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The morphology of the sphaeromatid brood pouch (Crustacea: Isopoda: Sphaeromatidae)

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The structure of the brood pouch and mouthparts of ovigerous female sphaeromatids is described. Taxonomically, these are shown to be important generic characters and some attempt is made to relate structure to function. Expanded maxillipeds (which produce a current of water through the marsupium) are shown to occur only in genera which have oostegites overlapping in the mid-line and reaching the mouthparts anteriorly. The reduction of the mouthparts of some genera cannot be explained, but it may conserve energy at the final moult. No platybranchiate genera (subfamily Cassidiniinae) have the mouthparts reduced but some have the maxilliped expanded. Some correlation between brood pouch structure and habitat is suggested. Genera with a brood pouch composed only of oostegites (and hence liable to disruption by turbulence and particle abrasion) occur sublittorally or, if intertidal, adopt a protected, crevice dwelling habit. Genera with a brood pouch composed of large opposing pockets (which are more able to resist disruption) occur intertidally or in shallow water, and may be found in wave-washed sand. Some wood-boring species of the genus *Sphaeroma* Latreille show a reduced number of oostegites when compared with non-boring species. This presumably relates to their burrowing habit.

KEY WORDS:—Isopoda – Sphaeromatidae – genera – females – morphology – brood pouch – mouthparts.

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INTRODUCTION

Representatives of the family Sphaeromatidae (the marine 'pill-bugs') are common in coastal waters world-wide. Recent taxonomic investigations of this family (e.g. Holdich & Harrison, 1981a; Harrison & Holdich, 1982a) have shown the form of the brood pouch of the adult ('ovigerous') female to be an extremely useful generic character. Unfortunately this structure has been much neglected by previous research workers, and for many genera brood pouch descriptions do not exist. The potential taxonomic usefulness of such descriptions has prompted a complete review and reassessment of ovigerous female sphaeromatids and the results of that investigation are presented here.

Prior to 1905 the brood pouch of ovigerous female sphaeromatids had virtually been ignored. In 1905, however, Hansen published his radical revision of the Sphaeromatidae in which he introduced two major features of taxonomic importance: (1) the structure of the pleopods (of all specimens); (2) the form of the brood pouch and mouthparts of ovigerous females. Hansen divided the family into major groups based on pleopod form. This character was instantly accepted by researchers and has been used continuously ever since. Unfortunately, the importance of the pleopod morphology appears to have overshadowed Hansen's work on the structure of the ovigerous female, which has received little subsequent attention.

For ovigerous specimens Hansen noted two important characters which appeared consistent at a generic level, (1) that while the mouthparts of ovigerous females of some genera resembled the mouthparts of males and immature specimens, the mouthparts of ovigerous females of other genera were considerably modified ('metamorphosed'), and (2) that the brood pouch could take a number of different forms for different genera.

In genera having all the mouthparts metamorphosed, during a cursory examination the modification is most obvious in the form of the mandibles. These appendages lose their usual dark brown incisor processes and are represented only by pale lobes which abut one another in the mid-line. Probably because this loss of coloration is so obvious, most authors since Hansen have included in their generic diagnoses statements to the effect, "ovigerous female with mouthparts metamorphosed" (or "not metamorphosed"). Unfortunately, few authors have followed Hansen's lead and described the form of the brood pouch; most have either ignored this structure or referred to Hansen's (1905) work.

A complete review here of the brood pouch descriptions which do exist might prove of little value beyond that of a checklist. Many authors' 'descriptions' are inadequate, while some are now known to be incorrect. It is worth noting that while Hansen's work on the brood pouch is by far the most important and extensive work to date, his brood pouch descriptions were inaccurate for 12 of the 19 genera he described! For these reasons it is not intended here to give a detailed discussion of the published literature. Rather than rely on this literature, the present author has examined preserved specimens belonging to as many genera as possible and the following descriptions are based on these personal observations unless otherwise stated. The descriptions given here are intended to supersede previously published descriptions and where discrepancies occur the current descriptions should (in the author's opinion) be accepted as the more accurate, regardless of whether the discrepancy has been discussed.

For the purpose of this work an 'ovigerous female' has been defined as any female with the brood pouch fully formed, regardless of whether a brood is present or not.

Ovigerous ('egg bearing') females retain the young, which are housed in specialized structures on the ventral percon. Several types of structure may be present, and different genera show different arrangements, but Fig. 1 gives a generalized view showing most of the possibilities. In the present work the sum of all the specialized features shown by any one female will be referred to as the 'brood pouch', regardless of the component structures.

The most common component in sphaeromatids (as in most peracarid crustaceans) is the 'oostegite' (or 'brood plate' or 'brood lamella'). This is a thin, flat plate of cuticle arising from the ventral surface near the base of a pereopod and extending towards the mid-line. Oostegites may be of various sizes and shapes, but always occur as a pair on any one segment.

Also present may be a fold of cuticle, either extending from the posterior margin of the ventrum and opening anteriorly, or extending from the anterior margin to open posteriorly. Such a structure is referred to here as a 'pocket' or 'ventral pocket', and may be short (e.g. sap in Fig. 1) or long (e.g. lpp in Fig. 1).

The enclosed space ventral to the sternites, produced by the presence of oostegites, pockets, or a combination of the two, is here referred to as a 'marsupium'.

In addition to, or instead of, the above structures, the ovigerous females of

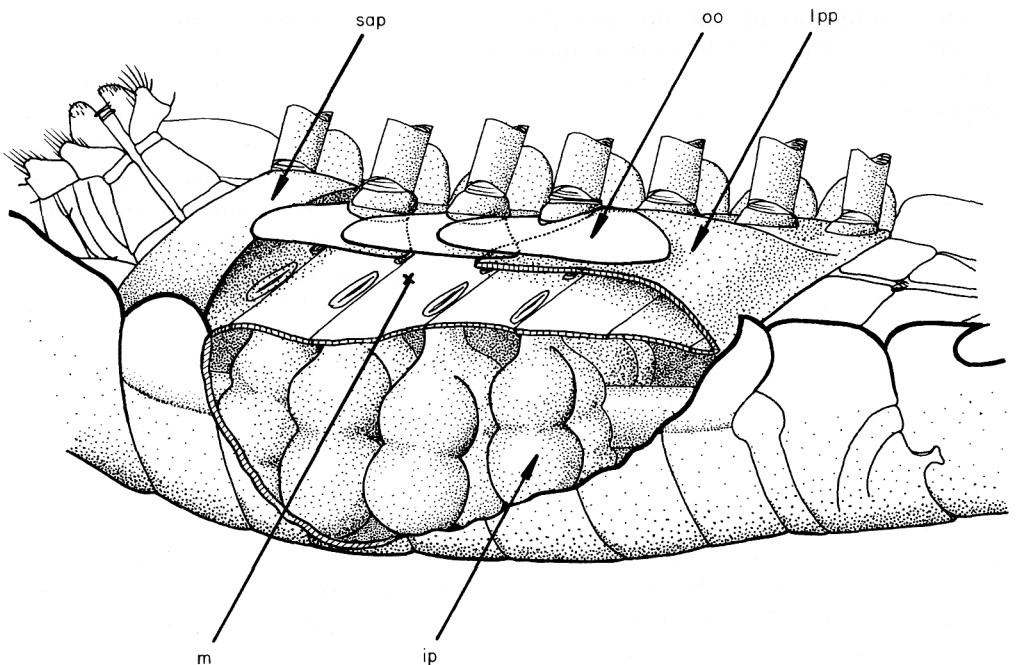


Figure 1. Generalized ovigerous female illustrating possible brood pouch components. (sap, short anterior pocket; oo, oostegite; lpp, large posterior pocket; m, marsupium; ip, internal pouch).

some genera bear paired invaginations of the ventral cuticle. These extend into the body cavity but open ventrally via narrow slits. Such invaginations are referred to here as 'internal pouches'.

As noted above, as well as bearing a brood pouch, ovigerous females of some genera have the mouthparts markedly modified. This metamorphosis usually takes the form shown in Fig. 2, but is more marked in species of *Dynamene* Leach (See Holdich, 1968a: 147) and less marked in some other genera (see Discussion below).

To avoid confusion when isolating ovigerous specimens, it should be noted that non-ovigerous females (i.e. females at the moult stage preceding the ovigerous condition) may bear indications of a developing brood pouch. In genera bearing oostegites, these are present in the non-ovigerous female as short, narrow, cylindrical, cuticular processes which may be referred to as 'oostegite buds'. In genera having internal pouches, these may be seen forming through the ventral cuticle of non-ovigerous females as faint discs. Pockets are not represented in non-ovigerous females, and non-ovigerous females never have the mouthparts metamorphosed.

In the present study it has been possible to trace or examine only a small number of ovigerous specimens for some genera, but where doubt exists as to the exact form of a structure, this has been indicated in the text. Particular problems exist in the determination of the precise number of internal pouches in females possessing this character. The number of pouches is represented by the number of ventral openings. Unfortunately, in many genera the pouch apertures are very small and are virtually invisible during most of the brood cycle. At one (unidentified) stage in the cycle, however, each aperture is rendered clearly visible. At this stage the aperture is surrounded by a thick circlet of white sub-cuticular tissue which emphasizes the opening and can be seen clearly through the sternites. In female specimens showing such a condition the number of pouches is obvious, but at other stages of the brood cycle—especially in females having thin, transparent sternites—the exact number of pouches is less clear, their existence being indicated only by the presence of the brood within the body. Accordingly, many of the following descriptions necessarily contain the phrase, "Brood held in internal pouches (number not known)".

In the following descriptions the museum location and reference numbers (if any) of the specimens examined have been indicated. The abbreviations for the museums are: AHF (Allan Hancock Foundation, University of Southern California); AM (Australian Museum, Sydney); AMBL (Amakusa Marine Biology Laboratory, Japan); BMNH (British Museum (Natural History)); CM (Zoological Museum, University of Copenhagen); EPML (Edward Percival Marine Laboratory, University of Canterbury, New Zealand); IBL (Institute of Biology, Ljubljana, Yugoslavia); NAIR (Personal loan from Professor Balakrishnan Nair, University of Kerala, India); NUZ (Nottingham University, Zoology Department); NZOI (New Zealand Oceanographic Institute); PM (Muséum National d'Histoire Naturelle, Paris); QM (Queensland Museum, Brisbane); SAfrM (South African Museum); SAustM (South Australian Museum, Adelaide); SM (Naturhistoriska Riksmuseet, Stockholm); USNM (United States National Museum); USSR (Zoological Institute, Academy of Sciences, Leningrad); VM (Natural History Museum, Vienna); WAM (Western

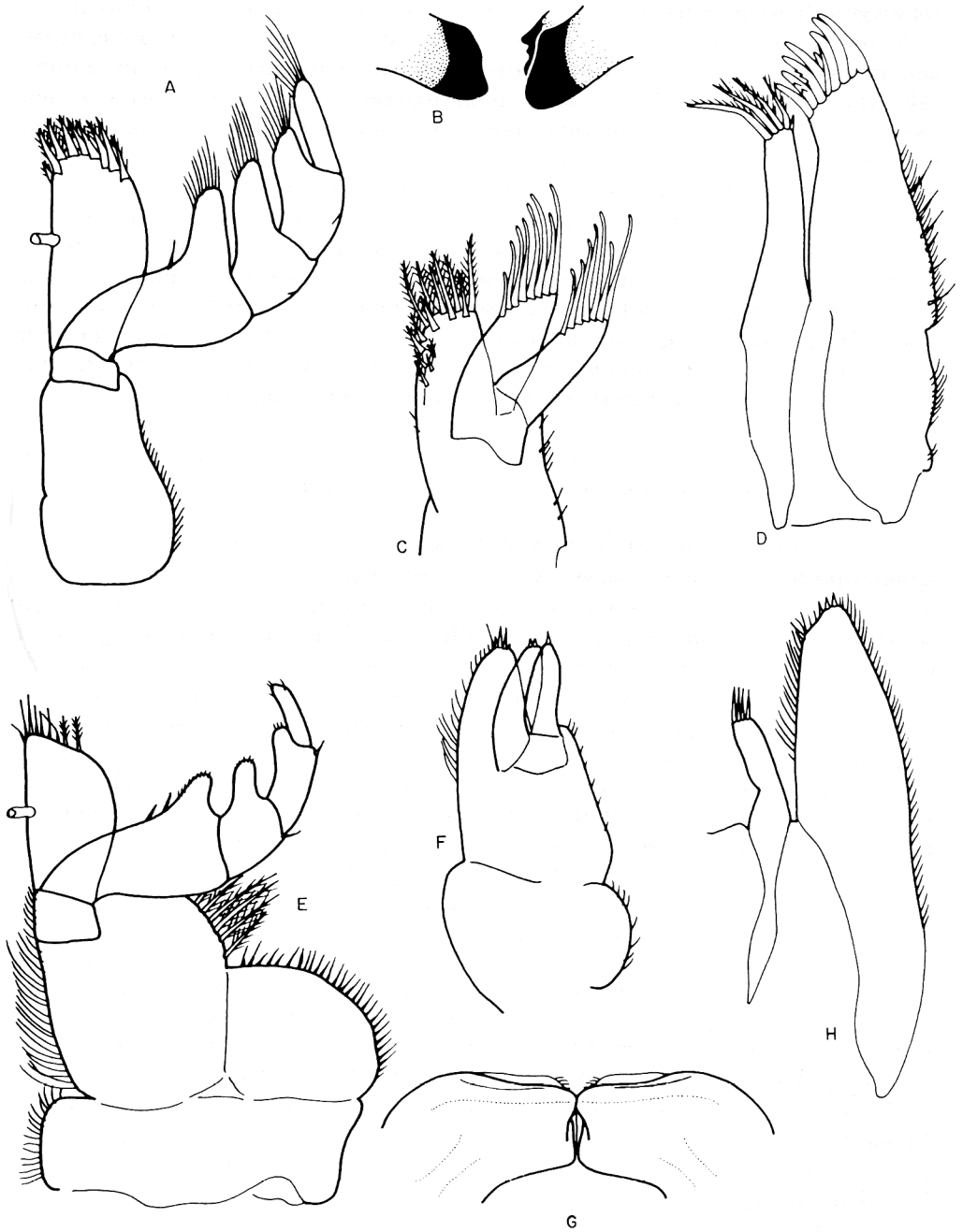


Figure 2. Illustrations of mouthparts showing usual form of metamorphosis in ovigerous female. Non-ovigerous specimen: A, maxilliped; B, incisor processes of mandibles; C, maxilla; D, maxillule. Ovigerous female: E, maxilliped; F, maxilla; G, incisor processes of mandibles; H, maxillule.

Australian Museum, Perth); and ZMUH (Zoological Museum, University of Hamburg).

The genera have been described below in alphabetical order and synonyms (if any) have been indicated. The subfamily to which each genus belongs has been indicated by one of the following codes placed in parentheses after the name: A (Ancininae Dana, 1852); T (Tecticipitinae Iverson, 1982); C (Cassidininae Iverson, 1982); S (Sphaeromatinae Milne Edwards, 1840); D (Dynameninae Bowman, 1981). The fossil subfamily Pleistosphaerominae Strouhal, 1954 is not represented in the present work.

The following results constitute a list of all known sphaeromatid genera except those containing only fossil forms. The fossil genera are: *Archaeosphaeroma* Novak, 1872; *Cyclosphaeroma* Woodward, 1890; *Eosphaeroma* Woodward, 1879; *Heterosphaeroma* Munier-Chalmas, 1872; *Palaeosphaeroma* Remeš, 1903; *Pleistosphaeroma* Strouhal, 1954; *Protosphaeroma* Bachmayer, 1949; *Unusuropode* Duarte & Silva Santos, 1962. Unfortunately nothing is known about the brood pouches of these fossil genera and they are included here only for completeness.

DESCRIPTIONS AND OBSERVATIONS

Genus Amphoroidea Milne Edwards, 1840 (D)

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4, and overlapping well in mid-line. In addition, large posterior pocket covering entire posterior ventrum and opening anteriorly between fourth pereopods; anterior lip bilobed and often pressed against sternites such that opening appears 'sealed'. Brood not held in marsupium thus formed but in 4 pairs of internal pouches.

Species examined: *A. falcifera* Thomson, 1879 EPML (KA497J). *A. media* Hurley & Jansen, 1971 EPML (KA497L). *A. longipes* Hurley & Jansen, 1977 (type specimens) EPML (KA497R).

Genus Amphoroidella Baker, 1908 (D)

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4, and overlapping well in mid-line. In addition, large posterior pocket covering entire posterior ventrum and opening anteriorly between fourth pereopods; anterior lip bilobed. Brood not held in marsupium thus formed but in internal pouches (number not known).

Species examined: *A. elliptica* (Baker, 1908) (type-species of genus) SAustM (C. 825).

Genus Ancinus Milne Edwards, 1840 (A)

Mouthparts: Not metamorphosed.

Brood pouch: Oostegites absent. Pouch formed from two opposing pockets covering entire ventral pereon and opening as narrow, transverse slit between

fourth pereopods. Brood housed in marsupium thus formed. Internal pouches absent.

Species examined: *A. panamensis* Glynn & Glynn, 1974 USNM (291052).

Remarks

The author has been able to examine only one ovigerous female specimen from museum collections. This specimen was not in perfect condition and, as the ventrum was torn, the brood pouch could not be detailed with certainty. However, the lack of oostegites in this specimen seemed to be the natural condition and not due to damage. Loyola e Silva (1971: 213) said of *Ancinus depressus* (Say, 1818) (the type-species of the genus) that the pouch took the form of "uma grande bolsa marsupial". His description of the opposing pockets of *Bathycopea* Tattersall (below) as "uma grande bolsa" supports the present observation that *Ancinus* also has two opposing pockets.

Genus Anoplocopea Racovitza, 1907 (C)

Specimens: Ovigerous female not seen.

Remarks

The author has seen only two syntype specimens of *A. hanseni* Racovitza (the type-species of the genus) (BMNH (1910.1.10.24–25)). One of these specimens was a male, the other a non-ovigerous female. The female bore rudimentary oostegites on pereonites 2, 3 and 4. There may also have been smaller oostegite buds on pereonite 1, but the specimen was very small, soft, and transparent, and details could not be seen with certainty. The ovigerous female will certainly bear at least three pairs of oostegites but the size of these, and the presence of other structures, is not known. *Anoplocopea* appears to be closely related to *Campecopea* Leach (below) and the brood pouches may be similar.

Genus Artopoles Barnard, 1920 (D)

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4 and just overlapping in mid-line. In addition, large posterior pocket covering entire posterior ventrum; lateral margins of pocket terminating at base of fifth pereopods, but anterior lip extending anteriorly as broad, rectangular flap, reaching level of second pereopods. Internal pouches apparently present in anterior half of ventrum but number not known.

Species examined: *A. natalis* Barnard, 1920 (type-species of genus) SAfrM (A14860).

Remarks

The specimen examined bore a number of large ova, some of which were in the posterior pocket, while the remainder were held within the body.

Genus Bathycopea Tattersall, 1904 (A)

Ancinella Hansen, 1905

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4 and overlapping well in mid-line. In addition, large posterior pocket covering entire posterior ventrum and opening anteriorly between fourth pereopods; also, short anterior pocket covering sternite of pereonite 1 and opening posteriorly between second pereopods. Brood held in marsupium thus formed. Internal pouches absent.

Species examined: *B. typhlops* Tattersall, 1904 (type-species of genus) SAfrM (A15461).

Remarks

Hansen originally described his *Ancinella profunda* Hansen, 1905 (a junior synonym of *Bathycopea typhlops*) as having a large pocket and (three pairs of) marsupial lamellae (Hansen, 1905: 79) ['three pairs' implied by his earlier statement that all members of this family which bore oostegites bore three pairs (1905: 75)]. In 1916 Hansen stated that he had subsequently discovered a fourth pair of oostegites on the first pair of pereopods of this species (1916: 176). Loyola e Silva (1971 : 217) said that the ovigerous female of *B. typhlops* bore three pairs of oostegites and "uma grande bolsa de incubação, que apresenta uma única abertura de nascimento que é transversal e que fica entre o quarto e o quinto par de pereiópodes". The present study supports Loyola e Silva's findings and the suggestion is that Hansen (1916) mistook the short anterior pocket for a pair of oostegites.

Genus Botryias Richardson, 1910 (C)

Specimens: Ovigerous female not known.

Remarks

This genus contains only one species, *B. fructiger* Richardson, 1910, which is known only from one specimen (USNM (41024)). Richardson did not state the sex of this specimen but the present investigation revealed it to be an adult male. It should be noted here that while Richardson stated that "The pleopods of the fourth and fifth pairs have both branches similar, of fleshy appearance and without marginal setae... This genus belongs therefore to the section of eubranchiata Sphaeromidae of Hansen" (1910: 31), this specimen actually shows a platybranchiate condition. Pleopods 4 and 5 each have both rami thickened but none shows any indication of branchial folds.

Genus Caecocassidias Kussakin, 1967 (D)

Mouthparts: Mandible, maxillule and maxilla unmodified. Maxilliped with palp unmodified, lobes bearing setae, but endite greatly expanded with proximal flaps and lobes.

Brood pouch: 5 pairs of oostegites arising from pereonites 1, 2, 3, 4 and 5, and overlapping well in mid-line. Brood held in marsupium thus formed. Pockets and internal pouches absent.

Species examined: *C. patagonica* Kussakin, 1967 (type-species of genus) (type specimens) USSR (I. 2/46721).

Remarks

Caecocassidias is a remarkable genus and deserves more attention than Kussakin gave it. Three points are worthy of especial mention:

(1) This is the only known genus to possess five pairs of oostegites (The posterior half of the body is not known to produce oostegites in any other genus)

(2) The pleonal tergite (neither described nor illustrated in detail by Kussakin) bears indication of all five 'original' segments. Ancestral isopods are believed to have possessed five separate pleonal segments. This is the condition shown by the family Cirolanidae today, and is one of the reasons why that family is considered to represent the most 'primitive' condition within the Flabellifera. It is a characteristic of the family Sphaeromatidae that the pleon segments are fused to produce at most two, or occasionally one, pleonal tergite. Most genera, however, show indications of the fused segments in the form of lateral 'suture lines', most of which are obsolete in the mid-line (e.g. Fig. 1). No other known genus shows more than three such lines, indicating, at most, four of the (evolutionarily) original segments. *Caecocassidias* has four clear suture lines at each side of the pleonal tergite (Fig. 3) thus indicating all five segments. All four suture lines are obsolete in the mid-line.

(3) Not only do pleopods 4 and 5 each bear branchial folds over the entire surface of both rami, but the endopod of pleopod 3 also bears branchial folds over its entire surface.

Points (1)–(3) are not known for any other extant sphaeromatid genus.

Genus Caecosphaeroma Dollfus, 1896 (C)

Vireia Viré, 1903

Mouthparts: Mandible, maxillule and maxilla unmodified. Maxilliped with palp unmodified, but endite with one small, proximal, external lobe at base.

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4. Anterior pair of oostegites just overlapping in mid-line; three remaining pairs large, overlapping well in mid-line. Brood held in marsupium thus formed. Pockets and internal pouches absent.

Species examined: *C. burgundum* Dollfus, 1898 PM (Is. 1188).

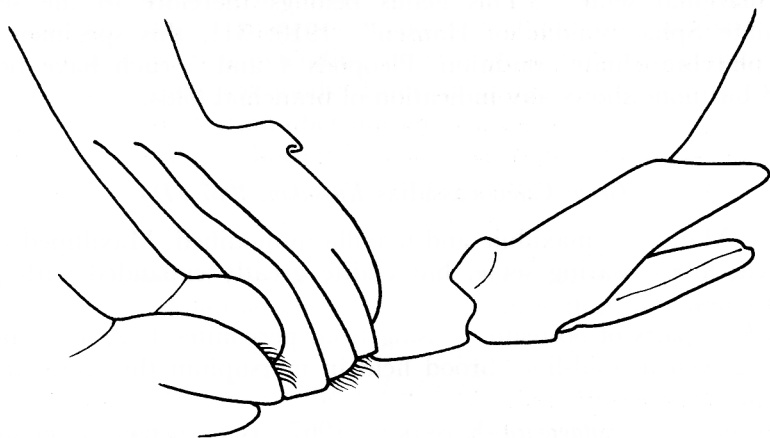


Figure 3. *Caecocassidias patagonica*. Dorso-lateral view of pleon and pleotelson of adult male paratype.

Remarks

Vireia is now treated as a sub-genus of *Caecosphaeroma*.

Genus Calcipila Harrison & Holdich, 1984 (S)

Mouthparts: Condition unknown.

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4 (see *Remarks*).

Species examined: *C. cornuta* Harrison & Holdich, 1984 (type-species of genus) (type specimen) (non-ovigerous female) QM (W. 9645).

Remarks

This genus is known only from the two type specimens (one adult male and one non-ovigerous female) of the type-species. The non-ovigerous female bears oostegite buds on pereonites 1, 2, 3 and 4, but it is not known whether these oostegites overlap in the mid-line in the adult. Also, it is not possible to tell whether the ovigerous female bears pockets and/or internal pouches.

Genus Campecopea Leach, 1814 (C)

Mouthparts: Not metamorphosed.

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4. Anterior pair of oostegites very short, not reaching mid-line; three remaining pairs overlapping in mid-line. In addition, large posterior pocket covering entire posterior ventrum and opening anteriorly between fourth pereopods (although curved lip arcs posteriorly to level of fifth pereopods in mid-line); also, short anterior pocket covering sternite of pereonite 1 and opening posteriorly between second pereopods. Brood held in marsupium thus formed. Internal pouches absent.

Species examined: *C. hirsuta* (Montagu, 1804) (type-species of genus) NUZ.

Remarks

Some authors have stated that *C. hirsuta* was founded (as *Oniscus hirsutus*) on the male of this species, while *C. cranchii* Leach, 1818 (a junior synonym of *C. hirsuta*) was based on the female (Omer-Cooper & Rawson, 1934: 47; Panouse, 1940: 93). This is not so. Montagu founded *O. hirsutus* on the female, as his description and illustration clearly show (Montagu, 1804: 71, tab. VI fig. 7). Leach (1814: 405; 1815: 367) described the female under the name *Campecopea hirsuta* (Montagu) and in 1818 he gave the first description of the male, correctly assigning it to *C. hirsuta*. Without stating reasons he then erected a new species, *C. cranchii*, for the female (1818: 341, 342).

Genus Cassidias Richardson, 1906 (D)

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule with two simple lobes. Maxilla with three simple lobes. Maxilliped with palp lobes lacking long setae; endite large, proximally expanded and lobed.

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4 and overlapping in mid-line. Brood not held in marsupium thus formed, but in internal pouches (number not known). Pockets absent.

Species examined: *C. argentinea* Richardson, 1906 (type-species of genus) (type specimens) USNM (32249; 32627).

Remarks

The male of *C. argentinea* is not known and this genus is based on the ovigerous female. Of the two other species housed in this genus: *Cassidias trituberculata* Thielemann, 1910 was based on the female of *Holotelson tuberculatus* Richardson; examination of type specimens of *Cassidias africana* Barnard, 1920 (in the British Museum (Natural History)) has shown that the ovigerous female has only three pairs of oostegites, the brood is in internal pouches (number unknown) and the mouthparts are only partly metamorphosed (see Discussion). *Cassidias africana* cannot be retained in *Cassidias* but its correct generic placement is not known.

Genus Cassidina Milne Edwards, 1840 (C)

Mouthparts: mandible, maxillule and maxilla unmodified. Maxilliped with palp unmodified, but endite with one small, proximal, external lobe at base.

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4, overlapping in mid-line and increasing in size posteriorly. Posterior pair of oostegites large, virtually covering entire marsupium. In addition, short posterior pocket covering sternite of pereonite 7 and opening anteriorly between sixth pereopods. Brood held in marsupium thus formed. Internal pouches absent.

Species examined: *C. typa* Milne Edwards, 1840 (type-species of genus) EPML (KA504F).

Genus Cassidinella Whitelegge, 1901 (S)

Specimens: Ovigerous female not known.

Remarks

The genus has only one species, *C. incisa* Whitelegge, 1901, which is known from only three specimens, none of which is an ovigerous female (*vide* Hansen, 1905: 75).

Genus Cassidinidea Hansen, 1905 (C)

Cassidisca Richardson, 1905

? *Dies* Barnard, 1951

Mouthparts: Not metamorphosed.

Brood pouch: Oostegites absent. Pouch formed from two opposing pockets covering entire ventral pereon and opening as narrow transverse slit between fourth pereopods. Brood housed in marsupium thus formed. Internal pouches absent.

Species examined: None. Above description paraphrased from Hansen, 1905: 80, 82.

Remarks

It has never been conclusively shown that *Dies* is a junior synonym of *Cassidinidea*. From the literature it would appear that the only major difference between the two genera is that the adult male of *Dies* has the penes fused as a single process. A detailed comparison of specimens belonging to these genera is needed, however, before the problem can be resolved.

Genus Cassidinopsis Hansen, 1905 (D)

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4 and overlapping in mid-line. Brood not held in marsupium thus formed, but in internal pouches (number not known). Pockets absent.

Species examined: *C. emarginata* (Guérin-Méneville, 1843) (type-species of genus) BMNH.

Genus Ceratocephalus Woodward, 1877 (S)

Bregmocerella Haswell, 1884

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule with two simple lobes. Maxilla with three simple lobes. Maxilliped with palp lobes lacking long setae; endite large, proximally expanded and lobed.

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4 and overlapping in mid-line. Anterior pair of oostegites narrow; remaining pairs increasing in size posteriorly. Brood not held in marsupium thus formed but in 5 pairs of internal pouches. Pockets absent.

Species examined: *C. grayanus* Woodward, 1877 (type-species of genus) BMNH.

Remarks

The species *Cymodopsis wardii* Baker, 1926 was apparently founded on a female specimen of *Ceratocephalus grayanus* (W. F. Seed, pers. comm.) and *C. wardii* is a junior synonym of *C. grayanus*.

Genus Cerceis Milne Edwards, 1840 (D)

Paradynamene Richardson, 1905

Circeis Baker, 1908 (*non Circeis* Saint-Joseph: Annelida)

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule with two simple lobes. Maxilla with three simple lobes. Maxilliped with palp lobes lacking long setae; endite large, proximally expanded and lobed.

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4 and overlapping in mid-line. Oostegites increasing in size from anterior to posterior. Brood (at least initially) not held in marsupium thus formed but in 4 pairs of internal pouches. Pockets absent.

Species examined: *Cerceis* sp. ZMUH (two ovigerous specimens of a species of *Cerceis* from Australia were examined, but these specimens could not be assigned to any known species with certainty).

Remarks

Hansen (1905: 108) stated that in *Cerceis* the brood was held in the marsupium. The ovigerous females examined here bore the brood in internal pouches. However, Hansen (loc. cit.) also said that in the related genus *Paracerceis* Hansen the brood was held in internal pouches, but the author has seen a female specimen of *Paracerceis* with a late stage brood in the marsupium. It seems possible that the early brood in both these genera is held in the internal pouches, while the later brood is held (at least for a short time prior to release) in the marsupium. This may also be true for some other genera which bear both internal pouches and a ventral marsupium.

Genus Chitonopsis Whitelegge, 1902 (C)

Mouthparts: Not metamorphosed.

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4 and overlapping well in mid-line. Oostegites increasing in size from anterior to posterior. Brood held in marsupium thus formed. Pockets and internal pouches absent, but sternite of pereonite 7 dilated ventrally as 'shelf' preventing posterior movement of ova out of marsupium.

Species examined: *C. spatulifrons* Whitelegge, 1902 (type-species of genus) (type specimen and non-type specimens) AM (G. 2152); SAustM.

Genus Cilicaea Leach, 1818 (S)

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule with two simple lobes. Maxilla with three simple lobes. Maxilliped with palp lobes lacking long setae; endite large, proximally expanded and lobed.

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4 and overlapping in mid-line. Brood not held in marsupium thus formed but in 5 pairs of internal pouches. Pockets absent.

Species examined: *C. latreillei* Leach, 1818 (type-species of genus) BMNH. *C. crassicaudata* Haswell, 1881 NUZ.

Genus Cilicaeopsis Hansen, 1905 (S)

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule with two simple lobes. Maxilla with three simple lobes. Maxilliped with palp lobes lacking long setae; endite large, proximally expanded and lobed.

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4 and overlapping in mid-line. Brood not held in marsupium thus formed but in 5 pairs of internal pouches. Pockets absent.

Species examined: *C. whiteleggei* (Stebbing, 1905) NUZ.

Genus Clianella Boone, 1923 (S)

Paradynoides Loyola e Silva, 1960

Dynoidella Pillai, 1965

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4, and

overlapping well in mid-line. Brood not held in marsupium thus formed but in internal pouches (number not known). Pockets absent.

Species examined: *C. elegans* Boone, 1923 (type-species of genus) USNM (154967). *C. brucei* Harrison & Holdich, 1984 (type specimens) NUZ.

Genus Cymodetta Bowman & Kühne, 1974 (C)

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4. Oostegites short, not overlapping in mid-line (extending only two-thirds of distance to mid-line). Brood held in 4 pairs of internal pouches. Pockets absent.

Species examined: *C. gracilipes* Holdich & Harrison, 1983 (type specimens) NUZ.

Remarks

Bowman & Kühne (1974: 236), describing *C. gambosa* Bowman & Kühne (the type-species of the genus), incorrectly stated that the ovigerous female bore four pairs of oostegites on pereonites 2, 3, 4 and 5. In fact, in common with all sphaeromatid genera except *Caecocassidias*, *Cymodetta* lacks oostegites on pereonite 5.

Genus Cymodoce Leach, 1814 (S)

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule with two simple lobes. Maxilla with three simple lobes. Maxilliped with palp lobes lacking long setae; endite large, proximally expanded and lobed.

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4, and overlapping in mid-line. Brood not held in marsupium thus formed but in 5 pairs of internal pouches. Pockets absent.

Species examined: *C. truncata* Leach, 1814 (type-species of genus) NUZ. *C. bipapilla* Harrison & Holdich, 1984 (type specimens) NUZ. *C. pelsarti* Tattersall, 1922 NUZ.

Remarks

Loyola e Silva (1963), in his paper on the mouthparts of *Cymodoce*, incorrectly stated that the genus bore three pairs of oostegites. He was presumably following Hansen (1905) who also made this mistake. Loyola e Silva's illustration (1963: 5) of the maxilliped of the ovigerous female of *Cymodoce brasiliensis* Richardson shows this appendage lacking external lobes on the endite. However, *C. brasiliensis*, like many species currently housed in the genus *Cymodoce*, bears little morphological resemblance to *C. truncata* (the type-species) and its congeneric status must be questioned. The present author sees no reason at present to suggest that the presence of such lobes is a variable character for species of *Cymodoce sensu stricto*.

Genus Cymodocella Pfeffer, 1887 (D)

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4, and overlapping well in mid-line. In addition, large posterior pocket covering entire

posterior ventrum and opening anteriorly between fourth pereopods. Brood not obviously housed in marsupium thus formed but embedded in ventral body wall.

Species examined: *C. tubicauda* Pfeffer, 1887 (type-species of genus) NZOI (Z1795). *C. egregia* (Chilton, 1892) EPML (KA497G).

Remarks

The brood appears to occupy a strange position in this genus (and in the closely related genus *Ischyromene* Racovitza—see below). Although the brood does not appear to be held in discrete internal pouches, it is embedded in the ventral cuticle either side of the nerve cord.

Genus *Cymodopsis* Baker, 1926 (*S*)

Specimens: Ovigerous female not known.

Remarks

The author has been unable to trace any ovigerous female specimens belonging to this rather ill-defined genus.

Genus *Discerceis* Richardson, 1905 (*D*)

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule with two simple lobes. Maxilla with three simple lobes. Maxilliped with palp lobes lacking long setae; endite large, proximally expanded and lobed. *Brood pouch:* 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4, and overlapping well in mid-line. Brood not held in marsupium thus formed but in internal pouches (number not known). Pockets absent.

Species examined: *D. granulosa* (Richardson, 1899) (type-species of genus) USNM (144660).

Genus *Dynamene* Leach, 1814 (*D*)

Nesaea Leach, 1814

Naesa Leach, 1815

Prochonaesea Hesse, 1873

Sorrentosphaera Verhoeff, 1944

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule with two simple lobes. Maxilla with three simple lobes. Maxilliped with palp much reduced; endite greatly expanded and lobed.

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4, and overlapping well in mid-line. Brood held in marsupium thus formed, but ventrum displaced dorsally such that brood appears to fill entire body. Pockets and internal pouches absent.

Species examined: *D. bidentata* (Adams, 1800) (type-species of genus) NUZ. *D. bifida* Torelli, 1930 NUZ. *D. curalii* Holdich & Harrison, 1980 (type-specimens) NUZ. *D. edwardsi* (Lucas, 1849) NUZ. *D. magnitorata* Holdich, 1968b NUZ. *D. torelliae* Holdich, 1968b NUZ. *D. tubicauda* Holdich, 1968b NUZ.

Remarks

Dynamene has the maxillipedal palp of the ovigerous female more reduced than any other known genus.

Genus Dynamenella Hansen, 1905 (D)

Mouthparts: Not metamorphosed.

Brood pouch: Oostegites absent. Pouch formed from two opposing pockets covering entire ventral pereon and opening as narrow, transverse slit between fourth pereopods. Brood housed in marsupium thus formed. Internal pouches absent.

Species examined: *D. perforata* (Moore, 1901) (type-species of genus) (type specimen) USNM (32649). *D. liochroea* Harrison & Holdich, 1982a (type specimens) NUZ. *D. ptychura* Harrison & Holdich, 1982a (type specimens) NUZ. *D. trachydermata* Harrison & Holdich, 1982a (type specimens) NUZ.

Remarks

Hansen's statement "marsupial lamellae overlap each other somewhat" for this genus (1905: 107) appears to have arisen by his confusing specimens of *Ischyromene* (which had not been described at that time) with his new genus *Dynamenella*. He did not examine ovigerous female specimens of *Dynamenella perforata* (*vide* Hansen, 1905: 78, 126) but assigned *Ischyromene eatoni* (Miers) (at that time placed in *Dynamene*) to *Dynamenella* (1905: 125). Hansen may have used ovigerous females of species of *Ischyromene* when compiling his description of *Dynamenella*.

Genus Dynameniscus Richardson, 1905 (C)

Mouthparts: Mandible, maxillule and maxilla unmodified. Maxilliped with palp unmodified, lobes bearing long setae; endite expanded with proximal lobes.

Brood pouch: 4 pairs of large oostegites arising from pereonites 1, 2, 3 and 4, and overlapping well in mid-line. Oostegites increasing in size from anterior to posterior. Brood held in marsupium thus formed. Pockets and internal pouches absent.

Species examined: *Dynameniscus* sp. CM.

Remarks

This genus is known from only two specimens, the non-ovigerous female type specimen of *D. carinatus* (Richardson, 1900) (the type-species of the genus) and the ovigerous female *Dynameniscus* sp. mentioned here. This second specimen of *Dynameniscus* is to be described in the near future by Mr E. W. Iverson (pers. comm.).

Genus Dynamenoides Hurley & Jansen, 1977 (D)

Specimens: Ovigerous female not known.

Remarks

This genus was erected for two new species from New Zealand, but no ovigerous female specimens were collected (*vide* Hurley & Jansen, 1977: 36).

Genus Dynamenopsis Baker, 1908 (D)

Mouthparts: Not metamorphosed (*vide* Hurley & Jansen, 1977: 38, 39).

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4. Brood held in 4 pairs of internal pouches (see Remarks).

Species examined: *Dynamenopsis* sp. (non-ovigerous female) WAM (57–80).

Remarks

The author has seen no ovigerous females of this genus. Ovigerous females are not known for *D. obtusa* Baker, 1908 (the type-species of the genus), and Hurley and Jansen did not describe the ovigerous female of *D. varicolor* Hurley & Jansen, 1971 (the only other species in this genus) beyond including "Female mouthparts not metamorphosed" in their description of the genus. The present description is based on a specimen of a species of *Dynamenopsis* from Western Australia (see Harrison & Holdich, 1982a). This non-ovigerous female bore rudimentary oostegites on pereonites 2, 3 and 4, and four pairs of developing pouch openings were visible through the ventral cuticle. It is not known whether the oostegites overlap in the mid-line in the ovigerous female, or whether pockets are present.

Genus Dynoides Barnard, 1914 (S)

Dynoidella Nishimura, 1976 (*non Dynoidella* Pillai, 1965)

Specimens: Ovigerous female not known.

Remarks

The author has been unable to trace any ovigerous females belonging to this genus, but due to their similarity it seems unlikely that the brood pouch and mouthparts will differ from those of the closely related genus *Clianella* Boone.

Genus Exocerceis Baker, 1926 (D)

Specimens: Ovigerous female not known.

Remarks

This genus is known only from the type specimens of the type-species *E. nasuta* (Whitelegge, 1902) (AM (G.2277; G. 2279)). There are no ovigerous females among these specimens (*pers. obs.*).

Genus Exosphaeroides Holdich & Harrison, 1983 (C)

Mouthparts: Not metamorphosed.

Brood pouch: 2 pairs of oostegites arising from pereonites 3 and 4. Oostegites short, not reaching mid-line. Brood held in 4 pairs of internal pouches. Pockets absent.

Species examined: *E. fluvialis* Holdich & Harrison, 1983 (type-species of genus) (type specimens) NUZ.

Genus Exosphaeroma Stebbing, 1900 (S)

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4. Oostegites short, not reaching mid-line. Brood held in 4 pairs of internal pouches. Pockets absent.

Species examined: *E. gigas* (Leach, 1818) (type-species of genus) BMNH.

Genus Geocerceis Menzies & Glynn, 1968 (D)

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule with two simple lobes. Maxilla with three simple lobes. Maxilliped with palp lobes lacking long setae; endite not expanded.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4, and just overlapping in mid-line. Brood not held in marsupium thus formed but in internal pouches (number not known). Pockets absent.

Species examined: *G. barbarae* Menzies & Glynn, 1968 (type-species of genus) (type specimen) USNM (269486).

Remarks

Menzies & Glynn (1968: 56) were not correct in saying that female specimens belonging to this genus do not have the mouthparts metamorphosed.

Genus Gnorimosphaeroma Menzies, 1954 (C)

Mouthparts: Not metamorphosed.

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4; anterior pair short, not reaching mid-line; remaining three pairs overlapping well in mid-line. Brood not held in marsupium thus formed but in 4 pairs of internal pouches. Pockets absent.

Species examined: *G. luteum* Menzies, 1954 USNM (293047). *G. ovatum* (Gurjanova, 1933) NUZ.

Genus Haswellia Miers, 1884 (D)

Calyptura Haswell, 1881 (*non Calyptura* Swainson: Aves)

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule with two simple lobes. Maxilla with three simple lobes. Maxilliped with palp lobes lacking long setae; endite large, proximally expanded and lobed.

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4, and overlapping well in mid-line. Oostegites increasing in size from anterior to posterior. Brood not held in marsupium thus formed but in 4 pairs of internal pouches. Pockets absent.

Species examined: *H. cilicoides* Baker, 1908 SAustM (C. 1046). *H. emarginata* (Haswell, 1882) SAustM (C. 1337).

Genus Hemisphaeroma Hansen, 1905 (S)

Specimens: Ovigerous female not known.

Remarks

This genus is known only from the two type specimens (one adult male and one sub-adult male (CM)) of the type-species *H. pulchrum* Hansen, 1905. However, as indicated by Hansen (1905: 75, 76) this genus is closely related to *Sphaeroma* Latreille (pers. obs.) and it is unlikely that the brood pouch will differ from the more usual form for that genus (see below).

Genus Holotelson Richardson, 1909 (D)

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule with two simple lobes. Maxilla with three simple lobes. Maxilliped with palp lobes lacking long setae; endite large, proximally expanded and lobed. *Brood pouch*: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4, and overlapping well in mid-line. In addition, large posterior pocket covering entire posterior ventrum and opening anteriorly between fourth pereopods (although curved lip arcs posteriorly to level of fifth pereopods in mid-line). Brood not held in marsupium thus formed but in internal pouches (number not known).

Species examined: *H. tuberculatus* Richardson, 1909 (type-species of genus) USNM (112369).

Remarks

Comparison of the description of *Cassidias trituberculata* Thielemann (Thielemann, 1910: 56–59) with female specimens of *H. tuberculatus* shows the two to be identical. *Cassidias trituberculata* is a junior synonym of *Holotelson tuberculatus*.

Genus Ischyromene Racovitza, 1908 (D)

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4, and overlapping well in mid-line. In addition, large posterior pocket covering entire posterior ventrum and opening anteriorly between fourth pereopods. Brood not obviously housed in marsupium thus formed but embedded in ventral body wall.

Species examined: *I. lacazei* Racovitza, 1908 (type-species of genus) NUZ.

Remarks

As in the closely related genus *Cymodocella* (which bears an identical brood pouch) the brood does not appear to be held in discrete internal pouches, but is embedded in the ventral cuticle either side of the nerve cord.

Genus Isocladus Miers, 1876 (S)

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4. Oostegites short, not reaching mid-line. Brood held in 4 pairs of internal pouches. Pockets absent.

Species examined: *I. armatus* (Milne Edwards, 1840) (type-species of genus) BMNH (1921.11.29.163–177). *I. excavatus* (Baker, 1910) NUZ.

Genus Leptosphaeroma Hilgendorf, 1885 (C)

Mouthparts: Not metamorphosed.

Brood pouch: 2 pairs of oostegites arising from pereonites 3 and 4. Oostegites short, not reaching mid-line (extending only two-thirds of distance to mid-line). In addition, two opposing pockets covering entire ventral pereon and opening as narrow, transverse slit between fourth pereopods. Brood held in marsupium formed by these pockets. Internal pouches absent.

Species examined: *L. gottschei* Hilgendorf, 1885 (type-species of genus) AMBL (Isopoda 34–36).

Remarks

Hansen (1905: 79, 80) stated that he examined an ovigerous female of a "new species of *Leptosphaeroma*" in which it was "impossible to detect even the slightest vestige of marsupial lamellae". As no species of *Leptosphaeroma* other than *L. gottschei* have been described, it must be assumed that Hansen's specimen belonged to a different genus, the identity of which remains unknown. (Any assumption that Hansen was examining a species of *Paraleptosphaeroma* Buss & Iverson (see below) must remain speculation.)

Genus Monolistra Gerstaecker, 1856 (C)

Spelaeosphaeroma Feruglio, 1904

Microlistra Racovitza, 1929

Mouthparts: Either (1) mandible, maxillule and maxilla unmodified, but maxilliped with endite bearing small external, proximal lobe (subgenera *Typhlosphaeroma* Racovitza, 1910 and *Microlistra* Racovitza, 1929); or (2) not metamorphosed (remaining subgenera).

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4, and overlapping well in mid-line. Brood held in marsupium thus formed. Pockets and internal pouches absent.

Species examined: *Monolistra (Monolistra) caeca* Gerstaecker, 1856 (type-species of genus) IBL (2155).

Remarks

Microlistra is now treated as a subgenus of *Monolistra*. Ovigerous females belonging to the subgenera *Microlistra* and *Typhlosphaeroma* have a slightly expanded maxilliped (with the palp unmodified); adult females of other species in this genus have all the mouthparts as in male and immature specimens.

Genus Moruloidea Baker, 1908 (D)

Vallentinia Stebbing, 1914a (non *Vallentinia* Browne: Coelenterata)

Evallentinia Stebbing, 1914b

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4, and overlapping well in mid-line. Brood not held in marsupium thus formed but in 4 pairs of internal pouches. Pockets absent.

Species examined: *M. darwini* (Cunningham, 1871) BMNH. *M. tumida* Harrison, 1984 (type specimen) WAM (259-82).

Remarks

In the specimens examined by the present author the exact number of internal pouches was not obvious. That there are four pairs is cited on the authority of Loyola e Silva (1974: 17).

Genus Naesicopea Stebbing, 1893 (D)

Mouthparts: Condition unknown.

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4. (See Remarks.)

Species examined: *N. abyssorum* (Beddard, 1886) (type-species of genus) (type specimen) (non-ovigerous female) BMNH.

Remarks

The genus is known only from the two type specimens (one adult male and one non-ovigerous female) of the type-species. The non-ovigerous female bears oostegite buds on pereonites 1, 2, 3 and 4, but it is not known whether these overlap in the mid-line in the ovigerous female. Also, it is not possible to tell whether the ovigerous female bears pockets and/or internal pouches.

Genus Neocassidina Roman, 1974 (D)

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule with two simple lobes. Maxilla with three simple lobes. Maxilliped with palp lobes lacking long setae; endite large, proximally expanded and lobed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4, and overlapping well in mid-line. Oostegites extending anteriorly to level of mouthparts. (See Remarks.)

Species examined: *N. perlata* Roman, 1974 (type-species of genus) (type specimen) NUZ.

Remarks

Roman said, for *N. perlata* (the only species known in this genus), that the ovigerous female lacked oostegites (even reduced oostegites) and that the brood was in internal pouches (1974: 357). This is not so. The present author has seen one ovigerous female paratype of this species. This female lacked a brood and was not in good condition. For this reason it is not possible to state with certainty that pockets were absent, although none were seen. With regard to internal pouches: the oostegites on pereonite 4 are extremely large, reaching the opposite side of the body and covering the other oostegites. It seems likely that Roman, finding a continuous ventral surface of cuticle, assumed this to represent the pereonal sternites. This would explain why she stated that the female lacked oostegites (as all the remaining oostegites would be obscured by one of the posterior pair). On finding the brood dorsal to this continuous sheet of cuticle, Roman may have assumed that the brood was held in internal pouches. As the present author has not examined a female with brood it is not possible to say

whether pouches are present, but now that it is known that large oostegites are present it must be considered possible that the brood is held in the marsupium formed by these, and not in pouches.

Genus Neonaesa Harrison & Holdich, 1982b (D)

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule as two simple lobes. Maxilla as three simple lobes. Maxilliped with palp lobes lacking long setae; endite large, proximally expanded and lobed.

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4, and overlapping well in mid-line. Oostegites increasing in size from anterior to posterior. Brood held in marsupium thus formed, but ventrum displaced dorsally such that brood appears to fill entire body. Pockets and internal pouches absent.

Species examined: *N. rugosa* Harrison & Holdich, 1982b (type-species of genus) (type specimens) NUZ.

Genus Neosphaeroma Baker, 1926 (S)

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4, and just overlapping in mid-line. Brood held in internal pouches (number not known). Pockets absent.

Species examined: *N. laticaudum* (Whitelegge, 1901) (type-species of genus) AM (P. 9524). *N. australe* (Whitelegge, 1902) QM (W. 8082).

Remarks

Like *Caecocassidias*, *Neosphaeroma* has the endopod of pleopod 3 folded, but in *Neosphaeroma* these folds do not cover the entire ramal surface and *Neosphaeroma* is otherwise a hemibranchiate, not a eubranchiate, form.

Genus Paracassidina Baker, 1911 (C)

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3, and 4, and overlapping in mid-line. In addition, short posterior pocket covering sternite of pereonite 7 and opening anteriorly between sixth pereopods. Brood held in marsupium thus formed. Internal pouches absent.

Species examined: *P. pectinata* Baker, 1911 (type-species of genus) (type specimen and non-type specimens) SAustM (C. 381); NUZ.

Genus Paracassidinopsis Nobili, 1906 (D)

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule with two simple lobes. Maxilla with three simple lobes. Maxilliped with palp lobes lacking long setae; endite large, proximally expanded and lobed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4, and overlapping well in mid-line. Oostegites extending anteriorly to level of

mouthparts. Brood not held in marsupium thus formed but in internal pouches (number not known). Pockets absent.

Species examined: *P. sculpta* Nobili, 1906 (type-species of genus) (type specimens) PM (Is. 1187).

Genus Paracerceis Hansen, 1905 (D)

Paracerceis Nierstrasz, 1931

Sergiella Pires, 1980

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule with two simple lobes. Maxilla with three simple lobes. Maxilliped with palp lobes lacking long setae; endite large, proximally expanded and lobed. *Brood pouch:* 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4. Anterior pair of oostegites just reaching mid-line; remaining three pairs overlapping well in mid-line. Brood (at least initially) not held in marsupium thus formed but in internal pouches (number not known). Pockets absent.

Species examined: *P. beddardi* (Stebbing, 1905) (type specimens) BMNH.

Remarks

See remarks following *Cerceis* (above).

Genus Paracilicaca Stebbing, 1910a (S)

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule with two simple lobes. Maxilla with three simple lobes. Maxilliped with palp lobes lacking long setae; endite large, proximally expanded and lobed. *Brood pouch:* 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4. Anterior pair of oostegites just reaching mid-line; remaining three pairs overlapping well in mid-line. Brood not held in marsupium thus formed but in 5 pairs of internal pouches. Pockets absent.

Species examined: *P. stebbingi* Baker, 1926 QM (W. 8059).

Genus Paradella Harrison & Holdich, 1982a (D)

Mouthparts: Not metamorphosed.

Brood pouch: 1 pair of oostegites arising from pereonite 4. Oostegites short, not reaching mid-line. In addition, two opposing pockets covering entire ventral pereon and opening as narrow, transverse slit between fourth pereopods. Brood housed in marsupium formed by these pockets. Internal pouches absent.

Species examined: *P. octaphymata* Harrison & Holdich, 1982a (type-species of genus) (type specimens) NUZ. *P. bakeri* (Menzies, 1962a) (type specimens) SM (Isopoda 9468). *P. diana*e (Menzies, 1962b) NUZ.

Remarks

The size of the oostegites may vary between species, those of *P. diana*e being shorter than those of the other two species mentioned. In none of the three species, however, did the oostegites reach the mid-line.

Genus Paraleptosphaeroma Buss & Iverson, 1981 (C)

Mouthparts: Not metamorphosed.

Brood pouch: Oostegites absent. Pouch formed from two opposing pockets covering entire ventral pereon and opening as narrow, transverse slit between fourth pereopods. Brood housed in marsupium thus formed. Internal pouches absent.

Species examined: *P. glynni* Buss & Iverson, 1981 (type-species of genus) (type specimens) AHF (782).

Genus Parasphaeroma Stebbing, 1902 (C)

Mouthparts: Not metamorphosed.

Brood pouch: 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4, and overlapping in mid-line. Brood not held in marsupium thus formed but in internal pouches (number not known). Pockets absent.

Species examined: *P. prominens* Stebbing, 1902 (type-species of genus) (type specimen and non-type specimens) BMNH.

Remarks

On the type specimen examined two pairs of pouch openings were obvious, but others may also be present. The number of pouches could not be ascertained for the non-type specimens. All sphaeromatid genera which bear internal pouches, and for which the number of pouches is known, possess four or five pairs (see Discussion). It seems probable that *Parasphaeroma* also bears four or five pairs.

Genus Parisocladus Barnard, 1914 (S)

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4. Oostegites short, not reaching mid-line. Brood held in 4 pairs of internal pouches. Pockets absent.

Species examined: *P. stimpsoni* (Heller, 1865) (type-species of genus) BMNH. *P. perforatus* (Milne Edwards, 1840) BMNH.

Remarks

Barnard (1914: 399) said for this genus "Marsupial plates overlapping in middle line". Only two species are known for this genus, and in the specimens examined by the present author the oostegites extended only half way to the mid-line.

Genus Pistorius Harrison & Holdich, 1982b (D)

Mouthparts: Not metamorphosed.

Brood pouch: Oostegites absent. Pouch formed from two opposing pockets covering entire ventral pereon and opening as narrow, transverse slit between fourth pereopods. Brood housed in marsupium thus formed. Internal pouches absent.

Species examined: P. bidens Harrison & Holdich, 1982b (type-species of genus) (type specimens) NUZ.

Genus Platycerceis Baker, 1926 (D)

Platycirceis Nierstrasz, 1931

Specimens: Ovigerous female not known.

Remarks

This genus currently contains only one species, *P. hyalina* Baker, 1926. Although the ovigerous female is not known for this species, it is unlikely that the mouthparts and brood pouch differ from those of the related genus, *Cerceis*.

Genus Platynympha Harrison, 1984 (S)

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule with two simple lobes. Maxilla with three simple lobes. Maxilliped with palp lobes lacking long setae; endite large, proximally expanded and lobed. *Brood pouch:* 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4, and overlapping in mid-line. Oostegites increasing in size from anterior to posterior. Brood not held in marsupium thus formed but in 5 pairs of internal pouches. Pockets absent.

Species examined: P. longicaudata (Baker, 1908) (type-species of genus) ZMUH.

Genus Platysphaera Holdich & Harrison, 1981b (C)

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4. Oostegites short, not reaching mid-line. Brood held beneath ventral cuticle (see Remarks).

Species examined: P. membranata Holdich & Harrison, 1981b (type-species of genus) (type specimens) QM (W. 6328; W. 6329).

Remarks

In the two ovigerous female specimens seen, no openings were visible in the ventral cuticle overlying the brood. For this reason it proved impossible to tell whether the brood was held in two large opposing pockets (with internal pouches absent) or in internal pouches (with pockets absent).

Genus Pseudocerceis Harrison & Holdich, 1982b (D)

Mouthparts: Metamorphosed. Mandible simple, fused with cephalosome. Maxillule with two simple lobes. Maxilla with three simple lobes. Maxilliped with palp lobes lacking long setae; endite large, proximally expanded and lobed. *Brood pouch:* 4 pairs of oostegites arising from pereonites 1, 2, 3 and 4, and overlapping in mid-line. Oostegites increasing in size from anterior to posterior. Brood not held in marsupium thus formed but in 4 pairs of internal pouches. Pockets absent.

Species examined: P. furculata Harrison & Holdich, 1982b (type-species of genus) (type specimens) NUZ. *Pseudocerceis* sp. (see Harrison & Holdich, 1982b) QM (W. 9651).

Genus Pseudosphaeroma Chilton, 1909 (D)

Paradynamenopsis Menzies, 1962a

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4, and overlapping well in mid-line. Oostegites increasing in size from anterior to posterior. Brood not held in marsupium thus formed, but in 4 pairs of internal pouches. Pockets absent.

Species examined: *P. campbellense* Chilton, 1909 (type-species of genus) (*sensu* Harrison, 1984) ZMUH.

Remarks

The specimens examined were those assigned to the species *P. campbellense* by Harrison (1984). The difficulty of identifying the species within this genus is discussed in that publication.

Genus Ptyosphaera Holdich & Harrison, 1983 (D)

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4, and overlapping in mid-line. Oostegites relatively narrow. Brood held in 4 pairs of internal pouches. Pouches opening as long, transverse slits. Pockets absent.

Species examined: *P. alata* (Baker, 1926) (type-species of genus) NUZ.

Genus Scutuloidea Chilton, 1883 (D)

Mouthparts: Not metamorphosed.

Brood pouch: 2 pairs of oostegites arising from pereonites 3 and 4, and overlapping well in mid-line. Brood held in internal pouches (number not known). Pockets absent.

Species examined: *S. maculata* Chilton, 1883 (Type-species of genus) EPML (KA219K).

Genus Sphaeramene Barnard, 1914 (S)

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4. Oostegites short, not reaching mid-line. Brood held in 4 pairs of internal pouches. Pockets absent.

Species examined: *S. polytylotos* Barnard, 1914 (type-species of genus) (type specimens) BMNH (1916.11.20.35-42).

Genus Sphaeroma Latreille, 1802 (S)

Europosphaera Verhoeff, 1942

Mouthparts: Not metamorphosed.

Brood pouch: Oostegites various (see Remarks). Brood held in 4 pairs of internal pouches. Pouches opening as long, transverse slits. Pockets absent.

Species examined: *S. annandalei annandalei* Stebbing, 1911 NAIR. *S. annandalei*

travancorensis Pillai, 1954 NAIR. *S. intermedium* (Baker, 1926) NUZ. *S. quoyanum* Milne Edwards, 1840 NUZ. *S. rugicaudum* Leach, 1814 NUZ. *S. serratum* (Fabricius, 1787) NUZ. *S. terebrans* Bate, 1866 NUZ. *S. triste* Heller, 1865 (type specimens) VM. *S. venustissimum* Monod, 1931 NUZ. *S. walkeri* Stebbing, 1905 NUZ.

Remarks

In several respects the genus *Sphaeroma* is unusually variable. One variation is in the form of the oostegites of different species. Most species have three pairs of oostegites arising from pereonites 2, 3 and 4, and all overlapping in the mid-line (e.g. *S. intermedium*, *S. quoyanum*, *S. rugicaudum*, *S. serratum*, *S. venustissimum*, and *S. walkeri*). However, some of the species known to bore into wood bear reduced oostegites. *Sphaeroma terebrans* has the two posterior pairs of oostegites overlapping in the mid-line, but the anterior pair are very short and rudimentary. In *S. triste* the anterior pair are absent; the remaining pairs arising from pereonites 3 and 4 and overlapping in the mid-line. In *S. annandalei annandalei* and *S. annandalei travancorensis* all oostegites are absent, the brood pouch being composed only of four pairs of internal pouches. (These are the only two taxa known to the author which do not have the openings of internal pouches protected by oostegites.) Additional variations may exist in species not examined here.

Genus *Sphaeromopsis* Holdich & Jones, 1973 (D)

Mouthparts: Not metamorphosed.

Brood pouch: Oostegites absent. Pouch formed from two opposing pockets covering entire ventral pereon and opening as narrow, transverse slit between fourth pereopods. Brood housed in marsupium thus formed. Internal pouches absent.

Species examined: *S. amathitis* Holdich & Jones, 1973 (type-species of genus) (type specimens) NUZ. *S. mourei* (Loyola e Silva, 1960) (type specimens) NUZ. *S. reticulata* (Stebbing, 1910b) NUZ. *S. serriguberna* Holdich & Harrison, 1981a (type specimens) NUZ.

Genus *Stathmos* Barnard, 1940 (C)

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4. Oostegites short, extending only half way to mid-line. Brood held in 4 pairs of internal pouches. Pockets absent.

Species examined: *S. coronatus* Barnard, 1940 (type-species of genus) SAfrM (A14957).

Genus *Striella* Glynn, 1968 (C)

Mouthparts: Not metamorphosed.

Brood pouch: Oostegites absent. Pouch formed from two opposing pockets covering entire ventral pereon and opening as narrow, transverse slit between

fourth pereopods. Brood held in marsupium thus formed. Internal pouches absent.

Species examined: *S. balani* Glynn, 1968 (type-species of genus) (type specimens) USNM (122858).

Genus Syncassidina Baker, 1929 (C)

Mouthparts: Not metamorphosed.

Brood pouch: 2 pairs of oostegites arising from pereonites 3 and 4. Oostegites short, not reaching mid-line. In addition, two opposing pockets covering entire ventral pereon and opening between fourth pereopods. Bilobed lip of posterior pocket overlapping curved lip of anterior pocket. Brood held in marsupium formed by these pockets. Internal pouches absent.

Species examined: *S. aestuaria* Baker, 1929 (type-species of genus) NUZ.

Genus Tecticeps Richardson, 1897a (T)

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4, and overlapping well in mid-line. Brood held in marsupium thus formed, but ventrum displaced dorsally such that brood appears to fill entire body. Pockets and internal pouches absent.

Species examined: *T. glaber* Gurjanova, 1933 BMNH. *T. renoculis* Richardson, 1909 BMNH.

Genus Thermosphaeroma Cole & Bane, 1978 (D)

Mouthparts: Not metamorphosed.

Brood pouch: Oostegites absent. Pouch formed from two opposing pockets covering entire ventral pereon and opening as narrow, transverse slit between fourth pereopods. Brood held in marsupium thus formed. Internal pouches absent.

Species examined: *T. thermophilum* (Richardson, 1897b) USNM (151227).

Genus Tholozodium Eleftheriou, Holdich & Harrison, 1980 (C)

Mouthparts: Not metamorphosed.

Brood pouch: Oostegites absent. Pouch formed from two opposing pockets covering entire ventral pereon and opening as narrow, transverse slit between fourth pereopods. Brood held in marsupium thus formed. Internal pouches absent.

Species examined: *T. ocellatum* Eleftheriou, Holdich & Harrison, 1980 (type-species of genus) (type specimens) NUZ.

Genus Waiteolana Baker, 1926 (S)

Mouthparts: Not metamorphosed.

Brood pouch: 2 pairs of oostegites arising from pereonites 3 and 4, and just

overlapping in mid-line. Brood held in internal pouches (number not known). Pockets absent.

Species examined: *W. gibbera* Harrison, 1984 (type specimen) WAM (68-80).

Genus Zuzara Leach, 1818 (S)

Cyclura Stebbing, 1874 (*non Cyclura* Harlan: Reptilia)

Cycloidura Stebbing, 1878

Mouthparts: Not metamorphosed.

Brood pouch: 3 pairs of oostegites arising from pereonites 2, 3 and 4. Oostegites short, not reaching mid-line. Brood held in 4 pairs of internal pouches. Pockets absent.

Species examined: *Z. semipunctata* Leach, 1818 (type-species of genus) BMNH (1980.217.6).

DISCUSSION

Before a general discussion of the above descriptions, some mention must be made of the genus *Sphaeroma*. This genus, the type of the family, shows an unusual interspecific variability in the number of oostegites. Most species have three pairs of oostegites, all overlapping in the mid-line; at least one (*S. terebrans*) has the anterior pair reduced; at least one (*S. triste*) has the anterior pair absent; and at least one (*S. annandalei*) lacks oostegites completely. Alternative implications of this variation are: (1) as *Sphaeroma* shows interspecific variation, then the form of the brood pouch cannot be assumed to be consistent in other genera and therefore cannot be treated as an important generic characteristic; (2) *Sphaeroma* is aberrant and its variation does not undermine the consistency of the brood pouch of other genera. There are good reasons for adopting the second opinion. Following his investigation of many species, Hansen (1905) clearly considered the form of the brood pouch to be a generic character and treated it as such. Similarly, the present author has found no variation in pouch structure between species of the same genus, except in *Sphaeroma*. Even in the genus *Dynamene*, where seven species were available for study, no variation was found. Perhaps more importantly, *Sphaeroma* is known to show variation in several other characters which are consistent in all other known genera. These are, the lobing of the articles of the maxillipedal palp (some species lacking lobes, others bearing lobes), and the presence of appendices masculinae in the adult male (*S. terebrans* apparently lacking an appendix while all other species possess this structure). At present it is not clear why *Sphaeroma* (and only *Sphaeroma*) shows such inconsistencies, but for the brood pouch, at least, there is an apparent relationship with wood-boring activity. Among the Sphaeromatidae only the genus *Sphaeroma* is known to contain species which bore into wood, and only those species known to be active borers show reduction of the oostegites. It seems probable that such reduction is related to the burrowing habit. For this reason, *Sphaeroma* will be treated here as an anomalous genus, and the consistency of brood pouch form for other genera will be assumed.

The family overall can now be discussed. The descriptions of the brood pouch and mouthparts are summarized in Table 1 (arranged by structure) and Table 2

(arranged by subfamily). Both Tables are arranged primarily with regard to oostegite number, as this is the most obvious feature for any brood pouch.

Brood pouch

As can be seen from Tables 1 and 2, all genera which lack oostegites bear a brood pouch composed of two large opposing pockets (cf. the aberrant species *S. annandalei*). Only three genera are known which bear both two large opposing pockets and oostegites. None of these three bears more than two pairs of oostegites and none of these oostegites reaches the mid-line. (As two opposing pockets alone are capable of producing an effective marsupium, this might explain the reduction of the oostegites (in both size and number) when such pockets are present.) It can further be seen that large anterior pockets do not occur unless large posterior pockets are present. Large posterior pockets may occur in the presence of only short anterior pockets, or in the absence of anterior pockets, but in such cases the large posterior pocket is always accompanied by at least three pairs of oostegites covering the anterior ventrum.

One observation that is not clear from the Tables but is clear from the descriptions is that the pereonites show a sequence of priority for the possession of oostegites. If an animal bears one pair of oostegites, these are always on pereonite 4; two pairs are on pereonites 4 and 3; three pairs are on pereonites 4, 3 and 2; and four pairs are on pereonites 4, 3, 2 and 1. (Similarly, Kinne (1954: 110) observed that in *Sphaeroma hookeri* Leach the females acquire the oostegites in successive moults, and that the oostegites appear first on pereonite 4, then 3, then 2.) If the presence of a brood pouch formed from oostegites is considered to be the 'usual' peracarid condition, and if ancestral sphaeromatids are considered to have had such a brood pouch (which seems probable), then certain sphaeromatid genera have—in evolutionary terms—lost some, or all, of these oostegites. This reduction in number always commences anteriorly and affects the subsequent pereonites in the sequence 2, 3, 4.

This 'all-or-nothing' reduction in the number of oostegites is paralleled by the size of the oostegites of many genera. The two oostegites on each pereonite are identical, but usually differ in size from those of the neighbouring pereonites, each oostegite being smaller than the oostegite posterior to it. Thus, reduction in both number and size commences anteriorly and moves posteriorly. When considering the range of brood pouch forms, pereonite 4 is always the last pereonite to lose its oostegites, and this pereonite always bears the largest oostegites.

In the foregoing the genus *Caecocassidias* has not been considered. *Caecocassidias* is unique among the sphaeromatid genera in having five pairs of oostegites. These are borne on pereonites 1–5, and their presence on pereonite 5 makes this the only known genus to bear oostegites on the posterior half of the body. In all other genera the only brood pouch component which occurs in the posterior half of the body is a posterior pocket (if present); oostegites and internal pouches—as well as anterior pockets—only occur in the anterior half.

Tables 1 and 2 show that Hansen's original (1905) claim that all genera which bear oostegites (i.e. all except his *Cassidinini*) have three pairs is not true. Racovitza (1910) and Hansen himself (1916) accepted this was the case and that some genera bore four pairs (although Hansen's claim that this was the case

Table 1. Brood pouch composition and mouthparts (arranged by structure)

Genus	Oostegites (No. of pairs)					Overlap	Pouches (pairs)		Pockets				MPTS	
	1	2	3	4	5		4	5	Ant		Post		EX-MXPD	RED'N
									S	L	L	S		
<i>Ancinus</i>										+	+			
<i>Cassinidea</i>										+	+			
<i>Dynamenella</i>										+	+			
<i>Paraleptosphaeroma</i>										+	+			
<i>Pistorius</i>										+	+			
<i>Sphaeromopsis</i>										+	+			
<i>Striella</i>										+	+			
<i>Thermosphaeroma</i>										+	+			
<i>Tholozodium</i>										+	+			
<i>Paradella</i>	+					-				+	+			
<i>Leptosphaeroma</i>		+				-				+	+			
<i>Syncassinina</i>		+				-				+	+			
<i>Exosphaeroides</i>		+				-	+							
<i>Scutuloidea</i>		+				0	?	?						
<i>Waiteolana</i>		+				0	?	?						
<i>Sphaeroma</i>		t	+			0	+							
<i>Moruloidea</i>			+			0	+							
<i>Pseudosphaeroma</i>			+			0	+							
<i>Ptyosphaera</i>			+			0	+							
<i>Clianella</i>			+			0	?	?						
<i>Neosphaeroma</i>			+			0	?	?						
<i>Cassinopsis</i>			+			0	?	?						
<i>Geocerceis</i>			+			0	?	?					+	
<i>Paracassinopsis</i>			+			0	?	?				+	+	
<i>Cymodetta</i>			+			-	+							
<i>Exosphaeroma</i>			+			-	+							
<i>Isocladus</i>			+			-	+							
<i>Parisocladus</i>			+			-	+							
<i>Sphaeramene</i>			+			-	+							
<i>Stathmos</i>			+			-	+							
<i>Zuzara</i>			+			-	+							
<i>Amphoroidea</i>			+			0	+				+			

for *Bathycopea* (1916: 176) was apparently based on a misobservation). Hansen's supposition that all the genera of his Cassidinini lacked oostegites can also be seen to be untrue, and while the variation in the genera known to Hansen was greater than he suspected, even more variation has been found in genera described since his work.

Mouthparts

Of the genera listed in the Tables, 17 have all the mouthparts metamorphosed, and a further four have just the maxilliped modified. Regarding the mouthparts Hansen (1905: 82) stated, "One is apt to suppose that this metamorphosis must be associated with one of the modifications of the incubatory chamber, but it is far from being so". This is not necessarily the case. Hansen viewed the metamorphosis of the mouthparts as a single feature, but as Racovitza showed (1910: 642, 643) it can be viewed as two separate components, (1) the proximal expansion of the maxillipedal endites, and

Table 1 (continued).

Genus	Oostegites (No. of pairs)					Overlap	Pouches (pairs)		Pockets				MPTS		
	1	2	3	4	5		4	5	Ant		Post		EX-MXPD	RED'N	
									S	L	L	S			
<i>Amphoroidella</i>			+			0	?	?				+			
<i>Artopoles</i>			+			0	?	?				+			
<i>Tecticeps</i>			+			0									
<i>Paracassidina</i>			+			0							+		
<i>Cymodocella</i>			+			0						+			
<i>Ischymene</i>			+			0						+			
<i>Bathycopea</i>			+			0			+			+			
<i>Chilonopsis</i>				+		0									
<i>Monolistra</i>				+		0								TM	
<i>Caecosphaeroma</i>				+		0								+	
<i>Dynameniscus</i>				+		0								+	
<i>Dynamene</i>				+		0								+	
<i>Neonaesa</i>				+		0								+	
<i>Gnorimosphaeroma</i>				+		0	+								
<i>Parasphaeroma</i>				+		0	?	?							
<i>Cerceis</i>				+		0	+							+	
<i>Haswellia</i>				+		0	+							+	
<i>Pseudocerceis</i>				+		0	+							+	
<i>Discerceis</i>				+		0	?	?						+	
<i>Paracerceis</i>				+		0	?	?						+	
<i>Cassidias</i>				+		0	?	?						+	
<i>Ceratocephalus</i>				+		0		+						+	
<i>Cilicaea</i>				+		0		+						+	
<i>Cilicaeopsis</i>				+		0		+						+	
<i>Cymodoce</i>				+		0		+						+	
<i>Paracilicaea</i>				+		0		+						+	
<i>Platynympha</i>				+		0		+						+	
<i>Cassidina</i>				+		0						+		+	
<i>Campecopea</i>				+		0			+			+			
<i>Holotelson</i>				+		0	?	?				+		+	
<i>Caecocassidias</i>					+	0								+	

Explanation: Only genera for which all details are known (except the number of internal pouches) are plotted. Genera for which a full description is not yet possible are omitted.

Oostegites: The number of oostegite pairs present are indicated (+). Five blank columns denote that the genus lacks oostegites. (t, the species *S. triste* bears only two pairs of oostegites. *S. annandalei* lacks oostegites).

Overlap: 0, at least some oostegites overlap in the mid-line. — none of the oostegites reach the mid-line.

Pouches: For those genera where the exact number of internal pouches is known, this is indicated (+). These genera always have 4 or 5 pairs, therefore only two possibilities are given in the tables despite the fact that for many genera the number is not known. ??, internal pouches are present but the number is not known; two blank columns denote that internal pouches are absent.

Pockets: Ant, anterior; Post, posterior; S, short (covering pereonite 1 or pereonite 7); L, large [covering pereonites 1-4 inclusive (anterior) or pereonites 7-5 inclusive (posterior)].

MPTS (metamorphosis of the mouthparts): the presence of an expanded maxilliped is indicated (+) in the column EX-MXPD. Mouthpart reduction is indicated in the column RED'N. (TM, the subgenera *Typhlosphaeroma* and *Microlistra* show weakly expanded maxillipeds).

(2) the distal reduction of the maxillipeds and anterior mouthparts. These two components, a posterior expansion and an anterior reduction, can be treated separately when being related to brood pouch form.

Maxilliped expansion

Expanded maxillipedal endites beat, drawing a current of water anteriorly through the marsupium of the ovigerous female (Hansen, 1905: 84; Holdich,

Table 2. Brood pouch composition and mouthparts (arranged by subfamily)

Genus	Oostegites (No. of pairs)					Overlap	Pouches (pairs)		Pockets				MPTS		
	1	2	3	4	5		4	5	Ant		Post		EX-MXPD	RED'N	
									S	L	L	S			
Cassidininae															
<i>Cassidinidea</i>											+	+			
<i>Paraleptosphaeroma</i>											+	+			
<i>Striella</i>											+	+			
<i>Tholozodium</i>											+	+			
<i>Leptosphaeroma</i>		+				-					+	+			
<i>Syncassidina</i>		+				-					+	+			
<i>Exosphaeroides</i>		+				-	+								
<i>Cymodetta</i>			+			-	+								
<i>Stathmos</i>			+			-	+								
<i>Paracassidina</i>			+			0							+		
<i>Chitonopsis</i>				+		0									
<i>Monolistra</i>				+		0								TM	
<i>Caecosphaeroma</i>				+		0								+	
<i>Dynameniscus</i>				+		0								+	
<i>Gnorimosphaeroma</i>				+		0	+								
<i>Parasphaeroma</i>				+		0	?	?							
<i>Cassidina</i>				+		0							+	+	
<i>Campecopea</i>				+		0			+			+			
Sphaeromatinae															
<i>Waiteolana</i>		+				0	?	?							
<i>Sphaeroma</i>		+				0	+								
<i>Clanella</i>			+			0	?	?							
<i>Neosphaeroma</i>			+			0	?	?							
<i>Exosphaeroma</i>			+			-	+								
<i>Isocladius</i>			+			-	+								
<i>Parisocladius</i>			+			-	+								
<i>Sphaeramene</i>			+			-	+								
<i>Zuzara</i>			+			-	+								
<i>Ceratocephalus</i>				+		0		+					+	+	
<i>Cilicæa</i>				+		0		+					+	+	
<i>Cilicæopsis</i>				+		0		+					+	+	
<i>Cymodoce</i>				+		0		+					+	+	
<i>Paracilicæa</i>				+		0		+					+	+	
<i>Platynympha</i>				+		0		+					+	+	

1968a: 138). Knowing this to be the function of such a modification, a number of assumptions can be made before examining the correlation between maxilliped form and brood pouch structure. These *a priori* assumptions are: (1) if the brood pouch was composed only of two opposing pockets, a lobed maxilliped could not produce a current of water within this marsupium; (2) if oostegites were present but did not meet in the ventral mid-line, then the 'marsupium' would not be ventrally enclosed and a current of water could not be produced through it by a lobed maxilliped; and (3) even if oostegites were present and did overlap in the mid-line, a lobed maxilliped could not produce a current of water through the marsupium if there was a significant gap between the anterior margins of the anterior oostegites (i.e. the anterior margin of the marsupium) and the maxilliped itself. Therefore, a lobed maxilliped could only produce a current of water through the marsupium if (a) the marsupium was composed of oostegites which overlapped in the mid-line, and (b) the oostegites

Table 2 (continued).

Genus	Oostegites (No. of pairs)					Overlap	Pouches (pairs)		Pockets				MPTS		
	1	2	3	4	5		4	5	Ant		Post		EX-MXPD	RED'N	
									S	L	L	S			
Dynameninae															
<i>Dynamenella</i>											+	+			
<i>Pistorius</i>											+	+			
<i>Sphaeromopsis</i>											+	+			
<i>Thermosphaeroma</i>											+	+			
<i>Paradella</i>	+					-					+	+			
<i>Scutuloidea</i>		+				0	?	?							
<i>Moruloidea</i>			+			0	+								
<i>Pseudosphaeroma</i>				+		0	+								
<i>Ptyosphaera</i>				+		0	+								
<i>Cassidinopsis</i>				+		0	?	?							
<i>Amphoroidea</i>				+		0	+					+			
<i>Amphoroidella</i>				+		0	?	?				+			
<i>Artopoles</i>				+		0	?	?				+			
<i>Geocerceis</i>				+		0	?	?						+	
<i>Paracassidinopsis</i>				+		0	?	?					+	+	
<i>Cymodocella</i>				+		0						+			
<i>Ischyromene</i>				+		0						+			
<i>Dynamene</i>					+	0							+	+	
<i>Neonaesa</i>					+	0							+	+	
<i>Cerceis</i>					+	0	+						+	+	
<i>Haswellia</i>					+	0	+						+	+	
<i>Pseudocerceis</i>					+	0	+						+	+	
<i>Discerceis</i>					+	0	?	?					+	+	
<i>Paracerceis</i>					+	0	?	?					+	+	
<i>Cassidias</i>					+	0	?	?					+	+	
<i>Holotelson</i>					+	0	?	?				+	+	+	
<i>Caecocassidias</i>						+	0						+		
Ancininae															
<i>Ancinus</i>												+	+		
<i>Bathycopea</i>											+		+		
Tecticipitinae															
<i>Tecticeps</i>												+			

Explanation: see Table 1.

extended anteriorly to reach or overlap the maxilliped. In practice these theoretical requirements give a good correlation with actual observations.

Examination of specimens shows that all genera with the maxilliped lobed bear oostegites, all of which overlap in the mid-line. All these genera except two bear oostegites on all four anterior pereonites (leaving no gap between the oostegites and the maxilliped). The two exceptions [*Neocassidina* (not included in the Tables) and *Paracassidinopsis*] each bear only three pairs of oostegites, and as there are no oostegites on pereonite 1, a gap would be expected between the oostegites and the mouthparts. In fact, both these genera have very large oostegites which extend anteriorly to cover pereonite 1 and reach the level of the maxillipeds. All remaining genera bearing three pairs of oostegites have these relatively smaller; have a gap anterior to the marsupium; and do not have the maxilliped expanded. No genus bearing less than three pairs of oostegites has any metamorphosed mouthparts.

All these observations agree with the theoretical requirements outlined above. However, the metamorphosis of the maxilliped is not as consistent as this might suggest. Although all genera with lobed maxillipeds bear oostegites which reach the mouthparts, five genera occur which bear four pairs of oostegites but do not have the maxilliped expanded. These are: *Campecopea*, *Chitonopsis*, *Gnorimosphaeroma*, *Monolistra* (except the subgenera *Typhlosphaeroma* and *Microlistra*) and *Parasphaeroma*. In *Campecopea* and *Gnorimosphaeroma* the anterior oostegites are short and do not reach the mid-line. As this produces a gap anterior to the marsupium, an unmodified maxilliped would be expected from the theoretical considerations. The three remaining genera each have all four pairs of oostegites overlapping, and it seems unusual that they do not have the maxilliped lobed. It may be significant, however, that all these genera are platybranchiate forms (subfamily Cassidininae).

Hansen stated (1905: 86) that it was probable that the mouthparts were unmodified in all platybranchs. Certainly, no known platybranch has the anterior mouthparts metamorphosed, but four genera (*Caecosphaeroma*, *Cassidina*, *Dynameniscus*, and the subgenera *Typhlosphaeroma* and *Microlistra* of *Monolistra*) have the maxilliped lobed. However, in *Caecosphaeroma*, *Cassidina* and *Monolistra* these lobes are very small. Among the platybranchs, only *Dynameniscus* has the maxilliped lobed as in hemibranchiate and eubranchiate forms (subfamilies Sphaeromatinae and Dynameninae respectively). Overall, therefore, the platybranchs show less tendency to have metamorphosed mouthparts than do other genera. The reason for this is not known. All hemibranchs and eubranchs bearing four pairs of oostegites have the maxilliped lobed.

From the above it can be seen that there is a good correlation between the form of the brood pouch and the lobing of the maxilliped, apparently related to the use of this appendage for creating a current of water through the marsupium. The metamorphosis of the anterior mouthparts (with the accompanying reduction of the maxillipedal palp and distal endite) must now be considered.

Mouthpart reduction

Hansen admitted (1905: 97) that he could offer no explanation for the overall reduction of the mouthparts of some genera, and no convincing explanation has been proposed since his work. At most, certain observations can be made.

Hansen's belief that a relationship existed between the reduction of the mouthparts and the presence of an apical pleotelsonic notch (1905: 86–88) was refuted by Racovitza (1910: 642, 643), and does not appear to hold when all known genera are examined. However, the reduction does appear to be partially related to pleopod morphology as no platybranchiate genera have the mouthparts reduced (this 'related to' does not imply a causal relationship, merely a morphological correlation). All hemibranchiate and eubranchiate genera bearing four pairs of oostegites have the mouthparts reduced. Only three additional genera (*Geocerceis*, *Neocassidina* and *Paracassidinopsis*) plus the currently displaced species '*Cassidias*' *africana*—all eubranchiate and with three pairs of oostegites—have reduced mouthparts. Thus, reduction also appears to be related to brood pouch structure. All genera showing reduction (except *Geocerceis* and *C. africana*) have oostegites which reach the mouthparts. Despite the two exceptions, this relationship appears significant and shows an obvious

similarity to the relationship between the expansion of the maxilliped and the form of the brood pouch.

As almost all known genera which have the mouthparts reduced also have the maxilliped expanded, the reduction could be causally related only to the lobing of the maxilliped. As this lobing is causally related to brood pouch structure (see above), this would give an apparent, direct relationship between reduction and brood pouch form. However, *Geocerceis* and *C. africana* (with reduction but no maxillipedal expansion) and *Caecocassidias* and *Dynameniscus* (with broad maxillipedal expansion but no reduction) show that mouthpart reduction and maxillipedal lobing are not mutually dependent. A direct relationship does appear to exist, therefore, between brood pouch structure and mouthpart reduction, although the existence of *Geocerceis* and *C. africana* (in which the oostegites do not reach the mouthparts) makes interpretation of this relationship difficult.

An understanding of the structural relationships is further hindered because the reason for the reduction is not known. As the oostegites never completely cover the mouthparts, there is no reason why the anterior mouthparts could not function normally.

It is possible, of course, that the external morphology of the mouthparts is not the important factor. The accompanying reduction of internal musculature must increase the space available within the body for housing the brood. Racovitza (1910: 644) suggested that the reduction was more pronounced in genera such as *Dynamene*, which have the brood pouch well formed. (In *Dynamene* and *Neonaesa* the brood appears to fill the entire body and extends anteriorly into the cephalosome.)

Alternatively, the reduction may not be the result of any morphological considerations, but rather energetic requirements. It is possible that ovigerous females of many genera do not feed. Kinne (1954: 117) observed that ovigerous females of *Sphaeroma hookeri* ingested little food, and Buss & Iverson (1981: 14) said that ovigerous females of *Paraleptosphaeroma glynni* rarely had food in their guts. (Both these species bear mouthparts that are unmodified and suitable for feeding.) Racovitza suggested (1910: 643) that ovigerous females are prevented from feeding by the distension of the brood pouch, and Holdich (1971: 42) showed that in *Dynamene* the body organs are compressed by the brood. If adult females of some genera do not feed, energy stores accumulated by these females in the subadult stages must be used to produce the new cuticle for the adult, and to provide the extra yolk put into the eggs following the final moult. For genera with expanded maxillipeds these stores must also provide the extra cuticle and musculature for these structures, and must provide the energy substrate to keep them beating during the ovigerous period. Stores must also be used to maintain the female's vital functions. These requirements would be expected to place marked energetic restrictions on the adult female. The energy store could be maximized if the female did not expend energy producing unnecessary structures at the moult to the ovigerous condition. Holdich (1971), examining *Dynamene bidentata*, showed that at the final moult the female underwent considerable degeneration of the internal musculature and connective tissues; the new cuticle was thinner than that of the male or the subadult stages; and the antennules were reduced. It is possible that the reduction of the mouthparts is another aspect of this degeneration. The production of spines, setae, and cutting

and triturating surfaces would be a waste of energy if these specialized structures were not to be used. Perhaps Hansen's observation (1905: 86) that the reduction must prevent feeding would be better expressed by saying that the lack of feeding allows the reduction to occur. Unfortunately, while these energetic considerations appear plausible, they would not explain the apparent relationship with oostegite number or the absence of reduction in platybranchiate genera.

Although the cause and function of the reduction are obscure, such reduction must play an important part in the life histories of the species concerned. In *Dynamene bidentata* (with reduced mouthparts) the female dies after release of the brood (Holdich, 1968a: 150; 1971: 35), while in *Sphaeroma hookeri* and *Paraleptosphaeroma glynni* (both with unmodified mouthparts) the females produce more than one brood. Presumably the females of these last two species feed between broods, and it may prove to be a general trend that ovigerous females of genera with reduced mouthparts produce only one brood before dying, while females of other genera may produce more than one.

As the above shows, within the family Sphaeromatidae the ovigerous females exhibit a wide range of structures for housing the developing brood. This variation, especially the development of features such as internal pouches, probably arose in parallel with the habit of rolling into a ball (or folding) which gives the family its name. The ovigerous females of many genera are still capable of this rolling despite the presence of the brood within the body (although in some genera—especially those with the brood held in a marsupium composed only of oostegites—this is no longer possible). Modification of the brood pouch, associated with a rolling habit, can also be found in some terrestrial isopods. Oniscoids belonging to the genera *Armadillo* Latreille and *Armadillidium* Brandt have a brood pouch composed of oostegites, but the ventral pereon also bears five pairs of invaginations which surround the gut within the body cavity. In the genus *Helleria* Czerniavsky females have a brood pouch composed of oostegites, but the marsupium extends posteriorly into the pleon as a large pouch (Mead, 1963: 775–777). In *Tylos granulatus* Krauss, Barnard observed that the sternites of the ovigerous female were displaced dorsally and pressed against the dorsal cuticle, with the brood filling the body. Barnard also observed that the internal organs of the female were much compressed by this arrangement, saying “this squeezing of the internal organs between the sternal and dorsal plates is carried to such an extreme that these organs appear to be quite degenerate” (Barnard, 1940: 438). All these oniscoids roll into a ball.

Although the similarities between the pouch modifications of these oniscoids and the sphaeromatids suggest that the variation of the sphaeromatid pouch is related to the rolling habit, it is difficult to understand why so much variation of structure occurs. It may be that modification of the brood pouch arose independently in a number of different groups within the Sphaeromatidae, with variation on each of these original modifications producing the range of forms found today. Some modification may have been the result of environmental pressures exerted on brooding females as the Sphaeromatidae colonized various habitats.

Among other isopod families variation of brood pouch structure occurs in groups showing different life styles. Some parasitic isopods show radical changes from the oostegite form of brood pouch. In cryptoniscids the oostegites decrease

in size and disappear, leaving a brood pouch formed by vento-lateral folds of the body wall; in specimens of *Hemioniscus* Buchholz the ventral cuticle 'delaminates' to produce a pouch which is never open; and in the gnathiid genus *Paragnathia* Omer-Cooper the ova develop within the ovaries (Klapow, 1970). Among free-living groups, the cirolanid genera *Exciorolana* Richardson and *Eurydice* Leach show modifications of the brood pouch which prove useful in aiding an understanding of some sphaeromatid forms.

In *Eurydice* there are five pairs of large oostegites, but in addition the ventrum of the female is displaced dorsally either side of the nerve cord, and the marsupium, containing the brood, fills the entire pereon, surrounding the gut (Chaix, 1974). In *Exciorolana* there are only three pairs of oostegites and these are short and do not function as a marsupium. The brood in *Exciorolana* is held internally in paired 'uteri' which fill the pereon either side of the gut (Klapow, 1970). The brood in *Exciorolana*, therefore, is completely internal and is protected by the unbroken ventral cuticle of the female. Klapow (1970) has suggested that these modifications of the brood pouches of *Eurydice* and *Exciorolana* are related to the fact that these genera are found in intertidal, wave-washed sand. (The related genus *Cirolana* Leach contains sublittoral species, and the brood pouch of this genus is composed only of oostegites.) Klapow suggested that in such an exposed intertidal environment an unmodified brood pouch, composed only of oostegites, would be vulnerable to disruption by mobile sand particles during strong wave action. Under these conditions a brood might suffer damage. Although *Eurydice* has the brood within the pereon, the brood pouch is still closed ventrally only by oostegites. However, ovigerous females of *Eurydice* are reported to move their position on the beach and appear to select a more sheltered region when brooding (Klapow, 1970: 368). Ovigerous females of *Exciorolana* do not appear to change their behaviour or position on the beach while brooding, but their internal brood would not be affected by sand abrasion.

These observations can be applied to a study of the sphaeromatid brood pouch. Of the genera having a marsupium composed of two large opposing pockets (the combination which might be considered best able to resist mechanical disruption by particle abrasion): *Tholozodium*, *Sphaeromopsis*, *Dynamenella*, *Ancinus*, *Leptosphaeroma* and *Paradella* have all been found in intertidal sand; *Pistorius*, *Paraleptosphaeroma* and *Striella* all contain only intertidal marine species, and specimens might be expected to be subjected to wave action; and specimens of *Cassinidea* and *Syncassinidea* are found in shallow water in muddy, brackish areas which would be liable to turbulence caused by wind and wave action. *Thermosphaeroma* has been found only in warm freshwater springs and *T. thermophilum*, at least, burrows into sediment (Shuster, 1981: 292). None of these genera is known to contain deepwater species.

Of the genera having a brood pouch composed only of oostegites: *Paracassinidea*, *Tecticeps*, *Chitonopsis*, *Dynameniscus* and *Caecocassinidea* all contain only sublittoral species, and *Monolistra* and *Caecosphaeroma* are subterranean freshwater genera. Only *Dynamene* and *Neonaesa* are found intertidally, but the ovigerous females of both these genera adopt a cryptic, crevice-dwelling habit when brooding; they have never been found in intertidal sand.

Apart from wave-washed sand, other environmental conditions may affect brood pouch structure. It is noteworthy that all the species of *Sphaeroma* known to

show reduction of the oostegites are timber-boring species; non-boring forms have all the oostegites fully formed. As the brood of *Sphaeroma* develops within the internal pouches, the oostegites of this genus are presumably less necessary for producing a marsupium *sensu stricto*, and may serve only to protect the (relatively large) openings to the pouches, preventing the entry of particles and detritus. Within a burrow, the ovigerous females of the boring species would be protected from much mechanical wave action, and in such a sheltered habitat the oostegites could presumably be reduced, or lost completely, without major disadvantage to the brood.

With regard to the mouthparts and their relationship to environmental conditions, the fact that some females generate a current of water through the marsupium, while others have a brood pouch (and mouthparts) that would not seem to allow such circulation, would suggest that the broods of different genera have different physical requirements. This, in turn, may reflect the different ambient environmental conditions experienced by the brooding females.

Unfortunately, the study of the sphaeromatid brood pouch is still at a very early, descriptive stage and many questions must remain unanswered. Only when more is known about the conditions within the pouch, and the life-cycles and habitat preferences of sphaeromatid species, will a greater understanding of the variation shown become possible.

Morphologically, the present study has shown that the brood pouch is more varied than was previously thought and deserves more attention from taxonomists. Its potential as an important generic character cannot be overstressed. However, although this character is important, due to the range of variation shown it would be unwise to attempt to re-organize the subfamily groupings and base them on the brood pouch. Most aspects of pouch structure vary within and between the existing subfamilies, and the only obvious trends which emerge from the tables are that no platybranchiate genera have the mouthparts reduced, and that all hemibranchiate genera have the brood in internal pouches and lack any form of pockets. These trends are striking, but whether they will persist when future genera are described cannot be predicted. None of the trends in the distribution of brood pouch characters conflicts with the current arrangement of the subfamilies.

Much work remains to be carried out on the brood pouch, but with the relationship between maxillipedal expansion and brood pouch structure now much clearer, and a relationship emerging between some forms of brood pouch and environmental conditions, the above will hopefully serve as a useful foundation for future investigations.

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