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The systematics and evolution of *Haplomunna* and its relatives (Isopoda, Haplomunnidae, New family)

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Introduction

Haplomunna caeca (Richardson, 1905), based on a single individual, has been a poorly known species since it was first described. In the original description Richardson placed it in *Munna*. In 1908 she erected the genus *Haplomunna* for this species in a footnote, but did not give any generic diagnosis. Menzies (1962 a) stated that *Haplomunna caeca* did not belong in the Munnidae but could not place it in a family. Wolff (1962) also relegated *H. caeca* to *incertae sedis*. In spite of Richardson's somewhat confusing illustration it was possible to determine from the description that *Haplomunna* might be related to some genera that were considered recently by Wilson & Hessler (1974). An examination of the holotype of *H. caeca* disclosed that Richardson's original description was generally correct but inadequate in terms of our modern taxonomy. After examining *H. caeca*, three specimens of a new species of *Haplomunna* were found in the Scripps Institution of Oceanography Benthic Invertebrate Collection.

This paper presents the new information gained from the inspection of this material and of isopods from Dr. Robert R. Hessler's collection. The enigmatic nature of *Haplomunna* is resolved with diagnoses for the genus, the type species, and a new species. Elucidation of the relationship between this genus and *Munella*, *Abyssaranea* and *Thylakogaster* permits the diagnosis of a new family. In order to come to conclusions regarding the Haplomunnidae, the Dendrotionidae are discussed using new information, and a hypothetical phylogeny for both families is presented. For the use of laboratories studying the deep-sea benthos, new geographic information on the Haplomunnidae and a key to the genera are given.

Systematic position of *Haplomunna* and related genera

Desire to examine *Haplomunna* was based on the suspicion that it bore affinity to *Thylakogaster*, *Munella* and *Abyssaranea*, and that it may be the most primitive of the four. All these genera have a small-to-minute uropod at the ventral margin of the pleotelson, a robust subchelate pereopod I, all other pereopods ambulatory, prominent corporal spines, particularly on the pleotelson, an antennula with many articles and aesthetascs, and an anus covered by the opercular pleopods. Though *Haplomunna*, *Thylakogaster*, *Munella* and *Abyssaranea* are superficially different when compared one to another, they nevertheless all have these basic similarities that, at the same time, prevent their inclusion in any previously defined paraselloid family (see discussion in Wilson & Hessler, 1974). It is these similarities that reveal a natural relationship between these genera distinct enough to merit the formal erection of a new family.

The greatest systematic problem involved with defining this new group is posed by a comparison of *Haplomunna* and *Acanthomunna* Beddard (1886). *Haplomunna* closely resembles some species of *Acanthomunna* (*A. tannerensis* Schultz (1966), for example) in details of body form such as the elevation and shape of the pleotelson, the shape and sculpturing of the body and cephalon, distribution of spines and the shape of the first pereopod. The author feels, with Wolff (1962), that *Acanthomunna* belongs in the Dendrotionidae since some species have morphologies found in other genera of this family (see fig. 1). *Acanthomunna* and the other dendrotionids, *Dendrotion* Sars (1872) and *Dendromunna* Menzies (1962 b), have large biramous uropods that are positioned dorsolaterally on the pleotelson. *Acanthomunna proteus* Beddard (1886) and species like it have an extremely long stylet on pleopod I, a feature which also appears in *Dendromunna* and *Dendrotion*. Some species of *Acanthomunna* exhibit an elongation of body and reduction of the pleotelson characteristic of other dendrotionids. In all three genera the tip of the pleotelson extends well beyond the insertion of the uropods and is acutely pointed (the males of some species of *Acanthomunna* have a tip that is truncate, flat and shelf-like). All dendrotionids are also similar in the spininess of their bodies and limbs, and in the morphology of the antennula, although these characters are not particularly unique.

To place *Haplomunna* (see fig. 3(*a*)) in the Dendrotionidae with *Acanthomunna* would seriously weaken the concept of that family; the tiny uropod of *Haplomunna* is very uncharacteristic of the Dendrotionidae. *Acanthomunna* does not even offer an intermediate condition for this situation; if anything its

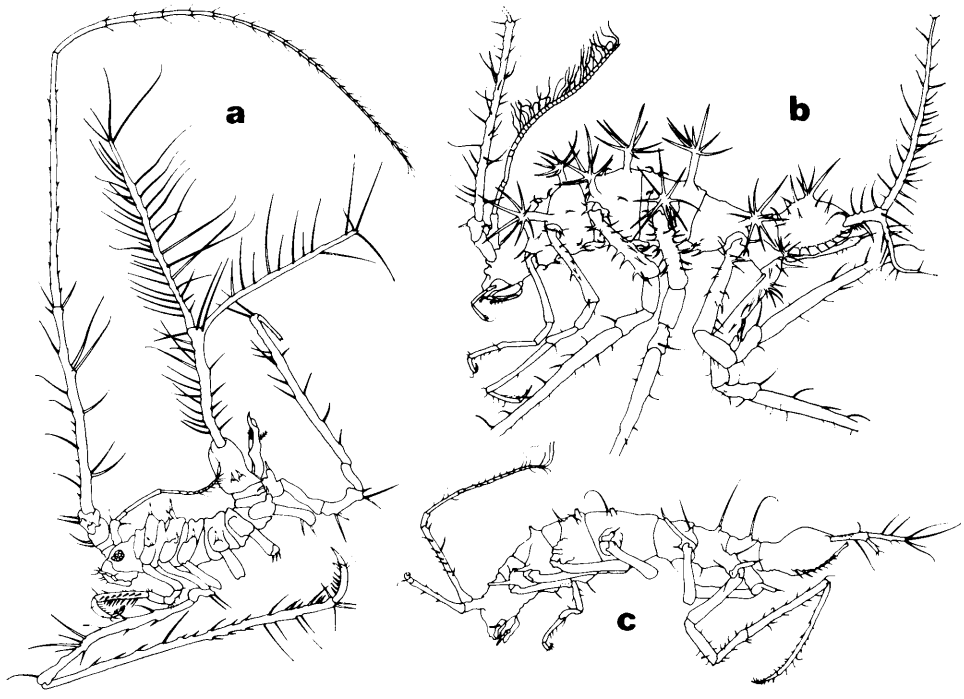

FIG. 1. Genera of the Dendrotionidae in lateral views. (*a*) *Acanthomunna* (after Vanhöffen, 1914); (*b*) *Dendromunna*; (*c*) *Dendrotion*. (*b*) and (*c*) are undescribed species.

uropods are incredibly hypertrophied (e.g. *A. spinipes* (Vanhöffen, 1914)). On *Acanthomunna* and other Dendrotionidae the uropods are dorsolateral in position while they are ventral on *Haplomunna*—a clear distinction. The tip of the pleotelson of *Haplomunna* is foreshortened and does not exhibit the sloping, pointed tip of the Dendrotionidae.

On the basis of these observations and the foregoing conclusions, a phylogeny can be suggested. The basic assumption is that all the above-mentioned genera developed from a long-legged, shallow-water janirid-like isopod with the following characteristics: antennula with articles 3 and 5 longer than the short article 4, uropod with a protopod and two well-developed rami (but not hypertrophied), the tip of the pleotelson pointed and extending well beyond the uropods, eyes present, pereopod I fairly strong with a robust carpus, and the antennae fairly long, matching perhaps the long legs. This creature would be similar in body form to *Haplomunna* and is most like *Acanthomunna* in the characters mentioned. Development toward the *Haplomunna* form proceeded with a reduction in the uropods and their migration ventrally. Since this radiation probably took place in the deep sea (all the present genera have distributions that reach into the bathyal or abyssal), the eyes were lost fairly early (Hessler & Thistle, 1975).

A trend of reductions in the uropod to two short segments, in the size of the antenna, and in the seventh pereopods and pereonite gave rise to the present day *Munella*, and continued further to produce the very specialized *Abyssaranea*. This genus has a small single-segmented uropod, a short antenna and a nearly absent seventh pereonite. Since *Munella* is still found in depths as shallow as 100 m (LoBianco (1903); in the Bay of Biscay) and still retains the extension of the pleotelson, it must be the more primitive member of this side line.

In another type of specialization the pleotelson of the ur-*Haplomunna* became enlarged and spinier, and underwent reductions of the pleotelson tip and the uropods. From this, the line leading to *Thylakogaster* was characterized by a reduction and fusion of the uropodal rami with the protopod, but special adaptations with the pereopods and mouthparts produced the unique morphology of this genus. The ur-*Haplomunna* became *Haplomunna* when the uropod reduced to a single segment, probably one of the rami. Thus, while *Haplomunna, sensu stricto* is specialized, the genus approximates the ancestral form in general.

In this phylogenetic scheme, *Acanthomunna* is a primitive morphology; the retention of eyes on *Acanthomunna* and its occurrence in shallow bathyal environments as well as in deep water favours this contention. The similarity between *Haplomunna* and *Acanthomunna* is explained as commonality of ancestry from which the latter is least modified. Convergence from unrelated groups to a common body form would be difficult to argue because the similarities are so many between these two genera.

Structural modifications within the Dendrotionidae took a different direction than in the genera with a small uropod. There is an overall tendency to elongate and narrow the body, to displace the uropods dorsally and to reduce the size of the first pereopod. These features appear in *Acanthomunna* on some species, but are most evident in *Dendromunna* and *Dendrotion*. An increase in size of the uropods also characterizes the dendrotionid line of radiation, although the

endopod of *Dendrotion* has been secondarily reduced (the protopod is still long on most species).

This proposed phylogeny serves to illustrate the basic difference between the Dendrotionidae and the four genera that have small uropods. While the presence of eyes and the condition of the uropods are the only characters which definitively separate *Acanthomunna* from *Haplomunna,* these two genera must belong to different evolutionary lines

Thus, in spite of the similarities of *Acanthomunna* with *Haplomunna* which blur the distinctiveness of the taxon composed of *Haplomunna, Thylakogaster, Munella* and *Abyssaranea,* there is good reason to separate these genera as a new family. This group should be called Haplomunnidae, after the genus *Haplomunna* which appears to be the least modified member of the family.

Taxonomy

HAPLOMUNNIDAE, fam. nov.

Synonym: Dendrotionidae Wolff, 1962, p. 64, pars.
Type genus: *Haplomunna* Richardson, 1908.
Genera included: *Haplomunna*, Richardson, 1908; *Munella*, Bonnier, 1896; *Thylakogaster* Wilson & Hessler, 1974; *Abyssaranea* Wilson & Hessler, 1974.

Diagnosis: Cephalon without eyes. Body with spines, generally deep, with posterior pereonites compressed and reduced. Antennula with many articles and aesthetascs, with a tendency for female to have fewer than male. Antenna with four proximal articles short and roughly same size, articles 5–6 much longer. Pereopod I strongly developed, subchelate, with major hinge between carpus and propodus. Pereopods II–VI, and VII, if present, longer than body, increasing in length posteriorly; those pereopods used for locomotion are ambulatory. Uropods greatly reduced, with no more than two segments, on or near ventral margin of pleotelson. Anus covered by opercular pleopods.

Discussion: Two subgroups can be discerned within the Haplomunnidae. *Munella* and *Abyssaranea* are distinctly related by a number of characters (Wilson & Hessler, 1974): pereonite 7 reduced and pereopod VII absent; pleotelson at most only slightly elevated from longitudinal axis of pereon; frons-clypeal ridge of cephalon not well developed; antenna as long as body or shorter, not longer; antenna with approximately seven articles in flagellum; opercular pleopods without spines. The second group, *Haplomunna* and *Thylakogaster*, is not as clearly intra-related as the first, mainly due to the uniqueness of *Thylakogaster*'s morphology. However, both have an elevated pleotelson, a well-developed frons-clypeal ridge, antennae that are much longer than the body, many more than seven articles in the antennal flagellum, and opercular pleopods with spines.

One interesting feature of the Haplomunnidae is that some genera are neotenic (i.e. have larval characters in the adult). *Munella* and *Abyssaranea*, as mentioned above, completely lack the seventh pereopod. Individuals of these genera could conceivably be confused with the manca I stage, although the presence of sexually mature adults in this condition precludes this possibility. The ' adult manca ' occurs fairly frequently in deep-sea Paraselloidea; an in-progress survey of the Atlantic isopod collection curated by this laboratory has revealed that the following groups lack the seventh pereopod: *Munella* and *Abyssaranea* (Haplomunnidae); *Dendromunna* and a species of *Dendrotion*

(Dendrotionidae); *Lipomera*, a related undescribed genus, and a species of *Munnopsurus* (Eurycopidae); and a species of *Haplomesus* (Ishnomesidae). Since this syndrome appears in completely unrelated and adaptively different groups it is clear there is no one reason for its presence.

However, for *Munella* and *Abyssaranea* the lack of the last leg may be explicable in light of the shape of the body of *Haplomunna* and *Thylakogaster*. Both of the latter genera have a dorsal flexure of the body such that the pleotelson is at an appreciable angle to the long axis of the body. In the above two genera and in unrelated taxa such as *Munna globicauda* Vanhöffen (1914), the flexure is found in the adult.

It is suggested that both morphologies found in the Haplomunnidae relate to the long-legged ambulatory habits of these animals. These habits may intensify selection to make the body easier to balance—in this case, more compact. The presence of reduced abdomens in very different arthropod groups (opilionid arachnids, decapod crabs, and pycnogonids) demonstrates that this selection must be important. Since the pleopods of haplomunnids supply the branchial structure, the pleotelson cannot be reduced as much as in the pycnogonids. As a result, we see two different answers to the same problem. Merely by retraining morphologies normally passed through in ontogeny, *Munella* and *Abyssaranea* have become adult in the manca form and, as a consequence, have reduced the long axial length of the body. *Abyssaranea* has continued this trend by compressing the abdomen forward. *Haplomunna* and *Thylakogaster*, on the other hand, have a dorsal flexure, thus balancing the body by putting the abdomen on the back.

Key to the genera of the Haplomunnidae

1 a Body with seven well-developed pereonites and pereopods 2
1 b Pereonite 7 reduced, pereopod VII absent 3
2 a Pleotelson huge, balloonlike, forms acute angle with longitudinal axis of pereon; mandibular palp absent . . . . . ***Thylakogaster***
2 b Pleotelson only partially expanded, forms obtuse angle with longitudinal axis of pereon; mandibular palp present . . . . . ***Haplomunna***
3 a Uropod with two articles; antenna same length as body . . . . . ***Munella***
3 b Uropod with one article; antenna shorter than body . . . . . ***Abyssaranea***

Geographic distribution

Since the description of *Thylakogaster*, *Abyssaranea* and the new species of *Munella* (Wilson & Hessler, 1974), new specimens of these three genera have been found. Although this material is too incomplete to formally describe, the geographic data provided by these specimens are interesting and may eventually give some insight into the past history of the Haplomunnidae. Data are given for each genus.

Haplomunna is known only from the abyssal waters off southern and Baja California in the Pacific.

Thylakogaster has the broadest known distribution of the Haplomunnidae; it has been found in the Atlantic near the Equator, in the Argentine Basin and on the Bermuda Slope at depths from 1135 m to 5223 m. New records are: north off Surinam ,WHOI (Woods Hole Oceanographic Institution) station 303, 8° 28·8′ N, 56° 4·5′ W, 2842–2853 m; south-west off Ireland, WHOI station 328, 50° 4·7′ N, 15° 44·8′ W, 4426–4435 m; east equatorial Pacific SIO

(Scripps Institution of Oceanography) station H-84, 3° 1·9′ N, 125° 0·8′ W, 4435–4438 m.

Munella has its known centre of vertical distribution in the bathyal deep sea; it has been found in the central Mediterranean, in the Bay of Biscay and on the Bermuda Slope in the Atlantic at depths from 100 to 1153 m. A new record is in the Atlantic, north of Surinam, WHOI station 299, 7° 55·1′ N, 55° 42·0′ W, 1946–2076 m.

Abyssaranea has been found in the equatorial Atlantic at depths of 3458–3783 m. A new record is in the east equatorial Pacific, SIO station H-84, 3° 1·9′ N, 125° 0·8′ W, 4435–4438 m. In the three stations where *Abyssaranea* has been collected, it co-occurs with *Thylakogaster*.

Haplomunna Richardson, 1908

Type species: *Haplomunna caeca* (Richardson, 1905).
Synonym: *Munna* (Richardson, 1905, p. 483) pars.

Diagnosis: Cephalon without eyes, rounded in dorsal view, much narrower than pereonite 1, with moderately developed frons-clypeal ridge and antennae raised on low projection. Body deep, ovate, in lateral view humped; first four pereonites of similar length. Dorsomedial portion of last three pereonites strongly compressed forward; lateral portions angling backward, with pereonites 6 and 7 extending underneath elevated pleotelson. Longitudinal axis of pleotelson nearly perpendicular to that of pereon; somewhat bilobed anteriorly, heart-shaped in dorsal view; smooth distal tip small, produced ventroposteriorly. Body surfaces and edges spinose, with two distinctly different sizes of spines: large robust spines, often on raised portions of cuticle, and small thin spines (Richardson's ' stiff hairs '); pereonites 5–7 with spines only on lateral edges, dorsal surfaces smooth. Dorsal surfaces of anterior pereonites sculptured, often with parallel transverse ridges arching across dorsum. Antenna at least 1·5 times longer than body, with many flagellar articles. Mandible normally formed; molar process truncate with two distal ridges: one ridge finely denticulate; other ridge with inner row of stout spines, and outer row of long, sharp, minutely serrate spines; lacinia mobilis and incisor process each with four teeth. Maxillipedal palp with segment 2 distinctly broader, segment 3 only slightly broader than segment 1; epipod approximately as long as basis, tapering distally. Pereopod I strong, subchelate; carpus somewhat elongate; distinct rows of many stiff, unequally bifid setae on occlusive margins of both carpus and propodus. Pereopods II–VII essentially similar to each other, longer than body, increasing in length posteriorly. All pereopods with two dactylar claws. Developing oostegites distinct on preparatory female. Opercular pleopods with strong spines. Uropod tiny, with single article, on ventral margin of pleotelson, directed ventroposteriorly. Anus covered by opercular pleopods.

Discussion: At the present time, *Haplomunna* has been collected only from the abyssal floor at the base of the Patton Escarpment off southern and Baja California. Members of this genus that we have examined have been uncharacteristically large for entirely ambulatory, deep-sea isopods, a feature that they share with a number of other isopod genera from this area. A robust, spiny body with an arched back and an elevated pleotelson with a tiny uropod

produce in creatures of this genus an appearance that is easy to recognize. Males have never been collected so we can only surmise that they are similar to the females though perhaps with a smaller maximum size, as this is the case with related genera.

Haplomunna caeca (Richardson, 1905)

(Figs. 2- 3)

Synonym: *Munna caeca* Richardson, 1905.

Holotype: Brooding female, cephalon-pereon length in lateral view (measured from clypeus to lateral extremity of pereonite 7) 5·7 mm, USNM (United States National Museum) catalogue number 32072.

Type locality: Pacific Ocean, off southern California. Albatross station 4390, 33° 2·15′ N, 120° 42·0′ W, 3998 m.

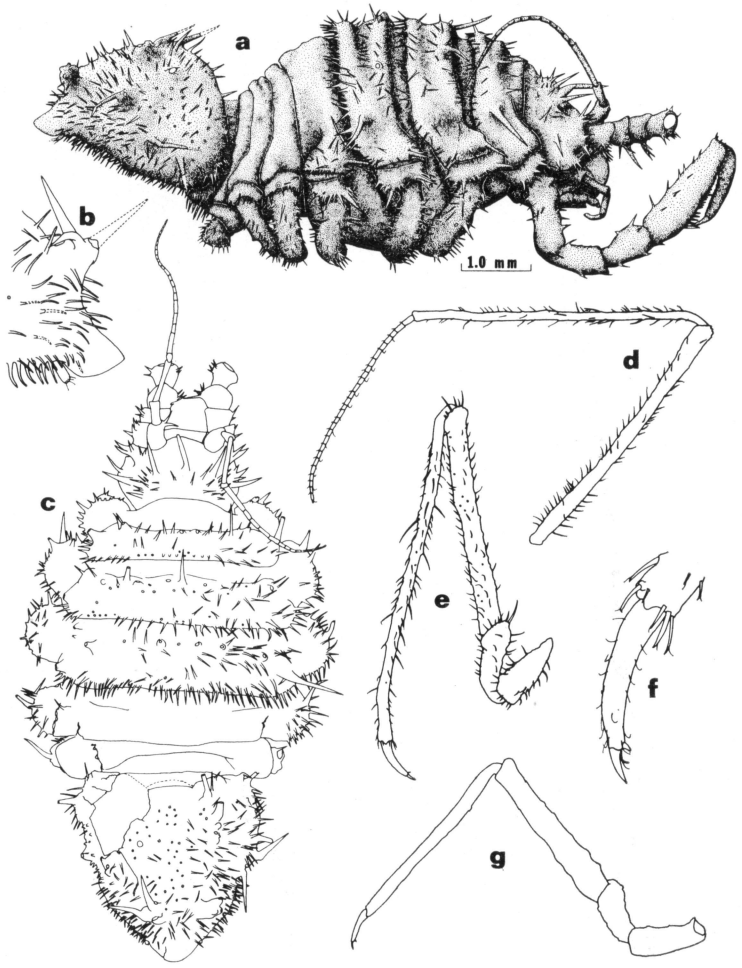

FIG. 2. *Haplomunna caeca* holotype, brooding female: (*a*) right lateral view; (*b*) left lateral view of pleotelson tip and three-spined tubercle; (*c*) dorsal view; (*d*) antenna; (*e*)–(*f*) posterior pereopod ((*e*) entire limb, (*f*) dactylus); (*g*) anterior pereopod without setae drawn. (*d*)–(*g*) were detached from holotype but in same vial.

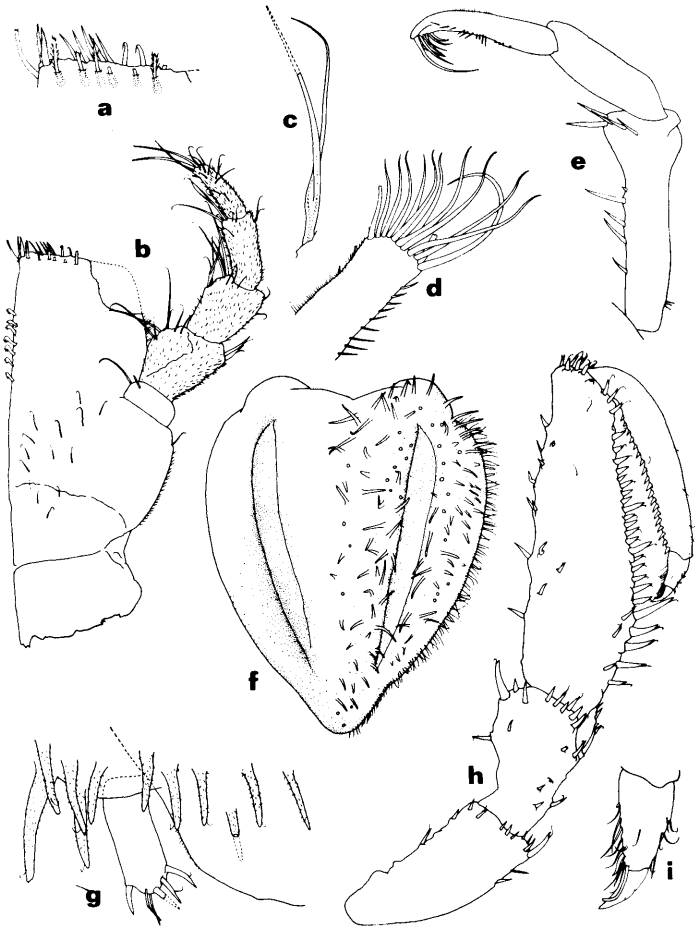

FIG. 3. *Haplomunna caeca* holotype: (*a*)–(*c*) maxilliped ((*a*) distal tip of endite; (*b*) entire appendage, epipodite missing; (*c*) equally bifid seta on inside margin of palp article 3); (*d*)–(*e*) palp of mandible drawn *in situ* ((*d*) distal tip, (*e*) entire appendage); (*f*) pleopod II; (*g*) left uropod, lateral view; (*h*)–(*i*) right pereopod I drawn *in situ* ((*h*) entire appendage, basis excluded, in lateral view, (*i*) dactylus). (*b*) and (*f*) were detached from holotype but in same vial.

Diagnosis: Surface of body with very many small spines in addition to large spines. Dorsal surface of pleotelson with pair of large stout protuberances posteriorly, each with three large spines distally. Body well sculptured, troughs between raised cuticular ridges of pereonites 1 and 2, 2 and 3 pronounced; ridge on pereonite 1 not strongly developed; lateral margins of cuticular ridges on pereonites 1–4 not marked by cuticular infolding.

Additional description: Body not heavily calcified (possibly a preservation artifact). Antennula approximately 3·9 mm long, 0·68 cephalon-pereon length, with 24 articles; third article very long, fourth article very short, 2·2 and 0·3 times length of article 2 respectively.

Antenna approximately 12 mm long, 2·1 cephalon-pereon length; article 6 slightly longer than article 5; flagellum 0·76 length of article 5, with 28 articles.

Mandibular palp with 13 curved setae on truncate distal tip, seta on dorsal corner much longer than other setae.

Maxilliped with seven coupling hooks; basis and endite length double the width. Pereopod I with 25 and 19 unequally bifid setae on occlusive margins of carpus and propodus respectively.

Of ambulatory pereopods (preserved but separated from holotype), propodus around 1·3 length of carpus on anterior pereopods while propodus approximately 1·6 length of carpus on more posterior pereopods.

Uropod more or less cylindrical, rounded distally, with two broom setae and four strong unequally bifid setae.

Remarks: The above description and diagnosis were made from the same individual that Richardson used in her 1905 monograph. As far as is known this species has not been collected since the Albatross collection was made. As can be seen in the drawing (fig. 2 *c*) the holotype has a damaged pleotelson. Figure 3 (*a*) of *H. hubbsi* sp. nov. illustrates the proper form of the body, and is probably equally applicable to this species. *Haplomunna caeca* can be immediately recognized by the three-spined protuberances (fig. 2 *b*) on the pleotelson and the many fine spines on the body surfaces.

Haplomunna hubbsi sp. nov.

(Figs. 4–5)

Etymology: This species is dedicated to Dr. Carl L. Hubbs whose collecting programmes in abyssal waters off the Patton Escarpment and elsewhere have brought to light many poorly known fishes and invertebrates, including this new species.

Holotype (fig. 4): Preparatory female, cephalon-pereon length in lateral view 7·6 mm, USNM catalogue number 154170.

Type locality: Pacific Ocean, off Baja California. SIO (Scripps Institution of Oceanography) station 70-94, 31° 14·4′ N, 120° 09·6′ W to 31° 36·0′ N, 120° 07·4′ W, 3706–3806 m; collected in 25 foot otter trawl.

Other material: Brooding female, SIO station 70–94 (fig. 5); preparatory female, SIO station 70–92, 31° 47·0′ N, 120° 12·0′ W to 31° 18·8′ N, 120° 14·8′ W, 3950–3880 m, collected in Isaacs-Kidd midwater trawl (struck bottom). This additional material is kept in the Scripps Institution of Oceanography Benthic Invertebrate Collection.

Diagnosis: Surface of body with few small spines and many large spines. Dorsal surface of pleotelson lacking pairs of posterior spinose protuberances, but with two large spines in their place. Troughs between raised cuticular ridges of pereonites 1 and 2, 2 and 3 not pronounced; ridge on pereonite 1 strongly developed, bulging; lateral margins of cuticular ridges on pereonites 1–4 demarcated by cuticular infolding (possibly the external expression of apodemes).

Additional description and differences from H. caeca: All specimens of this species that we have examined are around 2 mm larger than the holotype of *H. caeca* which was an adult female. Body heavily calcified with a shiny surface.

Antennula with 26–28 articles. Antenna with 32 flagellar articles.

Mandible with eight finely serrate setae next to lacinia mobilis, and ten stout and ten long minutely serrate setae on molar process. Palp with nine

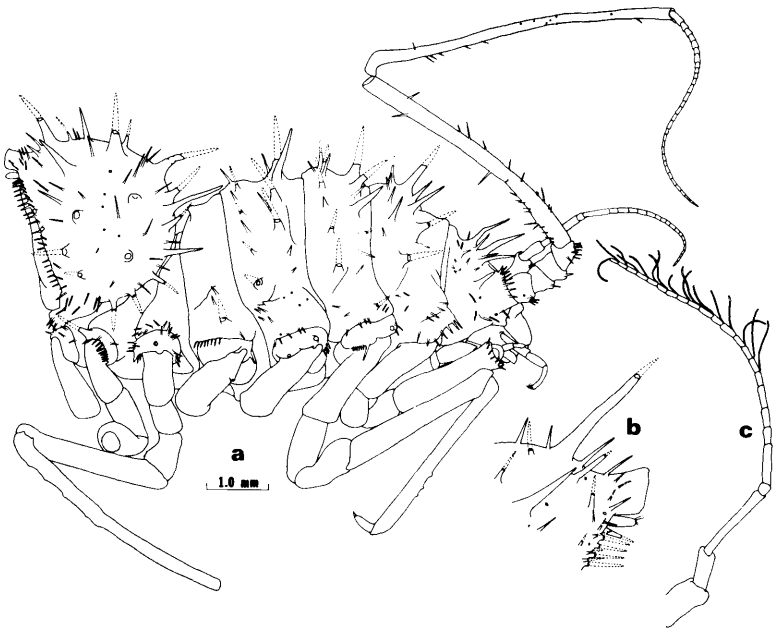

FIG. 4. *Haplomunna hubbsi*, sp. nov. holotype, preparatory female: (*a*) right lateral view; (*b*) distal tip of pleotelson, left lateral view; (*c*) antennula.

curved setae on truncate distal tip; setae on dorsal corner only slightly longer than other setae.

Maxillipedal epipod two times longer than wide, with setae on lateral edge and on ventral surface.

Remarks: As in *H. caeca*, this species is only known from females. It is interesting to note that *H. hubbsi* was collected roughly 100 miles south of the type locality for *H. caeca*. This large species can easily be recognized by its paucity of fine spines, the many large spines, the lack of the three-spined protuberances characteristic of *H. caeca* and by the heavily calcified, shiny cuticle.

Summary

A re-examination of *Haplomunna* Richardson (1908) reveals a close relationship between this genus and *Munella* Bonnier (1896), *Abyssaranea* Wilson & Hessler (1974) and *Thylakogaster ibid.* As a consequence, a new family, Haplommunidae, is erected to contain these four genera. The systematic problems with this new grouping, its relation to the Dendrotionidae, and some peculiarities of its members are discussed. A key and the geographical ranges of the four genera are included. A generic diagnosis for *Haplomunna* is given, and *H. caeca* (Richardson, 1905) and *H. hubbsi*, sp. nov. are described.

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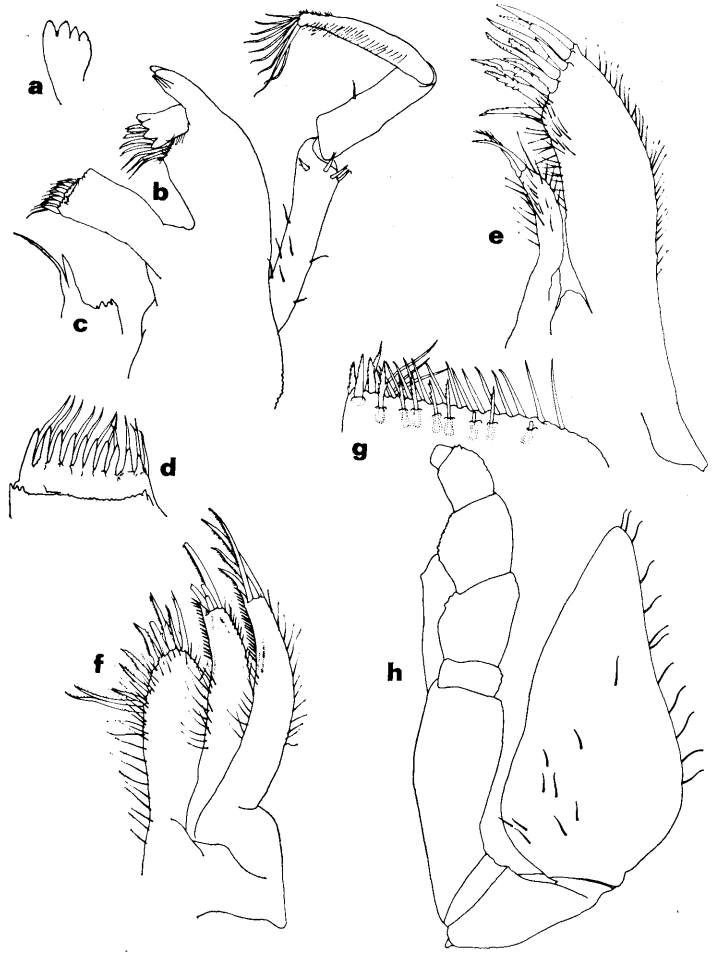

FIG. 5. *Haplomunna hubbsi*, sp. nov., mouthparts from a brooding female: (*a*)–(*d*) left mandible ((*a*) incisor process, ventral view, (*b*) entire appendage, (*c*)–(*d*) two views of molar process); (*e*) maxillula; (*f*) maxilla; (*g*)–(*h*) maxilliped ((*g*) endite, distal tip, (*h*) lateral view showing epipodite).

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