

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>Ischymene</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 *Syncassinida* 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: *Paracassinida*, *Tecticeps*, *Chitonopsis*, *Dynameniscus* and *Caecocassinidas* 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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