

LIST OF GENERIC SYNONYMS OF STENETRIOIDEA AND PARASELLOIDEA

(Author and year of description of all valid genera are given in Table 20, p. 276)

- Acanthoniscus* G. O. Sars, 1879 = *Acanthaspidia*
Antennuloniscus Menzies, 1962 = *Haploniscus*
Asellodes Stimpson, 1853 = *Janira*
Aspidarachna G. O. Sars, 1899 = *Ilyarachna*
Austrimunna Richardson, 1906 = *Austrosignum* and
Paramunna
Austroflilius Hodgson, 1910 = *Neojaera*
Austronanus Hodgson, 1910 = *Paramunna*
Austroniscus Vanhöffen, 1914 = ? *Caecianiropsis*
Brevipleonida Gnanamuthu, 1954 = *Angeliera*
Caecimunna Richardson, 1908 = *Munna*
Duslenia Lévi, 1950 = *Microcharon*
Echinozone G. O. Sars, 1899 = *Ilyarachna*
Eugerdia Meinert, 1890 = *Desmosoma*
Haliacris Pfeffer, 1887 = *Munna*
Henopomus Krøyer, 1846 = *Janira*
Iaira Meinert, 1877 = *Jaera*
Iamna Bovallius, 1866 = *Stenetrium*
Ianthe Bovallius, 1881 = *Ianthopsis*, *Iolella*, and *Janira*
Ilychthonos Barnard, 1920 = *Syneurycope*
Iolanthe Beddard, 1886 = *Ianthopsis* and *Janira*
Iole Ortmann, 1900 (see RICHARDSON 1905, p. 547)
= *Iolella*
Ischnosoma G. O. Sars, 1866 = *Haplomesus*, *Heteromesus*, and *Ischnomesus*
Jaeridina Milne-Edwards, 1840 = *Jaera*
Jamna – see *Iamna*
Janirella Sayce, 1900 = *Heterias*
Janthe – see *Ianthe*
Jolanthe – see *Iolanthe*
Jole – see *Iole*
Jorina Nierstrasz, 1918 = *Iathrippa*
Leptaspidia Bate & Westwood, 1868 = *Paramunna*
Mesostenus G. O. Sars, 1864 = *Ilyarachna* and
Pseudarachna
Metajaera Verhoeff, 1949 = *Jaera*
Metamunna Tattersall, 1905 = *Paramunna*
Mormomunna Vanhöffen, 1914 = *Acanthomunna*
Munnopsoides Tattersall, 1905 = *Munnopsis*
Notasellus Pfeffer, 1887 = *Iathrippa*
Notopais Hodgson, 1910 = *Ilyarachna*
Oniscoda Latreille, 1829 = *Janira*
Pleuracantha G. O. Sars, 1864 = *Pleurogonium*
Pseudomunna Hansen, 1916 = *Acanthomunna*
Pseudomunnopsis Hansen, 1916 = *Munnopsis*
Rhabdomesus Vanhöffen, 1914 = *Ischnomesus* and
Stylomesus
Tole Ortmann, 1900 = *Iolella*
Vana Meinert, 1890 = *Macrostylis*.

V. GENERAL PART

A. Postmarsupial development

Up to the present time only FORSMAN (1944) and BOCQUET (1953) have treated the postmarsupial development in Asellota in detail, both studying the ontogeny of the littoral *Jaera albifrons albifrons*.

Materials of bathyal and abyssal isopods generally consist of one or a few specimens only. However, a comparatively large material of the new species *Haploniscus helgei* was dredged by the *Galathea*, and found in the Copenhagen Museum are rather large and representative materials of two other species, *H. bicuspis* (G. O. Sars) and *H. spinifer* Hansen, collected by the *Ingolf* Expedition. In addition, the specimens of *H. antarcticus* Vanhöffen from the German Antarctic Expedition have been borrowed from the Berlin Museum.

Jaera albifrons albifrons

FORSMAN (l. c., p. 25) and BOCQUET (l. c., p. 231) both enumerate a number of stages which will be

briefly listed below. FORSMAN adopted the terms "Mancastadium", "Vorbereitungsstadium", etc., introduced by ZIMMER (1926) for Cumacea. I follow BOCQUET in allotting numbers to the various stages, thus indicating that it is as yet too early to attempt to correlate the very poorly known postmarsupial development of isopods and cumaceans.

Stage I (on leaving the marsupium): Head proportionately very large and pleon small. Head and pereonites 2-6 with one pair of lateral setae, prns. 1 and 7 with none. Prn. 7 much smaller than 6. Flagellum of antenna with 8 joints. No pereopods VII. Sex indeterminable, pleopods 2 forming an operculum. Length 0.9 mm.

Stage II: Head proportionately smaller and pleon larger. Head and prns. 1-6 with two pairs of lateral setae, prn. 7 with one. Prn. 7 still somewhat smaller than 6. Flagellum of antenna with 9 joints. No prps. VII. Sex indeterminable, plps. 2 forming an operculum. Length 1.0 mm.

Stage III: In comparison with the adult the head is still considerably larger, pleon about as large as, but more rounded than in the adult. The number of lateral setae varies. Prn. 7 a little smaller than 6. Flagellum of antenna with at least 11 joints. Prps. VII developing, strongly curved and with indistinct articulations. Sex determinable in most cases, due to the size of the pleotelson (larger in males than in females). In some specimens with larger pleotelson a subdivision in lobes – indicating sympods, endopods and exopods of male pleopods 2 – starts inside the female-like operculum during this stage; these are the “avant-prémâles” of stage III (BOCQUET, l. c.).

Males.

After stage III the number of stages before sexual maturity is reached varies, at least in the males, and seems to be influenced by the environment. If the “avant-prémâle” state is already reached in stage III the specimen inevitably becomes premale (“prémâle”) in stage IV. Generally, the “avant-prémâle” state occurs in stage IV, followed by the premale state in stage V; it is very rarely postponed until stage V which means that sexual maturity is not reached until stage VII.

Thus, the premale (or pre-puberty) state may occur in stages IV, V or VI and is limited to one stage only. It is characterized by (1) development of pleopods 1 (pre-operculum) which may be very diversely differentiated (BOCQUET's fig. 16), disregarding the stage in which the premale state is reached. However, even in the most advanced pleopods 1 the posterolateral hook, setae, and right-angled corner of the adult male are not yet present; (2) a further development of pleopods 2 (BOCQUET's fig. 15) which during the preceding moult become liberated from the operculum, having commenced differentiation inside the latter during the “avant-prémâle” state; (3) pereopods I sexually differentiated.

Stage IV: Whether the premale state is reached or not in this stage, pereopods VII have the normal shape, but are shorter than VI. A lobe on carpus of prps. VI and VII may either be present or still not developed.

Stage V: Prps. VII about as large as VI. Mature males of this stage have the lobes on prps. VI and VII fully developed, premares have these lobes somewhat smaller and with fewer setae.

Stage VI: In this stage the greater part of the males become sexually mature, with pleopods 1 and 2 fully developed (BOCQUET 1953, fig. 17 and SYE 1887, pl. III, 39).

Females.

Stage IV: Prps. VII of normal shape but shorter than VI – as in the males; pleopods 2 of course, remain opercular.

Stage V: Prps. VII about as large as VI.

Stage VI: Prps. VII slightly larger than VI.

Stage VII: The egg strings in the ovaries grow large and turn green.

Stage VIII: Sexual maturity is reached. The lamellar oostegites form a marsupium and the first eggs are laid.

Stage IX: During the breeding period each incubatory stage (with marsupium) is followed by a preparatory stage (without marsupium) before the next incubatory stage. The females of the preparatory stages are relatively smaller than those of the incubatory ones and oostegites are claimed to be absent (BOCQUET 1953, p. 242). See discussion on this latter point on p. 215.

Thus, in females it takes eight stages to reach sexual maturity, i. e. at least one and generally two stages more than in the males.

Pseudasellus nichollsi

In his description of this freshwater species from Tasmania, CHAPPUIS (1951, p. 15) mentions some specimens which he considers to be intersexes having a female predominance. The male pleopods 1 are more or less developed, but never as differentiated as in the adult male. The second pleopods are shaped as the female operculum, but being transparent, a differentiation in lobes is clearly visible (fig. 21). CHAPPUIS tentatively suggests that these lobes represent the endo- and exopods of the male pleopods 2.

In comparison with BOCQUET's fig. 14 (l. c.) of the slightly differentiated operculum in *Jaera albifrons* there is no doubt that this assumption is correct. CHAPPUIS does not mention the size of these supposed intersexes but it is most likely that they are somewhat or a little smaller than the typical male and female. In this case they are undoubtedly undergoing the normal stages of development, as those found in *J. albifrons* (the “avant-prémâle” state).

Although CHAPPUIS makes no mention of this, it is assumed that the developing male pleopods 1 are found simultaneously with the slightly differentiated, opercular pleopods 2. If so, *Pseudasellus* differs from *Jaera* in having pleopods 1 in a state of development while plps. 2 are still opercular (cf. discussion below, p. 212).

Other species

In the description of the available stages in the following species I have tried to correlate these with those found in *Jaera albifrons*. As shown by BOCQUET, the occurrence of the premale state in *Jaera* is not referable to a fixed stage, but may be found in stage IV, V or VI. For this reason, the correlation of stages from one species to another should probably be based rather on the successive development of pereopods VII than on that of the male pleopods. This has been done in the following eleven species:

Haploniscus bicuspis bicuspis

The study of the total material of this subspecies from altogether fifteen *Ingolf* stations (699-2465 m, -1.1 - -0.4°C .) disclosed two stages in which the sex is indeterminable and two later immature stages in which males and females could be determined, not only by size but also by differences in external morphology.

Stage II: Body (Fig. 138a) tapering more towards the hind end than in the adult (SARS 1885, pl. 10, 31; HANSEN 1916, pl. II, 2a). Pereonite 7 only faintly indicated. Flagellum of antennula and antenna with 3 and 9 joints respectively; process on joint 3 of peduncle of antenna very prominent (138b). Pereopods VII not developed. Uropods apparently not developed. Body length 0.9-1.0 mm (St. 141: 0.7 mm). In view of the almost equal in-

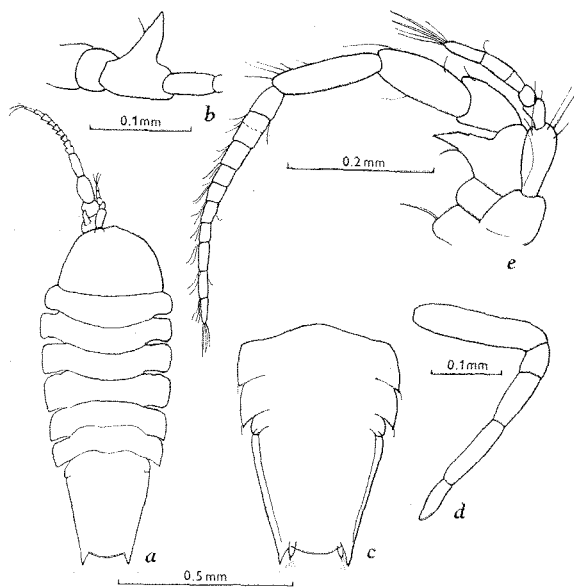


Fig. 138. *Haploniscus b. bicuspis* (G. O. Sars), from *Ingolf* St. 139; a, stage II; b, stage II, proximal joints of antenna from the side; c, stage III, pereonites 5-7 and pleon; d, stage III, pereopod VII; e, stage IV, ♀, antennula and antenna.

crease in size between the available stages of this species, it seems most likely that this is stage II rather than stage I.

Stage III: The posterior pereonites broader and the seventh more clearly visible (138c) than in stage II, although not fully developed. Flagellum of antennula and antenna with 3 and 10 joints respectively; prominent process on antenna. Prps. VII developing (138d). Uropods fully developed. Body length 1.4-1.5 mm.

Females.

Stage IV: Shape of body as in the adult; prn. 7 fully developed. Flagellum of antennula with 4 joints as in the adult ♀, of antenna with 10-11 joints (138e); both are stronger than in the adult; prominent process on antenna. Prps. VII fully developed and as long as prps. VI. Body length 1.7-1.8 (1.9) mm.

Stage V: Flagellum of antenna with 11 joints. Length 2.1 mm.

Stage VI (incubatory ♀): Sexual maturity reached. Ventral side of body concave throughout. Flagellum of antenna with 13 joints. Length 2.5-2.6 mm (St. 117) and 2.7-2.8 mm (St. 139). It seems probable that the incubatory stage in this species follows immediately after stage V, in view of the moderate increase in size.

Stage VII (preparatory ♀): Body narrower and less flattened. Sternum of prns. 1-4, and especially of 5-7, strongly vaulted. Length (2.4) 2.5-2.8 mm. None of a total of 43 adult females without marsupium had any developing oostegites; this probably means that there is no intermediate stage with this kind of oostegite between females without and females with fully developed oostegites (cf. p. 214).

Males.

Stage IV: In all details corresponding to the juvenile females of the same size and stage, except in the following respects: (1) Presence of developing pleopods 1 (Fig. 139a-b) which reach forwards to the posterior margin of the sternum of prn. 7, thus emerging from the vestigial pleonite in front of pleotelson; (2) sternum of prns. 5-7 less vaulted; (3) average length of postero-lateral processes greater (cf. Fig. 140); (4) the two distal joints of peduncle of antenna slightly thicker. Males of this stage differ from the adult males in the following respects: (1) pleopods 1 developing and plps. 2 forming an operculum; (2) no depression between posterior end of branchial cavity and anal doors; (3) postero-lateral processes shorter (Fig. 140); (4) flagellum of anten-

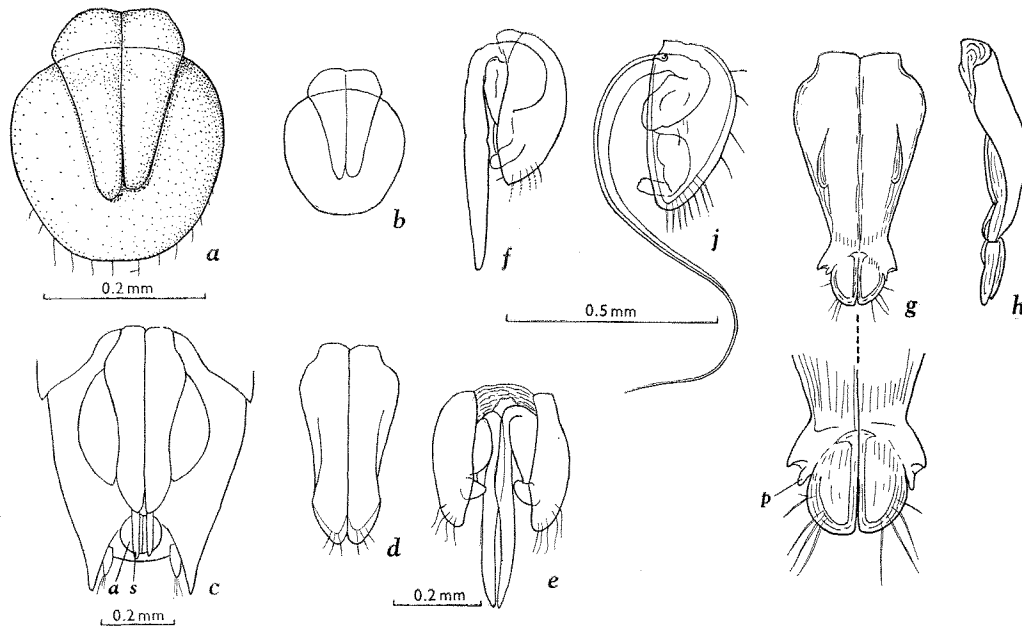


Fig. 139. *Haploniscus b. bicuspis* (G. O. Sars); male pleopods; a-b and f-j from *Ingolf* St. 117; c-e, from *Ingolf* St. 138; a-b, stage IV, plps. 1-2; c, stage V, pleon from below (a, anal door; s, tip of stylus of plps. 2); d-e, stage V, plps. 1-2; f, stage V, plps. 2; g-h, stage VI (adult ♂), plps. 1 from below (outside) and from the left side (p, uncalcified process); j, stage VI, plp. 2.

nula with 4 joints (5 in adult ♂) and of antenna with 10 joints (13 in adult ♂). Length 1.6-1.85 mm.

Stage V: Plps. 1 and 2 male-like but not fully developed and plps. 1 calcified throughout (Fig. 139c-f); the stylets of plps. 2 (s in 139c) reach a little beyond the anal doors (a). The depression between posterior end of branchial cavity and anal doors present, although not as deep as in the adult ♂. Otherwise as adult ♂. Length (1.93) 2.0-2.2 mm.

Stage VI (adult ♂): To the description of the pleopods given by HANSEN (1916, p. 30, pl. II, 2h-i) the following details can be added: The two small angles, or rather processes, on each side of the distal part of plps. 1 (p in Fig. 139g) are uncalcified, as is a broad stripe proximal to them. These stripes separate the greater calcified part of the pleopods and the distal, likewise calcified plates which are semi-circular and have a few long setae terminally. The

Table 10. Age distribution of the total collection of *Haploniscus b. bicuspis* from the *Ingolf* Expedition.

Station No.	Sex		Males (numbers and length in mm)			Females (numbers)				
	Age	?	Stage IV	Stage V	Adults	Stages IV and V	Adults			
							Without marsup.	Marsup. empty	With eggs	With embryos
102	1	-	-	-	1 (2.4)	-	1	-	-	-
103	-	-	2 (1.8-1.85)	1 (2.2)	-	1	-	-	-	-
104	1	-	-	1 (2.2)	1 (2.5)	1	6	1	2	-
105	1	-	-	-	-	-	2	-	-	-
113	2	-	-	-	1 (2.6)	1	3	-	-	-
116	1	1 (1.7)	-	-	1 (2.3)	1	8	-	-	-
117	1	1 (1.6)	1 (2.1)	1 (2.1)	3 (2.5-2.7)	1	6	9	4	5
118	-	-	-	-	1 (2.6)	-	-	-	-	-
119	-	-	-	4 (1.93-2.1)	2 (2.5)	1	6	3	1	1
120	2	-	-	-	-	1	-	1	-	-
124	-	1 (1.6)	1 (2.1)	1 (2.1)	-	-	2	1	-	-
125	-	-	-	-	1 (2.4)	-	1	-	-	-
138	1	3 (1.6-1.7)	2 (2.0)	2 (2.0)	-	1	1	-	2	-
139	5	6 (1.69-1.78)	-	-	3 (2.3)	9	6	2	-	-
141	6	-	-	-	1 (2.5)	1	1	-	-	-
Total number	21	14 (1.6-1.85)	10 (1.93-2.2)	15 (2.3-2.7)	18	43	17	9	6	

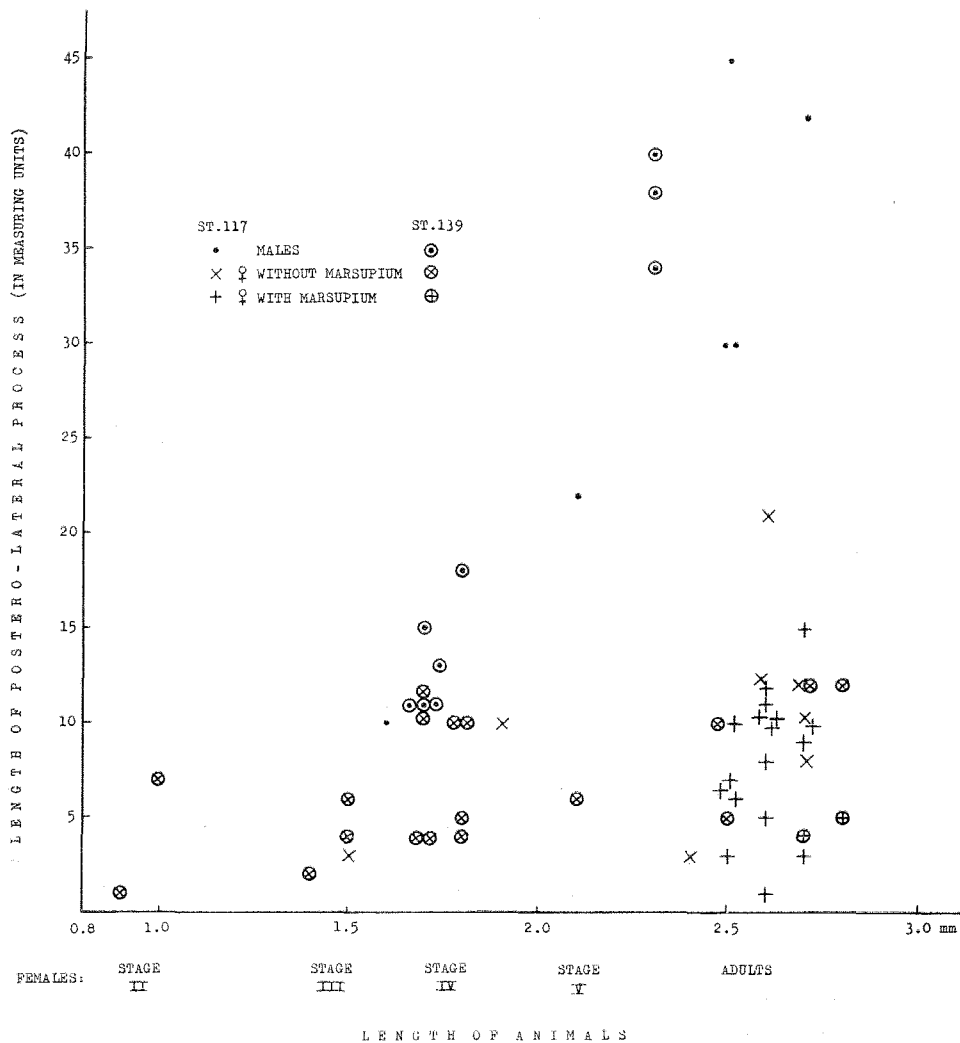


Fig. 140. Variation in length of postero-lateral processes in the collection of *Haploniscus b. bicuspis* from Ingolf Sts. 117 and 139.

postero-lateral and median margins of each semi-circle are thicker than the rest. Proximal part of plps. 1 furnished with two longitudinal keels and somewhat vaulted (139h). Distal end of plps. 1 of an adult ♂ from St. 139 is shown in Fig. 25c, p. 58. Plp. 2 according to Fig. 139j. Length 2.3-2.7 mm.

The number of specimens of the various age groups is given in Table 10. The predominance of adult females compared with adult males is remarkable (75 vs. 15) and is certainly explained by assuming that the females have two or more egg-bearing stages after maturity is reached. As the period of collecting was confined to one month only (from 10 July-11 August) no information about a possible seasonal reproduction can be deduced from the table.

One of the above named sexual differences, i. e. the length of the postero-lateral processes (spines) on pleon, shows considerable variation. In Fig. 140

the total length of males and females is plotted against the length of the processes (i. e. beyond the distal end of pleotelson medianly). In the males the length of the processes is proportional to the total length, in the females it varies greatly (in adult females without marsupium between 3 and 21 units on the measuring ocular, and in females with marsupium between 1 and 15 units).

Haploniscus spinifer

Stage II (2 specimens from Ingolf St. 36 (Table 2, p. 59) and 8 from St. 78): Pereonite 7 as in *bicuspis*. Flagellum of antennula with 3 joints and of antenna with 9. Pereopods VII not developed. Length 0.8-1.0 mm (St. 78) and 1.1-1.2 mm (St. 36).

Stage III (1 specimen from St. 22): Prn. 7 still much smaller than 6. Flagella as in stage II. Prp. VII developing (cf. Fig. 138d). Length 1.6 mm.

Females.

?Stage VII (preparatory ♀ from St. 36): Flagellum of antennula and antenna with 4 and 11 joints respectively. Length 2.3 mm.

Males.

Stage VI or later stages (1 adult ♂ from St. 36, 3 from St. 22): Flagella as in adult ♀. Length 2.6-2.9 mm. The variation in shape of body, etc. in these males was described p. 59 and will be further discussed (p. 228).

Haploniscus antarcticus

In his description of this species, VANHÖFFEN (1914, p. 558) mentioned and illustrated (fig. 85f) the first pleopods of a young male in which plps. 1 were in a state of development and plps. 2 operculum-shaped (as in e. g. *bicuspis* – Fig. 138a). Since a total of 18 specimens of *antarcticus* were collected during the German Antarctic Expedition I have – through the courtesy of Dr. H.-E. GRUNER – borrowed the entire material from the Berlin Museum. Unfortunately, only 12 specimens remain. According to VANHÖFFEN, the only adult male was collected on 30th March 1903 at 3397 m depth (Cat. No. 17707) together with two other specimens. All three specimens are still preserved, but of the adult male only pereonites 1-7 and the outermost part of pleotelson (Fig. 141c) are left. VANHÖFFEN's fig. 85a and g-h (of the entire animal and of male plps. 1-2) was undoubtedly based on this male. Fig. 85b-e (of antennula, antenna and mouthparts) was probably also based on this male, this being the reason why only the body now remains.¹ I have therefore found it in order to select the fragmentary adult male as lectotype and the adult female (with large embryos in the marsupium), collected at the same station, as allotype.

Stage I (Pl. XIV A): Body tapering towards the posterior end. Frontal projection hardly visible. Pereonite 7 not indicated. Flagellum of antennula and antenna with 4 and 9 joints respectively; process on joint 3 of peduncle of antenna not comparatively larger than in the adult (VANHÖFFEN's fig. 85b). Pereopods VII not developed. Uropods considerably larger and stronger than in the adult and

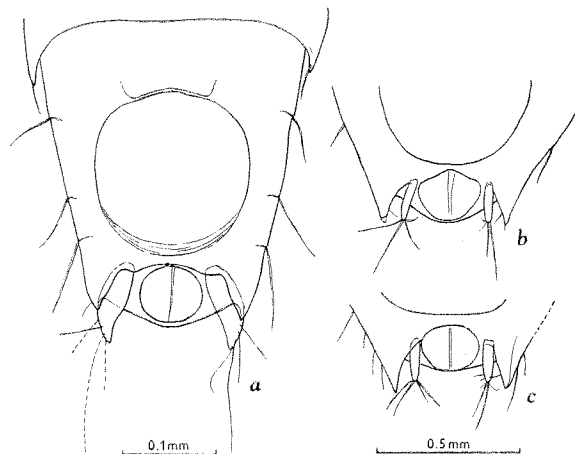


Fig. 141. *Haploniscus antarcticus* Vanhöffen; a, stage I, pleon from below; b-c, ♀ allotype and ♂ holotype, distal end of pleon from below.

curved somewhat inwards (Fig. 141 a); postero-lateral processes small. Length of 4 specimens 1.08-1.16 mm.

?Stage II (Pl. XIV B): Prn. 7 faintly visible. Flagellum of antennula and antenna with 4 and 10 joints respectively. Prps. VII probably still lacking (the specimen was mounted on a slide). Uropods stronger than in the adults, but relatively shorter than in the previous stage; postero-lateral processes a little longer than the uropods and slightly curved inwards terminally. Since prps. VII are almost certainly not in the developing stage as yet, I have referred this specimen to stage II in spite of the fact that in size (1.71 mm long) it is closer to stage IV (1.9-2.0 mm) than to stage I (1.1-1.2 mm).

Females.

Stage IV: Prn. 7 smaller than in the adult. Flagellum of antennula and antenna with 4 and 10 joints respectively. Prps. VII lost. Length 1.9 mm (1 specimen).

Stage VI (incubatory ♀): Shape of body oval (Pl. XIV C). Frontal projection directed downwards as a tiny hook. Posterior margin of pleotelson considerably convex, reaching almost as far backwards as the postero-lateral processes (Fig. 141 b). Flagellum of antennula and antenna with 5 and 12 joints respectively. Three specimens available: (1) 2.7 mm long (6 December 1902, 385 m), marsupium with about 23 embryos which are as large as those in McMURRICH's pl. IX, fig. 71 (1895); (2) 2.8 mm long (12 August 1902, 385 m), with further advanced (stretched) embryos; (3) 3.1 mm long (♀ allotype, 3397 m) with about 25 embryos of the same size as in (1).

1. Three poorly preserved slides (Nos. 552-554, Cat. No. 17706) of a specimen from the *Gauss* Station (17 December 1902) contain one antennula, one mandible and two maxillipeds, but it is unlikely that any of these formed the basis for VANHÖFFEN's fig. 85c-e.

Males.

Stage IV (Pl. XIV D): Prn. 7 and flagella as in female stage IV. Prps. VII as prps. VI, but one-third smaller. Pleopods 1 developing, plps. 2 forming a circular operculum (VANHÖFFEN's fig. 85). Length 2.0 mm (1 specimen).

Stage VI: (adult ♂, holotype). Body with subparallel margins (Pl. XIV E and VANHÖFFEN's fig. 85a). Frontal projection and flagella as in adult ♀. Posterior margin of pleotelson only moderately convex (Fig. 141 c). Length about 2.8 mm.

Haploniscus helgei

Females.

Stage V (Pl. XV G): With 13 joints in flagellum of antenna as in some adult females, and therefore, only differing from these in size. Length 6.6 and 6.9 mm.

Stage VI (incubatory ♀): Flagellum of antenna with 12-14 joints. Length 8.1-8.3 mm.

Males.

Stage IV (1 specimen): Pereonite 7 smaller than in the adult. Flagellum of antennula and antenna with 3 and 11 joints respectively. Pereopods VII as large as prps. VI. Pleopods 1 developing, a little more than half the diameter of the circular operculum-like plps. 2; these without setae along posterior margin (Fig. 142a). Length 5.2 mm.

?Pre-hermaphroditic stage or stage IVa (Pl. XV H) (1 specimen): Pereonite 7 as in the adult. Flagellum of antennula with 4 joints (as in the adult), of antenna with 15 joints. Pleopods 1 developing, plps. 2 forming an operculum of the same shape as in the adult female and with setae along the hind margin; plps. 1 almost reaching this margin (142b). Length 8.0 mm. This extraordinary specimen is further discussed below (p. 228).

Stage VI (adult ♂): Flagellum of antenna with 15-16 joints. Differences between adult ♀ and ♂ listed on p. 54.

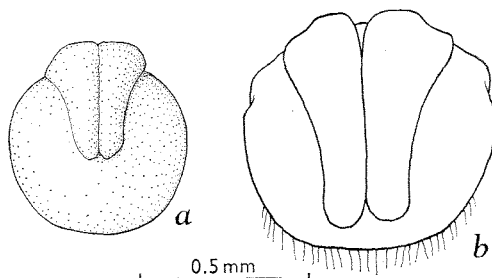


Fig. 142. *Haploniscus helgei* n. sp.; male pleopods 1-2; a, stage IV; b, ? pre-hermaphroditic stage or ? stage IVa.

Haploniscus tridens and *H. percavix*

In addition to the male holotype, female allotype and one fragment of *tridens* from one station, MENZIES (1962b) recorded two "intersexes" from another station. Three females and three males of *percavix* were recorded from three stations (l. c.); two of the males were termed "male intersex". No description or figures of the pleopods or pereopods VII of any of the so-called intersexes were given.

Janirella vema, *J. bifida* and *J. magnifrons*

MENZIES (1956b) founded the former species on a single specimen which is definitely immature, having pereonite 7 smaller and less developed than prn. 6 - and pereopods VII developing, consisting of six joints only (l. c., fig. 5 B); the number of joints in the antennula is also smaller than in related species. Furthermore, male pleopods 1 are developing and plps. 2 form an operculum, as in three of the above mentioned species of *Haploniscus*. According to the shape of prps. VII the specimen should be referred to stage III.

J. bifida and *magnifrons* were also described on a single specimen only (MENZIES 1962b). The former was termed "intersex", the latter "female intersex" but no description or figures of the pleopods were given. There is hardly any doubt that they are in the same developmental stage as *vema*.

Echinothambema ophiuroides

The holotype and only specimen (MENZIES 1956b) is in the same stage as the preceding, prn. 7, prp. VII, and pleopods 1-2 are as described above.¹

Ilyarachna multispinosa

The only specimen of *I. argentinae* (certainly identical with *multispinosa* - cf. p. 97) is an "intersex fragment" (MENZIES 1962b). The pleopods are not described or figured.

Conclusions

A comparison of certain features in all developmental stages available (Table 11) shows that it is impossible to find more than a few equal characters for the same stage in various species within different

1. The developing male pleopods 1 are unusually small (l. c., fig. 4D), reaching backwards only between one-third and one-fourth of the total length of the operculum.

Table 11. Comparison of morphological details in the developmental stages of males of some Asellota. (Lengths in mm; prn. = pereonite; prp. = pereopod; plp. = pleopod; sm. = smaller; (<) = slightly smaller than; << = smaller than; < < = smaller than; < < < = much smaller than; sl. = slightly smaller than; < < < < = much smaller than; f. = fully; diff. = differentiated).

Species	<i>Jaera a. albifrons</i> (some specimens) ¹	<i>Jaera a. albifrons</i> (the majority) ²	<i>Jaera albifrons</i> (a few specimens) ³	<i>Haplomisus</i> <i>b. bicuspis</i>	<i>Haplomisus</i> <i>spitifer</i>	<i>Haplomisus</i> <i>antarcticus</i>	<i>Haplomisus</i> <i>helgei</i>	<i>Janirella</i> <i>vemae</i>	<i>Echinothambema</i> <i>ophiuroides</i>
Stage I (Manca 1)	Length Prn. 7 Prps. VII	0.83-0.94 much smaller than prn. 6 lacking	—	—	—	1.8-1.16 lacking	—	—	—
Stage II (Manca 2)	Length Prn. 7 Prps. VII	0.91-1.03 smaller than prn. 6 lacking	(0.7) 0.9-1.0 << 6 lacking	0.8-1.2 << 6 lacking	1.71 << 6 (?) lacking	—	—	—	—
Stage III (Manca 3)	Length Prn. 7 Prps. VII Plps. 1 Plps. 2	1.09-1.26 (<) 6 developing lacking operculum	1.4-1.5 < 6 developing lacking operculum	1.6 << 6 developing lacking operculum	—	—	3.3 < 6 developing developing operculum	—	5.0 < 6 developing developing operculum
Stage IV (Jugend)	Length Prn. 7 Prps. VII Plps. 1 Plps. 2	1.23-1.46 as 6 as VI, but sm. developing lacking sl. diff.	1.7-1.8 (1.9) as 6 as VI developing operculum	— — — —	— — — —	1.91-2.0 < 6 < VI developing operculum	5.2 < 6 as VI developing operculum	— — — —	— — — —
Stage V (Vorbereitung)	Length Prn. 7 Prps. VII Plps. 1 Plps. 2	1.31-1.57 as 6 as VI developing developing	(1.93) 2.0-2.2 as 6 as VI developing developing	— — — —	— — — —	— — — —	— — — —	— — — —	— — — —
Stage VI (Adult ♂ 1) (except a few <i>J. a. albif.</i>) (Hochzeit 1)	Length Prn. 7 Prps. VII Plps. 1 Plps. 2	1.63-1.86 as 6 as VI fully developed fully developed	(2.3-2.6) as 6 as VI f. developed f. developed	(2.6-2.9) as 6 as VI f. developed f. developed	(c. 2.8) as 6 as VI f. developed f. developed	(8.6-8.9) as 6 as VI f. developed f. developed	— — — —	— — — —	— — — —
Stage VII (Adult ♂ 2) (Hochzeit 2)	Length	1.91-2.00	(2.3-2.6)	(2.6-2.9)	(c. 2.8)	(8.6-8.9)	—	—	—

1. Premales in stage IV.
2. Premales in stage V.
3. Premales in stage VI.

families and even in species of the same genus. Naturally, it cannot be taken for granted that the correlation is correct, i. e. that all specimens with developing pereopods VII really do belong to stage III. If this is not the case, however, it is even more difficult to find features which characterize the same developmental stages in the different species. It is especially noteworthy that in *Janirella vemae* and *Echinothambema ophiuroides* the presence of developing male pleopods 1 occurs simultaneously with developing prps. VII, i. e. as early as in stage III.¹

In *Haploniscus bicuspis* the material was sufficiently large to include both immature females with a typical operculum and equally large specimens with developing pleopods 1 (stage IV), immediately followed by distinctly immature males with somewhat further developed plps. 1 and typical, although not yet fully developed plps. 2 (premale stage V). This should indicate that also the specimens in stage IV are actually premales (or perhaps rather "avant-prémâles"). In view of this it is more probable that the only available specimens of *Janirella vemae* and *Echinothambema ophiuroides* are "avant-prémâles" rather than ambi-sexual or intersexes as stated by MENZIES (1956b, 1962b).

1. However, there is a certain possibility that the stage is in reality stage IV, the occurrence of developing prps. VII having thus, in these two species, been postponed to a later stage than usual.

B. Reproduction

Apart from the genus *Asellus*, very little is known about various aspects of reproduction in the Asellota, notably of course, in the deep-sea forms. In the following an attempt has been made to deal with some of these questions. The study is based not only on the *Galathea* material but also on applicable collections in this Museum or those borrowed from elsewhere.

NUMBER OF PREPARATORY STAGES

As mentioned above (p. 207), BOCQUET found (in *Jaera a. albifrons*) and I, myself (in *Haploniscus bicuspis*) that none of the adult females had developing oostegites. However, it has hitherto been generally accepted that the incubatory stage (with marsupium) in the Paraselloidea is preceded by two preparatory stages, the first of which shows no sign of oostegites, while in the second these are present

It is interesting that BOCQUET (1953, p. 240), in his very large collection of premales of *Jaera albifrons* with simultaneous development of pleopods 1 and 2, found one single instance of "well developed" plps. 1 on a specimen with plps. 2 shaped as an operculum. BOCQUET stressed that "il ne s'agissait nullement d'un cas d'intersexualité, mais de la dissociation, dans leur ordre d'apparition, de deux caractères dont la manifestation est normalement simultanée ... [L'animal] a, par la suite, donné un mâle tout à fait normal". Thus, *Jaera albifrons* differs from all the other species listed in Table 11 in having a simultaneous development of plps. 1 and 2 (or even a slight differentiation of the operculum in the "avant-prémâles" of the preceding stage), while in the others the first development of plps. 1 takes place before the differentiation of the operculum.

In the description of the embryos of *Storothyngura novae-zelandiae* (WOLFF 1956a, p. 122) it was shown that the operculum is established as a bilobed plate (fig. 37d) which was found comparable in all embryos. As also pointed out by MENZIES (1956b, p. 11) the presence of developing plps. 1 together with opercular plps. 2 further supports the suggestion that in the females of the Paraselloidea plps. 2 form the operculum while plps. 1 never become developed.

as conspicuous oval outgrowths (developing oostegites).

In order to obtain a clearer picture of this problem I have carefully gone through the total available material of Paraselloidea from depths exceeding 200 m, including more than 2000 specimens in 137 species¹ (Table 12). The survey revealed several extraordinary facts.

One preparatory stage before sexual maturity

First and foremost it was found that in three families – Haploniscidae, Munnidae and Macrostylidae – none of a total of 90, 133, and 22 adult females in the respective families had developing oostegites

1. A good many more species have been investigated, but were not entered in the table, as they were represented by subadult specimens only or were too fragmentary to decide either the sex or the presence of oostegites.

(cf. Table 14).¹ This seems to indicate that females in all species in these three families progress directly from the stage without oostegites to the incubatory stage, thus having only one preparatory stage.

As mentioned above, BOCQUET (1953) maintained that *Jaera a. albifrons* has no developing oostegites. This I found surprising since in all well represented species of other genera of the Janiridae (e. g. *Janira* and *Iolella*), females with developing oostegites are abundant (Table 12). It is impossible to judge the conditions in most other janirid genera owing to lack of material. In order to confirm BOCQUET's observation I have made a study of part of the *Jaera albifrons* material in this Museum. Females with developing oostegites were found to be present in material from such widespread localities as Finland, Denmark, the Faroes, W. Greenland and Maine in the U. S. A. It is true that these outgrowths are very difficult to observe (especially in transparent specimens), not only because the legs covering them must be bent aside but also because they are quite small and lunular in shape. Pl. XIV F shows the largest outgrowths it was possible to find in this rather extensive collection. It was also stated that they are present in another shallow water species of Janiridae, *Iais pubescens*.

Table 12 also shows that, on the other hand, no adult females without oostegites were present in the Nannoniscidae. Of a total of 126 females studied, all had either developing or fully developed oostegites. This is especially evident in *Nannoniscus analis* of which a large collection of 87 females was available from one locality.

It has not been possible to discover why Haploniscidae, Munnidae, Macrostylidae, and Nannoniscidae have only one preparatory stage before sexual maturity instead of two as in the other families. The depths and temperature range of the studied specimens (Table 12) shows that with one or two exceptions the Munnidae occur at moderate depths of less than 2000 m. However, the temperature – owing to distribution at high latitudes – is, in most of the species, below 4-5°C. This is also so in the Nannoniscidae, but conditions with regard to oostegite development are diametrically opposed in the two

1. The category "females without oostegites" naturally only includes those which were as large as or only a little smaller than females in the same assembly with developing oostegites (in the families where such females are represented), or those with a marsupium. It is thus believed that only those females without oostegites, which in the next stage would moult into females with developing oostegites or with a marsupium, have been included.

families. In contrast to the Munnidae, almost all the specimens of Haploniscidae occur deeper than 1500-2000 m and none at temperatures above 4°, but regarding oostegite development the conditions are identical. Nor do the four families in question differ from the other parasellid families as far as depth and temperature range is concerned.

Two preparatory stages before sexual maturity

In families where females without oostegites as well as those with developing oostegites are found, the relative number of these two categories varies considerably (Table 14). One would expect a slightly larger number of the former as these are the younger population, but this is only so in Dendrotionidae and Ilyarachnidae – which do have either many more of the former (Dendrotionidae) or almost twice as many (Ilyarachnidae). In all the other five families there is a correspondingly large predominance of females with dvl. oost.; this is especially true of Eurycopidae which has almost five times as many of the latter. A slight predominance of females with dvl. oost. might be explained by the fact that in all cases where I was in doubt as to whether a female without oostegites was subadult or adult, it was considered subadult, and therefore not counted. However, there were few doubtful cases of this type and they cannot completely account for this very marked predominance. The only explanation would seem to be that in the five families (Janiridae, Ischnomesidae, Desmosomatidae, and especially Eurycopidae and Munnopsidae) the preparatory stage following immediately after the first incubatory stage (with marsupium), consists of females with dvl. oost., this also being the case after all later incubatory stages.¹ Consequently, adult females without oostegites only occur once, viz. just before sexual maturity is reached. On the contrary, the large number of females without oostegites in Dendrotionidae and Ilyarachnidae may indicate that here the incubatory stages are consistently followed by two preparatory stages, one without oostegites and one with dvl. oost. – or perhaps by one stage only, viz. without oostegites (as in Haploniscidae, Munnidae, and Macrostylidae).

The latter presumption is supported by the fact that in *Dendrotion paradoxum* the stage with dvl. oost. seems to be absent at some time during the breeding period: Pl. XIV J shows a female lacking

1. Cf. the evidence in *Storthingura pulchra* of, at least, one stage with dvl. oost. after the first incubatory stage (p. 134).

Table 12. Number of adult males and of adult females with varying oostegite development, based on material of Paraselloidea specimens, from depths greater than 200 m, existing in the Museum of Copenhagen. Only species with at least five specimens each have been entered in the table; the remainder are listed below. Single localities (stations) with a considerable number of specimens are listed separately (*Go.* = *Godthaab* Station; *In.* = *Ingolf* St.; *Th.* = *Thor* St.); dvl. oost. = developing oostegites; ovig. = ovigerous (with eggs or embryos).

Species	No. of localities (stations)	Depth in m	Temp. in °C.	Females				Males
				No oost.	With dvl. oost.	With marsupium		
						Ovig.	Not ovig.	
JANIRIDAE								
<i>Ianthopsis pulchra</i>	4	1100-1510	1.2-4.5	8	10	0	1	10
<i>Janira maculosa</i>	19	200-1510	-0.4-6.1	5	10	14	6	9
<i>Iolella spinosa</i>	<i>Go.</i> 14	310	2.8	0	16	1	3	19
<i>Iolella laciniata</i>	10	300-1380	1.2-3.9	8	5	1	1	5
<i>Iolella vilhelminae</i>	1	400	-0.7	0	2	1	0	17
<i>Janirella bonnieri</i>	1	1227	13	0	0	0	4	3
<i>Katianira chelifera</i>	1	1510	4.5	3	0	0	0	3
7 spp. ¹	8			2	2	0	0	6
HAPLONISCIDAE								
<i>Haploniscus bicuspis</i>	13	700-2470	-1.1-0.4	31	0	6	6	9
<i>Haploniscus bicuspis</i>	<i>In.</i> 117	1890	-1.0	6	0	9	9	3
<i>Haploniscus bicuspis</i>	<i>In.</i> 139	1320	-0.6	6	0	0	2	3
<i>Haploniscus spinifer</i>	2	2700-3470	1.4-1.5	1	0	0	0	4
<i>Haploniscus helgei</i>	1	1360	3.5	4	0	0	3	5
5 spp. ²	6			4	0	3	0	2
MUNNIDAE								
<i>Munna acanthifera</i>	9	550-2090	-0.8-8.4	13	0	0	1	13
<i>Munna acanthifera</i>	<i>In.</i> 24	2260	2.4	18	0	0	0	4
<i>Munna acanthifera</i>	<i>In.</i> 32	600	3.9	15	0	0	0	0
<i>Munna acanthifera</i>	<i>In.</i> 35	680	3.6	30	0	0	0	12
<i>Munna hansenii</i>	3	550-1510	-0.5-6.1	4	0	0	2	4
<i>Munna hansenii</i>	<i>In.</i> 44	1030	4.8	8	0	0	1	3
<i>Munna boeckii</i>	2	200-320	5-7	9	0	7	2	4
<i>Pleurogonium intermedium</i>	3	370-890	-0.6-0.6	9	0	5	5	8
3 spp. ³	5			3	0	0	2	0
DENDROTIONIDAE								
<i>Acanthomunna hystrix</i>	1	1510	4.5	1	0	0	0	0
<i>Dendrotion paradoxum</i>	1	1510	4.5	8	0	0	0	2
<i>Dendrotion spinosum</i>	3	270-1510	4.5-7.5	2	0	0	1	1
<i>Dendromunna mirabile</i>	1	5230-5340	1.1	0	1	0	0	0
ISCHNOMESIDAE								
<i>Haplomesus quadrispinosus</i>	9	700-3520	-1.0-2.4	4	4	0	1	9
<i>Heteromesus frigidus</i> ¹¹	6	930-1440	-0.9-0.6	7	13	0	1	3
16 spp. ⁴	18			4	7	0	0	10
MACROSTYLIDAE								
<i>Macrostylis abyssicola</i>	3	3230-3520	1.3-1.4	5	0	1	0	6
<i>Macrostylis subinermis</i>	4	1320-1900	-1.0-0.6	6	0	0	4	0
5 spp. ⁵	6			4	0	1	1	4
NANNONISCIDAE								
<i>Nannoniscus simplex</i> ¹¹	2	1070-1510	4.4-4.5	0	1	0	5	4
<i>Nannoniscus reticulatus</i> ¹¹	1	550	-0.5	0	2	1	1	3
<i>Nannoniscus plebejus</i>	<i>In.</i> 24	1510	4.5	0	2	0	1	4
<i>Nannoniscus analis</i>	1	2260	2.4	0	60	5	22	18
<i>Nannoniscus oblongus</i>	2	260-1510	4.5-5.9	0	7	1	3	2
<i>Nannoniscus oblongus</i>	<i>In.</i> 32	600	3.9	0	8	0	0	0
5 spp. ⁶	6			0	2	3	2	1

Species	No. of localities (stations)	Depth in m	Temp. in °C.	Females				Males
				No oost.	With. dvl. oost.	With marsupium		
						Ovig.	Not ovig.	
DESMOSOMATIDAE								
<i>Desmosoma politum</i>	2	1070-1510	4.4-4.5	0	6	0	0	2
<i>Desmosoma simile</i>	1	2260	2.4	1	2	1	1	0
<i>Desmosoma gracilipes</i>	2	2260-2700	1.5-2.4	1	2	0	1	2
<i>Desmosoma insigne</i>	1	2700	1.5	0	5	0	1	3
5 spp. ⁷	5			2	5	0	2	2
ILYARACHNIDAE								
<i>Ilyarachna coronata</i>	6	220-1510	3.3-7	11	0	0	0	6
<i>Ilyarachna longicornis</i>	19	370-2470	-1.0-7	24	19	1	4	12
<i>Ilyarachna thori</i>	2	220-820	7.5-7.7	0	0	0	0	9
<i>Ilyarachna kermadecensis</i>	2	4540-7000	1.1-1.3	2	0	0	0	3
7 spp. ⁸	9			3	5	3	2	1
EURYCOPIDAE								
<i>Storhyngura novae-zelandiae</i>	1	2010	2.8	0	3	2	1	3
<i>Storhyngura benti</i>	4	5850-7000	1.2-1.3	1	10	0	3	4
<i>Storhyngura p. pulchra</i>	3	2490-3570	1.9	0	1	1	0	3
<i>Storhyngura p. kermadecensis</i>	1	6620-6730	1.3	0	4	0	0	3
<i>Storhyngura magnispinis</i>	2	2260-2700	1.5-2.4	2	1	0	1	2
<i>Eurycope cornuta</i>	Th. 26	250	6	1	4	0	2	14
<i>Eurycope complanata</i>	3	1920-2700	1.5-3.4	1	2	0	0	2
<i>Eurycope producta</i>	6	310-2150	-0.6-4.5	0	5	1	1	5
<i>Eurycope phalangium</i>	2	600-1100	3.3-3.9	3	1	1	1	1
<i>Eurycope brevirostris</i>	2	890-1090	-0.6	1	0	3	4	8
<i>Eurycope inermis</i>	14	550-1900	-1.0-5	5	16	1	1 + 1	26
<i>Eurycope inermis</i>	Th. 99	870-970	5	2	1	0	0 + 1	11
<i>Eurycope inermis</i>	In. 117	1890	-1.0	2	7	0	0	4
<i>Munnopsurus giganteus</i>	11	550-1470	-1.1-—0.4	0	15	0	2	8
<i>Munnopsurus giganteus</i>	In. 101	1010	-0.7	0	7	0	0	2
<i>Munneurycope murrayi</i> ¹²	15	c. 300-c. 1000	—	2	23	0	12 + 2	26
<i>Munneurycope murrayi</i> ¹²	Th. 76	0-900	—	0	5	0	0 + 1	5
<i>Munneurycope murrayi</i> ¹²	Th. 183	c. 600	c. 6	0	4	0	2 + 2	4
<i>Munneurycope murrayi</i> ¹²	Th. 190	c. 900	c. 7	0	5	0	1	7
<i>Bathypsurus nybelini</i>	4	4400-7900	1.1-2.7	1	3	0	0	1
27 spp. ⁹	40			9	18	3	7	19
MUNNOPSISIDAE								
<i>Paramunnopsis oceanica</i> ¹²	6	c. 300-c. 1000	—	0	5	0	4	3
<i>Munnopsis typica</i> ¹¹	16	200-790	2.5-5.3	4	12	1	6	16
<i>Munnopsis typica</i> ¹¹	Go. 84	240	-0.5	5	9	0	0	13
<i>Munnopsis typica</i> ¹¹	In. 32	600	3.9	0	4	0	2	10
<i>Munnopsis typica</i> ¹¹	In. 138	890	-0.6	0	11	0	0	1
<i>Munnopsis eximius</i> ¹¹	4	890-2700	1.5-5	3	2	0	0	3
<i>Munnopsis bathyalis</i>	1	490	6.5	2	0	0	0	4
3 spp. ¹⁰	5			1	4	0	0	4
<i>Munnopsis longiremis</i>	1	3570	1.9			4		33

1. 7 spp. = *Janira operculata*, *J. alta*, *Iolella spinosissima*, *Janthura abyssicola*, *Janirella spongicola*, *J. laevis*, and *Acanthaspida typhlops*.

2. 5 spp. = *Haploniscus armadilloides*, *H. antarcticus*, *H. ingolfi*, *H. kermadecensis*, and *Hydroniscus abyssii*.

3. 3 spp. = *Pleurogonium spinosissimum*, *P. latimanum*, and *P. pulchrum*.

4. 16 spp. = *Ischnomesus armatus*, *I. profundus*, *I. birsteini*, *I. bruuni*, *I. spärcki*, *I. anacanthus*, *I. roseus*, *Stylomesus inermis*, *Mixomesus pellucidus*, *Haploniscus angustus*, *H. insignis*, *H. modestus*, *Heteromesus dentatus*, *H. greeni*, *H. schmidti*, and *H. longiremis*.

5. 5 spp. = *Macrostylis elongata*, *M. spinifera*, *M. longipes*, *M. longiremis*, and *M. hadalis*.

6. 5 spp. = *Nannoniscoides angulatus*, *Nannoniscus arcticus*, *N. aequiremis*, *N. minutus*, and *N. affinis*.

7. 5 spp. = *Desmosoma plebejum*, *D. latipes*, *D. longispinum*, *D. coarctatum*, and *D. laterale*.

8. 7 spp. = *Ilyarachna quadrispinosa*, *I. dubia*, *I. bicornis*, *I. spinosissima*, *I. antarctica*, *I. nordenstami*, and *I. aspidophora*.

9. 27 spp. = *Acanthocope galathea*, *Syneurycope parallela*, *Storhyngura bicornis*, *S. chelata*, *S. herculea*, *S. furcata*, *S. abyssalis*, *S. serrata*, *S. robustissima*, *Eurycope cornuta*, *E. hanseni*, *E. furcata*, *E. parva*, *E. megalura*, *E. mutica*, *E. gaussi*, *E. sarsi*, *E. ovalis*, *E. vicarius*, *E. madseni*, *E. galathea*, *E. gibberifrons*, *Munnopsurus longipes*, *Munneurycope nodifrons*, *M. menziesi*, *M. elongata*, and *Paropsurus giganteus*.

10. 3 spp. = *Munnopsis beddardi*¹¹, *M. latifrons*, and *M. mandibularis*.

11. Developing oostegites very inconspicuous.

12. Pelagic.

Table 13. Length of developing oostegites in relation to length of the basipodites of the corresponding pereopods.¹ In some species the body lengths are recorded.

<i>Ianthopsis pulchra</i>		<i>Eurycope cornuta</i>		<i>Storthingura pulchra kermadecensis</i>		
<i>Ingolf St. 95</i>	prps. II-IV	<i>Thor St. 26</i>	prps. II-IV	<i>Galathea St. 650</i>	prp. I	prps. II-IV
3 ♀	$\frac{2}{3}$	♀ 12.9 mm	fully dvl.	Type	$\frac{3}{5}$	$\frac{1}{1}$
1 ♀	$\frac{2}{5}$	♀ 11.8 mm	fully dvl.	♀	$\frac{1}{2}$	$\frac{5}{6}$
<i>Ingolf St. 25</i>		♀ 12.2 mm	$\frac{3}{5}$	♀	$\frac{1}{2}$	$\frac{4}{5}$
2 ♀	$\frac{2}{5}$	♀ 11.9 mm	$\frac{1}{2}$	♀	$\frac{1}{3}$	$\frac{1}{2}$
2 ♀	$\frac{1}{3}$	♀ 9.3 mm	$\frac{1}{5}$	<i>Munnopsurus giganteus</i>		
<i>Ingolf St. 96</i>		♀ 9.0 mm	$\frac{1}{2}$	<i>Godthaab St. 112</i>	prps. II-IV	
1 ♀	$\frac{2}{5}$	♀ 8.7 mm	lacking	♀	$\frac{5}{4}$	
1 ♀	$\frac{1}{3}$				♀	$\frac{1}{2}$
<i>Munneurycope murrayi</i>		<i>Eurycope inermis</i>		<i>Ingolf St. 101</i>		
<i>Godthaab St. 1</i>	prp. III	<i>Ingolf St. 117</i>	prps. II-IV	1 ♀	$\frac{7}{8}$	
♀ 7.0 mm	$\frac{8}{7}$	♀ 9.3 mm	$\frac{1}{2}$	5 ♀	$\frac{1}{1}$	
♀ 5.6 mm	$\frac{1}{2}$	♀ 9.0 mm	$\frac{1}{2}$	1 ♀	$\frac{7}{8}$	
<i>Thor St. 190</i>		♀ 7.9 mm	$\frac{1}{2}$	<i>Bathypsurus nybelini</i>		
♀ 10.3 mm	$\frac{1}{1}$	♀ 7.6 mm	$\frac{1}{2}$	<i>Sw. Exp. St. 371</i>	prp. III	
♀ 5.0 mm	$\frac{1}{2}$	♀ 7.4 mm	$\frac{1}{2}$	Type	$\frac{1}{2}$	
♀ 5.2 mm	$\frac{1}{3}$	♀ 7.0 mm	$\frac{1}{2}$	♀	$\frac{8}{7}$	
<i>Thor St. 74</i>		♀ 6.5 mm	$\frac{1}{2}$	<i>Galathea St. 601</i>		
5 ♀	$\frac{1}{1}$	♀ 8.8 mm	$\frac{1}{10}$	♀	$\frac{2}{5}$	
1 ♀	$\frac{1}{2}$	♀ 6.7 mm	lacking			

1. As an example, in the first part of the table three females of *Ianthopsis pulchra* from *Ingolf St. 95* were found to have dvl. oost. two-thirds as long as basis of prps. II-IV.

oostegites but possessing nine large eggs in the ovary, just ready to be spawned into a marsupium after the next moult.

THE DEVELOPING OOSTEGITES

Length

In the sporadic references to dvl. oost. in the literature on Paraselloidea (i. e. in descriptions of new species, etc.) it was, at most, stated that the oostegites were "developing", "rudimentary", "half-sized", etc. No account was ever given of their relative length within a single species or a single population.

However, in some species I have found remarkable differences in their size (Table 13). Although this phenomenon occurred in several other species, in the present species it was especially pronounced, and the animals were large enough to estimate the size of the oostegites with certainty.

It is perhaps natural to suggest that this difference indicates that two stages with dvl. oost. are involved in the species in question. In *Munneurycope murrayi* the specimens with long oostegites are considerably larger than those with short ones. However, the

lengths of the oostegites do not fall into two well defined groups, as one could expect, and in *Eurycope cornuta* and *inermis*, females with short oostegites were found to be larger than females with much longer oostegites. This latter feature may of course be explained by supposing that larger females with short oostegites have already passed through one or more incubatory stages; this not being so with smaller females with long oostegites. In any case, it seems highly improbable that more than one preparatory stage (with dvl. oost.) occurs between the preparatory stage (without oost.) and the incubatory stage. The stage with dvl. oost. is even left out entirely in three families (Table 12).

In some of the species the dvl. oost. are so thin-skinned and bloated that there is a possibility that they may expand during the dvl. oost. stage, thus accounting for the difference in length. But in others, especially *Storthingura pulchra*, they are considerably calcified and this must, of course, prevent growth. In such species it appears that the dvl. oost. in specimens of the same species – even from a very restricted area – really *do* vary remarkably in length.

In some species the dvl. oost. were consistently

found to be very small. This is especially true of *Munnopsis typica*. Fig. A (Pl. XV) shows a specimen without oostegites, Fig. B a specimen with a minimum development of the oostegites (not to be seen on prp. IV and hardly discernable on prp. III) and Fig. C a specimen with a maximum development. In *M. eximius* they are a little more conspicuous and in *beddardi* still a little larger. In *latifrons* and *bathyalis*, respectively, those on prps. I are one-third and one-fourth as long as the corresponding basipodites, those on prps. II one-third and a half as long as the basipodites, and those on prps. III and IV as long as or a little longer than the short basipodites. They are more or less triangular in shape. In *Nannoniscus simplex* and *reticulatus* and in *Heteromesus frigidus* the dvl. oost. are also very small.

Number

The number of oostegites (developing as well as fully developed) was consistently four pairs and they were always found to be outgrown from the coxa of pereopods I-IV. There were, however, some curious exceptions.

In the following two species I have found – among a total of 23 specimens with fully developed oostegites (but all non-ovigerous – cf. Table 12) – that five specimens had fully developed oostegites only on pereopods I, and in two more specimens they were present on prps. I and IV. There was not the slightest trace of oostegites on the remaining four anterior pairs of pereopods.

The data are as follows:

(1) Oostegites on prp. I:

Eurycope inermis (Thor St. 99, 61°15'N, 9°35'W, 870-970 m).

Eurycope inermis (Ingolf St. 139, 63°36'N, 7°30'W, 1322 m).

Munneurycope murrayi (Thor St. 76, 59°52'N, 9°53'W, 1500 m wire).

Munneurycope murrayi (Thor St. 183, 61°30'N, 17°08'W, 1800 m wire).

Munneurycope murrayi (Godthaab St. 24, 62°19'N, 56°00'W, 1000 m wire).

(2) Oostegites on prps. I and IV:

Munneurycope murrayi (Thor St. 181, 61°34'N, 19°05'W, 1800 m wire).

Munneurycope murrayi (Thor St. 183 – see above)

It has not been possible to find any explanation how this variation came about in such scattered species and specimens.

THE INCUBATORY STAGE

Possible reasons for deficit of ovigerous females

In Table 14 the number of ovigerous females and of all females with marsupium is given together with their percentage of all adult females in the material. Not only is the percentage of ovigerous females very low, but the percentage of females with marsupium (incubatory females) is also less than that found for females without marsupium. Four or five factors may account for this.

(1) Greater mortality. The incubatory females have had the longest life-span and the mortality rate here must necessarily be higher than in females of the preceding one or two preparatory stages. The mortality rate may also be greater for breeding than for non-breeding females. In all probability, however, these factors are of slight importance.

(2) Behaviour. As suggested previously (WOLFF 1956b, p. 238), the females may, during the breeding period, prefer a more fossorial mode of life than normal, thus more successfully evading the trawl than non-breeding females and males. A more obscured mode of life is also suggested as being the reason why ovigerous females of common genera such as *Aega* and *Rocinela* are hardly ever collected (ZIMMER 1927, p. 726).

(3) Breeding with long intervals. It was also suggested (l. c.) that hadal isopods and tanaids grow unusually old, reproduction consequently taking place only every second or third year. A similar pattern may be valid for bathyal and abyssal species also. This assumption further leads to:

(4) The period with marsupium being short, considerably shorter than the preparatory period. The length of the incubatory period in *Asellota* has at present been studied only by UNWIN (1920) and STEEL (1961) who both worked on *Asellus*. UNWIN recorded 30-34 days, STEEL found it to be "less than three months and to exceed one month in duration". It seems reasonable that in the cold environment of the deep-sea the incubation period is probably longer, perhaps even between two and three months.

According to UNWIN (l. c.) the female *Asellus* moults "soon after the escape of the young". This can hardly be the case in deep-sea (or all marine?) asellotes. The material contained twice as many females with an empty marsupium as ovigerous females (Table 14). This can only be explained by assuming that a long period passes between the moment the young leave the marsupium and the female moults or dies. This period is, without doubt,

Table 14. Number and percentage of adult males and adult females with and without marsupium. Total of each of the families. Material and abbreviations as in Table 12. Percentage printed in heavy type.

Families	Females							Males		
	Without marsupium		With marsupium				Total no.	No.	% of all specimens	
	No. without oost.	No. with dvl. oost.	Ovigerous		No. of non-ovig.	Total no.				% of all ♀♀
			No.	% of all ♀♀						
Janiridae	26	45	17	17	15	32	31	103	72	41
Haplomiscidae	52	0	18	20	20	38	43	90	26	22
Munnidae	108	0	12	9	13	25	19	133	48	27
Dendrotonidae	11	1	0	0	1	1	8	13	3	19
Ischnomesidae	15	24	0	0	2	2	5	41	22	35
Macrostylidae	15	0	2	9	5	7	32	22	10	31
Nannoniscidae	0	82	10	8	34	44	35	126	32	20
Desmosomatidae	4	20	1	3	5	6	20	30	9	23
Ilyarachnidae	40	24	4	5	6	10	14	74	31	30
Eurycopidae	30	135	12	5	45	57	26	222	158	42
Munnopsidae	15	47	1	1	12	13	16	79 ¹	87	52
Total...	316	378	77	8	158	235	25	933	498	35

1. Including 4 *Munnopsis longiremis*.

at least as long as the incubatory period. Thus, the length of time in which the female possesses a marsupium (with eggs, embryos or empty) is certainly in the order of four months or more. Provided that the females breed every year, and that the above mentioned factors (1) and (2) are of little importance, the expected percentage of females with marsupium should be between 33 and 50, probably depending on the number of preparatory stages before each incubatory stage – one in some families, two in others.

(5) Seasonal breeding. The majority of the material presented in Tables 12 and 14 was collected by the *Ingolf* and *Thor* during the summer months (May-August). Thus it is obvious that the percentage of incubatory females must vary greatly in accordance with whether the animals are summer, winter, or year-round breeders.

Very little is known about the breeding time of bathyal and abyssal animals. The importance of temperature in controlling breeding in marine animals has been shown by many workers. From his observations, ORTON (1920, p. 353) claimed "that in those parts of the sea where temperature conditions are constant or nearly constant, and where biological conditions do not vary much, the marine animals will breed continuously". Such stenothermal places were to be found in the tropics, in the polar regions, and in the deep-sea. It is true that as far as the tropics are concerned, year-round breeding is very common. As pointed out by DUNBAR (1957), all Arctic and Subarctic forms so far studied have,

however, shown well-marked breeding seasons, often extending over only a short period of the year. A continuous breeding in deep-sea animals is a generally accepted factor (cf. e. g. REIBISCH 1927, p. 792), but actual evidence of this has not yet been given.

The very low percentage of incubatory females (Table 14) shows that the bathyal and abyssal aselotes, particularly in the North Atlantic, cannot as a general rule be summer breeders. In this case the number of ovigerous females must necessarily have been much higher, the material being almost entirely collected in summer months. The presence of at least some ovigerous females in the material must be explained by supposing that these species (or some of the specimens?) probably breed the year round. I could find no indication that the collecting of ovigerous females was restricted to the very earliest month (May) or the latest month (August) of the period during two successive years in which the *Ingolf* worked in the North Atlantic. This is in agreement with HULT (1941) who wrote (p. 194): "I have material from April to September inclusive, and in this case the material is unambiguous. When a species is fairly abundant at a locality it is possible to observe all the stages in the evolution of the females ... Consequently, it looks as though the species living in constant-boreal water might be able to propagate the whole year round, and this probably owing to the fact that the temperature within the area varies only slightly during the year. I have not been able to find anything corresponding to the

definite periods of breeding seasons of boreal species living in the upper littoral".

However, in my opinion, the most likely explanation for the deficit of ovigerous females in the material presented here is to assume that the breeding in the bathyal and abyssal depths of the North Atlantic is to a certain extent seasonal, taking place in the winter months from which no material is available. The majority of the species originate from cold stenotherm shallow water ancestors which must be supposed to have had, as a rule, a seasonal breeding – as is the case with shallow-water species in the polar region today. As far as the asellotes are concerned, this mode of reproduction has also been maintained in the deep-sea.

The marsupium

The marsupium of the Ischnomesidae has not been mentioned previously in the literature. Unfortunately, none of the specimens of this family in the Copenhagen Museum were ovigerous, but one *Haplomesus quadrispinosus* had fully developed oostegites. Their very large size (Fig. 143) shows that the marsupium also must be unusually large.

Eggs and embryos

The number of eggs and embryos in the marsupium of deep-sea asellotes has only very occasionally been recorded. VANHÖFFEN (1914) gives the following number of eggs (length of specimens given in mm, number of specimens added in parenthesis, when known):

	Length	No. of eggs
<i>Paramunna gaussi</i> (2)	1.3	6
<i>Munna schauinslandi</i>	1.5	c. 12
<i>Munna psychrophila</i>	1.5-2	12
<i>Haplomesus antarcticus</i> (2)	2.7; 3	23; 25 ¹
<i>Echinomunna horrida</i> (2)	3.5	9-12
<i>Acanthomunna spinipes</i> (1)	6	15
<i>Stenetrium acutum</i> (2)	9.5; 11	15; 16

HULT (1941, p. 193) found no variation in the number of eggs within his investigation area (Skagerrak and the North Atlantic). At a single locality the variation in number generally covered the entire known variation of the species. The small species (e. g. *Eurycope mutica* and *Desmosoma* spp.) had fairly low numbers (8-12-16) while the larger species had a larger number of eggs, *Eurycope cornuta* and

1. This is according to my own count (p. 211); VANHÖFFEN (l. c., p. 558) gave the number as 12-17.

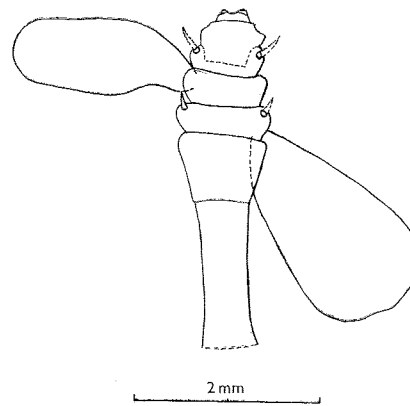


Fig. 143. *Haplomesus quadrispinosus* (G. O. Sars) from Ingolf St. 102; two of the fully developed oostegites.

Munnopsis typica showing 64 eggs in several cases and *Ilyarachna longicornis* up to 32. STEEL (1961, table 2) found that for *Asellus aquaticus* and *meredeanus* also, the mean brood size varies with the size of the female.

The number of eggs in several of the ovigerous females I have studied (cf. Table 12) has been counted (number of specimens in parenthesis):

	Length	No. of eggs
<i>Pleurogonium intermedium</i> (1)	1.3	5
<i>Eurycope mutica</i> (1)	1.5	9
<i>Nannoniscus minutus</i> (2)	1.5	3; 4
<i>Nannoniscus aequiremis</i> (1)	1.9	2
<i>Nannoniscus reticulatus</i> (1)	2	7
<i>Nannoniscus oblongus</i> (1)	2.5	4
<i>Macrostylis longiremis</i> (1)	2.5	10
<i>Nannoniscus analis</i> (5)	2.5-2.7	1; 2; 3; 4; 8
<i>Eurycope parva</i> (1)	2.7	c. 15
<i>Eurycope brevirostris</i> (2)	2.7	10; 11
<i>Macrostylis abyssicola</i> (1)	3	5
<i>Ilyarachna aspidophora</i> (1)	3.2	20
<i>Ilyarachna nordenstami</i> (1)	5.3	18
<i>Janira maculosa</i> (10)	6-8	c. 40-c. 70
<i>Iolella laciniata</i> (1)	8	19
<i>Eurycope inermis</i> (1)	10.5	22
<i>Storothyngura novae-zelandiae</i> (1)	12	c. 80
<i>Iolella vilhelminae</i> (1)	13	c. 75
<i>Storothyngura p. pulchra</i>	25	c. 75

Generally speaking, this primarily bathyal material also shows an increase of eggs in larger specimens.

The number of eggs in shallow water species has only been given occasionally. For five "Munniden" (2.5-4 mm long) ZIRWAS (1910) recorded a minimum and maximum as high as 70 and 136 eggs respect-

ively. In ten *Janira maculosa* from the North Sea he found on an average 52 eggs, the minimum being 31, the maximum 97, but generally ranging between 40-70, i. e. identical to the ten bathyal specimens of this species examined by me. For five *Jaera albifrons*, ZIRWAS recorded an average of 43 eggs (min.: 27, max.: 86). By examining 30 females of this species (3.5-4.5 mm long) from shallow water in various North European localities I found an average of 25 eggs (min.: 11, max.: 45). Unfortunately, I did not have access to material of ovigerous females from shallow water in tropical or subtropical areas.

On the whole, it seems that the boreal species of asellotes from the littoral have more numerous (and smaller?) eggs than bathyal and abyssal species of equal size. This is in accordance with findings on other marine bottom invertebrates (THORSON 1950) and deep-sea fishes (MARSHALL 1953).

In the comparatively rich material of *Haploniscus bicuspis* from Ingolf St. 117 (South of *Jan Mayen*, 1890 m, -1.0°C .) the number and size appears from the following list:

- ♀ No. 17: 12 eggs (0.26-0.30 mm)
- ♀ No. 18: 12 embryos (0.7 mm long)
- ♀ No. 19: 4 embryos (0.6 mm long)
- ♀ No. 24: 13 eggs (0.26-0.30 mm)
- ♀ No. 25: 14 embryos (0.8 mm long)
- ♀ No. 26: 18 embryos (0.7 mm long)
- ♀ No. 27: 18 embryos (0.6 mm long)

The embryos in Nos. 18, 26, and 27 were tightly packed together in the marsupium (Pl. XIV G).

Degeneration of embryos? In a typical adult female of *Haploniscus bicuspis* from Ingolf St. 117 a dark, brownish sphere was found inside the marsupium (Pl. XIV H). The sphere consisted of small fragments, but it was impossible to detect any distinguishable structures in them. The oostegites appeared undamaged – thus it seems unlikely that the sphere could have entered accidentally from outside. In the latter event, the only possible explanation is that the sphere represents degenerate remains of what were probably unfertilized eggs.

However, JENSEN (1955) reported that in the case of *Spaeroma hookeri* unfertilized eggs will remain in the ovary and degenerate there. JANCKE (1924, 1926) showed that in certain isopods (and amphi-

Pods) a considerable reduction in the number of eggs and embryos takes place during incubation. In *Asellus aquaticus* and *Idotea viridis* the reduction from spawned eggs to embryos ready to hatch is from about 150 to 80 and from 30-40 to 4-6, respectively. The reduction was explained by lack of space due to the growth of the embryos, and JANCKE claims to have actually seen eggs being passed out of the marsupium. None of the eggs exhibited any sign of being abnormal or less healthy than those remaining in the marsupium. In *Jaera albifrons* JANCKE recorded the reduction to be from 15-16 eggs to 3-4 full-grown embryos (occasionally 8-12 embryos), but a space factor cannot be involved here. STEEL (1961) also found a marked difference between the mean number of eggs and of embryos in *Asellus*. By keeping females in individual containers, however, very few eggs were found in the water during daily inspections. This could be due either to the parent eating the eggs soon after release or to the eggs decaying while still in the marsupium. He observed a few opaque eggs which were presumably dead, but these were very rare.

If the sphere in *Haploniscus bicuspis* does indeed represent degenerate eggs or embryos, it is difficult to understand why the female had not rid herself of them long since.

Males - sex ratio

The number of males in the bathyal and abyssal asellote material is recorded in Table 14. Only in Munnopsidae do the males exceed the females in number (due to a large predominance of males in *Munnopsis longiremis* – cf. Table 12.) In the other families the percentage of males lies between about 20 and 40.

In *Asellus*, SEITZ (1954) and STEEL (1961) found an average sex ratio of 1:1, although it was subject to considerable fluctuations throughout the year on account of the differential mortality rate of males and females. A similar fluctuation in the sex ratio has been demonstrated in marine crustaceans also, e. g. *Carcinus maenas* (BROEKHUYSEN 1936). Since the present material is relatively small, scattered over many species, and the time of reproduction uncertain, it is evident that only slight significance can be attached to the sex ratios recorded.

C. Hermaphroditism in Isopoda

a. Previous studies

The occurrence of sexually intermediate specimens in *Haploniscus* has induced me to make a study of the scanty and very sporadic literature on hermaphroditism and "intersexes"¹ in the isopods and to include a survey of it in the following.²

1. Flabellifera.

Cymothoidae. BULLAR (1877) was the first to give an account of hermaphroditism in isopods, viz., in the following five species: *Meinertia oestroides* Risso, *Nerocila maculata* (M.-Edw.), *N. bivittata* (Risso), *Anilocra physodes* (L.), and *A. mediterranea* (M.-Edw.). In these species the hermaphroditic gonad, as well as the secondary sexual characters, was typically protandrous. MAYER (1878) followed the development more thoroughly and confirmed the occurrence of hermaphroditism. MONTALENTI (1941) studied *Emetha audouini* (M.-Edw.) and *Anilocra physodes* in detail and found that sexual inversion takes place very suddenly in single individuals, and that their size at the point of transition may vary considerably. LEGRAND (1951, 1952) proved that in *A. physodes* the proximity of a female to a male (on the fish host) causes a marked prolongation of the male stage, while, on the contrary, the presence of a younger male accelerates the sexual inversion of the male. In addition to this phenotypical effect, hermaphroditism was also considered to be genotypically induced. Finally, BOWMAN (1960) found that *Lironeca puhi* Bowman was also a protandrous hermaphrodite and suggested similar effects from the presence or absence of females as in *Anilocra*.

Thus, within the Cymothoidae hermaphroditism

1. I follow GOLDSCHMIDT (1931) in his definition of an "intersex" (p. 12) as "ein Individuum, das nach seiner genetischen Beschaffenheit, XX oder XY, eigentlich ein Weibchen oder Männchen sein sollte, tatsächlich sich aber nur bis zu einem bestimmten Augenblick mit seinem eigentlichen Geschlecht entwickelt, von diesem Augenblick, dem Drehpunkt, an aber seine Entwicklung mit dem anderen Geschlecht vollendet". No cases of true zygotic intersexuality are yet known in isopods, corresponding to that found in certain amphipods (particularly in *Gammarus chevreuxi*) (SEXTON & HUXLEY 1921, SEXTON 1924). Thus, the term "intersex" should not be applied to any individual with intermediate sexual characters, primary or secondary or both.
2. The study had to be limited to morphological characteristics of the isopods, thus excluding first and foremost the modern physiological literature, preferably on decapods.

has been recorded in one subfamily only, the Cymothoinae, although MAYER (l. c.) did point out that in *Cirolana* and *Conilera* (Cirolaninae) he found three diverticles on the ovaries which he interpreted as being rudimentary testes, but no trace of ovaries was found on the testes. There is hardly any doubt that all Cymothoinae are protandrous hermaphrodites.

Sphaeromidae. LEICHMANN (1891) studied *Sphaeroma rugicauda* Leach and recorded the presence of, what he considered to be rudimentary testes, on the ovaries of almost all females, but could find no rudiment of female gonads on the testes of males. In his material of *Sphaeroma*, FORSMAN (1952) discovered a single specimen of *rugicauda* and of *hookeri* Leach which exhibited both male and female primary or secondary sexual characters; he regarded them as rare cases of protandrous hermaphrodites. KINNE (1954) recorded a single similar case in *hookeri* and suggested that the presence of a setiferous appendix masculina in 2% of the males may be due to female influence from a hermaphroditic gonad, but the sexual organ was not studied. PIGEULT (1957) investigated *S. rugicauda*, *serratum* (Fabr.), and *venustissimum* Monod in Morocco. In all three species the author repeatedly found a rudimentary ovary and oviduct in the males. Rudiments of testes diverticles were present in females *rugicauda* and *serratum*, and absent in *venustissimum*; a rudimentary vas deferens was probably present in all three species. Further, a study of *serratum* at Roscoff (in Brittany) disclosed a more advanced hermaphroditism in a limited number (6%), but without spermatogenesis and functioning vas deferens. In one specimen a hermaphroditically functioning gonad was found, but the specimen lacked penes. Accordingly, active hermaphrodites have not been demonstrated in the Sphaeromidae.

2. Epicaridea.

Cryptoniscidae. KOSSMANN (1884) was the first to realize that the mature males in this family are represented by cryptoniscian larvae which later develop into sessile, parasitic females; thus demonstrating evident protandrous hermaphroditism. He probably studied several genera, but gave no details. CAULLERY & MESNIL (1899, 1901) made a thorough investigation of *Cryptothir (Hemioniscus) balani* (Spence Bate), a parasite of *Balanus balanoides* and other balanids, and confirmed and supplemented KOSSMANN's findings. The oviducts are developed

at the same time as male maturity is reached and the ovaries start growing while the male is still mobile and the testes still functioning. PEREZ (1900) found a rudimentary ovary in one of the cryptoniscian males of *Crinoniscus equitans* Perez (parasitic in *Balanus perforatus* Bruguière) and suggested protandrous hermaphroditism although he did not – as did CAULLERY & MESNIL – follow the entire metamorphosis. In 1903 he recorded another instance of hermaphroditism in an unidentified species, probably belonging to *Eumetor* Kossman; this cryptoniscid is a parasite of *Sacculina* which is again a parasite of a *Pinnotheres* – a commensal of a *Spondylus* found in the Iranian Gulf. SMITH (1906) found that all the specimens of *Danalia curvata* (Fraisse) living parasitically on *Sacculina neglecta* or its host *Inachus dorsettensis*, were hermaphrodites which metamorphosed into females. Finally, CAULLERY (1908) followed the radical metamorphosis of *Danalia curvata* in detail and demonstrated protandrous hermaphroditism also in *Liriopsis monophthalma* Fraisse (parasitic on the hermit crab parasite *Peltogaster curvatus*).

3. Oniscoidea.

Squamiferidae. The first carcinologist to suggest protandrous hermaphroditism in woodlice was NEMEC (1896) who recorded, what he interpreted as rudimentary oviducts, in males of *Platyarthrus hoffmannseggii* Brandt and referred to SCHÖBL's old observation (1860) of the presence of vestigial copulatory organs in females of the same species. This led him to conclude that all isopods were originally successive hermaphrodites, a view strongly opposed by VANDEL (1925).

Oniscidae. ARCANGELI (1923, 1925) found that the Sardinian subspecies (*sardoa* Arcangeli) of *Chaetophiloscia elongata* (Dollfus) was a protandrous hermaphrodite. During the first year it is a typical male (although with rudimentary ovaries, oviducts and female genital openings) and fertilizes normal females of the same age. The following year it develops into a female existing side by side with the normal females, but probably always producing smaller broods (about ten young) compared with those of the normal female (about fifty). Since the small males are unable to fertilize the larger normal females these produce parthenogenetic eggs which develop into new normal females only, while the fertilized eggs of the young females develop into protandrous hermaphrodites.

Porcellionidae. A rather large number of inter-

mediate males and females have been described in this family (in most cases the gonads were not investigated): (1) Female-like males (together with normal males) of *Porcellio dispar* Verhoeff in Portugal (VERHOEFF 1901). (2) One intermediate specimen of *Nagara van namei* Arcangeli from Japan (ARCANGELI 1927). (3) Specimens from the Mediterranean island Scarpanto of *Porcellio* (*Porcellionides*) *steini* Arcangeli together with normal males and females (ARCANGELI 1929). (4) An apparently typical male of *Metoponorthus pruinosus* (Brandt) ab. *meleagris* Budde-Lund from Lemnos with a marsupium with two eggs (STROUHAL 1929). (5) In addition to normal males of *Porcellio laevis* Latreille, some with one or two ovaries with a few egg cells, but no oviducts – or (in one case) oviducts present, but ending blindly (ARCANGELI 1931). (6) One intermediate specimen of *Porcellio* (*Porcellio*) *pelseneri* from Morocco with a well developed, recently emptied marsupium and possessing in addition, male features from a suggested preceding male phase (ARCANGELI 1932). (7) A specimen of *Uramba triangulifera* Budde-Lund from East Africa which combined the presence of typical male secondary sexual characters with a marsupium with one egg (ARCANGELI 1941). In *Porcellio laevis* Latreille, VANDEL (1941, 1947) found not only males with more or less reduced secondary sexual characters (pereopods and pleopods) but also true intermediate forms with mixed secondary sexual characters and ovotestes – which in one case had produced both eggs and spermatozoans, thus functioning hermaphroditically. One similar intermediate form was found in *Metoponorthus pruinosus*. LEGRAND & LEGRAND (1947) showed that in *Porcellio dilatatus* Brandt 13 % of the males were normal but had oviducts opening on the surface which ended blindly at the proximal position; 13 % of the females showed intermediate secondary sexual characters, the smaller specimens having typical ovotestes, and the larger functional ovaries – thus suggesting a primitive hermaphroditism. The male phase is, however, too short for the testes to reach maturity (LEGRAND 1947). In their further examination of *P. laevis* and *dilatatus*, LEGRAND & VANDEL (1948) demonstrated that the developing gonad is initially hermaphroditic, being furnished with six mesodermous tracts along the inner margin which will develop according to the sex of the animal. In the male the three anterior tracts become the diverticles, the next two become suspensory filaments and the posterior tract develops into the vas deferens. In the female the

three anterior and two posterior tracts become suspensory filaments, while no. 4 will serve as the oviduct. According to LEGRAND & VANDEL, the hermaphroditic state of the initial gonad is the background for frequent cases of rudimentary protandrous hermaphroditism in several groups of isopods. Finally, LEGRAND (1956) showed that in populations of *P. dilatatus*, increased temperature would intensify the tendency for – preferably younger – females to acquire male secondary characters, and demonstrated that this tendency is hereditary.

Armadillidiidae. LEGRAND (1941) found a male of *Armadillidium vulgare* (Latreille) with reduced testes and intermediate female secondary characters (perhaps induced by the presence of a parasitizing tachinid larva), although other species of oniscids with the same parasite were perfectly normal sexually. COLLINGE (1946) recorded an apparently non-parasitized female of the same species with intermediate male characters, and similar cases of intermediate, non-parasitized specimens of *A. valonae* Arcangeli and *cinereum* Zenker were found (ARCANGELI 1942, 1951). VANDEL (1941, 1947) recorded functioning females of *A. vulgare* with pereopods more or less differentiated in the male sense; he also reported on males of this species with typical testes, but with the said secondary sexual characters considerably reduced.

Rhyscotidae. In 1928 JACKSON showed that *Rhyscotoides (Rhyscotus) ortonedae* Budde-Lund (and certainly all other species of this sole genus of the family) are protandrous hermaphrodites which – as *Chaetophiloscia elongata* – retain the unmodified external male genitalia during the female phase also, indicating an active persistence of the male stimulus throughout the life-span. One of the specimens studied even suggested the possibility of a later return of the male phase, with renewed activity of the residual testes. JOHNSON (1957a, 1957b, 1957c) made a histological study of the development of *Rhyscotoides legrandi* Johnson. The gonad is initially hermaphroditic and the spermatogenesis begins at a body length of 2.7 mm. After a purely male phase the oogenesis commences at a body length of 3 mm, but the spermatogenesis continues, resulting in a simultaneous male and female gametogenesis persisting throughout the life-span. However, as suggested by JACKSON, experiments indicated a hermaphroditism of alternating male and female phases (LEGRAND 1957c). It was also experimentally shown that parthenogenesis and self-fertilisation are excluded.

4. Asellota.

Aselloidea. RACOVITZA (1919) found an egg-bearing female of *Asellus communis* Say with male copulatory styles and UNWIN (1920) an egg-bearing female of *A. aquaticus* (L.) (or *meridianus* Racovitza?) with vestigial male pleopods 1 and 2. MAERCKS (1931) recorded several females of *A. aquaticus* which also had more or less developed copulatory styles, but lacked any trace of testes. Moreover, MAERCKS found a single hermaphroditic specimen, exteriorly a female, but having in addition to normal ovaries one testis with spermatozoans (which, however, was apparently without a vas deferens). According to MAERCKS it was “ein Fall von echtem pathologischen Hermaphroditismus”, but he gave no further explanation. An example of hermaphroditism in *aquaticus*, induced by a parasite, was given by MUNRO (1953) who found that one-third of the specimens parasitized by a larval acanthocephalan showed intermediate features in varying degrees, and that these forms also seemed to be modified females. The gonads were not studied.

Stenetrioidea. From the littoral zone in South Africa K. H. BARNARD (1940) described *Stenetrium syzygus* with the eyes reduced to three or four feebly pigmented ocelli. No females with operculum were represented; all the specimens available had typical male pleopods, but some had well developed oostegites and carried eggs or embryos. None of the specimens were dissected.

Paraselloidea. In 1899 SARS re-described and figured (pl. 50) males of *Nannoniscus oblongus* Sars, 1870, pointing out that in spite of the presence of a typical operculum in place of the male pleopods 1 and 2 he considered the two available specimens to be males because of “the greatly projecting sexual prominence¹ and ... the presence of well-developed testes shining distinctly through the integuments in their usual place” (p. 120). HANSEN (1905, p. 310; 1916, p. 87) showed that the two males should belong to another species for which he proposed the name *crassipes*. In addition to the operculum, the outline of the body and the antennae also exhibited exclusively female features. HANSEN therefore regarded the two specimens as protandrous hermaphrodites. As is the case of several of the aforementioned statements, this one also has been completely overlooked.

1. The large process ventrally on pereonite 7 does not have a sexual significance, being equally shaped in typical females and males of several other species of *Nannoniscus*, e. g. *minutus*, *armatus*, and *affinis*.

b. Own investigations

Haploniscus bicuspis bicuspis

In the extensive material of this species I found a single, fully grown specimen from *Ingolf* St. 117 which combined the presence of male pleopods 1 (although somewhat reduced – or still not fully developed) with the presence of a typically shaped female operculum. A similar combination (but with pleopods 1 not so well developed) is found in the juvenile male stage IV, described on p. 208.

The present specimen (Pl. XV D) is as long as two of the three typical adult males from the same station (2.5 mm). It exhibits the following

Male characters: (1) Antennula with five joints in flagellum (antennae lost); (2) pleopods 1 (Fig. 144) almost fully developed, but as in the juvenile males (stages IV and V, Fig. 139 a and d, p. 209) calcified in their total extent and lacking the two dorsal, longitudinal, lateral keels which fit into the second pleopods in the typical males; (3) postero-lateral processes as long as in a typical male from the same station.

Female characters: (1) Typically shaped operculum present; (2) no furrow connecting the branchial cavity with the anal doors (HANSEN 1916, pl. II, 2 1).

The specimen was sectioned but no identifiable organs were preserved.

Haploniscus helgei

In the description of a male and female of this new species (p. 54) the differences between the two sexes were pointed out; apart from the pleopods, differ-

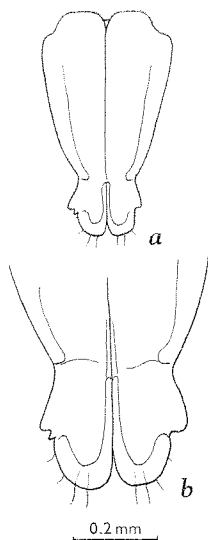


Fig. 144. *Haploniscus b. bicuspis* (G. O. Sars) from *Ingolf* St. 117; a, male pleopods 1 of intermediate specimen; b, distal, fully calcified part.

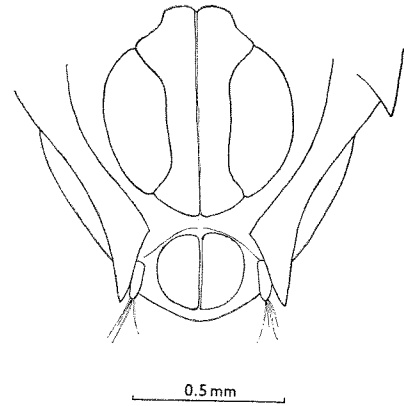


Fig. 145. *Haploniscus helgei* n. sp.; posterior end of typical, adult male (No. 3) from below.

ences are found mainly in the shape of the pleon and the position of the postero-lateral spines.

The total material of *H. helgei* (Table 15) contains:

(a) One immature male (No. 1), a typical representative of stage IV (cf. p. 212).

(b) Two immature females (Pl. XV G; Nos. 9 and 10) which belong to stage V (cf. p. 212).

(c) Three adult females with marsupium, including the allotype (Pls. I D and XV F; Figs. 13, 19). No variation found (except in flagellum of antennae).

(d) Three adult males, including the holotype (Pls. I E-F and XV E; Figs. 13-18 and 145). No variation found (except in number of joints in flagellum of antennae).

(e) One immature male (No. 2) which was described on p. 212 and is further mentioned below.

(f) Four specimens (Nos. 5-8), which are as large as or larger than the females with marsupium, have a female operculum and no trace of male pleopods (Pl. XVI F). However, they differ from the typical adult females in having pereonites 5-7 and pleon shaped as in the typical adult males (Fig. 13b, p. 52). Their anatomy is described below.

Sexual organs

With the much appreciated help of Professor K. G. WINGSTRAND of the Institute of Comparative Anatomy, some of the specimens of *H. helgei* (marked * in Table 15) were sectioned and the anatomy studied. Unfortunately, the entire material was originally preserved in 70 % alcohol only. The state of preservation is surprisingly good in specimens 7 and 8 but rather poor in the remainder.

Table 15. Details of the total material of *Haploniscus helgei* n. sp. Sectioned specimens marked *.

	Ref. No.	Total length (mm)	No. of joints in flag. of antenna
♂ (stage IV)	1	5.2	12
♂ (? pre-herm.) (? stage IV a)	2*	8.0	15
♂ adult (stage VI)	3*	8.6	15
	4	8.8	16
	holotype	8.9	16
Intermediate females	5	8.3	15
	6	8.4	12
	7*	8.4	
	8*	8.6	
♀ (stage V)	9	6.6	13
	10	6.9	
♀ adult (with marsupium) (stage VI)	allotype	8.1	13
	11*	8.3	14
	12*	8.3	12

1. Intermediate females (with male-shaped prns. 5-7 and pleon) (Nos. 7 and 8).

A reconstruction of the sexual organs was made by Professor WINGSTRAND, based on the microscopical material (Fig. 146).

The ovaries stretch from the anterior end of prn. 3 to prn. 6 and contain about 15 eggs each (Pl. XVII D). The oviduct opening is very conspicuous and situated somewhat laterally on prn. 5 (about halfway between the anterior and posterior margins (Pl. XVI A, o.o.)). The oviduct can be clearly seen only at the distal end; the proximal part is a delicate string.

A receptaculum seminis proved to be present in *H. helgei*. A similar receptaculum is also present in *Asellus aquaticus* but a marked difference was found between this and the former. While the receptaculum in *Asellus* is a dilatation of the oviduct and thus opens on the surface through the oviduct opening (LEICHMANN 1891, pl. III 7, 10 and Pl. XVI B in this paper), it has in *H. helgei* a separate duct and opening situated at the segment connexion between prns. 4 and 5, somewhat lateral to the oviduct opening (Fig. 146). From the opening a short duct lined with cuticle leads to a large bulbus, which apparently has strong radiating muscles (Pl. XVII A-C). From here the duct (still lined with a cuticle) proceeds forwards to the receptaculum and continues into the lumen of the receptaculum (Pl. XVI C) but the proximal end of the duct could not be clearly discerned. The receptaculum is large

and sac-like and situated laterally to the ovary; the wall consists of cubical epithelium (Pl. XVI C).

Attached to the ovary are further, three compact organs on each side (Fig. 146 and Pl. XVI G). The two posterior measure *c.* 100 μ in diameter, the anterior is somewhat smaller and less conspicuous and is situated immediately posterior to the receptaculum. Each organ is filled with cells (Pl. XVII D) which have a close resemblance to germinal cells in the testis – (cf. the germinal zone of a testis of *Asellus aquaticus* from November (Pl. XVII E)).

In view of the evident male shape of prns. 5-7 and pleon of the specimens in question, one would *a priori* interpret these organs as vestigial testes, the more so since there are three pairs, as in almost all other isopod tribes, and they have the same rounded shape as in *Asellus* (cf. G.O.SARS 1867, pl. X, 7). However, the testes are normally situated in the anterior part of the body – see e. g. *Nannoniscus oblongus (crassipes)* (G.O.SARS 1899, pl. 50) in which they are found in prns. 2-4, but in the present specimens the said organs are situated in prns. 5-6. This extraordinary position makes one doubt whether they really are vestigial testes. On the other hand, similar organs are not present in the typical females (see below). However, if they are not testes, I have no inkling of their nature or function.

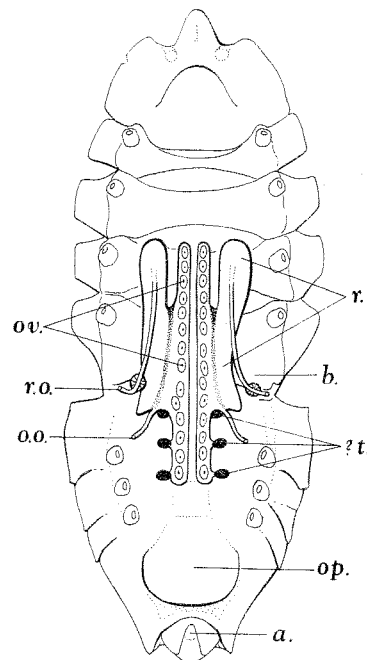


Fig. 146. *Haploniscus helgei* n. sp.; reconstruction of sexual organs in the intermediate females (Nos. 7 and 8); ov., ovary; o. o., oviduct opening; r., receptaculum; b., bulbus; r. o., receptaculum opening; ? t., ? testes; op., operculum; a., anus. (K. G. WINGSTRAND del.).

The shape of the alimentary canal is shown in Pl. XVI E. In contrast to that of *Asellus aquaticus* which is almost equally broad throughout (G.O. Sars 1867, pl. X, 1; LEICHMANN 1891, pl. III) it is considerably swollen in the anterior end and – curiously enough – also in the pleon. The contents of the gut are briefly mentioned on p. 239.

2. Preadult male (No. 2).

As described above (p. 212), this specimen is remarkable in having the first pleopods somewhat more developed than in the ordinary stage IV male, while the second pleopods are shaped like a female operculum. Although only one specimen was available at this stage it was decided to section it.

The hemocoel is filled with a large number of very small cells (*c.* 7 μ) with a pale nucleus, probably originating from a parasite (Pl. XVI H). The gonads are represented only by a narrow string on each side. The vas deferens is feebly developed and in contact with the gonad. The sexual opening is unpaired and situated on a conspicuous penis on the sternite, slightly in front of the proximal end of the first pleopods (Pl. XVI J). A similar penis was not to be seen externally on the two adult males (the third, sectioned male was very damaged in this region).

No trace of an oviduct opening could be found but a small receptaculum opening is present at the connexion between prns. 4 and 5 (situated in the same place as in the intermediate and normal females). The duct is short, without a bulbus and ends blindly.

3. Normal adult females (Nos. 11 and 12).

Female 12 has embryos in the marsupium. Thus, the ovaries are only feebly developed. The remaining organs of female 12 are poorly preserved, the interior of female 11 totally destroyed. The genital openings of both females are larger than the receptaculum openings. They are located as in the intermediate females (Nos. 7 and 8).

4. Normal adult male (No. 3).

The three testes on each side stretch from prn. 1 to the distal end of prn. 7. Two pairs only seem to be active. The vas deferens runs from the posterior end of the testis and opens medianly, probably immediately in front of the pleopods, which were crushed in male 3.

c. Conclusions

Unfortunately, the present material of *H. bicuspis* and *helgei* is very limited and not particularly suitable for anatomical studies. Thus, it seems premature to attach too much importance to it. On the other hand, the presence of no less than four intermediate females of *helgei* (of a total number of 14 specimens) indicates that this phenomenon is by no means rare in that species.

I find it most probable that in *Haploniscus* the species are normally gonochoristic (unisexual), but in some cases signs of hermaphroditism (but presumably not active hermaphroditism) may occur. As suggested by LEGRAND & VANDEL (1948) for *Porcellio* (cf. above) and LANG (1953) for the hermaphroditic *Apseudes spectabilis* Studer (= *hermaphroditicus* Lang – cf. LANG 1958), this instability could be due to the fact that not only in species with simultaneous hermaphroditism but also in many gonochoristic species, both kinds of sexual organs are initiated. As a rule, only one (the male or the female) develops and reaches maturity but sometimes a partial development of the sexual organ of the opposite sex influences secondary sexual characters, e. g. the male-like, posterior part of the intermediate females of *Haploniscus helgei*, the intermediate specimen of *H. bicuspis*, the variation in the length of the postero-lateral processes and the stylet of the second pleopods in *H. spinifer* (described on p. 59), and the intermediate females or males in *Sphaeroma*, *Platyarthrus*, *Porcellio*, etc., and in *Nannoniscus* referred to above.

The appearance of the immature male 2 of *Haploniscus helgei* can perhaps be explained in the same way. As shown in *H. bicuspis* where a sufficiently large material was at hand, the males normally pass two stages (IV and V), the first of which has rudimentary pleopods 1 and a female-shaped operculum while the second has further developed pleopods 1 and differentiated plps. 2, shaped almost as in the mature male, although still rudimentary. However, in *helgei* the typical male stage V is not represented in the material, but a transitional male (with an operculum) is found (male 2). It is possible that after the next moult this male would have developed into a (not active) hermaphrodite like the above described, intermediate specimen of *H. bicuspis*, with a combination of further developed male pleopods 1 and a female-shaped operculum.

However, if the cells found in male 2 of *helgei* do belong to a parasite, the fact should not be excluded

that its presence has caused the divergent appearance of this specimen. This serves as a parallel to the above-mentioned cases of pathological hermaphroditism in *Armadillidium* and *Asellus*.

A third explanation may be that male 2 simply represents an ordinary developmental stage; thus in *helgei* occurring between stage IV (with less developed plps. 1 and opercular plps. 2 – Figs. 139a and

142a) and stage V (with further developed plps. 1 and differentiated plps. 2 – Fig. 139c-f).

However this may be, a study of a large collection of one or more species of *Haploniscus* will without doubt prove interesting. Unfortunately, all known species of this genus are bathyal or abyssal, and therefore not easily obtainable.

D. Some characteristics of deep-sea *Asellota*

CORRELATION BETWEEN SIZE AND DEPTH

Previous evidence

The remarkable size of some of the most deeply-occurring isopods was first pointed out by the present author (WOLFF 1956a, p. 152). It was shown that hadal representatives of the genera under consideration were among the very largest (except in *Eurycope* and *Leptanthura*). It was also noted that the Antarctic species of various genera are large or very large.

A very striking correlation between increased size and either Antarctic or bathyal-abyssal distribution was shown for the tanaid genus *Apseudes* in a later paper (WOLFF 1956b, p. 237). It was also shown that the average length of species of the almost exclusively abyssal-hadal family Neotanaidae, was 1.5 times greater than the length of any known representative of the families Tanaidae and Paratanaidae (which both have numerous species).

ZENKEVICH & BIRSTEIN (1956) gave various examples of deep-water gigantism in crustaceans: *Haplo-mesus*, the mysid genera *Amblyops* and *Eucopia*, and the cirriped genus *Scalpellum*. BIRSTEIN (1957) demonstrated a positive correlation between the size of species of the genus *Storothyngura* and the depth at which they were recorded. He could find no correlation between their size and the temperature at which they occurred. It was suggested that abyssal gigantism is determined by the effect of hydrostatic pressure on the metabolism (see below p. 237). BIRSTEIN & VINOGRADOV (1958) recorded large-sized gammarid amphipods collected abysso- and hadopelagically and VINOGRADOV (1962b) showed a maximum of mean-size in pelagic copepods from depths between 500 and 4000 m.

Records of giants at great depths in animal groups other than Crustacea are scarce. MADSEN (1961 b, p. 201) gives an example of the very large solitary

hydroid *Branchocerianthus* (*Monocaulus*) from the *Challenger*. Among others are the foraminifer *Bathysiphon* from the N. W. Pacific (ZENKEVICH & BIRSTEIN 1956), and the remarkable gastropod *Cocculina superba* from 6100 m in the South Atlantic – by far the largest known species of the superfamily (CLARKE 1960).

The genera of the *Asellota*

In the following, a survey of the possible correlation between size and depth (and regional distribution) in asellote genera has been attempted. It was decided in the main survey to ignore genera with less than four species. I have also omitted all freshwater species, all unnamed specimens, all species wherein juveniles only are known, and all subspecies (except those of *Storothyngura pulchra*).

The size recorded is the largest body length for each species on record. This is entered in Table 18 (p. 249) which gives the length of both females and males (if available in the literature). Only the length of the largest known specimen of each species has been considered, notwithstanding whether it is a female or male (in some cases the female is larger than the male, and vice versa).

Unfortunately, most of Miss RICHARDSON's descriptions give no information on size. For his many new species, MENZIES (1962 b) records only the length of the holo- and allotype¹ without stating whether these are the largest specimens available. Moreover, he gives no measurements of his additional specimens of previously described species. This is regrettable inasmuch as most of the additional records show somewhat greater or much greater depths than any previous records. Omission of such information is, unfortunately, also the rule in most of the other papers consulted.

1. When new species are described on fragmentary specimens, only the length of the fragments is given. In all such cases I have myself estimated the total length of the animal (cf. the Systematic Part).

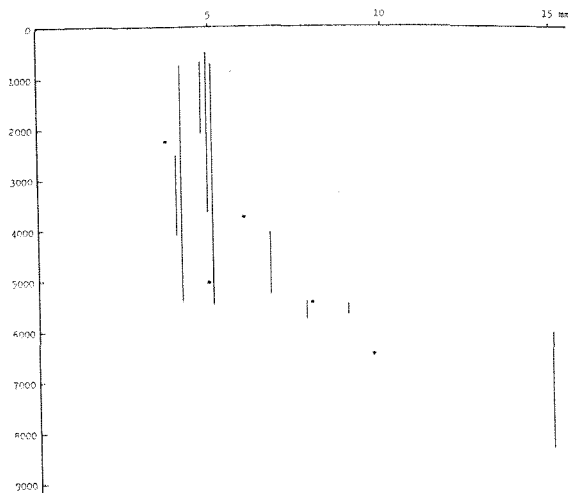


Fig. 147. Relation between size and depth within *Haplomesus*.

A diagrammatic presentation of asellote genera with at least 4 species gives the following result¹:

Good correlation found:

Haplomesus (Fig. 147) ranges from 4.3 to 15 mm. The hadal *H. gigas* (from the Kurile-Kamtschatka Trench) is one-third longer than the second largest species (*cornutus*) which is also hadal. Nos. 3, 4, and 5 in size are the three species with the deepest penetration into the abyssal zone.

Heteromesus (148) also shows good correlation but has fewer species and a more restricted size range (from 3.7-8 mm). The largest species is *bifurcatus* from 4100 m in the Caribbean Sea.

Ischnomesus (149) has a wide size range (from 3-37 mm). The smallest is *I. bispinosus*, the only species found on the continental shelf. By far the largest species is *I. planus*; it was described above (p. 82) on a fragmentary specimen from the East Pacific off Costa Rica and was estimated to be 35-40 mm in total length. If this somewhat dubious size

1. The occurrence of all species with a vertical range exceeding 200 m has been indicated by a vertical line in the diagrams. Antarctic species with a restricted bathymetric range have been indicated by +, those with a wider range by ⊥.

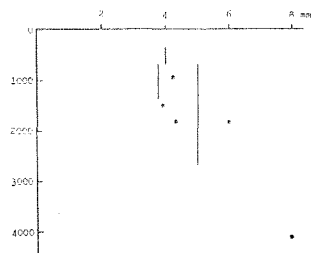


Fig. 148. Relation between size and depth within *Heteromesus*.

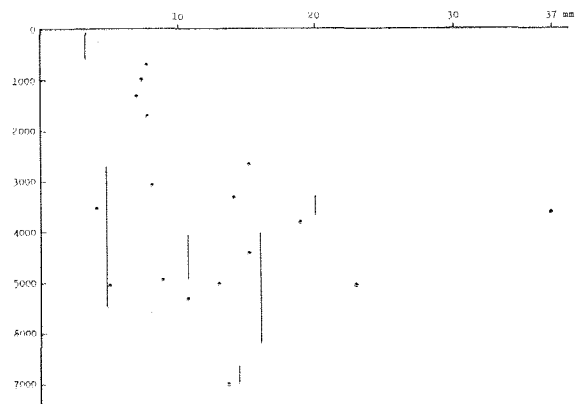


Fig. 149. Relation between size and depth within *Ischnomesus*.

record is not taken into account the correlation between size and depth is more convincing.

Stylomesus. The fourth genus of Ischnomesidae with a fair number of species (at least 8) is dealt with below, since it shows no correlation between size and depth. However, *Stylomesus* is restricted to abyssal depths between 2500 and 6000 m; thus one can hardly expect to find a correlation corresponding to that of the three other genera with several species, occurring at depths less than 2500 m.

Storothyngura (150) has a remarkable size range (from 2.3-45 mm). Eight of the nine largest species are either Antarctic (two) or hadal (six). Of the latter, the 45 mm long *S. herculea* (from the Kurile-Kamtschatka Trench) is a virtual giant compared to the others (the average size of the species and subspecies under consideration is 18.5 mm). On the other hand, some of the species between 4000 and 6000 m are among the smallest within the genus.

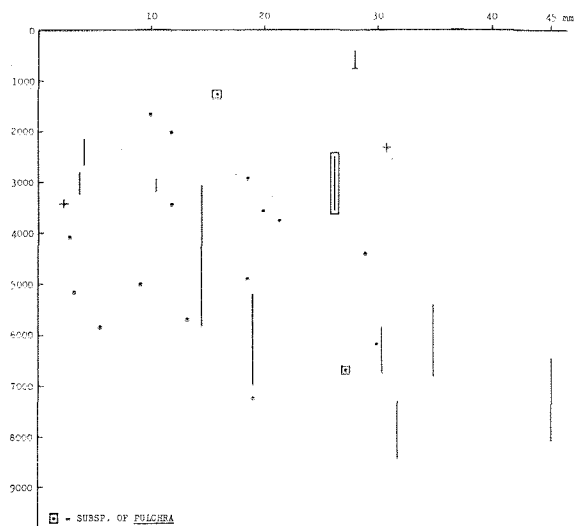


Fig. 150. Relation between size and depth within *Storothyngura*.

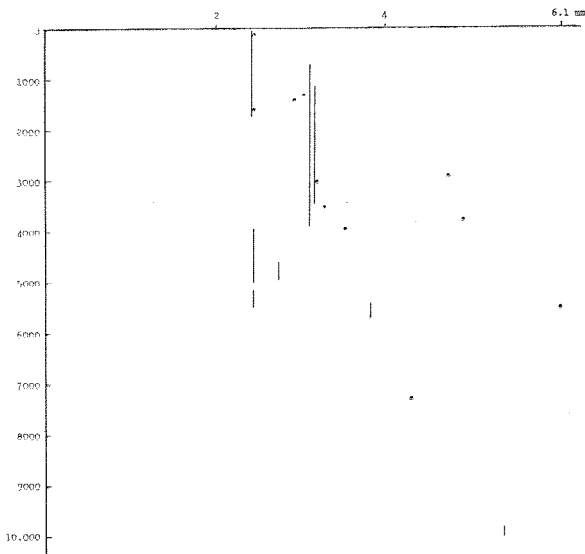


Fig. 151. Relation between size and depth within *Macrostylis*.

A rather unfortunate error is to be found in BIRSTEIN's diagram of the size-depth correlation in *Storthyngura* (1957, fig. 10). Between 0 and 1000 m he shows a dot at 500 m denoting a species measuring *c.* 3.1 mm. The only species of *Storthyngura* known at depths of less than 1000 m is the Antarctic *robustissima* (from 400 and 700 m). The length of the female is 24 mm (MONOD 1926, p. 18) or 28 mm (STEPHENSEN 1947, p. 8), the length of the male 18 mm (STEPHENSEN).

Macrostylis (151) shows as obvious an increase in size with increasing depth as the four above genera, but it should be noted that the size of the twenty species of the genus only ranges from 2.5 to 6.1 mm. *M. setifer* from 5500 m north of the West Indies is the largest, but three other *Vema* species from almost the same depth are among the smallest. As mentioned previously (WOLFF 1956a, p. 153), the two hadal species (*galathea* and *hadalis*) are among the largest within the genus.

Munneurycope (152) is another pronounced abyss-

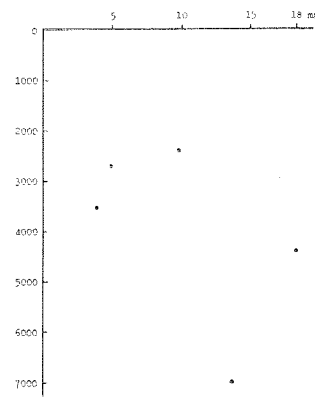


Fig. 152. Relation between size and depth within *Munneurycope*.

al genus which also shows a distinct correlation between depth and size. However, since it was only possible to study five species all known from one locality each, the correlation may prove to be accidental.

Stenetrium (153) differs from the genera of Ischnomesidae and the three last mentioned genera in being primarily a littoral genus. It is, however, characteristic that six of the seven species occurring deeper than 200 m are larger than any of the littoral species. By far the largest species are *S. haswelli* (from a depth of 1100 m in an area probably rich in nutrition off the mouth of the River Plate) and the Antarctic *acutum* (from 150-3400 m).

Fairly good correlation found:

Ilyarachna (154) ranges between 2 and 17 mm in size. The largest species, *I. quadrispinosa*, is Antarctic, followed by *kermadecensis*, the only species which penetrates into the hadal zone. However, a considerable number of the most deeply-occurring species (primarily collected by the *Vema* in the South Atlantic) are amongst the smallest representatives of the genus and – in addition to the Antarctic *quadrispinosa* – two other rather large species (*longi-*

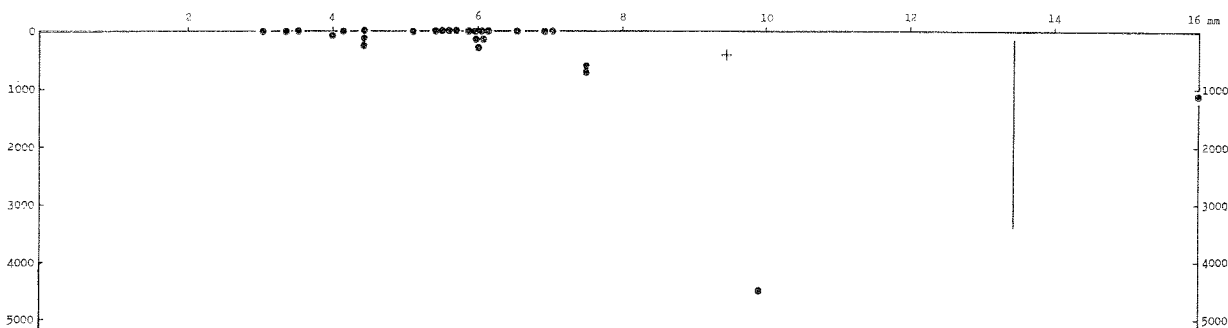


Fig. 153. Relation between size and depth within *Stenetrium*.

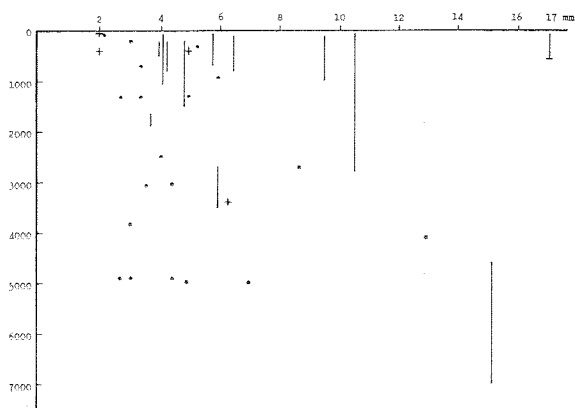


Fig. 154. Relation between size and depth within *Ilyarachna*.

cornis and *zachsi*) have part of their bathymetric distribution on the shelf.

Eurycope (155) has a very wide size range (from less than 1 mm to more than 25 mm). By far the largest species are the abyssal *E. scabra* from the Gulf of Panama and the likewise abyssal *sarsi* from the Subantarctic Indian Ocean; they are more than twice as large as any other species.

Ianthopsis (156) has almost the same size range (from 2.5 to 24 mm). The abyssal species *acanthonotus* from the Antarctic is extremely large. The only three species restricted to the continental shelf are, at the same time, the three smallest species.

Little or no correlation:

Each of the first four following genera have a large number of species (at least 18). They differ from the genera mentioned above (except *Heteromesus* and *Macrostylis*) in exhibiting a much more restricted range in size.

Nannoniscus (157) shows perhaps a slight correlation, the smallest species, *caspius* (from 4-6 m in

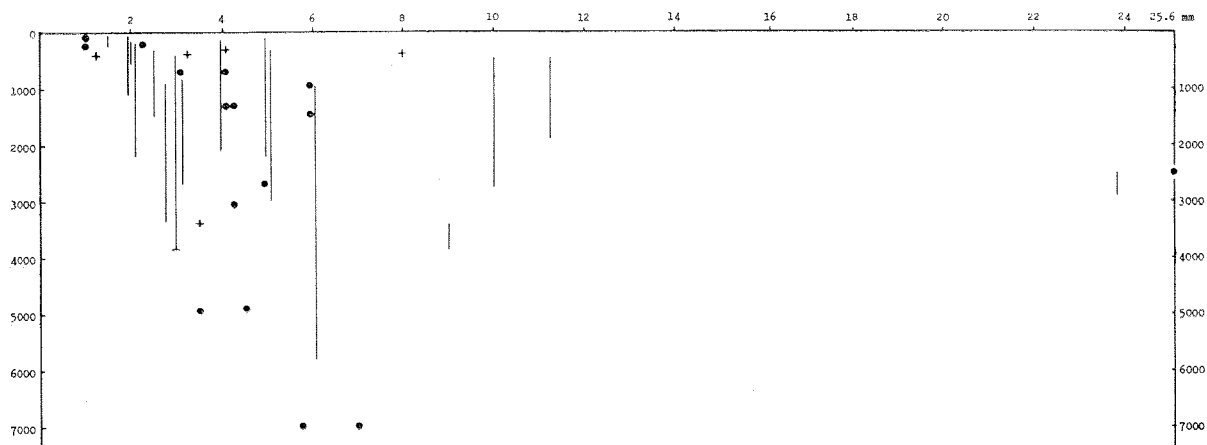


Fig. 155. Relation between size and depth within *Eurycope*.

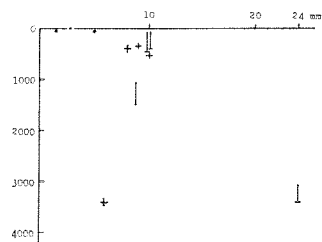


Fig. 156. Relation between size and depth within *Ianthopsis*.

the Caspian Sea) being the only real shallow water representative of the genus and the four largest species being either abyssal (three) or Antarctic (one).

Haploniscus (158) is a pronounced deep-sea genus but shows very little or no correlation between depth and size. By far the largest species (the bathyal *helgei* from south of Australia) is among spe-

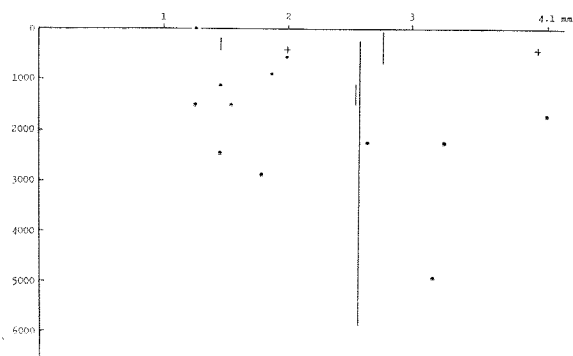


Fig. 157. Relation between size and depth within *Nannoniscus*.

cies recorded from the shallowest depths, while the two other species of considerable size are from about 4500 m.

Desmosoma (159). Both the two smallest and the third largest species occur at depths from 50-150 m.

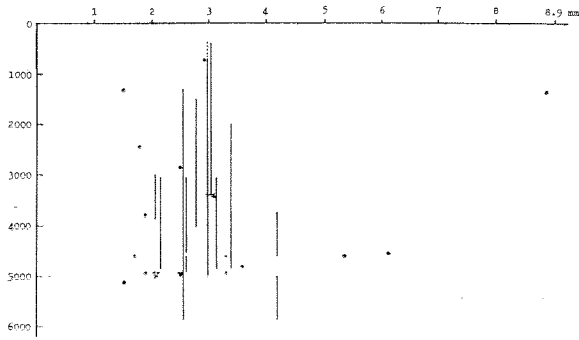


Fig. 158. Relation between size and depth within *Haploniscus*.

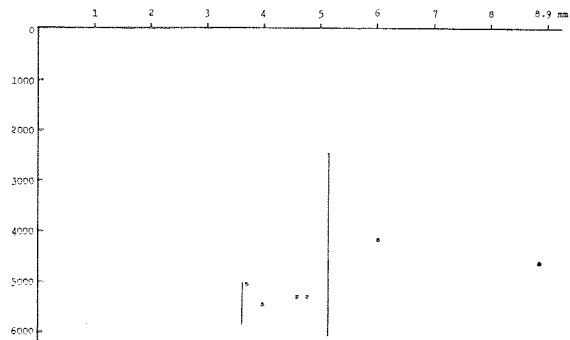


Fig. 161. Relation between size and depth within *Stylomesus*.

The largest species is *reticulata* from 700 m in the Arctic Ocean.

Munna (160) is primarily a littoral genus. The smallest and largest species are both eulittoral – *M. acarina* from Hawaii and *macquariensis* from the Subantarctic Macquarie Island, respectively. The bathyal species are of about average size, and the single abyssal species (*argentinae*) is only one-third the size of *macquariensis*.

Stylomesus (161) was mentioned above. The lack of correlation may be due to the deep-abyssal character of the genus. The largest species is *granulosus* from the South Atlantic Ocean.

Munnopsis (162) and *Munnopsurus* (163) show almost the same pattern. In the former, the tropical

bathyalis (a truly bathyal species) is the largest; in the latter, the primarily Arctic species *giganteus* (from 40-1500 m) is by far the largest – being more than twice as long as any other species. However, none of the genera have any truly abyssal species.

Janira (164) is peculiar in that the only abyssal species¹, *operculata* (described above, p. 44) is the smallest species. This may be due to the fact that *operculata* probably lives in water-logged wood (from which it was obtained).

Acanthomunna (165) and *Acanthaspidia* (166) are almost identical. The number of species is limited to four in both genera.

1. No length was recorded for *J. abyssicola*, which perhaps does not belong to *Janira* (cf. p. 42).

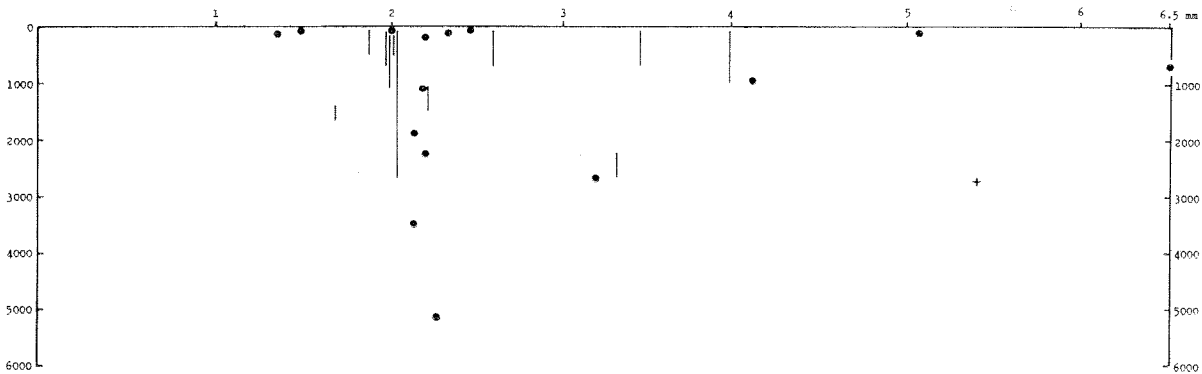


Fig. 159. Relation between size and depth within *Desmosoma*.

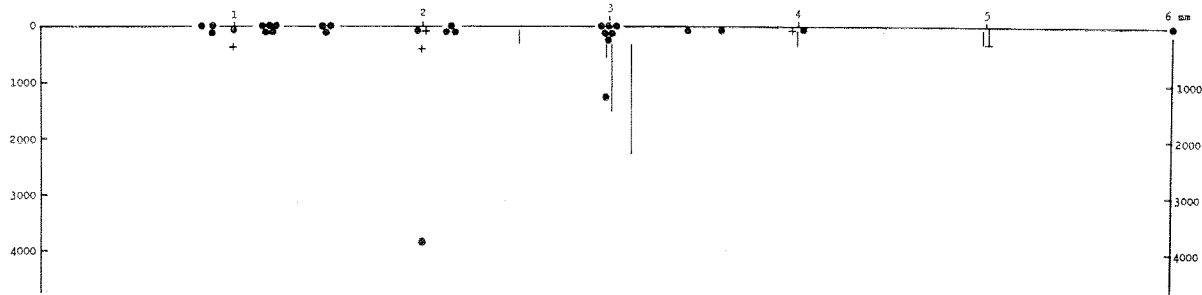


Fig. 160. Relation between size and depth within *Munna*.

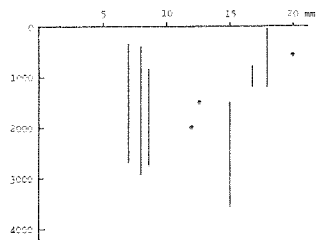


Fig. 162. Relation between size and depth within *Munnopsis*.

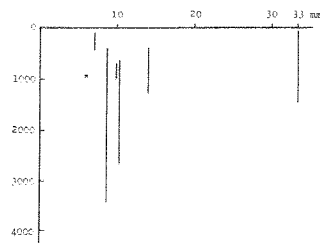


Fig. 163. Relation between size and depth within *Munnopsurus*.

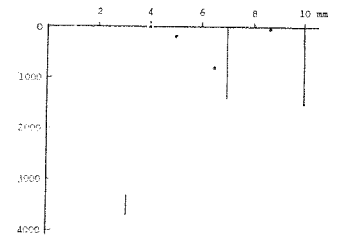


Fig. 164. Relation between size and depth within *Janira*.

The remaining three genera actually have a more or less pronounced decrease in size with increasing depth. These genera are *Janirella* (167), *Acanthocope*¹ (168), and *Syneurycope* (169). However, the size range is very limited in all three (from 3.2-7 mm, 2.8-7.3 mm, and 3.7-5 mm, respectively) and the number of species fairly small.

No correlation was found in the two genera, occurring between <100 m and 1500 m, viz. *Katianira*

which are almost entirely restricted to shelf areas: *Antias*, *Ianiropsis*, *Jaeropsis*, *Janiralata*, *Austrosignum*, *Iathrippa*, *Neojaera*, *Paramunna*, *Pleurosignum*, and *Pleurogonium*. Fig. 153 shows that in *Stenetrium* also there is no difference in size between eulittoral and sublittoral species.

To conclude, it can be stated that in all larger genera of Asellota, with species ranging from sublittoral or upper bathyal depths to well into the abyssal zone,

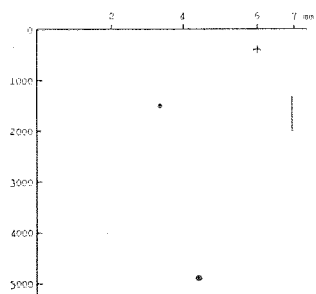


Fig. 165. Relation between size and depth within *Acanthomunna*.

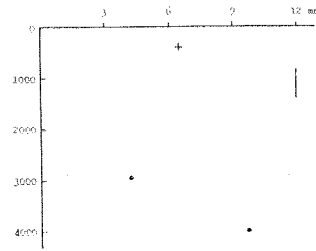


Fig. 166. Relation between size and depth within *Acanthaspida*.

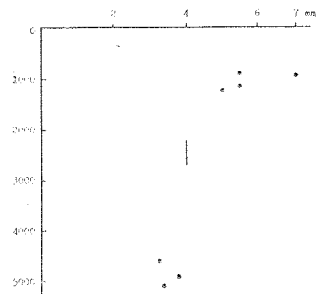


Fig. 167. Relation between size and depth within *Janirella*.

(170) and *Iolella* (171), of which the former has a limited size range and the latter a wide size range. Nor was it possible to find an increase in size in the deeper-occurring species of the following genera

1. Since the terminal spine varies considerably in length within the species of *Acanthocope*, the measurements have been made exclusive of this spine.

there is a more or less distinct indication of increasing size downwards. The only definite exceptions from this rule are the genera *Haploniscus*, *Desmosoma* and *Munna* – all of which are, however, characterized by a very small size range within the species.

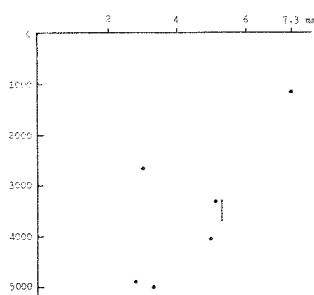


Fig. 168. Relation between size and depth within *Acanthocope*.

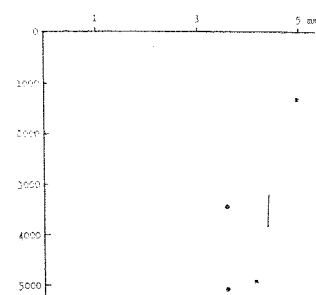


Fig. 169. Relation between size and depth within *Syneurycope*.

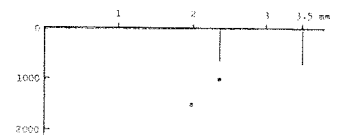


Fig. 170. Relation between size and depth within *Katianira*.

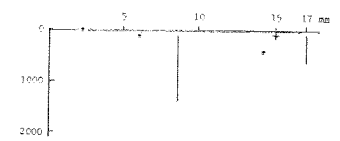


Fig. 171. Relation between size and depth within *Iolella*.

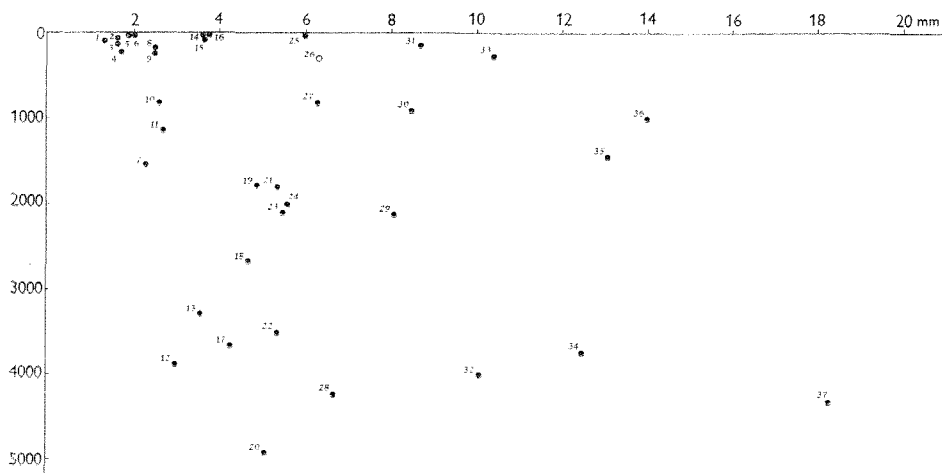


Fig. 172. Genera with at least four species. Relation between size and depth.

- | | | | |
|------------------------|------------------------|-------------------------|-------------------------|
| 1. <i>Paramunna</i> | 11. <i>Desmosoma</i> | 20. <i>Stylomesus</i> | 29. <i>Acanthaspida</i> |
| 2. <i>Austrosignum</i> | 12. <i>Haploniscus</i> | 21. <i>Eurycope</i> | 30. <i>Ianthopsis</i> |
| 3. <i>Pleurosignum</i> | 13. <i>Macrostylis</i> | 22. <i>Acanthocope</i> | 31. <i>Iathrippa</i> |
| 4. <i>Pleurogonium</i> | 14. <i>Ianiropsis</i> | 23. <i>Acanthomunna</i> | 32. <i>Munnerycope</i> |
| 5. <i>Antias</i> | 15. <i>Jaeropsis</i> | 24. <i>Ilyarachna</i> | 33. <i>Iolella</i> |
| 6. <i>Bagatus</i> | 16. <i>Jaera</i> | 25. <i>Janiralata</i> | 34. <i>Ischnomesus</i> |
| 7. <i>Nannoniscus</i> | 17. <i>Syneurycope</i> | 26. <i>Stenetrium</i> | 35. <i>Munnopsis</i> |
| 8. <i>Neojaera</i> | 18. <i>Janirella</i> | 27. <i>Janira</i> | 36. <i>Munnopsurus</i> |
| 9. <i>Munna</i> | 19. <i>Heteromesus</i> | 28. <i>Haplomesus</i> | 37. <i>Storhyngura</i> |
| 10. <i>Katianira</i> | | | |

The large size of the hadal species is especially remarkable. Table 16 shows that in all genera the length of the hadal species exceeds the average length of the genus.

The size and depth occurrence of genera with at least four species is compared in Fig. 172. Although the method is not quite satisfactory it was found necessary to base the comparison on the average length and the average depth occurrence of the species of each genus. There is a general tendency for the smallest genera to occur at depths of less than about 250 m and the largest at depths of more than 1000 m – but there are many exceptions:

There are six, comparatively very large, genera

from depths of less than 1000 m. One is *Stenetrium* all the other five belong to Janiridae (viz. *Janiralata*, *Janira*, *Ianthopsis*, *Iathrippa*, and *Iolella*) and all seem to be fairly closely related within this family. Some of the smallest genera (from depths < 1000 m) also belong to Janiridae (*Bagatus*, *Neojaera*, and *Katianira*) but they are not related to any of the five genera above.

Two typically bathyal genera (*Munnopsis* and *Munnopsurus*) are also exceptionally large, exceeding almost all the primarily abyssal genera in size.

On the other hand, some of the pronounced abyssal genera are very small, the following being below the average size of all genera considered

Table 16. Length of the hadal species compared to the average length of the genus. Species marked (*) are also recorded from depths of less than 6000 m.

	<i>Storhyngura</i>	<i>Ischnomesus</i>	<i>Munnerycope</i>	<i>Haplomesus</i>	<i>Eurycope</i>	<i>Ilyarachna</i>	<i>Macrostylis</i>
	Average <i>benti</i> * <i>tenuispinis</i> <i>pulchra kermadec.</i> <i>bicornis</i> <i>furcata</i> * <i>vitjazii</i> <i>chelata</i> * <i>herculea</i>	Average <i>brauni</i> <i>spärcki</i> <i>andriyashevi</i> *	Average <i>menziesi</i>	Average <i>cornutus</i> <i>gigas</i>	Average <i>galathea</i> <i>madsoni</i>	Average <i>kermadecensis</i> *	Average <i>hadalis</i> <i>galathea</i>
Length (mm)	18.3 19 19 27 30 30.5 32 35 45	12.5 13.5 16 16	10.1 13.5	6.7 9.8 15	5.4 5.8 6.9	5.6 15.2	3.6 4.4 5.5

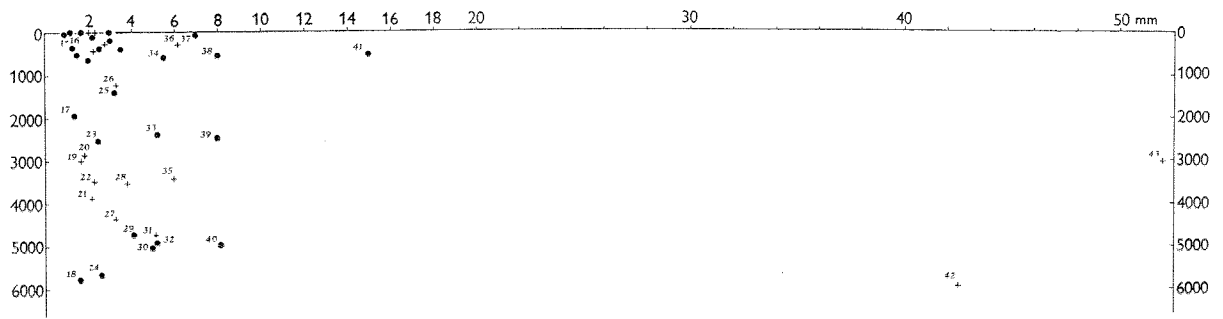


Fig. 173. Genera with 1-3 species. Relation between size and depth. ● one species, + 2-3 species.

- | | | | |
|---------------------------|---------------------------|---------------------------|-------------------------|
| 1. <i>Antennulosignum</i> | 12. <i>Nannoniscella</i> | 23. <i>Janthura</i> | 34. <i>Mixomesus</i> |
| 2. <i>Austroniscus</i> | 13. <i>Neasellus</i> | 24. <i>Microthambema</i> | 35. <i>Helomesus</i> |
| 3. <i>Astrurus</i> | 14. <i>Pleurocope</i> | 25. <i>Pseudomesus</i> | 36. <i>Coulmannia</i> |
| 4. <i>Caecianitropsis</i> | 15. <i>Pseudarachna</i> | 26. <i>Dendrotion</i> | 37. <i>Ectias</i> |
| 5. <i>Caecijaera</i> | 16. <i>Pseudojanira</i> | 27. <i>Hydroniscus</i> | 38. <i>Jaerella</i> |
| 6. <i>Echinomunna</i> | 17. <i>Schistosoma</i> | 28. <i>Dendromunna</i> | 39. <i>Thambema</i> |
| 7. <i>Echinopleura</i> | 18. <i>Abyssijaera</i> | 29. <i>Gomphomesus</i> | 40. <i>Xostylus</i> |
| 8. <i>Iais</i> | 19. <i>Nannoniscoides</i> | 30. <i>Echinothambema</i> | 41. <i>Microprotus</i> |
| 9. <i>Kuphomunna</i> | 20. <i>Notoxenoides</i> | 31. <i>Bactromesus</i> | 42. <i>Bathyopsurus</i> |
| 10. <i>Lipomera</i> | 21. <i>Abyssianira</i> | 32. <i>Vemathambema</i> | 43. <i>Paropsurus</i> |
| 11. <i>Munella</i> | 22. <i>Mesosignum</i> | 33. <i>Spinianirella</i> | |

1. See footnote p. 278.

(5.7 mm): *Haploniscus*, *Macrostylis*, *Syneurycope*, *Stylomesus*, and *Acanthocope*.

In Fig. 173 the same comparison has been made with all the remaining genera (with 1-3 species each). The great majority of genera from less than about 250 m are very small, but there is no similar preponderance of large-sized representatives among the primarily or exclusively abyssal genera – with two remarkable exceptions. By far the two largest genera of Asellota, *Bathyopsurus* and *Paropsurus*, both have a very deep depth occurrence (the former from 3900-7900 m, the latter from 2000-4400 m).

MADSEN (1961 b, p. 201) noted that pronounced examples of dwarfing also occur in some deep-sea species, exemplified by sessile suspension-feeders such as the gorgonarian *Primnoella* and the stalked crinoid *Bathyrinus*. He was of the opinion that this feature may be due to the sparse food supply available for this kind of animal. On the other hand, there are also extremely large suspension-feeders in the deep-sea, e.g. the previously mentioned solitary hydroid *Branchiocerianthus* (MADSEN, 1. c.). Similarly, the abyssal species of the cirriped genus *Scalpellum* are as large as or larger than the great majority of species from sublittoral or bathyal depths. No typical examples of deep-sea dwarfing are found in the asellotes although some abyssal species and even genera are almost as small as the smallest shallow water representatives (*Schistosoma*, *Abyssijaera*, *Nannoniscoides*, and *Notoxenoides* – cf. Fig. 173).

In a preliminary report on the collections from the *Vema* and *Theta* Expeditions, CLARKE (1959) stated that abyssal molluscs are usually small (mean length of specimens approximately 3 mm); in comparison with species of the same genera from shallower depths they show a tendency towards smaller size with increasing depth. However, this is not so with the collections of the *Galathea* Expedition (JØRGEN KNUDSEN, verbal communication). The small average size of the former collections may be due to the usage of a much smaller gear (cf. p. 13).

Causes for increase in size with depth.

In my opinion, it is evident that in many deep-sea species and genera (at least within crustaceans) there is a general increase in size with increasing depth. The cause of this increase is, however, difficult to explain.

I agree with ZENKEVICH & BIRSTEIN (1956) that the temperature factor cannot, in most cases, be of any great importance since the temperature between 2000 and 8000 m is generally the same. BIRSTEIN demonstrated (1957, fig. 11) that in *Storhynchura* there is no correlation between size and temperature; my investigations show the same in other asellote genera.

There are, however, examples of increased size at lower temperatures in a few deep-sea species. One instance was pointed out previously (WOLFF 1956 a, p. 153), viz. the North Atlantic *Eurycope inermis*

(HANSEN 1916, p. 143) of which all sixty large specimens (9-11.5 mm) were collected at low temperatures (-0.5--1.0°C.) while all forty small specimens (5.5-7 mm) were taken at temperatures above zero (1.2-4.1°C.); for both groups the depth was between some 600 and 1800 m. Another example is that of the two subspecies of *Haploniscus bicuspis* (p. 58). Of the nominate subspecies, fifteen adult males (2.3-2.7 mm long) were collected by the *Ingolf*, and consistently at temperatures below -0.4°C. (10 stations). The single adult male of *bicuspis tepidus* is only 1.7 mm long and was collected at 4.5°C. The depth of the former group of males is 700-2500 m, that of the *tepidus* male 1500 m.

Perhaps a third instance is that of the amphipod *Anonyx nugax* Phipps. STEPHENSEN (1923, p. 81) showed that all specimens of this species from boreal regions were smaller than 20 mm while all Arctic specimens were at least 30 mm, and some even above 40 mm. However, the large Arctic specimens are recorded from depths considerably greater than the boreal specimens (down to 1500 m); thus, it is possible that the size difference is rather a result of greater depth occurrence than of lower temperature.

ZENKEVICH & BIRSTEIN (1956) stated that "neither can differences in food habits and quality of food affect the body-size of deep-sea organisms, considering that deep-water giantism is observed in forms having different food habits and using various kinds of food". The authors thus assumed that the phenomenon must be caused by peculiarities in the metabolism. Furthermore, BIRSTEIN (1957) concluded that "the abyssal giantism is determined by the effect of the hydrostatic pressure on the metabolism", basing this assumption on experiments, i. a. by FONTAINE (1930) who showed that intensified pressure causes an increase in the rate of metabolism. This explanation was accepted by the present author (WOLFF 1960).

However, MADSEN (1961b, p. 201) strongly opposed it. The increased metabolic rate stated in the shallow water animals which were submitted to high pressure by FONTAINE "is quite another thing than the rate of metabolism in an animal living undisturbed in its natural milieu" (l. c.). After having exemplified cases of giantism under quite different ecological conditions (both on land and in the sea) he found it "most probable that the phenomenon of giantism in the deep-sea as understood by e. g. BIRSTEIN and WOLFF ... does not really exist". The increased size of some deep-sea forms may be determined by

greater longevity of the animals in general, the increased age being a result of fewer predators and the uniform ecological conditions prevailing in the deep-sea.

As stated above, I feel there is documented evidence enough to show that a tendency to overgrowth (but perhaps not "giantism", which is a rather ambitious word) does exist, at least in the majority of asellotes. Moreover, I feel convinced that hydrostatic pressure does, in some way or another, play a role. BRUUN (1957, p. 646) and BIRSTEIN (l. c.) reviewed statements made by a number of authors (e. g. EBBECKE, BRIDGMAN, KITCHING and MARS-LAND) on the important physiological effects of pressure. ZOBELL (1954, p. 25) recorded indication of growth acceleration in barophilic bacterians under high pressure.

It is probable that the overgrowth is determined by a combination of several factors, such as low temperature, large supply of food in restricted areas, and the effect of pressure, resulting in an increased metabolic rate or, alternatively, furthering the excess in size, e. g. by retarded sexual maturity and/or greater longevity.

Examples of overgrowth in Antarctic Asellota.

Evidence of overgrown species not only in the deep-sea but also in the Antarctic was previously given for various genera of isopods and the tanaid genus *Apseudes* (WOLFF 1956a, 1956b). There are other examples of this in the present material.

As shown in Figs. 150-171 in which all species restricted to Antarctic waters have been specially marked, there are some very overgrown Antarctic species from depths less than 1000 m in *Storthyn-gura*, *Stenetrium*, *Ilyarachna*, *Eurycope*, *Nannoniscus*, *Munna* and *Acanthomunna*. However, some of the smallest species in the first three of these genera are also Antarctic. The size records of *Ilyarachna quadrispinosa* are of interest in this respect. At Kerguelen, the largest female (ovigerous) was 6 mm (BEDDARD 1886b, p. 76) and at South Georgia, the size range of females (with developing oostegites and ovigerous) was 3.5-9.7 mm (NORDENSTAM 1933, pp. 271-272). However, on the Antarctic Continent MONOD (1926, pp. 23-24) reported females (with dvl. oost.) 10-11 mm and NORDENSTAM (l. c.) one female (with dvl. oost.) no less than 17 mm. Unfortunately, HODGSON (1902) omitted measurements for his specimens of *I. spinosa* (= *quadrispinosa*) from the Antarctic.

ELONGATION OF LEGS

There are several examples of deep-sea crustaceans with very long legs, e. g. *Parapagurus*, the caridean genus *Nematocarcinus*, and the amphipod genera *Lepechinella*, *Paralepechinella* and *Rachotropis* (PIRLOT 1933, 1934; DAHL 1959; J.L. BARNARD 1961).

The most remarkable example within the asellotes is that of *Munnopsis latifrons* (from a depth of about 800 m) in which pereopods III and IV are 116 mm, i. e. more than seven times longer than the body. The other species of *Munnopsis* are also extremely long-legged. Other examples are *Munna boeckii* and *limicola*, most species of *Ischnomesus*, *Macrostylis longipes* (with pereopod VII extremely elongated), *Ilyarachna aspidophora*, *Syneurycope parallela*, *Eurycope phalangium*, and *Munnopsurus longipes*. All these species are from soft bottom but only a few are typically abyssal; most occur at bathyal depths and a few (e. g. the two *Munna* species) at sublittoral depths. Similarly, five of the species of the three long-legged amphipod genera mentioned above are bathyal, one is abyssal and two are hadal.

Not all typically abyssal genera are long-legged. The legs in e. g. *Haploniscus* are as short as those of any shallow water genus.

EYES

All species described above are blind (except *Stenetrium* – cf. below) as are the majority of the asellotes. However, in both bathyal and abyssal species of *Munnopsis* (primarily *latifrons* (Pl. XII C) and *longi-*

remis) small nodules are found attached to the inner side of the head integument; they should probably be interpreted as vestigial eyes. The same perhaps applies to the oval, vaulted areas with a net-like pattern, found e. g. in the hadal *Ilyarachna kermadecensis* (WOLFF 1956a, fig. 25).

PIRLOT did not observe a single eye-bearing amphipod species from abyssal depths in the large *Siboga* collection (1936, p. 246) while BARNARD (1961) mentions the presence of vestigial eyes in a few abyssal species from the *Galathea* collections (*Eurythenes gryllus*, *E. obesus*, and *Leucothoe panpulco*). All the remaining abyssal species are completely devoid of eyes, whereas the majority of bathyal species have pigmented eyes.

In view of their deep occurrence (4500 m and 150-3400 m, respectively), the presence of pigmented eyes in *Stenetrium abyssale* and *S. acutum* is a curious feature within the asellotes. Owing to the scarcity of material, the histology of the eyes (of the former) has not been studied; thus it is not known whether the eyes actually function or are merely light-sensitive organs. As far as I am aware, *S. abyssale* and *acutum* are the only examples of abyssal asellotes with pigmented eyes. It is interesting that a distinct reduction of the eyes is recorded by K. H. BARNARD (1940, p. 432) for *S. syzygus*, although this species was "collected under rocks and among worm-tubes, ascidians, etc. in the littoral zone". The presence of pigmented eyes in *abyssale* and *acutum* may be explained by suggesting a late descent into the abyssal zone.

E. The food of some deep-sea Asellota

a. Previous studies

The intestine contents in marine asellotes have been very rarely studied. According to SYE (1887, p. 8), *Jaera albifrons* feeds on "pflanzliche Stoffe" but it also takes animal food, even dead specimens of its own species. In five specimens of *J. albifrons*, RAUCHENPLAT (1901, p. 97) found fragments of *Zostera*, algae and diatoms, and in one, also small crustacean fragments. As in other shallow water isopods, e. g. *Ligia* (NICHOLLS 1931) and *Idotea* (NAYLOR 1955b), this indicates an omnivorous diet, although there may be differences, depending on the habitat and locality and the size of the animals (NAYLOR, l. c.).

Bathyal and abyssal asellotes have not been investigated until recently. WOLFF (1956a) studied a hadal species, *Storothyngura pulchra*; identifiable re-

mains were shells of radiolarians, chaeta and a single jaw of polychaetes, spicules of sponges and a few fragments of legs and integuments belonging to crustaceans (Table 17). In *Acanthocope spinosissima*, in three specimens of *Eurycope* sp. and in *Janirella vemae*, MENZIES (1956a, 1956b) found large quantities of bacteria-size and -shape particles, somewhat larger globular or ovoid objects (identified as probable protozoans) and – except in *Acanthocope* – siliceous crystals. In the two former species, tests of foraminifers, diatoms and tintinoids were also found, and in *Acanthocope* some additional setae of a polychaete and sponge spicules. Thus, MENZIES regarded *Acanthocope* as both a carnivorous and deposit feeder, the others as omnivorous deposit feeders (Table 17).

SOKOLOVA (1958, p. 148) studied 10 *Eurycope* sp., 5 *Storothyngura* sp. (most certainly *herculea* Birstein), 5 Ischnomesidae, 5 *Antarcturus hirsutus* and 5 *A.* sp. In *Eurycope* and *Storothyngura* the contents were equal, 90% consisting only of moderately well sorted detritus with a few diatom tests, the remainder being chitinous fragments of crustaceans and ophiuroid skeletons and some sand grains. The detritus in the five specimens of Ischnomesidae was very well sorted, consisting exclusively of very fine, flake-like particles and small quantities of ooze. In *Antarcturus* sp. (which is from clayey ooze as *Eurycope* and *Storothyngura*), SOKOLOVA found a light, rather finely sorted detritus without ooze or animal remains, while in *A. hirsutus* from coarse sand and clay, half the contents consisted of sand. No intestine content showed the remains of algae, larvae of polychaetes and crustaceans, chaeta of polychaetes or mollusc shell fragments, which are commonly found in sublittoral animals.

Finally, TCHINDONOVA (1959) investigated 10 specimens of *Munneurycope (Eurycope) murrayi* collected pelagically at depths exceeding 500 m (at different horizons). The gut contents consisted mainly of phytoplankton, and in addition, small amounts of *Globigerina*, tintinoids, detritus and fragments of medusae. She thus considered this species to be a plant-eating filtrator, apparently able to make extensive vertical migrations. TCHINDONOVA compared the food of *M. murrayi* to that of certain specimens of *Storothyngura herculea* which had been taken in a vertical haul from 5000-0 m (depth to bottom: 7000 m). In the latter the intestine was completely filled with diatom ooze and benthic foraminifers (cf. above). It is interesting to note that, according to TCHINDONOVA, the integument of these pelagically captured, bottom-feeding specimens of *S. herculea* is thin, transparent and quite different to that of other specimens of this species collected in the same locality with a bottom trawl.

b. Own investigations

In all cases in the present material where there were sufficiently numerous specimens of species larger than 5-10 mm, the intestines were dissected. In general, only the posterior half of the gut was studied since this can be dissected fairly easily without too much damage to the specimen. The intestine was transferred directly to and mounted on a slide (in Faure-Berlese medium). The general results are

presented in Table 17¹ (which also includes records of the asellote gut contents mentioned above). The species are arranged in systematic order since the present material showed no difference in the sorting of the detritus. The following comments are found necessary:

Detritus. This consisted of unidentifiable objects. It was impossible to decide whether some of the particles were bacterians, as suggested by MENZIES (1956a, b), but it seems probable. The consistency was more or less fine, depending on the size of the animal, the particles being coarser in the large *Storothyngura* species, particularly in the very large *Paropsurus giganteus*, than in the remaining species. In No. 15 (*Munnopsis longiremis*) were many small, circular objects (50 μ) which are probably protozoans.

Mineral fragments are present in all samples, with the exception of the pelagic forms and a few others. In abundance, size and appearance, the fragments vary greatly. They are quite often of a greenish colour and resemble glass splinters, with sharp edges, keels etc. (Pl. XIX H-J) and are of considerable size (0.2-0.5 mm); they are particularly common in Nos. 19, 9, 21, 22, 20, and 24. In some specimens, fragments with a rather thread-like structure are also found (Pl. XIX J). Smaller, colourless fragments are particularly common in Nos. 1 and 23 (Pl. XIX K).

Plant material was present in several species. Mr. TYGE CHRISTENSEN of the Botanical Laboratory of the Copenhagen University has very kindly helped me with the identification and interpretation.

It is surprising and very interesting that the very large amount of plant material in specimens of *Bathyopsurus nybelini* from the Puerto Rico Trench and the Tasman Sea (Nos. 4-7 and 28), and the rarely occurring fragments in Nos. 1, 2, 19, and 22 all proved to be fragments of algae. In all cases the animal had apparently eaten the algae (in a fresh condition), just prior to capture. This can be seen in Pl. XVIII D, which shows two plasmolysed cells.

The abundant fragments in *B. nybelini* from the Puerto Rico Trench (Swedish Deep Sea Exp. St. 371) are in a very fine state of preservation (Pl. XVIII B-D, F, H, K). A comparison between some of these fragments and a specimen of *Sargassum fluitans* Børgesen (collected 29 January 1922 in the

1. In addition, the gut contents of the sectioned specimens of *Haploniscus helgei* (Pl. XVI E) were also studied. As far as could be made out they consisted of large amounts of detritus and some fragments of crustaceans and radiolarians.

Table 17. Intestine contents of 17 species (29 specimens) of benthic and 2 species (7 specimens) of pelagic Asellota. very rare; p = present; m. part = mouthpart(s); chit. fr. = chitinous fragment; isop. = isopod; amph. = amphipod; species is given by the recorded metre wire (mw)

Slide no.	Species	Locality	Depth (m)	Sediments in the locality	Detritus	Minerals	Algae or wood	Coccolitho- phorids	Diatoms
	<i>Janirella vemae</i>	Puerto Rico Tr.	5110	oz	cc	cc	—	—	r
	<i>Ischnomesidae</i>	Bering Sea	3820	cl/oz	cc	—	—	—	—
18	<i>Ilyarachna kermadecensis</i>	Kermadec Tr.	6960	cl	r	rr	—	—	—
	<i>Acanthocope spinosissima</i>	Caribbean Sea	1240	oz	?cc	?	—	—	+
	<i>Eurycope</i> sp.	Puerto Rico Tr.	5110	oz	cc	c	—	—	—
	<i>Eurycope</i> sp.	Aleutian Tr.	7250	cl/oz	cc	+	—	—	r
	<i>Storhyngura pulchra</i>	Kermadec Tr.	6620	cl	cc	?	—	—	?
19	<i>Storhyngura pulchra</i>	Off Costa Rica	3570	cl	c	cc	rr	—	—
8	<i>Storhyngura pulchra</i>	Panama Gulf	2690	oz	r	r	—	—	cc
35	<i>Storhyngura chelata</i> ¹	Japan Tr.	6475	?	cc	rr	rr	—	cc
33, 34	<i>Storhyngura chelata</i> ¹	Japan Tr.	6475	?	cc	rr	—	—	cc
9, 21	<i>Storhyngura furcata</i>	Kermadec Tr.	6660	cl	cc	cc	—	—	—
22	<i>Storhyngura furcata</i>	Kermadec Tr.	5850	s/cl	cc	cc	rr	—	—
20	<i>Storhyngura bentii</i>	Kermadec Tr.	6960	cl	cc	cc	—	—	—
	<i>Storhyngura herculea</i>	Aleutian Tr.	7250	cl/oz	cc	+	—	—	r
4, 28	<i>Bathyopsurus nybelini</i>	Tasman Sea	4400	oz	—	—	cc	—	—
5-7	<i>Bathyopsurus nybelini</i>	Puerto Rico Tr.	5850	oz	—	r	cc	—	rr
3	<i>Paropsurus giganteus</i>	Off Costa Rica	3570	cl	cc	r	—	—	c
1-2, 23-27	<i>Paropsurus giganteus</i>	Tasman Sea	4400	oz	cc	cc	r	—	rr
10	A <i>Munnopsis longiremis</i>	Off Costa Rica	3570	cl	+	—	—	+	cc
11	B <i>Munnopsis longiremis</i>	Off Costa Rica	3570	cl	+	c	—	+	+
12	C <i>Munnopsis longiremis</i>	Off Costa Rica	3570	cl	r	c	—	+	+
13	D <i>Munnopsis longiremis</i>	Off Costa Rica	3570	cl	+	—	—	c	+
14	E <i>Munnopsis longiremis</i>	Off Costa Rica	3570	cl	+	r	—	—	r
15	F <i>Munnopsis longiremis</i>	Off Costa Rica	3570	cl	r	cc	rr	—	cc
16	G <i>Munnopsis longiremis</i>	Off Costa Rica	3570	cl	r	c	—	—	cc
17	<i>Munnopsis bathyalis</i>	Bali Sea	550	s/cl	r	+	—	—	—
30	<i>Munnopsis latifrons</i>	East China Sea	800	?	+	c	—	rr	rr
29	<i>Munnopsis beddardi</i>	Davis Strait	2700	oz	rr	—	—	—	—
	<i>Munneurycope murrayi</i>	Kurile-Kamtch. Tr.	> 500	—	r	—	—	—	cc
39	<i>Munneurycope murrayi</i>	Davis Strait	2500 mw (2550)	—	rr	—	—	cc	—
32	A <i>Munneurycope murrayi</i>	S. of Iceland	1800 mw (> 2000)	—	rr	—	—	c	—
36	B <i>Munneurycope murrayi</i>	S. of Iceland	1800 mw (> 2000)	—	+	—	—	cc	rr
38	<i>Munneurycope murrayi</i>	S. of Iceland	1800 mw (2160)	—	r	—	—	rr	—
37	<i>Munneurycope murrayi</i>	S. W. of Iceland	2800-0	—	rr	—	—	—	rr
31	<i>Paramunnopsis oceanica</i>	Davis Strait	2500 mw (2550)	—	rr	—	—	cc	rr

1. From the stomach (No. 35) and from the intestine (Nos. 33 and 34) of the same specimen.

northern Caribbean Sea at 18°50'N, 79°07'W) (Pl. XVIII A, E, G, J) leaves no doubt that the fragments in question belong to the genus *Sargassum*. A determination of the genus has not been attempted with similar fragments found in other animals (more digested or less abundant), but there is little doubt that, generally, they belong in the

Fucales (cf. Pl. XVIII L). Some (if not all) may be holdfasts of kelps which are often transported far out into the open sea from the shore.

The size of the fragments in the Puerto Rico specimens (Pl. XIX D, O) is c. 0.3-0.5 mm, those in the Tasman Sea specimens c. 0.6-1 mm. The colour is always yellow-brown.

abbreviations: cl = clay; oz = ooze; s = sand; cc — c — + — r — rr = very common, common, abundant, rare, abundant; cop. = copepod; harp. = harpacticid. A, B, C, etc. = different specimens from the same station. The depth of the pelagic zone is indicated in the depth to the bottom in parenthesis.

Radolarians	Foraminifers	Spicules of sponges	Hydroids	Polychaetes (chaeta)	Crustaceans	Fragments of integument	Varia	Reference
—	r	—	—	—	—	—	—	MENZ. 1956 b
—	—	—	—	—	—	—	—	SOKOL. 1958
—	rr	r	—	—	?m. part	r	—	this paper
—	r	+	—	p	—	—	—	MENZ. 1956 a
—	—	—	—	—	—	—	—	MENZ. 1956 b
—	—	—	—	—	+	—	skeletons of ophiuroids	SOKOL. 1958
p	?	+	—	+ jaw	legs	p	—	WOLFF 1956 a
+	—	rr	—	—	amph.	—	—	this paper
+	r	+	—	—	—	—	tintinid (rr)	this paper
—	c	+	+	—	amph.	—	—	this paper
rr	c	c	—	—	chit. fr.	—	spine (echinoid?)	this paper
r	rr	r	—	—	amph.?	r	Halacarid; spine (echinoid)	this paper
+	c	—	—	—	—	—	—	this paper
rr	—	+	—	—	—	—	—	this paper
—	—	—	—	—	+	—	skeletons of ophiuroids	SOKOL. 1958
—	rr	rr	r	—	—	—	—	this paper
rr	—	rr	r	tube	amph.	rr	stiff setae; chit. fr.	this paper
—	r	cc	—	—	crust.	—	—	this paper
+	r	r	?	—	amph.; isop.	—	chit. fr.; skeletons of ophiuroid	this paper
cc	—	cc	—	—	—	—	sausage-shaped soft part	this paper
+	rr	rr	—	rr	m. part	—	—	this paper
+	—	rr	—	—	isop.	+	—	this paper
r	—	+	—	rr	chit. fr.; harp.	—	oval object (?)	this paper
r	—	rr	—	rr	—	r	—	this paper
cc	—	r	—	r	—	—	round protozoans (?)	this paper
—	—	rr	—	—	chit. fr.	—	—	this paper
—	cc	r	—	—	—	rr	spine (echinoid?)	this paper
—	+	r	—	—	—	—	spine (echinoid?)	this paper
—	—	rr	—	—	—	—	chit. fr.	this paper
—	r	—	—	—	—	—	fr. of medusae	TCHIND. 1959
—	rr	—	—	—	—	rr	—	this paper
rr	—	r	—	—	cop.	—	—	this paper
—	—	—	—	—	amph.	rr	—	this paper
—	—	—	—	—	isop.	rr	—	this paper
r	rr	—	—	—	—	—	spines (+)	this paper
rr	—	—	—	—	—	—	—	this paper

Other plant material consisted of one fragment of coniferous wood in No. 15 (Pl. XIX L-M) and a few fragments of a phanerogam in No. 35.

Coccolithophorids are very common in most of the pelagic specimens (Nos. 31-32, 36, 39) and also fairly common in several specimens of *Munnopsis longiremis*. Those in the former were identified by

Mr. VAGN HANSEN of the Danish Fishery- and Sea Investigations as *Coccolithus Huxleyi* (Pl. XVIII M-N). Although the large number found in Nos. 31 and 39, which are both from *Godthaab* St. 24, indicates that there must have been a large maximum in the photosynthetic zone the species was not recorded by GRÖNTVED & SEIDENFADEN (1938) in

their description of the phytoplankton from this station. This may be due to the fact that the coccolithophorids subsided so slowly to the depth at which they were eaten by the isopods that the surface maximum no longer existed by the time of collection. It is also possible that the absence of *C. Huxleyi* at the surface is explained by the plankton samples being net samples (VAGN HANSEN, *in litt.*).

Foraminifers are mainly pelagic forms, thus, dead tests which were accidentally swallowed with other bottom deposits. Due to the animals being mounted, identifications (by Dr. A. NØRVANG) could only be made tentatively. *Globigerina*-like forms were found in Nos. 8 (two types), 18, 3, and 17, ? *Trochammina* in No. 11 and aff. *Sphaeroidinella dehiscens* in No. 24. *Quinqueloculina*- and *Lagena*-type in No. 26, ? *Pyrgo* in No. 27, and a large (0.3 mm) rotaliform specimen (Pl. XIX N) are considered to be benthic forms.

Sponge spicules were sent to Professor CLAUDE LÉVI (Strasbourg) for possible identification. No. 19 contained one big spicule from *Hyalonema* sp. and others were from a lithistid sponge. Spicules (most certainly *Petrosia*) were found in No. 17. No. 12 contained a group of *Hyalonema bianchoratum* spicules (Pl. XIX Q); this sponge was collected at the same station (716) as the isopod (WOLFF 1961). Since the latter spicules were not distributed singly in the stomach contents (in the usual way) but apparently still *in situ* in the sponge tissue it might be possible that the isopod fed on sponges. However, according to Professor LÉVI (*in litt.*) it is more probable that in this case also the spicules have been swallowed accidentally with other bottom material. Finally, a specimen of *Munneurycope murrayi* (No. 32) contained a styloxe spicule of *Tethya* or *Aaptos*, a complete tylostyle of *Suberites* or *Cliona* and other spicules of uncertain origin (Pl. XIX P).

Hydroids were found on some of the *Sargassum* fragments in *Bathyopsurus*, consisting mostly of fragments of stolons and stalks (Pl. XIX D, O), but some hydrotheca were also present (Pl. XIX A). These were identified by Mr. KAY W. PETERSEN as *Campanularia* aff. *johnstoni* and were certainly swallowed accidentally along with the algae. Two other species, *Campanularia integra* and *C. sp.* (Pl. XIX B-C) were present in the stomach contents of No. 35, which otherwise contained large amounts of detritus, mineral fragments and diatoms. As the hydroids were so abundant it is most probable that they were deliberately eaten by the present species (*Storthyngura chelata*).

Polychaete spicules are rare in the samples. Those

in Nos. 11, 13 and 14 were identified (by Mr. J. B. KIRKEGAARD) as belonging to Cirratulidae – being characteristically arranged in bunches (Pl. XIX G). In No. 15 were several spicules from a species of Aphroditidae (Pl. XIX F). The concentration of spicules in all samples mentioned clearly shows that the polychaetes must have been eaten deliberately. In No. 5 there was a tube fragment, 1.7 mm long and 0.27 mm wide – probably from a polychaete.

Arthropods. An entire halacarid (excl. of legs) was found in No. 9 (Pl. XVII H), and copepod remains found in *Munneurycope murrayi*. All the remaining crustacean fragments appear to consist of either isopods or amphipods. Most abundant among them were pieces of body integument and fragments of mouthparts, pereopods, and uropods. In No. 19, as an example, the following amphipod fragments were preserved: Head and antennulae (Pl. XIX E), two pereonites, one pleonite, ischium-dactylus of prps. III or IV, coxa-ischium of prps. VI or VII, and four uropods. In most of the other specimens considerably fewer fragments were present.

Found in the gut of a specimen of *Munneurycope murrayi* (No. 38) was a uropod of the same species, measuring 0.75 mm (Pl. XVII J). The length of the examined specimen is 8.5 mm and its own uropod measures 1.1 mm. Thus, the length of the specimen devoured must have been about 5.5 mm, or two-thirds that of its cannibal attacker. The preserved propodus and dactylus of an amphipod or isopod (in No. 5) are also unusually large (1.5 mm) and must have belonged to a specimen of considerable size (impossible to estimate). However, the fragment comes from the gut of a specimen of *Bathyopsurus nybelini* which is about 40 mm long.

Chitinous fragments could in most cases be identified as being of crustacean origin.

Echinoderms. Found in No. 24 were two fragments of the arms of an ophiuroid (length of each joint 0.5 mm), and in several samples spine fragments of what were probably echinoids. All echinoderm remains were probably swallowed accidentally with the bottom deposits.

Unidentifiable objects include several setae of unknown origin. One is no less than 29 mm and rather stiff. It comes from the gut of the above-mentioned *B. nybelini* and is thus three-fourths the length of the entire animal. It was also found impossible to identify i. a. the serrated spine in No. 5 (Pl. XVII G) and the two chitinous fragments in Nos. 13 and 16 (Pl. XVIII O); the latter must certainly originate from a crustacean.

c. Discussion

Deposit feeding.

There can be hardly any doubt that all the benthic isopods considered – with the exception of the algae-feeding *Bathypsirus nybelini* – are primarily deposit feeders. The material at hand offered no opportunities for confirming SOKOLOVA's statement (1958) regarding a difference in the sorting of the material. In all species (of three families: Ilyarachnidae, Eurycopidae and Munnopsidae) the detritus appeared to be as coarsely sorted as that found by SOKOLOVA in *Eurycope* and *Storothyngura*. No specimens of Ischnomesidae (which according to SOKOLOVA sort the detritus much more finely) were available for study of the gut contents.

As already touched upon by MENZIES (1956b) and SOKOLOVA (1. c.), it is obvious that the food-value of the detritus greatly depends on its bacteria content. These largely consist of easily digestible proteins and lipids and many are rich in vitamins. ZOBELL (1952, 1954) and ZOBELL & MORITA (1959, p. 151) have estimated the standing crop of organic carbon in the cells of living heterotrophic bacteria to be from 0.2 to 2.0 mg per liter at the mud-water interface (where the isopods in question are believed to obtain their food), and have stressed their possible importance as a source of food in the deep-sea. Of course, a very important factor is the rate of reproduction, which is so far unknown for deep-sea bacteria *in situ*. In accordance with laboratory observations, ZOBELL & MORITA tentatively estimate a hundred or more bacterial generations per year but admit that "other dynamic factors must be evaluated before concluding that this is a reasonable estimate" (p. 151).

Diatom, radiolarian, and foraminifer tests are abundant in many samples (Table 17). As far as the foraminifers are concerned, it was mentioned above that practically all identifiable specimens were of epipelagic origin. No doubt all the tests of plankton organisms from the surface were empty when swallowed by the isopods in question, and thus without food-value. The vegetable plankton disintegrates almost entirely in the upper water layers (SKOPINZEV 1949; OHWADA 1960). No plasma even remains in shells of pteropods as large as 0.7-2.0 mm when they have sunk below 2000 m (VINOGRADOV 1962b).

Carnivorous feeding.

This is indicated by the relatively rich contents of remains of hydroids, polychaetes and crustaceans.

SOKOLOVA explains the presence of rather abundant remains of crustaceans and ophiuroids (also found by her) by suggesting that the isopods act as scavengers (necrophagi). I am not able to agree with this. In the first place, it probably occurs very rarely that dead specimens of e. g. crustaceans are encountered on the deep-sea bottom, where the overall amount of food is believed to be scarce in most places. Secondly, the general shape and the mouthparts of the deep-sea asellotes in question are not essentially different from those of e. g. *Mesidotea entomon*, which is a very active predator (GREEN 1957).

Crustaceans seem to constitute an essential part of the metazoan diet. They were found in all species studied (except *Storothyngura bentii* and three of the species of *Munnopsis*, in which there is no indication of occasional carnivorous feeding). In view of the abundance of isopods and amphipods at abyssal depths it is natural enough that most of the crustacean remains should be referred to one of these groups.

As mentioned above, there is hardly any doubt that *Storothyngura chelata* deliberately chooses hydroids as part of its diet. Apart from a dubious tube fragment in *Bathypsirus nybelini*, polychaetes appear to be eaten only by *Munnopsis longiremis* (the chaeta in *Acanthocope spinosissima* and the chaeta and jaw in *Storothyngura pulchra* (Table 17) may have been swallowed accidentally with the bottom deposits). SOKOLOVA mentioned (1. c.) that she found no polychaete remains.

The presence of ophiuroid skeleton fragments in the two largest species only (*Storothyngura herculea* and *Paropsirus giganteus*) is perhaps due to the fact that ophiuroids are only attacked by the larger species. It is also possible, however, that these fragments too were swallowed quite accidentally.

Herbivorous feeding.

There is no doubt that *Bathypsirus nybelini* feeds almost entirely on *Sargassum*. The entire intestine of all the specimens from both the Atlantic and the Pacific Oceans was packed with pieces of this alga to the exclusion of almost anything else¹. This is the first instance of an algae-eating animal from the deep-sea.

Similar pieces of masticated algae were also present in limited numbers in the related species *Paropsirus giganteus*. This may indicate that this species also feeds on algae, although not as regularly as

1. The presence of an amphipod leg fragment is an indication that the species may not feed exclusively on algae.

Bathyopsurus.¹ It is uncertain whether *Storthyngura pulchra* and *S. furcata* also choose algae as part of their diet or whether the presence of a few fragments in these two species was accidental.

It is extraordinary that algae found in all the said species were apparently fresh when eaten (cf. p. 239). This might indicate that these isopods are actually pelagic and able to ascend to the surface where the *Sargassum* weeds (and probably also the other algae in question) float around. However, both the rarity of these large isopod species and the fact that they all contained other remains which can only have been obtained on the bottom (minerals, spicules of sponges, etc.) clearly show that they are benthic at the great depths where they were collected. Thus, the algae must have been eaten very shortly after having reached the bottom from the surface layers. It seems probable that during a heavy gale large quantities of *Sargassum* (and other floating Fucales) may be forced downwards to such an extent that the vesicles burst and the plants start sinking to the bottom. In my opinion, this is the only feasible explanation for the presence of living (at the time of capture) algae in deep-sea isopods.

The rare occurrence of wood fragments in *Munniopsis longiremis* and shreds of leaves in *Storthyngura chelata* is probably an indication that the presence of these plant remains was quite accidental.

It is not certain whether *Janira operculata* which was obtained from a waterlogged tree trunk (see pp. 44 and 246) actually feeds on wood (as do certain shallow water Sphaeromidae: *Limmoria*, *Chelura* and *Sphaeroma*). The single specimen was too small to permit an examination of its intestine without the danger of damaging it.

There are only a few other examples of deep-sea animals known to feed on plant material. In *Parargissa galatheae*, J.L. BARNARD (1961, p. 56) found "bulky brown particles resembling woody debris", in addition to a few falcate flakes, small hooks (perhaps of polychaetes) and several flakes which were interpreted as bits of epidermis or comminuted muscle strands². The possibility cannot be excluded that the said brown particles could also conceivably be remains of *Sargassum* or related algae.

1. The mandibles of the genera *Bathyopsurus* and *Paropsurus* are remarkably equal and different from those of all other asellotes (cf. p. 170).

2. I have found several fragments of what must indisputably be striate muscle in *B. nybelini*, *P. giganteus* and *S. benti* (Pl. XVII F). They are of somewhat unequal size and I believe they derive from the animal itself, having been torn from the gut during dissection.

Another amphipod, *Onesimoides chelatus*, was extracted from the fruit of the *Nipa*-palm (BARNARD 1961, p. 44) and the gut content (a highly refractile fibrous material) was found to be identical in composition to the fruit meat. The contents of a specimen from another station could not be identified. BARNARD stated that "according to PIRLOT (1933) this species eats wood". This is not quite correct since PIRLOT (l. c., p. 138) only stated that *Onesimoides* had been extracted from pieces of wood. He did not examine the gut contents of this species or of *Paronesimoides lignivorus*, which was obtained from the same substratum. However, it is very likely that both feed on wood (as is also indicated by the name PIRLOT gave to the latter). The same applies to *Bathyceradocus stephensi* and *Melita lignorum* (BARNARD 1961, pp. 109, 111) and perhaps *Oradaria shoemakeri* (cf. below, p. 246).

Contrary to the view held by YONGE (1937), PURCHON (1941) and KNUDSEN (1961) find it likely that *Xylophaga* feeds on wood which may be decomposed through the action of bacteria living in the coecum. This certainly also applies to the *Teredo* recorded by WEBER (1902, p. 63) from a depth of 2053 m and by KNUDSEN (l. c.) from 5050 and 7250 m (it is, however, possible that the *Teredo* species do not belong to endemic deep-sea forms, as pointed out by KNUDSEN (p. 204)).

Finally, MORTENSEN (1938) reported that in three echinoids from 200-2000 m in the Philippines the intestinal canals were filled with bits of plants, mainly of land-plants, but also of fucacean algae. *Hygrosoma luculentum* from 400 m was also filled with plant remnants, as were two deep-sea species of *Micropyga* and *Pygmaeocidaris prionigera* (the latter found at a depth of 1960 m at Celebes). MORTENSEN expected that a vegetarian diet would prove to be common also in other regions which are rich in plant material on the bottom.

SOKOLOVA (1958) reported that herbivorous forms are very rarely found in the deep-sea. This certainly applies to the Kurile-Kamtchatka area - where her investigations took place. In that part of the world only very small amounts of plant material are carried out from land and deposited in the deep-sea. MORTENSEN may be right in stating that the echinoids mentioned will always prove to be facultative vegetarians, but on the other hand, the fact cannot be excluded that some species are so adapted to this type of food that they are restricted to areas (preferably off large rivers) where plant debris is found in sufficient quantity.

Food of the pelagic forms.

One bathypelagic species (*Paramunnopsis oceanica*) and one bathy-abyssopelagic species (*Munneurycope murrayi*) were investigated by the present author (Table 17). All six specimens had an almost empty intestine. In *Paramunnopsis* it contained only phytoplankton (generally coccolithophorids), in *Munneurycope* varying amounts of phytoplankton, and in most of the specimens mainly crustacean remains. The latter feature indicates a rather pronounced carnivorous diet (cf. below concerning the presence of sponge spicules in one specimen).

These records are not in agreement with the results arrived at by TCHINDONOVA (1959) and VINOGRADOV (1962b). The former stated that *Munneurycope* feeds exclusively on phytoplankton; in ten specimens she found no animal remains (with the exception of small amounts of medusae fragments). According to TCHINDONOVA, this plankton diet is synonymous with the shape of the mandible molar process, which she claimed to be well developed and with a large grinding surface in all filtrate-feeding phytophages. In contradiction, she stated that all carnivorous, bathy- and abyssopelagic decapods, euphausiids, amphipods and mysids investigated have a reduced molar process (or a reduction of the grinding surface) but a strongly developed cutting edge on the mandible. However, *Paramunnopsis oceanica* – as well as the two other pelagic species of *Paramunnopsis* – are characterized by having a greatly reduced, triangular molar process totally devoid of a grinding surface (cf. Table 9, p. 185).

Since I am convinced that TCHINDONOVA's claim is correct, that the molar process in pelagic carnivores is actually reduced, I suggest that *Paramunnopsis* is

also carnivorous – in spite of the fact that the single specimen studied gave no indication of this.

As far as *Munneurycope murrayi* is concerned, this species is probably not a true pelagic form. This can be seen by the curious presence of spines belonging to various species of sponges found in one of the specimens (No. 32) (cf. p. 242 and Pl. XIX P). The species was taken at a depth of about 600 m (1800 m wire), the depth to the bottom being at least 2000 m. Judging by the method of capture, *M. murrayi* is typically pelagic. It seems to have been collected at no less than 45 stations¹ (in the Atlantic, Indian Ocean and North Pacific – cf. p. 161) and consistently by means of a pelagic net, often towed over great depths. The only exception appears to be *Albatross* St. 4765 where specimens were collected with a bottom trawl (p. 157). Nevertheless, the presence of sponge spicules in No. 32 clearly shows that it is able to take at least part of its food from the bottom.

It is interesting to note that as a result of his analysis of the intestines of various amphipods, BARNARD (1961, p. 24) found that "several species thought to be strictly pelagic were shown to feed on the bottom, the evidence pertaining to mineral particles in the gut contents".

The mouthparts of *M. murrayi* are not essentially different from those of its closest relative, the benthic *M. harrietae* (p. 162), the main difference being that it has much fewer setae on the proximal joints of the maxillipedal palp. A similar paucity of setae is, however, found in many benthic species of the same family, e. g. in *Eurycope*.

1. This is exclusive of the unpublished data on the occurrence in the Kurile-Kamtchatka area (TCHINDONOVA 1959).

F. Habitat

1. BENTHIC OCCURRENCE

Substratum

It is not possible to gain a great deal of information from a study of the type of bottom on which the *Galathea* asellotes were caught. This is partly because the material is relatively small and scattered, partly because the short descriptions of the character of bottom deposits are only rough estimates (cf. BRUUN 1959, p. 21) – although they were practically always recorded by the same person throughout the expedition (the present author). Geological examinations of grain size, etc. are not yet available.

The species were collected from the following types of bottom (the ciphers in parenthesis give the number of records from the said type of bottom; species marked * were collected on different types):

Pumice in large quantities (no record of other deposits): *Dendromunna mirabile*, **Storthyngura benti*.

Sand (black): *Ilyarachna aspidophora*, *Eurycope gibberifrons*.

Sand and clay (mostly with stones): **Stenetrium abyssale*, *Haploniscus kermadecensis*, **Ischnomesus spärcki*, *I. birsteini*, **Ilyarachna kermadecensis*

(2), **Storothyngura benti*, **S. furcata*, *Munnopsis bathyalis*.

Clay (bluish, brown or dark, sometimes with pumice or stones): **Stenetrium abyssale*, *Ischnomesus bruuni*, **I. spärcki*, **I. roseus*, **Ilyarachna kermadecensis*, *Acanthocope galathea*, **Storothyngura benti* (3), **S. furcata* (2), *S. pulchra kermadecensis*, **S. p. pulchra*, *S. serrata*, *Eurycope madseni*, *E. galathea*, *Munneurycope menziesi*, **Bathyopsurus nybelini* (4)¹.

Muddy clay: *Janthura abyssalis*, *Ischnomesus planus*, **I. roseus*, *Macrostylis hadalis*, **Storothyngura p. pulchra*, **Paropsurus giganteus*, **Munnopsis longiremis*².

Very stiff clay: *Macrostylis galathea*, **Eurycope complanata*³.

Globigerina ooze: *Haploniscus helgei*, *Mixomesus pellucidus*, *Storothyngura abyssalis*, *Munneurycope harrietae*, **Bathyopsurus nybelini*, **Paropsurus giganteus*.

Pteropod ooze: *Ischnomesus anacanthus*, *I. sp.*

Only three species have been taken more than once on the same type of bottom (and only within a limited area in the Kermadec Trench). Five species are recorded from both sand & clay and clay alone, two from clay and muddy clay, one from clay and globigerina ooze, and one from muddy clay and globigerina ooze.

Although some of these deposits may not actually differ much in physical and chemical condition it seems that the present isopods are not strictly confined to a special type of bottom. Since comparisons of the type of bottom recorded in the various reports on deep-sea asellotes are subject to a great deal of uncertainty, and since the importance of the substratum character for the occurrence of this group is unknown, no further conclusions will be drawn from the present data.

In the remarks on the description of *Dendromunna mirabile* (p. 69) it was pointed out that there was reason enough to presume this species lives on sponge colonies – as do (probably) other members of the family Dendrotonidae.

A special substratum was found in the case of *Janira operculata* which was found inside a water-

1. The bottom deposit at the three stations where this species was previously caught was "red clay, poor in calcium carbonate" (NYBELIN 1951).
2. Recorded by RICHARDSON (1912b) from "globigerina ooze, corals, and mud".
3. Recorded by BONNIER (1896) from mud ("vase").

soaked tree trunk, dredged from the bottom at a depth of about 3300 m. There seems to be only one other record of isopods obtained from plant debris on the bottom. In his preliminary report on the results of trawlings during the *Siboga* Expedition, WEBER (1902, p. 63) recorded a small, specialised fauna associated with plant material: "Teredo et divers autres Bivalves, Ophiurides de coloration blanche, Chitons, Annélides, parfois aussi des Actinies et des Isopodes, tels étaient les hôtes très constants de ces débris végétaux". Apparently, none of the *Siboga* isopods and tanaids treated by NIESTRASZ (1913, 1931, and 1941) were collected from plant debris. Thus, the isopods to which WEBER refers are probably asellotes – this group of *Siboga* isopods having not yet been worked up.

WEBER (l. c.) was in some doubt as to whether animals found in the plant remnants had arrived there after the plant material subsided to the bottom or whether the animals had been able to survive the transition from the surface to the bottom (a matter of several thousand metres). In the case of the amphipod *Onesimoides chelatus* which the *Siboga* obtained from a piece of wood at a depth of 2053 m, PIRLOT (1933, p. 138) is quite convinced that this species is a typical representative of abyssal depths. During the *Galathea* Expedition 20 specimens of *O. chelatus* were collected inside one *Nipapalm* fruit, 58 specimens inside another (J.L. BARNARD 1961, photograph on p. 45). Other amphipods found in sunken wood are: *Paronesimoides lignivorus* (PIRLOT 1933, p. 143) and possibly *Oradaria shoemakeri* and *Bathyceradocus stephensi* (PIRLOT 1934, pp. 201 and 229). The latter species was actually collected by the *Galathea* from a sunken tree trunk (BARNARD l. c., p. 109). BARNARD also records *Melita lignophila* n. sp. from a similar substratum (p. 111).

J. KNUDSEN (1961) has – in connexion with the description of no less than 17 new species of the bivalve genus *Xylophaga* from plant debris, collected by the *Galathea* – reviewed several other instances of the special fauna of this highly specialised habitat. It is essential that future deep-sea expeditions should likewise devote attention to detailed examinations and make records of the remnants of terrestrial vegetation found on the sea bottom at all depths. This material serves not only as a substratum and a source of food for vegetarian bottom animals, but also as a food basis for bacteria and protozoans, which again, represent the first link of a food chain for all kinds of benthic feeders (BRUUN 1957, 1959).

It is extremely unlikely that the two other, very long-legged species, *Ischnomesus roseus* and *Acanthocope galathea*, captured at the same station as *Janira operculata*, also live in sunken wood.

The contents of algae and wood in the intestines of a few species (cf. p. 239) are indication that these also rely on plant debris.

2. PELAGIC OCCURRENCE

The larger majority of free-living isopods are benthic. A purely pelagic occurrence applies only to the larvae of Epicaridea, the genus *Xenuraega* Tattersall and *Barybrotus* Schiødte & Meinert, to species of *Eurydice* Leach within the Flabellifera, and four or five species of Asellota (cf. below). This is in strong contrast to the amphipods. In a recent survey of the abyssal amphipods, J.L. BARNARD (1961, p. 118) records 272 species but 106 of these are definitely pelagic (bathy- or abyssopelagic) while others are dubious or possibly inhabit pelagic hosts (e. g. tunicates and medusae). Thus, of a total of 272 abyssal species, only 81 are definitely benthic and 78 are probably benthic rather than pelagic.

The four probably exclusive pelagic asellotes are: *Paramunnopsis oceanica* (Tattersall), *P. longicornis* (Hansen), *P. spinifer* (Vanhöffen): Taken almost exclusively in nets operating pelagically (cf. p. 186).

Desmosoma chelatum Stephensen: Taken on one occasion in the Mediterranean near the surface (25 m wire); depth to bottom: 600 m. However, the furthest distance from land (Corsica) was only c. 20 km so it is possible that this is not a truly pelagic species (cf. HANSEN 1916, p. 5).

In addition, *Munneurycope murrayi* should probably be regarded as a demersal species, occasionally seeking its food on the bottom (cf. the discussion on diet, p. 245).

It is also possible that some of the little known species of *Munnopsis* are either pelagic or demersal (cf. Table 9, p. 185). The wide distribution of *Bathyporus nybelini* and *Paropsurus giganteus*, and their parchment-like integument, may indicate that they are demersal – although they do seek their food on the bottom.

I have only succeeded in finding two additional records of a pelagic occurrence. (1) SCOTT (1905, table III) found on one occasion among 68 plankton samples from the Firth of Clyde a single *Jaera albifrons* (and on another occasion one *Gnathia maxillaris* (Montagu)). These are no doubt casual stray-occurrences. (2) TCHINDONOVA (1959) recorded that *Storothyngura herculea* was taken in a pelagic haul from 5000-0 m (depth to bottom: 7000 m). The integument of the pelagically occurring specimens was thin and transparent, in contradiction to the calcified integument of other specimens of *herculea* taken with a bottom trawl in the same locality. The gut contents in the pelagic specimens (diatom ooze, etc.) indicate that they seek their food on the bottom and are able to make vertical migrations of at least 2000 m.

Apart from this one extraordinary record and the pelagic species mentioned above, there is not much evidence that even the more active asellotes move far from the bottom. The afore-mentioned record of a pelagic *Jaera albifrons* indicates that while lacking natatory legs, the species actually can swim (as can also *Asellus aquaticus*). On the other hand, three species of *Pleurogonium* kept in aquariums, have never been seen to swim (HULT 1941, p. 126). HULT has observed that two species of *Desmosoma*, which have oar-shaped pereopods V-VII, only swim for very short distances and then, only if alarmed. He recorded that the natatory legs in *Munnopsis typica* are capable of two different swimming movements – the second one depending on the animal becoming alarmed. After the swimming period, it continued to move “slowly about in the ordinary creeping manner” (SARS 1899, p. 134). Finally, *Eurycope mutica* is a particularly rapid swimmer, but “like *Munnopsis* it sat still most of the time except for a few breaks for some quick swimming strokes” (HULT l. c., p. 131). On a soft bottom it “moved nimbly and easily with the anterior pereopods”.

Thus, it seems that the majority of the species of asellote families with oar-shaped pereopods V-VII are benthic, but that they may occasionally swim away from the bottom for a short or longer period.