BATHYAL AND ABYSSAL AMPHARETIDAE (ANNELIDA: POLYCHAETA) (SEDENTARY SPECIES II)

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ABSTRACT

The bathyal and abyssal ampharetids from the Galathea Expedition 1950-1952 are treated. The material comprises at least 13 species. Four have been identified to the species level, five to the generic. Four new species: *Jugamphicteis galatheae*, *Lysippides caeca*, *Paramage tasmanensis*, and *Phyllocomus balinensis* are described. The taxonomy of the genus *Jugamphicteis* Fauchald & Hancock, 1981 is discussed. The species *Amphicteis sargassoensis* Hartman & Fauchald, 1971 is included in this genus as *Jugamphicteis sargassoensis* n. comb. *Amphicteis gunneri malayensis* Caullery, 1944 is raised to the rank of a full species: *Amphicteis malayensis*. The bathymetric distribution of the family is discussed.

Key words: Polychaeta, Ampharetidae, systematics, Galathea Expedition.

INTRODUCTION

The Ampharetidae is a family of polychaetous annelids. This family and the families Pectinariidae, Alvinellidae, Terebellidae, and Trichobranchidae constitute the order Terebellida (or Terebellomorpha). The family contains about 70 genera with more than 200 species (Holthe 1986a). Most of the species are marine, but a few live in fresh water. In the sea they are found from the shallow sub-littoral to the depths of the oceans. The ampharetids are common in all oceans and most inshore waters. They live in tubes which they build of sediment particles, feed on detritus by means of tentacles which can be retracted into the pharynx, and breathe by means of dorsal branchiae. The chaetae are capillaries on the notopodia and usually minute hooks (uncini) on the neuropodia. Some species have specialized chaetae, like paleae – enlarged first pair of notochaetae pointing forwards. The body is short, seldom more than 50 mm, and clearly divided into a thorax with chaetous notopodia and an abdomen without such notopodia.

The ampharetids in the *Galathea* material from depths exceeding 6000 m were treated by Kirkegaard (1956), and those from shelf depths off West Africa by Kirkegaard (1959). A rich material of littoral and sublittoral samples from the Galathea Expedition is still not examined.

MATERIAL AND METHODS

The material was kindly lent by the Zoological Museum, University of Copenhagen (ZMUC).

A complete list of the *Galathea* stations was given by Bruun (1958). The material has been studied in stereo microscope and light microscope; all drawings are free-hand.

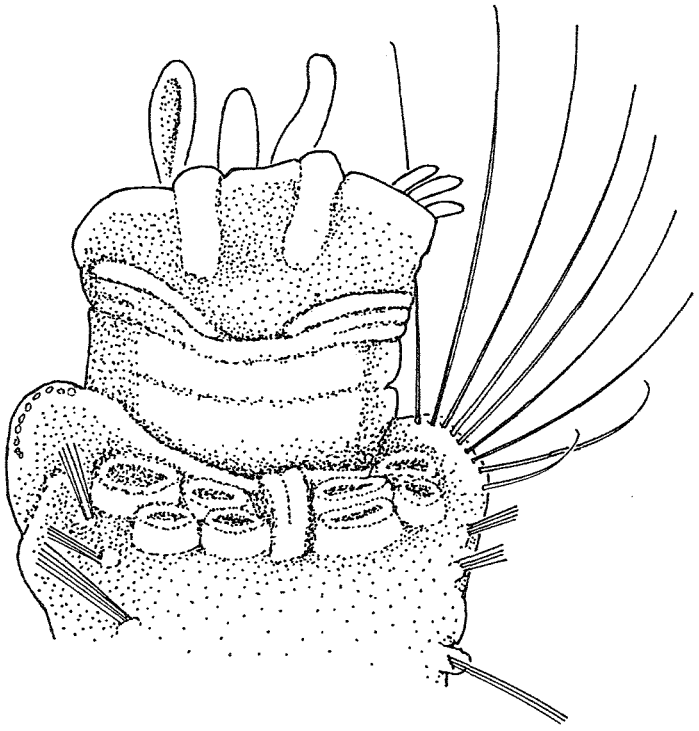

Fig. 1. *Amphicteis malayensis* Caullery, St. 311. Dorsal view of anterior part, branchiae lost, left paleae omitted.

SYSTEMATICS

Amphicteis Grube, 1850

Type of genus: *Amphitrite gunneri* Sars, 1835, by monotypy.

Amphicteis malayensis Caullery, 1944 new rank

Fig. 1

Originally described as *A. gunneri* var. *malayensis*. Type locality: South East Asian seas.

Material: St. 311, off Ganges Delta, 20°49′N, 88°40′E, 445 m, 1 spec.

Remarks: The specimen is complete, 14 mm long and 2 mm broad. Morphologically it is very close to Caullery's (1944) description and figures. I find it difficult to see this ampharetid as a subspecies of *A. gunneri*, and consequently propose that its rank should be raised to that of a full species.

Distribution: Sulu Sea, Java Sea, Bay of Bengal in 275-1330 m.

Amphicteis posterobranchiata Fauvel, 1932

Material: St. 99, off Angola, 8°40′S, 11°10′E, 2690 m, ZMUC-POL-906, 1 spec.; St. 302, Bay of Bengal, 19°42′N, 86°48′E, 1190 m, ZMUC-POL-907, 2 spec.

Remarks: The species was described from off Ceylon in 1000-1250 m. Its distribution now includes both the deep Indian and the deep South Atlantic Oceans.

Amphicteis sp.

Fig. 2

Material: St. 17, Dakar-Monrovia, 7°17′N, 13°28′W, 1260 m, ZMUC-POL-908, 1 spec.

Remarks: This anterior fragment of an *Amphicteis* was identified as such by J.B. Kirkegaard. It comprises the head region and 11 chaetigerous thoracic segments, width 4 mm at the broadest part.

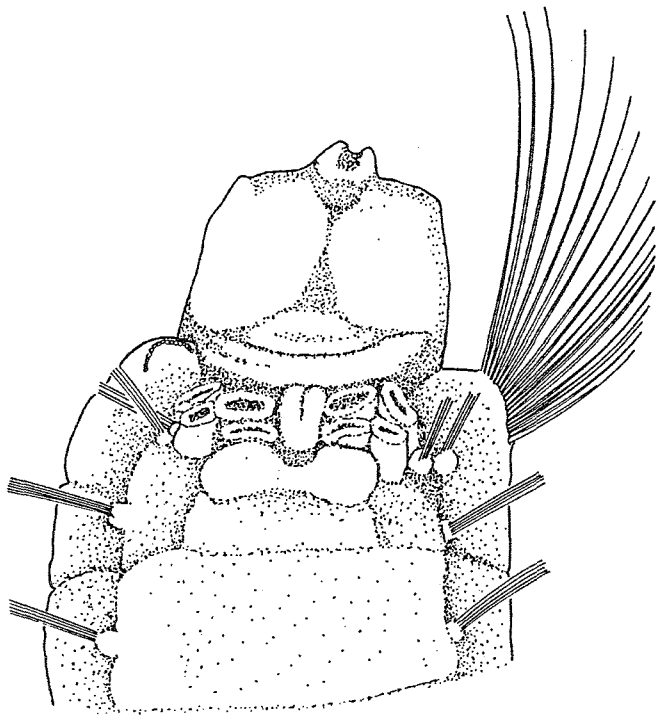

Fig. 2. *Amphicteis* sp., St. 17. Dorsal view of anterior part, branchiae lost, left paleae omitted.

The body is thick, and not smooth. Anteriorly the prostomium has a pair of very short ridges. No nuchal arches can be seen. The posterior part of the prostomium is nearly covered by a pair of cushion-like structures, a character known in some *Amphicteis* species. The paleae number 17-19 on each side, and are long, strong and golden with slightly bent tips. The most conspicuous character is the arrangement of the anterior, smaller two pairs of notopodia. The second pair is very close to, medial to and only slightly behind the first pair (Fig. 2).

Other *Amphicteis* species with a cushionlike posterior prostomium include *A. mucronata* Moore, 1923; *A. obscurior* Chamberlin, 1919; *A. orphnius* Chamberlin, 1919; and *A. uncopalea* Chamberlin, 1919. The present specimen conforms with no known ampharetid, but is too incomplete to allow the description of a new species.

Eclysippe Eliason, 1955

Type of genus: *Lysippe vanelli* Fauvel, 1936, by monotypy.

Eclysippe sp.

Material: St. 311, off Ganges Delta, 20°49′N, 88°40′E, 445 m, 1 spec.

This specimen is incomplete; the abdomen is broken off and the thorax is ruptured dorsally. Like the type species *E. vanelli*, it has long posterior thoracic segments and a triangular prostomium. The branchiae (only two left ones remaining in this specimen) are much shorter and thicker than those of *E. vanelli*.

Jugamphicteis Fauchald & Hancock, 1981

Type of genus: *Amphicteis sibogae* Caullery, 1944, by original designation.

Emended diagnosis: Prostomium with transverse or curved nuchal arches. No parallel glandular ridges. Four pairs of branchiae in close lateral groups, separated by a narrow median area. Paleae present. Seventeen thoracic segments with normal notopodia, the posterior fourteen also with uncinigerous tori. First abdominal segment with fanlike notopodial structures, connected at middorsum.

Key to species of *Jugamphicteis*:

1. Nuchal organs spirally coiled ..... *J. paleata*
– Nuchal organs not spirally coiled 2
2. Nuchal organs forming 4 horseshoe-shaped arches ..... *J. sibogae*
– Nuchal organs forming 2 transverse ridges 3
3. Nuchal ridge straight, paleae reaching forward to nuchal ridges ..... *J. sargassoensis*
– Nuchal ridges curved, paleae reaching forward past prostomium ..... *J. galatheae*

Remarks: When Fauchald & Hancock (1981) erected the genus *Jugamphicteis* for the type species *Amphicteis sibogae* Caullery, 1944 and described a new species, *J. paleata*, they briefly mentioned that two other species of *Amphicteis*, viz. *A. vega* Wirén, 1883 and *A. vestis* Hartman, 1965, also show modified notopodial structures on anterior abdominal segments. They concluded that neither of these two species had the characteristic structures present in *J. sibogae* and *J. paleata*, and therefore should not be included in the new genus. I agree that *A. vega* and *A. vestis* are different from the species of *Jugamphicteis*, and should not be included in this genus. Strangely enough, it seems that Fauchald & Hancock (1981) overlooked one species which Fauchald himself had participated in describing ten years earlier, *A. sargassoensis* Hartman & Fauchald, 1971. Indeed, Hartman & Fauchald (1971) emphasized the resemblance of *A. sargassoensis* to *A. sibogae*, and recently Fauchald (pers. comm.) has agreed in the transfer of *A. sargassoensis* to *Jugamphicteis*.

The four species of *Jugamphicteis* are likely to be closely related by sharing a conspicuous and most probably apomorphic structure as the notopodial fan: 'la rame sétigère dorsale est remplacée par une sorte d'expansion lamelleuse, formant un tablier à bord découpé en une quinzaine de lobes, et qui s'étend jusqu' à la ligne médiane;' (Caullery 1944); 'erect, broadly flaring notopodial membrane' (Hartman & Fauchald 1971); 'medially fused notopodial structures forming a valve between the thorax and abdomen' (Fauchald & Hancock 1981). All have characteristic nuchal ridges: 'organes nucaux ... dessinent une ligne transversale de quatre arceaux en fer à cheval, saillants, avec une bande pigmentée' (Caullery 1944); 'transversal nuchal ridges' (Hartman & Fauchald 1971); 'spiralled mediosuperior part; the edge of each spiral is formed by glandular ridges' (Fauchald & Hancock 1981). Interpreting the presence of notopodial fans and prominent nuchal ridges as synapomorphies, I find it most likely that the genus *Jugamphicteis* is monophyletic.

The four species are identical in the usual meristic characters, but can be told apart by the shape of the nuchal ridges, which are straight in *J. sargassoensis*, arched in *J. galatheae* n. sp., spiralled in *J. paleata*, and like a series of horseshoes in *J. sibogae*. The parallel glandular ridges typical of most *Amphicteis* species, including the Type of genus: *A. gunneri* (Sars, 1835), seem to be absent in *Jugamphicteis*.

Jugamphicteis galatheae n. sp.

Fig. 3A-F

Material: St. 664, Kermadec Trench, 36°34′S, 178°57′W, 4540 m, HOLOTYPE ZMUC-POL-909 (complete), 11 paratypes (1 complete) ZMUC-POL-1002; St. 178, Cape Town - Durban, 35°07′S, 30°35′E, 4470 m, ZMUC-POL-910, 1 spec.; St. 180, Cape Town - Durban, 34°56′S 36°31′E, 5220 m, ZMUC-POL-911, 1 spec.; St.182, Cape Town - Durban, 33°28′S, 38°32′E, 5110-5340 m, ZMUC-POL-912, 6 spec.; St. 194 off Durban, 34°09′S, 30°45′E, 4360 m, ZMUC-POL-913, 2 spec.; St. 663, Kermadec Trench, 36°31′S, 178°38′W, 4410 m, ZMUC-POL-914, 1 spec.

Description: Holotype nearly broken into two parts, must have been ca 35 mm long, width at widest part 2.5 mm. Body long, tapering towards pygidium. Prostomium- peristomium characteristically funnel-shaped, broad and deep in front (Fig. 3A-C). Prostomium with two transverse, raised and slightly curved nuchal ridges. Tentacles numerous, small and smooth. Four pairs of branchiae arranged in two lateral groups with two anterior and two posterior branchiae (Fig. 3A). The outer posterior branchia significantly thinner and shorter than the

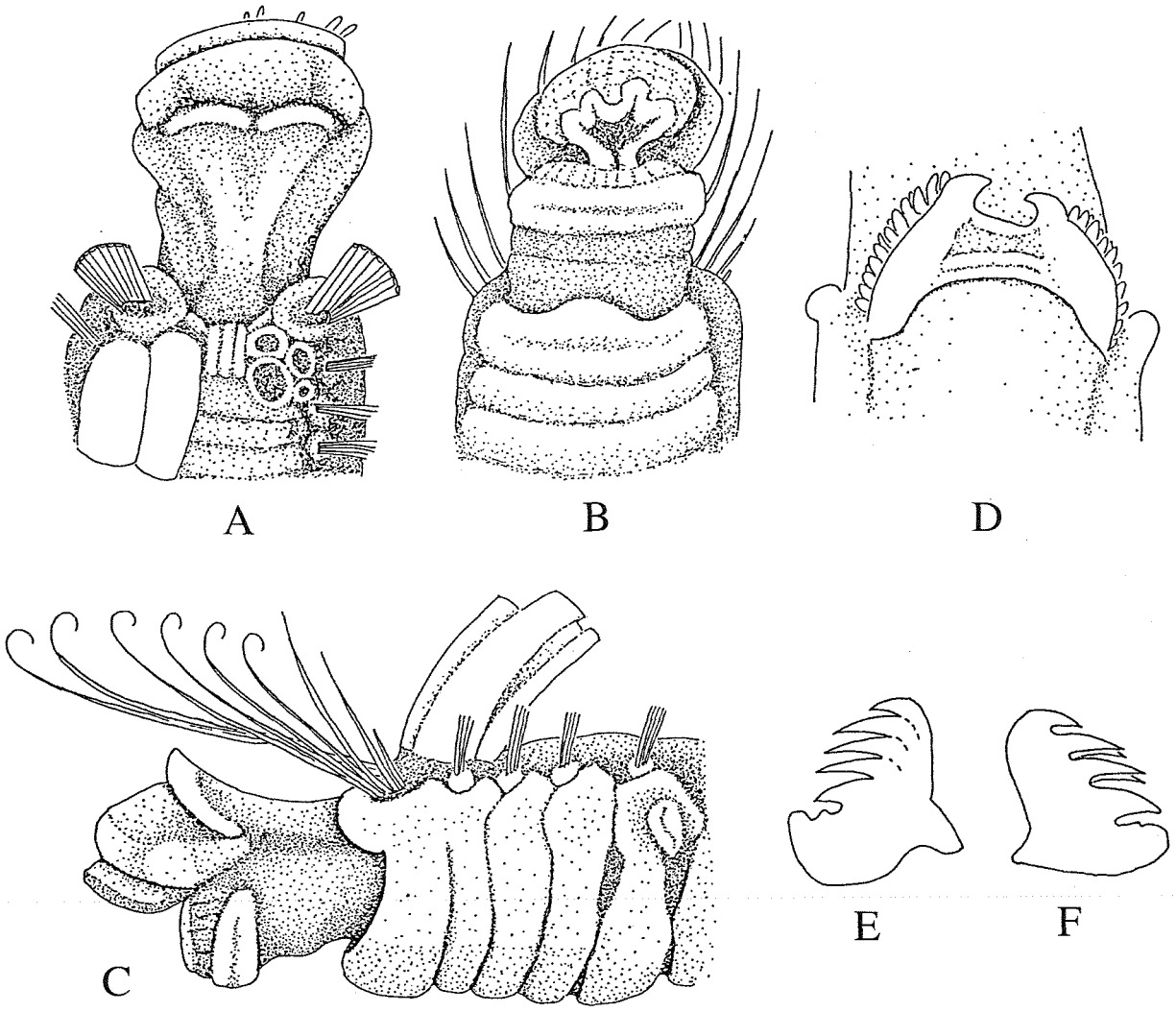

Fig. 3. *Jugamphicteis galatheae* n. sp., holotype. A, anterior region, dorsal view, right branchiae left out, only proximal part of paleae shown. B, anterior region, ventral view, tentacles lost. C, anterior region, left lateral view, only proximal parts of branchiae shown. D, frontal dorsal view of first abdominal segment. E, thoracic uncinus. F, abdominal uncinus.

other three. Long, slender paleae with curled tips reaching forward past the rim of prostomium (Fig. 3C). Three first thoracic segments with fully developed notochaetae, but lacking neurochaetae. Following 14 segments with notochaetae and uncinigerous tori. First abdominal segment with dorsal fan stretching across dorsum, but with a large median notch (Fig. 3D). Outer edges of fan with double rows of papillae. 14-16 abdominal segments (14 in HOLOTYPE), the anterior ones long, the posterior ones much shorter. Pygidium with a pair of long lateral cirri, sometimes unequally developed. Notochaetae slightly flattened distally before tapering into slender tips. Thoracic uncini with one row of four large teeth above a small rostrum (Fig. 3E). Abdominal uncini with one superior tooth and two rows of two teeth, each row above a small rostrum (Fig. 3F).

Colour in alcohol: pale yellow.

Tube: The entire material contains only two remnants of tubes, one of which belongs to one of the paratypes. Tube rather thin, close-fitting, covered with very fine sediment particles, greyish with a discernible circular pattern.

Etymology: This species is named after the expedition ship, *Galathea*.

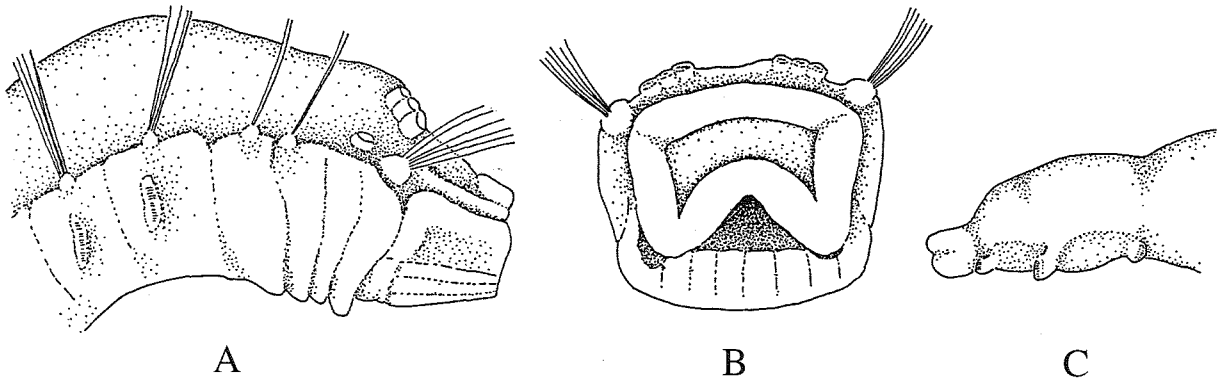

Fig. 4. *Lysippides caeca* n. sp., holotype. A, right lateral view of anterior region, branchiae lost. B, frontal view of head region, branchiae lost. C, right lateral view of last abdominal segments and pygidium.

Remarks: The wide distribution of this species conforms with those of several other deep-sea polychaetes, see Kirkegaard (1996).

Distribution: Kermadec Trench and off east coast of South Africa in 4360-5340 m.

Jugamphicteis sargassoensis (Hartman & Fauchald, 1971) n. comb.

Material: None.

Lysippides Hessle, 1917

Type of genus: *Amphicteis fragilis* Wollebæk, 1912, by monotypy.

Lysippides caeca n. sp.

Fig. 4A-C

Material: St. 478, South of Bali, 8°50′S, 114°55′E, 600 m, 1 spec., HOLOTYPE, ZMUC-POL-915.

Description: Holotype 14 mm long, 1.5 mm wide. Body evenly tapering from just behind the branchiae and throughout abdomen.

Prostomium simple and folded, without glandular ridges, nuchal organs or eyespots (Fig. 4A-B). Peristomium ventrally protruding, with longitudinal furrows. Branchiae lost in holotype, but the branchial pattern can be seen from the remaining short branchial stems. Four pairs of branchiae forming close groups of three in front, separated by a median space, and a pair of lateral branchiae behind the paleae (Fig. 4A). Small paleae present. Thorax with 16 chaetigerous segments, the last 14 ones also with uncinigerous tori. Notochaetae very fine and brittle. Uncini not examined, as the holotype is very delicate. Abdomen with 11 uncinigerous segments. Pygidium very small, without cirri (Fig. 4C).

Tube: unknown.

Colour in alcohol: very pale yellowish.

Etymology: Latin *caeca* meaning blind, as there are no eyespots in this species.

Remarks: The number of thoracic uncinigers and the branchial pattern clearly show that this species belongs to *Lysippides*. This species seems to be even more brittle than its only congener *L. fragilis* (Wollebæk, 1912). The notochaetae are extremely fine and easily broken. The holotype is nearly broken at the 11th thoracic uncinigerous segment; the two parts are barely connected by the skin. The main diagnostic character is the number of abdominal segments, 11 versus 8 in *L. fragilis*. The latter has a pygidium with lateral cirri, and has usually distinct eyespots.

Melinna Malmgren, 1866

Type of genus: *Sabellides cristata* Sars, 1851, by monotypy.

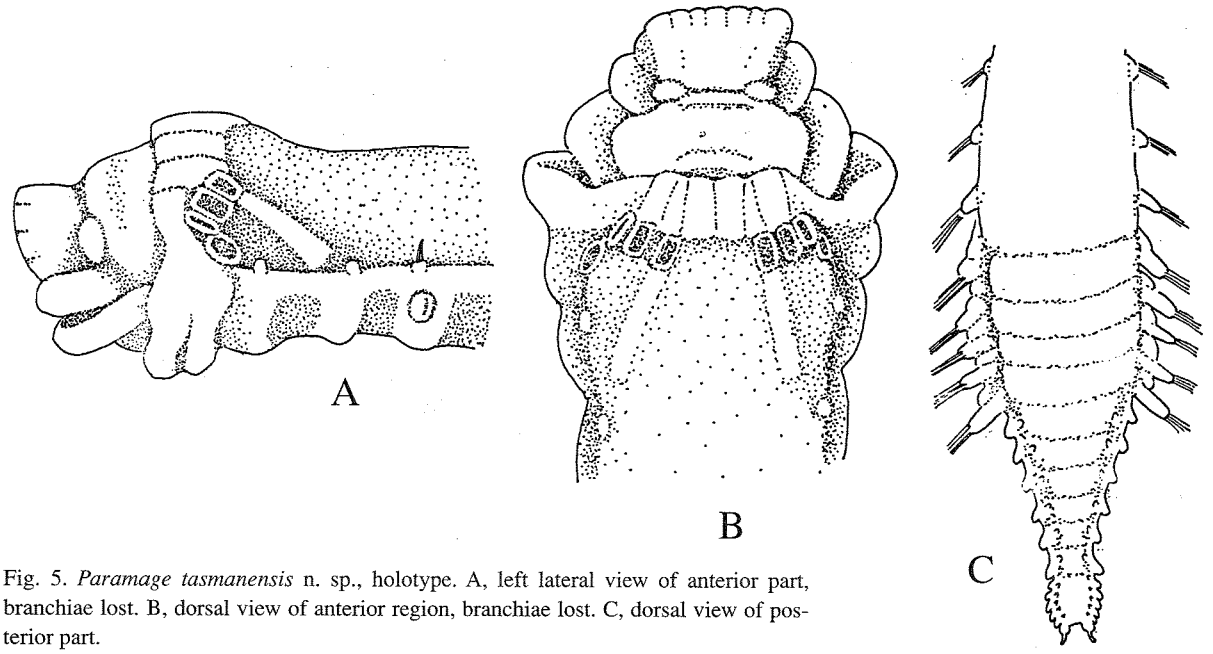

Fig. 5. *Paramage tasmanensis* n. sp., holotype. A, left lateral view of anterior part, branchiae lost. B, dorsal view of anterior region, branchiae lost. C, dorsal view of posterior part.

Melinna sp. or spp.

Material: St. 180, 1 spec.; St. 450, 1 spec.; St. 490, 1 spec.; St. 626; 1 spec.
None of these few specimens are complete, and in my opinion do not allow identification to the species level.

Melinnopsis McIntosh, 1885

Type of genus: *Melinnopsis atlantica* McIntosh, 1885, by monotypy.

Melinnopsis (?) sp. or spp.

Material: St. 190, 5 spec.; St. 217, 2 spec.; St. 599, 1 spec.; St. 663, 3 spec., St. 664, 2 spec.

One of the specimens from St. 664 resembles *M. annenkovae* Ušakov, 1952, but I hesitate to identify any of these specimens to the species level.

Paramage Caullery, 1944

Type of genus: *Paramage madurensis* Caullery, 1944, by monotypy.

Remarks: Contrary to Fauchald's (1977) diagnosis, rudimentary notopodia are present on the abdomen. These can be seen in the drawings by Caullery (1944) and Moore (1923). In Caullery's description of *P. madurensis* they are mentioned as: 'Tubercules correspondant aux rames dorsales'.

Paramage tasmanensis n. sp.

Fig. 5A-C

Material: St. 607, Tasman Sea, 44°18′S, 166° 46′E, 3830 m, 1 spec., HOLOTYPE, ZMUC-POL-916. Complete but for the loss of all branchiae, nearly broken into two parts in thorax.

Description: Holotype 16 mm long, width at widest part 3 mm. Branchial region wider than thorax. Thorax long, cylindrical, not tapering towards abdomen. Abdomen short, thick, tapering towards pygidium. Prostomium prominent; with a pair of oval nuchal organs, without glandular ridges or eyespots. Four pairs of branchiae arranged as three middle pairs, almost in a transverse line, and one outer pair behind the outermost of the inner branchiae (Fig. 5A-B). Wide space between left and right branchial groups. Branchiae lost in holotype. Branchial bases rectangular. Innermost pair has long bases, the proximal parts of which are attached to the dorsum, and cross obliquely backwards and outwards into segment V. No paleae. Segments IV and V with rudimentary notopodia

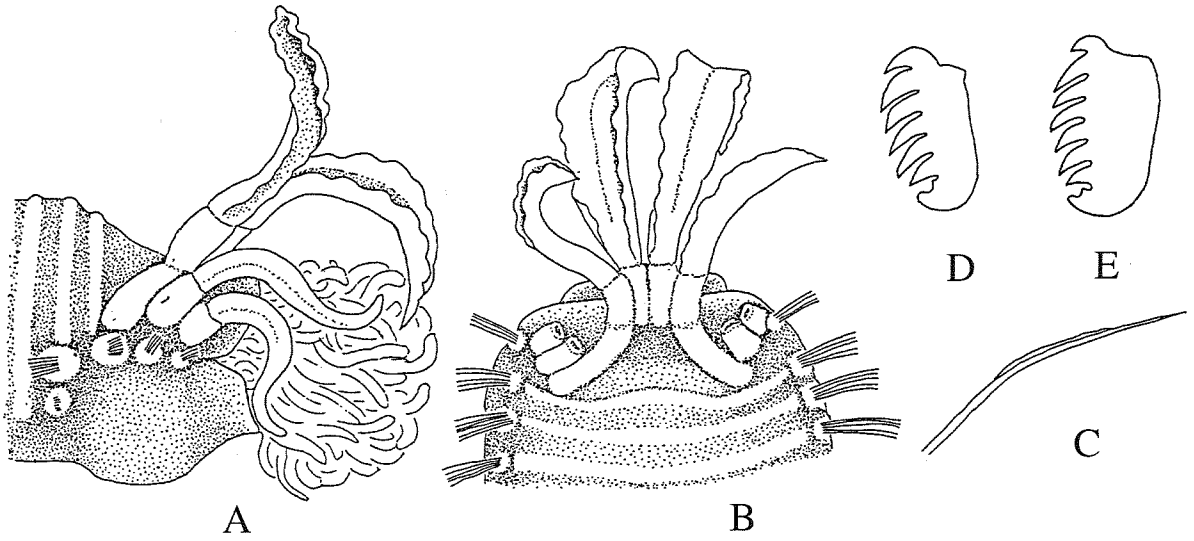

Fig. 6. *Phyllocomus balinensis* n. sp., holotype. A, right lateral view of anterior region. B, dorsal view of anterior region, first two pairs of lateral branchiae left out. C, notochaeta. D, thoracic uncinus. E, abdominal uncinus.

without chaetae. Twelve chaetigerous thoracic segments, all uncinigerous. First chaetigerous notopodia with only 2-3 short and thin bristles. Anterior thoracic segments long, with short notopodia. Posterior five thoracic segments short, with long notopodia (Fig. 5C). Abdomen with 11 uncinigerous segments. Six anterior segments long, five posterior ones short (Fig. 5C). Abdominal segments with a dorsolateral cirrus. Pygidium with a pair of lateral cirri with thick bases and slender tips.

Thoracic uncini with a simple row of five teeth above a small rostrum. Abdominal uncini with a simple row of six teeth above a small rostrum.

Tube: unknown.

Colour in alcohol: pale yellow.

Etymology: This species is named after its type locality, the Tasman Sea.

Remarks: This deep-sea species of *Paramage* resembles *P. madurensis* Caullery, 1944, which was described from littoral waters (69-91 m) in Indonesia. Both species are described from single specimens. Allowing for the possible difference in contraction of the two holotypes, I nevertheless find sufficient differences to erect a new species. The main diagnostic characters are the branchial bases and the branchial pattern. There is also a difference in the length of the anterior segments, which are longer in *P. tasmanensis*. This species moreover has six long abdominal segments, whereas *P. madurensis* only has two. The third species of the genus, *P. scutata* (Moore, 1923), is known from the shelf and slope off California. This species has much shorter anterior segments. As mentioned by Moore (1923), and shown in the drawing by Williams (1987), this species has a ridge connecting the innermost branchiae transversely across the dorsum with the parapodial region of segment IV. This seems to correspond to the prolonged branchial bases of *P. tasmanensis*.

Phyllocomus Grube, 1878

Type of genus: *Phyllocomus crocea* Grube, 1878, by monotypy.

Emended diagnosis: Four pairs of branchiae, at least two of these foliate. No paleae. No glandular ridges on prostomium. Twelve thoracic uncinigers. Abdomen long. Pygidium with rounded papillae.

Phyllocomus balinensis n. sp.

Fig. 6A-E

Material: St. 490, Bali Sea, 5°25′S, 117°03′E, 570-545 m, HOLOTYPE (complete), ZMUC-POL-917; 2 paratypes (1 complete), ZMUC-POL-918.

Description: Holotype 33 mm long, width at widest part 3 mm. Body soft, thorax short, broad and thick anteriorly, tapering towards abdomen. Abdomen long, slender, tapering slightly towards pygidium. Prostomium very short, rectangular, almost hidden beneath fused branchial bases; without glandular ridges or eyespots. A pair of barely discernible nuchal slits at posterior rim. Four pairs of branchiae arranged as 1st, 2nd and 3rd lateral pairs, and one middle pair (Fig. 6 A-B). First and 2nd lateral pairs have short bases and are almost normal, thick cirriform branchiae, only slightly flattened. Third lateral pair has long bases, the proximal parts of which are attached to the dorsum, and cross obliquely forward and inward to join the short bases of the middle pair. Distal parts of bases rising from dorsum together with those of the middle pair. Branchiae of 3rd lateral and middle pair large and foliate, with undulated brims. No distinct filiform tips. No paleae. 15 chaetigerous thoracic segments, the last 12 of which uncinigerous. Abdomen with 25-27 uncinigerous segments. Abdominal uncinigerous pinnulae protruding, each with a short dorsal cirrus. Pygidium with a few rounded papillae in a seemingly irregular pattern. Notochaetae with a distal bend and tapering tip, a very narrow brim running on the convex side from just before the bend and half way to the tip (Fig. 6C). Thoracic uncini with a simple row of five teeth above a small rostrum (Fig. 6D). Abdominal uncini with a simple row of six teeth above a small rostrum (Fig. 6E).

Tube: unknown.

Colour in alcohol: pale yellow. Thoracic dorsum and anterior abdomen can be translucent, showing a large, red, median vessel and gut contents, respectively.

Etymology: This species is named after its type locality, the Bali Sea.

Remarks: The unusual, distorted branchial pattern with the bases of the last pair of branchiae crossing the dorsum and joining those of the middle (first?) pair is similar to that of the type of the genus, *P. crocea* Grube, 1878, as drawn by Hartman (1966). The two patterns are, however, not identical. In *P. crocea* the next to last outer branchiae have bases as long as those of the last pair; in *P. balinensis*, those of the last pair have bases more than twice as long as all the other branchial bases. Another difference between the two species is the number of abdominal segments: about 45 in *P. crocea* and 25-27 in *P. balinensis*.

Terampharete Augener, 1918

Type of genus: *Terampharete luderitzi* Augener, 1918, by monotypy.

Terampharete luderitzi Augener, 1918

Type locality: Southwest Africa.

Material: St. 136, off Kunene River, SW Africa, 17°13′S, 11°12′E, 960 m, ZMUC-POL-919, 1 spec. Identified by J.B. Kirkegaard.

Distribution: Southwest Africa, from shallow water to 1000 m.

Sabellides Milne Edwards in Malmgren, 1866

Type of genus: *Sabella octocirrata* Sars, 1835, by monotypy.

Sabellides sp.

Material: St. 196, off Durban, 29°55′S, 31° 20′E, 425-430 m, many fragments of tubes and a few fragments of worms.

Samythella Verrill, 1873

Type of genus: *Samythella elongata* Verrill, 1873, by monotypy.

Samythella neglecta Wollebæk, 1912

Material: St. 771, Gulf of Biscay, 47°48′N, 08°26′E, 1920 m, 1 spec.

This small (10 mm long) complete specimen was first identified by J.B. Kirkegaard. The abdomen has fewer segments (24) than normal for the species (29-31). It is the southernmost and deepest record of the species, which mainly is distributed along the continental margin from Svalbard to Shetland in 100-960 m.

Ampharetidae indet.

In the Galathea material which I have examined, there are indeterminable fragments of ampharetids of the subfamily Ampharetinae from stations 161, 193, 194, 468, 626, 661, 664, 668.

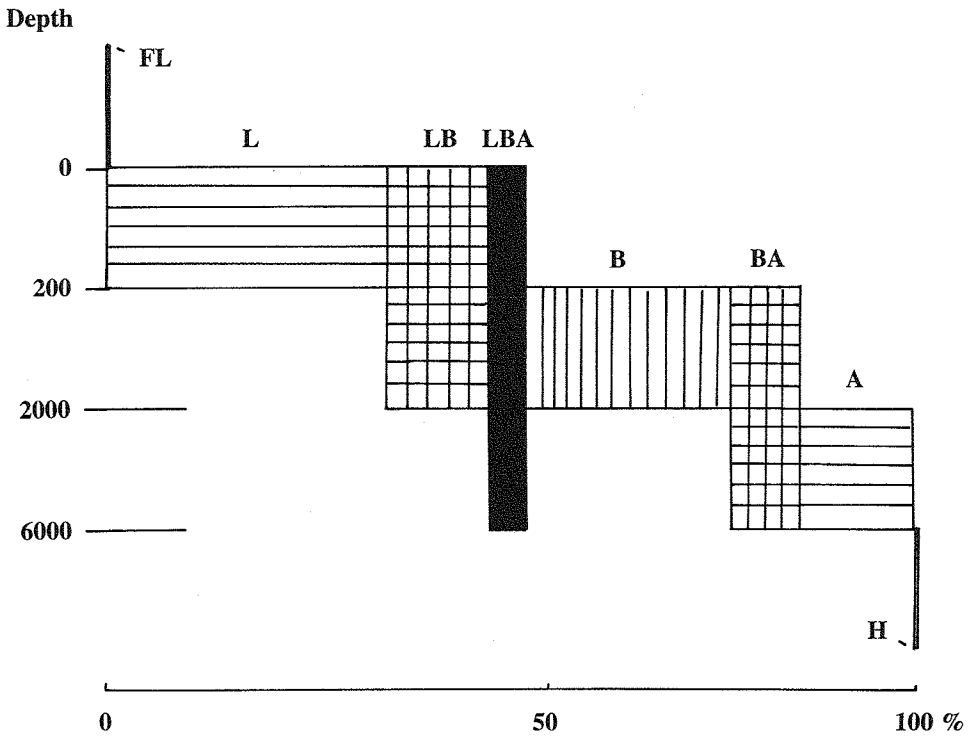

Fig. 7. Bathymetric distribution of the family Ampharetidae in fresh (F), littoral (L), bathyal (B), abyssal (A), and hadal (H) waters and combinations of these. Vertical scale depth as tiers with borders given in meters. Horizontal scale percentage of total number of species.

DISCUSSION

Holthe (1986a) lists 210 valid species of ampharetids. Later descriptions, including those in the present paper, have added 20 species to the list. Holthe (1986a) distinguishes between deep-sea species and shelf/upper slope species. The limit between these was set at about 1000 m. Of the present 230 species, 91 have been found in the deep sea, and 67 of these exclusively so. Thus, 24 species are found both in the deep sea and on the shelves or upper slopes. The latter must be considered eurybathic. The eurybathic species are normally found in only one deep-sea basin and on adjacent slopes and shelves. The exclusively deep-sea species are normally found in only one deep-sea basin or may in a few cases occur in adjacent basins.

Only two species have hitherto been found in widely separate ocean basins viz. *Ampharete finmarchica* (Sars, 1865): Atlantic and Pacific deep seas as well as slopes and shelves and *Amphicteis gunneri* (Sars, 1835): Atlantic and Indian Ocean deep seas as well as slopes and shelves.

These two species seem to be extremely eurybathic, and according to Holthe (1986b) *Ampharete finmarchica* is widely distributed in the northern hemisphere, from the upper sublittoral to depths exceeding 5000 m, whereas *Amphicteis gunneri* is almost fully cosmopolitan on the shelves and vertically distributed from the upper sublittoral to about 5000 m. At least five subspecies of *A. gunneri* (including the nominate subspecies) have been described. One of these, *Amphicteis gunneri malayensis* Caullery, 1944, is raised to the rank of a full species in the present paper, and I should not be surprised if the others would follow. One species, *Amphicteis midas* (Gosse, 1855), was for many years treated as a synonym of *A. gunneri*, but was restored as a separate species by Hartley (1985). Both Hutchings & Rainer (1979) and Hartley (1985) advocate a full revision of the genus *Amphicteis*. I fully agree that such revision is necessary, especially regarding the *Amphicteis gunneri* complex.

As a result of the present work, two more ampharetid species have been found in widely separate deep-sea basins, viz. *Amphicteis posterobranchiata* Fauvel, 1932: Atlantic and Indian Ocean deep seas and *Jugamphicteis galatheae* n. sp.: Indian Ocean deep sea and the Kermadec Trench.

Of the 91 species occurring in the deep sea, 5 are

found in the Arctic Ocean, 23 in the North Atlantic, 4 in the South Atlantic, 12 in the Antarctic Ocean, 3 in the Indian Ocean, 34 in the North Pacific, and 10 in the South Pacific. This distribution is clearly biased by varying sampling effort. The North Atlantic and the North Pacific are far more easily reached from established research facilities in Europe and North America than are the Indian Ocean and the South Pacific.

Adopting a more formal division between freshwater, littoral (0-200 m), bathyal (200-2000 m), abyssal (2000-6000 m), and hadal (below 6000 m) tiers, we get the following percentages of the total number of species: Freshwater and littoral: 0.5%; exclusively littoral: 35.1%; littoral and bathyal: 11.6%; exclusively bathyal: 24.8%; bathyal and abyssal: 8.8%; exclusively abyssal: 14.1%; littoral, bathyal, and abyssal: 4.6%; hadal: 0.5%. This distribution is shown in Fig. 7.

The Ponto-Caspian species, *Hypania invalida* (Grube, 1860), occurs in the Danube to above Passau in Germany (Kothé 1968, Hartmann-Schröder 1996). It is probably a relic from the Sarmatian inland sea of the Pliocene. The Sarmatian fauna was in turn composed of relics from the early Tertiary Paratethys Sea. Thus, species like *H. invalida* are characterized as ancient, thalassogenic freshwater animals (Kothé 1968). After the completion of the Danube-Main-Rhine Canal in September 1992, this species, according to information available on the Internet, seems to have spred to the rivers Main and Rhine, and even into the North Sea (Helgoland). The Danube-Main Canal reaches 406 m above sea level in the Swabian Alps.

Among the littoral species many are euryhaline, and some, like *Alkmaria romijni* Horst, 1919 and *Mugga wahrbergi* Eliason, 1955, are genuine brackish water species. Many are common within their respective biogeographical regions, and some are abundant at certain localities.

Some inshore localities may contain several species of ampharetids. One station at 50 m depth within the parameter of the city of Trondheim with a total sampled area of 6 m^2 yielded 7 species of ampharetids (Holthe 1977). Ampharetids are often widely distributed inshore and on the shelves, covering two or more biogeographical regions (Holthe 1986a). The biogeographical distribution of these ampharetids follows that of the order Terebellida in general (Holthe 1978, 1986a).

A majority of the ampharetid species, 63.9%, occur at bathyal or abyssal depths or both. As the littoral is definitely more frequently sampled, this percentage may be considerably higher in reality. Very close to half of the species (49.8%) have been found in the bathyal tier, which regarding the ampharetids contains the highest diversity.

Two of the abyssal species, *Amphisamytha galapagensis* Zottoli, 1983 and *Grassleia hydrothermalis* Solis-Weiss, 1993, are associated with hydrothermal vents of the Pacific. The rest seem to belong to the cold soft-bottom environment.

Again we have a small group (4.6%) of extremely eurybathic species (column marked 'LBA' in Fig. 7). Only a taxonomic revision of these 10 species will show to which extent this group is real.

Two fragmentary specimens have been found in hadal depths: Kermadec Trench, St. 658, 6660-6720 m, and Sunda Trench, St. 465, 6930-7000 m (Kirkegaard 1956). Thus, we know that the hadal ampharetids are there, but we need more samples to identify or describe the species. Presently we do not know whether these specimens belong to exclusively hadal species, or to species also occuring in the abyssal zone.

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