could still be present in the Merriganowry phyllollepid material, but it is difficult to see how evidence for it might be extracted from fossil specimens that have undergone strong tectonic deformation.

The cannibal from Cowra

If further confirmation was required concerning the topographic relationships of all the gnathal and visceral skeletal elements under the *Cowralepis* head shield it is provided by an unusual example of one individual that literally bit off more than it could chew!

AMF90011a, b is a moderately large *Cowralepis* specimen in which the vertebral column of a second, smaller *Cowralepis* is seen disappearing under the anterior margin of the head shield in the midline (Fig. 18E). That it is not just a case of accidental superposition of one fish on another is revealed by the counterpart showing the ventral surface (Fig. 18F) and by combining information from the part and counterpart (Fig. 19). In the larger individual most of the gnathal and branchial skeletal elements are present *in situ* and they even include the small left posterior superognathal (Sgn post.) exposed by separation of the articular from the ceratohyal.

The smaller fish skeleton is shown here in black (Fig. 19). The vertebrae continue posteriorly under the ventral margin of the head shield and over the right superognathal. They pass between the basihyal and the right ceratohyal into the buccal cavity where they terminate against the posterior margin of the ventral trunk plates of the smaller individual (PVL + AVL plates; shown in black), still in association. The size of the prey demonstrates that the mouth opening in *Cowralepis* was at least as wide as the anterior margin of the head shield.

The neural arches and their dorsal spines lie against the occlusal surface of the right superognathal and are overlain by the posterior part of the right inferognathal. Behind this the dorsal spines disappear under the anteromesial corner of the right ceratohyal that has been moulded over them. The vertebrae and associated trunk plates are partly overlain by several hypobranchial plates and the trunk plates disappear under the leading edge of the host's ventral shield (AVL plates); the left and right interolateral plates have swung forwards and the AMV is missing, as commonly occurs in phyllolepids.

This unique specimen confirms that the skeletal elements identified as basihyal, ceratohyals, articulars and hypobranchials, together with the inferognathals, all lay ventral to the palatoquadrate and superognathals.

An egg sac?

One of the most intriguing finds from Merriganowry, AMF127151, preserved in counterpart (but only as a natural mould) appears to be an egg sac (Fig. 18D). It is 3 cm long, 1 cm wide and contains perhaps 200 tightly packed, uniform, oval bodies, each 3-4 mm long and oriented parallel to, or slightly oblique to the long axis of the whole mass. The surface material of each oval body is finely granular. The well-defined margins suggest that these tightly packed oval bodies were originally enclosed in a membrane or sac. There is obviously no way to investigate what they once contained. The only animal remains recorded from Merriganowry are phyllolepid fishes, possible thelodont scales (in coprolites), and rare eurypterid fragments. It is at least possible that they represent unhatched fish eggs and are presented here for the record.

Relationships of phyllolepids

Since their first discovery in Scotland in the early 19th century (Agassiz 1844) the nature, origins and relationships of phyllolepids have been in dispute. At one time they were even thought to be ostracoderm agnathans (Woodward 1915, 1920) until Stensiö (1934, 1936, 1939) confirmed that they were rather aberrant placoderms.

Until the 1980s, phyllolepids were considered to be the sister group to the Arthrodira (Goujet 1984) and several workers have suggested a close relationship with a distinctive endemic Australian arthrodire, *Wuttagoonaspis* Ritchie, 1973 (cf. Janvier 1996, figs 4.44, 4.49). Phyllolepids and wuttagoonaspids, which have now been recorded over a wide area in Australia (Young and Goujet 2003), had a rather similar ridged ornament that has been interpreted as a shared derived character of the two groups. In contrast, I (Ritchie 1973) suggested that phyllolepids and wuttagoonaspids were only distantly related, a view supported by Dupret (2004, 48) who does not consider the ornament ridges in phyllolepids and wuttagoonaspids to be homologous and proposes *Wuttagoonaspis* as a sister group to all other arthrodires. Goujet and Young (1995, fig. 2) and Goujet and Young (2004, fig. 1) included both the Phyllolepida and *Wuttagoonaspis* in the Arthrodira, but as a polytomy, leaving their interrelationships unresolved.

Dupret (2004) reviewed the phylogenetic relationships between actinolepids (which, like phyllolepids, had a sliding neck joint,) and other arthrodires, e.g. phlyctaeniids and brachythoracids (which had a rotating neck joint with articular condyles on the anterior dorsolateral plates). He grouped Phyllolepida with “Actinolepids” in “Actinolepidoidei”, a paraphyletic assemblage, and suggested that Phyllolepida are the sister group to the Phlyctaenioidei (Phlyctaenii plus Brachythoraci).

Palaeogeographic distribution of phyllolepids

Of the ca 300 placoderm genera and eight placoderm orders that dominated the Devonian lakes, rivers and seas (Carr 1995), the phyllolepids display perhaps the most unusual stratigraphic distribution. In the former supercontinent of Laurussia (=Euramerica), where they were first found, phyllolepids are known only from the latest Devonian (Famennian). They are the only placoderm group with no Early or Middle Devonian fossil record in the Northern Hemisphere.

Fossil discoveries from Gondwana since the early 1980s provide a possible explanation for the sudden appearance of phyllolepids in the Northern Hemisphere and a solution to the mystery of their origins (Young 1986, 1987, 1990, 1993a, 1993b, 2003, in press a, b). With the exception of Venezuela and Antarctica, most of the phyllolepid finds from Gondwana have come from Australia, from much older deposits - Late Middle Devonian (Givetian) to Early Late Devonian (Frasnian) - than those in the Northern Hemisphere. They are also usually found, like their northern relatives, in freshwater sediments.

This disjunct distribution of phyllolepids, in time and space, provides strong support for a dispersal episode in the mid-Late Devonian (Frasnian-Famennian boundary) at which time northern Gondwana and Laurussia came close enough to each other to allow the exchange of predominantly freshwater fish faunas. Phyllolepid fishes survived in Laurussia until the end of the Devonian but have left no record in Asia.

It is clear that much more remains to be uncovered about the early history of phyllolepid placoderms and that Gondwana, and especially Australia, displays the greatest potential for discoveries illustrating the origins and radiation of the Phyllolepida.

Cowralepis mclachlani gen. et sp. nov. makes a major contribution to our knowledge of the Phyllolepida. The Merriganowry site in central west New South Wales provides an ideal base for a long-term, multi-disciplinary scientific research programme into the palaeontological, palaeoecological and sedimentological history of a Late Middle Devonian lake and its fauna covering tens, or hundreds, of thousands of years. Under proper scientific supervision, this can be combined with, and financially supported by, a unique, hands-on, educational facility and eco-tourism experience, with long-term economic benefits for rural New South Wales.

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I wish to thank the Director and Trust of the Australian Museum for appointing me as a Museum Research Fellow following my retirement as Museum palaeontologist in 1995 and for providing facilities and support enabling me to continue active research work on fossil fishes, especially in central west New South Wales.

Without the support of Mr Alex McLachlan, owner of the property on which Merriganowry is situated, this study would not have been possible. His generous action in fencing and securing the Merriganowry site for scientific investigation by the Australian Museum has preserved a unique, world-class fossil assemblage for posterity, the full scientific, educational and eco-tourism potential of which has yet to be realised.

The discovery of the Merriganowry site owes much to the late Mr Reg Dumbrell of Canowindra who discovered the remains of phyllolepid fossil fish near the Lachlan River and reported this to the Australian Museum.

The remarkable assemblage of fossil specimens illustrated here represents only part of the material excavated from Merriganowry between 1993 and 2004 by many hundreds of paying volunteers, supervised by myself and Dr Zerina Johanson from the Australian Museum. These groups have been organised by Ms Monica Yeung of Canberra and Mr Bruce Loomes of Canowindra, through Gondwana Dreaming Inc. of Canberra. My deepest thanks to them and to all the dig participants who (mostly willingly) relinquished their fossil finds to the Australian Museum for this project and whose financial contributions helped to fund our research.

Mr James Fairfax, of Bowral, New South Wales, generously funded our Canowindra Research Project (of which the Merriganowry study is part) for many years.

I thank my palaeoichthyological colleagues, most especially Dr Zerina Johanson, who has jointly supervised more than 60 weekend digs at Merriganowry; also Dr Gavin Young (Canberra), Dr John Long (Melbourne), Dr Robert Carr (Ohio), Dr Daniel Goujet (Paris), Dr Vincent Dupret (Paris) and many others for constructive discussions on phyllolepid anatomy and placoderm relationships. I would like to express particular gratitude to the referees, Dr Gavin Young and Dr Robert Carr, whose extensive and useful comments made this a much better paper. However, in the final analysis, the opinions expressed here are my own.

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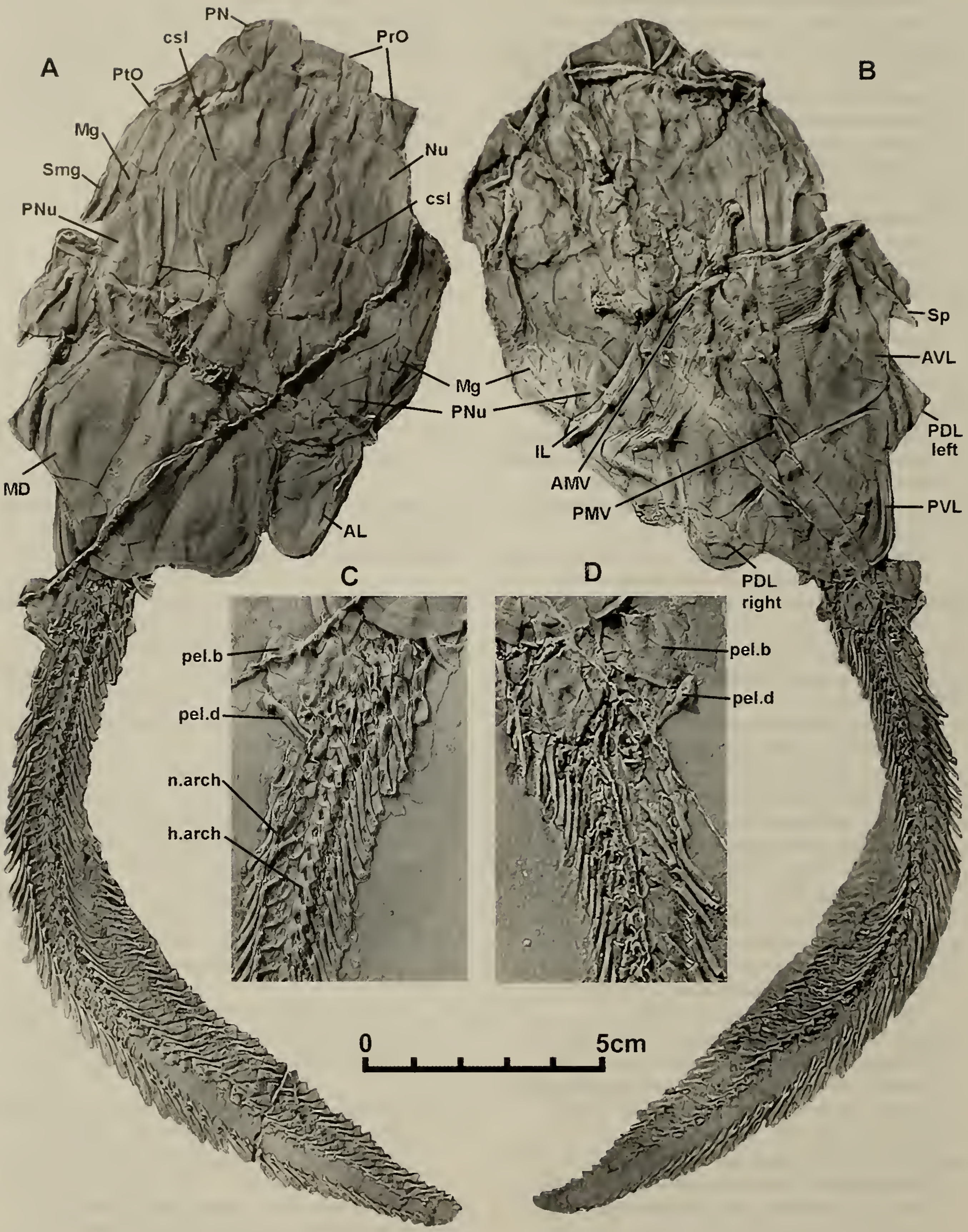

Figure 1A-D. *Cowralepis mclachlani* n. gen. and sp. AMF103767a, b. holotype, complete individual in part and counterpart. A) dorsal view; B) ventral view, C-D) detail, pelvic fins and vertebrae, in dorsal and ventral view respectively. Latex casts whitened with ammonium chloride sublimate.

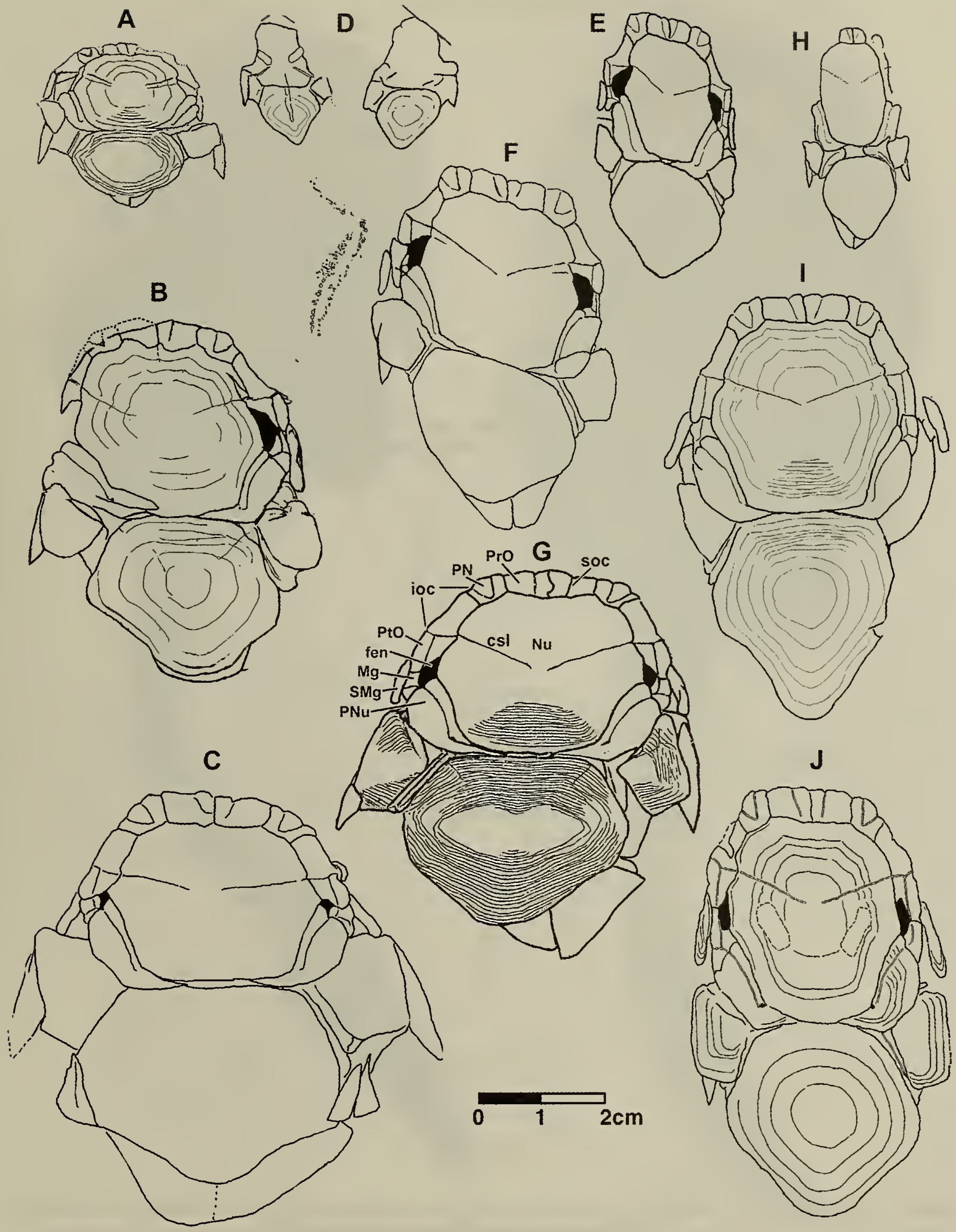

Figure 2A-J. *Cowralepis mclachlani* n. gen. and sp. Small to medium-sized individuals to the same scale illustrating the range of deformation in Cowralepis specimens from Merriganowry. A-C), short, broad symmetrical specimens; D-G) skewed specimens; (H-J) long, narrow symmetrical specimens. A) AMF103756; B) AMF90053; C) AMF90027; D) AMF90034a, b; E) AMF96750; F) AMF104157a; G) AMF96747a; H) AMF103784; I) AMF90044b; J) AMF103778a

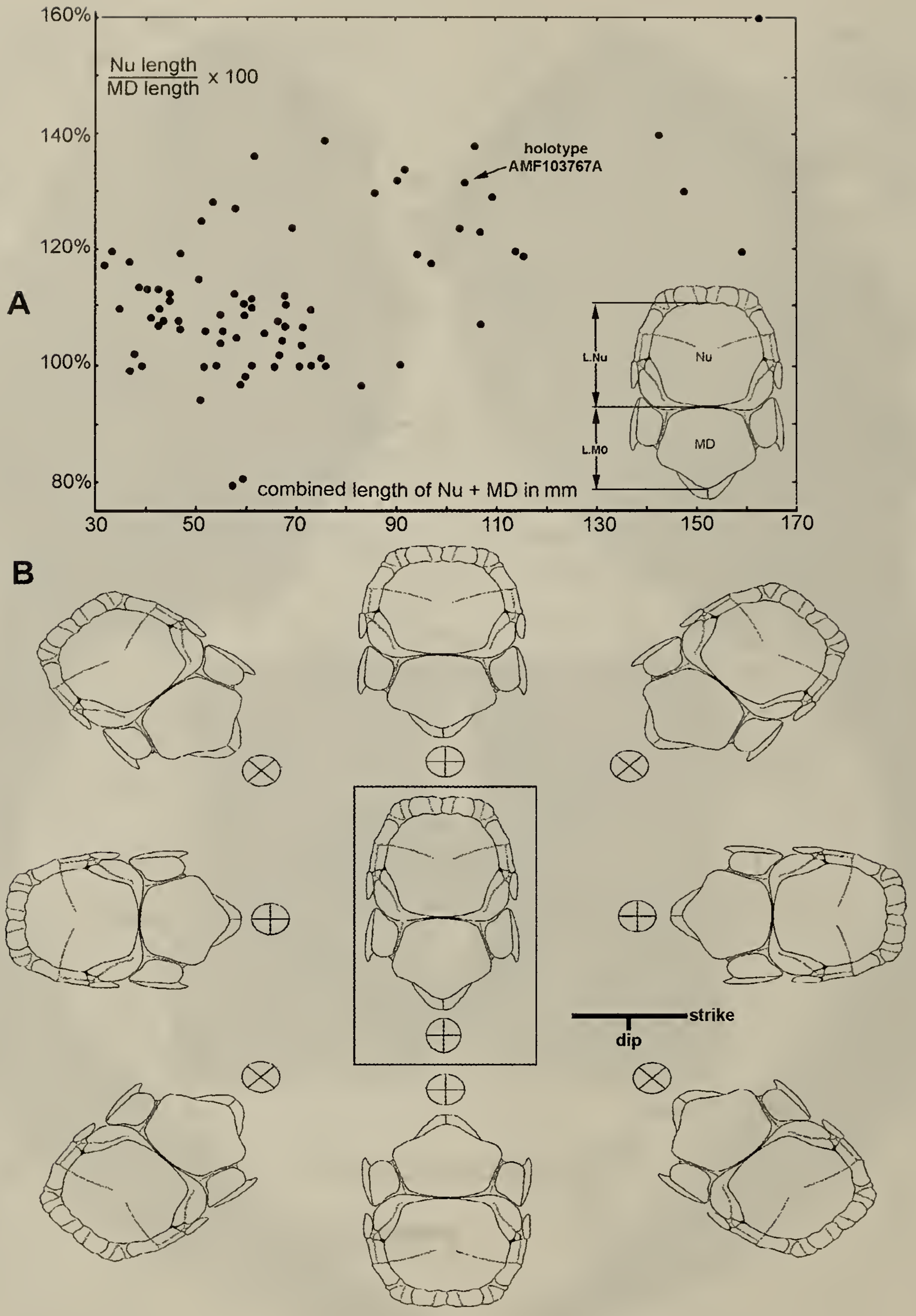

Figure 3A, B *Cowralepis mclachlani* n. gen. and sp. Tectonic deformation. A) relative lengths of dorsal plates in eighty *Cowralepis* specimens. Horizontal axis shows combined length of Nu+MD; vertical axis shows Nu/MD x 100. B) All *Cowralepis* specimens from Merriganowry have been tectonically deformed. The central figure depicts a hypothetical undeformed individual of *Cowralepis*. Surrounding figures, in different orientations, were enlarged by 10% in the direction of largest principal extension (GPE) and reduced by 10% in the direction of smallest principal extension (SPE), as indicated by accompanying strain ellipses. The strike anddip at Merriganowry are in register with the GPE and SPE of the strain ellipse, but this is probably coincidental.

Figure 4A, B. *Cowralepis mclachlani* n. gen. and sp. Two large individuals with tail. A) AMF90003a, dorsal view; B) AMF96762, ventral view (cf. Fig. 6 for digitally modified versions of both). Latex casts whitened with ammonium chloride sublimate.

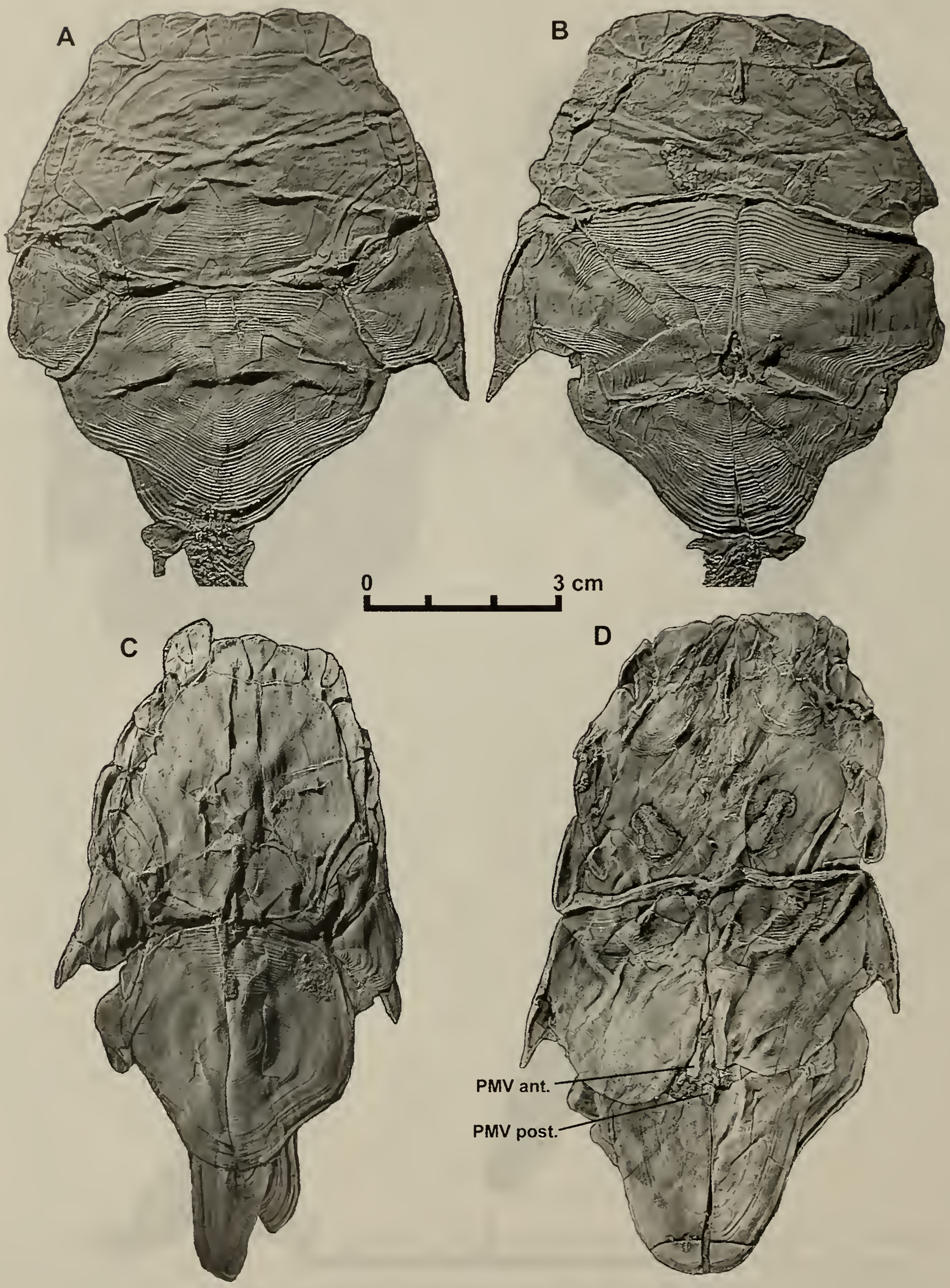

Figure 5A-D. *Cowralepis mclachlani* n. gen. and sp. Three symmetrical individuals illustrating short/broad and long/narrow examples of tectonic deformation. A, B) AMF103753a, b, dorsal and ventral (cf. Fig. 6C, D for same specimen after digital modification); C) AMF90051 dorsal view; D) AMF100018, ventral view. Latex casts whitened with ammonium chloride sublimate.

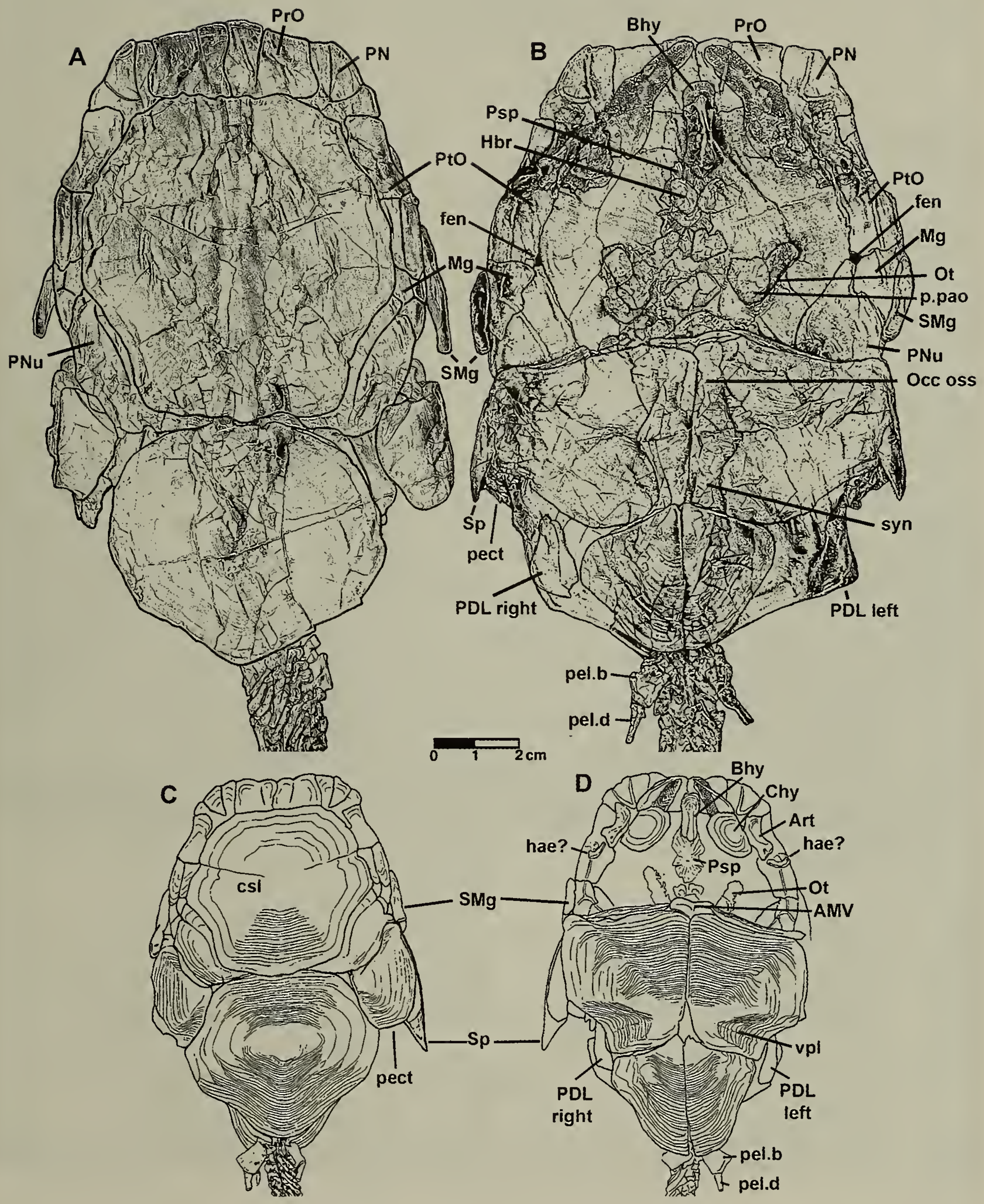

Figure 6A-D. *Cowralepis mclachlani* n. gen. and sp. Digitally modified versions of A,B) long/narrow and C,D) short/broad *Cowralepis* specimens restored approximately to original proportions. A) AMF.90003a, dorsal surface (cf. Fig. 4A); B) AMF96762, ventral surface (cf. Fig. 4B); AMF103753, dorsal and ventral views (cf. Fig. 5A, B).

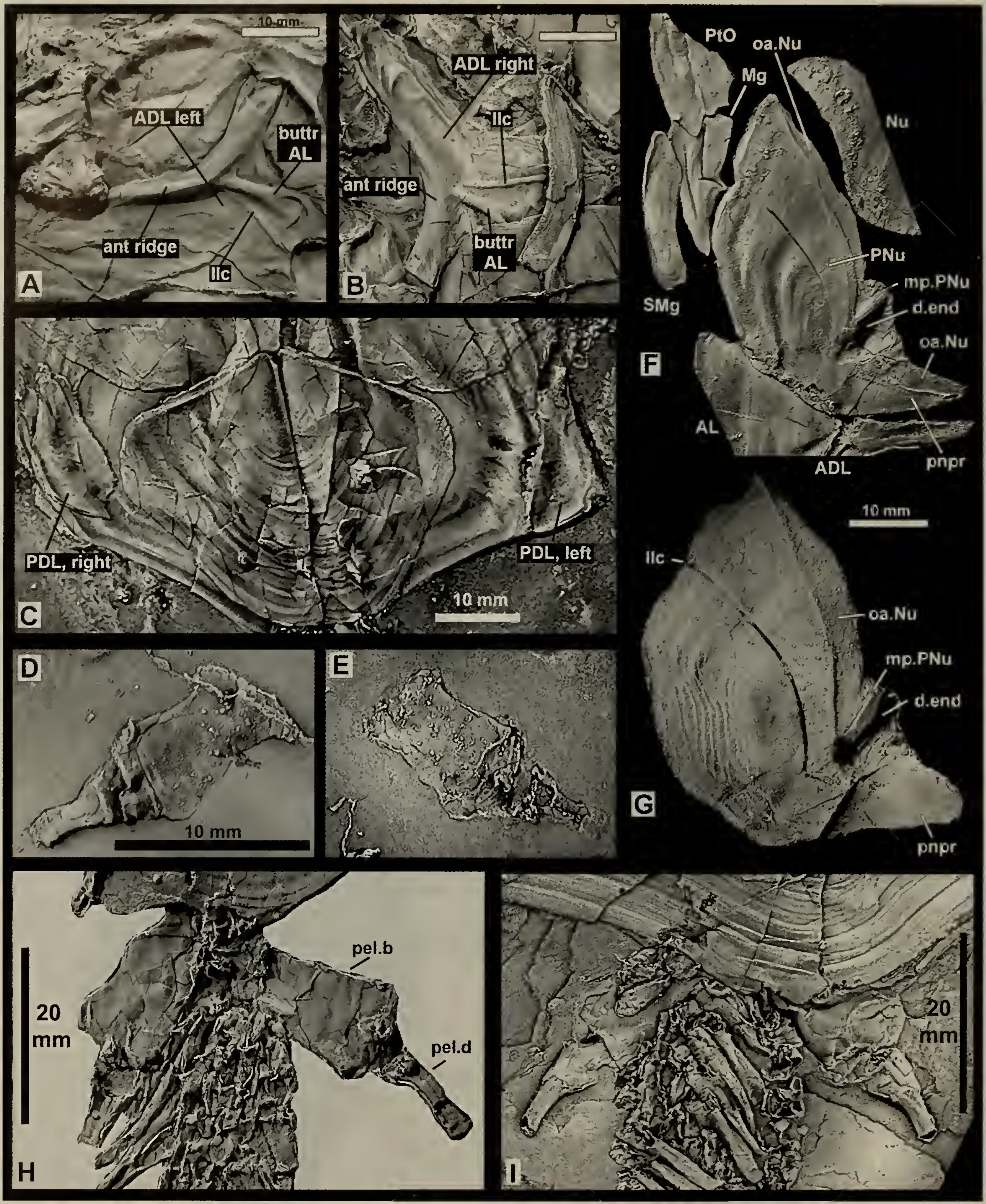

Figure 7A-I. *Cowralepis mclachlani* n. gen. and sp. A, B) AMF96779, left and right ADLs from same individual, in ventral view; C) AMF96762, left and right PDLs (cf. Figs 4B, 6B); D, E) AMF90054a, b, isolated pelvic fin skeleton, in counterpart; F) AMF96784, PNu with associated Mg, PMg and part of PtO, dermal view; G) AMF90029a, right paranuchal, dermal view; H) AMF90012, pelvic fins, dorsal view; I) AMF 103754, pelvic fins, dorsal view. Latex casts whitened with ammonium chloride sublimate.

Figure 8A-G. *Cowralepis mclachlani* n. gen. and sp. Ventral trunk plates. A) AMF104154, partial head and trunk, ventral view; B) IL, AMV and otolith; C) AMF103770, right IL; D) detail of ornament; E) AMF127152, anterior ventral margin with AMV and both IL plates slightly dislodged; F) AMF104160, AVL and PVL plates; no PMV visible; G) AMF127162, AVL and PVL plates; one PMV present. Latex casts whitened with ammonium chloride sublimate.

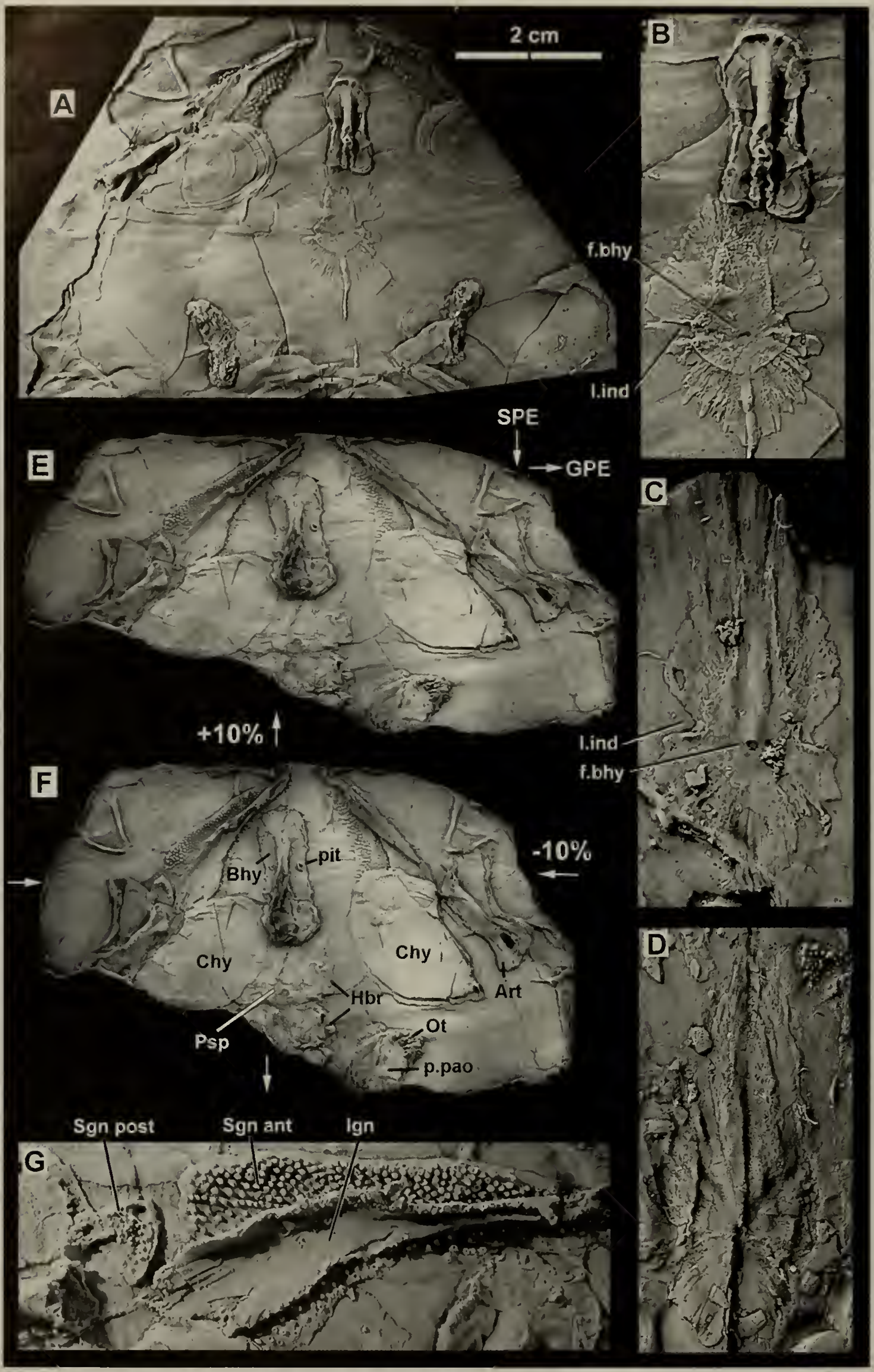

Figure 9A-G. *Cowralepis mclachlani* n. gen. and sp. A) AMF96781, ventral view; and B) AMF96781, detail of A); C) AMF104154, parasphenoid, ventral surface (cf. Fig. 8A); D) AMF103768, parasphenoid, dorsal surface; E) AMF96783, before digital modification; GPE and SPE indicate directions of Greatest and Shortest Principal Extension; F) AMF96783, after digital modification; arrows indicate direction and % of correction applied; G) AMF96783, right inferognathal and both superognathals in association. Latex casts whitened with ammonium chloride sublimate.

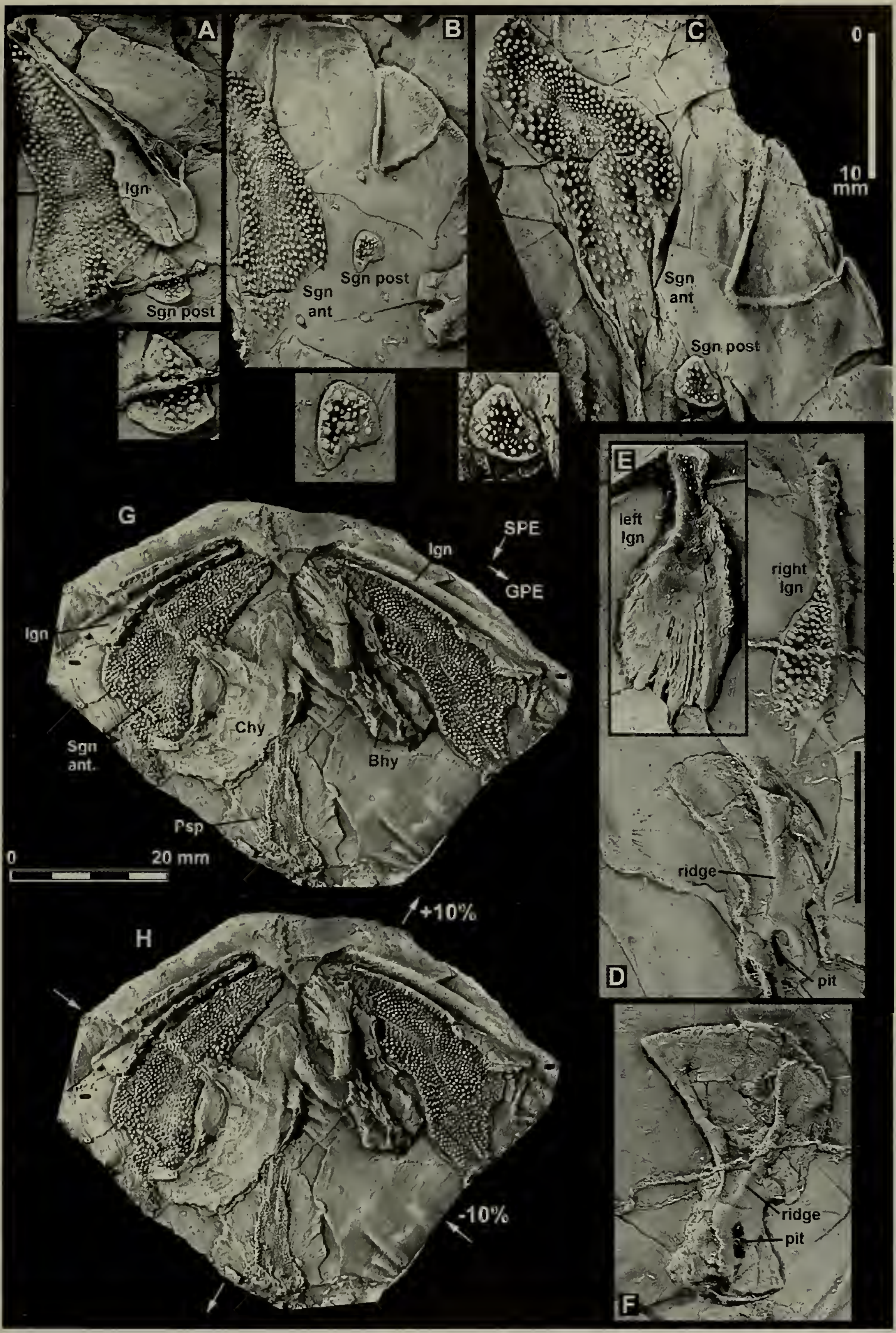

Figure 10A-G. *Cowralepis mclachlani* n. gen. and sp. Gnathal elements. A) AMF103755, left superognathals and inferognathal; B) AMF104164, left superognathals, inferognathal lost; C) AMF104155, left superognathals, inferognathal lost; D) AMF103787, right inferognathal and articular, Ign rotated to show occlusal surface; E) AMF96779, left inferognathal, ventral view; F) AMF96780, right articular, ventral view; G) AMF96786, before digital modification; GPE and SPE indicate directions of Greatest and Shortest Principal Extension; H) AMF96786, after digital modification; arrows indicate direction and % of correction applied. Latex casts whitened with ammonium chloride sublimate.

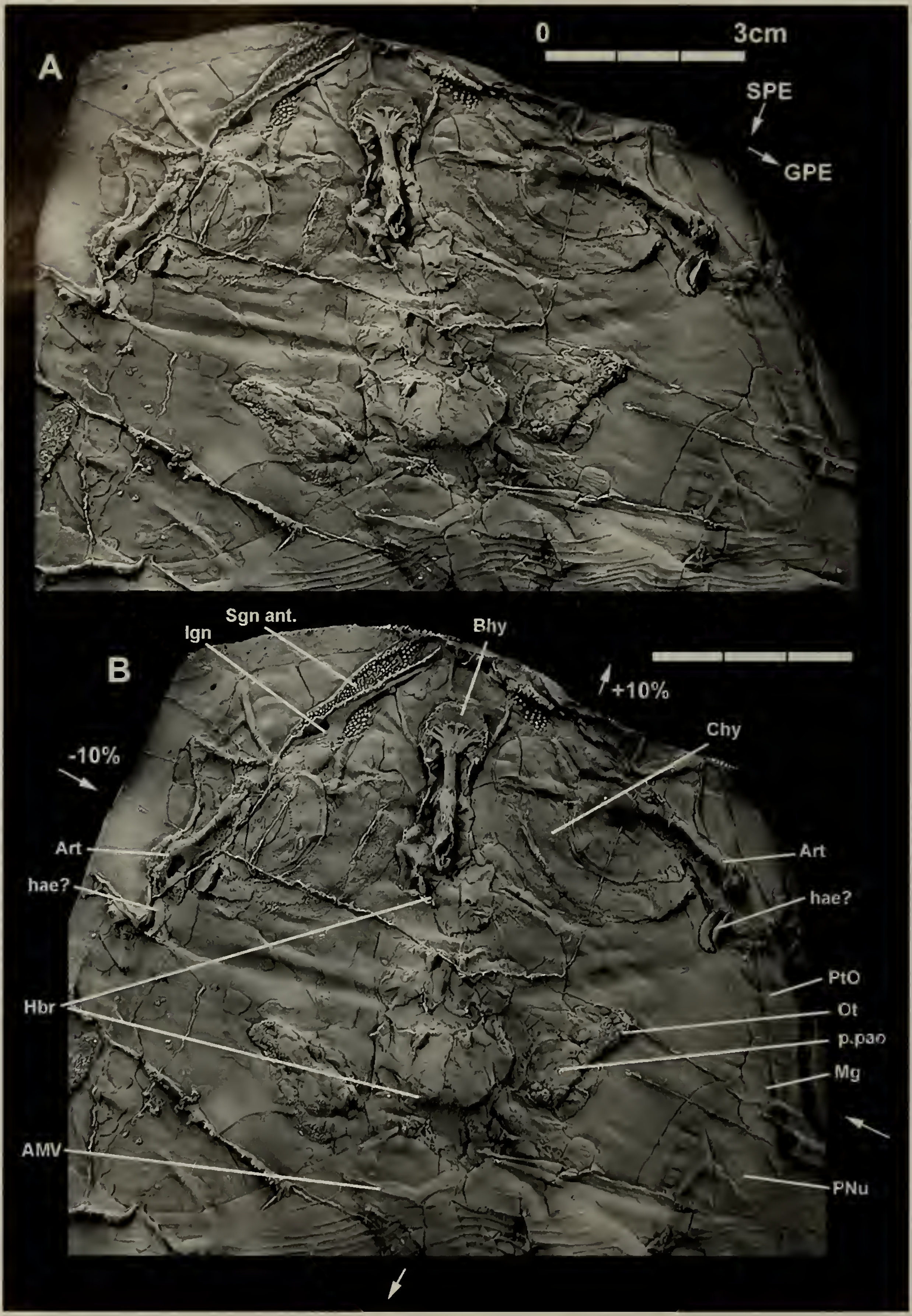

Figure 11A, B. *Cowralepis mclachlani* n. gen. and sp. AMF127156, ventral surface of head shield and anterior margin of ventral trunk shield, A) before digital modification; GPE and SPE indicate directions of Greatest and Shortest Principal Extension; B) after digital modification; arrows indicate direction and % of correction applied. (cf. Fig. 12B-D for stereo pairs of basihyal, articulars and ?hyoid arch element). Latex cast whitened with ammonium chloride sublimate.

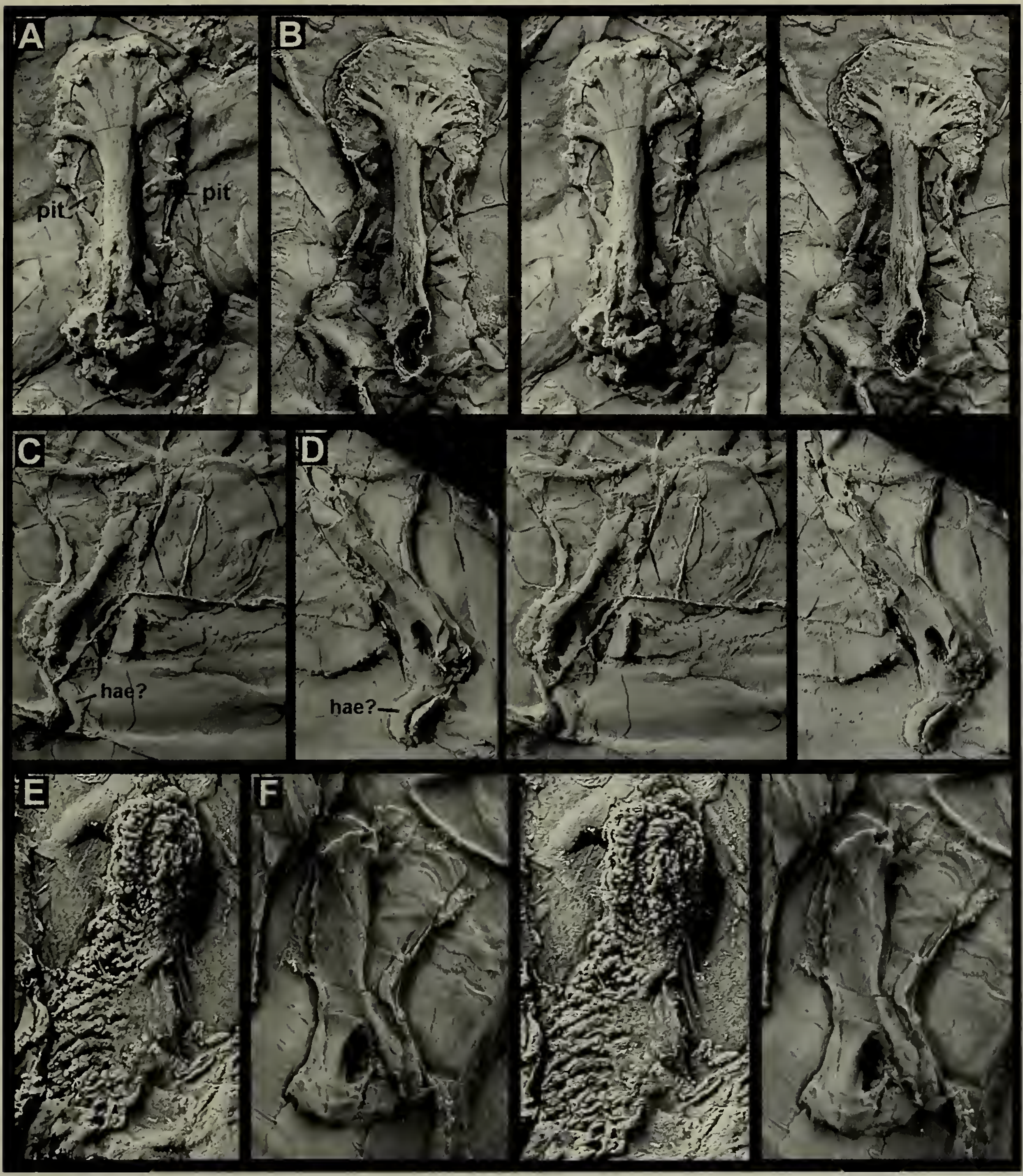

Figure 12A-F. *Cowralepis mclachlani* n. gen. and sp. Stereopair images of visceral skeletal elements and otolith. A) AMF90007b, basihyal (cf. Fig. 14A); B) AMF127156, basihyal (cf. Fig. 11A); C) right articular, ceratohyal and hyoid arch element? (cf. Fig.9); D) AMF127156, left articular and hyoid arch element? (cf. Fig. 9); E) AMF96779, left otolith, ventral view; F) AMF96783, left articular. Latex casts whitened with ammonium chloride sublimate.

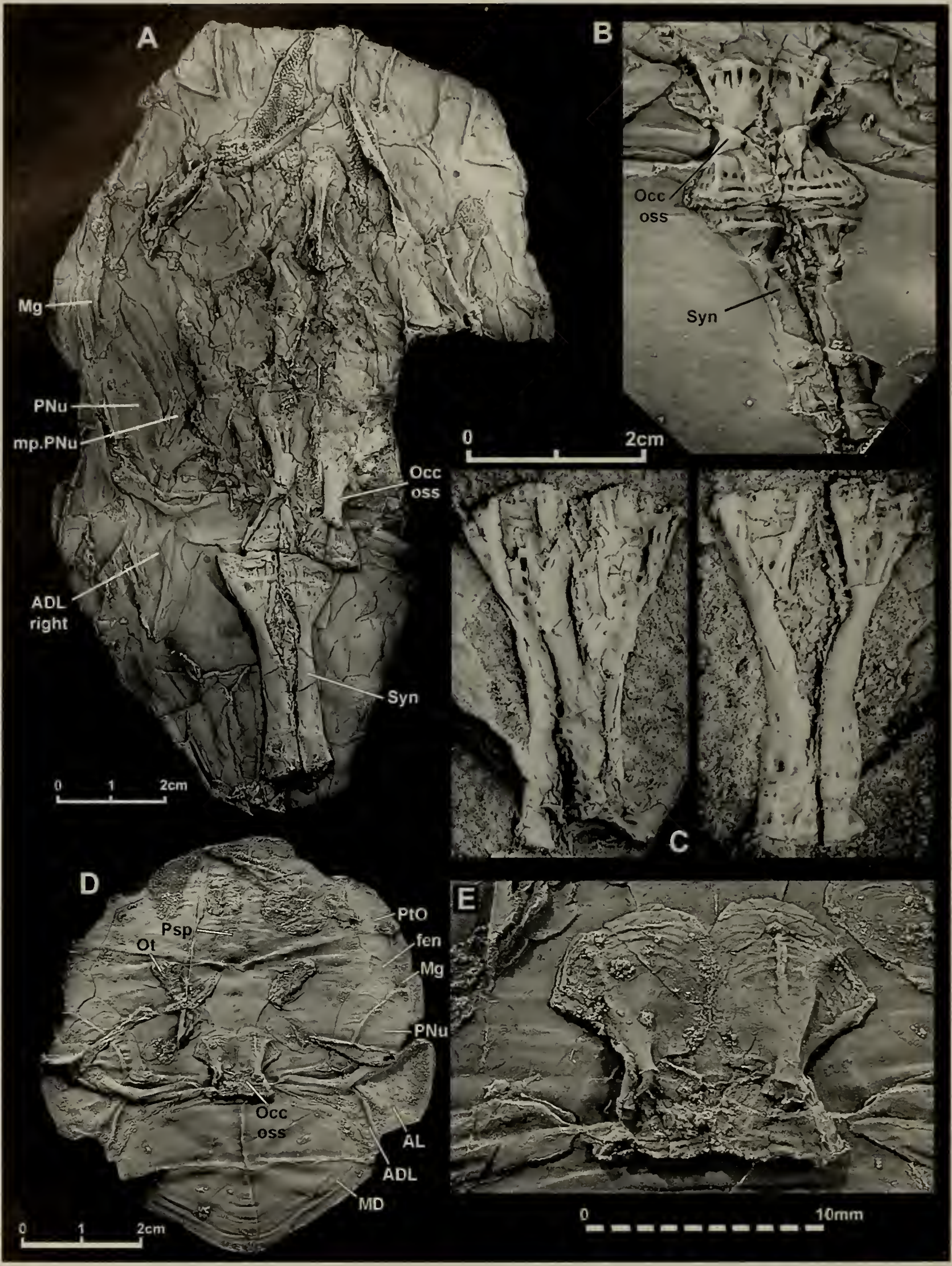

Figure 13A-E. *Cowralepis mclachlani* n. gen. and sp. Occipital and synarcual ossifications. A) AMF96751, head and trunk shields, ventral view; ventral shield lost, exposing axial skeleton; B) AMF103763, occipital ossification and synarcual, ventral view; C) AMF96753, isolated synarcual; dorsal (left) and ventral (right); D) AMF96785, juvenile dorsal shield, ventral view showing occipital ossification; synarcual lost. E) detail, ventral view. Latex casts whitened with ammonium chloride sublimate.

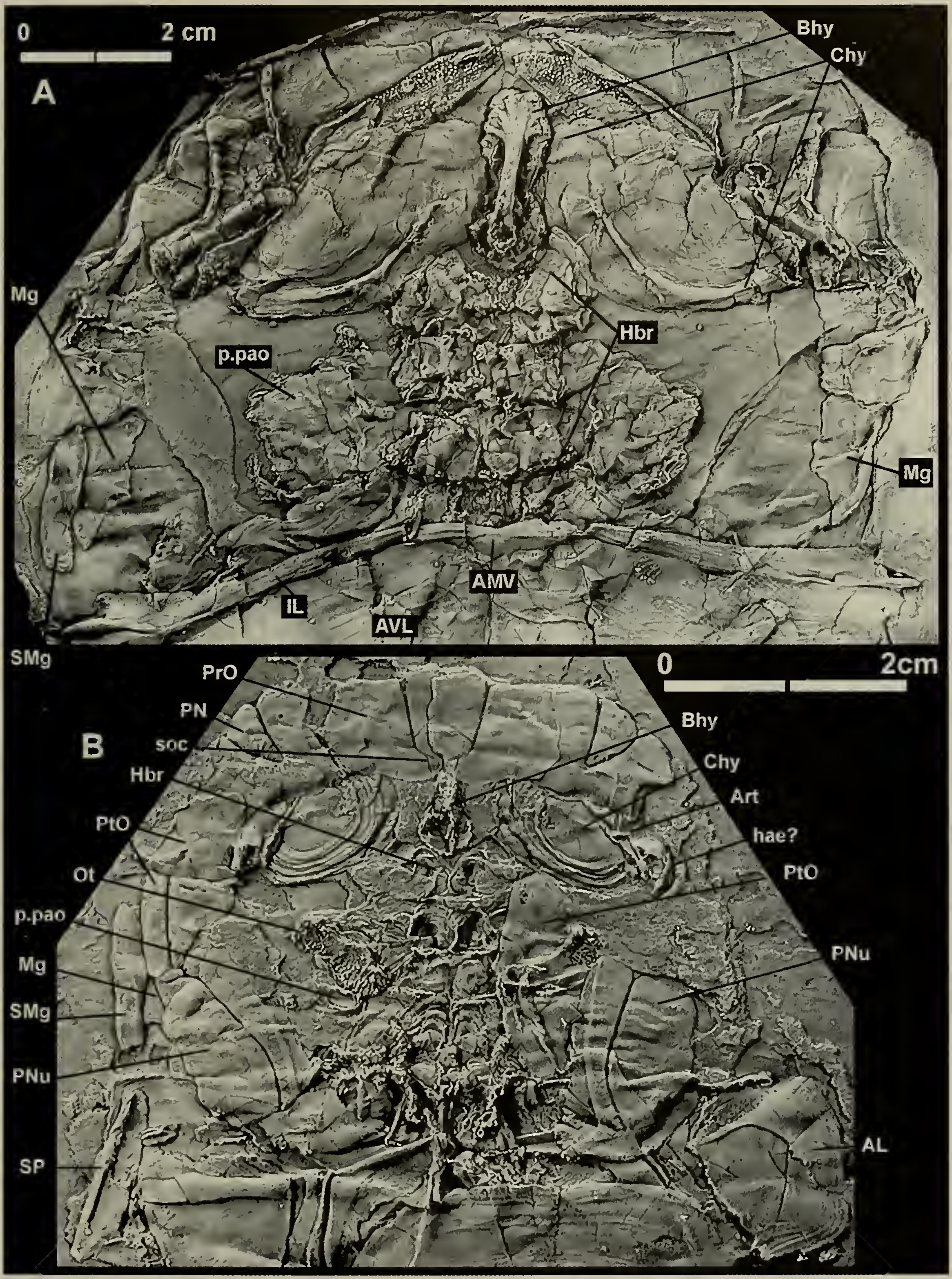

Figure 14A, B. *Cowralepis mclachlani* n. gen. and sp. A) AMF90007b, head shield of large individual, ventral view, showing all gnathal and visceral elements in association; B) AMF103776, smaller individual, head in dorsal view, Nu lost, exposing visceral branchial skeleton and otoliths in dorsal view, surrounded by circum-nuchal plates . Latex casts whitened with ammonium chloride sublimate.

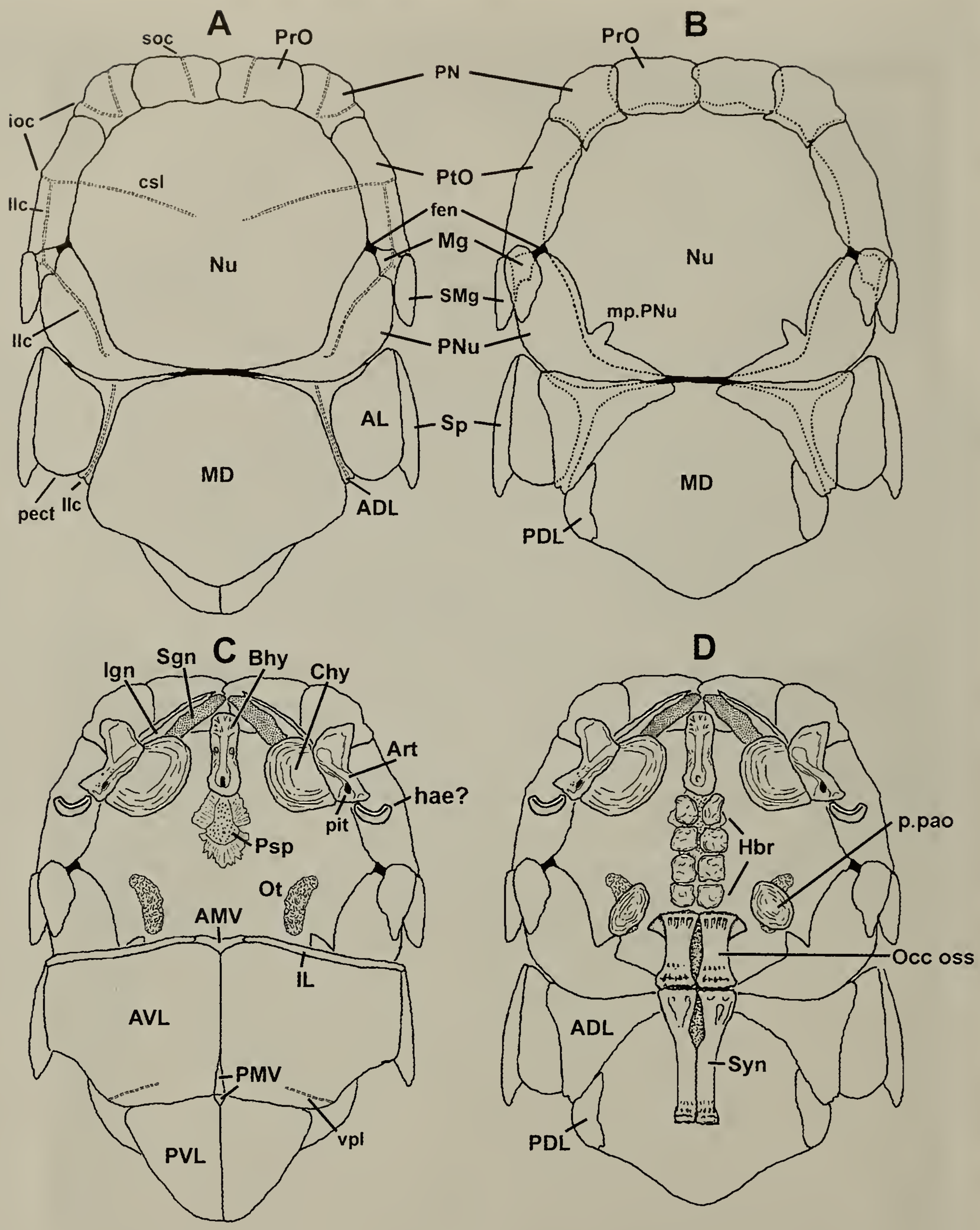

Figure 15A-D. *Cowralepis mclachlani* n. gen. and sp. A) reconstruction of craniothoracic armour, dorsal view; B) reconstruction of dorsal shield, ventral view (ventral shield omitted) showing overlap relationships of dorsal plates; C) reconstruction of craniothoracic armour, ventral view, showing gnathal elements, parasphenoid, otoliths, etc; D) reconstruction of dorsal shield, ventral view (ventral shield omitted) showing hypobranchials, occipital ossification and synarcual.

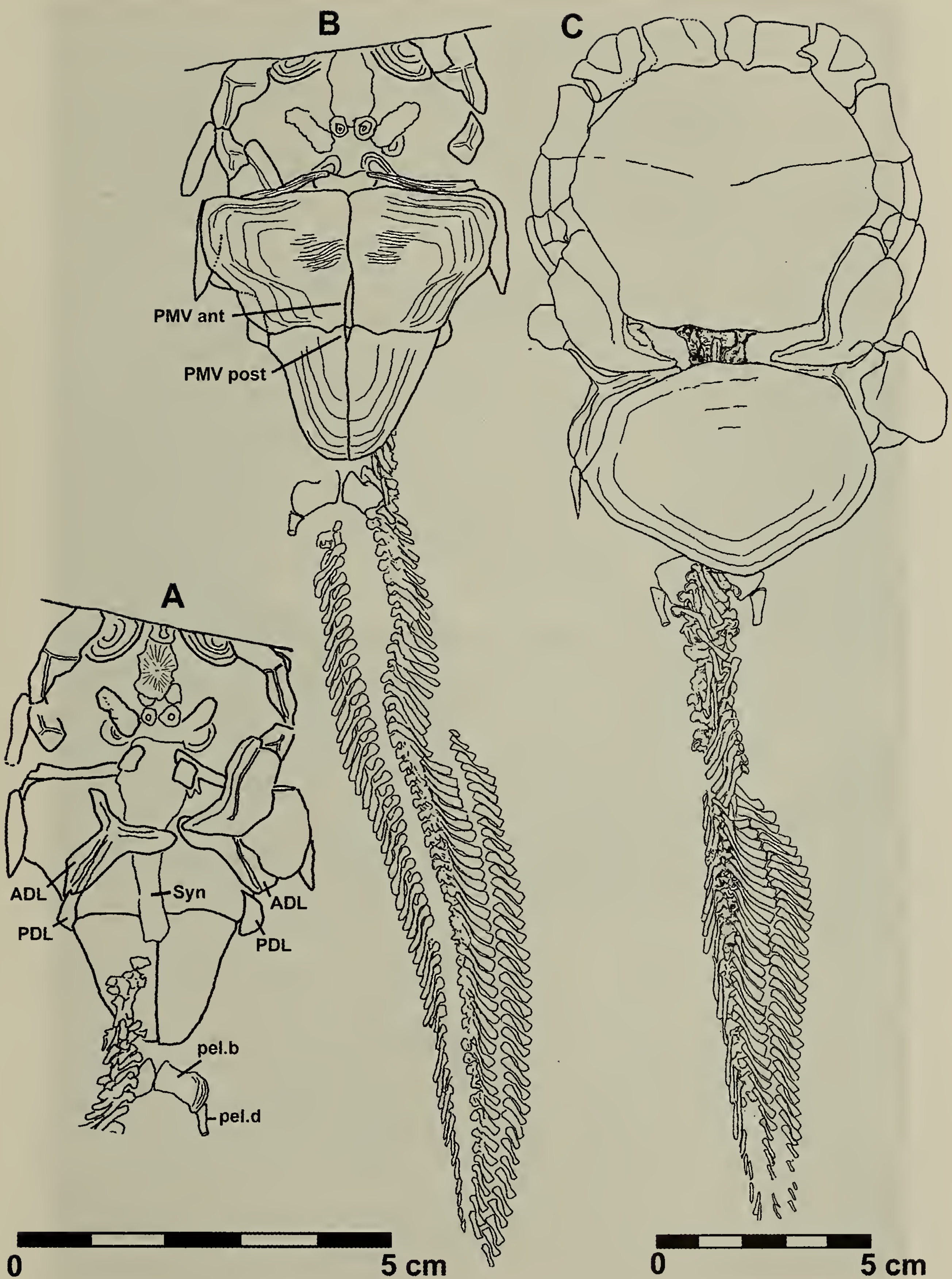

Figure 16A-C. *Cowralepis mclachlani* n. gen. and sp. A) AMF96764, dorsal view; Nu and MD plates lost, exposing ventral elements; B) AMF96765, counterpart showing ventral shield, pelvic fins and complete vertebral column; C) AMF90004, dorsal view. Both specimens digitally modified (to correct for tectonic deformation) and drawn to same length to illustrate the relative lengths of dermal armour/tail in smaller and larger individuals.of *Cowralepis*.

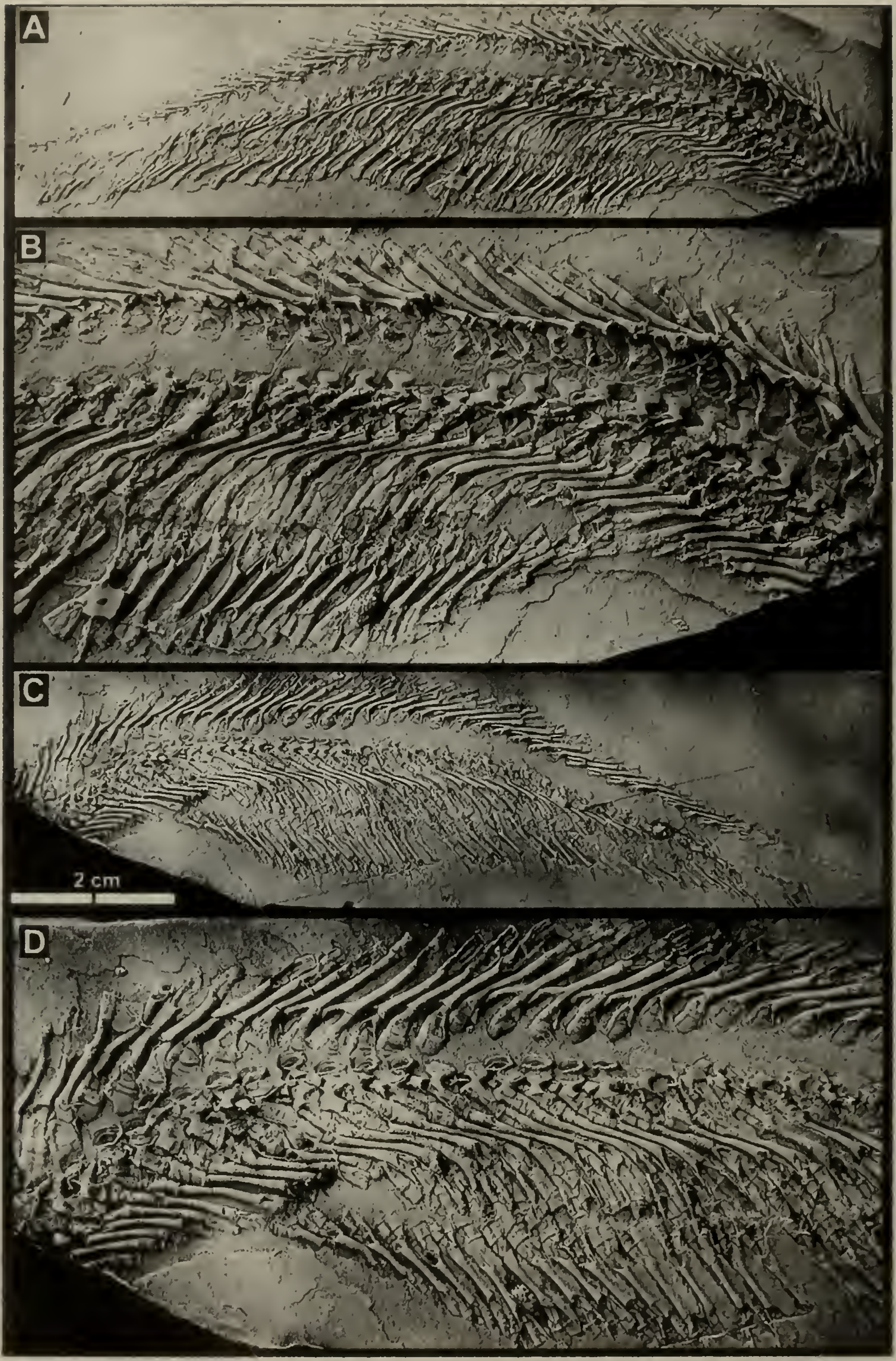

Figure 17A-D. *Cowralepis mclachlani* n. gen. and sp. Caudal fin. A. B) AMF90048a, caudal fin seen from right; B) detail of anterior region; C, D) AMF90048b, same caudal fin seen from left; D) detail of anterior region. Latex casts whitened with ammonium chloride sublimate.

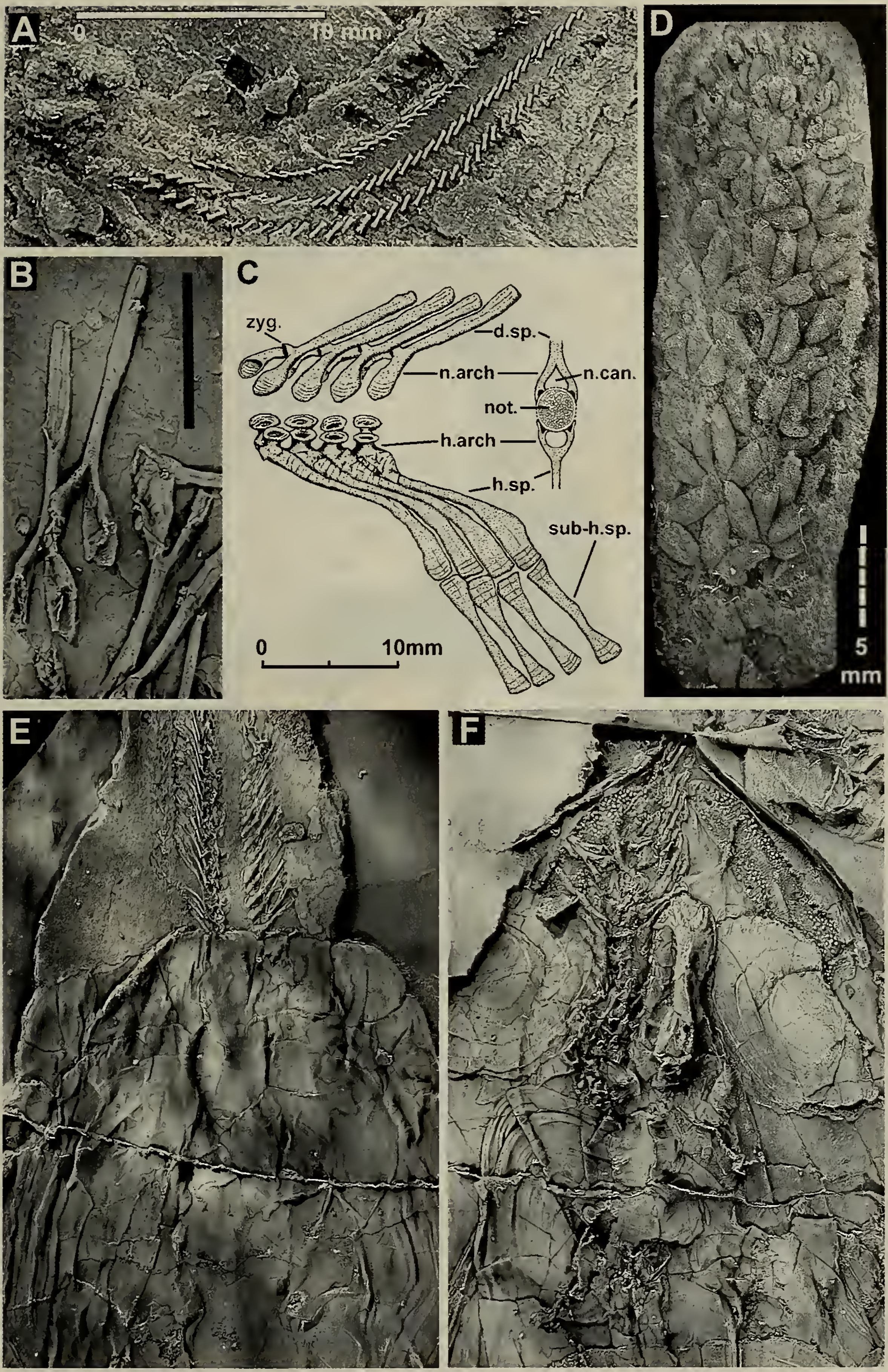

Figure 18A-F. *Cowralepis mclachlani* n. gen. and sp. A) AMF127159, juvenile vertebral column; B) AMF127154b, isolated neural arcualia: C) neural and haemal arcualia reconstructed from AMF90048 (cf Fig. 17); D) AMF127151a, egg sac from Merriganowry; E) AMF90011a, dorsal shield with smaller *Cowralepis* disappearing under anterior margin; F) AMF90011b, head shield in ventral view showing smaller *Cowralepis* inside buccal cavity (cf. Fig. 19 for interpretation). Latex casts whitened with ammonium chloride sublimate.

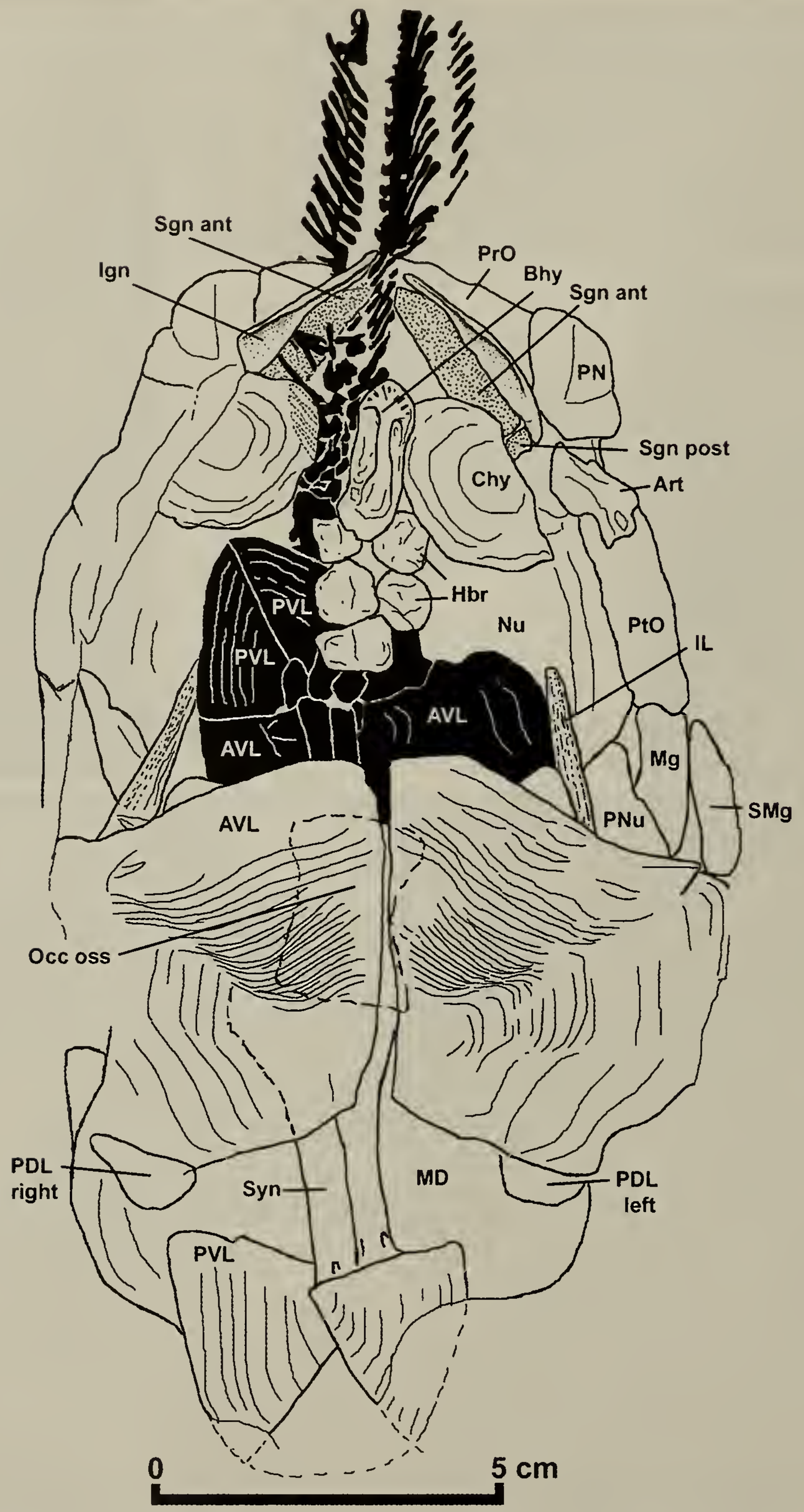

Figure 19. *Cowralepis mclachlani* n. gen. and sp. Combined sketch of the dorsal and ventral surfaces in AMF90011a, b. (cf. Fig. 18E, F). This individual appears to have died in the act of swallowing another *Cowralepis* individual that was too large, fortuitously providing invaluable information on the spatial relationships of the gnathal and branchial skeletal elements in *Cowralepis mclachlani.*

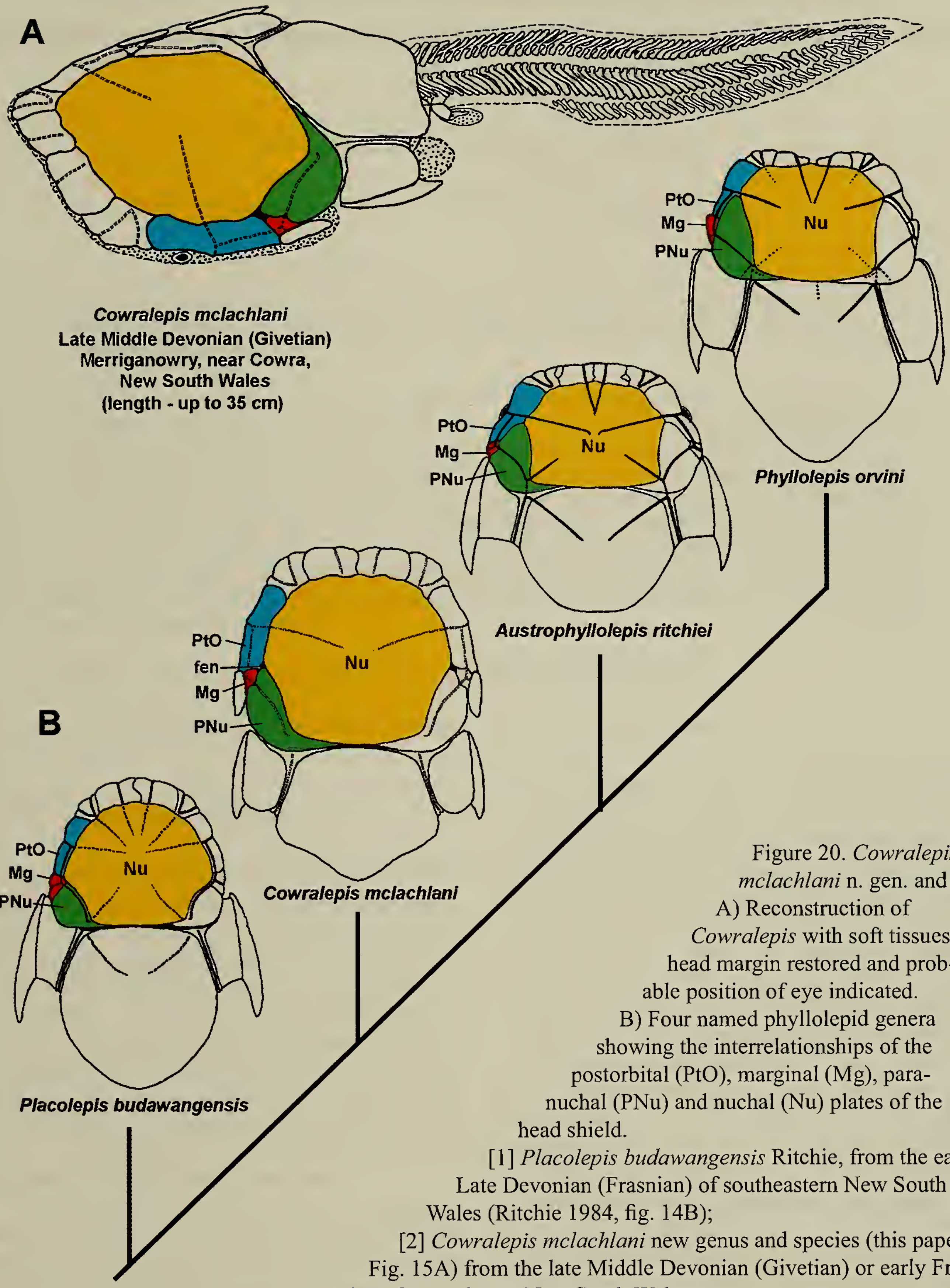

Figure 20. *Cowralepis mclachlani* n. gen. and sp. A) Reconstruction of *Cowralepis* with soft tissues of head margin restored and probable position of eye indicated. B) Four named phyllolepid genera showing the interrelationships of the postorbital (PtO), marginal (Mg), paranuchal (PNu) and nuchal (Nu) plates of the head shield.
[1] *Placolepis budawangensis* Ritchie, from the early Late Devonian (Frasnian) of southeastern New South Wales (Ritchie 1984, fig. 14B);
[2] *Cowralepis mclachlani* new genus and species (this paper Fig. 15A) from the late Middle Devonian (Givetian) or early Frasnian of central west New South Wales;
[3] *Austrophyllolepis ritchiei* Long from Mt Howitt, Victoria, originally dated as Frasnian, now thought to be Givetian (Young, pers. comm.). Long's reconstruction of *A. ritchiei* (1984, fig. 7A); digitally modified to correct for tectonic deformation at Mt Howitt.
[4] *Phyllolepis orvini* Heintz, from the Late Devonian (Famennian) of East Greenland (after Denison, 1978, fig. 29).

Larval Development and Autogeny in *Ochlerotatus camptorhynchus* (Thomson) (Diptera: Culicidae) from Southern Victoria

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Larval development and autogeny was examined in the mosquito *Ochlerotatus camptorhynchus* (Thomson) from southern Victoria. Larvae of *Oc. camptorhynchus* were reared in the laboratory at 5 constant temperatures (15, 20, 25, 30 and 35°C) and three constant salinities (0, 18 and 36 ppK). Of the five temperatures, survival ranged from 35.6% at 35°C to 84.4% at 20°C, and development times ranged from 12.1 to 37.1 days at 35°C and 15°C respectively. The minimum threshold temperature for development was 7.3°C, and the thermal constant was 324.0 ± 12.8 SE degree-days. No differences in development times or survival were detected for the three salinities. Adult mosquitoes reared from field-collected pupae and larvae reared on a high-nutrition diet displayed no autogenous egg development. A positive relationship was found between adult body size (wing length) and fecundity in blood-fed adults, with fecundity ranging from 40 to 112 eggs per female.

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Key Words Autogeny, culicidae, larval development, fecundity, *Ochlerotatus camptorhynchus*

INTRODUCTION

The southern saltmarsh mosquito, *Ochlerotatus camptorhynchus* (Thomson), is an abundant mosquito species in southern coastal Australia from southwest Western Australia around to the southern coast of New South Wales, including Tasmania (Dobrotworsky 1965; Russell 1993). It is a confirmed vector of Ross River virus (Ballard and Marshall, 1986) and suspected vector of Barmah Forest virus (Aldred et al. 1990; Russell 1995). *Ochlerotatus camptorhynchus* was also detected on the North Island of New Zealand during 1998 (Hearnden et al. 1999), and a large eradication program is now under way.

Larvae of *Oc. camptorhynchus* are typically found in brackish to fresh ground pools associated with coastal swamps and bushland (Dobrotworsky 1965; Lee et al. 1984), but also in some salinity-affected areas inland (Wishart 2002). No studies have previously investigated the responses of immature stages of *Oc. camptorhynchus* to different temperatures or salinities.

Autogeny, or the ability to develop an initial batch of eggs without a blood meal, has been described to varying levels in several Australian mosquito species including *Anopheles hilli* Woodhill and Lee (Sweeney et al. 1973), *Ochlerotatus vigilax* (Skuse) (Sinclair 1976; Hugo *et al.* 2003), *Culex annulirostris* Skuse (Kay et al. 1986), *Culex sitiens* Wiedemann (Fanning et al. 1992), *Ochlerotatus australis* (Erichson) (Brust 1997) and *Culex molestus* Förskal (Dobroworsky 1954). Of these mosquitoes, arguably the most closely related ecologically is *Oc. vigilax*, a saltmarsh mosquito replacing *Oc. camptorhynchus* as the dominant mosquito in northern coastal areas from southern New South Wales around to southern Western Australia (Lee et al. 1984; Russell 1993). Autogeny in *Oc. camptorhynchus* has not previously been investigated. Production of an autogenous egg batch may delay the first mosquito-host contact (Kay et al. 1986), and is thought to accelerate the rate of natural increase of mosquito populations (Tsuji et al. 1990).

The purpose of this study is to increase our understanding of the development and survival of larval *Oc. camptorhynchus*, which may provide for greater accuracy of timing of larvicide applications, as well as a better understanding of the basic ecological parameters of this important mosquito species.

METHODS

Larval development

Thirty newly hatched larvae (1st instar) of *Oc. camptorhynchus* (<12hrs old) from a saltmarsh at Breamlea (144°35' East, 38°13' South), near Geelong in southern Victoria, were put into each of six translucent plastic containers with 300 ml of water (salinity = 18 ppK). Sets of six containers (total = 180 larvae) were then placed in a water bath for each of 15, 20, 25, 30 and 35°C. Larvae were fed ground K9® Gold Fish Food (Go-Pet Petcare Solutions) at rates of: 1st and 2nd instars = 0.12 mg/larva/day, 3rd instar = 0.48 mg/larva/day, 4th instar = 0.96 mg/larva/day. Any excess food was removed daily. Subsamples of 20 adult females were taken from each temperature treatment, and those had a single wing removed and measurement with a graticule eyepiece at 10x magnification from the wing tip (excluding the fringe) to the arculus (Harbach and Knight 1980).

To evaluate salinity tolerance, seawater (36 ppK) was collected from near Breamlea and used as stock solution, diluted equally with distilled water to produce a concentration of 18 ppK, and with distilled water being used for the 0 ppK concentration. Thirty newly hatched larvae, again collected from the Breamlea saltmarsh, were added to 300 ml of each concentration (2 replicates each). Concentrations were kept constant by adding distilled water daily to compensate for evaporation. A constant temperature of 25°C was maintained with the use of a water bath. Larvae were fed as described above.

Average development time and survival for all immature stages were calculated using frequency-weighted means, based on daily counts. Analysis of Variance with Student Newman-Keuls post-hoc tests (SPSS v11) was used to compare differences in total development times and survival to adulthood between treatments. The relationship between larval development times and temperature, plus wing length and temperature, was examined using least squares linear regression. The day-degrees (K) needed for development at each experimental temperature (T°C) and duration of development (t days) was calculated from K = t (T-C), where C is an extrapolation of minimum temperature for development.

Autogeny

Autogeny was assessed in two categories of mosquito: 1) adults derived from field-collected pupae, and 2) adults derived from larvae reared on a high nutrition diet. All larvae and pupae were taken from a field site at Breamlea flora reserve near Geelong in southern Victoria (144°35' East, 38°13' South, Fig 3.1).

The field-sourced pupae were collected from the same site at Breamlea during September 2002 and October 2003 and were allowed to emerge over a 24-hour period in a cage of approx 0.5m^3. The laboratory-reared larvae were collected during October 2003 as first instar and reared with a high nutritional feeding regime at a daily rate of: 1st and 2nd instar = 0.16 mg/larva, 3rd instar = 0.64 mg/larva, and 4th instar = 1.28 mg/larva. The field-collected pupae and laboratory-reared larvae were kept in water taken from the field (36ppK) with salinity kept constant by topping up containers with distilled water. All emerged adult mosquitoes were given immediate access to 10% sucrose solution and males were not removed from the cages. Immatures and adults were kept at ambient laboratory temperatures (approx 20 ± 5°C). Ten days after emergence, all female mosquitoes were removed and cold anaesthetised before dissection. Ovaries were dissected and placed on slides with a saline solution for inspection of follicles at 200x magnification. Recording of stages of ovarian development was done with reference to Clements and Boocock (1984).

A separate sample of mosquitoes derived from pupae at Breamlea flora reserve (October 2003) was allowed to blood-feed three days after emergence. These mosquitoes were dissected seven days after the blood meal and their fecundity (number of eggs per female) recorded, as well as with wing length.

RESULTS

Larval development

At all temperatures tested, the first and fourth instars had the shortest and longest development times, respectively (Table 1). A significant difference between total development time and temperature was obtained (d.f. = 4, M.S. = 1313.06, F = 66.65, $P < 0.01$). Mean development was 12.1 ± 0.9 days at 35°C, and 37.1 ± 1.3 days at 15°C. Survival to adulthood was significantly different between the temperature treatments (d.f. = 4, M.S. = 205.55, F = 12.42, $P < 0.01$), with 84.4% survival at 20°C and 35.6% survival at 35°C. No difference was obtained for total immature development in different salinity treatments (d.f. = 2, M.S. = 2.99, F = 0.22, $P = 0.80$). No difference was obtained for immature survival between the salinity treatments (d.f. = 2, M.S. = 4.50, F = 1.50, $P = 0.35$).

Table 1 Duration, development rate and survival of immature stages of *Oc. camptorhynchus* at constant water temperatures and salinities. *Values followed by different letters are significantly different at the 5% level (Student-Newman-Keuls test). ^Proportion of immature development per day.

	Days (mean ± SE) in each stage							
Temperature °C	I	II	III	IV	P	Total*	Development rate^	%Survival*
15	4.1 ± 0.5	6.5 ± 1.0	8.1 ± 1.2	11.3 ± 1.2	7.1 ± 0.9	37.1 ± 1.3a	0.027	68.9 a,b
20	3.1 ± 0.8	4.2 ± 1.1	5.3 ± 1.2	7.5 ± 1.3	6.4 ± 1.2	26.5 ± 1.2b	0.038	84.4 a
25	2.4 ± 0.9	3.3 ± 1.0	4.0 ± 1.0	5.4 ± 1.1	5.1 ± 1.0	20.2 ± 1.0c	0.05	76.1a
30	1.8 ± 0.6	2.3 ± 0.7	2.6 ± 0.8	3.5 ± 1.0	3.1 ± 0.9	13.3 ± 0.9d	0.075	52.8 b
35	1.5 ± 0.6	2.3 ± 0.7	2.5 ± 0.7	28 ± 1.0	3.0 ± 0.8	12.1 ± 0.9d	0.083	35.6 c
Salinity (ppK) at 25°C								
0	2.5 ± 0.8	3.2 ± 1.0	4.1 ± 1.0	5.2 ± 1.1	4.0 ± 0.9	18.9 ± 1.1a	0.052	98.5 a
18	2.4 ± 0.8	3.2 ± 0.9	4.2 ± 1.0	5.2 ± 1.1	5.0 ± 1.0	20.0 ± 1.0a	0.05	88.3 a
36	2.5 ± 0.8	3.2 ± 1.0	4.1 ± 1.0	5.5 ± 1.1	4.5 ± 1.0	19.9 ± 1.0a	0.053	93.3 a

Table 2. Percentage ovarian development in two categories of adult female *Oc. camptorhynchus*, 10 days post emergence.

	Percent ovarian stage								
Source of adults	Ia	Ib	Iia	Iib	IIIa	IIIb	Iva	Ivb	V	Total No.
Pupae taken from field	0	19	51.2	26.2	3	0.6	0	0	0	168
Larvae reared on high diet	0	12.4	42.8	32.4	9	3.4	0	0	0	145

A significant linear relationship (d.f. = 1, M.S. = 0.01, F = 109.01, $P < 0.01$) was obtained between water temperature and rate of development with a coefficient of determination of $R^2 = 0.971$ (Fig 1). The lower threshold for development was extrapolated to 7.3°C, and the thermal constant required for complete development was calculated as 324.0 ± 12.8 SE degree-days. A significant negative linear relationship (d.f. = 1, M.S. = 1.12, F = 68.133, P < 0.01) was obtained for wing length and temperature (Fig 2.)

Autogeny

No autogeny was observed in either category of *Oc. camptorhynchus* assessed in this study. The most common stage of follicular development in the two categories examined was stage IIa (field = 51.2%, laboratory = 42.8%) (Table 2). The next highest percentage of follicular development was stage IIb (field = 26.2%, laboratory = 32.4%). All blood fed mosquitoes developed eggs to stage V, seven days after the blood meal. A significant linear relationship was found between body size (wing length) and the number of mature follicles per mosquito (d.f. = 1, MS = 5,668.00, F = 41.64, P < 0.01) (Fig 3). Fecundity of blood-fed females ranged from 40 to 112 eggs per mosquito (72.41 ± 2.99 SE, n = 34).

DISCUSSION

This study demonstrates that *Oc. camptorhynchus* is well adapted to cooler temperatures and is widely tolerant of different salinities. In contrast to *Oc. vigilax*, the Breamlea population of *Oc. camptorhynchus* exhibits no autogeny, indicating a different survival strategy to its more northern congener.

The development of larval *Oc. camptorhynchus* responded to temperature and was linear between 15 and 35°C. None of the temperatures tested were lethal to the Victorian strain *Oc. camptorhynchus*. The development threshold temperature of 7.3°C for *Oc. camptorhynchus* suggests development of immatures

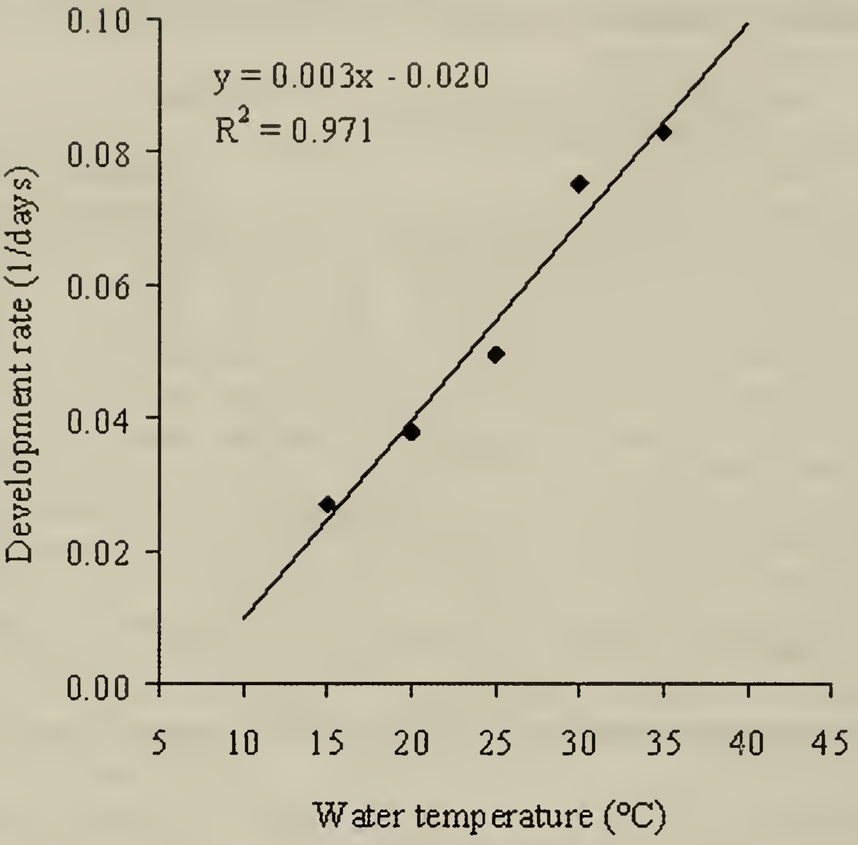

Figure 1. Relationship between development rate of immature stages of *Oc. camptorhynchus* and five constant water temperatures.

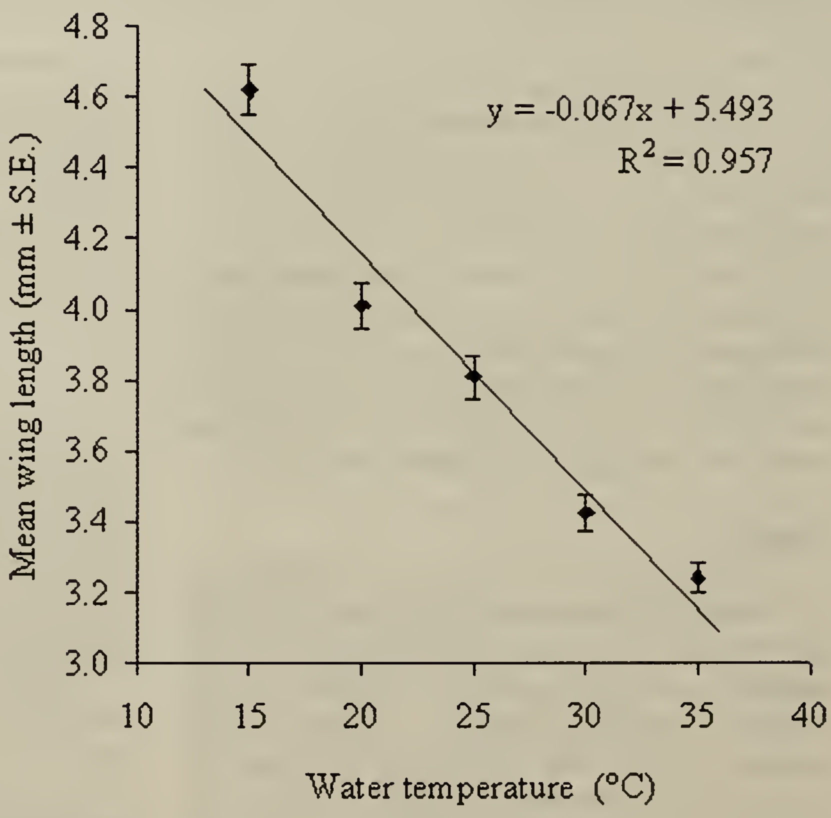

Figure 2. Relationship between wing length of adult female *Oc. camptorhynchus* and five constant water temperatures.

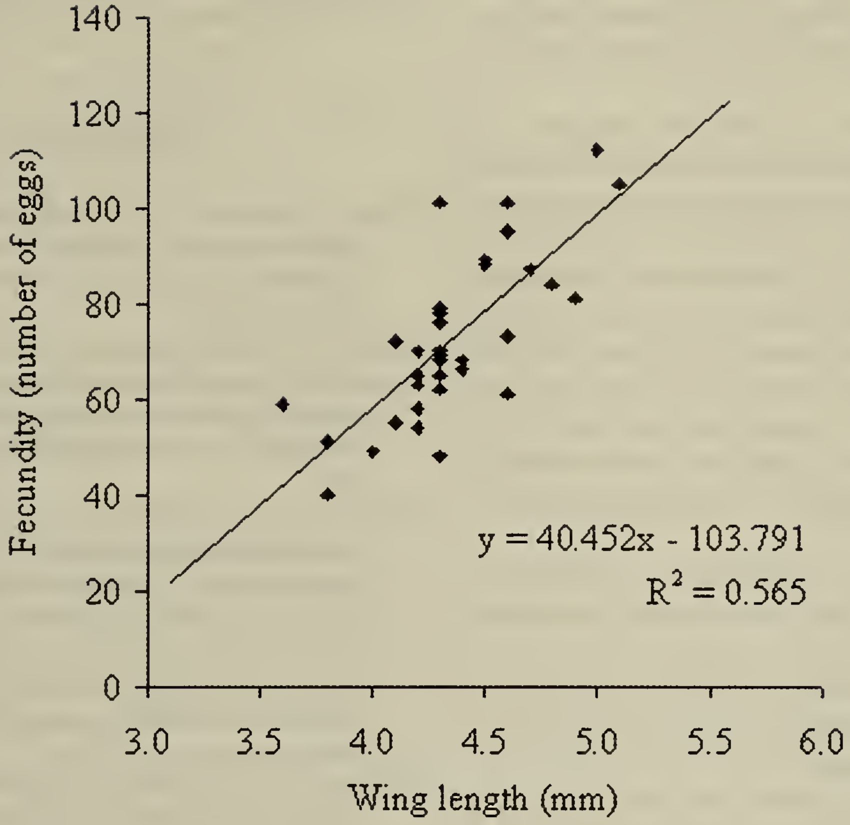

Figure 3. Relationship between wing length and fecundity for blood-fed *Oc. camptorhynchus* (n = 34).

will continue in winter in southern Victoria, where minimum temperatures of approximately 8°C commonly occur (Bureau of Meteorology 1993). The larvae of *Oc. camptorhynchus* at 15°C had higher survival (69%) and a lower development threshold (7.3°C) compared to more northern species reared at 15°C, such as *Cx. sitiens* from southeast Queensland (10% survival, 11.9°C threshold) (Mottram et al. 1994), *Cx. annulirostris* from northern Victoria (3 % survival, 9.7°C threshold) (McDonald et al. 1980) and *Ae. aegypti* from north Queensland (24% survival, 8.3°C threshold) (Tun-Lin et al. 2000).

At 25°C, the absence of any affect of salinity on the development or survival of larval *Oc. camptorhynchus* suggests a high level of adaptation to saline conditions. The mechanism for survival in high salinities is likely to be a capacity to produce non-toxic osmolytes (Bradley 1987), which can neutralise the harmful effects of high salt concentrations. Possible interaction between salinity and temperature was not examined and differences in survival and/or development may be observed at varying salinities at higher or lower temperatures.

During expected spring or summer temperatures of 15-25°C, and following inundation of larval habitat, survival of *Oc. camptorhynchus* will be high, depending on predation, and development may take 20-37 days. No threshold salinity, above which survival is curtailed, is apparent for *Oc. camptorhynchus* between 0ppK and 36ppK. Given the optimal stage for treatment with the control agent *Bacillus thuringiensis israelensis* are 2nd to 3rd instars, this suggests a large treatment window of approximately 7-15 days, and if s-methoprene were to be used, the time before treatment could be extended to 4th instar if necessary. However, in situations where prolonged temperatures of above 30°C occur, survival of *Oc. camptorhynchus* might be expected to be lower, and control may not be warranted. The operational criteria for control, therefore, should be based on larval densities, size of breeding site and on proximity to residential areas.

Adult *Oc. camptorhynchus* derived from field-collected pupae and larvae reared with high nutrition in the laboratory both failed to exhibit autogeny. This differs remarkably compared to the saltmarsh mosquitoes *Oc. vigilax* from Australia (Sinclair 1976; Hugo et al. 2003), and *Oc. taeniorhynchus* from the USA (O'Meara and Edman 1975), where autogeny rates of up to 100% and 94.4% were observed in these studies, respectively.

Of all the adults assessed for autogeny, the majority of displayed ovarian development to stages IIa or IIb, which is the previtellogenic resting stage described by Clements and Boocock (1984). At this developmental stage, it is thought that a blood meal is required to facilitate further follicular development and oviposition. That a greater percentage of adults reared on a high diet had follicles over stage IIb (12.4%) compared to adults derived from field-collected pupae (3.6%) suggests that nutrition may be important in influencing ovarian development in *Oc. camptorhynchus*.

The fecundity of blood-fed *Oc. camptorhynchus* increased with body size, a well-known relationship documented with other mosquitoes (Nayar and Sauerman 1975; Armbruster and Hutchinson 2002). Larger mosquitoes might therefore be expected to produce larger egg batches

The anautogeny apparent from the sampled *Oc. camptorhynchus* suggests this species may require blood meals for survival and egg development and therefore appetential dispersal after emergence might occur earlier, in relative terms, than for *Oc. vigilax*, as time for egg development and oviposition is not required. This in turn suggests that the role of *Oc. camptorhynchus* in biological transmission would commence earlier, as this species is unlikely to mature an autogenous egg batch. From an ecological standpoint, dispersal of anautogenous *Oc. camptorhynchus* would seem to be a risky survival strategy when suitable saltmarsh habitats are discontinuous, as on the Bellarine Peninsula where this study was performed. This result might be expected to change geographically, where different genetic and environmental factors may influence autogenous expression (Sota and Mogi 1995; Hugo et al. 2003), and is worthy of further study.

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BOOK REVIEW

Bibliography of Australian Entomology 1687-2000

by G. Daniels, 2004. Privately published by the author, P.O. Box 828, Mt Ommaney, Qld 4074. Email: g.daniels@uqconnect.net. Two volumes. viii, 1776 pages. A$275.

This very impressive work, in two large hard-bound volumes, documents the Australian entomological literature from the earliest published record to the year 2000 and partly beyond. It lists over 52,000 references and attempts to include every publication that mentions an Australian insect. Some three quarters of the work (1322 pages) is occupied in documenting the references while the remaining quarter (450 pages) comprises a very comprehensive index and a list of journal titles. The work begins with a Contents listing and a short Introduction. The two volumes are case bound for heavy use.

References are listed alphabetically by author and chronologically by date, in an easy to read format. Multi-authored works are cross referenced to each author. Taxonomic references are accompanied by a list of all new taxa described; these lists are sometimes extensive. Author's given-names are included where known and biographical summaries are included for some authors. The bibliography also includes references on Collembola and Protura, groups which until recently were included in the class Insecta.

While a serious attempt has been made to list every publication mentioning an Australian insect the author is aware that it is inevitable he has not achieved perfection. However, it is clear that this is by far the most comprehensive bibliography of Australian entomology ever published. Further, it is the only bibliography on all Australian entomological literature for the period 1931-2000.

In addition to author listings in the References there are entries for topics such as Australian Museum, ANIC, Coleopterorum Catalogus, Genera Insectorum, Royal Entomological Society of London, School of Public Health & Tropical Medicine, Zoological Catalogue of Australia and names of ships of famous voyagers cross-referenced to relevant literature. References with complex or controversial publication details are annotated with notes on dates of publication, pagination of parts, authors, etc.

The Index is an important part of this Bibliography. It is exceptionally detailed and comprehensive. References are arranged under 242 major subject areas such as Behaviour, Christmas Island, Distribution, Insecticides, Forensic Entomology, Fungal Diseases, Keys, Malaria, Morphology, Phylogeny, Sound, Taxonomy, Vision and Zoogeography. These are further divided by Order, Family (and species for economic groups), Author and Year. For example, entries under 'Biological Control of Insects' are listed under 18 subheadings which in turn are further divided into family headings and in some cases species headings, the total entry running to over 7 pages of small print. This enables the user to locate literature on almost any subject.

Works such as this require exceptional patience, perseverance and an eye for detail. It is evident that the author has these attributes in abundance. Typographical errors are exceedingly rare in the reference list and index, although a few have crept into the Introduction. The author is to be congratulated on a super- human effort that provides a basic tool for Australian entomologists. It is clear that anyone wanting to get into the literature on any subject concerning Australian entomology should consult this impressive work. It is not available electronically but this is of little consequence because the Index is so comprehensive. At least as hard copy it will always be readily accessible.

M.S. Moulds
Australian Museum

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(this is an abbreviated form – the full instructions can be obtained from our web site or from the Secretary)

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2. Manuscripts should be submitted to the Editor (M.L. Augee, PO Box 82, Kingsford NSW 2032). All manuscripts are sent to at least two referees and in the first instance three hard copies, including all figures and tables, must be supplied. Text must be set at one and a half or double spacing.

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Chapters or papers within an edited work:

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