

THE GENUS *EUAUGAPTILUS* (CRUSTACEA,  
COPEPODA). NEW DESCRIPTIONS AND A  
REVIEW OF THE GENUS IN RELATION TO  
*AUGAPTILUS*, *HALOPTILUS* AND  
*PSEUDAUGAPTILUS*

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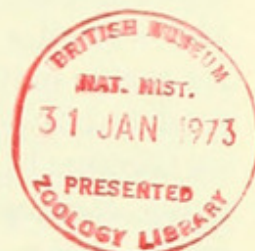
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By J. B. L. MATTHEWS



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## SYNOPSIS

Information on the species in the Augaptilidae is scattered and often poor. This can make identification difficult, particularly in the case of *Euaugaptilus* which has 59 accepted species, including four described in the present work, plus several supposed synonyms. All species names attributed to the four genera are listed in the paper, with notes where necessary and a summary of geographical distribution; structural details are tabulated. Several species of *Euaugaptilus* show intraspecific variation in size, the degree of reduction of the mandible and 1st maxilla, and in the setation, even the segmentation, of the swimming limbs. The species cannot, therefore, be classified on the basis of firm, concise definitions. Coefficients of overall similarity between each pair of species indicate that the genus can be divided into two groups which are defined polythetically and named after a typical member, *E. affinis* and *E. squamatus* respectively. The other three genera, particularly *Augaptilus* and *Pseudaugaptilus*, are much more homogeneous.



This numerical method possesses several advantages over others, and the recent description elsewhere of some new species provides an opportunity to test its practical application. These new species can be satisfactorily placed in the system and discussed without it being essential to repeat the computer programme.

#### GENERAL INTRODUCTION

THE family Augaptilidae Sars, 1905, is composed almost entirely of bathypelagic copepods. The first few species were described in 1863 by Claus who placed them in his genus, *Hemicalanus*. Giesbrecht described some additional species in 1889 and erected a second genus, *Augaptilus*, for those species with a reduced number of segments in the urosome. As Claus' use of the generic name *Hemicalanus* was predated by Dana in 1853, it became necessary to emend Claus' name and Giesbrecht (in Giesbrecht & Schmeil, 1898) proposed the name *Haloptylus* instead. (The generic name, *Hemicalanus* Dana, is no longer used either, as it has turned out to be a composite group. As it has never been officially suppressed, it is proposed here that *H. calaninus* be designated the type of Dana's genus, thus making *Hemicalanus* Dana a junior synonym of *Centropages* Krøyer, 1849.)

In the early years of this century many more new species were described, most of them by Sars from the collections made by Prince Albert I of Monaco. Some of these went into new genera distinguished by various special characters but the majority were closely related to the previously known species of *Augaptilus*. In 1920 Sars divided this genus, largely on the basis of the structure of the 1st maxilla; those species with greatly reduced setation remained in *Augaptilus*, while the rest were transferred to *Euaugaptilus*. There is now a total of twelve genera which have been erected in this family, as follows:

<i>Augaptilus</i> Giesbrecht, 1889	<i>Centraugaptilus</i> Sars, 1920
<i>Haloptylus</i> Giesbrecht, 1898	<i>Euaugaptilus</i> Sars, 1920
<i>Pontoptylus</i> Sars, 1905	<i>Heteroptylus</i> Sars, 1920
<i>Pseudaugaptilus</i> Sars, 1907	<i>Pachyptylus</i> Sars, 1920
<i>Pseudhaloptylus</i> Wolfenden, 1911	<i>Neoaugaptilus</i> Brodsky, 1950
<i>Augaptilina</i> Sars, 1920	<i>Disco</i> Grice & Hulsemann, 1965

Right from the start *Euaugaptilus* contained a large number of species and Sars recognized the desirability of further division, but was unable to find satisfactory taxonomic criteria. Since then two attempts have been made at subdivision. Sewell (1932, 1947) elaborated a system of grouping based largely, but not entirely, on the structure of the mandible and 1st maxilla; this has been accepted as useful but not generally as representative of true relationships (see Vervoort, 1965). Brodsky (1950) proposed the genus *Neoaugaptilus* for the species, *N. distinctus*, discovered by him, in which there was reduced segmentation of both rami of the 1st swimming limb; even if this genus were accepted it would still leave the great majority of species in *Euaugaptilus*.

The present study was prompted by the discovery of a single specimen of a new species of *Euaugaptilus* in a plankton sample taken off the west coast of Africa. In the course of the investigation a specimen of a second new species was received from Dr Hulsemann, then of Woods Hole Oceanographic Institution, and specimens of



two more new species and of two undescribed males were sent by Mr Roe of the National Institute of Oceanography, England; all these are described in the present paper. The size and confused state of the genus make it a good subject for analysis by modern techniques of numerical taxonomy. This taxonomic review of the genus has been carried out in conjunction with *Augaptilus*, *Pseudaugaptilus* and *Haloptylus* with a twofold purpose: first it provides an opportunity to review these genera in their own right and, secondly, the inclusion of other, well recognized, conventional taxa provides a basis for evaluating the results obtained for *Euaugaptilus*. Other genera of the family have not been included as they are clearly separated by special characters which cannot easily be incorporated into a study of this nature. The intention has been to rank the species and detect any subgroups by using as wide a range of morphological characters as possible, and submitting the results, expressed as coefficients of similarity, to a principal coordinates analysis. The calculations have been carried out on the Orion computer at the Rothamsted Experimental Station and the results deposited at the British Museum (Natural History).

Since taxonomic judgements must ultimately rely on original descriptions and type material, the morphological data on which the computer analysis is based have purposely been obtained from such descriptions, supplemented where necessary by examination of specimens, if possible type material. Original material has been obtained from Scripps Institution of Oceanography (the species described by Esterly), from the University Museum, Amsterdam (the species described by Scott), and from Professor Brodsky of Leningrad (the species described by him in 1950). Material has also been sent by Drs Grice and Hulsemann (specimens from the Indian Ocean and South Pacific), lent by the Bergen Museum (specimens from the Michael Sars North Atlantic Deep Sea Expedition, 1910) and examined at the British Museum (Natural History). The males of many species are still unknown and in other cases known males cannot yet be assigned with certainty. This investigation, therefore, has been limited to females, except for those males which have been described but not assigned to a known female; in such cases the name is included in the review of the genus but excluded from the computer analysis. Also excluded from the analysis are five species of *Euaugaptilus* and two of *Haloptylus*, whose descriptions by Park (1970) were published after this stage of the study had been completed. Their structural details are included and they are considered at the end of the numerical section as an example of how the conclusions reached in the present paper may be applied to future discoveries.

#### DESCRIPTIONS

##### *Euaugaptilus pachychaeta* sp. nov.

**MATERIAL AND LOCALITY:** 1 adult female in stramin-net haul from 600–0 m off the coast of Nigeria (5°49'N, 3°24'E) on 9 May 1962. Deposited at the British Museum (Natural History), reference number BM 1972.2.10.1A–F.

**DESCRIPTION OF THE FEMALE** (Figs 1 and 2, Table 5): The total length of the body is 7.0 mm. The length of the prosome is 2.5 times its width and 4.1 times the



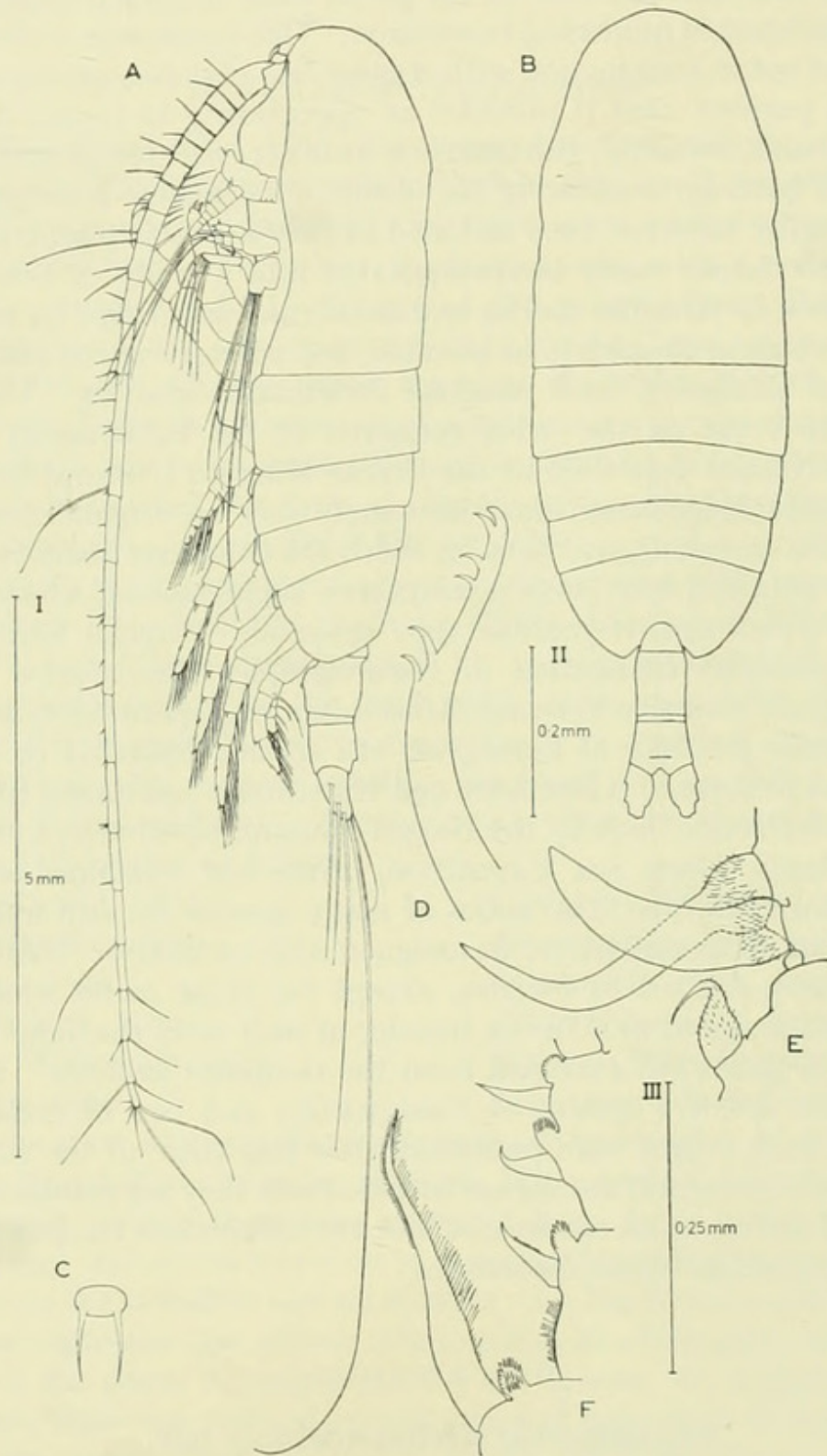


FIG. 1. *Euaugaptilus pachychaeta* ♀. A. Lateral view. B. Dorsal view. C. Rostrum in antero-ventral view. D. Mandibular gnathobase. E. Modified setae on protopodite of maxilliped. F. Distal outer border of exopodite of 1st swimming limb. A and B to scale I; C - E to scale II; F to scale III.



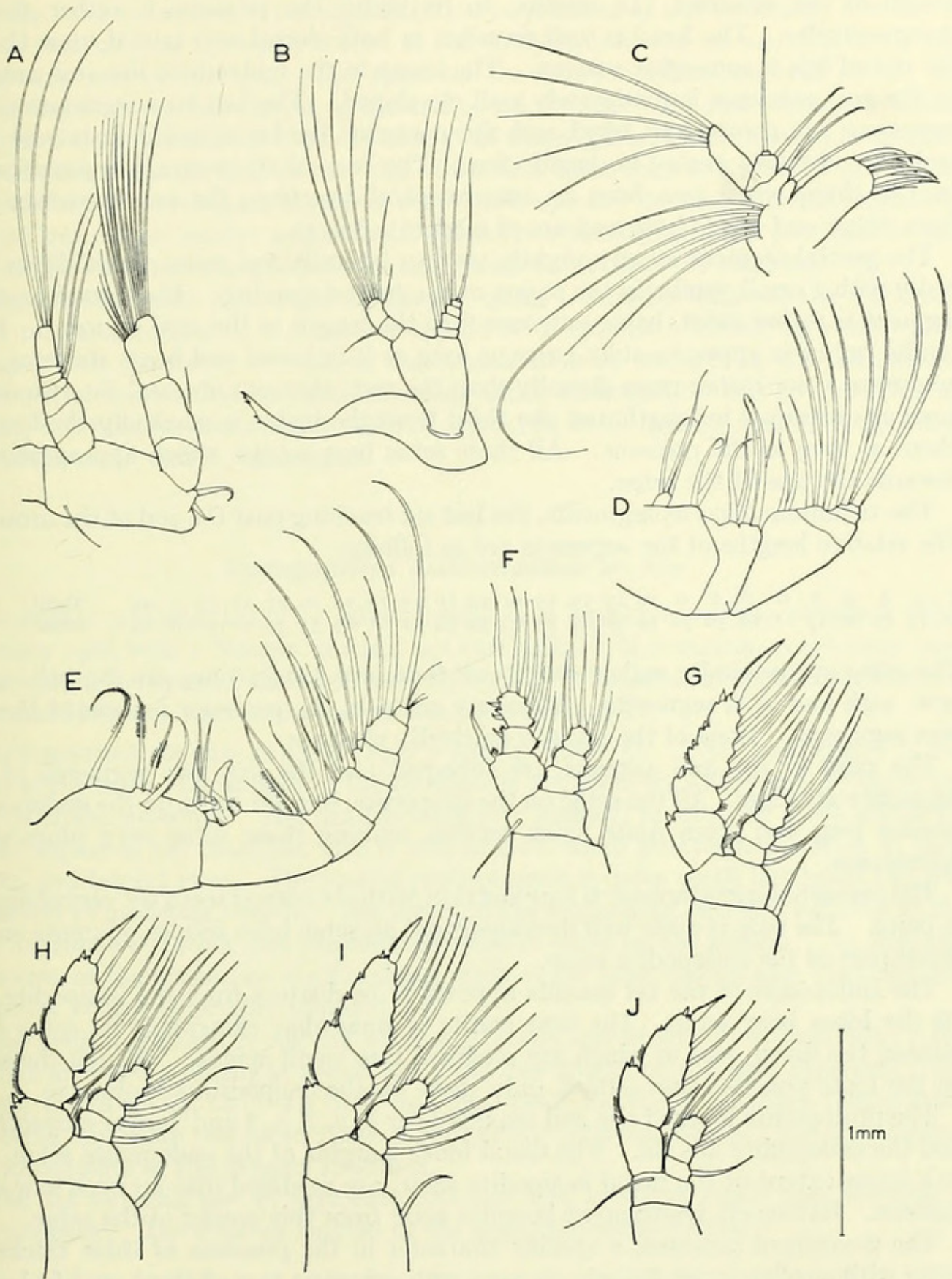


FIG. 2. *Euaugaptilus pachychaeta* ♀. A. 2nd antenna. B. Mandible. C. 1st maxilla. D. 2nd maxilla. E. Maxilliped. F. 1st swimming limb. G. 2nd swimming limb. H. 3rd swimming limb. I. 4th swimming limb. J. 5th swimming limb.



length of the urosome. In relation to its width the prosome is rather shallow dorsoventrally. The head is well rounded in both dorsal and lateral view though the dorsal line is somewhat uneven. The hump in the midventral line just anterior to the 2nd antennae is moderately well developed. The last two segments of the mesosome are completely fused and the posterior border rounded in lateral view and very obtusely angled in dorsal view. The base of the rostrum is pronounced, oval in shape when seen from an anteroventral direction; the two filaments arise from either end of the base and are of moderate length.

The genital segment is only slightly swollen laterally but more distinctly so ventrally with a small papilla in the region of the genital opening. The second urosome segment is rather short, being only one fifth the length of the anal segment. Each caudal ramus is approximately twice as long as it is broad and bears six setae; the innermost is set rather more dorsally than the rest; the next one and the two outermost are subequal in length and the third from the inside is markedly the longest, about as long as the prosome. All these setae bear setules which appear plumose towards the tips of the setae.

The 1st antenna has 25 segments, the last six reaching past the end of the urosome. The relative lengths of the segments are as follows:

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	Total
42	13	15	19	17	21	21	30	32	34	40	46	53	65	59	59	61	61	63	53	49	40	46	38	23	1000

The setae are generally rather short but there are longer ones on the 9th, 14th, 21st, 24th and 25th segments. There are setae on the posterior margin of the last four segments. None of the setae is markedly plumose.

The rami of the 2nd antenna are subequal and the last two segments of the exopodite are fused. All the setae on the exopodite, but not those on the endopodite, possess long and often quite thick setules, making these setae very plumose in appearance.

The mandibular gnathobase is long and thin, with six curved teeth set very obliquely in pairs. The palp is quite well developed and all setae have setules, plumose on the distal part of the endopodite setae.

The endopodite of the 1st maxilla appears to be distinct from the basipodite and all the lobes bear setae. The first endite is somewhat elongated; its setae bear setules, the distal ones of which are modified into small spines. Though the setae on the exite possess some setules, only those on the exopodite are plumose.

The protopodite lobes of the 2nd maxilla bear 3, 2, 2, 3, 2 and 3 setae respectively and the endopodite has six. The distal inner margins of the endopodite setae, and to a lesser extent of the distal basipodite setae, are modified into an open saw-edge pattern. Extremely transparent lamellae arise from this border of the setae.

The maxilliped possesses a specific character in the presence of three thickened setae with swollen bases densely covered with spinules; two of these modified setae are situated on the proximal part of the basipodite and the third, with its tip transformed into a hook and lying across the other two, arises from the distal part of the coxopodite. The long setae on the endopodite are modified in the same way as those on the 2nd maxilla.



There is no reduction in the segmentation or setation of the swimming limbs. A seta is present near the outer border of the basipodite of the 1st and 5th limbs but apparently not on the 4th. The spine on the first exopodite segment of the 1st swimming limb reaches almost to the end of the ramus. The other spines are short but stand out prominently. At the base of all these spines there is a small irregularly shaped protuberance; that at the base of the first spine ends in a number of digitate and spinose processes and is also covered with spines; the second one is similarly shaped but rather smaller and without spines over the surface; the processes on the end of the third are sharply pointed and those on the last are rounded.

The specific name (Gr. *παχύς* = thick + *χαιτή* = bristle) refers to the thickened setae on the maxilliped, a character shared with no other known member of the genus. This character, as well as the combination of features in the mandibular gnathobase, 1st maxilla and 1st swimming limb, distinguishes this species from all others, of which the most closely related appear to be *E. tenuispinus*, *E. marginatus*, *E. grandicornis*, and *E. squamatus*.

### *Euaugaptilus hulsemannae* sp. nov.

**MATERIAL AND LOCALITY:** 1 adult female in a plankton sample obtained 16/17 January 1966 with a Nansen vertical net (see Grice & Hulsemann, 1967) from 3000 to 2000 m in the South Pacific (34°20'S, 85°05'W). Deposited at the British Museum (Natural History), reference number BM 1972.2.10.2A-H.

**DESCRIPTION OF THE FEMALE** (Figs 3 and 4, Table 5): The total length of the body is 7.4 mm. The length of the prosome is 2.7 times its width and 3.7 times the length of the urosome. The head is relatively narrow, broadening quite markedly in the region of the maxillae, and it also bears a small prominence visible in both dorsal and lateral view. The rostral protuberance is quite small but bears two fine filaments of moderate length. The hump in the midventral line just anterior to the 2nd antennae is rather less pronounced than is usual in the genus. The last two segments of the mesosome are fused but signs of the joint can be seen laterally; the posterior border is broadly rounded.

The genital segment is slightly swollen laterally but distinctly so ventrally. The second urosome segment is about one third the length of the anal segment. The length of the caudal rami is a little less than twice the width and each ramus bears six setae, similarly placed to those described for *E. pachychaeta*. The two longest are incomplete in the present specimen.

The 1st antenna has 25 segments, the last two of which reach past the end of the urosome. The relative lengths of the segments are as follows:

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	Total
62	19	23	29	27	27	31	31	35	39	43	47	53	53	47	53	55	53	45	37	37	33	45	41	35	1000

The appendage appears evenly setose along its length except for rather longer setae towards the tip. The last four segments possess setae on their posterior margins. There are no plumose setae.



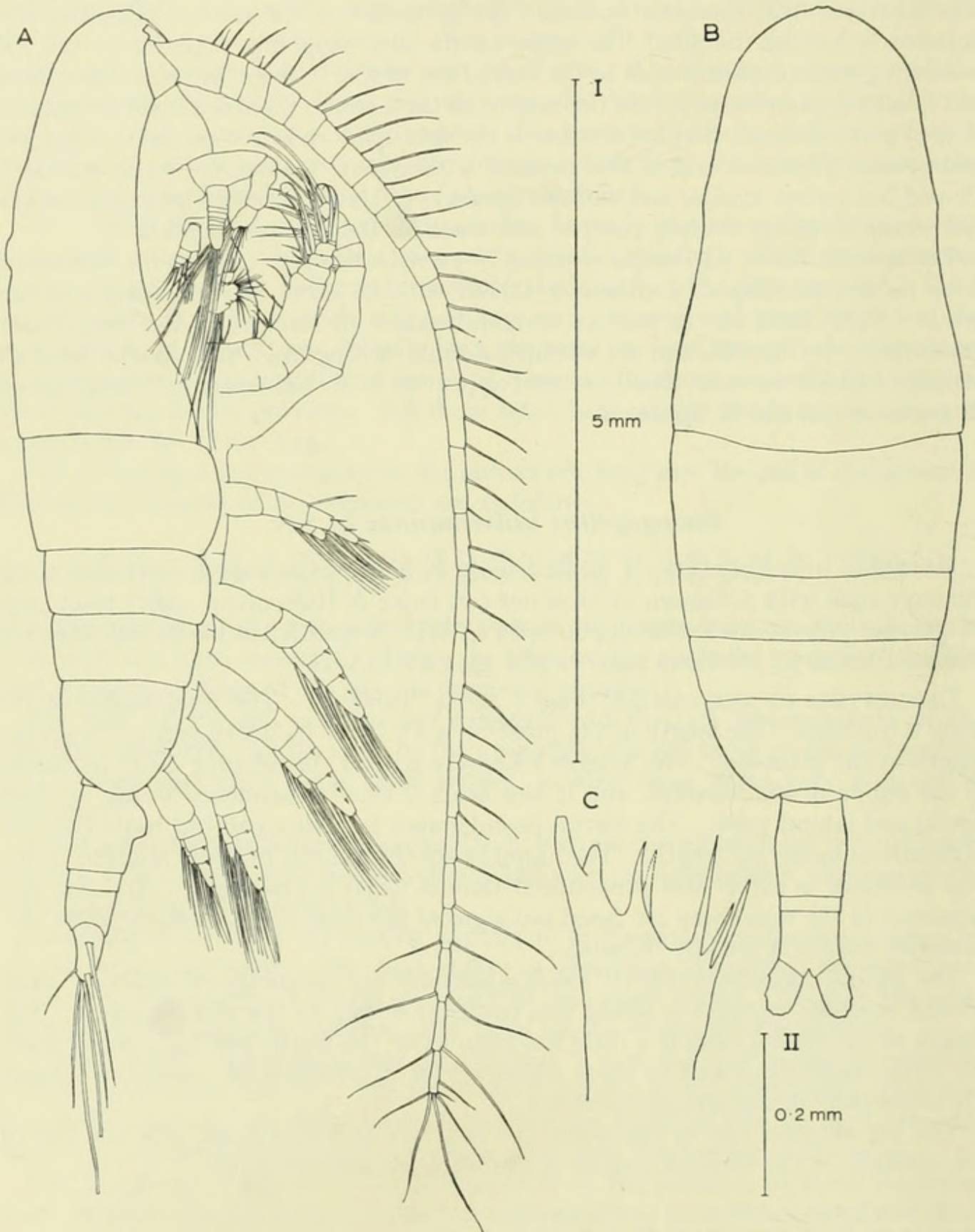


FIG. 3. *Euaugaptilus hulsemannae* ♀. A. Lateral view. B. Dorsal view. C. Mandibular gnathobase. A and B to scale I; C to scale II.



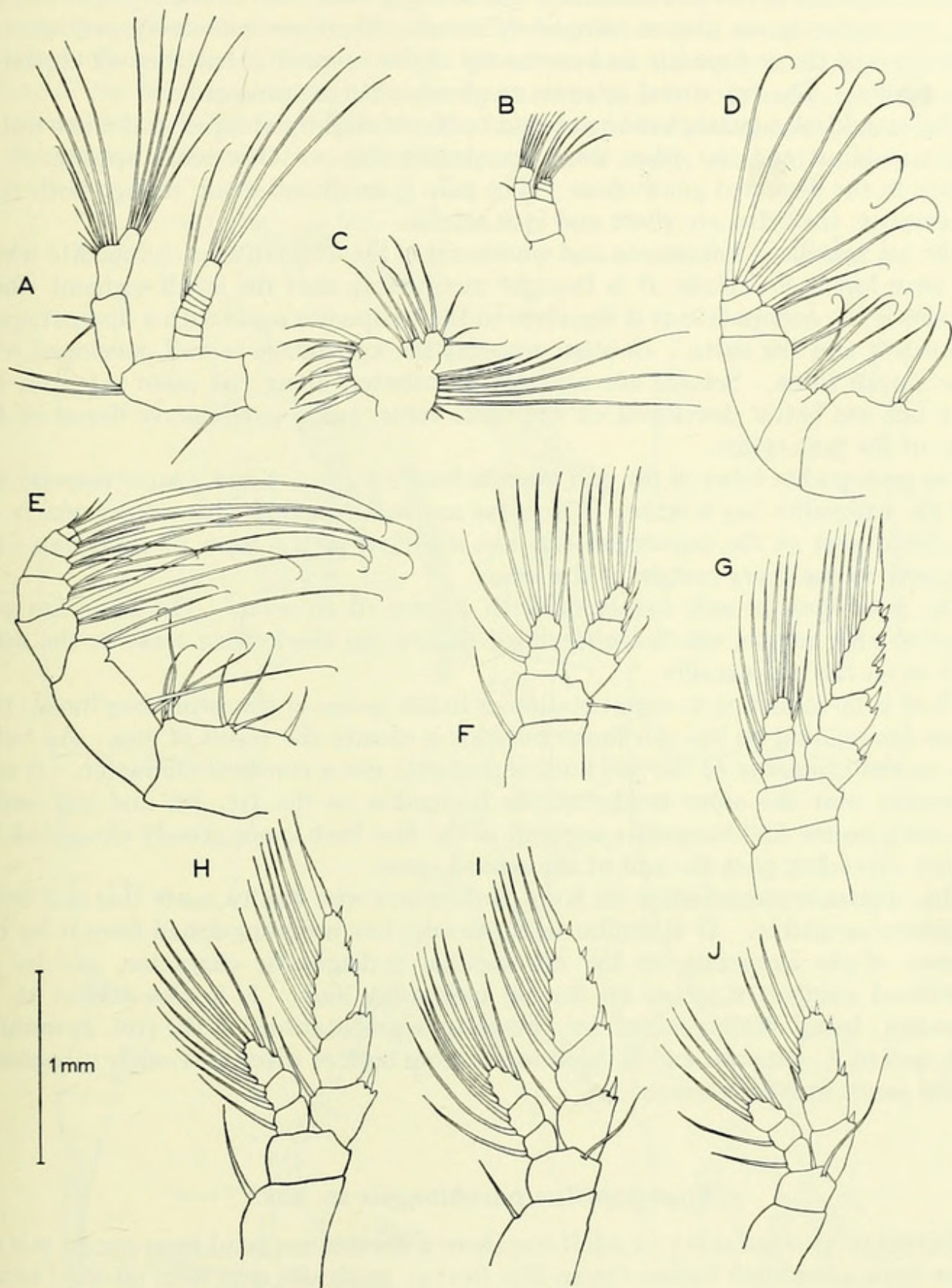


FIG. 4. *Euaugaptilus hulsemannae* ♀. A. 2nd antenna. B. Mandibular palp. C. 1st maxilla. D. 2nd maxilla. E. Maxilliped. F. 1st swimming limb. G. 2nd swimming limb. H. 3rd swimming limb. I. 4th swimming limb. J. 5th swimming limb.



The exopodite of the 2nd antenna is less strongly built than the endopodite and the last two segments are almost completely fused. There are well developed setae on both lobes of the endopodite and on the tip of the exopodite, but they all appear to lack setules. The two distal setae on the basipodite are plumose.

The mandibular gnathobase has seven teeth set slightly obliquely; the two outermost are blunt and the other three are slender spines. One tooth appears to be broken in the dissected gnathobase. The palp is small and weak, though both rami are present; the setae are short and lack setules.

The 1st maxilla is uniramous and whether it is the exopodite or endopodite which has been lost is uncertain; it is thought more likely that the small segment which remains is the endopodite as it lies close to the basipodite setae with a distinct space between it and the exite. In other respects the appendage is well developed with setae on all lobes. Setules are sparsely distributed along the main setae on the exite but are better developed on the inner setae, being particularly dense on the setae of the first endite.

The protopodite lobes of the 2nd maxilla bear 2, 0, 1, 3, 2 and 3 setae respectively and the exopodite has 6 setae. The setae are well supplied with setules which, on the distal part of the outermost six, are modified in the form of thin plates set obliquely to the inner margin of the setae.

The maxilliped is well developed with a total of 29 setae. The setae are well supplied with setules which are modified distally on the longest setae in the same form as on the 2nd maxilla.

There is no reduction in segmentation or in the spines of the swimming limbs; two spines are missing on the 5th limbs but this is clearly the result of loss. An extra seta on the exopodite of the 3rd limb is probably not a constant character. A seta is present near the outer border of the basipodite of the 1st, 4th and 5th limbs. The spine on the first exopodite segment of the first limb is not greatly elongated, its tip not extending past the end of the second spine.

This species is named after Dr Kuni Hulsemann who kindly made this and other specimens available. It is similar to *E. farrani* but is distinguished from it by the absence of the exopodite on the 1st maxilla, a diagnostic character, and by an unreduced number of spines on the 1st swimming limb. It is also similar to *N. distinctus*, being distinguished by complete segmentation of the 1st swimming limb, and to *E. elongatus* and *E. hyperboreus* from both of which it is easily recognized by the much broader prosome.

### *Euaugaptilus paroblongus* sp. nov.

**MATERIAL AND LOCALITY:** 1 adult female in a divided net haul from 940 to 700 m, taken with a modified Indian Ocean Net (N113), mesh size 0.33 mm, off the Canary Islands (28°07'N, 14°07'W) on 26 November 1965. Deposited at the British Museum (Natural History), reference number BM 1972.2.10.3A-G.

**DESCRIPTION OF THE FEMALE** (Figs 5 and 6, Table 5): The total length of the body is 8.2 mm. The length of the prosome is 2.8 times its width and 4.1 times the



length of the urosome. The widest point lies just behind the well-marked division between the cephalosome and mesosome. The head is rounded in lateral view though a little further back the dorsal margin becomes more uneven; in dorsal view the outline of the head appears rather more square due to lateral broadening level with the 1st antennae. The 'shoulders' by the insertion of the 2nd antennae are normal for the genus. The posterior end of the prosome is evenly rounded in both dorsal

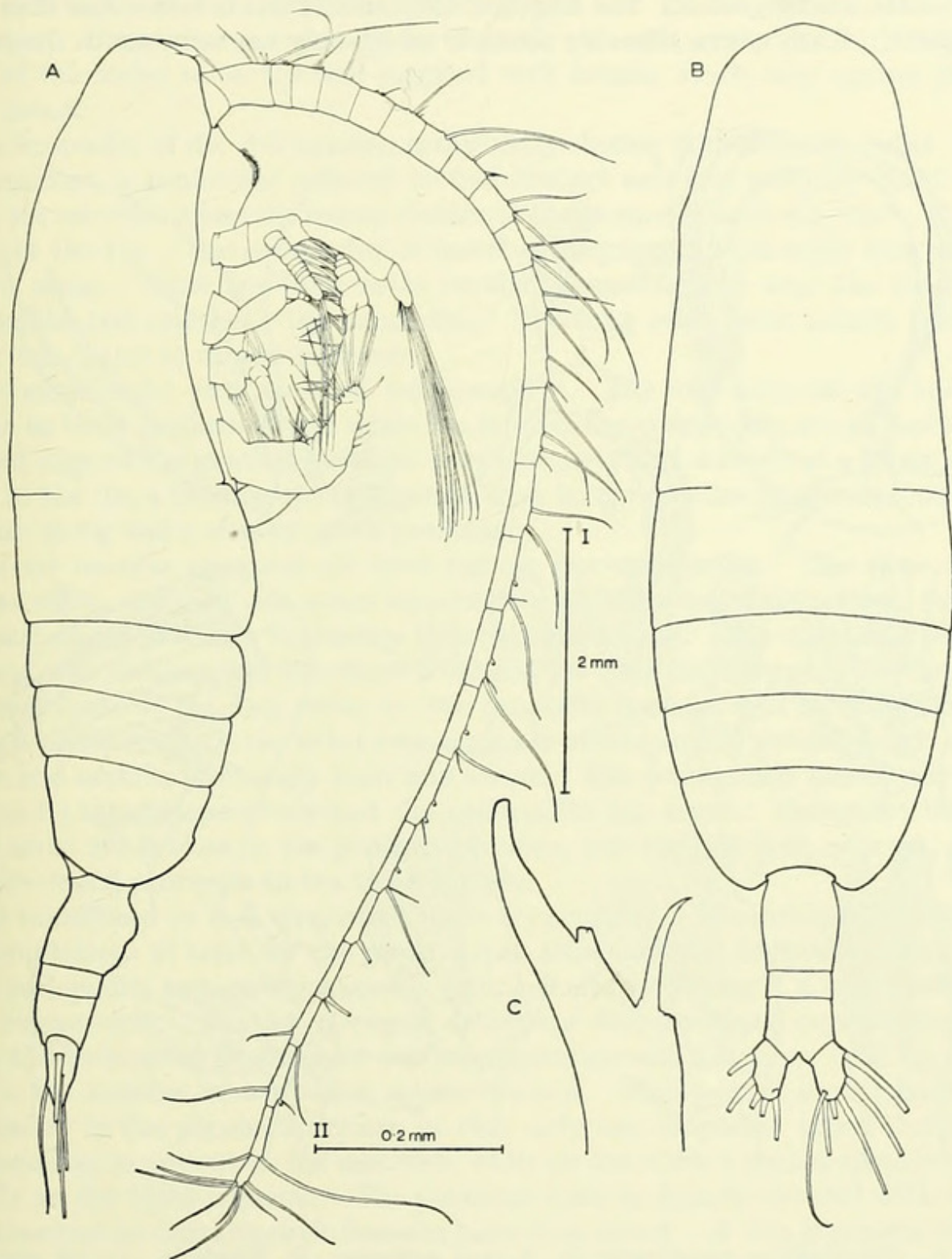


FIG. 5. *Euaugaptilus paroblongus* ♀. A. Lateral view. B. Dorsal view. C. Mandibular gnathobase. A and B to scale I; C to scale II.



and lateral view. The rostral protuberance is moderately well developed and bears two firm filaments of medium length. The mid-ventral hump just anterior to the 2nd antennae is prominent and has a partial covering of fine setae.

The genital segment is slightly swollen laterally and the swelling around the genital opening is also not very prominent. The middle segment of the urosome is proportionally longer than in most species of the genus, being over a third of the length of the anal segment. The length of the caudal rami is rather less than twice their width. Each ramus bears six setae, of which only one is intact in the present

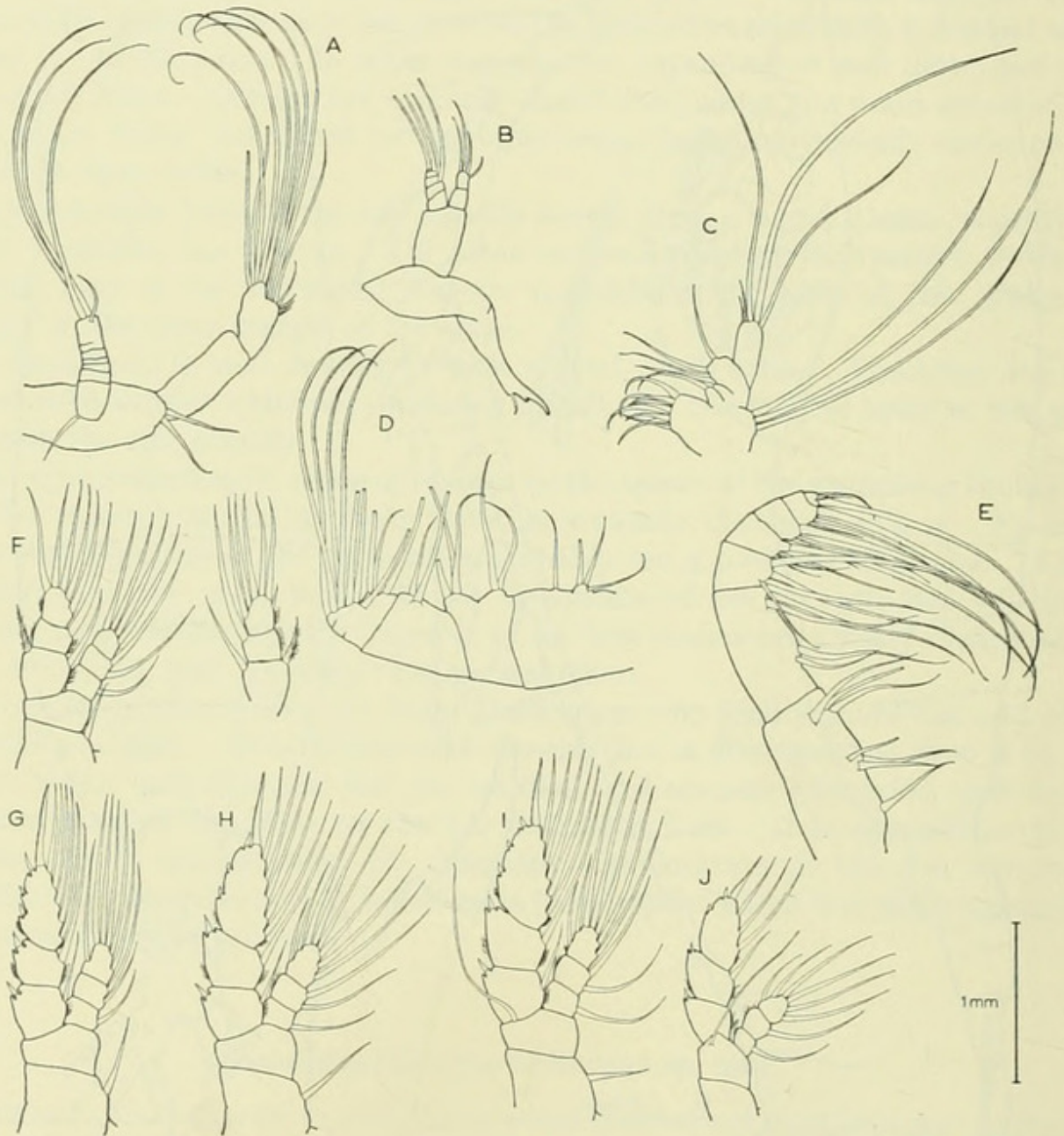


FIG. 6. *Euaugaptilus paroblongus* ♀. A. 2nd antenna. B. Mandible. C. 1st maxilla. D. 2nd maxilla. E. Maxilliped. F. 1st swimming limb, left and exopodite of right. G. 2nd swimming limb. H. 3rd swimming limb. I. 4th swimming limb. J. 5th swimming limb.



specimen; this seta, set on the dorsal surface near the inner margin, curves inwards and backwards, but only a little upwards.

The 1st antenna has 25 segments, the last four of which extend past the end of the urosome. The relative lengths of the segments are as follows:

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	Total
40	15	22	28	28	28	26	31	35	35	40	49	55	54	55	58	55	54	55	43	46	38	47	38	25	1000

It is well supplied with setae though these are not all complete in the present specimen. Long setae are present on the 1st, 7th, 9th, 16th, and 24th segments. Most of the major setae are well supplied with setules which may appear plumose when intact.

The exopodite of the 2nd antenna is distinctly shorter than the endopodite, and its segmentation is somewhat reduced to five distinct and two partially fused joints. There are no setae along the lateral border of the exopodite and only three, one very short, at the tip. The endopodite is quite well equipped, with eight long and five shorter setae. There are three setae on the basipodite, two near the base of the endopodite and one near the exopodite. The long setae bear setules which are rather too sparse to appear plumose.

The mandibular palp is small but complete. The four setae on the exopodite appear to be of medium length while the four on the endopodite are all short. The toothed edge of the gnathobase is set very obliquely and consists of a blunt, curved tooth at the tip, a blunt projection (which may be the remains of a broken-off tooth) halfway along and a slender tooth proximally.

The 1st maxilla possesses all lobes but no free endopodite. The three endites possess eight, one and one setae respectively and the basipodite three, of which the most distal probably represents endopodite setation. The exopodite possesses one long, two medium and two short setae and the exite three setae. The innermost and outermost of the long setae on the exopodite possess well developed setules, giving a plumose effect; the other long setae are more sparsely provided with setules.

The 2nd maxilla is strongly built and setose. The protopodite lobes bear 3, 1, 2, 3, 2, and 3 setae respectively and the endopodite has seven. Several of the more distal setae are broken in the present specimen, but the last four, at least, possess well developed processes on the inner margin.

The maxilliped is well developed, as is its setation. The coxopodite bears the full complement of setae for the genus, seven setae, and the basipodite four. Each of the endopodite segments possesses a principal seta, with 3, 3, 2, 2, and 2 subsidiary setae respectively. The seven longest setae bear well developed cup-like processes.

All the swimming limbs show full segmentation and setation; only in the 1st limb is the number of exopodite spines reduced. This pair of limbs shows some asymmetry in the present specimen in that only one exopodite spine, that on the first segment, is present on the one limb, while on the other a second spine is present distally on the third segment. The proximal spine is densely covered with setules, but otherwise no characteristic features have been noted. A seta is present towards the outer margin of the basipodite of the 4th and 5th limbs, but not of the 1st. The seta on the second exopodite segment of the 5th limb reaches just beyond the base of the next seta but one.



This species appears to be most closely related to *E. oblongus*, hence its specific name. It is distinguished by the longer rostral filaments, details of the mandibular teeth and the setae on the 1st maxilla, and by the reduced number of spines on the exopodite of the 1st swimming limb, though the last of these is obviously a variable character.

*Euaugaptilus roei* sp. nov.

**MATERIAL AND LOCALITY:** 1 adult female in a divided net haul from 900 to 750 m, taken with a modified Indian Ocean Net (N113), mesh size 0.33 mm, off the Canary Islands (28°05'N, 14°06'W) on 28 November 1965. Deposited at the British Museum (Natural History), reference number BM 1972.2.10.4A-J.

**DESCRIPTION OF THE FEMALE** (Figs 7 and 8, Table 5): The specimen had suffered some damage which made it difficult to represent accurately the form of the head region; this may be a little deeper than shown in the lateral view (Fig. 7A). It has also not been possible in this drawing to indicate the appendages in situ as they had previously been dissected.

The total length of the body is 5.2 mm. The length of the prosome is 2.7 times its width and 4.0 times the length of the urosome. The prosome, particularly the head region, is dorsoventrally shallow. The head is evenly rounded with no very prominent 'shoulders' at the level of the 2nd antennae. The division between the cephalosome and the mesosome is quite clearly marked. The posterior end of the prosome is broadly rounded on each side. The base of the rostrum is well developed and bears a pair of fine, fairly long filaments. The mid-ventral hump just anterior to the 2nd antennae is small.

The genital segment is long and bears a prominent, almost hemispherical, protuberance on the ventral side. The second urosome segment is one third of the length of the anal segment. Each caudal ramus is about one and a half times as long as it is broad and bears six setae. One of these is set dorsally towards the mid-line and is clearly seen in lateral view curving above the others. The other setae are positioned round the edge of the ramus, the innermost, the only one complete in the present specimen, being the shortest. The setules do not appear plumose.

The 1st antenna has 25 segments, the last five of which extend past the end of the body. The relative lengths of the segments are as follows:

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	Total
50	18	23	20	23	27	28	27	34	30	37	44	55	54	55	57	59	49	50	47	45	42	47	47	32	1000

The exact lengths of the setae are difficult to determine; though there are two setae on each segment and a few more on the first and last, they do not convey a setose appearance. None of the setae appears to be plumose.

The exopodite of the 2nd antenna is about half the length of the endopodite and is imperfectly divided into eight segments. There are three very long and one shorter terminal seta and one each on the 4th, 5th, and 6th segments. The endopodite possesses nine very long and two shorter terminal setae, but none on the lateral margin. There appears only to be a single seta on the basipodite. The long setae do not have a plumose appearance as the setules, though long, are rather sparse.



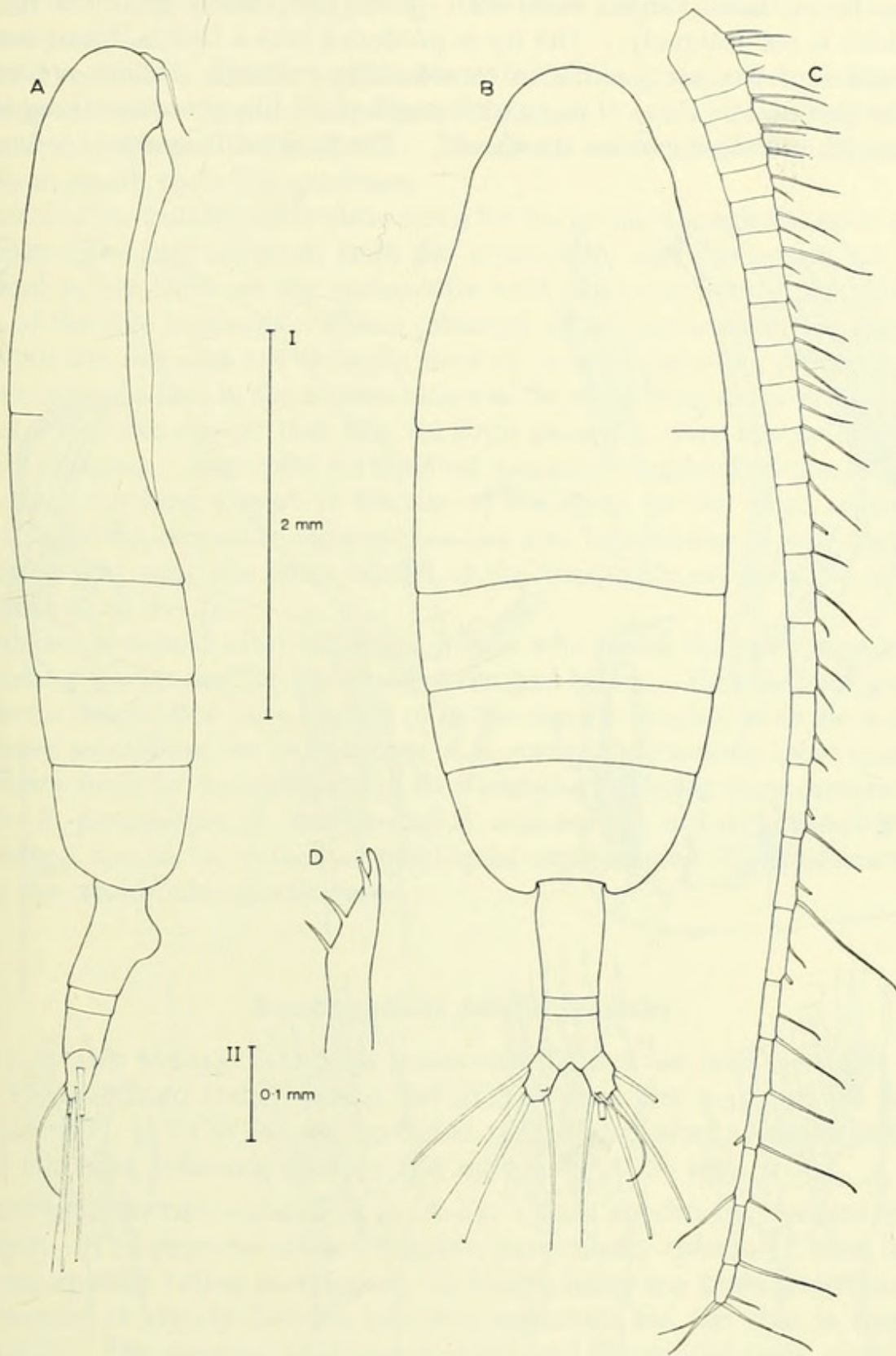


FIG. 7. *Euaugaptilus roei* ♀. A. Lateral view. B. Dorsal view. C. 1st antenna. D. Mandibular gnathobase. A - C to scale I; D to scale II.



The mandibular palp is well developed, with five setae of medium length on the exopodite, and four short and one very short seta on the endopodite. The gnathobase bears three pointed teeth with curved tips, evenly spaced along the end margin which is set obliquely. The tip is produced into a fourth, blunt tooth.

The setation of the 1st maxilla is considerably reduced. There are only four setae on the first endite, three of them with small, plate-like processes along one edge, and the second and third endites are absent. The basipodite bears no setae and the

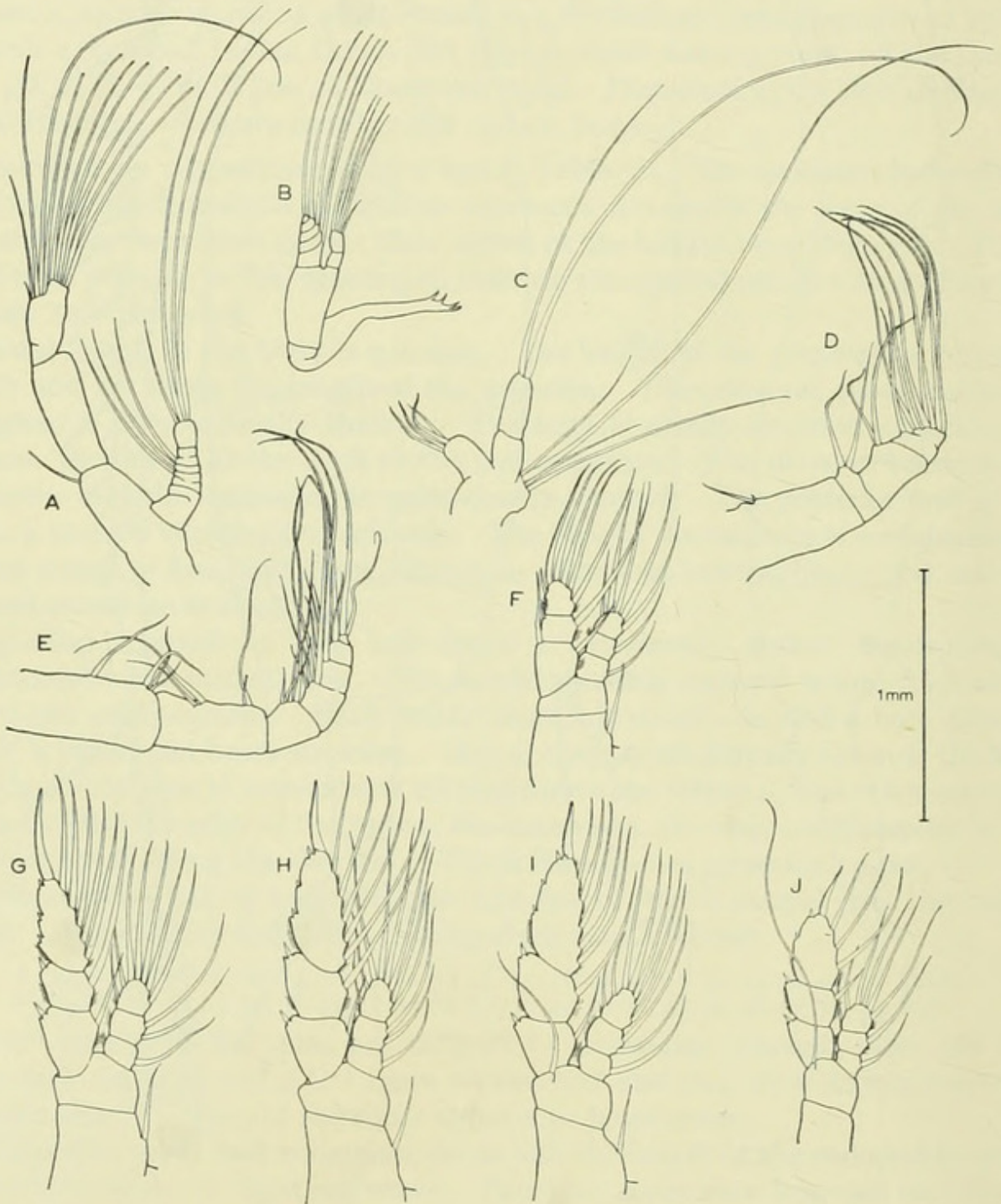


FIG. 8. *Euaugaptilus roei* ♀. A. 2nd antenna. B. Mandible. C. 1st maxilla. D. 2nd maxilla. E. Maxilliped. F. 1st swimming limb. G. 2nd swimming limb. H. 3rd swimming limb. I. 4th swimming limb. J. 5th swimming limb.



endopodite is absent. The exopodite bears one long and one very long seta. The proximal seta on the exite is of medium length, the second and fourth are rather short, and the third is extremely long. The two longest setae on this appendage have sparse setules.

The 2nd maxilla is slender and shows indistinct segmentation, at least distally. The protopodite lobes bear 1 (+ a reduced spine), 0, 0, 2, and 1 fairly short and weak setae, and the endopodite has seven. The distal inner margins of all but the first seta possess small, plate-like processes.

The form of the maxilliped is quite usual for the genus, though the setae are noticeably weak. The four setae on both the coxopodite and basipodite are all rather feeble, and so are those on the endopodite with the exception of the principal one on each of the five segments. These principal setae, particularly the last four, are longer than the rest and are the only ones to possess plate-like processes.

There is no reduction in the segmentation of the swimming limbs or in the numbers of spines and setae except that the 1st limb possesses only one spine on the last exopodite segment. The spine on the first exopodite segment of the 1st swimming limb is long, reaching almost to the tip of the spine on the third segment. The seta on the second exopodite segment reaches just beyond the base of the next seta. A seta is present near the outer border of the basipodite on both the 4th and 5th limbs, but not on the 1st.

The species is named after Mr H. S. J. Roe who found the specimens of this and the preceding species and the two males described below. He has kindly made them available for description here instead of in the more ecological work he is preparing. The reduced setation of the mouthparts of *E. roei* place it among those species which show affinity more to *Augaptilus* than to *Haloptylus*. Among these species it is most similar to *E. parabullifer*, *E. bullifer* and *E. vicinus*. It is distinguished from these, and all other, species by details of mouthpart setation and the arrangement of the teeth on the mandibular gnathobase.

### *Euaugaptilus facilis* (Farran)

**MATERIAL AND LOCALITY:** 2 adult males in a divided net haul from 940 to 700 m, taken with a modified Indian Ocean Net (N113), mesh size 0.33 mm, off the Canary Islands (28°07'N, 14°07'W) on 26 November 1965. Deposited at the British Museum (Natural History), reference number BM 1972.2.10.5A-G; 1972.2.11.7.

**DESCRIPTION OF THE MALE** (Fig. 9, A-C): Both specimens measure 5.0 mm in total length. The prosome is more angular, particularly anteriorly, than that of the female and appears rather more squat, its length being 2.9 times its greatest width. The mesosome is clearly divided into five segments but the first is fused to the cephalosome. The urosome is five-segmented and the caudal rami, about twice as long as they are wide, are the same as those of the female.

The 1st antennae are proportionally a little shorter than in the female, exceeding the length of the body by not more than the last three segments. There is some fusion of segments in the right-hand one so that it consists of only 22 free segments.



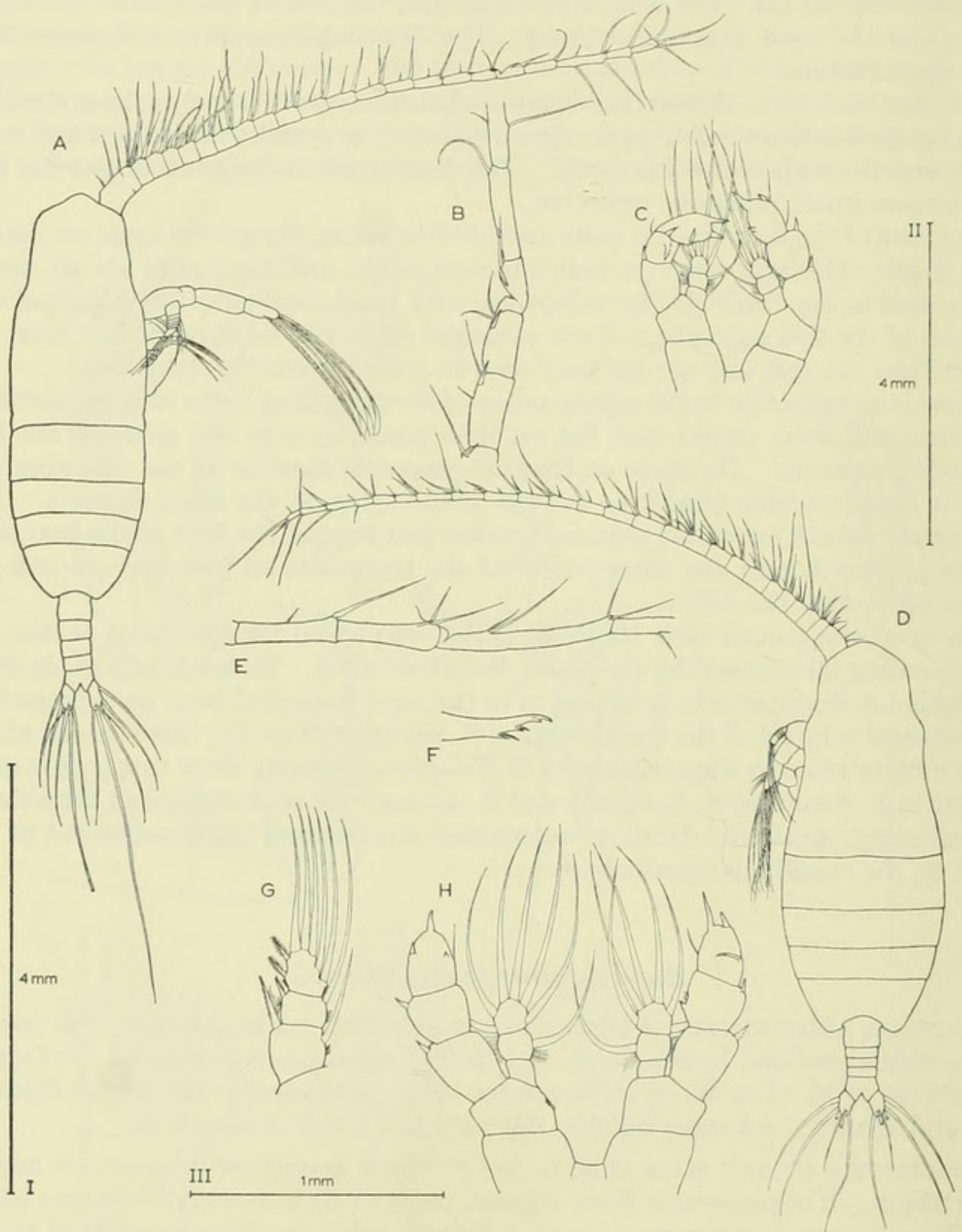


FIG. 9. *Euaugaptilus facilis* ♂. A. Dorsal view. B. Part of 1st antenna showing geniculate joint. C. 5th limbs in posterior view. *E. squamatus* ♂. D. Dorsal view. E. Part of 1st antenna showing geniculate joint. F. Mandibular gnathobase. G. Exopodite of 1st swimming limb. H. 5th limbs in anterior view. A to scale I; D to scale II; B, C, E - H to scale III.



The 18th segment possesses the geniculate joint, which is a fairly simple structure. The only associated modifications are a spinose projection lying close to the segment just distal to the joint and a seta on each of the three preceding segments which has been shortened and strengthened into a spine.

The 2nd antenna is a little stouter than shown by Sars (1925) for the female, but is structurally identical.

The mandibular gnathobase is identical to Sars' figure for the female, but the setae on the palp, of which there is one fewer on the endopodite, are longer than the female's.

The 1st maxilla is identical to that of the female, except that it has a fourth well developed seta on the exopodite.

The 2nd maxilla and the maxilliped are identical to those of the female.

The number of spines on the exopodite of the 1st swimming limb is reduced, as in the female, and the exopodites of the 3rd and 4th limbs bear just the same swellings at the distal outer corner of the second and third segments as are characteristic of the female. In all respects the first four swimming limbs resemble those of the female very closely.

The fifth limbs are modified in the usual manner for the genus. On the right-hand limb the spiny projection at the tip is a little longer than the terminal spine (their position appears reversed in Fig. 9C due to curling of the ramus in the mounted specimen). The projection on the inner margin of the second segment of this ramus is pointed and appears to be recurved. On the exopodite of the other limb the terminal projection is well developed and, in addition to the outer spine on the end segment, there is also a pointed projection on the inner side.

These specimens differ from descriptions of the female of *E. facilis* in the usual primary and secondary sexual characters, in the proportionally wider prosome and in small differences of proportion and setation of the mouth parts. It agrees with these descriptions, however, in all the main characters of the body, mouth parts and limbs, the most striking of which are the swellings on the exopodites of the 3rd and 4th swimming limbs.

### *Euaugaptilus squamatus* (Giesbrecht)

**MATERIAL AND LOCALITY:** 2 adult males in a divided net haul from 940 to 700 m, taken with a modified Indian Ocean Net (N113), mesh size 0.33 mm, off the Canary Islands (28°07'N, 14°07'W) on 26 November 1965. Deposited at the British Museum (Natural History), reference number BM 1972.2.10.6A-G; 1972.2.11.8.

**DESCRIPTION OF THE MALE** (Fig. 9, D-H): One specimen measures 5.9 and the other 6.4 mm in total length. The anterior end of the prosome is markedly narrower than the posterior part though the widest point is not far behind its middle. The urosome is five-segmented; the first of these segments is quite long, the next three are equal and short and the last is rather longer. The caudal rami are the same as in the female.

Only the last four segments of the 1st antenna extend past the end of the urosome,



as against eight in the female. The geniculate joint on the right-hand antenna is not very pronounced and the only associated modification is a spiny projection towards the distal end of the segment before.

The 2nd antenna lacks setae on the basipodite, but otherwise is the same as has been described for the female.

The mandibular palp is identical to that of the female and the gnathobase agrees with the figure given by Giesbrecht (1892), except that the middle and distal teeth are sharper; Sars (1925) figured an extra, fine tooth in the proximal group.

The 1st maxilla possesses eleven spines on the first endite, while Giesbrecht (*loc. cit.*) figured ten and a small seta and Sars (*loc. cit.*) showed only nine.

The 2nd maxilla agrees completely with earlier descriptions.

The maxilliped has one more small seta on the terminal segment than Sars (*loc. cit.*) has depicted.

The exopodite of the 1st swimming limb possesses a spine on the second segment. It is noted below (p. 42) that this is probably the normal condition. Otherwise the 1st—4th swimming limbs are the same as Sars (*loc. cit.*) has described for the female.

In the dissected specimen the right-hand 5th limb lacks a spine on the first exopodite segment, but this is almost certainly due to loss. The spiny projection on the end of this ramus is about twice as long as the terminal spine and the projection on the inner margin of the second segment is small, with a feeble tip and with some associated setules just distal to it. The left-hand limb is quite usual for the genus.

The specimens agree so closely with the female of *E. squamatus* in all morphological details common to both sexes that there can be no doubt that it belongs to the same species.

#### EMENDATION

#### *Euaugaptilus pacificus* nom. nov.

*E. similis* Brodsky, 1950, is a junior homonym of *E. similis* (Farran, 1909). The new name, *Euaugaptilus pacificus*, is therefore proposed for the former species.

#### OBSERVATIONS ON INTRASPECIFIC VARIABILITY

With so many species morphologically so similar that they cannot easily be grouped, identifications are often difficult. Several authors have therefore made tentative identifications and accompanied them with structural details which differ in some respects from the original descriptions; in particular the reported size range of several species is extremely wide. It is therefore important to examine the extent of intraspecific variability in size and morphology in order to arrive at an assessment of reliable taxonomic characters. Such an examination requires a fair number of specimens, a condition met by few species of *Euaugaptilus*, particularly if they are all to come from a single area to exclude geographical variation. This part of the study has therefore been confined to the most common species, *E. magnus*, in the collections from the Michael Sars Expedition, with some observations on two other species. It is assumed that the general conclusions which can be drawn from these are valid for the other species but it is not expected that all possible variations



will have been detected. The results are intended only as a guide to the reliability of the taxonomic characters used in this study and in no way as a study of intra-specific variability in itself. It is likely that some of the recorded variation, particularly in setation, may be the result of loss or damage but no attempt has been made to distinguish that from natural variation as it is equally likely to affect descriptions based on limited material.

Fourteen female specimens of *E. magnus*, three of *E. nodifrons* and two of *E. laticeps* were obtained on loan from the Bergen Museum. The total body length of each was measured and one mandible, both 1st maxillae and the 1st, 4th and 5th pairs of swimming limbs were dissected off and mounted on slides in polyvinyl lactophenol to which a few drops of ink had been added (Carrie, 1959).

One other specimen from the Bergen Museum, originally identified as *E. nodifrons*, probably on account of the absence of rostral filaments, was found to fit the description of *E. laticeps* in all other respects; the rostral protuberance was distinctly bifid and well developed and it is possible that the filaments had been broken off. Because of doubt over its identity it is included here only in the consideration of mandibular structure, in which it showed some asymmetry.

#### Body length

*E. magnus* was the only species of which there were enough specimens to yield data on this aspect of variation. The specimens ranged in total length from 5.53 to 7.40 mm with a mean of 6.55. The standard deviation was 0.62 mm and the coefficient of variability (percentage deviation from the mean) 9.5. Assuming a normal size distribution, one can anticipate a standard range (the range of a population of 1000 individuals) of 4.02, i.e. from 4.54 to 8.56 mm.

These specimens were all taken in the North Atlantic in the course of one expedition. The species, however, has an almost world-wide distribution, so the total size range of all populations may well be greater than that indicated here. Measurements for nine species, summarized by Vervoort (1965), show the upper limit of the size range to be anything from 19 to 51% above the lower limit and, if Sewell's record (1947) of *E. longimanus* is correct, it may be as much as 120% higher.

#### Mandible

In *E. magnus*, which is described as having six well-defined teeth on the gnathobase, the number of teeth was the same in all specimens examined and there was no noticeable difference in their arrangement. The palp possessed consistent setation throughout.

In *E. nodifrons*, which has numerous teeth on the gnathobase, an extra small point was present in one specimen though the general set of the teeth was almost identical. Setation did not vary.

In *E. laticeps* the teeth on the gnathobase showed no variation at all but there were five setae on the exopodite of one specimen and four on the other. (Sars (1925) figured five setae, while Sewell (1947) recorded four.)

The doubtful *E. laticeps* mentioned above was found to possess a typical *laticeps* gnathobase on one mandible but to have one tooth fewer on the other (Fig. 10).



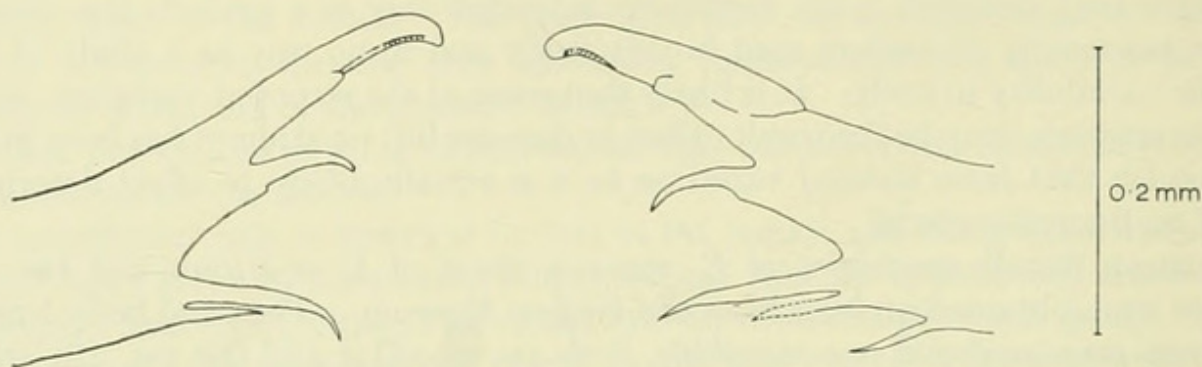


FIG. 10. Left and right gnathobases of a doubtful specimen of *Euaugaptilus laticeps*.

### 1st maxilla

Sars (1925) figured this appendage in *E. magnus* with ten setae on the first endite, one on the second, a small one on the third, one on the basipodite, two on the exopodite, and eight on the exite. In the present specimens there were invariably found to be eleven on the first endite. The second endite was also constant, with one seta, but on the third endite the single seta was further reduced in some specimens and in one case was absent altogether. The basipodite of one appendage out of the 28 examined bore a small additional seta. The exopodite in all cases had two principal setae, as described, but in most cases there were one, two or three subsidiary ones, so small as easily to be overlooked. The setation of the exite also showed some variation in the number of minor setae at the proximal end of the row.

The available material on *E. nodifrons* also indicated that only the small setae of the exopodite and exite showed any variation in number.

*E. laticeps*, however, showed greater variation. The 1st maxillae from one of the two specimens had eleven setae on the first endite and two on the second, while these appendages in the other specimen had ten and one respectively. The first specimen also possessed some additional small setae on the exopodite and exite. These two setal formulae agree with the descriptions by Sars (1925) and Sewell (1947) respectively.

### 1st, 4th and 5th swimming limbs

A total of 110 swimming limbs was examined and segmentation was invariably found to be normal. Only in two cases did the setation of the rami differ from the usual formula: one exopodite of the 1st pair of limbs in one specimen of *E. magnus* possessed eight setae, i.e. one extra, and one endopodite of the 5th pair of limbs in one specimen of *E. laticeps* also had an extra, ninth, seta. Among the specific characters of these limbs are the length of the spine on the first exopodite segment of the 1st pair of limbs, relative to the rest of the ramus, and the relative length of the seta on the second exopodite segment of the 5th pair of limbs. The relative length of the spine was found to be constant throughout and that of the seta to vary very slightly in the case of *E. magnus*; in some specimens the seta reached to the base of the next but one seta, in others to a little way past the base.

These three swimming limbs have in common the presence, at least sometimes, of a



seta on the basipodite, originating on the posterior surface near the outer margin. The occurrence of these setae in the specimens examined here is given in Table 1.

TABLE 1

Occurrence of a seta on the basipodite of the 1st, 4th and 5th swimming limbs. Numbers refer to the number of individuals.

Present on:	<i>E. magnus</i>			<i>E. nodifrons</i>			<i>E. laticeps</i>		
	1st	4th	5th	1st	4th	5th	1st	4th	5th
Both limbs	—	6	10	3	2	3	—	—	—
Left only	—	3	—	—	—	—	—	2	—
Right only	—	1	—	—	—	—	—	—	2
Neither	14	3	2	—	—	—	2	—	—

It appears that the presence or absence of this seta on the 1st swimming limbs may well be a sound taxonomic character. There may not be variation in the setae on the other limbs in *E. nodifrons* and *E. laticeps* either, but the small number of specimens and the apparent variability in *E. magnus* make this far from certain. It is possible, of course, that setae have been broken off but such loss without trace, if at all frequent, would destroy their value as a taxonomic character. Apart from this, however, real differences in the relative length of the seta on the 5th limb of *E. magnus* did occur; in one pair of 5th limbs the setae were greatly reduced so that total absence may well occur naturally.

### General

Comparison of original and subsequent descriptions supplements this brief report on variability. Sewell (1932, 1947) has redrawn parts of previously described species and some differences in setation exist between his figures and those of Sars (1925) (Table 2). Sewell's descriptions also indicate the possibility of variation in segmentation of the limbs; a stage V female which he attributed tentatively to *E. longicirrhus* possessed three-segmented rami in the 1st swimming limbs, while Sars (1925) described them as two-segmented in the adult.<sup>1</sup>

TABLE 2

Differences in setation of the 1st maxilla, according to previous descriptions.

	<i>E. angustus</i>		<i>E. elongatus</i>		<i>E. grandicornis</i>		<i>E. laticeps</i>		<i>E. longimanus*</i>		<i>E. tenuispinus</i>	
	Sars	Sewell	Sars	Sewell	Sars	Sewell	Sars	Sewell	Sars	Sewell	Sars	Sewell
Li1	10	10	11	10	9	11	10	10	3	3	9	11
Li2	1	1	2	2	1	1	2	1	0	1	1	1
Li3	0	0	2	2	0	1	2	2	0	0	1	1
B2	3	2-3†	3	4	4	4	3	3	1	1	3	2
Ri	—	—	3	3	—	—	—	—	—	—	—	—
Re	8	9	6	7	7	8	6	6	3	3	6	7
Le	4	4	8	9	6	7	8	4	5	5	7	9

\*Sewell's specimen was very much larger (9.50 mm) than is usual for this species (approx. 4.5-6.0 mm).

†Sewell mentioned two setae present on one side but drew three, presumably from the other side.

<sup>1</sup>See footnote on p. 63.



It is possible on this basis to draw certain conclusions on the reliability of morphological characters for taxonomic purposes within *Euaugaptilus*. First, gross and well-defined characters, such as body proportions, segmentation of both body and appendages, and the arrangement of teeth on the mandible, show little variation; neither does setation of the mouthparts when this concerns the well developed setae. Variation is most likely to be encountered in the setation of appendages where reduction has occurred, particularly when the number of setae is high.

THE SPECIES OF *EUAUGAPTILUS* SARS, 1920

As can be expected in a genus of this size, several synonyms have been proposed and generally accepted. A check for synonymy has been carried out separately from the computer analysis of similarity, since variability and incomplete descriptions often mask the identity of two forms. Fifteen of the least variable characters (Table 3) were chosen and presented as simple alternatives. Cards were punched for each species on the basis of the original description; where a character was undescribed or intermediate, both alternatives were punched. Comparison of each pair of cards produced a number of possible synonyms, each of which was carefully checked with the original descriptions and, where possible, with the original specimens. Some doubts must inevitably remain but for the most part it has been possible to accept or reject the synonymy of two (or more) names.

TABLE 3

The structural characters used in the check for possible synonymy within *Euaugaptilus*, with a definition of the alternative states.

	Class 1	Class 2
Rostral filaments	Absent	Present
Mandible		
Number of rami	1	2
Setting of teeth on gnathobase	Transverse	Oblique
Ist maxilla		
2nd endite	Not setose	Setose
3rd endite	Not setose	Setose
Basipodite	Not setose	Setose
Endopodite	Absent	Present
Maxilliped dimensions	Not elongated	Elongated
Ist swimming limb		
Exopodite segments	Reduced	Complete
Endopodite segments	Reduced	Complete
Basipodite seta	Absent	Present
Exopodite spines	Reduced no.	Full no.
Exopodite border	Unmodified	Modified
3rd and 4th swimming limbs		
Exopodite border	Unmodified	Modified
5th swimming limb		
Segments	Reduced	Complete



For ease of reference every specific name attributed to *Euaugaptilus* and *Neoaugaptilus*, including those attributed before 1920 to *Augaptilus* but properly belonging to *Euaugaptilus*, is included in the alphabetic list below. In the present state of knowledge 59 apparently valid species can be included. As further information on specific variability becomes available more may be merged; a small increase in the known range of variation would make this possible but it would not be justified at present.

The synonymy is intended to include the various scientific names which have been used for each species, references to descriptions, and references to the original records which have been used in compiling the distribution of each species. It is not a complete bibliography. The distribution given for the species includes Wilson's records (1942, 1950); as pointed out by Fleminger (1965) these records may not be fully reliable.

One of the main purposes of a generic review is to aid in the correct identification of specimens. Any dichotomous key, however, is impractical in the present case as specific variation of spine and setal counts would frequently lead to wrong alternatives being followed and some species have been inadequately described for this purpose. It is hoped instead that the table of structural characters (Table 5, facing p. 58) can be used for this purpose. It will be a relatively short task to note the salient characters (see Table 4, pp. 57-58) on a strip of paper, spaced according to the columns in Table 5. It is then a simple and quite rapid matter to run the strip down the table, noting the species with which there is good, but not necessarily complete, agreement. Most species will be eliminated in this way, so that detailed comparisons can be restricted to a few descriptions.

### *Euaugaptilus affinis* Sars, 1920

*Euaugaptilus affinis* Sars, 1920 : 13; Sars, 1924 : pl. 88; Sars, 1925 : 276; Björnberg, 1965 : 224; de Decker & Mombeck, 1965 : 12.

DISTRIBUTION. Recorded from the N.E. Atlantic between 32 and 46°N, from off the coast of Brazil at 13°S, and from the Indian Ocean in the region south of Madagascar. Known to occur at depths between 300 and 1000 m.

### *Euaugaptilus angustus* (Sars, 1905)

*Augaptilus angustus* Sars, 1905 : 10; Farran, 1908 : 16, 77.

*Euaugaptilus angustus*; Sars, 1924 : pl. 91; Sars, 1925 : 281; Sewell, 1932 : 322; Sewell, 1947 : 222, fig. 60E; Wilson, 1950 : 204; Tanaka, 1964 : 56, fig. 201; de Decker & Mombeck, 1965 : 12; Vervoort, 1965 : 140.

DISTRIBUTION. Widely distributed in the N. Atlantic between 1 and 55°N and as far as 43°W. In the Indian Ocean from the northern part of the Arabian Sea to south of Madagascar and as far as 75°E. Recorded in the eastern Pacific between 5 and 12°S and the western Pacific between 21 and 35°N. Known to occur between 600 and 1400 m depth.



***Euaugaptilus antarcticus*** (Wolfenden, 1911)

See under *E. laticeps*.

***Euaugaptilus brevicaudatus*** (Sars, 1905)

See under *E. squamatus*.

***Euaugaptilus brodskyi*** Hulsemann, 1967

*Euaugaptilus mixtus* (non *Augaptilus mixtus* Sars, 1907) Brodsky, 1950 : 379, fig. 268; Tanaka, 1964 : 58, fig. 202.

*Euaugaptilus niveus* nom.nud. Tanaka, 1953 : 135.

?*Euaugaptilus* sp. Grice & Hulsemann, 1965 : 224, 249, figs 4, 18g-k.

*Euaugaptilus brodskyi* Hulsemann, 1967 : 18; Grice & Hulsemann, 1967 : 30, figs 174-179.

DISTRIBUTION. One uncertain record from the North Atlantic (30°N, 23°W). Recorded from the western equatorial Indian Ocean south to 30°S. In the N.W. Pacific, off Japan, and the Bering Sea. Known to occur below 1000 m, possibly also somewhat higher.

***Euaugaptilus bullifer*** (Giesbrecht, 1889)

*Augaptilus bullifer* Giesbrecht, 1889 : 813; Giesbrecht, 1892 : 400, pl. 28 figs 6, 21, 24, pl. 39 fig. 46; Farran, 1908 : 16, 75; Scott, 1909 : 135.

*Euaugaptilus bullifer*; Sars, 1924 : pl. 85; Sars, 1925 : 272; Sewell, 1947 : 231; Wilson, 1950 : 204; Grice, 1963 : 496; Tanaka, 1964 : 67, fig. 207; de Decker & Mombeck, 1965 : 12; Grice & Hulsemann, 1965 : 224, 247, figs 4, 18a; Grice & Hulsemann, 1967 : 18; Owre & Foyo, 1967 : 83, figs 567, 568, 577.

*Euaugaptilus bulbifer*; Sewell, 1932 : 316.

DISTRIBUTION. Recorded from the subtropical and temperate N. Atlantic, between 15 and 55°N, and in the western part of the Indian Ocean from 20°N to 28°S. Widely distributed in the Pacific between 35°N and 23°S. Known to occur at 1000 m and deeper, occasionally as high as the uppermost 100 m.

***Euaugaptilus californicus*** (Esterly, 1913)

See under *E. squamatus*.

***Euaugaptilus clavatus*** (Sars, 1907)

*Augaptilus clavatus* Sars, 1907 : 23.

*Euaugaptilus clavatus*; Sars, 1924 : pl. 105 figs 1-8; Sars, 1925 : 301; Vervoort, 1965 : 142.

DISTRIBUTION. N. Atlantic between 1 and 40°N and as far as 28°W. Recorded from a depth of 600 m.



***Euaugaptilus curtus* Grice & Hulsemann, 1967**

*Euaugaptilus curtus* Grice & Hulsemann, 1967 : 18, 31, figs 180-186.

DISTRIBUTION. Recorded at 14°N, 70°E in the Indian Ocean, within a depth range of 1000-2000 m.

***Euaugaptilus depressus* (Esterly, 1913)**

See under *E. filigerus*.

***Euaugaptilus digitatus* Sars, 1920**

*Euaugaptilus digitatus* Sars, 1920 : 13; Sars, 1924 : pl. 87; Sars, 1925 : 275; Sewell, 1947 : 222; ?Owre & Foyo, 1967 : 83, figs 553-566.

DISTRIBUTION. Recorded at 47°N, 5°W and, doubtfully, 23°N, 83°W in the N. Atlantic, also in the N. Arabian Sea. Known to occur at 900 m depth.

***Euaugaptilus diminutus* Park, 1970**

*Euaugaptilus diminutus* Park, 1970 : 529, figs 300-312.

See p. 66 for a discussion of possible synonymy.

DISTRIBUTION. Recorded in the Caribbean Sea at 19°N, 82°W, at a depth between 155 and 450 m.

***Euaugaptilus distinctus* (Brodsky, 1950)**

*Neoaugaptilus distinctus* Brodsky, 1950 : 385, fig. 273.

See p. 63 for a discussion on the validity of the genus *Neoaugaptilus*.

DISTRIBUTION. Recorded from the N.W. Pacific between 1000 and 4000 m.

***Euaugaptilus elongatus* (Sars, 1905)**

*Augaptilus elongatus* Sars, 1905 : 13; Farran, 1908 : 16, 71.

*Euaugaptilus elongatus*; Sars, 1924 : pl. 84; Sars, 1925 : 270; Jespersen, 1940 : 60, 96; Lysholm, Nordgaard & Wiborg, 1945 : 38; Sewell, 1947 : 203, fig. 52; Wilson, 1950 : 204; Djordjevic, 1963 : 576; Grice, 1963 : 496; Grice & Hulsemann, 1965 : 224, fig. 4; Vervoort, 1965 : 134; Grice & Hulsemann, 1967 : 18.

DISTRIBUTION. Widely distributed in the N. Atlantic between 1 and 63°N and into the western Mediterranean. Recorded from the western Indian Ocean between 10°N and 14°S and twice in the Pacific, at 14°N, 121°E and 18°S, 178°E. Known to occur at depths between 600 and more than 1000 m, occasionally quite near the surface.



*Euaugaptilus facilis* (Farran, 1908)

*Augaptilus facilis* Farran, 1908 : 16, 73, pl. 3 figs 23, 24, pl. 8 figs 1-6; Wolfenden, 1911 : 188, 343, fig. 75, pl. 38 figs 1, 2.

*Euaugaptilus facilis*; Sars, 1924 : pl. 86; Sars, 1925 : 273; Sewell, 1932 : 322; Sewell, 1947 : 223; Wilson, 1950 : 204; Tanaka, 1964 : 62, fig. 204; Grice & Hulsemann, 1965 : 224, fig. 4; Vervoort, 1965 : 141; Grice & Hulsemann, 1967 : 18.

*Euaugaptilus* species 1 Grice & Hulsemann, 1967 : 19, 35, figs 215-224.

Grice & Hulsemann (1967) described the specimen, *Euaugaptilus* species 1, which closely resembled this species. One of the differences, the presence of an additional small seta on the exopodite of the 1st maxilla, is easily accounted for as a part of normal variability. Grice & Hulsemann considered that the cup-shaped ends to the exopodites of both the 3rd swimming limbs could be an abnormality; having also examined the specimen, the present author is of the same opinion. The absence of the mandibular palp, which is normally weakly developed in *E. facilis*, could likewise be abnormal.

DISTRIBUTION. Recorded from the N. Atlantic between 1 and 55°N and as far as 23°W, in the north-western part of the Indian Ocean between 10 and 18°N, in the eastern equatorial Pacific and off Japan, as well as once in the Antarctic. Known to occur at depths between 600 and 3000 m.

*Euaugaptilus farrani* Sars, 1920

*Euaugaptilus farrani* Sars, 1920 : 15; Sars, 1924 : pl. 96; Sars, 1925 : 288; Tanaka, 1964 : 48, fig. 196; Grice & Hulsemann, 1967 : 18.

DISTRIBUTION. Recorded once from the Atlantic at 34°N, 12°W, once from the Indian Ocean at 6°S, 65°E, and once from off the coast of Japan. Known to occur at a depth between 1000 and 1800 m.

*Euaugaptilus filigerus* (Claus, 1863)

*Hemicalanus filigerus* Claus, 1863 : 179.

*Augaptilus filigerus*; Giesbrecht, 1889 : 813; Giesbrecht, 1892 : 400, pl. 3 fig. 3, pl. 27 fig. 34, pl. 28 figs 4, 10, 13, 14, 20, 26-29, 36, pl. 29 fig. 26, pl. 39 fig. 49; Farran, 1908 : 16, 77; Scott, 1909 : 136; Wolfenden, 1911 : 188, 341.

*Euaugaptilus filigerus*; Farran, 1929 : 269; Sewell, 1932 : 321; Farran, 1936 : 114; Jespersen, 1940 : 61, 96; Wilson, 1942 : 184; Wilson, 1950 : 205; de Decker & Mombeck, 1965 : 12; Grice & Hulsemann, 1967 : 18; Grice, 1969 : 454; Park, 1970 : 477.

*Euaugaptilus filligerus*; Tanaka, 1964 : 51, fig. 198.

*Euaugaptilus filiger*; Sars, 1924 : pl. 90; Sars, 1925 : 279; Rose, 1937 : 165, figs 7-12; Lysholm, Nordgaard & Wiborg, 1945 : 38, 50; Björnberg, 1963 : tab. 6; Grice & Hulsemann, 1965 : 224, fig. 4; Vervoort, 1965 : 137.

*Euaugaptilus filliger*; Björnberg, 1965 : 223.

*Augaptilus depressus* Esterly, 1913 : 187, figs 11, 20, 26, 33, 38, 42, 44, 54; Brodsky, 1950 : 372, fig. 262.

*Augaptilus romanus* Esterly, 1913 : 188, figs 7, 24, 30, 32, 45, 47, 52.

Specimens originally described by Esterly (1913) as *A. depressus* (♀ only) and



*A. romanus* (♂ only) have been re-examined. These forms were not taken in the same haul (*A. romanus* occurred together with *A. californicus*) but they nevertheless agree closely in all characters constant between the sexes. Particularly striking are the form of the prosome, the arrangement of the teeth on the mandible, the setation of the 1st maxilla, and the structure of the 1st swimming limb. The specimens also agree closely with the descriptions given by Giesbrecht (1892) and Sars (1925) of *E. filigerus*; the only apparent difference occurs in the right 5th limb of the male, where the points of the terminal spine and seta come closer together in *A. romanus* than in *E. filigerus* (cf. Esterly, 1913, pl. 12 fig. 47 and Giesbrecht, 1892, pl. 29 fig. 26. The omission of the joint between the basipodite and the first exopodite segment in Esterly's figure is incorrect). The names, *A. depressus* and *A. romanus*, are therefore considered junior synonyms of *E. filigerus*.

Rose (1937) drew attention to some apparent differences between specimens caught in the Atlantic and others collected in the Mediterranean; he discussed the possible existence of two geographical races.

**DISTRIBUTION.** Widely distributed and frequently recorded in the Atlantic between 64°N and 24°S, and in the Mediterranean. In the western Indian Ocean from 14°N to south of Madagascar. Widely distributed in the Pacific between 35°N and 34°S. Recorded quite often at depths between 100 and 500 m, also deeper and occasionally shallower.

### ***Euaugaptilus fundatus* Grice & Hulsemann, 1967**

*Euaugaptilus fundatus* Grice & Hulsemann, 1967 : 18, 32, figs 187-192.

**DISTRIBUTION.** Recorded once from the Indian Ocean at 13°N, 70°E at a depth range of 1000-2000 m.

### ***Euaugaptilus fungiferus* (Steuer, 1904)**

See *E. magnus*. For the specimen identified by Wolfenden (1911) as *A. fungiferus* (?) see *E. laticeps*.

### ***Euaugaptilus gibbus* (Sars, 1905)**

This is a junior synonym and homonym of *E. gibbus* (Wolfenden), as pointed out by Sars (1907).

### ***Euaugaptilus gibbus* (Wolfenden, 1904)**

*Augaptilus gibbus* Wolfenden, 1904 : 111, 122, 145; Farran, 1908 : 16, 75; Wolfenden, 1911 : 187, 337, pl. 37 figs 2, 3.

*Euaugaptilus gibbus*; Sars, 1924 : pl. 104; Sars, 1925 : 300; Lysholm, Nordgaard & Wiborg, 1945 : 38, 50; Wilson, 1950 : 205; de Decker & Mombeck, 1965 : 12; Vervoort, 1965 : 142.

*Augaptilus gibbus* Sars, 1905 : 16.

**DISTRIBUTION.** Distributed in the Atlantic between 60°N and 10°S. Recorded



once in the Indian Ocean at 35°S, 44°E and in the Pacific at 34°N, 119°W. Known to occur at depths between 400 and 1300 m.

***Euaugaptilus gracilis* (Sars, 1905)**

*Augaptilus gracilis* Sars, 1905 : 12.

*Euaugaptilus gracilis*; Sars, 1924 : pl. 89; Sars, 1925 : 278; Lysholm, Nordgaard & Wiborg, 1945 : 38; Grice & Hulsemann, 1965 : 224, fig. 4; Grice & Hulsemann, 1967 : 18; Grice, 1969 : 454; Park, 1970 : 477.

DISTRIBUTION. Recorded in the N. Atlantic between 27 and 48°N and in the Caribbean. In the western Indian Ocean between 10°N and 3°S. Known to occur at depths between 1000 and greater than 4000 m.

***Euaugaptilus graciloides* Brodsky, 1950**

*Euaugaptilus graciloides* Brodsky, 1950 : 381, fig. 270.

DISTRIBUTION. So far only recorded once, from the N.W. Pacific at a depth between 1000 and 4000 m.

***Euaugaptilus grandicornis* Sars, 1920**

*Euaugaptilus grandicornis* Sars, 1920 : 14; Sars, 1924 : pl. 94; Sars, 1925 : 286; Sewell, 1947 : 207, fig. 54; Grice & Hulsemann, 1967 : 18; Grice & Hulsemann, 1968 : 325.

DISTRIBUTION. Recorded once in the Atlantic at 34°N, 37°W. Occurs in the Arabian Sea between 6 and 14°N. Also recorded once in the Pacific at 34°S, 82°W. Known to occur at depths between 1000 and 2000 m.

***Euaugaptilus hecticus* (Giesbrecht, 1889)**

*Augaptilus hecticus* Giesbrecht, 1889 : 814; Giesbrecht, 1892 : 400, pl. 1 fig. 3, pl. 27 fig. 30, pl. 28 figs 5, 9, 16, 30, 33, 37, pl. 29 fig. 18, pl. 39 fig. 45; Scott, 1894 : 35, pl. 1 figs 37-39, pl. 2 figs 1-4, 38-42; Scott, 1909 : 136; Wolfenden, 1911 : 188, 339; Lysholm, Nordgaard & Wiborg, 1945 : 37, 48.

*Euaugaptilus hecticus*; Farran, 1926 : 288; Farran, 1929 : 269; Sewell, 1932 : 323; Wilson, 1950 : 205, figs 297, 299; Grice, 1962 : 226, pl. 26 figs 15-17; Björnberg, 1963 : 54; Grice, 1963 : 496; Owre & Foyo, 1964b : 366; Tanaka, 1964 : 71, fig. 209; Björnberg, 1965 : 223; Grice & Hulsemann, 1965 : 224, fig. 4; Calef & Grice, 1967 : 93; Owre & Foyo, 1967 : 86, figs 61, 67, 569-572; Park, 1970 : 477.

*Hemicalanus longisetosus* Scott, 1892 (unpubl. MS).

DISTRIBUTION. Occurs widely in the Atlantic between 47°N and 24°S and in the Mediterranean, Caribbean and Gulf of Mexico. Recorded once in the Indian Ocean at 10°N, 75°E. Scattered records from the Pacific between 35°N and 34°S. Known to occur at depths between 30 and 700 m.



*Euaugaptilus hulsemannae* sp. nov.

DISTRIBUTION. Recorded once from the Pacific at 34°S, 85°W, from a depth between 2000 and 3000 m.

*Euaugaptilus humilis* Farran, 1926

*Euaugaptilus humilis* Farran, 1926 : 289, pl. 10 figs 4-10; Grice, 1963 : 496, 498, fig. 1h-j; Grice & Hulsemann, 1965 : 224, fig. 4; Grice & Hulsemann, 1967 : 18, 32; Park, 1970 : 477.

DISTRIBUTION. Recorded from the N. Atlantic, including the Caribbean, between 15 and 47°N and from the western Indian Ocean between 1 and 18°N. Known to occur at depths around 1000 m.

*Euaugaptilus hyperboreus* Brodsky, 1950

*Euaugaptilus hyperboreus* Brodsky, 1950 : 383, fig. 272.

DISTRIBUTION. Recorded from the central Arctic Ocean at a depth greater than 200 m.

*Euaugaptilus indicus* Sewell, 1932

*Euaugaptilus indicus* Sewell, 1932 : 319, fig. 105; Sewell, 1947 : 201, fig. 51; Grice & Hulsemann, 1967 : 18.

DISTRIBUTION. Hitherto recorded only from the western Indian Ocean, between 10°N and 6°S. Known to occur at depths less than 850 m and greater than 1000 m.

*Euaugaptilus laticeps* (Sars, 1905)

*Augaptilus laticeps* Sars, 1905 : 11; Farran, 1908 : 16, 72; Paulsen, 1909 : 37.

*Euaugaptilus laticeps*; Sars, 1924 : pl. 80; Sars, 1925 : 264; Farran, 1926 : 289; Farran, 1929 : 269; Sewell, 1932 : 321; Jespersen, 1940 : 59, 96; Lysholm, Nordgaard & Wiborg, 1945 : 38, 48; Sewell, 1947 : 209, figs 55, 56; Wilson, 1950 : 205; Vervoort, 1957 : 139, fig. 131; Grice, 1963 : 496; Tanaka, 1964 : 50, fig. 197; Björnberg, 1965 : 225; de Decker & Mombeck, 1965 : 12; Vervoort, 1965 : 136; Grice & Hulsemann, 1967 : 18; Tanaka & Omori, 1967 : 252.

*Augaptilus placitus* Scott, 1909 : 137, pl. 42 figs 10-19.

*Augaptilus antarcticus* Wolfenden, 1911 : 187, 334, 337, fig. 70, pl. 36 figs 6, 7.

?*Augaptilus fungiferus* (?) (non Steuer) Wolfenden, 1911 : 187, 336, fig. 71, pl. 36 fig. 8.

The synonymy of *A. antarcticus* with this species was suggested by Farran (1929) and by Sewell (1932, 1947) and accepted by Vervoort (1957). In the apparent absence of Wolfenden's type material it is impossible to be conclusive. The recorded body proportions are a little different and Wolfenden described seven segments in the exopodite of the 2nd antenna, against eight in *E. laticeps*. The first of these differences may be accounted for by natural variation or shrinkage at fixation, the second may be an error of observation. In all other recorded characters there seems to be little or no difference.



Sewell (1947) has also proposed that *A. placitus* Scott is a synonym of this species. A specimen of *A. placitus* from the Siboga Expedition has been re-examined and found to agree in all essential details with *E. laticeps* (see Table 5).

The specimen identified by Wolfenden (1911) as *A. fungiferus* (?) Steuer is certainly not that species, as the proportions of the body and the structure of the 1st maxilla are quite distinct. Although Wolfenden described this specimen alongside *A. antarcticus* and separated the two on the grounds of 'wesentliche Differenzen', there are only two characters mentioned by him which distinguish them: the length to width ratio of the prosome is given as 1.5 : 1 in *A. antarcticus* and as 2 : 1 in *A. fungiferus* (?), and there is reduced segmentation of the exopodite of the 2nd antenna in the latter. The first of these is a slight difference and the second an improbable one, though an easy mistake to make in observation. Vervoort (1965) commented on the wide range of size recorded for *E. laticeps* and expressed some doubt as to whether the specimens from various collections really represented a single species, though he said that no structural differences had yet been mentioned between small and large specimens. It is possible that Wolfenden's specimens represent two such forms or species at present combined under *E. laticeps*, though it must be pointed out that there was little difference in size between them.

**DISTRIBUTION.** Widely distributed in the Atlantic from 64°N to 16°S, including the Mediterranean. In the western Indian Ocean from the northern Arabian Sea to south of Madagascar. Widespread in the Pacific from 36°N to 25°S. Circumpolar in the Antarctic, extending to 72°S. Recorded from below 800 m, but usually not so deep, occasionally near the surface.

### *Euaugaptilus latifrons* (Sars, 1907)

*Augaptilus latifrons* Sars, 1907 : 22.

*Euaugaptilus latifrons*; Sars, 1924 : pl. 101; Sars, 1925 : 295; Sewell, 1932 : 323, fig. 106; Lysholm, Nordgaard & Wiborg, 1945 : 38; Sewell, 1947 : 232; Owre & Foyo, 1964b : 366; Vervoort, 1965 : 144; Owre & Foyo, 1967 : 86, figs 580-582.

**DISTRIBUTION.** Recorded in the Atlantic between 1 and 48°N, including the Caribbean. Also in the northern and central Arabian Sea. Known to occur at depths between 400 and 750 m.

### *Euaugaptilus longiantennalis* Park, 1970

See under *E. marginatus*.

### *Euaugaptilus longicirrhus* (Sars, 1905)

*Augaptilus longicirrhus* Sars, 1905 : 15.

*Euaugaptilus longicirrhus*; Sars, 1924 : pl. 98; Sars, 1925 : 291; ?Sewell, 1947 : 229, fig. 62.

**DISTRIBUTION.** Recorded from the N. Atlantic between 29 and 37°N and as far as 27°W. Probably also from the central Arabian Sea. Obtained in vertical hauls from 3000 m to the surface.



***Euaugaptilus longimanus* (Sars, 1905)**

*Augaptilus longimanus* Sars, 1905 : 17; Wolfenden, 1911 : 188, 340, fig. 73.

*Euaugaptilus longimanus*; Sars, 1924 : pl. 92; Sars, 1925 : 282; Lysholm, Nordgaard & Wiborg, 1945 : 38; Sewell, 1947 : 223, figs 60A-D, 61; Wilson, 1950 : 205; Grice, 1963 : 496; Owre & Foyo, 1964a : 343; Tanaka, 1964 : 69, fig. 208; Grice & Hulsemann, 1965 : 224, fig. 4; Vervoort, 1965 : 143; Furuhashi, 1966 : 307; Grice & Hulsemann, 1967 : 18; Owre & Foyo, 1967 : 86, figs 583-587; Tanaka & Omori, 1967 : 253, fig. 5.

DISTRIBUTION. Widespread in the Atlantic from 41°N to 18°S (Björnberg, unpubl.), including the Caribbean. In the western Indian Ocean from the Gulf of Oman to 22°S. Recorded from the Pacific between 35°N and 23°S. Known to occur at depths from below 1000 m to less than 600 m, occasionally near the surface.

***Euaugaptilus longiseta* Grice & Hulsemann, 1965**

*Euaugaptilus longiseta* Grice & Hulsemann, 1965 : 224, 247, figs 4, 18b-f; Grice & Hulsemann, 1967 : 18, 32, figs 193-195.

DISTRIBUTION. Recorded from the Atlantic at 40°N, 20°W and from the western Indian Ocean between 18°N and 3°S. Known to occur in the region of 2000 m depth.

***Euaugaptilus magnus* (Wolfenden, 1904)**

*Augaptilus magnus* Wolfenden, 1904 : III, 122, 142, 145; Farran, 1908 : 16, 77; Wolfenden, 1911 : 188, 337, 341, fig. 73, pl. 37 figs 4-9.

*Euaugaptilus magnus*; Sars, 1924 : pl. 79; Sars, 1925 : 262; Farran, 1926 : 289; Jespersen, 1940 : 58, 96; Wilson, 1950 : 206; Grice, 1963 : 496; Owre & Foyo, 1964a : 343; Owre & Foyo, 1964b : 366; Tanaka, 1964 : 53, fig. 199; de Decker & Mombeck, 1965 : 12; Grice & Hulsemann, 1967 : 18; Owre & Foyo, 1967 : 87, figs 588-591; Tanaka & Omori, 1967 : 253; Grice & Hulsemann, 1968 : 325; Park, 1970 : 478; typical form; Sewell, 1932 : 322; Vervoort, 1957 : 139.

*Euaugaptilus magnus* f. *fungiferus*; Sewell, 1947 : 213, fig. 57.

*Euaugaptilus magnus magnus*; Vervoort, 1965 : 139.

*Augaptilus fungiferus* Steuer, 1904 : 597.

*Augaptilus validus* Scott, 1909 : 138, pl. 43 figs 1-10.

*Euaugaptilus squamatus* (Giesbrecht, 1889) [part] Lysholm, Nordgaard & Wiborg, 1945 : 38, 39, 48.

Farran (1908) suggested that *A. fungiferus* was a synonym of this species and Sewell (1947) proposed two races, f. *fungiferus* and f. *magnus*, of the one species, *E. magnus*. There can hardly be any doubt that they do represent the same species; in fact the supposed differences between them are so slight as to raise doubts about the validity of the two races or subspecies. In particular the setting of the teeth on the mandibular gnathobase appears to be identical in the figures drawn by Sars (1925) and Sewell (1947), contrary to what is indicated by the latter author. Insufficient is yet known about the morphological variation between populations but, as this distinction into two forms retains some information, e.g. on body proportions, it is useful to keep it, at least for the time being.



Sewell (1947) proposed that *A. validus* Scott was also a synonym of *E. magnus*. Insofar as Scott's description (1909) covers the important structural characters, there is complete agreement, especially with the form *magnus*, except in the shape of the head which Scott described as being very much depressed with an extremely narrow forehead. The female recorded by Scott appears to be lost, so this proposed synonymy cannot be finally confirmed. See also p. 44.

Sars (1925) stated that he had earlier confused this species with *E. squamatus*. As he had been consulted by Lysholm and Nordgaard when the material from the Michael Sars Expedition, 1910, was being worked up, specimens identified as *E. squamatus* in those collections have been re-examined and have been found in the main to be *E. magnus*.

**DISTRIBUTION.** Widely distributed in the N. Atlantic south of 65°N, including the Caribbean, with occasional records from the S. Atlantic. In the Indian Ocean from the Gulf of Oman as far as 66°S. Widespread in the Pacific between 35°N and 34°S. Obtained mostly at depths between 440 and about 2500 m, occasionally near the surface.

***Euaugaptilus malacus* Grice & Hulsemann, 1967**

*Euaugaptilus malacus* Grice & Hulsemann 1967 : 18, 33, figs 196–200.

**DISTRIBUTION.** Recorded in the Indian Ocean at 28°S, 80°E, at a depth between 1000 and 2000 m.

***Euaugaptilus marginatus* Tanaka, 1964**

*Euaugaptilus marginatus* Tanaka, 1964 : 64, fig. 205.

*Euaugaptilus longiantennalis* Park, 1970 : 533, figs 318–324.

See p. 66 for a discussion of the synonymy.

**DISTRIBUTION.** Recorded once from the Caribbean Sea at 19°N, 82°W and once from the Pacific at 35°N, 139°E. Obtained at depths between 100 and 450 m.

***Euaugaptilus matsuei* Tanaka & Omori, 1967**

*Euaugaptilus matsuei* Tanaka & Omori, 1967 : 254, figs 6, 7.

**DISTRIBUTION.** Recorded once from the Pacific at 34°N, 139°E in a vertical haul from 1430 m to the surface.

***Euaugaptilus maxillaris* Sars, 1920**

*Euaugaptilus maxillaris* Sars, 1920 : 15; Sars, 1924 : pl. 95; Sars, 1925 : 287; Vervoort, 1965 : 135; Grice & Hulsemann, 1967 : 18.

**DISTRIBUTION.** Recorded from the Atlantic between 1 and 26°N and as far as 35°W. Once from the Indian Ocean at 28°S, 80°E. Known to occur at a depth of 600 m and between 1000 and 2000 m.



***Euaugaptilus mixtus* Brodsky, 1950**

See under *E. brodskyi*.

***Euaugaptilus mixtus* (Sars, 1907)**

*Augaptilus mixtus* Sars, 1907 : 22.

*Euaugaptilus mixtus*; Lysholm, Nordgaard & Wiborg, 1945 : 38; Hulsemann, 1967 : 163.

DISTRIBUTION. Recorded twice from the N. Atlantic, at 32°N, 25°W and 45°N, 25°W. Known to occur at a depth of 1000 m.

***Euaugaptilus modestus* Brodsky, 1950**

*Euaugaptilus modestus* Brodsky, 1950 : 382, fig. 271.

This species is known only from the male. It may belong to one of the numerous species of which only the female is known, but it has not been possible yet to assign it with any certainty.

DISTRIBUTION. Recorded from the N.W. Pacific at a depth between 1000 and 4000 m.

***Euaugaptilus niveus* Tanaka, 1953**

See under *E. brodskyi*.

***Euaugaptilus nodifrons* (Sars, 1905)**

*Augaptilus nodifrons* Sars, 1905 : 13; Farran, 1908 : 16, 72.

*Euaugaptilus nodifrons*; Sars, 1924 : pl. 82; Sars, 1925 : 267; Sewell, 1932 : 316, fig. 104; Jespersen, 1940 : 60, 96; Lysholm, Nordgaard & Wiborg, 1945 : 38, 50; Sewell, 1947 : 205, fig. 53; Wilson, 1950 : 206; Owre & Foyo, 1964a : 343; Tanaka, 1964 : 47, fig. 195; de Decker & Mombeck, 1965 : 12; Grice & Hulsemann, 1965 : 224, fig. 4; Vervoort, 1965 : 134; Grice & Hulsemann, 1967 : 33, figs 201-203; Owre & Foyo, 1967 : 88, figs 592-597; Tanaka & Omori, 1967 : 256, fig. 8; Park, 1970 : 478.

*Augaptilus simplex* Wolfenden, 1911 : 188, 345, fig. 76.

*Augaptilus simplex* Esterly, 1913 : 188, figs 10, 28, 34, 36, 41, 50, 60.

*Euaugaptilus simplex*; Brodsky, 1950 : 375, fig. 265.

Sewell (1932) suggested that *A. simplex* Wolfenden might be synonymous with this species and in 1947 he also suggested synonymy with *A. simplex* Esterly. Two of Esterly's specimens have been re-examined and found to agree completely with Sars' description (1925) of *E. nodifrons*. Esterly (1913, p. 189) stated, 'This species appears to resemble *A. nodifrons* . . .' At that time he only had Sars' original and very brief description to go on and may have discounted conspecificity on the grounds of distance between the two finds. Wolfenden's description differs slightly from that of *E. nodifrons*, in body proportions, the number of segments recorded in the exopodite of the 2nd antenna, and the setation of the exopodite and exite of the



1st maxilla. As these differences may well be due to individual variation or to error in observation, it seems reasonable to consider *A. simplex* Wolfenden, as well as *A. simplex* Esterly, synonymous with *E. nodifrons*.

DISTRIBUTION. Widespread in the N. and S. Atlantic, including equatorial regions, the Caribbean and Gulf of Mexico, and extending at least to 64°N. In the western Indian Ocean known to extend from the Gulf of Oman to south of Madagascar. Several records from the N. Pacific as far as 35°N and from off the coast of S. America. Known to occur at depths between 600 and more than 1000 m, occasionally near the surface.

***Euaugaptilus nudus* Tanaka, 1964**

*Euaugaptilus nudus* Tanaka, 1964 : 60, fig. 203.

DISTRIBUTION. Obtained once in the Pacific at 35°N, 139°E in a vertical haul from 1000 m to the surface.

***Euaugaptilus oblongus* (Sars, 1905)**

*Augaptilus oblongus* Sars, 1905 : 11.

*Euaugaptilus oblongus*; Sars, 1924 : pl. 81; Sars, 1925 : 266; Sewell, 1932 : 322; Jespersen, 1940 : 59, 96; Lysholm, Nordgaard & Wiborg, 1945 : 38, 48; Sewell, 1947 : 218, fig. 58; Wilson, 1950 : 206; Grice, 1963 : 496; Tanaka, 1964 : 55, fig. 200; de Decker & Mombeck, 1965 : 12; Vervoort, 1965 : 139; Grice & Hulsemann, 1967 : 19, 34; Owre & Foyo, 1967 : 88, figs 66, 70, 598-600; Tanaka & Omori, 1967 : 257, fig. 9; Park, 1970 : 478.

*Augaptilus rostratus* Esterly, 1906 : 73, figs 19, 42, 57, 63, 75.

*Euaugaptilus rostratus*; Brodsky, 1950 : 374, fig. 264; Owre & Foyo, 1964b : 366; Owre & Foyo, 1967 : 88, figs 605-608.

*Augaptilus subfiligerus* Wolfenden, 1911 : 188, 343.

Grice & Hulsemann (1967) have demonstrated that *A. subfiligerus* and *A. rostratus* are synonyms of this species.

DISTRIBUTION. Widely distributed in the Atlantic, including the Caribbean, from 63°N to 10°S. In the western Indian Ocean from 18°N to 36°S. In the Pacific from 35°N to 22°S. Known to occur at depths between 440 and 1400 m.

***Euaugaptilus pachychaeta* sp. nov.**

DISTRIBUTION. Recorded once from the equatorial Atlantic off Nigeria in a vertical haul from 600 m to the surface.

***Euaugaptilus pacificus* nom. nov.**

*Euaugaptilus similis* (non *E. similis* (Farran)) Brodsky, 1950 : 377, fig. 267.

See p. 22.

DISTRIBUTION. Recorded once from the N.W. Pacific at a depth between 1000 and 4000 m.



***Euaugaptilus palumbii*** (Giesbrecht, 1889)

*Augaptilus palumbii* Giesbrecht, 1889 : 813; Giesbrecht, 1892 : 400, pl. 27 fig. 32, pl. 28 figs 3, 15, 17, pl. 39 fig. 50.

*A. palumboi*; Cleve, 1904 : 182, 185; Farran, 1908 : 16, 75; Scott, 1909 : 137; Wolfenden, 1911 : 188, 340.

*Euaugaptilus palumboi*; Sars, 1924 : pl. 105, figs 9-19; Sars, 1925 : 302; Farran, 1926 : 288; Farran, 1936 : 114; Lysholm, Nordgaard & Wiborg, 1945 : 38, 50; Brodsky, 1950 : 374, fig. 263; Wilson, 1950 : 207; Grice, 1963 : 496; Tanaka, 1964 : 66, fig. 206; de Decker & Mombeck, 1965 : 34; Grice & Hulsemann, 1965 : 224, fig. 4; Furuhashi, 1966 : 310, 313; Grice & Hulsemann, 1967 : 19; Park, 1970 : 478.

Giesbrecht's spelling of the specific name is retained here as there seems to be no nomenclatural reason for changing it.

DISTRIBUTION. Widely distributed in the Atlantic, including the Caribbean and Gulf of Mexico, from 55°N to 12°S. In the western Indian Ocean from 14°N to 36°S. In the Pacific from 35°N to 16°S. Known to occur between depths of less than 500 and more than 1000 m.

***Euaugaptilus parabullifer*** Brodsky, 1950

*Euaugaptilus parabullifer* Brodsky, 1950 : 376, fig. 266.

DISTRIBUTION. Recorded once from the N.W. Pacific in a vertical haul from 4000 to 1000 m.

***Euaugaptilus paroblongus*** sp. nov.

DISTRIBUTION. Recorded once from the Atlantic at 28°N, 14°W at a depth between 940 and 700 m.

***Euaugaptilus penicillatus*** Sars, 1920

*Euaugaptilus penicillatus* Sars, 1920 : 16; Sars, 1924 : pl. 100; Sars, 1925 : 294; Sewell, 1947 : 205; Grice & Hulsemann, 1967 : 19.

DISTRIBUTION. Recorded once in the N. Atlantic at 36°N, 8°W, once in the N. Arabian Sea and once further south in the Indian Ocean at 17°S. Known to occur between 1000 and 1400 m depth.

***Euaugaptilus placitus*** (Scott, 1909)

See under *E. laticeps*.

***Euaugaptilus propinquus*** Sars, 1920

*Euaugaptilus propinquus* Sars, 1920 : 17; Sars, 1924 : pl. 102; Sars, 1925 : 297.

DISTRIBUTION. Recorded in the N. Atlantic between 31 and 39°N and as far as 24°W. Known to occur above 1550 m, possibly also deeper.



***Euaugaptilus pseudaffinis*** Brodsky, 1950

*Euaugaptilus pseudaffinis* Brodsky, 1950 : 381, fig. 269.

It is at least possible that this species is synonymous with *E. affinis*, as suggested by Grice & Hulsemann (1967). There is, however, some difference in the proportions of the prosome as well as in the characters mentioned by Brodsky (loc. cit.).

DISTRIBUTION. Recorded once from the N.W. Pacific at a depth between 1000 and 4000 m.

***Euaugaptilus quaesitus*** Grice & Hulsemann, 1967

*Euaugaptilus quaesitus* Grice & Hulsemann, 1967 : 19, 34, figs 204-209.

DISTRIBUTION. Known from the Indian Ocean at 10°N, 65°E in a vertical haul from 3000 to 2000 m.

***Euaugaptilus rectus*** Grice & Hulsemann, 1967

*Euaugaptilus rectus* Grice & Hulsemann, 1967 : 19, 35, figs 210-214.

DISTRIBUTION. Recorded from the western equatorial Indian Ocean at a depth between 275 and 2250 m.

***Euaugaptilus rigidus*** (Sars, 1907)

*Augaptilus rigidus* Sars, 1907 : 21.

*Euaugaptilus rigidus*; Sars, 1924 : pl. 103; Sars, 1925 : 298; Wilson, 1950 : 207, figs 61, 62; Owre & Foyo, 1964b : 366; Tanaka, 1964 : 72, fig. 210; Vervoort, 1965 : 145; Grice & Hulsemann, 1967 : 19; Owre & Foyo, 1967 : 88, figs 601-604.

DISTRIBUTION. In the N. Atlantic, including the Caribbean, between 15 and 34°N. In the western Indian Ocean at 3 and 28°S. In the N.W. Pacific at 35°N and in the S.E. Pacific at 23°S. Known to occur at a depth of 600 m and also below 1000 m.

***Euaugaptilus roei*** sp. nov.

DISTRIBUTION. One record from the N. Atlantic at 28°N, 14°W between 750 and 900 m depth.

***Euaugaptilus romanus*** (Esterly, 1913)

See under *E. filigerus*.

***Euaugaptilus rostratus*** (Esterly, 1906)

See under *E. oblongus*.



***Euaugaptilus sarsi*** Grice & Hulsemann, 1965

*Euaugaptilus sarsi* Grice & Hulsemann, 1965 : 224, 249, figs 4, 181-q, 19a-d.

DISTRIBUTION. Recorded from the N. Atlantic at 30°N, 23°W in a vertical haul from 1000 to 500 m.

***Euaugaptilus similis*** Brodsky, 1950

See under *E. pacificus* and p. 22.

***Euaugaptilus similis*** (Farran, 1908)

*Augaptilus similis* Farran, 1908 : 16, 75, pl. 8 figs 7-14.

*Euaugaptilus similis*; Lysholm, Nordgaard and Wiborg, 1945 : 40.

DISTRIBUTION. Recorded from the N. Atlantic between 31 and 55°N and as far as 35°W. Known to occur at a depth of 1400 to 1500 m.

***Euaugaptilus simplex*** (Esterly, 1913)

See under *E. nodifrons*.

***Euaugaptilus simplex*** (Wolfenden, 1911)

See under *E. nodifrons*.

***Euaugaptilus simulans*** Sars, 1925

See under *E. vicinus*.

***Euaugaptilus squamatus*** (Giesbrecht, 1889)

*Augaptilus squamatus* Giesbrecht, 1889 : 814; Giesbrecht, 1892 : 400, pl. 28 figs 1, 12, 18, 22, 25, 34, pl. 39 fig. 38; Steuer, 1904 : 598; Paulsen, 1909 : 37; Wolfenden, 1911 : 188, 341.

*Euaugaptilus squamatus*; Sars, 1924 : pl. 78; Sars, 1925 : 261; Jespersen, 1940 : 58, 96; [part] Lysholm, Nordgaard & Wiborg, 1945 : 38, 48; ?Wilson, 1950 : 207; Grice & Hulsemann, 1965 : 224, fig. 4; Vervoort, 1965 : 136.

*Augaptilus brevicaudatus* Sars, 1905 : 12; Farran, 1908 : 16, 73.

*Augaptilus californicus* Esterly, 1913 : 186, figs 4, 22, 31, 40, 43, 48; Brodsky, 1950 : 371, fig. 261.

*Euaugaptilus californicus*; Owre & Foyo, 1964a : 343; Owre & Foyo, 1964b : 366.

*Euaugaptilus laticeps* (non *Euaugaptilus laticeps* (Sars, 1905)) Owre & Foyo, 1967 : 86, figs 578, 579 (non 573-576).

This species was designated by Sars as the type of the genus.

Since Sars originally confused this species with *E. magnus* (see p. 36) the samples from the Michael Sars Expedition, 1910, have been re-examined. Only those found to contain *E. squamatus* are included in the distributional notes given below. The records given by Wilson (1950), which were also based on identifications by Sars, may be similarly affected.



The description of this species by Sars (1925) differs in three points of detail from Giesbrecht's description (1892): (1) the spine on the second exopodite segment of the 1st swimming limb is absent in Sars' description; (2) Sars figured seven, instead of eight, setae on the endopodite of the 5th swimming limb; (3) he figured an extra tooth on the mandibular gnathobase. These differences seem to be part of the natural variation, but the condition described by Giesbrecht was the more common in the specimens examined by the present author.

The type material of *A. californicus* has been re-examined by Dr Hulsemann and the present author and found to agree with Giesbrecht's description of *E. squamatus* (loc. cit.).

Some confusion has arisen over the identification of some specimens of *Euaugaptilus* as *E. californicus* by Owre & Foyo (1964a & b) and their subsequent transfer to *E. laticeps* (Owre & Foyo, 1967). The opportunity is taken here to clarify this matter with the aid of correspondence kindly sent by Drs Owre and Foyo and by Dr Hulsemann. Structurally, *E. squamatus* and *E. laticeps* are very close but Owre and Foyo's original figures (1967, figs 578, 579) of the 1st and 5th swimming limbs are more suggestive of *E. squamatus*. Dr Hulsemann has said (in litt.) that the specimens she examined 'were not misidentified *E. laticeps* but agreed with *E. squamatus* as described by Giesbrecht'. It seems, therefore, that these records should be corrected back to *E. squamatus*, but the drawings (loc. cit., figs 573-576), being taken from Sars (1925), refer to *E. laticeps*.

**DISTRIBUTION.** Widespread in the N. and S. Atlantic, including the equatorial region, and extending north to 63°N. Recorded in the Pacific between 33°N and 23°S. Usually obtained below about 500 m, but recorded by Wilson (1950) at the surface.

#### *Euaugaptilus subfiligerus* (Wolfenden, 1911)

See under *E. oblongus*.

#### *Euaugaptilus sublongiseta* Park, 1970

*Euaugaptilus sublongiseta* Park, 1970 : 527, figs 277-288.

See p. 66 for a discussion of possible synonymy.

**DISTRIBUTION.** Recorded once from the Caribbean Sea at 11°N, 79°W at a depth between 208 and 500 m.

#### *Euaugaptilus tenuicaudis* (Sars, 1905)

*Augaptilus tenuicaudis* Sars, 1905 : 15.

*Euaugaptilus tenuicaudis*; Sars, 1924 : pl. 99; Sars, 1925 : 292; Lysholm, Nordgaard & Wiborg, 1945 : 38, 50.

**DISTRIBUTION.** Only recorded from the N. Atlantic, between 29 and 40°N and as far as 29°W. Known to occur at a depth less than 1500 m.



*Euaugaptilus tenuispinus* Sars, 1920

*Euaugaptilus tenuispinus* Sars, 1920 : 16; Sars, 1924 : pl. 97; Sars, 1925 : 290; Sewell, 1932 : 322; Owre & Foyo, 1964a : 343; Vervoort, 1965 : 140; Grice & Hulsemann, 1967 : 19; Owre & Foyo, 1967 : 88, figs 609, 611.

*Euaugaptilus tenuispinus* var.; Sewell, 1947 : 219, fig. 59.

**DISTRIBUTION.** Recorded in the N. Atlantic, including the Caribbean, between 1 and 36°N, and in the N. Arabian Sea between 10 and 18°N. Known to occur at a depth of 900 m.

*Euaugaptilus truncatus* (Sars, 1905)

*Augaptilus truncatus* Sars, 1905 : 14; Farran, 1908 : 16, 75.

*Euaugaptilus truncatus*; Sars, 1924 : pl. 83; Sars, 1925 : 269.

Grice & Hulsemann found a female specimen of *Euaugaptilus* in the South Pacific (33°53'S, 90°34'W in a haul from 2000 to 970 m on 19 January 1966) which they have suggested (in litt.) may represent a new subspecies of *E. truncatus*. The specimen was slightly smaller (6.6 mm in body length) than recorded by Sars (7.6 mm) and differed from the typical structure in having one seta fewer than normal on the endopodite of the 1st swimming limb and two fewer on the first endite of the 1st maxilla (Fig. 11c), in having an extra tooth on the gnathobase (Fig. 11a), and in the greater reduction of the mandibular palp (Fig. 11b). The difference in body length and in setation of the 1st maxilla and 1st swimming limb can be attributed to possible natural variation; the difference in the mandibular structure may be an abnormality (cf. *E. facilis*). Until more is known about the occurrence of this form, it seems best to record it as a variant and to refrain from erecting a new subspecies, with the zoogeographical connotations this would imply.

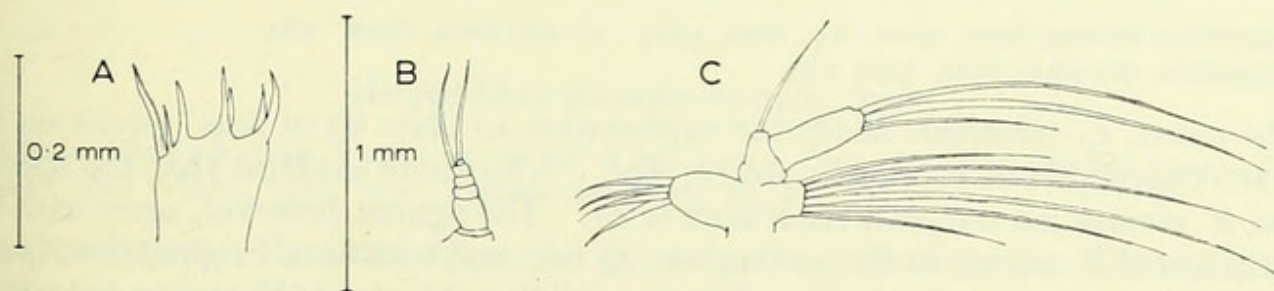


FIG. 11. An unusual specimen of *Euaugaptilus truncatus*. A. Mandibular gnathobase. B. Mandibular palp. C. 1st maxilla.

**DISTRIBUTION.** Recorded from the N. Atlantic between 28 and 55°N and as far as 26°W. One record of a variant from the S.E. Pacific.

*Euaugaptilus unisetosus* Park, 1970

*Euaugaptilus unisetosus* Park, 1970 : 533, figs 313-317.

See p. 66 for a discussion of possible synonymy.

**DISTRIBUTION.** Recorded once in the Caribbean Sea at 19°N, 82°W at a depth between 155 and 450 m.



***Euaugaptilus validus*** (Scott, 1909)

*Augaptilus validus* Scott, 1909 : 138, pl. 43 figs 1-10.

It appears that the specimens actually dissected and described by Scott are not now in the Siboga collections and their whereabouts are unknown. A male specimen in a vial labelled *A. validus* (containing also three females of *E. longimanus*, a species not recorded by Scott) and examined by the present author, may be the second male, though the shape of the head in lateral view is well rounded, in marked contrast to Scott's description of it as very much depressed and with an extremely narrow forehead. The other characters described by Scott, notably the structure of the mandibular gnathobase and the fifth limbs, agree well with the present specimen. The head and rostrum are identical with *E. oblongus* and it is certainly closely related to that species and to *E. squamatus*, *E. rectus* and rather less so to *E. magnus*, though in no case is it identical. The proposed synonymy of *E. validus* with *E. magnus* must therefore remain in doubt. Scott's description of *E. validus* is supplemented in Table 5 with details from this male, the extra data being marked with an asterisk.

***Euaugaptilus vescus*** Park, 1970

*Euaugaptilus vescus* Park, 1970 : 529, figs 289-299.

See p. 66 for a discussion of similarity.

DISTRIBUTION. Recorded once from the Caribbean Sea at 11°N, 79°W at a depth between 1000 and 1850 m.

***Euaugaptilus vicinus*** Sars, 1920

*Euaugaptilus vicinus* Sars, 1920 : 14; Sars, 1924 : pl. 93; Sars, 1925 : 284.

*Euaugaptilus simulans* Sars, 1924 : 37

The name, *E. simulans*, heads the explanation to plate 93 of Sars' report on the Monaco copepods but is found nowhere else. A footnote explains that the specific name, *E. vicinus*, on the plate itself is an error. The figures, however, agree with the description of *E. vicinus* in the accompanying text and with Sars' original description (1920) of that species. The name, *E. simulans*, therefore is at the most a subjective synonym of *E. vicinus*.

DISTRIBUTION. Recorded once from the N. Atlantic at 32°N, 25°W in a vertical haul from 3000 m to the surface.

***Euaugaptilus species*** Grice & Hulsemann, 1965

See under *E. brodskyi*.

***Euaugaptilus species 1*** Grice & Hulsemann, 1967

See under *E. facilis*.



***Euaugaptilus* species 2** Grice & Hulsemann, 1967

As concluded by Grice & Hulsemann (1967), it is not possible at this time to do more than point out that this male resembles the female of *E. affinis* more than any other; yet it shows sufficient differences to prevent its assignment to that species with any certainty.

***Euaugaptilus* species 3** Grice & Hulsemann, 1967

If this is the male of a known species it must be that of *E. rigidus*, but again there are differences which make any such assignment uncertain.

THE SPECIES OF *AUGAPTILUS* GIESBRECHT, 1889

*Augaptilus* sensu stricto, as defined by Sars (1920) is a well defined genus of augaptilid copepods in which the 1st maxilla shows marked reduction. The genus of seven species shows little interspecific variation. *A. zetesios* is accepted as a synonym of *A. glacialis* but data for both forms are entered in Table 5 and their similarities as shown by the computer analysis are discussed on p. 59. Some species described before the division of *Augaptilus* sensu lato have not been recorded since. They have not been included in the list below if in fact they belong to genera subsequently divided off from *Augaptilus*. In the case of species now belonging in *Euaugaptilus* the name has been included under that heading, in other cases they are listed among the species later transferred to other genera (p. 56).

***Augaptilus anceps*** Farran, 1908

*Augaptilus anceps* Farran, 1908 : 16, 79, pl. 8 figs 15-19; Sars, 1924 : pl. 77 figs 19-22; Sars, 1925 : 260; Wilson, 1950 : 170; Tanaka, 1964 : 75, fig. 211.

DISTRIBUTION. Recorded from the N. Atlantic, including the Mediterranean, between 35 and 55°N and as far as 28°W. In the N.W. Pacific between 14 and 35°N and in the S.E. Pacific between 6 and 22°S. Known to occur above 600 m depth, probably also deeper.

***Augaptilus cornutus*** Wolfenden, 1911

*Augaptilus cornutus* Wolfenden, 1911 : 187, 333, fig. 69; Brodsky, 1950 : 370, fig. 259; Grice & Hulsemann, 1965 : 224, fig. 4.

DISTRIBUTION. The three recorded specimens came from widely separate oceanic regions: the N. Atlantic at 30°N, the Antarctic and the N.W. Pacific. Known to occur between 2000 and 3000 m depth.



*Augaptilus glacialis* Sars, 1900

*Augaptilus glacialis* Sars, 1900 : 88, pls 26, 27; Sars, 1924 : pl. 76 figs 1-16; Sars, 1925 : 254; Jespersen, 1940 : 57, 96; Brodsky, 1950 : 367, fig. 258; Wilson, 1950 : 170; Vervoort, 1951 : 144, figs 80, 81; Vervoort, 1957 : 138, fig. 131; Tanaka, 1964 : 77, fig. 212; de Decker & Mombeck, 1965 : 11; Grice & Hulsemann, 1965 : 224; Vervoort, 1965 : 130; Calef & Grice, 1967 : 93; Grice & Hulsemann, 1967 : 18.

*Augaptilus zetesios* Wolfenden, 1902 : 369, pl. 3; Wolfenden, 1904 : 112, 122.

See p. 59 for a discussion of the similarity between accepted synonyms.

**DISTRIBUTION.** Widely distributed in the N. Atlantic from the equator to Arctic regions N.E. of Novaya Zemlya, also in the Atlantic sector of the Antarctic. In the Indian Ocean from 6°N to 55°S and in the N.E. and N.W. Pacific at 33 to 35°N. The known vertical distribution extends from below 1000 to the uppermost 130 m (in the Arctic); taken once in the uppermost 200 m in the tropical Atlantic.

*Augaptilus lamellifer* Esterly, 1911

*Augaptilus lamellifer* Esterly, 1911 : 329, figs 8, 36; Brodsky, 1950 : 371, fig. 260.

**DISTRIBUTION.** Recorded once in the N.E. Pacific off California at a depth less than 600 m.

*Augaptilus longicaudatus* (Claus, 1863)

*Hemicalanus longicaudatus* Claus, 1863 : 179, pl. 29 fig. 3.

*Augaptilus longicaudatus*; Giesbrecht, 1889 : 814; Giesbrecht, 1892 : 400, pl. 27 fig. 31, pl. 28 figs 2, 8, 11, 19, 23, 31, 32, 35, 38, 39, pl. 29 fig. 22, pl. 39 figs 37, 48; Scott, 1894 : 34, pl. 1 figs 24-26, pl. 2 fig. 5; Wolfenden, 1904 : 112, 135, 142, 144, 145; Farran, 1908 : 16, 78; Paulsen, 1909 : 37; Scott, 1909 : 136; Wolfenden, 1911 : 188, 341; Farran, 1920 : 16; Sars, 1924 : pl. 76 figs 17, 18; Sars, 1925 : 256; Farran, 1926 : 288; Farran, 1929 : 269; Farran, 1936 : 113; Jespersen, 1940 : 57, 96; Wilson, 1942 : 171; Lysholm, Nordgaard & Wiborg, 1945 : 37, 48; Sewell, 1947 : 232; Brodsky, 1950 : 367, fig. 257; Wilson, 1950 : 170; Grice, 1962 : 226, pl. 26 figs 6-14; Tanaka, 1964 : 79, fig. 213; de Decker & Mombeck, 1965 : 11; Vervoort, 1965 : 131; Calef & Grice, 1967 : 93; Owre & Foyo, 1967 : 82, figs 58, 59, 550-552; Park, 1970 : 477.

As the senior species this should be regarded as the type of the genus, in accordance with Sars' statement (1925, p. 254). Sewell's objection (1932, p. 325) on the grounds that Giesbrecht consistently named *A. filigerus* before *A. longicaudatus* is irrelevant as *A. filigerus* no longer remains in the genus.

**DISTRIBUTION.** Occurs widely in the N. Atlantic, including the Mediterranean and Caribbean, between 0 and 60°N, also once in the S. Atlantic. Recorded in the western Indian Ocean between 10°N and 34°S. Frequently recorded in the N. and particularly the S. Pacific between 35°N and 34°S. Known to occur at a depth between 750 and 1000 m, but usually higher up, often in the uppermost 200 m, and taken at the surface in a night sample.



***Augaptilus megalurus* Giesbrecht, 1889**

*Augaptilus megalurus* Giesbrecht, 1889 : 814; Giesbrecht, 1892 : 400, pl. 27 fig. 28, pl. 28 fig. 7, pl. 29 fig. 20, pl. 39 fig. 47; Farran, 1908 : 16, 80; Wolfenden, 1911 : 187, 339; Farran, 1920 : 16, 21; Sars, 1924 : pl. 77 figs 1-9; Sars, 1925 : 257; Sewell, 1932 : 326; Jespersen, 1940 : 58, 96; Wilson, 1950 : 171; Björnberg, 1965 : 223; Vervoort, 1965 : 132; Park, 1970 : 477.

DISTRIBUTION. Recorded from the Atlantic, including the Caribbean, between 65°N and 1°S. Also known from the central Arabian Sea and the Pacific between 14°N and 20°S. The known depth range extends from about 150 to below 1200 m.

***Augaptilus spinifrons* Sars, 1907**

*Augaptilus spinifrons* Sars, 1907 : 20; Sars, 1924 : pl. 77 figs 10-18; Sars, 1925 : 258; Farran, 1936 : 113; ? Lysholm, Nordgaard & Wiborg, 1945 : 37; de Decker & Mombeck, 1965 : 11; Park, 1968 : 563, pl. 12 figs 1-5.

DISTRIBUTION. Recorded from the N. Atlantic between 34 and 39°N and as far as 33°W, and from the Pacific at 32°N, 146°E and 16°S, 155°W. Known to occur at less than 150 m depth.

***Augaptilus zetesios* Wolfenden, 1902**

See under *A. glacialis*.

THE SPECIES OF *HALOPTILUS* GIESBRECHT, 1898

The original generic name, *Hemicalanus*, was retained by Giesbrecht in 1889 and 1892 when he divided off the species of *Augaptilus* s.l. It was finally dropped in 1898 after it was realized that Claus had used the name quite differently from Dana (see p. 4). Twenty-four species are analysed in Table 5.

***Haloptilus aculeatus* (Brady, 1883)**

*Hemicalanus aculeatus* Brady, 1883 : 4, 45, pl. 46 figs 2-4; ? Giesbrecht, 1889 : 813.

As a poorly described species which has not been rediscovered with certainty since its original description, this must be considered a doubtful species, though it has been included in the computer analysis.

DISTRIBUTION. Recorded from the southern Indian Ocean and from the Pacific at 28°N, 155°W and possibly 3°S, 99°W.

***Haloptilus acutifrons* (Giesbrecht, 1892)**

*Hemicalanus acutifrons* Giesbrecht, 1892 : 384, pl. 3 fig. 11, pl. 27 figs 4, 12, 18, 26, pl. 42 figs 12, 20.

*Haloptilus acutifrons*; Sars, 1903 : 122, pl. 83 fig. 2; Wolfenden, 1904 : 111, 135, 140, 145; Farran, 1908 : 16, 68; Farran, 1920 : 17, 19; Jespersen, 1923 : 131; Sars, 1924 : pl. 74 figs



1-11; Sars, 1925 : 250; Farran, 1926 : 285; Farran, 1929 : 267; Farran, 1936 : 113; Jespersen, 1940 : 56, 96; Wilson, 1942 : 188; Lysholm, Nordgaard & Wiborg, 1945 : 37, 48; Sewell, 1947 : 190; Brodsky, 1950 : 364, fig. 255; Wilson, 1950 : 235; Chiba, Tsuruta & Maéda, 1955 : 192; Vervoort, 1957 : 135; Grice, 1962 : 223, pl. 25 figs 1-8; Grice & Hart, 1962 : 293; Björnberg, 1963 : 54; Djordjevic, 1963 : 576; Gaudy, 1963 : 27; Giron, 1963 : 574; Grice, 1963 : 496; Owre & Foyo, 1964b : 366; Tanaka, 1964 : 42; Björnberg, 1965 : 223; [Chiba], 1965 : 129, 136; de Decker & Mombeck, 1965 : 12; Grice & Hulsemann, 1965 : 224, fig. 4; Furuhashi, 1966 : 313; Calef & Grice, 1967 : 93; Grice & Hulsemann, 1967 : 19; Owre & Foyo, 1967 : 81, figs 523-534; Park, 1970 : 478.

*Hemicalanus spinifrons* Sars, 1900 : 95, pl. 28.

**DISTRIBUTION.** Widespread in the Atlantic, including adjacent seas, from 84°N, 96°E in the Arctic to 30°S. In the western Indian Ocean from 10°N to 35°S. Recorded throughout the Pacific from 37°N to 44°S. Known to occur at various depths from near the surface to 500 m, once recorded below 1000 m.

### *Haloptilus angusticeps* Sars, 1907

*Haloptilus angusticeps* Sars, 1907 : 20; Sars, 1924 : pl. 72; Sars, 1925 : 246; Farran, 1926 : 285, pl. 9 fig. 14; Farran, 1936 : 113; Wilson, 1942 : 188; Lysholm, Nordgaard & Wiborg, 1945 : 37; Wilson, 1950 : 235; Björnberg, 1965 : 225; de Decker & Mombeck, 1965 : 12; Vervoort, 1965 : 125.

**DISTRIBUTION.** Recorded in the Atlantic, including the Mediterranean, between 47°N and 14°S and as far as 23°W. In the Indian Ocean at 37°S, 55°E. In the western Pacific between 39°N and 15°S. Known to occur as deep as 750-1000 m and also recorded from the uppermost 200 m.

### *Haloptilus austini* Grice, 1959

*Haloptilus austini* Grice, 1959 : 193, figs 1-18; Grice, 1962 : 223; Grice & Hart, 1962 : 293; Calef & Grice, 1967 : 93.

**DISTRIBUTION.** Recorded from the central and western Atlantic between 0 and 40°N and from the central Pacific between 0 and 28°N. Known to occur at less than 100 m depth.

### *Haloptilus bulliceps* Farran, 1926

*Haloptilus bulliceps* Farran, 1926 : 286, pl. 9 figs 15, 16, pl. 10 figs 1-3; Wilson, 1950 : 235; Björnberg, 1965 : 223.

Although this species has been recorded twice since its original description, only the male copepodid IV has yet been observed and described. It is therefore not included in the computer analysis although it certainly seems to be distinct from other known species.

**DISTRIBUTION.** In the Atlantic recorded from the Bay of Biscay and off the coast of Brazil. One record from the tropical western Pacific. Known to occur at a depth between 200 and 400 m and above 200 m.



***Haloptilus caribbeanensis*** Park, 1970

*Haloptilus furcatus* (non *H. furcatus* Sars) Grice, 1969 : 454.

*Haloptilus caribbeanensis* Park, 1970 : 537, figs 356-371.

DISTRIBUTION. So far only recorded from the Caribbean Sea and Gulf of Mexico. Known to occur at a depth between 980 and 1900 m.

***Haloptilus chierchiae*** (Giesbrecht, 1889)

*Hemicalanus chierchiae* Giesbrecht, 1889 : 813; Giesbrecht, 1892 : 384, pl. 27 figs 16, 17, 25, pl. 42 figs 2, 27, 28.

*Haloptilus chierchiae*; Wolfenden, 1911 : 187, 324; Sars, 1924 : pl. 70; Sars, 1925 : 244; Sewell, 1932 : 328; Sewell, 1947 : 190, fig. 49; Wilson, 1950 : 236; Grice & Hulsemann, 1967 : 19.

DISTRIBUTION. Recorded from the equatorial Atlantic to 47°N. In the western Indian Ocean between 6 and 18°N. In the S.E. Pacific from the equator to 17°S. Recorded from below 1000 m to the surface layers.

***Haloptilus fertilis*** (Giesbrecht, 1892)

*Hemicalanus fertilis* Giesbrecht, 1892 : 384, pl. 27 figs 2, 36, pl. 42 figs 5, 18, 26.

*Haloptilus fertilis*; Grice, 1962 : 223, pl. 25 figs 9-11; Owre, 1962 : 492; Björnberg, 1963 : 54; ?Björnberg, 1965 : 223; Vervoort, 1965 : 129; Calef & Grice, 1967 : 93; Owre & Foyo, 1967 : 81, figs 526-529; Park, 1968 : 561.

Only the male of this species has so far been described.

DISTRIBUTION. Known from the Atlantic, including the Mediterranean, between 25°N and 25°S. Recorded in the central Pacific between the equator and 32°N. Obtained at the surface and at a depth between 80 and 240 m.

***Haloptilus fons*** Farran, 1908

*Haloptilus fons* Farran, 1908 : 16, 69, pl. 7 figs 11-15; Sars, 1924 : pl. 71; Sars, 1925 : 245; Wilson, 1950 : 236.

DISTRIBUTION. Recorded in the N. Atlantic between 29 and 55°N and as far as 40°W. In the eastern and western Pacific between 8 and 17°N. Known to occur below 1200 and above 600 m depth.

***Haloptilus furcatus*** Sars, 1920

*Haloptilus furcatus* Sars, 1920 : 12; Sars, 1924 : pl. 75; Sars, 1925 : 252.

DISTRIBUTION. So far recorded only at 31°N, 24°W in the Atlantic, in a haul from 5000 m to the surface.



***Haloptilus longiceps* Tanaka, 1964**

*Haloptilus longiceps* Tanaka, 1964 : 44, fig. 194.

DISTRIBUTION. One record from the Pacific off the coast of Japan in a vertical haul from 1000 m to the surface.

***Haloptilus longicirrus* Brodsky, 1950**

*Haloptilus longicirrus* Brodsky, 1950 : 363, fig. 254; Grice, 1963 : 496, 498, fig. 1c-g; Vervoort, 1965 : 124; Park, 1970 : 535, figs 330-342.

See discussion under *H. longicornis*.

DISTRIBUTION. Recorded from the N. Atlantic, including the Caribbean and the Gulf of Mexico, between 1 and 26°N. Originally described from the N.W. Pacific. Occurs at depths from around 600 to below 1000 m.

***Haloptilus longicornis* (Claus, 1863)**

*Hemicalanus longicornis* Claus, 1863 : 179, pl. 29 fig. 1; Brady, 1883 : 4, 44, pl. 9 figs 1-7; Thompson, 1888 : 139; Giesbrecht, 1889 : 813; Giesbrecht, 1892 : 384, pl. 1 fig. 4, pl. 2 fig. 13, pl. 27 figs 3, 8-10, 23, 27, 29, 33, pl. 42 figs 15, 29; Scott, 1894 : 32.

*Haloptilus longicornis*; Sars, 1903 : 121, pls. 82, 83 fig. 1; Thompson, 1903 : 4, 8-10, 28; Wolfenden, 1904 : 111, 112, 140, 144, 145; Farran, 1908 : 16, 67; Scott, 1909 : 140; Wolfenden, 1911 : 187, 323; Farran, 1920 : 17, 19, 27, 28; Sars, 1925 : 240; Farran, 1926 : 286; Farran, 1929 : 269; Farran, 1936 : 113; Wilson, 1942 : 188; Lysholm, Nordgaard & Wiborg, 1945 : 37, 48; Brodsky, 1950 : 362, fig. 253; Wilson, 1950 : 236; Chiba, Tsuruta & Maéda, 1955 : 192, 199, 200; Honjo, Ohta, Kidachi, Umeda & Kudoh, 1957 : 121; Heinrich, 1960 : 31, 36, 39; Grice, 1962 : 223; Grice & Hart, 1962 : 296; Owre, 1962 : 492; Björnberg, 1963 : 54; Djordjevic, 1963 : 576; Gaudy, 1963 : 27; Giron, 1963 : 574; Grice, 1963 : 496; Owre & Foyo, 1964b : 366; Tanaka, 1964 : 39, fig. 192; Björnberg, 1965 : 223; [Chiba], 1965 : 129, 136; de Decker & Mombeck, 1965 : 38; Grice & Hulsemann, 1965 : 224, fig. 4; Vervoort, 1965 : 123; Furuhashi, 1966 : 310, 313; Calef & Grice, 1967 : 89, 93; Grice & Hulsemann, 1967 : 19; Owre & Foyo, 1967 : 81, figs 530-534; Park, 1968 : 561; Park, 1970 : 535, figs 325-329.

In recent years three new species, *H. longicirrus* Brodsky, *H. setuliger* Tanaka and *H. paralongicirrus* Park, have been described. These three species are structurally very similar to each other and to *H. longicornis*, and are likely to be included in some of the above references. *H. longicirrus* was apparently described from a single specimen (Brodsky, 1950) but has since been found in greater numbers, in geographical if not vertical association with *H. longicornis*, and has been more fully described and compared with the latter species (Vervoort, 1965; Park, 1970). *H. paralongicirrus* has been described on the basis of 28 specimens and distinguished from both *H. longicornis* and *H. longicirrus* found in the same area (Park, 1970), so it is clear that this, too, represents a recognizable population unit. *H. setuliger* was described from a total of four specimens in a survey which also included *H. longicornis*. *H. longicirrus* was not recorded at the same time but Tanaka (1964) pointed to certain



distinguishing characters in the structure of the 5th limbs (the presence in *H. setuliger* of one small seta on the inner margin of the basipodite and another on the second segment of the exopodite). In these details Park's redescription of *H. longicirrus* agrees with *H. setuliger*. If these setae were overlooked in the original description of *H. longicirrus*, then *H. setuliger* can be assumed to be a synonym of *H. longicirrus*. If there is a real difference, then Park's specimens, and perhaps Vervoort's, should be referred to *H. setuliger*. Because of this uncertainty *H. setuliger* Tanaka is retained for the present.

**DISTRIBUTION.** A very widespread and often abundant species. Recorded in the Atlantic and adjacent seas from 70°N to the Antarctic. In the Indian Ocean from 14°N to 35°S. In the Pacific from 35°N to 40°S. The known depth range extends from the surface to below 1000 m, though the deepest records may refer to the related species.

### *Haloptilus major* Wolfenden, 1911

*Haloptilus major* Wolfenden, 1911 : 187, 324.

**DISTRIBUTION.** Only recorded from the equatorial Atlantic at a depth between 1330 m and the surface.

### *Haloptilus mucronatus* (Claus, 1863)

*Hemicalanus mucronatus* Claus, 1863 : 179, pl. 29 fig. 2; Giesbrecht, 1889 : 813; Giesbrecht, 1892 : 384, pl. 3 fig. 10, pl. 27 figs 11, 13, 19, 22, 37, 39, pl. 42 figs 4, 6, 13, 14, 30; Scott, 1894 : 33.

*Haloptilus mucronatus*; Sars, 1924 : pl. 73 figs 11-15; Sars, 1925 : 249; Farran, 1929 : 268; Farran, 1936 : 113; Lysholm, Nordgaard & Wiborg, 1945 : 37, 48; Sewell, 1947 : 193; Wilson, 1950 : 236; Chiba, Tsuruta & Maéda, 1955 : 192; Owre, 1962 : 492; Björnberg, 1965 : 223; de Decker & Mombeck, 1965 : 12; Furuhashi, 1966 : 310; Calef & Grice, 1967 : 93; Owre & Foyo, 1967 : 81, figs 530-534.

**DISTRIBUTION.** Occurs widely in the warmer regions of the Atlantic, including the Mediterranean and Caribbean, between 37°N and 25°S. Recorded in the S.W. Indian Ocean as far as 27°S. In the Pacific, particularly the western part, from 30°N to 34°S. Most frequently recorded at depths from 200 m to the surface but known to extend down to below 1000 m.

### *Haloptilus ocellatus* Wolfenden, 1905

*Haloptilus ocellatus* Wolfenden, 1905 : 14, pl. 5; Wolfenden, 1908 : 42, pl. 3 figs 1, 2; Wolfenden, 1911 : 187, 324; Farran, 1929 : 268; Vervoort, 1951 : 143; Vervoort, 1957 : 138; [Chiba], 1965 : 129, 136; Seno, Komaki & Takeda, 1966 : 4, 5, 12.

**DISTRIBUTION.** This is characteristically a circumpolar Antarctic species but it has been reported to reach 5°N in the eastern Indian Ocean. Known to occur in the uppermost 100 m and down to below 500 m.



***Haloptilus orientalis*** (Brady, 1883)

*Hemicalanus orientalis* Brady, 1883 : 4, 45, pl. 9 figs 8, 9, pl. 10 figs 1-4.

This species was described from a female copepodid V and has not been recorded since. As the brief description is insufficient to decide whether or not *H. orientalis* is synonymous with a better known species, it seems best to reject the name.

***Haloptilus ornatus*** (Giesbrecht, 1892)

?*Hemicalanus plumosus* (non *H. plumosus* Claus) Giesbrecht, 1889 : 813.

*Hemicalanus ornatus* Giesbrecht, 1892 : 384, pl. 27 figs 1, 6, 7, 14, 15, 21, 24, 38, pl. 42 figs 1, 9, 17, 19, 22, 24.

*Haloptilus ornatus*; Scott, 1909 : 141; Wolfenden, 1911 : 187, 323; Sars, 1924 : pl. 73 figs 1-5; Sars, 1925 : 247; Sewell, 1932 : 328; Wilson, 1942 : 189; Lysholm, Nordgaard & Wiborg, 1945 : 37, 48; Sewell, 1947 : 194, fig. 50H; Wilson, 1950 : 236; Chiba, Tsuruta & Maéda, 1955 : 192; Grice, 1962 : 223, pl. 25 figs 12-16; Owre, 1962 : 492; Björnberg, 1965 : 223; [Chiba], 1965 : 129, 136; de Decker & Mombeck, 1965 : 12; Grice & Hulsemann, 1965 : 224, fig. 4; Vervoort, 1965 : 126; Furuhashi, 1966 : 307, 310; Calef & Grice, 1967 : 93; Owre & Foyo, 1967 : 81, figs 539-542; Park, 1970 : 478.

DISTRIBUTION. Widespread in the Atlantic, including the Mediterranean and Caribbean, between 38°N and 27°S. Recorded in the western Indian Ocean from 10°N to 30°S. In the central and western Pacific from 35°N to 20°S. Known to extend from the surface to below 150 m.

***Haloptilus oxycephalus*** (Giesbrecht, 1889)

*Hemicalanus oxycephalus* Giesbrecht, 1889 : 813; Giesbrecht, 1892 : 384, pl. 42 figs 7, 16, 23.

*Haloptilus oxycephalus*; Wolfenden, 1911 : 187, 324; Sars, 1924 : pl. 74 figs 12-16; Sars, 1925 : 252; Farran, 1929 : 268; Wilson, 1942 : 189; ? Lysholm, Nordgaard & Wiborg, 1945 : 37; Sewell, 1947 : 194; Wilson, 1950 : 237; Vervoort, 1951 : 142; Chiba, Tsuruta & Maéda, 1955 : 192; Honjo, Ohta, Kidachi, Umeda & Kudoh, 1957 : 121; Vervoort, 1957 : 136, figs 128-130; Owre, 1962 : 492; Djordjevic, 1963 : 576; Tanaka, 1964 : 43; [Chiba], 1965 : 129; de Decker & Mombeck, 1965 : 12; Vervoort, 1965 : 129; Furuhashi, 1966 : 303, 305, 313; Calef & Grice, 1967 : 93; Owre & Foyo, 1967 : 82, figs 543, 544.

DISTRIBUTION. Recorded from the Atlantic, including the Mediterranean and Caribbean, between 1 and 44°N with one record at 63°S (Björnberg, unpubl.). Extends from equatorial regions in the western Indian Ocean to 35°S. Widely distributed in the Pacific from 42°N to Antarctic regions at 78°S. Several times reported at 100 m depth or less but also recorded down to 600 m.

***Haloptilus pacificus*** Chiba, 1956

*Haloptilus pacificus* Chiba, 1956 : 48, fig. 38.

This species was described from a single female obtained off Bikini Reef in the Pacific. The description is too brief and uncertain for the species to be included



in the computer analysis and it has not been possible to obtain further details. Instead, the original description, translated by Dr Akira Fuji, is reprinted here so that any specimens which may subsequently be found may be identified and more completely described.

*Female*: Body transparent. Metasome [=prosome] 5-segmented, urosome 4-segmented. Ratio of length of metasome to urosome 24 : 5. Relative lengths of the segments as follows:

Metasome	1	2	3	4	5	Total
	54	18	9	8	11	100
Urosome	1	2	3	Furca		Total
	52	14	14	20		100

1st antenna reaching past the end of the body, 25-segmented, the last two each bearing one plumose seta; a long seta present on the 16th, 18th, 20th, 23rd, and 24th segments. Endopodite of 2nd antenna much longer than the exopodite. Posterior lateral corners of the last thoracic segment rounded. Genital segment very long and expanded, somewhat longer than the total of the other urosome segments. 5th pair of feet<sup>1</sup> symmetrical, each ramus bearing 5 furcal setae, one of which is very long. Both rami of the 5th limbs 3-segmented; the terminal segment of the exopodite with 4 plumose setae. The species is distinguished from the other known species by the structure of the 1st antenna and the great length of one of the furcal setae. Body length 3.2 mm.

### *Haloptilus paralongicirrus* Park, 1970

*Haloptilus paralongicirrus* Park, 1970 : 537, figs 343-355.

See discussion under *H. longicornis*.

**DISTRIBUTION.** So far only recognized in samples from the Caribbean Sea taken at a depth between 100 and 1850 m.

### *Haloptilus plumosus* (Claus, 1863)

*Hemicalanus plumosus* Claus, 1863 : 178, pl. 28 fig. 12, pl. 29 figs 4-7; Giesbrecht, 1892 : 384; Scott, 1894 : 33, pl. 2 fig. 6, pl. 6 fig. 6.

*Haloptilus plumosus*; Scott, 1909 : 141; Wolfenden, 1911 : 187, 323; Farran, 1926 : 287; Wilson, 1942 : 189; Gaudy, 1963 : 27.

This is the senior species in the genus, being the first to have been described by Claus.

**DISTRIBUTION.** Recorded in the Atlantic, including the Mediterranean, between 47°N and 28°S. Scattered records from the Pacific between 32°N and 34°S. Known to occur at depths of less than 100 to more than 1000 m.

<sup>1</sup>The number and form of the setae suggest that this should read 'caudal furca' instead of '5th pair of feet', a suspicion which is strengthened by the use of the word 'furcal' in the same sentence.



***Haloptilus princeps***

This name is listed in table D-8 (p. 129) of the preliminary report of one of the Japanese cruises taking part in the International Indian Ocean Expedition ([Chiba], 1965). It is likely to be a misprint for *H. spiniceps* which is listed in the subsequent table (D-9).

***Haloptilus pseudooxycephalus* Brodsky, 1950**

*Haloptilus pseudooxycephalus* Brodsky, 1950 : 365, fig. 256.

DISTRIBUTION. Known only from the N.W. Pacific and the Bering and Okhotsk Seas. Recorded both above 470 and below 1000 m.

***Haloptilus setuliger* Tanaka, 1964**

*Haloptilus setuliger* Tanaka, 1964 : 40, fig. 193.

See discussion under *H. longicornis*.

DISTRIBUTION. Recorded from the coast of Japan at a depth less than 1000 m.

***Haloptilus spiniceps* (Giesbrecht, 1892)**

*Hemicalanus spiniceps* Giesbrecht, 1892 : 384, pl. 27 figs 5, 20, 35, 40, pl. 42 figs 3, 8, 10, 11, 21, 25.

*Haloptilus spiniceps*; Thompson, 1903 : 4, 11, 28; Scott, 1909 : 141; Wolfenden, 1911 : 324; Sars, 1924 : pl. 73 figs 6-10; Sars, 1925 : 249; Farran, 1929 : 268; Farran, 1936 : 112; Wilson, 1942 : 189; Lysholm, Nordgaard & Wiborg, 1945 : 37, 48; Wilson, 1950 : 237; Grice, 1962 : 223, figs 17-20, pl. 26 figs 1-5; Owre, 1962 : 492; Björnberg, 1963 : 54; Grice, 1963 : 496; Owre & Foyo, 1964b : 366; Tanaka, 1964 : 43; Björnberg, 1965 : 225; [Chiba], 1965 : 136; de Decker & Mombeck, 1965 : 12; Vervoort, 1965 : 127; Furuhashi, 1966 : 310; Calef & Grice, 1967 : 93; Owre & Foyo, 1967 : 82, figs 60, 545-549; Park, 1968 : 563.

*Haloptilus spinipes*; Wolfenden, 1911 : 187.

DISTRIBUTION. Widely distributed in the Atlantic, including the Mediterranean and Caribbean, from 50°N to 28°S. Recorded in the eastern and western Indian Ocean between the equator and 35°S. Quite widespread in the Pacific from 38°N to 34°S. Recorded once at 700 m depth but otherwise the known depth range is in the uppermost 200-300 m.

***Haloptilus spinifrons* (Sars, 1900)**

See *H. acutifrons*.

***Haloptilus tenuis* Farran, 1908**

*Haloptilus tenuis* Farran, 1908 : 16, 68, pl. 7 figs 16-22; Sars, 1924 : pl. 69; Sars, 1925 : 243; Jespersen, 1940 : 56, 96; Wilson, 1950 : 237; Grice, 1963 : 496; de Decker & Mombeck, 1965 : 12; Grice & Hulsemann, 1967 : 19.

DISTRIBUTION. Recorded from the temperate N. Atlantic, including the Mediter-



anean, between 35 and 65°N. In the S.W. Indian Ocean between 6 and 38°S. One record from the Pacific at 29°N, 140°W. Known to occur over a wide depth range, from the uppermost 200 m to between 1000 and 2000 m.

***Haloptilus validus* Sars, 1920**

*Haloptilus validus* Sars, 1920 : 11; Sars, 1924 : pl. 68; Sars, 1925 : 241; Sewell, 1947 : 194, fig. 50A-G; Wilson, 1950 : 237; de Decker & Mombeck, 1965 : 12; Grice & Hulsemann, 1967 : 19.

DISTRIBUTION. One record from the eastern N. Atlantic at 28°N and one from the Mediterranean. Several records from the western Indian Ocean between about 10°N and 38°S. One record from the S.E. Pacific at 20°S, 103°W. Known to occur in the region of 600 m depth.

THE SPECIES OF *PSEUDAUGAPTILUS* SARS, 1907

This genus appears to be close to *Euaugaptilus*, differing chiefly in possessing an extra segment in the urosome, as in *Haloptilus*. Only three species have been described and they are structurally very similar.

***Pseudaugaptilus longiremis* Sars, 1907**

*Pseudaugaptilus longiremis* Sars, 1907 : 24; Sars, 1924 : pl. 109; Sars, 1925 : 310; Jespersen, 1940 : 62, 96; Lysholm, Nordgaard & Wiborg, 1945 : 40; Vervoort, 1951 : 144, fig. 82; Vervoort, 1957 : 140; Grice & Hulsemann, 1965 : 224, fig. 4; Grice & Hulsemann, 1967 : 19; Park, 1970 : 541.

Park (1970) has suggested that *P. orientalis* Tanaka is synonymous with this species. The main character distinguishing them, i.e. the presence or absence of a spine on the second segment of the exopodite of the 1st limbs, is one which in *Euaugaptilus* at least shows intraspecific variation. If *P. longiremis* and *P. orientalis* should prove to be distinct, however, Park's record (loc. cit.) should be transferred to the latter.

DISTRIBUTION. Recorded from the N. Atlantic, including the Gulf of Mexico, between 22 and 63°N. In the Indian Ocean at 10°S, 65°E. Also known from 66°S in the Atlantic and Indian sectors of the Antarctic. The known depth range extends from above 500 to below 1000 m.

***Pseudaugaptilus orientalis* Tanaka, 1964**

*Pseudaugaptilus orientalis* Tanaka, 1964 : 85, fig. 216.

See discussion under *P. longiremis*.

DISTRIBUTION. This species, if distinct from *P. longiremis*, has only been identified in a sample from the coast of Japan taken vertically from 1000 m to the surface.



*Pseudaugaptilus polaris* Brodsky, 1950

*Pseudaugaptilus polaris* Brodsky, 1950 : 391, fig. 278.

DISTRIBUTION. Recorded from the central area of the Arctic at a depth between 400 and 1000 m.

OTHER SPECIFIC NAMES ONCE ATTRIBUTED TO *AUGAPTILUS*

The following species, originally placed in *Augaptilus*, have since been transferred to *Centraugaptilus* Sars, 1920:

- C. cucullatus* (Sars, 1905)
- C. horridus* (Farran, 1908)
- C. lucidus* (Esterly, 1911)
- C. macrodus* (Esterly, 1911) = *C. rattrayi*
- C. pyramidalis* (Esterly, 1911) = *C. horridus*
- C. rattrayi* (Scott, 1894)

Farran (1908, p. 8) mistakenly wrote *Augaptilus pavoninus* instead of *Arietellus pavoninus*.

## NUMERICAL CLASSIFICATION OF THE SPECIES IN THE FOUR GENERA

## Introduction and method

Sewell's attempt at dividing the genus *Euaugaptilus* has been criticized for being based too much on the structure of the 1st maxilla and too little on other characters (see Vervoort, 1965). In trying to overcome this criticism the principles of numerical taxonomy, defined by Sokal & Sneath (1963, p. 48) as 'the numerical evaluation of the affinity or similarity between taxonomic units and the ordering of these units . . . on the basis of their affinities', have been applied to this study of the four closely related genera. The aims have been to obtain as broad a morphological base as possible and to achieve an objective approach. A summary of the principles and methods in this type of investigation has been given by Sheals (1964).

The Orion Classification Programme (CLASP) developed at Rothamsted Experimental Station, modified since its use by Sheals, has been employed in the present study. In this programme the structural characters are compared one by one for each combination of two species and assigned a score, *s*, which lies between 0 (total dissimilarity) and 1 (total similarity), and a count, *n*, which is 1 if there is a valid comparison and 0 if there is not. The coefficient of similarity, *S*, is then calculated as:

$$S_{ij} = \frac{\sum s_{ij}}{\sum n_{ij}},$$

where the subscripts *i* and *j* refer to the species being compared. All valid comparisons are given equal weight and invalid ones, due usually to one or other character being unknown, are rejected. It follows from the formula that the coefficients of similarity must lie between 0 (representing total dissimilarity) and 1 (representing total similarity).



Two types of characters have been used in the comparisons. The first consists of qualitative characters, where there is a number of classes which are mutually exclusive and unranked; these are scored on a match or mismatch basis. All other characters, in which there is a range of values on a linear scale, are treated quantitatively and scored as follows:

$$s = 1 - \frac{|x_i - x_j|}{r},$$

where  $x_i$  and  $x_j$  are the values for the two species being compared and  $r$  is the observed range of values for that character. Characters with a range of 1, e.g. presence or absence, are considered to be of this type although they are in effect two-class alternatives. For ease of computation all qualitative characters have been assembled at the end of the table of morphological data.

The choice of characters (see Table 4) has largely been determined by the nature of the sources. They include size and body proportions, shape and segmentation of

TABLE 4

Definition of the structural characters used in the computer study. Salient characters for use in identification are denoted by \*.

Character No.	Description
1	Total body length, in mm $\times 10$
2	Ratio of prosome width to length, (1:) $x \times 10$ , e.g. 1:2.7 written as 27
3	Ratio of urosome to prosome, (1:) $x \times 10$
4	Number of urosome segments
5	Ratio of genital segment to urosome, excluding furca, (1:) $x \times 10$
6	Ratio of width to length of caudal rami, (1:) $x \times 10$
7	No. of 1st antenna segments reaching past end of caudal furca
8	Proportions of rami of 2nd antenna - 1. equal or subequal. 2. grossly unequal
9	No. of exopodite segments on 2nd antenna
10	No. of exopodite setae on 2nd antenna
11	No. of endopodite setae on 2nd antenna
12	No. of distinct teeth (incl. spine) on mandibular gnathobase
*13	Setting of teeth on mandibular gnathobase - 1. transverse. 2. slightly oblique. 3. very oblique
14	No. of exopodite setae on mandible
15	No. of endopodite setae on mandible
*16	No. of endopodite segments on 1st maxilla
*17	No. of setae on 1st endite of 1st maxilla
*18	No. of setae on 2nd endite of 1st maxilla
*19	No. of setae on 3rd endite of 1st maxilla
*20	No. of setae on basipodite of 1st maxilla
*21	No. of setae on endopodite of 1st maxilla
*22	No. of setae on exopodite of 1st maxilla
*23	No. of setae on exite of 1st maxilla
24	Total no. of setae on 2nd maxilla
25	Cup-shaped appendages on some setae of 2nd maxilla - 0. absent. 1. poorly developed. 2. well developed
26	No. of setae on coxopodite of maxilliped



TABLE 4 (*cont.*)

Character	Description
27	No. of setae on endopodite of maxilliped
28	Cup-shaped appendages on some setae of maxilliped – as for character 25
29	Length of first exopodite spine on 1st swimming limb – 10. not reaching tip of second spine. 20. not reaching end of ramus. 30. reaching beyond end of ramus. Borderline cases given appropriate intermediate values
30	Length of seta on second exopodite segment of 5th swimming limb – 0. absent. 10. not reaching end of segment. 20. not reaching base of next seta. 30. not reaching base of next seta but one. 40. not reaching end of ramus. 50. reaching beyond ramus. Borderline cases given appropriate intermediate values
*31	Segmentation of the swimming limbs – 1. both rami of 1st reduced. 2. endopodite of 1st reduced. 3. no reduction (3 joints on both rami of all limbs). 4. both rami of 5th reduced. 5. endopodites of 1st and 5th reduced. 6. endopodite of 1st and both rami of 5th reduced
32	No. of spines on the swimming limbs (usual complement: 4,5,5,5,4) – 1. at least 2 missing on 1st, 3rd and 5th. 2. 1 missing on 3rd. 3. 3 missing on 1st. 4. 2 missing on 1st. 5. 1 missing on 1st. 6. usual complement. 7. 1 extra on 5th. 8. 1 missing on 5th. 9. 3 or 4 missing on 5th. 10. reduced no. on 3rd and 5th. 11. reduced no. on 1st and 5th
*33	Details of head structure – 0. no cephalic spine, no rostral filaments. 1. no spine but filaments present. 2. spine but no filaments. 3. spine and filaments present. 4. as for 3 but with longer cephalic spine
*34	Details of mouthparts – 1. one mandibular ramus, no unguiform setae on 2nd maxilla. 2. two rami and no unguiform setae. 3. two rami and unguiform setae. 4. as for 3 but unguiform setae more strongly developed
*35	Protopodite setae on 1st and 5th swimming limbs – 0. no setae on basipodite of 1st or coxopodite of 5th. 1. present on 1st but not on 5th. 2. seta on both.

the appendages, setal counts and some special features. Where information is good and there is much variation between species, as in the case of the 1st maxilla, a number of characters can be set up; where it is usually less detailed in species descriptions, as in the case of the 2nd maxilla, it is not possible to set up more than the one character of the total number of setae. Where particular values of a character are shared by only a few species positive comparisons have an exaggerated effect on the overall similarity. This effect can be overcome by transforming the data so that they show an approximately normal distribution, or by combining several such features, preferably associated ones such as the segmentation of the various swimming limbs. The present data were not always suitable for transformation, so combined, qualitative, characters have been used. To the extent that the choice of characters has been determined by the conventional form of description there is some weighting in favour of those features which have received most attention from previous authors of new species. All available data on these characters for all species of *Euaugaptilus* (including synonyms), *Augaptilus*, *Haloptilus* and *Pseudaugaptilus* are given in Table 5.

The coefficients of similarity are presented in a matrix which then requires sorting. The aims of sorting are to arrange the species so that as far as possible there is a continuous trend from one extreme to the other, and within the matrix to detect



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groups of similar species. To this end the method of principal coordinates analysis (Gower, 1966) has been used to give a multidimensional representation of the differences between the species. This type of analysis examines the spread of the species in  $n$  dimensions, the greatest spread being taken out by the first dimension with a progressive decrease in the subsequent ones.

## Results

The coefficients obtained for the species of *Augaptilus* have been checked first to assess the sensitivity of the technique. This genus shows little interspecific variation and possible synonyms may be expected not to be very obviously paired in such uniform surroundings. *A. zetesios* is an accepted synonym of *A. glacialis*; these two species can be used as an example to illustrate the level of similarity between such synonyms. Table 6a gives the similarity coefficients, expressed as percentages, for

TABLE 6A

Coefficients of similarity (CLASP programme), expressed as percentages, for the genus *Augaptilus*

<i>A. anceps</i>							
84.5	<i>A. cornutus</i>						
87.3	93.2	<i>A. lamellifer</i>					
88.8	90.6	94.6	<i>A. glacialis</i>				
92.2	89.7	93.9	96.7	<i>A. zetesios</i>			
90.2	88.3	93.7	95.3	96.1	<i>A. longicaudatus</i>		
90.7	89.2	92.3	94.1	94.1	93.2	<i>A. megalurus</i>	
84.3	85.0	87.2	89.4	89.6	89.6	90.4	<i>A. spinifrons</i>

the species of *Augaptilus*. *A. glacialis*, *A. zetesios* and *A. longicaudatus* are the only species to show mutual coefficients greater than 95%, and of these that between *A. glacialis* and *A. zetesios* is the highest. As a further check it may be postulated that synonyms will show similar affinity to all other species, so the coefficients for each pair of species have been compared in the following manner:

Q-no.	67	68	69	70	71	72	73	74
67	100.0	(84.5)	88.8	87.3	90.2	90.7	84.3	92.2
68	84.5	(100.0)	90.6	93.2	88.3	89.2	85.0	89.7

$$S_{67} - S_{68} \quad 15.5 \quad - \quad -1.8 \quad -5.9 \quad 1.9 \quad 1.5 \quad -0.7 \quad 2.5$$

$$\Sigma(S_{67} - S_{68})^2 = 290.9.$$

The results (Table 6b) emphasize the similarity between *A. glacialis* and *A. zetesios* and between *A. longicaudatus* and *A. zetesios*. *A. glacialis* and *A. longicaudatus* are very similar to each other, the only reported differences being in body proportions and the presence in the latter species of small spines on the distal surface of the caudal rami, a character not incorporated in the computer study. The body proportions of *A. zetesios*, as figured by Wolfenden (1902), are intermediate, while its size is closer to *A. glacialis*. Wolfenden did not mention spines on the caudal rami, but he was aware of the existence of *A. longicaudatus* and had specimens of it for comparison, so *A. zetesios* can be considered to be distinct. On the other hand,



TABLE 6B

Differences between coefficients,  $S$ , for each pair of species,  $i$  and  $j$ , of *Augaptilus*, expressed as  $\Sigma (S_{ia} - S_{ja})^2$ , where  $a$  is the species common to each comparison.

<i>A. anceps</i>						
291	<i>A. cornutus</i>					
297	131	<i>A. lamellifer</i>				
300	250	57	<i>A. glacialis</i>			
268	309	93	24	<i>A. zetesios</i>		
243	270	84	31	24	<i>A. longicaudatus</i>	
212	241	98	58	56	55	<i>A. megalurus</i>
254	266	306	315	347	281	232 <i>A. spinifrons</i>

Sars' assertion (1925, p. 256) that it is synonymous with *A. glacialis* cannot be accepted as final. As there is so little range of structure in the genus, the extra seta on the 1st maxilla may be more significant than a similar variation in *Euaugaptilus*.

In order to reduce the matrix of coefficients as far as possible to manageable proportions, assumed synonyms have been omitted from the *Euaugaptilus* results, though they were included in the computations. The coefficients for the groups of synonyms are given in Table 7; figures in bold face distinguish assumed synonyms, figures in italics are used where synonymy is less definite, and figures in ordinary type represent doubtful synonymy. The coefficient for *E. subfiligerus* and *E. rostratus* is the lowest for all assumed synonyms; this apart, 90% similarity at least is attained between all such pairs, though the general level is lower than in the case of *Augaptilus glacialis* and *A. zetesios*. There is general agreement between the likelihood of synonymy and the level of the similarity coefficient.

TABLE 7

Coefficients of similarity between assumed (bold face), likely (italics) and doubtful synonyms.

A	<i>E. laticeps</i>	B	<i>E. squamatus</i>
	<b>90.4</b> <i>E. placitus</i>		<b>93.5</b> <i>E. californicus</i>
	83.3 85.4 <i>E. antarcticus</i>		
	83.7 82.4 95.7 <i>E. fungiferus</i> ?		
C	<i>E. oblongus</i>	D	<i>E. magnus</i>
	<b>93.7</b> <i>E. subfiligerus</i>		92.7 <i>E. validus</i>
	<b>89.6</b> <b>86.9</b> <i>E. rostratus</i>		88.3 81.0 <i>E. fungiferus</i>
E	<i>E. filigerus</i>	F	<i>E. nodifrons</i>
	<b>91.0</b> <i>E. depressus</i>		<b>95.3</b> <i>E. simplex</i> (Esterly)
			<b>91.4</b> <b>92.2</b> <i>E. simplex</i> (Wolfenden)

In the principal coordinates analysis of the whole matrix, the first dimension took out 26% of the total spread and indicated the divisions between *Augaptilus*, *Euaugaptilus* and *Haloptilus*, though with some overlap between the last two. The second dimension took out a further 10% of the total spread and, taken in conjunction with the first, improved the separation between the three main genera, though *Pseudaugaptilus* remained indistinguishable from *Euaugaptilus*; it also indicated a



division of *Euaugaptilus* into two groups. The first three dimensions together took out 41% of the total spread and achieved reasonable separation of all the genera, as well as indicating the two groups within *Euaugaptilus* more clearly. As no two dimensions produced a satisfactory division, a three-dimensional figure has been constructed, photographed, and copied in two dimensions (Fig. 12). This has been used as the basis for the arrangement of the species in the matrix, with some adjustment by trial and error to accommodate as much as possible of the spread not already taken out by the first three dimensions.

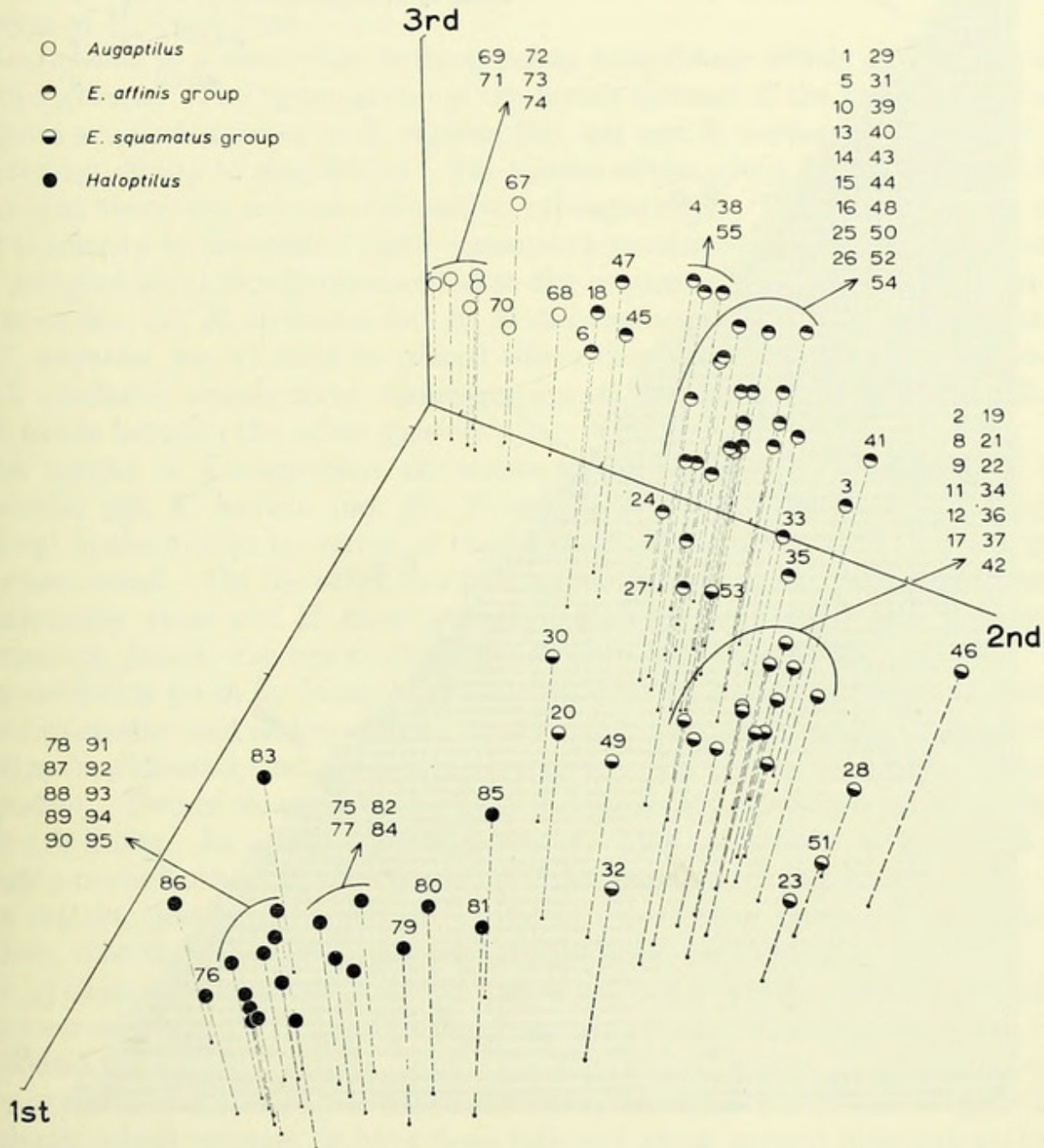


FIG. 12. The results of a principal coordinates analysis of the similarity coefficients produced by the CLASP programme. The small dots indicate the values of the first and second vectors; the circles are positioned according to the values of the third vector. The species are identified by their Q-numbers (see Table 5).



The results are presented in Fig. 13. As is to be expected, the most obvious groupings are those which combine the species within each genus; *Augaptilus* and *Pseudaugaptilus* are particularly homogeneous in this respect. *Pseudaugaptilus* does not fit well into any one place in the matrix and has been placed separately; it can be considered to represent an intermediate between *Augaptilus* and *Haloptilus* alternative to that of *Euaugaptilus*. The species of *Haloptilus* rank quite closely; at the

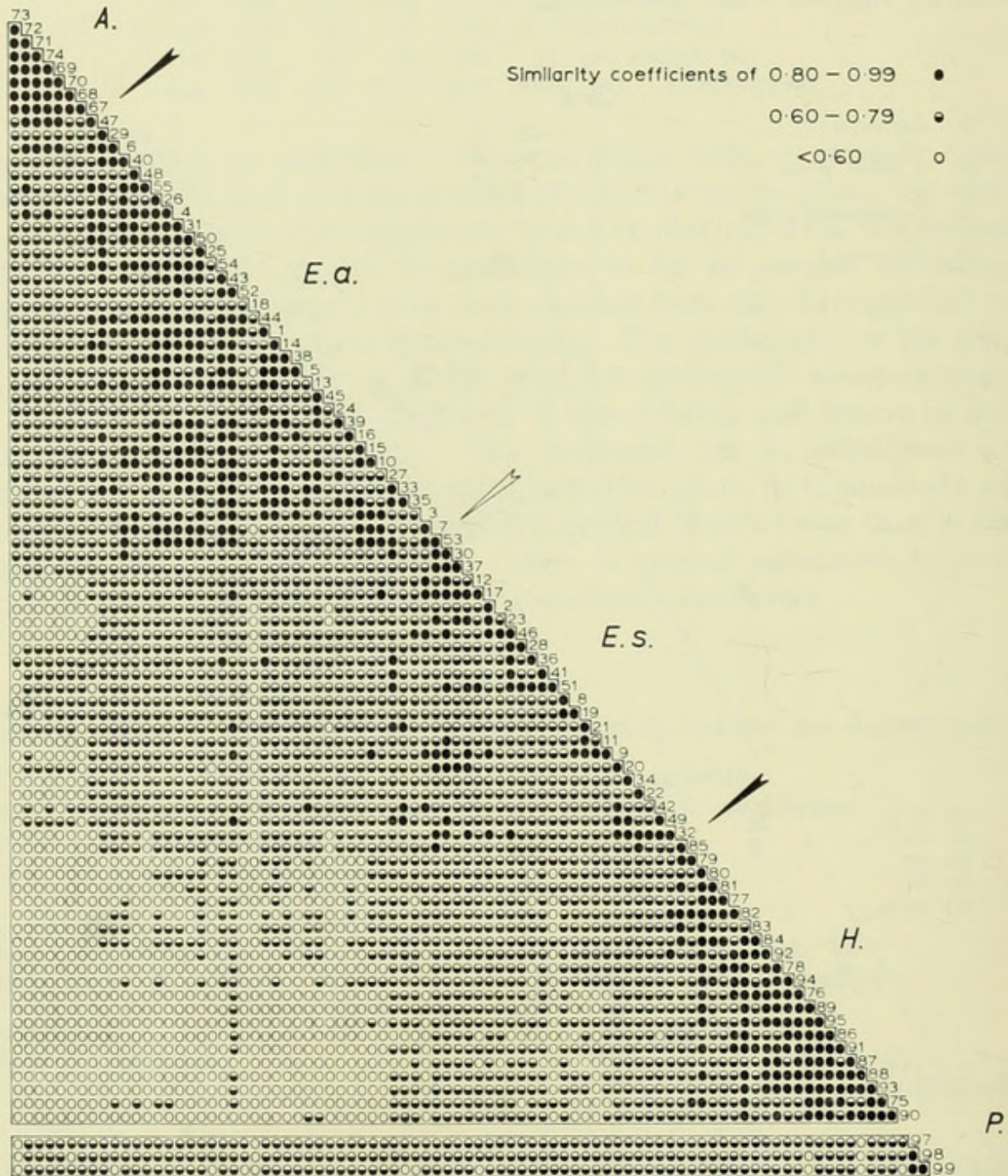


FIG. 13. The matrix of similarity coefficients produced by the CLASP programme, arranged in accordance with the principal coordinates analysis and adjusted by eye. A. *Augaptilus*. E.a. *Euaugaptilus affinis* group. E.s. *Euaugaptilus squamatus* group. H. *Haloptilus*. P. *Pseudaugaptilus*. The species are identified by their Q-numbers (see Table 5).



*Euaugaptilus* end *H. major* (Q-no. 85) is quite clearly the extreme species though at the other end the order is less clear-cut and several alternatives would be equally satisfactory. There are no notably aberrant species within this genus, though *H. major*, *H. fons* (no. 80) and *H. longicirrus* (no. 83) have rather lower coefficients than the others; in the case of *H. major* and *H. longicirrus* this is due to some extent to the exclusion of several characters which have not been described. It is noteworthy that there is a high coefficient between *H. longicornis* (no. 84) and *H. longicirrus*, two species which it is thought may often have been confused before Brodsky's description (1950) of the latter (see Vervoort, 1965); there are also high coefficients between these two and *H. setuliger* (no. 92) which Park (1970) has suggested is a synonym of *H. longicirrus*.

*Euaugaptilus* is a somewhat heterogeneous assemblage which appears to divide into two groups. The upper group is the better defined of the two and at the top end there are such species as *E. rigidus* (no. 47) and *E. curtus* (no. 6) which show quite strong affinity to *Augaptilus*. The species of this group form a triangle of high values and there are several alternative arrangements. The second group shows closer similarity to *Haloptilus*, but it possesses several species which deviate from the main morphological trends represented in the sequence; thus *E. nodifrons* (no. 34), *E. indicus* (no. 22), *E. distinctus* (no. 8), *E. hulsemannae* (no. 19), *E. magnus* (no. 28), and *E. angustus* (no. 2) must be placed where they are, although their low level of overall similarity causes some disintegration of the triangle of higher coefficients which exists between the other species.

Four species of *Euaugaptilus* are shown to be particularly aberrant; *E. longicirrus* (no. 25), *E. hecticus* (no. 18), *E. quaesitus* (no. 45) and *E. latifrons* (no. 24) stand out in the matrix by virtue of the low coefficients with which they are consistently associated. On the other hand, *E. affinis* (no. 1) and *E. pseudaffinis* (no. 44) are extremely close and it must remain a distinct possibility that the two are synonymous, despite the reported differences in body proportions.

The definition given by Brodsky (1950) of the genus *Neoaugaptilus*, i.e. a two-segmented exopodite and endopodite on the 1st swimming limb, covers *E. longicirrus*<sup>1</sup> as well as *N. distinctus*, and seven other species (see Table 5) possess a two-segmented endopodite. Two of these species, plus *E. hecticus*, also show reduced segmentation of the 5th limbs. In other respects, however, these ten species do not show close similarity to each other; *N. distinctus* and *E. longicirrus*, in particular, are far apart in the matrix, despite the identical segmentation of their limbs. It is suggested, therefore, that the genus *Neoaugaptilus* should not be maintained.

The 35 characters used in the calculation of similarity coefficients have been tested to discover which could be used in the diagnoses of the two groups indicated in the matrix and the vector diagram. Since the sequence of species is associated with a tendency towards simplification of the structure and setation of the head appendages, a tendency which appears to have been followed along several different pathways,

<sup>1</sup>The author has recently examined an adult female which was identical with Sars' description of *E. longicirrus* in all respects except that it possessed three segments on both the exopodite and endopodite of the 1st swimming limbs. It seems that even segmentation of appendages is subject to intraspecific variation.



no single character was sufficient to define the groups. Several species, moreover, show affinities with both groups, so any definition must to some extent be arbitrary in its placing of the division between the groups. For this reason the groups have not been given generic or subgeneric rank but are each named after a typical species. The most satisfactory definition is based on the structure of the 1st maxilla, as follows:

*E. affinis* group—The 1st maxilla is reduced to such an extent that there is rarely an endopodite and the third endite generally bears no setae; in no case are an endopodite and a setose third endite present together. The total number of setae and spines on this appendage never exceeds 22 and is usually considerably less. The cup-shaped appendages on certain setae of the 2nd maxilla and maxilliped are almost always well developed.

*E. squamatus* group—The 1st maxilla shows less reduction in setation and an endopodite is often present. Three species, *E. angustus*, *E. grandicornis* and *E. rectus*, lack both an endopodite and any setae on the third endite, but in all three there are at least 26 setae and spines on the whole appendage. Generally there is a total of between 24 and 40 setae and spines; only *E. marginatus* and *E. oblongus* have fewer, 21 and 23 respectively. The cup-shaped appendages on certain setae of the 2nd maxilla and maxilliped are often poorly developed or even absent.

The following species belong to the *affinis* group:

47. <i>E. rigidus</i>	31. <i>E. matsuei</i>	1. <i>E. affinis</i>	16. <i>E. graciloides</i>
29. <i>E. malacus</i>	50. <i>E. similis</i>	14. <i>E. gibbus</i>	15. <i>E. gracilis</i>
6. <i>E. curtus</i>	25. <i>E. longicirrhus</i>	38. <i>E. pacificus</i>	10. <i>E. facilis</i>
40. <i>E. parabullifer</i>	54. <i>E. truncatus</i>	5. <i>E. clavatus</i>	27. <i>E. longiseta</i>
55. <i>E. vicinus</i>	43. <i>E. propinquus</i>	13. <i>E. fundatus</i>	33. <i>E. mixtus</i>
48. <i>E. roei</i>	52. <i>E. tenuicaudis</i>	45. <i>E. quaesitus</i>	35. <i>E. nudus</i>
26. <i>E. longimanus</i>	18. <i>E. hecticus</i>	24. <i>E. latifrons</i>	3. <i>E. brodskyi</i>
4. <i>E. bullifer</i>	44. <i>E. pseudaffinis</i>	39. <i>E. palumbii</i>	7. <i>E. digitatus</i>

The following species belong to the *squamatus* group:

53. <i>E. tenuispinus</i>	23. <i>E. laticeps</i>	8. <i>E. distinctus</i>	34. <i>E. nodifrons</i>
30. <i>E. marginatus</i>	46. <i>E. rectus</i>	19. <i>E. hulsemannae</i>	22. <i>E. indicus</i>
37. <i>E. pachychaeta</i>	28. <i>E. magnus</i>	21. <i>E. hyperboreus</i>	42. <i>E. penicillatus</i>
12. <i>E. filigerus</i>	36. <i>E. oblongus</i>	11. <i>E. farrani</i>	49. <i>E. sarsi</i>
17. <i>E. grandicornis</i>	41. <i>E. paroblongus</i>	9. <i>E. elongatus</i>	32. <i>E. maxillaris</i>
2. <i>E. angustus</i>	51. <i>E. squamatus</i>	20. <i>E. humilis</i>	

The 'traditional' and numerical approaches—a comparison

The subdivision of *Euaugaptilus* proposed by Sewell can be compared with the results obtained in the present study in order to evaluate the different methods of approach. Full definitions of the groups into which Sewell divided the genus are to be found in his report (1947) on the copepods from the John Murray Expedition; only a few corrections and additions need to be made here. Sewell placed *E. hecticus* in group IVB although Giesbrecht (1892) described a setose third endite on the 1st



maxilla, a condition which is not included in Sewell's grouping; a subgroup IIB would therefore need to be set up to accommodate this species and two more recently described ones. It would also be necessary to set up a subgroup ID in which there is a well developed mandible and a 1st maxilla lacking setae only on the third endite. Group IVAb must be extended a little to include *E. pacificus* which is reported to have only six segments in the exopodite of the 2nd antenna. The subgroups based on this character are not clear-cut; *E. palumbii*, for example, is figured differently by Giesbrecht (1892) and Sars (1925) and *E. filigerus* appears to belong more properly in IIAa than in IIAb. Finally, *E. grandicornis* and *E. longimanus* can be placed according to both their original descriptions and Sewell's amendments; examination of specimens of *E. longimanus* by the present author confirms Sars' description, so the extra seta reported by Sewell must be a part of normal intraspecific variation.

The order in which Sewell (*loc. cit.*, pp. 196-198) placed the 32 species which were known to him and have been accepted here is similar (in reverse order) to the sequence obtained by numerical analysis, though the division indicated by the latter does not correspond exactly with any of Sewell's divisions. The nearest to this is the division between group IIA and IIB, but the present results indicate that Sewell's grouping would place *E. pacificus* (no. 33) too far from the *Augaptilus* end of the genus and *E. angustus* (no. 2), *E. marginatus* (no. 30) and *E. rectus* (no. 46) too far from the *Haloptilus* end.

The two methods of approach are thus comparable in the results obtained, but the numerical one has some advantages which are obvious in the case of *Euaugaptilus*, particularly in view of the intraspecific variability the genus exhibits. First of all, it obviates the need to set up priorities in the order in which characters are compared; all characters are assessed together and the estimate of similarity is not biased in favour of any particular characters. Secondly and almost more importantly, the quantitative treatment of the data ensures that intraspecific variation does not distort affinities between species; the recorded data need only be exemplary of the species; they do not need to be accurate for all individuals or embrace the whole range of variation. This difficulty is apparent in Sewell's approach where the presence or absence of a single seta, a part of normal intraspecific variation, can cause transfer across group boundaries; the small number of specimens usually available can make this a serious limitation, as it is impossible to determine the typical structure. Thirdly, unknown characters are less serious an obstacle than when classification is dependent on a number of characters taken in a predetermined order; thus lack of knowledge of the 1st maxilla of *E. distinctus* precludes the assignment of this species to any of Sewell's groups but does not prevent its inclusion in the numerical ranking. Finally, the system is repeatable and flexible. Three species discovered since Sewell classified the genus do not fit into any of the groups defined by him and the suggested new subgroups (ID and IIB) do not fit particularly well into the pattern common to the two classifications; the discovery of these few species could well lead to rejection of the groupings as originally laid out. Sewell's system, on the other hand, does have the advantage of speed and decisiveness in placing new species and identifying specimens, provided they fit the existing classification.



## Evaluation of subsequent species—a practical application

Species which still remain to be described can be incorporated in the numerical classification by repeating the computer programme. The computation necessary to represent a new species on the vector diagrams produced for a set of previously known species has been set out by Gower (1968). This will often be time-consuming, however, and the results obtained in the present study will be more generally useful if new species can be inserted into the system by conventional means. The species recently described by Park (1970) have been tested with this aim in mind.

In accordance with the definitions on p. 64, *E. unisetosus*, *E. diminutus* and *E. vescus* fit into the *affinis* group, and *E. longiantennalis* and *E. sublongiseta* into the *squamatus* group. Comparison of each of the new species with each other and with the previously known species, using the characters given in Table 5 in the manner suggested on p. 27, gave the following results:

New species	Compared with	Similarity
<i>E. unisetosus</i>	<i>E. fundatus</i>	Close
	<i>E. diminutus</i>	Close
	<i>E. quaesitus</i>	Fairly close (comparison incomplete)
<i>E. diminutus</i>	<i>E. unisetosus</i>	Close
	<i>E. fundatus</i>	Close
	<i>E. quaesitus</i>	Fairly close (comparison incomplete)
<i>E. vescus</i>	<i>E. diminutus</i>	Fairly close
	<i>E. quaesitus</i>	Fairly close (comparison incomplete)
<i>E. longiantennalis</i>	<i>E. marginatus</i>	Very close
	<i>E. sublongiseta</i>	Close
<i>E. sublongiseta</i>	<i>E. longiantennalis</i>	Close
	<i>E. marginatus</i>	Close
	<i>E. longiseta</i>	Fairly close

The similarity between two species is classified as very close when only slight differences occur between body proportions and/or details of setation which are considered earlier (see pp. 22–26) to be a part of normal intraspecific variation. Similarity is classified as close when there is one structural difference which exceeds known intraspecific variation, and as fairly close when there are two such differences.

These comparisons indicate clearly where the five new species belong in the sequence shown in Fig. 13: *E. unisetosus*, *E. diminutus* and *E. vescus* can be inserted adjacent to each other between *E. fundatus* (Q-no. 13) and *E. quaesitus* (Q-no. 45), while *E. longiantennalis* and *E. sublongiseta* belong together next to *E. marginatus* (Q-no. 30). It is remarkable that these five new species, based on a total of six specimens obtained with the same equipment on a cruise in a single geographical region, should group so distinctly, in contrast to the wide range of morphology which the genus exhibits as a whole. The fact that the descriptions of two of these species



and of the three others show such close resemblance does not confirm the initial impression that a vast number of species remains to be discovered, but suggests a rather greater degree of intraspecific variation than hitherto demonstrated. Until such variation can be proved it would be premature to propose synonymy on this basis. The similarity between *E. marginatus* and *E. longiantennalis*, however, is so close that their synonymy is here proposed.

The methods suggested in this paper for the identification of members of the three genera have proved to be practical. The evaluation of new species on the basis of the conclusions reached in the numerical section is straightforward and enables comparisons with other species to be depicted quite clearly, even though such comparisons are carried out without the help of a computer.

#### IN CONCLUSION

It is certain that much remains to be discovered about the Augaptilidae, in particular *Euaugaptilus*. New species are still being discovered and relatively few males have been described and assigned with certainty to known females. This has necessitated limiting the present study to adult females, although it is often the males of calanoid copepods which show the more distinct specific differences. Intraspecific variation seems to be great in *Euaugaptilus*, but until its limits are better known synonymy within the genus cannot be finally settled. It is hoped that the present assembling of known data and application of new techniques will provide a basis for a more definitive review when the necessary information is at hand.

In the definitions of the *affinis* and *squamatus* groups mention is made of the fact that the cup-shaped appendages, or 'buttons', on setae of the 2nd maxilla and maxilliped are better developed in the former group. The fine structure of these appendages in *Centraugaptilus horridus* has been studied by Krishnaswamy *et al.* (1967). They appear to vary quite considerably within *Euaugaptilus* and close examination may reveal distinct types with taxonomic significance.

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## REFERENCES

- BJÖRNBERG, T. K. S. 1963. On the marine free-living copepods off Brazil. *Bolm Inst. Oceanogr., S. Paulo* **13** : 3-142.
- 1965. The study of planktonic copepods in the south west Atlantic. *Anais Acad. bras. Cienc.* **37** (supl.) : 219-230.
- BRADY, G. S. 1883. Report on the Copepoda collected by H.M.S. Challenger during the years 1873-76. *Rep. sci. Res. 'Challenger', Zool.* **8** : 1-142, 55 pls.
- BRODSKY, K. A. 1950. Calanoida of the far eastern seas and the polar basin of the U.S.S.R. *Opred. Faune SSSR* **35** : 442 pp. (in Russian).
- CALEF, G. W. & GRICE, G. D. 1967. Influence of the Amazon River outflow on the ecology of the western tropical Atlantic. II. Zooplankton abundance, copepod distribution, with remarks on the fauna of low-salinity areas. *J. mar. Res.* **25** : 84-94.
- CARRIE, B. G. A. 1959. Notes on the counting and mounting of planktonic organisms. *Jl R. microsc. Soc.* **78** : 77.
- CHIBA, T. 1956. Studies on the development and the systematics of Copepoda. *J. Shimonoseki Coll. Fish.* **6** : 1-90 (in Japanese with English summary).
- [—] 1965. Data of planktological survey in the Indian Ocean from November 1962 to January 1963. *Data oceanogr. Obs. explor. Fish. Shimonoseki Univ. Fish.* No. 1 : 113-145.
- CHIBA, T., TSURUTA, A. & MAÉDA, H. 1955. Report on zooplankton samples hauled by larva-net during the cruise of Bikini-Expedition, with special reference to copepods. *J. Shimonoseki Coll. Fish.*, **5** : 189-213.
- CLAUS, C. 1863. *Die freilebenden Copepoden mit besonderer Berücksichtigung der Fauna Deutschlands, der Nordsee und des Mittelmeeres.* Leipzig, 230 pp., 37 pls.
- CLEVE, P. T. 1904. Plankton of the South African Seas. I. Copepoda. *Mar. Invest. S. Afr.* **3** : 177-210.
- DANA, J. D. 1853. Crustacea. In *U.S. Exploring Expedition during the years 1838-1842 under the command of Charles Wilkes* **13** (2) : 1019-1262, pls 70-88 (not seen).
- DE DECKER, A. & MOMBECK, F. J. 1965. South African contribution to the International Indian Ocean Expedition: (4) A preliminary report on the planktonic Copepoda. *Investl. Rep. Div. Fish. Rep. S. Afr.* No. 51 : 10-67.
- DJORDJEVIC, M. M. 1963. Observations sur les copépodes pélagiques en rade de Villefranche de mars à août 1962. *Rapp. P.-v. Réun. Commn int. Explor. scient. Mer Méditerr.*, **17** : 575-580.
- ESTERLY, C. O. 1906. Additions to the copepod fauna of the San Diego region. *Univ. Calif. Publs Zool.* **3** : 53-92, pls 9-14.
- 1911. Third report on the Copepoda of the San Diego region. *Ibid.* **6** : 313-352, pls 26-32.
- 1913. Fourth taxonomic report on the Copepoda of the San Diego region. *Ibid.* **11** : 181-196, pls 10-12.
- FARRAN, G. P. 1908. Second report of the Copepoda of the Irish Atlantic slope. *Scient. Invest. Fish. Brch. Ire.*, 1906 No. 2 : 104 pp., 11 pls.
- 1920. On the local and seasonal distribution of the pelagic Copepoda of the south-west of Ireland. *Publs Circonst. Cons. perm. int. Explor. Mer* No. 73 : 30 pp.
- 1926. Biscayan plankton collected during a cruise of H.M.S. Research, 1900. Part 14. The Copepoda. *J. Linn. Soc., Zool.* **36** : 219-310, pls 5-10.
- 1929. Crustacea. Part X.—Copepoda. *Nat. Hist. Rep. Br. Antarct. Terra Nova Exped.*, *Zool.* **8** : 203-306, 4 pls.
- 1936. Copepoda. *Scient. Rep. Gt Barrier Reef Exped.* **5** : 73-142.
- FLEMINGER, A. 1965. On some Pacific species of *Labidocera* and *Stephos* reported by C. B. Wilson. *Crustaceana* **8** : 121-130.



- FURUHASHI, K. 1966. Studies on the vertical distribution of copepods in the Oyashio region east of Japan and in the Kuroshio region south of Japan. *Publs Seto mar. biol. Lab.* **14** : 295-322.
- GAUDY, R. 1963. Campagne du navire océanographique 'Calypso' dans les eaux côtières du Brésil (Janvier-Février 1962). Copépodes pélagiques. *Recl Trav. Stn mar. Endoume* Bull. 30, Fasc. 45 : 15-42.
- GIESBRECHT, W. 1889. Elenco dei Copepodi pelagici raccolti dal tenente di vascello Gaetano Chierchia durante il viaggio della R. Corvetta 'Vettor Pisani' negli anni 1882-1885, e dal tenente di vascello Francesco Orsini nel Mar Rosso, nel 1884. *Atti Accad. naz. Lincei R.* **5**, sem. 1 : 811-815.
- 1892. Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel. *Fauna Flora Golf. Neapel* **19** : 831 pp., 54 pls.
- GIESBRECHT, W. & SCHMEIL, O. 1898. Copepoda I: Gymnoplea. *Das Tierreich*, Berlin, pt 6 : 169 pp.
- GIRON, F. 1963. Contribution à l'étude des copépodes de la Mer Alboran. *Rapp. P.-v. Réunion. Commn int. Explor. scient. Mer Méditerran.* **17** : 573-574.
- GOWER, J. C. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika* **53** : 325-338.
- 1968. Adding a point to vector diagrams in multivariate analysis. *Ibid.* **55** : 582-585.
- GRICE, G. D. 1959. A new species of *Haloptilus* (Copepoda: Calanoida) from equatorial and subtropical waters of the east central Pacific Ocean. *J. Wash. Acad. Sci.* **49** : 193-195.
- 1962. Calanoid copepods from equatorial waters of the Pacific Ocean. *Fishery Bull. Fish Wildl. Serv. U.S.* **61** : 171-246.
- 1963. Deep water copepods from the western North Atlantic with notes on five species. *Bull. mar. Sci. Gulf Caribb.* **13** : 493-501.
- 1969. Calanoid copepods from the Caribbean Sea and Gulf of Mexico. 1. New species and new records from midwater trawl samples. *Bull. mar. Sci.* **19** : 446-455.
- GRICE, G. D. & HART, A. D. 1962. The abundance, seasonal occurrence and distribution of the epizooplankton between New York and Bermuda. *Ecol. Monogr.* **32** : 287-309.
- GRICE, G. D. & HULSEMAN, K. 1965. Abundance, vertical distribution and taxonomy of calanoid copepods in the northeast Atlantic. *J. Zool. Lond.* **146** : 213-262.
- 1967. Bathypelagic calanoid copepods of the western Indian Ocean. *Proc. U.S. natn. Mus.* **122** : 1-67.
- 1968. Calanoid copepods from midwater trawl collections made in the southeastern Pacific Ocean. *Pacif. Sci.* **22** : 322-335.
- HEINRICH, A. K. 1960. On the subsurface plankton in the central Pacific. *Trudy Inst. Okeanol.* **41** : 42-47 (in Russian).
- HONJO, K., OHTA, H., KIDACHI, T., UMEDA, K. & KUDOH, S. 1957. Distribution of Copepoda in the 'Kuroshio' area, south of Honshu, May 1955. *Rec. oceanogr. Wks Japan, Spec. No.* : 120-129.
- HULSEMAN, K. 1967. Redescription of *Euaugaptilus mixtus* (Sars) (Copepoda, Calanoida). *Crustaceana* **12** : 163-166.
- JESPERSEN, P. 1923. Dr. Thorild Wulff's plankton-collections in the waters west of Greenland. Metazoa. *Meddr Grønland* **64** : 101-160.
- 1940. Non-parasitic Copepoda. *Zoology Iceland* **3** (33) : 116 pp.
- KRISHNASWAMY, S., RAYMONT, J. E. G., WOODHOUSE, M. A. & GRIFFIN, R. L. 1967. Studies on the fine structure of Copepoda. Observations on the fine structure of buttons on the setae of the maxilla and maxilliped of *Centraugaptilus horridus* (Farran). *Deep-Sea Res.* **14** : 331-335.
- KRØYER, H. 1849. Karcinologiske Bidrag. *Naturh. Tidsskr.* (2), **2** : 563-609, pl. 6.
- LYSHOLM, B., NORDGAARD, O. & WIBORG, K. F. 1945. Copepoda from the 'Michael Sars' North Atlantic Deep-Sea Expedition, 1910. *Rep. scient. Results Michael Sars N. Atlant. deep Sea Exped.* **5** (7) : 60 pp.





1972. "The genus *Euaugaptilus* (Crustacea, Copepoda). New descriptions and a review of the genus in relation to *Augaptilus*, *Haloptilus* and *Pseudaugaptilus*." *Bulletin of the British Museum (Natural History) Zoology* 24, 1–71.

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