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The Genera of the Sphaeromatidae (Crustacea: Isopoda): a Key and Distribution List

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Abstract

An illustrated key to the genera of the family Sphaeromatidae, based on adult male specimens, is provided. This is complemented by notes on the distribution of the 81 known genera. It is suggested that *Nishimuraia* Nunomura may be a junior synonym of *Gnorimosphaeroma* Menzies, but this requires confirmation. It is suggested that the current sphaeromatid subfamilies Cassidininae, Sphaeromatinae and Dynameninae, based only on the folding of pleopods 4 and 5, may not reflect a natural classification. A modern analysis of sphaeromatid systematics is long overdue.

Key words: Sphaeromatidae, genera, key, distribution.

Introduction

'Any person of impatient temper who has ever attempted, when pressed for time, to disentangle with unskilful fingers a knotted skein of string, may understand the plight of a busy naturalist who has Sphaeromidae to classify.'

T. R. R. Stebbing

The systematics of the family Sphaeromatidae needs extensive revision. Both in the literature and in museum collections many species have been assigned to inappropriate genera, while many environmental surveys make no attempt to identify members of this family, listing only 'sphaeromatid 1', 'sphaeromatid 2', etc. Such misidentification and non-identification is encouraged by the fact that a key to separate the genera of the Sphaeromatidae does not exist. The only key to all known genera that has ever been attempted was in Hansen's (1905) monograph. That key is no longer effective as nearly three times as many genera now exist. A modern key to all known genera is long overdue.

Sphaeromatids are common in shallow seas worldwide. As the family name suggests, many species are capable of rolling (or, more correctly, folding) into a ball by bringing the ventral surfaces of the head and tail together. However, some are markedly flattened dorso-ventrally and appear less sphere-like when folded. In addition to this ability, sphaeromatids can usually be identified as such by the form of the pleon, the uropods and the ventral surface of the cephalosome. The pleon in sphaeromatids bears, at most, two separate tergites (plus the pleotelson), sometimes one, although short suture lines are often visible at the lateral or posterior margins indicating the junctions of the ancestral segments. In sphaeromatids each uropod has the endopod fused immoveably to the basis. The proximal end of this fused endopod-basis (here called an 'endopod') articulates with the pleotelson and usually carries a moveable exopod. Anterior to the mouthparts, the labrum is embraced by a single fused frontal lamina/clypeus (the 'epistome'). In most other isopods the frontal

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lamina and clypeus are separate, the latter carrying the labrum. A generalised sphaeromatid is shown in Figs 1-4. For the purpose of the key the terms 'proximal' and 'distal' refer to the article or appendage under consideration; 'anterior', 'posterior', 'lateral', 'median', 'midline', etc. refer to the orientation of the entire animal.

Historical

The Sphaeromatidae was first recognised as a discrete group within the Isopoda by Latreille in 1825 (Jacobs 1987). Latreille's 'Sphaeromides' was retained by Milne Edwards, as the 'Sphéromiens', in his major crustacean revision of 1840 and the group was raised to family level by White (1847) as the 'Sphaeromidae'. Following Milne Edwards' review, various works were published on the species of this group but the next major revision was that of Hansen (1905). Hansen's Sphaeromidae comprised all the genera of the Sphéromiens, together with the genera *Limnoria* Leach and *Plakarthrium* Chilton, and he split this family into three subfamilies, the Sphaerominae, the Limnoriinae and the Plakarthriinae respectively. Subsequent authors have not followed Hansen's classification and these three taxa are now treated as full families.

In 1916 Dahl modified the name 'Sphaeromidae' to 'Sphaeromatidae' without comment or explanation. Indeed, the paper in which this modification occurred used both spellings. The investigations of Hurley & Jansen (1977: 6) indicate that either spelling could be grammatically correct, but 'Sphaeromatidae' is the more expected construction and has now gained general acceptance.

In his monograph, Hansen reviewed the taxonomy of the family, redefined the genera, described several new genera and species, and redistributed the species to the most appropriate genera. He also carried out a detailed study of the morphology of ovigerous female specimens. Hansen's work was by far the most extensive study that had ever been carried

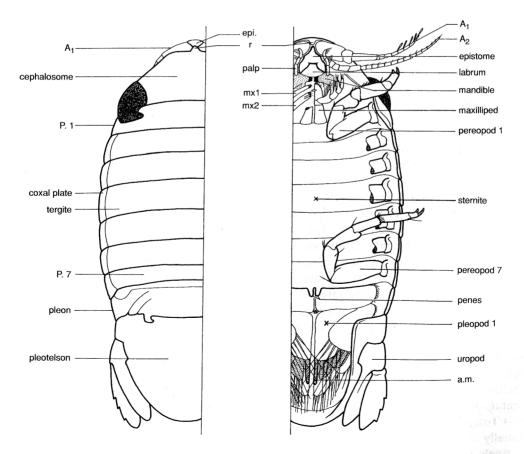


Fig. 1. Generalised sphaeromatid showing terminology: A1, antennule; A2, antenna; r, rostral process; mx1, maxillule; mx2, maxilla; P. 1, pereonite 1; a.m., appendix masculina.

out on this group and it has remained the standard text for sphaeromatid taxonomists despite the subsequent description of many new taxa.

The most significant of Hansen's observations concerned the structure of the fourth and fifth pleopods. Hansen noted that, while these pleopods were always biramous, in some species both rami were flat and membranous, in some species both bore marked transverse folding, while in others the endopod was folded and the exopod was flat. Hansen also noted that these possibilities were consistent at the generic level and he made them the basis of three supra-generic 'groups': the platybranchiatae ('flat gilled'), eubranchiatae ('well gilled') and hemibranchiatae ('half gilled'). The family has been divided on the basis of pleopod structure ever since.

In a brief note of 1905, followed by a full paper in the same year, Tattersall erected a new family, the Ancinidae, to house the genus Ancinus Milne Edwards and a new genus, Bathycopea. Dana (1852: 305) had already recognised the unusual nature of the genus Ancinus and had erected a subfamily, the 'Ancininae', to house it. It is not clear whether Tattersall was aware of Dana's action or was acting independently.

Richardson (1909) observed that Ancinus differed from other genera in that pleopod 1 bore only one ramus. Based on this she said that she preferred to keep Ancinus as the only genus in the Ancinidae, but if workers wished to keep Ancinus in the Sphaeromatidae then a fourth 'group' would be needed in Hansen's classification to house this genus. She called this group the 'colobranchiatae' (Greek 'colos' = docked, curtailed). Hansen had placed Ancinus in the platybranchiatae as the fourth and fifth pleopods lack folds. Subsequent workers have retained Ancinus in the Sphaeromatidae but the term colobranchiatae has been little used.

In 1969 Bodle, in an unpublished master's thesis, stated 'Tecticeps convexus does not fit into any of the categories established by Hansen. Hansen had not seen this species, but assigned the genus to the' ... 'platybranchiates on the basis of another species Tecticeps

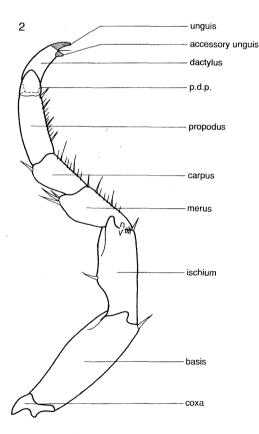


Fig. 2. Pereopod showing terminology: p.d.p., posterior distal plate.

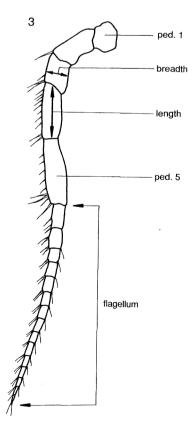


Fig. 3. Antenna showing terminology: ped., peduncle article.

alascensis Richardson. T. convexus has folds on both rami of pleopod 5 but no folds on either ramus of pleopod 4, and, for this reason, should be in a fourth group' (actually a fifth group). 'The term "pentadibranchiate" might be appropriate for this group' (1969: 23). Miller, who appears to have supervised Bodle's work, published the term 'pentadibranchiatae' in 1975.

Hurley & Jansen (1977) raised Hansen's three 'groups' to the level of subfamilies as Platybranchiatinae, Eubranchiatinae and Hemibranchiatinae. They did not mention the colobranchiatae or pentadibranchiatae.

Bowman (1981) observed that Hurley & Jansen were not justified in retaining Hansen's names for their subfamily groups, as under the International Code of Zoological Nomenclature (ICZN 1985) the names of family-group taxa must take their root from the name of an included genus. Hansen's names were descriptive terms, not modified generic names. Bowman, who considered only one eubranchiate genus, replaced the name Eubranchiatinae with 'Dynameninae', based on the eubranchiate genus *Dynamene*. Iverson (1982) replaced the remaining subfamily names. 'Platybranchiatinae' was replaced with 'Cassidininae', based on *Cassidina*. Iverson stated that 'Cassidininae' was a 'new name', but in 1905 Hansen had erected a 'section' Cassidinini in his 'group' platybranchiatae. In Hansen's classification this 'section' was at the rank of subtribe. In a modern classification, with the Sphaeromatidae as a full family, it would be a tribe. Iverson was therefore raising the level of Hansen's 'Cassidinini' within the family group and under Articles 35 and 36 of the ICZN, the name Cassidininae should be attributed to Hansen, 1905.

'Hemibranchiatinae', containing the genus *Sphaeroma*, the type genus of the family Sphaeromatidae, was the nominotypical subfamily and became 'Sphaeromatinae'. Iverson retained Tattersall's Anciniidae as a subfamily of the Sphaeromatidae, the 'Anciniinae', but seemed unaware of Dana's prior use of this name. The pentadibranchiatae, containing only representatives of the genus *Tecticeps*, became the 'Tecticipitinae'. [Despite Bodle's restriction of 'pentadibranchiate' to only one species, and Hansen's placement of *T. alascensis* in the platybranchiatae (with pleopods 4 and 5 lacking folds), Iverson (1982: 253) stated in his subfamily diagnosis 'Pleopod 5 with both rami with fleshy transverse folds', implying that this was the condition for all species in the genus *Tecticeps*. The present authors have not examined the pleopods of any species of *Tecticeps* and can render no opinion on Iverson's action.]

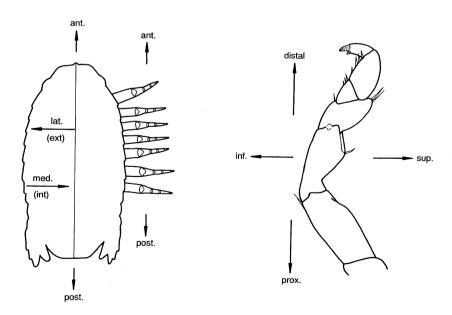


Fig. 4. Orientation of body and appendage showing terminology: ant., anterior; post., posterior; lat., lateral; ext, external; med., median; int, internal; prox., proximal; inf., inferior; sup., superior.

The family Sphaeromatidae therefore currently contains five subfamilies: Sphaeromatinae Latreille, 1825; Cassidininae Hansen, 1905; Dynameninae Bowman, 1981; Anciniinae Dana, 1852; and Tecticipitinae Iverson, 1982. The structures of pleopods 4 and 5 for these subfamilies are shown in Fig. 5.

In the subfamilies Sphaeromatinae, Cassidininae and Dynameninae, the folding of pleopods 4 and 5 is generally assumed to reflect a natural classification, indicating three monophyletic groups. However, this overlooks the variation within the folding patterns. The short, weak folds on the exopods of pleopods 4 and 5 in Ptyosphaera and the weak folding in Pseudosphaeroma appear to be intermediate between the condition found in the 'classic' hemibranchiates and eubranchiates. Also, there seems no logical reason to restrict a consideration of folding to pleopods 4 and 5. In Neosphaeroma there is folding of the endopods of pleopods 5, 4 and 3 (although the folding is only in the proximal region on pleopod 3); the exopods of all three pleopods are flat. In Caecocassidias the endopods of pleopods 5, 4 and 3 are fully folded, as are the exopods of pleopods 5 and 4. The folding of the endopod of pleopod 3 in two apparently unrelated species suggests that folding is not simply the inheritance of a pattern from a distant ancestor (sufficiently distant to be ancestral to dozens of current genera), but may be more intimately associated with the biological requirements of the animals. Pleopods 4 and 5 are the gills of sphaeromatids, and folding greatly increases their surface area. An understanding of folding patterns might profitably be pursued in the life histories of the species and the environmental conditions they encounter.

The Key

Several authors since Hansen have produced keys to the genera of selected geographical localities (Hale 1929, S. Australia; Loyola e Silva 1960, Brazil; Hurley & Jansen 1977, New Zealand; Kensley 1978, S. Africa). Apart from now being out of date, all these keys began with the same character. All authors followed Hansen in initially dividing the family, on the basis of pleopod morphology, into platybranchiatae, hemibranchiatae and eubranchiatae. They then devised keys to separate the genera of each of these divisions. Unfortunately, using pleopod form as an initial key character can create problems: (a) In some genera the entire pleopodal ramus is strongly folded (e.g. Cerceis-like genera), but in genera such as Pseudosphaeroma and Ptyosphaera there may be few folds. A non-specialist researcher who has seen a specimen with the folds well formed might have difficulty placing a specimen with the folds less well pronounced in the correct subfamily. (b) It can be difficult, without experience, to determine the exact form of the pleopods of small specimens. (c) If pleopods are mounted as permanent micro-slide preparations before examination, folds may be

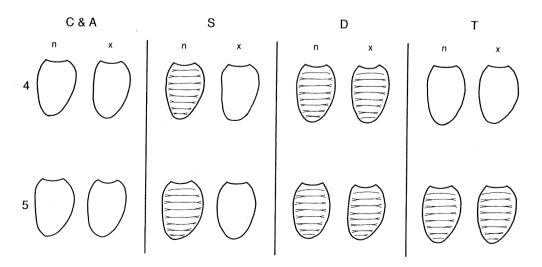


Fig. 5. Folding of pleopods 4 and 5 in the five subfamilies: n, endopod; x, exopod; C, Cassidininae; A, Anciniinae; S, Sphaeromatidae; D, Dynameninae; T, Tecticipitinae.

rendered non-obvious (pleopods should always be examined before mounting). (d) It is not uncommon for the pleopods of specimens to undergo apparent 'inflation' during preservation, thus making it impossible to determine whether folding was originally present. If a key uses pleopod structure as the initial separation factor, these difficulties can render such a key ineffective at the first couplet. The present authors have therefore not divided the family on the basis of pleopod structure. This feature is used only in the later stages to separate individual genera or small groups of genera.

A number of approaches are possible when devising a key to the genera of the Sphaeromatidae. It is felt here, however, that the greatest need for such a key lies with ecologists and other non-isopod specialists working in the field. The present key has been developed for use by field workers and this has imposed certain restrictions on the characters used. Many ecologists work with limited laboratory facilities. For this reason, whenever possible, the present key minimises the need for detailed microscopy or dissection. Unfortunately, microscopic examination is required in the initial stage of the identification to determine the sex of the specimen. Sphaeromatid species (and genera) are defined primarily on the form of the adult male. The females of many genera are similar and it is sometimes difficult to place females in the correct genus if accompanying males are not found. The following key is therefore based entirely on the form of the adult male. Females and immature specimens may not key to the correct genus, but at present it is not possible to devise a key to include all stages of the life-cycle. Workers can usually ascertain that their specimen is male by confirming that it has a pair of penes in the ventral mid-line of pereonite 7 (these are sometimes fused and sometimes tucked beneath the first pleopods), and that it is adult by examining the endopod of pleopod 2. In male specimens the inner margin of this endopod bears a copulatory structure, the appendix masculina, but only in adult males is this appendix free along its entire length. In subadult males it is partially fused to the endopod (Fig. 6). Unfortunately, in the genus Dynamene and the species Sphaeroma terebrans adult males lack an appendix masculina. However, as a general guide to their recognition, adult males of Dynamene can be distinguished by their two prominent, dorsal, backwardly projecting spines on the posterior margin of pereonite 6 (only adult males of Dynamene show this character), and all Sphaeroma species have long, stiff setae on the superior surfaces of pereopods 1 to 3, as in Fig. 10 of the key (and the mandibles 'normal' as in

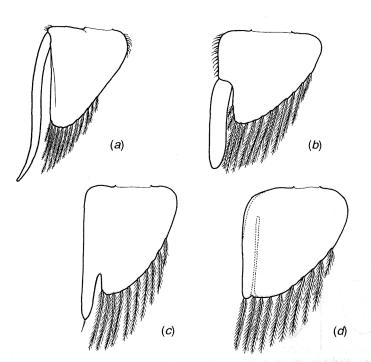


Fig. 6. Endopod of pleopod 2 in male sphaeromatids: (a) and (b), adult forms (note articulation between appendix and ramus); (c) and (d), immature forms.

Fig. 1, not as in Fig. 13 of the key). Sphaeroma terebrans will usually be found boring into wood.

Not all genera currently housed in the Sphaeromatidae are included in the following key. Fossil forms are excluded. The three exclusively fresh-water genera are also excluded because their restricted environment means that confusion with other genera should not occur. Thermosphaeroma is known only from hot inland springs in southern North America. No other sphaeromatid is known from this habitat. Monolistra and Caecosphaeroma are cave-dwelling genera known only from subterranean streams in central and southern Europe (Caecosphaeroma can be distinguished from Monolistra in having the pleon completely fused with the pleotelson in the dorsal mid-line). None of these three genera ever occurs in the sea or in open rivers. Of the remaining genera, which are all marine or estuarine in habit (although some contain species that may occur in rivers in very low salinities), three are not represented in the key. These are Dynameniscus, Cassidias and Stathmos (Fig. 7). These genera were, unwisely, founded on female specimens and, as the form of the adult male is not known, they must be omitted.

Nunomura (1988) described a new genus, Nishimuraia, from Japan. The type species (N. paradoxa Nunomura, 1988) appears to be a species of Gnorimosphaeroma. Nunomura stated that Nishimuraia is eubranchiate, but his illustration shows platybranchiate pleopods in which blood lacunae, not folds, are illustrated. The pleon of N. paradoxa is figured with one suture line extending to each lateral margin but the generic diagnosis states 'Pleon with 2 pairs of distinct suture lines'. The only distinction between Gnorimosphaeroma and Nishimuraia is Nunomura's claim that the uropodal exopod is absent in Nishimuraia. Given the contradictions in Nunomura's paper and the poor quality of his illustrations, N. paradoxa requires re-examination before the validity of Nishimuraia can be determined. Nishimuraia has not been included in the following key.

Basphaeroma Taberner (1988) is a junior synonym of Tholozodium Eleftheriou et al. (1980). Taberner erected Basphaeroma for the species Pseudosphaeroma rhombofrontale (Giambiagi) which had been placed in Tholozodium by Pires (1982) and by Holdich & Harrison (1983). Taberner stated that Basphaeroma differed from Tholozodium in lacking

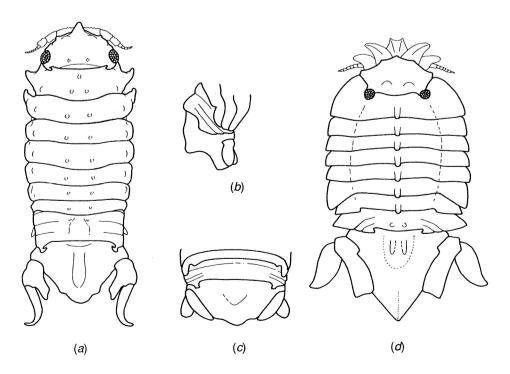


Fig. 7. Examples of sphaeromatid genera known only from females: (a) *Dynameniscus carinatus* Richardson, non-ovigerous female holotype (from a drawing provided by E. W. Iverson); (b) and (c) *Cassidias argentinea* Richardson (from Richardson 1906); (d) *Stathmos coronatus* Barnard (from Kensley 1978).

sutures on the pleon and between the coxal plates and tergites of pereonites 2 to 7, and by having the penes fused at the base. In fact, the sutures of *Tholozodium ocellatum* Eleftheriou et al. (the type species of the genus), are very faint and were discovered using a stereoscan electron microscope. The penes of P. rhombofrontale are only fractionally fused at the base and are not significantly different from those of T. ocellatum.

It should be emphasised that no key covers all the taxonomic characters diagnostic of the groups being separated. A key merely attempts to separate the groups using the smallest number of comparisons. Identifications made using a key should always be considered provisional and should be confirmed by consultation with a taxonomic specialist, or by comparison with reference specimens or detailed published descriptions. As a key provides limited information, it has been decided here to include details of the known distributions of the genera. This information may indicate occasions where the key has misled the reader (e.g. a worker should be suspicious if a specimen from a Mediterranean shore keys out to a genus only previously recorded from a depth of 2000 m off Indonesia!). These distributions are based on the restricted constitutions of the genera as outlined in Harrison & Holdich (1982a, 1982b, 1984) and Harrison (1984a). In addition to the known distribution, the subfamily in which each genus is placed is denoted in the distribution list by the following codes: C, Cassidininae; S, Sphaeromatinae; D, Dynameninae; A, Anciniinae; and T, Tecticipitinae. This gives an indication of the form of pleopods 4 and 5 and can also be used to indicate a failure of the key.

Although the key is based only on the form of the adult male, the structure of the brood pouch of adult females is usually consistent at the generic level. If females are found accompanying the males, an examination of the brood pouch morphology may be helpful in identification of the genus. The brood pouch alone will seldom indicate to which genus the females belong (different genera may share identical brood pouches), but it may indicate to which genera the females do *not* belong. This information may complement the identification of the males made using the key. Details of brood pouch structure for many sphaeromatid genera will be found in Harrison (1984b). See also Kensley (1987) for Harrieta and Javed & Ahmed (1988) for Paraimene.

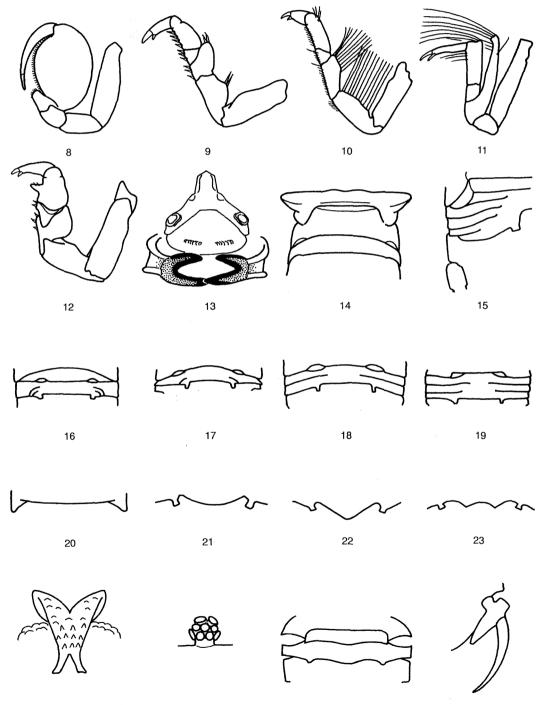
When using the following key it is important to read both parts of each couplet before proceeding. It is also helpful if the animal can be examined when flat, rather than folded. Note that phrases such as 'endopod longer than exopod' refer to the relative positions of the tips of the rami, not to the total length of each appendage.

Key to the Marine and Brackish Water Genera of the Sphaeromatidae (Crustacea: Isopoda)

(based on adult male specimens)

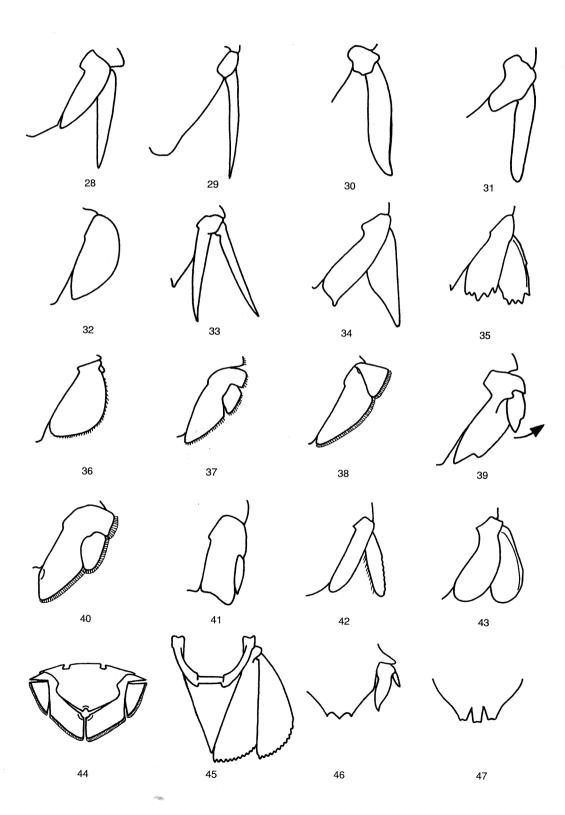
1.	Pereopod 1 markedly subchelate; propodus subovate (Fig. 8)
2(1).	Uropod biramous (e.g. Fig. 28) Tecticeps
2(1).	Uropod uniramous (e.g. Figs 29, 30)
3(2).	Posterior margin of pleon with short posterior projection at each side (these projections articulate with the pleotelson) (Fig. 21)
	Posterior margin of pleon lacking short projections (Fig. 20)
4(1).	Dorsal surface of cephalosome with 2 long, slender, anteriorly directed processes, 1 each side of epistome in dorsal view. Epistome narrow, greatly extended anteriorly, approx. 2×
	length of processes (Fig. 99)
	Cephalosome without long anterior processes. Epistome considerably shorter than that shown in Fig. 99
5(4).	Pereopod 1 scythe-shaped; merus with very long superior lobe (Fig. 11) Paracassidina
	Pereopod 1 ambulatory or weakly prehensile; merus may bear a short superior lobe, but not as in Fig. 11
6(5).	Pereopod 1 robust; inferior margin of propodus with blunt, conical, median tubercle (Fig. 12)
	Pereopod 1 slender or, if robust, propodus without median, conical tubercle (may bear
	spines)

7(6).	Mandibles with incisor processes greatly elongate, flat, deeply bifid (Fig. 13)
8(7).	Mandibles with incisor processes short, not as in Fig. 13
9(8).	Anterior margin of cephalosome not as in Fig. 14. Eyes usually obvious. Pleon with less than 4 suture lines at each side (suture lines may be absent) 9 Endopod of pleopod 1 modified as extremely long filamentous 'thread' (approx. 5 × length of exopod) Neocassidina Endopod of pleopod 1 lamellar (or absent), not modified as long 'thread' 10

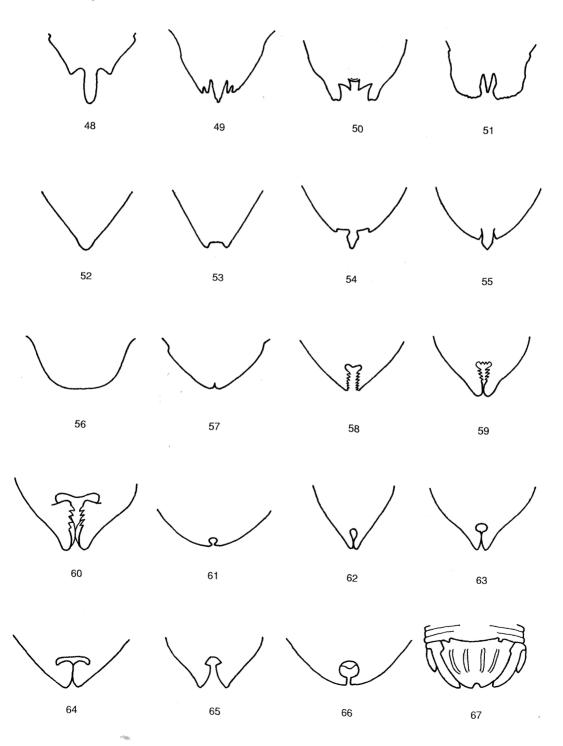


10(9),	Dorsal surface of body bearing large, prominent, spherical, tuberculate processes (each as in Fig. 25). Epistome deeply bifid (Fig. 24), projecting anteriorly beyond cephalosome in dorsal view
	Body not covered with large, prominent, tuberculate processes. If epistome bifid, distal tips rounded, not acute
11(10).	Uropod without an exopod; formed as one broad plate held alongside pleotelson (Fig. 32). Articles 1 and 2 of A1 peduncle not extended anteriorly as flattened plates
	Exopod of uropod present (may be minute and non-obvious, and housed in a notch on the external margin of the endopod). Articles 1 and 2 of A1 peduncle may or may not be extended anteriorly as flattened plates
12(11).	Article 1 of A1 peduncle with antero-distal angle extended distally as long, narrow, flat lobe (Fig. 101)
12(12)	anteriorly beyond cephalosome in dorsal view, e.g. Figs 100, 102, 103)
13(12).	Exopods of pleopods 1-3 with pronounced marginal teeth (especially obvious on pleopod 2) (Fig. 88). Penes and sternite of pereonite 7 separated from point of attachment of pleopod 1 by transverse band of cuticle bearing an elliptical region each side of mid-line (Fig. 89)
	Exopods of pleopods 1-3 without marginal teeth, at most slightly crenulate (Fig. 91). Penes and sternite of pereonite 7 adjoining point of attachment of pleopod 1 (Fig. 92) 20
14(13).	Pereonite 7 with pronounced, dorsal, posteriorly directed extension. Extension forming broad, finger-like process or flat, broad shield covering pleotelson
15(14).	Uropod with rami subequal, narrow, styliform, extending beyond pleotelsonic apex (Fig. 33). Body extremely flattened (approx. $5 \times$ as wide as deep), smooth Platycerceis Uropod with rami markedly unequal in length or, if subequal, flattened not styliform. Body not extremely flattened (less than $3 \times$ as wide as deep). Pleotelson (at least) with 1 or
16(15).	more tubercles or ridges
10(15).	endopod. Endopod not reaching level of pleotelsonic apex (e.g. Fig. 31)
	Both rami of uropod flattened. Endopod not reduced, reaching level of pleotelsonic apex (e.g. Figs 34, 35)
17(16).	Pleotelsonic apex with a notch bearing a pronounced median tooth which extends posteriorly beyond the level of the notch opening (e.g. Fig. 49)
	Pleotelsonic apex with a deep notch which either lacks a median tooth (e.g. Fig. 50) or has a median tooth which does not extend posteriorly beyond the level of the notch opening (e.g. Fig. 51)
18(16).	Anterior margin of cephalosome extended forwards; apex of median rostral process directed postero-ventrally. Epistome never visible in dorsal view (e.g. Figs 94, 95. Never as Fig. 98)
	Anterior margin of cephalosome not extended. Median rostral process directed anteroventrally. Epistome visible in dorsal view when cephalosome is rotated dorsally to bring mouthparts forwards (e.g. Fig. 98)
19(18).	Anterior margin of cephalosome dorso-ventrally flattened (e.g. Fig. 94). Article 1 of A1 peduncle with distal angles elongate, acute (Fig. 97). Exopod of uropod acute (e.g. Fig. 34)
	Anterior margin of cephalosome conical, blunt, not dorso-ventrally flattened (Fig. 95). Article 1 of A1 peduncle with distal angles blunt (e.g. Fig. 96). Exopod of uropod truncate, dentate (Fig. 35)
20(13).	Pereonite 6 with dorsal, posterior margin extended posteriorly as 1 or 2 pronounced, spine-like projections. Projections reaching level of pleotelson
21(20).	2 lobes; without freely projecting spine-like extensions
22(20).	Pereonite 6 with 2 spine-like projections, 1 each side of mid-line
	Pereonite 7 with posterior margin similar to that of preceding pereonites, or with 2 lobes, or transverse ridges, or 2 short acute processes, but not with 1 median spine
23(22).	Pleotelson with a subapical foramen connected to the apex by a narrow slit (Figs 62, 63)
	Pleotelson without a subapical foramen (may have an open notch)

24(23).	Pleotelsonic apex entire, acute (e.g. Fig. 52), or weakly emarginate with a longitudinal
	ventral groove (Fig. 53)
	Pleotelsonic apex with a terminal notch bearing a median tooth (e.g. Figs 54, 55)
	Zuzara
25(22).	Pleon with dorsal posterior margin bearing 1 median, posteriorly directed, spine-like process
	(e.g. Figs 84, 85), or a broad, flat, truncate process (e.g. Fig. 86)
	Posterior margin of pleon without a freely projecting median process (may be slightly
	deflected as in Figs 21-23)

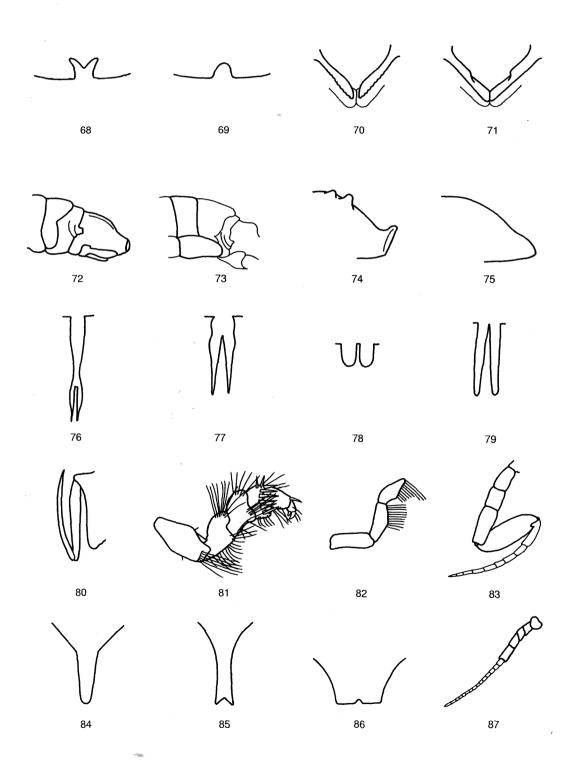


26(25).	Uropod with rami subequal, broadly rounded (e.g. Fig. 43). Apex of pleotelson with a narrow slit or foramen. Slit or foramen usually lined with small teeth (e.g. Figs 58, 59) Dynoide
	Uropod with endopod reduced, exopod long (e.g. Fig. 31). Apex of pleotelson notched
27(26).	Apical notch of pleotelson with a median tooth (e.g. Fig. 68)
28(25).	Endopods of uropods meet in mid-line posterior to pleotelsonic apex, and exopods reduced housed in notches on margins of endopods (e.g. Fig. 44)
29(28).	Proximal region of uropod, anterior to exopod, subrectangular (Fig. 40). Pleon without dorsa suture lines ————————————————————————————————————
30(28).	Proximal region of uropod, anterior to exopod, acute, spine-like (as in Fig. 44). Pleon with 2 suture lines extending to each lateral margin (e.g. Fig. 19) Leptosphaeroma Posterior margin of pleotelson with broad, flat, triangular extension. Extension longer than main dome of pleotelson. Uropod with rami subequal, broad, lamellar, with distally rounded, serrulate margins extending beyond pleotelsonic apex (Fig. 45, ventral view) Cephalosome with broad, dense, anterior patch of short setae
31(30).	Posterior margin of pleotelson without flat acute extension as shown in Fig. 45. Uropode relatively shorter than those in Fig. 45. Cephalosome without dense, anterior patch of setae (may bear sparse setae over entire surface)
32(31).	Apex of pleotelson either without enclosed foramen, or with antero-dorsally, dorsally, or postero-dorsally directed foramen, but never a posteriorly directed foramen in the form of a tube. Uropods various. Exopods of pleopods 4 and 5 folded or flat
33(32).	Fig. 61)
34(33).	Exopod of uropod reduced, housed in a notch on external margin of endopod, or positioned anterior to endopod. Exopod not capable of horizontal movement (e.g. Figs 36–38) Exopod of uropod not housed in notch on endopod. If reduced, exopod still capable of
35(34).	horizontal movement (e.g. Fig. 39, ventral view)
36(35).	105). Articles of A1 peduncle may or may not be expanded
37(35).	Exopod of uropod triangular, lying anterior to endopod (Fig. 38)
38(37).	Pereonite 7 reaching lateral margins of body in dorsal view
	40

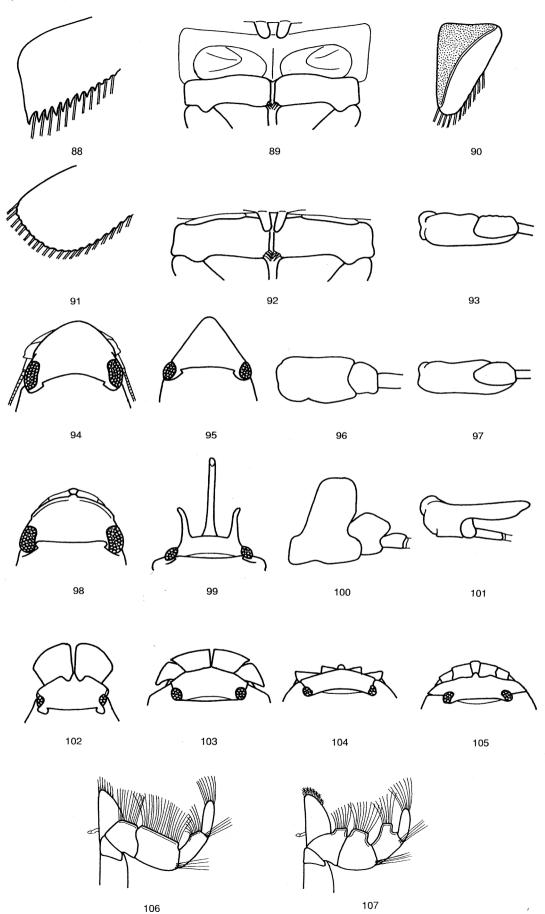


41(34) <u>.</u>	Article 1 of A1 peduncle expanded anteriorly as large plate (e.g. Fig. 102) Amphoroidea Article 1 of A1 peduncle not obviously expanded as flattened plate
42(41).	Penes narrow, elongate, proximally fused, tapering to very acute tips. Exopods of pleopods 4 and 5 flat, without transverse folds; endopods with transverse folds. Apex of pleotelson with foramen
	Penes separate or joined only at base; tips usually rounded. Exopods of pleopods 4 and 5 with or without folds. (If penes appear proximally fused with acute tips, then exopods of pleopods 4 and 5 have transverse folds.) Apex of pleotelson with or without foramen
43(42).	Body very flattened; pereonite 7 not reaching lateral margins in dorsal view (Fig. 26). Exopod of uropod styliform, curved, $2 \times$ length of endopod (Fig. 27)
44(43).	Fig. 26)
45(44).	Pleotelson without subapical foramen
46(45)	Pereonite 6 subequal in length to pereonite 5 in dorsal mid-line, not posteriorly bilobed. Pereonite 7 without short, acute, posterior projections
46(45).	Exopod of uropod cylindrical, approx. $5 \times$ length of endopod
47(46).	Dorsal surface of entire body covered with large separate tubercles. Pleopods 4 and 5 each with exopod flat, membranous; only endopod bearing transverse folds Sphaeramene Entire body not covered with large separate tubercles (pleotelson may bear large tubercles).
48(47).	Pleopods 4 and 5 each with both rami bearing transverse folds
	Pleopod 1 with endopod not obviously thickened. Penes tapering, fused at base (e.g. Fig. 77) 49
49(48).	Ventral margins of pleotelson with out-turned ridges which do not meet in posterior mid-line (e.g. Fig. 70, ventral)
50(44).	(e.g. Fig. 71), or without out-turned ridges
51(50).	A2 not enlarged, not reflexed (e.g. Fig. 87). Coxal plates of pereonite 5 not appearing to overlap those of both pereonites 4 and 6 when animal folded. Eyes various 51 Article 1 of A1 peduncle with infero-distal angle extended as acute process (Fig. 93). Uropod
	as in Fig. 33
52(51).	Apex of pleotelson with long, thick median process (Fig. 48). Uropod with rami subequal, rounded (e.g. Fig. 43). Pleopods 4 and 5 with both rami bearing transverse folds Holotelson
	Apex of pleotelson without long, thick median process; if apex appears tridentate, then exopods of pleopods 4 and 5 without transverse folds. Uropods various
53(52).	Apex of pleotelson tridentate in dorsal view (i.e. with a notch bearing a median tooth) (e.g. Figs 46, 47)
	Apex of pleotelson not tridentate; either with a notch which does not bear a median tooth, or without a notch
54(53).	Exopod of uropod minute; endopod not reaching pleotelsonic apex (Fig. 46). All coxal plates acute, separate
55(54).	Exopod of uropod narrow, subcylindrical or elliptical in cross-section; at least 2× length of endopod. Posterior margin of pleon with or without short, obtuse projection each side
	of mid-line

Exopod of uropod at least $3 \times$ length of endopod (or endopod apparently absent)	. 31
Exopod of uropod, at most, $2 \times$ length of endopod (may be subequal to or shorter th	nan
endopod)	59
Apex of pleotelson tapering, acute. Exopod of uropod extending just beyond pleotelson	
tip	?tta
Apex of pleotelson blunt, truncate, with median notch. Exopods of uropods extending beyo	ond
pleotelsonic apex for most of their length	58



5 ⁸ (57),	Pleotelson with large, broad, tuberculate, longitudinal, median ridge, with smaller longitudinal ridge at each side
	Pleotelson without a median longitudinal ridge, but with a smooth conical elevation each side of mid-line
59(56).	Pereopod 2 heavily calcified, modified for clasping (i.e. subterminal articles broad, flattened superior to inferior, with pronounced inferior spines). Pereopods 3–7 slender
	Pereopod 2 not heavily calcified or modified for clasping; slender, or flattened anterior to
	posterior. Pereopods 3-7 various
60(59).	Endopod of pleopod 3 with several transverse folds
61(60).	Endopod of pleopod 3 flat, without transverse folds
01(00).	(e.g. Fig. 10). Penes short (e.g. Fig. 78)
	Pereopods 1–3 each with ischium and merus without dense superior row of long, stiff, setae
	(pereopods may bear many long setae over all surfaces, but in this case penes are long, e.g. Fig. 79)
62(61).	Apex of pleotelson smoothly rounded and upturned (in lateral view, Fig. 74). Anterior region
	of pleotelson with several prominent tubercles each side of mid-line
	various (may be absent)
63(62).	Pleotelson with 4 pronounced, continuous, longitudinal ridges, and pleon with 2 suture lines
	extending to each lateral margin (Fig. 67)
	Pleotelson smooth or tuberculate. If tuberculate, pleon with suture lines extending to posterior
64(63).	margin (as in Fig. 16)
01(05).	thickened (Fig. 90). Pleotelson with pronounced apical notch. Pleopods 4 and 5 each with
	both rami bearing transverse folds
	Pleopod 1 with inner $\frac{1}{2}$ of endopod not noticeably thickened. Pleotelson with or without
65(64).	apical notch. Exopods of pleopods 4 and 5 with or without transverse folds 65 Pleon with 1 or 2 suture lines reaching lateral margins at each side (e.g. Fig. 19). Apex
	of pleotelson smoothly rounded, without apical notch (e.g. Fig. 56)
	Pleon with suture lines reaching posterior margin, not lateral margins (lines may reach postero-lateral angles, but in this case the pleotelson has a vertical apical notch which is
	not obvious in dorsal view)
66(65).	Pleopods 4 and 5 each with both rami bearing transverse folds
(7)(()	Exopods of pleopods 4 and 5 flat, without transverse folds
67(66).	Endopod of uropod broad, apically emarginate; exopod short, narrow, acute (Fig. 41) Cassidinopsis
	Uropod with rami relatively narrow, apically rounded, subequal or exopod slightly longer than
	endopod (e.g. Fig. 42)
68(66).	Eyes minute, not obvious. Mandible with palp reduced (with only 1 apical seta) or absent.
	Pereopods 3-6 robust, hirsute (e.g. Fig. 81)
	epistome). Pereopods not as robust as in Fig. 81
69(68).	Apex of pleotelson smoothly rounded (e.g. Fig. 56) or acute (e.g. Fig. 52), without median
	apical notch
	Apex of pleotelson narrowly truncate or with apical notch (notch may be very short and narrow or may be vertical and not obvious in dorsal view)
70(69).	Endopods of pleopods 4 and 5 with obvious transverse folds; exopods flat
	Exosphaeroma
	Pleopods 4 and 5 each with both rami flat, membranous, without transverse folds (pleopods
71(60)	may appear opaque and 'fleshy', but no indication of folding) Exosphaeroides
71(69).	Body flattened. Apex of pleotelson with short, median incision (Fig. 57). Exopod of uropod just shorter than endopod and apically rounded. Endopods of pleopods 4 and 5 flat,
	without transverse folds
	Body not flattened. Apex of pleotelson with deep vertical notch, or narrowly truncate. Exopod
	of uropod various. Endopods of pleopods 4 and 5 with transverse folds (folds may be
	weak)



Apex of pleotelson narrowly truncate, with very shallow ventral longitudinal groove, or with 72(71). pronounced apical notch which is clearly visible in dorsal view. Dorsal surface of body Apex of pleotelson with deep, narrow, vertical notch; dorsal lip of notch overhanging in lateral view, obscuring notch in dorsal view. Pereon (at least) dorsally smooth Maxillipedal palp without inferior lobes, margins straight (Fig. 106) Sphaeroma 73(61). 74(33). Apex of pleotelson with enclosed postero-dorsally directed foramen. Coxal plate of pereonite 7 only visible dorsal to coxal plate of pereonite 6 (Fig. 73). Pereonite 1 with lateral regions thickened, appearing to have a distinct coxal plate; this lateral region extended anteriorly Apex of pleotelson with deep, narrow, vertical slit. Coxal plate of pereonite 7 visible as a rod of cuticle postero-ventral to coxal plate of pereonite 6. Pereonite 1 without apparent coxal plate, lateral regions not thickened, extended anteriorly only to mid point of eye Body smooth; pleotelson with 1 posteriorly directed boss each side of mid-line. Exopod of 75(55). uropod 2× length of endopod, scimitar-like with acute, out-turned tip. Lateral margin of pereonite 1 directed postero-ventrally, broadly truncate. Coxal plate of pereonite 5 extending ventrally further than other coxal plates Harrieta Pleotelson, pleon and posterior region of pereon usually with tubercles, ridges and long setae. Exopod of uropod lanceolate; shorter than, or extending just beyond, endopod. Lateral margin of pereonite 1 directed postero-ventrally, but acute or narrowly rounded, not broadly truncate. Coxal plate of pereonite 5 not extended ventrally more than other coxal 76(42). Appendix masculina recurved (Fig. 80). Apex of pleotelson with narrow, deep, T-shaped slit Appendix masculina not recurved, acute tip extending beyond endopod of pleopod 2. Apex

exoped dominant univamous

Annotated List of Genera

Amphoroidea Milne Edwards, 1840 (D)

Synonyms. None.

Description. Hurley & Jansen, 1977: 27.

Type species. Amphoroidea typa Milne Edwards, 1840.

Approximate number of species. 6.

Distribution. S. and E. Australia; New Zealand; South America (Pacific coast). Intertidal and shallow sublittoral; especially on algae.

Amphoroidella Baker, 1908 (D)

Synonyms. None.

Description. Harrison, 1984a: 276.

Type species. Amphoroidea (Amphoroidella) elliptica Baker, 1908.

Approximate number of species. Monotypic.

Distribution. S. Australia. Shallow sublittoral; has been collected from sponges.

Ancinus Milne Edwards, 1840 (A)

Synonyms. None.

Description. Pires, 1987: 121; Glynn & Glynn, 1974: 401.

Type species. Naesa depressa Say, 1818.

Approximate number of species. 7.

Distribution. New World (Pacific coast from California to Panama; Atlantic coast from Massachusetts to Brazil). Intertidal and shallow sublittoral on sandy beaches.

Anoplocopea Racovitza, 1907 (C)

Synonyms. None.

Description. Racovitza, 1907: LXXXIV.

Type species. Anoplocopea hanseni Racovitza, 1907.

Approximate number of species. Monotypic.

Distribution. N. Mediterranean. Intertidal; under stones.

Artopoles Barnard, 1920 (D)

Synonyms. None.

Description. Kensley, 1978: 115.

Type species. Artopoles natalis Barnard, 1920.

Approximate number of species. 2.

Distribution. S. and SE. Africa. Sublittoral (10-20 m).

Bathycopea Tattersall, 1905a (A)

Synonyms. Ancinella Hansen, 1905.

Description. Silva, 1971: 215.

Type species. Bathycopea typhlops Tattersall, 1905a.

Approximate number of species. 4.

Distribution. Atlantic Ocean off Ireland and S. Africa; NW. Pacific Ocean; California; SE. Australia (N. L. Bruce, *in litt.*). Deep water (Atlantic, 680-830 m; NW. Pacific, 1600-4000 m) or sublittoral (California, 2-20 m).

Botryias Richardson, 1910 (C)

Synonyms. None.

Description. Richardson, 1910: 30.

Type species. Botryias fructiger Richardson, 1910.

Approximate number of species. Monotypic.

Distribution. Indonesia. Deep water (330 m).

Caecocassidias Kussakin, 1967 (D)

Synonyms. None.

Description. Kussakin, 1967: 237; Harrison, 1984b: 371.

Type species. Caecocassidias patagonica Kussakin, 1967.

Approximate number of species. Monotypic.

Distribution. Atlantic Ocean (off Argentina N. of Falkland Islands). Deep water (400-680 m).

Caecosphaeroma Dollfus, 1896 (C)

Synonyms. Includes Vireia Viré, 1903 as a subgenus.

Description. Sket, 1986: 427.

Type species. Caecosphaeroma virei Dollfus, 1896.

Approximate number of species. 2.

Distribution. S. Europe (inland). Freshwater underground streams.

Calcipila Harrison & Holdich, 1984 (S)

Synonyms. None.

Description. Harrison & Holdich, 1984: 319.

Type species. Calcipila cornuta Harrison & Holdich, 1984.

Approximate number of species. Monotypic.

Distribution. E. Australia (S. Queensland). Sublittoral (4-12 m); on particulate substrata.

Campecopea Leach, 1814 (C)

Synonyms. None.

Description. Naylor, 1972: 36.

Type species. Oniscus hirsutus Montagu, 1804.

Approximate number of species. Monotypic.

Distribution. E. Atlantic (from Wales to W. Africa). Intertidal; on rocky shores.

Cassidias Richardson, 1906 (D) (only females known)

Synonyms. None.

Description. Richardson, 1906: 20.

Type species. Cassidias argentinea Richardson, 1906.

Approximate number of species. Monotypic.

Distribution. Argentina (off River Plate). Sublittoral (20 m).

Cassidina Milne Edwards, 1840 (C)

Synonyms. None.

Description. Hurley & Jansen, 1977: 71.

Type species. Cassidina typa Milne Edwards, 1840.

Approximate number of species. Monotypic.

Distribution. New Zealand. Intertidal (lower shore) and sublittoral (0-1300 m).

Cassidinella Whitelegge, 1901 (S)

Synonyms. None.

Description. Whitelegge, 1901: 241.

Type species. Cassidinella incisa Whitelegge, 1901.

Approximate number of species. Monotypic.

Distribution. E. Australia (New South Wales). Sublittoral (78-146 m).

Cassidinidea Hansen, 1905 (C)

Synonyms. Cassidisca Richardson, 1905; ?Dies Barnard, 1951.

Description. Hansen, 1905: 113, 131.

Type species. Naesa ovalis Say, 1818.

Approximate number of species. 8 (including 6 in Dies).

Distribution. N. America (Atlantic coast); Caribbean and (as Dies spp.) Brazil, S. Africa, India. Very shallow brackish water; especially coastal lagoons.

Cassidinopsis Hansen, 1905 (D)

Synonyms. None.

Description. Hansen, 1905: 108, 128.

Type species. Cassidina emarginata Guérin-Méneville, 1843.

Approximate number of species. Monotypic.

Distribution. Sub-Antarctic (circum-polar on Tierra del Fuego, Falkland Islands, South Georgia, Crozet Islands, Kerguelen Island, Macquarie Island). Sublittoral (0-32 m); on algae.

Ceratocephalus Woodward, 1877 (S)

Synonyms. Bregmocerella Haswell, 1884.

Description. Woodward, 1877: 658; Haswell, 1884: 1004 (as Bregmocerella).

Type species. Ceratocephalus grayanus Woodward, 1877.

Approximate number of species. Monotypic.

Distribution. E. Australia (New South Wales and Tasmania). Sublittoral (18-70 m); on particulate substrata.

Cerceis Milne Edwards, 1840 (D)

Synonyms. Paradynamene Richardson, 1905; Circeis Baker, 1908 (unjustified emendation).

Description. Harrison & Holdich, 1982b: 433.

Type species. Cerceis tridentata Milne Edwards, 1840.

Approximate number of species. 10.

Distribution. Australia; Philippines; Malaya; Andaman Islands (NE. Indian Ocean); India; Kenya (personal observation). Intertidal and shallow sublittoral (0–13 m); has been collected from floating algae.

Chitonopsis Whitelegge, 1902 (C)

Synonyms. None.

Description. Holdich & Harrison, 1981a: 628.

Type species. Chitonopsis spatulifrons Whitelegge, 1902.

Approximate number of species. 2.

Distribution. S. and E. Australia; S. Indonesia. Sublittoral (6-91 m); on particulate substrata.

Cilicaea Leach, 1818 (S)

Synonyms. None.

Description. Harrison & Holdich, 1984: 346.

Type species. Cilicaea latreillei Leach, 1818.

Approximate number of species. 13.

Distribution. New Zealand; Australia; Indonesia; S. Philippines; Sri Lanka; S. Africa. Intertidal or, more usually, sublittoral (0-289 m).

Cilicaeopsis Hansen, 1905 (S)

Synonyms. None.

Description. Harrison & Holdich, 1984: 332.

Type species. Cilicaea granulata Whitelegge, 1902.

Approximate number of species. 6.

Distribution. W. and E. Australia; Coral Sea (E. of Australia); Indonesia; S. Philippines; Sri Lanka. Sublittoral (3-175 m); usually on particulate substrata.

Cliamenella Kussakin & Maljutina, 1987 (S)

Synonyms. None.

Description. Kussakin & Maljutina, 1987: 59 (in Russian with figures); Kussakin, 1979: 445 as Dynamenella fraudatrix (in Russian, with figures).

Type species. Dynamenella fraudatrix Kussakin, 1962.

Approximate number of species. Monotypic.

Distribution. Sea of Japan. Intertidal and sublittoral (0-8 m); among rocks with algae (can withstand significant reductions in salinity).

Clianella Boone, 1923 (S)

Synonyms. Paradynoides Loyola e Silva, 1960; Dynoidella Pillai, 1965.

Description. Harrison & Holdich, 1984: 363.

Type species. Clianella elegans Boone, 1923.

Approximate number of species. 5.

Distribution. Brazil; Tierra del Fuego; E. Australia; India. Intertidal; on rocky shores.

Cymodetta Bowman & Kühne, 1974 (C)

Synonyms. None.

Description. Holdich & Harrison, 1983: 127.

Type species. Cymodetta gambosa Bowman & Kühne, 1974.

Approximate number of species. 2.

Distribution. E. Australia. Shallow brackish water; usually found in estuaries.

Cymodoce Leach, 1814 (S)

Synonyms. Cymodice Leach, 1815 (lapsus calami?); Cymodyce Leach, 1815 (err. typ.?); Cymodocea Leach, 1818 (unjustified emendation).

Description. Harrison & Holdich, 1984: 301.

Type species. Cymodoce truncata Leach, 1814.

Approximate number of species. 23 (+9?).

Distribution. Japan; Korea; Indo-China; Malaya; Indonesia; Australia; India; Persian Gulf (personal observation); Red Sea; E. and S. Africa; Mediterranean; Atlantic coast of Europe; U.K.; Brazil. Intertidal and sublittoral (0-1547 m); usually shallow sublittoral and intertidal.

Cymodocella Pfeffer, 1887 (D)

Synonyms. None.

Description. Harrison & Holdich, 1982a: 106; Hurley & Jansen, 1977: 30.

Type species. Cymodocella tubicauda Pfeffer, 1887.

Approximate number of species. 13.

Distribution. Southern Hemisphere (circum-polar on Aukland Island; New Zealand; Chile; Brazil; South Sandwich Islands; South Georgia; Antarctica). Intertidal (on rocky shores) and sublittoral (0-245 m).

Cymodopsis Baker, 1926 (S)

Synonyms. None.

Description. Baker, 1926: 264.

Type species. Sphaeroma latifrons Whitelegge, 1902.

Approximate number of species. 4?.

Distribution. E. Australia (New South Wales). Sublittoral (44-49 m).

Dies (see Cassidinidea)

Discerceis Richardson, 1905 (D)

Synonyms. None.

Description. Richardson, 1905: x, 309.

Type species. Cilicaea granulosa Richardson, 1899.

Approximate number of species. 2.

Distribution. Mexico (Atlantic and Pacific coasts). Sublittoral (37-46 m).

Dynamene Leach, 1814 (D)

Synonyms. Nesaea Leach, 1814; Naesea Leach, 1814; Naesa Leach, 1815; Nesa Leach, 1818 (err. typ.?); Prochonaesea Hesse, 1873; Nesea Thomson, 1879; Sorrentosphaera Verhoeff, 1944.

Description. Holdich & Harrison, 1980: 163.

Type species. Oniscus bidentatus Adams, 1800.

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Approximate number of species. 8.

Distribution. U.K.; Atlantic coast of Europe; Mediterranean; NW. Africa; S. and E. Australia. Intertidal (on algae and in cryptic habitats) and shallow sublittoral (0-33 m).

Dynamenella Hansen, 1905 (D)

Synonyms. None.

Description. Harrison & Holdich, 1982a: 89.

Type species. Dynamene perforata Moore, 1901.

Approximate number of species. 11.

Distribution. Red Sea; Seychelles; India; Indo-China; Japan; Korea; E. Australia; Gambier Islands; Pacific coast of Panama; Brazil; Caribbean; Bermuda. Intertidal and shallow sublittoral (0-5 m).

Dynameniscus Richardson, 1905 (C) (only females known)

Synonyms. None.

Description. Richardson, 1905: x-xi, 319 (as Cilicaea).

Type species. Cilicaea carinata Richardson, 1900.

Approximate number of species. Monotypic.

Distribution. NE. Atlantic (off Georgia, U.S.A.); Caribbean. Deep water (804-1033 m).

Dynamenoides Hurley & Jansen, 1977 (D)

Synonyms. None.

Description. Hurley & Jansen, 1977: 36.

Type species. Dynamenoides vulcanatus Hurley & Jansen, 1977.

Approximate number of species. 2.

Distribution. New Zealand. Intertidal; on rocky shores.

Dynamenopsis Baker, 1908 (D)

Synonyms. None.

Description. Harrison & Holdich, 1982a: 105.

Type species. Dynamenopsis obtusa Baker, 1908.

Approximate number of species. 2.

Distribution. W. and S. Australia; New Zealand. Intertidal; on rocky shores.

Dynoides Barnard, 1914 (S)

Synonyms. Dynoidella Nishimura, 1976a.

Description. Harrison & Holdich, 1984: 363-370.

Type species. Dynoides seratisinus Barnard, 1914.

Approximate number of species. 5.

Distribution. Japan; Korea; N. China; E. Australia; S. Africa. Intertidal; on rocky shores.