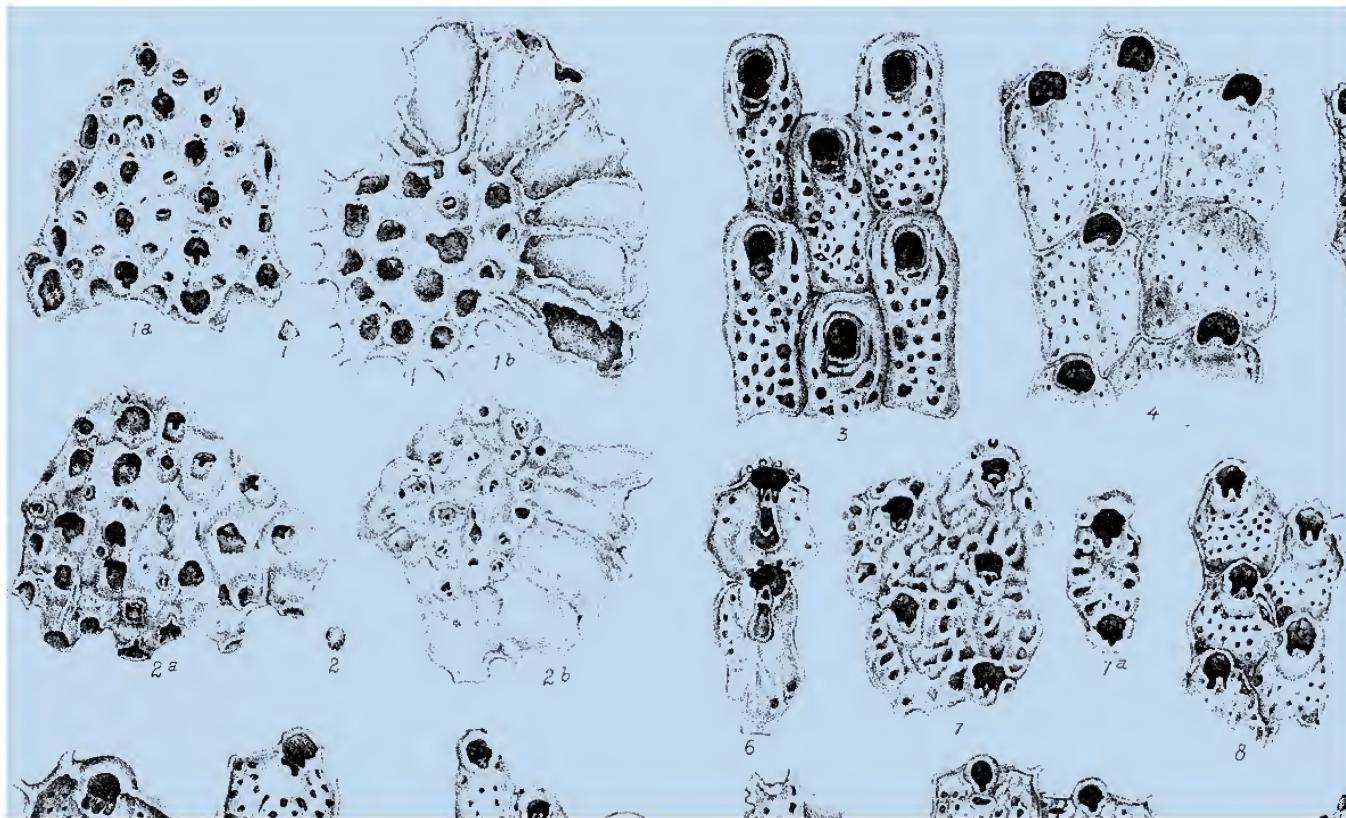
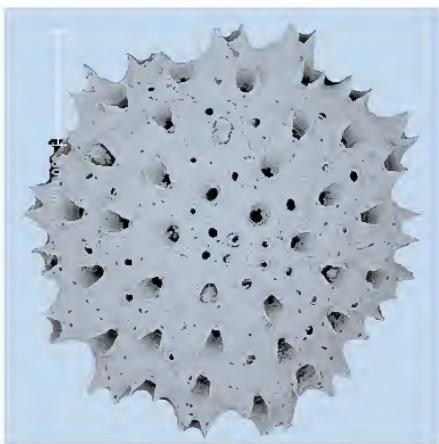


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Front cover Top left: Scanning electron micrographs of two species of bryozoans of the genus *Conescharella* from southern Australia described as new by Philip Bock and Patricia Cook in this volume.

Bottom: part of the original plate published by P. H. MacGillivray in 1895 in *Transactions of the Royal Society of Victoria* in which the same two species are illustrated.

A molecular and morphological revision of genera of Asterinidae (Echinodermata: Asteroidea)

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Abstract

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A molecular phylogeny has inspired a reappraisal of the systematics of the Asterinidae. New morphological characters are defined and illustrated and used to diagnose all genera. A table of the distribution of morphological characters among genera and key for genera of Asterinidae are provided. New genera of Asterinidae are erected: *Aquilonastraea* O'Loughlin, *Indianastra* O'Loughlin, *Parvulastra* O'Loughlin and *Pseudopatiria* O'Loughlin. *Patiria* is raised out of synonymy with *Asterina*. *Allopatria* is a junior synonym of *Asterina*, *Manasterina* is a junior synonym of *Disasterina*, and *Paxillasterina* is a junior synonym of *Asterinides*. The genus *Asterinopsis* and the genus and species *Desmopatiria flexilis* are nomina nuda. *Patiriella tangribensis* is a nomen dubium. Genera reviewed are: *Anseropoda*, *Asterina*, *Asterinides*, *Callopatria*, *Cryptasterina*, *Disasterina*, *Kampylaster*, *Meridiastra*, *Nepanthia*, *Paranepanthia*, *Patiria*, *Patiriella*, *Pseudasterina*, *Pseudonepanthia*, *Stegnaster*, *Tegulaster* and *Tremaster*. *Asterina cephea* var. *iranica* is raised to species status. *Enoplapatiria siderea* is a junior synonym of *Asterina stellifera*. *Disasterina leptalacantha* var. *africana* is no longer recognised as a subspecies. *Disasterina spinulifera* is a junior synonym of *Disasterina praesignis*. A synonymy of *Tremaster novacaledoniae* with *Tremaster mirabilis* is formalised. Asterinid species reassigned on the basis of molecular evidence and morphological congruity are new combinations: *Aquilonastraea anomala*, *A. batheri*, *A. burtoni*, *A. coronata*, *A. minor*, *A. scobinata*, *Meridiastra calcar*, *M. gunni*, *M. mediuss*, *M. mortensenii*, *M. occidens*, *M. oriens*, *Paranepanthia aucklandensis*, *Parvulastra calcarata*, *P. exigua*, *P. parvivipara*, *P. vivipara*, *Patiria chilensis*, *P. miniata*, *P. pectinifera*. Species reassigned on the basis of morphological evidence are new combinations: *Aquilonastraea cepheus*, *A. corallicola*, *A. heteractis*, *A. iranica*, *A. limboonkengi*, *A. rosea*, *Asterinides hartmeyeri*, *A. pilosa*, *A. pompom*, *Disasterina ceylanica*, *D. longispina*, *Indianastra inopinata*, *I. sarasini*, *Nepanthia pedicularis*, *Parvulastra dyscrita*, *Pseudonepanthia briareus*, *P. gracilis*, *P. grangei*, *P. nigrobrunnea*, *P. reinga*, *P.roughtoni*, *Pseudopatiria obtusa*, *Tegulaster alba*, *T. leptalacantha*, *T. praesignis*. Three species remain incertae sedis: *Asterina lorioli*, *Asterina novaezelandiae* and *Nepanthia brachiata*. A table of asterinid species is provided, with original and current combinations. It is concluded that Asterinidae is a cosmopolitan family, mainly of shallow-water narrow-range genera but including some more widespread in deeper waters of all oceans.

Keywords

Echinodermata, Asteroidea, Asterinidae, new genera, taxonomy, molecular, morphology

Introduction

Traditional systematic studies of asteroids have been confounded, to an extent, by morphological characters that are of dubious phylogenetic value and limited by observable size and historical choice (Clark and Downey, 1992). Some morphological characters currently used in asteroid systematics, for instance, may be subject to strong selection and thus remain stable while evolutionary divergence occurs in other characters (e.g. molecular divergence in living fossils; Avise et al., 1994). Hence taxa that are superficially similar, and perhaps congeneric on traditional morphological criteria, may prove to be

unrelated (O'Loughlin et al., 2002; Waters et al., 2004). Some other morphological characters may be plastic and readily diverge among taxa that are closely related (e.g. O'Loughlin et al., 2003). Current taxonomic treatments of asteroids may also be hindered by the possibility that certain morphological characters are phylogenetically informative for some clades but homoplasious and unreliable for others (Mah, 2000). The abundant phylogenetic information provided by DNA sequence data (Avise, 2000) presents a means of reassessing taxonomic relationships and stimulates reappraisal of morphological, behavioural, physiological and ecological traits.

The Asterinidae comprise 21 genera and about 116 species according to the comprehensive index of taxa by A.M. Clark (1993) and the subsequent work of Rowe (in Rowe and Gates, 1995), Campbell and Rowe (1997), O'Hara (1998), VandenSpiegel et al. (1998), A.M. Clark and Mah (2001), H.E.S. Clark and McKnight (2001), O'Loughlin (2002), O'Loughlin et al. (2002, 2003) and Dartnall et al. (2003). The need for a systematic revision was first commented on by Verrill (1913). Recently, Rowe (in Rowe and Gates, 1995), Campbell and Rowe (1997), O'Loughlin (2002) and O'Loughlin et al. (2002) noted continuing conflicting opinions on the systematic status of, and assignment of species to, the genera *Asterina* Nardo, 1834, *Asterinides* Verrill, 1913 and *Patiriella* Verrill, 1913.

O'Loughlin (2002) provided a restricted morphological review of Asterinidae and erected a new genus (*Meridiastra*) with three new species (*M. fissura*, *M. nigranota*, *M. rapa*). Hart et al. (1997) reported the first molecular phylogeny for 12 asterinid species assigned to the genera *Asterina* and *Patiriella*. The phylogeny indicated that neither *Asterina* nor *Patiriella* is monophyletic. O'Loughlin et al. (2002, 2003) reported two molecular phylogenies and the erection of four new Australasian asterinid species (*Patiriella medius*, *P. mortensenii*, *P. occidens*, *P. oriens*), provisionally assigned to *Patiriella* in the absence of molecular data from other genera. Hart et al. (2003) reported a molecular phylogeny on which Dartnall et al. (2003) erected an additional genus (*Cryptasterina*) and species (*C. hystera* Dartnall and Byrne, 2003). Waters et al. (2004) reported a molecular phylogeny (adapted in Fig. 1) for 31 asterinid species, predominantly Australasian. Their phylogeny showed strong resolution at shallow levels, with six well-supported clades. With additional species included, the polyphyletic assemblages of *Asterina* and *Patiriella* illustrated by Hart et al. (1997) were further elucidated. Some genera, defined on the basis of morphology, have molecular support. Other well-defined clades may deserve generic rank but need morphological support. Some genera as presently conceived appear polyphyletic. They invite reappraisal to explore whether morphology will support division into smaller unrelated genera.

This paper seeks congruence between morphological and molecular data: we evaluate the phylogenetic reliability of characters traditionally used to differentiate asterinid genera and explore the utility of new characters. Ideally, genera are monophyletic groups of species diagnosed by shared character states — morphological, behavioural and molecular — that reflect common descent (De Queiroz and Gauthier, 1992). Here we apply phylogenetically informative morphological characters to define genera anew and recognise new genera. The morphological analysis is extended to many asterinid genera and species for which there are currently no molecular data. Future molecular analyses will help to evaluate the decisions made here on the basis of morphology alone.

In the cladogram of Waters et al. (2004) basal relationships were unclear. It did not demonstrate the monophyly of the family as presently construed. *Demasterias* (Asteropseidae) was placed within the asterinid clade. It should be noted that this relationship received minimal phylogenetic support. The unresolved affinities of *Demasterias* have little bearing on the

objectives of this paper, which are to redefine genera currently assigned to the Asterinidae. On morphological evidence, the genus *Tremaster* Verrill, 1880 appears to be inappropriately included in Asterinidae. But a reassessment of what genera belong in Asterinidae, such as the inclusion or not of *Cycethra* Bell, 1881 (currently in Ganeriidae), and retention or not of *Tremaster*, should await appropriate molecular phylogeny data.

In this revision all of the species of all of the genera were reviewed, except for *Anseropoda* where a sample of species only was examined. Material for three asterinid species, for which the morphological descriptions raise doubts about their generic assignment, could not be found. They are placed incertae sedis.

Terminology follows that defined in the glossary and illustrated by Clark and Downey (1992, figs 2, 3), except that “papular space” (“restricted area with papular pores”, fig. 15f) is used for “papular area”, and “papulate areas” is used to refer to the parts of the abactinal surface where papulae occur (as defined by O'Loughlin, 2002). The form of spines and spinelets is of ten broad types (form frequently revealed by clearing with bleach): long and thin, needle-like, “acicular” (fig. 5c); round base and apical point, cone-shaped, “conical” (fig. 10g); long, thick, finger-like, “digitiform” (fig. 5e); short and thick, “granuliform” (fig. 5a), which may be subspherical, “globose” (fig. 5b), or “short columnar” (figs 15d, 16h); thin, few prominent points laterally and distally, “splay-pointed” (figs 5d, 6c, 9d); distal pointed glassy tip, “thorn-tipped” (fig. 17d); sac-like base and tapering distally to narrowly rounded end or point, “sacciform” (figs 5f, 8b, 8g, 9c); combination of “sacciform” and “splay-pointed” (fig. 5d). The armature of abactinal plates is consistently referred to as “spinelets”, irrespective of size. The armature of actinal plates is consistently referred to as “spines”, irrespective of size. Specimen size refers to preserved material, and is categorized as “small” (up to R = 25 mm), “medium” (R = 26–65 mm), and “large” (R greater than 66 mm). All measurements refer to preserved material.

Abbreviations for institutions are: AM, Australian Museum, Sydney; BMNH The Natural History Museum, London; MNHN, Muséum National d'Histoire Naturelle, Paris; MNZ, Museum of New Zealand, Te Papa Tongarewa, Wellington; NMV, Museum Victoria, Melbourne, Australia; TM, Tasmanian Museum, Hobart; UF, University of Florida, USA; USNM, United States Museum of Natural History, Smithsonian Institution, Washington; WAM, Western Australian Museum, Perth; YPM, Peabody Museum of Natural History, Yale University, New Haven; ZMUC, Zoological Museum, University of Copenhagen, Denmark. Photography for figures 4–18 was performed using a Leica MZ16 stereomicroscope, DC300 Leica digital camera, and “Auto-Montage” software for composition of images.

Invalid and junior synonyms of genera and species (indexed by A.M. Clark, 1993) are not repeated in this work unless their systematic status is reviewed. The summary distributional data given for the genera below are in part based on more detailed ranges given by A.M. Clark (1993), Rowe (in Rowe and Gates, 1995), O'Loughlin (2002), O'Loughlin et al. (2002, 2003), and Dartnall et al. (2003). Throughout the paper, “Rowe (1995)” refers to “Rowe (in Rowe and Gates, 1995)”. The erection of

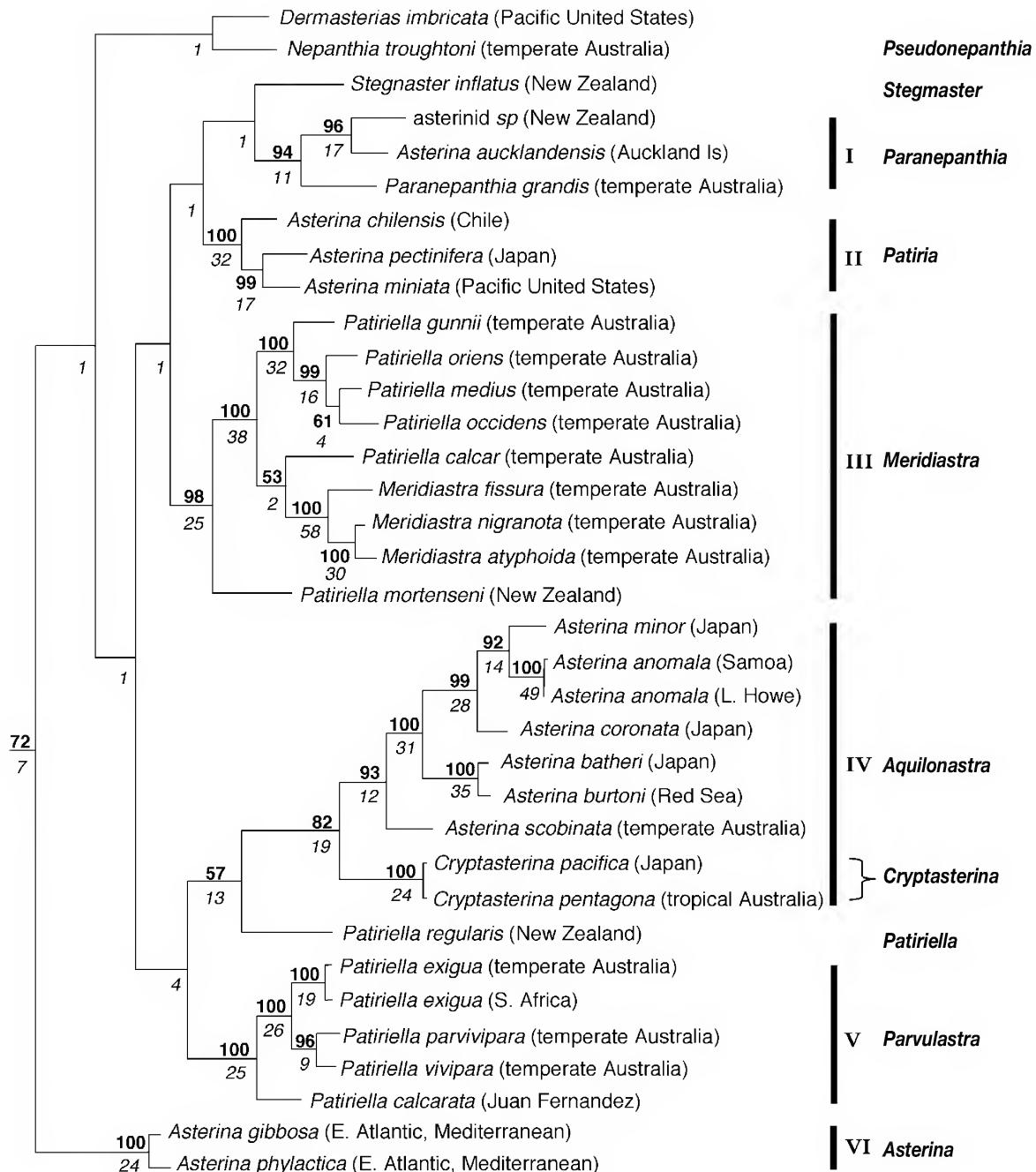


Figure 1. Phylogenetic relationships of asterinid mtDNA sequences (after Waters et al., 2004). Support for particular reconstructions is indicated by bootstrap values (>50%; in bold) and by decay indices (in italics). MtDNA Clades I–VI are identified on the basis of high bootstrap support. Generic assignments made in this paper appear on the right.

new genera and systematic decisions in this work are made by the first author (O'Loughlin).

Morphological diagnostic characters (see Table 1)

The molecular phylogeny of Waters et al. (2004) has provided evidence of relationships between species. Morphological examination of molecular clades has been a starting point for seeking and confirming characters which are useful for generic diagnoses. A significant outcome has been the recognition of internal skeletal plates as good diagnostic characters. Their absence and presence in different combinations vary across genera and are objective criteria.

Clark and Downey (1992) recognised these plates, and defined them collectively as “superambulacral plates”. These internal support plates are distinguished here as three independent types, which are each reliable diagnostically. The Clark and Downey (1992) definition of “superambulacral plate” is emended to: an internal plate articulating between the actinal end of an ambulacral plate, and actinal or marginal or abactinal plates (figs 4a, e, 14e, f; illustrated in A.M. Clark, 1983: fig. 5b). Two additional types of plates are defined. A “superactinal plate” is: an internal interradial plate articulating between abactinal plates, and actinal or other superactinal or superambulacral plates (figs 4b, d, 10d, 15c). “Transactinal plates” are: internal plates in transverse series across rays above the actinal plates (fig. 4f; illustrated but not defined in A.M. Clark, 1983: figs 5d, e [*brevis* a junior synonym of *belcheri*]). As with many diagnostic characters, the development and presence of internal plates may be related to size. They have not been observed in the pedomorphic species of some genera.

Body form, in terms of the degree to which rays are discrete and the form of the rays, is useful diagnostically. But both are subject to variation within a species and because of the habit of the animal and preservation artefact. The presence of noticeable body integument is consistent for some genera, but varies in the degree to which it is evident. Whether abactinal plates imbriicate, or form regular series, or are irregularly arranged, are useful criteria, but also vary. The presence of single large papulae or numerous small papulae in papular spaces distinguishes some genera but the distinction is not absolute. Whether actinal plates are in longitudinal series parallel to the furrow, or in oblique series from the furrow to the margin, are useful characters, but sometimes a combination of plate arrangements is evident and sometimes there is variation within a species (in one species apparently changing with size). The form of spinelets and spines is broadly useful for generic diagnoses, but there is variation in detail of form among and within species. Whether spinelets are judged to be “opaque” or “glassy” is attempted, but when denuded by bleach all spinelets appear crystalline and thus glassy. There is subjectivity in making diagnostic statements using the above characters.

The occurrence of pedicellariae is diagnostically reliable for some genera but in others they are present in only some of the species. Glassy convexities occur on the plates of many species. They are present on all species of some genera and absent in one genus, but within one genus they are present on one species and absent on another.

Some characters were found to vary within genera and species and are unhelpful for generic diagnostic purposes: extent of development of a carinal series of plates; presence of a border of five large radial and five small interradial plates around the disc; precise numbers of papulae and secondary plates per papular space; numbers of abactinal spinelets and actinal spines per plate; size of plates and spinelets and spines; fissiparity; and gonopore occurrence abactinally or actinally.

We acknowledge the limitations we face in diagnosing genera using morphological characters. These result from examination of few specimens of each species, consequent limited exposure to intraspecific variations and developmental variations, character variability such as noted above, and the subjectivity of decision-making when addressing continuous characters. Table 1 lists some morphological characters judged to be useful diagnostically and their occurrence in the asterinid genera confirmed or erected in this study.

Key to genera of Asterinidae

1. Furrow spines in longitudinal arrangement on adambulacral plates (fig. 16d); 2 series of tube feet in each ambulacrum; lacking internal plated brood chambers 2
- Furrow spines in vertical series on adambulacral plates (fig. 17f); 4 series of tube feet; internal plated brood chambers with abactinal and actinal interradial openings *Tremaster* Verrill
2. Rays narrow at base, to varying degrees subcylindrical or digitiform (fig. 2j) 3
- Rays broad at base or not discrete, not subcylindrical or digitiform (figs 2b, i) 6
3. Superambulacral series of plates present (fig. 4a) 4
- Lacking superambulacral, transactinal and superactinal plates (fig. 16g) *Pseudopatiria* O'Loughlin gen. nov.
4. Superactinal plates present (fig. 4b) 5
- Superactinal plates absent (fig. 14e) *Pseudonepanthia* A.H. Clark
5. Rays narrowly flat actinally, marginal edge weakly angular; pedicellariae present; transactinal plates present (fig. 4f) *Nepanthia* Gray
- Rays broadly flat actinally, marginal edge strongly angular (fig. 10d); lacking pedicellariae; lacking transactinal plates *Callopatria* Verrill
6. Interradii very thin; abactinal and actinal plates interiorly contiguous throughout the interradii (fig. 7) 7
- Interradii not very thin; abactinal and actinal interradial plates contiguous or connected by superactinal plates distally only (fig. 15c) 9
7. Body arched; furrow spines project actinally, in continuous series, with integument and granule cover (fig. 17c); actinal spines glassy thorn-tipped (fig. 17d) *Stegnaster* Sladen
- Body not arched; furrow spines not projecting actinally, in webbed groups on adambulacral plates, not covered with integument and granules; actinal spines not glassy thorn-tipped 8

8. Abactinal spinelets sacciform; interradial extensively supported by long thin articulating interior projections from abactinal and actinal plates (fig. 7) *Anseropoda* Nardo
- Abactinal spinelets granuliform; interradial extensively supported interiorly by contiguous imbricating abactinal and actinal plates *Pseudasterina* Aziz and Jangoux
9. Lacking superambulacral, transactinal and superactinal plates 10
- One or both of superambulacral and superactinal plates present 13
10. Abactinal body covered by thick integument with subgranular spinelets; body typically in high arched (domed) shape (fig. 17e); abactinal interradial plate arrangement irregular *Kampylaster* Koehler
- Body not covered by thick integument with subgranular spinelets; body rarely in high arched (domed) shape; abactinal interradial plate arrangement regular 11
11. Abactinal spinelets glassy, acicular or subsacciform, in tufts (fig. 8f) or paxilliform (fig. 8i); inferomarginal plates with distal tuft of spinelets (fig. 8h) *Asterinides* Verrill
- Abactinal spinelets opaque, granuliform or digitiform, not in tufts or paxilliform; inferomarginal spinelets not in distal tufts 12
12. Rays discrete; abactinal spinelets columnar to digitiform (fig. 6a) (Atlantic, Mediterranean) *Asterina* Nardo
- Rays not discrete, margin straight or slightly incurved; abactinal spinelets granuliform (fig. 5a) (temperate Indo-Pacific) *Meridiastra* O'Loughlin
13. Abactinal and actinal plates with dense subpaxilliform tufts of glassy acicular subsacciform spinelets and spines (fig. 5c); lacking superambulacral plates (fig. 15c) *Paranepanthia* Fisher
- Abactinal spinelets and actinal spines not in dense subpaxilliform tufts; superambulacral plates present 14
14. Abactinal spinelets glassy, acicular or sacciform or splay-tipped sacciform or long thin conical (fig. 13c) 15
- Abactinal spinelets opaque, granuliform or digitiform, or short thin to thick columnar (fig. 15d) 18
15. Abactinal plates with numerous firmly attached, glassy spinelets (fig. 9f); superomarginal spinelets same as those on abactinal plates (fig. 9d) *Aquilonastraea* O'Loughlin gen. nov.
- Abactinal plates with very fine glassy spinelets, numerous to none, weakly attached (fig. 13c); superomarginal spinelets few to none (fig. 13d) 16
16. Abactinal plates loosely contiguous leaving non-plated spaces (fig. 12); distal abactinal plates in series perpendicular or zig-zag to margin (fig. 12a); superomarginal plates small, not in regular series; inferomarginal plates with stout sacciform spinelets (fig. 10e) *Disasterina* Perrier
- Abactinal plates imbricate, always contiguous; distal abactinal plates not in perpendicular series to margin; superomarginal plates in distinct regular series; inferomarginal spinelets not stout sacciform 17
17. Body low; abactinal plates small, thin, deeply notched, up to 6 series along each side of rays (fig. 13b); inferomarginal spinelets acicular, in dense integument-covered tufts (fig. 13d) *Indianastra* O'Loughlin gen. nov.
- Body high; abactinal plates large, thick, shallow notches or crescentiform, up to 3 series along side of rays (fig. 18a); inferomarginal spinelets discrete, not in dense integument-covered tufts *Tegulaster* Livingstone
18. Form subpentagonal to medium-rayed stellate; large papular spaces; numerous papulae and secondary plates per space (fig. 15f) 19
- Form pentagonal to subpentagonal; small papular spaces; few papulae and secondary plates per space (fig. 11b) 20
19. Abactinal plates with close subpaxilliform cover of spinelets; spinelets thick to thin, short columnar or sub-globose (figs 15d, e); more than 3 spines on mid-interradial actinal plates *Patiria* Gray
- Spinelets on abactinal plates not in close subpaxilliform cover; spinelets granuliform or digitiform (fig. 16e); up to 3 spines on mid-interradial actinal plates *Patiriella* Verrill
20. Superomarginal plates typically in prominent series, longitudinally subrectangular; inferomarginal plates project narrowly to define the margin; abactinal papular spaces with predominantly 1 papula (fig. 11a); midray and distal actinal interradial plates frequently with 1 spine *Cryptasterina* Dartnall et al.
- Superomarginal and inferomarginal plates typically subequal; inferomarginal plates project prominently to define margin; abactinal papular spaces frequently with more than 1 papula (fig. 11b); midray and distal actinal interradial plates frequently with 2 spines (fig. 16c) *Parvulastra* O'Loughlin gen. nov.

Asterinidae Gray, 1840

Synonymy. See Clark and Downey, 1992.

Diagnosis. See Clark and Downey, 1992.

Genera. See Table 2.

Remarks. We do not revise the family diagnosis of Clark and Downey (1992). Changes to the list of genera in A.M. Clark (1993) are: *Cryptasterina* Dartnall et al., 2003, *Meridiastra* O'Loughlin, 2002, *Aquilonastraea* O'Loughlin gen. nov., *Indianastra* O'Loughlin gen. nov., *Parvulastra* O'Loughlin gen. nov. and *Pseudopatiria* O'Loughlin gen. nov. are added; *Allopatiria* Verrill, 1913 is a junior synonym of *Asterina* Nardo, 1834; *Patiria* Gray, 1840 is raised out of synonymy with *Asterina*; *Manasterina* H.L. Clark, 1938 is a junior synonym of *Disasterina* Perrier, 1875; *Paxillasterina* A.M. Clark, 1983 is a junior synonym of *Asterinides* Verrill, 1913, which is maintained as a valid genus; and *Asterinopsis* Verrill, 1913 and *Desmopatiria* Verrill, 1913 are rejected.

We agree with H.L. Clark (1938) that *Asterinopsis* Verrill, 1913 is nomen dubium. Verrill (1913) designated *Asterias penicillaris* Lamarck, 1816 (Indo-Pacific) the type species, and assigned *Asterina pilosa* Perrier, 1881 (West Indies) and *Asterina lymani* Perrier, 1881 (synonymous according to Clark and Downey, 1992) to *Asterinopsis*. Fisher (1919) added *Nepanthia pedicellaris* Fisher, 1913 to *Asterinopsis*. Mortensen (1933) judged that the type of *A. penicillaris* was lost and that no reliable specimens or image were available. H.L. Clark (1938, 1946) pointed out that Mortensen's case for the dubious

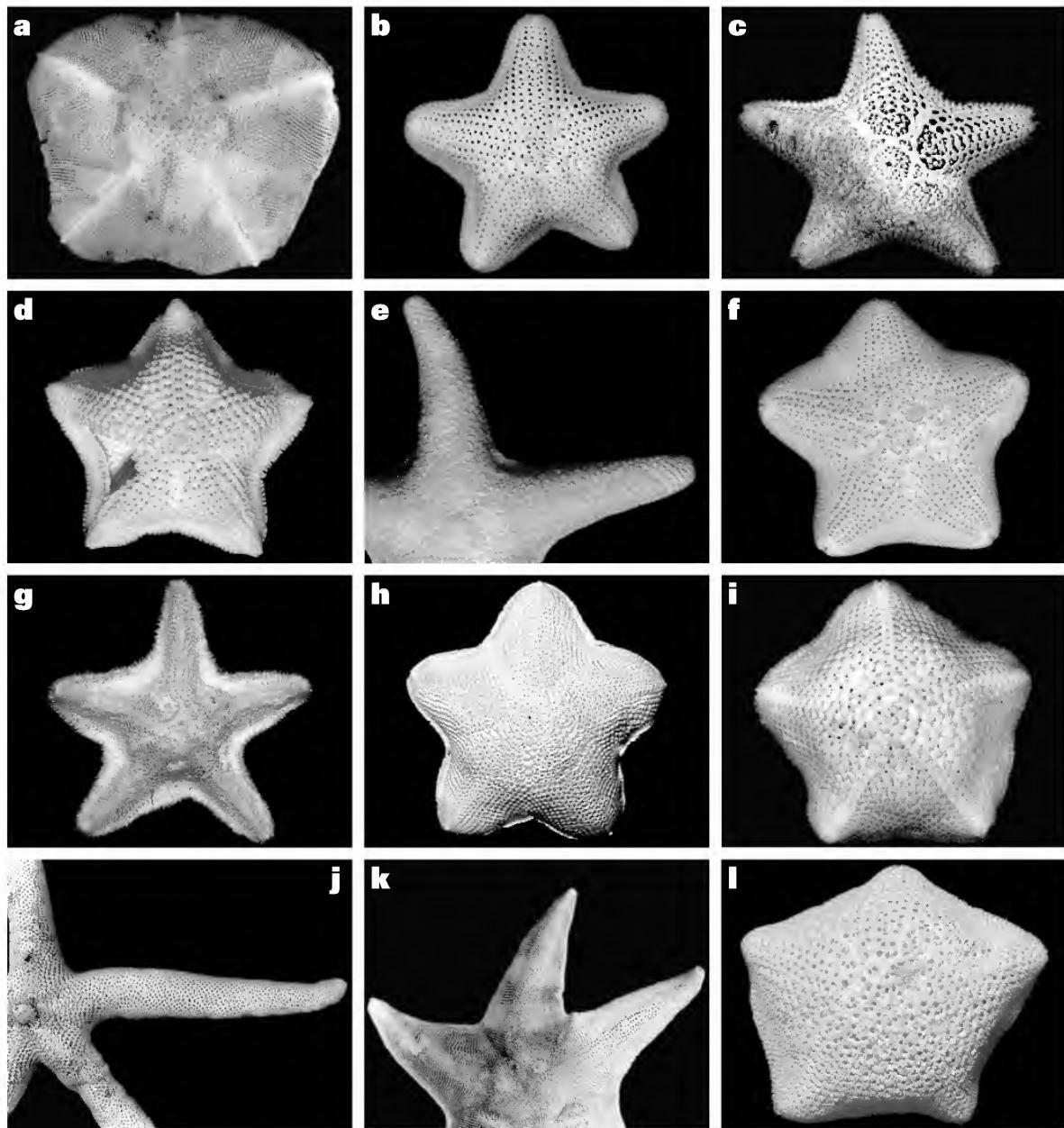


Figure 2. Abactinal views of type species of Asterinidae genera. a, *Anseropoda placenta* ($R = 31$ mm, AM J10714). b, *Aquilonastraea cepheus* ($R = 12$ mm, AM J8072). c, *Asterina gibbosa* ($R = 16$ mm, AM G11524). d, *Asterinides folium* ($R = 19$ mm, USNM E28573). e, *Callopattiria granifera* ($R = 50$ mm, NMV F98049). f, *Cryptasterina pentagona* ($R = 11$ mm, NMV F95959). g, *Disasterina abnormalis* ($R = 22$ mm, WAM Z6754). h, *Indianastra sarasini* ($R = 20$ mm, NMV F95802). i, *Meridiastra atypoida* ($R = 12$ mm, AM J9909). j, *Nepanthia maculata* ($R = 73$ mm, AM J13918). k, *Paranepanthia platydisca* ($R = 57$ mm, holotype, USNM 32644). l, *Parvulastra exigua* ($R = 11$ mm, neotype, TM H508).

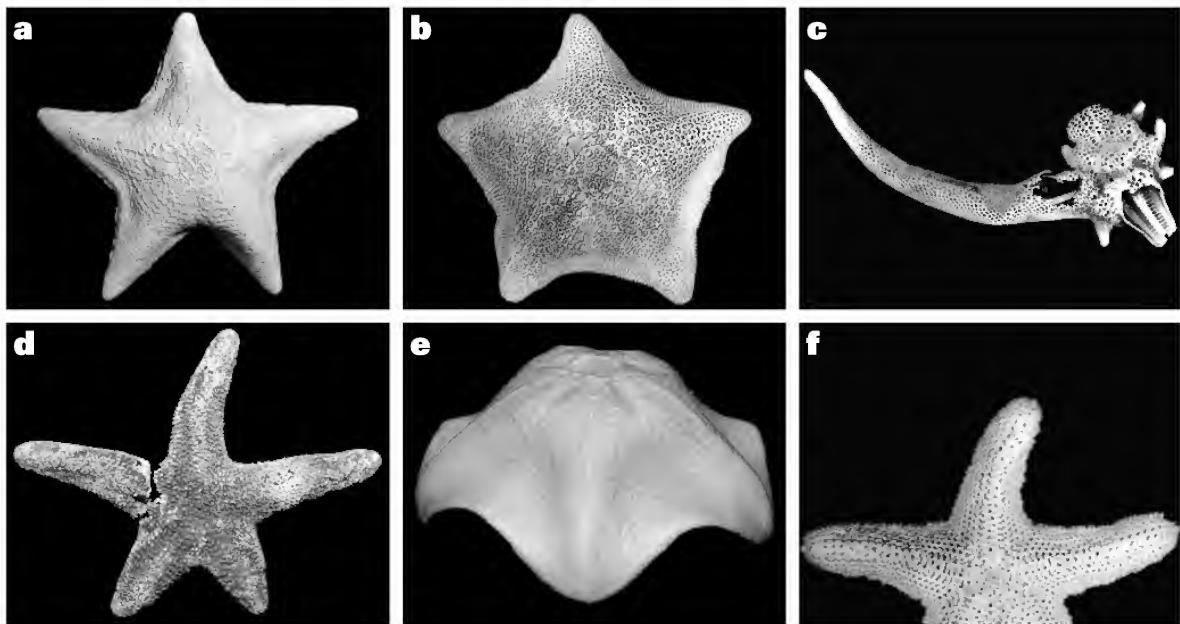


Figure 3. Abactinal views of type species of Asterinidae genera (continued; *Tremaster mirabilis* is figure 17e). a, *Patiria miniata* ($R = 67$ mm, NMV F98040). b, *Patiriella regularis* ($R = 31$ mm, AM J5594). c, *Pseudonepanthia gotoi* ($R = 74$ mm, holotype, USNM 36899). d, *Pseudopatiria obtusa* ($R = 54$ mm, holotype, BMNH 1938.6.23.24). e, *Stegnaster inflatus* ($R = 45$ mm, NMV F95675). f, *Tegulaster emburyi* ($R = 19$ mm, holotype, AM J5605).

state of *penicillaris* would render *Asterinopsis* also dubious. He further pointed out that *Asterinopsis* included both West Indian and Indo-Pacific species. A.M. Clark (1993) awaited reassessment, and listed *N. pedicellaris* and *A. pilosa* under *Asterinopsis*. In this work *N. pedicellaris* is referred to *Nepanthia* and *A. pilosa* is assigned to *Asterinidae*.

A.M. Clark (1993) listed *Desmopatiria* Verrill, 1913, but noted “validity doubtful since identity of type species doubtful”. The genus was erected for the new species *D. flexilis* Verrill, 1913. It was described from a single dry specimen, without a label, found in the YPM collections with some asteroids from Chile. A recent search of the YPM collections by Eric Lazo-Wasem (pers. comm.) failed to find the specimen. No subsequent specimen has been referred to the species or genus. In the absence of both type specimen and record of type locality, the species *D. flexilis* and genus *Desmopatiria* are judged to be nomina nuda.

Anseropoda Nardo

Figures 2a, 7, 8a-b

Anseropoda Nardo, 1834: 716.—Bell, 1891: 234–235.—Fisher, 1906: 1088.—Clark and Downey, 1992: 174–175.—A.M. Clark, 1993: 204–205.—Liao and Clark, 1995: 128.—Rowe, 1995: 32–33.—McKnight (in Clark and McKnight), 2001: 161. (For complete synonymy and discussion see Clark and Downey, 1992).

Diagnosis. Rays 5–18; body very thin, margin variably curved, rays short or not discrete, broadly rounded or pointed; narrow

raised radial areas with single papulae, in scattered or single longitudinal series, sometimes ringed by secondary plates; abactinal plates thin, in longitudinal and oblique series, not notched, each with subpaxilliform glassy, sacciform spinelets, few or tuft; pediculariae over papulae; actinal plates in longitudinal and oblique series; actinal spines few to numerous per plate, glassy, sacciform; lacking superambulacral plates, superactinal plates present or absent; interradial plates meet internally by long thin articulating projections, extensive in interradii.

Type species. *Asterias placenta* Pennant, 1777 (subsequent designation by Bell, 1891) (junior synonym: *Asterias membranacea* Retzius, 1783, by Bell, 1891).

Other species. *A. antarctica* Fisher, 1940; *A. aotearoa* McKnight, 1973; *A. diaphana* (Sladen, 1889); *A. fisheri* Aziz and Jangoux, 1985; *A. (Palmipes) grandis* Mortensen, 1933; *A. habracantha* H.L. Clark, 1923; *A. insignis* Fisher, 1906; *A. lobiancoi* (Ludwig, 1897); *A. ludovici* (Koehler, 1909); *A. macropora* Fisher, 1913; *A. novemradiata* (Bell, 1905); *A. pellucida* (Alcock, 1893); *A. petalooides* (Goto, 1914); *A. rosacea* (Lamarck, 1816); *A. tenuis* (Goto, 1914).

Material examined. *A. placenta*. NE Atlantic, off Great Britain, NMV F98043 (2).

A. rosacea. NW Australia, Broome, NMV F95811 (1); AM J7718 (1); Queensland, AM E1814 (1); Tasmania, AM E5037 (1).

Description with some species variations. Body very thin; rays 5 (*grandis*, *placenta*) or 6 (*insignis*) or 15–18 (*rosacea*), margin variably curved; rays not discrete or short, broad basally,

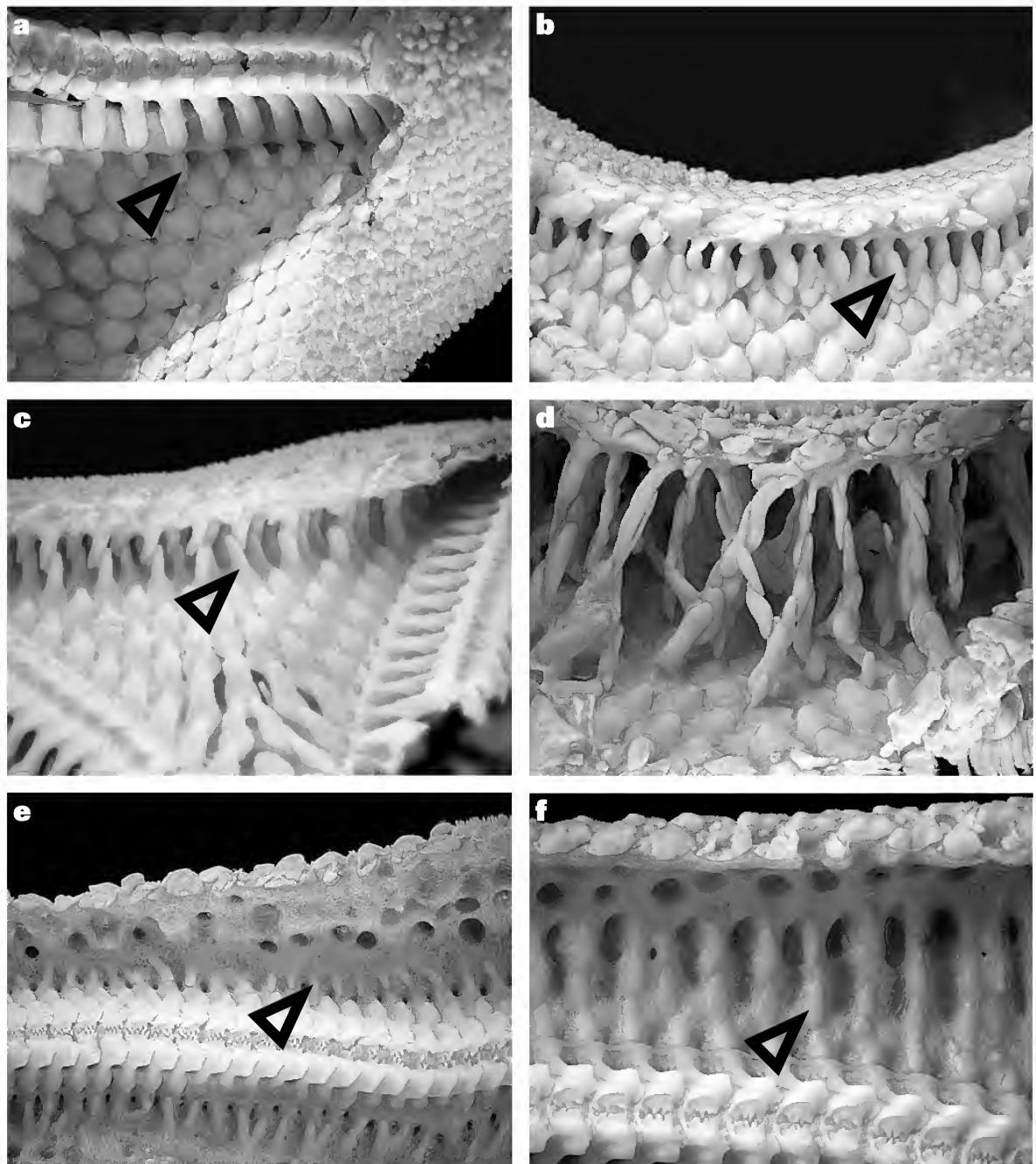


Figure 4. Abactinal views, with plates removed and cleared with bleach to show internal morphology. a–b, *Parvulastra dyscrita* ($R = 24$ mm, TM H854); a, series of superambulacral plates linking ambulacral and actinal plates; b, superactinal plates linking abactinal and actinal plates to support the interradial margin. c, *Meridiastra oriens* ($R = 28$ mm, NMV F73468); margin supported by internal contiguous projections of abactinal and actinal plates (arrow), absence of superambulacral and superactinal plates. d, *Patiria miniata* ($R = 65$ mm, NMV F97444); multiple superactinal plate struts supporting interradial margin. e, *Pseudonepanthia troughtoni* ($R = 85$ mm, NMV F73013); series of superambulacral plates, and thick internal tissue lining. f, *Nepanthia belcheri* ($R = 40$ mm, NMV F95806); transactinal plates extending transversely across actinal inner ray, and thick internal tissue lining.

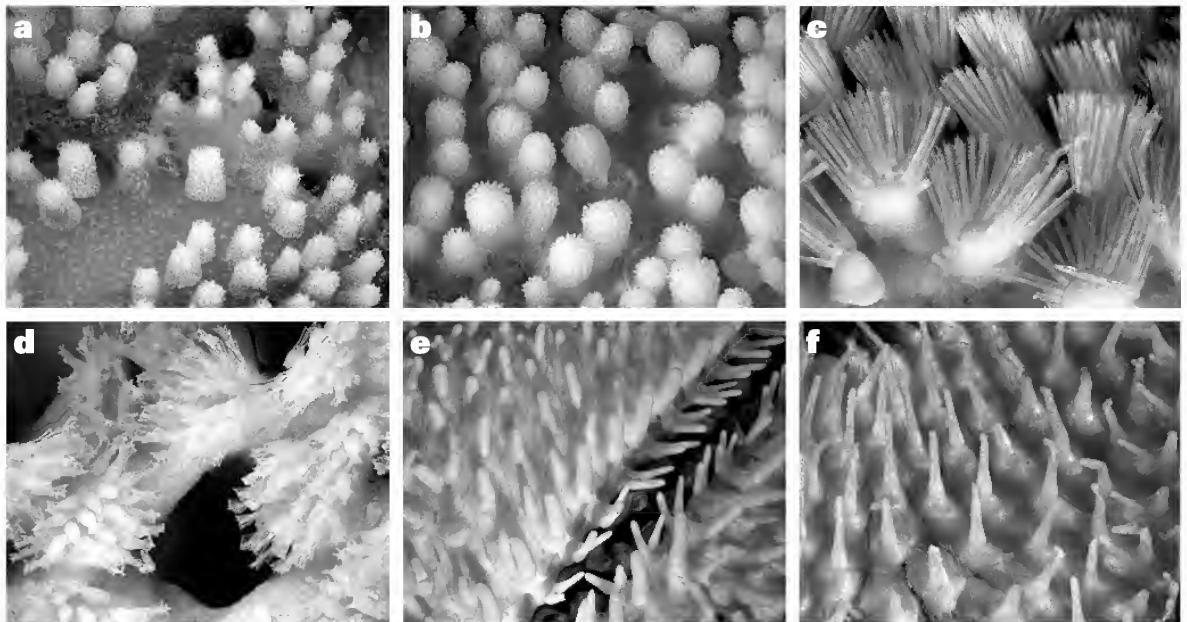


Figure 5. Forms of spinelets and spines. a, *Meridiastra gunnii* (NMV F73248): granuliform abactinal spinelets. b, *Parvulastra dyscrita* (TM H854): globose abactinal spinelets. c, *Paranepanthia grandis* (NMV F73976): acicular abactinal spinelets. d, *Pseudonepanthia gotoi* (USNM 36899): splay-pointed abactinal spinelets. e, *Parvulastra dyscrita* (TM H854): digitiform actinal spines. f, *Disasterina longispina* (WAM Z6760): sacciform actinal spines.

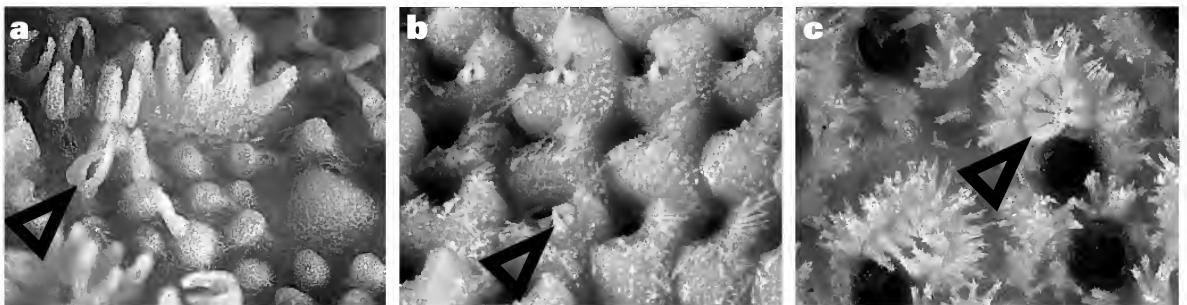


Figure 6. Forms of abactinal fasciculate pedicellariae. a, *Asterina ocellifera* (BMNH 1969.12.16.13). b, *Indianastra sarasini* (WAM Z6836). c, *Neopanthis belcheri* (NMV F95805).

rounded (*grandis*, *insignis*, *placenta*) or pointed (*rosacea*); rays slightly elevated as low ridges; size large (*grandis* up to $R = 130$ mm); pedicellariae present (*grandis*, *placenta*, *rosacea*); none fissiparous.

Abactinal plates thin, imbricate, narrow raised radial papulate area, extensive interradial non-papulate area; radial plates in regular (*grandis*) or irregular (*placenta*) distribution on narrow upper ray; single papulae scattered on upper ray (*rosacea*, *placenta*) or in 1–3 longitudinal series along each side of radial midline (*grandis*); papulae may be each surrounded by ring of up to 5 secondary plates (*placenta*, *rosacea*); interradial plates imbricate, rhombic to fan-shaped, in both longitudinal and oblique series, may be distally perpendicular to margin (*placenta*); disc not bordered; abactinal plates sometimes with

proximal low (*placenta*) to high (*rosacea*) spinelet-bearing elevation or dome; subpaxilliform tufts of spinelets (up to about 25 in *placenta*, up to 3 in *grandis*), sometimes multiple tufts per plate (*insignis*); spinelets glassy, sacciform, pointed (*placenta*, *rosacea*), sometimes more stout over papulae (*grandis*, *placenta*, *rosacea*; presumed to be pedicellariae); cleared abactinal plates sometimes with reticulate glassy appearance (*rosacea*), lacking glassy convexities; superom marginal and inferom marginal plates with abactinal-type spinelets, plates slightly larger than adjacent abactinals; margin defined by projecting inferom marginal plates. Actinal plates in longitudinal and oblique series; may be distally perpendicular to margin (*placenta*).

Actinal spines per plate: oral 5–8; suboral 3–10; furrow 4–9 proximally, webbed; subambulacral 2–7; actinal 3–12, webbed,

Table 1. Selection of morphological characters present (•) in the genera of the Asterinidae

Morphological characters	<i>Asterinopoda</i>	<i>Aquilonasteria</i>	<i>Asterina</i>	<i>Asternides</i>	<i>Callopeltida</i>	<i>Cryptasterina</i>	<i>Dissasterina</i>	<i>Indasterina</i>	<i>Kampylester</i>	<i>Meridiaster</i>	<i>Nepanthia</i>	<i>Paranepanthia</i>	<i>Parivalvata</i>	<i>Patiria</i>	<i>Patiriella</i>	<i>Pseudonepanthia</i>	<i>Pseudopalpida</i>	<i>Stegnaster</i>	<i>Tetulaster</i>	<i>Tremaster</i>
noticeable integument cover (fig. 10e)																				
interradii thin, inner surfaces connected (figs 2a, 7b)	•		•																	
habit arched, not flat (figs 3e, 17e)											•									
rays usually 5 only			•		•	•	•	•	•	•										
rays 5 and more	•	•	•								•	•								
margins straight to slightly curved (figs 2a, i, 3e)	•			•		•	•	•	•											
rays discrete, flat actinally, wide basally (figs 2b, c)	•	•	•	•		•	•	•	•											
rays discrete, flat actinally, narrow basally (fig. 2e)						•														
rays discrete, subcylindrical (figs 2j, 3c, d, 14e)																		•	•	
superambulacral plates present (figs 4a, 14e)		•				•	•	•	•											
transactinal plates present (fig. 4f)												•								
superactinal plates present (figs 4b, d, 15c)	•	•				•	•	•	•											
interradial internal articulating supports (figs 7a, b)	•																			
internal resinous body lining (figs 4e, f)						•						•						•	•	
abactinal plates imbricate (figs 8e, 10i, 15a)	•	•	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•	•
abactinal plates loosely contiguous (figs 12a, b)									•											
ray plates mostly in series (figs 2b, c, i, 9a, 13b)	•	•	•	•		•		•	•											
ray plates mostly not in series (figs 3b, 12a, b)								•	•											
few to many papulae per space (figs 10a, 15f)		•	•	•																
mostly single papula per space (figs 9f, 13b)	•	•				•	•	•	•											
spinelets opaque, stout, granuliform (figs 5a, b, 11b)						•			•	•										
spinelets opaque, stout, elongate (figs 6a, 16h)						•														
spinelets glassy, fine, acicular (figs 5c, 13d)						•														
spinelets glassy, fine, not acicular (figs 9c-f)	•	•		•	•		•													
spinelets absent, or glassy, very fine, often lost (fig. 13c)								•	•	•										
body with integument/granule cover (figs 17a, c, d)										•										
pedicellariae always present (fig. 6c)	•																			
pedicellariae sometimes present (figs 6a, b)		•	•																	
pedicellariae never present						•	•	•			•	•	•	•	•	•	•	•	•	•
glassy convexities always present (fig. 9c)		•				•	•	•			?	•	•							
glassy convexities never present		•					•				?						•	•	•	
superomarginal plates in regular series (figs 10c, 13d)	•	•	•	•	•	•			•		•	•	•	•	•	•	•	•	•	•
superomarginal plates irregular (fig. 10e)									•		•	•					•	•		
superomarginal plates absent																				
inferomarginals project narrowly, or not at all (fig. 16g)									•	•							•	•		
inferomarginal plates loosely contiguous (fig. 10e)										•										
inferomarginal spinelets large, sacciform (fig. 10e)											•									
inferomarginal spinelets acicular, dense tufts (fig. 13d)									•			•								
furrow spines in longitudinal series (figs 5e, 10h, 16d)	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
furrow spines in vertical series (fig. 17f)																				
tube feet rows biserial (fig. 15b)	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
tube feet rows quadrilateral																				
actinal plates in distinct oblique series (fig. 16c)																	•	•	•	

Table 2. List of genera and species of Asterinidae, including new synonymies and combinations, and species nomen dubium, nomen nudum, and incertae sedis. Type species with asterisk.

Combination, this paper, or senior synonym	Original combination
<i>Anseropoda antarctica</i> Fisher, 1940	<i>antarctica</i> , <i>Anseropoda</i> , Fisher, 1940
<i>Anseropoda aotearoa</i> McKnight, 1973	<i>aotearoa</i> , <i>Anseropoda</i> , McKnight, 1973
<i>Anseropoda diaphana</i> (Sladen, 1889)	<i>diaphana</i> , <i>Palmipes</i> , Sladen, 1889
<i>Anseropoda fisheri</i> Aziz and Jangoux, 1985	<i>fisheri</i> , <i>Anseropoda</i> , Aziz and Jangoux, 1985
<i>Anseropoda grandis</i> Mortensen, 1933	<i>grandis</i> , <i>Anseropoda</i> (<i>Palmipes</i>), Mortensen, 1933
<i>Anseropoda habracantha</i> H.L. Clark, 1923	<i>habracantha</i> , <i>Anseropoda</i> , H.L. Clark, 1923
<i>Anseropoda insignis</i> Fisher, 1906	<i>insignis</i> , <i>Anseropoda</i> , Fisher, 1906
<i>Anseropoda lobiancoi</i> (Ludwig, 1897)	<i>lobiancoi</i> , <i>Palmipes</i> , Ludwig, 1897
<i>Anseropoda ludovici</i> (Koehler, 1909)	<i>ludovici</i> , <i>Palmipes</i> , Koehler, 1909
<i>Anseropoda macropora</i> Fisher, 1913	<i>macropora</i> , <i>Anseropoda</i> , Fisher, 1913
<i>Anseropoda novemradiata</i> (Bell, 1905)	<i>novemradiata</i> , <i>Palmipes</i> , Bell, 1905
<i>Anseropoda pellucida</i> (Alcock, 1893)	<i>pellucida</i> , <i>Palmipes</i> , Alcock, 1893
<i>Anseropoda petalooides</i> (Goto, 1914)	<i>petalooides</i> , <i>Palmipes</i> , Goto, 1914
* <i>Anseropoda placenta</i> (Pennant, 1777)	<i>placenta</i> , <i>Asterias</i> , Pennant, 1777
<i>Anseropoda rosacea</i> (Lamarck, 1816)	<i>rosaceus</i> , <i>Asterias</i> , Lamarck, 1816
<i>Anseropoda tenuis</i> (Goto, 1914)	<i>tenuis</i> , <i>Palmipes</i> , Goto, 1914
<i>Aquilonastraea anomala</i> (H.L. Clark, 1921)	<i>anomala</i> , <i>Asterina</i> , H.L. Clark, 1921
<i>Aquilonastraea batheri</i> (Goto, 1914)	<i>batheri</i> , <i>Asterina</i> , Goto, 1914
<i>Aquilonastraea burtoni</i> (Gray, 1840)	<i>burtoni</i> , <i>Asterina</i> , Gray, 1840
* <i>Aquilonastraea cepheus</i> (Müller and Troschel, 1842)	<i>cepheus</i> , <i>Asteriscus</i> , Müller and Troschel, 1842
<i>Aquilonastraea corallicola</i> (Marsh, 1977)	<i>corallicola</i> , <i>Asterina</i> , Marsh, 1977
<i>Aquilonastraea coronata</i> (Martens, 1866)	<i>coronata</i> , <i>Asterina</i> , Martens, 1866
<i>Aquilonastraea coronata</i> (Martens, 1886)	<i>coronata fascicularis</i> , <i>Asterina</i> , Fisher, 1918
<i>Aquilonastraea coronata</i> (Martens, 1886)	<i>spinigera</i> , <i>Asterina</i> , Koehler, 1911
<i>Aquilonastraea heteractis</i> (H.L. Clark, 1938)	<i>heteractis</i> , <i>Asterina</i> , H.L. Clark, 1938
<i>Aquilonastraea iranica</i> (Mortensen, 1940)	<i>iranica</i> var. <i>iranica</i> , <i>Asterina</i> , Mortensen, 1940
<i>Aquilonastraea limboonkengi</i> (Smith, 1927)	<i>limboonkengi</i> , <i>Asterina</i> , Smith, 1927
<i>Aquilonastraea minor</i> (Hayashi, 1974)	<i>minor</i> , <i>Asterina</i> , Hayashi, 1974
<i>Aquilonastraea rosea</i> (H.L. Clark, 1938)	<i>rosea</i> , <i>Paranepanthia</i> , H.L. Clark, 1938
<i>Aquilonastraea scobinata</i> (Livingstone, 1933)	<i>scobinata</i> , <i>Asterina</i> , Livingstone, 1933
<i>Asterina fimbriata</i> Perrier, 1875	<i>fimbriata</i> , <i>Asterina</i> , Perrier, 1875
<i>Asterina gibbosa</i> (Pennant, 1777)	<i>gibbosa</i> , <i>Asterias</i> , Pennant, 1777
* <i>Asterina gibbosa</i> (Pennant, 1777)	<i>gibbosa</i> , <i>Asterina</i> , Pennant, 1777
<i>Asterina gracilispina</i> H.L. Clark, 1923	<i>gracilispina</i> , <i>Asterina</i> , H.L. Clark, 1923
<i>Asterina ocellifera</i> (Gray, 1847)	<i>ocellifera</i> , <i>Patiria</i> , Gray, 1847
<i>Asterina pancerii</i> (Gasco, 1870)	<i>pancerii</i> , <i>Asteriscus</i> , Gasco, 1870
<i>Asterina phylactica</i> Emson and Crump, 1979	<i>phylactica</i> , <i>Asterina</i> , Emson and Crump, 1979
<i>Asterina stellifera</i> (Möbius, 1859)	<i>stellifera</i> , <i>Enoplopatria</i> , Verrill, 1913
<i>Asterina stellifera</i> (Möbius, 1859)	<i>stellifera</i> , <i>Asteriscus</i> , Möbius, 1859
incertae sedis	<i>lorioli</i> , <i>Asterina</i> , Koehler, 1910
incertae sedis	<i>novaehollandiae</i> , <i>Asterina</i> , Perrier, 1875
* <i>Asterinides folium</i> (Lütken, 1860)	<i>folium</i> , <i>Asteriscus</i> , Lütken, 1860
<i>Asterinides hartmeyeri</i> (Döderlein, 1910)	<i>hartmeyeri</i> , <i>Asterina</i> , Döderlein, 1910
<i>Asterinides pilosa</i> (Perrier, 1881)	<i>lymani</i> , <i>Asterina</i> , Perrier, 1881
<i>Asterinides pilosa</i> (Perrier, 1881)	<i>pilosa</i> , <i>Asterina</i> , Perrier, 1881
<i>Asterinides pompom</i> (A.M. Clark, 1983)	<i>pompom</i> , <i>Paxillasterina</i> , A.M. Clark, 1983
<i>Callopatria formosa</i> (Mortensen, 1933)	<i>formosa</i> , <i>Parasterina</i> , Mortensen, 1933
* <i>Callopatria granifera</i> (Gray, 1847)	<i>bellula</i> , <i>Patiria</i> , Sladen, 1889
<i>Callopatria granifera</i> (Gray, 1847)	<i>granifera</i> , <i>Patiria</i> , Gray, 1847
<i>Cryptasterina hystera</i> Dartnall and Byrne, 2003	<i>hystera</i> , <i>Cryptasterina</i> , Dartnall and Byrne, 2003
<i>Cryptasterina pacifica</i> (Hayashi, 1977)	<i>pseudoexigua pacifica</i> , <i>Asterina</i> , Hayashi, 1977
<i>Cryptasterina pentagona</i> (Müller and Troschel, 1842)	<i>obscura</i> , <i>Patiriella</i> , Dartnall, 1971
* <i>Cryptasterina pentagona</i> (Müller and Troschel, 1842)	<i>pentagona</i> , <i>Asteriscus</i> , Müller and Troschel, 1842
<i>Cryptasterina pentagona</i> (Müller and Troschel, 1842)	<i>pseudoexigua</i> , <i>Patiriella</i> , Dartnall, 1971
nomen nudum (this work)	<i>flexilis</i> , <i>Desmopatiria</i> , Verrill, 1913

- **Disasterina abnormalis* Perrier, 1875
Disasterina abnormalis Perrier, 1875
Disasterina ceylanica Döderlein, 1888
Disasterina longispina (H.L. Clark, 1938)
Disasterina odontacantha Liao, 1980
Disasterina spinosa Koehler, 1910
- Indianastra inopinata* (Livingstone, 1933)
Indianastra inopinata (Livingstone, 1933)
Indianastra sarasini (de Loriol, 1897)
Indianastra sarasini (de Loriol, 1897)
Indianastra sarasini (de Loriol, 1897)
Indianastra sarasini (de Loriol, 1897)
- **Kampylaster incurvatus* Koehler, 1920
- **Meridiastra atypoida* (H.L. Clark, 1916)
Meridiastra calcar (Lamarck, 1816)
Meridiastra fissura O'Loughlin, 2002
Meridiastra gunnii (Gray, 1840)
Meridiastra gunnii (Gray, 1840)
Meridiastra mediuss (O'Loughlin et al., 2003)
Meridiastra modesta (Verrill, 1870)
Meridiastra modesta (Verrill, 1870)
Meridiastra mortensenii (O'Loughlin et al., 2002)
Meridiastra nigranota O'Loughlin, 2002
Meridiastra occidens (O'Loughlin et al., 2003)
Meridiastra oriens (O'Loughlin et al., 2003)
Meridiastra rapa O'Loughlin, 2002
- Nepanthia belcheri* (Perrier, 1875)
Nepanthia crassa (Gray, 1847)
Nepanthia fisheri Rowe and Marsh, 1982
*iNepanthia maculata Gray, 1840
Nepanthia pedicellaris Fisher, 1913
- incertae sedis
- Paranepanthia aucklandensis* (Koehler, 1920)
Paranepanthia grandis (H.L. Clark, 1928)
Paranepanthia grandis (H.L. Clark, 1928)
*iParanepanthia platydisca (Fisher, 1913)
- Parvulastra calcarata* (Perrier, 1869)
Parvulastra dyscrita (H.L. Clark, 1923)
*iParvulastra exigua (Lamarck, 1816)
Parvulastra parvivipara (Keough and Dartnall, 1978)
Parvulastra vivipara (Dartnall, 1969)
- Patiria chilensis* (Lütken, 1859)
*iPatiria miniata (Brandt, 1835)
Patiria miniata (Brandt, 1835)
Patiria pectinifera (Müller and Troschel, 1842)
- Patiriella inornata* Livingstone, 1933
Patiriella oliveri (Benham, 1911)
Patiriella oliveri (Benham, 1911)
Patiriella paradoxa Campbell and Rowe, 1997
*iPatiriella regularis (Verrill, 1867)
- nomen dubium (this work)
- **Pseudasterina delicata* Aziz and Jangoux, 1985
Pseudasterina granulosa Aziz and Jangoux, 1985
- Pseudonepanthia briareus* (Bell, 1894)
*iPseudonepanthia gotoi A.H. Clark, 1916
Pseudonepanthia gracilis (Rowe and Marsh, 1982)
Pseudonepanthia grangei (McKnight, 2001)
- **abnormalis*, *Disasterina*, Perrier, 1875
pulchella, *Habroporina*, H.L. Clark, 1921
ceylanica, *Disasterina*, Döderlein, 1888
longispina, *Manasterina*, H.L. Clark, 1938
odontacantha, *Disasterina*, Liao, 1980
spinosa, *Disasterina*, Koehler, 1910
- inopinata*, *Asterina*, Livingstone, 1933
perplexa, *Asterina*, H.L. Clark, 1938
lutea, *Asterina*, H.L. Clark, 1938
nuda, *Asterina*, H.L. Clark, 1921
orthodon, *Asterina*, Fisher, 1922
sarasini, *Palmipes*, de Loriol, 1897
- incurvatus*, *Kampylaster*, Koehler, 1920
- atypoida*, *Asterina*, H.L. Clark, 1916
calcar, *Asterias*, Lamarck, 1816
fissura, *Meridiastra*, O'Loughlin, 2002
brevispina, *Patiriella*, H.L. Clark, 1938
gunnii, *Asterina*, Gray, 1840
medius, *Patiriella*, O'Loughlin et al., 2003
agustincasoi, *Asterina*, Caso, 1977
modesta, *Asterina* (*Asteriscus*), Verrill, 1870
mortensenii, *Patiriella*, O'Loughlin et al., 2002
nigranota, *Meridiastra*, O'Loughlin, 2002
occidens, *Patiriella*, O'Loughlin et al., 2003
oriens, *Patiriella*, O'Loughlin et al., 2003
rapa, *Meridiastra*, O'Loughlin, 2002
- belcheri*, *Asterina* (*Nepanthia*), Perrier, 1875
crassa, *Patiria*, Gray, 1847
fisheri, *Nepanthia*, Rowe and Marsh, 1982
maculata, *Nepanthia*, Gray, 1840
pedicellaris, *Nepanthia*, Fisher, 1913
- brachiata*, *Nepanthia*, Koehler, 1910
- aucklandensis*, *Asterina*, Koehler, 1920
grandis, *Nepanthia*, H.L. Clark, 1928
praetermissa, *Asterinopsis*, Livingstone 1933
platydisca, *Nepanthia*, Fisher, 1913
- calcarata*, *Asteriscus*, Perrier, 1869
dyscrita, *Asterina*, H.L. Clark, 1923
I, Lamarck, 1816
parvivipara, *Patiriella*, Keough and Dartnall, 1978
vivipara, *Patiriella*, Dartnall, 1969
- chilensis*, *Asterina*, Lütken, 1859
coccinea, *Patiria*, Gray, 1840
miniata, *Asterias*, Brandt, 1835
pectinifera, *Asteriscus*, Müller and Troschel, 1842
- inornata*, *Patiriella*, Livingstone, 1933
nigra, *Patiriella*, H.L. Clark, 1938
oliveri, *Asterina*, Benham, 1911
paradoxa, *Patiriella*, Campbell and Rowe, 1997
regularis, *Asterina* (*Asteriscus*), Verrill, 1867
- tangribensis*, *Patiriella*, Domantay and Acosta, 1970
- delicata*, *Pseudasterina*, Aziz and Jangoux, 1985
granulosa, *Pseudasterina*, Aziz and Jangoux, 1985
- briareus*, *Patiria*, Bell, 1894
gotoi, *Pseudonepanthia*, A.H. Clark, 1916
gracilis, *Nepanthia*, Rowe and Marsh, 1982
grangei, *Nepanthia*, McKnight, 2001

<i>Pseudonepanthia nigrobrunnea</i> (Rowe and Marsh, 1982)	<i>nigrobrunnea</i> , <i>Nepanthia</i> , Rowe and Marsh, 1982
<i>Pseudonepanthia reinga</i> (McKnight, 2001)	<i>reinga</i> , <i>Nepanthia</i> , McKnight, 2001
<i>Pseudonepanthiaroughtoni</i> (Livingstone, 1934)	<i>roughtoni</i> , <i>Parasterina</i> , Livingstone, 1934
* <i>Pseudopatiria obtusa</i> (Gray, 1847)	<i>obtusa</i> , <i>Patiria</i> , Gray, 1847
* <i>Stegnaster inflatus</i> (Hutton, 1872)	<i>inflatus</i> , <i>Pteraster</i> , Hutton, 1872
<i>Stegnaster wesseli</i> (Perrier, 1875)	<i>wesseli</i> , <i>Asterina</i> , Perrier, 1875
<i>Tegulaster alba</i> (H.L. Clark, 1938)	<i>alba</i> , <i>Asterina</i> , H.L. Clark, 1938
* <i>Tegulasteremburyi</i> Livingstone, 1933	<i>emburyi</i> , <i>Tegulaster</i> , Livingstone, 1933
<i>Tegulaster leptalacantha</i> (H.L. Clark, 1916)	<i>leptalacantha</i> , <i>Asterina</i> , H.L. Clark, 1916
<i>Tegulaster leptalacantha</i> (H.L. Clark, 1916)	<i>leptalacantha</i> var. <i>africana</i> , <i>Disasterina</i> , Mortensen, 1933
<i>Tegulaster praesignis</i> (Livingstone, 1933)	<i>praesignis</i> , <i>Disasterina</i> , Livingstone, 1933
<i>Tegulaster praesignis</i> (Livingstone, 1933)	<i>spinulifera</i> , <i>Disasterina</i> , H.L. Clark, 1938
* <i>Tremaster mirabilis</i> Verrill, 1879	<i>mirabilis</i> , <i>Tremaster</i> , Verrill, 1879
<i>Tremaster mirabilis</i> Verrill, 1879	<i>novacaledoniae</i> , <i>Tremaster</i> , Jangoux, 1982

sometimes in fans (*grandis*, *insignis*, *placenta*); adradial row of actinal plates with complete series of spines; interradial actinal spines glassy, sacciform.

Superambulacral plates absent; superactinal plates absent (*rosacea*) or present proximally in multiple plate struts (*placenta*); abactinal and actinal interradial plates meet extensively internally by long thin articulating projections.

Distribution. Indo-West Pacific, South Africa, Australia, New Zealand, Antarctic Peninsula, North-East Atlantic, Mediterranean; 10–600 m.

Remarks. Molecular data are not available for any *Anseropoda* species. This restricted generic review is based on examination of specimens of *A. placenta* (type species) and *A. rosacea*, and original descriptions of *A. grandis* by Mortensen (1933) and *A. insignis* by Fisher (1906). Most of the species assigned to *Anseropoda* have not been examined and their generic placement has not been reviewed. The very thin body, and presence of extensive interradial internal thin projecting articulating supports distinguish *Anseropoda* from all other asterinid genera. The contrasting internal plate structures and presence or absence of superactinal plates in *A. placenta* and *A. rosacea* (Fig. 7) suggest that *Anseropoda* may not be monophyletic. Clark and Downey (1992) regarded the very small *Anseropoda lobiancoi* (Ludwig, 1897) from the Mediterranean (R about 8 mm) as being incompatible with *Anseropoda*.

Aquilonastrida O'Loughlin gen. nov.

Figures 1 (clade IV, part), 2b, 9a–f

Diagnosis. Rays 5 (6–8 in fissiparous species); interradial margin deeply incurved, form stellate; rays discrete, broad at base, tapering, rounded distally; flat actinally, high convex abactinally; abactinal plates in longitudinal series, not perpendicular to margin; papulate areas extensive; papulae predominantly single, large, in longitudinal series along sides of rays; abactinal plates with glassy convexities; abactinal spinelets and actinal spines predominantly fine, glassy, conical or sacciform or splay-pointed sacciform, in bands or tufts, numerous (10–40 per plate); actinal plates in longitudinal, not oblique, series;

superambulacral plates present for all of ray, sometimes for part of ray or absent in pedomorphic species; superactinal plates present.

Type species. *Asteriscus cepheus* Müller and Troschel, 1842.

Other species. *A. anomala* (H.L. Clark, 1921); *A. batheri* (Goto, 1914); *A. burtoni* (Gray, 1840); *A. corallicola* (Marsh, 1977); *A. coronata* (Martens, 1866) (junior synonyms: *Asterina coronata fascicularis* Fisher, 1918, possible synonymy raised by H.L. Clark, 1928, formalised by Rowe, 1995; and *Asterina spinigera* Koehler, 1911, by VandenSpiegel et al., 1998); *A. heteractis* (H.L. Clark, 1938); *A. iranica* (Mortensen, 1940) (raised to species status, this work); *A. limboonkengi* (Smith, 1927); *A. minor* (Hayashi, 1974); *A. rosea* (H.L. Clark, 1938); *A. scabinata* (Livingstone, 1933).

Material examined. *A. anomala*. Caroline Is, WAM Z6845 (2); Christmas I, Z6851 (1); Lord Howe I, AM J6169 (21); NMV F95593 (6); F97690 (6); F96699 (1); Maldives, Z6854 (1); Samoa, F96698 (2); Torres Strait, Darnley I, Z6849 (2); Western Australia, Kimberley, Z6843 (1).

A. batheri. Japan, Toyama Bay, NMV F97441 (1); AM J11564 (2); Oman, UF 70 (7).

A. burtoni. Gulf of Suez, AM J17892 (2); TM H1815 (2); Red Sea, Egyptian coast, H1814 (1).

A. cepheia iranica. Syntype. Persian Gulf, S of Bushire, coral reef, AM J17891 (1).

A. cepheus. Queensland, NMV F95594 (2), AM J23331 (1); Western Australia, Abrolhos Is, WAM Z6778 (7); J8321 (5); New Guinea, Trobriand Group, J22934 (1); Hong Kong, BMNH 1981.2.6.25 (1; previously identified as *Asterina limboonkengi*).

A. corallicola. Paratypes. Caroline Is, WAM Z1704 (3). *A. coronata*. Northern Territory, Darwin, NMV F95796 (4); AM J6613 (1); J8206 (2); Caroline Is, J13660 (1); Bombay, BMNH 1960.10.4.11-16 (2; previously identified as *Asterina lorioli*); Taiwan, J19956 (1); Japan, J11563 (2).

A. heteractis. Queensland, Townsville, AM J9541 (2); Heron I, J19449 (1).

A. limboonkengi. Oman, UF 1645 (2); UF 246 (1); UF 68 (6).

A. minor. Japan, NMV F96697 (2).

Paranepanthia rosea. Paratypes. Western Australia, Rottnest I, AM J6171 (3). Other material. Western Australia, Jurien Bay, AM J7437 (4).

A. scabinata. Holotype. Tasmania, AM J1241. Other material. Tasmania, Eaglehawk Neck, J9060 (3); Victoria, Phillip I, NMV F72998 (1); Port Fairy, F72985 (2); Killarney, F72997 (10).

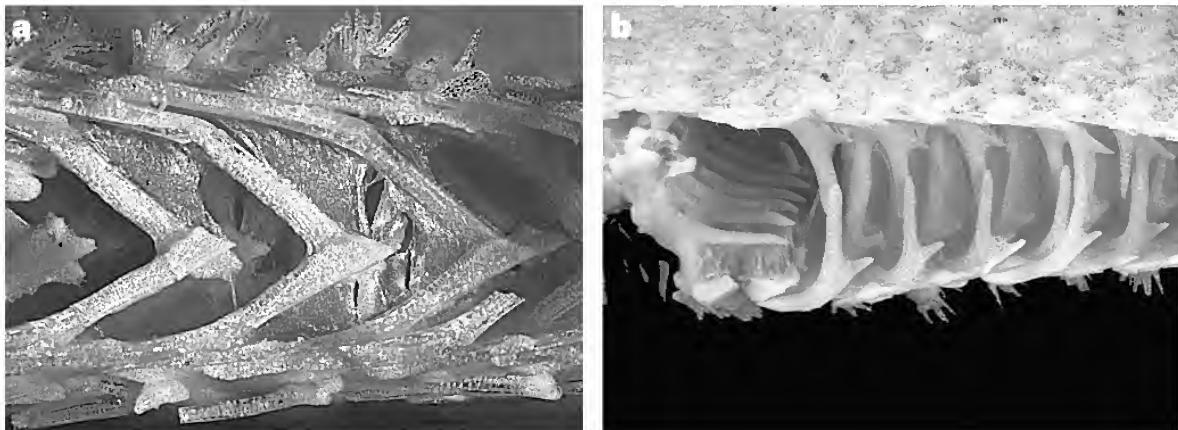


Figure 7. Longitudinal sections through interradial plates of *Anseropoda* species, showing internal contiguous projections from abactinal and actinal plates, and absence (b) of superambulacral plates. a, *Anseropoda placenta* ($R = 56$ mm, NMV F98043). b, *Anseropoda rosacea* ($R = 82$ mm, NMV F95811).

Description with species variations. Rays predominantly 5, or 6 (fissiparous *corallicola*, *heteractis*), or 6–7 (fissiparous *burtoni*), or 7–8 (fissiparous *anomala*); interradial margin deeply incurved, form stellate; rays discrete, broad at base, tapering, rounded distally; flat actinally, high convex abactinally; size medium (*iranica* up to $R = 35$ mm) to small (pedomorphic species *anomala*, *burtoni*, *corallicola*, *heteractis*, *minor* with R up to 10 mm); pedicellariae sometimes present, scattered (*iranica*) or few on proximal lateral rays above papulae (*batheri*, *coronata*); gonopores abactinal or actinal (*corallicola*, *scobinata*); fissiparity in 4 species.

Abactinal surface even, or very uneven with some paxilliform plates (*coronata*, *rosea*); plates in longitudinal series, not series perpendicular to margin; papulate areas extensive, to near distal end of rays, to near interradial margin; papular spaces small with few secondary plates and predominantly 1 large papula (rarely up to 3); 2–6 distinct longitudinal series of large papulae along each side of rays, series variably evident carinally; disc variably bordered by continuous series of 5 radial and 5 interradial plates (not in fissiparous species); abactinal plates predominantly singly notched for papulae, crescentiform on rays and interradially to near margin, round distally, with transverse or round spinelet-bearing proximal elevations; carinal series of plates absent, or proximal series of singly or doubly notched plates not widely separated by secondary plates, or doubly papulate to end of ray (*heteractis*); cleared abactinal plates with glassy convexities; abactinal spinelets glassy, conical or sacciform or splay-pointed sacciform; abactinal spinelets in transverse bands or tufts of 8–40 spinelets per plate, tufts sometimes multiple per plate (*batheri*, *cephalus*), spinelets sometimes 2 distinct forms (*coronata*), spinelets sometimes paxilliform (*coronata*, *rosea*); marginal plates with abactinal spinelets; superomarginal plates not larger than inferomarginals; acute margin formed by projecting inferomarginal plates (rounded margin in pedomorphic *corallicola*).

Actinal plates in longitudinal series, sometimes also oblique (*coronata*), or oblique (pedomorphic *heteractis*).

Actinal spines per plate: oral 5–9; suboral 3–12; furrow 3–9 proximally; subambulacral 2 up to tuft; adradial actinal plates fully spinous; actinal interradial spines similarly variable forms as abactinally, predominantly in tufts, up to 20 per plate.

Superambulacral plates present for all of ray, or distal half (pedomorphic *minor*), or absent (pedomorphic *corallicola*); superactinal plates present.

Distribution. Eastern Mediterranean, northern Indian and western Pacific Oceans, Gulf of Suez, Red Sea, Persian Gulf, Arabian Sea, southern Australia, Japan; 0–15 m.

Etymology. From the Latin *aquilonalis* (northern) and *astrum* (star), referring to the predominantly northern Indo-Pacific occurrence of the species of this genus (feminine).

Remarks. The new genus *Aquilonastrida* is represented on the molecular clade of Waters et al. (2004, clade IV, part) by six species: *A. anomala*, *A. batheri*, *A. burtoni*, *A. coronata*, *A. minor*, *A. scobinata*. These share a consistent morphology: discrete high rays; series of single large papulae along rays; fine glassy spinelets; presence of superambulacral and superactinal plates. Other species share this morphology and are included in the genus: *cephalus*, *corallicola*, *heteractis*, *limboonkengi* and *rosea*. The new genus shares some characters with *Cryptasterina* Dartnall et al., 2003: extensive papulate areas; small papular spaces with few secondary plates and single papulae per space; up to four longitudinal series of papulae along each side of the rays; doubly papulate carinal plates variably present, as short or long series or absent; margin formed by projecting inferomarginal plates; superactinal plates support the interradial margin. This similarity is supported by a sister taxon relationship on the molecular tree (clade IV, part). However, there are significant morphological differences

exhibited by *Cryptasterina*: form pentagonal or subpentagonal; abactinal spinelets granuliform; at most very low raised rounded spinelet-bearing elevations along the proximal projecting edge of abactinal plates; superom marginal plates larger than inferomarginals; actinal spines fewer (oral 4–5, suboral 1–2, furrow 2–3, subambulacral 1–2 proximally, actinal interradial 0–1 proximally 1–2 distally), conical to digitiform; adradial actinal series of plates with none to few spines; superambulacral plates not in complete series, few present.

In an electrophoretic study of five *Asterina* species from Japan, Matsuoka (1981) found them to be a heterogeneous phylogenetic group with *A. batheri* and *A. coronata japonica* closely related, *A. pseudoexigua pacifica* fairly closely related, and *A. pectinifera* and *A. minor* each probably belonging to separate lineages. This result is generally congruent with the molecular phylogeny of Waters et al. (2004), except that in their clades *A. minor* was not separate but in the same lineage as *A. batheri* and *A. coronata*.

H.L. Clark (1938) described juvenile specimens of *Paranepanthia rosea* (up to $R = 8$ mm). Material examined in this work from Jurien Bay was significantly larger (up to $R = 17$ mm) and characterised by: absence of two distinct ‘fields’ of abactinal plates; splay-pointed sacciform spinelets and spines; predominantly large single papulae in papular spaces; numerous longitudinal series of papulae along the sides of rays; actinal plates not in oblique series; presence of series of superambulacral plates; and single superactinal plate supports. *P. rosea* is removed from *Paranepanthia*. The inferomarginal plates define the margin in *P. rosea*, not superomarginal plates as stated by H.L. Clark (1938).

Mortensen (1940) distinguished a variety *iranica* for the species *A. cepheus* on the basis of having 5–6 suboral spines per plate and *A. cepheus* two (up to four seen in this work). Further to this observation, the variety is distinguished from *A. cepheus* (characters in brackets) by having: up to eight stout sacciform spinelets in single series across proximal abactinal plates (up to 20 fine spinelets in bands across plates); up to ten stout inferomarginal spinelets per plate (more than, 20); typically two actinal spines per plate (4–8). *Asterina cepheus iranica* is raised to species status.

Marsh (1977) compared the three similar small fissiparous Indo-Pacific asterinids *A. anomala*, *A. corallicola* and *A. heteractis*, and her confirmation of valid species status for all three is supported here. *A. heteractis* has some characters which are exceptional to those shared by other *Aquilonastridae* species: regular doubly papulate carinal series for length of ray; actinal plates in oblique series; fewer actinal spines per plate, with up to four oral, sometimes no suboral, up to four furrow, up to three actinal. These differences are not sufficient to justify assignment to another genus.

Smith (1927), Liao (1980) and Liao and Clark (1995) observed that *A. limboonkengi* was close to *A. cepheus* (Smith as close to *A. burtoni* from the Philippines, *A. burtoni* presumably *A. cepheus*). Liao and Clark (1995) described the differences between *A. cepheus* and *A. limboonkengi*. Our observations confirm that the abactinal spinelets in *A. cepheus* are long and fine, and those in *A. limboonkengi* short and stout. Rowe (1995) rejected the subspecies *A. coronata fascicularis* Fisher,

1918. The possible species status of the other subspecies of *A. coronata* (*cristata* Fisher, 1916 and *euerces* Fisher, 1917) has not been examined.

Pairs of abactinal spinelets on *A. anomala*, *A. cepheus*, *A. corallicola* and *A. minor* are sometimes angled and contiguous, suggesting that they may act as pedicellariae. But the spinelets are not differentiated in form.

Asterina Nardo

Figures 1 (clade VI), 2c, 6a, 8c–e

Asterina Nardo, 1834: 716.—Clark and Downey, 1992: 177–181.—A.M. Clark, 1993: 206–214.—Liao and Clark, 1995: 129.—Rowe, 1995: 33–35.—O'Loughlin, 2002: 278.—Waters et al., 2004: 874, 875, 877 (part). (For complete synonymy and discussion see Clark and Downey, 1992).

Allopatiria Verrill, 1913: 480.—Verrill, 1914: 273.—Tortonese, 1965: 174.—Spencer and Wright, 1966: U69.—A.M. Clark, 1983: 372–373.—Clark and Downey, 1992: 172.—A.M. Clark, 1993: 204. New synonym.

Diagnosis. Rays 5; body integument noticeable; interradial margin incurved to varying extents; rays discrete, short, distally broadly or narrowly rounded or pointed; flat actinally, convex abactinally; papular spaces with numerous small papulae and secondary plates; abactinal spinelets opaque, digitiform to conical, rounded distally; actinal plates in oblique and sometimes longitudinal series; actinal interradial spines digitiform to conical, up to 5 per plate; internal contiguous projections from abactinal and actinal plates support margin; lacking superambulacral and superactinal plates.

Type species. *Asterias gibbosa* Pennant, 1777 (subsequent designation by Fisher, 1906; full treatment by A.M. Clark, 1983) (junior synonym: *Asterina crassispina* H.L. Clark, 1928, by Rowe, 1995).

Other species. *A. fimbriata* Perrier, 1875; *A. gracilispina* H.L. Clark, 1923; *A. ocellifera* (Gray, 1847); *A. pancerii* (Gasco, 1870); *A. phylactica* Emson and Crump, 1979; *A. stellifera* (Möbius, 1859) (junior synonym: *Enoplopatria siderea* Verrill, 1913, this work).

Material examined. *A. fimbriata*. Argentina, Comodoro Rivadavia, AM J6411 (3).

A. gibbosa. Mediterranean, Tunisia, USNM E42476 (1); see O'Loughlin (2002).

A. gracilispina. South Africa, Cape Agulhas, BMNH 1975.10.29.47 (1).

A. ocellifera. Mauritania, Cape Lever, BMNH 1969.12.16.13 (1).

A. stellifer. Argentina, AM J6410 (1).

Enoplopatria siderea. Holotype. Panama (assumed here to be mistaken locality), YPM No. 9830. New synonym.

Description with species variations. Rays 5; interradial margin incurved to varying extents, rays discrete, distally narrowly (*gibbosa*) or broadly (*fimbriata*, *gracilispina*) rounded, or pointed (*ocellifera*, *stellifera*); size large (*ocellifera* up to $R = 81$ mm) to small (*phylactica* up to $R = 7.5$ mm); pedicellariae numerous abactinally, predominantly 2 valves, fasciculate (*gibbosa*, *ocellifera*, *stellifera*), or absent (*fimbriata*, *gracilispina*, *ocellifera*, *stellifera*) or actinal (*gibbosa*, *phylactica*); not fissiparous.

Extensive abactinal papulate area of weakly notched or shallow crescentiform or rhombic (*ocellifera*) plates, narrow interradial non-papulate margin of proximally rounded plates; upper rays with variably developed carinal series of doubly notched plates (*fimbriata*, *gibbosa*, *gracilispina*), or irregular plates (*stellifera*), or rhombic plates (*ocellifera*); up to 4 longitudinal series of plates along each side of rays; papular spaces large, secondary plates and papulae numerous, small secondary plates may partly obscure (*ocellifera*) or encroach on (*stellifera*) primary plates; disc bordered by series of 5 radial and 5 interradial plates (*gibbosa*, *gracilispina*) or not (*fimbriata*, *ocellifera*, *stellifera*); abactinal plates with spinelet-bearing ridges and domes; denuded plates with glassy convexities (*gibbosa*, *gracilispina*, *ocellifera*, *stellifera*) or reticulations (*fimbriata*); abactinal spinelets digitiform or conical, rounded distally; spinelets spaced on plates closely (*stellifera*) or widely (*fimbriata*, *gibbosa*, *gracilispina*, *ocellifera*), not in tufts; interradial plates in short series perpendicular to margin (*ocellifera*, *stellifera*) or not (*fimbriata*, *gibbosa*, *gracilispina*); superomarginal and inferomarginal plates in distinct series, covered with abactinal-type spinelets; projecting inferomarginal plates form marginal edge.

Actinal plates in oblique series (small specimens of *A. gibbosa*; longitudinal series in large specimens of *A. gibbosa*).

Actinal spines per plate: oral 4–9; suboral 1–4; furrow 2–5 proximally, webbed; subambulacral 1–3; adradial row of actinal plates with complete series of spines; actinal interradial predominantly 2–3 in mid-interradius; interradial actinal spines digitiform to conical.

Lacking superambulacral and superactinal plates; interradial margin supported by contiguous internal tongue-like extensions of abactinal and actinal plates.

Distribution. Atlantic Ocean, Europe, SW and S Africa, SE and S South America; Mediterranean Sea; 0–250 m.

Remarks. The principal characters in this new diagnosis of *Asterina* are: papular spaces with numerous small papulae and secondary plates, not predominantly single large papulae; abactinal spinelets opaque, digitiform to conical, not glassy and fine; actinal plates in oblique and longitudinal series; internal contiguous projections from abactinal and actinal plates support the margin; lacking superambulacral and superactinal plates.

Molecular evidence (Waters et al., 2004, clade VI) places *A. phylactica* as sister species of *A. gibbosa*. On the basis of the diagnosis the following species are removed from *Asterina* to other genera: *A. alba*, *A. anomala*, *A. aucklandensis*, *A. batheri*, *A. burtoni*, *A. cepheus*, *A. chilensis*, *A. corallicola*, *A. coronata*, *A. hartmeyeri*, *A. heteractis*, *A. inopinata*, *A. miniata*, *A. minor*, *A. pectinifera*, *A. sarasini*, *A. scobinata*.

A.M. Clark (1983) considered that the rhombic and non-crescentic form of the large primary plates in the radial field, and the proliferation of small secondary plates to the extent that abactinal plates become obscured peripherally, distinguish *Allopatiria* from *Asterina*. Clark and Downey (1992) noted superficial similarity of similarly sized specimens of *Allopatiria* and *Asterina*. We have found that the form of abactinal plates and number of secondary plates are not

generically significant. In diagnosing *Allopatiria*, Clark and Downey (1992) referred to “additional internal plates” supporting the margin. If such superactinal plates were present they might justify the retention of *Allopatiria*. But we did not confirm their presence. What could appear to be superactinal plates are long internal projections of distal abactinal and actinal plates. This is a character shared with *Asterina*, and *Allopatiria* is judged to be a junior synonym. A.M. Clark (1993) listed *Patiria* Gray, 1840 and *Asterinides* Verrill, 1913 as junior synonyms of *Asterina*. Rowe (1995) and Campbell and Rowe (1997) supported the validity of *Asterinides*. *Patiria* is raised out of synonymy in this work.

O’Hara (1998) synonymised *Asterina hamiltoni* Koehler, 1920 and *Cycethra macquariensis* Koehler, 1920 with *Asterina frigida* Koehler, 1917 and assigned *A. frigida* to *Cycethra* Bell, 1881 in the Ganeriidae. Rowe (1995) synonymised *Asterina crassispina* H.L. Clark, 1928 with *Asterina gibbosa*, and judged the northern Australia locality data to be incorrect. Based on an examination of the type of *Asterina spinigera*, VandenSpiegel et al. (1998) synonymised it with *Asterina coronata*.

Clark and Downey (1992) summarised the characters thought to distinguish *A. pancerii* from *A. gibbosa* as: flatter and near pentagonal shape; fewer and larger skeletal plates; plates with coarse crystal bodies; and more numerous, usually three, suboral spines. O’Loughlin (2002) noted in *A. gibbosa* material: some conspicuous glassy convexities around the margin of abactinal plates; and some plates with up to three suboral spines. The near pentagonal body form and relative size of plates have been found to show variation within species in this study. *A. pancerii* is probably conspecific with *A. gibbosa*. In the absence of molecular evidence, *pancerii* is retained here as a species of *Asterina*.

The holotype of *Enoplopatria siderea* was examined and found to conform in all morphological features with *Asterina stellifera*. The Panama type locality must be an error, since *A. stellifera* occurs on the east and west coasts of the South Atlantic.

Specimens of *Asterina lorioli* Koehler, 1910 and *Asterina novaezelandiae* Perrier, 1875 were not examined. Based on the descriptions, assignment to *Asterina* could not be confirmed. These species are placed incertae sedis, and discussed below.

All species placed here in *Asterina* are from the Atlantic and Mediterranean.

Asterinides Verrill

Figures 2d, 8f–i

Asterinides Verrill, 1913: 479.—Verrill, 1914: 263.—Verrill, 1915: 58.—Tommasi, 1970: 14–15.—A.M. Clark, 1983: 364.—Rowe, 1995: 33.—Campbell and Rowe, 1997: 131.—Clark and Mah, 2001: 335.—O’Loughlin, 2002: 291, 293.

Paxillasterina A.M. Clark, 1983: 373.—Clark and Downey, 1992: 193.—A.M. Clark, 1993: 227. New synonym.

Diagnosis. Rays 5 or 6; form subpentagonal or subhexagonal or discrete rays; abactinal plates in longitudinal series; extensive papulate areas, predominantly single papulae; abactinal plates singly notched; abactinal spinelets glassy, acicular to

subsacciform, in tufts or subpaxilliform or on paxilliform columns; lacking pedicellariae; superomarginal plates with tuft of spinelets; inferomarginal plates with distal dense subpaxilliform tuft of larger spinelets; actinal spines subsacciform, thin; lacking superambulacral and superactinal plates, distal interradial margin supported by inward projecting tongues from abactinal and sometimes actinal plates.

Type species. *Asteriscus folium* Lütken, 1860 (original designation).

Other species. *A. hartmeyeri* (Döderlein, 1910); *A. pilosa* (Perrier, 1881) (junior synonym: *A. lymani* Perrier, 1881, by Clark and Downey, 1992); *A. pompom* (A.M. Clark, 1983).

Material examined. *A. folium*. Holotype. Atlantic Ocean, Virgin Is (ZMUC). Other material. Atlantic Ocean, Caribbean Sea, USNM E28573 (1); Gulf of Mexico, USNM 38811 (3); Bermuda, USNM 38236 (4).

A. hartmeyeri. Atlantic Ocean, Caribbean Sea, USNM E49050 (2).

A. pilosa. Atlantic Ocean, Caribbean Sea, USNM E17973 (2); Gulf of Mexico, USNM E13707 (1); Venezuela, USNM E28411 (1).

A. pompom. Atlantic Ocean, Caribbean Sea, USNM E47755 (4); E47866 (1).

Description with species variations. Rays predominantly 5 (*folium, hartmeyeri, pompom*) or 6 (*pilosa*), interradial margin straight to slightly to deeply (*pilosa*) incurved, subpentagonal or discrete rays (*pilosa*); body thick, sides of rays steep (*folium, hartmeyeri, pilosa*), or thin (*pompom*); size small (*folium* up to $R = 20$ mm) to very small (*hartmeyeri* up to $R = 7$ mm); lacking pedicellariae; gonopores abactinal; one fissiparous (*pilosa*, *R* up to 10 mm).

Abactinal surface uneven due to raised proximal edge of thick imbricating plates (*folium*) or paxilliform columns (*pompom*); abactinal plates in longitudinal series; denuded appearance dominated by singly notched plates, heart-shaped to crescentiform; papulate areas extensive; papulae predominantly single, large, up to 4 longitudinal series along each side of rays; doubly notched and papulate carinal series variably present for most of ray, or upper ray plates irregular (*pilosa*); papular spaces fairly large, sometimes up to 3 papulae and 3 secondary plates per space; disc bordered by series of 5 radial 5 interradial plates (*folium*), or not (*hartmeyeri, pilosa*); denuded plates with glassy convexities (*folium, hartmeyeri*) or irregular texturing (*pompom*); plates with apical ridge or dome; spination variable, up to 3 subpaxilliform tufts across each plate proximally, each tuft with up to 20 spinelets, single subpaxilliform tufts distally (*folium*), or tufts of spinelets (*hartmeyeri, pilosa*), or soft paxillar columns and rounded domes, each with up to 50 spinelets (*pompom*); spinelets glassy, acicular to subsacciform; superomarginal plates with central tuft or pompom of spinelets; inferomarginal series projects to form margin, plates bare proximally, prominent marginal tuft of larger spinelets, sometimes on elevations (*folium, pompom*).

Actinal interradial plates in longitudinal series (*folium, pompom*), sometimes oblique (*folium*), or oblique (*hartmeyeri*).

Actinal spines per plate: oral 4–7; suboral 1–10; furrow 3–5, webbed; subambulacral 2–4 or clusters (*pilosa*); adradial actinal plates with complete series of spines; actinal 1–4 or clusters

(*pilosa*), webbed if more than 1; actinal interradial spines subsacciform, thin.

Lacking superambulacral and superactinal plates; distal interradial margin supported by internal contiguous tongue-like projections from abactinal and actinal plates (*folium, pompom*) or from abactinal plates only (*hartmeyeri*).

Distribution. W Atlantic, Florida, Bahamas, West Indies, Caribbean, Brazil; 0–256 m.

Remarks. Molecular data are not available for any species of *Asterinides*, and this review is based on morphology. Rowe (1995) and Rowe and Campbell (1997) considered *Asterinides* to be a valid genus. Verrill (1913) referred *Asteriscus folium* Lütken, *Asteriscus cepheus* Müller and Troschel, 1842 and *Asterina (Asteriscus) modesta* Verrill, 1870 to his new genus *Asterinides*. O'Loughlin (2002) removed *A. modesta* to his new genus *Meridiastera*. *A. cepheus* is removed here from *Asterinides* to *Aquilonastrida*. The genera *Aquilonastrida* and *Asterinides* share many morphological similarities, such as the multiple spinelet tufts per plate in *A. batheri* (*A. folium* also) and paxillar columns in *A. coronata* (*A. pompom* also). But the generic morphological difference evident in this study is the presence of superambulacral and superactinal internal skeletal plates in *Aquilonastrida* and absence in *Asterinides*.

A.M. Clark (1983) considered the paxillar columns on many abactinal plates of *P. pompom* to be of generic significance, but Clark and Downey (1992) noted some similarity between *A. folium* and *P. pompom*. Both papers considered the paxillar columns to be otherwise unknown among Asterinidae but *Aquilonastrida coronata* has similar columns. Their presence in two otherwise well-defined genera, *Asterinides* and *Aquilonastrida* argues against use of paxillar columns as a generic character. *Paxillasterina* is placed in synonymy with *Asterinides*.

The description of *A. folium* by O'Loughlin (2002) was of specimens up to $R = 15$ mm, and is superseded by the descriptive details here based on a specimen with $R = 19$ mm (USNM E28573). The earlier description referred to ad-disc interradial papular spaces, each with two lateral papulae separated by one or two secondary plates. In the larger specimen these spaces have up to three papulae and three secondary plates. Multiple spinelet tufts are evident on the abactinal plates of the larger specimen, but were not evident on smaller specimens. Clark and Downey (1992) discussed differences between *A. folium* and *A. hartmeyeri* recognising separate but similar species. *Asterina hartmeyeri* also belongs to *Asterinides*. *Asterinopsis pilosa* (Perrier, 1881) is assigned here to *Asterinides* since it shares the generic diagnostic morphological characters.

Callopatria Verrill

Figures 2e, 10a–d

Callopatria Verrill, 1913: 480.—A.M. Clark, 1983: 367–372.—Clark and Downey, 1992: 190–191.—A.M. Clark, 1993: 217.

Diagnosis. Rays 5, discrete, narrow basally, long rayed stellate; flat actinally, high convex abactinally, sides of rays close to perpendicular above angular margin; abactinal plate

arrangement irregular on upper rays, plates crescentiform; plates closely covered by numerous glassy spinelets, digitiform to sacciform on primary plates, thin conical pointed on secondary plates; lacking pedicellariae; papular spaces large, numerous papulae and secondary plates; inferomarginal series of plates project only slightly; actinal plates in oblique series; actinal spines digitiform, numerous per plate; interior resinous body lining; series of irregular superambulacral plates; superactinal plates fill interradial angular margin.

Type species. *Patiria bellula* Sladen, 1889 (original designation) (junior synonym of *Patiria granifera* Gray, 1847, by A.M. Clark, 1956).

Other species. *C. formosa* (Mortensen, 1933).

Material examined. *C. granifera*. South Africa, Western Cape Province, NMV F98049 (1).

Description with species variations. Rays 5, interradial margin deeply incurved, rounded proximally, rays discrete, narrow base tapering to rounded end, form long-rayed stellate; body flat actinally, wider actinally than breadth of upper ray, high convex abactinally, sides of rays close to perpendicular above angular margin; size medium, up to $R = 60$ mm (*granifera*); lacking pedicellariae; not fissiparous.

Abactinal surface coarse, irregularly arranged crescentiform plates only (*granifera*); sometimes also enlarged rounded plates distally, mostly bare of spinelets (*formosa*); lacking carinal series of plates; papulate areas extensive; papular spaces large, not clearly bordered, up to about 10 large to small secondary plates and up to about 10 papulae per space; abactinal plates irregularly notched for papulae, each plate with low rounded elevation, some subpaxilliform, closely covered with up to about 60 spinelets, glassy, digitiform to sacciform on primary plates, thin conical pointed on secondary plates; bare plate surface with large glassy convexities; sometimes longitudinal series of plates and papulae evident on sides of rays; series of large subequal superomarginal and inferomarginal plates, covered closely with digitiform spinelets, not in marginal tufts; inferomarginals projecting only slightly at almost right-angular margin.

Actinal plates in oblique series.

Actinal spines per plate: oral 6; suboral 5–6; furrow 4 proximally; subambulacral 3–4; actinal interradial up to 10 (fans proximally, clusters distally); adradial actinal plates with complete series of spines; actinal plates with spine-bearing low domes; interradial spines digitiform.

Superambulacral plates present as irregular series, variable size, sometimes paired or absent, contiguous with superactinals for most of ray; marginal angle filled with numerous superactinal plates; abactinal and actinal plates near margin lacking interior projections, meet at angle; superambulacral and superactinal plates embedded in resinous interior lining.

Distribution. Southern Africa; 0–82 m.

Remarks. Molecular data are not available for either species of *Callopatria*, and this review is based on a morphological examination of a specimen of *C. granifera* and the description of *C. formosa* by Clark and Downey (1992). *Patiria bellula* Sladen, 1889 was designated by Verrill (1913) as type species

of his new genus but it was subsequently assigned to *Parasterina* by H.L. Clark (1923) and Mortensen (1933). However, *Parasterina* is a junior synonym of *Nepanthia*. *Patiria granifera* Gray, 1847 was reassigned to *Asterina* by Perrier (1875), H.L. Clark (1923) and Mortensen (1933). Mortensen (1933) thought it highly probable that *P. bellula* and *P. granifera* were synonyms and A.M. Clark (1956) was more confident. Fisher (1940, 1941) rejected *Callopatria* as a junior synonym of *Patiria* but it was restored to generic status by A.M. Clark (1983), who noted similarities between *Callopatria* and *Nepanthia*.

Callopatria, *Nepanthia*, *Pseudonepanthia* and *Pseudopatiria* are unusual asterinid genera in having discrete narrow rays which are rounded abactinally. They also have irregularly arranged abactinal plates on the upper rays and narrowly or not projecting inferomarginal plates, characters shared with some other genera. *Callopatria* is separated diagnostically by having rays that are not subcylindrical, with a flat actinal surface significantly wider at mid-ray than upper ray breadth, and by a marginal angle supported internally by many superactinal plates.

Cryptasterina Dartnall, Byrne, Collins and Hart

Figures 1 (clade IV, part), 2f, 11a

Cryptasterina Dartnall et al., 2003: 3–4.

Diagnosis. Rays 5, form pentagonal to short rays rounded distally; body with noticeable integument; low convex abactinally; abactinal plates in longitudinal series, deeply notched for papulae, many U-shaped more than crescentiform; longitudinal series of predominantly single papulae along sides of rays; non-papulate interradial areas extensive; few (1–3) papulae per papular space; abactinal spinelets granuliform, spaced over plates; lacking pedicellariae; lacking glassy convexities; superomarginal series prominent, longitudinally subrectangular, inferomarginals predominantly project narrowly; non-plated actinal area distal to oral plates frequently present, not extensive; actinal interradial plates in oblique series; actinal spines short conical, predominantly 1 per plate, rarely 2–3 distally; very small superambulacral plates few, never as series; superactinal plates present, sometimes in multiple plate struts.

Type species. *Asteriscus pentagonus* Müller and Troschel, 1842 (original designation) (junior synonyms: *Patiriella pseudoexigua* Dartnall, 1971 and *Patiriella obscura* Dartnall, 1971, by Dartnall et al., 2003).

Other species. *C. hystera* Dartnall and Byrne, 2003; *C. pacifica* (Hayashi, 1977).

Material examined. *C. hystera*. Paratypes. Queensland, Yeppoon (Statue Bay), NMV F96255 (3). Other material. Statue Bay, F98457 (2); F97057 (6).

C. pentagona. Queensland, Cairns, NMV F96702 (2); Townsville, F97056 (2); F98452 (8); F98453 (1); Bowen (Airlie Beach), F97055 (4), F98454 (2); Mackay, F95959 (7); Hervey Bay, F98456 (2); Kurrimine, F95961 (2); Bingil Bay, F98455 (2).

Description with species variations. Rays 5 (rarely 4 or 6); interradial margin straight to slightly incurved, form pentagonal to short tapered rays rounded distally; body with

noticeable integument; flat actinally, low convex abactinally, sides of rays not steep; size small (*pentagona* up to $R = 17$ mm; *hystera* up to $R = 12$ mm); lacking pedicellariae; lacking actinal gonopores; not fissiparous.

Abactinal surface even; plates low, imbricate, deeply notched for papulae, many U-shaped more than crescentiform; plates in longitudinal series; papular spaces fairly large; papulae predominantly single, large (*pentagona*) or small (*hystera*), up to 3 per space; secondary plates 0–3 per papular space; carinal series of doubly or singly notched plates variably present; longitudinal series of papular spaces along sides of rays; disc variably bordered by 5 radial and 5 smaller interradial plates; abactinal spinelets granuliform, short columnar, spaced over plates; denuded abactinal plates with reticulate glassy ridges, not convexities; marginal plates with abactinal-type spinelets, slightly thinner and longer on inferomarginals; superomarginal series distinctive, longitudinally subrectangular; inferomarginal plates less conspicuous, predominantly project narrowly to form margin.

Actinal interradial plates in oblique series; non-plated actinal area distal to oral plates variably present, not extensive.

Actinal spines per plate: oral 5–6 (proximal separated from distal frequently in *hystera*); suboral 1–2; furrow 2–3 proximally; subambulacral 1; adradial actinal 0–1; actinal interradial predominantly 1 (rarely 2–3 distally); actinal spines short conical.

Small superambulacral plates few, especially distally, lacking series; superactinal plates present, sometimes in multiple plate struts.

Distribution. Tropical Indo-Pacific; NE Australia, Indonesia, Philippines, Solomon Is., Taiwan, Japan; littoral and shallow sublittoral.

Remarks. In the molecular clade IV of Waters et al. (2004), the label *P. pseudoexigua* (Japan) refers to *C. pacifica* and *P. pseudoexigua* (Australia) to *C. pentagona* (following Dartnall et al., 2003). These sister taxa are on a clade separate from *Aquilonastraea*. Hart et al. (2003) added two additional lineages to this clade (*C. hystera* and an undescribed species from Taiwan). Dartnall et al. (2003) erected *Cryptasterina* and provided a morphological diagnosis for the three species. The principal diagnostic characters of *Cryptasterina* seen here are: integument cover; pentagonal to short-rayed form; longitudinal series of plates on rays; granuliform spinelets; predominantly single papulae per space; absence of glassy convexities; prominent longitudinally elongate superomarginal plates; narrowly projecting inferomarginal plates; actinal interradial spines predominantly single in mid-ray; some superambulacral plates present; superactinal plates present. The similarities and differences for *Cryptasterina* and *Aquilonastraea* were discussed under the latter.

Disasterina Perrier

Figures 2g, 5f, 10e–f, 12a–b

Disasterina Perrier, 1875: 289.—Livingstone, 1933: 5–7.—H.L. Clark, 1946: 138.—Spencer and Wright, 1966: U69.—A.M. Clark, 1993: 218.—Liao and Clark, 1995: 131–132.—Rowe, 1995: 35.

Manasterina H.L. Clark, 1938: 157–158.—H.L. Clark, 1946: 139.—A.M. Clark, 1993: 220.—Rowe, 1995: 36. New synonym.

Diagnosis. Rays 5; body thin, covered by thick integument; form medium to long-rayed stellate, rays with wide base, tapering strongly, flat actinally, height low convex; abactinal plates thin, on broad upper rays predominantly irregular in shape, size and arrangement, loosely imbricate or contiguous or not contiguous leaving non-plated spaces; plates on lower rays in few irregular longitudinal series, sometimes weakly notched and crescentiform; interradii thin distally, small non-papulate plates in perpendicular or zig-zag series to margin; papulae few, irregular on rays; abactinal spinelets lacking or rare or few, glassy, sacciform, short or long; superomarginal plates small, not in distinct series; inferomarginal plates project widely, loosely contiguous, with distal fringe of few large sacciform spinelets; actinal interradial plates in oblique series; proximal actinal interradial areas frequently not plated; interradial actinal plates with 1–2 long sacciform spines; superambulacral plates irregularly present mid-ray and distally, lacking complete series; superactinal plates present as single plate struts.

Type species. *Disasterina abnormalis* Perrier, 1875 (monotypy) (junior synonym: *Habroporina pulchella* H.L. Clark, 1921, by Livingstone, 1933).

Other species. *D. ceylanica* Döderlein, 1888; *D. longispina* (H.L. Clark, 1938); *D. odontacantha* Liao, 1980; *D. spinosa* Koehler, 1910.

Material examined. *D. abnormalis*. New Caledonia, AM J5042; Queensland, Cairns, J4947 (2); Hayman I., J5699 (1); J5904 (4); J5957 (1); J7315 (1); Torres Strait, Murray I., Z6748 (1); N Western Australia, Rowley Shoals, WAM Z6749 (2); Scott Reef, Z6753–5 (3).

D. longispina. Western Australia, Houtman Abrolhos, WAM Z6758 (1); Z6760 (2).

D. odontacantha. Fiji, UF 2391 (1); UF 1116 (1); UF, 1874 (1); Guam, UF 1253 (1).

Description with species variations. Body thin, rays 5 (*abnormalis* 5–6); interradial margin deeply incurved, concave or acute proximally, form medium to long-rayed stellate; rays with wide base, tapering to narrowly or widely rounded end; body flat actinally, low convex abactinally; distal interradii wide and thin (*abnormalis*), or narrow and thin, rays rise distinctly from thin margin; body covered with thick integument; size medium (*abnormalis* up to $R = 38$ mm) to small (*spinosa* up to $R = 14$ mm); pedicellariae possibly present (*longispina*); none fissiparous.

Abactinal appearance irregular; abactinal plates on broad upper rays thin, irregular in form, size, arrangement; plates not distinguishable as primary and secondary, intergrade from large to small; plates weakly imbricating or contiguous or not contiguous leaving non-plated spaces on rays; lacking carinal series; plates on lower rays in few irregular longitudinal series; distal thin interradii with small rounded non-papulate plates in irregular series perpendicular or zig-zag to margin; plates on rays sometimes weakly notched for papulae and crescentiform (*spinosa*); papulae on rays only, single, few and sparse, large or small, irregular; disc not regularly bordered (*abnormalis*) or almost regular border (*longispina*, *odontacantha*); low domes sometimes present on abactinal plates (*longispina*); abactinal

plates frequently bare, or with few sacciform spinelets around disc (*abnormalis*), or sometimes with 1–2 spinelets, short proximally, long distally (*odontacantha*), or with 1–4 spinelets variable in form from digitiform to long, pointed or rounded, principally on ends of rays (*longispina*), or with 1–3 long sacciform spinelets proximally and on rays (*spinosa*); clusters of 2–4 undifferentiated spinelets possibly act as pedicellariae interradially (*longispina*); glassy convexities present on abactinal plates (*abnormalis*, *longispina*, *odontacantha*); superomarginal plates small, not in distinct series, bare (*abnormalis*, *longispina*) or with 1 (*odontacantha*) or few long spinelets (*spinosa*); inferomarginal plates project prominently, some elongate and almost entirely projecting (*abnormalis*, *longispina*, *odontacantha*), each plate with transverse distal fringe of 1–6 integument-covered long sacciform spinelets.

Actinal interradial plates in oblique series; proximal actinal interradial areas frequently not plated.

Actinal spines per plate: oral 4–8; suboral 1–3 (*odontacantha* 0); furrow 3–6 proximally, webbed; subambulacral 1–3; adradial bare (*abnormalis*, *odontacantha*) or with spines; actinal 1 or 2 (*spinosa*); interradial actinal spines long sacciform.

Superambulacral plates irregularly present mid-ray and distally (*abnormalis*, *longispina*), lacking complete series; superactinal plates present as single plate struts (*abnormalis*, *longispina*).

Distribution. Indo-West Pacific, South China Sea (Xisha Is), Ceylon, Bay of Bengal (Andaman Is), Indonesia, New Caledonia, Guam, Fiji, northern Australia, western Australia.

Remarks. Molecular data have not been obtained for species of *Disasterina* and the genus is reviewed on morphological grounds. Specimens of *D. ceylanica* and *D. spinosa* were not seen and morphological data were obtained from the original descriptions and figures by Döderlein (1888) and Koehler (1910).

Species previously assigned to *Disasterina* fall into two morphological groups, those close to the type *D. abnormalis* and retained here in *Disasterina*, and *D. leptalaantha* and *D. praesignis* (with junior synonym *D. spinulifera*) which are close to *Tegulaster emburyi* and are removed to *Tegulaster*. *Disasterina* differs from *Tegulaster* in having: body thin and low, not thick and high; abactinal plates thin and loosely contiguous, not thick and imbricating; non-plated abactinal spaces present, not absent; median band of irregular abactinal plates on rays wide, not narrow; distal interradial plates at margin in irregular perpendicular series, not longitudinal and thus crossed angled series; superomarginal plates small and irregular, not large and in distinct series; covering integument thick, not thin. The form and patterns of spinelets and spines are similar in the two genera. *Disasterina* also shares some morphological characters with *Indianastra* gen. nov. below, in particular spination, limited presence of superambulacral plates and presence of series of superactinal plates. The morphological differences between *Disasterina* and *Indianastra* are detailed under the latter.

Manasterina longispina H.L. Clark, 1938 was described from a single specimen and the genus distinguished from *Disasterina* by size, single minute spinelets on some abactinal

plates, long spinelets on rays distally, openly spaced abactinal plates, and absence of non-plated proximal actinal areas. None of these characters is of generic value. The long spinelets on distal ray plates is unique to the species. *M. longispina* is intermediate in size amongst species of *Disasterina*; species of *Disasterina* sometimes have spinelets on abactinal plates; and the extent of non-plated abactinal and actinal body wall varies amongst specimens of *M. longispina* and amongst species of *Disasterina*. *Manasterina* is synonymised here with *Disasterina*. Clusters of 2–4 undifferentiated interradial spinelets with their distal ends angled together and contiguous were observed on preserved *D. longispina* material, and possibly act as pedicellariae.

Livingstone (1933) considered *D. spinosa* to be inappropriately assigned to *Disasterina* but gave no reason. The single long sacciform spinelets on abactinal plates distinguish the species but are not grounds for rejecting its generic placement. *Disasterina ceylanica* Döderlein (1888) was reassigned to *Tegulaster* by Livingstone (1933). *Disasterina* and *Tegulaster* have some common characters but the reassignment is inappropriate.

Material from the University of Florida extends the distribution of *D. odontacantha* from China to Guam and Fiji.

Indianastra O'Loughlin gen. nov.

Figures 2h, 6b, 13a–f

Diagnosis. Rays 5, petaloid to subpentagonal; size small; body thin, integument-covered; abactinal and actinal interradial plates in longitudinal series; abactinal plates deeply notched for papulae, short crescentiform; numerous regular longitudinal series of plates with papulae along sides of rays; abactinal spinelets fine, glassy, inconspicuous, acicular to subsacciform, few to numerous per plate, in tufts or cover over plate, not on high raised ridges or domes, fragile, readily lost; pedicellariae sometimes present over papulae; superomarginal plates with rare spinelets or bare; inferomarginal plates with distal subpaxilliform dense tufts of acicular spinelets, covered by integument; actinal interradial plates in longitudinal series; plates with small clusters of webbed short sacciform spines; lacking superambulacral series of plates, rare single plates distally; superactinal plates as single plate struts.

Type species. *Palmipes sarasini* de Loriol, 1897 (junior synonyms: *Asterina lutea* H.L. Clark, 1938, *Asterina nuda* H.L. Clark, 1921, and *Asterina orthodon* Fisher, 1922 by Rowe, 1995).

Other species. *I. inopinata* (Livingstone, 1933) (junior synonym: *Asterina perplexa* H.L. Clark, 1938, by Rowe, 1995).

Material examined. *I. inopinata*. Holotype, 12 paratypes. Australia, New South Wales, AM J3077. Other material. New South Wales, NMV F93460 (3); Byron Bay, AM J15254 (6);

I. lutea. Paratypes. NW Australia, Broome, AM J6167 (4).

I. orthodon. Hong Kong, BMNH 1983.2.15.116 (1).

I. sarasini. NW Australia, WAM Z6833 (1); Broome, AM J6640 (5); NMV F95802 (2); Queensland, J4123 (1).

Description with species variations. Rays 5, petaloid (rays wide basally, rounded distally, subacute to narrowly rounded junctions) to narrowing rounded to subpentagonal (interradial margin straight to shallow incurved); body integument-

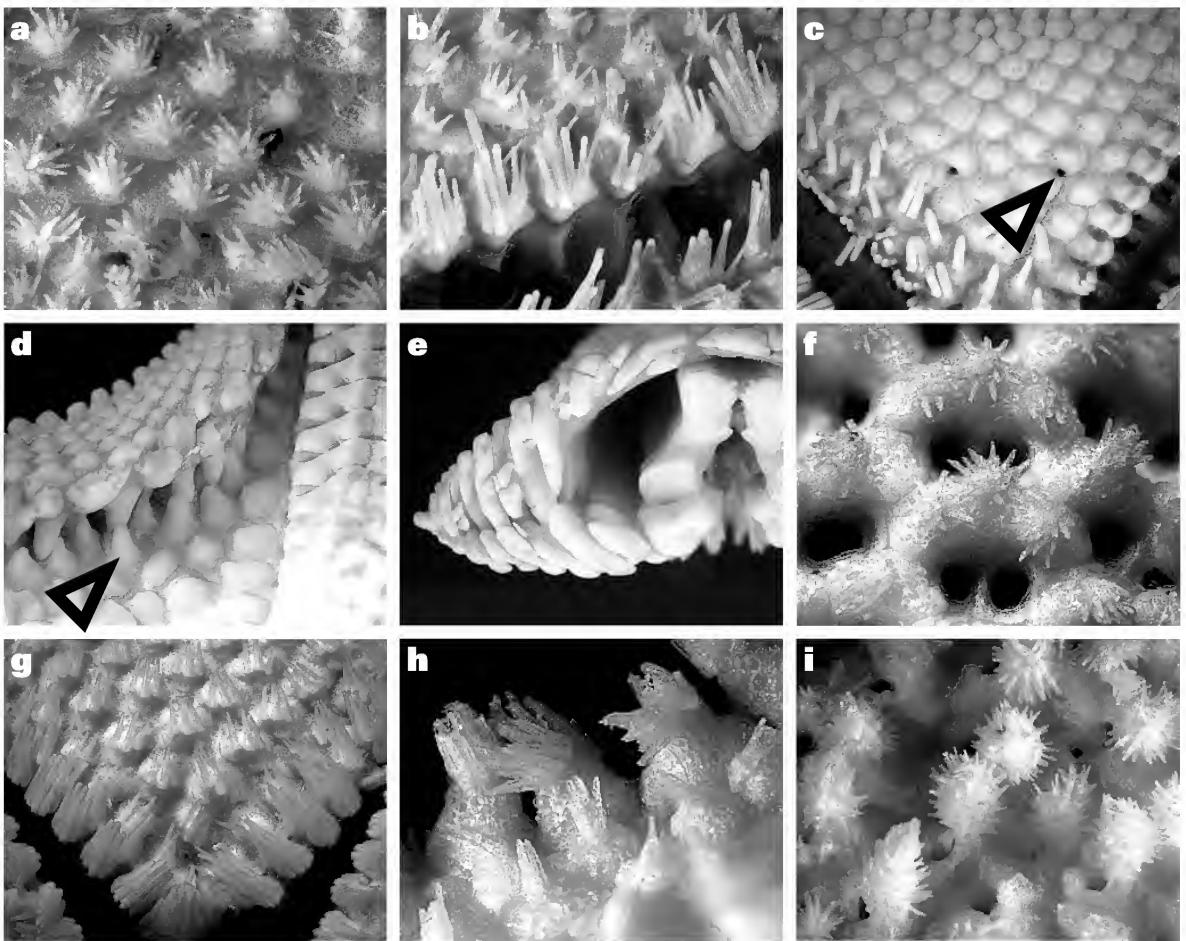


Figure 8. a, *Anseropoda placenta* ($R = 56$ mm, NMV F98043): abactinal plates, spinelets, papulae. b, *Anseropoda rosacea* ($R = 82$ mm, NMV F95811): adambulacral and actinal plates and sacciform spines. c-d, *Asterina gibbosa* ($R = 19$ mm, NMV F45108): c, actinal interradius with gonopores; d, margin supported by internal contiguous projections from abactinal and actinal plates, absence of superambulacral plates. e, *Asterina ocellifera* ($R = 37$ mm, BMNH 1969.12.16.13): margin supported by internal contiguous plate projections, absence of superambulacral and superactinal plates. f-h, *Asterinides folium* ($R = 20$ mm, USNM 28573): f, abactinal spinelet clusters and papulae; g, actinal interradius with sacciform spines; h, marginal plates with spinelets. i, *Asterinides pompom* ($R = 14$ mm, USNM 47866): abactinal plates with paxilliform elevations.

covered, flat actinally, low convex abactinally; size small (both species up to $R = 20$ mm); simple pedicellariae present over papulae, valves short, conical to sacciform, up to 6 valves (*sarasini* only); not fissiparous.

Abactinal appearance dominated by numerous regular longitudinal series of papulae along sides of rays; plates imbricate, deeply notched for papulae, interradially in longitudinal series to margin; papulate areas extensive, papular spaces fairly large, predominantly single large papula per space, up to 4 small papulae and 5 secondary plates per space; up to 6 longitudinal series of papulae along each side of rays; plates on narrow median upper rays irregular, carinal series of plates variably present, doubly notched; abactinal plates with low spinelet-bearing

elevations, on lower rays and proximal interradii predominantly singly notched for papulae, crescentiform only (*inopinata*), additional deep to almost closed pedicellarial notch proximally (*sarasini*); fine, glassy, fragile, inconspicuous, acicular to subsacciform spinelets, sparsely present in apical tufts or numerous in crescentiform cover on projecting proximal edge of plates, spinelets readily lost; glassy convexities (*sarsini*) or reticulations (*inopinata*) on plates; disc variably bordered by continuous series of 5 large radial 5 small interradial plates; superomarginal plates in series, rare spinelets (*inopinata*) or bare (*sarasini*); inferomarginal plates in series, project to form margin, bare proximally, distal subpaxilliform dense tuft of acicular spinelets projects laterally, integument-covered.

Actinal plates in longitudinal series.

Actinal spines per plate (lower numbers in *inopinata*): oral 8–11; suboral 4–9, webbed fan; furrow 5–9 proximally, webbed; subambulacral 3–9; adradial actinal plates with complete series; actinal 2–8 in mid interradius, webbed transverse clusters; actinal interradial spines short sacciform.

Lacking series of superambulacral plates, rare single plates distally (seen in *sarasini* only); margin supported by series of single superactinal plates, and internal tongue-like projections of abactinal plates contiguous with actinal plates.

Distribution. Indian West Pacific, Sri Lanka to southern China, N and E Australia, 0–25 m.

Etymology. From the first word of “Indian West Pacific” and the Latin *astrum* (star), referring to the region of occurrence of this genus (feminine).

Remarks. Molecular data are not available for either species and this review is based on morphological evidence. *Indianastra* shares some morphological characters with both *Disasterina* and *Tegulaster*, in particular the spination, limited presence of superambulacral plates and presence of series of superactinal plates. Morphological differences between *Indianastra* and *Disasterina* are: form petaloid to subpentagonal, or rays discrete; abactinal plates small, of uniform size and imbricate, or irregular in size, form and arrangement and loosely contiguous; abactinal plates deeply, or slightly notched; longitudinal series of papulate plates numerous and regular on rays, or few and irregular on lower sides of rays; abactinal interradial plates in longitudinal series, or series perpendicular to margin; superomarginal series of plates distinct and regular, or reduced and irregular; inferomarginal spinelets acicular, in dense tufts, or few, sacciform and discrete; actinal series of plates longitudinal, or oblique; actinal interradial spines short, in clusters, or long, 1–2. Morphological differences with *Tegulaster* are given under *Tegulaster* below. These morphological differences are the basis for the erection of the new genus.

Jangoux (1985) established a lectotype and paralectotype for *Palmipes sarasini*. Rowe (1995) formalised the synonymies of *I. lutea*, *I. nuda* and *I. orthodon* with *I. sarasini*, which had been suggested by Clark and Rowe (1971). Dartnall (1970, 1980) recorded *A. inopinata* from northern Tasmania, but records were based on material subsequently determined by O’Loughlin as *Meridiastra nigranota* O’Loughlin, 2002 (TM H1330), *M. atypoida* (H.L. Clark, 1916) (TM H841) and *Asterina scobinata* Livingstone, 1933 (TM H1746). The pedicellariae on *I. sarasini* are frequently difficult to detect because the valves are lost or close over the notch and are integument-covered.

***Kampylaster* Koehler**

Kampylaster Koehler, 1920: 136–137.—Fisher, 1940: 250–252.—Bernasconi, 1973: 344.—A.M. Clark, 1993: 220.

Diagnosis. Rays 5; body small, frequently arched, abactinally covered by integument and subgranular spinelets; rays 5, short petaloid; abactinal plates thin, not notched, irregular

arrangement; actinal plates in oblique series; actinal spines per plate few, subglobose; lacking superambulacral and superactinal plates; abactinal and actinal distal interradial plates lacking contiguous internal projections.

Type species. *Kampylaster incurvatus* Koehler, 1920 (original designation).

Material examined. *K. incurvatus*. Syntypes. Antarctica, Adelie Land, AM J3581 (2, A and B).

Description. Rays 5, petaloid to tapered from wide base; margin incurved and subacute interradially; body variably arched; size small, up to R = 15 mm; lacking pedicellariae; brood-protects under body.

Abactinal plates obscured by integument and close uniform cover of coarse subgranular spinelets; abactinal plates on rays large, thin, imbricating, not notched, irregular arrangement; papulae small, inconspicuous, single, irregular over rays (seen from coelomic side by Fisher, 1940; not seen here); abactinal spinelets subgranular, wide base, narrowed waist, convex and spinous distally; superomarginal plates similar to adjacent abactinal plates, covered with granular spinelets, not aligned with inferomarginals; series of thick rounded projecting inferomarginal plates define margin, covered with granular spinelets.

Actinal interradial areas small, series of plates oblique.

Actinal spines per plate: oral 3; suboral 0; furrow 2–3 proximally, webbed; subambulacral 1–2; actinal 1–3; adradial actinal plates with series of shorter spines; actinal spines short, thick, rounded, subglobose distally.

Lacking superambulacral and superactinal plates; abactinal and actinal distal interradial plates meet at an angle, lacking contiguous internal projections.

Distribution. Antarctica, Enderby Land to Scotia Sea; 93–750 m.

Remarks. Molecular data are not available for *incurvatus*, and this review is based on a morphological examination of syntypes and the observations of Fisher (1940). Distinctive diagnostic characters of *Kampylaster* are the integument and granular spinelet cover, irregular arrangement of thin abactinal plates, inconspicuous papulae, absence of a series of superomarginal plates, and absence of superambulacral and superactinal plates.

Koehler (1920) considered *Kampylaster* to be similar to *Tremaster* Verrill, 1880 and referable to the subfamily Tremasterinae. Fisher (1940) rejected the similarity because of the distinctive interradial perforations of *Tremaster*, and considered *Kampylaster* to be closer to *Stegnaster* Sladen, 1889. Additional reasons for rejecting a similarity with *Tremaster* are the quadriradial arrangement of tube feet and vertical furrow spines on adambulacral plates in *Tremaster*.

***Meridiastra* O’Loughlin**

Figures 1 (clade III), 2i, 4c, 5a, 10g–i

Meridiastra O’Loughlin, 2002: 280.—Waters et al., 2004: 874, 875, 877.

Diagnosis. Rays predominantly 5 or 6 or 7 or 8; interradial margin straight or incurved, rays not discrete; flat actinally, low

to high convex abactinally; abactinal plates in longitudinal series along rays, carinal series present for at least part ray length; papulae small, lacking longitudinal series of large papulae along sides of rays; abactinal spinelets granuliform; lacking pedicellariae; abactinal plates with glassy convexities; actinal plates in longitudinal series; actinal spines in mid-interradius digitiform or tapering or conical, 1–3; lacking superambulacral and superactinal plates, distal interradial margin supported by contiguous interior projections from abactinal and actinal plates.

Type species. *Asterina atypoida* H.L. Clark, 1916 (original designation).

Other species. *M. calcar* (Lamarck, 1816); *M. fissura* O'Loughlin, 2002; *M. gunnii* (Gray, 1840) (junior synonym: *Patiriella brevispina* H.L. Clark, 1938, by O'Loughlin et al., 2003); *M. medius* (O'Loughlin et al., 2003); *M. modesta* (Verrill, 1870) (junior synonym: *Asterina agustincasoi* Caso, 1977 by O'Loughlin, 2002); *M. mortenseni* (O'Loughlin et al., 2002); *M. nigranota* O'Loughlin, 2002; *M. occidens* (O'Loughlin et al., 2003); *M. oriens* (O'Loughlin et al., 2003); *M. rapa* O'Loughlin, 2002.

Material examined. See O'Loughlin (2002), O'Loughlin et al. (2002, 2003).

M. calcar: Australia, Victoria, Cape Paterson, NMV F73126 (4).

Description with species variations. Rays predominantly 5 (*atypoida*, *modesta*, *mortenseni*, *nigranota*, *rapa*), or 6 (*gunnii*, *medius*, *occidens*, *oriens*), or 7 (*fissura*), or 8 (*calcar*); interradial margin straight to incurved, rays sometimes distinct, narrowly rounded to pointed distally; integument noticeable; size medium (*gunnii* up to R = 56 mm) to very small (*rapa* up to R = 6.0 mm); pedicellariae absent; gonopores actinal (*nigranota*) or abactinal; fissiparity in one species (*fissura*).

Abactinal plates in longitudinal series; carinal series present to variable extent; abactinal appearance of two types, with papulate areas extensive, papular spaces large with numerous small papulae and secondary plates, plates distinctly doubly or singly notched with projecting proximal edge crescentiform except in distal plates (*calcar*, *gunnii*, *medius*, *mortenseni*, *occidens*, *oriens*), or with papulate areas small, papular spaces small with few small papulae and secondary plates, plates not distinctly notched and projecting proximal edge not crescentiform (*atypoida*, *fissura*, *modesta*, *nigranota*, *rapa*); lacking distinct longitudinal series of large papulae along sides of rays; disc variably distinct with border of continuous radial and interradial plates; abactinal plates sometimes with low spinelet-bearing elevation; cleared abactinal plates with glassy convexities; abactinal spinelets over projecting anterior edge of plates, not in tufts, granuliform, and stout, opaque and firmly attached (*calcar* group above) or fine, glassy and weakly attached (*atypoida* group above); series of subequal, spinelet-covered, superomarginal and inferomarginal plates; margin formed by projecting inferomarginal plates.

Actinal plates in longitudinal series, sometimes oblique (*atypoida*).

Actinal spines per plate: oral 4–7; suboral 0–2; furrow 2–5 proximally, webbed; subambulacral 1–3; actinal 1–3 in mid-interradius, up to 4 distally; adradial row of actinal plates with variably complete series of spines; interradial actinal spines thick, bulbous to short tapered to conical to digitiform.

Lacking superactinal and superambulacral plates; interradial margin supported by contiguous internal projections of the abactinal and actinal plates.

Distribution. Southern Australia, New Zealand, central and eastern South Pacific, Mexico, Panama; 0–59 m.

Remarks. *Meridiastra*, erected by O'Loughlin (2002) on morphological evidence only, is supported by the molecular phylogenetic relationships of the nine species included in clade III of Waters et al. (2004). The key morphological features of these nine species are: straight to shallow incurved interradial margins, rays not discrete; longitudinal series of abactinal plates; granuliform abactinal spinelets; lack pedicellariae; presence of conspicuous glassy convexities on plates; actinal plates in longitudinal series; low numbers of thick, tapering actinal spines; lack superambulacral and superactinal plates; have internal contiguous projections of distal interradial abactinal and actinal plates supporting the margin. Most of the species of *Meridiastra* were previously assigned to *Patiriella* which has irregularly arranged abactinal plates, actinal plates in predominantly oblique series, and superambulacral and superactinal plates present. The molecular phylogeny supports the separation of *Meridiastra* and *Patiriella*. *Meridiastra* is closest morphologically to *Asterina* which also lacks internal skeletal plates but which has more discrete rays, opaque spinelets which are elongate, and actinal plates in predominantly oblique series. The molecular phylogeny also supports the separation of *Meridiastra* (Indo-Pacific) from *Asterina* (NE Atlantic). The morphological similarities of these two genera could reflect convergent evolution, or the retention of ancestral character states, or a true sister relationship; the phylogeny of Waters et al., 2004 was uninformative in this regard.

Molecular clade III provides evidence of two groups of closely related species within the clade: *M. gunnii*, *M. oriens*, *M. medius* and *M. occidens*; and *M. fissura*, *M. nigranota* and *M. atypoida*. These closer molecular relationships are reflected in the morphological description above, where these two sets fall within the *M. calcar* and *M. atypoida* groups. Our decision to combine the two groups into a single genus is subjective but supported by the significant internal skeletal similarities.

Nepanthia Gray

Figures 2j, 4f, 6c, 14a–c

Nepanthia Gray, 1840: 287.—Sladen, 1889: 386–387.—Verrill, 1913: 480.—Fisher, 1940: 270–271.—Fisher, 1941: 451–455, figs, 20–22, pl. 70 fig. 2.—Spencer and Wright, 1966: U69.—Rowe and Marsh, 1982: 93.—A.M. Clark, 1983: 370.—A.M. Clark, 1993: 220.—Liao and Clark, 1995: 132–133.—Rowe, 1995: 36–37.—McKnight (in Clark and McKnight), 2001: 158.

Asterina (*Nepanthia*) Perrier, 1875: 320.

Diagnosis. Rays 4–7, subcylindrical, to varying degrees flat actinally with distinct to slight marginal edge; plates on upper rays irregular in arrangement; secondary plates present; abactinal and actinal interradial plates with dense clusters of thick or thin glassy spinelets, frequently on spinelet-bearing elevations; pedicellariae present; glassy convexities on plates; infero-

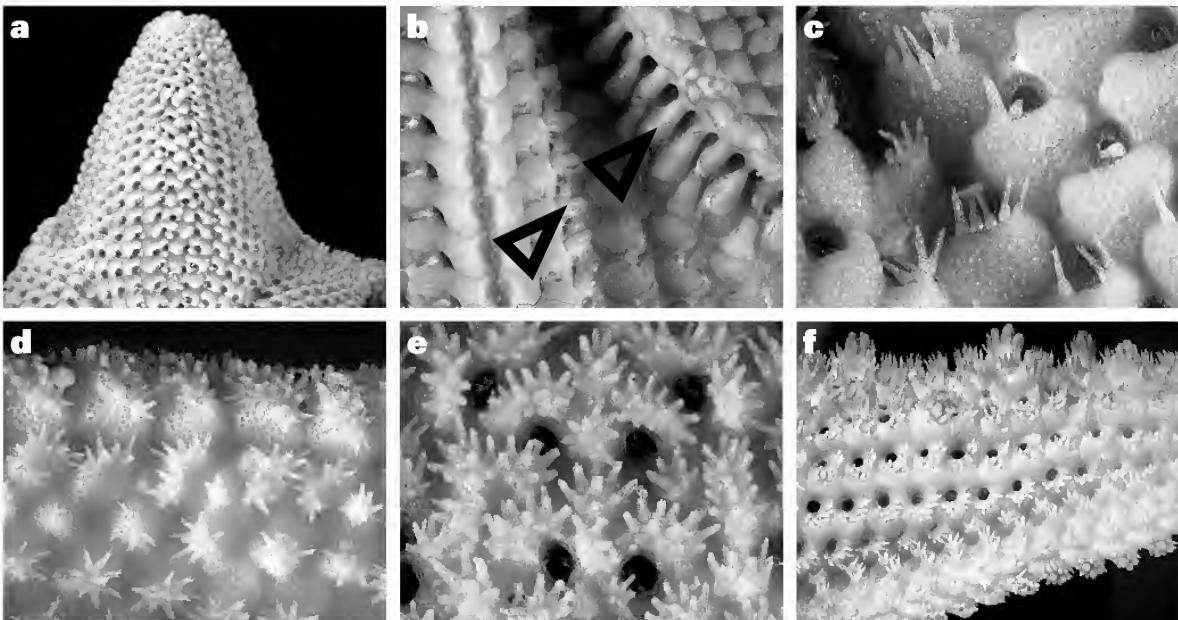


Figure 9. a-d, *Aquilonastraea cepheus*: a, cleared ray ($R = 17$ mm, NMV F95793); b, internal superambulacrals (left arrow) and superactinal (right arrow) plates ($R = 22$ mm, WAM Z6778); c, cleared abactinal plates with some sacciform spinelets ($R = 17$ mm, NMV F95793); d, abactinal margin ($R = 22$ mm, WAM Z6778). e, *Aquilonastraea batheri* ($R = 19$ mm, NMV F97441): abactinal carinal plates with tufts of spinelets. f, *Aquilonastraea coronata* ($R = 22$ mm, NMV F95796): side of ray with paxilliform elevations on upper ray.

marginal plates projecting slightly; oblique series of actinal plates variably evident; furrow spines 6 and more per plate; actinal spines predominantly thin, glassy, sometimes sacciform; superambulacrals, transactinal and superactinal plates present, embedded in interior resinous lining in most species.

Type species. *Nepanthia maculata* Gray, 1840 (restriction by Perrier, 1875; subsequent designation by Verrill, 1913).

Other species. *N. belcheri* (Perrier, 1875) (junior synonym: *N. variabilis* H.L. Clark, 1938 by Rowe and Marsh, 1982); *N. crassa* (Gray, 1847); *N. fisheri* Rowe and Marsh, 1982; *N. pedicellaris* Fisher, 1913.

Material examined. *N. belcheri*. Queensland, Magnetic I., NMV F97721 (1); Western Australia, Dampier, F95806 (1); Exmouth Gulf, F95805 (1).

N. crassa. Western Australia, Fremantle, AM J6165 (1); Ludlow Reef, J7418 (1).

N. fisheri. Timor Sea, AM J12649 (1).

N. maculata. Australia, Timor Sea, AM J13918 (2); Gulf of Carpentaria, J7404 (2); J10536 (1); J13063 (1).

N. pedicellaris. Holotype. Philippines, USNM 32643.

N. variabilis. Paratypes. Western Australia, Broome, AM J6187 (4).

Description with species variations. Rays 4–7, elongate, subcylindrical, equal or unequal lengths, tapering strongly (*fisheri*, *pedicellaris*) or slightly; large (*maculata* up to $R = 94$ mm) to small (*pedicellaris* up to $R = 23$ mm); integument variably evident; flat actinally, distinct to slight edge at margin; pedicellariae present, 2-valve (*fisheri*, *maculata*, *pedicellaris*) or multi-valve (*belcheri*, *crassa*); fissiparous (*belcheri*) or not.

Abactinal plates strongly imbricating, projecting proximal edge creating uneven surface, irregularly arranged on upper rays, in regular longitudinal sloping series on sides of rays; plates predominantly irregular in shape (*crassa*) or notched (*belcheri*, *fisheri*, *maculata*, *pedicellaris*), with spinelet-bearing curved elevations above notch (*belcheri*, *pedicellaris*) or raised ridges (*fisheri*, *maculata*) or domes (*crassa*), lower surface with glassy convexities; disc variably bordered; papulate areas extend to near margin; papular spaces with 1–2 large papulae and 1–8 secondary plates per space; spinelets thin, glassy, variably sacciform (*fisheri*, *maculata*, *pedicellaris*), some splay-pointed distally (*belcheri*, *crassa*), up to more than 40 per plate; variably regular superomarginal plates, inferom marginal series of plates project slightly at margin, covered with spinelets.

Actinal plates with spine-bearing elevations, variably in oblique series.

Actinal spines per plate: oral 9–10; suboral about 10–26, tall and short; furrow 6–10; subambulacrals 6–20; complete series of adradial actinal spines; interradial actinal 4–6 or dense subpaxilliform clusters, glassy, thin (*belcheri*), thick and thin (*crassa*), sometimes sacciform (*fisheri*, *maculata*, *pedicellaris*).

Superambulacrals, transactinal and superactinal plates present, embedded in internal resinous lining or not (*pedicellaris*).

Distribution. N, S, E and W Australia, Lord Howe I., Indonesia, Timor Sea, New Guinea, W Indonesia, Philippines, Vietnam, Burma, Mergui Archipelago, 0–123 m.

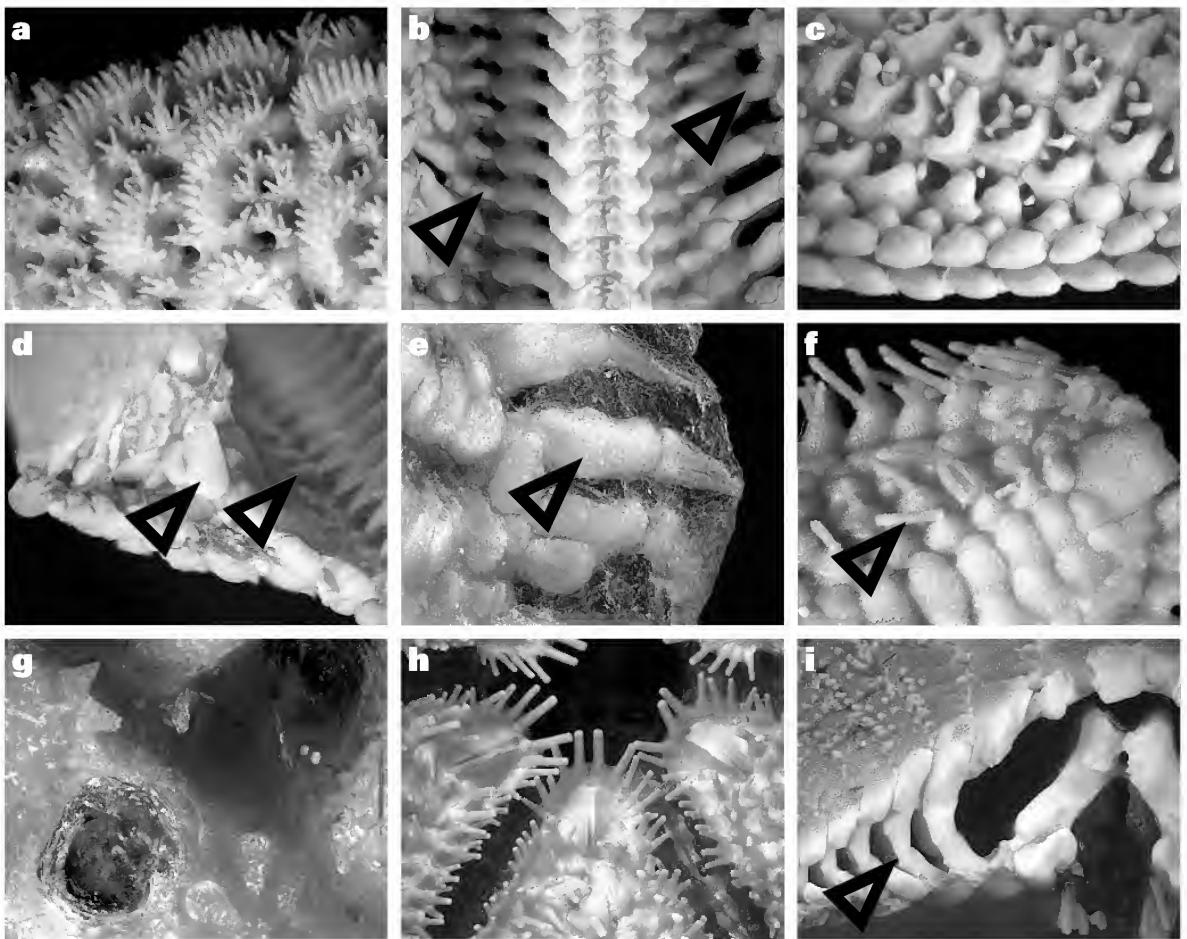


Figure 10. a–d, *Callopeltaria granifera* (R = 50 mm, NMV F98049); a, mid-ray abactinal primary and secondary plates, spinelets and papulae; b, internal superambulacral (left arrow) and superactinal (right arrow) plates; c, cleared lower lateral ray, with marginal plates, glassy convexities, papulae and secondary plates; d, section through ray showing superactinal (left arrow) and superambulacral (right arrow) plates. e, *Disasterina abnormalis* (R = 38 mm, WAM Z6749); integument-covered inferomarginal plate (arrow) with two distal sacciform spinelets. f, *Disasterina longispina* (R = 20 mm, WAM Z6760); abactinal tip of ray, with margin and long upper ray spinelet (arrow). g, *Meridiastra atyphoida* (R = 12 mm, NMV F87166); minute abactinal conical spinelets. h, *Meridiastra occidens* (R = 22 mm, NMV F73186); proximal actinal interradius, with oral spines. i, *Meridiastra gunni* (R = 40 mm, NMV F73248); interradial margin supported by contiguous projections from abactinal and actinal plates, absence of superambulacral and superactinal plates.

Remarks. Molecular data are not available for any species of *Nepanthia* and this review is based on a morphological examination. Six species previously assigned to *Nepanthia* are removed to *Pseudonepanthia*. The morphological characters which distinguish *Nepanthia* from *Pseudonepanthia* are: rays flat actinally, with a marginal edge; presence of secondary plates, pedicellariae and glassy convexities; furrow spines six and more per plate; presence of transactinal and superactinal plates.

Nepanthia pedicellaris Fisher, 1913 was referred by Fisher (1919) to *Asterinopsis* Verrill, 1913 (a nomen dubium). We return it to *Nepanthia*.

Paranepanthia Fisher

Figures 1 (clade I), 2k, 5c, 15a–c

Paranepanthia Fisher, 1917: 172.—Fisher, 1919: 419.—H.L. Clark, 1946: 136.—Spencer and Wright, 1966: U69.—A.M. Clark, 1993: 222.—Rowe, 1995: 39.—McKnight (in Clark and McKnight), 2001: 160.—Waters et al., 2004: 874, 875, 877.

Diagnosis. Rays 5, medium length, wide basally, pointed or rounded distally; flat actinally, rays elevated to low; abactinal and actinal interradial plates with subpaxilliform dense clusters of acicular subsacciform spinelets; abactinal plates mostly irregular on upper rays, mostly series perpendicular to

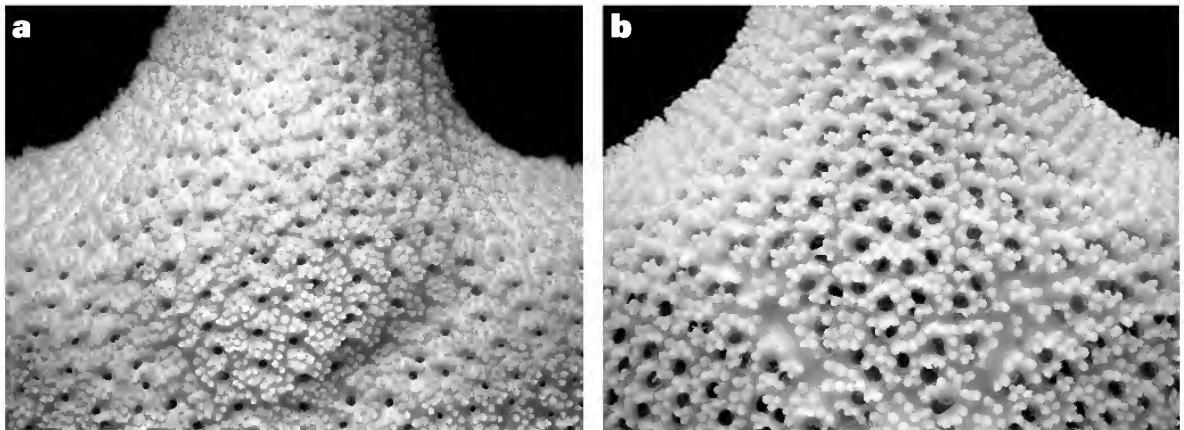


Figure 11. a, *Cryptasterina hysteria* ($R = 11$ mm, NMV F98457): abactinal surface with small papulae and granuliform spinelets. b, *Parvulastra exigua* ($R = 10$ mm, NMV F98062): abactinal surface with larger papulae and granuliform spinelets.

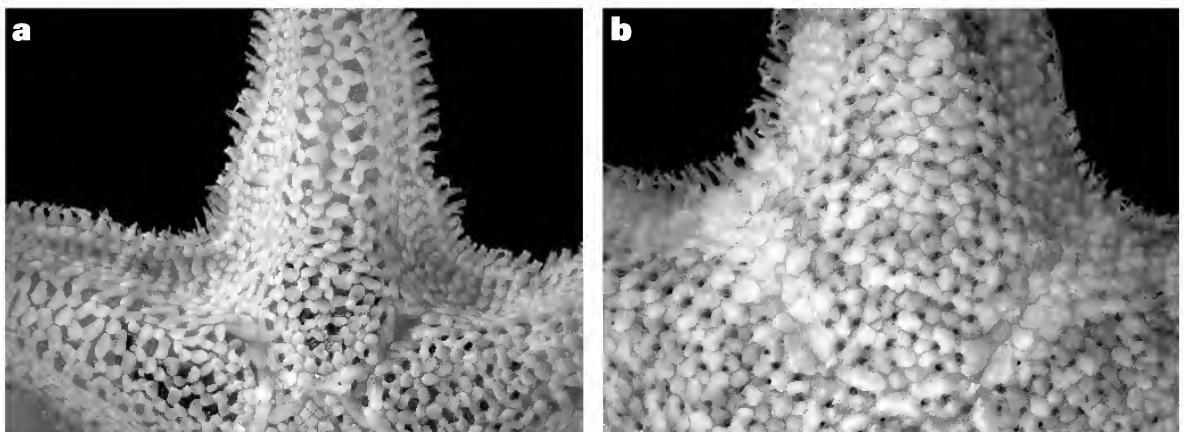


Figure 12. Abactinal views of *Disasterina* species. a, *Disasterina abnormalis* ($R = 11$ mm, WAM Z6753). b, *Disasterina longispina* ($R = 25$ mm, WAM Z6760).

margin in interradial; marginal plates subequal, in regular series, with dense tufts of spinelets, inferomarginals project prominently; actinal interradial plates in oblique series; superambulacral plates absent; superactinal plates present as multiple struts.

Type species. *Nepanthia platydisca* Fisher, 1913 (original designation).

Other species. *P. aucklandensis* (Koehler, 1920); *P. grandis* (H.L. Clark, 1928) (junior synonym *Asterinopsis praetermissa* Livingstone, 1933, by Rowe, 1995).

Material examined. *P. aucklandensis*. New Zealand, Auckland I., AM J5160 (2); J6023 (1).

Asterinopsis praetermissa. Holotype. Australia, New South Wales, Port Jackson, AM J4793.

Nepanthia platydisca. Holotype. Indonesia, 377 m, USNM 32644.

P. grandis. Australia, Victoria, NMV F72887 (1); Bass Strait, F98044 (1); South Australia, F73976 (4).

Description with species variations. Rays 5, interradial margin deeply incurved, rays distinct, ends of rays rounded (*aucklandensis*, *grandis*) or pointed (*platydisca*); body flat actinally, rays elevated or low (*platydisca*); distal interradial body thin (actinal to abactinal) or not (*aucklandensis*), area of non-papulate plates wide or not (*aucklandensis*); size medium (*grandis* up to $R = 65$ mm) to small (*aucklandensis* up to $R = 22$ mm); lacking pedicellariae; none fissiparous; gonopores abactinal.

Abactinal plates imbricate, distinct radial and interradial ‘fields’, plates on upper rays irregular in size, shape, arrangement (except *aucklandensis* with regular proximal carinal and upper ray series, and crescentiform plates), up to 3 fairly irregular longitudinal series along each side of rays; papular spaces large, with numbers of small papulae, variable numbers of secondary plates; interradial series of small plates perpendicular to margin (except longitudinal series in *aucklandensis*); disc not bordered or variably bordered (*aucklandensis*); abactinal plates with high (*grandis*) or low (*aucklandensis*, *platydisca*) spinelet-

bearing domes or ridges; glassy convexities on plates present (*aucklandensis*) or not (*grandis*, *platydisca*); subpaxilliform tufts of many acicular subsacciform spinelets; superomarginal and inferomarginal plates in distinct series, subequal; both series with spinelet-bearing domes and subpaxilliform dense tufts of acicular spinelets; inferomarginals define acute margin, projecting plates with narrowed waist (*aucklandensis*, *grandis*) or not (*platydisca*).

Actinal plates in oblique series; plates with high (*grandis*, *platydisca*) or low (*aucklandensis*) spine-bearing domes.

Actinal spines per plate: oral 8–12; suboral tufts or transverse series; furrow 7–10, webbed; subambulacral dense tufts; adradial and actinal interradial dense subpaxilliform tufts (up to about 40 spines); actinal interradial spines acicular subsacciform.

Lacking superambulacral plates; numerous superactinal plates in multiple plate struts; distal interradial margin supported by angled contiguous abactinal and actinal plates (*grandis*, *platydisca*), lacking internal projections (except *aucklandensis* with internal tongue-like projections from abactinal plates).

Distribution. E and S Australia, Indonesia, subantarctic New Zealand; 0–377 m.

Remarks. Three species cluster together in clade I of Waters et al. (2004). One of these is a species that has been assigned to *Paranepanthia* in the past and one is undescribed. The molecular evidence that *Asterina aucklandensis* is also a member of this clade is supported by morphological criteria. All three species of *Paranepanthia* were examined and the morphological integrity of the genus confirmed. *Paranepanthia* is characterised by the unique combination of subpaxilliform dense clusters of acicular spines and spinelets on the plates, absence of superambulacral plates, and presence of superactinal plates. *Paranepanthia rosea* has been removed to *Aquilonastera*.

Parvulastra O'Loughlin gen. nov.

Figures 1 (clade V), 21, 4a–b, 5b, e, 11b, 16a–d

Diagnosis. Rays 5, pentagonal to subpentagonal; noticeable integument; carinal series variably present; abactinal plates broadly notched for papulae, crescentiform more than U-shaped; papulate areas extensive, papulae large or small, a few per space; secondary plates a few per space; abactinal spinelets clustered or spread, not paxilliform; spinelets granuliform or digitiform or thin pointed; lack pedicellariae; superomarginal and inferomarginal plate series predominantly subequal; frequently extensive non-plated actinal area distal to oral plates; actinal interradial plates in oblique series; actinal interradial plates with frequently 2 spines mid-ray to distally, spines digitiform to conical; superambulacral plates present to varying extents, superactinal plates always present.

Type species. *Asterias exigua* Lamarck, 1816.

Other species. *P. calcarata* (Perrier, 1869); *P. dyscrita* (H.L. Clark, 1923); *P. parvivipara* (Keough and Dartnall, 1978); *P. vivipara* (Dartnall, 1969).

Material examined. *P. calcarata*. Juan Fernandez I., NMV F96703 (1); F96704 (1); F97445 (1); F97449 (1).

P. dyscrita. South Africa, False Bay, TM H800 (1); H854 (1); Jeffrey's Bay, NMV F98059 (3).

Patiriella exigua (Lamarck, 1816). Neotype (by Dartnall, 1971). South Africa, False Bay, TM H508. Other material. Cape Town, NMV F98062 (4); Durban, F98061 (4); Jeffrey's Bay, F97450 (5); Saint Helena, F98060 (4); Amsterdam I., F98063 (2); Australia, Victoria, Apollo Bay, F97054 (6); Gabo I., F73079 (9); Port Arthur, F97451 (12).

P. vivipara. Australia, SE Tasmania, NMV F77984 (3).

P. parvivipara. South Australia, Eyre Peninsula, NMV F97720 (3).

Description with species variations. Rays predominantly 5; interradial margin straight to slightly incurved, form pentagonal to subpentagonal; noticeable integument; flat actinally, low convex abactinally, size small (*dyscrita* up to $R = 24$ mm) to very small (*parvivipara* up to $R = 3$ mm); lacking pedicellariae; 2 smallest viviparous (*parvivipara*, *vivipara*); none fissiparous; gonopores abactinal (*calcarata*, *dyscrita*) or actinal (*exigua*).

Abactinal surface appearance granular, upper ray plates with regular carinal series except proximally (*calcarata*, *dyscrita*, *exigua*), or irregular (*parvivipara*, *vivipara*); plates in longitudinal series; plates broadly notched for papulae, crescentiform more than U-shaped; papulate areas extensive, non-papulate interradial areas not extensive, papular spaces large, a few papulae and secondary plates per space; papulae large (*exigua*, *parvivipara*, *vivipara*) or small (*calcarata*, *dyscrita*); disc variably bordered by series of 5 large radial and 5 small interradial plates; abactinal plates with raised spinelet-bearing elevations (*calcarata*) or not; abactinal spinelets in splayed clusters (*calcarata*) or fairly close cover over plates; spinelets both digitiform on primary plates and pointed on secondary and distal interradial plates (*calcarata*), or granuliform globose (*dyscrita*), or short columnar (*exigua*, *parvivipara*, *vivipara*); glassy convexities and reticulations variably evident on denuded plates; superomarginal and inferomarginal series of predominantly subequal plates; typically widely projecting inferomarginal plates define margin, with proximal abactinal-type spinelets, distal fringe of thinner and longer spinelets.

Actinal interradial plates in oblique series; actinal proximal areas of non-plated body wall frequently extensive.

Actinal spines per plate: oral 2 tall, 3–5 short sometimes grouped separately with distalmost frequently longest; suboral 1–2, thick; furrow 2 short, thin; subambulacral 1 tall, thick; adradial actinal spines present (*dyscrita*) or few (*vivipara*) or absent (*calcarata*, *exigua*); actinal interradial frequently 2 midray to distally; actinal interradial spines digitiform (*dyscrita*) or pointed or short conical.

Superambulacral plates present as series (in large *dyscrita*), or rare single, or distal only plates; superactinal plates present as single or multiple-plate series (neither seen in the pedomorphic *parvivipara*).

Distribution. Southern Pacific Ocean, southern Australia, southern Indian Ocean, southern Africa, SE Atlantic Ocean; 0–10 m.

Etymology. From the Latin *parvulus* (very small) and *astrum* (star), referring to the small to very small species of the genus (feminine).

Remarks. Four species previously included in *Patiriella* belong to a monophyletic clade V in Waters et al.'s (2004) analysis. They share a consistent morphology characterised by: subpentagonal form; longitudinal series of abactinal plates on rays; oblique series of actinal plates; granuliform and digitiform spinelets; a few papulae per space; and superambulacral and superactinal plates. The clade warrants generic rank. *Asterina dyscrita* shares these morphological characters and is assigned to the genus on this basis.

Morphologically, *Parvulastra* is similar to *Cryptasterina* and *Patiriella*. Waters et al.'s cladogram suggests that these three genera are not closely related on molecular grounds. Either the similar morphological characters have remained stable while divergence has occurred in characters not considered, or there is strong morphological convergence among the three unrelated genera, or the molecular data are unreliable at levels more basal than inter-species. Nevertheless, the genera can be differentiated by morphological characters. *Cryptasterina* is differentiated by predominantly single papulae per space, elongate superomarginal plates, narrowly projecting inferomarginal plates, and single mid-actinal spines. The characters which differentiate *Patiriella* are listed under that genus.

Patiria Gray

Figures 1 (clade II), 3a, 4d, 15d–f

Patiria Gray, 1840: 290.—Gray, 1847: 82–83.—Gray, 1866: 16.—Sladen, 1889: 384.—Verrill, 1913: 480, 482.—Verrill, 1914: 263–264.—Fisher, 1919: 410.—Fisher, 1940: 269.—Fisher, 1941: 451–455, pl. 70 fig. 1.—Spencer and Wright, 1966: U69.—Bernaconi, 1973: 336.—Clark and Courtman-Stock, 1976: 78.—Campbell and Rowe, 1997: 131, 135.—Dartnall et al., 2003: 12.

Diagnosis. Rays 5, medium to short-rayed stellate, not pentagonal, rays pointed distally; noticeable integument; flat actinally, convex abactinally; primary abactinal plates strongly or weakly crescentiform, close subpaxilliform cover of short, thick or thin, columnar or subglobose spinelets, not acicular or sacciform, secondary plates with smaller spinelets; lacking pedicellariae; papulate areas extensive, papular spaces large, numerous secondary plates and papulae per papular space; series of spinelet-covered superomarginal and inferomarginal plates, spinelets on thick rounded inferomarginals extend onto actinal surface; actinal plates in oblique series; actinal spines in mid-interradius thick, combs of 4–6; lacking complete superambulacral series of plates, present distally; superactinal plates present, multiple plate struts in larger specimens.

Type species. *Patiria coccinea* Gray, 1840 (original designation) (junior synonym of *Asterias miniata* Brandt, 1835 mistakenly recorded from South Africa, synonymy by Mortensen, 1933).

Other species. *P. chilensis* (Lütken, 1859); *P. pectinifera* (Müller and Troschel, 1842).

Material examined. *P. chilensis*. Chile, Arica, NMV F95674 (3); Peru, NMV F97442 (1); F97443 (1).

P. miniata. California, NMV F97444 (1); F97448 (1); F98040 (1); F98041 (1); F98042 (1).

P. pectinifera. Japan, Toyama Bay, NMV F95672 (7); F95673 (2).

Description with species variations. Rays 5 (sometimes 6); noticeable integument; interradial margin incurved, medium to short-rayed stellate, not pentagonal, rays distally pointed to narrowly rounded; flat actinally, convex abactinally, body thick, sides of rays steep; size large (*miniata* up to R = 85 mm) to small (*chilensis* up to R = 21 mm); lacking pedicellariae; gonopores abactinal.

Abactinal surface uneven; appearance dominated by subpaxilliform spinous primary plates, variably crescentiform, and large papular spaces with smaller spinous secondary plates; plates in irregular longitudinal series; papulate areas extensive, to near distal end of rays and near margin; papular spaces with numerous secondary plates and small papulae (up to about 25 of each); lacking longitudinal series of large single papulae along sides of rays; disc weakly bordered by discontinuous series of larger radial and smaller interradial plates; abactinal primary plates variably crescentiform or oval or round or linear, with spinelet-bearing elevations, variably with 1 or more notches for papulae; carinal series variably present, plates separated by large papular spaces; cleared plates with glassy convexities prominent (*chilensis*) or not; abactinal spinelets opaque, short columnar, thick (*miniata*), or subglobose (*pectinifera*), or thin (*chilensis*), in section round (*chilensis*, *pectinifera*) or square (*miniata*); spinelets on primary plates in subpaxilliform transverse or round clusters, very close and palisade-like (*miniata*) or slightly more spaced (*chilensis*, *pectinifera*), on secondary plates shorter, splayed; series of subequal superomarginal and inferomarginal plates, covered with spinelets; spinelets on thick rounded inferomarginals extend onto actinal surface; projecting inferomarginals form acute margin.

Actinal plates in oblique series.

Actinal spines per plate: oral 5–7; suboral 2–7; furrow 3–4 proximally; subambulacral 2–4; adradial actinal plates fully spinous; actinal interradial in combs of 3–8 proximally, 4–6 distally; actinal interradial spines conical to digitiform to spatulate.

Superambulacral plates not present as series, sometimes present in mid-ray (*chilensis*) or absent (*miniata*, *pectinifera*), present distally linking with actinal or superactinal or abactinal plates; superactinal plates present, multiple plate struts in larger specimens.

Distribution. N and E Pacific Ocean, Japan, Alaska, California, Peru, Chile; 0–300 m.

Remarks. Fisher (1908, 1911), Mortensen (1933), Hayashi (1940) and A.M. Clark (1983) considered *Patiria* to be a junior synonym of *Asterina*, while Verrill (1913), Fisher (1919, 1940, 1941) and Clark and Courtman-Stock (1976) maintained *Patiria* as a valid genus. Verrill (1914) considered it to be significant that *Patiria* lacked pedicellariae. Spencer and Wright (1966) listed *Callopatiria* and *Enoplopatiria* as junior synonyms of *Patiria*. Hayashi (1973) considered *Patiria* and *Patiriella* to be junior synonyms of *Asterina*. A.M. Clark

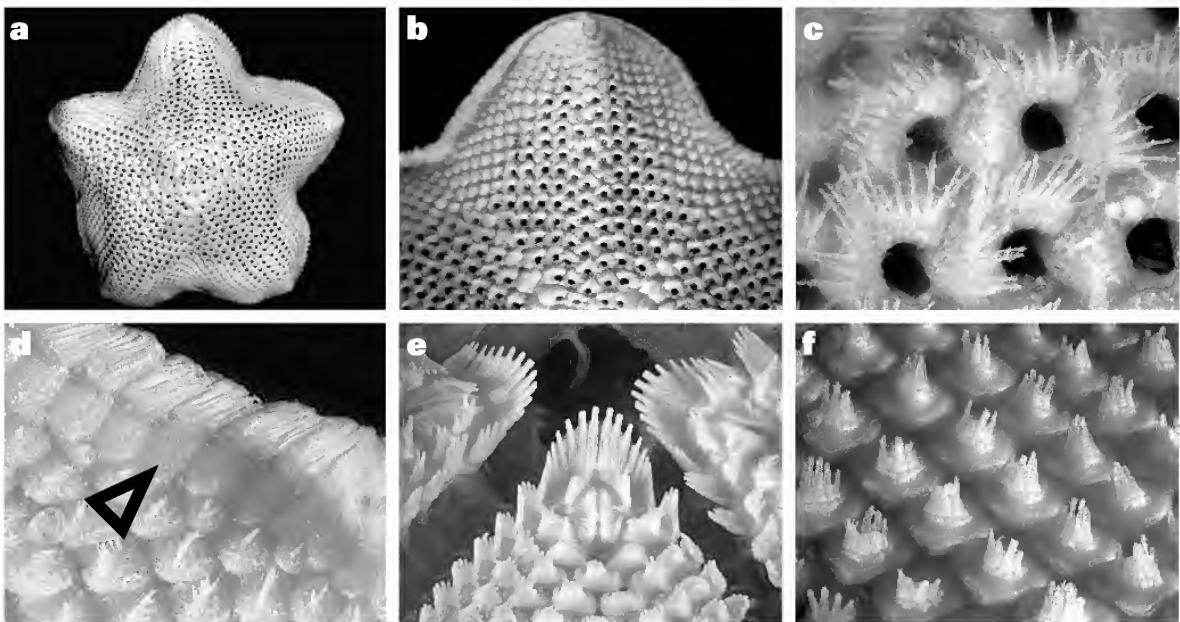


Figure 13. a, *Indianastera inopinata* ($R = 19$ mm, AM J15254): cleared abactinal surface. b–f, *Indianastera sarasini* ($R = 14$ mm, WAM Z6835): b, abactinal ray; c, abactinal elongate subsacciform spinelets, and papulae; d, bare superom marginal plates, and tufts of inferom marginal spinelets; e, oral and proximal actinal spines; f, actinal plates and spines.

(1983), Clark and Downey (1992) and A.M. Clark (1993) considered *Enoplopatiria* and *Patiria* to be junior synonyms of *Asterina*. Campbell and Rowe (1997) “accepted the separate generic status [of *Patiria*] until the matter is more clearly resolved”.

Waters et al. (2004) found that the three species of *Patiria*, including the type species, constituted a single clade (II). They confirmed an earlier result, based also on molecular data (Hart et al., 1997), that confirmed the type and one of the species to be sister taxa. Together there is strong molecular evidence for the generic status of *Patiria*, remote from *Asterina* and *Patiriella*. Morphologically, *Patiria* is distinguished from *Asterina* by the presence of superambulacral and superactinal plates, and from *Patiriella* by the discrete rays, dense subpaxilliform clusters of granuliform spinelets, and more numerous actinal interradial spines.

Patiriella Verrill

Figures 1, 3b, 16e–f

Patiriella Verrill, 1913: 480, 483–484.—Verrill, 1914: 263.—Fisher, 1919: 410.—H.L. Clark, 1946: 134.—Spencer and Wright, 1966: U69.—Shepherd, 1968: 745.—Dartnall, 1970: 73–74.—Dartnall, 1971: 39–40.—Bernasconi, 1973: 341.—Clark, A.M. and Courtman-Stock, 1976: 80.—Clark, A.M., 1983: 364–367, 378, fig. 3c, 4.—Clark, A.M. and Downey, 1992: 178, 192.—Clark, A.M., 1993: 224.—Rowe, 1995: 39.—Campbell and Rowe, 1997: 129–131.—McKnight (in Clark and McKnight), 2001: 155.—O’Loughlin et al., 2002: 701.—Dartnall et al., 2003: 11–12.—Waters et al., 2004: 874, 875, 877. (Part).

Diagnosis. Rays 5, interradial margin straight to incurved, subpentagonal to short discrete rays, ends pointed or broadly or narrowly rounded; noticeable integument; plates on rays irregularly arranged; abactinal spinelets granuliform to digitiform, not webbed, in close to spaced distribution over projecting surface of plates; regular series of granuliform or digitiform spinelet-covered superom marginal and inferom marginal plates; actinal plates in oblique series; actinal adradial spines in incomplete series; actinal spines digitiform to short conical, no more than 3 per plate; superambulacral plates present from midray or distally only; superactinal plates present as single and multiple-plate supports.

Type species. *Asterina (Asteriscus) regularis* Verrill, 1867 (original designation).

Other species. *P. inornata* Livingstone, 1933; *P. oliveri* (Benham, 1911) (junior synonym: *Patiriella nigra* H.L. Clark, 1938, by Rowe, 1995); *Patiriella paradoxa* Campbell and Rowe, 1997.

Material examined. *P. inornata* Livingstone, 1933. Holotype. Western Australia, AM J3198.

P. nigra. Paratype. Lord Howe I., AM J4439 (1).

P. oliveri. Kermadec Is., MNZ EC4805 (2 of 7); Lord Howe I., AM G11519 (2); G2247 (1).

P. paradoxa. Holotype. Oman, BMNH 1997.1016. Paratypes. BMNH 1997.1017 (1); BMNH 1997.1018 (2).

A. regularis. Syntypes. New Zealand, Auckland, H. Edwards, 1866, YPM 988A (1), B (1, partially cleared), C (2). Other material. See O’Loughlin et al. (2002).

Description with species variations. Rays 5, rarely 6; interradial margin straight to incurved, form subpentagonal to

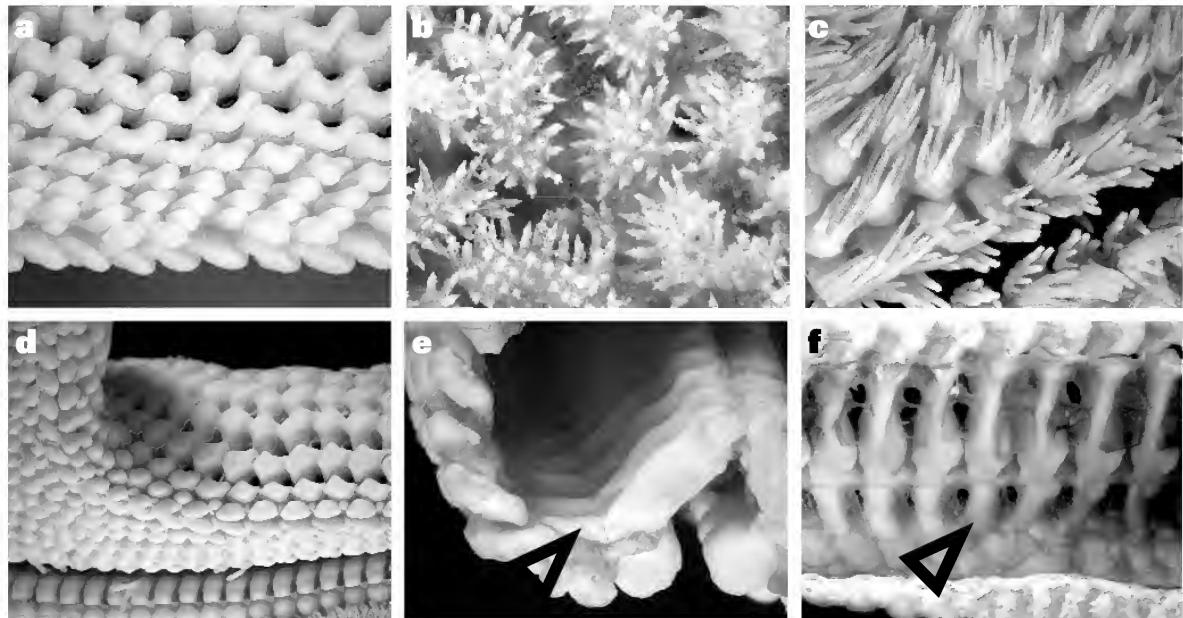


Figure 14. a–c, *Nepanthia pedicellaris* ($R = 23$ mm, holotype, USNM 32643): a, cleared lower lateral ray, and distinct margin; b, abactinal spinelets; c, adambulacral and actinal plates and spines. d, *Pseudoneopanthia trougtoni* ($R = 55$ mm, NMV F73977): cleared proximal lateral ray, margin, and ambulacrums. e, *Pseudoneopanthia nigrobrunnea* ($R = 85$ mm, NMV F95810): cleared section of ray with single series of superambulacral plates (arrow), and absence of transactinal and superactinal plates. f, *Pseudoneopanthia gotoi* ($R = 70$ mm, holotype, USNM 36899): internal cleared view of ambulacral plates, with series of superambulacral plates (arrow).

discrete rays with ends broadly rounded to pointed; integument cover sometimes evident (*regularis*); body flat actinally, low convex abactinally; rays elevated, sides steep; size medium (*regularis* up to $R = 39$ mm); lacking pedicellariae; rare evidence of fissiparity (*regularis*); abactinal gonopores.

Abactinal plates on upper rays in longitudinally series (*oliveri*) or irregular (*inornata*, *paradoxa*, *regularis*); carinal plate series ray length (*oliveri*) or short proximal (*regularis*) or not evident (*inornata*, *paradoxa*), plates doubly notched; variably regular longitudinal series of crescentiform plates on lower sides of rays; papulate areas extensive, non-papulate interradial area extensive (*inornata*, *oliveri*) or narrow (*paradoxa*, *regularis*); papular spaces large, 1–4 large (*inornata*, *paradoxa*) or numerous small papulae and irregular secondary plates per space (*oliveri*, *regularis*); proximal primary abactinal plates irregular (*inornata*, *paradoxa*) or crescentiform (*oliveri*, *regularis*), with spinelet-bearing ridges (*oliveri*, *regularis*) or not; glassy convexities below elevations on denuded plates (*oliveri*, *paradoxa*, *regularis*), or reticulations (*inornata*); abactinal spinelets granuliform, subglobose to subconical (*inornata*, *paradoxa*), or proximally short columnar, distally short subsacciform (*regularis*), or digitiform, many slightly widened terminally (*oliveri*); spinelets not webbed, in close arrangement on plates (*oliveri*, *paradoxa*, *regularis*) or spread (*inornata*); disc variably bordered by 5 radial and 5 interradial plates; supero-marginal and inferom marginal plates in regular series, with

typical abactinal spinelets; margin formed by projecting inferomarginals.

Actinal plates in oblique series (irregular proximally in *inornata*, *paradoxa*); proximal actinal interradial areas sometimes not plated.

Actinal spines per plate: oral 4–6; suboral 0–4; furrow 2–4 proximally, short, webbed; subambulacral 1–3, tall; adradial actinal 0–1, short, incomplete series; actinal interradial 1–3 proximally, 1–2 short distally; actinal interradial spines digitiform, slightly tapered (*regularis*), slightly swollen (*oliveri*), or short conical (*inornata*), or short thick columnar (*paradoxa*).

Superambulacral plates present distally (*inornata* not examined distally); superactinal plates present as single and multiple-plate struts.

Distribution. New Zealand, North and South Is, Stewart and Chatham Is; Australia, Lord Howe I., New South Wales, Tasmania; Western Australia; Oman; 0–92 m.

Remarks. O'Loughlin et al. (2002) did not report on the four syntypes of *Asterina regularis* Verrill, 1867 in their systematic review of *Patiriella*. They have now been examined and are consistent with O'Loughlin et al.'s (2002) redescription. Waters et al. (2004) presented a molecular phylogeny in which *P. regularis* fell on a clade remote from those on which all other species of *Patiriella* were included (clades III part, IV part, and V, in Fig. 1). The species in clade III (part) were removed to *Meridiastera*, those in clade IV (part) to *Cryptasterina* by Dartnall et al. (2003), and those in clade V to *Parvulastra*.

The diagnostic characters of *P. regularis* are: subpentagonal to very short-rayed form; abactinal plates on rays not in longitudinal series; spinelets granuliform, short columnar; large papular spaces with numerous papulae and secondary plates; actinal plates in oblique series; few superambulacral plates; superactinal plates present. *Patiriella* is distinguished from *Meridiastra* by lacking longitudinal series of plates on the rays, by oblique series of actinal plates, and by having superactinal plates. *Patiriella* is distinguished from *Cryptasterina* and *Parvulastra* by lacking longitudinal series of plates on the rays, and by having large papular spaces with numerous papulae and secondary plates.

On morphological grounds *P. inornata* and *P. paradoxa* are retained in *Patiriella*. Rowe (1995) transferred *Asterina oliveri* to *Patiriella*. *P. oliveri* has many of the characters of *Patiriella*, but is retained in *Patiriella* with reservation because of the regular carinal and longitudinal series of plates on the rays. On morphological grounds, *Asterina dyscrita* H.L. Clark, 1923 is removed from *Patiriella* to *Parvulastra*.

Patiriella tangribensis Domantay and Acosta, 1970 is judged to be nomen dubium. Domantay and Acosta (1970) established the species without type material being designated, and the description and figures are not adequate to diagnose the material (reference was made to an absence of marginal plates). It was distinguished only from *Patiriella exigua*, which does not occur in the type locality (Philippines).

Pseudasterina Aziz and Jangoux

Pseudasterina Aziz and Jangoux, 1985: 283-284.—A.M. Clark, 1993: 227.

Diagnosis. Small thin body; rays 5, discrete, broad base, rounded or pointed distally, medium-rayed stellate; abactinal upper ray plates variably regular in form and arrangement; interradial plates small, long imbricating oblique series; papulae along upper rays only, sparse, single; short columnar granuliform abactinal spinelets; superomarginal series of large plates with granuliform spinelets; inferomarginal plates project narrowly, with glassy subsacciform spinelets; actinal plates in oblique series; actinal interradial plates with numerous glassy subsacciform spines principally on proximal edge, few distally; lacking superambulacral and superactinal plates; very thin interradii, with abactinal and actinal imbricate plates angled and meeting internally throughout the interradii.

Type species. *Pseudasterina delicata* Aziz and Jangoux, 1985 (original designation).

Other species. *P. granulosa* Aziz and Jangoux, 1985.

Material examined. *P. delicata*. Tonga, 149–157 m, MNHN EcAs11704 (2); Wallis and Futuna Is, 250 m, MNHN EcAs11706 (1).

Description with species variations. Rays 5, discrete, broad base, distally rounded (*delicata*) or pointed (*granulosa*), medium-rayed stellate; body flat, thin; size small (*granulosa* up to $R = 18$ mm); lacking pedicellariae; neither fissiparous.

Abactinal appearance dominated by imbricating small interradial plates in oblique series from upper rays to

margin; papulate areas confined to narrow upper rays; papular spaces small, papulae single, rare secondary plates; abactinal plates on narrow upper rays variably regular in form and arrangement, some notched, some indented for papulae, proximal doubly or singly papulate carinal series sometimes present; disc distinctly bordered; abactinal plates with short columnar stout granuliform spinelets, weakly attached, spaced not clustered, up to 10 on proximal edge or covering plate, closer and slightly larger over some papulae; glassy reticulations on plates, not convexities; superomarginal plates larger than adjacent abactinals, regular series, longitudinally subrectangular, covered with granuliform spinelets; margin formed by narrowly projecting inferomarginal plates, each with numerous conical to subsacciform to splay-pointed sacciform spinelets.

Actinal interradial plates in distinct imbricating oblique series.

Actinal spines per plate: oral up to about 10, webbed; suboral up to about 15, short, glassy conical; furrow up to about 10 on furrow edge, webbed, up to about 10 on surface of plate; subambulacral, adradial actinal, and actinal interradial about 10, predominantly on proximal edge of plates; actinal spines glassy, short, pointed, sacciform.

Lacking superambulacral and superactinal plates; thin interradii with abactinal and actinal plates imbricating and angled interiorly to meet throughout the interradii; no tongue-like inner projections from abactinal or actinal plates.

Distribution. Philippines, Wallis, Futuna and Tonga Is, 130–250 m.

Remarks. No molecular data are available and this review is based on morphology. Until recently the two species were known only from the type material from the Philippine Is (*Pseudasterina delicata* holotype, MNHN EcAs10065; paratype, MNHN EcAs10066. *P. granulosa* holotype, MNHN EcAs10067). None of the type material could be located. Recently A.J. Dartnall determined material in the MNHN collections as *P. delicata*. These specimens have been examined in this study. The distinctive characters of *Pseudasterina* are: abactinal long imbricating oblique series of small plates from narrow upper radii to margin, and similar series from furrow to margin actinally; very thin interradii, with abactinal and actinal imbricate plates angled and meeting internally throughout the interradii; short columnar, granuliform, readily-detached spinelets on abactinal and superomarginal plates, but glassy, subsacciform, sometimes splay-pointed, spinelets on the inferomarginal plates. The spination characters given by Aziz and Jangoux (1985) for distinguishing *P. delicata* and *P. granulosa* appeared to be all variably present on the *P. delicata* specimens observed here, suggesting that *P. granulosa* may be a junior synonym. Aziz and Jangoux (1985) distinguished *Pseudasterina* from all other asterinid genera by the distinctive series of large superomarginal plates. This diagnostic character is a feature of *Cryptasterina* also, from which *Pseudasterina* differs in abactinal and actinal plate arrangement and spination, and in the absence of superambulacral and superactinal plates.

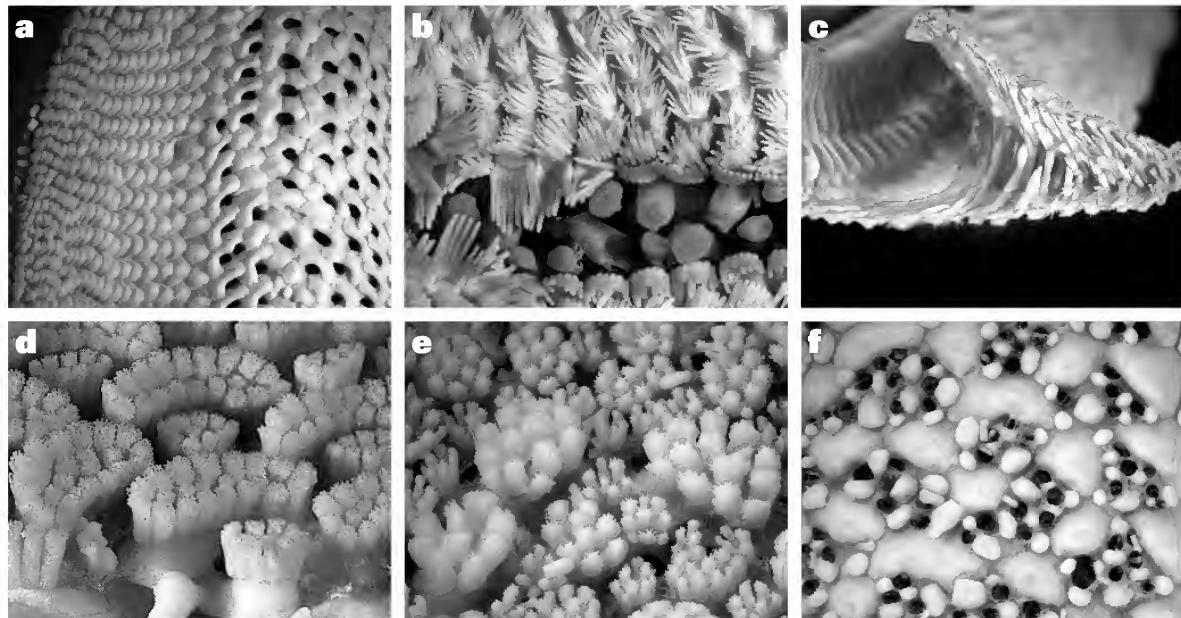


Figure 15. a–b, *Paraneanthia platydisca* ($R = 55$ mm, holotype, USNM 32644): a, cleared abactinal ray from upper ray to margin; b, ambulacrum with adambulacral and actinal plates and spines. c, *Paraneanthia grandis* ($R = 50$ mm, NMV F73976): section of ray showing superactinal plates supporting margin, and absence of superambulacral plates. d–f, *Patiria miniata* ($R = 65$ mm, NMV F97444): cleared abactinal surface with subpaxilliform clusters of granuliform spinelets. e–f, *Patiria pectinifera* ($R = 40$ mm, NMV F95672): e, cleared abactinal surface, with subpaxilliform globose spinelets; f, cleared abactinal surface, with papular spaces, secondary plates and papulae.

Pseudonepanthia A.H. Clark

Figures 1, 3c, 4e, 5d, 14d–f

Pseudonepanthia A.H. Clark, 1916: 118.—A.M. Clark, 1993: 227.

Diagnosis. Rays 4–10, subcylindrical, not flat actinally, lacking marginal edge; integument variably noticeable; lacking secondary plates; abactinal spinelets thick or thin or subsacciform, covering plates or in tufts; lacking pedicellariae; plates lacking glassy convexities; inferomarginal plates not projecting; furrow spines up to 5 per plate; actinal interradial spines digitiform, up to 7–30 per plate; series of superambulacral plates present, rare transactinal plates; lacking superactinal plates.

Type species. *Pseudonepanthia gotoi* A.H. Clark, 1916 (original designation).

Other species. *P. briareus* (Bell, 1894); *P. gracilis* (Rowe and Marsh, 1982); *P. grangei* (McKnight, 2001) (in Clark and McKnight); *P. nigrobrunnea* (Rowe and Marsh, 1982); *P. reinga* (McKnight, 2001) (in Clark and McKnight); *P.roughtoni* (Livingstone, 1934).

Material examined. *P. briareus*. Mariana Is, Guam, 118–152 m, UF 226 (1).

Pseudonepanthia gotoi. Holotype. Japan, Sagami Bay, 90 m, USNM 36899.

P. gracilis. Australia, New South Wales, AM J12874 (2); J11880 (2).

P. nigrobrunnea. New South Wales, Coffs Harbour, NMV F95810 (2); Byron Bay, F95804 (1).

Parasterina rooughtoni. Holotype. Western Australia, Albany, AM J3978. Other material. Victoria, Cape Woolamai, NMV F73013 (1);

Wilsons Promontory, F73017 (1); South Australia, Cape Jervis, F73977 (4).

Description with species variations. Rays 4–10, distinct, elongate, subcylindrical, tapered slightly (*nigrobrunnea*, *roughtoni*) or strongly (*briareus*, *gotoi*, *gracilis*, *grangei*, *reinga*), some irregular (*briareus*, *gotoi*, *nigrobrunnea*); integument variably noticeable; margin rounded, rays not flat actinally, lacking marginal edge; size large (*roughtoni* up to $R = 87$ mm) to medium (*grangei* up to $R = 33$ mm); lacking pedicellariae; gonopores sometimes actinal (*roughtoni*); one fissiparous (*briareus*).

Abactinal plates imbricating, projecting proximal edge creating uneven surface, irregular in form and arrangement on upper rays, oblique longitudinal series along sides of rays; lacking secondary plates; papulate areas extending to near margin; papular spaces with single large papula or a few (*nigrobrunnea*); abactinal plates with spinelet-bearing elevations or not (*roughtoni*); spinelets glassy, subsacciform with splayed points distally (*briareus*, *gotoi*), or subsacciform (*gracilis*), or fine columnar (*nigrobrunnea*, *roughtoni*); spinelets covering plates closely (*gotoi*, *gracilis*, *nigrobrunnea*, *roughtoni*) or in splayed groups (*briareus*); disc not bordered; cleared plates lacking glassy convexities; superomarginal plates in regular or irregular series; marginal plates covered with abactinal type spinelets; inferomarginal plates in predominantly regular series, frequently longitudinally elongate, not projecting.

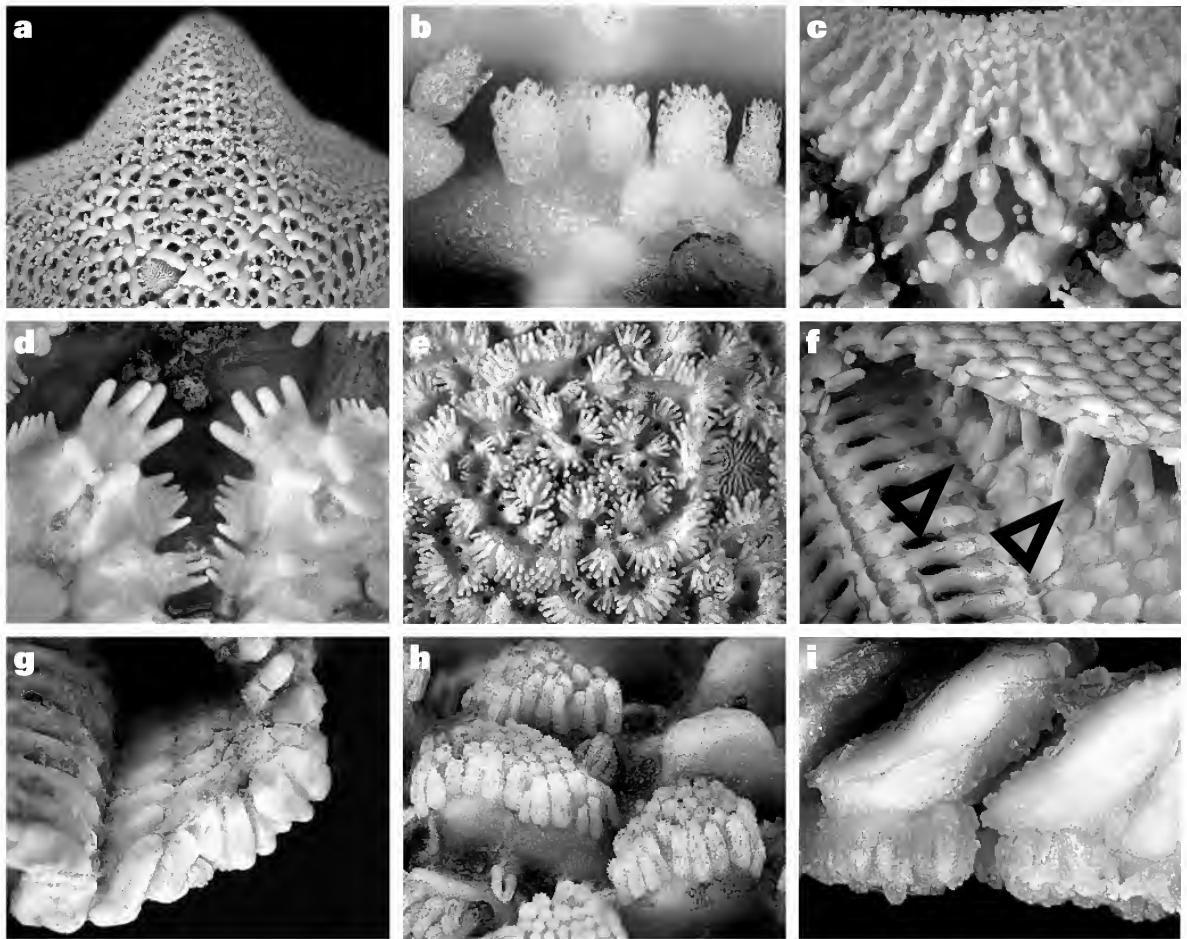


Figure 16. a–d, *Parvulastra exigua*: a, cleared ray ($R = 10$ mm, NMV F98062); b, denuded abactinal granuliform spinelets (NMV F98062); c, actinal interradius ($R = 9$ mm, NMV F98062); d, oral spines ($R = 10$ mm, NMV F97450). e–f, *Patiriella oliveri* ($R = 28$ mm, MNZ EC4805): e, abactinal disc and spinelets; f, absence of superambulacrinal plates (left arrow), presence of superactinal plates (right arrow). g–i, *Pseudopatiria obtusa* ($R = 54$ mm, holotype, BMNH 1938.6.23.24): g, section of ray with absence of both superambulacrinal and superactinal plates; h, abactinal subpaxilliform spinelets, and pedicellariae (lower left); i, actinal spines.

Actinal plates with spine-bearing elevations or not (*troughtoni*); not in oblique series.

Actinal spines per plate: oral 3–10; suboral 4–12; furrow 3–5; subambulacrinal 6–10; actinal 7–30; adradial row of actinal plates with complete series of spines; interradial actinal spines digitiform.

Superambulacrinal plates present as predominantly single series along ambulacrum, sometimes contiguous with inferomarginal plates across floor of ray (*briareus*, *troughtoni*) or with abactinal plates (*nigrobrunnea*); rare transactinal plates (sometimes irregularly present in *gracilis*); lacking superactinal plates; interior of rays with resinous lining.

Distribution. Mariana Is., SE Japan, South China Sea, Philippines, E Indonesia, E and S Australia, New Zealand; 0–540 m.

Remarks. Molecular data are available for *P. troughtoni* only. This review is based on morphology. Six species are removed from *Nepanthia* to *Pseudonepanthia* which is distinguished by: rays not flat actinally, lacking a marginal edge; absence of secondary plates, pedicellariae and glassy convexities; furrow spines fewer than 6 per plate; absence of transactinal and superactinal plates.

McKnight (in Clark and McKnight, 2001) referred *Nepanthia grangei* and *N. reinga* “provisionally” to *Nepanthia*. Material has not been examined, and internal skeletal plates not observed. Based on the descriptions, the absence of secondary plates and pedicellariae, and presence of up to five furrow spines per plate, fit the diagnosis of *Pseudonepanthia* to which both species are reassigned.

***Pseudopatiria* O'Loughlin gen. nov.**

Figures 3d, 16g–i

Diagnosis. Rays 5; interradial margin deeply incurved, rays distinct, unequal in size, subcylindrical, narrowly flat actinally; margin weakly defined by irregular series of transversely elongate inferom marginal plates; abactinal plates irregular; abactinal spinelets opaque, digitiform to short columnar, dense subpaxilliform clusters; pedicellariae present in papular spaces; papulate areas extensive; papular spaces large, numerous secondary plates and small papulae; actinal interradial plates irregular in size and arrangement; actinal spines short columnar, dense subpaxilliform clusters; lacking superambulacral and superactinal plates; lacking interior contiguous projections of abactinal and actinal plates.

Type species. *Patiria obtusa* Gray, 1847.

Material examined. *P. obtusa*. Holotype. Panama, 11–18 m, BMNH 1938.6.23.24 (dry; poor condition).

Description. Rays 5, subcylindrical, unequal in length, up to $R = 54$ mm; rays narrowly flat actinally, poorly defined margin; fasciculate pedicellariae between abactinal plates, 2–3 curved digitiform valves; not fissiparous.

Abactinal surface uneven, with abactinal plates domed and irregular in size and arrangement on upper rays, in angled series on sides of rays; papulate areas extensive, to near margin; papular spaces large, numerous large secondary plates intergrading with primary plates, numerous papulae; single large madreporite; disc not bordered by regular series of radial and interradial plates; abactinal plates crescentiform or elongate or rounded, with high dome, lacking glassy convexities; spinelets thick, digitiform to short columnar, distally minutely spinous, typically 0.4 mm long, in close subpaxilliform clusters of about 40 spinelets per plate; superomarginal and inferomarginal plates in irregular series, inferomarginals frequently transversely elongate, projecting slightly to define margin.

Actinal interradial plates irregular in size and arrangement.

Actinal spines per plate: oral 6, some thick subspatulate; suboral, cluster, some thick subspatulate; furrow 3, subspatulate; subambulacral and actinal dense clusters of up to 20 per plate; spines short columnar, typically 0.5 mm long.

Superambulacral, transactinal and superactinal plates absent; margin not supported by contiguous internal projections of abactinal and actinal plates; internal resinous body lining.

Distribution. Panama; 11–18 m.

Etymology. From the Latin *pseudo* (false), with *Patiria*, referring to the significant internal skeletal differences with the genus *Patiria*.

Remarks. Gray (1866) and Verrill (1870) retained *obtusa* in *Patiria*, but Perrier (1875) referred the species to *Asterina*. Verrill (1913) referred it to *Callopatiria*. A.M. Clark (1983 figs 5a, 7) also discussed the generic placement and noted the absence of what are referred to in this work as superambulacral and superactinal plates. A.M. Clark (1993) noted the need for a reassessment of generic status and opined that the single specimen was “probably from the Pacific side of Panama”. No

molecular data are available, and a morphological reassessment is undertaken here. The unique characters of this asterinid genus are: subcylindrical rays; irregular abactinal and actinal plate arrangements; plates with subpaxilliform dense clusters of opaque, thick, short columnar spinelets and spines; presence of pedicellariae; and absence of superambulacral, transactinal and superactinal plates.

***Stegnaster* Sladen**

Figures 1, 3e, 17a–d

***Stegnaster* Sladen, 1889: xxxiv, 375, 376 (key).—Fisher, 1911: 254 (key).—Verrill, 1913: 481 (key).—Verrill, 1915: 65.—Spencer and Wright, 1966: U69.—Clark and Downey, 1992: 194.—A.M. Clark, 1993: 227.—McKnight (in Clark and McKnight), 2001: 161–162.**

Diagnosis. Rays 5, subpentagonal, frequently arched, integument cover, rays with median ridge, body very thin interradially; abactinal cover of fine granules only; glassy convexities present; projecting inferom marginal plates lack fringe of spinelets; projecting furrow spines covered by continuous granule-covered integument; actinal interradial plates with thorn-tipped short spines; lacking superambulacral plates, proximal interradius supported by multiple superactinal plate struts, wide thin interradius supported internally by downward projecting abactinal plate extensions meeting actinal plates.

Type species. *Pteraster inflatus* Hutton, 1872 (original designation).

Other species. *S. vesseli* (Perrier, 1875).

Material examined. *S. inflatus*. New Zealand, North Island, AM J1856 (1); South Island, NMV F95675 (1); no locality data, AM G2030 (1).

Description with species variations. Rays 5, narrowly elevated median ridge, interradii very thin, form subpentagonal to rounded, body frequently in high domed (arched) shape, body covered by integument; size medium (*inflatus* up to $R = 53$ mm) to small (*vesseli* up to $R = 20$ mm); lacking pedicellariae; not fissiparous; gonopores abactinal (*inflatus*), actinal (*vesseli*).

Abactinal surface even, continuous cover of granuliform spinelets partly obscured by integument, larger globose spinelets on crown of plates (*inflatus*), spinelets slightly enlarged around pores (*vesseli*); cleared plates with prominent glassy convexities; plates of radii in longitudinal series, not to end of ray; carinal series in midray raised, longitudinally oblong, not notched; plates on upper sides of rays slightly notched for papulae; secondary plates rare to absent; papulate areas not extensive, confined to narrow raised radii; papular spaces large (*inflatus*) with up to 6 small papulae per space, to small (*vesseli*) with single papulae in longitudinal series; distinct pentagonal disc bordered by 5 raised radial and 5 small interradial plates; interradial areas extensive, not papulate, small plates in regular series perpendicular to margin; superomarginal and inferomarginal plates subequal, regular series, granule and integument cover; margin formed by inferomarginals, without a fringe of spinelets, continuous with actinal series of plates.

Actinal interradial plates in oblique series.

Actinal spines per plate: oral 3; suboral 0; furrow 2–3, project actinally, continuous integument and granule cover; sub-ambulacral none to rare; adradial series present; actinal 1 proximally, up to 6 distally, partly obscured by granule-covered integument; actinal spines short, thick basally, tapering distally to needle-like glassy point (thorn).

Lacking superambulacral plates; superactinal plates numerous proximally, multiple plate struts between actinal plates and inward projecting extensions of abactinal plates; superactinals absent distally, wide thin interradius supported internally by downward projecting abactinal plate extensions meeting actinal plates.

Distribution. West Indies, Venezuela, New Zealand, Chatham Is; 0–183 m.

Remarks. This morphological review is based on material examined and description of *S. wesseli* by Clark and Downey (1992). The phylogenetic trees of Waters et al. (2004) placed *S. inflatus* on a clade separate from three species placed in *Paranepanthia* but this distinction received only weak support. Both genera lack superambulacral plates but significant morphological differences reflect the clade separation, such as the dense subpaxilliform tufts of acicular spines and spinelets in *Paranepanthia*. Distinctive characters of *Stegnaster* are: noticeable integument and granuliform spinelet cover; furrow spines projecting actinally and covered by continuous granule-covered integument; thorn-tipped spines actinally; lacking superambulacral plates; superactinal plates proximally; wide thin interradii supported internally by downward projecting abactinal plate extensions meeting actinal plates.

Tegulaster Livingstone

Figures 3f, 18a–b

Tegulaster Livingstone, 1933: 11–12.—H.L. Clark, 1946: 143.—Spencer and Wright, 1966: U69.—A.M. Clark, 1993: 228.—Rowe, 1995: 41.

Diagnosis. Rays 5, size small, body thick, covered by thin integument; rays discrete, form medium to long-rayed stellate, flat actinally, rays elevated, narrow or broad basally; abactinal plates thick, imbricating, shallow notch and crescentiform, irregular in form and arrangement on narrow median band of upper rays; plates and papulae in few series along sides of rays; papulae predominantly single per space; secondary plates rare; abactinal spinelets few to none on plates, glassy, sacciform or conical or acicular; glassy convexities present; superomarginal plates in regular series; inferomarginal plates each with up to 7 discrete short spinelets or tuft of acicular spinelets; actinal interradial plates in oblique series; actinal interradial plates each with 1–2, long or short, sacciform spines; superambulacral plates rare, or in distal series, not in complete series; superactinal plates present as single plate struts.

Type species. *Tegulaster emburyi* Livingstone, 1933 (original designation).

Other species. *T. alba* (H.L. Clark, 1938); *T. leptalacantha* (H.L. Clark, 1916) (unrecognised subspecies: *Disasterina leptalacantha africana* Mortensen, 1933, this work); *T. praesignis* (Livingstone, 1933) (junior synonym: *Disasterina spinulifera* H.L. Clark, 1938, this work).

Material examined. *Asterina alba*. Paratypes. Lord Howe I., AM J6170 (5); NMV F45118 (2). Other material. J16575 (1).

T. emburyi. Holotype. Capricorn Group, Queensland, shallow sublittoral, AM J5605.

Asterina leptalacantha. Holotype. Queensland, Capricorn Group, AM J3082. Other material. J6097 (1); Mauritius, 24 m, UF 2499 (1).

Disasterina praesignis. Holotype. Queensland, Port Curtis, AM J5059. Other material. J19314 (3); NMV F94009 (1); F94010 (1).

D. spinulifera. N Western Australia, Lacepede I., WAM Z6773 (1).

Description with species variations. Body thick, covered by thin integument; rays 5, discrete, flat actinally, high convex abactinally, narrow at base (*emburyi*) or broad basally tapering distally to widely (*alba*) or narrowly (*leptalacantha*, *praesignis*) rounded; size small (*leptalacantha* up to R = 25 mm; *alba* up to R = 7 mm); pedicellariae present over papulae (*emburyi*, 2 conical valves), or not; none fissiparous; gonopores abactinal or actinal (*alba*).

Abactinal surface uneven, dominated by projecting proximal edges of imbricating thick plates; narrow median band of upper rays plates irregular in form and arrangement; part carinal series variably evident on upper rays (*alba*, *emburyi*, *praesignis*); secondary plates rare (*emburyi*) or absent (*alba*), or primary plates grading from large to small (*leptalacantha*, *praesignis*); up to 3 series of papulate plates with shallow notch and crescentiform along each side of rays; papular spaces small, predominantly single large papulae per space, irregular on upper rays, series on sides of rays; disc bordered by 5 radial and 5 interradial plates, variably regular; abactinal plates with spinelet-bearing raised rounded proximal edge (*alba*) or domes (*leptalacantha*); abactinal spinelets frequently lacking, or sometimes up to 12, glassy, sacciform to conical, spinelets across proximal edge of plates (*alba*), or present distally as tufts of small sacciform spinelets (*emburyi*), or with tufts of acicular sacciform spinelets on distal interradial plates (*leptalacantha*), or rarely a few short sacciform spinelets on apex of plates (*praesignis*); glassy convexities on bare plates; superomarginal and inferomarginal plates predominantly subequal, in regular series; superomarginal plates with a few abactinal-type spinelets (*alba*), or with spinelets only in mid-interradius (*emburyi*), or bare (*leptalacantha*), or with rare spinelets (*praesignis*); projecting inferomarginal plates with cover of up to 7 short acicular spinelets per plate (*alba*), or series of up to 6 short spinelets (*emburyi*, *praesignis*), or tuft of long acicular sacciform spinelets (*leptalacantha*).

Actinal interradial plates in oblique series; proximal interradial non-plated areas sometimes present (*leptalacantha*, *praesignis*).

Actinal spines per plate: oral 6–9; suboral 1 (*alba*, *leptalacantha*, *praesignis*) or 2 large, 4 small (*emburyi*); furrow 4–7, webbed; subambulacral 1–5; adradial actinal spines present; actinal predominantly 2 (*emburyi*) or 1; actinal interradial spines sacciform, long or short (*alba*).

Superambulacral plates rare (*alba*, *emburyi*) or series distally (*leptalacantha*, *praesignis*), not in complete series; superactinal plates present as single plate struts.

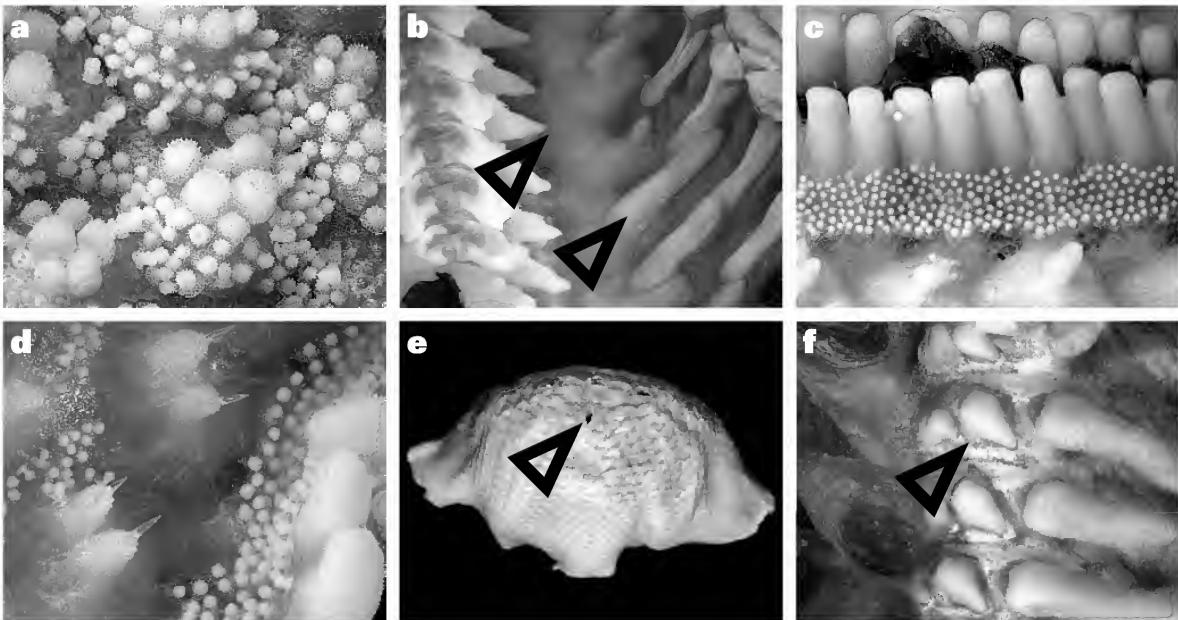


Figure 17. a–d, *Stegaster inflatus* (cleared, $R = 45$ mm, NMV F95675): a, abactinal globose spinelets and granules; b, internal adradial interradius, showing absence of superambulacral plates (left) and presence of superactinal plates (right); c, actinal furrow spines, and granule-covered integument; d, actinal glassy thorn-tipped spines. e–f, *Tremaster mirabilis* ($R = 60$ mm, NMV F67741): e, arched body, with abactinal brood chamber pore (arrow); f, ambulacrum showing vertical series of furrow spines.

Distribution. Northern Australia, Lord Howe I., Norfolk I., Mauritius, South Africa; 0–366 m.

Remarks. Molecular data are not available and this review is based on morphological evidence. Two species have been removed from *Disasterina* to *Tegulaster* and the reasons are discussed under the former. *Tegulaster* also shares some morphological characters with *Indianastra* gen. nov. above, in particular the spination, limited presence of superambulacral plates and presence of series of superactinal plates. The features distinguishing *Tegulaster* from *Indianastra* are: body thick with discrete rays, not thin with petaloid to subpentagonal form; abactinal plates large thick in few irregular series along sides of rays, not small thin in numerous regular series along rays; abactinal plates at most slightly notched and crescentiform, not deeply notched; inferomarginal spinelets discrete, not acicular in dense integument-covered tufts; actinal interradial spines per plate up to 2, not small webbed fans; actinal interradial plates in oblique series, not longitudinal series.

Livingstone (1933) established *D. praesignis* for a single specimen ($R = 14$ mm) from Port Curtis (NE Australia). H.L. Clark (1938) established *D. spinulifera* for a single specimen ($R = 8$ mm) from Broome (NW Australia), and did not distinguish it from *D. praesignis*. Specimens of both species were compared and found to be identical; *D. spinulifera* is a junior synonym of *D. praesignis*. *Asterina alba* has all the diagnostic characters of *Tegulaster*. Livingstone (1933) assigned *Disasterina ceylanica* to his new genus *Tegulaster* but it has the characters of *Disasterina*. *D. leptalacantha* var. *africana* was

established by Mortensen (1933) on the basis of its geographical separation (South Africa) from the *D. leptalacantha* type locality (NE Australia). Material from Mauritius has been determined as *T. leptalacantha* and no evidence found to justify the retention of variety *africana*.

Tremaster Verrill

Figures 17e–f

Tremaster Verrill, 1879: 201.—Sladen, 1889: xxxiv, 375, 394.—Spencer and Wright, 1966: U69.—Jangoux, 1982: 155–158, 161–162.—Leeling, 1984: 263–274.—Clark and Downey, 1992: 195–196.—A.M. Clark, 1993: 228.—McKnight (in Clark and McKnight), 2001: 163.

Diagnosis. Rays 5, subpentagonal, frequently strongly arched; 5 plated ducts between proximal abactinal and proximal actinal conspicuous interradial openings; abactinal plates with integument cover and large conical (proximal) and small granular (overall) spinelets; lacking series of superomarginal plates; 4 rows of tube feet in each ambulacrum; furrow spines in vertical series on adambulacral plates; actinal spines single, tall, slender, spatulate, in oblique series; lacking superambulacral and superactinal plates, wide thin interradial body supported by interior distal keels on actinal plates meeting abactinal plates.

Type species. *Tremaster mirabilis* Verrill, 1879 (original designation) (junior synonym: *Tremaster novaecaledoniae* Jangoux, 1982 proposed by Leeling, 1984 and confirmed in this work).

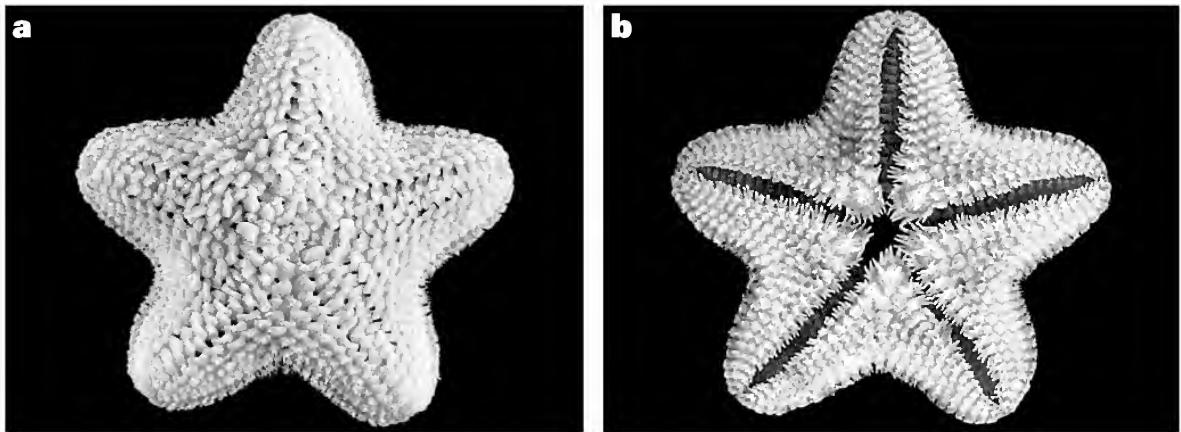


Figure 18. *Tegulaster alba* ($R = 5$ mm, paratype, NMV F45118): a, abactinal view; b, actinal view.

Material examined. *T. mirabilis*. Southern Ocean, Heard I., 226–252 m., NMV F67741 (6), F87362 (1), F67363 (1).

Description. Rays 5; interradial margin straight or slightly convex or concave; body frequently strongly arched; conspicuous proximal abactinal interradial openings to plate-lined ducts and chambers, opening actinally distal to oral plates; wide very thin body distally; size large (up to $R = 85$ mm); 4 rows of tube feet in each ambulacrum; lacking pedicellariae; ducts act as brood chambers.

Appearance dominated by domed form of body, 5 proximal duct openings, regular fish-scale plates, large conical spinelets on free edge of proximal plates, small granuliform spinelets on plates; abactinal proximal plates large, rhombic, thin, irregular on upper rays, singly notched for papula on upper sides of rays, distal plates small, covered by integument and weakly attached small granuliform spinelets; papular spaces small, predominantly single papula, secondary plates absent; 3–4 longitudinal series of small papulae along each upper side of rays; proximal abactinal plates with series of conical spinelets on proximal edge over papular space; cleared plates lacking conspicuous glassy convexities; abactinal interradial plates in longitudinal series, irregular distally, not in series perpendicular to margin; lacking series of superomarginal plates; acute margin formed by projecting series of inferomarginal plates; margin fragile, frequently broken off.

Actinal plates in oblique series, each plate with prominent proximal spine-bearing dome, series separated by decalcified body wall.

Actinal spines per plate: oral 1 tall proximally, adjacent pair, few upper small conical; suboral 0; furrow vertical series of 4–5, short to tall actinally; subambulacral 1 tall; adradial actinal series present; actinal 1 (rarely 2); actinal spines tall, slender, spatulate, subsacciform.

Lacking superambulacral plates; wide thin interradial margin supported by interior distal keels on actinal plates meeting abactinal plates; lacking superactinal plates.

Distribution. Atlantic, Pacific and Southern Oceans; 150–1060 m.

Remarks. No molecular data have been obtained for *T. mirabilis*, and this review is based on morphology. Leeling (1984) questioned the specific status of *T. novaecaledonicae* as its characters fell within the variation seen in *T. mirabilis*. We agree with her proposed synonymy. The significantly different characters of *Tremaster* from other asterinid genera are: abactinal and actinal duct openings, and internal plated brood chambers; absence of superomarginal series of plates; four rows of tube feet in each ambulacrum; furrow spines in vertical series on adambulacral plates; and extensive thin interradial margin supported by internal keels on actinal plates.

Incertae sedis

Asterina lorioli Koehler

Asterina lorioli Koehler, 1910: 129–131, pl. 19 figs 5–8.—A.M. Clark, 1993: 211.

Remarks. The description and illustrations by Koehler (1910) of abactinal granuliform spinelets and actinal spination suggest that *A. lorioli* is not a species of *Asterina*. Without material we have not been able to examine the internal skeleton.

Asterina novaezelandiae Perrier

Asterina novaezelandiae Perrier, 1875: 308.—Koehler, 1920: 135–136, pl. 35 figs 8–9.

Patiria novaezelandiae—Verrill, 1913: 482.

Remarks. The single type specimen of *A. novaezelandiae* was reported by Perrier (1875) from New Zealand but A.M. Clark (1993) noted “holotype originally with specimens of *Patiriella gunnii* supposedly from New Zealand but almost certainly from southern Australia”. If this is the case, it may be a five-rayed form of a species of *Meridiastra*. The description of three furrow spines and three subambulacral spines suggests *Meridiastra medius* (O’Loughlin et al., 2003). The specimen could not be found.

Nepanthia brachiatia Koehler

Nepanthia brachiatia Koehler, 1910: 133–135, pl. 19 figs 14–15.—Fisher, 1917: 173.—Fisher, 1919: 420.—Clark and Rowe, 1971: 70.—A.M. Clark, 1993: 222.

Remarks. Fisher (1917, 1919) and Clark and Rowe (1971) referred *N. brachiata* to *Paranepanthia*. The type specimen could not be found. Based on the description and figures by Koehler (1910), *N. brachiata* is characterised by: discrete narrow rays, flat actinally with narrow thin margins, not subcylindrical; absence of two distinct 'fields' of abactinal plates; predominantly large single papulae in papular spaces; few suboral, subambulacral and actinal interradial spines; webbed combs of digitiform actinal spines. This combination of characters is not found in *Nepanthia* or *Paranepanthia* or *Pseudonepanthia*. Without material we have not been able to examine the internal skeleton.

Biogeography

Waters et al. (2004) noted a link between the phylogeny suggested by molecular evidence and biogeographic patterns. The shallow marine genera *Paranepanthia* (clade I) in southern Australia and New Zealand, *Patiria* (clade II) in the northern and eastern Pacific, *Meridiastra* (clade III) in southern Australia and New Zealand, *Aquilonastraea* and *Cryptasterina* (clade IV) in the northern Indo-West Pacific, *Parvulastra* (clade V) in the southern temperate waters from South Africa to South America, and *Asterina* (clade VI) in the north-eastern and southern coastal Atlantic and Mediterranean, all have localised distributions. Additional species added to these genera on morphological grounds do not alter this pattern. Other genera, not included in the molecular phylogeny, *Asterinides* in the West Indies, *Calloptiria* in southern Africa, *Disasterina* and *Indiaastraea* and *Pseudasterina* and *Tegulaster* in the northern Indo-West Pacific, *Nepanthia* and *Pseudonepanthia* around Australia and the Indo-West Pacific, and *Patiriella* in southern Australasia and the north-west Indian Ocean, are likewise regionally localised.

The remaining genera with more widespread distributions, *Anseropoda* in the Atlantic and Indo-Pacific, *Stegnaster* in the West Indies and New Zealand, and *Tremaster* in the Atlantic and Pacific and Southern Oceans, show significant morphological differences from the other asterinid genera and all occur in deeper water. *Anseropoda* also shows morphological evidence of possibly being paraphyletic.

It can be concluded that Asterinidae is a cosmopolitan family, mainly of shallow-water narrow-range genera but including some more widespread in deeper waters of all oceans.

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A new genus of millipedes (Diplopoda: Polydesmida: Dalodesmidae) from wet forests in southern Victoria, with brief remarks on the Victorian Polydesmida

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Abstract

Mesibov, R. 2004. A new genus of millipedes (Diplopoda: Polydesmida: Dalodesmidae) from wet forests in southern Victoria, with brief remarks on the Victorian Polydesmida. *Memoirs of Museum Victoria* 61(1): 41–45.

Victoriombrus gen. nov. is erected for *Victoriombrus acanthus* sp. nov. from the Otway Ranges and *V. seminudus* sp. nov. from the Mt Donna Buang area. Four species of Dalodesmidae and 15 species of Paradoxosomatidae have now been described from Victoria. A diverse fauna of non-paradoxosomatid Polydesmida remains to be described from Victorian wet forests.

Keywords

Diplopoda, Polydesmida, Dalodesmidae, millipede, Australia, Victoria

Introduction

At the time of writing, there are 18 valid names for native polydesmidan millipedes known or believed to occur in Victoria (Table 1). Sixteen of these taxa are in Paradoxosomatidae, a family with numerous representatives in the dry forests and woodlands of eastern and western Australia. Paradoxosomatids also occur in Victoria's wetter forests, where they share moist microhabitats with Polydesmida most closely related to forms found in the wet forests of Tasmania and New Zealand. This non-paradoxosomatid, wet-forest polydesmidan fauna is very poorly known, yet collections by the author and others have shown it to be diverse and to include undescribed species in the genera *Asphalidesmus* Silvestri, 1910, *Lissodesmus* Chamberlin, 1920 and *Paredrodesmus* Mesibov, 2003.

In this paper I describe two wet-forest species in a genus with a novel gonopod structure. Victorian species of *Lissodesmus* will be reviewed in a forthcoming paper.

All material examined has been preserved in 75–80% ethanol. Preliminary drawings on graph paper were made using an eyepiece graticule. Gonopods were cleared and temporarily mounted in 60% lactic acid; other body parts were temporarily mounted in glycerine jelly. A Philips Electroscan ESEM 2020 operated in high-vacuum mode was used to examine material which had been air-dried before sputter-coating with gold. SEM images were acquired digitally. Abbreviations are as follows: NMV, Museum Victoria, Melbourne, Vic.; QVM, Queen Victoria Museum and Art Gallery, Launceston, Tas.

Order Polydesmida Leach, 1815

Suborder Dalodesmidea Hoffman, 1980

Dalodesmidae Cook, 1896

Victoriombrus gen. nov.

Type species. *Victoriombrus acanthus* sp. nov., by present designation.

Diagnosis. Dalodesmids c. 15 mm long with head + 20 segments, rounded and somewhat swollen paranota and pore formula 5, 7, 9–19. Telopodite of gonopod short, wide, divided by a transverse constriction into a setose, posteromesally excavated basal portion and a bare distal portion bearing a small mesal branch comprising a long, tapering solenomere accompanied by a distally flattened and roughened process, a much larger lateral branch, and between the two a narrow, more or less rod-like process arising posteromesally.

Description. Head with moderately deep impression lateral to antennal base; bases separated by about twice a socket diameter; vertigial sulcus faintly indicated; head moderately setose with moderately long setae on clypeus and frons, a few long setae on the vertex. Antenna (Fig. 1) short, slender; antennomere 2 the longest, 6 the widest. Collum about as wide as head and second somite; sparsely setose with moderately long setae; posterior margin straight, anterior margin gently convex, corners rounded. Somite 2 with lateral margin of paranotum well below collum corner, somite 3 margin at about the level of the collum corner. Somites with well-defined waist (Fig. 1); a

Table 1. Native Polydesmida from Victoria.

Taxon	Published localities
Dalodesmidae	
<i>Gephyrodesmus cineraceus</i> Jeekel, 1983	Drummer State Forest, 15 km E of Cann River (Jeekel, 1983)
<i>Lissodesmus martini</i> (Carl, 1902)	
Paradoxosomatidae	
<i>Archicladosoma magnum</i> Jeekel, 1984	Australia (Jeekel, 1984; ¹); Ferntree Gully National Park, 18 km NNE of Dandenong (Jeekel, 1984; tentative identification)
<i>Australiosoma laminatum</i> Jeekel, 1984	Australia (Jeekel, 1984) ¹
<i>Cladethosoma forceps</i> (Verhoeff, 1941)	Gippsland (Verhoeff, 1941)
<i>Dicranogonus pix</i> Jeekel, 1982	13 km SE of Buchan; 4 km ESE of Bruthen; Mt Taylor, 11 km NNW of Bairnsdale (Jeekel, 1982)
<i>Hoplatessara nigrocingulata</i> Jeekel, 1984	Australia (Jeekel, 1984) ¹
<i>H. pugiona</i> Verhoeff, 1941	Whittlesea (Verhoeff, 1941) ² ; Belgrave (Jeekel, 1984)
<i>Hoplatria clavigera</i> Verhoeff, 1941	Australia (Jeekel, 1984) ¹ ; Gippsland (Verhoeff, 1941)
<i>Isocladosoma guttatum</i> Jeekel, 1984	Glenaladale National Park, 28 km WNW of Bairnsdale (Jeekel, 1984)
<i>I. maculatum</i> Jeekel, 1984	Australia (Jeekel, 1984) ¹
<i>I. pallidulum</i> Jeekel, 1984	Gunyah Gunyah, 32 km SSW of Morwell (Jeekel, 1984)
<i>Pogonosternum adrianae</i> Jeekel, 1982	Toongabbie, 18 km NNE of Traralgon (Jeekel, 1982)
<i>P. coniferum</i> Jeekel, 1965	Australia (Jeekel, 1965, 1982) ¹
<i>P. laetificum</i> Jeekel, 1982	Ferntree Gully National Park, 18 km NNE of Dandenong (Jeekel, 1982)
<i>P. nigrovirgatum infuscum</i> Jeekel, 1982	Mt Taylor, 11 km NNW of Bairnsdale (Jeekel, 1982)
<i>P. nigrovirgatum nigrovirgatum</i> (Carl, 1902)	Melbourne (Carl, 1902)
<i>Somethus biramus</i> Jeekel, 1984	Drummer State Forest, 15 km E of Cann River; 13 km SE of Buchan; also NSW and SA (Jeekel, 1984)

¹ Jeekel (1982, 1984) believed that the type specimens of these species are from Victoria because they were collected by Victorian naturalist Charles Barrett and, in the case of *Isocladosoma* and *Pogonosternum* spp., because congeners are known from Victoria.

² Verhoeff (1941: 14) gives "Whettlera bei Melbourne", probably an error for 'Whittlesea', c. 40 km north of Melbourne.

few setae on somite 2, remaining somites bare and apparently smooth (very small seta-like processes scattered over dorsal surface of metazonite, only visible under high magnification); paranota on most somites just above midlateral (Fig. 1), somewhat swollen, laterally with a very narrow, upwardly concave groove bordered by a slightly thickened margin; from above, anterior margin of paranotum gently curved, lateral margin very slightly convex, posterior margin slightly concave on anterior somites, more so on posterior somites, where the posterior corner projects slightly and bluntly; limbus a comb of fine, straight teeth. Ozopores small, opening dorsolaterally just above and near the posterior end of the paranotal groove on somites 5, 7 and 9–19. Sternites slightly longer than wide, cross impressions well-defined. Anterior legs (Fig. 1) with swollen podomeres, prefemur strongly arched dorsally; posterior legs less swollen; tarsus about as long as next longest podomere, the femur. Sphaerotrichomes on tibia and tarsus only, from leg 3 rearwards, diminishing in number on the more posterior legs and absent from the last leg. Dense 'brushes' of setae ventrally on prefemur, femur and postfemur of most legs from 3 rearwards. Leg 2 coxa somewhat extended mesally, the genital opening a simple pit on this extension. Legpairs 4 and 5 not separated at bases, legpairs 6 and 7 well-separated; flexed gonopod telopodites reaching to legpair 6. Spiracles simple in structure with slightly raised rims; on diplosegments the anterior spiracle just above and anterior to the anterior leg, the posterior spiracle just anterior to the midway point between the leg

bases. Preanal ring moderately setose; epiproct tapering to blunt, rounded and depressed tip extending well past anal valves; hypoproct paraboloid in outline.

Gonopod aperture ovoid (Figs 2, 4), wider than long, about one-half width of somite 7 prozonite, with posterior margin in the form of a flattened 'V' and posterolateral portions of rim projecting ventrally. Gonocoxa in overall form a truncated cone, tapering distally, with moderately long setae on posteromesal surface; gonocoxae fairly firmly joined along midline but not quite fused into a syncoxite. Cannula prominent. Gonopod telopodites (Figs 2, 4), short, wide, closely appressed but not joined; partly fused with gonocoxa on anterior side of base; basal portion clearly separated from branched distal portion by a transverse constriction; basal portion excavated posteromesally, sparsely setose, mainly posterolaterally; distal portion bare, divided into a small mesal branch with a long, tapering solenomere joined basally to a distally flattened and roughened process, a much larger lateral branch, and a narrow, more or less rod-like posterior process arising posteromesally.

Females somewhat larger than males, with the same colouring; legs smaller than corresponding male legs and not swollen; posterior rim of epigynum projecting slightly, more so in centre; cyphopods not examined.

Distribution. Southern Victoria.

Etymology. Victoria + Greek *ombros* ("rainshower"), masculine.

Remarks. It is not clear how *Victoriombrus* is related to other Australian dalodesmid genera. The new genus shares with Tasmanian *Bromodesmus* (Mesibov, 2004) a long, tapering, acutely pointed solenomere and telopodite elements fringed with teeth, but the gonocoxae in *Victoriombrus* are more nearly fused into a syncoxite than in the Tasmanian genus, the telopodites are much shorter and wider, and the pore formula is 5, 7, 9–19 instead of 5, 7, 9, 10, 12, 13, 15–19.

Victoriombrus acanthus sp. nov.

Figures 1, 2, 3, 6 (map)

Material examined. Holotype. Male, Australia, Victoria. Young Creek Road, 0.2 km NE of Ciancio Creek crossing, 38°40'S, 143°29'E, pitfall 15.xi.1994–31.i.1995, G. Milledge, *Nothofagus* forest, sample NOH-1079, NMV K-8842.

Paratypes. 1 stadium 7 juvenile male, same details as holotype, NMV K-8843; 2 females, Aire Crossing Track, 0.5 km N of Aire River crossing, 38°40'S, 143°29'E, pitfall 15.xi.1994–31.i.1995, G. Milledge, *Nothofagus* forest, sample NOH-1084, NMV K-8844, K-8857; 1 male, same details but pitfall 31.i.–11.iv.1995, NMV K-8845; 2 males, 1 female, Maits Rest, 10 km W of Apollo Bay, 22.x.1991, K. Walker, *Nothofagus* litter and moss, NMV K-8846, K-8874, K-8875; 1 male, Beauchamp Falls, 38°39'S, 143°36'E, pitfall 6.ix.–15.xi.1994, G. Milledge, *Nothofagus* forest, sample NOH-1089, NMV K-8847; 2 females, same details but pitfall 15.xi.1994–31.i.1995, sample NOH-1090, NMV K-8848, K-8858; 5 males, Turtons Pass, 38°38'39"S, 143°41'20"E, 12.xii.2003, R. Mesibov and T. Moule, wet eucalypt forest litter, NMV K-8849, K-8859–K8862; 2 females, 9 stadium 7 juvenile males, 1 stadium 7 juvenile female, same details, NMV K-8851, K-8863–K8873; 1 stadium 7 juvenile male, same details but 38°38'43"S, 143°40'36"E, NMV K-8850.

Diagnosis. Differs from *V. seminudus* sp. nov. in the form of the gonopod, notably the posterior curvature of the solenomere and the presence of small, branched, spiny processes on the lateral division of the telopodite.

Description. Males c. 15 mm long, c. 1.2 mm in maximum vertical diameter. In alcohol, freshly collected specimens with pale yellow head and antennae; ground colour of body pale yellow, patterned with brown patches: prozonite with a patch laterally and a pair of paramedian patches dorsally, metazonite with a triangular mid-dorsal patch anteriorly, a quadrangular mid-dorsal patch posteriorly, a small patch anteroventrally on paranotum; posterior margin of metazonite and distal podomeres brown.

Gonopod telopodites (Figs 2, 3) short, wide, closely appressed basally but not joined. Basal portion of telopodite excavated posteromesally, with variably long setae on postero-lateral surface and surrounding the excavate area. Telopodite with a transverse constriction at between one-third to one-half its length, separating setose basal portion from bare distal portion, the latter divided basally into mesal, posteromesal and lateral branches. Mesal branch divides basally into a long, tapering, acutely pointed solenomere and a long, flattened process arising posterior to solenomere. Solenomere curves first anteriorly and basally, then turns sharply distally, curving slightly posteriorly but remaining parallel to long axis of telopodite, terminating at about two-thirds telopodite length. Prostatic groove running along mesal surface of telopodite,

following curvature of the solenomere and terminating at its tip. Laterally flattened process accompanying the solenomere curves first mesally, then anteriorly, terminating just distal to solenomere; tip of process and a somewhat expanded portion at about mid-length with numerous marginal teeth and a roughened surface. Just distal and posterior to solenomere origin, posteromesal process arising as a narrow, rod-like, tapering process, laterally flattened from about half its length, curving slightly mesally, then laterally. Lateral branch of telopodite by far the largest, complicated in structure (Figs 2, 4), basically a laterally flattened process, curving slightly laterally and somewhat concave mesally, with marginal teeth of varying sizes; posterior edge giving rise to a mesally curving process ending in a rounded, somewhat expanded tip resembling a spanner or wrench midway between solenomere origin and tip; lateral and anterior surfaces of main process armed at about one-third the process length with small, short, branched, spiny structures resembling the tips of a thorny shrub.

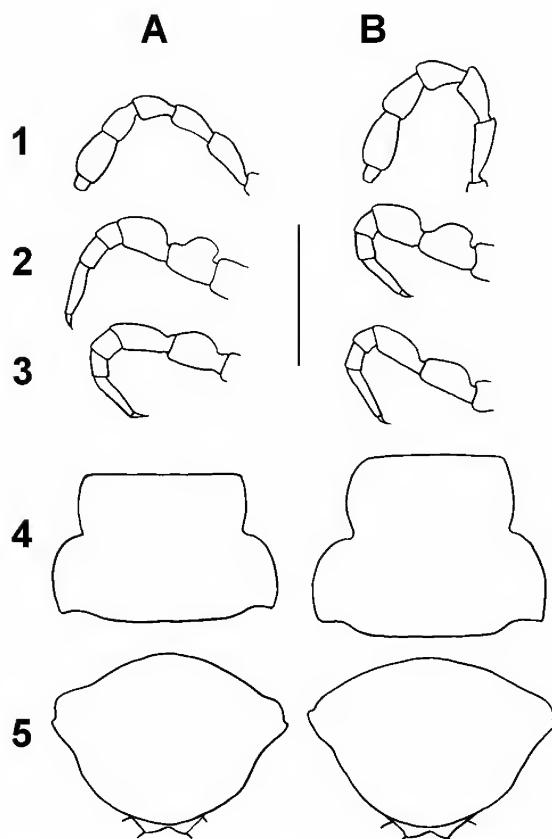


Figure 1. *Victoriombrus* spp. details. A, *V. acanthus* sp. nov., male paratype from NMV K-8849; B, *V. seminudus* sp. nov., male paratype from NMV K-8856. 1, Antenna; 2, posterior leg on somite 6; 3, posterior leg on somite 12; 4, dorsal outline view of somite 12; 5, posterior outline view of somite 12. Scale bar = 1.0 mm; setation and antennal cones not shown.

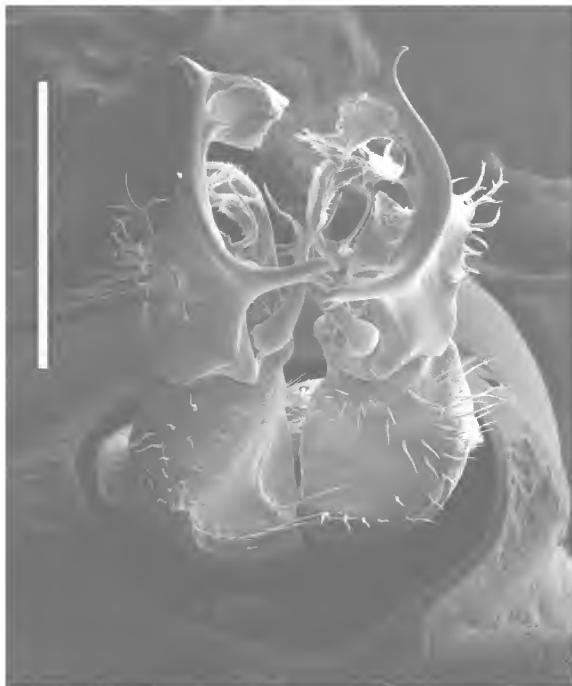


Figure 2. *Victoriombrus acanthus* sp. nov., male, paratype. Posterior view of gonopods in situ (specimen from NMV K-8849). Scale bar = 0.5 mm.

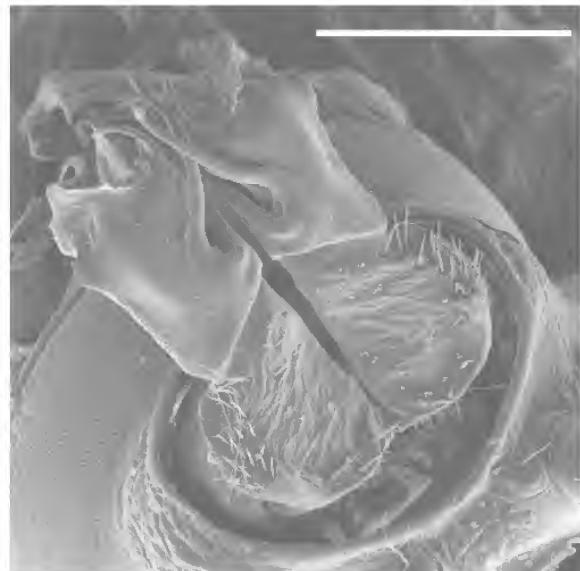


Figure 4. *Victoriombrus seminudus* sp. nov., male, paratype. Posterior view of gonopods in situ (specimen from NMV K-8853). Scale bar = 0.5 mm.

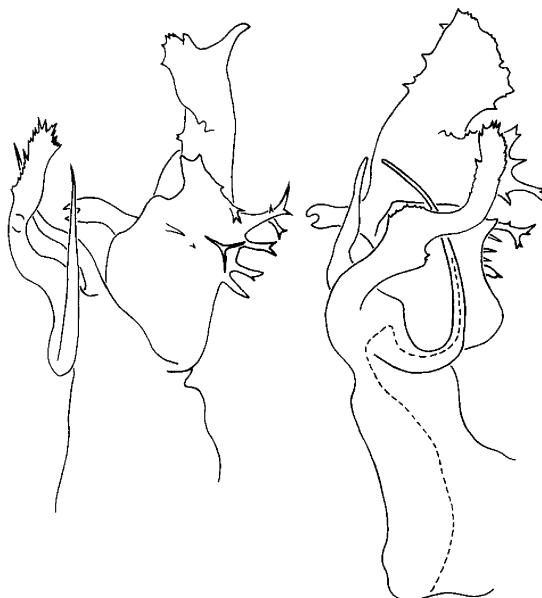


Figure 3. *Victoriombrus acanthus* sp. nov., male, paratype. Anterior (left) and mesal (right) views of right gonopod (specimen from NMV K-8849). Dashed line indicates course of prostatic groove; for clarity, the continuation of the groove to the solenomere tip is not indicated.

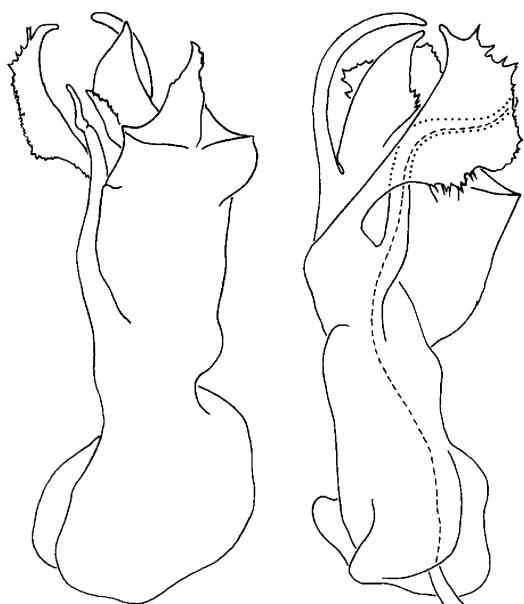


Figure 5. *Victoriombrus seminudus* sp. nov., male, paratype. Anterior (left) and mesal (right) views of right gonopod (specimen from NMV K-8856). Dashed line indicates course of prostatic groove.

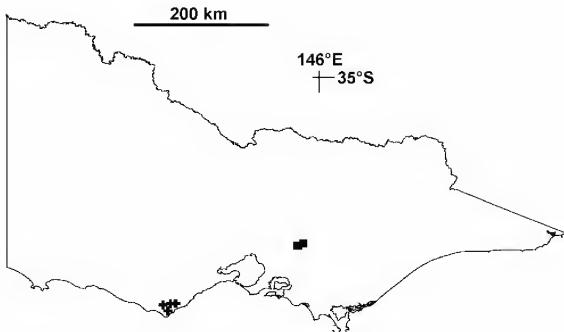


Figure 6. Localities in Victoria of *Victoriombrus acanthus* sp. nov. (crosses) and *V. seminudus* sp. nov. (squares).

Distribution and microhabitat. In wet eucalypt and *Nothofagus* forest litter in the Otway Ranges (Fig. 6).

Etymology. Latin *acanthus* ("prickly shrub"), noun in apposition, from the appearance of the gonopod telopodite.

Victoriombrus seminudus sp. nov.

Figures 1, 4, 5, 6 (map)

Material examined. Holotype. Male, Australia, Victoria. Myrtle Gully Reserve, 3.4 km WSW of Mt Donna Buang, 37°43'S, 145°38'30"E, pitfall 29.xi.1994–20.i.1995, G. Milledge, *Nothofagus* forest, sample NOH-1840, NMV K-8852.

Paratypes. 1 male, 7 females, 1 stadium 7 juvenile female, same details as holotype, K-8853, K-8876–K-8883; 1 male, same details but pitfall 21.i.–7.iv.1995, sample NOH-1841, NMV K-8854; 2 males, 2 females, Road 26, 0.2 km WNW of Donna Buang Road junction, 37°43'S, 145°39'30"E, pitfall 29.xi.1994 to 20.i.1995, G. Milledge, *Eucalyptus* forest, sample NOH-1846, NMV K-8855, K-8884–K-8886; 1 male, Acheron Gap, 6 km NE of Mt Donna Buang, 37°40'43"S, 145°44'20"E, pitfall 28.xii.1995–21.ii.1996, G. Milledge, *Nothofagus* forest, sample NOH-1853, NMV K-8856.

Diagnosis. Differs from *V. acanthus* sp. nov. in the form of the gonopod, notably the anterior curvature of the solenomere and the absence of small, branched, spiny processes on the lateral division of the telopodite.

Description. Males c. 15 mm long, 1.2 mm in maximum vertical diameter. In alcohol, well-coloured specimens with pale yellow antennae and yellow-orange head, legs and paranota; prozonite and metazonite ground colour pinkish-brown; metazonite reddish-brown below paranota and with mid-dorsal, triangular reddish-brown patch; posterior margin of metazonite and distal podomeres reddish-brown.

Gonopod telopodites (Figs 4, 5) short, wide, closely appressed basally but not joined. Basal portion of telopodite excavated posteromesally, with variably long setae on postero-lateral surface. Telopodite with a transverse constriction at between one-third to one-half its length, angled distad from lateral to mesal, separating setose basal portion from bare distal portion, latter divided basally into mesal, posteromesal and lateral branches. Mesal branch divides basally into a long, tapering, acutely pointed solenomere and a long, flattened process arising posterior to solenomere. Solenomere extends

distally, then turns abruptly anteriorly at about three-quarters the length of the telopodite before terminating in a short, distally directed tip. Prostatic groove running along mesal surface of telopodite, following curvature of the solenomere and terminating at its tip. Laterally flattened process accompanying the solenomere directed anterodistally and slightly mesally, expanding in its distal half into a large flattened, fan-like structure with numerous marginal teeth and a roughened surface. Just distal and posterior to solenomere origin, posteromesal process arising as a narrow, rod-like, tapering process, curving mesally and anteriorly and terminating just distal to the most distal teeth of the process accompanying the solenomere. Lateral branch of telopodite by far the largest, greatly inflated basally, terminating in toothed crests anteriorly and posteriorly.

Distribution and microhabitat. In wet eucalypt and *Nothofagus* forest litter in the Mt Donna Buang area (Fig. 6).

Etymology. Latin *semi-* (half) + *nudus* (naked), adjective, because the setose basal portion of the gonopod telopodite is so clearly separated by a transverse constriction from the bare distal portion.

Acknowledgements

This study was supported by a grant from the Plomley Foundation. I am grateful to David Steele (University of Tasmania) for acquiring the SEM images, and to Peter Lillywhite (Museum Victoria) for the loan of specimens and for his hospitality during my visit to Museum Victoria in March 2004. A draft of this paper was improved by suggestions from Sergei Golovatch.

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Biosystematics of Australian mygalomorph spiders: descriptions of three new species of *Teyl* from Victoria (Araneae: Nemesiidae)

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Abstract

Main, B.Y. 2004. Biosystematics of Australian mygalomorph spiders: descriptions of three new species of *Teyl* from Victoria (Araneae: Nemesiidae). *Memoirs of Museum Victoria* 61(1): 47–55.

Revised diagnostic notes on the tribe Teylini and the genus *Teyl* Main are presented. Three new species of *Teyl* from Victoria are described: *T. harveyi*, *T. walkeri* and *T. yeni*. The biogeography of the genus is briefly discussed.

Keywords

Araneae, Mygalomorphae, Nemesiidae, *Teyl*, Teylini, new species, biogeography, taxonomy

Introduction

The genus *Teyl* Main, 1975 is one of four genera of the tribe Teylini (Main, 1985b). *Teyl luculentus* Main, 1975 is the only named species attributed to the genus. However, many undescribed species are recognised in south-western Western Australia and further north in the Carnarvon Basin (Main, 1985b, 1996, 1999, Main et al., 2000). While it was formerly stated that the genus was confined to south-western Western Australia (Main, 1985b) examination of specimens in the South Australian Museum and Museum Victoria shows that it also occurs in Eyre Peninsula and western Victoria (Main, 1996: 168, 1997: 119, 1999: 237). Main (1999) suggested that the distribution of *Teyl* was fragmented in southern Australia during the Cretaceous inundation of central Australia and that the radiation of the genus in southern Western Australia has resulted from the continuing isolation in relictual habitats which have retained aspects of Gondwanan conditions. Similarly, occurrence of the genus in Eyre Peninsula and western Victoria may be related to persistence of microhabitats simulating Gondwanan characteristics.

Specimens collected from the Little Desert in Victoria by Museum Victoria are attributed to three new species described below. All specimens are lodged in Museum Victoria, Melbourne (NMV). Measurements are in millimetres. Abbreviations are as follows: ALE, anterior lateral eyes; AME, anterior median eyes; PLE, posterior lateral eyes; PME posterior median eyes; d, dorsal; pd, prolaterodorsal; rd, retro-laterodorsal; v, ventral; pv, prolateroventral; rv, retrolateroventral; PMS, posterior median spinnerets; PLS, posterior lateral spinnerets; WA, Western Australia; SA, South Australia; WAM, Western Australian Museum.

In the species descriptions the leg formula is obtained by dividing the length of the leg by the length of the carapace. The patella width is measured across the dorsal proximal base (= knee); an indication of the relative thickness of the legs is given by the tibial index which = (100 x width of patella) divided by (length of tibia + patella) (Petrunkevitch, 1942).

Tribe Teylini Main

Teylini Main 1982: 274.—Main, 1983: 925.—Main, 1985b: 744.—Raven 1985: 82, 87.

Diagnosis. The main diagnostic features of the Teylini (and which distinguish the tribe from the Anamini) are: the narrow band of cuspules on the maxillae (covering no more than a third of the length of the maxillae) in contrast to the broader distribution in Anamini (*Chenistonia* Hogg, 2001 and some possibly misplaced species of *Aname* Koch, 1872 are exceptions); absence of a spine-bearing spur on tibia I of males except in *Teyloides* and the spherical, subspherical or gourd shaped bulb of the male palp with the embolus arising equatorially or from the apex; embolus sometimes reflexed, usually tapering but may be flanged proximal to or at tip. Inclusion of *Merredinia* Main, 1983 (which lacks a tibial spur) in the Anamini has already been noted as tentative (Main, 1985b).

Remarks. Main (1982) erected the tribe Teylini (to include at that time only the genus *Teyl*) as distinct from the Anamini. However it was not fully described until 1985 (Main, 1985b) when the four genera *Teyl* Main, 1975, *Namea* Raven, 1984, *Teyloides* Main, 1985 and *Pseudoteyl* Main, 1985 were attributed to it. Remarks by Raven (1985: 5 December 1985) that Teylini was a nomen nudum were redundant in that they were

predated by publication of a description of the tribe (Main, 1985b: 17 September 1985).

Representatives of the tribe occur in southwestern Western Australia, southern South Australia, western Victoria and the border country of southeastern Queensland and northeastern New South Wales.

Teyl Main

Teyl Main, 1975: 74.

Type species. *Teyl luculentus* Main, 1975 by monotypy (female holotype from 14.5 km N of Bruce Rock, WA, (WAM 75-944).—Raven, 1981: 341.—Main, 1982: 73.—Main, 1983: 925.—1985a: 39.—1985b: 746.—Raven, 1985: 82, 87, 88.

Diagnosis. As in Main (1985b) but with the following modifications/additions. Small to medium-sized spiders (carapace length 2.0 to 10.0 mm). Scopula sparse or absent on tarsi of palp and anterior legs of female. Scopula of male complete (i.e. covering whole ventral face) on tarsi I and II, on apical part only (if present) on anterior metatarsi. Metatarsus I of males straight (unmodified) or with “elbow” i.e. “bowed”; with many, few or no spines. Palpal bulb and embolus of male variable, as for tribe and with embolus short or long (based on described and undescribed species). Differs from *Namea* by the broad sternum which is convex behind labium and the short ovoid terminal segment of the posterior lateral spinnerets; from *Teyloides* by lacking a spined spur on tibia I in the male and lobate, not coiled, internal genitalia in the female; and from *Pseudoteyl* by absence of dark smudges on the legs.

Remarks. Raven (1985: 88) incorrectly stated that the holotype of *Teyl luculentus* was a “male”. The holotype is a female (Main, 1975: 74). The comment by Raven (1985: 88) “cymbium ... aspinose” requires modification in that some undescribed species and one species described here have spines on the male palpal tarsus. The first part of the third couplet of the key (Main, 1985b) requires modification as follows “Southwest WA, Eyre Peninsula, SA and western Victoria (instead of “Southwest WA only”). Species (including many undescribed) occur in southwestern Western Australia, Eyre Peninsula South Australia and western Victoria.

Key to males of species of *Teyl*

1. Spines on palp tarsus *T. harveyi*
- Palp tarsus without spines 2
2. Embolus tip tapering; metatarsus I with spines 3
- Embolus tip flanged; metatarsus I without spines
..... *T. walkeri*
3. Metatarsus I with few spines *T. yeni*
- Metatarsus I with many spines *T. luculentus*

Teyl harveyi sp. nov.

Figures 1–9, table 1

Material examined. Holotype, male, Victoria, 24.9 km SE of Murrayville, 35°24'S, 141°24'E (site 79), drift fence pitfall trap, Jun 1986, A.L. Yen (NMV T-3011). Paratype, male, Victoria, 20.3 km SE of Murrayville 35°24'S, 141°20'E (site 76), drift fence pitfall, Jun 1986, A.L. Yen (NMV T-3012).

Table 1. *Teyl harveyi* sp. nov. Holotype, male. Leg measurements and leg formulae

	F	P	T	MT	T	Total
I	2.8	1.8	2.2	2.1	1.4	10.3
II	2.5	1.3	2.0	2.0	1.0	8.8
III	2.2	1.2	1.6	2.1	1.3	8.4
IV	3.0	1.3	2.7	2.8	1.7	11.5
Palp	1.8	1.1	1.3	—	1.1	5.3

Width of patella I at knee = 0.4. Tibial index = 10.00.

Width of patella IV at knee = 0.4. Tibial index = 10.00.

Leg formulae: 4/3.7, 1/3.32, 2/2.83, 3/2.7.

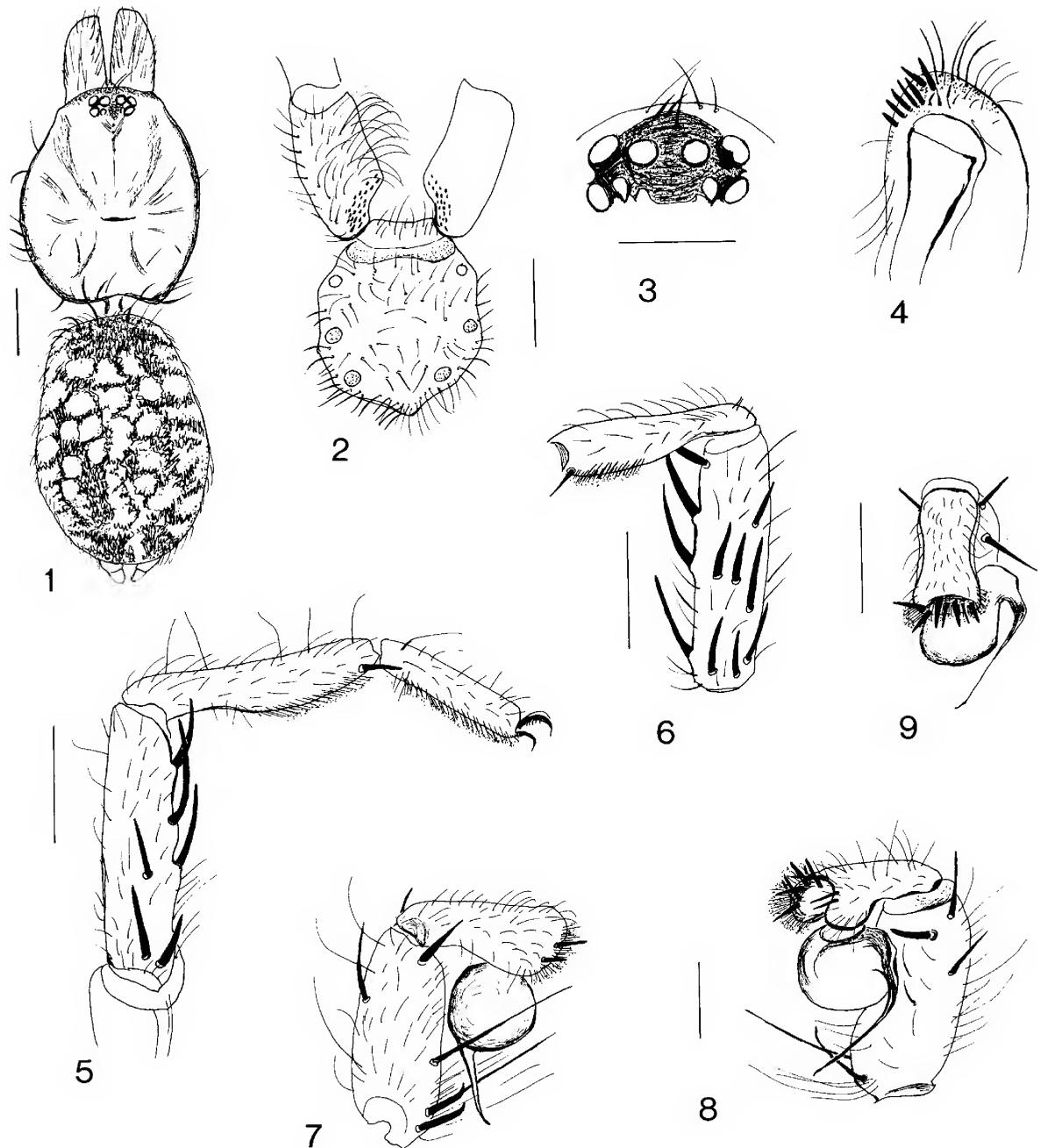
Diagnosis. Male. Light tan brown, glabrous carapace with sparse and delicate posterolateral spines. Abdomen with dorsal dark reticulated pattern, ventrally yellow with a few speckles anterior to spinnerets. Retrolateral spines of palp tibia: 1 heavy apical, 2 heavy proximal and 2 long, tapering spines on retroventral margin. A group of heavy apical, dorsal spines on palp tarsus. Embolus tapering. Metatarsus I with pair of thin apical ventral spines, moderate “elbow”. Tibia I with spines on all faces; a line of 4 megaspines on retroventral angle.

The group of dorsal apical spines on palp tarsus distinguishes the species from *T. luculentus* and the other two species (*T. walkeri* and *T. yeni*) described here; the presence of a pair of ventral apical spines on metatarsus I further distinguishes it from *T. walkeri* which lacks spines and *yeni* which has additionally several prolaterodorsal spines.

Female. Unknown.

Description of male (holotype). Carapace glabrous, light tan brown with darker margin and dark radial lines; abdomen with dorsal pattern of dark, mottled reticulations, venter pale yellowish with a few dark speckles in front of spinnerets. Carapace with few marginal spines, all delicate, median lateral group and posterior marginal group. Fovea straight. Carapace length 3.1, width 2.6mm; abdomen length 3.7, width 2.3. Eye group on mound 0.5 long; eye group 0.3 mm long, 0.7 wide; diameters of eyes: ALE 0.2, AME 0.2, PLE 0.15, PME 0.5. Sternum slightly convex, length 1.9, width 1.6; evenly covered with fine bristles; sigilla small, faint, submarginal; labium length 0.3. Chelicerae with pseudorastellum of about 8 thick spines on apical inner edge of paturon; groove with 8 proximal teeth, proximal two large and separated by a gap from others; a few basal granular teeth on retromargin. Maxillae with 33 cuspules on right maxilla; about 30 on left, some damaged.

Legs with scopula on tarsi I and II (thin on II), and distal half of metatarsi I and II. Tarsal claws with double combs of superior claws with about 15, fine, close-set teeth decreasing in size proximally; median claw long and curved. Spination of legs – I, femur d 6, patella rv 1, tibia rv 3 megaspines on slight mounds in a line followed by 1 heavy proximal spine, r 1-1, v 2-2, pv 1-1-1, metatarsus pv 1 apical, rv 1 apical, tarsus 0. II, femur d 6, patella 0, tibia v 1-2-2, pd 1-1, metatarsus v 2-2, pd 1-1. III, femur d 6, patella pd 1-1, tibia v 2-2-4, pd 1-1, rd 1-1, metatarsus v 2-2-3, pd 1-1-1, rd 1-1-1, tarsus 0. IV, femur d 6,



Figures 1–9. *Teyl harveyi* sp. nov. Holotype, male. 1, dorsal view, carapace, chelicerae and abdomen; 2, sternal area; 3, eye group; 4, apical region left chelicera; 5, right leg I, retrolateral view tarsus, metatarsus and tibia ; 6, right leg I, tibia and metatarsus (ventral aspect of tibia); 7, tarsus and tibia of right palp, retrolateral; 8, tarsus and tibia of right palp, prolateral; 9, right palp tarsus and palpal organ, dorsal. Scale = 1.0 mm. (figs 1, 2, 5, 6, 9); 0.5 mm. (figs 3, 7, 8).

patella, pd 1 apical, rd 1, tibia v 2-2-3, pd 1-1-1, rd 1-1-1, metatarsus v 2-1-2-3, pd 1-1-1, rd 1-1-1, tarsus 0.

Palp (Left palp missing). Tarsus with apical group of about 10 thick spines. Tibia with 2 heavy terminally hooked and 2 long thin proximal retrolateral spines, prolaterally with 2 tapering heavy apical spines and 1 finer spine. Bulb spherical but viewed dorsally, gourd shaped with embolus arising at sharp angle (reflexed); embolus finely tapering.

Variation. Paratype carapace length 3.0, width 2.5.

Etymology. The species is named as a tribute to M. S. Harvey for his vast contribution to arachnology.

Teyl walkeri sp. nov

Figures 10–30, table 2

Material examined. Holotype, male, Victoria, 17.8 km SE of Murrayville, 35°22'S, 141°19'E (site 74), drift fence pitfall, Jun 1986, A.L. Yen (NMV T-3008). Paratypes. Allotype female, 27.2 km SE of Murrayville, 35°25'S, 141°11'E, drift net fence pitfall trap (site 79), Jun 1986, A.L. Yen (NMV T-3009). Male, 20.3 km SE of Murrayville, 35°24'S, 141°20'E (site 76), drift fence pitfall, Jun 1986, A.L. Yen (NMV T-3010).

Diagnosis. Male. Generally pale yellow, abdomen with irregular dark brown, median dorsal pattern. Carapace non hirsute, heavy marginal bristles. Palp tarsus without spines; tibia retrolaterally with 2 hooked, proximal spines, 1 long tapering spine and 1 apical spine. Embolus slightly reflexed, flanged tip; bulb large, spherical but in some views gourd-shaped. Legs moderately hirsute, heavily spinose. Metatarsus I without spines. Tibia I with 4 large spines in retroventral line (3 megaspines terminally hooked, distal 2 on low mounds).

Absence of spines on metatarsus I and the flanged embolus tip distinguish the species from *T. luculentus*, *T. harveyi* and *T. yeni*.

Female. Small (< 4 mm), uniformly pale yellow except abdomen greyish with dorsal median darker streak; carapace glabrous. Legs with dark spines and sparse hairs and bristles.

The presence of thin, sparse scopula on tarsi of palps and legs I and II differs from *T. luculentus* which lacks scopula in female. Tibia I with fewer heavy spines than *T. luculentus*. Internal genitalia lobate with short, thick stems.

Description of male (holotype). Uniformly pale yellow except for ocular area black, abdomen dorsally with irregular dark

brown median pattern. Carapace non hirsute, with heavy marginal bristles. Legs not glabrous, moderately hirsute, heavily spinose. Fovea straight. Carapace length 3.2, width 2.5; abdomen length 3.5. Eye tubercle slightly wider than edges of ALE/PLE, tubercle 0.4 high; length of eye group 0.3, width 0.7. Diameters of eyes: ALE 0.15, AME 0.12, PLE 0.1, PME 0.1. Sternum length 1.5, width 1.3; labium 0.2. Chelicerae with heavy apical bristles intermixed with a few reduced spine-like bristles. Fang groove with 7 teeth on promargin and 6 or 7 small granule-like teeth retrobasally. Maxillae with narrow band of 18–20 cuspules (left and right).

Legs. Scopula present on tarsi and apical half of metatarsi I and II. Tarsal claws with 11 or 12 teeth in each line of all claws. Spination I, femur d 1-1-3-1 (pd apical), patella pd 1 (apical), tibia rd 1-1, pv 1-1-1, pd 1-1-1, r 1-1-1-1 (distal 3 megaspines with slightly hooked tip), metatarsus 0. II, femur 1-3-1-1 (pd apical), patella pd 1 apical, tibia pd 1-1, v 2-2, metatarsus pd midregion 1, rv midregion 1. III (right missing) left femur 1-1-3-2, patella pd 1 apical, rd 1 mid region, tibia d 1-3-2, metatarsus about 3 spines in a line on each face. IV, femur d 3 median, pd 3, rd 3, patella 0, tibia 2 or 3 spines in a line on each face, metatarsus about 3 spines in a line on each face (difficult to determine exact 'side'). (Note: also a half circle of dorsal curved bristles on trochanters). Metatarsus I with slight proximal ventral depression and slight "elbow" (Figs 14–16).

Palp. Tarsus without spines; tibia retrolaterally with 2 proximal, terminally hooked, stout spines and 1 long, bristle-like tapering spine, 1 midretrodorsal spine and 1 retrolateral apical spine, prolaterally with 3 stout spines and 2 prolateral-ventral proximal tapering bristle-like spines. Bulb subspherical to gourd-shaped, height 0.6 mm, width 0.5 mm; embolus arising mid (equatorial) region (Figs 19–21). Embolus not distinctly reflexed, tip flanged.

Comments on paratype. Carapace damaged on posterior edge (length approximately 3.0, width 2.5); retrolateral spination of right palp tibia as for holotype; retrolateral aspect of tibia I lacks median spine; abdomen missing.

Description of female (paratype). Uniformly pale yellow except abdomen greyish with dorsal median dark brown streak reaching about two-thirds from anterior margin. Legs with sparse hairs and bristles; brown spines. Carapace glabrous and

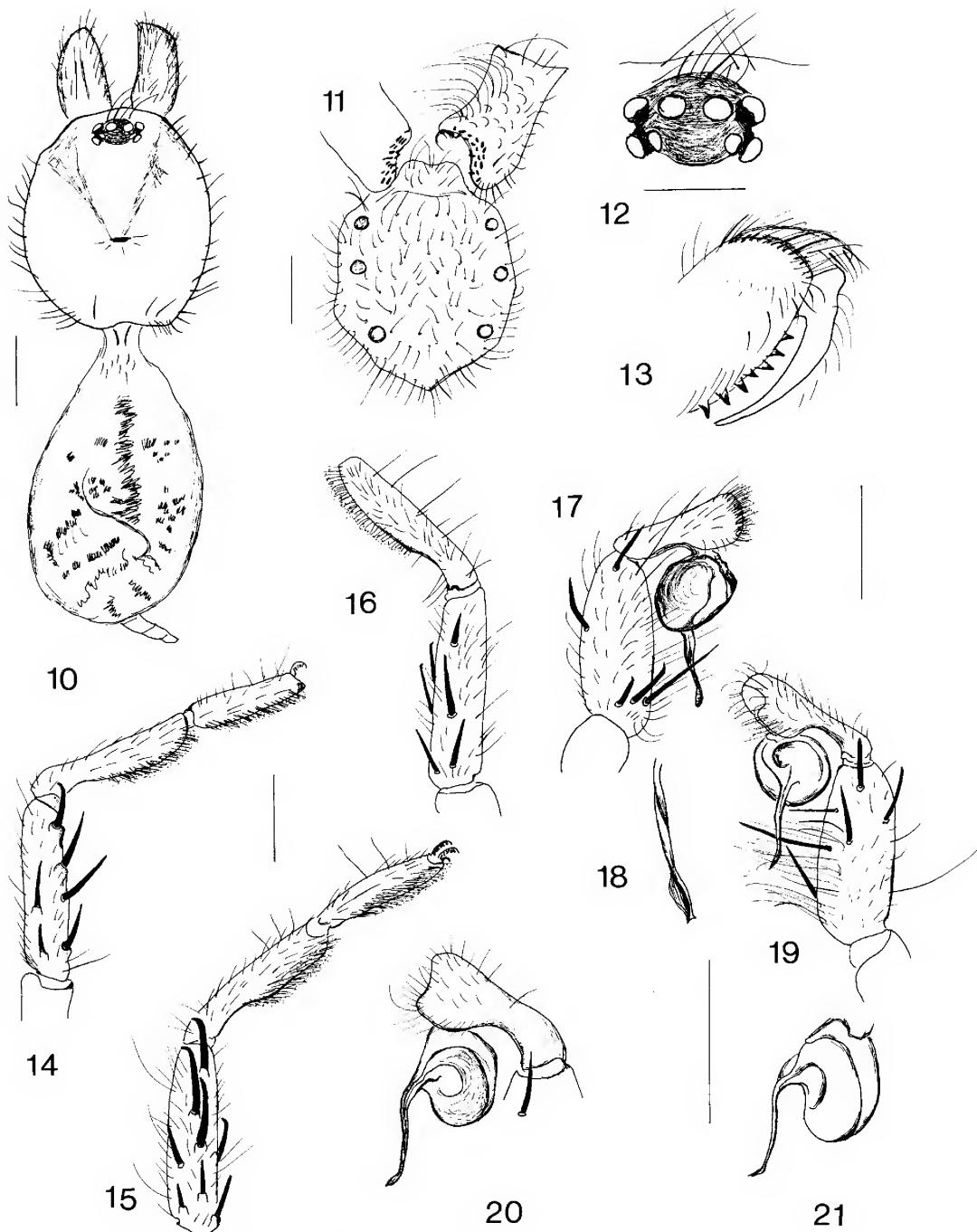
Table 2. *Teyl walkeri* sp. nov. Holotype, male and paratype, female. Leg measurements and leg formulae, male with female measurements in parentheses.

	F	P	T	MT	T	Total
I	2.8 (2.7)	1.5 (1.7)	2.1 (2.0)	1.6 (1.9)	1.4 (1.2)	9.4 (9.5)
II	2.6 (2.5)	1.2 (1.5)	1.9 (1.8)	1.9 (1.8)	1.5 (1.4)	9.1 (9.0)
III	2.4 (2.5)	1.1 (1.4)	1.7 (1.7)	2.1 (2.1)	1.3 (1.3)	8.6 (9.0)
IV	3.0 (3.1)	1.3 (1.6)	2.6 (2.7)	2.6 (2.9)	1.6 (1.6)	11.1(11.9)
Palp	1.8 (1.8)	0.8 (1.1)	1.2 (1.3)	—	1.0 (1.0)	4.8 (5.2)

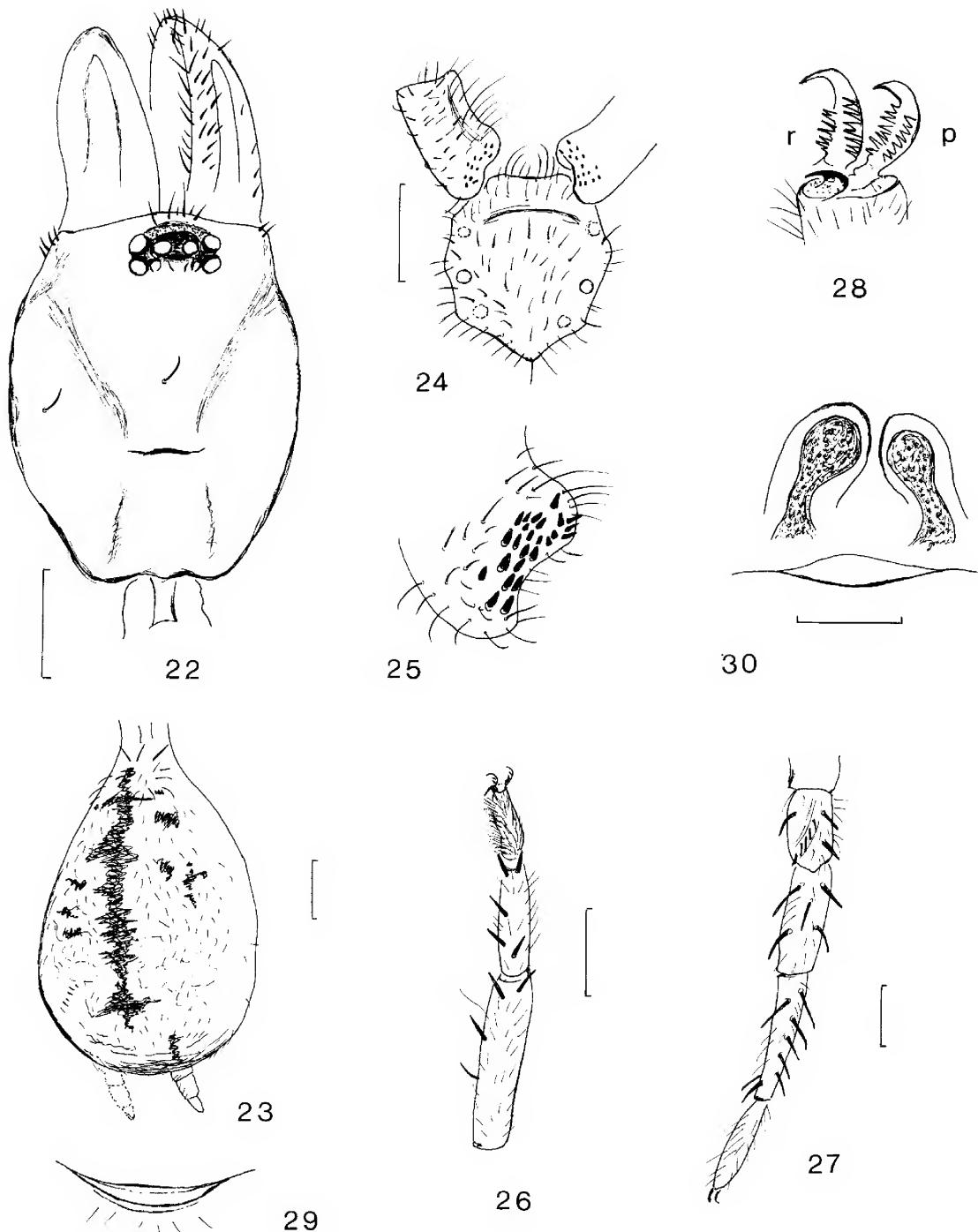
Width of patella I at knee = 0.45 (0.45). Tibial index = 12.5 (12.16).

Width of patella IV at knee = 0.40 (0.5). Tibial index = 10.2 (11.62).

Leg formulae: 4/3.0 (3.6), 1/2.9 (2.9), 2/2.8 (2.72), 3/2.7(2.72).



Figures 10–21. *Teyl walkeri* sp. nov. Holotype, male. 10, carapace, chelicerae and abdomen, dorsal view; 11, sternal area and maxillae; 12, eye group; 13, left chelicera, pro-view; 14, leg I, tarsus, metatarsus, tibia, retrolateral view; 15, right leg I, tarsus, metatarsus, tibia, retroventral view; 16, right leg I, metatarsus and tibia prolateral view; 17–21, right palp; 17, tibia, tarsus and palpal organ, retrolateral; 18, same view as for 17, palpal tip enlarged; 19, tibia, tarsus and palpal organ, prolateral view; 20, tarsus and palpal organ, prolaterodorsal; 21, palpal organ (bulb and embolus) dorsal. Scale = 1.0 mm. (figs 10, 14–17, 19); 0.5 mm. (figs 11, 12); 13 and 18 not to scale.



Figures 22–30. *Teyl walkeri* sp. nov. Paratype (allotype), female. 22, carapace and chelicerae; 23, abdomen, dorsal view; 24, sternal area and maxillae; 25, right maxilla, proximal with cuspules; 26, right leg I ventral, tarsus, metatarsus and tibia; 27, right leg III dorsal, tarsus, metatarsus and tibia and patella; 28, right leg I, tarsal claws, p, prolateral, r, retrolateral; 29, genital lobe/aperture; 30, internal genitalia (spemathecae). Scale = 1.0 mm (figs 22–24, 26, 27); 0.5 mm (fig. 30); figs 25, 28, 29 not to scale.

with black ocular area. Fovea straight. Carapace length 3.3, width 2.7, caput width 1.9; abdomen length 6.2. Carapace lacks marginal spines. Eye group 0.85 long, 0.4 wide. Diameters of eyes: ALE 0.2, AME 0.15, PLE 0.15, PME 0.5; ALE apart 0.55. Sternum length 1.7, width 1.5. Labium 0.3 long. Chelicerae with pseudorastellum of stout bristles and long thin spines. Fang groove with 7 (left), 8 (right) promarginal teeth and 5 basal retromarginal teeth. Maxillae with cuspules in narrow band around incurved edge (about 22 on left maxilla, 35 on right), small rounded heel.

Legs. Scopula thin on palp tarsus and tarsus I; a few proximal scopula hairs on tarsus II; a few thin apical hairs on metatarsus I. Tarsal claws. Palp claw with 6 prolateral teeth (left) (right claw detached); legs with 6–9 teeth in each row of all claws. Spination I, femur pd 1 apical, rd a few, patella pd 1-1-1 bristle-like, tibia rv 1-1, v 2 bristle-like, metatarsus v 2-1 (rv) -2. II, femur pd 1 apical, patella pd 1 apical, tibia v 1-1-2 (bristles), pd 1-1, metatarsus v 2-2-2, pd 1. III, femur pd 1 apical, patella d 2-1, tibia v 1-2-2 (bristles), d 3-2, metatarsus v 2-2-3, d 8 or 9 spines and heavy bristles. IV, femur pd 1 apical, patella rd 1, tibia v 2-2-2, rd 1-1, metatarsus v 2-2-3, d 2-1-1-2-1.

Palp, tibia pv 4 distal, pd 1 proximal, tarsus pv 1 proximal. Internal genitalia lobate with short, thick stems, terminally bulbous (Fig. 30).

Etymology. The species is named in honour of Dr Ken Walker in recognition of his entomological and arachnological work.

Teyl yeni sp. nov.

Figures 31–40, table 3

Material examined. Holotype, male, Victoria, 22.2 km SE of Murrayville, 35°25'S, 141°21'E (site 77), drift fence pitfall trap, Jun 1986, A.L. Yen (NMV T-3013). Paratype, male, Victoria, 17.8 km SE of Murrayville, 35°23'S, 141°19'E (site 74), drift fence pitfall trap, Jun 1986, A.L. Yen. (NMV T-3014).

Diagnosis. Male. Generally pale yellowish brown with dark median pattern on abdomen dorsum. Palp tibia retrolaterally with 2 basal and 1 apical stout, heavy spines and 2 long thin tapering spines. Tarsus without apical spines. Embolus base arising equatorially and slightly reflexed, tapering. Metatarsus I slightly bowed, 2 retrolateral spines in proximal half. Tibia I retrolaterally with 3 megaspines in proximal line.

Differs from *T. harveyi* by having 2 retrolateral spines (instead of 1) on metatarsus I, and further from *T. harveyi* and *T. walkeri* by having more metatarsal spines (including a pro-laterodorsal line) on metatarsus I. Differs from *T. luculentus* by having a more strongly “bowed” metatarsus I, the strongly hooked retrolateral spines on the palp, smaller size and delicate marginal spines on carapace and from all the other species by the more widely spread maxillary cuspules.

Female. Unknown.

Description of male (holotype). Carapace, sternum, legs yellowish brown with faint smudge of darker brown. Abdomen pale yellowish brown with reticulated dark brown pattern on median dorsal area. Legs with short evenly distributed hairs and sparsely scattered strong spines. Carapace with delicate

Table 3. *Teyl yeni* sp. nov. Holotype, male. Leg measurements and leg formulae.

	F	P	T	MT	T	Total
I	4.4	2.0	3.4	3.3	2.3	15.4
II	4.2	1.9	3.1	3.2	2.3	14.7
III	4.3	1.4	2.5	3.0	2.1	13.3
IV	3.9	1.8	3.7	4.5	2.3	16.2
Palp	2.7	1.5	2.1	—	1.0	7.3

Width of patella I at knee = 0.4. Tibial index = 7.4.

Width of patella IV at knee = 0.4. Tibial index = 7.27.

Leg formulae: 4/4.26, 1/4.05, 2/3.86. 3/3.5

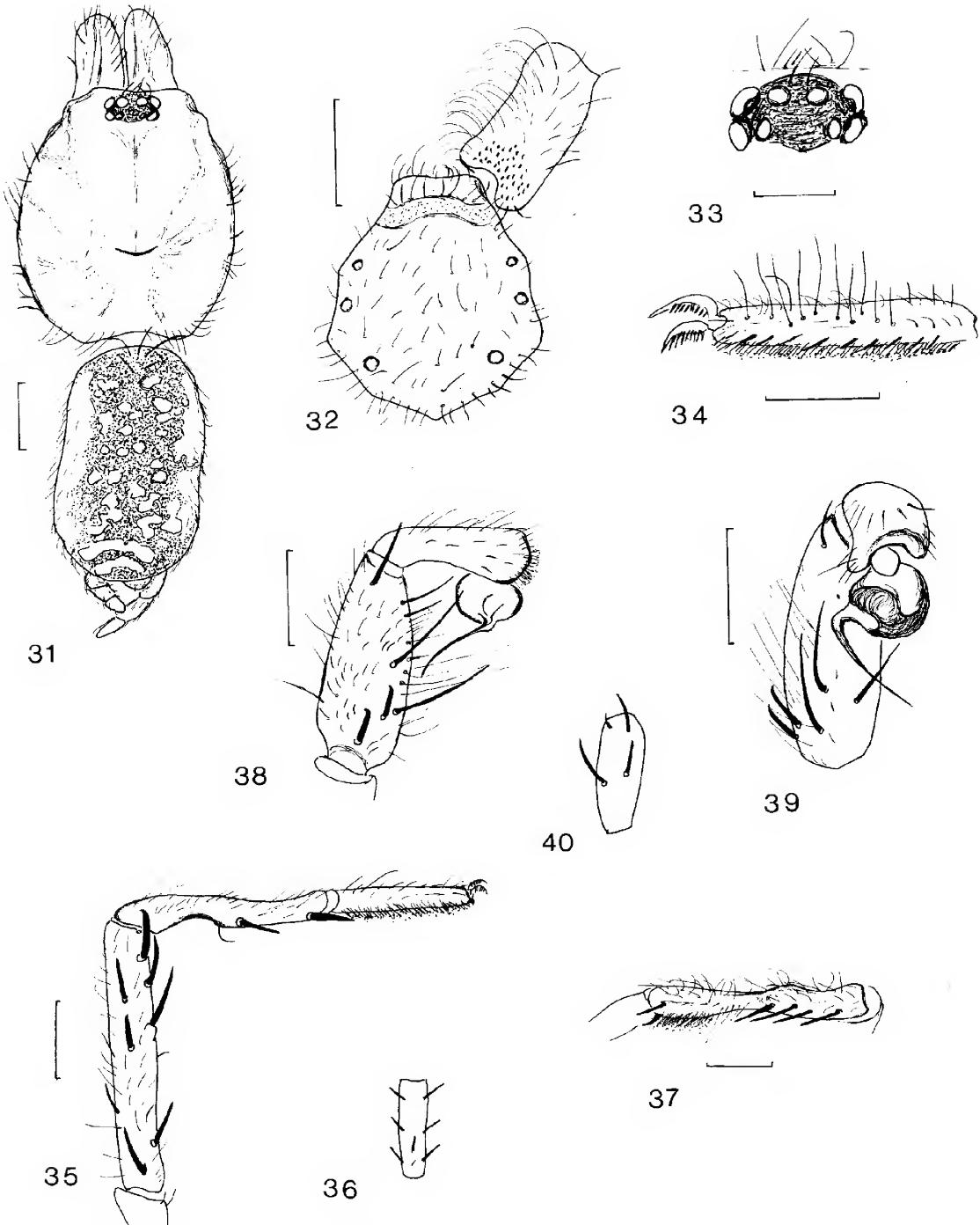
marginal spines. Caput low. Height of carapace at fovea 0.6, at eyes 1.0. Fovea straight, slightly reflected at edges. Carapace length 3.8, width 3.5, caput width 2.0. Abdomen length 4.2, width 2.4. Eye group broad on low tubercle 0.4 long, 0.9 wide. Diameters of eyes: ALE 0.25, AME 0.2, PLE 0.2, PME 0.1. Sternum length 2.3, width 2.0; with long fine bristles uniformly scattered. Labium 0.3 long. Sternal sigilla small, round, indistinct, marginal although posterior pair separated by a marginal line of bristles. Chelicerae long and narrow with a pseudorastellum of short apical spines on inner edge. Promargin of cheliceral groove with 8 teeth, 5 basal retromarginal teeth. Maxillae with broad band of about 50 cuspules around inner edge (extending farther from inner edge than is usual for *Teyl* specimens).

Legs. I, metatarsus “bowed” i.e. with a distinct “elbow”. Scopula complete (that is covering full extent of segment) on tarsus I, thin on II, sparse and divided by a line of bristles on III and IV; present on metatarsi I and II only (apical half). Trichobothria. Palp tarsus at least 8. Tarsus I with about 9, plus four rigid, vertical hairs, metatarsus about 12 trichobothria. Tarsal claws 8–12 teeth on each comb of paired claws, basal ones may be fused. Spination, I, femur d 14, patella pd 2, tibia d 2-1-2-2 (including pd and rd), rv 3 megaspines in apical half, 1 in lower third (Fig. 35), metatarsus pd 1-1-1-1 (left 1-1-0-1), rv 2 distal to elbow, pv 1 apical. II, femur d 11, patella pd 2, tibia d 7, v 2-2-3, metatarsus d 5, v 2-2-2. III, femur d 11, patella pd2, rd 1, tibia d 3-3-3, v 2-2-2, metatarsus d 9, v 2-2-3. IV, femur d 11, patella d 0, tibia d 6, v 2-2-2, metatarsus d 2-1-1-2-3.

Spinnerets. PMS length 0.4, PLS, basal segment 0.6, median 0.4, terminal 0.5.

Comments on paratype. Specimen larger than holotype; carapace length 4.4, width 4.0. Left palp with 3 basal retrolateral heavy spines (instead of 2). Right legs II, III, IV and left III, IV missing. Tibia I spination (right) d 2-1-1-2, rv 5 in a line (2 proximal, 3 distal megaspines), pv 2-1, metatarsus pd 1-1 (proximal) - 1 (distal/apical), rv 1 distal to elbow and 1 very small apical spine; (left) d 2-1-2-2, rv 3 in line (1-1-1 distal megaspines), pv 1-1-1, metatarsus pd 1-1-1, rv 1-1 distal to elbow.

Etymology. The species is named in recognition of Dr Alan Yen's untiring activities in entomology and arachnology.



Figures 31–40. *Teyl yeni* sp. nov. Holotype, male. 31, dorsal view, carapace, chelicerae and abdomen; 32, sternal area and left maxilla; 33, eye group; 34, right tarsus I, prolaterodorsal; 35, right leg I, retrolateral, tibia, metatarsus, tarsus; 36, schematic dorsal spination right tibia I; 37, right metatarsus I, prolaterodorsal; 38, right palp, retrolateral; 39, right palp, prolateroventral; 40, schematic spination of right palp tibia, prolateral. Scale = 0.1 mm (figs 31, 32, 34, 35, 37–39); 0.5 mm (fig. 33); figs 36, 40 not to scale.

Acknowledgements

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Chirostylidae from north-western Australia (Crustacea: Decapoda: Anomura)

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Abstract

Ahyong, S.T., and Baba, K. 2004. Chirostylidae from north-western Australia (Crustacea: Decapoda: Anomura). *Memoirs of Museum Victoria* 61(1): 57–64.

New records and a new species of Chirostylidae from north-western Australia are reported. Prior to the present study, two chirostylids were known from north-western Australia. The present collection comprises seven species arrayed in three genera: *Chirostylus*, *Eumunida* and *Uroptychus*. Five species are newly recorded from Australian waters: *Eumunida ampliata*, *E. funambulus*, *E. pacifica*, *Uroptychus joloensis* and *U. nigricapillis*. *Chirostylus dolichopus* is newly reported from the Northern Territory. One species from the North West Shelf, *U. oxymerus* is new to science. A total of 40 species of Chirostylidae are now known from Australian waters.

Keywords

Crustacea, Decapoda, Anomura, Chirostylidae, Uroptychus, new species

Introduction

The Australian deep-water squat lobsters of the family Chirostylidae are known from relatively few studies (Henderson, 1885, 1888; Haig, 1974; Baba, 1986, 2000; de Saint Laurent and Macpherson, 1990; de Saint Laurent and Poupin, 1996; Ahyong and Poore, 2004). Of the 34 chirostylids recorded from Australia (Ahyong and Poore, 2004), only two are known from north-western Australia: *Chirostylus dolichopus* Ortmann, 1892 and *Uroptychus brucei* Baba, 1986. The present study is based on miscellaneous chirostylid collections from north-western Australia in the collections of the Australian Museum, Museum Victoria, and the South Australian Museum. Of the seven species reported below, five represent range extensions into Australian waters, and one is new to science. A total of 40 species of Chirostylidae is now known from Australian waters.

Measurements of specimens, given in millimetres (mm), indicate the carapace length including the rostrum unless indicated otherwise. Specimens are deposited in the Australian Museum, Sydney (AM), Natural History Museum, London (BMNH), Museum Victoria, Melbourne (NMV), and the South Australian Museum, Sydney (SAM).

Chirostylidae Ortmann, 1892

Chirostylus Ortmann, 1892

Chirostylus dolichopus Ortmann, 1892

Chirostylus dolichopus Ortmann, 1892: 246, pl. 11, figs 2, 2b, 2c,

2e, 2i, 2z [type locality: Kadsiyama (= Katsuyama), Sagami Bay, Japan].—Haig, 1974: 447.—Davie, 2002: 30.

Material examined. AM P25058, 1 male (4.4 mm), Timor Sea, Northern Territory, 9°30'S, 132°34'E, 124 m, MV *San Pedro Sound*, P. Colman, 9 Nov 1969.

Remarks. *Chirostylus dolichopus* was reported from tropical Western Australia by Haig (1974) without mention of a specific locality. The present specimen represents a new record for the Northern Territory.

Distribution. Western Indian Ocean, Sulu Archipelago, Japan, Western Australia and now the Northern Territory; 35–140 m (Baba, 1988).

Eumunida Smith, 1883

Eumunida (*Eumunida*) *funambulus* Gordon, 1930

Eumunida funambulus Gordon, 1930: 744, figs 1c, 2a, b, 3b, 4b, 5 [type locality: Gulf of Aden].

Eumunida (*Eumunida*) *funambulus*.—de Saint Laurent and Poupin, 1996: 350–352.

Material examined. SAM C725, 1 female (38.8 mm), Timor Sea, off Palmerston [now Darwin], Northern Territory, P. Foelske, Nov 1890.

Remarks. The single specimen agrees well with published accounts. Unfortunately, the depth of capture was not recorded for this and other specimens of *Eumunida* reported herein.

Distribution. Gulf of Aden to Indonesia, the Philippines, Japan (de Saint Laurent and Poupin, 1996) and now from Timor Sea, Northern Territory; 130–732 m.

***Eumunida (Eumunida) pacifica* Gordon, 1930**

Eumunida pacifica Gordon, 1930: 746, figs 6–7 [type locality: Timor Sea, Indonesia].

Eumunida (Eumunida) pacifica.—de Saint Laurent and Poupin, 1996: 359–362, figs 4a, b, 12a.

Material examined. SAM C724, 1 female (43.0 mm), Timor Sea, off Palmerston [now Darwin], Northern Territory, P. Foelske, Nov 1890; SAM C725, 4 males (16.9–32.1 mm), 1 female (20.0 mm), Timor Sea, off Palmerston [now Darwin], Northern Territory, P. Foelske, Nov 1890.

Remarks. The present specimens of *E. pacifica* are all in dry condition. One lot (SAM C725) forms part of a larger series of *Eumunida* that includes *E. funambulus* and *E. ampliata* (see below) registered as a single lot.

Distribution. Indonesia (Timor Sea, Moluccas, Kai Islands) and now from northern Australia; 204–304 m (de Saint Laurent and Poupin, 1996); 293–605 m (de Saint Laurent and Poupin, 1996).

***Eumunida (Eumunidopsis) ampliata* de Saint Laurent and Poupin, 1996**

Eumunida (Eumunidopsis) ampliata de Saint Laurent and Poupin, 1996: 368–371, figs 7a–e, 8a–e, 12c [type locality: Timor Sea].

Material examined. SAM C725, 2 males (21.8–25.9 mm), 2 females (23.1–28.1 mm), Timor Sea, off Palmerston [now Darwin], Northern Territory, P. Foelske, Nov 1890.

Remarks. The specimens are fragmented but nevertheless identifiable as *E. ampliata*.

Distribution. Indonesia (Kai Islands, Sahul Bank) and now from northern Australia; 204–304 m (de Saint Laurent and Poupin, 1996).

***Uroptychus* Henderson, 1888**

***Uroptychus joloensis* Van Dam, 1939**

Figure 1

Uroptychus joloensis Van Dam, 1939: 395–398, figs 2, 2a, 2b, 2c [type locality: Jolo, Indonesia].

Material examined. NMV J21046, 2 males (5.6–7.3 mm), ovigerous female (7.8 mm), North West Shelf between Port Hedland and Dampier, 18°45'S, 118°24'E, 142 m, trawl, G. Poore and H. Lew Ton, 5 Jun 1983 (stn NWA-23).

Diagnosis. Carapace lateral margins convex; dorsum unarmed; with anteriorly directed anterolateral spine and 2 lateral spines in advance of midlength; with low, narrow, marginal ridge extending from orbital to posterior margin. Sternal plastron with faintly concave anterior margin, and median notch. Cornea not dilated, about one-third length of remaining stalk. Antennal basal segment with small lateral spine; ultimate and penultimate segments of peduncle each with long distal spine. Antennal scale not exceeding apex of ultimate peduncle segment. Chelipeds smooth but sparsely setose; ischium with 2 dorsal and 1 ventral spine. Walking legs similar, slightly decreasing in length posteriorly, sparsely setose, segments

smooth; propodus with paired movable spines on distal flexor margin; dactylus with 6 or 7 strong, widely spaced, perpendicularly (or near perpendicularly) directed corneous teeth on flexor margin.

Description. Carapace: Length excluding rostrum slightly less than breadth. Lateral margins convex; with anteriorly directed anterolateral spine and 2 lateral spines in advance of midlength; with low, narrow, marginal ridge extending from orbital to posterior margin. Rostrum narrow, triangular, dorsally excavate. Outer orbital angle produced to small acute spine. Dorsum smooth, with scattered setae. Pterygostomian flap visible in dorsal view; with strong anterior spine, otherwise unarmed.

Sternum: Plastron about as long as wide, subquadrate. Sternite 3 (at base of maxilliped 3) with faintly concave or irregular anterior margin; with narrow, U-shaped median notch; anterolateral angle with blunt tubercle; anterior margin level with or very slightly exceeding sternite 4. Sternite 4 (at base of pereopod 1) with anterolateral margins angular.

Abdomen: Segments smooth, sparsely setose. Telson about one-third as long as broad; distal portion broadly convex posteriorly, shorter than proximal portion.

Eye. Cornea not dilated, about one-third length of remaining stalk; reaching approximately to midlength of rostrum.

Antenna: Basal segment with distolateral spine. Peduncle extending almost to apex of rostrum. Ultimate segment longer than penultimate segment, both with long distomesial spine. Antennal scale slightly wider than opposite peduncular segments, extending almost to apex of ultimate segment (excluding distal spine).

Maxilliped 3: Dactylus and propodus unarmed. Carpus with proximal spine on extensor margin. Merus with distolateral spine and 2 small flexor spines. Ischium with small distal spine lateral to rounded flexor distal margin. Crista dentata denticulate for length of ischium.

Pereopod 1 (cheliped): About 4 times carapace length; smooth but sparsely setose. Palm 5 times as long as high. Fingers crossing, opposable margins dentate and each with low process proximally; slightly longer than one-third palm-length. Carpus about as long as palm. Merus with 2 or 3 small spines on lower proximal margin. Ischium with 2 dorsal spines; ventrally with short subterminal spine on mesial margin.

Pereopods 2–4 (walking legs): Similar, slightly decreasing in length posteriorly, sparsely setose; segments smooth. Merus shorter than carapace. Propodus more than twice as long as carpus, not broadened distally, with paired movable spines on distal flexor margin. Dactylus with 6 or 7 strong, widely spaced, perpendicularly (or near perpendicularly) directed corneous teeth on flexor margin.

Remarks. The present specimens generally agree with the type account of *U. joloensis* Van Dam, 1939, based on a specimen from Jolo, Indonesia, in carapace shape and lateral spination, the armature of the dactyli of the walking legs, and small eyes. The present specimens differ from the type account of *U. joloensis* chiefly in the following features: the rostrum lacks distolateral spines, the fingers of the cheliped are longer than one-third instead of about one-quarter the length of the propodal palm, the anterior margin of the sternal plastron (sternite

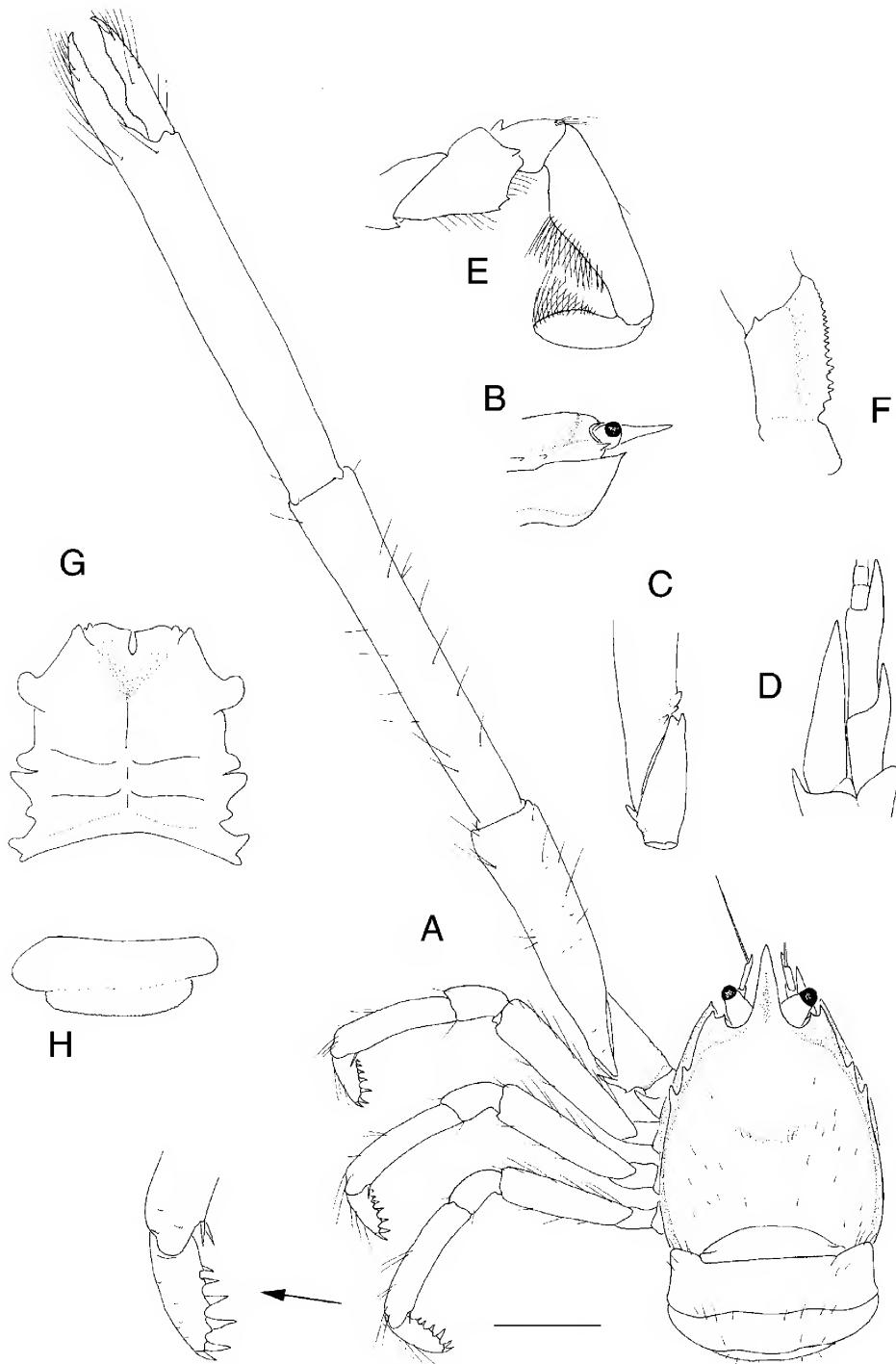


Figure 1. *Uroptychus joloensis* Van Dam, 1939, ovigerous female (7.8 mm), NMV J21046. A, dorsum. B, anterior carapace, right lateral view. C, right cheliped, proximal mesial view. D, right antenna, ventral view. E, right maxilliped 3, lateral view. F, crista dentata, right. G, sternal plastron. H, telson. Scale A–C, G = 3.0 mm, D–F = 0.7 mm, H = 1.5 mm.

3) does not distinctly exceed that of sternite 4, and the median notch of the sternal plastron is distinctly narrowed rather than a broad U-shape. The difference in rostral spination, whether apically trifid (as in the type) or singular (as in present material) is variable in this species as also in *U. tridentatus* (Henderson, 1885) and *U. zejuensis* Kim, 1972 (Baba, unpublished). The last mentioned differences appear to be within the range of expected morphological variation. As only the second record of the species, a description and figures of Australian material are provided.

Distribution. Jolo, Indonesia, and now from north-western Australia at depths between 37.8–56.7 m and 142 m.

Uroptychus nigricapillus Alcock, 1901

Figures 2A–I

Uroptychus nigricapillus Alcock, 1901: 282–284, pl. 3 fig. 3, 3a [type locality: Andaman Islands].—Alcock and McArdle, 1902, pl. 56 fig. 3.

Material examined. AM P67832, 1 ovigerous female (11.0 mm), North West Shelf, 240 km NW of Port Hedland, Western Australia, 500 m, J. Paxton, 7 Apr 1982 (stn S02/82/31).

Diagnosis. Carapace excluding rostrum distinctly longer than broad; lateral margins slightly divergent; with 3 or 4 small spines behind base of cervical groove; with anteriorly directed anterolateral spine; posterior quarter with low ridge. Rostrum sharply triangular, exceeding one-third length of remaining carapace. Outer orbital angle produced to small spine extending to level of anterolateral spines. Dorsum with pair of distinct epigastric spines. Sternite 3 anterior margin deeply emarginate, with pair of median spines separated by narrow notch. Antennal basal segment with small outer spine; ultimate and penultimate segments unarmed. Antennal scale extending slightly beyond midlength of ultimate peduncular segment. Chelipeds smooth, fingers setose. Pereopod 4 slightly shorter than pereopods 2 and 3; sparsely setose; propodi with 6–9 movable spines on distal flexor margin, none paired; distalmost flexor spine remote from distal margin; dactyli with 8–10 small spines on flexor margin, oriented oblique to dactylar margin, distal 2 appressed.

Description. **Carapace:** Length excluding rostrum distinctly greater than breadth. Lateral margins slightly divergent; with 3 or 4 small spines behind base of cervical groove, anterior-most spine with small additional dorsal spine; with anteriorly directed anterolateral spine; posterior quarter with low carina. Rostrum sharply triangular, exceeding one-third length of remaining carapace; margins unarmed. Outer orbital angle produced to small spine extending to level of anterolateral spines. Dorsum smooth, with pair of distinct epigastric spines; cervical groove distinct medially. Pterygostomian flap with small anterior spine.

Sternum: Plastron broader than long, widening posteriorly. Sternite 3 (at base of maxilliped 3) depressed, anterior margin narrow, deeply emarginate, with pair of median spines separated by narrow notch; with distinct anterolateral tooth. Sternite 4 (at base of pereopod 1) with distinct anterolateral tooth extending anteriorly to level of base of emargination of sternite

3; margins dentate, irregular; demarcation between sternites 4 and 5 dentate.

Abdomen: Abdominal segments glabrous. Telson length about half breadth; distal portion posteriorly emarginate, about twice length of proximal portion.

Eye: Cornea moderately dilated, subequal to length of peduncle; reaching to distal quarter of rostrum;

Antenna: Basal segment with small outer spine. Peduncle extending to distal third of rostrum. Flagellum about 3 times as long as peduncle. Ultimate and penultimate segments unarmed; ultimate segment about 2.5 times length of penultimate segment. Antennal scale slightly wider than opposite peduncular segments, extending slightly beyond midlength of ultimate peduncular segment.

Maxilliped 3: Dactylus, propodus, carpus and merus unarmed. Crista dentata distinctly serrate on proximal two-thirds of ischium, extending onto basis.

Pereopod 1 (cheliped): Slender, cylindrical, about 3.5 times carapace length; glabrous dorsally; fingers setose. Palm about 4 times as long as high, about 1.5 times as long as fixed finger; lower margin with row of low granules. Fingers crossing, opposable margins dentate; occlusal margin of movable finger with obtuse process proximally; occlusal margin of fixed finger without distinct prominence. Carpus longer than merus and propodal palm; glabrous. Merus usually with several low granules on inner proximal margin. Ischium with short, slender spine on dorsolateral margin.

Pereopods 2–4 (walking legs): Similar; sparsely setose; decreasing in length posteriorly. Pereopod 1 merus longer than carapace. Merus extensor margin smooth. Carpus about 0.5 merus length, about two-thirds propodus length. Propodi not broadened distally, with 6–9 movable spines on distal flexor margin; distalmost flexor spine remote from distal margin. Dactyli setose marginally, with 8–10 small spines on flexor margin, oriented oblique to dactylar margin, distal 2 appressed. Pereopod 4 slightly shorter than pereopods 2 and 3.

Ova: Diameter 0.8 mm.

Remarks. The single Australian specimen agrees well with the original account and figures of *U. nigricapillus* in most respects (Alcock, 1901; Alcock and McArdle, 1902) and represents the first record from Australian waters. It differs from figures of the holotype in having relatively longer legs, such that the merus of the first walking leg in the Australian specimen is longer than, instead of shorter than, the carapace length (excluding rostrum). In a series of Indian Ocean specimens (from several localities) attributed to *U. nigricapillus*, Tirmizi (1964) noted considerable variation in the ornamentation of the sternites, the distinctness of the epigastric and lateral spines on the carapace, and length of the antennal scale – features normally considered diagnostic in many species. Unfortunately, the sternum of the holotype of *U. nigricapillus* was neither figured nor described by Alcock (1901). A Java Sea specimen figured by Van Dam (1940: fig. 2), however, bears a transverse row of tubercles behind the dentate anterior margin of sternite 4 in contrast to the Australian specimen which lacks tubercles. Tirmizi (1964) also noted variation in the sternal armature, in which the sternum of only one specimen resembled Van Dam's (1940) figure.

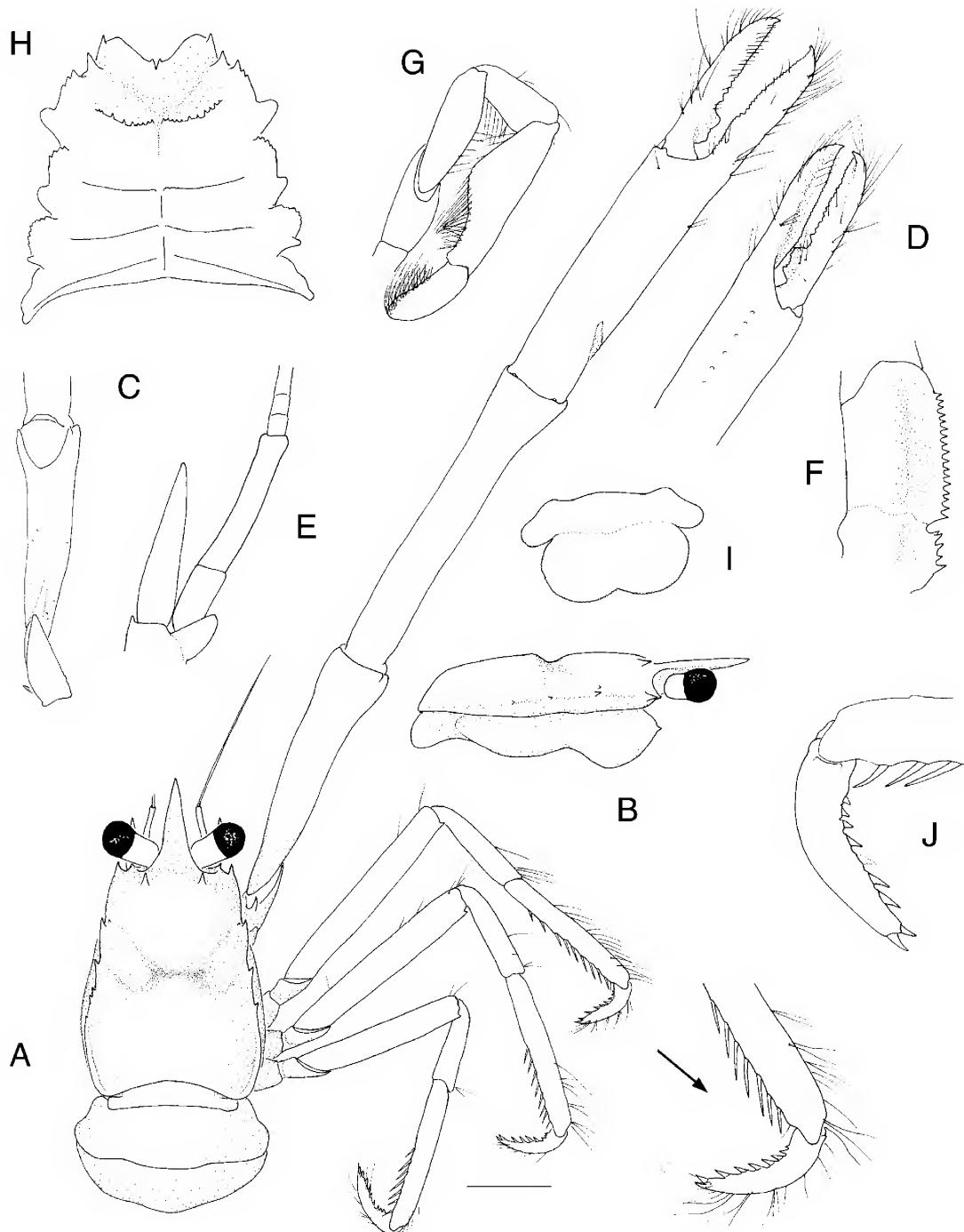


Figure 2. A–I, *Uroptychus nigricapillus* Alcock, 1901, ovigerous female (11.0 mm), AM P67832. J, *Uroptychus gracilimanus* (Henderson, 1885), female (9.4 mm), AM P65825. A, dorsum. B, carapace, right lateral view. C, cheliped, proximal ventral view. D, cheliped, distal ventral view. E, right antenna, ventral view. F, right maxilliped 3, lateral view. G, crista dentata, right. H, sternal plastron. I, telson. J, left pereopod 2, dactylus and distal propodus. Scale A–D = 3.0 mm, E–F = 0.7 mm, G–J = 1.5 mm.

The Australian specimen bears well-developed epigastric spines, and small but distinct lateral carapace spines as in Alcock's (1901) account. Variation in the presence and degree of epigastric ornamentation is also known in other congeners (e.g. *U. australis* (Henderson, 1885), *U. gracilimanus* (Henderson, 1885), *U. vandamae* Baba, 1990). However, variation in other characters mentioned by Tirmizi (1964) and other studies (e.g. Baba, 1981, 1988), namely, the lateral carapace spination and ornamentation and morphology of the sternal plastron, suggests that more than one species could be confused under *U. nigricapillis*. In view of morphological variation in *U. nigricapillis* reported in previous studies, the Australian specimen is described and illustrated.

Uroptychus nigricapillis closely resembles *U. gracilimanus*, described from off Port Jackson, in general habitus, armature of the dactyli of the walking legs, and in variation in the presence and size of the epigastric spines. *Uroptychus nigricapillis* differs, however, in the presence of lateral spines on the carapace margins, in bearing a short slender spine instead of a low tooth on the cheliped ischium, and in the spination of the propodi of the walking legs. Thus, in *U. nigricapillis* and the distal flexor spine on the propodi of the walking legs is positioned more remotely from the distal margin than in *U. gracilimanus* (Fig. 2A). The distal-most of the flexor spines is located close to the articulation with the dactylus, a fact confirmed by examination of the holotype of *U. gracilimanus* (BMNH 1888: 33, off Port Jackson). In the specimen of *U. gracilimanus* figured by Ahyong and Poore (2004: fig. 10, AM P65825, off Port Jackson), some of the movable propodal spines on the walking legs are damaged or lost. The dactylus and distal portion of the propodus of the left first walking leg of the same specimen of *U. gracilimanus* is shown (Fig. 2J) for comparison with the condition in *U. nigricapillis*.

Distribution. Western Indian Ocean, Andaman Sea, Indonesia, the Philippines and now from north-western Australia at 66–1930 m depth.

Uroptychus oxymerus sp. nov.

Figure 3

Material examined. Holotype: NMV J21040, male (>6.5 mm), North West Shelf, between Port Hedland and Dampier, 184 m, G. Poore and H. Lew Ton, 6 Jun 1983 (stn NWA-24).

Diagnosis. Carapace lateral margins convex; dorsum unarmed; with strong, anteriorly directed anterolateral spine and 5 or 6 stout lateral spines. Rostrum apically trifid; dorsally excavate. Sternal plastron with faintly concave anterior margin, and median notch. Cornea not dilated, about one-third length of remaining stalk. Antennal basal segment with outer spine; ultimate and penultimate segments of peduncle each with long distal spine. Antennal scale exceeding apex of ultimate peduncle segment. Chelipeds rugose, setose; merus with row of strong, stout spines on mesial ventral margin. Walking legs similar, slightly decreasing in length posteriorly, setose, segments rugose; propodus distal flexor margin with 2 or 3 movable spines, distal most paired; dactylus with 6 or 7 strong, widely

spaced, perpendicularly (or near perpendicularly) directed corneous teeth on flexor margin.

Description. Carapace: Length excluding rostrum subequal to breadth. Lateral margins convex; with anterolateral spine and 5 lateral spines and spinule above third lateral spine; anterolateral spine, strong, directed anteriorly; first and second lateral spine slender; third and fourth lateral spines stout, larger than others; fifth lateral spine low, blunt. Rostrum apically trifid; dorsally excavate. Outer orbital angle produced to small acute spine. Dorsum smooth, with scattered setae. Pterygostomian flap with strong anterior spine and field of spines and tubercles on anterior half.

Sternum: Plastron about as long as wide, subquadrate. Sternite 3 (at base of maxilliped 3) anterior margin shallowly concave, with narrow U-shaped median notch, anterolateral angle blunt. Sternite 4 (at base of pereopod 1) with anterolateral margins pointed, not produced beyond anterior concavity of sternite 3.

Abdomen: Segments glabrous. Telson about half as long as broad; distal portion posteriorly emarginate, longer than proximal portion.

Eye: Cornea not dilated, about half as long remaining stalk; not reaching beyond midlength of rostrum;

Antenna: Basal segment with distolateral spine. Peduncle extending beyond distal half of rostrum. Ultimate segment about twice as long as penultimate segment, both with long distomesial spine; ultimate also with 2 small marginal spines. Antennal scale slightly wider than opposite peduncular segments, extending slightly beyond apex of ultimate segment.

Maxilliped 3: Dactylus and propodus unarmed. Carpus with distal and 2 proximal spines on extensor margin. Merus with distal extensor spine and 2 distal flexor spines. Ischium with small spine lateral to distal end of flexor margin. Crista dentata denticulate for length of ischium.

Pereopod 1 (cheliped): About 4 times carapace length; all segments rugose and setose. Palm 3 times as long as high, about 2.5 times as long as fixed finger; surface with short, transverse, depressions. Fingers crossing, opposable margins dentate and each with low process proximally. Carpus with small lower distal spine adjacent to each articular condyle of propodus. Merus with row of 5 stout spines on mesial ventral margin and group of 3 spines proximally. Ischium with 2 dorsal spines and 1 ventral spine; distal dorsal spine slender, depressed.

Pereopods 2–4: Similar, slightly decreasing in length posteriorly, strongly setose; segments rugose, setose. Merus shorter than carapace. Propodus more than twice length of carpus, not broadened distally, with 2 or 3 movable spines on distal flexor margin, distalmost paired. Dactylus with 6 or 7 strong, widely spaced, perpendicularly (or near perpendicularly) directed corneous teeth on flexor margin.

Etymology. From *oxy*, sharp, and *merus*, the fourth limb segment, in reference to the sharp, stout spines on the merus of the cheliped that distinguish the new species from *U. tridentatus* and *U. zejuensis*.

Remarks. *Uroptychus oxymerus* sp. nov. closely resembles *U. tridentatus* (Henderson, 1885), described from Indonesia,

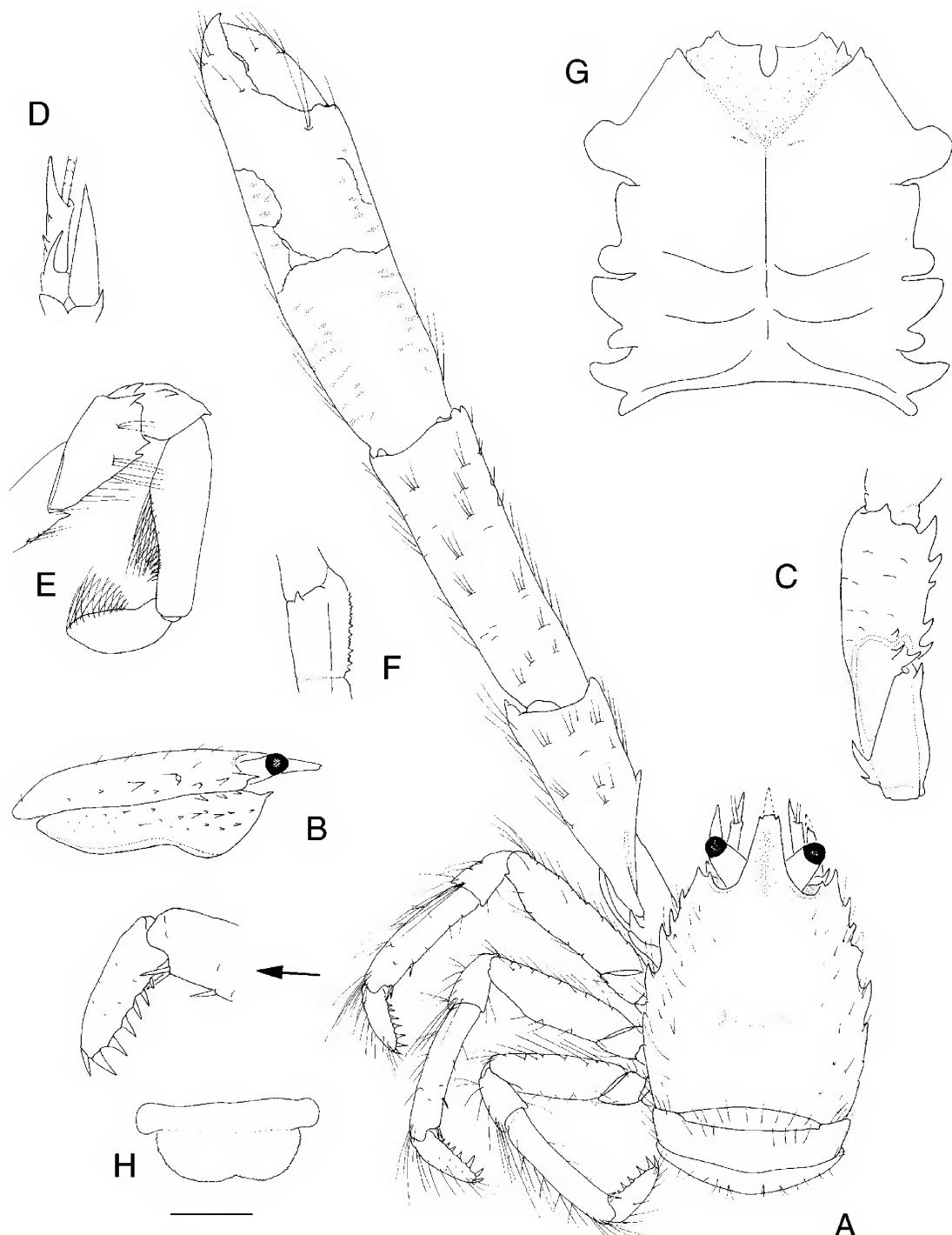


Figure 3. *Uroptychus oxymerus* sp. nov., holotype male (+6.5 mm), NMV J21046. A, dorsum. B, carapace, right lateral view. C, right cheliped, proximal mesial view. D, left antenna, ventral view. E, right maxilliped 3, lateral view. F, crista dentata, right. G, sternal plastron. H, telson. Scale A–C = 2.0 mm, D–H = 1.0 mm.

and *U. zezuensis* Kim, 1972 from Korea, in almost all respects including the spinose carapace margins, distally spinose segments of the antennal peduncle, armature of pereopods 2–4, and shape of the sternal plastron. The new species is readily distinguished from both *U. tridentatus* and *U. zezuensis* by having a row of large, stout spines instead of a cluster of spines on the mesial ventral margin of the merus of the cheliped, in having three instead of two spines on the extensor margin of the carpus of the third maxilliped, and in having spines along the lower margin of the ultimate segment of the antennal peduncle in addition to the distal spine.

Four species of *Uroptychus* are now known from the North West Shelf. *Uroptychus oxymerus* is readily distinguished from *U. joloensis* by having distinctly more spinose lateral carapace margins (5 or 6 instead of 2); from *U. nigricapillis* by lacking a pair of epigastric spines on the carapace and in having a distal spine on the ultimate and penultimate segments of the antennal peduncle; and from *U. brucei* by having lateral carapace spines.

Distribution. Known only from the type locality at 184 m depth.

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Sicafodiidae, fam. nov. for *Sicafodia stylos*, gen. nov., sp. nov., from the marine bathyal of south-eastern Australia (Crustacea: Amphipoda: Gammaridea)

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Abstract

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A new genus and species, *Sicafodia stylos*, is described from bathyal depths (400–1277 m) off south-eastern Australia. Following a discussion of its possible placement in existing families, a new family, Sicafodiidae, a potential sister taxon to the Pardaliscidae, is established. The new species is characterised by the extreme elongation of its conically bundled mouthparts including the inner plate of the maxilliped, a completely smooth body, short, broadly rounded coxal plates, slender, simple but strongly dissimilar gnathopods and elongate pereopods. An analysis of the functional morphology of the mouthparts, including muscles in the upper lip and epistome, indicates that *Sicafodia stylos* feeds by piercing its prey and sucking up macerated/liquefied food. The actual food items are not known.

Keywords

Crustacea, Amphipoda, Sicafodiidae, fam. nov., *Sicafodia*, deep-sea, Australia

Introduction

The new species described below was collected as part of the South-Eastern Australian Slopes Program of Museum Victoria and the Victorian Institute of Marine Sciences. The program commenced in 1986 with sampling at bathyal depths (approximately 200 to 2900 metres) off southern New South Wales, Bass Strait and eastern Tasmania, followed by a similar sampling program in 1988. A highly diverse and novel fauna of Peracarida was brought to light. A preliminary analysis of the composition and diversity of Isopoda and comments on other groups of Crustacea, together with environmental data from this stretch of continental margin towards the Tasman Sea, was provided by Poore et al. (1994).

The length of specimens was measured from the tip of the rostrum along the dorsal curvature to the tip of the telson. The specimens are deposited in the collections of Museum Victoria, Melbourne, Australia.

Classification of the new species

Using Barnard and Karaman's (1991) key to families, the new species falls among Ochlesidae (as Ochlesinae in their broad concept of the Iphimediidae) and Lafystiidae on account of its lack of a mandibular molar and the reduced number of articles (three) in the maxillipedal palp. Using the key in Coleman and

Barnard (1991) the species keys out in the vicinity of Lafystiidae and Laphystiopsidae on account of its simple gnathopod 1, rounded, non-elongate coxae 1–3, and lack of mandibular raker setae. None of these characters is unique to those families. Bousfield (1983), Barnard and Karaman (1991) and, by implication, Coleman and Barnard (1991) assumed that at least Lafystiidae, and for the last two works possibly also Laphystiopsidae, are basically related to the iphimedioids. A recent phylogenetic analysis of amphipod families (Berge et al., 2000), however, places those two families in separate clades, neither with iphimedioid families. The Lafystiidae do, however, show some similarities with the iphimedioids (see discussion below) in the elongate, acuminate coxa 4 and short, robust pereopods with curved dactyli, the conically pointed, but weakly modified mouthparts, simple gnathopod 1 and subchelate gnathopod 2. For these reasons, the family is implicitly included in the general discussion of the iphimedioids below. Laphystiopsidae have simple, identical gnathopods similar to, but smaller than, pereopods 3 and 4, and quadrately bundled unmodified mouthparts. Laphystiopsidae bear little resemblance to the new species and will not be discussed further. For Ochlesidae see discussion below.

The most immediately obvious characteristics of *Sicafodia stylos* is the extreme elongation and acuteness of the downward, backward pointing mouthpart bundle. Conically bundled, pointed mouthparts are uncommon in gammaridean

Amphipoda. They are found primarily in the conicostomatid group of genera in the Lysianassoidea (see Lowry and Stoddart, 1983), in monotypic Didymocheliidae, in the iphimedioids, and in two genera of the Pardaliscidae.

Sicafodia stylos clearly does not belong in the Lysianssoidea, species of which have a characteristic body shape and an elongate ischium and mitten shaped propodus of gnathopod 2. Whilst there are some similarity in the mouthparts, notably in the enlarged, folded outer plate and the elongate inner plate of the maxillipeds in some conicostomatid genera, these similarities must have been independently derived to serve a similar function (see section on mouthpart function below).

The three known species of *Didymochelia* (see Bellan-Santini and Ledoyer, 1986, Lowry and Stoddart, 1995) have moderately conical mouthpart bundles, but little or no modification of mouthparts with regard to elongation or reductions. Furthermore, didymocheliids have gnathopods 1 and 2 chelate, pereopods 3–7 short and strong with curved dactyli, uropod 3 reduced to a stubby ramus only, and the telson shorter than wide, entire. *Sicafodia stylos* cannot be referred to the Didymocheliidae.

Coleman and Barnard (1991) divided the non-eusiroid iphimedioids into six families: Iphimediidae, Ochlesidae, Acanthonotozomatidae, Acanthonotozomellidae, Dikwididae and Odiidae. Berge et al. (1999) merged Ochlesidae and Odiidae under the former name. Species in these families have conically bundled, more or less elongate mouthparts with a variety of strong or less strong reductions. The strongest elongations and reductions are found in species of Ochlesidae s.s. None, however, exhibits the extremes found in *Sicafodia stylos*. Iphimedioids have moderately compressed bodies (broadly rounded dorsally in *S. stylos*), dorsal spines and/or carina (smooth), one or more of coxae 1–4 elongate, tapering and acuminate, or elongate and oddly shaped (Ochlesidae s.s.) (approximately as long as broad, non-tapering, apex broad, rounded), one or more of pleonal sideplates 1–3 with acute posteroventral corner and often with additional cusp on posterior margin of sideplate 3 (broadly rounded, no cusps), pereopods 3–7 short, strong, ‘clinging’ with strong, curved dactylus (slender, elongate, dactylus slender, nearly straight). Some iphimedioid families have simple, similar or dissimilar gnathopods 1 and 2; in some families both gnathopods are subchelate or chelate; in others a combination; while they are carpo- or merochelate in Ochlesidae s.s. Simple gnathopods occur in many gammaridean families. Thus, there are no characters that unequivocally places *S. stylos* within the iphimedioids, while its smooth dorsum, elongate, slender pereopods 3–7 and short, rounded coxae 1–4 in particular preclude such an allocation.

Sicafodia stylos shares with Pardaliscidae a smooth body, short simple coxae 1–4, simple gnathopods 1–2, slender pereopods 3–7 (5 and 7 assumed), and lanceolate uropodal rami. However, the gnathopods in *S. stylos* are highly dissimilar, whereas in the Pardaliscidae they are generally of similar shape and size. Pardaliscids normally have quadrately bundled mouthparts, with broad molar incisors and strongly reduced (or absent) inner plate of the maxillipeds (prominent and much

elongate in *S. stylos*). The exceptions to quadrate mouthparts in pardaliscids are *Halicella* Schellenberg (monotypic) and *Rhynohalicella* Karaman (monotypic), in both of which mouthparts form a small downward or forward pointed cone respectively, but the structure and reductions of individual mouthparts differ significantly from those of *S. stylos*.

Conical bundling with some elongations and reductions in mouthparts clearly has been independently derived in several non-related families, and therefore does not in itself place *S. stylos* within any of the groups discussed. Disregarding the mouthparts, *S. stylos* appears to be closer to the Pardaliscidae than to any of the other families mentioned. The prominent inner plate of the maxillipeds and the dissimilar gnathopods would appear to preclude the inclusion of the new species in that family, although it could be conceived as representing a separate subfamily taxon in the Pardaliscidae with extremely apomorphic mouthparts, but having retained a plesiomorphic inner plate of the maxillipeds, reduced or lost in all other members of the family (the sister clade). However, because of the lack of males, and lack of complete antennae 1 and 2 and pereopods 5 and 7 in all specimens, which might provide firmer clues to the placement of this species, I hesitate to place *Sicafodia stylos* in the Pardaliscidae. Instead, I refer it to a new family, Sicafodiidae, a potential sister taxon of Pardaliscidae.

Sicafodiidae fam. nov.

Diagnosis. Body broad, smooth; cuticle smooth. Cephalon short with well developed rostrum. Pereonite 1 enlarged, partly overlapping cephalon. Pleonal sideplates broadly rounded. Primary flagellum of antennae multiarticulate (not confirmed for antenna 2), accessory flagellum present, 1-articulate, antenna 1 with callynophore commencing on first flagellar article. Coxal plates 1–4 apically rounded, barely longer than broad, overlapping, forming an even ventral curve, coxa 4 barely excavate posteriorly. Mouthparts elongate, grouped into sharply pointed downward-backward pointing cone. Upper lip apically notched. Mandibles without molar and spine row, with 3-articulate palp, both mandibles with rod-shaped lacinia mobilis. Lower lip with mandibular lobes, inner lobes absent. Maxilla 1 without palp, inner plate digitiform, outer plate with 9 distal spine-like setae. Maxilla 2 plates slender, with apical and subapical setae only. Maxilliped with 3-articulate palp, outer and inner plates of subequal length. Gnathopods 1 and 2 simple, strongly dissimilar. Pereopods 3–7 slender, dactyls slender, nearly straight, pereopods 5–7 with article 2 expanded. Urosomites free. Uropods with full complement of slender, lanceolate rami, peduncle of uropod 3 short. Telson short, laminate, apically incised. Coxal gills simple sacks, on pereopods 2–7. Oostegites on pereopods 2–5, 2–4 broad, sparsely setose, 5 linear.

Type genus. *Sicafodia* gen. nov.

***Sicafodia* gen. nov.**

Type and only species. *Sicafodia stylos* sp. nov.

Diagnosis. With the characters of the family.

Etymology. The name of the genus is derived from Latin, *sica*, dagger, and *fodio*, to stab, hence ‘the one that stabs with a dagger’, alluding to the shape of the mouthpart bundle. Feminine.

***Sicafodia stylos* sp. nov.**

Figures 1–4

Material examined. Holotype. Female with developing ovaries, 3.7 mm, Australia, eastern Tasmania, off Freycinet Peninsula, 41° 57.50'S, 148° 37.90'E, 400 m, coarse biogenic rubble, mud, WHOI epibenthic sled, M.F. Gomon et al., RV *Franklin*, 27 Jul 1986 (stn SLOPE-48), NMV J23915 (condition: antennae, some pereopods and tip of some uropods broken).

Paratypes (5 specimens, all from Australia). Same data as holotype, NMV J23916 (female A, with apparent traces of broken oostegites; condition: antennae and most pereopods and uropods broken, telson missing). Eastern slope of Bass Strait, 38° 21.90'S, 149° 20.00'E, 1000 m, WHOI epibenthic sled, G.C.B. Poore et al., RV *Franklin*, 23 July 1986 (stn SLOPE-32), NMV J23917 (female B, with fully developed oostegites, 4.6 mm; condition: antennae, some pereopods and uropods broken), NMV J23918 (female C, with fully developed oostegites; condition: half specimen, everything posterior to pereonite 6 missing, antennae and most pereopods broken), NMV J23919 (female D, with fully developed oostegites; condition: half specimen, everything posterior to pereonite 7 missing, antennae and most pereopods broken). Eastern Bass Strait slope, 67 km S of Point Hicks, 38° 23.78'S, 149° 17.02'E, 1119–1277 m, fine mud, WHOI epibenthic sled, G.C.B. Poore et al., RV *Franklin*, 25 Oct 1988 (stn SLOPE-67), NMV J23920 (1 specimen, condition: antennae, all pereopods and most of uropods broken).

Description. Cephalon depth approximately 2.5 times mid-lateral length. In lateral view cephalon tapering towards right angled ventral corner. Ocular lobes broadly rounded, continuing in nearly straight line to ventral corner. Eyes absent. Rostrum about as long as deep in lateral view, apex rounded triangular, approximately half length of non-rostral part of cephalon, ventrally forming a narrow angle with elongate, convex frons part of cephalon. Epistome short, unproduced.

Pereonite 1 as long as its anterior depth, as long as 2 and 3 combined. Pleosome dorsal length equalling combined length of pereonites 2–7, pleonites of equal length.

Coxal plates 1–4 with smoothly rounded ventral margin; plates 1–3 of subequal length when flattened, (appear to increase in length from 1 to 3 in Fig. 1 habitus, due to 1 and 2 curving slightly inwards), of rounded rectangular shape but increasing in width from 1 to 3; coxa 1 length:width 1.25, coxa 2 length:width 1.20, coxa 3 length:width 1.0, coxa 4 length:width 0.70, with rounded angular posterior projection and weak concavity posterior to projection; coxa 5 with lobes equally deep, anterior lobe wider, evenly rounded, posterior lobe rounded rectangular; coxa 6 similar to 5, but posterior lobe approximately third deeper than anterior lobe; coxa 7 an evenly rounded semicircle. Pleonal sideplates with smooth margin; plate 1 with weakly angular apex, 2 and 3 rounded.

Antenna 1, peduncular article 1 as long as 2 and 3 combined, approximately 10% longer than lateral width, articles 2 and 3 of subequal length, both somewhat telescoped into preceding article, article 3 with lateral apical margin extended beyond

insertion of accessory flagellum; *accessory flagellum* approximately half length of flagellar article 1, distally tapering, with 1 apical and 1 subapical setae; article 1 of flagellum approximately two-fifths as wide as long, with single-field callynophore composed of 4–5 irregular rows of aesthetascs, article 2 and 3 with 2 distal rows of similar aesthetascs. Antenna 2 with broad, apically pointed antennal cone; peduncular article 4 approximately twice as long as wide, reaching to apex of flagellar article 1 of antenna 1. (Antennae otherwise broken in all specimens, but the shape of the proximal parts known suggests that the flagellum of both antennae is simple, multiarticulate). Upper lip approximately 2.5 times longer than wide at base (anterior view), narrowing in middle, tapering towards bilobed apex, apical notch forming a narrow angle. Mandibles styliform distal to insertion of palp, reaching to apex of upper lip; left mandible with irregularly notched apex, lacinia mobilis a long slender rod terminating in strongly oblique cutting edge with 6 or 7 small denticles; right mandible with 3 blunt teeth apically, lacinia mobilis quarter to half length of left lacinia mobilis, with bifid apex; strong palp inserted in proximal third of mandibular body, reaching slightly beyond apex of mandible, article 1 as long as broad, article 2 approximately 4 times longer than broad with 2–3 distal setae, article 3 approximately three-quarters length of 2, with up to 4 setae on posterior margin and approximately 4 apical setae, lateral surface partly covered with fine setules. Lower lip with styliform lobes, lobes finely setose apically not quite reaching apex of mandibles; mandibular lobes short, slender, pointing directly backwards. Maxilla 1 outer plate approximately 11 times longer than greatest width; distal 9 spine-like setae falling into three groups: 2 apical setae (one coarsely serrate along entire length, one finely serrate in distal quarter), 5 setae closely set on strongly oblique margin (regularly denticulate in distal half), 2 poorly articulating, flattened more proximal setae closely adpressed to medial surface of plate, coarsely and irregularly serrate along entire margin; inner plate approximately third length of outer, slender, cylindrical, tapering towards rounded apex, without setae. Maxilla 2 outer plate approximately 9 times longer than greatest width, with tuft of approximately 6 unequally long apical setae; inner plate approximately 80% length of outer, with 4 apical simple setae and 3 short, subapical medial bi- or trifid setae. Maxilliped palp article 1 ovoid, approximately 50% longer than wide, article 2 approximately 80% length of 1, of similar shape, article 3 as long as 1 and 2 combined, third width of 2, approximately 9 times longer than wide with 3 or 4 groups of 2 or 3 setae on midlateral surface and tufts of apical and subapical setae; outer plates broad in proximal third, tapering towards truncate apex, apex with row of at least 8 blunt, rod-like setae evenly decreasing in length from medial to penultimate lateral seta, lateralmost seta stouter than the rest, approximately as long as medialmost one, curved mediad, with denticles in distal quarter, (because of the natural forward folding of outer plates around remaining mouthparts, Fig. 2C mxp dv, the lateralmost, denticulate seta, Fig. 2A mxp op, is functionally in a medial position, cf. above); inner plates nearly as long as outer plates, each plate slender with nearly parallel margins, terminating in bluntly pointed apex with what appears to be glandular tissue in terminal part (Fig. 2C mxp ip), plates

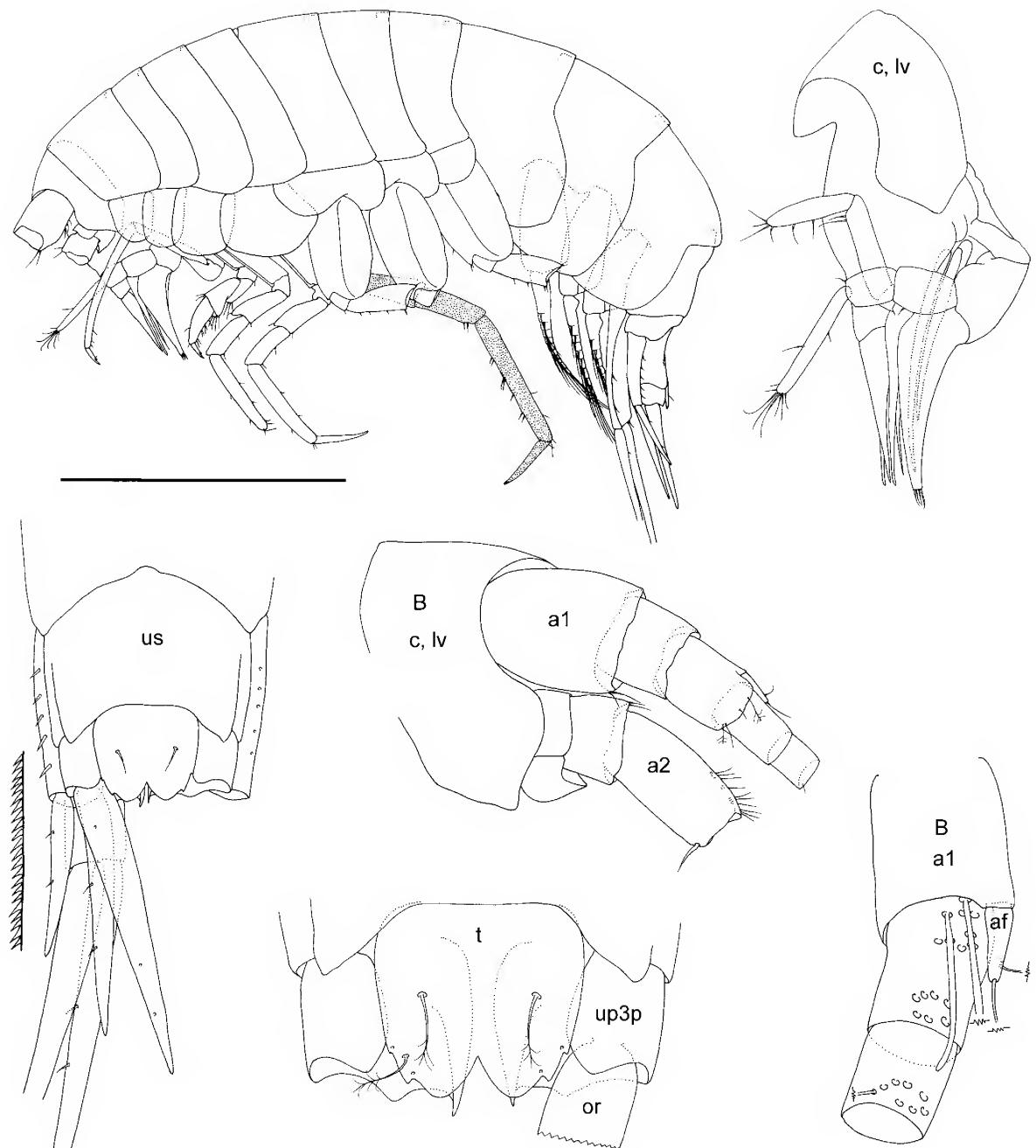


Figure 1. *Sicafodia stylos*, gen. nov., sp. nov. Holotype, except B, paratype, female B (NMV J23917). a1, antenna 1; a2, antenna 2; af, accessory flagellum; c, head; lv, lateral view; or, outer ramus up3; t, telson; up3p, uropod 3 peduncle; us, urosome. Habitus scale bar: 1 mm.

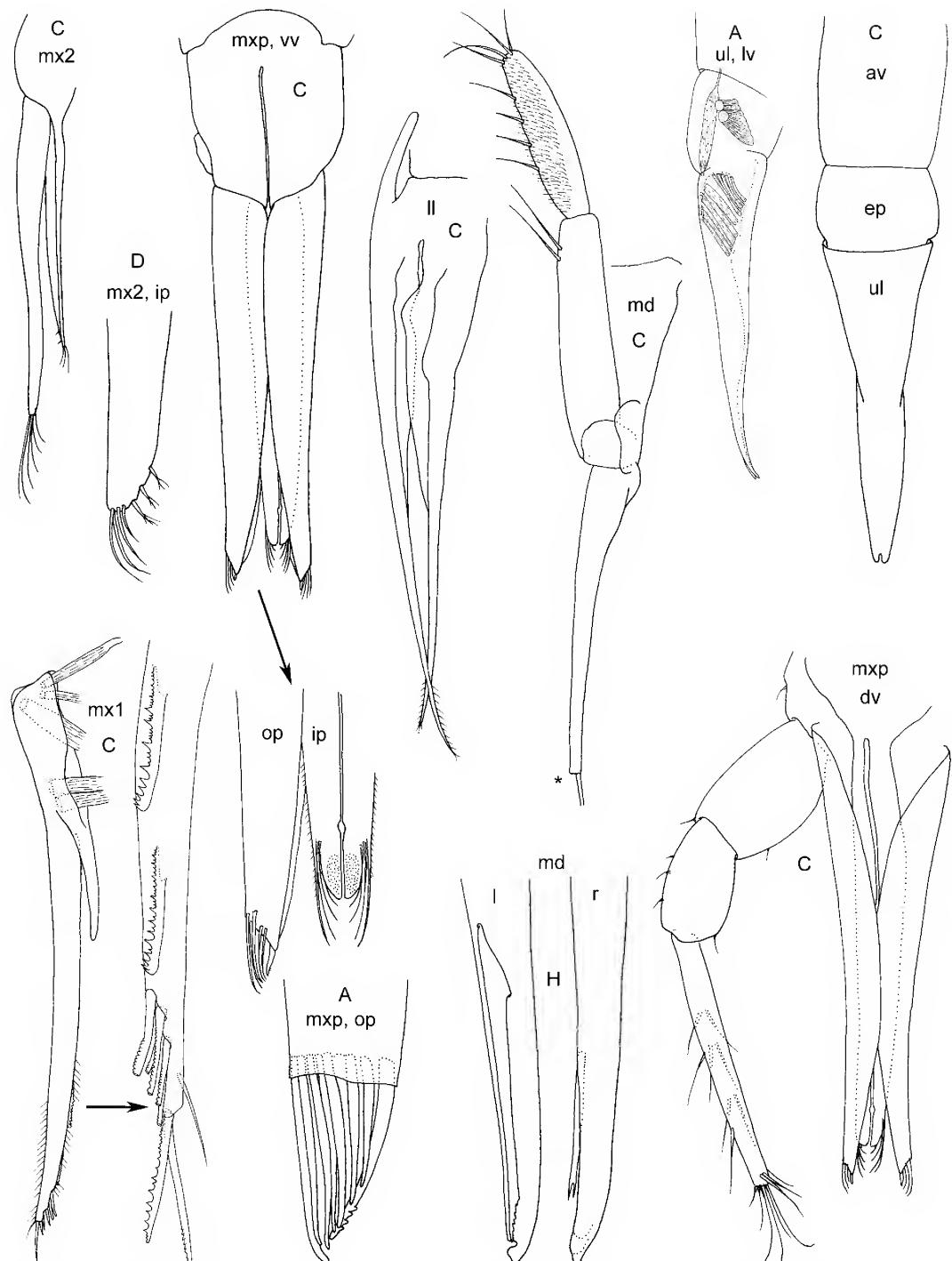


Figure 2. *Sicafodia stylos*, gen. nov., sp. nov. A, paratype, female A (NMV J23916); C, paratype, female C (NMV J23918); D, paratype, female D (NMV J23919); H, holotype. av, anterior view; dv, dorsal view; ep, epistome; ip, inner plate; I, left; II, lower lip; l, r md, mandible; mx1, 2, maxilla 1, 2; mxp, maxilliped; op, outer plate; r, right; ul, upper lip; vv, ventral view; asterisk: tip of mandible and lacinia mobilis broken.

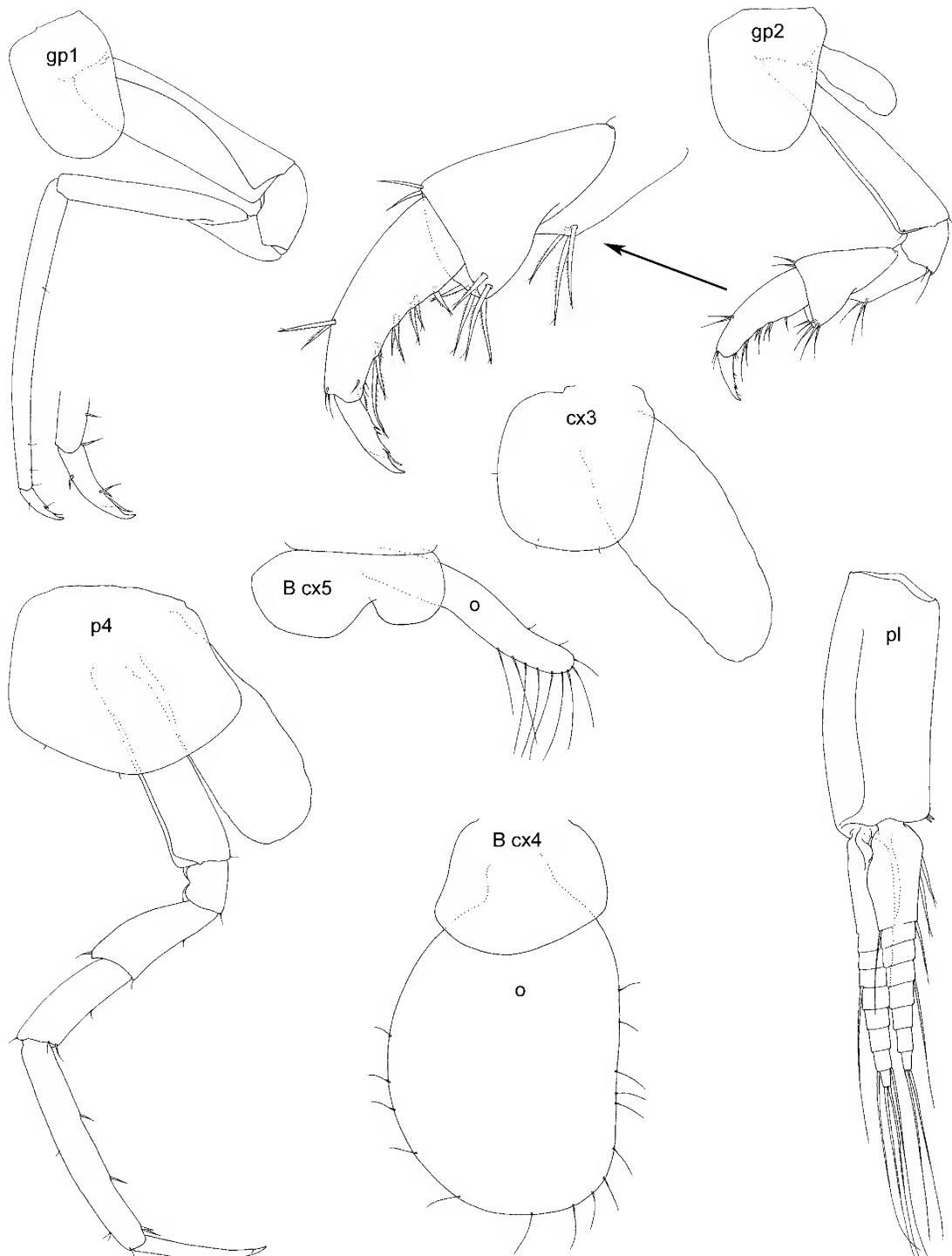


Figure 3. *Scafodia stylos*, gen. nov., sp. nov. Holotype, except B, paratype, female B (NMV J23917). cx, coxa; gp, gnathopod; o, oostegite; p, pereopod; pl, pleopod.

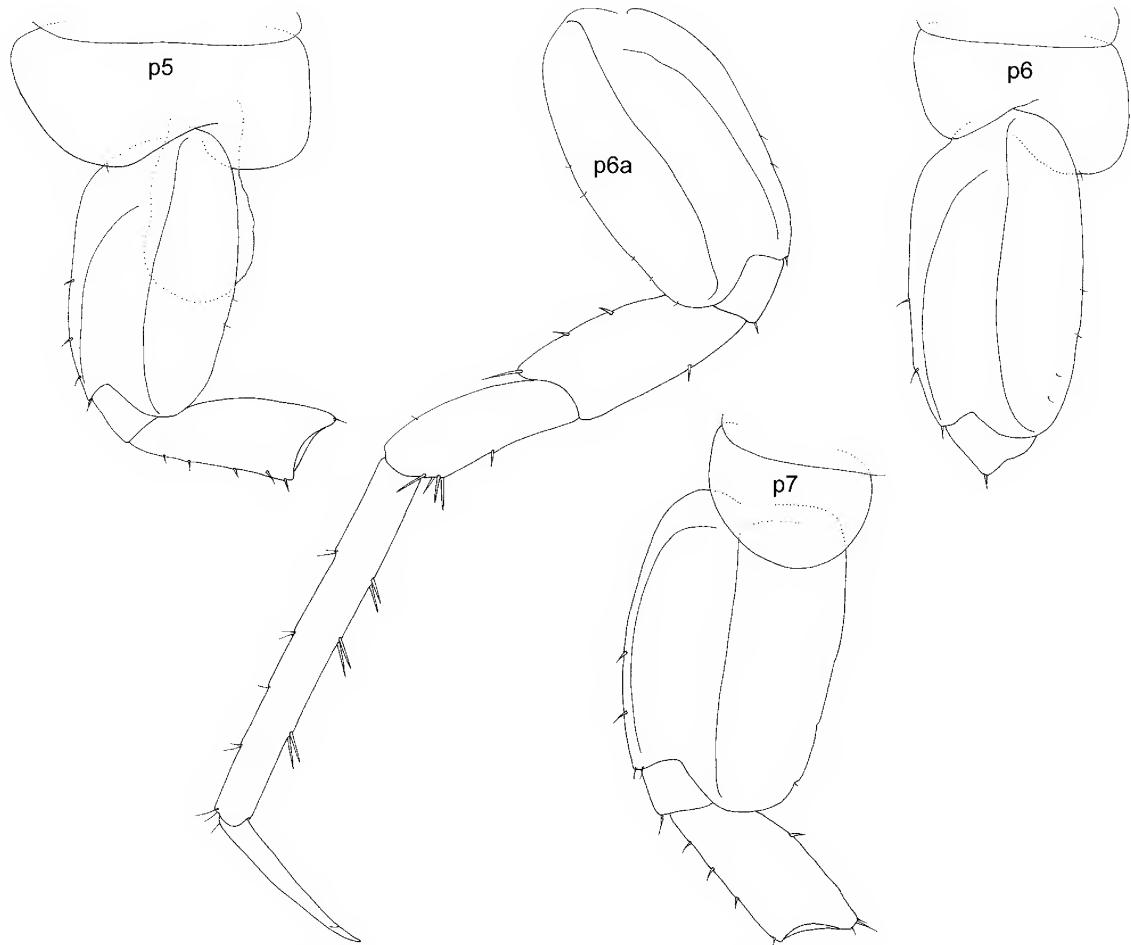


Figure 4. *Scafodia stylos*, gen. nov., sp. nov. Holotype. p5–7, left pereopods 5–7; p6a, right pereopod 6.

with small opposing notch in medial margin proximal to 'gland', each plate laterally, between notch and 'gland', with tuft of 4 or 5 inward curving setae decreasing in length from lateral to medial.

Gnathopod 1 basis approximately 4 times longer than broad, as long as merus and carpus combined, with anterior longitudinal concavity to receive article 5 when fully folded back; ischium approximately twice as long as lateral width; merus triangular, anteriorly pointed, approximately as long as ischium, with carpus inserted on anterior margin; carpus slender, twice as long as merus, with parallel margins, approximately 6 times longer than wide, unarmed; propodus approximately 65% longer than carpus, 12 times longer than broad at base, slightly curved and faintly tapering distally, with a few short posterior setae; dactylus weakly curved, approximately sixth length of propodus, with posterior tooth near base of stout, curved unguis, 1 straight, simple seta level with tooth and 2 curved, blunt, simple setae at posterior base of and adpressed to unguis.

Gnathopod 2 little more than half the length of 1, without elongate elements; carpus approximately 80% the combined length of ischium and merus, triangular, approximately 50% longer than lateral distal width, posterodistal lobe setiferous, not projecting along propodus; propodus approximately 10% longer than carpus, moderately curved, tapering distally, with 4 or 5 posterior groups of stiff, pectinate setae, anterior margin with group of similar setae at distal two-thirds; dactylus half length of propodus, similar to that of gnathopod 1 but with 2 small midposterior teeth.

Pereopods 3 and 4 similar, slender, approximately 4 times longer than respective coxal plates; merus and carpus subequal in length, combined as long as basis; propodus twice as long as carpus; merus, carpus and propodus with a few posterior and anterior small setae, propodus with small posterodistal robust seta; dactylus half length of propodus, nearly straight, length approximately eight times width at base. *Pereopods 5–7* apparently alike (*pereopod 6* the only entire limb known, hence

relative lengths of 5–7 not known, but probably of subequal length), with posteriorly expanded distally rounded basis, posterior margin smooth with scattered setules, with midlateral and anterolateral ridges; at least pereopod 6 approximately third longer than pereopods 3 and 4, but otherwise of similar shape and proportions, carpus posterodistally and propodus posteriorly with groups of slender robust setae.

Pleopods strong, alike; peduncle approximately twice as long as wide (posterior view), with 2 mediodistal coupling hooks; subequal rami as long as peduncle, proximal part of rami with opposing surfaces excavate, outer ramus with posterior proximal locking projection.

Urosomite 1 as long as 2 and 3 combined; urosomite 2 dorsal length approximately quarter that of elongate 3; urosomite 3 dorsally flattened to slightly concave in transverse section. *Uropods* 1 and 2, peduncles with lateral robust setae; uropod 1 overreaching 2 and outer ramus of 3, (tip of uropod 1 rami broken in all specimens, but proportions between rami and peduncle probably approximating those in uropod 2); uropod 2 shorter than 1, reaching nearly to tip of outer ramus of 3, outer ramus as long as peduncle, inner ramus approximately 40% longer than outer; uropod 3 biramous (inner ramus lost in all specimens, but presence indicated by socket and musculature), peduncle as long as wide, reaching to tip of telson, outer ramus approximately 5 times longer than peduncle; rami of all uropods slender lanceolate, without terminal seta(e), but apparently all with a few small lateromarginal setae, margins finely serrate. *Telson* approximately 10% broader than long, reaching to distal margin of peduncle of uropod 3, quarter cleft in open V-shape; lobes rounded, each with 2 distolateral marginal teeth, 2 or 3 small apposite setae level with teeth and 1 long similar seta at mid-surface.

Size. Largest female, 4.7 mm. Male not known.

Etymology. The species name is derived from the Latin *stylus* meaning pointed instrument or pen, and *os* meaning mouth, alluding to the long, pointed mandibles. Noun in apposition.

Distribution. South-eastern Australia, 400–1277 m depth.

Function of the mouthparts

Conically bundled, elongate, pointed mouthparts are frequently referred to as having piercing and possibly sucking functions. In most cases the piercing action can be readily understood, whereas the subsequent transport of food (particles, macerated tissue, body fluids) has not been studied in detail. Dahl (1964) discussed the probable function of the mouthparts and adjacent parts of the digestive tract in *Acidostoma neglecta* Dahl, 1964 (Lysianassoidea; ectoparasite on sea anemones, Vader, 1983). He found that muscles in the oesophagus and the anterior part of the stomach may create the necessary negative pressure to lift up food through the narrow passageways of the conically bundled mouthparts.

In spite of many differences in mouthpart details, the general outline of the bundle is quite similar between *Acidostoma* and *Sicafodia*. *Sicafodia* also seems to possess the two prerequisites necessary for sucking up food through the mouth cone, viz., a tight lumen, and a sucking mechanism. When the

maxillipeds are brought fully forward, a tight funnel may be created between the forward-inward folded outer plates and the elongate upper lip (as in *Acidostoma*); the equally elongate inner plates of the maxillipeds will help seal the funnel posteriorly. Once the apex of the mouthpart cone is embedded in the food item tissue and a tight funnel has been established, a sucking devise may be found in the proximal part of the upper lip, where obliquely set transverse muscles (Fig. 2A ul, lv) will, on contraction, pull the soft-walled posterior surface of the upper lip forward thus drawing liquid or semi-liquid food upward through the funnel. The obliquely transverse muscles in the epistome may have a similar function, bringing food closer to the oesophagus. Additional mechanisms, like those described by Dahl (1964), have not been observed but may be present to finally lift food into the stomach.

Following the initial piercing by the mandibles, the apical and subapical spine-like setae located on the maxillipedal outer plate and the outer plate of maxilla 1 may help in extending the wound and shredding the tissue. If the tips of the maxillipedal inner plates are indeed glandulariferous as suggested in the description, such glands may release proteolytic enzymes into the wound and thus help speeding up the maceration process before suction transport.

The actual food items of *Sicafodia stylos* are not known. However, the lack of grasping gnathopods or strongly dactylate, clinging pereopods suggest that *Sicafodia* is not a fish parasite. In view of its slender epibenthic/pelagic pereopods 3–7 and the strongly developed pleosome the species is probably a roaming predator on some group or groups of sessile or sluggish benthic or epibenthic invertebrates.

Acknowledgments

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Pseudidotheidae (Crustacea: Isopoda: Valvifera) reviewed with description of a new species, first from Australia

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Abstract

Poore, G.C.B., and Bardsley, T.M. 2004. Pseudidotheidae (Crustacea: Isopoda: Valvifera) reviewed with description of a new species, first from Australia. *Memoirs of Museum Victoria* 61(1): 75–83.

The family Pseudidotheidae, comprising only four species of *Pseudidothea*, is reviewed. A new highly-ornamented species from south-eastern Australia, *Pseudidothea hoplites*, is described. A key to species of the genus and family is provided.

Keywords

Isopoda, Valvifera, Pseudidotheidae, *Pseudidothea*, new species, south-west Pacific, Australia

Introduction

The family Pseudidotheidae Ohlin, 1901 was erected for the east Patagonian genus and species *Pseudidothea bonnieri* Ohlin, 1901 on the basis of the male first pleopods being modified for a copulatory function, a character never before recorded in the Isopoda. Ohlin also noted that the second to seventh pereopods are of virtually the same size and form. He regarded the Pseudidotheidae as an intermediate link between the Idoteidae Samouelle, 1819 and Arcturidae Dana, 1849. Barnard (1920) noted that the Pseudidotheidae have a flattened body, pereonite 4 never elongate, pereopod 1 prehensile and pereopods 2–4 stout. In Arcturidae the body is cylindrical, pereonite 4 often elongate, pereopod 1 setiferous and pereopods 2–4 slender and setiferous. Nordenstam (1933) added another character: penial processes fused but distally cleft or bilobate.

Pseudidotheidae are distinguished, with other arcturoid valviferans, from Idoteidae and similar families by having the head fused to pereonite 1 (with a few exceptions not so in Idotidae), penial processes fused but distally cleft, and pleopod 1 with an elongate peduncle and modified exopod in the male. Wägele (1989, 1991) treated the family as one of four subfamilies of Arcturidae, the others being Arcturinae, Xenarcturinae Sheppard, 1957 and Holidoteinae Wägele, 1989. He included *Arcturides* Studer, 1882 with *Pseudidothea* in Pseudidotheinae which, he believed, shared the synapomorphy of all pleonites fused and not divided by furrows. This state is true of all arcturoid families, with rare reversals in two genera (Poore, 2001). Arcturidae Poore, 2001 (*Arcturides* alone),

Pseudidotheidae and Xenarcturidae were treated as families by Poore (2001), three members of an unresolved clade. Poore (2001) separated pseudidotheids from other arcturoid families by the uniquely undifferentiated pereopods 2–4, similar to more posterior ambulatory pereopods. While it is true that all limbs are ambulatory and 2–4 do not bear long filtering setae of the arcturid type, pereopods 2 and 3 are more robust than 4–7. In Xenarcturidae, only pereopods 2 and 3 are slender, setose and arcturid-like while pereopods 4–7 are ambulatory. In Arcturidae, pereopods 2–7 are all similar and ambulatory. Holidoteidae was only remotely related in Poore's (2001) cladogram (see revision by Poore, 2003).

The family contains only *Pseudidothea*, the type species of which is a junior synonym of an earlier described species, "*Idothea Miersii*" Studer, 1884, an observation suggested by Ohlin, suspected by later authors, and confirmed here. *Microarcturus scutatus* Stephensen, 1947 from the South Shetland Islands, was transferred to *Pseudidothea* by Sheppard (1957). Hurley (1957) described *Pseudidothea richardsoni* from New Zealand. Here, a fourth species is described from southern Australia.

All limbs are drawn from the left side unless otherwise stated. The following abbreviations are used in figures: A1, A2, antennae 1, 2; MD, mandible; MP, maxilliped; MX1, maxilla 1; MX2, maxilla 2; P1–P7, pereopods 1–7; PL1–PL5, pleopods 1–5; U, uropod; l, left; r, right. Material is lodged at Museum Victoria, Melbourne (NMV); the Canterbury Museum, Christchurch, New Zealand (CMNZ), Museum of New Zealand (Te Papa Tongarewa) (MNZ), Zoological Institute and Museum, Hamburg, and Museum für Naturkunde, Berlin.

Pseudidotheidae Ohlin

Pseudidotheidae Ohlin, 1901: 274–276.—Stebbing, 1905: 43.—Barnard, 1920: 381.—Nordenstam, 1933: 112–113.—Hale, 1946: 168.—Sheppard, 1957: 173–174.—Poore, 2001: 227.

Pseudidotheinae.—Wägele, 1989: 137–138.—Wägele, 1991: 80–81.

Diagnosis. Body strongly vaulted. Head and pereonite 1 fused. Pereonite 4 of similar length to pereonite 3. All pleonites fused into pleotelson. Body variously tuberculate or spinose; pleotelson without dorsolateral ridges ending in mediobursal posterior spine, never with posterior dorsolateral pair of strong spines; limbs and most of surface covered with fine setae that trap sediment. Dorsal coxal plates 2–7 obsolete, bases of pereopods exposed. Mouthparts and pereopod 1 visible in lateral view. Eyes well developed. Antenna 2 flagellum of 2 or 3 articles plus distal claw. Pereopod 1 a gnathopod, pereopods 2 and 3 differentiated from ambulatory pereopods 4–7. Pereopod 1 dactylus evenly curved along anterior margin, evenly tapering. Pereopods 2 and 3 with propodus able to close on carpus, articles broad and with posterior robust setae; with prominent dactylus, unguis short. Pereopods 4–7 similar and ambulatory. Pereopods of males without dense mat of fine setae. Uropodal exopod (smaller ramus) tapering (with terminal setae only), more than half as long as endopod. Oostegites 1–4 functional, not supported by coxal lobes; oostegite 5 present or absent. Penes fused as a single penial plate, apically simple or barely slit. Pleopod 1 peduncle more elongate than on other pleopods; with marginal setae on rami longer than or equal to length of rami. Pleopod 1 exopod of male thickened and with groove on posterior face, with few simple setae along straight lateral margin; with groove on posterior face of exopod ending on tapering distolateral apical extension. Pleopod 2 of male with appendix masculina about as long as endopod, basally less than half width of endopod.

Remarks. The diagnosis is rephrased from Poore (2001) to better define limb differentiation. We note that the body is covered with fine setae, not illustrated in the new species and indicated or mentioned only in passing for other species by Hurley (1957) and Brandt and Wägele (1990). Such setation is not a typical valviferan characteristic. Poore (2001) defined the family as lacking oostegites on pereopod 5; this is true of three species but not of *P. scutata*. The presence of a fifth pair of oostegites in one species is anomalous among arcturoid families. It is seen elsewhere only in Austrarcturellidae Poore and Bardsley, 1992 where oostegites 5 are vestigial and act as egg guides rather than as part of the marsupium.

Wägele (1989) considered *Arcturides* a family member but Poore (2001) erected a separate family for this genus.

Pseudidothea Ohlin, 1901

Pseudidothea Ohlin, 1901: 276.—Nordenstam, 1933: 113.—Hale, 1946: 168.—Sheppard, 1957: 174.—Hurley, 1957: 15.—Wägele, 1991: 84–87.

Type species. *Pseudidothea bonnieri* Ohlin, 1901 (by monotypy).

Diagnosis. As for family.

Remarks. Ohlin (1901) was “almost convinced” that *Pseudidothea bonnieri* was identical to *Idotea miersii* Studer, 1884 and noted that “the localities where they were dredged are nearly the same.” He nevertheless, erected his new species. He also expressed his “suspicion” that his new genus was identical to *Arcturides* Studer, 1883. Hale (1946) listed three characters that separated the two genera. In *Arcturides*, the coxae of pereonites 2–7 are distinctly marked off, the antenna 2 flagellum is of three articles and the uropodal exopod as long as endopod. Hale’s view was confirmed by Poore (2001) whose phylogenetic analysis concluded the two genera belong in different families.

Key to species of *Pseudidothea*

1. Pereonites 2 and 3 with forked dorsolateral spines; all pereonites with lateral rows of blade-like ridges, each with anteriorly and posteriorly directed spines; tergites produced laterally over coxae to form a shield with 3 points; *Pseudidothea hoplites*
- Pereonites with low or high flat tubercles; tergites produced laterally as large tubercles or rounded or flattened laterally; 2
2. Pereon with large high flat tubercles; pereonite 1 with dorsal pair, pereonites 2–4 with dorsal and lateral pair and pereonites 5–7 with dorsal, dorsolateral and lateral pair; male pleopod 2 with appendix masculina twice as long as rami *Pseudidothea scutata*
- Pereon with low irregular tubercles; male pleopod 2 with appendix masculina and rami subequal 3
3. Uropodal exopod with a single strong setae, endopod with 3 pappose setae; antenna 2 peduncle with long fine setae on articles 3–5; pereopods without tubercles; male pleopod 1 endopod with 5 lateral spinules proximally, 5 apical plumose setae; exopod with 15 spinules on lateral margin, tapering distally to an obtuse apex *Pseudidothea richardsoni*
- Uropod rami each with single seta; antenna 2 peduncle with short setae on articles 3–5; pereopods with tubercles; male pleopod 1 endopod with plumose setae marginally; exopod with 16–17 spinules laterally, with acute apex bent outwards *Pseudidothea miersii*

Pseudidothea hoplites sp. nov.

Figures 1–3

Material examined. Holotype. Western Bass Strait, 70 km W of Cape Farewell, King Island, Tasmania ($39^{\circ}38.2'S$, $143^{\circ}07.2'E$), 127 m, sand, epibenthic sled, R. Wilson on RV *Tangaroa*, 21 Nov 1981 (stn BSS 195), NMV J8705 (male, 4.4 mm).

Paratypes. Type locality, NMV J8706 (1 female); 36 km SSW of Stokes Point ($40^{\circ}26.7'S$, $143^{\circ}41.4'E$), 85 m, rock dredge, 22 Nov 1981 (stn BSS 198), NMV J8709 (1); 59 km WNW of Cape Farewell ($39^{\circ}28'S$, $143^{\circ}17'E$), 103 m, Smith-McIntyre grab/pipe dredge, G.C.B. Poore on HMAS *Kimbla*, 10 Oct 1980 (stn BSS 81), NMV J8703 (1).

Victoria, 80 km SSE of Cape Otway ($39^{\circ}26'S$, $142^{\circ}57'E$), 113 m, 9 Oct 1980 (stn BSS 67), NMV J8701 (2); NMV J23186 (1 ovigerous female, 5.1 mm, figured); 51 km SSW of Cape Otway, Victoria

(39°16'S, 143°17'E), 90 m, 10 Oct 1980 (stn BSS 73), NMV J8702 (1); 45 km SSW of Cape Otway (39°15'S, 143°19'E), 94 m (stn BSS 74), NMV J8704 (2 males); 55 km SW of Cape Otway (39°16.7'S, 143°06.7'E), 95 m, rock dredge, R. Wilson on RV *Tangaroa*, 21 Nov 1981 (stn BSS 193), NMV J8707 (male, female); 44 km SW of Cape Otway (39°06.3'S, 142°55.6'E), 81 m (stn BSS 192), NMV J23077 (1); 60 km SW of Cape Otway (39°06.3'S, 142°55.6'E), 84 m, fine shell (stn BSS 191), NMV J8708 (1).

Other material. Tasmania. Breaksea Island, Bathurst Harbour (43°20'S, 145°57'E), 4 m, NMV J23085 (1 ovigerous female, SEM examination). Isle des Phoques (42°25'S, 148°10'E), NMV J23084 (1). Bicheno, eastern side of Waubs Bay, reef (41°53'S, 147°18'E), 7 m, *Macrocystis* holdfasts (stn TAS 94), NMV J23081 (1); E side of Waubs Bay, reef local name "Split Rock" (41°53'S, 147°18'E), 11 m, red and brown algae (stn TAS 102), NMV J23083 (2); granite reef 50 m offshore, N end of "The Gulch" (41°53'S, 147°18'E), 7 m, erect red algae (stn TAS 88), NMV J53071 (1); reef close to base of "Split Rock" (41°53'S, 147°18'E), 12 m, fine sand from base of reef (stn TAS 96), NMV J23082 (1).

Victoria. "Harry's Hole", W side of Twin Reefs, Venus Bay (38°41'S, 145°39'E), 9 m, rocky (stn CPA 8), NMV J23079 (1). 75 m SW of Eagles Nest (38°40'S, 145°40'E), 8 m (stn CPA 3), NMV J23078 (1). Off Eagles Nest (38°40.67'S, 145°38.76'E), 10–11 m, mixed algae (stn BUN 3), NMV J53073 (1). Aireys Inlet (38°28'S, 144°06'E), from *Sphaerelaria*, NMV J23080 (1).

Diagnosis. Head dorsally strongly elevated, with paired double or single spines. Pereonite 1 with 1 pair of small dorsal spines, 2 small lateral spines. Tergites 2–7 each produced laterally in form of a with 3 points, anteriorly, posteriorly and laterally. Pereonites 2 and 3 with small paired middorsal spines, large paired dorsolateral forked spines, and lateral ridges produced acutely anteriorly and posteriorly; pereonites 4–7 with dorsolateral and lateral ridges, each produced acutely anteriorly and posteriorly, and several anterodorsal and posterodorsal spines. Pleotelson with anterolateral processes, paired anterodorsal convexities, a series of 3 spines on each side (dorsal-lateral) and pair of mediobursal convexities, remaining pleotelson tapers to an obtuse apex.

Male antenna 1 flagellum with 6 clusters of aesthetascs. Antennae and pereopods with tubercles. Antenna 2 with short setae on articles 3–5. Male pleopod 1 endopod about 1.5 times as long as peduncle with plumose setae apically; exopod longer, 8 spinules on lateral margin, tapering distally, thickened and folded laterally to partially cover a groove that runs to the apex. Male pleopod 2 appendix masculina styliform, slightly longer than endopod. Uropodal exopod about two-thirds as long as endopod; exopod with a strong apical seta; endopod with 3 brush setae and 2 setules. Oostegite absent from pereopod 5.

Description. Ornamentation. Head dorsally strongly elevated, with paired double or single spines. Eyes prominent, arising laterally. Lateral margin of head armed with about 7 small teeth, extending downwards and outwards. Head fused to pereonite 1, partial suture visible laterally. Pereonite 1 with pair of small dorsal spines, 2 small lateral spines, lateral margin with about four small teeth. Tergites 2–7 produced laterally to form a shield with 3 spines, laterally, anteriorly and posteriorly. Pereonites 2 and 3 with small paired dorsal spines, large paired dorsolateral forked spines, and lateral ridges finished

anteriorly and posteriorly with a small spine. Pereonite 4–7 with dorsolateral and lateral ridges, finished anteriorly and posteriorly with a small spine. Pereonite 4 with 4 anterodorsal and posterodorsal spines, pereonites 5 and 6 with 3 and pereonite 7 with 2 and a single dorsal denticle.

Sculpture of pleotelson from anterior to posterior as follows. A central pair of dorsal convexities each with an anteriorly directed spine, lateral to these a series of 3 anteriorly directed spines on each side, followed by large lateral convexities on each side, followed by a pair of central dorsal convexities, remaining pleotelson tapers to an obtuse apex.

Antennae, mouthparts and limbs (from male). Antenna 1 peduncle articles with brush setae, articles rounded and becoming successively smaller; flagellum article 1 very short; article 2 with 6 aesthetascs and setules. Antenna 2 peduncle articles 3–5 with blunt tubercles on lower margin, bearing robust setae, especially on articles 4 and 5; flagellum almost as long as peduncle article 5, articles becoming successively smaller, first with distal robust seta and setules, second with setules, third a short claw.

Mandible incisor with 4 uneven teeth; left lacinia mobilis almost as wide as incisor, with 3 teeth; right lacinia mobilis an unevenly toothed column; left molar process with concave face rimmed by obscure teeth and bearing a setal cluster; right molar process with face ending with row of blunt teeth and bearing setal cluster. Maxilla 1 inner lobe with 2 long pappose setae; outer lobe with 11 apical setae, some obscurely dentate. Maxilla 2 inner lobe oblique margin with 6 pappose setae along posterior edge, 5 setae on anterior edge; middle lobe with 2 longer pappose setae; outer lobe with 3. Maxilliped endite with complex of thin pappose setae and rows of blunt tubercles; palp with tubercles and long setae on mesial margins of articles 2–5; articles 1 and 2 short, 3 and 4 of subequal length, 3 produced mesially, article 5 one-fifth as long as 4, almost as long as wide; epipod apex with small blunt tooth.

Pereopod 1 held close to the mouthparts; merus-propodus with uneven posterior tubercles and stout pectinate setae; propodus almost as wide as long, with rows of mesial pectinate setae along anterodistal margin; proximal part of dactylus linear, about 2.5 times as long as greatest width, complexly setose with mesial pectinate setae, 1 spinule on posterior margin, posterodistal corner of dactylus with a spinule, seta and 2 setules; unguis a strong claw, less than half length of dactylus.

Pereopod 2 basis–merus short, subequal, carpus–dactylus longer; merus with complex tubercle on lower margin bearing short setae; carpus longer than greatest width, with tuberculate ridge on lower margin bearing 2 long robust setae; propodus robust, about twice as long as wide, with 2 robust setae on lower margin opposing carpus; proximal part of dactylus almost 3 times as long as wide, unguis a short claw. Pereopod 3 similar to pereopod 2. Pereopods 4–7 basis–merus with blunt tubercles on upper margin, most articles with well spaced setae on lower margin; basis about 1.5 times as long as wide; ischium–carpus subequal, about as wide as long; propodus about 2.5 times as long as wide, dactylus similar to pereopod 2.

Male pleopod 1 peduncle twice as long as wide, with 4 coupling hooks; endopod lamellar with 6 apical plumose setae;

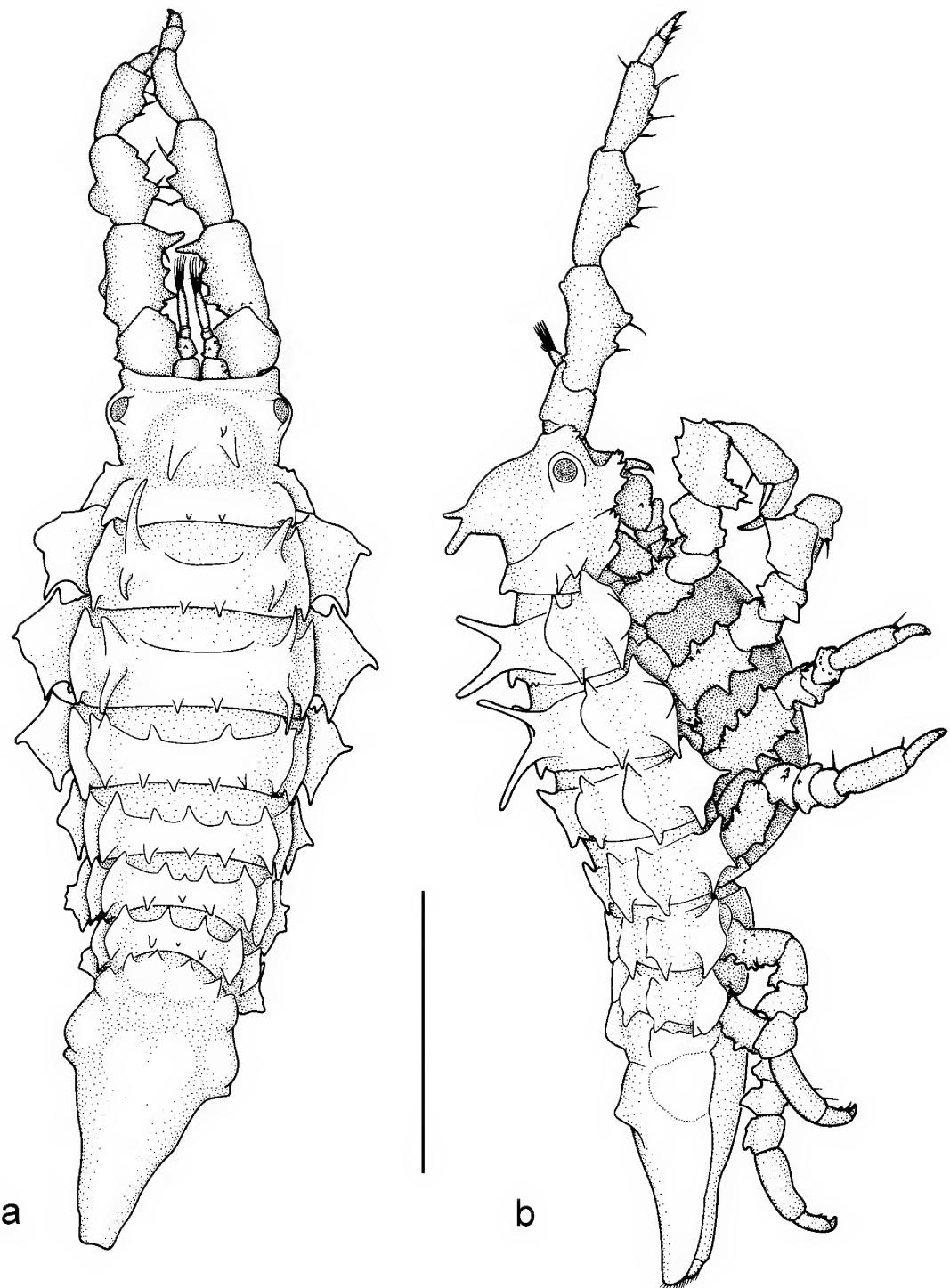


Figure 1. *Pseudidothea hoplites*. Paratype female, NMV J23186. Dorsal and lateral views. Scale bar 2 mm.

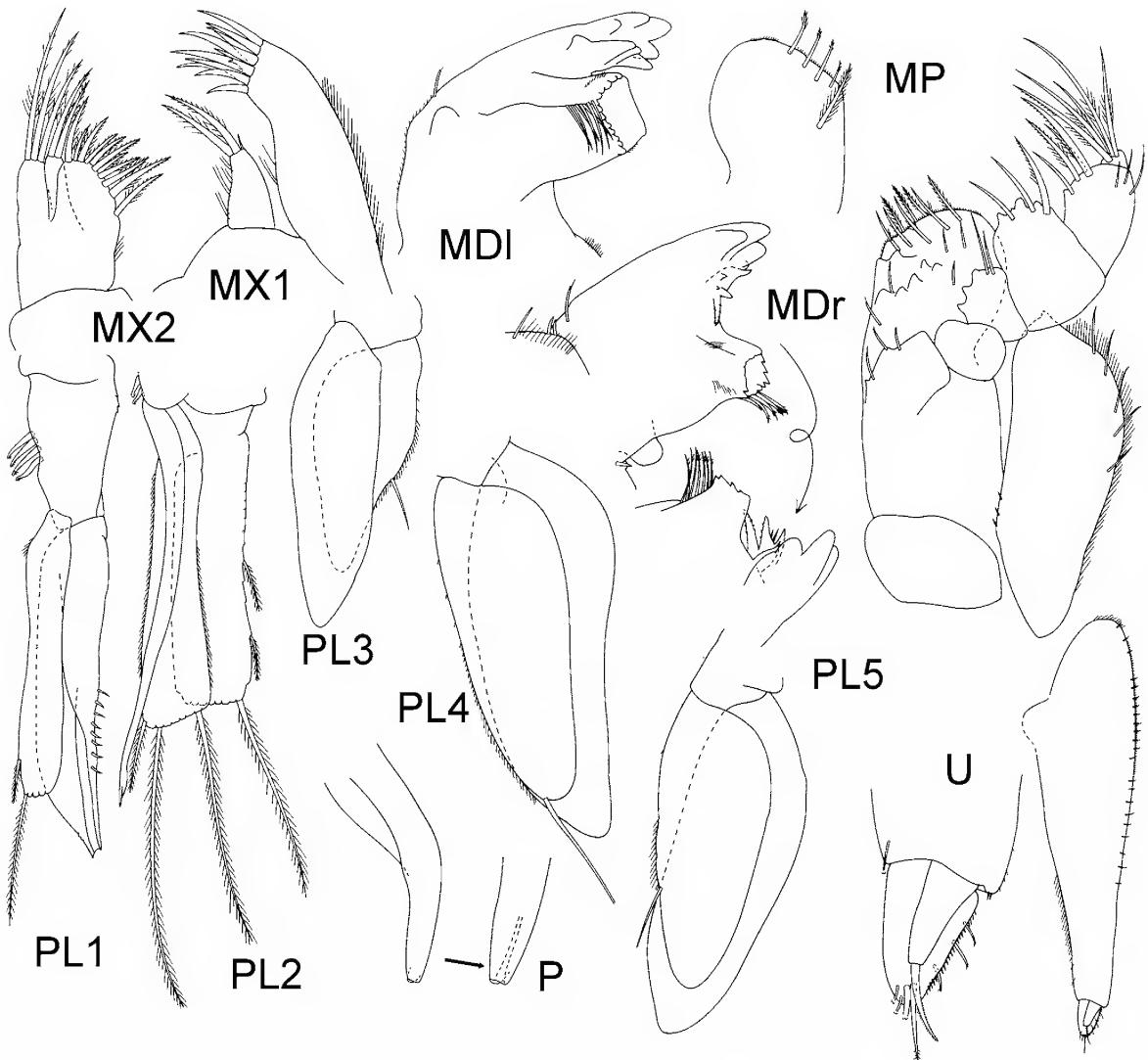


Figure 2. *Pseudidothea hoplites*. Holotype male, NMV J8705. Left and right mandibles, maxillae 1 and 2, maxilliped with detail of anterior face of endite. Pleopods 1–5; penial process; uropod with detail of rami.

exopod longer than endopod with 8 spinules on lateral margin, tapering distally, thickened and folded laterally to partially cover a groove that runs to the apex. Male pleopod 2 rami apically flattened, endopod with 9 apical plumose setae; exopod with 21 marginal plumose setae; appendix masculina styliform, slightly longer than endopod. Pleopods 3–5 becoming successively larger, rami apically rounded with single simple seta on endopod.

Uropod unarmed, rounded anteriorly, tapering posteriorly; exopod about two-thirds as long as endopod, conical, with apical seta; endopod broader, apically rounded with 4 distal setae and 3 lateral setae.

Sexual differentiation. Female differs from male in broader

body, especially of pereonites 2–4; ornamentation more developed; antenna 1 flagellum with 3 clusters of aesthetascs on article 2; pereopods 1–4 with oostegites, pereopod 5 without oostegite; penial process absent; pleopods 1 and 2 without male modifications. Male with ventral terga separate on pereonites 1–4 and fused across midline of pereonites 5–7.

Etymology. *Hoplites* (Gr.), man in armour, in reference to the elaborate spines and ridges.

Distribution. South-eastern Australia (Victoria and Tasmania), 4–127 m depth.

Remarks. *Pseudidothea hoplites* is distinguished from other species of *Pseudidothea* by the complex ornamentation of the

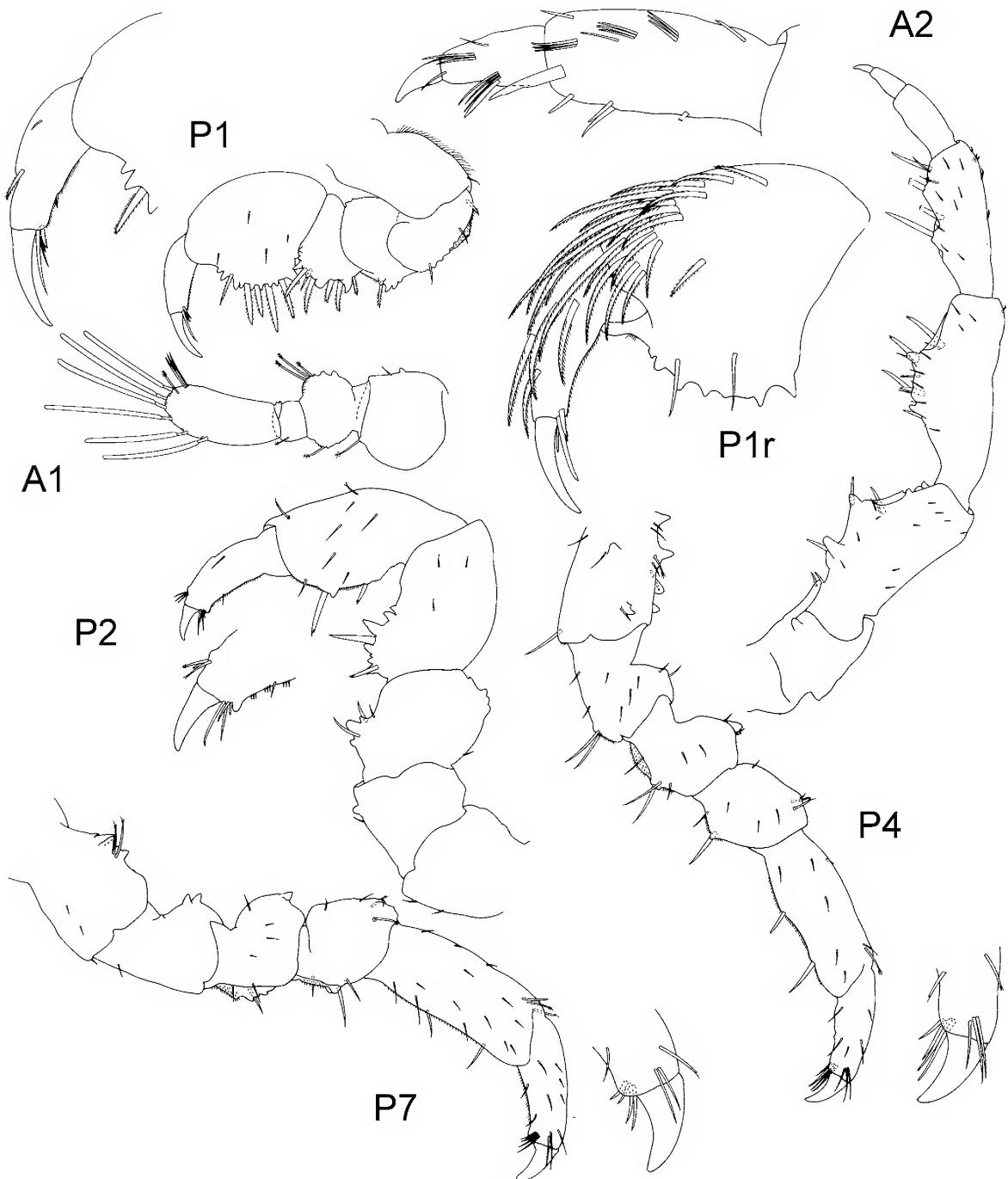


Figure 3. *Pseudidothea hoplites*. Holotype male, NMV J8705. Antennae 1 (not all aesthetascs drawn) and antenna 2; left pereopod 1 with detail of dactylus; inner face of right pereopod 1 propodus. Pereopods 2, 4 and 7, with details of dactyli.

pereon comprising forked projections on pereonites 2 and 3, and dorsolateral and lateral lobes produced front and back. It is most similar to *P. richardsoni* from New Zealand but is much more ornamented. The lateral projections of pereonites 2 and 3 are more exaggerated but both species have anterior and posterior spines.

Pseudidothea miersii (Studer)

Idothea Miersii Studer, 1884: 17, pl. 1 fig. 5. (lapsus for *Idotea*)
Pseudidothea bonnieri Ohlin, 1901: 276–281, fig. 6.—Nordenstam, 1933: 114, fig. 27.—Sheppard, 1957: 175–176.
Pseudidothea miersii.—Barnard, 1920: 380–381.—Nordenstam, 1933: 114.—Shepherd, 1957: 175–176, figs 1d, 14a–f.—Kussakin, 1967: 267–269, figs 28, 29.
Arcturides miersii.—Nierstrasz, 1941: 262.

Diagnosis. Head dorsally convex; pereon with irregular minute tubercles. Pleotelson with blunt anterolateral processes, dorsally smooth, tapering to broadly truncate and slightly upturned apex. Male antenna 1 flagellum with about 6 clusters of aesthetascs. Antennae and pereopods without tubercles. Antenna 2 peduncle with short setae on articles 3–5. Pereopods minutely setose and with tubercles. Male pleopod 1 endopod about 1.5 times as long as peduncle with marginal plumose setae; exopod longer, 16–17 spinules on lateral margin, tapering distally, to acute apex bent outwards, with oblique furrow opening at apex. Male pleopod 2 appendix masculina tapering to acute point, slightly longer than endopod. Uropodal exopod with strong apical setae, endopod with 1 short seta; exopod about two-thirds as long as endopod (Ohlin, 1901). Oostegite absent from pereopod 5 (Sheppard, 1957).

Distribution. East Patagonia, Falkland Islands, 115–500 m depth.

Remarks. Studer (1884) based his new species *Idothea miersii* on a specimen 9 mm long, collected by the *Gazelle* Expedition off the east coast of South America at 47°1'6"S, 63°29'6"W at 63 fathoms (110 m). In the same paper he redescribed his earlier named species, *Arcturides cornutus*. Ohlin (1901) based *Pseudidothea bonnieri* on two males, 9 mm long, in the Hamburg Museum. When Ohlin (1901) described *P. bonnieri* he was almost convinced that his specimens were identical with *Idothea miersii* (Studer) and in a footnote reported how he had tried to borrow Studer's material from the Museum für Naturkunde in Berlin but "got the reply that, as there were only two of them, it would be against the regulations to send them away from the Museum." Angelika Brandt compared material from the museums in Hamburg and Berlin on our behalf:

from Hamburg, a 4 mm manca and a 6.4 mm male (ZMH K-1877) labelled and catalogued "Pseudidothea bonnieri, Pisagua, Chile, 19°27'S, 70°10'W, K. Kophamel 1877–1889"; and

from Berlin, a 6.2 mm male (18804) labelled "Zool. Mus. Berlin 18804 Pseudidothea bonnieri (Syntype) Ohlin, 1901 Leg. Kap. Kophamel, 3.VI.1888, 43°6'S, 60°W" and on another label "Pseudidothea bonnieri Ohlin, 1901 (*Idothea miersii* (Studer))", and catalogued in Berlin with further information, "Hamburger Museum ded. Pisagua".

Brandt (pers. comm.) could find no differences between the specimens and concluded that one of Ohlin's two males had been donated to the museum in Berlin. This seems certain. The locality recorded by the two museums, but not the coordinates and collecting date of the Berlin specimen, is at odds with the type locality and more recent records of the species and is clearly wrong. Ohlin must have included antennae in his total length of 9 mm while Brandt's measurements of 6.2 and 6.4 mm do not. The manca was not mentioned by Ohlin. Studer's material can not now be found although Ohlin's footnote tells that it existed in 1901. It is tempting to speculate that, being unable to borrow Studer's material and convinced of the synonymy of his species *bonnieri* with Studer's *miersii*, Ohlin sent one of his syntypes to Berlin for comparison. This may explain why the Berlin male has two species names but whoever concluded this remains a mystery.

Sheppard (1957) examined many specimens from the Falklands region, reported them as *Pseudidothea bonnieri* but thought too that *I. miersii* was a synonym. Kussakin (1967) also illustrated a species using the older species name, as *Pseudidothea miersii*, and noted that *P. bonnieri* is probably a synonym. He observed that slight differences exist: in *P. bonnieri* the second article of the peduncle of antenna 1 bears a rounded tubercle with four setae (referring to Sheppard, 1957); in Kussakin's specimens there is a slight swelling with five setae. The epipod of the maxilliped in Sheppard's illustration of *P. bonnieri* has slightly concave lateral margins, while in Kussakin's specimens it has a regular oval form with convex lateral margins. We consider that these minor differences can be attributed to intraspecific variation or mounting.

To add to the confusion, Nierstrasz (1941) synonymised Studer's two species, *Pseudidothea bonnieri* and *Arcturides cornutus*, without explanation. It seems improbable that Studer could confuse his own two species in one paper and specimens of *A. cornutus* in our possession look nothing like a pseudidotheid; in fact, Poore (2001) placed the two species in different families.

We conclude, with Kussakin (1967), that *P. bonnieri* should be treated as a junior synonym of *P. miersii*. We treat as additional evidence the observation that all authors have reported only one species like this off eastern South America; the only other in the genus in the region, *P. scutata* Stephenson, 1947 is quite different.

Pseudidothea richardsoni Hurley

Figure 4

Pseudidothea richardsoni Hurley, 1957: 15–17, figs 74–91.

Material examined. New Zealand, Banks Peninsula region. Off Lyttelton, 4 fm [7.3 m], H. Suter, CMNZ (4 females, 5.1–6.1 mm; 4 males, 4.8–5.1 mm, 1 figured); NMV J47116 (1 female, 1 male). Big Bay, mud bottom, 12 m, MNZ CR-9846 (2). Beacon Rock, mud bottom, 10–12 m, MNZ CR-9850 (1). E side of Port Levy, mud bottom, MNZ CR-9855 (1).

Diagnosis. Head with anterior margin vaguely tuberculate, dorsally with tubercles, pereon finely setose and vaguely tuberculate; tergites slightly laterally produced. Pleotelson with blunt anterolateral processes, laterally tuberculate, dorsally

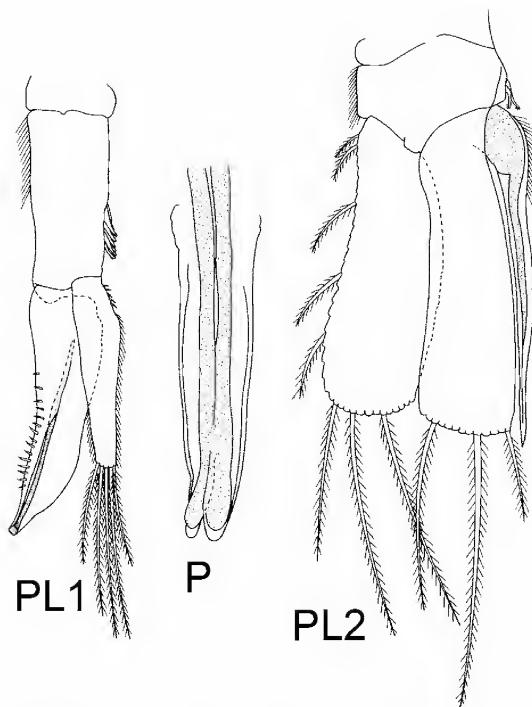


Figure 4. *Pseudidothea richardsoni*. Male, CMNZ. Pleopods 1 and 2; penial process.

smooth, tapering to a blunt apex. Male antenna 1 flagellum with about 7 clusters of aesthetascs. Antennae and pereopods without tubercles. Pereopods finely setose. Antenna 2 peduncle with long, fine setae on articles 3–5. Male pleopod 1 endopod about as long as peduncle, with plumose setae apically; exopod longer than endopod, with 15 spinules on lateral margin, tapering distally, thickened and folded laterally to partially cover groove that runs to apex. Male pleopod 2 appendix masculina styliform, about as long as endopod. Uropodal exopod with strong apical setae, endopod with 3 pappose setae; exopod about two-thirds as long as endopod. Oostegite absent from pereopod 5.

Descriptive notes. We examined a male specimen of *P. richardsoni* and here figure and describe pleopods 1 and 2 and the penial process:

Male pleopod 1 peduncle twice as long as wide, with 8 coupling hooks mesially; endopod lamellar with 5 lateral spinules proximally, tapering distally with 5 apical plumose setae; exopod longer than endopod with 15 spinules on lateral margin, tapering distally, thickened and folded laterally to partially cover a groove that runs to the obtuse apex. Male pleopod 2 endopod with 13 apical plumose setae; exopod with 39 marginal plumose setae; appendix masculina styliform, about as long as endopod. Penial process fused, distally bilobate.

Distribution. Cook Strait and Lyttelton Harbour, New Zealand, 7–146 m depth.

Remarks. Hurley (1957) observed that *P. richardsoni* is close to “*P. bonnieri* Ohlin” (=*P. miersii*) but he considered there are sufficient differences to warrant a separate species; these include uropodal endopod with three pappose setae, lack of tubercles on the pereopods and antenna 2 peduncle with long fine setae on articles 3–5.

The first male pleopods are also different from those of *P. miersii*. *Pseudidothea miersii* has a male pleopod 1 peduncle with 6–7 coupling hooks, endopod with plumose setae marginally, exopod with 16 or 17 spinules laterally and with an acute apex bent outwards, almost at right angles. In contrast, *P. richardsoni* has a peduncle with eight coupling hooks, an endopod with five lateral spinules proximally and five apical plumose setae, and an exopod with 15 spinules on its lateral margin, tapering distally to an obtuse apex.

Pseudidothea scutata (Stephensen)

Microarcturus scutatus Stephensen, 1947: 15–17, figs 5, 6.

Pseudidothea scutata Sheppard, 1957: 176–180, figs 15, 16.

Pseudidothea scutatas.—Brandt and Wägele, 1990: 97–105, figs 1–3 (lapsus)

Material examined. Antarctica, Western Weddell Sea, A. Brandt on RV *Polarstern*, Jan–Feb 2002 (ANDEEP stns): 61°09.82'S, 54°33.40'W, 302–306 m, NMV J47401 (1 male); 61°11.94'S, 54°37.37'W, 302–306 m, NMV J47402 (1 male); 61°20.51'S, 55°28.66'W, 159–117 m, NMV J47403 (1 female); 61°44.88'S, 58°1.54'W, 256–295 m, NMV J47404 (1 male); 59°52.21'S, 59°58.75'W, 3643–3622 m, NMV J47405 (1 specimen).

Diagnosis. Head smooth, peronites with large, high, flat tubercles: peronite 1 with 1 pair of dorsal tubercles and 3 pairs of shorter lateral processes; peronites 2–4 with 1 pair of dorsal and 1 pair of lateral tubercles and 1 or 2 pairs of shorter dorsolateral processes; peronites 5–7 with 1 pair each of dorsal, dorsolateral and lateral tubercles. Pleotelson with subacute anterolateral processes, 3 pairs of mediadorsal spines and shorter and more irregular processes, apically acute and bent dorsally. Male antenna 1 flagellum with about 25 clusters of aesthetascs. Antenna 2 and pereopods 2 and 3 with tubercles. Antenna 2 peduncle with long, fine setae on articles 3–5. Male pleopod 1 endopod about as long as peduncle with plumose setae laterally and apically; exopod longer than endopod, with diagonal groove, apically tapering, bent outwards and terminating in an acute tooth, proximal half of lateral margin with short setae, distal half with longer, plumose setae. Male pleopod 2 appendix masculina apically acute, about twice as long as rami (Stephensen, 1947). Uropodal exopod about two-thirds as long as endopod, each ramus with single seta (Sheppard, 1957). Oostegite present on pereopod 5.

Distribution. South Shetland Islands, Antarctic Peninsula, 159–3622 m depth.

Remarks. Sheppard (1957) included Stephensen's *Microarcturus scutatus* in the synonymy of what she called “*Pseudidothea scutata* sp. n.”. She admitted that Stephensen's “species appears to be identical with my specimens” and that she received Stephensen's paper after making her own descriptions and figures. Her intention would appear to

have been be to make a new combination rather than a new species.

The species differs from all other species of *Pseudidothea* in the presence of well developed oostegites on pereopods 5 (Sheppard's 1947 observation confirmed in new material). Although the pair of fifth oostegites meet in the middle, they are flat and do not help in enclosing the eggs.

The dorsal and lateral pereonal tubercles of the holotype, a 20-mm long male, are separated by gaps smaller than the tubercle diameters. In the same-sized female described by Brandt and Wägele (1990) the tubercles are relatively smaller and separated by gaps equal to their diameters. The uropodal rami of the two specimens also differ: the endopod of the male being shorter and narrower than the exopod while the two are subequal in the female. In the absence of other material, we assume these differences are sexual rather than specific. The new material collected during the 2002 ANDEEP cruise is typical of this well-described species. The individual dredged from 3643–3622 m depth, much deeper than the usual depths of a few hundred metres, could not be distinguished from the rest.

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The long-horned caddisfly genus *Oecetis* (Trichoptera: Leptoceridae) in Australia: two new species groups and 17 new species

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Abstract

Wells, A. 2004. The long-horned caddisfly genus *Oecetis* (Trichoptera: Leptoceridae) in Australia: two new species groups and 17 new species. *Memoirs of Museum Victoria* 61(1): 85–110.

Among Australian caddisflies (Insecta: Trichoptera), the leptocerid genus *Oecetis* McLachlan is one of the most widespread and diverse genera. This paper brings to 53 the number of described species recorded for Australia, and at least a further 15 to 20 species remain to be described. Here 17 newly described species are assigned with 12 others to an informal *laustra*-group, defined by having the phallus simple and lacking parameres. Three other newly described species are placed in another informal group, the *longiterga*-group, based on the broad form of the forewing and strongly pronounced venation. Distributions are plotted for most species, new records extending distributions considerably; of the 29 *laustra*-group species included here, 15 are known in Australia only from the north of the continent. Keys are provided to the informal species-groups recognised for Australia, and to males of the *laustra*- and *longiterga*-groups.

Keywords

Taxonomy, Trichoptera, Leptoceridae, *Oecetis*, new species, Australia

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Introduction

Oecetis McLachlan, 1877 (Leptoceridae), a cosmopolitan genus of long-horned caddisflies, is one of several genera of Trichoptera represented Australia-wide, occurring even in the arid inland. Light trap samples of caddisflies in Australia seldom fail to include several species and often adults and immatures of some species are abundant. Adults of most Australian species are rather nondescript in appearance, although some have distinctive wing markings, and many members of one group have patches of scales on the forewing.

On the basis of features of wing venation and male genitalia, however, five distinct groups can be recognised among Australian species of *Oecetis*. Two of these were dealt with recently. Males of the *reticulata*-group (Neboiss, 1989), have an amour-like, sculptured dorsal plate formed by the extension of abdominal tergite VIII over the terminal segments of the abdomen. In the *complexa*-group (Wells, 2000), males are characterised by external spiny processes or parameres associated with the phallus, and forewing fork 1 with a footstalk. Here, two further groups are recognised, the *laustra*- and *longiterga*-groups. A fifth group, the *pechana*-group, will be dealt with in a subsequent paper.

The *laustra*-group is distinguished by having the phallus very simple, lacking parameres or spines of any kind (Fig. 3). This group, its name taken from a widespread and common Australian species, comprises 29 species, 17 of them newly described. Most of these have the forewing with a distinct footstalk on fork 1, the feature upon which Chen (1992), in his unpublished revision, based a subgroup in one of his subgenera. Several species, however, have the footstalk very short (indistinct), and several have fork 1 sessile.

The *longiterga*-group, named for a New Guinea species, share a wing form atypical in the Australian fauna (Figs 91, 94), with pronounced veins and fork 1 sessile. Three new Australian species are included: *O. crosslandi* sp. nov., *O. ancalia* sp. nov. and *O. digitata* sp. nov. Another unpublished New Guinean species is known that shares this wing form (Chen, 1992: fig. 4.3).

Species of the *laustra*-group vary in tibial spur counts: spur formulae may be 0, 2, 2 or 1, 2, 2. A count of 2, 2, 2 for *O. scirpicula* Neboiss, 1977 was reported, but has not been verified in material checked in this study. Variation is seen, too, in length of wing setae, with some species having long downy setae along veins while others have the vestiture uniformly short over the wing laminae, although always longer on the distal margins. Some wings are uniformly fuscous, yet others show distinctive patterns, with darker brown to black markings produced by differences in wing membrane colour, emphasised by the colour of the setae. Wing shape varies. Forewings are generally slender, having length to width ratios close to 4, but are broader in some species. The position of transverse veins in the forewing, especially the *posterior anastomosis* (Fig. 1, following terminology of Ruiter, 2000, after Schmid, 1980), varies across the group. The crossveins are denoted t1 for that closing discoidal cell, t2 for r-m, and t3 for the vein closing the thyridial cell. In some species, t1, t2, and t3 are more or less contiguous, or linear — as in *O. scirpicula*, in others no two transverse veins are aligned — as in *O. multipunctata* Ulmer, 1916 and *O. parka* Mosely, 1953. Variation within some species is apparent. Thus, in *O. laustra* the posterior anastomosis is linear in some populations, while the crossveins are slightly out of alignment in others. None of the *laustra*-group species has wing-scales such as occur in most of the *pechana*-group.

Assignment of males to the five *Oecetis* species groups using the key provided here is reasonably straightforward. Using the key to *O. laustra*-group species, however, may be difficult. Where possible, wing features are used for differentiation and several species are readily identified by their

characteristic wing markings. For others, the often more cryptic genitalic features must be used. It is recommended that, when identifications are being made, close attention be given to the illustrations provided and to notes on variation within species.

Extensive collections in Museum Victoria (NMV), Australian National Insect Collection (ANIC) and Northern Territory Museum and Art Galleries (NTM) were available for this study; other depositories of types or new material are The Natural History Museum, London (BMNH), Queensland Museum (QM) and Waite Agricultural Research Institute (WARI). For all established species, only a diagnosis, illustrations and new distribution data are given. For the more commonly collected species, only distribution maps are given — the detailed locality data are not included here, or are included for type material only; these data are available from the author or from NMV. Members of the *laustra*-group occur in all Australian states and territories, and tend to be more or less peripherally distributed on the mainland; several species are found in Tasmania and one is described from Lord Howe Island. Some species appear to be localised, and others to have disjunct distributions (see Table 1); similar patterns were reported for *complexa*-group species (Wells, 2000). Fifteen *laustra*-group species are known only from northern Australia, and the richest diversity — 16 species — is recorded for Queensland (see Table 1), with most records being from along the eastern seaboard; four of these species have been collected from northern Queensland only, and one is known from Queensland and New Guinea. Few species in this group are recorded for south-western Western Australia or South Australia. Two species assigned to the *longiterga*-group are recorded only from northern Australia; the third is widespread — collected from northern Western Australia, the north of the NT, south-eastern Qld, eastern NSW and south-central Victoria.

As for species of the *complexa*-group, few females can be associated with males with certainty. Thus, new species are diagnosed on the basis of males only. Several observations on biology are pertinent, some deduced from label data. For example, locality data for *O. laustra* include a large number of lacustrine sites. Larvae of this species build their case from portions cut from stems of aquatic macrophytes and live amongst and on these plants (Wells, 1991; St Clair, 1994); the cases are very light and would readily be swept free of the substratum by currents. In contrast, it appears from label data that *O. arcada* Mosely, 1953, *O. asmanista* Mosely, 1953 and *O. cymula* Neboiss, 1982 are probably adapted to swiftly flowing waters. I have found the sand grain-cased larvae of *O. digitata* sp. nov. in sand in the direct flow of water under small rocky falls, and those of *O. koobarra* sp. nov. amongst sand on ledges in the bedrock of small permanent creeks that have moderate flow, but are subject to occasional spates. Larvae and pupae of *O. erskinensis* sp. nov., from Lord Howe Island, were collected from crevices, ridges and ledges in the main flow of a small stream. Like many other species, *O. brevidentata* sp. nov. constructs sand-grain cases and is found associated with boulders and cobbles in sand- or cobble-based creeks or rivers.

Table 1. *Oecetis laustra*-group species clustered according to state/territory of occurrence with the exception that a distinction is made between the north-west and south-west of Western Australia, and Lord Howe Island is included (LHI). Arrangement designed to emphasize commonalities between parts of Australia. (Abbreviations: Qld, Queensland; NSW, New South Wales; Vic., Victoria; Tas., Tasmania; SA, South Australia; SWWA south-western Western Australia; NWWA, north-western Western Australia; NT, Northern Territory; LHI, Lord Howe Island).

SPECIES	SW WA	NW WA	NT	Qld	NSW	Vic.	Tas.	SA	L H I
<i>Oecetis erskinensis</i> sp. nov.									+
<i>Oecetis scripicula</i> Neboiss, 1977									+
<i>Oecetis crena</i> sp. nov.						+			
<i>Oecetis arcada</i> Mosely, 1953						+	+		
<i>Oecetis asmanista</i> Mosely, 1953						+	+		
<i>Oecetis paracymula</i> sp. nov.						+			
<i>Oecetis terania</i> sp. nov.						+			
<i>Oecetis minasata</i> Mosely, 1953						+	+	+	
<i>Oecetis parka</i> Mosely, 1953					+	+	+		
<i>Oecetis aduncata</i> sp. nov.					+	+	+		
<i>Oecetis curta</i> sp. nov.					+	+			
<i>Oecetis inscripta</i> Kimmings, 1953					+	+	+	+	+
<i>Oecetis laustra</i> Mosely, 1953	+	+	+	+	+	+	+	+	+
<i>Oecetis atarpa</i> Mosely, 1953	+	+		+	+	+	+	+	+
<i>Oecetis aeoloptera</i> Kimmings, 1953				+	+	+			
<i>Oecetis dosilinei</i> sp. nov.					+				
<i>Oecetis dilata</i> sp. nov.				+	+	+			
<i>Oecetis spicata</i> sp. nov.				+	+	+			
<i>Oecetis cepaforma</i> sp. nov.				+	+	+			
<i>Oecetis papposa</i> sp. nov.				+	+				
<i>Oecetis cracenta</i> sp. nov.				+	+				
<i>Oecetis brevidentata</i> sp. nov.				+					
<i>Oecetis koobarra</i> sp. nov.				+					
<i>Oecetis pseudolaustra</i> sp. nov.					+				
<i>Oecetis falcata</i> sp. nov.					+				
<i>Oecetis quadrata</i> sp. nov.					+				
<i>Oecetis multipunctata</i> Ulmer, 1916					+				
<i>Oecetis ornata</i> Kimmings, 1962					+				
<i>Oecetis cymula</i> Neboiss, 1982		+							
Total species	3	7	10	16	10	10	7	3	

Generally, larval morphology of *Oecetis* species is remarkably uniform, a major difference being colour patterns on the head and pro- and mesonota, and occasional differences are apparent in ventral head and thoracic sternal sclerites, and in setation (Floyd, 1995; St Clair, 2000). However, mandibles of at least one *laustra*-group species, *O. brevidentata* sp. nov., are short and stout (Wells, 1991), suggesting a different diet from that of most species. The more characteristic mandible form is slender and sharply pointed.

Key to males of *Oecetis* species groups in Australia

1. Abdominal tergite VIII sculptured, expanded and extended distally, forming shield over terminal abdominal segments and genitalia *reticulata*-group (see Neboiss, 1989)
- Abdominal tergite VIII unmodified 2
2. Wings with veins strongly pronounced, fork 1 without a footstalk (sessile) (Figs 91, 94) *longiterga*-group

- Wings with veins normal, not particularly well pronounced, fork 1 with or without footstalk (Figs 1, 30, 53) 3
- 3. Phallus simple, lacking parameres (Figs 3, 38, 72) *laustra*-group (see below)
- Phallus with one or more internal or external parameres or spines 4
- 4. Forewing fork 1 sessile, wing lamina often bearing patches of scales (androconia); phallus usually with a single internal paramere or spine *pechana*-group
- Forewing fork 1 stalked, wing never bearing patches of scales; phallus with one or more external parameres *complexa*-group (see Wells, 2001)

Key to males of the *Oecetis laustra*-group in Australia

1. Forewing with distinct footstalk on fork 1 (Fig. 1) 2
- Forewing with fork 1 sessile (Figs 80, 87, 88), or very nearly so 25

2. In hind wing, M unbranched (Fig. 73); in male genitalia in lateral view, inferior appendages about same width basally and apically, constricted mesially (Fig. 72) *O. papposa*
 — In hind wing, M branched; male genitalia not as above 3
3. In hind wing, Cu1 and Cu2 arise at crossvein M-Cu (Fig. 53) *O. quadrata*
 — In hind wing, Cu1 and Cu2 arise distal to crossvein M-Cu 4
4. In forewing, at least 2 crossveins contiguous (linear), or nearly so, in posterior anastomosis (Figs 10, 12) 5
- In forewing, crossveins of posterior anastomosis all clearly stepped (Figs 29, 30) 13
5. Forewing with distinctive dark lines marking parts of veins, including diagonal mark linking t1, t2, t3 (Fig. 12)
 *O. inscripta*
 — Forewing not as above 6
6. In genitalia, inferior appendages in lateral view swollen basally, distally reduced to at least one-third basal width and strongly curved dorsad 7
- In genitalia, inferior appendages in lateral view not as above (Figs 18, 39) 10
7. In genitalia, in ventral view, inferior appendages tapered gradually towards apex, mesial margin slightly denticulate or with a single sharp mesial hook (Fig. 2) 8
- In genitalia, in ventral view, inferior appendages sharply excavated at about one-third length, distally slender, mesial margin smooth (Figs 8, 26) 9
8. In genitalia, in ventral view, inferior appendages with a small mesial tooth (Fig. 2) *O. laustra*
 — In genitalia, in ventral view, inferior appendages with a sharp anteriorly directed mesial hook (Fig. 4)
 *O. pseudolaustra*
9. Forewing with dark membrane marking posterior anastomosis; genitalia in lateral view with peg-like process ventral to preanal appendages (Fig. 9) *O. atarpa*
 — Forewing without dark markings at posterior anastomosis (Fig. 10); without peg-like process ventral to preanal appendages (Fig. 11) *O. scirpicula*
10. In forewing t3 well proximal to t1 and t2, with M3+4 arising distal to t3; wing lamina patterned with dark marking on crossveins t1, t2 and M forming a short dark distal cross (Fig. 15) *O. brevidentata*
 — In forewing t3 only slightly proximal to t1 and t2, with M3+4 arising at t3; wing lamina mottled, without distinct marking 11
11. In genitalia in ventral view, inferior appendages broad in basal two-thirds, mesial margin rounded then abruptly constricted, curved inwards towards apices, not sharply angled (Fig. 19); tergite X slim, digitiform *O. asmanista*
 — In genitalia in ventral view, inferior appendages broad-based with meso-ventral angle slightly lobed, mesial margin strongly constricted to form a narrow lobe latero-distally, with apex sharply angled inwards (Figs 21, 24); tergite X a broad membrane 12
12. In genitalia in ventral view, phallus with apex sharply delineated and deeply V-shaped (Fig. 24) *O. erskinensis*
 — In genitalia in ventral view, phallus with apex rounded, very shallowly cleft (Fig. 21) *O. minasata*
13. In forewing, t1 more distal than t2 or t3 (Figs 64, 73) 14
 — In forewing, t2 more distal than t1 or t3 (Fig. 30) 17
14. Male genitalia with prominent, unequal sclerotised spines dorsally (Figs 65–67) *O. falcata*
 — Male genitalia without any sclerotised spines (Figs 60, 62)
 15
15. Forewing fork 1 and its footstalk about equal length; on forewing a zig-zag pattern marks posterior anastomosis (Fig. 63) *O. koobarra*
 — Forewing fork 1 longer than its footstalk; forewing posterior anastomosis not marked by zig-zag pattern 16
16. Male genitalia, in ventral view, with inferior appendages stout throughout length, about 1.5 times width, rounded mesially, apically a small curved lateral process (Fig. 57); tergite X broad, apically truncate (Figs 58, 59) .
 *O. dilata*
- Male genitalia, in ventral view, with inferior appendages stout basally, gradually constricted to about half basal width; tergite X excavated mesially to form a pair of apically acute lateral processes (Figs 47, 48)
 *O. spicata* (N Qld form)
17. Male genitalia, in lateral view, with a small digitate lobe dorsal to base of inferior appendages (Fig. 38) *O. parka*
 — Male genitalia, in lateral view, without a small lobe as above 18
18. Male genitalia, in ventral view, with a lobe on mesial side of inferior appendages (Fig. 69) *O. terania*
 — Male genitalia, in ventral view, without a lobe as above 19
19. Wings uniformly fuscous, vestiture short, dense; in male genitalia, tergite X comprising a median, tapered lobe between a pair of broadly rounded, membranous lateral lobes (Figs 42, 45) 20
- Wings mottled or with some small markings, or spotted; tergite X not as above 21
20. Male genitalia, in lateral view, with inferior appendages about same width throughout length, apices not down-turned (Fig. 43) *O. cymula*
 — In genitalia, in lateral view, inferior appendages dilated baso-ventrally, apices down-turned, rounded (Fig. 46)
 *O. paracymula*
21. In genitalia, in ventral view, inferior appendages broad-based, abruptly narrowed, expanded slightly mesially, distally about width of narrower basal section (Fig. 50); in lateral view, inferior appendages with a broadly rounded basodorsal lobe, distally tapered, slender (Fig. 52)
 *O. crena*
- In genitalia, in ventral view, inferior appendages not as above 22
22. In genitalia, in lateral view, inferior appendages truncate apically, in distal half about half width at base (Fig. 40); in ventral view, a distinct notch on mesial margin at about two-thirds length (Fig. 39) *O. arcada*
 — Not as above 23
23. In genitalia, inferior appendages in lateral view expanded dorsally, narrow in distal two-thirds (Fig. 36); in ventral view gently curved inwards and tapered to acuminate apices (Fig. 34) *O. cracenta*
 — Not as above 24

24. In genitalia, in ventral view, inferior appendages stout basally gradually curved and constricted to narrowly rounded apex; preanal appendages rounded (Figs 31–33) *O. multipunctata*
 — In genitalia, in ventral view, inferior appendages stout at base, abruptly narrowed to form slender disto-lateral lobes; preanal appendages in dorsal view triangular, in lateral view slender, tapered (Figs 26–28) *O. aeoloptera*
25. Forewing distinctly and coarsely patterned, dark brown and fuscous (Fig. 80) *O. ornata*
 — Forewing not as above, but may be spotted, moth-like 26
26. Male genitalia with, tergite X hairy, rounded, cleft medially (Fig. 75) *O. curta*
 — Tergite X not as above 27
27. In genitalia, tergite X membranous with apicolateral angles acute (Fig. 48) *O. spicata* (NT form)
 — In genitalia, tergite X not as above 28
28. Wings not spotted; in genitalia, in lateral view, preanal appendages narrow, length 2x width (Figs 78, 79)
 *O. aduncata*
 — Wings spotted (Figs 87, 88); in genitalia, in lateral view, preanal appendages broadly rounded or subtriangular (Figs 86, 89) 29
29. In genitalia, tergite X in dorsal view minaret-shaped (Fig. 85); inferior appendages in ventral view with tiny hook at mesial angle *O. cepaforma*
 — Male genitalia with, tergite X in dorsal view broad, apically truncate (Fig. 90); inferior appendages in ventral view without tiny hook at mesial angle
 *O. dostinei*

Key to males of *Oecetis longiterga*-group in Australia

1. Forewing Cu1a straight (Fig. 94); in genitalia a single paramere with apex spiked and toothed (Figs 98, 100) *O. crosslandi*
 — Forewing Cu1a with distinct curve (Fig. 91); male genitalia not as above 2
2. Male genitalia with, in lateral view, a sclerotised process dorsal to inferior appendages (Fig. 97); in ventral view, forming a stout structure, angled mesially at midlength (Fig. 95) *O. ancala*
 — Male genitalia without any sclerotised processes (Figs 92, 93) *O. digitata*

Species of the *laustra*-group

Oecetis laustra Mosely

Figures 1–3, 101

Oecetis laustra Mosely in Mosely and Kimmins, 1953: 295, fig. 209.—Neboiss, 1977: 146, figs 788–791.—Neboiss, 1982: 321, figs 129–131.

Material examined. Holotype. Male, Yanchep, WA, 31°32.9'S 115°41.2'E (BMNH).

Other material. About 180 samples in ANIC, NTM, NMV and WARI.

Diagnosis. Wings slightly mottled, fuscous-brown/grey, with short hair on veins; forewing (Fig. 1) length 4 times maximum width, footstalk of fork 1 slightly shorter than fork, posterior anastomosis almost linear, to linear, very slightly oblique; hindwing (Fig. 1) with M branched; in male genitalia, inferior appendages (Figs 2–3) broad and stout, in ventral view, a small mesial tooth at about two-thirds length, in lateral view broadly rounded above and below in basal half, distally about one-third maximum basal width; preanal lobes short, rounded.

Distribution. Widespread in Australia, in lentic and slower lotic waters, but not collected from arid central Australia (Fig. 101).

Remarks. The stouter inferior appendages distinguish *O. laustra* from *O. atarpa* and *O. aeoloptera*, the absence of a sharp, anteriorly directed mesial hook on the inferior appendages distinguishes it from *O. pseudolaustra* sp. nov. *Oecetis laustra* is one of the most widespread and abundant of Australian *Oecetis* species, although unlike *O. pechana* it has not been collected from the natural and artificial waterbodies of arid inland Australia. In its present concept, the species is quite variable across its range, and may eventually be demonstrated to be several species. The posterior anastomosis of the forewing is usually more or less linear, but may be slightly stepped; and in the male genitalia, the form of the mesial margin of the inferior appendages may be more or less dentate (Mosely and Kimmins, 1953: fig. 209c, d; Neboiss, 1986: 269).

Oecetis pseudolaustra sp. nov.

Figures 4–6, 102

Material examined. Holotype, male, Qld, Lakefield NP, Sweetwater Lagoon, 11 Oct 2002, G. Theischinger (ANIC).

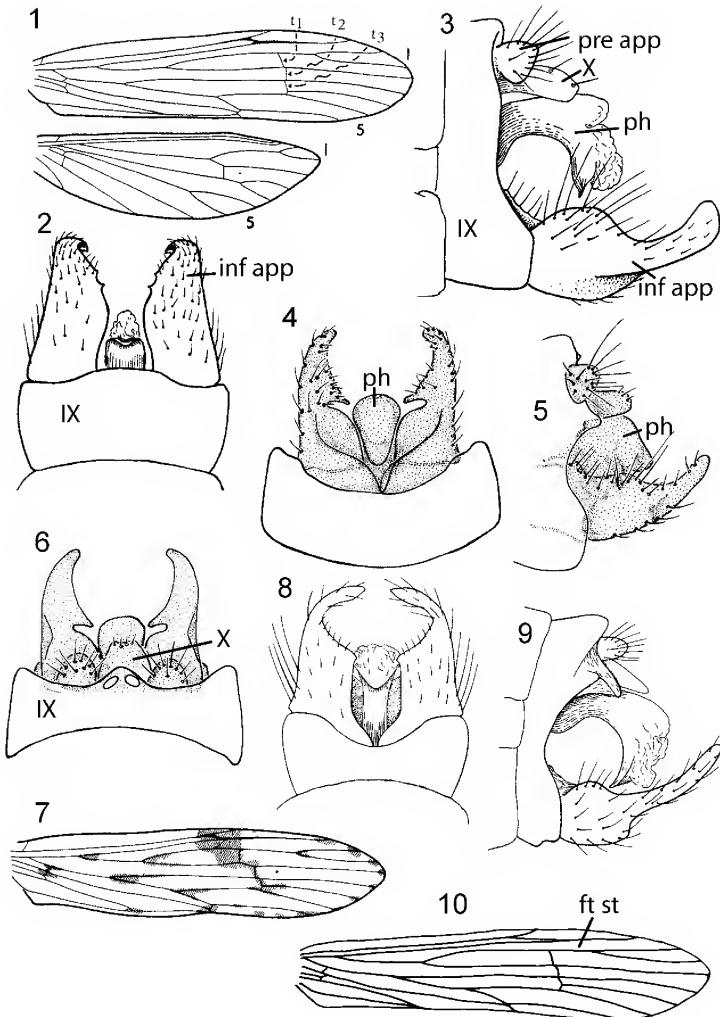
Paratypes. 21 males, 1 female, data as for holotype (ANIC); 18 males, 3 females, Cape York Peninsula, Wenlock River crossing (to Iron Range), 5 Oct 2002, G. Theischinger (ANIC, NMV, QM).

Diagnosis. As *O. laustra* except inferior appendages with a sharp anteriorly directed mesial hook.

Description. Tibial spurs 1, 2, 2. Male forewing length 3.4–5.0 mm. Wings as for *O. laustra*, mottled fuscous/brown, densely covered with short hair. Male genitalia as in Figs 4–6. Preanal appendages in dorsal view rounded apically and about as long as wide. Tergite X a single membranous plate, narrowly truncate apically. Inferior appendages stout, in lateral view broadly rounded above and below in basal half, distally about one-third maximum basal width, in ventral view with a sharp mesial hook on inner margin. Phallus length in lateral view equal to width.

Distribution. Far north of Cape York Peninsula, northern Qld (Fig. 102).

Remarks. At the Lakefield National Park site, this species was collected together with several specimens of *Oecetis laustra*, which could be distinguished by their slightly darker colour as well as the distinctive difference in male genitalia. The stouter inferior appendages distinguish *O. pseudolaustra* and *O. laustra* from *O. atarpa* and *O. aeoloptera*.



Figures 1–3, *Oecetis laustra* Mosely, 1953: 1, wings, labelled to indicate forks present and terminology applied to crossveins of posterior anastomosis; 2–3, male genitalia, ventral and lateral views [after Mosely and Kimmins, 1953]. inf app, inferior appendages; ph, phallus; pre app, pre-anal appendage; IX, X, abdominal segments IX and X; 1, 5, forks in wing venation.

Figures 4–6, *O. pseudolaustra* sp. nov., male genitalia, ventral, dorsal and lateral views. X, abdominal segment X.

Figures 7–9, *O. atarpa* Mosely: 7, forewing; 8, 9, male genitalia, ventral and lateral views [from Mosely and Kimmins, 1953].

Figure 10, *O. scirpicula* Neboiss, forewing [after Neboiss, 1977]. ft st, foot stalk of fork 1.

Oecetis atarpa Mosely

Figures 7–9, 103

Oecetis atarpa Mosely and Kimmins, 1953: 287, fig. 202.

Material examined. Paratype. Male, National Park [Royal National Park], NSW, 34°33.9'S 151°3.1'E (BMNH).

Other material. 27 samples in ANIC and NMV.

Diagnosis. Forewing (Fig. 7) length 3–4 times maximum width, fork 1 with footstalk, posterior anastomosis with t2 and t3 contiguous, t1 more proximal than both t2 and t3; in the male

genitalia (Figs 8, 9) abdominal segment IX in lateral view produced distally in a down-turned peg ventral to preanal lobe; and inferior appendages in lateral view long and slender distally, rounded and swollen basally with basal third about 4 times broader than distal two-thirds which is less than twice length of basal section.

Distribution. Throughout Australia but only small scattered collections taken in NT (Fig. 103).

Remarks. Closely resembling *Oecetis scirpicula* and *O. aeoloptera* in form of male genitalia but distinguished by the

stepped arrangement of crossveins in the posterior anastomosis in forewing, and the dorsolateral 'peg' on abdominal segment IX. The very slight difference between *O. atarpa* and *O. scirpicula* Neboiss—mainly the more strictly linear posterior anastomosis in the forewing of the latter and in the male genitalia a small difference in proportions in inferior appendages—is well within the range of variation exhibited by other Australian *Oecetis*, particularly those with temperate to tropical distributions. For the present, however, the two names are retained.

Oecetis scirpicula Neboiss

Figures 10, 11, 104

Oecetis scirpicula Neboiss, 1977: 149, figs 804–807.

Material examined. Tas.: 2 males, Canal at Interlaken, 42°8.8'S 147°10.5'E, 2 Feb 1966, G.E. Edmunds (ANIC); males, females, Navarre River, 42°9.5'S 146°8.6'E, 12 Feb 1967, E.F. Riek (ANIC); 1 male, Olga-Hardwood River, Saddle buttongrass plain, 42°57.8'S 145°55.3'E, 4 Apr 1977, Allbrook, Richardson, Swain (NMV); 2 males, 12 km NNE Bronte Park, 42°02'S 146°33'E, 2 Feb 1983, J.C. Cardale (ANIC); male, 2 females, Pelion Hut, 3 km S Mt Oakleigh, 41°50'S 146°03'E, Feb 1990, E.S. Nielsen, It trap (ANIC).

Diagnosis. Forewing (Fig. 10) length about 4 times maximum width, veins of the posterior anastomosis contiguous; in male genitalia (Fig. 11), abdominal segment IX produced posteriorly to form a triangular process ventral to preanal appendages and inferior appendages with distal slender distal portion twice length of basal portion.

Distribution. Tas. (Fig. 104).

Remarks. Although males of this species closely resemble those of *O. atarpa*, as noted above, the name *scirpicula* is retained here for these Tasmanian specimens. The two species have only slight difference in forewing venation and in the genitalia—proportions of the inferior appendages, differences that are well within the range of variability accepted for other species. Size differences, however, are considerable, the anterior wing length of around 9 mm for *O. scirpicula* being several millimetres longer than in *O. atarpa*. In addition, females of *O. scirpicula* lack the broadly rounded dorsal lobes seen in *O. atarpa* (Moseley and Kimmins, 1953: fig. 203c), having in their place a pair of almond-shaped lobes.

Oecetis inscripta Kimmins

Figures 12–14, 105.

Oecetis inscripta Kimmins in Moseley and Kimmins, 1953: 294, fig. 208.—Neboiss, 1977: 148, figs 801–803.—Neboiss, 1982: 323, figs 127, 128.

Material examined. Holotype. Male, Bathurst, NSW (BMNH). 52 samples in ANIC, NMV and WARI.

Diagnosis. Forewing (Fig. 12) length almost 5 times maximum width, lamina marked with bold dark streaks, not the more usual dark spots or patches; footstalk on fork 1, and t1 and t2 contiguous, t3 more proximal than the 2 other crossveins

of the posterior anastomosis. In the male genitalia (Figs 13, 14), a rounded basodorsal lobe on the inferior appendages and inferior appendages in ventral view slender with length 3 times maximum width, irregularly tapered towards apex.

Distribution. Eastern Australia from Tas, northwards almost to Cairns, north-eastern Qld, probably widespread in Murray–Darling basin (Fig. 105).

Oecetis brevidentata sp. nov.

Figures 15–18, 106

Oecetis sp. E.—Wells, 1991: figs 138, 172–176.

Material examined. Holotype, male, NT, Katherine River Gorge National Park, 13°23.9'S 133°10.0'E, 13 Aug 1979, J. Blyth (NMV T-18524).

Paratypes. NT: 4 males, 3 females, same data as for holotype (NMV); 1 male, Kakadu National Park, Jim Jim Creek, 3 km below falls, 13°15.9'S 132°51.1'E, 1 Sep 1979, J. Blyth (NMV); 1 male, ARRS, South Alligator River, at Gimbat OSS Station, 13°34.3'S 132°36.7'E, 24 May 1988, A. Wells and P. Suter (NMV); 9 males, 1 female, South Alligator River below BHP camp, 25 May 1988, P. Suter and A. Wells (NMV); 2 males, ARRS, SAR site 1, 14 Jun 1988, P. Dostine (NTM); 1 male, 1 female, ARRS, South Alligator River, at Gimbat OSS Station, 13°34.3'S 132°36.7'E, 28 Apr 1989, P. Dostine (NTM); 2 males, 1 female, 12°48'S 132°49'E, Kakadu National Park, Baroalba Springs, 4 Oct 1991, A. Wells (NTM).

Other material. NT: male, 3 females, ARRS South Alligator River above Fisher Creek jcn, 13°34'S 132°34'E, 18–20 Apr 1989, Suter and Wells (NTM); 2 males, female, Gunlom (as UDP Falls), 13°24.9'S 132°26.0'E, 18–19 Jul 1980, M.B. Malipatil (NTM).

Diagnosis. Forewing with length about 5 times maximum width, lamina marked by a distinctive cross formed by dark membrane and setae on t1 and t2 and their junction with R3–4; t1 and t2 contiguous, t3 well proximal of both. In male genitalia, inferior appendages in ventral view slender and curving, and in lateral view with apices acute and directed ventrally, rather than straight as in *O. multipunctata*.

Description. Tibial spurs 1, 2, 2. Male forewing length 6.1–7.8 mm. Wings with vestiture of even length, without spots, but forewing (Fig. 15) with distinctive dark cross marking the junctions of t1 and t2 with R, footstalk on fork 1 longer than fork. Male genitalia as in Figs 16–18. Segment IX widest midlaterally; preanal appendages separate, ovoid. Segment X elongate, membranous, dorsal process short, slender. Inferior appendages narrow, tapered, slightly bowed, apices down-turned in lateral view. Phallus with length about twice width, beak-like apically.

Distribution. Alligator Rivers region of northern NT (Fig. 106).

Remarks. The larva of this species is unique among Australian *Oecetis* species. Associated as 'sp. E' by Wells (1991), it is the only *Oecetis* species of which I am aware that has short, blunt mandibles. This feature suggests that *O. brevidentata* has dietary habits quite different from other congeners. It may well be a detritivore.

Etymology. Latin, descriptive of the larval mandibles.

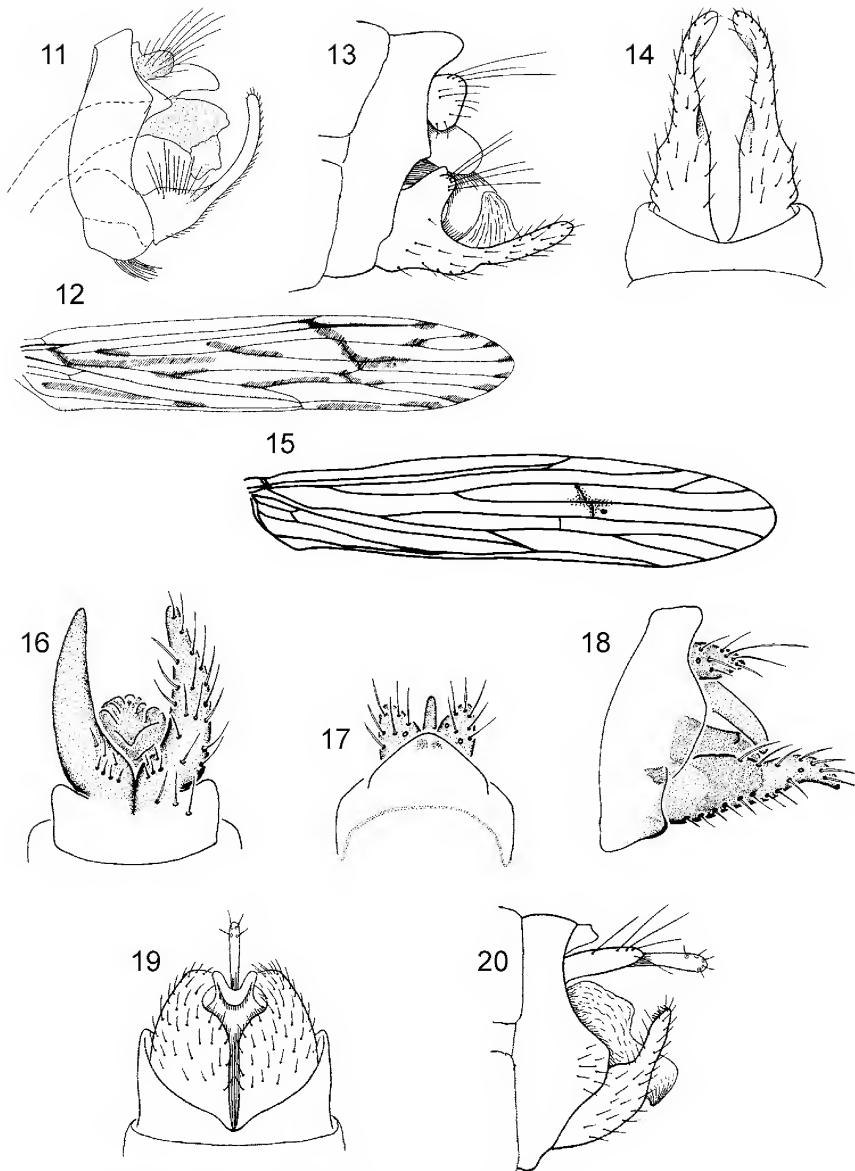


Figure 11, *Oecetis scirpicula* Neboiss, male genitalia, lateral view [from Neboiss, 1977].

Figures 12–14, *O. inscripta* Kimmins: 12, forewing; 13, 14, male inferior appendages in ventral view, genitalia in lateral view [from Mosely and Kimmins, 1953].

Figures 15–18, *O. brevidentata* sp. nov.: 15, forewing; 16–18, male genitalia, ventral, dorsal and lateral views.

Figure 19, 20, *O. asmanista* Mosely, male genitalia, ventral and lateral views [from Mosely and Kimmins, 1953].

Oecetis asmanista Mosely

Figures 19, 20, 107

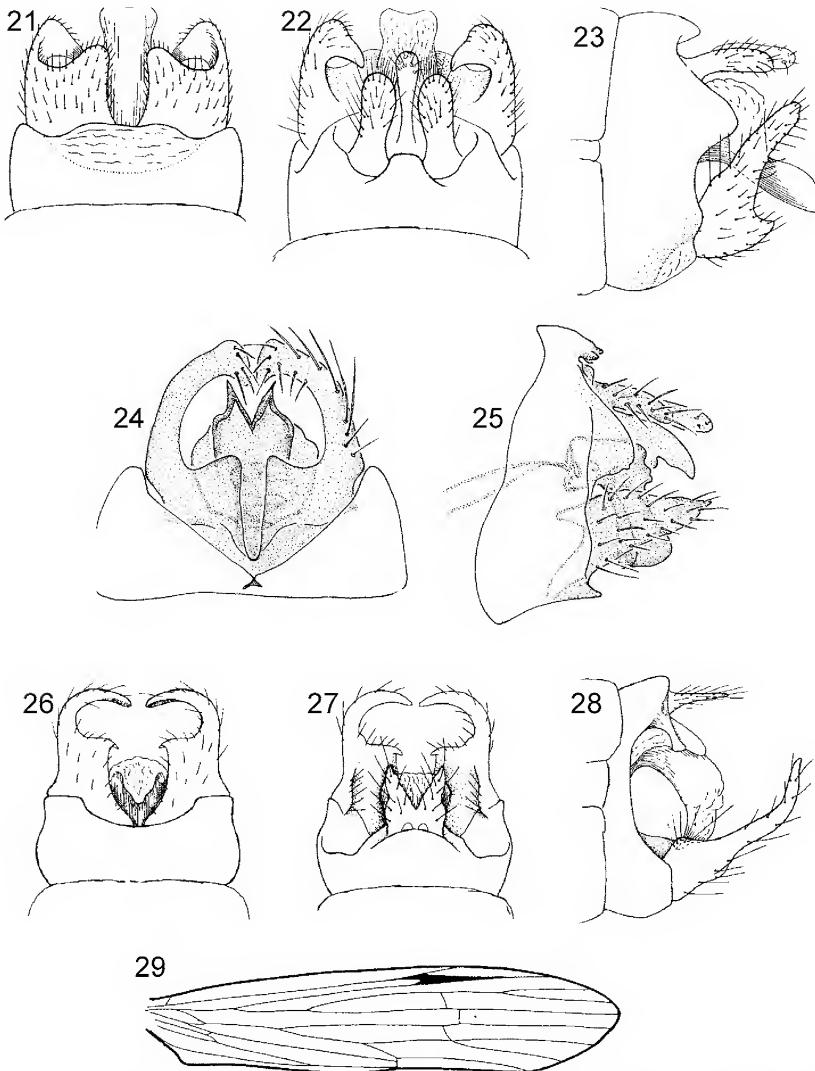
Oecetis asmanista Mosely and Kimmins, 1953: 282, fig. 199. — Neboiss, 1977: 147, figs 792–795.

Oecetis ochracea Jaquemart, 1965: 23. [Junior homonym of *Oecetis ochracea* (Curtis, 1825)], (synonymy by Neboiss, 1977: 147).

Oecetis gevestonia Neboiss, 1974: 15. [Unnecessary replacement name for *O. ochracea* Jaquemart.]

Material examined. Holotype. male, Tas. (BMNH).

Tas.: Male, female, Derwent Bridge, 12 Feb 1967, E.F. Riek (ANIC); male holotype (BMNH); 1 male, Olga Camp, Gordon-Smith River junction, 42°39.1'S 145°48.0'E, 2 Feb 1976, Howard, Suter (NMV); males, females, West Bay River, Margate, 43°1.7'S



Figures 21–23, *Oecetis minasata* Mosely, male genitalia, ventral, dorsal and lateral views [from Mosely and Kimmins, 1953].

Figures 24–25, *O. erskinensis* sp. nov., male genitalia, ventral, dorsal and lateral views.

Figures 26–29, *O. aeoloptera* Kimmins: 26–28, male genitalia, ventral, dorsal and lateral views; 29, forewing [from Mosely and Kimmins, 1953].

147°15.7'E, 6 Jan 1977, Coleman, Neboiss, Allbrook (NMV); males, females, Franklin River-Roaring Creek junction, 4 km above Gordon River junction, 8 Jan 1977, Coleman, Neboiss, Allbrook (NMV); 1 female, Swamp nr Olga River, 19 km above Gordon River Junction, 42°42.8'S 145°46.8'E, 13 Jan 1977, Neboiss and Swain (NMV); 3 males, Pelion Hut, 3 km S Mt Oakleigh, 41°50'S 146°03'E, 6–11 Mar 1991 at light, M. Horak, P. McQuillan (ANIC). Vic: male, Tanjil River Jcn, 10 km N of Willow Grove, 38°4.2'S 146°10.6'E, 18 Dec 1973, A. Neboiss (NMV).

Diagnosis. Forewing length over 4 times maximum width, fork 1 with footstalk and t1 and t2 contiguous, t3 only slightly more proximal than t1 or t2. In male genitalia (Figs 19, 20), inferior appendages skittle-shaped in lateral view being roundly

constricted at two-thirds length, narrow distally; tergum X a narrow process, almost twice as long as preanal appendages.

Distribution. Tas. and south-central Vic. (one specimen only) (Fig. 107).

Oecetis minasata Mosely

Figures 21–23, 108

Oecetis minasata Mosely in Mosely and Kimmins, 1953: 282, fig. 198. —Neboiss, 1977: 146, figs 784–787.

Material examined. Holotype. Male, Tas. (BMNH).

21 samples in ANIC and NMV.

Diagnosis. Wings dark brownish, unicolorous, with long downy hair on the veins; forewing length 4 times maximum width, posterior anastomosis contiguous. In male genitalia (Figs 21–23) in ventral view, inferior appendages with basal portion as long as wide, roundly produced ventromesally, and constricted and sharply returned forming dorsolateral lobes; preanal appendages about 3 times as long as wide.

Distribution. South-eastern Australia: from south-eastern NSW, ACT, Vic. and Tas. (Fig. 108).

Remarks. Males of *O. minasata* are distinguished from those of *O. erskinensis* by the rounded apex of the phallus, and from *O. asmanista* by the angular ventral expansion of the inferior appendages and the shorter median process of tergum X. The female lacks the patches of bristles characteristic of *O. asmanista*. In form of male genitalia, *O. cymula* and *O. paracymula* also show resemblance, but *O. minasata* can be distinguished from the two species by the crossveins of the posterior anastomosis contiguous, not stepped.

Oecetis erskinensis sp. nov.

Figures 24, 25

Material examined. Holotype, male, Lord Howe Island, Erskine Valley, Erskine Creek, 21–22 Nov 1996, Wells and Mound (ANIC).

Paratype. Male, data as for holotype (ANIC).

Other material. Larvae, pupa, locality as for holotype, 24 Dec 2001, Wells and Mound (ANIC).

Diagnosis. As for *O. minasata*, but in male genitalia (Figs 24, 25) setae on inturned apices of inferior appendages are all about equal in size and length, and in ventral view the apex of phallus is divided to form 2 apically acute, sclerotised lobes.

Description. Spurs 1, 2, 2. Male forewing length, 7.9 mm. Wings of typical shape, forewing fork 1 with footstalk less than half length of fork, posterior anastomosis with t1 and t2 linear, oblique, t3 slightly more proximal, angled. Male genitalia, Figs 22, 25. Segment IX narrow, preanal appendages more than twice as long as wide, rounded apically. Segment X slender, almost same width throughout length. Inferior appendages in ventral view clasper-shaped, inturned subapically, apices obliquely truncate. Phallus very short, with distal sharply downturned section almost twice length of basal portion, rounded basally, bifurcate, lobes sclerotised, acute apically.

Remarks. *Oecetis minasata* and *O. erskinensis* are closely similar, possibly sister species, distinguished by genitalic character states as noted under *O. minasata*.

Etymology. Named for the collecting site.

Oecetis aeoloptera Kimmings

Figures 26–29, 109

Oecetis aeoloptera Kimmings in Mosely and Kimmings, 1953: 287, fig. 201.

Material examined. Holotype. Male, Murwillumbah, NSW (BMNH). 21 samples in ANIC and NMV.

Diagnosis. Forewing (Fig. 29) length 4 times maximum width, posterior anastomosis clearly non-linear, with t2 more distal than t1 and t3 which are both approximately equal; in male genitalia (Figs 26–28) inferior appendages pincer-shaped in ventral view, in lateral view long and slender distally; preanal lobes discrete, triangular.

Distribution. Eastern Vic., more north-eastern NSW, south-eastern and northern Qld, northern NT to northern WA (Fig. 109).

Remarks. In male genitalic features *O. aeoloptera* closely resembles *O. atarpa* and *O. scirpicula* but is distinguished by the more attenuate inferior appendages, and preanal lobes elongate triangular in ventral view, in lateral view, slender, tapered, rather than rounded.

Oecetis multipunctata Ulmer

Figures 30–33, 110

Oecetis multipunctata Ulmer, 1916: 19. —Mosely and Kimmings, 1953: 293, fig. 206.

Material examined. 48 samples in ANIC and NMV.

Diagnosis. Wings with pattern of dark spots (Fig. 30); forewing length about 4.5 times maximum width, fork 1 with footstalk and veins of the posterior anastomosis clearly stepped. In male genitalia (Figs 31–33) segment X simple, short and slender; inferior appendages without any lobes or processes, length about 3 times width, tapered distally; and phallus curved downwards.

Distribution. Widespread in northern and eastern Qld, and also collected from north-eastern NSW (Fig. 110).

Remarks. *Oecetis ceaformia*, *O. dostinei* and *O. parka* also have spotted wings, but *O. ceaformia* and *O. dostinei* have the forewings broad and ‘floppy’ compared to those of *O. multipunctata* and *O. parka*. These last two species are distinguished by male genitalic features, particularly the presence of the digitate laterobasal lobe on the inferior appendages of *O. parka*, and the more rounded, rather than angular shape of the inferior appendages of *O. multipunctata*. The male genitalia of *Oecetis multipunctata* closely resemble those of the NT *O. brevidentata* from which *O. multipunctata* is distinguished by its spotted wings and shape of the phallus. Also in *O. multipunctata*, in lateral view, the inferior appendages are almost straight, whereas in *O. brevidentata* sp. nov. the apices are down-turned.

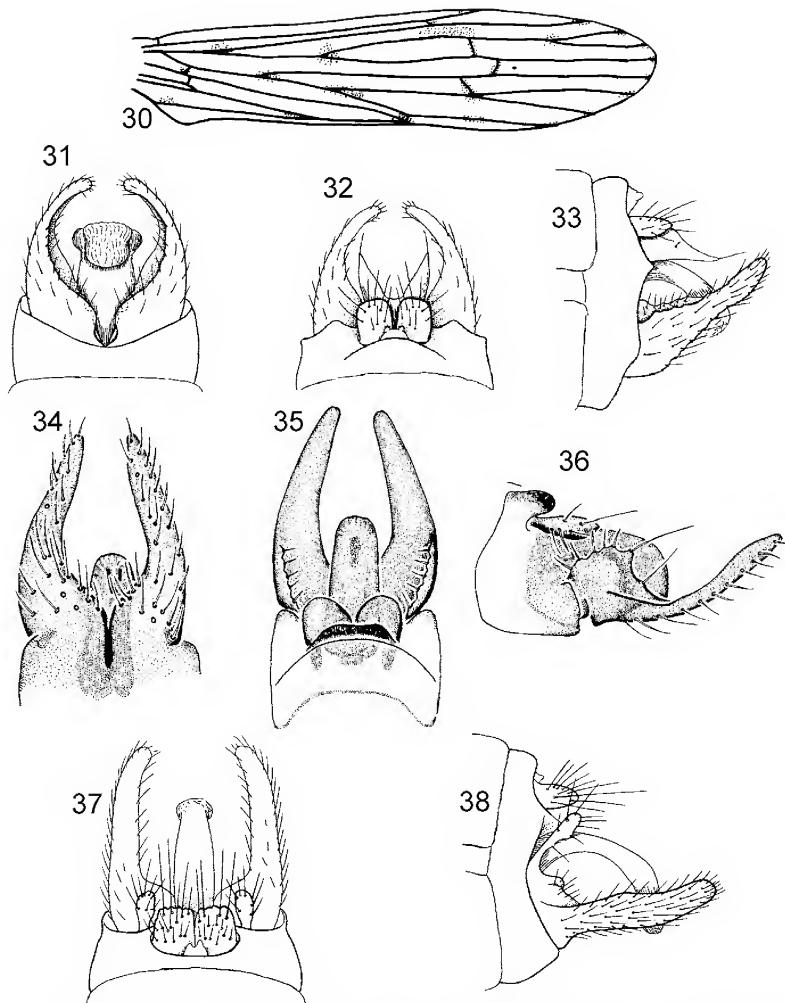
Oecetis cracentia sp. nov.

Figures 34–36, 111

Material examined. Holotype, male, WA, King Edward River, 4–5 May 1992, 14°52.57'S 126°12.08'E, P.S. Cranston (ANIC).

Paratypes. NT: 2 males, 3 females, Litchfield National Park, Florence Falls, 13°03'S 130°47'E, 9 Apr 1991, Wells and Horak (NMV).

Diagnosis. Wings mottled, not noticeably spotty; forewing length about 4 times maximum width, fork 1 with footstalk, and



Figures 30–33, *Oecetis multipunctata* Ulmer: 30, forewing; 31–33, male genitalia, ventral, dorsal and lateral views [from Mosely and Kimmins, 1953].

Figures 34–36, *O. cracenta* sp. nov., male genitalia, ventral, dorsal and lateral views.

Figures 37, 38, *O. parka* Mosely, male genitalia, dorsal and lateral views [from Mosely and Kimmins, 1953].

crossveins of posterior anastomosis clearly stepped. In male genitalia, in ventral view, the inferior appendages taper smoothly from base to apex and lack a mesial process, and the preanal appendages are rounded.

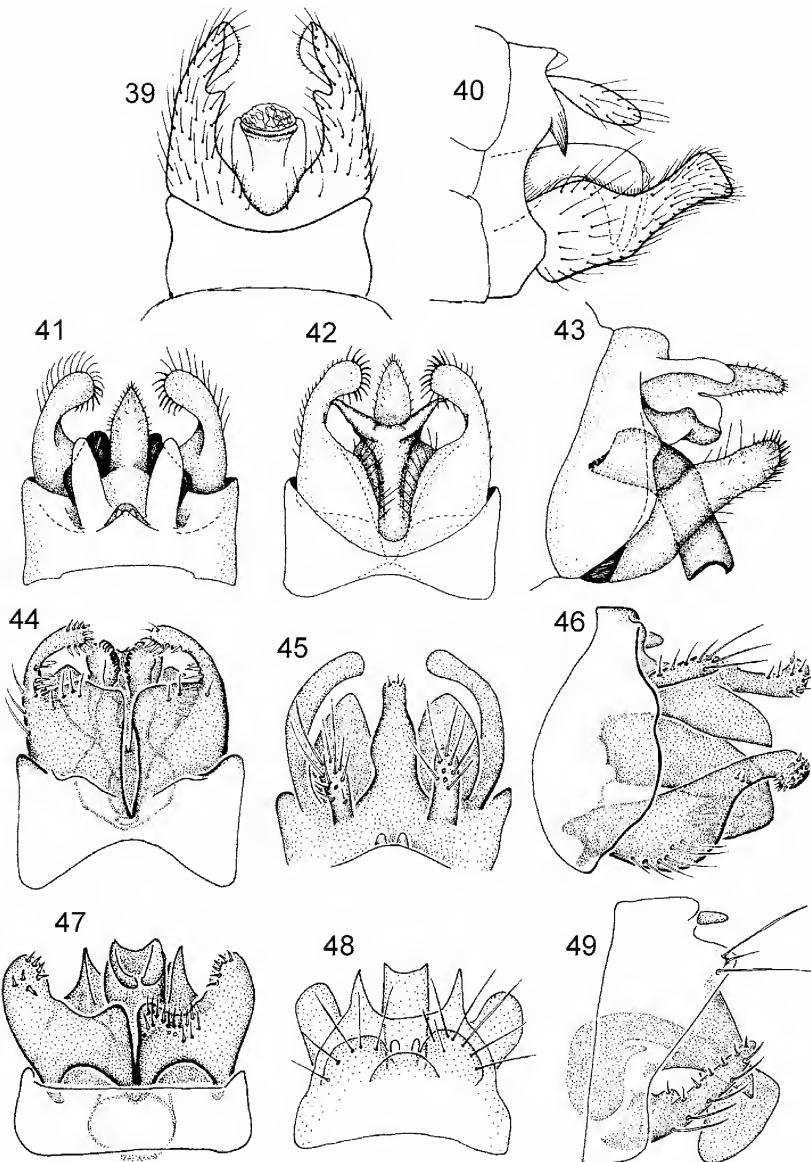
Description. Tibial spurs 0, 2, 2. Male forewing length 4.9–5.4 mm. Wings with vestiture of even length, without scales or spots, but forewing with a distinctive dark line marking the distal crossveins; forewing with footstalk on fork t1 and t2 more distal than t1 and t3. Male genitalia as in Figs 34–36. Segment IX short; preanal appendages in lateral view narrow at base and apically rounded, in ventral view stout, rounded. Inferior appendages in lateral view slightly expanded basodorsally,

slender in distal two-thirds, in ventral view closely appressed basomesially, tapered to narrow apices, curved mesially, straighter distally. Phallus strongly downturned, sharply ‘beaked’ apically.

Distribution. Kimberley region of northern WA, and northern NT (Fig. 111).

Remarks. Seen in lateral view, the male genitalia of this species resemble closely those of *O. crena* from which it is distinguished by the smoothly rounded inner margin of the inferior appendages.

Etymology. Latin, descriptive of the male inferior appendages.



Figures 39, 40, *Oecetis arcada* Mosely, male genitalia, ventral and lateral views [from Mosely and Kimmins, 1953].

Figures 41–42, *O. cymula* Neboiss, male genitalia, ventral, dorsal and lateral views [from Neboiss, 1982].

Figures 43–46, *O. paracymula*, sp. nov., male genitalia, ventral, dorsal and lateral views.

Figures 47–49, *O. spicata* sp. nov., male genitalia, ventral, dorsal and lateral views.

Oecetis parka Mosely

Figures 37, 38, 112

Oecetis parka Mosely in Mosely and Kimmins, 1953: 290, fig. 205.

Material examined. Holotype. Male, NSW, National Park [?the Royal National Park] (BMNH).

15 samples in ANIC and NMV.

Diagnosis. Wings spotted; forewing length about 4 times maximum width, footstalk present, veins of posterior anastomosis clearly stepped with t2 more distal than t1 and t3. In male genitalia (Figs 37, 38) an unusual dorsal digitiform process arises at the base of the inferior appendages, which are about 4 times as long as wide, and almost rod-shaped and straight in distal three-quarters of length.

Distribution. Eastern Vic., east-central NSW and north-eastern Qld (Fig. 112).

Remarks. The dorsal process at the base of the inferior appendages is unique among Australian *Oecetis*, but closely resembles similar structures seen in some *Setodes* species described by Schmid (1987), for example *S. apitayati* and *S. uttamavarna*. This species is never common in collections.

Oecetis arcada Mosely

Figures 39, 40, 113

Oecetis arcada Mosely, in Mosely and Kimmins, 1953: 290, fig. 204. —Neboiss, 1977: 148, figs 796–800.

Oecetis albodecorata Jaquemart, 1965 (Synonymy by Neboiss, 1977: 148)

Material examined. Holotype of *O. arcada*. Male, Cradle Mountains, Tas. (BMNH).

18 samples in NMV and ANIC.

Diagnosis. Male genitalia (Figs 39, 40), with the inferior appendages curving upwards and apically truncate; preanal appendages almost 3 times longer than wide. Forewing length less than 4 times maximum width; footstalk on fork 1 and t2 more distal than t1 and t3.

Distribution. Widespread in Tas. (Fig. 113).

Oecetis cymula Neboiss

Figures 41–43, 114

Oecetis cymula Neboiss, 1982: 323, figs 132–136.

Material examined. WA: 3 paratype males, same data as for holotype (ANIC); paratypes, females, same locality as holotype, 22 Nov 1978, A. Neboiss (ANIC); males, females, 15 miles NW of Walpole, 15 Nov 1958, E.F. Riek (ANIC); males, females, Harvey River nr Harvey Falls, 15 km E of Harvey, 33°5.5'S 116°2.0'E, 21 Nov 1978, A. Neboiss (ANIC).

Diagnosis. Forewing length almost 5 times maximum width, footstalk on fork 1 about half as long as the fork, long downy hairs along wing veins, and t2 more distal than t1 and t3. In male genitalia (Figs 41–43), ventral view, tergum X tapers to an attenuate apex; length of median process of tergum X exceeds length of preanal appendages and inferior appendages are well separated mesially, thus lacking (when viewed laterally) an expanded ventral projection near the base. Females have on each side on segment VIII an area of bristle-like setae.

Distribution. South-western WA (Fig. 114)

Remarks. *Oecetis cymula* closely resembles *O. paracymula* but has a tibial spur count of 1, 2, 2, whereas the latter has 0, 2, 2, and *O. cymula* has fine setae apically and on the mesial margin on the inferior appendages whereas *O. paracymula* has shorter, stout almost peg-like setae.

Oecetis paracymula sp. nov.

Figures 44–46, 115.

Material examined. Holotype, male, NSW, Upper Manning River, 20 km NNW Rawdon Vale, 31°34'S 151°34'E, 19 Feb 1980, A.A. Calder (NMV T-18511).

Paratypes. NSW, 2 males, data as for holotype (NMV); male, Barrington Tops, 16 Nov 1953, A. Neboiss (NMV).

Other material. 4 females, data as for holotype (NMV).

Diagnosis. Adults densely hairy; forewing shape as for *O. cymula*, footstalk on fork 1, and t2 more distal than t1 or t3. In male genitalia, in ventral view, median process of tergum X constricted close to its base, then swollen, narrowest distally; inferior appendages in ventral view loosely turned inwards in distal third and in lateral view down-turned apically.

Description. Spurs 0, 2, 2. Male forewing length 8.7 mm. Wings with long downy hair along veins; forewing narrow proximally expanded more distally, rounded apically, footstalk on fork 1 about one-fifth length of fork, discoidal and thyridial cells about equal length, anterior anastomosis stepped with t1 and t2 almost level, t3 well anterior to other 2 veins; hind wing slender, narrow. Male genitalia (Figs 44–46). Segment IX broadly convex in lateral view, preanal appendages elongate, slender, more robust in dorsal view, about two-thirds length of median process of tergum X. Tergum X with the membranous ventral plate forming a pair of widely almond-shaped lobes, median process constricted towards base, slightly swollen medially, narrower distally, in lateral view, about twice length of anal appendages. Inferior appendages slender in postero-lateral half, in lateral view form resembling *O. minasata*, down-turned apically and with short stout setae on terminal third. Phallus stout, strongly down-turned distally.

Distribution. North-eastern NSW (Fig. 115).

Etymology. Showing close resemblance to *O. cymula*.

Oecetis spicata sp. nov.

Figures 47–49, 116.

Material examined. Holotype, male, Gunshot Creek at Telegraph Crossing, 11°42.9'S 142°20.0'E, 14–15 Feb 1992, D. Cartwright and A. Wells (ANIC).

Paratypes, Qld: males, 5 females, Palmer River, 20 Jun 1971, E.F. Riek (ANIC: WTH-1390); 21 males, Laura, Cape York Peninsula, 15°33.9'S 144°27.1'E, 7 Oct 1979, M.S. and B.J. Moulds (NMV); 1 male, Qld, Seary's Creek, Rainbow Beach, 25°52'S 153°04'E, 6 Dec 1984, G. Theischinger (NMV); 1 male, Bertie Creek, 1 km SE Heathlands HS, 11°49.9'S 142°29.0'E, 5 Feb 1992, D. Cartwright and A. Wells (QM); 6 females, Tributary of Bertie Creek, 250 m SW Heathlands HS, 11°45'S 142°35'E, 11 Feb 1992, D. Cartwright and A. Wells (QM); 1 male, Cape York Peninsula, Heathlands, Bertie Creek, 11°49.9'S 142°29.0'E, 23 Mar 1993, M. Crossland (ANIC).

Other material. Qld: male, Mossman, 12 Jun 1971, E.F. Riek (ANIC); males, females, Palmer River, 20 Jun 1971, E.F. Riek (ANIC); male, Peach Creek Crossing, 25 km NNE of Coen, 4–5 Jul 1976, G.B. and S.R. Monteith (ANIC); male, Cockatoo Creek Crossing, 17 km NW Heathlands, 11°39'S 142°27'E, 25.vii–19 Aug 1992, P. Zborowski, J.C. Cardale, open forest, Malaise #5 (ANIC); male, Cape York Peninsula, Heathlands, Bertie Creek, 23 Mar 1993, M. Crossland (ANIC). NT: 1 male, South Alligator River, UDP Falls [Gunlom], 13°24.9'S 132°26.0'E, 7 Sep 1974, J. Blyth (NTM); 3 males, South Alligator River, UDP Falls [Gunlom], 13°24.9'S 132°26.0'E, 18–19 Jul 1980, M.B. Malipatil (NTM); 2 males, ARRS, South Alligator River, at Gimbat OSS Stn, 13°34.3'S 132°36.7'E, 28 Apr 1988, P. Dostine (NTM); male, ARRS, 5 km W South Alligator River OSS Stn, 19 Apr

1988, Wells and Suter, 13°33'S 132°34'E (NMV); male, Litchfield NP, Walker Creek, 18–19 Apr 1992, Wells (NTM). WA: 2 males, 2 females, Bell Gorge, Melaleuca Hole, 17°01'S 125°14'E, I. Edwards (NMV).

Diagnosis. Male genitalia, in ventral view, with inferior appendages broad-based, slightly produced apicomediately, lateral lobes almost twice basal section, and tergite X a simple, broad membranous plate with acute apicolateral angles.

Description. Spurs 1, 2, 2. Forewing length 4.5–5.1 mm. Wings of typical slender shape, neuration variable with forewing fork 1 with a short footstalk (N Qld forms) or sessile (NT form), t1 slightly more distal than t3 (N Qld) or both t1 and t3 well distal of t2; wing membrane dark along cross veins of posterior anastomosis. Male genitalia, Figs 47–49. Segment IX narrow, preanal appendages short, broad-based, rounded apically. Segment X broad at base and apex, a wide apicomosal concavity resulting in acute apicolateral processes. Inferior appendages in ventral view broad-based, extending apico-laterally as stout short lobes, in lateral view more or less straight but with a basi-ventral notch. Phallus strongly arched in lateral view.

Distribution. South-eastern and northern Qld, northern NT and northern WA (Fig. 116).

Remarks. The forewing venation of *O. spicata* varies from footstalk short on forewing fork 1 (N Qld form) to having fork 1 sessile (NT form), and crossveins of the posterior anastomosis varied, as indicated above. However, the males from NE Queensland, N Northern Territory and NW Western Australia show such close similarities in genitalic structures that, tentatively, the differing position of the fork on the forewing is considered simply to be variation within a local population.

Etymology. From Latin *spica* — point, for the apicolateral processes on segment X.

Oecetis crena sp. nov.

Figures 50–52, 117

Material examined. Holotype, male, Vic., Gibbo River at Exhibition Creek junction, 20 km N Benambra, 16 Jan 1982, A. Wells (NMV T-18512).

Paratypes, Vic.: 1 male, 5 females, Mitta Mitta river, 8 km NE of Benambra, 5 Feb 1974, A. Neboiss (NMV); 1 male, Wellington River, 23 km NNE of Licola on Tamboritha Road, 21 Feb 1978, NMV Survey Department (NMV); 1 male, Yarra River, East Warburton, ii.1980, I Campbell (NMV); 1 male, 2 females, Nongungarra and Crooked River junction, 4 Feb 1981, J. Blyth (NMV); male, Cobungra River, at Anglers Rest, 15 January 1982, A. Wells (NMV).

Other material. Vic.: male, 4 females, Porepunkah River, 26 Jan 1960, A. Neboiss (NMV).

Diagnosis. Male genitalia inferior appendages clasper-shaped, with a median expansion on the inner margin and fringes of short setae dorso-basally; in the forewing a footstalk on fork 1, and t2 more distal than t1 and t3.

Description. Spurs 1, 2, 2. Forewing length 7.1–8.1 mm. Wings with long downy setae along veins; forewing fork 1 about twice length of footstalk, anterior anastomosis with t1 and t2 almost level, more distal than t3. Male genitalia, Figs 50–52. Segment

IX short, a triangular projection midlaterally on apical margin, preanal appendages small, ovoid, separated. Segment X simple, membranous. Inferior appendages elongate, slender, in ventral view with a medial notch on inner margin; in lateral view a knob dorsally at base, slender and tapered distally. Phallus short, down-turned medially.

Distribution. Eastern Vic. (Fig. 118).

Etymology. Latin, *crena* — notch or rounded projection.

Oecetis quadrata sp. nov.

Figures 53–56, 118

Material examined. Holotype, male, North Qld, Zarda Creek nr Mt Misery, W of Mossman, 1200 m, 23 Nov 1974, M.S. Moulds (NMV T-18513).

Other material. Qld: male, Birthday Creek, 6 km NWW Paluma, 18°59'S 146°10'E, 25 Sep 1980, J.C. Cardale (ANIC).

Diagnosis. Cu1 and Cu2 in the hind wing arising at crossvein m-cu, and preanal appendages exceedingly large, rectangular, free.

Description. Tibial spurs 1, 2, 2. Male forewing length 7.6 mm. Wings (Fig. 53) slender, forewing length about 4 times maximum width, footstalk on fork 1 about as long as fork, posterior anastomosis stepped with t2 more distal than t1, t3 distal of t1 and t2; in hind wing Cu1 and Cu2 arise at crossvein m-cu. Male genitalia, Figs 54–56. Segment IX broad ventrally and laterally, narrow middorsally, preanal appendages large, subquadrate. Segment X membranous, bifid. Inferior appendages broad in basal half, strongly constricted medially, narrow distally. Phallus short, apex strongly down-turned.

Distribution. North-eastern Qld (Fig. 118).

Remarks. When viewed laterally, the genital features of *O. quadrata* males generally resemble those of *O. inscripta*. The species has been collected from two disjunct localities only.

Etymology. Latin, *quadrata* — four-cornered, for the unusual shape of the preanal appendages.

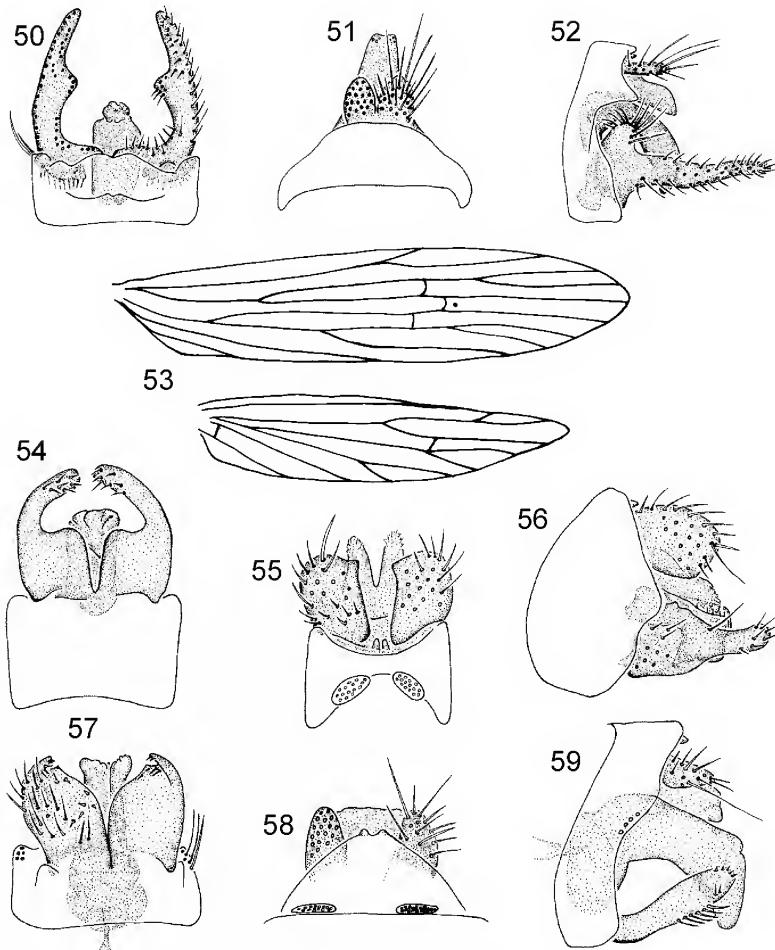
Oecetis dilata sp. nov.

Figures 57–59, 119

Material examined. Holotype, male, WA, 9 km N of Kununurra, 19 Sep 1979, J. Blyth (NMV T-18514).

Paratypes, WA: 3 males, 2 female, same data as for holotype (NMV); 2 males, Geikie Gorge, 18°06'S 125°42'E, 5 Oct 1996, I. Edwards (NMV). Qld: 2 males, female, McLeod River, 15 km W of Mt Carbine, 22–23 Jun 1975, S.R. Monteith (ANIC); 2 males, Cape York Peninsula, Laura, 15°33.9'S 144°27.1'E, 7 Oct 1979, M.S. and B.J. Moulds (NMV); 2 males, 2 females, 11°08'S 142°21'E, Jardine River, 19 Oct 1992, P. Zborowski and T. Weir (ANIC). NT: 2 males, Daly River, 13°45'S 132°42'E, 9–10 Aug 1980, M.B. Malipatil (NMV).

Diagnosis. Forewing length about 4 times maximum width, footstalk present on fork 1, t1 more distal than t2 or t3. Males genitalic features, inferior appendages, in ventral view have width about 0.75 times length, and are rounded towards the



Figures 50–52, *Oecetis crena* sp. nov., male genitalia, ventral, dorsal and lateral views.

Figures 53–56, *O. quadrata* sp. nov.: 53, fore- and hind wings; 54–56, male genitalia, ventral, dorsal and lateral views.

Figures 57–59, *O. dilata* sp. nov., male genitalia, ventral, dorsal and lateral views.

apex, with a small apicolateral lobe, and in lateral view, have length about 4 times width.

Description. Spurs 1, 2, 2. Male forewing length 4.8–5.4 mm. Forewing with footstalk on fork 1 slightly shorter than fork; posterior anastomosis stepped with t1 more distal than t2, t3 oblique, slightly distad of t2. Male genitalia, Figs 57–59. Segment IX uniformly narrow, preanal appendages ovoid, widely separated. Segment X simple broad, apically truncate. Inferior appendages stout, apically rounded with short, thin lobe laterally; narrow and straight in lateral view, rounded apically. Phallus stout, rounded, strongly curved downwards.

Distribution. Far northern Qld, NT and WA (Fig. 119).

Etymology. Latin, *dilata* — enlarge, for the unusually broad inferior appendages.

Oecetis koobarra sp. nov.

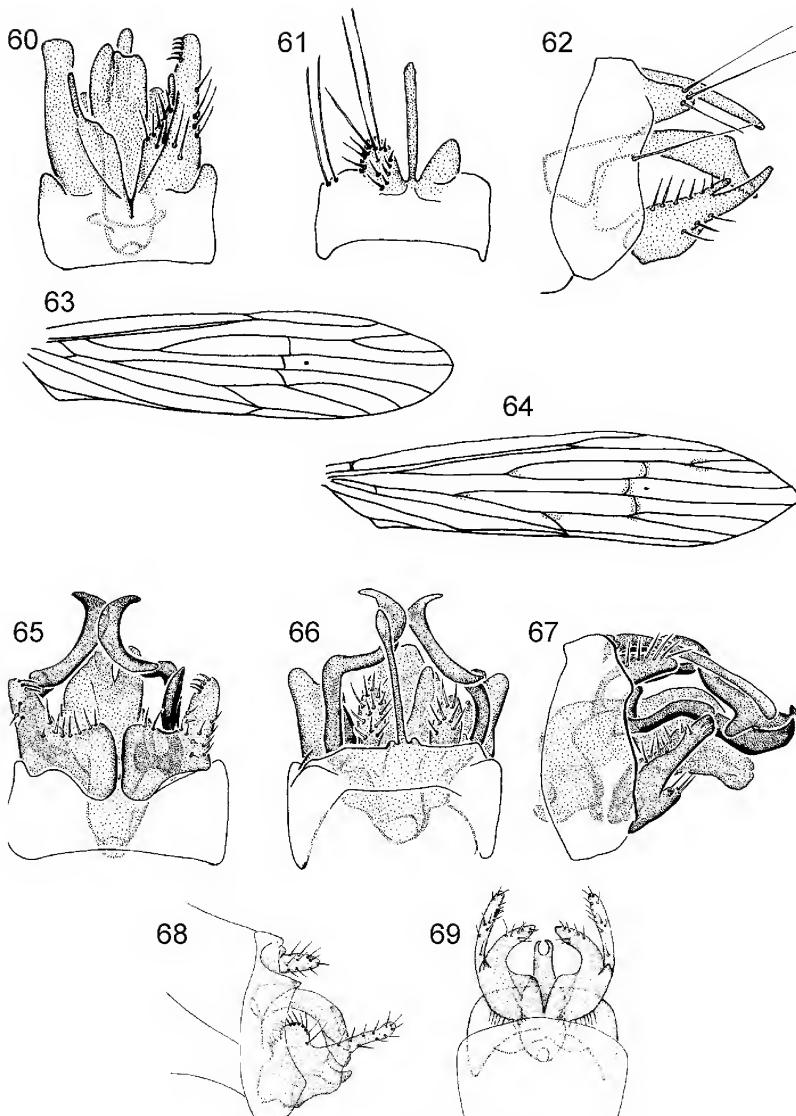
Figures 60–63, 120

Oecetis sp. 'H' —Wells 1991: fig. 139.

Material examined. Holotype, male, NT, Kakadu National Park, Radon Creek, 3 Sep 1979, J. Blyth (NTM).

Paratypes. NT: 15 males, ARRS, Radon Springs, 13/14 Apr 1988, Suter and Wells (NTM and NMV); male, Magela Creek, 7 Apr 1993, P. Dostine (NTM).

Other material. NT: male, 3 females, 12°50'S 132°51'E, 16 km EbyN of Mt Cahill, 13 Jun 1973, J.C. Cardale (ANIC); male, 12°48'S 132°49'E, Kakadu National Park, Baroalba Springs, 16 Jan 1992, Wells and Webber (NTM); pupa, Litchfield National Park, Walker Creek, 18 Apr 1992, A. Wells (NMV); 2 males, Litchfield National Park, Walker Creek, 18/19 Apr 1992, A. Wells (NMV); 4 males, 12°48'S 132°49'E, Kakadu National Park,



Figures 60–63, *Oecetis koobarra* sp. nov.: 60–62, male genitalia, ventral, dorsal and lateral views; 63, forewing.

Figures 64–67, *O. falcata* sp. nov.; 64, forewing; 65–67, male genitalia in ventral, dorsal and lateral views.

Figures 68, 69, *O. terania* sp. nov., male genitalia in lateral and ventral views.

Baroalba Springs, 25 Apr 1991, Wells and Webber (NTM); 3 males, 1 female, 12°48'S 132°49'E, Kakadu National Park, Baroalba Springs, 29 May 1991, Wells and Webber (NTM); male, Melville Island, 11°36'S 130°43'E, 4 Oct 1996, G.R. Brown (NTM); male, Melville Island, nr Pickertaramoor, 11°46'S 130°53'E, 10 Oct 1996, G.R. Brown (NTM).

Diagnosis. Dark zig-zag mark on forewing (Fig. 63) formed by pattern on wing membrane around the stepped posterior anastomosis; overall straight-sided male genitalia, phallus narrow mesially, with apex obliquely truncate.

Description. Tibial spurs 1, 2, 2. Male forewing length 4.6–5.6 mm. Wing laminae with vestiture of equal length; forewing (Fig. 63) with a zig-zag pattern marking posterior anastomosis, a footstalk on fork 1, t1 more distal than t2, t2 and t3 contiguous. Male genitalia, Figs 60–62. Segment IX almost uniform in length all round, preanal appendages well separated, ovoid. Segment X with long, slender dorsal process. Inferior appendages straight-sided, stepped in midlength on inner margin, and with a slender dorsal lobe at midlength. Phallus in lateral view slender medially, obliquely angled towards apex.

Distribution. Northern NT (the 'Top End'), and offshore Melville Island in the Tiwi Islands Group (Fig. 120).

Remarks. *Oecetis koobarra* is distinctive for both its wing markings and its very angular male genitalia. It is probably most closely allied to *O. parka*. An associated pupa is from a cornucopia-shaped sand case.

Etymology. Koobarra, now the official name for Baroalba Springs, one of the collecting localities.

***Oecetis falcata* sp. nov.**

Figures 64–67, 121

Material examined. Holotype, male, Upper Jardine River, Cape York, Qld, 11°14'S 142°36'E, 26 Oct 1979, M.S. and B.J. Moulds (NMV T-18515).

Paratypes. Qld: 72 males, females, same data as for holotype (NMV, ANIC).

Other material. Qld: male, female, Iron Range, Cape York Pen., 2–Jun 1971, E.F. Riek (ANIC); male, female, Mt Molloy, 13 Jun 1971, E.F. Riek (ANIC); male, 2 females, Iron Range, West Claudio River, 17 Sep 1974, Moulds (NMV); male, Iron Range, Middle Claudio River, 2–9 Oct 1974, Moulds (NMV); male, Jardine River, Cape York, 11°09'S 142°27'E, 11 Oct 1979, M.S. and B.J. Moulds (NMV); 7 males, 4 females, Jardine River, Cape York, 11°08'S 142°35'E, 14 Oct 1979, M.S. and B.J. Moulds (NMV); 3 males, Jardine River, Cape York, 11°17'S 142°35'E, 17 Oct 1979, M.S. and B.J. Moulds (NMV); 8 males, 2 females, Jardine River, Cape York, 11°19'S 142°37'E, 22 Oct 1979, M.S. and B.J. Moulds (NMV); 2 males, Jardine River, Cape York, 11°14'S 142°36'E, 24 Oct 1979, M.S. and B.J. Moulds (NMV); male, Qld, Tributary of Bertie Creek, 250 m SW of Heathlands HS, 11°45'S 142°35'E, 11 Feb 1992, Cartwright and Wells, 11°45'S 142°35'E (QM) (slide); 3 males, 1 female, Cape York Peninsula, Pascoe River crossing (to Iron Range), 4.10.2002, G. Theischinger (ANIC); 6 males, 7 females, Cape York Peninsula, Dul-hunty River crossing at Telegraph rd, 7.10.2002, G. Theischinger (ANIC).

Diagnosis. Forewing length about 4 times maximum width, footstalk on fork 1 almost equal in length to the fork. In the male genitalia, a pair of asymmetrical, scythe-like, sclerotised processes dorsally, one at each side of the phallus

Description. Spurs 1, 2, 2. Male forewing length 4.1–5.2 mm. Wings (Fig. 64): forewing with patches of dark membrane at crossveins of posterior anastomosis and, more proximally, triangles of dark membrane at several forks; narrow, tapered distally; footstalk on fork 1 equal in length to fork; t1 and t3 at about same level in wing, t2 more proximal. Male genitalia, Figs 65–67. Abdominal segment IX narrow, but broader than in *O. ancala*. Preanal appendages about twice as long as wide. Tergite X very slender, reaching almost to length of other genitalic parts. Inferior appendages in ventral view broad-based, laterally produced to about twice length of basal section, in lateral view more slender. Phallus broad. Dorsolateral processes unequal, the left one twisted in basal half, curved outwards in distal half, right one more or less that same shape, but less twisted.

Distribution. Far northern Qld (Fig. 121).

Remarks. As with *O. ancala*, grouping of this species is equivocal, as the homologies of the processes are uncertain.

Etymology. Latin, *falcata* — sickle-shaped, for the shape of the lateral processes.

***Oecetis terania* sp. nov.**

Figures 68, 69, 122

Material examined. Holotype, male, NSW, Terania Creek, N of Lismore, 28°25'S 153°18'E, 21 Jan 1986, G. Theischinger (NMV T-18516) (slide).

Paratypes. 2 males, 1 female, same data as holotype (NMV) (one male on slide).

Diagnosis. Wings with dense vestiture of downy hair and male genitalia with inferior appendages bifurcate in lateral half, the ventral lobes curving and clasper-like, the dorsal lobes more slender and straight.

Description. Spurs 1, 2, 2. Male forewing length 6.0–6.1 mm. Wings typical form, tapered distally; footstalk on fork 1 about half length of fork; t2 more distal than t1 or t3. Genitalia, Figs 68, 69. Abdominal segment IX narrow. Preanal appendages discrete, about twice as long as wide in lateral view, more or less conical in dorsal view. Tergite X a short, narrow membrane, about length of preanal appendages. Inferior appendages in ventral view broad-based, bilobed in distal half, with the ventral lobes almost meeting mesially, dorsal arms slender and straight; in lateral view stout and irregular in shape basally, the dorsal arm almost straight, extending well beyond the ventral arm. Phallus curved ventrally.

Distribution. North-eastern NSW (Fig. 122).

Remarks. In shape the male inferior appendages of this species more closely resembles those of some *complexa*-group species, but the phallus lacks spines or parameres of the kind seen in that group. The species is known only from the type locality.

Etymology. For the creek at the collecting site.

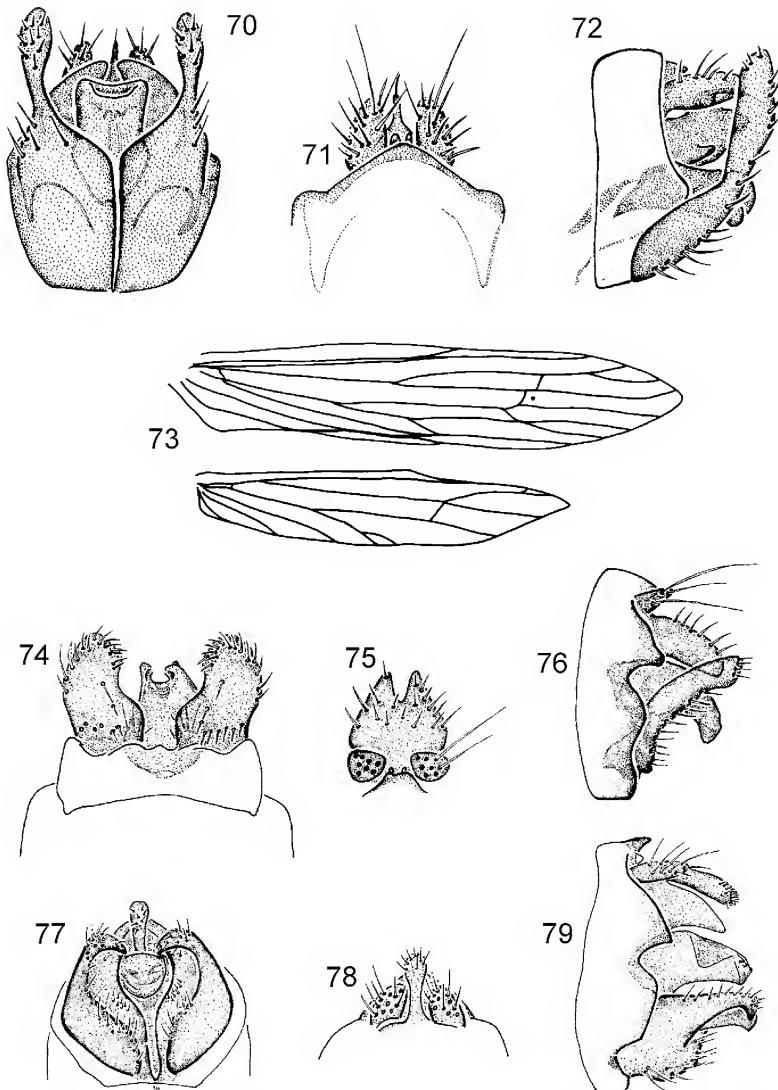
***Oecetis papposa* sp. nov.**

Figures 70–73, 123

Material examined. Holotype, male, NT, South Alligator River, UDP Falls [Gunlom], 13°24.9'S 132°26.0'E, J. Blyth (NMV T-18517).

Paratypes. NT: male, Jim Jim Creek, 3 km below falls, Kakadu National Park, 1 Sep 1979, J. Blyth (NMV); male, Katherine River Gorge National Park, 13 Aug 1979, J. Blyth (NMV); male, ARRS Creek 5 km W of OSS South Alligator field station, 19 Apr 1989, Wells and Suter (NMV); 6 males, ARRS, Radon Springs, 13–14 Apr 1989, Suter and Wells (NTM); 1 male, 12°42'S 132°57'E, Kakadu National Park, Magela Creek, OSS Site 009, 15 Mar 1991, Wells and Webber (NTM); male, 12°48'S 132°49'E, Baroalba Springs, 4 Apr 1991, Wells and Webber (NTM); male, 12°48'S 132°49'E, Baroalba Springs, 16 Aug 1991, Wells and Webber (NTM); 4 males, 2 females, 12°48'S 132°49'E, Baroalba Springs, 25 Apr 1991, Wells and Webber (NTM); 2 males, female, 12°48'S 132°49'E, Baroalba Springs, 4 Oct 1991, Wells and Webber (NTM).

Other material. NT: male, Litchfield National Park, Florence Falls, 13°03'S 130°47'E, 9 Apr 1991, Wells and Horak (NMV); 4 males, 12°48'S 132°49'E, Baroalba Springs, 16 Jan 1992, Wells, Webber and Bickel (NTM); male, Litchfield National Park, Walker Creek, 18–19 Apr 1992, A. Wells (NTM). WA: 4 males, Drysdale River headwaters, 30 km NW Mt Elizabeth H.S., 30 Sep 1979, J. Blyth (NMV); 9 males,



Figures 70–73, *Oecetis papposa* sp. nov.: 70–72, male genitalia in ventral, dorsal and lateral views; 73, fore- and hind wings.

Figures 74–76, *O. curta* sp. nov., male genitalia, ventral, dorsal and lateral views.

Figures 77–79, *O. aduncata* sp. nov.: male genitalia, ventral, dorsal and lateral views.

King Edward River, 14°54'S 126°12'E, 3 Sep 1996, I. Edwards (NMV); 6 males, Pearson's Creek S edge of Prince Regent Res., 16°01'S 125°35'E, 5 Sep 1996, I. Edwards (NMV); males, females, Drysdale River upper reaches, 16°09'S 125°58'E, 7 Sep 1996, I. Edwards (NMV); males, females, Manning River nr Mt Barnett, 16°40'S 125°56'E, 8 Sep 1996, I. Edwards (NMV).

Diagnosis. Hindwing vein M unbranched; in male genitalia, short, straight phallus and elongate inferior appendages with a strong medial constriction.

Description. Spurs 0, 2, 2. Wings (Fig. 73) narrow, length over 4 times maximum width, with downy hair (readily lost in preserved specimens). Male forewing length 4.2–5.4 mm. Forewing with footstalk on fork 1 of variable length, less than or equal to length of fork; posterior anastomosis in part obliquely linear, t3 more proximal than t1 and t2. Hind wing with venation strongly reduced, M unbranched. Maxillary palps very long, all segments of equal length. Male genitalia, Figs 70–72. Segment IX excavated midventrally, preanal

appendages elongate-ovate, separated. Segment X in form of a pair of stout, membranous lobes, with setate, digitiform mesal process. Inferior appendages in ventral view broad-based, slender distally, slightly dilated towards apices, in lateral view, slender but constricted medially. Phallus short, straight, with only a slight apicoventral lip.

Distribution. Northern NT and northern WA (Fig. 123).

Etymology. From Latin, *pappus* — hair, for the hairy wings.

***Oecetis curta* sp. nov.**

Figures 74–76, 124

Material examined. Holotype. Male, Qld, Girraween National Park, nr Wyberba, 10 Oct 1973, A. Neboiss (NMV T-18518).

Paratypes. Qld: male, same data as for holotype; 1 male, Mothar Mtn, 32 km SE of Gympie, 29 Oct 1980, A. Neboiss (NMV); male, Cape York Pen, Laura, 15°33.9'S 144°27.1'E, 7 Oct 1979, M.S. and B.J. Moulds (NMV). NSW: 3 males, female, 48 km N of Singleton, 'Tuglo' alt. 760 m, 5 Oct 1975, M.S. Moulds; (NMV); 16 males, 4 females, Terania Creek, N of Lismore, 28°25'S 153°18'E, 21 Jan 1986, G. Theischinger (NMV); 6 males, female, Wilson River, NW of Wauchope, 31°14'S 152°34'E, 30 Oct 1981, Wells and Carter (NMV).

Diagnosis. Wings uniformly fuscous to mottled; forewing without footstalk on fork 1. In male genitalia, tergite X covered with short setae and shallowly cleft apically; inferior appendages elongate and straight to slightly curved in lateral view.

Description. Spurs 1, 2, 2. Male forewing length 6.6–8.6 mm. Wings rounded apically, hair along veins long, downy in appearance, forewing fork 1 sessile or with a very short footstalk; t1 more distal than t2 and t3 which are almost contiguous, all three crossveins marked by darkened membrane. Male genitalia, Figs 74–76. Segment IX with lateral cleft, preanal appendages small, rounded, widely separated. Segment X robust and setate, cordate but with apex cleft. Inferior appendages stout, in ventral view separated basally, rounded apically, uniformly stout along length; in lateral view slender, apically obliquely truncate. Phallus short, rounded in ventral view, in lateral view down-turned distally.

Distribution. Eastern NSW, and south-eastern and far northern Qld (Fig. 124).

Remarks. The unusual, hairy segment X may represent the medial process of segment X such as is seen in *O. aduncata* or *O. minasata*, but expanded. A similar plate is seen in *O. cepaforma*, but that species has setae only distally, and is not cleft apically.

Etymology. Latin, *curta* — short, for the phallus.

***Oecetis aduncata* sp. nov.**

Figures 77–79, 125

Material examined. Holotype, male, NSW, Boonoo Boonoo River, 10 km upstream of falls, 28°37.9'S 152°15.1'E, 31 Oct 1975, A. Neboiss (NMV T-18519) (slide).

Paratypes. NSW: 1 male, Bargo River, 10 km SW of Picton, 34°14.9'S 150°34.0'E, 30 Dec 1977, A. Neboiss (NMV). Vic: 1 male, Watson's Creek, 37°42'S 145°16'E, 16 Dec 1951, A. Neboiss (NMV);

1 male, Yae River, 7 km S of Glenburn, 37°25.4'S 145°25.3'E, 1 Dec 1972, A. Neboiss (NMV); 1 male, Belles Clearing, 6 km S of Aberfeldy, 37°39.7'S 146°26.4'E, 8 Feb 1977, T131, A.A. Calder (NMV) (slide); 1 male, Gibbo River, Exhibition Creek, 20 km N of Benambra, 36°44.6'S 147°44.4'E, 16 Jan 1982, A. Wells (NMV) (slide).

Other material. Qld: 1 male, Tewah Creek, Tin Can Bay, 25°48.9'S 153°1.0'E, 17–18 Oct 1971, S.R. Monteith (ANIC); 2 males, The Crater, nr Herberton, 25°2.9'S 148°24.1'E, 18 Dec 1974, M. Moulds (slides) (NMV); 3 males, 15°17'S 145°10'E, 5 km WbyN Rounded Hill nr Hope Vale Mission, 7 Oct 1980, J.C. Cardale (ANIC); 2 males, 15°47'S 145°17'E, Moses Creek, Finnigan, 14 Oct 1980, J.C. Cardale (ANIC).

Diagnosis. Fork 1 in forewing sessile and wings mottled. In forewing, t1 more distal than t2 or t3; in male genitalia, inferior appendages broad and strongly ridged along their length, in lateral view with tips sharply down-turned and phallus in lateral view appearing as if it has a triangular fold subapically.

Description. Spurs 1, 2, 2. Male forewing length 6.1–7.1 mm. Wings tapered apically; forewing fork 1 sessile, posterior anastomosis obliquely stepped, t1 more distal than other two crossveins. Male genitalia, Figs 77–79. Segment IX with apical margin excavated midventrally and midlaterally, preanal appendages, small, well separated, ovate. Segment X broad, membranous, in lateral view broad and down-curved, medial process club-shaped. Inferior appendages appear to be slender and strongly in-turned apically, but are actually broad and deeply ridge, in lateral view broad-based, tapered distally and down-turned apically. Phallus short, simple, down-turned, in lateral view always with a more or less triangular area dorsolaterally before apex.

Distribution. Eastern Australia, from eastern Vic. to south-eastern Qld (Fig. 125).

Etymology. Latin, *aduncata* — bent inwards, for the shape of the inferior appendages.

***Oecetis ornata* Kimmins, 1962**

Figures 80–83, 126

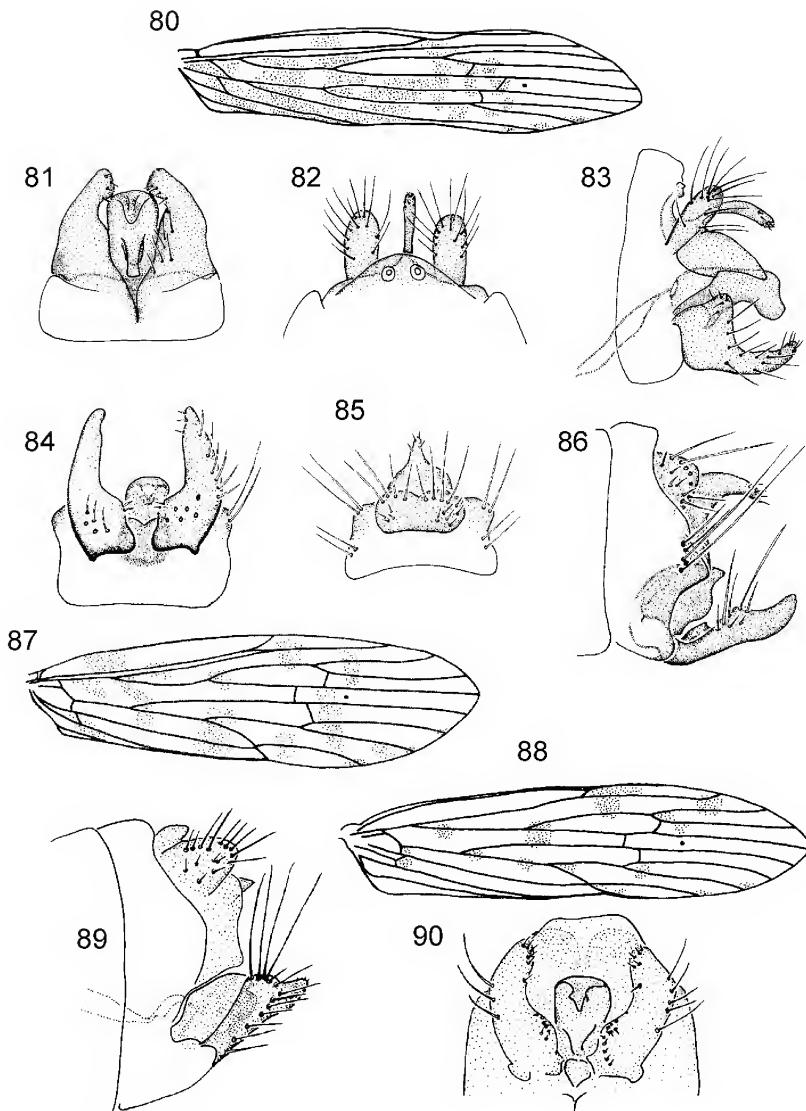
Oecetis ornata Kimmins, 1962: 157–158.

Material examined. Holotype. Male, Humbolt Bay, Dutch New Guinea [Irian Jaya] (BMNH).

Male, Qld, 3 km ENE Mt Tozer, 12°44'S 143°14'E, 2 Jul 1986, J.C. Cardale (ANIC).

Diagnosis. Forewing (Fig. 80) strongly and coarsely patterned, with dark brown markings on the proximal two-thirds. In forewing fork 2 sessile; in male genitalia, phallus with a sclerotised digitate process subapically on ventral side.

Remarks. The single male specimen available for study varies slightly from the type as illustrated by Kimmins (1962). However, given the proximity to New Guinea of the collecting locality in far northern Qld and that the species was described from a single male, the specimen is referred to *O. ornata* for the present. Differences are mainly genitalic — shape of the pre-anal lobes and of the inferior appendages in lateral view. Figures drawn from the Australian specimen are provided for comparisons (Figs 81–83).



Figures 80, *O. ornata* Kimmins, forewing (drawn from Australian specimen).

Figures 81–83, *Oecetis ornata* Kimmins: 79–81, male genitalia, ventral, dorsal and lateral views (drawn from Australian specimen).

Figures 84–87, *O. cepaforma* sp. nov.: 84–86, male genitalia, ventral, dorsal and lateral views; 87, forewing.

Figures 88–90, *O. dostinei* sp. nov.: 88, forewing; 89, 90, male genitalia, ventral, dorsal and lateral views.

Distribution. New Guinea and far northern Qld (Fig. 126).

Oecetis cepaforma sp. nov.

Figures 84–87, 127

Oecetis sp. D.—Wells, 1991: 61 (in key).

Material examined. Holotype. Male, Qld, Erwin Falls on Eliot Creek, 100 km S of Bamaga, 7 Nov 1988, K. Walker (NMV T-18520) (slide).

Paratypes. NT: male, Radon Springs, 13–14 Apr 1989, Suter and Wells (NTM); 2 males, female, same locality and collectors, 18–19

May 1988 (NTM); 2 males, 1 female, same locality and collectors, 14 Apr 1989 (NTM); 1 male, 12°31'S 132°54'E, 9 km N by E of Mudginberri HS, 10–11 Jun 1973, J.C. Cardale (ANIC); Other material. 35 samples in ANIC, NMV, NTM and QM.

Diagnosis. Forewing broad, length scarcely 3 times maximum width, spotted and moth-like, footstalk on fork 1 sessile. In male genitalia inferior appendages with length about 4 times width, a small spur on the baso-mesial angle; tergite X extended to an elongate-triangular apex, tipped with several short setae.

Description. Spurs 1, 2, 2. Male forewing length 5.5–5.7 mm. Wings, broad, forewing (Fig. 87) with fork 1 sessile and with large dark spots extending across membrane away from veins; posterior anastomosis stepped, t1 more distal than t3 which is more distal than t2. Male genitalia, Figs 84–86. Segment IX widest midlaterally, preanal appendages large, broadly rounded laterally, fused medially. Segment X onion-shaped in outline in dorsal view, without medial process. Inferior appendages clasper-shaped, widely separated at bases, narrower distally beyond a mesial angle bearing a spur and a cluster of short setae; in lateral view with a medial notch dorsally. Phallus very short.

Distribution. Qld, NT and WA (Fig. 127).

Remarks. The soft, broad, spotted wings give this species a truly moth-like appearance. The male genitalia vary as follows: specimens from northern Qld have the inferior appendages more slender than those from NT, with the several setae at the meso-basal angle shorter and stouter. Larvae build cornucopia-shaped sand grain cases.

Etymology. Latin for onion- or minaret-shaped — *cepaforma*, being descriptive of the shape of segment X,

Oecetis dostinei sp. nov.

Figures 88–90, 128

Oecetis sp. G.—Wells, 1991: fig. 144.

Material examined. Holotype male, Qld, Mulgrave River W of Gordonvale, 17°13.9'S 145°57.1'E, 29 Apr 1979, A. Wells (NMV T-18521, slide).

Paratypes. Qld: male, data as for holotype (NMV) (slide); male, Hann River, 73 km NW by W Laura, 15°12'S 143°52'E, 27 Jun 1986, JC Cardale (ANIC). NT: male, female, UDP Falls [Gunlom], 13°24.9'S 132°26.0'E, 18–19 Jul 1980, MB Malipatil (NTM); male, ARRS South Alligator River at Gimbat OSS Stn, 13°34.3'S 132°36.7'E, 24 Mar 1988, Wells and Suter (NMV); 2 males, same loc., 28 Apr 1988, P. Dostine (NTM); male, Litchfield National Park, 13°03'S 130°47'E, 6 Jun 1991, Wells and Webber (NTM); male, Butterfly Gorge, Katherine River Gorge National Park, 27 Jan 1977. M.S. and B.J. Moulds (NMV).

Diagnosis. Forewing length scarcely 4 times maximum width, spotted and moth-like, but with wing markings on the forewing smaller than in *O. cepaforma*, fork 1 on forewing sessile. In male genitalia inferior appendages with length about equal to 3 times width, without a small spur on the basomesial angle; tergite X truncate apically.

Description. Spurs 1, 2, 2. Male forewing length 6.1–6.4 mm. Wings, broad and spotted, forewing (Fig. 88) with fork 1 sessile and posterior anastomosis stepped, with t1 more distal than t3 which is more distal than t2. Genitalia, Figs 89, 90. Segment IX widest midlaterally, preanal appendages large, rounded to broadly conical in dorsal view, in contact in midline, but not fused. Segment X broad, apically truncate, without medial process. Inferior appendages clasper-shaped, widely separated at bases, curving outwards beyond a mesial angle bearing a cluster of short stout setae. Phallus very short.

Distribution. Northern NT and northern Qld (Fig. 128).

Species of the *longiterga*-group

Oecetis digitata sp. nov.

Figures 91–93, 129

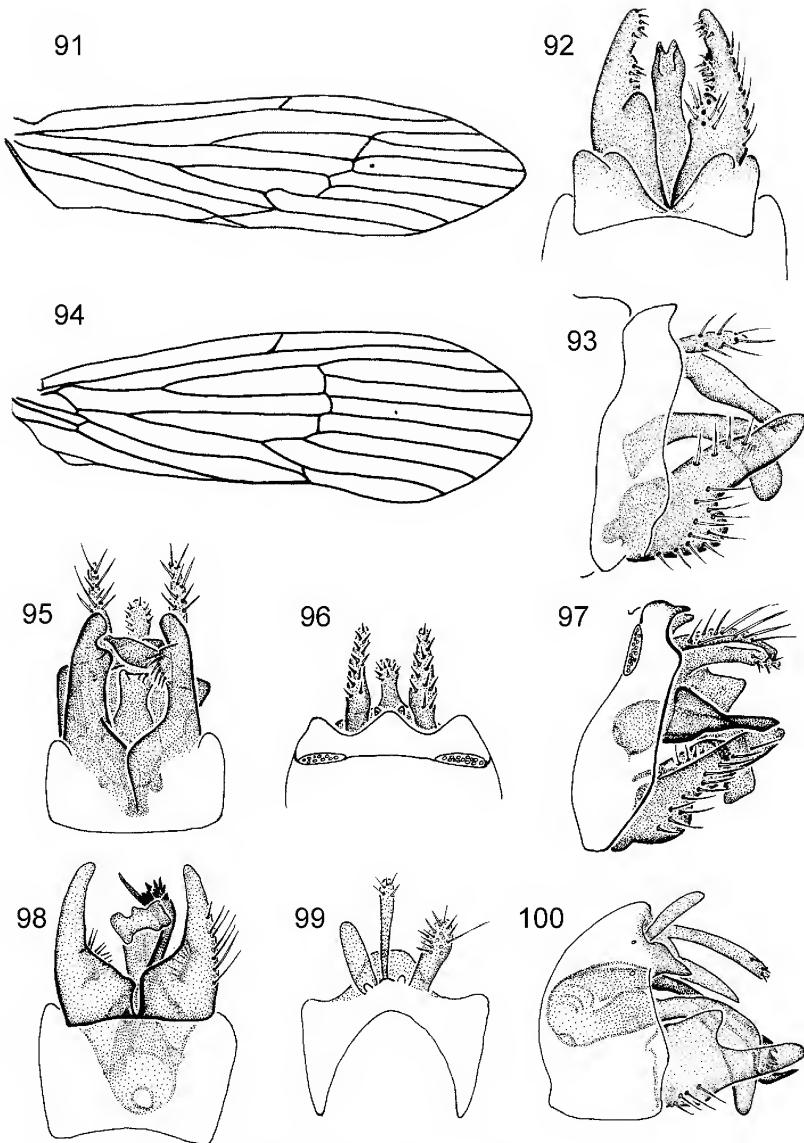
Material examined. Holotype, male, NT, Jim Jim Waterhole, Kakadu National Park, 5 September 1979, J. Blyth (NMV T-18522).

Paratypes. NT: 7 males, 3 females, Muirella Park, 12 Oct 1972, E.F. Riek (ANIC); male, 12°06'S 133°04'E, 19 km E by S of Mt Borrodaile, 5–6 Jun 1973, J.C. Cardale (ANIC); male, Jim Jim Creek, 19 km WSW of Mt Cahill, 12°5'S 132°33'E, 17 Jun 1973, J. Cardale (ANIC); 1 male, 1 female, Gulungul Billabong, East Jabiru, 23 Feb 1988, P. Dostine (NTM); 1 male, 12°38'S 132°53'E, Gulungul Billabong, East Jabiru, 20 May 1989, A. Wells and P. Suter (NTM); 1 male, ARRS, South Alligator River at Gimbat OSS Station, 13°34.3'S 132°36.7'E, 24 May 1988, A. Wells and P. Suter (NTM); 3 males, ARRS, Kambolgie Creek, 13°28.9'S 132°22.0'E, 25 May 1988, A. Wells and P. Suter (ANIC); 1 male, ARRS, East Alligator River at Cahills Crossing, 27 May 1988, A. Wells and P. Suter (NTM); 2 males, SAR site 1, 30 Sep 1988, P. Dostine (NTM); 5 males, 12°48'S 132°49'E, Baroalba Springs, 25 Apr 1991, Wells and Webber (NMV); 1 male, 12°42'S 132°57'E, Kakadu National Park, Magela Creek, OSS Site 009, 8 Jun 1991, Wells and Webber (NTM); 1 male, 12°48'S 132°49'E, Little Baroalba Creek, 10 Jul 1991, Wells and Webber (NTM); 5 males, female, Alligator River, Two Mile Hole, 12°42'S 132°09'E, 5 Aug 1996, I. Edwards (NMV).

Other material. WA: Kimberley, Four Mile Creek, 2 Feb 1979, J.E. Bishop (ANIC) (slide); male, female, 14°25'S 126°38'E, CALM site 13/H 12 km S of Kalumburu Mission, 7–11 Jun 1988, T.A. Weir (ANIC); 5 males, female, NT, Alligator River Two Mile Hole, 12°42'S 132°09'E, 5 Aug 1996, I. Edwards, NMV. Qld: female, Palmer River, 20 Jun 1971, E.F. Riek (ANIC); male, 15°41'S 145°12'E, Annan River, 3 km W by S Black Mountain, 17 Sep 1980, J.C. Cardale (ANIC); male, 4 females, 15°25'S 141°53'E, Hann River, 7 km NW by W Laura, 27 Jun 1986, J.C. Cardale (ANIC). NT: male, 12°57'S 132°33'E, Jim Jim Creek, 19 km WSW of Mt Cahill, 17 Jun 1973, J.C. Cardale, ANIC; female, Howard Creek, 3 km E of Howard Springs, 12°27.5'S 131°3.1'E, 17 Aug 1979, J. Blyth (NMV); 1 female, Magela Creek at Ranger pipe outlet, 20 May 1988, P. Suter and A. Wells (NTM); female, Magela Creek at Ranger Pipe Outlet, Suter and Wells, 23 May 1988 (NMV).

Diagnosis. Forewing length less than 4 times width, veins sclerotised, appear very prominent, footstalk absent on fork 1; an unusual forward bulge present at base of vein Cu1a. In male genitalia, inferior appendages with mesial margin irregular, not smoothly curved; phallus smoothly arched, length about 4 times width.

Description. Spurs 1, 2, 2. Male forewing length 6.6–8.1 mm. Wings strongly sclerotised with veins dark, hair short; in forewing (Fig. 91) fork 1 sessile, anterior anastomosis with t1 and t2 almost linear, and well distad of t3, a forwardly directed bulge on Cu1a. Male genitalia, Figs 92, 93. Segment IX almost of uniform length on all sides, but excavated deeply midventrally; preanal appendages slender, elongate. Segment X elongate in lateral view, slightly swollen towards base. Inferior appendages in ventral view with small inner lobe at about half length. Phallus curved, slender with length about 4 times width.



Figures 91–93, *Oecetis digitata* sp. nov.: 91, forewing; 92, 93, male genitalia, ventral and lateral views.
Figure 94, *O. crosslandi* sp. nov., forewing.

Figures 95–97, *O. ancala* sp. nov., male genitalia, ventral, dorsal and lateral views.

Figures 98–100, *O. crosslandi* sp. nov., male genitalia, ventral, dorsal and lateral views.

Distribution. Qld, NT, Kimberley Region of northern WA (Fig. 129).

Remarks. Several of the New Guinean *Oecetis* species resemble *O. digitata* in having broad wings with bold or prominent venation, and may be allied to this species. However, none has Cu1a as in *O. digitata* and *O. ancala* sp. nov.

Etymology. Latin, *digitata* — having fingers, for the finger-like appearance of the male genitalia in lateral view.

Oecetis ancala sp. nov.

Figures 95–97, 130

Material examined. Holotype, male, SE Qld, Bulimba Creek, nr Brisbane Site R1, near Kimmax Street riffle, 23 Oct 1979 (NMV T-18523).

Paratypes. Qld: 3 males, Camp Mountain, 31 Mar 1967, N. Dobrotworsky (NMV); 2 males, female, Coondoo Creek, 30 km NE of Gympie, Toolara State Forest, 28 Oct 1980, A. Neboiss (NMV); 3 males, female, Cooloola National Park, Freshwater Lake, 27 Nov 1985, D. Bickel and G. Cassis (NMV).

Other material. WA: male, N end of Lake Argyle nr Kununurra, 6 Feb 1977, M.S. and B. Moulds (NMV); 7 males, female, Geikie Gorge, 18°06'S 125°42'E, 5 Oct 1996, I. Edwards (NMV). NT: 2 males, 2 females, Nourlangie Creek, 6 km E of Mt Cahill, 12°52'S 132°46'E, 18 Nov 1972, J.C. Cardale (ANIC); male, Katherine River Gorge National Park, 13 Aug 1979, J. Blyth (NMV); male, 2 females, Adelaide River, 15 km E of Stuart Highway, 15 Aug 1979, J. Blyth (NMV); male, Devil Devil Creek, 70 km SW of Daly River Mission, 23 Aug 1979, J. Blyth (NMV); 2 males, 2 females, 12°52'S 132°46'E, Nourlangie Creek, 6 km E of Mt Cahill, 18 Nov 1972, J.C. Cardale (ANIC); male, ARRS, SAR at Gimbat OSS Stn, 13°34.3'S 132°36.7'E, Wells and Suter, 24 May 1988 (NTM); 3 males, ARRS, Kambolgie Creek, 13°28.9'S 132°22.0'E, 25 May 1988, Wells and Suter (NTM); male, 12°36'S 132°53'E, ARRS, Gulungul Creek, Inlet to Gulungul Billabong, 20 Apr 1989, Wells and Suter (NTM); 2 males, SAR Site 1, 30 Sep 1988, P. Dostine (NTM); male, 3 females, 12°42'S 132°57'E, Kakadu National Park, Magela Creek, OSS Site 009, 15 Feb 1991, Wells (NTM); male, 12°42'S 132°57'E, Kakadu National Park, Magela Creek, OSS Site 009, 8 Jul 1991, Wells and Webber (NTM). Qld: males, female, Cape York Peninsula, Pascoe River crossing (to Iron Range), 4 Oct 2002, G. Theischinger (ANIC); Cape York Peninsula, Dulhunty River crossing at Telegraph rd, 7 Oct 2002, G. Theischinger (ANIC). NSW: Barrington Tops, Barrington Tops Country Retreat, Dam, 22 Dec 2000, A. Wells (ANIC). Vic: male, Tyers River, LRES, 24 Feb 1974, Site 22 (NMV) (slide); male, female, Yarra River, below Upper Yarra Dam, 28 Feb 1976, A. Neboiss (NMV); male, female, Yarra River, Diamond Creek junction, 14 Mar 1976, A. Neboiss (NMV).

Diagnosis. Forewing as for *O. digitata*. In male genitalia, paired, sharply angled, sclerotised processes ventral to tergite X, in ventral view appearing to be lateral to the phallus.

Description. Spurs 1, 2, 2. Male forewing length 7.9–9.4 mm. Wings, broad: forewing with fork 1 sessile, veins prominent; posterior anastomosis almost linear, oblique, marked by dark membrane forming a line across wing; Cu1a with a proximally directed bulge. Male genitalia, Figs 95–97. Segment IX narrow, preanal appendages discrete, slender, elongate, apices obliquely truncate in lateral view. Tergite X slender, setose. Inferior appendages stoutly clasper-shaped in ventral view, a subapical notch mesially, in lateral view swollen basoventrally, then rod-shaped to rounded apex. Phallus long for a *laustra*-group species, arched ventrally. A pair of slender processes occur ventral to tergite X, appearing to be lateral to phallus in ventral view, sharply angled inwards at about half their length (ankle-shaped), in lateral view broad-based, tapered and slender distally.

Distribution. Northern WA, northern NT, south-eastern Qld, eastern NSW and south-central Vic (Fig. 130).

Remarks. The homologies of the unusual lateral processes are obscure, being impossible to determine from the prepared slides. In lateral view they seem to be associated in some way with tergite X, although in ventral view they appear to be closely associated with the phallus. If they are derived from the phallotheca, then this species should probably be placed in the *complexa*-group in the Australian fauna, but for the present they are dealt with as part of the *laustra*-group. Only few specimens have been collected at any one time, which suggests that the species may be far more widespread, but not often collected. This is consistent with the very curious distribution.

Etymology. Latin, *anca* — a bent arm, descriptive of the structures lateral to the phallus.

Oecetis crosslandi sp. nov.

Figures 94, 98–100, 131

Material examined. Holotype male, Qld, Gunshot Creek at Telegraph Crossing, 11°44'S 142°29'E, 4–5 Apr 1992, M. Crossland (ANIC). Paratypes. 2 males, Qld: Heathlands, 11°45'S 142°35'E, T. Weir (ANIC).

Diagnosis. Forewing broad, length about 3 times width; fork 2 sessile and wing veins strongly pronounced, but without bulge in vein Cu1a. In male genitalia a single heavily sclerotised dorsal paramere with a group of teeth and spikes subapically.

Description. Wings broad, veins pronounced; forewing (Fig. 94) apex rounded, fork 1 sessile, Cu1a almost straight. Male forewing, 5.3 mm. In male genitalia (Figs 98–100), abdominal segment IX ventrally about 3 times middorsal length; preanal appendages elongate, length about 4 times width, apically rounded. Tergite X comprising a slender, elongate median lobe dorsal to a short rounded membranous plate. Inferior appendages broad-based, in ventral view sharply constricted on mesial margin, tapered to narrow apices, in lateral view with a short dorsal lobe. Phallus slender, downcurved in distal third, laterally on right, an elongate heavily sclerotised paramere with a subapical twist below a cluster of teeth and spikes.

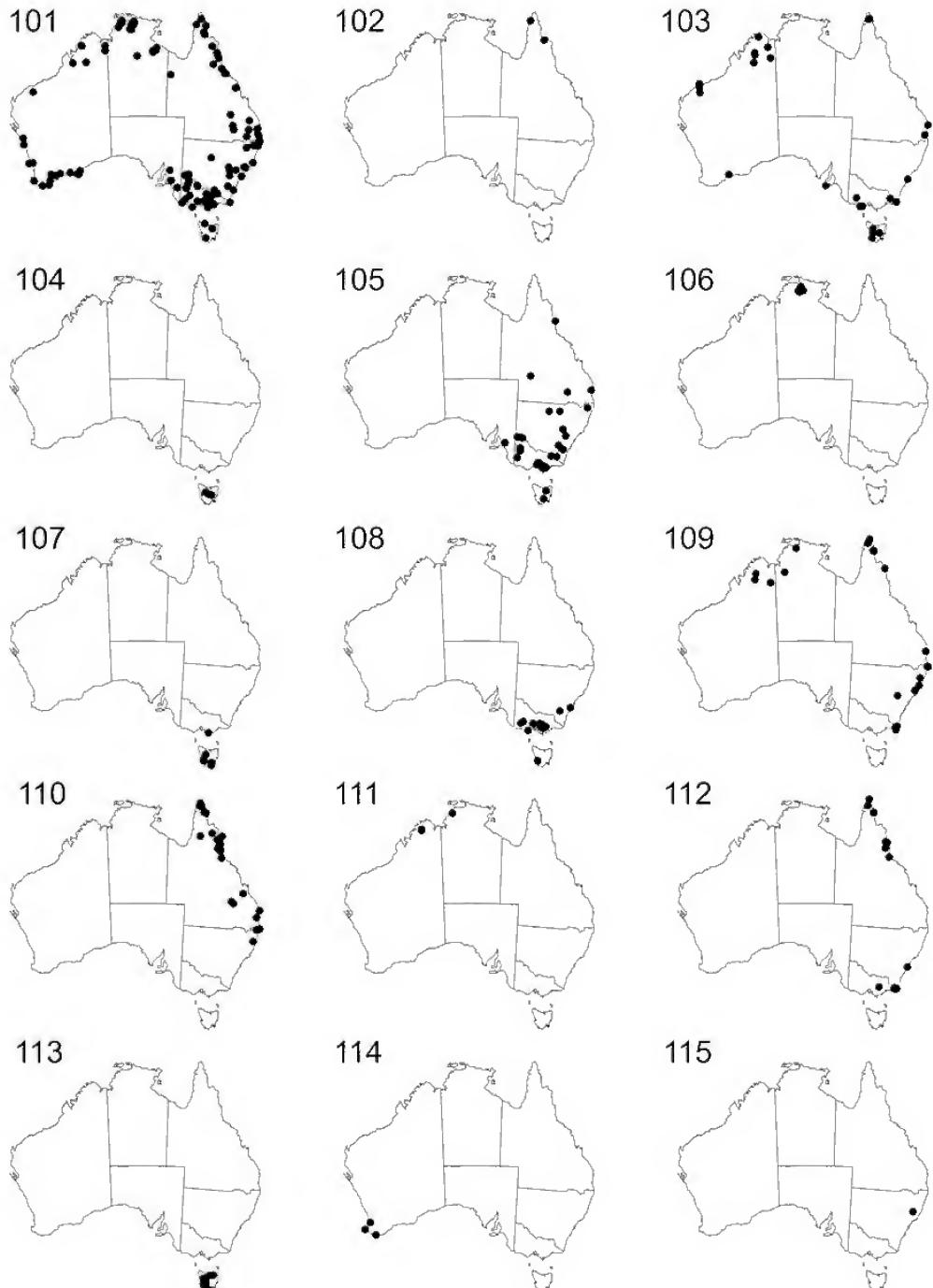
Distribution. Northern Cape York, Qld (Fig. 131).

Remarks. One can only speculate on which features of *O. digitata*, *O. ancala* and *O. crosslandi* are homoplasious. I have assumed here, tentatively, that the synapomorphy for the group is the unusual form of the wing, which is shared by the New Guinean *O. longiterra* and at least one other New Guinean species (see Chen, 1992). However, *Oecetis longiterra* has a pair of internal parameres in the phallus, which feature could otherwise place it in the *O. pechana*-group; *O. ancala* and the New Guinea species of Chen's unpublished work have paired external parameres, somewhat similar to the arrangement in the *O. complexa*-group species (Wells, 2000); and *O. digitata* has the phallus simple, without parameres, which is characteristic of the *O. laustra*-group.

Etymology. Named for Michael Crossland.

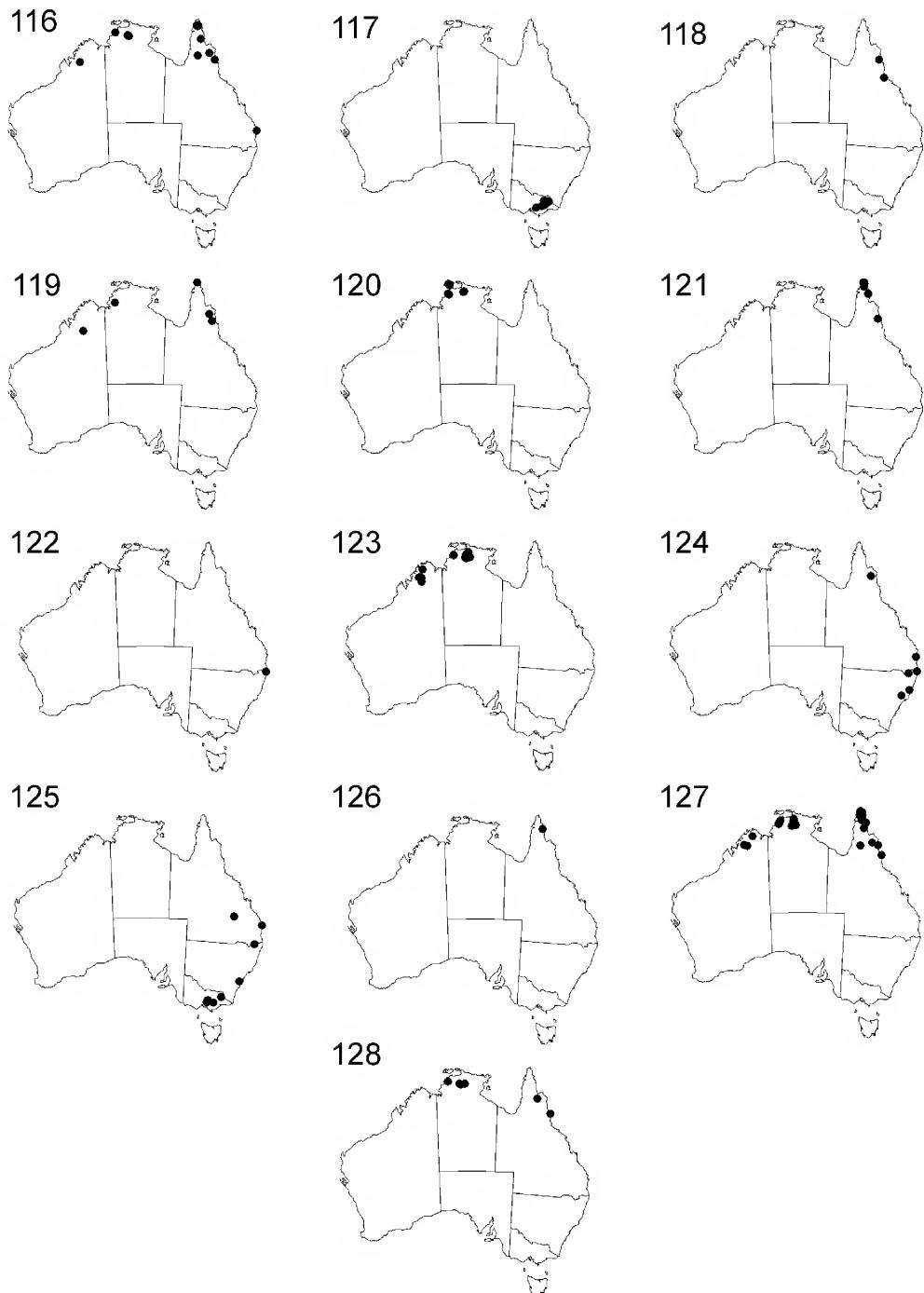
Acknowledgements

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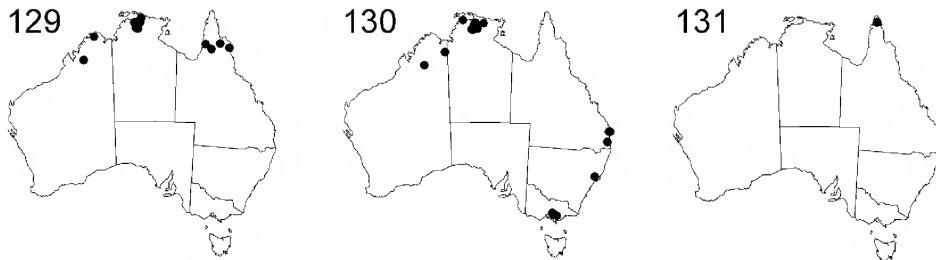
Figures 101–115, distribution of species within Australia:

101, *Oecetis laustra* Mosely; 102, *O. pseudolaustra* sp. nov.; 103, *O. atarpa* Mosely; 104, *O. scirpicula* Neboiss; 105, *O. inscripta* Kimmings; 106, *O. brevidentata* sp. nov.; 107, *O. asmanista* Mosely; 108, *O. minasata* Mosely; 109, *O. aeoloptera* Kimmings; 110, *O. multipunctata* Ulmer; 111, *O. cracenta* sp. nov.; 112, *O. parka* Mosely; 113, *O. arcada* Mosely; 114, *O. cymula* Neboiss; 115, *O. paracymula*, sp. nov.



Figures 116–128, distribution of species within Australia:

116, *Oecetis spicata* sp. nov.; 117, *O. crena* sp. nov.; 118, *O. quadrata* sp. nov.; 119, *O. dilata* sp. nov.; 120, *O. koobarra* sp. nov.; 121, *O. falcata* sp. nov.; 122, *O. terania* sp. nov.; 123, *O. papposa* sp. nov.; 124, *O. curta* sp. nov.; 125, *O. aduncata* sp. nov.; 126, *O. ornata* Kimmins; 127, *O. cepaforma* sp. nov.; 128, *O. dostinei* sp. nov.



Figures 129–131, distribution of species within Australia: 129, *O. digitata* sp. nov.; 130, *O. ancala* sp. nov.; 131, *O. crosslandi* sp. nov.

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Descriptions of new species and a new genus of leptophlebiid mayflies (Insecta: Ephemeroptera) from the Northern Territory, Australia

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Abstract

Dean, J.C., and Suter, P.J. 2004. Descriptions of new species and a new genus of leptophlebiid mayflies (Insecta: Ephemeroptera) from the Northern Territory, Australia. *Memoirs of Museum Victoria* 61(1): 111–118.

Adults and nymphs of a new monotypic genus (*Manggabora* gen. nov.) and three new species of leptophlebiid mayflies (*Manggabora wapitja* sp. nov., *Atalophlebia gubara* sp. nov. and *Tillyardophlebia dostinei* sp. nov.) are described from Kakadu National Park in northern Australia.

Key words

mayflies, Leptophlebiidae, taxonomy, new species, new genus, Australia, Kakadu

Introduction

Although the Ephemeroptera (mayflies) of the Northern Territory have been reasonably well known since environmental monitoring programs were commenced in the early 1980s, their taxonomy has been neglected and most species remain undescribed. The first serious attempt to document the fauna was by Suter (1992) who sampled extensively in the Alligator Rivers Region, associated adults with immature aquatic stages by rearing, and produced identification keys to both adults and nymphs of recognised voucher species. This study formed the basis for inclusion of Northern Territory taxa in subsequent identification guides to Australian mayfly nymphs (Suter, 1997, 1999; Dean, 1999).

Suter (1992) recorded nine species of the family Leptophlebiidae placed in five genera, and Dean (1999) recognised ten species in seven genera. A recent attempt to collect additional material was only partially successful, primarily due to unsuitable conditions at the end of the dry season. Three new species are described below, and a new genus is erected to accommodate one of them.

Material has been preserved in alcohol, with parts of some specimens mounted on microscope slides. Terminology follows Peters et al. (1978). All type material is lodged in the Museum of Victoria, Melbourne (NMV). The following abbreviations are used for material examined: MI male imago; FI female imago; MSI male subimago; FSI female subimago; N nymph.

Family Leptophlebiidae

Subfamily Atalophlebiinae

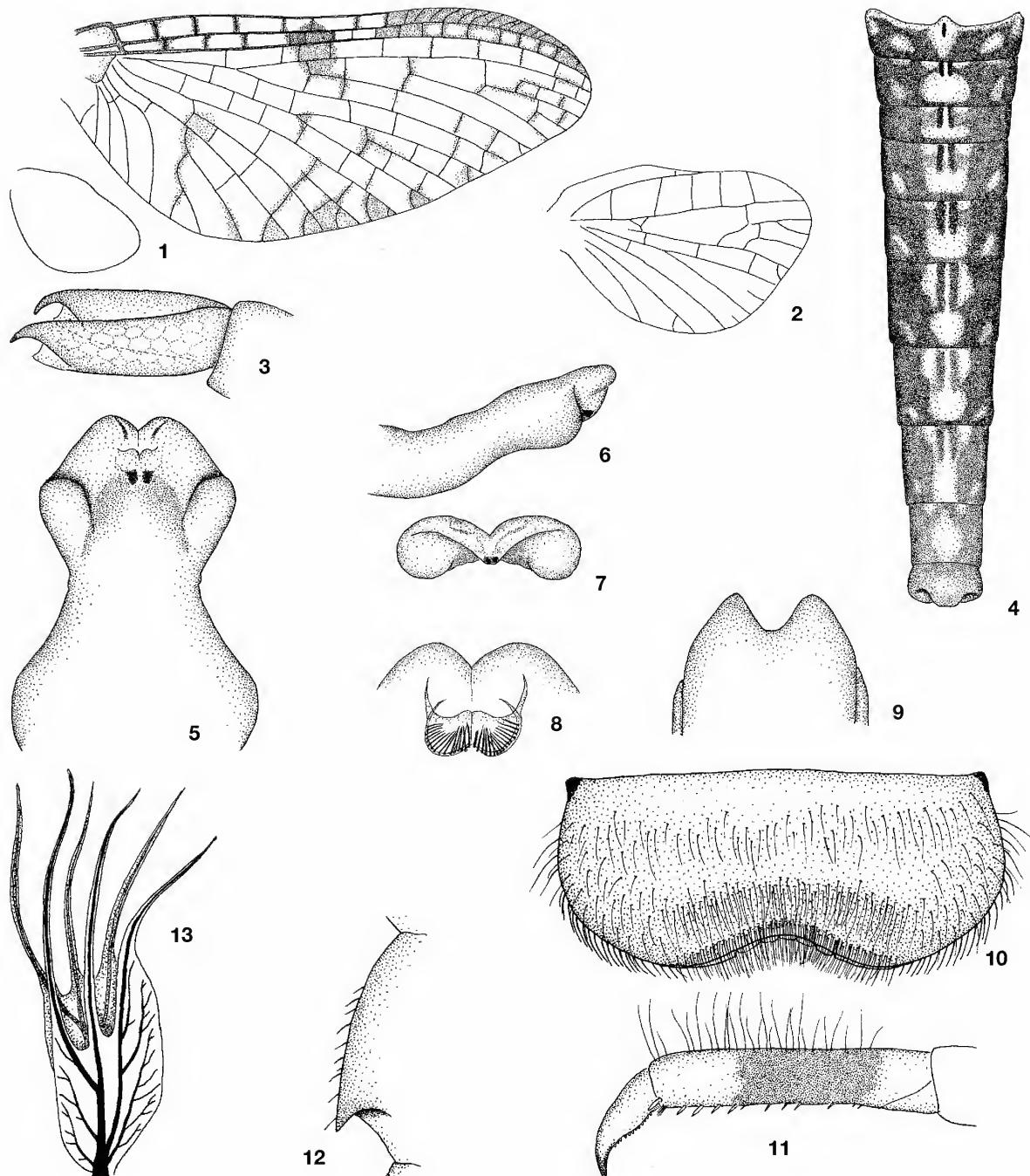
Atalophlebia gubara sp. nov.

Figures 1–13

Type material. Holotype: male imago, Gubara (Baroalba Springs), Kakadu National Park, Northern Territory, 12°49'S 132°53'E, 14 Aug 1999, J.Dean (NMV T-18498).

Paratypes: collected with holotype, 8 male imagos (NMV T-18499–T-18506).

Other material examined. Northern Territory. 3MI, 2N, Gubara (Baroalba Springs), 12°49'S 132°53'E, 14 Aug 1999, J. Dean; 1FSI, 1N, Gulungul Creek (Radon Springs), 12°45'S 132°55'E, 18 May 1988, P. Suter; 4N, Gulungul Creek (Radon Springs), 12°45'S 132°55'E, 13 Aug 1999, J. Dean; 3N, Manggabor Creek, Arnhem Land, 12°17'S 134°05'E, 26 Aug 1999, J. Dean; 1MSI, 1FI (both reared from nymphs), Walker Creek, Litchfield National Park, 13°05'S 130°42'E, 31 Aug 1999, J. Dean; 2MSI, 2FSI, (all reared from nymphs), 3FI, 2N, Magela Creek, Bowerbird Billabong, 12°47'S 133°02'E, 30 June 1990, P. Suter; 1N, Magela Creek, 1.5 km d/s Bowerbird Billabong, 12°46'S 133°02'E, 28 May 1988, P. Suter; 7N, Magela Creek, d/s Bowerbird Billabong, 12°47'S 133°02'E, 3 May 1990, D. Cartwright; 1N, South Alligator River, d/s Gimbat, 13°35'S 132°36'E, 2 May 1990, D. Cartwright; 1N, South Alligator River, Koolpin Crossing, 13°32'S 132°33'E, 18 Aug 1999, J. Dean; 1MI, 1FI, South Alligator River, Koolpin Crossing, 13°32'S 132°33'E, 14 Oct 1987, P. Dostine; 2N, South Alligator River, Coronation Hill, 13°36'S 132°37'E, 20 Apr 1987, P. Dostine.



Figs 1–13. *Atalophlebia gubara*. Male imago: 1, forewing and outline of hind-wing; 2, hind-wing enlarged; 3, foretarsal claws; 4, abdominal terga, dorsal; 5, penes lobes, ventral; 6, penes lobes, lateral; 7, penes lobes, apical; 8, penes lobes, ventral pockets (cleared slide preparation, spine-like setae internal). Female imago: 9, sternum, abdominal segment IX. Nymph: 10, labrum; 11, foretarsus; 12, lateral margin, abdominal segment V; 13, gill, abdominal segment IV.

Description. Imago. Length of male: body 6.8–7.9 mm, forewing 6.1–6.9 mm; Length of female: body 6.5–7.9 mm, forewing 6.0–7.0 mm. Head medium brown; antennae medium brown; male eyes with upper lobes medium brown, lower lobes grey, upper lobes separated by distance approximately equal to diameter of median ocellus. Thorax with meso- and metascutum medium brown; thorax laterally pale yellow, with small patches of dark brown pigment. Forelegs medium brown, femora with dark brown bands a little beyond midlength and at apex, tibiae with dark band at base and more heavily pigmented in apical half. Middle and hind legs paler, yellowish, femora with dark bands as in foreleg, tarsal segments also darker brown. Tarsal claws similar, with apical hook and opposing ventral flange (Fig. 3). Forewings hyaline, cross veins in costal and subcostal spaces washed with brown pigment; elsewhere in forewing many crossveins and cells washed with pale brown (Fig. 1). Male abdomen dark brown, pattern of paler yellow maculae, predominantly along midline (Fig. 4); abdominal sterna pale, with some darker brown markings. Penes narrow at midlength, broader in apical half, the two halves fused almost to apex; a pair of large ventro-lateral lobes at about three-quarters length, and closer to the apex a smaller ventro-median lobe (Figs 5–7); median lobe underlying deep pockets with internal spine-like setae (Fig. 8). Male imago with 3 apical filaments, dark brown in basal half and white in apical half. Female abdominal colour pattern similar to male; abdominal sternum 9 with posterior margin deeply excised (Fig. 9); strongly projecting egg guide on posterior margin of abdominal sternum 7. Subimago. Wings yellow-pale brown, forewing with suffusion of darker brown covering most cross veins. Abdominal colour pattern similar to imago but lateral pale areas more strongly developed. Nymph. General colour medium to dark brown, paler markings on abdominal terga; legs yellowish with brown bands on all segments. Labrum broad, width approximately 2.5 times length along median line (Fig. 10). Foretarsus with about 10 ventral spine-like setae, each seta less than one-sixth diameter of tarsus (Fig. 11). Abdominal segments 2–9 with relatively short posterolateral spines, those on segment V about one-eighth length of segment (Fig. 12). Gills on abdominal segments 1–7; all gills with upper and lower lamella tridigitate (Fig. 13).

Etymology. The species is named for the type locality.

Comments. Although previously undescribed, this species has been included in keys as *Atalophlebia* sp.1 (Suter, 1992) and *Atalophlebia* sp.AV16 (Dean, 1999). The species is distinguished from all other species of the genus by the structure of the male genitalia, and in the nymph by the shape of the gills, the size and number of ventral spines on the foretarsus and the short posterolateral abdominal spines.

Manggabora gen. nov.

Type species. *Manggabora wapitja* sp. nov.

Diagnosis. Imago. Forewing length-width ratio 2.8–3.0 (Fig. 14); membrane hyaline, except costal and subcostal cells in apical third of wing which are opaque, white; costal crossveins

basal to bulla very faint, difficult to see, crossveins elsewhere weakly developed; IC_u usually linked to CuA-CuP crossvein, terminating free in some individuals; IC_u₁ and IC_u₂ parallel as wing margin approached. Hindwing approximately 0.22 length of forewing; costal margin with shallow concavity a little beyond midlength; vein Sc joining costal margin at about 0.85 wing length (Fig. 15). Legs with tarsal claws dissimilar, one with an apical hook and opposing ventral flange, the other large, pad-like (Fig. 16). Male genitalia (Figs 19–22) with claspers three-segmented, penes extending beyond narrowing of claspers; penes lobes narrow, fused almost to apex, ventral surface with a robust, medial projection; each lobe with a stout, retractable apical spine. Female ninth sternum strongly projecting, posterior margin entire (Fig. 23). Subimago. Wings uniformly pale grey-yellow, without pattern. Mature nymph. Labrum a little broader than clypeus; maximum width about 2.3 times length along median line (Fig. 25); anterior margin overhanging medial notch; frontal setae sparse, arranged as narrow band. Mandibles (Figs 26, 27) with outer incisors slender; outer margin swollen at base of incisor. Maxillae with subapical row of 12–15 pectinate setae on ventral surface (Fig. 28). Labium with glossae slightly dorsal to paraglossae, not turned under ventrally (Fig. 29); labial palp with terminal segment about half length of middle segment, without spine-like setae along inner margin. Femora with long spine-like setae and hair-like setae along outer margin (Fig. 30); tarsi with all ventral spines similar in length; tarsal claws with ventral teeth (Fig. 31). Abdominal segments with posterolateral spines on segments 4 or 5–9; posterior margins of abdominal terga with an almost continuous series of very small triangular spines, about 10 µm long, interspersed with fewer long hair-like seta (Fig. 33); gills linear, lateral tracheae very weakly developed or absent (Fig. 32). Caudal filaments (Fig. 34) with apical whorl of flattened, triangular spines on each segment, and between each spine a series of 4 or 5 fine setae about half segment length.

Etymology. The genus is named after Manggabora Creek, Arnhem Land, one of the collection localities for the species. Feminine.

Remarks. *Manggabora* is a member of the *Austrophlebioides* lineage, as evidenced by the following features: (1) adult tarsal claws dissimilar; (2) forewing with IC_u₁ usually linked to CuA-CuP crossvein; (3) sternum 9 of female with apical margin entire; (4) mouthparts of nymph with labrum broader than clypeus; (5) mandibles with outer incisors slender; (6) terminal segment of labial palp, short, about half length of middle segment. The lineage is restricted to the Southern Hemisphere, and includes the Australian genera *Austrophlebioides*, *Tillyardophlebia* and *Kirrara*. *Manggabora* can be distinguished from all other genera in the lineage by the following combination of characters: (1) penes lobes relatively slender, fused almost to apex, with large ventral projection near apex; (2) anterior margin of labrum overhanging central notch; (3) maxillae with only 12–15 pectinate setae in subapical row; (4) absence of elongate ventral spines from all tarsi; (5) posterolateral spines on abdominal segments 4 or 5–9 only.

Manggabora wapitja sp. nov.

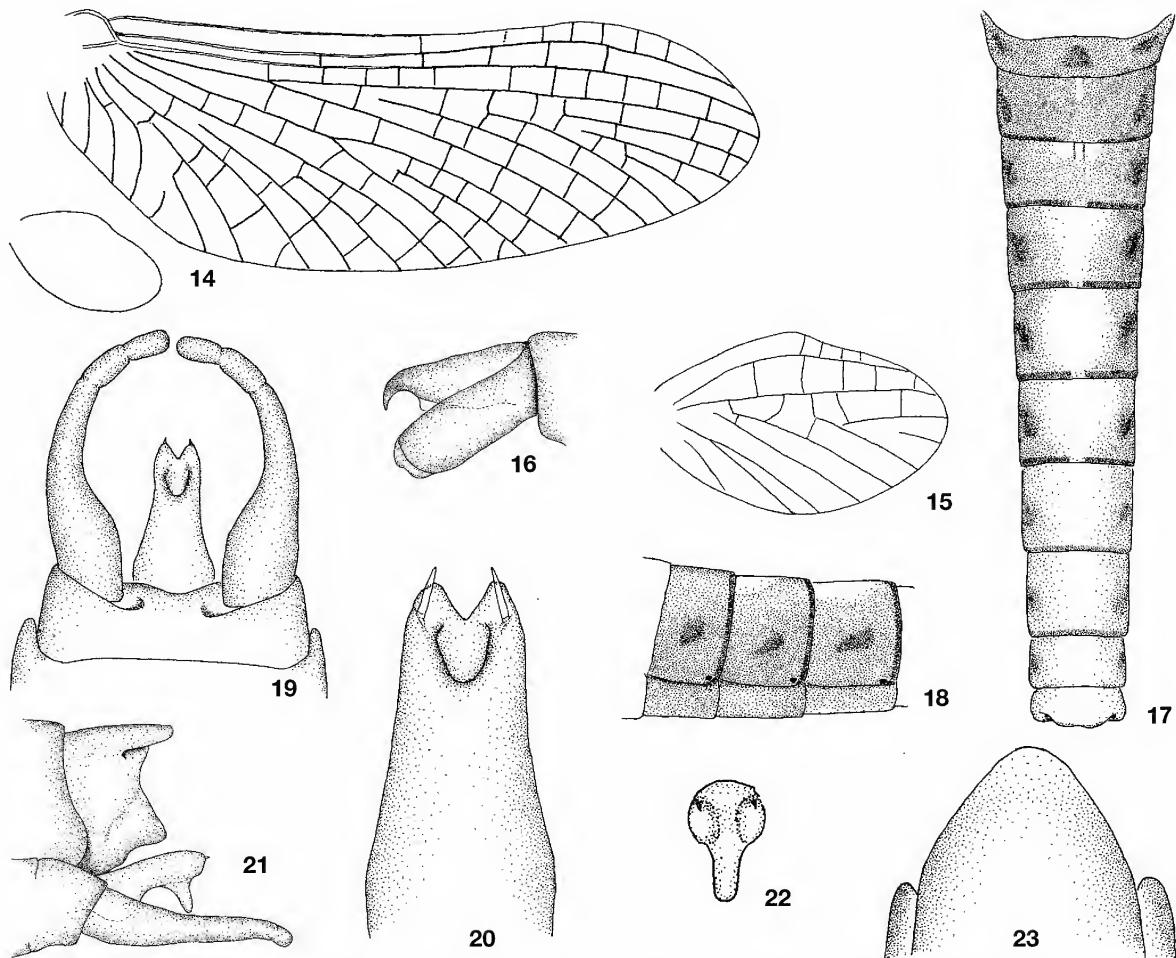
Figures 14–34

Type material. Holotype: male imago (reared from nymph), Coobanbora Spring, Kakadu National Park, Northern Territory, 12°24'S 132°40'E, 21 Aug 1999, J. Dean (NMV T-18491).

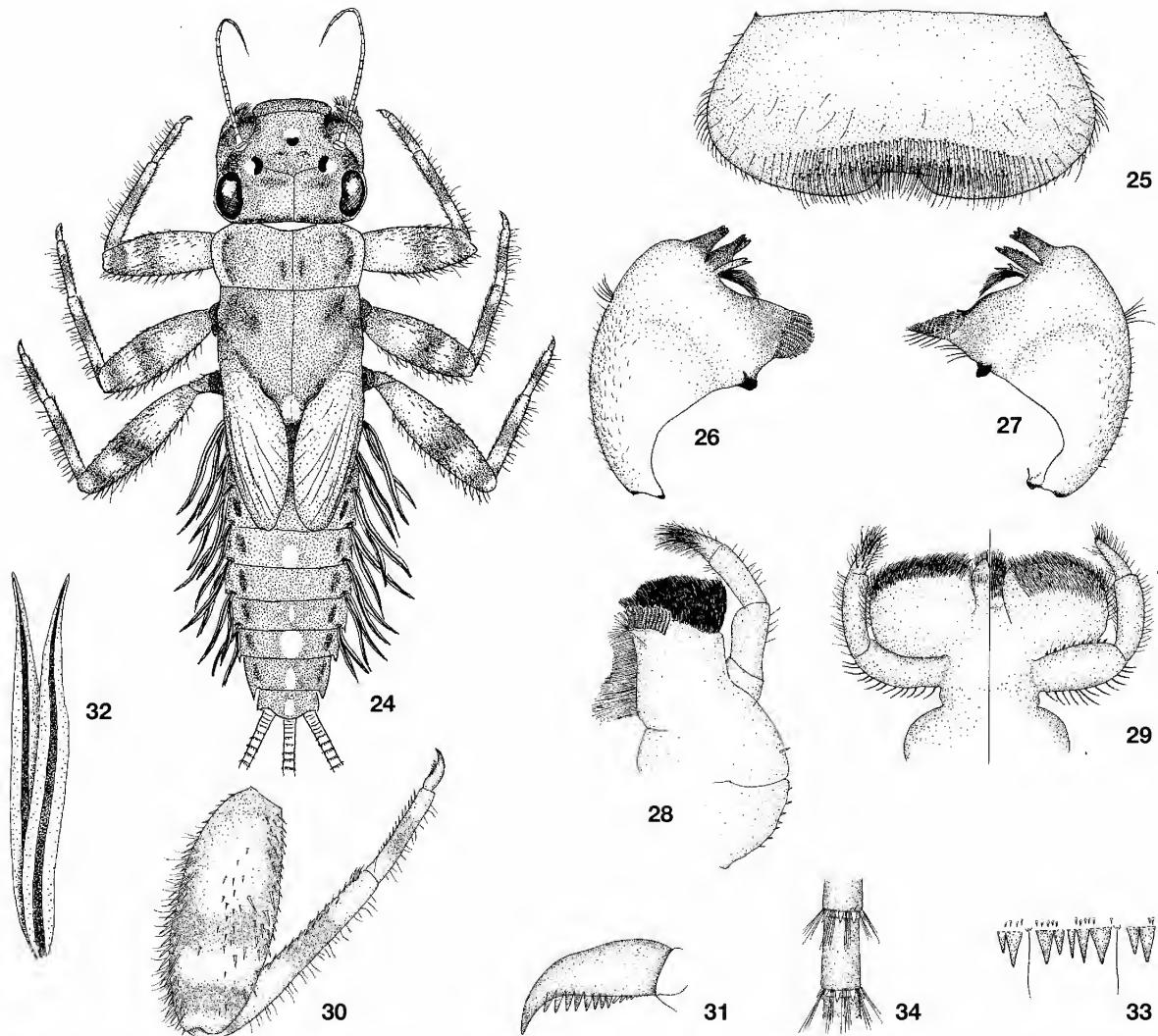
Paratype: male imago (reared from nymph; wings, legs and nymphal exuvia mounted on slides), collected with holotype (NMV T-18492).

Other material examined. Northern Territory. 10N, Coobanbora Spring, Kakadu National Park, Northern Territory, 12°24'S 132°40'E, 21 Aug 1999, J. Dean; 1MI, 17N, Koolpin Gorge, Kakadu National Park, 13°30'S 132°35'E, 18 Aug 1999, J. Dean; 1MI, 1FSI, 11N, Walker Creek, Litchfield National Park, 13°05'S 130°42'E, 31 Aug 1999, J. Dean; 14N, Florence Falls, Litchfield National Park, 13°06'S 130°47'E, 31 Aug 1999, J. Dean; 1FSI, 21N, Tolmer Falls, Litchfield

National Park, 13°12'S 130°43'E, 31 Aug 1999, J. Dean; 2MI, 20N, Mann River, Arnhem Land, 12°22'S 134°08'E, 26 Aug 1999, J. Dean; 6N, Liverpool River, Arnhem Land, 12°21"S 134°07'E, 26 Aug 1999, J. Dean; 1FI, 22N, Manggabor Creek, Arnhem Land, 12°17'S 134°05'E, 26 Aug 1999, J. Dean; 1FI, 56N, Kambolgie Creek, Kakadu National Park, 13°31'S 132°23'E, 16–19 Aug 1999, J. Dean; 3N, Kambolgie Creek, Kakadu National Park, 13°31'S 132°23'E, 1 May 1990, D. Cartwright; 13N, Barramundie Gorge, Kakadu National Park, 13°19'S 132°26'E, 22 Aug 1999, J. Dean; 1FI, 3N, Gerowie Creek, 7 km N of Bubbuluk Lookout, Kakadu Highway, 13°26'S 132°16'E, 19 Aug 1999, J. Dean; 32N, creek 2 km N of Bubbuluk Lookout, Kakadu Highway, 13°29'S 132°15'E, 19 Aug 1999, J. Dean; 1FI, 1N, South Alligator River, Koolpin Crossing, 13°32'S 132°33'E, 18 Aug 1999, J. Dean; 13N, South Alligator River, Gunlom Road Crossing, 13°30'S 132°29'E, 19 Aug 1999, J. Dean; 2N, South Alligator River, d/s Gimbat, 13°35'S 132°36'E, 1 May 1990, D. Cartwright; 1MI, 1MSI, 1FSI, Jim Jim Creek, 3 km d/s Falls, 1 Sep 1979, J. Blyth; 2N, Magela



Figs 14–23 *Manggabora wapitja* Male imago: 14, forewing and outline of hind-wing; 15, hind-wing enlarged; 16, foretarsal claws; 17, abdominal terga, dorsal; 18, abdominal segments 3–5, lateral; 19, genitalia, ventral; 20, penes lobes, ventral; 21, genitalia, lateral; 22, penes lobes, apical. Female imago: 23, sternum, abdominal segment IX.



Figs 24–34 *Manggabora wapitja* Nymph: 24, nymph; 25, labrum; 26, left mandible, dorsal; 27, right mandible, dorsal; 28, left maxilla, ventral; 29, labium, dorsal (left of midline) and ventral (right of midline); 30, foreleg; 31, foretarsal claw; 32, gill, abdominal segment IV; 33, spines, posterior margin of abdominal tergum V; 34, terminal filament, midlength.

Creek, u/s Bowerbird Billabong, 3 May 1990, D. Cartwright; 16N, Radon Springs, Kakadu National Park, 12°45'S 132°55'E, 23 Apr. 1990, D. Cartwright; 4N, Gulungul Creek, Radon Springs, Kakadu National Park, 12°45'S 132°55'E, 13 Aug 1999, J. Dean; 25N, Baroalba Creek, Kubarra Pools, 12°49'S 132°52'E, 28 Apr 1990, D. Cartwright; 11N, Baroalba Creek, Kubarra Pools, 12°49'S 132°52'E, 14 Aug 1999, J. Dean; 6N, Harris Creek, u/s South Alligator River, 1 May 1990, D. Cartwright. **Western Australia.** 27N, King Edward River, Mitchell River Road, 25 Sep 1995, L. Metzeling.

Description. Imago. Length of male: body 4.7–5.0 mm, forewing 5.1–5.2 mm; Length of female: body 4.1–5.9 mm, forewing 4.9–6.3 mm. Head predominantly medium brown; antennae pale yellow; ocelli white, black at base; male eyes

with upper lobes pale orange-brown, in contact dorsally, lower lobes grey. Thorax with meso- and metascutum golden-yellow; lateral surfaces golden with some patches of medium brown. Forelegs with femora reddish-brown, tibiae pale yellow with apex medium brown, tarsi pale yellow; middle and hind legs uniformly pale yellow; forelegs of male with ratios of segment lengths 0.69–0.70; 1.00 (1.74–1.75 mm); 0.05; 0.27–0.31; 0.28; 0.18–0.21; 0.10–0.11; tarsal claws dissimilar, one claw with apical hook and ventral flange and the other expanded and pad-like, without terminal hook (Fig. 16). Forewings hyaline except for pterostigma, which is white and opaque; veins predominantly unpigmented (Fig. 14). Male abdomen reddish, dorsally pale tending to hyaline; each segment with narrow band of

medium brown along posterior margin and pair of weakly developed brown lateral markings (Figs 17, 18); abdominal sterna pale, tending to hyaline. Penes lobes (Figs 19–22) narrow, fused almost to apex, each lobe with a stout, retractable apical spine; subapically with a robust, medial projection on the ventral surface. Female abdominal colour pattern similar to male, although generally a little darker, reddish-brown; abdominal sternum 9 strongly projecting, without apical excision (Fig. 23). Subimago. Wings pale greyish-yellow, abdominal colour pattern similar to imago. Mature nymph. General colour yellow. Mouthparts as in Figs 25–29. Legs yellow, all segments banded; foretarsus with 10–15 ventral spine-like setae, relatively uniform in length; tarsal claws with ventral teeth (Figs 30, 31). Abdomen yellow, each segment with pair of brown lateral markings (Fig. 24); gills linear, lateral tracheae very weakly developed or absent (Fig. 32).

Etymology. The name wapitja is derived from the word for ‘digging stick’ in the Dät^liwy language of eastern Arnhem land (Ganambarr, 1999), and refers to the appearance of the male genitalia in lateral view.

Remarks. The genus is monotypic. Suter (1992) included this species in his keys as “Leptophlebiidae Genus A sp.1”, and Dean (1999) designated the nymph “Genus V sp.AV1”.

Tillyardophlebia dostinei sp. nov.

Figures 35–47

Type material. Holotype: male imago (reared from nymph), Rockhole Mine Creek, Kakadu National Park, Northern Territory, 13°30'S 132°30'E, 24 Jun 1995, P. Dostine (NMV T-18493).

Paratypes: male imago (reared from nymph; wings, legs and nymphal exuvia mounted on slide, labelled specimen 01), Rockhole Mine Creek, Kakadu National Park, Northern Territory, 13°30'S 132°30'E, 24 Jun 1995, P. Dostine (NMV T-18494); male imago, 2 female imagos (all reared from nymphs), Rockhole Mine Creek, Kakadu National Park, Northern Territory, 13°30'S 132°30'E, 31 May 1995, P. Dostine (NMV T-18495–T-18497).

Other material examined. Northern Territory. 1MSI (reared from nymph), Rockhole Mine Creek, Kakadu National Park, Northern Territory, 13°30'S 132°30'E, 24 Jun 1995, P. Dostine; 3N, Rockhole Mine Ck, 2 May 1990, D. Cartwright.

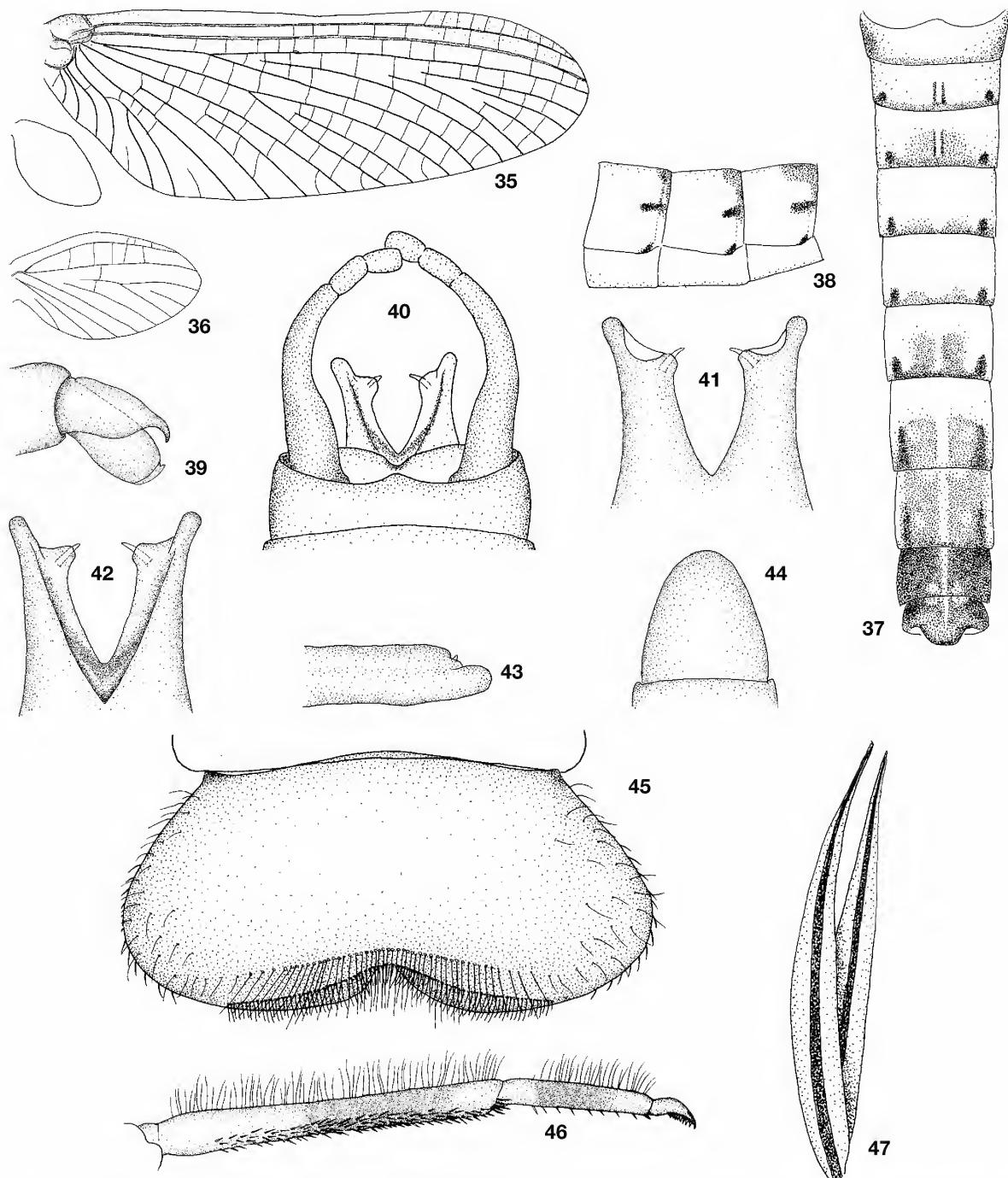
Description. Imago. Length of male: body 5.6–6.5 mm, forewing 6.0–6.6 mm; Length of female: body 5.5–5.6 mm, forewing 6.0–6.4 mm. Eyes of male with upper lobes brownish-pink, in contact dorsally, lower lobes black. Thorax orange-brown. Forewing with membrane hyaline (Fig. 35); costal and subcostal cells in apical third of wing translucent, whitish; length-width ratio 2.8–3.0; costal crossveins absent or weakly developed basal to the bulla, 10–15 distal to the bulla; MA forked at 0.37–0.39 wing length; MP₁ attached by crossvein to MP₂ at about 0.18 wing length; ICu₁ linked to CuA-Cup crossvein, ICu₁ and ICu₂ weakly diverging as wing margin approached. Hindwing 0.20–0.22 length of forewing; costal margin convex at about midlength, relatively straight basal and distal to midpoint (Fig. 36); vein Sc joining costal margin a little less than 0.9 wing length; hindwing with 3–5 costal crossveins and 5–6 subcostal crossveins, all weakly developed. Legs pale, not banded, but slightly darker brown at apex of

femur and tibia; tarsal claws dissimilar, one claw with an apical hook and without an opposing ventral flange, the other large, pad-like (Fig. 39); forelegs of male with ratios of segment lengths 0.72–0.73; 1.00 (2.4 mm); 0.07–0.08; 0.31–0.32; 0.29–0.30; 0.22; 0.08–0.09. Abdomen predominantly pale yellow, restricted dark brown markings on segments 1–6, more strongly developed markings on segments 7–9 (Figs 37, 38). Male genitalia with claspers three-segmented, narrowing gradually at about one-third length (Fig. 40); penes extending beyond narrowing of claspers, lobes moderately broad, widely separated in apical two-thirds and fused in basal third; each lobe with a stout, inwardly directed subapical spine and a ventral longitudinal ridge (Figs 41–43). Female ninth sternum with posterior margin entire, strongly convex, protruding beyond apex of segment 10 (Fig. 44). Mature nymph. Head prognathous. Mouthparts: Clypeus with lateral margins slightly diverging to anterior. Labrum clearly broader than clypeus, width about 2.4 times length along median line; 2 setal fringes close to anterior margin, each fringe extending across more than half width of labrum; anterior margin with broad central notch, the base of which is concealed beneath an overhanging canopy (Fig. 45). Mandibles with incisors slender. Maxillae with subapical row of about 25 pectinate setae. Legs with tibiae and tarsi relatively slender (Fig. 46); tibiae with ventral spine-like setae relatively dense right to apex; tarsi with 10 or fewer ventral spine-like setae, relatively uniform in length; tarsal claws with ventral teeth, progressively larger apically. Abdominal segments without setae on lateral margins, strongly developed posterolateral spines on segments 2–9. Gills present on abdominal segments 1–7, each gill narrowly lanceolate without lateral tracheae (Fig. 47).

Etymology. The species is named for Peter Dostine, who collected the type material and associated nymphs with adults.

Remarks. This species was not included in the original keys to mayflies of the Alligator Rivers region presented by Suter (1992). The nymph has previously been designated *Tillyardophlebia* sp.AV8 (Dean, 1999), albeit with a comment that the species should perhaps be placed in a new genus. While we have opted to retain the species in *Tillyardophlebia* pending completion of further study of two undescribed Queensland species and a detailed phylogenetic analysis, we are of the opinion that these three northern Australia species will eventually be transferred to a new genus. The nymphs of the species from northern and southern Australia are very similar, with no obvious characters to justify generic separation. In the imagoes, however, there are clear differences in the structure of the male genitalia. The species from south-eastern Australia form a monophyletic group with long, narrow and widely separated penes lobes, each lobe bearing a large curved ventral spine (*Tillyardophlebia* sensu stricto). Species from northern Australia have more robust penes lobes, which are fused either in the basal third or along most of their length, and each lobe has a single subapical spine.

Although confirmed material of this species has only been collected from the type locality, it is probably more widely distributed. We have examined nymphs from Manning Gorge in north-western Australia which we believe are conspecific.



Figs 35–47 *Tillyardophlebia dostinei* Male imago: 35, forewing and outline of hind-wing; 36, hind-wing enlarged; 37, abdominal terga, dorsal; 38, abdominal segments 4–6, lateral; 39, foretarsal claws; 40, genitalia, ventral; 41, penes lobes, dorsal; 42, penes lobes, ventral; 43, penes lobes, lateral. Female imago: 44, sternum, abdominal segment IX. Nymph: 45, labrum; 46, foretibia and foretarsus; 47, gill, abdominal segment IV

Acknowledgements

We would like to thank management and staff at the Alligator Rivers Research Institute, who provided encouragement and material assistance during several field trips to the region. In particular we would like to single out Peter Dostine and Chris Humphrey; we greatly appreciate their friendship, hospitality and the valuable time and knowledge they were able to provide. Alice Wells, Peter Cranston and John Hawking are thanked for assistance in the field.

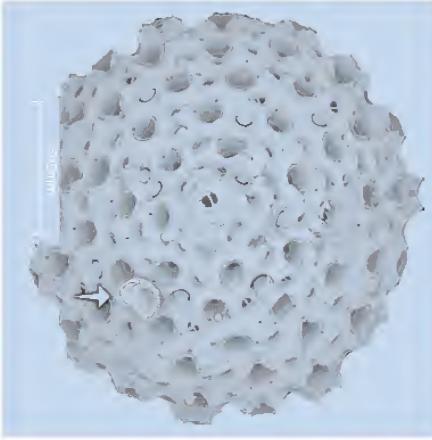
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