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A REVIEW OF LATERITE STUDIES IN SOUTHERN SOUTH AUSTRALIA

*By Robert P. Bourman**

Summary

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Key Words: laterite, laterite profiles, ferricrete, polygenetic profiles, peneplains, deep weathering, palaeoclimatic indicators, multicyclic landscapes, morpho-stratigraphic markers.

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In southern South Australia interpretations of landscape evolution have depended heavily on recognition of parts of an original normal laterite profile, consisting of a pallid, bleached zone successively overlain by a mottled zone and laterite, a ferruginous and/or aluminous crust. This profile has been associated with formation on a peneplain surface under a humid, but seasonally dry, tropical climate. The possible preservation of a pristine laterite surface of great antiquity in the modern landscape on uplifted peneplains has been entertained by some workers, but questioned by others. Alternatives to this approach are provided by stratigraphic investigations of polygenetic profiles, and a continual weathering model of laterite formation that results in lateral variability in the distribution of pallid, mottled and laterite materials on a surface initially with irregular topography. Interpretations of lateritised landscapes include differential dissection of a complete laterite profile on an uplifted peneplain surface, multicyclic landscapes successively lateritised and the formation and lateritisation of high level surfaces during uplift.

Evidence of laterite formation under non-tropical conditions questions the climate-laterite correlation as does the lack of reliable minerals as climatic indicators of lateritisation. Furthermore, the recognition of lateritisation occurring throughout the Mesozoic and Cainozoic restricts the usefulness of laterite as a palaeoclimatic and morpho-stratigraphic marker.

KEY WORDS: laterite, laterite profiles, ferricrete, polygenetic profiles, peneplains, deep weathering, palaeoclimatic indicators, multicyclic landscapes, morpho-stratigraphic markers.

Introduction

There is a long history of research on materials called laterite in South Australia. The general distribution of lateritic materials in southern South Australia is shown in Fig.1. Specifically, these materials include ferruginous and aluminous crusts, variably described as 'ortstein', 'ferruginous duricrust' (Lang 1965), 'duricrust' (Woolnough 1927), 'ironstone' (Teale 1918), 'ironstone cappings' (Segnit 1937), 'indurated zones', 'ironstone gravels' (Prescott 1931) and 'ferricrete' (Firman 1967a; Bourman 1969[1]; Milnes *et al.* 1985), weathered bedrock, sediments and soils, variably ferruginised, mottled and/or bleached. This paper summarises and critically comments on these definitions. Issues addressed include the diversity of interpretations concerning the nature of laterite, processes of laterite development, laterite profiles, the topographic and climatic requirements for its formation, its age, and reconstructions of, and interpretations drawn from, lateritic landscapes.

The term 'laterite' has been in the scientific literature since the publication of Buchanan (1807). David (1887) discussed the origin of laterite in the New England district of New South Wales, but did so without reference to Buchanan's work, and the term did not appear in the South Australian literature until more than 100 years after its first usage (Teale 1918). Nevertheless, features subsequently regarded as laterite were discussed by early workers under labels such as 'Desert Sandstone' (Woolnough 1927) and 'Upland Miocenes' (Tate 1879).

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[1] BOURMAN, R. P. (1969) Landform Studies near Victor Harbour. B.A. (Hons) thesis, The University of Adelaide (unpubl.).

With few exceptions, the majority of investigators in South Australia have followed the view that laterite formed as a result of intense chemical weathering in a seasonally dry tropical climate on a peneplain surface, largely during the Tertiary. These conditions favoured the development of a laterite profile comprising a leached sandy A-horizon successively underlain by laterite, a mottled zone and a pallid zone resting on unweathered bedrock (Fig.2). Generally, the present discontinuous distribution of these materials has been ascribed to differential erosion following tectonic uplift of the peneplain.

Definition of laterite

Laterite as a rock unit

Early studies of laterite in southern South Australia were undertaken by geologists, who considered laterite to be a rock or sedimentary unit and equated it with 'Desert Sandstone' (silcrete) or with terrestrial deposits referred to as 'Upland Miocenes'. For example, Tate (1879, p. lix) regarded 'evenly-bedded sandrock, mottled clayey sands and ironstone conglomerates', occupying flat-topped localities in the Adelaide foothills and within the ranges as 'Upland Miocenes'. He

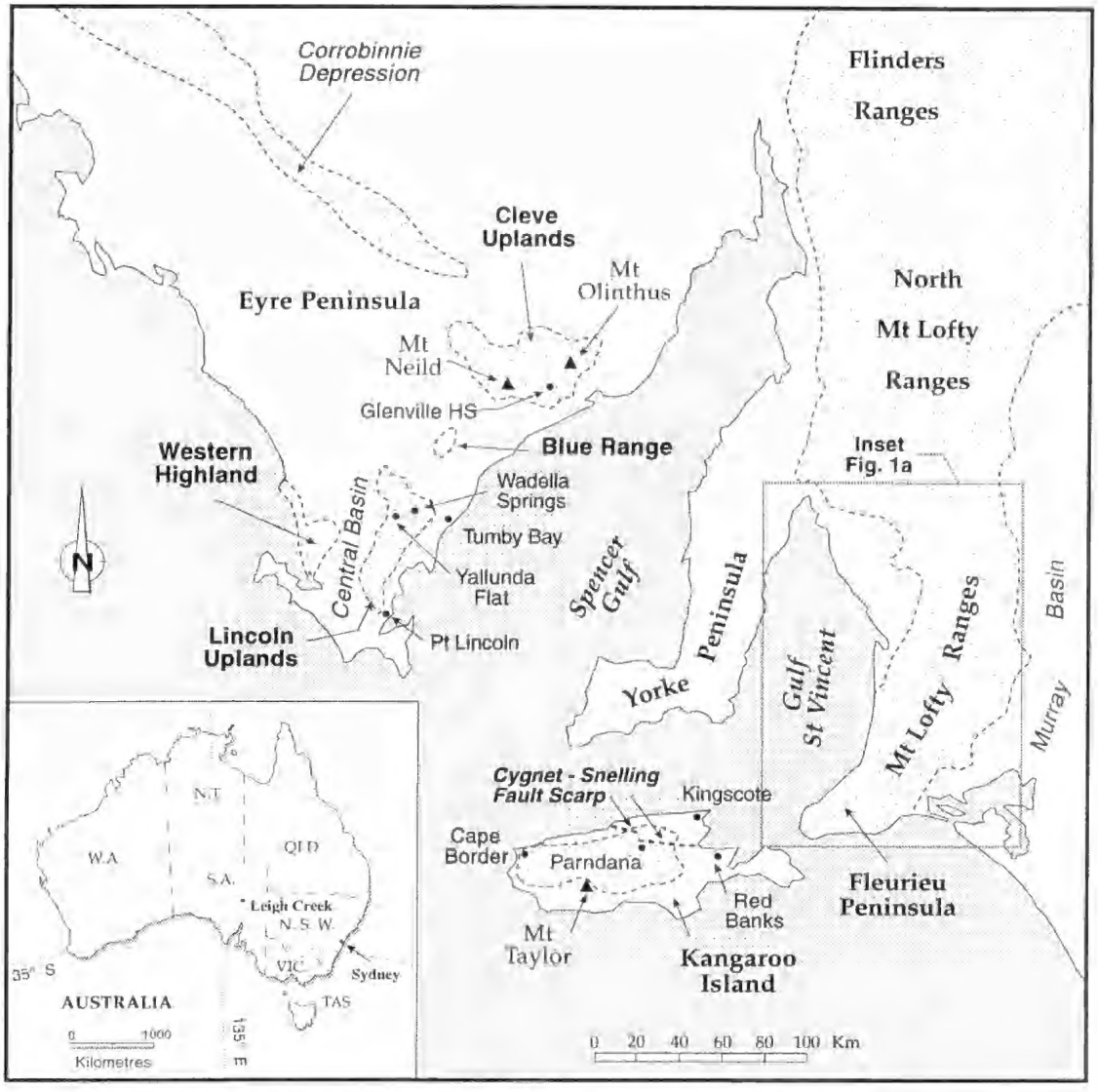
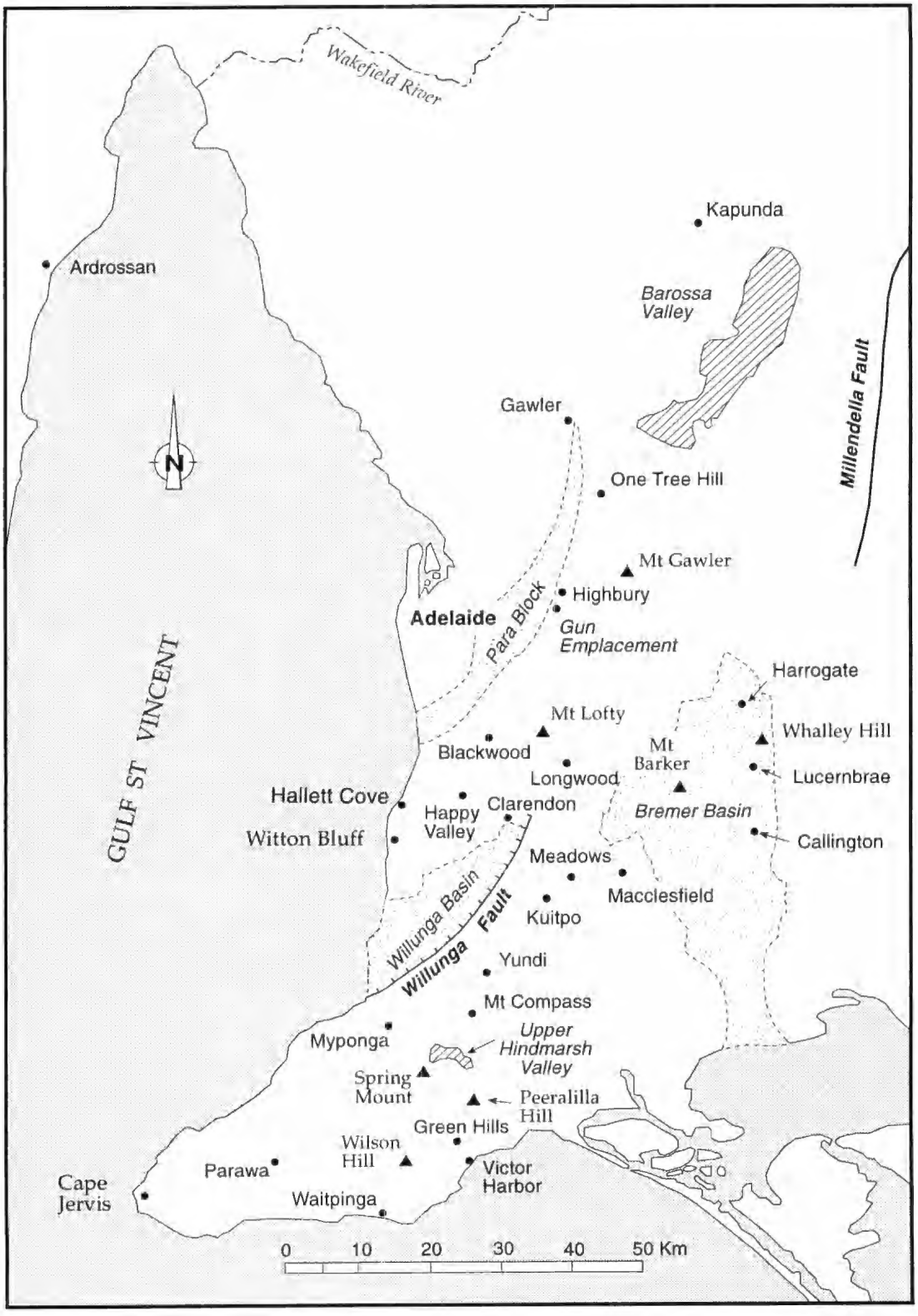


Fig. 1. Map showing the localities of lateritic areas in southern South Australia referred to in the text.

Fig. 1A. (Opposite page). Inset in Figure 1.


Wakefield River
Kapunda
Ardrossan
Barossa Valley
Millendella Fault
N
Gawler
One Tree Hill
Mt Gawler
Highbury
Adelaide
Para Block
Gun Emplacement
Harrogate
Mt Lofty
Whalley Hill
Blackwood
Mt Barker
Longwood
Lucernbrae
GULF ST VINCENT
Hallett Cove
Clarendon
Happy Valley
Bremer Basin
Witton Bluff
Callington
Meadows
Willunga Basin
Fault
Macclesfield
Kuitpo
Willunga
Yundi
Mt Compass
Myponga
Upper Hindmarsh Valley
Spring Mount
Peeralilla Hill
Green Hills
Wilson Hill
Parawa
Victor Harbor
Cape Jervis
Waitpinga
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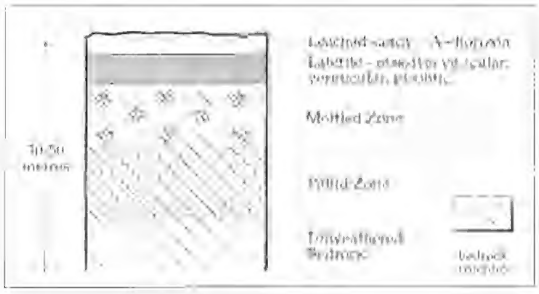


Fig. 2. Sketch of the pedogenic model of the normal or standard laterite profile incorporating a sandy, bleached A horizon above a laterite horizon, successively underlain by companion materials of mottled and bleached bedrock (Stephens 1946), considered to have developed on a peneplain under humid tropical conditions.

considered them to be correlative both with terrestrial clays overlying fossiliferous limestone at Adelaide and Tertiary terrestrial sediments bordering the Mt Lofty Ranges. Later work has demonstrated that these sediments vary in age from Pleistocene to Eocene. Furthermore, the limestone exposed in Adelaide is now known to be Late Pliocene (Ludbrook 1980) rather than Miocene as assumed by Tate.

The Desert Sandstone in northern South Australia, currently known as silcrete, was interpreted by Tate (1879) as an extensive lacustrine deposit contemporary with river gravels and sands of the Upland Miocenes. Thus silcrete and laterite were not distinguished and they were both considered to be sediments or rocks. Whereas Tate (1879) equated sediments within the ranges and on their flanks as Upland Miocenes, Benson (1906) separated them into two groups, with an older Miocene series capping hills and a younger series flanking the western escarpment of the Mt Lofty Ranges.

More recent papers have also considered laterite to be a rock unit. For example, Major & Vitols (1973, p. 46) described laterite on Kangaroo Island as a 'massive rock composed of pebble-sized pisolites of maghemite and limonite and fine-grained quartz sand cemented by limonite'. This crust, up to 1 m thick, was overlain by white, fine-grained quartz sand and underlain by mottled yellow and red clay or rocks of the weathered Kanmantoo Group metasediments. The crust occurred as boulders where ripped up by ploughs and loose pisolites, mixed with white or yellow sand, were recorded on the margins of the inland plateau.

[2] Bourne, J. A. (1974) Chronology of denudation of Northern Eyre Peninsula. M.A. thesis, The University of Adelaide (unpubl.).

Laterite as an iron-rich horizon

Many geological studies have been concerned with laterite in only a very incidental fashion, and almost any iron-rich horizon has been regarded as laterite (e.g. Glaessner 1953a; Olliver 1964). At various locations within and on the margins of the Mt Lofty Ranges, Tertiary sediments, variably weathered and ferruginised, have been reported to contain laterite. For example, at Happy Valley, Olliver (1964) described a sequence of Eocene marine Blanche Point Marls and North Maslin Sands overlain by Pliocene freshwater sands and clays capped and preserved by a lateritic horizon at about 200 m above sea level. The laterite consisted of a band of iron-impregnated sandy sediment. Similar occurrences were described in many sand quarries in Tertiary sands in the Adelaide region by Harris & Olliver (1964) and Olliver & Weir (1967).

Laterite as a weathering product

The association of lateritic crusts with weathering profiles (Walther 1889; Maclaren 1906) was introduced to Australian studies by Simpson (1912) and Walther (1915). They espoused the view that laterite formed as iron and aluminium oxide effloresences were transported in solution from the water table by capillarity. Walther (1915) assigned the term 'laterite' to the complete profile.

However, laterite in South Australia has most commonly been considered to be an indurated ferruginous horizon in a weathering profile (Stephens 1946; Hallsworth & Costin 1953; Connah & Hubble 1960), which is quite different from the original laterite, described by Buchanan (1807) as a low-level sedimentary deposit consisting of massive, unstratified iron-rich clay material, full of cavities and pores, which hardened once cut into blocks and exposed to the atmosphere.

Lang (1965) followed Hallsworth & Costin (1953), restricting the term 'laterite' to crusts associated with well-differentiated profiles apparently formed by *in situ* relative accumulation of iron oxides. 'Ortstein' was used by Lang (1965) to describe crusts developed by laterally derived absolute accumulations. Where ortstein crusts formed above weathered profiles and simulated *in situ* weathering profiles they were called 'duricrusts'. Lang considered that laterites on the oldest surfaces were only occasionally developed from materials recognisable in the pallid zone, and he assumed that a discontinuous layer of Tertiary sediments overlay older rocks throughout the lateritic area. Maud (1972) also considered that only soils containing ironstones overlying mottled and pallid zones should be regarded as laterites. This definition has sometimes been ascribed the descriptor 'true laterite' (e.g. Bourne 1974[2]).

Classification of laterite

There has been little attempt to classify lateritic materials in South Australia. Teale (1918) used the term 'ironstone' to describe ferruginous materials, which were noted to affect all materials except alluvium. They were categorised into four main types: loose, concretionary gravels in deposits up to 1 m thick, iron-cemented sands and gravels, ferruginised slates and quartzites, and lateritic ironstone forming hard sheets.

Laterite was categorised by Forrest (1969[3]) as 'fossil or relict', which referred to the complete normal laterite profile, 'truncated', where the upper horizon was absent, 'immature', where the percentage of iron in the capping was low and the underlying bedrock was only partially weathered, 'derived', when the capping had been derived from the reworking of higher crusts and where this reworked capping rested on weathered bedrock, and 'ferricrete' where an iron-rich crust incorporated partially-rounded quartz pebbles and overlay fresh bedrock.

The use of the term 'ferricrete', coined by Lamplugh (1902) to describe a ferruginous conglomerate, has been extended to apply to all iron-cemented and indurated continuous horizons and crusts in preference to laterite by some workers (e.g. Milnes *et al.* 1985; Bourman 1989[4]). Ferricrete was classified by Milnes *et al.* (1987) and Bourman (1989[4]) as simple types, which included ferruginised bedrock and clastic and organic sediments, and complex types such as pisolitic, nodular, slabby and vermiform ferricrete. The different forms of ferricrete were noted to display differences in micromorphology, mineralogy and chemistry that reflect the nature of the parent material, environmental conditions during iron impregnation and subsequent transformations during landform evolution. Mottled (Fig. 3) and bleached materials (Fig. 4) were regarded as having developed independently of the ferricretes by Bourman (1989[4]).

[3] FORREST, G. J. (1969) Geomorphological evolution of the Bremer Valley. B.A. Hons thesis, The University of Adelaide (unpubl.).

[4] BOURMAN, R. P. (1989) Investigations of ferricretes and weathered zones in parts of southern and southeastern Australia - A reassessment of the laterite concept. Ph.D. thesis, The University of Adelaide (unpubl.).

Fig. 3. Strongly mottled zone with a crude vertical orientation in Precambrian bedrock south of Kapunda in the Mid North. Mottles (dominantly hematitic) and adjacent bleached zones display a pronounced vertical orientation. There is no overlying laterite crust.

Processes of laterite formation

It is necessary for the various potential processes of laterite formation to be understood so that more reliable interpretations of ages and relationships to underlying companion materials can be provided. For example, does laterite formation require a peneplain surface, as many workers in South Australia have claimed? Furthermore, with respect to pisoliths, is it possible to distinguish formation in place from transported origins? Many theories of laterite origins have concentrated on vertical translocations of minerals in the regolith that involve capillary rise, vertical leaching and fluctuating water tables. However, Milnes *et al.* (1985) and Bourman *et al.* (1987) demonstrated that ferricrete development in southern South Australia has been almost exclusively related to lateral physical and chemical transport to, and accumulation of iron and or aluminium minerals in, discrete preferred sites.

Capillarity

Teale (1918) favoured the role of capillarity in laterite formation. He concluded that laterite formation depended upon a ferruginous rock or subsoil for an iron source, dissolution of iron, largely by organic acids, and a hot season to 'pump the iron salts' to the surface, causing oxidation and precipitation of limonite.

Laterite development by prolonged chemical weathering during the late stages of the cycle of erosion (Davis 1909, 1920), on a Miocene continental peneplain with sluggish surface drainage, in a seasonally dry tropical climate that encouraged capillary rise of iron and aluminium in solution, was described by Woolnough (1927), who had widespread experience of duricrust in Australia. He considered the 'Upland Miocenes' of South Australia to be 'veritable Duricrust albeit of somewhat aberrant type' (p. 46). He noted similarities between ferruginous cappings in the Mt Lofty Ranges with examples in Western Australia, and regarded some of the ferruginous materials on highlands as 'thoroughly typical lateritic crusts' (p. 46) and that the ferruginous surface of much of the 'Mount Lofty Plateau' was underlain by highly decomposed arenaceous rocks, similar to those related to 'Duricrust'. Laterite, 'Upland Miocenes' and 'Desert Sandstone' were thus considered as contemporary and equivalent duricrusts, resting on weathered rock materials (Woolnough 1927).

Fig. 4. Bleached and kaolinised Precambrian Aldgate Sandstone exposed by quarrying at Longwood, in the South Mount Lofty Ranges at 400 m above sea level. The depth of the section is 30 m.

The capillarity model of laterite formation should result in the reversal of soil A and B-horizons, with the surface laterite being the illuvial B-horizon and the underlying iron-depleted clay being the eluvial A-horizon. Thus, this model requires the cogenetic formation of the complete laterite profile.

Leaching

The interpretation of laterite as the B-horizon of a fossil podzolic soil was pursued by Prescott (1931) in view of evidence of the dominance of leaching of bases in laterite profiles, as opposed to capillary uplift, evaporation and surface precipitation of iron and aluminium oxides. Tropical podzolisation became the most pervasive view on laterite formation in South Australia, with the laterite horizon being regarded as a fossil illuvial B-horizon where laterite occurs in areas of aridity.

Johns (1961a) proposed that poorly drained soils on Eyre Peninsula were leached (which appears to be contradictory), during presumed humid pluvial conditions of the Pliocene, leading to the accumulation of iron oxides and the *in situ* formation of laterite.

Combinations of water table movements, leaching and capillarity

Both Whitehouse (1940) and Stephens (1946) concurred with the general podzolic origin of laterite but envisaged sources of iron not only from the overlying leached A-horizon but also from iron-depleted, weathered bedrock by water table fluctuations and capillary rise.

Hallsworth & Costin (1953) questioned that the upper podzolised layers of southern Australian laterites comprised parts of original laterite profiles, and suggested that they resulted from intense leaching after lateritisation. However, Prescott & Pendleton (1952) had pointed out that, in spite of current semi-aridity, relic podzolic soils with ironstone gravels in Western Australia remain acid, re-emphasising their hypothesis of the pedogenic origin of laterite.

The interpretation of laterite as the indurated, iron-rich B-horizon of a fossil, podzolic soil profile was favoured by Stephens (1946), who proposed a dynamic pedological model of soil formation, subsequent upon dissection of the lateritic regions in South Australia. He regarded laterite as a pedogenic material and suggested that ferruginous concretionary gravels accumulated in the soil profile in the zone of oscillating seasonal water table as a result of alternating reducing and oxidising conditions. He associated the water table fluctuations with a low relief and a humid climate. Under these conditions the concretionary gravels were assumed to form an indurated horizon by their progressive enlargement and coalescence. Later uplift and dissection of the landscape was postulated to explain the laterite mantling remnants of former peneplains. A major contribution to pedological studies was made by Stephens (1946) who recognised the influences of soil development on both the *in situ* weathered bedrock and the eroded, transported debris. This model proved to be very productive for other pedologists (e.g. Northcote 1946; Northcote & Tucker 1948; Rix & Hutton 1953).

Stephens (1971) later modified some of his views on laterite formation when he investigated a possible cogenetic relationship between silcrete and laterite. He considered that laterite formed by the accumulation of hydrated oxides, kaolinisation of mottled and pallid zones and the acidification of the whole profile, with pronounced leaching losses of silica and bases. Laterite was noted to form by both relative and absolute accumulation but he believed that relative accumulation was predominant. He also concluded that although laterite formation was associated with a fluctuating water table, it was not dependent on either perfect plantation surfaces or tropical climates, views that have largely been ignored in the local literature.

Wetting and drying processes

In opposition to Prescott & Pendleton (1952), Bauer (1959[5]) favoured the view that laterite may currently be forming in southern Australia where the regolith is affected by wetting and drying. He postulated that under these conditions ferrous iron would migrate upward during waterlogging and convert to stable ferric iron in dry, oxygenating periods. He recognised a ready source of iron from decomposing country rock and a temperature regime warm enough to allow the reduction, migration and oxidation of iron.

Weathering transformations of materials rich in ferrous iron

Mawson (1907a) described a large saucer-shaped body of bog iron ore, with a maximum thickness of 10 m, forming a flattish-topped hill about 200 m above sea level at Wadella Springs on Eyre Peninsula. He concluded that the deposit had originated from spring waters, with iron sulphate having derived from the oxidation of underlying pyrite bodies. Thus Mawson, without confusing the occurrence with laterite, had observed and explained the formation of a distinctive type of ferricete.

[5] BAUER, F. H. (1959) The regional geography of Kangaroo Island. Ph.D. thesis, Australian National University, Canberra (unpubl.).

The formation of ferruginous crusts, in such places as the Telford and Murray basins, by weathering transformations of minerals containing ferrous iron such as glauconite, siderite, chamosite and pyrite to ferric iron minerals dominated by goethite has also been recorded (Bourman 1989[a]; Bourman *et al.* 1995).

Lacustrine laterite

The view of ironstone formation as lacustrine (e.g. Fermor 1911) or swamp deposits on a peneplain surface close to sea level, with the water table close to the ground surface was suggested for South Australian samples by Segnit (1937). He also noted the occurrence of three types of ironstone cappings on high level ground and slopes in the Mt Lofty Ranges. Vesicular ferricrete, formed by iron oxide replacement of organic material in former swamp environments, has been recorded (Bourman 1989[a]) in various landscape positions in the Mt Lofty Ranges (Fig. 5) and on Kangaroo Island.

Relative and absolute accumulation: in situ versus transported laterite

Laterite formation by relative (*in situ*) and absolute (lateral) accumulation has long been recognised with different workers attributing differing significance to these processes. For example, Stephens (1971) attributed laterite formation dominantly to relative accumulation. Crocker (1946) agreed with the *in situ* formation of some ferruginous gravels but considered that some others have secondary origins. Milnes *et al.* (1985) and Bourman *et al.* (1987) presented evidence of dominant lateral transport in ferricrete and pisolith formation in the Mt Lofty Ranges, although the possibility of *in situ* formation was not rejected (Fig. 6). Johns (1961a) also conjectured that most of the sediment deposited on the coastal plains and Central Basin of southern Eyre Peninsula was material resorted from the uplands and included pisolitic or massive ironstone gravels. Johns believed that during lateritisation the previously peneplained basement rocks underwent deep weathering, ferruginisation and kaolinisation. Lithological variations in the basement rocks were thought to have had no influence on the final weathering products.

Maud (1972), following d'Hoore (1954) proposed absolute and relative sources of iron and aluminium oxides for the formation of laterite. The accumulation of iron and aluminium oxides was attributed either to the removal of silica and bases or their accumulation from outside sources. Well-developed lateritic ironstones on Permian glacigene sediments were explained by the concentration of iron oxides from lateral sources, whereas thinner crusts on pre-Permian rocks were ascribed to *in situ* weathering losses of silica and bases (Maud 1972). Maud (1972) believed that following landscape rejuvenation and lowering of the water table, the zones of iron-enrichment irreversibly

Fig. 5. View of bulldozer excavation on Peeralilla Hill showing ferruginous crust of vesicular ferricrete and light-coloured clays (bottom left of photograph) that include calcite and barite. This deposit of ferricrete occurs on the summit surface but below the level of surrounding hills. Borehole evidence indicates that this deposit is underlain by sandy sediments. Excavation 2.5 m deep.

hardened into lateritic ironstones. Brock (1964[6]) also agreed with d'Hoore (1954) that dissection of lateritic terrain, accompanied by lateral water movement, may have redeposited iron oxides on gentle slopes to form cappings.

Wopfner (1972) carried out an analytical investigation of mottled materials that in other contexts have been referred to as lateritic. He discussed maghemite in mottled Cainozoic sediments at Hallett Cove, where both primary and reworked maghemite were identified. Maghemite was reported from two locations: small amounts (2%) of maghemite in conspicuous red mottles, within medium grained white sandstone, were used as evidence of *in situ* formation, whereas maghemitic sub-rounded ironstone pebbles in a conglomeratic horizon were considered to be indicators of reworking. The profiles and crusts were considered to be genetically related with the conglomerate forming by reworking of an original *in situ* crust.

[6] Brock, E. J. (1964) The denudation chronology of Fleurieu Peninsula. M.A. thesis, The University of Adelaide (unpubl.).

Many soils associated with uplifted peneplains in Australia have been noted to contain concretionary ironstone gravels, attributed by Prescott (1934) to former wetter periods when waterlogging of soils and shallow water tables were more common than at present. Chemical analyses of ferruginous gravels were interpreted by Prescott (1934) to demonstrate the concretionary character of the ironstone gravels. However, many pisoliths in southern South Australia appear to have formed dominantly by disintegration of ferruginous materials such as mottles, followed by physical transport and modifications in soils resulting in increases in iron content as well as a mineralogy dominated by hematite and maghemite (Milnes *et al.* 1987; Bourman *et al.* 1987). Transported pisoliths typically are associated with stone lines, have different chemical and mineralogical compositions to surrounding matrix materials and display multiple rinds. Milnes *et al.* (1985) also considered that ferricretes in southern South Australia, as well as pisoliths, are dominantly remnants of iron impregnated sediments, originally formed in former valley bottoms and depressions.

Fig. 6. Road cutting on the Victor Harbor-Cape Jervis road west of the Waitpinga road, exposing bands rich in pisoliths, at a depth of about 1 m, in ferruginous sandy sediments of probable Pliocene age and of aeolian origin. Other pisoliths occur at the ground surface and in the upper soil mantle. The pisoliths at depth contain only goethite, whereas those at the surface have higher iron contents and contain dominantly hematite and maghemite. Geological hammer 33 cm long.

Although there is general agreement that ferruginous materials can form both by processes operating *in situ* and those related to transportation, there has been confusion in the use of the term *in situ*. For example, some workers have considered that ferricrete, formed during landscape downwasting, which involves both vertical and lateral movement of clasts, formed *in situ*. Such ferricretes may be better regarded as residual with *in situ* weathering applying more strictly only to isovoluminous weathering (Bourman 1993b).

Laterite profiles

The normal laterite profile

Throughout the South Australian literature, following Stephens (1946), runs the thread of the normal laterite profile, which has influenced many palaeo climatic and palaeo-environmental reconstructions. Only rarely have studies departed from this model. The normal lateritic profile (Stephens 1946), was envisaged as essentially a podzol with A, B and C horizons of eluviation, illuviation and weathering, with an accessory laterite horizon usually above a clayey B-horizon. Occasionally several lateritic horizons were noted in one profile. Stephens believed that the normal laterite profile was restricted to southern Australia; in Queensland laterite was thought to occur as an horizon in red earth profiles (Bryan 1939; Whitehouse 1940), which contained silicified zones, suggesting the incomplete removal of dissolved silica.

The model presented by Stephens has considerable merit as it emphasises the dynamic nature of landform change and pedogenesis. However, its dependence on the widespread occurrence of a former normal laterite profile related to former regional water table fluctuations, is unrealistic and has led to simplistic explanations of landscape development. Furthermore there are various objections to the view that the original laterite is the illuvial horizon of a fossil podzolic soil.

Widespread lateritic soils on the elevated peneplain of Kangaroo Island, the Mt Lofty Ranges, Yorke Peninsula and Eyre Peninsula were reported by Crocker (1946), who observed that they contained considerable percentages of louse and indurated lateritic ironstone gravels. Some of these gravels were considered to have formed *in situ*, but on dissected marginal slopes secondary origins for them were suggested. Crocker (1946) followed the view of Prescott (1931) that laterite is the fossil illuvial horizon of a tropical Pliocene podzolic soil. Thus he reiterated the then current thoughts about laterite and further promulgated the association of laterite, peneplains, tropical climates and the Pliocene (or Tertiary), thereby setting the stage for the generation of circular arguments. Sprigg (1946) concurred with Prescott (1931) and Crocker (1946) concerning laterite genesis.

The pedogenic origin of laterite was promoted by Northcote (1946) and Northcote & Tucker (1948). These workers mapped and described a relic normal laterite profile of Pliocene age, the Eleanor Sand, on the lateritic plateau of Kangaroo Island. Crocker (1946) commented that lateritic residuals on Kangaroo Island were covered by grey and white siliceous sands derived from resorted A-horizons, originally developed on Pleistocene coastal calcareous sand dunes. However, Northcote (1946) claimed that the constant ratio of coarse to fine sand throughout the profile indicated that it had formed *in situ* and that the surface had not received accessions of wind blown sand. Consequently he regarded the Eleanor Sand as a relatively undisturbed fossil soil of Pliocene age, with a lateritic horizon developed *in situ* and preserved on an uplifted peneplain. However, Mulcahy (1960) has suggested that such sand may not be fossil, but may have derived from laterite destruction, thus yielding a similar grain size analysis to that determined by Northcote. Twidale (1983) considered that this sandy A-horizon provides evidence for the preservation of an original Mesozoic laterite profile.

Rix & Hutton (1953) regarded the summit surface in the south Mt Lofty Ranges as a block-faulted, uplifted and dissected peneplain. They followed Sprigg (1946), considering that by Early Tertiary times Precambrian rocks had been reduced to a base surface and subsequently buried by a Tertiary lacustrine and marine covermass. The soil pattern suggested to them that a further cycle of erosion had removed the greater part of the covermass, leaving isolated areas of varying extents thereby creating a new peneplain, with remnants of Tertiary deposits preserved in topographic lows. They postulated lateritisation of soils on the peneplain, prior to major faulting and dissection, concurring with Whitehouse (1940) that there had been contemporaneous laterite formation throughout Australia in the Pliocene. Residual lateritic soils were only mapped on hill summits and spurs so they suggested that erosion had removed most of a lateritic sandplain following uplift and dissection.

One soil, the Yaroona Gravelly Sand, was regarded as an original laterite profile and described as a massive band of laterite 22-30 cm thick, containing water-washed grits, gravels and sands, unconformably overlying kaolinised Precambrian shales (Fig. 7). Rix & Hutton (1953) described other residual podzols in the area as exhibiting normal profiles of ferruginous, mottled and pallid zones, overlying unweathered country rock. These workers were strongly influenced in their interpretations by the normal laterite profile model of Stephens (1946) and presented a convoluted explanation of an anomalous laterite profile, preserved in a road cut south of Clarendon, in order to account

for a mottled zone overlying a laterite zone. The section can also be interpreted as a geological sequence of Precambrian rocks weathered in pre-Tertiary times, and overlain by fluvial gravels, grits and sands of Eocene age (Mawson 1953). Subsequently these sediments were partially silicified and superficially stained red by small amounts of iron oxides in groundwaters. A thin grey soil with pisoliths occurs at the surface. The above example demonstrates how complex deductive arguments, within framework of the model of the normal laterite profile, were used to introduce events, for which there was no evidence, in order to explain apparently aberrant observations. Despite this, Rix & Hutton (1953) produced a detailed soil map.

In southern South Australia the normal laterite profile of Stephens (1946) has been given excessive consideration, sometimes resulting in simplistic interpretations of landscape development. This has occurred despite observations indicating great variability in lateritic weathering profiles and despite the view of Stephens (1971) that the 'normal profile' is the exception rather than the rule. Bauer (1959[5]) and Alley (1977) disagreed with the interpretation of laterite as a tropical fossil soil profile developed on a peneplain. However, their views have not been generally accepted.

Polygenetic profiles - Alternatives to the normal laterite profile

Stratigraphic Approach To Investigations Of Lateritic Materials

Firman (1967a, b, 1976, 1981, 1994) placed weathered zones and palaeosols within a stratigraphic framework. For example, he gave formal status to ferruginised clastic sediments and bedrock weathering profiles consisting of sesquioxides of iron and forming ironstone crusts, by introducing the name Yallunda Ferricrete. The Yallunda Ferricrete was reported to exceed 1 m in thickness in its type area at high levels over interfluves of the Lincoln Uplands (Eyre Peninsula) and on remnants of old high surfaces elsewhere. The term 'ferricrete' was used to describe ferruginous layers and crusts both independent of, and in association with, weathered profiles. Firman (1976) interpreted the various zones of the so-called normal laterite profile as having formed by different processes at different times, with the profile as old as the initial transformation of the parent material.

Ferricretes in various stratigraphic situations, including ferricrete above and below Lower Tertiary sediments in the Barossa Valley, as well as ferricretes

Fig. 7. Section in road cut near Clarendon, exposing the Yaroona Gravelly Sand of Rix & Hutton (1953), showing angular unconformity with ferruginised pebbles, grits and sands of Eocene age overlying weathered, bleached and partly kaolinised Precambrian meta-siltstones. Section is approximately 3 m high.

in the highlands of the Mt Lofty Ranges and the Lincoln Uplands were recorded by Firman (1967a). He also suggested that there were equivalents of upland ferricretes in the sedimentary succession of the Murray Basin. These included oolitic siderite-rich sediments and laterite in the Early Pliocene Bookpurnong Beds, as well as ferruginous beds and cappings in the Late Pliocene Parilla Sand near the Victoria-South Australia border. Some of the ferricretes, however, have resulted from the relatively recent oxidation of pre-existing iron-rich sediments containing glauconite and siderite and cannot be used as reliable soil stratigraphic markers.

Firman (1976) considered that between Permian and Early Tertiary times, some 200 Ma, the Mt Lofty Ranges region was a land mass experiencing prolonged weathering and erosion, so that by Early Tertiary times a subdued and deeply weathered landscape had developed. Associated bleached profiles were considered to have originated in the Mesozoic. A range of different ages of weathering and lateritisation was reported. Decomposed, bleached or mottled bedrock underlying Eocene sediments was ascribed to pre-Tertiary weathering; a laterite profile developed in Eocene gravelly sands was used to indicate post-Eocene weathering; silicified and ferruginous zones in Early Pleistocene sediments, overlying older bleached zones were argued to have equivalents in laterite profiles in the adjoining uplands; and ferruginisation in carbonaceous and pyritic Eocene sediments was attributed to recent exposure and oxidation.

The work of Firman is significant in attempting to establish stratigraphic ages for different weathering features. Nevertheless, correlating weathering phases simply on shapes, sizes and colours of mottles may be unreliable, as similar weathering patterns occur in profiles of different ages. Furthermore, Firman observed modification of some profiles by later weathering, obscuring earlier weathering products. Firman apparently took no account of local environmental conditions, which may have favoured synchronous bleaching in one area and mottling in another. Various questions remain unanswered, such as what happened to the iron derived from the bleaching of the Arckaringa Palaeosol; where did the iron for the development of the San Marino Palaeosol come from; and how was it concentrated in discrete, but more-or-less uniformly distributed mottles within previously bleached bedrock?

Polygenetic Profiles and Continual Weathering Model of Ferricrete Formation

Milnes *et al.* (1985, 1987) and Bourman *et al.* (1987) combined investigations of the field relationships of ferricretes and weathered zones with micromorphological, chemical and mineralogical analyses and questioned the former development of normal laterite profiles. These studies have suggested that there was complex reworking and continuous weathering of relic landscapes since the Early Mesozoic, and that ferricretes are dominantly remnants of iron-impregnated sediments of ancient valleys or depressions. Some ferricretes may be the culmination of processes beginning in the Mesozoic but still proceeding, resulting in the repeated dissolution, break up and neo-formation of ferricretes, as well as the ongoing and current formation of mottles and bleached zones.

Some ferricretes may have developed as suggested by McFarlane (1976), who postulated ferricrete development by the surface accumulation of ferruginous materials during landscape downwasting, the formation of gibbsitic-rich zones in near-surface situations and continued development of ferricretes and bleached zones after uplift. However, some other features of her model do not fit the observations in South Australia; there is evidence for some bleached zones and mottled zones being older than the ferricretes (Bourman 1989[a]) and no evidence has been observed of progressive development of profiles, with horizons having formed from progenitors resembling those currently beneath them. An extension of this model is the continual weathering hypothesis of Bourman (1989[a], 1993a), which proposes ongoing epigenetic transformations of ferricretes and weathered zones, with rates of change influenced by climate and events such as tectonism, sedimentary burial and submergence beneath lakes and the sea.

Topographic requirements for laterite formation

Peneplain concept in laterite development

Many workers have associated laterite formation and preservation with peneplained surfaces. However, Sprigg (1946) considered it unwise to associate laterite formation with peneplanation, which implied formation over a very long period, since he believed that lateritisation occupied only a relatively short time span. This interpretation has important implications for landscape evolution as laterite formation would first require the development of an extensive planation surface. The peneplain concept of laterite development began early (Benson 1911; Mawson 1907b; Teale 1918; Woolnough 1927), and has persisted (Campana & Wilson 1954; Brock 1964[b]; Ward 1966; Twidale 1968, 1983; Maud 1972). For example, the summit surface of the Mt Lofty Ranges was interpreted as an Early Tertiary differentially uplifted and dissected 'peneplain, surmounted by monadnocks' such as Mt Lofty, Mt Barker and Mt Gawler (Benson 1911). Tate (1879) attributed the discontinuous distribution of the 'Upland Miocenes', separated by deep ravines, to extensive denudation after uplift of the ranges.

Mawson (1907b) extended the peneplain concept to Eyre Peninsula where he described peneplains in the Port Lincoln area at about 100 m and 6 m above sea level. He equated mottled clay beds underlying the lower surface with freshwater Miocene beds near Adelaide.

Some extremely perspicacious comments on the nature and formation of ferruginous materials in the south Mt Lofty Ranges were made by Teale (1918) and his work represents the most comprehensive, detailed and objective discussion of iron oxides among all of the early investigators, particularly on classification and theories of origin of ironstone crusts. Teale (1918) interpreted the summit surface of the ranges as dislocated and eroded remnants of a former extensive peneplain. Woolnough (1927) suggested that the distribution of remnants of the terrestrial Upland Miocenes agreed completely with the physiographic conditions postulated for duricrust formation i.e. a peneplain with sluggish drainage.

In the southern part of the Mt Lofty Ranges, Campana & Wilson (1954) described a planation surface at levels up to 420 m above sea level, as a pre-Tertiary peneplain, uplifted during Tertiary and Quaternary times and deeply dissected by subsequent cycles of erosion and Brock (1964b) identified remnants of an ancient landsurface on the spine of Fleurieu Peninsula covering an area of 25 km²; the remnants were described as having little relief and a capping of the normal laterite profile of Stephens (1946). Ward (1966) also described flat surfaces preserved on the crests and gentle back slopes of the western blocks of the Mt Lofty Ranges as relics of a pre-deformational Mt Lofty peneplain, mantled by deep weathering and laterite. Twidale (1968) described the summit surface of the Mt Lofty Ranges as a lateritised peneplain, surmounted by a few residual remnants or monadnocks.

Today the term 'peneplain' is rarely used in geomorphic literature because, among other things, it carries with it an undemonstrable, highly theoretical mode of genesis. The terms 'erosion surface' or 'planation surface' are preferred.

Irregular surfaces

Not all workers have considered peneplains necessary for laterite formation. If peneplain surfaces are necessary for laterite formation, the implication is that laterite formation follows peneplanation, although irregular surfaces suggest that laterite can form during, and as a result of, landscape downwasting. Some investigators such as Campana (1955) have demonstrated great complexities and irregularities in weathering and landscape evolution. Working near Gawler in the north Mt Lofty Ranges, Campana (1955) noted a leached lateritic soil overlying gneisses, schists and Tertiary fluviatile deposits resting on a pre-Tertiary weathered erosion surface. He reported gravels and coarse sands cemented by iron oxides within the Tertiary sediments. The mapping of the Tertiary (Early Eocene) strata in this area indicated that deposition occurred in a system of lakes and rivers on a weathered surface of moderate relief, above which ridges of harder rocks projected. Campana (1955) considered that the non-marine strata and older rocks had been subjected to widespread lateritisation between the Early Eocene and the Miocene. The sequence outlined by Campana (1955) illustrates pre-Tertiary weathering and bleaching of basement rocks, the deposition of Tertiary terrestrial sediments over a dissected landscape, differential ferruginisation of suitable host rocks and the inhibition of this by marine submergence.

Bauer (1959) noted that regardless of elevation, the laterite profile, the Eleanor Sand, occurs on areas of low relief and poor drainage that would have suited periodic waterlogging and drying (Fig. 8). Thus he thought that topography might have been important in assisting the formation of a distinctive soil in two differing physiographic locations, that is, on a stepped topography with flat treads, but not necessarily a peneplain.

Lang (1965) reported on soils and geomorphology of the Yundi area within the south Mt Lofty Ranges. His work represents a departure from that of many earlier workers as he invoked different types of weathering, erosional and sedimentary influences to explain the current landscape and he envisaged lateritisation and duricrust formation as proceeding over long periods of time, on landscapes of variable relief and positions above sea level. In the same area, Maud (1972) noted lateritised surfaces occurring across infilled glacial valleys and correlated them with the summit surface despite their lower landscape positions. The gentle non-tectonic inclinations of ironstone cappings were regarded as original valley morphologies, and Maud (1972) concluded that the original erosion surface was one of considerable relief.

Bourman (1989a, 1993a) presented a model of laterite formation involving an original landscape of some relief that provided lateral local environmental variability. This resulted in bleaching of higher parts of the landscape and iron accumulation on plateau margins, in depressions, swamps and valley bottoms. Primary iron minerals mobilised in sub-surface zones affected by water table fluctuations were concentrated in hematitic mottles. Landscape downwasting concentrated and fragmented mottles at the surface, further weathering modified them, formed pisoliths, cemented them to form ferricrete at the surface and further modified the ferricrete. Portions of the summit surface of the Mt Lofty Ranges have been continually affected by weathering and erosion since the Permian

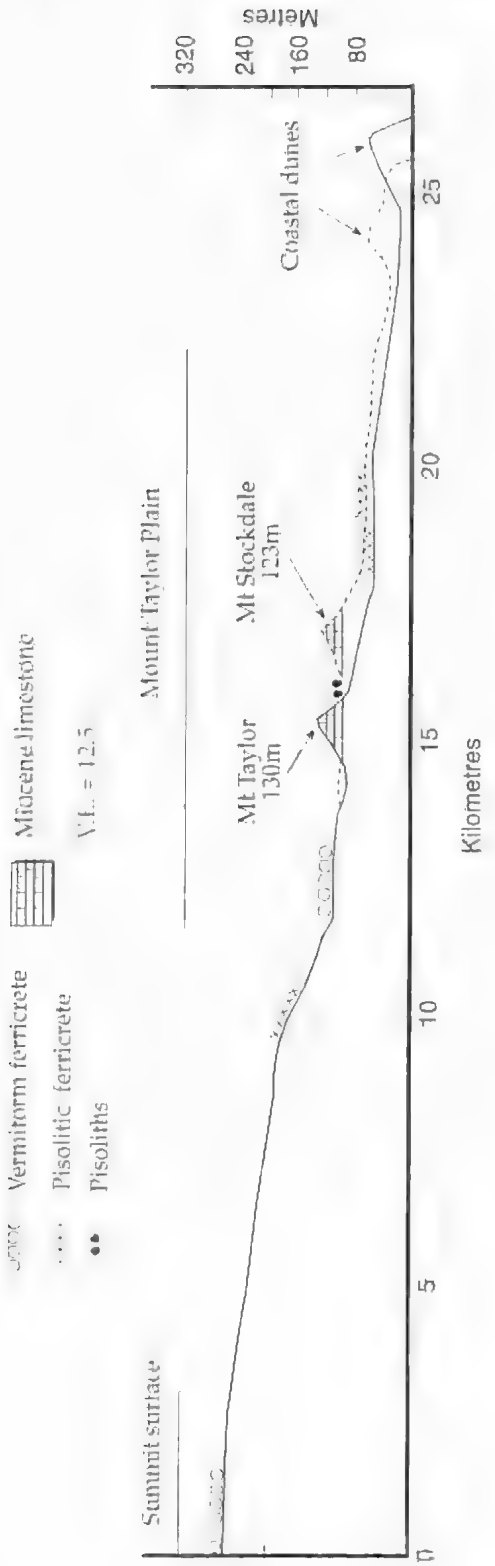


Fig. 8. Cross section of the Mount Taylor Plain, Kangaroo Island, showing the relationships of identical vermiform ferricrete on a high pre-Miocene summit surface and a low post-Miocene surface.

This suggests ferricrete formation during landscape evolution rather than being dependent on the presence of a planation surface. The continual weathering model postulates ongoing variable weathering, interrupted by tectonic activity, sedimentary burial or marine or lacustrine submergence.

Climatic conditions required for laterite formation

The vast majority of workers has equated laterite formation with a hot, seasonally dry tropical climate favouring the operation of intensive weathering processes. Low topographic relief and tropical climates were considered ideal for laterite formation, generating many circular arguments related to the laterite-tropical climate-peneplain association.

A tropical climate with pronounced wet and dry seasons, such as that of Darwin, was considered ideal for the formation of laterite by Walther (1915). This view has persisted. Stephens (1946), Sprigg (1946), Crocker (1946) and Northcote (1946) associated laterite formation with a pluvial period in the Pliocene and Johns (1961a) believed that low relief and high tropical temperatures had favoured the removal of silica, with seasonal oscillations of the water table leading to the concentration of iron oxides. More recent workers such as Bourne (1974[2]), Daily *et al.* (1974), Twidale & Bourne (1975a), McGowran (1979a), and Twidale (1976b, 1983) also favoured torrid, tropical conditions for lateritisation. The timing of lateritisation has commonly been associated with independent evidence for tropical climates. For example, Twidale & Bourne (1975a) noted that palaeontological considerations favoured the Triassic as providing the most suitable humid, tropical climatic conditions for the formation of laterite in the Mt Lofty Ranges.

In marked contrast, Firman (1981) proposed different climatic conditions for separate parts of the profiles. For example, the bleached zone of the Arckaringa Palaeosol was not considered to have been genetically associated with younger ferruginous zones but to have preceded the development of mottles and ferricretes. He ascribed bleaching to early cool climates and ferruginisation to tropical conditions.

Other workers such as Bauer (1959[5]) and Campana & Wilson (1954) considered that lateritic material might be forming at present in southern Australia so that climate for lateritisation need be no different from that of today. Maud (1972) also argued that the process of

iron oxide-enrichment of sediments is currently proceeding on broad valley floors in the Mt Lofty Ranges under current climatic conditions. Furthermore, there is considerable evidence of modern iron mobilisation and precipitation in southern South Australia (e.g. Bourman 1989[a]; Ferguson *et al.* 1984), so that a humid tropical climate need not be a prerequisite for bleaching and iron enrichment.

The role of climatic influences in the formation of ferruginous and siliceous duricrusts was examined by Alley (1977), who provided evidence that both laterite and silcrete formed together, for at least some time during the Tertiary, on identical strata and under similar climatic conditions, suggesting that some other factor(s) must have controlled the processes of weathering. Only the base levels of erosion differed between the silcreted and lateritised surfaces and silcrete developed on a surface, the drainage of which flowed sluggishly into Tertiary lakes. Palynological data were interpreted by Alley (1977) to demonstrate that the Eocene appeared to have been warm and temperate with a very high rainfall and that the Miocene was similar, with perhaps slightly warmer temperatures and a slightly lower precipitation. The concentration of silica at the landsurface was attributed to high alkalinity, slow groundwater movement and a high water table close to the lakes. Alley (1977) concluded that laterite and silcrete co-existed for part of the Early Cainozoic in adjacent drainage basins. Consequently, laterite and silcrete were not thought to form through the mechanism proposed by Stephens (1971) which involved the formation of silcrete by deposition of silica in dry zones after having been derived from lateritic weathering elsewhere. Furthermore, the view that laterite is associated with tropical conditions and silcrete with aridity was not supported because both formed in similar climatic and biotic regimes; only the base levels and groundwater conditions varied.

Using chemical (Hutton 1977), palynological and stratigraphic evidence to support their argument McGowran *et al.* (1978) disagreed with Alley (1977) that laterite and silcrete formed concurrently on similar rocks and under broadly similar climatic conditions from Eocene to Miocene times. However, Alley (1978) countered the arguments presented by McGowran *et al.* (1978) and made a valuable contribution to the study of laterite genesis by highlighting the influence of local topographic and groundwater conditions in its formation, as well as questioning climatic influences on laterite and silcrete development.

Minerals as climatic indicators of lateritisation

As noted above lateritisation is commonly associated with intensive weathering under tropical climatic conditions and certain minerals are suggested as indicators of climatic conditions. For example, Wopfner (1972) suggested that maghemite in mottles is a climatic indicator, originating by thermal dehydration of lepidocrocite formed by oxidation under fluctuating water table levels and warm climatic conditions. He concluded that lepidocrocite and goethite may have formed as gels that were subsequently dehydrated and crystallised as maghemite and hematite under conditions of low relief, warm climate and heavy seasonal rainfall.

However, maghemite in lateritic mottles is very rare in southern South Australia as they are dominantly hematitic (Bourman 1989[a]). Moreover, in lateritic areas of the Mt Lofty Ranges, potentially weatherable minerals including felspars, muscovite, vermiculite, chlorite and smectite have been identified (Bourman 1989[a]). In some cases there may have been neoformation of these minerals but it does seem anomalous that they should be so widespread in areas considered to have been affected by lateritic weathering processes. Previously, Crawford (1965) had noted fresh felspar gravel in mottled material at Ardrossan and used this to argue against lateritic weathering.

Palaeoclimatic indicators

Depending on the climatic conditions considered essential for laterite formation, the presence of laterite has palaeoenvironmental implications. There is little doubt that the operation of chemical processes is accelerated under hot moist conditions but there is a growing body of evidence suggesting that iron mobilisation and kaolinisation can occur under various climatic regimes – see Bourman (1993a) for a summary – so that there are considerable uncertainties linking laterite formation with a specific climate. For example, there are many reports of modern iron mobility from localities in the Mt Lofty Ranges, Kangaroo Island and Fisherman Bay (Ferguson *et al.* 1984) under current Mediterranean and semi-arid climatic conditions. These observations may also cast doubt on the reliability of correlating terrestrial ferruginous crusts with evidence of warm, humid climates derived from marine climatic indicators (McGowran 1979b).

Interpretation of lateritic landscapes

Many different hypotheses have been presented to explain the distribution and evolution of laterite. These include the development of laterite on a surface of low relief, close to sea level, followed by differential tectonic uplift and dissection of the lateritic surface, development of multiple erosion surfaces affected by episodic weathering and laterite formation, differential weathering and laterite formation on a landscape formed by uplift and dissection of a surface originally of low relief, and the weathering, erosion and sedimentation of a landscape before, during and after uplift.

Reconstruction of lateritised landscapes

The models of landscape evolution presented to explain the development of laterite depend on preconceptions of how laterite forms. For example, it is often assumed that isolated occurrences of laterite represent dissection of a former continuous laterite surface and that the different horizons of laterite profiles formed contemporaneously. In the past, many workers have tacitly assumed that the present day isolated and sporadic occurrences of laterite represent the erosional dissection of a former contiguous and uniform laterite-mantled planation surface and that these remnants are excellent and reliable morphostratigraphic markers (e.g. Twidale 1983). However, discontinuous distributions may reflect only localised formation in favourable localities (Bourman 1993a) where optimum topographic and climatic conditions did not generally prevail. Hence, the occurrence of laterite need not necessarily indicate a former extensive erosion surface.

Preservation of uplifted peneplains

Interpretations of landscape evolution have commonly depended upon recognition of uplifted and dissected former peneplains, and the preservation of parts of the original weathered surface, which can be used to reconstruct the former surface. A review of the character and age of the summit high plain of the Mt Lofty Ranges was presented by Twidale (1976b), who argued that the summit surface is of Mesozoic age and has been preserved for some 200 Ma (Twidale, 1976a). Recurrent uplift of the Mt Lofty Ranges, it was argued, postponed the ultimate degradation of the ranges by exposing new land to the area undergoing reduction. However, other workers have suggested that the best preservation of laterite is in relatively low lying points and least in areas of greatest uplift (Milnes *et al.* 1985). The development of the Mt Lofty Ranges on an anticline, the flanks of which are faulted, was one factor used by Twidale (1976a) to explain the preservation of the laterite-capped plateau. It was maintained that the bulk of the plateau is centrally located close to the resistant compressional zone of the anticline and remnants near the western margin are buttressed by sandstone and limestone outcrops. However, the folding, which occurred in the Cambrian, was very complex and did not result in the formation of a simple anticline. Moreover, erosion of this complex structure has been so pronounced that vertical and near-vertical rock structures are exposed. Furthermore, subsequent tensional faulting has occurred within the ranges (Glaessner 1953a), so that the core of the ranges should not be considered to be in compression. The preservation of the Mesozoic sandy A-horizon of the laterite profile was thought to have assisted palaeosurface preservation by providing an absorbent cushion to protect the underlying ferruginous horizon from rainfall (Twidale 1976a). However, no evidence has been found by the present author of 200 Ma old sandy A-horizons in the ranges. Conversely, sandy soils are common, especially on Permian glacigene sediments and occur in landsurfaces, demonstrably of post-Mesozoic ages. A permeable and porous ferruginous crust of the laterite profile was also thought to render this zone resistant to erosion. However, ferruginous crusts are relatively rare and discontinuous with the thickest crusts occurring in positions well below the level of the postulated ancient surface.

Gully gravure, involving the alternation of the locus of intense erosion through the protective influence of coarse debris, was implied to reduce the rate of scarp retreat (Twidale 1976a). However, no specific sites were discussed and the present author has not observed the extensive operation of this process in the Mt Lofty Ranges. The unequal activity of rivers, which incise more rapidly than they erode laterally, was also suggested as a contributory factor in summit surface preservation (Twidale 1976a). While river incision may operate more rapidly than valley-side processes in some situations, the operation of the processes of weathering, surface wash and gullying on valley slopes and hill summits for 200 Ma has led to considerable modification of the landscape (Milnes *et al.* 1985; Bourman 1993a).

A model of landscape evolution involving increasing relief amplitude in order to account for the preservation of these presumed ancient palaeoforms was presented, and evidence supporting this model for other areas, was discussed. However, it is unlikely that the summit surface of the Mt Lofty Ranges has survived essentially unchanged for this enormous period of time.

Dissection model

The dissection model assumes relic induration at the top of former complete and continuous profiles and the lack of preservation of complete profiles is often taken to imply dissection (Stephens 1946; Thomson & Horwitz 1962; Johns 1961a, b; Maud 1972; Robertson 1974; Daily *et al.* 1974; Twidale 1983). Johns (1961a) considered that much of the Lincoln Uplands of southern Eyre Peninsula is obscured by fossil laterite and lateritic gravels and conglomerates, a formerly continuous mantle now partly stripped following regional uplift, drainage rejuvenation and erosion. Johns (1961b) also interpreted the accordance of summit levels in the eastern Mt Lofty Ranges as a base-levelled terrain of Pliocene age, carrying sporadic occurrences of ferruginous grits and laterites. He believed that once-continuous ironstone cappings of Pliocene or post-Pliocene age have been largely removed by erosion. The best exposures of ironstones were reported from "Lucernbrae" where deposits about

1 m thick were noted to mantle Kanmantoo Group metasedimentary rocks.

Maud (1972) noted that although laterite profiles in the southern Mt Lofty Ranges are typically thick, with well developed mottled and pallid zones, laterite horizons are rare. He attributed this to erosional truncation of the profile. Robertson (1974) reported ironstone fragments and deeply weathered and kaolinised rocks in the central section of the Mt Lofty Ranges at about 450 m above sea level. He also interpreted the weathered material as a remnant of a Tertiary laterite profile.

Geologists and geomorphologists have been particularly interested in laterite, primarily to establish denudation chronologies, to establish the ages of particular landforms, to correlate widely spaced planation surfaces and to throw light on the tectonic behaviour of upland areas. Examples of the use of lateritic weathering in interpreting landscape evolution are provided by the work of Sprigg (1945), Brock (1964[b]), and Twidale & Bourne (1975a). Sprigg (1946) considered laterite formation in the Mt Lofty Ranges to be short-lived, correlated it with mottled Pleistocene sediments and believed that faulting and uplift of a peneplain occurred after laterite formation, indicating land movements of between 180 m and 300 m during the Pleistocene Kosciusko epoch of block faulting. This interpretation provides a very young age for lateritisation and faulting, whereas Brock (1964[b]) interpreted the summit surface as a peneplain formed after prolonged subaerial weathering and erosion in the Palaeozoic, culminating in a phase of crustal stability in the Mesozoic and Early Tertiary, when lateritisation occurred prior to uplift and dissection of the surface.

Even greater antiquity of the Mt Lofty Ranges was proposed by Twidale & Bourne (1975a) who investigated the geomorphic evolution of the eastern Mt Lofty Ranges. A summit high plain (Tungkillo Surface) at 200 - 300 m above sea level, an etch surface, occasionally surmounted by scattered lateritic residuals up to 10 m high (Whalley Surface), was identified. The scattered lateritic remnants were interpreted as remnants of a once-contiguous weathered surface of low relief. The Whalley Surface and its associated deep weathering were considered to be of Mesozoic age by extrapolation from Kangaroo Island (Daily *et al.* 1974). They also argued that it developed under a humid, tropical climate. Dislocation of the Whalley Surface by faulting was proposed although there was no evidence of buried laterite on the downthrown side of the Milendella Fault. Its absence, if it ever existed, was explained by sub-surface dissolution of the iron oxides.

Kennedy model of development of lateritised surface

Twidale (1968) accounted for the absence of downfaulted remnants of the lateritised erosion surface by proposing an alternative to the traditional explanation of the summit surface of the Mt Lofty Ranges that it is an extensive lateritised surface of erosion, developed close to regional base level in the Late Tertiary, and subsequently upthrust along ancient fault lines, after which it suffered dissection. While conceding that the ferruginous crusts of the postulated laterite profile might have been removed by sub-surface solution, the possible development of an extensive landsurface in relationship to local base levels in the upper reaches, one of the possibilities suggested by the work of Kennedy (1962), was proposed. However, no critical evidence was presented to show that the summit surface of the Mt Lofty Ranges developed in this fashion

Alternatives to truncated laterite profiles

While carrying out regional geological investigations on Yorke Peninsula, Crawford (1965) described Pleistocene deposits, exposed in the sea-cliffs at Ardrossan, as mottled dark red to olive green argillaceous sediments - The 'Ardrossan Clays and Sandrock' of Tepper (1879). He suggested that the mottling could be due to lateritisation, with the upper indurated zone having been removed by erosion and the pallid zone occurring sub-surface. However, fresh felspar gravel in the mottled material argued against lateritic weathering. Consequently, an alternative non-lateritic explanation of mottling produced by alternate wetting and drying in an environment of low relief was also suggested. Crawford (1965) obviously considered laterite within the framework of the standard laterite profile and attempted to fit his observations into it by postulating the erosional removal of an upper indurated zone. He did, however, also consider an alternative non-lateritic explanation for his observations.

The validity of accounting for incomplete profiles by erosional truncation in landscape interpretation was questioned (Bourman *et al.* 1987; Bourman 1993a) by demonstrating great lateral variability in the spatial distribution of bleached, mottled and ferricreted zones, the development of which depended closely on local micro-environments (Bourman, 1993a). Presumed remnants of laterite crusts have been shown to be lags of ferruginous mottles accumulating at the surface during landscape downwasting (Bourman 1989[a]) and thus laterite crusts, as such, may never have existed.

Double planation theory of Fenner

Fenner (1930, 1931) presented a double peneplanation hypothesis to account for the evolution of the Mt Lofty Ranges, providing a geomorphic and tectonic framework for the use of subsequent authors. The greater part of the Mt Lofty Ranges was thought to

have been stripped of an easily eroded Miocene marine covermass. He saw the double planation theory as necessary to explain transverse drainage and exhumed surfaces in the ranges. He postulated that a pre-Miocene peneplain blanketed with a Miocene marine covermass had been affected by block-faulting, tilting and differential uplift in the Late Miocene or Early Pliocene. Subsequently, this irregular surface was thought to have been peneplaned, resurrecting the older surface in places and developing a new peneplain on both Precambrian and Miocene rocks. Following this, Pleistocene (Kosciusko Epoch) tectonism renewed erosion. Some fault blocks remained buried by Tertiary sediments and others, exhumed from beneath the covermass, were subjected to renewed weathering and erosion.

Today it is generally agreed that the Mt Lofty Ranges were not totally immersed by the Miocene seas, so that the double planation theory cannot be accepted in its entirety. However, large areas of the Mt Lofty Ranges and Kangaroo Island (Milnes *et al.* 1983) were covered by Miocene seas at heights in excess of 200 m above sea level and there is evidence in the Brenter, Myponga and Upper Hindmarsh valleys that the shorelines were even higher than this (Bourman 1989[4]). Moreover, even though the covermass of marine deposits may not have totally covered the ranges, Tertiary terrestrial sediments occur extensively and at higher levels than do the marine sediments. Consequently, the double planation theory has considerable merit but it is still inadequate to account for all of the geomorphic complexities of the ranges, which have been variably exposed to processes of weathering, erosion and sedimentation for immense periods of time.

According to Sprigg (1945) laterite in the Mt Lofty Ranges formed on both a Precambrian or Cambrian bedrock undermass and a covermass of Tertiary limestones and lacustrine sediments. Initially critical of the double peneplanation theory, Sprigg (1945) subsequently made the observation that the widespread occurrence of laterite over the Mt Lofty Ranges presented a potent argument in favour of this theory.

Landscapes with multiple surfaces

Landscapes with multiple erosional surfaces have frequently been described in South Australia, with the surfaces being marked by different weathering responses. Some examples follow, which illustrate varying interpretations of multicyclic landscapes.

Bourman (1969[1], 1973[2]), identified a multicyclic landscape marked by two major erosion surfaces, the Spring Mount Plateau, developed during the time from the Mesozoic to the Eocene and the Green Hills Surface of Pliocene age on Fleurieu Peninsula. The former, underlain by a lateritic weathering profile consisting of pallid, mottled and ferruginous-rich zones, occurred at about 400 m above sea level. The surface was considered to have been tilted to the southeast. The second erosional surface, 170–100 m above sea level, was capped in places by ferricrete, a term used to describe iron-cemented crusts not underlain by deep weathering profiles. The Green Hills ferricreted surface was thought to have formed from reworking of lateritic material from the summit surface. Using stranded river gravels and river profiles, Bourman (1973[2]) suggested that base level during erosion of the Green Hills Surface in the Pliocene was approximately 60 m above sea level when fluvial action modified a resurrected pre-Miocene erosion surface.

Forrest (1969[3]) examined the geomorphic evolution of the Bremer Valley in the eastern Mt Lofty Ranges and identified two erosional surfaces of low relief which he considered had formed prior to a major marine transgression in the Miocene. Consequently, both the surfaces and their associated cappings of lateritic material were interpreted as pre-Miocene in age. The Miocene sea was presumed to have transgressed an area with relief similar to that of today and lateritisation of the bedrock was presumed to have followed the development of the Whalley Hill and Lucernbrae erosion surfaces prior to the Miocene. Another surface, an exhumed one with a remnant of derived ferricrete, and thought to have formed by stripping of the Miocene limestone cover, was considered to be of Pliocene age.

In a study of landsurface development in the Mid North of South Australia, Alley (1969[5], 1973, 1977) identified remnants of a laterite surface, occurring high in the landscape but below resistant quartzite ridges. Remnants of the laterite surface were noted to be most common at stream-heads but also to occur on prominent hills that stand nearly 100 m above modern valley floors. The laterite capping of angular quartz fragments set in a matrix of iron oxides was observed to overlie severely weathered and locally kaolinitic bedrock and to be consistently thicker on lower slopes. Sections of the laterite surface were thought to have been down-faulted in the Early Tertiary and later buried by Middle Tertiary sediments. A consistently lower silcrete-capped landsurface was considered to be younger than the laterite surface.

In interpretations of multicyclic landscapes and the recognition of the ages of different landsurfaces there are inevitably many disagreements and workers in South Australia have not escaped these. An example follows. King (1976) recognised several of his world

[1] BOURMAN, R. P. (1973) Geomorphic evolution of southeastern Fleurieu Peninsula. M.A. thesis, The University of Adelaide (unpubl.).

[2] ALLEY, N. E. (1969) The Cainozoic History of the Mid North of South Australia. M.A. thesis, The University of Adelaide (unpubl.).

wide erosional surfaces in the Mt Lofty Ranges of South Australia. He considered that south of the Willunga Fault, 'laterite-encrusted tablelands' represented the Moorlands planation ('great Australian denudation cycle') of Late Cretaceous to middle Cainozoic age, whereas north of the fault, the Mt Lofty Ranges were thought to be surmounted by his Rolling landsurface of Miocene age that lacked a true laterite. The Widespread landscape of Pliocene age was recognised in broad valleys and basins accordant with a Pliocene coastal plain at about 180 m above sea level, and the Youngest Cycle was related to deep valleys and gorges in the ranges.

On the other hand, Twidale (1978) considered that the summit surfaces both north and south of the Willunga Fault were contiguous and of the same early Mesozoic age. However, areas of laterite mapped by Twidale (1978) north and west of the Willunga Fault on the Eden and Clarendon Blocks are variably covered with weathered and ferruginised Eocene to Pliocene sediments (Sprigg 1942, 1946; Ward 1966). In places these have been eroded to expose an underlying weathered pre-Tertiary surface, eroded and reweathered since exhumation (Sprigg 1945). Consequently, the summit surface here cannot be of early Mesozoic age. Furthermore, there may be some support for King's generalised scheme, as weathered zones have been stripped from large areas of the summit surface north of the Willunga Fault, especially in the eastern Mt Lofty Ranges (Twidale & Bourne 1975a), allowing further erosion and the potential development of a younger surface, possibly equivalent to King's Rolling surface.

Age of laterite

It is very difficult to ascribe ages to laterite materials because they may have developed over long time periods, some may have several possible modes of genesis, others are polygenetic having been considerably reworked and reweathered, and there are severe limitations on dating techniques applied to weathered materials (Bourman 1993a). Furthermore, there are rarely constraining sediments. These difficulties are apparent in South Australia, where lateritisation has been ascribed to periods from the early Mesozoic to the present. There have been many assertions about the age of laterite in South Australia, often without presentation of convincing evidence. There has also been a tendency to prescribe a single time of lateritisation, when evidence of the timing has commonly been derived from limited study areas, from where there has often been widespread extrapolation. The following discussion of evidence presented by different workers in South Australia highlights the great variability in the ages attributed to lateritisation

Early-Middle Tertiary

Woolnough (1927) considered that lateritisation occurred during one period, in the Miocene, and many subsequent workers have generally supported the view of a Tertiary age for lateritisation (e.g. Prescott & Pendleton 1952) but not necessarily in the Miocene. Aitchison *et al.* (1953) reported Early Tertiary lacustrine mottled sands, argillaceous sandstone and clays occurring sub-horizontally on a pre-Tertiary erosion surface in the Adelaide area, implying lateritisation in the Tertiary, and Campana (1955) favoured widespread lateritisation between the Early Eocene and the Miocene.

Sections of a laterite surface in the Mid North of South Australia were thought to have been down-faulted in the Early Tertiary and later buried by Middle Tertiary sediments, so that Alley (1973) regarded the laterite surface to be of (?)Early to pre-Tertiary age and considered that it persisted until the Middle Tertiary in the Barossa area.

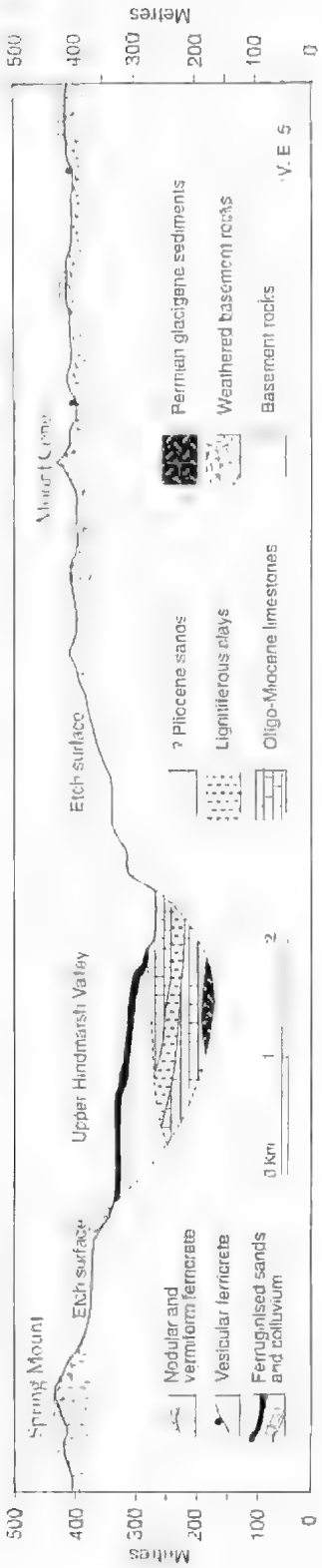
Iron-stained rounded quartz grains and ferruginous pellets were reported from within a fossiliferous marine limestone of probable Upper Eocene age (Bourman & Lindsay 1973), intersected in a drill hole at -36 m underlying part of the Waitpinga Creek drainage basin, and at an elevation of about 60 m above sea level. This observation was interpreted as indicating the development of lateritisation, or at least ferruginisation, prior to the Eocene.

Pliocene

Many concurred with Prescott (1931) and Whitehouse (1940) that there had been widespread laterite formation throughout Australia in the Pliocene (e.g. Stephens 1946; Crocker 1946; Northcote 1946; Rix & Hutton 1953; Johns 1961a, b). Fenner (1930, 1931) also implied a post-Miocene or Pliocene age for laterite in the Mt Lofty Ranges.

Working on Fleurieu Peninsula, Crawford (1959) identified laterite capping Wilson Hill at 320 m, around which an area was mapped as the lower part of a laterite profile developed on Kanmantoo Group metasedimentary rocks. The occurrence of areas of hard laterite at lower elevations (100 m above sea level), on quartzose sediments, was interpreted as indicating a very irregular original lateritised surface of Late Tertiary age. Subsequently, Bourman (1973) demonstrated that the two occurrences were distinctive and probably of two different ages, with Miocene limestone separating the two types.

The evidence presented by Horwitz (1960) for major lateritisation in the Pliocene is also equivocal. In the intramontane Upper Hindmarsh Valley of Fleurieu Peninsula over 150 m of cross-bedded and mottled brown ferruginous sands, capped by a crust of limonite-



cemented gravels, were reported. By extrapolation these were considered to overlie fossiliferous Early Miocene limestones. The sands were thus tentatively assigned to the Pliocene. Horwitz also considered that these lateritised Pliocene sands were continuous with limonite-cemented gravels on the high plateau (Fig. 9). Thus he assigned them to the same Pliocene age. Brock (1964[6], 1971) questioned the contemporaneity of the high-level and low-level crusts and Bourman (1969[1], 1973[7]) highlighted their different characters and suggested that the higher crust was of pre-Miocene age and the lower one of Pliocene age.

Harris & Olliver (1964) reported on palynological analysis of organic material preserved in "coal balls" exposed in Tertiary sands in the Barossa Valley. The basal Tertiary unit was described as a lateritic sand and gravel overlain by laminated silty and sandy clays and was considered to be of Early Tertiary age. The clays were capped by an upper laterite. Previously the sands had been assigned to the Eocene (Glaessner 1955) or Pliocene (Hossfeld 1949) but Harris & Olliver (1964) suggested that the microfloras indicated a Miocene or possibly an Early Pliocene age for the sediments.

Twidale (1968) concluded that the deep weathering in the Mt Lofty Ranges occurred late in the Tertiary (Pliocene) and may have even continued into the early part of the Pleistocene. Major & Vitols (1973) suggested that ferruginous pisolites on the western end of Kangaroo Island were of Late Pliocene or Early Pleistocene age as an aeolian calcarenite (Middle Pleistocene Bridgewater Formation) was thought to overlie pisolites, and elsewhere blocks of ferruginous pisolite were noted to overlie marine limestone of probable Late Pliocene age.

Pleistocene

Sprigg (1946) noted similarities between mottled zones of laterite of the Mt Lofty Ranges and mottled Pleistocene clays of the nearby gulf lowland and correlated the two disparate occurrences assigning lateritisation to a humid pluvial period in the Pleistocene. Bauer (1959[5]) also favoured a Pleistocene age for lateritisation when he addressed problems associated with lateritic soils on Kangaroo Island. He noted that the Eleanor Sand, regarded by Northcote (1946) as a Pliocene fossil lateritic soil, occurs both on a Pliocene plain of marine abrasion at 50 m to 100 m above sea level (Mt Taylor Plain) and on the highest

Fig. 9 Spur-line cross section through the Spring Mount-Upper Hindmarsh Valley-Mount Cone area showing the relationships of ferricretes to Tertiary limestone. Note particularly the distribution of nodular to vermiform ferricrete and that consisting of ferruginised sands, which Horwitz (1960) regarded as of the same Pliocene age.

portions of an undissected Tertiary plateau surface at heights up to 300 m above sea level. Regardless of whether the Eleanor Sand formed in two separate periods or one, Bauer (1959[a]) considered that both were no older than the Early Pleistocene.

Bauer (1959[a]) also challenged the view of Prescott & Pendleton (1952) that laterite is an exposed podzolic illuvial horizon of Tertiary age, as he noted the occurrence of laterite on presumed Pleistocene surfaces. Several anomalous laterite occurrences were examined by Bauer (1959[a]), who interpreted them to favour *in situ* laterite formation although Northcote (pers. comm. to Bauer) suggested that the ironstones had been derived by transport and could not have formed *in situ* because of the small amounts of associated clays. However, Bauer (1959[a]) doubted this explanation on age and topographic grounds. Subsequent work (Milnes *et al.* 1983) revealed that the critical limestones used by Bauer (1959[a]) to date the laterites are older than he thought. Consequently, many of his objections to transported origins for the laterites may be removed.

Lateritisation has also been ascribed to the Pleistocene by Horwitz & Daily (1958), Crawford (1965) and Wopfner (1972) who described mottled Pleistocene sediments in various locations.

Multiple periods of lateritisation

A detailed stratigraphic study by Glaessner (1953b) and Glaessner & Wade (1958) on the western margin of the Mt Lofty Ranges allowed them to suggest several periods of lateritisation, provide information on the character and timing of tectonic activity and to elucidate aspects of landscape evolution. Rocks and sediments of Precambrian, Cambrian, Permian and Tertiary ages were noted to be variably lateritised or to contain blocks of laterite. However, many of the iron oxides within these sediments attributed to lateritisation may have formed since exposure, in recent times, by oxidation of primary iron minerals such as glauconite and siderite.

Several groups of workers have considered that lateritic weathering has proceeded over long periods of time. For example, Campana & Wilson (1954) attributed lateritisation to Pliocene to Recent weathering, Brock (1964[b]) from Mesozoic to the Early Tertiary and Firman (1981) observed weathering affecting materials varying in age from the Proterozoic to the Pleistocene. Milnes *et al.* (1985) considered that weathering has been ongoing since the Permian.

After investigations on Fleurieu Peninsula and in the Mid North, Horwitz (1960, 1961) considered evidence relating to the nature and age of laterite, which suggested two major periods of lateritisation, in the pre-Eocene and Pliocene. Boutman (1973[1]) also presented evidence for two ferruginous duricrusts of different ages, one on the summit surface and the other on the sands that overlie Miocene limestone in the Upper Hindmarsh Valley. Previously, Horwitz (1960) had regarded these crusts as contiguous and of the same Pliocene age. Bourman (1973[1]) also favoured the view that deep weathering proceeded after summit surface uplift.

Ward (1966) believed that the peneplain of the western Mt Lofty Ranges is not of the same age everywhere and was no younger than the Early Pliocene. Relationships between soil morphologies and degrees of lateritisation of materials were noted, as were well-developed lateritic mottled zones formed beneath surfaces attributed to the Late Pliocene, Early Pleistocene and Late Pleistocene. In contrast, Maud (1972) noted scattered erosional remnants of laterite surviving above the level of Miocene limestones deposited in partly exhumed glacial valleys. This suggested that the laterite surface pre-dated the Miocene, by which time it was being destroyed. Consequently, Maud (1972) believed that faulting and tilting of the lateritised surface had occurred earlier than the Pleistocene age favoured by Sprigg (1942), with the lateritised surface antedating the major period of diastrophism. He equated the surface with the Australian Surface of King (1962). Furthermore, Maud (1972) interpreted outcrops of lateritic ironstone at various levels in the landscape as relics of episodic lateritisation, affecting alluvial sediments, including reworked crusts, on former broad valley floors. He suggested that the ironstone terrace remnants varied in age from Pliocene for the highest to Recent for the lowest. These valley ironstones were described as forming parts of typical laterite profiles, with bleached, though rarely kaolinised, pallid zones.

Mesozoic

Daily *et al.* (1974) argued that evidence on Kangaroo Island enabled direct and precise dating of the laterite developed on the uplifted planate summit surface of the Mt Lofty Ranges. They described Kangaroo Island as a dissected, tilted and block-faulted plateau with a caprock of laterite, in places, breached by faults. Adjacent lowlands were noted to be essentially coincident with Permian glacigene sediments that were also lateritised and overlain by basalt of Jurassic age.

The lateritic capping of the summit plateau surface of Kangaroo Island was described as part of a laterite profile and they explained the lack of a complete laterite profile in the Late Palaeozoic sediments beneath the basalt by erosion of the ferruginous horizons prior to basalt extrusion. No evidence of deep weathering on the basalt was observed during their investigations. Consequently, they ruled out the possibility of the surface on the basalt being an etch surface.

They argued that as the basalt is of Middle Jurassic age, both the laterite and the summit surface must be older. The laterite was regarded as an indicator of a humid tropical climate and as a reliable morphostratigraphic marker. Using stratigraphic and palaeoclimatic evidence they suggested that the summit surface was eroded and lateritised during the Late Triassic, Early Jurassic, or both. Support for this conclusion was derived from evidence of warm, humid conditions associated with the Triassic flora of Leigh Creek, in the Flinders Ranges, and evidence of tectonism and uplift of a deeply weathered kaolinised zone during the Mid-Jurassic, which had led to the development of the Polda Basin on Eyre Peninsula and the extrusion of the Kangaroo Island basalt.

A Middle to Late Tertiary age for the lateritised surface was preferred by Northcote (1979) who considered that the correlation of the summit surface weathering with that beneath the Jurassic basalt was unresolved.

Schmidt *et al.* (1976) presented palaeomagnetic evidence that required sub-basaltic weathering during a Late Oligocene to Early Miocene period of dominant lateritic weathering. Idnurm & Senior (1978) favoured a synchronous Australian-wide laterite remagnetisation over this period during a major weathering event. The superimposition of a Mid-Tertiary weathering event on the earlier weathering profile was accepted by Daily *et al.* (1979) but they also presented further evidence for deep lateritic pre-Eocene weathering. Milnes *et al.* (1982) also pointed out problems with the sub-basaltic weathering hypothesis, including the preservation of a sharp basalt/weathered zone contact, the absence of leaching or kaolinisation of the basal basalt, and the fact that the basalt everywhere is largely unweathered.

Subsequent isotopic dating of kaolinite (Bird 1988[9]) and alunite (Bird *et al.* 1990), collected by the present author from the sub-basaltic weathered zone at Kingscote, together with kaolinised bedrock from the summit surface of Kangaroo Island and Fleurieu Peninsula suggests that the kaolinitic weathering beneath the basalt is of Early Mesozoic age, but that the summit surface kaolinite samples are of Middle Tertiary age. Furthermore, the alunite is not synchronous with the pre-Jurassic weathering but possibly relates to the posulated Middle Tertiary iron mobilisation of Schmidt *et al.* (1976). This illustrates the complexities involved in some weathering materials and highlights potential dangers in extrapolating even over quite short distances, and especially interregionally (e.g. Bourne 1974[2]; Twidale & Bourne 1975a, b; Twidale *et al.* 1976; Twidale 1983).

[9] Bird, M. J. (1988). An oxygen- and hydrogen-isotope study of lateriles and deep weathering. Ph D. thesis, Australian National University, Canberra (unpubl.).

The many conflicting views on the age and development of lateritic materials, largely arise from investigations in isolated localities and extrapolation from them over sub-continental areas. These apparent conflicts may be resolved by the application of the ongoing weathering hypothesis.

Ongoing weathering

The evidence presented for a wide variety of possible ages for lateritisation and reworking of ferruginous materials in southern South Australia, ranging throughout the Mesozoic and Cainozoic including the present (see Fig. 2 in Bourman 1993b), prompted Bourman (1989[4], 1993b) to propose continual lateritic development interrupted by geological events and ongoing transformations of ferricretes over long periods of time. There may have been some times when weathering was more extreme but there is no reliable evidence of discrete and episodic periods of lateritisation.

Laterite as a morphostratigraphic marker

Duricrusts including laterite have been widely used as morphostratigraphic markers for dating and correlating land surfaces, in some cases of continental extent. Some workers, such as Twidale (1983) regard duricrusts as excellent morphostratigraphic markers and Firman (1981) considered that original materials, now ferricreted, have separate lithostratigraphic status and that continuous sheet ferricrete has both rock and soil stratigraphic status. However, there are difficulties in using duricrusts as morphostratigraphic markers. For example, they may take long periods of time to form so that any correlation would be extremely coarse. Furthermore, as noted in the section on the ages of lateriles, even short distance correlation of apparently similar materials can be unreliable.

Horwitz (1960) used lateritic materials in morphostratigraphy when he associated glazed pisolites, pebbles and limonite pisolites with a pre-Tertiary surface on Fleurieu Peninsula, after observing similar ferruginous materials elsewhere beneath Tertiary limestone. However, the correlation of ferruginous materials, which superficially appear similar, may not be reliable. For example, a surface in the lower Hindmarsh Valley, carrying alleged Early Tertiary pisoliths could not have developed until post-Miocene times (Bourman (1973[2]) as it had been covered by the Miocene seas. Moreover, the occurrence of pisoliths in reworked Early Tertiary sediments is not a critical indicator of their maximum possible age. They may be of variable ages, or be older clasts reincorporated into younger sediments. In addition, it appears that some of these pre-Eocene ferruginous materials represent the transgressive marine Compton

Conglomerate (Oligocene) of the Murray Basin (Ludbrook 1961; Lindsay & Williams 1977), and do not relate to exposure in a terrestrial environment.

A useful and innovative approach to morphostratigraphy was reported by Wopfner (1972) who recorded identical mottled profiles from the Mid North and the South East regions of South Australia, where maghemitic mottled profiles in Cainozoic sediments were capped by brown ferruginous and maghemitic crusts. Magheumte was regarded as a climatic indicator and as presenting opportunities for correlation of the Cainozoic sediments.

Twidale and co-workers (e.g. Twidale *et al.* 1976; Twidale & Bourne 1975a, b; Bourne 1974[2]; Twidale 1983) have used duricrusts extensively as morphostratigraphic markers in southern Australia. For example, Twidale *et al.* (1976) described eight palaeosurfaces on Eyre Peninsula. Among these was an epigene surface of low relief (Lincoln Surface) protected by a lateritic duricrust and formed under humid tropical climatic conditions during the early Mesozoic. A younger surface characterised by a ferruginous duricrust was ascribed to the Late Tertiary. These surfaces were used as evidence for the progressive exposure of inselbergs on Eyre Peninsula. The Lincoln Surface was regarded as a laterite-capped dissected peneplain formerly contiguous with summit surfaces in the Mt Lofty Ranges and on Kangaroo Island and disrupted by faulting.

However, the summit surface of Blue Range described by Bourne (1974[2]) and Twidale *et al.* (1976) as the most northerly occurrence of a postulated Mesozoic true laterite surface, and equivalent to summit surfaces on the Lincoln Uplands, Kangaroo Island and the Mt Lofty Ranges was thought to have no continuous laterite profile beneath it (Bourman 1989[1]). Near-horizontal Precambrian metasediments are bleached and mottled but the mottles were interpreted as superficial stains of iron oxides (Bourman 1989[2]). Tabular blocks of iron-stained and iron-impregnated sandstone litter the surface and superficially resemble a crust but they were considered to be remnants of flat-lying strata within the Precambrian bedrock. Furthermore, fringing the highest sections of Blue Range, are bleached Precambrian metasediments overlain by up to 2 m of calcareous fine earth, out of sympathy with a leached lateritic environment, and capped by a sandy grey soil containing fragments of ferruginised sandstone bedrock and glazed magnetic pisoliths. Thus the surface is a complex feature, much younger than the suggested Mesozoic age.

Pedogenic accumulations of iron oxides lacking mottled and pallid zones were reported by Twidale *et al.* (1976) at lower elevations below relics of silcrete duricrust assigned to the Middle Tertiary and thus were attributed to the Late Tertiary and correlated with similar ferricretes on Yorke Peninsula and in the southern Mt Lofty Ranges. The Glenville Surface was also mapped in the area and was regarded as an etch plain equivalent of the laterite surface.

A summary of views concerning duricrusts has been presented by Twidale (1983). Laterites and bauxites were regarded as ferruginous and aluminous members of comparable origins with similar physiographic and climatic implications, developed on contiguous land surfaces and of the same age ranges in given regions. A map of Australia was compiled, reaffirming the general peripheral distribution of laterite and an interior preservation of silcrete in arid Australia (e.g. Stephens 1971). Both primary laterite and silcrete were regarded as reliable stratigraphic markers, useful in dating landforms and landscapes.

Twidale (1983) considered that the dating of laterite, silcrete and their associated surfaces has been confused by the assumption that all relic laterites are of the same age and that primary and secondary laterites have been confused. This may have been the case in some areas, but in the Mt Lofty Ranges, Brock (1964[6]), Bourman (1969[1]) and Forrest (1969[3]) clearly distinguished laterites formed in place and those developed by transport. Although some workers have stressed the influence of geomorphic processes affecting laterite development during deep weathering (e.g. Alley 1973, 1977), Twidale (1983) considered that these processes had not been given sufficient appreciation. Twidale (1983) also thought that silcrete developed mainly during the Early and Middle Tertiary, forming under warm-humid to sub-humid conditions, but is today preserved in aridity. This is in contrast to the views expressed in McGowran *et al.* (1978).

Twidale (1983) believed that during the Late Mesozoic and Tertiary much of Australia was base-levelled and this surface of low relief was deeply weathered under humid, warm conditions; laterite and bauxite formed in the marginal areas with external drainage, while silcrete developed in interior catchments. The formation of the duricrust was interpreted as having been interrupted by geologic and geomorphic events so that the duration and timing of events were not everywhere the same. Climatic conditions suitable for duricrusting were thought to have lasted for at least 60 Ma and possibly for 200 Ma and ferruginous and siliceous crusts were related to the same extended period of warm, humid climate but were separated from analogous Cainozoic development by tectonic rather than by climatic events (see also Alley 1977).

Bourman (1993b) noted that the reliability of duricrusts (ferricrete) and weathered mottled and bleached zones as morphostratigraphic markers depends on whether lateritisation has been ongoing or discrete, episodic and related to periods of intense tropical weathering. Evidence of continual weathering in

southern South Australia throughout the Mesozoic and Cainozoic favours the former view. Even where lateritic materials are stratigraphically constrained there is no evidence that they relate to humid tropical conditions or that their cessation depended on climatic change rather than burial by sediments. Most commonly, there are no constraining sediments and some lateritic materials have been affected by ongoing transformations over long time periods.

Conclusions

This review of the laterite literature of southern South Australia reveals many fundamental conflicts concerning the nature of laterite, its classification, the processes of laterite formation, the relationships of horizons within laterite profiles, the topographic and climatic requirements for laterite formation, the interpretation of lateritic landscapes, the age of laterite and its viability as a morphostratigraphic and palaeoclimatic marker.

In particular, there is considerable confusion and lack of consistency about the nature of materials called laterite, these varying from superficially iron-stained sediments, without associated profile differentiation, to iron-mottled and kaolinised bedrock forming part of a weathering profile. Different types of laterite fabrics have long been recognised but until recent work (e.g. Milnes *et al.* 1987; Bourman *et al.* 1987; Bourman 1993a) there has been no recognition nor discussion of their significance. Resulting from these factors there is no precise definition of the term by many workers. Distinctively different materials have often been regarded as equivalents leading to the allocation of spurious ages for the laterites. On the basis of much equivocal evidence, the tectonic behaviour of parts of the Mt Lofty Ranges and ages of lateritisation have been implied.

Many studies have been merely coincidental to other geological investigations and others have been very broad scale geomorphic reports that have involved inter-regional correlations based on the use of laterite as morphological and palaeosol-stratigraphic markers. Until quite recently there has been a dearth of studies involving detailed chemical, mineralogical and micromorphological analyses (Milnes *et al.* 1987; Bourman *et al.* 1987; Bourman 1993a).

There has been a shackling effect on landscape interpretaion by the model of the normal laterite profile, which implies the original occurrence of a complete profile including ferruginous, mottled and pallid zones having developed by the *in situ* weathering of regolith materials. Evidence of former lateritisation has been attributed to the occurrence of weathered, bleached and mottled bedrock as well as to ferruginous crusts. Thus, often, the present distribution of lateritic materials on upland areas has been explained by the dissection of formerly continuous laterite after disruption and uplift by faulting. The absence of ferruginous and/or mottled zones has been explained by various degrees of truncation of an original and complete profile, rather than considering differential development of, and lateral variability in, the distribution of ferricretes, mottled and bleached zones, depending on local environments of formation. Surprisingly, often only the laterite crust has been reported missing, even though this is likely to be the most resistant part of the profile. Where crusts are present they are all younger than the immediately underlying materials.

The common association of laterite development with humid, tropical conditions on peneplains close to base level (sea level) has led to the development of circular arguments relating climate, topography and laterite and there have been implied or specified associations of laterite with deep weathering by most previous workers, whereas hypotheses offering alternative explanations to the view of laterite being a fossil soil profile formed on peneplains under tropical climatic conditions have failed to find general acceptance.

There have been suggestions of the age of laterite formation varying from the Mesozoic to the present. The views have been promulgated that laterite of great antiquity persists in pristine form in the contemporary regolith environment and that it is an excellent morphostratigraphic marker, thereby facilitating inter regional extrapolations. This interpretation is at odds with the view that lateritic materials are demonstrably complex, polygenetic features, having been weathered and modified over long periods of time and are notoriously difficult to date. There have also been some questionable correlations of lateritic materials between remote locations, based on relatively superficial observations such as the shape, size and colour of iron oxide mottles.

As laterite formation has often been equated with humid, torrid conditions it has also been used as a palaeoclimatic indicator although some workers have considered that current climatic conditions may be suitable for its formation. There is a paucity of isotopic and palaeomagnetic data and other age dating associations, such as palynology, in demonstrating the timing of lateritisation. Clearly there is a need for far more analytical work to be carried out in the investigation of laterite in South Australia.

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CLADOCERA RECORDED FROM AUSTRALIA

By R. J. Shiel & J. A. Dickson**

Summary

Shiel, R. J. & Dickson, J. A. (1995) Cladocera recorded from Australia. Trans. R. Soc. S. Aust. 119(1), 29-40, 31 May, 1995.

One hundred and sixty-five taxa of Cladocera, in 53 genera, are recognized from Australia. Seventy-two of these are endemic, with another five also recorded from New Zealand. Species names, with published synonymy, are listed systematically, Distributions are given by State/Territory only.

Key Words: Crustacea, Branchiopoda, Anomopoda, Ctenopoda, cladocerans, Australia, checklist, taxonomy, distribution.

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Introduction

The small branchiopod crustaceans commonly called cladocerans are vital links in aquatic food webs as intermediate grazers between algae and bacteria and higher order consumers, e.g. macroinvertebrates and fish. They generally have been neglected in Australian ecological studies, in part because of the lack of suitable local taxonomic references or expertise.

The first brief descriptions of Australian cladocerans appeared in the expedition reports of Dana (1852, 1853), with more detailed descriptions of peculiarly Australian cladocerans by King (1853, 1854, 1866), from the neighbourhood of Sydney. Later, G.O. Sars (e.g. 1885, 1888, 1889, 1896, 1897), working in Norway, described specimens raised from dried mud mailed to him from Australia. Subsequent incidental records, e.g. Henry (1919, 1922), Gurney (1927), Serventy (1929), Brehm (1953a, b), Petkovski (1973a, b) brought to ca 60 the taxa of cladocerans known from Australia.

Early records were collated, and new taxa described, by Smirnov & Timms (1983), in the first revision of the Australian Cladocera. They listed 125 taxa, and provided keys and figures for most of them. Subsequently, significant taxonomic changes were made (e.g. Benzie 1988; Korovchinsky 1992) and a further 45 cladocerans were described (e.g. Frey 1991a, b; Sergeev 1990a, b; Sergeev & Williams 1985; Smirnov 1989a, b, 1992). Five additional indigenous chydorid taxa are described in manuscripts only partly completed by the late D. G. Frey (Indiana University). Frey was working on Gondwanan chydorids, with emphasis on the radiation of the family in Australia, when he died in 1992.

Particularly as a result of Frey's highly detailed work, it has become apparent that many of the cladocerans recorded from Australia, but described from elsewhere, are not conspecific with the nominate species. The wide dissemination of authoritative (albeit northern hemisphere) taxonomic references is partly to blame, compounded by lack of careful discrimination. Also, possibly as a consequence of the widespread acceptance of cosmopolitanism, some earlier authors did not figure their finds, but merely listed them. It is thus impossible to determine the true identity of an animal if the description is minimal, there are no figures, or the original material has been lost.

Our intention in providing a checklist of the cladocerans recorded from Australia is to bring together a disparate and often inaccessible literature. The listing below is a starting point and includes all the taxa and references which have appeared since the revision by Smirnov & Timms (1983). We stress that it is our opinion that at least some of the taxa named are not conspecific with the nominate species, particularly those described initially from the northern hemisphere. It will clearly take considerable effort to resolve the systematic uncertainties.

Systematics

We continue to use "Cladocera" because it is familiar, although the term no longer has taxonomic significance. The classification of the Crustacea: Branchiopoda is outlined by Dodson & Frey (1991). Most Australian cladoceran families are placed in the Anomopoda (families Daphniidae (5 genera/21 species), Moinidae (2/7), Bosminidae (2/2), Ilyocryptidae (1/4), Macrothricidae (5/24) and Chydoridae (29/101)). Only one of the two families in Ctenopoda occurs here - Sididae (5/11), the Holopedidae do not. Similarly, only one of the three families in Onychopoda occurs here - Podonidae (marine, 4/5). The Polyphemidae and Cercopagidae are not recorded here. Neither are the Haplopoda: Leptodoridae known from Australia. This zoogeographic disparity is significant

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ecologically; these absent families contain the larger carnivorous cladocerans.

Cladocera recorded from Australia

In the following checklist, all genera and species of cladocerans recorded from Australia are listed alphabetically in their respective families. Original authors are cited fully in the reference list to facilitate location of original descriptions. See also references cited by Hawking (1994) and Shiel (1995). The first recorded Australian locality follows the describing author, with subsequent finds outside the State/Territory of first record also given with citing author(s). To minimize repetitive citation, exhaustive listings of later finds in the same State/Territory are not given. Published synonymies or reassignments relevant to the Australian fauna also are given, as are authors of synonymy. In the following list, * = endemic to Australia, ** = Australia and New Zealand, 'A "?" with the locality record indicates that the taxon was listed with a "cf." and is not positively identified from that State/Territory. Unless specifically noted, all records are from Australian inland waters, both fresh and athallasic saline. Families are treated systematically in the sequence as given by Smirnov & Timms (1983). However, the *Ilyocryptus* species are separated into the family Ilyocryptidae as proposed by Smirnov (1992). For convenience genera and species within each family are listed alphabetically. In the author citations, two authors who are sometimes confused are separated as follows: (O.F.) Müller, with umlaut, who published in the late 1770s-80s and (P.E.) Mueller, with ue, who published in the 1860s.

Family Sididae Baird, 1850

Diaphanosoma Fischer, 1850

**D. australiensis* Korovchinsky, 1981; Qld (Korovchinsky 1981). Later finds all in Qld

D. excisum Sars, 1885; Qld (Sars 1885); NSW (Jolly 1966); SA (Shiel *et al.* 1982); NT (Tait 1982[1]); WA (Timms 1988)

D. sarsi Richard, 1894; Qld (Korovchinsky 1981); NT (Tait *et al.* 1984); WA (Timms 1988)

**D. unguiculatum* Gurney, 1927; Qld (Gurney 1927); Vic., NSW (Walker & Hillman 1977); SA (Shiel *et al.* 1982); NT (Tait 1982[1]); WA (Brock & Shiel 1983); ?Papua-New Guinea (Korovchinsky 1992)

D. vulzi Stingelin, 1905; NSW (Korovchinsky 1981)

Latonopsis Sars, 1888

L. australis Sars, 1888; Qld (Sars 1888); Vic., NSW (Shiel 1978); NT (Julli 1986); WA (Timms 1988)

**L. brehmi* Petkovski, 1973; WA, NSW (Petkovski 1973b); NT (Julli 1986); Qld (Timms 1986)

Penilia Dana, 1852

P. avirostris Dana, 1852; NSW (marine, coastal) (Dakin & Colefax 1940)

Pseudosida Herrick, 1884

**P. australiensis* Smirnov & Timms, 1983; NSW (Korovchinsky, in Smirnov & Timms 1983)

P. szalayi Daday 1898; Qld, NT, WA (Timms 1988)

Sarsilatona Korovchinsky, 1985

S. papuana (Daday, 1901); *Pseudosida papuana* Daday, 1901; *Sarsilatona papuana*: Korovchinsky (1985); NT (Korovchinsky 1985); Qld, WA (Timms 1988)

Family Podonidae Mordukhai-Boltovskoi, 1968

Pleopsis Dana, 1852

P. polyphemoides (Leuckart, 1859); E. Australia (marine) (Dakin & Colefax 1940)

Pseudevadne (Claus, 1877)

P. tergestina (Claus, 1877); E. Australia (marine) (Dakin & Colefax 1940)

Podon Lilljeborg, 1853

P. intermedius Lilljeborg, 1853; Vic. (estuarine) (Neale & Bayly 1974)

Evadne Lowen, 1836

E. spinifera Mueller, 1867; E. Australia (marine) (Dakin & Colefax 1940)

E. nordmanni Lowen, 1836; E. Australia (marine) (Dakin & Colefax 1940)

Family Chydoridae Stebbing, 1802

Acroperus Baird, 1843

A. alanoides Hudendorff, 1876; NSW (Smirnov 1971); Qld (Timms 1988)

A. harpae (Baird, 1834); *Lynceus harpae* Baird, 1834; *Acroperus harpae*: Baird (1843); NSW (Smirnov 1971)

A. neglectus Lilljeborg, 1900; *Acroperus avirostris* Henry, 1919: Smirnov & Timms (1983); NSW (Henry 1919)

**A. sinuatus* Henry, 1919; NSW (Henry 1919)

Alona Baird, 1843

A. archeri Sars, 1888; Qld (Sars 1888)

**A. beverleyae* Smirnov, 1989; Qld (Smirnov 1989a)

A. cambouei Guerne & Richard, 1893; NSW (Henry 1919); Vic. (Shiel 1976); Qld, NT, WA (Timms 1988)

**A. clathrata* Sars, 1888; Qld (Sars 1888); NSW (Henry 1922)

A. costata Sars, 1862; NSW (Smirnov 1971); Vic. (Timms 1973[2]); NT (Tait 1982[1])

[1]TAIT, R. D. (1982) Plankton of Magela billabongs, N.T. M.Sc. thesis, Macquarie University, unpubl.

[2]TIMMS, B. V. (1973) A comparative study of the limnology of three maar lakes in western Victoria. Ph.D. Thesis, Monash University, unpubl.

A. crassicaudata Sars, 1916; Qld, NT, WA (Timms 1988)

A. diaphana King, 1853; *Alonella diaphana* (King): Sars (1888); *Alona davidi* Richard, 1895: Frey (1991a); *Alona davidi* var. *iheringi* Richard, 1897: Frey (1991a); *Alona punctata* Daday, 1898. Frey (1991a); see Frey (1991a) for comments on synonymy; NSW (King 1853); Qld (Sars 1888); Vic. (Shiel 1976); SA (Shiel 1981[3]); NT (Tait *et al.* 1984); WA (Timms 1988)

A. guttata Sars, 1862; *Alona microtata* Henry, 1922: Smirnov & Timms (1983); NSW (Henry 1922); Vic. (Timms 1973[2]); SA (Shiel *et al.* 1982); NT (Tait *et al.* 1984); Qld, WA (Timms 1988)

A. intricalata Shen Chia-jui, Sung Ta-hsiang & Chen Kuo-hsiao, 1964; Vic. (Morton & Bayly 1977); Tas. (Smirnov & Timms 1983)

**A. investis* Smirnov & Timms, 1983; Vic. (Smirnov & Timms 1983)

**A. laevissima* Sars, 1888; Qld (Sars 1888); NSW (Henry 1922)

**A. macracantha* Smirnov & Timms, 1983; NSW (Smirnov & Timms 1983)

A. monacantha Sars, 1901; NT (Julli 1986); Qld (Timms 1988)

A. popperi Richard, 1897; Vic. (Shiel 1981[3])

A. pulchella King, 1853; NSW (King 1853); Vic. (Shiel 1981[3]); ?Qld, NT, WA (Timms 1988)

A. quadrangularis (Müller, 1785); *Lynceus quadrangularis* Müller, 1785; *Alona quadrangularis*: Smirnov (1971); Vic., WA (Smirnov & Timms 1983)

A. rectangula Sars, 1862; Qld, SA (Smirnov 1971); Vic., (Shiel 1976), NSW (Walker & Hillman 1977); NT, WA (Timms 1988)

**A. sculoides* Smirnov & Timms, 1983; WA (Smirnov & Timms 1983)

A. striolata Sars, 1916; "tropical Australia" (Smirnov 1989a)

**A. truncata* Smirnov, 1989; Qld (Smirnov 1989a)

**A. unguiculata* Smirnov, 1989; Qld (Smirnov 1989a)

Alonella Sars, 1862

A. clathratula Sars, 1896; NSW (Sars 1896); SA (Shiel 1981[3]); NT (Julli 1986); Qld (Timms 1986); WA (Timms 1988)

A. excisa (Fischer, 1854); *Lynceus excisus* Fischer, 1854; *Alonella excisa*: Sars 1862b; NSW (Henry 1922); Vic. (Shiel 1976); SA (Shiel 1981[3]); Qld (Hawkins 1988); ?WA (Bayly 1992)

A. exigua (Lilljeborg, 1853); *Lynceus exiguus* Lilljeborg, 1853; *Alonella exigua*: Mueller, 1867; NSW (Smirnov 1971); NT (Tait *et al.* 1984)

**Archepleuroxus* Smirnov & Timms, 1983

**A. baylyi* Smirnov & Timms, 1983; Vic., Tas., WA (Smirnov & Timms 1983)

**Australochydorus* Smirnov & Timms, 1983

**A. aporus* Smirnov & Timms, 1983; Qld, NSW (Smirnov & Timms 1983); NT (Tait *et al.* 1984); WA (Timms 1988)

Biapertura Smirnov, 1971

**B. abbreviata* (Sars, 1896); *Alona abreviata* (sic) Sars, 1896; *Biapertura abreviata* (sic): Smirnov & Timms 1983; NSW (Sars 1896)

Comment: The spelling of the species name with a single b as *abreviata* in the original description (Sars 1896: 40) appears to be a typographical error, as it is later spelt (p. 43 text; p. 79 fig. caption) as *abbreviata*.

B. affinis (Leydig, 1860); *Lynceus affinis* Leydig, 1860; *Alona whiteleggii* Sars, 1896: Henry 1922; *Alona affinis*: Sars 1901; *Alona longirostris* Henry, 1919: Smirnov 1971; *Biapertura affinis*: Smirnov & Timms 1983; NSW (Sars 1896); Vic. (Timms 1973[2]); WA (Williams 1979); SA (Shiel 1981[3]); NT (Tait 1982[1]); Qld (Timms 1986)

**B. duoodonta* (Henry, 1922); *Alonella duoodonta* Henry, 1922; *Biapertura duoodonta*: Smirnov & Timms 1983; NSW (Henry 1922) ?NT (Tait *et al.* 1984)

**B. imitatoria* Smirnov, 1989; WA (Smirnov 1989a)

B. intermedia (Sars, 1862); *Alona intermedia* Sars, 1862; *Biapertura intermedia*: Smirnov 1971; Qld (Gurney 1927); NSW (Smirnov 1971); Vic. (Shiel 1978); WA (Bayly 1982); NT (Timms 1988)

B. karua (King, 1853); *Alona karua* King, 1853; *Alonella karua*: Sars, 1888; *Biapertura karua*: Smirnov & Timms 1983; NSW (King 1853); Qld (Sars, 1888); Vic. (Morton 1973[4]); NT (Tait 1982[1]); WA (Timms 1988)

Comment: King's description is inadequate by modern standards. There are differences in the post-abdomen morphology of his species and that later hatched from Qld mud by Sars (1888), although Sars considered the taxa identical. There is now good evidence that *B. karua* represents a species complex worldwide (Alonso & Pretus 1989). In our opinion the 1000 km separation of the King and Sars taxa is sufficient to doubt conspecificity, hence their respective identities are not satisfactorily resolved at this time. The problem is compounded by errors in Smirnov & Timms (1983) (see *Incertae sedis* below).

**B. kendallensis* (Henry, 1919); *Alona kendallensis* Henry, 1919; *Biapertura kendallensis*: Smirnov 1971; NSW (Henry 1919); Qld (Smirnov 1971); Vic. (Timms 1973[2]); NT (Julli 1986); WA (Crowns *et al.* 1992)

[1]Still, R. J. (1981) Plankton of the Murray-Darling river system, with particular reference to the zooplankton. Ph.D. Thesis, University of Adelaide, unpubl.

[4]Morton, D. W. (1973) Studies on some temporary Victorian waters with special reference to the Microcrustacea. B.Sc. (Hons) Thesis, Monash University, unpubl.

B. longiqua Smirnov, 1971; NSW, Qld (Smirnov 1971); Vic. (Shiel 1981[3]); WA (Timms 1988)

B. macrocopa (Sars, 1894): *Alona macrocopa* Sars, 1894; *Biapertura macrocopa*: Smirnov & Timms 1983 (author date given as 1895); Qld (Gurney 1927); Vic. (Morton & Bayly 1977); WA (Bayly 1982); NSW (Timms 1982)

B. rigidicaudis Smirnov, 1971; *Alona intermedia* Gurney 1927 (misidentification): *Biapertura rigidicaudis*, Smirnov 1971: Qld (Gurney 1927); Vic. (Shiel 1976); NSW (Timms 1976); SA (Shiel 1981[3]), WA (Bayly 1982); NT (Julli 1986)

B. rusticoides Smirnov & Timms, 1983; Tas. (Smirnov & Timms 1983)

B. setigera (Brehm, 1931); *Alona guttata setigera* Brehm, 1931; *Alona setigera*: Petkovski 1973a; *Biapertura setigera*: Smirnov & Timms 1983; NSW (Bayly 1970); Vic. (Shiel 1976); SA (Shiel 1981[3]); Qld (Timms 1986) ?WA (Storey *et al.* 1993).

B. verrucosa (Sars, 1901); *Alona verrucosa* Sars, 1901; *Alona rectangula pulchra* Hellich, 1874; Smirnov 1971 and Smirnov & Timms 1983; *Biapertura verrucosa*: Smirnov 1989; Qld (Smirnov 1971); NT (Julli 1986); WA (Timms 1988)

B. willisi Smirnov, 1989; Qld (Smirnov 1989)

Camptocercus Baird, 1843

**C. australis* Sars, 1896; NSW (Sars 1896); Vic. (Shephard *et al.* 1918); Qld (Smirnov 1971); NT (Tait 1982[1]); WA (Timms 1988)

Celsinotum Frey, 1991

C. hypsilophum Frey, 1991; NSW (Frey 1991a)

C. parboensis Frey, 1991; NSW (Frey 1991a)

C. platamodes Frey, 1991; NSW (Frey 1991a)

Chydorus Leach, 1816

C. eurynotus Sars, 1901; Qld (Timms 1967); Vic (Walker & Hillman 1977)

C. herrmanni Brehm, 1933; Qld (Timms 1967); Vic. (Shiel 1981[3])

C. kallipygos Brehm, 1933; NSW (Petkovski 1973a); Qld (Hann 1975[5])

Comment: Smirnov & Timms (1983) regarded Petkovski's record as a misidentification of *C. eurynotus*. However Hann (1975[5]) independently recorded *C. kallipygos* from NSW and Qld. Petkovski's record should stand until a thorough revision of the genus is made.

C. obscurirostris Frey, 1987; NT, WA (Frey 1987)

C. opacus Frey, 1987; NT, Qld, WA (Frey, 1987)

C. parvus Daday, 1898; "tropical Australia" (Smirnov 1989a)

C. pubescens Sars, 1901; NT, Qld, WA (Timms 1988)

C. reticulatus Daday, 1898; "tropical Australia" (Smirnov 1989a)

Comment: This species was listed without comment by Smirnov (1989). It is given as a synonym of *C. sphaericus* (Müller) in Flössner (1972). The relationship of this taxon to the other *'faviformis*-like' reticulated taxa described by Frey (1987) remains unresolved. We consider it unlikely to be Daday's species.

C. sphaericus (Müller, 1785); *Lynceus sphaericus* Müller, 1785; *Chydorus sphaericus*; Baird 1843; *Chydorus ehlandi* Henry, 1919 was synonymized with *Chydorus leonardi* by Henry (1922); *Chydorus leonardi* King, 1853: Smirnov (1971) *C. leonardi* was attributed to Sars, 1896 by Smirnov & Timms (1983); NSW (King 1853); Vic. (Morton 1967); Qld (Timms 1967); NT (Tait 1982[1]); SA (Shiel *et al.* 1982); ?WA (Bayly 1992)

Comment: In view of the restricted distribution of *Chydorus sphaericus s.str.* (Frey 1980), it is likely that a complex of species occurs in Australia, none of which is the nominate taxon (D.G. Frey pers. comm.).

Dadaya Sars, 1901

D. macrops (Daday, 1898): *Alona macrops* Daday, 1898; *Dadaya macrops*: Sars 1901; Qld (Smirnov 1971); NT (Tait *et al.* 1984); WA (Timms 1988)

Disparalona Fryer, 1968

D. acutirostris (Birge, 1879); *Pleuroxus acutirostris* Birge, 1879; *Alonella acutirostris*: Frey 1959 *Disparalona acutirostris*: Fryer 1971; "tropical Australia" (Smirnov 1989a)

Dunhevedia King, 1853

D. crassa King, 1853; NSW (King 1853); Qld (Sars 1888); SA (Henry 1922); Tas. (Brehm 1953a), Vic. (Morton 1973[4]); NT (Tait *et al.* 1984); WA (Timms 1988)

Ephemeroporus Frey, 1982

E. tridentatus (Bergamin, 1939); *Chydorus tridentatus* Bergamin, 1939; *Chydorus barroisi* Richard, 1894: Fig. 329 in Smirnov 1971; *Ephemeroporus tridentatus*: Frey 1982a; Qld (Smirnov 1971); Vic. (Shiel 1981[3]); NT (Tait *et al.* 1984); WA (Timms 1988)

Comment: see *Incertae sedis* for other taxa referred to this genus in Australia.

Euryalona Sars, 1901

E. orientalis (Daday, 1898); *Alonopsis orientalis* Daday, 1898; *Euryalona occidentalis* Sars, 1901: Smirnov 1971; *Euryalona orientalis*: Daday 1905; Qld (Smirnov & Timms 1983); NT (Tait *et al.* 1984); WA (Timms 1988)

Graptoleberis Sars, 1862

G. testudinaria (Fischer, 1848): *Lynceus testudinarius* Fischer, 1848 (cited as 1851 in Smirnov & Timms [1983]); *Graptoleberis testudinaria*: Kurz, 1874; NSW (Henry 1919); Vic (Shiel 1976); NT (Tait 1982[1]); Qld; WA (Timms 1988)

[5]HANN, B.J. (1975) Taxonomy of Chydoridae in Ontario and genus *Chydorus* worldwide. MSc. Thesis, University of Waterloo, Ontario, unpubl.

Kurzia Dybowski & Grochowski, 1894

K. latissima (Kurz, 1874); *Alonopsis latissimus* Kurz, 1874; *Kurzia latissima* Dybowski & Grochowski 1894; Vic. (Shiel 1976)

K. longirostris (Daday, 1898); *Alona longirostris* Daday, 1898; *Kurzia longirostris*: Harding 1957; NSW (Timms 1972); NT (Tait *et al.* 1984), Qld, WA (Timms 1988)

**Leberis* Smirnov, 1989

**L. aenigmatosa* Smirnov, 1989; WA (Smirnov 1989b)

Leydigia Kurz, 1874

L. acanthocercoides (Fischer, 1854); *Lynceus acanthocercoides* Fischer, 1854; *Leydigia acanthocercoides*, Kurz, 1874: NSW (Timms 1970), NT (Julli 1986); Qld, WA (Timms 1988)

L. australis Sars, 1885; Qld (Sars 1885); NSW (Shiel 1978); Vic., SA (Shiel 1981[3])

L. ciliata Gauthier, 1939; NSW, Qld (Smirnov 1971); Vic. (Shiel 1981[3])

**L. laevis* Gurney, 1927; Qld (Gurney 1927); NSW (Shiel 1981[3]); WA (Growns *et al.* 1992)

L. leydigi (Schoedler, 1863); *Alona leydigii* Schoedler, 1863; *Leydigia leydigi*: Daday 1902; SA (Henry, 1922); Vic. (Shiel 1976); NT (Tait 1982[1]); WA (Growns *et al.* 1992); NSW (Kobayashi 1992)

**Monope* Smirnov & Timms, 1983; *Monoporus* Smirnov, 1977: Smirnov & Timms (1983: 34)

**M. reticulata* (Henry, 1922); *Pleuroxus reticulatus*: Henry 1922; *Monoporus henryae* Smirnov, 1977; *Monope reticulata*: Smirnov & Timms 1983; non *Pleuroxus reticulatus* Henry, 1918; Frey 1991b; NSW (Henry 1922); WA (Bayly 1992)

Comment: Henry's (1918) taxon as figured is, according to Frey (1991b), a species of *Alonella*, probably *A. clathratula* Sars, 1896.

Monospilus Sars, 1862

**M. diporus* Smirnov & Timms, 1983; SA (Shiel 1978) (as *Monospilus* sp. nov.); WA (Brock & Shiel 1983) (as *Monospilus* sp.); NSW (Shiel 1981[3]) (as *Monospilus* n. sp. 1); Vic. (Shiel & Croome, unpubl. data)

**M. elongatus* Smirnov & Timms, 1983; SA (Shiel 1981[3]) (as *Monospilus* n. sp. 2)

Comment: Neither of these taxa is referrable to *Monospilus* s. str.; indeed they are probably not even congeneric (D.G. Frey, pers. comm.).

Notoalona Rajapaksa, 1986

N. globulosa (Daday, 1898); *Alona globulosa* Daday, 1898; *Notoalona globulosa*: Rajapaksa & Fernando 1987. The nominate species is not recorded from Australia. However a geographic subspecies is known:

**N. globulosa australiensis* (Rajapaksa & Fernando, 1987); *Indialona* (Petkovski, 1966); Rajapaksa & Fernando 1987; NT (Smirnov & Timms 1983 as *Indialona* sp.); Qld (Rajapaksa & Fernando 1987; WA (Timms 1988)

Comment: *Indialona* was reported from the NT by Smirnov & Timms (1983), species not given. Julli (1986) reported *I. globulosa*, also from the N.T. As Rajapaksa & Fernando obtained their material from B.V. Timms, who also collected the Smirnov & Timms material and identified the Julli material, it is probable that all N.T. records are *N. globulosa australiensis*.

Oxyurella Dybowski & Grochowski, 1894

O. singalensis (Daday, 1898); *Alonopsis singalensis* Daday, 1898; *Oxyurella singalensis*: Smirnov 1971; Qld (Smirnov & Timms 1983); NT (Julli 1986); WA (Timms 1988)

O. tenuicaudis (Sars, 1862); *Alona tenuicaudis* Sars, 1862; *Alona wallaciana* Henry, 1919, *Oxyurella wallaciana*: Smirnov 1971; *Oxyurella tenuicaudis*: Smirnov & Timms 1983; NSW (Henry, 1919); ?Vic. (Timms 1973[2]) (as *Oxyurella* sp.)

**Planicirelas* Frey, 1991

**P. alticarinatus* Frey, 1991; WA (Frey 1991b)

**Plurispina* Frey, 1991

**P. chauliodis* Frey, 1991; WA (Frey 1991b)

**P. multituberculata* Frey, 1991; WA (Frey 1991b)

Pleuroxus Baird, 1843

**P. foveatus* Frey, 1991; WA (Frey 1991b)

**P. inermis* Sars, 1896; *Chydorus denticulatus* Henry, 1919; Frey (1991b); NSW (Sars 1896); Vic. (Haase 1903); ?Qld (Gurney 1927); SA (Shiel 1981[3]); WA (Bayly 1992)

**P. jugosus* (Henry, 1922); *Chydorus jugosus* Henry, 1922; Smirnov & Timms (1983); NSW (Henry 1922)

Comment: Frey (1991b) states that close study of the type specimen did not reveal enough positive characters to make a firm decision (regarding *Pleuroxus* cf. *jugosus*), and hence this taxon, at least for the present, must be regarded as a *nomen dubium*. *Pleuroxus jugosus* in Smirnov & Timms (1983) is not *Chydorus jugosus* Henry, 1922: rather most of the description and all of the illustrations in this paper are for *Plurispina chauliodus* Frey, 1991.

**P. kakaduensis* Smirnov, 1989; NT (Smirnov 1989b)

P. laevis Sars, 1862; NT, Qld, WA (Timms 1988)

P. similis Vavra, 1900; *P. australis* Henry, 1922; Smirnov & Timms 1983; NSW (Henry 1922)

Comment: Probably absent from Australia (Frey 1991b)

**P. truncellatus* Smirnov, 1989; WA (Smirnov 1989b)

Pseudochydorus Fryer, 1968

P. globosus (Baird, 1843); *Chydorus globosus* Baird, 1843; *?Chydorus augustus* King, 1853; Sars (1888); *Pseudochydorus globosus*; Fryer 1968; ?NSW (King 1853); Vic. (Shephard *et al.* 1918); Qld (Timms & Midgley 1969); SA (Smirnov 1971); NT, WA (Timms 1988)

Rak Smirnov & Timms, 1983
**R. labimsus* Smirnov & Timms, 1983; SA, Tas, Vic WA (Smirnov & Timms 1983)
**R. obtusus* Smirnov & Timms, 1983; NSW, WA (Smirnov & Timms 1983); Qld (Timms 1988)
Comment: Several new species of *Rak* from W.A. are included in an incomplete MS by the late D.G. Frey. He also found *Rak* in South Africa.
The *Rak* MS will be completed by RJS.
**Rhynchochydorus* Smirnov & Timms, 1983
**R. australiensis* Smirnov & Timms, 1983, *Amblyrynchus*: Bayly 1992 (*nomen nudem*); NSW (Smirnov & Timms 1983); WA (Bayly 1992)
***Saycia* Sars, 1904
***S. cooki* (King, 1866); *Eurycercus cooki* King, 1866; *Saycia orbicularis* Sars, 1904: Smirnov 1966; *Saycia cooki*: Smirnov 1966; NSW, Qld (King 1866); Vic. (Sars 1904)
Comment: After examining a N.Z. population, Frey (1971) concluded that it represented a new geographic subspecies, *Saycia cooki novaezealandiae* Frey, 1971. The Australian subspecies is designated *Saycia cooki cooki* (King, 1866): Smirnov & Timms 1983

Family Ilyocryptidae Smirnov, 1992

Ilyocryptus Sars, 1862
I. brevidentatus Ekman, 1905; Vic. (Shiel 1981[3]), NT (Tait *et al.* 1984)
**I. varidentatus* Smirnov, 1989; WA (Smirnov 1989b)
I. sordidus (Lievin, 1848); *Acanthocercus sordidus* Lievin, 1848; *Ilyocryptus sordidus*: Sars 1896; NSW (Sars 1896); Vic. (Henry 1922); SA (Shiel 1981[3]), NT (Tait *et al.* 1984)
I. spinifer Herrick, 1882; *I. longiremis* Sars, 1888: Smirnov & Timms (1983); *I. halyi* Brady, 1886 in Gurney (1927): Smirnov & Timms (1983); Qld (Sars, 1888); ?Vic. (Timms 1973); WA (Williams 1979); SA, NSW (Shiel 1981[3]); NT (Julli 1986)

Family Macrothricidae Baird, 1843

Grimaldina Richard, 1892
G. brazzai Richard, 1892; Qld, NT (Timms 1988)
Macrothrix Baird, 1843; *Echinisca* Lievin, 1848: Smirnov 1992
**M. breviseta* Smirnov, 1976; Qld (Smirnov 1976); Vic. (Shiel 1981[3]); WA (Growns *et al.* 1992); ?NSW (Timms 1993)
M. capensis (Sars, 1916); *Echinisca capensis* Sars, 1916: Smirnov 1992; Vic. (Smirnov 1976); NSW (Shiel 1981[3]); Tas., WA (Smirnov & Timms 1983); Qld, NT (Timms 1988)
**M. carinata* (Smirnov, 1976); *Echinisca carinata* Smirnov, 1976: Smirnov (1992); Qld (Smirnov 1976); NSW, Tas., WA (Smirnov & Timms 1983)
**M. flabelligera* Smirnov, 1992; Qld (Smirnov 1992)
**M. flagellata* (Smirnov & Timms, 1983); *Echinisca flagellata* Smirnov & Timms, 1983; Smirnov 1992; Tas. (Smirnov & Timms, 1983)
**M. hardingi* Petkovski, 1973: *Echinisca hardingi* Smirnov 1976; WA (Petkovski 1973b); NSW (Shiel 1981[3])
M. hirsuticornis Norman & Brady, 1867; Vic. (Smirnov 1976); SA (Mitchell 1980[6])
**M. hystrix* Gurney, 1927; Qld (Gurney 1927); NT (Julli 1986)
**M. indistincta* Smirnov, 1992; NSW, WA (Smirnov 1992)
**M. longiseta* Smirnov, 1976; Vic. (Smirnov 1976); "tropical Australia", Tas. (Smirnov 1992)
M. malayensis Idris & Fernando, 1981; Qld (Timms 1988)
**M. pectinata* (Smirnov, 1976); *Echinisca pectinata* Smirnov, 1976; Smirnov 1992; Qld, Vic. (Smirnov 1976); NSW (Smirnov & Timms 1983)
M. rosea (Lievin, 1848); *Echinisca rosea* Lievin, 1848; Smirnov 1992; Qld (Smirnov & Timms 1983)
M. schaunslandi Sars, 1903; *Macrothrix bursalis* Smith, 1909: Smirnov & Timms (1983); Tas (Smith 1909); Vic., "tropical Australia" (Smirnov 1992)
M. spinosa King, 1853; NSW (King, 1853); Vic., SA (Shiel 1981[3])
**M. timmsi* (Smirnov, 1976); *Echinisca timmsi* Smirnov, 1976; Smirnov 1992; NSW (Smirnov 1976); Qld (Timms 1986)
M. triserialis Brady, 1886; *Echinisca triserialis* Smirnov 1976; ?NSW (Henry 1922); Qld, Vic., SA (Smirnov & Timms, 1983); NT (Julli 1986); WA (Timms 1988)
**M. williamsi* (Smirnov & Timms, 1983); *Echinisca williamsi* Smirnov & Timms, 1983; Smirnov 1992; Qld (Smirnov & Timms 1983); NT (Julli 1986)
Neothrix Gurney, 1927
***N. armata* Gurney, 1927; Qld (Gurney 1927); Vic. (Morton 1973[4]); WA (Bayly 1982); NSW (Kobayashi 1992)
**N. paucisetosa* Smirnov, 1989b; *Macrothrix paucisetosa* Smirnov 1989b: WA (Smirnov 1989b)
**N. superarmata* Smirnov, 1989b; Qld (Smirnov 1989b)
***Pseudomoina* Sars, 1912
***P. lemnae* (King, 1853); *Moina lemnae* King, 1853; *Pseudomoina lemnae* Sars 1912; NSW (King 1853); Vic. (Shephard *et al.* 1918); Tas. (Smirnov & Timms 1983); SA (Shiel & Koste 1985)

[6]MITCHELL, B.D. (1980) The ecology of waste stabilization ponds. Ph. D. thesis, University of Adelaide, unpubl

Streblocerus Sars, 1862

S. serricaudatus (Fischer, 1849); *Daphnia laticornis* Fischer, 1849; *Streblocerus serricaudatus* Lilljeborg, 1900; Smirnov 1976; Vic. (Smirnov 1976); Qld, Tas. (Smirnov & Timms 1983)

Family Moinidae Goulden, 1968

Moina Baird, 1850

***M. australiensis* Sars, 1896; NSW (Sars 1896); Vic. (Shiel 1981[3]); WA (Smirnov & Timms 1983); NT (Tait *et al.* 1984)

**M. baylyi* Forró, 1985; *Moina mongolica* Daday, 1901 in Bayly (1976), Smirnov (1976), Smirnov & Timms (1983) (misidentified); SA (Bayly 1976); NSW (Williams 1986); Qld (Timms 1987)

**M. flectuosa* Sars, 1897; WA (Sars 1897)

M. micrura Kurz, 1874; *Moina propinqua* Sars, 1885; Goulden (1968); *Moina dubia* Richard in Gurney (1927) (misidentified); Goulden (1968); Qld (Sars 1885); NSW (Timms 1970); Vic. (Timms 1973[2]); SA (Shiel 1978); NT (Smirnov & Timms 1983)

**M. tenuicornis* Sars, 1896; NSW (Sars 1896); Vic. (Henry 1922).

Comment: Possibly also from South Africa (unverified); Goulden (1968)

Moinodaphnia Herrick, 1887

M. macleayi (King, 1853); *Moina macleayi* King, 1853; *Moinodaphnia macleayi*: Sars 1888; NSW (King 1853); Qld (Smirnov & Timms 1983); NT (Julli 1986); WA [Timms 1988])

Family Bosminidae Sars, 1865

Bosmina Baird, 1845

B. meridionalis Sars, 1903 (not 1904 as in Smirnov & Timms [1983]).

For extensive synonymy, see Smirnov & Timms (1983). See also *Incertae sedis* below; Tas. (Smith 1909, as *B. rotundata*); NSW (Jolly 1966); Qld (Timms & Midgley 1969); Vic. (Timms 1973[2]); SA (Shiel *et al.* 1982); NT (Tait *et al.* 1984); WA (Timms 1988)

Bosminopsis Richard, 1895

B. dietersi Richard, 1897; NSW (Jolly 1966); NT (Tait 1981); Qld (Timms 1986); WA (Timms 1988)

Family Daphniidae Straus, 1820

Ceriodaphnia Dana, 1852

C. cornuta Sars, 1885; Qld (Sars 1885); NSW (Henry 1922); Vic. (Shiel 1978); NT (Tait 1981); SA (Shiel *et al.* 1982); Tas. (Koste & Shiel 1987); WA (Berner 1987)

Comment: Evidently more than one small species of *Ceriodaphnia* with an acute "beak" occurs in tropical Australia (cf. Berner 1987). Until a thorough revision of the genus has been made, these taxa should be referred to *C. cornuta* s.l.

C. dubia Richard, 1894; Qld (Gurney 1927); Vic. (Shiel 1976); ?NSW (Timms 1989)

C. laticaudata Mueller, 1867, ?Vic. (Shiel 1978); ?Qld (Timms 1988)

C. quadrangula (Müller, 1785; *Ceriodaphnia hakea* Smith, 1909; Brehm (1953a); ?*Ceriodaphnia planifrons* Smith; Brehm (1953a); Tas. (Smith 1909); NSW (Jolly 1966); Vic. (Timms 1973[2]); SA (Shiel 1978)

C. rotunda Sars, 1862; Vic. (Shephard *et al.* 1918)

Daphnia Müller, 1785

D. carinata King, 1853 s.l. For extensive synonymy, see Benzie (1988: 136-139); NSW (King 1853); Vic. (Shephard 1898); Tas. (Shephard 1917); WA (Serventy 1929); Qld (Timms 1968); SA (Mitchell 1978); NT (Timms & Morton 1988)

D. cephalata King, 1853; For synonymy, see Benzie (1988: 129); NSW (King 1853); Vic. (Sars 1914)

**D. jollyi* Petkovski, 1973; WA (Petkovski 1973a)

D. lumholtzi Sars, 1885; For synonymy, see Benzie (1988: 113-114); Qld (Sars 1885); NSW, Vic., SA (Shiel 1981[3]); WA (Timms & Morton 1988)

**D. nivalis* Hebert, 1978; For synonymy, see Benzie (1988: 122); NSW (Hebert 1977)

**D. occidentalis* Benzie, 1986; WA (Benzie 1986a)

Daphniopsis Sars, 1903

**D. australis* Sergeev & Williams, 1985; Tas. (Sergeev & Williams 1985); SA, Vic. (Williams 1986)

**D. pusilla* Serventy, 1929; WA (Serventy 1929); Vic., SA (Bayly & Edward 1969); Tas. (Sergeev & Williams 1983)

**D. quadrangulus* Sergeev, 1990; Vic. (Sergeev 1990a)

**D. queenslandensis* Sergeev, 1990; Qld (Sergeev 1990b)

Scapholeberis Schoedler, 1858

S. kingi Sars, 1903; *Daphnia mucronata* Müller, 1785; King 1853 (misidentification); *Scapholeberis kingii*: Sars, 1888 (*nomen nudem*); Smirnov & Timms 1983; *Scapholeberis kingi* Sars, 1903; NSW (King 1853); Vic. (Henry 1922); NT (Julli 1986); Qld (Timms 1988); WA (Halse *et al.* 1993)

Simocephalus Schoedler, 1858

S. acutirostratus (King, 1853); *Daphnia elisabethae acutirostrata* King, 1853; *Simocephalus acutirostratus*: Sars 1888; *Simocephalus dulvertonensis* Smith, 1909; Dumont in Smirnov & Timms 1983; NSW (King 1853); Vic. (Haase 1903); Tas. (Smith 1909); NT (Tait *et al.* 1984); Qld (Timms 1988)

S. expinosus australiensis (Dana, 1852); *Daphnia australiensis* Dana, 1852; *Simocephalus australiensis*: Sars, 1888, *S. exspinosus australiensis*: Dumont in Smirnov & Timms (1983); Qld (Sars 1888); NSW (Sars 1896); ?Tas. (Smith 1909); SA (Henry 1922); WA (Serventy 1929); Vic. (Morton 1973[4])

S. latirostris Stingelin, 1906; ?*S. iheringi* Richard, 1897; Dumont in Smirnov & Timms (1983); ?NSW (Henry 1922); NT (Tait *et al.* 1984); Qld, WA (Timms 1988)

S. serrulatus (Koch, 1841); NT (Hall 1986); Qld (Timms 1988)

S. vetulus (Müller, 1776); 2 ssp. recognized from Australia (see comments by Dumont, in Smirnov & Timms [1983: 98-102])

S. vetulus elisabethae (King, 1853); *Daphnia elisabethae* King; *Simocephalus elisabethae*: Sars (888; NSW (King 1853); Vic. (Shiel 1978); SA (Shiel 1981[3]); Qld, NT (Timms 1988)

S. vetulus gibbosus (Sars, 1896); *Simocephalus gibbosus* Sars, 1896; *Simocephalus vetulus gibbosus*: Dumont in Smirnov & Timms 1983; NSW (Sars 1896); Vic. (Shephard *et al.* 1918); SA (Shiel 1981[3])

?S. victoriensis Dumont, 1983; Vic. (Dumont in Smirnov & Timms 1983)

Incertae sedis

Alona bairdii King, 1853; NSW (King 1853: Description inadequate.

Alona karua King, 1853; NSW; *Biapertura karua* in Smirnov & Timms (1983) is erroneously referred to King. They list King's *Alona karua* as *incertae sedis*. The species they have mislabelled is *Alonella karua* in Sars (1888), which is apparently a misidentification of another species, not the nominate *A. karua*. As figured by Sars, it is clearly not the taxon figured by King, and should be relocated if King's species is rediscovered.

Alona mascula King, 1853; NSW: Inadequately described.

Bosmina maritima Mueller, 1867; "off the Abrolhos, 300 miles north of Fremantle, Western Australia, in November, 1910" (Searle 1936: 172). Not recorded again, or mentioned by Korinek in Smirnov & Timms (1983). *B. maritima* is recorded as a synonym of *B. longispina* Leydig, 1860 in Flössner (1972). This is the only record of a marine bosminid from Australia and its identity is uncertain.

Chydorus barroisi (Richard, 1894); Qld (Smirnov 1971): = *Ephemeroporus barroisi*, *nomen dubium* (See Frey 1982a). Frey noted (p. 234) that the figured specimens from Prospect Reservoir, NSW, in Smirnov (1971 Figs 328, 330, 331, 332) are not conspecific with *E. tridentatus* (Fig. 329 in the same series), nor are they conspecific with *E. barroisi* s. str.

Chydorus hybridus Daday, 1905; Qld, NSW (Smirnov & Timms 1983); Frey (1982a) relocated *C. hybridus* s. str. to a new genus, *Ephemeroporus*, and the taxon became *E. hybridus* (Daday). The limited features of the Australian taxon assigned to "*C. hybridus*" as figured in Smirnov & Timms (1983) are neither *Chydorus* nor *Ephemeroporus*, but more correctly those of *Rak* (Frey, in MS).

Chydorus ovalis Kurz, 1874; NSW (Henry 1922); No figures or material are available of the taxon identified by Henry and it has not been recorded again. It is a Holarctic species and regarded as absent from Australia by Smirnov & Timms (1983).

Daphnia honorata King, 1853; NSW (King 1853); A species of *Ceriodaphnia*, inadequately described and figured. Sars (1888) considered it close to the European *C. reticulata* (Jurine, 1820), but specifically distinct.

Dunhevedia podagra King, 1853; NSW: Not seen since original description, which is inadequate.

Eurycercus cunninghami King, 1853; NSW (King, 1853); A chydorid, but not referable to *Eurycercus*.

Eurycercus spinosus King, 1853; NSW (King, 1853); A chydorid, but not referable to *Eurycercus*.

Pleuroxus aduncus (Jurine, 1820) in Smirnov & Timms (1983); *Alonella nasuta* Smith, 1909; *Chydorus denticulatus* Henry, 1919; *Chydorus unispinus* Henry, 1922; southern Australia: Smirnov & Timms (1983): These taxa were synonymized with the northern hemisphere *P. aduncus* by Smirnov & Timms (1983: 24). Frey (1991b), after examination of these and other extensive materials, considered that *P. aduncus* does not occur in Australia. The identities of these various taxa have yet to be resolved.

P. denticulatus Birge, 1879; non *Chydorus denticulatus* Henry, 1919; NSW (Smirnov 1971); Vic. (Timms 1973[2]); ?Qld, ?NT, ?WA (Timms 1988).

Comment: After examination of the available material in the Australian Museum labelled as *P. denticulatus*, Frey (1991b) concluded that none of the specimens was of the nominated taxon and they were certainly not conspecific. He considered that the species probably was absent from Australia.

Zoogeography

Our comments here must be considered preliminary, given the rapid changes in cladoceran taxonomy in recent years. Widespread recognition of non-cosmopolitanism has provided a significant impetus to a more critical approach (cf. Frey 1982b). It is clear, particularly from some of the last works of Frey (1991a, b), that a considerable degree of endemism is obscured

by cosmopolitan 'names' in the Australian fauna. In our opinion, any cladoceran in Australia referred to a species described from the northern hemisphere should be viewed with suspicion until critical reviews of all families, to the standard of Frey (1991b), are achieved.

On present evidence, Australia has more cladoceran species: 165 vs ca. 120 (Europe) and 140 (U.S.A.) than are found in other comparable areas. Overall the level of endemicity stands at 43%, with five additional taxa also known from New Zealand, i.e. Australasian endemicity is ca. 46%. To the endemic genera *Neothrix*, *Pseudomoina* (Macrothricidae), *Archepleuroxus*, *Australochydorus*, *Monope*, *Rak*, *Rhynchochydorus* and *Sawcia* (Chydoridae) listed by Smirnov & Timms (1983), *Celsinotum*, *Leberis*, *Planicirclus* and *Plurispina* (Chydoridae) are added.

Most radiation appears to have occurred in the Chydoridae: 45 of the 94 recognized species (48%) are endemic. Australia may differ from other regions in the selective pressures which cause genetic divergence (cf. Frey 1991b). In any event there has been marked speciation in areas where water is limited, e.g. southwestern W.A., where the habitats are not those 'normally' indicative or supportive of a diverse aquatic microfauna, e.g. rock pools, salinized wetlands. The aquatic microfauna of these habitats, in common with those of billabongs and wetlands on the opposite side of the continent, have generally been ignored. We suspect that a diverse array of indigenous cladocerans is yet to be discovered.

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SKUSEMYIA ALLOCASUARINAE, A NEW GENUS AND SPECIES OF CECIDOMYIIDAE (DIPTERA) DAMAGING LATERAL BRANCH BUDS OF DROOPING SHEOAK, ALLOCASUARINA VERTICILLATA IN AUSTRALIA

*By P. Kolesik**

Summary

Kolesik, P. (1995) Skusemyia allocasuarinae, a new genus and species of Cecidomyiidae (Diptera) damaging lateral branch buds of drooping sheoak, Allocasuarina verticillata in Australia. Trans. R. Soc. S. Aust. 119(1), 41-46, 31 May, 1995.

A new gall midge genus Skusemyia and a new species S. allocasuarinae are described from South Australia. Detailed descriptions of the larva, pupa, male and female of the new species as well as its gall on drooping sheoak, Allocasuarina verticillata, are given. The new genus is placed in the subtribe Schizomyiina within the tribe Asphondyliini.

Key Words: Cecidomyiidae, Cecidomyiinae, Cecidomyiidi, Asphondyliini, Schizomyiina, Skusemyia gen. nov., Skusemyia allocasuarinae sp. nov., Allocasuarina verticillata, South Australia.

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KEY WORDS: Cecidomyiidae, Cecidomyinae, Cecidomyiidi, Asphondyliini, Schizomyiina, *Skusemyia* gen. nov., *Skusemyia allocasuarinae* sp. nov., *Allocasuarina verticillata*, South Australia.

Introduction

This paper is the second part of a study on the South Australian Cecidomyiidae. Kolesik (in press) described the first South Australian gall midge species, *Eocinctiomia malarskii*, from *Eucalyptus fasciculosa*. A new species is described here that was found damaging the lateral branch buds of drooping sheoak, *Allocasuarina verticillata* (Lam.) L. Johnson (Casuarinaceae) in South Australia. The large numbers of infested and ultimately killed branch buds at one site indicate that this species could become a serious pest (Fig. 3I). The new gall midge has one generation per year in Adelaide, South Australia.

A new genus is erected for the new species. It belongs to the subfamily Cecidomyiinae and supertribe Cecidomyiidi. It is compared to other known genera of the subtribe Schizomyiina of the tribe Asphondyliini.

Materials and Methods

A survey of the Cecidomyiidae associated with galls on plants in nature conservation parks around Adelaide was carried out between November 1992 and May 1993. All galls sampled were dissected and examined. Those which contained larvae of Cecidomyiidae were described, photographed and conserved for later authoritative identification of the host plant species. The larvae from the gall kind described here were processed in two ways. A small number was preserved in 70% ethanol after notes were made on their colour. The larger number was brought to the laboratory to rear to adults. Here the galls were carefully dissected and the larvae transferred with entomological tweezers into rearing pots containing sterilised, wet sand (Skuhravá & Skuhravý 1960). Pots were examined daily and emerged adults preserved together with their pupal skins in 70% ethanol after their colour had been noted. Microscope mounts of a series were prepared by maceration in 20% KOH, followed by processing through distilled water, 70 and 99% ethanol and xylene to Canada balsam mountant for examination by interference-contrast and bright-light microscopy. Larvae, entire or dissected into two pieces, and entire pupae, were mounted dorso-ventrally or laterally. Adults were dissected into four (female) or five (male) pieces and the particular parts were mounted separately. Wing and head were mounted frontally, thorax laterally, abdomen dorso-ventrally or laterally and male genitalia dorso-ventrally. Measurements were made with an eyepiece reticule. Drawings were done with the aid of a camera lucida. The type series and other material retained in 70% ethanol are deposited in the South Australian Museum, Adelaide [SAM] and United States National Museum, Washington [USNM].

Genus *Skusemyia* gen. nov.

Adult

Wings with R_5 joining C at wing apex, Rs weak, R_1 joining C near wing mid-length. M_{1+2} absent. M_3 weakly developed, Cu forked. Maxillary palpus with 4 segments. Male antenna with 12 flagellomeres. Female antenna with 11 flagellomeres, the last three successively and progressively shorter, the last apparent flagellomere evidently a combination of the eleventh and twelfth. Flagellomeres cylindrical with necks, first and second not fused, with long and stout setae in two whorls, bearing closely appressed circumfila. Tarsi with first segment substantially shorter than the second.

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first tarsomeres lacking ventrodistal spine, tarsal claws simple, empodia much shorter than claws. Male terminalia: gonocoxites free ventrally, produced to form a roundly triangular apical process; gonostylus situated dorsally on gonocoxite, short and wide, with truncated apex bearing teeth of uniform length; cerci simple, rounded apically; hypoproct divided into two apical lobes; claspettes large; aedeagus long, stout, tapering distally. Female abdominal sternite 7 longer than sternite 6. Ovipositor protractile, elongate, sclerotized, without basal lobes; cerci fused, divided at apex, setose.

Larva

Head capsule with short posterolateral apodemes. Antenna short. Sternal spatula bilobate. Anus ventral. Thoracic and first through seventh abdominal segments with 6 dorsal, 2 pleural and 4 ventral papillae. Eighth abdominal segment with 2 dorsal, 2 pleural and 2 ventral papillae. Terminal segment with 8 dorsal and 4 anal papillae. All collar, thoracic and abdominal papillae asetose with exception of the dorsal papillae on the terminal segment that are bearing very short setae.

Pupa

Frons without projections. One of three lower facial papillae with a seta. Lateral facial papillae absent. Cephalic sclerite with two strongly chitinized swellings and two papillae with long setae. First through seventh abdominal segments with 6 dorsal asetose papillae and one pleural setose papilla. Second through eighth abdominal segments dorsally with 3 indistinct transverse rows of spines on anterior half. Last abdominal segment with large pouch, emarginate medially but not completely divided in two parts.

Type species: Skusemyia allocasuarinae sp. nov.

Etymology

The genus is named after E.A.A. Skuse, author in 1888/1890 of the first taxonomic studies on Australian Cecidomyiidae.

Remarks

Skusemyia fits in the tribe Asphondyliini of the superttribe Cecidomyiidi because the female seventh abdominal sternite is 1.5 times as long as the sixth sternite and the eighth tergite is wider than the seventh tergite, combined with the male genitalia having a ventroapical gonocoxal lobe and a dorsally situated gonostylus that is about as broad as long; it belongs to the subtribe Schizomyiina because the first tarsomeres lack a ventrodistal spine, the male genitalia have claspettes, and the female lacks cerci-like lobes immediately posterior to the eighth tergite (Gagné 1994). Within the subtribe Schizomyiina, *Skusemyia* resembles most closely *Placorhela* Rubsaamen, known from three European and one El Salvadorean species (Möhn 1960, Skuhravá 1986). The male antennae of the two genera are the only ones in the subtribe with relatively simple circumfila and with flagellomeres made up of a bulbous basal node and long neck and resembling those of *Dasineura* and relatives (Oligotrophini: Lasiopteridi). The female antennae of *Skusemyia* and *Placorhela* are also similar except that the eleventh and twelfth flagellomeres of the new genus are apparently amalgamated, which is unique in Asphondyliini. The genitalia of both sexes are generally similar also (Möhn 1961), except in details of the ovipositor, which differs in *Skusemyia* because the cerci are discrete, at least at their apices, and the distal setae are longer. The immature stages of *Skusemyia* are unique in Schizomyiina. The pupal cephalic sclerite has two swellings that are longer than the antennal horns. The larva has very reduced papillar setae, and the papillae of the terminal segment are all situated at the end of separate lobes.

Skusemyia allocasuarinae sp. nov.
FIGS 1-3

Holotype: ♂, Black Hill Conservation Park, South Australia [34°53'S., 138°44'E.]; 15.iii.1993, P. Kolesik, reared from larva from lateral branch bud gall of *Allocasuarina verticillata* (Lam.) L. Johnson sampled 25.ii.1993, 121270 [SAM].

Allotype: ♀, same data but emerged 16.iii.1993, [2127] [SAM].

Paratypes (all sampled with holotype): 4♂♂ and 4♀♀, emerged 13-19.iii.1993; 7 pupae, emerged 13-18.iii.1993; 8 larvae [SAM].

Other material: 4♂♂, 3♀♀ [SAM], 3♂♂, 3♀♀ [USNM], 3 pupae [SAM] and 3 pupae [USNM], same data as holotype but emerged 16-22.iii.1993: 6 [SAM] and 3 larvae [USNM], same data but sampled 25.iii.1993: 3 larvae, Wistow, South Australia [35°07'S., 138°53'E.], 23.iii.1993, P. Kolesik, on *A. verticillata*

Description

Male (Fig 1)

Colour: antenna grey, head black, thorax brown, abdomen with sclerotized parts black and non sclerotized red, legs yellow, all setae black. Total length of the body 3.24 mm (range 3.15 - 3.33 mm), Wing length 2.44 mm (2.33 - 2.52), width 0.98 mm (0.93 - 1.00). Wing membrane and especially veins densely covered with setae, 50 - 60 µm. Antenna total length 1.72 mm (1.57 - 1.83); flagellomeres with stout setae, 54 - 160 µm, longer at the distal whorl than at the basal whorl; closely appressed circumfila consisting of one transverse and one longitudinal bands. Eye bridge 5 to 6 facets medially, eye facets rounded. Claws curved beyond the second third, 39 µm (37 – 41). Empodium 11 µm (8 – 16).

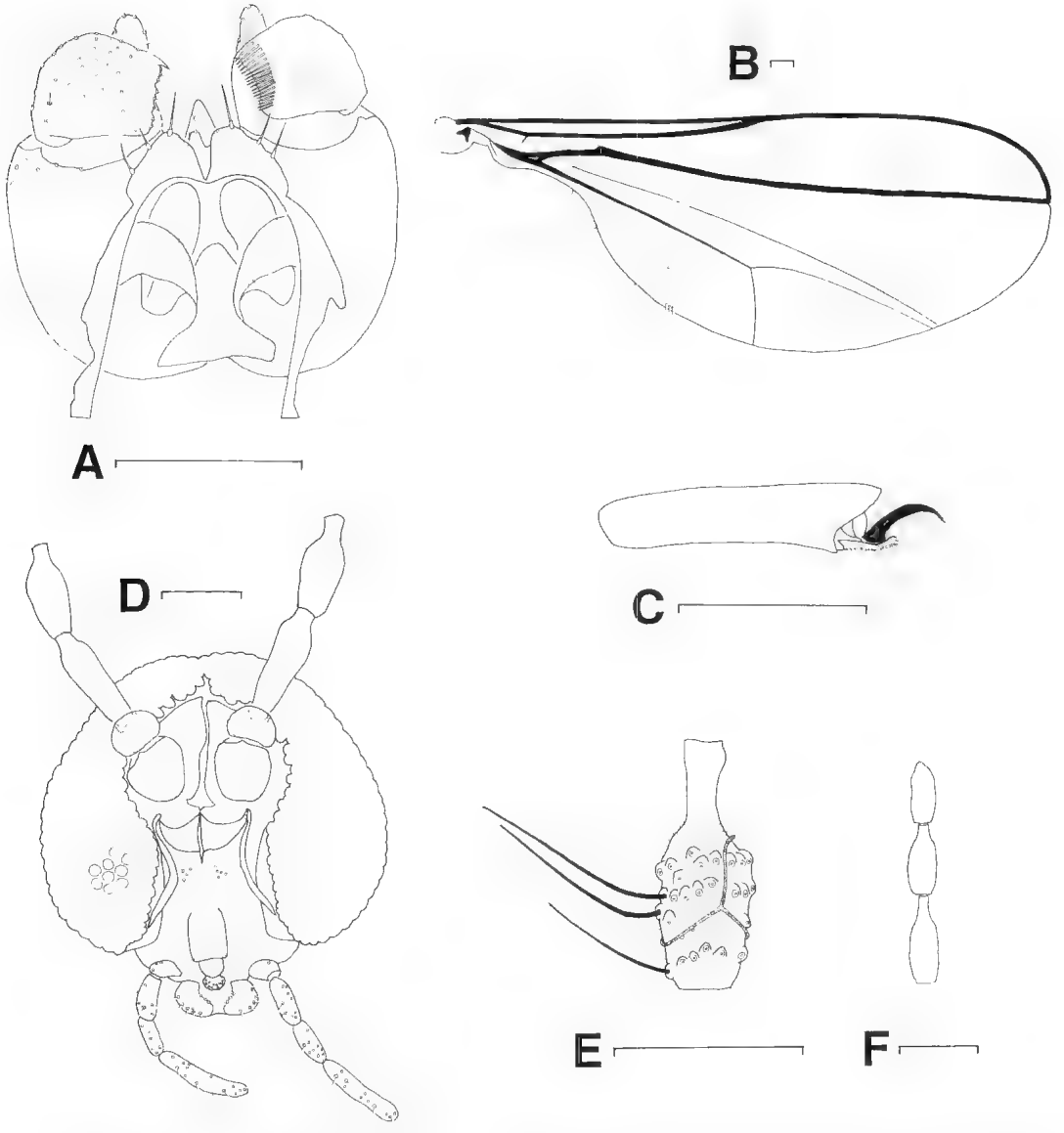

Fig. 1. Male of *Skusemyia allocasuarinae* gen. et sp. nov.: A. genitalia in dorsal view; B. wing; C. last tarsal segment with claw and empodium; D. head in frontal view; E. sixth flagellomere; F. last three flagellomeres. Scale bars = 100 μm.

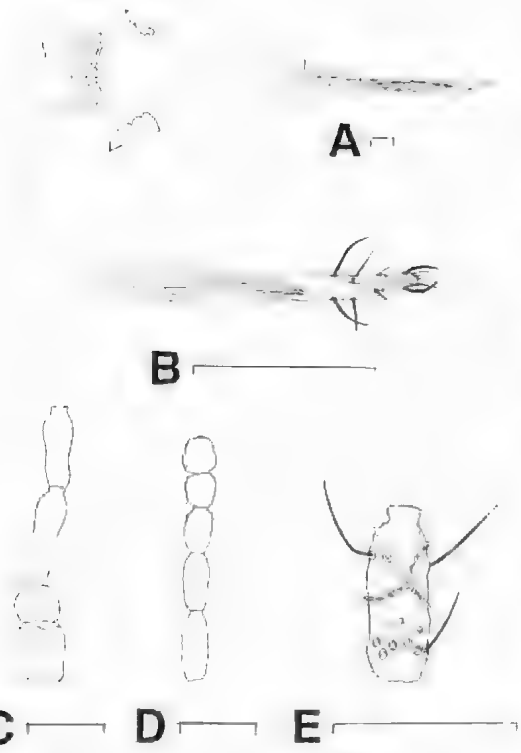

Fig. 2. Female of *Skusemyia allocasuarinae* gen. et sp. nov.: A. ovipositor in ventral view; B. end of ovipositor in ventral view; C. first four antennal segments; D. last five flagellomeres; E. sixth flagellomere. Scale bars = 100 μm.

Terminalia: gonocoxite setose and setulose; gonostylus setose and setulose, bearing 17 - 20 sclerotized tapering teeth that are narrow and about 15 μm in length; hypoproct bearing one seta on each lobe, setulose; cerci deeply divided medially, setose and setulose; claspettes setulose.

Female (Fig. 2)

Total length of the body 3.63 mm (3.41 - 3.80). Wing length 2.65 mm (2.32 - 2.80), width 0.89 mm (0.74 - 1.00). Antenna total length 1.12 mm (0.95 - 1.20); flagellomeres with setae, 51 - 115 μm. Last flagellomere with a shallow constriction medially. Seventh abdominal sternite about 1.5 times longer than sternite 6. Ovipositor with one ventral sclerotized longitudinal band forked distally, distal half of ovipositor with 8 - 9 pairs of 6 - 9 μm long setae, cercus with 8 pairs of 5 - 48 μm long setae. Colour and other characters as in male.

Mature larva (Fig. 3A-D)

Colour red. Total length 3.70 mm (3.24 - 4.44). Integument smooth, ventrally with several transverse rows of spiculae on anterior half of each segment. Head capsule width 61 μm (53 - 77), length 63 μm (51 - 74), length of posterolateral apodemes 61 μm (51 - 64). Antenna 17 μm (15 - 20). Sternal spatula 268 μm (230 - 320) in length, with apical enlargement 86 μm (77 - 105) in width and 42 μm (38 - 51) in length. Terminal segment dorsally with 8 lobes bearing papillae: 6 with very short setae and 2 with corniform setae.

Pupa (Fig. 3E-H)

Colour: prothoracic spiracle, cephalic swellings and antennal horns dark brown, remaining parts pale brown. Total length 3.03 mm (2.46 - 3.56). Integument covered with spiculae, ventrally 2 - 4 μm and dorsally 4 - 6 μm long. Antennal horns 33 μm (28 - 38) long. Cephalic swellings 77 μm (74 - 80) in length. Cephalic papilla with seta 76 μm (58 - 90). One of three lower facial papillae with seta 45 μm (38 - 51). Prothoracic spiracle 146 μm (140 - 151) long and 23 μm (20 - 28) wide across the base, with trachea ending at apex. Seta on pleural papilla 9 μm (8 - 10). Dorsal spines of the first row 13 - 20 in number, 5 - 30 μm; spines of the second row 13 - 20 in number, 25 - 45 μm; spines of the third row 9 - 12 in number, 35 - 65 μm.

Gall (Fig. 3I)

Swollen lateral branch bud, forming spherical to spindleform rosette, 7 - 12 mm in diameter, polythalamous, pale brown in colour. One larva in each of the 2 - 3 cells. Galls appear in January - March. Larvae leave galls to pupate in the soil.

Etymology

Derived from the generic name of the host plant.

Acknowledgments

I thank the South Australian Museum, Division of Natural Science, for providing the facilities that assisted this work. I am grateful to the museum collaborators Ms J. A. Forrest, Dr E. G. Matthews and Mr D. B. Hirst for their support. The Ministry of Environment and Planning, South Australia, kindly gave permission to collect in the nature conservation parks of Black Hill, Morialta and Cleland. I wish to thank Mr M. C. O'Leary, State Herbarium of South Australia, Adelaide, for the identification of the host plant species. I am grateful to Dr Raymond J. Gagné, Systematic Entomology Laboratory, U.S. National Museum, Washington, for careful review of the manuscript.

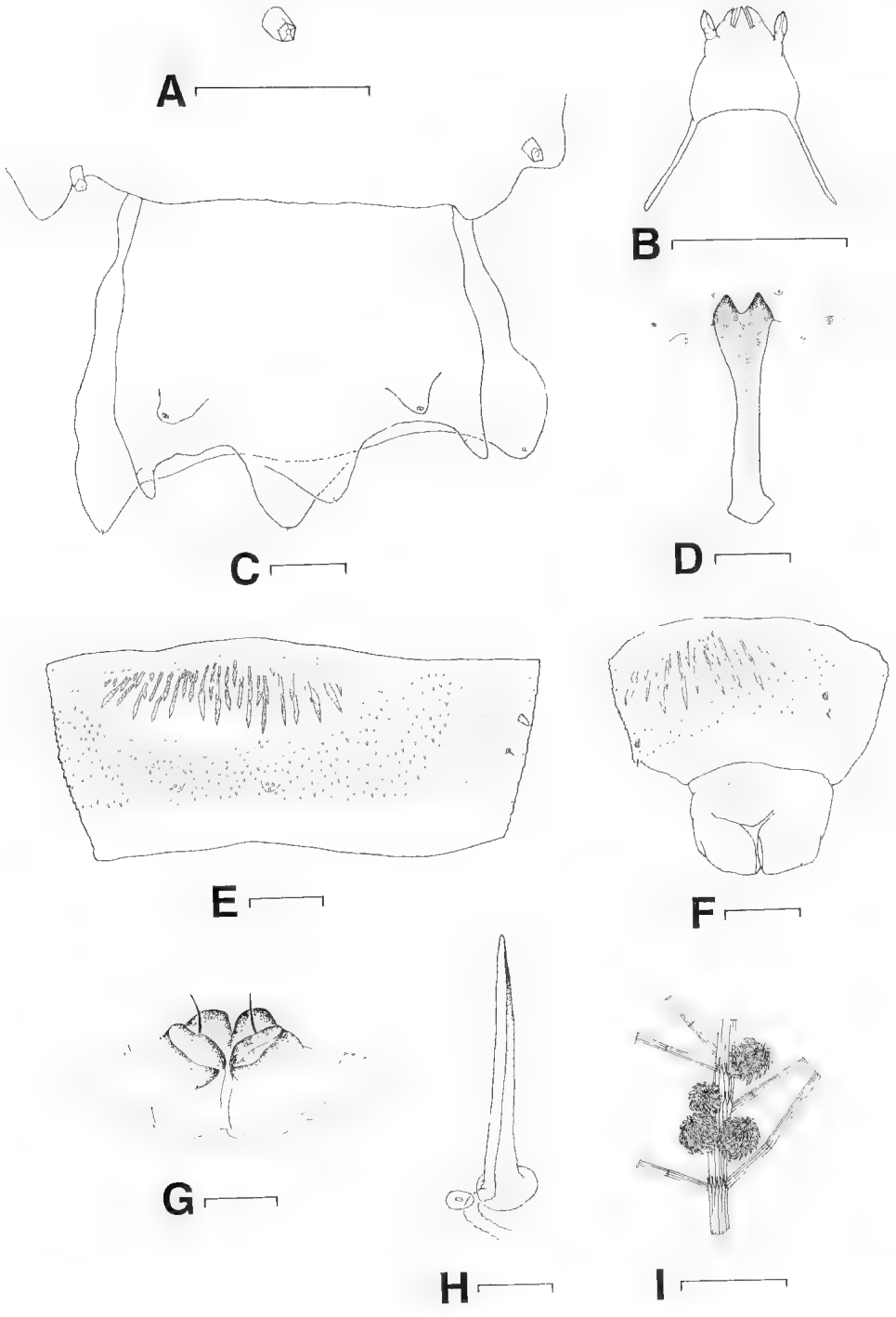

Fig. 3. *Skusemyia allocasuarinae* gen. et sp. nov.: A. - D. larva; E. - H. pupa; I. gall. A. stigma; B. head capsule in dorsal view; C. anal segment in dorsal view; D. sternal spatula; E. sixth abdominal segment in dorsal view; F. last abdominal segment in dorsal view; G. anterior end in ventral view; H. prothoracic spiracle; I. *Allocasuarina verticillata* - lateral branch bud galls caused by *Skusemyia allocasuarinae* gen. et sp. nov. Scale bars = 100 μm. A. - H.; 2 cm I.

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TRANSACTIONS OF THE

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VOL. 119, PART 2

NEW GENERA, SPECIES AND A NEW SUBFAMILY OF XYALIDAE (NEMATODA: MONHYSTERIDA) FROM OCEAN BEACHES IN AUSTRALIA AND THAILAND

By Warwick L. Nicholas & Aimorn C. Stewart**

Summary

Nicholas, W. L. & Stewart, A. C. (1995) New genera, species and a new subfamily of Xyalidae (Nematoda: Monhysterida) from ocean beaches in Australia and Thailand. Trans. R. Soc. S. Aust. 119(2), 47-66, 31 May, 1995.

Five new species of Xyalidae are described from Australian ocean beaches and one from Thailand. Gullanema fragilis gen. nov., sp. nov., possesses many long cervical and somatic setae, but is distinguishable from other similarly hirsute Cobbiinae by a distinctive narrow peri-buccal region. Rhynchonema tomakinese sp. nov., R. collare, sp. nov. and Prorhynchonema gourbaultae sp. nov., in the Rhynchonematinae, differ from congeneric species by their spicules and amphidial regions. R. chiloense Lorenzen, 1975 and R. gerlachi Vitiello, 1967, and P. warwicki, Gourbault, 1982 are commented upon. Two new species with characters intermediate between the Cobbiinae and Rhynchonematinae are placed in a new subfamily, the Corononeminae. The cervical region, enclosing a cylindrical buccal cavity, is shorter and less attenuated than in Rhynchonematinae, longer and narrower than Cobbiinae. The labial region is set off from the buccal region by a narrow indented ring. Corononema parvum, gen. nov., sp. nov., is described from Australia and C. thai sp. nov., from Thailand, the two differing in the shape of the head.

Key Words: Taxonomy, nematodes, Xyalidae, beaches, Gullanema, gen. nov., Rhynchonema, Prorhynchonema, Corononema, gen. nov.

Transactions of the Royal Society of S. Aust. (1995), 119(2), 47-66

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by WARWICK L. NICHOLAS* & AIMORN C. STEWART*

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KEY WORDS: Taxonomy, nematodes, Xyalidae, beaches, *Gullanema*: gen. nov., *Rhynchonema*, *Prorhynchonema*, *Corononema*, gen. nov.

Introduction

Nematodes have been collected from sandy beaches on the southern, eastern and northern coasts of Australia and southern Thailand. Previously we (Stewart and Nicholas 1994), described eight new species of Xyalidae Chitwood, 1951 belonging to well-known genera of Cobbiinae de Coninck, 1965. In this paper we describe a new species and genus of Cobbiinae, namely *Gullanema fragilis* gen. nov., sp. nov., and three new species from the other subfamily of Xyalidae, the Rhynchonematinae de Coninck, 1965, namely *Rhynchonema tomakinense*, sp. nov., *R. collare*, sp. nov. and *Prorhynchonema gourbaultae* sp. nov. Species of *Rhynchonema* Cobb, 1920 are common in Australian sandy beaches, as in other parts of the world, and we comment on Australian specimens belonging to two previously described species. The genus was comprehensively reviewed by Lorenzen (1975). We also erect a new subfamily, Corononeminae, to hold *Corononema parvum* gen. nov., sp. nov. and *C. thai* sp. nov., with characters intermediate between Cobbiinae and Rhynchonematinae. The last named species is from Thailand.

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Materials and Methods

Collections were made on the 90 Mile Beach at Seaspray, Victoria (147° 23'E, 38° 46'S); South Moruya, Broulee, Rosedale, Tomakin and Kioloa beaches, New South Wales (between 150° 9'E, 35° 55'S and 150° 20'E, 35° 32'S); Southport beach, Queensland (153° 25'E, 27° 58'S) and Rapid Creek beach, a suburb of Darwin, Northern Territory (130° 50'E, 12° 23'S). Some specimens were also collected from Pathaya beach, Chonburii, Thailand (100° 53'E, 12° 45'N). Specimens were collected in samples of sand dug up at low tide between the tidemarks to a depth of 40 cm. Exceptions were samples of sub-littoral sand taken from a boat in shallow water off Cronulla, New South Wales (151° 10'E; 34° 05'S).

Nematodes were extracted from the sand by re-suspension in tap water, allowing the sand to settle and collecting the nematodes on a 50 µm nylon mesh sieve. The nematodes were washed off the sieve into sea water, then fixed in 5% formalin in sea water.

Specimens were picked up under the microscope with a fine pipette and transferred to 5% aqueous glycerol which was slowly dehydrated to anhydrous glycerol at 40°C. Permanent mounts were made in anhydrous glycerol, and the cover slips ringed with Glyceel (Gurr). Glass beads (ballatini), selected under the microscope to approximate the diameter of the nematodes, were used to support the cover slips.

Drawings and measurements were made using a camera lucida. When mounted the nematodes lie on their sides presenting a lateral view (except in Fig. 19). Our drawings show setae on one side only, that lying uppermost as mounted.

Measurements are in μm from specimens fixed and mounted in this way. De Man's ratios are given, i.e. a = body length divided by greatest body width, b = length divided by length of pharynx, c = length divided by tail length, c′ = tail length divided by width at anus; V = anterior end to vulva as a percentage of body length, and spicule measurements are arc length. For Rhynchonematinae, Lorenzen's (1975) formula has been used to summarise the characteristic features of each species described. In this formula a letter code, referring to drawings of characteristic structural features, is used to describe successively the form of body annulation, symmetry of the spicules, form of the spicules, annulation surrounding the amphids, relative size of amphids in both sexes, position of amphids relative to end of buccal tube, form of buccal cavity, and form of the vulva. An important character is the direction, either towards the anterior or towards the posterior, of the saw-tooth edge of cuticular annulation (*reifenartig dick mit sägeartiger Aussenkontur*). In some species there is an abrupt mid-body change in direction. Where this is so, the distance from the head end to the inversion is expressed as a percentage of body length. In other species only the cervical and tail regions have saw-tooth annulation, the mid region of the body having rounded annule profiles.

Scanning electron micrographs (SEM) were made from specimens that had been post-fixed in 1% aqueous osmium tetroxide, freeze-dried and coated with gold palladium. Type material is deposited in the South Australian Museum, Adelaide, and the museum's numbers are given in the text. Holotype numbers (all males) follow SAMA and the prefix V. Some paratypes are on the same slide, to give both a male and a female. Other paratypes are on slides labelled AHC followed by a number.

Taxonomic descriptions

Family Xyalidae Chitwood, 1951.

Annulated cuticle, circular cryptospiral amphids, female with single prodelphic ovary situated to left of gut, male with one or two testes, anterior situated to left of gut, posterior if present to right of gut.

Subfamily Cobbiinae de Coninck, 1965

With characters of family. Head and cervical region only slightly attenuated, base of buccal cavity conical, enclosed by pharyngeal musculature, 10 sensilla in second ring of cephalic sensilla, usually segmented.

Genus *Gullanema* gen. nov.

Type species: *Gullanema fragilis*

Diagnostic definition

With characters of Cobbiinae. Cephalic region surrounding conical buccal cavity cylindrical, set off from wider cervical region. Strong mouth ring supporting six labial setae and six thin flexible lips. Very long annulated double and triple sets of cervical setae and numerous long single and double somatic setae extending as far as the anus.

Etymology

Named after Dr Penelope Gullen in the School of Life Sciences, Australian National University.

Gullanema fragilis sp. nov.
(FIGS 1-12)

Holotype: Male, SAMA V4259, Kioloa beach, NSW, 27.xi.1986.

Paratypes: 4 males, AHC 24808 and 24813, Kioloa beach, NSW, 27.xi.1986, 15.xi.1987 respectively; AHC 24809 and 24812, Broulee beach, NSW, 3.viii.1980; 8 females, AHC 24810 and 24813-15, Kioloa beach, NSW, 27.i.1986, 3.viii.1980, 26.vii.1978 and 15.xi.1987 respectively; AHC 24812, Broulee beach, NSW, 3.viii.1980; AHC 24816, Moruya beach, NSW, 7.xii.1988; AHC 24817, Seaspray beach, Vic. 3.xii.1988.

Measurements: Table 1.

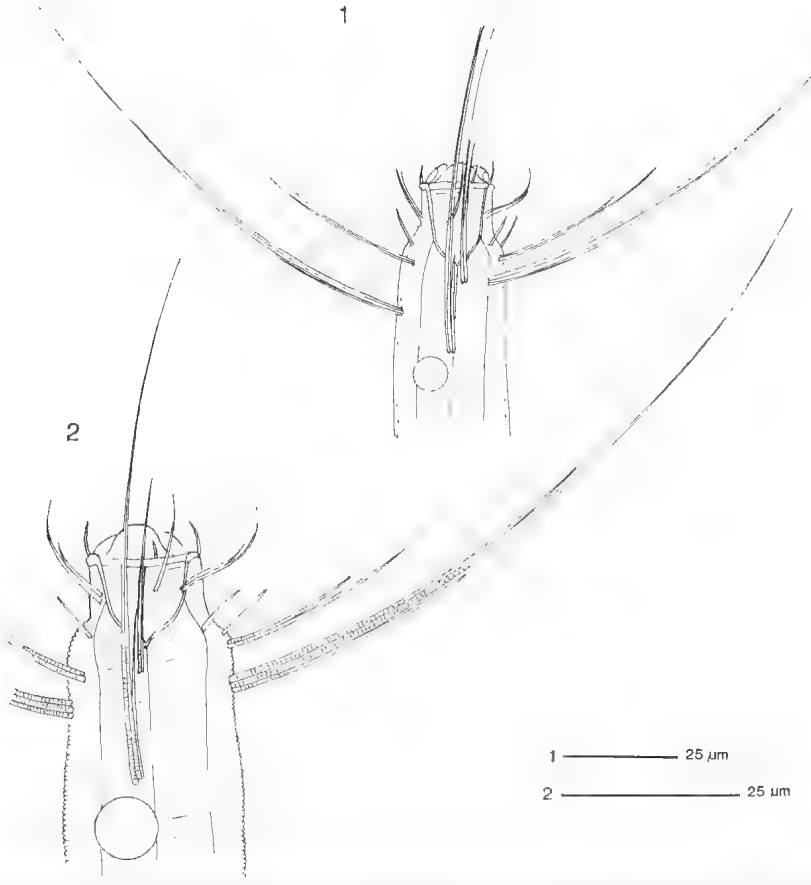
Description of Holotype male.

Body cylindrical, cuticle finely annulated, tail a long narrow tapering cylinder. Head widens sharply at base of narrow peri-buccal 'turret-like' region enclosing buccal cavity. Almost cylindrical buccal cavity, tapered at base, six longitudinal bars reinforce buccal cavity, strong circum-oral mouth ring, surmounted by six flexible very thin lips, about 6 μm high, and six 4μm long inner labial setae. Six 18 μm outer labial, four 12 μm cephalic setae, in one ring, insert near base of peri-buccal 'turret'. Complex hexaradiate array of cervical setae insert between base of buccal region and amphids: most anterior, six 11 μm short setae; next, six longer unequal pairs of cervical setae, 36 and 19 μm; then six longer triplets of unequal length, 166, 102 and 50 μm. The successive sets of cervical setae not inserted in rings around the body at the same level, but each set slightly staggered relative to the long axis of body. Labial, cephalic and cervical setae segmented. Amphids, almost circular, 9 μm diameter, 31 μm behind mouth. Long unequal pairs and single setae insert irregularly between amphids and anus, longest, 209 μm, in pharyngeal region. Also a few short setae along body continue posterior to anus. Two caudal setae, 168 and 145 μm long, at tip of 230 μm long tail. Pharynx cylindrical, cardia conical, rectum short. Two

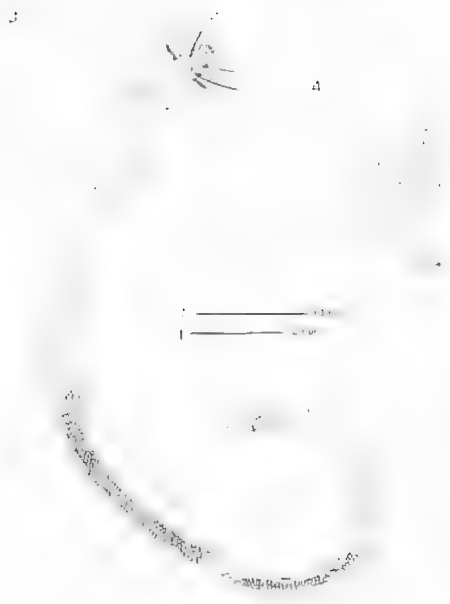
TABLE 1. *Measurements of* Gullanema fragilis *gen. nov., sp. nov.*

Type	Holo Male	Male Paratypes n = 4 Range	Mean ± SD		Female Paratypes n = 8 Range	Mean ± SD	
Length	1443	1368 - 1482	1444	258	1251 - 2025	1580	261
Width	36	24 - 36	29	4.85	35 - 62	47	8.82
Lips	5	3 - 8	5.5	2.10	5 - 9	6.9	0.58
Inner labial setae	4	8 - 10	9	1.16	7 - 9	8	0.93
Outer labial setae	18	22 - 26	24	2.07	22 - 29	25	2.06
Cephalic setae	12	13 - 19	16	2.50	15 - 20	17	0.53
Amphid diameter	9	7 - 8	7.8	0.50	7 - 9	7.8	0.70
Mouth to amphid	31	27 - 35	30	3.78	22 - 45	32	7.28
Buccal cavity	11	9 - 18	13	3.78	10 - 23	15	4.30
Nerve ring	81	68 - 90	77	9.27	82 - 130	100	17
Pharynx	310	262 - 330	290	30	275 - 365	328	28
Mouth to vulva	-	- -			751 - 1279	981	160
Mouth to anus	1213	1015 - 1293	1200	126	1019 - 1645	1332	213
Tail	230	171 - 225	199	24	30** - 380	279*	* -
Anal Width	23	21 - 33	26	5.25	21 - 48	34	7.91
Spicule	48	37 - 46	42	4.43	-	-	-
De Man's a	40.1	41 - 55	51	6.74	26 - 43	34	7.36
" b	4.7	4.4 5.4	5	0.43	3.9 - 5.5	4.8	0.50
" c	6.3	6.5 - 9	7.3	0.70	41.7** - 8.6	6*	*
" c'	10.0	6.8 - 9.1	7.83	1.01	1.1** - 11	8.2*	* -
" V%		- -	-	-	74 - 81	76	2.58

* Excluding female with truncated tail (n=7) **Truncated tailed female



Figs 1 and 2. Head of male *Gullanema fragilis* sp. nov. Setae, which are annulated, are illustrated only on one side of the body.



Figs 3 and 4. *Gullanema fragilis* sp. nov. 3. entire male. 4. spicules.

outstretched testes, anterior to left of gut, posterior to right, gonoduct filled with spermatozoa, spicules weak, hardly cephalated, uniformly curved, blunt bifid tips, 48 μm long.

Paratypes: The numbers and location of somatic setae are rather variable, especially the number of caudal setae, which vary from one to three of unequal length, possibly due to breakage during preparation. The number and location of short cervical setae are variable, 9-14 μm long. Two sets of longer cervical setae are consistently present, the first set of six doublets of unequal length, the second of six triplets also of unequal length, but with the points of insertion of each group staggered with respect to the longitudinal body axis. As an example of setal length in one female paratype: doublet 58, 42, triplet 99, 62, 45, cervical 200, 55 μm. The post-amphidial setae apparently not inserted in regular rows or circles, the most anterior the longest, decreasing to short scattered setae behind the anus. The distance the amphid lies behind the mouth is rather variable both in absolute terms and relative to pharyngeal length. Female paratypes differ significantly from males only in reproductive organs. Females are monodelphic and prodelphic.

Most specimens of both sexes have long tails, but occasional specimens with much shorter tails have been found; an extreme case is illustrated in Fig. 5 (on slide AHC 24810, which also contains a second female with a slightly longer tail). Because the degree of truncation is variable and found on infrequent individuals amongst numerous long-tailed individuals, the short-tailed form is not considered a separate taxon but an infrequent aberration. Because of the variation in tail length, the position of the vulva is more usefully related to the percentage distance from head to anus rather than the more usual head to tip of tail.

Differential diagnosis

The new genus resembles *Steineria* Micoletzky, 1922, and less closely *Trichotheristus* Wieser, 1956, in possessing many very long setae. In *Steineria*, as in *Gullanema*, but unlike *Trichotheristus*, groups of long cervical setae are inserted between the mouth and the amphid. *Gullanema* is quite unlike either genus in the form of the head and shape of the buccal cavity. In these two genera the head tapers gradually to the base of the large lips, whereas in *Gullanema* gen. nov. the head narrows sharply to a cylindrical 'turret-like' region surrounding the buccal cavity. The outer labial and cephalic setae are inserted near the base of the turret, the inner labials at the mouth ring. The lips are smaller, supported by a very strong mouth rim. At the specific level, the weakly cephalated spicules with blunt bifid tips are an important character.

Habitat

Sandy ocean beaches.

Distribution

New South Wales, Victoria.

Subfamily Rhynchonematinae de Coninck, 1965.

After Lorenzen, 1975: head and mouth region very attenuated, buccal cavity long and tubular, cuticle strongly annulated, first cephalic annule wider, amphids circular, tail conical. Uncertainty regarding cephalic sensilla because of difficulty in resolving tiny head with light microscope, inner labial sensilla undescribed, single ring of 6 or 10 cephalic setae. Less than 900 μm long.

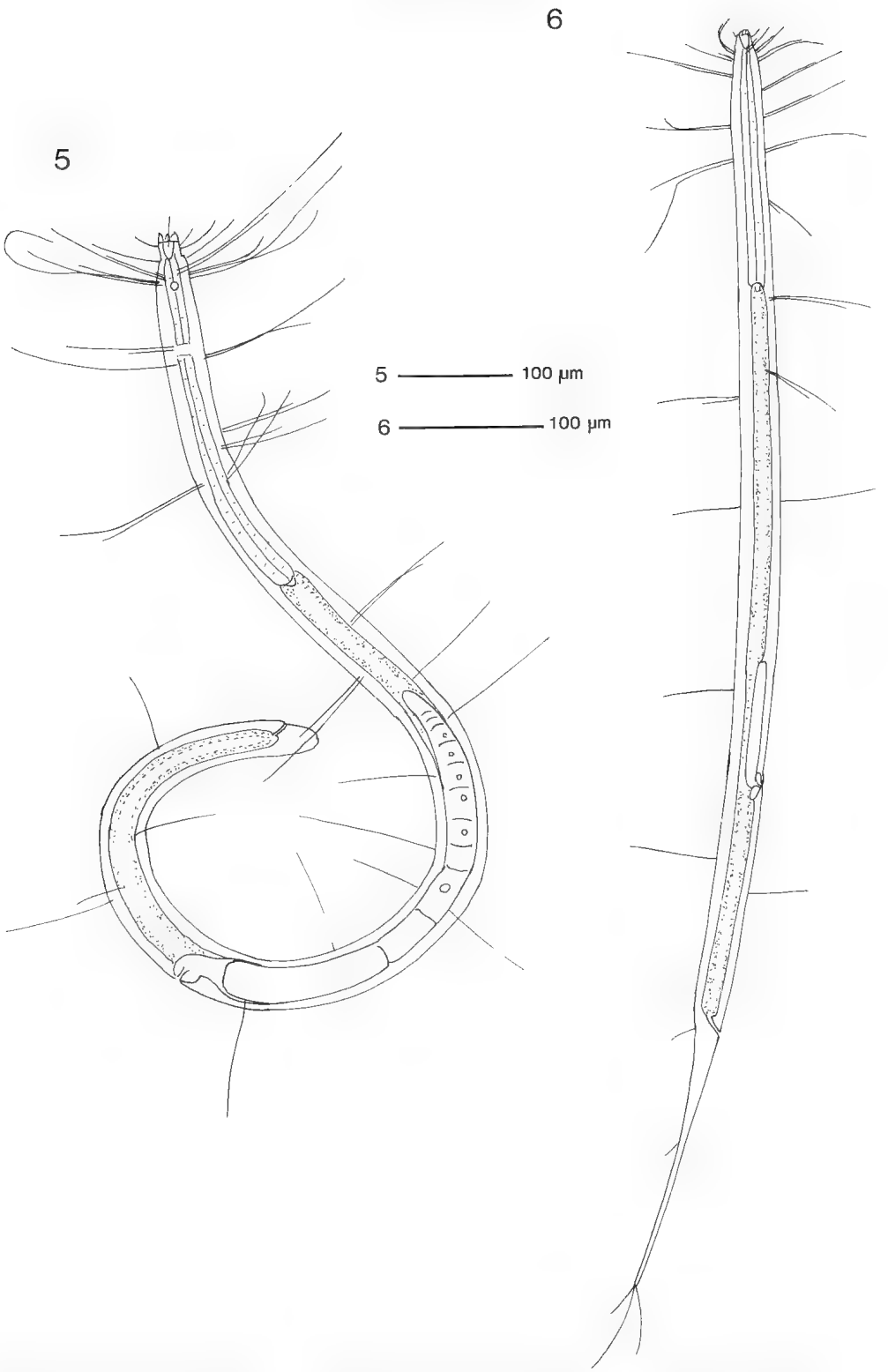
Genus *Rhynchonema* Cobb, 1920

Buccal cavity in two parts; short anterior chamber, at level of cephalic setae, narrow tubular part at least 25 μm long., Amphids placed over or very close to end of buccal tube. Male with two testes.

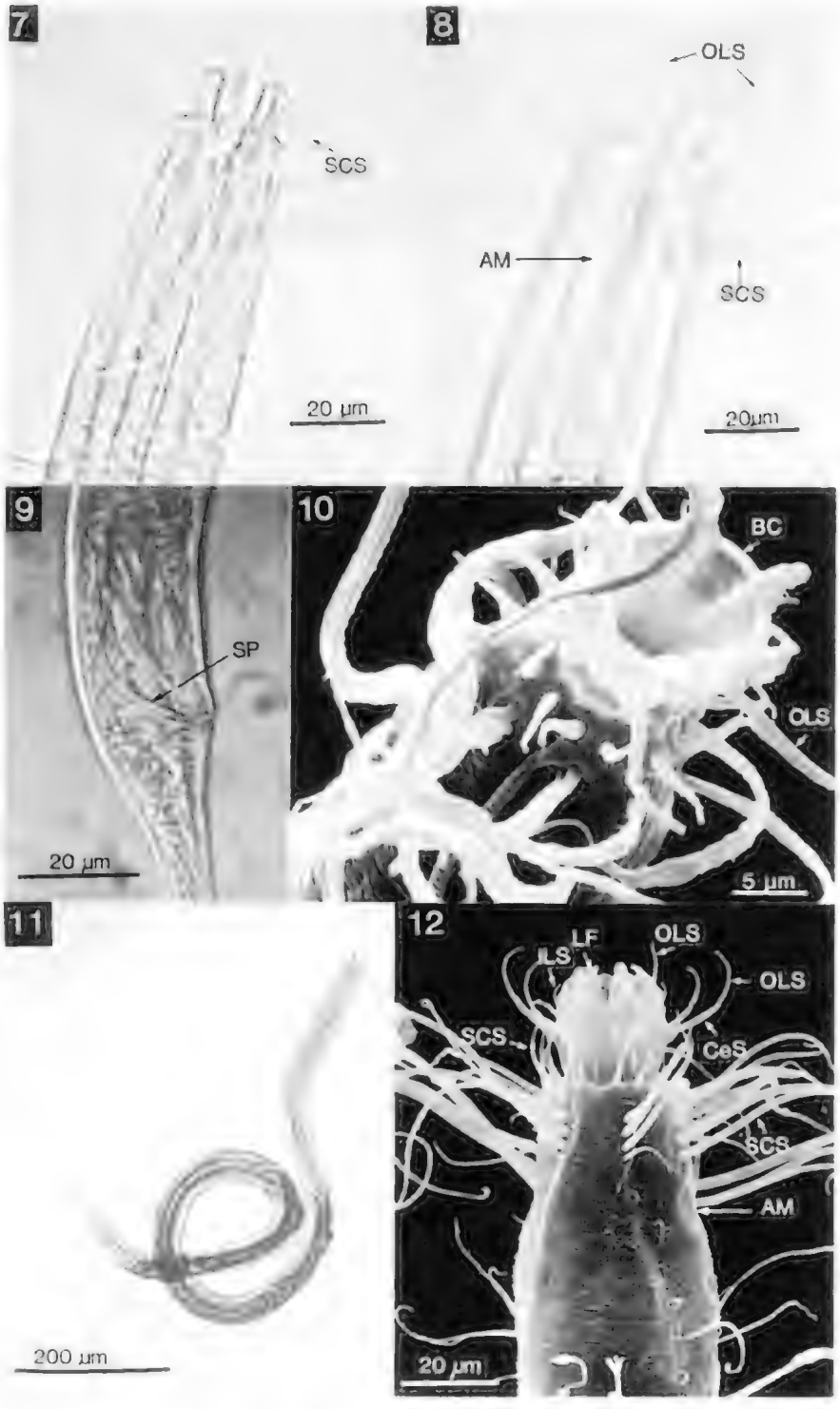
Rhynchonema collare sp. nov.
(FIGS 13-18, 25-30)

Holotype: Male, SAMA V4260, Rosedale beach, NSW, 5.ii.1986.

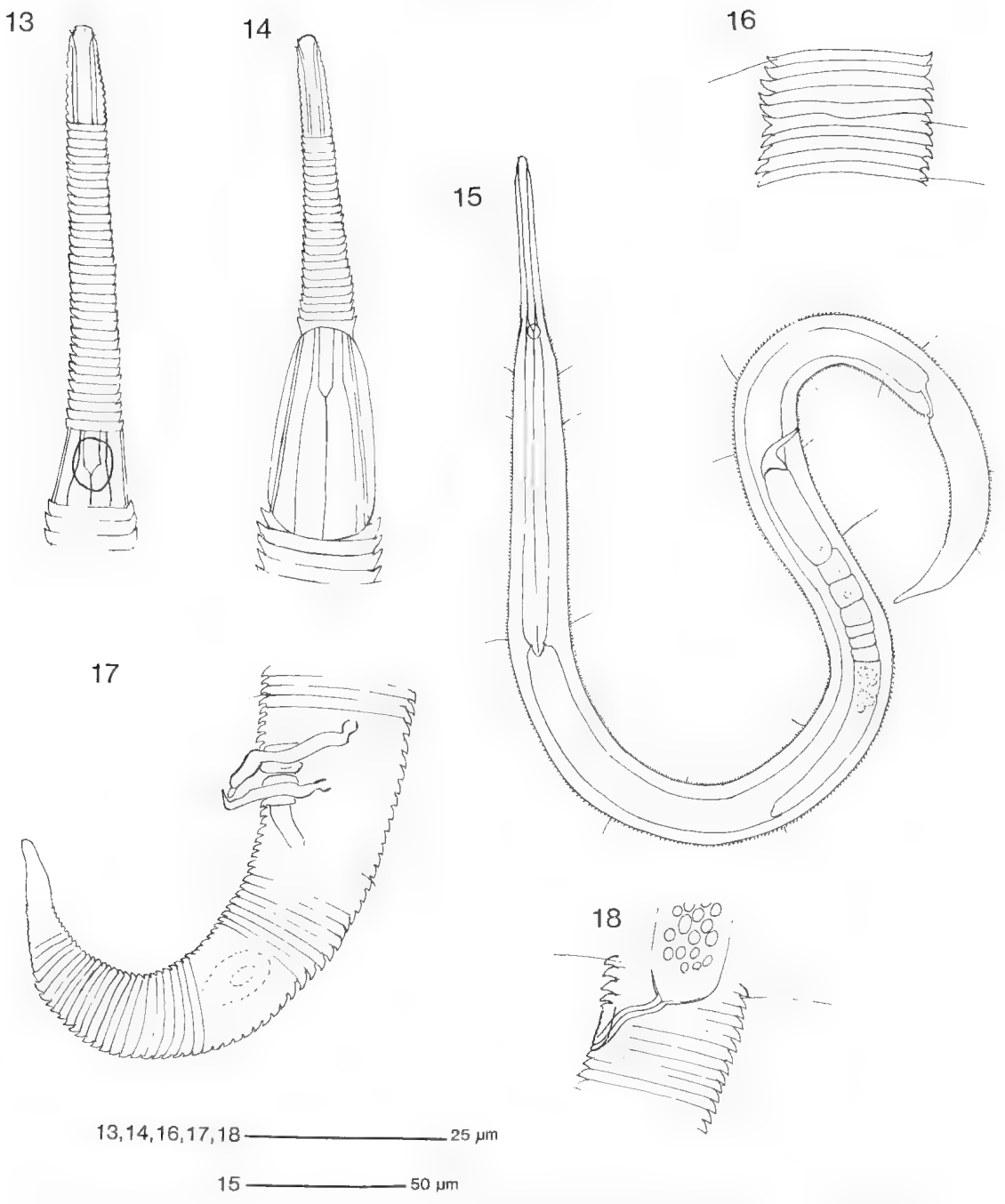
Paratypes: 2 males, AHC 24818, Rosedale beach, NSW, 5.iii.1986 and AHC 24819a Broulee, NSW, 3.viii.1980; 7 females, AHC 24819b-e, Broulee beach, NSW, 3.viii.1986.



Figs 5 and 6. *Gullanema fragilis* sp. nov. 5. female, infrequent short tail form. 6. common long tailed female.



Figs 7-12. *Gullanema fragilis* sp. nov. 7. head to show buccal region. 8. showing amphid. 9. spicules. 10. SEM of buccal cavity. 11. entire nematode. 12. SEM cephalic and sub-cephalic setae. SCS sub-cephalic setae, OLS outer labial setae, AM amphid, SP, spicule, BC, buccal rim, LF, lip flaps, ILS inner labial setae, CeS, cephalic setae.



Figs 13-18. *Rhynchonema collare* sp. nov. 13. female head. 14. male head. 15. entire female. 16. inversion of annules. 17. male tail and spicules. 18. female vulva and operculum.

TABLE 2. *Measurements of* Rhynchonema collare *sp. nov.*

Type	Holo Male	Male Paratypes Male	Male	Female Paratypes n = 8 Range	Mean	± SD
Length	476	412	579	511 - 552	533	19
Width	20	19	17	20 - 24	21.8	1.10
Body setae	-	13		17 - 17	17	0.00
Buccal cavity	53	38	52	47 - 54	51	2.65
Amphid, length	21	18	19	6 - 9.5	8	1.32
Amphid, width	10	10	12	6 - 7	6.7	0.45
Mouth to amphid	52	30	42	44 - 55	49	4.06
Mouth to nerve ring	-		88	84 - 93	90	3.87
Pharynx	125	104	162	124 - 152	138	13
Mouth to vulva				316 - 391	365	35
Mouth to inversion%	56	55	58	56 - 73	60	5.67
Mouth to anus	399	328	515	439 - 483	468	19
Anal width	17	18	16	15 - 17	15.6	0.89
Tail	77	65	75	54 - 74	65	8.72
Spicule, long	16.8	18.7	16.2	- -	-	-
Spicule, short	13.7	13.2	12.8	- -	-	-
De Man's a	24	22	34	22 - 26	24	1.52
" b	3.8	4.0	3.6	3.6 - 4.1	3.8	0.27
" c	6.2	6.3	7.7	7.1 - 9.9	8.3	1.12
" c'	4.5	3.6	4.7	3.0 - 4.9	4.2	0.43
" V%	-	-	-	61 - 73	69	5.41

Measurements: Table 2.

Description of Holotype male

Very small, with long attenuated cervical region, plump post-cervical region, rather long broad curved conical tail, recurved at tip. Cuticle strongly annulated, annule profiles sharply angled forward on front half of body, backward on posterior, abruptly changed (inverted) at 56% body length; very thin somatic setae spaced uniformly between amphid and anus. Buccal cavity a shallow cup leading into long narrow parallel-sided tube with strongly cuticularised walls extending length of narrow cervical region to level of middle of amphid. Six cephalic setae at base of buccal cup, extremely large elongated amphids enclosing posterior 40% of narrow cervical region; no annulation between amphids. Pharynx cylindrical, cardia heart-shaped. Spicules unequal, weakly cephalated, lacking rectangular bend, tips turned up. Large gubernaculum encloses mid region of spicules, strong dorso-caudal apophysis.

Paratypes: Amphids strongly dimorphic, in females relatively large, but much smaller than in males, separated by strong non-annulated cuticle. Vulva with operculum, on which annulation greatly reduced or absent. Terminal vaginal canal cuticular. Lorenzen's formula:- b,a,o*,g,+,2,o,w: *new letter because spicules do not correspond to any of those figured by Lorenzen (1975).

Differential diagnosis

The new species can be distinguished from some other species by possessing sharply angled annulation along the whole body and by the possession of sexually dimorphic amphids. It lacks the pre-anal supplements and strong somatic setae and equal spicules found in *R. hirsutum* Hopper, 1961. It more closely resembles *R. chiloense* Lorenzen, 1975, and *R. scutatum* Lorenzen, 1971 but has quite differently shaped spicules. The male amphids are larger than either of these species. It differs from *R. tomakinense* sp. nov. in the larger male amphid, absence of annulation between amphids, and in possessing a cuticular vaginal canal.

Habitat

Sandy ocean beaches.

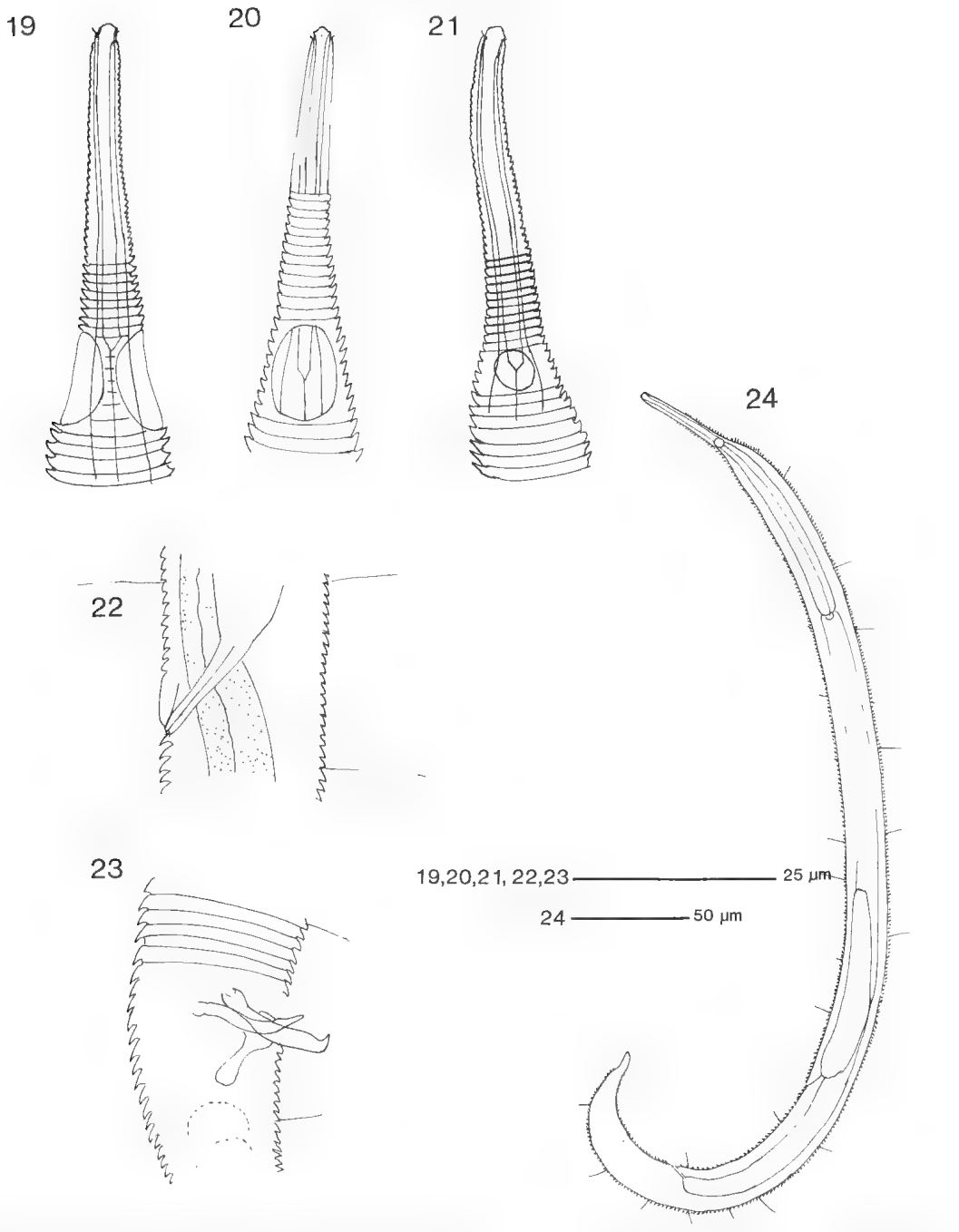
Distribution

New South Wales.

Rhynchonema tomakinense sp. nov.
(FIGS 19-24)

Holotype: Male, SAMA V4261, Tomakin beach, NSW, 11.xi.1986.

Paratypes: 3 males and 5 females, additional male and 3 females on holotype slide; male and female, AHC 24820a, Rosedale beach, NSW, 22.xi.1986 and female, AHC 24820b, Rosedale beach, 5.ii.86; male, AHC 24821, Rapid Creek beach, NT, 31.vii.1986.



Figs 19-24. *Rhynchonema tomakinense* sp. nov. 19. male head, dorsal view. 20. male head, lateral view. 21. female head. 22. vulva and operculum. 23. spicules. 24. entire female.

TABLE 3. *Measurements of* Rhynchonema tomakinense *sp. nov.*

Type	Holo	Male Paratypes n = 3		Female Paratypes n = 5	
	Male	Range	Mean ± SD	Range	Mean ± SD
Length	551	438 - 495	485 30	489 - 592	545 38
Width	22	19 - 25	20 3.12	22 - 24	23 1.51
Body setae	11	9 - 18	12.6 -	13 - 16	14.6 -
Buccal cavity	44	48 57	49 4.73	14 - 49	47 1.52
Amphid, length	14	9 - 12	12 1.73	6 - 9	7.2 1.10
Amphid, width	10	8 - 12	8 2.31	6 - 8	6.4 0.89
Mouth to amphid	38	40 - 43	43 1.58	38 - 44	42 2.68
Pharynx	121	105 - 110	110 108	120 - 149	134 11
Mouth to vulva	-	- -	- -	545 - 430	386 36
Mouth to inversion%	54	52 - 66	57 7.57	51 - 58	55 2.86
Mouth to anus	474	382 - 439	413 29	423 - 524	476 38
Anal width	18	17 - 18	17 0.58	15 - 18	16 1.52
Tail	77	56 68	60 6.93	64 - 73	68 3.65
Spicule	18	11 19	14.6 4.04	- -	- -
Gubernaculum	11	- -	- -	- -	- -
De Man's a	25	22 - 24	23 1.00	20 26	24 2.45
" b	4.6	4.1 4.7	4.4 0.30	3.5 - 4 5	4.1 0.43
" c	7.2	7.1 - 8.8	7.9 0.85	7.4 8.7	8.0 0.63
" c'	4.3	3.1 - 4.0	3.4 0.52	4.2 - 3.7	4.2 0.40
" V%	-	- -		66 - 73	71 2.83

Measurements: Table 3.

Description of Holotype male

Very small, cervical region long and attenuated, post-cervical region plump, tail curved, conical, rather long and broad with recurved tip. Strongly annulated, sharp border angled forward, especially in amphidial region, direction sharply inverted 54% from anterior end. Six very small cephalic setae inserted at base of buccal cup, from which narrow, parallel-sided cuticular buccal tube extends length of cervical region. Large circular amphids located over end of buccal tube, annulation continues between amphids. Cylindrical pharynx, heart-shaped cardia. Thin setae spaced along body from cervical region to anus. Spicules cephalated, asymmetric, slightly unequal size, without strong rectangular curvature, tips turned up. Gubernaculum encloses middle of spicules, strong dorso-caudal apophysis.

Paratypes: Amphids dimorphic, smaller in female, vulva with operculum, vaginal canal not cuticularised. Lorenzen's formula:- b,a,p*,r,+,2,o,u. *new letter because spicules do not correspond to any of those figured by Lorenzen (1975).

Differential diagnosis

This species is very close to *R. collare* sp. nov. The two are sibling species from the same beaches but can be clearly distinguished by several features. Annulation continues between the amphids in both sexes, whereas there is smooth cuticle in *R. collare* sp. nov. The male amphids are not as large. The vaginal canal is not cuticular and the spicules show greater asymmetry. *R. tomakinense* resembles *R. chiloense* Lorenzen, 1975, and *R. scutatum* Lorenzen, 1971, but has quite differently-shaped spicules.

Habitat

Sandy ocean beaches.

Distribution

New South Wales, Northern Territory.

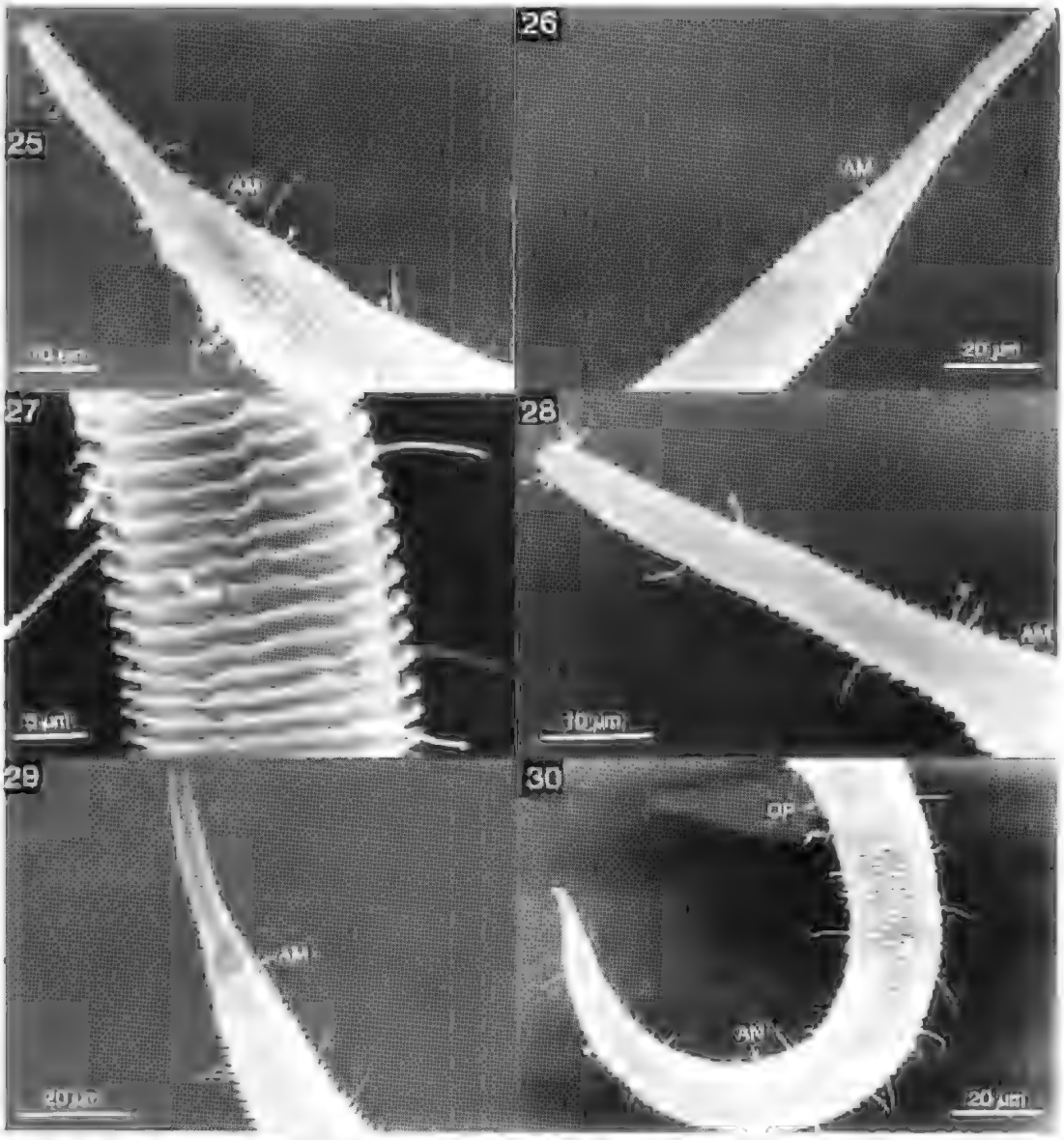
Rhynchonema chiloense Lorenzen, 1975

Material examined

One male and one female and juvenile, off-shore, Cronulla, NSW, one female, Rapid Creek beach, NT.

Description

Lorenzen's formula:- b,s,i,r,+,2,o,u. De Man's ratios:- a = 18-23, b = 3.2-3.6, c = 8-10, V = 73%; inversion of annulation 52%. Spicule arc length 26, more than twice length given in Lorenzen's paper, but that seems by comparison with the drawing to be chord length, and by comparing drawings our male's spicules are only slightly longer in a larger male. The cuticle and body setae are stronger than in the other species of *Rhynchonema* we have found



Figs 25-30. *Rhynchonema collare* sp. nov. by SEM. 25. male head, and cervical region. 26. female head and cervical region. 27. annulation pharyngeal region; *Rhynchonema tamakuense* sp. nov. 28. female head and cervical region. 29. male cervical region. 30. female posterior; AM amphid, OP operculum, AN anus

Habitat

Sandy ocean beach and shallow sub-littoral sand.

Distribution

New South Wales and Northern Territory.

Rhynchonema gerlachi Vitiello, 1967

Material examined

Three males and one female, off-shore Cronulla, NSW.

Description

Lorenzen's formula:- i,s,g,r,=,2,u. Agrees with Vitiello's (1967) description except that he did not illustrate the vulva. Our specimens possess an operculum but no strongly cuticular terminal duct corresponding to u in Lorenzen's formula. According to Vitiello the spicules have bifid tips, but his figure shows sharply pointed tips with one spicule rotated on its long axis. The spicules in our specimens are just like his illustration. According to Vitiello there are three pre-anal papillae in males but these are not shown in his illustration. We observe one to three minute pre-anal bumps, but cannot determine whether they contain papillae because of the strong annulation. Our specimens are smaller than Vitiello's adult specimens, L = 390-632 compared with 742-793 but De Man' ratios in our specimens:- a = 20-26, b = 3.5-4.8, c = 6.3-10.2, c' = 2.8-3.9, V = 75% are in agreement with Vitiello's.

Habitat

Shallow sub-littoral and intertidal beach sand.

Distribution

New South Wales

Prorhynchonema Gourbault, 1982

Buccal cavity in two parts; anterior short, at level of cephalic setae, posterior tubular, not more than 15 μm. Amphids circular, placed well posterior to end of buccal tube.

Prorhynchonema gourbaultae sp. nov.
(FIGS 31-35)

Holotype: Male, SAMA V4262, Kioloa beach, NSW, 31.vii.1986.

Paratypes: 3 males and 3 females, AHC 24822, Kioloa beach, NSW, 31.ii.1976.

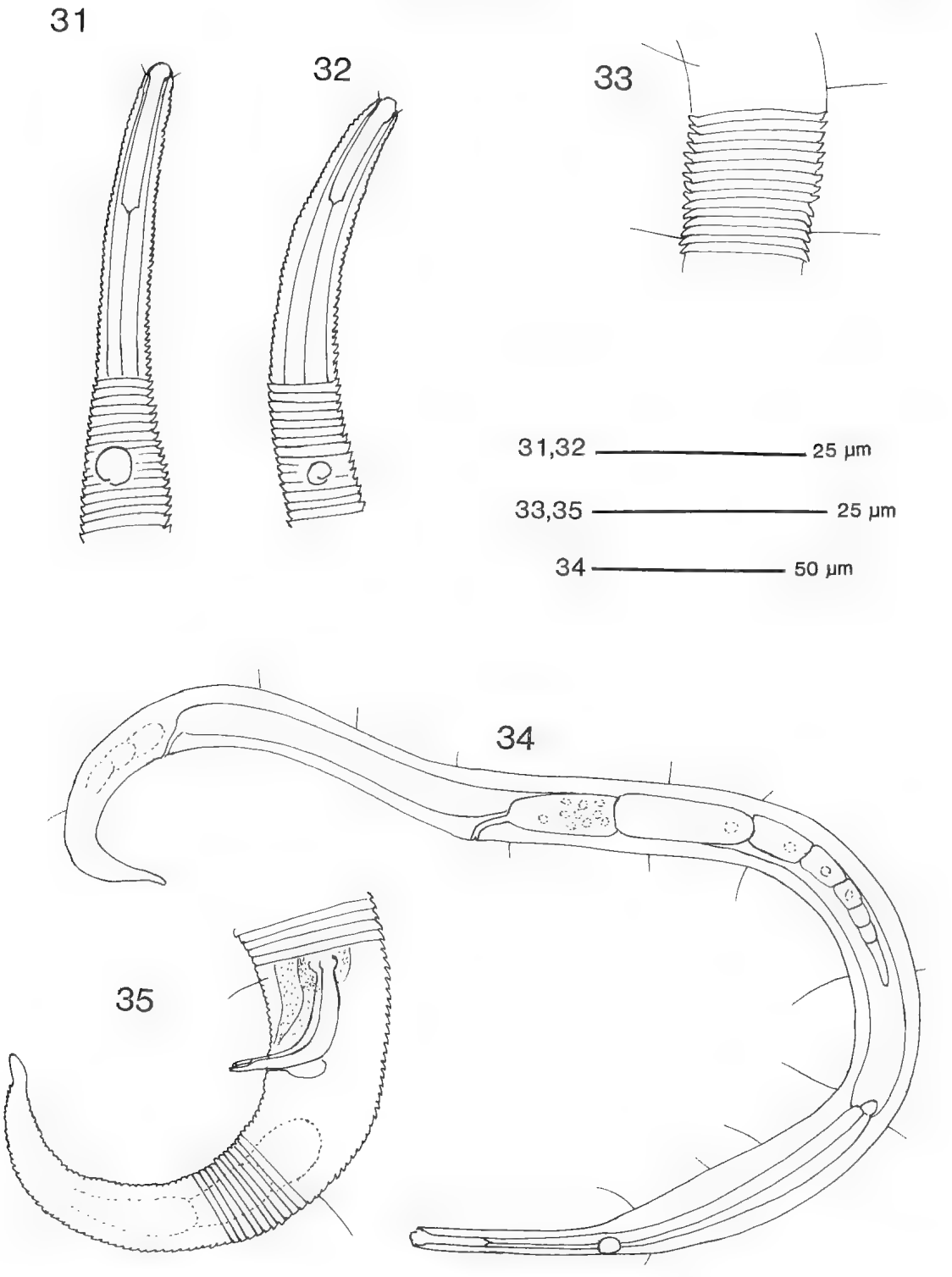
Measurements: Table 4.

Description of Holotype male

Body cylindrical, anterior attenuated from level of amphids to small head, about 10% of body length; tail conical, curved ventrally, tip slightly reflexed. Cuticle weakly annulated, annules about 1 μm wide, first annule wider, inversion of annule direction 50%; sparse thin somatic setae, 11 μm long. Inner labial setae not visible, six short cephalic setae in one ring, less than 1 μm long, amphids circular, cryptospiral, 30% body width, situated much farther posterior, 9.5% of length, about 55 annules from mouth, well beyond end of buccal tube. Buccal cavity long narrow parallel-sided tube, 3.8% of body length, slightly expanded at level of cephalic setae; pharynx cylindrical, widens gradually as body widens behind level of amphid, cardia rounded. Spicules cephalated, smoothly curved, slightly attenuated narrow spoon-shaped rounded tip, gubernaculum simple plate with small caudo-dorsal apophysis, three post-anal caudal glands.

TABLE 4. *Measurements of* Prorhynchonema gourbaultae *sp. nov.*

Type	Holo	Male Paratypes n = 3		Female Paratypes n = 3	
	Male	Range	Mean	Range	Mean
Length	452	460 - 491	476	439 - 453	445
Width	15	16 - 18	17	19 - 20	19
Buccal cavity	17	15 - 16	16	15 - 16	15
Amphid	2.6	2.5 - 3	2.8	3 - 3.5	3.3
Mouth to amphid	43	40 - 47	43	39 - 42	41
Pharynx	144	102 - 122	117	128 - 138	132
Mouth to vulva	-	- -	-	308 - 322	314
Mouth to anus	384	390 - 420	408	380 - 396	382
Anal breadth	14	14 - 14	14	14 - 14	14
Tail	66	62 - 71	68	53 - 62	57
Spicule	22	23 - 25	24.5	- -	
De Man's a	30	27 - 31	29	22 - 24	23
" b	3.1	3.8 - 4.4	4.1	3.2 - 3.5	3.4
" c	6.8	6.6 - 7.7	7.1	7.1 - 8.3	7.8
" c'	4.7	4.4 - 5.1	4.8	3.8 - 4.4	4.1
" V%	-	-	-	70 - 71	71



Figs 31-35. *Prorhynchonema gourbaultae* sp. nov. 31. male head. 32. female head. 33. inversion of annules. 34. entire female. 35. male tail and spicules.

Paratypes: Female paratypes resemble male holotype, apart from reproductive organs, but amphids slightly larger, 2.7-3.5 μm cf 2.6-3 μm. Single anterior ovary, vulva simple not cuticularised, no operculum.

Habitat

Intertidal sandy beaches.

Distribution

New South Wales.

Differential diagnosis

The new species differs from the other described species, *P. warwicki* Gourbault, 1982, by having very different spicules and a longer cervical region and buccal tube. The relative length of the buccal tube is similar to *R. brevituba* Gerlach, 1953 but the spicules are different and in *R. gerlachi* annulation does not show inversion.

Prorhynchonema warwicki Gourbault, 1982.

Material examined

Three males and 3 females from Rosedale and Tomakin beaches, New South Wales.

New subfamily Corononeminae

With characters of family. Buccal cavity cylindrical, deep and wide, not enclosed by pharyngeal musculature; amphid situated above base of buccal cavity. Cervical region only slightly attenuated. Six inner labial setae in one ring, six outer labial and four cephalic setae in second ring. Strong cuticular annulation begins at base of buccal region.

Genus ***Corononeema*** gen. nov

Type species: *Corononeema parvum*

Diagnostic definition

Cuticle strongly annulated with eight longitudinal ridges. Lips high, incised. Deep groove around the head just posterior to the insertion of six inner labial setae, in front of outer labial and cephalic setae, sets off the lip region from the slightly tapered buccal region.

Etymology

Corona, Latin for crown, because the head appears to be crowned by the incised lips, set off from the cylindrical buccal region by a deep groove.

Corononeema parvum sp. nov.
(FIGS 36-40, 50-53)

Holotype. Male, SAMA V4263, Rapid Creek beach, NT, 31.vii.1986.
Paratypes. 6 males, 5 AHC 24823a-e, Rapid Creek beach, NT, 31.vii.1986; 1 male, AHC 25824, Southport beach, Qld; 7 females, 6, AHC 24823, Rapid Creek beach, NT, 31.vii.1986; 1, AHC 24824, Southport beach, Qld, 31.vii.1986.

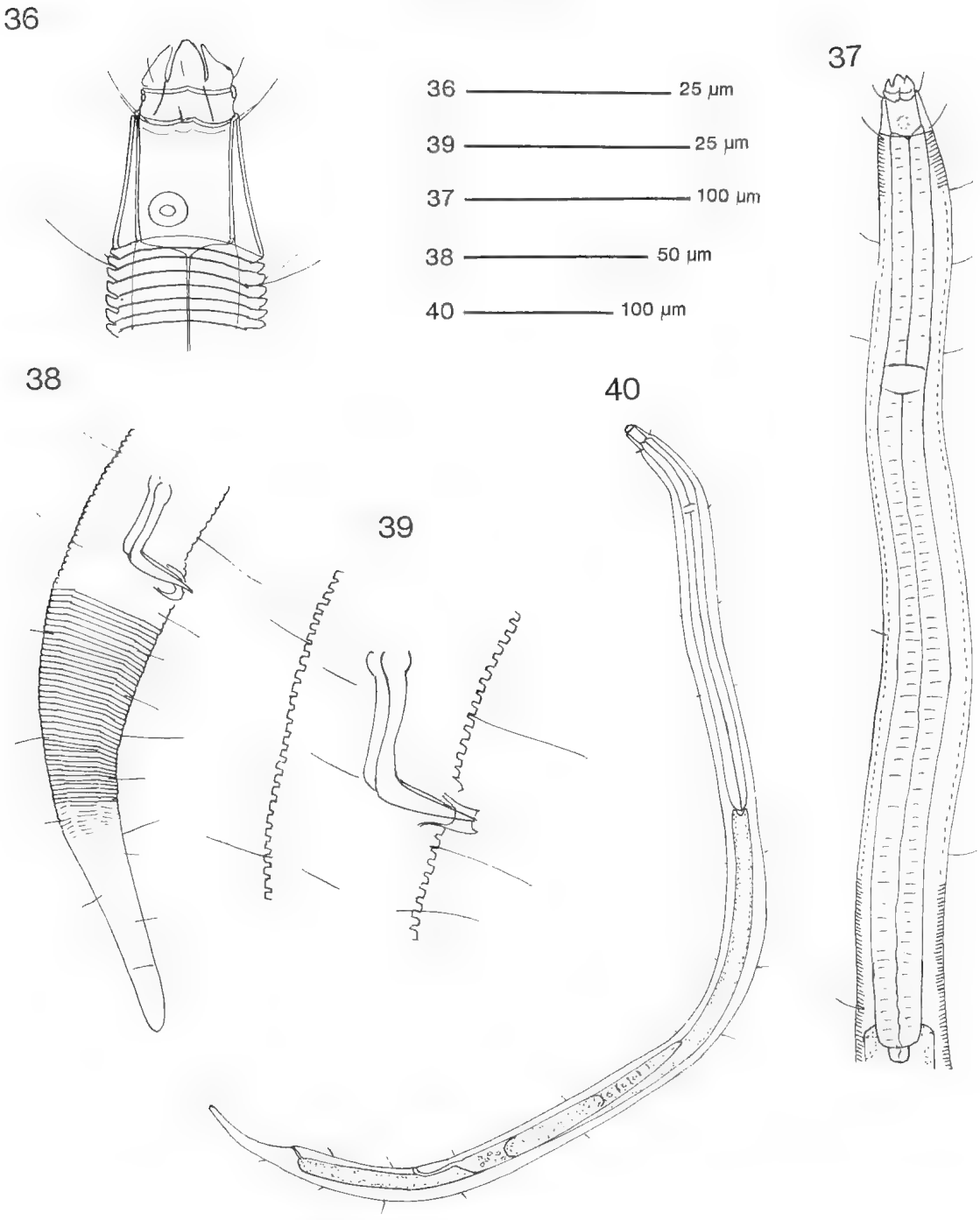
Measurements: Table 5

Description of Holotype male.

Cuticle strongly annulated, annules 1.8 μm, with eight equidistant longitudinal ridges, weakly developed in cervical region, pronounced mid-body, which is polygonal in cross section, extending almost to blunt

TABLE 5. *Measurements of* Corononeema parvum *sp. nov.*

Type	Holo	Male Paratypes n = 6			Female Paratypes n = 6		
	Male	Range	Mean	± SD	Range	Mean	± SD
Length	855	800 - 1045	911	111	840 - 1084	977	71
Width	27	22 - 26	24	1.36	22 - 38	28	4.63
Annulation	1.6	1.5 - 2	1.8	0.19	1.7 - 2	1.9	0.12
Lip height	5.5	4.5 - 6	5.4	0.59	4 - 5.5	5	0.50
Outer labial setae	5	4 - 6	4.6	0.89	6 - 9	6.9	1.01
Sub-cephalic setae	12	11 - 19	15.4	2.97	10 - 12	11	1.00
Body setae	11	13 - 19	16.2	2.39	9.5 - 21	13.5	3.99
Amphid	5	4 - 4.8	4.6	0.40	4.4 - 6	5.3	0.82
Buccal cavity, length	13	11 - 16	13.3	1.97	13 - 18	15.7	1.80
Buccal cavity, width	9	8 - 10	9	0.63	8 - 11	9.9	0.95
Mouth to nerve ring	97	90 - 120	100	11	100 - 132	107	13
Pharynx	322	285 - 360	314	30	310 - 380	352	26
Mouth to vulva	-	- -	-	-	687 - 870	799	63
Mouth to anus	781	714 - 973	843	107	762 - 975	900	74
Width at anus	21	19 - 23	21	1.33	20 - 23	22	1.27
Tail	74	72 - 87	79	5.92	68 - 105	80	12
Spicule, arc	27	25 - 31	27.8	2.56	- -	-	
De Man's a	32	32 - 44	37	5.01	26.0 - 40.0	35.0	4.91
" b	2.7	2.6 - 3.6	2.9	0.36	2.4 - 3.1	2.8	0.27
" c	11.6	9.3 - 14.5	11.6	2.01	9.8 - 15.2	12.4	1.91
" c'	3.5	3.3 - 4.5	3.8	0.47	3.20 - 5.30	3.80	0.71
" V%	-	- -	-	-	80 - 84	81	1.38



Figs 36-40. *Corononema parvum* sp. nov. 36. male head. 37. head and pharyngeal region. 38. male tail. 39. spicules. 40. entire female.

cylindrical tip of tail. Cervical region enclosing buccal cavity not annulated or ridged, slightly attenuated towards mouth. Deep groove, with less strong cuticle, surrounds buccal region just below the lips, two scalloped cuticular rings lie just within mouth. Six incised leaf-like lips, six inner labial setae at base of lips, six outer labial and four cephalic setae insert posterior to the groove: four strong cervical setae, 12 μm insert at base of non-annulated buccal region on first annule, numerous body setae, amphid fovea situated over base of buccal cavity, 5 μm diameter, 25% head width. Wide, deep buccal cavity with strong almost parallel-sided walls. Cylindrical pharynx. Two outstretched, inactive testes; spicules cephalated, rectangular curvature, simple pointed tips; gubernaculum surrounds spicule tips.

Paratypes: The spicules differ somewhat in the degree of curvature and may appear different because of partial rotation about their axes and the pointed tips may be turned outwards. Females, apart from the reproductive organs, closely resemble males. Females possess a single anterior gonad; the vulva has no operculum. The labial and cephalic setae are difficult to measure by light microscopy because of their small size, but from scanning electron microscopy the inner labials are about 1.2 μm long, the outer labials about 0.5 μm and the cephalic about 2 μm long.

Differential diagnosis

The deep parallel-sided buccal cavity, without teeth, with four strong setae at the base is distinctive. The indented weakly cuticular groove below the insertion of the lips is unlike that found in other Xyalidae.

Habitat

Sandy ocean beaches.

Distribution

Tropical and sub-tropical beaches in the Northern Territory and Queensland, Australia.

Coronunema thai sp. nov.
(FIGS 41-49, 54-56)

Holotype: Male, SAMA V4264, Pathaya beach, Chonburii, Thailand, 30.ix.1985.
Paratypes: 4 males, AHC 24825, and 7 females, AHC 24826 Pathaya beach, Chonburii, Thailand, 30.ix.1985.

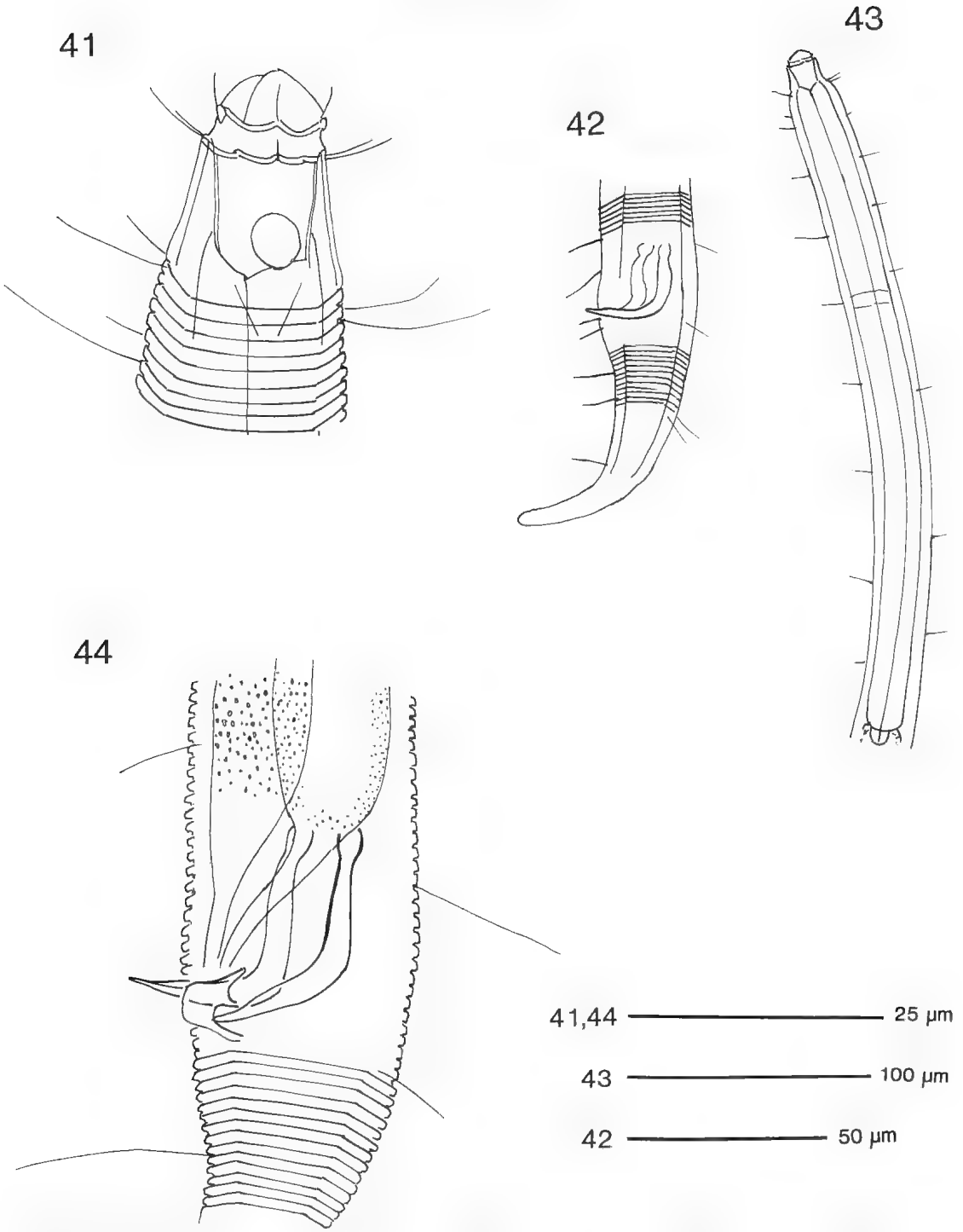
Measurements: Table 6

Description of Holotype male

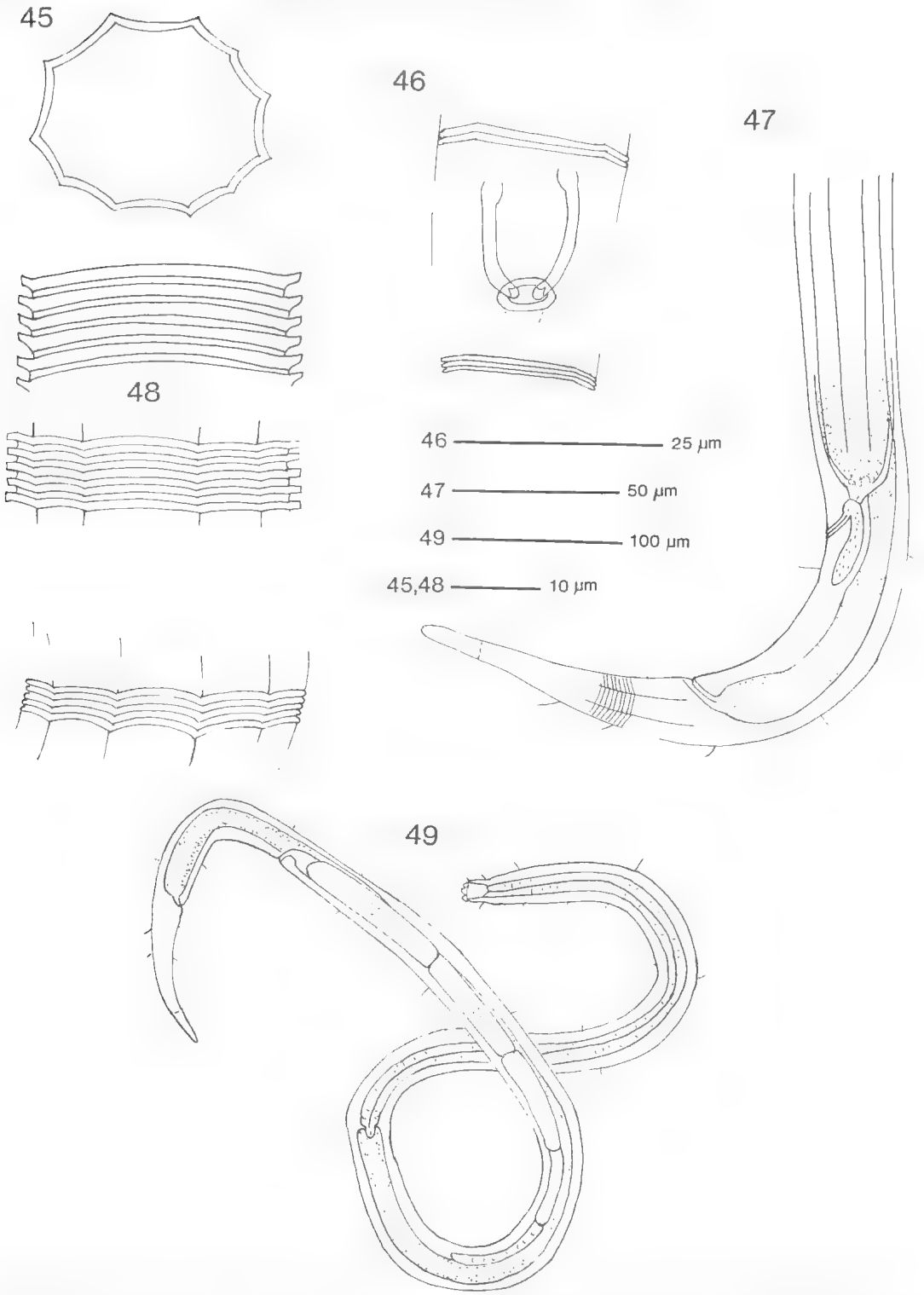
Strongly annulated cuticle, annules 1.6 μm wide, 8 longitudinal ridges from buccal region almost to tip of tail. Buccal region not attenuated, only slightly widening from mouth to base, enclosing deep, wide unarmed buccal cavity. Lips high, leaf-like, fold over wide mouth. Lip region separated from buccal region by deeply indented weakly cuticular circum-oral ring sandwiched between two circum-oral crenellated cuticular rings. Six inner labial setae inserted at base of lips, six outer labial and four cephalic setae inserted below indented ring. Long thin body setae spaced along body, six cervical setae inserted on first annule at base of buccal region. Cylindrical pharynx. Two outstretched testes, anterior to left of gut, posterior to right; spicules cephalated, rectangular curvature, simple pointed tips; gubernaculum surrounds spicule tips.

TABLE 6. *Measurements of* Coronunema thai *sp. nov.*

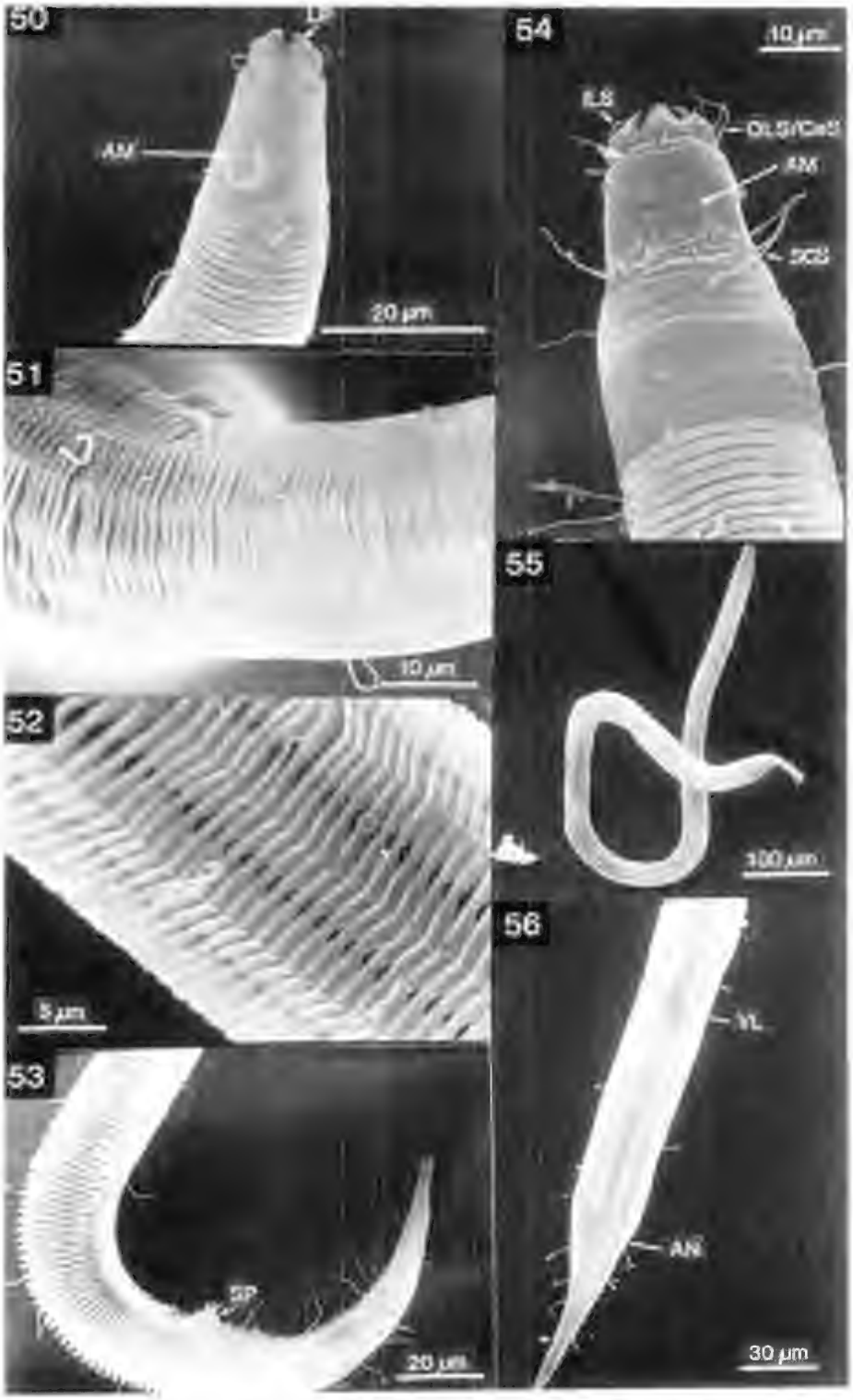
Type	Holo	Male Paratypes n = 4			Female Paratypes n = 6		
	Male	Range	Mean ± SD		Range	Mean ± SD	
Length	990	652 - 958	754	138	790 - 1082	946	106
Width	27	25 - 28	21	1.29	31 - 35	32	1.51
Annulation	1.6	1.6 - 1.7	1.6	0.05	1.4 - 1.8	1.6	0.15
Lip height	4.4	4 - 5	4.8	0.05	6.5 - 7.5	7	0.50
Outer labial setae	6	5 - 8	6.9	1.44	6 - 10	9.3	1.63
Sub-cephalic setae	14	9 - 14	12	2.50	10 - 12	11	1.00
Body setae	13	10 - 16	12.8	2.50	11 - 14	12.4	1.52
Amphid	4.7	4 - 5.5	4.6	0.75	4 - 6	5.4	0.76
Buccal cavity, length	12	9 - 16	12.5	2.89	11 - 13	11.7	0.82
Buccal cavity, width	12	8 - 11	9.8	8.00	10 - 12	11	1.11
Mouth to amphid	7	6 - 15	10	3.74	5 - 7.4	5.8	1.17
Mouth to nerve ring	76	84 - 118	95	16	70 - 92	82	8.51
Pharynx	264	241 - 288	262	21	285 - 424	320	52
Mouth to vulva	-	- -		-	650 - 871	768	8.50
Mouth to anus	19	589 - 895	691	138	722 - 988	858	100
Width at anus	24	20 - 24	22	1.71	22 - 26	24.2	1.33
Tail	71	61 - 68	64	2.99	68 - 101	86	13
Spicule, arc	32	26 - 32	28	2.63	- -		
De Man's a	37	24.0 - 38.0	29.0	6.56	23.0 - 34.0	29.3	3.93
" b	3.8	2.5 - 3.5	2.9	0.45	2.6 - 3.4	3.0	0.34
" c	13.9	10.3 - 15.2	11.9	2.28	9.0 - 13.3	11.2	1.74
" c'	0.3	2.6 - 3.1	3.0	0.24	3.10 - 4.00	3.60	0.44
" V%				-	80 - 84	81	1.60



Figs 41-44. *Corononema thai* sp. nov. 41. male head. 42. male tail. 43. head and pharyngeal region. 44. spicules.



Figs 45-49. *Corononema thai* sp. nov. 45. cross section drawn from fractured specimen viewed by SEM. 46. spicules in ventral view. 47. female posterior end. 48. annulation by SEM successively near head, mid-body and near tail. 49. entire female.



Figs 50-56. *Corononema* gen. nov. by SEM. 50-53. *C. parvum* sp. nov. 54-56. *C. thai* sp. nov. AM amphid, LP lips, 1LS inner labial setae, OLS/CeS outer labial and cephalic setae, SCS sub-cephalic setae, SP spicules, VL vulva, AN anus

Paratype: Female paratypes possess a single anterior ovary, vulva without operculum, prominent post-vulval gland, otherwise females closely resemble males.

Differential diagnosis

C. thai sp. nov. differs from *C. parvum* sp. nov. by possessing a shorter broader head. As an index of this difference the ratio of length to breadth of the pre-annulated buccal region has been measured. In *C. parvum* the ratio ranged from 0.87 to 1.04 (n=30), in *C. thai* from 0.64 to 0.75 (n=10). The annulation is shallower in *C. thai*. Both these properties are most clearly seen in scanning electron micrographs of the head (Fig. 52).

Habitat

Tropical sandy beaches.

Distribution

Thailand.

Discussion

The taxonomic position and rank of the Corononeminae presents difficulties. The circular cryptospiral amphids and single prodelphic female gonad are characteristic of Xyalidae. The strongly annulated cuticle and buccal cavity lacking teeth are also shared with most Xyalidae, although some possess tooth-like ridges in the buccal cavity. The deep unarmoured buccal cavity with strong cylindrical walls is found in other Xyalidae, such as *Omicronema* and all Rhynchonematinae, but whereas in Rhynchonematinae the buccal cavity terminates as a narrow tube of varying length, the buccal cavity of *Corononcma* is relatively wide and short. The cephalic region is attenuated, but not to the marked degree so characteristic of Rhynchonematinae. For these reasons the new genus, *Corononcma*, is best placed within the Xyalidae, but would stretch the definition of the two previously recognised subfamilies too far so that the erection of a new subfamily seems warranted.

Lorenzen (1978) in his review of the superfamily Monhysteroidea does not recognise any subfamilies within the Xyalidae, noting, in this regard, that essential aspects of the phylogenetic relationships within the Monhysteroidea have not been cleared up. We do not find this sufficient reason to abandon the previously recognised division of the Xyalidae into two clearly separable subfamilies, namely the Cobbiinae and Rhynchonematinae. Whether we are justified in creating another subfamily for two species with intermediate characters must be a matter of personal judgement. In *Corononcma* the form of the cervical region and buccal cavity are intermediate between that found Rhynchonematinae from Cobbiinae, but there is no overlap and clear differences remain between the three taxa. The deeply incised labial region and a flexible indented ring separating the cephalic region from the buccal region are in our view significant distinguishing attributes of the Corononeminae. It may well be when the very poorly known nematode faunae of Australia and South East Asia are better known more species will be found assignable to the subfamily.

The indented circum-oral ring is probably flexible and may facilitate the ingestion of larger particles than would otherwise be possible. A flexible oral region has been observed to facilitate the ingestion of relatively large diatoms by other Xyalidae such as *Daptonema*.

Acknowledgments

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A NEW GENUS AND SPECIES OF CRANGONYCTOID AMPHIPOD (CRUSTACEA) FROM WESTERN AUSTRALIAN FRESH WATERS

By J. H. Bradbury & W. D. Williams**

Summary

Bradbury, J. H. & Williams, W. D. (1995) A new genus of crangonyctoid amphipod (Crustacea) from Western Australian fresh waters. Trans. R. Soc. S. Aust. 119(2), 67-74, 31 May, 1995.

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Key Words: Amphipoda, Totgammarus, Western Australia, crangonyctoid, Paramelitidae.

Transactions of the Royal Society of S. Aust. (1995), 119(2), 67-74

A NEW GENUS AND SPECIES OF CRANGONYCTOID AMPHIPOD (CRUSTACEA) FROM WESTERN AUSTRALIAN FRESH WATERS

by J. H. BRADBURY* & W. D. WILLIAMS*

Summary

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A new genus of crangonyctoid amphipod (Crustacea) from Western Australian fresh waters, *Totgammarus*, with a single species, *T. eximius*, is described. The species was collected from roadside pools in the south-west of Western Australia.

KEY WORDS: Amphipoda, *Totgammarus*, Western Australia, crangonyctoid, Paramelitidae.

Introduction

All known crangonyctoid species of Australian fresh waters to 1987 were comprehensively reviewed by Williams & Barnard (1988). In their review, known species were re-examined and redescribed, and some new species were described. They dealt with a total of 12 genera and 33 species. They considered the number of genera probably represented about half the number expected to occur in Australia and noted that the number of species within genera was probably small. Further work (Barnard & Williams, in press) supports this view; they described two new genera, each monotypic, as well as a further new species of both *Austrogammarus* and *Uroctena*. This second review by Barnard & Williams (in press) described, *inter alia*, most material available to them from Western Australia. They did not describe, however, a taxon from that State represented by only a single specimen, pending the collection of further material. Unfortunately, all attempts to obtain more specimens have proven unsuccessful; exhaustive examination of all the known collections from the area have yielded no further specimens and nor did collections made in 1994 on our behalf by A. J. Boulton.

Since the single available specimen represents in our view a new genus, and to facilitate further studies of freshwater amphipods in Western Australia in particular and Australia in general, we now consider it appropriate to describe this single specimen.

Methods of dissection, description and notation follow those of Williams & Barnard (1988). To expedite the use of figures in the present publication, the abbreviations are as follows; "Antennal sinus" refers only to the cephalic sinus receiving antenna 2. A - antenna; Abd - abdomen; acc - accessory; art -article; C - coxa, cox - coxal; d - dorsal; dact - dactylus; e - eye; E - epimeron; flag - flagellum; g - gill; G - gnathopod; Hd - head; i - inner; l - left; lac - lacinia mobilis; lat - lateral; LL - lower lip; MD - mandible; med - medial; mol - molar; MP -maxilliped; MX - maxilla; o - outer; O - oostegite; p -palp; P - pereopod; PC - prebuccal complex; pl - plate; post - posterior; Pp - pleopod; r - right; ret -retinaculum; st - sternal; T - telson; U - uropod; UL -upper lip; v - ventral; 1,2,3...7 - first, second, third...seventh.

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Genus *Totgammarus* gen. nov.

Etymology

Named for the combination of features of several genera.

Type species: *Totgammarus eximius*

Diagnosis

Pleon with sparse dorsal setation, rostrum weak. Lateral cephalic lobes strongly projecting, antennal sinus moderate, eye not discernible in preserved specimen. Flagellum of first antenna lacking major armaments, moderately long, about 0.5x body length, twice A2. Ratio of peduncular articles 2:2:1. Flagellum of second antenna and peduncle of sub-equal length, calceoli of type 9 present (Lincoln & Hurley 1981).

Ratio of mandibular palp articles about 2:9:6, article 2 moderately setose, article 3 falcate, setae = ABDE (Barnard & Barnard 1983). Labium lacking inner lobes. Maxillae 1 - 2 medially setose, inner plate wholly or marginally pubescent. Maxilla 1 outer plate ovate, medially and laterally setose, palps asymmetric; left with thin apical spines, right with thick apical spines. Maxilla 2 inner plate with row of apico-medial weakly sub-marginal setal spines, medial margin heavily setose. Maxillipedal palp articles 2 – 3 with few lateral setae, article 3 with fine facial pubescence dorsally and a ventro-facial row of moderately long, curved setae.

Coxae 1 - 3 with a row of posterior spines, coxae 1 - 4 moderately elongate, coxa 1 tapering below, coxa 4 deeply emarginate post-dorsally, coxae 5 - 6 shorter than 4, coxa 7 shorter than 5 - 6. Gnathopods unequal, gnathopod 1 0.5x gnathopod 2. Carpus of gnathopod 1 long, of gnathopod 2 short. Scythe spine absent from article 4 of both gnathopods, each with a weak lobe. Propodus of both gnathopods rectangular, palms weakly to moderately convex, palmer corners prominent, turned out. First gnathopod lacking strong spines at palmar corner, second with 6 strong spines. Spines along palms of both gnathopods short, simple, without triggers, numerous.

Pereopods 3 - 4 with posterior spine sets on article 6 evenly spaced, P5 - 7 moderately elongate, article 2 broadly expanded, lobate. Dactyls with 1 - 3 spinules.

Coxae 2 - 7 with sac-like gills. Thoracic segments 2 - 7 with lateral sternal gills.

Basomedial setae on inner rami of pleopods 1 - 3 plumose, peduncles each with paired retinacula and paired (first and second pleopod) or single (third pleopod) plumose accessory retinacula.

Pleonites with few dorsal setae and/or spines. Epimera with few ventral spines, posterior margins weakly setulate. Rami of uropods 1 - 2 extending subequally, each with 2 rows of spines. Facial armaments of uropod 1 weak, largely absent on uropod 2 which bears a strong, elongate apico-medial spine. Uropod 3 extended, magniramous, peduncle short, outer ramus 2 articulate, article 2 short.

Telson longer than broad, 100% cleft, not laterally turnid, apically and disto-laterally weakly setose, bearing a single sub-apical spine on either lobe.

Additional description

Flagellum of A1 - 2 lacking major armaments. Apical margin of labrum extended. Accessory blades (rakers) on mandibles with inter-raker plumose setae interspersed among rakers and additional short plumose setae lying between rakers and molar. Molar triturative, with plumose apical seta. Mandibular palp article 3 shorter than 2, palp article 2 lacking baso-anterior setae with few median and apico-anterior setae. Both plates of second maxillae with rows of long distal setae. Maxillipedal palp moderately long. Article 3 weakly produced and finely pubescent at the apex which bears long terminal setae; baso-medially bearing a single sub-marginal seta; medially with a row of scythe setae extending to the base of the dactyl; setae of the ventral face constituting a comb row, as well as a single long mid-facial seta and a row of short setae basal to the comb row; the mid-distal dorsal face bearing fine pubescence.

Dactyl of first gnathopod not reaching palmar corner, bearing a small, bent, inner tooth-spine. Dactyl of second gnathopod reaching to end of palm, bearing 2 small inner spines. Pereopod 7 shorter than 6. Article 2 of pereopods 5 - 7 equally setose posteriorly.

Sternal processes: fleshy sausage-shaped gills on thoracic segments 2 - 7, attached to mid-lateral margins of segments.

Postero-ventral apex of epimera 1 - 3 blunt, as in *Austrogammarus*. Pleopods similar, except for numbers of retinaculae, rami approximately equal. Outer ramus of uropods 1 - 2 slightly shorter than inner ramus. Apicolateral corner of peduncle of uropod 1 with 2 spines, rami of both first and second uropods with 5 apical spines. The third uropod extending beyond the first and second in the entire animal, peduncular spines apical and sub-apical, some medial setae of each ramus plumose. Ventrodistal spine on urosomite 1 at base of uropod 1 short, as in *Austrogammarus*.

Relationship

This genus displays the characteristics of crangonyctoid amphipods in possessing (1) sternal gills (2) an accessory flagellum of the first antenna with two or more articles (3) calceoli of type 9 or linear (4) uropod 1 lacking a basofacial spine on the peduncle (5) a lower lip without inner lobes (6) a first gnathopod that is not melitoid or mitteniform in shape (7) a first gnathopod that does not dominate the second, and (8) a mandibular palp of typical form (Williams & Barnard 1988).

The new genus fits the essential criteria of the family Paramelitidae in possessing sausage-like sternal gills, dorsal setae on the telson, and linear or type 9 calceoli. It differs from the Neoniphargidae in the absence of rugosities on the third article of the maxillipedal palp and gnathopods, the form of the gnathopods (not small and mitteniform), the form of the carpi (not short and lobate), and non-dendritic or lump bearing sternal gills. It differs from the Perthiidae in that the first antenna is significantly longer than the second, the mandibular molar is normally developed and triturative, the outer plate of the maxilliped is not very small, the gnathopods are not large, nor are the carpi short and deeply lobate, the carpi and propodi are not eusirid, and the sternal gills are not dendritic.

Tolgammarus bears features in common with other paramelitid genera, such as blindness, which occurs in several, and in possession of an elongate spine on the second male uropod (as in some *Uroctena* spp.). The combination of characteristics however, is unique. The genus varies from *Austrogammarus*, the most primitive Australian paramelitid genus, in several ways. In *Tolgammarus*, dorsal setation of the pleonites is weak, the lateral cephalic lobes project strongly, the antennal sinus is moderate, eyes are absent, and the

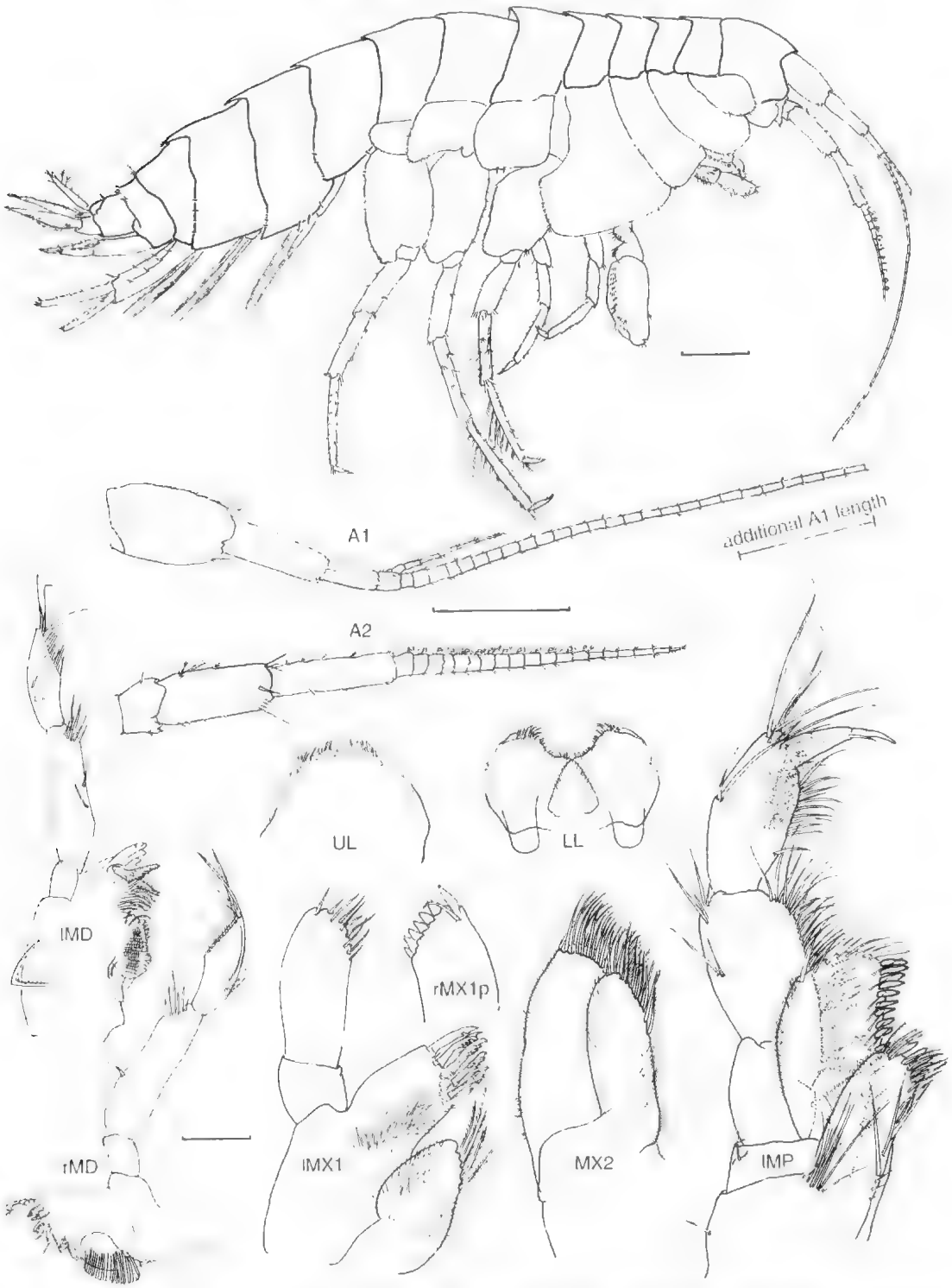

Fig. 1. *Totgammarus eximus*, sp. nov. holotype, male 10.6 mm. Whole animal, antennae and mouthparts. Scale bars: adult and antennae = 1 mm, mouthparts = 200 μm.

second article of the mandibular palp is relatively long with few apico-anterior and no baso-anterior setae. Additionally, there is an extension of the apical margin of the labrum, 5 rather than 3 apical spines occur on the inner plate of the maxilliped, coxae 1 - 4 are moderately long rather than elongate, the apex of coxa 1 tapers, pereopods 5 - 7 are more even in length, and a scythe spine is not present on article four of the gnathopods although a small lobe is present. The dactyls of legs 3 - 7 are multi-spinose. The peduncles of the pleopods are moderately setose, the apico-lateral and apico-medial spines of peduncles of the first uropod differ, as do the relative lengths of the uropod rami which also bear baso-facial armaments. The third uropod is magniramous.

Totgammarus eximius sp. nov.
FIGS 1 - 3.

Etymology
From *eximius*, meaning exceptional or alone.

Type locality
Temporary roadside water in sands along the Scott River Road, south-western Western Australia.

Diagnosis
With the characteristics of the genus (only male known).

Material Examined Holotype
Western Australian Museum WAM14-95, male 10.6 mm in type series.
No other specimens available.

Description of holotype (male)
Body (Fig.1), pleonites 3 - 6 with sparse transverse dorsal setation and dorso-lateral spines on 5 - 6.

First antenna (Fig. 1): primary flagellum sparsely setose, flagellum of 35 articles, 1.8 x peduncle. No calceoli. Accessory flagellum 7 - 8 articulate, reaching to article 8 of the primary flagellum. Second antenna (Fig. 1): length 0.25 x body length, peduncular articles 4 - 5 subequal, flagellum of 19 articles, setae sparse. Calceoli on articles 1 - 13. Labrum (Fig. 1): broadly rounded with apex slightly extended, laterally and apically pilose. Labium (Fig. 1): medially and laterally pilose with 10 curved apico-medial spines on either lobe.

Left mandible (Fig. 1): palp article 3 setation 1A -2B - 1D - 4E, article 2 with 2 medial setae and oblique row of 6 apico-medial setae. Incisor 6-toothed, lacinia mobilis 4-toothed, 9 setose accessory blades, 3 short plumose setae and 1 short blunt spine toward base of molar. Anterior of molar densely pilose. Molar with short plumose seta. Right mandible (Fig. 1): incisor 4-toothed, lacinia mobilis bifid with 4 denticulate teeth on one side and 9 cuspate teeth and a blunt terminal tooth on the other, accessory blades of 3 toothed spines and 4 setose inter-rakers, 3 short plumose setae and 1 narrow blunt spine toward the base of the molar. Molar with 1 setose median, short, blunt spine, and long plumose seta.

Left first maxilla (Fig. 1): palp article 2 with 10 thin apical spines, otherwise naked. Outer plate medially setose, 10 denticulate terminal spines. Inner plate ovate, laterally and medially with sparse straw-like pubescence, 5 apico-medial plumose setae. Right first maxilla (Fig. 1): palp article 2 with 6 thick apical spines, 1 disto-lateral moderately long spine and 1 lateral sub-apical curved spine. Outer plate with 10 denticulate terminal spines and 1 antero-medial plumose seta, median area with long pubescence. Inner plate as for left side.

Second maxillae (Fig. 1): symmetrical, outer plate laterally setose, sub-terminal row of 10 curved spines, terminal row of many curved setae. Inner plate laterally setose, sub- marginally pubescent; medial margin with fine setae proximally, row of setal spines distally.

Maxilliped (Fig. 1): palp article 3 with 9 medial scythe setae, 16 antero-facial comb row setae extending from M0.4 to the sub-apex, 4 long terminal setae, 2 mid lateral setae and 1 median seta. Dactyl bearing 1 distal and 1 medial accessory spines and, dorsally, 4 short post-facial setae basal to the comb row; outer plate laterally setose, apically bearing sub- terminal row of 8 strong curved spines, a disto-medial sub-facial row of 10 tooth spines and 13 setae, setae distally sub-facial to the teeth, proximally facial. Inner plate terminating in 5 strong tooth spines and 8 plumose setae; medially 6 long setal spines, the distal 4 plumose; basal to the inner plate a transverse row of 8 medium to long naked setae.

First gnathopod (Fig. 2): coxa tapered, 3 posterior spines, weakly setose marginally; carpus moderately long, sub-equal to propodus, not lobed; propodus rectangular, palmar corner prominent, extended posteriorly, palm acute, convex, dactyl reaching corner of palm, bearing small bent inner tooth, 5 plumose and 1 naked spines at palmar corner; numerous short spines along palm.

Second gnathopod (Fig. 2): larger than the first (Left 2x, Right 1.7x); coxa with row of 4 or 5 posterior spines, few small distal setae; carpus short, about 0.5x propodus; propodus rectangular, longer than wide, palmar corner with 2 strong, naked spines and 4 plumose spines, corner prominent and slightly extended posteriorly; dactyl not reaching corner, but reaching to the second naked spine, bearing 2 inner teeth at approximately M0.5; palm slightly convex with numerous short spines.

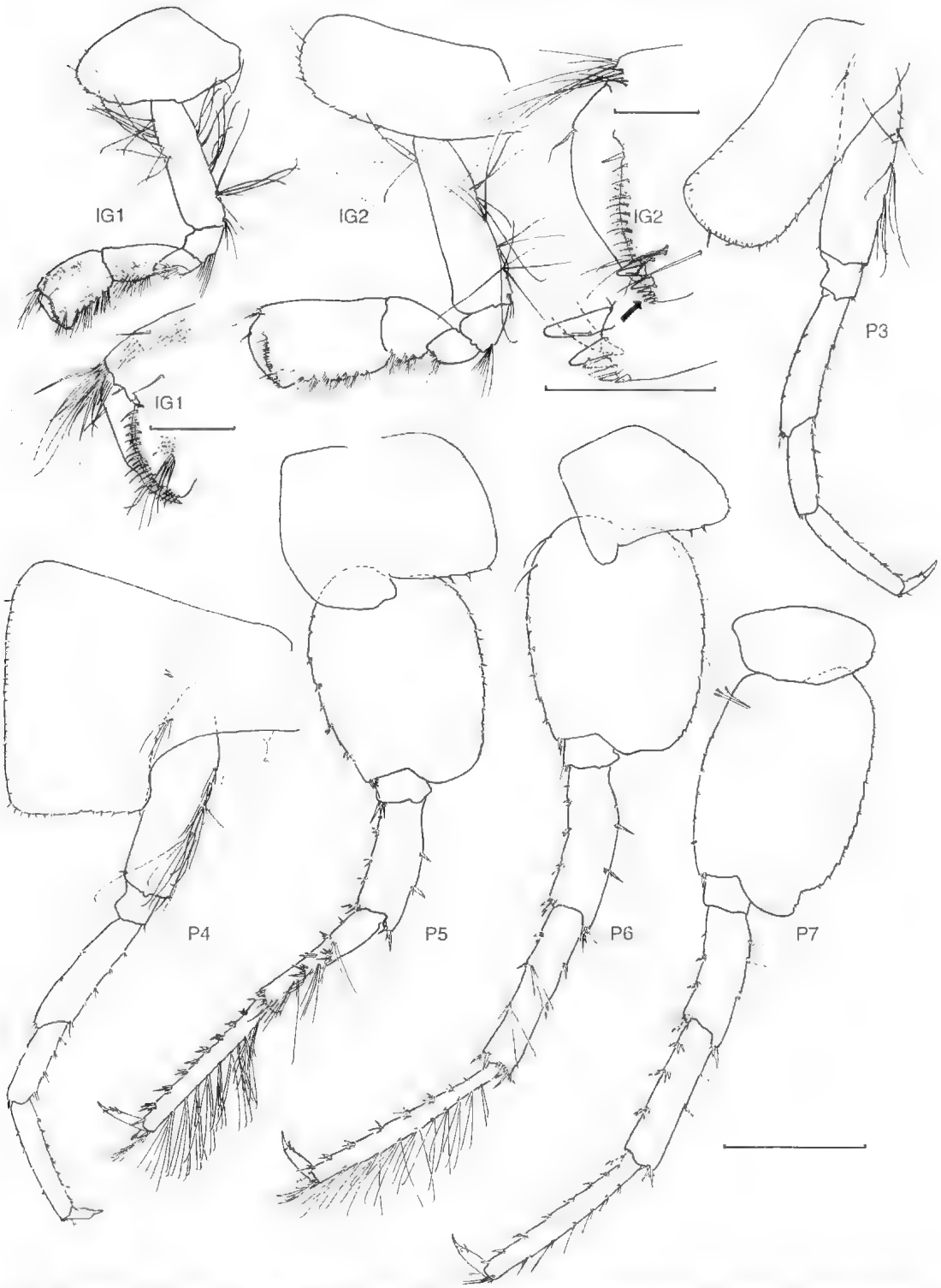

Fig. 2. *Totgammarus eximius*, sp. nov. holotype, male 10.6 mm. Gnathopods and pereopods. Scale bars: gnathopods and pereopods = 1 mm, dactylar enlargements = 200 μm.

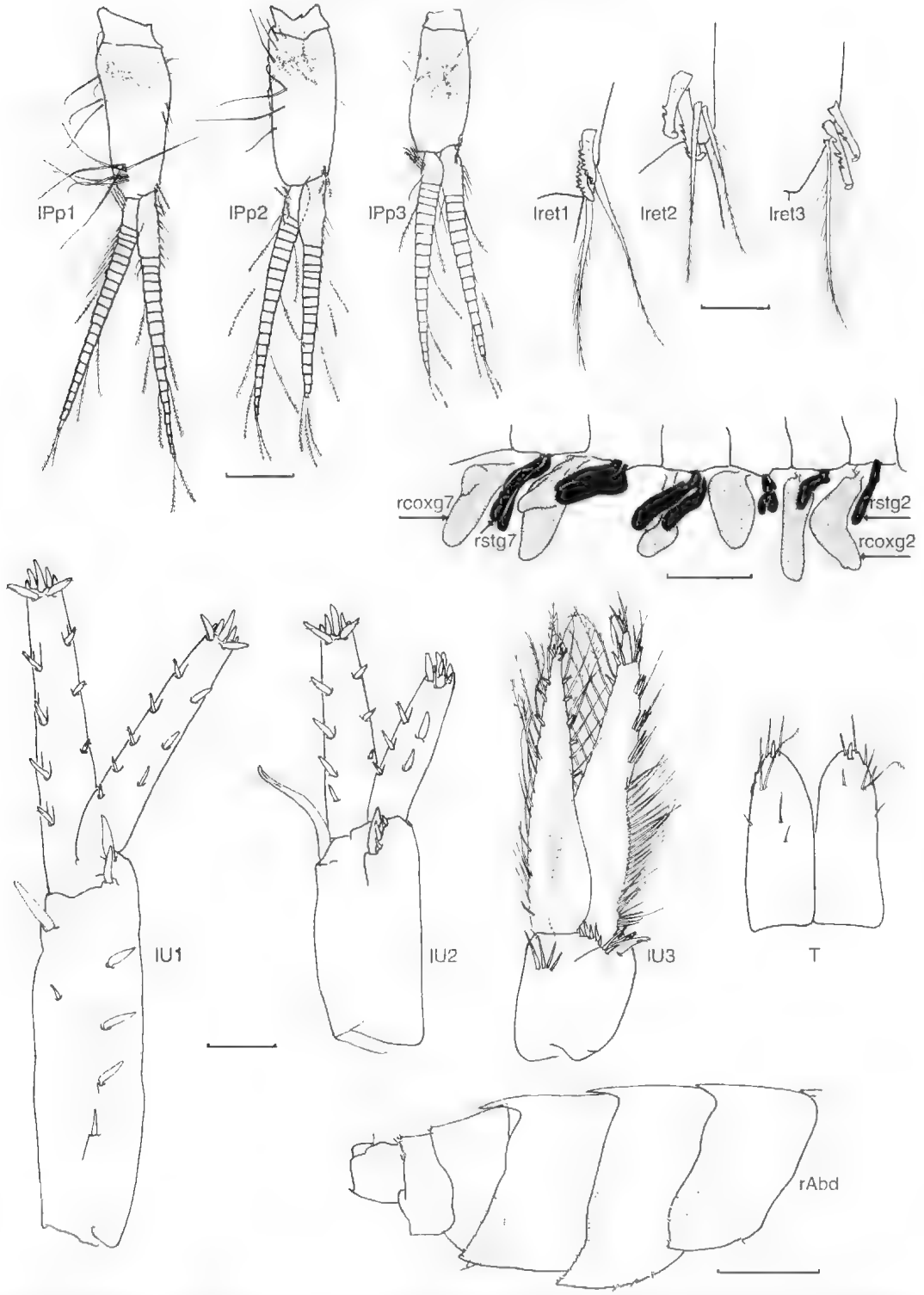

Fig. 3. *Totgammarus eximius*, sp. nov, holotype, male 10.6 mm. Pleopods, uropods, telson, gills and abdomen. Scale bars: abdomen and gills = 1 mm, pleopods, uropods and telson = 200 μm, retinaculae = 50 μm.

Pereopods (Fig. 2): coxa 3 with 9 posterior spines, coxa 4 deeply emarginate, small setae and spines below, no posterior spines. Coxa 5 bearing 3 posterior ventral spines, coxa 6 with 3 posterior ventral spines and 4 small posterior setules. Coxa 7 with 4 posterior spines. Pereopods 3 - 4 length 1.2 x G2, subequal, article 2 of both bearing long posterior setae. Article 5 of P3 apico-posterior spine formula (proximal to distal): 1 - 2 - 2 - 2, article 6; 1 - 3 - 3 - 3 - 2 - 2 - 2, article 5 of P4; 2 - 3 - 3 - 4, article 6; 3 - 3 - 3 - 3 - 3 -3 -3. Pereopods 5 - 7 of approximately equal length. Pereopod 5 articles 5 - 6 bearing long apico- posterior setae, apico-anterior spine formulae 2 – 3 – 2 and 3 - 4 - 4 - 4 - 3 - 3 - 4 - 4. Pereopod 6 article 5 bearing few long setae, article 6 many apico-posterior setae; spine formulae 4 - 3 - 4 - 0 and 2 - 4 - 4 -5 - 0 - -3 respectively. Pereopod 7 apico-anterior spine formulae: article 5: 4 - 6 - 6 and article 6: 3 - 3 - 4 - 4 - 4 - 3.

Gills (Fig.3): coxall gill 5 slightly reduced, gills 5 -7 bi-lobed. Sternal gills 2-7 lateral.

Epimera (Fig. 3): with few ventro-facial spines, posterior margins with few small setules. Epimeron 1 slightly rounded posteriorly with single antero-ventral spine. Epimeron 2 with 3 small mid-ventral setae only. Epimeron 3 naked ventrally.

Pleon (Fig. 3): pleonites 3 - 6 with dorsal spines and/or setae. Pleonite 5 with 5 spines in transverse groups of 2 and 3. Urosomite 6 with 1 dorsal spine on either side.

Pleopods: pleopods 1 and 2 bearing paired, hooked retinaculae and paired accessory retinaculae, pleopod 3 lacking second accessory retinacula. Uropods (Fig. 3): first uropod: peduncle length 1.2 x rami, outer margin with 1 apico-facial spine, 2 medial spines, and strong row of 5 dorsal spines, without setae. Rami subequal, terminating in a cluster of 5 spines. Second uropod: peduncle length equal to rami, lacking spine rows, but with a cluster of 1 large and 4 short apico-facial spines. Inner medial angle with elongate spine 0.5 x length of peduncle, terminally spoon shaped. Inner ramus 1.3 x length of outer, lacking setae. Both rami terminating in a cluster of 5 spines. Third uropod: peduncle length 0.35 x length of outer ramus, about the same length as urosomite 3, bearing median transverse row of 5 spines, distal transverse row of 7 spines at the base of the outer ramus and a group of 4 apico-lateral spines. Outer ramus proximal article strongly setose baso-laterally with 4 disto-lateral clusters of spines and setae, paired medial and single lateral trigger spines apically; medially a single sub-apical trigger spine and evenly spaced plumose setae. Small distal article, 0.13 x proximal, terminating in 3 short and 2 long setae. Inner ramus of a single article, equal to the length of the proximal article of the outer ramus, marginally setose, the medial setae plumose, 6 lateral and 5 medial trigger spines distally, 2 terminal spines and 4 setae.

Telson (Fig. 3): 1.25 x urosomite 3, cleft 100%. Disto-lateral margins and apex with sparse dorsal setation, paired penicillate setules sub-marginal at M.80. Single sub-apical spine on either lobe.

Distribution

Western Australia (south west), Scott River Road, sands in a roadside ditch coll. K. Davies, B. Knott, 03 Oct., 1981.

Acknowledgments

The authors wish to thank Dr A. J. Boulton (University of New England, NSW) for his efforts to collect further samples of the species in January and February 1994. A.B.R.S. support during the finalization of the manuscript is gratefully acknowledged.

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ARROWIPORA FROMENSIS A NEW GENUS AND SPECIES OF TABULATE-LIKE CORAL FROM THE EARLY CAMBRIAN MOOROWIE FORMATION, FLINDERS RANGES, SOUTH AUSTRALIA

By Margaret K. Fuller, & Richard J. F. Jenkins**

Summary

Fuller, M. K., & Jenkins, R. J. F. (1995) Arrowipora fromensis, a new genus and species of tabulate-like coral from the Early Cambrian Moorowie Formation, Flinders Ranges, South Australia. Trans. R. Soc. S. Aust. 119(2), 75-82, 31 May, 1995.

The recently discovered Early Cambrian tabulate-like coral Arrowipora fromensis gen. et. sp. nov. occurs in the Moorowie Formation of the eastern Flinders Ranges. It is found in an ancient reefal environment in association with Moorowipora chamberensis Fuller & Jenkins 1994 and Flindersipora bowmanii Lafuste 1991. Arrowipora fromensis has tabulate-like characteristics including the cerioid form of the corallum, wedge-shaped to spine-like septa and strongly developed dissepiment-like tabulae. Although unlike any other Early Cambrian coral, skeletal characteristics are similar to some micheliniids, which have a time range from the Late Silurian to the Late Permian. Arrowipora fromensis provides further evidence that the time range of the Subclass Tabulata possibly extended to the Early Cambrian.

Key Words: Arrowipora fromensis, Early Cambrian, Moorowie Formation, tabulate-like coral, Flinders Ranges, South Australia.

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by MARGARET K. FULLER*, & RICHARD J. F. JENKINS*

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The recently discovered Early Cambrian tabulate-like coral *Arrowipora fromensis* gen. et sp. nov. occurs in the Moorowie Formation of the eastern Flinders Ranges. It is found in an ancient reefal environment in association with *Moorowipora chambersensis* Fuller & Jenkins 1994 and *Flindersipora bowmani* Lafuste 1991. *Arrowipora fromensis* has tabulate-like characteristics including the cerioid form of the corallum, wedge shaped to spine-like septa and strongly developed dissepiment-like tabulae. Although unlike any other Early Cambrian coral, skeletal characteristics are similar to some michelinids, which have a time range from the Late Silurian to the Late Permian. *Arrowipora fromensis* provides further evidence that the time range of the Subclass Tabulata possibly extended to the Early Cambrian.

KEY WORDS: *Arrowipora fromensis*, Early Cambrian, Moorowie Formation, tabulate-like coral, Flinders Ranges, South Australia.

Introduction

Arrowipora fromensis gen. et sp. nov. occurs in the Early Cambrian Moorowie Formation in the eastern Flinders Ranges of South Australia in association with *Moorowipora chambersensis* Fuller & Jenkins 1994, and *Flindersipora bowmani* Lafuste 1991. It is present in slumped reefal blocks within a megabreccia at a site close to the disused Moorowie Mine (Fig. 1) described in Fuller & Jenkins (1994). The corals are preserved as upright coralla relative to bedding and clearly are in life position within individual slump blocks. They occur in association with both fragmental and encrusting remains of the calcimicrobes *Renalcis* Vologdin 1932, *Girvanella* Nicholson & Etheridge 1878 and *Epiphyton* Bornemann 1886, and current-deposited archaeocyaths. The ancient reefal system may have been established on a marginal fan comprising a coarse breccia (Savarese *et al.* 1993). The high energy marine environment was responsible for the influxes of sediment preserved within the framework of the coral colonies. *Arrowipora fromensis* and the two previously described corals from Moorowie have few skeletal characteristics in common.

Preservation

The available material, collected many years ago by Mr Brent Bowman, then a technical assistant at the University of Adelaide, shows parts of probably one

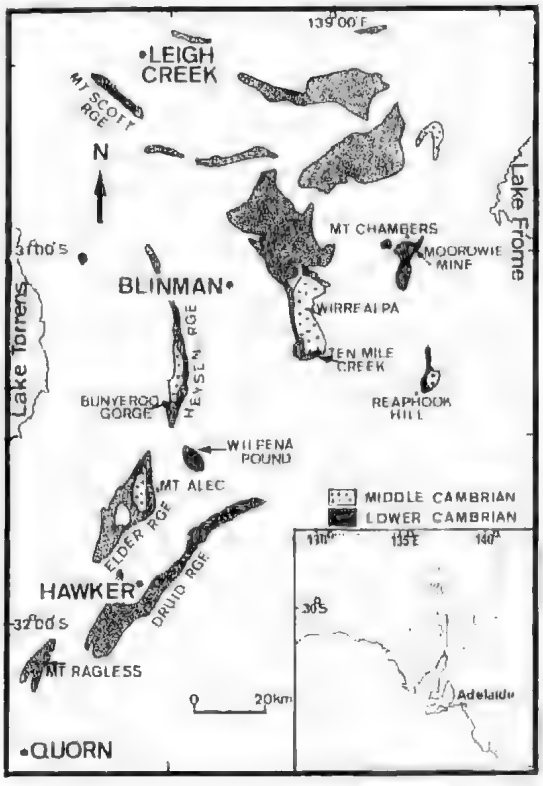

Fig. 1. Location map showing fossil occurrence near the Moorowie Mine and the distribution of Early and Middle Cambrian outcrops in the Flinders Ranges of South Australia.

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Fig. 7. Holotype SAM P5487 (complete specimen), illustrating rectangular shelves extending from a large colony (x1.6)

Fig. 3. Holotype SAM P34167 (reverse side of specimen shown in Fig. 2) with shelf-like projections across adjacent sediment (x1.0).

colony broken from a large specimen (Figs 2,3). During life the colony appears to have been repeatedly but partly covered by centimetre thick layers of fine sediment which now fill large spaces between lateral expansions of the corallum. Many corallites were smothered, allowing only a limited number to continue their growth. Subsequent corallites grew either inclined or spread laterally above the lenses of sediment. Transverse and oblique sections of small archaeocyaths lying on their sides relative to bedding are evident in cavities between extended shelves of the corallum (Figs 2,3). The geopetal infilling of the archaeocyaths further indicates that they were transported into the cavities with the sediment.

Calcareous sediments filling small cavities between the corallites have generally been recrystallized, while the calices (together with larger cavities) are usually filled with very fine sand or silt. Laterally extended shelves of the specimen SAM P34167 are irregularly rectangular or platy and project over the bioclastic and/or calcarenite matrix (Figs 2,3). Corallites also show indications of being eroded by rapid, energetic influxes of coarse sand. Calcite-filled fractures apparently related to post-diagenetic deformation of the corallum occur rarely (Figs 4B,C).

Recrystallization has affected all of the colony and some of the skeletal structures observed may be artifacts of diagenesis. There are, however, domains within the recrystallized fabric where some evidence of the primary structure of the skeleton appears to be preserved. These relic, rather robust fibrous elements which evidently formed the sclerenchyme (calcareous skeleton of corallites), are seen as either lineations across the walls of corallites (in transverse section) and/or divergent bundles (in longitudinal section) (Figs 4E,5D).

In longitudinal section, upturned spines along some corallite walls (Fig. 4C), and spines situated on the upper surface of some tabulae (Fig. 4D) are represented by bundled fibres, giving both the wall and tabulae a bumpy appearance. In transverse section, most septa appear to terminate in fan-shaped arrays of fibres, or similar arrays arise from the walls (Fig. 5C). The bundled fibres resemble primitive trabeculae. However, fan-shaped tufts in carbonates often result from diagenesis (Oekentorp 1989).

Systematic palaeontology

Phylum: CNIDARIA
Class: ANTHOZOA
Subclass: ?TABULATA
Family: uncertain

Genus: ***Arrowipora*** gen. nov.
Type species: *Arrowipora fromensis* sp. nov.

Etymology

For the Arrowie Basin, an Early Cambrian shallow marine basin, extending over much of the area of the present Flinders Ranges of South Australia.

Diagnosis

Corallum large, massive cerioid, comprising polygonal corallites; corallites prismatic and irregularly cylindrical; walls separated by a medial plane, thick, wavy to crenate, sometimes almost straight; tabulae numerous, rarely complete, commonly dissepiment-like tabellae; septa numerous or absent, numbering up to 35 in each corallite; where present septa form short wedge- to spine-like projections into the lumen; mural pores absent.

Arrowipora fromensis sp. nov.
FIGS 2-5

Etymology

For nearby Lake Frome.

Diagnosis

As for genus.

Type specimens: The specimens described in this paper are held at the South Australian Museum (SAM). Holotype SAM P34167, a polished slab of a broken part of a corallum and thin sections SAM P34167-1, SAM P34167-2. Paratype SAM P31962-1, SAM P31962-2, counterparts comprising two triangular, large, cut, polished slabs approximately 34 cm normal to bedding and 28 cm parallel to bedding, containing either two coralla or more likely the disjunct parts of one large corallum which formed numerous platy shelves. Thin section SAM P34168-1. The material was collected from the Moorowie Formation, near the Moorowie Mine in the eastern Flinders Ranges (Fig. 1).

Description

Colony large, more than 24 cm tall and extending laterally well in excess of 23 cm. In longitudinal section the corallum may broaden upward, or more commonly, forms wide shelves extending laterally over the adjacent sediment. Shelves are either irregularly rectangular in shape, with corallites tending to diverge slightly, or are plate-like. Individual shelves measure up to 70 mm high and 130 mm in width (Figs 2,3). The upper surface of the shelves is irregularly horizontal to concave, and calices may extend up to 7 mm above the uppermost tabellae. In transverse section (Figs 5A,B,C), the cerioid corallites, are seen as 5-8 (generally 6) sided polygons, varying between 10 and 14 mm in diameter.

Walls are relatively thick, varying between 0.1 mm and 1.0 mm, and are wavy to almost straight. The inner surfaces of the walls are irregular, due to the insertion

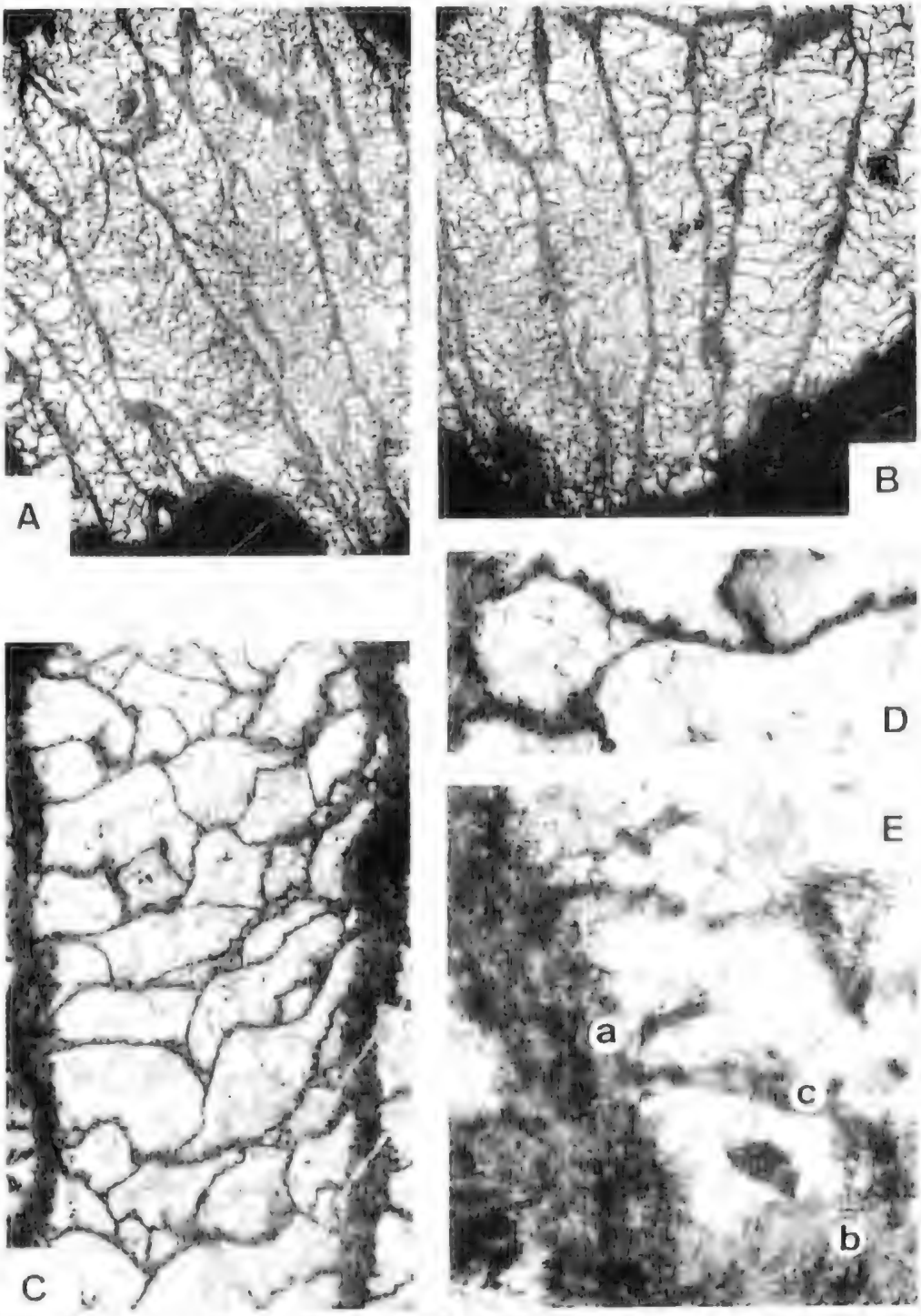

Fig. 4. Longitudinal sections of Holotype SAM P34167 A,B Adjoining sections illustrating general shape of the corallites, tabulae, vertical and basal corallite walls (x2.4). C. The irregular surface of the walls and upper surface of tabulae. Two fractures which post date growth are observed mid-to lower-right of figure, together with the recrystallized fabric within the corallite (x10.6). D. Enlarged section (x2.4) of corallite (lower right Fig. 4B) illustrating tabulae with possible septal spinules on the upper surface. E. Higher magnification (x40) of a corallite section illustrating diverging fibres of a vertical wall, a; and the similar structure of the basal wall, b; and tabulae, c.

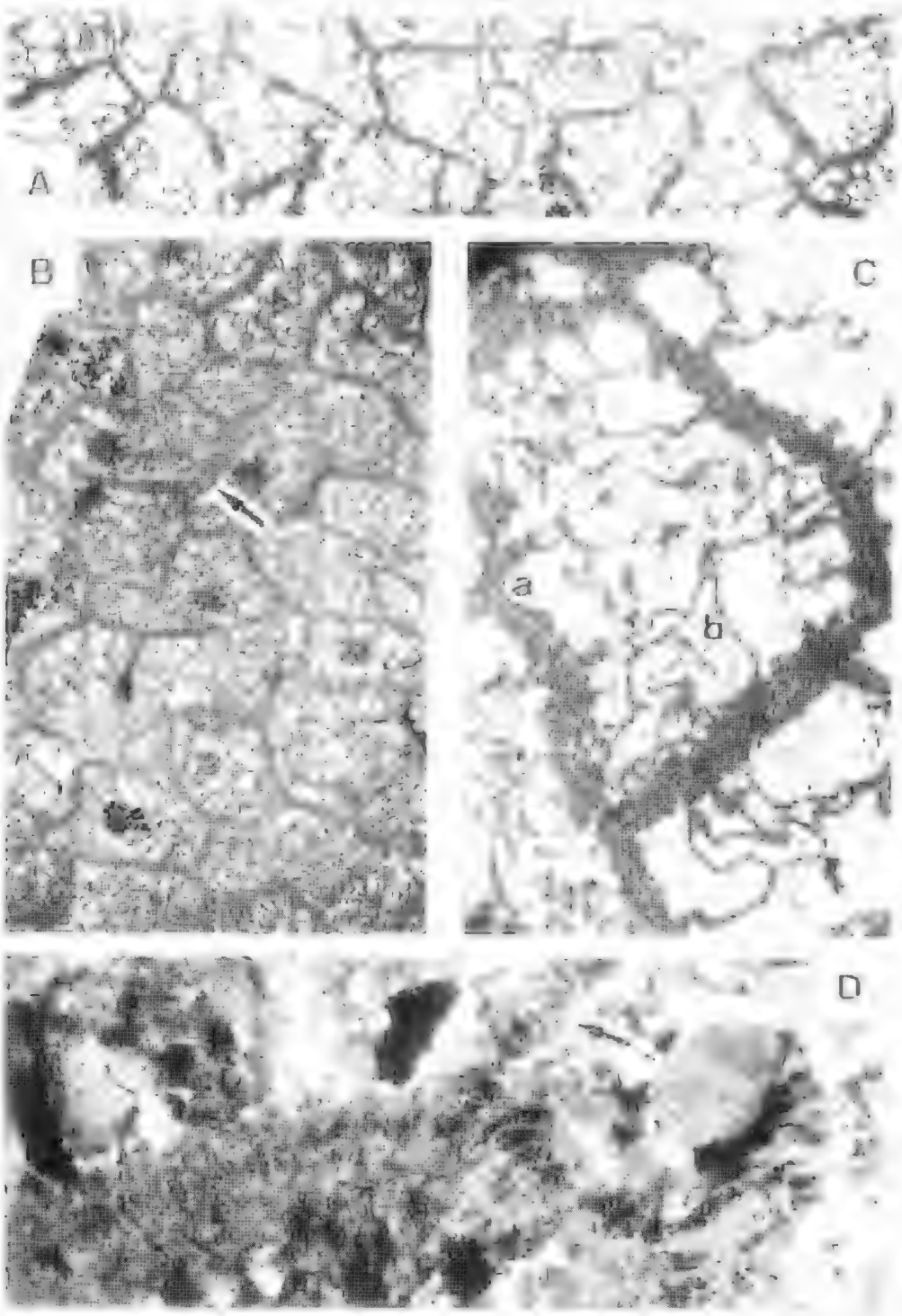

Fig. 5 A. Transverse section of Holotype SAM P34167 (x3.8). B. Transverse section of Paratype SAM P34168 (x4.5) showing variation in corallite shape and septa. Tabulae are observed as irregular lines crossing the corallite: the midline of the wall (arrowed) may be seen in some adjoining corallites. C. Enlarged section (x10.5) of 5A illustrating septa, wall irregularities, midline a and tabulae b. The recrystallized fabric is observed within the corallite. D. Corallite walls (x40) showing the bundles of fibres which cross the wall (arrowed) in sections of the specimen.

of numerous tabellae and septal spines. In thin sections, a medial line divides the walls of adjoining corallites (Figs 5A,C).

In transverse section at low magnifications (up to X 40) straight to slightly diverging fibres crossing the walls between adjacent corallites are commonly disrupted by the medial line (Figs 5A,B,C,D). In longitudinal section, fibrous elements diverge outward and upwards from the medial line and often protrude into the lumen giving the walls an irregular appearance. The walls which truncate parent corallites and form the base of subsequent corallites, are composed of vertical to slightly inclined fibres. These partitions arise from the vertical walls and are usually V-shaped, but may be undulating, horizontal or inclined (Figs 4C,D,E).

In longitudinal section (Figs 2,3,4A,B,C), individual corallites are prismatic to irregularly cylindrical and up to 14 mm wide and 47.5 mm long. Corallites vary little in diameter and length, prior to the addition of new corallites (increase). Increase is both lateral and peripheral intracalicular parricidal within the established body of the colony (Figs 2,4A,B).

Tabulae are numerous, commonly formed of incomplete, globose and dissepiment-like tabellae. Occasionally some are continuous across very narrow corallites. Tabellae may arise from the walls or from adjacent tabellae, extending inward and curving downwards to rest upon other tabellae. They are very thin, generally less than 0.06 mm, often wavy and rarely straight. Small projections often occur on the upper surface of tabulae (Fig. 4D). In transverse section, tabellae are seen as wavy and crenate, arising from the walls and anastomosing with adjacent tabellae (Figs 5A-C). At low magnification, the fibrous structure of the tabellae is similar to that of the walls, with some bundles extending to give the small projections on the upper surface. In longitudinal section, the fibrous elements are normal to the base of the tabellae.

In transverse section, septal spines vary from numerous (about 35) to absent and are often difficult to distinguish from other irregularities on the wall (Figs 5A,B,C). Where present they are short (up to c. 0.25 mm), generally equal in length, blunt triangular or spine-like in shape and equidistant from each other (about 0.25 to 0.5 mm). They are commonly present on some walls while absent on others within a single corallite. Septal spines appear to be continuations of bundles of fibres of the fibrous wall, usually terminating as, or being seen as fan-shaped tufts (see above - **Preservation**). In longitudinal section, the generally upturned septal spines are observed to occasionally form short vertical rows on corallite walls.

Discussion

A. fromensis is unlike the two previously described Early Cambrian corals from the same location, *Flindersipora bowmani* Lafuste 1991 (e.g. Lafuste *et al.* 1991) and *Moorowipora chamberensis* Fuller & Jenkins 1994. *A. fromensis* is distinguished from *F. bowmani* by the size and general form of the colony, the position and shape of tabulae and septa, as well as the mode of increase. In *F. bowmani*, tabulae are mostly complete and concave proximally; there are 6-16 strongly developed slightly curved septa, the edges of which bear very short blunt spines; the walls are very short segments between the septa. Increase is by longitudinal fission.

The main differences between *A. fromensis* and *M. chamberensis* are in the size and form of the colonies, the size and shape of the corallites and the arrangement and shape of tabulae. Although both are cerioid in colonial form, the former is much larger and usually has parallel corallites, while those in *M. chamberensis* are generally divergent. Corallites are prismatic to cylindrical and up to 14 mm in diameter and 47.5 mm in length in *A. fromensis*, but much smaller (up to 5 mm in diameter and 19.5 mm in length) and tuboroid to irregularly cylindrical in *M. chamberensis*. The presence or absence of septal spines is common to both corals; when present they are about the same size and shape.

Tabulae differ greatly, being incomplete, globose and dissepiment-like (tabellae) in *A. fromensis* and complete, undulating and horizontal to concave upward in *M. chamberensis*. Although the microstructure has not been studied at high magnification, there are some similarities between the above corals at low magnification. These include the parallel fibrous elements of the sclerenchyme evident in transverse section, and the parallel to diverging fibrous elements in longitudinal section. Fan-like arrays of fibres are not present in *M. chamberensis*. A medial line within walls of adjacent corallite occurs in both corals. Medial lines in the walls are common in tabulate corals, and represent the external epitheca (Hill 1981).

A. fromensis is unlike any of the previously described Cambrian corals suggested by Scrutton (1979) to have tabulate affinities, but does have skeletal characteristics in common with some of the Late Silurian to Late Permian michelinids.

The diagnostic characteristics for the genus *Michelinia* De Koninck 1841 include thin to moderately thick walls with a medial suture, short septal trabeculae, tabulae incomplete and globose sometimes with septal spinules on the upper surface, and large mural pores (Hill 1981). The walls and tabulae are similar to those seen in *A. fromensis* but the present taxon lacks mural pores.

Michelinia expansa White 1883 [*Tabellaephyllum peculiare* Stumm 1948] (Stumm 1948) from the Early Carboniferous of Arizona, is similar to *A. fromensis* with respect to the form of the colony, the size and shape of corallites and the arrangement of tabellae. Corallites are up to 15 mm in diameter in the former and 14 mm in the latter. Corallites are also of a similar shape, being generally 4, 5 or 6 sided, but differ by the lack of septa in *M. expansa*. A most noticeable similarity between the two is the placement, size and shape of the tabellae. They are incomplete and globose and are arranged in similar manner in both taxa, arising from either the walls or adjacent tabellae. The tabellae in *A. fromensis* appear to be less globose, spaced slightly further apart, and have a more irregular and wavy surface.

Although *A. fromensis* most closely resembles some of the michelinids, because of the long time separation between them (~120 million years) it is highly unlikely that they are related and more probable their skeletal similarities result from convergent evolution (Scrutton 1979, 1984, 1992; Hill 1981). It has been described as primitive, cerioid, of simple morphology, aseptate, but with tabulae and rare mural pores (Bassler 1950; Flower 1961; McLeod 1979; Scrutton 1984; Laub 1984). Although *A. fromensis* lacks mural pores, it has a similar skeletal structure to some michelinids which post-date *Lichenaria*. Most of the skeletal aspects of *A. fromensis* are characteristic of Palaeozoic tabulate corals. These are (1) the cerioid form of the colony; (2) walls separated by a medial line reflecting individual corallites (Scrutton 1987); (3) the spine-like to wedge-shaped septa occasionally situated in longitudinal rows (Hill 1981); (4) individual corallites which spread above the pockets of sediment within the colony, this habit being usual for cnidarians following influxes of sediment (Scrutton 1979); (5) lateral increase common, with peripheral intracalicular increase being described in some Favositidae (Hill 1981). Although tabulae are incomplete and dissepiment-like, they are consistently and strongly developed both within individual and between adjacent corallites in *A. fromensis*.

A. fromensis has anthozoan structural characteristics, most of which are evident in tabulate corals. It should therefore probably be included in the known group of tabulates, thus extending the time range of this group to the late Early Cambrian.

Conclusions

The three described corals from the Moorowie Formation, *A. fromensis*, *M. chamberensis* and *F. bowmanii*, are very different in form and arrangement of the skeleton. The diverse nature of the corals from this ancient reefal environment indicates that during the Early Cambrian, variability in polyp form and skeletal morphology was well established.

The genus *Lichenaria* has been recognized as the earliest tabulate coral, with a time range from the base of the Early Ordovician to the early Late Ordovician

Acknowledgments

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CHARACTER AND INTERPRETATION OF THE REGOLITH EXPOSED AT POINT DRUMMOND, WEST COAST OF EYRE PENINSULA, SOUTH AUSTRALIA

By E. Molina Ballesteros, E. M. Campbell†, J. A. Bourne† & C. R. Twidale†*

Summary

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The weathering mantle developed on granodiorite at Point Drummond, Eyre Peninsula, South Australia is examined using thin section and XRD analyses. Stages in the alteration of the granodiorite can be deduced by examination of the zonation of the regolith; release of oxides and hydroxides from the parent rock; removal of iron and kaolinisation; new concentrations of haematite in micropores; development of nodular structure and renewed removal of oxides and hydroxides. The possible age relationships of this profile with laterites and Plio-Pleistocene ferricretes from other South Australian sites are discussed. The age of weathering is uncertain but it predates the calcarenite (? Pleistocene) and is probably post Permian, with Plio-Pleistocene the most likely.
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The weathering mantle developed on granodiorite at Point Drummond, Eyre Peninsula, South Australia is examined using thin section and XRD analyses. Stages in the alteration of the granodiorite can be deduced by examination of the zonation of the regolith: release of oxides and hydroxides from the parent rock; removal of iron and kaolinisation; new concentrations of haematite in micropores; development of nodular structure and renewed removal of oxides and hydroxides. The possible age relationships of this profile with laterites and Plio-Pleistocene ferricretes from other South Australian sites are discussed. The age of weathering is uncertain but it predates the calcarenite (? Pleistocene) and is probably post Permian, with Plio-Pleistocene the most likely.

Key Words: regolith, ferruginisation; Point Drummond.

Introduction

The west coast of Eyre Peninsula is characterised by high cliffs eroded in dune calcarenite (also known as aeolianite: see e.g. Crocker 1946) of Middle and Late Pleistocene age (Wilson 1991[1]). The calcarenite rests unconformably on Precambrian rocks, mostly igneous and metamorphic, with granite and gneiss prominent, but including sandstone and conglomerate near Talia. The unconformity is uneven and the base of the calcarenite commonly extends below sea-level. Elsewhere, the Precambrian basement is exposed in rather irregular shore platforms and in the lower sections of the cliffs which, however, are composed mainly of the calcarenite. At several sites remnants of the pre-calcarenite regolith are developed on the Precambrian basement. One of the best exposures of the regolith, in terms of thickness, completeness and lateral extent, occurs at Point Drummond, a westerly projecting promontory located on the west coast of southern Eyre Peninsula, some 80 km north-west of Port Lincoln (Figs 1 & 2).

The purpose of this short paper is to describe the mineralogical variations between horizons within the regolith, and to discuss their genetic implications. The site is on the southern portion of Point Drummond. Two profiles, one from a south-projecting peninsula and one from the cliff adjacent to the access steps several hundred metres to the north, were examined. The samples were selected on the basis of colour and textural variations. The profiles are so similar both in appearance and upon analysis that they can be treated as one.

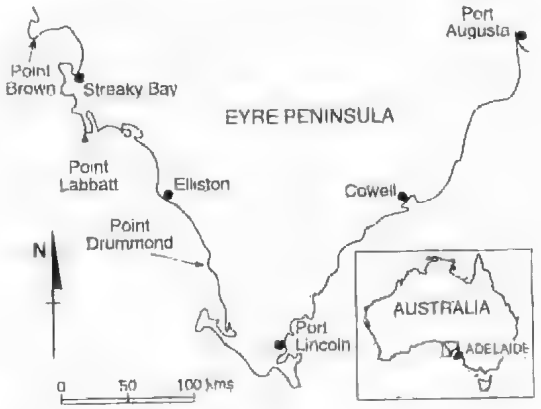

Fig. 1. Location Map.

Description of the profile

The profile, approximately 18 m thick, was subdivided from the base to the top into five horizontal zones on the basis of their colour and texture (Fig. 3). Mineralogy and texture have been studied in thin section (using samples impregnated with a thinned araldite to prevent any disturbance of the original structures) and by XRD analysis of bulk samples.

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1 Wilson, C. C. (1991) Geology of the Quaternary Bridgewater Formation of southwest and central South Australia. Ph.D. thesis, University of Adelaide, Adelaide (Unpubl).

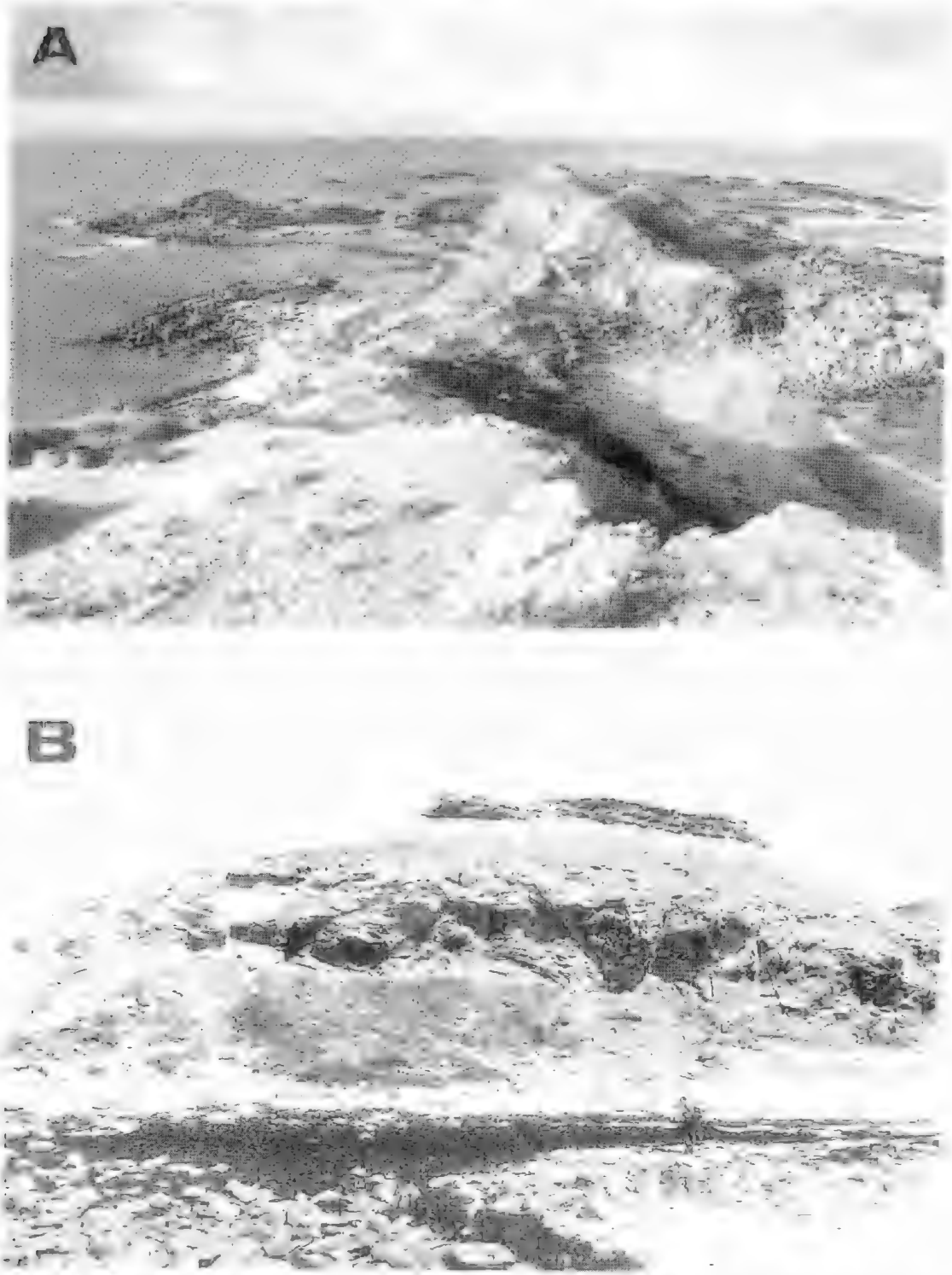

Fig. 2A. General view of Point Drummond, Eyre Peninsula, South Australia. 2B. The weathering profile sample site, Point Drummond peninsula, showing the coastal platform developed in granodiorite, the goethite rich zone at the base of the cliff and above this the white kaolinised zone, the haematite zone and the calcarenite remnant at the surface.

Zone I

The parent rock is a gneiss of granodioritic composition consisting mainly of quartz, plagioclase, biotite and muscovite with some orthoclase. Secondary minerals resulting from hydrothermal alteration of the rock prior to weathering include sericite, chlorite (from biotite), epidote-zoisite and calcite (from plagioclase - Sample 1, Fig. 3, Munsell Rock Colour N8, white to N3, dark gray - dry. The colours of other samples are Munsell Soil Colours - 1994). The granodiorite is intruded by amphibolitic and quartzitic veins. Schistose shear zones are also present. These various rocks are all members of the Sleaford Complex, dated at 2,700-2,300 Ma and thus of late Archaean or Palaeoproterozoic age (Flint *et al.* 1984; Parker *et al.* 1985) though the shear zones may result from the Kimban Orogeny (~1700 Ma - Thomson 1969).

Stages in the weathering of the gneiss can be traced by examination of the zonation of the regolith or weathered mantle, assuming that the weathering front, or lower limit of weathering, has descended into the rock mass from the surface. Hence, in these terms, the initial stages of weathering are represented by the zone immediately above the weathering front and the most advanced by the near surface horizon.

The coastal platform eroded in granodiorite and located between high and low tide levels, is irregular with many blocky and bouldery rises and intervening clefts. Many of the outcrops are superficially altered, with rinds of ferruginous oxides and hydroxides developed at the margins of blocks, boulders and other exposures. The rinds are also found bordering fissures (Sample 2, 7.5YR 7/6, reddish yellow to 7.5YR 7/3, pink). In this zone the thickness of the rinds increases up the profile, but nowhere exceeds 5 cm.

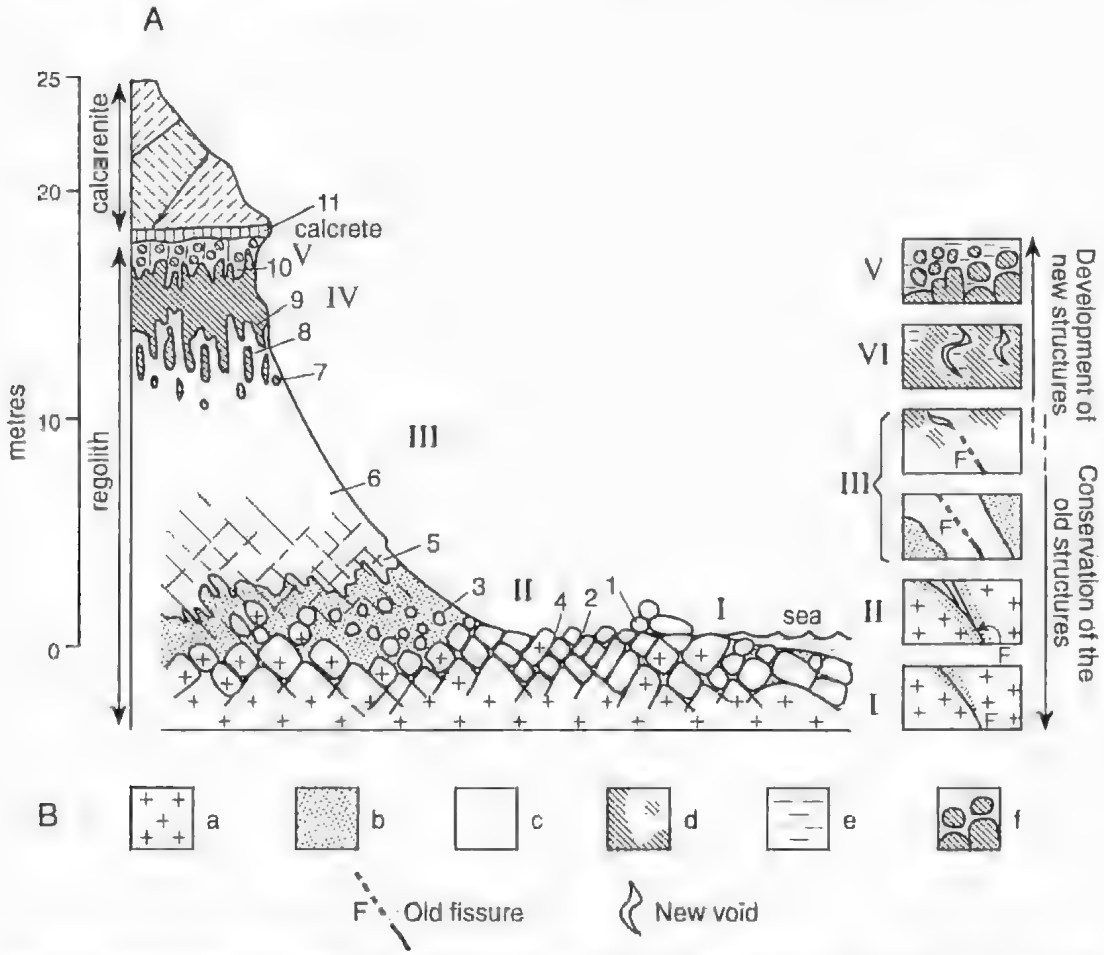

Fig. 3. Schematic diagram of the weathering profile on the peninsula, Point Drummond. A. Profile I-V, Zones of weathering (see text for explanation); 1-11, sample numbers (sample 5 similar to 6). B. Principle processes: a. Unweathered parent rock. b. First stage of weathering (goethite-rich zone). c. Kaolinisation. d. Formation of new structures and concentration of haematite. e. Removal of iron and plasmic separation. f. Development of peds and nodules.

The first stage of weathering discernible is the development of the rinds around the corestones. In these the epidote-zoisite minerals are dissolved and the alteration of plagioclase is manifested by the appearance of zones of randomly oriented clays. The clay minerals are preferentially developed along fissures presumably because the latter allow penetration of water. Biotite changes colour from green to brownish-yellow, reflecting a release of iron which, as goethite, is concentrated in cracks and fissures.

Zone II

Here, though the original rock structures are everywhere distinguishable, some of the blocks and boulders are entirely discoloured and the rinds are thicker than those in Zone I (Samples 3 & 4, 10YR 8/4, very pale brown to 10YR 7/6, yellow) with a white rind (N8) developed on the outside, and a strong brown (7.5YR 5/6) interior. Again the rind increases in thickness up the profile and, as in Zone I, is also found along partings. The contact between the weathered rind and the interior of the corestones low in the profile is sharp but is more diffuse at higher levels.

The rinds are pale in colour and voids are apparent in thin section. Plagioclase is progressively reduced higher in the profile and essentially isotropic clays, believed to be mainly kaolinite, become dominant. With the XRD method used, it is difficult to differentiate any other polymorphs of kaolin. Resistates such as quartz and muscovite are present.

Zone III

Almost the entire rock in this zone is white (Sample 6, N8) but most of the original textures and structures are preserved and remnants of the yellow and red iron oxides occur as spots in the upper part of the zone. At the top of Zone III loss of material has led to the formation of voids. The weathering plasma (in the sense of Nahon 1991, p. 63), derived from weathering of the parent materials, begins to appear anisotropic, especially in areas close to voids [the vosepic plasma separation of Brewer (1964, 1976)]. Some, though not all, oxide concentrations are related to voids.

Zone IV

The yellow and red spots present in Zone III here merge to give a mixture of oxides and hydroxides of iron in differing degrees of dehydration and crystallisation (Sample 7, 5YR 4/4, reddish brown to 7.5YR 6/8, reddish yellow to 10R 4/3, weak red; Sample 8, 10YR 8/8 yellow to 10R 4/3, weak red; Sample 9, 10R 4/3, weak red to 10R 5/6 red). The zone is up to four metres thick. None of the original structures survives.

XRD analysis shows that haematite is dominant in the weak red patches, kaolinite having been removed. On the other hand, where there is no iron oxide or hydroxide, the kaolinitic alteroplasma is well preserved. Muscovite remains, albeit weathered to varying degrees and quartz is corroded and in some instances clearly disaggregated. At the top of Zone IV voids are common.

This zone is similar to the "mottled clay" horizon from a laterite profile described by Nahon (1987), of which alumina (not analysed in this study) is a typical component.

Zone V

The lower part of this zone is characterised by irregular ill-defined fissures in the mottled clay. Also, a new structure occurs in the form of polyhedral peds some centimetres across. They become smaller and more rounded upwards, where they take the form of soft nodules 0.5–1.0 cm in diameter, reddish yellow in colour but with red oxide concentrations in the interior (Sample 10, 7.5YR 6/6, reddish yellow to 10R 4/6, red) (Fig. 4). The partings which define the polyhedral peds

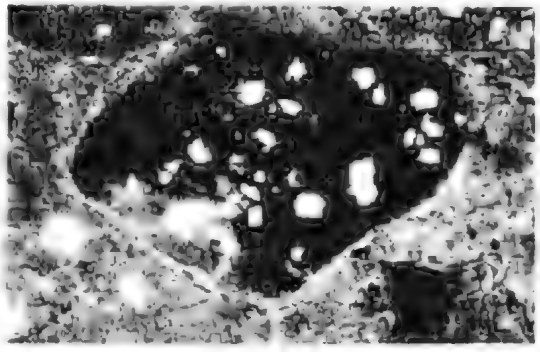

Fig. 4. Thin section (crossed polars, plain light, x25) of upper part of Zone V. Kaolinite plasma surrounds the ferruginous nodule (dark area). The light-coloured material in both the nodule and the surrounding plasma is quartz.

are preferential zones of leaching. Removal of oxides and hydroxides has resulted in zones of concentration of skeletal grains (mainly quartz) from the parent material, and in the appearance of a kaolinitic clay plasma (a pedoplasma in the sense of Boulet 1974). It grades from asepic, where oxyhydroxides are abundant, to skelsepic, vosepic and even masepic where the oxyhydroxides have disappeared (Brewer 1964, 1976). The development of the nodules is a centripetal process involving the removal of oxides and hydroxides from the margins of the peds and their concentration in the nodules, the redistribution of clays and the concentration of skeletal grains in the leached zones.

Both the promontory and the cliff profiles are overlain by a calcareous crust (calcrete - Sample 11, 2.5Y 7/2, light gray), located at the base of the calcarenite but developed on the weathered material and including nodules like those found in Zone V (Fig. 3).

Interpretation

Various stages in the weathering of the granodiorite are evidenced:

1. The penetration of meteoric waters from the surface and release of oxides and hydroxides from minerals in the parent rock, especially biotite, is the initial process in evidence. The iron oxides are concentrated in fissures at the weathering front, at the margins of blocks and boulders and adjacent to joint partings. The hydrothermally altered minerals are dissolved and the plagioclases are weathered to clays.

2. Removal of iron and kaolinisation are represented by the appearance of white rinds. These processes are usually achieved in acid reducing solutions, which appear to have leached most of the calcium, iron and sodium and some of the silica and produced the newly formed mass of isotropic to insepic materials (see Brewer 1964, p. 309), mainly kaolinite. Inside this isotropic plasmic material are resistates such as quartz and muscovite {skeleton grains, of Brewer (1964, 1976)}. On the whole, however, kaolinite is dominant.

3. Ferruginisation results from the progressive development of a kaolinitic plasma, and a new porosity plus the destruction of the original textures and structures. Micropores, especially, become the sites of new concentrations of oxides (weak red spots), particularly haematite (Fig. 4), due to the decreased mobility of the solutions in these pores (Didier *et al.* 1983; Tardy & Nahon 1985). This is the origin of the 'mottled clay horizon' typical of profiles developed under seasonally wet and dry climates.

4. The development of nodular structure is related to the removal of oxides and hydroxides by solutions probably emanating from an overlying soil. A new kaolinitic plasma is developed as the oxyhydroxides are removed. The mobility of the materials is governed by the amount of oxyhydroxides: the less oxyhydroxide the more plasmic movement and hence better re-organisation of the soil mass.

5. The removal of oxides and hydroxides requires acid solutions (i.e. those which are poor in carbonates), so that the processes described in paragraphs 1-3 inclusive predate the development of the calcrete and the deposition of the dune calcarenite.

The age of the profile, and the events to which it relates, are mainly problematic. It is clearly younger than the Proterozoic rocks on which it is developed, and predates the calcarenite which, according to Wilson (1991), is Middle and Late Pleistocene in age (maximum c. 700,000 years). But allocating it to an hiatus of some 1500-2000 Ma is neither precise nor informative. The extent of the hiatus can be reduced if two general arguments are accepted. First, although regoliths have survived the passage of ice sheets (see e.g. Fogelman 1985), the profile, which has apparent equivalents at several points along the west coast of Eyre Peninsula (e.g. Point Brown, Point Labatt, Talia), is unlikely to have survived the Early Permian glaciation, which evidently affected most of the present state of South Australia (e.g. Ludbrook 1969), and subsequent erosion; for the regolith has readily been eroded by marine agencies and by gullying. In these terms the regolith under debate is less than 250 Ma old.

Second, the hiatus is further reduced if it is conceded that the regolith is most likely immediately to predate the cover material, that is the calcarenite. This last suggestion assumes that even if the development of the regolith began long before the deposition of the dune limestone, it would have continued to evolve (see e.g. McFarlane 1986; Bourman 1993) up to (and even beyond) being covered. In these terms the young date for the regolith is of the order of 700,000 years, though, because it must have developed over a long period, it ought to be assigned an age range and could reasonably be labelled Plio-Pleistocene.

Broader considerations support this suggestion. First, with what other regoliths might the Point Drummond profile be related? Ferruginous regoliths are known from various parts of South Australia (e.g. Hossfeld 1926[2]; Northcote 1946; Miles 1952; Horwitz & Daily 1958; Campana 1958; Glaessner & Wade 1958; Horwitz 1960; Wopfner 1967; Daily *et al.* 1974; Twidale *et al.* 1976; Wright 1985; Milnes *et al.* 1985; Bourman *et al.* 1987). They have been variously defined and interpreted (see e.g. Bourman 1993 - but see also McFarlane e.g. 1986; Firman 1994). Some, characterised by a sandy or silty A-horizon, a massive, commonly pisolitic, ferruginous horizon overlying a thick bleached zone, have been labelled laterite. Others, consisting of either a ferruginous crust alone, or a crust resting on a thin bleached horizon, have been termed ferricretes (e.g. Lamplugh 1902; Twidale 1976, p. 196-197). The Point Drummond profile does not sit easily with either of these, but is perhaps closer to the ferricrete than to the laterite, particularly if it is considered together with other stratigraphically comparable regoliths such as that exposed at Point Brown. Ferricretes in southern South Australia have been dated by various means, but on Yorke Peninsula (Horwitz & Daily 1958) local stratigraphy indicates a Pliocene age. Equally, occurrences in the interior of Eyre Peninsula have, on stratigraphic grounds, also been attributed to the Tertiary, some being considered Eocene but others clearly Pliocene or post-Pliocene (Rankin & Flint 1991; Flint & Rankin 1991; Flint 1992). Given the Middle-Late Pleistocene age of the overlying

2 Hossfeld, P. (1926) The geology of portions of the Counties of Light, Eyre, Sturt and Adelaide. M.Sc. thesis, University of Adelaide, Adelaide (Unpubl).

calcarenite, a later rather than an earlier Tertiary age seems appropriate for the Point Drummond exposure, and on balance a Plio-Pleistocene attribution is in keeping with the available evidence.

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A REVISION OF THE GENUS TIKUSNEMA (NEMATODA: ACUARIOIDEA) WITH THE DESCRIPTION OF A NEW SPECIES FROM THE FALSE WATER-RAT XEROMYS MYOIDES FROM QUEENSLAND

*By Lesley R. Smales**

Summary

Smales, L. R. (1995) A revision of the genus Tikusnema (Nematoda: Acuarioidea) with the description of a new species from the false water-rat, Xeromys myoides from Queensland. Trans. R. Soc. S. Aust. 119(2), 89-94, 31 May, 1995.

The genus Tikusnema Hasegawa, Shiraishi & Rochman, 1992 is redescribed. The species Molinacuaria indonesiensis Gibbons, Cranshaw & Rumpus, 1992 was found to be synonymous with Tikusnema javaense Hasegawa, Shiraishi & Rochman, 1992, the two species having been described almost simultaneously from the rice field rat, Rattus argentiventer. A new species of Tikusnema from the false water-rat Xeromys myoides is described. Tikusnema vandycki sp. nov. can be distinguished from T. javaense by the size of the adult male and female, the shape of the cuticular leaves on the pseudolabia, the length of the male tail and spicules, the length of the female tail and size of eggs. The implications of the presence of acuariid nematodes, normally found in birds, in a range of small mammalian hosts, are discussed. The significance of the presence of Tikusnema in Indonesian and Australian hosts cannot be determined until its presence or absence on the island of New Guinea is confirmed.

Key Words: Tikusnema, Nematoda, Acuarioidea, Xeromys myoides, false water-rat, mammalian hosts.

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The genus *Tikusnema* Hasegawa, Shiraishi & Rochman, 1992 is redescribed. The species *Molinacuaria indonesiensis* Gibbons, Crawshaw & Rumpus, 1992 was found to be synonymous with *Tikusnema javanense* Hasegawa, Shiraishi & Rochman, 1992, the two species having been described almost simultaneously from the rice field rat, *Rattus argentiventer*. A new species of *Tikusnema* from the false water-rat *Xeromys myoides* is described. *Tikusnema vandycki* sp. nov. can be distinguished from *T. javanense* by the size of the adult male and female, the shape of the cuticular leaves on the pseudolabia, the length of the male tail and spicules, the length of the female tail and size of eggs. The implications of the presence of acuariid nematodes, normally found in birds, in a range of small mammalian hosts, are discussed. The significance of the presence of *Tikusnema* in Indonesian and Australian hosts cannot be determined until its presence or absence on the island of New Guinea is confirmed.

KEY WORDS: *Tikusnema*, Nematoda, Acuarioidea, *Xeromys myoides*, false water-rat, mammalian hosts.

Introduction

The false water-rat *Xeromys myoides* Thomas, 1889 is a small dark grey semi-aquatic rat whose preferred habitat is shallow coastal wetlands, such as swamps, mangroves, forests, lagoons, or sedged lakes (Van Dyck 1994). They are currently known from only six sites in north-central and north-eastern Australia. Their current conservation status is vulnerable and likely to progress to endangered because of human proclivity to drain and develop swamps (Van Dyck 1992). They forage on the mud flats for food items including aquatic invertebrates, such as crabs, mud-lobsters, mussels, marine pulmonates and polyclads (Van Dyck 1994).

Nematodes dissected from specimens of *X. myoides*, collected by staff of the Queensland Museum were found to be species belonging to the Acuarioidea. The genus *Tikusnema* was erected for specimens from *Rattus argentiventer* (Robinson & Kloss, 1916), the rice field rat from West Java by Hasegawa *et al.* (1992). Almost simultaneously a new species of *Molinacuaria* was described, also from *R. argentiventer* from Java, by Gibbons *et al.* (1992).

Comparison of material from *X. myoides* with type specimens of both species described from *Rattus argentiventer* suggest that the nematodes from *X. myoides* are new species of *Tikusnema* while all the material from *R. argentiventer* is con-specific. *Molinacuaria indonesiensis* therefore falls as a synonym of *Tikusnema javanense*.

Materials and Methods

Six false water-rats, *Xeromys myoides*, were collected from Myora Swamp, Stradbroke Island, Queensland during 1992. Faecal pellets from two hosts were examined. The alimentary tracts of the four other hosts were dissected for helminth parasites after the bodies had been fixed whole in 10% formalin. The nematodes so collected were cleared in lactophenol for microscopic examination. Figures were drawn with the aid of a drawing tube. Measurements, of 10 specimens in μm unless otherwise stated, with the range followed by the mean, were made with the aid of an ocular micrometer, drawing tube and measuring wheel.

Specimens of *Molinacuaria indonesiensis* Gibbons, Crawshaw & Rumpus, 1992 and *Tikusnema javanense* Hasegawa, Shiraishi & Rochman, 1992 from *Rattus argentiventer* were also examined for comparison.

The terminology used for morphological features in the descriptions is that of Bird and Bird (1991) and the taxonomic system of Anderson (1992) is followed. Abbreviations are: Queensland Museum QM; Australian Helminthological Collection South Australian Museum SAM; United States National Museum Helminthological Collection USNM; International Institute for Parasitology IIP.

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Systematics

Order Spirurida
Suborder Spirurina
Superfamily Acuarioidea
Family Acuariidae
Sub family Seuratiinae
Genus *Tikusnema* Hasegawa, Shiraishi & Rochman, 1992

Type species *Tikusnema javaense* Hasegawa, Shiraishi & Rochman, 1992.

Tikusnema
Hasegawa, Shiraishi & Rochman, 1992.

Revised generic diagnosis

Cephalic end inflated and set off from body by constriction. Oral opening laterally compressed. Pseudolabia large, triangular in lateral view, each with two cephalic papillae and an amphid. Pseudolabia attached to each other apically, separated dorsally and ventrally by cordons and indented deeply at level of anterior extremity of cordons. Posterior end of each pseudolabium forms two cuticular leaves each subdivided into teeth. Cordons small, not extending posteriorly. Buccal capsule long, cuticular wall thick, not striated. Pharynx divided into anterior muscular and posterior glandular portions. Deirids small, bicuspid. A pair of cuticular ornamentations present laterally, posterior to deirids. Parasitic in the stomach or intestine of rodents.

Tikusnema javaense
Hasegawa, Shiraishi & Rochman, 1992.

Synonym *Molinacuaria indonesiensis* Gibbons, Crawshaw & Rumpus, 1992: pp. 175-181

Material examined

From *R. argentiventer*: 1 ♂ allotype. *Tikusnema javaense* USNM 82223 Pusakanagara, West Java, Indonesia; 1 ♂ paratype IIP B1055B from Sukamandi, West Java, Indonesia.

Description

As in Hasegawa *et al.* (1992). From the combined measurements of both Hasegawa *et al.* (1992) and Gibbons *et al.* (1992) the dimensions become as follows:

Male: length 9-21 mm, width 277-440. Buccal capsule 359-490 long, muscular portion of pharynx 410-560, glandular portion 1130-1980 long. Deirids 296-440, nerve ring 450-560, excretory pore 525-830 from anterior end. Right spicule 190-210, left spicule 491-570 long; tail 556-990 long.

Female: length 11.0-24.5 mm, width 293-510. Buccal capsule 330-490 long, muscular portion of pharynx 402-630, glandular portion 860-2030 long. Deirids 273-430, nerve ring 410-630, excretory pore 502-870 from anterior end. Vulva 5.02-12.21 mm from anterior end. Tail 230-520 long. Eggs 28-31 by 38-44

Remarks

Tikusnema javaense and *M. indonesiensis* were described almost simultaneously by Hasegawa *et al.* (1992) and Gibbons *et al.* (1992), the descriptions appearing in different journals. Both descriptions referred to material collected on the island of Java from *Rattus argentiventer*. A careful examination of the descriptions given by each group of authors, together with a comparison of the material they examined, has revealed that they are of the same species. Any differences in measurements between the two sets of material relate only to the fact that the specimens described by Hasegawa *et al.* (1992) were smaller than those described by Gibbons *et al.* (1992). The females described by Gibbons *et al.* (1992) for example are larger, gravid females containing embryonated eggs while the smaller females described by Hasegawa *et al.* (1992) contain unfertilized eggs.

Hasegawa *et al.* (1992) describe and figure a pair of cuticular ornamentations much larger than the deirids in the adult worms and even more prominent in the 4th stage larva. Gibbons *et al.* (1992) did not mention this feature in their description of their more mature worms. Therefore it appears that the cuticular ornamentations may be a more prominent feature of juvenile than mature worms. This would account for their apparent absence in the specimens examined by Gibbons *et al.* (1992).

The interpretation of the cephalic ends of the specimens, in particular the origins of the cuticular leaves, by Hasegawa *et al.* (1992) appears consistent with both sets of material. As discussed in Hasegawa *et al.* (1992) the cuticular leaves of *Tikusnema* originate directly from the pseudolabia without separating furrows. *Tikusnema* also has small cordons not extending posteriorly. By contrast the genus *Molinacuaria*, although characterized by the absence of pseudolabia (Wong & Lankaster 1985), does have grooves located immediately anterior to ptilina. *Molinacuaria* can be further differentiated from *Tikusnema* by a lack of cordons. *Molinacuaria indonesiensis* therefore falls as a synonym of *Tikusnema javaense*. The species name *javaense* has priority because it was published in October 1992, while *indonesiensis* did not appear until in November of that year.

Tikusnema vandycki sp. nov.
FIGS 1-16

Material examined

From *Xeromys myoides*: 54 immature adults and fourth stage larvae, 31 anterior ends, 40 mature ♂♂, 26 mature ♀♀ from Myora Swamp, Stradbroke Island, Queensland.

Description

Long, slender worms with tapered extremities, cuticle thin, with fine annulations. Lateral alae absent. Cephalic cuticular leaves each divided into 4-5 teeth, lateral tooth largest (Figs 2,3,5,16). Cordons rod-like in dorso-ventral view (Fig. 2). Cordons and dorsal and ventral rim of pseudolabia faintly striated (Figs 2,8). Muscular portion of pharynx narrower and shorter than glandular portion, pharynx about 1/7 body length (Figs 1,15). Nerve ring near anterior end of muscular portion, excretory pore posterior to nerve ring. Deirids tiny, bifid, between nerve ring and excretory pore (Fig. 1). A pair of cuticular ornamentations, small, inconspicious at about mid level of glandular portion of pharynx (Fig. 12).

Male: Length 27 (25-30) mm, width at midbody 412 (317-476). Cephalic end 177 (156-245) long, 240 (215-260) wide. Posterior end of cuticular leaf 220 (208-266) from anterior extremity. Buccal capsule 269 (260-287) long; muscular portion of pharynx 435 (370-680) long, glandular portion 3229 (2975-3872) long. Deirids 307 (186-325), nerve ring 377 (338-410), excretory pore 499 (442-559), cuticular ornamentation (one measurement only) 2685 from anterior end. Posterior region curved ventrally. Caudal papillae arranged in 10 pairs, 4 pairs pre-anal, 6 pairs post anal, large pedunculate; 1st and 2nd pairs grouped together; 3rd and 4th pairs grouped together; 1st and 3rd more lateral; 8th and 9th pairs grouped together 9th more lateral; 10th pair close to tail tip. Longitudinal cuticular ridges present anterior to cloaca (Fig. 13). Spicules dissimilar; right spicule short robust, rounded distal tip 241 (208-266) (Fig. 9); left spicule, trifid distal tip 746 (682-813) long (Figs 4,14); longest spicule about 1:36 body length, tail 721 (598-845) (Fig. 11).

Female: Length 34.8 (30-41) mm, width at mid body 555 (510-629). Cephalic end 188 (156-201) long, 255 (240-273) wide. Posterior end of cuticular leaf 238 (188-260) from anterior extremity. Buccal capsule 282 (266-292); muscular portion of pharynx 461 (325-650) long, glandular portion 4040 (3111-4675). Deirids 336 (273-383), nerve ring 399 (357-422), excretory pore 500 (455-546) from anterior end. Vulva circular, without lips, 16.5 (13.6-19.4) mm from anterior extremity. Ovejector amphidelphic; vagina vera directed transversely, 550 (one measurement), vagina uterina 250 (one measurement) parallel to body wall (Fig. 6). Tail 621 (510-748) (Figs 7,10). Eggs thick shelled, 33.8 (32-34) by 48 (44-53).

Etymology

The specific name *vandycki* is given in recognition of Steve Van Dyck who first noticed the presence of these worms in the host.

Host: *Xeromys myoides*

Location: Stomach

Locality: Stradbroke Island, Queensland

Type specimens: Holotype male, QM211925; Allotype female, QM211926.

Paratypes: QM211927-30; SAM24832.

Remarks

Tikusnema vandycki can be distinguished from *T. javaense* by the shape of the cuticular leaves. In *T. vandycki* the leaves are subdivided at the edge into 4-5 teeth, but in *T. javaense* the leaves have three teeth, the middle one being the most prominent. *Tikusnema vandycki* can be further distinguished by its larger size; males up to 30 mm long, females up to 41 mm as compared with 21 and 24.5 in *T. javaense* respectively. The spicules of *T. vandycki* are longer (208-266 and 682-813) than those of *T. javaense* (190-210 and 500-570). However since *T. vandycki* is a larger worm than *T. javaense* the proportion of left spicule to body length is smaller for *T. vandycki* (1:36) than for *T. javaense* (1:18). Male *T. vandycki* have a shorter tail (598-845) than do *T. javaense* (840-990). The eggs of *T. vandycki* (44-53 x 32-34) are larger than those of *T. javaense* (38-44 x 28-31). Comparative measurements of *T. javaense* and *T. vandycki* are given in Table 1. Since the specimens examined by Hasegawa *et al.* (1992) are smaller immature adults only the measurements from Gibbons *et al.* (1992) of mature specimens are used. This allows an easier comparison of the relative sizes of mature adult specimens of each species. The paired cuticular ornamentations at the level of the glandular portion of the pharynx are tiny and difficult to find in *T. vandycki* but more prominent in *T. javaense*. The vagina vera of *T. vandycki* appears to consist of two parts, a globular heavily cuticularized part leading into a more tubular less cuticularized part, which in turn opens into vagina uterina (Fig. 6). The vagina vera of *T. javaense* is similarly figured in Gibbons *et al.* (1992). Further investigation is needed to determine whether the vagina vera is actually bipartite or whether the distal, globular part is actually an elaboration of the vulva.

Fourth stage larvae and immature adults of *T. vandycki* show similar morphological features to those of *T. javaense*. A detailed comparison and analysis, particularly of the development of the cephalic structures, is being prepared for a subsequent paper.

Discussion

The spirurid superfamily Acuarioidea is usually found in birds. However an increasing number of genera has now been reported from mammals. The genera *Stammerinema* Osche, 1955, *Antechiniella* Quentin & Beveridge, 1986, *Chandlerinema* Little & Ali, 1980, and now *Tikusnema* occur exclusively in

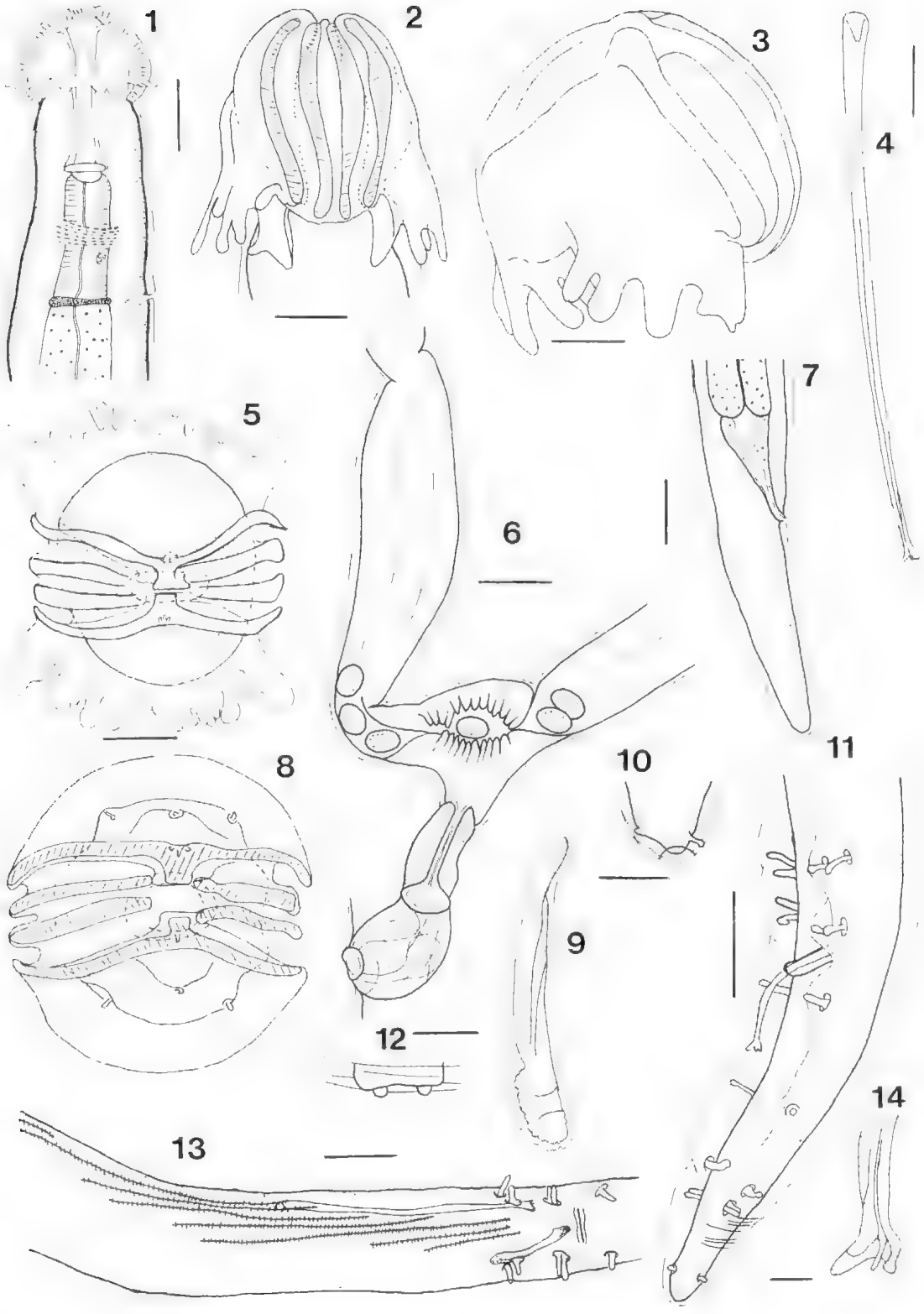
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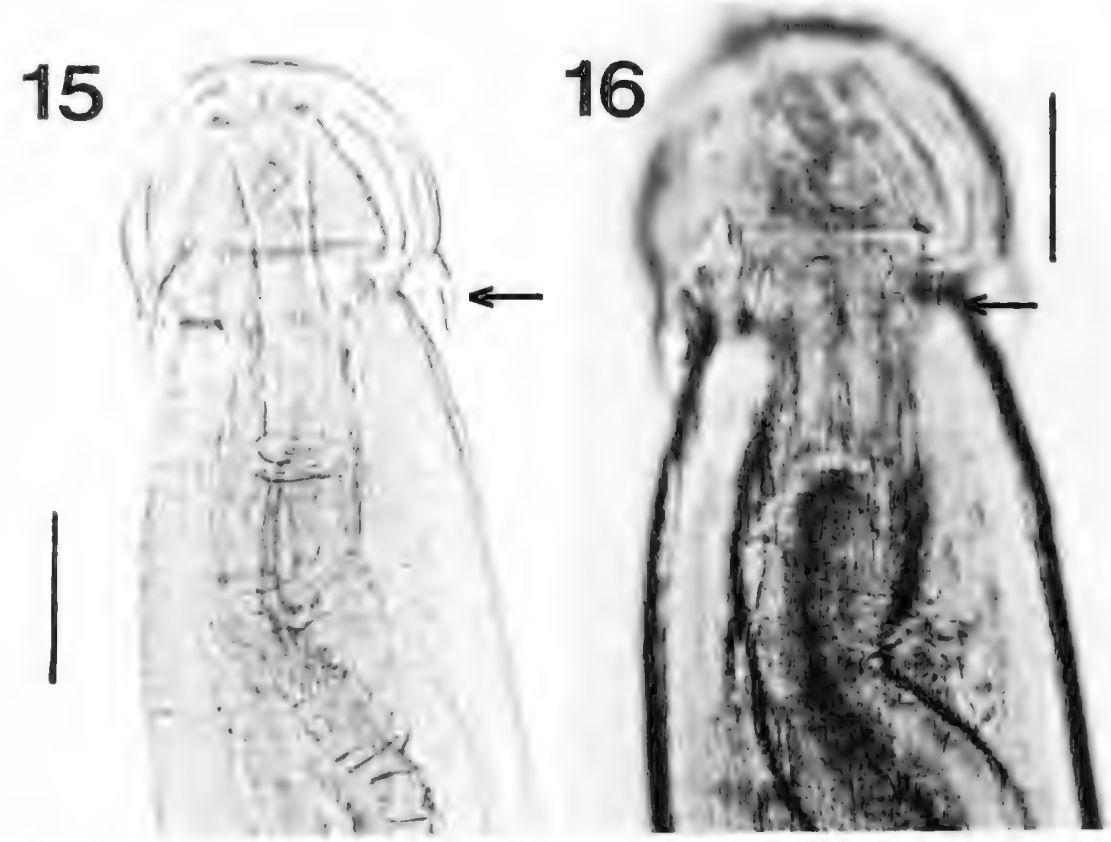
TABLE 1. *Mean measurements, in μm unless otherwise idicated, of* Tikusnema *species. Measurements of* T. javaense *are from Gibbons* et al. *1992. Standard deviations are given for the measurements of* T. vandycki.

	T. vandycki	*T. javaense*	*T. vandycki*	*T. javaense*
	Male		Female	
No. of specimens measured	10	4	10	2
Length in mm	27 ± 2.15	20.19	34.8 ± 3.16	23.5
Width	412 ± 43.39	410	555 ± 43.67	445
Length buccal capsule	269 ± 13.91	465	282 ± 31.55	515
Length muscular pharynx	435 ± 95.09	540	461 ± 89.07	585
Length glandular pharynx	3229 ± 383.86	1870	4040 ± 578.37	1935
Deirid to anterior end	307 ± 48.85	390	336 ± 33.15	410
Nerve ring to anterior end	377 ± 22.09	550	399 ± 24.96	585
Excretory pore to anterior end	499 ± 37.45	765	500 ± 27.58	825
Right spicule	241 ± 19.73	200	-	-
Left spicule	746 ± 53.62	535	-	-
Tail	721 ± 67.32	915	621 ± 65.41	505
Vulva to anterior end in mm (one specimen)	-	-	16.5	12.21



Figs 15,16. Photomicrographs of the anterior end of *Tikusnema vandycki* sp. nov. lateral aspects. Fig. 15. optical section. Fig. 16. showing the cuticular leaves of the pseudolabia. Scale bars = 100μm. Arrows indicate cuticular leaves.

Figs 1-14. *Tikusnema vandycki* sp. nov. Fig. 1 Anterior end, lateral view. Fig. 2. Cephalic region, dorsal view. Fig. 3. Cephalic region, lateral view. Fig. 4. Left spicule. Fig. 5. Cephalic region, enface view showing cuticular leaves. Fig. 6. Vulva, vagina and uteri, lateral view. Fig. 7. Posterior end female, lateral view. Fig. 8. Cephalic end, enface view, optical section showing cordons. Fig. 9. Right spicule. Fig. 10. Female tail tip. Fig. 11. Posterior end male, lateral view. Fig. 12. Cuticular ornamentation in pharyngeal region. Fig. 13. Posterior end male, ventral view showing cuticular ridges arising anterior to the cloaca. Fig. 14. Left spicule tip. Scale bars: Figs 1,6,4, = 100 μm; Figs 2,3,5,8, = 50 μm; Figs 7,11,13, = 200 μm; Figs 9,10,12, = 50 μm; Fig. 14, = 25μm.

mammals (Gibbons *et al.* 1992) while others, *Synhimantus* Railliet, Henry & Sissoff, 1912, *Paracuaria* Rao, 1951 and *Skrjabinoclava* Sobolev, 1943 although primarily found in birds, also occur in mammals. Various arthropods and fish serve as intermediate hosts for the life cycle stages of acuariids (Anderson 1992). The link between mammalian host and acuariid parasite therefore may be one of dietary habit (Smales 1991). A particular set of dietary preferences and habits of a few mammals thus allows these odd occurrences of infection by acuariids of biologically unrelated host species, in geographically unrelated regions of the world. Shrews from Bulgaria, Israel, Alaska, Europe; rice rats, racecoons, muskrats, from USA; rice field rats from Indonesia; pyrenean desmans from Spain; *Antechinus* species, water-rats and false water-rats from Australia are all able to be parasitized by acuariids under appropriate circumstances (Quentin & Beveridge 1986; Hasegawa *et al.* 1992; Alvarez *et al.* 1994; Andersón & Wong 1994). The precise nature of the link would probably differ from one mammalian host to another. For example the diet, including crustaceans, and semi-aquatic habits of *X. myoides* appear to fit the required pattern.

Australian rodents are all included within the family Muridae. Their ancestors are believed to have evolved in South-east Asia about 25 million years ago (Watts & Aslin 1981). Then some 15-20 million years ago members of the lineage colonized the Indonesian and possibly some Melanesian islands. Geological changes during this period isolated the islands for greater or lesser periods of time allowing further speciation to occur. By 5-10 million years ago Australia and New Guinea had moved close enough to these islands to allow colonization by what has become known as the old endemic rodents.

The Australian water rat group, the Hydromyini form part of that old endemic fauna. The suggested period of divergence within the group (Watts & Aslin 1981) would have the Australian and false water-rats evolving along separate lineages before their arrival in Australia. Both genera have closer affinities with various New Guinean rat species, in body form and ecological niche, than they do with each other. The fact that both genera have acuariid parasites can be seen as a reflection of their aquatic to semi-aquatic life-styles and the inclusion of crustaceans in their diet. However, the acuariids found in *H. chrysogaster*, *Antechinella* and *Synhimantus* are also found in Australian dasyurid marsupials whilst *Tikusnema* from *X. myoides* also occurs in *R. argentiventer* from Indonesia. This is consistent with the scenario proposed by Watts & Aslin (1981) that *X. myoides* is a more recent arrival in Australia than *H. chrysogaster*. How the radiation of the Hydromyini is related to the murids of Southeast Asia is unknown (Watts & Kemper 1989). A survey of the parasites of the Papua New Guinean Hydromini is needed to determine which, if any, acuariid parasites are present. Conclusions may then be able to be drawn as to whether the appearance of *Tikusnema* in *R. argentiventer* and *X. myoides* has any significant bearing on murid relationships in South-east Asia, Papua New Guinea and Australia.

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MASTOPHORUS MURIS (NEMATODA: SPIROCERCIDAE) FROM THE MUSKY RAT-KANGAROO, HYPSIPRYMNODON MOSCHATUS

BRIEF COMMUNICATION

Summary

The Musky Rat-kangaroo, Hypsiprymnodon moschatus Ramsay, 1876, the smallest and most primitive of the macropodoids, occurs exclusively in the rainforest of northern Queensland.[1] It forages in the leaf litter of damp areas of the forest for fungi, fallen fruits and invertebrates. H. moschatus has a sacciform stomach intermediate in structure between the simple stomach of the phalangerids and the complex, compartmentalized stomachs of the potoroos and macropods.[2] Apparently the Musky Rat-kangaroo has not adapted to a diet with a high content of cellulose dependent on a fore-stomach fermentation chamber, but rather has retained an omnivorous diet of higher nutritive value.[1]

Transactions of the Royal Society of S. Aust., (1995), **119**(2), 95–96.

BRIEF COMMUNICATION

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A small colony of *H. moschatus* has been maintained, for research purposes, at the Queensland National Parks and Wildlife facilities, Pallarenda, Townsville. One of these animals died in its pen in 1994 and was subsequently made available for dissection. Twenty male and 17 female *Mastophorus muris* (Gmelin, 1790) were found in the stomach. The worms were fixed in 10% formalin, stored in 70% ethyl alcohol and then cleared in lactophenol for microscopic examination. The males measured up to 25 mm and the females 63 mm long. The worms appeared mature and healthy, the females being gravid. *Mastophorus muris* is a nematode from the family Spirocercidae, cosmopolitan in rodents of the families Microtidae and Muridae[3]. It has previously been recorded from rats, a "mouse" and cats in Australia.[4,5,6,7] A range of insect species including cockroaches has been found to be suitable intermediate hosts.[7]

Both cockroaches and rats are attracted to human food stores such as those kept to feed the captive animals at Pallarenda. If *M. muris* were established in an infective cycle, including cockroaches and rats living in close proximity to the pens, then such cockroaches when eaten by Musky Rat-kangaroos could be the link between normal rodent hosts and the accidental macropodoid host. Once ingested *M. muris* is apparently able to establish itself in the simple non-fermenting Rat-kangaroo stomach. The environment here could more closely resemble that of rodent stomach than that of the more complex fermentative stomach of macropods and potoroos.

This is the first record of *M. muris* occurring in a macropodoid marsupial. The only other records of *M. muris* from marsupials are from a phalangeroid, the Brushtail possum, *Trichosurus vulpecula* (Kerr, 1792). Worms from infected possums were first described from Queensland[9,10] and then reported from New South Wales[11,12] as *Protospirura marsupialis* Baylis, 1927. This material was subsequently reexamined and determined to be *M. muris*[13].

The diet of the Brushtail possum, including fruits and meat if offered,[2,14] is more similar to that of the Musky Rat-kangaroo than to that of other macropodoids. The non-fermenting environment within the possum's stomach is probably also similar to that of *H. moschatus*. Therefore it is likely that, as with *H. moschatus*, *T. vulpecula* could also become accidentally infected with *M. muris* from time to time.

I am indebted to P. M. Johnson for the opportunity to examine the Musky Rat-kangaroo. All the nematodes collected have been deposited in the Australian Helminthological Collection, South Australian Museum, Adelaide.

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OTOLITHS AS POTENTIAL INDICATORS OF AGE IN COMMON CARP, CYPRINUS CARPIO L. (CYPRINIDAE: TELEOSTEI)

BRIEF COMMUNICATION

Summary

The common carp, Cyprinus carpio L., was among the first species of fish for which techniques of age estimation were developed[1]. The annuli of scales (seasonal zones of slow growth) have been used as growth indicators in carp from Asia, Europe and North America[2-5], Opercular bones[6-8], fin rays[9] and spines[10,11] have proven useful, and the eye lens may also have value[12] although it is unreliable for older fish[13,14], Otoliths have been used successfully for the cyprinid Phoxinus phoxinus[15-20], but not for carp[11,21].

Transactions of the Royal Society of S. Aust., (1995), **119**(2), 97–98

BRIEF COMMUNICATION

OTOLITHS AS POTENTIAL INDICATORS OF AGE IN COMMON CARP, *CYPRINUS CARPIO* L. (CYPRINIDAE: TELEOSTEI)

The common carp, *Cyprinus carpio* L., was among the first species of fish for which techniques of age estimation were developed[1]. The annuli of scales (seasonal zones of slow growth) have been used as growth indicators in carp from Asia, Europe and North America[2–5]. Opercular bones[6–8], fin rays[9] and spines[10,11] have proven useful, and the eye lens may also have value[12] although it is unreliable for older fish[13,14]. Otoliths have been used successfully for the cyprinid *Phoxinus phoxinus*[15–20], but not for carp[11,21].

It is not clear whether the authors considered the full complement of otoliths in these studies. Carp, and teleost fish in general, have three pairs of utricular, saccular and lagenar otoliths, respectively named the lapilli, sagittae and asterisci. Given the peculiar morphology of the lower part of the inner ear of cyprinids (and other ostariophysan fish), the asterisci and the lapilli are much larger than the comparatively thin, elongate sagittae[22]. Lapilli have been used to distinguish daily growth increments in the fallfish *Semotilus corporalis*[23] and the rose bitterling *Rhodeus ocellatus ocellatus*[24], and a diurnal rhythm of calcium deposition has been reported in the asterisci of young goldfish *Carassius auratus*[25]. Unspecified otoliths have been used to age tench, *Tinca tinca* in Europe[26], but it is likely that these were asterisci or lapilli rather than sagittae.

In recent work on the ecology of carp we have been able consistently to recover well formed otoliths with patterns that appear to represent a chronological record. As validation is necessarily a protracted procedure we believe that a preliminary communication is warranted. This work has special significance in Australia because carp are an introduced species that is widely believed responsible for the degradation of wetlands throughout the Murray-Darling Basin[27]. If the impact of carp is to be evaluated the ability to estimate the ages of individual fish, providing for measurements of growth, recruitment and other population parameters, is crucial.

Samples for this study were obtained by gill-netting in backwaters of the River Murray at Swan Reach and at Gurra Gurra Lakes near Berri, from January to April 1994. Body weight (to within 0.1 g) and fork length (1 mm) were measured before recovering the otoliths and recording the weights of the asterisci (0.1 mg).

Annuli (translucent bands) were counted on the distal side of whole asterisci. When more than three annuli were present the earliest ones, particularly the first and second, were often obscured by calcium deposition. When more than 5–6 annuli were present the outermost ones were more easily discernible in transverse thin sections than in whole otoliths. The lapilli proved useful only when 2–3 annuli were present, and otherwise underestimated the counts from the asterisci. The sagittae showed no recognisable pattern. For these reasons, asterisci appear to be potentially more useful as indicators of age in this carp population.

In Figures 1a–c the asteriscus weight, fork length and body weight of 63 carp are plotted against the numbers of annuli on the asteriscus. Strong correlations are evident in each plot (respectively, Spearman rank correlation coefficient $r_S = 0.873$, $P < 0.001$; $r_S = 0.851$, $P < 0.001$, $r_S = 0.842$, $P < 0.001$), suggesting that the annuli are related to the size and weight of the fish and the weight of the asteriscus. The pattern of alternating translucent and opaque bands on the asterisci is comparable to that of other fish. The lapilli may provide complementary readings, especially where there are few annuli. We conclude that the asterisci, and to a lesser extent the lapilli, may provide a chronological record. Validation procedures are now underway to obtain data from fish of known age.

This paper is part of a PhD program being undertaken by the senior author. The Division of Fisheries, Department of Primary Industries, Adelaide provided a permit to net fish. We are grateful to Mr Ian Pettman, Institute of Freshwater Ecology, England, for library assistance, and to Mr John Pillar, Berri, for assistance in the field.

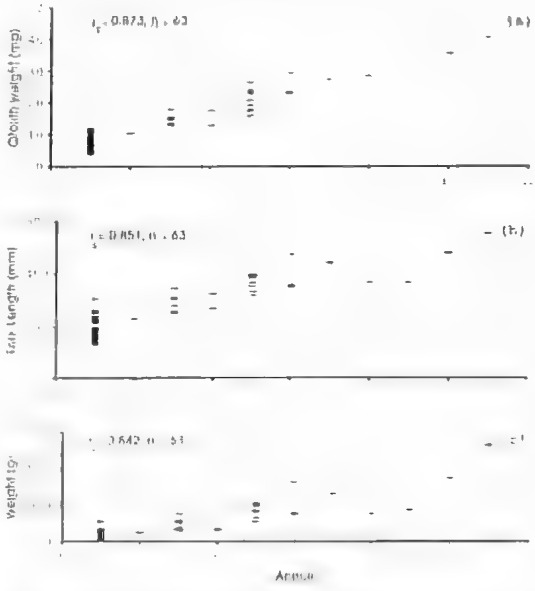

Fig. 1. Relationships between the numbers of annuli on the otoliths (asterisci) of carp from the River Murray, January–April 1994, (a) otolith weight (mg) (b) body size (Fork Length, mm), (c) body weight (g).

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VOL. 119, PART 3

COMMENTS ON SOME SOUTHERN AUSTRALIAN FORAMINIFERA AND DESCRIPTION OF THE NEW GENUS PARREDICTA

By Qianya Li & Brian McGowran**

Summary

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The distribution and relationship of 20 benthic foraminiferal genera from southern Australia are reviewed, and ranges of some stratigraphically useful species are revised. Among these, Crespinella, Crespinina, Hofkerina, Maslinella and Wadella are endemic to the Australian-New Zealand region. Others contain species which are either endemic or cosmopolitan forms or those migrating into the region at various times. The new genus Parredicta is described to include two endemic species, Planulina kalimnensis Parr (early Miocene-late Pliocene) and Valvulineria porifera Parr (Pleistocene-Recent).

Key Words: benthic foraminifera, Eocene, Oligocene, Miocene, southern Australia, Parredicta, new genus.

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by QIANYU LI* & BRIAN McGOWRAN*

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KEY WORDS: benthic foraminifera, Eocene, Oligocene, Miocene, southern Australia, *Parredicta*, new genus.

Introduction

Foraminifera are single-celled protozoans widely employed in stratigraphy and marine geology for age-dating and palaeoenvironmental interpretation. Howchin's (1889, 1891) work, which appeared in this *Transactions*, laid the foundation for surveying local foraminiferal assemblages. Foraminiferal studies in the early part of this century in Australia were cultivated particularly by W. J. Parr. Like his New Zealand counterpart H. J. Finlay, Parr published many papers on recent and fossil foraminifera and supplied numerous specimens for J. A. Cushman to describe (Glaessner 1950). Recent and modern students, including Carter (1958, 1964), Quilty (1974, 1977, 1981, 1982--mainly small benthics) and Chaproniere (1984--larger benthics), tend to emphasize the foraminiferal biostratigraphic application, as well as lineage classification. Systematic treatments of southern Australian foraminifera, however, have not yet reached the standard of Hornibrook *et al.* (1989) from New Zealand. Local marine sequences have been correlated with standard biostratigraphy (e.g. McGowran 1979), but the correlation lacks cross-reference to the geomagnetic record, and the range of many species is not well defined. Confusion over synonyms adds difficulties to any attempt for systematic compilations.

As a prelude to such a compilation, this paper summarizes current knowledge of some important Cenozoic taxa based on material from several southern Australian basins. The records of these taxa, as reported elsewhere (Loeblich & Tappan 1987), are revised. The new genus *Parredicta* is proposed to accommodate *Valvulineria porifera* Parr and *Planulina kalimnensis* Parr.

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The Material

The late Eocene to early Oligocene samples were taken mainly from two localities: Maslin Bay on the southwest coast of Adelaide, South Australia and Browns Creek, Aire District in Victoria (Fig. 1). The Maslin Bay sequence has been described and discussed in great detail by McGowran & Beecroft (1986) and McGowran (1990), and both sections by McGowran *et al.* (1992). The Lakes Entrance oil shaft section from Gippsland Basin spanning the late Oligocene-late Miocene was the focus of our study of faunal overturn and ecostratigraphy (McGowran & Li 1993, 1995; Li & McGowran 1995), and thus forms part of the material here. We also examined 29 samples from the early middle Miocene Morgan-Cadell section from the Murray Basin (Ludbrook 1961). As well, we refer to the material during a recent biofacies study of dredged samples from the Lacepede Shelf (Li *et al.* 1995). Other material includes random samples from Castle Cove (near Browns Creek) and WMC core 703 in Kingston, South Australia. Relevant type specimens deposited in the South Australian Museum and in the Department of Geology & Geophysics, The University of Adelaide, were also examined. Several scanning photographs, originally taken by J. M. Lindsay on material from the South Australian Department of Mines and Energy, are also reproduced.

Localities are shown in Fig. 1, and ranges of taxa discussed in Fig. 2. The generic references to these taxa refer to Loeblich & Tappan (1987). Appendix 1 alphabetically lists all genera and species mentioned in this report.

Systematic Remarks

Order Foraminiferida Eichwald, 1830
Suborder Rotaliina Delage & Hérouard, 1896
Family Almaenidae Myatlyuk, 1959
Genus *Almaena* Samoylova, 1940

Synonymy and Type species: see Loeblich & Tappan 1987, p. 622.

Remarks

In their compilation of *Almaena*, Loeblich & Tappan (1987) apparently overlooked its record in southern Australia. From the Gippsland Basin, Carter (1964) described *Almaena gippslandica* (Fig. 4, 1a, b), a form undoubtedly belonging in this genus.

Carter (1964) correctly indicated that *Almaena gippslandica* was restricted to the region, as it has to date never been reported from any other localities. It ranges from 347 m - 320 m in the Lakes Entrance section, in an interval equivalent to planktonic foraminiferal Subzone N4b, earliest Miocene (Li & McGowran 1995).

It is not known whether *A. gippslandica* is synonymous with any European taxon or whether it represents a migratory species from Paratethys where the genus first evolved in the later Eocene (Loeblich & Tappan 1987)

Family Asterigerinatidae Reiss, 1963
Genus *Asterigerinella* Bandy, 1949

Synonymy and Type species: see Loeblich & Tappan 1987, p. 606.

Remarks

According to Loeblich & Tappan (1987), this genus differs from the similarly stellate *Asterigerina* d'Orbigny in having a flattened lenticular test and a high aperture. The wall is papillate on both sides of the test, in contrast to the smooth surface in *Asterigerina*. Loeblich & Tappan (1987) found the type species *A. gallowayi* from Alabama to be the only record.

Howchin's (1891) taxon, *Truncatulina margaritifera* var. *adelaidensis*, bears every feature of *A. gallowayi* and must be a form of *Asterigerinella*. Lindsay (1969, pl. 2, fig. 2, 4) illustrated a topotype of *A. adelaidensis* and Lindsay (1985, p. 203, as *Asterigerina*) indicated that the species ranged from the top of South Maslin

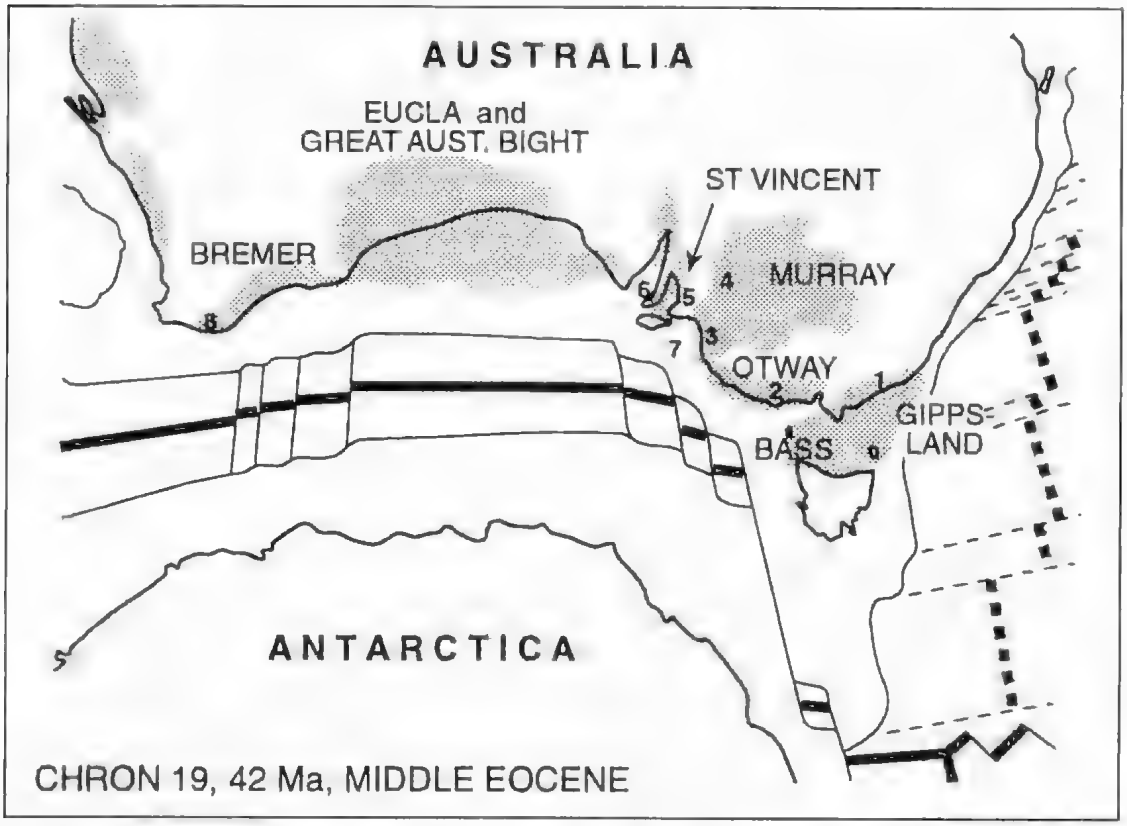

Fig. 1. Southern Australia in the later middle Eocene, showing major Tertiary sedimentary basins (adapted from Falvey & Mutter 1981). It was not until this time that sedimentation became widespread along the southern margin. Numbers 1-7 are section localities: 1. Lakes Entrance, Victoria. 2. Browns Creek and Castle Cove, Victoria. 3. WMC core 703, Kingston, South Australia. 4. Morgan and Cadell, Murray Basin, South Australia. 5. Maslin Bay (Tortachilla, Blanche Point), South Australia. 6. Yorke Peninsula (Port Vincent), South Australia. 7. Lacepede Shelf, South Australia. 8. Nanarup, Western Australia.

Sand to Perkana Member of the Blanche Point Formation, Zones Pl3-Pl5 in modern biostratigraphical correlation (McGowran *et al.* 1992). This view is confirmed again here in our recent observations.

As illustrated in Fig. 4, 2, 3, *A. adelaidensis* can be differentiated from the slit-apertured *A. gallowayi* by its almost circular aperture.

Family Bronnimanniidae Loeblich & Tappan, 1984
Genus *Bronnimannia* Bermúdez, 1952

Synonymy and Type species: see Loeblich & Tappan 1987, p. 563.

Remarks

Forms of *Bronnimannia* are rare in southern Australia, although the closely related *Discorbinella* and *Planulina* have been widely reported (Parr 1950; Carter 1964; Quilty 1977). Our record of *B. haliotis* from Cadell Marl section (Zones top N8 to lower N9, early middle Miocene) thus confirms the occurence of the genus in the region. Quilty (1994, pers. comm.) recently informed us that he has found similar forms in the Swan River estuary, Western Australia.

Bronnimannia haliotis (Fig. 4, 4a, b) is similar to the type species *B. palmerae* in the auricular biconcave test. Unlike the latter taxon, however, the South Australian species is much flatter and lacks a distinct marginal keel. The strongly concave, evolute (ventral) side is coarsely perforate, with limbate, imperforate sutures. All these suggest that the illustrated form is a distinct, perhaps endemic, species.

Family Cibicididae Cushman, 1927
Genus *Cibicides* de Montfort, 1808

Synonymy and Type species: see Loeblich & Tappan 1987, p. 582.

Remarks

The cibicidids are one of the most abundant and diverse foraminiferal groups found in many parts of southern Australia. This group includes trochospiral forms with an extraumbilical aperture which may extend around the periphery and onto the spiral (dorsal) side. With these features, *Cibicides*, *Cibicidoides* and *Heterolepa* may be lumped as cibicidids in a classical study of biofacies (e.g. Hornibrook *et al.* 1989). Although Loeblich & Tappan (1987) demonstrated different hyaline walls between *Cibicides* and *Cibicidoides* and classified them in two different superfamilies, these two genera are always associated in a faunal community and some of their species show transitional characters, particularly in the flat to convex dorsal side.

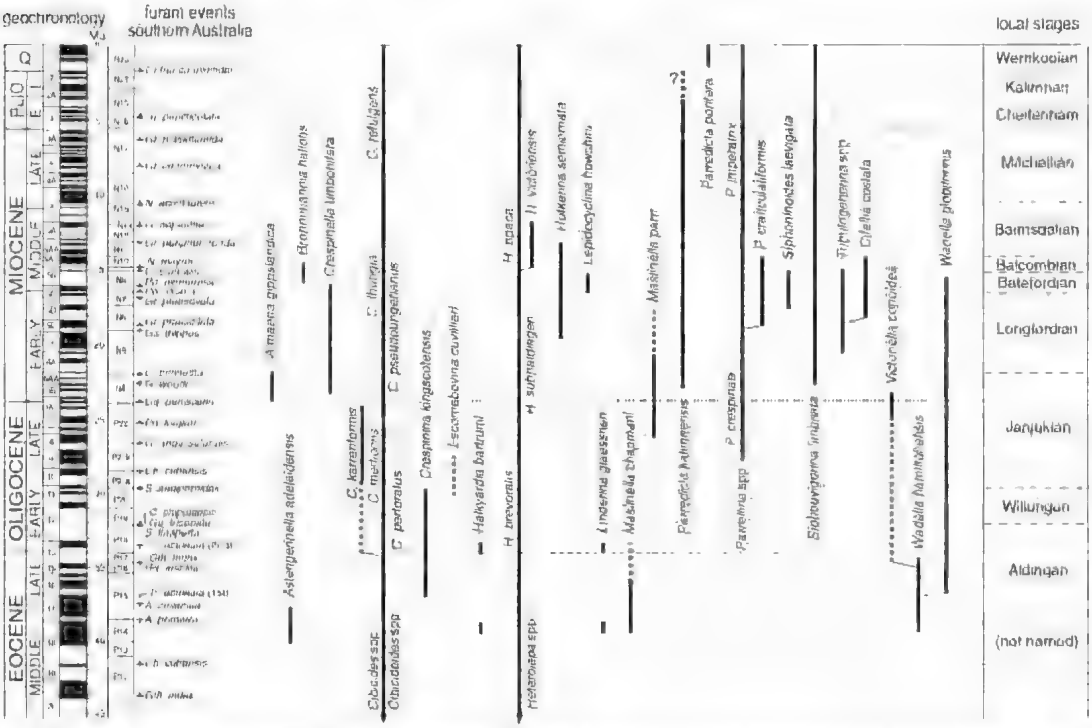

Fig. 2. Ranges of the taxa discussed. Geochronology after Cande & Kent (1992) and N/P zones after Berggren *et al.* (1985a, b). Correlation of local planktonic foraminiferal data and regional stages follows McGowran *et al.* (1971), Heath & McGowran (1984), and McGowran & Li (1993, 1994).

Quilty (1982, p. 10) listed over 20 cibicidid species known from the Tertiary of southern Australian and New Zealand. Together with the biconvex allied *Cibicidoides*, the planoconvex genus *Cibicides* averages 20% - 50% of total fauna in most samples. Typical cibicidid forms include *Cibicides ihungia* (Fig. 4, 7, 8), *C. mediocris* (Fig. 4, 9, 10), *C. vortex* (Fig. 4, 6a, b), *Cibicidoides perforatus* (Fig. 4, 11) and *C. pseudoungerianus* (= *Cibicides neoperforatus*) (Fig. 4, 12, 13). The evolution of *C. pseudoungerianus* from *C. perforatus* was in the late Eocene, by a reduction of coarse perforations from both sides (on *C. perforatus*) and restriction to the spiral side of the test. The stratigraphically most useful species is *C. karreriformis* Hornibrook, occurring in the Oligocene (Fig. 2). Other previously described species, such as *C. subhaidingeri* and *C. opacus*, are now placed in the genus *Heterolepa* (see below).

Three cibicidids characterising the modern biofacies on Lacepede Shelf, South Australia, are *Cibicides refulgens* (Fig. 4, 5), *C. mediocris* and *Cibicidoides pseudoungerianus* (Li *et al.* 1995).

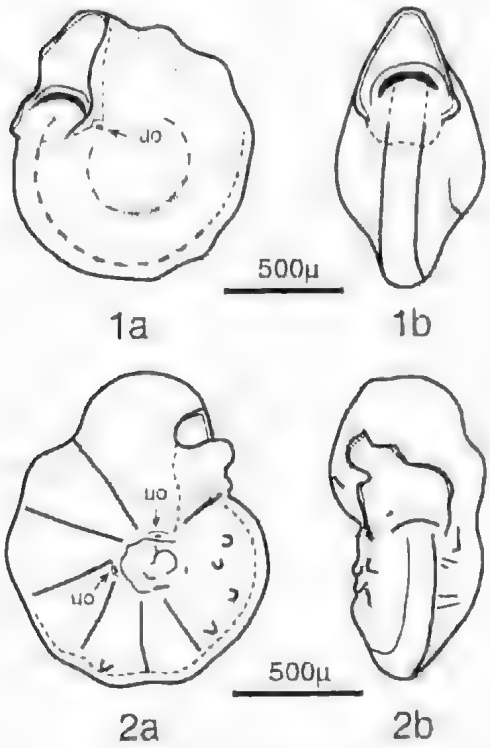

Fig. 3. 1a, b. *Crespinella umbonifera*: sketches of the holotype of *?Operculina umbonifera* Howchin & Parr (1938) (see also the scanning micrographs in Fig. 4, nos. 14a, b). 2a, b *Maslinella chapmani* Glaessner & Wade (1959): sketches of the holotype. Both types are deposited in the South Australian Museum. Note that the final chamber on both tests is missing, but umbilical openings (uo) are present.

Family Eponididae Hofker, 1951
Genus *Crespinella* Parr, 1942

Synonymy and Type species: see Loeblich & Tappan 1987, p. 579.

Remarks

Parr (1942) erected the early Miocene taxon *?Operculina umbonifera* Howchin & Parr as the type species of his genus *Crespinella*, separating this simple form from similarly planispiral but internally complex *Operculina*.

Crespinella was monospecific until Quilty (1980) added to it another species, *C. parri*, with a low trochospiral (other than planispiral) coiling. The overall morphological similarity between *C. umbonifera* and *C. parri* led Quilty (1980) to imply that both *C. parri* and *C. umbonifera* are phylogenetically related, with *C. parri* being the predecessor. Loeblich & Tappan (1987), however, rejected this statement on the basis of the distinct trochospiral coiling and supplementary sutural openings in Quilty's species. Such confusion over the generic status of *C. parri* needs to be clarified.

Li has inspected the holotype of *C. umbonifera*, which was made available from the South Australian Museum, and found that it also possesses an opening on the umbilical side (Fig. 3, 1a, b; Fig. 4, 14a, b). It is an incomplete specimen with the final chamber missing, and a small opening can be observed at the base of the relic part of the missing chamber, close to the margin of the pronounced umbilical boss. No umbilical openings, however, were found related to any previous chambers. We thus conclude that the species *C. parri* is correctly assigned to *Crespinella*, a genus having species with a very low trochospiral to planispiral coiling and one or more supplementary openings on the umbilical side.

Genus *Hofkerina* Chapman & Parr, 1931

Synonymy and Type species: see Loeblich & Tappan 1987, p. 551.

Remarks

Geographically *Hofkerina semiornata* (Fig. 5, 11, 12) is similar to *Almaena gippslandica*, as both are confined to the southeastern corner of southern continental margin (Carter 1958, 1964). *Almaena gippslandica* is an earliest Miocene form and apparently has affinities with species from Paratethys (see above), whereas *Hofkerina semiornata* seems to be entirely endemic to the region with a range from the early Miocene to early middle Miocene.

It is noteworthy that both *Hofkerina semiornata* and *Crespinella umbonifera*, above, have a similarly thick wall, which mimics the wall in the Eocene *Maslinella chapmani* (see below). Unlike *H. semiornata*, however, *C. umbonifera* and *M. chapmani* have also been recorded from South Australia and Western Australia (Quilty 1980, 1981). It is not clear whether the thick wall in these endemic taxa signals a high $CaCO_3$ buildup in local waters during the warming phases of the later Eocene and early-middle Miocene.

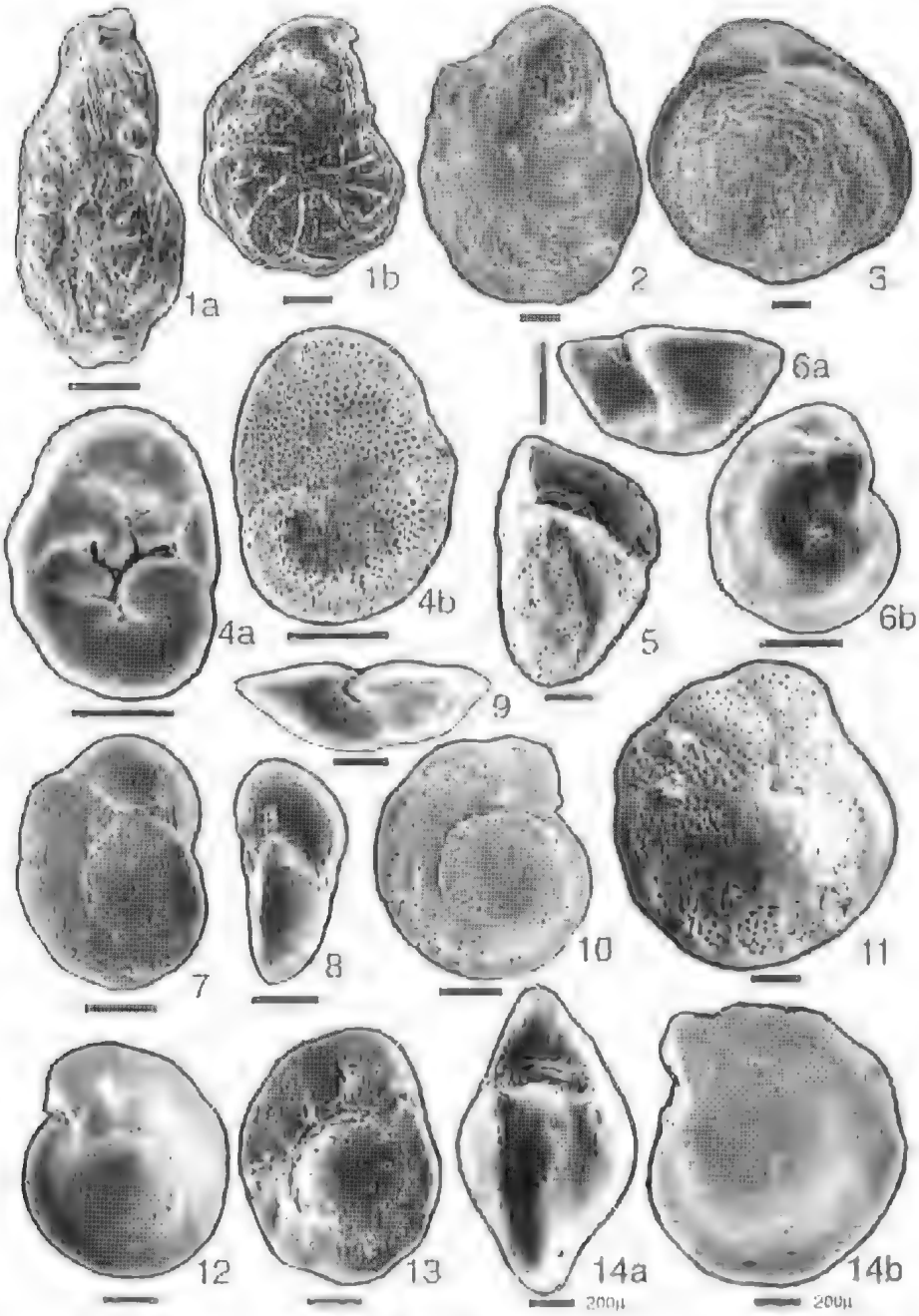

Fig. 4. Scale bar = 100 µm, unless otherwise indicated. 1a, b. *Almaena gippslandica* Carter: two views of a single specimen, latest Oligocene, Lakes Entrance, Sample 1156. 2, 3. *Asterigerinella adelaidensis* (Howchin): two specimens, later middle Eocene, Tortachilla Limestone, Maslin Bay, Sample AB-Tor. 4a, b. *Bromimannia haliotis* (Heron-Allen & Earland): single specimen from the early middle Miocene, Cadell Marl section, Sample C9. 5. *Cibicides refulgens* de Montfort: Recent, Lacepede Shelf, Sample 89-1, water depth 171 m. 6a, b. *Cibicides vortex* Dorreen: single specimen, early Miocene, Lakes Entrance, Sample 808. 7, 8. *Cibicides ihunyia* Finlay: two specimens, early Miocene, Lakes Entrance, Samples 992 and 732. 9, 10. *Cibicides meduceris* Finlay: two specimens, late Oligocene and early Miocene, Lakes Entrance, Samples 828 and 1196. 11. *Cibicidoides perforatus* (Karrer): late Eocene, Blanche Point Formation, Maslin Bay, Sample A3-091. 12, 13. *Cibicidoides pseudoungerianus* (Cushman): two specimens, late Oligocene and early Miocene, Lakes Entrance, Samples 1196 and 956. 14a, b. *Crespinella umbonifera*: two views of the uncoated holotype of *?Operculina umbonifera* Howchin & Parr, using a Philips XL20 scanning electron microscope at the University of Adelaide (CEMMSA).

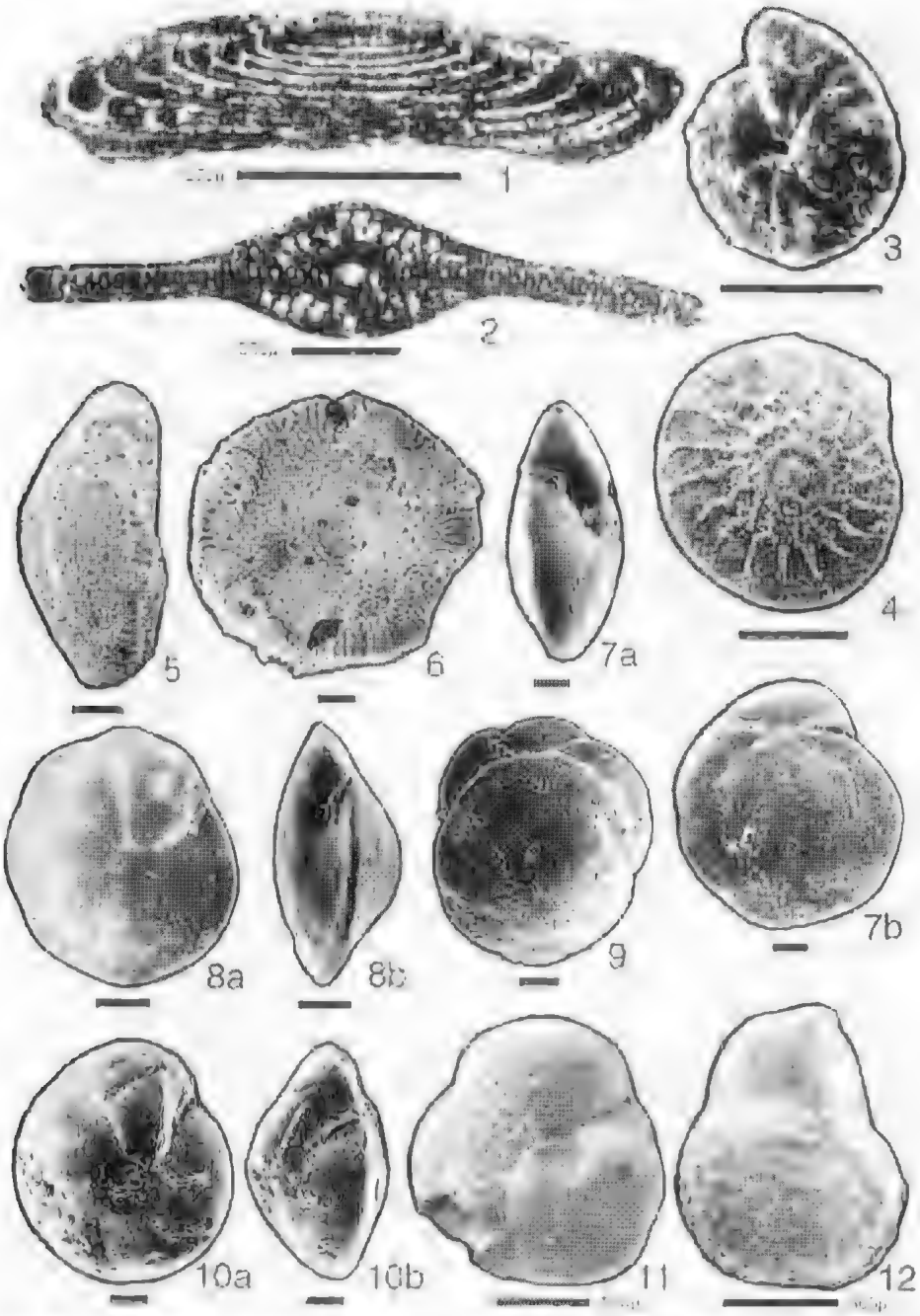

Fig. 5. Scale bar = 100 μm, unless otherwise indicated. 1. *Crespinina kingscotensis* Wade: axial section, early Oligocene, Port Vincent Limestone, Yorke Peninsula, Sample BS1. 2. *Lepidocyclina howchini* Chapman & Crespin: axial section, early middle Miocene, lower Morgan Limestone, Mannum, Sample Li/93-1. 3, 4. *Escornebovina cuvillieri* (Poignant): two specimens, earliest Oligocene, SADME bore A40, western Murray Basin (3), Ff 805, and SADME South Parklands Bore, Adelaide (4), Ff 808, both from Lindsay (1981, pl. 44, figs. 1, 3). Note that Lindsay[1], 1994 (pers. comm.) considered the form in no. 4 not a typical specimen of that species. 5, 6. *Halkyardia bartrumi* Parr: two specimens, late Eocene, Castle Cove, Sample RJEJ 19. 7a, b. *Heterolepa opaca* (Carter): single specimen, early Miocene, Lakes Entrance, Sample 724. 8-9. *Heterolepa brevoralis* (Carter): two specimens, early Miocene, Lakes Entrance, Samples 788 (8a, b) and 984 (9). 10a, b. *Heterolepa subhaidingeri* (Parr): single specimen, early Miocene, Lakes Entrance, Sample 852. 11, 12. *Hofkerina semiornata* (Howchin): two specimens, earliest Miocene, WMC 703, Samples 45.35 m and 45.65 m

Family Chapmaninidae Thalmann, 1938
Genus *Crespinina* Wade, 1955

Synonymy and Type species: see Loeblich & Tappan 1987, p. 668.

Remarks

This genus, together with its only species *C. kingscotensis* (Fig. 5, 1), apparently represents one of the numerous taxa endemic to southern Australia. It has been recorded in South Australia (Wade 1955; Ludbrook 1961), Victoria (Carter 1958) and Western Australia (Quilty 1981). Quilty (1981) also noted that tests of *C. kingscotensis* became larger and more robust from east to west, indicating a warmer temperature towards the western part of the southern continental margin.

Crespinina kingscotensis occurs mainly in the later middle Eocene to early Oligocene (Wade 1955). In the Port Vincent Limestone from Yorke Peninsula (Fig 1), it is associated with some planktonic foraminifera such as *Guembelitria*, an early Oligocene marker in local biostratigraphy (McGowran & Beecroft 1985), and its last appearance precedes the first appearance of *Amphistegina*. The latter datum in the region was within the late Oligocene (Lindsay 1985).

Family Gavelinellidae Hofker, 1956
Genus *Escornebovina* Butt, 1966

Synonymy and Type species: see Loeblich & Tappan 1987, p. 633.

Remarks

Specimens referable to *E. cuvillieri* were found in the basal Ettrick Formation (Oligocene) from the western Murray Basin and eastern St Vincent Basin (Lindsay 1981[1]), but this record has never been made public. These specimens were compared with the near-topotypes of *E. cuvillieri* from Escornebéou, France, supplied to Lindsay by Professor C. W. Drooger (Utrecht). This record thus extends the geographic distribution of this taxon from Paratethys to southern Australia.

Two of Lindsay's specimens are shown in Fig. 5, 3, 4.

Family Cymbaloporidae Cushman, 1927
Genus *Halkyardia* Heron-Allen & Earland, 1918

Synonymy and Type species: see Loeblich & Tappan 1987, p. 593.

Remarks

The conical *Halkyardia bartrumi* (Fig. 5, 5a, b) has been widely recorded in New Zealand from where it was originally named (Hornibrook *et al.* 1989). In southern Australia, Ludbrook (1961, as *Halkyardia* sp.) found similar forms in the western Murray Basin, and Quilty (1981) recorded it in the Nanarup Limestone near Albany, Western Australia (Fig. 1). On the eastern margin of the St Vincent Basin, this species makes two brief appearances, in the Tortachilla Limestone and the basal Port Willunga Formation (Lindsay 1967). McGowran *et al.* (1992) recently correlated these two intervals as from top P14 to early P15 in the later middle Eocene, and upper P18 in the early Oligocene respectively.

No record of this taxon has been reported to date from the eastern corner of southern Australia.

Family Heterolepidae Gonzáles-Donoso, 1969
Genus *Heterolepa* Franzenau, 1884

Synonymy and Type species: see Loeblich & Tappan 1987, p. 632.

Remarks

Many species of *Heterolepa* were previously recorded as *Cibicides* in southern Australia. The genus *Heterolepa* differs from the radially walled *Cibicides* in having a granular wall and an aperture which does not extend far onto the spiral side (Loeblich & Tappan 1987). *Cibicides brevoralis* (Fig. 5, 8-9), *C. opacus* (Fig. 5, 7a, b) and *C. subhaidingeri* (Fig. 5, 10a, b) all appear to have these features, and are accordingly transferred to the genus *Heterolepa*.

Also included in this genus is *Cibicides victoriensis* (see also Lindsay 1969, 1981[1]), a species confined to the middle Miocene, or Zones N9-N13 equivalents. Morphologically, *H. victoriensis* is similar to both *H. brevoralis* and *H. subhaidingeri*, but differs from the latter two in the strongly limbate sutures on the spiral side.

At the Morgan-Cadell section, western Murray Basin, *Heterolepa* decreases from the lower Morgan Limestone, disappears in the Cadell Marl, and reappears in the upper Morgan Limestone. The Cadell Marl is composed mainly of bioskeletons including abundant miliolid and discorbid foraminifera, and represents a restricted, but highly productive, environment. The marly sequence is dated at about 15 Ma, in the later part of the Miocene climatic optimum (Li & McGowran 1995). Its absence from the Cadell Marl indicates that *Heterolepa* may be an open marine genus only, in contrast to the ubiquitous *Cibicides*.

Family Lepidocyclinidae Scheffen, 1932
Genus *Lepidocyclina* Gümbel, 1870

Synonymy and Type species: see Loeblich & Tappan 1987, p. 614.

Remarks

The last occurrence of *Lepidocyclina sensu lato* was

[1] LINDSAY, J. M. (1981) Tertiary Stratigraphy and Foraminifera of the Adelaide City Area, St Vincent Basin, South Australia. Unpubl. M.Sc. Thesis, The University of Adelaide.

in the middle Miocene (Zone N9), if not the late Miocene or early Pliocene (Adams 1992). This has been apparently misquoted to be in the Aquitanian (N4, earliest Miocene) by Loeblich & Tappan (1987).

The local representative of this genus is *L. howchini* (Fig. 5, 2), a species widely reported from various localities in southern Australia (Ludbrook 1961; Lindsay 1969; Lindsay & Giles 1973; McGowran 1979; Quilty 1982; Chapponiere 1984; Lindsay 1985). Associated with many other larger forms, it was confined to the latest early Miocene to earliest middle Miocene, or Zones N8 and N9 equivalents. Its occurrence in the region has been hailed as a signal of the Miocene climatic optimum (McGowran 1979; Frakes *et al.* 1987; McGowran & Li 1993, 1995).

Family Linderinidae Loeblich & Tappan, 1984
Genus *Linderina* Schlumberger, 1893

Synonymy and Type species: see Loeblich & Tappan 1987, p. 645.

Remarks

The species *Linderina glaessneri* is large, discoid and internally complex with numerous chamberlets (Fig. 6, 1). Like *Halkyardia bartrumi*, above, it was restricted to the central and western parts of the region and has never been recorded from either Gippsland or Bass basins in the southeastern corner. The stratigraphical occurrence of *Linderina glaessneri* is also similar to that of *H. bartrumi* in two short intervals: later middle Eocene (Zones top P14-lower P15) and earliest Oligocene (upper P18). This record thus extends the range of that genus into the early Oligocene from the originally middle and late Eocene (Quilty 1981).

Family Elphidiidae Galloway, 1933
Genus *Parrellina* Thalmann, 1951

Synonymy and Type species: see Loeblich & Tappan 1987, p. 677.

Remarks

Wade (1957) emended *Parrellina*, a planispiral elphidiid which appears to have been restricted to southern Australian waters during its early evolutionary history. It first appeared in the middle Oligocene, Zone P21 equivalents, about 15 Ma after the evolution of its trochospiral ancestor *Notorotalia* Finlay.

The New Zealand taxon, *Discorotalia*, is similar to *Parrellina* in many morphological aspects except the distinct evolute spiral side, and both are believed to have evolved from the trochospiral *Notorotalia* (Eocene-Recent) in the late Oligocene. It is difficult, however, to separate *Parrellina* from *Discorotalia*, as some of our Oligocene-early Miocene specimens of *Parrellina crespinae* and *P.* cf. *imperatrix* tend to be also low-trochospiral (Fig. 6, 5-6). Typical planispiral *P. imperatrix* (Fig. 6, 7) seems to have occurred only from the early Miocene to Recent. Modern specimens of *P. imperatrix* from offshore southern Australia may grow a test >1 mm in diameter, while its allied form *P. verriculata* is much smaller and without peripheral spines. A large, typically planispiral species existing in the early to middle Miocene (N6-N10) is *P. craticulatiformis* (Fig. 6, 8).

Family Siphonidae Cushman, 1927
Genus *Siphoninoides* Cushman, 1927

Synonymy and Type species: see Loeblich & Tappan 1987, p. 572.

Remarks

A smooth form described by Howchin (1889) as *Truncatulina echinata* var. *laevigata* is apparently a *Siphoninoides* (Fig. 6, 4). Whether the smooth wall has been subject to the effect of cold waters is not known. This consistent feature guarantees that the taxon is a distinct species. The generic description of *Siphoninoides*, as in Loeblich & Tappan (1987), should be revised to embrace this feature.

We found numerous specimens of *S. laevigata* in samples from the Cadell Marl section, western Murray Basin (Fig. 1). The age of these samples is within Zones top N8 to N9 equivalents, early middle Miocene. Quilty (1994, pers. comm.) indicated that a similar form exists in the modern Swan River estuary, Western Australia.

Family Uvigerinidae Haeckel, 1894
Genus *Siphouvigerina* Parr, 1950

Synonymy and Type species: see Loeblich & Tappan 1987, p. 525.

Remarks

This genus was supposed to occur only in the Holocene (Loeblich & Tappan 1987). However, we recently discovered forms similar to the type species *S. fimbriata* from the Lakes Entrance section, Gippsland Basin, in a level correlated to the earliest Miocene. One of the specimens is illustrated in Fig. 6, 9). Our record thus extends the range of this genus down to the early Miocene, although the form was found only sporadically.

Revets (1993) recently found the type specimen of *S. fimbriata* to be biserial throughout, a finding contrasting the conventional definition of the genus (e.g. Parr 1950; Loeblich & Tappan 1987). However, many uvigerinid and angulogerinid forms are triserial initially and change to biserial at any later stage. The triserial part of the test would be difficult to define if early chambers are loosely coiled, a case most likely existing in *S. fimbriata*.

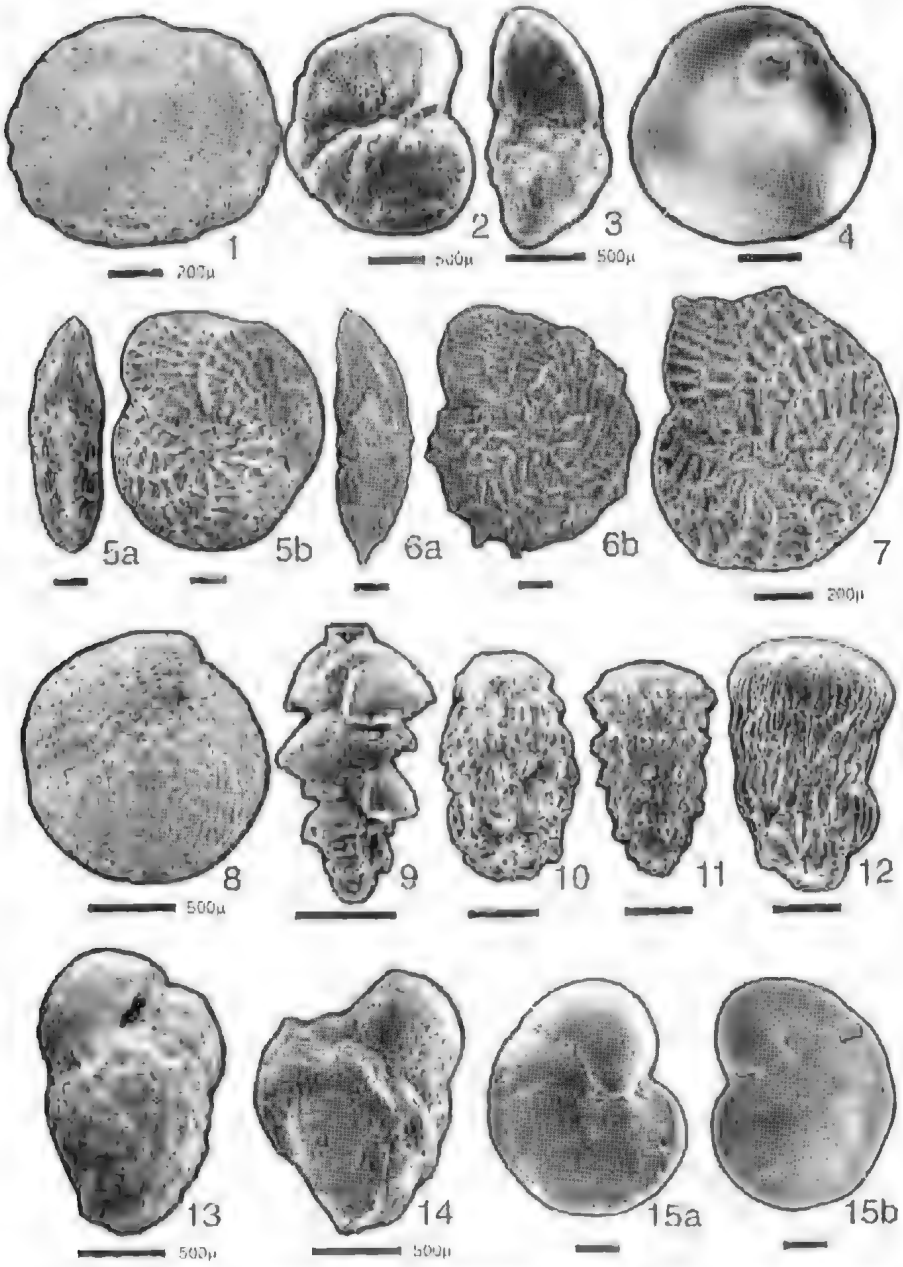

Fig. 6. Scale bar = 100 µm, unless otherwise indicated. 1. *Linderina glaessneri* Quilty; late Eocene, Castle Cove, Sample RJFJ 19. 2, 3. *Maslinella chapmani* Glaessner & Wade, two specimens, late Eocene, Adelaide area (Children's Hospital), Sample 19.2-19.5 m, Ff 955 and Ff 956, both from Lindsay (1981, pl. 48, figs. 1, 4). 4. *Siphoninoides laevigatus* (Howchin); later early Miocene, Lower Morgan Limestone, Sample LM2. 5a, b. *Parrellina crespinae* Cushman; single specimen, earliest Miocene, Lakes Entrance, Sample 1140. 6a, b. *Parrellina* cf. *imperatrix* (Brady); single specimen, early Miocene, Lakes Entrance, Sample 992. 7. *Parrellina imperatrix* (Brady); Recent, Lacepede Shelf, Sample 89 60, water depth 82 m. 8. *Parrellina craticulaniformis* Wade; later early Miocene, Lower Morgan Limestone, Sample LM2. 9. *Siphogenerina fimbriata* (Sidebottom); earliest Miocene, Lakes Entrance, Sample 1140. 10. *Tubulogenerina ferax* (Heron-Allen & Earland); later early Miocene, Lakes Entrance, Sample 700. 11. *Tubulogenerina moorabooleensis* Cushman; later early Miocene, Lakes Entrance, Sample 868. 12. *Cifellia costata* (Heron-Allen & Earland); later early Miocene, Lakes Entrance, Sample 708. 13. *Victorella conoidea* (Rutten); earliest Miocene, WMC 703, Sample 45.65 m. 14. *Wadella hamiltonensis* (Glaessner & Wade); late Eocene, Blanche Point Formation, Maslin Bay, Sample 099. 15a, b. *Parrecteta kalimnensis* (Parr); single specimen, later middle Miocene, Lakes Entrance, Sample 416.

Family Siphogenerinoididae Saidova, 1981
Genus *Tubulogenerina* Cushman, 1927

Synonymy and Type species: see Loeblich & Tappan 1987, p. 520.

Remarks

Gibson (1987, 1989; Gibson *et al.* 1991) conducted a series of studies on the evolution and distribution of *Tubulogenerina* and related taxa. Two main conclusions from his studies are: (1) this genus ranged from early Eocene to Pliocene, with Europe being the site of its first evolution, and (2) species seem to have migrated westward from Europe, through the Atlantic, to Pacific and Indian Oceans. According to Gibson (1989), mid-latitude Miocene species were largely confined to the later early Miocene to early middle Miocene, or Zones N6 to N8 equivalents.

Quilty (1977) reported *T. mooraboolensis* from the early Miocene in Tasmania. In the Lakes Entrance oil shaft, we found three tubulogenerinines (Fig. 6, 10-12): *T. fenix*, *T. mooraboolensis* and *Cifellia costata*. The combined range of these species is from 263 m – 157 m in the section, which is mid-N5 to early N10 in our correlation (McGowran & Li 1993, 1995).

We follow Gibson (1989) in considering *C. costata* a tubulogenerinid without a toothplate. Revets (1991), however, classified *Cifellia* and *Tubulogenerina* into two different superfamilies, on the absence and occurrence of toothplates in these two genera respectively. Whether the toothplate ever exists in the early part of *C. costata* is not known, and little evidence has been found to resolve problems such as the development and reduction or function of foraminiferal toothplates (Revets 1993).

Family Victoriellidae Chapman & Crespin, 1930
Genus *Maslinella* Glaessner & Wade, 1959

Synonymy and Type species: see Loeblich & Tappan 1987, p. 596.

Remarks

Similar to several other endemic taxa, this genus is also monospecific. *Maslinella chapmani* (Fig. 6, 2, 3) is a large but internally simple form ranging from the later middle Eocene to earliest Oligocene. Although not mentioned in the original description, sutural openings occur on the umbilical side of some specimens (Fig. 6, 2), possibly resulting from relic apertural extensions. This feature can be seen even in the holotype, sketched in Fig. 3 (compare Glaessner & Wade 1959, pl. 1, fig. 7).

Crespinella parri Quilty, above, is morphologically similar to *Maslinella chapmani* at least in the following: (1) a large, low trochospiral test which tends to be planispiral in the final stage, (2) a distinct peripheral keel, (3) sutural openings on the umbilical side, and (4) a thick, laminated wall, though perforations on *M. chapmani* were much coarser. All these indicate that *C. parri* is morphologically, if not phylogenetically, closely related to *Maslinella*. The occurrence of *C. parri* in the late Oligocene is cryptogenic, and pending studies of its relationship with *M. chapmani* are necessary.

Genus *Victoriella* Chapman & Crespin, 1930

Synonymy and Type species: see Loeblich & Tappan 1987, p. 596.

Remarks

Glaessner & Wade (1959) emended this genus and discussed its affinities. They found the type species *Victoriella plecte* to be a junior synonym of *Carpenteria conoidea*, now *V. conoidea* (Rutten) (Fig. 6, 13). The total range of *V. conoidea* in southern Australia is from the latest Eocene (P17) to earliest Miocene (N4). Ludbrook (1971, p. 64) noted the transition of *V. conoidea* from *Carpenteria hamiltonensis* (now *Wadella hamiltonensis*, see below), in the earliest Oligocene *Globigerina angiporoides angiporoides* Zone.

The Eocene-Oligocene record of that species, however, is relatively rare. Only in the latest Oligocene and earliest Miocene did *V. conoidea* become common and southern Australia-wide, as well as from northeastern Australia (Quilty 1993). It is conspicuous in the carbonate-chert association of the Gambier Limestone in the Otway Basin (G. Moss, 1994, pers. comm.).

Genus *Wadella* Srinivasan, 1966

Synonymy and Type species: see Loeblich & Tappan 1987, p. 596.

Remarks

The genera *Wadella* and *Victoriella* are similarly large and high trochospiral. However, *Wadella hamiltonensis* (Fig. 6, 14) can be distinguished from *V. conoidea* by its smooth test lacking pillars and less regular coiling.

In the later middle to late Eocene, *Wadella hamiltonensis* was one of many large species endemic to southern Australia and New Zealand. Prior to the late Eocene, in southern Australia, *Wadella hamiltonensis* achieved a wider distribution than *V. conoidea* (Cooper 1979; Quilty 1981; Lindsay 1985). In the Maslin Bay section, *W. hamiltonensis* was found in the Tortachilla Limestone and basal Blanche Point Formation, in an interval equivalent to Zones upper P14 to P15 (McGowran *et al.* 1992). *Wadella globiformis* also evolved in the late Eocene, and ranged into the early Miocene. Unlike *W. hamiltonensis*, *W. globiformis* developed a low trochospiral test and globular chambers.

Family Bagginidae Cushman, 1927
Genus ***Parredicta*** gen. nov
(FIG. 7)

Type species: Valvulineria porifera Parr, 1950

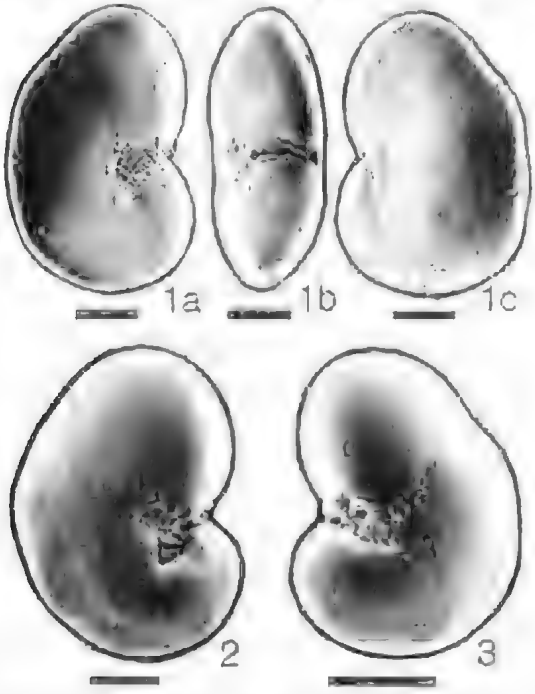

Fig. 7. *Parredicta porifera* (Parr). Scale bar = 200 μm. 1a-c. Scanning micrographs of the uncoated holotype of *Valvulineria porifera* Parr. 2, 3. Two specimens from Lacepede Shelf, Samples 89-3 and 89-1, in water depths 123 m (2) and 171 m (3) respectively.

Etymology

This genus is named in honour of W. J. Parr, who was one of the most influential and prolific foraminiferal students in southern Australia in the early part of this century, and who originally described the species on which this new genus is based; *edictum* (Latin) = proclamation or decree.

Description

Test medium to large, low trochospiral, biconvex; chambers high, enlarging regularly, more than 6 in the final whorl; 1½ to 2½ whorls in adult tests; surface smooth; sutures radiate to strongly curved, depressed or flush on ventral side, flush and limbate on the dorsal (spiral) side; umbilicus small; depressed or closed with shell material, but without a distinct umbilical boss; periphery narrowly rounded to weakly keeled; wall calcareous hyaline, distinctly perforate except a small area immediately above the apertural lip; aperture large, arched or slit-like, extending from periphery to marginal area of the umbilical depression; apertural lip distinct, regular or irregular; supplementary openings common, resulting from either irregular growth of the lip or relic extension of the aperture on the umbilical side.

Remarks

This genus differs from *Valvulineria* in having an oval test outline, angular periphery and supplementary openings, and lacking apertural flaps. *Valvulineria* Cushman has a pronounced apertural flap which projects over the umbilicus (Loeblich & Tappan 1987, p. 547). Many species of *Valvulineria* are rounded in outline, with a distinctly lobate margin which is broadly rounded in peripheral view, and have no supplementary openings on the umbilical side.

Parredicta is introduced to accommodate two species which were originally considered as *Planulina kalimnensis* Parr (Fig. 6, 15a, b) and *Valvulineria porifera* Parr (Fig. 7). Among others, Carter (1964) and Quilty (1980) recorded *Parredicta kalimnensis* (both as *Valvulineria kalimnensis*) in the Miocene of Victoria and Tasmania. In the Lakes Entrance oil shaft, it was found from 340 m to the top of sampling level (63.6 m), i.e. the earliest Miocene to late Miocene (Li & McGowran 1995). The younger occurrence of *P. kalimnensis* was reported by Quilty (1985) from the Pliocene in Flinders Island, Bass Strait. *Parredicta porifera* (Parr), on the other hand, seems to be a Quaternary species. On the Lacepede Shelf of South Australia, *P. porifera* occurs frequently between 50 m and 200 m, and some specimens grow up to about 1.5 mm (height) x 1 mm (width), with over 15 chambers in the final whorl (Li *et al.* 1995).

Quilty (1980) suggested that *Crespinella parri* was the probable ancestor of both *C. umbonifera* and *P. kalimnensis*. His view is upheld here. The evolution of this lineage might have begun from *C. parri* in the later Oligocene, but the radiation of both *Crespinella umbonifera* and *Parredicta kalimnensis* did not occur until the early Miocene. This was probably implemented by a morphological change from low trochospiral to planispiral (*C. parri* > *C. umbonifera*) and from keeled to weakly keeled or non-keeled (*M. parri* > *P. kalimnensis*). The loss of the umbilical filling (boss) also took place in the early Miocene and subsequently became a diagnostic feature in younger specimens of *P. kalimnensis* and, particularly, in the much younger *P. porifera* (Fig. 7).

Distribution

Southern Australia, early Miocene to Recent

Acknowledgments

Amanda Beecroft compiled and scanned most of the Eocene species. J. M. Lindsay generously allowed the use of his unpublished data and scanning micrographs, and he and P. G. Quilty read an early draft and shared with us their knowledge on the distribution of many species. The manuscript was reviewed by P. G. Quilty and S. A. Revet, whose comments are acknowledged. We are indebted to S. Shafik for the Lakes Entrance

material and to Y. Bone for dredged samples from the Lacepede Shelf. G. Trevelyan did thin sections and B. Shubber took several optical photographs. B. McHenry arranged the loan of type material from the South Australian Museum. J. Terlet assisted in scanning the uncoated type specimens. R. Barrett reproduced Figs. 4-7. This work was supported by an Australian Research Council grant.

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Appendix 1. A list of genera and species

Almaena Samoylova
A. gippslandica Carter
Amphistegina d'Orbigny
Asterigerinella Bandy
*A. galloway*i Bandy
A. adelaidensis (=*Truncatulina margaritifera* var. *adelaidensis* Howchin)
Bronnimannia Bermúdez
B. palmerae (=*Discorbis palmerae* Bermúdez)
B. haliotis (=*Discorbis haliotis* Heron-Allen & Earland)
Cifellia Gibson
C. costata (=*Chrysalidina costata* Heron-Allen & Earland)
Cibicides de Montfort
C. ihungia Finlay
C. mediocris Finlay
C. refulgens de Montfort
C. vortex Dorreen
Cibicidoides Thalmann
C. neoperforatus Hornibrook
C. perforatus (=*Rotalia perforata* Karrer)
C. pseudoungerianus (=*Truncatulina pseudoungerianus* Cushman)
C. karreriformis Hornibrook
Crespinella Parr
C. parri Quilty
C. umbonifer (=?*Operculina umbonifera* Howchin & Parr)
Crespinina Wade
C. kingscotensis Wade
Discorotalia Hornibrook
Escornebovina Butt
E. cuvillieri (=*Rotalia cuvillieri* Poignant)
Halkyardia Heron-Allen & Earland
H. bartrumi Parr
Heterolepa Franzenau
H. brevoralis (=*Cibicides brevoralis* Carter)
H. opaca (=*Cibicides opacus* Carter)
H. subhaidingeri (=*C. subhaidingeri* Parr)
H. victoriensis (=*Cibicides victoriensis* Chapman, Parr & Collins)
Hofkerina Chapman & Parr
H. semiornata (=*Pulvinulina semiornata* Howchin)
Lepidocyclina Gümbel
L. howchini Chapman & Crespin
Linderina Schlumberger
L. glaessneri Quilty
Maslinella Glaessner & Wade
M. chapmani Glaessner & Wade
Nonorotalia Finlay
Operculina d'Orbigny
Parrencheta Li & McGowran
P. kalimnensis (=*Planulina kalimnensis* Parr)
P. porifera (=*Valvulineria porifera* Parr)
Parrellina Thalmann
P. craticulatiformis Wade
P. crespinae (=*Elphidium crespinae* Cushman)
P. imperatrix (=*Polystomella imperatrix* Brady)
P. verriculata (=*Polystomella verriculata* Brady)
Siphoninoides Cushman
S. laevigata (=*Truncatulina echinata* var. *laevigata* Howchin)
Siphouvigerina Parr
S. fimbriata (=*Uvigerina porrecta* var. *fimbriata* Sidebottom)
Tubulogenerina Cushman
T. ferox (=*Bigenerina ferox* Heron-Allen & Earland)
T. mooraboolensis Cushman
Victoriella Chapman & Crespin
V. conoidea (=*Carpenteria conoidea* Rutten)
Victoriella plecte (=*Carpenteria proteiformis* var. *plecte* Chapman)
Wadella Srinivasan
W. hamiltonensis (=*Carpenteria hamiltonensis* Glaessner & Wade)
W. globiformis (=*Carpenteria globiformis* Chapman)

THE POPULATION BIOLOGY OF THE TEMPERATE REEF FISH CHEILODACTYLUS NIGRIPES IN AN ARTIFICIAL REEF ENVIRONMENT

*By Michael Cappo**

Summary

Cappo, M. (1995) The population biology of the temperate reef fish Cheilodactylus nigripes in an artificial reef environment Trans. R. Soc. S. Aust. 119(3), 113-122, 30 November, 1995.

Underwater surveys and observations of tagged fish were used to examine spatial distribution, temporal variation in abundance, habitat use and agonistic behaviour of a small population of Magpie Perch, Cheilodactylus nigripes, in a 1176 m^2 site beneath a pier over two winters. A marked decline in numbers of small fish in the population was observed in one year and the number of larger fish was more stable. The unstratified density of fish was between 1.6 and 3.4 fish 100 m^2 but locations of fish sightings were strongly positively correlated with two dimensional cover of hard substrata within the site. Cheilodactylus nigripes was a diurnally active micro-carnivore which used hard substrata for shelter and for feeding on benthic invertebrates. Movement patterns were measured or inferred from spatial patterns of distribution and were found to be restricted to small areas within the confines of the pier. Home range was estimated to be 26 m^2 for one juvenile fish. Only juveniles <= 12 cm TL defended space aggessively against intrusion by conspecifics and fish >19 cm TL engaged in lateral displays with colour changes in agonistic encounters. These displays were considered to be related to maintenance of spatial patterns.

Key Words: temperate reef fish, habitat use, agonistic behaviour, feeding, Cheilodactylus nigripes.

Transactions of the Royal Society of S. Aust. (1995), 119(3), 113-122

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by MICHAEL CAPPO†

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Underwater surveys and observations of tagged fish were used to examine spatial distribution, temporal variation in abundance, habitat use and agonistic behaviour of a small population of Magpie Perch, *Cheilodactylus nigripes*, in a 1176 m² site beneath a pier over two winters. A marked decline in numbers of small fish in the population was observed in one year and the number of larger fish was more stable. The unstratified density of fish was between 1.6 and 3.4 fish 100 m⁻² but locations of fish sightings were strongly positively correlated with two-dimensional cover of hard substrata within the site. *Cheilodactylus nigripes* was a diurnally active micro-carnivore which used hard substrata for shelter and for feeding on benthic invertebrates. Movement patterns were measured or inferred from spatial patterns of distribution and were found to be restricted to small areas within the confines of the pier. Home range was estimated to be 2.7 m² for one juvenile fish. Only juveniles <= 12 cm TL defended space aggressively against intrusion by conspecifics and fish >19 cm TL engaged in lateral displays with colour changes in agonistic encounters. These displays were considered to be related to maintenance of spatial patterns.

Replenishment of the pier population was observed to occur in spring from recruitment of 5 cm TL juveniles. These data indicate the importance of relatively small marine protected areas as refuges from spearfishing for *C. nigripes*.

KEY WORDS: temperate reef fish, habitat use, agonistic behaviour, feeding, *Cheilodactylus nigripes*.

Introduction

Cheilodactylid fishes are a numerically important component of the cool temperate reef fish faunas in Australia, New Zealand, South Africa, South America and Japan (Lincoln Smith *et al.* 1989; Branden *et al.* 1986; Leum & Choat 1980; van der Elst 1981; Nielsen 1963; Sano & Moyer 1985). They are relatively large, slow moving and can be easily approached underwater, making them very popular targets for spearfishers. In south-eastern Australia they dominate the catches made in spearfishing competitions (Johnson 1985a; Lincoln Smith *et al.* 1989) and there is evidence that spearfishing is a major cause of localised depletion of cheilodactylids in New Zealand (Cole *et al.* 1990).

Assessment of effects of recreational spearfishing on cheilodactylid populations requires a knowledge of habitat use by the fish, their patterns of movement and abundance and the sources of population replenishment. These data are essential for the implementation of marine protected areas (Edyvane 1993) at the proper spatial scale as a means of managing temperate reef fisheries. A knowledge of feeding habits is also desirable to determine the role of cheilodactylids in trophic dynamics and to predict any subsequent changes in benthic community structure which may result from the effects of high fishing mortality. Their behavioural traits make these fish ideal subjects for underwater studies yet little is known of the patterns of distribution and ecology of temperate cheilodactylids, especially those that inhabit the coastal reefs of southern Australia.

Cheilodactylus nigripes is an abundant inhabitant of shallow (<30 metres) limestone and basaltic reefs in southern New South Wales, Victoria, Tasmania, South Australia and southern Western Australia (Hutchins & Swainston 1986). It is commonly found in association with the hard substrata provided by artificial tyre reefs, ship wrecks and piers. This species attains 41 cm in length and rarely takes a baited hook although it comprises a major portion of the spearfishers' catch in South Australia (Johnson 1985a). Limits to the speared catch are enforced by competition bag limits and legislated closure of marine reserves and all piers to spearfishing.

With the exception of counts of *C. nigripes* in surveys of reef faunas in the Great Australian Bight (Kuiter 1983; Branden *et al.* 1986), and frequency in catches at spearfishing competitions (Johnson 1985a,b), there have been no studies of the ecology of this species in Australia.

The present study documents the patterns of spatial and temporal abundance, habitat use and agonistic behaviour in a protected population of *C. nigripes*

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below a South Australian pier. Specific aims of the study were to:
(1) map the spatial and temporal patterns of abundance of the population in relation to the microhabitats provided by the pier,
(2) describe the feeding morphology and diet of the species and
(3) describe the agonistic behaviour amongst individuals and its importance in the maintenance of spatial patterns.

Methods

The study site

Edithburgh pier is located on the western side of Gulf St Vincent, South Australia at 35.5°S, 137.45°E (Fig. 1). The seabed below the pier sloped seaward to a maximum depth of approximately 4.5 m at low tide and consisted of a base of coarse sands, gravels and shell. The predominant hard substrata were artificially placed, in the form of fallen pier materials, discarded ship's ballast and debris and a limestone shelf produced by dredging along the northern side. Large expanses of seagrasses surrounded the structure.

The configuration of pylons and major features of the hard substrata below the pier were mapped (Fig. 2). The entire pier was 168 metres long bounded by 53 rows of timber pylons in 4-5 columns. The study site was under the outer half of the pier seaward of row 23 (Fig. 1). It comprised an area of 1176 m² and was divided into 120 quadrats from 9-11 m² in area with reference to the grid of pylon rows and columns (Fig. 2).

Topographic complexity (Leum & Choat 1980) was described for the site by estimating the two dimensional "cover" of hard substrata within each quadrat, using three ordinal categories of topographic complexity. A total of 804 m² in 81 quadrats was "simple" (cover $\leq$ 10%), 225 m² in 24 quadrats had a "middle" level of cover (cover = 11-25%) and 147 m² in 15 quadrats were classified as "complex" (cover $\geq$ 25%). The seaward end and the southern side of the pier had the most hard substrata, in the form of boulders, slabs and blocks that were usually less than 0.8 m high.

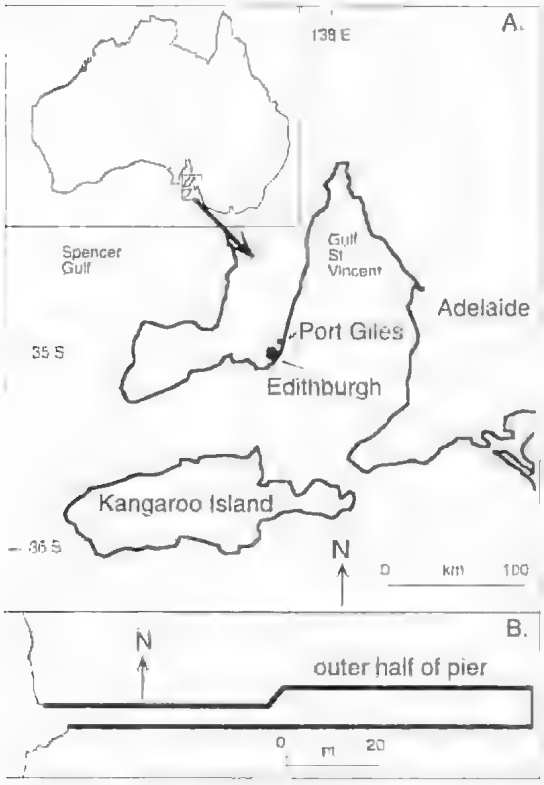

Fig. 1. Location and aspect of Edithburgh pier in Gulf St Vincent, South Australia.

Distribution

Seven visual censuses of the population were made during March-September 1980 using SCUBA. On each census the whole habitat was searched and the position of each fish recorded. The total length (TL) of each fish was estimated to the nearest centimetre and a note was made if the fish were feeding when sighted. Fish were approached to within one metre or less and length estimates were frequently made in direct comparison to a 40 cm plastic ruler. Four censuses of the size frequency under the pier were made by another diver in April-July 1981 and fish lengths were estimated to the nearest centimetre (K. Wehr unpubl. data).

In analyses fish lengths (TL) were categorised as: R recruits (<6 cm); C1 (6-12 cm); C2 (13-19 cm); C3 (20-26 cm); C4 (>26 cm). The choice of distinction between C1 and C2 was made to separate young-of-the-year from older fish. These were biologically meaningful divisions of the population, as colour and morphological differences occurred amongst them. The usual colour pattern of *C. nigripes* was three broad, vertical, dark bands on the white background of the body and caudal peduncle and a dark cheek stripe through the eye (Figs 3a, 4a). Recruits had a bright orange caudal fin and pale orange caudal peduncle with black tips on the caudal lobes. The mouth was more terminal than inferior and angled slightly upward giving these fish a shorter snout and deeper chin than larger fish. Size class C1 fish had the same caudal fin colouration but this faded with size to dusky or reddish in larger classes. There were protuberant crests on the preorbital bone of the two largest size classes which were not observed on smaller fish.

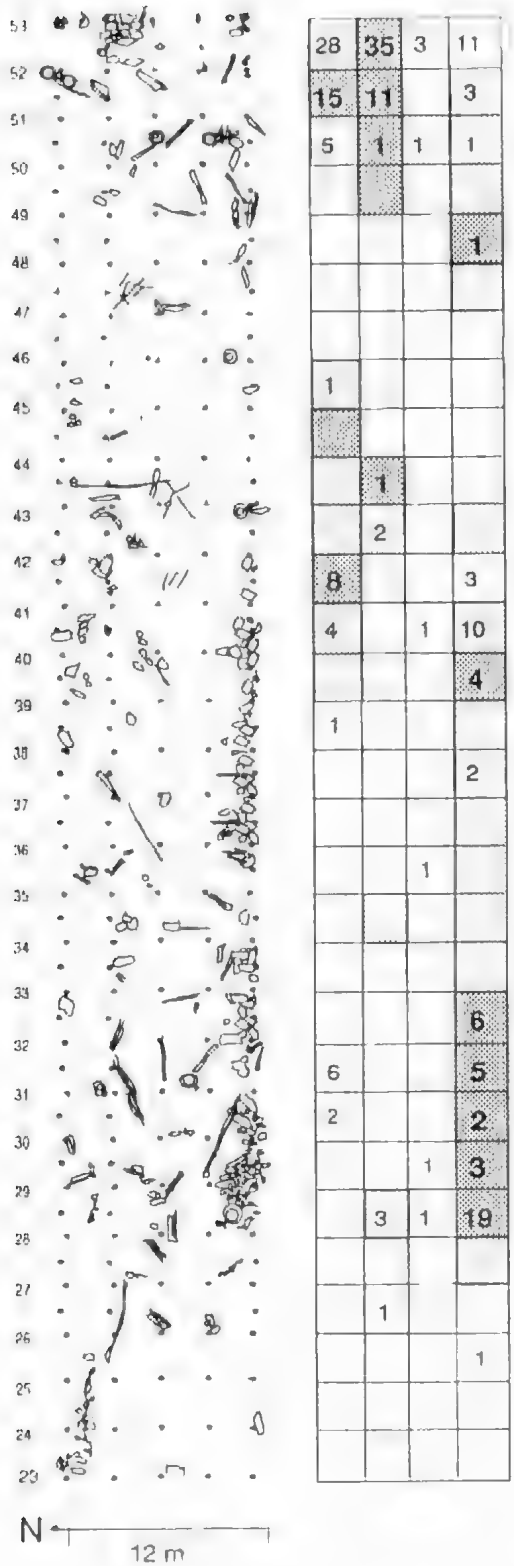

Fig. 2. Comparison of pooled sightings of *C. nigripes* in 1980 and an index of topographic complexity in quadrats (right) with the mapped study site (left). Pylon rows are numbered in ascending order seaward from row 23. "Simple" cover of hard substrata $<=10\%$ (no shading); "middle" cover 11-25% (mild shading); "complex" cover $>25\%$ (dark shading)

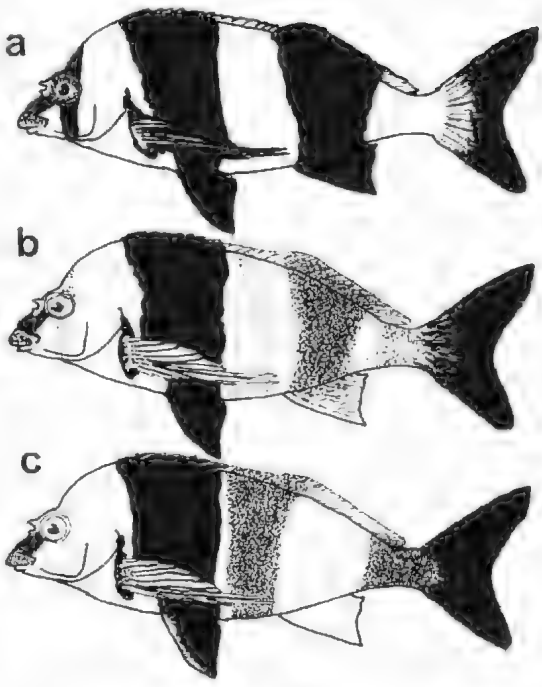

Fig. 3. Summary of colour changes displayed by large *C. nigripes*. a. Normal banding pattern. b. Transitional banding pattern. c. Modified banding pattern - note dark midriff band and caudal peduncle, loss of posterior and cheek bands, white iris and white demarcation between dark bands.

Feeding habits

To avoid sacrificing the small population in the study site a sample of 21 Magpie Perch (TL 21-36 cm) was speared on 25 September 1980 under Port Giles pier 12 km NNE of Edithburgh pier (Fig. 1). Immediately after capture the alimentary tracts were removed and preserved. The food bolus in each tract was dispersed evenly in water and taxa in four field views (×7) were identified as far as possible. The volume of each taxon in the pooled contents of the alimentary tracts was estimated by a water displacement method.

Observation of movement and behaviour

Underwater behavioural observations were made in 60-minute periods at dawn, midday, dusk and midnight on five days during August-September 1980 from a single vantage point amongst limestone slabs at the seaward end of the pier in pylon row 53 (Fig. 2).

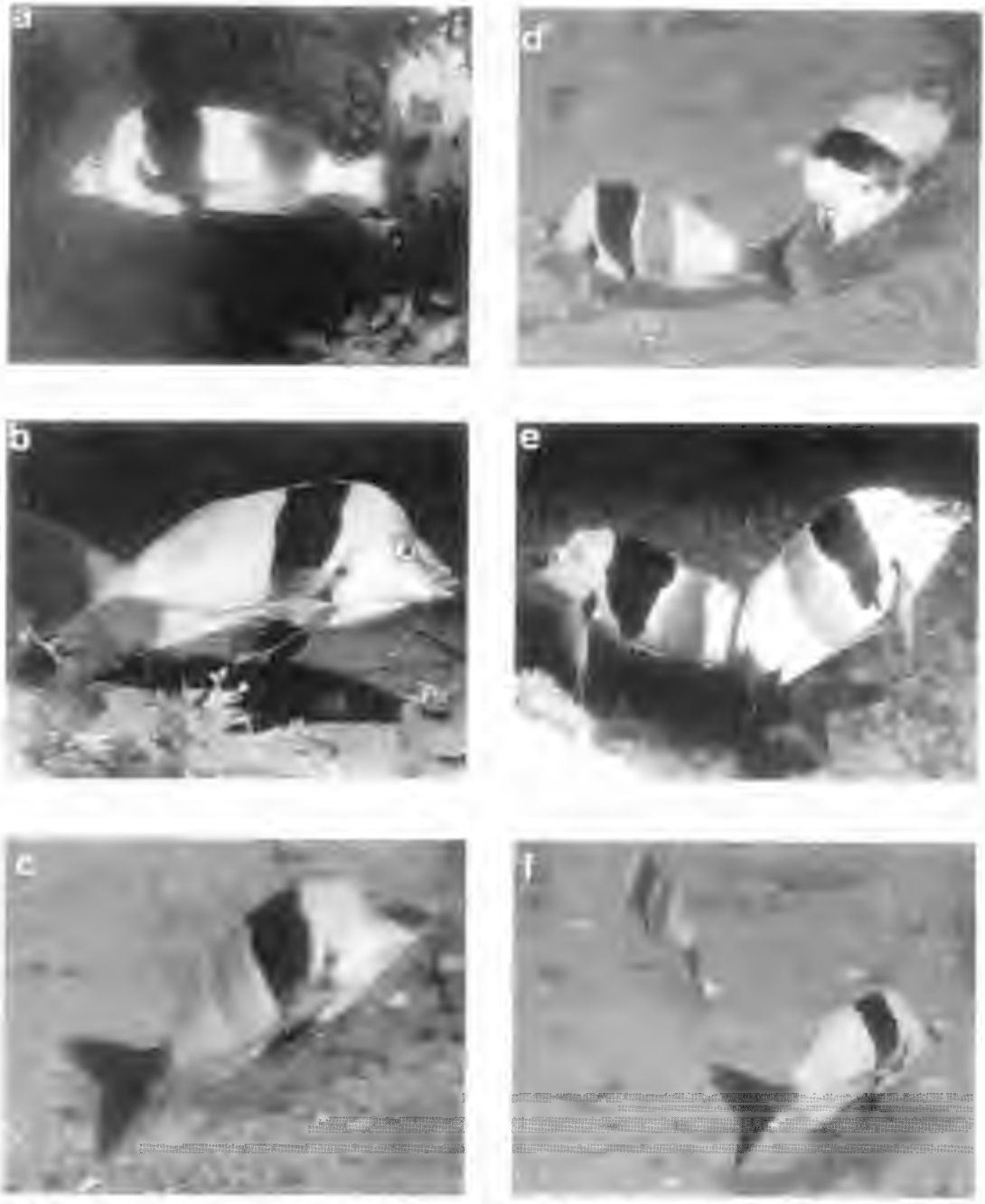

Fig. 4. Photographs of colour change and lateral displays. a. Normal banding pattern. b. Loss of posterior dark band. c. Transitional banding pattern. d. Circling and leaning displays. e. Anti parallel orientation and modified banding. f. Break in encounter and transitional banding.

Observations began before sunrise and finished after sunset to include crepuscular periods of activity. The movements of four fish at this location were monitored simultaneously during the dawn observation periods. Each fish was recognised individually by tags or body markings. Further observations were made at a variety of locations on an opportunistic basis during 1981-1987.

Data on the movement patterns of tagged individuals were collected during 1980. Seventeen fish were tagged with "T bar" anchor tags individually coded with coloured paints. Fish were captured with a large hand-net, tagged underwater, measured and released immediately at the site of capture, and a numbered stake was used to mark each release site. During subsequent dives the sightings of tagged fish were recorded on the site map. The larger fish in the population evaded capture and the tagged sample (TL 10.5-23.0 cm) did not include C4 fish.

Results

Temporal changes in abundance and size composition

The sightings of fish of the five size classes are shown for each sampling date in Fig. 5. The mean numbers of total sightings for each census were similar for the two years with 29.85±4.30 fish sighted in 1980 (95% CI = 19.32-40.37) and 30.50±1.55 fish in 1981 (95% CI = 25.55-35.44), but seasonal declines in sightings were different.

In 1980 sightings declined from a March high of 53 fish to an August low of 18 (Fig. 5). This was partly due to the low visibility (<=0.75 m) encountered during the August census. The decline was evident for all size classes from March to April when both C1 and C2 declined by one half. The steady decline in C1 numbers may be partly accounted for by growth into the C2 size class which showed an increase in abundance. Recruits were first observed in early September 1980, and increased by late September (Figs 5, 6). Predation may play a role in size-specific mortality as a Southern Calamari squid *Sepioteuthis australis*

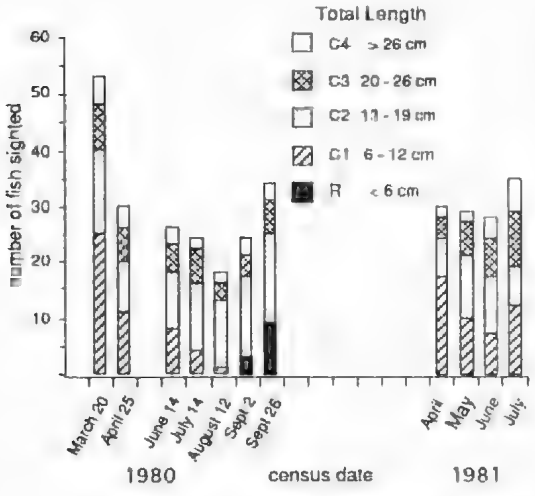

Fig. 5. Changes amongst months in the number of five size classes of *C. nigripes* at Edithburgh pier during 11 underwater visual censuses in 1980 and 1981

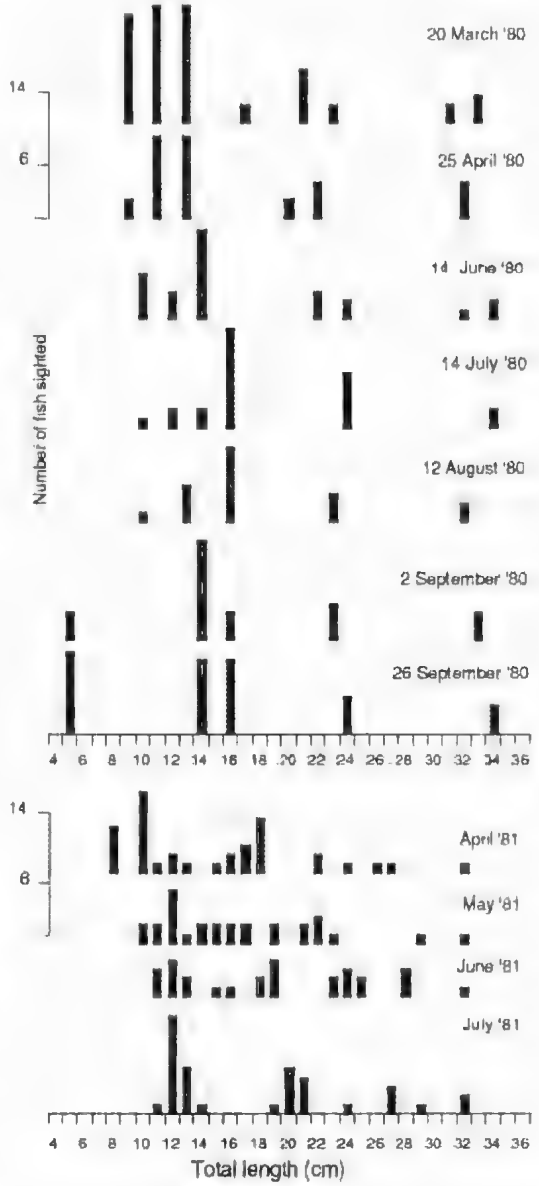

Fig. 6. Modal progression in estimated total length of *C. nigripes* sighted at Edithburgh pier during 1980 and 1981.

was observed to make several attacks on some newly recruited juveniles before capturing and consuming one in 1982.

This pattern was not seen in the 1981 winter surveys although there was a slight decline in the proportion of class C1 fish from April to July. The June low was attributable partly to low visibility (<=0.6 m) encountered during that census. In both years the winter population counts were at comparative levels in the study site. Changes in abundance were relatively small in the two largest size classes amongst months, and between years (Fig. 5). However, the sample sizes and numbers of fish were low, precluding meaningful statistical comparisons. Caution is therefore used in the interpretation of these data.

Modal progression is evident in Fig. 6 for the smaller fish from 1980 to 1981 showing maximum growth rates of about 0.46 cm month^{-1} for C1 fish and about 0.77 cm month^{-1} for recruits. These are in general agreement with the measured rate of 0.46 cm month^{-1} growth of a tagged fish from 13.7 cm to 15.0 cm over five months in 1980. However, the accuracy and precision of length estimation were not determined for either observer so further estimation of growth from modal progression was not possible.

Spatial distribution

The overall density of fish in the study area was estimated at 1.64-3.43 fish per 100 m^2 in 1980 using 95% confidence limits for the mean number of fish sighted divided by the area surveyed. Localised densities were much higher and the number of *C. nigripes* sighted in quadrats under the pier was positively associated (Spearman R = 0.5487, P = 0.000) with the amount of hard substrata within quadrats using Spearman's rank correlation procedure (Zar 1984). Fifteen "complex" quadrats comprised only 12.5% of the study area but gave 55% of sightings compared to 30% in "middle" quadrats and only 15% in the remaining 68% of the study area defined as "simple" (Fig. 2). Nearly 18% of all sightings were made in one quadrat on the seaward end of the pier where large limestone slabs and other hard substrata occurred. These slabs were the highest (0.6 – 1.2 m) and most rugose hard substrata in the study area and provided extensive shelter (Fig. 2). Fish were rarely sighted in quadrats with 10% or less of hard substrata, with the exception of quadrats containing tall three-dimensional structures not well described by the two-dimensional method used to classify quadrats. For example, clusters of buffer pylons on the seaward corners of the pier were fused together by encrusting organisms and provided shelter sites.

There was no clear relationship between water depth and fish size due to the shallow nature of the habitat and the overriding influence of three-dimensional reef structure. However, the largest fish were generally restricted to the deepest water and were not seen in the area shoreward of pier row S1 (Fig. 2). New recruits were seen throughout the study area, but mainly near the sea surface on pylons at the deepest seaward end, amongst arborescent bryozoans.

Movement of fish in the study area

Observations throughout the day and in the night showed that individual *C. nigripes* emerged from shelter sites just after dawn and retreated to the same sites during sunset. No fish were seen to be active at night. In five night dives two of the largest fish in the population were seen in the same shelter site in a crevice between close pylons, resting motionless on outstretched pectoral fins with raised spinous dorsal fins. It appeared that largest fish emerged earlier and retreated later than smaller size classes. The movements of three fish were monitored in each of the five dawn observation periods but the fourth and smallest (C1) fish was only seen for the first three days. The largest fish (C4) traversed an average of 8.0 ± 1.0 metres, a 23.0 cm tagged fish moved 7.8 ± 0.37 metres and a 14.0 cm tagged fish moved 2.5 ± 0.55 metres in the 60 minutes after emergence from their individual shelter sites. The smallest individual moved only 0.83 ± 0.28 metres. Only the largest fish moved far from the confines of the pier, foraging amongst low limestone shelves within 10 metres of the seaward end.

Seven of the tags (41%) were not seen after application, three others persisted for only 9 days, and only five tags were sighted after 60 days. The movement of large Magpie Perch could not be assessed from the tagging program because the mean length at release for these remaining five fish was only 15.4 cm (C1,C2) and the largest was 23.0 cm (C3). Only four tagged fish were present at the end of the 1980 study period and each of these fish was seen during every census following tagging. The loss of tags from the population was at least partly due to tag shedding. On two occasions fish were observed to scrub the tag rill against hard objects. The sightings of all tagged fish were restricted to the habitat underneath the pier within 7 metres of the tagging site with the exception of two individuals. Several weeks after tagging these two fish were found to be resident for the remainder of the study in quadrats about 10 metres away from the tagging site. Tagged fish were never seen to traverse the seagrass beds on the southern side of the pier which appeared to act as natural boundaries to the pier habitat.

Wilson (1975) defined "home range" to be the area that an animal learns thoroughly and habitually patrols, and "core area" to be the area of heaviest regular use within the home range. Only a single tagged fish was seen frequently enough to confidently estimate these two areas. This small C2 fish (13.7 cm) was sighted 18 times within 7 metres of the tagging site. The home range of this fish was estimated to be only 26 m^2 by measuring the area of a polygon joining the outermost

sightings (Leum & Choat 1980). Similarly, the core area was estimated at 1.7 m² to be the area encompassing 50% of sightings. The focus of this area was a small shelter site within a cavern amongst limestone blocks on the southern side of the pier in pylon row number 28 (Fig. 2). This fish was only sighted once outside the shaded confines of the pier and the furthest displacements were northward under the pier and westward along the pylons.

Feeding morphology and diet

Cheilodactylus nigripes had a small mouth with thick fleshy lips and a single row of widely spaced peg-like teeth on the dentary and premaxillary. In the throat there were a pair of upper, and a single lower, pharyngeal tooth pads covered with bands of villiform teeth. There were 15 long and fine gillrakers on the first gill arch and the stomach was small with a large pyloric region containing five short pyloric caeca.

The fish were observed to inspect closely pockets of sediment in crevices or amongst fronds of arborescent organisms and fed in a pecking motion. The mouth was rapidly opened, forming a suction with the fleshy lips, and benthos was ingested with an audible clicking sound. By rapidly opening and closing the opercula, fine silt was strained out through the gill chambers and larger particles were ejected from the mouth. Large polychaetes were wrenched from the substratum and vigorously shaken to break them up into pieces suitable for swallowing. When close observations were made, no evidence of prey was seen near the fish and they appeared to select feeding substrata, but not the benthic organisms within, although fish directed repeated feeding "pecks" at large prey such as polychaetes once they were detected.

The fish fed mainly on benthic invertebrate fauna with gammarid amphipods about 4 mm long predominant in the pooled sample. Of the 60% of food volume identifiable, the fourteen major taxa were ranked as: gammarids (25.6%); Polychaeta (10%); ostracods (7.5%); Bivalvia (6.6%); Brachyura (3.2%); Mysidacea (2.7%); and Tanaidacea, Archaeogastropoda, Polyplacophora, Gastropoda, Isopoda, Ophiuroidea, and caprellid and tubiculous amphipods (each less than 1%).

There did not appear to be any size-related difference in the feeding behaviour of *C. nigripes* with the exception that small fish were observed to feed more often than larger ones. Of all sightings made in 1980 the following proportions were engaged in feeding when sighted: R 75%; C1 76%; C2 79%, C3 49%; C4 45%.

Agonistic behaviour

Wilson (1975) defined agonistic behaviour to be any activity related to fighting, whether aggression or conciliation and retreat. Agonistic behaviour in *C. nigripes* was directed toward only conspecifics of a similar size and three size-specific patterns were described for the smallest and largest size classes.

The smallest fish (<=12 cm), classified as recruits (R) and C1, aggressively defended space. Most common was a short pursuit of incoming R or C1 fish away from a foraging area. Also observed was the head-on approach of C1 fish to within about 4 cm followed by sustained pursuit, darting in small circles with the dorsal fin fully raised. Biting was evident as audible sounds and tail damage from broken caudal rays. This was termed "carousel fighting" by Chiszar (1978).

Three slow lateral display patterns were observed amongst fish more than about 19 cm long (C3, C4) which did not involve such pursuit. The first involved pairs of C3 fish which approached each other head-on and met head-to-tail in a parallel orientation, often within centimetres, and one or both fish tilted upward slowly. The two fish then swam in slow circles in close proximity with some lateral displays, but no colour change, before parting.

An elaboration of this theme occurred during the approach of the large C4 fish when a characteristic colour change occurred. The posterior band began to pale and the white midriff darkened with the development of a sharp white line between them (Figs 3b,c, 4c,d). When the fish met they assumed an anti-parallel orientation separated by only a few centimetres for about 15 seconds, during which they slowly tilted 30 degrees to a head-up, tail-down position (Fig. 4e). The posterior band blanched and the darkening of the midriff and caudal peduncle deepened. Other colour changes were also striking, including blanching of the anal fin, cheek band, iris and pectoral fins, and definition of a black patch around the pectoral axil (Fig. 3b,c). When one fish withdrew the other followed and both began lateral "leaning displays" with lowered or raised dorsal spines, described by Chiszar (1978) as defensive posturing (Fig. 4d). The entire sequence lasted one to two minutes and once the fish broke off the encounter the midriff band quickly resumed its former white state but the other bands were slower to return (Fig. 4c,f).

These displays were clearly identified to occur when fish met and appeared to relate to the position of the fish within the habitat, although it was not possible to define the home ranges and spatial boundaries involved in eliciting the agonistic behaviour. The significance of a third type of behaviour was more obscure and involved the loose aggregation of large fish into a slowly circling group above the seabed. Most of the circling fish had a pale posterior band and some of the fish exhibited a leaning display towards others. There was insufficient information to recognise characteristics of "winners" or "losers" and no attempt was made to identify the sex of the participants, but these lateral displays were considered to relate to habitat use.

Discussion

The low variability in counts of *C. nigripes* amongst most months in winters of two years, the very close association between fish sightings and topographic complexity and the restricted movements of tagged fish were all evidence for a high degree of site specificity of *C. nigripes* under the Edithburgh pier. Rugose, hard substrata were used as sleeping and sheltering sites and as feeding substrata and the concept of a small home range may best describe the use of this space by *C. nigripes*.

These patterns of habitat use indicate that relatively small artificial habitats such as piers can act as important marine protected areas for this species. Marine protected areas can fulfil a number of important functions in fisheries management including protection of "critical habitats" and provision of areas for stock replenishment, for fishery-independent monitoring of stock fluctuations and for resolution of conflict amongst competitors for use of marine resources and habitats. (Edyvane 1993). Planning the spatial scale and habitat composition of marine protected areas for temperate reef fishes requires knowledge of sources of population replenishment, ontogenetic movement patterns, home range size, habitat requirements and natural habitat boundaries. Some of these can be inferred for *C. nigripes* from the simple observations presented here supported by comparison with other detailed studies of the cheilodactylids associated with reefs.

Distribution and movement

In translation of the pier observations to natural reef populations of *C. nigripes* in South Australia it is essential to recognise that major biological features of the habitat have been shown to affect the distribution of temperate reef fish at a variety of spatial scales and these patterns have been maintained over long time scales (Jones 1988; McCormick 1989b). In this regard the artificial nature of the pier habitat is considered to differ from nearby natural reefs in two main ways. Unlike the algal-dominated reefs surveyed by Branden *et al.* (1986), the habitat beneath Edithburgh pier lacked macrophyte cover, perhaps because of shading. There may thus be more suitable feeding substrata there for *C. nigripes*, as Choat & Ayling (1987) found that larger carnivorous reef fishes, including cheilodactylids, forage preferentially in open reef areas which support greater densities of their invertebrate prey in comparison to areas dominated by laminarian algae. The amount of habitat for feeding and refuge is further enhanced under the pier by the presence of the pylons and the fouling communities that encrust them. Secondly, the density of *C. nigripes* beneath the pier (1.6-3.4 per 100 m^2) was six-fold higher than an estimate for unexploited reefs of the Great Australian Bight (0.2 - 0.6 per 100 m^2) calculated from the survey data in Branden *et al.* (1986). The home range sizes, movement patterns and agonistic behaviour on natural reefs may be different as a consequence.

The microhabitat requirements of *C. nigripes* for shelter sites and feeding substrata were not described with the simple habitat classifications used here but can determined by studying associations between abundance and habitat at small spatial scales. McCormick & Choat (1987) stratified estimates of density of the morwong *Cheilodactylus spectabilis* in New Zealand by ten habitat types and depth, and reported averages of 0.25-2.09 fish per 100 m^2, with the exception of the topographically complex "tumble boulderbank" habitat where the density was 15.87 fish per 100 m^2.

There is also a clear role for ontogenetic movements along environmental gradients in establishing patterns of cheilodactylid abundance and these should be considered in selection of reef areas for protection. After first recruiting in surge zones (Leum & Choat 1980) cheilodactylids are known to move to progressively deeper parts of the reef habitat as they grow (Sano & Moyer 1985; McCormick 1989a,b). Although the seagrass beds around the pier appeared to act as habitat boundaries which smaller *C. nigripes* did not traverse, it was not possible to describe immigration and emigration of fish with the simple techniques used in the study. Replenishment of the pier population was observed to occur only through the spring arrival of new recruits.

The autumn decline in numbers of these young-of-the-year in 1980 was not observed in 1981 censuses, and it was not possible to resolve the roles of size-specific natural mortality, tag-induced mortality or counting biases in the decline of such a small population. Properly replicated censuses stratified to identify individual fish and detect counting biases and diurnal and seasonal differences in activity, would help clarify these temporal changes. The pier map and census data presented here provide a baseline for future surveys to examine long-term variations in patterns of abundance of *C. nigripes* at Edithburgh.

It is possible that home ranges and movements on natural reefs may be more extensive amongst all size classes of *C. nigripes*, and it is unknown whether the distributions reported here were more, or less restricted during warmer months outside the study period. Leum & Choat (1980) attributed significant winter declines in numbers of *C. spectabilis* sighted to an extension of home range during cooler months. The estimates of home range for *C. nigripes* were relatively small in comparison to those constructed for *C. spectabilis* by Leum & Choat (1980) on natural reefs and may depend on fish density as well as habitat type. Juvenile *C. spectabilis* had home ranges $\leq$ 100 m^2, which were about three times that estimated here for *C. nigripes* using the same technique. Similarly the largest *C. nigripes* were always sighted in a relatively

small area at the seaward end of the Edithburgh pier but Leum & Choat (1980) observed that larger *C. spectabilis* moved large distances and had home ranges up to 50-70 thousand m^2.

Feeding habits

Cheilodactylus nigripes were diurnally active, benthic carnivores feeding mainly on gammaridean amphipods and other small benthic invertebrates. Their mode of feeding is common to other reef-associated morwongs in the same genus. Bell (1979) reported that *C. fuscus* and *C. spectabilis* use their thick fleshy lips to wrench and suck animals off the substratum, mainly polychaetes, brachyurans, amphipods, gastropods, and bivalves. Sano & Moyer (1985) reported that the Japanese *C. zebra* feeds mainly on epifauna, especially gammaridean amphipods and decapods, while the sympatric *C. zonatus* tends to take both epifauna (mainly gammaridean amphipods, isopods, sponges and decapods) and infaunal polychaetes.

Agonistic behaviour

Juvenile *C. nigripes* $<= 12$ cm TL were observed to defend space aggressively, but such defence may have been energetically uneconomic for larger fish >19 cm TL occupying larger home ranges. It is proposed here that the lateral displays and colour-change during agonistic encounters amongst larger *C. nigripes* were related to the maintenance of some undefined spatial pattern of overlapping home ranges. Such patterns were mapped by Leum & Choat (1980) for *C. spectabilis* which directed agonistic behaviour only towards conspecifics of similar size and only smaller size classes vigorously defended space outside of the spawning season. The habitat of *C. spectabilis* was described as a mosaic of exclusive territories occupied by smaller fish through which the larger size classes foraged in larger, overlapping home ranges (Leum & Choat 1980) and this may be a useful model for future studies of habitat use by *C. nigripes*.

Using Chiszar's (1978) definitions of lateral displays in agonistic behaviour, the description of "carousel fighting" fits well the behaviour of *C. nigripes* juveniles, whereas the various colour phases of larger fish can be interpreted as varying degrees of threat in a typical "colour fight". The anti-parallel orientation adopted during these reciprocal lateral displays is widespread in fishes, and some species with long dorsal spines, such as the chaetodontids, are reported to tilt the raised spines towards the other fish in a defensive posture called "rolling" or "leaning" if it approaches too closely (Chiszar 1978).

The possibility of a reproductive basis for some agonistic behaviours cannot be discounted for all observations of *C. nigripes*, as McCormick (1989a) found that large male *C. spectabilis* aggressively defended territories during the spawning season by "rolling" down on to intruders and restrained visiting females by "tight circling, pursuit and blocking" or chasing and tail-nipping. Some of the larger *C. nigripes* at Edithburgh pier were observed to have tentacular protuberances on the preorbital bones which have been used in studying sexual dimorphism and separating the sexes of *C. spectabilis* and *C. fuscus* by external characters in visual counts (McCormick 1989a; Schroeder *et al.* 1994). The high population densities of *C. nigripes* at some deeper South Australian piers may provide the best chances of clarifying the spatial and sexual significance of agonistic behaviour of *C. nigripes* through observation and morphometric studies.

Future research

The resilience of *C. nigripes* to spearfishing and recovery of depleted populations depend on growth rates and the sources and rate of population replenishment. This study suggests that widespread movement of *C. nigripes* amongst habitats is not an important source of replenishment but further studies at appropriate scales are necessary to determine the contributions of recruitment and post-recruitment processes in determining spatial patterns of abundance. These data are needed to determine if marine protected areas should include shoreline surge zones as recruitment sites with corridors of hard substrata linking them to adjacent deeper reef, or if isolated offshore habitats such as artificial reefs are adequate.

The magnitude and frequency of changes in population structure are likely to be directly related to the longevity of *C. nigripes* as variable recruitment will have least effect and spearfishing the greatest effect on the population size of long lived species. When fishing mortality is absent in such cases age classes accumulate and temporal consistency in population size may mask an underlying instability in the age composition (Jones 1988). Consequently, future studies of *C. nigripes* population dynamics may require analyses of age compositions of unexploited populations in conjunction with recruitment surveys (Doherty & Fowler 1994) and monitoring of the survival, growth and movement of individually recognisable fish from time of recruitment in permanent quadrats (Connell & Jones 1991). The results presented here form a basis for such studies and for longer-term assessment of temporal consistency in the patterns of abundance of *C. nigripes* in a mapped habitat.

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THE MOST VIGOROUS SOUTH AUSTRALIAN TIDE

By C. Schluter, J. A. T. Bye†, & P. Harbison‡*

Summary

Schluter, C., Bye, J. A. T., & Harbison, P. (1995) The most vigorous South Australian tide. Trans. R. Soc. S. Aust. 119(3), 123-132, 30 November, 1995.

Harmonic analysis of tidal records for the region between the city of Port Augusta and Yorkey Crossing in the upper Spencer Gulf indicates that the most vigorous South Australian tide probably occurs just north of the Whyalla Railway bridge and has a maximum range of about 4.1 m, just short of being classified as macrotidal. The special property of South Australian tides, that the semi-diurnal constituents (M_2 and S_2) have about equal amplitudes, results in very interesting shallow water tidal interactions, in particular the generation of a large amplitude quarter-diurnal constituent (MS_4). The intertidal environment of mangrove forests and especially the samphire flats of the upper Spencer Gulf is shown to be finely tuned to this shallow water tide.

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Introduction

The tides of South Australia have attracted interest for over 100 years (Chapman 1892; Easton 1970). However there appears to be no account of the region in which the largest tide occurs. This region is of interest to tidal theory because both Gulf St Vincent and Spencer Gulf have large semi-diurnal tides at their heads and also because the major lunar (M_2) and solar (S_2) constituents are of similar magnitude. The diurnal tide progresses from west to east along the Southern Shelf as a Kelvin wave which enters the South Australian sea where its amplitude and phase increase regularly and gradually towards the head of the gulfs. The semi-diurnal tides, on the other hand, displays a much more energetic response.

Tidal characteristics in Gulf St Vincent and Spencer Gulf

An almost progressive wave enters Investigator Strait and becomes converted into a standing oscillation within Gulf St Vincent (Bye 1976). Bowers & Lennon (1990) investigated the tidal character using the classical model (Bowden 1983) in which an incoming wave is reflected at the head of the gulf in the presence of a frictional force linearly proportional to the tidal current velocity. Particular attention was given to the importance of Backstairs Passage in this process. The system can be best described as a quarter-wave resonance of the open sea tide.

In Spencer Gulf the tidal resonance is more complex and lies closer to a three-quarter resonance in which a tidal node occurs between the head and the mouth of the gulf. This behaviour results in a minimum semi-diurnal tidal amplitude near Wallaroo, beyond which there is a rapid increase in amplitude towards the head of the gulf. Easton (1978) has given an elegant mathematical demonstration of this resonance which also uses a frictional term linearly proportional to the tidal current velocity. Numerical models of the tides of Spencer Gulf have been developed by Noye *et al.* (1981) and Bills and Noye (1986), including fine resolution models of tidal eddies in upper Spencer Gulf (Noye 1984; Noye *et al.*, 1994).

In both gulfs mangrove forest and samphire flats are extensive, especially near Port Wakefield, Port Adelaide[1] (Schluter 1993), Franklin Harbour and Port Augusta. The tides are of great ecological significance to these areas. The most vigorous tidal system in South Australia occurs between Port Augusta and Yorkey Crossing in upper Spencer Gulf. This distinctive region has the character of a brine estuary (Bye & Harbison 1990).

The action of tidal currents is responsible for internal mixing of the water column. Stabilising forces, such as surface heating and horizontal salinity gradients, tend to result in a stratified water column, the lower stratum being denser than the upper. The dynamics of the mixing process have been extensively studied, initially in temperature stratified environments such as the shallow European seas (Simpson & Bowers 1981), and more recently in the salinity stratified environment of the South Australian sea (Samarasinghe 1989). Stratification occurs when the ratio of the horizontal density gradient multiplied by the depth and

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[1] SCHLUTER, C. G. (1994) The Generation of Shallow Water Tides within a Mangrove Environment, MSc Thesis, The Flinders University of South Australia (unpubl.)

divided by the density and the root mean square of the slope of the water surface due to the tide exceeds a critical value (Bye 1990).

In upper Spencer Gulf the tidal currents maintain a vertically well mixed water column whereas in mid Spencer Gulf a very detailed and extensive observational programme has shown that transient stratification occurs (Nunes & Lennon 1987). At the mouth of Spencer Gulf the horizontal density gradient maintains a stratified exchange for about nine months of the year (Bye & Whitehead 1975; Lennon *et al.* 1987). In the summer months, however, the horizontal density gradient is reduced due to the reversal of sign in the temperature gradient and vertical mixing can also occur. These considerations highlight the significance of the tidal regime in the dispersion of dissolved material introduced into the water column in the coastal provinces of upper Spencer Gulf, especially in the brine estuary.

The Site

Previously, measurements of the tide in Spencer Gulf extended only as far north as Port Augusta. Recent tidal measurements (Bye & Harbison 1987, 1991, 1994) north of Port Augusta (Fig. 1), indicate that a very vigorous tidal regime exists. The site of the investigations was an old wooden bridge on which an abandoned mineral railway to a salt works crossed over Spencer Gulf. On the eastern shore of the gulf the salt bridge was originally connected with an embankment which cuts through the mangrove forest and into the samphire flats. The maximum span height of 4.4 m is just greater than high water springs, and at low water springs, the water is confined to a few central spans where the maximum depth is about 30 cm (Fig. 2a). The piers and spans are ideally suited for instrument deployments. Tide gauges were secured to the piers and current meters were suspended from the spans or mounted by poles driven into the ground. On the western side, beyond a narrower fringe of mangroves, the bridge leads directly to the salt works. The tidal observations undertaken at this site extended from 28 February to 28 March, 1986 (Bye & Harbison 1987).

Tide gauges and current meters were also deployed for shorter periods between the Central Australian Railway bridge and Yorkey Crossing. This station lies approximately 4 km further north of the salt bridge and is bordered on both sides by samphire flats (Fig. 2b) which are covered at high water springs and also during the rare floodings which originate on the Pirie-Torrens plains north of Yorkey Crossing (Bye & Harbison 1994).

Since the above observations were of limited time span, a second more extensive period was initiated in 1993. The choice and location of tidal equipment was based upon the pilot investigations. An Inter-Ocean S4 current meter was located within the town of Port Augusta at an abandoned road bridge using a cradle mooring device. The current meter is based upon an electromagnetic flux measurement and thus has no moving parts as do the conventional current meters. This makes the current meter immune to the effect of algal growth. The current meter obtained data between 27 July 1993 and 27 August 1993. A tide gauge located at this site proved faulty. The tidal constants in Table 1 were obtained from the Port Augusta power station tide gauge for the same period as the salt bridge deployment.

A bottom mounted pressure tide gauge was deployed at the Whyalla Railway bridge north of Port Augusta between 28 July and 30 October 1993. Another bottom mounted tide gauge was deployed at the salt bridge, but this gauge was destroyed by vandals. A bottom mounted tide gauge was deployed at the Central Australian Railway bridge between 18 September and 31 October 1993. This gauge clearly indicates the unusual tide of the region.

Tidal Analysis

To distinguish between a progressive and standing wave situation the phase differences between the tidal currents and elevations must be known. One of the most important aspects of tidal systems is the definition of standing and progressive waves. With standing waves, the phase difference between the tidal elevations and currents is 90° while for a progressive wave the phase difference is 0°. A standing wave may be considered as being the sum of two progressive waves, one directed landward and one of equal amplitude directed seaward. The landward energy flux associated with the incident wave is, in this case, balanced by the seaward energy flux of the reflected wave and thus there is no net energy flux. In dissipative situations the reflected wave will be frictionally attenuated and must be smaller in amplitude than the inbound wave and thus a perfect standing wave is impossible. As the tide propagates from the open ocean, various nonlinear distortions occur in the tidal signal. These distortions are primarily influenced by nonlinear mechanisms including frictional interactions and interactions with surrounding bathymetric features, as well as atmospheric effects and continuous freshwater discharges. The interactions of the primary astronomical tide discussed above may be represented by the growth of the shallow water tides which indicate the degree of nonlinear distortion of the primary signal.

In the analysis of tidal signals, it is common practice to decompose the tidal signal into a harmonic series of amplitudes and phases. The total tidal elevation or current may thus be represented by the sum of the

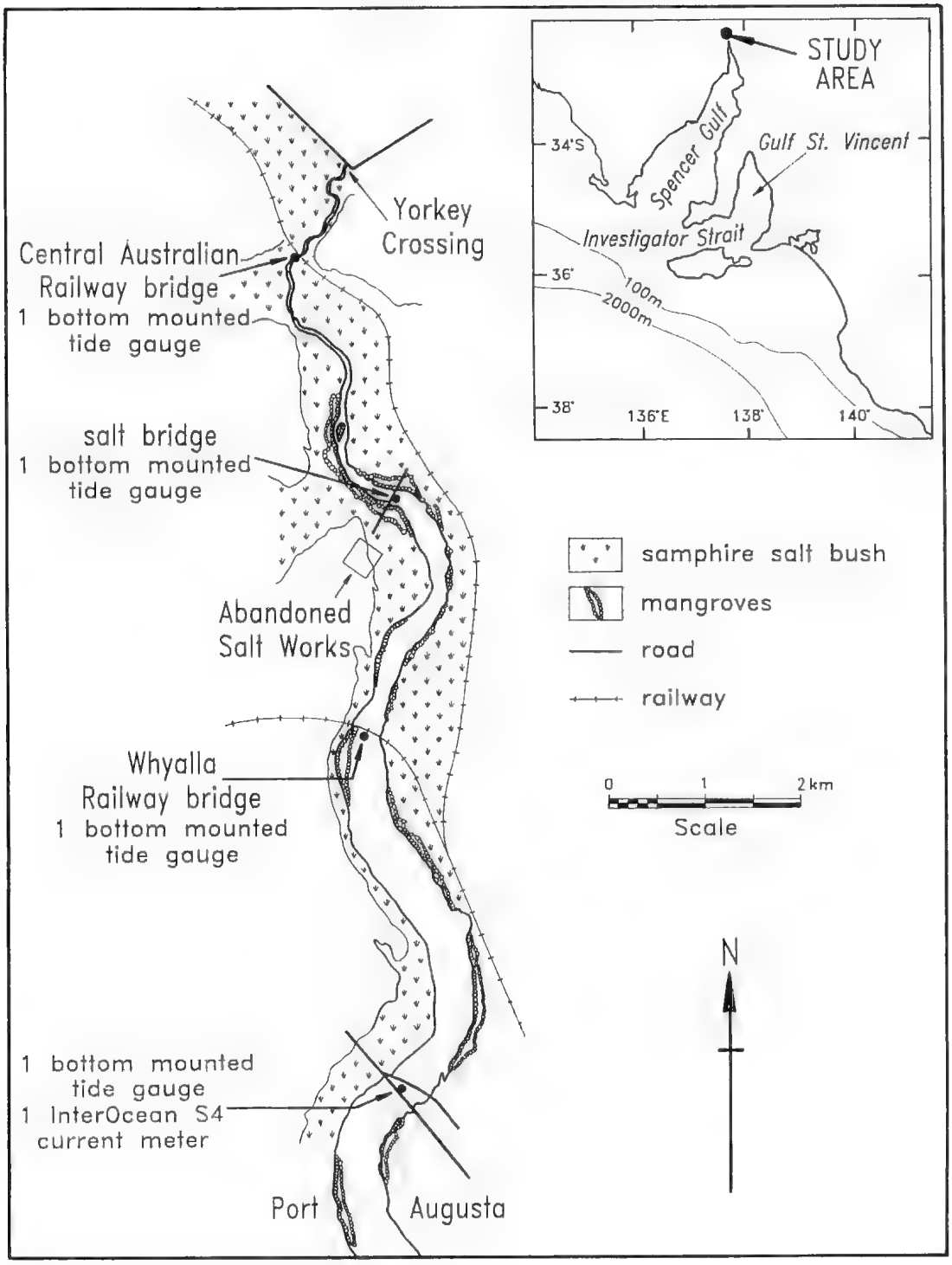

Fig. 1. Locality map of upper Spencer Gulf.

Fig. 2. (a). View of the salt bridge looking westward. Note an investigator (Pat Harbison) on the fringe of the mangrove forest, and the abandoned salt works in the background. (b). View looking southward from just before Yorkey Crossing. Note the samphire flats on the western side of the channel, and the Central Australian Railway bridge in the background. Both views were taken a short time after low water.

TABLE 1. *Tidal constituents for the upper Spencer Gulf.*
a = amplitude; g = phase in degrees. The tidal elevations are in mm and the currents are in cm/s. Currents are related to the magnetic bearing. The record lengths used with the analysis are given in the text.

	Elevations								Currents			
Constituent	Port Augusta (1986)		Whyalla Railway bridge		salt bridge (1986)		Central Aust Railway bridge		Port Augusta (East)		Port Augusta (North)	
	a	g	a	g	a	g	a	g	a	g	a	g
O_1	248	39	265	42	263	51	149	75	0.75	322	2.98	337
K_1	453	73	462	74	451	80	308	90	0.68	1	2.14	4
M_2	617	206	611	210	559	223	245	227	2.14	140	9.28	139
S_2	644	257	704	267	680	275	301	288	2.62	198	10.8	202
$3M_2S_2$	44	68	24	15	5	278	35	19	0.18	63	0.58	109
Meu_2	138	224	121	300	92	310	33	289	0.28	218	1.15	274
$2SM_2$	149	93	107	76	111	121	33	21	0.52	52	2.45	57
$3S_2M_2$	42	165	13	18	31	175	26	85	0.19	347	0.42	350
MO_3	9	91	17	63	10	175	28	284	0.03	79	1.38	172
SO_3	38	231	41	200	61	242	59	356	0.45	200	3.15	219
SK_3	3	194	13	208	28	359	76	358	0.18	337	1.11	276
M_4	12	325	3	317	29	57	50	132	0.25	59	1.18	18
MS_4	34	9	12	295	77	104	136	138	0.29	142	1.41	32
S_4	11	302	16	323	53	173	78	185	0.45	276	0.54	307
$4MS_6$	3	229	4	345	7	48	1	337	0.05	71	0.37	39
M_6	10	9	9	352	5	129	10	64	0.13	355	0.26	349
$2MS_6$	8	40	14	28	22	149	21	44	0.17	79	0.46	45
$2SM_6$	18	139	11	93	44	211	14	76	0.26	168	1.63	169
S_6	2	286	9	130	21	285	4	265	0.13	36	0.39	27
$4SM_6$	4	242	6	35	4	308	4	14	0.17	202	0.56	221

predicted harmonic series and the residual signal, i.e.

$$\zeta_{Obs}(t) = \zeta_{Pred}(t) + \zeta_{Res}(t)$$

where $\zeta_{Obs}(t)$ is the observed tidal elevation or current, $\zeta_{Pred}(t)$ is the predicted tidal elevation or current, $\zeta_{Res}(t)$ is the difference between the observed and predicted tidal elevation and current.

The predicted harmonic amplitude is given by

$$\zeta_{Pred}(t) = \sum_{i=1}^{n} a_i \cos(\sigma_i t - g_i)$$

where a_i is the amplitude of the ith constituent, σ_i is the frequency of the ith constituent, t is the local time of the data and g_i is the corresponding phase lag.

The residual signal includes all tidal frequencies which are not harmonically analysed as well as atmospheric storm surges. These storm surges usually persist for 2 to 4 days depending on atmospheric conditions.

The harmonic analysis of all tidal constituents (Table 1) utilising programs developed by the National Tidal Facility shows the important aspects of the upper Spencer Gulf tide

Results

The four major primary constituents (M_2, S_2, K_1, and O_1) are the main energy source for the region, and the interactions of the dominant semi-diurnal doublet (M_2 and S_2) generate suites of quarter-diurnal (M_4, MS_4, S_4), frictional semi-diurnal ($3M_2S_2$,μ_2[2], $2SM_2$ and $3S_2M_2$) and frictional sixth-diurnal ($4MS_6$, M_6, $2MS_6$, $2SM_6$, S_6, and $4SM_6$) shallow water constituents (Pugh 1987). Terdiurnal (MO_3, SO_3, and SK_3) shallow water constituents are also generated through interactions between the four major primary constituents. The MK_3 constituent, however, is not resolvable from the SO_3 constituent owing to the short length of our records. The tidal energy spectrum at the Central Australian Railway bridge (Fig. 3) clearly shows energy peaks for each of these bands, and also that this energy is resolved by the harmonic analysis. Two prominent higher frequency bands not presented in Table 1, are also shown

Table 1 indicates that the primary constituents have a maximum amplitude between the Whyalla Railway bridge and the salt bridge and also that their phases increase between Port Augusta and the Central Australian Railway bridge. At Port Augusta the tidal currents lead the tidal elevation by about 60°, indicating a northwards propagation of energy.

Each group of the shallow water constituents appears to behave differently, although there is large variability between the constituents within the groups. The

[2] Only part of μ_2 is a shallow water constituent, μ_2 also is a minor primary tide.

clearest signal is shown by the quarter-diurnal constituents, the amplitudes of which are far greater at the Central Australian Railway bridge. The amplitudes are approximately in the ratio of 1:2:1 for most stations in agreement with theoretical prediction (Gallagher & Munk 1971) and differ by about 180° between Port Augusta and the salt bridge (Table 1). This is consistent with a node occurring near the Whyalla Railway bridge where the quarter-diurnal amplitudes are a maximum. The phase of the terdiurnal constituents also differs by about 180° between Port Augusta and the Central Australian Railway bridge where the amplitudes are about half of the quarter-diurnal amplitudes.

The frictional sixth-diurnal constituents, on the other hand, tend to have maximum amplitudes at the salt bridge and very variable phases. Finally, the frictional semi-diurnal constituents show maximum amplitudes at Port Augusta, with the suggestion of secondary maxima at the salt bridge.

Discussion

The propagation of the primary tidal constituents (and also the frictional semi-diurnal shallow water constituents) into upper Spencer Gulf gives rise to the most vigorous tide in South Australia which occurs between the Whyalla Railway bridge and the salt bridge where there is a generation of frictional shallow water tidal energy. The position of this maximum tide coincides approximately with the node of the quarter-diurnal tide. The maximum tidal range is defined as the summation of the mean spring semi-diurnal range (MSR) and the mean spring diurnal range (MDR) where MSR = 2 (M_2 + S_2) and MDR = 2 (K_1 + O_1) (Easton 1978). Following the above definition the maximum recorded tidal range for South Australian waters occurs at the Whyalla Railway bridge and corresponds to an elevation of 4.1 m, compared to the range at Port Augusta of 3.9 m. This tidal range identifies the tide as being at the very upper end of the mesotidal range (2.1 - 4.2 m)

Friedrichs and Aubrey (1988) have classified estuaries in which the lunar semi-diurnal tide (M_2) is dominant over the solar semi-diurnal tide (S_2) into ebb dominant and flood dominant. In an ebb dominant estuary, much greater tidal currents occur during the ebb following the exposure of mudflats and the release of intertidal storage. To overcome these effects the duration of the ebb tide is far less than the flood tide. The consequence of ebb dominance is to provide a mechanism for the long-term outwelling of sediments and pollution. In the reverse situation of flood dominance, the estuary usually does not contain intertidal mudflats and thus the duration of the flood tide is less than the ebb and as a result the currents are greater on the flood tide. Flood dominant estuaries

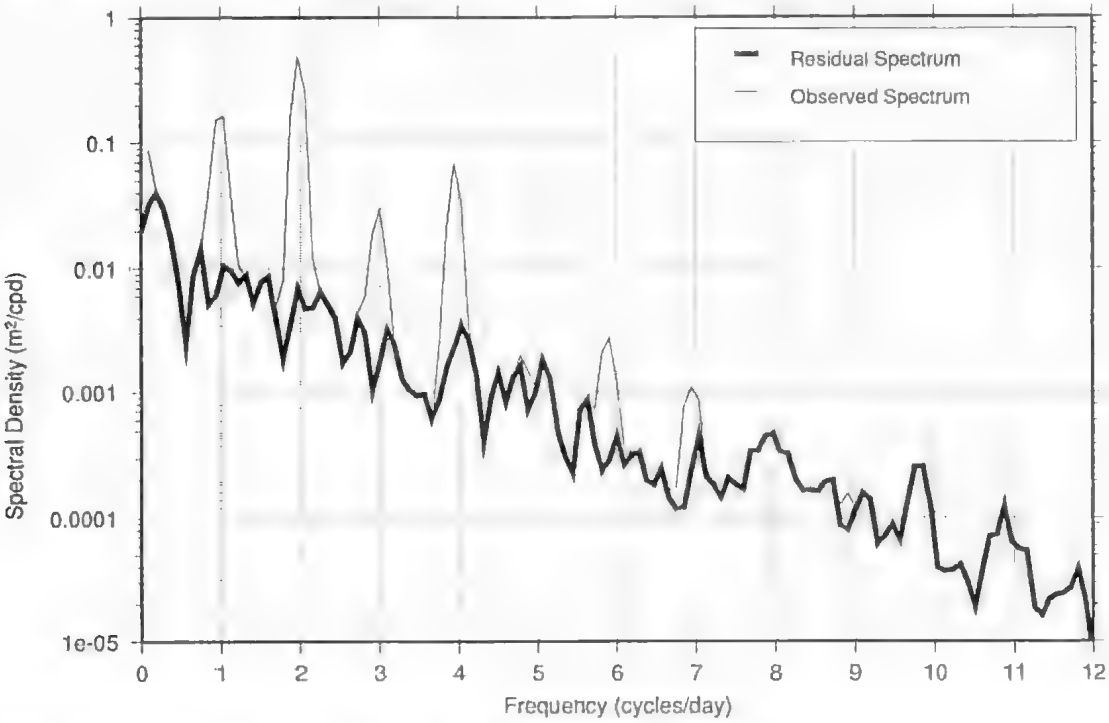

Fig. 3. Power spectrum of tidal energy at the Central Australian Railway bridge.

usually consist of more unstable geometries and in the long term become filled with fine sediments which arise from the net transport into the estuary. This classification is based on the phase difference between the primary lunar tides (M_2) and the major shallow water tide (M_4). In the ebb dominant situation the minimum M_4 current approximately coincides with the maximum of the M_2 current, and in the flood dominant situation the maximum of the M_4 current approximately coincides with the maximum of the M_2 current.

We find that this classification is not appropriate for the brine estuary of upper Spencer Gulf, which behaves either as high water or low water dominant. High water dominant conditions occur when the differences between the high water level and mean sea level are much greater than those between the low water level and mean sea level; the opposite occurs for low water dominant conditions. In high water dominant situations the maximum of the dominant shallow water constituent approximately coincides with the maximum of the primary tidal amplitude and vice versa. For example, at the Central Australian Railway bridge, the phase difference between the MS_4 constituent and its corresponding astronomical generating tide is (M_2+S_2)-$MS_4 = 17°$.

The high water dominant environment consists of a well defined channel which is very shallow at low water, but which can accommodate the propagation of the incoming and outgoing tides except very near high water when overbank flow on the samphire banks occurs. However, with the low water dominant environment, the channel is deep enough to have a negligible effect on low water levels, but as high tide approaches, large volumes of water spill into the adjacent mangrove areas filling up the intertidal depressions and truncating the high water level. The node between these two environments where the most vigorous tide occurs marks the position where these two opposite effects are in balance. These properties appear to be due to the almost equal amplitudes of M_2 and S_2 (see below).

High water dominant conditions are well developed at the Central Australian Railway bridge such that the low water levels appear to be "cut-off" (Fig. 4b). There are four interesting features of this record. First, the low water levels at the neap tide are lower than at the spring tide. It is believed that this is the result of the formation of intertidal pools of gulf water trapped between the Central Australian Railway bridge and Yorkey Crossing. Water is held in this region on the ebbing tide which is slowly drained until the tide turns but during the neap cycle, less water is able to be stored in the upper reaches and subsequently the low water level is less than the spring tidal level.

Second, the diurnal inequality of the tide produced by the beating of the diurnal and semi-diurnal constituents is significantly modulated at the Central Australian Railway bridge relative to the Whyalla Railway bridge due to the generation of the terdiurnal tides.

Third, the residual records show that storm surges are usually greatly attenuated between Whyalla and Central Australian Railway bridges.

Fourth, the drainage from the samphire flats retards the low tide much more than the high tide. The approximate lags between Yorkey Crossing and Port Augusta, determined directly from the short tidal records of the pilot study, were high water 35 min, low water 180 min. Similar results can be obtained from Fig. 4a and b. The difference between the lags is primarily due to the major quarter diurnal shallow water tide (MS_4), as can be seen from Fig. 5a in which the three tidal constituents M_2, S_2 and MS_4 are represented as well as the combination of the three. An interesting feature of Fig. 4b is the form of the tidal range curve during the ebb, which resembles an exponential drainage curve, and is clearly reproduced in Fig. 5a. Thus the drainage from the samphire flats is explained harmonically by the existence of MS_4. This appears to be a unique property of the system in which M_2 and S_2 have approximately the same amplitude. The corresponding current record (Fig. 5b), which is constructed by differentiating the tidal elevations with respect to time, and scaling to give maximum tidal velocities similar to the observations ($\sim$0.35 ms^{-1}) shows characteristic current spikes at the beginning of both the ebb and flood tides which are of similar amplitude and also a slow ebb ($\sim$3 cms^{-1}) during low tide. This structure was observed in the short period current meter deployments just south of Yorkey Crossing and at the salt bridge (Bye & Harbison 1987, 1994).

Flattening of high water can be seen in the Whyalla Railway bridge record (Fig. 4a) but the importance of MS_4 (Table 1) is much smaller here than in the high tide dominant conditions at the Central Australian Railway bridge.

Conclusions

Following an extensive field programme of tidal elevations and currents, the largest tide in South Australia is believed to exist in upper Spencer Gulf, north of Port Augusta. This tide is the peak of the three-quarter resonance in Spencer Gulf which gives rise to a rapid increase in amplitude northwards from near Wallaroo. The location of the Whyalla Railway bridge was observed to have the largest amplitudes of the major astronomical tidal constituents (namely the M_2, S_2, K_1 and O_1 tides) giving a tidal range which lies within 4 to 4.5 m where typically the tidal range in both gulfs is closer to 2.5 to 3 m. Just beyond the bridge

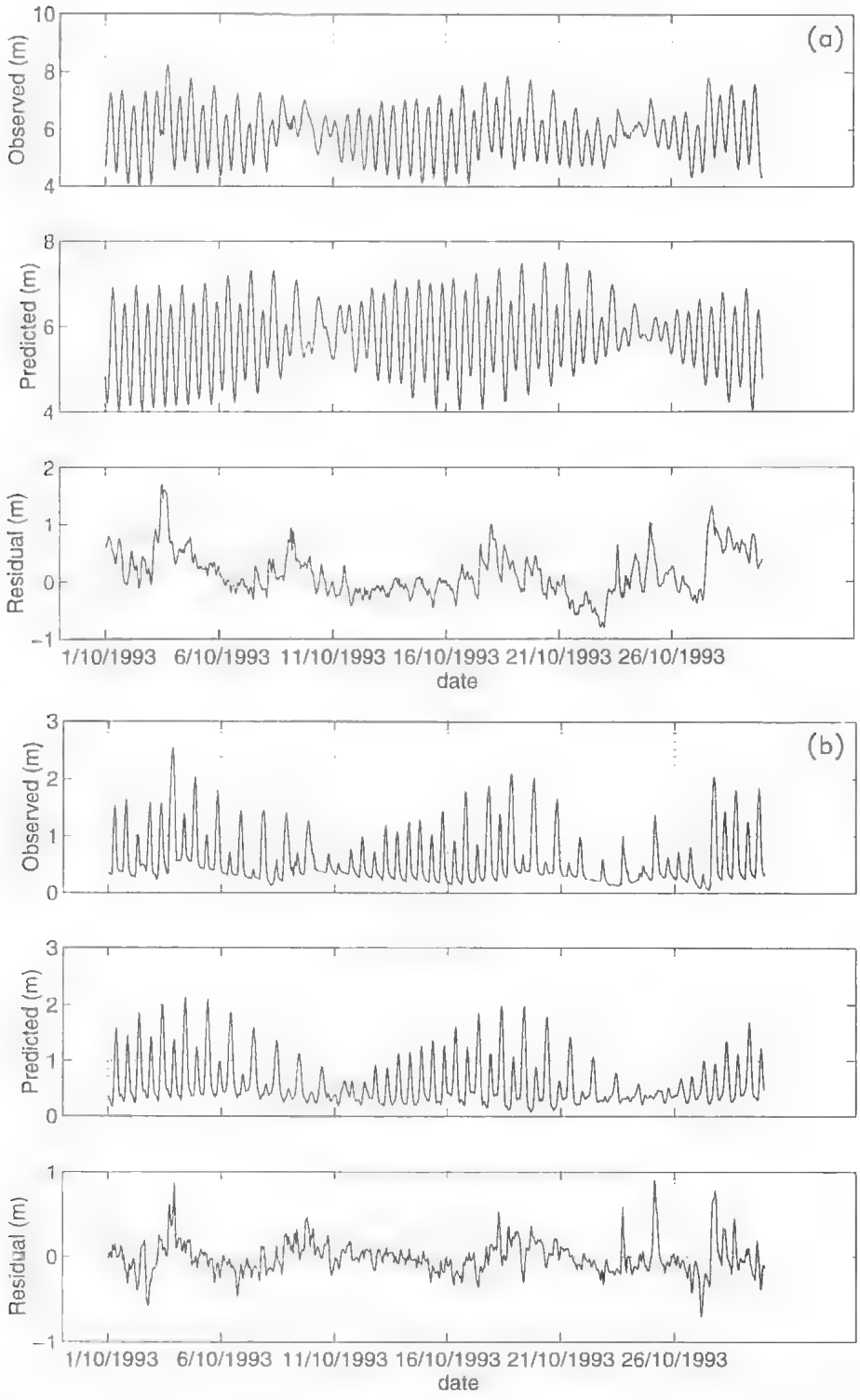

Fig. 4. Tidal observations for October 1993. (a). The Whyalla Railway bridge. (b) The Central Australian Railway bridge. The residual (Res) = the observed (Obs) - the predicted (Pred) tidal elevation.

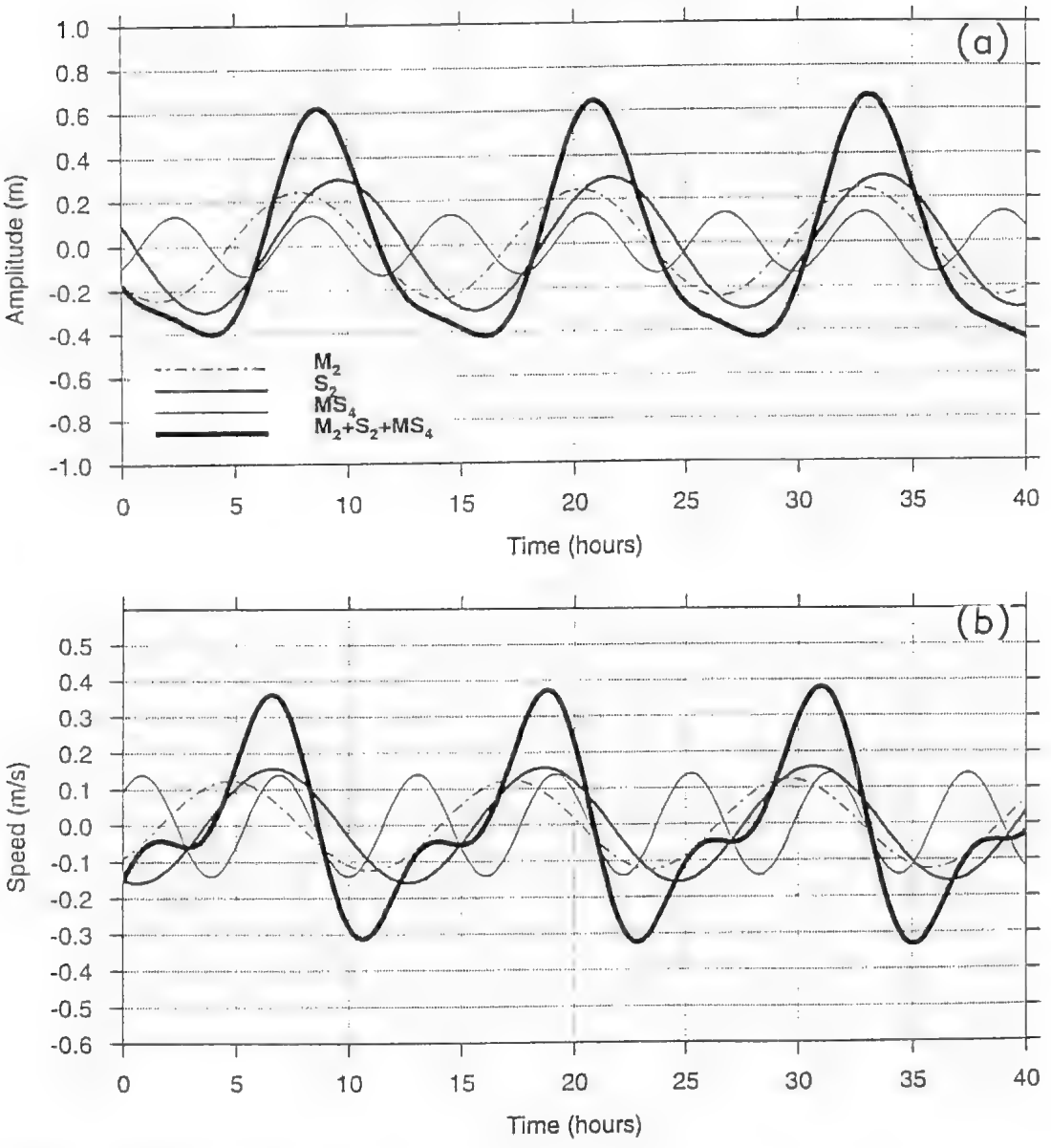

Fig. 5. (a) Tidal elevations and (b) Tidal currents at the Central Australian Railway bridge, constructed using the tidal constituents M_2, S_2, and MS_4.

a shallow water tidal node occurs and we identify this location as the probable position of the largest tidal range. As in all tidal studies, however, the longer the length of tidal records, the better is the harmonic analysis. In this study we have relied on one-two month deployments at several locations. Longer records would be necessary to improve the accuracy of the tidal constants.

The nonlinear interaction between the major astronomical constituents and the surrounding bathymetric features leads to the generation of significant shallow water tides, especially the quarter diurnal MS_4 constituent which dominates because of the similar amplitudes of the M_2 and S_2 tides.

These observations prompt the speculation that the samphire flats and mangrove forest environment have evolved as a positive feedback to the shallow water tidal interactions. In other words, in the absence of the unusual South Australian tidal regime in which the major semi-diurnal tidal constituents (M_2 and S_2) have a similar amplitude, the intertidal environment would be quite different.

It is also likely that the changes in the intertidal environment of upper Spencer Gulf and its northward extension into the Pirie-Torrens plains that have occurred due to sea level changes have been decisively influenced by shallow water tidal interactions.

Acknowledgments

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STUDIES ON EUTOBRILUS HEPTAPAPILLATUS (NEMATODA: TOBRILIDAE) THE PREDOMINANT NEMATODE INHABITING THE BOTTOMS OF LAKE ALBERT AND ALEXANDRINA, SOUTH AUSTRALIA

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KEY WORDS: *Eutobrilus heptapapillatus*, nematodes, Lake Albert, Lake Alexandrina, sediment, eggs, morphology, measurements, crystalloids.

Introduction

The nematode *Eutobrilus heptapapillatus* (Joubert & Heyns, 1979) Tsalolikhin, 1981 has a world-wide distribution in a range of freshwater habitats. In South Australia this nematode occurs at various sites on the shores of Lake Alexandrina and Hindmarsh Island at the mouth of the Murray River (Nicholas *et al.* 1992) and was the most common species extracted from a sample dredged from a depth of 3 m at the southern end of Lake Alexandrina. To date no studies have been published on measurements of this nematode nor of its presence or absence at the bottom of the adjacent Lake Albert.

In this paper I compare measurements of males and females of *E. heptapapillatus* from Lakes Albert and Alexandrina with those from South African populations (Swart & Heyns 1988). I also describe their habitats and their proportions to other nematode species found in these habitats, as well as the percentage of *E. heptapapillatus* containing crystalloid inclusions.

Materials and Methods

Collection of material

Samples were collected using a benthic grab from the bottoms of Lakes Albert and Alexandrina at the following localities. For Lake Alexandrina the collecting site was at the navigation marker No. 84 (Fig. 1 site [1]). The Lake Albert collecting site was 2-3 km off shore from the town of Meningie with compass bearings 135° on the town's water tower, 285° on trees on the Coorong side of the lake, 205° on a headland on the port side and 85° on a barren hill top on the starboard side (Fig. 1 site [2]). In each case the contents of the benthic grab were placed in a plastic bag and stored in a cooled insulated container.

The dry weight of the sediment was determined by allowing it to gravitate from the water included in the benthic sample in a graduated cylinder. The supernatant was removed by suction and the sediment was then spooned into a weighed beaker which was placed in an incubator at 40°C. Dehydration was maintained until a constant weight was reached.

Membrane (0.2 μm) filtered water samples from the lakes were taken simultaneously with the sediment samples taken with the benthic grab. Salinity was calculated from electrical conductivity (Nicholas *et al.* 1992) and a range of elements was analysed using the technique of Zarcinas and Cartwright (1983). Particle size of these samples was measured using various techniques as described by Beech (Nicholas *et al.* 1992).

A large plastic container was filled with lake water from the sampling site and this water was used to dilute the samples during the sieving procedures used to separate the nematodes. This consisted of passing the samples through 2 mm, 850 μm, 710 μm, 250 μm, 120 μm and 90 μm sieves. In samples containing much sand, further sieving through 75 μm, 53 μm and 38 μm sieves was undertaken. However, in the case of Lake Albert samples, the sediment which passed through the 90 μm sieve would have blocked the remaining three sieves. Accordingly, the material obtained on the 120 μm and 90 μm sieves was diluted to facilitate microscopic observation and aliquots were examined under the dissecting microscope. The nematodes were picked out alive on mounted eyelashes, their movement indicating their presence in the sample.

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They were placed in a test tube in a small volume of filtered lake water and an equal volume of boiling double strength FA 4: 1 solution (20 ml 40% formaldehyde and 2 ml glacial acetic acid in 78 ml of distilled water) (Hooper 1986) was added to the shaken suspension of nematodes. These specimens were processed to pure glycerol using Seinhorst's (1959) method and mounted in anhydrous glycerol on slides sealed to a coverslip by molten paraffin as described by De Maeseneer and D'Herde (1963). Nematodes fixed and processed into glycerol in this manner were photographed with Ilford Pan F film. Living nematodes, for example females laying eggs, were photographed using Ilford Delta 400 film. These nematodes were observed and photographed using a Vanox AHBT research microscope equipped with bright field and interference contrast (Nomarski) optics.

Results

The water environment

Lake Albert is a relatively large body of water about 16 km x 10 km connected to Lake Alexandrina, which is approximately 30 km x 15 km, by a narrow channel of water (Fig. 1).

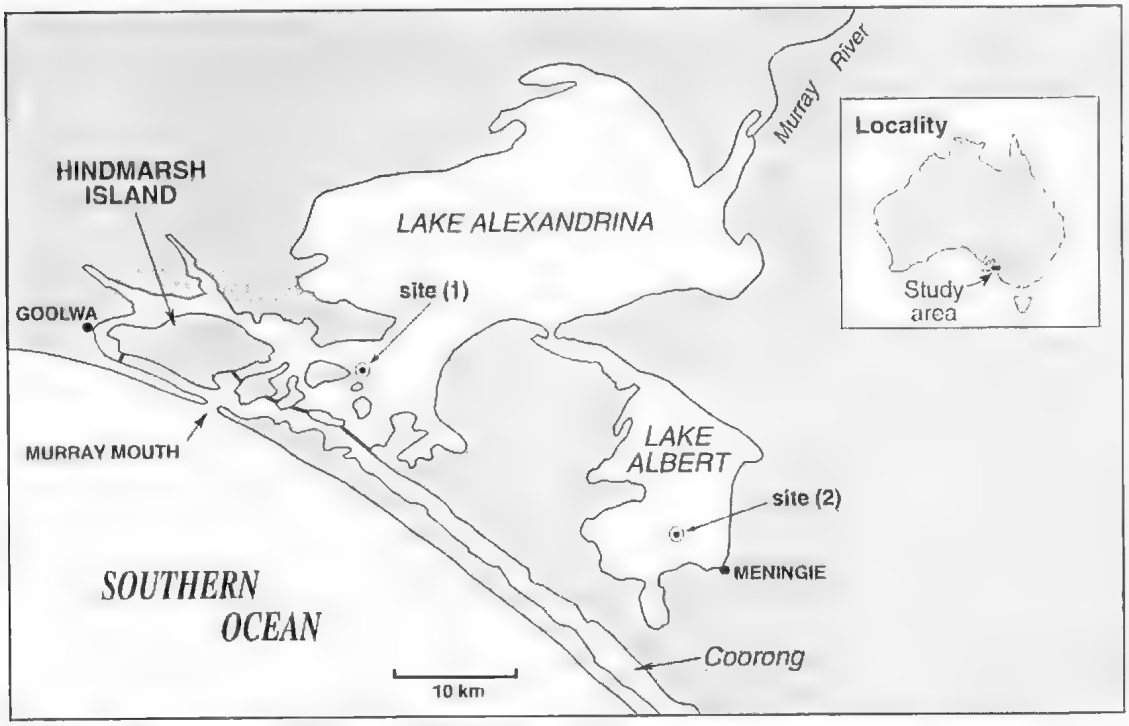

Fig. 1 Map showing the location of collecting sites (1) and (2) in Lakes Alexandrina and Albert respectively.

TABLE 1. *Analyses of major soluble ions in water from the shores of Lakes Alexandrina and Albert sampled on the same day at a six monthly interval and from water sampled from the middle of Lake Albert at a later date.*

Date (Site)	Locality	Na	Cl	Ca	Mg	K	S	E.C.[a] ds m^{-1}	TSS[b] %
				mg l^{-1}					
29 April 1993	Alexandrina	48	82	15	11	5	6	0.42	0.03
(shore)	Albert	214	348	38	33	12	22	1.6	0.10
22 Oct. 1993	Alexandrina	54	105	9	8	3	7	0.4	0.03
(shore)	Albert	200	375	34	31	10	22	1.5	0.10
20 May 1994 (mid-lake)	Albert	188	265	34	28	10	16	1.23	0.06

[a] E.C. = electrical conductivity (deci-siemens m^{-1})
[b] TSS = total soluble salts (estimated percentage)

The results of the analyses of water collected from Lakes Albert and Alexandrina are given in Table 1. From these results it can be seen that there is mostly a three-to four-fold difference in the total soluble salts in water samples collected from the shores of the two lakes on the same day. These differences in the major ions persisted in water samples taken six months later (Table 1).

The sediment environment

The surface 15 cm of the soil at the bottom of Lake Albert consists of a slimy sediment, largely composed of clay which made up 48-61% of samples of this surface sediment or slime taken from various parts of the lake as the top component of core samples (Taylor & Poole 1931).

It was estimated that only 1/6th of the sediment from Lake Albert consisted of solid material. This material comprised 67% clay, 25% silt, 5% fine sand and less than 1% coarse sand.

The nematode

The most common nematode in the Lake Albert sediment, *Eutobrilus heptapapillatus*, comprised up to 87% of the nematode population; the remainder mostly consisted of monhysterids. Similarly the benthic sample from Lake Alexandrina comprised up to 85% *E. heptapapillatus*.

The ratios of larvae, males and females were similar in two different collections from Lake Albert. In one instance an aliquot containing 137 nematodes had 43% larvae, 16% males and 41% females. In the other harvest the ratios were 39% larvae, 23% males and 38% females. In an aliquot containing *E. heptapapillatus* from the Lake Alexandrina benthic sample, the ratios were 51% larvae, 37% males and 12% females. An obvious difference between these two populations was the presence of crystalloid inclusions (Fig. 2) in 32% of the nematodes from Lake Albert whereas none was observed from the Lake Alexandrina sample.

Comparison of populations of E. heptapapillatus.

Specimens from both lakes were measured and compared with each other and with those from South Africa (Swart & Heyns 1988). It can be seen (Table 2) that the males of these three populations are similar in many respects. For example, they are of similar length, have the same body width at the anus and have similarly-sized copulatory spicules. Differences in maximum body width and pharynx length could not be analysed statistically due to the absence of certain measurements of the South African population. There is, however, a significant difference in tail length ($P<0.001$) between the Australian populations (Lake Albert with a mean of 179 μm and Lake Alexandrina with a mean of 173 μm) and the South African population (mean of 244 μm). This significant difference in tail length is not so pronounced ($P<0.01$) in the females of these populations (Table 3). The males of *E. heptapapillatus* (Figs 3, 4) have a diorchic reproductive system consisting of a pair of testes, a vas deferens and ejaculatory duct connecting with the copulatory spicules. The most obvious components of the male's accessory structures are the seven supplementary organs (Fig. 4) from which its specific name is derived.

The distances between these supplementary organs in the South African population have been measured (Swart & Heyns 1988) and so can be compared with the Australian populations. Measurements of the Australian populations are expressed as percentages of the sum of these distances rather than as direct measurements. This is because direct measurements using coiled and uncoiled nematodes revealed a significant difference in the mean value of the distance between supplements in the coiled (27.9 μm) and the uncoiled (41.4 μm) ($P<0.001$). However, when these distances were expressed as percentages of the sum of the distances between supplements, there was no

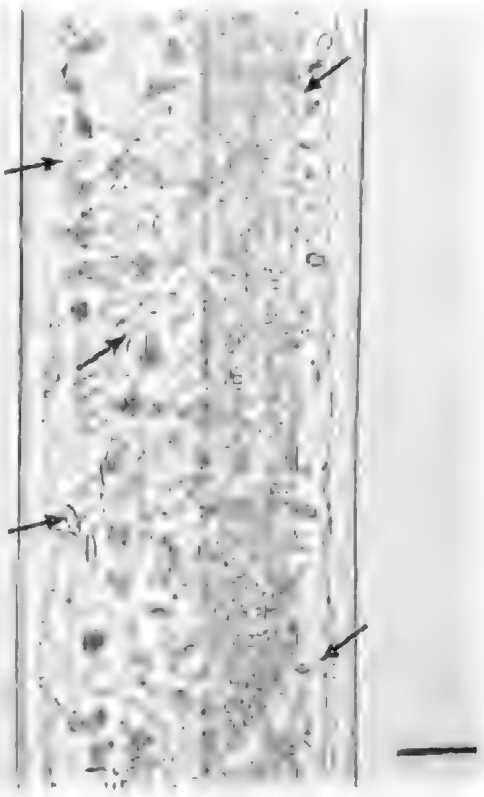

Fig. 2. Photograph of part of an adult female *Eutobrilus heptapapillatus* that had been maintained in shallow distilled water in a Petri dish for over a month prior to being photographed. Bright field optics showing the presence of numerous crystalloid bodies (small arrows). Scale bar = 20 μm

TABLE 2. *Comparison of measurements of different populations of males of* Eutobrilus heptapapillatus.

All measurements μm	Tsitsikama Forest Cape Province, South Africa (Swart & Heyns 1988) n = 7		Lake Albert South Australia (present study) n = 5			Lake Alexandrina South Australia (present study) n = 5		
Parts measured	Range	Mean	Range	Mean	SD	Range	Mean	SD
Body length (L)	1550-2120	1920	1873-2000	1931	±57	1800-1990	1896	±68
Max. body width		53*	66-77	71	±5	60-70	66	±4.1
Pharynx length		369*)	305-327	311	19	270-315	290	±18
Tail length	211-300	244	168-191	179	19	140-192	173	±20
Body width at anus		38*)	36-41	38	±2.7	32-40	38	±3.6
Spicule	48-57	53	50-55	54	±2.2	52-56	53	±1.8
Gubernaculum	35-39	37.0	23-36	31	±5.7	30-36	33	±2.7
De Man's indices a	32.1-41.3	36.2	25.6-30	27	±1.8	28.1-31.3	29	±1.3
De Man's indices b	5.1-5.3	5.2	5.7-6.6	6.2	±0.3	6.1-7.0	6.6	±0.4
De Man's indices c	6.2-8.8	7.9	10.4-11.6	10.8	±0.5	9.9-12.9	11.1	±1.1
De Man's indices c'	5.8-8.0	6.5	4.4-5.3	4.7	±0.4	4.4-4.8	4.6	±0.2

) ,) calculated from data of Swart & Heyns (1988)

TABLE 3. *Comparison of measurements of different populations of females of* Eutobrilus heptapapillatus.

All measurements μm	Tsitsikama Forest Cape Province, South Africa (Swart & Heyns 1988) n = 21		Lake Albert South Australia (present study) n = 5			Lake Alexandrina South Australia (present study) n = 5		
Parts measured	Range	Mean	Range	Mean	SD	Range	Mean	SD
Body length (L)	1720-2280	2040	2182-2254	2209	±30	1940-2200	2094	±128
Max. body width		80*)	82-95	88	±6	65-82	74	±8.2
Pharynx length		385*)	336-382	358	±18	285-345	320	±22
Tail length	228-337	292	246-268	242	±20	224-296	261	±27
Body width at anus		34*)	41-45	42	±2	36-40	38	±2
De Man's indices V	39-48	42	41-47	45	±1	33-48	40	±6.0
De Man's indices a	26-41	34	23-27	25	±2	26-34	28	±3.2
De Man's indices b	4.8-5.9	5.3	5.9-6.6	6.2	±0.3	6.1-6.9	6.6	±0.3
De Man's indices c	6.1-9.0	7.1	8.2-10.2	9.2	±0.8	7.4-8.7	8.1	±0.5
De Man's indices c'	6.8-10.0	8.7	5.3-6.5	5.8	±0.5	6.2-7.4	6.8	±0.4

) ,) calculated from data of Swart & Heyns (1988)

significant difference ($P>0.05$) between the means of coiled (14.3%) and uncoiled (also 14.3%) nematodes. Thus expressing distances between supplements as percentages rather than actual measurements when making comparisons between nematodes that are coiled into various shapes provides a standardised measure for differently-coiled nematodes.

Measurements of the Australian populations were combined to obtain a pooled estimate of the means and standard deviations. Because these values appeared normally distributed, standard deviations of the South African values were calculated assuming a normal distribution (Table 4).

The positions of the Australian population male supplementary organs differ in some respects from those of the South African population (Table 4) although these differences are not significant except for the S_2 and S_3 ($P<0.01$). These differences appear minor compared with the similarities that exist between the populations. Thus the females (Table 3) are of similar length and have a similar vulval position although the South African population appears narrower with a longer pharynx and a significantly longer tail. The females of this species (Figs 5, 6) are didelphic amphidelphic. The genital tract (Fig. 6) consists of ovary, short oviduct, pars dilatata and uterus that may contain oval-shaped sperm.

Egg laying

The laying process was observed in a specimen collected the previous day from Lake Alexandrina. It was in a sitting drop slide in filtered Lake Alexandrina water (0.2 μm membrane). Egg laying took place at 23°C and was very rapid, the actual emergence of the egg being completed in several seconds. The whole process was filmed (Fig. 7) (Ilford XP 1 400 film). The egg is shown moving from the pars dilatata into the uterus (Fig. 7A, B) and from there into the vagina (Fig. 7C, D). During the final stages of laying, the egg moves from the vagina to the exterior through the vulva (Fig. 7E, F, G, H). The egg which is oval (ellipsoidal) within the nematode assumes a spherical shape soon after laying (Fig. 8). It has a mean diameter of 70.8 μm (±2.9 SD) including the shell which has a mean thickness of 8.4 μm (±0.6 SD). This compares with *in utero* measurements of fixed material of 73.5 μm x 48.9 μm including an egg shell thickness of 5.5 μm (Swart & Heyns 1988).

Discussion

Over 60 years ago Taylor and Poole of CS&IR Division of Soil Research (now CSIRO Division of Soils) published the results of a soil survey of the bed of Lake Albert (Taylor & Poole 1931). This work resulted from a request by the appropriate branches of both the State

TABLE 4. *Comparison of measurements of distances between supplementary organs, expressed as percentages of the sum of the distances between supplements, in different populations of males of* Eutobrilus heptapapillatus.

Parts measured			Tsitsikama Forest Cape Province, South Africa (Swart & Heyns 1988) n = 5			Lake Albert South Australia (present study) n = 5			Lake Alexandrina South Australia (present study) n = 6		
			Range	Mean	SD*	Range	Mean	SD	Range	Mean	SD
Cloaca	→	S7	7.6-11.4	9.3	±1.6	4.7-11.8	8.5	±2.6	9.1-11.8	9.8	±1.1
S7	→	S6	7.6-9.2	8.3	±0.7	6.0-9.9	8.1	±1.4	8.7-12.3	10.3	±1.3
S6	→	S5	8.8-11.3	10.2	±1.1	9.7-12.2	11.1	±1.2	10.3-13.0	11.6	±0.9
S5	→	S4	16.2-17.8	17.4	±0.7	16.5-23.1	20.1	±2.8	17.0-21.7	19.1	±1.6
S4	→	S3	14.4-17.6	15.6	±1.4	13.2-15.3	14.3	±1.0	12.3-15.3	13.6	±1.1
S3	→	S2	19.9-21.6	20.8	±0.7	15.3-19.7	17.2	±1.7	15.4-18.2	16.7	±1.0
S2	→	S1	16.4-20.3	18.4	±1.6	18.6-25.0	20.7	±2.5	15.1-20.8	18.9	±2.0

*= estimated using sample size and range and assuming normal distribution

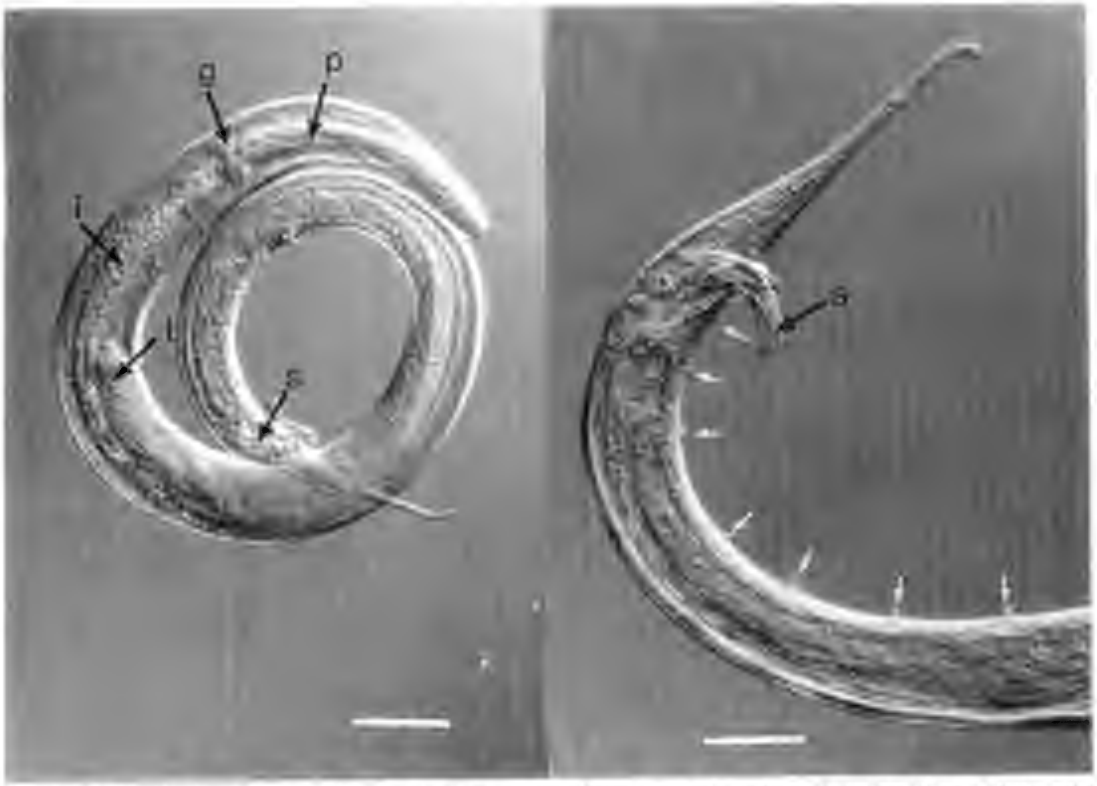

Fig. 3. Photograph of an adult male *Eutobrilus heptapapillatus* from Lake Albert. Nomarski optics showing pharynx (p), intestine (i), pharyngeal glands (g), testis (t), retracted copulatory spicules (s). Scale bar = 100 μm.

Fig. 4. Photograph of an enlarged portion of an adult male *Eutobrilus heptapapillatus* from Lake Albert. Nomarski optics showing the seven supplementary organs (small arrows) and the everted copulatory spicules (s). Note relatively short tail. Scale bar = 50 μm.

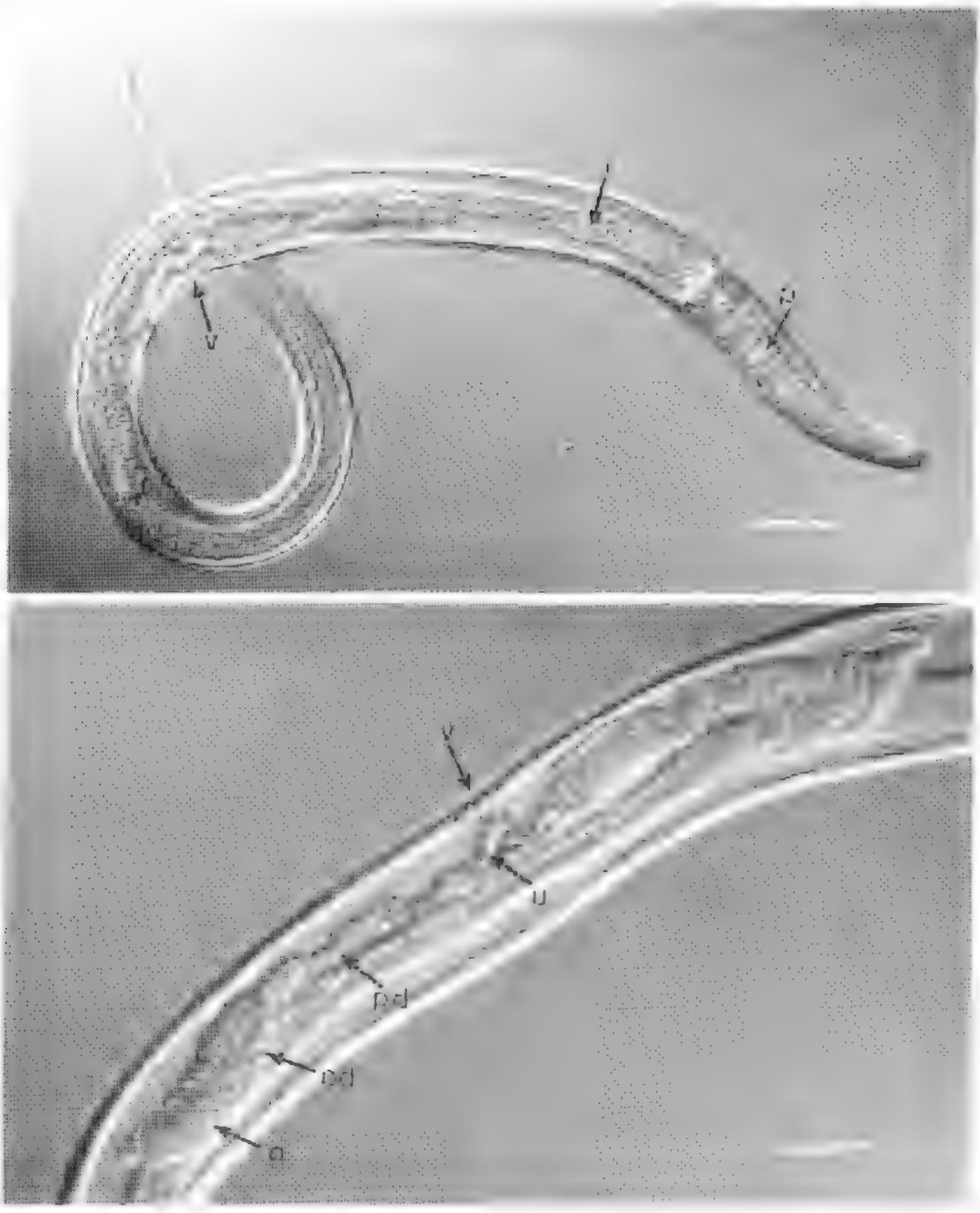

Fig. 5. Photograph of an adult female *Eutobrilus heptapapillatus* from Lake Albert. Nomarski optics showing pharynx (p), intestine (i) and vulva (v). Scale bar = 100 μm.

Fig. 6. Photograph of an enlarged portion of an adult female *Eutobrilus heptapapillatus* from Lake Albert. Nomarski optics showing the didelphic reproductive system consisting on each side of ovary (o), short uterus (u), pars dilatata (pd), uterus (u) and vulva (v). Scale bar = 50 μm.

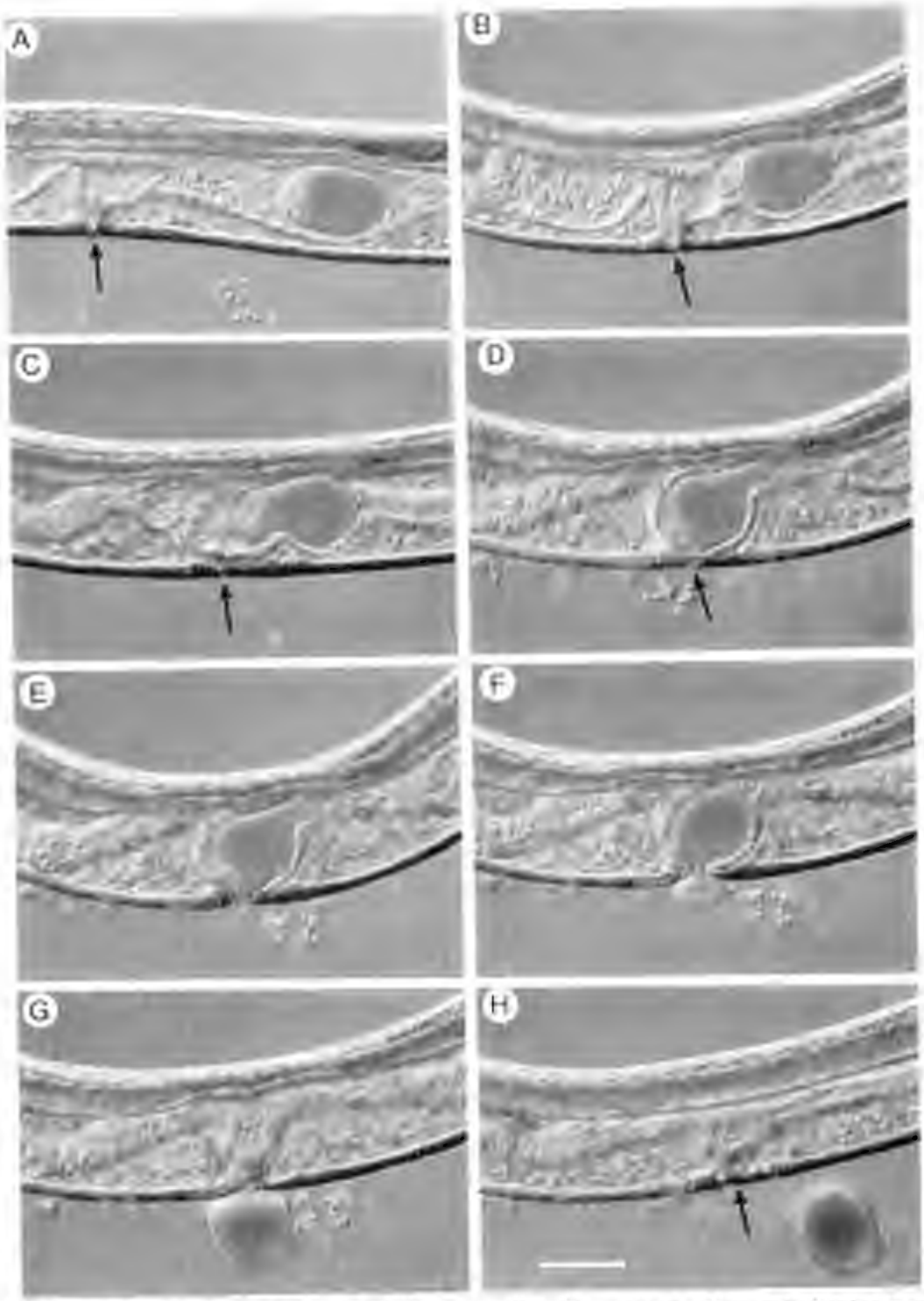

Fig. 7 Photographic sequence of egg laying in *Eutobrilus hepatopapillatus*. Nomarski optics. Arrows indicate vulval opening. A., B. Movement of the egg from the pars dilatata to the uterus. C., D. Movement of the egg from uterus to vagina. E., F., G. The process of laying as the egg passes from the vagina to the exterior via the vulva. H. The newly laid egg. Scale bar = 50 μm.

and Commonwealth Governments regarding the feasibility of using the soil at the bottom of the lake for agriculture after it had been drained. Taylor and Poole (1931) showed that the drained lake would be unsuitable for agricultural purposes. Thus, at a time when the clearing of land was in full swing, these workers were able to show, as a result of their soil survey, conducted under difficult conditions, that drainage of this lake would have been a costly mistake. Furthermore, their detailed results (Taylor & Poole 1931) provided valuable information on which to base further studies of the lake's benthos.

Taylor & Poole (1931) reported that Lake Albert was once connected to the saline waters of the Coorong by an ancient river channel which persists today as a lagoon extending from the southern side of the lake (Fig. 1). Thus, although Lake Albert is not now flushed through by waters of the River Murray, as is Lake Alexandrina, it may once have been when the river was in flood.

The barrages at the mouth of the River Murray were not built until 1940 so that at the time of Taylor's and Poole's survey during March to April 1930 when the river was running low, Lake Alexandrina had become very saline as a result of incoming sea water. Thus water from Lake Alexandrina was making the water from Lake Albert more saline and "was not potable for humans and taken unwillingly by stock until accustomed to it" (Taylor & Poole 1931). Today, due to the presence of the barrages, Lake Alexandrina is much less saline than it was and although the quantities of soluble salts contained in its water can and do vary from time to time depending on river flushings, it is clear from the samples collected on the same day from both lakes at a six-monthly interval (Table 1) that Lake Albert has a higher concentration of soluble salts than Lake Alexandrina during normal river flow. Nicholas *et al.* (1992) have shown that the concentration of soluble salts in water collected from sites on the shore of Lake Alexandrina varies from month to month and hence it was necessary to collect water from the two lakes on the same day so that valid comparisons could be made.

It is interesting to speculate whether or not the presence of crystalloid bodies observed in *E. heptapapillatus* from Lake Albert but not in specimens of the nematode collected on the same day from Lake Alexandrina when its soluble salt values were low, might be associated with increased salinity in these lakes. Crystalloid bodies were found in *E. heptapapillatus* collected from Lake Alexandrina both at the water's edge and from the bottom of the lake in 97% of the nematodes examined (Bird *et al.* 1991) but no correlation was made with the salinity of the lake at that time. However, examination of these data shows that the concentrations of sodium and chloride ions (Table 2 - Nicholas *et al.* 1992) were greater than those obtained from this lake during the present study (Table 1). Furthermore, contrary to our findings that nematodes maintained in aquaria over a period of two months "appeared to be free of crystalloids," I have found that there was an almost three-fold increase in both numbers of *E. heptapapillatus* and their crystalloid content when mud from Lake Albert was placed in an aquarium tank, covered with Lake Albert water and left for four months with occasional aeration. Under these conditions, the ratio of larvae to females to males was 85 : 12 : 3 of which 93% contained crystalloids. The large number of larvae present would probably be due to relatively recent hatching from eggs and the low number of adults to lack of food. The increase in the percentage of crystalloids present from 32% to 93% in nematodes kept in an aquarium tank for four months would probably be due to an increase in the concentration of soluble salts due to evaporation from the tank. This particular batch of Lake Albert water (collected on 20 May 1994) had initial sodium and chloride ion readings of 188 and 265 mg l^{-1} respectively (Table 1) which are apparently high enough to induce the development of crystalloids.

The occurrence and possible functions of crystalloids in a number of genera of aquatic free-living nematodes have been recorded by various workers (Bird *et al.*

Fig. 8. Photograph of freshly laid eggs of *Eutobrilus heptapapillatus*. Bright field optics showing vulva (v) and spherical eggs (e) with their relatively thick shells (es). Scale bar = 20 μm.

1991) but as yet no clear-cut evidence for their function has been obtained.

Clearly further research is required to test whether these crystalloid structures are produced in the nematodes in response to changes in their environment and whether or not they are a manifestation of a diseased state, since they appear to be associated with small regular particles that resemble icosahedral viruses in some respects (Bird *et al.* 1991).

I think that this nematode which predominates in the sediment at the bottom of these lakes is *E. heptapapillatus* although, as will be discussed below, there are some differences between the Australian and South African populations. It has all the characteristics of its Subfamily (Eutobrilinae) described by Tsalolikhin (1983) namely, hedgehog-like supplementary organs (Fig. 3), a muscular vagina and well-differentiated female genital system (Fig. 5) and well-developed and rounded pharyngeal glands. Similarly, it is less than 3.5 mm in length and it has the described species characteristics of a cuticle without pronounced annulations, head bristles that do not exceed 14 μm and, most obvious of all, males with seven supplementary organs. It does not quite fit Tsalolikhin's key in having females whose tails are not ten times greater than the body width at the anus (Table 3) but this also applies to the South African specimens (Swart & Heyns 1988). However, these various morphological differences are likely to be reflections of variability between different populations of this species of nematode rather than suggesting that the Australian and South African nematodes are different species.

Another apparent difference is that the egg, although oval-shaped when within the female, becomes round when laid (Figs 7, 8). However, it seems likely that egg measurements in the past may have all been made while the eggs were within the female in fixed material. The transition from oval within the female to spherical on laying is, however, illustrated by Tsalolikhin (1983) in his book. Since eggs of these species can not be identified unless laid from an identified female, their shape for taxonomic purposes is listed in the description of the genus *Eutobrilus* as oval (Tsalolikhin 1983). Furthermore, since fixation leads to shrinkage, measurements from fixed material will always be lower than those for unfixed, freshly laid eggs.

The combination of characters described above places these worms firmly in the Tobrilidae. Minor differences between the populations in South Australia and South Africa are not considered significant and the worms are confidently referred to as *E. heptapapillatus*.

Much remains to be learnt about this cosmopolitan nematode. Its feeding habits, rates of growth and longevity in the lakes are unknown. Such information is needed if its value as an indicator of environmental pollution in these environments is to be determined.

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DISTRIBUTION OF SPECIES OF TRICHOSTRONGYLOID NEMATODE PARASITES IN THE SMALL INTESTINE OF THE BUSH RAT, RATTUS FUSCIPES

By L. F. Skerratt, I. Beveridge* & M.-C. Durette-Desset†*

Summary

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Key Words: Parasite, ecology, niche, Trichostrongyloidea, Rattus, interaction.

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KEY WORDS: Parasite, ecology, niche, Trichostrongyloidea, *Rattus*, interaction.

Introduction

One mode by which parasite evolution may occur is "host switching" (Chabaud 1965). This involves a break-down in host specificity allowing the transfer of a parasite from its usual host to an unrelated host species occupying the same environment. The new host may be infected through the skin by free-living stages of the parasite or may ingest the infective form of the parasite with its food (Chabaud 1965). The mechanism of host switching appears to be common among parasitic nematodes (Chabaud 1982) and is based on the assumption that the invading nematode parasite is occupying a previously vacant niche within the new host. In the case of intestinal parasites this is usually defined as a restricted longitudinal or radial distribution within the gut of the host (Schad 1963). Host switching within the nematode superfamily Trichostrongyloidea is well documented (Durette-Desset 1985), yet few studies have examined whether the invading nematode actually occupies a separate or previously-vacant niche.

The trichostrongyloid nematode parasites of the native bush rat, *Rattus fuscipes*, offer the opportunity to examine such an hypothesis. At one locality in Victoria (Blackwood) Obendorf (1979) found that *R. fuscipes* was parasitised by three species of trichostrongyloids, the heligmosomes *Nippostrongylus magnus* (Mawson, 1961) and *Odilia bainae* Beveridge & Durette-Desset, 1992 and the herpetostrongylid *Paraustrostrongylus ratti* Obendorf, 1979 (Obendorf 1979; Beveridge & Durette-Desset 1992a,b, 1993). *P. ratti* belongs to a genus which otherwise occurs exclusively in marsupials and which presumably has switched to its current eutherian host (Obendorf 1979). It is considered (Obendorf 1979) to be one of only two examples of trichostrongyloid nematodes switching from marsupials to native rodents, the other being *Woolleya hydromyos* in the water rat, *Hydromys chrysogaster* (see Mawson 1961, 1973). *O. bainae* belongs to a genus which is parasitic primarily in hydromyine rodents and species of the genus were considered by Durette-Desset (1985) to have switched secondarily to murine rodents such as *R. fuscipes*. Only *Nippostrongylus magnus* can be considered an original parasite of this murine rodent (Beveridge & Durette-Desset 1992a).

The current study was therefore undertaken to determine the ecological niches occupied by *N. magnus*, *O. bainae* and *P. ratti* within the small intestine of *R. fuscipes* and to examine the extent of overlap between them to establish whether or not each occupies a distinctive intestinal niche.

Materials and Methods

Ten bush rats, *Rattus fuscipes*, were trapped from along the banks of the Lerderderg River, Blackwood, Victoria, Australia (37° 29' S, 144° 19' E) using collapsible aluminium traps baited with peanut butter. Immediately following euthanasia with chloroform, the small intestine was removed and divided into sixteen equal parts. The total length of the small intestine was measured. Gut segments were incubated in saline at 37°C for at least 2 hours and all nematodes which emerged from the mucosa were fixed in hot 70% ethanol before being counted. *P. ratti* was distinguished

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from other species based on the description of Obendorf (1979) using a stereomicroscope, whereas *N. magnus* and *O. bainae* were differentiated using the descriptions of Beveridge & Durette-Desset (1992 a,b) and a compound microscope following clearing in lactophenol. The rats were also routinely examined for other helminth parasites.

The number of each species of nematodes in individual sections of the small intestine was converted to a percentage of the total number of each species present. For each species, the positions of the anterior, median and posterior nematodes were determined using the method of Bush & Holmes (1986), such that the section number in which nematodes occurred was converted to a percentage of the total length of the small intestine. It was assumed that nematodes were uniformly distributed within each section.

Differences in distribution between species were tested statistically using values calculated from a 2 x 5 contingency table (species x sector of intestine) for each species pair. Sections 5 to 16 of the intestine, where very few nematodes were found, were combined to form a single cell in the table.

The extent of niche overlap between the three species was determined using the equation

$$Cxy = 1 - \tfrac{1}{2}(\Sigma|Pxi - Pyi|)$$

where

$$Pxi = \frac{xi}{\bar{X}} \quad , \quad Pyi = \frac{yi}{\bar{Y}}$$

(Hurlbert 1978)

such that Pxi and Pyi are the proportions of two species, x and y, in different segments of the intestine.

This equation was used to calculate the "fundamental overlap" between species pairs, which is the extent of overlap (Cxy) in the mean distributions of the two nematode species and the "realised overlap" which is obtained by determining the extent of overlap (Cxy) between two nematode species in individual rats and then computing the average of the individual overlaps.

Differences between fundamental and realised overlaps, that is when the realised overlap was substantially less than the fundamental overlap, were used to infer the presence of competition between nematode species.

Seven laboratory rats, *R. norvegicus*, were infected either subcutaneously or orally with 200 - 900 infective larvae of *N. magnus* or *O. bainae* (Table 3). The infective larvae were obtained by culturing a mixture of faeces from naturally infected rats with activated charcoal on moist filter paper and recovering developed larvae by sedimentation in water. Larvae were separated on the basis of morphological differences (shape of the tail) identifiable using a stereomicroscope (unpublished observations). Infected rats were killed with chloroform 14 days after infection and the distribution of nematodes in the small intestine determined in a similar fashion to that described above. Experimental infections with *P. ratti* via oral, subcutaneous and percutaneous routes were unsuccessful.

TABLE 1. *Position of mean anterior, median and posterior individuals (± standard error of mean) of* Nippostrongylus magnus, Odilia bainae *and* Paraustrostrongylus ratti *as percentage distances along the small intestine in ten naturally infected bush rats,* Rattus fuscipes.

	Anterior	Median	Posterior
N. magnus	1.01 ± 0.64	15.14 ± 4.84	56.63 ± 10.17
O. bainae	2.17 ± 0.84	18.23 ± 3.07	48.40 ± 6.47
P. ratti	3.22 ± 1.62	19.06 ± 2.25	49.40 ± 4.42

Results

Nematode distributions in wild rats

N. magnus occurred in 100% of the wild bush rats examined, with a mean intensity of 67 and a range of 11-183. *O. bainae* was present in 100% of wild rats examined, with a mean intensity of 64 and a range of 11-173. *P. ratti* was present in 90% of wild rats examined with a mean intensity of 171 and a range of 1-1094 (Table 4).

Other parasites found in the ten naturally infected bush rats were very small numbers of *Capillaria* sp. (Nematoda) in the first segment of the small intestine and *Capillaria gastrica* (Baylis, 1926) within the squamous epithelium of the stomach in five rats. There was no pathological reaction to adult *Capillaria* or eggs within the squamous epithelium. *Heterakis spumosa* (Schneider, 1866) was found in the large intestine of eight rats. The cestodes *Choanotaenia rutticola* (Sandars, 1957), *Hymenolepis diminuta* (Rudolphi, 1819) and *Bertiella anapolytica* Baylis, 1934 were found in the small intestine. *C. rutticola* inhabited the opening of the bile duct, causing hyperplasia of the bile duct epithelium. *H. diminuta* and *B. anapolytica* were found in segments 4-12 and 5-16 respectively. However, *H. diminuta* was distributed anteriorly to *B. anapolytica* when both species occurred in rats.

N. magnus occurred mainly (64%) in the anterior two segments of the small intestine in naturally infected rats, with maximum intensity in the first segment, and its numbers declined progressively in the remaining sections (Fig.1). The majority of *O. bainae* (82%) inhabited the five most anterior segments in naturally infected bush rats with a maximum intensity (30%) in the second segment (Fig. 1). The majority of *P. ratti* (87%) were distributed throughout the five anterior segments of the small intestine in naturally infected rats (Fig. 1) with maximum intensity occurring in segments 1 to 4. Small intestine lengths ranged from 56-92 cm (mean 71 cm) and hence the average length of each segment was 4.5 cm.

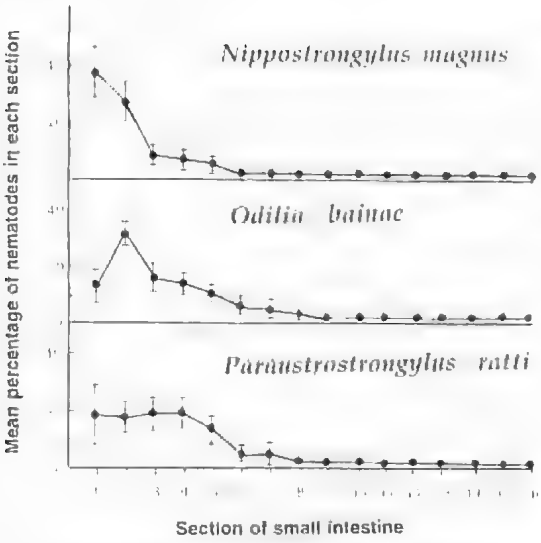

Fig. 1 Distribution (mean percentage ± standard error [error bars]) of *Nippostrongylus magnus*, *Odilia bainae* and *Paraustrostrongylus ratti* in each segment (sixteenths) of the small intestine of ten naturally infected bush rats, *Rattus fuscipes*

N. magnus, *O. bainae* and *P. ratti* were sequentially distributed along the small intestine of naturally infected bush rats but differed in the positions of their mean anterior, posterior and median individuals (Table 1). The mean anterior and median individuals of *N. magnus* were anterior to those of *O. bainae* which were more anterior to those *P. ratti*. However, the mean posterior individual of *N. magnus* was posterior to both *O. bainae* and *P. ratti*. This was due to *N. magnus* inhabiting the posterior quarter of the small intestine in two rats, whereas *O. bainae* and *P. ratti* were not found in this segment. The distributions of the three nematode species were significantly different. Chi-squared values obtained for pair-wise comparisons were *N. magnus* - *O. bainae*, $\chi^2_4 = 77.5$ ($p<0.001$), *O. bainae* – *P. ratti*, $\chi^2_4 = 90.9$ ($p<0.001$), *N. magnus* - *P. ratti*, $\chi^2_4 = 18.5$ ($p<0.001$). There was no correlation between mean positions of nematodes with intensity of infection, except in the case of the posterior position of *O. bainae* ($r^2 = 0.68$, $p = 0.004$).

The variation in numbers of trichostrongyloid nematodes in each segment of the intestine of naturally infected bush rats was large (Table 4), with the standard deviation equal to or greater than the mean (see standard error bars in Fig. 1). Despite this variation, the difference in distribution was greater in individual rats (1- realised overlap) than the difference in their mean distributions (1- fundamental overlap). The realised overlap was lower than the fundamental overlap in 25 of 28 species interactions. The mean realised overlap between *N. magnus* and *P. ratti* was lower than the overlap between *N. magnus* and *O. bainae* and between *O. bainae* and *P. ratti* (Table 2). The total numbers of each species of nematode in individual rats and the realised overlaps in natural infections varied between individuals but the two parameters were independent of one another ($r^2 < 0.3$). *Capillaria* sp. occurred in such low numbers that

TABLE 2. *Fundamental and realised overlap between niches of* Nippostrongylus magnus, Odilia bainae *and* Paraustrostrongylus ratti *in the small intestine of ten naturally infected bush rats*, Rattus fuscipes.

Nematode species pair	No. of rats infected with both species	Fundamental overlap	Realised overlap (± standard deviation)
N. magnus – O. bainae	10	0.68	0.55 ± 0.14
N. magnus – P. ratti	9	0.61	0.40 ± 0.27
O. bainae – P. ratti	9	0.82	0.55 ± 0.23

TABLE 3 *Percentage of* Nippostrongylus magnus *and* Odilia bainae *occurring in 16 segments of the small intestine of laboratory reared* Rattus norvegicus *following oral or percutaneous infection with third stage larvae*

Segment no. of intestine	Mean percentage of nematodes in segment (± standard error)	
	Nippostrongylus magnus	*Odilia bainae*
No. of rats	4	3
1	85.3 ± 13.1	91.0 ± 5.8
2	2.3 ± 2.2	7.0 ± 6.7
3	2.5 ± 2.5	2.3 ± 2.3
4	10.0 ± 6.8	0
5 - 16	0	0

Table 4. *Numbers of nematodes*, Nippostrongylus magus, Odilia bainae *and* Paranstrostrongylus ratti *in sections (1/6) of the small intestine of ten naturally infected bush rats*, Rattus fuscipes.

Section of intestine	Rat number 1	2	3	4	5	6	7	8	9	10
1	14,5,0	0,0,1	2,1,1	5,0,1	31,11,0	5,13,7	42,22,10	42,2,2	37,3,1	49,4,238
2	1,0,0	8,9,8	6,18,0	19,3,5	0,16,0	8,32,6	4,31,36	29,11,1	33,17,19	40,16,366
3	2,0,0	2,6,2	1,9,0	3,3,2	3,36,2	0,9,6	4,9,25	20,10,5	13,7,40	11,2,225
4	2,3,0	1,1,2	3,7,0	8,2,13	0,12,0	1,0,12	4,7,56	7,21,18	3,12,26	9,5,133
5	0,2,0	0,0,0	6,1,0	5,5,18	0,13,1	0,9,0	3,2,16	1,9,9	3,10,34	9,2,76
6	0,1,0	0,0,1	0,0,0	2,4,4	2,4,0	0,6,1	0,1,22	0,1,4	1,17,10	4,3,39
7	0,0,0	0,0,0	0,0,0	10,3,18	0,1,0	0,7,0	0,0,7	0,5,1	0,30,11	2,0,15
8	0,0,0	0,0,0	0,0,0	2,1,4	2,5,0	0,1,2	0,1,5	0,1,1	6,25,2	1,0,2
9	0,0,0	0,0,0	0,0,0	2,1,2	2,2,0	0,0,0	0,0,1	0,0,1	13,13,1	0,0,0
10	0,0,0	0,0,0	0,0,0	1,0,1	1,1,0	0,0,0	0,0,0	0,0,0	12,13,1	0,0,0
11	0,0,0	0,0,0	0,0,0	1,0,1	1,1,0	0,0,0	0,0,0	0,0,0	12,13,1	0,0,0
12	0,0,0	0,0,0	0,0,0	1,0,1	1,1,0	0,0,0	0,0,0	0,0,0	12,13,0	0,0,0
13	1,0,0	0,0,0	0,0,0	10,0,0	0,0,0	0,0,0	0,0,0	0,0,0	10,0,0	0,0,0
14	0,0,0	0,0,0	0,0,0	9,0,0	0,0,0	0,0,0	0,0,0	0,0,0	10,0,0	0,0,0
15	0,0,0	0,0,0	0,0,0	9,0,0	0,0,0	0,0,0	0,0,0	0,0,0	9,0,0	0,0,0
16	0,0,0	0,0,0	0,0,0	9,0,0	0,0,0	0,0,0	0,0,0	0,0,0	9,0,0	0,0,0
Total	20,11,0	11,16,14	18,36,1	96,22,70	43,103,3	14,77,34	57,73,178	99,60,42	183,173,146	125,32,1044

its possible interactions with the trichostrongyloid nematodes were not considered.

Nematode distributions in experimentally infected rats

N. magnus occurred primarily in the anterior segment of experimentally infected laboratory rats, with a relatively small population of nematodes established in segments 2 to 4 (Table 3). Similarly, *O. bainae* became established primarily in the first segment of the intestine, with small numbers of nematodes present in segments 2 to 3. The mean intensity of infection was 10 for *N. magnus* and 14 for *O. bainae*.

Discussion

The significantly distinct sequential distributions of the three species of trichostrongyloid nematode along the small intestine in natural infections and experimental infections suggest that each species occupies a distinct niche. Furthermore, the fundamental overlaps in natural infections between the species pairs *N. magnus* - *O. bainae* (68%) and *N. magnus* - *P. ratti* (61%) were lower than the 70% value suggested by several authors (Pianka *et al.* 1979; Holmes & Price 1980; Bull *et al.* 1989) to indicate the existence of ecologically relevant differences. Only the fundamental overlap between the species pair *O. bainae* - *P. ratti* (82%) was greater than 70%. However, the mean realised overlap (55%) between these two species was substantially less than 70%, indicating that these two species interact to separate their niches in individual rats. The distribution of *O. bainae* in experimental infections (Table 3) differed when compared with natural infections (Fig. 1) in that in monospecific infections it occurred in the most anterior segment of the duodenum and this may be due to the absence of competition from *N. magnus* or *P. ratti*. However, other contributing factors may have been the different species of host, the smaller sample size in experimental infections or the smaller numbers of *O. bainae* in experimental infections.

These observations suggest that the nematode community in *R. fuscipes* is an interactive one. Holmes and Price (1986) separated communities of parasites into two categories, isolationist and interactive, based on their infrapopulations, that is, populations in individual hosts. They suggested that an interactive community has no vacant niches, parasites are not distributed independently and realised distributions of parasites are dependent on other guild members. Some of these features are present in the case of the trichostrongyloid nematode parasites of the bush rat, since the realised overlap was less than the fundamental overlap in most interactions in natural infections.

However, the small intestine of the bush rat does appear to have vacant niches in natural infections despite the above evidence for an interactive community. Although host immunity may reduce the size of apparent vacant niches (Noble *et al.* 1989) and low transmission rates may prevent parasites filling all available niches (Price 1980), the distribution of the trichostrongyloids in individual rats was independent of nematode numbers. Thus, assuming vacant niches occur, the trichostrongyloids of the bush rat also demonstrate one feature of an isolationist community (Holmes & Price 1986). The "population concentration" and "individual response" hypotheses both explain why the species *N. magnus*, *O. bainae* and *P. ratti* should occupy distinct niches even when additional vacant niches are available (Holmes & Price 1986). The "population concentration" hypothesis has two components, that narrow niche occupation is essential for the maintenance of intraspecific contact for mating purposes (Rohde 1979, 1982) and that the occupation of discrete niches is important as a

reproductive isolating mechanism preventing hybridization (Sogandares-Bernal 1959; Martin 1969). The "individual response" hypothesis (Price 1984) argues that parasites adapt to the environment they inhabit and consequently fill narrow niches.

The distribution and overlap of trichostrongyloid nematodes in individual bush rats vary greatly from the means but are independent of nematode numbers except in the case of the posterior extent of *O. bainae* in the intestine. The variability in these infracommunities may be due to the biological features of the nematodes and their interactions with one another but may also be caused by variability in the characteristics of the host which influence parasite infracommunities such as host diet (Croll 1976) and blood supply (Croll & Ma 1977). The non-specific host response, pathological responses and acquired immune responses of the host may also influence the distribution of parasites.

The three trichostrongyloid nematode species found in *R. fuscipes* have different biogeographical origins. The genus *Nippostrongylus* occurs primarily in *Rattus* spp. in south-east Asia and in other rodents in Asia and the Middle-East, with a single species in dermopterans (Beveridge & Durette-Desset 1992a). Since the endemic species of *Rattus* in Australia probably reached the continent from south-east Asia (Watts & Aslin 1981), it is likely that *Nippostrongylus* reached Australia with them and that subsequent co-speciation led to the evolution of *N. magnus* in *R. fuscipes* (see Beveridge & Durette-Desset 1992a). The genus *Odilia* occurs primarily in hydromyine or "old endemic" rodents in Australia, principally in the genera *Melomys* and *Uromys*. Species occurring in *Rattus* spp. have been interpreted as transfers from "old endemic" rodents, which probably evolved between 5 and 15 million years ago, to the "new endemic" *Rattus* spp. which have been present on the continent for about 1 million years (Watts & Aslin 1981). Species of *Paraustrostrongylus* occur in possums (Phalangeridae, Petauridae, Burramyidae) and rat kangaroos (Potoroidae) (Spratt *et al.* 1991), with a single species, *P. rani* in a rodent. The transfer of *Paraustrostrongylus*, and probably *Odilia*, is therefore presumed to be of recent origin (less than 1 million years).

Holmes (1973) suggested that stable communities are older than interactive ones and since most parasite communities are stable, he concluded that they are relatively old. The interactive component of the trichostrongyloid infracommunity in bush rats suggests that it is a comparatively young community. This is consistent with the hypothesis that *P. ratti* and possibly also *O. bainae* are recent invaders. Following their invasion of *R. fuscipes*, *P. ratti* and *O. bainae* have occupied distinctive niches within the new host possibly due to isolationist forces and/or their interactions with the other trichostrongyloid nematode species present in the small intestine. It is possible that *P. ratti* colonised a previously vacant niche at the time of switching since *N. magnus* and *O. bainae* do not occupy this niche even when *R. ratti* is absent.

The other parasites found in the small intestines of bush rats appear to occupy completely different niches from those inhabited by the trichostrongyloid nematodes or to occur at a very low intensity and prevalence (*Capillaria* sp.) and therefore were not considered in the interactions of the trichostrongyloid community in the present study. The distributions of *H. dimunuta* and *B. anapolytica* overlapped. However, the two species were never found in the same segment of the small intestine although only two rats were infected with both species. Because of interactions which may occur between them, they may occupy separate niches (Holmes 1973). A larger sample of rats would be needed to examine the extent of interaction between their cestode parasites.

Acknowledgments

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TRANSACTIONS OF THE

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VOL. 119, PART 4

EIGHT NEW SPECIES OF AUSTRALIAN BUPRESTIDAE (INSECTA: COLEOPTERA)

*By S. Barker**

Summary

Barker, S. (1995) Eight new species of Australian Buprestidae (Insecta: Coleoptera). Trans. R. Soc. S. Aust. 119(4), 149-156, 30 November, 1995.

Six new species of Castiarina namely C. corallina sp. nov., C. ernestadamsi sp. nov., C. euknema sp. nov., C. octopunctata sp. nov., C. oedemerida, sp. nov. and C. prolata sp. nov., one new species of Themognatha, T. viridescens sp. nov., and one species of Astraeus, A, powelli sp. nov. are described.

Key Words: Coleoptera, Buprestidae, New species, Castiarina, Themognatha, Astraeus.

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EIGHT NEW SPECIES OF AUSTRALIAN BUPRESTIDAE (INSECTA: COLEOPTERA)

by S. BARKER*

Summary

BARKER, S. (1995) Eight new species of Australian Buprestidae (Insecta, Coleoptera). *Trans. R. Soc. S. Aust.* 119(4), 149-156, 30 November, 1995.

Six new species of *Castiarina* namely *C. corallina* sp. nov., *C. ernestadamsi* sp. nov., *C. euknema* sp. nov., *C. octopunctata* sp. nov., *C. oedemerida*, sp. nov. and *C. prolata* sp. nov., one new species of *Themognatha*, *T. viridescens* sp. nov., and one species of *Astraeus*, *A. powelli* sp. nov. are described.

KEY WORDS: Coleoptera, Buprestidae, New species, *Castiarina*, *Themognatha*, *Astraeus*

Introduction

Despite the increase in specialist collecting of Australian Buprestidae undertaken by amateur entomologists over the last twenty years, new species are still being found. This reflects the vastness of the continent as well as the cyclic nature of the life histories of many of the arid area species. Of the species described herein, specimens of *Astraeus powelli* have been available since 1970 but the specimens in the South Australian Museum collection were inadvertently sorted into a tray full of *A. aberrans* v. de Poll, the closest species, and it was only through the alertness of Mr M. Powell that this species has been recognised. *Themognatha viridescens* was collected many years ago in inaccessible country at Iron Range, Cape York Peninsula. A series has now become available from the Jack Macqueen collection, lodged with the Australian National Insect Collection (ANIC). Three species, have only recently been collected. *Castiarina oedemerida* and *C. prolata* in Queensland and *C. corallina* in Western Australia. *Castiarina euknema* was known for some years from two female specimens and a male has only been located recently in the collection of ANIC. *Castiarina octopunctata* specimens have been collected frequently but until now have not been distinguished from *C. parallela*. Until recently *C. ernestadamsi* has been confused with *C. straminea* MacLeay.

Materials and Methods

Male genitalia were prepared and displayed by the method described by Barker (1987). The holotype is illustrated in all species. Measurements given are mean total body length and width with standard error, except where there are insufficient specimens available to make the last calculation. Codens used in the text for museum and private collections following the four letter system of Watt (1979) and Arnett *et al.* (1993) are: AIMS: Australian Institute of Marine Science, Townsville; ANIC: Australian National Insect Collection, CSIRO, Canberra; SAMA: South Australian Museum, Adelaide; WAMA: Western Australian Museum, Perth; JHIQ: Mr J. Hasenpusch, Innisfail; MHSA: Mr T. M. S. Hanlon, Sydney; MPWA: Mr M. Powell, Melville; GWQA: Mr G. Wood, Atherton.

Castiarina corallina sp. nov.
(FIGS 1D, 2C)

Holotype: ♂, 144 km NW Wittenoom, W.A., 25.iii.1994, M. Golding, M. Powell, WAMA.

Allotype: ♀, 140 km NW Wittenoom, W.A., 25.iii.1994, M. Golding, M. Powell, WAMA.

Paratypes: 2 ♀♀, Millstream Stn, W.A.; 25.iii.1994, M. Golding, M. Powell, MPWA; 1 ♂, same data as allotype, MPWA; 4 ♂♂, 145 km NW Wittenoom, MPWA, SAMA.

Colour

Head, antennae dark blue. Pronotum red-brown, in some specimens with medial smudge of dark blue along basal margin. Scutellum dark blue. Elytra red-brown with the following markings: dark blue along basal margin, in some specimens with mark extended to surround scutellum; large post-medial spot on each elytron; apical mark. Ventral surface: pre-sternum red-brown; meso- and meta-sternum dark blue; abdomen red-brown except laterally at base variably dark blue; legs dark blue.

Shape and sculpture

Head closely punctured, broad median sulcus, short muzzle. Antennae, antennomeres 1-3 obconic, 4-11 toothed. Pronotum closely punctured, narrow basal fovea; apical margin projecting medially, basal margin bisinuate; laterally parallel-sided at base, angled outwards, rounded to widest pre-medially, tapered to apex. Scutellum cordiform, glabrous, flat. Elytra punctate-striate, intervals convex, punctured; laterally

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parallel-sided at base, rounded at humeral callus, concave rounded post-medially, narrowed to spineless apex; apices hardly diverging, apical margin subserrate. Ventral surface, shallowly punctured, edges of abdominal segments glabrous, without hairs, S_7; apically rounded in both sexes.

Size

Males, 14.3 ± 0.48 x 5.3 ± 0.14 mm (6). Females, 16.8 x 6.5 mm (3).

Aedeagus (Fig. 1D)

Parameres angled outwards from basal piece, rounded apically. Penis pointed, sides acutely angled away. Apophysis of basal piece medium width, tapered, rounded apically.

Remarks

The dorsal markings of this species resemble those of *Castiarina quadriplagiata* (Carter) which has only been collected in Queensland. However, *C. corallina* is a narrower species, it is a paler red than *C. quadriplagiata* and the male genitalia differ (Fig. 1C).

Etymology

Derived from L. *-corallinus*, coral coloured.

Castiarina oedemerida sp. nov
(FIGS 1H, 2F)

Holotype: ♂, Georgetown, Qld, 28.ii.1993, J Hasenpusch, SAMA I 21285.

Paratype: Qld: 1♂, Georgetown, 1.iii.1993, J Hasenpusch, JHIA.

Colour

Head black. Antennae dark blue. Pronotum brown with the following black markings: medial spot, smaller spot on each side, narrow basal border, expanded anteriorly on each side. Scutellum black. Elytra yellow-brown with the following black markings; M-shaped mark along anterior margin, arms covering humeral callus; post-medial fascia reaching margin, expanded anteriorly and posteriorly along suture; apical mark. Ventral surface: prosternum yellow-brown; meso-sternum and meta-sternum and coxae dark blue; abdomen yellow-brown, S_5 with lateral black spot, S_6 with lateral black bar, S_7 black apical edge, edges of S_5, S_6, S_7, testaceous; legs dark blue. Hairs silver.

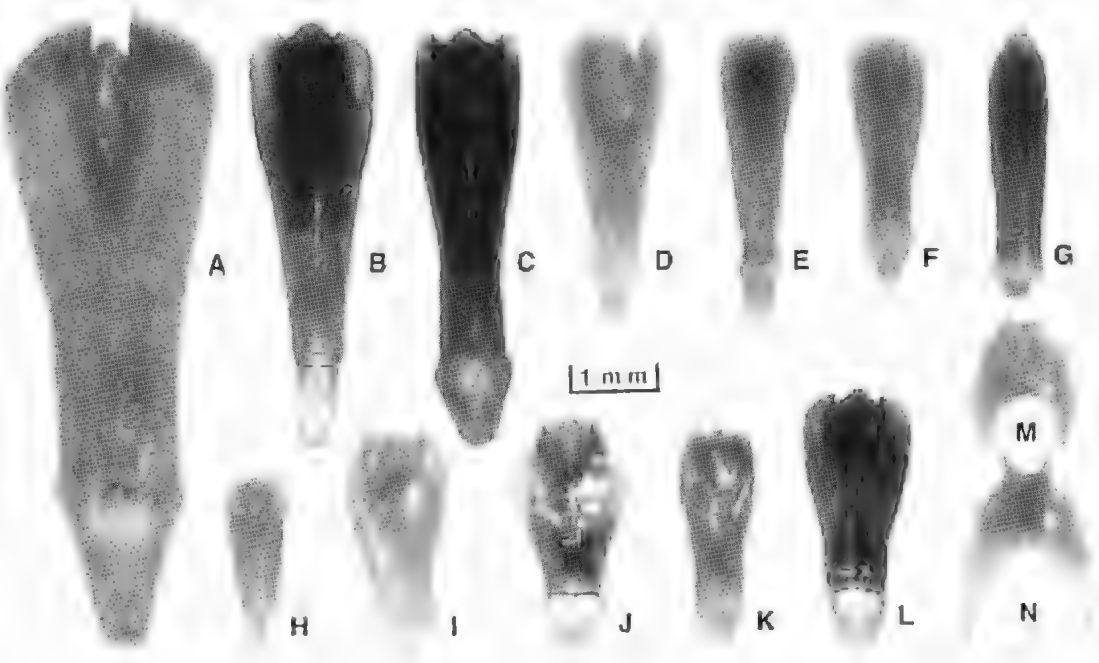

Fig. 1 Photomicrographs of male aedeagi of the following *Castiarina*, *Astraeus* and *Themognatha* species. A. *Themognatha virtdescens*. B. *Castiarina acuminata* Kerremans. C. *Castiarina quadriplagiata* Carter. D. *Castiarina corallina* sp. nov. E. *Castiarina prolata* sp. nov. F. *Castiarina octopunctata* sp. nov. G. *Astraeus powelli* sp. nov. H. *Castiarina oedemerida* sp. nov. I. *Castiarina ernestadamsi* sp. nov. J. *Castiarina straminea* Saunders. K. *Castiarina eukinema* sp. nov. L. *Castiarina rufipes* MacLeay. Photomicrographs of proctigers of types of *Castiarina octopunctata* sp. nov. M. Holotype male. N. Allotype female.

Shape and sculpture

Punctured over entire dorsal surface. Head closely punctured, median sulcus, short muzzle. Antennae, antennomeres 1-3 obconic, 4 ½ toothed, 5-11 toothed. Pronotum closely punctured, glabrous area surrounding basal fovea, fovea at each angle; apical margin straight, basal margin barely bisinuate; laterally rounded from base to apex, widest pre-medially. Scutellum scutiform, punctured, excavate. Elytra punctate-striate, intervals convex, heavily punctured; laterally angled out from base, rounded at humeral callus, concave, rounded post-medially at widest part to bispinose apex; small marginal spine, small sutural spine, margin rounded and indented between spines, apices slightly diverging. Ventral surface closely punctured, edges of abdominal segments glabrous, few short hairs. S_7: males truncate, indented medially; females unknown. Legs: in male tarsomeres 1-3 without pulvilli, replaced by median longitudinal ridge.

Size

Males, 10.0 x 3.5 mm (2).

Aedeagus (Fig. 1H)

Parameres angled outwards from basal piece, rounded at apex. Penis blunt, sides acutely angled away. Apophysis of basal piece medium width, tapered, rounded apically.

Remarks

This species appears to be an oedemerid mimic as its colour and pattern are similar to known oedemerid species; the model is unknown. It is not close to any other known species.

Etymology

The name is derived from that of the beetle family Oedemeridae.

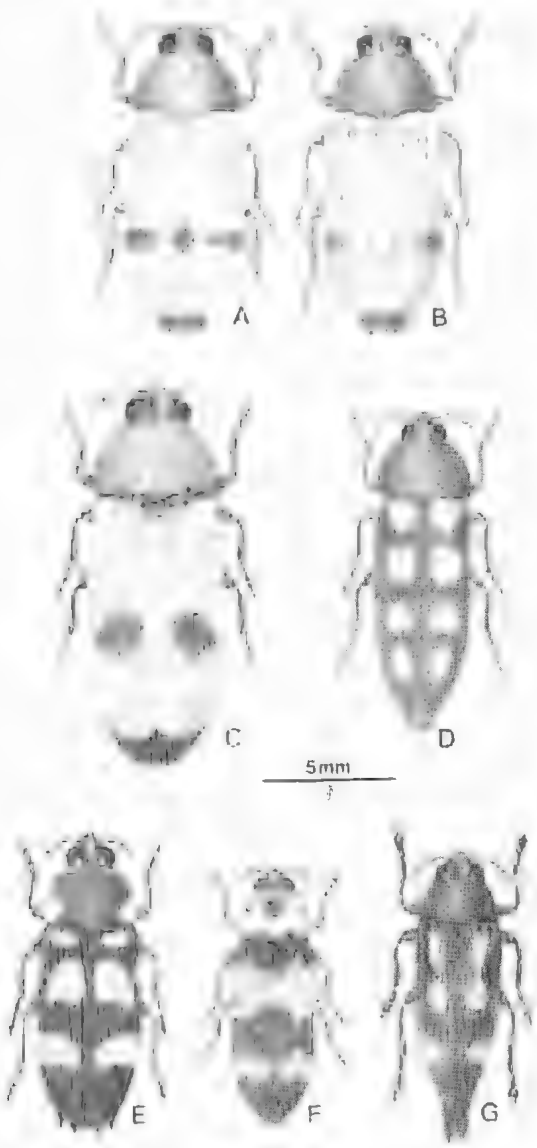

Fig. 2. Habitus illustrations of the following *Castiarina* species. A, *C. ernestadamsi* sp. nov. holotype. B, *C. strigata* MacLeay. C, *C. coralina* sp. nov. holotype. D, *C. octopunctata* sp. nov. holotype. E, *C. euknema* sp. nov. holotype. F, *C. oedemerida* sp. nov. holotype. G, *C. pustata* sp. nov. holotype.

Castiarina euknema sp. nov.
(FIGS 1K, 2E)

Holotype: ♂, Surveyor's Pool, W.A., 15.viii.1983, I. D. Naumann, J. C. Cardale, ANIC.

Allotype: ♀, 2 km N Jabiluka, N.T., 21.iii.1981, M. Cappo, SAMA I 21286.

Paratype: W.A.: ♀, 34 km S Roebuck, W.A., 8.vii.1984, M. Powell, M. Golding, MPWA.

Colour

Head black with yellow reflections, elongate yellow frontal spot. Antennae blue-green. Pronotum: anterior and basal margins black with yellow reflections; yellow laterally; medial black mark with yellow reflections in the shape of sleeveless T-shirt, the neck enclosing a very small yellow spot. Scutellum black with yellow reflections. Elytra yellow with the following black markings; narrow basal margin; pre-medial fascia with ends expanded anteriorly over humeral callus reaching anterior margin and enclosing yellow basal spot, posteriorly reaching margin and enclosing yellow spot on margin; post-medial fascia reaching margin and meeting posterior extension of pre-medial fascia and with it enclosing yellow medial spot; mark covering whole apex, elongate yellow mark reaching margin, but not suture, lying between this and post-medial

fascia. In allotype black marks less prominent and apical mark encloses a small yellow apical spot. Ventral surface yellow, edges of sutures black with green reflections, S_4, S_5, S_6 with lateral spots coalesced with marks along edges. Legs: femora and tibia blue; tarsomeres dark blue. Hairs silver.

Shape and sculpture

Head shallowly punctured, shallow median sulcus, medium length muzzle. Antennae compressed, antennomeres 1-4 obconic, 5-11 toothed. Pronotum shallowly punctured, basal fovea extending forwards to middle as glabrous line, basal notches on each side closer to margin than middle; apical margin straight, basal margin barely bisinuate; laterally rounded from base, widest pre-medially, rounded and narrowed to apex. Scutellum scutiform, without punctures, excavate along anterior margin. Elytra punctate-striate, intervals flat anteriorly, convex apically; laterally angled out from base, rounded at humeral callus, concave, rounded post-medially and narrowed to trispinose apex; marginal and sutural spines equal, medial spine slightly larger, margin rounded and indented between spines, apices slightly diverging. Ventral surface with shallow punctures, edges of abdominal segments glabrous, few short hairs. S_7 truncate both sexes.

Size

Male, 10.9 x 4.2 mm (1). Female, 11.9 x 4.5 mm (2).

Aedeagus (Fig. 1K)

Parameres parallel-sided from basal piece, rounded medially then parallel-sided, rounded at apex. Penis pointed, sides angled away. Apophysis of basal piece medium width, tapered, rounded apically.

Remarks

This species has similar markings to those of *C. rufipes* MacLeay, except that the legs are blue whereas they are red in the other species. The male genitalia are quite different (Fig. 1L).

Etymology

Derived from Gr. *euknemos*, beautiful legs.

Castiarina prolata sp. nov.
(FIGS 1E, 2G)

Holotype: ♂, Cardwell Ra., Qld, 23.xii.1993, J. Hasenpusch, SAMA I 21287.

Allotype: ♀, same data as holotype, SAMA I 21288.

Paratypes: 1 ♂, 1 ♀ same data as holotype, JHQA.

Colour

Head and antennae black with green and gold reflections. Pronotum black with green reflections at base. Scutellum black with blue reflections. Elytra yellow with black markings coalesced forming an elongate yellow basal mark, a round yellow pre-medial mark and a predominantly red sub-apical mark, touching margin not reaching suture and merging into yellow closest to it. Ventral surface green with yellow reflections. Legs: femora, dorsal surface deep blue, ventral surface green with gold reflections; tibia and tarsi dark blue. Hairs silver.

Shape and sculpture

Head shallowly punctured, broad median sulcus, short muzzle. Antennae, antennomeres 1-3 obconic, 4-11 toothed. Pronotum shallowly punctured, glabrous, small basal fovea, larger fovea at each basal angle; apical margin projecting slightly medially, basal margin bisinuate; rounded from base, narrowed to apex. Scutellum tulipiform, few punctures, glabrous, flat. Elytra anteriorly punctate-striate, intervals raised posteriorly, intervals convex; laterally parallel-sided at base, rounded at humeral callus, rounded and tapered posteriorly, then attenuated, rounded at apex to pointed marginal spine, deeply indented and rounded to minute sharp sutural spine, apices diverging. Ventral surface with shallow punctures, edges of abdominal segments glabrous, sparse medium length hairs. Mesosternal process inflated. Elytra cantilevered over last visible abdominal sternite. Legs: femora and tibia long and thin; tarsomeres with enlarged pulvilli. S_7 truncate both sexes.

Size

Males, 10.9 x 3.4 mm (2). Females, 12.4 x 3.6 mm (2)

Aedeagus (Fig. 1E)

Parameres elongate, angled outwards from basal piece, apically rounded. Penis pointed, sides obtusely angled away. Apophysis of basal medium width, elongate, tapered, rounded apically.

Remarks

This species is a '*C. producta*' group mimic. It resembles *C. acuminata* Saunders which also has greatly attenuated apical spines but is heavily costate. The apical spines of *C. prolata* are both obvious whereas in *C. acuminata* the marginal spine is absent. Male genitalia differ (Fig. 1B).

Etymology

Derived fotm L. *prolatus*, elongate.

Castiarina ernestadamsi sp. nov
(FIGS 1I, 2A)

Holotype: ♂, Mourangee, Edungalba, Qld, 26.xii.1979, E. E. Adams, SAMA I 21289.

Paratypes: Qld: 3 ♂ ♂, Mourangee, Edungalba, S. A. Adams & E. E. Adams, SAMA.

Colour

Head maroon at base blending into blue-green, blue muzzle. Antennae, antennomeres 1-2 blue-green, 3-11

bronze green. Pronotum maroon. Scutellum blue or blue-green. Elytra pale yellow with following dark blue markings: narrow basal margin; small mark over each humeral callus; remnant post-medial fascia touching lateral margin reaching half way to suture, small remnant mark on suture; small apical mark. Ventral surface: sternum maroon; abdomen testaceous; legs blue. Hairs silver.

Shape and sculpture

Head shallowly punctured, medium sulcus, short muzzle. Antennae, antennomeres 1-3 obconic, 4-11 toothed. Pronotum shallowly punctured, basal fovea extending forwards to middle as glabrous line, basal notches represented by glabrous area on each side closer to margin than middle; apical margin projecting medially, basal margin barely bisinuate; laterally parallel-sided at base, angled outwards and rounded to widest pre-medially, rounded and narrowed to apex. Scutellum scutiform, glabrous, flat. Elytra punctate-striate, intervals convex, lightly punctured; laterally angled outwards from base, rounded at humeral callus, concave, rounded post-medially and narrowed to bispinose apex; both spines small and sharp, margin rounded and indented between spines, apices hardly diverging, apical margin subserrate. Ventral surface with shallow punctures, edges of abdominal segments glabrous, sternum with few medium length hairs, abdomen almost hairless. S_7 males truncate; female unknown.

Size

Males, 12.4 ± 0.09 x 4.8 ± 0.04 mm (4).

Aedeagus (Fig. 1I)

Lightly tanned. Parameres parallel-sided from basal piece, pre-medially rounded, parallel-sided then rounded to apex. Penis pointed; sides obtusely angled away. Apophysis of basal piece narrow, rounded apically.

Remarks

This species was previously confused with *C. straminea* MacLeay. However it is smaller, it has a smooth pronotum with small punctures whereas *C. straminea* has heavy punctation. It has darker elytral markings than *C. straminea* and the male genitalia differ (Fig. 1J). A form of *C. strigata* MacLeay (Fig. 2B) occurs in the type locality, similar in size and pattern but not in colour. It has very light elytral markings, the post-medial fascia being considerably reduced. The head and pronotum are green with reddish reflections in some specimens.

Etymology

In honour of Mr E. E. Adams, octogenarian, Edungalba, Queensland who has assisted my research for many years.

Castiarina octopunctata sp. nov.
(FIGS 1F, 2D)

Holotype: ♂, 91 km NNE Zanthus, W.A., 21.x.1986, M. Powell, WAMA.

Allotype: ♀, Wialki, W.A., 21.ix.1970, S. Barker, SAMA I 21290.

Paratypes: W.A.: 1 ♂, SAMA; 1 ♀, summit Mt Cooke, 10.xi.1956, S. Barker, SAMA; 1 ♀, Wialki, 18.ix.1957, S. Barker, SAMA; 2 ♂♂, Kalbarri N.P., 23.ix.1969, F. H. Uther Baker, SAMA; 4 ♂♂, 2 ♀♀, Beverly T. O., Brookton Hwy, 19.ix.1970, S. Barker, SAMA; 2 ♂♂, same data as allotype, SAMA; 1 ♂, 6 km S Tammin, 8.xi.1970, S. Barker, SAMA; 3 ♂♂, 3 ♀♀, 1/2 way between Glen Eagles and Brookton Hway, 13.x.1980, S. Barker, SAMA; 1 ♀, 8 km E Woolgangie, 22.x.1980, S. Barker, P. G. Kempster, SAMA; 1 ♂, 10 km E Merredin, 12.x.1990, S. Barker, SAMA; 1 ♂, 4 km W Zanthus, 21.x.1986, M. Powell, MPWA; 1 ♂, same data as holotype, MPWA; 1 ♀, Moora, WAMA; 1 ♀, McDermid Rock, 27.ix/3.x.1978, T. F. Houston, WAMA; 2 ♂♂, 1 ♀, Lake Ningham, WAMA; 1 ♀, Merredin, WAMA; 1 ♂, Karlgarin, W. Duboulay, WAMA; 1 ♀, Dedari, 7.x.1978, T. M. S. Hanlon, WAMA; 1 ♀, 21 km W York, 4.xi.1978, T. M. S. Hanlon, WAMA; 1 ♂, 1.5 km S Mt Jackson, 5/11.ix.1979, T. F. Houston *et al.*, WAMA; 1 ♂, 1 ♀, 12 km NNE Bungalbin Hill, 11/18.ix.1979, T. F. Houston *et al.*, WAMA; 1 ♂, 1 ♀, 14 km NNE Bungalbin Hill, 11/18.ix.1979, T. F. Houston *et al.*, WAMA; 3 ♂♂, 1 ♀, 15 km NNE Bungalbin Hill, 11/18.ix.1979, T. F. Houston *et al.*, WAMA; 2 ♀♀, Dedari, 21.ix.1979, T. M. S. Hanlon WAMA; 1 ♂, Mt Dale, 29.ix.1980, T. M. S. Hanlon, MHSA; 1 ♂, Muckinbuddin, 10.x.1979, R. P. McMillan, WAMA; 1 ♂, Mt Walker, 34 km E Narembeen, 23.x.1980, R. P. McMillan, WAMA; 3 ♂♂, 1 ♀, Mt Observation, 21.x.1987, R. P. McMillan, WAMA; 1 ♀, Beacon, 20.x.1981, R. P. McMillan, WAMA; 1 ♀, 20.ix.1990, Bonnie Rock, S. Barker, SAMA; 1 ♂, 10 km E Merredin, 12.x.1990, S. Barker, SAMA; 3 ♂♂, 2 ♀♀, Dedari, 22.x.1991, T. M. S. Hanlon, MHSA.

Colour

Head, antennae, pronotum dark coppery-purple. Scutellum dark blue with coppery-purple reflections. Elytra yellow with coalesced dark blue markings with coppery-blue reflections forming the following yellow marks: 4 large medial spots in a row on each elytron, the basal, pre-medial and post-medial roundish, the pre-apical elongate; narrow margin from base, not reaching apex. Ventral surface and legs brown with coppery-purple reflections. Hairs silver.

Shape and sculpture

Head closely punctured, broad median sulcus, short muzzle. Antennae, antennomeres 1-3 obconic; 4-11

toothed. Pronotum closely punctured, basal fovea extending forwards to middle as glabrous impressed line; apical margin projecting broadly medially, basal margin almost straight; laterally parallel-sided at base, slightly rounded, widest medially, slightly rounded to apex. Scutellum scutiform, glabrous, excavate. Elytra punctate-striate, intervals convex, smooth medially, punctured and rough laterally; laterally angled out from base, rounded at humeral callus, concave, rounded post-medially and narrowed to spineless apex, last interval indented and straight, apices slightly diverging. Entire ventral surface covered in dense, flat hairs, also present around lateral margins of pronotum and in some specimens encroaching onto dorsal surface. S_7; males truncate; females rounded and slightly pointed.

Size

Males, 11.9 ± 0.46 x 4.0 ± 0.06 mm (35), Females, 12.7 ± 0.48 x 4.2 ± 0.07 mm (25)

Aedeagus (Fig. 1F)

Parameres angled outwards and gradually widened from basal piece, rounded at apex. Penis pointed, angled away obtusely. Apophysis of basal piece medium width, rounded apically. Proctiger with apex bluntly bilobed, the two projections variable (Fig. 1M).

Female terminalia (Fig. 1N)

Proctiger; apex with two narrow, pointed lobes.

Remarks

A species complex exists in Western Australia which includes *C. parallela* (White) with a more or less continuous gradation in size from the smallest (*C. parallela*) to larger species. *C. parallela* also occurs in eastern Australia. Until now I have not been able to separate the individual species in the western complex. *C. xanthopilosa* Hope and *C. vittata* Saunders are closely related species but only occur in eastern Australia. From examination of the terminal abdominal segments, it now appears as if males and females of both eastern and western specimens of *C. parallela* have a rounded proctiger and can be distinguished on that basis and on their colour, size and structure of male genitalia. Both sexes of the larger western species have an ornamented proctiger. *C. octopunctata* is distinguishable on the basis of the structure of male genitalia and the lack of apical spines on the elytra. Further work is required to delimit the remaining species.

Etymology

The name is derived from L., *octo*, eight and L., *punctatum*, spotted.

Thremognatha viridescens sp. nov. (FIGS 1A, 3)

Holotype: ♂, Iron Ra., Qld, 20.vi.1980, G. Wood, SAMA I 21291.

Allotype: ♀, Iron Ra., Qld, 30.iv.1966, J. Kerr, ANIC.

Paratypes: Qld: 2 ♀♀, Iron Ra., 3/9.v.1966, J. Kerr, ANIC; 1 ♂, Iron Ra., 24.v.1974, M. Walford-Huggins, MHSA; 1 ♀, Iron Ra., Qld, 19.v.1978, G. Wood, GWQA; 1 sex indeterm, 5.v.1966, J. Macqueen, J. Kerr, ANIC.

Colour

Head, antennae, pronotum and scutellum bright green with yellow reflections. Elytra yellow with following dark green markings: narrow basal margin; medial fascia not reaching margin, apical mark connected along suture to fascia. Ventral surface mainly bright green with yellow reflections, male with testaceous patches on S_6 and S_7, abdomen all green in female; legs bright green with yellow reflections.

Shape and sculpture

Head punctation fine, even, dense, median impressed basal line; frons moderately hairy; labrum longitudinally divided and pointed. Pronotum narrower than elytra, L:W 0.6, punctation fine moderately dense; sides rounded from base to 1/3 distance to apex, then explanate and converging anteriorly, laterally flattened; anterior margin bisinuate, posterior margin almost straight; median glabrous line from base to near apex. Scutellum scutiform, anterior margin straight, concave without punctures, 1/8 width of elytra. Elytra slightly wider than thorax; elytral interneurs long and with scutellary striole, strongly marked with heavy punctation and additional punctation on shoulders; intervals flat, sides sub-parallel then tapering to pre-apical areas; apex bisinuate, both spines prominent, interval between sinuous, lateral spine anterior to medial spine. Ventral surface: prosternum hairy, finely punctured, with a definite forward medial projection; pro-episternum finely punctured with deep smooth fossa in posterior angle; mesosternum and metasternum smooth medially with coarser punctation laterally; hairy, hair long and fine medially, shorter

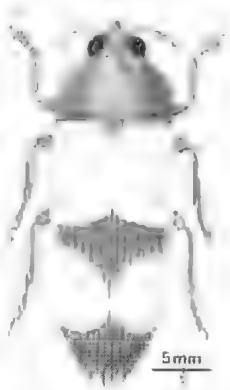

Fig. 3. Habitus illustration of *Thremognatha viridescens* sp. nov. holotype

and coarser laterally; abdomen smooth and shiny in male, punctation very fine, apically hairy in female. S_5: male deeply concave; female rounded. Feet: tarsal claws without a notch.

Size

Male, 31.4 x 11.4 mm (2). Females, 30.7 x 11.8 mm (4).

Aedeagus (Fig. 1A)

Parameres parallel-sided from basal piece, angled outwards premedially, rounded at apex. Penis pointed, sides acutely angled away. Apophysis of basal piece medium width, tapered, rounded at apex.

Remarks

This is an unusual species as it shows two characters found in the related genus *Calodema* C&G. It has a small medial projection on the anterior margin of the prosternum, but not as large as those found in *Calodema*. The scutellum is wider than in other *Themognatha* in relation to the elytral width, although not as wide as any of the known *Calodema* species. However, the body is not sinuous in lateral profile, the pronotum is not as wide as the elytra and the elytral interneurs are clearly defined as in *Themognatha*. The tarsal claws are not notched, but this is a variable character found in some *Themognatha* and not in others.

Etymology

Derived from L. *viridis*, green.

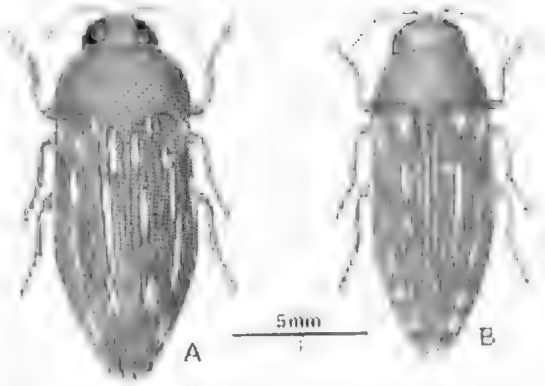

Fig. 4. Habitus illustrations of the following *Astraeus* species. A, *A. aberrans* v. de Poll. B, *A. powelli* sp. nov. holotype.

Astraeus (Depollus) powelli sp. nov. (FIGS. 1G, 4B)

Holotype: ♂, Quairading, 7.xi.1970, S. Barker, SAMA I 21292.

Allotype: ♀, Quairading, 26.i.1991, M. Golding, M. Powell, WAMA.

Paratypes: W.A.: 1 ♂, Tammin, 8.xi.1970, S. Barker, SAMA; 1 ♂, 17 km E Dowerin, 21.x.1989, M. Golding, M. Powell, MPWA; 1 ♂, 6 km SE Tamunin, 15.xii.1990, M. Golding, M. Powell, MPWA; 1 ♂, 43 km E Merredin, 26.x.1991, M. Golding, M. Powell, MPWA; 2 ♂♂, 32 km E Yellowdine, 21/22.x.1991, T. M. S. Hanlon; 2 ♀♀, Quairading, 27.xii.1991, K. K., MPWA; 4 ♀♀, Quairading, 1.1.1992, M. Golding, K. K., MPWA.

Colour

Head, antennae, pronotum black with blue and purple reflections. Elytra black with following yellow markings: irregular marks along width of one striae, mainly concentrated along 4th and 8th intervals from suture and along the margin on basal half. Ventral surface and legs purple; lateral yellow spots on S_3, S_4, S_5 in most specimens last one absent in holotype. Hairs silver.

Shape and sculpture

Head punctures small medially, larger laterally, small glabrous median keel near apex merging into impressed line basally. Pronotum punctures smaller medially, larger and in form of shallow fovea laterally, glabrous median area; anterior margin projecting medially, basal margin strongly bisinuate, laterally hairy. Elytral intervals between striae convex and smooth, laterally parallel-sided from base, rounded post-medially and narrowed to apex, small pre-apical notch on margin, broad outwardly curving sutural spine, hairy overall. Ventral surface and legs punctured and hairy.

Size

Males, 12.6 ± 0.22 x 4.4 ± 0.11 mm (7). Females, 15.3 ± 0.38 x 5.6 ± 0.12 mm (7).

Aedeagus (Fig. 1G)

Parameres parallel-sided from basal piece, gradually widening until rounded to pointed apex. Apophysis of basal piece medium width, rounded apically.

Remarks

This species has been confused with *A. aberrans* v. de Poll (Fig. 4A). It differs from that species by being narrower, having most of the yellow elytral marks medial and post-medial whereas in *A. aberrans* they are more evenly distributed, by having single outcurving sutural spines on the elytra while in *A. aberrans* the sutural spines are small and there is a definite small marginal spine.

Etymology

In honour of Mr M. Powell of Melville, W.A. who has assisted my research for many years.

With the addition of the above new species the key to *Astraeus (Depollus)* (Barker 1975, p.107) requires the following replacement:

Replace 4. *aberrans* van de Poll with:

4a. small, almost straight marginal spine
. . . . . *aberrans* van de Poll

4b. broad, outcurving marginal spine
. . . . . *powelli* Barker

With the addition of this species the sub-genus *Depollus* now contains nine species.

Acknowledgments

I thank the following for their assistance: Dr T. F. Houston, WAMA; Mr T. A. Weir, ANIC; Mr M. Cappo, AIMS; Ms H. Vanderwoude, Department of Zoology, University of Adelaide. I thank the following collectors for the loan of specimens: Mr E. E. Adams, Edungalba; Mr T. M. F. Hanlon, Hunters Hill; Mr J. Hasenpusch, Innisfail; Mr M. Powell, Melville; Mr G. Wood, Atherton.

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A NEW SPECIES OF CALLULOPS FROM NEW GUINEA AND COMMENTS ON THE STATUS OF C. HUMICOLA COMPTUS (ZWEIFEL) (ANURA: MICROHYLIDAE: ASTEROPHRYINAE)

By Stephen J. Richards, Thomas C. Burton†, Michael J. Cunningham‡ & Andrew J. Dennis**

Summary

Richards, S. J., Burton, T. C., Cunningham, M. J. & Dennis, A. J. (1995) A new species of Callulops from New Guinea and comments on the status of C. humicola comptus (Zweifel) (Anura: Microhylidae: Asterophryinae). Trans. R. Soc. S. Aust. 119(4), 157-162, 30 November, 1995.

Callulops sagittatus sp. nov. from the summit of Mt. Binnie, Western Province, Papua New Guinea is described. It is a moderately large species (males 44.1-47.8 mm, a female 56.3 mm S-V) distinguished from congeners by the presence of an orange stripe from the tip of the snout dorsally across each eyelid, forming an arrow-shaped mark on the crown. The advertisement call is a series of 11-12 deep croaks uttered from the entrance to, or deep within, crevices between rocks. The female paratype contains large (4.5 mm diameter) unpigmented eggs indicating that, like other Australopapuan microhylids, larval development is completed with the egg capsule. Among the Asterophryinae, Callulops sagittatus and C. h. humicola share a unique condition of the mandibular branch of the trigeminal nerve suggesting that C. sagittatus and not C. h. comptus is the closest relative of C. h. humicola. This and a number of other consistent morphological differences indicate that C. h. comptus warrants elevation to specific status.

Key Words: Anura, Microhylidae, Asterophryinae, frog, new species, Callulops sagittatus sp. nov., Callulops humicola, Callulops comptus, New Guinea.

Transactions of the Royal Society of S. Aust. (1995), 119(4), 157-162

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KEY WORDS: Anura, Microhylidae, Asterophryinae, frog, new species, *Callulops sagittatus* sp. nov., *Callulops humicola*, *Callulops comptus*, New Guinea.

Introduction

Microhylid frogs of the subfamily Asterophryinae are restricted to the New Guinea mainland and nearby islands (Zweifel & Tyler 1982). This ecologically and morphologically diverse group occurs from sea level to subalpine meadows high in the central cordillera (Zweifel 1972). In a review of the Asterophryinae Burton (1986) recognised eight genera and 43 species. Blum & Menzies (1988) subsequently described nine new species of *Xenobatrachus* and *Xenorhina*, and Richards *et al.* (1994) described a new species of *Asterophrys*, bringing the total to 53. Additional undescribed species occur in museum collections, and field work continues to reveal unnamed taxa.

During a survey of the fauna of Mt Binnie, Western Province, Papua New Guinea (Dennis *et al.* 1995)[†] three of us (SR, AD, MC) collected an undescribed species of the asterophryine genus *Callulops*. The discovery of this new species necessitates a reassessment of the relationships of the taxa currently recognised as subspecies of *Callulops humicola*. Here *we describe the new species and demonstrate that Callulops humicola comptus* warrants elevation to specific status.

Materials and Methods

Specimens are deposited in the Biology Department, University of Papua New Guinea, Port Moresby (UPNG) and the Queensland Museum, Brisbane (QM).

Recordings of mating calls were made in the field with a Sony Professional Walkman tape recorder with an Electret Condenser Microphone ECM-Z200 and were analysed using the sound analysis program "Canary" (Cornell Ornithology Laboratory, 1994).

Measurements were made to the nearest 0.05 mm with dial callipers or to the nearest 0.1 mm using a binocular microscope with an ocular micrometer. Methods of measurement follow Zweifel (1985) except the snout-naris measurement, taken from the tip of the snout to the centre of the naris. Measurements (mm) were: snout-vent length (S-V); tibia length (TL); eye diameter (EYE); eye-naris distance (EN); internarial distance (IN); snout-naris distance (SN); head width at angle of the jaws (HW); head length from tip of snout to angle of the jaws (HL); horizontal diameter of tympanum (EAR); hand length (HD); foot length (FT). The rather featureless palmar and plantar surfaces of the hands and feet, and the poorly defined tympanic annulus made measurement of the hands, feet and tympanum difficult, and the measurements should be treated with caution. One of us (TCB) dissected the superficial throat and jaw musculature under a Wild M3Z microscope with the aid of topical application

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† Division of Biological and Chemical Sciences, La Trobe University, Bendigo, PO Box 199, Bendigo, Vic. 3550.
‡ Zoology Department, University of Queensland, Qld 4072.

† DENNIS, A., RICHARDS, S. & CUNNINGHAM, M. (1995) Preliminary survey of mammals, birds, reptiles and frogs on the summit of Mt Binnie, Western Province, PNG. 20-23 November, 1994. Report to Ok Tedi Mining Limited (unpubl.)

of the iodine-potassium iodide solution of Boek & Shear (1972). The squamosal bone was also examined.

Systematics

Callulops Boulenger is applied to asterophryine microhylid frogs formerly referred to *Phrynomantis* Peters, following the recommendation of Dubois (1988). *Callulops* is distinguished by two skull characters: two supplementary slips to the M. intermandibularis arise from the dentary; one via a tendon and the other directly, and run together, more or less parallel to the mandible, to insert upon the ventral fascia of the M. submentalis and sometimes also upon the adjacent medial aponeurosis of the M. intermandibularis (Burton 1986). The second character is that the otic ramus of the squamosal bone is about the same length as the zygomatic ramus, and it is not twisted i.e. the postero-lateral surface of the otic ramus is continuous with the lateral surface of the zygomatic ramus (Burton 1986).

In his revision of the asterophryines, Zweifel (1972) described *Callulops h. humicola* and *C. h. comptus*. These taxa resemble each other superficially apart from relatively longer legs in *C. h. humicola*, and an orange postocular stripe in adult *C. h. comptus* which is only "somewhat developed in young *humicola*" (Zweifel 1972 p. 476). The geographic ranges of these taxa abut. Zweifel reported only one instance of sympatry, and was reluctant to assign the taxa to species status in the absence of evidence of reproductive isolation.

Burton (1986) added two further characters to distinguish the taxa. First, in *C. h. humicola* the M. depressor mandibulae arises from the dorsal fascia, with some fibres from the otic ramus of the squamosal and the posterior surface of the adjacent prootic; in *C. h. comptus* and all other *Callulops*, additional fibres arise from the entire posterior and ventral surfaces of the tympanic ring. Second, in *C. h. humicola* the mandibular branch of the trigeminal nerve passes directly ventro-laterally through the M. adductor mandibulae posterior longus on its way to the mandibular musculature; in *C. h. comptus* and all other asterophryines this nerve passes antero-laterally between the M. a. m. posterior longus and the M. m. anterior longus, and then postero-ventrally across the lateral surface of the M. a. m. posterior longus before plunging towards the mandibular musculature. Burton (1986) made no taxonomic recommendation regarding the status of these taxa.

Callulops sagittatus sp. nov.
(FIGS 1-5)

Holotype: UPNG 9051 an adult male collected by S. J. Richards, M. Cunningham and A. Dennis on 20.xi.1994 at an altitude of 2200 m on the summit of Mt Binnie, Western Province, Papua New Guinea (141° 7' 30"E, 5° 12'S).

Paratypes: UPNG 9052 (adult female), QMJ 60231 (adult male), same data as holotype.

Definition

A moderately large and robust species (males 44.1-47.8 mm S-V, a female 56.3 mm S-V) distinguished from congeners by a combination of the following characters: fingers and toes without expanded discs, a distinct orange stripe dorsally on the head from the snout extending across each eyelid, tympanum indistinct, advertisement call a series of deep "crawks" with a dominant frequency of 609 Hz, a note repetition rate of 1.85-2.2/s and a pulse rate of 11.89-14.02/ms.

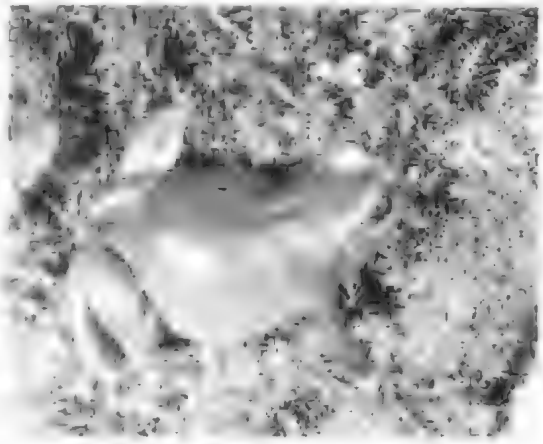

Fig. 1. *Callulops sagittatus* sp. nov. in life (S-V 56.3 mm).

Description of holotype

Body robust, almost pear shaped (Fig. 1), head broader than long (HW/HL 1.23) with nares closer to tip of snout than to eye (SN/EN 0.6) and directed laterally. Internarial distance greater than distance from eye to nares (EN/IN 0.78), eyes large (EYE/S-V 0.119). Snout blunt, broadly rounded in dorsal view and rounded in lateral view (Fig. 2). Canthus rostralis rounded, loreal region steep, slightly concave. Tympanum indistinct, annulus barely visible. Dorsal and ventral surfaces minutely granular, a weak supratympanic fold. Anterior palatal ridge long, smooth, posterior palatal ridge with 11 distinct denticles.

Limbs short (TL/S-V 0.38), relative lengths of fingers 3>4>2>1, fourth finger only marginally longer than second. Fingers unwebbed, tips without expanded discs, subarticular tubercles low, rounded. Palm smooth except for a low inner metacarpal tubercle. Relative lengths of toes 4>3>5>2>1. Toes

unwebbed, tips without expanded discs, subarticular tubercles low, rounded. A low, oval inner metatarsal tubercle; no outer tubercle (Fig. 3).

Colour in life uniform deep red-brown dorsally on body and limbs, grading laterally into a uniform lighter brown ventral surface. Throat slightly darker brown than rest of venter. Head deep red-brown with an orange stripe dorsally from tip of snout along canthus and over eye, forming distinct arrow shape on crown. Slight orange tinge on upper surface of thigh. No other markings dorsally or ventrally. In preservative brown with a mauve tinge dorsally, brown ventrally, stripes on head very pale pink.

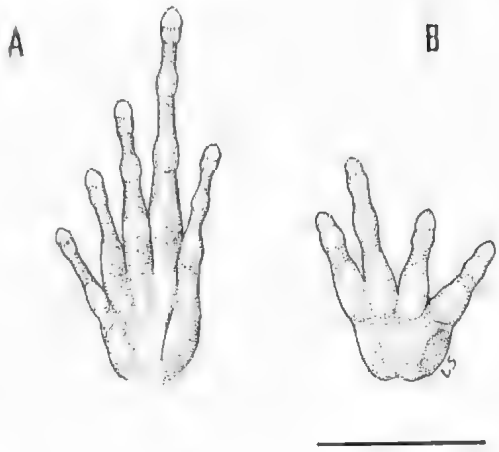

Fig. 3. Hand and foot of *Callulops sagittanus* sp. nov. holotype (UPNG 9051). A. Plantar view of foot. B. Palmar view of hand. Scale bar = 10 mm.

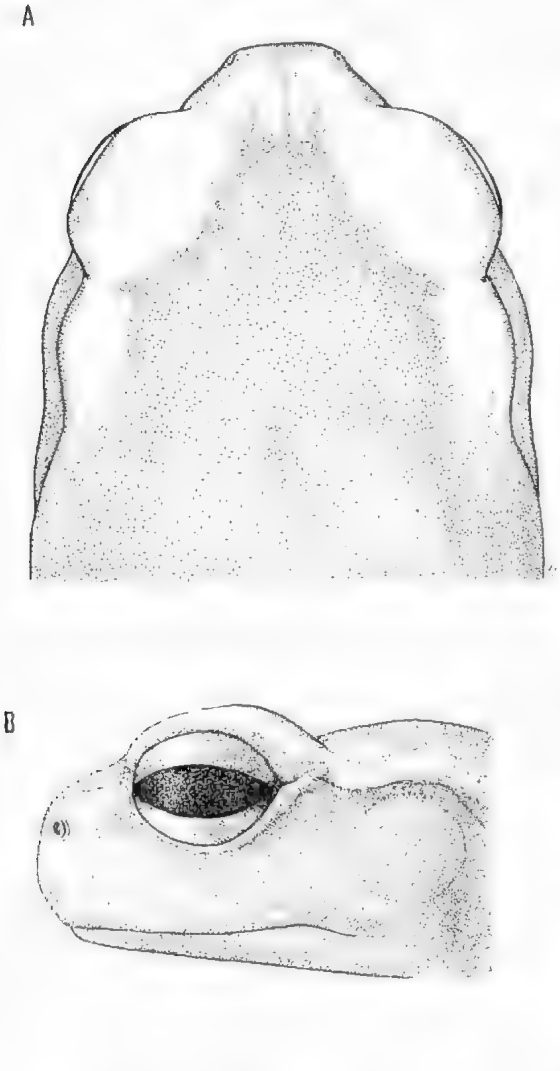

Fig. 2. Views of head of *Callulops sagittanus* sp. nov. holotype (UPNG 9051). A. Dorsal view. B. Lateral view. Scale bar 10 mm.

Dimensions of holotype

S-V 47.8; TL 18.2; EN 3.3; SN 2.0; IN 4.2; EYE 5.7; HW 17.0; HL 13.8; HD 12.5; FT 19.3; EN/IN 0.785; TL/S-V 0.38; HW/HL 1.23; EYE/S-V 0.119; HW/S-V 0.355; width of toe tip on fourth toe 1.0 (width of penultimate phalanx 0.8); width of toe tip on third finger 0.9 (1.0).

Musculature

The superficial throat musculature and squamosal form conform to the definition of *Callulops*. The M. depressor mandibulae arises predominantly from the dorsal fascia, but also receives substantial contributions from the otic ramus and the posterior and ventral margins of the tympanic ring. The mandibular branch of N. trigeminalis passes directly ventro-laterally from the brain case and penetrates the M. adductor mandibulae posterior longus on its way to the mandibular musculature (Fig. 4).

Advertisement call

We recorded two call sequences but only one of these is of sufficient quality for detailed analysis. The mating call is a series of deep, guttural croaks "crawk, crawk, crawk...". The recordings contained 11 and 12 notes lasting a total of 5.57 and 5.186 seconds respectively (note repetition rate = 1.85/s and 2.2/s). Both calls had a dominant frequency of 609Hz. Individual notes in the 11-note call lasted 118.9-182.3 ms (mean = 154.2), contained 10-13 pulses (mean = 11.63) at a rate of 11.89-14.02/ms (mean = 13.23). Fig. 5 illustrates the first four notes of an 11-note call recorded at the type locality on 20.xi.94 at an air temperature of 13.5 °C.

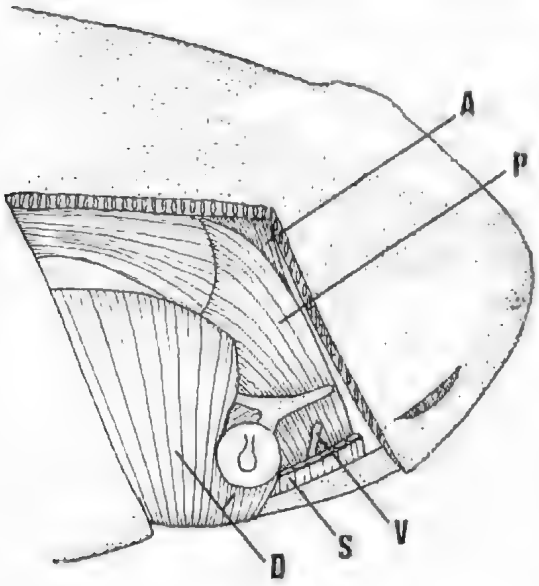

Fig. 4. Dorso-lateral view of musculature of right jaw of *Callulops sagittatus* sp. nov. A. M. adductor mandibulae anterior longus; D. M. depressor mandibulae; P. M. adductor mandibulae posterior longus; S. M. adductor mandibulae externus superficialis (severed); V. mandibular branch of trigeminal nerve. Scale bar = 5 mm.

The calls were uttered at irregular intervals, with long periods (often over five minutes) between calls. On several occasions we heard a melodious, dove-like "coo coo...." vocalisation uttered immediately following, or from the same vicinity as, one of the call types described above but we were unable to confirm whether it was part of the vocal repertoire of this species.

Natural history

The type series was collected in disturbed rainforest and secondary regrowth at altitudes over 2000 m along the access road to the summit of Mt Binnie. One male was calling from the entrance to a deep crevice between rocks in a vertical road cutting, and the other was calling from deep within a labyrinth of crevices among large rocks in the road cutting. The female was collected on the surface and appeared to be approaching the latter male. Additional males were heard calling within crevices adjacent to the road but we were unable to trace them due to the sporadic nature of calling and their subterranean habitats.

The female contains large, unpigmented eggs indicating that development occurs within the egg capsule like other Australopapuan microhylids (Zweifel & Tyler 1982). Two mature eggs measured in the ovary were 4.5 mm in diameter.

The skin of this species is thick and glandular (Fig. 4) and the animals exuded a slimy mucus when handled, apparently as a defensive mechanism.

Variation

The colour pattern is consistent in the three available specimens, all of which exhibit the distinctive orange stripes on the head. Some of the fingers and toes of each specimen are dehydrated making accurate measurement difficult, but none has expanded discs; some fingers and toes have faint, vestigial grooves on the tips. Measurements and proportions of the two paratypes (UPNG 9052/QMJ60231) are: S-V 56.3/44.1; TL 19.8/14.6; EN 3.4/3.3; SN 2.1/2.0; IN 4.6/3.9; EYE 6.0/5.2; HW 19.0/17.7; HL 16.0/16.1; FT 21.0/19.0; HD 13.2/11.7; EN/IN 0.76/0.846; TL/SV 0.35/0.33; HW/HL 1.18/1.09; EYE/S-V 0.106/0.118; HW/S-V 0.337/0.401; width of toe tip on fourth toe (width of penultimate phalanx) 1.1 (0.9)/0.8 (0.7); width of toe tip on third finger 1.0 (1.0)/1.0 (1.0).

Comparison with other species

Callulops (sensu Dubois (1988)) now includes 15 species. Morphologically they are rather conservative, and there is extensive overlap in most body proportions among species (Zweifel 1972 Table 6). The comparisons below are based largely on the detailed descriptions of taxa presented by Zweifel (1972).

The presence of orange stripes dorsally on the head distinguishes *C. sagittatus* from known congeners. *Callulops boettgeri*, *C. eurydactylus* and *C. slateri* further differ from *C. sagittatus* in having greatly expanded finger and toe discs (vs no discs). *Callulops doriae*, *C. dubius*, *C. fuscus*, *C. humicola humicola* and *C. h. comptus*, *C. kopsteini*, *C. personatus* and *C. robustus* have small grooved discs on the fingers and toes. *Callulops doriae* (100 mm), *C. personatus* (72.5 mm) and *C. robustus* (73 mm) are much larger species and *C. dubius* appears to be a much smaller species (maximum S-V = 24 mm). Although sample size is small, there appear to be differences between the mating calls of *C. sagittatus* and those of both *C. personatus* and *C. robustus*. Two calls of *C. personatus* have a dominant frequency of about 1000-1500 Hz (vs 609 Hz) and contained 5 notes (vs 11-12). Calls of *C. robustus* from Misima Island (the type locality) have a dominant frequency of about 800Hz (J. Menzies unpubl. data). *Callulops h. comptus* is the only other species in which adults have orange stripes on the head, but in this species the orange markings are restricted to a short lateral post-ocular stripe. *Callulops sagittatus* shares with *C. h. humicola* the condition of the mandibular branch of the trigeminal nerve. As this condition is unique among the asterophryines it appears to be a synapomorphy indicating a close phylogenetic relationship between these taxa. However, *C. h. humicola* differs from *C. sagittatus* in the possession

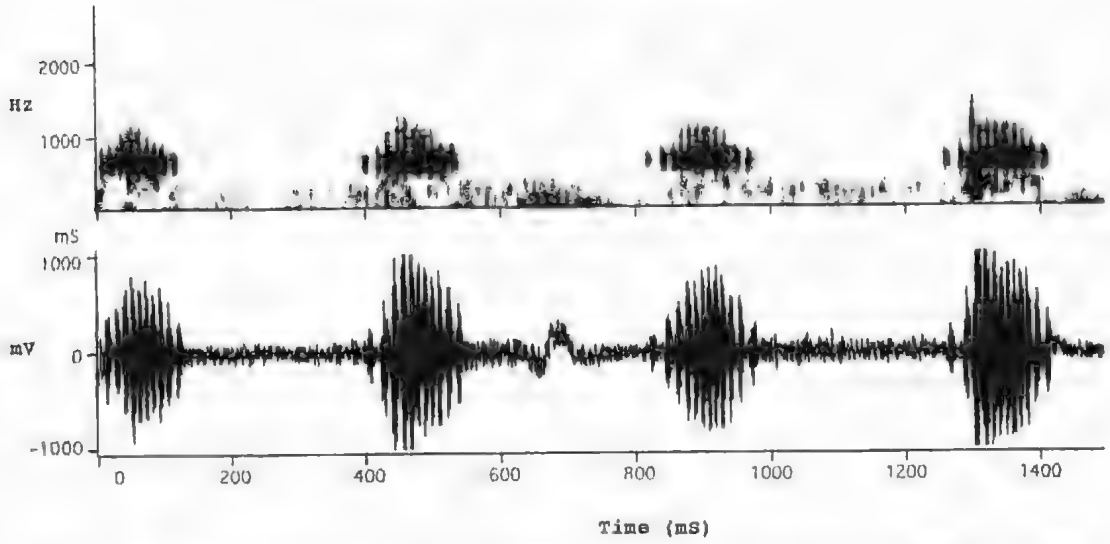

Fig. 5. Audiospectrogram (top) and wave form (bottom) of first four notes of an 11-note call sequence of *Callulops sagittatus* sp. nov. recorded at the type locality. Air temperature 13.5°C.

of grooved discs on the fingers, and lack of orange stripes on the head. Three species, namely *C. glandulosus*, *C. stictogaster* and *C. wilhelmanus* share with *C. sagittatus* the lack of finger and toe discs. *Callulops glandulosus* differs from *C. sagittatus* in having a coarsely mottled ventral surface (vs uniform) and in having a well-developed glandular area behind the ear, whereas *C. stictogaster* is a larger species (to 80 mm) and has a distinct tubercle between the eye and the nostril (lacking in *C. sagittatus*). *Callulops wilhelmanus* closely resembles *C. sagittatus* and has a similar call (J. Menzies unpubl. data), size and colour pattern. It is distinguished predominantly by the absence of orange markings on the crown and the condition of the mandibular branch of the trigeminal nerve.

Zweifel (1972) discussed four specimens of *Callulops* from Busilmin on the northern slopes of the Star Mountains that he tentatively assigned to *C. robustus*. This population is geographically close to the type locality and is at a similar altitude. The frogs are within the size range of *C. sagittatus* but none exhibits the orange stripes typical of this species and their identification remains uncertain.

Status of Callulops h. humicola *and* C. h. comptus

Although we still lack calls or other reproductive data for these taxa, their classification as a single species is no longer tenable, given the evidence that the taxon most closely related to *C. h. humicola* is not *C. h. comptus* but *C. sagittatus*. In light of this and previously reported consistent morphological differences (Burton 1986; Zweifel 1972) we propose that *C. humicola comptus* be elevated to specific status as *Callulops comptus* (Zweifel) new combination. Zweifel (1972) presented a thorough description of these two taxa and a detailed comparison with each other and all other *Callulops* except *C. sagittatus*, with which they are compared above.

Etymology

From the *L. Sagitta* (= arrow) with reference to the arrow-shaped orange markings on the crown.

Acknowledgments

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MANUNEMA PECTENOPHORA SP. NOV. (PERESIANIDAE, LEPTOLAIMINA), A NEMATODE POSSESSING UNUSUAL MALE SUPPLEMENTARY ORGANS

*By Aimorn C. Stewart & Warwick L. Nicholas**

Summary

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Manunema pectenophora, sp. nov., with three unique pre-anal male supplementary organs, is described. These are comb-like organs held clear of the body on short rods. Two previously described species of Manunema, the sole genus in the Peresianidae, possess tubular supplements. M. pectenophora also differs from the other species in that the single testis is anterior. All Manunema species possess four long cephalic setae, no labial setae or papillae, circular amphids, a strongly annulated cuticle, a narrow tubular buccal tube, a narrow cervical region expanding to accommodate the strongly muscular pharynx, two outstretched ovaries ventral to the gut and simple curved spicules. The taxonomic placement of the Peresianidae is difficult but the conclusion of other taxonomists that it belongs within the Leptolaimina is supported.

Key Words: Taxonomy, marine nematodes, Peresianidae, Manunema.

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Manunema pectenophora, sp. nov., with three unique pre-anal male supplementary organs, is described. These are comb-like organs held clear of the body on short rods. Two previously-described species of *Manunema*, the sole genus in the Peresianidae, possess tubular supplements. *M. pectenophora* also differs from the other species in that the single testis is anterior. All *Manunema* species possess four long cephalic setae, no labial setae or papillae, circular amphids, a strongly annulated cuticle, a narrow tubular buccal tube, a narrow cervical region expanding to accommodate the strongly muscular pharynx, two outstretched ovaries ventral to the gut and simple curved spicules. The taxonomic placement of the Peresianidae is difficult but the conclusion of other taxonomists that it belongs within the Leptolaimina is supported.

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Introduction

Manunema pectenophora sp. nov. possesses prominent male supplementary organs, i.e. ventral pre-anal organs found in many male nematodes, but in the new species they are unlike those described previously. The Peresianidae contains a single genus, *Manunema*, comprising only two previously-described species, namely *M. proboscidis* Gerlach, 1957, and *M. annulata* (Vitiello & de Coninck 1968) Riemann, *et al.* 1971.

The taxonomic placement of the Peresianidae has proved a problem. Some characters suggest placing the family in the Leptolaimina (Chromadorida), others are closer to the Desmoscolecoidea (Monhysterida).

Materials and Methods

Specimens were collected from the intertidal zone of beaches at Darwin NT. Samples of about 2 kg of sand were dug up at low tide and the meiofauna present was briefly suspended in 5 litres of tap water with vigorous stirring. As soon as the sand had settled, the water was passed through a 60 μm nylon sieve and the fauna retained on the sieve back-washed into a beaker with sea water. They were immediately fixed by adding formalin to give a final concentration of 5%. Later, the meiofauna was examined in petri dishes under a binocular microscope. The new species was isolated by pipette from the many hundreds of other nematodes collected and the nematodes mounted on microscope slides in anhydrous glycerol. Cover slips were supported by glass beads (Ballotini) selected under the microscope to be slightly wider than the nematodes and the cover slips were ringed with Glyceel (Gurr).

Measurements are in μm from specimens fixed and mounted in this way. De Man's indexes (ratios) (Fortuner 1990) are given, i.e. a = body length divided by greatest body width, b = length divided by length of pharynx, c = length divided by tail length, c' = tail length divided by width at anus, V = anterior end to vulva as a percentage of body length, and spicule measurements are arc length.

Drawings and measurements were made using a camera lucida. When mounted, the nematodes lie on their sides presenting a lateral view, and our drawings, with the exception of all four cephalic setae, show setae on one side only, those lying uppermost as mounted.

For scanning electron microscopy, some specimens in 5% formalin were washed in phosphate buffer, pH 7, containing 3% sucrose, post-fixed by the addition of 2% osmium tetroxide, washed, sonicated and finally freeze-dried. The specimens were mounted on metal stubs and coated with gold/palladium before examination in the microscope.

Type specimens are deposited in The South Australian Museum, SAMA, Adelaide, and their numbers in the Museum's Australian Helminth Collection, AHC, are given in the text.

Manunema pectenophora sp. nov.
(FIGS 1-11)

Holotype: Male, Rapid Creek beach, Darwin, NT, 19.x.1992, SAMA, AHC 30000.

Measurements: Table 1

* Division of Botany and Zoology, Australian National University, Canberra ACT 0200.

TABLE 1. *Measurements of* Manunema pectenophora *sp. nov.*

Type	Holo-Male	Male paratypes n = 3 Range	Mean	+SD	Female paratypes n = 4 Range	Mean	+SD
Length	488	468-506	490	20	475-508	497	17
Maximum width	15	11-12	13	0.58	16-20	18	1.83
Cephalic setae	13	10-16	13	3.06	12-18	15	2.50
Body setae	11	11-14	12	1.73	10-14	12	1.83
Mouth to amphid	12	10-11	10	0.58	9-9	9	0.50
Amphid diameter	3.7	3.0-3.2	3.1	0.12	3.6-3.6	3.6	0.00
Width at amphid	6.5	5.0-6.5	5.8	0.76	5.6-5.6	5.6	0.05
Buccal cavity	30	32-36	34	2.08	31-34	33	1.50
Width at buccal cavity	12	9-11	10	1.15	9-12	11	1.50
Mouth to nerve ring	57	54-60	57	3.06	55-60	58	2.08
Width at nerve ring	13	13-14	13	0.58	14-18	16	1.73
Pharynx	83	77-83	80	3	82-88	85	2.58
Width at cardia	14	14-17	14	2.52	10-18	14	2.99
Mouth to vulva	-	-	-	-	252-273	265	10
Width at vulva	-	-	-	-	15-20	18	1.83
Egg	-	-	-	-	44-79	57	20
Mouth to anus	341	391-434	412	22	407-438	426	14
Tail	81	72-84	78	6	67-74	71	3.77
Width at anus	11	11-11	11	0	8-11	10	1.29
Spicule, arc length	24	23-25	24	1			
Gubernaculum	11	10-11	10	0.99			
Anus to 1st supplement*	6.8	4.5-7.3	6.4	1.57	-		
Anus to 2nd supplement*	13	11-15	13	2.25	-		-
Anus to 3rd supplement*	34	31-34	33	1.62	-	-	-
De Man's a	33	36-39	39	2.63	25-30	28	2.6
De Man's b	5.9	5.6-6.6	6.1	0.47	5.7-6.2	5.8	0.24
De Man's c	6	5.9-7.0	6.3	0.63	6.9-7.3	7.0	0.22
De Man's c'	7.4	6.5-7.6	7.1	0.55	6.7-8.5	7.5	0.96
De Man's V%	-	-	-	-	51-55	53	1.48

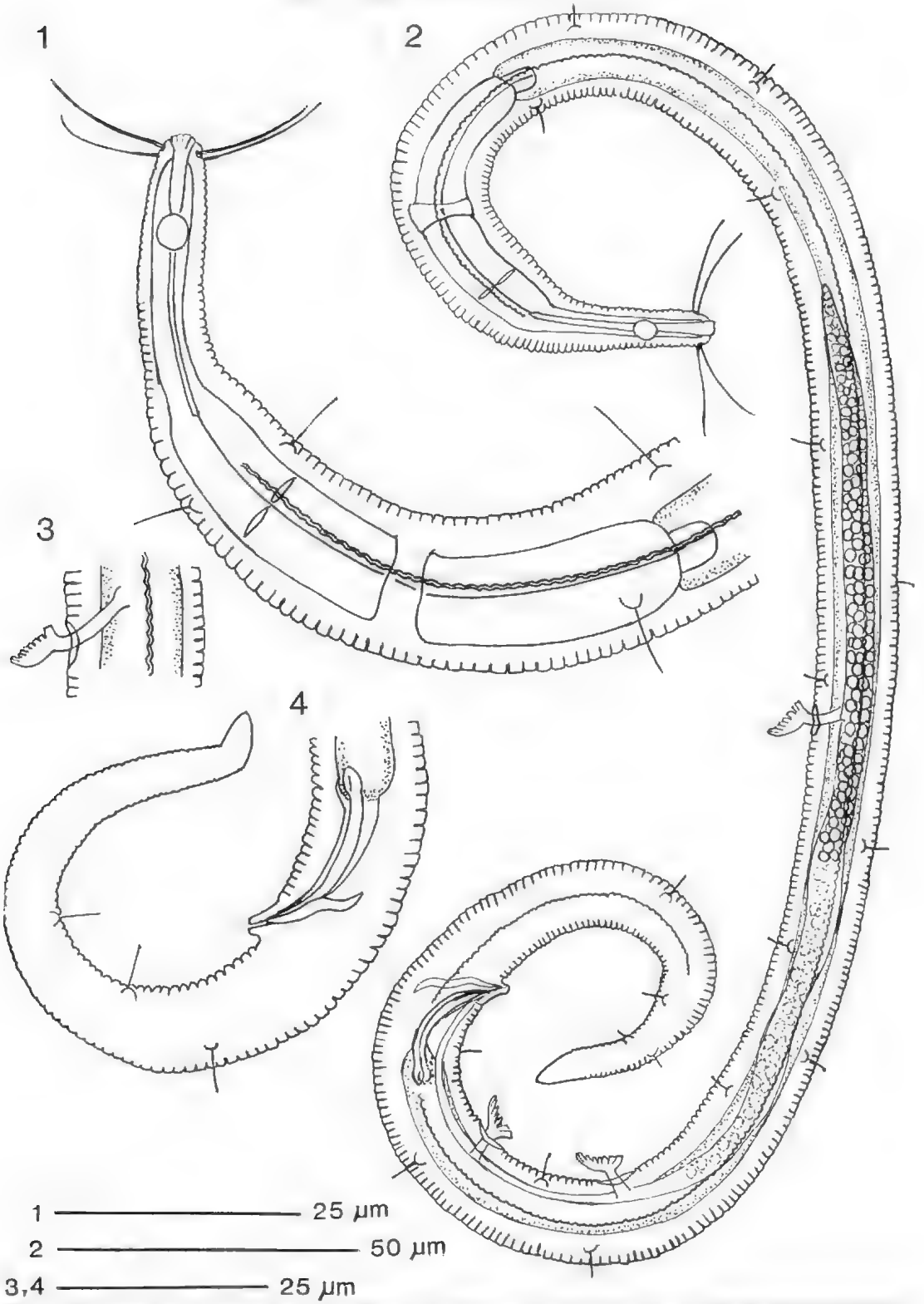
*As percentage of body length

Description of Holotype male

Small, body when fixed strongly curved, head and cervical region folded back along body, tail curled. Cuticle strongly annulated; lateral ridges from mid-pharyngeal region to mid tail, wavy in register with annules; four rows of prominent body setae, arising from pronounced cuticular hemispherical swellings, dorso-lateral setae alternate with ventro-lateral setae. Four long cephalic setae arising form sockets; labial setae absent; amphid circular. Buccal cavity, with minute ridges around mouth, initially narrowly conical extending posteriorly as a narrow parallel-sided tube. Pharynx, in cervical region (35% of pharynx length) narrow parallel-sided, encloses buccal tube, then a wider muscular cylinder, somewhat constricted by prominent nerve ring, two cytoplasmic clefts between nerve ring and expansion; cardia short, cylindrical. Intestine simple tube, anus and rectum project slightly from body contour; caudal glands not observed (probably obscured by strong annulation). Single testis to left of intestine; spicules cephalated, smoothly curved, tips pointed; gubernaculum slightly curved plate. Three pre-anal supplementary organs, most anterior one about mid-way between cardia and anus, the other two close to anus. Each supplement resembles an outwardly and slightly forwardly directed comb, with about 11 prongs, mounted on a cuticular rod arising deep in the body wall.

Paratypes: SAMA, AHC 30001-7. Measurements of three males and four females are given in Table 1. In paratype males, as in the holotype, anterior supplement about 33% of body length in front of anus, second and third supplements, closer to anus, apparently more variable in position, probably due to different degrees of body curvature. Long testis, to left of intestine, with many developing sperm, begins just anterior to mid body, continues as long sperm duct. SEM of another male, Figs 6 and 7, shows a tenous transparent film overlapping the base of a supplement and adjacent cuticle. We interpret this as mucus, present over the surface of freshly fixed specimens and preserved by freeze-drying but lost when specimens are transferred to glycerol for light microcopy.

Females (Fig. 5) similar to males apart from reproductive organs and absence of supplementary organs. Didelphic, two very short ovaries outstretched, ventral to gut. Three females each have single large egg, 43, 48 and 79 μm long, respectively, overlapping the vulva, to left of intestine. The largest is probably at an early stage of the first cleavage division.



Figs 1-4. *Manunema pectenophora* sp. nov. 1. Male head. 2. Entire male. 3. Supplementary organ. 4. Spicules and gubernaculum.

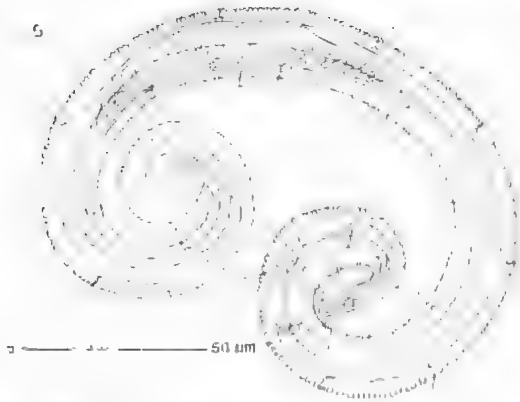


Fig. 5. Female *Manunema pectenophora* sp. nov.

Differential diagnosis

The form of the supplement distinguishes *M. pectenophora* sp. nov. from the other described species of *Manunema*, none of which possesses comb-like structures mounted on rods. The new species differs from *M. annulata* in the orientation of the single testis.

Habitat

Sandy ocean beach.

Distribution

So far known only from Rapid Creek beach, a suburb of Darwin, Northern Territory.

Etymology

Named from L. *pecten*, a comb.

Discussion

Supplementary organs are common in many families of Adenophorea, where they are associated with sensilla, and are generally believed to play a part in copulation. They may be tubular, setose or papilliform and are often associated with cuticular ornamentation but none like the organs described here has previously been reported. They do not appear to be associated with sensilla and conceivably serve some mechanical role in copulation. *M. proboscidis* possesses two pre-anal tubular male supplementary organs (Gerlach 1957). Vitiello & de Coninck (1968) claimed that supplements were lacking in *M. annulata*, but Riemann *et al.* (1971) redescribed *M. annulata*, reporting two pre-anal tubular supplements. Neither Gerlach (1957) nor Vitiello & de Coninck (1968) comment on the buccal cavity. We agree with Riemann *et al.* (1971) that the buccal cavity is long and tubular. Lorenzen (1981) includes a long tubular buccal cavity as one of the diagnostic characters of the Peresianidae.

The taxonomic position of the Peresianidae, to which *Manunema* belongs, has been the subject of some doubt, partly because their small size has led to some uncertainty about taxonomically important characters. It is significant that scanning electron microscopy does not show either outer labial papillae or setae, nor any external manifestation of inner labial sensilla. All the described species have four long sub-median cephalic setae inserted in sockets.

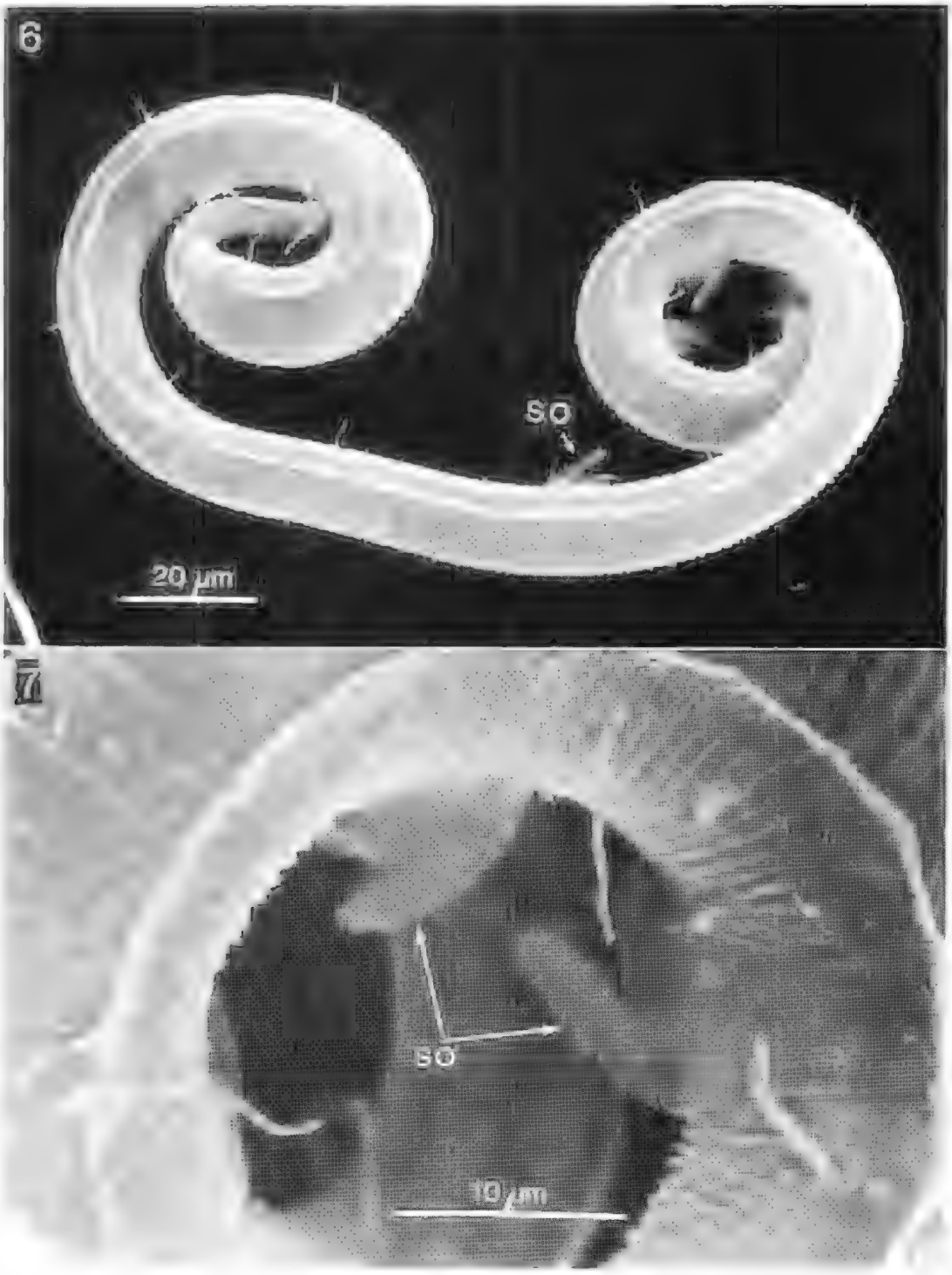
In Lorenzen's (1981) phylogenetic classification of the Adenophorea, ovaries ventral to the intestine and a single posterior testis are significant characters in *Manunema*, consistent with the placement of the Peresianidae in the Leptolaimina but, while the location and form of the ovaries in *M. pectenophora* are the same as in *M. proboscidis*, we have observed a single anterior testis in three males of *M. pectenophora*. The form of the amphids, the long narrow buccal tube and tubular supplementary organs are consistent with Leptolaimina; ventral outstretched ovaries are not (Lorenzen 1981). In the possession of four cephalic setae, the absence of outer labial setae, the possession of four sub-median rows of alternating body setae arising from peduncles and the anus on a protrusion from the body cavity, *Manunema* resembles the Desmoscolecoidea, within the Monhysterida, rather than the Leptolaimina.

In Vitiello and de Coninck's (1968) view, the similarities between *Peresiana annulata*, now renamed *Manunema annulata* Riemann *et al.* (1971), and *Meylia spinosa* Gerlach 1956 indicated a phylogenetic link between the Halliplectidae (Leptolaimina in Lorenzen's classification) and the Desmoscolecida, in which they placed the new species. The similarities to which they drew attention were the four cephalic setae and the position of the non-vesicular amphids, but in other respects the species are unalike, differing in the structure of the cuticle, buccal cavity, pedunculate setae and the location of the anus. In fact, as Riemann *et al.* (1971) point out, there are similarities between *Manunema* and other Desmoscolecoidea, for example with *Tricoma mirabilis* Timm 1961, although *Manunema* shows greater similarity with such Leptolaimina as *Anomonema haplostoma* Hopper 1963 and *Leptolaimus triubulatus* Boucher and Helléouët 1977.

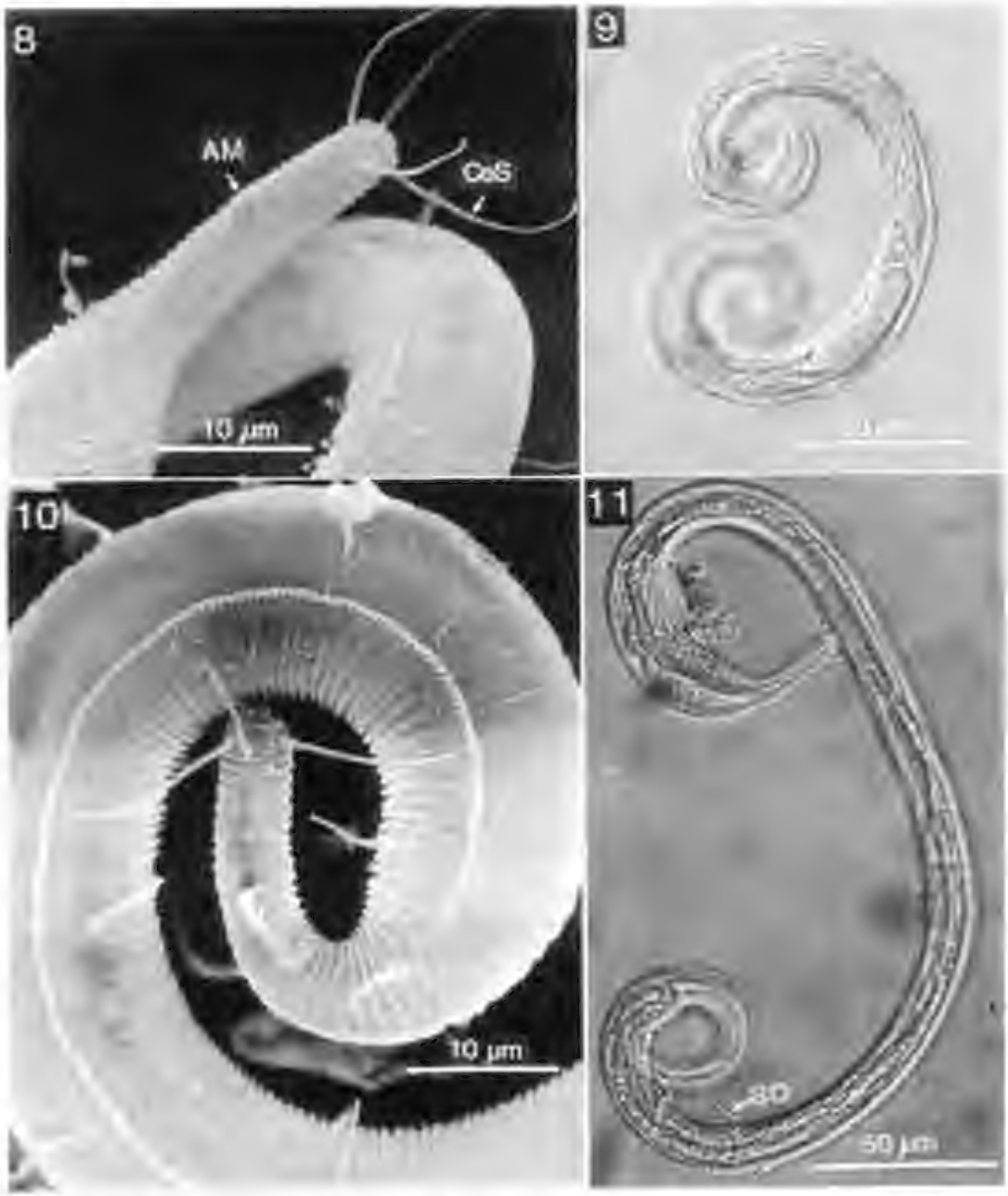
Although *M. pectenophora* does not possess tubular supplementary organs or a posterior testis (leptolaimid characters of *Manunema proboscidis* and *M. annulata*) we concur with the placement of Peresianidae in the Leptolaimina, with a possible link between Leptolaimina and Desmoscolecoidea.

Acknowledgments

We thank Dr Russell Hanley for providing facilities in The Northern Territory Museum and the Australian Biological Survey for financial support for one of us to work in Darwin.



Figs 6 and 7. Scanning electron microscopy of *Manunema pectenophora* sp. nov. 6. Entire male. 7. Enlargement to show supplementary organs. SO supplementary organ.



Figs 8-11. 8. Scanning electron microscopy of female *Marasmina pectinophora* sp. nov. CeS cephalic seta, AM amphid. 9. Female by light microscopy. 10. SEM of female head. 11. Male by light microscopy. SO supplementary organ.

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ASPHONDYLIA DODONAEAE, A NEW SPECIES OF CECIDOMYIIDAE (DIPTERA) DAMAGING LEAVES AND BRANCHES OF HOP-BUSH, DODONAEA VISCOSA (SAPINDACEAE) IN AUSTRALIA

*By P. Kolesik**

Summary

Kolesik, P. (1995) Asphondylia dodonaeae, a new species of Cecidomyiidae (Diptera) damaging leaves and branches of hop-bush, Dodonaea viscosa (Sapindaceae) in Australia. Tran. R. Soc. S. Aust. 119(4), 171-176, 30 November, 1995.

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Key Words: Cecidomyiidae, Asphondylia dodonaeae sp. nov., Dodonaea viscosa, South Australia.

Transactions of the Royal Society of S. Aust. (1995), 119(4), 171-176.

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KEY WORDS: Cecidomyiidae, *Asphondylia dodonaeae* sp. nov., *Dodonaea viscosa*, South Australia.

Introduction

The new gall midge species described here was found infesting leaves and terminal branches of hop-bush, *Dodonaea viscosa* Jacq. subsp. *spathulata* (Smith) J. G. West (Sapindaceae) in South Australia.

Dodonaea viscosa Jacq. is a shrub or tree up to 8 m tall. It occurs throughout Australia and extends into tropical Asia, America and Africa and into temperate southern Africa, New Zealand and Pacific islands (Reynolds & West 1985). Its leaves are used in various parts of the world in folk medicine to control fever, colic, inflammation, swellings, rheumatism and pain (West 1984; Ahmad *et al.* 1987; Wagner *et al.* 1987; Mata *et al.* 1991). In several countries it is used as firewood, material for tool handles and for reclamation of unused or degraded landscape areas such as sand dunes, marshlands and mine wastes (Norem *et al.* 1982; Reynolds & West 1985). In Australia a purple-leaved form is grown widely in gardens and the foliage is valued for its decorative appearance.

The hop-bush is a common shrub in remnants of the original flora around Adelaide where it forms a substantial part of the medium-high vegetation cover in the nature conservation parks. During 1992-1993 large numbers of galls were found on almost all shrubs surveyed in Morialta and Cleland Conservation parks. The new gall midge appears to have two generations in the Adelaide area, the first from January to February, the second from September to October. Shrubs bearing galls from two successive generations of the gall midge can often be found.

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Materials and Methods

Leaf and branch stem galls of *Dodonaea viscosa* subsp. *spathulata* were sampled in Morialta (27.xi.1992 and 26.ix.1993) and Cleland Conservation Parks (3.i.1993). The parks are adjacent and located about 13 km north-east of Adelaide. The galls obtained on 26.ix.1993 were processed in two ways. A small number was dissected and the larvae (along with one larva from 27.xi.1992) and pupae were preserved in 70% ethanol after notes were made on their colour. A larger number, with larvae and pupae retained within galls, was brought to the laboratory to rear to adults. Branches with galls were kept in plastic bags. Larvae pupated in their galls. Plastic bags were examined daily and emerged adults preserved together with their pupal skins in 70% ethanol after their colour had been noted. Canada balsam mounts of a series for microscopic examination were prepared according to the technique outlined by Kolesik (1995). The type series and other materials retained in 70% ethanol together with dried examples of the galls are deposited in the South Australian Museum, Adelaide [SAM], Australian National Insect Collection, CSIRO, Canberra [ANIC] and United States National Museum [USNM], Washington DC USA.

Asphondylia dodonaeae sp. nov.
(FIGS 1-19)

Holotype: ♂, Morialta Conservation Park, South Australia [34°54′S, 138°44′E], 29.ix.1993, P. Kolesik, reared from larva from leaf gall of *Dodonaea viscosa* Jacq. subsp. *spathulata* (Smith) J. G. West, sampled 26.ix.1993. 121272 [SAM].

Allotype: ♀, same data, I2I273 [SAM].

Paratypes: 3♂♂, 3♀♀, 4 larvae, 4 pupal skins [SAM], 2♂♂, 2♀♀, 2 larvae, 2 pupal skins [ANIC], all same data; 1 larva, sampled 27.xi.1992 [SAM].

Other material: 10♂♂, 10♀♀ [SAM], 5♂♂, 5♀♀, [USNM], 10 pupal skins [SAM], 5 pupal skins [USNM], 10 pupae, all same data as holotype, 5 larvae [SAM], 5 larvae [USNM], all collected with holotype.

Diagnosis

Wings with R_5 joining C at wing apex, Rs absent, R_1 joining C at wing mid-length, M_{1+2} absent, M_1 weakly developed, Cu forked, Sc cell opaque. Flagellomeres 12 in number, cylindrical with short necks, first and second not fused, with short and stout setae and bearing anastomosing slightly appressed circumfila. Male flagellomeres all about same length, female ones, especially the apical three, successively and progressively shorter. Tarsus: first segment substantially shorter than second, bearing ventroapical spine; claws simple; empodia longer than claws. Male terminalia: gonocoxites free ventrally, short, with small apical lobe; gonostylus situated dorsally on gonocoxite, short, bearing two teeth merged basally; hypoproct and cerci bilobate; aedeagus long, stout, tapering distally. Female abdominal sternite 7 about three times longer than sternite 6. Ovipositor: elongate, sclerotized, with large basal lobes; cerci fused, glabrous, bearing few microsetae.

Male (Figs 1-7)

Colour: sclerotized parts of body dark brown, setae and scales black, non-sclerotized parts of abdomen orange. Wing length 2.4 mm (range 2.2 - 2.6), width 1.1 mm (1.0 - 1.2). Wing membrane and veins densely covered with setae, 55 - 120 μm, microtrichia dense, about 0.5 μm long. Flagellomeres with stout setae, 33-38 μm, more or less equally positioned on the segments. Circumfila: two long and two short longitudinal bands with long bands connected to each other by transverse circular bands on both ends; each of the short bands attached on both ends to one of the long ones by short transverse arch; the transverse circular bands on the distal end of the flagellomere arched strongly. Eye facets rounded, eye bridge 8-9 facets long. Maxillary palpus 3 or 4 segmented, often specimens with different number of segments in left and right maxillary palpus can be found; however, total length of both palpi about the same. Palpiger weakly developed. Legs covered with setae and scales, the latter serrated at distal end.

Female (Figs 8-12)

Wing length 2.6 mm (2.6 – 2.7), width 1.2 mm (1.2 1.3). Flagellomeres with stout setae, 30 – 35 μm. Circumfila comprising two transverse bands connected by two short longitudinal bands. Claws somewhat stronger than in male. Abdominal sternite seven 3.2 times (3.1 - 3.3) longer than sternite six. Setae of cerci 6 - 8 in number and less than 1 μm in length. Other characters as in male.

Mature larva (Figs 13-15)

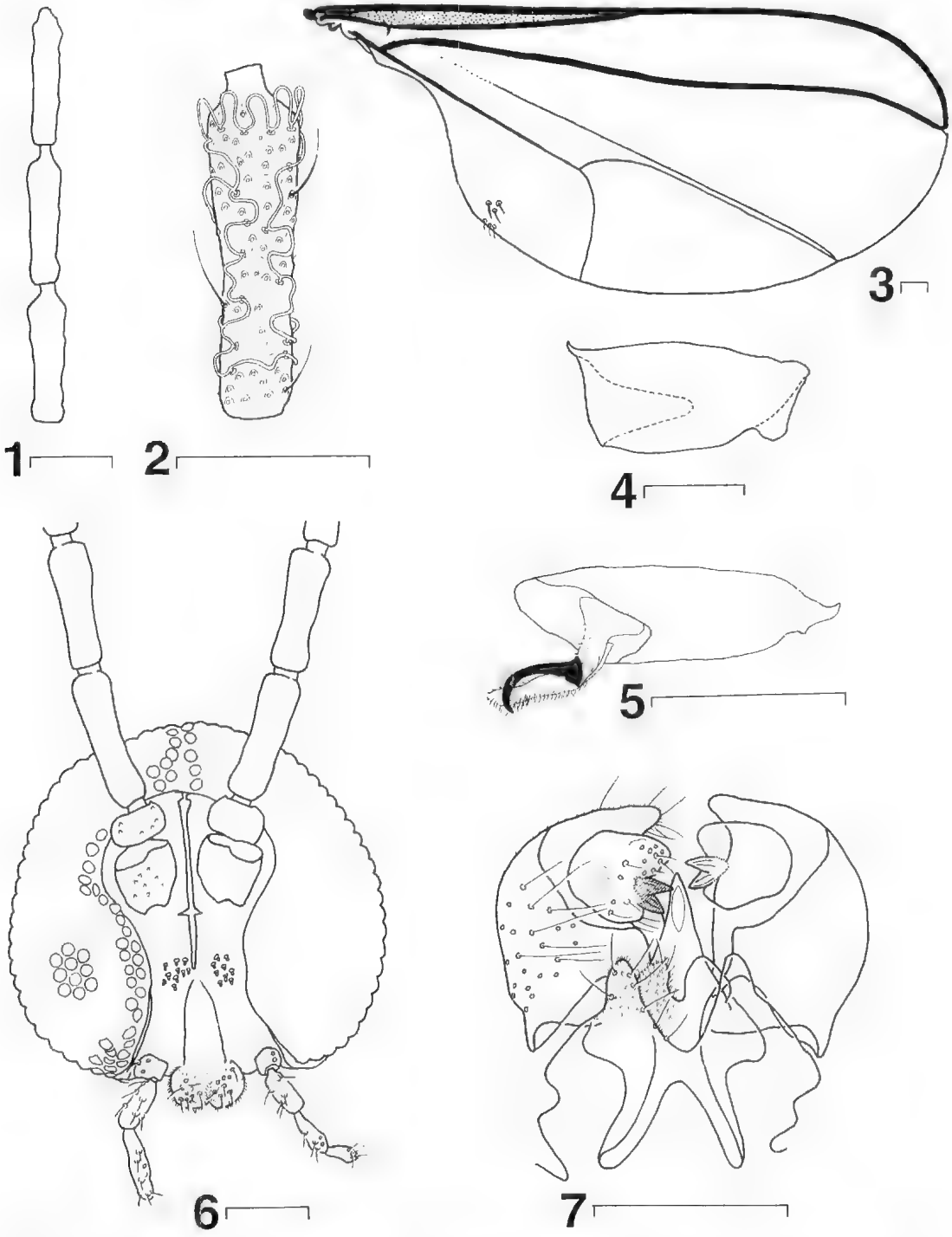
Colour pale orange. Total length 1.9 mm (1.7 - 2.2). Head capsule width 91 μm (90 - 92), length 29 μm (26 - 31), length of posterolateral extensions 10 μm (9 – 10). Antenna 14 μm (13 - 15). Sternal spatula bilobate, 111 μm (108 - 116) in length, with apical enlargement 68 μm (64 - 74) in width and incision 34 μm (31 - 38) in depth. Area around spatula not sclerotized. Anus dorsal. One pair of sternal papillae on thoracic and first to seventh abdominal segments. One pair of ventral papillae on collar, second and third thoracic and first to eighth abdominal segments. Two pairs of lateral papillae on thoracic segments. Pleural papillae: first and third thoracic and first to eighth abdominal segments with one pair, second thoracic segment with two pairs. Dorsal papillae: collar, third thoracic and last two abdominal segments with one pair, first two thoracic and first to seventh abdominal segments with two pairs. The setae on lateral papillae 3 – 5 μm long, those on other papillae 4 - 20 μm long.

Pupa (Figs 16-18)

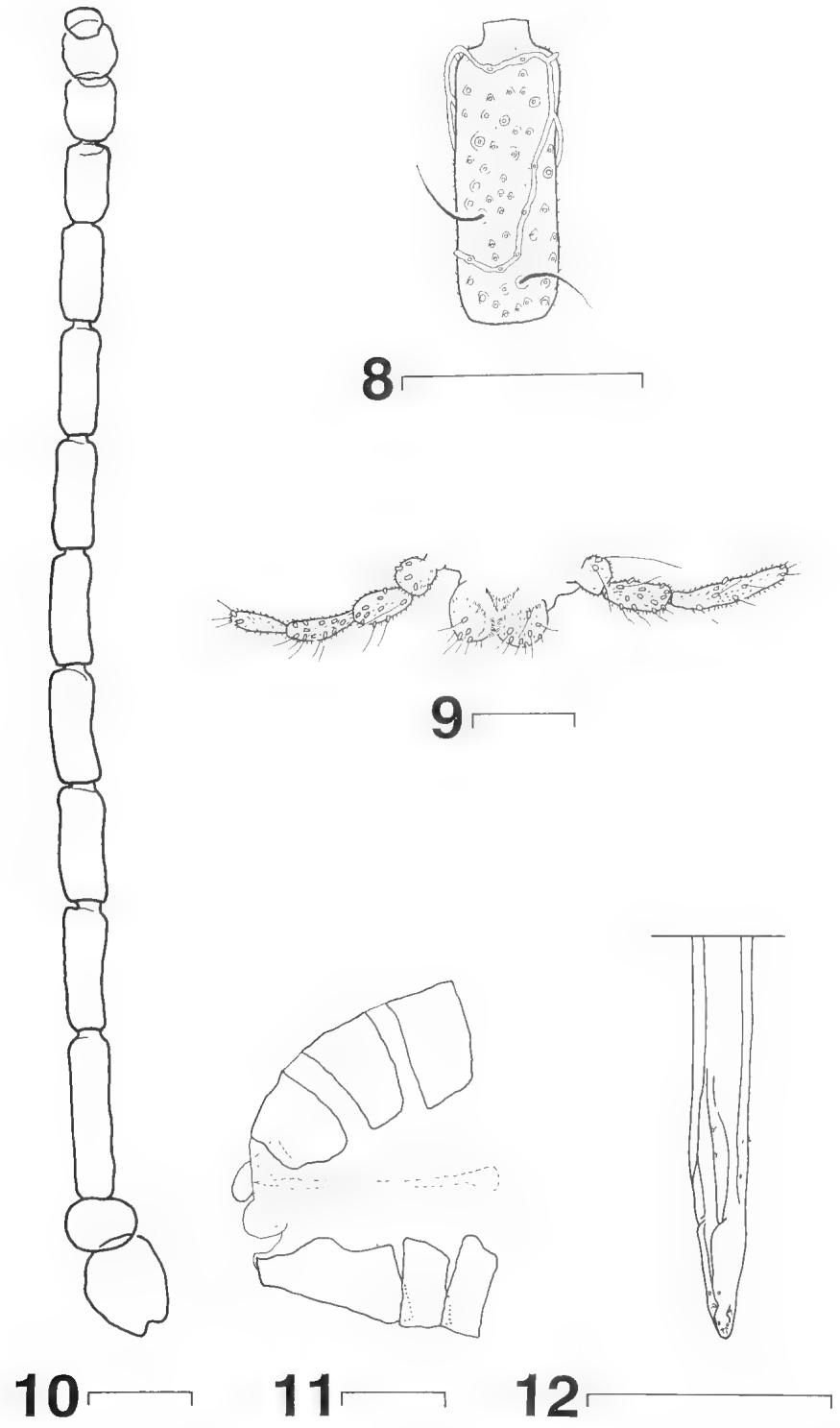
Colour: antennal horns, prothoracic spiracles and dorsal spines dark brown, remaining parts pale brown. Total length 3.0 mm (2.7 – 3.2). Antennal horns triangular, serrated, 161 μm (147 - 182) in length. Cephalic papillae with seta 39 μm (36 - 44). Upper and lower frontal horns absent. Two pairs of lower facial papillae, each consisting of one setose (5 - 15 μm) and one asetose papilla. Two triplets of lateral facial papillae, each consisting of two setose (about 2 μm) papillae and one asetose papilla. Prothoracic horn with trachea ending at its mid-length, 96 μm (83 - 103) long. Second to eighth abdominal segments with two pairs of dorsal papillae (length of setae 8 - 13 μm), two pairs of pleural papillae (19 - 31 μm) and one pair of ventral papillae (12 - 14 μm). Dorsal spines simple, 46 - 104 in number and 8 - 41 μm in length, with length and number increasing from second to ninth segments.

Gall (Fig. 19)

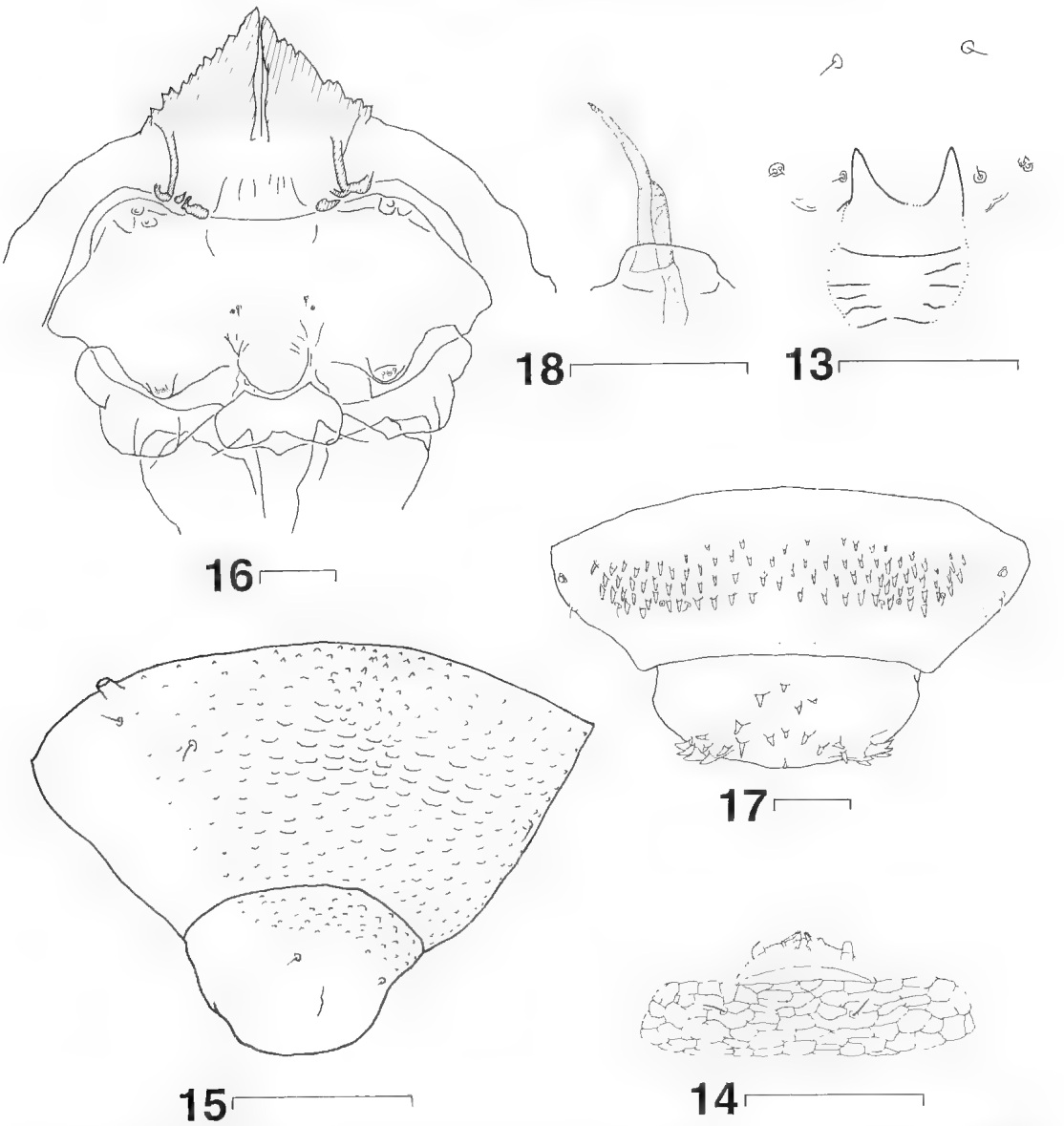
This species forms subglobular monothalamous galls on terminal branch stems and leaf main veins, glabrous, 4 mm long and 3 mm in diameter, green in colour. One larva occupies each gall. Pupation takes place inside the gall. Circular necrotized tissue area, brown in colour, appears on the top of the gall before the pupa cuts a circular opening with its antennal horns by moving its body up and down. The lid to this opening remains attached to the gall by a thin strip of uncut tissue. The pupa raises two thirds of its body outside the gall shortly before emergence as adult. On 24



Figs 1-7. Male of *Asphondylia dodonaeae* sp. nov. 1. Last three flagellomeres. 2. Sixth flagellomere. 3. Wing. 4. First tarsomere. 5. Last tarsomere with claw and empodium. 6. Head in frontal view. 7. Genitalia in dorsal view. Scale bars = 100 μm.



Figs 8-12. Female of *Asphondylia dodonaeae* sp. nov. 8. Sixth flagellomere. 9. Mouth parts in frontal view. 10. Antenna. 11. End of abdomen in lateral view. 12. End of ovipositor in ventro-lateral view. Scale bars = 100 μm.



Figs 13-18. *Asphondylia dodonaeae* sp. nov, 13-15 larva, 16-18 pupa. 13. Sternal spatula. 14. Head capsule and collar segment in dorsal view. 15. Last two abdominal segments in dorso-lateral view. 16. Anterior part in ventral view. 17. Last two abdominal segments in dorsal view. 18. Prothoracic spiracle. Scale bars = 100 μm.

Fig. 19. Galls of *Asphondylia dodonaeae* sp. nov. on *Dodonaea viscosa* Jacq. subsp. *spathulata* (Smith) J. G. West. Scale bar = 2 cm.

November 1992, the vast majority of the galls were dried, only a few of them still contained larvae. On 3 January 1993, the galls were fresh and contained immature larvae. On 26 September 1993, most of the galls were occupied by pupae, with a few occupied by larvae and a few already empty. Empty galls retained pupal skins in openings. On each of the latter occasions a few dried galls from the previous generation were present on the shrubs. The species seems to have two generations in the area surveyed – adults of the first generation appear possibly from January to February and those of the second generation from September to October.

Etymology

The species name is derived from the generic name of the host plant.

Remarks

The new species can be assigned to the genus *Asphondylia* because the female seventh abdominal sternite is more than 1.5 times longer than the sixth, the male genitalia have a ventroapical gonocoxal lobe and dorsally situated gonostylus that is about as broad as long, combined with the first tarsomeres having a ventrodistal spine, the gonostylus bearing two basally merged teeth and the ovipositor having large basal lobes (Gagné 1994). Within the genus *Asphondylia* it is distinguished from other species by lacking both upper and lower frontal horns in the pupa.

Acknowledgments

The Ministry of Environment and Planning, South Australia, kindly permitted collection within the nature conservation parks of Morialta and Cleland. Martin C. O'Leary, State Herbarium of South Australia, Adelaide, courteously identified the host plant species. I am grateful to David B. Hirst, South Australian Museum, Natural Science, John D. Gray, University of Adelaide, Department of Horticulture, Viticulture and Oenology and Raymond J. Gagné, Systematic Entomology Laboratory, USDA, Washington DC USA, for their comments on an early draft of the manuscript.

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CONTARINIA BURSARIAE, A NEW SPECIES OF CECIDOMYIIDAE (DIPTERA) INFESTING FRUITS OF SWEET BURSARIA, BURSARIA SPINOSA (PITTOSPORACEAE) IN AUSTRALIA

*By P. Kolesik**

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Key Words: Cecidomyiidae, Contarinia bursariae sp. nov., Bursaria spinosa, South Australia.

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KEY WORDS: Cecidomyiidae, *Contarinia bursariae* sp. nov., *Bursaria spinosa*, South Australia.

Introduction

Bursaria spinosa Cav., sweet bursaria or Christmas bush, is a shrub usually 1-3 m tall. The genus is endemic to Australia. *Bursaria spinosa* can be found in South Australia, Queensland, New South Wales, Victoria and Tasmania where it is common in woodland vegetation (Bennett 1986). Voluminous clusters of white flowers make the shrub a useful honey plant (Cunningham *et al.* 1981). The gall midge species described here was found to prevent seed production in *B. spinosa* in Morialta Conservation Park, near Adelaide.

Materials and Methods

Fruit capsules of *Bursaria spinosa* were surveyed in Morialta Conservation Park (13 km north-east of Adelaide) on 19 February 1995. Those which contained larvae of the new species were brought to the laboratory where the fruits were cut open and the extracted larvae processed in two ways. A small number was preserved in 70% ethanol after their colour had been noted. The remainder were transferred with entomological forceps into pots containing sterilised, wet sand and reared to the adult stage. Pots were examined daily and emerged adults preserved together with their pupal skins in 70% ethanol after their colour had been noted. For microscopic examination adults, larvae and pupae were mounted on slides in Canada balsam according to the technique outlined by Kolesik (1995). The type series and other material retained in 70% ethanol are deposited in the South Australian Museum, Adelaide [SAM] and Australian National Insect Collection, CSIRO, Canberra [ANIC].

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Contarinia bursariae sp. nov. (FIGS. 1-13)

Holotype: ♂, Morialta Conservation Park, South Australia [34°54'S, 138°44'E], 2.iii.1995, P. Kolesik, reared from larva from fruit of *Bursaria spinosa* Cav., sampled 19.ii.1995, I21274 [SAM].

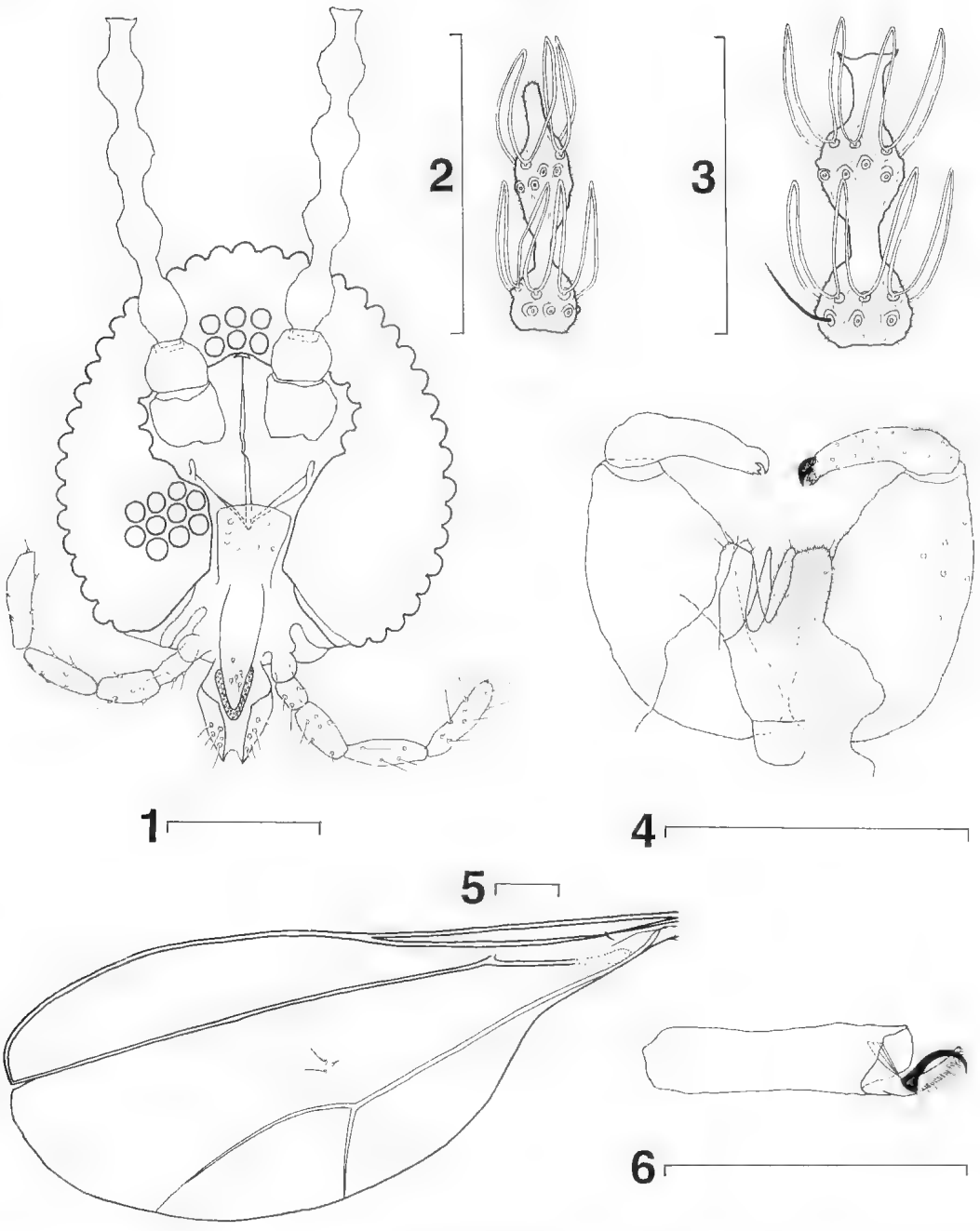
Allotype: ♀, same data, I21293 [SAM].

Paratypes: 2♂♂, 2♀♀, 1 pupal skin [SAM], 2♂♂, 2♀♀, 1 pupal skin [ANIC], all same data but emerged 2.iii.1995 - 6.iii.1995, 4 larvae [SAM], 2 larvae [ANIC], sampled with holotype.

Other material: 21 larvae, sampled with holotype [SAM].

Male (Figs 1-6)

Colour: antenna grey, head black, thorax brown, abdomen with sclerotized parts brown and non sclerotized parts yellow, legs grey with black scale strips along segments. Wing length 1.26 mm (1.19 - 1.31), width 0.47 mm (0.44 - 0.51). Vein C broken at juncture with R_{s}, M_{1} in form of stripe of setae, R_{5} sclerotized on base only. Wing membrane covered with setae, 17 - 22 μm long. Abdominal tergites 2 - 6 with caudal setae only. Head with postvertical peak present. Eye facets rounded, eye bridge 8 - 10 facets long medially. Eight fronto-clypeal setae in all specimens. Antenna total length 1.43 mm (1.32 - 1.54). Length measurements of third flagellomere (μm): proximal node 30 (28 - 32), proximal neck 17 (14 - 18), distal node 36 (34 - 38), distal neck 28 (24 - 31). Circumfilar loops reaching the mid-length of the next node. Tarsal claws curved at mid-length, about as long as empodium. Genitalia: gonocoxite setose and setulose; gonostylus with strongly sclerotized claw and an array of plates below it, sparsely setose with densely setulose pouch at base; hypoproct deeply divided medially, with one seta on each lobe, setulose; cerci deeply divided medially, setose and setulose; aedeagus as long as hypoproct and cerci.



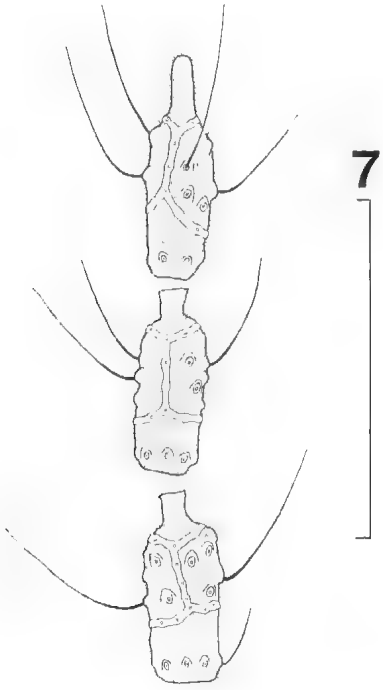
Figs 1-6. Male of *Contarinia bursariae* sp. nov. 1. Head of frontal view. 2. Last flagellomere. 3. Fourth flagellomere. 4 Genitalia in dorsal view. 5. Wing. 6. Last tarsomere with claw and empodium. Scale bars = 100 μm.

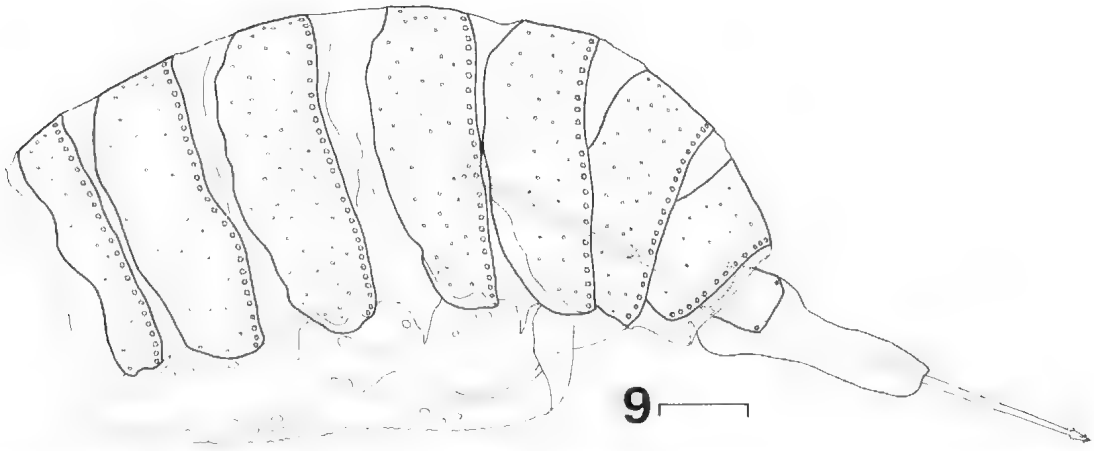
Female (Figs 7-9)

Wing length 1.28 mm (1.23 - 1.37), width 0.48 mm (0.43 - 0.53). Antenna total length 0.79 mm (0.69 - 0.83). Third flagellomere with node 45 μm (43 -49) and neck 6 μm (5 -8) long. Circumfila appressed, consisting of two transverse rings connected by two longitudinal bands. Other characters as in male.

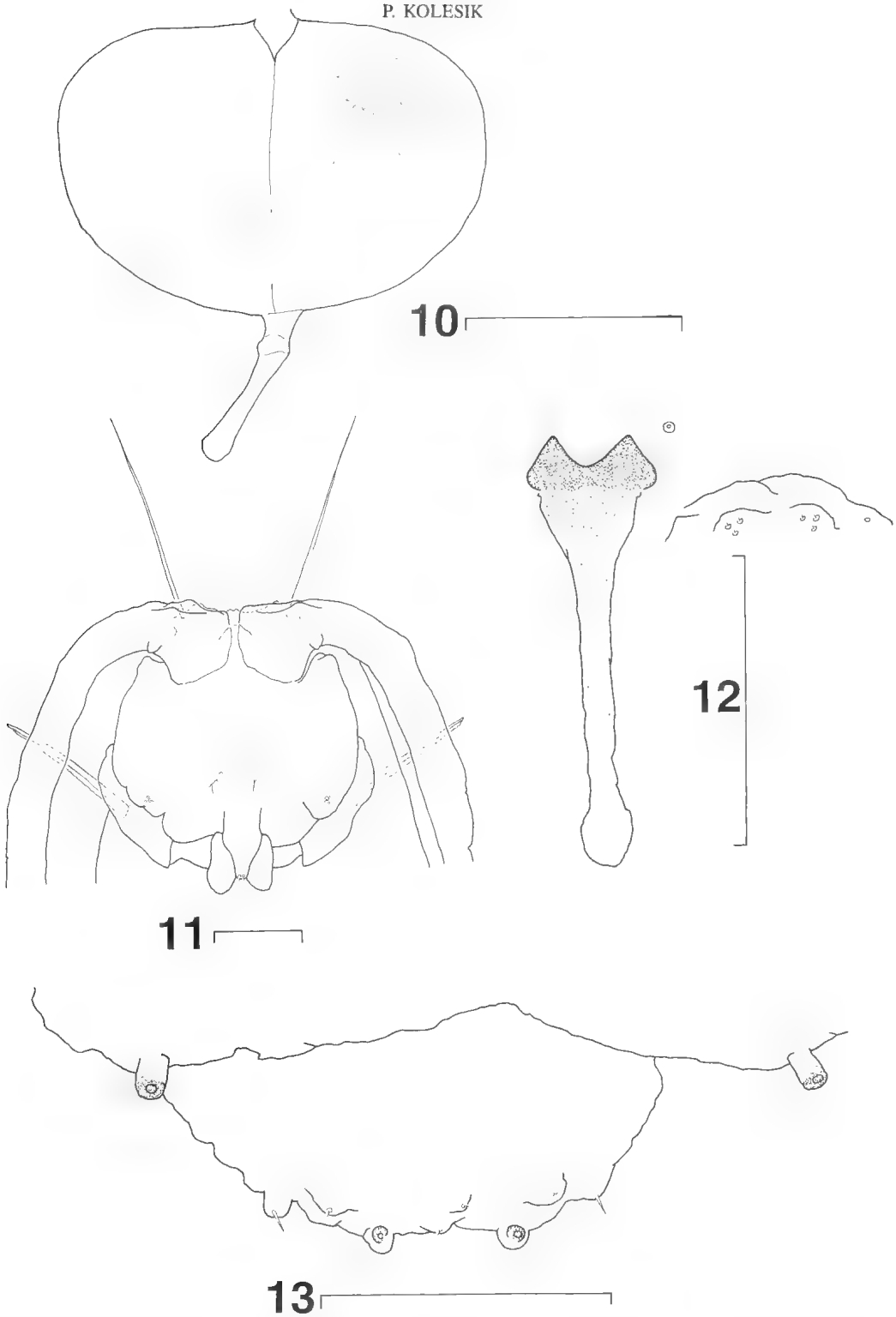
Mature larva (Figs 12-13)

Colour yellow. Total length 2.44 mm (2.20 – 2.75), diameter 0.18 mm (0.14 – 0.21). Integument smooth, ventrally with several transverse rows of spiculae on anterior half of each segment as well as with longitudinal rows around anus. All ventral, pleural, lateral and dorsal papillae with minute setae, sternal





Figs 7-9. Female of *Contarinia bursariae* sp. nov. 7. Last three flagellomeres. 8. End of ovipositor in dorsal view. 9. Abdomen in lateral view. Scale bars = 100 μm in 7 & 9; 10 μm in 8.



Figs 10-13. *Contarinia bursariae* sp. nov. 10. Larvae inside fruit capsule of *Bursaria spinosa* Cav. (left loculus with fruit, right one infested). 11. Anterior part of pupa in dorsal view. 12. Sternal spatula of larva. 13. Terminal segment of larva in dorsal view. Scale bars = 5 mm in 10; 100 μm in 11-13.

papillae asetose. Terminal segment with one pair of stublike, asetose papillae and three pairs of setose papillae, with one of the three pairs having longer setae than the other two. Head capsule width 51 μm (43-54), length 40 μm (37-45), length of posterolateral apodemes 42 μm (35-46). Sternal spatula 152 μm (139-175) in length, with apical enlargement 44 μm (41-47) in width and 20 μm (19-21) in length. Larva can jump short distances by arching its body and inserting its posterior end between the spatula enlargement and the integument and by subsequent quick releasing of the posterior end.

Pupa (Fig. 11)

Head with small, angular, slightly sclerotized antennal horns. Cephalic papillae with seta 223 - 250 μm long. Two pairs of lower facial papillae, one of each pair setose (11 - 23 μm) and one asetose. Two triplets of lateral facial papillae, one of each triplet setose (about 5 μm) and two asetose. Prothoracic spiracle with trachea ending at its apex, 133 to 168 μm long. Second to eighth abdominal segments with strongly sclerotized, simple dorsal spines, 5 - 15 in number and 4 - 25 μm in length.

Infestation symptoms (Fig. 10)

The infestation of *Bursaria spinosa* by *Contarinia bursariae* can easily be overlooked because there is no apparent malformation of the fruit capsules. However, in transmitted sunlight several larvae can be recognised inside the capsule. The larvae occupy one or both locules of the capsule, preventing the development of seeds. Up to eight larvae were observed within individual fruits. Despite the absence of seed in infested fruit no significant decrease in the total seed production per plant was observed due to the low infestation incidence in comparison to the enormous number of fruit per plant.

Etymology

Derived from the generic name of the host plant.

Remarks

The genus *Contarinia* is one of the largest genera of Cecidomyiidae represented in all zoogeographical regions. Larvae of all known species are phytophagous, most live gregariously in flowers, buds and fruits which are often malformed to galls. Others are found in malformed leaves and stems. Almost all known species are host-specific, sometimes with different species living on the same plant. The genus *Contarinia* in the context of this paper is defined as below. Larva: terminal segment with 6 setose papillae and 2 large, stublike, asetose papillae. Adults: maxillary palpus with 4 segments, antenna with 12 flagellomeres; wings with R_5 joining C beyond wing apex; tarsal claws simple on all legs. Male: flagellomeres binodal, with a single series of circumfilar loops on each node; genitalia with stout, unlobed gonocoxite, slightly tapered gonostylus, bilobed hypoproct and simple, short, distally tapering aedeagus. Female: ovipositor very long, retractable, the cerci tiny, dorso-ventrally flattened, and closely approximated mesally.

The genus *Contarinia* is known in Australia from 12 species, all of them from inflorescences and seed heads of Graminae and Cyperaceae (Harris 1979). The species described here differs morphologically from the previously-described Australian species in the number of setae on female cerci and the relative length of male circumfilar loops: female cerci bear eight setae in *C. bursariae*; those in all the other species bear more than 14: male circumfilar loops reach the mid-length of the next node in *C. bursariae*; those in the other species never extend beyond the base of the next node.

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A REVIEW OF THE SCALE INSECT SUBTRIBE ANDASPIDINA (HEMIPTERA: COCCOIDEA: DIASPIDIDAE) AND A NEW GENUS, NOTANDASPIS, FOR TWO AUSTRALIAN SPECIES

By D. J. Williams & H. M. Brookes†*

Summary

Williams, D. J. & Brookes, H. M. (1995) A review of the scale insect subtribe Andaspidina (Hemiptera: Coccoidea: Diaspididae) and a new genus, Notandaspis, for two Australian species. Trans. R. Soc. S. Aust. 119(4), 183-189, 30 November, 1995.

The subtribe Andaspidina is recognised as one of three subtribes of the scale insect tribe Lepidosaphini. A review of the literature is presented and diagnostic keys are given to subtribes and to genera of the subtribe Andaspidina. Notandaspis gen. nov. is described for Mytilaspis (Coccomytilus) hymenantherae Green, a species described originally from Victoria and presently included in Andaspis and for a new species Notandaspis oodnadattae sp. nov. from South Australia. The new species is unusually large for the subtribe.

Key Words: Coccoidea, Diaspididae, Andaspidina, Notandaspis gen. nov., Notandaspis hymenantherae (Green), Notandaspis oodnadattae sp. nov., scale insects, Australia.

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A REVIEW OF THE SCALE INSECT SUBTRIBE ANDASPIDINA (HEMIPTERA: COCCOIDEA: DIASPIDIDAE) AND A NEW GENUS, *NOTANDASPIS*, FOR TWO AUSTRALIAN SPECIES

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Summary

WILLIAMS, D. J. & BROOKES, H. M. (1995) A review of the scale insect subtribe Andaspidina (Hemiptera: Coccoidea: Diaspididae) and a new genus, *Notandaspis*, for two Australian species. *Trans. R. Soc. S. Aust.* **119**(4), 183-189, 30 November, 1995.

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KEY WORDS: Coccoidea, Diaspididae, Andaspidina, *Notandaspis* gen. nov., *Notandaspis hymenantherae* (Green), *Notandaspis eodnadattae* sp. nov., scale insects, Australia.

Introduction

Although nearly 250 species of Australian armoured scale insects (family Diaspididae) have so far been described, most of the endemic species cannot be recognised from the original descriptions without referring to authentic specimens in collections. A few species have been redescribed as part of revisions of genera but there is a pressing need for a complete revision of all the named species. Since a catalogue of world species was published by Borchsenius (1966) it would be fairly easy to extract most of the pertinent literature on Australian species. However, the work involved in also describing the new species already in collections, and those still to be discovered, estimated at many hundreds, could take many years. Numerous exotic species have also become established in Australia, some causing damage to cultivated crops and trees and these also need revision.

In the present work two species are described in the subtribe Andaspidina. Australian species at present assigned to this group are *Andaspis hymenantherae* (Green), *A. incisor* (Green), *A. numerata* Brimblecombe and *Metandaspis recurvata* (Froggatt). *A. hymenantherae* is assigned to a new genus in which a new species with an unusually large adult female is also included.

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Materials and Methods

The species are described from slide-mounted specimens of the adult female and the illustrations show the dorsal aspect on the left and the ventral aspect on the right. Morphological terminology is the same as that used in Williams & Watson (1988) where reference may also be made to a generalised illustration of the adult female. Further specimens have been prepared on microscope slides for this study using the techniques discussed by Williams & Watson (1988).

The term megaduct was adapted by Takagi (1992) from the term megapore proposed originally by Balachowsky (1954). These ducts, when present, numbering 2-7 on each side of the pygidial margin, are enlarged and are much larger than any others on the dorsum of the pygidium. The orifice of each megaduct is longitudinally elliptical and surrounded by a heavily sclerotised rim.

Abbreviations of the depositories are as follows:
ANIC, Australian National Insect Collection, CSIRO, Canberra, Australia.
BMNH, The Natural History Museum, London, U.K.

Historical Review of *Andaspis* and related genera

In the present work two tribes, Diaspidini and Lepidosaphini are recognised in the subfamily Diaspidinae. Based on the works of Borchsenius (1966) and Balachowsky (1968) the subtribes Andaspidina, Lepidosaphina and Coccomytilina are available in the tribe Lepidosaphini and are here accepted. Genera of the subtribe Andaspidina include *Andaspis* MacGillivray, *Caia* Williams, *Parandaspis* Mamet, *Metandaspis* Williams, *Saotomaspis* Balachowsky and the new genus *Notandaspis* gen. nov. here described.

The names Lepidosaphini and Lepidosaphina are used here without inflection formed from the nominal genus *Lepidosaphes* Shimer despite the various spellings Lepidosaphedini, Lepidosaphidini, Lepidosphedina and Lepidosaphidina.

The genus *Andaspis* was named by MacGillivray (1921) with *Mytilaspis flava* var *hawaiiensis* Maskell as type species. MacGillivray also included the Australian species *Lepidosaphes incisor* Green. Hall (1946) accepted the genus and included the African species *Lepidosaphes punicae* Laing. Rao & Ferris (1952) revised *Andaspis* and included 10 species, eight of which were from Asia. Brimblecombe (1960) described the new species *A. numerata* from Queensland. Takagi & Kawai (1966) described four new species of *Andaspis* from Japan and added further records of previously described species.

In a detailed study of adult males, Ghauri (1962) accepted the subtribe Lepidosaphidina to include *Lepidosaphes* Shimer and *Andaspis*. Lepidosaphidina was accorded equal rank to the Diaspidina of the tribe Diaspidini.

Williams (1963), in a review of *Andaspis*, accepted 22 species and provided a key. Also included in the review were the new genera *Caia*, with *C. quernea* Williams from Pakistan as type species, and *Metandaspis* with *Mytilaspis recurvata* Froggatt described from New South Wales as type species. He also included *Metandaspis javanensis* Williams from Java and stated that both new genera were related to *Andaspis*.

In a catalogue of so-called Diaspidoidea of the world, Borchsenius (1966) recognised the tribe Lepidosaphidini Shimer and the two subtribes Lepidosaphidina and Coccomytilina Borchsenius. He included *Andaspis* and *Caia* in the subtribe Lepidosaphidina and *Metandaspis* in the subtribe Coccomytilina and transferred the Australian species *Mytilaspis (Coccomytilus) hymenanthera* Green to *Andaspis*.

Mamet (1967) described the new genus *Parandaspis* with *P. vinsoni* Mamet from Mauritius as type species.

Borchsenius (1967) described the genera *Raoaspis* Borchsenius with *Andaspis mori* Ferris as type species, *Pararaoaspis* Borchsenius with *Lepidosaphes meliae* Green as type species and *Roonwalaspis* Borchsenius with type species *Roonwalaspis quercicola* Borchsenius. The new species *Raoaspis indica* Borchsenius, *R. raoi* Borchsenius and *Roonwalaspis quercicola* described in the same paper were purported to be Indian in origin but Danzig (1968) indicated that the localities on all the original labels were in China. Takagi (1970), discussing the Diaspididae of Taiwan, synonymised the names *Raoaspis*, *Pararaoaspis* and *Roonwalaspis* with *Andaspis* but suggested that the genera may be valid in some degree as species-groups. All three genera described by Borchsenius possess pygidial megaducts.

Balachowsky (1968), unaware of Mamet's *Parandaspis*, described the new genus *Parandaspis* with *P. castelbranchi* Balachowsky as type species. He also discussed the tribe Lepidosaphedini and erected a new subtribe Andaspidina to include *Andaspis*, *Caia*, *Metandaspis* and his new genus *Parandaspis*. He provided a key to the three subtribes Lepidosaphedina, Coccomytilina and Andaspidina and a key to the genera of the subtribe Andaspidina.

Balachowsky (1973), realising that the name *Parandaspis* Balachowsky was a junior homonym of *Parandaspis* Mamet, proposed the name *Saotomaspis* Balachowsky to replace *Parandaspis* Balachowsky with *S. castelbranchi* as type species.

Williams (1980) synonymised the name *A. dasi* Williams, described from India, with *A. numerata* Brimblecombe and commented on its distribution in Australia and the Pacific region and its association with the symbiotic fungus *Septobasidium* sp.

Williams & Watson (1988) discussed the Pacific species of *Andaspis* including two new species from Papua New Guinea.

Takagi (1992) commented on some unusual genera of the Lepidosaphedini as a tribe of the subfamily Diaspidinae and suggested that *Metandaspis javanensis*, based on a study of the first instar and adult female, was a 'somewhat odd form' but could belong to the tribe.

Danzig (1993) recently accepted only the tribe Lepidosaphini without subtribes.

Systematics

Superfamily Coccoidea Fallén, 1814.
Family Diaspididae Targioni Tozzetti, 1868.
Subfamily Diaspidinae Targioni Tozzetti, 1868.
Tribe Lepidosaphini Shimer, 1868.

Most genera of the family Diaspididae or armoured scales are included in the two subfamilies Aspidiotinae and Diaspidinae. The subfamily Aspidiotinae, based on characters of the adult female, contains genera with peetinae or plates and lobes that are never bilobed. In the subfamily Diaspidinae the plates are replaced by gland spines and the lobes anterior to the median lobes are often bilobed. The Diaspidinae are usually subdivided into the tribes Diaspidini and Lepidosaphini. Major characters of the Lepidosaphini, mostly defined by Takagi (1969) and never found in the Diaspidini, include megaducts, a pair of gland spines between the median lobes and abdominal segments II-IV with either lateral tubercles or spurs. One or more of these characters may be absent.

In the present work the subtribe Andaspidina is recognised and can be separated from the two other subtribes of the tribe Lepidosaphini by the following key adapted from Balachowsky (1968).

Some genera and species assigned to the tribe Lepidosaphini are difficult to place in any of the subtribes. *Mercetaspis calligoni* Borchsenius, for instance, lacks lobes and gland spines but possesses megaducts. The species is nevertheless related to other species of *Mercetaspis* Gómez-Menor possessing gland spines and well-developed or reduced lobes (Danzig 1993). *Phaulomytilus* Leonardi, an Australian genus, has small conical lobes, lacks gland spines but possesses megaducts. It was included in the subtribe Lepidosaphina by Borchsenius (1966). Another Australian genus, *Allantomytilus* Leonardi, has small triangular lobes but lacks megaducts. Borchsenius (1966) included this genus in the subtribe Coccomytilina. According to Takagi (1992), *Mitulaspis* MacGillivray, with more or less triangular lobes, is a primitive genus of the tribe Lepidosaphini, probably of the subtribe Coccomytilina. *Howardia* Berlese & Leonardi also belongs to the tribe Lepidosaphini but its position remains obscure. The genus possesses median lobes similar to those of *Andaspis*. Each median lobe of *Howardia* has a narrow, transverse paraphysis at each basal corner and, in addition, a large club-shaped sclerosis arising from the inner basal corner. Although Takagi (1992) tentatively included *Howardia* in the subtribe Coccomytilina, the name Howardiina Borchsenius is available for it but this subtribe was erected originally to include other genera also, presently in the tribe Diaspidini. In the following key to subtribes, only those genera possessing well-developed median lobes in the adult female are included, omitting the genus *Howardia* for the present. The correct assignment of many genera must await more detailed research possibly of first and second instar nymphs.

Key to subtribes of the tribe Lepidosaphini with well-developed median lobes (adult females)

1. Median lobes with parallel or subparallel sides, each lobe either without notches or with a single outer notch. Dorsal marginal megaducts on the pygidium present or absent 2

   Median lobes not with parallel sides, each lobe with inner margin straight, diverging slightly, curving round to a long oblique outer margin, the margin either smooth or serrated. Dorsal marginal megaducts on the pygidium either present or absent . . . . . Andaspidina Balachowsky

2. Dorsal marginal megaducts always present on the pygidium, numbering 2–7 on each side . . . . . Lepidosaphina Shiner

   Dorsal marginal megaducts always absent from pygidium . . . . . Coccomytilina Borchsenius

Genus *Notandaspis* gen. nov

Type species: *Mytilaspis (Coccomytilus) hymenanthae* Green

Diagnosis

Adult female on microscope slide elongate oval, segmentation of thorax and prepygidial segments distinct. Spiracles with quinquelocular pores. Antennae each usually with 3 long setae. Pygidium rounded with median lobes prominent, set close together, triangular or oval, inner edges short and diverging, outer edges long. Second, third and fourth lobes small, represented by sclerotised points. Megaducts absent. Macroducts of pygidium, including marginal ducts, all about same size. Gland spines short between median lobes; anteriorly about same length as median lobes. Venter with microducts and gland tubercles present as far forward as head.

Discussion

This genus is erected for the type species described from Victoria and a new species from South Australia. In lacking megaducts and possessing dorsal pygidial macroducts all about the same size, the new genus is related to *Saotomaspis*, an anomalous genus without gland spines in the adult female but with all the other characters of the subtribe Andaspidina.

Etymology

The name *Notandaspis* is based on the Greek word *notos*, meaning south, combined with the present generic name *Andaspis*.

The new genus *Notandaspis* can be separated from other genera of the subtribe by the following key.

Key to genera of the subtribe Andaspidina (adult females)

1. Pygidium always with 4–7 dorsal marginal megaducts on each side, these much larger than other dorsal ducts 2

   Pygidium always without dorsal marginal megaducts, any marginal ducts present always about same size as other dorsal ducts 4

2. Median lobes each with single notch on outer margin. Anal opening situated towards apex of pygidium . . . . . *Cuna* Williams

   Median lobes each with outer margin smooth or finely serrated. Anal opening situated towards base of pygidium 3

3. Gland tubercles present on ventral surface of head . . . . . *Parandaspis* Mamet

   Gland tubercles absent from ventral surface of head . . . . . *Andaspis* MacGillivray

4. Dorsal ducts of pygidium, including any marginal pygidial ducts, always in the form of microducts only . . . . . *Metandaspis* Williams

   Dorsal ducts of pygidium not in the form of microducts always in the form of macroducts and all about same size 5

5. Gland spines absent from pygidial margins . . . .
Saiomaspis Balachowsky
Gland spines present on pygidial margins
Notandaspis Williams & Brookes gen. nov.

Notandaspis hymenantherae (Green) comb. nov.
(FIG. 1)

Mytilaspis (Coccomytilus) hymenantherae Green 1905: 5. Lectotype ♀, Victoria, Myrniong, on stems and twigs of *Hymenanthera banksii* (BMNH) (here designated) [examined].
Lepidosaphes hymenantherae (Green), Sanders 1906: 17.
Coccomytilus hymenantherae (Green), MacGillivray 1921: 293.
Andaspis hymenantherae (Green), Borchsenius 1966: 71.

Adult female

Scale described originally as "reddish-brown, more or less covered by fibres of the bark upon which it rests".

Adult female on microscope slide elongate-oval, about 1.8 mm long and 1.1 mm wide, widest at about first abdominal segment; body membranous to lightly sclerotised, pygidium moderately sclerotised. Abdominal segments strongly lobed laterally. Lateral spurs absent. Anterior spiracles each with a group of 4-7 quinquelocular pores; posterior spiracles each with 2 or 3 quinquelocular pores. Antennae each with 3 setae all about same length.

Pygidium rounded. Median lobes prominent, set close together, almost triangular, each with rounded apex, outer edge finely serrated and longer than inner edge; a short, blunt paraphysis arising from inner and outer basal angles. Second, third and fourth lobes represented by short, sclerotised projections. Gland spines minute and barely perceptible between median lobes; a short pair present between each median and second lobe and groups of three gland spines about as long as median lobes present between each second and third lobe and each third and fourth lobe. Anal opening situated towards base of pygidium. Vulva present near middle of pygidium. Perivulvar pores absent. Dorsal ducts of pygidium all about same size, each about 20 μm long, arranged in loose marginal to submedian groups on each segment. Other dorsal ducts on abdomen about same size as pygidial ducts, present around margins and in submedial groups of 6-10 on segment V, submedial groups of 4-9 on segment IV and usually submedial groups of 1-3 ducts on segment III. Ducts around margins becoming progressively smaller to mesothorax.

Ventral surface with marginal gland spines as far forward as abdominal segment III. Gland tubercles present on thorax and first abdominal segment. Submarginal microducts present on prothorax mesothorax and lateral lobes of abdominal segments. Small ducts situated on margins of thorax and first abdominal segment.

Diagnosis

The presence of almost triangular median lobes on the pygidium is a good distinguishing character of this species. Each outer edge of a median lobe is, nevertheless, longer than the inner edge.

The lectotype designated is one of six specimens on a single slide labelled 'Mytilaspis hymenantherae Green, Type, from *Hymenanthera dentata*, Victoria, Australia, coll. J. Lidgett No. 63' and is clearly marked in red ink. It is further located on a diagram showing the positions of all six specimens on a separate label fixed to the back of the slide. The other five specimens are here designated paralectotypes (BMNH).

Notandaspis oodnadattae sp. nov.
(FIG. 2)

Material examined

Holotype, ♀, ANIC, South Australia, 70 km west of Oodnadatta, on stems of *Acacia aneura*, I.x.1976, F. D. Morgan.

Paratypes: same data as holotype, 8 ♀♀ (ANIC), 5 ♀♀ (BMNH).

Adult female

Scale dull white, 4 mm long, exuviae apical, pale white, cork layer of plant in some instances growing in strands over scale cover.

Adult female on microscope slide, elongate oval, largest available specimen 3.2 mm long, 1.2 mm wide, widest at metathorax, moderately sclerotised throughout, pale brown, pygidium light brown, segments well constricted behind head and prothorax and between thoracic and prepygidial segments. Anterior spiracles each with a group of 4-6 quinquelocular pores, posterior spiracles each with 1 or 2 quinquelocular pores, occasionally absent. Antennae each with 3 setae, one thicker and longer than others.

Pygidium rounded. Median lobes prominent, each almost oval, the short inner edge and long outer edge finely serrated. A pair of slender paraphyses present, each arising from inner and outer basal angles, directed antero-medially or almost transversely but not meeting. Second, third and fourth lobes represented by small sclerotised points. Gland spines short and minute between median lobes, a subequal pair present between each median and second lobe, a group of three, all about as long as median lobes, situated between each second and third lobe. Anal opening lying near middle of pygidium. Vulva situated anterior to position of anal opening, at about one third length of pygidium from base. Perivulvar pores absent. Dorsal ducts of pygidium

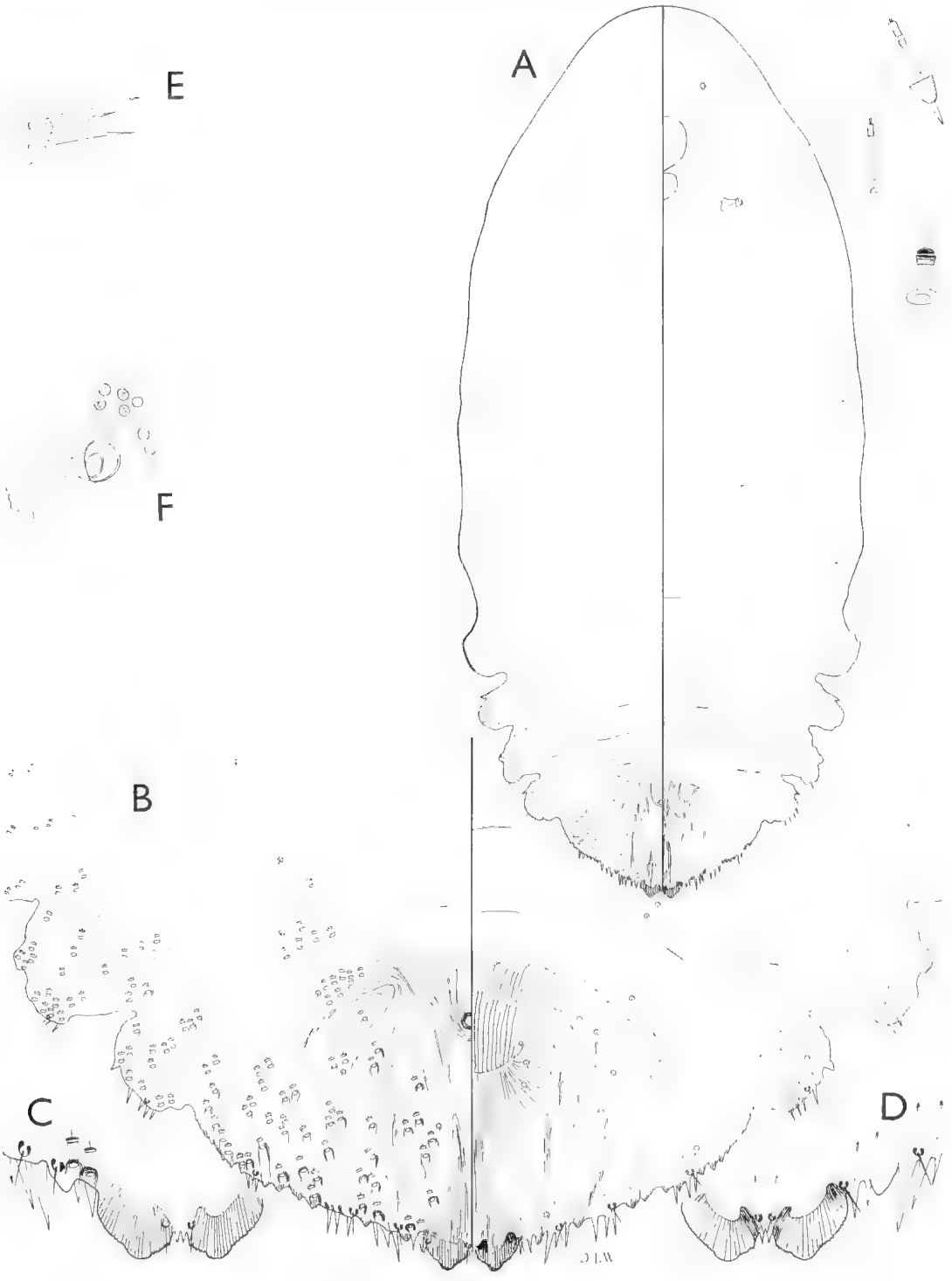

Fig. 1. *Notandaspis hymenantherae* (Green) comb. nov. A. Adult female, general aspect. B. Pygidium. C. Dorsal margin of pygidium. D. Ventral margin of pygidium. E. Antenna. F. Anterior spiracle.

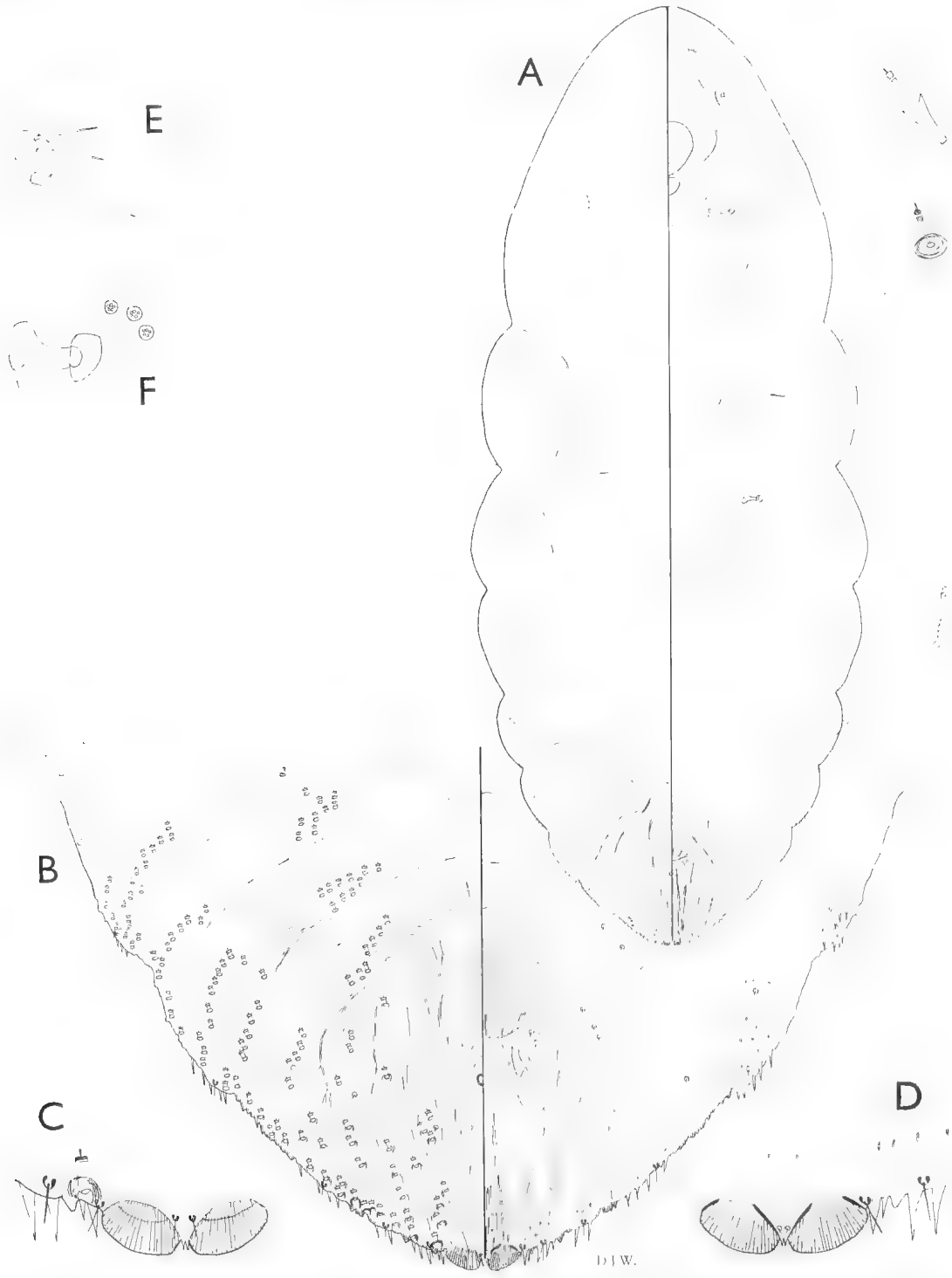

Fig. 2. *Notandaspis oodnadattae* sp. nov. A. Adult female, general aspect. B. Pygidium. C. Dorsal margin of pygidium. D. Ventral margin of pygidium. E. Antenna. F. Anterior spiracle.

all about same size, each approximately 20 μm long, numerous along margins and arranged in ill-defined rows to middle of pygidium except on segments III-V where they form distinct submarginal rows and submedian groups of 7-10. Ducts around margins becoming progressively smaller anteriorly as far forward as mesothorax.

Ventral surface with submarginal microducts of two types. An elongate type, each about 15 μm long, present in submarginal groups on abdominal segments IV and V. A shorter type, each about 10 μm long and with area surrounding opening sclerotised; present in marginal groups on head, thoracic segments and second abdominal segment, and others present in small groups near labium and medial area of head. Gland spines present in groups on prepygidial margins and minute, truncate gland tubercles present submarginally on prothorax and near inner edges of groups of microducts.

Diagnosis

This is a large species compared with others in the subtribe Andaspidina with the scale cover reaching 4 mm long and the adult female 3 mm long. The scale cover of most other species scarcely exceeds 2 mm long and the adult female is rarely more than 1 mm long. At first sight the scale of *N. oodnadattae* resembles an ovisac of many species of *Eriococcus* (Eriococcidae). Although each of the median lobes is almost oval there is a distinct, short inner edge and a long outer edge as in all species of the subtribe. The shape of the median lobes distinguishes the species from *N. hymenantherae* which possesses almost triangular median lobes. The positions of the anal opening and vulva are reversed in both species, the anal opening of *N. oodnadattae* lying posterior to the position of the vulva and in *N. hymenantherae* the anal opening lying anterior to the position of the vulva.

Etymology

The name is based on the place-name 'Oodnadatta'.

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DIET OF JUVENILE KING GEORGE WHITING SILLAGINODES PUNCTATA (PISCES: SILLAGINIDAE) IN THE BARKER INLET – PORT RIVER ESTUARY, SOUTH AUSTRALIA

*By Rod M. Connolly**

Summary

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Key Words: Sillaginodes punctata, fish diet, predation, crustacea, seagrass, Zostera.

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The diet of juvenile King George whiting, *Sillaginodes punctata* (Cuvier & Valenciennes), was determined by examining the stomach contents of fish collected over two years from shallow eelgrass and unvegetated habitats in the Barker Inlet - Port River estuary, South Australia. Estimates of weight of prey actually ingested by fish were made by combining abundances and sizes of prey found in stomachs with data on the size - weight relationship of potential prey items collected separately. Fish ate epifaunal invertebrates exclusively. A range of crustaceans formed the main prey, with smaller fish taking mostly harpacticoid copepods. Amphipods were more prominent in the diet of larger fish, which also fed upon polychaete worms. Fish fed mainly during the day. Fish collected at night typically had very little food in their stomachs, as measured by a fullness index (ratio of estimated ash-free dry weight of ingested prey to dry weight of fish). Relatively few fish were caught over unvegetated habitat, but where comparisons could be made, polychaetes rather than crustaceans predominated.

KEY WORDS: *Sillaginodes punctata*, fish diet, predation, crustacea, seagrass, *Zostera*

Introduction

Fish from shallow, soft-substratum habitats are typically carnivorous, preying mainly on small, motile invertebrates. Invertebrates associated with the seagrass canopy or sediment surface (epifauna) are more important than invertebrates from within sediment (infauna) (Klumpp *et al.* 1989). Despite the high levels of primary production sustained by shallow seagrass meadows (Hillman *et al.* 1989), few fish actually consume seagrass in temperate waters (Klumpp *et al.* 1989).

The diets of small fish from seagrass habitats in South Australia have not been reported. The diets of fish in Western Port, Victoria, an enclosed waterway with vegetation similar to that in the Barker Inlet - Port River region, have been studied by Robertson (1984) and Edgar *et al.* (1993)' who confirm the importance of epifaunal invertebrates, especially crustaceans. The diet of juvenile King George whiting (*Sillaginodes punctata*) in Western Port is described in Robertson (1977). Fish of this species fed on crustaceans (harpacticoid copepods, mysids and amphipods) after settling from a planktonic larval stage into eelgrass beds. Larger juveniles (>40 mm length) fed upon ghost prawn (*Callianassa*) larvae and polychaetes, primarily in unvegetated patches adjacent to eelgrass.

A wide variety of measures and indices involving gut analyses has been used in attempts to quantify the relative importance of food categories to fish (Berg 1979; Hyslop 1980). Frequency of occurrence, abundance, weight and volume have been used but any one of these may be misleading (Berg 1979). Indices combining in various ways the basic measures listed above have been devised (e.g. Pinkas *et al.* 1971) but no index is advantageous in all situations. Different food categories gain prominence depending on the weighting given to the different variables in the index. Berg (1979) recommends that where an index combining abundance, weight or volume, and perhaps frequency of occurrence, is used, values for the separate variables should also be shown. I consider that it may be as informative to forego the index, given that it is influenced by the weighting given to each variable, and simply present results based on, for example, abundances and weights.

Decisions about the importance of food categories to fish are best based not on the weight or volume of prey remaining in the gut but on the weight or volume of prey ingested. The ideal way of calculating weight or volume of food intake for prey such as motile invertebrates is to determine the weight - size (e.g. length) relationship for all prey categories using whole animals, and then to estimate the weight or volume of ingested prey based on the number and size of individual items found in fish. Edgar *et al.* (1993)' describe an approximate method for estimating weights in which prey items are allocated to a size-class known to represent the range of sizes retained on a particular

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EDGAR, G. J., HAMMOND, L. S. & WATSON, G. F. (1993) Consequences for commercial fisheries of loss of seagrass beds in southern Australia. Report to Fishing Industry Research & Development Committee (unpubl.)

sieve mesh size within a stack of hierarchically arranged sieves. The size of invertebrates is then used to estimate their weight (Edgar 1990).

In calculating the relative importance of food types by dividing the number or weight of a food type by the number or weight of all food in a particular fish, no distinction is made between a fish having in its stomach one harpacticoid copepod and one calanoid copepod and a fish having 50 harpacticoids and 50 calanoids. Many studies therefore include some estimate of gut fullness. The most common method has been to assign guts to one of several subjective categories of fullness (Berg 1979). A measure more repeatable by other workers is *l' indice de repletion* of Hureau (1969, described by Berg 1979) in which the weight of ingested food is presented as a proportion of the total weight of the fish.

The primary aim of the present study was to record the diet of juvenile *S. punctata* in the Barker Inlet - Port River estuary. This estuary has been declared an aquatic reserve in recognition of its importance in providing habitat for juvenile fish, especially *S. punctata* (Jones 1984), the most important species economically in both the commercial and recreational fisheries of South Australia. A secondary aim was to compare diets of fish from eelgrass (*Zostera muelleri*) and unvegetated habitats.

Materials and Methods

Juvenile *Sillaginodes punctata* were collected over two years during surveys comparing the fish fauna of eelgrass and unvegetated habitats in the Barker Inlet - Port River region (138° 30' E, 34° 45' S) (for descriptions of the estuary and the surveys, see Connolly 1994a). At each sampling period, the stomachs and oesophagi of all fish (or of 10 randomly selected fish where more than 10 fish were caught) from each site were removed, and the contents examined. The number of sites and total number of fish examined at each period are shown in Table 1.

The most satisfactory way of determining what fish eat is to examine items only from the anterior part of the tract. This is because food items from the oesophagus and stomach are more likely to be intact and are more easily recognised than items further along the gut, the bias caused by differential gut passage rates or digestion rates of different food items is likely to be reduced (Berg 1979) and items towards the anterior end of the tract give a more reliable guide to the diet of fish just prior to capture. This is an advantage for the secondary aim of this study, namely comparison of the diet of fish caught over eelgrass and unvegetated habitat. The tract of *S. punctata* less than about 25 mm long is a simple, uncoiled tube, narrowing posteriorly; contents of these smaller fish were examined from the section anterior to the narrowing.

TABLE 1. *Sillaginodes punctata examined for stomach contents: number of sites at which S. punctata were caught, number of fish examined, and median length of fish, separately for each habitat at each sampling period.*

All fish were collected during the daytime except those marked **Night**

Habitats: E = eelgrass, U = Unvegetated.

Sampling period	Habitat	Number of sites	Number of fish examined	Median length (mm)
January 1990	E	8	66	80
	U	2	11	109
April 1990	E	9	68	110
	U	1	4	150
August 1990	E	8	65	24
	U	2	2	25
October 1990	E	8	68	32
	U	4	17	35
February 1991	E	8	71	90
	U	4	15	103
June 1991	E	4	34	21
	U	4	7	23
June 1991 **Night**	E	7	54	21
	U	1	4	22
October 1991	E	8	67	25
	U	4	17	29
Oct. 1991 **Night**	E	3	28	26
	U	1	1	28

Individual items were mostly either intact or nearly so, and were identified to major taxa and counted. Animals were measured using a graticule in the microscope eye-piece and were assigned to a sieve mesh size-class so that weights of ingested prey could be estimated using the length - weight relationship described by Edgar (1990). The majority of prey items were crustaceans and where individuals were not whole, sizes were estimated by roughly piecing together parts of an animal (in the case of large crustaceans such as amphipods and mysids) or by using other individuals of the same taxon as a guide (for copepods). The only taxa recorded other than crustacea were polychaetes and chironomid larvae. Chironomid larvae were rare and were always whole. Although polychaetes were often whole, they were sometimes in pieces; estimating sizes of polychaetes chopped into pieces was the most problematic part of this method. In these cases the number of anterior ends was counted and lengths were estimated to try to take account of the general size of individuals.

Each prey item was assigned to a size-category relating to the range of lengths of that taxon retained on different mesh sizes. These size ranges were

determined by measuring the length of numerous specimens of each taxon from epifaunal samples taken at the time of fish collections. For each taxon, relative length - frequency histograms were plotted for each mesh size, and a range of lengths was chosen as representative of a mesh size by selecting upper and lower limits where histograms from adjacent mesh sizes crossed. Size ranges for each taxon are shown in Table 2. The mean ash-free dry weight (AFDW) of invertebrates can be related to sieve mesh size using Edgar's (1990) equation, $\log B = a + b \log S$ (where B = AFDW (mg), S = sieve size (mm) and a and b vary depending on broad taxonomic category). Since each sieve size retains animals ranging from that sieve size to the next, S is expressed as a geometric mean calculated using the equation, $\log S = (\log S_i + \log S_{i+1})/2$, in which S_i = mesh size of the ith sieve and S_{i+1} = mesh size of the next size up (Edgar 1990).

For each fish, the percentage abundance of each food category was calculated as n/N, where n is the number of individuals of the food category and N is the total number of individuals of all categories in that fish. The same calculation was made for each category based on estimated weight (AFDW). The average percentage abundance and weight of each food category were calculated for each site. The average percentage abundance and weight at each sampling period (with night collections in June and October 1991 treated as sampling periods) were then calculated separately for eelgrass and unvegetated sites.

The total estimated weight (AFDW, mg) of the stomach contents of a fish was recorded as a proportion of the estimated total weight of the fish (dry weight, g). This proportion gives the same information as Hureau's (1969, described by Berg 1979) *indice de repletion*, although Hureau's index used the same units in numerator and denominator and is reported as a percentage. By using mg as the unit for the numerator, the ratio (fullness index) used here minimises the occurrence of numbers less than one. The weight of the whole fish, including stomach contents, was estimated using the relationship between dry weight and fish length. Fifty *S. punctata* collected from different periods and ranging from 18 to 133 mm total length were weighed after being dried to constant weight (at least 48 h) at 60°C. The dry weight of a fish is best estimated by its length using the relationship $\log W = 3.261 \log L - 6.396$, where W is dry weight (g) and L is total length (mm) ($r^2 = 0.997$).

Fullness indices of fish from eelgrass and unvegetated sites were compared using Mann-Whitney U-tests at periods when fish were collected from enough unvegetated sites to make useful comparisons. Indices were also compared for fish from eelgrass sites between day and night samplings at June and October 1991. The Mann-Whitney U-test is less powerful than a t-test if data meet the assumptions of normality and homoscedasticity but, in cases such as these where sample sizes are very small and tests of normality are impossible, it is a more reliable method of testing differences in central tendencies (here, medians).

TABLE 2. *Size ranges (mm) of prey types matching mesh sizes.*
Blank cells indicate that prey type was not found on that mesh.

Prey type	Mesh size (mm) 4	2	1	0.5	0.25	0.125	0.075
Harp				>0.8	>0.68-0.8	0.55-0.68	<0.55
Por				>0.6	<0.6		
Cycl					>0.65	0.55-0.65	<0.55
Cola				>1	0.71	<0.7	
Ostr			>1.6	>0.8-1.6	0.5-0.8	<0.5	
Amph	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		
Capr		>7	3.8-7	<3.8			
Mysi		>5	3-5	<3			
Tana		>5	>2.6-5	1.2-2.6	<1.2		
Chma		>6.5	4-6.5	<4			
Carr	>9.5	6-9.5	<6				
Poly	>11	>5-11	>2.9-5	>1.3-2.9	0.6-1.3	<0.6	
Chir		>4.8	>2.6-4.8	1.2-2.6	<1.2		

Results

The diet of juvenile *Sillaginodes punctata* consisted entirely of invertebrates. Thirteen categories were recorded, as shown in Table 3. Prey were either crustaceans or polychaetes, except for a small number of chironomid larvae taken in October 1990. Porcellid harpacticoids and caprellid amphipods were counted separately from their general taxa (harpacticoids and amphipods, respectively) because of their different form. Porcellid harpacticoids have a wide, flattened, shield-like shape and caprellids are extremely long and thin compared to gammarid amphipods. The prominence of small items such as copepods, especially harpacticoids, was greater when based on abundance than when based on weight. The prominence of larger items such as amphipods and polychaetes was, conversely, more obvious when based on weights. Notwithstanding these different emphases, the change

TABLE 3. *Stomach contents of* Sillaginodes punctata *based on abundances.*
Habitats: E = eelgrass, U = Unvegetated. Numbers are mean percentage of food category from all sites, with standard errors (SE) in parentheses. * = no SE because fish were caught at only one unvegetated site. ** = no SE because only polychaetes were recorded from fish at unvegetated sites. Food category abbreviations are as follows: Harp = Copepoda - Harpacticoida; Porc = Copepoda - Harpacticoida - Porcellidiidae; Cycl = Copepoda - Cyclopoida; Cala = Copepoda - Calanoida; Ostr = Ostracoda; Amph = Amphipoda Gammaroidea; Capr = Amphipoda - Caprellidae; Mysi = Mysidacea; Tana = Tanaidacea; Cuma = Cumacea; Cari = Caridea; Poly = Polychaeta; Chir = Chironomidae, larvae

Sampling period	Habitat	Harp	Porc	Cycl	Cala	Ostr	Amph	Capr	Mysi	Tana	Cuma	Cari	Poly	Chir
January 1990	E	7 (4.5)					24 (10)		2.5 (2.5)	7 (4)			60 (11.5)	
	U						13 (13)		3 (3)				83 (17.5)	
April 1990	E						31 (12.5)		14 (7.5)				55 (14.5)	
	U												100 (**)	
August 1990	E	87 (3)	1 (0.6)	3 (1)	0.5 (0.5)	0.4 (0.4)	7 (2.7)			1.1 (1.1)			0.7 (0.7)	
	U	83 (3)					17 (3)							
October 1990	E	69 (8)		0.1 (0.1)	5.1 (2.2)		21 (6)	1.5 (1.2)	1.2 (1.9)					2.3 (2.3)
	U	73 (12)		3.8 (3.8)	1.3 (0.9)		2 (1.5)						20 (11)	
February 1991	E						14 (11)		9.5 (4.5)	6.3 (5.6)		2.5 (2.5)	68 (11)	
	U									1.3 (1.3)			99 (1.3)	
June 1991	E	92 (3)		1.1 (1.1)	3 (3)		3.5 (1.5)							
	U	78 (11)		1.4 (1.4)	2.5 (2.5)	0.5 (0.5)	2.7 1.7						15 (9)	
June 1991 Night	E	82 (14)			7 (7)		11 (7)							
	U	100 (*)												
October 1991	E	74 (5)		2.1 (2.1)	1.2 (0.8)		20 (6)	2 (1)	0.1 (0.1)		1 (0.5)			
	U	72 (14)			4 (4)		12 (4)		1 (1)				11 (11)	
October 1991 Night	E	59 (29.5)			31.5 (27)		8 (4)						1.6 (1.6)	
	U	87 (*)											13 (*)	

in diet of *S. punctata* as fish grew larger is shown clearly in Tables 3 and 4. The median length of fish at each period is reported in Table 1.

At sampling periods in the second half of the year (August, October 1990; June, October 1991), when fish were small, harpacticoid copepods were the most conspicuous prey by abundance, and amphipods along with harpacticoids were dominant by weight. The abundance and weight of amphipods were noticeably lower in June 1991 than at later periods and this may be attributable to the smaller size of fish at this period. Cyclopoid and calanoid copepods, which are typically more planktonic than harpacticoids, were taken consistently at these periods but were small contributors to diet by abundance or weight. Ostracods, caprellid amphipods, mysids, tanaids and polychaetes occurred occasionally but were not important by abundance or weight. Cumaceans were recorded in

TABLE 4. *Stomach contents of* Sillaginodes punctata *based on weight.*
All labels and symbols as for Table 3.

Sampling period	Habitat	Harp	Porc	Cycl	Cala	Ostr	Amph	Capr	Mysi	Tana	Cuma	Cari	Poly	Chir
January 1990	E	6 (4)					11 (5)		2.5 (2.5)	11 (7)			69 (10)	
	U						4 (4)		10 (10)				87 (13)	
April 1990	E						22 (11)		14 (8)				64 (13)	
	U												100 (**)	
August 1990	E	59 (7)	3 (2)	6 (2.7)	0.7 (0.7)	0.9 (0.9)	25 (8.6)			4.6 (4.6)			0.1 (0.1)	
	U	58 (20)					42 (20)							
October 1990	E	38 (8)		0.1 (0.1)	10 (4)		37 (9)	7 (4.5)	4.5 (2.9)					3.1 (3.1)
	U	54 (8)		3.1 (3.1)	3.9 (2.5)		11 (6.2)						29 (11)	
February 1991	E						10 (8.5)		8.2 (4)	2.8 (2.7)		2.5 (2.5)	76 (8)	
	U									0.3 (0.3)			100 (0.3)	
June 1991	E	85 (6)		1.1 (1.1)	5.5 (5.5)		8 (3)							
	U	68 (16)		1.4 (1.4)	5.5 (5.5)	2.8 (2.8)	(6) (5)						(17) (10)	
June 1991 Night	E	76 (16)			7 (7)		17 (11)							
	U	100 (*)												
October 1991	E	50 (7)		4 (4)	3 (2)		33 (11)	7 (4.5)	1.5 (1.5)		2.2 (2)			
	U	66 (13)			5.5 (5.5)		11 (4)		3 (3)				15 (15)	
October 1991 Night	E	37 (20)			25 (14)		27 (15)						10 (10)	
	U	48 (*)											52 (*)	

small numbers in October 1991.

At sampling periods in the first half of the year (January, April 1990; February 1991), when larger fish were examined, polychaetes were the main food category by abundance and weight. There was an obvious difference in the size of polychaetes taken by fish in periods in the second half of the year compared with the first half of the year. Polychaetes taken in June 1991 were small, ranging from less than 1 mm to 3 mm long (although the larger of these are large relative to other prey). Polychaetes taken in October 1990 and 1991 were 2 - 10 mm, Polychaetes in fish from periods in the first half of the year ranged from 7 - 50 mm in length. Amphipods were the second most important category by abundance, although by weight amphipods were no more prominent than the other two frequently-recorded categories, mysids and tanaids. Harpacticoids were found in a small number of fish in January 1990. Fish in which harpacticoids were found had no other categories of prey present, so that although the harpacticoids were not numerous and were small, they comprised 100% of the food in those fish based, on

abundance or weight. Caridean shrimps were recorded infrequently in February 1991.

The percentage of fish having empty stomachs is shown in Table 5. Very few of the fish caught during the day had empty stomachs at any sampling period and no difference is evident between sites from eelgrass and unvegetated habitat. The weight of stomach contents, as a proportion of total fish weight, varied markedly from site to site but did not seem to vary consistently with season (Table 5). In periods when fish were caught at enough unvegetated sites to make a reasonable comparison possible, the weight of stomach contents did not differ between eelgrass and unvegetated habitats (Mann-Whitney U-test results: October 1990, $p = 0.234$; February 1991, $p = 0.734$; June 1991, $p = 0.773$; October 1991, $p = 0.174$). Results of tests were identical for all periods whether or not fish with empty stomachs were included.

TABLE 5. *Numbers of fish with no food in stomach, and fullness indices, separately for each habitat at each sampling period.*
Habitats: E = eelgrass, U = Unvegetated. The number of fish with empty stomachs is shown firstly by number (n) and secondly as a percentage (%), but percentages should be interpreted cautiously for unvegetated habitat where total fish numbers are very small. Fullness index is weight of stomach contents (mg AFDW) as a proportion of weight of whole fish (g dry weight). Fullness indices are shown as means of site means, with standard errors in parentheses (n/a = fish caught at one site only, therefore no SE available). (a) = excluding fish with empty stomachs (b) = including fish with empty stomachs (and fullness index of zero).

Sampling period	Habitat	Empty (n)	Empty (%)	Fullness index (a)	Fullness index (b)
January 1990	E	3	5	4.18 (0.51)	4.01 (0.50)
	U	0	0	4.80 (1.84)	4.80 (1.84)
April 1990	E	0	0	2.94 (0.49)	
	U	0	0	2.04 (n/a)	
August 1990	E	0	0	4.07 (0.81)	
	U	0	0	2.55 (0.26)	
October 1990	E	2	3	4.29 (0.71)	4.20 (0.69)
	U	0	0	2.60 (1.36)	2.60 (1.36)
February 1991	E	7	10	4.23 (1.23)	4.06 (1.26)
	U	0	0	3.60 (0.63)	3.60 (0.63)
June 1991	E	0	0	2.52 (0.73)	2.52 (0.73)
	U	1	14	3.33 (0.89)	3.11 (1.04)
June 1991	E	33	61	1.14 (0.33)	0.52 (0.14)
Night	U	2	50	0.96 (n/a)	0.48 (n/a)
October 1991	E	3	5	4.04 (0.84)	4.72 (0.79)
	U	0	0	3.35 (0.76)	3.35 (0.76)
October 1991	E	18	64	2.99 (0.91)	1.00 (0.21)
Night	U	0	0	0.98 (n/a)	0.98 (n/a)

More than half the fish caught at night in June and October 1991 had empty stomachs. In fish caught at night with food in their stomachs, the types of food were similar to those in fish caught during the day. For a given period, the quantity of food in fish caught at night was significantly less than in fish caught during the day when fish with empty stomachs were included (Mann-Whitney U-test results: June 1991, $p = 0.047$; October 1991, $p = 0.014$), but was not significantly different when fish with empty stomachs were excluded (June 1991, $p = 0.186$; October 1991, $p = 0.221$).

Comparisons of the diet of fish caught over eelgrass and unvegetated habitat are limited by the small number of *S. punctata* caught over unvegetated habitat and the small number of unvegetated sites at which fish were caught. Over all periods, polychaetes seemed to predominate in fish from unvegetated habitat. In October 1990 and 1991, when fish were caught at 4 unvegetated sites, increasing the chance that the data are representative of the habitat more generally, only fish from unvegetated sites had taken polychaetes. Fish from eelgrass sites tended to contain a greater range of crustaceans. Caprellid amphipods, for example, were recorded only from fish caught over eelgrass at both periods.

Discussion

The diet of *Sillaginodes punctata* fits within the typical diet for fish from shallow, soft-substratum habitats. Stomach contents at the periods sampled give no indication of feeding on anything other than motile invertebrates. Juvenile *S. punctata* caught at periods in the first half of the year were large enough to be able to take small individuals of other fish species but there was no evidence of this. Although gastropods are eaten by some fish species, none was found in the present study. The prominence of harpacticoids and amphipods in the diet of smaller juveniles and an increased prominence of polychaetes in older juveniles matches the pattern in *S. punctata* from Western Port, Victoria (Robertson 1977).

Bruce (1995) has suggested that the shift in diet towards larger crustaceans and polychaetes with increasing fish size may be related to the timing of gut coiling. Bruce's study of larval and postlarval *S. punctata* from South Australian waters shows that coiling of the gut tube and migration of the anus begin in fish 21 - 24 mm long, and are complete in fish of 26 mm. Most fish caught in October 1990 and 1991 during the present study were >26 mm long and did have coiled guts. These fish had a predominance of small crustaceans such as harpacticoids, however, indicating that the shift towards larger crustaceans and polychaetes does not happen until after gut coiling.

Results suggest that *S. punctata* feed on a narrower range of prey and include more polychaetes in their diet when over unvegetated habitat. Lubbers *et al.* (1990) have also reported that for juveniles of several species of fish from an estuary in Chesapeake Bay, USA, diets of fish collected from unvegetated areas included a much greater proportion of polychaetes than diets of fish collected from vegetated areas. Evidence from the present study is, however, obtained from only a small number of fish from very few sites. The small number of fish examined from unvegetated sites could account for the failure to find food types such as caridean shrimps recorded infrequently in fish from eelgrass sites.

Evidence from the two night sampling periods suggests that juvenile *S. punctata* feed mainly during the day. The stomachs of fish collected at night were often either empty or contained only a small quantity of food. Either fish feed in a limited way at night or food in the stomach of fish collected at night remained from feeding during daylight hours. The time between sundown and collection of fish at night ranged from four to seven hours. The rate at which food is evacuated by juvenile, carnivorous, marine fish of a similar size to the fish studied here has been shown to range variously from 2.7 to 4.8 h (Rosenthal & Paffenhofer 1972), 6 h (Archambault & Feller 1991) and from 10 to 30 h (Ryer & Boehlert 1983). These laboratory estimates of gut evacuation times, however, tend to be overestimates (Lockwood 1980). Food is presumably clear of the stomach before it is fully evacuated from the gut, so stomach emptying times could be shorter than those mentioned above. On the other hand, gut passage rates are much slower in colder water (Durbin *et al.* 1983; Ryer & Boehlert 1983) and, in the evening water temperatures of June and October 1991 of about 14°C, food may have remained in guts much longer. It is therefore impossible to distinguish between the possibilities of limited nocturnal feeding and food remaining in stomachs from daytime feeding.

The ratio of ingested food to total fish weight did not seem to vary consistently with the size of fish taken at different periods. This contrasts with the study of silver hake (*Merluccius bilinearis*) and Atlantic cod (*Gadus morhua*) by Durbin *et al.* (1983), using the same measure, in which it was found that the ratio was greater in larger fish. Durbin *et al.* (1983), however, used a much larger size range, including juvenile and adult fish. Differences in the ratio for *S. punctata* might occur in larger fish.

Any differences in gut passage rates or rates of digestion for different food types could have affected the apparent relative importance of food types. These biases were not determined during the present study but should have been limited by examining food only from the oesophagus and stomach of fish. Differential digestion rates tend to underestimate the importance of soft-bodied invertebrates (Scholz *et al.* 1991) and, for juvenile *S. punctata*, this means that polychaetes are the taxon most likely to be underestimated.

This study confirms that juvenile *S. punctata* within the Barker Inlet - Port River estuary feed on epifaunal invertebrates. Experiments in the same estuary have shown that removal of eelgrass canopy reduces epifaunal invertebrate productivity (Connolly 1995). Abundances of juvenile *S. punctata* are not reduced directly by removal of eelgrass canopy but are correlated with levels of invertebrate productivity (Connolly 1994b). The ongoing threat to the health of eelgrass in the estuary from human activities such as treated sewage and stormwater discharge should therefore be viewed as a potentially detrimental influence on *S. punctata* populations.

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