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.

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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 antennulc 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 <i>Cymodocella ankylosauria</i> sp. nov.
-	Body not rugose, smooth or with nodules; antennule peduncle article 1 anterodistal angle not strongly produced
2.	Antennule peduncle articles 2 and 3 colinear; pereopod 2 robust, similar to pereopod 3; pleopod 1 endopod medial margin indurate
_	Antennule peduncle article 2 with anterodistal lobe, article 3 posteriorly offset; per-
	eopod 2 distinctly longer and more slender than pereopod 3; pleopod 1 operculate,
	indurate
3.	Posterior margin of perconites 2-7 with low setose nodules; pleotelson nodulose with 2 longitudinal nodular ridges; penial processes short; appendix masculina basally attached
-	Body unornamented; penial processes elongate; appendix masculina on posteriorly directed lobe
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.	Body margin ovate; pereonite 7 narrow, not extending to lateral margins of body out- line
-	Body margin sub-parallel; pereonite 7 extending to lateral margins of body outline

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 tubetail: 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.

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, percopod 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 $(10\mu m)$; B, right mandible $(10\mu m)$; C, molar process $(10\mu m)$; D, pereopod 2, dactylus, with diatoms $(100\mu m)$; E, pereopod 2, dactylus, trifid secondary unguis $(10\mu m)$; F, maxillule lateral lobe $(10\mu m)$.

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 \circ and \circ , 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. \circ (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 \circ (2.0, 2.1, 2.2, 2.3 dissected, 2.4 mm), φ (non-ovig 2.5 mm), manca (1.7 mm), same data as holotype (AM P42556, 1 male, ZMUC CRU317). φ (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.



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. \circ (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 \circ (3.4 dissected, 3.3 mm), 18 \circ (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.



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 $(100\mu m)$; B, mandible, incisor at left of picture $(100\mu m)$; C, molar process $(10\mu m)$; D, maxillule lateral lobe, gnathal spines $(10\mu m)$.

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. \heartsuit (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 \heartsuit (4.2 dissected, 4.0 mm), 2 \heartsuit (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.

green and red algae, large forms, coll. S. Shepherd (NMV J36988; 1 male ZMUC CRU318). 2 \circ (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). \bigcirc (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). \bigcirc (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). \bigcirc (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 (100μ m); C, mandibular spine row (10μ m); D, maxillule lateral lobe spines (10μ m); E, pereopod l (100μ m); F, lateral cuticle, pereonite 4, showing pit (10μ m).

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-