NEW AND RARE CALANOID COPEPODS FROM THE GREAT METEOR SEAMOUNT, NORTH EASTERN ATLANTIC

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ABSTRACT

Nine benthopelagic calanoid taxa belonging to seven genera were found in 11 samples collected at the Great Meteor Seamount, northeastern Atlantic at depths from 295 to 560 m by means of an epibenthic sledge during a cruise of RV "Meteor" in 1998. A new species of Xanthocalanus (family Phaennidae), X. meteorae sp. nov. is described, as well as a male of Paracomantenna minor, which is the first description of a male in this genus. The following known benthopelagic calanoids could be identified: Bradyidius armatus Giesbrecht, 1897, B. luluae Grice, 1972, Paracomantenna minor (Farran, 1905), Tharybis macrophthalma Sars, 1902, Metacalanus inaequicornis (Sars, 1902). Pseudocyclopia sp., Paramisophria sp. and P. cf. spooneri also are reported. A great similarity exists between the fauna of benthopelagic calanoids found at the Great Meteor Seamount and those occurring in Norwegian waters.

Key words: Great Meteor Seamount; benthopelagic calanoid copepods, Xanthocalanus sp. nov.

INTRODUCTION

The benthic boundary layer, waters immediately above the sea floor, is numerically dominated by copepods (e.g., Wishner 1980a). More than seventy new species of calanoid copepods were described from this benthopelagic habitat during recent decades (Bradford-Grieve, in press). However, biodiversity of this habitat is expected to increase with the increased number of benthopelagic collections. To date, zooplankton samples from the near bottom waters are scarce. Hence, the fauna of benthopelagic species remains poorly known. A main problem is the technical difficulty of collecting plankton in the proximity to the bottom. Different types of traps (e.g., McWilliams et al. 1981; Jacoby

and Greenwood 1988; Ohtsuka et al. 1998; Nishida et al. 1999), nets (e.g., Matthews 1964; Grice 1972; Grice and Hulsemann 1970; Campaner 1978a; 1986; Wishner 1980b) and sledges (e.g., Fosshagen 1968; Ohtsuka 1984; Imabayashi and Endo 1968; Brandt and Barthel 1995) have been employed, all with different success dependening on the depth (shallow - deep) and on the topographic relief of the sea floor. Another problem is the contamination by typically pelagic organisms when the collecting gear does not close tightly during the descent and ascent (Grice 1972).

The depth of the plateau of the Great Meteor Seamount is between 275 and 400 m. The epibenthic sledge samples studied here were collected in the region of 29°-30'N 28°-28° 30'W. They contained benthopelagic calanoids as well as, species which are considered typical inhabitants of the water column due to the incomplete closing of the epibenthic sledge (Brenke et al. 2000). Zooplankton samples were collected using a multiple opening-closing net at the plateau and slope stations (Schiel et al. 2000). Pelagic calanoids were common in the multinet tows whereas the benthopelagic species were absent with the exception of the genera Tharybis and Xanthocalanus. Species of these two genera were found in the deepest depth strata sampled at slope and plateau stations (Tharybis at three slope and four plateau, and Xanthocalanus at one slope station). Sampling is described more detailed in "Material and Methods" in the end of main text. The pelagic species are not further considered

The following abbreviations are used in the

descriptions: P1-P5, swimming legs 1-5. Setal elements of the antennule are designated as: first meaning - seta, second meaning - aestethasc, if setal element is broken - it is designated under question mark (?). Ramal segments of Mx2 are considered exopodal (Ferrari 1995) and the tip of Mx2 is considered a complex of exopodal segments plus the sixth enditic lobe on the basis (Ferrari and Markhaseva 1996); Mxp syncoxa with 3 praecoxal lobes and 1 coxal lobe (Martinez Arbizu 1997; Ferrari and Ambler 1992; Ferrari and Markhaseva 2000 a, b; Ferrari and Ivanenko 2001).

RESULTS

The benthopelagic calanoid copepod fauna from shallow coastal water and the deep-sea are quite different. Representatives of only seven genera (Paramisophria, Bradyidius, Diaixis, Brachycalanus, Xanthocalanus, Cenognatha and Tharybis) are known to be common for both habitats (Ohtsuka et al. 2002; Bradford-Grieve in press). However, there are many data of typical pelagic calanoid species collected in the benthopelagic samples (Campaner 1986; Grice 1972; Gowing and Wishner 1992; Grice and Hulsemann 1970; Matthews 1964; Wishner 1980a). It is probable that pelagic calanoids are found in the benthopelagic samples not only due to the imperfect sampling, but also, at least in shallow waters, due to their diel or seasonal migrations, or to hitherto unknown peculiarities of their life cycle.

A new species of *Xanthocalanus* is described as well as a male of *Paracomantenna minor*. Two benthopelagic calanoids could not be identified to species level (Table 1): *Pseudocyclopia* sp. occurred as copepodite stage V and 2 adult females of *Paramisophria* sp. were extremely damaged. The most abundant species found at the Great Meteor Seamount were *Bradyidius armatus* and *Tharybis macrophthalma*.

The other species occurred only sporadically in low numbers (Table 1).

TAXONOMY

Family Phaennidae Sars, 1902 Xanthocalanus meteorae sp. nov.

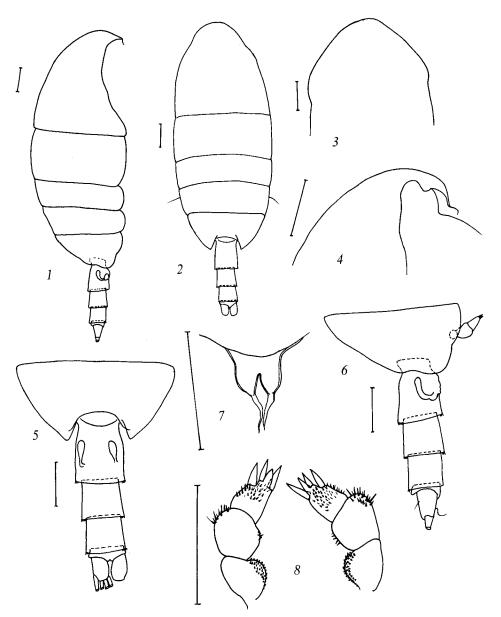
(Figs 1-21)

Material. – Holotype. N 90737. Female (total length: 1.3 mm), collected 20 September 1998, epibenthic sledge, depth 565 m, Great Meteor Seamount, northeastern Atlantic.

Paratypes: N 90738, two females (1.2-1.3 mm) from the same sample; N 90739, four females (1.2 mm), collected 18 September 1998, epibenthic sledge, depths about 460-470 m; N 90740, three females (1.2-1.3 mm), collected at 14 September 1998, epibenthic sledge, depths about 500 m.

Holotype and paratypes are kept at the Zoological Institute of the Russian Academy of Sciences, St. Petersburg.

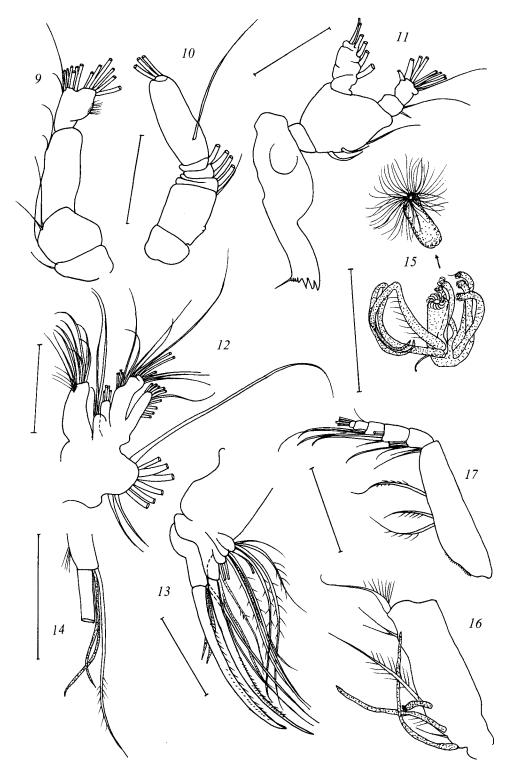
Description - Female. Total length 1.2 - 1.3 mm. Anterior part of cephalosome rounded in dorsal view (Fig. 3). Cephalosome and first pedigerous somite separate. Fourth and fifth pedigerous somites fused. Prosome nearly 3 times as long as urosome. Posterior corners of fifth pedigerous somite obtuse-rounded in lateral view and triangular in dorsal view (Figs 1-2, 5-6). Spermathecae elongate and curve anteriorly (Figs 1, 6). Caudal rami with 4 terminal, 1 ventral and 1 small dorsolateral seta. Rostrum as a subdivided base with filaments (Fig. 7). Antennule in all specimens broken. Setal armament broken at nearly all segments. Intact part has one aestethase at each of the 2nd to 3rd, 5th. 7th, 8th, 11th, 13th, and 18th articulated segments. Aestethasc at the 13th segment is the longest and reaches the distal part of the 17th segment. Coxa of antennae with 1 seta; basis with 2 setae; first exopodal segment lacking setae; second-sixth exopodal segments with 1 seta each; seventh exopodal segment with 1 seta proximally and 3 setae terminally (Fig. 10); first endopodal segment with 2 setae distally; second endopodal segment with 6 plus 8 setae (Fig. 9). Mandibular palp base with 3 setae, first endopodal segment with 2 setae, one short and spine-like; second endopodal segment with 9 terminal setae (Fig. 11). Maxillule praecoxal arthrite with 9 terminal setae and 4 posterior setae; coxal endite with 3 setae; first basal endite with 4 setae; second basal endite with 5 setae; endopod with 9 setae; exopod with 10 setae, coxal epipodite with 9 setae (Fig. 12). Maxilla proximal praecoxal endite with 5 setae; distal praecoxal and proximal coxal endites with 2 sclerotized and 1 sensory setae each; distal coxal endite with 1 strong spinulated spine, 1 sclerotized and 1 sensory setae; basal endite with 1 strong spinulated spine, 1 sclerotized and 2 sensory setae (Figs 13-14). Maxilla exopod with 9 setae: 2 worm-like and 6 brush-like sensory setae and 1 short, partly sclerotized seta (Fig. 15). Syncoxa of maxilliped with 1 worm-like sensory seta on proximal praecoxal



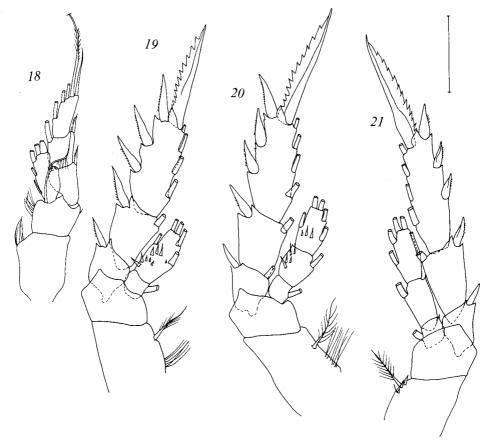
Figs 1-8. Xanthocalanus meteorae sp. nov. Female, paratype. 1, right lateral general view; 2, dorsal general view; 3, cephalon, anteriorly; 4, cephalon and rostrum in right lateral view; 5, prosomal posterior corners and urosome in dorsal view; 6, the same in right lateral view; 7, rostrum in ventral view; 8, P5. Scale lines 0.1 mm.

lobe; 1 worm-like sensory plus 1 sclerotized seta on middle praecoxal lobe, and 1 brush-like sensory seta plus 1 sclerotized seta on distal praecoxal lobe; coxal lobe with 3 setae. Basis of maxilliped with 3 setae in the middle part of limb and 2 setae distally; endopod of 5 articulated segments with 4, 4, 4, 3+1 and 4 setae (Figs 16-17).

P1 with 1-segmented endopod and 3-segmented exopod. Lateral spines on first and second segments of exopod do not reach the base of spines on second and third exopodal segments (Fig. 18). P2 with 2-segmented endopod; second endopodal segment with groups of posterior surface spinules (Fig. 19). P3 endopod and exopod 3-segmented; second and third



Figs 9-17. Xanthocalanus meteorae sp. nov. Female, paratype. 9, antenna endopod; 10, antenna exopod; 11, mandible; 12, maxillue; 13, maxilla (without exopod); 14, maxilla, basal endite; 15, sensory setae of maxilla exopod; 16, maxilliped, syncoxa; 17, maxilliped, basis and endopod. Scale lines 0.1 mm.



Figs 18-21. Xanthocalanus meteorae sp. nov. Female, paratype. 18, P1; 19, P2; 20, P3; 21, P4. Scale lines 0.1 mm.

endopodal segment with groups of posterior spinules (Fig. 20). P4 exopod and endopod 3-segmented; coxa with small spines varying in number from 1 to 4, situated near the base of medial seta (Fig. 21). P5 3-segmented with terminal spine-like attenuation of the segment and 3 terminal articulated spines; all segments are spinulated (Fig. 8).

Male unknown.

Etymology – The species name is derived from the name of the RV "Meteor". It is a noun in the genitive singular.

Remarks – To date more than 50 species are included in the phaennid genus Xanthocalanus. Many species of the genus are poorly described and their placement in Xanthocalanus is tentative (Bradford et al. 1983). For this reason the genus awaits rediagnosis. However, the new species fits well the existing definition of Xanthocalanus (Bradford 1973; Bradford et al.

1983). Xanthocalanus meteorae sp. nov. differs from other species in the genus in the following combination of characters: the obtuse rounded posterior prosomal corners; the shape of the rostrum with medium size of filaments; the maxilla exopod with 2 worm-like and 6 brush-like sensory setae plus 1 small partly sclerotized seta; the maxilla distal praecoxal and coxal endites with one of the setae sensory; the syncoxa of the maxilliped with 2 worm-like and 1 brush-like sensory setae; P5 with 3 terminal articulated spines and 1 terminal spine-like attenuation of terminal segment. The new species is a small representative of the Xanthocalanus (1.2-1.3 mm), while most species in the genus have sizes over 2 mm and up to 7.30 mm.

Xanthocalanus meteorae sp. nov. is similar with Xanthocalanus echinatus Sars, 1907, X. fallax Sars, 1921, and Xanthocalanus obtusus Farran, 1905.

Xanthocalanus meteorae sp. nov. shares the fol-

lowing characters with X. echinatus: small size (2.10 mm in X. echinatus); 3 articulated spines plus 1 spine-like attenuation on distal segment of P5 and 2 worm-like sensory setae on maxilliped syncoxa (however it has one worm-like sensory seta on the praecoxal proximal lobe, while in X. echinatus the sensory seta is situated on the distal lobe). The new species differs from X. echinatus in: the terminal position of the inner articulated spine on the distal P5 segment (the spine is situated in medial position in X. echinatus); number, structure and composition of the maxilla exopod sensory elements: 2 worm-like plus 6 brush-like sensory setae, one of brush-like setae on maxilla larger than others (Fig. 15), plus 1 small partly sclerotized seta (in X. echinatus there are 2 wormlike and 5 (?) brush-like sensory setae, brushes are of nearly the same size and small sclerotized seta absent); the maxilla distal praecoxal and coxal endites with one of the setae sensory (sensory setae on maxilla endites absent in X. echinatus); P1 lateral spines on the first and second segments of the exopod do not reach the bases of the spines on second and third exopod segment (in X. echinatus they exceed the bases of these spines); and P2-P4 posterior surfaces in X. meteorae sp. nov. are noticeably less spinulated than in X. echinatus (according to Sars (1924) these surfaces are densely spinulated). This new species shares with X. fallax P1 and P5 of similar structure, but it differs from X. fallax in its size (2.90 mm for X. fallax); the shape of posterior corners of prosome (triangular pointed in lateral and dorsal view in X. fallax), and the longer rostral filaments (moderately short filaments in X. fallax). Xanthocalanus meteorae sp. nov. and X. obtusus have similar shape of posterior corners of the prosome and terminal P5 segment. The new species differs from X. obtusus in its smaller size (size of X. obtusus is 2.4-3.3 mm); the 3 articulated spines of the terminal segment of P5, and the terminal spinelike attenuation (in X. obtusus all 4 terminal spines are apparently articulated). The maxilla exopod of X. meteorae sp. nov. with 9 setal elements: 2 worm-like, 6 brush-like sensory setae plus 1 small sclerotized seta; distal praecoxal and both coxal endites have sensory seta, while X. obtusus, redescribed by Vyshkvarzeva (2002), has maxilla exopod with 1 worm-like and 7 brush-like sensory setae, the later identical in structure and only the proximal coxal endite has sensory seta.

Family Aetideidae Giesbrecht, 1892 Paracomantenna minor (Farran, 1905)

(Figs 22-51)

Bryaxis minor Farran, 1905:32, pl. 4, figs. 1-5, 7-12; Rose, 1933: 102, fig. 75; Vervoort, 1952 (sheet 43): 2, fig. 6 (a, b, f, g).

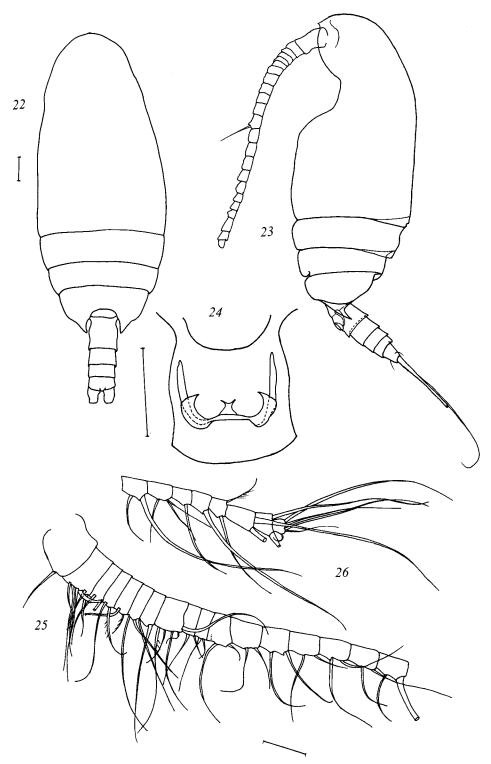
Paracomantenna minor Campaner, 1978: 871; Markhaseva, 1995: 229; 1996: 238, fig. 190.

Material examined: 3 females, 2 males, 1 female CV, 3 males CV from Great Meteor Seamount, depths from 300 to 537 m, collected by epibenthic sledge in 5 samples on the 13th, 14th, 18th and 20 September 1998.

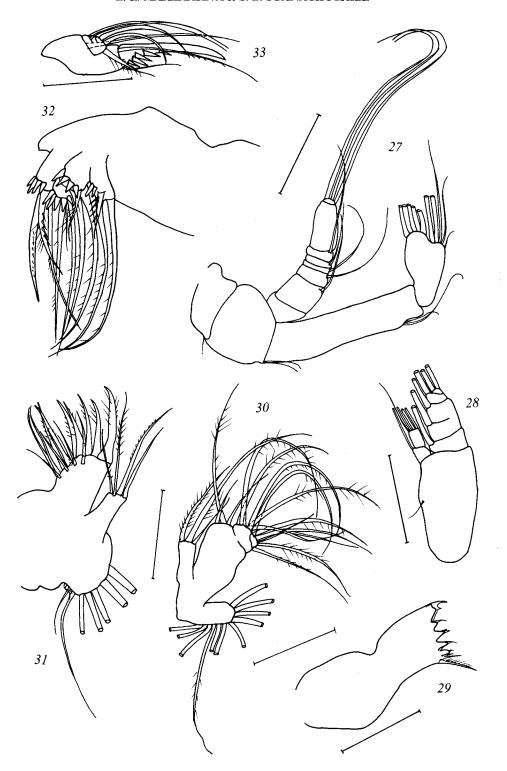
Description – Female. Total length 1.45-1.60 mm. Prosome - urosome ratio: 3.9. Cephalosome and first pedigerous somite fused (Fig. 22). Fourth and fifth pedigerous somite incompletely fused, suture is visible in lateral view (Fig. 23). Posterior corners of fifth pedigerous somite pointed and curved dorsally (Fig. 23). Caudal rami with 4 terminal, 1 ventral and 1 short lateral setae. Rostrum absent. Spermathecae elongate and curve anteriorly (Fig. 24). Antennule of 24 articulated segments. Setal armament: segment 1 with 1 seta, segment 2 with 6 setae, segments 3-7 with 2 setae each, segment 8 with 5 setae, segments 9-17 with 2 setae each, segment 18 with 3 setae, segments 19 and 20 with 1 seta each, segments 21-23 with 2 setae each, and segment 24 with 5 setae (Figs. 25-26).

Coxa of antenna with 1 small seta; basis with 2 setae; first segment of exopod without seta; segments 2–6 of exopod with one seta each, segment 7 of exopod with 3 terminal setae (Fig. 27); endopodal segment 1 with 2 setae distally; endopodal segment 2 with 5 plus 5 setae.

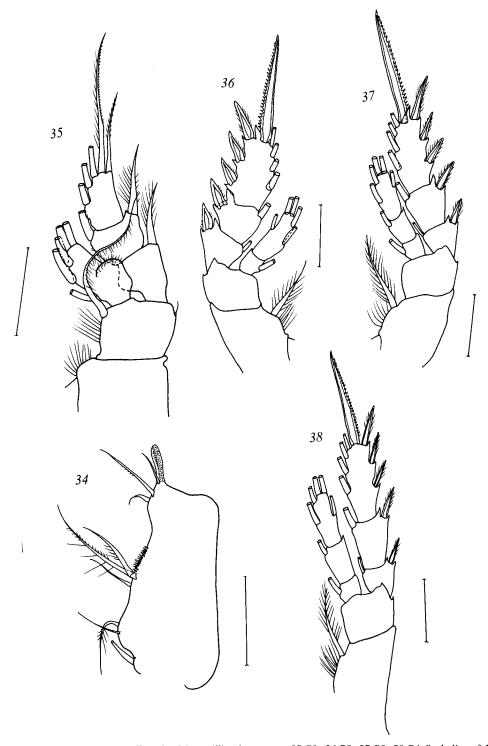
Mandibular palp basis with 1 small seta; first endopodal segment with 1 seta; second endopodal segment with 4 terminal setae (Fig. 28). Cutting edge of mandibular gnathobase with 5 teeth and one articulated seta (Fig. 29). Maxillule praecoxal arthrite with 9 terminal, 4 posterior and 1 anterior setae; coxal endite with 4 setae (Fig. 31); first and second basal endites with 3 setae each; endopod with 12 setae; exopod with 11 setae (Fig. 30); coxal epipodite with 5 large, 2 medium-sized and 2 tiny setae (Fig. 31). Maxilla praecoxal and proximal coxal endites with 3 setae each; distal coxal endite with 1 seta and 2 strongly sclerotized spine-like setae. Maxilla praecoxal and coxal endites with surface robust short spines (Fig. 32). Basal endite with a strong spine sup-



Figs 22-26. Paracomantenna minor. Female. 22. general dorsal view; 23, general left lateral view; 24, genital somite in ventral view; 25, antennule: articulated segments 1-17th; 26, antennule: articulated segments 17th-24th. Scale lines 0.1 mm.



Figs 27-33. Paracomantenna minor. Female. 27, antenna; 28, mandibular palp; 29, mandible gnathobase; 30, first and second basal endites, endopod and exopod of maxillule; 31, maxillule: praecoxal arthrite, coxal endite and coxal epipodite; 32, praecoxal and coxal endites of maxilla; 33, maxilla, basal endite plus exopod. Scale lines 0.1 mm.



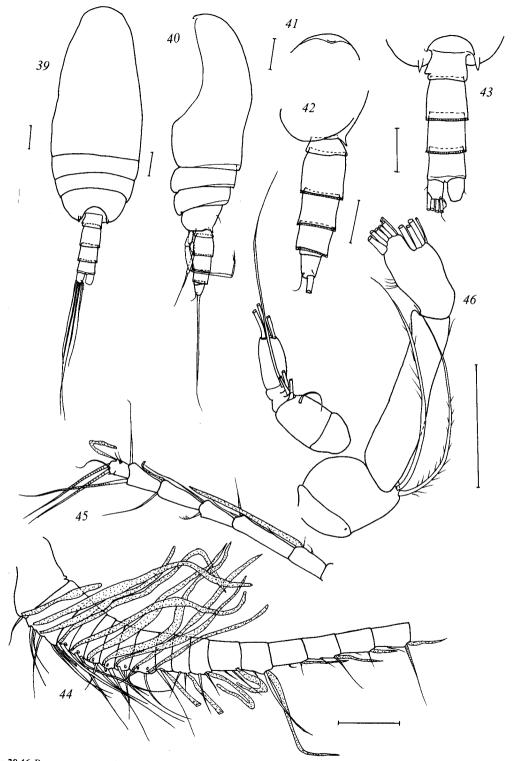
Figs 35-38. Paracomantenna minor. Female. 34, maxilliped, syncoxa; 35, P1; 36, P2; 37, P3; 38, P4. Scale lines 0.1 mm.

plied with large teeth and 2 setae; maxilla's exopod with 6 setae (Fig. 33). Syncoxa of maxilliped with 1 seta on proximal praecoxal lobe, 2 setae on middle praecoxal lobe, 3 setae on distal praecoxal lobe and coxal lobe with a group of 3 setae plus a digitiform sensory appendage (Fig. 34). Maxilliped basis with 3 setae in proximal half of the segment and 2 setae distally; endopod of 5 articulated segments with 4, 4, 4, 3+1, and 4 setae respectively. P1 endopod 1-segmented; exopod 3-segmented; endopod lateral lobe wide, with hairs along lateral margin; lateral spines on first and second segments of exopod reaching at least the mid length of the following spine (Fig. 35). P2 endopod 2-segmented, all other rami of P2-P4 3-segmented (Figs 36-38). P5 is absent.

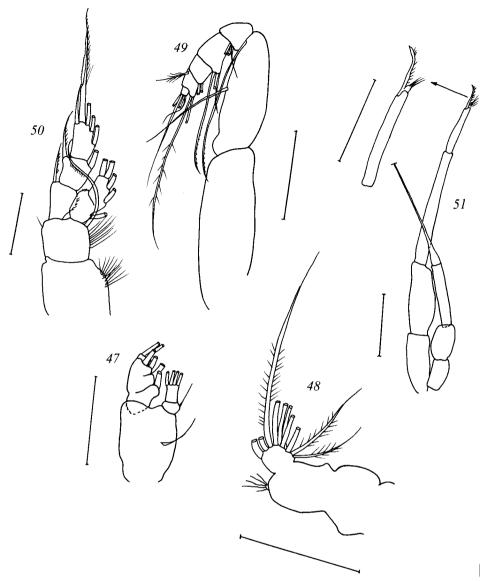
Male. Total length 1.20-1.25 mm. Prosome: urosome ratio: 3.0-3.2. Cephalosome and first pedigerous somite fused. Fourth and fifth pedigerous somites incompletely separated (Figs 39-40, 42-43). Posterior corners of fifth pedigerous somite pointed and directed dorsally (Figs 39-43). Rostrum absent. Caudal rami with 4 large terminal, 1 small lateral and 1 ventral setae. Antennule of 23 articulated segments reaching fourth-fifth pedigerous somite. Antennule setal armament as following: first articulated segment with 1+1 setal elements; segment 2 with 5+2; segments 3-7 with 2+1+?; segment 8 with 3+2+2?; segment 9 with 1+1; segments 10-18 with 2+1; segment 19 with 3; segment 20 with 2; segment 21 with 1+1; segment 22 with 2, and segment 23 with 6+1 (Figs 44-45). Coxa of antenna with 1 setal element (broken); basis with 2 long setae; endopod is enlarged compared with that of the female (Figs 27 and 46). Antenna exopod of 6 indistinctly articulated segments (second and third segments articulated in females are fused in males): first segment without seta, second with 2 setae, third to fifth segments with 1 seta each, sixth segment with 3 terminal setae (Fig. 46). Antenna first endopodal segment with 1 seta distally; second endopodal segment with 4 plus 6 setae. Mandibular palp basis as in females (Fig. 47); mandibular gnathobase is very reduced. Maxillule very reduced, only endopod and exopod bear setae; endopod with 5 small setae; exopod with 10 setae (Fig. 48). Maxilla very reduced to a small lobe lacking setae. Maxilliped syncoxa without setae; basis with 1 seta at about middle length and 1 distal seta; endopod of 5 articulated segments with 3, 3, 2, 2+1, and 4 setae (Fig. 49). P1 endopod outer lobe is less well developed compared with the female (Figs 35 and 50). P2-P4 as in females, except P4 coxa lacking medial hairs at the base of medial seta. Right P5 4-segemented, distal segment elongate and spine-like terminally. Left P5 5-segmented; distal segment elongate, its proximal (basal) part is lobe-like with terminal hairs and distal part is covered with hairs along its border (Fig. 51).

CV male. Total length 1 mm. The shape of posterior corners of prosome and main characters of oral parts similar to those of adult females. Oral parts differ in details of setation. Antenna: second and third exopodal segments incompletely fused; second endopodal segment with 6+6 setae, in other characters as in adult female. Seta on mandibular palp basis was not found, in other characters limb is as in adult female. Maxillule with 2 setae on second basal endite (3 setae in adult females) and 10 setae on exopod (11 in adult females), identical in other characters to maxillule of adult females. Maxilla is identical to that in adult females. Maxilliped syncoxa with digitiform appendage on coxal lobe as in adult female; endopod of 5 articulated segments, with 3, 3, 2, 2+1, and 4 setae respectively. Both left and right P5 are uniramous; right is 3-segmented, distal segment with 2 small lateral spines and 1 distal spine; left is 4-segmented, penultimate segment with small lateral spine and distal segment with 2 distal spines: 1 small and 1 nearly as long as terminal segment.

Remarks – The male of Paracomantenna minor is described for the first time; this is the first male known for the genus. The sensory appendage in the distal part of syncoxa of the maxilliped (coxal lobe) in Paracomantenna females and CV males is a key character, and is another example of the presence of sensory elements on the maxilliped syncoxa in the superfamily Clausocalanoidea to which the Aetideidae belongs. Clausocalanoidean families Diaixidae, Parkiidae, Phaennidae, Scolecitrichidae, and Tharybidae possess sensory elements on maxilla and maxilliped syncoxa. Their sensory elements originate from the transformation of sclerotized seta into a sensory seta (Nishida and Ohtsuka 1997). On the maxilliped they are usually situated (if present) on praecoxal lobes of the syncoxa: proximal, middle, or distal, but never on the coxal lobe (the distal lobe of segment). In aetideids there is another origin and placement of sensory element on the same segment. The aetideid genera Bradyetes, Comanten-



Figs 39-46. Paracomantenna minor. Male. 39, general dorsal view; 40, general lateral view; 41, cephalon, anterior part in ventral view; 42, prosomal posterior corners in left lateral view; 43, prosomal posterior corners in dorsal view; 44, antennule: 1-17th articulated segments; 45, antennule: 18-23rd articulated segments; 46, antenna. Scale lines 0.1 mm.



Figs 47-51. Paracomantenna minor. Male. 47, mandibular palp basis; 48, maxillule; 49, maxilliped; 50, P1; 51, P5. Scale lines 0.1 mm.

na, Mesocomantenna, Paracomantenna and Pseudeuchaeta have a sensory element on the maxilliped syncoxa associated with the coxal lobe near a group of three sclerotized setae, which (i.e., 3 sclerotized setae here) is typical of clausocalanoideans. The sensory element in aetideids is not a transformed sclerotized seta, but the poorly sclerotized attenuation of the maxillipedal coxal lobe edge, digitiform in shape. Thus we observe the evolutionary independent origination of sensory structures in

clausocalanoideans that may function as chemoreceptors in the detection of food (Nishida and Ohtsuka 1997; Ohtsuka et al. 1998).

Based on the morphology of females Comantenna, Mesocomantenna and Paracomantenna are considered related genera; Alvarez (1986) discussed placement of their species in single genus. Males of Mesocomantenna are unknown. The male of Comantenna brevicornis (Sars, 1902) is the only known male of that genus. Its P5

structure is quite different from that of P. minor; both legs of C. brevicornis are biramous (Matthews, 1964). In P. minor male P5 is uniramous. The right P5 of P. minor is 4-segemented and left is 5-segmented, of simple configuration with segments of elongate cylindrical shape, and lacking complex structures. If to compare oral parts of P. minor and C. brevicornis they appear much more similar than their males P5 (Markhaseva 1993; 1996). The morphology of the oral parts in the related taxa of benthopelagic Aetideidae apparently change in the process of speciation less abruptly than change structures connected with the process of copulation. It is probable that mating behavior and copulation of the related taxa living in the similar near-bottom conditions can differ significantly and there are consequently equally large differences in the morphology of structures involved at the process (genital complex in females and P5 in males).

In P5 structure and segmentation Paracomantenna minor male is more similar to Bradyidius angustus (Tanaka 1957) and Bradyidius spinifer (Bradford 1969) (while right leg is considered 5-segmented in later species). However, Bradyidius cannot be considered related to Comantenna, Mesocomantenna and Paracomantenna due to the high morphological difference.

DISCUSSION

The well developed sensory appendage of P. minor on the coxal lobe of maxilliped syncoxa is a derived character unique within Clausocalanoidea (as well as for Calanoida in general). It is found in the family Aetideidae only in some benthopelagic genera: Bradyetes Farran, 1936, Comantenna Wilson, 1924, Crassantenna Cole et. al, 1972, Mesocomantenna Alavarez, 1986, Paracomantenna Campaner, 1978 and Pseudeuchaeta Sars, 1905. Presence of this derived structure is combined with a primitive morphology of P5 in males of these genera (in Crassantenna and Mesocomantenna males unknown). Pelagic aetideids (except Chiridiella) share males P5 of simple, or complex structure, but usually with one-segmented endopods (if present at all), and exopods: right 2-segmented and left 3-segmented (Markhaseva 1993; 1996). The most primitive type of male P5 registered in aetideids (both exopods 3-segmented and both endopods indistinctly 2-segmented), is known for benthopelagic species Parabradyidius angelikae (Schulz and Markhaseva 2000).

As mentioned above, P5 of primitive aetideid

type is retained in males of *Bradyetes*, *Comantenna*, and *Pseudeuchaeta* as biramous P5 of simple configuration with segments of elongate cylindrical shape, and lacking complex structures, with 2-segmented left endopod (*Bradyetes* and *Comantenna*), or both exopods 3-segmented (*Pseudeuchaeta*). Primitive P5 of males in these genera combined with the presence of such derived structures as the sensory element on the maxilliped syncoxa is a good example of benthopelagic aetideids morphology, which is usually characterized by the mosaic of primitive and derived morphological features (Markhaseva 1993).

It has been suggested that benthopelagic calanoid copepods share similar characters such as a compact body, robust long external spines on swimming leg exopods, short antennules and smaller numbers of setae on the mouthparts (Bowman and Gonzalez 1961; Bradford 1969). Aetideidae, the family of calanoid superfamily Clausocalanoidea has been well studied including its benthopelagic representatives (e.g., Campaner 1978a; Bradford and Jillet 1980; Alvarez 1986; Markhaseva 1996; Schulz 2002; Schulz and Markhaseva 2000). Nevertheless some near-bottom aetideid genera do not have such characters, or at least not the complete set of the features listed above.

Ancestral Clausocalanoidea in general were more probably pelagic inhabitants (Park, 1986). Ancestral Aetideidae were apparently pelagic also. Bradford-Grieve (2002) considers that "members of Clausocalanoidea of the families Aetideidae, Diaixidae, Phaennidae, Pseudocyclopiidae, Stephidae and Tharybidae appear to have secondarily returned to the benthopelagic environment, although it is impossible to determine when and how often it occurred". Aetideid species have re-invaded the near-bottom localities perhaps more than once in the shallow and deep waters; a near-bottom mode of life is apparently a secondary, later adaptation for the group.

The extant benthopelagic aetideids can be characterized by the presence of the combination of primitive and derived features (Markhaseva, 1993), that is not typical of extant pelagic aetideids. Recent pelagic aetideids have lost some primitive features retained by benthopelagic descendants from their pelagic ancestors. In the same time the benthopelagic aetideids show little resemblance among each other (Markhaseva, 1993). This lack of similarity may be an evidence for several invasions of

their pelagic ancestors to the near-bottom layers.

Matthews (1964) studied the biology of some aetideids (Aetideopsis armata (Boeck, 1872) (as Chiridius armatus), Bradyidius armatus Giesbrecht, 1897 (as Bradyidius bradyi), Aetideus armatus (Boeck, 1872), Comantenna brevicornis and phaennids Xanthocalanus fallax Sars, 1921 and X. minor Giesbrecht, 1892. He suggested that hyperbenthic (benthopelagic) and pelagic copepods differ in their biology. The degree of adaptation depends on how closely they are associated with the sea floor. Some benthopelagic copepods species, for example lay far fewer eggs than pelagic species, some have a shorter naupliar phase (e.g., phaennids), some only very few naupliar stages (Aetideidae), and some have self-adhesive eggs or eggs that are stuck to the sea bed by females (Aetideidae). There is little information available about the feeding behaviour of benthopelagic calanoids. Gowing and Wishner (1986, 1992) concluded from gut content studies of Xanthocalanus spp. that they are predominantly detritivores in the deep-sea habitat. Ohtsuka and Mitsizumi (1990) studied the gut content of Paramisophria platysoma Ohtuska and Mitsuzumi, 1990 from shallow waters and found this species feed carnivorously on epibenthic harpacticoids. However, studies of calanoid biology are few and much more investigation is required.

The benthopelagic calanoids found at the Great Meteor Seamount include seven genera, all previously described from other regions. Bradyidius armatus and Tharybis macrophthalma

were the most numerous and abundant species found at the Great Meteor Seamount (Table 1).

The genus Bradyidius is globally represented by many species both in shallow and deep waters. B. armatus and B. luluae were recorded off the Norwegian coast; B. armatus also is known from the Norwegian and Barents Seas and off the coast of Great Britain, and B. luluae from the northwestern Atlantic (Markhaseva 1996; 1998a). The genus Paracomantenna is known from the Brazilian coast (Campaner 1978a; Alvarez 1986) and from the eastern tropical Pacific (Markhaseva 1995). Paracomantenna minor is known from a single record off the west coast of Ireland (Farran 1905). Many species of the genera Xanthocalanus and Tharybis are recorded worldwide where they inhabit all depths from epi- to the bathypelagic environment (e.g., Sars 1902, 1924-25; Tanaka 1960; Matthews 1964; Grice and Hulsemann 1970; Campaner 1978b; Schulz and Beckmann 1995; Bradford et al. 1983; Gowing and Wishner 1986; Markhaseva 1998b; Ohtsuka et al. 1998; Andronov 2002; Vyshkvartzeva 2002). T. macrophthalma has a wide distributional range and is known also from Norwegian waters, northwestern Ireland, the Azores, off western Spain, and the Mediterranean and Adriatic Seas (Razouls 1995). The genera Paramisophira and Metacalanus are both widely distributed and inhabit shallow coastal waters (see for references Ohtsuka et al. 2002). However Paramisophria ovata Heinrich, 1996 and P. rostrata Heinrich, 1996 were recently found at depths of 500 and 1200 m (Heinrich

Table 1: Frequency and total numbers of the benthopelagic species collected with an opening/closing epibenthic sledge in September 1998 on the Great Meteor Seamount

Species	Frequency of	Total number found		
	occurrence (%)	Female	Male	Copepodids
Family Actideidae Giesbrecht, 1892				
Bradyidius armatus Giesbrecht, 1897	55	>298	>54	>195
B. luluae Grice, 1972	36	7 1	1	47
Paracomantenna minor (Farran, 1905)	45	3	2	5
Family Phaennidae Sars, 1902				
Xanthocalanus meteorae sp. nov.	27	10	0	(
Family Pseudocyclopiidae T. Scott, 1894				
Pseudocyclopia sp.	9	0	0	1
Family Tharybidae Sars, 1902				
Tharybis macrophthalma Sars, 1902	82	51	17	>426
Family Arietellidae Sars, 1902				
Metacalanus inaequicornis (Sars, 1902)	9	1	0	(
Paramisophria sp.	55	2	0	11
P. cf. spooneri	18	5	3]

1996). P. spooneri (to which Paramisophria cf. spooneri may be conspecific) and M. inaequicornis (first described as Scottula inaequicornis by Sars (1902) and removed to the genus Metacalanus by Campaner (1984)) are known from a single record each, from the Plymouth area (Krishnaswamy 1959) and from Norway (Sars 1902), respectively.

Similarity on a species/generus level is observed when comparing benthopelagic calanoid fauna of the Great Meteor Seamount with that of Norwegian waters. Four of the benthopelagic calanoids found at the Great Meteor Seamount are known from Norway: Bradyidius armatus, B. luluae, Metacalanus inaequicornis, and Tharybis macrophthalma, as well as representatives of the genera Pseudocyclopia and Paramisophria. If we characterize Great Meteor Seamount benthopelagic calanoid species by their distributional ranges within the latitudinal zones of the World Ocean (Nesis 1982; Markhaseva 1998a), they may be considered mostly restricted to the Boreal Atlantic zone.

MATERIAL AND METHODS

Calanoid copepods were studied by analyzing samples collected with an epibenthic sledge during the RV "Meteor" cruise 42 to the Great Meteor Seamount (northeastern Atlantic) in September 1998. As part of a larger sampling programme (Pfannkuche et al. 2000), samples from the benthic boundary layer were collected with an opening/closing epibenthic sledge in order to investigate the specific community of benthic and pelagic invertebrates associated with the bottom. The sledge was employed at eleven stations at depths from about 295 to 553 m (Brenke et al. 2000). At four stations the epibenthic sledge consisted of the epinet of 500 µm mesh size. At the nine stations an additional supranet of 300 µm was mounted above the epinet (see Brandt and Barthel 1995). The mechanism of the opening/closing device did not work satisfactorily and, hence, contamination from the water column is probable. At the first station the sledge was employed for 20 minutes, but due to the relatively large amount of sediment sampled, the tow time had to be reduced to ten minutes. Immediately after sampling the organisms were concentrated on sieves (1000 µm mesh size) to elutriate the sediment and than transferred to 80% ethanol.

Zooplankton samples were collected using a 100 µm mesh multiple opening-closing net. Stratified sampling included the water column

down to 2500 m at oceanic stations; at the plateau and slope stations the multinet was stopped between about 10 and 100 m above the sea floor. The samples were preserved in 4% borax-buffered formaldehyde seawater solution (Schiel et al. 2000).

The specimens selected were dissected under a microscope. All figures were prepared using *camera lucida*.

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