OPHELIA **43** (2): 127-180 (November 1995)

THE TAXONOMY AND PHYLOGENY OF TUBE-TAILED SPHAEROMATID ISOPODS (CRUSTACEA) WITH DESCRIPTIONS OF NEW SPECIES AND A NEW GENUS FROM SOUTHERN AUSTRALIA

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ABSTRACT

The genus *Cymodocella* Pfeffer, 1887, is revised and three new species are described from southern Australian coastal waters: *Cymodocella ambonota* sp. nov., from the central New South Wales coast, *Cymodocella glabella* sp. nov. (incertae sedis) from Lord Howe Island, and *Cymodocella ankylosauria* sp. nov. (incertae sedis) from coastal islands off South Australia. The genus is characterized by having an elongate, posteriorly directed, ventrally closed tube to the pleotelson, pleopod one with a medially indurate endopod and the antennule with colinear peduncular articles. *Diclidocella* gen. nov. is established for those tube-tailed Dynameninae with operculate first pleopods, short epistome and antennule peduncular article 2 posteriorly offset; three new species are described: *Diclidocella bullata* sp. nov., *Diclidocella ngake* sp. nov. and *Diclidocella yackatoon* sp. nov. (the latter two species being provisionally regarded as incertae sedis). The genus is recorded from Tasmania, Victoria, South Australia and southern Western Australia.

Species of *Cymodocella* and *Diclidocella* gen. nov. belong to a distinct group of southern hemisphere genera. The diagnostic characters of this group are presented. Character states of the tube-tailed genera are reviewed. The phylogenetic significance and homoplasy of certain characters is assessed, in particular the occurrence of tube-tails within the Sphaeromatidae. Cladistic analysis of the species of *Cymodocella* suggests that the genus is a polyphyletic taxon. The phylogeny of the species and their geographic distribution are briefly discussed.

Two species, on the basis of character evaluation resulting from examination of the types, are transferred to *Ischyromene: I. bicolor* (Barnard, 1914) comb. nov. and *I. magna* (Barnard, 1954) comb. nov.

A key is given to the Australian genera and species of tube-tailed sphaeromatids.

Key words: Isopoda, taxonomy, Sphaeromatidae, *Cymodocella,* new genus, new species, Australia.

INTRODUCTION

The family Sphaeromatidae presents several difficulties that appear to be peculiar to the family when compared to other families of the Flabellifera. The

very large number of genera, now fast approaching 100, a figure likely to be rapidly exceeded, and the large number of species (no accurate assessment exists at present; Bruce 1993, quoted more than 400, a very conservative estimate), has resulted in few workers undertaking global generic revisions. Many of the larger genera therefore contain numerous species that are incompatible with the generic diagnosis and the type species of the genus in which they have been placed. Harrison & Holdich (1984) discussed this situation for many of the genera that they treated, and the scope of the problem can be judged from their remarks. In some genera there are more "undescribed" species (i.e. named and diagnosed only) than there are species with full descriptions. Most specialists on the family have worked on a regional basis, and in many cases the lack of specialist attention has resulted in an inconsistency of character data available from existing descriptions. This lack of consistent character data considerably impedes progress of revisionary studies, and also results in an inability to assess what constitutes reliable and informative generic level characters within the family. *Cymodocella* is a genus that epitomises these points.

The genus *Cymodocella* Pfeffer, 1887, has long been accepted as having an exclusively southern hemisphere distribution (Harrison & Holdich 1982), with the preponderance of species being recorded from southern Africa. Harrison & Holdich (1982) rediagnosed the genus, but redescribed none of the species. Other than the type species, which was redescribed in detail by Brandt & Wägele (1989), none of the 13 species listed by Harrison & Holdich (1982) could be considered as adequately known.

This present work initially set out to document those species of the genus that occurred in southern Australian waters, but the morphological diversity shown by these species, especially in structures such as penes and appendix masculina, which are often of critical generic importance, and also of the mandibular morphology, raised two issues. The first was whether or not the genus and its constituent species could still be considered conceptually viable. The second was that the apparently unique and easy to recognize character of the telsonic tube could be a homoplasy, and not be of phylogenetic significance. An answer has been attempted for both of these points, but the results suggest that the genus as presently constituted is not monophyletic.

I thank Drs P.B. Berents and J.K. Lowry (Australian Museum, Sydney), Drs G.C.B. Poore and R.S Wilson (Museum of Victoria), Mr W.Zeidler (South Australian Museum) and Ms Liz Hoenson (South African Museum, Cape Town) for the loan of material in their charge. This study was supported by the Australian Biological Resources Study (Grant 89/1844). I thank Jørgen Olesen for his inking of my original drawings. I also thank Dr D. Eibye-Jacobsen for his considerable assistance in demonstrating the operation and the workings of the Hennig '86 programme and for his comments on the manuscript; Drs D.M. Holdich (Nottingham University) and G.C.B. Poore (Museum of Victoria) for their comments on an early version of this article. I thank Dr H.-G. Müller (Tropical Research Laboratory, Wetzlar, Germany) for allowing me access to his work in preparation.

MATERIAL AND METHODS

Material

Specimens for study were principally borrowed from the collections of the Australian Museum, Sydney, and the Museum of Victoria, Melbourne. Specimens, mostly types, of all of K.H. Barnard's species from southern Africa were borrowed from the South African Museum, Cape Town, and examined in detail. Specimens of *Cymodocella egregia* (Chilton) from Akaroa Harbour, New Zealand (collected circa 1897-1900, ZMUC CRU310-312) and syntypic specimens of *Cymodocella guarapariensis* (ZMUC CRU089) were examined.

Examination and preparation of specimens follows that outlined in Bruce (1994a), with the exceptions that high power microscopy drawings were made using Nomarski interference lighting, and that the SEM used was a Jeol JSM 840.

Specimens are categorized according to their type status; the section Additional material includes that which is explicitly excluded from the type series by virtue of uncertain status, disparate location, or that the specimens were merely identified after completion of the description and therefore not examined in the process of formulating the description.

Character analysis

The analysis was performed using Hennig'86 (Farris 1988). Characters were polarised using *Sphaeroma* Bosc and *Ischyromene* Racovitza as the outgroups, with further reference to the Cirolanidae for some ambiguous characters. Characters were coded as binary in most cases, with additive binary multistate characters. Trees were generated using the mh* and implicit enumeration command, followed by successive character weighting (xs w).

Initially 52 characters were scored, this being reduced to 34 following the removal of characters common to all taxa or shown by a single species only. The taxa included are the type species, all Australian species and all those southern African species for which adequate data could be obtained.

Abbreviations: AM- Australian Museum, Sydney, NSW; NMV- Museum of Victoria, Melbourne, Vic; NSW- New South Wales; SA- South Australia; SAM- South Australian Museum, Adelaide, SA; SAfM- South African Museum, Cape Town, Republic of South Africa; Vic- Victoria; WA- Western Australia; ZMUC- Zoological Museum, University of Copenhagen, Denmark.

BL- body length; PMS- plumose marginal setae; SMS- simple marginal setae.

TAXONOMY

Order Isopoda Latreille, Family Sphaeromatidae Latreille, 1825, Subfamily Dynameninae Bowman, 1981.

The genus *Cymodocella* belongs to a group of genera that I term the "*Ischyromene*-group", after the first described genus. Characters that would appear to be common to the "*Ischyromene*-group" of genera are: 1, the presence of a short pleonal sternite; 2, antennule peduncle article 2 is always relatively long (>40% length of article 1); 3, antennule peduncle article 3 is short (equal in length or shorter than article 2) [compared to most hemibranchs and several other genera e.g., the *Cymodoce, Cerceis* and *Cilicaeoposis* genus groups]; 4, pereopods accessory unguis with 2 accessory (= secondary) cusps*; 5, posterior margin of pereopodal dactylus with flattened cuticular scales; 6, pleopod 1 endopod medial margin is indurate*; 7, pleopod 2 endopod distinctly longer than exopod*; 8, pleopods 3 and 4 exopods always lacking a transverse suture; 9, basally attached appendix masculina which extends beyond the ramus; 10, presence of clubbed spines on the maxilliped endite distal margin(*?); 11, the brood pouch of ovigerous females with a posterior pocket; 12, sexual dimorphism weak or absent. Additionally all have the pleonal sutures running to the posterior of the pleon when present. Characters marked * are apparently unique to the group. The other characters are known to occur in some other genera in all of the subfamilies.

The genera that can be recognized as belonging to the *Ischyromene*-group are: *Amphoroidea* Milne Edwards, 1840, *Amphoroidella* Baker, 1908, *Cymodocella* Pfeffer, 1887, *Dynamenopsis* Baker, 1908, *Ischyromene* Racovitza, 1908, *Juletta* Bruce, 1993, *Maricoccus* Poore, 1994, *Margueritta* Bruce, 1993 and the new genus described here. There are at least a further two undescribed southern Australian genera that belong to this group. It can be seen at once that this group is almost exclusively southern hemisphere in distribution, with most genera and species being recorded from Australia, New Zealand and South Africa.

There is a group of genera, superficially similar to the *Ischyromene*-group, that includes *Clianella* Boone, (see Harrison & Holdich 1984), *Cliamenella* Kussakin & Malyutina, 1987, *Dynamenella* Hansen, 1905, *Dynoides* Barnard, 1914, *Paradella* Harrison & Holdich, 1982, and *Parameine* Javed & Ahmed, 1988. These genera differ by having antennule peduncle article 2 short and 3 long (although this is not as clearly expressed as in *Sphaeroma* or *Cymodoce* for example), having the penial processes at least basally fused (except *Parameine),* usually with a simple accessory unguis to the dactylus (this character is not always clearly recorded in the literature), usually with pleopod 3 exopod with a distinct transverse suture or articulation, and there is obvious sexual dimorphism, with the male being more ornate than the female.

The difference in the relative length pleopod 2 endopod is very clear: in *Cymodocella,* the length of the endopod in relation to the exopod ranges from 1.43 to 1.69 for Australian species (excluding *C. ankylosauria* sp. nov.) and 1.08 to 1.17 for the South African species (excluding *C. sublevis* 0.83). The range for most other sphaeromatid genera, illustrated by the following examples, is

between about 0.6-1.0 (S = Sphaeromatinae; D= Dynameninae): *Sphaeroma* (S) 0.72-0.83; *Cymodoce* (S) 0.82-0.85; *Cerceis* (D) 0.69; *Paracilicaea* (S) 0.66-0.75; *Cilicaeoposis* (S) 0.63-0.83; *Dynamenella* (D) 0.08-1.05; *Clianella* (D) 1.0.

Significantly, this group includes genera with vaulted body shapes (e.g., *Cymodocella, Dynamenopsis, Ischyromene)* and others which are strongly dorsoventrally flattened (e.g., *Amphoroidella* and *Maricoccus).* These flattened genera are otherwise unrelated to those flattened sphaeromatids of the Cassidininae s.stricto (see Bruce 1994b), indicating that flattened body shape is a convergent character. Similarly *Amphoroidea* and *Amphoroidella* have antennule peduncle articles 1 and 2 flattened and anteriorly expanded, a character often (but not always – *Cassidinidea* lacks this character state while *Cassidinella akania* Bruce, 1994a, a vaulted species, also has it) associated with flattened body shape, and similarly homoplasious.

Major divisions within this genus-group seem to revolve around operculate pleopod 1 (or not), antennule peduncle article 2 with an anterodistal lobe (or not) and article 3 posteroventrally attached (versus colinear), short epistome (or long), and slender pereopod 2 (or not). The first three characters seem closely linked, and apply to several other Australian genera: *Juletta, Margueritta, Maricoccus,* and *Diclidocella* gen. nov.

KEY TO AUSTRALIAN MALE TUBE -TAILED SPHAEROMATIDS

1. Body rugose, pitted, dorsally covered with prominent processes; antennule peduncle article 1 (male) anterodistal angle strongly produced ..... *Cymodocella ankylosauria* sp. nov.
- Body not rugose, smooth or with nodules; antennule peduncle article 1 anterodistal angle not strongly produced 2

2. Antennule peduncle articles 2 and 3 colinear; pereopod 2 robust, similar to pereopod 3; pleopod 1 endopod medial margin indurate 3
- Antennule peduncle article 2 with anterodistal lobe, article 3 posteriorly offset; pereopod 2 distinctly longer and more slender than pereopod 3; pleopod 1 operculate, indurate 4

3. Posterior margin of pereonites 2-7 with low setose nodules; pleotelson nodulose with 2 longitudinal nodular ridges; penial processes short; appendix masculina basally attached ..... *Cymodocella ambonota* sp. nov.
- Body unornamented; penial processes elongate; appendix masculina on posteriorly directed lobe ..... *Cymodocella glabella* sp. nov.

4. Pereonites 1, 6 and 7 with dorsal bosses; telsonic tube elongate, about 20 % body length ..... *Diclidocella bullata* sp. nov.
- Pereonites unornamented; telsonic tube short, about 5 % body length 5

5. Body margin ovate; pereonite 7 narrow, not extending to lateral margins of body outline ..... *Diclidocella yackatoon* sp. nov.
- Body margin sub-parallel; pereonite 7 extending to lateral margins of body outline ..... *Diclidocella ngake* sp. nov.

Genus *Cymodocella* Pfeffer

Cymodocella Pfeffer, 1887: 69.- Hansen, 1905: 80, 107; Stebbing, 1910: 430; Hodgson, 1910: 31; Barnard, 1914: 421; Menzies, 1962: 138; Hurley & Jansen, 1977: 29; Kensley, 1978: 87; Harrison & Holdich, 1982: 106.
Not *Cymodocella* Gómez Simes, 1981: 160 (= *Ischryomene* Racovitza, 1908).

Type species: *Cymodocella tubicauda* Pfeffer, 1877, by monotypy.

Description

Male. Body dorsally strongly vaulted, surface smooth to heavily ornamented. Cephalon with rostral process in ventral position; eyes lateral, round, facets distinct. Pereonite 1 longest, 2-6 subequal in length. Pereonite 7 extending to lateral body margins or slightly narrower, coxae not concealed by pereonite 6; dorsal posterior margin weakly produced. Pleon with 4 segments, segment 1 entire, 2 separate sutures running to posterior margin of pleon. Pleotelson strongly vaulted, indistinctly bidomed; posteriorly formed into ventrally closed tube, aperture of which opens posteriorly or slightly towards a dorsal position; tube extends beyond posterior of uropod rami. Pereonite 1 without sternal extensions; narrow pleonal sternite present.

Antennule peduncle 3-articled, article 1 longest, article 2 greater than 40 % length of article 1; article 3 as long as or shorter than article 2, with short fused fourth article; articles 2 and 3 colinear, article 3 articulating terminally with article 2; flagellum shorter than peduncle. Antenna peduncle slender, articles 1-3 short, 5 longest; flagellum about equal in length to peduncle.

Epistome more than half as long as labrum, anteriorly produced, usually anteriorly quadrate; apex separating antennule bases. Mandible morphology variable, usually: incisor 1- to 5-cuspid; left mandible with prominent 3-cuspid lacinia mobilis; spine row prominent, with serrate and plumose spines; molar process prominent, keratinized, with nodular crushing surface and proximal marginal teeth. Maxillule medial lobe usually with 4 long fringed or plumose spines and 2 short simple acute spines; lateral lobe with about 13 spines on gnathal surface, medial group of which are pectinate. Maxilla entire, setae on lateral and middle lobes anteriorly pectinate or finely nodular. Maxilliped palp articles 2-4 medial margins with prominent setose medial lobes, lobes of articles 3 and 4 between 1 and 2 times as long as distal articulating margin; endite distal margin subtruncate, with stout clubbed and plumose sinuate spines, and single smooth spine at distomesial angle; distal dorsomedial margin with 2-3 stout circumplumose spines.

Pereopods all ambulatory, 1 shorter and stouter than 2-7 which are all subsimilar; dactylus posterior margin with cuticular scales; accessory unguis with 2 secondary cusps; posterior margins of ischium to propodus usually with setulose or scale fringe; dorsal margin of ischium usually with 1 medial spine and 1

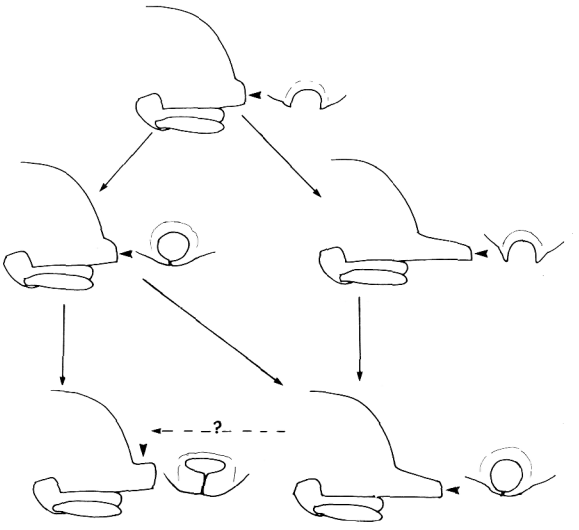

Fig. 1. Potential evolutionary routes from which the sphaeromatid tube-tail can be derived from a pleotelson with a short simple notch.

proximal simple spine; pereopods 6 and 7 usually with biserrate spines on distal margin of carpus.

Penes separate, usually short, close set, distally blunt; usually not extending to pleopod rami.

Pleopod 1 endopod medial margin indurate; exopod lamellar, lateral margin shallowly concave or straight along middle part; endopod as long as or shorter than exopod. Pleopod 2 exopod distinctly shorter than endopod (Australian and type species) or subequal in length (South African species); appendix masculina basal in position, extending beyond distal margin of endopod. Pleopod 3 exopod distinctly shorter than endopod, without transverse suture. Pleopods 4 and 5 with thickened rami, ridges weakly developed or absent; exopod of pleopod 4 without transverse suture, that of 5 with; exopod of pleopod 5 with 3 scale patches, 2 apical and one proximal to suture. Uropod rami not extending beyond posterior margin of pleotelson; usually with both rami lamellar, exopod more than half as long as endopod, articulating in ventrolateral position.

Female. Similar to the male; mouthparts not metamorphosed; brood pouch consisting of large oostegites arising from the coxae of pereonites 2 – 4 and overlapping at midline, and posterior pocket opening anteriorly at pereonite 4.

Remarks. The genus *Cymodocella* has always been one that appeared to be relatively easy to recognize. The presence of a distinct tube arising from the posterior margin of the pleotelson would appear to present few problems in recognition. But when is a tube not a tube? And when does a tube cease to be "posteriorly pointing" and become "upwardly directed"? There is no definable

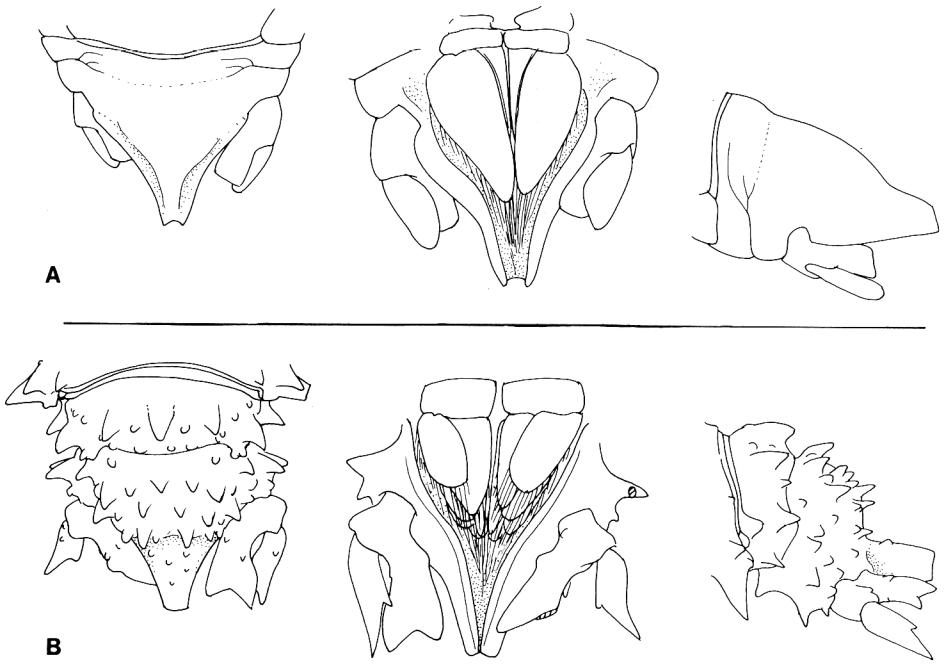

Fig.2. Sphaeromatids displaying convergent (homoplasious) tube-tail or partly developed tube-tail: A, undescribed sphaeromatid from the southern Australian coast; B, undescribed female sphaeromatid from deep-water off New Caledonia.

answer to those questions, and some species do not show a clear cut state, and therefore would have to be placed on the basis of other characters. Within the Dynameninae a perforate pleotelson is common, and shows a diversity of forms. Can the tube-tail be regarded as a unique apomorphy? It can easily be demonstrated that it is not, and can be derived from two different pathways (Fig. 1). Additionally closed "tube-tails" can be shown to occur in taxa that do not belong to the *Ischyromene*-group, such as *"Cymodocella" hawaiiensis* Bruce, 1994c, *Dynamene* Leach, 1814 (e.g., see Holdich & Harrison 1980) and open tube-tails of the two undescribed taxa illustrated here, one from deep water off New Caledonia and one from southern Australia (Fig. 2).

The sole character that can be currently recognized as separating *Cymodocella* from *Ischyromene* is the presence of a produced, ventrally closed pleotelsonic tube in the former. Harrison & Holdich (1982) described *Ischyromene* as having "a number of variable characters", and state "the pleotelsonic apex may have a simple groove or an enclosed foramen"; no reference was made to the directional position of the opening. An enclosed foramen is little different to a short tube, the condition shown by most of the South African species and *Diclidocella yackatoon* sp. nov. for example.

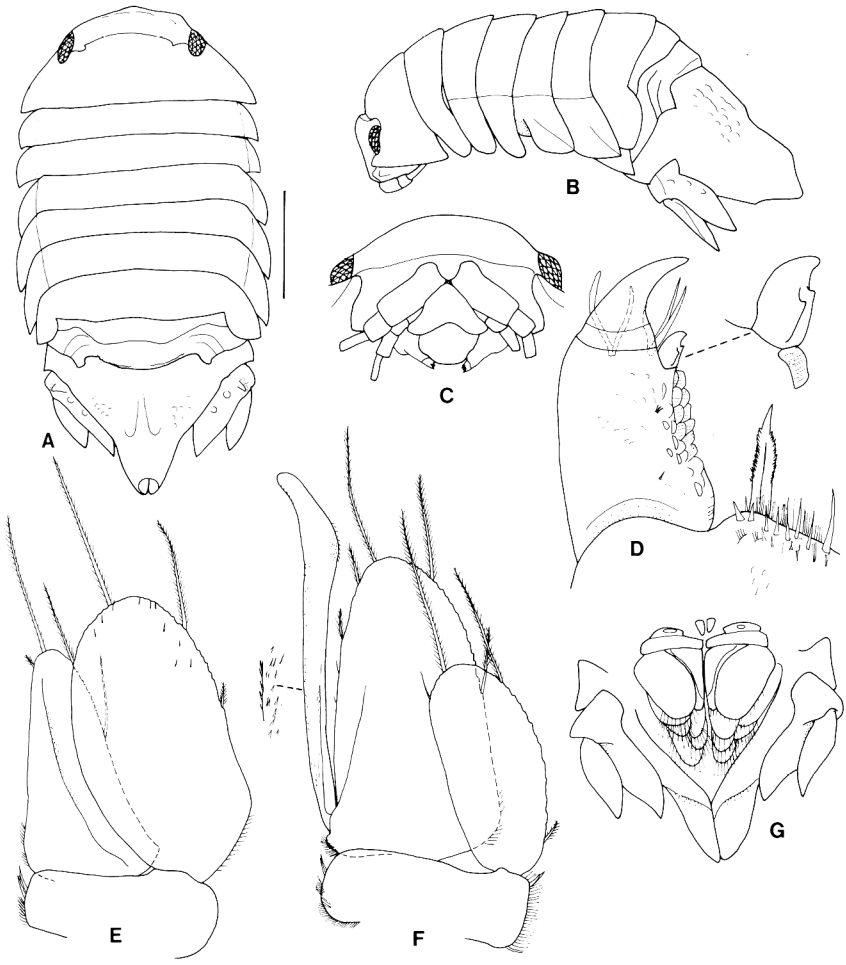

Fig. 3. *Cymodocella tubicauda* Pfeffer. All male 9.7 mm, NMV J4826. A, dorsal view; B, lateral view; C, frons; D, pereopod 1, dactylus; E, pleopod 1; F, pleopod 2; G, pleon, ventral view. Scale 2.0 mm.

4758

Of the species placed in the genus, I regard only four as belonging to the genus sensu stricto. The remaining species are all categorised as incertae sedis due to lack of adequate data or material to describe from (the species *C. algoensis, C. cancellata, C. diateichos, C. eutylos),* or the species differing in certain characters of the mouthpart, pereopod and pleopod morphology that suggests their generic placement is in question (remaining species, and see the species list).

Species included: Species regarded as belonging to the genus sensu stricto: *Cymodocella ambonota* sp. nov.; *Cymodocella capra* Hurley and Jansen, 1977; *Cymod-*

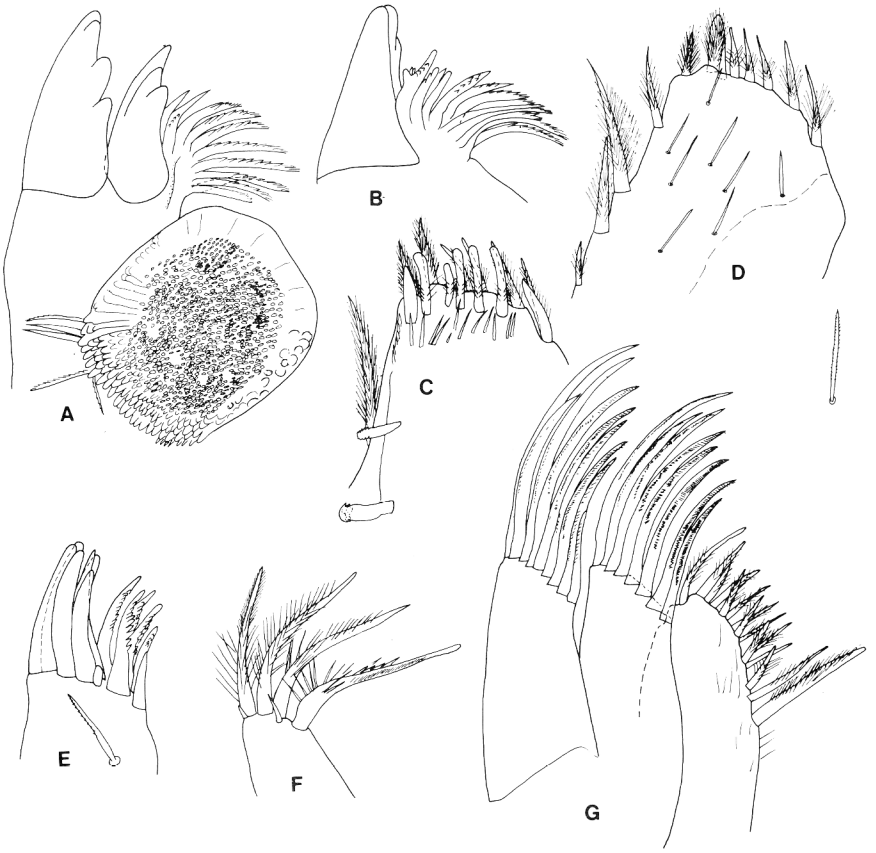

Fig. 4. *Cymodocella tubicauda* Pfeffer. All male 9.7 mm, NMV J4826. A, left mandible; B, right mandible incisor and spine row; C, maxilliped endite, distal margin; D, maxilliped endite, dorsal margin, showing spread of serrate setules: E, maxillule exopod apex; F, maxillule endopod apex; G, maxilla.

ocella egregia (Chilton, 1892); *Cymodocella tubicauda* Pfeffer, 1887, type species.

Species here regarded as incertae sedis are: *Cymodocella algoensis* (Stebbing, 1875); *Cymodocella ankylosauria* sp. nov., *Cymodocella cancellata* Barnard, 1920; *Cymodocella diateichos* Barnard, 1959; *Cymodocella eutylos* Barnard, 1954; *Cymodocella glabella* sp. nov.; *Cymodocella guarapariensis* Loyola e Silva, 1965; *Cymodocella pustulata* Barnard, 1914; and *Cymodocella sublevis* Barnard, 1914.

Species excluded: Cymodocella bicolor Barnard, 1914 and *Cymodocella magna* Barnard, 1954, which are here transferred to *Ischyromene.*

"Cymodocella" hawaiiensis Bruce, 1994c, is not considered to belong to the *Ischyromene*-group (see section Analysis of Taxa).

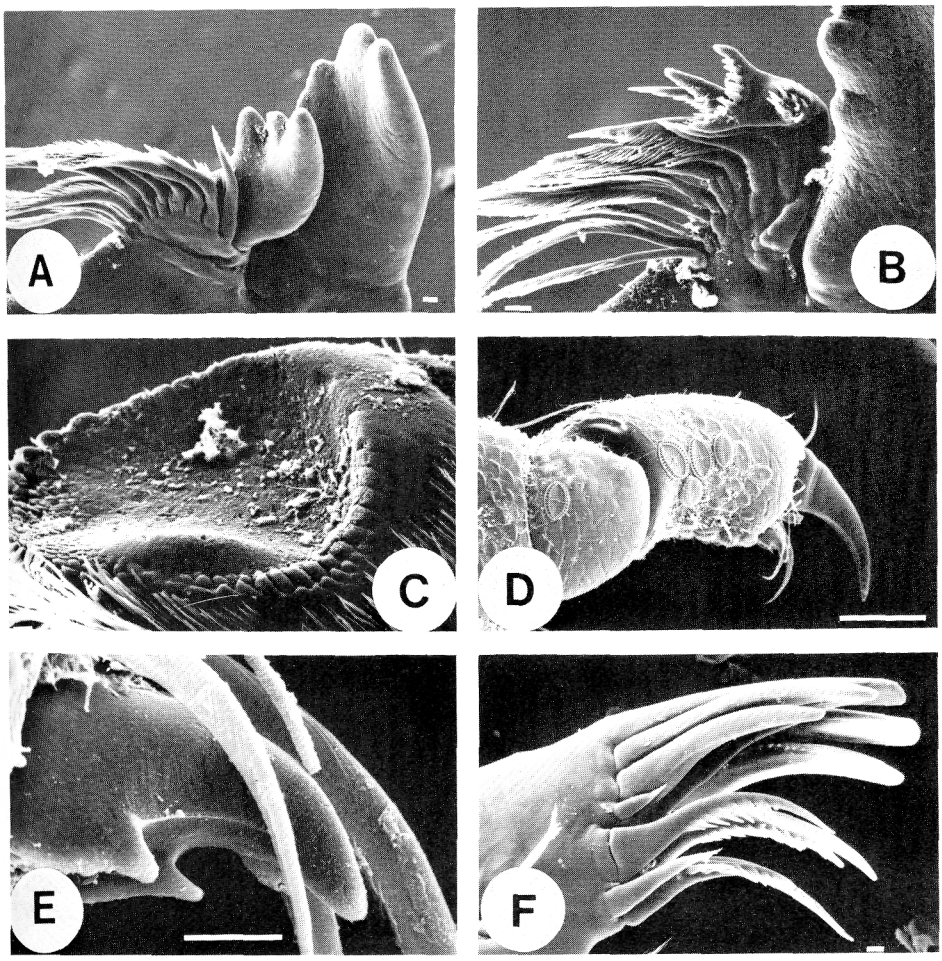

Fig. 5. *Cymodocella tubicauda* Pfeffer. SEMs, male, 6.9 mm, NMV J4826. A, left mandible (10μm); B, right mandible (10μm); C, molar process (10μm); D, pereopod 2, dactylus, with diatoms (100μm); E, pereopod 2, dactylus, trifid secondary unguis (10μm); F, maxillule lateral lobe (10μm).

Cymodocella tubicauda Pfeffer

Figs 3-5

Cymodocella tubicauda Pfeffer, 1887, 70-75, pl 2, fig. 8, pl 6, figs 11, 12; Richardson, 1908: 4; 1913: 6; Chilton, 1909: 657; Hodgson, 1910: 31; Tattersall, 1921: 222; Monod, 1931: 25; Nierstrasz, 1931: 214; Hale, 1937: 21; Stephensen, 1947: 30; Hurley, 1961: 271, 287; Kussakin, 1967: 236; Amar & Roman, 1974: 582; Hurley & Jansen, 1977: 32, fig. 20; Brandt & Wägele, 1989: 206, figs 1-14.

Cymodocella georgiana Pfeffer, 1887: 18 (nomen nudum); Brandt & Wägele,

1989:209.

Cymodocea antarctica Hodgson, 1902: 243, pl. 32, fig. 2.

Cymodocella tibicauda Kussakin, 1982: 75 (lapsus).

Material Examined: About 160 ♂ and ♀, Davis Station, Antarctica, 68°38'S, 77°48'E, 6 Jan 1989, coll. M. Tucker (NMV J4826). 6 specimens, South Georgia Island, Swedish South Pole expedition, 25 Oct 1903, on old kelp (ZMUC CRU308). 1 specimen, Ranvik, Peter Island, 69.75°S, 90.50°W, 1 Feb 1929, 80 m, coll. O. Olsted (ZMUC CRU309).

Remarks. This species, despite frequent literature records, was only recently redescribed in detail (Brandt & Wägele 1989). Figures given here are of generically important characters, and of details not previously fully illustrated. The pleopods, as illustrated by Brandt & Wägele (1989), lack thickened ridges or folds.

Distribution. Antarctic and subantarctic coastal waters (Hurley & Jansen 1977, Brandt & Wägele 1989).

Cymodocella ambonota sp. nov.

Figs 6-8

Material Examined: Holotype. ♂ (2.4 mm), off Nelson Head, Port Stephens, NSW, 32°43'S, 153°10'E, 27 Oct 1980, 18 m, sand and shell grit, coll. J. Hall and I. Loch (AM P42555). Paratypes. 6 ♂ (2.0, 2.1, 2.2, 2.3 dissected, 2.4 mm), ♀ (non-ovig 2.5 mm), manca (1.7 mm), same data as holotype (AM P42556, 1 male, ZMUC CRU317). ♀ (ovig 2.8 mm), Nelson Head, Port Stephens, NSW, 32°37'S, 152°04'E, 10 Oct 1980, 18 m, tufted bryozoans and hydroids, coll J. Hall (AM P42557).

Description

Male. Body about twice as long as wide, lateral margins sub-parallel. Cephalon anteriorly with low nodules. Posterior margins of pereonites 2-6 raised into thickened ridge with low nodules; dorsal posterior margin of pereonite 7 somewhat posteriorly produced, with median indentation; most pereonal nodules dorsally minutely setose. Coxal sutures indistinct; coxae dorsally thickened, forming lateral longitudinal ridge. Pleon short, largely concealed in lateral view, about 4-5% BL. Pleotelson with 2 submedial longitudinal indistinct nodulose ridges; dorsal surfaces with scattered small nodules; telsonic tube short, about 7% BL, very slightly upturned, ventrally entirely closed.

Antennule peduncle article 2 50% as long as article 1; article 3 about 80% as long as article 2; flagellum about 23 % as long as peduncle, with 2 articles. Antenna flagellum 64 % as long as peduncle, with 8 articles, first 3 of which

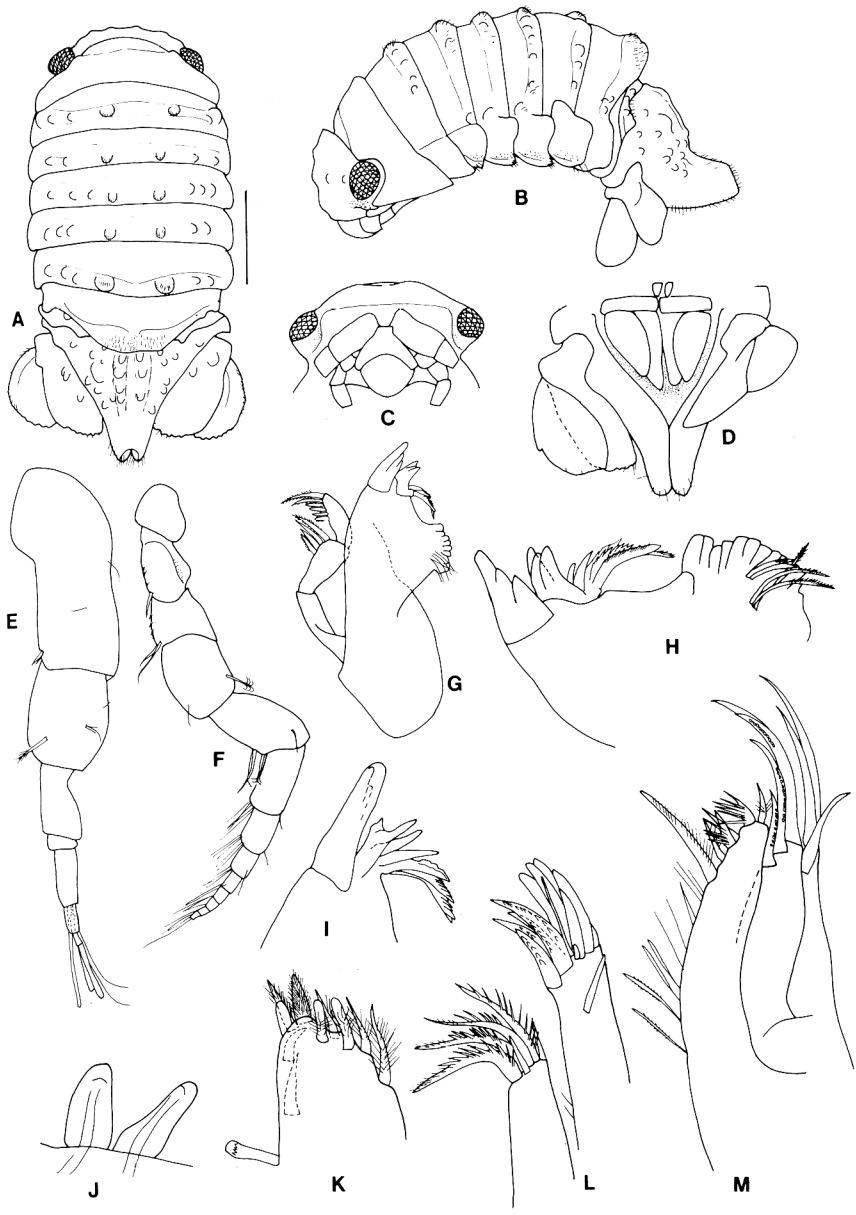

Fig. 6. *Cymodocella ambonota* sp. nov. A-D holotype, remainder male paratype 2.4 mm. A, dorsal view; B, lateral view; C, frons; D, pleon, ventral view; E, antennule; F, antenna; G, right mandible; H, right mandible, distal margin; I, left mandible; J, penes; K, maxilliped endite, distal margin; L, maxillule. Scale 0.5 mm.

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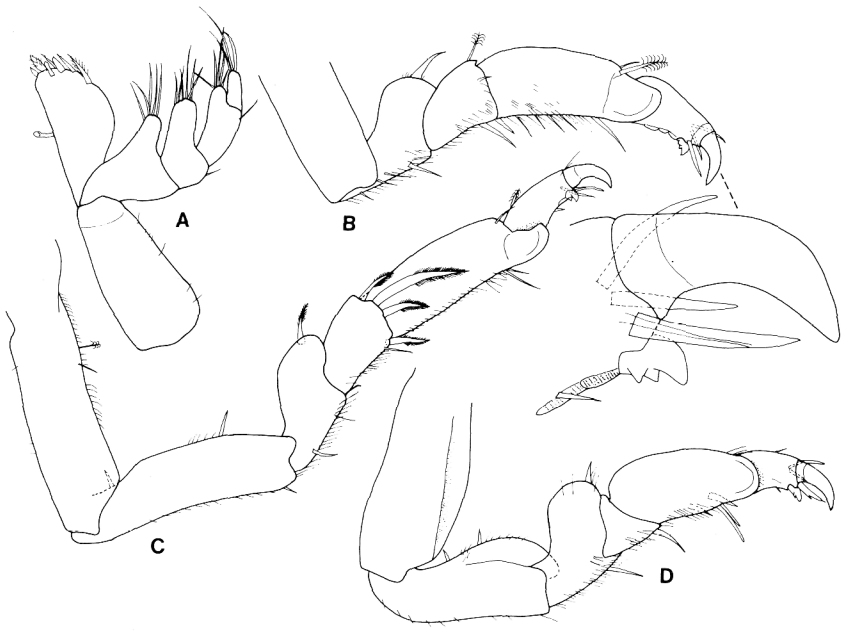

Fig. 7. *Cymodocella ambonota* sp. nov. All figs male paratype 2.4 mm. A, maxilliped; B, pereopod 2; C, pereopod 7; D, pereopod 1.

are distinctly longer than the remainder; antenna peduncle articles 4 and 5 longest, relatively stout, being respectively 1.25 and 1.64 as long as wide, article 4 about 0.9 as long as article 5.

Epistome about 0.6 as long as labrum, anterior margin quadrate. Mandible incisor multicuspid; left mandible with 3-cuspid lacinia mobilis; spine row with 6-8 spines; molar process with nodular ridged surface; palp article 2 with 4 stout biserrate spines, article 3 with 6. Maxillule as for type species. Maxilla lateral lobe with 3 spines, middle with 4; medial lobe with stout coarsely setulose spines. Maxilliped endite with 2 clubbed spines and 3 acute plumose spines on distal margin.

Pereopods all with 2 accessory cusps on secondary unguis. Pereopod 1 without stout or serrate spines on posterior margins; single spine at anterodistal angle of merus; posterior margins of merus, carpus and propodus with setulose fringe. Pereopods 2 and 3 similarly ornamented to pereopod 1. Pereopod 7 carpus with 4 prominent biserrate spines on distal margin.

Penes short, bluntly rounded, not reaching pleopod rami, about twice as long as basal width.

Pleopod 1 endopod with medial margin distinctly indurate; endopod shorter (0.76) than exopod, with distinct proximolateral point; exopod lateral margin sinuate; endopod and exopod with 5 and 6 PMS respectively. Pleopod 2

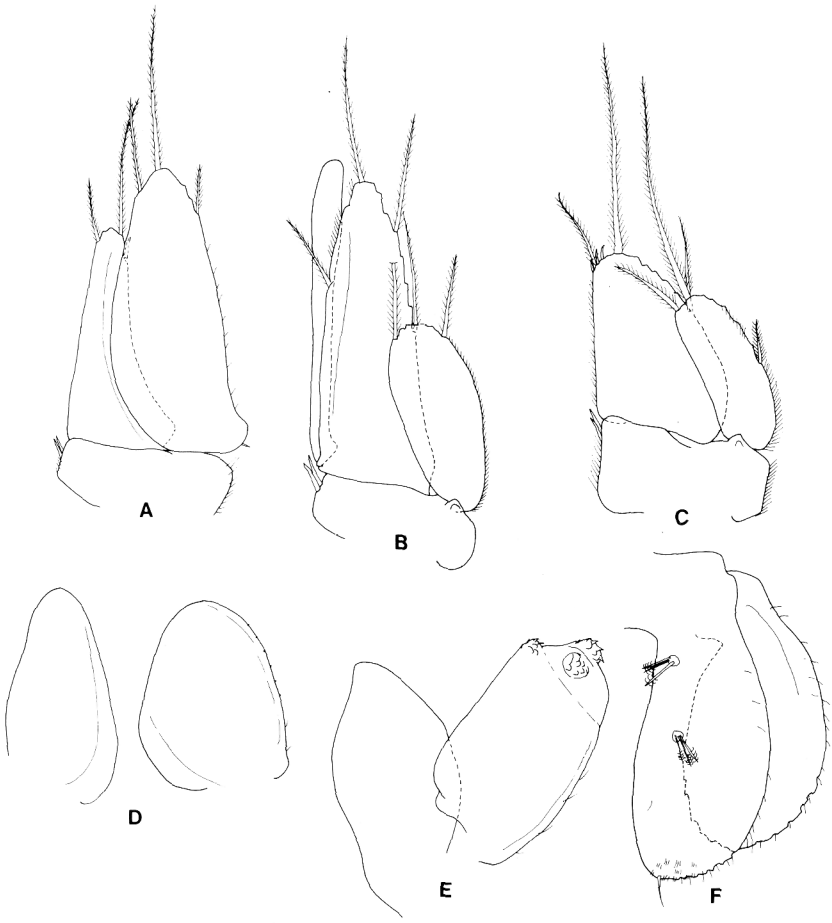

Fig. 8. *Cymodocella ambonota* sp. nov. All figs male paratype 2.4 mm. A-E, pleopods 1-5 respectively; F, uropod.

endopod manifestly longer (1.7) than endopod; appendix masculina arising sub-basally, extending slightly beyond distal margin of ramus, subequal in length to endopod, apex rounded; endopod and exopod with 11 and 6 PMS respectively. Pleopod 3 endopod with 3 short spines at distomedial angle; endopod and exopod each with 11 PMS. Pleopods 4 and 5 lamellar; pleopod 5 with indistinct transverse suture. Uropod exopod 0.86 as long as endopod; rami with margins weakly scalloped, distally rounded.

Female. Similar to the male.

Colour. Pale tan in alcohol.

Size. Adults are between 2.0 and 2.5 mm.

Remarks. Known only from two samples from the central New South Wales coast, this species presents little variation from the genus diagnosis. It is readily recognized by the prominently thickened coxal ridge, transverse nodular pereonal ridges, the presence of two submedial longitudinal nodular ridges on the pleotelson, and the broadly rounded lamellar uropod rami.

Distribution. Known only from the vicinity of Port Stephens, New South Wales, at a depth of 18 metres.

Etymology. The epithet is derived from the Greek words *ambon,* (ridge or crest) and *noton* (back), and alludes to the dorsal transverse ridges.

Cymodocella glabella, sp. nov.

Figs 9-12

Material Examined: Holotype. ♂ (3.9 mm), Old Gulch, Lord Howe Island, NSW, 31°33'S, 159°05'E, 17 May 1977, lower sides of lower littoral boulders, among algae, coll. G.D. Fenwick (AM P42553). Paratypes. 2 ♂ (3.4 dissected, 3.3 mm), 18 ♀ (ovig 4.6, 3.9, 3.7, 3.6, 3.5, 3.5, 3.5, 3.3, 3.1, non-ovig 3.6, 3.3, 3.3, 3.3, 3.0, 2.6, 2.6, 2.5, 2.3 mm), 18 mancas (1.5-2.3 mm), same data as holotype (AM P41394, 3 females ZMUC CRU316) .

Description

Male. Body about twice as long as wide, unornamented; lateral margins subparallel. Coxal sutures distinct; coxae of pereonite 6 largest, posteriorly overlapping those of pereonite 7. Pleon short, about 4-7% BL in lateral view; with anterolateral lacuna at position of coxae of pereonite 7. Pleotelson bidomed, dorsal surface smooth; pleotelsonic tube short, about 5 % BL, slightly upturned, ventrally entirely closed.

Antennule peduncle article 2 58% as long as article 1; article 3 about 86% as long as article 2; flagellum about 40% as long as peduncle, with 6 articles. Antenna flagellum 90% as long as peduncle, with 11 articles, becoming progressively shorter distally; antenna peduncle articles 4 about 0.66 as long as article 5.

Epistome about 0.7 as long as labrum, anterior margin quadrate. Mandible incisor with single acute cusp; lacinia mobilis and spine row absent; molar process reduced, unornamented; palp article 2 with 5 stout biserrate spines, article 3 with 10. Maxillule as for type species. Maxilla lateral lobe with 5 spines, middle with 5; medial lobe with stout, relatively short setulose spines. Maxilliped endite with 3 clubbed spines and 4 acute plumose spines on distal margin.

Pereopods all with 2 prominent accessory cusps on secondary unguis. Pereo-

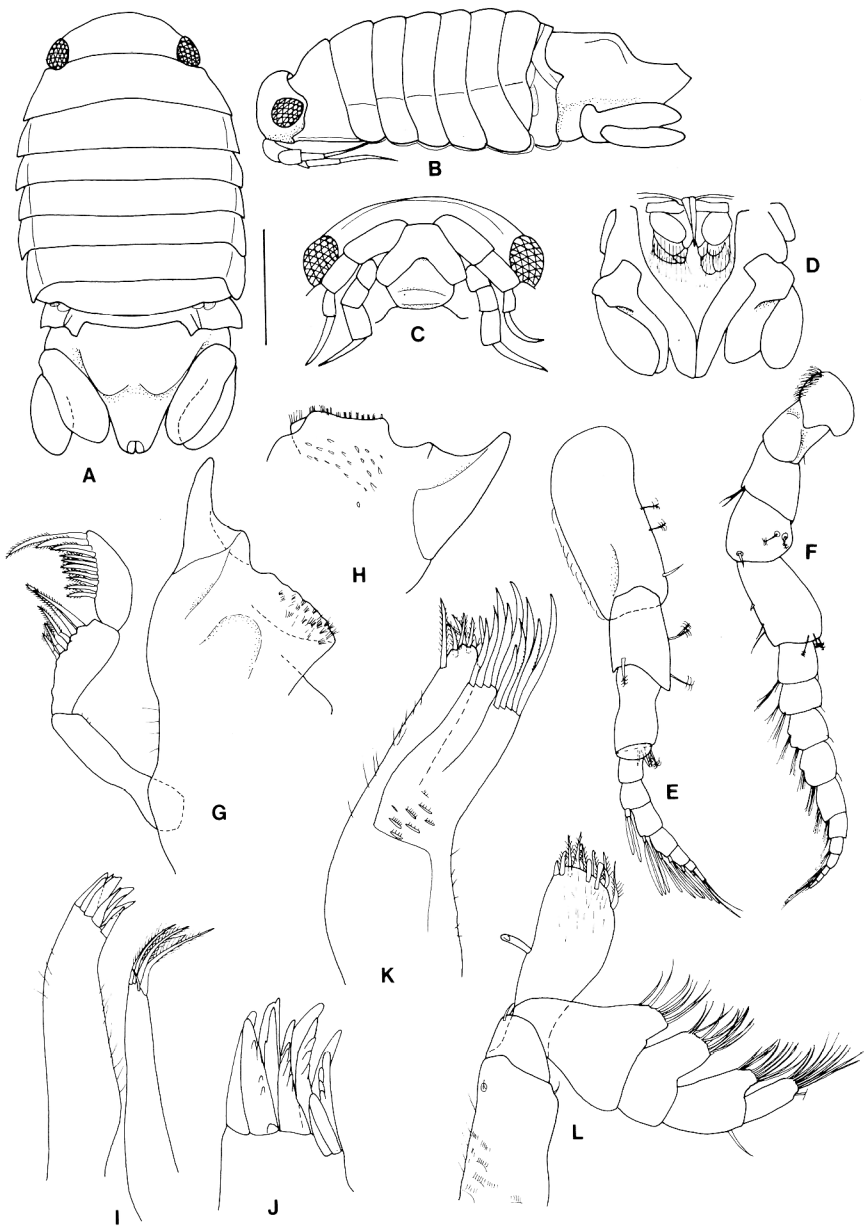

Fig. 9. *Cymodocella glabella* sp. nov. A-D holotype, remainder 3.4 mm male paratype. A, dorsal view; B, lateral view; C, frons; D, pleon, ventral view; E, antennule; F, antenna; G, right mandible; H, left mandible; I, maxillule; J, maxillule exopod, apex; K, maxilla; L, maxilliped. Scale 1.0 mm.

4670

Fig. 10. *Cymodocella glabella* sp. nov. All figs 3.4 mm male paratype. A, pereopod 1; B, pereopod 1, dactylus; C, pereopod 2; D, pereopod 6; E, pereopod 7; F, penes.

pod 1 with serrate spine at posterodistal margin of propodus; anterior margins without prominent spines; posterior margins of merus, carpus and propodus with setulose fringe. Pereopods 2 and 3 similarly ornamented to pereopod 1, but setulose fringe more strongly developed. Pereopod 7 carpus with 2 prominent biserrate spines on distal margin; ischium anterior margin with prominent flange.

Penes elongate, apex acute, about 4.6 times as long as basal width, extending to pleopod rami.

Pleopod 1 endopod with medial margin distinctly indurate, with dense covering of setules; endopod and exopod subequal in length; endopod with distinct proximolateral point; exopod lateral margin sinuate; endopod and exopod with 13 and 21 PMS respectively. Pleopod 2 endopod manifestly longer (1.6) than endopod; appendix masculina arising on proximally directed lobe, extending beyond distal margin of ramus, about 1.7 times as long as endopod, apex acuminate, acute; endopod and exopod with 16 and 13 PMS respectively.

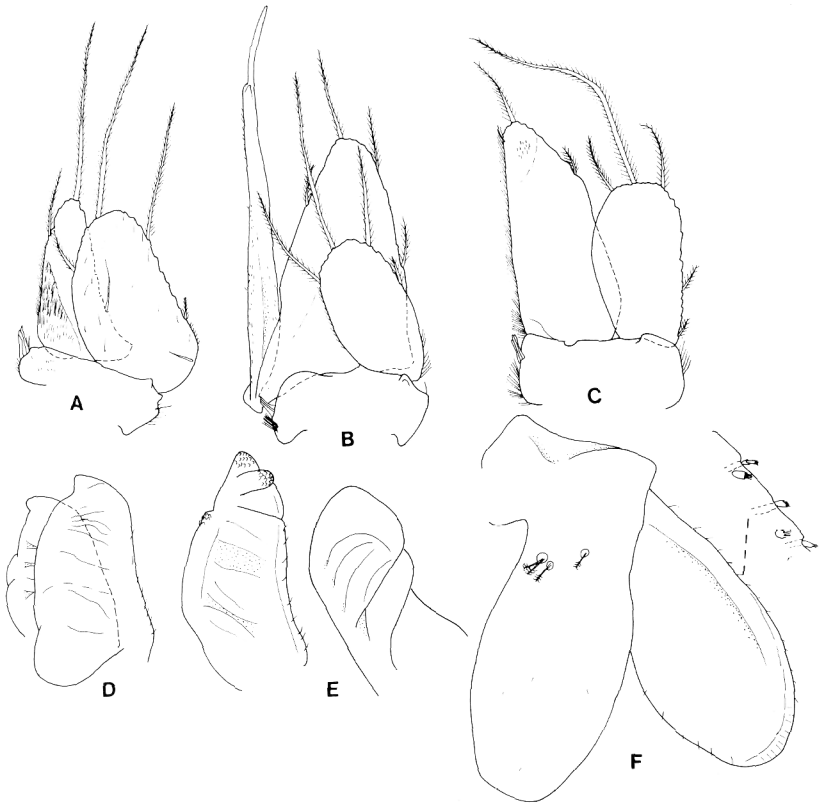

Fig. 11. *Cymodocella glabella* sp. nov. All figs 3.4 mm male paratype. A-E, pleopods 1-5 respectively; F, uropod.

Pleopod 3 endopod with cuticular setule patch at distomedial angle; endopod and exopod with 10 and 25 PMS respectively. Pleopods 4 and 5 with indistinct and weak ridges; pleopod 5 with incomplete transverse suture. Uropod exopod 0.81 as long as endopod; rami with margins smoothly rounded.

Female. Similar to the male.

Colour. Pale tan in alcohol.

Size. Adults measure between 2.3 and 4.6 mm; the largest manca was 2.3 mm.

Remarks. Known only from two samples from Lord Howe Island, *Cymodocella glabella* is easily identified by the lack of dorsal ornamentation. This species differs from the type species, and most other species currently placed in the genus, in having elongate penial processes, pleopod 1 rami subequal in length and an elongate appendix masculina borne on a proximomedial lobe. The mandible shows reduced states in having a unicuspid incisor, lacking a lacinia

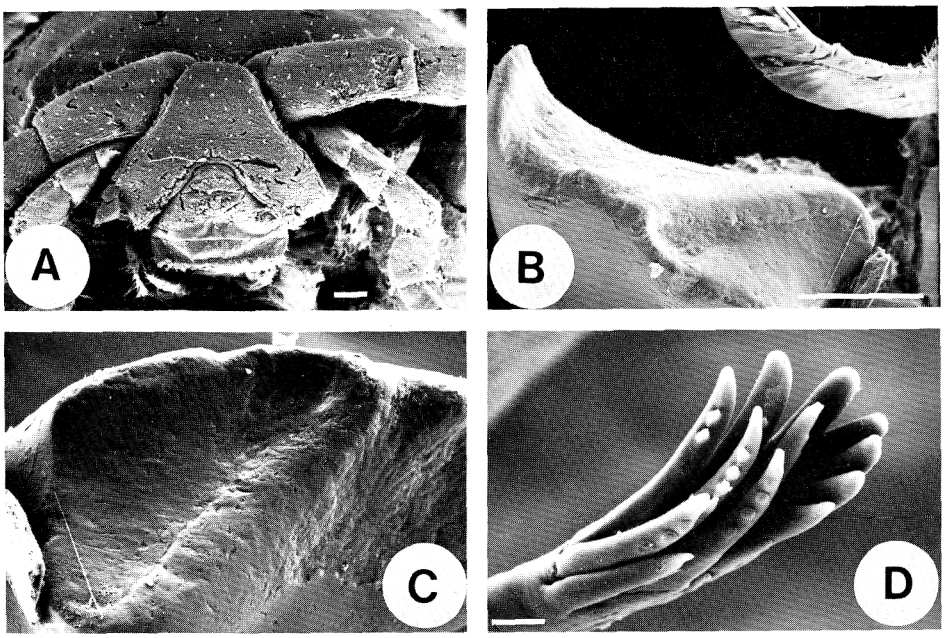

Fig. 12. *Cymodocella glabella* sp. nov. SEMs, appendages 4.6 mm ovig female paratype. A, frons (100μm); B, mandible, incisor at left of picture (100μm);C, molar process (10μm); D, maxillule lateral lobe, gnathal spines (10μm).

mobilis and spine row and in having the molar process flattened and unornamented. The penial and pleopod 2 characters are shared with the South African species *Cymodocella cancellata* Barnard, 1920 and *C. sublevis* Barnard, 1914, although *C. cancellata* differs in many other characters, including body ornamentation. Most South African species have pleopod 1 rami subequal in length.

Distribution. Known only from Lord Howe Island, New South Wales.

Etymology. The Latin word glabellus is the diminutive of glabra and refers to the lack of ornamentation.

Cymodocella ankylosauria sp. nov.

Figs 13-16

Material Examined: All material is from South Australia. Holotype. ♂ (4.9 mm), "The Hotspot" reef, 5 nautical miles west of north end of Flinders Island, 33°40.5'S, 134°22.0'E, 19 Apr 1985, 17 m, tufted bryozoa on exposed rock face, coll. G.C.B. Poore (NMV J36997). Paratypes. 2 ♂ (4.2 dissected, 4.0 mm), 2 ♀ (ovig 3.8, 3.5 mm), same data as holotype except: assorted brown,

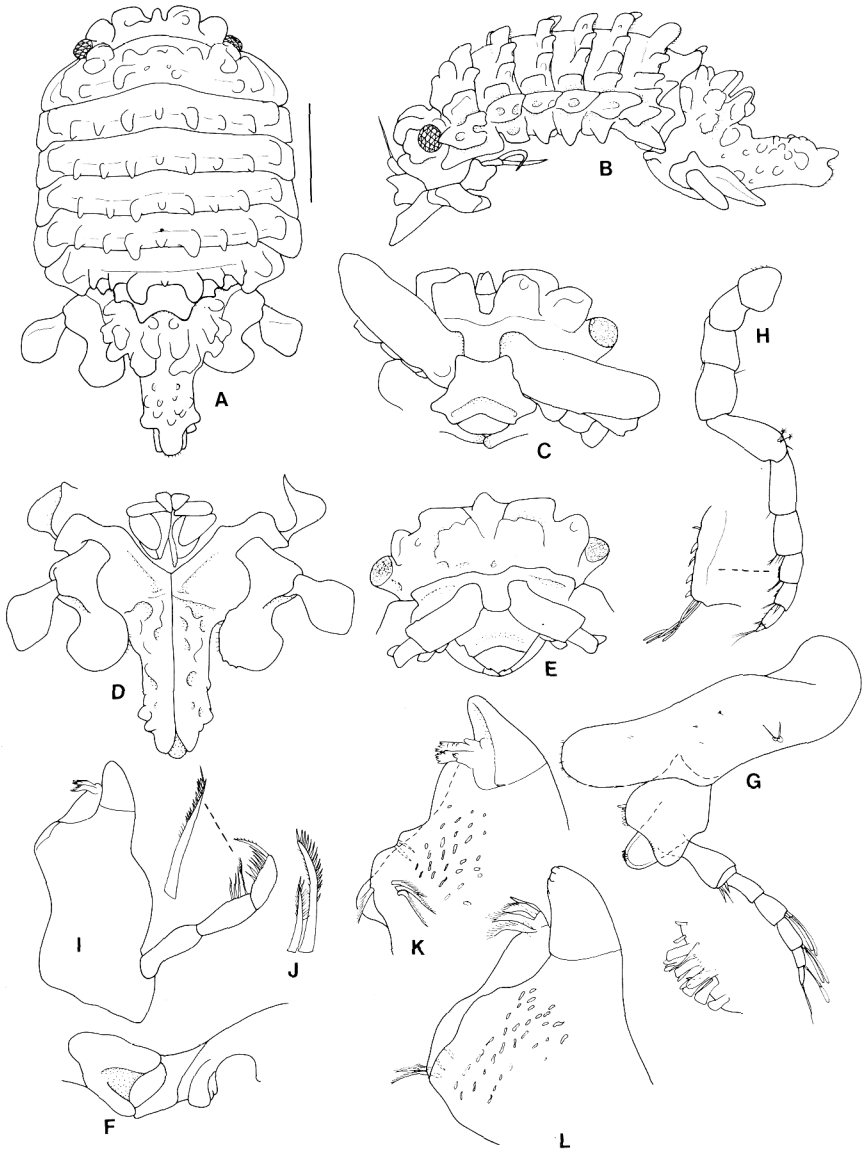

Fig. 13. *Cymodocella ankylosauria* sp. nov. A-D holotype; E, F female paratype NMV J36988; remainder male paratype NMV J36988. A, dorsal view; B, lateral view; C, frons; D, pleon, ventral view; E, frons, female; F, pleonites, lateral view; G, antennule; H, antenna; I, right mandible; J, spines, distal end of mandible palp article 3; K, left mandible; L, right mandible. Scale 1.0 mm.

4611

green and red algae, large forms, coll. S. Shepherd (NMV J36988; 1 male ZMUC CRU318). 2 ♀ (non-ovig 3.8, 3.2 mm), manca (1.6 mm), same data as

holotype except: tufted red algae on flat exposed rock face (NMV J36998). ♀ (ovig 4.4 mm), manca (1.5 mm), Pearson Island, in bay on east side, 33°57.3'S, 134°15.7'E, 17 Apr 1985, 10 m, algae in *Posidonia* meadow, coarse sand, coll. G.C.B. Poore (NMV J36987) . ♀ (ovig 5.3 mm), imm (3.4 mm), Stoke's Bay, northern coast of Kangaroo Is., 35°37'S, 137°12'E, 4 Mar 1978, 7 m, mixed algae, coll. I. Loch (AM P42558). ♂ (4.4 mm), Knobs Bluff, Kangaroo Island, 5 Mar 1978, 18 m, mixed algae on rocky bottom, coll I. Loch (AM P41142).

Description

Male. Body about 1.6 times as long as wide, lateral margins sub-parallel; surfaces ornamented and pitted. Cephalon with prominent ventral rostral process; anterior margin with distinct ridge; dorsal surface with several prominent bilaterally paired bosses, and 1 anterior median boss. Pereonite 1 nodular, with paired anterolateral bosses and 2 sublateral posteriorly directed bosses. Coxal sutures indistinct; coxae with dorsal prominent posteriorly acute boss, ventrally with an acute process; pereonites 2-7 each with 8 prominent posteriorly acute tubercles on posterior margin, these forming longitudinal rows; 2 submedial tubercles largest. Pereonite 7 lateral margins largely concealed by coxae of pereonite 6. Pleon largely concealed by pereonite 7, only posterolateral angles visible in lateral view. Pleotelson with paired bimedian processes, and several other smaller paired bosses; tube straight, elongate, about 20 % BL, ventrally entirely closed, opening posteriorly.

Antennule peduncle article 2 60 % as long as article 1; article 3 about 83 % as long as article 2; flagellum about 34% as long as peduncle, with 5 articles; peduncle article 1 anterodistal angle produced into prominent lobe about half as long as article 1; peduncle article 2 with rounded anterior dorsal lobe and ventral anterodistal lobe. Antenna flagellum 56% as long as peduncle, with 5 articles, articles becoming progressively shorter distally; antenna peduncle article 4 about 0.68 as long as article 5.

Epistome about as long as labrum, anterior margin quadrate. Mandible incisor with single blunt cusp; lacinia mobilis absent; spine row with 3-4 spines; molar process reduced, unornamented, unkeratinized; palp article 2 with 4 stout biserrate spines, article 3 with 8. Maxillule as for type species. Maxilla lateral lobe with 5 spines, middle with 5; medial lobe with relatively slender setulose spines. Maxilliped endite with 3 clubbed spines and 4 acute plumose spines on distal margin.

Pereopods lacking accessory cusps on secondary unguis. Pereopod 1 with serrate spine at posterodistal margin of propodus; anterior margins without prominent spines; anterior margin of ischium with setulose fringe; posterior margins of merus, carpus and propodus with teeth like cuticular scales, setule fringe absent; anterior margin of ischium and merus produced, forming rounded lobe. Pereopods 2 and 3 similarly ornamented to pereopod 1, but set-

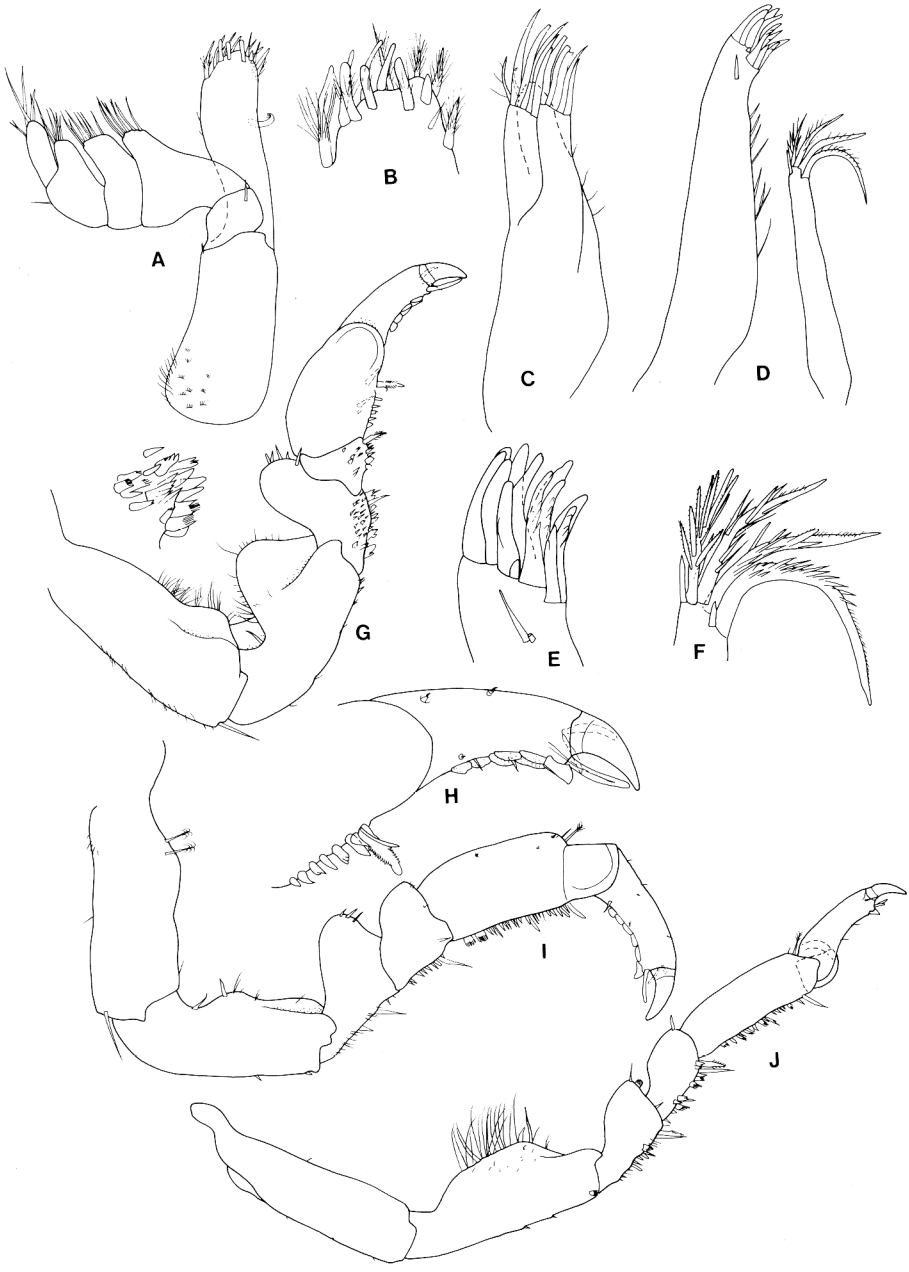

Fig. 14. *Cymodocella ankylosauria* sp. nov. All figs of male paratype NMV J36988. A, maxilliped; B, maxilliped endite, distal margin; C, maxilla; D, maxillule; E, maxillule exopod apex; F, maxillule endopod apex; G, pereopod 1; H, pereopod 1, dactylus; I, pereopod 2; J, pereopod 7.

ulose fringe more present on posterior margins of merus and carpus. Pereopod 7 carpus with 1 biserrate spine at posterodistal angle; ischium anterior margin with setulose fringe.

Penes short, apex bluntly rounded, about 3 times as long as basal width, not extending to pleopod rami.

Pleopod 1 endopod with medial margin indistinctly indurate, with dense covering of setules; endopod shorter (0.78) than exopod in length; endopod without distinct proximolateral point; exopod lateral margin straight; endopod and exopod with 3 and 2 PMS respectively. Pleopod 2 endopod manifestly longer (1.2) than endopod; appendix masculina arising sub-basally, extending beyond distal margin of ramus, about 1.2 times as long as endopod, apex dilated, broadly rounded; endopod and exopod with 8 and 18 PMS respectively. Pleopod 3 endopod distally truncate; endopod and exopod with 10 and 15 PMS respectively. Pleopods 4 and 5 with indistinct ridges; pleopod 5 with complete transverse suture. Uropod exopod about 0.6 as long as exopod, ovate in shape, articulating freely from endopod; endopod with prominent medial indentation on lateral margin, distal margin widely rounded; dorsal surface with 2-3 nodules.

Female. Similar to the male, with the exception of the antennule peduncle which lack the flanged processes present in the mature males.

Colour. Pale tan in alcohol, chromatophores not apparent.

Size. Males measured between 4.0 and 4.9 mm, females 3.2 to 4.4 mm.

Variation. In some specimens the dorsal tubercles and bosses are reduced, and are eroded in appearance.

Remarks. The highly ornate dorsal armature immediately separates *Cymodocella ankylosauria* from all other congeners, and also all other sphaeromatids. The South African species *C. cancellata* is similarly ornate, but the dorsal pereonal tubercles are far smaller, and the pleotelson has only two prominent acute processes; additionally the uropods are distinct, the South African species having a narrowly rounded exopod and truncate exopod.

The lack of accessory cusps on the secondary unguis of the pereopods is remarkable. This character state is shown by all genera and species in what can be termed the *Ischyromene*-group of genera, and is one of the defining apomorphies for that group. The mandible of *C. ankylosauria* shows several reductions, having a unicuspid incisor, lacking the lacinia mobilis and molar process, and having a reduced spine row of only 3 to 4 spines. The pleonal sternite is present, but in a very reduced state. The lateral margin of pleopod 1 endopod is not distinctly thickened, but pleopod 2 is similar to that shown by others of the genus. The uropod rami, with the distinctly separate (non-overlapping) articulation of the exopod is also unique. All these characters suggest that *C.*

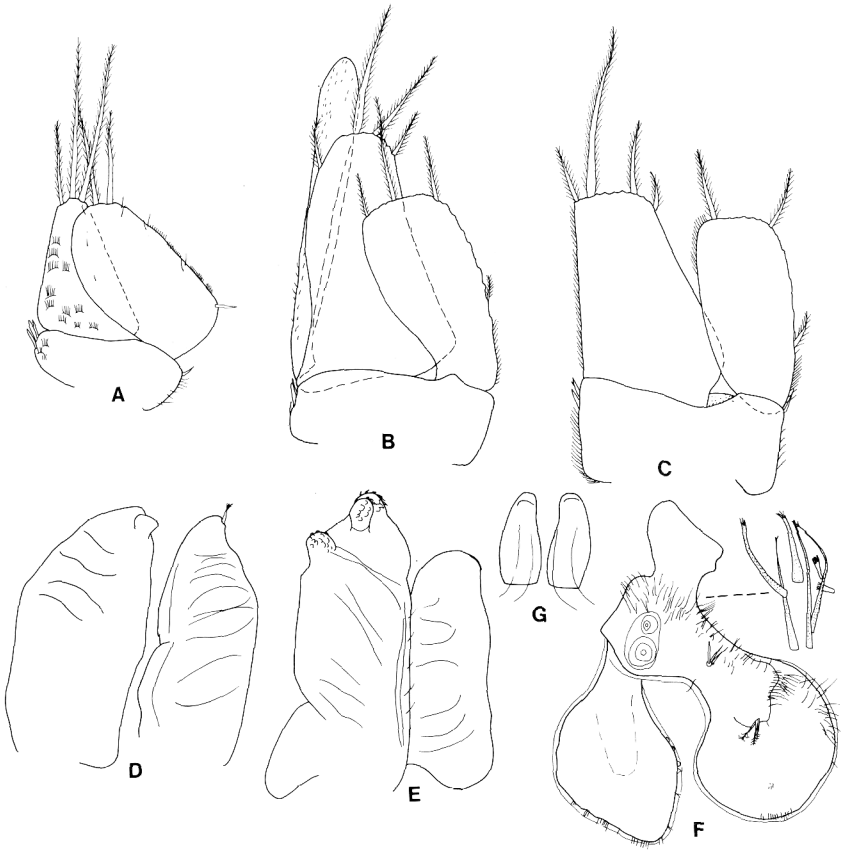

Fig. 15. *Cymodocella ankylosauria* sp. nov. All figs of male paratype NMV J36988. A-E, pleopods 1-5 respectively; F, uropod; G, penes.

ankylosauria occupies a place apart within the genus, and that the species should be regarded as incertae sedis.

Distribution. Known only from islands off the coast of South Australia.

Etymology. The epithet is taken from the dinosaurs known as ankylosaurs, in reference to the heavily "armoured" back of this species.

Genus *Diclidocella* gen. nov.

Type species: *Diclidocella bullata* sp. nov., here designated.

Description

Male. Body dorsally strongly vaulted, smooth or ornamented. Cephalon with

rostral process in ventral position; eyes lateral, round, facets distinct. Pereonite 1 longest, 2-6 subequal in length; pereonite 7 narrower than lateral body margins, dorsal posterior margin weakly or not produced. Pleon with 4 segments, segment 1 entire, 2 separate sutures running to posterior margin of pleon. Pleotelson strongly vaulted, indistinctly bidomed; posteriorly formed into ventrally closed tube, aperture of which opens posteriorly; tube extends beyond posterior of uropod rami. Pereonite 1 without sternal extensions; narrow pleonal sternite and sternal process present.

Epistome short, about half as long or less than labrum; not anteriorly produced, not separating antennule bases. Antennule peduncle 4-articled, article 1 longest; article 2 greater than 40% length of article 1, article 3 as long as or shorter than article 2, articulating in ventral or posteroventral position; article 2 with short anterodistal lobe, article 3 positioned subterminally on posterior margin; flagellum shorter than peduncle. Antenna peduncle slender, articles 1-3 short, 5 longest; flagellum about equal in length to peduncle. Mandible incisor 1- to 5-cuspid; left mandible with prominent 3-cuspid lacinia mobilis, or lacinia mobilis absent, spine row prominent, with serrate and plumose spines; molar process prominent keratinized, with nodular crushing surface or smooth. Maxillule medial lobe with 3-4 slender long fringed or plumose spines and 2 short simple acute spines; lateral lobe with about 13 spines on gnathal surface, medial group of which are pectinate. Maxilla entire, setae on lateral and middle lobes smooth or weakly anteriorly pectinate. Maxilliped palp articles 2-4 medial margins with prominent medial lobes, lobes of articles 3 and 4 between 1 and 2 times as long as distal articulating margin; endite distal margin subtruncate, with stout clubbed and plumose sinuate spines, and smooth spine at distomesial angle.

Pereopods all ambulatory, 1 shorter and stouter than 3-7 which are all subsimilar; pereopod 2 markedly more slender than other pereopods; dactylus posterior margin with cuticular scales; accessory unguis with 2 secondary cusps; posterior margins of ischium to propodus with weak setule fringe; pereopods 6 and 7 usually with biserrate spines on distal margin of carpus.

Penes separate, short, close set; not extending to pleopod peduncles.

Pleopod 1 operculate; exopod lateral margin convex; endopod distinctly shorter than exopod. Pleopod 2 exopod distinctly shorter than endopod; appendix masculina basal in position, extending beyond distal margin of endopod. Pleopod 3 exopod distinctly shorter than endopod, without transverse suture. Pleopods 4 and 5 with ridges weakly to well developed; exopod of pleopod 4 without transverse suture; exopod of pleopod 5 with transverse suture, with 3 scale patches. Uropod rami not extending beyond posterior margin of pleotelson; both rami lamellar, exopod about half to subequal in length to endopod, articulating in ventrolateral position.

Female. Similar to the male; mouthparts not metamorphosed; brood pouch

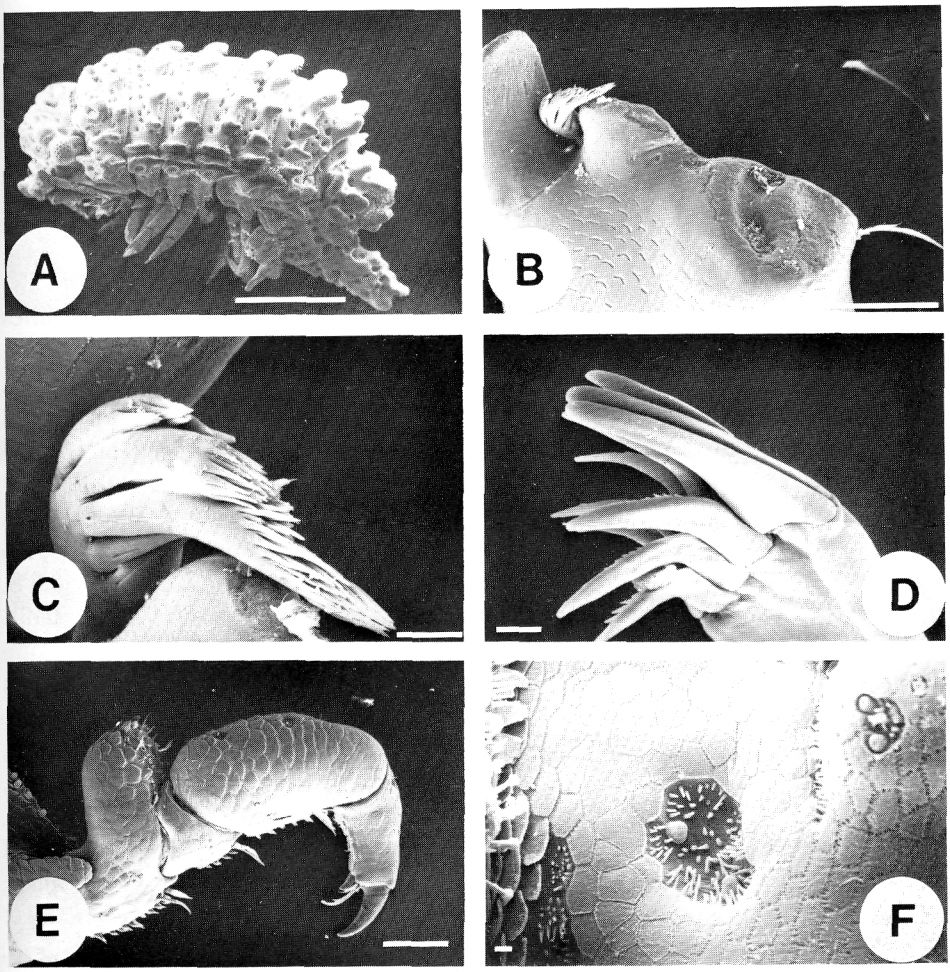

Fig. 16. *Cymodocella ankylosauria* sp. nov. SEMs, 3.5 mm, female paratype NMV J36988. A, lateral view (1 mm); B, mandible (100μm); C, mandibular spine row (10μm); D, maxillule lateral lobe spines (10μm); E, pereopod 1 (100μm); F, lateral cuticle, pereonite 4, showing pit (10μm).

consisting of large overlapping oostegites arising from the coxae of pereonites 2-4, and posterior pocket opening anteriorly at pereonite 4.

Remarks. The genus is readily separated from others of the *Ischyromene*-group by the combinations of antennule peduncle third article being posteriorly offset from the second article, a slender second pereopod, presence of operculate pleopods and pleotelsonic tube in combination with a very short epistome. Of these characters only the pleotelsonic tube is shared with *Cymodocella*.

Etymology. The name is obtained from the Greek diklidos meaning double-fold-

ing doors, in combination with the ending -cella, indicating the affinity to *Cymodocella.*

Species included: Diclidocella bullata sp. nov.; *Diclidocella yackatoon* sp. nov., *Diclidocella ngake* sp. nov.

Diclidocella bullata sp. nov.

Figs 17-19

Material Examined. Holotype. ♂ (2.3 mm), "The Hotspot" reef, 5 nautical miles west of north end of Flinders Island, 33°44.5'S, 134°22.0'E, 19 Apr 1985, 12 m, assorted brown and red algae, coll. S. Shepherd (NMV J36991). Paratypes. **South Australia:** 10 ♂ (1.8- 2.3 mm, mean 2.01 mm), 8 ♀ (6 ovig 2.0-2.5 mm, mean 2.22 mm, non-ovig 1.8 mm), 2 mancas (1.0, 1.1 mm), same data as holotype (NMV J36994(♀), J36995(♂); 3 ♂, 3 ♀ ZMUC CRU313). 2 ♂ (2.0, 1.9 mm), 2 ♀ (2.2, 2.1 mm), manca (1.0 mm), same data as holotype except: 17 m (NMV exJ26187). ♂ (2.0 mm), imm ♂ (1.5 mm), 2 females (non-ovig 2.0, 1.6 mm), 3 mancas (0.9, 1.0, 1.0 mm), same data as holotype except: 33°40.8'S, 134°22.5'E, 20 Apr 1985, large red algae, coll. G.C.B. Poore (NMV exJ26049). ♂ (2.8 mm), 2 ♀ (ovig 2.3, 2.2 mm), imm (1.5 mm), southeastern Cape Thomas, between Godfrey Islands, 16 Feb 1989, 3-6 m, soft rock, algae, sand; from red algae, coll. W. Zeidler and K. Gowlett-Holmes (SAM C5590, C5592). **Western Australia:** ♀ (ovig 2.0 mm), Israelite Bay, north of Point Dempster, 33°37'S, 123°52.2'E, 10 Apr 1984, 3 m, *Posidonia* epiphytes, coll. G.C.B. Poore and H. M. Lew Ton (NMV J36989, J36992). 6 ♂ (1.5-2.1 mm), 4 ♀ (ovig 1.9, 2.0, 2.3, non-ovig 2.0 mm), 2 mancas (0.9, 1.0 mm), Mississippi Bay, 48 km east of Esperance, 34°00'S, 122° 17'E, Jan 1972, 2 m, exposed head at west end of bay, mixed algae, coll. W.F. Ponder and J. M. Ponder (AM P42554). **Tasmania:** 2 ♂ (2.2, 2.3 mm), 1 immature damaged, Waterhouse Point, 24 Apr 1992, 5 m, *Amphibolis antarctica,* coll. G. Edgar (NMV J36966).

Description

Male. Body about 1.6 times as long as wide, cuticle smooth; lateral margins irregular. Cephalon anteriorly with 2 rounded bosses. Pereonite 1 with paired lateral boss and large anterior submedial bilobed boss. Pereonite 2 with 2 small lateral bosses, pereonites 3 and 4 unornamented, pereonite 5 and 6 with paired lateral submedial and coxal bosses, pereonite 7 posterior dorsal margin produced into medially indented lobe. Coxal sutures indistinct; coxal margins of pereonites 3 and 4 short, those of pereonite 7 not extending to lateral margin of pereonite 6, but not overlapped by 6. Pleon short, about 4-5 % BL. Pleotelson with 2 submedial prominent bosses; telsonic tube long, about 23% BL, straight, ventrally entirely closed.

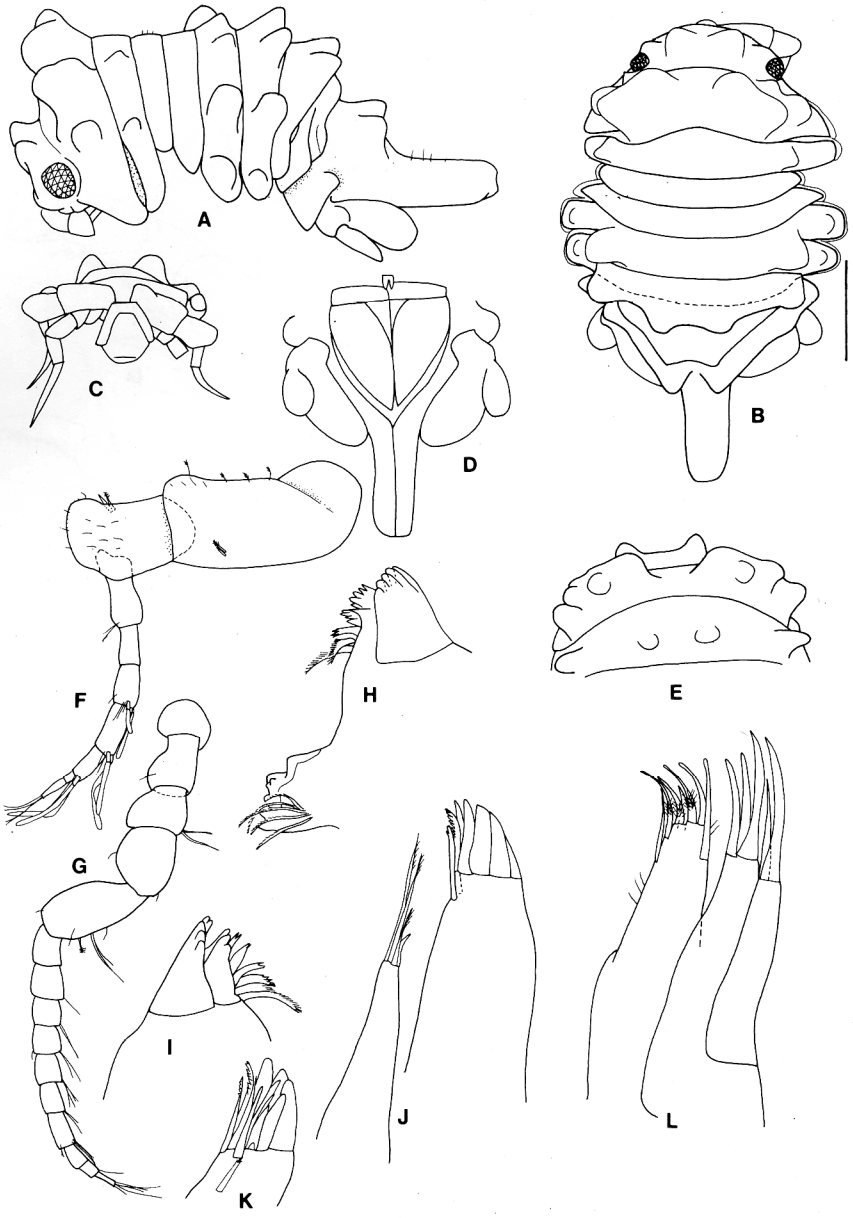

Fig. 17. *Diclidocella bullata* sp. nov. A-D holotype; E, 2.5 mm ovig female, NMV J36994, F, G, 2.3 mm male and H-L 2.2 mm male paratypes, NMV J36995. A, lateral view; B, dorsal view; C, frons; D, pleon, ventral view; E, anterior, female; F, antennule; G, antenna; H, right mandible; I, left mandible; J, maxillule; K, maxillule exopod, apex; L, maxilla. Scale 0.5 mm.

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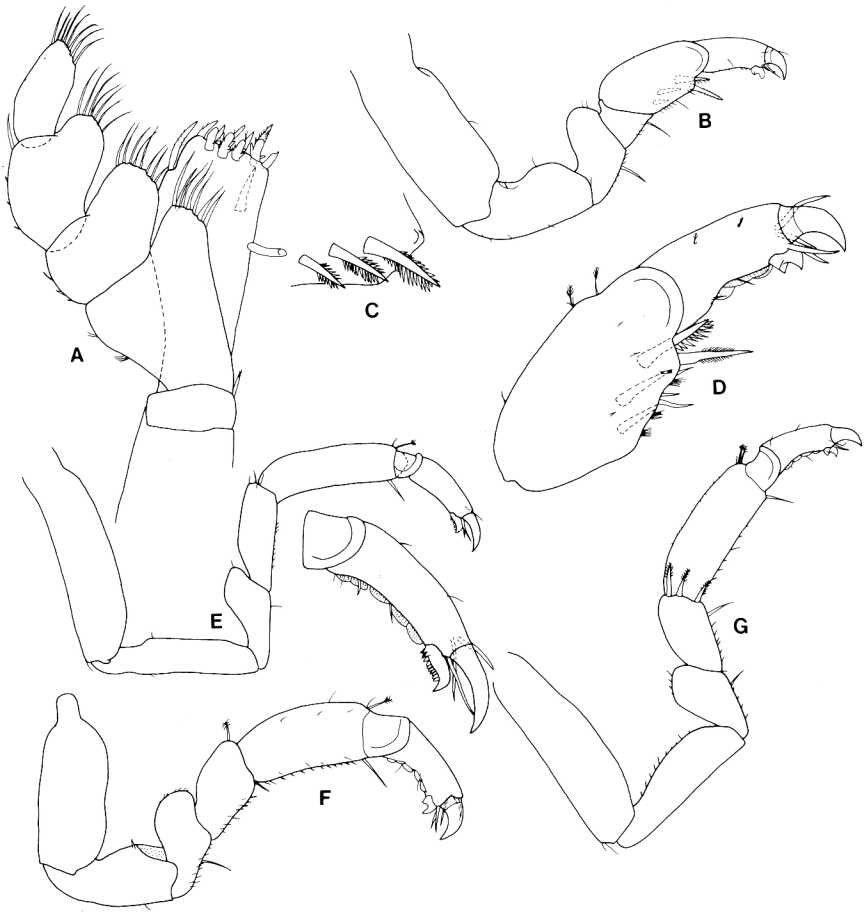

Fig. 18. *Diclidocella bullata* sp. nov. All 2.2 mm male paratype NMV J36995. A, maxilliped; B, pereopod 1; C, pereopod 1, propodus and dactylus; D, pereopod 2; E, pereopod 3; F, pereopod 7. G, pereopod 7.

Antennule peduncle article 2 66% as long as article 1; article 3 about 70% as long as article 2; article 2 with anterodistal margin weakly lobate; flagellum about 23% as long as peduncle, with 2 articles: Antenna flagellum about (0.94) as long as peduncle, with 11 articles; antenna peduncle articles 4 and 5 longest, arcticle 4 relatively short, about 1.2 times as long as wide, article 5 being 1.4 times as long as article 4 .

Epistome about 0.25 as long as labrum. Mandible incisor 5-cuspid; left mandible with 3-cuspid lacinia mobilis, right mandible with conspicuous lacinoid spine; spine row with about 6 spines; molar process narrow, projecting, with nodular ridged surface; palp article 2 with 4 stout biserrate spines, article 3 with 6. Maxillule medial lobe with 3 long and 1 short slender feebly plumose

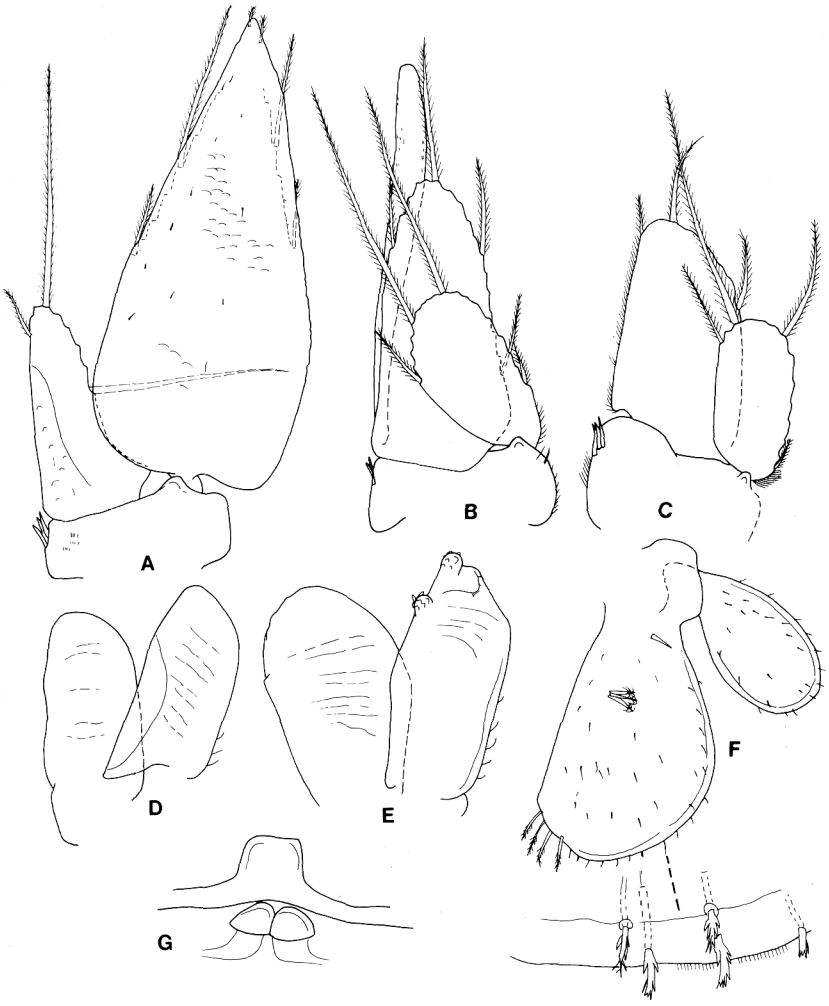

Fig. 19. *Diclidocella bullata* sp. nov. All 2.2 mm male paratype NMV ex J26184. A-E, pleopods 1-5 respectively; F, uropod; G, penes and sternal process.

spines; lateral lobe with lateralmost spines broad based and closely spaced, only 1 pectinate spine present. Maxilla lateral lobe with 2 spines, middle with 3, all spines being unornamented; medial lobe with slender terminally blunt setulose spines. Maxilliped endite with 4 clubbed spines and 5 acute plumose spines on distal margin.

Pereopods all with 2 accessory cusps on secondary unguis. Pereopod 1 with stout serrate spines on posterodistal and medial margins of propodus, posterior margin of merus and carpus each with single stout simple seta; setulose fringe absent. Pereopods 2 and 3 similarly ornamented to pereopod 1. Pereo-

pod 2 without spines; accessory unguis prominently pectinate. Pereopod 7 carpus with 3 prominent biserrate spines on distal margin.

Penes very short, bluntly rounded, not reaching pleonal sternite, about 0.84 as long as basal width.

Pleopod 1 endopod with medial margin distinctly indurate; endopod distinctly shorter (0.45) than exopod, with distinct proximolateral point; exopod margins converging to acute apex; endopod and exopod with 9 and 14 PMS respectively, those of exopod positioned submarginally on dorsal side. Pleopod 2 endopod manifestly longer (1.75) than endopod; appendix masculina arising sub-basally, extending beyond distal margin of ramus by about 0.3 of its length, about 1.3 as long as endopod, apex rounded; endopod and exopod with 16 and 17 PMS respectively. Pleopod 3 endopod and exopod with 9 and 14 PMS respectively. Pleopods 4 and 5 with very weakly developed ridges; pleopod 5 with indistinct transverse suture. Uropod exopod about 0.55 as long as endopod, distal margins both smoothly rounded.

Female. Similar to the male, except that the anterior sublateral bosses are wider and trilobate rather than bilobate. Females may be reliably identified as such using this character.

Colour. Pale in alcohol, with dark brown patches.

Size. Adults 1.5-2.8 mm; a little more than 20% of the total body length is accounted for by the long telsonic tube, which makes this species one of the smallest sphaeromatids known, with an adult body length usually of less than 2 mm.

Remarks. This very small species can at once be identified by the operculate rami of pleopod 1, in conjunction with the long telsonic tube and the pereonal ornamentation. The only other species placed in the genus *D. yackatoon* sp. nov. and *D. ngake* sp. nov., have a very short telsonic tube, and unornamented body surfaces, and are also far larger.

Distribution. From Tasmania and the central coast of South Australia (134°E) to the central southern coast of Western Australia (122°E); at depths of 3 to 17 m, mostly recorded from algae.

Etymology. The epithet is derived from the Latin word bulla meaning knob or boss, and alludes to the prominent dorsal bosses.

Diclidocella yackatoon sp. nov.

Figs 20-23

Material Examined. Holotype. ♂ (4.5 mm), near 'Map of Australia' reef, east side of Cape Northumberland, 38°03.8'S, 140°39.5'E, 16 May 1990, 2 m, coral-

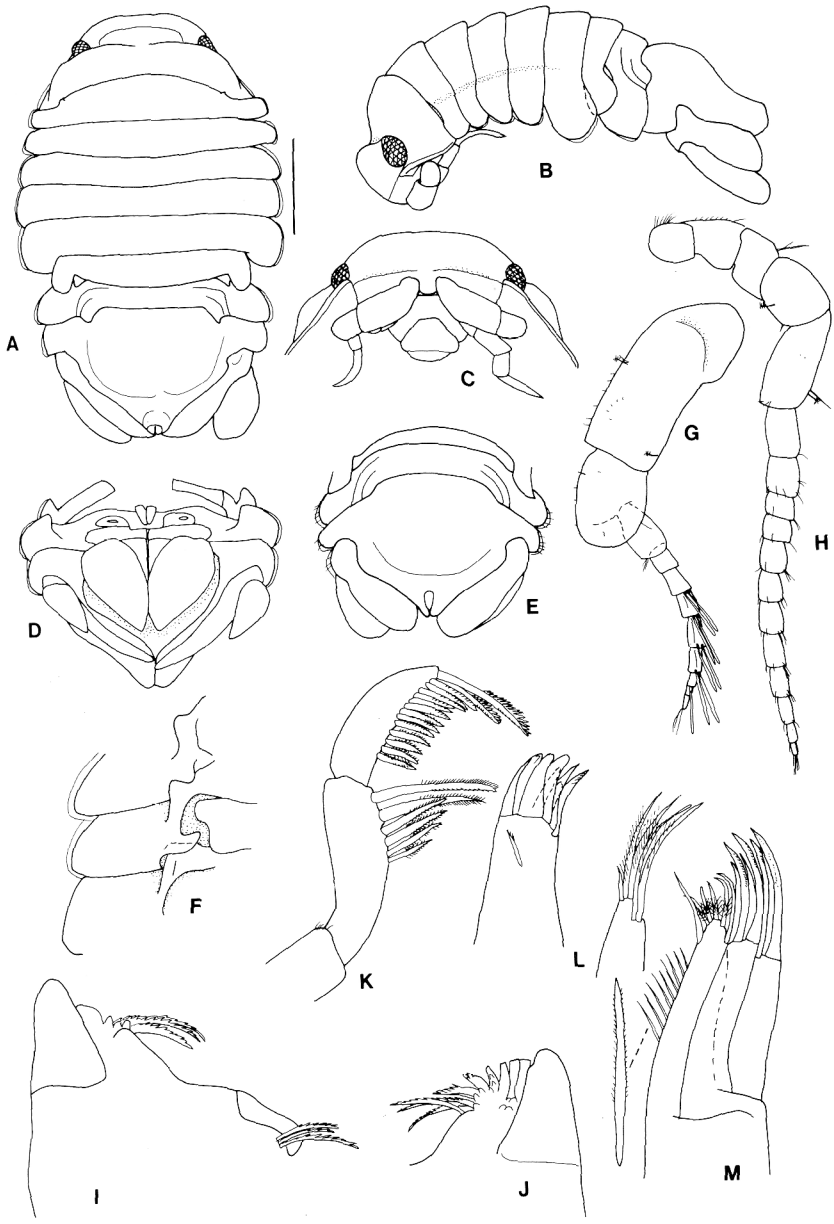

Fig. 20. *Diclidocella yackatoon* sp. nov. A-D holotype, E, F, 3.5 mm ovig female paratype, remainder 3.8 mm male paratype, NMV J34068. A, dorsal view; B, lateral view; C, frons; D, pleon, ventral view; E, pleon and pleotelson, female; F, coxae 4 and 5, ventral view; G, antennule; H, antenna; I, right mandible; J, left mandible; K, mandibular palp; L, maxillule; K, maxillule exopod, apex; M, maxilla. Scale 1.0 mm.

line algal turf on limestone reef, coll G.C. B. Poore and R. S. Wilson (NMV J36990). Paratypes. **South Australia:** ♂ (3.8 mm), 5 ♀ (ovig 3.3, 3.5 non-ovig 2.8, 3.0, 3.5 mm), 2 mancas (1.3, 2.3 mm), same data as holotype (NMV J34068, 1 female ZMUC CRU315). ♂ (3.9 mm), 2 ♀ (non-ovig 2.3, 2.8 mm), 4 mancas (2.0-2.5 mm), Middle point, near Cape Northumberland, 38°45'S, 140°58'E, 19 Mar 1974, 6 m, on brown algae, 600 metres from shore, coll S. Shepherd (AM P41144). 5 ♀ (ovig 3.6, 3.8, non-ovig 3.5, 3.9 mm + 1 broken), "The Hotspot" reef, 5 nautical miles west of north end of Flinders Island, 33°44.5'S, 134°22.0'E, 19 Apr 1985, 12 m, assorted brown, green and red algae, large forms, coll. S.A. Shepherd (NMV J36996). **Victoria:** ♂ (4.5 mm), 2 ♀ (ovig 3.6, 3.9 mm), east side of South Point, Twin Reefs, 38°41'S, 145°39'E, 4 Mar 1982, 11 m, rocky, coll. C. Larsen, G. Barber and R.S. Wilson (NMV J34055). ♂ (4.3 mm), 2 ♀ (non-ovig 3.5, 3.9 mm broken), 2 mancas (1.7, 1.6 mm), Henty Reef, Apollo Bay, 38°47.0'S, 143°40.5'E, 25 Apr 1988, 4.5 m, algae, coll. R.T. Springthorpe and P.B. Berents (AM P41348).

Additional material. 2 ♂ (3.5, 4.2 mm), Point Lonsdale, Port Phillip Bay, Vic., 38°18.0'S, 143°37.0'E, 5 Mar 1991, 0 m, pool on western rock platform, red and brown algae, *Caulerpa,* coll. G.C.B. Poore (NMV J26410, J26407).

Description

Male. Body about 1.6 times as long as wide, unornamented, cuticle smooth; widest at pereonite 6, lateral margins weakly ovate; gel-layer present on coxal and pereonal margins. Coxal sutures indistinct, coxae of pereonites 2-4 shorter than those of 5 and 6; coxae of pereonite 7 not extending to lateral margin of pereonite 6, but not overlapped by 6. Pleon about 10% BL in lateral view. Pleotelson dorsally weakly bidomed; telsonic tube short, about 5 % BL, opening posteriorly.

Antennule peduncle article 2 47% as long as article 1; article 3 about 66% as long as article 2; article 2 with anterodistal margin weakly lobate; flagellum about 56% as long as peduncle, with 8 articles, article 4 longest. Antenna flagellum longer than (1.3) peduncle, with 12 articles, article 1 of which is longest; antenna peduncle articles 4 and 5 longest, article 4 relatively short, about 1.3 times as long as wide, article 5 being 1.3 times as long as article 4 .

Epistome about 0.57 as long as labrum, anterior margin truncate. Mandible incisor unicuspid, blunt; left mandible without distinct lacinia mobilis; spine row with about 6-9 spines, proximal spines being smooth and terminally truncate; molar process keratinized, smooth; palp article 2 with 6 stout biserrate spines, article 3 with 15. Maxillule medial lobe with 4 long feebly plumose spines; lateral lobe with lateralmost spines broad based and closely spaced, only 1 pectinate spine present. Maxilla lateral lobe with 3 spines, middle with 4, all spines being finely serrate; medial lobe with slender terminally blunt set-

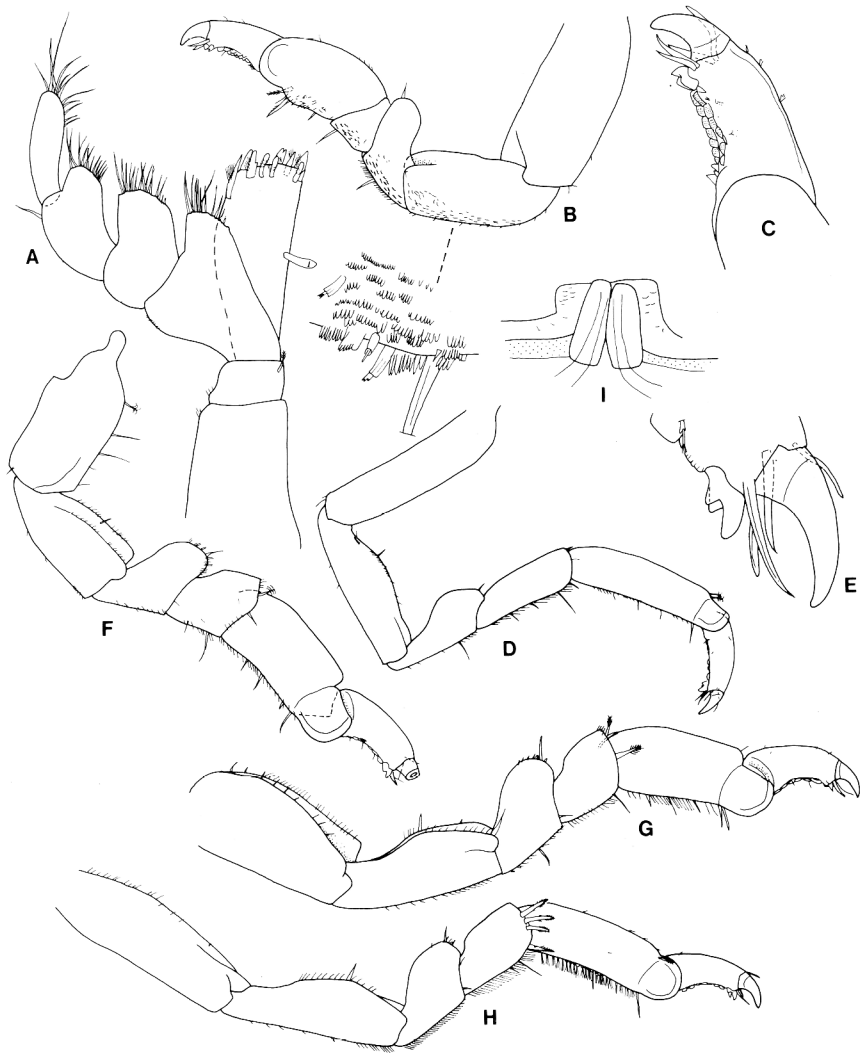

Fig. 21. *Diclidocella yackatoon* sp. nov. All figs 3.8 mm male paratype, NMV J34068. A, maxilliped; B, pereopod 1; C, pereopod 1, dactylus; D, pereopod 2; E, pereopod 2, dactylus apex; F, pereopod 3; G, pereopod 6; H, pereopod 7. I, penial process.

ulose spines. Maxilliped endite with 4 clubbed spines and 6 acute plumose spines on distal margin.

Pereopods all with 2 prominent accessory cusps on secondary unguis. Pereopod 1 with stout serrate spine on posterodistal margins of propodus, posterior margin of merus and carpus each with single stout simple seta; setulose fringe absent, dense cuticular scale-spines present. Pereopods 2 without scale-spines, posterior margins of carpus and propodus with weak setulose fringe; accessory

unguis similar to pereopod 1. Pereopod 3 similar in ornamentation to pereopod 1. Pereopod 7 carpus with 4 prominent biserrate spines on distal margin; posterior margins distal ischium to propodus with weak setulose fringe.

Penes short, bluntly rounded, extending to pleonal sternite, about 2.5 as long as basal width.

Pleopod 1 endopod with medial margin distinctly indurate; endopod distinctly shorter (0.68) than exopod, with distinct proximolateral point; exopod margins converging to narrowly rounded apex; endopod and exopod with 16 and 21 PMS respectively. Pleopod 2 endopod manifestly longer (1.65) than endopod; appendix masculina arising sub-basally, extending beyond distal margin of ramus by about 0.07 of its length, about as long as endopod, subdistally dilated, apex rounded; endopod and exopod with 36 and 35 PMS respectively. Pleopod 3 endopod and exopod with 21 and 39 PMS respectively. Pleopods 4 and 5 with very strongly developed ridges; pleopod 5 with distinct transverse suture. Uropod exopod about 0.72 as long as endopod, distal margins both smoothly rounded, with distinct gel-layer.

Female. Similar to the male, except that the telsonic tube opens in a more dorsal position and is slightly ovate.

Colour. Pale brown in alcohol.

Size. Males measure 3.8-4.5 mm; ovigerous females 3.3-4.3 mm, non-ovigerous females 2.8-3.8 mm.

Remarks. This species, while agreeing on the generic characters presented for *Diclidocella,* differs in certain other characters, which suggests that its placement in *Diclidocella* should be regarded as provisional, and the species as incertae sedis.

All species of the genus have operculate first pleopods, but those of *D. yackatoon* and *D. ngake* differ little in shape and proportion from those of *Cymodocella,* while those of *D. bullata* have the endopod smaller, the exopod coming to an acute point and the marginal setae dorsally attached. The telsonic tube of *D. yackatoon* and *D. ngake* is scarcely produced, although it is ventrally closed in the male; without such a tube, there is little except the operculate pleopods and slender second pereopod to separate the species from *Ischyromene,* and females of these two species do superficially resemble that genus. However, the antennule morphology and short epistome of *Diclidocella* clearly distinguishes the genus from *Ischyromene,* and indicates an affinity with the southern Australian genera *Juletta* Bruce, 1993 and *Margueritta* Bruce, 1993. The mandible of *D. yackatoon* in particular is similar to that of those two genera, having in common a unicuspid incisor, a spine row with distal truncate spines and proximal serrate spines, and the molar process reduced and smooth, but still keratinized. *Juletta* and *Margueritta* are immediately separated from *Diclidocella* by having the pleotelson totally fused to the pleon.

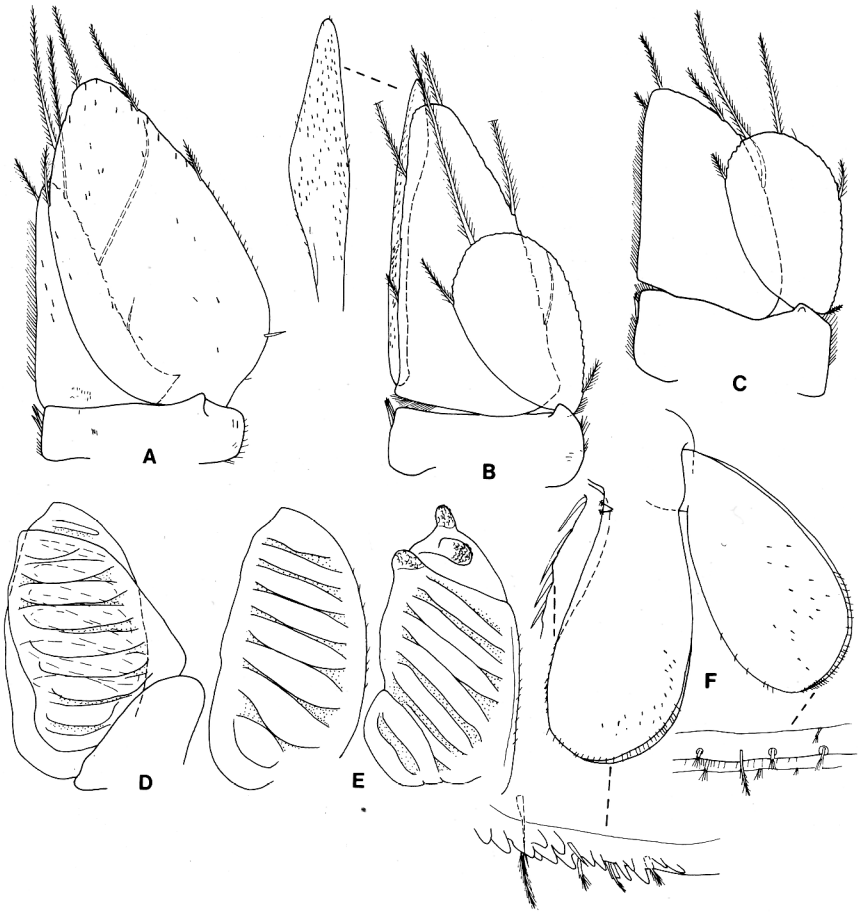

Fig. 22. *Diclidocella yackatoon* sp. nov. All figs 3.8 mm male paratype, NMV J34068. A-E, pleopods 1-5 respectively; F, uropod.

Distribution. From the central southern Australian coasts from Victoria (145°E) to South Australia (134°E).

Etymology. The epithet is an Aboriginal word meaning happy, and alludes to nothing in particular.

Diclidocella ngake sp. nov.

Figs 24-26

Material Examined. Holotype. ♂ (3.8 mm), Bay of Islands, Warrnambool, Vic, 38°35'S, 142°49.5'E, 28 Apr 1988, 2.5 m, brown algae, coll. R.T. Springthorpe and P.M. Berents (AM P42552). Paratypes. 63 ♀ (ovig 3.0, 15 non-ovig 3.3#1,

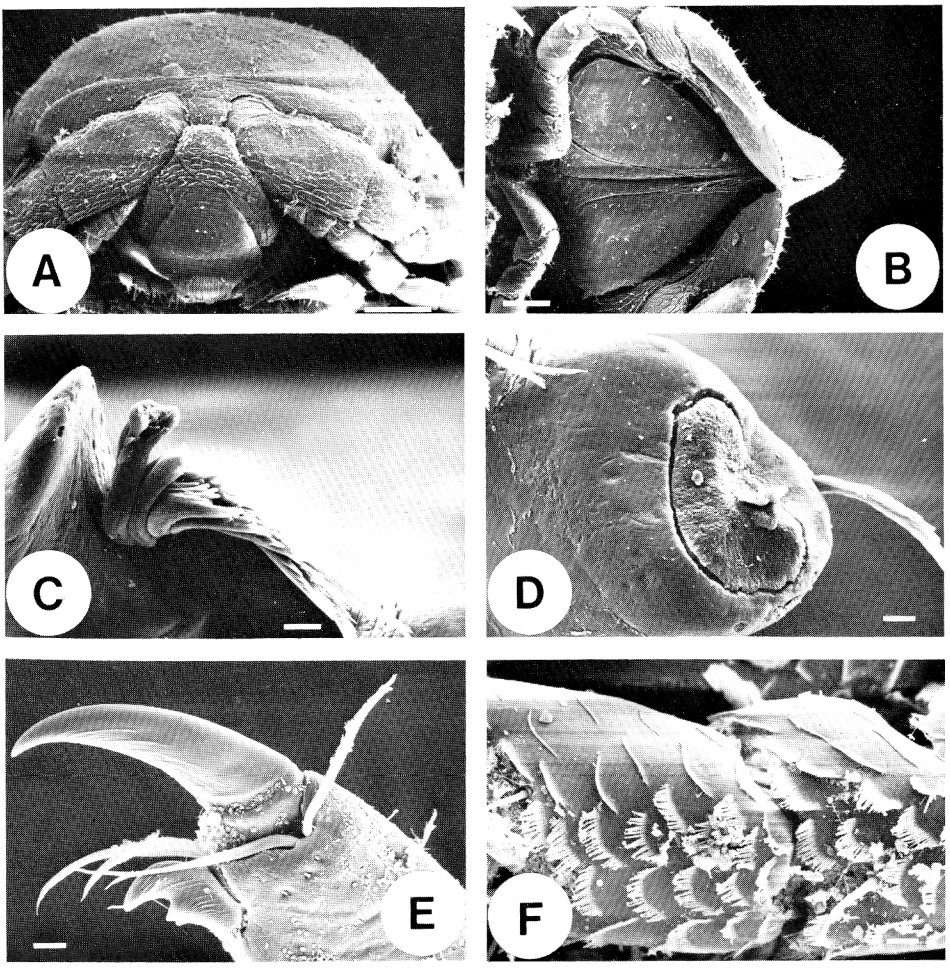

Fig. 23. *Diclidocella yackatoon* sp. nov. SEMs of manca and damaged female, AM P41348. A, frons (100μm); B, pleotelson, in ventral view (100μm); C, left mandible, distal end (10μm); D, molar process (10μm); E, pereopod 2 dactylus (10μm); F, pereopod 7, merus and carpus (10μm).

3.0#2, 3.0, 3.0, 2.9, 2.9, 2.8, 2.8, 2.8, 2.8, 2.7, 2.7, 2.6, 2.6, 2.4 mm, + 47 unmeasured), 38 mancas (0.8-1.3 mm), same data as holotype (AM P41349, 4 females ZMUC CRU314).

Additional material. ♂? (3.9 mm), Waterhouse Point, Tasmania, 24 Apr 1992, 5 m, *Amphibolis antarctica,* coll. E. Edgar (NMV J40507). ♂ (4.5 mm), 3 ♀ (ovig 3.5, 3.6, 4.0 mm), Stokes Bay, Kangaroo Is,. S.A., 35°42'S, 137°10'E, 4 Mar 1978, low tide, algae, coll. K. Handley (AM P41030).

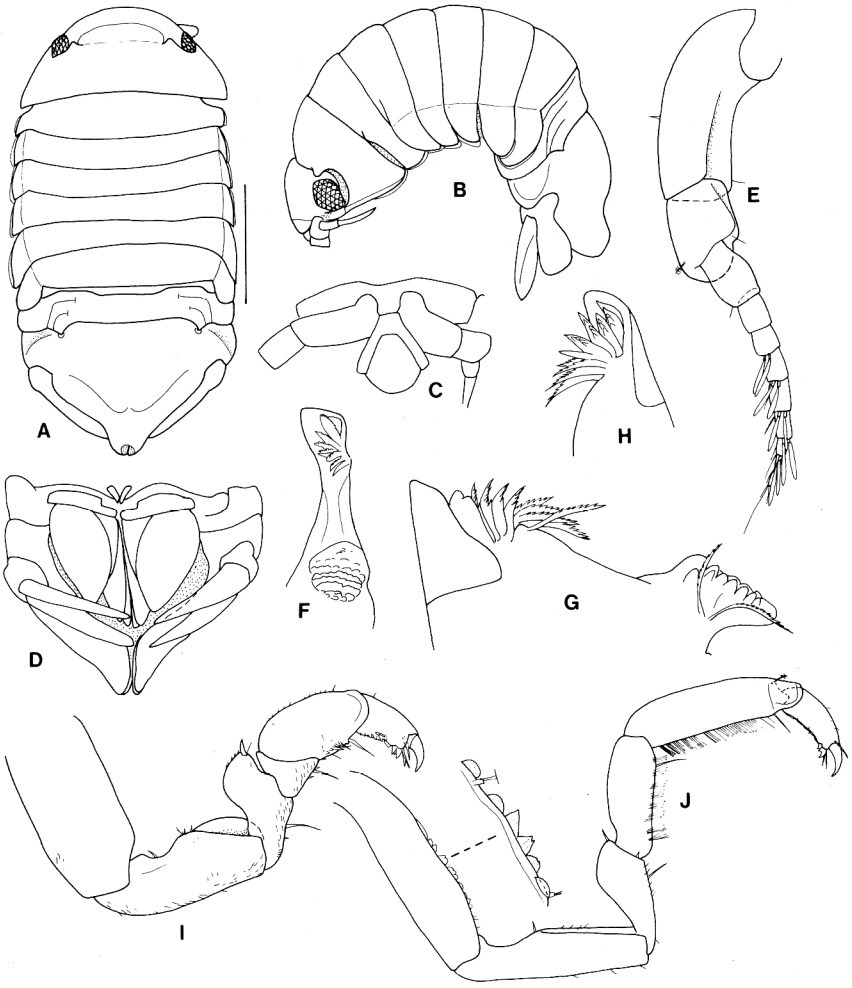

Fig. 24. *Diclidocella ngake* sp. nov. A-D holotype, remainder 3.3 mm female paratype. A, dorsal view, B, lateral view; C, frons; D, pleon, ventral view; E, antennule; F, left mandible, en face; G, left mandible; H right mandible; I, pereopod l; J, pereopod 2. Scale l.0 mm

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Description

Male. Body about 1.9 times as long as wide, unornamented, cuticle smooth; widest at pereonitc 6, lateral margins subparallel; gel-layer present on coxal and pereonal margins. Coxal sutures 3-7 distinct; coxae of pereonite 7 extending to lateral margin of pereonite 6, larger than those of pereonite 6. Pleon about 8% BL in lateral view. Pleotelson dorsally weakly bidomed; pleotelsonic tube short, about 5% BL, opening posteriorly.

Antennule peduncle article 2 50% as long as article 1; article 3 about 61% as

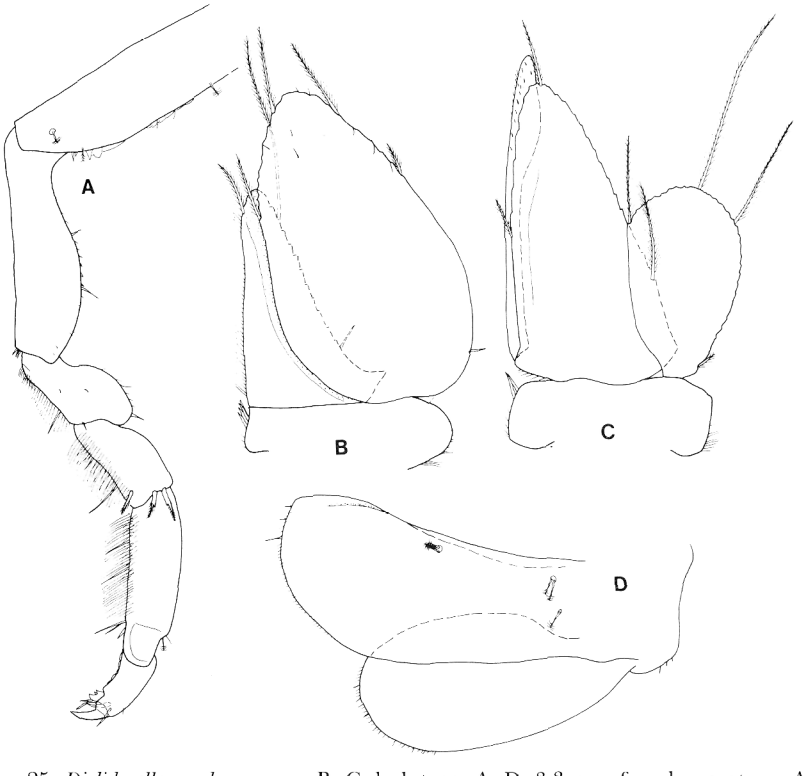

Fig. 25. *Diclidocella ngake* sp. nov. B, C, holotype, A, D, 3.3 mm female paratype. A, pereopod 7; B, pleopod 1; C, pleopod 2; D, uropod.

long as article 2; article 2 with anterodistal margin lobate; flagellum about 65 % as long as peduncle, with 8 articles, articles 1 and 4 subequal in length and longest. Antenna similar to that of *D. yackatoon,* flagellum with 13 articles.

Epistome about 0.36 as long as labrum, anterior margin truncate. Mandible incisor unicuspid, distally truncate; left mandible without distinct lacinia mobilis; spine row with about 9 spines, distal spines robust, proximal slender; molar process small, keratinized, nodular; palp article 2 with 5 stout biserrate spines, article 3 with 11. Maxillule and maxilla, and maxilliped as for *D. yackatoon.*

Pereopods all with 2 prominent accessory cusps on secondary unguis. Pereopod 1 without stout serrate spines; posterior margin of merus and carpus each with single stout simple seta; setulose fringe absent, dense cuticular scale-spines present. Pereopod 2 without scale-spines, posterior margins of carpus and propodus with dense setulose fringe; accessory unguis similar to pereopod 1. Pereopod 3 similar in ornamentation to pereopod 1. Pereopod 7 carpus with 3 prominent biserrate spines on distal margin; posterior margins ischium to propodus with dense setulose fringe.

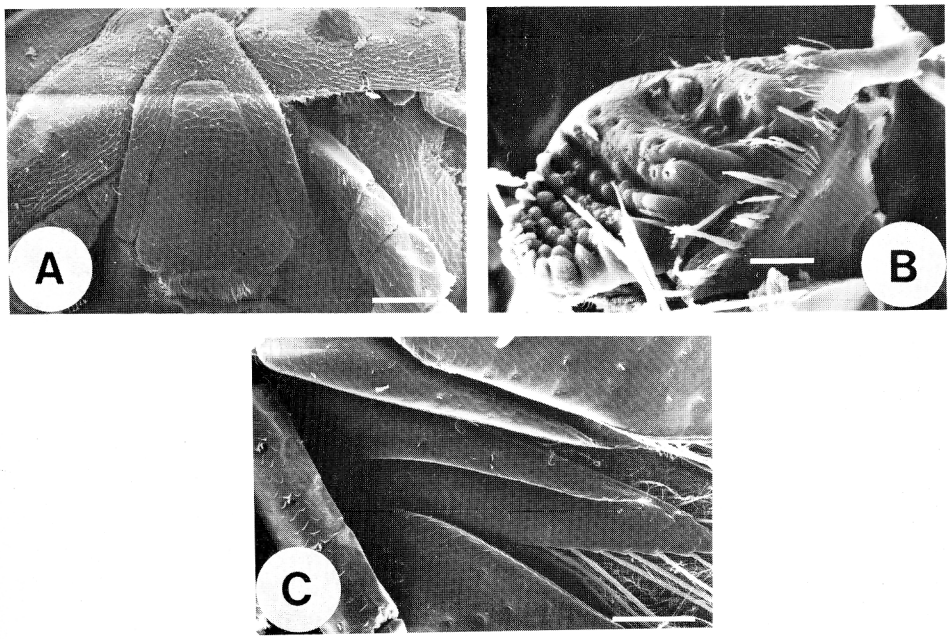

Fig. 26. *Diclidocella ngake* sp. nov. SEMs, 2.8 mm non-ovig female paratype. A, frons (100μm); B, molar process (10μm); C, pleopod 1, in situ, showing thickened medial margin (100μm).

Pencs short, bluntly rounded, extending to pleonal sternite.

Pleopod 1 endopod with medial margin distinctly indurate; endopod distinctly shorter (0.66) than exopod, with distinct proximolateral point; exopod margins converging to narrowly rounded apex; endopod and exopod with 19 and 24 PMS respectively. Pleopod 2 endopod manifestly longer (1.60) than endopod; appendix masculina arising sub-basally, extending beyond distal margin of ramus by about 0.10 of its length, about as long as endopod, subdistally dilated, apex rounded; endopod and exopod with 25 and 34 PMS respectively. Pleopods 3-5 as for *D. yackatoon*. Uropod exopod about 0.70 as long as endopod, distal margins both smoothly rounded.

Female. Similar to the male.

Colour. Pale brown in alcohol.

Size. Adult females 2.4-3.3 mm.

Remarks. This species is readily separated from the very similar *D. yackatoon* by having subparallel body margins, and pereonite 7 as wide as pereonite 6 as well as having larger coxal plates. The first pair of pleopods, while clearly operculate, are not as heavily indurate as those of *D. yackatoon*. While the mouthparts of the two species are nearly identical, the incisor, spine row and molar are distinct, that of *D. ngake* showing the plesiomorphic states.

Distribution. Recorded from Warrnambool, Victoria, and Kangaroo Island, South Australia; one specimen (male, damaged, NMV exJ36966) from Tasmania is provisionally identified as this species, suggesting a southern coast distribution from Tasmania to South Australia.

Etymology. The epithet is an Aboriginal word meaning close (to), and alludes to the similarity in appearance of this species to *Diclidocella yackatoon.*

ANALYSIS OF THE TAXA

Species of Cymodocella initially assessed with notes

Initially all species of tube-tailed sphaeromatids, including some undescribed taxa, were included in the analysis. Those that lacked the characters of the *Ischyromene*-group were removed.

Outgroups used were *Sphaeroma* and *Ischyromene.* The tree was rooted using *Sphaeroma.* The genus is well known and characterized, with an imperforate telson, biramous lamellar uropods which together with the mouthparts, indicate that the genus displays a relatively plesiomorphic condition in comparison to *Cymodocella.* The genus *Ischyromene,* while clearly closer to *Cymodocella,* is a diverse genus of uncertain monophyly, and potentially overlaps with the ingroup, at least in part. *Ischyromene* is in need of revision as the most recent diagnosis is based on Australian taxa and the diversity of the species contained, rather than on the type species. For these reasons the genus was excluded from the analysis.

Cymodocella tubicauda Pfeffer, 1887. Type species.

Australian species: *Cymodocella ambonota* sp. nov.; *Cymodocella ankylosauria* sp. nov.; *Cymodocella glabella* sp. nov., *Diclidocella bullata sp.* nov.; *Diclidocella yackatoon* sp. nov.; *Diclidocella ngake* sp. nov.

South African species: *Ischyromene bicolor* (Barnard, 1914) comb. nov.; *Cymodocella cancellata* Barnard, 1920; *Ischyromene magna* (Barnard, 1954) comb. nov.; *Cymodocella pustulata* Barnard, 1914; *Cymodocella sublevis* Barnard, 1914.

South Atlantic, Brazil: *Cymodocella guarapariensis* Loyola e Silva, 1965.

Ischyromene bicolor (Barnard, 1914) comb. nov.

Differs very little from *Ischyromene,* and specifically lacks a posteriorly directed ventrally enclosed telsonic tube. The only differences to *Ischyromene* s. str. are that the epistome anterior margin is quadrate, and pleopod 1 endopod has the medial margin indistinctly thickened. The distribution of these characters within *Ischyromene* is, as a whole, not known. As this species shares far fewer of the characters of *Cymodocella* it seems more appropriate to place it in *Ischyromene.*

Ischyromene magna (Barnard, 1954) comb. nov.

Lacks a tube tail, the produced telsonic apex being ventrally open and short.

Excluded from the analysis

Cymodocella algoensis (Stebbing, 1875). No material is available for this very poorly known species, and I have not been able to locate the types. Recorded from Algoa Bay, South Africa. Stebbing (1910) later cast doubt on its provenance, suggesting that it may have come from Australia. The original figure bears little resemblance to any of the Australian species.

Cymodocella diateichos Barnard, 1959. Omitted due to lack of adequate material and lack of males.

Cymodocella eutylos Barnard, 1954. Omitted due to lack of adequate material and lack of males.

Cymodocella egregia (Chilton, 1892). Specimens from Akaroa Harbour, New Zealand (ZMUC) were examined. The species has an anteriorly produced and acute epistome. The species is readily separated from the larger *Cymodocella tubicauda* by lacking pleotelsonic ornamentation, and by having a far shorter uropodal exopod and rounded endopod. Pleopods 4 and 5 have light but distinct ridges.

Cymodocella capra Hurley & Jansen, 1977. An inadequately described species from New Zealand; has an anteriorly produced and acute epistome, and appears close to *C. tubicauda.*

Cymodocella hawaiiensis Bruce, 1994c. Hawaii; known from females only. Lacks the rostral point, posterior pocket to the brood pouch, pereopod dactylus accessory unguis is simple, pleopod 1 endopod lacks a distinct indurate medial margin and the rami are subequal in size as are those of pleopod 2. This species therefore does not belong to the *Ischyromene*-group of genera. This species is regarded as incertae sedis, and males are needed before it can be assigned to its correct generic position within the Dynameninae.

New Caledonia tube-tail (Fig. 2B). An undescribed species that belongs to no existing genus. Differs in most characters, and is not a member of the *Ischyromene*-group. None the less it does have a posteriorly closed tube tail.

Discussion of characters

Pereon: Coxal plates are variously expanded in the family, with those of pereonite 6 in some cases largely or even totally concealing the coxae of pereonite 7. Pereonite 7 may be narrower than pereonite 6 and not extend to the lateral margin of the body outline. Both of these characters are usually, but not always, consistent within a genus.

Sternal process: Anterior to the point of attachment of the first pleopods is a band of cuticle, most clearly seen in the genus *Cerceis.* This feature is present in a shorter form in many sphaeromatid genera, but in some it is absent. In many cases the presence of the character has never been noted and consequently its distribution is uncertain.

Pleotelson: In sphaeromatid taxonomy the varied and diverse shape and ornamentation of the posterior margin of the pleotelson has long been regarded as of fundamental importance in defining genera. This analysis is concerned only with the tube-tail. This may be elongate and ventrally entirely closed, as in *Cymodocella ankylosauria* and *Diclidocella bullata,* short and distinct as in the type species and upwardly turned as in *C. glabella,* and equally can be ventrally closed but scarcely produced. Lack of a tube is the plesiomorphic state, and presence of a tube apomorphic; short and long tubes are both scored as 1 as a long tube can be derived in more than one way (see Fig. 1).

Epistome: The most commonly occurring sphaeromatid epistome shape is that of an anteriorly narrowed laterally constricted shield, as occurs in *Cymodocella tubicauda.* The very short epistome with straight lateral lobes encompassing the labrum, occurs in some Cassidininae and several southern Australian genera of the *Ischyromene*-group.

Antennule: Typical antennule peduncle morphology in the Sphaeromatidae is with three colinear articles (as in most Flabellifera), with articles 1 and 2 heavily calcified, article 2 being very short, less than half the length of 1, and article 3 elongate and slender, not heavily calcified. Such an antennule peduncle occurs in, for example, *Sphaeroma* and related genera, *Cymodoce* Leach, and the group of genera related to *Cilicaea* Leach; in the Dynameninae it is present in the *Cerceis*-group of genera. In *Diclidocella* the second peduncular article is long, and the third not colinear with the first two but offset.

Mandibles: The mandible provides a rich source of data, but previously little attention has been given to details of sphaeromatid mouthpart morphology. In some larger genera (e.g., *Paracassidina* Baker, 1911, see Bruce 1994b; *Cymodoce* sensu strictu, see Dumay 1972 and earlier references, Harrison & Holdich 1984) morphology is essentially uniform. Character states of mandible are particularly difficult to homologise as most apomorphies involve loss of structures. The reduced incisor, spine row and lacinia mobilis in *C. glabella* (Fig. 12B) and *Cymodocella ankylosauria* (Fig. 16B) are clearly different. The mandible incisor has been scored 1 where reduced, but should be regarded as a homoplasy. The actual details of the spine row and incisor for the species pair *D. yackatoon* and *D. ngake* are the same and differ little from genera such as *Juletta,* but the surface of the molar process of the two species (Figs 23D and 26B) differ considerably. Without knowledge of the functional morphology of these structures it is not possible to be sure of the significance of such differences.

Pereopods: Pereopods have in the past featured little in the definition of genera, although many genera present a pereopodal morphology that is recognizable as that of the genus, often showing a consistent spine ornamentation and pattern. In most sphaeromatids, pereopods are described as ambulatory, with 1-3 subsimilar, and 4-7 more slender, 7 usually being shorter than 6. Some genera,

such as *Paracassidina* (see Bruce 1994b), may have exceptionally distinctive first pereopods with the other pereopods being subsimilar. Among the species treated here some have a notably slender second leg. The secondary unguis at the base of the dactylus unguis is in the Sphaeromatinae always simple. In the *Ischyromene*-group, and several other genera there are two small cusps at the base of the secondary unguis. The distribution of the pectinate secondary unguis, in the species considered here on the second leg only, is uncertain. This character can occur on pereopods 1-3 (Müller, new genus in press) and on pereopod 1 in some Cassidininae (Bruce 1994b).

Pleopods: In the Sphaeromatidae the first and second pair of pleopods usually have rami that are of about equal length, the first pair are not operculate, and pleopods 1-5 forming a rank. The medial margin of pleopod 1 endopod is usually thickened, and pleopod 1 is generally slightly more robust than the remainder. In the *Ischyromene*-group the first pleopod has a distinctly demarcated indurate medial portion; several genera have operculate first pleopods which may also be indurate. Secondary loss of the indurate medial margin is not possible to distinguish from the plesiomorphic state. The second pair of pleopods commonly have rami of subequal length; an elongate endopod is an apomorphy for the *Ischyromene*-group; basal attachment of a short appendix masculina is considered plesiomorphic.

Pleopods 4 and 5 with thickened ridges on both rami or exopod only is an apomorphy for the family, but one that is repeatedly lost. The absence of thickened ridges or folds on pleopods 4 and 5 can be shown to be an homoplasious occurrence in some sphaeromatid genera, or regarded as the retention of a plesiomorphic condition in other genera. While the presence of thickened ridges on the exopods only (Sphaeromatinae) or on both rami (Dynameninae) is probably significant, the subsequent loss of these ridges is not. Currently there are several genera which have some species that lack these ridges (e.g., *Cymodocella, Diclidocella, Exosphaeroma* Stebbing, 1900, *Benthosphaera* Bruce, 1994d). In some other genera the expression of this character is unclear (e.g., *Apemosphaera* Bruce, 1994b, *Pseudosphaeroma* Chilton, 1909 [see Harrison 1984], *Waiteolana* Baker, 1926 [see Harrison 1984]). It is increasingly evident that the phylogenetic interpretation of this character alone must be cautious.

For the purposes of this analysis presence of ridges on the rami is considered the plesiomorphic condition.

FINAL CHARACTER LIST

Somatic

1. Sternal process: absent (0); present (1).
2. Pereonite 6 coxae: not produced (0); posteriorly produced, concealing lateral margins of pereonite 7 (1).

3. Pereonite 7: about as wide, forming part of body margin (0); narrower than 6, not part of body margin (1).
4. Pereonite 7 dorsal posterior margin: not extended (0); extended (1).
5-6. Pleotelson posterior margin: without tube (00); short, posteriorly directed, ventrally closed tube (10); elongate, posteriorly directed ventrally closed tube (11).
7. Sexual dimorphism of body ornamentation: absent (0); present (1).

Appendages

8. Antennule peduncle article 3: colinear with 2 (0); posteriorly offset (1).
9. Antennule bases: set together, not widely separated by epistome (0); set apart, separated by epistome (1).
10. Epistome: medially anteriorly produced, about as long as labrum (0); not medially produced, much shorter than labrum (1).
11. Epistome anterior margin: anteriorly acute (0); anteriorly quadrate (1).
12. Mandible incisor: multicuspid (0); unicuspid (1).
13. Mandible with lacinia mobilis: present (0); absent (1).
14. Mandible with spine row: present (0); reduced or absent (1).
15. Mandible: with molar process (0); molar process absent (1).
16. Mandible with molar process: prominent, nodular or ridged (0); smooth (1).
17. Maxillule medial lobe: with 4 plumose spines (0); with 3 spines or less (1).
18. Pereopods: with setulose fringe on posterior margin (0); without setulose fringe (1).
19. Pereopod 2 accessory unguis: as other pereopods (0); pectinate (1).
20. Pereopods 2 and 3: similar (0); pereopod 2 markedly slender (1).
21. Penial process: short, blunt, not reaching pleopod rami (0); long, apically narrowed or acute, extending to pleopod bases (1)
22. Pleopod 1: endopod and exopod subequal in length (0); endopod markedly shorter than exopod (1) .
23. Pleopod 1 endopod: broad, less than 1.4 x basal width (0); elongate, more than 1.5 x longer than basal width (1).
24. Pleopod 1 endopod medial margin: indistinctly thickened or indurate (1); distinctly indurate (0).
25. Pleopod 1 rami: lamellar, not operculate (0); rami operculate (1).
26-27. Pleopod 1 exopod: lateral margin convex (00); lateral margin straight (10); lateral margin concave (01).
28. Pleopod 2: rami subequal in length [endopod 0.8-1.2 x length of exopod] (0); endopod markedly longer [> 1.3 x] than exopod (1).
29. Pleopod 2: without proximomedial lobe (0); male endopod with proximomedial lobe (1) .

Table 1. Character state and distribution of the 34 characters used in the analysis.

	0 12345	0 67890	1 12345	1 67890	2 12345	2 67890	3 1234
Sphaeroma	00000	00000	00000	00000	00000	00000	0000
C. tubicauda	10001	10000	00000	00100	01110	01101	0001
C. ambonota	?0011	10010	10000	00000	01110	01100	0010
C. glabella	10101	10010	11111	11000	10110	01111	0100
C. ankylosauria	01101	10110	11111	10000	00000	10101	0000
D. bullata	10111	11111	10000	01111	01111	00101	0010
D. yackatoon	10101	00111	11100	10001	01111	00100	0000
D. ngake	10001	00111	11100	00001	01111	00100	0000
C. bicolor	01000	00000	11000	0?000	00010	10001	0000
C. cancellata	00001	1?100	1????	??000	10100	01011	1100
C. magna	?0000	00000	00000	0?000	10000	10001	01??
C. pustulata	10111	0?000	11000	00011	00100	00101	0000
C. sublevis	00001	00000	10000	0?000	11000	10001	1100
C. guaraparien	00101	1?000	00000	00111	?0000	101??	??00

30-31. Appendix masculina: as long as endopod, not longer (00); longer than endopod, extending beyond distal margin of ramus [1.1-1.5 x length of endopod] (10); elongate [< 1.7 x length of endopod] (11).

32. Appendix masculina: apically rounded, blunt (0); apically narrowed or acuminate (1).

33-34. Pleopods 4 and 5: with thickened ridges or folds (00); lamellar (10); smooth, but thickened (01).

RESULTS AND DISCUSSION OF THE ANALYSIS

The analysis undertaken here is regarded as provisional and experimental, and was performed in order to find some direction in the search for useful characters within the Sphaeromatidae. The results carry little implication beyond the ingroup other than in demonstrating the homoplasious nature of many characters used in sphaeromatid taxonomy, and perhaps in drawing attention to characters that have not previously been regarded as useful or worth noting.

The Sphaeromatidae is a large family, currently with over 90 named genera. The only recent attempt to present a phylogenetic analysis is that of Wägele (1989). This presentation used 22 selected genera and "genus groups", less than 30 % of the total genera known. In using only 30 characters to analyse the family, and with several of the groups containing many genera, the resultant cladogram can only be considered as highly unresolved. In some cases recognizably homoplasious characters (e.g., flattened antennule peduncular

articles, flattened body shape) were used to group dissimilar genera such as *Amphoiroidella* with *Cassidina*. The "Gruppe *Cymodocella*", characterized by the homoplasious perforate or slit pleotelson, contained genera of the here defined *'Ischyromene*-group' as well as several genera close to *Dynamenella* and also *Dynamenoides* Hurley & Jansen, 1977. Brusca & Wilson (1991), in their analysis of isopod relationships, correctly recognized the still urgent need for a thorough taxonomic and cladistic revision of the sphaeromatid genera. Currently there is no accepted pattern of relationships which can be used to identify potential sister groups and, furthermore, the monophyly of many of the larger genera, including the potential sister groups for this analysis, is very uncertain.

Initial analysis using unit weight for all characters (Table 1) resulted in 4 equally parsimonious trees with a length of 183, and a consistency index of 44, retention index of 51. Successive character weighting resulted in a single tree (Fig. 27) with a length of 183, and a consistency index of 69, retention index of 77. Of particular note is that of the 34 characters used, 21 can be identified as homoplasies, and of the remaining synapomorphies 5 have associated reversals. Of the synapomorphic characters that are apparently unique, comparison of these to the wider distribution of apparently similar characters in the Sphaeromatidae suggests that further consideration is necessary before their phylogenetic significance can be fully understood.

DISCUSSION OF THE TREE

The clade comprising *I. bicolor, I. magna* and *C. sublevis* is not supported by any unique characters, but only by the lateral margin of pleopod 1 exopod being straight (character 26), a character state also present in *Cymodocella ankylosauria*. Two of these species (*I. bicolor* and *I. magna*) have been transferred to *Ischyromene* as they lack a posteriorly directed ventrally enclosed pleotelsonic tube.

The remaining species are characterized by four characters (3, 6, 23, and 28), all of which have at least one reversal. The elongate pleotelsonic tube (6) is reversed once in *Diclidocella yackatoon* and *D. ngake*. The character state of pereonite 7 narrower than 6 (character 3) is reversed twice (*C. cancellata* and *D. ngake*), and the width of pereonite 7 is known to be variable in other sphaeromatid genera (e.g., *Cassidinella*, see Bruce 1994a). Character 23 (relative length of pleopod 1 endopod) reverses in *Cymodocella ankylosauria* and *C. guaraapariensis*, and character 28 (relative length of pleopod 2 rami) once in *C. cancellata*.

The clade containing *Cymodocella ankylosauria, C. glabella* and *C. cancellata* is supported by 2 synapomorphies, both effectively the loss of a character (characters 14 and 15, the spine row and molar process). It is a moot point whether or not these reductions are homologous, and the actual form of the incisor

and molar (Figs 12B, 12C, 16C) in the Australian species clearly indicates that they are not. Within this group, the species pair of *Cymodocella glabella* and *Cymodocella cancellata* share the synapomorphy of having the elongate appendix masculina on a prominent posteriorly directed lobe (character 29), a character state also known to occur in the otherwise unrelated genera *Cassidinidea* Hansen, 1905 and *Syncassidina* Baker, 1929 (see Bruce 1994b).

The remaining taxa have in common a slender pereopod 2 (character 20), and the clade is also characterized by the appearance of a pectinate accessory unguis on pereopod 2 (character 19). The former character state is widely distributed in the Dynameninae (e.g. also *Amphoroidea, Cassidinopsis* Hansen, 1905, *Scutuloidea* Chilton, 1883 and some *Dynamenella).* The latter character is reversed once in *Diclidocella yackatoon* and *D. ngake.* The pectinate accessory unguis is a character that also needs to be treated with caution. The unguis of *Diclidocella yackatoon* and *D. ngake* is of the form typically found in others of the *Ischyromene*-group (i.e., distally recurved with 2 proximal cusps) and is not of a different shape or ornamentation that could be ascribed as an independent derivation from the flattened comb form. Furthermore the accessory unguis of pereopod 1 in the genus *Paracassidina* Baker, 1911 (see Bruce 1994b) varies from being strongly pectinate to smooth, although not homologous (being straight, apically acute and lacking the 2 proximal cusps) with that of the *Ischyromene*-group.

Within this analysis the genus *Diclidocella* is supported by the appearance of two unique synapomorphies: the very short epistome (character 10) and operculate first pleopods (character 25). These two characters are also shared with several other genera of Sphaeromatidae, all with a southern Australian distribution, also in conjunction with the antennule peduncle having an elongate second article with an anterodistal lobe and a posteriorly offset third article (character 8). These genera are *Juletta, Margueritta,* and *Maricoccus.* Other characters require comment in this group of species. In *Diclidocella bullata* the presence of a multicuspid mandible incisor is scored as a reversal, and indeed is not of the form of taxa such as *Sphaeroma* or *Cymodocella tubicauda,* the cusps being finer and subequal in size. The very similar species pair of *Diclidocella yackatoon* and *D. ngake* each have a very different mandibular molar process, that of *D. yackatoon* being totally smooth, while that of *D. ngake* has prominent rounded nodules (an autapomorphy), suggesting that this character needs careful recording and interpretation for all genera and species of Sphaeromatidae.

CONCLUSIONS

The resultant cladogram (Fig. 27) demonstrates that *Cymodocella* as currently constituted is a polyphyletic taxon, defined primarily by the homoplasious character state of the pleotelson having a posteriorly directed and ventrally

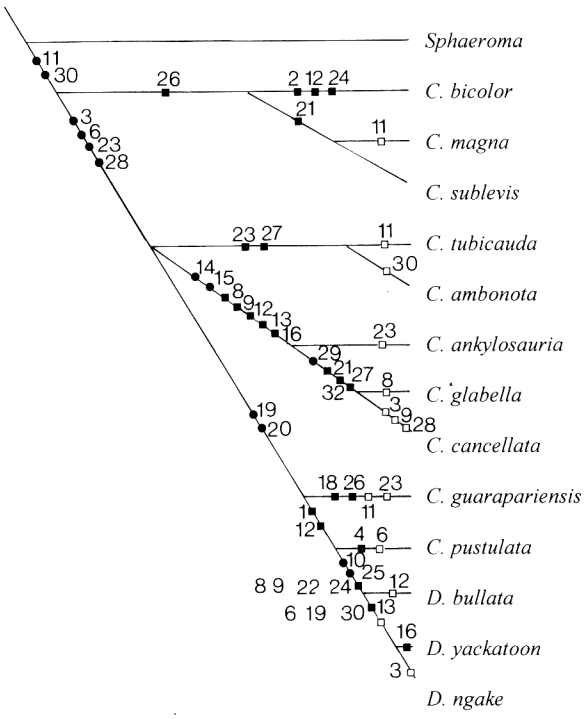

Fig. 27. Cladogram for species of *Cymodocella* and *Diclidocella* based on the characters in Table 1. The outgroup is *Sphaeroma*. Only synapomorphies and certain of the homoplasies and reversals are shown. Key: ○ – apomorphy; ● – homoplasy; □ – reversal.

enclosed tube. The high level of character homoplasy (71 %) and reversals (41% of the synapomorphies) further support the polyphyly of the examined group. As the ingroup is not monophyletic, the results therefore have to be treated with caution. The monophyly of most potential sister groups is equally uncertain, and until such time as these genera are revised meaningful analysis of the relationships between the genera is not possible.

The result of the analysis suggests that the southern African species belong to a discrete clade, while *Diclidocella* could accommodate all those taxa with slender second pereopods with a pectinate accessory unguis. The remaining clade includes the tube-tails with elongate closed tube and robust pereopods. This scheme cannot be acted upon for several reasons. The characters delimiting the South African clade are weak, and at present of uncertain significance; all southern African tube-tails need to be redescribed before they can be assigned with confidence to new or existing genera.

The three species of *Diclidocella* cannot be housed in *Cymodocella* nor can *Diclidocella* accommodate *C. guaraparíensis* and *C. pustulata,* as it has three significant apomorphic characters that sets it apart from those species, *Cymodocella* and also *Ischyromene:* antennule peduncle article 3 posteriorly offset, a short epistome and an operculate pleopod 1. These characters place *Diclidocella* in

the group of southern Australian genera that includes *Juletta, Margueritta* and *Maricoccus* and several undescribed genera, while on the basis of those same characters *C. guarapariensis* and *C. pustulata* are closer to *Cymodocella* and *Ischyromene.*

At present *Cymodocella* sensu strictu can be regarded as having only four species that belong to it. All others are regarded as incertae sedis, and sensu lato, provisionally include tube-tailed species that cannot be placed in other genera or in unambiguously defined new genera. It will also be necessary for the monophyly of the potential sister groups such as *Ischyromene, Paradella, Dynamenella* to be resolved before classificatory changes can be made.

Within the group of tube-tailed species analyzed there is a group of South African species that is characterized by the retention of plesiomorphic character states, some of the characters being shared with some of the Australian taxa *(Cymodocella glabella* and *C. ankylosauria). Cymodocella* (sensu strictu) appears to be restricted to southern Australian, New Zealand and subantarctic waters. The northern hemisphere species attributed to the genus, one from Hawaii (Bruce 1994a), Japan (personal observation) and one from the Bahamas (Miller 1968), can be shown to be not closely related to *Cymodocella* and related austral genera.

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