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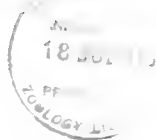
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THE GENUS *EUAUGAPTILUS*  
(CRUSTACEA, COPEPODA). NEW  
DESCRIPTIONS AND A REVIEW OF  
THE GENUS IN RELATION TO  
*AUGAPTILUS*, *HALOPTILUS* AND  
*PSEUDAUGAPTILUS*



J. B. L. MATTHEWS

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*PSEUDAUGAPTILUS*

BY

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*Pp.* 1-71; 13 *Text-figures*

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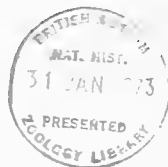
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# THE GENUS *EUAUGAPTILUS* (CRUSTACEA, COPEPODA). NEW DESCRIPTIONS AND A REVIEW OF THE GENUS IN RELATION TO *AUGAPTILUS*, *HALOPTILUS* AND *PSEUDAUGAPTILUS*

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 *Haloptilus* 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 *Haloptilus*, 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

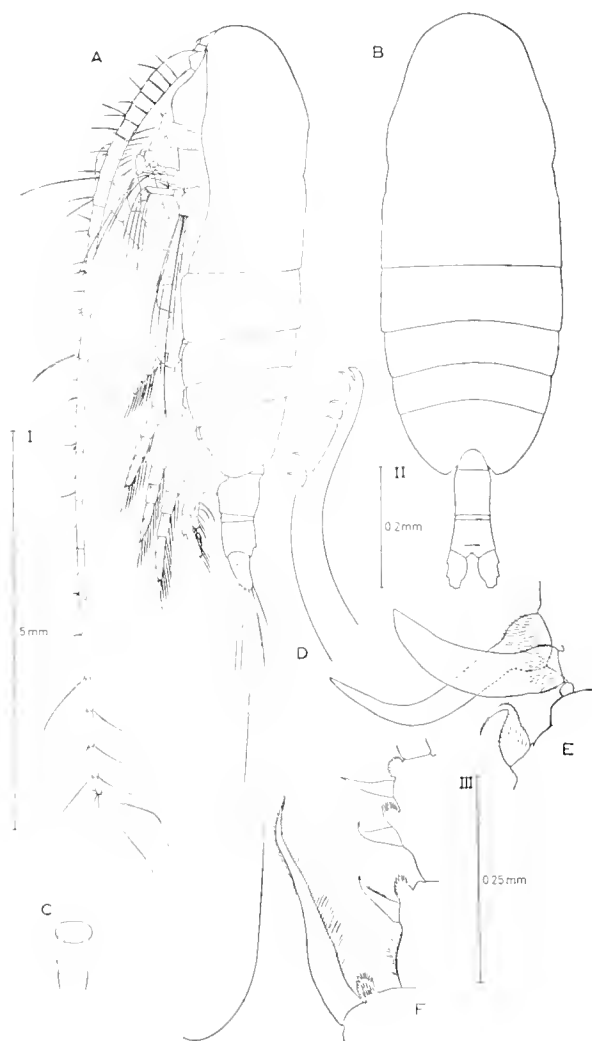


FIG. 1. *Euaugaptilus pachychaeta* ♀. A. Lateral view. B. Dorsal view. C. Rostrum in antero-ventral view. D. Mandibular gnathobase. E. Modified setae on protopodite of maxilliped. F. Distal outer border of exopodite of 1st swimming limb. A and B to scale I; C - E to scale II; F to scale III.

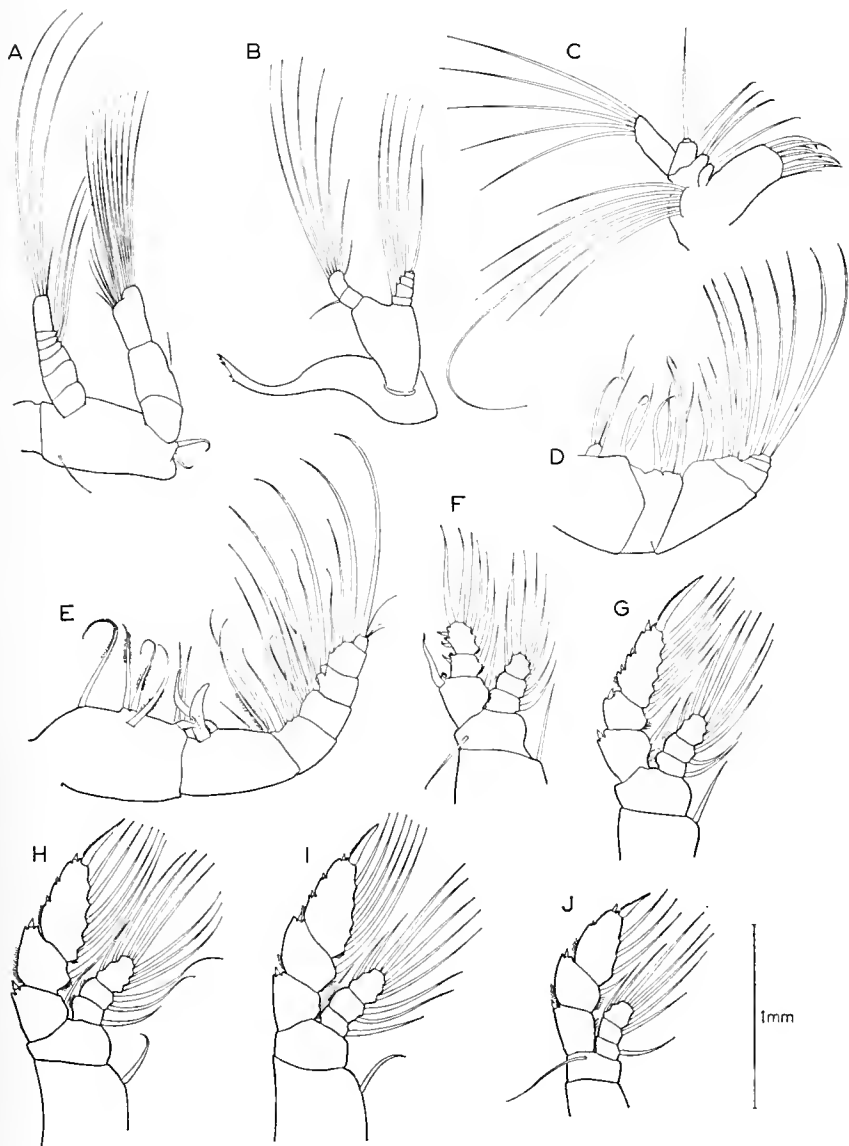


FIG. 2. *Euauogaptilus pachychaeta* ♀. A. 2nd antenna. B. Mandible. C. 1st maxilla. D. 2nd maxilla. E. Maxilliped. F. 1st swimming limb. G. 2nd swimming limb. H. 3rd swimming limb. I. 4th swimming limb. J. 5th swimming limb.

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.  $\pi\alpha\chi\upsilon\varsigma$  = thick +  $\chi\alpha\tau\tau\eta$  = 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.

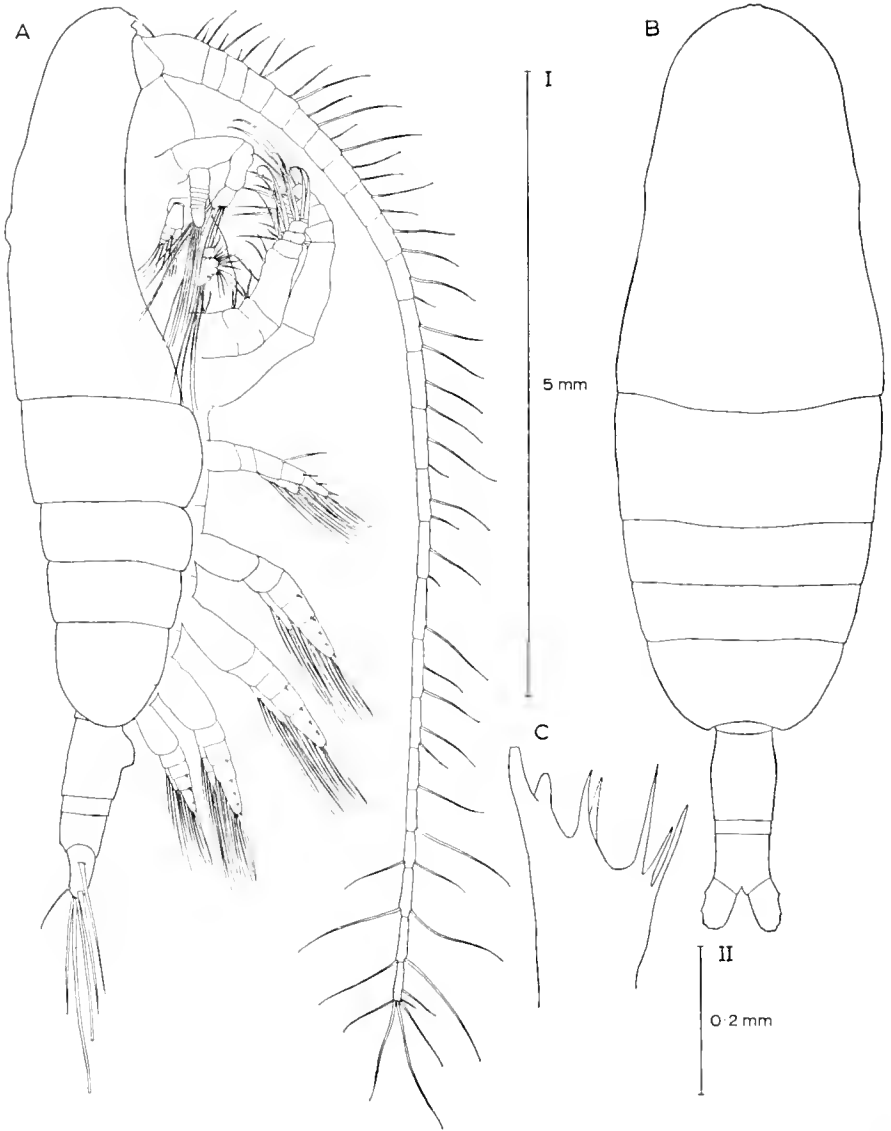


FIG. 3. *Euaugaptilus hulsemannae* ♀. A. Lateral view. B. Dorsal view. C. Mandibular gnathobase. A and B to scale I; C to scale II.

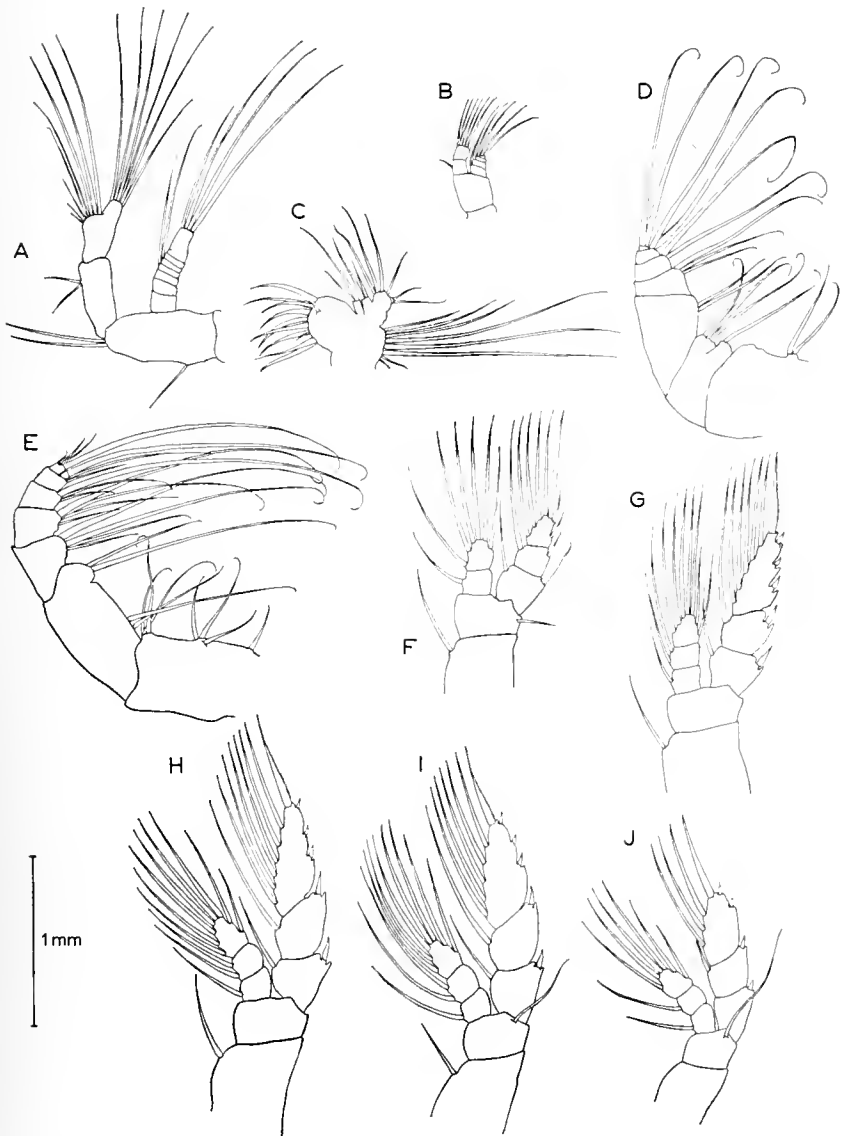


FIG. 4. *Euangaptilus hulsemannae* ♀. A. 2nd antenna. B. Mandibular palp. C. 1st maxilla. D. 2nd maxilla. E. Maxilliped. F. 1st swimming limb. G. 2nd swimming limb. H. 3rd swimming limb. I. 4th swimming limb. J. 5th swimming limb.

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 propodite 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

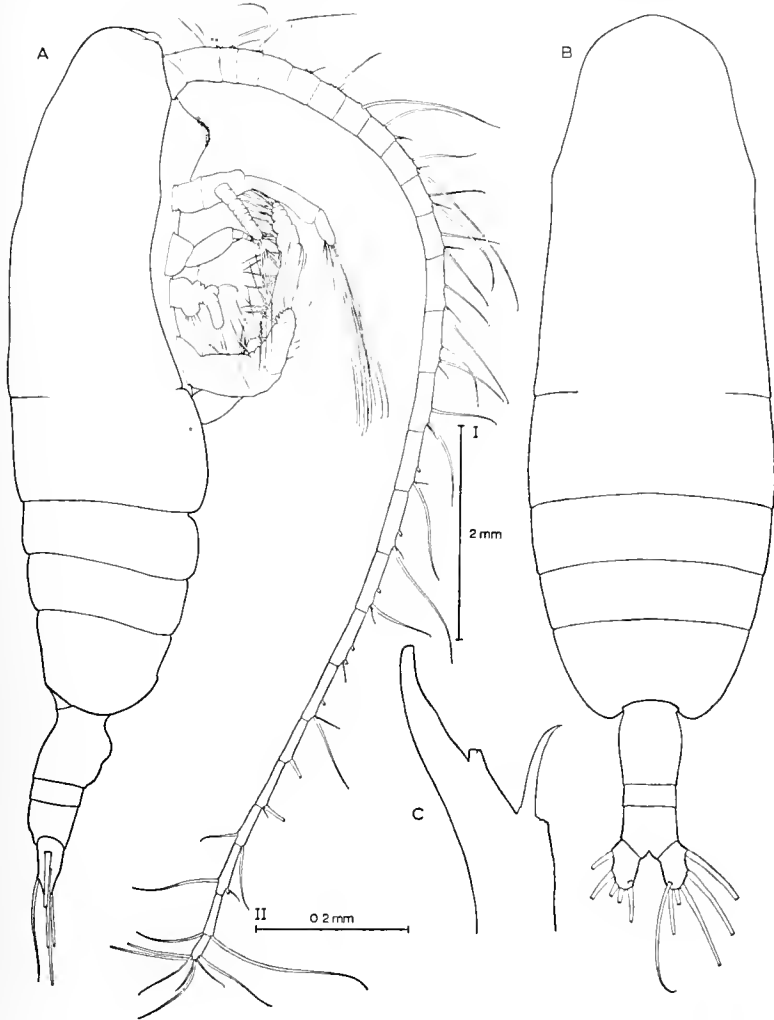


FIG. 5. *Euauogaptilus paroblongus* ♀. A. Lateral view. B. Dorsal view. C. Mandibular gnathobase. A and B to scale I; C to scale II.

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

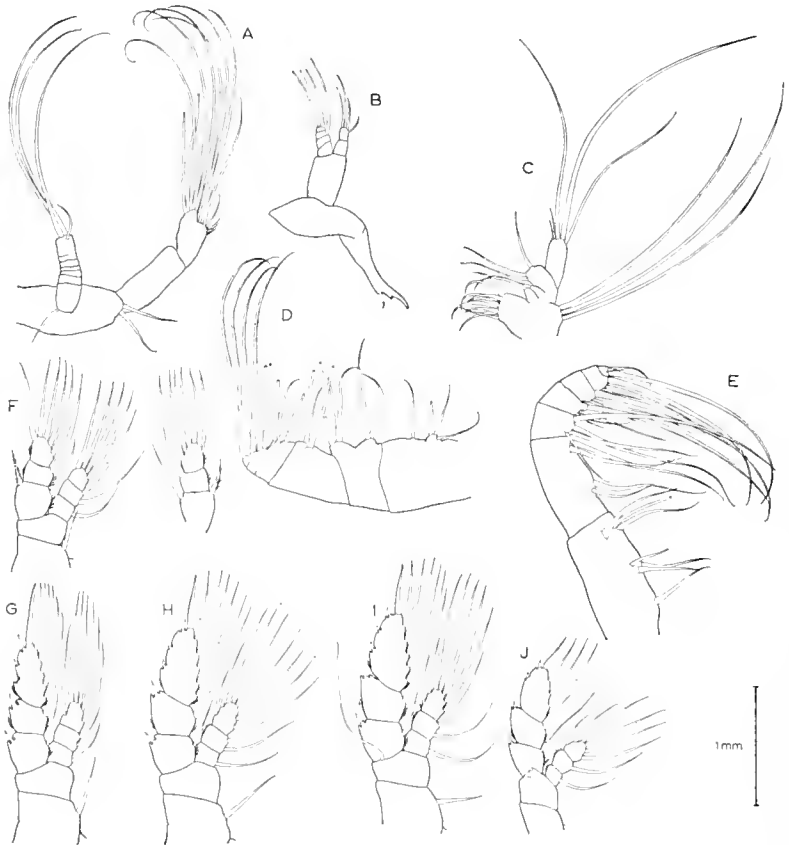


FIG. 6. *Euaugaptilus paroblongus* ♀. A. 2nd antenna. B. Mandible. C. 1st maxilla. D. 2nd maxilla. E. Maxilliped. F. 1st swimming limb, left and exopodite of right. G. 2nd swimming limb. H. 3rd swimming limb. I. 4th swimming limb. J. 5th swimming limb.

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	5 <sup>8</sup>	55	54	55	43	46	3 <sup>8</sup>	47	3 <sup>8</sup>	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.

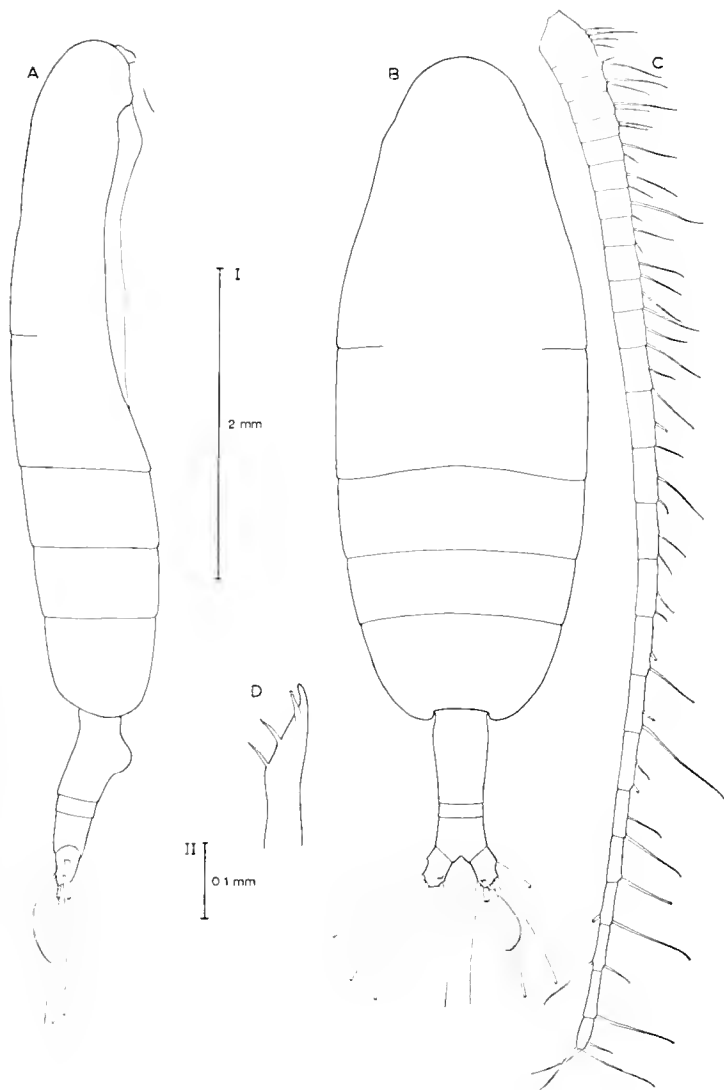


FIG. 7. *Euaugaptilus roei* ♀. A. Lateral view. B. Dorsal view. C. 1st antenna. D. Mandibular gnathobase. A - C to scale I; D to scale II.

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

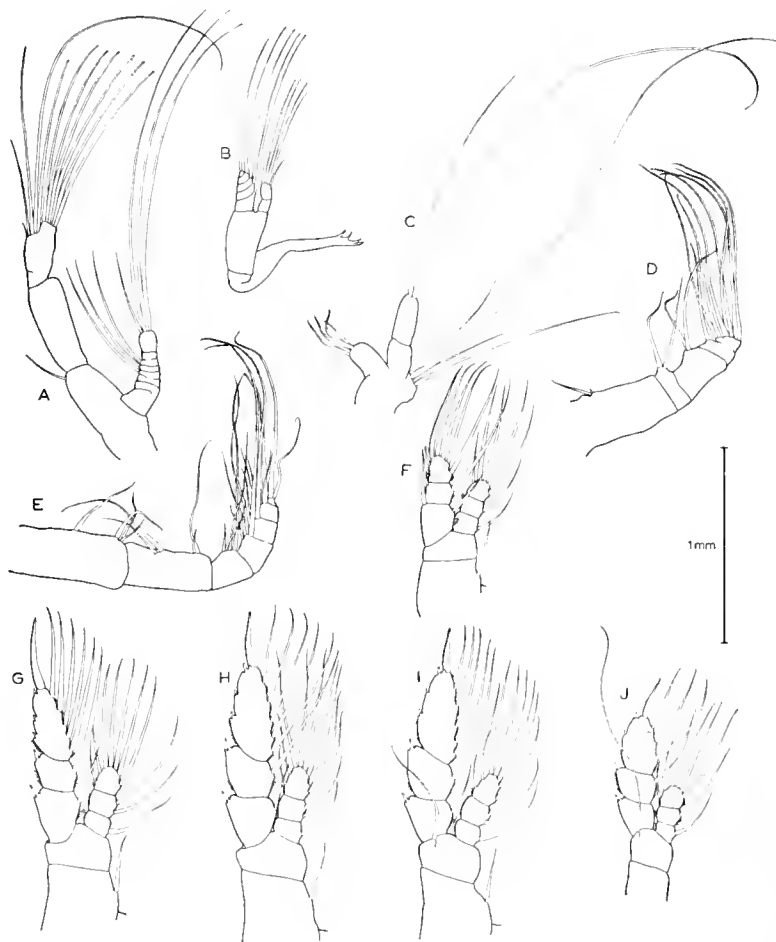


FIG. 8. *Euaugaptilus roei* ♀. A. 2nd antenna. B. Mandible. C. 1st maxilla. D. 2nd maxilla. E. Maxilliped. F. 1st swimming limb. G. 2nd swimming limb. H. 3rd swimming limb. I. 4th swimming limb. J. 5th swimming limb.

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 *Haloaptilus*. 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.

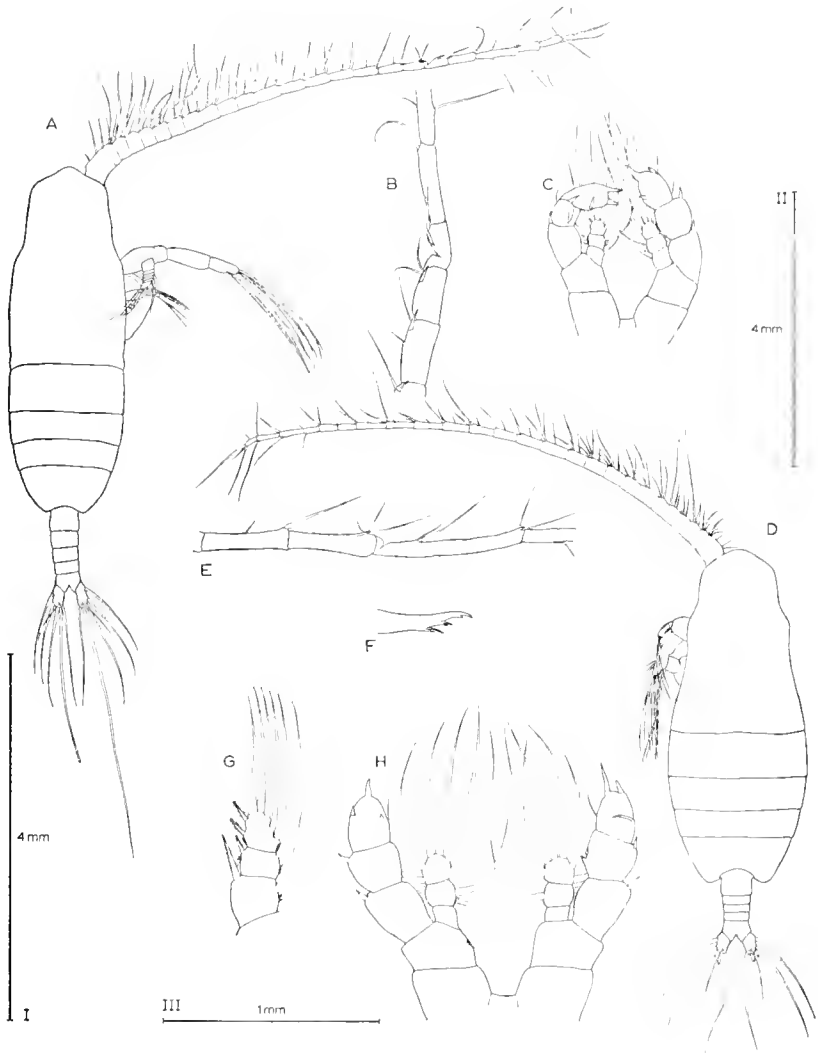


FIG. 9. *Euaugaptilus facilis* ♂. A. Dorsal view. B. Part of 1st antenna showing geniculate joint. C. 5th limbs in posterior view. *E. squamatus* ♂. D. Dorsal view. E. Part of 1st antenna showing geniculate joint. F. Mandibular gnathobase. G. Exopodite of 1st swimming limb. H. 5th limbs in anterior view. 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. longicirrus* 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
1st 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 placilus* 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 : 111, 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.

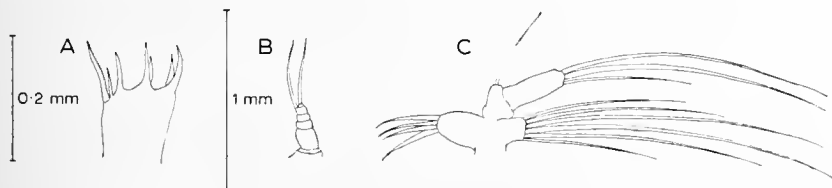


FIG. 11. An unusual specimen of *Euaugaptilus truncatus*. A. Mandibular gnathobase. B. Mandibular palp. C. 1st maxilla.

**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 : 103, 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 chierchiaie* (Giesbrecht, 1889)**

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

*Haloptilus chierchiaie*; 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 & Mombbeck, 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 pseudoxycephalus* Brodsky, 1950

*Haloptilus pseudoxycephalus* 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-

ranean, 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:) $\times \times 10$ , e.g. 1:2.7 written as 27
3	Ratio of urosome to prosome, (1:) $\times \times 10$
4	Number of urosome segments
5	Ratio of genital segment to urosome, excluding furca, (1:) $\times \times 10$
6	Ratio of width to length of caudal rami, (1:) $\times \times 10$
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*, *Haloptylus* 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







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.

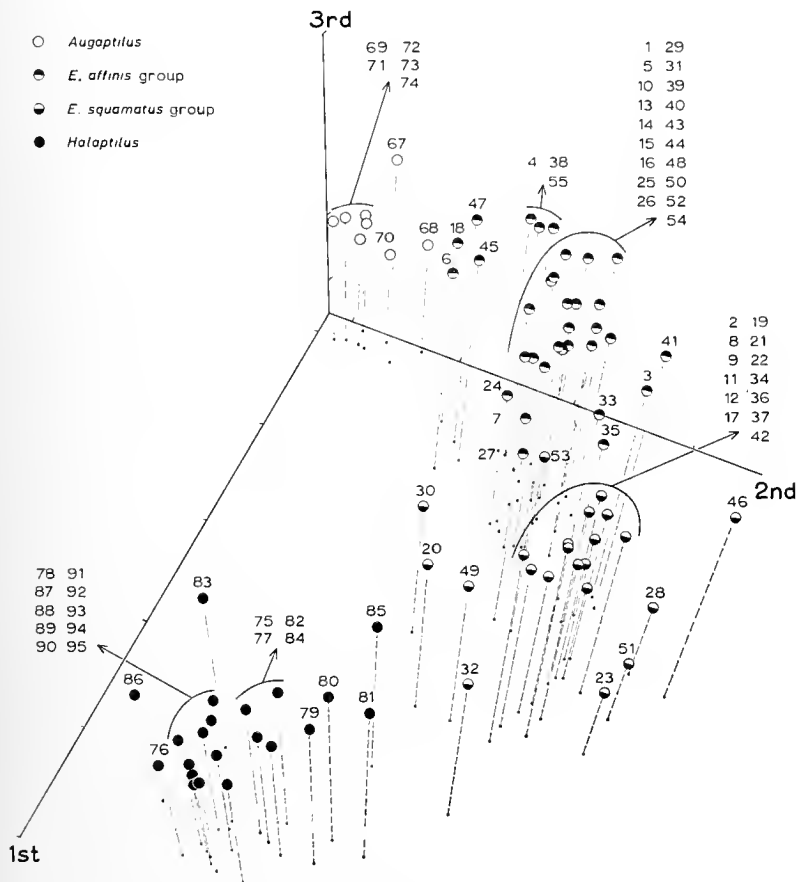


FIG. 12. The results of a principal coordinates analysis of the similarity coefficients produced by the CLASP programme. The small dots indicate the values of the first and second vectors; the circles are positioned according to the values of the third vector. The species are identified by their Q-numbers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

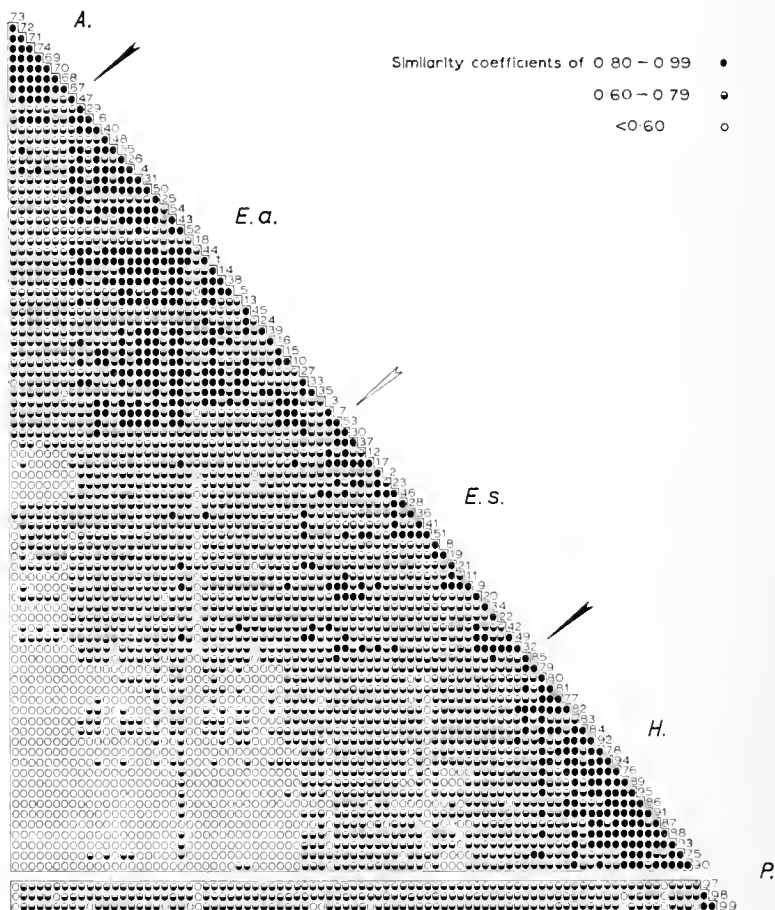


FIG. 13. The matrix of similarity coefficients produced by the CLASP programme, arranged in accordance with the principal coordinates analysis and adjusted by eye. A. *Augaptilus*. E.a. *Euaugaptilus affinis* group. E.s. *Euaugaptilus squamatus* group. H. *Haloptilus*. P. *Pseudaugaptilus*. The species 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>	5. <i>E. longicirrus</i>	38. <i>E. pacificus</i>	10. <i>E. facilis</i>
40. <i>E. parabullifer</i>	24. <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. farvani</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>	<i>E. sublongiseta</i>	Close
	<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*<sup>1</sup>, 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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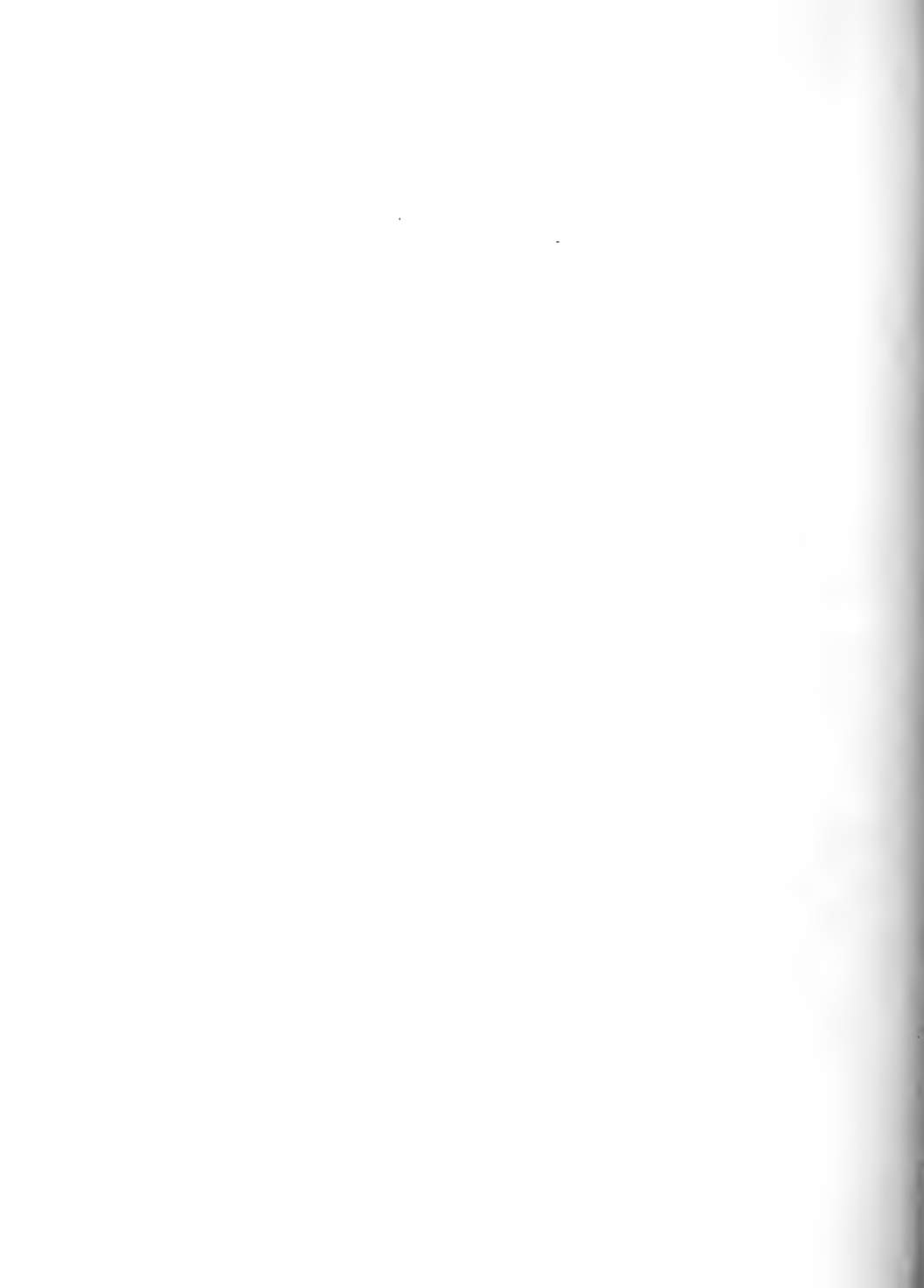
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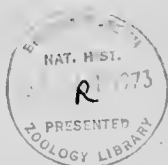




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By AILSA M. CLARK

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THIS paper deals primarily with a number of crinoids entrusted to the author by the Smithsonian Oceanographic Sorting Center and collected in the course of the International Indian Ocean Year from the research ships 'Anton Bruun' and 'Te Vega'. Some Pacific specimens taken on the latter vessel are dealt with in an appendix. Additional relevant material from the British Museum collections is also discussed, notably some fine specimens from Madagascar sent by Professor A. G. Humes of Boston University. Two new species and two new subspecies are described, of which the holotypes not belonging to the British Museum will be deposited in the National Museum of Natural History, Smithsonian Institution, Washington. Several of the species have rarely been recorded hitherto and the additional material has made possible some studies on variation, mainly expressed in tabular form. The most interesting discovery is an anatomical one, namely the complete perforation of the centrodorsal in adult specimens of *Pterometra pulcherrima* (family Asterometridae) by radially-placed coelomic canals opening on the dorsal (aboral) surface. Similar complete canals have formerly only been recorded in an immature specimen of *Notocrinus virilis* (Notocrinidae) and in some Cretaceous comatulids, though incomplete homologous coelomic pits have been found in other recent Asterometrids. Under the headings of *Heterometra* and *Democrinus* the problem of

size criteria for multiradiate comatulids and stalked crinoids is discussed. The arrangement of genera and species within the families is alphabetical.

## Family COMASTERIDAE

### *Capillaster multiradiatus* (Linnaeus)

*Asterias multiradiata* Linnaeus, 1758 : 663.

*Actinometra coccodistoma* P. H. Carpenter, 1883 : 747.

*Capillaster multiradiata*: A. H. Clark, 1909d : 364; 1911b : 8, 13, 16; 1931 : 173-209, pl. 3, fig. 5, pl. 11, fig. 30, pl. 13, fig. 34, pl. 14, figs 35, 36, pl. 81, figs 222, 223.

*Capillaster multiradiata* var. *coccodistoma*: A. H. Clark, 1911b : 16.

*Capillaster coccodistoma*: A. H. Clark, 1931 : 212-214.

*Capillaster multiradiatus*: A. M. Clark, 1967a : 26-27; Clark & Rowe, 1971 : 15.

MATERIAL. 'Anton Bruun' cruise 1, st. 18A, 07°34'N : 98°00'E (between Malaya and the Nicobar Islands), 77 metres; 9 specimens.

'Anton Bruun' cruise 1, st. 20, 09°13'N : 97°51'E (SW from Mergui Archipelago, Burma), 58-60 metres; 2 large specimens.

'Anton Bruun' cruise 1, st. 28A, 11°52'N : 92°49'E (Andaman Islands), 66 metres; 4 specimens.

'Anton Bruun' cruise 1, st. 37, 13°28'N : 97°19'E (N of Mergui Archipelago), 64 metres; 6 specimens.

'Anton Bruun' cruise 1, st. 38, 14°07'N : 97°05'E (W of Moskos Islands, Burma), 69-73 metres; 35 specimens.

'Anton Bruun' cruise 1, st. 39A, 14°52'N : 96°39'E (SW of Gulf of Martaban, Burma), 48-64 metres; 1 broken specimen.

'Anton Bruun' cruise 1, st. 43, 15°08'N : 94°04'E (S of Cape Negrais, Burma), 55 metres; 6 specimens.

'Anton Bruun' cruise 1, st. 47B, 19°50'N : 92°55'E (off Akyab, Burma), 22-30 metres; 3 specimens.

'Anton Bruun' cruise 9, st. KA 13, Grand Comoro Island; 1 specimen.

'Anton Bruun' cruise 9, st. KA 14, Mounimeri, Comoro Islands; arms only.

'Anton Bruun' cruise 9, st. RU 272, reef on NW corner of Mounimeri, Comoro Islands; 1 broken specimen.

Prof. A. G. Humes's st. R 741, Ampombilara, Nosy Bé, Madagascar, on millepore, 0.5-1 metre; 6 specimens.

REMARKS. The specimens from Madagascar, the type-locality of *Capillaster coccodistoma*, show that this nominal species was based on immature specimens of *C. multiradiatus* with less than 20 arms and up to only 23 cirrus segments. All six of them have about 30 arms and the maximum number of cirrus segments between 24 and 28 and are not distinguishable from the other mature specimens of *C. multiradiatus* in the collection. The 35 specimens from 'Anton Bruun' station 38 have the arm number ranging from 10 to 39.

The small specimens which have only 10 arms are most easily identified by the

V-shaped ridges on the distal cirrus segments dorsally, the usual distinctive position of the first brachial syzygy at  $2 + 3$  being only developed when the arms exceed 10 and some are based on IIBr or subsequent division series.

### *Comanthus parvicirrus* (J. Müller)

*Alecto parvicirra* J. Müller, 1841 : 185.

*Alecto timorensis* J. Müller, 1841 : 186.

*Comanthus parvicirra*: A. H. Clark, 1911b : 8, 17, 19<sup>2</sup>, 20<sup>2</sup>; 1931 : 631-684, pl. 29 fig. 88, pl. 65, fig. 184, pl. 73, fig. 200, pl. 78, figs 209, 210, pl. 79, figs 211-214, pl. 80, figs 215-218, pl. 81, fig. 221.

*Comanthus timorensis*: A. H. Clark, 1931 : 603-631, pl. 64, fig. 181, pl. 75, fig. 204, pl. 76, fig. 205, pl. 77, figs 206, 207.

MATERIAL. 'Anton Bruun' cruise 1, st. 18A, 07°34'N : 98°00'E (between Malaya and the Nicobar Islands), 77 metres; 1 specimen.

'Anton Bruun' cruise 7, st. 372Q, 25°57'S : 33°02'E (off S Mozambique), 42 metres; 2 specimens.

'Anton Bruun' cruise 8, st. 400C, 20°30'S : 35°43'E (Ponte da Barra Ralsa, near Beira, Mozambique), 62 metres; 4 specimens.

'Anton Bruun' cruise 9, st. 447, 10°00'N : 51°15'E (N Somalia), 59-61 metres; 1 specimen.

The specimen from the Bay of Bengal (st. 18A) has about 40 arms and probably all the IIIIBr series are of four ossicles. There are about XVI cirri mostly with about 17 segments but not forming a complete ring.

### *Comanthus wahlbergi* (J. Müller)

*Alecto wahlbergii* J. Müller, 1843 : 131.

*Comanthus wahlbergii*: A. H. Clark, 1931 : 588-593, pl. 65, fig. 183; Gislén, 1938b : 8-10, fig. 7.

The present collection includes what I believe should be regarded as a distinct subspecies of the South African *Comanthus wahlbergi* restricted to the isolated Walter's Shoal to the south of Madagascar.

It should be pointed out that *Comanthus wahlbergi* does not run down to the genus *Comanthus* in A. H. Clark's monograph (1931 : 83) but to *Comanthoides* on account of the presence of transverse dorsal ridges on the distal cirrus segments, though in smaller specimens these ridges may be so short as to resemble small spines, certainly when viewed in profile. *Comanthoides* A. H. Clark, 1931, is a monotypic genus including only *Comanthus spanoschistum* H. L. Clark from Tasmania and Victoria, Australia, and was referred to the subfamily Capillasterinae by A. H. Clark despite the fact that P<sub>1</sub> only occasionally arises from Br<sub>1</sub> rather than the usual Br<sub>2</sub> on arms based on IIBr (or subsequent) series and the first syzygy is rarely at  $2 + 3$  on such arms, the proximal position of both pinnule and syzygy being the primary characters for distinguishing this subfamily. The status and

position of both *Comanthoides spanoschistum* and *Comanthus wahlbergi* need further investigation. They can be distinguished from each other by the very ornate spinose dorsal processes on the bases of the proximal pinnules in the Australian species.

Gislén (1938b) has described two small Comasterids from South Africa (precise locality uncertain but possibly in the vicinity of Durban) as a new species *Comissia serrata*, the specimen more fully described having ten arms while he says the other has 'abnormally eleven arms', the supposed abnormality being presumably because he was referring the species to *Comissia*, which is otherwise known to have only ten arms. In the British Museum there are samples of specimens from off the Tugela River mouth, Natal and from Port Elizabeth, totalling 92 in all, of which only 16% (15 specimens) have more than ten arms, the maximum positive number (owing to breakage) being only 12 arms. The total of 22 IIBr series includes 13 (59%) of four ossicles, 7 (32%) of two ossicles and two abnormal ones with one ossicle. Only two of the 44 arms based on IIBr series have  $P_1$  on  $Br_1$  and these were based on IIBr series of four ossicles not two, contrary to the condition supposed to be characteristic of the Capillasterinae to which A. H. Clark referred *Comissia*. Nevertheless I have no doubt that they are conspecific with *Comissia serrata*, in the eleven-armed paratype of which the single IIBr series is 4(3 + 4) followed by  $P_1$  on  $Br_2$  and the first syzygy is evidently not at 2 + 3. A. H. Clark (1931 : 245) says, 'Taken as a whole *Comissia* is a rather heterogeneous assemblage and some of the species groups within it seem to have little in common with others beyond the possession of only ten arms.' Apart from the small numbers of arms, I can find little difference between these predominantly ten-armed specimens and *Comanthus wahlbergi* and I believe that they should be regarded as conspecific though *serrata* can be retained at the subspecific level and may prove to be restricted geographically to the eastern half of the range of *C. wahlbergi*.

***Comanthus wahlbergi serratus* (Gislén) n. comb.**

*Comanthus wahlbergii* (part): A. H. Clark, 1931 : 390 (specimens from Algoa Bay).

*Comissia serrata* Gislén, 1938b : 7-8, figs 3, 4, pl. 1, fig. 1.

**MATERIAL.** 'Anton Bruun' cruise 7, st. 357B, 29°11'S : 32°02'E (off Natal), c. 68 metres; 1 specimen, in poor condition.

Some descriptive remarks about this subspecies are given under the heading of the new subspecies of *Comanthus wahlbergi* described below; these are based on specimens in the British Museum collections and from Cape Town University Ecological Survey stations in the vicinity of Port Elizabeth.

***Comanthus wahlbergi tenuibrachia* subsp. nov.**

(fig. 1)

**MATERIAL.** 'Anton Bruun' cruise 7, st. 381A-C, 33°13'S : 43°51-53'E (Walter's Shoal, S from Madagascar), 38-46 metres; c. 215 specimens.



DIAGNOSIS. A subspecies of *Comanthus wahlbergi* (J. Müller) with relatively few arms, less than 15 in 90% of specimens and only ten in nearly 50%, not known to exceed an arm length of about 50 mm; arms moderately slender, maximum arm length : breadth (at the first syzygy) averaging  $>30 : 1$ ; usually six or seven consecutive proximal pinnules with terminal combs.

[DIAGNOSIS OF *C. wahlbergi wahlbergi* FOR COMPARISON. Arm number generally 15–20, or even more, sometimes less; arms markedly tapering, arm length : breadth averaging  $<25 : 1$ ; less than five consecutive pinnules with combs when the arm length is not more than 50 mm.]

DESCRIPTION. The holotype of *C. wahlbergi tenuibrachia* has the centrodorsal completely flat and discoidal, 2.6 mm in diameter. Around the edge there are XVI well developed cirri and two very small rudimentary ones forming an almost continuous though slightly staggered ring except for three narrow gaps in one quadrant. There are up to 18 cirrus segments and the maximum cirrus length is 10.5 mm. The fifth segment is generally the transition one, its distal end (or edge) abruptly shiny like the following segments, the basal ones having a matt texture. The fourth and longest segment measures 0.85 mm in length and 0.40 mm median breadth, a ratio of over  $2 : 1$ . The distal segments are broader dorso-ventrally so that the median breadth of the fourth from the tip is 0.6 mm. There is a slight transverse dorsal ridge across the distal end of each segment from the seventh one, giving the effect of a small dorsal spine when viewed in profile. This is only a little enlarged on the penultimate segment forming a small opposing spine. The terminal claw is fairly large, curved, acute and hyaline.

The arms are markedly asymmetrical, ranging from 50 mm long on one side to only 25 on the other. They number 13. In the larger ones, the breadth at the first

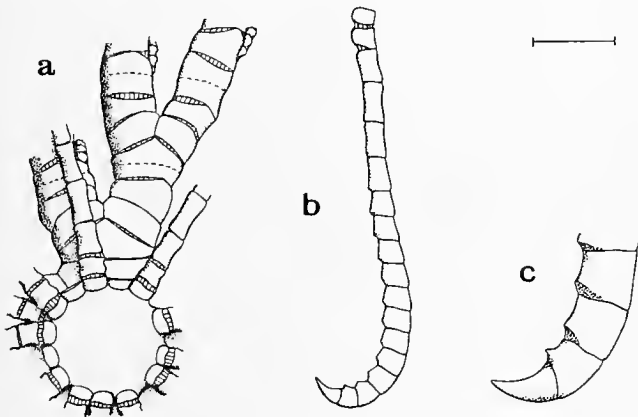


FIG. 1. *Comanthus wahlbergi tenuibrachia* subsp. nov. Holotype. 'Anton Bruun' st. 381B, Walter's Shoal. a. Dorsal view of centrodorsal and proximal part of one post-radial series; b. side view of mature cirrus and c. latero-dorsal view of cirrus tip, enlarged further. [The scale equals 2 mm for a and b but 1 mm for c.]

syzygy on arms based on IBr series is 1.4 mm or after IIBr series 1.3 mm. The length from the proximal edge of the IBr<sub>1</sub> to 3 + 4 (after a IIBr series of four ossicles) is 5.3 mm. All three of the IIBr series have four ossicles. The brachials are flared at their distal ends but the first ten at least have fairly smooth distal edges, though the following ones become spinose.

P<sub>D</sub>, the pinnule on the IIBr<sub>2</sub>, has 37 segments and measures 9.2 mm; there is a comb of nine teeth from the 29th segment.

P<sub>1</sub> with 26 segments measures 4.8 mm and has a comb of eight teeth. P<sub>2</sub> has about 22 segments. All the pinnules to P<sub>7</sub> have a comb though the more distal ones have only about six teeth.

Where there is no IIBr series, P<sub>1</sub> resembles P<sub>D</sub> and so on.

VARIATIONS. The arms of 173 of the more nearly intact specimens were counted, the numbers being as follows:

78 with 10 arms  
27 with 11 arms  
24 with 12 arms  
14 with 13 arms  
11 with 14 arms  
4 with 15 arms  
6 with 16 arms  
5 with 17 arms  
2 with 18 arms  
and 2 with 19 arms.

The mean arm number is 11.7.

In 20 specimens examined closely, out of 28 IIBr series, two consisted of only two ossicles and a third of three with a syzygy at IIBr<sub>2</sub> + 3; all the rest were 4(3 + 4).

The ratio of maximum arm length to the breadth at the first syzygy, after a IBr series only, ranges from 23 to 43 : 1 with a mean of 31 : 1 (i.e. an arm breadth 3.2% of the length), this is in specimens with maximum arm length 25–50 mm. The arm breadth at 3 + 4 on arms arising from IIBr series may be the same as on those from IBrs but is usually smaller, up to almost a fifth less.

The cirri number about XII in the smaller specimens increasing to a maximum of XX but in the largest specimens some of the sockets have become obsolete after losing their cirri and the number is most often about XVI. Larger numbers of arms also seem to be correlated with reduction in the cirri, a specimen with 17 arms up to 40 mm long having only XII. The maximum number of cirrus segments increases from 14 to 18 and their length from 6.3 mm to 10.8 mm. The cirrus length varies from 19 to 31% of the maximum arm length and is relatively less in the larger specimens.

AFFINITIES. In comparison with *Comanthus wahlbergi wahlbergi* the most obvious difference is the smaller number of arms. A. H. Clark (1931 : 590) gives the number as 13–21, usually 16–20 for *wahlbergi* from the South African mainland and, apart from the specimens which he mentions from Algoa Bay with only 10–12 arms which

are probably referable to *C. wahlbergi serratus*, the 23 individuals dealt with descriptively average 17.8 arms.

The maximum size is also greater for the subspecies from the mainland, judging from the present sample from Walter's Shoal, the arm length reaching 80 mm rather than only 50 mm. Also the arms are more slender in *C. wahlbergi tenuibrachia*; while a specimen of *C. wahlbergi wahlbergi* from False Bay, South Africa, has arms only 30 mm long at 1.4 mm breadth of 3 + 4 (on arms based on IIBr series), in the Walter's Shoal specimens with the same breadth the maximum arm length is 45-50 mm. Fifteen specimens from the mainland waters have a mean ratio of arm length : breadth 22 : 1, compared with a mean of 33 : 1 in the twelve specimens of *C. wahlbergi tenuibrachia* measured which have IIBr series present to provide a comparable measurement. However, there is some overlap since the range in this ratio in the twelve of *tenuibrachia* is from 25 to 45 : 1, overlapping that of *wahlbergi*, which is 19-29 : 1.

The cirri appear to be relatively shorter in *C. wahlbergi wahlbergi* measuring up to only c. 7 mm in specimens with arm length 30-50 mm, compared with 8-10+ in *C. wahlbergi tenuibrachia*. The transition segment is usually the fifth in the latter but more often the sixth in the mainland specimens.

Finally *C. wahlbergi wahlbergi* may differ in having fewer consecutive proximal pinnules with combs at a comparable size.

As for *Comanthus wahlbergi serratus*, this does resemble *tenuibrachia* in the relatively small number of arms but these are again stouter basally than in the specimens from Walter's Shoal, the ratio of arm length : breadth (after IBr series in this case) ranging from 15-26 : 1 with a mean of 21 : 1 for 26 specimens of *serratus* compared with a range of 23-43 : 1 and a mean of 31 : 1 in the 20 of *tenuibrachia* measured.

The number of cirrus segments may be slightly less in *C. wahlbergi serratus*, usually 13-15 at arm length 25-30 mm compared with 14-16 in *tenuibrachia* at this size. Even the holotype of *serratus* with arm length c. 40 mm was described as having only 13-15 cirrus segments; it has over XX cirri according to Gislén, which may also be a significant difference.

PENTACRINOIDS. Several pentacrinoids were observed attached to the cirri of a number of specimens, as also noted by A. H. Clark in *C. wahlbergi wahlbergi*.

### *Comaster distinctus* (P. H. Carpenter)

*Actinometra distincta* P. H. Carpenter, 1888 : 295-296, pl. 55, fig. 1.

*Antedon brevicirra* Bell, 1894 : 400.

*Comaster parvus* A. H. Clark, 1909 : 144; 1912a : 88-89, 315, fig. 3; Gislén, 1927 : 9-10, figs 5, 6.

*Comaster distincta* : A. H. Clark, 1911a : 533; 1912a : 87-88; 1931 : 448-451, pl. 52, fig. 153.

*Comaster brevicirra* : A. H. Clark, 1931 : 444-447, pl. 29, figs 84-86.

*Comaster* sp. ? nov. aff. *distinctus* : A. M. Clark in Humes & Ho, 1970 : 15.

*Comaster distinctus* and *brevicirrus* : A. M. Clark & Rowe, 1971 : 16.

MATERIAL. 'Anton Bruun' cruise 1, st. 18A, 07°34'N : 98°00'E (between Malaya and the Nicobar Islands), 77 metres; 2 specimens.

'Anton Bruun' cruise 9, st. KA 14, Mounimeri, Comoro Islands; one post-radial series and arms [probably of *C. distinctus*].

Prof. A. G. Humes's no. 1298, 13°29'S : 48°06'E (S of Nosy Bé, Madagascar, 47 metres; 7 specimens. B.M. reg. nos 1969.5.13.117-122.

Dr L. Fishelson's nos NS 6317-6320, Gulf of Akaba; 3 specimens and one IIBr series with arms. B.M. 1970.10.8.45 (1 specimen).

REMARKS. The inclusion in *Comaster distinctus* of the fine specimens from Madagascar and the Gulf of Eilat extends both the geographical and the size ranges of the species, which was hitherto unknown either from the western Indian Ocean or to reach an arm length of more than 110 mm.

Some counts and measurements of most of these specimens are given in the following table together with others from the holotypes of *Comaster distinctus* and *brevicirrus* and a specimen in the British Museum collection from the South China Sea, N. of Sarawak (B.M. no. 1964.3.17.15). The arm lengths given are for the longest arms left intact, or almost. Since all possible IIBr series are present in all these specimens, the number of IIBr series of 4 can be found by deducting the number of IIBr 2 series from 10. Except in the seventh specimen listed, the additional III or IVBr series are internal in position.

TABLE I  
Numerical data from specimens of *Comaster distinctus*

Specimen	Arms		Cirri			Division Series				
	No.	Length (mm)	No.	Segs.	Length (mm)	IIBrs		IIIIBrs		IVBrs
						2	2	4	2	4
AB st. 18A	30	c. 55	XIX	10	6.8	5	9*	0	0	0
Sarawak	33 (?+)	80	XVIII	13	9.2	0	13	0	0	0
<i>C. brevicirrus</i>										
HOLOTYPE	c. 50	c. 50	XXV	11	6.8	7	12	4	13	0
<i>C. distinctus</i>										
HOLOTYPE	36 (?+)	c. 75	XXX	12	9.0	0	16	0	0	0
Eilat	c. 40	c. 100	XXVIII	12	10.8	0	18	0	1	0
Madagascar	36	150	XX	13	8.7	4	13	2	1	0
"	41	125	XVII	13	8.4	2†	17	0	3	1
"	41	120	XX	13	8.9	4	14	4	3	0
"	c. 40**	140	XVI	13	8.9	2	11+	2	1	0
"	39	150	XV	13	9.7	4††	15	1	2	1
"	41	170	XIX	13	10.3	2	13	3	5	0
"	48	140	XXXVI	14	10.3	2	19	0	9	0

\* One IIIBr 3 series also present.

† One IIBr 3 series also present.

\*\* One IBr and one IIBr series broken, probably about 10 arms lost.

†† One IIBr 3 series also present.

The specimen with arms 170 mm long (last but one in the table) has the arm breadth (on arms arising from IIIIBr series) measured at Br<sub>2-3</sub> (which is a tangential suture unlike Br<sub>1+2</sub>) measuring 1.6 mm and the length from the proximal edge of the IBr<sub>1</sub>

to this same suture is 8.4 mm. The brachials from about Br<sub>12</sub> have rugose distal edges but the proximal ossicles are smooth.

The flattened centrodorsal has the dorsal pole 2.1-2.9 mm in diameter, the cirri encroaching unevenly upon it. A mature cirrus measuring 10.3 mm in length has the fourth segment longest, with length : median breadth 1.02 : 0.37 mm (=2.76 : 1). Since the cirri deepen considerably distally, the breadth of the antepenultimate segment (excluding its small dorsal distal projection) measures 0.60 mm. The distal segments each have a short transverse dorsal ridge distally, in profile resembling a small spine. Only the opposing spine on the penultimate segment is narrow.

On an arm preceded by both IIBr 4 and IIIBr 4 series, P<sub>1</sub> (in this case the third pinnule, following the P<sub>D</sub> and P<sub>P</sub>) has 32 segments and is 9.5 mm long; its comb of seven long teeth starts abruptly and finishes two segments short of the tip. P<sub>2</sub> with about 29 segments measures 6.3 mm and has a comb of nine teeth. Combs are lacking from P<sub>3</sub> and P<sub>5</sub> but present on P<sub>4</sub>, P<sub>6</sub> and P<sub>7</sub> and scattered more distal pinnules. P<sub>D</sub> has 36 segments and is 11.5 mm long with a comb of nine teeth but an internal P<sub>1</sub> with 32 segments has the last 13 bearing teeth. The genital pinnules are relatively short with stout segments; the gonads are undeveloped. The distal pinnules are much more elongated.

In most of the specimens the joint in the IBr series appears to be usually a pseudosyzygy but in some cases the ends of the radiating ridges characteristic of proper syzygies can be distinguished superficially. The first joint in IIBr series of four ossicles is also rarely syzygial in contrast to that in IIIBr series or the first two brachials.

The key to the species of *Comaster* given in A. H. Clark's monograph (1931) has a dichotomy c (after a<sup>2</sup>b<sup>2</sup>) based on more or less than 40 arms, cutting across the present specimens which run down to *C. schoenovi* A. H. Clark, 1918, if one opts for 40+ arms or to *C. brevicirrus* (35-40 arms) or *distinctus* (<35 arms) otherwise. As noted already (A.M.C. & Rowe, 1971 : 16) the number of arms is probably not a valid distinction between *schoenovi*, *brevicirrus* and *distinctus*. Indeed the holotype of *C. brevicirrus* probably had about 50 arms. It came from Macclesfield Bank in the South China Sea, while the holotype of *C. schoenovi* with 60 arms was from the coast of China. The specimen from Singapore figured under the name of *C. schoenovi* by A. H. Clark (1931, pl. 64, fig. 179) appears to have about 45 arms.

In the holotype of *C. brevicirrus* the cirri certainly are shorter and stouter than those of the holotype of *C. distinctus*, having the fourth and longest segment with length : median breadth 0.95 : 0.58 mm (=1.64 : 1) as opposed to 1.00 : 0.53 (=1.89 : 1) but I doubt if this difference is significant. The specimen from Sarawak has cirri of similar proportions to those of the holotype of *C. brevicirrus*. I do not think that the high incidence of IIBr series of only two ossicles (7 out of 10) is significant and I can find no other characters by which to distinguish specifically the holotypes of *C. brevicirrus* and *distinctus*. Accordingly, *C. brevicirrus* is here returned to the synonymy of *C. distinctus*, A. H. Clark having made the same move in 1912 but reversed it in 1931. I think that *C. schoenovi* will also prove to be a synonym of *C. distinctus*, certainly the Singapore specimen is straddled geographically and in arm number by the material of Carpenter's species. *Comaster pulcher* A. H. Clark,

1912, known from only a single specimen from the Kei Islands with 40 arms c. 85 mm long has cirri with as many as 15-17 segments up to 15 mm long and may well be distinct on this account. Unfortunately, immature specimens of the other species such as *C. multifidus*, which completely lack cirri as adults following reduction during growth, also need to have their relationships with *C. distinctus* evaluated. Much better samples, especially from the western tropical Pacific, are needed to allow this to be done.

### *Comaster gracilis* (Hartlaub)

*Actinometra gracilis* Hartlaub, 1890 : 170, 187; 1891 : 111-112, pl. 5, fig. 55.

*Comaster gracilis*: A. H. Clark, 1910 : 139; 1912a : 84; 1913 : 12; 1931 : 430-435, pl. 47, figs 143, 144; Gislén, 1934 : 32, 34-35; 1940 : 5; A. M. Clark & Rowe, 1971 : 16

MATERIAL. 'Te Vega' cruise 2, st. 65, Pulau Hantu, SW of Singapore, reef, intertidal; 1 broken specimen.

'Te Vega' cruise 2, E St John's, Singapore, 'sublittoral'; 2 broken specimens.

'Te Vega' cruise 3, Gan, Maldivé Islands, shore; 1 fragmented specimen [with commensal shrimp].

'Te Vega', F. C. Zieshenne's st. 64-11, 4°17'50"N : 73°33'42"E (between Male and Fadiffolu, Maldivé Islands), reef, 1-3 feet; 1 broken specimen.

REMARKS. This species has already been collected at Singapore and the Maldivé Islands by Svend Gad and Stanley Gardiner respectively. The multiplicity of proximal syzygies renders it very easily broken in preservation and hampers comparison with *Comaster multifidus*, of which it is thought by Gislén to be a synonym. These specimens, including the two from St John's, Singapore, are more slender than the one from that locality which I am referring to *C. multifidus*.

### *Comaster multifidus* (J. Müller)

*Alecto multifida* J. Müller, 1841 : 188.

*Comaster multifida*: A. H. Clark, 1911c : 247-248; 1912a : 84-85; 1931 : 413-430, pl. 46, figs 140, 141; Gislén, 1940a : 4-6. [Non *C. multifida*: Gislén, 1919 : 14-19, which is *Comanthus parvicirrus*.]

MATERIAL. 'Te Vega' cruise 2, E St John's, Singapore, 'sublittoral'; 1 specimen.

### *Comatella maculata* (P. H. Carpenter)

*Actinometra maculata* P. H. Carpenter, 1888 : 307, pl. 5, fig. 1, pl. 55, fig. 2.

*Comatella maculata*: A. H. Clark, 1910 : 138; 1931 : 112-118, pl. 20, fig. 50.

MATERIAL. 'Te Vega' cruise 3, st. 132, S Nilandu Atoll, Maldivé Islands; 1 specimen (somewhat decalcified).

This specimen has 21 arms, the only III Br series 2(1 + 2).

*Comatella stelligera* (P. H. Carpenter)

*Actinometra stelligera* P. H. Carpenter, 1880 : 198, pl. 12, fig. 26; 1888 : 308-309, pl. 5, fig. 5, pl. 58, figs 1, 2.

*Comatella stelligera*: A. H. Clark, 1910 : 136; 1911a : 530-531; 1912a : 68, 70; H. L. Clark, 1921 : 13, pl. 2, fig. 2; Gislén, 1922 : 18-21, figs 7-9; A. H. Clark, 1931 : 98-112, pl. 4, figs 6-9; Gislén, 1940a : 3-4.

**MATERIAL.** 'Anton Bruun' cruise 1, st. 47B, 19°50'N : 92°55'E (off Akyab, Burma), 22-30 metres; 1 specimen.

**REMARKS.** This species has been recorded from the nearby Mergui Archipelago. The present specimen has about 40 arms and up to 27 cirrus segments, the latter bringing it within the range of *Comatella nigra* (P. H. Carpenter, 1888) as given in A. H. Clark's key (1931 : 91-92), though specimens with up to 50 arms have been recorded as *C. stelligera*, contrary to his key but allowed for in the diagnosis. I think it very likely that *nigra* will prove to be not specifically distinguishable; unlike *C. stelligera* it has not been recorded from the Indian Ocean.

*Comatula pectinata* (Linnaeus)

*Asterias pectinata* Linnaeus, 1758 : 663.

*Comatula pectinata*: A. H. Clark, 1910 : 148; 1912a : 80-81; H. L. Clark, 1921 : 14, pl. 1, fig. 3, pl. 3, fig. 2; A. H. Clark, 1931 : 339-360, pl. 20, fig. 49, pl. 33, fig. 100, pl. 34, fig. 101, pl. 35, fig. 102, pl. 36, fig. 103, pl. 37, fig. 104, pl. 38, figs 105-107; H. L. Clark, 1938 : 18-20.

**MATERIAL.** 'Anton Bruun' cruise 1, st. 38, 14°07'N : 97°05'E (W of the Moskos Islands, Burma), 69-73 metres; 2 specimens.

'Anton Bruun' cruise 1, st. 47B, 19°50'N : 92°55'E (off Akyab, Burma), 22-30 metres; 2 specimens.

**RANGE.** This predominantly west Pacific species has been recorded from the Straits of Malacca but these are the first positive records from within the Bay of Bengal.

*Comissia hartmeyeri* A. H. Clark

(fig. 2)

*Comissia hartmeyeri* A. H. Clark, 1912f : 386-387; 1931 : 267-269, pl. 28, figs 78, 79, pl. 29, figs 80-82.

**MATERIAL.** 'Anton Bruun' cruise 9, st. HA-39, 27°16'38"N : 33°47'01"E (just S of the Gulf of Suez, Red Sea), 3-5.5 metres; 7 specimens.

Dr Fishelson's no. NS 4477, Ras-Atantur, Sinai Peninsula, Gulf of Akaba, 1 metre, in hole under dead coral; 2 specimens. B.M. reg. no. 1969.5.13.1 and Tel-Aviv University research collection.

The only other record of this small comasterid is that of the type-material, which

was taken at Tor (El Tur) on the Gulf of Suez side of the Sinai Peninsula. It will probably be found to be quite widespread but has escaped attention because of its small size and self-effacing habit.

DESCRIPTION. One of the larger 'Anton Bruun' specimens has arm length c. 30 mm, breadth at the first syzygy 0.7 mm and the length from the proximal edge of the  $IBr_1$  to this syzygy 2.5 mm. There are XV cirri with 12 or 13 segments and length up to 5.8 mm; the fourth and longest segment has length : median breadth 0.8 : 0.25 mm (= 3.2 : 1) and the distal breadth, in the middle of the antepenultimate segment, is 0.4 mm. The second syzygy is at 11 + 12 on eight of the nine remaining arms and at 12 + 13 on the ninth. There are up to seven teeth in the comb on  $P_1$ .

The larger Sinai specimen has arm length 47 mm and the breadth at 3 + 4 1.15 mm. The centrodorsal is c. 2 mm in diameter. There are XX cirri with up to 15 segments and length c. 8 mm; the fifth and longest segment has length : breadth 0.90 : 0.35 mm (= < 3 : 1). The sixth segment is slightly broader, especially at the distal end and the cirrus is distinctly deeper from the seventh segment to the penultimate so that the mean distal breadth is c. 0.55 mm. The last six segments are shorter than their median breadths. There are small median distal dorsal spines or short transverse ridges. The brachials are flared but not markedly spinose, at least in the proximal half of the arm. The pinnule segments are both flared and spinose. There are no dorsal processes at the bases of the proximal pinnules.  $P_1$  with 26 segments has the last six with teeth making the comb; it is c. 9 mm long.  $P_2$  is much smaller with 15 segments, four with teeth; the length is c. 4 mm.  $P_3$  is a genital pinnule. There are eggs on the exterior of some genital pinnules and a pentacrinoid attached to a cirrus of the second Israeli specimen, the same being true of an 'Anton Bruun' specimen and also of the type series.

Both the shore specimens have eleven arms but the 'Anton Bruun' individuals

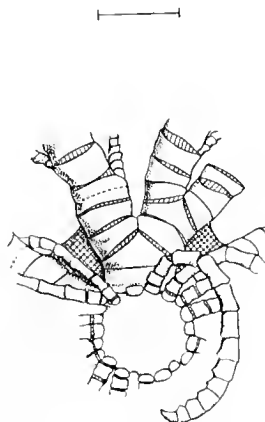


FIG. 2. *Comissia hartmeyeri* A. H. Clark. B.M. reg. no. 1969.5.13.1, SE Sinai peninsula. Arm br 1.15 mm (after  $IBr$  series only). Dorsal view of centrodorsal and proximal part of one post-radial series. [The scale equals 2 mm.]



all have ten. The IIBr series, where present, have two ossicles in one specimen and four in the other.

REMARKS. These specimens serve to show that some of the characters used in A. H. Clark's key to the species of *Comissia* (1931 : 246-247), such as the number of cirrus segments and cirri, are correlated with size, *C. hartmeyeri* being supposedly characterized by having not more than 14 cirrus segments, the longest more than three times as long as broad, arms not more than 45 mm long and less than XX cirri, all of which clearly applies only to not fully grown specimens.

### Family EUDIOCRINIDAE

#### *EUDIOCRINUS* P. H. Carpenter

*Eudiocrinus* P. H. Carpenter, 1882 : 493; A. H. Clark, 1941 : 145-149. [Type-species *Ophiocrinus indivisus* Semper, 1868.]

A. H. Clark (1941) recognized twelve nominal species of *Eudiocrinus* including a new one, *E. eoa*, rather incompletely described from a single specimen from the Philippine Islands, which seems to me to be close to, if not conspecific with, *E. tenuissima* Gislén, 1940, from the Marshall Islands, the description of which appeared while Clark's monograph was in the press. Most of the numerical characters of these two which were mentioned in the descriptions are given in Table 2 together with comparable data of the other species in the order in which they appear in A. H. Clark's key. The approximate entries for relative length of the longest cirrus segments are estimates from his comparisons of length with either proximal or distal breadth, rather than the usual median breadth. The T.V. ('Te Vega') and A.B. ('Anton Bruun') specimens are likely to be deposited in the U.S. National Museum and the Swain Reefs (Great Barrier Reef) specimen of *E. serripinna* in the Australian Museum. Only the holotype of *Antedon granulatus* Bell (a synonym of *E. indivisus*) was hitherto in the British Museum collections, the specimen of *E. gracilis* from the Maldive Islands being in the Cambridge Zoological Museum.

Unfortunately little is known about the range of variation in the species of *Eudiocrinus* and the present collection does little to help rectify this, though it does serve to extend the range of no less than three species into the Bay of Bengal from the Pacific, namely *E. indivisus*, *serripinna* and *venustulus*, if my identifications on the basis of A. H. Clark's key are correct. However, I suspect that not all the nominal species he recognized will prove to be valid.

#### *Eudiocrinus indivisus* (Semper)

*Ophiocrinus indivisus* Semper, 1868 : 68.

*Eudiocrinus indivisus*: P. H. Carpenter, 1882 : 495; A. H. Clark, 1912a : 102; Gislén, 1922 : 68-69; A. H. Clark, 1941 : 163-169, pl. 11, fig. 42.

*Eudiocrinus granulatus* Bell, 1894 : 397-398, pl. 23.

MATERIAL. 'Anton Bruun' cruise 1, st. 21, 09°54'N : 97°42'E (SW of Mergui Archipelago), 70 metres; 1 broken specimen.

DESCRIPTION. The arm length is 35 plus possibly about 25 mm; the breadth at  $3 + 4$  is 1.4 mm and the length of the first five post-radial ossicles (i.e. to  $3 + 4$  since the first two count as  $IBr_1$  and  $_2$  by A. H. Clark's terminology) is 3.3 mm. The centrodorsal is 2.6 mm in diameter. There are c. XXII cirri but only one peripheral one of 23 segments is complete; it measures 17 mm, the fifth and longest segment has length : median breadth 1.0 : 0.5 mm and the distal breadth is 0.7 mm.

The arms are smooth, the brachials not flared. Only parts of three remain and two of them do not have a syzygy at  $3 + 4$ , the brachial syzygies following that between the two IBr ossicles being:  $3 + 4$ ,  $9 + 10$ ;  $7 + 8$ ,  $12 + 13$ ;  $15 + 16$ ,  $19 + 20$ . In spite of this anomaly in the joints, the last arm has the pinnules on the usual brachials, as on the first arm, no pinnule occurring on  $Br_3$  even though it is not a hypozygal; however, the second arm does have a pinnule on  $Br_3$ .

$P_C$  on the second ossicle,  $IBr_2$ , has 14 segments and is 5.3 mm long. It is prismatic and most markedly flattened horizontally with a lateral flange.  $P_1$  is a similar shape, with 13 segments and is 5.3 mm long.  $P_a$  is relatively huge, very stout, smooth and gradually tapering, with 18 segments and length 10.0 mm.  $P_2$  is similar to  $P_a$  with 20 segments and is 10.5 mm long; the segments have parallel sides and only the distal ones have a small spine at their distal ends.  $P_b$  is variable in size; it may be more slender, with 19 segments and length only 6.8 mm, or almost equal to  $P_a$ , while on one arm it is the longest pinnule since  $P_a$  is relatively small, only 6.2 mm long.

RANGE. This record extends the known range of *E. indivisus* into the Indian Ocean; it was previously known only from the East Indies, Philippines and South China Sea to the Bonin Islands.

### *Eudiocrinus minor* A. H. Clark

(fig. 3)

*Eudiocrinus minor* A. H. Clark, 1909b (17 April) : 75-76; 1912a : 102-103, fig. 5.

*Eudiocrinus ornatus* A. H. Clark, 1909b : 76 (nom. nud.); 1909c (19 June) : 633-635; 1912a : 99-101, fig. 4; 1918 : 70, pl. 17, fig. 29; 1941 : 172-175, pl. 11, fig. 40, pl. 12, fig. 47.

NOMENCLATURE. The dating of A. H. Clark's two papers of 1909 contradicts his treatment of 1918 and 1941, where *E. minor* is referred to the synonymy of *E. ornatus* despite its clear priority and the fact that in 1941 he qualified the entry for *E. ornatus* in the earlier of the two 1909 references as a nomen nudum. I cannot agree with his statement in the text that this earlier paper provided sufficient 'indication' to establish the name since it was not differentiating *E. ornatus* from *E. minor* in any way but likening the two. The relevant passage at the end of the description of *E. minor* reads 'Arms and pinnules as in *E. ornatus*, the overlapping of the brachials and pinnules being moderately marked'. Despite the change away from the usage in A. H. Clark's monograph—the definitive work on this family—I consider that the name *Eudiocrinus minor* is the proper one to use for this species.

MATERIAL. 'Anton Bruun' cruise I, st. 18A,  $07^{\circ}34'N$  :  $98^{\circ}00'E$  (between Malaya and the Nicobar Islands), 77 metres; 1 specimen.

Species	anules			
	P <sub>a</sub>		P <sub>2</sub>	
	Segs.	L.	Segs.	L.
<i>juvencus</i> A.H.C., 1912	15	11	15	11
<i>philenor</i> A.H.C., 193	15	8	—	—
<i>venustus</i> A.H.C., 1	12	5	similar	
	14	5.3	15	5.5
<i>tenuissima</i> Gis., 194	7	2	similar	
<i>eo</i> A.H.C., 1941	7	2	similar	
<i>serripinna</i> A.H.C., 1	—	—	—	—
	12	5.3	12	5.3
	11	5.3	11	5.0
<i>minor</i> A.H.C., 1909	15	8.5	similar	
	larger		18	12
	10	5.0	11	5.3
	—	—	—	—
<i>indivisus</i> (Semp.), 1	—	—	—	c. 8
	18	10.0	20	10.5
	17	9.0	15	9.0
	10	7.5	11	8
<i>pulchellus</i> Gis., 1922	10	4	12	4
	8	2	—	—
	10	3.5	10	3.2
<i>gracilis</i> A.H.C., 191	10	7	—	—
	11	9	—	—
	16	9	15	8
<i>pinnatus</i> A.H.C., 19	17	11	17	11
	16	12	similar	
<i>loveni</i> Gis., 1922	11	5	11	5
<i>variegatus</i> A.H.C., 1	similar		c. 12	c. 4.5
	12	4	12	4

TABLE 2

Numerical data for the species of *Eudiocvinus* P. H. Carpenter

Species	Specimen	Arms		Cirri				Cirrus L. as % arm length	Pinnules							
		Length	Breadth	No.	Segs.	Length	L : Br longest segment		Segs.	P <sub>c</sub>	P <sub>1</sub>		P <sub>a</sub>		P <sub>2</sub>	
										L.	Segs.	L.	Segs.	L.	Segs.	L.
<i>juncus</i> A.H.C., 1912b	holotype	90	—	XXV	22	23	say 4·2	26	15	6·5	14	6·5	15	11	15	11
	T.V. st. 60	c. 30	0·7	XXI	17	10·5	4·5	35	c. 10	3·5	—	—	—	—	—	—
<i>philenor</i> A.H.C., 1932	holotype	c. 40	—	XXV	15	10	4·0	25	11	4	12	4	15	8	—	—
<i>venustus</i> A.H.C., 1912b	holotype	60	—	XII	16	6·5	say 1·4	11	10	3·0	similar		12	5	similar	
	A.B. st. 21	c. 40	0·9	XX	18	6·3	1·5	16	8	2·2	10	2·9	14	5·3	15	5·5
<i>tenuissima</i> Gis., 1940	holotype	45	0·5	XV	11	c. 4	2·5	9	7	1·5	similar		7	2	similar	
<i>coa</i> A.H.C., 1941	holotype	?	—	XV	12	?	2·5	—	7	1·5	similar		7	2	similar	
<i>servipinna</i> A.H.C., 1908	holotype	65	—	XIX	16	10	say 1·2	15	—	—	—	—	—	—	—	—
	Swain Reefs	c. 60	1·4	XXII	17	8	1·4	13	11	3·7	11	3·7	12	5·3	12	5·3
	A.B. st. 18A	40+	1·3	XVI	20	9	1·2	c. 20	10	3·3	10	4·0	11	5·3	11	5·0
<i>minor</i> A.H.C., 1909a	<i>ornatus</i> HT	85	—	XVIII	18	20	say 2·2	24	12	5·5	12	—	15	8·5	similar	
	Siboga st. 294	c. 50	—	XXI	18	12	say 2·2	24	12	5	15	7·5	larger		18	12
	A.B. st. 18A	c. 32	1·1	c. XX	15	9·5	2·7	30	10	3·0	10	3·4	10	5·0	11	5·3
	<i>minor</i> HT	15	—	XII	12	5	2	33	—	—	—	—	—	—	—	—
<i>indivisus</i> (Semp.), 1868	holotype	80	—	XVI	20	9	c. 2	11	—	—	—	—	—	—	—	c. 8
	A.B. st. 21	c. 60	1·4	XXII	23	16·8	2·0	28	14	5·3	13	5·3	18	10·0	20	10·5
	<i>granulatus</i> HT	c. 90	1·7	XXV	21	14·5	1·8	16	13	5·3	13	5·3	17	9·0	15	9·0
Bock st. 59	—	c. 1·9	XIX	21	15	2	—	10	4	10	4	10	7·5	11	8	
<i>pulchellus</i> Gis., 1922	holotype	40	0·8	XIX	15	6·5	c. 2	16	10	2·5	10	3	10	4	12	4
	Bock st. 46	30	—	XVII	14	6·5	c. 3?	15	6	1·5	6	—	8	2	—	—
	Bock st. 45	c. 20	—	XX	12	3	—	22	8	2	8	2	10	3·5	10	3·2
<i>gracilis</i> A.H.C., 1912b	holotype	55	—	X	16	9	say 2·2	16	10	3·5	10	4·5	10	7	—	—
	paratype	—	—	XIII	18	12	—	—	10	4	—	—	11	9	—	—
	S. G. Maldives	100	1·6	c. XX	20	11	1·4	11	14	5	15	5·3	16	9	15	8
<i>pinnatus</i> A.H.C., 1912b	holotype	75	—	XVII	22	11	l < br	15	11	4	12	4·5	17	11	17	11
	Jolo, Kei Is.	—	—	XV	17	—	say 1·2	—	15	6	14	6+	16	12	similar	
<i>loveni</i> Gis., 1922	holotype	45	1·4	XX	21	10	1·25	22	9	3·5	10	4	11	5	11	5
<i>variegatus</i> A.H.C., 1908	holotype	75	—	XXV	15	9	say 1·3	12	9	4	12	6	similar		c. 12	c. 4·5
	Hamburg Mus.	40	—	XVII	15	5	say 1·2	12·5	9	3	9	3	12	4	12	4

DESCRIPTION. The arm length is only 27 plus about 5 mm; the breadth at 3 + 4 is 1.1 mm and the length to this syzygy 2.6 mm. The diameter of the centrodorsal is 2.1 mm, of which the dorsal pole occupies the greater part, being bounded by a staggered row of cirri, mostly only one deep. The cirri number c. XX, have up to 15 segments and are up to 9.5 mm long. The fourth and most attenuated segment has length : median breadth 0.8 : 0.3 mm but is so constricted medially that its distal breadth is 0.5 mm. The antepenultimate segment is also longer than broad with br 0.4 mm.

The brachials are slightly flared at their distal ends so that the profile is uneven but they are not spinose or carinate.

$P_c$  arises on the left side of the  $IBr_1$  and has 9 or sometimes 10 segments, its length being 2.8–3.0 mm; it tapers evenly from a stout base.  $P_1$  with 10 segments is 3.4 mm long.  $P_a$  again with 10 segments is larger, 5.0 mm long, the segments being stouter and more flared at their distal ends as well as finely spinose.  $P_2$  with 11 segments is 5.3 mm long.

REMARKS. This specimen agrees fairly well with A. H. Clark's description of the holotype of *E. ornatus*, which is also from the Bay of Bengal but nearer the Andaman Islands, allowing for the much larger size, arm length c. 85 mm. The fewer cirri of the type, only XVIII, probably have little significance and could be attributable

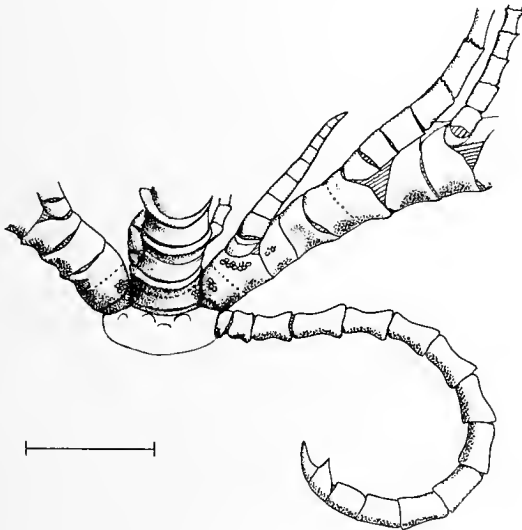


FIG. 3. *Eudiocrinus minor* A. H. Clark. 'Anton Bruun' st. 18A, N Malacca Strait. Arm br 1.1 mm. Side view of calyx with mature cirrus and the bases of three post-radial series, the median one foreshortened, that on the right showing  $P_c$  and the bases of  $P_a$  and  $P_b$ , the centrodorsal drawn only in outline, being obscured by the cirri. [The scale equals 2 mm.]

to A. H. Clark's more conservative estimates of cirrus numbers. The main difference appears to be the smoother brachials in the 'Anton Bruun' specimen (see fig. 3), whereas the holotype has brachials with 'a somewhat concave dorsal surface and very prominent distal ends which are strongly overlapping and give the animal a curiously ornate appearance'. This condition may approximate to that in *E. venustulus* (see fig. 5) from which the holotype of *E. ornatus* differs in having prismatic basal segments to the proximal pinnules and no large dorsal crests. Since *E. venustulus* was also taken at station 18A, the two are sympatric and a study of their variation is desirable. The holotype of *E. minor*, also from the vicinity of the Andaman Islands, is relatively small, the arms only 15 mm long and the XII cirri with up to only 12 segments.

A. H. Clark (1941) notes that *E. philenor* A. H. Clark, 1932, known only from the nearby Mergui Archipelago, is the species most closely related to *E. ornatus*. It seems to differ in having more elongated cirrus segments, up to four times as long as the median width, while  $P_a$  and  $P_2$  are relatively longer, the proximal ossicles carinate and their distal edges less produced. In the holotype of *E. philenor* the arm length is 40 mm and  $P_a$  is 8 mm long with 15 segments, almost as long as that of the holotype of *E. ornatus* where the arm length is twice as long.

### *Eudiocrinus serripinna* A. H. Clark

(fig. 4)

*Eudiocrinus serripinna* A. H. Clark, 1908b : 211; 1918 : 71; 1941 : 169-171, pl. 12, fig. 49.

MATERIAL. 'Anton Bruun' cruise I, st. 18A, 07°34'N : 98°00'E (between Malaya and the Nicobar Islands), 77 metres; 1 specimen.

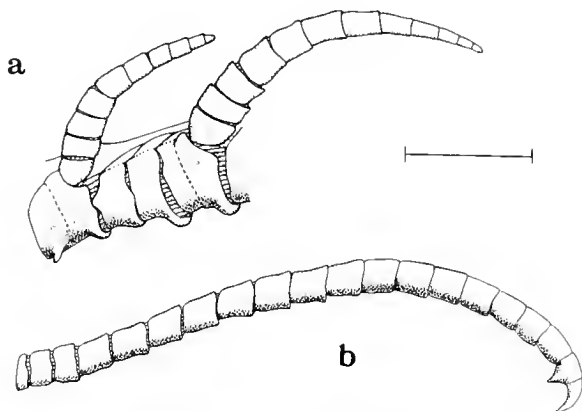


FIG. 4. *Eudiocrinus serripinna* A. H. Clark. 'Anton Bruun' st. 18A, N Malacca Strait. Arm br 1.3 mm. a. side view of base of one post-radial series showing  $P_c$  and  $P_a$ ; b. mature cirrus. [The scale equals 2 mm.]

DESCRIPTION. The arms are all broken by 16 mm from the calyx but were possibly 40–50 mm, judging from the breadth at 3 + 4, which is 1.3 mm while the length to this syzygy is 2.5 mm. The centrodorsal is 2.0 mm in diameter. There are XVI cirri with up to 20 segments and length up to 9.2 mm; the segments are relatively short, the fifth and longest having length : median breadth 0.55 : 0.45 mm and there is little change in the proportions of the segments distally, the antepenultimate being only fractionally shorter but equally as broad as the fifth.

The proximal post-radial ossicles are markedly flared at their distal ends with median peaks on about the first five (i.e. IB<sub>1</sub> to Br<sub>3</sub> or 4); also the IB<sub>1</sub> and 2 have ventro-lateral flanges.

P<sub>c</sub> (on the left) and P<sub>1</sub> are markedly prismatic, both with 10 segments and length respectively 3.3 and 4.0 mm. P<sub>a</sub> and P<sub>2</sub> with 11 (or 12) segments are 5.3 and 5.0 mm long but P<sub>b</sub> with 10 segments is only 3.4 mm long; it has the segments more flared at their distal ends than the earlier pinnules.

REMARKS. The maximum number of cirrus segments in the Pacific specimens described by A. H. Clark is only 16, corresponding with arm lengths of up to 65 mm, although a specimen from the Great Barrier Reef which I have recently studied (and which provides a further extension of range) has up to 17 cirrus segments at arm length c. 60 mm. However, the cirrus segments are relatively short in *E. serripinna* in comparison with those of the two other species taken at station 18A, *E. minor* and *E. venustulus*, where the ratio of length : median breadth is c. 2 : 1 or more. The proportions of the cirrus segments provide most of the primary dichotomies in A. H. Clark's key to the species of *Eudiocrinus* (1941 : 148–149).

RANGE. This record provides an extension of the known range of *E. serripinna* into the Indian Ocean, previous records being from the Philippines, Kei and Lesser Sunda Islands.\*

### *Eudiocrinus venustulus* A. H. Clark

(fig. 5)

*Eudiocrinus venustulus* A. H. Clark, 1912b : 27–28; 1918 : 68–70, pl. 17, figs 27, 28; 1941 : 160–162, pl. 12, figs 45, 46.

MATERIAL. 'Anton Bruun' cruise 1, st. 18A, 07°34'N : 98°00'E (between Malaya and the Nicobar Islands), 77 metres; 2 specimens.

'Anton Bruun' cruise 1, st. 21, 09°54'N : 97°42'E (SW of the Mergui Archipelago), 70 metres; 1 specimen.

DESCRIPTION. All three specimens are similar in size with arm length probably 35–40 mm, the breadth at 3 + 4 c. 1.0 mm and length from IB<sub>1</sub> to 3 + 4 2.3–2.8 mm. One of the specimens from station 18A has its cirri closely curled round the branches of a hydroid and is hard to examine with respect to the centrodorsal and

\*Since this paper went to press, I have received from Tel-Aviv University a specimen of *Eudiocrinus serripinna* (no. NS 6094) taken off Taba, near Eilat, Gulf of Akaba, in 25 metres, extending the range farther still.

cirri. The two others have the centrodorsal 1.7 and 2.1 mm in diameter, with the dorsal pole 1.1 and 1.7 mm across respectively, the staggered ring of cirri being doubled for varying extents. In both there are c. XX cirri with up to 16 or 18 more or less constricted segments, the longest cirri up to 6.4 mm long, while the fifth and longest segment has length : median breadth c. 0.5 : 0.3 mm, its flared distal end being 0.45 mm broad; the antepenultimate segment is barely longer than broad, c. 0.40 : 0.35 mm. The distal edges of the radials and the immediately following ossicles are flared and ornamented to some extent with beading or more or less elongated tubercles (see fig. 5a). The distal median projections on the brachials may give the effect of a keel.

$P_c$  is on the left in each case, as usual; it has 8 segments and measures c. 2.3 mm. The first two segments are much enlarged and have very high dorsal crests.  $P_1$  is similar but slightly larger, with 9 or 10 segments and c. 2.8 mm long.  $P_a$  is much

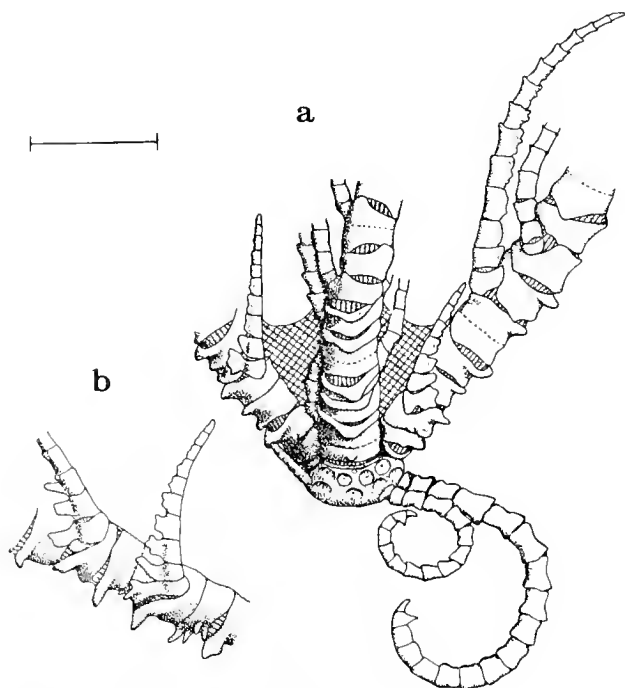


FIG. 5. *Eudiocrinus venustus* A. H. Clark. a. 'Anton Bruun' st. 21, SW Burma. Arm br 0.9 mm. Side view of calyx with mature peripheral and apical cirri and the bases of three post-radial series, the median one foreshortened, that on the left showing  $P_1$  and that on the right  $P_c$ ,  $P_a$  and the base of  $P_b$ ; the disc cross-hatched; b. 'Te Vega' st. 60, S China Sea. Arm br 0.8 mm. Side view of part of an arm from  $IBr_2$  to  $Br_6$  showing  $P_1$  and  $P_2$ . [The scale equals 2 mm.]



larger with 11 or 14 segments and is c. 5.3 mm long. The first two segments bear much smaller dorsal crests and the following ones are finely spinose dorsally and at their flared distal ends.

Two of the specimens show signs of double longitudinal brownish stripes along the arms, zigzagging slightly according to the offset of the apices of the plates. In one  $P_2$  has a marked purple stripe.

One of the specimens from station 18A has a large elongated cyst covered by scale-like alternating platelets on the right side of a  $Br_1$ .

**RANGE.** This material provides an extension of the known range of *E. venustus* into the Indian Ocean, previous records being restricted to the Philippines and Lesser Sunda Islands.

[See also p. 151.]

### Family ZYGOMETRIDAE

#### *Zygometra comata* A. H. Clark

(fig. 6)

*Zygometra comata* A. H. Clark, 1911e : 762; 1918 : 61; Gislén, 1936 : 8, fig. 1; A. H. Clark, 1941 : 110-120, pl. 4, figs 13, 14, pl. 5, figs 15-17.

**MATERIAL.** 'Anton Bruun' cruise 1, st. 37, 13°28'N : 97°19'E (N of Mergui Archipelago, Burma), 64 metres; 4 small broken specimens.

'Anton Bruun' cruise 1, st. 38, 14°07'N : 97°05'E (W of the Moskos Islands, Burma), 69-73 metres; 2 specimens.

**DESCRIPTION.** The two specimens from station 38 have respectively 14 arms, 45 plus c. 10 mm long and 12 (?13) arms c. 45 mm long. Br at 3 + 4 on arms based on a IIBr<sub>4</sub> series is 1.0 mm in both and on arms based on IBr series c. 1.15 (including the lateral flanges in each case). The length from the proximal edge of the IBr to 3 + 4 including a IIBr<sub>4</sub> series is 4.7 and 4.2 mm respectively. The cirri number c. XXII and XVI, with up to 24 or 25 segments, the maximum length 12.1 and 11.0 mm, while the sixth and longest segment has length : median breadth 0.7 : 0.6 mm and the segments from the sixth (sometimes the fifth) have attenuated, sharp, erect dorsal spines. Two of the four IIBr series in the 14-armed specimen are of 2 ossicles, the others are all 4. The division series and basal brachials have distinct,

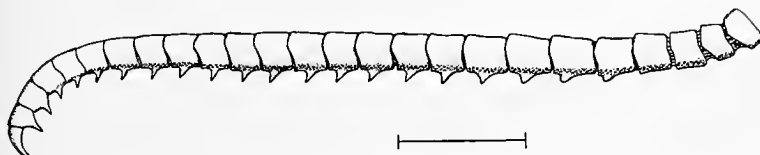


FIG. 6. *Zygometra comata* A. H. Clark. 'Anton Bruun' st. 38. Arm br 1.0 mm (after IIBr<sub>4</sub> series). Mature cirrus. [The scale equals 2 mm.]

continuous, straight-edged lateral flanges. The two specimens have  $P_1$  to  $P_3$  on arms based on IBr series with the following segment numbers and lengths:

$$\begin{array}{l} P_1 \text{ 24, 7.4 mm; } P_2 \text{ 29, 9.2 mm and } P_3 \text{ 15, 4.0 mm} \\ \text{26, 6.8 mm; } \quad \text{25, 7.9 mm and } \quad \text{17, 4.7 mm} \end{array}$$

The second specimen has a  $P_D$  (on IIBr<sub>2</sub>) 25, 7.1 mm followed by  $P_1$  27, 9.2 mm and  $P_2$  25, 7.9 mm, the second pinnule, whatever its designation, being the largest in each case. The basal pinnules have high crests, are angular in cross section and taper to flagellate tips. One specimen has a relatively massive sausage-shaped cyst, probably caused by a myzostome, superimposed on a  $P_1$ , consisting of irregular platelets and with an opening at the dorsal end.

REMARKS. These relatively small specimens have about the minimum number of arms and cirrus segments given by A. H. Clark for *Z. comata*; indeed one of the specimens from station 37 may not have had more than ten arms. Consequently they could run down to *Z. punctata* from the Aru Islands and northern Australia in A. H. Clark's key to the species of *Zygometra* (1941: 82). However, they differ from a specimen of *Z. punctata* of similar arm length from the Great Barrier Reef in the smoother, more rounded ossicles and the more slender cirri with sharper hyaline dorsal spines. In this specimen of *Z. punctata* none of the cirrus segments are appreciably longer than broad.

LECTOTYPE. The naming of this species has pursued a very ramshackle course. *Antedon comata* was a nomen nudum published by von Graff in 1887 when describing myzostome parasites from some crinoids collected in the Mergui Archipelago and given this provisional manuscript name by P. H. Carpenter who abandoned it before his crinoid report was published. In 1911 (e, p. 762) the first valid mention by A. H. Clark of the name *Zygometra comata* was in the form of a footnote to *Z. elegans* pointing out that *Z. fluctuans* (Carpenter) is a synonym of *Z. elegans* (Bell), necessitating another name for the Singapore and Mergui Archipelago specimens of *Zygometra* which he had previously mentioned under one or other of these names. The synonymy given in A. H. Clark's monograph (1941, p. 111) shows that in 1911 there were four sources of material which he considered as belonging to the species, namely:

- (1) the Mergui Archipelago, Anderson collection, referred to *Antedon elegans* Bell by P. H. Carpenter, 1888 and 1889;
- (2) the Philippines, Semper collection, referred to *A. elegans* by Carpenter, 1889;
- (3) the Philippines, collected by the 'Albatross' at stations 5137, 5138 and 5358, referred to *Zygometra elegans* by himself in 1908(b) and to *Z. comata* (as a nomen nudum) in 1911(a); finally
- (4) Singapore, Gad collection, referred to *Z. fluctuans* by himself in 1909 (*Vidensk. Medd.*, actually published in 1910).

In the 1911 footnote A. H. Clark refers to his own description of Singapore material to establish the species *Z. comata* and notes that it also occurs in the Philippine Islands.

There are thus three localities—the Mergui Archipelago, Singapore and the Philippines—for the type-series of the species as defined in article 72(b) of the Code

of Nomenclature, although, if the type-locality is to be narrowed down by selection of a lectotype, material from Singapore is probably to be preferred, following the wording of A. H. Clark's footnote. Also the Mergui specimens have the lowest priority for selection, not having been studied by A. H. Clark himself. Correspondence with Dr Madsen of the Copenhagen museum and Dr Pawson and Miss M. Downey of the U.S. National Museum reveals that in neither institution is there material labelled as type or types of *Zygometra comata*. The specimen from Singapore shown in plate 4 figure 13 of A. H. Clark's monograph (1941) appears to answer the description given in 1910, having about 19 arms. Unfortunately this specimen cannot be traced in either museum. However, the fine specimen from 'Albatross' station 5138 shown in plate 5 figs 15-17 is recognisable in the U.S. National Museum collection, catalogue number 35137. One post-radial series has been detached, so clearly the specimen was particularly examined by A. H. Clark and it also has the virtue of having over 20 arms, thereby showing well the 2, 1, 1, 2 arrangement of arm branching said by him to be characteristic of the species in contrast to *Z. elegans*—a feature less obvious in the specimens from Singapore which evidently tend to have few arms in comparison with those from the Philippine area. Accordingly I propose that this specimen be regarded as the lectotype of *Zygometra comata*.

### Family MARIAMETRIDAE

Mariametridae A. H. Clark, 1911f : 649; 1941 : 391-396.

Except for *Mariametra* itself with its spinose ossicles and the monotypic *Pelometra* (known from only a single specimen) with peculiar glassy keels on the genital pinnules, the taxa included by A. H. Clark in this family are very poorly defined in view of the degree of variation found in most of the characters used by Mr Clark to try and distinguish between them. That he himself had considerable reservations about them is obvious from some of his remarks: for instance (on *Oxymetra*) 'as herein understood (it) includes three closely related species that may eventually prove to be simply more or less distinct forms of the same species'; (on four of the nominal species of *Stephanometra*) 'there is really no hard and fast line of division between these forms'; (on two of the three nominal species of *Liparometra*) these 'are very closely related and may eventually prove to be different forms of the same species, or possibly even identical'; (on the two nominal species of *Lamprometra*) 'It is quite possible that *L. klunzingeri* is simply the western form of *L. palmata*'; (on the nominal species of *Dichrometra*) 'these seven species are all very much alike, and the differences between them are slight'. At the generic level Gislén (1922 : 76) comments 'It seems to me to be rather unfortunate within this family to base the characteristics of genus on the relation between the length of  $P_1$ ,  $P_2$  and  $P_3$ , as has been done in the genera *Liparometra*, *Lamprometra* and *Dichrometra*, which are surely very closely related to each other'. I fully agree with Gislén and think that *Liparometra* and *Lamprometra* will prove to be better referred to the synonymy of *Dichrometra* with *Stephanometra* probably included as well since it seems to me to

intergrade with *Lamprometra palmata*. I have often found difficulty in deciding whether to refer specimens to *S. indica indica* (sensu A. H. Clark, 1941) or to *Lamprometra*. A. H. Clark's dogmatic diagnosis of *Stephanometra* (1941 : 407) with 'one or more of the oral pinnules enlarged, greatly stiffened, sharp pointed, and spinelike' clearly needs qualification after reading in his key to *S. indica indica* (p. 409) that  $P_2$  is 'somewhat less enlarged (than in *S. indica protectus*) and stiffened, usually more or less strongly recurved (i.e. bending towards the arm tip), distally becoming very slender and delicate, though not flagellate, composed of 15-20 segments of which the fourth and fifth are not noticeably different from the rest'. For comparison his description of *Lamprometra palmata palmata* (p. 481) reads ' $P_2$  is the longest and stoutest pinnule on the arm and is usually much longer and stouter than either  $P_1$  or  $P_3$  . . . It is more or less strongly stiffened, though tapering to a delicate and flagellate tip. It is usually more or less, and often strongly, recurved towards the arm tip, but it may be straight and almost spinelike . . . It is composed of 16-40 (most commonly 25-30) segments'. Apart from the segment number, the difference seems to depend on the interpretation of 'flagellate', for which figure 10 g and e provide a comparison. The first is of an external  $P_2$  of the specimen of *S. indica* from Rodriguez (which is in fact the holotype), described by A. H. Clark (1913 : 29) as slender distally but not flagellate; while the second is from the specimen from Muhlos, Maldives, described (also under the name *S. indica* at the same time) as 'enlarged and stiff but distally flagellate'. During Jeffery Bell's lifetime it was not politic to relabel specimens he had otherwise identified and, on a subsequent visit, A. H. Clark re-named and labelled this same Muhlos specimen as *Lamprometra palmata*, recording it as such in 1929 (p. 641) without reference to his earlier treatment of it. In his monograph the record appears twice over; on p. 453 it is referred to *Stephanometra indica protectus* and on p. 502 to *Lamprometra palmata palmata*.

If the shape of  $P_2$  cannot always be relied upon to distinguish between *Stephanometra* and *Lamprometra* then what about the shape of the division series? A. H. Clark (1941 : 407) specifies that those of *Stephanometra* are 'well separated, and the component ossicles bear rounded ventro-lateral extensions' as opposed to *Lamprometra* (p. 473) where they are 'usually in very close lateral contact with more or less broadly and sharply flattened sides, more rarely just in contact with the sides slightly or not at all flattened'. I would say that in *Lamprometra* too the division series are not always very close together and the sides may have ventro-lateral flanges, though these are usually blunter than in *Stephanometra* and normally have a continuous straight edge, whereas in *Stephanometra* the flange of each ossicle tends to be rounded off at the ends so as to give a scalloped outline when viewed dorsally (compare figures 9f and 10f). When the disc has been lost in preservation, the prominence of the ventro-lateral flanges may be emphasized.

Unfortunately there are specimens such as three taken by the 'Te Vega' at East St John's, Singapore (fig. 10b), in which the division series are slightly scalloped at the edges but the very large  $P_2$  has more than 25 segments and its tip is slender and could be described as flagellate. One of the three from Singapore has less disparity between  $P_2$  and the other basal pinnules than in the two other specimens

and this inclines me to identify all three as *Lamprometra palmata*. [However, it should be noted that a fourth specimen from St John's, though taken by a different collector (J. Kelts) and separately preserved, is undoubtedly referable to *Stephanometra indica protecta* (sensu A. H. Clark) having markedly scalloped, though blunt, flanges on the division series and  $P_2$  perfectly straight, stiff throughout and with only twelve segments.] Four rather similar specimens from the sudanese Red Sea in the British Museum collections (fig. 9e and f) add a further problem, however; they have  $P_2$  relatively huge, especially on arms based on IBr series, inclined inwards over the disc and stiff for the proximal two-thirds but slender and slightly flexible distally and again with more than 25 (26-32) segments; also the division series are slightly scalloped, their ventro-lateral flanges being fairly well developed but the edges of these not perfectly straight. In one of the four,  $P_3$  is almost as stout and as long as  $P_2$  but in the rest it is markedly smaller. These specimens are also remarkable for having distinct keels on the proximal pinnules along the edge facing the arm tip, as in *Lamprometra palmata gyges*, as opposed to *L. klunzingeri*, according to A. H. Clark. Despite this, the relatively large size of  $P_2$  and the form of the division series, it seems impossible to me to identify these specimens as anything other than *L. klunzingeri*, if that is to be recognized as distinct from *L. palmata*, the fauna of the Red Sea being so restricted. In A. H. Clark's key, *L. klunzingeri* is supposedly distinguished from *L. palmata palmata* by having  $P_2$  neither markedly stouter than the other proximal pinnules, nor with the proximal segments of the early pinnules more than very slightly carinate. This single sample simultaneously negates the validity of both these distinctions.

Unfortunately the British Museum collections have only a poor representation of the species of *Liparometra* and *Dichrometra*, which should certainly be included in any detailed revision of the relationships within the family Mariametridae, so it seems better to defer such a revision to another occasion.

A new species of *Dichrometra* is described below, being necessitated by the unusual arrangement of the division series, not by any difference in the proximal pinnules.

### *Dichrometra afra* A. H. Clark

(fig. 7)

*Dichrometra flagellata* var. *afra* A. H. Clark, 1912g : 23-24.

*Dichrometra afra* A. H. Clark, 1913 : 31; 1941 : 558-562, pl. 58, figs 269, 270.

*Liparometra multicirra* H. L. Clark, 1923 : 232-233, pl. 8, fig. 2.

*Liparometra* sp. A. M. Clark in Humes & Ho, 1970 : 7, 11.

**MATERIAL.** 'Anton Bruun' cruise 8, st. 400C, 20°30'S : 35°43'E (off Beira, Mozambique), 62 metres; 2 specimens.

Prof. A. G. Humes' no. 1082, off Pte Lokobe, Nosy Bé, Madagascar, 15 metres; 1 specimen. B.M. reg. no. 1969.5.13.114.

Prof. Humes' no. 125I, c. 13°29'S : 48°10'E (near Nosy Bé), 23-27 metres, M/V 'Vauban'; 1 specimen. 1969.5.13.115.

Prof. Humes' no. 1336, W. of Ambatoloaka, Nosy Bé, 35 metres; 1 specimen. 1969.5.13.116.

DESCRIPTION. Some numerical details of the specimens are given in Table 3.

The diameter of the centrodorsal is 3.8 mm in the smaller specimen from st. 400C and 4.5 mm in the specimen from Ambatoloaka. The dorsal spines on the eirri begin as a raised keel, sometimes interrupted slightly in the middle of its length giving the dorsal profile a double peak, or else the projection is 'roman-nosed', the high bridge diminishing on the distal segments.

The first IIIBr, or IVBr series when present, to appear are external in position, the corresponding internal (or adradial) series only appearing subsequently. All the division series are of two ossicles and have slightly rugose lateral projections which form a continuous straight-edged lateral flange each side of the post-radial series. The dorsal surface of the division series and arm bases is smooth and there are low rounded synarthrial tubercles just distinguishable.

The relative proportions of the proximal pinnules are very variable, possibly to some extent eorrelated with the maturity of the individual arms.  $P_3$  is either similar to  $P_2$  or slightly longer and stouter, sometimes distinctly so, or conversely it may be shorter. The first six or seven segments are not appreciably longer than broad but the rest are somewhat elongated though probably all not more than twice as long as broad. Specimen no. 1969.5.13.114 has only immature external arms based on IIIBr series with intact proximal pinnules and here  $P_3$  is distinctly smaller than  $P_2$ ; this is also true on an external arm based on a IIBr series.

REMARKS. Owing to the similarity between  $P_2$  and  $P_3$ , which contradicts A. H. Clark's diagnosis of *Dichrometra*, I made the same mistake with this species as H. L. Clark (1923) in my preliminary determination of Professor Humes' specimens

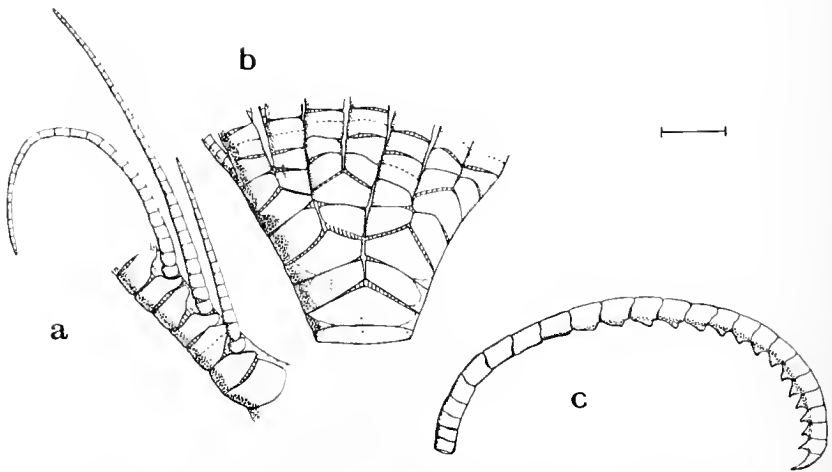


FIG. 7. *Dichrometra afra* A. H. Clark. B.M. reg. no. 1969.5.13.116, Nosy Bé, Madagascar. Arm br 1.3 mm (after IIIBr series). a. side view of first eight brachials showing  $P_1$  to  $P_3$  of an external arm; b. dorsal view of one post-radial series; c. mature cirrus. [The scale equals 2 mm.]

as referable to *Liparometra*. Further study indicates that his two specimens which I formerly labelled '*Dichrometra* sp. ?*afra*' should be referred to a distinct species, described below, leaving the present specimens instead attributable to *D. afra*. This is in spite of A. H. Clark's statement in his key (1941 : 538, d<sup>1</sup>) that P<sub>2</sub> and P<sub>3</sub> are 'composed of segments most of which are not longer than broad'. Although these segments of these pinnules are relatively short, this is an exaggeration, at least for the specimens I have seen, those from Madagascar approximating to the type-locality. As for the relative lengths of these pinnules, in the holotype of *D. afra* P<sub>3</sub> is only 5% longer than P<sub>2</sub> and in the holotype of *Liparometra multicirra*, which A. H. Clark reckons is a synonym of *D. afra*, P<sub>3</sub> is similar to or smaller than P<sub>2</sub>. P<sub>3</sub> is also smaller in the two specimens from 'Anton Bruun' st. 400C which, like the holotype of *L. multicirra* (from off northern Natal) came from the vicinity of the African mainland rather than from Madagascar. It is interesting that all three of these show cirri of relatively large size and more segments than the specimens from Madagascar but much more material is needed to clarify the range of variation in these characters.

In comparison with the specimens from Madagascar which I have called *Lamprometra klunzingeri*, the main differences are that *D. afra* has better developed dorsal spines on the distal cirrus segments and P<sub>2</sub> and P<sub>3</sub> not markedly dissimilar whereas in *L. klunzingeri* P<sub>3</sub> is much smaller. It seems to me that these characters are hardly of generic weight, especially in view of the considerable variation in the relative proportions of the proximal pinnules throughout this family. A detailed assessment of the affinity of the type-species of *Dichrometra*, *Lamprometra* and *Liparometra* is needed on the basis of large samples. Certainly if *Dichrometra afra* is to be retained in that genus then the species of *Liparometra* should also be referred to *Dichrometra*, which is the oldest of the three generic names.

COMMENSALS. The copepods *Pseudanthessius major* and *minor* were found associated with the specimens from Madagascar, as also with the following species of *Dichrometra* and *Lamprometra klunzingeri* as well as the himerometrin *Heterometra africana*.

***Dichrometra austini*\* sp. nov.**

(fig. 8)

*Dichrometra* sp. ?*afra* A. M. Clark in Humes & Ho, 1970 : 7, 11, 13. [Non *D. afra* A. H. Clark.]

MATERIAL. Prof. A. G. Humes's no. 802, Ambariobé, near Nosy Bé, Madagascar, 6-8 metres; 1 fragmented specimen. B.M. reg. no. 1969.5.13.112.

Prof. Humes's no. 876, Ambarioto, near Nosy Bé, 2 metres; the holotype. B.M. 1969.5.13.113.

DIAGNOSIS. A species of *Dichrometra* in which the IIIBr series develop first internally on the post-radial series, not externally, the ossicles of the division series have individual ventro-lateral rounded processes not forming a continuous lateral

\*Named after Austin H. Clark.

flange and the distal cirrus segments are simply carinate dorsally, without spines. In comparison with the sympatric *D. afra* also  $P_3$  is notably stouter relative to  $P_2$ .

DESCRIPTION. Some numerical details of the holotype and paratype are given in Table 3.

The centrodorsal is 5.3 mm in diameter and c. 1.8 mm high with the slightly concave dorsal pole 2.6–2.9 mm in diameter. The irregularly-placed cirri are two or three deep around the sides. The seventh cirrus segment is approximately the longest, measuring 1.2 mm in length while length : median breadth is 1.2 : 1. After about the tenth segment a low median dorsal keel begins to develop, at first straight but becoming convex in profile on the shorter distal segments. The opposing spine and terminal claw are relatively small in comparison with those of *D. afra*.

The length from the proximal edge of the  $IBr_1$  to the syzygy at  $Br_{3+4}$ , including I, II and  $III Br$  division series, is 8.4 mm. All the division series are of two ossicles. Synarthrial tubercles are barely appreciable but laterally the axillaries have abruptly projecting short rounded flanges externally and the  $II Br_1$  and  $Br_1$  have similar ventro-lateral projections for most of their lengths but rounded off at the ends so that the resultant flange is discontinuous. Internally the pairs of ossicles following each axillary are contiguous for two-thirds of their lengths and then diverge abruptly so that the arms are separated from each other basally, unlike those of *D. afra* which are closely contiguous. All five of the  $III Br$  series present are internal in

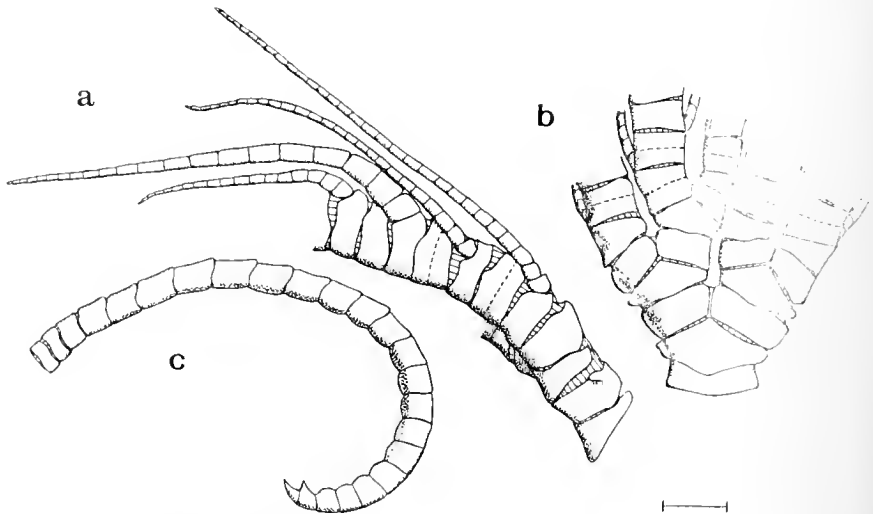


FIG. 8. *Dichrometra austini* sp. nov. Holotype. B.M. reg. no. 1969.5.13.113, Nosy Bé, Madagascar. Arm 1.7 mm (after  $III Br$  series). a. side view of proximal part of a post-radial series from  $IBr_2$  to  $Br_{10}$  (including a  $II Br$  series) showing  $P_1$  to  $P_4$ ; b. dorsal view of proximal part of one post-radial series; c. mature cirrus. [The scale equals 2 mm.]



Numerical values except where marked

Specimen	P <sub>3</sub>		P <sub>4</sub>	
	Segs.	Length	Segs.	Length
<i>Dichrometra afra</i>				
Holotype	24	10	—	—
1969.5.13.115	34	17.4	20	7.6
	—	—	21	8.7
1969.5.13.116	29	11.3	17	11.0
1969.5.13.114	—	—	—	—
'Liparometra multicir	= or < P <sub>2</sub>		= P <sub>1</sub>	
'A.B.' st. 400C	c. 20*	c. 11	smaller	
'A.B.' st. 400C	? = P <sub>1</sub> +		—	—
<i>Dichrometra austini</i>				
Holotype	21†	13.7	16†	7.4
Paratype	c. 17	c. 14	—	—
	c. 20†	c. 13.5	15†	5.5
<i>Dichrometra ciliata</i>				
Syntypes	31	18.5	12	11.5
'A.B.' st. 22A	22	12.1	19	8.2
<i>Lamprometra klunzingeri</i>				
1969.5.13.83	15	4.5	14	3.4
	—	—	14	3.2
1969.5.13.82	14	3.4	11	2.9

\* Pinnules from arm

† Pinnules from arm

\*\* Quadriradiate specimen

TABLE 3

Numerical data from some specimens of *Dichrometra* and *Lamprometra*, that from the arms taken from arms based on III Br series except where marked

Specimen	Arms		Br at 3 + 4	Cirri					Pinnules							
	No.	Length		No.	Segs.	Length	1st seg. with 'spine'	l : br longest seg.	P <sub>1</sub>		P <sub>2</sub>		P <sub>3</sub>		P <sub>4</sub>	
								Segs.	Length	Segs.	Length	Segs.	Length	Segs.	Length	
<i>Dichrometra afra</i>																
Holotype	29	c. 85	—	XX	29	18	9, 10	l > br	25	8	25	9.5	24	10	—	—
1969.5.13.115	c. 27	100	1.5	c. XXXV	28	23	9	1.5 : 1	—	—	34	15.8	34	17.4	20	7.6
									21	7.4	26	9.7	—	—	21	8.7
1969.5.13.116	c. 36	c. 85	1.3	XLV	25	18	9	1.5	18	6.1	33	10.5	29	11.3	17	11.0
1969.5.13.114	c. 25-30	c. 55	0.9	c. XVII	24	12.5	9, 10	1.5	—	—	—	—	—	—	—	—
'Liparometra multicirra'	c. 50	c. 85	—	XLIII	36	—	10, 11	l = br(+)	21	10	26	13	= or < P <sub>2</sub>		= P <sub>1</sub>	
'A.B.' st. 400C	c. 45-50	c. 70	1.2	c. XL	42	32	13	1.05	21*	9.0	24*	14.2	c. 20*	c. 11	smaller	
'A.B.' st. 400C	41	c. 45	1.1	XXXVI	31	22	11	1.3	15	5.8	19	9.5	? = P <sub>1</sub> +		—	—
<i>Dichrometra austini</i>																
Holotype	25	130	1.7	c. XL	25	23	—	1.2	30†	13.7	26†	12.1	21†	13.7	16†	7.4
Paratype	22+	c. 100	1.5	XLIV	26	24	—	1.4	24	10.8	c. 20	c. 14.5	c. 17	c. 14	—	—
									c. 24†	—	23†	12.6	c. 20†	c. 13.5	15†	5.5
<i>Dichrometra ciliata</i>																
Syntypes	34-42	110-120	—	XXVII	29-35	30	10-13	—	29	11.5	34	17	31	18.5	12	11.5
'A.B.' st. 22A	c. 40	c. 110	1.4	c. XXX	39	c. 35	11, 12	1.3	25	8.2	27	10.3	22	12.1	19	8.2
<i>Lamprometra hlunzingeri</i>																
1969.5.13.83	29	c. 70	1.2	c. XXXV	25	14	10	1.4	27	6.8	28	11.0	15	4.5	14	3.4
									25	6.8	24	9.0	—	—	14	3.2
1969.5.13.82	31**	c. 60	1.1	XXVII	23	13.5	10	1.2	22	6.8	25	9.5	14	3.4	11	2.9

\* Pinnules from arm based on IVBr series.

† Pinnules from arm based on IIBr series.

\*\* Quadriradiate specimen with only four IBr series.

position, two of them occurring on the same post-radial series, which is symmetrical.

The first two pinnules are slender with basal breadth c. 0.7 mm, or  $P_2$  may be slightly broader;  $P_3$  is markedly stouter, the first segment c. 1.0 mm broad, but the total length is not appreciably greater than that of the previous pinnules, in fact  $P_2$  may be the longest. However,  $P_4$  is much shorter. On the inner side,  $P_b$  is nearly always markedly stouter than  $P_c$ , while on internal arms  $P_2$  is more often than not the stoutest.

The disc has been lost.

The whole animal is notably smooth in all its ossicles.

The paratype consists of a centrodorsal with two incomplete post-radial division series, one of which has both internal and external IIIBr series one side; the arms are all detached from their bases. A separate post-radial series with four arms attached has two internal IIIBr series but none external. The centrodorsal is 4.7 mm in diameter and the dorsal pole about 2.4 mm. There were XLIV cirri but no intact ones remain attached. Five loose cirri have 24 segments and another has 26; the development of keels on the distal segments is just like that in the holotype.

$P_1$  on the single external arm on the detached post-radial series has 18+ segments; it is curled round between two arms but is probably only about two-thirds the length of  $P_2$  which is much stouter with 23 segments, very attenuated distally and with basal breadth 0.85 mm compared with  $P_3$ , the basal breadth of which is 0.70 mm. The segment numbers and lengths of these pinnules are the second series given in Table 3. One other detached arm which may also have been external in position (it has a division series still attached) has  $P_3$  distinctly stouter basally than  $P_2$  while three other loose arms have  $P_2$  and  $P_3$  similar in size. However, eleven more loose arms have  $P_2$  markedly the largest pinnule; in one,  $P_2$  with c. 20 segments is c. 15.5 mm long with basal breadth 0.95 mm, corresponding with a  $P_3$  having only 13 segments, measuring 5.8 mm, with basal breadth 0.70 mm. Possibly all such arms were internal in position.

The colour of the paratype in life is given as brownish with alternating dark reddish brown and cream bands on the arms.

**AFFINITIES.** The development of IIIBr series internally rather than externally in both specimens sets this species aside from all the other members of the Mariametridae and possibly could justify a generic separation, though A. H. Clark (1941 : 439) mentions a specimen of *Stephanometra indica*, also from Madagascar, with internal not external IIIBr series. In Gislén's analysis of the arm ramification of the recent comatulids (1934 : 25) *D. austini* would fall into section 41, characteristic only of the thalassometrid *Stylometra spinifera* and some species of the charitometrid genus *Crinometra*, whereas most of the mariametrids (but also two thalassometrids and some representatives of other families) fall into sections 42 and 43 with IIIBr's external or both external and internal.

In comparison with *Dichrometra afra* and *Lamprometra klunzingeri*, *D. austini* may also differ in the simply carinate distal cirrus segments without any sort of spines and the individual rounded ventro-lateral processes on the division series coupled with the separated arm bases. In fact the processes on the division series

resemble those of *Stephanometra* but that genus is distinguished by the erect, stiffened form of  $P_2$  and sometimes also  $P_3$ .

COMMENSALS. The copepods *Pseudanthessius major* and *minor* were both associated with this species as well as with *D. afra*, *Lamprometra klunzingeri* and *Heterometra africana*.

### *Dichrometra ciliata* A. H. Clark

*Dichrometra ciliata* A. H. Clark, 1912a : 319-320; 1932 : 558; 1941 : 565-566, pl. 57, figs 263, 264, pl. 58, figs 265-268.

MATERIAL. 'Anton Bruun' cruise 1, st. 18A,  $07^{\circ}34'N$  :  $98^{\circ}00'E$  (between Malaya and the Nicobar Islands), 77 metres; 1 small specimen.

'Anton Bruun' cruise 1, st. 22A,  $10^{\circ}37'N$  :  $97^{\circ}34'E$  (SW of the Mergui Archipelago, Burma), 75-80 metres; 1 specimen.

'Anton Bruun' cruise 1, st. 36A,  $13^{\circ}00'N$  :  $97^{\circ}41'E$  (off Cape Tavoy, S Burma), 68 metres; 1 small specimen.

REMARKS. Details of the specimen from station 22A are given in Table 3 facing p. 100. The two smaller specimens both have an arm length of c. 35 mm, which probably accounts for the fact that  $P_3$  is similar to or, more often, smaller than  $P_2$ . There are up to 21 cirrus segments, with fairly large nose-like dorsal spines from about the eighth one. The large specimen has the pinnules very variable; in series other than the one included in the table,  $P_1$  has 23, 26 or 27 segments, in the last case the length being 0.5 mm and a  $P_4$  has 24 segments and is 11.8 mm long.

### *Lamprometra klunzingeri* (Hartlaub)

(fig. 9)

*Antedon klunzingeri* Hartlaub, 1890 : 175; 1891 : 46-47, pl. 2, figs 22, 25.

*Lamprometra klunzingeri*: A. H. Clark, 1909b : 144; 1929 : 641; 1937 : 89; 1941 : 527-536, pl. 55, fig. 256; Tortonese, 1953 : 26-27, pl. 1, fig. 1; A. M. Clark, 1967a : 28-29; A. M. Clark in Humes & Ho, 1970 : 6, 11.

MATERIAL. 'Anton Bruun' cruise 8, st. 412D (RU 180),  $12^{\circ}46'S$  :  $47^{\circ}45'E$  (NW of Madagascar), 44 metres; 1 specimen, poorly preserved.

Prof. A. G. Humes's no. 690, Pte Ambarionaomby, Nosy Komba, near Nosy Bé, Madagascar, 1 metre; 1 specimen. B.M. reg. no. 1969.5.13.82.

Prof. Humes's no. 1372, opposite Antsiabe, Nosy Komba, 13 metres; 1 specimen. 1969.5.13.83.

DESCRIPTION. Humes's no. 690 is unusual in being quadriradiate, each of three rays having as many as eight arms, including one external IVBr series, while the fourth has seven. All three specimens are rather slender and the arms and division series are not closely flattened against each other basally, though many other specimens of *Lamprometra* do also show this condition, contrary to A. H. Clark's diagnosis. The lateral spacing is of course particularly noticeable in the quadriradiate

specimen, though the division series fan out sharply to take up the space. In comparison with the other *Mariametrinae* from Madagascar now under study, the dorsal spines of the distal cirrus segments are low and blunt, smaller than those of *Dichrometra afra* but more asymmetrical in profile than the low keels of *D. austini*. However, the cirri of *Lamprometra palmata* are very variable and this may well be true also in *L. klunzingeri*.

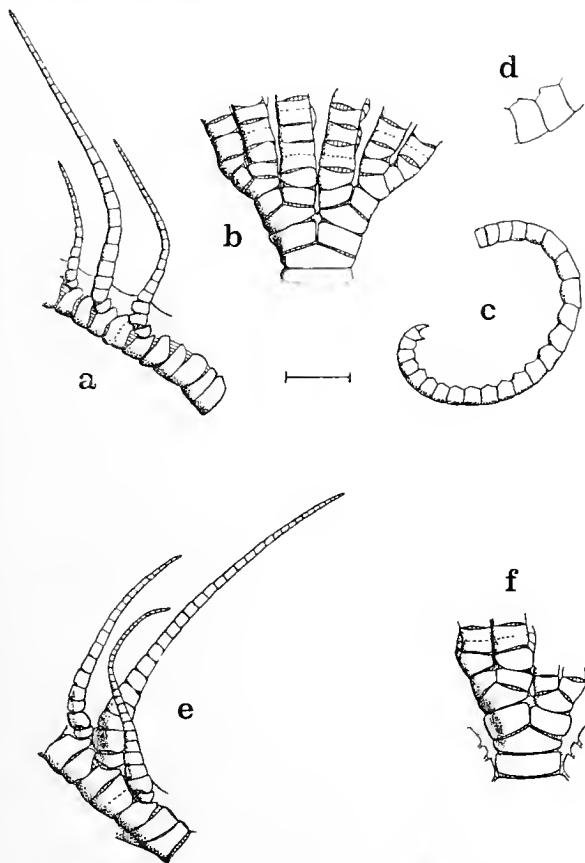


FIG. 9. *Lamprometra klunzingeri* (Hartlaub). a-d. B.M. reg. no. 1969.5.13.83, Nosy Komba, Madagascar. Arm br 1.0 mm. a. side view of proximal part of one post-radial series from IIBr<sub>1</sub> to Br<sub>7</sub> showing P<sub>1</sub> to P<sub>3</sub>; b. dorsal view of proximal part of one post-radial series; c. mature cirrus with d. segments 19 and 20 enlarged; e and f. B.M. reg. no. 1951.5.7.17 (pt.), Sudanese Red Sea. Arm br 1.15 mm (after IBr series) or 1.05 mm (after IIBr series). (Specimen with P<sub>2</sub> especially large.) e. side view of proximal part of one post-radial series from IBr<sub>2</sub> to Br<sub>7</sub> showing P<sub>1</sub> to P<sub>3</sub>; f. dorsal view of proximal part of one post-radial series, the IIBr<sub>2</sub> and following ossicles on the right regenerating. [The scale equals 2 mm for a-c, e and f but 1 mm for d.]

AFFINITIES. As noted in the discussion of the family Mariametridae, *Lamprometra palmata* and *klunzingeri* are poorly distinguished from one another. A. H. Clark (1941) gives a key to no less than sixteen named forms of *L. palmata* (including the subspecies *gyges*), most of them supposedly distinguished only by rather small variations in the shape and size of the proximal pinnules. Also, apart from the geographical isolation of *L. klunzingeri* around the Arabian peninsula, he could only distinguish it from *L. palmata* by  $P_2$  being neither keeled basally nor markedly stouter than  $P_1$  and  $P_3$ , neither of which characters is completely reliable, as already noted. In an analysis of the geographical distribution of Indo-West Pacific echinoderms from shallow water (down to c. 20 m), of nearly 1000 species of the other four major groups, more than 5% extend throughout the area, from the Red Sea and SW Indian Ocean to the South Pacific and Hawaiian Islands but not a single one of the 138 nominal species of crinoids represented has such a wide distribution. I think this is a false picture and may be attributed to undue weighting of certain characters by A. H. Clark resulting in fragmentation of a number of species, including *Lamprometra palmata*, to the synonymy of which *L. klunzingeri* should probably be referred.

RANGE. These records extend the known range of *Lamprometra* to the southwest Indian Ocean, although *L. klunzingeri* was provisionally recorded from Zanzibar by A. H. Clark (1929) on the basis of a small specimen in the British Museum collections. This specimen has  $2I + 2$  or 3 arms c. 40 mm long and its cirri agree with those of *L. klunzingeri*. Most of the pinnules are broken but  $P_3$  appears to have been distinctly smaller than  $P_2$  so that it agrees best with this species. The same may well be true of the broken specimen from Dar-es-Salaam in the Berlin Museum recorded by A. H. Clark in 1912 without realizing that the locality was outside the Red Sea. The Zanzibar specimen has an unusual anomaly in that one  $P_2$  is triple, three pinnules arising from the same brachial.

### *Lamprometra palmata palmata* (J. Müller)

(fig. 10a-e)

*Alecto palmata* J. Müller, 1841 : 185.

*Lamprometra palmata* : A. H. Clark, 1929 : 641 ; 1932 : 557-558, pl. 19, fig. 9; Gislén, 1940a : 10; A. H. Clark, 1941 : 474-517, pl. 53, figs 243-246, pl. 54, figs 248-252, pl. 55, fig. 257.

MATERIAL. 'Anton Bruun' cruise 1, st. 18A,  $07^{\circ}34'N$  :  $98^{\circ}00'E$  (between Malaya and the Nicobar Islands), 77 metres; 1 specimen.

'Anton Bruun' cruise 1, st. 47B,  $19^{\circ}50'N$  :  $92^{\circ}55'E$  (off Akyab, Burma), 22-30 metres; 6 specimens.

'Te Vega' cruise 2,  $01^{\circ}14'N$  :  $103^{\circ}51'E$  (East St John's, Singapore), 'sublittoral'; 3 specimens.

The specimen figured and the other two from Singapore have the division series widely separated laterally and not much flattened. Also the very large  $P_2$  is usually

inclined proximally over the disc and stiffened in the basal part, though flagellate distally and with about 30 segments, affiliating them with *Lamprometra* rather than *Stephanometra* with its straight tapering  $P_2$ .

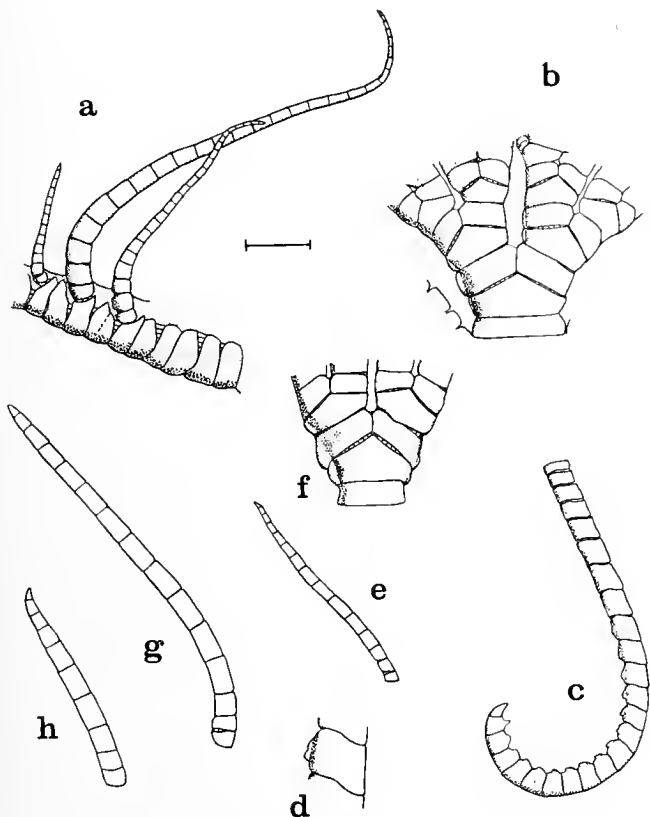


FIG. 10. a-e. *Lamprometra palmata palmata* (J. Müller). a-d. 'Te Vega' cruise 2, E St John's, Singapore. Arm br 1.4 mm (after III Br series). a. side view of proximal part of one post-radial series from IIBr<sub>1</sub> to Br<sub>7</sub> (including a III Br series) showing P<sub>1</sub> to P<sub>3</sub>; b. dorsal view of proximal part of one post-radial series; c. mature cirrus with d. segment 13 enlarged; e. B.M. reg. no. 1902.3.13.46, Muhlos, Maldive Is. Arm br 1.15 mm (after I Br series). P<sub>2</sub> from arm based on I Br series; f-h. *Stephanometra indica* (Smith); f. 'Te Vega' cruise 2, E St John's, Singapore. Arm br 1.25 mm (after I Br series), dorsal view of proximal part of one post-radial series; g. holotype, B.M. reg. no. 76.5.5.24, Rodriguez. Arm br 1.4 mm (after either I Br or III Br series), external P<sub>2</sub> from arm based on III Br series. (Internal P<sub>2</sub>s may be slightly larger with up to 17 segments, as described by Smith.) h. 'Anton Bruun' st. 412D, NW Madagascar. Arm br 1.25 mm (after I Br series), P<sub>2</sub> from arm based on I Br series. [The scale equals 2 mm for a-c and e-h but 1 mm for d.]

*Mariametra vicaria* (Bell)

*Antedon vicaria* Bell, 1894 : 400.

*Mariametra vicaria*: A. H. Clark, 1912a : 142-143; 1941 : 573-579.

MATERIAL. 'Anton Bruun' cruise 1, st. 18A, 07°34'N : 98°00'E (between Malaya and the Nicobar Islands), 77 metres; 1 specimen.

'Anton Bruun' cruise 1, st. 22A, 10°37'N : 97°34'E (SW of the Mergui Archipelago, Burma), 75-80 metres; 14 specimens.

DESCRIPTION. Numerical details of seven specimens are given in Table 4. The maximum arm length and number of cirrus segments exceed the 65 and 36 given by A. H. Clark.

The centrodorsal is low but convex, though the dorsal pole is more or less flat. I think the shape of the whole ossicle is better described as flattened hemispherical rather than discoidal. The longest cirrus segments, about the seventh, have length : median breadth 1.35-1.65 : 1 and are distinctly constricted medially and flared distally. Dorsal spines develop from about the thirteenth segment; those on the short distal segments are sharp.

IIIBr series are usually, but not exclusively, external. The ossicles of the division series and brachials are all abruptly flared with spinose distal edges, even at the syzygies; also the purple mid-line along each arm is raised above the rest of the surface, whereas in the holotype the profile is relatively smoother and the mid-line flush, though other specimens described by A. H. Clark also have everted, more or less spinose or rugose, ossicles. The division series are wall-sided and their lateral parts are particularly spinose but this lessens dorsally. A rugose or spinose texture extends on to the centrodorsal around the cirrus sockets.

The pinnules are rather variable in relative proportions, as usual in this family. P<sub>1</sub> may have as many as 20 segments.

TABLE 4

Numerical data from specimens of *Mariametra vicaria*, the arm breadth taken from arms based on IIBr series and the pinnule data from similar arms except where marked \*, which measurements are from arms based on IIIBrs

Arms			Cirri			Pinnules					
No.	Length	Br at	No.	Segs.	Length	P <sub>1</sub>		P <sub>2</sub>		P <sub>3</sub>	
		3 + 4				Segs.	L.	Segs.	L.	Segs.	L.
26	c. 60	1.0	XXIV	41	21	18*	5.8	23*	7.6	c. 23*	11.6+
c. 28	c. 55	1.1	XXV	40	20	16	5.0	16+	7.0+	21	11.8
21	c. 60	1.2	XX	39	21	18	4.5	19	8.2	21	10.5
27	c. 65	1.1	XXII	43	22	17	5.5	16	6.8	17	10.0
25	—	1.2	XIX	43	22	—	—	—	—	—	—
c. 26	70	1.2	XXVI	42	22	17	5.8	18	8.2	19	10.5
23	80-90	1.2	XX	44	23	13*	3.2	13*	3.7	c. 22*	13.7



*Stephanometra indica* (Smith)

(fig. 10f-h)

*Comatula indica* Smith, 1876 : 406; 1879 : 564, pl. 51, figs 3, 3b [not 3a].*Stephanometra indica*: A. H. Clark, 1911b : 26; 1913 : 29; 1937 : 88-89; A. M. Clark in Humes & Ho, 1970 : 6, 12.*Stephanometra indica indica*: A. H. Clark, 1941 : 436-443, pl. 51, figs 233, 234.*Stephanometra indica protectus*: A. H. Clark, 1941 : 443-459, pl. 49, fig. 222, pl. 50, figs 225-230, pl. 51, figs 231, 232.

MATERIAL. 'Anton Bruun' cruise 8, st. 412D, 12°46'S : 47°45'E (NW of Madagascar), 44 metres; 1 specimen.

'Anton Bruun' cruise 9, st. RU 296, 12°30'S : 45°16'E (inner side of Bandeli Reef, Mayolta Islands, Comoro Islands), c. 1 metre; arms detached.

'Te Vega' cruise 2, 1°14'N : 103°51'E (E St John's, Singapore), 'sublittoral', rock and coral; 1 specimen.

'Te Vega' st. FZ 64-20, 06°55'28"N : 73°11'55"E (N end Filadu Island, Tiladummati Atoll, Maldives Islands), 0-1 metre; 1 specimen.

Prof. A. G. Humes's no. 932, E of Pte Ambarionaomby, Nosy Komba, near Nosy Bé, Madagascar, 6 metres; 1 specimen. B.M. reg. no. 1969.5.13.18.

Prof. Humes's no. 1139, Antsiabe, S shore of Nosy Komba, 2 metres; 1 specimen. 1969.5.13.19.

Prof. Humes's no. 1303, pass between Nosy Komba and Nosy Bé, 17 metres, on sponge; 1 specimen. 1969.5.13.111.

Prof. Humes's no. 1371, opposite Antsiabe, 13 metres; 1 specimen. 1969.5.13.110.

Dr J. D. Taylor, S of East Channel, Aldabra Island; 1 specimen. 1969.5.1.124.

Mr W. Humphreys, off Settlement, Aldabra, night; 1 specimen. 1971.3.2.2.

DESCRIPTION. The specimen from 'Anton Bruun' station 412D has  $P_2$  particularly stout (fig. 10h) with only 10 segments of which the fourth, fifth and sixth are especially large and the last four segments taper rather abruptly in the only intact external  $P_2$  (which is slightly bent at the penultimate segment in preservation but was probably quite straight in life). This form of  $P_2$  is very like that supposed to be characteristic of *S. indica protectus* (Lütken in P. H. Carpenter), according to A. H. Clark (1941 : 409), which subspecies ranges westwards only to the Maldives Islands. In the holotype of *S. indica* from Rodriguez, an intact external  $P_2$  (fig. 10g) with 15 segments is rather more elongated but still quite stout and with the last three segments tapering fairly abruptly and hardly 'slender and delicate' as given in A. H. Clark's key to *S. indica indica* (as opposed to *protectus*). On account of these specimens I am inclined to doubt whether it is worthwhile retaining the subspecies *protectus* (or *protecta* if its gender is matched with that of *Stephanometra*), which in any case was very ill-founded nomenclatorially. It dates from a quote by P. H. Carpenter (1879 : 19) of a passage from an MS of Lütken's noting that the oral pinnules in *Antedon* are 'only slightly differentiated from the others, or are transformed into strong rigid spines, forming a protective covering over the disc [*A. protectus*, mihi]'. This statement might equally well apply to a species such as *Himerometra martensi* and is completely inadequate on its own to identify the

species concerned. Also subsequent examinations of specimens from Tonga distributed by the Godeffroy Museum and the basis of Lütken's *Antedon protectus*, have shown that some of them at least, like the one in the British Museum collections, are referable to *Lamprometra palmata* and not to *Stephanometra* at all. However, in 1881 (p. 192) P. H. Carpenter noted that his new species *Antedon* (now *Stephanometra*) *spicata* 'is closely allied to the Fijian *Antedon protecta* Lütken MS which has nearly 50 cirri, smoother arm joints, and a relatively smaller pinnule on the fifth brachial', and this does serve to narrow down the identity of the species, though the quote of 1879 may be considered as supplying sufficient indication to establish the name from that date. If the Malagasy and some other western Indian Ocean specimens can be referred to *S. indica protecta* then the geographical range of that subspecies becomes co-extensive with the range of *S. indica indica* and I think the rank should be even less than subspecific.

Of the present specimens, the two collected by the 'Te Vega' may both be referred to *protecta* but the remaining specimens have P<sub>2</sub> more gradually tapering, quite straight and usually erect but sometimes appressed to the arm and inclined distally, though probably only in preservation; it has 15-17 segments.

The colour of specimen RU 296 in life was black and yellow.

COMMENSALS. The copepods *Pseudanthessius angularis* and *major* were associated with Professor Humes's specimens from Madagascar; the latter was also found on *Lamprometra klunzingeri*, *Dichrometra afra* and *austini*, as well as *Heterometra africana* and *Cenometra emendatrix* but the former only on *D. austini*.

### *Stephanometra spicata* (P. H. Carpenter)

*Antedon spicata* P. H. Carpenter, 1881 : 190-192; 1889 : 310-311, pl. 27, figs 3-5.

*Stephanometra spicata*: A. H. Clark, 1911d : 183; Gislén, 1936 : 11-12; A. H. Clark, 1941 : 424-436, pl. 49, figs 223, 224.

MATERIAL. 'Te Vega' cruise 2, st. 65, Pulau Hantu, SW of Singapore, intertidal; 4 specimens.

## Family HIMEROMETRIDAE

### *Amphimetra mollerii* (A. H. Clark)

*Himerometra mollerii* A. H. Clark, 1908a : 222.

*Amphimetra mollerii*: A. H. Clark, 1910 : 156; Gislén, 1936 : 10; A. H. Clark, 1941 : 349-358, pl. 38, figs 169-171.

MATERIAL. 'Anton Bruun' cruise 1, st. 20, 09°13'N : 97°51'E (SW from Mergui Archipelago, Burma), 58-60 metres; 7 specimens.

DESCRIPTION. These specimens have been referred to *Amphimetra mollerii* since they are certainly conspecific with another in the British Museum collections from NW of Penang which was determined as *A. mollerii* by A. H. Clark himself. Also this is the only member of the genus which has been recorded from within the

TABLE 5

Numerical data from specimens of *Amphimetra mollevi*, the last being derived from A. H. Clark's description of the holotype from the 'Indian Ocean'. The specimen marked \* is B.M. no. 1923.8.28.4, from NW of Penang. The cirrus measurements are in micrometer scale units, of which 19 = 1 mm. The distal cirrus breadth measurements include the height of the dorsal spine, which is 6 units or 0.3 mm in the fifth specimen listed.

Arms		Cirri				Pinnules							
Length	Br at	No.	Segs.	L.	L : br 8th seg.	L : br roth from tip	1st seg. with spine	P <sub>1</sub>		P <sub>2</sub>		P <sub>3</sub>	
								Segs.	L.	Segs.	L.	Segs.	L.
35 + c. 10	1.1	XVIII	29	13	11 : 14 = 1 : 1.3	8 : 15.5 = 1 : 1.9	9	15	4.7	15	5.8	c. 10	c. 4.0
22 + c. 15	1.2	XV	28	15	12.5 : 18	9 : 18.5	8	15	6.0	13	5.2	13	4.2
40 + c. 20	1.6	XX	—	—	13.5 : 22	11 : 24	(7)	20	7.1	15	7.1	12	5.2
40 + c. 20	1.8	XX	32	23	14 : 25	13 : 28	8	15	5.8	16	7.6	14	4.7
60 + c. 25	2.2	XXII	35	28	16 : 32	2.0	10	20	9.0	16	10.3	16	9.2
70 + c. 25	2.5	XXIV	35	30	18 : 39	2.2	11	19	9.0	17	10.5	15	9.5
* 35 + +	3.0	XXII	36	30	18 : 28	1.6	11	23	11.0	22	13.2	22	11.6
50 + +	3.2	XXVI	43	40	18 : 33	1.8	13	23	9.5	c. 22	c. 12.7	20	11.8
II5	—	XVI	37	20	c. 2		6	18	10	21	15	sim.	II

Bay of Bengal, though *A. tessellata discoidea* and *A. ensifera* are known from Singapore. However, there are some respects in which they do not agree with A. H. Clark's key to the species of *Amphimetra* (1941 : 346-347). Firstly *A. molleri* comes within the section having 'very flexible and more or less evenly curved cirri with the distal segments very slightly longer than the proximal ones', whereas the present specimens appear to have the cirri somewhat stiffer proximally than distally and the distal segments are usually slightly *shorter* than the proximal ones (see Table 5). The primary dichotomy in the key also depends on the stoutness of the cirri, which can be seen from the table to increase with size. The early position of the first cirral spine on the sixth segment in the holotype does not seem significant either since not only does A. H. Clark record other specimens with the first spine on about the eleventh segment but also the specimen from NW of Penang has the first spine absent from up to 14 segments, though its usual position is at about the tenth or eleventh. In general I think it unwise to put much faith in the precise form of the cirri as providing characters of specific weight in this genus and I think that some of the nominal species recognized by A. H. Clark will prove to be untenable. This is particularly true of *A. spectabilis* A. H. Clark, 1918, which is based on two large Philippine specimens with 45-51 cirrus segments, these being exceptionally broad with spines only from about the sixteenth, as would be expected in very large specimens of *A. molleri*.

### HETEROMETRA A. H. Clark

*Heterometra* A. H. Clark, 1909d : 11; 1941 : 225-235; A. M. Clark & Rowe, 1971 : 21. [Type-species *Antedon quinduplicava* P. H. Carpenter, 1888.]

A. H. Clark made three attempts to draw up a satisfactory key to the 26 nominal species of this genus which he recognized, using mainly the following characters:

- Cirri*:
1. Number of segments.\*
  2. Length : breadth of the proximal and/or distal segments.\*
  3. Development of spines or tubercles on distal segments.
  4. Abruptness of appearance of spines or tubercles.
  5. Degree of taper.†
- Division series*:
1. Occurrence of IIIBr series of four ossicles.
  2. Ruggedness or convexity of surface.
- Arms*:
1. Number.†
  2. Relative length of brachials.\*
  3. Obliqueness of articulations beyond the base.
  4. Smoothness of profile.
- Pinnules*:
1. Number of segments.\*
  2. Stoutness.
  3. Development of basal keel facing the arm tip.†

4. Development of distal processes on the segments or prismatic form. †
5. Size of  $P_2$  relative to  $P_3$ .\*
6. Size of  $P_1$  relative to  $P_2$  and  $P_3$ .\*

Some of these characters (marked \*) are certainly modified during growth and others (shown by †) exhibit some degree of variation in specimens of similar size. It should help to clarify the interrelationships if data could be related more precisely to size. However, in a genus such as this where the multibrachiate condition prevails (i.e. the number of arms normally exceeds ten), can the arm length alone be used as the criterion of size still or should a further factor for the arm number be included? Table 6 shows numerical data derived from some specimens of *Heterometra* from the western part of the Indian Ocean including 14 specimens from Madagascar, which I am referring to *H. madagascarensis*. These 14 are arranged in the mean sequence derived from averaging the size sequences suggested by all but the last of the 17 columns, assuming that, apart from increases in the proportions and segment numbers, the relative breadth of the cirrus segments increases and the position of the first dorsal spine shifts distalwards in the later-developed cirri. These 14 specimens indicate that, in *H. madagascarensis* at least, the longest cirrus segments are at first longer than broad but become distinctly broader than long in more mature specimens. Also the length of  $P_2$  relative to  $P_3$  changes from larger to smaller.

It is significant that the specimen with the fewest but longest arms comes last in the average sequence. Since augmentation in arm number occurs by autotomy and regeneration of two arms in place of one, all but two of the arms in this eleven-armed individual are the original ones and have been able to develop uninterruptedly, whereas the 22-armed specimen has no original arms and the regeneration involved may well have served to retard the growth of the cirri, which are not disproportionately large although they do have more numerous segments. In this genus at least it therefore seems that arm number could be disregarded in size estimates.

Because of the discussions on interrelationships, the species of *Heterometra* dealt with here are not treated in alphabetical order but geographically, those from the western Indian Ocean, including *H. delagoae* and *H. madagascarensis*, first. These two species need to be compared with *H. africana*, recorded from the East African mainland and from Karachi, and *H. savignii* from the Red Sea, Persian Gulf and Gulf of Oman. Some measurements and counts from five specimens from Karachi determined as *H. africana* by A. H. Clark are given in Table 6 together with others from the few specimens available from East Africa. The Karachi specimens do not show any significant differences from the others in the characters tabulated, agreeing even in having  $P_3$  consistently smaller than  $P_2$ , unlike *H. madagascarensis*. The shape of the basal pinnules varies somewhat in these Karachi specimens, in some of them being very smooth, as in *Heterometra savignii*, with no trace of a secondary dorsal ridge in addition to the usual keel facing the arm tip, while in other specimens a dorsal ridge is quite distinct, as in most, but not all, of the specimens of *H. madagascarensis*. The segments of the proximal pinnules also have similar proportions

to those of *H. africana* from East Africa, in contrast to the corresponding pinnules of *H. savignii*, where the segments, especially of  $P_D$  and  $P_1$ , are much more attenuated. Other differences from *H. savignii* include the flanged approximating division series of *H. africana*, those of *H. savignii* being more or less rounded laterally and widely separated, also *H. savignii* has distinctly more elongated cirrus segments, the longest ones with length : median breadth usually c. 1.5 : 1. The geographical limits between *H. africana* and *H. savignii* remain to be determined. A. H. Clark in 1912 recorded as *H. savignii* not only the specimens from Karachi but also some from the Straits of Ormuz (Hormuz) between the Persian Gulf and the Gulf of Oman, both of which he subsequently (1941) referred to *H. africana*. The Ormuz material had the longest cirrus segments 'from slightly longer than broad to slightly broader than long' and the division series 'in lateral contact with sharply flattened sides, which are produced . . .', both features agreeing with *H. africana*. However, Gislén (1940b) records as *H. savignyi*\* fourteen specimens from within the Persian Gulf, noting that these have 'rather long cirrus joints—though not as long as those which I have seen from the Red Sea—narrow arm bases and almost smooth proximal pinnules'.

A. H. Clark (1911b) also described briefly two further nominal species of *Heterometra* from East Africa in the vicinity of Zanzibar, each from a single specimen. These are *H. joubini* and *H. gravieri*.

The holotype of *Heterometra joubini* has 20 arms about 80 mm long and XXII cirri with as many as 39–43 segments and measuring c. 30 mm, even the longest cirrus segments are distinctly broader than long and the dorsal spines are blunt. This last character together with the large number of cirrus segments may serve to distinguish the species.

The holotype of *H. gravieri* has 19 arms also c. 80 mm long and XXVIII cirri with 36–39 segments but cirrus length only c. 21 mm; the cirri are also more slender than those of *H. joubini*, the longest segments distinctly longer than broad.  $P_3$  is slightly smaller than  $P_2$ , as it is also in *H. joubini*.

Several further species have been recorded (mostly by A. H. Clark) from the Maldive Islands and the west coast of India. These are *Heterometra flora* (A. H. Clark), *H. compta* A. H. Clark, *H. producta* (A. H. Clark) and *H. reynaudi* (J. Müller), though the two last I have explained (1966) are doubtful records. In addition *Heterometra ater* (A. H. Clark) (better as *atra*) from the Red Sea is not well known and needs to be included in any comparative survey with the other nominal species.

### *Heterometra delagoae* Gislén

*Heterometra africana* var. *delagoae* Gislén, 1938b : 10–12, figs 8–11, pl. 1, fig. 3.

*Heterometra delagoae* : A. H. Clark, 1941 : 334–335.

MATERIAL. 'Anton Bruun' cruise 8, st. 403A, 19°09'S : 36°20'E (NE of Beira, Mozambique), 27–30 metres; 7 specimens.

\* His spelling.

DESCRIPTION. Numerical data for three of the more nearly intact specimens is given in Table 6. Another arm of the first specimen detailed has  $P_1$  to  $P_3$  with only three-quarters as many segments and also only three-quarters the length (except for  $P_3$  which is barely half as long) of the corresponding pinnules in the table, though the preceding  $P_D$  is similar. It is likely that this arm is chronologically younger than the first one though its length is about equal.

The number of arms is probably about thirty in all the specimens, which agrees with the type material. Also in contrast to *H. madagascarensis* the number of cirri is consistently greater, averaging c. XXX in comparison with XXI in the fourteen specimens from Madagascar seen. However, the specimen of *H. africana* from Wasin, Kenya, has likewise c. XXX cirri by my reckoning (including fractions for the immature ones according to size, whereas A. H. Clark's estimate of only XX ignores all but the fully-grown cirri). In relation to arm length there may also be a small difference in *H. delagoae* in the stoutness of the cirrus segments, the longest of which are 1.3-1.6 times as broad as long at an arm length of c. 80 mm, the median breadth of these segments being 1.1 mm, proportions only matched in the specimen of *H. madagascarensis* with arms 150 mm long, the specimens with arm length c. 80 mm having the cirrus breadth only c. 0.8 mm. However, further material may show that this difference is not consistent.

### *Heterometra madagascarensis* (A. H. Clark)

(fig. 11)

*Craspedometra madagascarensis* A. H. Clark, 1911b : 23.

*Heterometra madagascarensis* : A. H. Clark, 1918 : 78; 1941 : 295-297, pl. 29, figs 120-122.

*Heterometra africana* : A. M. Clark in Humes & Ho, 1970 : 5, 11. [Non *H. africana* (A. H. Clark, 1911)]

MATERIAL. Professor A. G. Humes's nos. 1166, 1188, 1255, 1273, 1300, 1304, 1312, 1313, 1350-1352, 1361-1363, Madagascar: off Pte. Lokobe, Nosy Bé, 17 metres; near Ambatoloaka, Nosy Bé, 29 and 34 metres; N of Nosy Varona, near Nosy Bé, 18 metres and SW of Nosy Bé, 25 metres; 14 specimens, B.M. reg. nos. 1969.5.13.5-17 & 96.

I formerly identified these specimens for Professor Humes as *Heterometra africana* since they failed to run down to *H. madagascarensis* in A. H. Clark's key (1941 : 230-232) because that species is included there in section d<sup>2</sup>, p. 231, with relatively small blunt spines on the cirri developing gradually, and then in section g<sup>2</sup>, p. 232, which has cirrus segments longer than broad. These specimens show some variation in the development of the cirrus spines, which are quite large and pointed in some specimens and develop to their full size over only two or three segments. They are particularly prominent in the specimen with arm length 120 mm (see Table 6) which gives the data shown in Table 7 in comparison with the specimen from Wasin, Kenya, in the British Museum collections, identified as *H. africana* by A. H. Clark, which had arm length c. 100 mm.

TABLE 7

Comparison of spine development on the cirri of  
*Heterometra madagascarensis* and *H. africana*

	Madagascar	Kenya
A. Cirrus length (mm)	25	18
B. Height of opposing spine	0.35	0.25
C. Remaining breadth of penultimate segment	1.00	0.70
D. Maximum cirrus breadth at fourth segment	1.30	0.95
A : B	72 : 1	72 : 1
A : C	25 : 1	26 : 1
A : D	19 : 1	19 : 1

The development of the opposing spine is directly proportional to that of the other dorsal spines on the distal segments and is clearly indistinguishable in these two specimens.

As for the relative length of the cirrus segments, A. H. Clark's key and diagnosis to *H. madagascarensis* are directly contradicted by his description of the holotype which gives the longest cirrus segments as 'from only slightly broader than long to

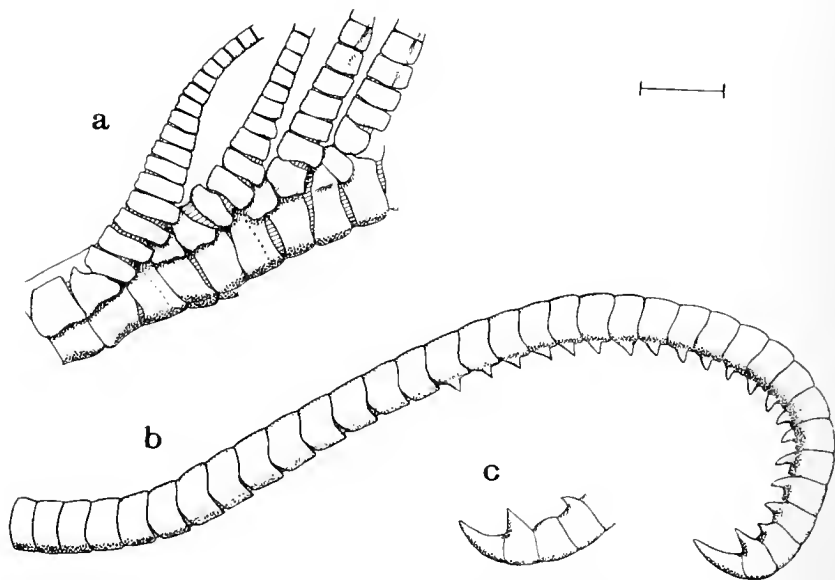


FIG. 11. *Heterometra madagascarensis* (A. H. Clark). B.M. reg. no. 1969.5.13.7, Nosy Bé, Madagascar. Arm br 2.1 mm (after II Br series). a, side view of proximal part of one post-radial series from II Br<sub>1</sub> to Br<sub>7</sub> showing P<sub>D</sub> and P<sub>1</sub> to P<sub>3</sub>; b, mature cirrus and c, tip of another cirrus without a spine on the antepenultimate segment. [The scale equals 2 mm.]



Species and locality		P <sub>3</sub>		Lengths
<sup>2</sup>	L.	Segs.	L.	P <sub>3</sub> : P <sub>2</sub>
<i>H. africana</i>				
Zanzibar	7.4*	20*	8.9*	—
"	12.6	—	? similar	—
Wasin	—	24	12.6	—
Karachi	8.9	19	6.3	0.71 : 1
"	14.5	23	9.7	0.67
"	9.2	21	7.1	0.78
"	13.4	28	12.1	0.96
"	13.4	27	12.9	0.96
<i>H. delagoae</i>				
Mozambique	16.8	28	14.5	0.86
"	13.7	26	13.1	0.98
"	—	—	—	—
<i>H. madagascare</i>				
Madagascar	—	—	—	—
"	8.1	21	7.9	0.98
"	8.4	—	larger	—
"	—	23	8.7	—
"	10.8	c. 22	c. 10.5	c. 1.0
"	9.5	21	11.6	1.23
"	10.8	22	10.8	1.00
"	11.0	—	smaller	—
"	—	23	10.5	—
"	—	26	12.9	—
"	10.5	26	15.0	1.43
"	12.1	c. 27	14.2	1.18
"	15.3	—	larger	—
"	14.2	33	19.5	1.38

TABLE 6

Numerical data from some specimens of *Heterometra africana*, *H. delagoae* and *H. madagascarensis*, that from the arms taken from arms based on IIBr series except where marked \*

Species and locality	Arms			Cirri					Pinnules								
	Length	No.	Br at 3 + 4	No.	Segs	Length	Br : L longest segment	First seg. with spine	Segs.	P <sub>D</sub> L.	Segs.	P <sub>1</sub> L.	Segs.	P <sub>2</sub> L.	Segs.	P <sub>3</sub> L.	Lengths P <sub>3</sub> : P <sub>2</sub>
<i>H. africana</i>																	
Zanzibar	c. 55	10	1.5*	XX	29	18	1.0 : 1	10	—	—	22*	4.2*	20*	7.4*	20*	8.9*	—
"	65	19	1.6	XVIII	33	22	1.0	10, 11	30	7.9	31	10.5	23	12.6	—	? similar	—
Wasin	c. 100	23	1.6	XXX	28	18	1.0	10, 11	32	8.9	32	10.0	—	24	12.6	—	—
Karachi	c. 75	18	1.7	XX	32 (36)	17	1.2	9, 10	20	5.8	23	8.4	24	8.9	19	6.3	0.71 : 1
"	c. 75	19 (?20)	1.7	XVIII	35	18	1.3	10-12	c. 29	c. 8.5	c. 28	c. 13.5	c. 29	c. 14.5	23	9.7	0.67
"	70	20	1.8	XXI	32	24	1.25	10 (11)	27	6.3	24	6.6	21	9.2	21	7.1	0.78
"	c. 95	17	1.9	XXVI	34	24	1.1	13	28	8.1	32	10.0	30	13.4	28	12.1	0.96
"	110	16 (?19)	1.8	XXIV	36	24	1.1	12, 13	26	7.4	29	8.9	27	13.4	27	12.9	0.96
<i>H. delagoae</i>																	
Mozambique	c. 75	30	1.5	XXVIII	35	c. 22	1.4	14	34	12.1	33	12.6	33	16.8	28	14.5	0.86
"	c. 75	30+	1.5	XXXI	31+	—	1.3	12	27	9.5	25	9.5	31	13.7	26	13.1	0.98
"	c. 85	c. 30	1.5	XXVIII	35	23	1.6	13	—	—	—	—	—	—	—	—	—
<i>H. madagascarensis</i>																	
Madagascar	55	11	1.3*	XVIII	25	14	0.9	8, 9	—	—	—	—	—	—	—	—	—
"	70	12	1.2	XX	29	19	0.85	(9) 10	28	6.8	—	—	24	8.1	21	7.9	0.98
"	65	16 (?17)	1.3	XVI	31	17	1.0	9-11	20	5.2	23	6.3	c. 23	8.4	—	larger	—
"	80	13 (?14)	1.4	XVIII	29	19	1.0	8 (9)	25	6.3	—	—	—	23	8.7	—	—
"	80	11 (?13)	1.6	XXIII	30	22	1.0	11	26	7.4	22	8.1	26	10.8	c. 22	c. 10.5	c. 1.0
"	100	13	1.8	XVIII	32	20	1.1	—	24	6.8	25	7.1	24	9.5	21	11.6	1.23
"	90	15	1.8	XX	32	22	1.1	12, 13	30	8.4	29	9.5	27	10.8	22	10.8	1.00
"	85	16	1.3	XXII	32	23	1.25	12, 13	24	7.4	c. 27	c. 9.2	28	11.0	—	smaller	—
"	100	16 (?17)	2.0	XXIV	31	c. 19	1.05	10, 11	29	8.4	32	13.7	c. 27	—	23	10.5	—
"	95	20	1.9	XX	32	19	1.15	(12) 13	34	9.0	28	8.7	—	26	12.9	—	—
"	110	22	1.8	XX	36	23	1.1	10-12	32	7.6	31	8.9	29	10.5	26	15.0	1.43
"	100	16	2.0	XXIII	34	21+	1.2	(9) 10	33	10.5	31	10.8	32	12.1	c. 27	14.2	1.18
"	120	14	2.1	XXII	34	c. 26	1.05	13	36	10.5	39	12.6	35	15.3	—	larger	—
"	150	11	2.0	XXVIII	35	c. 27	1.4	14	40	12.6	36	12.1	30	14.2	33	19.5	1.38

one-third again as broad as long', that is *not* longer than broad, which is in agreement with all but the smallest of Humes's specimens from Madagascar. There is thus no significant difference between *H. madagascarensis* and *H. africana* in the proportions of the cirrus segments.

However, when it comes to pinnule shape there is a very appreciable difference between the Wasin specimen of *H. africana* and the malagasy specimens. One of the latter with arms c. 90 mm long was used for comparison, yielding the data in Table 8.

TABLE 8

Comparison of the breadth of the first two pinnules in  
*Heterometra madagascarensis* and *H. africana*

	Madagascar	Kenya
P <sub>D</sub> Length (mm)	8.4	8.9
Segment number	30	32
Breadth at 20th segment	0.15	0.35
P <sub>1</sub> Length	9.5	10.0
Segment number	29	32
Breadth at 20th segment	0.20	0.35
Breadth at 10th segment	0.35	0.75
Breadth at 3rd segment	c. 0.9	c. 0.9

In the malagasy specimen there are very conspicuous basal crests on the edge of the proximal pinnules facing the arm tip but the pinnules become rapidly attenuated and their distal halves are much more flagellate than those of the specimen from Kenya, which is unfortunately the only well-developed example of *H. africana* available from the vicinity of the type-locality (the Zanzibar area).

Other characters used by A. H. Clark to distinguish between these two geographically approximating species are the supposedly more tapering cirri of *H. madagascarensis* and the longer, more wedge-shaped brachials. Table 7 shows that there may not be any appreciable difference in the degree of taper of the cirri, while comparative counts of brachials over lengths of 20 mm in the proximal and distal halves of the Kenya specimen of *H. africana* and one of *H. madagascarensis* of comparable size show fewer but longer brachials in the former! [The numbers are 32 : 38 proximally, counting from the 20th brachial, and 43 : 50 distally.] However, there happen to be more syzygies in this Madagascar specimen, syzygial brachials being naturally shorter. I cannot distinguish any appreciable difference in the obliqueness of the articulations between the brachials.

Apart from the difference in shape of the basal pinnules between the two species, it seems likely that there is also a difference in their proportions, at least as far as this can be judged from the available material. Unfortunately the few East African specimens of *H. africana* in the British Museum collections are small, apart from the Wasin specimen which has no P<sub>2</sub> left intact. However, five specimens from Karachi, which were identified as *H. africana* by A. H. Clark, consistently have P<sub>3</sub> smaller than P<sub>2</sub>, though in the larger ones with arm length c. 100 mm these two pinnules

are almost equal. The holotype of *H. africana* has  $P_3$  similar to or smaller than  $P_2$ . As can be seen from Table 6, in *H. madagascarensis*  $P_3$  and  $P_2$  are approximately equal until the arm length exceeds 80–90 mm when  $P_3$  becomes distinctly larger. Much more material is needed to establish whether these proportions and growth changes are consistent.

*Heterometra madagascarensis* was previously known only from the three type specimens in the U.S. National Museum, the precise locality of which in Madagascar was not known. The present material extends the range of arm number from 13–18 up to 11–22 and the number of cirri to a maximum of XXVIII (though A. H. Clark underestimates cirrus number in comparison to me by counting only the fully mature ones). The number of cirrus segments and the length of the cirri do not exceed his maximum but inevitably there is a bigger range in the proximal pinnules owing to the greater range of size of the specimens.

A notable feature is that a few specimens have no trace of a dorsal spine on the antepenultimate segment of some cirri, there being a distinct gap in the series (fig. 11c). The shape of the dorsal spine varies from blunt to sharp and is often roman-nosed with a subsidiary proximal peak. The specimen with 14 arms has one IIBr series present. Another with 22 arms has several irregularities in the division series, one of the seven IIBr having only two ossicles instead of the usual four, while there is another IIBr series of five ossicles (with a syzygy still at 3 + 4) followed by a IIBr series of only a single (axillary) ossicle; two other IIBr series have the usual two ossicles. On arms based on IBr series,  $P_4$  is about equal to  $P_3$  in length though with a few less segments; otherwise  $P_4$  is distinctly smaller than the preceding pinnule.

### *Heterometra* sp. ? *H. bengalensis* (Hartlaub)

*Antedon bengalensis* Hartlaub, 1890 : 182; 1891 : 19–21, pl. 1, fig. 2, pl. 2, fig. 16.

*Heterometra bengalensis*: A. H. Clark, 1941 : 321–325, pl. 30, figs 127–130.

MATERIAL. 'Anton Bruun' cruise 1, st. 22A,  $10^{\circ}37'N$  :  $97^{\circ}34'E$  (SW of Mergui Archipelago, Burma), 75–80 metres; 1 specimen.

DESCRIPTION. The arm length is  $90 + 10$ –20 mm; the breadth at the first syzygy on arms based on IIBr<sub>4</sub> series is 1.75 mm and the length from the proximal edge of the IBr<sub>1</sub> to this syzygy is 6.3 mm. There are 19 arms and two IIBr series each of two ossicles. The cirri numbered XXV–XXX (the exact number being uncertain since a piece is broken off the centrodorsal). All are broken off short but a detached cirrus caught between the arms has 33 segments and measures 27 mm in length. It is mature and could be a peripheral cirrus. The fifth and longest segment has length : breadth 1.2 : 0.85 mm. The dorsal spines appear abruptly on the eighth segment; all are rather blunt. The distal end of the cirrus is not tapered, the sixth segment from the tip (measured since the fifth has the spine broken) is 1.05 mm broad including the spine, or 0.85 mm without the spine.

The division series are smooth, straight-sided and the proximal brachials are all more or less wedge-shaped.

$P_D$  has 17+ segments and is 5.8+ mm long.  $P_1$  is similar but larger. Both of them have a thin high crest on segments 2 to 6.  $P_2$  is much larger, 15.25 mm long, with 29 or 30 segments; very stout basally and with a lower crest on segments 2 to 5, then becoming prismatic and attenuated distally.  $P_3$  is slightly smaller, 13.2 mm long and more attenuated; it has 26 segments. In another series from an arm also based on a IIBr<sub>4</sub> series,  $P_3$  is the largest pinnule although it is regenerated from the tenth segment and broken at the 23rd, at least five segments having been lost; the length is 14.75+ mm and the first ten segments measure 7.1 mm, whereas the first ten segments of  $P_2$  are only 6.4 mm long.

**AFFINITIES.** This specimen agrees with *Heterometra bengalensis* in most characters except that the proximal brachials are more or less wedge-shaped and do not have strongly produced ends; also the number of cirrus segments exceeds 30. On this account it runs down, in A. H. Clark's first key, to *H. compta* A. H. Clark (known from SW of India between Goa and Cochin) except that  $P_3$  is not markedly smaller than  $P_1$  or  $P_2$ . The British Museum collections include only two specimens named *H. bengalensis*. These are from Singapore and were determined in 1929 by A. H. Clark as *H. aspera*, which he treated as a synonym of *H. bengalensis* in 1941. These two specimens are badly broken. They agree with *H. bengalensis* in having relatively few arms (c. 12) and the profile irregular but most of their brachials are distinctly wedge-shaped rather than discoidal and I think they may be conspecific with *H. singularis*, also known from Malacca Strait.

### *Heterometra flora* (A. H. Clark)

*Amphimetra flora* A. H. Clark, 1913 : 23.

*Heterometra flora* : A. H. Clark, 1918 : 77; 1941 : 333; A. M. Clark, 1966 : 604-606.

**MATERIAL.** 'Anton Bruun' cruise 1, st. 28A, 11°52'N : 92°49'E (Andaman Islands), 66 metres; 1 specimen.

**DESCRIPTION.** The arm length is 55 + c. 50 mm; the breadth at the first syzygy on arms based on IIBr<sub>4</sub> series is 2.25 mm and the length from the proximal edge of the IBR<sub>1</sub> to this syzygy is 7.1 mm. There are 13, possibly 14 arms and two of the three IIBr series are unusual in having only two ossicles. The centrodorsal has a concave dorsal pole. The cirri are XXIV; all are broken though one peripheral may lack only 2-4 segments beyond the 26 that are left. All the segments are shorter than broad. There are dorsal spines from about the ninth segment and the more proximal ones are doubled or abruptly truncated.

Few of the brachials are particularly wedge-shaped but most are more or less discoidal and flared.

The only external post-radial series with IIBr<sub>4</sub> has the pinnules increasing in stoutness to  $P_4$ , which is forked abnormally from the third segment.  $P_D$  with 20 segments is huge basally with a high crest on the first and second segments but is rapidly attenuated distally; it is 7.4 mm long.  $P_1$  is possibly regenerating; it has 18 segments, is similar in shape to  $P_D$  but measures only 6.3 mm.  $P_2$  with 21 segments

ments is 8.7 mm long and P<sub>3</sub> with 18 segments is 8.4 mm long. P<sub>4</sub>, if normal, would probably have been the longest pinnule as well as the stoutest basally, since P<sub>5</sub> is also very stout and equal in length to P<sub>3</sub>. An arm based on a IBr series has P<sub>4</sub> the stoutest pinnule basally.

Except for the truncated or doubled cirrus spines, this specimen agrees with the type material of *H. flora*.

RANGE. This record extends the known range of the species from the Maldive Islands into the Bay of Bengal.

### *Heterometra reynaudi* (J. Müller)

*Comatula (Alecto) reynaudi* J. Müller, 1846 : 178.

*Heterometra reynaudii*: A. H. Clark, 1911c : 251; 1912a : 121-124, fig. 9.

*Heterometra reynaudi*: A. H. Clark, 1941 : 302-311, pl. 32, figs 137-143.

MATERIAL. 'Anton Bruun' cruise 1, st. 47B, 19°50'N : 92°55'E (off Akyab, Burma), 22-30 metres; 8 specimens.

DESCRIPTION. The largest specimen has arm length 50 + c. 50 mm; the breadth at the first syzygy on arms based on IBr<sub>4</sub> series is 1.7 mm and the length from the proximal edge of the IBr<sub>1</sub> to this syzygy is 5.5 mm. There are c. 22 arms. The cirrus number can be expressed as XXVIII, based on XXI mature cirri and X more or less immature ones. The longest are 26 mm with up to 40 segments, none of which are longer than broad. The dorsal spines start between the fourteenth and seventeenth segments, usually at the fifteenth; they are not particularly sharp. Two series of P<sub>D</sub>, P<sub>1</sub>, P<sub>2</sub> and P<sub>3</sub> are as follows:

24, 6.3 mm; 33, c. 10 mm; 35, 15 mm; 33, 18 mm  
26, 6.0 mm; 34, c. 14 mm; 34, 20 mm; 30, 16 mm

REMARKS. A. H. Clark's first key (1941 : 230-232) contradicts his text where *Heterometra reynaudi* is concerned, since he includes it in h<sup>1</sup> (bottom of p. 231) with 'P<sub>3</sub> as large as, or larger than, P<sub>2</sub>', whereas his diagnosis states that P<sub>2</sub> is the largest pinnule. It is clear from his description that in this instance length was his size criterion but, as the measurements above show, either P<sub>2</sub> or P<sub>3</sub> may be the longest pinnule and this character is not reliable.

### *Heterometra singularis* A. H. Clark

*Heterometra singularis* A. H. Clark, 1909c : 638-639; 1912a : 128-130, fig. 11; 1941 : 290-293 pl. 36, figs 161-163.

?*Heterometra pulchra* A. H. Clark, 1912a : 317-318; 1941 : 287-289, pl. 36, figs 164, 165.

MATERIAL. 'Anton Bruun' cruise 1, st. 21, 09°54'N : 97°42'E (SW of the Mergui Archipelago, Burma), 70 metres; 4 specimens.

'Anton Bruun' cruise 1, st. 22A, 10°37'N : 97°34'E (SW of the Mergui Archipelago), 75-80 metres; 2 specimens.

'Anton Bruun' cruise 1, st. 38, 14°07'N : 97°05'E (W of the Moskos Islands, Burma), 69-73 metres; 1 specimen (? *H. singularis*).

Cable ship 'Patrol', 05°38'45"N : 99°39'40"E (off Penang, Malaya), 55 metres; 2 specimens, B.M. reg. no. 1929.7.16.6.

DESCRIPTION. The most nearly intact specimen from 'Anton Bruun' st. 21 has the arm length 80 + 10-20 mm, 19 or possibly 20 arms, the breadth at the first syzygy following a IIBr<sub>4</sub> series 1.7 mm and the length to this syzygy 5.5 mm. The cirri number c. XXIII and have up to 50 segments, the maximum length being c. 38 mm. The twelfth and longest segment has length : breadth 1.1 : 1.0 mm. The maximum breadth is 1.1 mm at about the fifth segment and the cirri taper distally so that the fifth segment from the tip is only 0.6 mm excluding the dorsal spine or 0.75 mm including the spine. The spines are pointed, though relatively small and distally-directed, starting gradually between the 24th and 30th segments.

The division series are flanged laterally with straight edges; they approximate closely laterally. Only one IIIBr series is present; it consists of two ossicles.

In one pinnule series, P<sub>D</sub> has 29 segments and is 7.6 mm long; segments two to five have a very high thin crest beyond which the pinnule becomes very attenuated. P<sub>1</sub> with 20 segments measures 7.9 mm; its crest is slightly more extended and the distal segments are relatively longer than those of P<sub>D</sub>. P<sub>2</sub> with c. 22 segments measures 11.0 mm; its first eight segments together measure 5.0 mm, the crest is borne by segments two to four. P<sub>3</sub> is regenerating distally, with 19+ segments, the first eight of which are original and measure 4.5 mm so the length was probably little less than that of P<sub>2</sub>. P<sub>2</sub> was probably the largest pinnule in most cases but the external ones are mostly broken or on regenerating arms.

A slightly smaller specimen from this station is badly broken. It has arms c. 95 mm long and 1.5 mm broad at the first syzygy. The centrodorsal is 4.75 mm in diameter and the dorsal pole c. 3.2 mm. Again the longest cirrus segments are slightly longer than broad and the cirri taper distally.

The larger of the two specimens from station 22A had arm length only c. 50 mm and 12 arms with breadth at the first syzygy 1.2 mm. There are up to 31 cirrus segments, the sixth and longest with length : breadth 0.9 : 0.5 mm; the dorsal spines start between the twelfth and fourteenth segments; they are fairly large and sharp but on some cirri are truncated abruptly or double-peaked. Although taken at the same station as the specimen doubtfully referred to *H. bengalensis*, these two are marked off by the much more distal appearance of the cirrus spines at about segment thirteen rather than eight.

The specimen from station 38, which is only provisionally referred to *H. singularis*, has arm length 35 + 20-30 mm and only ten arms with breadth at the first syzygy 1.2 mm. There are c. XX cirri with up to 30 segments and length up to c. 20 mm. The fifth and longest segment has length : breadth 0.90 : 0.65 mm and the dorsal spines begin at the eighth or ninth segment of the mature cirri but not until about the twelfth in the immature ones. The spines are large and sharp. P<sub>1</sub> with 15 segments is 3.7 mm long. P<sub>2</sub> and P<sub>3</sub> with 18 segments are 6.6 mm long.

REMARKS. In spite of the slightly shorter P<sub>3</sub> relative to P<sub>2</sub>, which links it with

*Heterometra singularis*, the first specimen described above, which is the only mature reasonably intact one, agrees much more closely with A. H. Clark's description of the type-material of *H. pulchra* from Cape Negrals, Burma (arms 85+ mm long), than with that of *H. singularis* from the southern part of the Malacca Strait (arm length only c. 40 mm), especially in the distal position of the earliest cirrus spines beyond the twentieth segment, whereas the holotype of *H. singularis* has spines as far proximally as the seventh cirrus segment. The size difference is not enough to account for this since a small specimen also from 'Anton Bruun' station 21 with arms only c. 40 mm has two mature peripheral cirri with respectively 31 segments and spines from the fourteenth, or 27 segments with spines from the eleventh. The specimens from NW of Penang which A. H. Clark (1929) referred to *H. singularis* are all large (arm length 90 mm or more) and have cirrus spines starting from about the fifteenth segment or beyond on the larger cirri though more proximally on the apical ones. [A. H. Clark said that there are six of these specimens collected by the C.S. 'Patrol' in the British Museum collections which is true but only four of them, no. 1923.8.28.1-2, were labelled as *Heterometra singularis* by him, the other two, 1929.7.16.6, with locality 5°38'45"N : 99°39'40"E (which is also NW of Penang) were simply labelled as 'Crinoids' until 1950 but must have been the balance of the sample studied by Mr Clark. On both of these specimens, on mature arms following IIBr series, P<sub>3</sub> is distinctly larger than P<sub>2</sub>, a characteristic of *H. pulchra* according to him, although on arms based on IBr series it is smaller in at least one case, as he describes for *H. singularis*.] These specimens from off Penang are clearly conspecific with the specimens described above (with the possible exception of the one from station 38) and accordingly I am referring the 'Anton Bruun' material to *H. singularis* although I am not certain whether they are also conspecific with the holotype. If this provision does hold good then *H. pulchra* should be referred to the synonymy of *H. singularis* but this cannot be checked until a good series of specimens, preferably from the Malacca Strait, can be examined.

### *Himerometra sol* A. H. Clark

*Antedon palmata*: Bell, 1902 : 224. [Non *Alecto palmata* Müller, 1841.]

*Himerometra sol* A. H. Clark, 1912a : 115-116; 1941 : 188-189.

**MATERIAL.** 'Te Vega', F. C. Ziesenhenné's st. 64-20, small island at end of reef W of N end Filadu I., Tiladummati Atoll, Maldive Is., under loose coral boulders; 1 specimen.

**DESCRIPTION.** The arms are reflected dorsally and difficult to count all round but three radii together have 29 arms so the total is probably c. 50. Their length is c. 120 mm. The cirri have 24-33 segments, which develop a median dorsal convexity, becoming a small blunt tubercle on the segments of the outer third of each cirrus. All the segments are broader than long. One cirrus with 27 segments is c. 30 mm long. The IIIBr series are normally of four ossicles externally and two internally. There are low synarthrial tubercles. The only P<sub>D</sub> (pinnule on IIBr<sub>2</sub>) and P<sub>F</sub> (on



III<sub>Br</sub><sub>2</sub>) which are visible for their whole length both have the tip regenerated; they have respectively 31 segments measuring c. 22 mm and 29 segments measuring c. 21 mm. The P<sub>1</sub> of two different series have 23 or 25 segments and are c. 16 and 15 mm long; P<sub>2</sub> is much smaller.

This is only the second record of *Himerometra sol*. The holotype and paratype were also from the Maldive Islands.

### Family COLOBOMETRIDAE

#### *Cenometra emendatrix madagascarensis* subsp. nov.

(fig. 12)

*Cenometra emendatrix*: A. M. Clark in Humes & Ho, 1970 : 5.

**MATERIAL.** Prof. A. G. Humes's no. 1360, Banc de Dzamandzar, Nosy Bé, Madagascar, 20 metres; 12 specimens including nos. 1, 2 and 12 in Table 9. B.M. reg. no. 1969.5.13.84-90.

Humes's no. 947, NW coast of Nosy Ovy, Radama Islands, E Madagascar, 10 metres; the holotype and another specimen, nos. 10 and 8 in Table 9. B.M. 1969.5.13.93.

Humes's no. 702, S of Tany Kely, near Nosy Bé, 20 metres; 6 specimens, nos. 3, 4, 6, 7, 9 and 11 in Table 9. B.M. 1969.5.13.91, 92, 106-107.

Prof. J. Stock's no. MD 25, same locality, on 'sea-whip', c. 14 metres; 1 specimen, no. 5 in Table 9. Amsterdam Museum.

Since identifying these specimens from Madagascar for Professors Stock and Humes simply as *Cenometra emendatrix*, a detailed comparison with material from Mauritius, the type-locality, and the Seychelles, has revealed consistent differences not only in the number of arms and cirri but also in the proximal pinnules of specimens with comparable arm length, sufficient to justify the recognition of a distinct subspecies from Madagascar in my opinion.

**DESCRIPTION.** The holotype has the centrodorsal 5.0-5.8 mm in diameter and 1.3 to 1.7 mm in height. The dorsal pole is irregular in outline due to variable encroachment of the cirrus sockets, which are two or three deep around the sides, so that the diameter of the naked part ranges from 1.1 to 2.6 mm; it is slightly sunken in the middle.

The cirri number XXXIII with up to 46 segments and length up to 30 mm. All the segments are broader than long, the longer ones (around the tenth) with length : median breadth c. 0.8 : 1.2 mm = 0.67 : 1. The dorsal 'spines' begin between the tenth and twelfth segments.

The division series are widely separated laterally and have abrupt ventro-lateral flanges, though these are not quite continuous longitudinally, being cut off just short of the proximal and distal edges of each ossicle. There are slight synarthrial convexities. The arms are flat-sided without flanges. There are 28 (possibly 30) arms, the longest remaining one 120 plus probably about 5 mm in length and the breadth at 3 + 4 after either IIBr or IIIBr series is 1.6 mm.

On one arm  $P_1$  with 26 segments is 8.4 mm long; it is slender with most segments distinctly longer than broad and br at the fifth segment 0.5 mm.  $P_2$  is much stouter, as usual in the genus, with most segments broader than long; there are c. 25 segments and the length is 14.2 mm, br at the fifth is 0.75 mm and there are distal spinose projections starting at about the fourth segment, while the second to fourth segments bear a slight longitudinal, more or less rounded, crest on the side facing the arm tip, whereas on the following pinnules the third to fifth (sometimes also the second) segments have better developed squarer and sharper axe-like keels.  $P_3$  is much smaller than  $P_2$ , with 17 segments and is 6.0–6.5 mm long.

**VARIATIONS.** Some of the numerical variations are indicated in Table 9, the entries in which are arranged in a size sequence derived from the product of arm length, breadth and number for the specimens from Madagascar (nos. 1–21) and separately for *Cenometra emendatrix emendatrix* from Mauritius and the Seychelles (nos. 22–28). In four cases, pinnules from two different arms were counted to give some idea of the variation within a single individual.

**AFFINITIES.** Of the specimens from Madagascar, excepting the two smallest which do have less than 20 arms, the other 19 have the arm number ranging from 24 to 32 (possibly more), with a mean of 30 compared with a maximum number of 22 and a mean of 17 in the specimens from Mauritius and the Seychelles. The

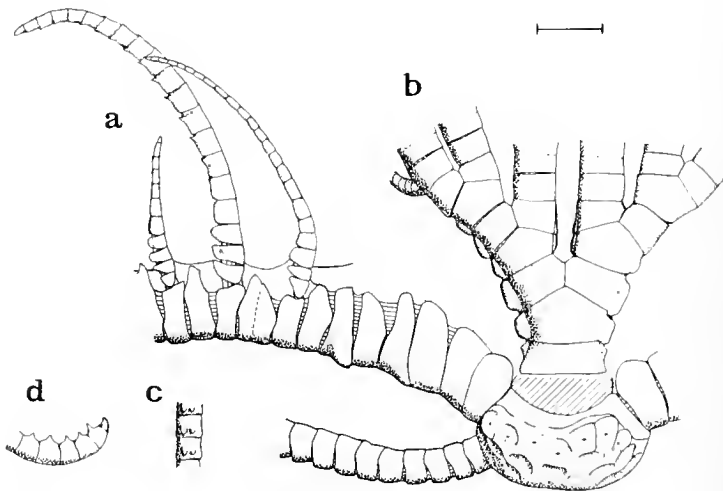


FIG. 12. *Cenometra emendatrix madagascavensis* subsp. nov. Holotype and paratype. B.M. reg. no. 1969.5.13.93. E Madagascar. Arm br 1.6 mm (after either II Br or III Br series) and 1.5 mm. a. paratype, side view of calyx with cirrus base and proximal part of one post-radial series to  $Br_7$  showing  $P_1$  to  $P_3$ ; b. holotype, dorsal view of proximal part of one post-radial series; c. dorsal view of segments from middle of cirrus showing paired spines and d. cirrus tip. [The scale equals 2 mm.]

increase in arm number during growth is most often by multiple augmentation (Gislén, 1923 : 14), the synarthry between the first two brachials on arms following IBr series being very easily broken, the subsequent regeneration resulting in simultaneous development not just of an axillary IIBr<sub>2</sub> and a pair of arms but of another division series (a IIIBr) in place of the external arm followed by a simple pair, resulting in three arms in place of one rather than the more usual two. This tendency for rapid augmentation in arm number is more marked in the Malagasy specimens where most post-radial series are symmetrical with six arms, the two median ones based on IIBr axillaries while the external four are paired on IIBr series. In the Mascarene and Seychellois specimens the average number of arms derived from each radial is four, the asymmetrical arm on one side being based on the IBr series having survived after loss and replacement of its opposite number.

As can be seen from the table, apart from the greater arm number, the number of cirri is also much greater in the specimens from Madagascar even though the centro-dorsal is similar in size, its diameter being most often about 5.0-5.5 mm in the specimens from both areas. However, the composition and length of the cirri themselves may not be significantly different, though unfortunately those of the syntypes of *C. emendatrix emendatrix* are unknown.

In a direct comparison of individual specimens, if the product of arm length, breadth and number is used as the criterion of size then specimen no. 3 of *C. emendatrix madagascarensis* in the table is most closely comparable with no. 27 of *C. e. emendatrix*. The cirri are similar in segments number and length in these two but there are nearly twice as many of them in the Malagasy specimen. Also the lengths of P<sub>1</sub> and P<sub>3</sub> at least are significantly greater, while P<sub>1</sub> also has more segments. These differences still hold good if specimens with individual arms of similar proportions are compared, for instance nos. 4 and 5 against 24, all with arms c. 90 mm long and 1.4 mm proximal br. The syntypes of *C. e. emendatrix* are rather variable with regard to the shapes of P<sub>1</sub> and P<sub>2</sub>; one has quite a stout P<sub>1</sub> with br at the fifth segment 0.6 mm compared with 0.8 mm br at the fifth segment of P<sub>2</sub>, which has particularly short segments in this specimen, most of them distinctly shorter than broad. Another syntype has a much slimmer P<sub>1</sub> with more prominent crests on segments two to five. With regard to these crests, in my opinion none of the three larger syntypes of *C. e. emendatrix* has the carination of P<sub>2</sub> really 'high and conspicuous' (see A.M.C. & Rowe, 1971, fig. 7a, p. 18) as given as characteristic of the species in A. H. Clark's key to *Cenometra* (1947 : 27), even if it was so in Möbius' specimen from Mauritius. Clark's key leans heavily on the development of basal crests on the various proximal pinnules for distinguishing the species of *Cenometra* and I would not be surprised if the poorly-described *C. herdmani* A. H. Clark, 1909, from Ceylon and southern India, with crests only on P<sub>1</sub> and P<sub>3</sub>, does not prove to be conspecific with *C. emendatrix*. *C. cornuta* A. H. Clark, 1911, from Australia has relatively shorter cirrus segments, P<sub>2</sub> much shorter, P<sub>1</sub> somewhat stouter and the division series less widely separated, though again with distinct ventro-lateral flanges, judging from a direct comparison of the holotype with the present material. The small number of cirri, only XIV, given by A. H. Clark for the type of *C. cornuta* might be thought to provide a further distinction but I estimate that there are (or

TABLE 9

Numerical data from specimens of *Cenometra emendatrix madagascarensis* subsp. nov. (nos 1-21) and *C. emendatrix emendatrix* (22-28); nos. 25, 26 and 28 are syntypes

No.	Arms			Cirri			Pinnules						
	No.	Length	Br at 3 + 4	No.	Segs.	Length	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Segs.	L.	Segs.	L.
1	18	—	1·0	XIV	31	16	—	—	—	—	—	—	—
2	16	—	1·2	XVII	—	—	24	6·8	23	11·3	—	14	4·2
3	32	c. 90	1·3	XL	38	21	26	8·9	23	11·0	—	16	6·3
4	29 (230)	c. 90	1·4	XXVII	39	25	24	9·5	23	12·1	—	17	5·3
5	30	c. 90	1·4	XXXV+	41	20	25	9·5	23	13·2	—	16	6·3
6	32	60+ +	1·4	XXX	49	32	20	8·7	26	13·9	—	15	5·5
7	c. 30	90	1·5	XXIX	43	30	25	10·0	25	14·7	—	17	6·3
8	28 (220)	40+ +	1·5	XL	42	27	23	8·4	25	14·7	—	18	6·6
9	29 (230)	40+ +	1·6	XXXVII	41	24	25	10·8	27	15·8	—	14	5·5
10	28 (230)	c. 125	1·6	XXXIII	46	30	26	8·4	25	14·2	—	17	6·3
11	12 + (233)	c. 100	1·5	XXXV	51	35	27	10·3	34	15·8	—	18	6·8
12	31 (232)	120	1·6	XXXII	45	25	30	11·0	—	—	—	17	6·3
13-21	Arm no. 24-32 (237) in nine more or less broken specimens												
Range	24-32 (237)	90-125	1·3-1·6	XXVII-XL	38-51	21-35	24-30	8·4-11·0	23-34	10·5-15·8	—	14-21	5·3-8·4
Mean	30			XXXII			25	9·6	25	13·6	—	17	6·4
22	12	c. 70	1·3	XVI	34	17	13	4·7	17	8·2	—	12	2·9
23	13 (216)	80	1·3	XV	—	—	16	5·3	18	7·9	—	13	4·0
24	14	90	1·4	XX	41	c. 27	18	5·8	—	—	—	13	4·2
25	10	c. 75	1·5	XXIII	—	—	20	8·7	20	11·6	—	13	4·0
26	21	c. 70	1·6	XIX	—	—	20	6·6	18	9·5	—	14	5·8
27	22	c. 115	1·4	XXII	36	c. 22	20	6·6	—	—	—	14	5·0
28	14 (216)	90	1·6	XVIII	—	—	(17)	6·6	20	13·1	—	14	5·0
Range	18-22	70-125	1·3-1·6	XV-XXIII	34-41	17-27	13-20	4·7-8·7	17-22	7·9-13·1	—	12-14	2·9-5·8
Mean	17			XIX			18	6·3	19	10·1	—	13	4·2

were) XV mature cirri and an additional six immature ones, giving a total of, say, XVIII, which lessens the discrepancy. I have no material of the oldest known species, *C. bella* (Hartlaub, 1890), recorded from the South Pacific islands to Burma, only the largest specimens of which are said to have any sign of pinnule crests.

### *Colobometra discolor* A. H. Clark

*Colobometra discolor* A. H. Clark, 1909c : 640-641; 1912a : 166-168, fig. 25; 1947 : 128-132, pl. 15, figs 72-75, pl. 16, figs 76-79.

MATERIAL. 'Anton Bruun' cruise I, st. 18A, 07°34'N : 98°00'E (between Malaya and the Nicobar Is.), 77 metres; 17 specimens.

DESCRIPTION. Measurements and counts were made on four specimens. These have:

arm length	c. 80 mm	c. 90 mm	c. 85 mm	c. 65 mm
breadth at 3 + 4	1·7 mm	1·6 mm	1·6 mm	1·5 mm
length to 3 + 4	4·0 mm	4·1 mm	4·0 mm	3·4 mm
cirrus number*	XVIII + vi	XX + iv	XXII + iii	XVIII + iv
cirrus segments	47-49	40-42	40-42	35-39
cirrus length	25-30 mm	c. 28 mm	c. 23 mm	22-23 mm
P <sub>1</sub> segs and length	18, 7·6 mm	17, 7·1 mm	16, 5·5 mm	18, c. 5 mm
P <sub>2</sub> segs and length	19, 11-12 mm	17, 13·4 mm	17, 10·5 mm	14, 8·7 mm
P <sub>3</sub> segs and length	15, 8·7 mm	17, 12·6 mm	17, 10·0 mm	15, 7·6 mm

The cirrus segments are flared distally, the dorsal spines stout; the longest segments (about the eighth) have length : median breadth c. 1·0 : 0·7 mm in the first specimen. The dorsal pole of the centrodorsal is 2·0-2·6 mm in diameter. P<sub>1</sub> is relatively smooth and tapering; P<sub>2</sub> is much stouter with elongated, distally-flared and spinose segments; P<sub>3</sub> is similar to P<sub>2</sub> but shorter.

The maximum number of cirrus segments given by A. H. Clark is 48 (though up to only 40 are mentioned in his diagnosis); otherwise these specimens fall within the ranges he gives for the various characters.

### *Cotylometra gracilicirra* (A. H. Clark)

(fig. 13)

*Oligometra gracilicirra* A. H. Clark, 1908b : 221-222; 1912a : 168, 323, fig. 26.

*Cotylometra gracilicirra* : A. H. Clark, 1918 : 128, pl. 28, fig. 110.

*Cotylometra gracilicirra gracilicirra* : A. H. Clark, 1947 : 49-51, pl. 8, figs 38-40, pl. 9, figs 41, 42.

MATERIAL. 'Anton Bruun' cruise I, st. 18A, 07°34'N : 98°00'E (between Malaya and the Nicobar Is.), 77 metres; 2 specimens.

\*Roman capitals signify the number of more or less mature cirri and small roman numerals of immature cirri. The numbers of segments and cirrus length refer only to mature peripheral cirri.

DESCRIPTION. The larger specimen has arms  $40 + c. 5$  mm long and the breadth at the first syzygy,  $3 + 4$ , is 1.2 mm. The very thick discoidal centrodorsal is 1.1 mm high and 2.4 mm in maximum diameter; the diameter of the flat but markedly spinose dorsal pole is 1.7 mm. The cirri number XII; the three remaining have 33, 33 and 35 segments; the last measures 12.0 mm in length. The longest cirrus segment, about the eighth, has length : median breadth 0.55 : 0.60 mm with maximum breadth 0.65 mm including the dorsal projection. This projection takes the form of a single distally directed spine from about the twelfth segment measuring up to c. 0.1 mm in height but on several segments preceding the twelfth there is an additional slightly smaller spine each side making a transverse row of three.  $P_1$  has 10 or 11 segments and measures c. 2.6 mm.  $P_2$  with 12 segments is c. 4.0 mm long and  $P_3$  with 10 segments 3.4 mm long.  $P_2$  and the following pinnules have markedly spinose and flared distal ends to the segments after the basal two and are distinctly prismatic in their distal halves.  $P_a$  is absent throughout and  $P_1$  on one arm.

The smaller specimen has arms c. 35 mm long; the breadth at the first syzygy is 1.05 mm. There are 30 segments in two mature cirri counted. The dorsal spines are sharper and more prolonged than in the other specimen (see fig. 13c) and are usually single from the tenth segment, being preceded on several segments by a transverse ridge of three spines.

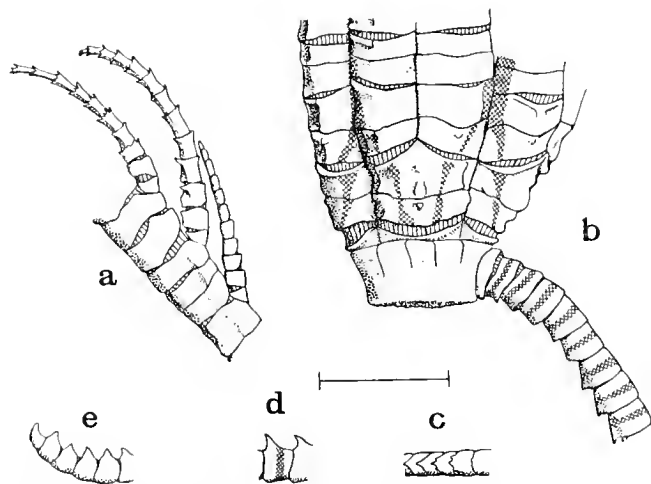


FIG. 13. *Cotylometra gracilicirra* (A. H. Clark). 'Anton Bruun' st. 18A, N Malacca Strait. Arm br 1.2 mm (after IIBr series). a. side view of proximal part of an external arm from Br<sub>2</sub> to Br<sub>7</sub> showing  $P_1$  to  $P_3$ ; side view of calyx, bases of post-radial series and a cirrus; c. dorsal view of cirrus segments 8-11 of smaller specimen showing transition from small multiple spines to single large one; d. side view of segment 12 and e. of cirrus tip. (The colour pattern is indicated by cross-hatching.) [The scale equals 2 mm.]

REMARKS. In spite of its original inclusion in *Oligometra* by A. H. Clark, *Cotylometra gracilicirra* does not fit very well into the family Colobometridae on account of its laterally compressed cirri with even the proximal segments lacking the characteristic flattened dorsal surface with paired tubercles or spines. Although there is a transverse ridge on a few segments, this is highest in the middle. However, the frequent absence of  $P_a$  allies it with some members of the Colobometridae, while the prismatic, spinose pinnules mark it off from the subfamily Perometrinæ of the Antedoninae—which also shows a tendency for reduction of  $P_a$ .

As can be seen from figure 13b, the larger of the two 'Anton Bruun' specimens has a distinct keel on each division series and a median tubercle on the first brachial of each arm. A. H. Clark distinguished four specimens from east of Borneo showing this condition, together with marginal tubercles on the division series and first two brachials, as *Cotylometra gracilicirra* variety (later subspecies) *ornata* but such modifications in ornamentation are often variable and the present specimens suggest that the carinate condition may occur throughout the range of the species. I think that further material will probably show little justification for maintaining the subspecies.

### *Cyllometra manca* (P. H. Carpenter)

*Antedon manca* P. H. Carpenter, 1888 : 226–227, pl. 44, figs 2, 3.

*Cyllometra manca*: A. H. Clark, 1907 : 357; Gislén, 1922 : 80–81, figs 66, 67; A. H. Clark, 1947 : 137–169, pl. 17, fig. 86, pl. 18, fig. 87, pl. 19, figs 91–96, pl. 20, figs 99, 100, pl. 21, fig. 101, pl. 22, figs 102–108; Utinomi & Kogo, 1965 : 276–277, fig. 8.

MATERIAL. 'Anton Bruun' cruise 1, st. 21, 09°54'N : 97°42'E (SW of Mergui Archipelago), 70 metres; 1 specimen.

'Anton Bruun' cruise 1, st. 22A, 10°37'N : 97°34'E (SW of Mergui Archipelago), 75–80 metres; 9 specimens.

'Anton Bruun' cruise 8, st. 420A, 02°42'N : 40°53'E (off Kenya–Somalia border), 140 metres; 1 specimen.

'Anton Bruun' cruise 9, st. 437, 09°25'N : 50°54'E (off N Somalia), 85–95 metres; 1½ specimens.

'Anton Bruun' cruise 9, st. 442, 09°33'N : 50°59'E (off N Somalia), 70–80 metres; 6 specimens.

'Anton Bruun' cruise 9, st. 444, 09°36'N : 51°01'E (off N Somalia), 78–82 metres; 5 specimens.

'Anton Bruun' cruise 9, st. 447, 10°00'N : 51°15'E (off N Somalia), 59–61 metres; 1 specimen.

DESCRIPTION. Of the fourteen specimens from off Somalia, all but three have more than ten arms, the maximum number (in one of the smallest specimens) being 17. The largest specimen from st. 442, arm length c. 90 mm, breadth at the first syzygy (after IBr series) 1.25 mm, contrasts with the rest not only in having the purple colour much more widespread but also in having most of the cirri with the maximum dorsal height predominantly median rather than in the form of paired

tubercles and  $P_3$  almost as stout as  $P_2$ . On the mature cirri the last ten or more segments before the penultimate have a crescentic dorsal elevation with a more or less sharp apex, though proximally there is sometimes more of a transverse ridge with one or more tubercles each side of the median projection. This form of the cirri resembles that in the larger specimens from Japan described under the name of *Cyllometra alboburpurea* by Gislén (1922), regarded by A. H. Clark (1947) as a synonym of *C. manca*, together with *C. disciformis* (P. H. Carpenter), *C. anomala* A. H. Clark, *C. soluta* A. H. Clark and *C. pulchella* Gislén. If A. H. Clark is right then *C. manca* is an extremely variable species, especially with regard to the cirri. Detailed correlation of the variable characters relating them to absolute size is needed before a proper assessment of the specific limits in *Cyllometra* can be arrived at. Unfortunately the genus is poorly represented in the British Museum collections.

The large specimen from station 442 has 14 arms. Its centrodorsal is 3.7 mm in maximum diameter with the dorsal pole 3.0 mm across. The division series are smooth, widely separated laterally, as usual in *Cyllometra*, especially in contrast with *Cotylometra*, without synarthrial tubercles, though the arm bases are slightly carinate.  $P_1$  is very slender with 16 extremely elongated segments and length 7.9 mm. No  $P_2$  is complete or unregenerated; likewise  $P_3$  though both these pinnules appear similarly stout and their segments are flared at their distal ends with a rugose dorsal tuft. The cirri, described above, have up to 31 segments and the longest measure c. 16 mm.

The largest of the other specimens from this station have arm length c. 60 mm and mostly have small paired dorsal spines on the cirri giving way to a single spine for the last five or so segments before the penultimate.

RANGE. The records from off Somalia represent an extension of the known range of this species, the previous westernmost locality known being the entrance to the Persian Gulf. [See also p. 152.]

### *Decametra mylitta* A. H. Clark

*Decametra mylitta* A. H. Clark, 1912d : 36; 1918 : 118-120; 1947 : 188-191, pl. 22, fig. 110, pl. 23, figs 116, 117, pl. 24, fig. 118.

MATERIAL. 'Anton Bruun' cruise 1, st. 28A, 11°52'N : 92°49'E (Andaman Is.), 66 metres; 1 specimen (?*D. mylitta*).

'Anton Bruun' cruise 1, st. 47B, 19°50'N : 92°55'E (off Akyab, Burma), 22-30 metres; 2 specimens, one badly broken.

DESCRIPTION. The more nearly intact specimen from st. 47B has arms up to 65 mm long, breadth at the first syzygy (3 + 4) 1.4 mm and length from the proximal edge of the IBr<sub>1</sub> to this syzygy 3.3 mm. The maximum and dorsal pole diameters of the centrodorsal are 3.3 and c. 2.0 mm. There are XXII cirri with up to 25 segments and length up to 11.5 mm; the longer segments about the ninth have



length : breadth 0.55 : 0.80 mm and the antepenultimate 0.45 : 0.65 mm. There are small paired tubercles from about the ninth segment, fusing into a single slightly larger one about four segments before the penultimate. The division series have synarthrial tubercles of moderate size, also the first two brachials. There are no lateral flanges though the adjacent division series are less widely spaced than in *Cyllometra*.  $P_1$ ,  $P_2$  and  $P_3$  have 15, 16 and 15 segments and measure 5.0, 7.6 and 5.5 mm in length,  $P_2$  being stoutest; it develops a small spinose tuft dorsally at the distal end of the fourth segment with slightly larger tufts shifting to the edge facing the arm tip on the following segments; otherwise the pinnules are fairly smooth.  $P_a$  is only found on two arms. There are small pink spots on many brachials and one each side of many pinnule segments.

The specimen from station 28A is only provisionally referred to this species since it has  $P_a$  present, as in *Oligometra*; however, this is often rather variable. The arms are c. 75 mm long. The stout cirri have 20 or 21 short segments, mostly with transverse ridges though a few have paired tubercles. The first three pinnules have 16, 17 and 13 segments and measure 5.5, 9.0 and 5.3 mm; they are nearly cylindrical and smooth distally. There are five acorn barnacles, *Octolasmis orthogonia* (Darwin) (named by Dr K. McKenzie), on the cirri.

RANGE. This is now extended into the Bay of Bengal, Singapore being the previous westernmost record.

### *Oligometra serripinna* (P. H. Carpenter)

*Antedon serripinna* P. H. Carpenter, 1881 : 182.

*Oligometra serripinna*: A. H. Clark, 1910 : 179-180; 1912a : 169-174, 323-324, fig. 28; 1947 : 216-217 (varieties and subspp. treated separately).

MATERIAL. 'Anton Bruun' cruise 1, st. 22A, 10°37'N : 97°34'E (SW of Mergui Archipelago), 75-80 metres; 2 specimens.

'Anton Bruun' cruise 1, st. 37, 13°28'N : 97°19'E (N of Mergui Archipelago), 64 metres; 1 specimen.

'Anton Bruun' cruise 1, st. 47A, 20°16'N : 92°32'E (NW of Akyab, Burma), 13-15 metres; 5 specimens.

'Anton Bruun' cruise 1, st. 47B, 19°50'N : 92°55'E (off Akyab, Burma), 22-30 metres; 8 specimens.

'Anton Bruun' cruise 8, st. 400C, 20°30'S : 35°43'E (off Beira, Mozambique), 62 metres; 4 specimens.

Prof. A. G. Humes's no. 948, NW coast of Nosy Ory, Radama Is., Madagascar, 10 metres; 3 specimens. B.M. reg. no. 1969.5.13.94.

Mr W. Humphreys, Passe du Bois, Aldabra; 1 specimen. 1971.3.3.1.

All these specimens run down to the subspecies *O. serripinna serripinna* in A. H. Clark's key (1947 : 216-217) except for the one from off Mozambique which has very ornate processes on the proximal pinnules and could be referred to the variety

electrae and the one from Aldabra, which conversely has the earlier pinnules hardly serrate in profile and could be called variety *occidentalis*.

Several immature specimens of Colobometrids cannot be determined with any certainty without more knowledge of the growth changes and variation within this family:

#### Colobometrid sp. A

MATERIAL. 'Anton Bruun' cruise 7, st. 371D, 24°46'S : 35°20'E (SE of Inhambane, Mozambique), 165 metres; 2 specimens.

One has 11 arms 20 + 5-10 mm long, breadth at the first syzygy 0.55 mm and c. XV cirri with 16 segments, c. 5 mm long. P<sub>2</sub> is the largest pinnule on some arms and there is no P<sub>a</sub>. The other specimen has ten arms c. 25 mm long, breadth 0.50 mm and c. XII cirri with 16 segments, c. 4.5 mm long.

Both have relatively narrow division series and may be referable to *Cyllometra manca* but, despite the extension westwards to Somalia in the known range of that species in this paper, without more mature specimens from further south off the East African coast I hesitate to refer them to *C. manca*.

#### Colobometrid sp. B

MATERIAL. 'Anton Bruun' cruise 8, st. 393A, 29°32'S : 31°17'E (NE of Durban, Natal), 50-53 metres; 1 specimen.

The ten arms were c. 33 mm long; the breadth at the first syzygy is 0.65 mm. The short cirri have up to 13 segments and measure only 3.8 mm. The proportions of the proximal pinnules are difficult to determine but P<sub>1</sub> may be larger than P<sub>2</sub> which has c. 10 segments. P<sub>a</sub> is absent. The division series and first brachial of each arm have ventro-lateral flanges, unlike *Cyllometra*.

#### Colobometrid sp. C

MATERIAL. 'Anton Bruun' cruise 1, st. 21, 09°54'N : 97°42'E (SW of Mergui Archipelago), 70 metres; 1 specimen.

The ten arms were c. 38 mm long; the breadth at the first syzygy is 0.90 mm. The centrodorsal is finely papillose; the cirri are all lost. P<sub>1</sub>, P<sub>2</sub> and P<sub>3</sub> have 12, 14 and 11 segments and are 3.0, c. 4.2 and 2.8 mm long, P<sub>2</sub> being the stoutest. There is no P<sub>a</sub>.

#### Colobometrid sp. D

MATERIAL. 'Anton Bruun' cruise 1, st. 21, 09°54'N : 97°42'E (SW of Mergui Archipelago), 70 metres; 7 specimens.

The ten arms are 20-30 mm long; one specimen has the breadth at the first

syzygy 0.35 mm. There are only c. 12 cirrus segments which are very short with fine sharp spines. The division series and brachials are all flared at the edges so that the profile of the arms is very serrate. The pinnules have long fine spines at the distal ends of the segments.  $P_a$  is absent.

Possibly these may be referred to *Decametra*.

### Family TROPIOMETRIDAE

#### *Tropiometra carinata carinata* (Lamarck)

*Comatula carinata* Lamarck, 1816 : 534.

*Tropiometra carinata* : A. H. Clark, 1911b : 34-35; Humes & Ho, 1970 : 1.

*Tropiometra carinata carinata* : A. H. Clark, 1947 : 291-337, pl. 35, figs 183, 184, pl. 36, figs 187, 188.

MATERIAL. 'Anton Bruun' cruise 8, st. 420A, 02°42'S : 40°53'E (off Kenya-Somalia border), 140 metres; c. 50 specimens.

'Anton Bruun' cruise 9, st. KA-13, reef on W shore, Grand Comoro I., 5-15 metres; 3 specimens.

'Anton Bruun' cruise 9, st. 447, 10°00'N : 51°15'E (off N Somalia), 59-61 metres; 2 specimens.

'Anton Bruun' cruise 9, st. RU 295, 13°30'S : 45°16'E (outer and inner sides, Bandeli Reef, Mayotta I., Comoro Is.), c. 1 metre; 5 specimens.

J. Rudloe's st. 29, Ambatoaka Beach, Nosy Bé, Madagascar; 1 specimen.

J. Rudloe's st. 30, Ambarionaombi Point, Nosy Bé; 1 specimen.

Professor A. G. Humes, Nosy Bé area (various stations, see Humes & Ho, 1970); 104 specimens.

#### *Tropiometra magnifica* A. H. Clark

*Tropiometra magnifica* A. H. Clark, 1937 : 90-91, pl. 1, fig. 1; 1947 : 266-268, pl. 33, figs 170-173.

MATERIAL. 'Anton Bruun' cruise 8, st. 420A, 02°42'S : 40°53'E (off Kenya-Somalia border), 140 metres; 5 specimens.

DESCRIPTION. This fine species was previously only known from the holotype taken in the Gulf of Aden by the John Murray Expedition.

Unfortunately all the arms of these specimens are somewhat broken; the longest, detached from its calyx, is 210+ mm. It is noticeable that the centrodorsal in this species is much higher relatively than in any of the numerous examples of *Tropiometra carinata* studied, in which it is quite flat with only a single peripheral row of cirri. There are purple stripes or spots along the arms and markings on the cirri, but not as bold as in the holotype.

The last specimen in the table has peripheral cirri with 43 or 44 segments measuring 4.0-4.5 mm. Its dorsal pole is distinctly convex.  $P_2$  and  $P_3$  have 26 and 27

segments and measure c. 21 and c. 22 mm. [Owing to the relatively large size these measurements are all taken with the naked eye, the need for precision being countered by variation.]

The holotype of *Tropiometra magnifica* with arm length 265 mm (A. H. Clark's estimate) has the breadth at the first syzygy only 3.7 mm so the 'Anton Bruun' specimens are all even larger.

RANGE. This record provides a small extension of range southwards from the Gulf of Aden.

TABLE 10

Numerical data from the four least broken specimens of *Tropiometra magnifica*, only 5, 3, 6 and 9 arms remain respectively

Diam.	Centrodorsal		Arm br. at 3 + 4	Cirrus no.	Segs.	P <sub>1</sub>		2nd syzygy at 9 + 10
	Ht.	D. pole				L.		
15	5.5	10.0	5.5	XXXIV	32*	c. 25	4/5	
14	4.5	8.5	5.5	XXIX	37	c. 30	2/3	
14	5.5	10.0	5.0-5.5	XXVI	35	c. 28	6/6	
12	5.0	c. 7	4.5-5.0	XXXIV	39	c. 32	8/9	

\* Possibly regenerated from the seventh segment after which the segments are abruptly shorter though not narrower.

### Family CALOMETRIDAE

#### *Neometra spinosissima* (A. H. Clark)

*Calometra spinosissima* A. H. Clark, 1909b : 79-80.

*Neometra spinosissima*: A. H. Clark, 1912a : 181-183, fig. 30; 1947 : 364-366, pl. 39, fig. 203.

MATERIAL. 'Anton Bruun' cruise 1, st. 18A, 07°34'N : 98°00'E (between Malaya and the Nicobar Is.), 77 metres; 2 specimens.

DESCRIPTION. The larger specimen has 17 arms on four radii, the fifth IBr series being broken; there were probably 21 arms. All the division series are of two ossicles and are very constricted laterally. The breadth at the first syzygy (3 + 4) after a IIBr series is 1.3 mm and the length from the proximal edge of the IBr<sub>1</sub> to this syzygy is 7.5 mm. The complete arm length was probably just over 100 mm. The cirri are XV + iii, the longest intact one with 47 segments and c. 30 mm in length (all are considerably incurled in the distal part). The longest cirrus segments have length : breadth c. 1.0 : 1.0 mm. Dorsal spines 'roman-nosed' in profile start from about the twelfth segment. P<sub>1</sub> has 36 segments and measures 11.0 mm in length. No P<sub>2</sub> or P<sub>3</sub> remains intact; they are progressively stouter than P<sub>1</sub> and their first 14 segments measure respectively 11.3 and 14.0 mm. P<sub>4</sub> is similar to P<sub>3</sub> except that the first two segments are less extravagantly enlarged.

The smaller specimen probably had c. 20 arms and XV cirri with c. 46 segments.

These specimens conform well with the holotype and only known specimen.

RANGE. This record provides a small extension of range southwards from the Andaman Islands.

### Family ASTEROMETRIDAE

Asterometridae Gislén, 1924 : 231; A. H. Clark, 1947 : 415-416.

A. H. Clark (1947) distinguishes two genera in this family, having split off *Pterometra* from *Asterometra* in 1909. In his key (1947 : 416), *Pterometra* is characterized by having 20-30 arms, cirri with the longer proximal segments more or less constricted medially and usually with a *ventral* projection at their distal ends, as well as pinnules of the proximal third of the arms not shorter than the distal but with many segments medially constricted and distally flared and spinose. *Asterometra* is said to have only 10-16 arms, the longer cirrus segments not constricted or produced ventrally and proximal pinnules shorter than the distal ones with only their distalmost segments at all modified. The main specific characters used in his keys include the length of the cirri relative to the arms, the development and extent of keels on the division series and the relative breadth of the proximal part of the animal. He also notes that the colour is pale in *Asterometra* but more or less brown or reddish in *Pterometra*.

The large sample of c. 70 asterometrids taken at 'Anton Bruun' station 18A (between Malaya and the Nicobar Islands) shows a range in arm number from 11 to 20, though with a mean of c. 19 if the smaller specimens are excluded (approximating perhaps more to *Pterometra*), the longer cirrus segments not notably constricted and, except in nine specimens, lacking any trace of ventral processes (which agrees more with *Asterometra*, as do the form and proportions of the pinnules, only the distalmost segments of the proximal ones being at all flared and spinose, though the darkish colour of many specimens again allies them with *Pterometra*). Then the length of the cirri relative to the arms ranges from 0.69 to 1.17 : 1 and the division series vary from having sharp median keels to being perfectly smooth, while it seems to me that the relative breadth of the proximal part of the animal depends too much on the attitude of the arms in preservation to be of use as a distinguishing character.

Further study of A. H. Clark's keys shows that two of the five species of *Pterometra* are, in fact, not supposed to have ventral cirral spines, in contradiction to the generic key, these two being *P. magnifica* and *P. pulcherrima*. However, A. H. Clark has referred to the latter species a specimen from the Gulf of Martaban (Burma) in which prominent ventral spines *are* present on the cirri. This record is the only one for the whole family from the Indian Ocean and, since A. H. Clark has referred mature specimens with as few as 12 arms to *P. pulcherrima* despite his generic diagnosis, I am referring the 'Anton Bruun' specimens to this species. However, I am very doubtful whether it is worth retaining *Pterometra* as a distinct genus. Unfortunately the family is poorly represented in the British Museum collections and I cannot at present try and ascertain the extent of variation in any of the other species.

Some additional descriptive notes on the holotype of *Asterometra longicirra* are given in the Appendix on p. 152.

*Pterometra pulcherrima* (A. H. Clark)

(fig. 14)

*Ptilometra pulcherrima* A. H. Clark, 1909f : 400-402.

*Asterometra pulcherrima* : A. H. Clark, 1912a : 193.

*Pterometra pulcherrima* : A. H. Clark, 1918 : 145, pl. 9, pl. 28, fig. 104; 1947 : 427-432, pl. 43, figs 218, 219.

MATERIAL. 'Anton Bruun' cruise 1, st. 18A, 07°34'N : 98°00'E (between Malaya and the Nicobar Is.), 77 metres; c. 70 specimens.

REMARKS. Fortunately in this family the arms are strong and end abruptly after tapering sharply, to such an extent that with the naked eye they look almost as if they are regenerating after breakage. It is therefore possible to relate their length to other measurements and counts with a fair degree of precision, though in the calculations for the data given in Table 11 the arm lengths were taken to the nearest 5 mm, allowing a little for variation of the individual arms. It is notable that the sample consists mainly of specimens showing a small size range, arm length 55-70 mm, only two specimens having arms less than 40 mm long.

About one specimen in eight was found to have even the longest segments of the peripheral cirri barely longer than broad and with a prominent ventral spine projecting from the distal end of each, as in the 'Investigator' specimen also from the Bay of Bengal, described by A. H. Clark. Also none of the specimens with such cirri have any development of a keel on the division series. However, this latter character is not restricted to the specimens with ventral cirrus spines and the range in the relative length of the longest cirrus segments overlaps that in the bulk of the material. The number of cirrus segments is no greater in the specimens with ventral cirrus spines and consequently the length of their cirri tends to be less, relative to the arm length, than in the main part of the sample. (It should be noted though that unfortunately the peripheral cirri are more often broken than the arms, so that estimates of their length and segment number may be too low, not being based on the largest ones.) Although there is some correlation between the form of the cirri and the lack of modification of the division series in these specimens, I do not think it is sufficient to justify a nomenclatorial difference, though the specimens concerned are segregated in Table 11. Also separated off from the bulk of the sample are seven specimens which are relatively small in mass, having either unusually few arms (e.g. 12, though with an arm length of c. 65 mm) or unusually short arms (only 40 mm long in one specimen, though numbering as many as 19).

In addition the table includes for comparison some summarized data from Gislén (1922 : 111) on *Asterometra anthus* (A. H. Clark) from the Bonin Islands, S. of Japan, this being the only other good sample of any member of the family for which details

Numerical data from s

	No.	Br st : r)	Pinnules				
			P <sub>1</sub>		P <sub>2</sub>		L.P <sub>2</sub> : L.P <sub>1</sub>
			Segs.	L. (mm)	Segs.	L. (mm)	
<i>erometra pulcherrima</i>							
all specimens:							
Range	11-19	81	9-15	4.0-4.7	10-13	5.0-5.8	1.22-1.36
Mean and number	14 (6)	7)	11	4.3 (5)	11	5.5 (6)	1.28 (5)
in sample:							
Range	16-20	76	12-15	4.2-6.3	12-16	5.2-9.0	1.05-1.55
Mean and number	19 (47)	17)	13	5.3 (41)	14	6.9 (43)	1.29 (40)
S.D.	1.02		0.88	0.50	1.08	0.69	0.14
specimens with short cirrals:							
Range	20-21	27	10-17	4.2-6.8	10-17	5.3-10.0	1.15-1.69
Mean and number	20 (9)	9)	13	5.6 (18)†	13	7.4 (18)†	1.33 (18)†
type material (from A.H.C.,							
947)	20		—	—	—	—	—
Holotype	20		16	8	19	12.5	1.56
investigator' st. 387							
from A.H.C.)	20		15	7	15	10	1.43
<i>erometra anthus</i>							
arger specimens							
(from Gislén, 1922):							
Range	10-16		8-14	4-7	9-14	5.0-9.5	1.00-1.39
Mean and number	11 (32)		11.4	5.6 (24)	11.6	6.7 (25)	1.18 (24)
<i>erometra longicirra</i>							
otype	10		11	6.3	12	8.4	1.34

This value is probably slightly low since some true figure may be c. 1.0 : 1.

Several pinnules were measured from each s

This maximum must be an error if the hol

TABLE II

Numerical data from specimens of *Pterometra pulcherrima*, also *Asterometra anthus* and the holotype of *A. longicirra* for comparison.  
The cirrus counts include consolidated fractions for immature ones

	Arms			Centrodorsal			Cirri					Pinnules					
	No.	L. (mm)	Breadth at 3 + 4 (mm)	Length to 3 + 4 (mm)	Ht. (mm)	Diam. : Ht. ( : 1)	Cirrus L : Arm L.	No.	Segs.	L. (mm)	L. of longest seg. (mm)	L : Br longest seg. ( : 1)	P <sub>1</sub>		P <sub>2</sub>		
													Segs.	L. (mm)	Segs.	L. (mm)	L.P <sub>2</sub> : L.P <sub>1</sub>
<i>Pterometra pulcherrima</i>																	
Small specimens:																	
Range	11-19	33-65	0.8-1.2	4.7-6.2	1.6-3.2	1.05-1.40	0.69-1.14	XIV-XX	58-93	35-61	0.85-1.15	1.31-1.81	9-15	4.0-4.7	10-13	5.0-5.8	1.22-1.36
Mean and number	14 (6)	47.5 (7)	1.04 (7)	5.4 (7)	2.4 (7)	1.32 (7)	0.95 (6)	XVII (7)	70 (6)	43 (6)	1.00 (7)	1.46 (7)	11	4.3 (5)	11	5.5 (6)	1.28 (5)
Main sample:																	
Range	16-20	55-70	1.2-1.5	5.5-7.4	2.4-4.5	0.87-1.88	0.69-1.17	XV-XXV	70-100	40-70	0.90-1.30	1.06-1.76	12-15	4.2-6.3	12-16	5.2-9.0	1.05-1.55
Mean and number	19 (47)	64 (47)	1.3 (47)	6.3 (47)	3.2 (47)	1.33 (47)	0.91* (38)	XX (47)	84 (40)	57 (40)	1.13 (47)	1.35 (47)	13	5.3 (41)	14	6.9 (43)	1.29 (40)
S.D.	1.02	5.30	0.07	0.39	0.50	0.20	0.11	2.30	7.35	6.33	0.09	0.16	0.88	0.50	1.08	0.69	0.14
Specimens with short cirrals:																	
Range	20-21	55-70	1.2-1.3	5.3-6.3	2.4-2.9	1.38-1.73	0.64-0.84	XV-XXIV	68-87	40-50	0.95-1.05	1.00-1.27	10-17	4.2-6.8	10-17	5.3-10.0	1.15-1.69
Mean and number	20 (9)	61 (7)	1.3 (9)	5.9 (9)	2.7 (9)	1.54 (9)	0.72 (5)	XX (9)	79 (8)	44 (8)	1.00 (9)	1.08 (9)	13	5.6 (18)†	13	7.4 (18)†	1.33 (18)†
Type material (from A.H.C., 1947)																	
Holotype	20	70-120	—	—	—	—	0.75-1+	XII-XXV**	80-120	78-128	—	—	—	—	—	—	—
'Investigator' st. 387 (from A.H.C.)	20	100	—	—	5	1.2	c. 0.8	XXXV	80-85	75-80	—	c. 1.4	16	8	19	12.5	1.56
Type material (from A.H.C., 1947)																	
Holotype	20	70	—	—	—	c. 2	c. 0.7	XXV	72-88	46-54	—	c. 1.3	15	7	15	10	1.43
<i>Asterometra anthus</i>																	
Larger specimens (from Gislén, 1922):																	
Range	10-16	55-105	—	—	—	—	0.50-0.88	XV-XXIII	64-100	35-73	—	—	8-14	4-7	9-14	5.0-9.5	1.00-1.39
Mean and number	11 (32)	80 (30)	—	—	—	—	0.73 (31)	XIX (32)	75 (31)	54 (31)	—	—	11.4	5.6 (24)	11.6	6.7 (25)	1.18 (24)
<i>Asterometra longicirra</i>																	
Holotype	10	80-95	2.3	8.2	3.7	1.29	c. 1.0	XVIII	85	90	1.5	1.28	11	6.3	12	8.4	1.34

\* This value is probably slightly low since some specimens may have had the longest cirri all broken;  
the true figure may be c. 1.0 : 1.

† Several pinnules were measured from each specimen, accounting for the extra number.

\*\* This maximum must be an error if the holotype really does have as many as XXXV.



have been published. As a result of his observations Gislén synonymized with *A. anthus* two other nominal species of *Asterometra* described by A. H. Clark.

Since so many of the specimens have one or more complete arms, it was possible to make some measurements of length for correlation with the numbers of brachials. Some variation was found in the length of individual arms in the same specimen, to a maximum of c. 10 mm in the largest, so that, even though the maximum length given in the table is 70 mm, some individual arms c. 75 mm long occur but balanced by others in the same specimen less than the mean value used in the figures. Gislén also found (1922) that it is not practicable to estimate arm length within about 5 mm. The number of brachials is closely correlated with the arm length so that in a single specimen with six complete arms these range in length from 65 to 75 mm and their brachial counts from 110 to 130. A relatively small specimen with arms c. 35 mm long has only 74 brachials on two arms counted.

Apart from the variable features mentioned above and in the discussion of the family, the centrodorsal shows a considerable range of shape from higher than its maximum breadth in a few cases to almost twice as broad as high, the dorsal pole being either dome-shaped or, more often, with five radial convexities of varying degrees of prominence. (A. H. Clark's description of these as *interradial* in his Burmese specimen I think must be a mistake; in the main description of *P. pulcherrima* he notes they are radial.) As shown in fig. 14 there are openings in the calcified part of the centrodorsal, if not in the overlying body wall, on the apices of these convexities, or in similar positions when the dorsal pole is simply domed. These

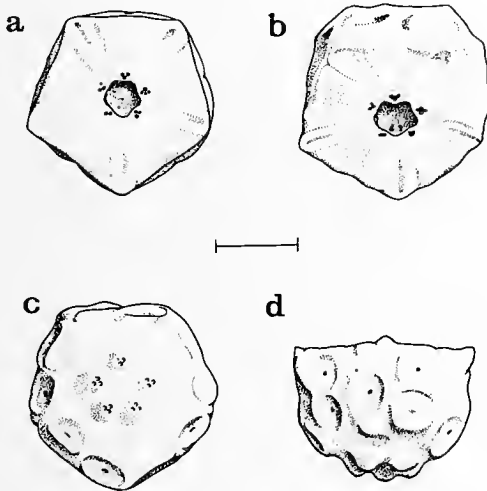


FIG. 14. *Pterometra pulcherrima* (A. H. Clark). 'Anton Bruun' st. 18A, N Malacca Strait. Centrodorsal 4.3 mm in diameter in a. ventral, b. oblique ventral, c. dorsal and d. side views, showing radial canals. [The scale equals 2 mm.]

are the aboral ends of vertical radial canals which perforate the entire centrodorsal outside the chambered organ and are subdivided by partial vertical septa, so that the canal in each radius branches and anastomoses irregularly into up to four separate passages with considerably more surface area than a single canal. However, preliminary sectioning indicates that these canals do not open to the exterior on the dorsal pole. In comparison, the radial pits described and figured by Gislén (1924, figs 287 and 288, p. 209, also fig. 293, p. 217) in *Notocrinus virilis* Mortensen, *Pterometra trichopoda* (A. H. Clark) and *Asterometra anthus* (A. H. Clark) are not only blind, stopping short by a third or less of the total height of the centrodorsal, but also single.

The discovery of complete radial canals perforating the centrodorsal in a recent comatulid supports the presence of similar ones in fossil species such as some of those of *Glenotremites*, *Loriolometra* and *Semiometra* figured by Gislén (1924) and Rasmussen (1961), the existence of which was dismissed by A. H. Clark (1915 : 229). It is also likely that complete canals through the centrodorsal exist, at least in some stage in the ontogeny, in other species of the Asterometridae. All the other species of *Pterometra* described by A. H. Clark usually have five radial convexities (tubercles in his terminology) on the dorsal pole and though in *Asterometra macropoda* he describes such tubercles as interradiar, his figure 190 (1915 : 235) shows them as radial. Although in the fossil species with aboral openings in the skeleton of the centrodorsal these are sunk into stellate hollows, in recent species it could be that they are correlated with convexities instead.

Unfortunately the absence of any really small specimens in the present sample prevents an ontogenetic study of this feature. Mortensen (1918 : 2) notes a fine pore in the centre of the apex of the dorsal pole of his smaller ('half-grown') specimen of *Notocrinus virilis*, surrounded by five radially-placed, possibly blind, pits, the latter having disappeared in the fully-grown specimen. This suggests that if radial perforations exist at any stage then this is likely to be younger rather than older. A fully-grown specimen of *N. virilis* in the British Museum collection decalcified and sectioned shows radial canals penetrating about two-thirds of the height of the centrodorsal. Without either dissolving the skin from the centrodorsal or decalcifying and sectioning it, it is impossible to be certain as to the presence of complete canals but they are present in all four of the 'Anton Braun' specimens so prepared, of both large and medium size, and external examination suggests that at least several more, if not the whole sample, also have them.

#### Familt THALASSOMETRIDAE

#### *Cosmiometra gardineri* A. H. Clark

*Cosmiometra gardineri* A. H. Clark, 1911b : 38; 1950 : 63-64.

MATERIAL. Stanley Gardiner; Saya da Malha Bank (between the Seychelles and the Mascarene Islands), c. 250 metres; the holotype. B.M. reg. no. 1907.7.1.135. 'Anton Bruun' cruise 9, st. 463, 11°24'N : 51°35'E (near Cape Gardafui, Somalia), 75-175 metres; 4 specimens.

DESCRIPTION. The holotype was only cursorily described by A. H. Clark in the form of a comparison with *Cosmiometra woodmasoni*. Some numerical details of it are given at the head of Table 12.

All its division series are of two ossicles. The centrodorsal is low and flattened with height : diameter 3.0 : 5.0 mm; it is somewhat tubercular around the base. There are XIX mature and iii immature cirri; all the mature peripheral ones are broken by the twenty-eighth segment, the data in the table being based on an immature cirrus. The transition segment, usually the ninth, measures 2.4 : 1.0 mm in one mature cirrus and 2.0 : 1.0 in another. The division series bear a smooth, slightly rounded, median keel and are squared off laterally, adjacent ones being fairly well appressed. The IB<sub>r1</sub> are rather irregular. The 20 arms are carinate throughout, finely spinose in the distal half, each brachial having a truncated median distal keel.

TABLE 12

Numerical data from the holotype and four other specimens of  
*Cosmiometra gardineri*

Arms		Cirri			Pinnules			
L. (mm)	Br at 3 + 4 (mm)	No.	Segs.	L. (mm)	P <sub>1</sub> Segs.	L. (mm)	P <sub>2</sub> Segs.	L. (mm)
1.40	2.0	c. XX	(c. 33)	c. 33	14	10.5	II	6.3
c. 80	1.5	XVIII	40	34	—	—	—	—
c. 70	1.5	c. XVI	—	—	17	8.7	II	5.3
—	1.5	XIV	c. 37	c. 27	19	9.0	—	—
c. 75	1.4	XII	—	—	17	8.4	14	6.6

The proximal pinnules are laterally compressed. The longest segments of P<sub>1</sub> have length : breadth 1.3 : 1. P<sub>2</sub> is stout basally, tapering in the distal half. The pinnules after P<sub>7</sub> have slightly broader median segments, prismatic in cross section. The distal pinnules are longer, P<sub>37</sub> with 19 segments being 10.5 mm long.

The 'Anton Bruun' specimens are more broken than the holotype but probably also had about 20 arms. The centrodorsal is rounded conical in the second specimen tabulated, with height : breadth 2.9 : 4.0 mm, fairly high rounded hemispherical in the next two with height : breadth c. 3.0 : 4.3 mm and the dorsal pole smooth, but low rounded conical in the last one. In the third specimen tabulated there is a slight raised ridge midradially in two radial areas but the other three have a median cirrus arising in this position. On the cirri the transition segment is usually the sixth or seventh but in one with 40 segments it is the eighth; this cirrus has dorsal spines starting from the ninth segment, in shape like the truncated lip of a jug, though as the segments shorten distally the lip becomes narrower and sharper. The division series and arms are much as in the type, laterally appressed basally and with distinctly acute keels except on the IB<sub>r</sub> series where they are slightly blunted.

REMARKS. This species does not run down easily to *Cosmiometra* in A. H. Clark's key to the genera of Thalassometridae (1950 : 5) since the carination of the division series is fairly well-marked, contrary to the diagnosis of the genus, leading one to *Stenometra*.

RANGE. The new record extends the known range northwards into the Arabian Sea.

*Crotalometra* sp. ?*C. sentifera* A. H. Clark

*Crotalometra sentifera* A. H. Clark, 1909e : 147 (?); 1937 : 92; 1950 : 91-92, pl. 32, figs 100-103.

*Thalassometra sentifera* : A. H. Clark, 1912a : 201-203, fig. 37.

*Crotalometra* sp. ?*sentifera* : A. M. Clark, 1967b : 158-161.

MATERIAL. Eastern and Associated Cable Co., C.S. 'Electra', January, 1911 [assuming this date is that of capture, then the locality must be the Red Sea or, more likely, the Gulf of Aden]; 1 specimen. B.M. reg. no. 1911.7.29.2.

DESCRIPTION. Some numerical details are given in Table 13. The centro-dorsal is conical with large apical papillae. The cirri are arranged in ten paired columns of two to four in each, the pairs of columns contiguous adapically but separated peripherally by a triangular, slightly sunken, space in each radius. There are XXV mature and v-x immature cirri. The sixth cirrus segment is usually the transition one except on two of the peripheral cirri where it is the seventh and one apical one where it is the fifth. The first five segments of the mature peripheral cirri are shorter than broad; there are dorsal spines from about the fifteenth segment and these are small, sharp and distally-directed at first, even the distal ones being highest at the distal end with the profile slightly convex proximal to the apex of each spine, like an aquiline beak.

The IBr series and first two ossicles following (IIBr<sub>1</sub> and <sub>2</sub> or Br<sub>1</sub> and <sub>2</sub>) have an angular median keel; also the proximal and distal edges of these ossicles are flared into frills, though these are only finely spinose. There is a coarse median tubercle on each radial. The brachials are rounded and, although the profiles of the arms become somewhat serrated in the distal half, the median angular projection on each brachial is neither very sharp nor markedly spinose. The joint between brachials one and two is usually fine and non-muscular, though more like a pseudosyzygy than a true syzygy, a broken one showing almost flush joint faces with some slight tubercles and a bare suggestion of the peripheral radiating ridges characteristic of a syzygy.

The first pinnule, P<sub>D</sub>, is massive basally, prismatic and markedly tapering beyond the base; two studied have 18 and 21 segments but both measure 10.3 mm in length. P<sub>1</sub> with 17 segments is 7.9 mm long and P<sub>2</sub> with 11 is 5.5 mm and much more slender throughout.

There is an acorn barnacle on one cirrus and, as in one of the Deutsche Tiefsee-Expedition specimens, a parasitic gall on the disc.

REMARKS. In 1967 I described under the name of '*Crotalometra* sp. ?*sentifera*', two specimens from the Deutsche Tiefsee-Expedition taken off Kenya, commenting

that they are conspecific with the two John Murray Expedition specimens from the Maldive Islands if not with the little-known and badly-broken syntypes from the Laccadive Islands. The same is true of the 'Electra' specimen since there is clearly considerable variation in the shape and ornamentation of the centrodorsal, cirrals, division series and brachials, as well as in the number of cirri and the nature of the joint between the first two brachials. The two Kenyan specimens differ markedly in the number of cirri and the two Maldive ones in the shape of the centrodorsal and the development of papillae.

[It should be noted that there are two errors in my 1967 paper with regard to this species: p. 160, paragraph 5, line 4, should read 'on the IIBr<sub>2</sub>' (not IIBr<sub>3</sub>) for the position of P<sub>D</sub> and paragraph 6, line 1, should have 'The arm breadth at the syzygy between brachials 3 + 4 is', etc.]

RANGE. If my surmise as to locality is correct, this record extends the known range of the species (whether or not it can be called *C. sentifera*) northwards into the Gulf of Aden.

TABLE 13

Numerical data from two John Murray Expedition specimens, one from the Deutsche Tiefsee-Expedition (in the Munich Museum) and the 'Electra' specimen of *Crotalometra* sp. ?*C. sentifera*

No.	Arms			Centrodorsal		Cirri				L : Br trans. seg. ( : 1)
	L. (mm)	Br at 3 + 4 (mm)	L. to 3 + 4 (mm)	Ht. (mm)	Diam. : Ht. ( : 1)	No.	Segs.	L. (mm)	Trans. seg.	
18 (? + 1)	—	1.6	10.5	3.7	1.35	XIX	57	c. 45	8	2.2
15 (? + 5)	—	1.7	10.5	3.7	1.15	XVII	65	c. 47	9 (8)	2.1
19	c. 130	1.6	8.5	5.25	1.32	XXXV	72	55	7	1.9
18	c. 130	1.8	10.0	4.2	1.05	XXX	71	60	6	1.6

## Family ANTEDONIDAE

## Subfamily ANTEDONINAE

*Andrometra* sp. ?*A. psyche* (A. H. Clark)

(fig. 15)

*Antedon psyche* A. H. Clark, 1908c : 241, pl. 1, figs 2, 3.*Andrometra psyche* : A. H. Clark, 1918 : 210; A. H. & A. M. Clark, 1967 : 81-84, fig. 5.*Andrometra aequipinna* Gislén, 1922 : 129-131, figs 114-116, pl. 2, fig. 11.

MATERIAL. 'Anton Bruun' cruise 9, st. 445, 09°41'N : 51°03'E (off N Somalia), 60-70 metres; 1 specimen.

'Anton Bruun' cruise 9, st. 447, 10°00'N : 51°15'E, 59-61 metres; 1 specimen.

DESCRIPTION. The specimen from station 447 is reasonably complete. The arm length is up to 57 mm; the breadth at the first syzygy, 3 + 4, is 1.0 mm and the length from the proximal edge of the  $IBr_1$  to the second syzygy, 9 + 10, is 5.5 mm.

The shape of the centrodorsal is obscured by the cirri but it is probably low conical since the irregular papillose dorsal pole is only c. 0.5 mm in diameter while the peripheral diameter is 1.8 mm; the height is c. 0.8 mm. There are c. XXXV cirri, the stout peripheral ones with 14–16 fairly short segments and c. 7 mm long. On one cirrus the fourth segment from the base has median breadth 0.42 mm while the fourth segment from the tip is 0.55 mm broad, the distal enlargement being only moderate. The apical cirri have c. 11 segments and measure c. 3 mm in length.

The division series are well separated laterally, the  $IBr_1$  having converging sides so that the lateral angles of the rhombic axillaries project well beyond them. The proximal angle of the axillary is very obtuse and only slightly elevated in an indistinct synarthrial tubercle. The two first brachials of each pair of arms are in contact beyond the distal angle of the axillary.

$P_1$ ,  $P_2$  and  $P_3$  have respectively 8 (or 9), 10 and 9 segments and lengths c. 6.3, 7.9 and 5.0 mm. Their segments are elongated after the first one (or two) and mainly cylindrical and smooth but becoming slightly flared and spinose at their distal ends.

The second specimen has nine of the arms broken at the first syzygy and the tenth at the second. Its cirri have up to 14 segments and are incurved over the centrodorsal so as to obscure its shape again.  $P_1$ ,  $P_2$  and  $P_3$  have 8, 11 and 10 segments and are 4.2, 6.2 and 4.3 mm long in the one series remaining.

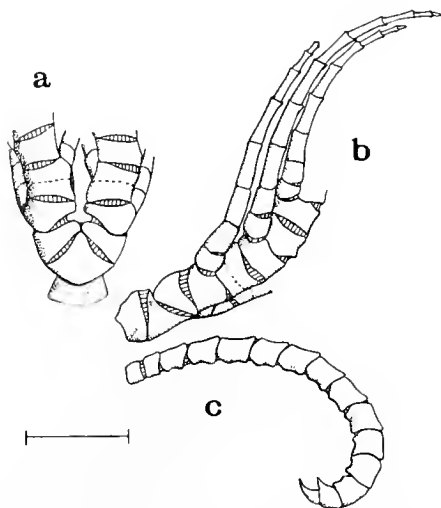


FIG. 15. *Andrometra* sp. ?*A. psyche* (A. H. Clark). 'Anton Bruun' st. 447, off Somalia. Arm br 1.0 mm. a. dorsal and b. side views of proximal part of one post-radial series, the arm in b. to  $Br_7$  showing  $P_1$  to  $P_3$ ; c. mature peripheral cirrus. [The scale equals 2 mm.]

**AFFINITIES.** These specimens agree well with *Andrometra psyche* from southern Japan except that specimens of *A. psyche* with arm length c. 60 mm have up to 18 cirrus segments, the division series approximate to each other laterally, the IB<sub>1</sub> having parallel sides, and the pinnules are relatively smaller, P<sub>1</sub>, for instance, being not more than 4 mm long. The geographically closer *Andrometra indica* (A. H. Clark) from the Andaman Islands differs much more in having the conical centro-dorsal bathymetrin-like, its height equal to its diameter, while the cirrus sockets number as many as LXX (the cirri themselves being unknown). *Antedon arabica* (A. H. Clark) from southern Arabia has heavier cirri with up to only 12 segments and its proximal pinnules are very different, P<sub>1</sub> with c. 20 short segments being much longer than P<sub>2</sub>.

### *Antedon parviflora* (A. H. Clark)

*Compsometra parviflora* A. H. Clark, 1912c : 133; Gislén, 1922 : 124-126, figs 109-113.

*Antedon parviflora* : A. H. & A. M. Clark, 1967 : 147-151, fig. 9b, c.

**MATERIAL.** 'Te Vega', F. C. Ziesenhenné's st. 64-19, 05°58'N : 73°79'E, lagoon off Kendikolu I., Miladummadulu Atoll, Maldives Is., 44-46 metres; 1 specimen.

**DESCRIPTION.** The arms are all broken at the first syzygy except one which remains to the second. The breadth at the first syzygy is 0.5 mm. The centro-dorsal is low hemispherical, 1.2 mm in diameter with c. XXV cirrus sockets; the central part has obsolete sockets and the surface is irregular. Only four cirri remain attached, none of which are mature or peripheral. The two larger ones have ten medially constricted segments flared at the joints and measure 2.8 mm in length. The fifth and longest segment is 0.4 mm long with length : median breadth 2.7 : 1. An apical cirrus has eight segments.

The axillaries are hexagonal with short projecting lateral flanges.

P<sub>1</sub> appears relatively huge; it has 9 or 10 +1(?) segments and was probably c. 4.2 mm long when complete. The first two segments are short but the next is very stout, long and flared distally. P<sub>2</sub> with 5 +1 (or 2) segments is c. 1.6 mm long. P<sub>3</sub>, the first genital pinnule, had 5 +1 (or 2) segments and is also c. 1.6 mm long.

**RANGE.** The Maldives Islands is the only locality in the Indian Ocean from which this species has been recorded. It was taken at Suvadiva Atoll by the 'Snellius' Expedition.\*

### *Dorometra mauritiana* (A. H. Clark)

*Iridometra mauritiana* A. H. Clark, 1911b : 40-42.

*Dorometra mauritiana* : A. H. & A. M. Clark, 1967 : 69-71.

**MATERIAL.** 'Anton Bruun', Tulear, Madagascar, offshore reef; 1 specimen.

\*Since this paper went to press, I have received from Tel-Aviv University two specimens of *Antedon parviflora* (nos NS 4444 and 4446) taken at Dahab, Gulf of Akaba, in 7 and 25 metres, extending the range farther still.

DESCRIPTION. The arm length was probably c. 37 mm; the breadth at the first syzygy, 3 + 4, is 0.8 mm and the length from the proximal edge of the  $IBr_1$  to this syzygy is 1.8 mm; the length to the second syzygy at 9 + 10 is 4.5 mm. The centrodorsal is 1.8 mm in diameter, almost completely covered with cirrus sockets; it has no distinct dorsal pole. All but one of the cirri have been lost, this one is from the second row from the periphery and has 11 segments, the length being 5.0 mm. The fourth and longest segment is flared at the ends, especially the distal end, and has length : median breadth 3 : 1, the length being 0.6 mm; the antepenultimate segment is 0.4 mm long with length : breadth 1.5 : 1.

$P_1$  and  $P_2$  are straight and tapering.  $P_1$  with 11 segments is 3.4–3.7 mm long;  $P_2$  with 10 segments is c. 2.7 mm long and  $P_3$  with 17 segments is c. 7.5 mm long; it is the first genital pinnule. The following pinnules are smaller than  $P_3$  but have stouter gonads.

### *Dorometra nana* (Hartlaub)

*Antedon nana* Hartlaub, 1890 : 170–171; 1891 : 89–90, pl. 5, figs 57, 58.

*Dorometra nana*: A. H. Clark, 1918 : 216; Gislén, 1922 : 133–135, figs 123, 124; 1940 : 15, pl. 2, figs 9–11; A. H. & A. M. Clark, 1967 : 71–75, fig. 3d.

MATERIAL. 'Te Vega', F. C. Ziesenhenné's st. 64–19, 05°58'N : 73°79'E, lagoon off Kendikolu I., Miladummadulu Atoll, Maldives Is., 44–46 metres; 2 specimens.

DESCRIPTION. Both specimens are badly broken. The larger one has the arm breadth at the first syzygy, 3 + 4, 0.7 mm; the length from the proximal edge of the  $IBr_1$  to the second syzygy at 9 + 10 is c. 4.0 mm for the single, recurved, arm left beyond the first syzygy. The low rounded hemispherical centrodorsal is 1.6 mm in diameter. The cirri have all become detached and could belong to either specimen; the larger ones have 12–14 segments and measure c. 7 mm in length; the fifth and longest segment is 0.75 mm long with length : median breadth 2.8 : 1; only the first two segments are not longer than broad. There are c. XXV cirrus sockets.  $P_1$ ,  $P_2$  and  $P_3$  have segment counts and lengths of: 7, 2.1 mm; 7, 2.6 mm and 9 + c. 2, c. 7 mm.

The smaller specimen has  $P_3$  with 12 segments, 3.4 mm long; the last few segments are very attenuated.

The larger specimen retains some pink colour in spirit but the smaller is banded with brown and off-white.

REMARKS. In 1967 (in Clark & Clark, 1967) I referred to *Dorometra mauritiana* five specimens from Male Atoll, also in the Maldives Islands, which A. H. Clark had originally identified as *D. nana*, since these five have as many as 21–25 segments in  $P_3$ , the maximum recorded in *D. nana* being 16. The male specimens have the arm breadth at the first syzygy c. 1.1 mm and the smaller number of segments in the pinnules of Capt. Ziesenhenné's specimens might be attributable to their smaller size. However, the holotype of *D. mauritiana* and the 'Anton Bruun' specimen from Madagascar also have  $P_3$  c. 7 mm long, like the larger of the present two, but with 17–20 segments. Accordingly it seems better to refer these two to *D. nana*.



RANGE. With this record, the range of the species is once again extended westwards to the Maldive Islands.

Subfamily **BATHYMETRINAE**

*Fariometra liobrachia* sp. nov.

(fig. 16)

MATERIAL. 'Anton Bruun' cruise 9, st. 423, 06°52'S : 39°54'E (off Tanzania), 200 metres; the holotype and ten paratypes.

DIAGNOSIS. A species of *Fariometra* in which the brachials are smooth, the two first brachials of each pair of arms are inwardly contiguous, the division series have parallel sides, the cirri have c. 20–25 segments, the longest segments four or five times as long as the median breadth, P<sub>1</sub> is much longer than P<sub>2</sub> or P<sub>3</sub>, and P<sub>4</sub> is usually the first genital pinnule.

DESCRIPTION. Some numerical details of the holotype and paratypes are given in Table 14.

In the holotype the centrodorsal is rounded conical, two-thirds of its height being covered with crowded, irregularly-placed cirrus sockets, giving a honeycomb effect. The adapical obsolete sockets are occupied by rounded papillae but these stop short of the apex. Peripherally there are about five sockets opposite each radial.

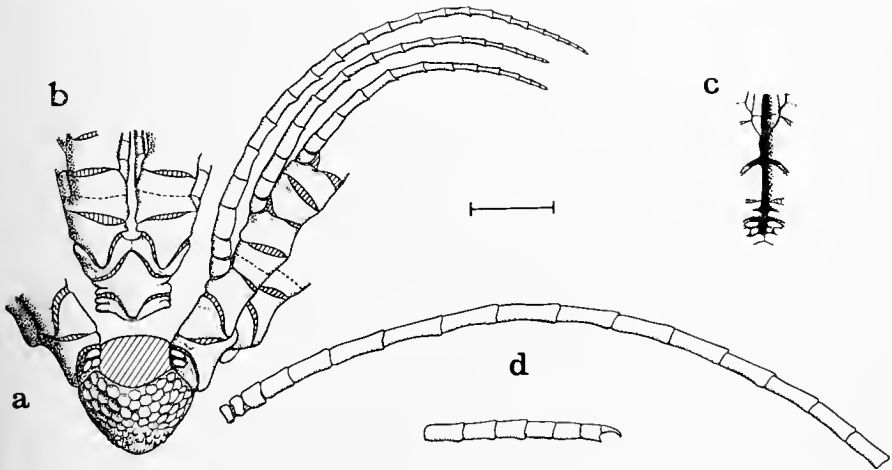


FIG. 16. *Fariometra liobrachia* sp. nov. Holotype. 'Anton Bruun' st. 423, off Tanzania. Arm br 1.35 mm. a. side view of calyx and proximal parts of two post-radial series, that on the right to Br<sub>7</sub> showing P<sub>1</sub> to P<sub>3</sub>; b. dorsal view of proximal part of one post-radial series; c. dorsal view, interradially, showing flattened faces of two adjoining post-radial series with notches corresponding to the synarthrial joints between IB<sub>1</sub> and 2 and Br<sub>1</sub> and 2; d. mature cirrus (probably not peripheral), drawn in two parts. [The scale equals 2 mm.]

TABLE I4

Numerical data from the ten paratypes and the holotype (last) of *Farionetra itobrachia* sp. nov.  
Numbers in brackets signify non-peripheral cirri

L. (mm)	Arms		Centrodorsal			Cirri			Pinnules								
	Br	at	D.	D. : Ht. (: 1)	No. (approx.)	Segs.	L. (mm)	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Segs.	L. (mm)	Segs.	L. (mm)	Segs.	L. (mm)	
40 + c. 10	3	4	2.25	1.4	LXV	—	—	20	10.8	13	7.1	13	5.8	1.2	13	5.8	1.2
—	1.2	6.4	2.25	1.4	LXV	21	14.2	21	12.5	13	7.25	10	5.4	1.35	13	6.5	1.05
50 + c. 10	1.2	6.7	2.3	1.4	LXX	(23)	(17)	19	10.8	15	6.8	13	6.5	—	—	—	—
—	1.2	—	2.75	1.6	LXXXV	—	—	18	10.8	—	—	—	—	—	—	—	—
—	1.25	6.8	2.5	1.4	LXXXV	—	—	21	11.7	12	6.7	11	5.5	1.2	—	—	—
—	1.25	—	2.5	1.6	LXV	24	17.0	23	12.5	—	—	—	—	—	—	—	—
35 + c. 15	1.25	6.9	2.7	1.3	LXXXV	—	—	19	10.0	c. 15	c. 8	15	6.7	1.2	—	—	—
—	1.35	c. 6.3	2.9	1.3	LXXXV	—	—	18	10.0	15	8.6	—	—	—	—	—	—
—	1.4	7.5	2.9	1.6	LXXX	—	—	—	—	—	—	—	—	—	—	—	—
—	1.35	7.6	2.7	1.3	LXXX	(22)	(14.6)	18	11.25	11	6.25	15	7.7	0.8	—	—	—
c. 60	1.35	7.9	2.6	1.4	LXXXV	(21)	(17.4)	23	13.2	17	9.2	13	7.0	1.3	—	—	—

There are no peripheral cirri left, the largest intact cirrus from among the middle ones has 21 segments and measures 17.4 mm in length. [A detached cirrus of 22 segments 17.6 mm long has the first two segments short, the third as long as broad, the seventh and longest 1.3 mm long with length : median breadth 4.8 : 1, the more distal segments only gradually becoming shorter so that the antepenultimate still has length : median breadth 1.75 : 1.]

The radials are almost completely occluded by the centrodorsal. The axillary has a conspicuous proximally-directed median angle so that the  $IBr_1$  is deeply concave distally. Similarly the second brachial has a pronounced proximal angle at the synarthry. However, these synarthrial tubercles are not very high in profile. Laterally the proximal and distal edges of the  $IBr_1$  are thickened and raised forming two or three coarse raised knobs. The proximal joints are markedly notched laterally, which is especially evident between the bases of each pair of arms where the space is T-shaped since the two first brachials, though short inwardly, are fully contiguous with each other distal to the angle of the axillary but then have a free tangential face leading to the constricted joint with the second brachial (see fig. r6b). The axillaries have length : maximum breadth 1.9 : 1.7 mm. The arms are quite smooth. The distal intersyzygial interval is three muscular joints.

Most of the segments of  $P_1$  are elongated and in side view have almost parallel sides, though they become slightly flared at the joints with a few fine spinelets dorsally.  $P_2$  and  $P_3$  are progressively more tapering than  $P_1$ .  $P_4$  is the first genital pinnule; it has 13 segments and is 5.8 mm long.

VARIATIONS. There is some variation in the relative height of the centrodorsal so that the diameter : maximum (interradial) height ranges from 1.3 : 1 to 1.6 : 1. The apex is more angular in some specimens. Owing to their irregular arrangement and crowding the number of cirrus sockets is difficult to estimate accurately but there are well over fifty in all the specimens. The radials are more evident in some of the specimens than in the holotype, especially laterally where they may have a convexity forming a cluster with the elevations on the  $IBr_1$ , while the proximal lateral corner of the axillary can also be thickened and raised. There are small differences in the relative lengths of the proximal pinnules; although  $P_2$  is normally distinctly longer than  $P_3$ , in one specimen the reverse is true. The pinnules on different arms of the same specimen may vary slightly; for instance, an apparently mature  $P_1$  in the tenth specimen in the table has only 15 segments and measures 9.6 mm compared with 18 segments and 11.25 mm in the one cited.

AFFINITIES. Of the other species of *Fariometra* recorded from the Indian Ocean, this new species differs from *F. sokotrae* John in the relatively lower centrodorsal, that of *F. sokotrae* being nearly as high as broad, the more numerous cirri, about five rather than three opposite each radial round the periphery, the smooth brachials and the position of the first genital pinnule, which is  $P_2$  in the species from Sokotra. *Fariometra sewelli* A. H. Clark, from the Maldive area, has a centrodorsal of similar lowish conical shape but its cirrus segments are relatively shorter, the division series and arms are finely spinose and again  $P_2$  is the first genital pinnule. The closest morphologically is probably the specimen from Deutsche Tiefsee-Expedition

station 265 off Somalia which I named '*Fariometra* sp. A' in 1967 (b : 163); this is very similar in size to the holotype of *F. liobrachia* and has  $P_5$ , sometimes  $P_4$ , the first genital pinnule but the centrodorsal is higher, the cirrus segments are probably more numerous and the division series and brachials are finely spinose.

### Family PENTAMETROCRINIDAE

#### *Pentametrocrinus varians* (P. H. Carpenter)

*Eudiocrinus varians* P. H. Carpenter, 1882 : 496-497; 1888 : 81-82, pl. 7, figs 3-7.

*Pentametrocrinus varians* : A. H. Clark, 1912a : 251; 1937 : 97; A. H. & A. M. Clark, 1967 : 804-810.

**MATERIAL.** 'Anton Bruun' cruise 7, st. 369F,  $24^{\circ}04'S$  :  $36^{\circ}15'E$ - $24^{\circ}07'S$  :  $36^{\circ}11'E$  (off Mozambique), 1630-1600 metres; 2 specimens.

**DESCRIPTION.** Both specimens are very badly broken and one of them is very small with no more than eight brachials of any arm left. There is a synarthry between the first two brachials so, in spite of the pinnule on the second one, this is a *Pentametrocrinus* not a *Eudiocrinus*. *P. varians* is the only known species of the genus in which  $P_1$  is developed. Unfortunately all the pinnules are broken at their bases. The brachials are alternately flared and constricted.

The larger specimen has the centrodorsal 3.2 mm in diameter. The cirri probably numbered c. XII but there are about six other, probably obsolete, sockets. All the cirri are broken but two with more than four segments have the first three markedly shorter than broad, the fourth with length 1.6 mm and length : median breadth 1.9 : 1 and the sixth with length : median breadth 2.7 : 0.7 = 3.9 : 1, though its flared distal end is 1.0 mm broad. A loose incomplete cirrus of 16 segments has lost about five segments proximally and one or two distally; it shows considerable taper.

The longest piece of arm remaining is broken at the twentieth brachial and measures 23 mm. The breadth at the first syzygy (4 + 5) is 2.4 mm and the length from the first brachial to the second syzygy when this is at 10 + 11 is 11.3 mm (in one case the second syzygy is at 11 + 12).

The smaller specimen has the centrodorsal rounded conical and the radials are comparatively long, whereas in the larger one they are almost completely occluded by the centrodorsal.

### Family BATHYCRINIDAE

#### *Democrinus chuni* (Döderlein)

(fig. 17)

*Rhizocrinus* sp. Döderlein in Chun, 1900 : fig. on p. 488.

*Rhizocrinus chuni* Döderlein, 1907 : 14-15, pl. 1, fig. 5, pl. 6, fig. 6.

*Rhizocrinus* (*Bythocrinus*) *chuni* : Döderlein, 1912 : 14-16, figs 3a, 5, 6, pl. 3, figs 1-7, pl. 5, figs 2, 4, pl. 7, figs 1-5, pl. 8, figs 1-10.

*Rhizocrinus* (*Bythocrinus*) *braueri* Döderlein, 1912 : 16-18, figs 3b, 7, pl. 4, figs 1-6, pl. 5, fig. 3, pl. 6, figs 1-6.

*Democrinus chuni* : Gislén, 1938a : 26-27; 1938b : 21-22, pl. 2, fig. 8.

MATERIAL. 'Anton Bruun' cruise 7, st. 369F, 24°04'S : 36°15'E-24°07'S : 36°11'E (off Mozambique), 1630-1600 metres; 4 specimens.

'Anton Bruun' cruise 7, st. 389E, 30°09'S : 31°37'E (off Durban), 930 metres; 41 specimens.

'Anton Bruun' cruise 7, st. 389G, 29°57'S : 31°31'E (SE of Durban), 700 metres; 9 specimens.

'Anton Bruun' cruise 8, st. 407A, 18°24'S : 42°11'E (Mozambique Channel), 2125 metres; 1 specimen.

REMARKS. This is the only stalked crinoid taken by the 'Anton Bruun'. Unfortunately, as usual in this family, the arms are badly broken in the great majority of specimens and in fact only three have any brachials left beyond the first one.

Although Döderlein has given some idea of the variation in the material taken by the Deutsche Tiefsee-Expedition and Gislén (1927) has discussed growth changes in *D. japonicus*, it seems worth while to include here some numerical data to try and show variations and growth changes by relating some of the proportions to others. In Table 15 the individual specimens have been grouped into three lots using the mean size sequence derived from the sequences obtained by: (1) the length  $\times$  maximum breadth of the calyx (basals and radials together), which is an unreliable criterion of size on its own owing to differences in *shape*, (2) the diameter of the top of the stalk, (3) the maximum length of an unspecialized columnal (omitting the sporadic double columnals sometimes found) and (4) the length of the ten proximal-most columnals. Using the mean sequence from all these, inevitably there is some overlapping in the individual measurements such as calyx length, which could alternatively be used itself alone as criterion of size, or any of the above four measurements. However, I think a more accurate estimate is obtained by taking the four into consideration.

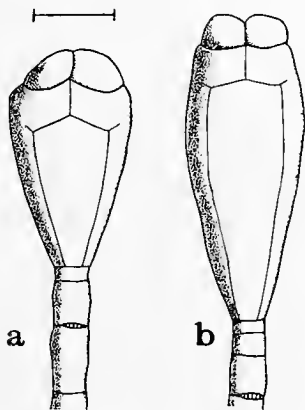


FIG. 17. *Democrinus chuni* (Döderlein). 'Anton Bruun' st. 389E, off Natal. Two specimens (arms lacking beyond the first brachial and only the proximal-most part of the stalk drawn) to show the two basic shapes of calyx, A and B, corresponding to a. and b. [The scale equals 2 mm.]

TABLE 15

Summarized numerical data from 52 specimens of *Demarcinus chuni* taken by the 'Anton Bruun', divided into three successive size groups (see text) followed by the totals. The excessive numbers in brackets are for abnormal specimens or ones possibly misplaced in the size estimates

	Range	No.	Mean	Range	No.	Mean	Range	No.	Mean	Total range	No.	Mean	S.D.
Calyx length (mm)	1.5-2.8	17	2.3	2.1-3.7 (4.8, 6.3)	17	3.2	3.8-8.5	17	5.6	1.5-8.5	—	—	—
Calyx max. breadth (mm)	1.0-1.5	17	1.3	1.3-1.9	17	1.5	1.5-2.5	18	1.9	1.0-2.5	—	—	—
Basals max. length (mm)	1.0-2.4	17	1.7	1.6-3.4 (4.3, 6.0)	17	2.7	3.5-7.9	17	5.1	1.0-7.9	—	—	—
Radials length (mm)	0.4-0.6	17	0.5	0.4-0.8	17	0.5	0.3-0.7	18	0.5	0.3-0.8	52	0.5	0.11
Top of stalk diameter (mm)	0.3-0.5	16	0.4	0.4-0.6	17	0.5	0.6-1.2	18	0.8	0.3-1.2	—	—	—
Basals length as % of calyx length	71-87	17	78	73-93	17	83	87-94 (85)	17	91	71-94	51	84	7.4
Calyx breadth as % of calyx length	43-75	17	60	20-68	17	51	23-44 (55)	17	35	23-75	51	49	13.8
Calyx shape: A, AB or B	10 : 2 : 5	—	—	4 : 2 : 11	—	—	0 : 6 : 12	—	—	14 : 10 : 28	—	—	—
Stalk length (mm)	19-29	9	24	28-35 (50)	4	32	50-82 (95+)	6	70	19-82 (95+)	—	—	—
Columnals no.	26-36	9	29	31-35 (39+)	4	34	37-53 (60+)	6	47	26-53 (60+)	—	—	—
Columnals no. to first 'cirrus'	24-30 (33)	14	27	25-35	13	30	26-50	11	40	24-50	—	—	—
First ten columnals length (mm)	4.7-7.6	16	6.3	6.8-10.0	17	7.8	8.8-14.5	18	11.1	4.7-14.5	—	—	—
Longer columnals individual length (mm)	0.8-1.0 (0.7)	16	0.9	0.9-1.3	17	1.1	1.2-2.6	18	1.6	0.8-2.6 (0.7)	—	—	—
Longer columnals length : median breadth ( : 1)	2.1-4.0	16	2.9	1.9-3.4	17	2.6	1.6-2.7	18	2.0	1.6-4.0	—	—	—
First ten columnals length as % of stalk length	22-31	9	27	21-27	4	23	15-19	6	16	15-31	19	23	5.4
Br1 length (mm)	0.4-1.1	17	0.8	0.4-1.4	16	0.7	0.5-0.8	15	0.6	0.4-1.4	48	0.7	0.25
Br1 length : median breadth ( : 1)	0.7-1.7	17	1.2	0.6-1.7	16	1.1	0.6-0.9	15	0.8	0.6-1.7	48	1.0	0.3

The two basic calyx shapes A and B correspond approximately to those of the holotypes of *D. chuni* and *D. braueri*, the former being the immature, inverted conical, relatively short, form and the latter the mature elongated more or less cylindrical (flask-shape according to Döderlein) shape. Gislén (1938) has referred *D. braueri* to the synonymy of *D. chuni*, with which I fully agree. Of the specimens shown in Döderlein's plates, only one of seven enlarged figures of *D. braueri* has the calyx length less than 3.0 mm, while only two of eleven of *D. chuni* are more than 3 mm long in the calyx.

This comparative study shows that the forms of both stalk and calyx are very variable. The length of the stalk does not appear to show any fixed relation to the length of the calyx. On some columnals a raised belt around the middle is found, the ossicle otherwise being barrel-shaped; other large columnals are, however, constricted medially. The 'rooted' part of the stalk also varies considerably; there may be a main 'tap-root' but more often the stalk becomes bifid or trifid basally.

In the calyx, it is clear that the radials do not increase in length, all the longitudinal growth being in the basals. The first brachial is very variable in size and shape, usually tapering slightly distally but not always; it is relatively broader in larger specimens.

DESCRIPTION. The most nearly intact specimen has an arm of 17 brachials probably almost complete and measuring 7.4 mm in length. The arms do not start to taper until Br<sub>3</sub>. The first pinnule is on the right side of Br<sub>6</sub>, it has 6 (?7) segments and is 2.1 mm long. The next pinnule, on Br<sub>8</sub>, has 8 segments and is 2.4 mm long. There are four more pinnules succeeding these but only two segments of the last are left; it is broken level with the end of Br<sub>17</sub>, which may have been the last brachial since its breadth is barely wider than that of the pinnule.

The calyx is 7.6 mm long with the basals making up 7.2 mm of this; the maximum breadth is 2.0 mm. The basals are therefore 94% of the calyx length and the maximum breadth is only 27%, the calyx being very slender with the radials tapering inwards slightly at the top. The diameter of the top of the stalk (and the bottom of the calyx) is 0.85 mm. At c. 1.6 mm above the base of the calyx there is a straight transverse suture around the basal ring and below this some additional irregular sutures making something of a mosaic. Sixty columnals of the stalk remain; these are stout, mostly barrel-shaped (except for the more distal ones) and together measure 95 mm but probably at least 10 mm of the basal part has been lost. There are radicular cirri from the forty-eighth segment (counting downwards), usually near the upper end of each columnal and projecting at right angles, with enlarged ones on the 54th, 55th, 57th and 60th. The uppermost columnal is very short discoidal with indistinct sutures; the second and third are also broader than high. The longest normal columnals have length : median breadth 1.60 : 0.95 mm but there are two abruptly enlarged ones, possibly formed by the fusion of two columnals, one of which measures 2.2 : 1.2 mm (see Döderlein's figure 7, 1912). These irregular ossicles have median raised belts. One columnal is also deformed by a parasitic gall. The ten uppermost together measure 10.5 mm but this would be more if not for the immature topmost segment.

Another specimen has a complete arm of 14 brachials measuring 4.5 mm, the calyx length being 3.0 mm. Br<sub>12</sub> is axillary-like with a pinnule from one side and the arm tip almost equal in size on the other. The third specimen with some brachials left beyond the first has no more than seven. Unlike the other two, it appears to have the joint between brachials 1 and 2 a syzygy.

At least two specimens have the stalk abruptly narrowed in the upper half, as has also been observed in some specimens of *Rhizocrinus lofotensis*. A second specimen, as well as the one with the longest arms, has an additional suture around the basals though not lining up perfectly where it intersects the longitudinal sutures. It lies at 3 mm from the base, the total calyx length being 6.3 mm. Gislén (1927) has also noted subdivided basals in *Democrinus japonicus*.

An interesting feature is that three specimens have a well marked constriction around the calyx near its upper end, in two cases in the radials and in the third at the upper end of the basals. Such a constriction is supposed to be characteristic of *D. parfaiti* Perrier from the North Atlantic.

ABNORMAL SPECIMEN. One of the two specimens excluded from the table has seven barrel-shaped columnals at the free (distal) end of the stalk with length : median breadth c. 0.7 : 0.5 mm. It then abruptly narrows into more elongated segments c. 0.8 : 0.3 mm, the first ten of which have usually bases of broken radicular cirri at their upper ends. There are then 16 other columnals gradually shortening before the very elongated calyx, 5.3 mm long by 1.7 mm in maximum breadth with a narrow groove around the middle of its length and the upper half distorted and asymmetrical, constricting abruptly 0.7 mm from the top so that the free ends of the radials and the five first brachials are much narrower, the radial ring only 1.0 mm in diameter. Also the sutures between basals and radials are not distinguishable and the basals are unnaturally swollen just above the base.

AFFINITIES. Gislén's key to the species of *Democrinus* (1938a : 26) distinguishes *D. chuni* and *D. japonicus* (Gislén, 1927) by the diameter of the top of the stalk (0.3-0.6 mm in *D. chuni* and 0.8-1.0 mm in *D. japonicus*) and the proportions of the longest columnals (length 2-3 × breadth as opposed to only 1.5-1.75). The present sample shows a range in proximal stalk diameter from 0.3 to 1.2 mm and 1.6 to 4.0 : 1 in the length : breadth ratio of the longest columnals, so only the geographical separation is left to distinguish between them. Until a proper study is made of growth changes in *Democrinus weberi* (Döderlein) from the East Indies, which is only known from specimens having proximal stalk diameter at least 2 mm, it seems inadvisable to make further alterations to the nomenclature.

#### APPENDIX PACIFIC MATERIAL

*Comanthus bennetti* (J. Müller). 'Te Vega' cruise 1, st. 35, 11°42'S : 166°51'E, Vanikoro I., Santa Cruz Is., just inside lagoon, W side of entrance; 1 specimen.

*Comanthus parvicirrus* (J. Müller). 'Te Vega' cruise 1, st. 27, 18°50'30"S : 178°32'10"E, SW shore, Mbulia I., Great Astrolabe Reef, Fiji Is., 4.5-6 metres; 1 specimen.



'Te Vega' cruise 1, st. 35, 11°42'S : 166°51'E, Vanikoro I., Santa Cruz Is., just inside lagoon, W side of entrance; 1 specimen.

***Comanthus samoanus*** A. H. Clark. 'Te Vega' cruise 1, st. 35, 11°42'S : 166°51'E, Vanikoro I., Santa Cruz Is., just inside lagoon, W side of entrance; 1 specimen.

The specimen of *Comanthus parvicirrus* from this locality is referable to the subspecies *timorensis*, having no cirri at all. In contrast, this specimen has XI large cirri and vi small ones, the larger being stout and laterally compressed with 17 (in one case 18) segments, the distal ones distinctly shorter and with well marked transverse ridges dorsally; the maximum length is c. 10 mm. Also the IIBr division series and all but one of the 13 IIIBr series are of four ossicles. This character as well as the relatively well-developed cirri serve to ally the specimen with *C. samoanus* rather than with *C. parvicirrus* although the number of arms (33) is well in excess of the 20-25 usually found in *C. samoanus*. However, A. H. Clark himself has referred a specimen from Tonga with 39 arms to *C. samoanus*. The arm length of this Vanikoro specimen is c. 65 mm.

***Eudiocrinus junceus*** A. H. Clark. 'Te Vega' cruise 1, st. 60, 4°44'N : 113°23'E (S China Sea, c. 60 miles off Sarawak), 100 metres; 1 specimen.

*Eudiocrinus junceus* A. H. Clark, 1912b : 25-26; 1918 : 65-67, fig. 3, pl. 17, figs 31, 32; 1941 : 149-151, pl. 10, figs 35, 36.

DESCRIPTION. The arm length is 16 + c. 10-15 mm; the breadth at 3 + 4 is 1.7 mm and the length from the proximal edge of the first ossicle (IBr<sub>1</sub> by A. H. Clark's enumeration) to this syzygy is 2.1 mm. There are XXI extremely attenuated cirri, the peripheral ones with up to 17 segments and maximum length 10.5 mm but the apical much smaller with only c. 10 segments and length c. 3 mm. The fifth and longest segment of the peripheral cirri has length : median breadth 0.9 : 0.2 mm = 4.5 : 1.

Most of the proximal pinnules are broken. One P<sub>C</sub> has c. 10 segments which are slender beyond the basal ones; the length is 3.5 mm. P<sub>1</sub> is similar to P<sub>C</sub> but P<sub>a</sub> is distinctly larger, as usual in the genus.

REMARKS. The holotype and only other specimen known has arm length 90 mm, which relatively large size accounts for its larger number of cirrus segments, up to 22, and the greater cirrus length of 23 mm. It was collected in the Moluccas so the extension of range is small.

***Eudiocrinus venustus*** A. H. Clark. 'Te Vega' cruise 1, st. 60, 4°44'N : 113°23'E (S China Sea, c. 60 miles off Sarawak), 100 metres; 1 specimen

This specimen is more ornate than those from the Bay of Bengal (see p. 92) having not only elaborate crests on the basal segments of the proximal pinnules but also tall single mid-radial tubercles on the proximal brachials with a few smaller ones each side, at least to Br<sub>1</sub> (see fig. 5b).

***Himerometra robustipinna*** (P. H. Carpenter). 'Te Vega' cruise 1, st. 35, 11°42'S : 166°51'E, Vanikoro I., Santa Cruz Is., just inside lagoon, W side of entrance; 2 specimens.

*Actinometra robustipinna* P. H. Carpenter, 1881 : 201-202.

*Himerometra robustipinna*: A. H. Clark, 1908b : 213; 1941 : 193-203, pl. 16, fig. 60, pl. 17, fig. 63, pl. 18, figs 68, 69.

RANGE. This record provides an extension of range to the NE from the Great Barrier Reef; the species is otherwise known from Ceylon to the S China Sea, the Moluccas and Kei Islands.

?*Cyllometra manca* (P. H. Carpenter). 'Te Vega' cruise 1, st. 60, 4°44'N : 113°23'E (S China Sea, c. 60 miles off Sarawak), 100 metres; 1 specimen.

The cirri are rather different in this individual from those of the Indian Ocean specimens (p. 127). There are XV in a single row around the discoidal centrodorsal, with up to 31 segments and c. 12.5 mm length; the sixth and approximately the longest segment has length : median breadth 0.7 : 0.6 mm. A median distal dorsal spine develops on the fifth to seventh segments and then a pair of smaller spines, one each side of it, which disappear at about the fourteenth segment leaving a single sharp median spine on the distal segments. This compares with the more usual condition of two small dorsal spines between about segments seven and fifteen, though A. H. Clark (1947 : 140) notes that occasionally the spines may be triple. In fact, the dorsal armament of the cirri in this specimen agrees with A. H. Clark's description of that of *Cyllometra gracilis* from the Lesser Sunda Is., though in that species the cirrus segments are much elongated, the longest with length over twice the median breadth (twice the proximal breadth according to A.H.C.). In the 'Te Vega' specimen there are eleven arms 35 + c. 10? mm; breadth at the first syzygy is 0.8 mm and the length to this syzygy is 2.6 mm. P<sub>1</sub> has 15 segments and measures c. 4.5 mm; P<sub>2</sub> with 19 segments is 8.2 mm and P<sub>3</sub> with 16 is 6.3 mm long and very attenuated distally. There is no P<sub>a</sub>.

The colour is purple except for the cirri which are white and a slightly paler mid-line on the arms.

The form of the cirri is also rather like that of *Cotylometra gracilicirra*, known from the neighbouring Sulu Archipelago, in the sharp median distal dorsal spines, but that species differs in having smaller and more spinose pinnules, even P<sub>2</sub> only c. 3 mm long at about the same arm length as the 'Te Vega' specimen.

*Asterometra longicirra* (P. H. Carpenter). 'Challenger' st. 192, 5°49'15"S : 132°14'15"E (near the Kei Is.), 256 metres; the holotype. B.M. reg. no. 88.11.9.8.

*Antedon longicirra* P. H. Carpenter, 1888 : 103-104, pl. 17.

*Asterometra longicirra*: A. H. Clark, 1947 : 439-441.

Although not taken in recent collections, this specimen was studied in connection with the identification of *Pterometra pulcherrima* and a supplementary description to Carpenter's rather brief one seems worthwhile.

DESCRIPTION. The ten arms are 80-95 mm long, fairly attenuated distally and very compressed with a sharp keel for the distal two-thirds of their length. The breadth at the first syzygy, 3 + 4, is 2.3 mm and the length from the proximal edge of the IB<sub>1</sub> to this syzygy is 8.2 mm.

The centrodorsal is conical, maximum height : diameter 3.70 : 4.75 mm. The dorsal pole is slightly bumpy but there are no distinct radial convexities. The

cirri are XVI + iv; two of the longest have 84 and 84 + 2 or 3 segments and measure up to 90 mm; the tenth and longest segment of a stout peripheral cirrus has length : median breadth 1.5 : 1.2 mm. The first segment is distinctly deeper than those immediately following but, as the segments shorten and develop dorsal spines, the cirri deepen again (i.e. broaden in side view). The distal dorsal edge starts to project between the 20th and the 25th segment on the peripheral cirri but between the fifteenth and 20th on the smaller ones, this projection turning into a keel. The maximum breadth on the distal segments, including the dorsal keel, is 1.7 mm but without the keel the breadth is only 1.25 mm.

The division series have low blunt keels, the crest on each ossicle stopping short of the joints; there is a Y-shaped elevation on the axillaries and a smaller slightly elongated tubercle on the first brachial. The IB<sub>1</sub> are joined laterally for the first two-thirds of their length, then the division series and arm bases have parallel flattened edges but no real lateral flange.

P<sub>1</sub> is very smooth and prismatic, rapidly tapering from a stout base; it has 11 segments and measures 6.3 mm. P<sub>2</sub> is similar but longer with 12 segments and 8.4 mm length. P<sub>3</sub> with 11 segments is 7.6 mm long. The distal pinnules have about 22 segments and are c. 16 mm long; most of their segments are cylindrical but the last ten are somewhat flared distally and finely spinose.

Unfortunately the existence and extent of radial pits in the centrodorsal cannot be determined in this species without more material.

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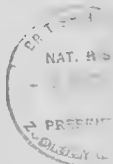
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# SOME CESTODE PARASITES OF THE ELASMOBRANCHS *RAJA BATIS* AND *SQUALUS ACANTHIAS* FROM ICELAND

By B. R. MANGER

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## SUMMARY

SEVERAL Cestode parasites were collected from five specimens of skate (*Raja batis*) and seven piked dogfish (*Squalus acanthias*), caught off the Western coasts of Iceland. The skate yielded seven species of Tetraphyllidean Cestodes, including three new species, all of which are new records for the area. The worms described are *Acanthobothrium parvum* sp. nov., *A. icelandicum* sp. nov., *Acanthobothrium* sp. innom., *Echeneibothrium dubium* Beneden, 1858, *E. minutum* Williams, 1966, *E. faxanum* sp. nov. and *Phyllobothrium* sp. innom. *A. parvum* sp. nov. is a small worm with between 64 and 79 testes, and has hooks measuring from 0.116 to 0.144 mm in length, a combination not found in any other species of *Acanthobothrium*. *A. icelandicum* sp. nov. is very similar to *A. septentrionale* Baer & Euzet, 1962, but differs in having only one accessory sucker to each bothridium (instead of three), an 'H'-shaped ovary, and a distinct vaginal sphincter. *E. faxanum* has 20 to 26 testes, a well-formed myzorhynchus, and 14 loculi to each bothridium, this last feature distinguishing the worm from *E. variabile* Beneden, 1849, with which it has some similarities. An examination of the spiral valve of *S. acanthias* showed the presence of *Gilquinia squali* (Fabricius, 1794) in four of the fishes, whilst *Trilocularia*

*acanthiaevulgaris* (Olsson, 1867) was found in the spiral valve, or stomach, or in both organs of every piked dogfish collected. Both of these worms are very common parasites of *S. acanthias* and the latter has previously been recorded from Icelandic waters.

#### INTRODUCTION

In October 1966, when on the staff of the British Museum (Natural History), the author was given the opportunity of accompanying the M.A.F.F. Research Vessel 'Clione' on a cruise to Iceland.

Although the parasites of fishes from Icelandic waters have been little studied, it was proposed to restrict investigations to the Cestodes of the Elasmobranchs found in this region.

During the course of the cruise a total of forty-three trawls were made on all but the Northern coasts of Iceland. Every Elasmobranch netted throughout the voyage was collected, comprising in all some twenty-two *Raja radiata*, five *Raja batis* and seven *Squalus acanthias*. However, in the present paper only *R. batis* and *S. acanthias* will be considered, these being caught on the Western coasts and mainly in Faxa Bay.

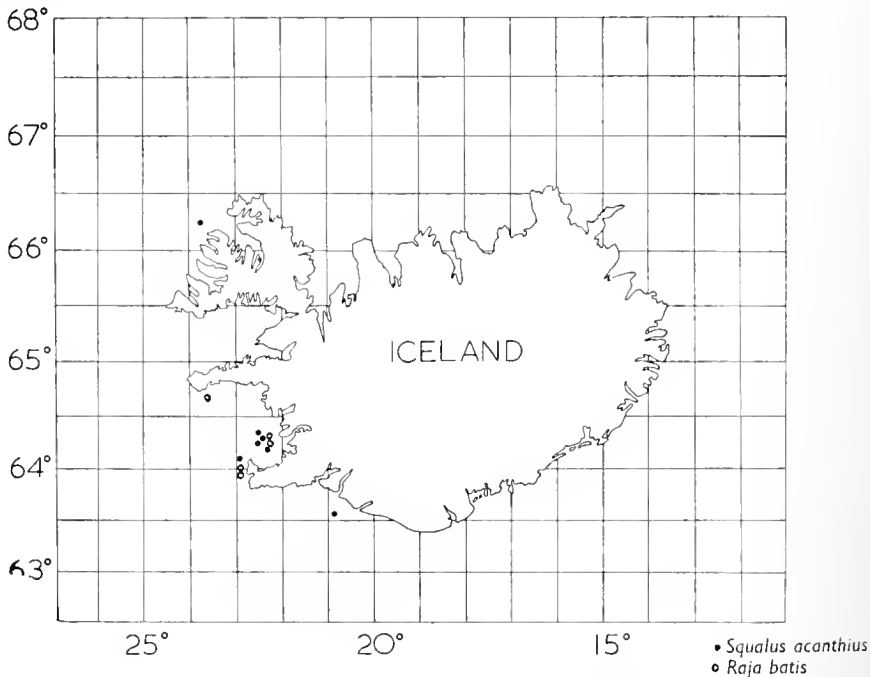


FIG. 1. Geographical distribution of fishes examined.



Fish	Length	Locality	Depth (Fathoms)	Date
<i>Squalus acanthias</i>	75 cm	63°31' 20°54' (Vestermann Is.)	50	20.x.66
<i>Raja batis</i>	61 cm	64° 38' 23° 39' (Faxa Bay)	57-60	21.x.66
<i>S. acanthias</i>	90 cm	64°22' 22°33' (Faxa Bay)	41-44	21.x.66
<i>R. batis</i>	48 cm	" " "	"	"
<i>R. batis</i>	65 cm	64°18' 22°20' (Faxa Bay)	35-37	22.x.66
<i>S. acanthias</i>	84 cm	" " "	"	"
<i>S. acanthias</i>	85 cm	" " "	"	"
<i>S. acanthias</i>	76 cm	" " "	"	"
<i>S. acanthias</i>	84 cm	64°04' 22°54' (Faxa Bay)	42	23.x.66
<i>R. batis</i>	144 cm	64°01' 22°55' (Faxa Bay)	45	23.x.66
<i>R. batis</i>	166 cm	" " "	"	"
<i>S. acanthias</i>	79 cm	66°13' 23°18' (Isafjord)	48-61	28.x.66

Every fish was dissected immediately after capture and the organs of the alimentary system were removed and separated. These were then opened, washed and individually preserved, together with their contents, in a formalin acetic saline solution and subsequently examined for parasites. It was hoped that an analysis of the stomach contents of the fish would reveal their diet, but unfortunately most of the *S. acanthias* had regurgitated their food on capture and thus had empty stomachs. Nevertheless, from an examination of those fish which had retained their food, the diet would appear to consist of small Crustacea and Polychaete worms in the smaller specimens, larger fish supplementing a diet of fairly large Crustacea with small fish.

Whilst searching for tapeworms, some specimens of *Otodistomum* (Trematoda; Azygiidae) were recovered from the anterior region of the stomach of two *R. batis*, and several Skate harboured *Calicotylo* (Monogenea; Monocotylidae) in the rectum posterior to the rectal gland. Some small, unidentified Digenetic Trematodes were found in the stomach and spiral valve of *S. acanthias*, and Nematodes occurred throughout the gut of both species of fish.

Altogether, nine species of Cestodes were recovered. These were stained with Gower's paracarmine or aceto-carmine and mounted *in toto*, or were serial-sectioned at a thickness of 15 $\mu$  and stained with Ehrlich's haematoxylin and eosin.

All the specimens, including the type-specimens of the three new species described, are deposited in the collection of the British Museum (Natural History), and their registration numbers are included in the following list.

#### LIST OF CESTODES RECOVERED

##### Order TETRAPHYLLIDEA

##### Family PHYLLOBOTHRIIDAE Braun, 1900

*Phyllobothrium* sp. innom. from *Raja batis*, Faxa Bay. Reg. no. 1969.2.24.1-10, 11-12.

*Echeneibothrium dubium* Beneden, 1858, from *Raja batis*, Faxa Bay. Reg. no. 1969.2.24.41-60.

*Echeneibothrium minutum* Williams, 1966, from *Raja batis*, Faxa Bay. Reg. no. 1969.2.24.61-65.

*Echeneibothrium faxanum* sp. nov. from *Raja batis*, Faxa Bay. Reg. no. 1969.2.24.13-20.

*Trilocularia acanthiaevulgaris* (Olsson, 1867) from *Squalus acanthias*, Faxa Bay, Isafjord and Vestermann Is. Reg. no. 1969.2.19.1-40.

Family **ONCHOBOTHRIDAE** Braun, 1900

*Acanthobothrium icelandicum* sp. nov. from *Raja batis*, Faxa Bay. Reg. no. 1969.2.24.21-40.

*Acanthobothrium parvum* sp. nov. from *Raja batis*, Faxa Bay. Reg. no. 1969.2.24.251-261.

*Acanthobothrium* sp. innom. from *Raja batis*, Faxa Bay. Reg. No. 1969.2.24.262.

#### Order TETRARHYNCHIDEA

Family **GILQUINIIDAE** Dollfus, 1942

*Gilquinia squali* (Fabricius, 1794) from *Squalus acanthias*, Faxa Bay, Isafjord and Vestermann Is. Reg. no. 1969.2.24.263-300.

The piked dogfish (*S. acanthias*) was found to harbour only two species of tapeworm, both very common, and one of them, *Trilocularia acanthiaevulgaris*, already having been recorded from Iceland (Rees, 1953). The parasitic fauna of the skate (*Raja batis*) proved to be more varied, with mixed infestations consisting of seven species of Cestodes whose occurrence is perhaps best illustrated in the following table.

TABLE I  
Cestode infestations of *Raja batis*

Parasite	Individual specimens of <i>Raja batis</i>				
	48 cm	61 cm	65 cm	144 cm	166 cm
<i>Phyllobothrium</i> sp. innom.			X	X	
<i>Echeneibothrium dubium</i>	X	X	X	X	X
<i>E. minutum</i>		X	X	X	X
<i>E. faxanum</i>					X
<i>Acanthobothrium icelandicum</i>				X	X
<i>A. parvum</i>		X	X		
<i>Acanthobothrium</i> sp. innom.				X	

The Skate, as a host for helminth parasites, has been fairly extensively studied, and so it is somewhat surprising that three new species of Cestodes should have been found during these investigations. A possible explanation for this fact is the lack of knowledge of fish-parasites in Icelandic waters. There do not appear to be any records of the helminths of *Raja batis* from this region, which may mean that the fish is supporting an endemic parasitic fauna that has so far been overlooked. This seems particularly plausible if the habits of the Skate are considered. For instance, these fish do not make long migrations, but remain in the same area throughout their lives, and specimens from Iceland probably never leave Icelandic coastal waters.

## DESCRIPTION OF SPECIES

*Acanthobothrium icelandicum* sp. nov.

(Figs 2-3; Plates 1 and 2)

Material was collected from two skate (*Raja batis*) in Faxa Bay, on 23 October 1966, and consisted of six specimens from one fish and seventeen from the other, three of which were immature forms. In both cases many fragments and apolytic segments were also obtained.

The largest specimen measures 67.4 mm in length and 1.1 mm in maximum width, bearing 140 proglottids, whilst the small immature worms are only just showing signs of segmentation and measure up to 4 mm in length. The terminal proglottid is about 2 mm long and 0.7 mm wide, and the free segments vary from 2.4 to 9.4 mm in length by 0.7 to 2.1 mm in width.

The scolex (Fig. 2a, plates 1 and 2) varies considerably in size, measuring from 0.98 to 1.2 mm in length and from 0.51 to 1.22 mm in width. The four very variable bothridia are divided by two transverse septa into three loculi, of which the anterior

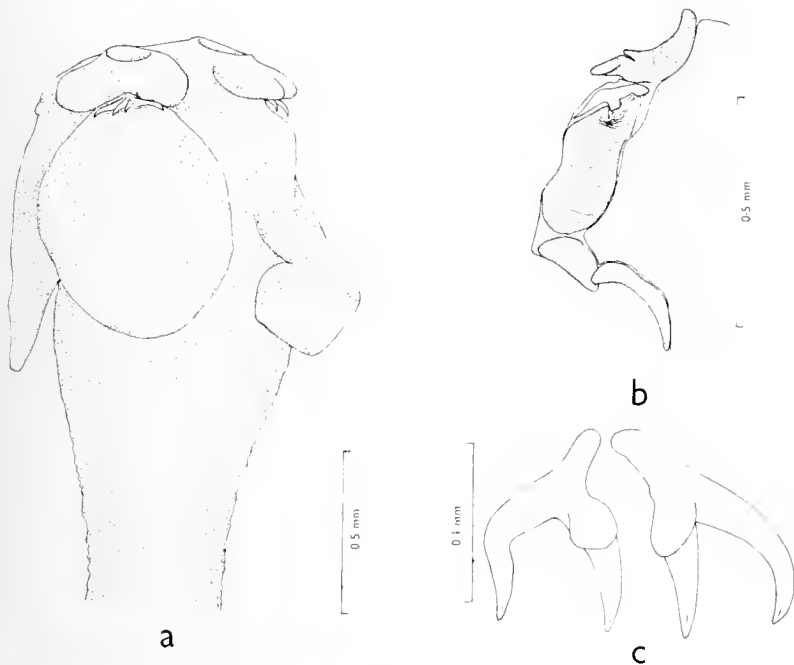


FIG. 2. *Acanthobothrium icelandicum*. (a) Scolex. (b) Longitudinal section of scolex. (c) Hooks.

is usually two or three times the length of the other two. The bothridia measure from 0.52 to 0.79 mm long, by 0.42 to 0.68 mm wide.

Each bothridium is armed with one pair of bifid hooks, measuring 0.12–0.16 mm long, and having a handle of 0.04–0.065 mm, an inner blade of 0.075–0.1 mm and an outer blade measuring 0.084–0.108 mm in length (Fig. 2c). On each bothridium there is an accessory sucker, measuring 0.168–0.23 mm in diameter, situated on a roughly triangular muscular cushion (Plate 1A–B).

The cephalic peduncle ranges from 2 mm to 7.7 mm in length, and when *in situ* is completely buried in the intestinal mucosa of the host, the anterior region bending back on itself to face the site of entry, thus ensuring a very secure attachment. This evokes considerable host-tissue reaction, which is evident in all the specimens of *Acanthobothrium* encountered.

A neck is present (0.36–0.65 mm long), but it is often difficult to distinguish from the base of the cephalic peduncle in specimens which have been stained and mounted *in toto*.

The irregularly alternating genital pores are situated in the posterior half of each segment. There are two layers of longitudinal muscle-fibres. The outer forms an unbroken ring of bundles, each bundle consisting of 2–15 fibres, whilst the inner musculature comprises 7–14 bundles of fibres in the ventral field and 6–10 bundles in the dorsal field, each bundle containing 4–30 fibres. The transverse and oblique musculature is very poorly developed. On each side of the strobila the longitudinal excretory vessels are of almost the same diameter, the dorsal being very slightly narrower than the ventral.

Both genital ducts pass between the longitudinal excretory vessels. The cirrus-sac is globular or pyriform, and ranges in size from 0.1 mm  $\times$  0.046 mm in young male segments to 0.38  $\times$  0.16 mm in mature female segments, attaining dimensions of 0.41 mm  $\times$  0.28 mm in ripe, detached proglottids. The vas deferens coils within the cirrus-sac to form a seminal vesicle, then leaves the pouch to lie between the testes in the median, anterior field of the segment (Fig. 3a). There is a strongly-spined cirrus present (Fig. 3b), which measures 1.09 mm in length and 0.15 mm in diameter at a bulbous swelling near the base (which contains the tightly coiled vas deferens). The cirrus can be very frequently found in a fully extended state in detached proglottids, but not so often in segments along the length of the strobila.

There are between 92 and 114 testes, contained in the area between the excretory canals, with 48 to 59 occurring in the aporal field and 40 to 61 porally (30 to 50 in front of the pore and 9 to 15 postporally). In transverse section the testes are found to occupy most of the vertical field between the longitudinal muscle-bands. In later mature segments the vasa efferentia leading from the testes become heavily swollen with sperm and reach proportions sometimes greater than the testes themselves.

An anomalous condition in which the number of testes on one side of the segment was very reduced, occurred not infrequently in one particular worm. In the same strobila a proglottid containing an additional, inverted, female system with no opening to the exterior, was encountered. (Fig. 3a).

A short distance behind the female genital pore there is a well-developed muscular vaginal sphincter (Fig. 3b). The thick-walled vagina passes ventrally and slightly

anteriorly to the cirrus-pouch, turning in mid-segment to run back to the oötype, situated behind the central portion of the ovary.

The two unequal lobes of the ovary are connected midway along their length by a long isthmus, giving the organ an 'H'-shaped appearance, with the posterior arms of the 'H' turning inwards to the middle of the segment (Fig. 3a). It is contained in the area within the longitudinal excretory vessels, and occupies the whole of the depth of the field between the longitudinal musculature, except for the connecting isthmus, which spans the ventral field of the segment.

The vitellaria are disposed in two continuous longitudinal rows laterally to the excretory canals, being broken only by the genital ducts on the poral side. The uterus initially has many small lobes, which grow until they occupy the whole of the segment. The rounded eggs measure 0.018–0.022 mm and contain embryos measuring 0.01–0.014 mm in diameter.

These specimens are very similar in many respects, especially in the shape and size of the hooks and the number of testes, to *A. septentrionale* Baer & Euzet, 1962. This species was erected to represent *A. coronatum* (Rud., 1819) of Johnstone, 1906, from *R. clavata* and *R. batis*; *A. ijimai* Yoshida, 1917, of Southwell, 1925, from *Raja* spp.; and *A. coronatum* (Rud., 1819) of Linton, 1925 (*pro parte*). However, according to their respective authors, all these worms have three accessory suckers in front of

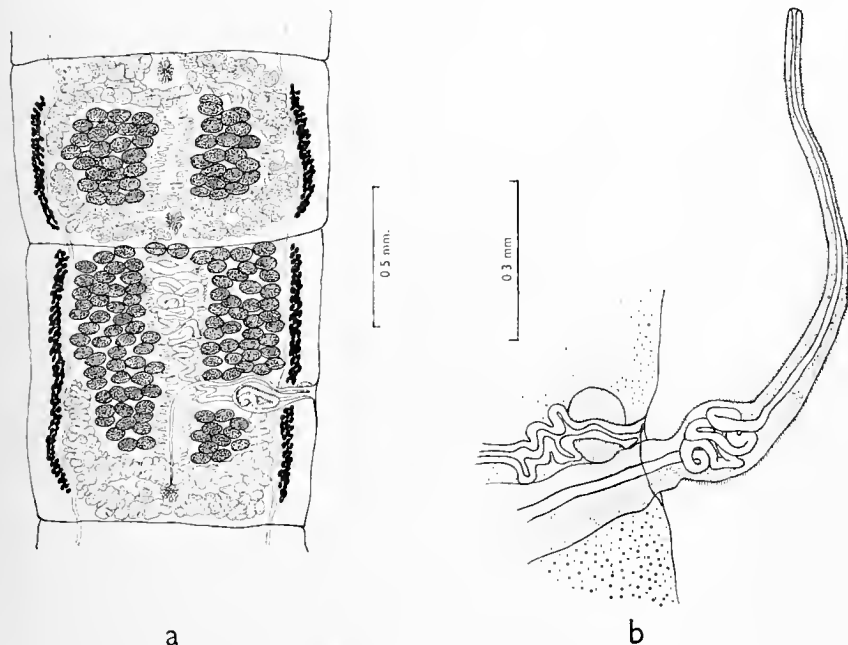


FIG. 3. *Acanthobothrium icelandicum*. (a) Portion of strobila containing an atypical segment with an additional, inverted set of female organs, and a typical mature segment. (b) Extruded cirrus, in transverse section.

each bothridium, a character which Baer & Euzet do not mention in their description. The present material, when examined *in toto* under the light microscope, also appeared to have three accessory suckers, but on subsequent examination under the scanning electron microscope this condition was not confirmed. Instead there appeared a triangular structure provided with an anteriorly-disposed sucker (Plate 1). Transverse sections showed the structure to be very muscular, and substantiated the presence of a single accessory sucker (fig. 2b). Rees and Williams (1965) interpret the prebothridial structures found in *A. coronatum* as muscular cushions, an interpretation which seems most applicable in this case. Further features in which *A. septentrionale* differs from *A. icelandicum* are the 'U'-shaped rather than 'H'-shaped ovary, and the apparent lack of a vaginal sphincter. Southwell (1925) in his description of *A. ijimai*, states that the dorsal excretory vessel is wider than the ventral, an unusual feature which does not occur in *A. icelandicum*.

The only other species of *Acanthobothrium* which agree in the size of the hooks and number of testes with the material collected from Iceland are *A. robustum* Alexander, 1953, from *Rhinobatos productus*, Southern California, and *A. dasybati* Yamaguti, 1934, from *Dasybatus akajei*, Japan. The former differs from the species described here in having an accessory spur to the hooks, and the latter by the lack of an accessory sucker (and also, in an amended description by Yamaguti (1952) in the number of testes). Both species occur in totally different hosts and in localities widely separated from the distribution of *Acanthobothrium icelandicum*.

### *Acanthobothrium parvum* sp. nov.

(figs 4-5)

Only a few specimens of this worm were retrieved from the spiral valve of two Skate (*Raja batis*) from Faxa Bay on 21 and 22 October 1966. The material consists of only two whole worms, but includes five fragments with scoleces attached, together with a few apolytic segments.

The worms are of small size for the genus, the largest measuring 19.3 mm in length, and the maximum width varies between 0.35 and 0.56 mm. The highest number of segments counted in a single strobila is 85.

The dimensions of the scolex vary with the state of contraction of the worm, the diameter ranging from 0.54 mm to 0.73 mm and length from 0.6 mm to 0.76 mm (fig. 4a). The four bothridia measure 0.456-0.564 mm. long by 0.3-0.41 mm wide. There is quite a considerable variation in the comparative sizes of the three very muscular loculi, although in the present material the middle loculus is the smallest, and the most anterior is usually fractionally larger than the posterior. The bothridial armature consists of one pair of bifid hooks to each bothridium (fig. 4b). The hooks measure between 0.116 mm and 0.144 mm in length, the measurement being taken from the base of the handle to the tip of the outer blade. The handle is 0.04-0.06 mm long, the inner blade 0.08-0.108 mm and the slightly larger outer blade 0.08-0.11 mm in length. Each bothridium is surmounted by a very muscular cushion bearing a single accessory sucker which varies in diameter between 0.1 and 0.16 mm.

There is a long, unarmed cephalic peduncle present, 1.4–3.5 mm in length, and segmentation begins from 0.2 mm to 3.5 mm behind this structure.

The irregularly alternating genital pores are situated approximately midway along each segment. The outer longitudinal musculature is very well developed, forming a complete circle of bundles each containing up to twenty fibres, and very closely applied to the body-wall of the worm. The less well-developed inner musculature consists of 5–10 bundles, each having up to 35 fibres, in both the dorsal and ventral layers.

The ventral excretory canal is very much wider than the dorsal, the genital ducts passing between the two longitudinal canals. The cirrus-sac is somewhat fusiform in mature segments (fig. 5a), but attains a considerably larger size and becomes rather more oval or pyriform as the segments develop further (fig. 5b). It may only measure 0.022 mm in diameter and 0.12 mm in length in early proglottids, but reaches a diameter of 0.172 mm and a length of 0.28 mm with further maturation. The cirrus-sac contains a coiled vas deferens, swollen with sperm to form a seminal vesicle, which on leaving the pouch turns forwards to lie in the anterior median field, where it becomes very convoluted and may occupy much of the region between the excretory canals. The protracted cirrus is large, measuring over 0.26 mm in length and 0.052 mm in diameter, and is covered with spines up to 0.01 mm long.

There are usually between 64 and 79 testes in each proglottid (although in one case only 58 and in another 85 are present), restricted to the area between the excretory vessels and in front of the ovary. They are distributed with 31–44 in the aporal field and 26–39 in the poral half of each segment, with 5–9 testes situated postporally.

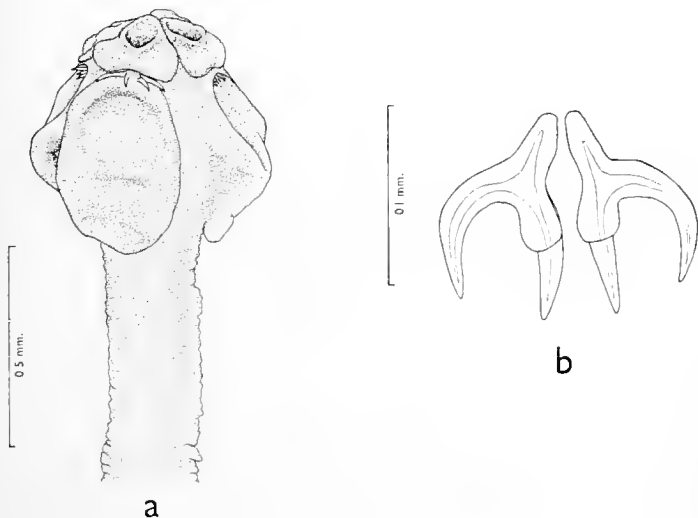


FIG. 4. *Acanthobothrium parvum*. (a) Scolex. (b) Hooks.

The vagina is very muscular, and in transverse sections can be seen to lie dorsally to the cirrus-sac. It crosses over the external vas deferens behind the cirrus pouch, to pass back to the oötype in the hindmost region of the ovary. The 'H'-shaped ovary appears to be bi-lobed, of which the aporal lobe is sometimes longer, extending beyond the cirrus-sac. Early in its development the ovary occupies from a quarter to a third of the posterior region of the segment, but may expand to over half the proglottid in terminal segments. Initially the uterus is saccular with a few lateral indentations but in later segments attains greater proportions, becoming much lobed, and is difficult to distinguish from the seminal vesicle.

The vitellaria are densely packed into the region outside of the excretory canals. They are round to oblong and form one or two rows.

The terminal segment varies between  $1.42 \times 0.51$  mm and  $4.1 \times 0.9$  mm, the latter being the stage at which the testes are beginning to atrophy and the uterus is expanding, which appears to be the furthest state of maturation attained whilst still attached to the strobila (fig. 5b).

Amongst the apolytic segments collected there are none that have reached the fully gravid stage, so that no record of the egg size can be obtained, but in the more

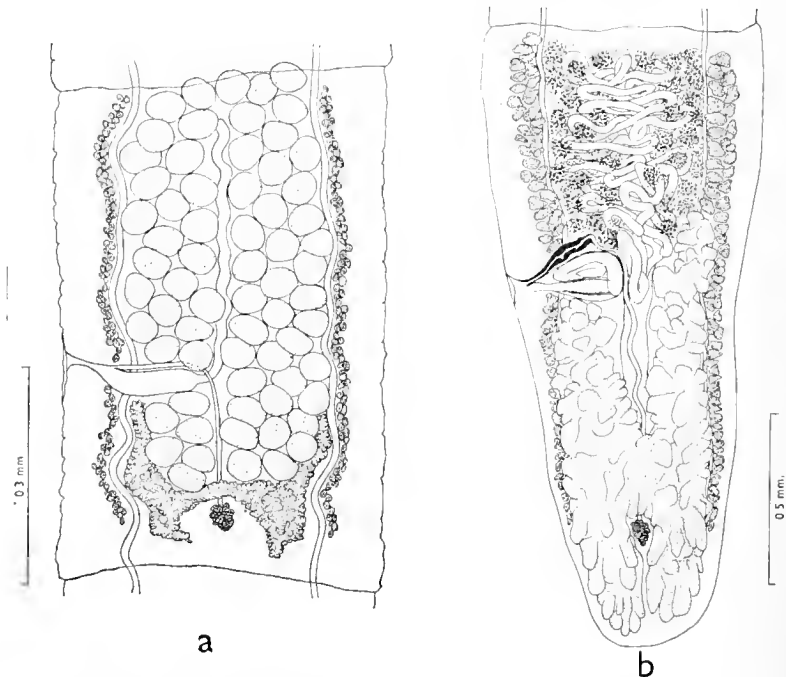


FIG. 5. *Acanthobothrium parvum*. (a) Mature segment. (b) Terminal segment, in which the testes are beginning to atrophy.



mature free proglottids, measuring about  $4 \times 1$  mm, the developing eggs measure approximately 0.02 mm in diameter.

The over-riding diagnostic characters of this small worm are the number of testes per segment, and the size of the bothridial hooks, a combination which cannot be found in the descriptions of any other species of *Acanthobothrium*.

A species commonly found in the Skate is *A. rajaebatis* (Rud., 1809). Although this worm has a similar range in the number of testes to *A. parvum*, it is a much larger worm reaching 60 mm in length and has proportionally greater dimensions throughout, the hooks alone measuring up to 0.30 mm long.

Yamaguti (1952) in his redescription of *A. dasybati* Yamaguti, 1934, (from a number of Japanese species of rays) gives the worm a comparable number of testes with the species described here, but the hooks have very much shorter prongs, the ovary is quadrilobed, and he states that there is no accessory sucker (although signs of one can be seen in his figure). Also *A. dasybati* has not been recorded from rays in European waters nor from *Raja batis*.

*A. maculatum* Riser, 1955, from *Aetobatus californicus*, California, agrees in many respects with the morphology of *A. parvum*, but differs in having a very long anterior loculus to each bothridium, a very small cirrus-pouch, and different proportions to the hooks, quite apart from the differences in host and distribution.

Very similar hooks to those described here can be found in *A. batailloni* Euzet, 1955, from *Myliobatis aquila* at Sète, but this particular species has small accessory suckers, a spiny neck and only 37-64 testes.

Neither Goldstein (1967), nor Williams (1969), in their respective publications on the genus *Acanthobothrium*, includes any worm comparable with *A. parvum* amongst the many species described, and there can be found nowhere in literature examined any reference to a worm from Elasmobranchs that fits the description of *A. parvum*.

***Acanthobothrium* sp.**

(fig. 6)

One immature specimen 1.8 mm long was collected from *Raja batis* in Faxe Bay on 23 October 1966.

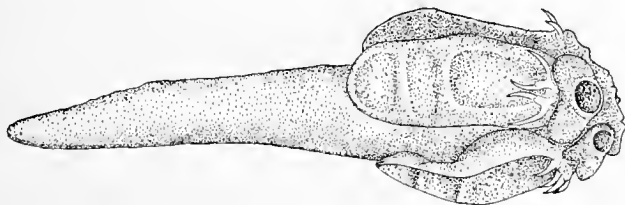


FIG. 6. *Acanthobothrium* sp.

The scolex, bothridia, and hooks, together with the overall size, are the few morphological characters available in this young worm. The bothridia measure 0.39 mm to 0.4 mm in length, and the hooks are from 0.108 to 0.12 mm long. The handle measures 0.046–0.056 mm, the inner blade 0.072–0.074 mm and the outer blade 0.074–0.08 mm.

There is some speculation as to the stage in development at which the hooks of *Acanthobothrium* and allied genera stop growing, and for this reason the above specimen has not been allotted to a new, or previously-described species.

*Echeneibothrium minutum* Williams, 1966

(figs 7 and 8a)

Many complete worms, together with several fragments, were found in four *Raja batis* caught in Faxe Bay on 22 and 23 October 1966. The worms are slightly larger than the specimens described by Williams, measuring between 1.29 mm and 3.75 mm in length (one specimen, however, reaches 5.48 mm) as opposed to 2 mm for Williams' material. There is a corresponding increase in the number of segments (up to thirty instead of ten), the myzorhynchus is fractionally larger, and the spine-covered, muscular bothridia may be a good deal longer. In the original description of *E. minutum* the bothridia are quoted as being 0.27 mm long, but are figured at about 0.5 mm. In the present material the bothridia are usually between 0.5 and 0.7 mm in length, but can reach a size of 0.9 mm, varying in shape and size quite considerably

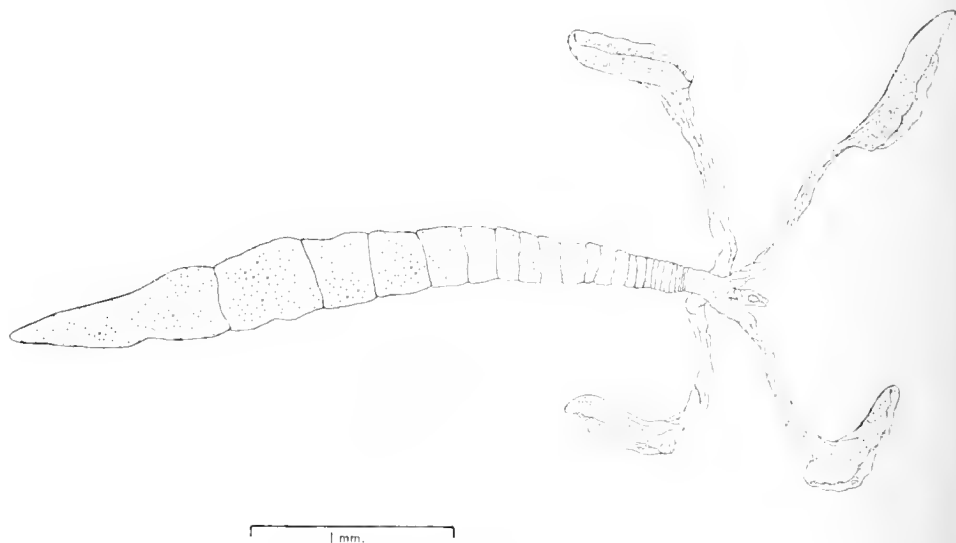


FIG. 7. *Echeneibothrium minutum*.

according to the degree of contraction or relaxation of the musculature at the time of fixing the worms. *E. minutum* has twenty loculi to each bothridium, as indeed do all the worms in this collection, but there appears in several instances to be only eighteen loculi on at least one bothridium of a worm whose other bothridia most definitely possess twenty, and in one case twenty-two loculi are apparent. In many other specimens the bothridia are so relaxed that it is very difficult, even with these structures individually mounted, to distinguish septa at all, let alone count the loculi with any degree of accuracy.

All the other features of this worm correspond closely with the original description of *E. minutum*, although a greater variation in the number of testes occurs, ranging from nine to fifteen per segment. Within the present material it is possible to divide the worms into two groups according to the number of testes. Specimens from three fish have 10-14 testes, whilst those from a fourth Skate have only between 9 and 11 per segment. This single character, however, does not justify the separation of the two groups as they are otherwise morphologically indistinguishable.

Two species of *Echeneibothrium* that have a comparable number of loculi to the bothridia and a similar number of testes to these specimens, are *E. maculatum* var. *exiguum* Euzet, 1959, and *Echeneibothrium* sp. Williams, 1966. However, they are larger worms, the former measuring 3-10 mm and the latter up to 7 mm in length, and occur in a different definitive host, *Raja clavata*.

Of the other recorded species of *Echeneibothrium*, there are several with similar proportions in the bothridia to the Icelandic material, but they all have a considerably higher number of testes, usually more than twenty per segment, and are altogether larger worms.

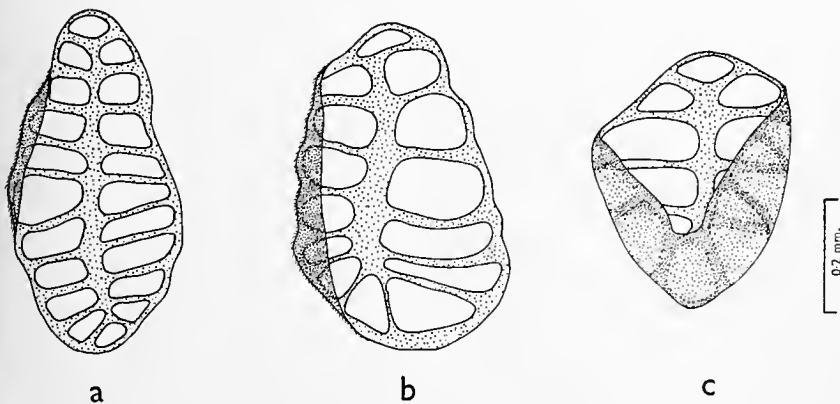


FIG. 8. Diagrammatic comparison of the bothridia of the three species of *Echeneibothrium* encountered: (a) *E. minutum*. (b) *E. faxanum*. (c) *E. dubium*.

*Echeneibothrium faxanum* sp. nov.

(figs 8b and 9)

*Echeneibothrium* sp. Williams, 1966.

This species was found in the spiral valve of only one Skate (*Raja batis*) caught in Faxe Bay, and the total collection is represented by only a few complete specimens and several fragments. The largest worm examined attains 14.63 mm in length and the smallest 10.5 mm. The number of segments varies from 27 to 42 and the maximum width recorded is 0.3 mm.

The specimens can be readily distinguished from the other worms present by the enormity of the myzorhynchus. When contracted this structure swells the scolex to a diameter of up to 0.28 mm and a length of 0.51 mm (fig. 9a), and when extruded the total length of the myzorhynchus may be up to 0.92 mm. The large terminal sucker on the fully-extended myzorhynchus measures 0.36–0.383 mm long by 0.22–0.28 mm in diameter (fig. 9b).

The four bothridia are borne on spiny stalks up to 0.9 mm long, and vary from 0.54 to 0.76 mm in length by 0.24 to 0.39 mm in width, with their external surfaces covered with small spines. There are 14 loculi to each bothridium, comprising one anterior, one posterior and twelve lateral loculi (fig. 8b). It is difficult to differentiate between the base of the tapering scolex and the beginning of the short neck, nevertheless, segmentation begins some 0.3 mm behind the scolex.

The genital pores are lateral and irregularly alternating, as is usual for the genus, and open in the posterior third of the proglottid. There are two pairs of longitudinal excretory canals, the ventral being wider than the dorsal, with no cross-connections readily visible.

The cirrus-sac is pyriform and contains a large spiny cirrus (in every worm examined the cirrus was invaginated) followed by a coiled, and much swollen with sperm, vas deferens, which, on leaving the pouch becomes further convoluted and lies in the median field of the segment. When fully developed the cirrus-sac extends across the segment to reach the aporal excretory canals, and measures 0.18 mm long by 0.09 mm wide.

In early proglottids the testes are spherical with a diameter of 50–70 $\mu$ , but increase in size with further maturation, adopting a more oval outline and measuring up to 120  $\times$  85 $\mu$ . They are disposed in two rows between the excretory vessels and occupy the anterior two-thirds of each segment (fig. 9c). The usual range in the number of testes is between 20 and 26, although there may be as few as nineteen, and in one case 27 were counted.

The vagina is anterior and slightly ventral to the cirrus-sac, turning abruptly in mid-field to run posteriorly to an oötype situated in the region behind the isthmus of the ovary. The ovary itself lies within the area bordered by the excretory canals in the posterior  $\frac{1}{3}$ – $\frac{1}{2}$ rd of the segment and consists of four longitudinal lobes, all roughly equal in length, connected almost terminally by a short isthmus. This gives the ovary almost a 'U' shape rather than the 'H' configuration more commonly encountered in the genus. In all segments examined the uterus is tubular and rather indistinct, not having attained any degree of development, and runs the

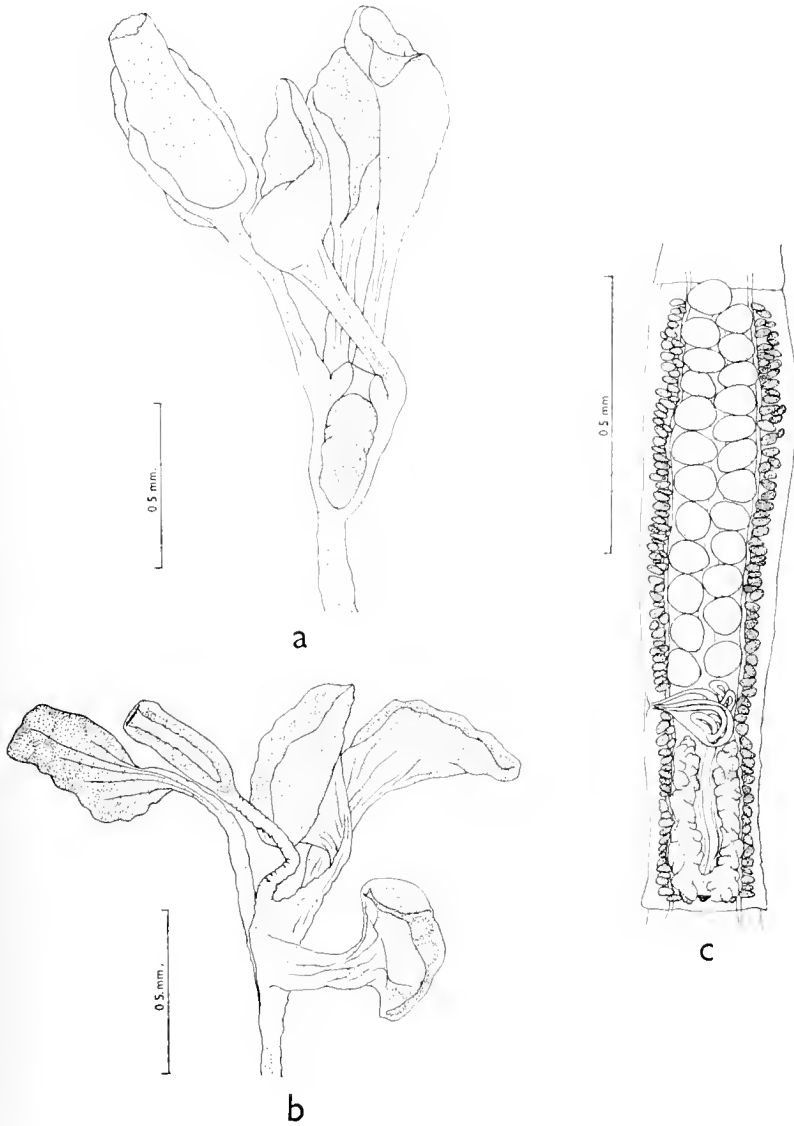


FIG. 9. *Echeneibothrium favanum*. (a) Scolex with contracted myzorhynchus. (b) Scolex with myzorhynchus extruded. (c) Mature proglottis.

length of the median line of the proglottid in the ventral field. The compact vitellaria are roughly circular to oval measuring in the region of 0.05 mm in diameter in mature segments. They are marginal, lying in one or two longitudinal rows in the area outside the excretory canals.

The terminal segment varies from 1.82 to 3.56 mm in length with a maximum width of between 0.2 and 0.3 mm, and contains fully-mature male and female reproductive organs.

No free proglottids were retrieved which could be allotted to this species with any degree of certainty, consequently the morphology of the gravid segments and eggs of this worm remain unknown.

*Echeneibothrium faxanum* has a very similar morphology in many respects to *E. variabile* Beneden, 1849, but differs in having only 14 loculi, as opposed to 16 in the latter, in the characteristic shape and comparatively small size of the myzorhynchus, and in its occurrence in the spiral valve of *Raja batis* (*E. variabile* is more commonly found in *R. clavata*). Euzet (1959) describes a variety of *E. variabile* from *R. batis* with a comparable number of loculi to *E. faxanum*, but the huge size of the myzorhynchus renders it unlikely to be synonymous with the species described here. *E. demensiae* Euzet, 1959, has affinities with *E. faxanum*, particularly in the similar shape and size of the myzorhynchus, but can be discounted as there are eighteen distinct loculi to each bothridium. Finally, Williams (1966) describes a worm from *R. batis* caught in British waters as *Echeneibothrium* sp., which although it is slightly smaller, corresponds so closely with these specimens of *E. faxanum* that it is almost certainly the same species.

### *Echeneibothrium dubium* Beneden, 1858

(figs 8e, 10 and 11)

This is by far the most common worm encountered, inhabiting in large numbers the spiral valve of every specimen of *Raja batis* caught in Faxe Bay.

The worms measure from 3.55 mm to 15.7 mm in length, and have from 35 to over 130 segments, rather more than is usual for this species.

The delicate bothridia may have their external surfaces covered with many small spines, and have a characteristic pyriform outline with the posterior border eup-shaped (fig. 8c). There are 14 distinct loculi. The myzorhynchus when fully extended is long and slender with a small sucker at its tip (fig. 10a), but when retracted assumes a vase-like appearance (fig. 10b).

Apart from the very wide range in the number of testes, the internal anatomy of these specimens tallies closely with all descriptions of *E. dubium*. There are between 11 and 22 testes per segment in these worms from Iceland. Initially it was thought that this large variation must be due to the presence of more than one closely-allied species whose range in testes overlap. However, on counting the testes from every segment of a number of randomly selected worms, it can be seen (fig. 11) that although the highest variation in the testes per individual worm is only five, the

shallow gradation in numbers throughout the whole group extends this range to ten, indicating that no clear-cut distinction can be made between the specimens.

Several species of *Echeneibothrium* have 10 loculi to their bothridia and have a testes number which falls within the range of this material. *E. myzorhynchum* Hart, 1936, *E. dolichoophorum* Riser, 1955, and *E. macrascum* Riser, 1955, all come into this category, but quite apart from numerous morphological differences, all

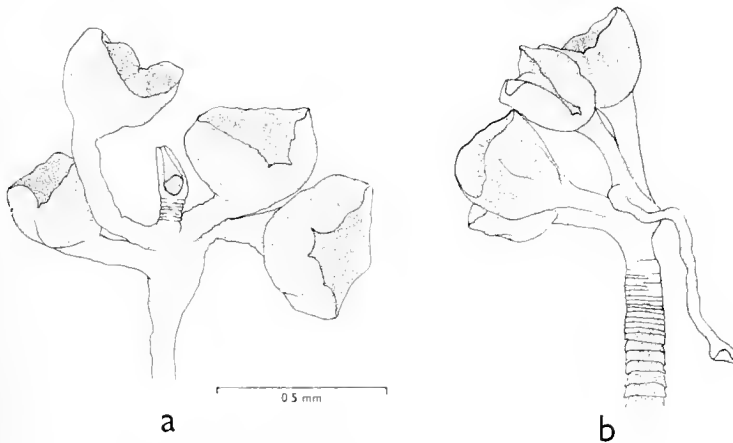


FIG. 10. *Echeneibothrium dubium*. (a) Scolex with contracted myzorhynchus. (b) Scolex with myzorhynchus extruded.

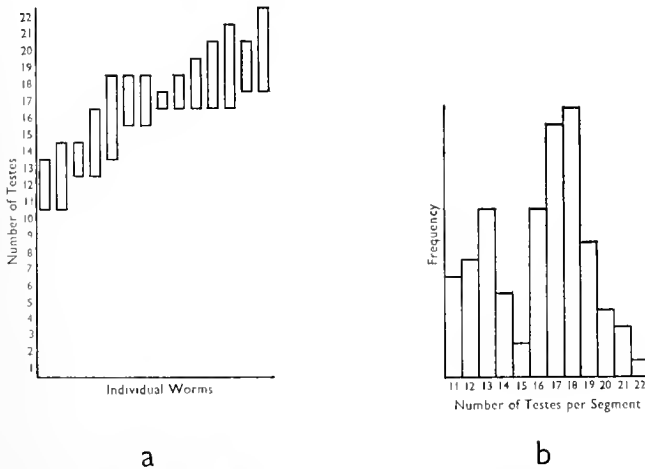


FIG. 11. *Echeneibothrium dubium*, showing the variation in the number of testes per segment. (a) Range within a group of individuals. (b) Frequency of testes per segment in the same group.

three species occur in Rays found on American coasts (*R. binoculata*, *R. rhina* and *R. montereyensis*, respectively), and are therefore unlikely to be found in *R. batis* off Iceland.

Other worms that have some similarities to this material are *E. maculatum*, *E. minimum* and *E. variabile* (pro-parte), with which species in fact *E. dubium* has at times been synonymized by various authors. However, the specimens collected from Iceland cannot reasonably be ascribed to any of these species, and the author can but only agree with Williams' (1958) conclusions in his very adequate elucidation of the status of *E. dubium*.

***Trilocularia acanthiaevulgaris* (Olsson, 1867)**

(fig. 12)

All seven specimens of *Squalus acanthias* yielded examples of this worm, either from the stomach, or spiral valve, or from both organs. The worms are all immature with no signs of segmentation, and are shaped rather like an inverted pyramid, with the broadest region at the scolex.

Those specimens from the spiral valve measure from 2 mm to 7.5 mm in length, whereas the smaller specimens found in the stomach only range between 1.8 and 2.4 mm.

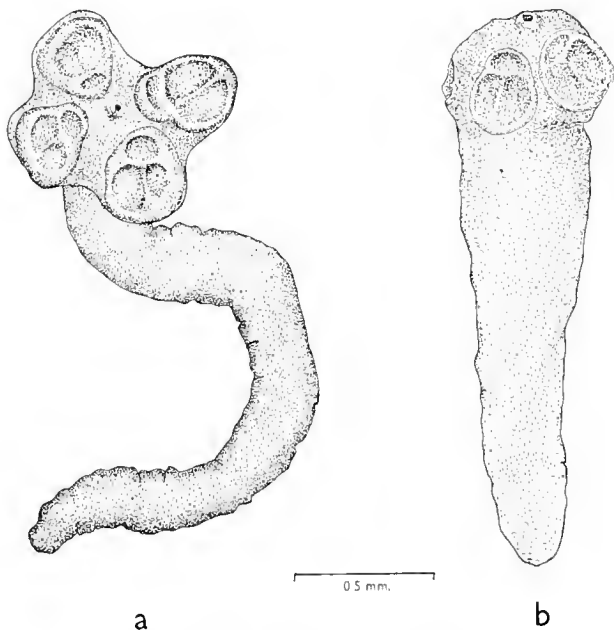


FIG. 12. *Trilocularia acanthiaevulgaris*. From the spiral valve (a) and stomach (b) of *Squalus acanthias*.



The normal variation in scolex diameter is from 0.7 mm to 0.85 mm, although in one worm the measurement is 1.0 mm. The bothridia have the characteristic tripartite shape, with one anterior, and two adjacent posterior loculi (fig. 12). The anterior loculus measures 0.06–0.17 mm  $\times$  0.14–0.24 mm, whilst the posterior region of the bothridium is 0.2–0.3 mm in width by 0.14–0.24 mm in length, and is divided into two equal loculi by a vertical septum. There is a small terminal sucker to the scolex, with a diameter of between 0.06 mm and 0.11 mm.

In one dogfish, the only specimens to be found in the spiral valve were three mature free segments with the characteristic spiny anterior region and posteriorly situated cirrus-sac and genital pore. There were, however, entire immature worms in the stomach of this fish. Alexander (1963) has also recorded the occurrence of only free proglottids on two occasions from dogfish in New Zealand.

This worm has been assigned to a number of genera, being originally described by Olsson as *Phyllobothrium acanthiae-vulgaris*, but later (1869) it is included by him in the genus *Trilocularia* Olsson. Since then this species has been transferred to the genera *Monorygma* Diesing, *Phyllobothrium* Beneden, and then back to *Trilocularia*.

The distribution of *T. acanthiae-vulgaris* appears to be very widespread, being recorded from *Squalus acanthias* in New Zealand by Alexander, from Southern France by Euzet; there are numerous records of the worm from British waters, and Rees (1953) has described specimens from the East coast of Iceland.

### *Phyllobothrium* sp.

Two immature specimens both measuring approximately 6 mm in length, and five adult worms 27–32 mm long with a maximum width of 2 mm, were found together with many apolytic segments in the spiral valve of *Raja batis* from Faxe Bay. Another Skate from the same locality yielded a further two immature specimens which measure 2 mm and 2.5 mm in length and show no signs of segmentation.

Unfortunately, the contracted condition of the preserved worms renders positive identification beyond the generic level virtually impossible, and so the worms have not been ascribed to any previously-recorded species of *Phyllobothrium*.

### *Gilquinia squali* (Fabricius, 1794)

These worms were found with their scoleces firmly embedded in the mucosa of the anterior region of the spiral valve of four specimens of *Squalus acanthias* from Faxe Bay, Isafjord and North of the Vestermann Islands.

The length of the worms ranges from 13.1 mm to 34.8 mm, having a maximum width of between 1.05 and 1.65 mm, and bearing up to 51 segments.

In general morphology these specimens correspond so closely with the definition of *G. squali* given by Dollfus (1942) in his monograph on the Tetrarhynchs, that any further description here is unnecessary.

## ACKNOWLEDGMENTS

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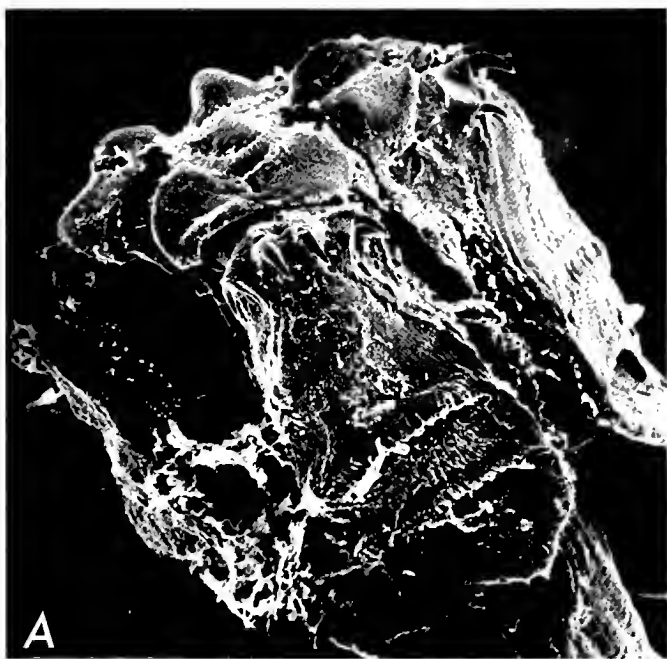
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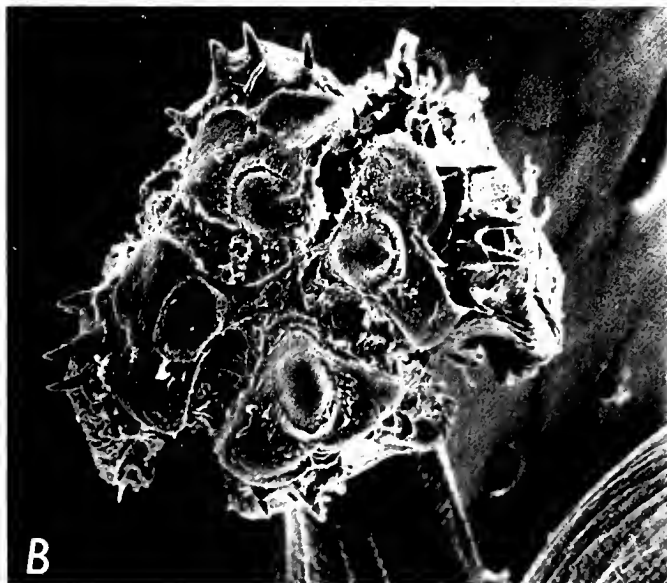
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PLATE 1

*Acanthobothrium icelandicum*. Scanning electron micrographs. A, Lateral view of scolex.  $\times 135$ ; B, Dorsal view of scolex showing the four accessory suckers with their triangular cushions.  $\times 122$ .



A



B









# THE CESTODE *TAENIA KREPKOGORSKI* (SCHULZ & LANDA, 1934) IN THE ARABIAN SAND-CAT (*FELIS MARGARITA* LOCHE, 1858) IN BAHRAIN

By R. A. BRAY

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## SYNOPSIS

*Taenia krepkogorski* is redescribed from the Arabian sand-cat (*Felis margarita*) in Bahrain and its relationship to other species of *Taenia* is discussed.

## INTRODUCTION

A NUMBER of parasitic worms from the intestine of an Arabian sand-cat (*Felis margarita*) obtained in Bahrain were presented to the British Museum (Natural History) by Major M. D. Gallagher. The following species were present in the collection.

Cestoda:

*Diplopylidium noelleri* (Skrjabin, 1924)

*Taenia krepkogorski* (Schulz & Landa, 1934)

Nematoda:

*Ancylostoma braziliense* de Faria, 1910\*

*Rictularia affinis* Jägerskiöld, 1904\*

Acanthocephala:

*Echinopardalis atrata* Meyer, 1931\*

This appears to be the first record of *A. braziliense* and *E. atrata* in this host.

The cestode *Taenia krepkogorski* is little known, and doubts have been expressed as to its validity as a distinct species (Verster, 1969). Originally, this worm was

\*Thanks are due to Miss Eileen A. Mitchell who identified these worms.

reported as a strobilocercus larva in *Gerbillus meridianus* from the Northern Caucasus and in *Rhombomys opimus* from Kazakhstan (Schulz & Landa, 1934). The adult worm appears to have been described only by Petrov & Potekhina (1951, 1953) from *Felis ornata caudata* [= *Felis libyca caudata*] in Tadzhikistan. With these facts in mind, it has been thought that a further description of this species, based on material other than that already described, would be useful.

#### DESCRIPTION

### *Taenia krepkogorski* (Schulz & Landa, 1934) Verster, 1969

*Hydatigera krepkogorski* Schulz & Landa, 1934.

Fifteen worms were found in the intestine of the sand-cat, and of these six were stained with Mayer's paracarmine and prepared as whole mounts. Series of transverse and horizontal sections stained with Ehrlich's haematoxylin and counter stained with erythrosin were also prepared.

The worms measure from 12 to 31 mm in length and up to 3 mm in maximum width, which generally occurs in the region of the later mature segments. The longest strobila consists of 99 segments. In all the specimens the mature segments are about seven times as broad as long (e.g., 2.7 mm  $\times$  0.4 mm), while the early gravid segments are about four times as wide as long (e.g., 2.5 mm  $\times$  0.66 mm). Later gravid segments tend towards a squarish outline, and the last three segments in the longest specimen are longer than wide.

The scolex has a width of between 0.56 mm and 0.84 mm, while the everted rostellum is 0.40–0.56 mm in diameter. The rostellum bears a double crown of hooks, of which there are between 68 and 76. The hooks were measured in preparations where the scolex had been placed *en face* on a slide in Berlese fluid, and pressure applied to spread the hooks conveniently for measuring (see Burse & Burt, 1970). The arrangement of hooks was examined on a scolex mounted *en face*, but not squashed, and also on scanning electron micrographs. As is usual in the genus *Taenia* the hooks are of two sizes, arranged alternately in two crowns the larger hooks forming the anterior circle. When examined *en face* on a light microscope the arrangement of the hooks appeared typically in two circles (Plate 1a), while the stereoscan pictures show the larger hooks disposed in two alternating circles, thus giving the rostellum the appearance of carrying three distinct crowns of hooks (Plate 1b and c). The larger hooks measure from 300–330  $\mu$ m in length and the smaller hooks 200–222  $\mu$ m (fig. 1). The suckers are either rounded (about 230  $\mu$ m dia.) or, more often, oval (232–280  $\mu$ m  $\times$  125–212  $\mu$ m).

The segments which occur close behind the scolex are wider than the scolex, and they increase in size to almost the maximum width of the body at about the twentieth segment. Some of the shorter strobila show a distinct neck measuring up to 0.6 mm, while the remainder of specimens, presumably due to contraction, show signs of segmentation immediately behind the scolex.

In transverse section the longitudinal musculature can be seen to form two distinct concentric layers of bundles. Those in the outer layer are usually about half the

size of those in the inner. Complete bundles in the inner layer contain about 38–42 fibres, while those in the outer layer have about 19–30 fibres which appear to be rather more closely packed. The bundles in both layers are weakly developed and very numerous. A single layer of circular muscle-fibres lies inside the longitudinal layers (fig. 2b).

The ventral excretory vessels are much larger than the dorsal and are more laterally disposed. In cross-section the lumen of the ventral canal is about 0.15 mm in diameter, and that of the dorsal canal about 0.01 mm. The two ventral vessels are connected by a transverse canal lying near the posterior margin of the segment. No corresponding connection between the dorsal vessels has been made out either in whole preparations or in serial sections. The longitudinal nerve-cords lie close to the ventral canals and directly lateral to them.

The genital pores alternate irregularly, and are situated at about the middle level of the segment margin. The genital ducts pass ventrally to the excretory canals and open into the base of a genital atrium, which is narrow and 0.2–0.25 mm deep.

The cirrus-sac, as seen in transverse and horizontal sections, is more or less club shaped, usually reaching to the ventral excretory vessel and measuring 310–430  $\mu\text{m}$  by 70–90  $\mu\text{m}$ . It contains an uncoiled tubular cirrus. An everted cirrus was not seen. A tightly coiled vas deferens leads into the cirrus-sac. The maximum number of testes counted in a single horizontal section was about 145, while an estimate of their number from an examination of whole mounts varies between 360 and 400. Each testis is globular, or nearly so, and measures 25–35  $\mu\text{m}$  in diameter. They are arranged in two lateral groups of roughly equal size, joined by a narrow band of testes disposed anteriorly to the ovary. The lateral fields do not meet behind the vitelline gland (fig. 2a).

The ovary is distinctly bilobed, each lobe consisting of a number of follicles arranged fan-wise. Posteriorly to the ovary lies the vitelline gland, which is transversely elongate and measures about 0.5 mm across. A conspicuous shell-

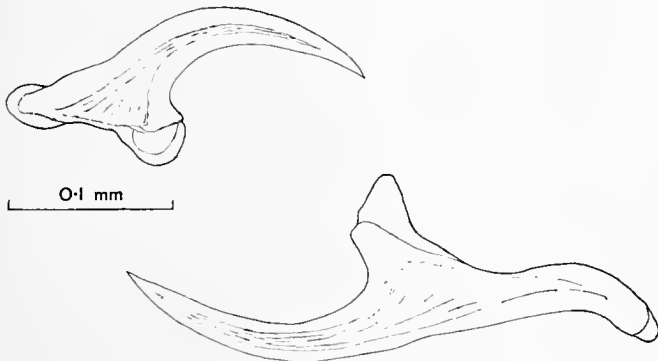


FIG. 1. *Taenia krepkogorski*: hooks.

gland lies in the median line between the ovarian lobes. From the shell-gland the vagina runs anteriorly to the poral lobe of the ovary and opens into the genital atrium posteriorly to the cirrus-sac. The vagina, especially at the distal end is strongly muscular, but it appears that there is no differentiated portion which might be described as a distinct sphincter.

The uterus has four or five main branches on each side of the median longitudinal stem, and these divide again into up to six secondary branches (fig. 3). Only one

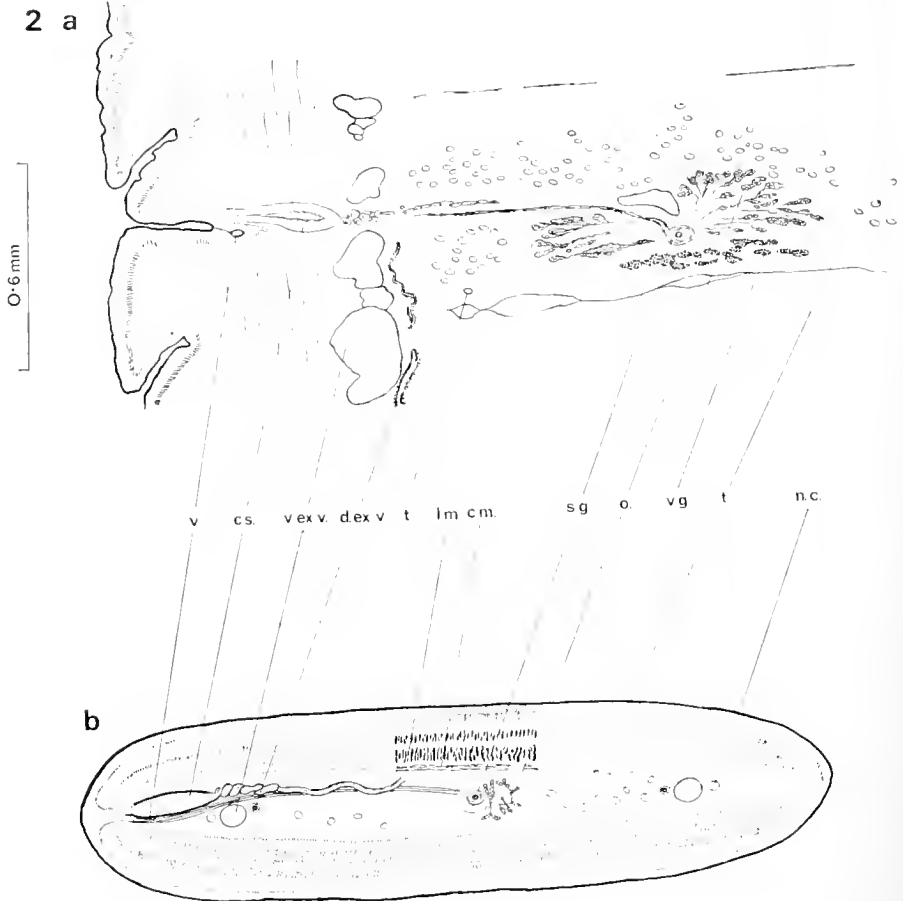


FIG. 2. *Taenia krepkogorski*: a, horizontal section of mature segment (aporal extremity omitted). b, transverse section of mature segment (diagrammatic—small section of musculature shown in detail). Abbreviations: c.m.—circular muscles; c.s.—cirrus sac; d.ex.v.—dorsal excretory vessel; l.m.—longitudinal muscles; n.c.—nerve cord; o.—ovary; s.g.—shell-gland; t.—testis; v.—vagina; v.ex.v.—ventral excretory vessel; v.g.—vitelline gland.

specimen contained fully-developed eggs, these were to be found in the last four segments of the longest specimen. The eggs, measured *in utero*, are 30-33  $\mu\text{m}$   $\times$  23-25  $\mu\text{m}$ . The egg-shell is thick, about 4  $\mu\text{m}$ , and the oncosphere about 15  $\mu\text{m}$  in diameter. The embryonic hooks were not seen, presumably they had not yet developed.

#### DISCUSSION

The material examined appears to be closely related to the adult worms described by Petrov & Potekhina (1951) as *Hydatigera krepkogorski*. In number, size and shape the hooks correspond closely to those described by these authors and also to those originally described by Schulz & Landa (1934) in the larva. The one feature of the hooks not corresponding exactly is the size of the smaller hooks which, in the present material, are very slightly larger on average.

While the length of the worms is rather less than that previously described, the number of segments present is similar. Most of the segments, being much wider

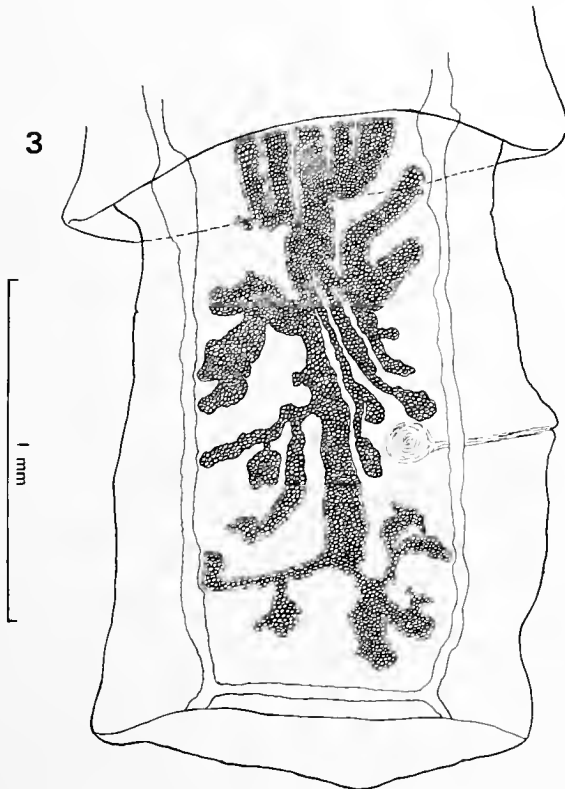


FIG. 3. *Taenia krepkogorski*: gravid segment.

than long, suggest that the worms are contracted, either owing to the method of fixation used or to conditions prevailing in the host.

Other slight differences between these specimens and those previously described, are the smaller size of the scolex and suckers and the fewer lateral branches of the uterus. These minor differences seem to lie within the range of variation usually shown by a species of the genus *Taenia*.

The similarity in the hooks, the general morphology of the segments and the egg-size would appear to place these specimens readily into the concept of the species *Taenia krepkogorski*.

#### RELATIONSHIPS

Verster (1969) in a revision of the species of the genus *Taenia* designates *T. krepkogorski* as a species of uncertain status and postulates its possible identity with either *Taenia taeniaeformis* (Batsch, 1786), *T. macrocystis* (Diesing, 1850) or *T. endothoracica* (Kirschenblatt, 1948).

*Taenia taeniaeformis* is a common parasite of felines and is widespread in its distribution. Undoubtedly it is closely related to *T. krepkogorski*, but differs in having fewer hooks of larger size. A number of specimens determined as *T. taeniaeformis* in the collections of the British Museum (Natural History) have been examined, and they agree closely in number of hooks with the numbers found by Verster (i.e., 34-36). Nevertheless, one specimen with 40 hooks was encountered. *T. taeniaeformis* has large hooks 370-402  $\mu\text{m}$  long, and small hooks 210-261  $\mu\text{m}$  long (Verster, 1969) and in both cases these measurements exceed those of *T. krepkogorski*. The latter species lacks a vaginal sphincter, a feature which Verster considers characteristic of *T. taeniaeformis* and which has been seen in the specimens of *T. taeniaeformis* examined for this study. Both species possess a strobilocercus-type larva, but Schulz and Landa mention that in *T. krepkogorski* the larva is found encysted in the mesenteries and that several larvae may occur in each cyst, a condition not normally associated with the strobilocercus of *T. taeniaeformis* which usually occurs singly in the liver of its host.

Of the species of *Taenia* with over 60 hooks, and, as far as it is known, no vaginal sphincter, only *T. laticollis* Rudolphi, 1819, *T. macrocystis* and *T. endothoracica* have hooks of a size and shape similar to those of *T. krepkogorski*. According to Verster *T. laticollis* has 58-62 hooks, with the larger being 307-407  $\mu\text{m}$  and the smaller 183-247  $\mu\text{m}$  in length. The genital ducts of this species pass between the excretory canals. These features readily separate this species from *T. krepkogorski*.

Verster states that Petrov & Potekhina's (1951) description of *T. krepkogorski* appears to be identical with *T. macrocystis*, and her study of the latter species is based solely on material from South and North America. *T. krepkogorski* differs from this American form in the average number of hooks, the overall spread being from 54-74, according to various authors (see Table 1). In *T. macrocystis* the genital ducts pass between the excretory canals, as in *T. laticollis*, and this is therefore another differentiating feature. *T. macrocystis* has also been recorded a number of times from Russia. Gubanov (1956) has described the adult form from an experi-

mental infection of a wolf cub, the larval material having been found in a mountain hare in the Yakutsk Republic. The hook number in the adult is given as 56, and in the larva from 56-60. No indication is made of the course of the genital ducts in relation to the excretory canals. Davlatov (1967) in his description of a larval *T. macrocystis* from a gerbil states that there are 60 hooks present and in both descriptions the size of the larger hooks exceeds those reported for *T. krepkogorski*. Thus on hook number and size alone a difference between *T. krepkogorski* and *T. macrocystis* from Russia can be detected. As will be mentioned later, it seems conceivable that the Russian specimens determined as *T. macrocystis* may not be conspecific with the American form.

TABLE I

Number and length of hooks in *T. krepkogorski*, *T. macrocystis* and *T. endotheracica*

*Taenia krepkogorski* (Schulz & Landa, 1934)

Author	Number of hooks	Length of large hooks in $\mu\text{m}$	Length of small hooks in $\mu\text{m}$	Host and locality
Schulz & Landa, 1934	66-74*	265-315	182-200	gerbils, Caucasus and Kazakhstan.
Petrov & Potekhina, 1951	64-76	312-345	188-204	<i>Felis libyca caudata</i> , Tadjikistan.
Sadikhov, 1954	60-64	354.6	218.4	<i>Vulpes vulpes</i> , Azerbaijan.
Sadikhov, 1962b	60-74	354	188-204	<i>Felis</i> spp., <i>V. vulpes</i> , Azerbaijan.
Present material	68-76	300-330	200-222	<i>Felis margarita</i> , Bahrain.

*Taenia macrocystis* (Diesing, 1850)

Lühe, 1910	60+	320-340	180	<i>Felis</i> spp., S. America.
Hall, 1919	60-74	320-365	180-200	<i>Lynx</i> spp., U.S.A.
Riser, 1956	—	320-340	190	lynx, Wyoming.
Little & Hopkins, 1969	—	330-340	190	<i>Lynx rufus</i> , Texas.
Verster, 1969	58-60	297-370	183-223	<i>Sylvilagus brasiliensis</i> , <i>Felis wiedii</i> , S. America.
Burse & Burt, 1970	54-70	336-430	198-247	<i>Lynx</i> spp., <i>Lepus americanus</i> , Canada.
Gubanov, 1956	56-60	336-384	183-216	mountain hares, Yakutsk Rep.,
Davlatov, 1967	60	352-360	192-208	wolf-cub, exp. great gerbil, Uzbekistan.

*Taenia endotheracica* (Kirschenblatt, 1948)

Kirschenblatt, 1948**	52-56	314-332	203-218	<i>Meriones erythrourus</i> , Georgia, U.S.S.R.
Dubnitski, 1952	52-60	351-372	224-241	<i>V. vulpes</i> , Kazakhstan.
Dollfus, 1956	52-64	300-378	201-241	<i>Meriones blackleri</i> , Iran.
Gvozdev & Agapova, 1963	56-64	350-370	210-220	<i>Rhombomys opimus</i> , U.S.S.R., <i>Vulpes</i> spp. and dog, exp.
Dollfus, 1965	56-62	335-360	205-219	<i>Meriones</i> spp., Iran.
Verster, 1969	54	329-338	209-218	<i>M. blackleri</i> , Iran.

\*Schulz & Landa (1934) give the number of hooks as 66-72 in the text, but show 74 in their figure

\*\*according to Verster (1969).

Lühe (1910) was the first to draw attention to the unusual arrangement of the larger hooks in *T. macrocystis*, in that they appear to be arranged in two distinct alternating rows. The specific importance of this feature has been stressed by Hall (1919), Riser (1956), Verster (1969) and Bursey & Burt (1970). The figure given by Petrov & Potekhina (1951) of the arrangement of the hooks does not indicate a similar condition in *T. krepkogorski* and neither does the *en face* view of the present material viewed by light microscope (Plate 1a). The stereoscan pictures of the latter material of *T. krepkogorski* (Plate 1b & c), however, shows this unusual arrangement very clearly. It would seem, therefore, that this feature may not be a reliable one for identification purposes, as its appearance varies with the method of examination.

*Taenia endothoracica* has between 52 and 64 hooks and therefore has fewer than *T. krepkogorski*, the larger hooks being between 300  $\mu\text{m}$  and 372  $\mu\text{m}$  in length, with a higher upper limit of size than those so far recorded for *T. krepkogorski*. It appears that the course of the genital ducts in *T. endothoracica* has yet to be described, and Verster places this species in her Group 1 (genital ducts passing between excretory vessels), explaining in a footnote that it is done for convenience only.

As the course of the genital ducts of *T. endothoracica* and the Russian specimens of *T. macrocystis* is not known, certain biological features of these two species and *T. krepkogorski* are compared.

As stated above, *T. krepkogorski* was first recorded as a strobilocercus larva from the mesenteries of the abdominal cavity of *Rhombomys opimus* in Kazakhstan and of *Gerbillus meridianus* from the Northern Caucasus. The larval form has since been found in *R. opimus* in Uzbekistan and Tadzhikistan (Golodnoi Steppe) and in *Meriones erythrourus* in Uzbekistan (Buliginskaya, Vladimirov & Markov, 1956 & 1959; Shleikher & Samsonova, 1953 and Sultanov, Muminov & Adysheva, 1962). The adult has been recorded in various felines. Sadikhov (1962a), has found this cestode in *Felis chaus* and *F. silvestris* in Azerbaijan, and, as already mentioned, Petrov & Potekhina have described it from *F. libyca caudata* in Tadzhikistan. More recently Agapova & Sapozhenkov (1961) have recovered *T. krepkogorski* in *F. libyca ocreata* and *F. margarita* in Turkmeniya. Sapozhenkov (1961) found this worm in *F. margarita* in East Turkmeniya along with *Taenia taeniaeformis* and other helminths, whilst carrying out an ecological survey on this cat. He notes that the cat's main food consists of members of the 'Giberrellinae' [? Gerbillinae] and jerboas. *T. krepkogorski* has been recorded less frequently in canines. Sadikhov (1964) assigned worms from *Vulpes vulpes* in Azerbaijan to this species, and Agapova & Sapozhenkov (1961) record it from *V. vulpes karagan* in Turkmeniya. Verster suggests that the record given by Agapova & Sapozhenkov from *V. vulpes* may in fact refer to *T. endothoracica*, but as these authors give no description of their material Miss Verster presumably draws this conclusion solely from the fact that the host is a canine. However, the partial description given by Sadikhov of material from *V. vulpes*, in which the number of hooks is given as 60-64, suggests that this record, at least, may refer to *T. endothoracica*. *T. krepkogorski* therefore appears to have a preference for felines as definitive hosts and to occur solely in gerbils in its strobilocercus stage, being restricted in distribution to the desert areas of southwestern central Asia.



*T. endotheracica* has so far been recorded naturally as an adult only in *Vulpes vulpes* in Kazakhstan and the Caucasus by Dubnitski (1952). Gvozdev & Agapova (1963) have studied the experimental life-history of this species and have gained positive results in *V. vulpes*, *V. corsac* and the dog. I have not been able to discover any references to this species occurring in carnivores other than canines. The larva has been described a number of times. It is polycephalic and has been found in many species of gerbils in southwestern Asia and north Africa (Gvozdev & Agapova, 1963; Dollfus, 1956 and 1965). This species differs from *T. krepkogorski*, therefore, in its preference for canine definitive hosts and in the form of its larval stage.

*Cysticercus macrocystis* was originally described by Diesing (1850) as a larval form in *Lepus brasiliensis* [= *Sylvilagus brasiliensis*] in Brazil. The adult was first described by Lühe (1910) as *Taenia macrocystis* from various cats in Brazil and Paraguay, and since then the worm has been recorded a number of times from felids in North and South America (see Table 2). The larval stage, a strobilocercus, has been found in lagomorphs in North and South America (Lühe, 1910; Hall, 1919; Grundmann, 1958; Verster, 1969; Burse & Burt, 1970). This species was first recorded in Russia by Petrov & Potekhina (1953) from *Vulpes vulpes* in Tadzhikistan, and the larval stage has since been recorded from hares, squirrels and gerbils in central Asia (Gubanov, 1956 and 1958; Gubanov & Fedorov, 1956; Kontrimavichus, 1959; Davlatov, 1967). Davlatov mentions the discovery of this species in a fox in Uzbekistan, and, as has already been stated, Gubanov (1956) successfully infected a wolf cub with material originating from a hare. In Russia this parasite has only once been recorded in a cat, that was in a lynx in Belorussia by Shimalov (1963). Both Gubanov and Davlatov have described the larva of this cestode. Gubanov (1956) calls the larva a cysticercus and makes it clear from his description that the scoleces are invaginated in the larval cyst. Davlatov (1967) states that the larva is a bladder-shaped helminth containing three capsules and twelve specimens. Neither description appears to refer to a strobilocercus-type larva, and it would seem that Davlatov's description is particularly ambiguous and could fit either a polycephalic or a coenurus larva, which according to Mahon (1954) may be related larval forms and quite distinct from a strobilocercus. Therefore the Russian form of *T. macrocystis* appears to differ from *T. krepkogorski* in larval type and in its host preference in both larval and adult stages.

The above statement also applies when comparing the Russian and the American forms of *T. macrocystis*. In Russia the adult shows an inclination to infest canines, a condition which has not been demonstrated in America, neither has the larva been found in rodents in America as it has, in a number of cases, in Russia. These facts indicate that these two forms may not be conspecific, and also suggest that a closer comparison with *T. endotheracica*, with its polycephalic larva and preference for canine hosts is very desirable.

To sum up, from the evidence presented above it appears that *Taenia krepkogorski* is a distinct species, occurring primarily in cats in southwestern central Asia, and is probably restricted in its larval (strobilocercus) form to gerbils. Moreover, it can be seen from the description that *T. krepkogorski* should be placed in Group II of Verster's classification of *Taenia* as the genital ducts pass ventrally to both excretory

TABLE 2

Records of adult *T. krepkogorski*, *T. macrocystis* and *T. endotheracica* in Felidae and Canidae

Species	Felidae	Canidae	Reference	
<i>T. krepkogorski</i>	<i>Felis libyca caudata</i> , Tadzhikistan	.	Petrov & Potekhina, 1951	
	<i>Felis libyca ocreata</i> , <i>Felis margarita</i> , Turkmeniya	<i>Vulpes vulpes</i> , Azerbaijan	Sadikhov, 1954	
	<i>F. margarita</i> , Turkmeniya	<i>V. vulpes karagan</i> , Turkmeniya	Agapova & Sapozhenkov, 1961	
	<i>Felis chaus</i> , <i>Felis silvestris</i> , Azerbaijan		Sapozhenkov, 1961 Sadikhov, 1962a	
	<i>F. margarita</i> , Bahrain		Present Study	
	<i>T. macrocystis</i>	<i>Felis wiedii</i> , <i>Felis yagouaroundi</i> , <i>Galictis</i> sp., <i>Felis</i> sp., Brazil, Paraguay		Lühe, 1910
		<i>Lynx rufus</i> , <i>L. rufus baileyi</i> , U.S.A.		Hall, 1919
		<i>Felis (Oncooides) macroura</i> , Brazil		Baer, 1927
		bobcat-lynx, Wyoming		Riser, 1956
		<i>L. rufus pallescens</i> , Utah		Grundmann, 1958
<i>L. rufus</i> , Colorado			Leiby, 1961	
<i>L. rufus</i> , N. and S. Carolina			Miller & Harkema, 1968	
<i>L. rufus</i> , Texas			Little & Hopkins, 1969	
<i>F. wiedii wiedii</i> , Brazil			Verster, 1969	
<i>Lynx canadensis</i> , Alaska				
<i>L. rufus</i> , New Brunswick		Burse & Burt, 1970		
<i>L. canadensis</i> , Newfoundland	wolf-cub, exp. (Yakutsk)	Gubanov, 1956		
lynx, Belorussiya	<i>V. vulpes</i> , Tadzhikistan	Petrov & Potekhina, 1953 Shimalov, 1963		
<i>T. endotheracica</i>		<i>V. vulpes</i> , Kazakhstan and Caucasus	Dubnitski, 1952	
		<i>V. vulpes</i> , <i>V. corsac</i> and dog, all exp. (U.S.S.R.)	Gvozdev & Agapova, 1963	

vessels. In addition a comment is made concerning those specimens of *T. macrocystis* recorded in Russia which, it is suggested, may not be conspecific with the worm as it is known in the Americas, and may be comparable with *T. endotheracica*.

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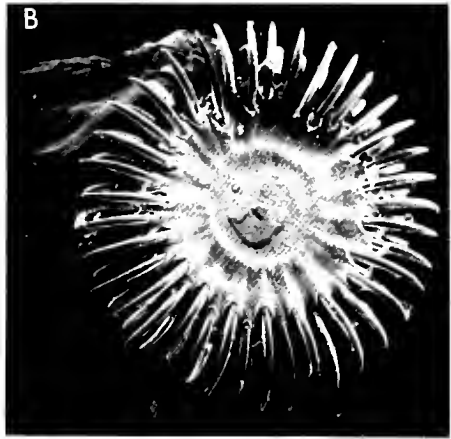
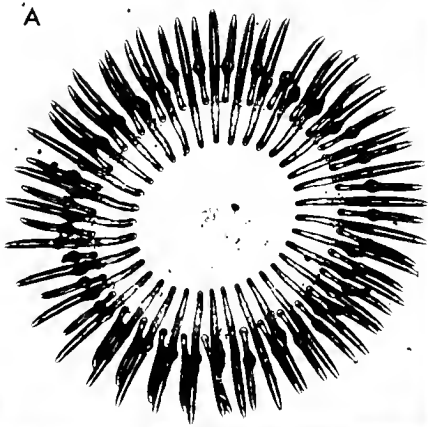
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PLATE 1

*Taenia krepkogorski*: views of scolex showing arrangement of the rostellar hooks.

- a. light microscope *en face* view
- b. stereoscan microscope *en face* view
- c. stereoscan microscope side view.







# ARCACEA (MOLLUSCA : BIVALVIA) TYPES IN THE BRITISH MUSEUM (NATURAL HISTORY)

By Mrs S. E. STEVENSON

THE following list of type specimens of the bivalve superfamily Arcacea in the BMNH includes details of locality and probable present taxonomic position. A list has also been made of types which could have been deposited in this Museum but which have not been isolated and may reside elsewhere.

When the type lot included more than one specimen, then all specimens are regarded as syntypes, figured specimens thus do not automatically become holotypes. Lectotypes are only referred to where they have been selected by earlier authors. The localities refer to that published and where relevant, details of that accompanying the specimen are given in square brackets. The probable present taxonomic position of each species has been arrived at after the curation of the collections but this decision has been greatly assisted by the following authors: Keen (1958), Lamy (1907), Lynege (1909), Olsson (1961) and Prashad (1932).

I wish to thank all members of the Mollusca Section of the BMNH for their help and guidance, particularly Dr J. D. Taylor, under whose supervision this work was carried out.

**aceraea** Melvill and Standen 1899 : 186, pl. 10, fig. 15, as *Acar* (*Barbatia*) loc. Torres Strait. 1 Syntype. Reg. no. 1899.2.23.23. = *Arcopsis aceraea* (Melvill and Standen, 1899).

**adamsiana** Dunker, 1866 : 88, pl. 29, fig. 4, as *Arca* loc. China Seas. 2 Syntypes. Reg. no. 1969241. = *Barbatia bistrigata* (Dunker, 1866).

**africana** Sowerby, 1904 : 4, pl. 6, fig. 4, as *Arca* (*Scapharca*) loc. 18 m N.W. Mouth of Tugela River, South Africa, 55 fm. Holotype. Reg. no. 1904.12.23.171. = *Anadara ferruginea* (Reeve, 1844).

**alternata** Sowerby, 1833 : 17, as *Byssoarca* loc. West Columbia. 3 Syntypes. Reg. no. 1969233. = *Barbatia alternata* (Sowerby, 1833).

**americana** d'Orbigny, 1846 : 632, as *Arca* loc. Brazil. Holotype. Reg. no. 1854.12.4.782. = *Lunarca campechiensis* (Gmelin, 1791).

**anaclima** Melvill and Standen, 1907 : 794, pl. 54, fig. 6, as *Arca* (*Bathyarca*) loc. (i) Gulf of Oman, Persian Gulf. 24°58'N 56°54'E 156 fms. (ii) 25°10'N 60°34'E 40 fms [not located in B.M.(N.H.)]. 8 ×  $\frac{1}{2}$  Syntypes. Reg. no. 1907.5.3.69-72. = *Bathyarca anaclima* (Melvill and Standen, 1907).

**angicostata** Reeve, 1844 : sp. 57, as *Arca* loc. Not known. [Specimen label: North Western Australia, sand banks low water.] Possible Holotype. Reg. no. 1969252. = *Anadara clathrata* (Reeve, 1844).

**angulata** King and Broderip, 1832 : 336 as *Arca* loc. Juan Fernandez. [Specimen label: Cumberland Bay.] 2 Syntypes. Reg. no. 1969202. = *Arca angulata* King and Broderip, 1832.

*Bull. Br. Mus. nat. Hist. (Zool.)* 24, 3

- avellanaria** Melvill and Standen, 1907 : 797, pl. 54, fig. 3, as *Barbatia* (*Acar*) loc. Gulf of Oman, Persian Gulf. 24°58'N 56°54'E. 156 fms. 3 ×  $\frac{1}{2}$  Syntypes. Reg. no. 1907.5.3.55-7. = *Bentharcia avellanaria* (Melvill and Standen, 1907).
- aviculoides** Reeve, 1844 : sp. 63 as *Arca* loc. St Elena. [Specimen label: St Elena and Ceylon.] 3 Possible Syntypes. Reg. no. 1969215. = *Anadara aviculoides* (Reeve, 1844).
- barbadensis** d'Orbigny, 1846 : 321, as *Arca* loc. Cuba. [Specimen label: Martinique.] 2 Syntypes. Reg. no. 1854.10.4.589. = *Arca noae* (Linnaeus, 1758).
- bensoni** H. Adams, 1872 : 14, pl. 3, fig. 24, as *Scaphula* loc. Not known. 3 Syntypes. Reg. no. 1878.1.2.8.86. = *Scaphula pinna* Benson, 1856.
- bicarinata** Sowerby, 1901 : 211, pl. 22, fig. 14, as *Arca* loc. Island of Cebu, Philippines. 3 Syntypes. Reg. no. 1901.10.3.6-8. = *Arca ventricosa* Lamarck, 1819.
- bicops** d'Orbigny, 1846 : 652, as *Arca* loc. Rio de Janeiro, Brazil. Holotype. Reg. no. 1854.12.4.781. = *Anadara chemnitzii* (Philippi, 1851).
- bifrons** Carpenter, 1857 : 134 as *Arca* loc. Mazatlan. Lectotype (Selected by Keen, 1968). Reg. no. 1969209. Paralectotype. Reg. no. 1969259. = *Anadara bifrons* (Carpenter, 1857).
- birleyana** Melvill and Standen, 1907 : 794, pl. 53, fig. 8, as *Arca* (*Scapharca*) loc. Thairi, Persian Gulf. Holotype. Reg. no. 1907.5.3.5. = *Anadara vellicata* (Reeve, 1844).
- bistrigata** Dunker, 1866 : 87, pl. 30, fig. 4-6, as *Arca* loc. Bombay. 2 ×  $\frac{1}{2}$  Syntypes. Reg. no. 1969242. = *Barbatia bistrigata* (Dunker, 1866).
- brevifrons** Sowerby, 1833 : 22, as *Arca* loc. Tumbez, Peru. Holotype. Reg. no. 1969256. = *Lunarca brevifrons* (Sowerby, 1833).
- britannica** Reeve, 1844 : sp. 98, as *Arca* loc. Devonshire coast, Britain. [Specimen label: Britain.] 3 Possible Syntypes. Reg. no. 1969199. = *Arca tetragona* Poli, 1795.
- bullata** Reeve, 1844 : sp. 107, as *Arca* loc. Not known. 3 Syntypes. Reg. no. 1969218. = *Barbatia helblingii* (Bruguière, 1789).
- caelata** Reeve, 1844 : sp. 110, as *Arca* loc. Not known. Holotype. Reg. no. 1969224. = *Barbatia caelata* (Reeve, 1844).
- carpenteri** Dunker, 1866 : 86, pl. 30, figs 7-9, as *Anomalocardia* loc. Australia. [Specimen label: South Australia.] Holotype. Reg. no. 1969176. = *Anadara ? indica* (Gmelin, 1791).
- cepoides** Reeve, 1844 : sp. 66, as *Arca* loc. San Miguel, South America. Holotype. Reg. no. 1969217. = *Anadara cepoides* (Reeve, 1844).
- chalcanthum** Reeve, 1844 : sp. 43, as *Arca* loc. San Nicolas, Island of Zebu, Philippines. [Specimen label: Island of Zebu.] 3 Syntypes. Reg. no. 1969162. = *Anadara gubernaculum* (Reeve, 1844).
- cibotina** Melvill and Standen, 1907 : 795, pl. 54, fig. 4, as *Arca* (*Scapharca*) loc. Gulf of Oman, Persian Gulf. 24°58'N 56°54'E. 156 fms. 7 ×  $\frac{1}{2}$  Syntypes. Reg. no. 1907.5.3.12-14. = *Samacar cibotina* (Melvill and Standen, 1907).
- clathrata** Reeve, 1844 : sp. 48, as *Arca* loc. Island of Burias and Ticao, Philippines. 2 ×  $\frac{1}{2}$  Syntypes. Reg. no. 1969172. = *Anadara clathrata* (Reeve, 1844).
- cometa** Reeve, 1844 : sp. 111, as *Arca* loc. Sarsogan, Island of Luzon, Philippines. [Specimen label: Island of Luzon.] 3 Syntypes. Reg. no. 1969185. = *Barbatia cometa* (Reeve, 1844).

- concinna** Sowerby, 1833 : 20, as *Arca* loc. Central America. [Specimen label: Gulf of Nicoya.] 3 Syntypes. Reg. no. 1969231. = *Anadara concinna* (Sowerby, 1833).
- congenita** Smith, 1885 : 264, pl. 17, fig. 6, 6a, as *Arca* (*Acar*) loc. Sta. 201, off West coast Mindanao, Philippines. 82 fms, stone and gravel. 2 Syntypes. Reg. no. 1887.2.9.3122. = *Barbatia plicata* (Dillwyn, 1817).
- consociata** Smith, 1885 : 266, pl. 17, fig. 7, 7a, as *Arca* loc. Sta. 189, Arafura Sea. 25 fms. 3 Syntypes. Reg. no. 1887.2.9.3128. = *Anadara ferruginea* (Reeve, 1844).
- contraria** Reeve, 1844 : sp. 55, as *Arca* loc. Not known. Holotype. Reg. no. 1969246. = *Noetia ponderosa* (Say, 1822).
- cornea** Reeve, 1844 : sp. 16, as *Arca* loc. Basey, Island of Samar, Philippines. 3 Syntypes. Reg. no. 1969171. = *Anadara cornea* (Reeve, 1844).
- corpulenta** Smith, 1885 : 263, pl. 17, fig. 5-5b, as *Arca* (*Barbatia*) loc. (i) Sta. 184 E. of Cape York, North Australia. 1400 fm. (ii) Sta. 194 S. of Amboina. 200 fm. (iii) Sta. 198 off N.E. extremity of Celebes. 2150 fm. (iv) Sta. 216A N.W. of New Guinea. 2000 fm. (v) Sta. 271 Mid Pacific 2425 fm. (vi) Sta. 300 near I. of Juan Fernandez off Chilean coast. 1375 fm. [Not located in BMNH] 6 Syntypes. Reg. no. (i) 1887.3.9.3120-1. (ii) 1889.11.11.13. (iii) 1887.2.9.3118. (iv) 1889.11.11.132. (v) 1889.11.11.134. = ? *Bathyarca corpulenta* (Smith, 1885).
- crebricostata** Reeve, 1844 : sp. 61, as *Arca* loc. Not known. 2 Syntypes. Reg. no. 1969165. = *Anadara crebricostata* (Reeve, 1844).
- culebrensis** Smith, 1885 : 268, pl. 17, fig. 9-9b, as *Arca* (*Scapharca*) loc. Sta. 24, off Culebra Island, West Indies. 390 fm. 2 Syntypes. Reg. no. 1887.2.9.3138. = *Bathyarca culebrensis* (Smith, 1885).
- cunealis** Reeve, 1844 : sp. 87 and erratta, as *Arca* loc. Zanzibar.  $2 \times \frac{1}{2}$  Syntypes. Reg. no. 1969198. = *Arca avellana* Lamarck, 1819.
- cuneata** Reeve, 1844 : sp. 37, as *Arca* loc. Zanzibar. [Specimen label: Shanghi.] Possible Holotype. Reg. no. 1969180. = *Anadara granosa* (Linnaeus, 1758).
- cuneata** Reeve, 1844 : sp. 87 (non sp. 37), as *Arca* see **cunealis** Reeve, 1844.
- cylindrica** Wood, 1828 : 6, pl. 2, fig. 3, as *Arca* loc. Not known. Holotype. Reg. no. 1969191. = *Barbatia barbata* (Linnaeus, 1758).
- cymbaeformis** Reeve, 1844 : sp. 31, as *Arca* loc. Not known. Possible Holotype. Reg. no. 1969212. = *Anadara* ? *cornea* (Reeve, 1844).
- dalli** Smith, 1885 : 269, pl. 17, fig. 10-10b, as *Arca* (*Macrodon*) loc. Sta. 233a, off Kobe, Japan. 50 fms. Holotype. Reg. no. 1887.2.9.3141. = *Poterius dalli* (Smith, 1885).
- decussata** Sowerby, 1833 : 18, as *Byssarca* loc. Pacific Ocean. [Specimen label: Lord Hood's Island.] 3 Syntypes. Reg. no. 1969232. = *Barbatia helblingii* (Bruguière, 1789).
- deshayesii** Hanley, 1843 : 157, pl. 18, fig. 42, as *Arca* loc. Indian Ocean. [Specimen label: no locality.] Possible Holotype. Reg. no. 1907.10.28.126. = *Anadara deshayesii* (Hanley, 1843).
- disparilis** Reeve, 1844 : sp. 59, as *Arca* loc. Not known. 1 Syntype. Reg. no. 1969164. = *Anadara inaequalis* (Bruguière, 1792).
- divaricata** Sowerby, 1833 : 18, as *Byssarca* loc. Annaa Island and Chain Island. [Specimen label: Annaa Island.]  $2 \times \frac{1}{2}$  Syntypes. Reg. no. 1969226. = *Barbatia plicata* (Dillwyn, 1817).

- dubia** Baird, 1873 : 453, pl. 42, fig. 5-6, as *Arca* (*Byssarca*) loc. New Caledonia. Holotype. Reg. no. 1969239 = *Barbatia domingensis* (Lamarck, 1819).
- eximia** Dunber, 1866 : 90, pl. 30, fig. 1-3, as *Barbatia* loc. Not known. Holotype. Reg. no. 1969192. = *Barbatia barbata* (Linnaeus, 1758).
- fasciata** Reeve, 1844 : sp. 90, as *Arca* loc. Not known. [Specimen label: Sydney, under stones low water.] 3 Possible Syntypes. Reg. no. 1969182 = *Barbatia fasciata* (Reeve, 1844).
- ferruginea** Reeve, 1844 : sp. 39, as *Arca* loc. Not known. [Specimen label: China Seas.] 3 Possible Syntypes. Reg. no. 1969178. = *Anadara ferruginea* (Reeve, 1844).
- formosa** Sowerby, 1833 : 20, as *Arca* loc. Gulf of Tehuantepec, Central America. 2 Syntypes. Reg. no. 1969234 = *Anadara formosa* (Sowerby, 1833).
- fultoni** Sowerby, 1907 : 302, pl. 25, fig. 11, as *Arca* (*Scapharca*) loc. Manila, Philippines. Holotype. Reg. no. 1907.8.28.30. = *Anadara crebricostata* (Reeve, 1844).
- gambiensis** Reeve, 1844 : sp. 36, as *Arca* loc. Mouth of River Gambia, Africa. 3 Syntypes. Reg. no. 1969211 = ?*Sheldonella gambiensis* (Reeve, 1844).
- gibbosa** Reeve, 1844 : sp. 20, as *Arca* loc. Not known. 1 Syntype. Reg. no. 1969216. = *Anadara* ? *gibbosa* (Reeve, 1844).
- glacialis** Gray, 1824 : 244, as *Arca* loc. Not given. [Specimen label: Prince Regents Inlet.] 12 Syntypes. Reg. no. 1841.4.19.14-22. = *Bathyarca glacialis* (Gray, 1824).
- globosa** Reeve, 1844 : sp. 52, as *Arca* loc. Catbalonga, Island of Samar, Philippines. 4 fms, in coarse sand and gravel. 2 Syntypes. Reg. no. 1969166. = *Anadara inaequalis* (Bruguière, 1792).
- gradata** Broderip and Sowerby, 1830 : 365, as *Arca* loc. Mazatlan, Pacific Ocean. [Specimen label: no locality.] Possible Holotype. Reg. no. 1858.5.12.100. = *Barbatia gradata* (Broderip and Sowerby, 1830).
- gubernaculum** Reeve, 1844 : sp. 14, as *Arca* loc. Basey, Island of Samar, Philippines. 4 fms, coarse sand and shell. 3 Syntypes. Reg. no. 1969168. = *Anadara gubernaculum* (Reeve, 1844).
- lians** Reeve, 1844 : sp. 62, as *Arca* loc. Not known. [Specimen label: Ceylon.] Possible Holotype. Reg. no. 1969179. = *Anadara* ? *indica* (Gmelin, 1790).
- holoserica** Reeve, 1844 : sp. 11, as *Arca* loc. Island of Samar, Philippines. [Specimen label: Catbalonga, Island of Samar.] 3 Syntypes. Reg. no. 1969174. = *Anadara wopignmelana* (Bory St Vincent, 1824).
- illota** Sowerby, 1833 : 18, as *Byssarca* loc. Central America. [Specimen label: Gulf of Nicoya.] 3 Syntypes. Reg. no. 1969235. = *Barbatia illota* Sowerby, 1833.
- imitata** Smith, 1885 : 321, as *Arca* (? *Barbatia*) loc. Sta. 244 Mid-North Pacific 2900 fms. 3 Syntypes. Reg. no. 1887.2.9.3350-2. = *Bathyarca imitata* (Smith, 1885).
- inaequisculpta** Smith, 1885 : 267, pl. 17, fig. 8, 8c, as *Arca* (*Scapharca*) loc. Sta. 24 off Culebra Island, West Indies 390 fm. 9 +  $\frac{1}{2}$  Syntypes. Reg. no. 1887.2.9.3132-7. = *Bathyarca inaequisculpta* (Smith, 1885).
- inflata** Reeve, 1844 : sp. 30 as *Arca* loc. Ilo Ho, Island of Panay, Philippines. 2 Syntypes. Reg. no. 1969167. = *Anadara broughtoni* (Schrenck, 1867).
- insignis** Dunker, 1867 : 93 pl., 31 fig., 11-13, as *Arca* loc. Not known. Holotype. Reg. no. 1969201. = *Arca noae* Linnaeus, 1758.

- japonica** Reeve, 1844 : sp. 32 as *Arca* loc. Coast of Japan. 3 Syntypes. Reg. no. 1969169. = *Anadara indica* (Gmelin, 1790).
- labiosa** Sowerby, 1833 : 21, as *Arca* loc. Tumbes, Peru. [Specimen label: Peru.] 3 Syntypes. Reg. no. 1969210. = *Anadara labiosa* (Sowerby, 1833).
- laminata** Angas, 1865 : 697, as *Barbatia (Acar)* loc. St Vincent's Gulf, South Australia. [Specimen label : South Australia.] 2 Syntypes. Reg. no. 1870.10.26.43. = *Barbatia plicata* (Dillwyn, 1817).
- lateralis** Reeve, 1844 : sp. 15, as *Arca* loc. Philippine Islands. 2 Syntypes. Reg. no. 1969244. = *Sheldonella lateralis* (Reeve, 1844).
- lima** Reeve, 1844 : sp. 101, as *Arca* loc. Island of Burias and Corrigidor, Philippines. [Specimen label: Philippines.] 2 Syntypes. Reg. no. 1969219. = *Barbatia helblingii* (Bruguière, 1789).
- lithodomus** Sowerby, 1833 : 16, as *Byssosarca*. loc. Monte Christo. [Specimen label: West Columbia.] 3 Syntypes. Reg. no. 1969230. = *Litharca lithodomus* (Sowerby, 1833).
- loricata** Reeve, 1844 : sp. 58, as *Arca* loc. Not known. 3 Syntypes. Reg. no. 1969253. = *Anadara cornea* (Reeve, 1844).
- lurida** Sowerby, 1833 : 19, as *Byssosarca*. loc. Santa Elena. 3 Syntypes. Reg. no. 196728. = *Barbatia lurida* (Sowerby, 1833).
- luzonica** Reeve, 1844 : sp. 44, as *Arca*. loc. Island of Luzon, Philippines. 2 Syntypes. Reg. no. 1969163. = *Anadara gubernaculum* (Reeve, 1844).
- maculata** Sowerby, 1833 : 17, as *Byssosarca*. loc. Pacific Ocean. [Specimen label: Lord Hood's Island]. 3 Syntypes. Reg. no. 1969207. = *Arca avellana* (Lamarck, 1819).
- maculosa** Reeve, 1844 : sp. 24, as *Arca*. loc. North Coast, Australia. [Specimen label: Australia]. 2 Syntypes. Reg. 1969170. = *Anadara antiquata* (Linnaeus, 1758).
- margarethae** Melvill and Standen, 1907 : 797, pl. 54, fig. 5, as *Barbatia (Acar)* loc. Gulf of Oman, Persian Gulf. 24°58'N 56°54'E. 154 fms. 4 Syntypes. Reg. no. 1907.5.3.27-31. = *Barbatia plicata* (Dillwyn, 1817).
- minuta** Reeve, 1844 : sp. 112, as *Arca* loc. Philippine Islands. 12 Syntypes. Reg. no. 1969221. = *Bathyarca minuta* (Reeve, 1844).
- mutabilis** Sowerby, 1833 : 17, as *Byssosarca*. loc. West Columbia. 3 Syntypes. Reg. no. 1969165. = *Arca imbricata* Bruguière, 1792.
- myristica** Reeve, 1844 : sp. 42, as *Arca*. loc. Jimamailan, Island of Negros, Philippines. [Specimen label: I. of Negros.] 3 Syntypes. Reg. no. 1969213. = *Anadara clathrata* (Reeve, 1844).
- navicella** Reeve, 1844 : sp. 114, as *Arca* loc. Calipan, Island of Mindoro, Philippines. [Specimen label: I. of Mindoro.] 4 Syntypes. Reg. no. 1969249. = *Arcopsis navicella* (Reeve, 1844).
- nodifera** von Martens, 1860 : 17, as *Arca*. loc. Bangkok. 2 Syntypes. Reg. no. 1969175. = *Anadara granosa* (Linnaeus, 1758).
- novaealedoniae** Baird, 1873 : 452, pl. 42, fig. 4, as *Arca*. loc. New Caledonia. Holotype. Reg. no. 1969240. = *Anadara antiquata* (Linnaeus, 1758).
- novaezealandiae** Smith, 1885 : 88, pl. 2, fig. 1,2, as *Arca (Barbatia)*. loc. St. 96, North of New Zealand. 70 fms. 3 Syntypes. Reg. no. 1852.3.13.110-2. = *Barbatia helblingii* (Bruguière, 1789).

- nux** Sowerby, 1833 : 19, as *Arca* loc. Xipixapi, Peru. [Specimen label: Peru.] 3 Syntypes. Reg. no. 1969229. = *Anadara nux* (Sowerby, 1833).
- obesa** Sowerby, 1833 : 21, as *Arca* loc. West Columbia [Specimen label: Atacamas] 3 Syntypes. Reg. no. 1969237. = *Anadara obesa* (Sowerby, 1833).
- obliquata** Wood, 1828 : 6, pl. 2, fig. 4, as *Arca* loc. Not known. Holotype. Reg. no. 1969190. = *Barbatia obliquata* (Wood, 1828).
- obtusa** Reeve, 1844 : sp. 77, as *Arca* loc. Coast of Japan 3 Syntypes. Reg. no. 1969189. = *Barbatia obliquata* (Wood, 1828).
- occlusa** Reeve, 1844 : sp. 64, as *Arca* loc. Not known. 1 Syntype. Reg. no. 1969160. = *Anadara ? cornea* (Reeve, 1844).
- ocellata** Reeve, 1844 : sp. 102, as *Arca* loc. Singapore. Holotype. Reg. no. 1969200. = *Arca ocellata* Reeve, 1844.
- olivacea** Reeve, 1844 : sp. 113, as *Arca* loc. San Nicolas, Island of Zebu, Philippines. [Specimen label: Island of Zebu.] 3 Syntypes. Reg. no. 1969245. = *Striarca olivacea* (Reeve, 1844).
- ovata** Reeve, 1844 : sp. 49, as *Arca* loc. St Elena, South America. 2 Syntypes. Reg. no. 1969214. = *Anadara aequatorialis* (d'Orbigny, 1847).
- pacifica** Sowerby, 1833 : 17, as *Byssarca* loc. St Elena. [Specimen label: South America.] 2 Syntypes. Reg. no. 1969197. = *Arca pacifica* (Sowerby, 1833).
- parva** Sowerby, 1833 : 10, as *Byssarca* loc. Pacific Ocean Island. [Specimen label: Ducie I.] 4 Syntypes. Reg. no. 1969206. = *Barbatia parva* (Sowerby, 1833).
- pectinoides** King and Broderip, 1832 : 336, as *Arca* loc. Rio de Janeiro. 2 ×  $\frac{1}{2}$  Syntypes. Reg. no. 1969255. = *Lunarca pectinoides* (King and Broderip, 1832).
- pectunculiformis** Dunker, 1866 : 88, pl. 28, fig. 4-6, as *Barbatia* loc. Borneo Coast. Holotype. Reg. no. 1969257. = *Striarca ? afra* (Gmelin, 1790).
- pilula** Reeve, 1844 : sp. 8, as *Arca* loc. Island of Burias, Philippines. 3 Syntypes. Reg. no. 1969161. = *Anadara pilula* (Reeve, 1844).
- pteroessa** Smith, 1885 : 262, pl. 17, fig. 4-46, as *Arca* (*Barbatia*) loc. (i) Sta. 24 off Culebra, West Indies 390 fm. (ii) Sta. 71, West of Azores 1675 fm. (iii) Sta. 73, West of Azores 1000 fm. (iv) Sta. 246 Mid North Pacific Ocean, 2050 fms. 7 Syntypes (2 with Binds disease)\*. Reg. no. (i) 1887.2.9.31159. (ii) 1887.2.9.31114 (iii) 1887.2.9.31113. (iv) 1887.2.9.31115-7. = *Bathyarca asperula* (Dall, 1881).
- pulchella** Reeve, 1844 : sp. 122, as *Arca* loc. Algeria. 4 Syntypes. Reg. no. 1969223. = *Barbatia pulchella* (Reeve, 1844).
- pusilla** Sowerby, 1833 : 18, as *Byssarca* loc. Iquiqui, Peru. Holotype. Reg. no. 1969236. = *Barbatia domingensis* (Lamarck, 1819).
- quadrilatera** Sowerby, 1833 : 22, as *Arca* loc. Real Llejos. [Specimen label: Bay of Guayaquil.] 2 Possible Syntypes. Reg. no. 1969228. = *Larkinia grandis* (Broderip and Sowerby, 1829).
- radula** Smith, 1885 : 260, pl. 17, fig. 3-3b, as *Arca* (*Barbatia*). loc. (i) Port Philip, South Australia. (ii) Sta. 162 off East Moncoeur Island, Bass Strait 38 fm. 5 Syntypes. Reg. no. (i) 1969183. (ii) 1887.2.9.3109-11. = *Barbatia fasciata* (Reeve, 1844).

\* Result of acetic acid (which exudes from English oak, old cotton wool and old glass) reacting with calcium carbonate to form calcium acetate.

- reeveana* d'Orbigny, 1846 : 635, as *Arca* loc. Payta, Peru. 2 Syntypes. Reg. no. 1854.12.4.786. = *Barbatia reeveana* (d'Orbigny, 1846).
- requiescens* Melvill and Standen, 1907 : 793, pl. 54, fig. 2, as *Arca* loc. Gulf of Oman, Persian Gulf. 24°58'N 56°54'E 156 fms. 4 ×  $\frac{1}{2}$  Syntypes. Reg. no. 1906.5.3.51-54. = *Samacarc requiescens* (Melvill and Standen, 1907).
- reversa* Sowerby, 1833 : 20, as *Arca* loc. Peru. [Specimen label: Tumbes.] 3 Syntypes. Reg. no. 1969254. = *Noetia reversa* (Sowerby, 1833).
- rufescens* Reeve, 1844 : sp. 53, as *Arca* loc. Not known. Holotype. Reg. no. 1969173. = *Anadara inaequivalvis* (Bruguière, 1792).
- sanctahelenae* Smith, 1890 : 305, pl. 2, fig. 8-8b, as *Arca* loc. St Helena. 3 Syntypes. Reg. no. 1889.10.1.2432-4. = *Arca bouvieri* (P. Fischer, 1874).
- sculptilis* Reeve, 1844 : sp. 118, as *Arca* loc. Baclayon, Island of Bohol, Philippines. [Specimen label: Island of Bohol.] 3 Syntypes. Reg. no. 1969250. = *Striarca afra* (Gmelin, 1790).
- secticostata* Reeve, 1844 : sp. 38, as *Arca* loc. Not known. 3 Syntypes. Reg. no. 1840.6.11.33-35. = *Anadara secticostata* (Reeve, 1844).
- setigera* Reeve, 1844 : sp. 94, as *Arca* loc. Zanzibar. 2 ×  $\frac{1}{2}$  Syntypes. Reg. no. 1969181. = *Barbatia lacerata* (Linnaeus, 1758).
- solida* Sowerby, 1833 : 18, as *Byssosarca* loc. Payta, Peru. 2 Syntypes. Reg. no. 1969243. = *Striarca afra* (Gmelin, 1790).
- sowerbyi* d'Orbigny, 1846 : 637, as *Arca* loc. Guayaquil, Ecuador. Holotype. Reg. no. 1854.12.4.785. = *Anadara biangulata* (Sowerby, 1833).
- striata* Reeve, 1844 : sp. 121, as *Arca* loc. Not known. 3 Syntypes. Reg. no. 1969251. = *Striarca lactea* (Linnaeus, 1758).
- subrubra* Dunker, 1866 : 83, pl. 28, fig. 1, 2, as *Anomalocardia* loc. Philippine Islands. 2 Syntypes. Reg. no. 1969177. = *Anadara antiquata* (Linnaeus, 1758).
- symmetrica* Reeve, 1844 : sp. 117, fig. 120, as *Arca* loc. Manila Bay, Philippines. [Specimen label: I. of Luzon.] 3 Possible Syntypes. Reg. no. 1969260. = *Striarca afra* (Gmelin, 1790).
- tenebrica* Reeve, 1844 : sp. 105, as *Arca* loc. Basey, Island of Samar, Philippines. [Specimen label: I. of Samar.] 3 Syntypes. Reg. no. 1969247. = *Striarca tenebrica* (Reeve, 1844).
- tenella* Reeve, 1844 : sp. 91, as *Arca* loc. Island of Burias, Philippines. 3 Syntypes. Reg. no. 1969184. = *Barbatia tenella* (Reeve, 1844).
- triangularis* Gray, 1857 : 371 as *Noetia* loc. Not known. Holotype. Reg. no. 1968856. = *Noetia reversa* (Sowerby, 1833).
- truncata* Sowerby, 1833 : 19, as *Byssosarca* loc. Galapagos Islands. 3 Syntypes. Reg. no. 1969205. = *Arca ventricosa* Lamarck, 1819.
- tuberculosa* Sowerby, 1833 : 19, as *Arca* loc. Real Llejos. [Specimen label: Real Llejos, Central America.] Holotype. Reg. no. 1969227. = *Anadara tuberculosa* (Sowerby, 1833).
- velata* Sowerby, 1833 : 18, as *Byssosarca* loc. Pacific Ocean Island. [Specimen label: Lord Hood's and Chain Islands.] 3 Syntypes. Reg. no. 1969238. = *Barbatia helblingii* (Bruguière, 1789).

- vespertilio** Carpenter 1857 : 140, as *Byssosarca* loc. Mazatlan. Holotype. Reg. no. 1969258. = *Barbatia lurida* (Sowerby, 1833).
- virescens** Reeve, 1844 : sp. 97, as *Arca* loc. Catbalonga, Island of Samar, Philippines. [Specimen label: I. of Samar] 2 ×  $\frac{1}{2}$  Syntypes. Reg. no. 1969188. = *Barbatia obliquata* (Wood, 1828).
- volucris** Reeve, 1844 : sp. 109, as *Arca* loc. Island of Burias, Philippines. [Specimen label: Philippines.] 3 Syntypes. Reg. no. 1969196. = *Arca avellana* Lamarck, 1819.
- zebuensis** Reeve, 1844 : sp. 120, fig. 117, as *Arca* loc. Island of Zebu, Philippines. 3 Syntypes. Reg. no. 1969248. = *Stiarca afra* (Gmelin, 1790).

## TYPE SPECIMENS NOT ISOLATED IN B.M.(N.H.)

- americana** Wood, 1828 : 6, pl. 2, fig. 1, as *Arca* loc. Bay of Campeachy.
- ambigua** Reeve, 1844 : sp. 65, as *Arca* loc. Not known.
- anomala** Reeve, 1844 : sp. 9, as *Arca* loc. Not known.
- auriculata** Sowerby, 1833 : 20, as *Arca* loc. St Elena.
- blangulata** Sowerby, 1833 : 21, as *Arca* loc. Atacamas, West Columbia.
- cardiiformis** Sowerby, 1833 : 22, as *Arca* loc. San Blas, Gulf of California.
- clstula** Reeve, 1844 : sp. 29, as *Arca* loc. Not known.
- crassicosata** H. Adams, 1873 : 209 loc. Persian Gulf.
- crenata** Reeve, 1844 : sp. 51, as *Arca* loc. Not known.
- donaciformis** Reeve, 1844 : sp. 104, as *Arca* loc. Mozambique Channel.
- emarginata** Sowerby, 1833 : 20, as *Arca* loc. Pacific Ocean: Atacamas, Real Llejes, Xi pisapi, Panama & Gulf of California.
- hanbeyana** Reeve, 1844 : sp. 68, as *Arca* loc. Harbour of Mozambique.
- labriata** Sowerby, 1833 : 21, as *Arca* loc. Real Llejes & Tumbes.
- lobata** Reeve, 1844 : sp. 19, as *Arca* loc. ? West Indies.
- multicosata** Sowerby, 1833 : 21, as *Arca* loc. Central America.
- nlvea** Reeve, 1844 : sp. 96, as *Arca* loc. Zanzibar.
- nodosa** Wood, 1828 : 6, pl. 2, fig. 8, as *Arca* loc. Not known.
- obliqua** Reeve, 1844 : sp. 41, as *Arca* loc. West coast of Africa.
- pertusa** Reeve, 1844 : sp. 28, as *Arca* loc. Mouth of Gambia, Africa.
- pygmaea** H. Adams, 1872 : 11, as *Scapharca* loc. Red Sea.
- radiata** Reeve, 1844 : sp. 40, as *Arca* loc. Not known.
- rotundicosata** Reeve, 1844 : sp. 46, as *Arca* loc. Not known.
- transversalis** H. Adams, 1872 : 11, pl. 3, fig. 16, as *Anomalocardia* loc. Red Sea.
- vellicata** Reeve, 1844 : sp. 33, as *Arca* loc. Not known.



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A NEW SPECIES OF *ANOPS* FROM MATO  
GROSSO, BRAZIL.  
(REPTILIA : AMPHISBAENIA)

By A. F. STIMSON

INTRODUCTION

In 1967 the Royal Society and Royal Geographical Society Xavantina-Cachimbo Expedition visited northeastern Mato Grosso State to study natural sciences and medicine. A base camp was set up to the east of the Xavantina-São Felix road at 12°49'S : 51°46'W and between September 1967 and May 1969 a collection of reptiles was made under the supervision of the leader of the expedition, Mr Iain R. Bishop of Leicester University. This collection was subsequently sent to the British Museum (Natural History) where it was found to contain five examples of an undescribed species of *Anops*, a genus hitherto considered monotypic.

Under an agreement between the organizers of the expedition and the Brazilian government the holotype and one paratype have been deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP). Of the other three paratypes, two have been deposited in the British Museum (Natural History) (BMNH) and one in the University of Michigan Museum of Zoology (UMMZ).

METHODS

Methods and terminology follow Gans & Alexander (1962) and Gans (1966). In describing characters peculiar to *Anops* I have followed Gans & Rhodes (1964). In *Anops kingii* Bell (1833 : 99) the scales between the oculars and the rostral are irregular and variable and Gans & Rhodes (1964 : 15) preferred not to name them individually. In the present species the single scale between the ocular and the rostral is referred to as the prefrontal and the paired scales between the oculars as frontals, terms used for scales occupying similar positions in the related genus *Mesobaena*. Dorsal annuli are counted along the paravertebral row of segments.

*Anops bilabialatus* sp. nov.

(Text-figs 1-2, pl. 1)

MATERIAL EXAMINED. HOLOTYPE: MZUSP 21276 (lizard collection) an adult female; 12°49'S : 51°46'W, 260 km north of Xavantina, Estado do Mato Grosso, Brazil, 400 m.

PARATYPES: BMNH 1971.1028 an adult male, UMMZ 131700 an adult female, BMNH 1971.1029 a juvenile and MZUSP 21277 (lizard collection) an incomplete specimen, same locality as holotype.

All material was collected by members of the Xavantina-Cachimbo Expedition between September 1967 and May 1969. They were taken on the surface of the forest floor during rains or in the surface layers of soil pits under forest cover. BMNH 1971.1028 was taken in a soil pit on 3 December 1967.

DIAGNOSIS. A species agreeing with *Anops kingii* Bell (1833 : 99) and differing from all other known New World amphisbaenians in possessing a strongly compressed snout with an enlarged, vertically keeled, keratinized rostral shield. The high number of body annuli (358-372) and the presence of only two supralabials and two infralabials enable this species to be readily distinguished from *A. kingii* (fig. 1). There are 15 to 19 dorsal and 18 to 21 ventral segments in a midbody annulus; two to four lateral and 15 to 16 caudal annuli. The male possesses a pair of well-defined precloacal pores situated anterior to and lateral to the eloea and separated from each other by four pore-less segments. In the females these pores are much weaker and may not be visible to the naked eye. The tip of the tail forms a blunt vertical ridge with a median dorsoventral suture similar to the 'doubled vertical ridge' (Gans 1971:4) of *Mesobaena huebneri* Mertens (1925 : 170).

DESCRIPTION OF HOLOTYPE. The rostral extends dorsally to the vertical of the posterior border of the first supralabial and is covered by a thick layer of keratin on all but its posterior and oral borders. The nasal is situated in a postero-ventral notch in the rostral and contacts the first and second supralabials and the prefrontal. The second supralabial is in broad contact with the prefrontal and has an oral border equal to that of the first supralabial. The large prefrontal, which is in point contact with its fellow behind the rostral, is the only shield between the ocular and the rostral. The much reduced triangular ocular is in the posterior angle of the prefrontal and second supralabial. It is bordered behind by a dorsoventrally elongated segment of the first body annulus. A single pair of frontals, wider than long, are bordered anteriorly by the prefrontals and posteriorly by the segments of the first body annulus. The mental is longer than wide, as wide as and shorter than the pentagonal postmental which is in broad contact with the second infralabial and narrowly in contact with the first infralabial. There are two infralabials of which the second is approximately five times as large as the first. The single pair of postgenials are a little larger than the malars which just fail to contact the postmental. The postmalar row is continuous with the postoculars and postfrontals (parietals) and with them forms the first body annulus, in which there are a total of 16 segments.

There are 372 body annuli, two laterals and 16 caudal annuli of which the 7th is slightly narrowed laterally and presumed to mark the site of caudal autotomy. There are 18 to 19 dorsal and 19 to 20 ventral segments in a midbody annulus, 28 segments in the autotomy annulus and 31 segments in the first post-autotomy annulus. The lateral groove separating the dorsal from the ventral segments is absent on the anterior 30 annuli and is irregular and indistinct between the 31st

and 52nd annuli. Thereafter there is a well defined straight groove that continues to the last body annulus. It is absent on the lateral and caudal annuli. The ventral sulcus forms a distinct groove anteriorly which peters out at about the 30th annulus and thereafter is indicated only by an alignment of the intersegmental sutures. The dorsal sulcus is indicated anteriorly by the presence of slightly enlarged intersegmental granules and, intermittently, by the non-alignment of the left and right halves of the dorsal half-annuli. On the posterior two-thirds of the body it is indicated only by an alignment of the intersegmental sutures. Precloacal pores are present as small brown dots not visible to the naked eye. There are ten precloacal and 17 postcloacal segments.

In alcohol the holotype is cartridge buff (sensu Ridgway 1912 : pl. 30) with rather indistinct light brown pigment spots confined to the dorsal segments. These spots are absent on the anterior third of the body and thereafter gradually increase in number and intensity posteriorly. At midbody this pigmentation is so weak as to be barely discernible and just before the vent the dorsum is only slightly darker than the unpigmented venter. Heavier pigmentation of the dorsal and dorsolateral caudal segments gives the tail a mottled brown appearance.

VARIATION. Variation in meristic characters is shown in Table 1. All the paratypes differ from the holotype in having the oral border of the second supralabial a little longer than that of the first supralabial. The mental may (BMNH 1971.1028-9) or may not (UMMZ 131700, MZUSP 21277) contact the second infralabial and is a little narrower than (MZUSP 21277) or a little wider than (BMNH 1971.1029) the postmental. The malars are in point contact with the postmental in two paratypes (BMNH 1971.1029 and UMMZ 131700). There are 15 to 17 segments in the first body annulus, 28 to 30 segments in the autotomy annulus and 28 to 31 segments in the first post-autotomy annulus.

The ventral sulcus is present anteriorly on BMNH 1971.1028 and absent on the other three paratypes. The variation of this groove is probably the result of differences in the state of the neck muscles at the time of death and is unlikely to

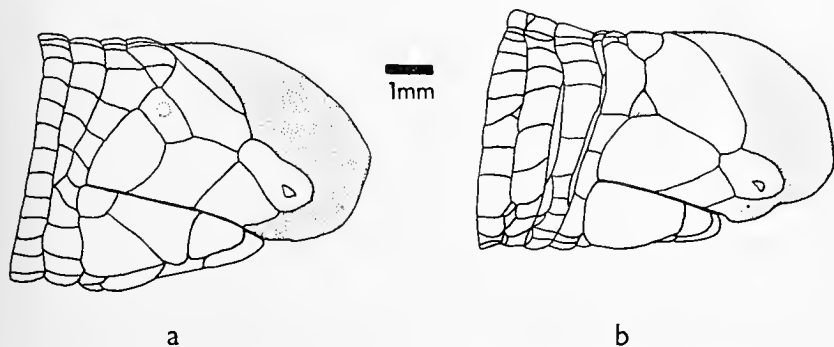


FIG. 1. Lateral view of head. A. *Anops kingii*, BMNH 86.3.10.3 - Rio Grande do Sul.  
B. *Anops bilabialatus*, Holotype. Stippling shows keratinization.

be due to real morphological differences. The lateral groove is absent on the first 33 to 39 annuli and becomes well defined between the 43rd and 55th annulus.

The precloacal pores are well developed on BMNH 1971.1028, fainter on UMMZ 131700 and not visible to the naked eye on BMNH 1971.1029. These pores are situated on the terminal segments of the first lateral annulus (fig. 2)

The coloration of the paratypes is basically the same as that of the holotype, BMNH 1971.1028 and MZUSP 21277 being more heavily pigmented and BMNH 1971.1029 and UMMZ 131700 less so.

In alcohol the eye is not visible externally and there is no indication that the ocular scale is more translucent than the adjacent cephalic scales. Dissection of MZUSP 21277 reveals a small pigmented eye with a discernible pupil situated below the posteroventral angle of the ocular.

**BODY ANNULI.** Gans & Rhodes (1964 : 16) discussed irregularities in the arrangement of body annuli of *A. kingii* and remarked upon the lack of intercalated dorsal half-annuli. *A. bilabialatus* has up to six supernumerary dorsal half-annuli and exhibits numerous other annular irregularities, most of which occur in the anterior third of the body. These take the form of intercalated half-, quarter- and part-annuli and the fusion of one or more segments with those of an adjacent annulus. Shifts in alignment of halves and sometimes quarters of annuli are common and often result in combining two or more annuli into a single spiral. A good example of this occurs in the holotype where nine annuli (49th to 57th) form a continuous spiral. Supernumerary dorsal half-annuli are calculated by simply deducting the ventral count from the dorsal count. In view of the intermittent vertebral non-alignment of annuli and other irregularities it was felt that a better picture of the extent of

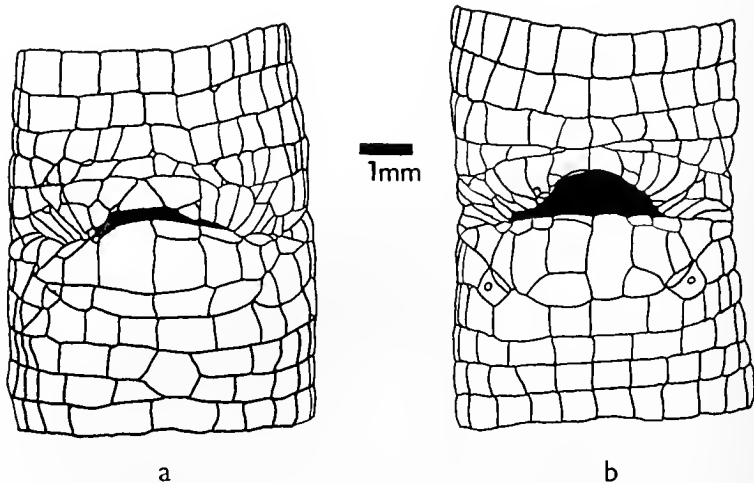


FIG. 2. Ventral view of cloaca of *Anops bilabialatus*. A. Holotype. B. BMNH 1971.1028.



TABLE I

Data for *Anops bilabialatus*

Collection and number	Sex	Annuli:		Midbody segments Dorsal/ventral	Pre- cloacals	Post- cloacals	Length in mm Snout-vent + tail
		Body + lateral + (autotomy) caudal	Body + lateral + (7) 16				
MZUSP 21276 (Holotype)	♀	372 + 2 + (7) 16	17-19/19-21	10	17	250 + 15	
BMNH 1971.1028 (Paratype)	♂	360 + 4 + (7) 16	18-19/19-20	10	16	230 + 15	
UMMZ 131700 (Paratype)	♀	358 + 4 + (7) 15	15-17/18-19	10	17	224 + 14	
MZUSP 21277 (Paratype)	?	298 + +	16-17/18-20	—	—	—	
BMNH 1971.1029 (Paratype)	♀?	366 + 3 + (6) 16	16-18/18-19	9	17	131 + 10	

TABLE 2

Body annuli counts of *Anops bilabialatus*

Collection and number	Ventral		Dorsal		Supernumerary quarter-annuli			
	Left	Right	Left	Right	Dorsal Left	Dorsal Right	Ventral Left	Ventral Right
MZUSP 21276	372	377	378	383	6	6	5	5
BMNH 1971.1028	360	366	365	370	5	4	6	5
UMMZ 131700	358	357	361	363	3	6	-1	2
MZUSP 21277	298 +	300 +	298 +	304 +	0	4	2	6
BMNH 1971.1029	366	368	371	373	5	5	2	2

dorsal supernumeraries would be obtained by making ventral and dorsal annuli counts on the right as well as left side of the body. These produced some remarkable results (Table 2). Not only do there appear to be more dorsal than ventral half-annuli but also more right than left half annuli. Similar variation in supernumerary dorsal half-annuli has been reported for members of the genus *Amphisbaena* (Gans & Alexander 1962 : 102) although its adaptive significance has not been discussed. That the left and right annular counts should differ in a species possessing so many irregularities is not surprising, but that there should be such a marked tendency for the supernumeraries to be on one side rather than the other is not easy to explain. Until further material is collected it seems best to assume that this apparent bilateral asymmetry reflects nothing more significant than uneven sampling.

**SKELETAL ELEMENTS.** X-rays were taken of all five specimens and, for comparison, of five examples of *Anops kingii*.

The skull is a little more elongate than that of *A. kingii* and extends to about the eighth body annulus. The holotype has 171 body, three lateral and 14 clearly defined caudal vertebrae. In BMNH 1971.1028 and 1029 these counts are 169, three, 14 and 174, three, 15 respectively. A terminal process, presumably the result of fusion and expansion of the last two or three caudal vertebrae, is present on each of the four complete specimens. The pectoral girdle, said by Zangerl (1945 : 778) to be minute in *A. kingii*, does not appear on my X-rays of either species. Perhaps it is too small and/or lies too close to the vertebral column to be discerned. The pelvic girdle consists of a pair of bent rod-like bones not significantly different from those of *A. kingii*.

Alexander & Gans (1966) reported the typical dermal-vertebral ratio of 2 : 1 for *A. kingii*. In *A. bilabialatus* this ratio varies from 2.10 : 1 to 2.17 : 1 suggesting that in addition to the dorsal and right supernumerary quarter-annuli there are between 18 and 30 intercalated annuli even in the left ventral quarter. Intercalated dermal annuli, although atypical, have been recorded in amphisbaenians, notably in species of the sympatric but not closely related genus *Leposternon*.

The most remarkable skeletal difference between *A. bilabialatus* and *A. kingii* is the presence in the former of a fusion and expansion of the terminal caudal vertebrae. Similar modifications are known to occur in several species of fossorial and sub-fossorial snakes and some amphisbaenians. Its occurrence in *Amphisbaena alba* (Linnaeus) has been noted and figured by Gasc (1967 : 85). Zangerl (1945 : 778) in his discussion on the post-cranial skeleton of *A. kingii* states that there are '5 clearly defined caudal vertebrae' and 'an undeterminable number of fused ones at the tip of the tail'. Presumably he had a specimen with an autotomized tail. My own observations show the two terminal vertebrae of *A. kingii* to be fused but well defined and not in any way expanded.

**SYSTEMATIC POSITION.** The present species is the third amphisbaenian with a vertically keeled rostral process to be recorded from South America. Of the three, *Anops kingii* and *A. bilabialatus* agree in having an exceedingly sharp, rounded keel whilst the other species, *Mesobaena huebneri* has a much blunter and more pointed keel. Outside South America only the African genera *Baikia* and *Ancylocranium*

have sharply and vertically keeled snouts but major cranial differences suggest that these are not closely related to the South American forms (Parker 1942 : 57 and Gans & Kochva 1965 : 88).

*A. bilabialatus*, although clearly related to *A. kingii*, is in some respects intermediate between that species and *Mesobaena*. This is not altogether unexpected since its geographical position is also intermediate, *Mesobaena* occurring in Amazonian Colombia and Venezuela and *A. kingii* inhabiting extreme southern Brazil, Uruguay and northern Argentina. Apart from the differences in the nature of the rostral process the diagnosis of *Anops* has to be changed to separate it from *Mesobaena* when *A. bilabialatus* is taken into consideration (Table 3, nos 2-5). Several characters are diagnostic at the species level but I can find no obvious character, apart from the nature of the rostral shield, that will readily separate both species of *Anops* from *Mesobaena*. However the marked difference in the nature of the rostral keel suggests that *Mesobaena* should continue to be recognized as a separate genus.

A key to the two genera will now have to employ a combination of characters and I suggest the following:

Rostral longer than high with a blunt vertical keel; two precloacal pores separated by a median hiatus and three supralabials . . . . .	<i>Mesobaena</i>
Rostral higher than long with a sharp vertical keel; four precloacal pores in a continuous series or two supralabials . . . . .	<i>Anops</i>

TABLE 3

## Diagnostic characters

	<i>Anops kingii</i>	<i>Anops bilabialatus</i>	<i>Mesobaena huebneri</i>
1. Rostral keel	strong	strong	moderate
2. Mental contacts 2nd infralabial	no	yes or no	yes
3. Precloacal pores	4, continuous	2, separated	2, separated
4. Tip of tail	elliptical	with doubled vertical ridge	with doubled vertical ridge
5. Supralabials	3	2	3
6. Postmental larger than a malar	no	yes	no
7. Body annuli	214-249	358-372	259-281

ETYMOLOGY. The new species is named *bilabialatus* with reference to the two supralabials, taking new latin *labiala* as equivalent to a labial scale.

## ACKNOWLEDGMENTS

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in taking X-rays and to Dr Garth Underwood for assistance in sexing the specimens and examining the eye. I would also like to thank Mr Iain R. Bishop and the other members of the Xavantina-Cachimbo Expedition who, through the courtesy of the Brazilian government, provided the type series of *Anops bilabialatus*.

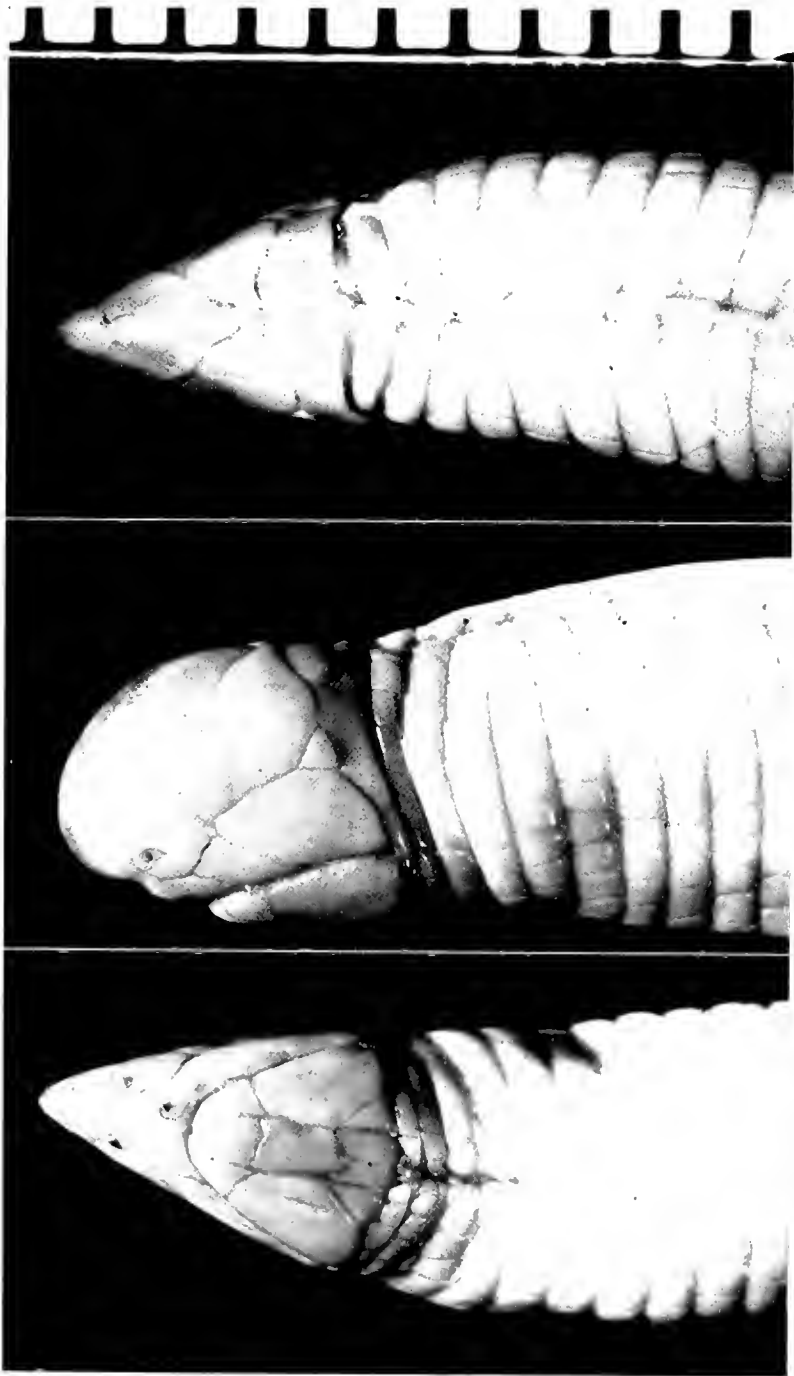
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PLATE 1

Dorsal, lateral and ventral views of head of *Anops bilabialatus* holotype. Scale in 1 mm divisions.











METASTENASELLUS WIKKIENSIS SP.N., FROM  
WARM-WATER SPRINGS IN NORTH-EASTERN  
NIGERIA (ASELLOTA : ASELLIDAE :  
STENASELLINAE)

By R. J. LINCOLN

INTRODUCTION

THE sub-family Stenasellinae has its centre of distribution in southwestern Europe where it is represented by the genus *Stenasellus* containing about 15 recognised species. It was thought for a long time that the group was restricted to the northern hemisphere, indeed that it did not occur south of the Mediterranean, except for the species *purpurea* described by Monod (1924) from Algeria and placed in the monotypic genus *Johannella*. However, in 1938 Remy described a new species *chappuisi* from a well at Gabu in Guinea, the first indication that the group was to be found in tropical regions with a much wider distribution than was previously realized. Since that time 7 further species have been described: *africanus* from the Ivory Coast (Monod, 1945), *guinensis* from Guinea (Braga, 1950), *congolensis* and *leleupi* (Chappuis, 1951) and *dartevellei* (Chappuis, 1952) from the Congo Basin, and finally from Somalia on the east coast *pardii* (Lanza, 1966) and *costai* (Lanza *et al.*, 1970). All of these tropical species were placed by their authors in the genus *Stenasellus* although it was apparent that those from the western part of Africa differed in a number of ways from the diagnosis of the genus proposed by Racovitza. In 1966 Magniez published a critical review of the status of *Stenasellus* and erected two new genera for the west African species: *Metastenasellus* to contain *congolensis*, *dartevellei* and *leleupi* from the Congo, and *Parastenasellus* for *chappuisi* from Guinea. The remainder of the species were left within *Stenasellus*. Later in the same year Lanza (1966) described new material from near the equator in Somalia and discussed further the taxonomy of the group. In view of the peculiar and apparently primitive conformation of the male copulatory organs of *africanus* a new genus *Magniezia* was proposed for this species, and although the male of *guinensis* was not known at the time it was thought to fit satisfactorily into the new taxon. Thus, the Stenasellinae are represented in central west Africa by three genera: *Parastenasellus* in Guinea, *Magniezia* in Guinea and the Ivory Coast, and *Metastenasellus* in the basin of the Congo. On the eastern side of the continent *Stenasellus* is found in Somalia.

A recent collection of asellids from Nigeria has provided a hitherto undescribed species belonging to the Stenasellinae, the structure of the male copulatory apparatus and other characters showing clear affinities with the congolese genus *Metastenasellus*.

The presence of this genus in Nigeria fits into the general pattern of distribution of asellids in central Africa but it extends considerably the known northerly range of *Metastenasellus* from south of the equator to northern Nigeria.

*Metastenasellus wikkiensis* sp. n.

(Text-figs 1a-c, 2a-d, 3a-c, 4a-c)

**MATERIAL EXAMINED.** 37 ♂ and 12 ♀ specimens collected by C. N. Pearson from Wikki Warm Springs, Yankari Game Reserve, Bauchi Province, North Eastern State, Nigeria. The holotype ♂ reg. no. 1971 : 158, allotype ♀ reg. no. 1971 : 159 and paratypes reg. no. 1971 : 160 are deposited in the collections of the British Museum (Natural History), London.

**DIAGNOSIS.** Body of relatively large size with extremely prominent uropods. In the male the uropod is almost twice the length of the pleotelson, the peduncle being a little shorter than the sub-equal rami. In the female the uropod is relatively shorter; the peduncle is equal to only about half the length of the rami and the complete uropod is about the same length as the pleotelson. Pleopod 1 ♂ without coupling hooks; pleopod 2 ♂, basal article large, endopodite forming a single conical process, slightly twisted apically with circular opening surrounded by ring of small chitinous teeth, exopodite 2-articulate, distal article flat, almost triangular with 3 long setae on outer margin; pleopod 2 ♀ small, triangular, the pair fused proximally, each with 2 strong marginal setae and 2-3 short spines on ventral surface.

**DESCRIPTION.** Length of body excluding uropods 5.0-8.0 mm in the male and 4.0-7.5 mm in the female, width of body at the level of tergite 6 from 0.9-1.4 mm in male and 0.7-1.5 mm in female; colour pale straw, without any traces of pigmentation; body (fig. 1a) more or less rectangular, long and slender, margins fringed with a number of small setae; head short, anterior margin evenly concave, eyes absent; peraeon tergites reaching maximum length at segment 7 and maximum width at 6 or 7; dorsal surface of peraeon with numerous small upright setae, and postero-lateral corners of tergites with conspicuous groups of small spines; the two free pleon tergites sub-equal, about half length of last peraeon tergite and a little narrower; pleotelson with lateral margins weakly concave proximally, posterior margin convex with small median process (in intact specimens the weak concavity of the sides of the pleotelson is somewhat obscured by the underlying pleopod 3 exopodites); appendages, antenna 1 (fig. 3e) small, reaching only a little beyond the end of peduncle antenna 2, article 1 and 2 of peduncle well developed, article 3 small, flagellum slightly longer than peduncle, 8-articulate, distal 6 articles bearing aesthetascs; antenna 2 (fig. 3d) reaching about one-third length of body, peduncle robust with articles increasing in length from 4-6, article 3 with small rudimentary exopodite, flagellum 25-35 articulate (number of articles in flagellum tends to increase with size of the individual); mandible (fig. 2c) with a 3-articulate palp, article 1 with 2 strong spines, article 2 with group of strong plumose setae, terminal article fringed with about 10 plumose setae on inner margin, incisor process and lacinia

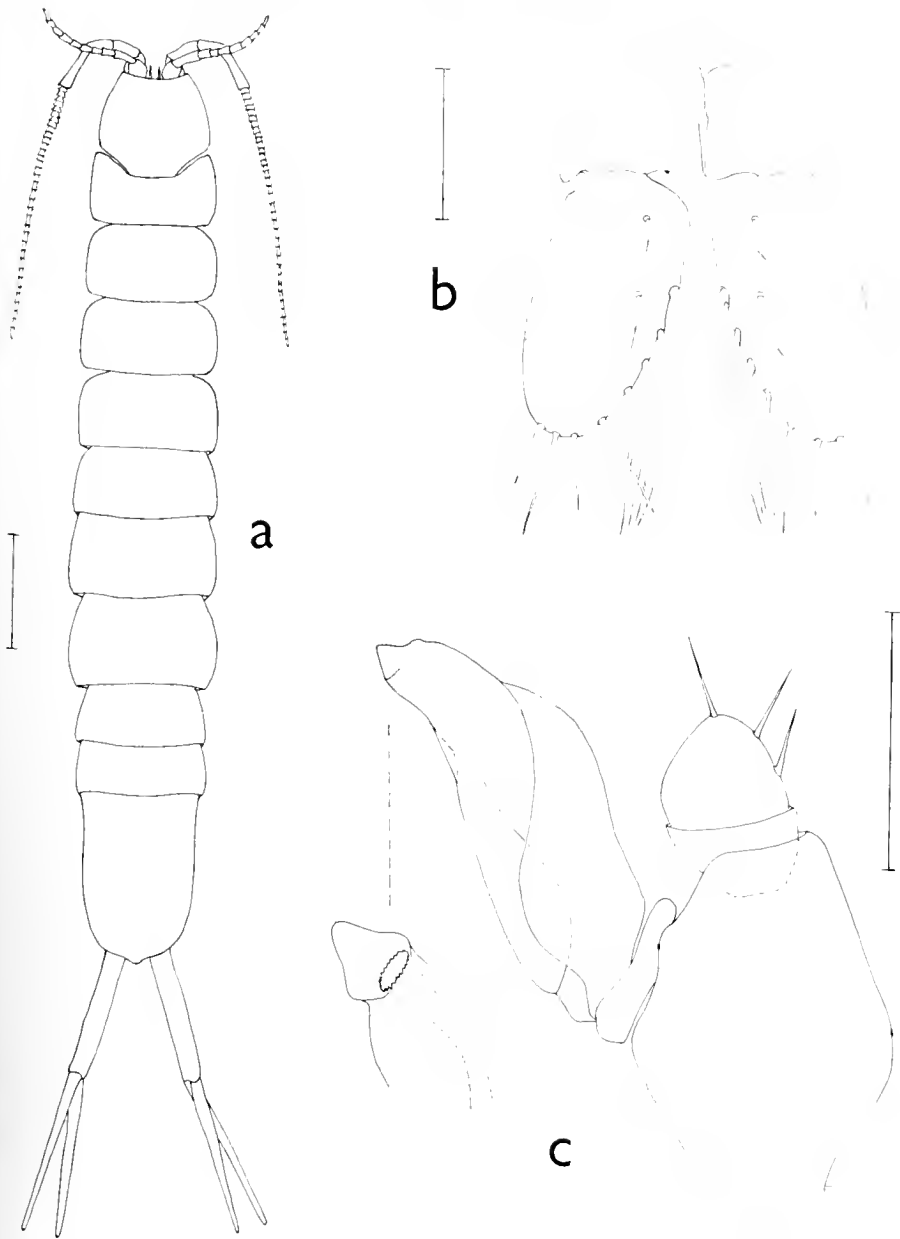


FIG. 1. *Metastenasellus wikkiensis* sp. n. ♂ paratype; a, dorsal body, entire, bar scale 1.0 mm; b, pleopod 1; c, pleopod 2 (apex of endopodite inset); bar scale 0.25 mm.

mobilis each composed of 4 processes, mandibular lobe with about 12 serrate spines and molar process with row of some 10 long setae; maxilla 1 (fig. 2a), outer ramus has 8 serrate spines and inner ramus 4 ciliated spines; maxilla 2 (fig. 2b), outer and middle lobe each with 6 long serrate spines, inner lobe bearing 3 ciliated and 2 non-ciliated spines; maxilliped (fig. 2d) has short inner masticatory lobe carrying 4 terminal ciliated spines, and a pair of coupling hooks on inner margin, palp 5-articulate, articles 2-3 broader than long, all articles with many long setae on inner margin; peraeopod 1 (fig. 3c), ischium and merus short having 1 and 5 stout spines on inner margins respectively, propodus broad proximally, outer margin strongly convex, palm straight with row of 4 stout spines proximally and 6 curved serrate spines distally, dactylus slightly curved, inner margin carrying 5 strong, closely applied, spines; peraeopods 2-7 (fig. 4a), basis broad and oval, merus with very strong apical spine, propodus and dactylus becoming more slender towards the posterior peraeopods and with inner margin strongly spinose, the large apical spine on merus equal to length of propodus in peraeopod 5 and almost so in 6; a pair of penis lobes are present on ventral side of peraeon segment 7 in male, long and slender, directed backwards and towards mid-line; pleopod 1 ♂ (fig. 1b), basal article slightly broader than long, outer margin strongly convex and inner margin without coupling hooks, exopodite twice as long as broad, having 7 setae along inner margin, setae becoming longer proximally, and 2 prominent spines on ventral surface; pleopod 2 ♂ (fig. 1c) basal article broad, endopodite conical and rigidly seated on basal article; pleopod 2 ♀ (fig. 4e) triangular, the pair fused proximally; pleopod 3 (fig. 4b), exopodite twice as long as broad, covering the entire ventral surface of the pleotelson, distal lobe two-thirds length of proximal and with 4 terminal and 4 outer marginal setae, proximal lobe with 8-9 long setae (from the dorsal side these setae give a setose appearance to the margin of the pleotelson), endopodite simple, fleshy, extending slightly beyond the proximal article of the exopodite; pleopod 4 and 5 (figs 4c, d) fleshy, twice as long as broad, exopodite with traces of an oblique suture towards the end, endopodite simple, reaching just beyond the suture line on the exopodite, no marginal setae; uropods (figs 3a, b) very long in large males reaching twice the length of pleotelson, rami sub-equal with tuft of long terminal setae; in smaller males the uropod is relatively shorter, and in all females and the smallest males the uropod is only about equal to the length of the pleotelson with the peduncle half the length of the rami.

**HABITAT NOTES.** The animals were found living amongst tree roots submerged in water; the temperature of the spring water at the time of collection was 33°C. The apparent photophobic response of the animals, which keeps them hidden deep in the matted, partly decayed root vegetation, makes collection quite a laborious process. Although the animals are colourless when preserved in alcohol for a number of weeks, living specimens are a bright pink colour presumably due to a blood pigment. This colouration is characteristic of many asellid species.

**AFFINITIES.** The conformation of the second male pleopod of *wikkiensis* fits well within the concept of the genus *Metastenasellus*; this is characterized particularly by a uni-articulate endopodite forming a single conical copulatory stylet. In

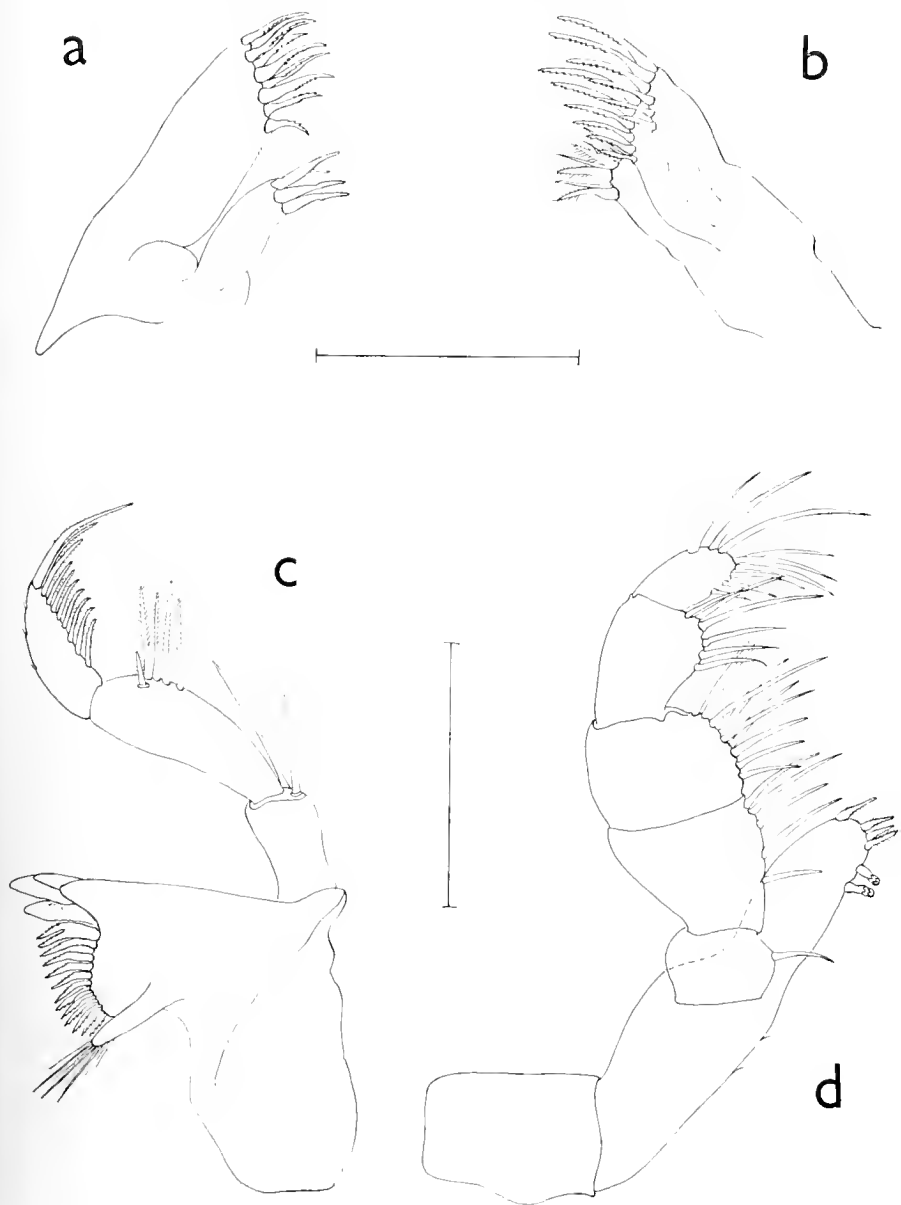


FIG. 2. *Metastenasellus wikkiensis* sp. n. ♂ paratype; a, maxilla 1, b, maxilla 2; c, mandible; d, maxilliped; bar scale 0.25 mm.

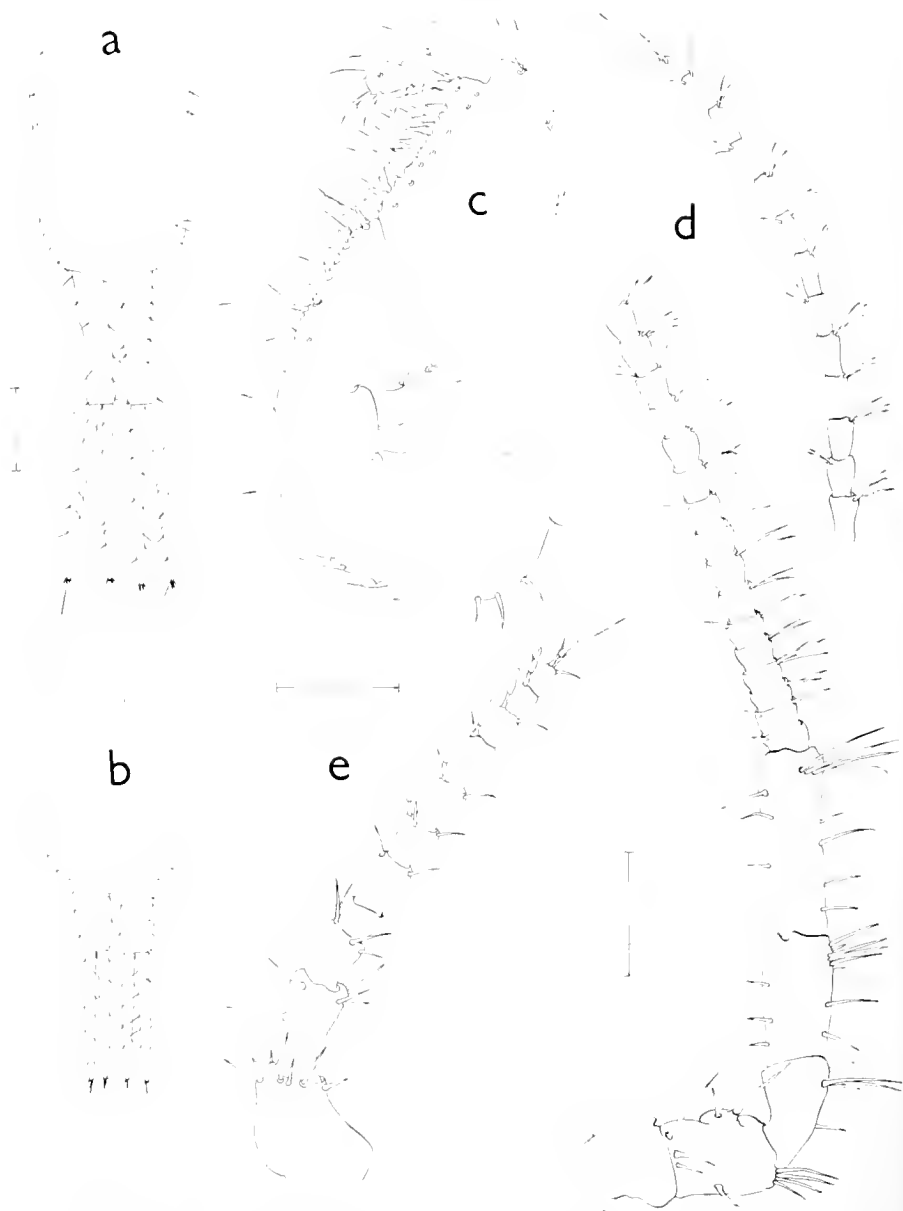


FIG. 3. *Metastenasellus wikkiensis* sp. n. paratypes; a, pleotelson and uropods of large male; b, pleotelson and uropods of large female; bar scale 0.5 mm; c, peraeopod 1 male; d, antenna 2; e, antenna 1; bar scale 0.25 mm.



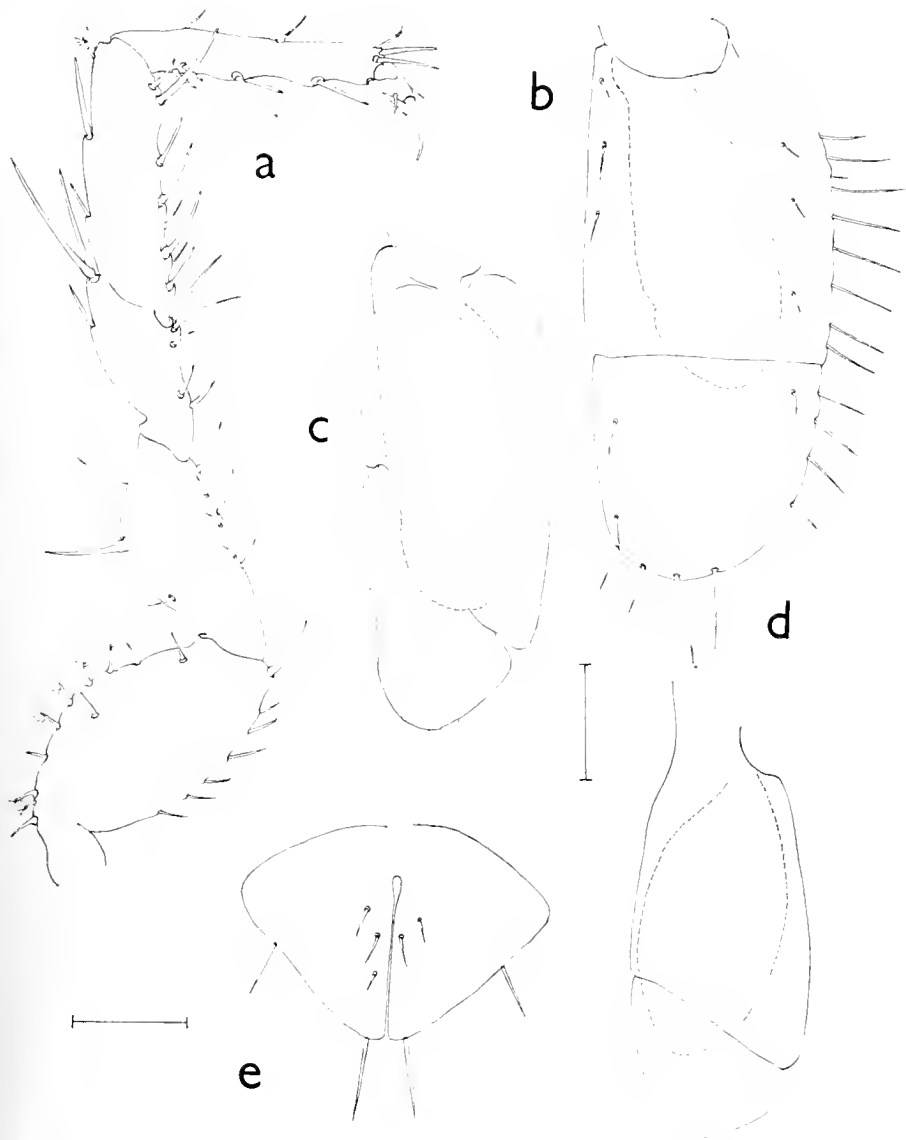


FIG. 4. *Metastenasellus wikkiensis* sp. n. a-d ♂ paratype; a, peraeopod 7; b, pleopod 3; c, pleopod 4; d, pleopod 5; e, ♀ paratype, pleopod 2; bar scale 0.25 mm.

the other allied genera this copulatory endopodite is composed of two distinct articles. Although generally compatible with other species of *Metastenasellus*, the detailed structure of the endopodite of the second male pleopod of *wikkiensis* differs on a number of points. In *congolensis* and *dartevellei* the proximal part of the endopodite forms a stout conical process, thickened at its base into a chitinous ring, and spiralling apically to an acute tip. The apex in *congolensis* has a small group of chitinous teeth, and in *dartevellei* these teeth form a long row following the apical spiral. This arrangement differs somewhat in *wikkiensis*; the proximal part of the endopodite is conical and has a thickened ring at the base. (This ring has the appearance of a separate compressed segment but is in fact formed as an expansion of the basal part of the endopodite.) The endopodite has an opening at its base towards the mid line of the animal which results from the rolling up of an otherwise laminate process; the two edges can be seen clearly overlapping along the centre. A flat leaf-like endopodite is considered to be a primitive asellid feature, and is still seen in one species, *africana*; it was this character which led Lanza (1966) to create a new genus *Magniezia* to accommodate *africana*. The apical part of the endopodite of *wikkiensis* is not formed into a strong spiral as in other species of *Metastenasellus*, but is instead only slightly twisted, the tip forming a small triangular lobe adjacent to a circular opening ringed by tiny chitinous teeth. It appears that the rolling up of the endopodite which is responsible for the spiral nature of the apex in *congolensis* and *dartevellei* is much less developed and probably more primitive in *wikkiensis* resulting in a much more open structure.

The other feature of *wikkiensis* by which it is readily distinguished from its close allies is the extremely large size of the uropods. They attain their maximum size in large male individuals where they can be nearly twice the length of the pleotelson, the peduncle being almost equal in length to the rami. In smaller males and in all females the uropods are much shorter and only equal to the length of the pleotelson, and the peduncle is about half as long as the rami. In other *Metastenasellus* the uropods are always shorter than the pleotelson.

#### KEY TO AFRICAN STENASELLINAE

- |   |  |   |   |
|---|--|---|---|
| 1 | Uropods less than one fifth length of pleotelson . . . . .   | <i>Johannella purpurea</i> Monod          |   |
| - | Uropods always more than one fifth length of pleotelson . . . . .  |   | 2 |
| 2 | Pleon tergites 1 and 2 only one quarter length of peraeon tergite 7, partly hidden; pleopod 1 ♂, inner margin of ramus folded onto ventral face . . . . .  | <i>Parastenasellus chappuisi</i> (Remy)   |   |
| - | Pleon tergites 1 and 2 more than half length of peraeon tergite 7, not hidden; pleopod 1 ♂, ramus not folded . . . . .   |   | 3 |
| 3 | Pleopod 2 ♂, endopodite in form of a single conical process; pleopods 2 ♀ fused together proximally along mid-line; basal article pleopod 1 ♂ without coupling hooks . . . . .   | ( <i>Metastenasellus</i> spp.)            | 4 |
| - | Pleopod 2 ♂, endopodite formed of distinct proximal and distal parts with articulation between; pleopods 2 ♀ not fused along mid-line; basal article pleopod 1 ♂ with or without coupling hooks . . . . .  |   | 7 |
| 4 | Pleopod 2 ♂, endopodite swollen proximally and narrow, tubular distally, an internal spiral canal prominent; exopodite with 2/3 marginal setae; pleopod 1 ♂, ramus with parallel sides; pleopod 2 ♀ with 2 marginal setae only; uropods much shorter than pleotelson . . . . . | <i>Metastenasellus leleupi</i> (Chappuis) |   |

- These characters not present . . . . . 5
- 5 Pleopod 2 ♂, endopodite almost rectangular but tapering distally, exopodite with 3 long marginal setae; pleopod 1 ♂, ramus margins convex; pleopod 2 ♀ triangular, 2 marginal setae; uropods in male up to twice length of pleotelson, in female at least as long as pleotelson . . . . . *Metastenasellus wikkiensis* sp.n.
- These characters not present . . . . . 6
- 6 Body size, length up to 14 mm; antenna 1, flagellum 14-18 articulate; pleopod 1 ♂ outer margin of ramus strongly concave; pleopod 2 ♀ with small group of 4/6 terminal setae . . . . . *Metastenasellus congolensis* (Chappuis)
- Body length less than 10 mm; antenna 1, flagellum 7-articulate; pleopod 1 ♂ outer and inner margins strongly convex . . . . . *Metastenasellus dartavellei* (Chappuis)
- 7 Pleopod 2 ♂, distal article of endopodite forming oval, folded lamina; basal article pleopod 1 ♂ without coupling hooks . . . . . (*Magniezia* spp)
- Pleopod 2 ♂, distal article of endopodite narrow and elongate; basal article pleopod 1 ♂ with coupling hooks . . . . . (*Stenasellus* spp.)
- 8 Pleopod 2 ♀ longer than broad, outer margin strongly concave . . . . . *Magniezia africana* (Monod)
- Pleopod 2 ♀ broader than long, more or less triangular . . . . . *Magniezia* (?) *guinensis* (Braga)
- 9 Large body size, up to 20 mm length; uropods equal to length of pleotelson; antenna 2 long and reaching to end of peraeon . . . . . *Stenasellus costai* Lanza
- Small body size, less than 10 mm length; uropods not equal to half length of pleotelson; antenna 2, short, not reaching half length of peraeon . . . . . *Stenasellus pardii* Lanza

## ACKNOWLEDGMENT

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# NOTES ON THE PREPARATION OF NATURAL HISTORY SPECIMENS FOR SCANNING ELECTRON MICROSCOPY

By R. H. HARRIS, B. S. MARTIN, & C. G. OGDEN

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## INTRODUCTION

In the course of assisting members of the five Departments of the British Museum (Natural History) in the preparation of their materials for examination by scanning electron microscopy, the authors have gained considerable experience in dealing with a variety of specimens requiring different treatments. Although it would be impracticable to describe all the methods used on such diverse specimens, an attempt is made here to present an account of the basic techniques used in these preparations.

As most biological materials are non-conductors, it is necessary to apply a conductive covering over the entire surface of the object before examination. The biological specimens referred to here can be divided into two groups, loosely described as being either soft or hard. The soft specimens, whether fresh, fixed or preserved, are usually freeze-dried to maintain their natural appearance, whilst the hard materials require the minimum of treatment prior to coating. Regardless of the number of stages through which the material is passed, it is essential to take the utmost care with the preparations to ensure that the specimens maintain their shape and structure, and to guard against the introduction of artifacts.

The importance attached to preparation is perhaps more easily explained by considering the example in which only a few specimens are available. If, after processing, it is seen that extraneous material is adhering to the surface, it is possible that it will be obscuring essential detail. Under these circumstances valuable information could be lost, because the removal of the conductive layer from biological specimens is difficult, and this prevents the possibility of their being cleaned and recoated.

No attempt is made to include reference to the numerous publications containing details relating to the preparation of specific tissues or specimens, but reference is made to some recent general accounts.

#### FIXATION

In certain circumstances it is not convenient to treat fresh material by direct freeze drying. This applies to specimens like blood-cells which are difficult to separate from the surrounding plasma, and to specimens that are difficult to maintain outside their natural environment. In these cases the use of a chemical fixative prior to freeze drying is recommended.

The purpose of using a fixative is to preserve the detail of the material faithfully at the time of fixation. Although this would appear to apply only to transmission electron microscopy, in which detail of cellular structure is examined down to the molecular level, it applies equally to scanning electron microscopy, even though the fine structure is confined mainly to the external surface.

In general, the conventional transmission electron microscopy fixatives, glutaraldehyde and osmium tetroxide both suitably buffered, have proved to be satisfactory. There are, however, some exceptions, for example, human blood-cells when treated for one hour in neutral Kaeserling I fixative produce good results (Pl. 1, fig. A). Some success has been achieved with Parducz's fixative, as recommended by Small & Marszalek (1969), but the subsequent washing required to ensure the removal of the introduced salts, makes this method tedious. In some circumstances it has been found necessary to narcotize the specimens prior to fixation. Certain oligochaetes and platyhelminthes not only contract violently if plunged directly into fixatives, but also secrete mucous which is often so finely dispersed (Pl. 1, fig. B) that it is only detected on examination at magnifications outside the range of the optical microscope. The conventional narcotic substances, menthol, ethyl urethane, magnesium chloride, chloral hydrate and alcohol, are suitable for most specimens. Nevertheless, marine zooplankton produce better results when treated with a solution of  $100 \text{ mg l}^{-1}$  tricaine methanesulphate. The specimens must be washed thoroughly after using fixatives to ensure that no salts are deposited in the subsequent freeze drying.

#### FREEZE DRYING

The tissue to be examined is carefully washed in several changes of distilled water, with a final rinse in triple glass distilled water. Normal and double distilled water leave a considerable deposit of dissolved salts after sublimation. Each specimen is treated separately in a Durham's fermentation tube, sufficient water being retained with delicate tissues to support them in a life-like position, whilst all the water is drained from firm tissues.

The specimens are rapidly frozen by spraying them for a few seconds with Polar Spray (100% dichlorodifluoromethane in an aerosol container). They are immediately placed in the specimen-chamber of an Edwards Ef2 freeze dryer, previously pumped down to a working pressure of  $50 \mu\text{m Hg}$  (0.05 Torr), with a specimen



temperature of  $-15^{\circ}\text{C}$  and condenser temperature of  $-40^{\circ}\text{C}$ . The apparatus is activated and sublimation is carried out for twelve hours. When the specimens are taken from the chamber they are placed into a small desiccator containing silica gel for at least half an hour. This allows any condensation, formed on removal from the cool chamber, to be adsorbed.

In some cases the specimens, particularly preserved materials, have an excess of debris adhering to them, but it is possible to clean these by using liquid-nitrogen. Care must be taken in handling liquified gases, and it is essential that all equipment is cooled prior to use. The material to be treated must also be pre-cooled to prevent the formation of a 'Leidenfrost envelope', which could cause considerable damage to cell-membranes.

The specimens to be treated with liquid-nitrogen, after washing and draining, are cooled for a few seconds using a Polar Spray. Then, using a pair of pre-cooled forceps, the tubes are carefully dipped beneath the surface of liquid-nitrogen. A small thermos flask, previously cooled to  $-20^{\circ}\text{C}$  for several hours, provides a suitable liquid-nitrogen container. The tubes are removed from the liquid-nitrogen and immediately placed in the specimen chamber of a freeze dryer and sublimated as before. The small amount of liquid-nitrogen remaining in the tubes boils rapidly, and this effectively removes the surface contamination from the specimen.

#### ADHESIVES AND MOUNTANTS

The Cambridge 'Stereoscan' specimen stub is a circular, aluminium platform, 13 mm in diameter, with grooved edges for handling. The critical dimensions are those of the shank which has a diameter of 3.2 mm ( $\frac{1}{8}$ " ) and a length of 8 mm. Alternative specimen supports can be used, for example,  $\frac{1}{8}$ " , flat-headed, aluminium rivets, but these are difficult to handle and the standard stub is preferred.

A large number of adhesives are used to attach specimens to the stubs, but only a few of these appear to be suitable. An investigation by Muir & Rampley (1969), together with observations made in this Museum, suggest that most adhesives are easily damaged by the electron beam. This damage appears to the viewer as 'squares' or 'lines' of sharply different contrast compared with the remaining areas of the exposed adhesive surface. In addition, some are unstable and change their dimensions constantly in the high vacuum of the coating unit and the microscope specimen-chamber, possibly due to slow solvent evaporation. Specimens are prone to move under these conditions, making focusing difficult, and accurate recording impossible. Decomposition products are also produced which gradually contaminate the microscope column.

Three commercially available adhesives, 'Araldite', 'Silver Dag' and 'Silver Mounting Compound', are stable in the scanning electron microscope. 'Araldite' is a good adhesive, but has the disadvantage of being an electrical insulator, whereas 'Silver Dag' is electrically conductive, but has inferior adhesive properties. 'Silver Mounting Compound' is a general term for a series of epoxy resin/colloidal silver mixtures, produced by Johnson-Matthey Ltd., which combine the best properties of both materials.

There are occasions when the adhesives recommended above are not convenient to use. Some entomological specimens, for example, are more easily mounted on double-sided adhesive tape. This tape exhibits all the defects mentioned above and ages badly. This latter feature causes a breakdown of electrical continuity over the stub surface, which becomes apparent on re-examination after a short period of storage. Such adhesives are acceptable, provided that the disadvantages are borne in mind and a more suitable product is used whenever possible.

A point often overlooked when mounting specimens is the part played by the adhesive in the background of the anticipated micrographs. Double-sided tape (Pl. 1, fig. C) and 'Silver Dag' have an unpleasant and confusing appearance, whilst the stub itself is scored with machine marks and small pits. A clean, clear background is easily obtained by sticking a 10 mm diameter, circular, glass cover-slip on to the stub-surface with 'Silver Dag', to ensure that good contact is made with the coating material.

#### SPECIMEN COATING

All biological specimens are electrical insulators and it is necessary to coat them with a conductive layer, usually an evaporated metal, to provide an electrical path to earth. The absence of this layer causes an electrical charge to accumulate on the specimen with resulting loss of resolution (Pl. 1, fig. C), and the appearance of bright patches that obscure detail. This progresses until the whole image area becomes speckled with bright flashes or streaked in the direction of the scanning beam. The maximum resolution of the Stereoscan is 20 nm, and it is inadvisable to exceed this thickness with the coating material if an accurate record is to be obtained. In practice a coating thickness of between 10 and 15 nm is considered satisfactory for most specimens.

Aluminium, magnesium, tin, cadmium, molybdenum, gold, gold/palladium alloy, silver, copper, platinum, carbon and anti-static solutions have been tried as coating materials with varying degrees of success. Aluminium has a high secondary electron emission and probably gives the strongest signal image formation. It has, however, two disadvantages, both of which cause coating instability. Any change in specimen dimensions due to shrinkage or local heating effects are inclined to cause cracks that charge, and the rapid oxidation of the metal surface in air causes local areas of insulation. The advantage it has over gold, is that it can be easily removed (Sylvester-Bradley, 1969) by immersion in a freshly made solution of sodium hydroxide. The precious metals, due to their malleability and inherent stability, appear to give the most satisfactory results. Gold is preferred, because it is easy to handle, it does not form an alloy with the tungsten filaments from which it is evaporated and it is readily available in wire form. In addition, it is removable (Hansen, 1968) by using an alkaline solution of sodium cyanide, although this only applies to hard materials.

Some specimens, mainly entomological, have features whose origins are situated in recesses below the general surface level, for example, insect appendages and setae. In these cases, it is impossible for the evaporated metal to reach these innermost

regions and make a continuous conductive layer. This can be remedied by soaking the specimens in a solution of 0.5% Duron, in iso-butyl alcohol, for a period of between twelve and twenty-four hours. Duron is an anti-static solution, and was initially used by Sikorski, *et al.* (1967), as a direct coating preparation for certain polymers. After soaking, the specimens are removed from the solution, washed briefly with iso-butyl alcohol and allowed to dry. They are then coated in the normal manner using evaporated metal. It is necessary to take the utmost care in the washing stage of this sequence, to ensure that the anti-static solution is washed from the exposed body surface, but not out of the recesses.

The coating metal is evaporated, in vacuo, from 'V'-shaped, tungsten filaments. During evaporation the specimen stubs are rotated by means of an apparatus (Plate 2, figs A & B) developed from that described by Boulton & Brabazon (1968). Four filaments are used to ensure that, in conjunction with the changing attitude of the stubs during rotation, the metal is coated evenly over the specimen through a complete range of angles from glancing (Plate 2, fig. B) to normal incidence. It cannot be too strongly emphasized that coating failures frequently occur if the lower filaments, which provide coating at very low angles to the stub-surface, are badly positioned or omitted. The stub-platten (Plate 2, fig. B) is rotated at about one revolution per second, and each stub revolves on its own axis between five and six times per second. As the total evaporation time is between ten and fifteen seconds an even coating is ensured.

The thickness of the metal coat on any given specimen is difficult to determine. However, if one considers the specimen to be flat, it is possible to estimate the mass of metal required for a known coating thickness. It is considered that metal deposited from filaments 1 & 2 (Plate 2, fig. A) will not contribute significantly to the coating on that part of the specimen normal to filaments 3 & 4, and vice versa. Making this assumption, the metal required for each filament can be calculated as follows:

$$m = \frac{8 \pi \cdot t \cdot R^2 \cdot \rho}{3}$$

where,  $m$  = mass of metal per filament (g);  $t$  = coating thickness required (cm);  $R$  = average filament to specimen stub distance (cm) and  $\rho$  = density of metal used ( $\text{g}\cdot\text{cm}^{-3}$ ).

Alternatively, this may be expressed in terms of wire length as:

$$l = \frac{8 \cdot R^2 \cdot t}{3 \cdot r^2}$$

where,  $r$  = radius of wire (cm) and  $l$  = length of wire (cm).

In practice, using 36 swg (0.0193 cm diameter) gold wire, each of the four filaments carries 6 cm of metal and is positioned at a distance of 12 cm from any given stub. This gives a coating thickness of 15 nm, which has been confirmed by measurements obtained using a quartz crystal thickness monitor. Evaporation takes place in a vacuum coating unit at a pressure of  $10^{-4}$  Torr, each filament being heated to allow evaporation to be completed within ten to fifteen seconds.

The success of this coating procedure depends on the adequate physical contact between the specimen and the stub. Large specimens such as pieces of rock and

marine shells often lack this contact, as do insects which are frequently attached to the stub solely by means of their appendages or other fine structures. In these cases filling the gap between the lower surface and the stub with 'Silver Dag' improves the electrical contact. Alternatively, a second coating from the lower pair of filaments often solves the problem. It is thought that the surface of some specimens tends to repel the metal coat, due to a waxy or oily covering. In these circumstances, the only alternative appears to be the evaporation of a larger quantity of metal in the hope that sufficient will adhere. The surface tension of molten gold is such that longer lengths of wire cannot be wound on a normal 'V' filament, but this is overcome by making a double 'V' filament.

The coating on the surface of chitinous materials, such as hair and insect cuticle, is often seen to be crazed (Plate 1, fig. D). No means of eliminating this effect has yet been found, but prolonged air drying prior to mounting appears to reduce it to an acceptable level.

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PLATE 1

FIG. A. Human erythrocytes.  $\times 10,000$ .

FIG. B. Cuticle of a nematode (*Memis nigrescens*) showing mucus pattern.  $\times 1,420$ .

FIG. C. Two mites (*Dermanyssus gallinae*), the upper of the two shows typical charging. The background pattern is due to double-sided adhesive tape.  $\times 75$

FIG. D. The cuticle of a mite, showing the crazing effect associated with chitinous surfaces.  $\times 75,000$ .









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SPIRORBINAE (SERPULIDAE:  
POLYCHAETA) FROM  
SOUTH-EASTERN AUSTRALIA.

A NEW GENUS,  
FOUR NEW SUBGENERA  
AND SEVEN NEW SPECIES

PHYLLIS KNIGHT-JONES



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*Pp. 229-259; 9 Text-figures*



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# SPIRORBINAE (SERPULIDAE: POLYCHAETA)

## FROM SOUTH-EASTERN AUSTRALIA.

### A NEW GENUS, FOUR NEW SUBGENERA AND SEVEN NEW SPECIES

By PHYLLIS KNIGHT-JONES

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#### SYNOPSIS

*Metalaeospira*, represented by one new species, has its embryos adhering to the body, but lacks any attachment stalk. *Protolaeospira* (inc. *Marsipospira*) is represented by two new species. The incubatory stalk characteristic of this genus is also found in the dextral form *Protolaeospira falklandica* (Pixell) (which is made the type of a new subgenus) and in *Helicosiphon*. A somewhat similar but funnel-like stalk is found in *Romanchella*, which is represented here by a new species. Southern *Romanchella* spp. have the collar folds fused dorsally, and a new subgenus is proposed for northern *Romanchella* spp. which have unfused collars and a more symmetrical distribution of uncini. A new subgenus is proposed for species of *Pileolaria* which lack sickle setae. The new genus represented by a single species, has '4½ segments' in the thoracic region but some affinities with *Pileolaria*. A new species of *Janua* (*Dexiospira*) has a tube with perforated ridges. A new subgenus of *Janua* is erected, with a new species as type, for form close to *Dexiospira* but with unfused collar folds.

#### INTRODUCTION

WISELY'S (1962) description of two species and Straughan's (1967) record of another seem to have been the only notable contributions to knowledge of Australian Spirorbinae so far published. Other authors who have dealt with these forms (Lamarck, 1818; Mörch, 1863; Bush, 1904) have offered just a few inadequate descriptions, several based on empty tubes, none of which had characters sufficiently distinctive for identification.

The following descriptions are based on material collected by Dr Leighton C. Llewellyn from South Australia (January 1967) and Sydney (July 1967). All the new species were present on the coast of Kangaroo Island, South Australia, namely at Cape du Couedic (S.W. tip), Sou' West River (south coast) and Kingscote (east coast), and two of them were also present off the mainland, at Brighton and Moanna, south of Adelaide. No new species were found at Sydney.

The material was preserved mainly in 5% formaldehyde in sea water (some in 70% alcohol) and examined early in 1970. Due to the length of time in fixative it was not possible to record the colours. The presence or absence of collar fusion (Pillai, 1970) was demonstrated by probing with a mounted eyelash (Knight-Jones, 1972). This and details of the tubes and opercula were distinguished in reflected light. Setae were examined in polyvinyl-lactophenol preparations (Knox, 1951; Gee, 1964; Harris, 1969) in which the clearing was considerably aided by gently warming on a hot plate for at least 48 hours. These preparations were viewed by phase contrast, with quartz-iodine illumination, and drawings were made on squared paper with the help of squared eyepiece graticules. The setae and uncini chosen for illustration were always the largest of their type. Light microscopy was used for all drawings, but in some species the finer details (particularly of the uncini) were confirmed from stereoscan electron-micrographs.

The species were compared with type material from several sources (p. 257). The classification into genera used below is mostly a compromise between the views of Bailey (1969b) and Pillai (1970), with amendments explained previously (Knight-Jones, 1972). It appears that the Spirorbinae of Australia may be remarkably different from those of Europe, in lacking any representative of the genus which Pillai called *Laeospira* Caullery and Mesnil, but which should rather (on priority grounds) be called *Spirorbis* Daudin. The nearest Australian genus would appear to be *Eulaeospira* Pillai. The reason originally given for separating this genus from *Spirorbis sensu stricto* was that its representatives lack sickle setae in the third thoracic fascicles. In fact, however, both the Australian form *Eulaeospira convexis* Wisely and the type species from Ceylon *Eulaeospira orientalis* Pillai were found on examination to be quite different from *Spirorbis* in having a bilaterally asymmetrical distribution of abdominal uncini and embryonic masses fixed to the body of the parent within the faecal groove. *Spirorbis* has the embryos fixed not to the body of the parent but to the wall of the tube (Bailey, 1969b).

#### TAXONOMY

The collections included 15 species, 7 of which were new, the rest comprise:—

- Eulaeospira convexis* (Wisely, 1962)
- Pileolaria* (*Pileolaria*) *militaris* (Claparède, 1868)
- Pileolaria* (*Simplicaria*—see p. 245) *pseudomilitaris* (Thiriot-Quévieux, 1965)
- Janua* (*Janua*) *pagenstecheri* (Quatrefages, 1865)
- Janua* (*Dexiospira*) *pseudocorrugata* (Bush, 1904—see p. 256)



*Janua (Dexiospira) formosa* (Bush, 1904) (Knight-Jones, 1972)

*Janua (Dexiospira) lamellosa* (Lamarck, 1818) (Wisely, 1962)

*Janua (Dexiospira) steueri* (Sterzinger, 1909) (Knight-Jones, 1972)

The recent references quoted above give descriptions of most of these forms. The others have been described recently by Bailey (1969a) and Zibrowius (1968). As shore ecologists may still find some difficulty in identifying these taxa, even after consulting the literature cited, it is hoped to complete, without much delay, an illustrated key to the fifteen species found, with notes on the ecology and distribution (Knight-Jones, Knight-Jones & Llewellyn, 1973). The two species described by Wisely have not yet been found outside Australia, but the distribution of the remaining six seems to be almost world-wide in warm-temperate and tropical seas.

Descriptions of the new species follow, starting with the genus that seems to be taxonomically nearest to *Eulaeospira*, judging from the way in which the embryos are attached to the parent's body (p. 236).

#### Genus *METALAEOSPIRA* Pillai, 1970 (amended)

Sinistral coiling; three rows of thoracic tori on the concave side; embryos incubated in the faecal groove, but without a specialised thoracic attachment stalk; collar setae with simple blades; thoracic uncini slender and with a blunt anterior peg; thoracic and abdominal uncini much more numerous on the concave side (Fig. 7b); tori large throughout most of the setigerous region; abdominal setae less than a quarter the length of the collar setae (Fig. 6b), and with vestigial brush-like blades.

**TYPE.** *Spirorbis pixelli* Harris, 1969 nom. nov. pro *Spirorbis antarcticus* Pixell, 1913.

#### *Metalaespira tenuis* sp. n. (Fig. 1)

*Tube* up to 2.5 mm across, sinistral, porcellaneous, thin-walled and somewhat triangular in cross section, having a smooth median ridge with sloping sides. At the mouth, the tube becomes rounded, often bearing a swollen ring where growth was presumably interrupted. Occasionally two such rings are present, indicating a period of renewed growth. The mouth may ascend slightly, but usually all the whorls (three to five) lie flat against the substratum and increase regularly in size and height so that the central region forms a shallow dish-like depression (Fig. 1a).

*Operculum* borne on a remarkably long stiff stalk, usually resembling in outline that of *Conopomatus acuiconus* Pillai, 1960. The distal calcification is in the form of a white, finely-granular thin-walled truncated cone, which is shallower in young specimens (Fig. 1c & d). In mounted specimens (polyvinyl-lactophenol) the cone is often dislodged, showing that the ampulla below has a fine membranous upper surface bearing a few small, scattered denticles (Fig. 1e).

*Thorax.* Collar margins not fused dorsally. Collar setae resembling those of the second and third fascicles in bearing slender simple blades with smooth margins

(Figs 1f & g), but smaller, particularly on the concave side. Capillary setae also present in the first fascicles and sickle setae (Fig. 1h) in the third. Three rows of tori on the concave side. Uncini slender, with a rounded anterior peg followed by four longitudinal rows of teeth and fewer rows of larger teeth posteriorly (Fig. 1j).

*Abdomen.* The asetigerous region is very long, but its proportionate length is not so great, because the whole abdomen is remarkably attenuated, particularly in older specimens (Fig. 1m). Setae (up to five per fascicle) are brush-like with blunt teeth. Many of the posterior fascicles include hooked capillary setae (Fig. 1l). Uncini with about eight longitudinal rows of very fine teeth and a broad, blunt anterior peg (Fig. 1k).

*Setation* (Figs 6b & 7b).

*Incubation.* Up to thirteen embryos in a single row, closely adhering to the faecal groove of the abdomen, mainly along the asetigerous region and occasionally well into the thoracic region. Careful examination showed that the embryo chains were attached to the body by delicate transparent strands. The attachment was generally near the first abdominal uncinus, but it involved different parts of the embryo chain, depending on the position of the latter relative to the body (Figs 1m, n, o & p). Only one specimen seemed to show a thoracic attachment and this was merely by a somewhat elastic thread. The faecal groove and particularly its spiral course is not obvious, because of the extreme attenuation of the animal. The comparatively large spawned eggs are associated with an indentation along the body, however, which may be due to retraction and compression of the animal on addition of fixative, but is nevertheless in the normal position of a faecal groove. One specimen seemed to have two separate large eggs lying in the more posterior part of the groove (Fig. 1p).

*Location.* Brighton. Collected by L. C. Llewellyn, January 1967. Very abundant (including type specimen) on a red alga, *Jeanerettia pedicellata*, presumed to have been washed up from sublittoral reefs, and some on a marine angiosperm *Amphibolis* (= *Cymodocea*) *antarctica*. Also found at Moanna on *Sargassum linearifolium*; Sou' West River and Cape du Couedic on *Amphibolis antarctica*.

HOLOTYPE. British Museum (Nat. Hist.) Reg. No. ZB 1971:8a.

PARATYPES. British Museum (Nat. Hist.) Reg. No. ZB 1971:9. Australian Museum Reg. No. W4473.

REMARKS. This genus has been represented previously only by the type *M. pixelli* (Harris, 1969), a species with which *M. tenuis* has strong affinities, particularly in setation and the distinctive form of the tube. It differs mainly in opercular detail. Pixell says of her species 'Small circular perforations occur in the calcareous plate and through these project small membranous projections which are generally thorn-shaped'. There are 'membranous thorns' similar in form but much fewer in number below and within the conical 'plate' of *M. tenuis* (Fig. 1e), but examination of numerous specimens showed the cone to be entire, without perforations and distal projections. Furthermore *M. pixelli* has an opercular talon, but *M. tenuis* has none.

The method of incubation of *M. pixelli* has not so far been described, but material of this species was available from South Georgia (identified by Harris, 1969, and kindly provided by the British Museum (Natural History)). Examination revealed

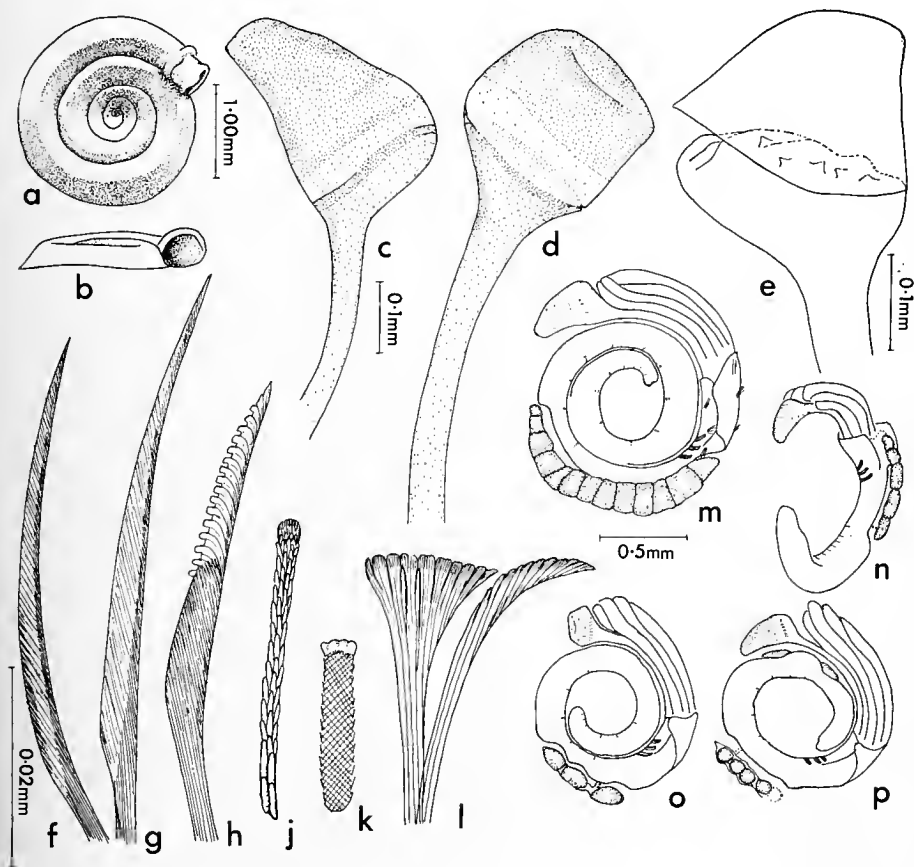


FIG. 1. *Metalaospira tenuis* sp. n. a) tube from above; b) tube, side view; c) operculum side view; d) operculum of a younger individual, dorsal view; e) operculum showing membranous denticles on the upper surface of the ampulla, within the cone; f) collar seta; g) seta representative of most in the second and third fascicles; h) sickle seta from the 3rd fascicle; j) thoracic uncinus; k) abdominal uncinus, cross hatched to represent teeth almost beyond resolution by light microscope; l) abdominal seta with associated hooked capillary seta; m) whole mature animal dorsal view showing the position of a fully developed egg string; n), o) and p) showing smaller egg strings and tenuous attachments to the faecal grooves.

Scales: b) as a); d) as c); g), h), j), k) and l) as f); n), o) and p) as m).

an egg string tightly compressed against the faecal groove, with the anterior end approximately level with the first abdominal torus. The method of attachment of the egg mass could not be discerned but it seems likely that direct attachment to the body surface, as described above, is the method characteristic of *Metalaeospira*. In that respect this genus differs from *Romanchella* and *Marsipospira* but resembles *Eulaeospira*, to judge from observations on *Eulaeospira orientalis* (Pillai, 1960) and *E. convexis* (Wisely, 1962), (Knight-Jones, Knight-Jones & Llewellyn, 1973). Further resemblances to *Eulaeospira* include the asymmetrical distribution of abdominal uncini and the presence of hooked capillary setae on several abdominal segments. The opercular stalk also resembles that of *Eulaeospira orientalis*, but not that of *E. convexis*.

Genus **PROTOLAEOSPIRA** Pixell, 1912 (redefined)  
(inc. *Marsipospira* Bailey, 1969b; *Pixellia* Pillai, 1970)

Coiling usually sinistral (see below); three rows of tori on the concave side of the thorax; other traces of a fourth thoracic segment may or may not be present; embryos incubated in the faecal groove and attached to a stalk which arises dorsally from the floor of the groove, in the thoracic region and towards the left side; collar setae with separate fins and blades which are usually cross-striated; sickle setae present in the third fascicle; thoracic and abdominal uncini much more numerous on the concave side (Fig. 7c & d, p. 250); thoracic uncini usually very long and slender, with a blunt, bilobed anterior peg; abdominal setae less than a quarter the length of the collar setae (Fig. 6c & d, p. 248); and with vestigial brush-like blades; opercular talon massive and usually bearing lateral projections; single white larval attachment gland may be present.

Bailey (1969b), in a valuable taxonomic review, first united these forms into a single subgenus, with *Marsipospira striata* (Quiévreux, 1963) as the type, but they must include *Spirorbis* (*Protolaeospira*) *ambilateralis* Pixell, 1912. This was originally separated into a monotypic subgenus, because it has all four parapodial rudiments appropriate to a fourth thoracic segment, thus differing from *Paralaeospira* in which the fourth segment is usually represented by a single torus (the neuropodium of the concave side). Pixell described her species as having a thoracic brood stalk but did not regard this character as helping to distinguish it from *Paralaeospira* because she described a similar stalk in *Spirorbis* (*Paralaeospira*) *racemosus*. The latter was made the type of a new genus *Pixellia* by Pillai (1970), but as Zibrowius (1968) showed there is probably no important difference between a complete or incomplete fourth thoracic segment and indeed the number of rudiments developed varies with the size of the specimen (Caullery and Mesnil, 1897; Crisp, Bailey, Knight-Jones, 1967; Bailey, 1969a). *Pixellia* and *Protolaeospira* must therefore be reunited and the rules of priority unfortunately necessitate use of the name *Protolaeospira*, in spite of the risk of confusion which redefinition entails.

It is also unfortunate that the name seems inappropriate. The stalk is unlikely to be primitive and not all these forms are sinistral. The direction of coiling in the diagnosis above must be qualified as being *usually* sinistral, because of the characters

of what has hitherto been called *Spirorbis* (*Paradexiospira*) *falklandicus* Pixell, 1913. Schizosyntypes of this species from the British Museum (Nat. Hist.) clearly showed the egg mass to have a thoracic attachment stalk like that typical of *Protolaeospira*. This species is thus quite different from the type species of *Paradexiospira*, i.e. *P. vitrea* (Fabricius, 1780), of which numerous live specimens from Cornwall, U.K. were examined (kindly provided by Mr Hedley Brown.) In *P. vitrea* the egg mass is attached to the tube and not to the animal. Clearly the subantarctic species cannot remain in the genus *Paradexiospira*. It has recently been shown that the direction of coiling is not very useful in distinguishing between genera in Spirorbinae (Knight-Jones, 1972). It is quite a useful character, however, at subgeneric level, so it seems best to institute herewith a new subgenus ***Dextralia***, within the genus *Protolaeospira*, with *P.(D.) falklandica* as the type species.

Before reaching the above decision on priority it was of course necessary to check the method of incubation in the type of *Paralaeospira* (i.e. *P. aggregata* Caullery and Mesnil, 1897, kindly loaned by the Museum National d'Histoire Naturelle, Paris). In this form the egg mass lies in the faecal groove, but no thoracic attachment stalk is present. *Spirorbis* (*Paralaeospira*) *lebruni* (Caullery and Mesnil, 1897) has the specialized attachment stalk, however, so must now be placed in *Protolaeospira* (see page 240).

TYPE. *Spirorbis* (*Protolaeospira*) *ambilateralis* Pixell, 1912.

***Protolaeospira* (*Protolaeospira*) *triflabellis* sp. n.** (Fig. 2)

Tube sinistral, large (up to 4 mm across), ornamented by high, round, smooth transverse ridges which converge into a longitudinal ridge on the innermost edge of the single visible whorl. The walls are thick and hard, but in no way translucent (Fig. 2a).

*Opercular* plate concave, densely calcified and very oblique, with a massive calcified talon bearing three irregularly fluted projections which appear fan-like in dorsal view. The terminal 'fan' is thick in profile and fluted on both sides (Fig. 2b & c).

*Thorax*. Collar margins unfused dorsally. Three pairs of tori. Three fascicles of setae on the concave side and four fascicles on the convex, forming what some authors have described as '3 $\frac{3}{4}$  segments'. Collar setae with fins, and cross-striations, which are confined to about a third of the width of the blades (Fig. 2d). Setae of the second, third and fourth fascicles have simple slender blades, with smooth margins (Fig. 2f). Also present in the third and fourth fascicles are sickle setae with the distal portions unusually small and bearing remarkably fine recurved teeth (Fig. 2g). Capillary setae (Fig. 2e) are present in all the fascicles. Uncini unusually numerous, elongated, each with a single longitudinal row of large teeth along most of its length, but with finer more numerous teeth adjoining the blunt, gouge-like anterior peg (Fig. 2k).

*Abdomen* with a long asetigerous region, followed by up to thirty-four rows of tori on the concave side. Uncini with about ten longitudinal rows of teeth and a blunt fluted anterior peg (Fig. 2l). Very small setae, up to four per fascicle and

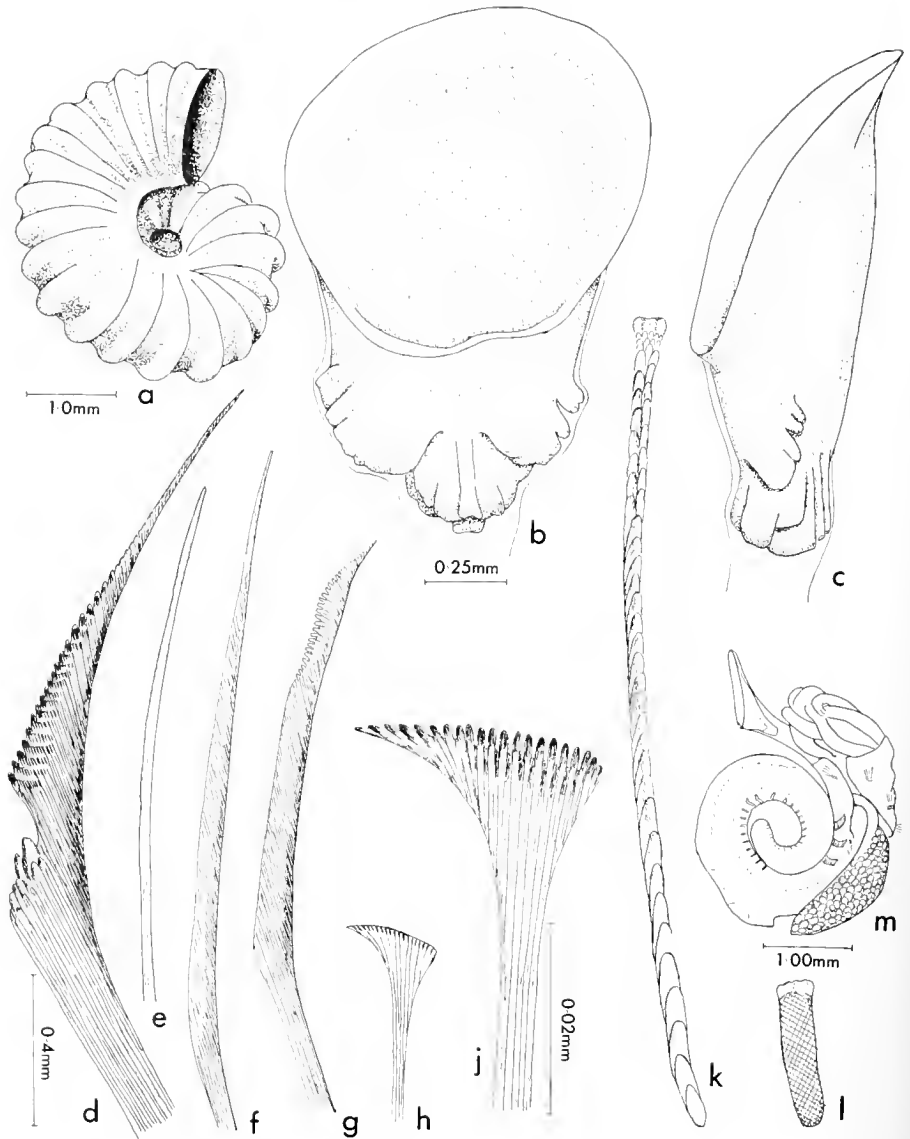


FIG. 2. *Protolacospira (P.) triflabellis* sp. n. a) tube; b) operculum, dorsal view; c) operculum side view; d) collar seta; e) capillary seta as in the first and third fascicles; f) simple seta, as in the second, third and fourth fascicles; g) sickle seta, as in the third and fourth fascicles; h) abdominal seta; j) abdominal seta shown to a larger scale; k) thoracic uncinus; l) abdominal uncinus (cross-hatching denotes teeth almost beyond resolution by the light microscope); m) whole animal viewed dorsally showing the egg mass and position of attachment stalk.

Scales: c) as b); e), f), g) and h), as d); k) and l) as j).

somewhat brush-like in appearance, with the short blade bordered by dense, well separated ovate teeth (Fig. 2j).

*Setation* (Figs 6d & 7d).

*Incubation.* About two hundred embryos lying in the faecal groove in an elongated mass which is attached to a thoracic stalk. The latter arises dorsally from the floor of the faecal groove on the concave side, just anterior to the first thoracic torus (Fig. 2m).

*LOCATIONS.* Cape du Couedic. Collected by L. C. Llewellyn January 1967. Occur sublittorally on kelp holdfasts (*Ecklonia radiata*) and on stones and shells in shaded places in the littoral zone (5 specimens). A few of these empty but highly characteristic tubes were also found at Moanna.

*HOLOTYPE.* British Museum (Nat. Hist.) Reg. No. ZB 1971:10, 10a & 10b.

*PARATYPES.* British Museum (Nat. Hist.) Reg. No. ZB 1971: 11. Australian Museum Reg. No. W4474.

*REMARKS.* This species resembles *Protolaeospira striata* and *P. racemosa* in having a tube with remarkably prominent transverse folds, but differs from them in having no spur ornamenting the ventral side of the talon. Its talon somewhat resembles that of a species from the Galapagos Islands, *P. translucens* (Bailey & Harris, 1968), but that has a translucent tube with indistinct transverse ridges, uncini with three to four longitudinal rows of teeth, and sickle setae of different proportions. Examination of *P. striata* showed that its attachment stalk also arises from the left side of the dorsal groove, just anterior to the first thoracic torus, and not in close association with the branchial crown, as was indicated by Pixell (1912) and Quévreur (1963). It seems unlikely therefore to be a modified branchial tentacle, as Bailey (1969b) suggested. The full complement of branchiae may be said to be present without it, for the peduncle of the operculum in all these species arises in the normal (for Spirorbinae) position of second on the left, the most dorsal tentacle being of the usual pinnate form. Hartman (1953), however, noted the position of a similar thoracic stalk in her description of *Helicosiphon biscoeensis* Gravier, 1907. 'The egg sack is attached to a thick stalk that arises from the dorsal side of the body between the first and second setigerous segment'. Examination of this species from the South Orkneys (Knight-Jones, Knight-Jones & Bregazzi, 1973) confirmed that the method of brood attachment in *Helicosiphon* is similar to that in *Protolaeospira*. It also resembles that found in *Romanchella sensu stricto* (p. 243), but further studies of this are desirable.

***Protolaeospira (Protolaeospira) canina* sp. n. (Fig. 3)**

*Tube* sinistral, bearing two longitudinal ridges (of which the inner may be the most prominent), with slight transverse grooves between them (Fig. 3a & b). A wide striated flange slopes down from the outer ridge and projects somewhat in front of the mouth, which may or may not ascend.

*Opercular plate* slightly concave with a massive talon; in side view this is somewhat like a dog's tooth, but a dorsal view shows faint bulges on each side (one higher than the other) and an indistinct median longitudinal ridge (Fig. 3c & d).

*Thorax.* Collar margins unfused dorsally. A fourth 'segment' represented by only a third torus on the concave side. Uncini long and slender, each with a single longitudinal row of teeth for most of its length and finer more numerous teeth behind the anterior peg, which is like a gouge (Fig. 3k). Collar setae with a fin and an indistinctly cross-striated blade (Fig. 3e & f). Capillary setae are also present. Setae of the second and third fascicles are simple with smooth margins (Fig. 3g) and there are also sickle setae (Fig. 3h) in the third fascicles.

*Abdomen.* About seventeen abdominal 'segments' closely spaced, except that the first is equidistant between the third thoracic torus and the second abdominal torus, resulting in what could be called a relatively short asetigerous region (see legend Fig. 7). Uncini with about nine rows of longitudinal teeth, which seem to occlude the anterior peg (Fig. 3). Setae small, up to six per fascicle and somewhat brush-like (Fig. 3j).

*Setation* (Figs 6c & 7c).

*Incubation.* The egg mass (up to 17 embryos) lying in the faecal groove and attached anteriorly by a stalk-like process, which arises from the floor of the groove level with the first thoracic torus on the concave side.

**LOCATION.** Cape du Couedic. Collected by L. C. Llewellyn January 1967. Twenty-seven specimens on stones in midlittoral pools.

**HOLOTYPE.** British Museum (Nat. Hist.) Reg. No. ZB 1971: 12.

**PARATYPES.** British Museum (Nat. Hist.) Reg. No. ZB 1971: 13. Australian Museum Reg. No. W4475.

**REMARKS.** This species is closely related to *P. lebruni*, material of which, collected from the Falkland Isles and recently described by Harris (1969), was kindly loaned by the British Museum (Nat. Hist.). Further specimens from New Zealand were kindly made available by Dr Peter Vine. Study of these showed the embryo mass to be held in position by a thoracic groove attachment stalk as in the above and preceding species. The opercular plate of *P. lebruni* varies from being slightly convex to prominently conical, perhaps with increasing age, but it is always adorned with brown concentric rings peripherally and apically. The talon too shows great variability in the size and angle of its lateral protuberances, though a ventral cavity and dorsal longitudinal ridge are usually present.

The range of variation includes that described by Harris (1969) as a separate species, *Spirorbis auricularis*. Paratypes of this from the British Museum (Nat. Hist.) were examined and found to be the same as *P. lebruni*, having the same setation and characteristic brown rings. The talon in *P. canina* is more massive and much simpler in outline, whilst the distal plate is concave and lacks brown rings, irrespective of the size of the animal. The anterior uncini are less numerous, the first, second and third thoracic tori on the concave side containing approximately 50, 70, and 60, compared with 80, 110 and 100 uncini, whilst the first abdominal torus



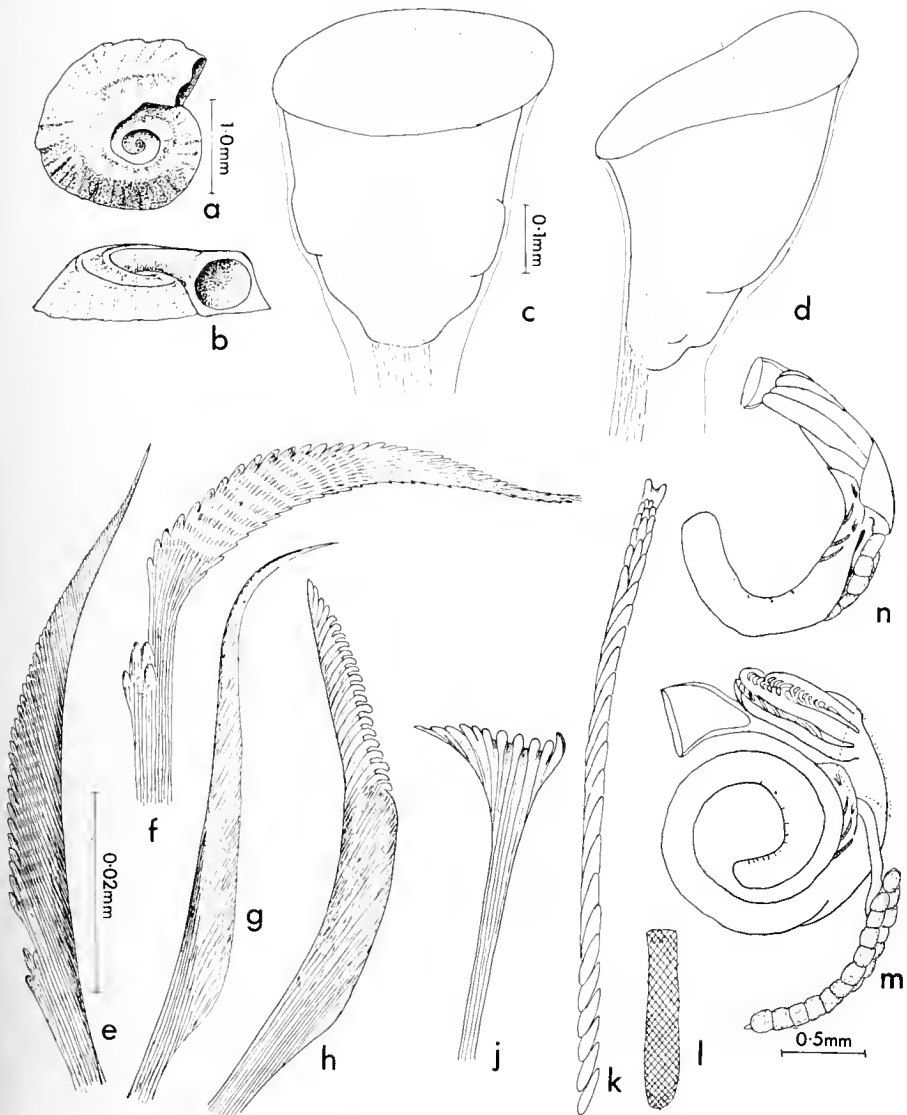


FIG. 3. *Protolaospira (P.) canina* sp. n. a) tube from above; b) tube, side view; c) operculum, dorsal view; d) operculum, side view; e) collar seta, viewing side of 'blade'; f) collar seta, viewing front of 'blade'; g) simple seta as in second and third fascicles; h) sickle seta as in third fascicles; j) abdominal seta; k) thoracic uncinus; l) abdominal uncinus (cross-hatching denotes teeth almost beyond resolution by light microscope); m) whole animal viewed from the dorsal side showing the egg mass and the position of the attachment stalk; n) another specimen showing the egg mass lying in its natural position, following the spiral course of the faecal groove.

Scales: b) as a); d) as c); f), g), h), j), k), l) as e); n) as m).

contains 40, compared with the remarkably large number of 110. The ridges of the tube are more distinct than in *P. lebruni* from the Falkland Islands, but less prominent than in those from New Zealand. Both *P. canina* and *P. lebruni* (including the form *auricularis*) have collar setae with indistinct cross-striations.

The constancy of the characters of *P. canina* (particularly its operculum) suggests that this is more than a variety of *P. lebruni* and that specific status is justifiable. Both these forms are different from other species of *Protolacospira* in that the first abdominal torus is the largest (cf Figs 7c & 7d), whilst the attachment stalk seems to arise in a slightly more posterior position.

#### Genus **ROMANCHELLA** Caullery and Mesnil, 1897 (amended)

Sinistral coiling; incubation in the faecal groove; simple collar setae; only two pairs of thoracic tori; sickle setae present in the third fascicles; abdominal setae less than a quarter the size of the collar setae (Fig. 6a, p. 248), usually paired and strongly geniculate, with small tapered blades, but one of a pair is often a hooked capillary seta; thoracic uncini with a blunt gouge-shaped anterior peg; white larval attachment glands probably not present.

#### Subgenus **ROMANCHELLA** Caullery and Mesnil, 1897

Margins of the collar fused to form a tunnel over the mid-dorsal thoracic groove; incubation in an egg mass attached anteriorly by a stalk arising in the thoracic groove and level with the tori; collar setae few compared with those of the other thoracic fascicles (Fig. 7a, p. 250), and small on the concave side (Fig. 6a, p. 248); uncini numerous on the concave side of the abdomen and sparse on the convex side, with the largest tori near the anterior end of the setigerous region (Fig. 7a, p. 250).

TYPE. *Spirorbis (Romanchella) perrieri* Caullery and Mesnil, 1897.

It seems best to adopt the narrow definition of this group outlined above, in order to exclude from it certain northern-hemisphere forms which fall within the definition of the genus. Of these I have studied mostly *Romanchella evoluta* (Bush, 1904) from the Smithsonian Institution and hereby designate it as the type of a new subgenus **Bushiella**, with the characters of the genus *Romanchella* and with separate dorsal collar margins; collar setae comparatively numerous and well developed; thoracic uncini long and narrow and bearing no more than two rows of longitudinal teeth; no marked bilateral asymmetry in the distribution of abdominal tori; and the largest tori about half way along the setigerous region. The poor preservation of the type material did not allow proper study of the method by which the egg masses were held in the faecal groove. A lectotype has been selected for the Smithsonian Institution. In the closely related form *Romanchella (Bushiella) media* (Pixell, 1912) also from the Smithsonian, there is a flap of skin from one side of the faecal groove, extending from the thorax to approximately the sixth abdominal 'segment' and partially covering the egg mass. *Romanchella coronata* (Zachs, 1933), kindly

supplied from the National Museum, Tokyo, and *Romanchella asperata* (Bush, 1904), from the Smithsonian Institution, also seem to be closely related to these and have unfused collar folds.

*Romanchella (Romanchella) quadricostalis* sp. n. (Fig. 4)

*Tube* sinistral, thick-walled, porcellaneous, with four to five high smooth longitudinal ridges, three of which form prominent teeth at the mouth. The upper whorl is often irregularly evolute, whilst the lower is tightly coiled and very firmly attached to the algal filament which forms the substratum.

*Opercular* plate slightly concave, oblique and bearing towards the dorsal edge a shallow broad talon with a central cleft forming shallow bilobed 'lips' terminally. Sometimes the outer surface of the plate shows incipient delamination and occasionally two lobed plates may be seen, one above the other (Fig. 4e).

*Thorax*. Collar margins fused dorsally (Fig. 4p). Collar setae simple and finely serrate, with those on the concave side smaller than the others. Setae of the second and third fascicles are similar, but larger and with smooth margins. Capillary setae are also present in the first fascicle and sickle setae in the third (Fig. 4k). Two pairs of tori, each uncinus broad and with unusually numerous minute teeth in about twelve to fifteen longitudinal rows, which almost cover a wide, blunt anterior peg (Fig. 4n).

*Abdomen*. Asetigerous region short and followed by about seventeen 'segments'. Uncini numerous on the concave side (sparse on the convex) and similar to those of the thorax, but with about fifteen to twenty longitudinal rows of teeth. Setae often in pairs and strongly geniculate, with sharply tapering blades bearing recurved teeth. Usually the second seta of the last few fascicles of mature specimens is in the form of a hooked capillary (Fig. 4m).

*Incubation* in the faecal groove. The egg mass (up to 25 orange embryos) is attached dorsally by a stalk-like process which arises from the floor of the thoracic groove, between the second and third thoracic 'segments'. The usual spiral course of the faecal groove and its associated egg 'string' can be seen particularly clearly because the body is short and relatively fat (Fig. 4q).

*Setation* (Fig. 6a and Fig. 7a).

**LOCATIONS.** Numerous (including the type specimens) on a red alga *Pterocladia capillacea* in the lower littoral zone at Cape du Couedic and a few attached to the base of various epiphytes on detached algae, presumed to have been cast ashore from the sublittoral reef about 100 m off Sou' West River. Collected by L. C. Llewellyn January 1967.

**HOLOTYPE.** British Museum (Nat. Hist.) Reg. No. ZB 1971: 14 & 14a.

**PARATYPES.** British Museum (Nat. Hist.) Reg. No. ZB 1971: 15. Australian Museum Reg. No. W4476.

**REMARKS.** Dorsal collar fusion, similar setation (including sickles) and an egg-mass attachment process were found in *R. (R.) perrieri* from New Zealand (identified and made available by P. Vine), *R. (R.) perrieri* from Falkland Isles and *R. (R.)*

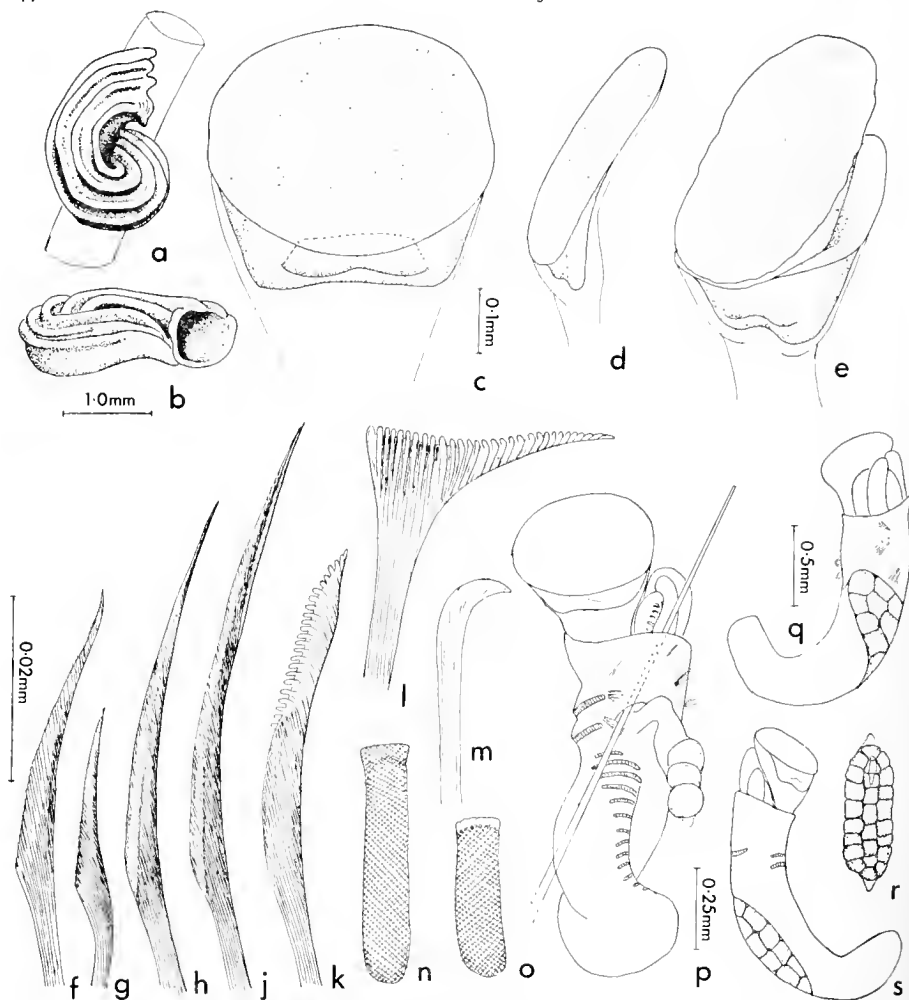


FIG. 4. *Romanchella (Romanchella) quadricostalis* sp. n. a) tube from above; b) tube, side view; c) operculum, dorsal view; d) operculum, side view; e) operculum showing delamination of an outer plate; f) collar seta from convex side of animal; g) collar seta from concave side; h) simple seta as in second fascicles; j) simple seta as in third fascicles, showing the tip of the blade in edge-on view; k) sickie seta as in third fascicles; l) geniculate abdominal seta; m) hooked capillary abdominal seta; n) thoracic uncinus (cross-hatching denotes teeth almost beyond resolution by light microscope); o) abdominal uncinus; p) whole animal viewed from the dorso-concave side, showing egg mass, position of the attachment stalk and probe inserted to demonstrate the fused collar folds; q) dorsal view of specimen with a fully developed egg mass obscuring the attachment stalk; r) detached egg mass, showing area of attachment near its anterior end; s) ventral view of q) showing the egg mass conforming with the spiral course of the faecal groove.

Scales: b) as a); d) and e) as c); g), h), j), k), l), m), n) and o) as f); r) and s) as q).

*scoresbyi* (Harris) and *R. (R.) inventis* (Harris) from Tristan Da Cunha (loaned by the British Museum (Natural History)). However, the tubes, opercula and uncini showed that all these were distinct species.

Collar fusion in dextral opercular incubators has been noted by Day (1961) and Pillai (1970) and has since been observed in sinistral forms of *Janna* (Knight-Jones, 1972; Vine, 1972a), but not hitherto in any genus of tube-incubators. Attachment stalks have previously been noted in *Protolaeospira* and *Helicosiphon*, but these arise in a slightly more anterior position and are long and thin, like unbranched tentacles. A transverse section of part of the thoracic region of *R. (R.) quadricostalis* showed the attachment stalk to be a hollow 'funnel' connecting with the coelomic cavity by a pore through the body wall (Knight-Jones, Knight-Jones & Vine, 1972). In whole animals it appears membranous and is often hidden under a mass of embryos.

The occasional appearance of delamination from the opercular plate recalls the periodic moulting described in other Spirobrinae by Thorp (1961), the function of which is presumably to get rid of epiphytes and epizoites. The opercular plate is usually double in *Romanchella (Bushiella) media* and it is presumably through more prolonged retention of such delaminations that the multiple operculum of *R. (R.) perrieri* is built up.

#### Genus *PILEOLARIA* Claparède, 1868 (amended)

Sinistral coiling; only two pairs of thoracic tori; incubation in the operculum; each collar seta with a fin, separated from a blade which is usually coarsely serrated and cross-striated; sickle setae may or may not be present; thoracic uncini very slender, with one to three rows of teeth and a blunt anterior peg; abdominal setae obliquely geniculate (with tapering blades) and usually about half the size of the collar setae; abdominal uncini fairly symmetrical in bilateral distribution; the largest abdominal tori lie in the posterior half of the setigerous region; larvae have single, white, mid-dorsal attachment glands.

**TYPE.** *Pileolaria militaris* Claparède.

This is a large and rather diverse genus. Vine (1972a) advocates grouping *Pileolaria koehleri* (Caullery & Mesnil, 1897) and related forms with multiple opercular plates and a divided first abdominal torus, into a separate subgenus. Another convenient criterion for dividing the group is the presence or absence of sickle setae. Pillai (1970) indeed regards this as a criterion for separating genera. Most species of *Pileolaria* have sickle setae, including the type species *P. militaris* (Claparède, 1868) and the others mentioned above. A few lack them and for these a new subgenus *Simplicaria* is here proposed, with *Pileolaria (Simplicaria) pseudomilitaris* (Thiriot-Quévieux, 1965) as the type. According to some authors, *P. moerchi* (Levinsen, 1883) and *P. berkleyana* (Rioja, 1942) also lack sickles, but other authors disagree and it will be necessary to study material from type localities to elucidate this problem. *P. (S.) pseudomilitaris* and *P. militaris* are both common off Australia and redescrptions from Australian material will be given in a separate paper (Knight-Jones, Knight-Jones & Llewellyn, 1973).

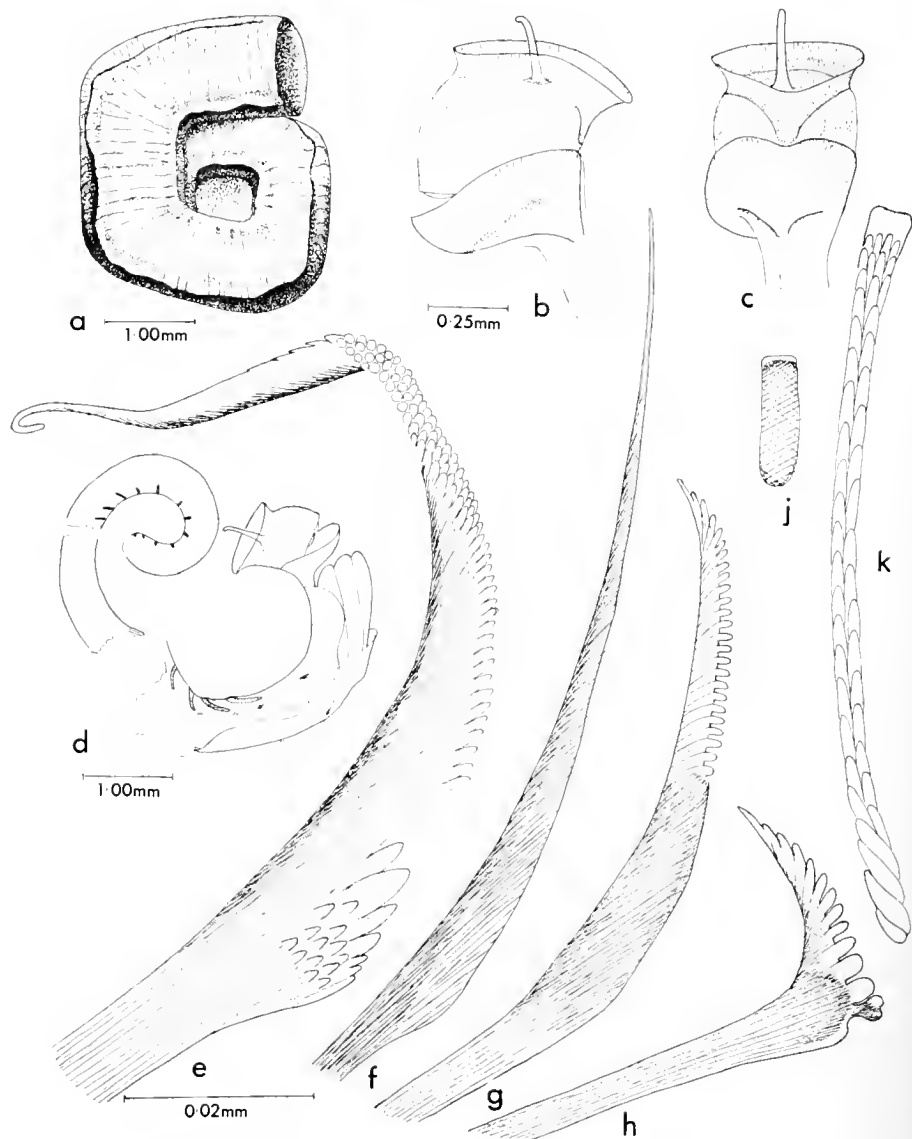


FIG. 5. *Amplavia spiculosa* sp. n. a) tube; b) operculum from side; c) operculum, dorsal view; d) whole animal, showing unfused dorsal collar margin; e) collar seta; f) seta of second or third fascicles; g) sickle seta, as in third fascicles; h) abdominal seta; j) abdominal uncinus (cross-hatching denotes teeth almost beyond resolution by light microscope); k) thoracic uncinus. Scales: c) as b); f), g), h), j), and k) as e).

Genus *AMPLARIA* gen. n.

Sinistral coiling; four thoracic tori and four fascicles of setae on the concave side, and three tori and five fascicles on the convex; incubation in the operculum; fin and blade collar setae without cross-striations; sickle setae present in the third and fourth fascicles; thoracic uncini slender and with a blunt anterior peg; abdominal setae geniculate, with a prominent indentation at the 'heel', less than a quarter the size of the collar setae (Fig. 6e) and with short tapering blades; abdominal uncini somewhat asymmetrical in bilateral distribution, with the largest tori about halfway along the setigerous region of the abdomen (Fig. 7e).

The name is derived from the latin *amplus*, referring to the large number of thoracic segments, with a termination to signify the apparent affinities with *Pileolaria* (see below).

TYPE. *Amplaria spiculosa* sp. n.

*Amplaria spiculosa* sp. n. (Fig. 5)

*Tube* sinistral, thick-walled, with two blunt and widely spaced ridges making the cross-section somewhat square (Fig. 5a).

*Opercular plate* rather flat, but depressed dorsally to form a sharp 'V'. It bears peripherally a high transparent collar, the distal edge of which is yellow or horny in appearance. From the centre of the plate arises a strong, slender hooked spine which is also yellow (Fig. 5b, c). The walls of the incubatory chamber below the plate are lightly calcified, with faint longitudinal granulations. The base of the chamber is within a cup-like secondary opercular plate. A scarcely visible, flexible 'rod' extends from this plate into the opercular stalk.

*Thorax*. The collar is unfused dorsally and extensive distally, partially covering the tentacles (Fig. 5d). There are four rows of tori and four fascicles of setae on the concave side and three tori and five fascicles on the convex. The collar setae have fins and blades, which are not cross-striated (Fig. 5e). Capillary setae were not observed. The second fascicles contain slender simple setae, which are similar to setae in the third, fourth, and fifth fascicles. Sickle setae (Fig. 5g) are also present in the third, fourth and perhaps the fifth fascicles. Uncini slender, with two longitudinal rows of teeth along most of the length and with a blunt, somewhat gouge-shaped anterior peg (Fig. 5k).

*Abdomen*. A long aseptigerous region followed by twelve pairs of tori. Uncini small and with about 10 longitudinal rows of teeth (Fig. 5j). The setae are distinctive in having a deep indentation and a bulbous 'spine' at the distal end of the shaft and a short tapering geniculate blade with large marginal teeth (Fig. 5h).

*Setation* somewhat asymmetrical (Figs 6e & 7e).

LOCATION. Kingscote on stones intertidally, associated with *Pileolaria* (*Simpli-caria*) *pseudomilitaris* and *Janua* (*Janua*) *pagenstecheri*. Collected by L. C. Llewellyn January 1967.

HOLOTYPE. British Museum (Nat. Hist.) Reg. No. ZB 1971: 16 & 16a.

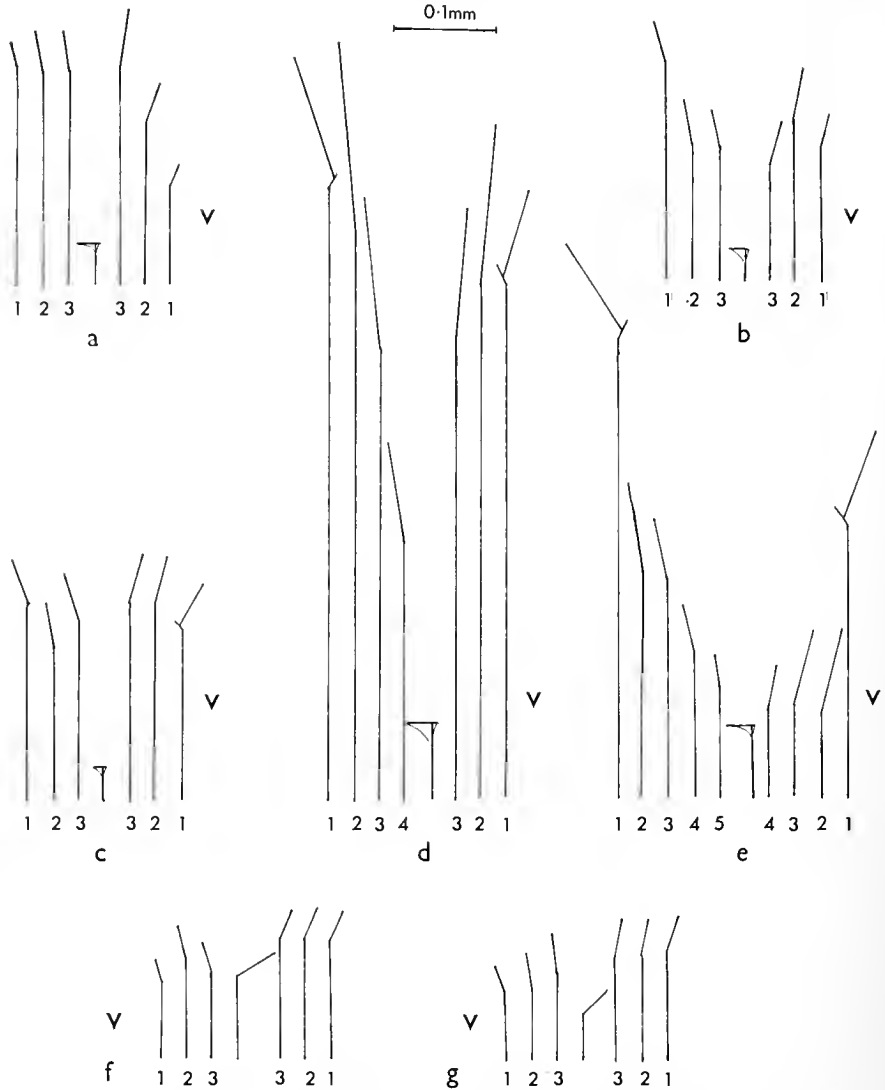


FIG. 6. Diagrams showing sizes of seta and their blades in a) *Romanchella (Romanchella) quadricostalis*; b) *Metalacospira tenuis*; c) *Protolacospira canina*; d) *Protolacospira triflabellis*; e) *Amplaria spiculosa*; f) *Janua (Pillaiospira) trifurcata*; g) *Janua (Dexiospira) fenestrata*.

'V' denotes the concave side. 1, 2, 3 (4 and 5) mark the thoracic fascicles and the middle seta represents the largest abdominal seta. The length of the blade and the angle at which it comes off from the shaft is indicated for each seta. All are to the same scale.



REMARKS. *Amplaria spiculosa* is almost unique among Spirorbinae in having a thorax with what some authors might call '4½ segments', the only other form sharing this character being a Red Sea species found recently by Dr Peter Vine (1972a). His species, however, differs from *A. spiculosa* in having dextral coiling, small thoracic uncini with multi-pronged anterior pegs, no sickle setae and simple collar setae, the blades of which are not much larger than those of the abdominal setae. Such characters suggest some affinities with *Janua* (see below), whereas *Amplaria* would appear to have affinities with *Pileolaria*, to judge from its large fin-and-blade collar setae, narrow elongated thoracic uncini and the posterior position of the largest abdominal tori (Fig. 7e). It differs from *Pileolaria* in having rudiments of two extra thoracic 'segments', a more asymmetrical distribution of abdominal uncini, a different type of abdominal setae and an operculum quite different in structure, though somewhat reminiscent of the *Pileolaria koehleri* 'group'.

Although only one specimen was found, it was felt that this species could not be an abnormal mutant of any *Pileolaria* and thus the erection of a new genus was inevitable. Moreover Dr Peter Vine has since found the same species off the Poor Knights Island, not far from Auckland, New Zealand.

#### Genus *JANUA* Saint-Joseph, 1894 (amended)

Mostly with dextral coiling; only two pairs of thoracic tori; incubation in an opercular brood chamber, below which a secondary plate (rudiment of next opercular plate) is formed soon after spawning; collar setae without toothed fin; abdominal setae with elongated blades as big as or bigger than those of the collar setae (Fig. 6f & g) and often accompanied by secondary setae, with rudimentary shafts (Vine, 1972a—see also Fig. 9q); thoracic uncini with anterior pegs narrow and more or less pointed in surface view; largest abdominal tori lie in the anterior half of the setigerous region (Fig. 7f & g); larvae have paired white attachment glands in the thoracic region.

#### Subgenus *JANUA* Saint-Joseph, 1894

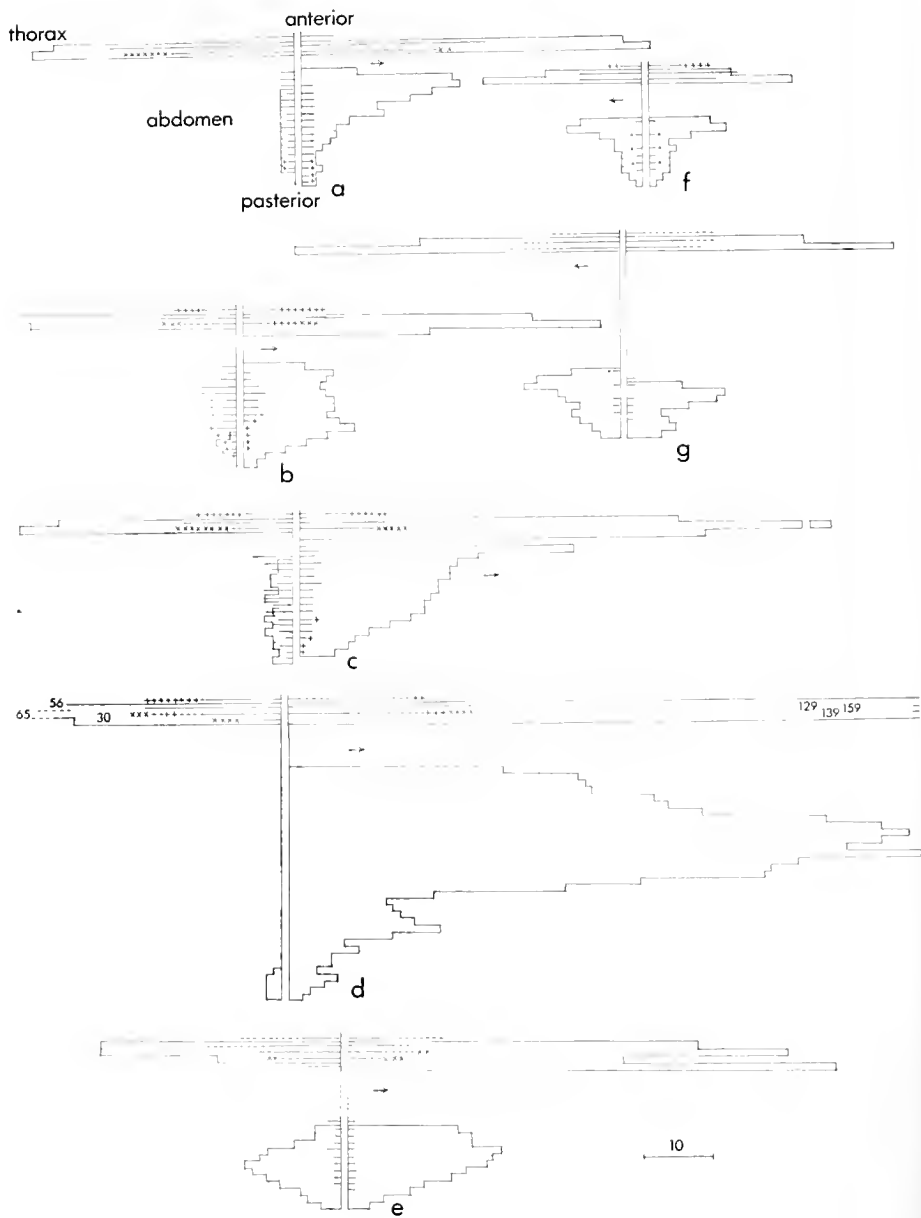
Dextral coiling; sickle setae present in the third thoracic fascicles; thoracic collar not fused dorsally.

TYPE. *Spirorbis pagenstecheri* Quatrefages, 1865.

#### Subgenus *DEXIOSPIRA* Caullery and Mesnil, 1897 (amended) (syn. *Neodexiospira* Pillai, 1970, see p. 253)

Coiling usually dextral; sickle setae absent; collar margins fused to form a tunnel over the mid-dorsal thoracic groove.

TYPE. *Spirorbis pseudocorrugatus* Bush, 1904 (= *Spirorbis corrugatus*: Caullery and Mesnil, 1897, non Montagu, 1803—see p. 256).



*Janua (Dexiospira) fenestrata* sp. n. (Fig. 8)

*Tube* may coil in one plane or the last whorl may ascend. Three very prominent equidistant longitudinal ridges, the outer of which projects as far as or beyond the area of attachment to the substratum. Between the ridges are deep transverse furrows, which in many specimens extend to form holes (tunnels) through the two outer ridges, giving a 'lacy' appearance from above (Fig. 8a, b & c).

*Opercular plate* with a central calcified disc surrounded by an upturned, brown rather membranous rim. A peg-like talon bilobed terminally, extends proximally from the dorsal edge of the plate (Fig. 8d & e). Mature opercula lose their talons and develop lightly calcified walls through which the embryos can be seen. A secondary plate develops below the embryos (Fig. 8f).

*Thorax.* Collar setae on the convex side have simple blades with coarsely serrated margins and indistinct, widely spaced cross-striations (Fig. 8g). Collar setae on the concave side (Fig. 8h) are like those of the second and third fascicles (Fig. 8j) with almost smooth margins. Capillary setae are also present in the first fascicle. Uncini have about five longitudinal rows of teeth, and a pointed anterior peg (Fig. 8l).

*Abdomen.* Asetigerous region is remarkably long (Fig. 7g) and followed by about ten pairs of tori. Setae have elongated, obliquely geniculate blades with recurved teeth (Fig. 8k). Secondary setae are occasionally present. Uncini have numerous (possibly ten) rows of minute teeth and a broad flared anterior peg (Fig. 8m).

*Incubation.* About six to eight embryos in the opercular chamber.

*Setal distribution* (Figs 6g & 7g) fairly symmetrical.

**LOCATION.** Cape du Couedic. Collected by L. C. Llewellyn January 1967: Fourteen specimens mainly on rock and stones in the midlittoral zone. One also found on a holdfast of *Ecklonia radiata*.

**HOLOTYPE.** British Museum (Nat. Hist.) Reg. No. ZB 1971: 17 & 17a.

**PARATYPES.** British Museum (Nat. Hist.) Reg. No. ZB 1971: 18. Australian Museum Reg. No. W4477.

FIG. 7. Distribution of setae in: a. *Romanchella quadricostalis*; b. *Metalaospira tenuis*; c. *Protolaospira canina*; d. *Protolaospira triflabellis*; e. *Amplaria spiculosa*; f. *Janua (Pillaiospira) trifurcata*; g. *Janua (Dexiospira) fenestrata*. Each diagram represents a worm straightened out and viewed from the ventral side (so that the concave side, indicated by an arrow, appears to the observer's right if the species is sinistral). The histograms represent the number of uncini per segment and the continuous lines (—) within the histograms the number of simple setae or collar setae. Each plus sign (+) represents a capillary seta in the thorax or a hooked capillary seta in the abdomen. A cross (X) represents a sickle seta and a dot (.) a secondary abdominal seta. Indeterminate setae are represented by short dashes (---). The length of the asetigerous region relative to the length of the nearest abdominal segment is represented by the gap between the histograms for thoracic and abdominal segments. In c) the anterior abdominal segment is unusually long, thus the asetigerous region appears relatively short. Each diagram relates to a single typical individual except for d), which is a composite diagram from two individuals, neither of which alone was suitable for determining the distribution of abdominal setae.

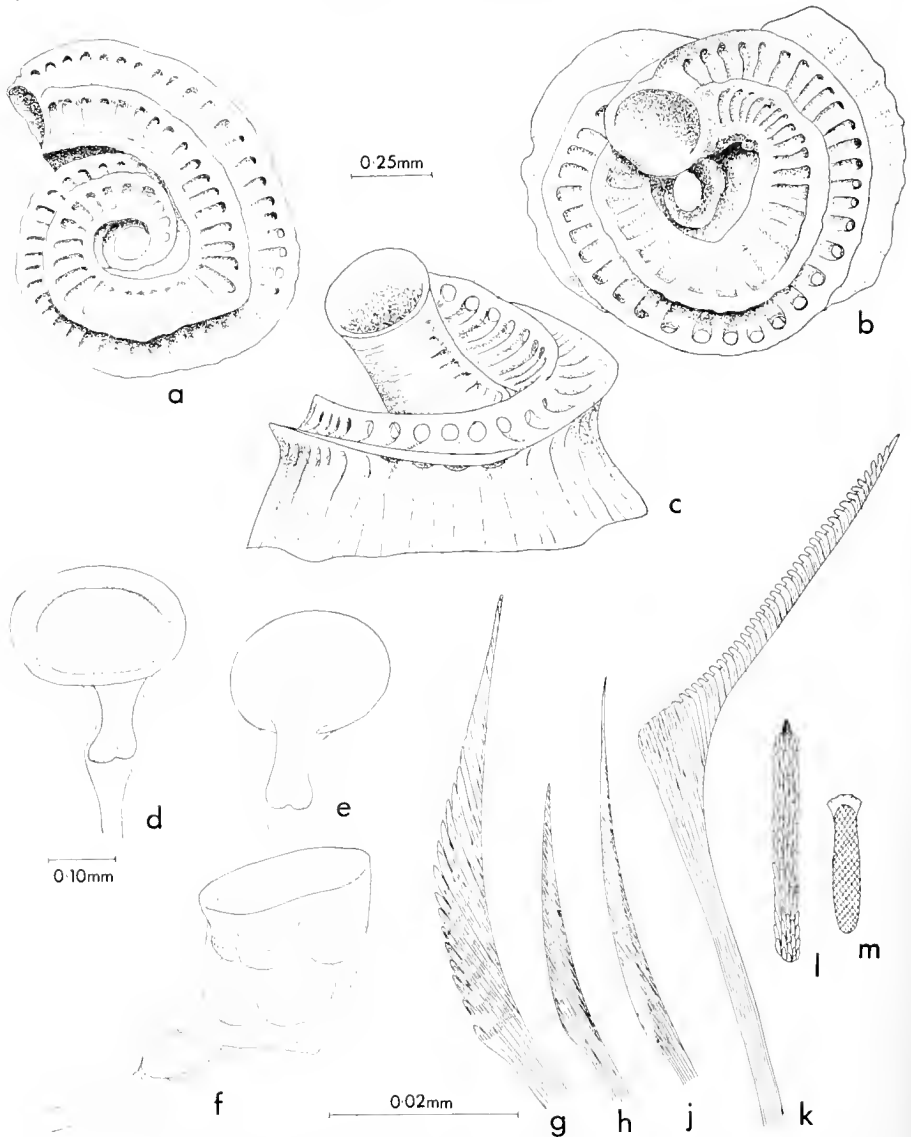


FIG. 8. *Janua (Dexiospiya) fenestrata* sp. n. a) tube with only three perforations; b) tube with numerous perforations; c) side view of b); d) juvenile operculum, dorsal view; e) same operculum viewed ventrally and from below; f) mature operculum with embryos and secondary plate; g) collar seta from convex side of animal; h) collar seta from concave side, which is like the setae from the second fascicles; j) seta from third fascicles; k) abdominal seta; l) thoracic uncinus; m) abdominal uncinus (cross-hatching denotes teeth almost beyond resolution by light microscope).

Scales: b) and c) as a); e) and f) as d); h), j), k), l) and m) as g).

REMARKS. The perforations of the tube recall the name *Spirorbis foraminosus* Moore & Bush, 1904, type material of which was kindly loaned by the Smithsonian Institution. Examination of a tube remnant showed that this species probably lacks prominent ridges (and associated perforations) and has a brood chamber and setae quite different from those of *J. (D.) fenestrata* (see p. 256).

Ridge perforations occur in *Spirorbis alveolatus* Zachs, 1933, but to judge from the original description the tube of that species is semi-transparent and incubation probably takes place within it. The name *alveolatus* has more recently been given to *Janua (Dexiospira) nipponica* (Okuda, 1934) by Imajima and Hartman (1964), but in fact Zach's description, although scarcely adequate, appears to belong to a species quite different from the Japanese form (see p. 256), which is itself quite different from *J. (D.) fenestrata*.

Bush (1904) inadequately described an empty tube from Port Phillip Australia, which may possibly have resembled that of *J. (D.) fenestrata*, although there is no mention of intercostal furrows (or perforations). She gave to it the name of *Spirorbis tridentatus*, however, which is a junior homonym for a common European species of *Spirorbis sensu stricto*.

The lectotype of *J. (D.) ceylonica* (Pillai, 1960), kindly made available by the British Museum (Natural History), differs from that of *J. (D.) fenestrata* in having unequally spaced low ridges and vestigial intercostal depressions which are not perforate. No other material was available and there has been no description of a juvenile form of operculum nor of setal distribution in this species. Further studies of *J. (D.) ceylonica* are necessary to establish whether it is a senior synonym for the present form.

The only adequately described forms to which *J. (D.) fenestrata* may be closely related are two new species from the Red Sea and Hawaii collected and studied by Peter Vine (1972a and 1972b). These resemble *J. (D.) fenestrata* in having simple talons, a brood chamber with lightly calcified walls, similar setae and a remarkably long asetigerous region. They differ in that the talons are spear-like, not bilobed, the rims of the opercular plates are narrow and more laterally placed and the tubes less deeply sculptured, without perforations. Both species have collars fused dorsally. It is uncertain whether those of *J. (D.) fenestrata* are fused, because the specimens had become very hardened. It seems likely that the material had been allowed to dry out, for the displacement of the secondary plate (Fig. 6f) seems likely to have resulted from dehydration. Because of this uncertainty, inclusion in this subgenus (rather than in the one that follows) is tentative and suggested only because of the close resemblance to the two species of *Dexiospira* mentioned above, coupled with the fact that this group contains most of the world's dextral opercular incubators, including most of such forms from Australia.

#### Subgenus *PILLAIOSPIRA* subgen. n.

Lacking sickle setae and collar folds not fused dorsally.

Pillai (1970) separated *Neodexiospira* from *Dexiospira* since he was led to believe, from examination of material misidentified by Fauvel (1914) that the type species

of *Dexiospira* has unfused collar folds. In this he was mistaken (see Knight-Jones, 1972), but discovery of the species below has confirmed that there is at least one species which is closely related to *Dexiospira*, but nevertheless has collar folds unfused. It is proposed to institute a new subgenus for this named after Dr G. Pillai, who first proposed a taxonomic division on this basis.

TYPE. *Janua trifurcata* sp. n.

*Janua (Pillaiospira) trifurcata* sp. n. (Fig. 9)

*Tube* dextral, round in cross section and bearing three longitudinal ridges, with 'chevron' sculpturing between (Fig. 9a & b). Most of the tubes were somewhat decalcified, so it is not certain whether this distinctive intercostal pattern is present in fresh material.

*Opercular plate* in juvenile specimens is convex, with the dorsal edge asymmetrically folded to form a latero-dorsal peak (always towards the right) and a deep 'U' shaped peripheral depression dorsally, with which a flattened peg talon is associated (Fig. 9c & d). The first incubatory chamber is formed by the development of finely granular calcified walls from the periphery of the plate (Fig. 9e & f). A secondary plate develops below the embryos and forms the distal part of the next brood chamber. This second stage chamber has an undulating thick rim surrounding a flat distal plate and no talon (Fig. 9g & h). There is no marked bilateral asymmetry as in the earlier forms. The wall of an empty chamber in reflected light shows rather widely spaced longitudinal markings (Fig. 9h). When damaged the chamber tends to break in the position of these lineations (Fig. 9j).

*Thorax* with the dorsal margins of the collar unfused. Collar setae on the convex side have simple, finely serrate blades (Fig. 9k). Those on the concave side (Fig. 9l) resemble those of the second and third fascicles (Fig. 9m) in being simple with almost smooth margins. Capillary setae are also present in the first fascicles. Two pairs of tori. Uncini with four longitudinal rows of teeth and a strongly trifurcate anterior peg (Fig. 9o).

*Abdomen* with about ten pairs of tori and uncini with about ten longitudinal rows of teeth, some of which obscure the anterior peg (Fig. 9p). Setae large and obliquely geniculate (Fig. 9n). Secondary setae (Fig. 9q) occasionally present.

*Setation* (Figs 6f & 7f) as in most *Janua*.

*Incubation* about six to eight embryos in the opercular chamber.

LOCATIONS. Twenty-nine specimens from Brighton (including types) and nine from Sou' West River on a small red alga, *Hypnea* (possibly *muciformis*) presumed to have been cast ashore from the sublittoral zone. Collected by L. C. Llewellyn January 1967.

HOLOTYPE. British Museum (Nat. Hist.) Reg. No. ZB 1971: 19 & 19a.

PARATYPES. British Museum (Nat. Hist.) Reg. No. ZB 1971: 20. Australian Museum Reg. No. W4478.

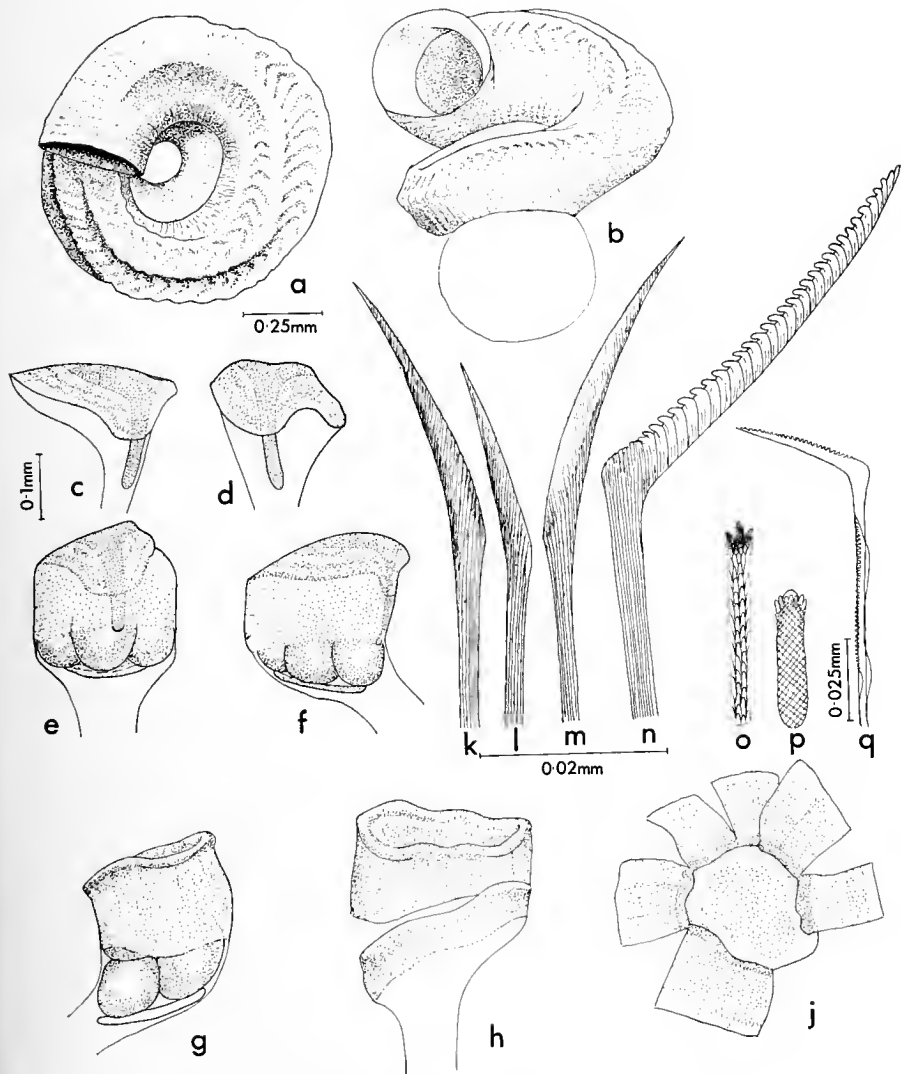


FIG. 9. *Janua (Pillaiospira) trifurcata* sp. n. a) tube viewed from above; b) tube, side view (attached to an algal filament seen in cross-section); c) juvenile operculum, side view; d) as c, but viewed dorsally; e) first stage mature operculum with embryos dorsal view; f) as e, but side view; g) second stage mature operculum with embryos; h) second stage mature operculum showing dehiscence (presumably after release of embryos) and the developing brood chamber below; j) a smashed brood chamber, showing tendency to break into sections resembling staves of a barrel; k) collar seta from convex side; l) collar seta from concave side; m) seta representative of second and third fascicles; n) abdominal seta; o) thoracic uncinus; p) abdominal uncinus (cross-hatching denotes teeth so small as to be almost beyond resolution by light microscope); q) secondary seta lying alongside shaft of an abdominal seta.

Scales: b) as a); d), e), f), g), h) and j) as c); l), m), n), o) and p) as k).

REMARKS. This species is very unusual amongst its close relatives, in having a marked difference between the shape of the distal plate in the first and second stage brood chambers, and somewhat unusual in having well defined three-pronged anterior pegs to the thoracic uncini. The only other forms described as having such anterior pegs are *Janua nipponica* (Okuda, 1934) and those from South Africa reported by Day (1961) as *Spirorbis foraminosus*. Japanese material thought to be the former species, but labelled *Spirorbis alveolatus* (see p. 253) was kindly supplied by Dr M. Imajima of the National Science Museum, Tokyo. The material agreed well with Okuda's description but also contained young forms (not previously described) with a rather flat distal plate and a broad, faintly bifid talon reminiscent of that in *J. (D.) pseudocorrugata* (Bush) and thus unlike that of *J. (P.) trifurcata*. The first stage incubatory chamber resembles that of most *Janua* (but not that of *J. (P.) trifurcata*) in being bilaterally symmetrical and flat distally, with a distinct fine rim. Later incubatory chambers (with no talon) differ from *J. (P.) trifurcata* only in that the rim is thinner and without undulations, whilst the calcified walls have very closely spaced lineations. The only other notable difference is that the collar folds in *Janua nipponica* were found to be fused. The setae and uncini of both species are very similar.

Professor Day kindly made available a specimen labelled *Spirorbis foraminosus* from Inhaca Island, Mozambique. Its operculum was similar to the juvenile operculum of *J. (D.) nipponica* and its other characters described by Day (he mentioned that the collar is continuous dorsally) agree well with *J. (D.) nipponica*.

The type material from Japanese waters of *Spirorbis foraminosus* Moore & Bush (see p. 253) proved to have uncini with a single anterior peg; faintly cross-striated collar setae; abdominal setae having rather broad (though elongated) blades with very fine recurved teeth and a remarkably slender opercular brood chamber with an unusually large flared rim, to which the elongated tentacles reach. It is thus a *Janua*, but very different from *J. (P.) trifurcata*. The talon figured by Bush could not be seen owing to decalcification in preservative.

The unusual and characteristic pattern of fracture seen in broken opercula of *J. (P.) trifurcata* (Fig. 9j) recalls the description by Langerhans (1880) of a dextral species from Madeira, with simple cylindrical brood chambers, the walls of which were easily smashed into pieces, like the staves of a barrel. He regarded it as possibly related to *Spirorbis corrugatus* (Montagu, 1803). Caullery and Mesnil (1897) also misapplied this name to a dextral species from France, which they thought agreed well with the description of Langerhans, but Bush (1904) pointed out that Montagu's name referred to a sinistral species. In fact Montagu's species was inadequately described, but the grouping of species in his account clearly shows that Bush was right, in spite of what Fauvel (1914) has written to the contrary. Caullery and Mesnil's dextral species, which should now be called *Janua (Dexiospira) pseudocorrugata* (Bush), was collected abundantly from France, Portugal and the Mediterranean and found to have collar folds fused dorsally (Knight-Jones, 1972). It has lightly calcified brood-chamber walls, bearing closely spaced granular lineations, which are indeed arranged longitudinally (as are the staves of a barrel) but do not form lines of fracture. These brood chambers in fact shatter irregularly.



The virtually unnamed description from Madeira does not agree with this but could agree with *J. (P.) trifurcata*. Langerhans noticed that the collar had an entire margin, slit open dorsally, as in the subgenus *Pillaiospira* here defined.

## SUMMARY

The collections, mostly from near Adelaide, included eight previously known species (one *Eulaeospira*, two *Pileolaria* and five *Janua*) and seven new species. The latter represent four existing genera, all of which are redefined. Four new subgenera are also described.

- (1) *Metalaeospira tenuis* **sp. n.** is close to the type of the genus, but has a smooth operculum.
- (2) *Protolaeospira* (including *Marsipospira* and *Pixelia*) is elevated to generic rank. The incubatory stalk characteristic of *Protolaeospira* is found too in the dextral form *P. falklandica* (which is made the type of *P. (Dextralia) subgen. n.*) and in *Helicosiphon*.
- (3) *Protolaeospira (P.) triflabellis* **sp. n.** has  $3\frac{3}{4}$  thoracic setigers and a tube with transverse ridges. *Protolaeospira (P.) canina* **sp. n.** is close to *P. lebruni (=auricularis)*.
- (4) *Romanchella (R.) quadricostalis* **sp. n.** also has an incubatory stalk, similarly located but shorter and funnel-like.

In *R. (Romanchella)* the collar folds are fused dorsally and *R. (Bushiella) subgen. n.* is proposed for northern *Romanchella* spp. which have unfused collars and a more symmetrical distribution of uncini.

*Pileolaria (Simplicaria) subgen. n.* lacks sickle setae.

- (5) *Amplaria spiculosa* **gen. et sp. n.** has  $4\frac{1}{2}$  thoracic setigers, but affinities with *Pileolaria*.
- (6) *Janua (Dexiospira) fenestrata* **sp. n.** has a tube with perforated ridges.
- (7) *Janua (Pillaiospira) trifurcata* **subgen. et sp. n.** (subgenus type by monotypy). The subgenus contains forms close to *J. (Dexicspira)* but with unfused collar folds.

Species (1) and (4) above were particularly numerous and found only on algae. All these southern hemisphere tube-incubators differ from the opercular incubators (and from *Spirorbis*) in having the abdominal uncini distributed asymmetrically.

## ACKNOWLEDGMENTS

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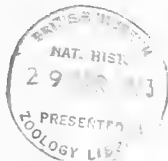
Dr M. Imajima of the National Science Museum, Tokyo; Dr Marian Pettibone of the Smithsonian Institution of Washington; and Dr Peter Vine, who will soon be publishing the results of extensive studies on the Spirorbinae made particularly from the Universities of Townsville and Auckland.

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ON THE CYPRINID FISH  
*BARBUS ALLUAUDI* PELLEGRIN:  
A POSSIBLE INTERGENERIC HYBRID  
FROM AFRICA

STUDIES ON AFRICAN CYPRINIDAE  
PART I



K. E. BANISTER

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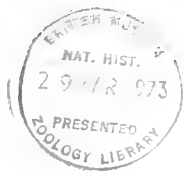




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BY  
KEITH EDWARD BANISTER



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# ON THE CYPRINID FISH *BARBUS ALLUAUDI* PELLEGRIN: A POSSIBLE INTERGENERIC HYBRID FROM AFRICA

## STUDIES ON AFRICAN CYPRINIDAE PART I

By KEITH EDWARD BANISTER

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### INTRODUCTION

WHILE identifying the fishes collected in the Mubuku and Sibwe rivers, Uganda (fig. 1) by Dr. I. G. Dunn of the Royal Society—International Biological Programme African Freshwater Research Team, Lake George, Uganda, I came across two specimens referable to *Barbus alluaudi* Pellegrin 1909. These two specimens were morphologically intermediate between the other cyprinid species collected, *Barbus somereni* Boulenger 1911 and *Varicorhinus ruwenzorii* (Pellegrin) 1909. The two specimens were collected upstream of the road bridge over the Mubuku river near Kasese, Uganda. More specimens were necessary before a full investigation could be pursued and these were obtained by Mr. Paul Ready and Mr. T. Slade of the Imperial College, London University, expedition to the Ruwenzori mountain range in 1971; they collected in the Mubuku and Sibwe rivers and obtained a further eight specimens of *Barbus alluaudi* from the Dunn locality and another specimen from the Sibwe river. The eight *Barbus alluaudi* were caught with 142 *Varicorhinus ruwenzorii* within a 30 yards stretch of river upstream from the road bridge.

Between these two events I had examined the types of *B. alluaudi* which were kindly loaned to me by Madame M. L. Bauchot of the Paris Museum. These two specimens were collected in the Wimi river (=Ruimi river) which is on the eastern flank of the Ruwenzori Mountain range (fig. 1).\*

Hybrids between the genera *Barbus* and *Varicorhinus* have been reported before (Steinitz and Ben Tuvia, 1957, from Israel; although Karaman, 1969, has now placed *Varicorhinus damascinus* in the genus *Capoeta*). Demetrashvili (1963) noted

\*The Wimi river does not appear on any modern maps. I have, however, been able to establish that it is an old name for the Ruimi river thanks to the detailed description of the expedition of Prince Luigi by Filippi (1908).

a hybrid between *Cyprinus carpio* L. and *Varicorhinus capoeta* Berg (*Capoeta capoeta* fide Karaman *op. cit.*) from the Khramsk reservoir, Georgia, U.S.S.R.

Slastenenko (1957) in his list of natural fish hybrids of the world does not list any hybrids between the genera *Varicorhinus* and *Barbus*.

In this paper I intend to offer evidence to support my hypothesis that specimens referred to the nominal species *Barbus alluandi* are hybrids between *Barbus somereni* and *Varicorhinus ruwenzorii*.

It would seem that our knowledge of African freshwater fishes has only recently reached the stage at which hybrids can be determined. Hubbs (1955) predicted the presence of hybrids in African fishes and suggested that they may have been misidentified as distinct and rare species. Hybrids have been described for *Tilapia* (see bibliography in Elder, Garrod and Whitehead 1971) but *Tilapia* has long been cultivated in ponds and special emphasis has been placed on its systematics because of its commercial importance. Jubb (1967 : 119) mentions a fish taken from a dammed stretch of river at Roodewal farm, Piet Retief district, South Africa

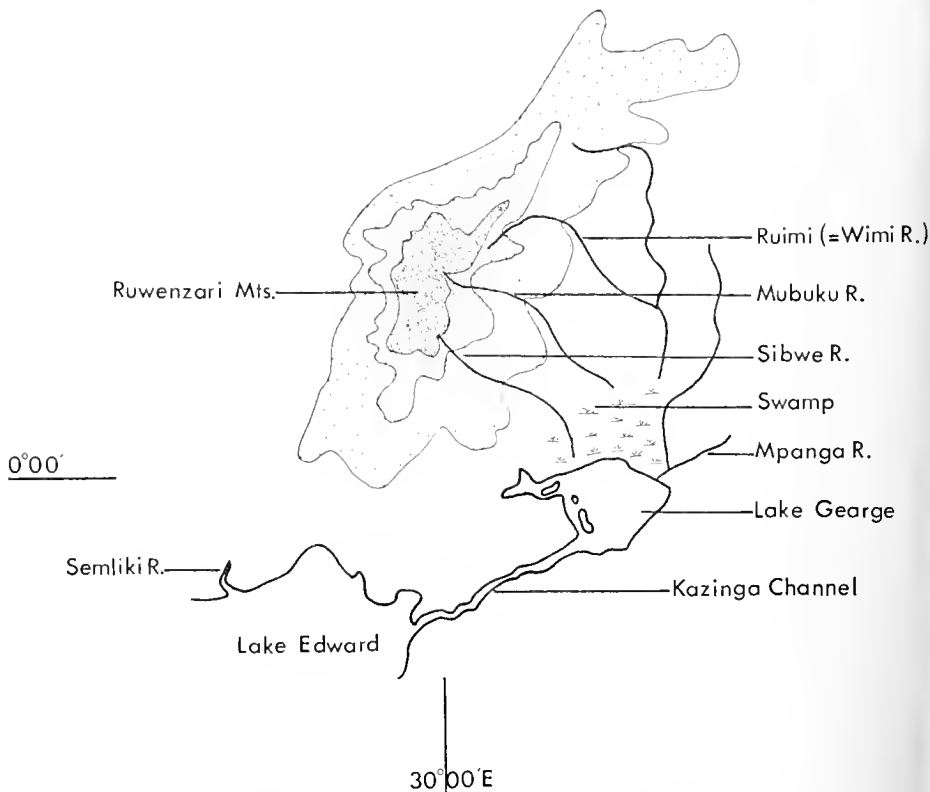


FIG. 1. A sketch map of the Ruwenzori region showing the rivers mentioned in the text.

(Maputo system), which he thought was a natural hybrid between *Varicorhinus nelspruitensis* Gilchrist and Thompson and *Barbus polylepis* Boulenger. I have not been able to examine this fish, but Jubb was of the opinion that hybridisation occurred as a result of the alteration of the environment; however, further specimens (Jubb, 1968) led Jubb to the conclusion that it was a natural variety of *B. polylepis*.

It may be noted that African *Barbus* and *Varicorhinus* have been, to some extent, problem genera. Groenewald (1958) demonstrated that in certain circumstances *Barbus* can achieve a 'Varicorhinus'-like appearance, especially of the mouth.

It is not my intention in this paper to define the generic limits of either genus, but work is in progress on this problem and it is here implied that *Barbus somereni* and *Varicorhinus ruwenzorii* rightly belong in separate genera.

#### MATERIALS AND METHODS

A total of 63 specimens of *Varicorhinus ruwenzorii*, including the types, were examined. Two of these specimens were prepared by the alizarin technique and used in the osteological descriptions. Fifty one *Barbus somereni*, including the holotype, were examined and two were prepared by the alizarin technique.

One specimen of *Barbus alluaudi* BM(NH) No. 1971.1.5 : 135 was first partially dissected to study the jaw muscles and ligaments and then prepared by the alizarin method.

The standard length (S.L.) was taken as the distance from the end of the snout to the end of the hypural bones. This distance was measured with dial calipers. The eye diameter (I) was measured as the horizontal distance across the eye. In long-preserved specimens the tissues around the eye had shrunk and exposed more of the orbit so that, in this paper, the eye diameter was only measured on specimens sufficiently fresh for there to be no noticeable wrinkling or shrinking of the tissues around the eye. The eye diameter ratio in long preserved specimens was the same in *Barbus somereni* as in *Varicorhinus ruwenzorii*, the differences were only noticeable in the fresh material. The mouth width (M.W.) is the greatest width of the lower jaw. The head length (H) is the horizontal distance from the anterior margin of the snout to the posterior extremity of the operculum. The interorbital width (I.O.) is the least distance across the bony part of the interorbital space. The dorsal fin 'spine' (D.Sp.)—the last unbranched ray—was measured from its base to the proximal articulation which is almost always at the base of the flexible tip of the ray. Where measurements were repeatable and different on both sides of the specimen, the larger one was accepted unless the structure measured showed signs of gross abnormality.

Sections were cut of the testes of a *Barbus somereni* and of a *Barbus alluaudi*; some were stained with haemalum and eosin, whilst others were stained with Feulgen and light green in an attempt to show the presence of D.N.A.

Radiographs were taken of all three species. The vertebral counts include all the vertebrae from the first to P.U.<sub>2</sub> of Rosen and Greenwood (1970). This includes the four vertebrae involved in the Weberian mechanism and excludes all after and including P.U.<sub>2</sub>—the vertebra which supports the parhypural. The abbreviations

used in the text and not mentioned above are Ab = anterior barbel; Pb = posterior barbel; N = the number of specimens considered.

#### THE PUTATIVE PARENT SPECIES

An interesting feature shared by the putative parent species and by *B. alluaudi* is the colour pattern. This is a deep olive-brown on the back which changes sharply into an ochreous yellow on the flanks and then fades on the belly. The dark olive of the back, however, is continued on to the lower lobe of the caudal fin. The upper lobe of the caudal fin and the dorsal fin are pale brown.

Specimens that have been stored in alcohol for a long time become uniformly brown.

A small specimen of *Varicorhinus ruwenzorii* (less than 40 mm S.L. and not included in the data) has a colour pattern consisting of a grey back, a dark lateral stripe ending in a dark spot on the caudal peduncle, and pale flanks and belly. There is just a trace of dark pigment on the caudal fin.

#### *Barbus somereni* Boulenger 1911

##### Plate 1a

**HOLOTYPE.** A fish of 172 mm S.L. BM(NH) 1911.7.26 : 1 from the Sibwe River, Ruwenzori mountains, Uganda.

There is no significant difference between certain morphometric ratios in *Barbus somereni* and in *Varicorhinus ruwenzorii*, so the only data discussed are those in which there is a noticeable difference.

The size range of the 51 specimens examined was from 66 to 279 mm S.L. The specimens came from the Sibwe river, Mubuku river, Tokwe river, Kirimia river and Ruimi river.

TABLE I

	N	$\bar{x}$	Range	S	Se
H	51	25.9	21.6-28.8	1.4	0.2
I	22	5.15	4.3- 6.6	0.7	0.14
M.W.	51	7.5	6.3- 9.2	0.8	0.14
Ab.	51	7.8	5.6- 9.6	1.0	0.1
Pb.	51	7.8	6.3-11.6	1.2	0.2
D.Sp.	51	13.8	8.7-21.2	2.9	0.4

All measurements are expressed as percentages of the standard length.

The mouth (fig. 2) is subterminal and horseshoe shaped. The anterior margin of the lower jaw is curved, the lips are soft, continuous and not usually enlarged. The isthmus extends a long way forward and the muscles are covered only by a thin layer of tissue below the skin.

The barbels are long and fleshy. The snout is gently curved and does not noticeably overhang the mouth. The eyes are usually visible in ventral view. The dorsal

fin has its origin in advance of the pelvic fins. It has four unbranched rays, the last one of which is ossified into a smooth spine. There are nine or ten branched rays.

The anal fin has three or four unbranched rays. The first ray, in the fishes with four rays, is extremely small and hidden below the skin so that it is only visible in radiographs or alizarin transparencies. The scales of *Barbus somereni* bear striae which do not conform neatly to either of the three divisions described by Boulenger (1911a). The striae on the exposed part of the scale vary between typically parallel and typically radiate; the number modally is about 18. In each case the fifth scale from the row above the lateral line has been examined. The buried portion of the scale has about the same number of striae but they are disposed more radially (fig. 3).

The number of scales in the lateral line varies from 26 to 34: 26 (f.1); 27 (f.2); 28 (f.3); 29 (f.5); 30 (f.11); 31 (f.12); 32 (f.7); 33 (f.7); 34 (f.1). This is expressed graphically in fig. 22.

There are twelve scales around the caudal peduncle;  $5\frac{1}{2}$  (sometimes  $4\frac{1}{2}$ , rarely  $6\frac{1}{2}$ ) between the mid-dorsal line and the lateral line and  $4\frac{1}{2}$ – $6\frac{1}{2}$  (very rarely  $7\frac{1}{2}$ ) between the lateral line and the mid-ventral line. Two and a half to  $3\frac{1}{2}$  (modally 3) scale rows are present between the lateral line and the base of the pelvic fin.

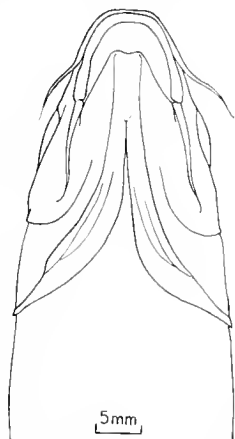


FIG. 2. The underside of the head of *Barbus somereni*.

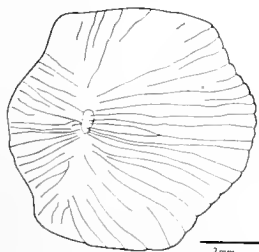


FIG. 3. A scale from the shoulder of *Barbus somereni* showing the position of the striae.

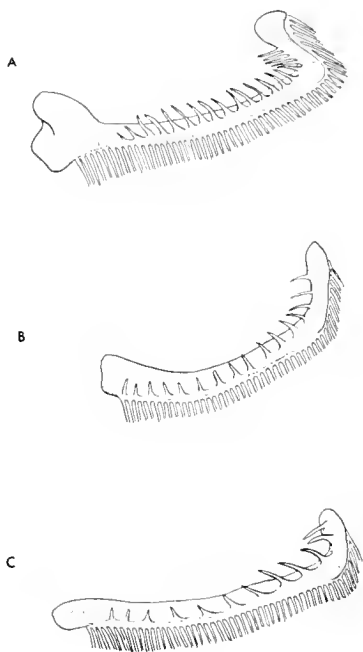


FIG. 4. Lateral aspects of the first gill arch in (a) *Varicorhinus ruwenzorii*, (b) *Barbus alluaudi*, (c) *Barbus somereni*.

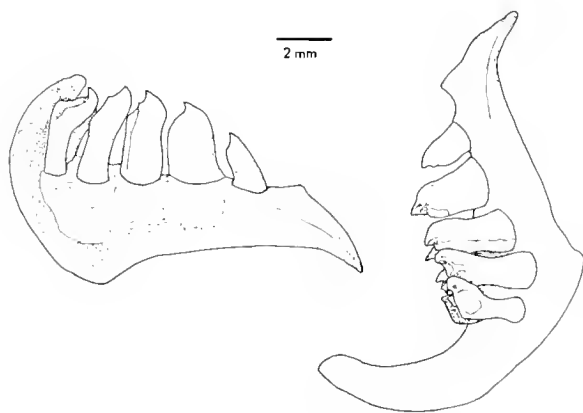


FIG. 5. The left pharyngeal bone of a *Barbus somereni* of 170 mm S.L.



The gill rakers on the first gill arch (fig. 4C) number modally  $10 + 2$  within the range  $8 + 2$  and  $11 + 2$ . They are strong and slightly hooked. The second tooth in the inner pharyngeal row of a specimen 170 mm S.L. shows no significant molarisation. The first tooth is stout, about  $\frac{2}{3}$  of the length of the second tooth and angled towards it. Teeth three to five become progressively more recurved with hooked crowns (fig. 5). The teeth of the second and third rows are smaller versions of the third, fourth and fifth teeth of the inner row.

The pharyngeal bone is broad, the anterior process (*sensu* Matthes, 1963) bears a sharp longitudinal ridge on the occlusal face of the bone and a moderately well defined lateral flange is present. The bone in a specimen of 170 mm S.L. measured 16 mm in a direct line from the extremity of the ascending process to the end of the anterior process. The vertebrae in ten specimens examined numbered 37 (f.3); 38 (f.6); 39 (f.1). The 37 vertebrae comprise 20 abdominal + 17 caudal (f.2) or 21 + 16 (f.1), the 38 comprise 19 + 19 (f.1); 20 + 18 (f.1) or 21 + 17 (f.4), the 39 comprise 18 + 21.

#### Suspensorium and jaws

An exploded diagram of the suspensorium is shown in fig. 6.

The dentary is long with a large based coronoid process. The rami of the lower jaw (fig. 7) smoothly taper rostrad and gently curve in towards their symphysis. The dotted line in fig. 7 represents the outer limit of the lower lip.

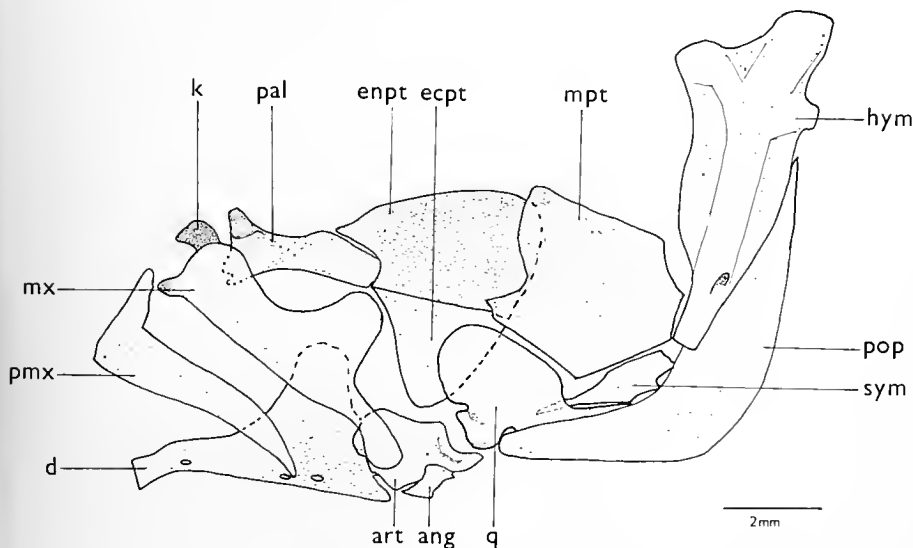


FIG. 6. A diagram of a partially disarticulated suspensorium of *B. somereni*. ang = angular; art = articular; d = dentary; ecpt = ectopterygoid; enpt = endopterygoid; hym = hyomandibula; mpt = metapterygoid; mx = maxilla; pal = palatine; pmx = premaxilla; pop = preoperculum; q = quadrate; sym = symplectic; k = kinethmoid.

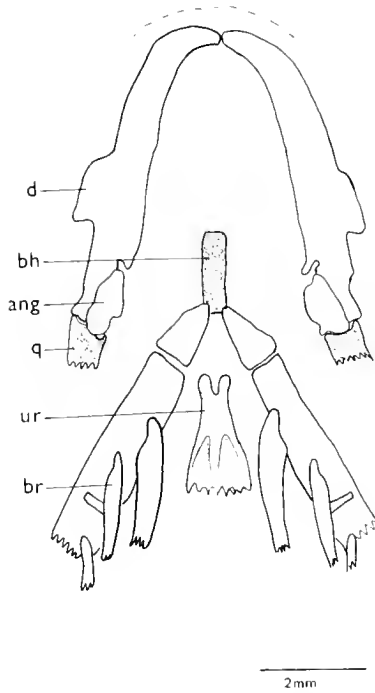


FIG. 7. Ventral aspect of the head and hyoid region of an alizarined specimen of *B. somereni*. Key as in fig. 6 except, br = branchiostegal ray; bh = basihyal; ur = urohyal. The dotted line indicates the edge of the lower lip.

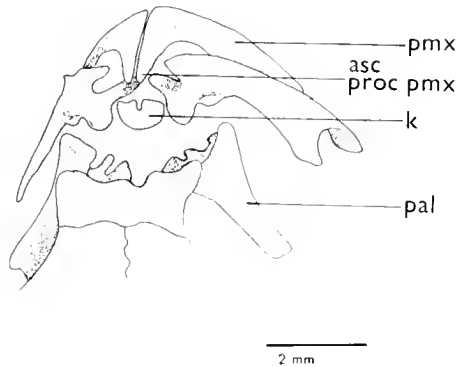


FIG. 8. Dorso-lateral view of the upper jaws and ethmoid region of *B. somereni*. asc proc pmx = ascending process of premaxilla.

The premaxilla (figs 6 & 8) has an ascending process approximately as long as the labial part of the premaxilla is deep.

#### Visceral cavity

The colour of the peritoneum in preserved specimens varies from light grey to dark grey. Matthes (1963) comments that the peritoneum is darker in herbivorous fishes than in carnivorous fishes. Steinitz and Ben Tuvia (1957) have noted that the peritoneum is black in *Varicorhinus damascinus* C. and V. but lighter in *Barbus longiceps* C. and V. and intimate that this character is not of any value in the problem under investigation, because of its variability. The cause of the variability is unknown but may reflect the *in vivo* state or may be the result of post mortem changes.

The alimentary tract of five specimens was measured with the following results: 200 mm S.L.—gut length 700 mm; 178 mm S.L.—gut length 570 mm; 168 mm S.L.—gut length 400 mm; 160 mm S.L.—gut length 350 mm; 160 mm S.L.—gut length 300 mm. This gives an overall gut to standard length ratio of from 1.9 to 3.5. All these specimens came from the Sibwe river. The gut length was only measured to the nearest 10 mm as in some specimens decay had started before fixation became effective and the gut had to be reconstructed, hence precise measurements would be meaningless.

#### Habitat

Little is known of the habitat of *B. somereni*. Greenwood (1966) states that it is found in streams up to an altitude of 5,500 feet. The Imperial College expedition noted that in the River Sibwe *B. somereni* would be found in stretches of fast, deep, smooth water without boulders. The food seemed mostly to be insects.

#### *Varicorhinus ruwenzorii* (Pellegrin) 1909

##### Plate 1(b)

*Varicorhinus ruwenzorii* was described by Pellegrin as *Capoeta* (*Pterocapoeta*) *ruwenzorii* from three specimens from the Wimi river; Paris Museum Nos. 09-583, 09-584, 09-585 of standard lengths 67, 70 and 65 mm respectively.

The size range of the specimens examined was from 57-231 mm S.L.

TABLE 2

	N	$\bar{x}$	Range	S	Se
H	63	21.87	19.2-30.2	1.54	0.33
I	32	3.9	2.8- 4.85	0.55	0.09
M.W.	63	9.07	7.5-10.2	1.02	0.22
Ab.	63	—	—	—	—
Pb.	63	—	—	—	—
D.Sp.	63	7.6	5.9-11.4	1.75	0.38

All measurements are expressed as a percentage of the standard length.

The anterior barbel is invariably absent. The posterior barbel is usually present as a small protuberance, too small to measure, at the corner of the mouth.

The mouth is wide and ventral. The anterior margin of the lower jaw is nearly straight in fishes of over 60 mm S.L. (fig. 9) and its horny covering is visible. In a specimen of 40 mm S.L. the lower jaw is more rounded anteriorly and lacks the horny edge.

The isthmus is short and the anterior gular surface has a smooth, padded appearance due to the presence of fatty deposits between the skin and the muscles. The snout is fleshy and overhangs the mouth, forming a rostral flap (Matthes, 1963). There is a well marked rostral groove in front of the upper jaw. The eye is small and not visible from below. The dorsal fin has its origin in front of the pelvic fin. There are four unbranched rays, the last one is weaker than in *Barbus somereni*, thinner and with persistent articulations throughout the distal two-thirds. There are nine or ten branched rays. The anal fin has three unbranched and five branched rays.

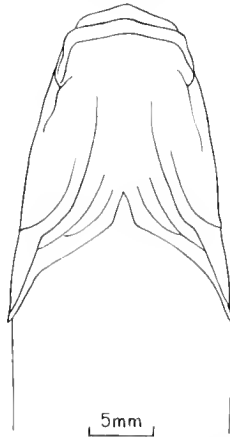


FIG. 9. Ventral view of the head of *Varicorhinus ruwenzorii*.

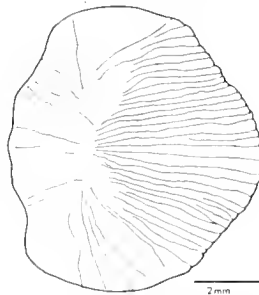


FIG. 10. A scale from the shoulder of *Varicorhinus ruwenzorii* showing the position of the striae.

The scales (fig. 10) have many more striae on the exposed part of the scale than in *Barbus somereni*. The fifth scale from the row above the lateral line has 34 striae on the posterior part of the scale but only a few incomplete striae on the anterior part.

There are from 38 to 44 scales in the lateral line; 38 (f.3); 39 (f.18); 40 (f.17); 41 (f.17); 42 (f.5); 43 (f.2); 44 (f.1). This is expressed graphically in fig. 22. There are from 12 to 15 scales around the caudal peduncle, 12 (f.33); 13 (f.16); 14 (f.10); 15 (f.1). There are  $6\frac{1}{2}$  (rarely  $5\frac{1}{2}$ ) scale rows from the mid-dorsal line to the lateral line, and from  $7\frac{1}{2}$  to  $10\frac{1}{2}$  scale rows between the lateral line and the mid-ventral line. The size of the scale rows on the ventral surface varies considerably and in some cases the scales are very reduced. Four scale rows (rarely  $3\frac{1}{2}$  or  $4\frac{1}{2}$ ) are present between the lateral line and the base of the pelvic fin.

The gill rakers on the first gill arch (fig. 4A) range from 16-18 + 4 in number and are long and fine.

The pharyngeal bones (fig. 11) are very much shorter than in equal sized specimens of *Barbus somereni*; the bones illustrated, from a specimen of 166 mm S.L. (c.f. *Barbus somereni* of 170 mm S.L.) measured only 9.7 mm from tip to tip (see page 269), less than  $\frac{2}{3}$  of the measurement in *Barbus somereni*.

All the specimens examined had four teeth in the inner row. The teeth tend to be longer and thinner than their counterparts in *Barbus somereni* but are of the same general pattern. The teeth are more crowded in *V. ruwenzorii* than in *B. somereni*. There is hardly any lateral flange in the former species. The other differences in shape can be seen by comparing figs 5 and 11.

The vertebral number is 38 (f.1); 39 (f.6) and 40 (f.3) in the ten specimens radiographed. The 38 vertebrae comprise 18 abdominal + 20 caudal, the 39 comprise

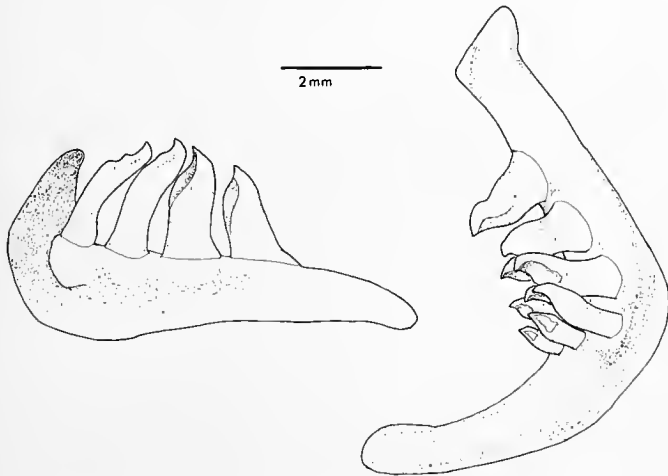


FIG. 11. The left pharyngeal bone of a specimen of *V. ruwenzorii* of 166 mm S.L. Compare with fig. 5.

19 + 20 (f.1) or 20 + 19 (f.5) and the 40 vertebrae comprise 20 + 20 (f.2) and 21 + 19 (f.1).

### Suspensorium

A diagram of a slightly disarticulated suspensorium is given in fig. 12. The symplectic and preopercular are shorter than in *B. somereni*; generally the bones are thicker and more robust.

The rami of the lower jaw (fig. 13) are very much stouter than in *B. somereni* and anteriorly bend sharply, almost at a right angle, towards the symphysis. The dotted line in fig. 13 represents the anterior extent of the horny edge of the lower jaw. The second branchiostegal ray in fig. 13 is not in its life position but as a result of maceration is on its side and therefore appears thicker than in its normal position.

The premaxilla in *V. ruwenzorii* is much stouter than in *B. somereni* and lacks the ascending process (fig. 14). The maxilla is of the same fundamental shape in both species and its articulations are similar.

### Visceral cavity

The peritoneum varies from black to grey, the range is such that its value as a taxonomic character is small. *Varicorhinus ruwenzorii* appears to feed largely on diatoms. The gut length in three specimens was measured with the following

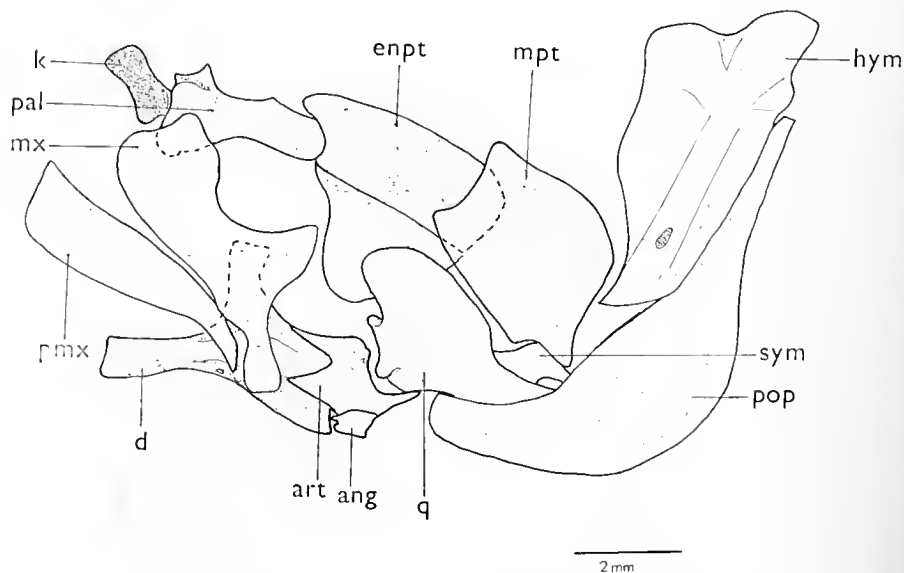


FIG. 12. A diagram of a partially disarticulated suspensorium of *V. ruwenzorii*. Key as in fig. 6.

results; S.L. 157 mm—gut length 580 mm; S.L. 160 mm—gut length 740 mm; S.L. 162 mm—gut length 635 mm. This gives a gut/standard length ratio of from  $3\frac{1}{2}$  to  $4\frac{1}{2}$ .

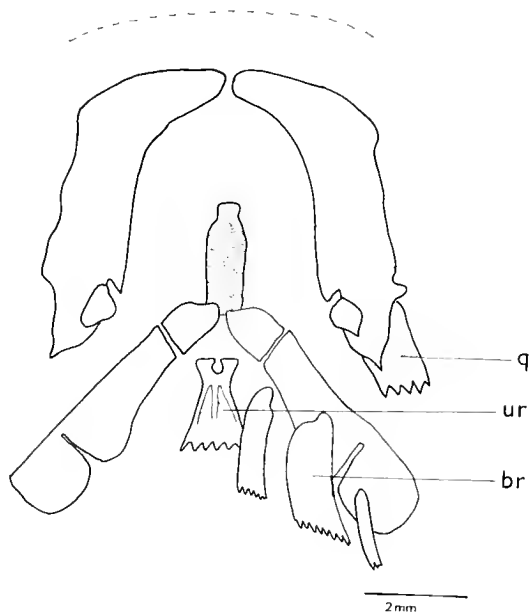


FIG. 13. The lower jaw and hyoid region of *V. ruwenzorii*. Key as in fig. 7.

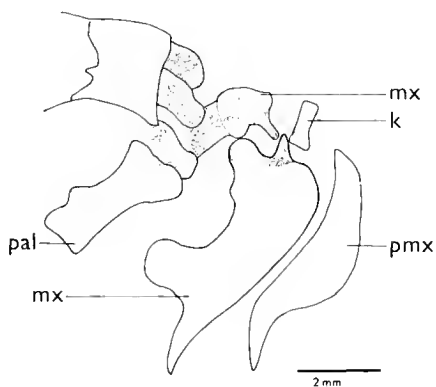


FIG. 14. Dorso-lateral view of the upper jaws and ethmoid region of *V. ruwenzorii*. Key as in fig. 6.

## Habitat

*Varicorhinus ruwenzorii* was most frequently encountered by the Imperial College expedition in stretches of fast turbulent broken water with many boulders behind which the fishes sheltered.

***Barbus alluaudi*** Pellegrin 1909

## Plate 1(c)

*Barbus alluaudi* was based on two small fishes from the Wimi (=Ruimi) river; Paris Museum Nos. 09-586 and 09-587 of S.L. 67 and 58 mm respectively. The size range of the 13 specimens examined is from 58 mm to 198 mm S.L. The nine specimens collected by the Imperial College expedition are in the 168 mm to 198 mm S.L. range. The two specimens collected by Dr. I. G. Dunn are of 67 mm and 106 mm S.L.

TABLE 3

	N	$\bar{x}$	Range	S	Se
H	13	23.1	21.1-27.6	2.03	0.56
I	10	4.14	3.8- 5.0	0.33	0.1
M.W.	13	7.50	6.9- 8.1	0.42	0.13
Ab.	11	2.25	+ - 3.0	0.60	0.18
Pb.	13	3.05	2.7- 4.7	0.71	0.19
D.Sp.	12	10.27	8.5-13.8	2.05	0.85

All measurements are expressed as percentages of the standard length.

The mouth is ventral, its width modally about the same as in *B. somereni* but the lower jaw is not so long, nor is its anterior curvature so extreme. There is no horny covering, but the anterior edge of the lower jaw is firm and sharp. As can be seen in fig. 15, the development of the isthmus is intermediate between that of each of the putative parent species, and a certain amount of firm fatty tissue is present between the dentaries. A rostral flap is developed but is less marked than in *V. ruwenzorii*. The eyes are just visible in ventral view in some of the specimens and just hidden in others.

There are four barbels. In 09-587, a Paris Museum specimen of *B. alluaudi*, the anterior barbel is present only on one side; in other specimens the anterior barbels are present although they are about as small as the posterior barbels of *V. ruwenzorii*. The barbels are fleshy and clearly visible.

The dorsal fin has four unbranched rays. The last ray is ossified and intermediate in length and strength between this ray in the putative parent species. The number of branched rays varies from 8 to 10; 8 (f.1); 9 (f.9); 10 (f.3). The anal fin has three unbranched rays and five branched rays. The dorsal fin origin lies anterior to the pelvic fin origin.

The number of striae on the exposed part of the scales examined, and their distribution is intermediate between that of *B. somereni* and *V. ruwenzorii*; 26 striae



are present on the fifth scale of the row above the lateral line (fig. 16). The striae on the buried portion of the scale are radiately disposed and are stronger than in *V. ruwenzorii*. The lateral line has from 35 to 38 scales; 35 (f.4); 36 (f.5); 37 (f.6); 38 (f.1). Three specimens have different counts on either side. There are 12 (f.9) or 13 (f.4) scales around the caudal peduncle. There are  $5\frac{1}{2}$  (f.4) or  $6\frac{1}{2}$  (f.9) scale rows between the mid-dorsal line and the lateral line and  $6\frac{1}{2}$  (f.2);  $7\frac{1}{2}$  (f.6) or  $8\frac{1}{2}$  (f.1) scales between the lateral line and the mid-ventral line. Between the lateral line and the base of the pelvic fin there are  $3\frac{1}{2}$  (f.7) or 4 (f.6) scales.

The gill rakers number between  $11 + 3$  and  $14 + 3$  on the first gill arch (fig. 4B).

The pharyngeal bones (figs 17 and 18) are intermediate in size between those of *B. somereni* and *V. ruwenzorii*. The bone shown in fig. 17 from a specimen of 173 mm S.L. measures 14 mm from tip to tip (see p. 269). The degree of development of the lateral flange and the shape of the anterior process is intermediate between those of the putative parent species, as is the size of the bone in equal-sized fishes.

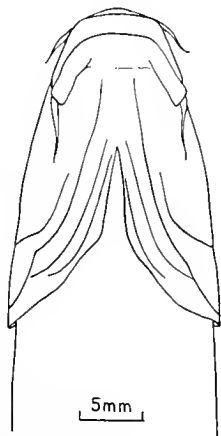


FIG. 15. Ventral view of the head of *Barbus allaudi*.

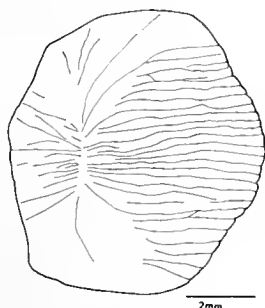


FIG. 16. A scale from the shoulder of *Barbus allaudi* showing the position of the striae.

The bone bears either 5 teeth in the inner row (fishes from the Mubuku and Sibwe rivers) or 4 teeth (the types from the Wimi river). When 5 teeth are present the first tooth in the inner row is smaller than it is in *B. somereni* (cf. fig. 5). The teeth otherwise resemble more closely those of *B. somereni* than they do those of *V. ruwenzorii*. The pharyngeal bones of the types of *B. alluaudi* (fig. 18) have only 4 teeth in the inner row. The shape of the teeth is more like that in *V. ruwenzorii* than in *B. somereni*.

The vertebrae were counted in eight specimens. There are modally slightly fewer vertebrae than in the samples from the putative parent species; 37 (f.2); 38 (f.5); 39 (f.1).

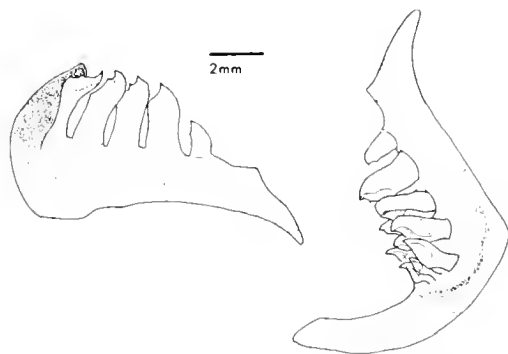


FIG. 17. Left pharyngeal bone from a specimen of *B. alluaudi* of 173 mm S.L. Compare with figs 5 and 11.

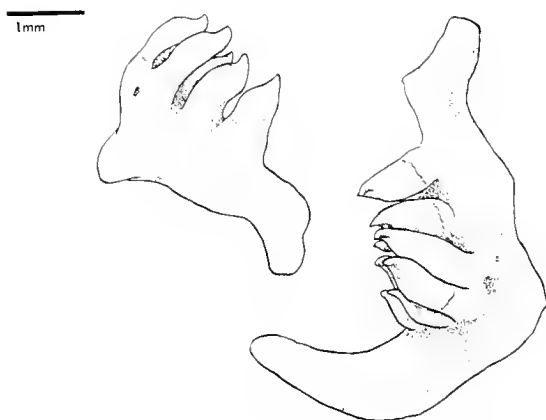


FIG. 18. Left pharyngeal bone from one of the types of *B. alluaudi*.

The 37 vertebrae comprise 18 abdominal + 19 caudal (f.1) or 19 + 18 (f.1); the 38 vertebrae comprise 18 + 20 (f.1); 19 + 19 (f.1); 20 + 18 (f.2) or 21 + 17 (f.1); the 39 vertebrae comprise 20 + 19 (f.1).

### Suspensorium and jaws

A lateral view of a partially disarticulated suspensorium is shown in fig. 19. The symplectic resembles the *B. somereni* condition more than it does the *V. ruwenzorii* condition, whilst the reverse is true of the preoperculum. The quadrate is more compact than in either of the putative parent species.

The ascending process of the premaxilla (fig. 21) is intermediate in length between those of *V. ruwenzorii* and *B. somereni*. The slope at the anterior end of the ethmoid, the curvature of the rami of the lower jaw (fig. 20) and the extent of the lower lip development are also mixtures of the characters in the supposed parents. There is less fat between the rami of the lower jaw than in *V. ruwenzorii*.

### Visceral cavity

The colour of the peritoneum varies considerably from light to dark grey. In any individual specimen the colour is not always uniform; dense black patches of melanin are sometimes present on a paler background.

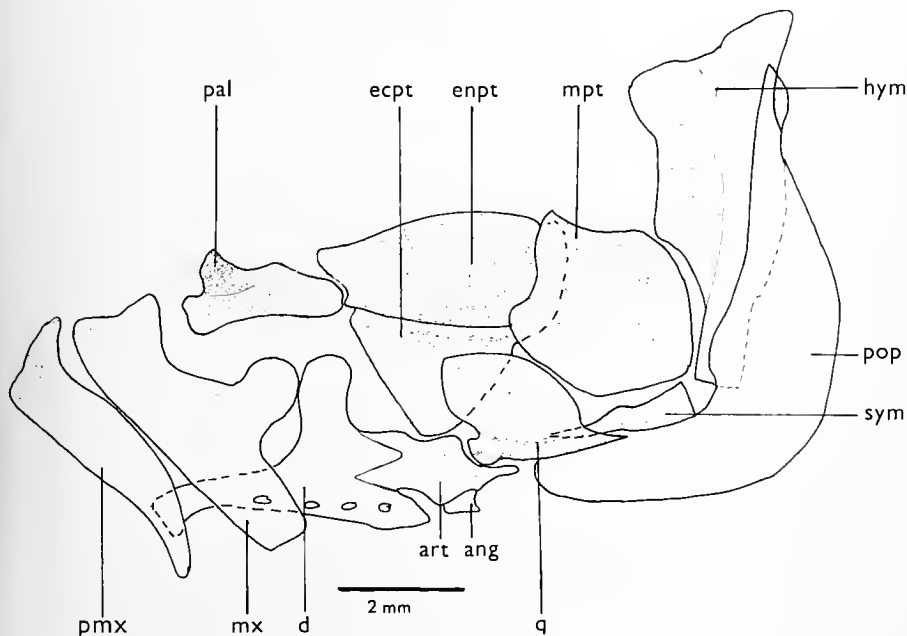


Fig. 19. A diagram of a partially disarticulated suspensorium of *B. alluaudi*. Key as in Fig. 6.

The gut lengths of two specimens were measured with the following results: S.L. 198 mm—gut length 490 mm; S.L. 175 mm—gut length 450 mm. This gives a gut/standard length ratio of about  $2\frac{1}{2}$ , a ratio below that of *V. ruwenzorii* but within the upper part of the range of *B. somereni*.

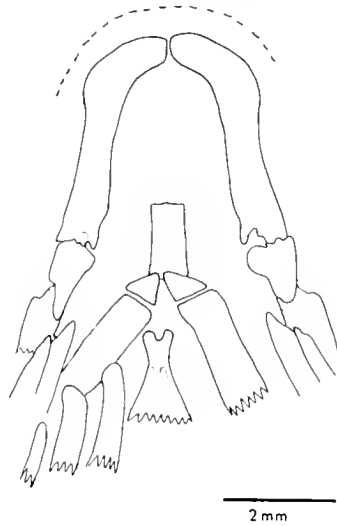


FIG. 20. The lower jaw and hyoid region of *B. alluaudi*.

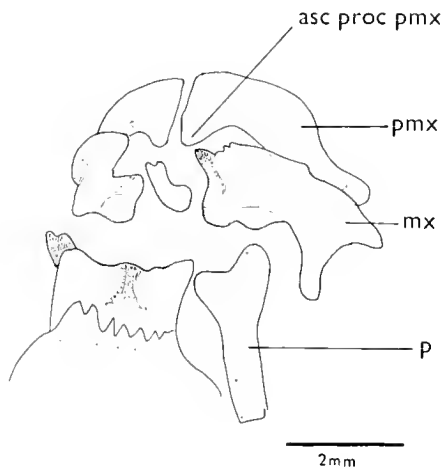


FIG. 21. Dorso-lateral view of the upper jaw and the ethmoid region of *B. alluaudi*. Key as in fig. 8.

### Habitat

The Imperial College expedition specimens were caught in turbulent water about six feet deep in an area slightly sheltered from the main force of the stream. The bed of the river was largely composed of small stones.

### DISCUSSION

It would seem from the differences between *Barbus somereni* and *Varicorhinus ruwenzorii* that there can be no doubt as to their specific integrity. It is most unlikely that the consistent differences in scale counts, dorsal spines and pharyngeal teeth could represent less than specific distinction, although the mouth form and its associated structures could, arguably, be the result of particular responses to the environment (Groenewald, 1958).

At the outset I must admit that all the evidence for the suggested hybridisation between these species is circumstantial. Breeding experiments would help to strengthen the hypothesis but these are, for the moment, impractical and I have had to rely heavily on the morphological intermediacy of the *B. alluaudi* specimens. The morphological intermediacy of aquarium bred hybrids has been noted before (e.g. Holčík and deWitt, 1962a, 1962b; Hubbs and Hubbs, 1932; Hubbs and Miller, 1952). The morphological intermediacy of hybrids in the wild has been described by Hubbs (1955).

I have used the Schultz and Schaefer technique (1936) for estimating the probability of morphological characters in the hybrids falling within the known range of variability for these characters in the putative parent species.

The absence of information on hybrids from African freshwaters can have at least two possible explanations. The study of African fish systematics lags behind that for North America and Europe. Secondly, there are many more species and species flocks in Africa than in the colder northern waters and this also makes the identification of hybrids more difficult.

Hubbs, Hubbs, and Johnson (1943) quote for the North American ostariophysans *Catostomus macrocheilus* and *C. syncheilus*, the proportion of hybrids to parent species collected from the same river system as respectively 6.4 and 4.2 per cent. Nelson (1968) gives a figure of approximately 7.0 per cent as the abundance of hybrids in the combined parental population for *Catostomus commersonii* and *C. macrocheilus*. Hubbs, Hubbs and Johnson (*op. cit.*) state that some hybrids are much rarer and perhaps one catostomid in a hundred on the average is an inter-specific hybrid in parent sympatric areas.

In the short stretch of the River Mubuku where the Dunn and Imperial College collection were made, *V. ruwenzorii* was the only putative parent species caught. The latter collectors found nine *B. alluaudi* specimens amongst 142 *Varicorhinus ruwenzorii*, a proportion of 6.4 per cent.

*Barbus alluaudi* is much rarer in the wild than either *Barbus somereni* or *Varicorhinus ruwenzorii* and it is known from only three localities. At one of the localities (the Mubuku river) its relative abundance is of the same order of magnitude as the relative abundance of the hybrid catostomids in North America. These facts,

coupled with the conspicuous morphological intermediacy between *B. somereni* and *V. ruwenzorii* possessed by *B. alluaudi* suggest that it is unlikely that *B. alluaudi* is a good species.

My arguments for the hybrid origin of *B. alluaudi* are similar to those of Hubbs and Miller (1952) for the hybrid origin of the catostomid *Xyrauchen uncomphagre*. Hubbs and Miller (*op. cit.*) rely on the infrequent occurrence of the nominal species in the wild, its association with the species whose characters it shares and the intermediacy of its characters between those of its associated, putative parent, species.

The possibility that *B. alluaudi* represents an extreme example of either parent species must now be considered. The techniques of Schultz and Schaeffer (1936) and of Hubbs, Hubbs and Johnson (1943) have been used here to evaluate the probability of a *B. alluaudi* character falling within the range of variation for that character in either of the putative parent species. The results are shown in Table 4.

TABLE 4

Character	N	$\bar{x}$	S	%R	%S	P
<b>H</b>						
<i>V. ruwenzorii</i>	63	21.87	1.54			0.1
<i>B. alluaudi</i>	13	23.10	2.03	69	31	
<i>B. somereni</i>	51	25.89	1.40			0.1
<b>I</b>						
<i>V. ruwenzorii</i>	32	3.93	0.55			.30
<i>B. alluaudi</i>	10	4.14	0.33	83	17	
<i>B. somereni</i>	22	5.15	0.68			.01
<b>I.O.</b>						
<i>V. ruwenzorii</i>	63	8.48	0.55			.04
<i>B. alluaudi</i>	13	8.13	0.51			
<i>B. somereni</i>	51	8.47	1.13			.33
<b>M.W.</b>						
<i>V. ruwenzorii</i>	63	9.07	1.02			.01
<i>B. alluaudi</i>	8	7.50	0.42	1	99	
<i>B. somereni</i>	51	7.48	0.84			.95
<b>D.Sp.</b>						
<i>V. ruwenzorii</i>	63	7.60	1.75			.01
<i>B. alluaudi</i>	8	10.27	2.05	57	43	
<i>B. somereni</i>	51	13.84	2.91			.01
<b>Ab.</b>						
<i>V. ruwenzorii</i>	63	—				
<i>B. alluaudi</i>	8	2.25	0.60			
<i>B. somereni</i>	51	7.83				.01
<b>Pb.</b>						
<i>V. ruwenzorii</i>	63					
<i>B. alluaudi</i>	8	3.05	0.71			
<i>B. somereni</i>	51	8.56	1.20			.01

For the characters H, I, M.W. and D.Sp. the mean for *B. alluaudi* lies between the means for the other two species. The per cent R refers to the percentage distance of this mean from the mean for *V. ruwenzorii* and per cent S refers to the percentage distance from the mean for *B. somereni*. Thus a per cent R of 50 indicates the *B. alluaudi* lies exactly halfway between the other two. The probability, P, refers to the probability of observing a mean equal to the *B. alluaudi* value had the sample come from one of the other two species. Thus, for H, the probability of observing a mean of 23.10 is 0.1 for *V. ruwenzorii* and 0.1 for *B. somereni*. A low value of P

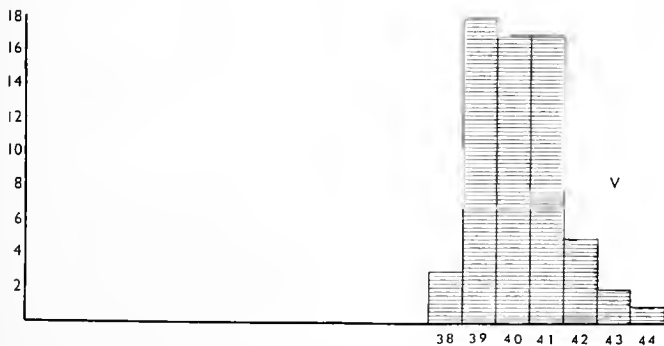
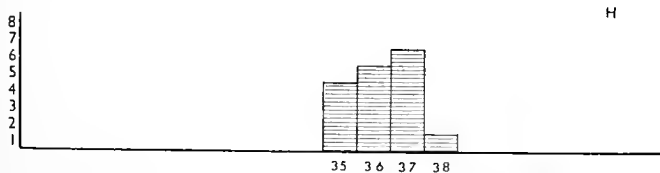
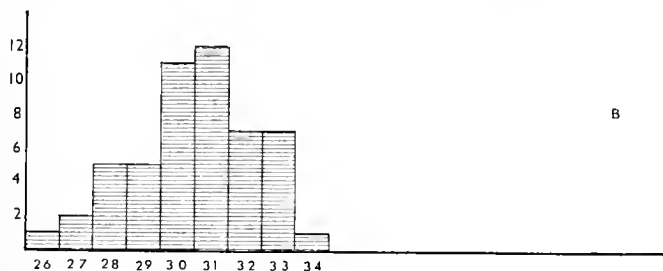


FIG. 22. Histograms to show the frequencies of the lateral line scale counts in *Varicorhinus ruwenzorii* (V); *Barbus somereni* (B); and *Barbus alluaudi* (H).

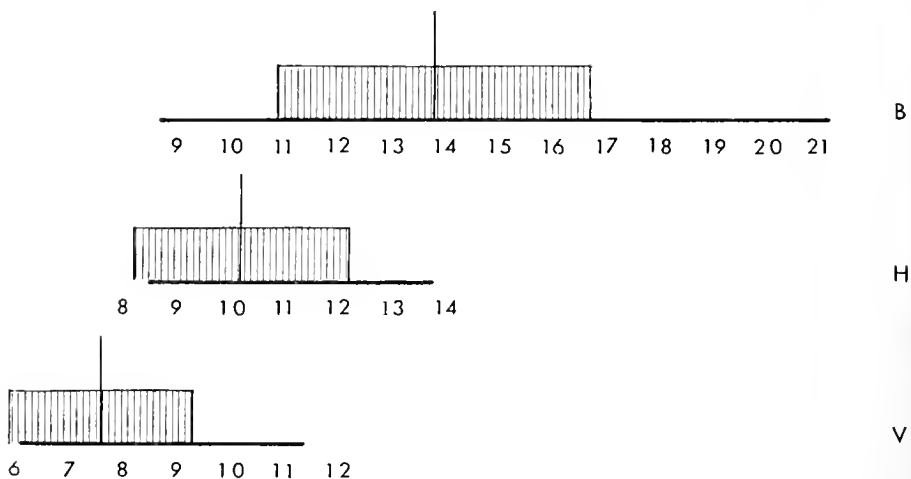


FIG. 23. A comparison of the ranges, mean and standard deviation of the dorsal spines in the three species. The base line represents the range; the vertical line represents the mean and the shaded area covers one standard deviation either side of the mean. The figures are the lengths of the dorsal spines expressed as a percentage of the standard length.

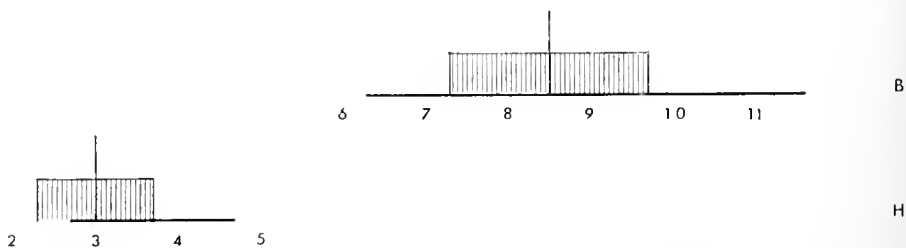


FIG. 24. A comparison of the posterior barbel lengths in *B. somereni* and *B. alluaudi*. Details as in fig. 23.

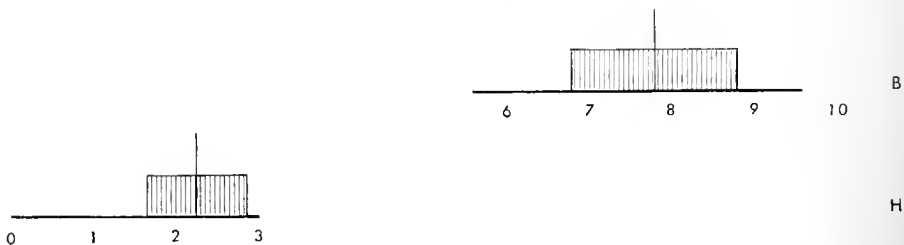


FIG. 25. A comparison of the anterior barbel lengths in *B. somereni* and *B. alluaudi*. Details as in fig. 23.



means that it is unlikely that the *B. alluaudi* differs from the putative parent species purely because of random variation. On this basis the values for the proportions of the dorsal spine (D.Sp.) provide strong evidence that the sample of *B. alluaudi* could not have come from either of the putative parent species.

It is most unlikely that the hybrids belong to either *V. ruwenzorii* or to *B. somereni* and the overall result hints most strongly at nearly perfect intermediacy.

Intermediacy has been advocated as a very significant distinguishing character of hybridisation by many authors (e.g. Hubbs, 1955; Berry and Low, 1970).

The lateral line scales for the three groups are compared in histogram form above (fig. 22). There is no overlap in the ranges of *B. somereni* and the hybrids, but the

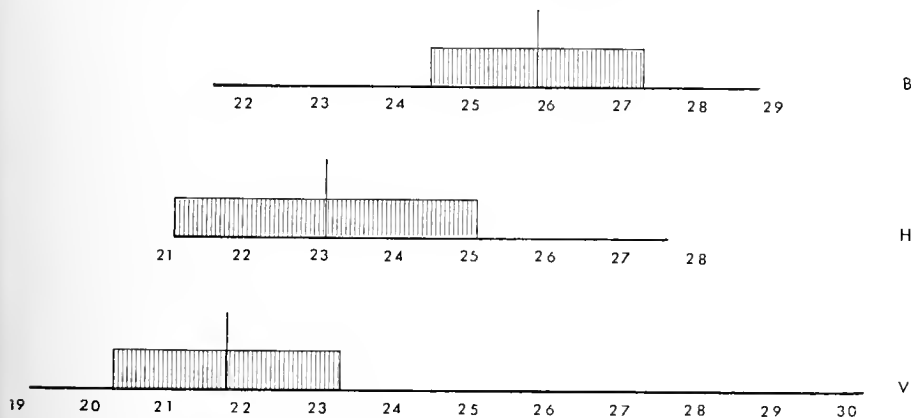


FIG. 26. A comparison of the head lengths of the three species. Details as in fig. 23.

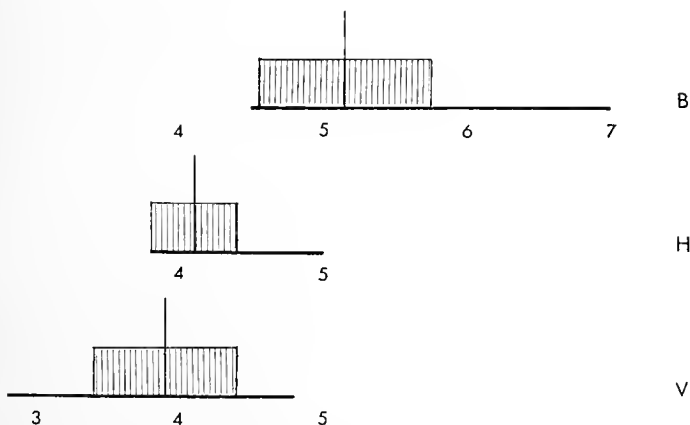


FIG. 27. A comparison of the eye diameters in the three species. Details as in fig. 23.

hybrids (1) and *V. ruwenzorii* (3) have 38 scales in common. The mean values for the hybrids and *V. ruwenzorii* are closer than those for *B. somereni* and the hybrids.

The range, mean and one standard deviation each side of the mean are shown graphically below. All are expressed as percentages of the standard length. Most of these graphs are self-explanatory and show the relation of the hybrid data to those of the parent species. The disappointing result for the mouth width has been mentioned above.

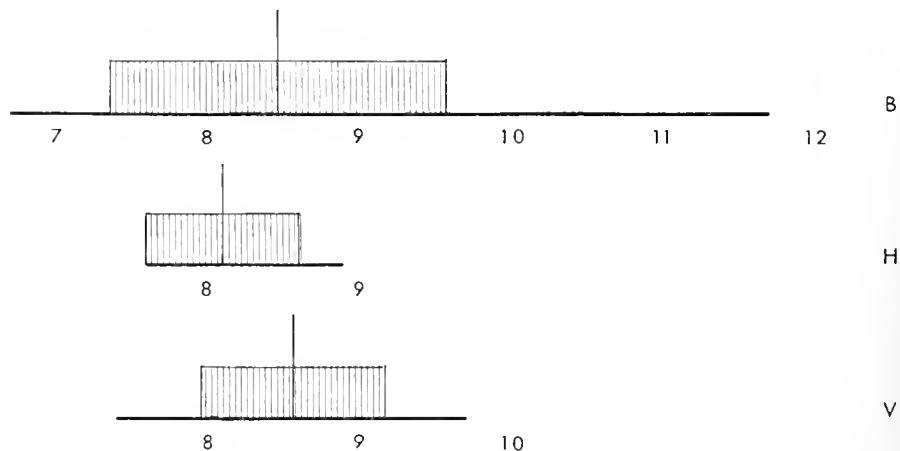


FIG. 28. A comparison of the interorbital widths in the three species. Details as in fig. 23.

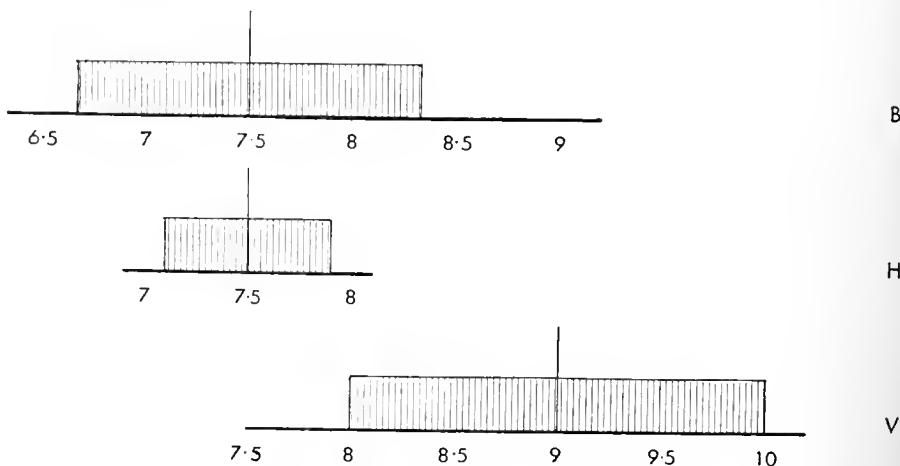


Fig. 29. A comparison of the mouth widths in the three species. Details as in fig. 23.

The graph for the interorbital width (fig. 28) shows two interesting factors. Firstly that the mean interorbital widths differ hardly at all in the parent species but both are slightly greater than in the hybrid. The increased mouth width in the *Varicorhinus* is not therefore reflected by an overall increase in head width. The visibility of the eyes in ventral view in the three groups of fishes has been noted above. The large standard deviation for this character in *B. somereni* (Table on page 282) is due to the relatively wider interorbital space in the very large *Barbus somereni*. The second point is that this is the only character in which the hybrid is not intermediate. There are instances of similarly anomalous results in hybrids. Steinitz and Ben Tuvia (1957) noticed the same phenomenon for the head length/eye diameter ratios in *Barbus longiceps* and *Capoeta damascinus* hybrids.

Hybrids may also have meristic characters which show great variability. Hubbs (1956) observed the great variability of the  $F_1$  hybrids of *Notropis lepidus* and *N. prosperinus* which in some characters exceeds the range of the parent species, e.g. in the number of dorsal and anal fin rays. Hubbs (1951) describes the increase beyond the parental ranges of the anal fin rays of the hybrids between *Notropis heterolepis* and *Hybognathus hankinsoni*. The Steinitz and Ben Tuvia results most closely resemble the interorbital width results shown above.

The pharyngeal bones in the hybrids have either four (as in the types) or five teeth in the inner row. The size of the fifth tooth, when present, is of some importance; it is always smaller than the same tooth in an equally large pharyngeal bone from *B. somereni*; in other words it is satisfactorily intermediate. The presence of only 4 teeth in the Wimi river specimens is more difficult to understand, for it reflects the *Varicorhinus* condition perfectly.

With such a small sample of hybrids and without a complete size range it is unwise to speculate on reasons for the possession of four or five teeth. Various other characters which are not readily quantifiable e.g. the shape of the bones of the jaws and suspensoria still serve to show the mixture of parental characters present in the hybrids.

The nine specimens collected by the Imperial College expedition were all males. Assuming that the fishes do not segregate by sexes the chances of a random sample all being male is sufficiently low to suggest that the sex ratio is unbalanced. Holčík and deWit (1962b) noticed that all of the  $F_1$  of a *Rhodeus sericeus*, *Rhodeus ocellatus* cross were male. Hubbs and Hubbs (1932) observed the predominance of male offspring in sunfish (Centrarchidae) hybrids. Hubbs (1961), reviewing earlier work, points out that the  $F_1$  male hybrids are usually sterile, although occasional exceptions are found both in the sense of an individual within a brood and in cases like *Molliensia sphenops* and *Molliensia latipinna* where the males are almost fully fertile but the females only rarely so. If the males are sterile (as the lack of evidence of  $F_2$  generations and backcrosses would suggest) then this might be displayed in the detailed structure of the testes. Accordingly, a hybrid specimen and a male of *B. somereni* of approximately the same size, caught on the same day, were compared. None of the specimens was preserved especially for histological examination, so this comparison of two specimens, treated in the same way, was the best that could be done. The specimens were preserved in formalin on the same day they were

captured but the preservative must have taken some time to become fully effective as decay was evident in the alimentary canal (p. 271). It could only be assumed that both specimens had undergone the same post-mortem changes and that a comparison between the two would have some validity.

The testes of the hybrid were longer than those of the *B. somereni* by about a quarter and thicker by the same amount. Histological sections were prepared as described above (p. 265).

The sections of the hybrid testes showed large vacuoles, hardly any interstitial tissue and the sperm mother nuclei gave an appearance of abnormality especially in the variation of size and shape when compared with the *B. somereni* sperm mother nuclei. In *Barbus somereni* there were no vacuoles, plenty of interstitial tissue and clumps of sperm. With the naked eye the D.N.A. stain showed up in dense patches in the *Barbus somereni* but only diffusely in the hybrid testes sections.

I have no information about the testicular cycle in *Barbus somereni* so I cannot justifiably draw any conclusions from these meagre observations. Much more histological work is necessary before any valid conclusions can be reached about the possible sterility of the testes of *B. alluaudi*.

With these assumptions, which is all the evidence currently available, it would seem that the sex ratio in *Barbus alluaudi* is unbalanced. This suggests that the fishes referred to *Barbus alluaudi* are hybrids.

The question why the hybrids should be relatively common in the Mubuku river is difficult to answer. The spawning habits of cyprinids are such that chance fertilisation of an egg by a foreign sperm is quite possible and has apparently not infrequently happened in North America and Europe, so an occasional hybrid would not be too surprising. However, the breeding habits of *Barbus somereni* and *Varicorhinus ruwenzorii* are not known. It can only be assumed that the eggs are freely scattered and the sperm shed into the water in their proximity as generally happens in cyprinids. But whether these two species breed at the same time or not is unknown.

*Barbus somereni* is either rare in the Mubuku or inhabits parts as yet uncollected. The Imperial College Expedition caught none in the Mubuku but found they were plentiful in the Sibwe (fig. 1). Ian Dunn collected only one specimen in the Mubuku. *Varicorhinus ruwenzorii*, on the other hand, is as abundant in the Sibwe as in the Mubuku.

It is possibly significant that *B. alluaudi* is commonest in the Mubuku river where *B. somereni* is scarce. Hubbs (1951) identified the unique specimen of *Notropis germanus* as a hybrid between *Hybognathus hankinsoni* and *Notropis heterolepis*. The interest here lies in the fact that *N. heterolepis* no longer lives in the Smoky Hill river where the hybrid was collected. It appears to have been rare in 1885 when '*N. germanus*' was collected. Only one specimen of this cross is known and Hubbs suggested that the *N. heterolepis* hybridised when their numbers became very low. Similar evidence is put forward for catostomids by Hubbs and Miller (1952). Perhaps the relative abundance of the hybrid in the Mubuku river is due to the disparity in numbers between *Barbus somereni* and *Varicorhinus ruwenzorii*.

The evidence for the hybrid origin is circumstantial, but the two arguments in

favour of this hypothesis are, (i) the presence of only three large cyprinids in the streams in question with the rarest of the three displaying conspicuous morphological intermediacy between the other two, (ii) the fact that *Barbus alluaudi* is most frequently encountered in a stream where one of the putative parent species is very scarce.

Although this does not prove the hybrid origin of *Barbus alluaudi*, the morphological intermediacy of this nominal species does conform to previously studied inter-specific fish hybrids. On the balance of evidence I suggest that *Barbus alluaudi* is an intergeneric hybrid between the cyprinid species *Barbus somereni* and *Varicorhinus ruwenzorii*.

#### SUMMARY

The three species of large cyprinids living in the streams on the Ruwenzori mountain range, Uganda viz. *Barbus somereni*, *Varicorhinus ruwenzorii* and *Barbus alluaudi* are described. The comparative scarcity of *B. alluaudi* (about 6 per cent of the population at one site) and the fact that many of its characters are intermediate between those of the other two species suggest that it is a hybrid. Further arguments in favour of this hypothesis are the apparently unbalanced sex ratio in *B. alluaudi* and the fact that it is most abundant where one of the putative parent species is rare.

The intermediate characters of *B. alluaudi* are discussed and compared with those of *Barbus somereni* and *Varicorhinus ruwenzorii*.

The hybrid origin of *B. alluaudi* cannot be proved but a strong circumstantial case can be constructed for it.

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PLATE I

(a) *Barbus somereni*

(b) *Varicorhinus ruwenzorii*

(c) *Barbus alluaudi*. A specimen from the Mubuku river collected by the Imperial College Expedition.





(a)



(b)



(c)





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THE CYPRINID FISHES OF  
*ACANTHOBRAMA* HECKEL AND  
RELATED GENERA



M. GOREN, L. FISHELSON and E. TREWAVAS

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Tel Aviv University  
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## SYNOPSIS

The genus *Acanthobrama* has been redefined to exclude *A. terraesanctae* Steinitz. This has been made the type of a new genus, *Mirogrex*, characterized by the high numbers and slender form of the gill-rakers. Two subspecies of *M. terraesanctae* are recognized and defined and a description is given of a new species of *Acanthobrama* from the Mediterranean rivers of Israel. The relationships of these genera are discussed.

## INTRODUCTION

THE part of this work on collections in European museums was done by Trewavas many years ago in connection with the naming of Tigris specimens. The discovery by Fishelson and Goren of a new species of *Acanthobrama* renewed interest in the genus and we decided to amalgamate our contributions as a revision of the genus. We independently discovered the differences between the Lake Kinnereth (Tiberias) and Huleh populations of *Acanthobrama terraesanctae* Steinitz and regarded them as subspecies, finally deciding to separate them from *Acanthobrama* as a new genus.

### Measurements, abbreviations and geographical names

SL = standard length, i.e. without caudal fin. The last dorsal or anal ray cleft to the base or the last two in contact at the base are counted as one, the usual practice in Cyprinidae. Vertebral counts start behind the complex vertebra with the first bearing a normal rib and include the urophore as one.

The names Sea of Galilee, Lake Tiberias and Lake Kinnereth are synonymous. We use the spelling Huleh for the former lake and swamp region and Hula for the part of it that remains as Hula Natural Reserve. Names of localities in Syria and Iraq, although variously transliterated, will, we believe, present no difficulty.

*ACANTHOBARAMA* and related genera

In southwest Asia there are recognized two cyprinid genera, *Acanthobrama* Heckel and *Capoetobrama* Berg, that have in common:

1. A smooth, rigid last simple dorsal ray.
2. A keel on the belly between the pelvic fins and the anus. In this place there is no median ventral row of scales, but the two ventral rows meet at a sharp angle or are narrowly separated by a narrow strip of naked skin ('soft keel').
3. A single row of pharyngeal teeth on each side.
4. 13-23 rays in the anal fin.

We now propose the separation of *Acanthobrama terraesanctae* Steinitz as type species of a third genus, *Mirogrex* nov. The characteristics of the three genera are set out in Table 1.

TABLE 1. Differences between the genera *Acanthobrama*, *Mirogrex* and *Capoetobrama*.

	<i>Acanthobrama</i>	<i>Mirogrex</i>	<i>Capoetobrama</i>
Geographical range	Orontes to Yarkon; Jordan Valley; Tigris-Euphrates	Jordan Valley	Aral Sea basin
Mouth: position	terminal or subterminal	terminal	ventral
shape	horse-shoe	narrow horse-shoe	slightly curved, nearly transverse
angle with horizontal	20°-40°	40°-50°	0° (horizontal)
Length of head, % SL	22.5-28.0	25-29	18-20
Length of lower jaw, % SL	8-11	9.5-12.5	6.5-7.0
Outer gill-rakers on			
first arch: lower part	8-12	13-20	12-13
whole arch	12-15	(17) 20-28	14-16 (17)*
Anal fin-rays	12-23	14-18	18-23
Scales lat. line	51-100	69-80	54-64
D-lat. line	9½-20	11½-17½	8-10
Vertebrae	32-38	34-36	38-40

\* 17 is the number given by Nikolskii (1938). The other numbers are taken from 5 specimens in the B.M.(N.H.).

The monotypic genus *Capoetobrama*, type species *C. kuschakowitschi* (Kessler), is, to judge by its mouth, its long intestine ( $3\frac{1}{4}$  times SL according to Berg) and compressed, bevelled pharyngeal teeth, adapted to feeding on mud. It differs from *Acanthobrama* in much the same way as *Varicorhinus* (or *Capoeta*) differs from *Barbus*. In two species of *Acanthobrama* and in *Mirogrex* (our new genus) we obtain measurements for the intestine of 81-133% SL.

Both geographically and structurally *Capoetobrama* is more distinct from *Acanthobrama* than is *Mirogrex*. The latter comes within the range of *Acanthobrama* both geographically and in most of the characters tabulated, but differs from both other genera in the high numbers and slender form of the gill-rakers (fig. 1), adapted to a largely planktonic diet. The parallel suggested here is with *Engraulicypris*, the plankton-feeding cyprinid of African lakes, which seems to be derived from the mainly fluviatile *Barilius*, a predator on invertebrates and fishes.

## ACANTHOBRAMA Heckel

Heckel, 1843 : 1033.

*Trachibrama* Heckel, l.c. (lapsus for *Acanthobrama*, see Heckel, op. cit. vol. 3, 1846 : 359).

TYPE SPECIES: *Acanthobrama marmid* Heckel, 1843 : 1075, designated by Bleeker, 1863 : 210.

DEFINITION: A soft keel between the ventral rows of scales for half or more of the distance from anus to pelvic base; pharyngeal teeth 5-5 or 5-4; scales 51-100 in the lateral line (excluding 2 or 3 on the caudal fin); last simple dorsal ray strong and rigid for one half to the whole of its length; gill-rakers 8-12, usually 9-11, on lower part of anterior arch (unknown in *A. centisquama*), 12-15 on the whole arch; 12-23 rays in the anal fin; length of head 22.5-28% of SL, of lower jaw 8-11%.

DISTRIBUTION: Tigris and Euphrates and their tributaries; R. Kueik at Aleppo; R. Orontes and Amik Göl; waters of Damascus; Jordan system; Mediterranean rivers of Israel from Na'amén to Yarkon.

*Acanthobrama mirabilis* Ladiges (1960 : 132 fig. 4) from R. Menderes (Meander) seems to be a *Vimba vimba tenella* (Nordmann) and there is no reliable record of *Acanthobrama* west of the Orontes, unless one of *A. marmid* from near Tarsus, quoted from Kosswig MS by Ladiges (1960) is verified.

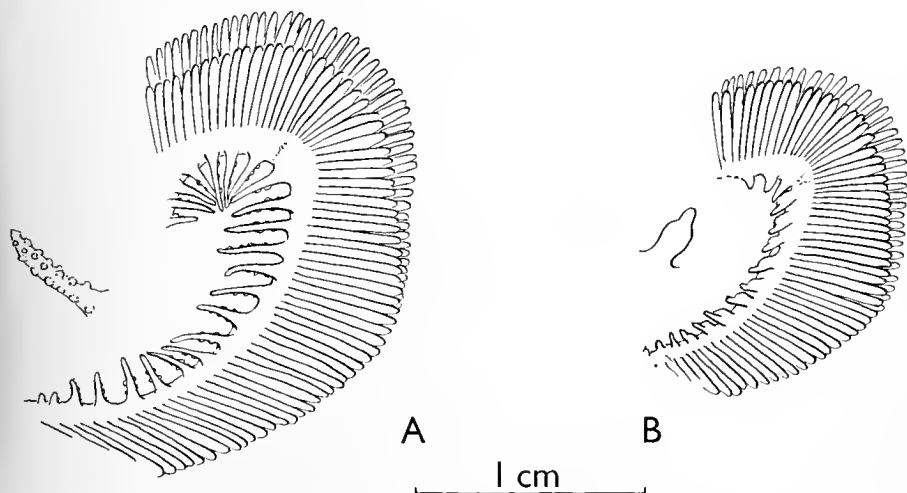


FIG. 1. First gill-arch with outer series of gill-rakers of, (A) *Mirogrex terraesanctae*, a specimen of 143 mm SL from Lake Tiberias; and (B) *Acanthobrama marmid*, a specimen of 116 mm SL from Houreira, Syrian Euphrates. For each a single raker is shown enlarged in oral aspect.

## KEY TO THE SPECIES

- |   |  |           |                     |
|---|--|-----------|---------------------|
| 1 | Branched dorsal rays 8, rarely 7 or 9; total anal rays 17-23                   | . . . . . | 2                   |
| - | Branched dorsal rays 7, rarely 8; total anal rays 12-16 (17)                   | . . . . . | 3                   |
| 2 | Anal rays 23; scales in l.l.90-100; last simple dorsal ray 27% SL              | . . . . . | <i>centisquama</i>  |
| - | Anal rays 17-22; scales in l.l.54-72; last simple dorsal ray 15-26% SL         | . . . . . | <i>marmid</i>       |
| 3 | Scales in l.l.59-69; rigid part of stiffened dorsal ray about 70% of whole ray | . . . . . | <i>lissneri</i>     |
| - | Scales in l.l.51-60; rigid part of stiffened dorsal ray 50-65% of whole ray    | . . . . . | <i>telavivensis</i> |

*A. centisquama* and *A. marmid* reach a larger size (up to 150 mm SL) than any recorded for *A. lissneri* and *A. telavivensis* (up to 113 mm SL).

*Acanthobrama centisquama*

(Figs 2A and 4A)

Heckel, 1843 : 1074 pl. 9 fig. 1 (Damascus); Tortonese, 1952 : 272 (Amik Göl in the Orontes basin).

Holotype in the Vienna Museum.

The following description is compiled from Heckel's description and figure and Tortonese's brief note.

Depth of body 28.3% of the Standard Length, length of head 23.6%, length of dorsal spine 27% (Heckel, fig.) or more (Tortonese). Pectoral fin extending to above base of pelvic.

Snout projecting slightly beyond the oblique mouth. Diameter of eye 25% of length of head, interorbital width about 31.5%. Pharyngeal teeth 5-5 (fig. 4A).

Scales small, without radii, 90-100 in the lateral line, 20 between origin of dorsal and lateral line, 10 below lateral line.

Dorsal iii 8, the third ray very strong and rigid to its extremity. Anal iii 20.

Colour silver-white with bluish grey back and blackish fins (Heckel, on a preserved specimen).

Heckel's only specimen (the holotype) measured 7 Viennese inches in total length. If, as is probable, the figure is natural size, the standard length was about 127 mm. The specimen could not be found in Vienna when Trewavas examined the types of Heckel's other species, but the pharyngeal bone was separately preserved. Tortonese's single specimen was a 'large' one.

Tristram (1884) recorded this species from the upper affluents of the Jordan, but preserved no specimens. He may have seen *A. lissneri* there (see also Steinitz, 1953 : 225).

The shape of the snout and angle of the mouth are more like these features in *Mirogrex* than in other species of *Acanthobrama*. If this species proves to have gill-rakers like *Mirogrex* it should be transferred to that genus.

*Acanthobrama marmid*

(Fig. 1B, 2B, 3, 4B)

Heckel, 1843 : 1075, pl. 9, fig. 2 (Aleppo, R. Kueik); Berg, 1949 : 839 (R. Karasu and Lake Balikli, nr. Erzerum); Steinitz, 1952 : 294, fig. 2.

*A. arrhada* Heckel, 1943 : 1076 (footnote); 1846 : 237, pl. 18, fig. 2 (Tigris at Mosul).

*A. cupida* Heckel, 1843 : 1077 (footnote); 1846 : 235, pl. 18, fig. (R. Kueik at Aleppo).

*A. marmid orontis* Berg, 1949 : 839 (R. Orontes).

*A. marmid morpha elata* Berg, 1949 : 839 (Lake Balikli).

Syntypes of *A. marmid*, *A. arrhada* and *A. cupida* in Vienna (see below, p. 8).

Syntypes of *A. m. orontis* and *A. m. morpha elata* in U.S.S.R. (Leningrad?).

DESCRIPTION based on the 43 specimens listed below, namely the syntypes of *A. marmid*, *A. cupida* and *A. arrhada* and samples from the Shatt-al-Arab, Tigris system, Euphrates system in Syria and the Hatay Province of Turkey; some of

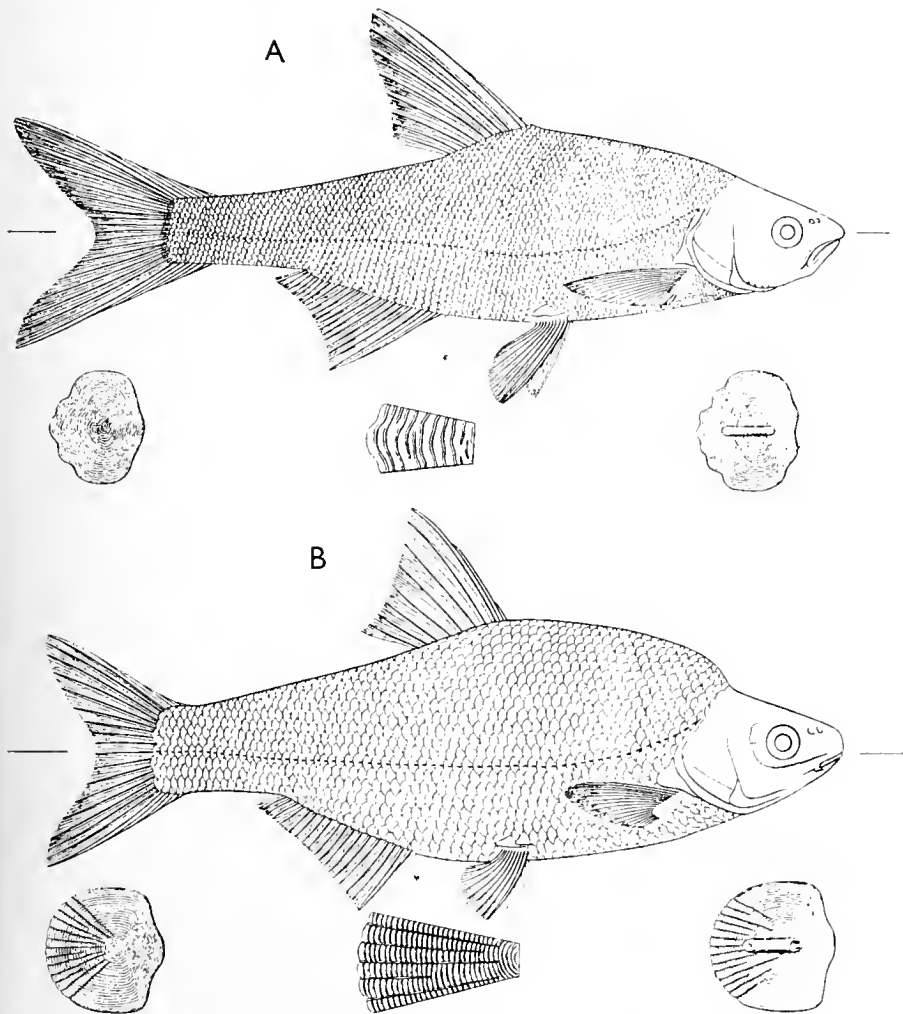


FIG. 2. (A) *Acanthobrama centisquama* and (B) *A. marmid* from pl. IX figs 1 and 2 of Heckel in Russegger's Reisen.

Heckel's types are from R. Kueik, a separate system related to the Euphrates. The description also takes into account Berg's descriptions of samples from the source region of the Euphrates and from the Orontes.

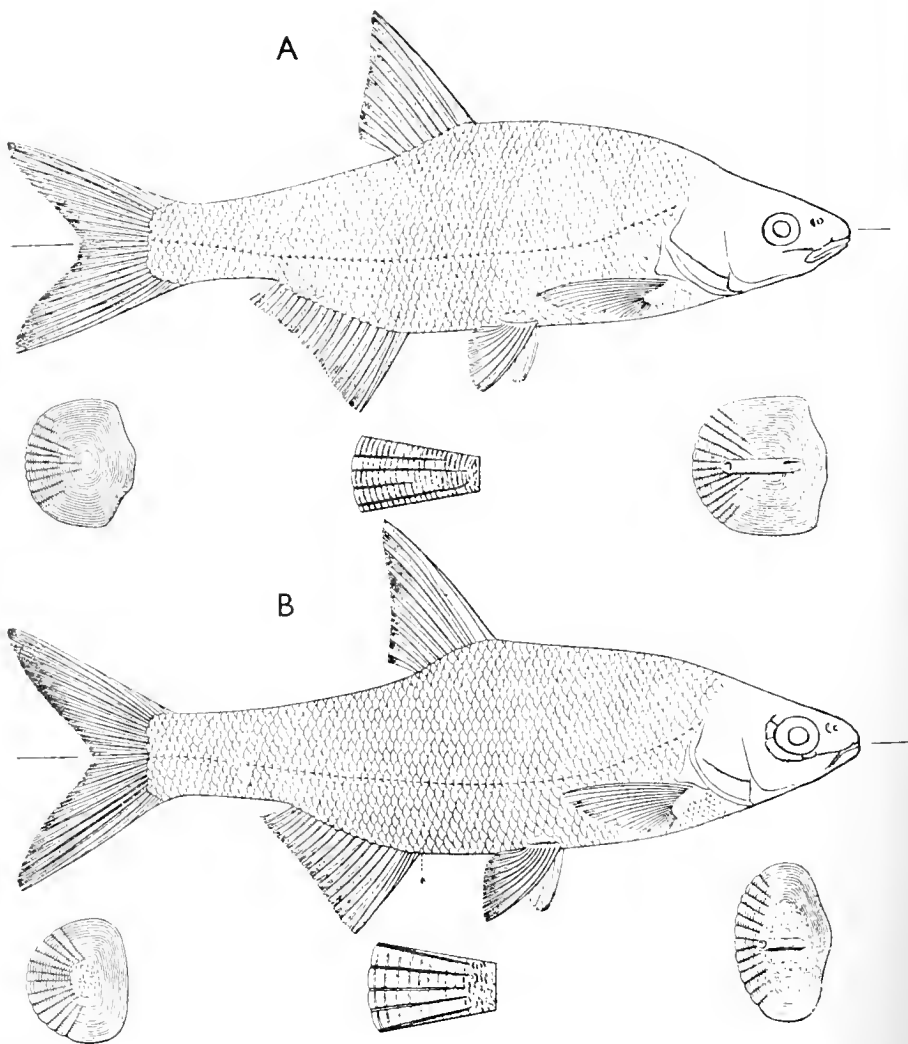


FIG. 3. (A) *Acanthobrama cupida* and (B) *A. arvhada* from pl. XVIII, figs 1 and 2 of Heckel in Russegger's Reisen, both names considered synonyms of *A. marmid*.

Depth of body 26–35% of SL, in none of the Tigris or Shatt-al-Arab specimens exceeding 32%, in none of the Euphrates or Kueik specimens less than 30% (except three young of 44–63 mm SL). Length of caudal peduncle 14.5–20% SL, 1.2–1.8 times its own depth.

Length of head 22.5–27.8% SL; less than 24 only in a few specimens longer than 130 mm SL and in some of the (rather badly preserved) specimens from Basra.

Length of pectoral fin 17–24% SL; fin extending nearly or quite to base of pelvic.

Length of rigid part of last simple dorsal ray 17–22.6% SL in most specimens of all samples; but in one of the 8 specimens from Mosul (types of *A. arrhada*) it is 26%, in one of 10 from Basra 24, in one of 4 from an eastern tributary of the Tigris 25. In contrast, three of 6 from R. Kueik have a short spine of 15–16% (Table 2).

Diameter of eye 23.5–38.5% of length of head, negatively allometric; interorbital width 29–37.5%; length of lower jaw 33–42%. Jaws meeting evenly in front or lower a little behind upper; mouth nearly horizontal.

Gill-rakers in outer series of first arch (2–4) + (0–1) + (9–11), short, with a basal swelling (fig. 1B). Pharyngeal teeth 5–5 in four sets prepared by Heckel in the Vienna Museum, three labelled *A. marmid* and one 'No. 55. *Trachybrama leucopsis*' from Mosul. The latter was evidently a MS name, replaced for publication by *Acanthobrama arrhada* (The name *leucopsis* was never published, but *Trachibrama* (sic) slipped in once on p. 1033 where, as Heckel explained in vol. 3 of the same work, it is a *lapsus* for *Acanthobrama*). One set has a tooth missing from each side, but its base is present on the bone, probably at the stage where the replacement tooth had not yet been ankylosed to it. The anterior tooth on each is compressed and bluntly pointed, the others are bevelled, often with a good cutting edge. (See also Steinitz, 1952, fig. 2).

Scales with radii; 54–69 (72) in the lateral line (excluding 1–3 on the caudal base), eight specimens from Mosul covering most of this range (Table 2); 10–13 between origin of dorsal and lateral line, 4–7 between lateral line and pelvic base.

Dorsal iii 8 in 37 individuals, iii 7 in 1, iii 9 in 1; origin above base of pelvic.

Anal 17–22, of which the first 3 are simple; 19 and 20 are the commonest numbers, found in 18 of 24 Tigris fishes and 14 of 18 from R. Kueik and the Syrian Euphrates. Origin below hind end of base of dorsal or just behind this vertical.

Sexual dimorphism: Heckel's material has not been examined for nuptial tubercles. No tubercles were found in the specimens in B.M.(N.H.), most of which are immature or, if mature, are ♀♀.

#### Notes on the synonymy

Most authors are agreed in regarding *A. cupida* as a synonym of *A. marmid*, considering the higher body of *A. marmid*, in extreme cases with a hump at the nape, as an ecological form. There is even no evidence that the types of *A. cupida* came from a separate locality. Berg found the high form again in Lake Balikli, considered it probably characteristic of still waters and named it according to his system 'morpha *elata*'. By analogy with other fishes, it seems sounder not to base a name on a feature that may characterize populations or individuals according to the degree of nourishment. Trewavas has tested on Heckel's material the other features

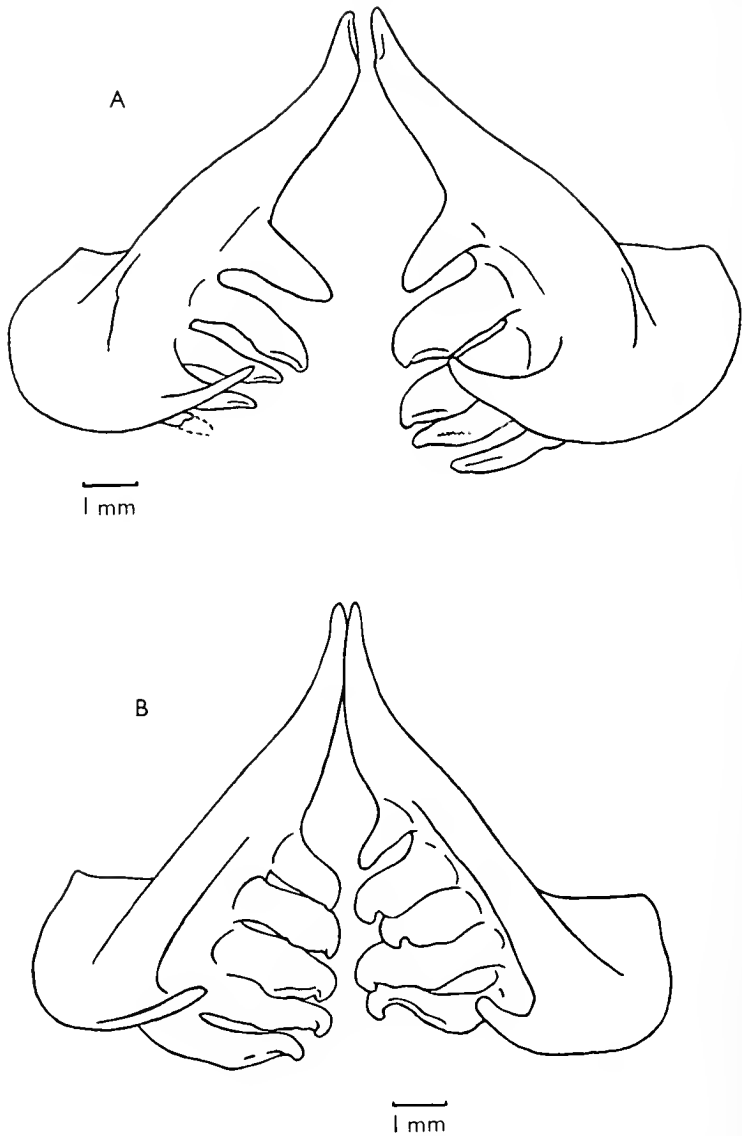


FIG. 4. Pharyngeal bones of, (A) *Acanthobrama centisquama*, a preparation by Heckel in the Vienna Museum; and (B) *A. marmid*, a preparation in the Vienna Museum under the name '*Trachybrama leucopsis*', a MS name, replaced for publication by *Acanthobrama arrhada*, regarded as a synonym of *A. marmid*.



in which the species were stated to differ and finds that variation, allometric or individual, within the samples disposes of all of them.

*A. arrhada* was distinguished mainly on its longer, stronger dorsal spine. Table 2 shows that the length is very variable within a population. On the available evidence the highest ranges are found in the Tigris system, the lowest in R. Kueik, but this does not seem sufficient basis for specific or subspecific divisions.

*A. m. orontis* was established on the basis of two specimens with respectively 54 and 55 scales in the lateral line; but 54 are found not only in this but in 3 from Basra and 1 from an eastern tributary of the Tigris. Berg's specimens from the upper Euphrates region were equally exceptional in the other direction, having a range of 65-72. While it is possible that the upper Euphrates holds a small-scaled population and the Orontes a large-scaled one, the samples are too small to prove this in view of the wide range at Mosul. Parallel local ranges are found in populations of *Varicorhinus damascinus* in the same area (see Kosswig, 1952, fig. 1).

## MATERIAL EXAMINED

Museum and reg. no.	No. of specimens	SL (mm)	Locality	Collector or donor
Vienna 55346	2	87,125	R. Kueik at Aleppo	Kotschy
" 55348 (syntypes of <i>A. marmid</i> )	2	114,133	" " "	"
Vienna 55340 (syntype of <i>A. cupida</i> )	1	125.5	" " "	"
Vienna 55342 (syntype of <i>A. cupida</i> )	1	101.5	" " "	"
Vienna 55334 (syntypes of <i>A. arrhada</i> )	6	65-146	R. Tigris at Mosul	"
Vienna 55335 (syntype of <i>A. arrhada</i> )	1	151	" " "	"
Vienna 55336 (syntype of <i>A. arrhada</i> )	1	145	" " "	"
University of Mosul B.M.(N.H.)	1	96	" " "	University of Mosul
1920.3.3.147-56	12	69-92	Basra, Shatt-al-Arab	C. Christy
1931.12.21.22-25	4	66-85	R. Tigris at Mosul	Bombay Nat. Hist. Soc.
—	4	50-109	Greater Zab (eastern trib. of Tigris) at Eski Kelek	Government of Iraq
—	1	86	R. Tenjera, trib. of Diyala, Tigris system	" " "
1935.9.12.30	1	108	Kara Su, trib. of Euphrates in Hatay Province, Turkey	Bird
1968.12.13.108-112	5	44-111	Quadi Khneizer, Syrian Euphrates system	Beckman
1968.12.13.113-118	6	56-117	Syrian Euphrates at Hooreira	"

TABLE 2. *A. marmid*. Data on the length of the last simple dorsal ray, expressed as % of SL; and ranges of numbers of scales in the lateral line (l.l) in the same samples. The samples have been divided into size groups and show that the variation does not follow any regular allometric pattern.

Locality	No.	SL (mm)	Whole ray	Rigid part	l.l.
Basra	1	69	29	24	54-60
	7	83-92	22.4-26.0	17.0-18.6	
Trib. Tigris	3	49-64	24-30	18-22	54-64
	1	86	30	25	
Mosul	2	61, 64	21.3, 21.7	—	56-69
	1	96	28	22	
	2	100, 120.5	—	20, 21	
	3	138-146	22.0, 22.6, 30.5	19, 17, 26	
Syrian Euphrates	1	151	—	18.7	56-66
	1	44	31	16	
R. Kueik	4	47-117	26-29.5	18.8-22.6	61-67
	1	87	24.8	18.8	
R. Orontes (Berg)	5	101-133	19-21	15-18	54, 55
	2	106, 121	21.5	—	

### *Acanthobrama lissneri*

(Figs 5, 6A, 8)

*Leuciscus zeregi* (part. nec Heckel); Günther, 1868 : 220 (Lake Tiberias); Annandale, 1913 : 31 (after Günther).

*Alburnus sellal* (nec Heckel); Lortet, 1883a : 169 (but not pl. xvi fig. 2, which is probably a true *A. sellal* from the Orontes) (Lake Tiberias); Tristram, 1884 : 176 (record, after Lortet); Barrois, 1894 : 273 (record, after Lortet); Annandale, 1913 : 31 (after Lortet).

*Acanthobrama lissneri* Tortonese, 1952 : 271 (L. Tiberias).

Holotype, SL 75 mm, and two paratypes, 60 mm and 69 mm, in the Zoological Museum, University of Turin, Italy. A third paratype, SL 67 mm, in B.M.(N.H.) (1951.12.4.1).

DESCRIPTION, based on 25 specimens recently collected in L. Tiberias, on the material listed below in the British Museum (Natural History) and on a specimen of 113 mm SL in Lortet's collection from L. Tiberias, with certain details from his ten smaller specimens (Mus. Lyon 3637) and incorporating details from Tortonese's description of the holotype.

Depth of body 21.5-26.5% SL, length of head 2.4-28%; length of caudal peduncle 18.5-24.0%, 1.7 to 2.6 times its own depth.

Snout 25.0-30.0% length of head, diameter of eye 27.0-38.0% (negatively allometric), interorbital width 30.0-35.0%, length of lower jaw 36.0-43.0%.

Angle of mouth 20-40° with the horizontal. Gill-rakers on first arch (2-3) + (0-1) + (8-11), but 5 on the upper limb in the largest specimen examined. Pharyngeal teeth 5-5.

Scales 59-69 in the lateral line, 9½-14½, mode 10½, between origin of dorsal and lateral line, 4½-6½, mode 5½, between lateral line and pelvic fin. The scales are thinner than in other species.

Origin of dorsal fin behind vertical of origin of pelvic, but over or just behind pelvic base. Origin of anal at or just behind vertical of posterior end of dorsal base. D ii-iii 7-8 (8 in only one of fourteen counted). Last simple ray (in four in

which it is complete) 21-24% SL, its rigid part about 70% of the whole (where both could be measured). Anal of 12-17 rays, two or three of which are simple, the first a mere nodule; modal numbers 14 and 15 with nearly equal frequency (table 3).

Pectoral not extending to origin of pelvic, its length 17-21% SL. Pelvic reaching anal fin.

Vertebrae behind complex 35 or 36 (table 6).

Sexual dimorphism: Among those in the B.M.(N.H.) one ♂ of SL 54 mm and two ♀♀ of 54 and 55.5 mm have gonads starting to swell. In the ♂ there are a few tubercles on the upper sides of the pectoral fins.

All the *Tiberias* specimens at Lyon assigned by Lortet to *Alburnus sellal* belong to this species, and it was from one of these that he took the uniseriate pharyngeals described. Specimens collected by Chantre in the 'Lac d'Antioche' and determined by Sauvage (Mus. Lyon 3655) (see Sauvage, 1882 and Lortet, 1883b) are true *Alburnus*, with the pharyngeal teeth in two series.

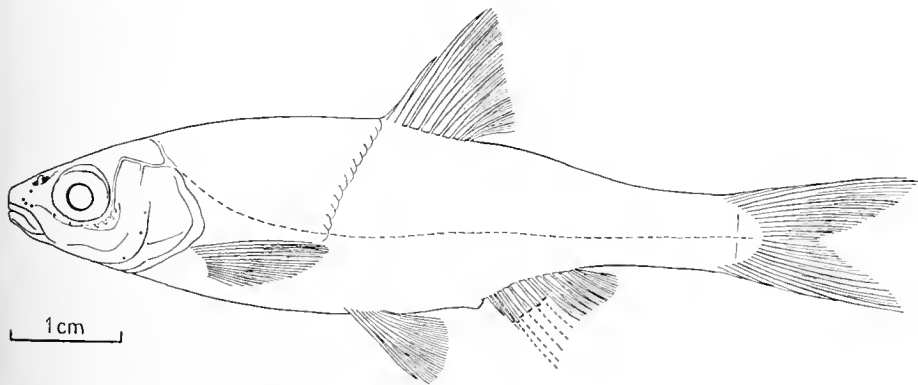


FIG. 5. *Acanthobrama lissneri*, paratype, B.M.(N.H.) 1951.12.4.1.

MATERIAL EXAMINED.

Museum and reg. no. B.M.(N.H.)	SL (mm)	Locality	Collector or donor
1949.9.16.50-54	51-55.5	Samakh, at S. end of L. Tiberias, nr. outflow of R. Jordan	C. K. Ricardo- Bertram
1949.10.10.65-66	42, 53.5	S. of Galilee	Craig-Bennett Beddome
1863.11.3.6-7	43.5, 51.5	" "	H. Steinitz coll., E. Tortonese pres.
1951.12.4.1. (paratype)	67	L. Tiberias	W. C. Beckman
1968.12.13.119-123	41-47	Springs of Muzerib Nr. Deraa, Syria (Yarmuk system)	
Mus. Lyon 3637 (7 specimens)	55-113	L. Tiberias	Lortet
" (4 " )	62.5-80.5	"	"

Museum and reg. no. B.M.(N.H.)	SL (mm)	Locality	Collector or Donor
Tel-Aviv University			
P 3113	50-104	L. Tiberias	M. Goren
P 3016	92-102	Nahal Amud (Jordan drainage)	"
P 3017	76-92	Beith Netofa	"
P 3019	36	R. Kiny (Kishon drainage)	"
P 3020	25-50	R. Kishon	"
P 3022	28-35	Beith Sh'an Valley	"
P 148	65-75	Hula	?

***Acanthobrama telavivensis* n. sp.**  
(Figs 6B, 7, 8)

*Rutilus tricolor* (nec Lortet)?; Bodenheimer, 1935 : 431.

Holotype ♂ 50 mm in SL, no. 3001 and 3 paratypes, 58-72 mm SL, nos. 3002-4 in collection of Department of Zoology, University of Tel-Aviv; all collected by M. Goren in Rosh Ha'ayin (Yarkon springs, near Tel-Aviv) 30.VIII.1968; 3 paratypes in B.M.(N.H.).

DESCRIPTION, based on the holotype and paratypes and additional material listed below.

Depth of body 25.5-30.5% SL, length of head 23.0-27.5, length of caudal peduncle 20.0-22.5, 1.5 to twice its own depth.

Snout 24.0-27.0% length of head, diameter of eye 27.0-31.0 (36% at SL 38 mm), interorbital width 32.5-38.0%, length of lower jaw 37.0-41.5.

Mouth subterminal, at an angle of 20°-40° with the horizontal; lower jaw closing within upper. Gill-rakers short, (2-3) + (0-1) + (8-11) on anterior arch. Pharyngeal teeth 5-5 or 5-4.

Scales 51-60 in lateral line, 11½-14 between lateral line and origin of dorsal, 4-7 between lateral line and base of pelvic.

Origin of dorsal behind origin of pelvic and in some behind whole of pelvic base; origin of anal a little behind vertical of posterior end of dorsal base. D ii-iii 7 (f. 11) or iii 8 (f. 2); length of last simple ray 23.0-28.5% SL, of which about 50-65% is rigid, moderately thick. Anal of 14-16 (17) rays, of which the first three are simple, the first a nodule (table 3).

Pectoral fin extending to origin of pelvic or nearly, its length 20.0-21.5% SL. Pelvics not reaching anus in female, extending beyond it in male.

Vertebrae behind complex 32-34, mode 33 (table 6).

Sexual dimorphism: In two ♂♂ of 78 mm from Na'amen there are tubercles on the upper sides of the pectoral fins. Other specimens examined were either female or not caught in breeding condition and had no tubercles.

Colour silvery on flanks, countershaded from grey above to white beneath; a dark longitudinal band from behind head to base of caudal at two thirds height of body.

Size: up to 80 mm SL.

Distribution: Coastal rivers of Israel, except Kishon; abundant in R. Yarkon, but (now) rare in Na'aman, Taninim and Rubin.

## MATERIAL EXAMINED.

Museum and reg. no.	SL (mm)	Locality	Collector
Tel-Aviv University P 3001 Holotype	50	Rosh Ha'Ayin Yarkon Springs	M. Goren
P 3002-4 Paratypes	58-72	"	"
P 3005-6	15-95	"	"
P 3212	25-65	Nahal Tuth, R. Dalia drainage	"
B.M.(N.H.)			
1969.11.19.22-24 (formerly Tel-Aviv P 2871-3) Paratypes	58-68	R. Yarkon	L. Fishelson
1920.12.23.1-2	38, 80	Nahal Rubin	Aharoni
1949.9.16.15-22	60-79	R. Na'aman	C. K. Ricardo-Bertram
Hebrew University, Jerusalem 3114	63	R. Na'aman	?

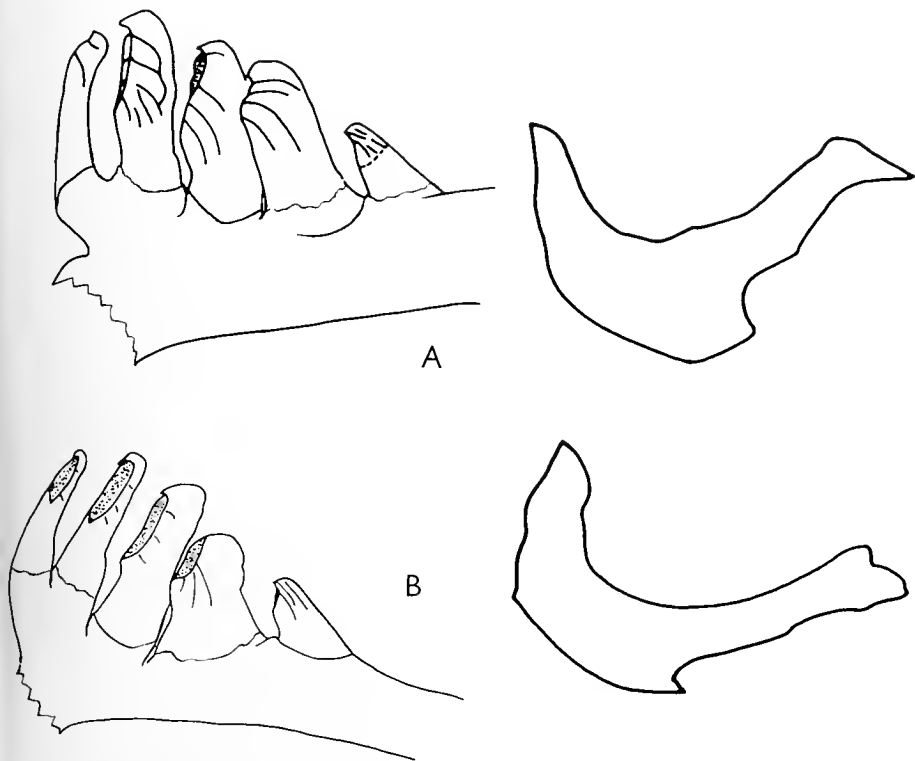
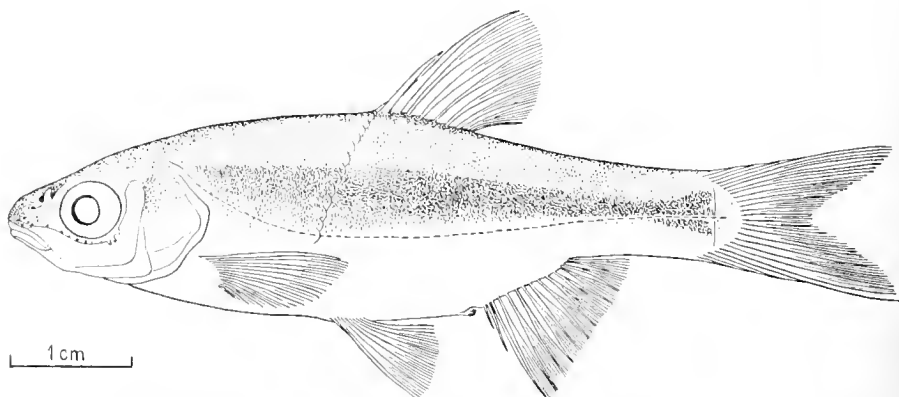


FIG. 6. Pharyngeal teeth and bone of right side in, (A) *Acanthobrama lissneri*; (B) *A. telavivensis*; teeth viewed from the right with flange of bone omitted.

TABLE 3. Frequencies of numbers of anal rays in samples of *Acanthobrama lissneri* and *A. telavivensis* examined by Goren and Trewavas respectively.

No. of rays	<i>A. lissneri</i>					Mean $\pm$ SD	<i>A. telavivensis</i>					Mean $\pm$ SD
	12	13	14	15	16		14	15	16	17		
Goren	1	2	13	12	3	14.4 $\pm$ 0.9	2	20	8		15.2 $\pm$ 0.5	
Trewavas		4	6	8	1	14.3 $\pm$ 0.9	3	5	4	1	15.2 $\pm$ 0.9	
Totals	1	6	19	18	4		5	25	12	1		

FIG. 7. *Acanthobrama telavivensis* from R. Yarkon. B.M.(N.H.) 1969.11.19.22; paratype.***Mirogrex* nov.***Acanthobrama* (part.); Steinitz, 1952.TYPE-SPECIES: *Acanthobrama terraesanctae* Steinitz.As *Acanthobrama*, but gill-rakers 13–20 on lower part of first arch, (17) 20–28 on whole arch (fig. 1). Length of head 25.0–29.0% SL, of lower jaw 9.5–12.25%.Etymology: from Latin *mirus*, wonderful, *grex*, a flock or shoal in reference to the 'miraculous draught' of fishes, which may have been of this species or *Tilapia galilaea*.***Mirogrex terraesanctae* (Steinitz)**

For synonymy see the subspecies.

***Mirogrex t. terraesanctae***

(Fig. 1A, 8, 9, 10)

*Alburnus sellal* (nec Heckel); Tristram, 1884 : 167; Vinciguerra, 1926 : 219; Norman in Hornell, 1935 : 82; Ricardo-Bertram, 1944 : 7 (bionomics and fishery). All these records, Lake Tiberias.*Acanthobrama terraesanctae* Steinitz, 1952 : 295, fig. 1; 1953 : 212; 1959 : 43–64, figs 1–6, tables i–xvi (bionomics); Komarowsky, 1952 (food).

Holotype: ♂ SL 147 mm, Hebrew Univ. Jerusalem. Cypr. 976. Paratypes: ♂ SL 123 mm, ♀ SL 153 mm, Hebrew Univ. Jerusalem. Cypr. 977 and 978. All collected in Lake Tiberias by Dr Steinitz, 20.III.1950.

DESCRIPTION based on data from Steinitz (1952 and 1959) and on samples in the B.M.(N.H.) collected in 1935, 1938 and 1943 with some meristic data from specimens collected by Goren 1968/9. Proportions are taken from specimens of 95–150 mm SL, meristic characters also from some smaller.

Depth of body 21.5–26.0% of SL, length of head 25.0–29.0, length of pectoral fin 17.0–20.5, length of caudal peduncle 17.5–23.0, 1.7–2.4 times its own depth.

Snout flat or very slightly decurved, its length 26.5–31.5% length of head at SL 70 mm and more. Diameter of eye 31.5% length of head at 70 mm SL to 22% at 150 mm SL; depth of preorbital bone 18–21, interorbital width 29–33, length of lower jaw (36) 38–42. Mouth oblique, with the mental process of the lower jaw slightly projecting; angle of cleft of closed mouth 40–50°.

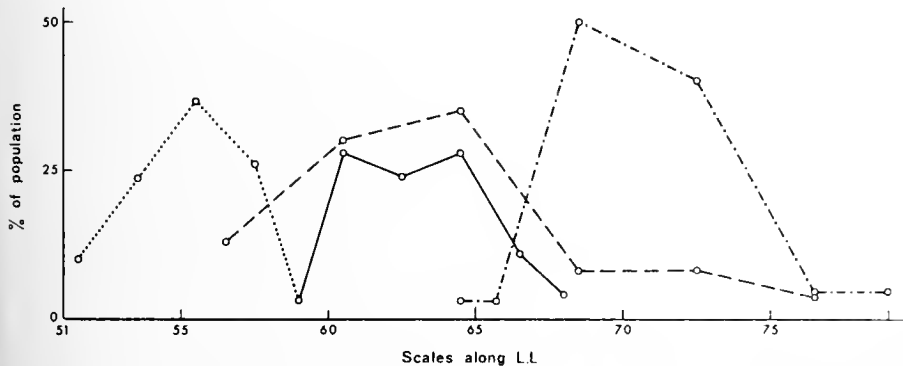


FIG. 8. Number of scales in the lateral line in ——— *A. lissneri*, ..... *A. telavivensis*, — · — · — *Mirogrex t. terraesanctae* and — — — — *M. t. hulensis*.

Gill-rakers on first arch (5–8) + (0–1) + (16–20) (table 4); usual numbers on lower part of arch in B.M.(N.H.) samples 17–19, in Steinitz' account 19–20 (1959 : 57). Rakers slender, tuberculate (fig. 1).

Pharyngeal teeth 5–5 (5–4 in one of many, according to Steinitz, 1952), the anterior tooth short and sturdy with a pointed tip, the other four moderately compressed and bevelled with short hooked tips, in some with slightly jagged edges of the bevelled area.

Scales 55–80 (usually 69–80) in the lateral line, 15–16 (Steinitz) or 13½–17½ (Goren) from origin of dorsal to lateral line, 4½–7½ between lateral line and pelvic fin. Ventral keel not prominent, belly rounded but no median scales between pelvics and anus; the two ventral rows of scales may meet or may be separated by a narrow strip of naked skin ('soft keel').

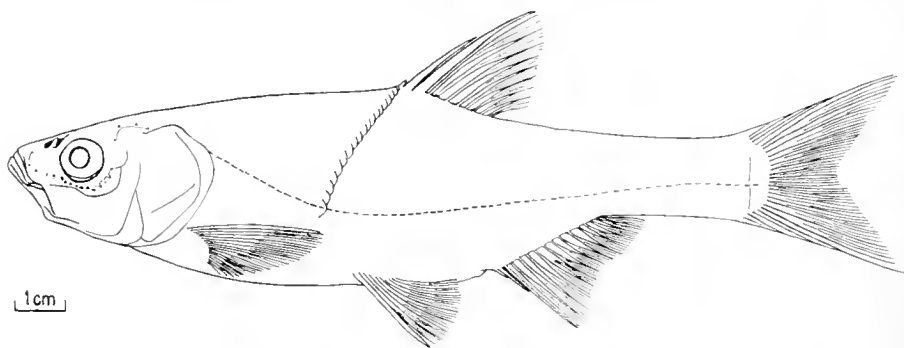


FIG. 9. *Mitrogrex terraesanctae terraesanctae*, L. Tiberias.

Dorsal fin originating just behind vertical of anterior end of base of pelvic fin; first ray usually a mere nodule, third with thickened, rigid proximal portion and flexible tip, the whole 18.5–19.0% SL, of which the rigid part is 72–86% in specimens over 100 mm SL. Formula iii 8, rarely iii 7 or iii 9 (a total of 13 in one of a sample of 760 according to Steinitz).

Anal fin originating at the vertical just behind base of dorsal. Total number of rays 14–18, usually 16 or 17 according to Steinitz, 15 or 16 (iii 12 or 13) in the B.M.(N.H.) samples.\*

Pectoral fin not extending to origin of pelvic; with 15–19 rays, usually 17 (Steinitz, 1959 : 56, table ix).

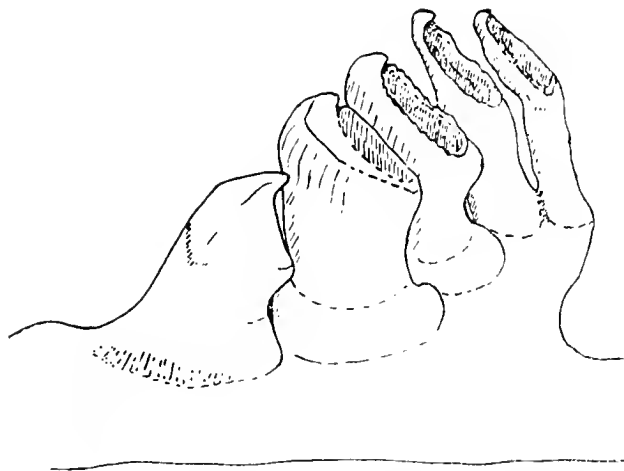


FIG. 10. Pharyngeal teeth of left side from holotype of *M. t. terraesanctae*. From Steinitz, 1952, fig. 1.

\* Possibly Steinitz counted the two last, often closely apposed rays separately; see p. 293.



TABLE 4. Frequencies of gill-raker numbers on lower part of anterior arch in *M. t. terraesanctae* and *M. t. hulensis* excluding one at the epi-ceratobranchial joint.

Gill-rakers	13	14	15	16	17	18	19	20
<i>M. t. terraesanctae</i>								
B.M.(N.H.)				3	8	13	8	2
Tel-Aviv			1	7	9	10	3	
<i>M. t. hulensis</i>								
B.M.(N.H.)		1	8	3	1	1		
Tel-Aviv	3	11	8	1				

Pelvic usually not reaching vent; with 8 or 9 rays (Steinitz, 1959 : 56 table x).

Vertebrae, excluding the complex vertebra, 34-37, mode 36 (the figures 39-41, mode 40 quoted from Lissner by Steinitz, 1959, must have counted the complex vertebra as 4 or 3 according as the urophore was counted or not).

Colour: Silvery to steel-blue, with counter-shading; top of head dark grey, a dark blotch on anterior part of operculum; skinny edge of operculum yellowish. Bases of pelvic and anal fins and parts of caudal yellowish, this colour spreading and becoming more intense, even reddish, at the breeding season.

Size: Ricardo Bertram (1944) records that individuals may occasionally reach 20 cm in total length; samples examined by Lissner and Steinitz ranged up to 19 cm in total length\*; B.M.(N.H.) samples to 18 cm total length and 150 mm SL. Of these, all that could be sexed above 13 cm (Steinitz) or 14 cm (B.M.) total length were females. Ricardo Bertram also reports that the average length of 791 females was 13.6 cm, of 986 males 10.3 cm.

Sexual dimorphism: In addition to the difference in size of maturity and maximum size between the sexes, ripe males have rows of small pointed tubercles along the upper sides of pectoral and pelvic fins and a few also on the anal.

Bionomics: for all that is known of the bionomics see Ricardo Bertram (1944), Steinitz (1959) and Komarowsky (1952). Briefly, *M. terraesanctae* in L. Tiberias is a pelagic fish, feeding on plankton, mainly zooplankton. The species forms big shoals and migrates to the shallows for spawning from December to the beginning of April.

#### MATERIAL EXAMINED.

Museum and reg. no.	SL (mm)	Locality	Collector or donor
B.M.(N.H.)			
1935.3.28.3	150	Lake Tiberias	Hornell
1935.11.1.9-10	70, 120	"	Craig-Bennett
1949.10.10.61-64	135-146	"	" " (1938)
1949.9.16.23-28	70-115	"	C. K. Ricardo-Bertram
1949.9.16.29-49	90-152	"	"
Tel-Aviv University			
P 3014, 3018	95-120	"	M. Goren

\* Steinitz gives 'total length' for his length classes in tables xv and xvi of 1959, but mentions 'standard length' for the same ranges on p. 61. Probably total length was correct, i.e. including caudal fin with the lobes folded together as usual in fishery research.

Ripe ovarian eggs measure 1.1 to 1.9 mm in diameter and when laid adhere to the pebbles. In adult fish outside the spawning season reserves of fat accumulate among the viscera.

*Mirogrex t. hulensis* subsp. n.

(Fig. 11)

*Alburnus sellal* (nec Heckel); Norman & Trewavas in Washbourn & Jones, 1938 : 55 (Lake Huleh).

Holotype of the subspecies: ♀, 158 mm SL collected in the former L. Huleh by R. Washbourn in 1936. B.M.(N.H.) 1936.4.6.20. Paratypes 6 others with same data as holotype, B.M.(N.H.) 1936.4.6.21-26; and 5, 104-205 mm SL collected by M. Goren in Hula Natural Reserve, the part of L. Huleh remaining after drainage of the main part of the lake and swamps. Tel-Aviv University nos. 3007-3010.

Data are taken from the holotype and paratypes, 7 other specimens collected in 1943 by Dr C. K. Ricardo-Bertram and 19 collected by Goren and used for frequencies and means of the contrasting characters.

*M. t. hulensis* differs from *M. t. terraesanctae* in the deeper body, contrasting in both the greatest depth and the depth of the caudal peduncle; in the lower numbers of gill-rakers; and in having a pharyngeal formula of 5-4 in all specimens examined for this purpose (tables 4 and 5).

The pharyngeal teeth were examined in seven specimens in the B.M.(N.H.) and several in the Tel-Aviv collection. In those (4 examined) collected by Washbourn in 1935 (and others collected by Goren) the shape of the teeth is like that in the nominate subspecies, but in the 3 examined from Dr Ricardo-Bertram's collection of 1943 the anterior tooth or two anterior teeth on each side is (or are) stout and flat-topped (fig. 11).

The differences in the gill-rakers and pharyngeal teeth doubtless reflect a different balance in the food. The former Lake Huleh was shallow with broad swampy areas and abundant stands of emergent vegetation including papyrus, to the submerged stems of which adhered an epiphytic fauna and flora including dense colonies of the gastropods *Melanopsis costata* (Olivier) and *Theodoxis jordani* (Sowerby), as noted by Tristram (1865 : 588). Tristram did not find these molluscs alive in Lake Tiberias, but Bodenheimer (1935) says they occur everywhere in running water, and Barrois lists them as the two commonest species along the shores of Lake Tiberias.

TABLE 5. Contrasting proportions and numbers of scales in lateral line in *M. t. terraesanctae* and *M. t. hulensis* between total lengths of 65 and 225 mm. BD = depth of body, PH = height of caudal peduncle, PL = length of caudal peduncle, all expressed as % SL; l.l. = scales in lateral line.

	<i>M. t. hulensis</i> n = 23		<i>M. t. terraesanctae</i> n = 30		t(v) test for level of significance
	Range	Mean ± SD	Range	Mean ± SD	
BD	22.0-33.1	28.4 ± 2.2	18.3-23.8	20.8 ± 2.1	0.5%
PH	3.9-12.3	11.0 ± 1.3	7.6-9.6	8.7 ± 1.4	0.5%
PL	18.9-24.4	20.6 ± 1.3	18.0-20.7	19.4 ± 1.0	0.5%
l.l.	55-76	64.02 ± 4.81	66-80	70.05 ± 3.06	0.5%

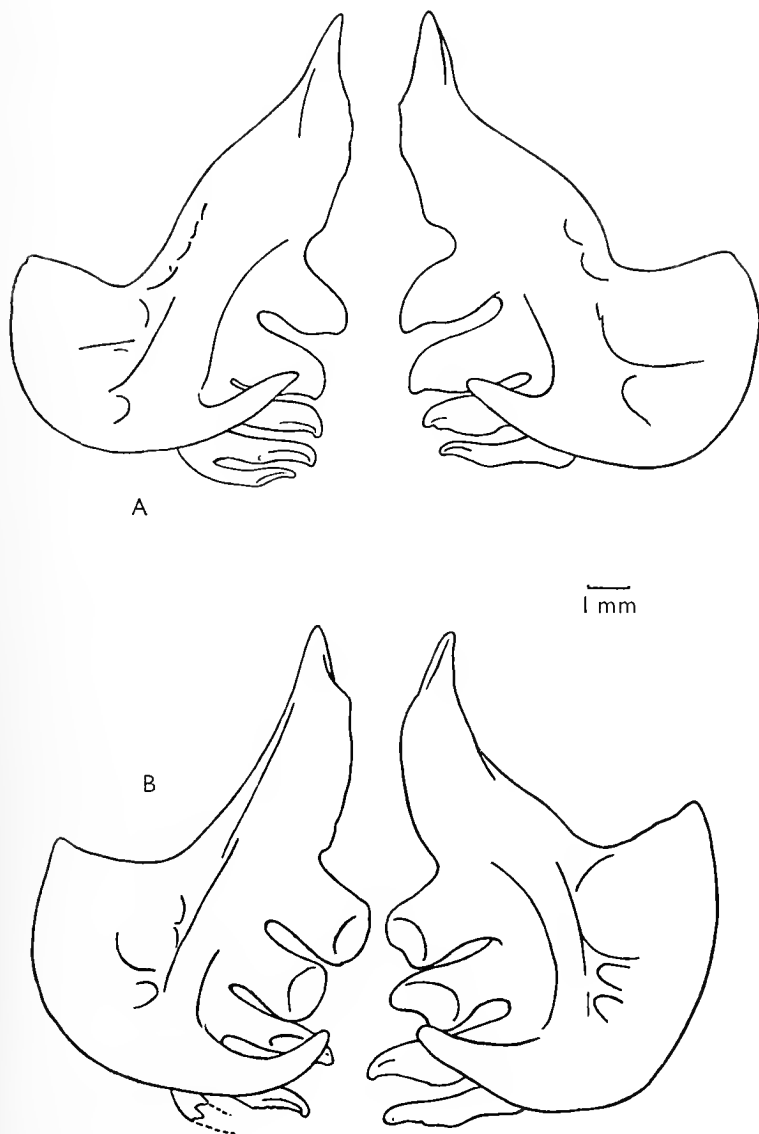


FIG. 11. *Mirogrex t. hulensis*, pharyngeal bones from two individuals collected by, (A) R. Washbourn in 1935; and (B) C. K. Ricardo-Bertram in 1943.

In any case, the two lakes present many contrasts and it is likely that the specialization towards a plankton diet would have gone much farther in Tiberias than in Huleh. We have as yet no evidence that the stronger teeth were used to crush snail shells, but it would be interesting to compare the food of the two populations, for the small reserve that was retained after Lake Huleh was drained is still strongly contrasted with *L. Tiberias* ecologically.

A parallel suggests itself with the cichlid fish *Astatoreochromis alluaudi* Pellegrin, which in Lake Victoria has massive pharyngeal bones with molariform teeth and subsists largely on aquatic snails, but in Lake Edward, where snails are not abundant, uses softer food-items and has a much weaker pharyngeal dentition carried on much smaller bones. Greenwood (1965) has recorded evidence that *A. alluaudi* is still flexible in respect of this striking morphological feature. Dr Greenwood tells us that there is an even closer comparison within the Cyprinidae, between the populations of *Barbus altianalis* of the East African lakes.

#### MATERIAL EXAMINED.

Museum and reg. no.	SL (mm)	Locality	Collector or donor
B.M.(N.H.) 1936.4.6.20-26 Holotype and Paratypes	131-158	Lake Huleh	R. Washbourn
Tel-Aviv University P 3007-3011 Paratypes	104-205	Hula Reserve	M. Goren
B.M.(N.H.) 1949.9.16.1-7 Tel-Aviv University	108.5-168	L. Huleh	C. K. Ricardo-Bertram
P 143-145	83-160	Hula Reserve	

#### DISCUSSION

*A. telavivensis* has so much in common with *A. lissneri* that our first care was to establish the distinctions between these two. The most trenchant distinction appeared when both were X-rayed for vertebral counts, when it was found that *A. telavivensis* was in this feature below the range of our other species of *Acanthobrama* and *Mirogrex* (except one specimen of the 28 *Mirogrex* radiographed). The additional vertebrae in both genera are in the caudal region, and this accounts for the higher values in *A. telavivensis* for proportions expressed as % SL.

Table 6 demonstrates the uniqueness of *A. telavivensis*, and also that its range (32-34 behind the Weberian complex) is identical with that of '*Rutilus*' *tricolor* Lortet—or at least those specimens in Paris and London that have been radiographed.

The general resemblance between *A. telavivensis* on the one hand and '*R.*' *tricolor* and '*Alburnus*' *vignoni* Lortet on the other led one of us (E.T.) to go to Lyon to examine Lortet's types. Both these species have scale-numbers within the range for *A. telavivensis*, 12-13 anal rays, (6) 7-8 soft dorsal rays, 8-11 gill-rakers on the lower part of the first arch and pharyngeal teeth in a single row. But the last simple dorsal ray is no thicker than the first branched and there is no ventral keel. In most specimens examined there are a few median ventral scales just behind the pelvic

base, followed by 4 or 5 paired, which may overlap or may be separated by a narrow strip of skin. They could not be admitted into the genus *Acanthobrama*. Specifically they differ from *A. telavivensis* also in having the mouth at an angle of 40°–50° with the horizontal.

If we accept *A. telavivensis* as an *Acanthobrama* in spite of its low vertebral numbers, its likeness to '*R.*' *tricolor* would indicate that the ancestor of *Acanthobrama* was very much like '*R.*' *tricolor*.

The generic position of '*R.*' *tricolor* has not been determined. Dr Banarescu (personal communication) suggests that it may be related to subgenus *Orthroleucos* Derzhavin (1937), in which he would include not only the type species *R. (O.) atropatensis* Derzhavin of Azerbaidjan but certain southern European forms, including *R. (O.) rubilio* (Bonaparte). This brings into consideration species with lower numbers of scales and anal rays, but from them '*R.*' *tricolor* and *A. telavivensis* must have diverged very close together.

*R. tricolor* and '*Alburnus*' *vignoni* Lortet, both described from the waters of Damascus, are very much alike. Comparison is complicated by the fact that the syntypes of *A. vignoni* are all bigger than those of *R. tricolor*. Allowing for the difference in size and condition (the *A. vignoni* are all plump fishes) the only important distinction seems to be in the longer, more pointed vertical fins of *R. tricolor*. The specimens identified by Pellegrin (1923) as *R. tricolor* cover the size-ranges of the syntypes of both Lortet's species, but at all sizes they have fins of the relative proportions of *A. vignoni*. They are probably all conspecific, the syntypes of *R. tricolor* perhaps representing a long-finned subpopulation, but only more field work can decide this.

Another question left open is the generic status of *Acanthobrama centisquama*, which can only be settled when more material is available and the gill-rakers can be examined.

TABLE 6. Frequencies of numbers of vertebrae behind the complex vertebra in some Cyprinidae of south-western Asia.

	32	33	34	35	36	37	38	39	40
<i>Capoetobrama kuschakewitschi</i>							1		1
<i>Mirogrex t. terraesanctae</i>			1	2	18	1			
<i>M. t. hulensis</i>				5	1				
<i>Acanthobrama marmid</i>									
Basra				1	6				
Mosul							2	2	
Syrian Euphrates				1	1	2	2		
<i>Acanthobrama lissneri</i>				2	8				
<i>Acanthobrama telavivensis</i>	2	12	6						
' <i>Rutilus</i> ' <i>tricolor</i>	1	3	4						

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Vertebral counts were made from radiographs prepared in Tel-Aviv University and the British Museum (Natural History).

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California State University, Fullerton

*Pp.* 317-339; 9 *Text-figures*



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# SYSTEMATIC COMPARISON OF THE STROMATEID FISHES *STROMATEUS* *BRASILIENSIS* FOWLER AND *STROMATEUS* *STELLATUS* CUVIER FROM COASTAL SOUTH AMERICA WITH A REVIEW OF THE GENUS

By MICHAEL H. HORN

## SYNOPSIS

Two populations of stromateid fishes occur along opposite coasts off southern South America and are recognized as distinct species. The available names are *Stromateus brasiliensis* Fowler, 1906, for the Atlantic population and *Stromateus stellatus* Cuvier, 1829, for the Pacific population. These allopatric species can be completely distinguished on the basis of vertebral counts. Differences also exist in median fin-ray numbers, pectoral fin length, head length, and otolith length. The genus *Stromateus* is described and a key is provided to the three species. The third and quite distinct species, *S. fiatola*, occurs in the Mediterranean and off West Africa. The two South American species occupy an intermediate systematic position between *S. fiatola* and *Peprilus Snyderi*, the most primitive species of an advanced stromateid genus.

## INTRODUCTION

*Stromateus*, one of the three genera of stromateid fishes (Haedrich, 1967), is widely distributed along the coasts of the Mediterranean, along the west African coast to Cape Town, and along the southern Atlantic and Pacific coasts of South America (Text-fig. 1). It is the only genus of the family with a transoceanic distribution—across the South Atlantic. According to Haedrich (1967), the genus contains the most primitive species of the family, *Stromateus fiatola*, but is not the direct ancestor of the other genera but rather must share a common ancestor with them.

Two apparently allopatric and quite similar populations of *Stromateus* occur in temperate waters on the continental shelf off the coast of South America—one off the Atlantic coast, and one off the Pacific coast. While names are available for each population, *Stromateus brasiliensis* Fowler, 1906, for the Atlantic population, and *S. stellatus* Cuvier, 1829, for the Pacific population, a junior synonym of the latter, *S. maculatus*, Cuvier and Valenciennes, 1833, is frequently applied to both populations. The status and relationships of the populations have long been uncertain. The availability of a series of specimens from both coasts has permitted a comparison of the two populations and provided a basis for the reinterpretation of specific relationships in the genus.

This paper presents a morphological and distributional comparison of the two populations and offers evidence for recognizing each as a separate species. The genus is reviewed, and an account is given of the distinct Eastern Atlantic and Mediterranean species, *S. fiatola*. The generic relationships in the family are discussed with particular emphasis on the limits, relationships, and zoogeography of *Stromateus* and *Peprilus*.

#### MATERIALS AND METHODS

Most of the specimens examined are in the British Museum (Natural History), London (BMNH), or were obtained from the Smithsonian Oceanographic Sorting Center, Washington, D.C. (SOSC). The latter are listed as uncatalogued specimens of the Museum of Comparative Zoology, Harvard University (MCZ). Other specimens studied are in the collections of the Academy of Natural Sciences, Philadelphia (ANSP), American University, Beirut, Lebanon (AUB), Museum National d'Histoire Naturelle, Paris (MNHN), Institut für Seefischerei, Hamburg (ISH), Zoological Museum, Copenhagen (ZMC), United States National Museum (USNM), the MCZ, and the Woods Hole Oceanographic Institution (WHOI). The AUB specimens are temporarily located at WHOI. The WHOI specimens will ultimately be catalogued in the MCZ. Fifteen specimens of *Stromateus brasiliensis* were received from the Instituto de Biología Marina, Mar del Plata, Argentina, and have not been deposited in an institution.

The methods of counting, measuring, and illustrating conform to those described by Horn (1970).

**MATERIAL EXAMINED.** The number of specimens, the range of standard lengths, and the locality appear in that order within the parentheses. Those specimens marked with an asterisk (\*) have been radiographed. The number radiographed equals the number measured unless otherwise indicated.

*Stromateus fiatola*. \*AUB P-717 (4 : 52.5-85.0 mm, Antelias, Lebanon); \*BMNH 87.3.2.30 (1 : 75.3, Lower Congo); BMNH 98.9.10.1 (1 : 111.3, Mossel Bay, Cape of Good Hope, South Africa); BMNH 1920.9.7.3 (1 : 203.0, Nahr Rubin, near Jaffa, Israel); \*BMNH 1922.1.13.56 (1 : 181.0, Durban, South Africa); \*BMNH 1925.9.19.100-101 (2 : 64.9, 93.9, Port Said); BMNH 1929.8.31.4 (1 : 150.0, Port Said); \*BMNH 1930.8.26.68 (1 : 294.0, Accra, Ghana); \*BMNH 1938.11.1.61 (1 : 191.0, near Haifa, Israel); \*MCZ 16729 (1 : 257.0, Mediterranean? from Vienna Museum); \*WHOI uncat. (1 : 176.7, Nigeria, Federal Fishery Service of Nigeria No. 4046); \*WHOI uncat. (6 : 199.8-240.0, Guinean Trawling Survey I Gulf of Guinea, 7° 20.5' N, 12° 40' W, 30 meters depth); \*WHOI uncat. (2 : 195.0, 290.0, Guinean Trawling Survey II, Gulf of Guinea, 3° 28' S, 10° 36' E, 20 meters); ZMC 73-75 (3 : 26.5-34.6, near Naples Zoological Station, Italy).

*Stromateus brasiliensis*. ANSP 11354 (1 : 278.0, holotype of *Stromateus brasiliensis* Fowler, 1906, Rio Grande do Sul, Brazil); \*BMNH 1925.6.10.1 (1 : 290.0, off northern coast of Tierra del Fuego); \*BMNH 1932.6.9.1-3 (3 : 253.0-273.0, Falkland Islands); \*BMNH 1935.9.11.8.9 (2 : 245.0, 283.0, off Uruguay, 34° S, 50° W); \*BMNH 1936.6.9.1-10 (10 : 227.0-285.0, Falkland Islands); \*BMNH 1936.8.26.1072-



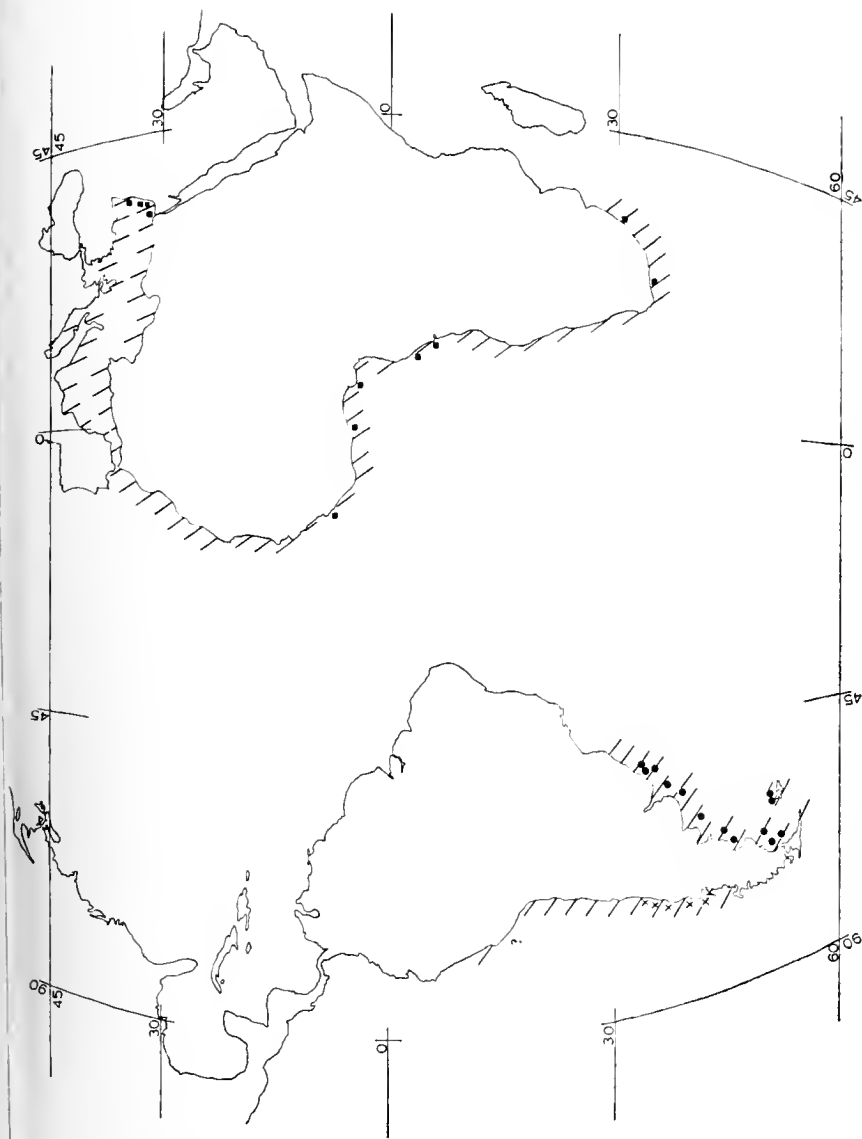


FIG. 1. Distribution of *Stromateus*. The slanted lines indicate the total known distribution of each species. Localities from which specimens were examined in this study are represented by an X for *S. stellatus*, by a filled circle (●) for *S. brasiliensis*, and by a filled square (■) for *S. fatola*. The question mark (?) in the northern part of the distribution of *S. stellatus* indicates the doubtful or rare occurrence of the species in that region.

74 (3 : 156.6-247.0, 44° 14' S, 63° 22' W); \*BMNH 1936.8.26.1075-8 (4 : 266.0-308.0, off Argentina); \*BMNH 1936.8.26.1079-83 (5 : 237.0-298.0, South Atlantic, 'DISCOVERY' Station W. S. 78/51.015, 91-93 meters); \*BMNH 1936.8.26.1084-7 (5 : 112.2-167.3, South Atlantic, 'DISCOVERY' Station W. S. 847, 51-56 meters); \*ISH 1463a-f/66 (6 : 116.0-285.6, South Atlantic, 45° 29' S, 66° 52' W, 'WALTHER HERWIG' Station 371/66, 85 meters, 4 radiographed); \*ISH 1186/66 (1 : 254.0, South Atlantic, 36° 49' S, 54° 37' W, 'WALTHER HERWIG' Station 250/66, 100 meters); \*MCZ 4599 (3 : 254.0-285.0, Rio Grande do Sul, Brazil); Uncatalogued (10 measured: 75.7-122.5, Mar del Plata, Argentina, received from Instituto de Biologia Marina, Mar del Plata, 15 radiographed).

*Stromateus stellatus*. \*BMNH 1935.6-12.20-22 (3 : 139.6-163.2, Dichato, Chile); BMNH 1935.8.27.29-33 (5 : 102.6-220.0, Bahia de Coronch, Chile); MNHN 264.11.3.1-2 (2 : 144.3, 163.5, types of *Stromateus maculatus* Cuvier and Valenciennes, 1833, Valparaiso, Chile); \*MCZ uncatalogued (10 : 50.5-99.4, 34° 03.6' S, 71° 58.4' W, R/V ANTON BRUUN Cruise 18A, Station 684, 40 meters); \*MCZ uncatalogued (11 : 106.5-210.0, 35° 22' S, 72° 33' W, R/V ANTON BRUUN Cruise 18A, Station 688B, 27 meters); \*MCZ uncatalogued (11 : 52.1-215.0, 37° 10.5' S 72° 21.5' W, R/V ANTON BRUUN Cruise 18A, Station 692, 18 meters); \*MCZ uncatalogued (2 : 205.0, 240.0, near Corral, Chile, 39° 42' S, 73° 27' W, 36-45 meters); \*USNM (1 : 193.0, Ancud, Chile, Chiloe Bay, 41° 52' S, 73° 53' W); WHOI uncatalogued (2 : 230.0, 237.0, Castro Bay, Chile, 42° 29' S, 72° 46' W).

#### SYSTEMATICS

##### Genus *STROMATEUS* Linnaeus, 1758

*Stromateus* Linnaeus, 1758 : 248. (Type species: *Stromateus fiatola* Linnaeus, 1758 : 248, by monotypy, Mediterranean.)

*Chrysostronus* Lacépède, 1802 : 697. (Type species: *Chrysostronus fiatoloides* Lacépède, 1802 : 697, by monotypy. Mediterranean. A synonym of *Stromateus fiatola* Linnaeus, 1758 : 248.)

*Fiatola* Cuvier, 1817 : 342. (Type species: *Stromateus fiatola* Linnaeus, 1758 : 248, by monotypy. Mediterranean.)

*Seserinus* Cuvier, 1817 : 342. (Type species: '*Seserinus Rondelet*' (*Seserinus rondeleti*) Cuvier 1817 : 343, by subsequent designation of Jordan, 1923 : 106. Mediterranean. A synonym of *Stromateus fiatola* Linnaeus, 1758 : 248.)

*Pterorhombus* Fowler, 1906 : 118. (Subgenus. Type species: *Fiatola fasciata* Risso, 1826 : 289, by original designation. Mediterranean. A synonym of *Stromateus fiatola* Linnaeus, 1758 : 248.)

**DIAGNOSIS.** The genus *Stromateus* is distinguished from other stromateid genera by the combination of moderately deep body, moderately long pectoral fins, usually five to seven small spines anterior to the rays of the dorsal fin, spotted body pattern, pelvic fins in the young (of one species), and no ventral spine on the pelvic bone. *Stromateus* is particularly distinguished from *Pampus* in having six rather than five branchiostegal rays and in having a movable rather than a fixed maxillary bone. *Stromateus* is further distinguished from *Peprilus* in having 41 to 49 vertebrae versus 29 to 36.

DESCRIPTION. Body moderately deep to elongate, depth 31 to 53 per cent of standard length, highly compressed. Caudal peduncle short, slender, and compressed. Dorsal and ventral profiles convex and similar, anterior dorsal profile slightly to moderately convex. Snout short and blunt, jaws equal. Eye small to moderate with surrounding adipose tissue reaching to nostrils; eye diameter either equal to or less than length of snout depending upon age. Nostrils double, anterior round, posterior a slit, moderate in size, directly anterior to eye, near end of snout. Dorsal and anal fins with long base, similar to each other, slightly to moderately falcate as produced by elongation of the first 10 to 13 rays; dorsal and anal coterminous, just anterior to caudal peduncle. Dorsal fin with five to seven small spines anterior to and continuous with the fin-rays; 42 to 56 total elements. Anal fin shorter than dorsal (fewer rays), with usually two or three small spines preceding and continuous with the fin-rays; 33 to 48 total elements. Posteriormost spines of anal and dorsal often difficult to distinguish from anteriormost soft rays. Pectoral fin lateral, just below level of eye, moderately long, either somewhat fan-like or pointed, base of fin slightly inclined, 15 to 30 per cent of standard length; 18 to 25 rays. Pelvic fins present in the juveniles of one species; small, inserting under end of pectoral fin base; fins absent in adult but two dark skin flaps often indicate the former presence of fins. No ventral spine on pelvic bone. Caudal fin moderately long to very long, moderately to deeply forked, about 17 to 32 per cent of total length; lobes equal.

TABLE I. Number of dorsal fin elements in species of *Stromateus*.

Species	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
<i>brasiliensis</i>						2	5	3	11	12	7	3	4	1	2
<i>stellatus</i>	1		1	1	3	9	10	10	9	1					
<i>fiatola</i>	1	2	5	4	3	2	4	2	2						

TABLE II. Number of anal fin elements in species of *Stromateus*.

Species	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
<i>brasiliensis</i>								1	6	7	9	11	6	5	2	1
<i>stellatus</i>				1		3	8	8	10	9	4	2		1		
<i>fiatola</i>	3	8	8	3	2	1										

TABLE III. Number of pectoral fin-rays in species of *Stromateus*.

Species	18	19	20	21	22	23	24	25
<i>brasiliensis</i>	1	7	21	19	2	2	1	
<i>stellatus</i>		8	17	20	2			
<i>fiatola</i>				3	4	9	7	2

TABLE IV. Number of gill rakers in species of *Stromateus*.

Species	14	15	16	17	18	19	20	21	22	23
<i>brasiliensis</i>					4	11	17	12	5	
<i>stellatus</i>					1	5	12	11	15	2
<i>fiatola</i>	2	1	1	12	6	2				

TABLE V. Number of vertebrae in species of *Stromateus*.

Species	41	42	43	44	45	46	47	48	49
<i>brasiliensis</i>					4	24	14	0	3
<i>stellatus</i>	3	6	32	4					
<i>jiatola</i>			4	13	3				

Scales small, cycloid, irregular in shape, deciduous, very small scales extending on to fins; cheek, suborbital area, preopercle, and sometimes opercle scaled; top of head and nape generally scaleless; scales usually absent in preserved material. Lateral line of trunk of simple, tubed scales which are often less deciduous than those of rest of body; lateral line above intermuscular septum, following dorsal profile and extending onto caudal peduncle but not to base of caudal fin. A branch of lateral line extends from immediately above eye posteriorly to head of hyomandibula where it joins a similar branch then turns upward toward mid-dorsal line in a wide, bony tract; not visible in all specimens. Cephalic lateral line of pores and canals on cheek, opercular area, snout, lower jaw, and top of head. Subdermal canal system apparently not well developed; pores on trunk lacking, top of head and nape underlain by a series of dendritic canals. As in other stromateoids, distinction between cephalic lateral line components and subdermal canal system not clear. Head length about 20 to 35 per cent of standard length depending upon species and age. Premaxilla not protractile, maxilla movable and not or just barely reaching anterior edge of eye; lacrimal bone reduced; end of maxilla exposed when mouth is closed. No supramaxilla. Jaw teeth small, uniserial, close-set, laterally flattened, usually with three subequal cusps, covered laterally by a membrane. Vomer, palatines, and basibranchials toothless. Gill membranes united across isthmus, divided from about level of anterior part of eye. Opercle and preopercle thin, flat, margins entire; opercle rounded, with two weak, ill-defined spines; angle of preopercle broadly rounded, projecting backward slightly. Gill rakers similar among the species, slightly less than one-half the length of the filaments, not toothed, fairly closely set, three to eight on epibranchial, one at junction of elements, and 10 to 15 on lower elements of first arch (cerato- and hypobranchials). Pseudobranch with no rudimentary rakers. Six branchiostegal rays, four on ceratohyal, two on epihyal. Vertebrae 41 to 49, 17 to 21 precaudal, 24 to 30 caudal. Three free interneurals ahead of dorsal fin. Two or three epural and four hypural elements in caudal apparatus. Sclerotic bones well ossified. Toothed pharyngeal sac behind last gillarch, joining tubular esophagus; stomach a simple sac; intestine long and in loops, about two to three times the standard length of the body; pyloric caeca numerous, short, in a dendritic mass adjacent to stomach. Swimbladder thin-walled, physoclistous, continuous with dorsal peritoneum, regressed in fishes larger than about 75 to 100 mm SL. Buccal and pharyngeal cavities light in colour; peritoneum silvery with a peppering of black pigment. Gonads paired, in postero-dorsal region of body cavity; ovary in mature and maturing individuals elongate, yellowish, and granular; eggs in ripe ovary spherical, yellowish, less than one millimeter in diameter; testis in mature and maturing specimens elongate, yellowish-white, and smooth in texture. No external sexual dimorphism apparent.

Colour in life iridescent bluish or greenish-silver dorsally to silver ventrally; numerous spots of varying colour on dorsal and upper ventral surfaces. The young of one species have five to nine dark vertical bands. Colour in preservative varying from bluish-brown to brown dorsally to silver ventrally or body completely brown or bluish-brown. The round or nearly round spots are dark in preservative and tend to disappear in one species. Individual melanophores conspicuous in specimens up to about 80 to 100 mm SL. Fins may be darker or lighter than the body; melanophores present on the membranes between the fin-rays. Eye usually darker than rest of body; lens opaque surrounded by iris which may be black, partly black and partly yellowish-white, or all yellowish-white

KEY TO THE SPECIES OF *Stromateus*

- 1 (2) Vertical bars on sides and pelvic fins present in juveniles of usually less than 100 mm SL; two dark skin flaps or scars indicate former presence of pelvic fins in adults; spots of varying colour on adults but usually lost in preservation; 33 to 38 total anal fin elements (Text-figs 2 and 3) . . . . . *S. fiatola* Linnaeus, 1758
- 2 (1) Vertical bars and pelvic fins never present; dark spots along upper sides of body, the number generally increasing with age; 36 to 48 total anal fin elements . . . . . 3
- 3 (4) Vertebrae 45 to 49; total dorsal fin elements 47 to 56; total anal fin elements 40 to 48; pectoral fin relatively short, 15 to 26 per cent of SL (Text-fig. 4) . . . . . *S. brasiliensis* Fowler, 1906
- 4 (3) Vertebrae 41 to 44; total dorsal fin elements 42 to 51; total anal fin elements 36 to 46; pectoral fin relatively long, 23 to 30 per cent of SL (Text-fig. 5) . . . . . *S. stellatus* Cuvier, 1829

*Stromateus fiatola* Linnaeus, 1758

(Text-figs 2 and 3)

*Stromateus fiatola* Linnaeus, 1758 : 248 (original description, Mediterranean, holotype not seen); Regan, 1902 : 203; Pellegrin, 1905 : 137; Metzelaar, 1919 : 227; Chabanaud and Monod, 1926 : 261, fig. 21; Fowler, 1936 : 672, fig. 303; Irvine, 1947 : 195, fig. 115; Barnard, 1947 : 193, Pl. XXXII, fig. 5; Smith, 1949 : 841; 1961 : 303, Pl. 63; Ben-Tuvia, 1953 : 19; Haedrich, 1967 : 102, fig. 39.

*Chrysostromus fiatoloides* Lacépède, 1802 : 697 (original description, Mediterranean, holotype not seen).

*Seserinus rondeleti* Cuvier, 1817 : 343 (original description, Mediterranean, holotype not seen).

*Fiatola fasciata* Risso, 1826 : 289 (original description, Nice, Mediterranean, holotype not seen); Fowler, 1906 : 118.

*Seserinus microchirus* Cuvier and Valenciennes, 1833 : 416 (original description, holotype not seen); Regan, 1902 : 204; Gilchrist and von Bonde, 1923 : 11, pl. XIX.

*Stromateus capensis* Pappe, 1853 : 26 (original description, Cape Town, South Africa, holotype not seen); Gilchrist and von Bonde, 1923 : 11; Fowler, 1925 : 212.

*Stromateus microchirus*, Günther, 1860 : 398; Pellegrin, 1905 : 137; Gilchrist and von Bonde, 1923 : 11.

*Stromateus fasciatus*, Fowler, 1936 : 673; Smith, 1949 : 841; 1961 : 303, pl. 97; Ben-Tuvia, 1953 : 19.

DIAGNOSIS. *S. fiatola* is a moderately deep to elongate species distinguished from the two other species of *Stromateus* in that the juveniles have pelvic fins and dark vertical bands. The scars or remnants of the pelvic fin remain in the adults.

DESCRIPTION. Proportional measurements are given in Table VI and meristic values in Table VII. Body moderately deep to elongate, anterior dorsal profile slightly to moderately convex. Eye diameter usually less than length of snout. Dorsal fin most frequently with five small spines and anal fin with two or three small spines preceding the rays. Pectoral fin somewhat rounded, fan-like. Pelvic fins small, disappearing with age with only dark flaps of skin or scars remaining. Caudal fin long to very long, moderately to deeply forked, about 22 to 32 per cent of total length. Three epural elements in caudal structure.

Colour in life iridescent blue or green with silvery aspect ventrally. Young have five to nine dark vertical bands which disappear with age; adults have spots over much of the upper surface of the body which vary from yellow to black in colour and from oblong to round in shape. Vertical bands of young usually remain visible in preservative but spots of adult often disappear to give uniform brown or bluish-brown colour.

Maximum length probably about 500 mm SL.

VARIATION. Coefficients of variation (V) for proportional measurements range from nine to 25 (Table VI) and from one to about seven for meristic characters (Table VII). *S. fiatola* is more highly variable in the morphological characters studied than the other two species of *Stromateus*, and this is largely associated with ontogenetic changes which are described below.

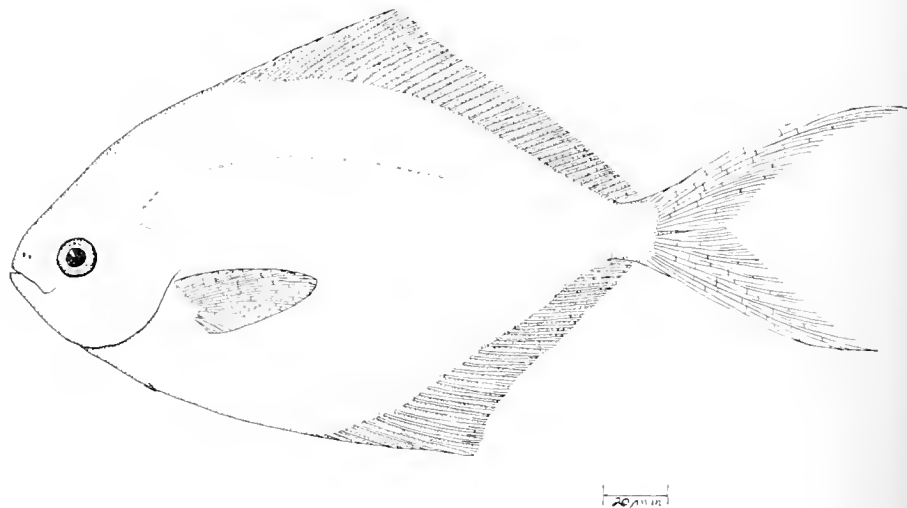


FIG. 2. *Stromateus fiatola*, 207.6 mm SL, 7° 20.5' N, 12° 40' W, Guinean Trawling Survey I. Spots usually present on fish of this size have disappeared on this specimen in preservative.

The frequency distribution of the number of dorsal fin-rays, anal fin-rays, pectoral fin-rays, gill rakers, and vertebrae for this and the other two species are presented in Tables I and V, respectively.

No geographic variation was detected in this species.

*S. fiatola* undergoes comparatively marked changes with age and to such an extent that the juveniles and adults have frequently been treated as separate species. *S. fasciatus* and *S. microchirus* are the names most often applied to the juveniles (see synonymic list above). The juveniles have five to nine dark vertical bands on the sides of the body and small pelvic fins. At a size of 100 mm SL, the fish has lost the vertical bands and the pelvic fins although small skin flaps or scars may persist in the pelvic area. The swimbladder is usually completely regressed by the time the fish reaches the above size.

The adults have spots of varying size and colour on the sides of the body. No marked morphometric changes occur with age although head length, eye diameter, and upper jaw length tend to decrease as a percentage of SL with age.

**DISTRIBUTION.** (Text-fig. 1) *S. fiatola* occurs throughout the Mediterranean Sea and along the Atlantic coast of Africa south to Cape Town. The species is confined to the continental shelf and inhabits relatively shallow water. Poll (1959) reported the adults to be common in depths of 12 to 50 meters off the coast of West Africa. Longhurst (1965) listed the fish as one of the associated species (i.e., not dominant) in the 'sub-thermocline sparid sub-community' on the Nigerian continental shelf.

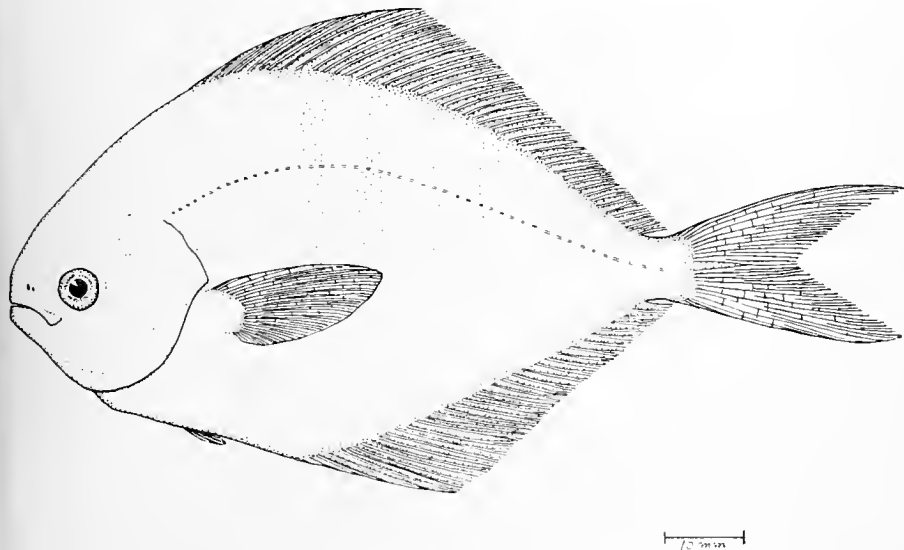


FIG. 3. *Stromateus fiatola*, 85.0 mm SL, eastern Mediterranean, off coast of Lebanon.

This sub-community begins at a depth of 45 to 50 meters and near the 20°C isotherm and is found over both hard and soft deposits below the thermocline to near the continental edge. Juveniles frequently occur with jellyfish medusae in surface waters.

TABLE VI. Proportional measurements of *Stromateus fiatola*. N = number of specimens; R = range of values;  $\bar{X}$  = mean; SE = standard error of mean; V = coefficient of variation. Size range, 26.5-294.0 mm SL; mean size, 153.4 mm SL.

	N	R	$\bar{X}$	SE	V
In thousandths of SL:					
Head length (HL)	26	225-351	271	6.93	13.05
Snout length	26	660-905	676	1.71	11.47
Eye diameter	26	0.35-0.92	0.62	3.07	25.26
Length of upper jaw	26	0.60-1.28	0.82	3.60	22.40
Interorbital width	26	0.91-1.33	1.09	2.41	11.27
Length of pectoral fin	26	1.83-2.67	2.24	4.70	10.71
Predorsal distance I	25	2.97-4.38	3.62	8.02	11.08
Predorsal distance II	24	2.01-3.12	2.37	6.17	12.76
Preanal distance	26	4.17-5.96	4.85	9.34	9.82
Maximum depth of body	26	3.59-5.29	4.70	9.54	10.35
Least depth of caudal peduncle	26	0.68-0.98	0.85	1.58	9.48
In thousandths HL:					
Eye diameter	26	1.55-2.89	2.24	6.01	13.67
			Mean V value		13.44

TABLE VII. Meristic values of *Stromateus fiatola*. Symbols as in Table VI.

	N	R	$\bar{X}$	SE	V
Dorsal fin rays*	25	42-50	46.0	0.45	4.87
Anal fin-rays*	25	33-38	34.8	0.26	3.68
Pectoral fin-rays	25	21-25	23.0	0.23	4.96
Total gill rakers	24	14-19	17.0	0.26	7.47
Total vertebrae	20	43-45	44.0	0.14	1.39
			Mean V value		4.47

\* Total fin elements

### *Stromateus brasiliensis* Fowler, 1906

(Text-fig. 4)

*Stromateus brasiliensis* Fowler, 1906 : 116, fig. 2 (original description, Rio Grande do Sul, Brazil, holotype seen, 278.0 mm SL, ANSP 11354); Haedrich, 1967 : 102.

*Stromateus maculatus*, Norman, 1937 : 118 (of *S. maculatus* Cuvier and Valenciennes 1833 : 399, in part—the population on the Atlantic coast of South America); Fordice, 1884 : 314, in part, specimen of description from Atlantic, but gives coast of Chile as the habitat; Abbot, 1899 : 337, in part, gives Atlantic coast northward to Patagonia as part of distribution; Hart, 1946 : 359.

DIAGNOSIS. *S. brasiliensis* is an elongate species with round, dark spots on the dorsal and upper ventral surfaces and with no pelvic fins. It is distinguished from the closely related *S. stellatus* by having 45 to 49 vertebrae compared to 41 to 44 in



*S. stellatus*. Characters that distinguish *S. brasiliensis* from *S. fiatola* are listed in the diagnosis of the latter species.

**DESCRIPTION.** Proportional measurements are given in Table VIII and meristic values in Table IX. Body elongate, anterior dorsal profile slightly convex. Dorsal fin usually with about five to seven small spines and anal fin with two or three small spines preceding the rays. Pectoral fin somewhat rounded, fan-like. No pelvic fins. Caudal fin moderately long to long, moderately forked, about 17 to 22 per cent of total length. Two epural elements in caudal structure.

Colour generally as described for the genus. The young in preservative have round, dark spots on the dorsal surface as do the adults, the number of spots increasing with age.

Maximum length probably about 450 mm SL.

**VARIATION.** Coefficients of variation (V) for proportional measurements range from about 5 to about 28 (Table VIII) and from about 2 to about 5 for meristic characters (Table IX).

No geographic variation was detected in this species.

*S. brasiliensis* does not undergo striking changes with age. The number of spots on the body tends to increase with size, and eye diameter as a percentage of SL decreases with increase in size of the fish.

**DISTRIBUTION.** (Text-fig. 1) *S. brasiliensis* occurs along the Atlantic coast off southern South America from southern Brazil to the Falkland Islands and beyond to Tierra del Fuego, almost to 55° S, and as far eastward in this southern vicinity as 57° W.

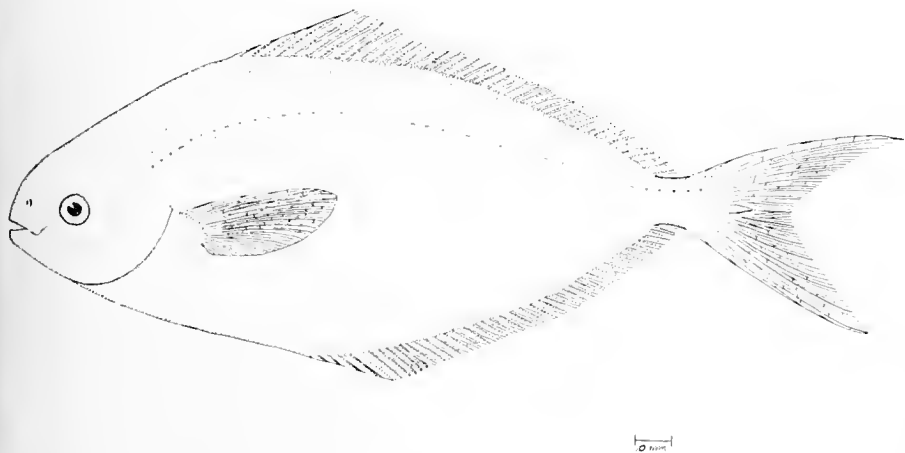


FIG. 4. *Stromateus brasiliensis*, 204.0 mm SL, 45° 29' S, 66° 52' W, 'Walther Herwig' Station 371/66.

TABLE VIII. Proportional measurements of *Stromateus brasiliensis*. Symbols as in Table VI. Size range, 75.7-308.0 mm SL; mean size, 210.4 mm SL.

	N	R	$\bar{X}$	SE	V
In thousandths of SL:					
Head length (HL)	54	198-305	235	2.78	8.70
Snout length	50	053-083	068	0.95	9.93
Eye diameter	50	031-085	050	1.99	28.16
Length of upper jaw	50	048-077	059	1.03	12.36
Interorbital width	49	067-106	084	1.44	11.99
Length of pectoral fin	54	154-259	216	3.29	11.18
Predorsal distance I	50	268-451	314	6.15	13.85
Predorsal distance II	49	179-271	216	3.14	10.01
Preanal distance	49	388-502	427	3.32	5.44
Maximum depth of body	54	310-463	398	4.56	8.43
Least depth of caudal peduncle	50	052-084	066	0.97	10.44
In thousandths of HL:					
Eye diameter	50	146-296	208	6.05	20.57
			Mean V value		12.59

TABLE IX. Meristic values of *Stromateus brasiliensis*. Symbols as in Table VI.

	N	R	$\bar{X}$	SE	V
Dorsal fin-rays*	50	47-56	51.0	0.30	4.16
Anal fin-rays*	48	40-48	43.1	0.29	4.64
Pectoral fin-rays	53	18-24	20.5	0.15	5.27
Total gill rakers	49	18-22	20.1	0.16	5.52
Total vertebrae	54	45-49	46.7	0.14	2.21
			Mean V value		4.36

\* Total fin elements.

### *Stromateus stellatus* Cuvier, 1829

(Text-fig. 5)

*Stromateus stellatus* Cuvier, 1829 : 213 (original description, coast of Peru, holotype not seen); Haedrich, 1967 : 102.

*Stromateus maculatus* Cuvier and Valenciennes, 1833 : 399 (original description, Valparaiso, Chile, holotype not seen); Guichenot, 1848 : 248, pl. 3, fig. 1; Fordice, 1884 : 314 (in part, lists coast of Chile in distribution but specimen of description from Rio Grande do Sul, Brazil); Abbott, 1899 : 314 (in part, Pacific coast); Regan, 1902 : 204; Evermann and Radcliffe, 1917 : 64; Norman, 1937 : 118 (in part, Pacific coast).

DIAGNOSIS. *S. stellatus* is an elongate species closely related to *S. brasiliensis* and has round, dark spots on the dorsal and upper ventral surfaces and no pelvic fins. Characters which distinguish the species from *S. brasiliensis* and *S. fiatola* are listed in the diagnosis of each of those species, respectively.

DESCRIPTION. Proportional measurements are given in Table X and meristic values in Table XI. Body elongate, anterior dorsal profile slightly convex. Dorsal fin with about five to seven small spines and anal fin with two or three small spines preceding the rays. Pectoral fin somewhat pointed. No pelvic fins. Caudal fin moderately long to long, moderately forked, about 20 to 24 per cent of total length. Two epural elements in caudal structure.

Colour generally as described for the genus. Small juveniles in preservative sometimes have no spots, but most frequently round, dark spots are present on the body and generally increase in number with age.

Maximum length probably 400 mm SL.

VARIATION. Coefficients of variation (V) for proportional measurements range from about 4 to 33 (Table X) and for meristic characters from about 2 to about 6 (Table XI).

No geographic variation was noted in this species.

*S. stellatus* does not undergo marked changes with age and has the lowest mean V values of the three species for the characters considered. However, eye diameter expressed as a percentage of SL has the greatest variation among the species and is due to change with age, the eye becoming relatively smaller. As in *S. brasiliensis*, the number of spots on the body tends to increase with age.

DISTRIBUTION. (Text-fig. 1) *S. stellatus* occurs along the Pacific coast off South America from southern Peru to southern Chile. Valenciennes (quoted in Cuvier (1829) and Abbott (1899)) stated that the fish was common in the fish markets of Lima from May to July; however, it probably occurs only infrequently or seasonally this far north. The most southerly locality encountered in the present study was Castro Bay, Chile at 42° 29' S. *S. stellatus* probably seldom occurs as far south as Tierra del Fuego.

TAXONOMIC COMMENTS. Whitley (1935) described a new species of *Stromateus*, *S. advectitius*, from a rough sketch of a fish collected on an Australian voyage (to New South Wales) in the late 1700's. The fish was later tentatively referred to as

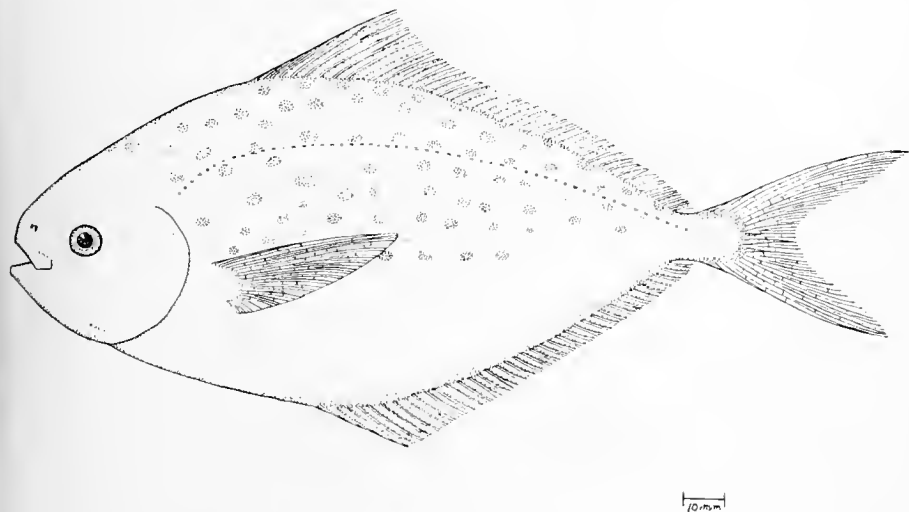


FIG. 5. *Stromateus stellatus*, 180.0 mm SL, 33° 22' S, 72° 33' W,  
R/V Anton Bruun Cruise 18A, Station 688B.

*Stromateus? maculatus*. Because Whitley was not certain of the identity and because *S. maculatus* was preoccupied, he named it *S. advectilius*. However, no other record of *Stromateus* from the southwestern Pacific exists, and the fish was quite likely not a member of this genus. The identity of this fish remains unknown.

TABLE X. Proportional measurements of *Stromateus stellatus*. Symbols as in Table VI. Size range, 50.5-240.0 mm SL; Mean size, 139.0 mm SL.

	N	R	$\bar{X}$	SE	V
In thousandths of SL:					
Head length (HL)	47	240-347	280	4.03	0.87
Snout length	47	068-082	077	0.50	4.42
Eye diameter	47	038-104	066	3.17	33.00
Length of upper jaw	46	055-091	070	1.32	12.80
Interorbital width	47	078-108	096	1.75	12.49
Length of pectoral fin	45	229-304	274	3.06	7.49
Predorsal distance I	46	302-396	340	3.86	7.70
Predorsal distance II	45	214-309	253	4.31	11.42
Preanal distance	47	404-483	437	2.56	4.01
Maximum depth of body	47	342-423	392	2.86	5.01
Least depth of caudal peduncle	47	057-070	064	0.45	4.88
In thousandths of HL:					
Eye diameter	47	158-347	229	7.88	23.61
			Mean V value		11.39

TABLE XI. Meristic values of *Stromateus stellatus*. Symbols as in Table VI.

	N	R	$\bar{X}$	SE	V
Dorsal fin-rays*	45	42-51	48.1	0.17	2.33
Anal fin-rays*	46	36-46	40.8	0.28	4.58
Pectoral fin-rays	47	19-22	20.3	0.12	4.04
Total gill rakers	46	18-23	20.0	0.18	5.60
Total vertebrae	45	41-44	42.8	0.10	1.61
			Mean V value		3.05

\* Total fin elements.

#### Comparison of *S. brasiliensis* and *S. stellatus*

The populations of *Stromateus* off the coasts of southern South America are quite similar and closely related. However, divergence in several morphological features has occurred, and two distinct populations are easily recognized. The populations are apparently allopatric—there are no records for extreme southern South America (Text-fig. 1). Because there has been no post-isolation contact of the divergent populations, the decision as to their taxonomic rank must remain a somewhat arbitrary one.

The two populations can be completely separated on the basis of vertebral number, the Atlantic form (*S. brasiliensis*) having 45 to 49 vertebrae and the Pacific form (*S. stellatus*) 41 to 44. Although vertebral number as a systematic character must often be used with caution, it can be used with some confidence in stromateid fishes.

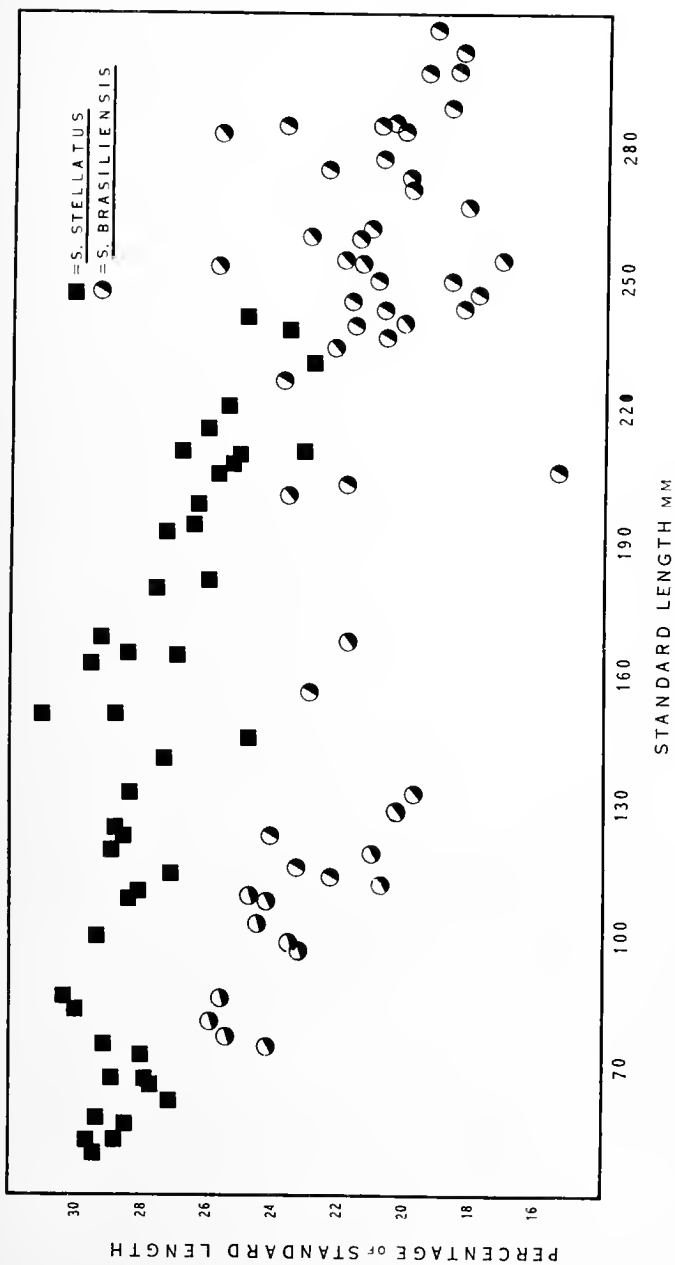


FIG. 6. Scatter diagram of pectoral fin length as a percentage of standard length in *Stromateus brasiliensis* and *Stromateus stellatus*.

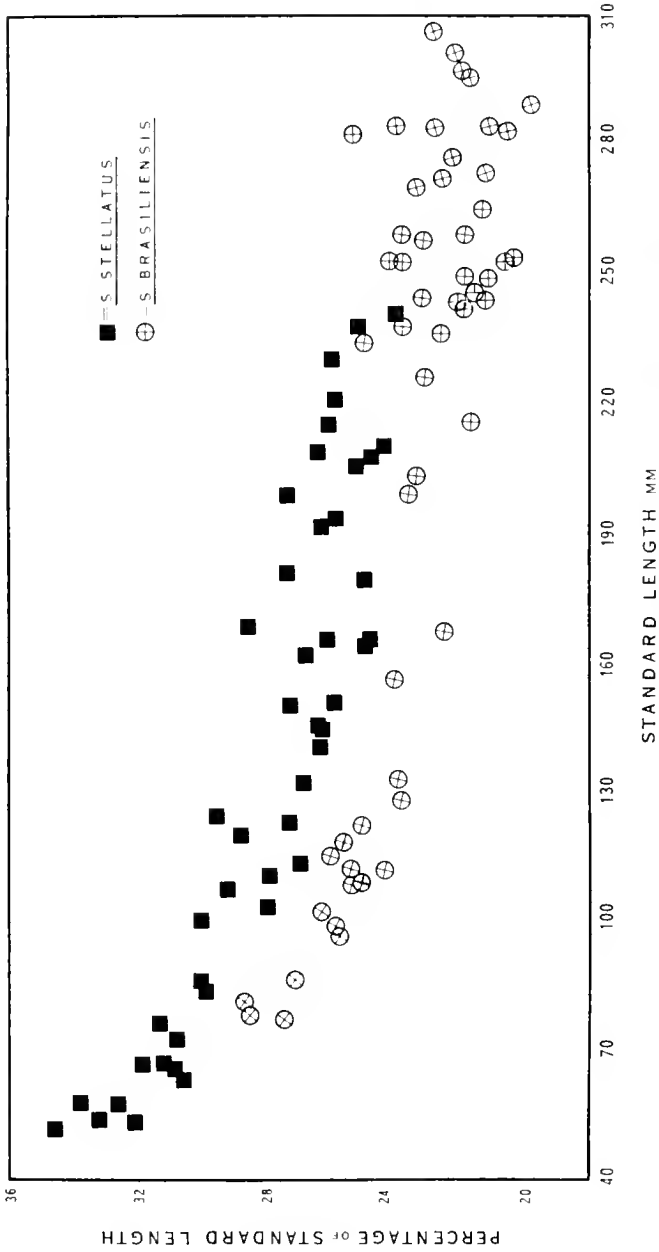


FIG. 7. Scatter diagram of head length as a percentage of standard length in *Stromateus brasiliensis* and *Stromateus stellatus*.

In the genus *Peprilus*, vertebral number varies little within a species and has been used to distinguish closely related species (Horn, 1970). In the Stromateidae, vertebral number appears to be of selective value, perhaps in association with trends in body shape.

The Atlantic population has a higher mean number of dorsal and anal fin-rays (Tables IX and X) although the populations overlap considerably in both.

Differences also exist in the relative length of the head and the pectoral fin, especially in the latter character. The Pacific form generally has both a longer head and a longer pectoral fin in relation to standard length (Text-figs 6 and 7). These differences, particularly in the length of the pectorals, may reflect divergence in behaviour and mode of life between the two populations. The shorter, more fan-like pectoral of *S. brasiliensis* may indicate a difference in locomotion and possibly in specific gravity, the fish perhaps being nearer neutral buoyancy as an adult than *S. stellatus*.

The otoliths of the two fishes are quite similar in shape and sculpturing (Text-fig. 8) but those of the Pacific population tend to be slightly more elongate than those of comparably-sized fish in the Atlantic (Text-fig. 9).

It is difficult to compare the ecology of the two forms since so little is known of this aspect, particularly of the Pacific population. Hart's (1946) discussion of the seasonal movements and potential economic importance of the Atlantic population provides a solid base on which to make future comparisons.

While little can be said about the comparative biology of the fishes, something can be said about the two habitats in which they exist and which may partially explain the observed divergence. The two coastlines differ considerably in the width of the continental shelf. The Atlantic side has a much broader shelf so that, if these fishes are restricted to the shelf region as they and other stromateids seem to be, the Atlantic has a larger preferred coastal habitat. Such a difference might be reflected in relative population size and perhaps even in size of individual fishes. From poor comparative data, the population size and individual size of *S. brasiliensis* seem probably to be larger than those of *S. stellatus*. Hart (1946) found that *Stromateus* in the Atlantic ranked third in total weight in one trawling survey and fifth in total

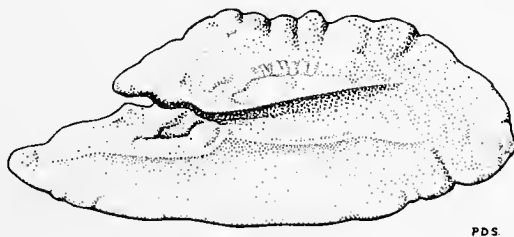


FIG. 8. Right otolith of *Stromateus brasiliensis*, median view ( $\times 13\frac{1}{2}$ ).  
From specimen 157.4 mm SL.

number during three surveys all on the Patagonian shelf. He considered the fish to be one of the most potentially valuable food fishes of the region. There is no indication to date that such a large population exists on the Pacific side.

The two coastlines are subject to different current conditions and thus have different temperature regimes at comparable latitudes. The cold, northward-flowing Peru Current pushes low temperatures farther north in the Pacific than does the cold, but weaker Falkland Current flowing northward along the Atlantic coast. The Brazil Current flows southward along the Atlantic coast to about 35° S and contributes to temperatures that are warmer than at the same latitudes in the Pacific. For example, the 25°C surface isotherm for February is at about 5° S latitude in the Pacific but at about 25° S latitude in the Atlantic (Sverdrup, *et al.*, 1942).

The two populations occupy a temperate, perhaps more nearly warm temperate, region with *S. stellatus* having a more northerly range presumably due to the effects of the Peru Current. The overall distribution in the Pacific in February, discounting any seasonal movements, would encompass a surface temperature range of from about 15° to about 20°C; in August the distribution would cover an isothermal range

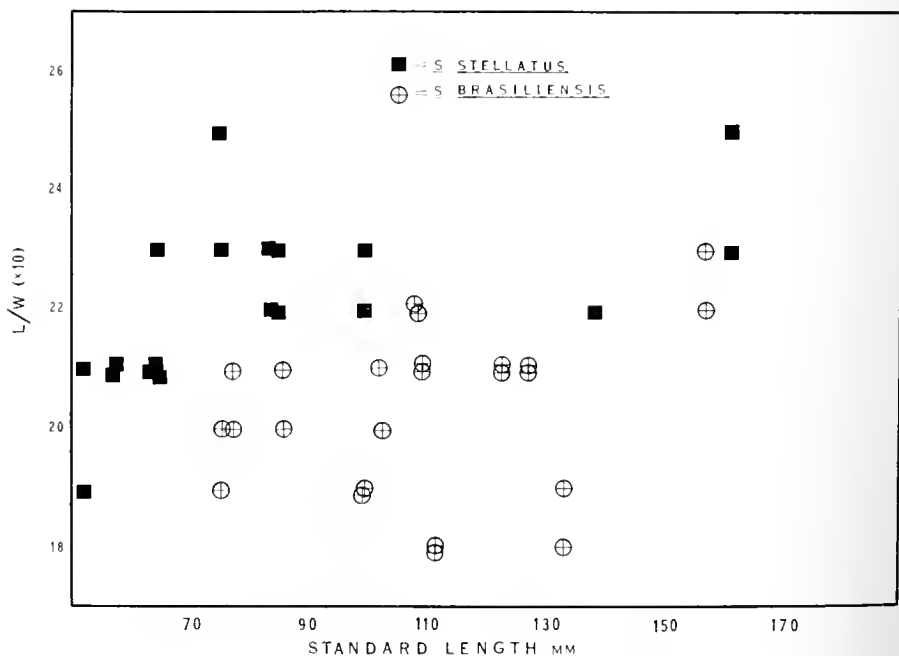


FIG. 9. Scatter diagram of otolith size in relation to standard length in *Stromateus brasiliensis* and *Stromateus stellatus*. (Length of otolith (L) divided by width (W) of otolith multiplied by 10.)



of from about 10° to about 17°C. The Atlantic population, discounting any seasonal movements, occupies a region approximately between the 10° and 25°C surface isotherms in February, and approximately between the 5° and 20°C surface isotherms in August. *S. brasiliensis* is, however, known to migrate seasonally (Hart, 1946), and the bulk of the population is probably most frequently found in the warmer parts of the range. It is not known how regularly or in what abundance *S. stellatus* occurs in the northern part of its range but probably infrequently. Most of the known collections are from farther south down to the vicinity of Chiloe Island which Ekman (1953) suggests is a possibly poorly defined southern limit for the warm temperate fauna.

In summary, the two populations appear to occupy similar temperature regimes although the Pacific one may be confined to a narrower range. The populations appear to be isolated by several hundred miles of coastline at the tip of South America and probably only in favourable periods in the past, perhaps during interglacial periods in the Pleistocene, has there been any significant migrations in either direction.

Recognition of the two populations as distinct species is based on the following evidence and reasoning: The populations show divergence in several morphological and meristic characters, and in one, vertebral number, there is no overlap. Divergence seems to be developing through both the reduction or absence of gene flow and adaptation to local conditions. The degree of divergence is comparable to that found in allopatric species of another stromateid genus, *Peprilus*, in which vertebral number is often an important character and apparently of selective value (Horn, 1970). In *Peprilus*, closely related species tend to either replace one another latitudinally along a continuous coastline (e.g., *P. simillimus* and *P. snyderi*) or parallel one another along opposite coastlines in different oceans (e.g., *P. paru* and *P. medius*; *P. simillimus* and *P. triacanthus*). A similar situation seems to exist in *Stromateus*. Less importantly, names are available in the literature for each population so that recognition of the populations at the species level requires no new names.

#### Position of *Stromateus* in the Family Stromateidae

Both Haedrich (1967) and Horn (1970) have suggested a Tethyan distribution for early members of the Stromateidae. Disruption of the Tethys Sea in the Miocene probably resulted in isolated populations and subsequently in the evolution of the three extant genera. Haedrich (1967 : 102) considers *Stromateus fiatola* to be the most primitive species in the family; characters considered to be primitive include the presence of pelvic fins in the young and three epural elements in the caudal structure. Haedrich considered *Pampus* to be the most highly derived genus. *P. paru*, the most highly derived species of *Peprilus*, parallels in several characteristics the advanced condition of *Pampus* (Horn, 1970 : 241).

*S. brasiliensis* and *S. stellatus* are then the derived members of *Stromateus* having completely lost the pelvic fins. They approach *P. snyderi*, the most primitive species of *Peprilus* (Horn, 1970 : 190), in several characteristics including the

presence of two epural elements in the caudal skeleton, the lack of pelvic fins, and an increased number of anal fin-rays. Indeed, a possible evolutionary route for *Peprilus* could have been from basic stromateid stock across the Atlantic via the southern coasts of South America to *Peprilus snyderi* presently found on the Pacific coast of Central America and Mexico. It is equally possible, however, that the ancestral stock of *Peprilus* was an element of the western Tethyan fauna.

*S. brasiliensis* and *S. stellatus* occupy an intermediate systematic position between the most primitive species of *Peprilus*, *P. snyderi*, and the most primitive stromateid, *S. fiatola*. The two species of *Stromateus* approach *P. snyderi* in the characters mentioned above but also retain affinities with *S. fiatola* in having a high vertebral number, a high number of dorsal fin-rays, low dorsal and anal fin lobes distinct dark spots on the body, and in attaining a relatively large size. Generic separation of the South American species might be justified but the decision should await thorough study of the osteology and other internal features.

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# THE MARINE MOLLUSCA OF THE TRUCIAL COAST, PERSIAN GULF

H. E. J. BIGGS



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*Pp. 341-421; 6 Plates, 10 Text-figures,*



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# THE MARINE MOLLUSCA OF THE TRUCIAL COAST, PERSIAN GULF

By H. E. J. BIGGS

## INTRODUCTION

THIS report on the Mollusca of the Trucial coast, at the southern end of the Persian Gulf, is based on a collection made by a team of geomorphologists from the Imperial College of Science and Technology, London led by Dr G. Evans. One hundred and ninety eight species are recorded including many new records for the Persian Gulf; five new species are described.

Little has been written on the Mollusca of the Trucial Coast although there is a considerable literature on the Persian Gulf. Melvill and Standen (1901, 1907) and Melvill (1928) record a total of 1618 species for the Persian Gulf, but only 32 of these are recorded for the southern coasts and these are all from Dubai. Haas (1952) records 40 species for the area based on the 1950 Peabody Museum Harvard Expedition to the Near-East which visited Dubai and Sharja; this list was expanded by Haas (1954), to include 64 species for the same area. For a more complete bibliography of the Persian Gulf than given in this work reference should be made to Melvill and Standen (1901, 1907) and Melvill (1928).

In this work the Persian Gulf refers to that area bounded by the 150 m depth contour at the northern end of the Gulf of Oman. As the stations in the Khor-al-Bazm were so numerous they are reported here as Eastern Khor, for material collected by Dr Sir Patrick d'E. Skipwith at 75 stations, and as Western Khor for that collected by Dr C. G. St. C. Kendall at 73 stations. For the list of species collected at each station see Biggs (unpublished MS) in the Library of the British Museum (Natural History).

The synonymies are restricted to records of the species in the Persian Gulf, south Arabia coast and Red Sea areas. Unannotated lists e.g. Shopland (1902) for Aden and Cooke (1885-6) for Suez Bay have not been cited unless more detailed records are unavailable. As Haas (1952, 1954) reports on the same area as this work reference is made to those lists. The identifications of all records placed in synonymy were not verified, the work of the authors cited is accepted unless otherwise stated.

Only some of the ecological data collected by Dr Evans and his team has been incorporated in this work, for more detailed information reference should be made to Kendall (1966), Kinsman (1964b) and Skipwith (1966). Photographs taken by members of the team in the region near Abu Dabi are included.

The majority of molluscs were collected dead and are worn but some specimens were collected live and preserved, where relevant the gross anatomy of such specimens has been figured. Unless otherwise indicated the material listed are adult specimens collected dead. The collection on which this work is based has been deposited in the Zoology Department of the British Museum (Natural History).

## THE TRUCIAL COAST

Contributed by Dr Graham Evans

The Trucial Coast forms the southern seaboard of the Persian Gulf from the Mussandam peninsular in the east to the base of the Qatar peninsular in the west. It is a low coastline bordered by numerous low islands and shallow banks which enclose shallow lagoons for much of its length (Evans, Kinsman, Sherman 1964), considerable geomorphological and sedimentological detail is contained in a series of unpublished theses of London University by Kinsman (1964), Skipwith (1966) and Kendall (1966). Inland is a narrow coastal plain which passes landwards in the west and central parts into the extensive desert area of the Rub-el-Khali. In the extreme east the coastal beaches and dunes are backed by outwash plains cloaked with dunes which run up to the foot of the Oman Mountains, and lagoons are less common. The coastline is composed almost entirely of Quaternary sediments which are usually unconsolidated but are sometimes cemented to form a friable rock. These sediments are composed almost exclusively of calcium carbonate produced by chemical and biochemical precipitation add breakdown as no freshwater drainage reached the area and there is no supply of sediment to the coast or open waters of the Gulf in this area except for some wind carried material. In a few localities low hills of Tertiary rocks form small scattered headlands.

Off shore there is a wide shallow marine area—the Great Pearl Banks—where the bottom rarely exceeds 120 ft. Low islands and banks rise from this shallow sea floor. These off shore islands are mostly salt plugs and show a great variety of rock types and they are often surrounded by soft Quaternary sediments. Coral is some-

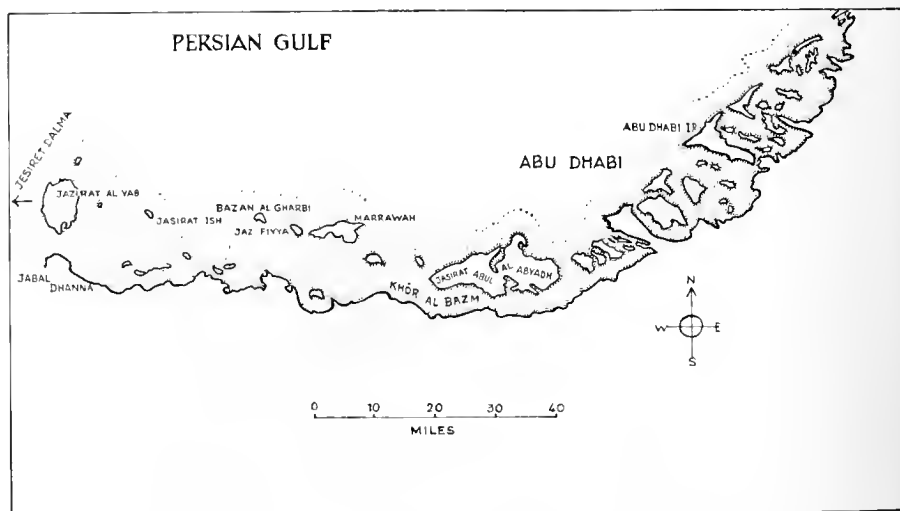


FIG. 1. Persian Gulf.

times found capping the banks and fringing the islands. The general Geology, Physiography and Oceanography of the area has been reviewed by Evans (1966).

The Persian Gulf is an area of unusually high temperatures and salinities. The temperatures range from 23°–32°C. in the Straits of Hormuz to 16°–32°C. at the head of the Gulf. The salinity ranges from 37‰–38‰ at the entrance to the Gulf and 38‰–41‰ at the north west end. Temperature and salinities are particularly high in the inshore area around the Trucial Coast, where there is no fresh water inflow and rainfall is only a few inches a year. Salinities range from 42‰–44.5‰ in the nearshore waters and 53.6‰–66.9‰ in the inner lagoons. Water temperatures range from 23°C.–34°C., in the coastal waters, to 22°C.–36°C. in the inner lagoons. In water pools on the exposed algal flats the temperature and salinities reach greater extremes (e.g. 77.4‰ at 36°C.). Large diurnal variations in temperatures are found in the lagoonal area.

The principal wind is the 'Shamal' which blows from the north west and consequently the wave attack is also from the north west. A diurnal on-off shore system also exists. Tidal ranges are low (7 ft. approx. max.) in the nearshore waters and are even lower in the lagoons (approx. 3 ft.). Strong inshore winds may, however, raise the nearshore waters to several feet above their normal level and then flood the coastal plains. Tidal and other currents are generally weak except in the inlets leading into the lagoons where surface waters may reach speeds of 2 ft./sec.

The low islands and banks bordering the coast form a low barrier which parallels the coastline and protects a large lagoon—the Khor-al-Bazm—in the west of the area. In the eastern part however the islands are orientated mainly perpendicularly to the coastline and almost reach the mainland in many places. The lagoons in this part are thus a series of small enclosed water bodies.

The islands are fronted by sandy beaches and dunes. In some places small corals have colonized the sea floor in front of the islands and have developed small barrier reefs which enclose small mud filled lagoons; in other cases the corals have built up fringing reefs on the fronts of the islands and banks particularly in the west (to form fringing reefs). Where the waters from the lagoons gain access to the shallow southern Persian Gulf large tidal deltas have formed to produce wide shoal areas stretching up to a mile off shore. These deltas are covered by calcareous sands and often have wide areas of weed growing on them, particularly where rocky floors exist. These are only covered by about 6 ft. of water at low water. Elsewhere the sea floor deepens fairly sharply in front of the islands to an average depth of 24 ft.–30 ft.

Seaward of the tidal deltas and fronts of the islands the floor of the southern Persian Gulf is very shallow. It is covered by sand and muddy sand with the finer grained sediments occupying the depressions. Again the sediment is composed almost entirely of CaCO<sub>3</sub>. Seagrasses and weed are sometimes found growing on the floor.

In the east of the area large tidal channels up to 40 ft. deep run back into the lagoons and eventually die out as traced towards the mainland. They separate shallow banks from the islands and are bounded by broad shallow terraces where the water depths rarely exceed 4 ft.–6 ft., patches of weed are often found in the

channels and at scattered localities where rock is exposed on the terraces. Coral is found developing small reefs on the outer parts of the lagoons on the sides and in some places on the floor of the channels, but it never extends far into the lagoons. Elsewhere the floor of the channels are covered with coarse gravelly calcareous sand, and sometimes Quaternary limestone is exposed. However at their landward ends the channels may be filled with muddy sand and mud. In the Khor-al-Bazm a large area of calcareous mud is found behind the shelter of the coastal barrier.

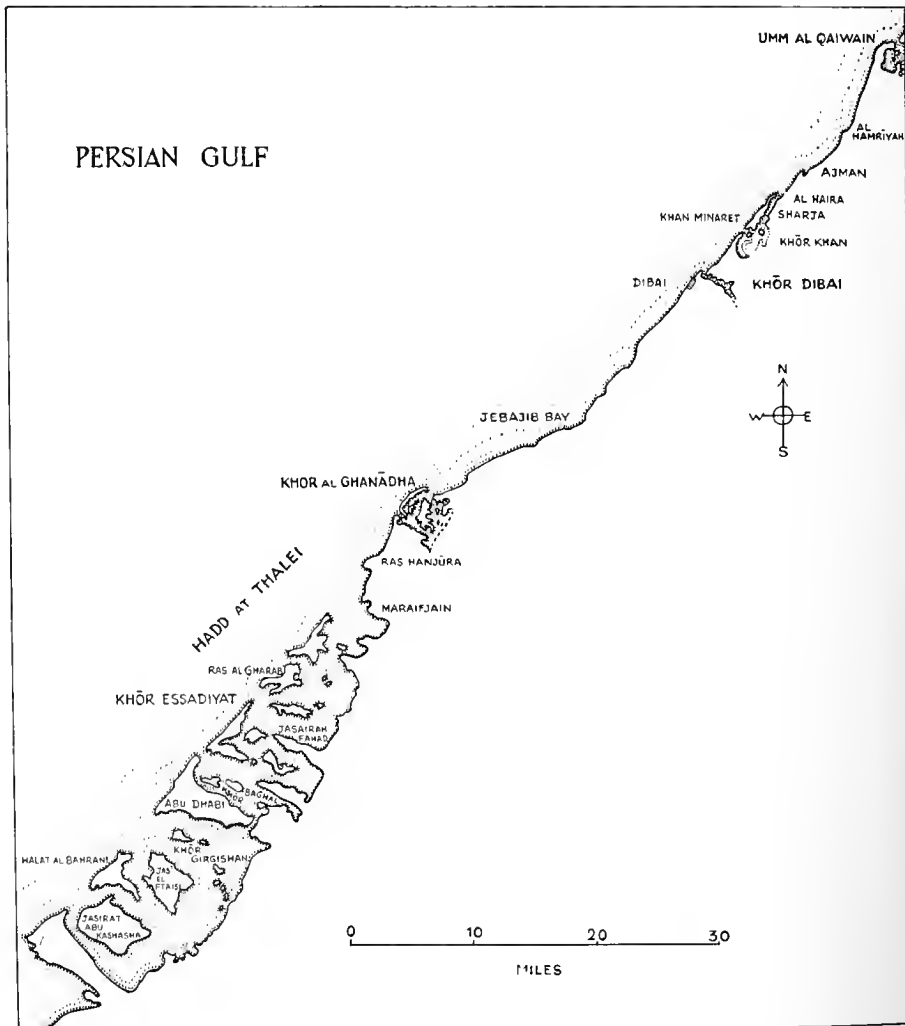


FIG. 2. Persian Gulf.

The terraces are covered with calcareous, slightly muddy sand or, more rarely calcareous sandy mud, and again bare rock is sometimes exposed. In places Quaternary limestones form small rocky islands in the lagoons and these provide hard rocky shores. Elsewhere the islands and mainland shores are fringed with narrow beach and dune ridges, and broad intertidal flats. These are sometimes colonised by blue-green algae, particularly along the mainland shore and the algal flats are often up to half a mile across. Extensive Mangrove swamps (*Avicennia marina* Försskål) occur fringing the islands and mainland (Plate 1, fig. 2) in some lagoons. The beach ridges and intertidal flats bordering the mainland shore pass into a wide low coastal plain—the sabkha. Its outer part is made up of old beach ridges and intertidal features which are now stranded far from the sea. This outer part of the plain has developed by extensive intertidal flat and beach ridge accretion in the same way that salt-marsh areas grew in more temperate latitudes. (Evans, Kendall and Skipwith, 1964).

The samples described were collected by a team of geologists led by Dr Graham Evans from the Imperial College, London. It included D. J. J. Kinsman, C. G. St. C. Kendall, and Sir Patrick A. d'E. Skipwith. The main collections were made between October 1961 and December 1965. Most of the collections were made on the beaches, intertidal flats, lagoons and near-shore zones by hand or by using a small grab. In addition some samples (designation Gh.) were collected with a grab from the deeper water areas off the Trucial Coast. When living organisms were encountered they were immediately preserved in alcohol and transported back to England in that state. In other cases lone shells were collected. This study is part of a much larger programme. The sediments are being studied at the Department of Geology, Imperial College, and have already been reported on in some theses and a few preliminary publications. The ostracods of the area are being studied by Dr R. Bate, British Museum (Natural History) and foraminifera collected in the samples are being studied by Dr J. R. Murray, Bristol University. Various other groups have been described by members of the Museum staff.

The expeditions were financed largely by N.E.R.C. with considerable help from Shell Oil Company Research Laboratory, The Hague, Holland. Mobil Oil Co. Research and Development, Dallas, U.S.A. also helped in financing the field work.

G.E.

## CLASS LORICATA

### Order CHITONIDEA

#### Family ISHNOCHITONIDAE

Genus *ISCHNOCHITON* Gray, 1847

*Ishnochiton yerburyi* Smith, 1891

*I. yerburyi* Smith, 1891 : 420, pl. 33, fig. 6.

MATERIAL. Sta. 102, 1 live.

This juvenile was found attached to *Pinna atropurpurea* Sowerby from the intertidal zone near the north cape of Abu Dhabi I. This is the first record of this species

from the Persian Gulf. It was described by Smith from Aden and is similar to specimens collected by Winckworth at Manora, Karachi and now in the B.M.(N.H.).

CLASS *GASTROPODA*

Sub Class *PROSOBRANCHIA*

Superfamily **PLEUROTOMARIACEA**

Family **FISSURELLIDAE**

Genus *EMARGINULA* Lamarck, 1801

*Emarginula planulata* A. Adams, 1853

(Plate 2, figs 1, 2)

*E. planulata* A. Adams, 1853 : 86. Reeve, 1873 : 19, sp. 20.

**MATERIAL.** Sta. 98, 1 live, B.M.(N.H.) Reg. No. 1968751.

This is a new record for the Persian Gulf. The shell is 11.5 mm long 7.2 mm broad and 3.4 mm high. The upperside is flesh-pink except for the apex which is yellowish; there are 47 radial ridges ornamented with closely placed imbrications, the ridges are alternately high and low, at the posterior end they are almost equal in height and at the anterior end the contrast in height is very marked. The inner side is thickened in the central part, rather dark yellow where the animal is attached; edges pale pink; area round the siphonal split thickened by the accretion of shelly matter, whitish. The inner edge of the shell is crenulate. Apex of the shell yellowish, very recurved, situated a little anterior to the median line. The fissure is narrow, extending to about halfway between the edge of the shell and the apex but after that it continues as a furrow to the apex where it disappears. Round the outer edge of the shell and on the upper side is a line which marks the limit of the overlap of the mantle.

The animal is deep crimson in colour throughout; the shell is somewhat buried in the mantle. Foot length 12.0 mm, breadth 10.0 mm. The mantle, which is irregularly serrate overlaps the shell about 1.5 mm. These measurements are based on an animal which has been in alcohol for some time.

The type series of 4 specimens in the B.M.(N.H.) have no locality but are from coarse sand and shells, 7 fms. Adams (1853) gives Singapore as the locality while Reeve (1873) gives the Philippines. The specimen figured is here selected lectotype (B.M.(N.H.) Reg. No. 196616/1). The differences between the types and the specimen here recorded are probably due to the former being worn.

A juvenile specimen from the Maldive Is. collected by Gardiner and a specimen from Port Blair, Nicobar I. were also examined.



Genus *DIODORA* Gray, 1821

*Diodora funiculata* (Reeve, 1850)

*Fissurella funiculata* Reeve, 1850, 19 : Sp. 65.

*Glyphis funiculata* Melvill and Standen, 1901 : 344.

*D. funiculata* Haas, 1952 : 115. Haas 1954 : 46. Biggs, 1958 : 271. Biggs and Grantier, 1960 : 387.

MATERIAL. Sta. 50, 1; Sta. 70A, 1 juvenile; Western Khor, 1 juvenile; Unlocated, 1 live.

*Diodora imbricata* (Sowerby, 1862)

*Fissurella imbricata* Sowerby, 1862 : 194, pl. 242, fig. 162.

MATERIAL. Sta. 12, 1 live, juvenile.

This is the first record of this species from the Persian Gulf. No locality is given for the type, the only other specimen examined was a juvenile from Karachi collected by Winckworth.

Superfamily TROCHACEA

Family TROCHIDAE

Genus *EUCHELUS* Philippi, 1847

*Euchelus angulatus* Pease, 1867

*E. angulatus* Pease, 1867 : 283, pl. 23, fig. 27.

*E. foveolatus angulatus* Melvill and Standen, 1901 : 350.

MATERIAL. Western Khor, 1.

Melvill and Standen (1901) record this species from Charbar, Makran Coast and Angas Bank, India. In the collection of the B.M.(N.H.) there are two specimens from Jask, Persian Gulf.

*Euchelus asper* (Gmelin, 1791)

*Trochus asper* Gmelin, 1791 : 3583

*E. asper* Melvill and Standen, 1901 : 350. Biggs, 1958 : 271. Biggs and Grantier, 1960 : 387.

This species is recorded as common by Kinsman (1964b) for the reef of the Trucial Coast, by Melvill and Standen (1901) for Karachi where it occurs 'amongst muddy rocks at low tide', by Biggs and Grantier (1960) for Ras Tanura and Biggs (1958) for Hormuz I. Haas (1952, 1954) does not record the species for the Trucial coast.

*Euchelus bicinctus* (Philippi, 1849)

*Trochus* (*Phorus*) *bicinctus* Philippi, 1849 : 102. Issel, 1869 : 226, 328.

*E. bicinctus* Tomlin, 1927 : 298. Moazzo, 1939 : 207.

MATERIAL. Eastern Khor, 9; Western Khor, 4.

Although not recorded by Melvill and Standen there are specimens in the B.M.(N.H.) collected on the Makran Coast in 3-7 fms. Moazzo (1939) reported the species in the Suez Canal as far north as Lake Timsah.

Genus *TURCICA* A. Adams, 1854

Sub-genus *PERRINIA* H. & A. Adams, 1863

*Turcica* (*Perrinia*) *stellata* A. Adams, 1863

*T. stellata* A. Adams, 1863 : 508.

*T. (P.) stellata* Melvill and Standen, 1901 : 301.

MATERIAL. Eastern Khor, 9 dead from 8 Stations; Western Khor, 19 dead from 12 Stations.

The above specimens are all much smaller than the type, which is from the 'China Sea', but this is not unusual for populations living in the warmer and more saline waters of the Persian Gulf. Melvill and Standen (1901) record the species from Charbar on the Makran Coast (dead shells), the Gulf of Oman (live in 15 fms.), Dabai on pearl oysters.

Moazzo (1939) includes the species in his synonymy of *Tectarius armatus* Issel under Littorinidae.

There is doubt about the authenticity of the type locality for this species, Tomlin has written on the type specimen tablet, 'Prob. from Gulf of Suez'. Certainly the existence of this species in Chinese waters needs confirmation.

Genus *TROCHUS* Linnaeus, 1758

Sub-genus *INFUNDIBULOPS* Pilsbry, 1889

*Trochus* (*Infundibulops*) *erythraeus* Brocchi, 1821

*T. erythreus* Brocchi, 1821 : 223.

*T. (I) erythraeus* Sturany, 1901 : 265. Tomlin, 1927 : 298.

MATERIAL. Sta. 12, 1; Sta. 9, 1; Eastern Khor, 1; Beach, 22.

A very common species in the area. Kinsman (1964b) reports that it is common on the off shore shelf.

Genus **GIBBULA** Risso, 1826

Sub-genus **ENIDA** A. Adams, 1860

**Gibbula (Enida) townsendi** Sowerby, 1895

*G. (E) townsendi* Sowerby, 1895 : 279, pl. 18, figs 7-9. Melvill and Standen, 1901 : 349.

MATERIAL. Western Khor, 2 juveniles.

This is a new record for the Persian Gulf as the specimens of Melvill and Standen (1901) are from the Makran Coast, the type locality. The species has not been recorded for the Red Sea but I have specimens collected by Mr W. Reed, from Dongonab Bay, north of Port Sudan.

Genus **MINOLIA** A. Adams, 1860

**Minolia gradata** Sowerby, 1895

*M. gradata* Sowerby, 1895 : 279, pl. 18, figs 5 and 6. Melvill, 1928 : 97. Sturany, 1903 : 265

MATERIAL. Eastern Khor, 4; Western Khor, 3.

**Minolia holdsworthiana** (G. & H. Nevill, 1871)

*Gibbula holdsworthiana* Nevill G. and H., 1871 : 3, pl. 1, fig. 18.

*M. (Conotrochus) holdsworthiana* Melvill and Standen, 1901 : 350.

*M. holdsworthiana* Melvill, 1928 : 97.

MATERIAL. Eastern Khor, 11 from 5 stations; Western Khor, 31 from 10 stations.

As Melvill (1928) states that his (1901) record was in error for *Minolia variabilis* A. Adams, this may be considered as the first record for the Persian Gulf.

**Minolia variabilis** A. Adams, 1873

*M. variabilis* A. Adams, 1873 : 207, pl. 23, fig. 10. Melvill, 1928 : 97.

*M. holdsworthiana* (in error) Melvill and Standen, 1901 : 350.

MATERIAL. Western Khor, 2.

Melvill (1928) records this species from Reshire, Gulf of Oman (abundant), Karachi (in mud, 3 to 7 fms). It is possible that the *Margarita variabilis* A. Adams listed by Shoplund for Aden is this species.

Genus *MONILEA* Swainson, 1840

Sub-genus *PRIOTROCHUS* Fischer in Kiener, 1879

*Monila (Priotrochus) obscura* (Wood, 1828)

*Trochus obscurus* Wood, 1828 : pl. 5, fig. 26. Issel, 1866 : 409.

*M. (P) obscura* Moazzo, 1939 : 208.

*Cantharidus kotschii* (in error) Biggs, 1958 : 271. Biggs and Grantier, 1960 : 387.

MATERIAL. Sta. 36, 10; Sta. 49, 7; Sta. 59, 13, 6 live; Sta. 60, 7; Sta. 61, 4 live; Sta. 63, 13; Sta. 64, 1; Sta. 68, 15 live; Sta. 92, 4 live; Eastern Khor 79; Western Khor, 50.

A common intertidal species. It is evident from the material studied (including some from Kuwait) that there is considerable variation in size, shape and markings of the shell of *obscura* and the South African specimens may be an extreme form of this species.

Genus *UMBONIUM* Link, 1807

*Umbonium vestiarius* (Linnaeus, 1758)

*Trochus vestiarius* Linnaeus, 1758 : 758.

*Rotella vestiaria* Issel, 1866 : 410.

*U. vestiarius* Fischer, 1891 : 227. Melvill and Standen, 1901 : 351. Biggs, 1958 : 271. Biggs and Grantier, 1960 : 387.

MATERIAL. Sta. 70, many; unlocated 3; Eastern Khor, 1; Western Khor, 3.

Family **CYCLOSTREMATIDAE**

Genus *CYCLOSTREMA* Marryat, 1818

*Cyclostrema quadricarinatum* Melvill and Standen, 1901

*C. quadricarinatum* Melvill and Standen, 1901 : 346, pl. 22, fig. 2.

MATERIAL. Western Khor, 8.

This is a new record for the Persian Gulf, the species was described from the Gulf of Oman, in 225 fms. on sand and mud. The present record is from the intertidal.

Family **TURBINIDAE**

Genus *TURBO*

*Turbo coronatus* Gmelin, 1791

*T. coronatus* Gmelin, 1791 : 3594. Melvill and Standen, 1901 : 352. Haas, 1952 : 115. Biggs, 1958 : 272. Biggs and Grantier, 1960 : 388.

MATERIAL. Sta. 27, 8 live; Sta. 53, 3 live; Sta. 63, 17 live; Sta. 68, 3 live; Sta. 70, 3; Sta. 86, 5 live juveniles; Sta. 92, 3 live; Eastern Khor, 21; Western Khor, 7.

As reported by Kinsman (1964b) this is a common intertidal species.

*Turbo radiatus* Gmelin, 1791

*T. radiatus* Gmelin, 1791 : 3594. Moazzo, 1939 : 200. Biggs and Grantier, 1960 : 387.

*T. Chemnitzianus* Sturany, 1903 : 78, 264.

MATERIAL. Eastern Khor 13 + 3 live.

The live specimens were from a coral bank in the Middle of the Khor-al-Bazm.

Genus *TRICOLIA* Risso, 1826

*Tricolia fordiana* (Pilsbry, 1888)

*Phasianella fordiana* Pilsbry, 1888 : 173.

*P. elachista* Melvill and Standen, 1901 : 351.

MATERIAL. Western Khor, 49.

The species is common at the Western end of the Khor-al-Bazm but unrecorded in the eastern end of the Khor. I am indebted to Dr Robert Robertson, of Philadelphia, for pointing out the identity of Melvill's species with one previously described by Pilsbry.

Genus *PHASIANELLA* Lamarck, 1804

*Phasianella solida* (Born 1778)

*Helix solida* Born 1778 : 408.

*P. nivosa* Reeve, 1862, 13 : sp. 8.

*P. variegata nivosa* Melvill and Standen, 1901 : 352.

MATERIAL. Sta. 39, 2 live, 1 juvenile; Eastern Khor, 8; Western Khor, 3; unlocated, 2.

Melvill and Standen (1901) record this species for the Makran Coast and Karachi, 'usually found from 3 to 7 fms, sand and mud'. This is a new record for the Persian Gulf, it appears to be fairly common.

Superfamily *NERITACEA*Family *NERITIDAE*

Genus *SMARAGDIA* Issel, 1869

*Smaragdiana rangiana* (Récluz, 1841)

*Nerita rangiana* Récluz, 1841 : 339.

*N. (S.) rangiana* Sturany, 1903 : 264.

*S. rangiana* Barnard, 1963b : 204.

MATERIAL. Eastern Khor 6; Western Khor, 6.

This is the first record of this species in the Persian Gulf.

Superfamily **NERITACEA**Family **PHENACOLEPADIDAE**Genus **PHENACOLEPAS** Pilsbry, 1891***Phenacolepas evansi*** n. sp.

(Pl. 2, figs 3, 4)

Shell white, semitransparent, broadly oval, rather flat; apex small, bulbous, smooth, inclined posteriorly but not projecting over the margin of the shell; ribs radiate from the apex, increasing in size towards margin, ribs with flat imbrications increasing towards the margin; interspaces with fine concentric striations, these are continuous over ribs between striations; margin slightly crenulate; interior of shell white, striated, the muscle scar is rounded at the anterior and posterior ends but deeply indented laterally.

TYPE MATERIAL. HOLOTYPE B.M.(N.H.) Reg. No. 1968757 Western end, Khor-al-Bazm, Oman. Length 5.6 mm, width 4.7 mm, height 2.0 mm.

PARATYPE A B.M.(N.H.) Reg. No. 1968758 Western end Khor-al-Bazm. Length 6.1 mm, width 5.7 mm, height 2.3 mm.

PARATYPE B B.M.(N.H.) Reg. No. 1968759, Sta. 58. Length 7.4 mm, width 6.8 mm, height 2.7 mm.

Compared with *Phenacolepas granocostata* (Pease) which appears to be its nearest relative this species is (a) flatter and broader, (b) with radial ribs higher and imbricate, (c) the apex is not so arched and does not protrude over the posterior end of the shells as in *granocostata*.

The species is named in honour of Dr Graham Evans as an acknowledgement of his careful collecting of mollusca and on whose work this paper is based.

***Phenacolepas omanensis*** n. sp.

(Pl. 2, figs 5, 6)

Shell white, thin, ovate; apex sub-central, inclined posteriorly but not overlapping the posterior end of the shell; protoconch globular, smooth, nipple-like, distinctly separated from the rest of the shell by a growth-line; surface of shell generally irregularly imbricated in latitudinal rows which are denser towards the edge of the shell; interior white, porcellaneous, with a thickened fold or ridge parallel to the edge of the shell and situated posteriorly fading out as it reaches the sides; muscle-scar distinct, entire with two distinct lobes on each side separated by a sinus, rim of shell somewhat crenulate.

TYPE MATERIAL. HOLOTYPE B.M.(N.H.) Reg. No. 1968755, Sta. 101 live. Length 8.2 mm, width 7.0 mm, height 2.8 mm.

PARATYPE B.M.(N.H.) Reg. No. 1968756, Sta. 101 live. Length 8.5 mm, width 7.0 mm, height 2.9 mm.

The chief feature which separates this proposed new species from *evansi* n.sp is the fact that the imbrications are not placed regularly and are not on longitudinal ridges as in *evansi*.

This is the first record of the genus *Phenacolepas* in the Persian Gulf and after examination of further material it may be necessary to separate them under a new sub-generic name.

### Superfamily LITTORINACEA

#### Family LITTORINIDAE

#### Genus *NODILITTORINA* v. Martens 1897

#### *Nodilittorina subnodosa* (Philippi 1847)

*Tectarius subnodosa* Philippi, 1847 : 161, pl. 3, fig 8, 9. Moazzo 1939 : 183.

*Littorina subnodosa* Cooke, 1885b : 269. Issel, 1869 : 191.

**MATERIAL.** Sta. 57, 16 live; Sta. 61, 10 live; Sta. 68, 2 live; Sta. 72, 275 live; Sta. 73, 7 live; Sta. 75A, 45 live; Sta. 92, 3 live; Sta. 99, 6 live; Eastern Khor 3; Western Khor, 1.

This species is generally found on intertidal flats which have a substrate of muddy sand, but in one case it was in the high intertidal zone with blue-green algal flat as substrate. The salinity was about 42‰ and the temperature ranged from 22°C. in December to 33°C. in July/August. However one locality, Station 73, in the outer lagoon near Abu Dhabi I. had a salinity of 50.05‰ in July/August 1966 with a temperature of 34°C. (= about 93°F.) at the same time of the year.

The colour of the specimens was generally a dull gray-green, possibly due to corrosion. In order to ascertain the actual colours a number of specimens from Sta. 57 and Sta. 73 have been washed in 10% HCl to remove the encrustations and variable colour patterns have been revealed ranging from uniform dark brown (occasionally almost black), banded (brown with white bands, white with brown bands, white or black with orange bands) to entirely orange.

Average measurements of a sample of 14 from Sta. 75A, height 12.8 mm, breadth 9.0 mm.

The specimens from Sta. 72 and Sta. 73 show a large amount of variation in sculpture, ranging from heavily noduled to almost smooth; all specimens have corrugations on the body whorl near the suture.

Specimens from the southern end of the Qatar Peninsular (collected by Illing) and from near Ras Tanura (collected by Grantier) were also examined.

Superfamily **RISSEOCEA**Family **HYDROBIIDAE**Genus **IRAVADIA** Blanford, 1867***Iravadia trochlearis*** (Gould, 1861)*Rissoina trochlearis* Gould, 1861 : 400.*I. trochlearis* Melvill and Standen, 1901 : 369.

MATERIAL. Sta. 12, 2; Western Khor 9.

The specimens from Sta. 12 was in 115 feet of water which suggests the species may not be confined to littoral zones as would be inferred from former records.

Family **RISSOIDAE**Genus **RISSOINA*****Rissoina distans*** (Anton, 1839)*R. distans* Anton, 1839 : 62.*R. (Rissolina) distans* Melvill and Standen, 1901 : 367.

MATERIAL. Sta. 72, 2; Eastern Khor, 3.

This is a new record for the Persian Gulf, as the Melvill and Standen record of the species is for Bombay and Anton does not give a locality for the type.

***Rissoina savignyi*** Jousseau, 1894*R. savignyi* Jousseau, 1894 : 101.

MATERIAL. Eastern Khor, 1.

It is possible that this species is synonymous with *R. clathrata* A. Adams which is recorded by Melvill and Standen for the Persian Gulf, Makran Coast and Karachi.

***Rissoina seguenziana*** Issel, 1869*R. seguenziana* Issel, 1869 : 209. Moazzo, 1939 : 188.*R. (Phosinella) seguenziana* Melvill and Standen, 1901 : 369.

MATERIAL. Sta. 70, 1.



Superfamily **CERITHIACEA**Family **TURRITELLIDAE**Genus **TURRITELLA** Lamarck, 1799***Turritella auricincta*** v. Martens, 1882

*Turritella auricincta* von Martens, 1882 : 107. Sturany, 1903 : 233. Moazzo, 1939 : 180. Tryon, 1886 : 208.

**MATERIAL.** Eastern Khor 17 specimens, mostly fragments; Western Khor 29 specimens, mostly fragments.

This is a new record for the Persian Gulf. Pilsbry (1886) includes the name amongst his 'unfigured, undetermined and spurious species' but gives Friendly Islands as the locality for the species. It is therefore not clear just which of the adjectives Pilsbry wished to apply to this species.

***Turritella fascialis*** Menke, 1828

Menke, 1828 : 83.

**MATERIAL.** Sta. 77, 1.

A new record for the Persian Gulf; Kinsman (1964b) records the species as rare on the reef in mid-lagoon.

Family **PLANAXIDAE**Genus **PLANAXIS** Lamarck, 1822***Planaxis sulcatus*** (Born, 1778)

*Buccinum sulcatum* Born, 1778 : 251.

*P. sulcatus* Melvill and Standen, 1901 : 377. Thorson, 1940 : 162. Biggs, 1958 : 272. Biggs and Grantier, 1960 : 388. Barnard, 1963 : 140.

*P. sulcatus savignyi* Sturany, 1903 : 263.

**MATERIAL.** Sta. 61, 13, 6 live; Sta. 68, 9; Sta. 92, 2; Western Khor, 2.

This species is widely distributed in the Indo-Pacific region. Details of its reproduction and development in the Persian Gulf have been recorded by Thorson (1940).

Family **POTOMIDIDAE**Genus **CERITHIDEA** Swainson, 1840***Cerithidea cingulatus*** (Gmelin, 1791)*Murex cingulatus* Gmelin, 1791 : 3561.*Potamides fluviatilis* Fischer, 1891 : 225.*P. (Tympanatomus) fluviatilis* Melville and Standen, 1901 : 375.*C. cingulatus* Haas, 1952 : 115. Haas, 1954 : 47. Biggs, 1958 : 272. Biggs and Grantier, 1960 : 388.

**MATERIAL.** Sta. 35, 4 juvenile; Sta. 57, 12 live; Sta. 59, 4; Sta. 60, 4; Sta. 71, 17 juvenile; Sta. 97, 2; Eastern Khor, 69; Western Khor, 6.

Both this species and *Pirenella conica* are able to flourish in the most extreme conditions. In Bundar Abbas, where the salinity is about 27‰ the species is not only abundant but of large size (Biggs, 1958), and on the opposite side of the Gulf on the Trucial Coast, it tolerates a salinity of 42‰ although the specimens are somewhat smaller. In the north of the Gulf it occurs more sparingly at Ras Tanura (Biggs and Grantier, 1960). Unfortunately I have not seen any records of the salinity in that area, but with the outflow from the Shatt-al-Arab and the Karun River it could be very much lower than either of the above two localities.

Genus **PIRENELLA** Gray, 1847***Pirenella conica*** (Blainville, 1829)*Cerithium conicum* Blainville, 1829 : 158.*P. cailiaudi* Potiez and Michaud, 1844 : 359.*P. conica* Tomlin, 1927 : 296.*Potamides (P.) conica major* Moazzo, 1939 : 176.

**MATERIAL.** Sta. 57, 12 live; Sta. 67, 24; Sta. 72, 25; Eastern Khor, 21; Western Khor, 13.

As with *Cerithidea cingulatus* this species can tolerate extreme conditions, those taken at Station 72 were living on muddy sand in about 6 inches of water with a salinity of 42‰. The species is also found in polluted water in Aden harbour.

Genus **TEREBRALIA** Swainson, 1840***Terebralia palustris*** (Bruguère, 1792)*Cerithium palustris* Bruguère, 1792 : 486.

**MATERIAL.** Sta. 51, 2.

This is a new record for the Persian Gulf. Both the specimens above were dead and damaged. It seems remarkable that such a large and conspicuous species has not been recorded before and there is just the possibility these specimens may have come in with ballast.

Family **DIASTOMIDAE**Genus ***FINELLA*** Adams, 1860***Finella pupoides*** (A. Adams, 1860)*Finella pupoides* A. Adams, 1860 : 336.*Fenella pupoides* Melvill and Standen, 1901 : 370. Taylor, 1968 : 200.

**MATERIAL.** Sta. 5, 27; Sta. 7, 22; Sta. 13, many; Sta. 14, 2; Sta. 77, 1; Eastern Khor, 4; Western Khor, 39.

This species is fairly common in the Persian Gulf, Melvill and Standen (1901) report it from Bushire, Dr L. V. Illing took some in both 15 and 18 metres of water off the south-east side of Qatar Peninsular (Biggs Colln.).

***Finella reticulata*** (A. Adams, 1860)*Dunkeria reticulata* A. Adams, 1860a : 422.*Fenella reticulata* A. Adams, 1864 : 40. Tryon, 1887, 9 : 395. Melvill and Standen, 1901 : 370.

**MATERIAL.** Western Khor, 9.

This species is extremely variable, Tryon (1887) places it in the synonymy of *O. scabra*, A. Adams; he figures *O. reticulata*. Even in the small sample from the Khor-al-Bazm there is much variation and two of them are extremely tall as compared with the others.

***Finella scabra*** (A. Adams, 1860)*Dunkeria scabra* A. Adams, 1860a : 421.*Fenella scabra* A. Adams, 1864 : 40. Taylor, 1868 : 200.*Finella scabra* Tryon, 1887, 9 : 395.

**MATERIAL.** Sta. 5, 10. Sta. 7, many; Eastern Khor, 6; Western Khor, 51.

This is a new record for the Persian Gulf.

Genus ***SCALIOLA*** A. Adams, 1860***Scaliola arenosa*** A. Adams, 1862*S. arenosa* A. Adams, 1862 : 421. Melvill and Standen, 1901 : 370. Taylor, 1968 : 200.

**MATERIAL.** Sta. 7, many; Sta. 14, many; Sta. 62, 4; Eastern Khor, 1; Western Khor, 30.

This species is the commonest of the genus in the material from the Trucial Coast. It is a new record for the Gulf as Melvill and Standen (1901) record it from Karachi and Bombay.

*Scaliola bella* A. Adams, 1860

*S. bella* A. Adams, 1860 : 120.

MATERIAL. Sta. 12, 1; Western Khor, 2.

New record for the Persian Gulf.

*Scaliola elata* Issel, 1869

*S. elata* Issel, 1869 : 198. Melvill and Standen, 1901 : 370. Moazzo, 1939 : 190.

MATERIAL. Western Khor, 2.

Writing of this and the two former species Melvill and Standen write 'with *Dialae*, *Fenellae*, &c. in much profusion, and appearing to be a small variety'. On the Trucial Coast the same observation applies.

Genus *DIALA* A. Adams, 1861*Diala semistriata* (Philippi, 1849)

*Rissoa semistriata* Philippi, 1849 : 34.

*Alaba semistriata* Issel, 1869 : 207. Moazzo, 1939 : 184.

*Litiopa (Diala) semistriata* Melvill and Standen, 1901 : 371. Sturany, 1903 : 263.

*D. semistriata* Tomlin, 1924 : 297.

MATERIAL. Western Khor, 53.

Melvill and Standen (1901) record this species from Muskat in the Gulf of Oman and for Bombay, so this is the first record of the species for the Persian Gulf. According to Moazzo (1939) and other writers on the Suez Canal fauna, this species had penetrated the Canal as far as Lake Timsah by 1939.

*Diala* cf. *hardyi* Melvill, 1895

*D. cf. hardyi* Melvill, 1895 : 118.

MATERIAL. Western Khor, 9.

This identification is tentative as I have not examined the type and a conclusive identification was not possible from the original description and figure.

Genus *BITTIUM* Leach in Gray, 1847*Bittium (Bittium) caudatum* Melvill, 1904

*B. caudatum* Melvill, 1904 : 161, pl. 10, fig. 8.

MATERIAL. Western Khor, 1.

Unfortunately the above specimen is damaged and the attenuated top of the shell, a character of the species (Melvill, 1904) had been lost.

Genus *CERITHIUM**Cerithium caeruleum* Sowerby, 1855

*C. caeruleum* Sowerby, 1855 : 866, pl. 179, fig. 61, 62. Issel, 1869 : 147. Melvill and Standen, 1901 : 373. Sturany, 1903 : 261. Moazzo, 1939 : 170. Barnard, 1963 : 132.

MATERIAL. Sta. 92, 2 live, Sta. 93, 1 live.

*Cerithium petrosum* (Wood, 1828)

*Strombus petrosus* Wood, 1828 : 34.

*C. petrosus* Sturany, 1901 : 261. Biggs, 1958 : 272.

MATERIAL. Sta. 36, 1; Sta. 61, 7; Sta. 70, 100; Eastern Khor, 15; Western Khor, 48.

I have separated this species from the following on grounds of general shape and ornamentation which I consider valid specific differences. Cooke (1885b : 44) states that *Cerithium petrosus* Wood is 'quite indistinguishable from *rugosum* Wood, in which species *petrosus* must be merged'.

*Cerithium rugosum* (Wood, 1828)

*Strombus rugosus* Wood, 1828 : 34.

*C. rugosum* Tomlin, 1924 : 295. Melvill and Standen, 1928 : 101.

MATERIAL. Sta. 36, 1; Sta. 60, 2; Sta. 62, 10; Sta. 63, 19; Sta. 64, 5; Sta. 86, 2, juvenile; Sta. 92, 1 live juvenile; Western Khor, 18.

*Cerithium scabridum* Philippi, 1848

*C. scabridum* Philippi, 1848 : 23. Cooke, 1885b : 42. Melvill and Standen, 1901 : 374. Sturany, 1903 : 260. Tomlin, 1924 : 295. Biggs, 1958 : 273.

*C. yerburyi* Smith, 1891 : 417, pl. 33, fig. 4. Moazzo, 1939 : 174.

*C. (Vulgoerithium) scabridum* Pallary, 1912 : 110.

*C. (Thericium) scabridum* Moazzo, 1939 : 173.

MATERIAL. Sta. 92, 1 live; Sta. 30, 57 juvenile; Sta. 50, 1 juvenile; Sta. 54, 3 juvenile; Sta. 63, 11; Sta. 67a, 4 live, 19 juvenile; Eastern Khor, 159 from 31 Sta.; Western Khor 342 from 20 Sta. 1 live; unlocated 5.

This is a common species and, with the two preceding species, probably makes up the bulk of the geological formations now being laid down along the Trucial Coast.

It is a very variable species, Smith (1891) has named the Aden form *C. yerburyi* and Cooke (1885b : 42) has put *C. ruppelli* Philippi, into the synonymy.

The species appears able to tolerate high temperature and salinity; Kinsman (1964b) records it as very common on the shelf, in mid-lagoon, inner lagoon, tidal creeks and algal mats. According to Moazzo (1939) the species has penetrated the Suez Canal to Port Said but Pallary (1912) states 'L'espèce remonte sur les côtes de la Syrie jusqu'à Jaffa'. One would like evidence that these were live specimens

in view of the fact that the current flows past the Egyptian delta and up the coast of Israel and so dead shells might have been carried by it and deposited at Haifa; a not unusual happening.

*Cerithium* sp.

A sample from the Western Khor (Tr. B2) must be left as belonging to the *rugosum-petrosum* species complex as I have been unable to assign them to either species.

Genus *CLAVA* Martyn, 1784

*Clava (Clava) fasciata* (Bruguière, 1792)

*Cerithium fasciatum* Bruguière, 1792 : 474.

*Cerithium (Vertagus) fasciatum* Melvill and Standen, 1901 : 374.

*Clava (Clava) fasciata* Haas, 1954 : 47.

MATERIAL. Western Khor, 2 live; Sta. 70, 3.

It is interesting to note that the specimens recorded by Melvill and Standen (1901) are from Muskat, dredged in 10-15 fathoms on muddy sand, whilst the two from Khor-al-Bazam are from the middle of a coral reef.

*Clava (Clava) kochi* (Philippi, 1848)

*Cerithium kochi* Philippi, 1848 : 21.

*Cerithium (Vertagus) kochi* Melvill and Standen, 1901 : 374.

*Cerithium (?Vertagus) kochii* Sturany, 1903 : 261.

MATERIAL. Western Khor, 1 live.

Genus *TRIPHORA* Blainville, 1828

*Triphora acuta* (Kiener, 1841-42)

*Cerithium acutum* Kiener, 1841-2 : 79, pl. 32, fig. 2.

*Triforis acutus* Melvill and Standen, 1901 : 376.

*Triphora acuta* Melvill, 1928 : 102. Hudson, Eames and Wilkins, 1957 : 397.

MATERIAL. Sta. 12, 1 dead; Western Khor, 1 dead.

*Triphora* sp.

(Pl. 4, figs 4, 5)

Shell straight sided, whorls 11-12, gradually increasing in size, protoconch eroded, whorls ornamented with latitudinal rows of 16 shining gemmules, 3 rows on each whorl except the body whorl which has 4 and the gemmules increase to 18; the adapical row is brown in colour, the middle one cream and the abapical one pearly white, on each whorl these are joined latitudinally by relatively high ridges which are nearly straight on the upper whorls but on the body whorl they are at an angle to the columella thus giving the shell a reticulated appearance. The suture is

fairly deep and distinct. Mouth rounded with a sharp lip, embayment at the point of juncture with the body whorl, channel at the base of the columella strongly curved and reflected. Animal unknown.

**MATERIAL.** Sta. 67a; 4 live.

I am unable to specifically identify the above specimens and two other juveniles collected by Winckworth in the B.M.(N.H.) are left undescribed, as the protoconch is eroded. Barnard (1963) pointed out 'a description of the protoconch is essential' for the acceptance of species in this genus.

The specimens examined closely resemble *Triphora acuta* (Kiener) but differ in the two upper rows of gemmules being more widely spaced than in *acuta* and also having the rows of gemmules of approximately equal size while in *acuta* the middle row is reduced in size.

### Superfamily CALYPTRACEA

#### Family CALYPTRAEDAE

Genus *CALYPTRAEA* Lamarck, 1799

#### *Calyptrea pellucida* (Reeve, 1859)

*Trochita pellucida* Reeve, 1859 : sp. 2.

*C. pellucida* Melvill and Standen, 1901 : 362. Thorson, 1940 : 172.

**MATERIAL.** Eastern Khor, 29 from 17 stations; Western Khor, 56 from 24 stations, dead; unlocated, 1.

I agree with Melvill and Standen (1901) and Thorson (1940) that there is little discernible difference between this species and *Calyptrea sinensis* L. from the Mediterranean. The genus has not been recorded for the Suez Canal or Red Sea.

### Superfamily STROMBACEA

#### Family XENOPHORIDAE

Genus *XENOPHORA* Fischer, 1807

#### *Xenophora caperata* Philippi, 1849

*X. caperata* Philippi, 1849 : 100. Biggs and Grantier, 1960 : 388.

**MATERIAL.** Sta. 13, 1; Eastern Khor, 2; unlocated 1 juvenile.

The specimen from Sta. 13 was very old and had bivalves (*Mytilacea* and *Arcacea*) attached.

#### *Xenophora corrugata* (Reeve, 1843)

*Phorus corrugata* Reeve, 1843 : 163.

*X. corrugata* Melvill and Standen, 1901 : 361.

**MATERIAL.** Khor-al-Bazam, 1 juvenile.

Only small fragments of greyish-black coral debris are attached to the keel of this specimen.

Family **STROMBIDAE**Genus **TEREBELLUM** Röding, 1798**Terebellum terebellum** (Linnaeus, 1758)*Conus terebellum* Linnaeus, 1758 : 718.

MATERIAL. Sta. 13, 1.

Melvill and Standen (1901) record *Seraphs* (= *Terebellum*) *terebellum* from the Gulf of Oman in 18-40 m. The Trucial Coast specimen was found on a sand and rock bottom in 15-20 m and may be a new record for the Persian Gulf proper.

**Strombus decorus** Röding, 1798ssp. **persicus** Swainson, 1821*S. persicus* Swainson, 1821 : pl. 53.*S. beluchiensis* Melvill, 1898 : 37. Melvill, 1901 : 380. Biggs, 1958 : 27.

MATERIAL. Sta. 13, 2; Beach, 50.

Reported by Kinsman (1964b) to be common on the shelf.

**Strombus** sp.

MATERIAL. Unlocated beach, 5.

These specimens have not yet been determined; they do not appear to agree with any of the species as yet reported from the Persian Gulf.

Superfamily **NATICACEA**Family **NATICIDAE**Genus **NATICA** Scopoli, 1777**Natica lineata** Link, 1807*Natica lineata* Link, 1807 : 140.

MATERIAL. Sta. 32, 1; Sta. 33, 1; Western Khor, 1.

This is a new record for the Persian Gulf.

**Natica** sp.

MATERIAL. Sta. 101, 2 egg masses.

These egg-masses seem to be identical with *Natica* sp.B. referred to by Thorson (1940) but considerably smaller. Thorson's example measured 20-25 mm average depth, these are between 14 and 17 mm in depth. The specimens were found in the intertidal zone.



Genus *SINUM* Röding, 1798

*Sinum (Eunaticina) papilla* (Gmelin, 1791)

*Nerita papilla* Gmelin, 1791 : 3675.

*Sigaretus papilla* Issel, 1869 : 188.

*Sigaretus (Eunaticina) papilla* Melvill and Standen, 1901 : 360.

*Eunaticina papilla* Biggs and Grantier, 1960 : 388.

MATERIAL. Beach, I.

Superfamily CYPRAEACEA

Family CYPRAEIDAE

Genus *CYPRAEA* Linnaeus, 1758

*Cypraea caurica* (Linnaeus, 1758)

*C. caurica* Linnaeus, 1758 : 723. Melvill and Standen, 1901 : 382.

*Erronea (Erronea) caurica caurica* Haas, 1954 : 47.

MATERIAL. Eastern Khor, I.

*Cypraea grayana*. Schilder, 1930

*Mauritia grayana* Schilder, 1930b : 75.

*C. arabica* Biggs, 1958 : 273.

MATERIAL. Beach I.

*Cypraea lentiginosa* Gray, 1825

*C. lentiginosa* Gray, 1825 : 489, pl. 7, pl. 12, fig. 1. Melvill and Standen, 1901 : 383.

MATERIAL. Sta. 10, I live.

*Cypraea turdus* Lamarck, 1810

*C. turdus* Lamarck, 1810 : 94. Issel, 1869 : 111. Sturany, 1903 : 255. Moazzo, 1939 : 166.

*C. ovata* Melvill and Standen, 1901 : 384.

MATERIAL. Sta. 15, 2 live; Sta. 54, 1; Sta. 55, 1; Sta. 51, 1 juvenile.

This variable species was reported common on the shelf by Kinsman (1964b).

## Superfamily MURICACEA

## Family MURICIDAE

Genus *MUREX* Linnaeus, 1758*Murex (Hexaplex) küsterianus* Tapparone Canefri, 1875

(Pl. 5, figs 1-5, 8, 9)

*M. küsterianus* Tapparone Canefri, 1875 : 635, pl. 19, figs 1, 2. Biggs, 1969 : 203.*M. spinosus* Tryon, 1880 : 106, pl. 28, fig. 257.*M. (Phyllonotus) turbinatus* Melvill and Standen, 1901 : 398. Thorson, 1940 : 197.*M. anguliferus* Biggs, 1958 : 273. Biggs and Grantier, 1960 : 388.

MATERIAL. Sta. 6, 1 live; Sta. 8, 1 live; Sta. 9, 1 live juvenile; Sta. 10, 3 live; Sta. 13, 1 live; Sta. 34, 1 live; Sta. 61, 2 live; Sta. 92, 3 live juvenile; beach, many.

In the past there has been considerable confusion as to the correct identification of this species. Tapparone Canefri based the description of *M. küsterianus* on two fossil specimens from a raised beach on the Red Sea coast, but added a further record of a living specimen from West Africa. The locality for the latter is probably an error as all other records are from the Persian Gulf, South Arabian coast and Red Sea. The type specimens have not been located in the museum at either Geneva, Genoa or Turin, therefore for comparison the original figure is reproduced here (Pl. 5, fig. 3), together with photographs of the type of *M. turbinatus* Lamarck (Pl. 5, figs 6, 7), and the probable type of *M. spinosus* Adams (Pl. 5 figs 1, 2). The latter is a synonym of *M. küsterianus* although Tryon (1880) incorrectly synonymized it with *M. turbinatus*. Material reported by Thorsen (1940) belongs to *M. küsterianus* and it is presumed that the *M. turbinatus* reported by Melvill and Standen (1901) is also this species.

Further material of *M. küsterianus* has been examined from Muscat; Hormuz I. (Biggs 1958); Ras Tanura; Masirah I; S. Arabian coast (Biggs 1969).

*Murex scolopax* Dillwyn, 1817

*M. scolopax* Dillwyn, 1817 : 681. Sturany, 1903 : 238. Melvill, 1928 : 104. Biggs and Grantier, 1960 : 388.

MATERIAL. Sta. 50, 1 juvenile; Sta. 51, 1; Sta. 54, 4 fragments; Beach, 2 fragments.

Genus *THAIS* Röding, 1798*Thais carinifera* (Lamarck, 1822)*Purpura carinifera* Lamarck, 1822 : 241. Fischer, 1841 : 224.*Cuma carinifera* Melvill and Standen, 1901 : 400. Hudson, Eames and Wilkins, 1957 : 396.*T. carinifera* Tomlin, 1927 : 294. Melvill, 1928 : 105. Moazzo, 1939 : 163, pl. 13, fig. 1. Biggs, 1958 : 273. Biggs and Grantier, 1960 : 389.*T. (Cuma) carinifera* Thorson, 1940 : 202.*T. (Cymia) carinifera* Haas, 1952 : 116.

MATERIAL. Sta. 63, 1.

*Thais pseudohippocastanum* (Dautzenberg, 1929)

*Purpura* (*Thalassa*) *pseudohippocastanum* Dautzenberg, 1929 : 427.

*Thais* (*Thalassa*) *hippocastaneum* Melvill and Standen, 1901 : 399.

*Thais pseudohippocastanum* Biggs, 1958 : 273. Biggs and Grantier, 1960 : 389.

MATERIAL. Sta. 61, 1 live; Sta. 92, 5 live.

Dautzenberg (1929) introduced the name *P. pseudohippocastanum* for *P. hippocastanum* Kiener (non Linnaeus, nec Lamarck).

*Thais tissoti* (Petit, 1852)

*Purpura tissoti* Petit, 1852 : 163, pl. 7, fig. 4a, b.

*T. tissoti* Smith, 1891 : 409. Biggs, 1958 : 273. Biggs and Grantier, 1960 : 389.

MATERIAL. Sta. 63, 1 live; Sta. 80, 4 juvenile; Sta. 92, 1 live juvenile.

Genus *DRUPA* Röding, 1798*Drupa margariticola* (Broderip, 1833)

*Murex margariticola* Broderip, 1833 : 177.

*Sistrum margariticola* Melvill and Standen, 1901 : 400.

*D. margariticola* Biggs, 1958 : 273.

MATERIAL. Sta. 37, 2; Sta. 38, 1 live; Sta. 39, 1; Sta. 45, 2 live; Sta. 61, 1; Sta. 63, 6; Sta. 92, 3 live; Western Khor, 5.

Most of the specimens are very corroded possibly due to the high salinity of the intertidal waters it inhabits. The above specimens are larger than those from Hormuz I. (Biggs, 1958).

Superfamily **BUCCINACEA**Family **COLUMBELLIDAE**Genus *MITRELLA* Risso, 1826*Mitrella* (*Mitrella*) *cartwrighti* (Melvill, 1897)

(Pl. 4, figs 1-3)

*Columbella* (*M.*) *cartwrighti* Melvill, 1897 : 8, pl. 6, fig. 14.

MATERIAL. Western Khor, 3, 2 juvenile; Eastern Khor, 3.

Three possible syntypes are in the B.M.(N.H.), Reg. no. 1897.7.30.III-114.

***Mitrella (Mitrella) blanda*** (Sowerby, 1844)

(Pl. 3, figs 1-4)

*Columbella blanda* Sowerby, 1844 : 137, pl. 39, fig. 145, 146.*C. doriae* Issel, 1865 : 395, pl. 1, fig. 3, 4.*C. (M.) blanda* Melvill and Standen, 1901 : 403. Thorson, 1940 : 204.*M. blanda* Hudson, Eames and Wilkins, 1957 : 397.*Pyrene (M.) blanda* Biggs, 1958 : 273.

**MATERIAL.** Sta. 29, 10 live; Sta. 31, 5 live; Sta. 40, 1; Sta. 57, 1; Sta. 59, 2+2 live; Sta. 60, 4; Sta. 62, 1; Sta. 63, 5; Sta. 68, 3; Sta. 70, 45; Sta. 81, 3; Sta. 86, 1 live; Sta. 92, 2 live; Sta. 97, 1; Eastern Khor, 17; Western Khor 22; unlocated 10.

There is confusion as to the type locality of this species, on the label with the type is written 'Loanda Africa under stones low water' but the type locality was published as 'Africa on the shore'. The species has otherwise only been recorded from the Persian Gulf and Karachi. From the three specimens in the type series I wish to select a lectotype, reg. no. 1968764.

This species shows a large degree of variation in shell form and colour patterns, which may be regionally distributed.

***Mitrella (Mitrella) misera*** (Sowerby, 1844)*Columbella miser* Sowerby, 1844 : 50. Shopland, 1902 : 173.**MATERIAL.** Sta. 79, 2 live.

This is a new record for the Persian Gulf, Melvill & Standen (1901) include *misera* Sowerby in the synonymy of *Columbella (Mitrella) zebra* Gray from the Makran coast. These shells have lighter markings when compared with Aden specimens.

Genus **PYRENE** Röding, 1798***Pyrene atrata*** (Gould, 1860)*Columbella (Anachis) atrata* Gould, 1860 : 334.*P. atrata* Barnard, 1959 : 180.**MATERIAL.** Eastern Khor, 3; Western Khor, 8.***Pyrene (Seminella) phaula*** (Melvill & Standen, 1901)*Columbella (S.) phaula* Melvill and Standen, 1901 : 405.*C. (S.) selasphora* Melvill and Standen, 1901 : 406, pl. 33, fig. 7. Melvill, 1903 : 30.**MATERIAL.** Western Khor, 6; Eastern Khor, 2.

After examination of the above specimens and a sample from Kuwait it is obvious that *P. phaula* and *P. selasphora* are conspecific. The colour and patterns and shape show continuous variation. The type locality for *selasphora* is Karachi.

Family **NASSARIIDAE**Genus **NASSARIUS** Froriep, 1806*Nassarius pullus* (Linnaeus, 1758)*Buccinum pullus* Linnaeus, 1758 : 737.*Nassa pulla* Issel, 1896 : 125. Melvill and Standen, 1901 : 409.*Nassa pullus* Sturany, 1903 : 243.*Nassarius pullus* Melvill, 1928 : 106. Biggs, 1958 : 274. Biggs and Grantier, 1960 : 389.*Nassa (Nassa) pulla* Haas, 1952 : 116.

MATERIAL. Sta. 29, 8 live; Sta. 31, 1 live; Sta. 32, 1 live; Sta. 40, 1 live; Sta. 48, 12 live; Sta. 86, 1 live.

*Nassarius stigmarius* (A. Adams, 1852)*Nassa stigmaria* A. Adams, 1852 : 96.*Nassa (Niotha) stigmaria* Melvill and Standen, 1901 : 412. Melvill, 1928 : 106.*Nassarius stigmarius* Biggs and Grantier, 1960 : 389.

MATERIAL. Sta. 43, 1 live; Sta. 77, 1 live; Sta. 100, 1 live.

Family **FASCIOLARIIDAE**Genus **FUSINUS** Rafinesque, 1815*Fusinus townsendi* (Melvill, 1899)*Fusinus townsendi* Melvill, 1899 : pl. 2, fig. 1. Melvill, 1901 : 418.*Fusinus townsendi* Melvill, 1928 : 107.

MATERIAL. Sta. 15, 1; Sta. 10, 1; beach, 2.

Melvill (1901) records the species from 7-50 fms., and the above specimens were from fairly deep water. The species has only been recorded from the Persian Gulf and Karachi.

Superfamily **VOLUTACEA**Family **OLIVIDAE**Genus **ANCILLA** Lamarck, 1799*Ancilla cinnamomea* Lamarck, 1801*Ancilla cinnamomea* Lamarck, 1801 : 73. Melvill and Standen, 1901 : 427. Melvill, 1928 : 110.

Biggs and Grantier, 1960 : 389.

*Ancillaria castanea* Sowerby, 1830 : 5.*Ancillaria cinnamomea* Tryon, 1853, 5 : 93.

MATERIAL. Sta. 14, 1 live; Sta. 63, 1 live; Sta. 70, 1; Sta. 90, 1 live; Sta. 100, 1 live; Eastern Khor, 2; unlocalised, 6.

I have followed Tryon (1883) who placed *castanea* in the synonymy of *cinnamomea*. Melvill and Standen (1901) and Melvill (1928) regard the two as distinct species.

*Ancilla eburnea* (Deshayes, 1830)

*Ancillaria eburnea* Deshayes, 1830 : 42.

*Ancilla eburnea* Melvill and Standen, 1901 : 427.

MATERIAL. Sta. 58, 2; Sta. 70, 1; Sta. 76, 1 live; Sta. 82, 4 live.

This is a new record for the Persian Gulf as Melvill and Standen record the species for Jask eastwards along the Makran Coast.

Genus *OLIVA* Bruguière, 1789

*Oliva bulbosa* (Röding, 1798)

*Porphyria bulbosa* Röding, 1798 : 37.

*O. bulbosa* Melvill and Standen, 1901 : 426. Biggs, 1958 : 274.

MATERIAL. Beach, 46.

*Oliva caerulea* (Röding, 1798)

*Porphyria caerulea* Röding, 1798 : 33.

MATERIAL. Beach, 7.

## Family MARGINELLIDAE

Genus *PERSICULA* Schumacher, 1817

*Persicula* cf. *asellina* (Jousseaume, 1875)

*Gibberula asellina* Jousseaume, 1875 : 243, pl. 7, fig. 6.

MATERIAL. Eastern Khor, 1.

This shell was damaged hence the tentative identification. The type locality is Mauritius.

*Persicula isseli* (Nevill, 1875)

*Marginella isseli* Nevill, 1875 : 95.

*M. (P.) oodes* Melvill, 1898 : 16, pl. 1, fig. 16.

*M. oodes* Melvill, 1928 : 109.

MATERIAL. Western Khor, 3.

Specimens were also examined from 40 km E. of Ras Mussandam and 40 km N.-N.E. of Ras Mussandam.

*Persicula mazagonica* (Melvill, 1893)

*Marginella (Gibberula) mazagonica* Melvill, 1893 : 57, pl. 1, fig. 10. Melvill and Standen, 1901 : 425. Melvill, 1928 : 109.

*M. mazagonica* Shopland, 1902 : 173.

*G. (Cysticus) mazagonica* Hudson, Eames and Wilkins, 1957 : 396.

MATERIAL. Western Khor, 4.

***Persicula shoplandi*** (Melvill, 1897)

*Marginella (Cryptospira) Shoplandi* Melvill, 1897 : 8.

*M. (Gibberula) shoplandi* Melvill and Standen, 1901 : 425.

MATERIAL. Eastern Khor, 1.

***Persicula subflava*** (Preston, 1906)

*Marginella subflava* Preston, 1906 : 35.

MATERIAL. Sta. 81, 2.

This is a new record for the Persian Gulf.

## Family MITRIDAE

Genus **MITRA** Röding, 1798

Subgenus **SCABRICOLA** Swainson, 1840

***Mitra (Scabricola) bovei***. Kiener, 1839

*Mitra bovei* Kiener, 1839 : 9, pl. 2, fig. 5. Issel, 1869 : 117, 352. Cooke, 1885a, 334. Melvill and Standen, 1901 : 418. Shopland, 1902, 173. Moazzo, 1939 : 146.

MATERIAL. Sta. 9, 1.

Sub-class **OPISTHOBRANCHIA**

Superfamily **PTENOGLOSSA**

Family **PYRAMIDELLIDAE**

Genus **EULIMELLA** (Forbes) Gray, 1847

***Eulimella kaisensis*** Melvill, 1898

*Eulimella kaisensis* Melvill, 1898 : 21, pl. 2, fig. 5. Melvill, 1911 : 181, pl. 4, fig. 9.

MATERIAL. Western Khor, 3.

Although only recorded for the Persian Gulf and Gulf of Oman, I have examined specimens from the Biggs collection from Dongonab Bay, Red Sea.

Genus **TURBONILLA** (Leach) Risso, 1826

***Turbonilla icela*** Melvill, 1911

*Turbonilla icela* Melvill, 1911 : 185, pl. 4, fig. 15.

MATERIAL. Eastern Khor, 1; Western Khor, 5.

Melvill (1911) records this species from less saline waters than those now reported on.

Family **STILIFERIDAE**Genus **MUCRONALIA** A. Adams, 1860***Mucronalia lepida*** Melvill, 1906*Mucronalia lepida* Melvill, 1906 : 73, pl. 7, fig. 8.

MATERIAL. Sta. 30, 1.

This is a new record for the Persian Gulf. The type locality is Gulf of Oman, 156 fms.

Superfamily **CEPHALASPIDEA**Family **ACTAEONIDAE**Genus **SOLIDULA** Fischer von Waldheim, 1807***Solidula*** sp.

MATERIAL. Sta. 70, 1.

This specimen is possibly the worn shell of *Solidula solidula* Linnaeus.Family **RINGICULIDAE**Genus **RINGICULA** Deshayes, 1838***Ringicula propinquans*** Hinds, 1844*Ringicula propinquans* Hinds, 1844 : 96. Melvill and Standen 1901 : 457.

MATERIAL. Western Khor, 6.

Family **BULLARIIDAE**Genus **BULLARIA*****Bullaria ampulla*** (Linnaeus, 1758)*Bulla ampulla* Linnaeus, 1758 : 727. Issel, 1869 : 167. Melvill and Standen, 1901 : 456.

Sturany, 1903 : 268. Moazzo, 1939 : 136.

*Bulla (Bulla) ampulla* Haas, 1952 : 116.*Bullaria ampulla* Biggs, 1958 : 274. Biggs and Grantier, 1960 : 389.

MATERIAL. Sta. 9, 1 specimen juvenile; Sta. 12, 1; Sta. 52, 1; Sta. 66, 1; Eastern Khor, 9; Western Khor, 19; beach, 30.



Family **ATYIDAE**Genus **ATYS*****Atys cylindricus*** (Helbling, 1779)

*Bulla cylindrica* Helbling, 1779 : 122.

*Alicula cylindrica* Issel, 1869 : 168.

*Atys (Alicula) cylindrica* Melvill and Standen, 1901 : 454.

*Atys cylindricus* Sturany, 1903 : 268. Melvill, 1928 : 112.

MATERIAL. Sta. 70, 1; Western Khor, 5.

Family **RETUSIDAE**Genus **RETUSA** Brown, 1827***Retusa omanensis*** Melvill, 1903

*R. omanensis* Melvill, 1903 : 321, pl. 23, fig. 19. Melvill, 1928 : 112.

MATERIAL. Western Khor, 7.

This is a new record for the Persian Gulf. The type localities are the Gulf of Oman in 314 m and 80 m in Charbar Bay, Makran Coast, so these dead specimens may have been washed in from deeper water.

Family **AGLAJIDAE**Genus **AGLAJA*****Aglaja*** sp. c.f. ***nigra*** von Martens, 1879

*Doridium nigrum* von Martens, 1879 : 738.

MATERIAL. Sta. 82A, 1 live.

This is the first record of the genus in the Persian Gulf. The locality is in the low intertidal zone, outer lagoon, 1 mile N.E. of Halat al Bahraini.

Order **ACOELA**Superfamily **DORIDACEA**Family **DORIDIDAE**Genus **CASELLA** H. & A. Adams, 1854***Casella atromarginata*** (Cuvier, 1804)

*Doris atromarginata* Cuvier, 1804 : 452, 473.

*C. atromarginata* Vayssière, 1912, 55. Haas, 1920 : 139. O'Donoghue, 1929 : 726. White, 1951 : 248. Marcus and Marcus, 1960 : 902.

MATERIAL. Eastern Khor, 2 live.

Little seems to have been written on the Nudibranch fauna of the Persian Gulf. Melvill and Standen do not mention any and Thorson (1940) only mentions four

species. The first record of this species is in Mareus and Marcus (1960) who mention neither the exact locality nor the number of specimens found, only stating that it occurs at 18 m depth in the Gulf. White (1951) records the species for Suez Bay.

Superfamily **ONCHIDIACEA**

Family **ONCHIDIIDAE**

Genus **ONCHIDIUM** Buchanan, 1800

***Onchidium peronii*** Cuvier, 1805

*P. peronii* Cuvier, 1805 : 37. White, 1951 : 241.

*O. (Peronia) peronii* Issel, 1869 : 153. Sturany, 1903 : 269.

*P. peronii* O'Donoghue, 1929 : 833.

MATERIAL. Sta. 96, 2 live; unlocated 1 live juvenile.

In the adult specimens the foot is lighter than the dorsum whilst in the juvenile it is the same colour.

Sub-Class **PULMONATA**

Order **BASOMMATOPHORA**

Superfamily **ELLOBIACEA**

Family **ELLOBIIDAE**

Genus **MELAMPUS** Montford, 1810

***Melampus lividus*** (Deshayes, 1830)

*Auricula livida* Deshayes, 1830 : 91.

*M. lividus* Fischer, 1901 : 96. Moazzo, 1939 : 130. Biggs, 1958 : 274.

MATERIAL. Sta. 92, 1.

The only previous record for the Persian Gulf for this species is from Bundar Abbas (Biggs, 1958), but there are several unrecorded specimens from Bushire in the Liverpool Museum collected by Dr Blair in 1915-1916.

***Melampus*** sp.

MATERIAL. Sta. 72, 1.

Genus **LAEMODONTA** Philippi, 1846

***Laemodonta (Laemodonta) rapax*** (Dhorn, 1859)

*Plecotrema rapax* Dhorn, 1859 : 204.

*Laemodonta bicolor* Biggs, 1965 : 339.

MATERIAL. Sta. 72, 1; Sta. 70, 1; Eastern Khor, 1.

Not previously reported from the Persian Gulf.

Superfamily **SIPHONARIACEA**Family **SIPHONARIIDAE**Genus **SIPHONARIA** Sowerby, 1824***Siphonaria asghar*** Biggs, 1958*S. asghar* Biggs, 1958 : 249.

MATERIAL. Sta. 75, 4 live.

This record extends the known distribution of the species into the Persian Gulf as the original locality was Hormuz Island. Other records of this species of *Siphonaria* in the British Museum (Natural History) consist of a long series of this species from East Pier, Karachi (Winckworth) and two specimens from Muscat (Townshend) and some from Bombay (Blanford and Peile).

***Siphonaria rosea*** Hubendick, 1943*S. rosea* Hubendick, 1943 : 1, pl. 1, fig. 1a, b. Hubendick, 1946 : 53, pl. 4, figs 12-15. Biggs and Grantier, 1960 : 389.

MATERIAL. Sta. 61, 1 live; Sta. 63, 4 live; Sta. 92, 1 live.

The type locality is N.W. of Bushire, northern end of the Persian Gulf; it is possibly distributed throughout the Gulf but not yet recorded outside this area.

Class **BIVALVIA**Superfamily **NUCULACEA**Family **NUCULANIDAE**Genus **NUCULANA** Link, 1807***Nuculana confusa*** (Hanley, 1860)*Leda confusa* Hanley, 1860 : 119, pl. 228, fig. 85.*N. (N.) confusa* Prashad, 1932 : 19.

MATERIAL. Western Khor, 16 valves.

This is a new record for the genus and species for the Persian Gulf.

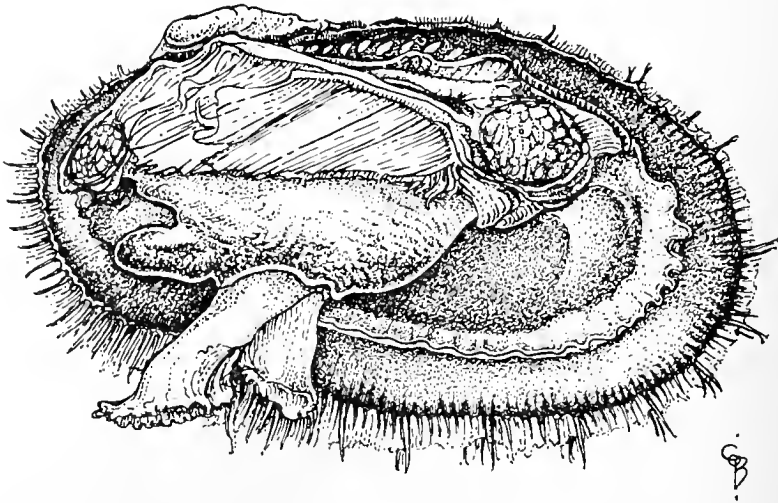
## Superfamily ARCACEA

## Family ARCIDAE

Genus *ACAR* H. & A. Adams, 1857*Acar plicata* Dillwyn, 1817*Arca plicata* Dillwyn, 1817 : 228.*Arca divaricata* Fischer, 1891 : 228. Tomlin, 1927 : 301.*Barbatia divaricata* Sturany, 1901 : 289.*Arca (Acar) plicata* Moazzo, 1939 : 55. Haas, 1952 : 116. Haas, 1954 : 47.*Arca (Acar) divaricata* Biggs, 1958 : 274. Biggs and Grantier, 1960 : 389.

MATERIAL. Sta. 31, 1 live; Sta. 63, 3 live; Sta. 67a, 1 live; Sta. 97, 2 live; Eastern Khor, 2 live; Western Khor, 2 live.

It is interesting to note the variety of habitats from which this species was collected. Those from the Khor-al-Bazm were generally from a sandy bottom but one live specimen from the eastern end was collected from 4 ft of water at a temperature of 69.5°F, pH 7.8. Two specimens from the western end (nearer the open sea) were collected in the middle of a coral bank. Station 97 was in the intertidal zone; Kinsman (1964b) records the species as common in the Mid-Lagoon.



ACTUAL SIZE, 48 m.m.

FIG. 3. *Barbatia lacerata* (Bruguière) lateral view with left valve and mantle removed to show general anatomical characters.

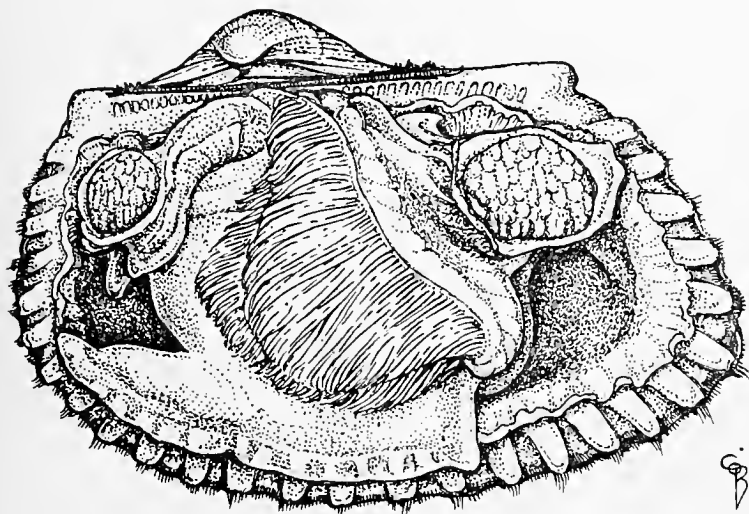
Genus *BARBATIA* Gray, 1842*Barbatia lacerata* (Bruguère, 1789)

(Text-fig. 3)

*Arca lacerata* Bruguère, 1789 : 101. Tomlin, 1927 : 319.*Arca* (*Barbatia*) *lacerata* Moazzo, 1939 : 53.

MATERIAL. Sta. 10, 1 live; Sta. 90, 1 live; Sta. 94, 3 live; Western Khor, 1 live; unlocated, 2 live; Eastern Khor, 1 valve; beach 21.

This is a new record for the Persian Gulf, which seems surprising in view of the variety of habitats. Kinsman (1964b) notes that it is common on the shelf, on the reef and the oolite delta (intertidal zone); Evans collected it on the reef and the intertidal zone whilst Kendall (1966) records it from the Khor-al-Bazm in the intertidal. The species also occurs at Ras Tanura at the northern end of the Persian Gulf and was collected by Grantier (personal communication).



ACTUAL SIZE, 38 m. m.

FIG. 4. *Anadara antiquata* (Linnaeus) lateral view with left valve and mantle removed to show general anatomical characters.

Genus *ANADARA* Gray, 1847

*Anadara antiquata* (Linnaeus, 1758)

(Text-fig. 4)

*Arca antiquata* Linnaeus, 1758 : 694. Jeffreys, 1879 : 571.

MATERIAL. Sta. 10, 1 live; Sta. 13, 5 live; Sta. 3, 1 valve.

This is a new record for the Persian Gulf. It is remarkable that this species was not recorded by Melvill and Standen (1907) who were reporting on dredged material rather than littoral collections in view of the fact that the above 6 live specimens were all taken at a depth of over 50 feet.

*Anadara ehrenbergi* (Dunker, 1868)

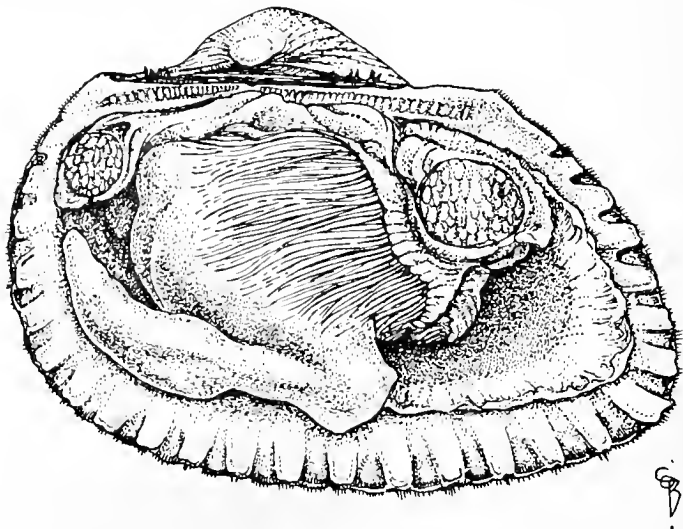
*Arca ehrenbergi* Dunker, 1868 : pl. 38, figs. 17, 18.

*Arca (Anomalocardia) ehrenbergi* Issel, 1869 : 91, 258.

*Arca (Anadara) ehrenbergi* Moazzo, 1939 : 52, pl. 5, fig. 1.

MATERIAL. Sta. 7, 1; unlocated, 9.

This is a new record for the Persian Gulf.



ACTUAL SIZE, 34 m.m.

FIG. 5. *Anadara wropigmelana* (Bory St. Vincent) lateral view with left valve and mantle removed to show general anatomical characters.

*Anadara uropigmelana* (Bory de St. Vincent, 1824)

(Text-fig. 5)

*Arca uropigmelana* Bory de St. Vincent, 1824 : 156, pl. 307, fig. 2. Biggs and Grantier, 1960 : 389.*Arca (Anadara) uropigmelana* Moazzo, 1939 : 52.*Arca (Arca) uropigmelana* Haas, 1952 : 116, Haas, 1954 : 47.

MATERIAL. Sta. 14, 1 live; Sta. 3, 1 valve; Sta. 54, 3 valves; Sta. 58, 3 valves; Sta. 70A, 1 valve; unlocated, 12 valves.

Reported by Kinsman (1964b) as an uncommon species on the shelf.

Genus *SCAPHARCA* Gray, 1847*Scapharca tricenica* Nyst, 1848*Arca tricenica* Nyst, 1848 : 74.*Arca (Anadara) tricenica* Prashad, 1932 : 39.

MATERIAL. Sta. 14, 1 live.

This is a new record for the Persian Gulf, it appears to be a rare shell. The example collected was dredged in 50-60 feet of water and on a sandy bottom with small amounts of rock. Two specimens in the B.M.(N.H.) collection (Winckworth collection) were dredged off Muscat in 1932.

*Scapharca vellicata* (Reeve, 1844)

(Text-fig. 6)

*Arca vellicata* Reeve, 1844, 2 : Sp. 33. Issel, 1869 : 257.*Arca (Scapharca) birleyana* Melvill and Standen, 1907 : 794. Melvill, 1928 : 113.*Arca (Anadara) vellicata* Lamy, 1907 : 251.*Arca (Anadara) birleyana* Prashad, 1932 : 41.

MATERIAL. Sta. 3, 1; Sta. 8, 1 live; Sta. 13, 1 live; Sta. 14, 4 live.

Genus *TRISIDOS* Röding, 1798*Trisidos tortuosa* (Linnaeus, 1758)*Arca tortuosa* Linnaeus 1758 : 693. Fischer, 1891 : 228.*Parallelipipedum tortuosum* Melvill and Standen, 1907 : 796.*Arca (Trisidos) Tortuosa* Barnard, 1964 : 369.

MATERIAL. Western Khor, 2 fragments.

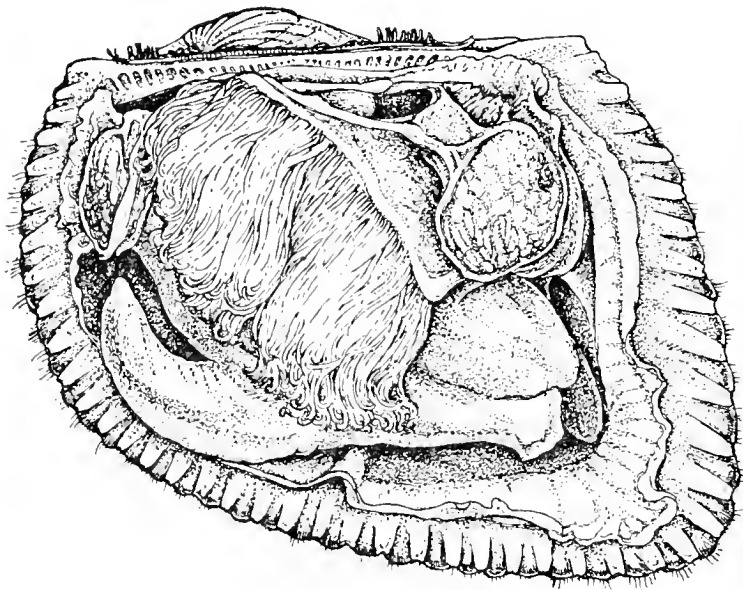
## Superfamily LIMOPSACEA

## Family GLYCYMERIDAE

Genus *GLYCYMERIS* da Costa, 1778*Glycymeris hoylei* Melvill and Standen, 1899*G. hoylei* Melvill and Standen, 1899 : 187, pl. 11, fig. 24.

MATERIAL. Western Khor, 9 valves, juvenile.

Material from Tuticorin (Winckworth) and Providence I, north of Madagascar (Gardiner) in the B.M.(N.H.) were also examined. A specimen from the latter locality had a breadth of 35 mm while the maximum measurement for those from the Western Khor is 11.5 mm.



ACTUAL SIZE, 35 m.m.

FIG. 6. *Scapharca vellicata* (Reeve) lateral view with left valve and mantle removed to show general anatomical characters.



***Glycymeris lividus*** (Reeve, 1843)

*Pectunculus lividus* Reeve, 1843 : sp. 51, Moazzo, 1939 : 58, pl. 5, fig. 3.  
*Pectunculus heroicus* Melvill and Standen, 1907 : 798 : pl. 55, fig. 1.

MATERIAL. Sta. 51, 1 valve; Sta. 70A, 1 valve.

After comparing the types of *P. lividus* Reeve and *P. heroicus* Melvill and Standen I consider them conspecific.

***Glycymeris pectunculus*** (Linnaeus, 1758)

*Arca pectunculus* Linnaeus, 1758 : 695.

MATERIAL. Sta. 1, 2 live; Sta. 9, 1 live juvenile; Sta. 10, 1 live, 1 dead; Sta. 13, 2 live; Sta. 70A, 1; Sta. 11, 1 valve; Sta. 12, 1 valve; Western Khor, 2 valves.

All these stations are on the off-shore shelf, one being about 7 miles N.E. of Jeziret Dalma.

***Glycymeris striatularis*** (Lamarck, 1819)

*Pectunculus striatularis* Lamarck, 1819 : 52. Melvill and Standen, 1907 : 789.

MATERIAL. Sta. 42, 1 live; Sta. 85, 1 live; Sta. 50, 4 valves; Sta. 54, 19 valves; Sta. 55, 3 valves; Sta. 56, 200 valves; Sta. 57, 40 valves; Sta. 70A, 7 valves; Western Khor, 1 valve; Es-Saddiyat I., 32 valves; beach, 57 valves.

A common intertidal species.

## Superfamily MYTILACEA

## Family MYTILIDAE

Genus **CRENELLA** Brown, 1827***Crenella adamsiana*** Melvill and Standen, 1907

*C. adamsiana* Melvill and Standen, 1907 : 801, pl. 55, fig. 2. Melvill, 1928 : 113.

MATERIAL. Eastern Khor, 6 valves; Western Khor, 19 valves; unlocated, 4 valves.

Melvill (1928) reports that a rounded form of this species is found in 40 fms, Charbar Bay (Makran Coast). The above specimens are also of this form.

Genus **MODIOLUS** Lamarck, 1799***Modiolus rhomboidea*** Reeve, 1857

*Modiola rhomboidea* Reeve, 1857, 10 : sp. 28. Melvill and Standen, 1907 : 800.

MATERIAL. Western Khor, 2 juveniles.

This is a new record for the Persian Gulf. The specimens from the Khor were in a sponge when received, and those mentioned by Melvill and Standen (1907) were also in sponges, at 10 fms.

Genus **BRACHIDONTES** Swainson, 1840***Brachidontes variabilis*** (Krauss, 1848)

*Mytilus variabilis* Krauss, 1848 : 25, pl. 2, fig. 5. Issel, 1869 : 94. Sturany, 1901 : 288. Melvill and Standen, 1907 : 709.

*Brachydontes variabilis* Fischer, 1870 : 178. Tomlin, 1927 : 302.

*M. (Hormomya) variabilis* Moazzo, 1939 : 43.

*Brachidontes variabilis* Rees and Stuckey, 1952 : 197. Hudson, Eames and Wilkins, 1957 : 397. Barnard, 1964 : 395.

*Brachidontes (H.) variabilis* Haas, 1952 : 116.

**MATERIAL.** Sta. 10, 1 live; Sta. 28, many live; Sta. 36, 2 live; Sta. 44, 1 live juvenile; Sta. 59, 1 live; Sta. 62, 17 live; Sta. 63, 2 live; Sta. 68, many; Sta. 86, 5+2 valves; Eastern Khor, 22 live, 30 valves; Western Khor, 117 valves.

This is the third most common bivalve on the Trucial Coast. Specimens were found in a wide variety of habitats including rock, coral, sand and on Mangrove rhizophores. The depth ranged from the littoral to 150 m.

Genus **SEPTIFER** Recluz, 1848***Septifer bilocularis*** (Linnaeus, 1758)

*Mytilus bilocularis* Linnaeus, 1758 : 705.

*S. bilocularis* Melvill and Standen, 1907 : 799. Moazzo, 1939 : 48. Barnard 1964 : 395. Taylor, 1968 : 203.

**MATERIAL.** Sta. 10, 8 live; Sta. 11, 1.

Melvill and Standen (1907) record this species from Kuwait and further south (27°N, 52°E) at 10 fms and 40 fms respectively. Barnard (1964) records dead shells at 55 fms from South Africa. The above specimens were collected at 8-14½ fms, some attached to *Pinctacta radiata* Leach and some to a sponge.

Genus **MUSCULUS** Röding, 1798***Musculus*** spp.

**MATERIAL.** Sta. 78, 1 live; Western Khor, 1 valve.

The above specimens are the only ones which can be referred to this genus with any certainty, the remainder of the material being too worn.

Genus **LITHOPHAGA** Röding, 1798***Lithophaga lithophaga*** (Linnaeus, 1758)

*Mytilus lithophagus* Linnaeus, 1758 : 705.

**MATERIAL.** Sta. 94, 4 live; Eastern Khor, 1 juvenile, live.

From a study of the shell it appears that this name should be applied to these specimens in spite of the fact that it is usually considered a Mediterranean one. In the collection of the B.M.(N.H.) are specimens from Aden (Dinshau Collection)

which have been referred to this species by Dr R. Turner and Dr K. Boss who studied the genus some years ago. This supports the view that *Lithophaga lithophaga* (Linnaeus) should be accepted as a species common to both seas.

This is a new record for the Persian Gulf. Melvill and Standen (1907) record *Lithodomus attenuatus* Deshayes for the area and comment 'Locality not precisely specified'. The few specimens collected were found boring in corals  $\frac{1}{2}$  m north of the north coast of Jeziret el Ftaiis by Kinsman (1964b) who records the species as common on the reef.

### Superfamily PTERIACEA

### Family ISOGNOMONIDAE

Genus *ISOGNOMON* Lightfoot, 1786

### *Isognomon ehippium* (Linnaeus, 1758)

*Ostrea ehippium* Linnaeus, 1758 : 700.

*I. ehippium* Biggs and Grantier, 1960 : 390.

*Melina ehippium* Spry, 1964 : 10, pl. 1, fig. 20.

MATERIAL. Sta. 9, 1; Eastern Khor, 1; juvenile, live.

### *Isognomon legumen* (Gmelin, 1791)

*Ostrea legumen* Gmelin, 1791 : 3399.

*I. legumen* Dautzenberg, 1929 : 566.

MATERIAL. Sta. 31, 1 live; Sta. 91, 1 live; Sta. 94, 3 live.

This is a new record for the Persian Gulf. The above specimens were found on hard substrate. The specimen from Sta. 91 where the salinity was 42‰ is distorted and curled into a semi-lunar shape.

### *Isognomon dentifer* (Krauss, 1848)

*Perna dentifera* Krauss, 1848 : 28.

*Parviperna dentifera* Barnard, 1964 : 410.

*Melina dentifera* Spry, 1964 : 10.

*Isognomon dentifer* Taylor, 1968 : 203.

MATERIAL. Sta. 61, 1 live; Sta. 68, 19 live; Sta. 93, 2 live; Western Khor, 26, 23 live.

This is the first record of the species in the Persian Gulf, it appears to be very common occurring in colonies attached to rock and coral. Specimens from the Persian Gulf and Gulf of Aqaba seem to be smaller than those from other localities.

Genus *MALLEUS* Lamarck, 1799*Malleus regula* (Forsskål, 1775)*Ostrea regula* Forsskål, 1775 : 124.*M. regula* Issel, 1869 : 97. Smith, 1891 : 434. Tomlin, 1927 : 301. Moazzo, 1939 : 41. Barnard, 1964 : 406.*M. cf. regula* Biggs and Grantier, 1960 : 390.

MATERIAL. Sta. 93, 1 live; Western Khor, 5 live, 1 juvenile.

This is a new record for the Persian Gulf, confirming Biggs and Grantier (1960). It is a common species on the reef Kinsman (1964b) and also on a different substrate in the Khor.

## Superfamily PTERIACEA

## Family PTERIIDAE

Genus *PINCTADA* Röding, 1798*Pinctada margaritifera* (Linnaeus, 1758)*Mytilus margaritifera* Linnaeus, 1758 : 704.*Meleagrina margaritifera* Issel, 1860 : 95. Sturany, 1901 : 289.*Margaritifera margaritifera* Melville and Standen, 1907 : 803.*P. margaritifera* Biggs, 1958 : 275. Biggs and Grantier, 1960 : 390. Reed, 1966 : 26.

MATERIAL. Western Khor, 2 juveniles; unlocated, 2 juveniles.

The ecology of this species in the Red Sea was reported on by Reed (1966).

*Pinctada radiata* (Leach, 1814)*Avicula radiata* Leach, 1814 : 98, pl. 43.*Perlamater vulgaris* Schumacher, 1817 : 108.*Perlamater inflata* Schumacher, 1817, 108.*Pteria* (*Pinctada*) *vulgaris* Moazzo, 1939 : 42, pl. 4, fig. 1.*Pinctada vulgaris* Biggs, 1958 : 275.*Pinctada radiata* Ranson, 1961 : 7.

MATERIAL. Sta. 10, 3 live juveniles; Sta. 12, 3 live; Sta. 38, 2 juveniles; Eastern Khor 1 live, 3 valves; Western Khor, 1+1 valve; beach, 174 valves.

As reported by Ranson (1961) this species has been erroneously recorded as *vulgaris* Schumacher and *inflata* Schumacher.

*Pinctada* spp.

I am unable to specifically identify a large number of very young specimens found in the samples of the deposits from the Khor-al-Bazm.

Family **PINNIDAE**Genus **PINNA** Linnaeus, 1758***Pinna atropurpurea*** Sowerby ssp. ***mutica*** Reeve, 1858*P. atropurpurea mutica* Reeve, 1858, 11 : sp. 33.

MATERIAL. Sta. 102, 1.

This is a new record for the Persian Gulf. J. Murray (personal communication) reports this species in Sea Grass in 9 ft of water off Abu Dhabi in the central part of the lagoon between that island and Es Sadiyat I.

***Pinna bicolor*** Gmelin, 1791*P. bicolor* Gmelin, 1791 : 3366. Melvill and Standen, 1907 : 806. Moazzo, 1939 : 40. Barnard, 1964 : 417.

MATERIAL. Sta. 87, 1 valve, damaged.

Superfamily **PECTINACEA**Family **PECTINIDAE**Genus **PLICATULA** Lamarck, 1801***Plicatula plicata*** (Linnaeus, 1767)*Spondylus plicata* Linnaeus, 1767 : 1136.*P. plicata* Moazzo, 1939 : 27. Barnard, 1964 : 433.

MATERIAL. Sta. 66, 1.

This is a new record for the Persian Gulf.

Genus **CHLAMYS** Röding, 1798***Chlamys ruschenbergerii*** (Tryon, 1870)*Pecten ruschenbergerii* Tryon, 1870 : 171, pl. 14, fig. 1.*C. ruschenbergerii* Eames and Cox, 1956 : 13, pl. 3, figs 2, 3. Biggs and Grantier, 1960 : 390.

MATERIAL. Sta. 9, 1 live, juvenile; Sta. 12, 3 live; Sta. 54, 1 valve juvenile; Sta. 58, 1 juvenile; Eastern Khor, 1 juvenile; Western Khor, 2 fragments; unlocated, 3 valves.

Kinsman (1964b) records the species as common on the off-shore shelf and the live specimens collected by Evans stations 9 and 12 were from a coral zone well off shore.

One of the examples from Sta. 12 contained a small starfish which Miss Ailsa M. Clark of the B.M.(N.H.) has determined as a juvenile *Amphioplus* sp.; this lay in the curve of the gills and immediately behind the adductor muscle. As there were a number of calcareous pellets in the lobes of the mantle on either side of the ligament it is difficult to say whether or not the starfish had been washed in by chance, as

had the pellets, or whether it was there by its own action, it was near the centre of the visceral cavity. Thomson (1934, p. 171) states that ' . . . the little pea-crab (*Pinnotheres pisum*) that is often found inside the Norway cockle (*Cardium norvegicum*), gets food as well as shelter there.'

Eames and Cox (1956) record this species from the Miocene and Pliocene of Persia.

Genus *SPONDYLUS* Linnaeus, 1758

*Spondylus exilis* Sowerby, 1895

*S. exilis* Sowerby, 1895 : 280, pl. 18, fig. 14. Melvill and Standen, 1907 : 811.

MATERIAL. Sta. 10, 1 juvenile live; Sta. 50, 1 valve; Sta. 51, 6 valves; Sta. 54, 2 valves; Sta. 56, 2 valves; Sta. 58, 5 valves; Sta. 69, 1 valve; Sta. 70a, 2 valves; Sta. 93, 1 live; Western Khor, 3 valves; Eastern Khor, 3 valves; unlocated 21 valves.

Kinsman (1964b) records this species as common on the coastal shelf. The only live shell collected was from intertidal waters, on a rocky shore with limestone boulders. The specimen from Station 10 was from a depth of 50-88 ft., attached to *Pinctada radiata*.

Family LIMIDAE

Genus *LIMA* Bruguière, 1797

*Lima (Lima) tenuis* (H. Adams, 1870)

*Radula tenuis* H. Adams, 1870 : 793.

*L. tenuis* Shopland, 1902 : 179.

MATERIAL. Sta. 11, 1 live; Eastern Khor, 1+4 valves; Western Khor, 1+5 valves; Sta. 46, 1 valve.

The above specimens are conspecific with one from Aden in the B.M.(N.H.) (Dinshau ex Shopland) determined by Jousseume. Moazzo (1939) includes *tenuis* in the synonymy of *Lima (Mantellum) fragilis* Lamareck ex Chemnitz which is found in the Suez Canal to Lake Timsah and Suez Bay.

Subgenus *LIMATULA* S. Wood, 1839

*Lima (Limatula) leptocarya* Melvill, 1898

*L. (L.) leptocarya* Melvill, 1898 : 28, pl. 2, fig. 2. Melvill, 1907 : 812.

MATERIAL. Western Khor, 1 valve.

A new record for the Persian Gulf as both Melvill's records are for the Gulf of Oman.

## Superfamily OSTRACEA

## Family OSTREIDAE

## Genus CRASSOSTREA

*Crassostrea cucullata* (Born, 1778)

*Ostrea cucullata* Born, 1778 : 100. Sturany, 1901 : 291. Melvill and Standen, 1907 : 806.

Rees and Stuckey, 1952 : 198.

*O. (Alectryonia) cucullata* Biggs, 1958 : 275.

*C. cucullata* Barnard, 1964 : 446.

MATERIAL. Sta. 93, 2 live.

Kinsman (1964b) reports the species as common on the reef and shelf divisions of the coastline; the above specimens are a flat form of this extremely variable species.

## Superfamily ASTARTACES

## Family CRASSATELLIDAE

## Genus CUNA Hedley, 1902

*Cuna coxi* Eames and Wilkins, 1957

*C. coxi* Eames and Wilkins 1957 : 199, pl. 27, fig. 1, 2, 3. Hudson, Eames and Wilkins, 1957 : 387

MATERIAL. Sta. II, 1 valve; Western Khor, 1+4 valves.

The species was described from fossil material collected near Lake Hamar, Busra, Iraq. This is the first record of its occurrence in the Persian Gulf. Station II was in 70 ft of water. The specimen from the Western Khor shows some brown colour, the type is white.

*Cuna majeeda* n. sp.

(Pl. 6, fig. 5-8. Text-figs 7)

Shell very small, thin, triangular, equilateral, equivalve, chestnut-brown colour, ornamented with 10 relatively smooth radial ribs but which tend to become ornamented with small nodules near the ventral edge of the shell; interstices relatively smooth, not deep, as wide as the ribs; dorsal margin sharply angled at umbo; umbos medial and close set; internally the shell is smooth and shining chocolate-brown, the external ribbing shows through, margins fluted, no palial sinus; ligament not retained.

TYPE MATERIAL. HOLOTYPE B.M.(N.H.) Reg. no. 1968769, Western end Khor-al-Bazm. Length 1.6 mm, height 1.4 mm, width 0.6 mm.

PARATYPES B.M.(N.H.) Reg. nos. 1968770, 1968771, 1968773, Western end Khor-al-Bazm

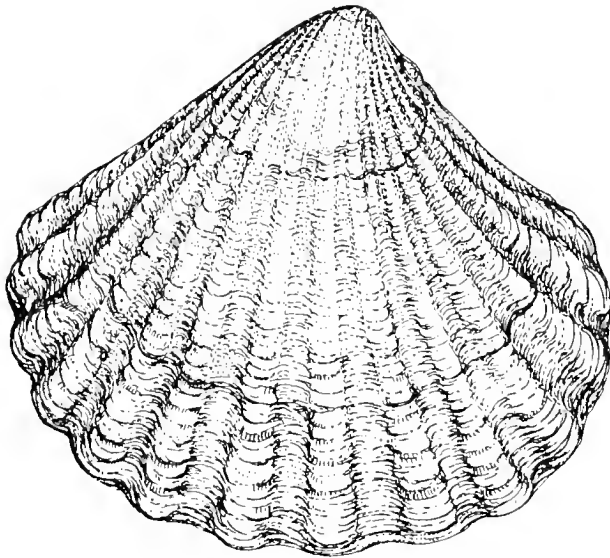
B.M.(N.H.) Reg. no. 1968772, Sta 105

B.M.(N.H.) Reg. no. 1968778, Sta. 62.

B.M.(N.H.) Reg. no. 1968779, Eastern Khor.

The holotype is possibly juvenile and differs from the paratypes in being brown in colour, the latter are orange. Also in the paratypes there is a tendency for the ribs to bear heavy nodules and for the inter-spaces to be wider than the ribs. The range of rib count in the paratypes is 9-14 (mean 11). The largest paratype is 2.5 mm long and 2.3 mm high.

The equilateral shape of this species distinguishes it from the strongly inequilateral *C. coxi* also the ribs are closer than in *C. coxi*. The figure on plate 6, shows very clearly the difference in shape between *coxi* Eames and Wilkins and the proposed new species.

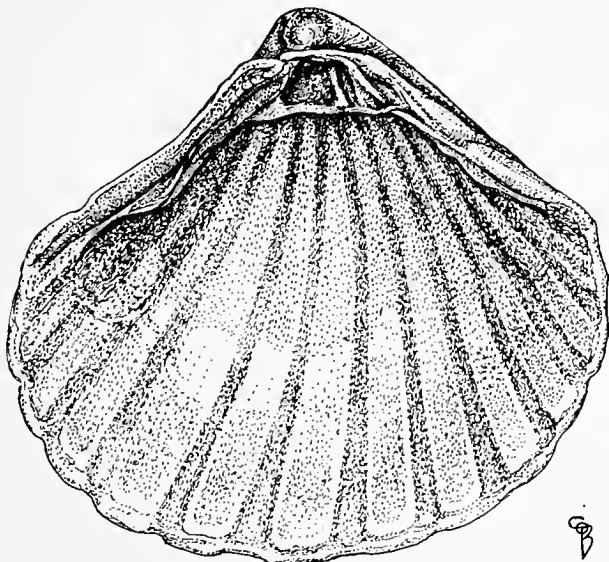


— = x6

ACTUAL SIZE, 1m.m.

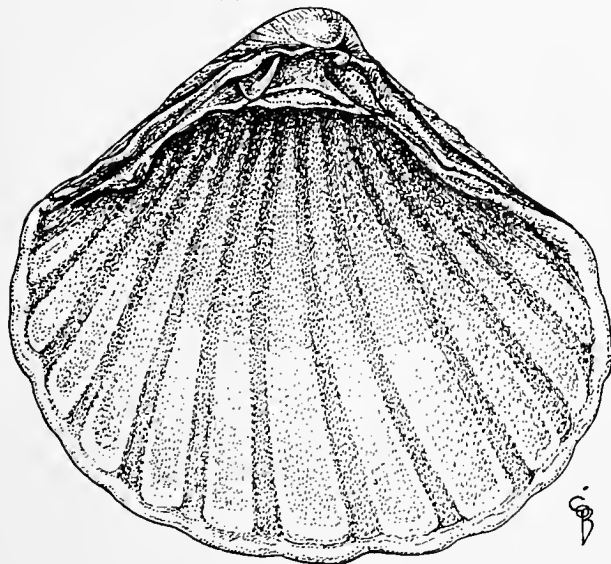
FIG. 7. *Cuna majeeda* n. sp. (A) left valve exterior.





— × 6

ACTUAL SIZE, 1 m. m.  
(B) left valve interior.



— = × 6

ACTUAL SIZE, 1 m. m.  
(c) right valve interior.

*Cuna* sp.

MATERIAL. Western Khor, 1+1 valve.

Superfamily **CARDITACEA**Family **CARDITIDAE**

Genus **CARDITA** Bruguière, 1792

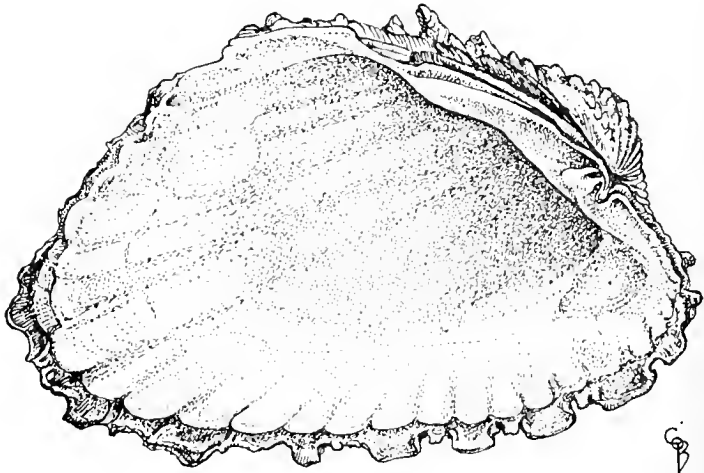
*Cardita antiquata* (Linnaeus, 1758)

*Chama antiquata* Linnaeus, 1758 : 691.

*Cardita antiquata* Melvill and Abercrombie, 1893 : 28. Sturany, 1901 : 287. Melvill and Standen, 1907 : 812.

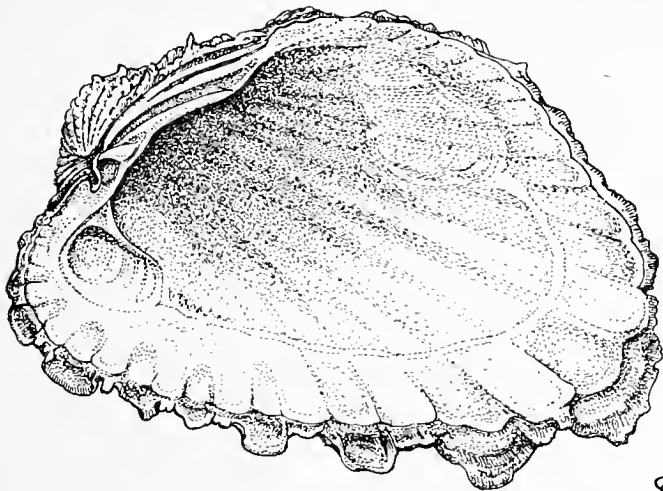
MATERIAL. Sta. 50, 3 valves; Sta. 54, 6 valves; Sta. 56, 32 valves; Sta. 58, 15 valves; Sta. 70a, 3 valves; unlocated, 6 valves.

The above determination is made with some reserve. Haas (1952 and 1954) reports the species *Cardita bicolor* Lamarck from the Trucial coast. Reeve (1843) makes *bicolor* Lamarck a synonym of *antiquata* Linnaeus. Melvill and Standen, (1928) reported *Cardita antiquata* (author in error) from Dabai in 8 fms but express doubts as to the determination.



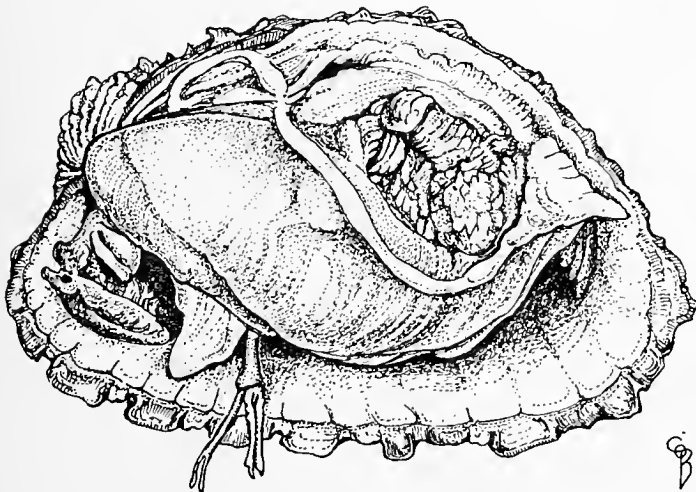
ACTUAL SIZE, 43 m.m.

FIG. 8. *Cardita finchi* Melvill (A) left valve interior.



ACTUAL SIZE, 43 m.m.

(B) right valve interior.



ACTUAL SIZE, 43 m.m.

(c) lateral view with left valve and mantle removed to show general anatomical characters.

*Cardita finchi* (Melvill, 1898)

(Text-fig. 8)

*Mytilicardia finchi* Melvill, 1898 : pl. 2, fig. 17. Melvill and Standen, 1907 : 813.

MATERIAL. Sta. 10, 1 live.

The generic name *Mytilicardia* used by Melvill is perhaps a *lapsus calami* for *Mytilocardia* (Blainville) L. Agassiz which Thiele (1936) makes a synonym of *Mytilicardia* Anton 1839. This genus Thiele makes a subgenus of *Beguina* Röding 1798. As it appears that this species has not the shell form of *Beguina* I feel obliged to include *finchi* in *Cardita*.

The species is apparently quite rare, and a specimen in the B.M.(N.H.), Reg. no. 1899.12.27.122 from the type locality, Muscat was examined. This is a new record for the Persian Gulf and also the first live specimen recorded.

The type locality is Muscat 10 fms, on coral sand, the Trucial Coast specimen came from a depth of 50-88 ft 4 miles off the north coast of Jeziret al Yas, on the off-shore shelf where rock was exposed on the bottom. This specimen has a weak byssus and was possibly attached to the rock.

## Superfamily CYPRINACEA

## Family TRAPEZIIDAE

Genus *TRAPEZIUM* Muhlfield, 1811*Trapezium sublaevigatum* (Lamarck, 1819)*Cardita sublaevigata* Lamarck, 1819 : 26.*Cypricardia vellicata* Reeve, 1843 : sp. 7.*Libitina vellicata* Melvill and Abercrombie, 1893 : 28. Melvill and Standen, 1907 : 814.*T. (Neotrapezium) sublaevigatum* Solem, 1954 : 71.

MATERIAL. Eastern Khor, 1.

The above specimen is considerably larger than the type as figured by Solem (1955). Blair (unpublished) collected specimens 'within a mile or two of Bushire', apparently all dead, between 1914 and 1918 and these are now in the Liverpool Museum.

## Superfamily LUCINACEA

## Family UNGULINIDAE

Genus *DIPLODONTA* Bronn, 1831*Diplodonta raveyensis* Sturany, 1901*D. raveyensis* Sturany, 1901 : 285, pl. 6, fig. 8-11. Melvill and Standen, 1907 : 816.

MATERIAL. Sta. 105, 3 valves; Eastern Khor, 4 valves.

This is a new record for the Persian Gulf as Melvill and Standen (1906) recorded it for the Gulf of Oman and Makran Coast. One of the specimens from the Khor-al-

Bazm is rather larger than the type from the Red Sea (height 12.5 and 9.8 mm, breadth 13.0 and 10.4 mm respectively). As this is the opposite to the expected trend in the warmer and more saline waters of the Khor it is possible that Sturany's specimen is a juvenile.

### Family LUCINIDAE

Genus *PHACOIDES* Blainville, 1825

Subgenus *BELLUCINA* Dall, 1901

#### *Phacoides (Bellucina) semperiana* (Issel, 1896)

*Lucina semperiana* Issel, 1869 : 82. Sturany, 1901 : 284. Cooke, 1886b : 99.

*L. (Cyclas) semperiana* Melvill and Standen, 1907 : 815.

*P. semperiana* Barnard, 1964 : 475.

MATERIAL. Eastern Khor, 1, 28 valves; Western Khor, 72 valves.

The above records are from deposits in the Khor, Melvill and Standen (1907) record the species from shell sand off Charbar Bay (Makran Coast) and from Bombay, in shell sand.

Genus *DIVARICELLA* Martens, 1830

#### *Divaricella cumingi* (Adams and Angus, 1863)

*Lucina (Cyclas) cumingi* Adams and Angus, 1863 : 426, pl. 37, fig. 20.

*D. dalliana* Biggs and Grantier, 1960 : 390

MATERIAL. Sta. 20, 2 valves; Sta. 50, 1 valve; Sta. 54, 2 valves; Sta. 55, 1 valve; Sta. 70A, 1 valve; unlocated, 2 valves.

None of the published lists for the Persian Gulf, Bombay or Aden has any reference to a species of *Divaricella*. Biggs and Grantier (1960) recorded *dalliana* Vanetta from Ras Tanura but Barnard (Personal communication) queried this determination. After re-examining this material I accept Barnard's view that *dalliana* is confined to South Africa.

Genus *CTENA* Morch, 1860

#### *Ctena divergens* (Philippi, 1850)

*Lucina divergens* Philippi, 1850 : 103, pl. 2, fig. 4. Fischer, 1891 : 230.

*Codokia (Jagonia) divergens* Moazzo, 1939 : 112.

MATERIAL. Sta. 97, 1; Sta. 20, 1 valve; Western Khor, 1 valve.

Kinsman (1964b) records the species as uncommon in the area of the lagoon between Halat-al-Bahrani and Abu Dhabi I.; Moazzo (1939) says it is rare in Suez Bay. The above sparse material seems to confirm the fact that it is a rare species.

Genus *CODAKIA* Scopoli, 1777

Subgenus *JAGONIA* Recluz, 1869

*Codakia (Jagonia) fischeriana* (Issel, 1869)

*Lucina fischeriana* Issel, 1869 : 104, pl. 1, fig. 8. Sturany, 1901 : 285. Shopland, 1902 : 178.

Tomlin 1927 : 308.

*Loripes fischerianus* Moazzo, 1939 : 114.

**MATERIAL.** Sta. 62, 1 live + 2 + 26 valves; Sta. 70, 2 valves; Sta. 58, 7 valves; Sta. 64, 1 valve; Eastern Khor, 13 valves; Western Khor, 87 valves.

Cook (1886b) records this species from the Persian Gulf but does not give the exact locality. The live specimen and one other valve are orange-pink, but the remainder are bleached.

Issel (1869) states that the margin of the shell is 'simple' but Cooke (1886b) states that it is dentated; the Persian Gulf specimens conform with Cooke's description but some of the worn specimens are smooth, which suggests that again Issel was describing a new species from beachworn specimens.

Genus *ANODONTIA* Link, 1807

*Anodontia edentula* (Linnaeus, 1758)

*Genus edentula* Linnaeus, 1758 : 689.

*Lucina edentula* Moazzo, 1939 : 110. Barnard, 1964 : 470.

**MATERIAL.** Western Khor, 1 specimen, 1 valve; unlocated, 5 valves.

This species has not previously been recorded for the Persian Gulf.

Superfamily **CHAMACEA**

Family **CHAMIDAE**

Genus *CHAMA* Linnaeus, 1758

*Chama brassica* Reeve, 1847

*Chama brassica* Reeve, 1847 : b : sp. 31. Biggs, 1958 : 275. Biggs and Grantier, 1960 : 390.

**MATERIAL.** Sta. 10, 1 valve; unlocalised 2, 1 juvenile.

The type locality was 'Philippines, under stones at low water'. Station 10 was on an 'exposed rock bottom' but at a good depth. Biggs (1958) records it on rocks at low water for Hormuz I. The distribution range in depth as well as its geographical range seem to be considerable.

Superfamily **CARDIACEA**Family **CARDIIDAE**Genus **LAEVICARDIUM** Swainson, 1840***Laevicardium papyraceum*** (Bruguière, 1789)*Cardium papyraceum* Bruguière, 1789 : 260.*C. (Papyridea) papyraceum* Melvill and Standen, 1907 : 839. Tomlin, 1927 : 305. Moazzo, 1939 : 64. Biggs and Grantier, 1960 : 391.*P. papyracea* Barnard, 1964 : 494.

MATERIAL. Eastern Khor, 1 valve juvenile; many fragments; Western Khor, 2 valves juveniles.

Genus **TRACHYCARDIUM** Mörch, 1853***Trachycardium lacunosum*** (Reeve, 1845)*Cardium lacunosum* Reeve, 1845, 2 : sp. 81.*C. (T.) lacunosum* Melvill and Standen, 1907 : 837. Melvill, 1928 : 116.*T. lacunosum* Biggs and Grantier, 1960 : 390.

MATERIAL. Sta. 8, 1 live; Sta. 9, 1+1 live; Sta. 13, 4 live; Sta. 50, 1 valve; Sta. 54, 5 valves; Sta. 56, 11 valves; Sta. 58, 13 valves; Sta. 70a, 7 valves; Eastern Khor, 1 valve; Western Khor, 1 valve; beach, 31 valves; unlocated, 16 valves.

***Trachycardium maculosum*** (Wood, 1815)*Cardium maculosum* Wood, 1815 : 218. Sturany, 1901 : 282.*C. (T.) maculosum* Melvill and Standen, 1907 : 837. Melvill, 1928 : 116.

MATERIAL. Sta. 3, 1 live; Sta. 4, 1 live; Sta. 9, 1 live; Sta. 15, 1 live; Western Khor, 1 juvenile, 2 valves; Eastern Khor, fragments.

Genus **PARCIVARDIUM** Monterosato, 1884***Parvicardium sueziensis*** (Issel, 1869)*Cardium sueziensis* Issel, 1869 : 76, 252, pl. 3, fig. 4.*Cardium (?Acanthocardium) sueziense* Melvill and Standen, 1907 : 839.*Cardium (Cervastoderma) sueziense* Tomlin, 1924 : 305. Moazzo, 1939 : 68.*Cardium (Acanthocardium) sueziense* Melvill, 1928 : 116.

MATERIAL. Sta. 58, 1 valve; Sta. 70, 2 valves; Eastern Khor, 11 valves; Western Khor, 44 valves.

Only one shell from the Western Khor has the brown flecks referred to by Issel in his original description as 'castaneis notata', all the remainder are pure white. The only other specimen I have seen with flecks is in the Manchester Museum and came from the Red Sea.

Superfamily **VENERACEA**Family **VENERIDAE**Genus **LIOCONCHA** Mörch, 1853**Lioconcha picta** (Lamarck, 1818)*Cytherea picta* Lamarck, 1818 : 569.*L. picta* Sturany, 1901 : 280. Melvill and Standen, 1907 : 830. Moazzo, 1939 : 80.**MATERIAL.** Western Khor, 2 valves juvenile.

This is the first record for the Persian Gulf, Melvill and Standen recorded it for Muskat and Karachi.

Genus **GAFRARIUM** Röding, 1798**Gafrarium arabicum** (Lamarck, 1818)*Cytherea arabica* Lamarck, 1818 : 571.*Cytherea (Lioconcha) arabica* Issel, 1869 : 65.*Meretrix (L.) arabica* Fischer, 1891 : 229.*L. arabica* Sturany, 1901 : 280. Melvill and Standen, 1907 : 830. Moazzo, 1939 : 79.*G. arabicum* Tomlin, 1927 : 306.*Circe arabica* Biggs and Grantier, 1960 : 391.**MATERIAL.** Beach, 1+10 valves; Sta. 70, 17+1 valve; Sta. 90, 1 live; Sta. 95, 5 live.**Gafrarium dispar** (Dillwyn, 1817)*Venus dispar* Dillwyn, 1817 : 199.*Cytherea (Crista) dispar* Issel, 1869 : 65.**MATERIAL.** Sta. 47, 1 live, juvenile.

This is a new record for the Persian Gulf. The specimen was found in a cora crevice.

**Gafrarium pectinatum** (Linnaeus, 1758)*Venus pectinatum* Linnaeus, 1758 : 689.*Crista pectinata* Sturany, 1901 : 280. Melvill and Standen, 1907, 831. Moazzo, 1939 : 80.*G. pectinatum* Tomlin, 1927 : 306, 316. Barnard, 1964 : 502.*G. (Circe) pectinatum* Spry, 1964 : 32.**MATERIAL.** Eastern Khor, 1 live.

This specimen was attached to seaweed.



Genus *CIRCE* Schumacher, 1817

*Circe (Circe) intermedia* Reeve, 1863

*C. intermedia* Reeve, 1863, 14 : sp. 26. Shopland, 1902 : 178.

*Gafrarium intermedia* Biggs and Grantier, 1960 : 391.

MATERIAL. Sta. 10, 1 live.

Little seems to be known of the distribution of this species. Reeve, in his original description, gives no locality for the type, but someone had written in pencil on the B.M.(N.H.) copy of Reeve, 'Hab. Aden, (Yerbury)'. The above record is from fairly deep water, 16 m to 30 m and 4 miles north of Jeziret al Yas.

The measurements are length 38 mm and height 33 mm. The ligament is only 7 mm long and rather weak. The adductor muscles are nearly equal in size so approximating to *Circe arabicum* (Lamarck) rather than *Circe scripta* (Linnaeus); in specimens of the latter examined from the Trucial Coast the two muscles are unequal in size. Cooke (1886) reports the species from habitats 2-10 fathoms for Suez Bay.

*Circe (Circe) scripta* (Linnaeus, 1758)

*Venus scripta* Linnaeus, 1758 : 689.

*C. scripta* Issel, 1869 : 71, 251. Sturany, 1901 : 280. Melvill and Standen, 1907 : 831.

Moazzo, 1939 : 78. Barnard, 1964 : 501. Spry, 1964 : 31.

*C. (C.) scripta* Haas, 1952 : 116.

*Gafrarium (C.) scripta* Haas, 1954 : 48.

*G. scripta* Biggs and Grantier, 1960 : 391.

MATERIAL. Sta. 9, 3 live, juvenile; Sta. 13, 1; Sta. 54, 1; Sta. 103, 2 live; Sta. 105, 1 juvenile; Eastern Khor, 1, 2 valves; Western Khor, 1+8 valves; Sta. 7, 1 valve.

This species was found on the off shore shelf (Sta. 9) and inshore (Sta. 103).

Subgenus *PARMULOPHORA* Dall, 1915

*Circe (Parmulophora) corrugata* (Dillwyn, 1817)

*Venus corrugata* Dillwyn, 1817 : 201.

*C. corrugata* Issel, 1869 : 71, 360. Sturany, 1901 : 280. Melvill and Standen, 1907 : 831.

Tomlin, 1927 : 306. Moazzo, 1939 : 76.

*C. (P.) corrugata* Spry, 1964 : 31.

MATERIAL. Sta. 54, 2; Sta. 56, 1; unlocated, 1; Eastern Khor, 10 valves juvenile; Western Khor, 6 valves juvenile.

This species is reported by Kinsman (1964b) as being uncommon on the shelf but I have collected the species in abundance in sand in Suez Bay and in Lake Timsah on the canal.

Genus *DOSINIA* Scopoli, 1777*Dosinia alta* (Dunker, 1848)*Artemisia alta* Dunker, 1848 : 184.*Artemis alta* Issel, 1869 : 72.*D. alta* Melvill and Standen, 1907 : 835. Moazzo, 1939 : 85. Biggs, 1958 : 275. Biggs and Grantier, 1960 : 391

MATERIAL. Sta. 56, 2 valves; Sta. 58, 1 valve juvenile.

*Dosinia hepatica* (Lamarck, 1818)*Cytherea hepatica* Lamarck, 1818 : 572.*D. hepatica* Melvill and Standen, 1928 : 511. Moazzo, 1939 : 83. Barnard, 1964 : 511.

MATERIAL. Eastern Khor, 1 valve juvenile; Western Khor, 1 valve juvenile.

*Dosinia histrio* (Gmelin, 1791)*Venus histrio* Gmelin, 1791 : 3287.*D. histrio* Sturany, 1901 : 282. Melvill and Standen, 1907 : 835. Moazzo, 1939 : 84.

MATERIAL. Western Khor, 1 live, 13 valves and fragments.

*Dosinia* spp.

MATERIAL. Sta. 70, 1; Sta. 67, 1.

Both these specimens are juveniles hence the hesitation in referring them to a species.

Genus *BASSINA* Jukes-Browne, 1914*Bassina calophylla* Philippi, 1836*Venus calophylla* Philippi, 1836 : 229, pl. 8, fig. 2.*Anaitis calophylla* Melvill and Standen, 1907 : 833.

MATERIAL. Western Khor, 1 live, 32 valves and fragments.

According to the measurements given by Philippi in his description of the species all the specimens from the Khor-al-Bazm must either be juveniles or a small race of the species.

Genus *TIMOCLEA* Brown, 1827*Timoclea farsiana* n. sp.

(Pl. 6, figs 1-4. Text-fig. 9)

Shell small, rather thin, equivalve, inequilateral, contracted posteriorly, anterior margin evenly rounded, posterior margin forming a truncated obtuse angle; shell colour externally creamy white with irregular dull purple-brown maculations,

internally milky white with purple-brown maculations; sculpture—about 13 parallel, sharp-edged, upturned costae which are interrupted somewhat where they are crossed by the radiating ribs on the anterior half of the shell but these ribs are dominant over the costae and continuous on the posterior end where they also bear foliations. Prodissoconch more or less smooth but with incipient radiating ridges. Interior margin of the shell strongly crenulate. Teeth, 3 cardinals in each valve. Lunule moderately broad, brownish purple with thin radiating ribs. Ligaments unknown. Escutcheon long, ovate and relatively smooth. Animal unknown.

TYPE MATERIAL. HOLOTYPE B.M.(N.H.) Reg. No. 1968774 Khor-al-Bazm, Trucial Coast, Persian Gulf. Length 6.3 mm, height 4.6 mm.

Material collected, Eastern Khor-al-Bazm, 34 valves, Western Khor-al-Bazm, 204 valves.

This species is intermediate between *Timoclea arakana* Nevill and *Timoclea macfadyeni* Dance and Eames. From the former it differs by being considerably smaller and by the costae being sharp-edged and upturned; from the latter it differs by having the costae placed relatively further apart and not being rounded but turned up, in general shape by being oval.

There is considerable variation in the number and spacing of the costae; in three examples from the Western Khor there is a proliferation of the costae by the interposition of smaller costae between the larger ones towards the ventral edge. A number of unidentified specimens in the British Museum (Natural History) from Muscat, Gulf of Oman (Winckworth Collection) may be large specimens of this species. I have also examined a sample from shallow water southern end of Qatar Peninsular (Biggs collection). The largest paratype is 9.5 mm long and 6.75 mm high.

### Genus *AMIANTIS* Carpenter, 1864

#### *Amiantis erycina* (Linnaeus, 1758)

*Venus erycina* Linnaeus, 1758 : 686.

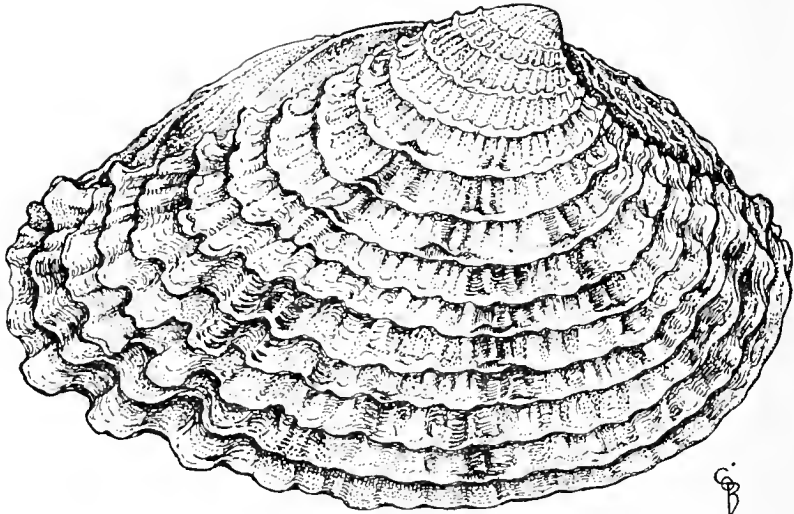
*Callista erycina* Melvill and Standen, 1904 : 829.

*Macrocallista (Paradione) erycina* Haas, 1952 : 116.

*Pitarvia (M.) erycina* Biggs and Grantier, 1960 : 391.

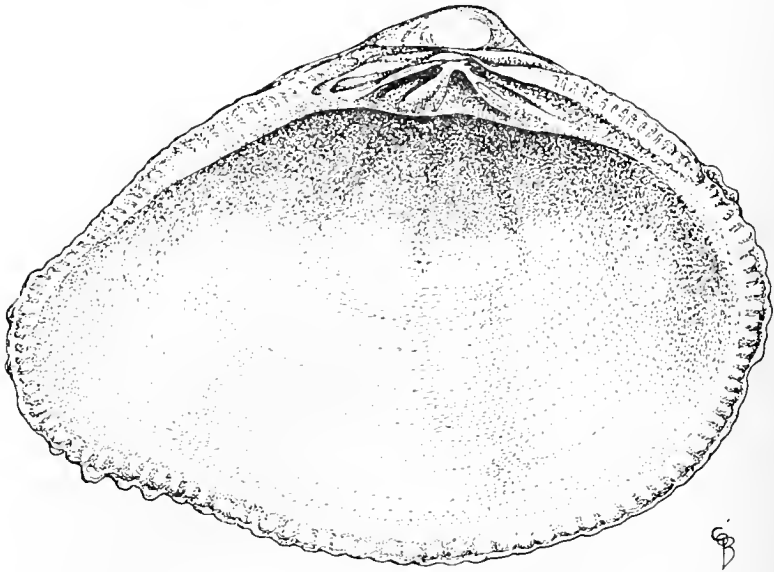
MATERIAL. Sta. 56, 1 valve juvenile; 4 valves.

The above is all worn material, juveniles of this species and the adults of the following species are sometimes difficult to distinguish.



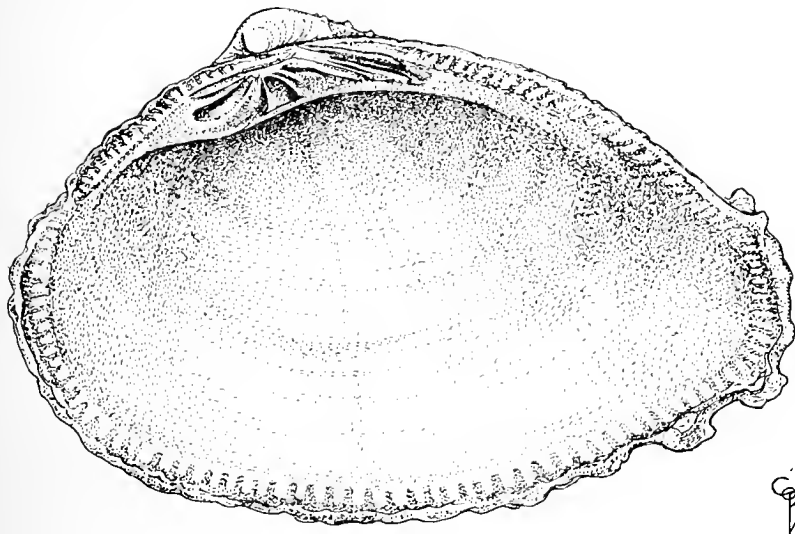
ACTUAL SIZE, 6 m.m.

FIG. 9. *Timoclea farsiana* n. sp. (A) right valve exterior.



ACTUAL SIZE, 6 m.m.

(B) left valve interior.



ACTUAL SIZE, 6 m. m.

(c) right valve interior.

*Amiantis hagenowi* (Dunker, 1849)

*Cytherea hagenowi* Dunker, 1849 : 184.

*Cytherea (Callista) Hagenowi* Issel, 1869 : 69.

*Callista hagenowi* Melvill and Standen, 1907 : 829.

MATERIAL. Eastern Khor, 33 valves; Western Khor, 22 valves.

The Melvill and Standen record is for Dubai on the Trucial Oman Coast, it has not yet been recorded for farther north. Most of the valves here recorded are juveniles and some reserve in accepting this determination is necessary as they may be juveniles of the previously recorded species.

Genus *SUNETTA* Link, 1807

*Sunetta effosa* (Hanley, 1842)

*Cytherea effosa* Hanley, 1842 : 123.

*S. effosa* Melvill and Abercrombie, 1893 : 45. Melvill and Standen, 1907 : 831. Biggs and Grantier, 1960 : 391.

MATERIAL. Western Khor, 7 live.

These live specimens were collected near the western end of the Khor-al-Bazm in the intertidal zone on a sandbank. Kendall (personal communication) comments that specimens of this species 'kept popping up from the sand as I walked'.

*Sunetta* spp.

MATERIAL. Sta. 55, 1 valve; Sta. 58, 5 valves; unlocated (on Es Sa'diyat I.) 1 valve.

Genus *MERETRIX* Lamarck, 1799

*Meretrix meretrix* (Linnaeus, 1758)

*Venus meretrix* Linnaeus, 1758 : 686.

*Cytherea zonaria* Lamarck, 1818 : 562.

*M. zonaria* Melvill and Standen, 1907 : 829.

*M. meretrix* Biggs and Grantier, 1960 : 391.

MATERIAL. Sta. 62, 3 live, 2 juveniles; Sta. 83, 4 live; Sta. 88, 2 live juvenile; Sta. 95, 4 live juvenile; Eastern Khor, 1 valve; beach, 50 valves.

Genus *TIVELA* Link, 1807

*Tivela ponderosa* (Koch in Philippi, 1844)

*Cytherea ponderosa* Koch, 1844 : 149.

*T. ponderosa* Sturany, 1901 : 279. Melvill and Standen, 1907 : 828. Haas, 1952 : 116.

MATERIAL. Sta. 54, 3 valves; Sta. 56, 1 fragment.

Genus *KATELYSIA* Romer, 1857

*Katelysia marmorata* (Lamarck, 1818)

*Venus marmorata* Lamarck, 1818 : 600.

*Tapes (Hemitapes) marmorata* Melvill and Standen, 1907 : 833.

MATERIAL. Sta. 9, 1 live.

This is a new record for the Persian Gulf as that of Melvill and Standen (1907) was for Bombay where it was taken on mud at low tide. This specimen was found in deep water 3 miles north of Jeziret el Yas.

Genus *IRUS* Schmidt, 1818

*Irus irus* (Linnaeus, 1758)

*Donax irus* Linnaeus, 1758 : 683.

*Venerupis macrophylla* Deshayes, 1853 : pl. 18, fig. 8, Cooke, 1886b : 103. Sturany, 1901 : 282.

Melvill and Standen, 1907 : 836.

*I. irus* Tomlin, 1927 : 315.

*Notirus macrophylla* Taylor, 1968 : 204.

MATERIAL. Eastern Khor, 1 valve.

This is a new record for the Persian Gulf. The relationship between this species and *I. macrophylla* Deshayes has been referred to on a number of occasions. Smith

(1891) recording the species for Aden says '*V. macrophylla* and *V. irus* are certainly identical'. Sturany reporting on the Red Sea equates the two species, Cooke (1886b) although using the name *macrophylla* notes 'These Suez shells are quite undistinguishable from the familiar *irus* L . . .' Tomlin (1927) records *Venerupis irus* Linnaeus on his list of species common to both the Mediterranean and Red Seas. This species inhabits cavities in rocks and tends to vary with the type of rock in which it bores.

### Superfamily MACTRACEA

#### Family MACTRIDAE

Genus *MACTRA* Linnaeus, 1767

#### *Maetra olorina* Philippi, 1846

*M. olorina* Philippi, 1846 : 72, pl. 2, fig. 2. Issel, 1869 : 52, 357. Fischer, 1891 : 229. Sturany, 1901 : 247, 276. Tomlin, 1924 : 308. Melvill, 1928 : 116. Moazzo, 1939 : 103, pl. 9, fig. 3, pl. 10, fig. 2. Hudson, Eames and Wilkins, 1957 : 397.

**MATERIAL.** Sta. 50, 3 valves; Sta. 54, 11 valves; Sta. 55, 3 valves; Sta. 56, 37 valves; Sta. 58, 38 valves; Sta. 70a, 18 valves; Eastern Khor, 1 valve; Western Khor, 1 valve; beach, 51 valves.

After examination of material from the Persian Gulf and South Arabian coast it appears that there is a species complex involving *olorina* Lamarck, *furoti* Jousseaume, *lilacina* Lamarck and according to Moazzo (1939) *isthmia* Jousseaume. I have tentatively placed all the specimens under *olorina* but the problem needs further study.

### Superfamily TELLINACEA

#### Family GARIIDAE

Genus *ASAPHIS* Modeer, 1793

#### *Asaphis deflorata* (Linnaeus, 1758)

*Venus deflorata* Linnaeus, 1758 : 687.

*A. violascens* Sturany, 1901 : 277.

*A. violascens* Issel, 1869 : 56.

*A. deflorata* Melvill and Standen, 1907 : 842. Moazzo, 1939 : 97. Biggs and Grantier, 1960 : 391.

*A. (A.) deflorata* Haas, 1954 : 48.

**MATERIAL.** Sta. 90, 1 live; beach, 8 valves.

Kinsman (1964b) reports that this species is very common on the off-shore shelf.

## Family PSAMMOBIIDAE

Genus *SOLECURTUS* Blainville, 1824*Solecurtus australis* (Dunker, 1861)*Macha australis* Dunker, 1861 : 424.*Solenocurtus (Macha) australis* Moazzo, 1939 : 100.*Solecurtus strigilatus* Biggs and Grantier, 1960 : 392.

MATERIAL. Western Khor, 2 valves, damaged.

The *Solecurtus strigilatus* Linnaeus recorded by Biggs and Grantier (1960) is this species. Issel (1869) reports *S. strigilatus* (Linnaeus) from Suez Bay based on material collected before the opening of the Suez Canal, it is possible that this was an error for the present species as Moazzo (1939) records *australis* in Suez Bay.

## Family TELLINIDAE

Genus *TELLINA* Linnaeus, 1758Subgenus *ARCOPAGINULA* Lamy, 1918*Tellina (Arcopaginula) inflata* Gmelin, 1891

(Text-fig. 10)

*Tellina inflata* Gmelin, 1791 : 3230.*Tellina (Tellinella) inflata* Melvill and Standen, 1907 : 819.*Tellina (A.) inflata* Moazzo, 1939 : 118.

MATERIAL. Sta. 3, 1 live; Sta. 5, 1+3 valves; Sta. 7, 1+3 valves.

This is a new record for the Persian Gulf. It was reported from Muscat, 10 fm mud, by Melvill and Standen (1907). The specimen from station 3 was gravid (see figure), it was taken in December or January when the temperature of the water was 21°C (70°F) on the bottom and the salinity 43‰ to 48‰.



FIG. 10. *Arcopagia (Arcopaginula) inflata* Gmelin lateral view with right valve and mantle removed to show general anatomical characters.



Subgenus *ARCOPAGIA* Brown, 1827

*Tellina (Arcopagia) isseli* (H. Adams, 1870) -

*Tellina (Arcopagia) isseli* H. Adams, 1870 : 790, pl. 48, fig. 10. Melvill and Standen, 1970 : 821.  
Moazzo, 1939 : 118.

MATERIAL. Sta. 11, 1.

Subgenus *PISTRIS* Thiele, 1934

*Tellina (Pistris) pristin* Lamarck, 1818

*T. pristin* Lamarck, 1818 : 531.

*T. (P.) pristin* Moazzo, 1939 : 119.

MATERIAL. Western Khor, 1 live.

Another new record for the Persian Gulf. Unfortunately the only specimen collected was badly broken when received.

Subgenus *PINGUITELLINA* Iredale, 1927

*Tellina (Pinguitellina) robusta* Hanley, 1844

*T. robusta* Hanley, 1844 : 63.

*Arcopagia (P.) robusta* Biggs, 1965 : 339.

*P. robusta* Taylor, 1968 : 204.

MATERIAL. Eastern Khor, 5+102 valves; Western Khor, 3+75 valves; Sta. 7, 3 valves.

Genus *EXOTICA* Lamy, 1918

Subgenus *JACTELLINA* Iredale, 1929

*Exotica (Jactellina) rhomboides* (Quoy and Gaimard, 1835)

*Tellina rhomboides* Quoy and Gaimard, 1835 : 502.

*T. (Moera) rhomboides* Melvill and Standen, 1907 : 820.

MATERIAL. Western Khor, 1 live, 6 valves; Eastern Khor, 1; unlocated, 3 valves.

This is the first record for the species in the Persian Gulf, Melvill and Standen record the species from Muskat, Gulf of Oman. The live specimen from the Khor-al-Bazam is greenish white in colour with pinkish maculations which appear to be the remains of five rays, there is one specimen from Japan in the collection of the B.M.(N.H.) showing similar markings. The costae near the ventral edge and the diagonal striations on the centre of the shell are very close.

Genus *MACOMA* Leach, 1819

*Macoma arsinoensis* (Issel, 1869)

*Tellina* (*M.*) *arsinoensis* Issel, 1869 : 59.

*T. arsinoensis* Cooke, 1886b : 106.

*T. (Angulus) arsinoensis* Moazzo, 1939 : 120.

MATERIAL. Sta. 59, 1 live juvenile; Western Khor, 1 live juvenile, 20 valves; Eastern Khor, 1 live.

The type series from Suez Bay measured length 13-17 mm, breadth 9.5-12.25 mm while the largest of the above sample is 11.3 mm in length, 8.3 mm in breadth.

*Macoma jeanae* Dance and Eames, 1966

*Macoma jeanae* Dance and Eames, 1966 : 36, pl. 4, fig. 1, 2.

MATERIAL. Eastern Khor, 1, 2 valves; Western Khor, 14 valves.

The species was described from a single valve from alluvium at 16 ft at Gaumat Ali in S.E. Iraq. The dimensions of the type are length 3.3 mm, height 2.3 mm while the range of the above sample is length 6.8-9.8 mm, height 4.0-5.3 mm. Mr Dance identified some of the above Trucial coast specimens.

Genus *TELLIDORA* H. and A. Adams, 1856

*Tellidora pellyana* H. Adams, 1873

*T. pellyana* H. Adams, 1873 : 208, pl. 23, fig. 14, Melvill and Standen, 1907 : 824.

MATERIAL. Sta. 3, 1 valve juvenile; Sta. 7, 2 valves juveniles; Eastern Khor, 2 valves; Western Khor, 10 valves.

Originally described from the Persian Gulf, Melvill and Standen (1907) record the species from Karachi. Haas (1952) records *Tellidora* sp. from Dukhan on the Qatar Peninsular which may well be this species. It is apparently rare and of very limited distribution.

Superfamily **SOLENACEA**

Family **SOLENIDAE**

Genus *CULTELLUS* Schumacher, 1817

*Cultellus cultellus* (Linnaeus, 1758)

*Solen cultellus* Linnaeus, 1758 : 673.

*C. cultellus* Sturany, 1901 : 276. Melvill and Standen, 1907 : 844. Moazzo, 1939 : 99.

MATERIAL. Sta. 7, 1 valve.

Superfamily **MYACEA**Family **CORBULIDAE**Genus **CORBULA** Lamarck, 1799***Corbula acutangula*** Issel, 1869*C. acutangula* Issel, 1869 : 246, pl. 5, fig. 1.**MATERIAL.** Western Khor, 1, juvenile, 11 valves.

This is a new record for the Persian Gulf. No exact locality was given for the type which is a sub-fossil specimen from a raised beach.

***Corbula modesta*** Hinds in Reeve, 1843*C. modesta* Hinds in Reeve, 1843, 2 : Sp. 14. Hinds, 1843 : 57. Melvill and Abercrombie, 1893 : 83. Melvill and Standen, 1907 : 843.**MATERIAL.** Western Khor, 1 valve.***Corbula subquadrata*** Melvill, 1907*C. subquadrata* Melvill and Standen, 1907 : 843, pl. 61, fig. 7, 7a. Melvill, 1928 : 117. Taylor, 1968 : 205.**MATERIAL.** Eastern Khor, 1; Western Khor, 6+30 valves.

Although the figure given by Melvill (1907) shows a more compact shell than those from the Khor-al-Bazm they conform well to specimens in the B.M.(N.H.) from Madras (Winckworth) and Bombay (Piele).

Superfamily **GASTROCHAENACEA**Family **GASTROCHAENIDAE**Genus **GASTROCHAENA** Spengler, 1783***Gastrochaena cuneiformis*** Spengler, 1783*G. cuneiformis* Spengler, 1783 : 179, pl. 1, fig. 8-11. Moazzo, 1939 : 108. Barnard, 1964 : 562. Taylor, 1968 : 205.**MATERIAL.** Sta. 65, 3 live; Sta. 104, 1 live; Western Khor, 1.

This species was found boring in limestone (Station 104) and in coral clumps (Station 65), Moazzo (1939) reports it in Suez Bay boring in coral.

## DISCUSSION

The conditions on the Trucial Coast, particularly in the inner lagoon areas, provide habitats with a wide range of temperatures and salinities (see Murray 1965, 1966). The variation in habitat, form and conditions makes this an interesting area for study as associated with these features are found many morphologically variable populations in a wide variety of taxa.

Kinsman (1964) has shown that on the reef north of Abu Dhabi certain corals survived temperatures and salinities previously regarded as lethal.

The collections were made primarily for geological study and hence are not random which would account for the absence of certain groups and the presence of large numbers of small gastropods and bivalves. The most common species in general collecting is *Cerithium scabridum* and eleven of the twenty most common gastropods belong to the Cerithiacea.

The most common bivalves in order of frequency are, *Glycymeris striatularis*, *Brachidontes variabilis*, *Pinctada radiata*, and *Tellina robusta*.

## ACKNOWLEDGEMENTS

The author wishes to thank those who collected the material on the Trucial Oman Coast, Dr Graham Evans and the team of workers under his direction, Dr D. J. J. Kinsman, Dr C. St. G. Kendall and Dr Sir Patrick d'E. Skipwith, and to the Trustees of the British Museum (Natural History) through whom this interesting collection reached his hands. Thanks are also due to the same team for their kindness in allowing the writer to use material from their manuscripts. Also to Mr P. R. Bush, of the Imperial College for technical help, and to Mrs O'Brien for the text-figures.

My thanks are also due to Dr E. Binder of Geneva for the photograph of *Murex turbinatus* Lamarck, Lamarck's type which is in his care and also for permission to reproduce the same. To Dr Myra Keen for much help and advice on taxonomy (especially with regard to Tellinacea); to Dr Rosewater for help with *Nodilittorina*; and Dr Robert Robinson for help with *Tricolia*, my thanks for guidance.

## LIST OF SPECIES IN TAXONOMIC ORDER

Listed below are the species here reported plus those recorded by Melvill and Standen (1901, 1907, 1928) and Haas (1952, 1954) for the Trucial Coast. No attempt has been made to revise the nomenclature of the latter. As difficulty was found in tracing the references of some species recorded by Haas some dates have been omitted.

\*—Recorded by Melvill and Standen only.

†—Recorded by Melvill and Standen and the author.

‡—Recorded by Haas only.

§—Recorded by Haas and the author.

## Class LORICATA

## Family ISHNOCHITONIDAE

*Ishnochiton yerburyi* Smith 1891

## Family CHITONIDAE

*Chiton* sp.

## Class GASTROPODA

## Superfamily ZEUGOBRANCHIA

## Family FISSURELLIDAE

*Emarginula planulata* A. Adams, 1851

*Diodora funiculata* (Reeve, 1850)§

*Diodora imbricata* (Sowerby, 1862)

## Superfamily TROCHACEA

## Family TROCHIDAE

*Euchelus angulus* Pease, 1867

*Euchelus asper* (Gmelin, 1791)

*Euchelus bicinctus* (Philippi, 1849)

*Turcica* (*Perrinia*) *stellata* A. Adams, 1863

*Trochus* (*Infundibulops*) *erythraeus*

Brocchi, 1821

*Trochus* (*Infundibulops*) *cariniferus* Beck

in Reeve, 1842‡

*Gibbula* (*Emida*) *townsendi* Sowerby, 1895

*Gibbula pulcherrima* A. Adams, 1854\*

*Minolia gradata* Sowerby, 1895

*Minolia holdsworthiana* (G. and H. Nevill, 1871)

*Minolia variabilis* A. Adams, 1873

*Minolia* (*Priotrochus*) *obscura* (Wood, 1828)

*Umbonium vestiarium* (Linnaeus, 1758)†

## Family CYCLOSTREMALIDAE

*Cyclostrema quadricarinatum* Melvill, 1907

## Family TURBINIDAE

*Turbo coronatus* Gmelin, 1791§

*Turbo radiatus* Gmelin, 1791§

*Tricolia fordiana* (Pilsbry, 1888)

*Phasianella solidula* (Born, 1778)

## Superfamily NERITACEA

## Family NERITIDAE

*Nerita plexa* Chemnitz‡ (= *textilis* Dillwyn)

*Smaragdia rangiana* (Récluz, 1841)

## Family PHENACOLEPADIDAE

*Phenacolepas evansi* n.sp.

*Phenacolepas omanensis* n.sp.

## Superfamily LITTORINACEA

## Family LITTORINIDAE

*Nodilittorina subnodosa* (Philippi, 1847)

## Superfamily RISSOACEA

## Family HYDROBIIDAE

*Iravadia trochlearis* (Gould, 1861)

## Family RISSOIDAE

*Rissoina distans* (Anton, 1839)

*Rissoina savigny* Jousseaume

*Rissoina* (*Phosinella*) *sequenziana* (Issel, 1869)

## Superfamily CERITHIACEA

## Family TURRITELLIDAE

*Turritella auricincta* v. Martens, 1882

*Turritella fascialis* Menke, 1828

*Turritella illustris* Melvill, 1904\*

*Turritella* (*Haustator*) *maculata* (Reeve, 1849)‡

## Family PLANAXIDAE

*Planaxis sulcatus* (Born, 1792)

## Family POTAMIDIDAE

*Cerithidea cingulatus* (Gmelin, 1791)

*Pirenella conica* (Blainville, 1829)

*Terebralia palustris* (Bruguière, 1792)

## Family FINELLIDAE

*Finella pupoides* (A. Adams, 1860)

*Finella reticulata* (A. Adams, 1860)

*Finella scabra* (A. Adams, 1860)

*Scaliola arenosa* A. Adams, 1862

*Scaliola bella* A. Adams, 1860

*Scaliola elata* Semper in Issel, 1869

Family **CERITHIIDAE**

- Diala semistriata* (Philippi, 1849)  
*Diala* cf. *hardyi* Melvill, 1895  
*Bittium* (*Bittium*) *caudatum* Melvill, 1904  
*Bittium* (*Bittium*) *tricarinatum* (Pease, 1860) ‡  
*Cerithium caeruleum* Sowerby, 1865  
*Cerithium echinatum* (Lamarck, 1822) ‡  
*Cerithium petrosum* (Wood, 1828)  
*Cerithium rugosum* (Wood, 1828)  
*Cerithium scabridum* Philippi, 1848  
*Cerithium* sp.  
*Clypeomorus clypeomorus* Jousseaume ‡  
*Clava* (*Clava*) *fasciata* (Bruguière, 1792)  
*Clava* (*Clava*) *kochi* (Philippi, 1848)

Family **TRIPHORIDAE**

- Triphora acuta* Kiener, 1841-2.  
*Triphora* sp.

Superfamily **CALYPTRAEACEA**Family **CALYPTRAEIDAE**

- Calyptraea pellucida* (Reeve, 1859)  
*Calyptraea* (*Crucibulum*) *violacea* (Carpenter, 1856) ‡

Superfamily **STROMBACEA**Family **XENOPHORIDAE**

- Xenophora caperata* Philippi, 1849  
*Xenophora corrugata* (Reeve, 1843)

Family **STROMBIDAE**

- Terebellum terebellum* (Linnaeus, 1758)  
*Strombus decorus persicus* Swainson, 1821  
*Strombus* sp.

Superfamily **NATICACEA**Family **NATICIDAE**

- Natica lineata* Link, 1807  
*Natica* sp.  
*Sinum* (*Eunaticina*) *papilla* (Gmelin, 1791)  
*Polinices* (*Polinices*) *manilla* (Linnaeus, 1758) ‡  
*Polinices* (*Neverita*) *ampla* (Gmelin, 1891) ‡

Superfamily **CYPRAEACEA**Family **CYPRAEIDAE**

- Cypraea caurica* Linnaeus, 1758 §  
*Cypraea grayana* Schilder, 1930  
*Cypraea fimbriata* Gmelin, 1791\*  
*Cypraea lentiginosa* Gray, 1825  
*Cypraea turdus* Lamarck, 1810 §  
*Erronea* (*Melicerona*) *felina* (Gmelin, 1791) ‡  
*Notocypraea pulicaria* (Reeve, 1846) ‡

Superfamily **DOLIACEA**Family **GYMATIIDAE**

- Cymatium* (*Gutturium*) *sarostoma* Reeve, 1844\*

Family **BURSIDAE**

- Bursa rubeta* (Linnaeus, 1758)\*  
*Cymatium ranzani* (Bianconi, 1850) ‡

Superfamily **MURIGACEA**Family **MURIGIDAE**

- Rapana bulbosa* (Solander) [Dillwyn, 1817] §  
*Chicoreus* (*Chicoreus*) *anguliferus* (Lamarck, 1822) ‡  
*Hexaplex* (*Hexaplex*) *turbinatus* (Lamarck, 1822) ‡  
*Murex küsterianus* Tapparoni Canefri 1875  
*Murex scolopax* Dillwyn, 1817  
*Murex* (*Ocenebra*) *flexirostris* Melvill, 1898\*  
*Murex* (*Murex*) *ternispina* Lamarck, 1822 ‡  
*Thais cavinifera* (Lamarck, 1822) §  
*Thais pseudohippocastanum* (Deutzenberg, 1929)  
*Thais tissoti* (Petit, 1852)  
*Drupa margariticola* (Broderip, 1798)  
*Drupa* (*Morula*) *concatenata* (Lamarck, 1822) ‡  
*Drupa* (*Morula*) *siderea* (Reeve, 1846) ‡

Superfamily **BUCCINACEA**Family **COLUMBELLIDAE**

- Mitrella* (*Mitrella*) *cartwrighti* (Melvill, 1897)  
*Pyrene atrata* (Gould, 1860)  
*Pyrene phaula* (Melvill and Standen, 1901)

Family **NASSARIIDAE**

- Nassarius pullus* (Linnaeus, 1758)  
*Nassarius stigmarius* (A. Adams, 1852)  
*Nassarius* (*Hebra*) *echinatus* (A. Adams, 1851)\*  
*Nassa* (*Nassa*) *persica* von Martens ‡

Family **FASCIOLARIIDAE**

- Fusinus townsendi* (Melvill, 1899)  
*Fusus* (*Fusus*) *colus* (Linnaeus, 1758) ‡

Family **FASCIDARIIDAE**

- Latirus arabicus* Melvill, 1898\*  
*Latirus* (*Peristernia*) *corallinus* Melvill, 1898\*

Superfamily **VOLUTACEA**Family **OLIVIDAE**

- Ancilla castanea* (Sowerby, 1830) ‡  
*Ancilla cinnamomea* (Lamarck, 1801) §  
*Ancilla eburnea* (Deshayes, 1830)  
*Oliva bulbosa* (Röding, 1798)  
*Oliva caerulea* (Röding, 1798)  
*Oliva (Oliva) elegans elegans* Lamarck, 1811 ‡  
*Oliva (Carmione) inflata* Lamarck, 1811 ‡  
*Oliva (Oliva) ispidula* (Linnaeus, 1758) ‡

Family **MITRIDAE**

- Mitra (Scabricola) bovei* Kiener, 1839

Family **MARGINELLIDAE**

- Persicula cf. asellina* (Jousseaume, 1875)  
*Persicula mazagonica* (Melvill, 1893)  
*Persicula shoplandi* (Melvill, 1897)  
*Persicula subflava* (Preston, 1906)  
*Marginella (Gibberula) charbarena* Melvill, 1897\*

Superfamily **CONACEA**Family **CONIDAE**

- Conus generalis* Linnaeus, 1758\*  
*Conus quercinus* Lightfoot, 1786\*

Sub-Class **OPISTHOBRANCHIA**Superfamily **AGLOSSA**Family **MELANELLIDAE**

- Strombiformis bivittata* H. and A. Adams,\*

Family **STILIFERIDAE**

- Mucronalia lepida* Melvill, 1906

Superfamily **PTENOGLOSSA**Family **PYRAMIDELLIDAE**

- Eulimella kaisensis* Melvill, 1898  
*Turbonilla iclea* Melvill, 1911  
*Turbonilla (Tropaeas) ruppelli* Jickeli, 1882 ‡

Superfamily **CEPHALASPIDAE**Family **ACTEONIDAE**

- Solidula* sp.

Family **RINGICULIDAE**

- Ringicula propinquans* Hinds, 1844

Family **BULLARIIDAE**

- Bullaria ampulla* (Linnaeus, 1758) §

Family **ATYIDAE**

- Alys cylindricus* (Helbling, 1779)

Family **RETUSIDAE**

- Retusa omanensis* Melvill and Standen, 1903

Family **AGLAJIDAE**

- Aglaja cf. nigra* (von Martens, 1879)

Order **ACOELA**Superfamily **DORIDACEA**Family **DORIDIDAE**

- Casella atromarginata* (Cuvier, 1804)

Superfamily **ONCIDIACEA**Family **ONCIDIIDAE**

- Oncidium peronii* Cuvier, 1805

Class **PULMONATA**Superfamily **ACTOPHILA**Family **ELLOBIIDAE**

- Melampus lividus* (Deshayes, 1830)  
*Melampus* sp.  
*Laemodonta (Laemodonta) rapax* (Dhorne, 1859)

Superfamily **PATELLIFORMIA**Family **SIPHONARIIDAE**

- Siphonaria asghar* Biggs, 1958  
*Siphonaria rosea* Hubendick, 1943

Class **BIVALVIA**Superfamily **NUCULACEA**Family **NUCULIDAE**

- Nuculana confusa* (Hanley, 1860)

Superfamily **ARCACEA**Family **ARCIDAE**

- Arca (Acar) plicata* Dillwyn, 1817 §  
*Barbatia lacerata* Bruguière, 1789  
*Barbatia nivea* Gmelin, 1791\*  
*Arca (Barbatia) fusca* Bruguière, 1792 ‡  
*Anadara antiquata* (Linnaeus, 1758)  
*Anadara ehrenbergi* (Dunker, 1868)  
*Anadara uropigmelana* (Bory St. Vincent, 1824) §  
*Arca (Scapharca) natalensis* Krauss, 1848\*  
*Arca (Scapharca) rufescens* Reeve, 1844\*  
*Scapharca tricenicosta* (Nyst, 1848)  
*Scapharca vellicata* (Reeve, 1844)  
*Trisidos tortuosa* (Linnaeus, 1758)

Family **GLYCYMERIDAE**

- Glycymeris hoylei* Melvill and Standen, 1899  
*Glycymeris lividus* (Reeve, 1843)  
*Glycymeris pectunculus* (Linnaeus, 1758)  
*Glycymeris striatularis* (Lamarck, 1819)  
*Glycymeris (Pectunculus) nodosus* (Reeve, 1843) ‡  
*Glycymeris (Pectunculus) pectiniformis* (Lamarck, 1819) ‡  
*Glycymeris (Glycymeris) taylori* (Angas, 1879) ‡

## Superfamily MYTILACEA

- Crenella adamsiana* Melvill and Standen, 1907  
*Modiolus rhomboideus* (Reeve, 1857)  
*Brachidontes (Hormomya) variabilis* (Krauss, 1848)  
*Septifer bilocularis* (Linnaeus, 1758)  
*Lithophaga lithophaga* (Linnaeus, 1758)

## Superfamily PTERIACEA

## Family ISOGNOMONTIDAE

- Isognomon ephippium* (Linnaeus, 1758)  
*Isognomon legumen* (Gmelin, 1791)  
*Isognomon dentifer* (Krauss, 1848)  
*Malleus regula* (Forsskål, 1775)

## Family PTERIIDAE

- Pteria (Pinctada) inflata* (Schumacher, 1817)‡  
*Pinctada margaritifera* (Linnaeus, 1758)  
*Pinctada radiata* (Leach, 1814)  
*Pinctada* sp.

## Family PINNIDAE

- Pinna atropurpurea* Sowerby *mutica* Reeve, 1858  
*Pinna bicolor* Gmelin, 1791

## Superfamily PECTINACEA

## Family PECTINIDAE

- Plicatula plicata* (Linnaeus, 1767)  
*Chlamys ruschenbergerei* (Tryon, 1870)  
*Spondylus exilis* Sowerby, 1895  
*Spondylus foliacus* Chemnitz, 1784‡  
*Spondylus gloriandus* Melvill, 1907\*  
*Pecten (Vola) dorothea* Melvill, 1907\*  
*Pecten (Chlamys) senatorius* Gmelin, 1790‡

## Family LIMIDAE

- Lima squamosa* Lamarck, 1801\*  
*Lima (Lima) tenuis* (H. Adams, 1870)  
*Lima (Limatula) leptocarya* Melvill, 1898

## Superfamily OSTREACEA

## Family OSTREIDAE

- Crassostrea cucullata* (Born, 1778)  
*Ostrea (Lopha) cristagalli* Linnaeus, 1758‡

## Superfamily ASTARTACEA

## Family GRASSATELLIDAE

- Cuna coxi* Eames and Wilkins, 1957  
*Cuna majeeda* n.sp.  
*Cuna* sp.

## Superfamily CARDITACEA

## Family CARDITIDAE

- Cardita antiquata* Linnaeus\*  
*Cardita (Cardita) bicolor* Lamarck, 1819‡  
*Cardita echinaria* Melvill, . . . \*  
*Cardita finchi* (Melvill, 1898)

## Family TRAPIZIIDAE

- Trapezium sublaevigatum* (Lamarck, 1819)

## Superfamily GRASSATELLACEA

## Family GRASSATELLIDAE

- Crassatella indica* Smith, 1895\*

## Superfamily LUCINACEA

## Family UNGULINIDAE

- Diplodonta ravayensis* Sturany, 1901

## Family LUCINIDAE

- Divaricella cunningi* (Adams and Angus, 1863)  
*Ctena divergens* (Philippi, 1850)  
*Codakia (Jagonia) fibula* (Reeve, 1850)‡  
*Codakia (Jagonia) fischeriana* (Issel, 1860)  
*Anodontia edentula* (Linnaeus, 1758)  
*Phacoides (Bellucina) semperianus* (Issel, 1860)

## Superfamily CHAMACEA

## Family CHAMIDAE

- Chama brassica* Reeve, 1847

## Superfamily CARDIACEA

## Family CARDIIDAE

- Laevicardium papyraceum* (Bruguère, 1780)  
*Laevicardium (Trachycardium) flavum* (Linnaeus, 1758)‡  
*Laevicardium (Trachycardium) unicolor* (Sowerby, 1841)‡  
*Trachycardium lacunosum* (Reeve, 1845)  
*Trachycardium maculosum* (Wood, 1815)  
*Cardium (Trachycardium) vertebratum* Jonas, 1844\*  
*Parvicardium sueziensis* (Issel, 1869)

## Superfamily VENERACEA

## Family VENERIDAE

- Lioconcha callipygia* (Born, 1778)‡  
*Lioconcha picta* (Lamarck, 1818)  
*Gafrarium arabicum* (Lamarck, 1818)  
*Gafrarium dispar* (Dillwyn, 1817)  
*Gafrarium pectinatum* (Linnaeus, 1758)



- Gafrarium (Circe) lenticulare* (Deshayes, 1853) ‡  
*Circe (Circe) intermedia* Reeve, 1863  
*Circe (Circe) scripta* (Linnaeus, 1758) §  
*Circe (Parmulophora) corrugata* (Dillwyn, 1817)  
*Dosinia alta* (Dunker, 1848)  
*Dosinia hepatica* (Lamarck, 1818)  
*Dosinia histrio* (Gmelin, 1791) ‡  
*Dosinia* sp.  
*Dosinia (Dosinida) contracta* Philippi, 1845 ‡  
*Dosinia (Dosinida) laminata* Reeve, 1850 ‡  
*Venus (Chione) lilacina* Lamarck, ‡  
*Chione lamarcki* Gray, 1843\*  
*Chione trigona* (Reeve, 1863) ‡  
*Amiantis erycina* (Linnaeus, 1758)  
*Amiantis hagenowi* (Dunker, 1844) ‡  
*Sunetta effosa* Hanley, 1842  
*Sunetta meroe* (Linnaeus, 1758)\*  
*Sunetta* sp.  
*Sunetta (Sunetta) scripta* (Linnaeus, 1758) ‡  
*Meretrix meretrix* (Linnaeus, 1758)  
*Tivela ponderosa* Koch in Philippi, 1844  
*Bassina calophylla* Hanley †  
*Timoclea farsiana* n. sp.  
*Katelysia marmorata* (Lamarck, 1818)  
*Irus irus* (Linnaeus, 1758)
- Superfamily **MACTRACEA**  
 Family **MACTRIDAE**  
*Maetra olorina* Philippi, 1846  
*Maetra (Maetra) grandis* Gmelin, 1791 ‡  
*Maetra (Maetra) lilacina jickelii*  
 Weinkauff, 1881 ‡

- Superfamily **TELLINACEA**  
 Family **PSAMOBIIIDAE**  
*Asaphis deflorata* (Linnaeus, 1758) §  
*Solecurtus australis* Dunker, 1861

- Family **TELLINIDAE**  
*Tellina (Arcopaginula) inflata* Gmelin, 1791  
*Tellina (Arcopagia) isseli* (A. Adams, 1870)  
*Tellina (Pistris) pristis* Lamarck, 1818  
*Tellina (Pinguitellina) robusta* Hanley, 1844  
*Angulus (Homala) triradiatus* H. Adams, 1870 ‡  
*Exotica (Jacetellina) rhomboides* (Quoy and Gaimard, 1835)  
*Macoma arsinoensis* (Issel, 1869)  
*Macoma jeanae* Dance and Eames, 1966  
*Tellidora pellyana* H. Adams, 1873

- Superfamily **SOLENACEA**  
 Family **SOLENIDAE**  
*Cultellus cultellus* (Linnaeus, 1758)

- Superfamily **MYACEA**  
 Family **CORBULIDAE**  
*Corbula acutangulata* Issel, 1869  
*Corbula modesta* Hinds, 1843  
*Corbula subquadrata* Melvill, 1907

- Superfamily **GASTROCHAENACEA**  
 Family **GASTROCHAENIDAE**  
*Gastrochaena cuneiformis* Spengler, 1783

## STATION LIST

Station No.	Locality	Habitat
'Al Ghazal' Stations dredged by G. Evans		
1	5 m S.W. of Jazirat az Zarqa.	60 ft sandy bottom.
2	2½ m N.E. of Oil Company's jetty.	49 ft sandy with plant fragments.
3	2½ m N.E. of Oil Company's jetty.	39-43 ft sandy, some weed coated friable rock.
4	3 m E. of Jazirat al Yas.	70 ft sandy bottom.
5	3 m E. of Jazirat al Yas.	70 ft muddy sand.
6	3 m E. of Jazirat al Yas.	44-74 ft sandy, no rock, algal covered, shells.
7	3 m E. of Jazirat al Yas.	51-64 ft sandy, no rock, many echinoids.

STATION LIST—'Al Ghazal' Stations dredged by G. Evans—*cont.*

Station No.	Locality	Habitat
8	2 m N.E. of Jazirat al Yas.	50-60 ft sandy, small fragments of rock.
9	3 m N. of Jazirat al Yas.	54-70 ft many rock fragments with dead brain coral and staghorn coral, many echinoids.
10	4 m N. of Jazirat al Yas.	50-88 ft rock exposed on bottom.
11	4 m N. of Jazirat al Yas.	70 ft sandy.
12	7 m E. of Jazirat al Dalma.	115 ft sandy
13	16 m N.E. of Jazirat al Dalma.	50-60 ft sandy, small amounts of rock.
14	20 m N.E. of Jazirat al Dalma.	50-60 ft sandy, small amounts of rock.
15	21½ m N.E. of Jazirat al Dalma.	50-60 ft sandy, small amounts of rock.

*Halat al Bahrani Stations collected by G. Evans*

16	near Lagoon N.W. Halat al Bahrani.	Beach.
17	N.W. Halat al Bahrani.	Dune flat.
18	N.W. Halat al Bahrani.	Spit.
19	S.W. Halat al Bahrani.	Beach.
20	—	Shell concentrate at base of beach.
21	½ m off N.E. Halat al Bahrani.	Beach.
22	S.E. Halat al Bahrani.	Flat hummocky beach.
23	—	Flat hummocky beach.
24	Inland, S.E. Halat al Bahrani.	Edge of upper beach.
25	—	Flat beach.
26	Jazirat Sir Abu Nu'air.	Beach.
27 to 30	Halat al Bahrani.	Low tide terrace.

*Stations collected by G. Evans and J. Kinsman*

31, 32	E. side of Halat al Bahrani.	Shoreline, center of Lagoon.
33	—	—
34, 35	S. side of Halat al Bahrani.	Shoreline.
36	N.E. of Halat al Bahrani.	Shoreline.
37	½ m N.W. of Halat al Bahrani.	Coral patch on small bank at mouth of Abu Dhabi channel.
38	½ m off Jazirat al Fuṭaysi.	Outer lagoon.
39	½ m W. of Jazirat al Fuṭaysi.	Outer lagoon.
40	N. side of Halat al Bahrani.	Small lagoon, protected by sand pit.
41	N. side of Halat al Bahrani.	Beach face.
42	1¾ m off N.W. coast of Halat al Bahrani.	10 ft on slope in front of tidal delta.
43	2¾ m off N.E. corner of Halat al Bahrani.	Nearshore shelf.
44	N. of Halat al Bahrani.	Small reef.
45	¼ m off N.W. coast of Halat al Bahrani.	Shallow platform.
46	N. of Jazirat al Fuṭaysi.	Channel.
47	N. of Jazirat al Fuṭaysi.	Coral clumps.
48	N. of Jazirat al Fuṭaysi.	Habitat

STATION LIST—*cont.*

Station No.	Locality	Habitat
<i>Stations collected by G. Evans Autumn 1962</i>		
49	S.W. Jazirat as Sa'diyat.	Rock platform, low tide covered with veneer of sand.
50	S.W. Jazirat as Sa'diyat.	Beach.
51	S.W. Jazirat as Sa'diyat.	Wind scoured flat behind beach.
52	Abu Dhabi—Jazirat as Sa'diyat lagoon.	Oyster shell concentrate on channel floor at entrance to lagoon.
53	S.W. Jazirat as Sa'diyat.	Intertidal flat just outside lagoon.
54	N.E. Jazirat as Sa'diyat.	Beach face.
55	N. coast Jazirat as Sa'diyat.	Low tide terrace, sandy bottom.
56	Coast of Jazirat as Sa'diyat.	Beach.
57	N.E. Abu Dhabi Island.	Muddy sand, outer intertidal flat.
58	N. coast Jazirat as Sa'diyat.	Shell concentrate on beach face.
59	Abu Dhabi—Jazirat as Sa'diyat lagoon.	Inner lagoon floor, sandy mud overlying rock.
60	Abu Dhabi—Jazirat as Sa'diyat lagoon.	Inner lagoon, floor mud.
61	Abu Dhabi—Jazirat as Sa'diyat lagoon.	Undercut at low tide on small rocky island.
62	Abu Dhabi—Jazirat as Sa'diyat lagoon.	Intertidal flat on inner edge of shallow terrace, mid-lagoon, muddy sand.
63	Abu Dhabi—Jazirat as Sa'diyat lagoon.	Sandy floor overhanging rock of a bank in outer lagoon.
64	Abu Dhabi—Jazirat as Sa'diyat lagoon.	Intertidal flat on inner edge of terrace, muddy sand, mid-lagoon.
65	Abu Dhabi—Jazirat as Sa'diyat lagoon.	Outer lagoon sand patch between coral clumps channel floor.
66	N.E. shore of Abu Dhabi.	Intertidal flat, muddy sand just inside lagoon.
67	Abu Dhabi lagoon.	Intertidal flat, muddy sand on a small island, outer lagoon.
67a	N.E. Abu Dhabi I. on margin of lagoon channel.	10 ft, muddy sand.
68	Abu Dhabi lagoon.	Thick sand overlying rock, shallow terrace, mid-lagoon.
69	Abu Dhabi lagoon.	Shell mound on island in mid-lagoon.
70	Shuweihat, W. coast Jebel Dhanna.	Beach concentrate, open beach.
70a	Sila, foot of Qatar Peninsula.	Beach face.
71, 72	N.E. shore Abu Dhabi I.	Tidal flat, muddy sand.
73	N.E. shore Abu Dhabi I.	Tidal flat, muddy sand, outer lagoon.
74, 75	Trucial coast.	
<i>Stations collected by D. J. J. Kinsman, Autumn, Winter 1961, Spring 1963</i>		
76	E. Halat al Bahrani.	Middle of intertidal zone in outer lagoon channel bank, sandy.
77	E. Halat al Bahrani.	Middle of lower intertidal zone, channel bank, sandy.
78	E. Halat al Bahrani.	Lowermost intertidal zone, channel bank, sandy.
79-85	1 m N. of N.E. Halat al Bahrani; outer lagoon.	Low intertidal zone on oolite shoal.

STATION LIST—Stations collected by G. Evans and J. Kinsman—*cont.*

Station No.	Locality	Habitat
86	N. shore Halat al Bahrani.	Lower intertidal zone; oolite sand substrate.
87	N. shore Halat al Bahrani.	Sub-tidal, oolite sand substrate.
88	1 m N. of Halat al Bahrani.	Intertidal oolite shoal.
89	Unknown	
90-93	N. Jazirat al Fuṭaysi.	Intertidal zone, rocky shore, limestone boulders.
94	$\frac{1}{4}$ m N. of N. Jazirat al Fuṭaysi.	Coral reef.
95	Off N. Jazirat al Fuṭaysi.	Mixed rock and sand bottom, low intertidal zone on channel side.
96	W. coast in mid-lagoon, Jazirat al Fuṭaysi.	Intertidal zone, sandy mud near limestone rocks.
97	1 m off W. Jazirat al Fuṭaysi.	Low intertidal zone, rocky limestone substrate.
98	$\frac{3}{4}$ m N. of N. Jazirat al Fuṭaysi.	Coral reef.
99	N.E. Jazirat al Fuṭaysi, in mid-lagoon.	High intertidal zone, blue-green algal flat, sandy.
100	N. Jazirat al Fuṭaysi.	Intertidal zone, sandy and rocky substrate.
101	$\frac{1}{4}$ - $\frac{1}{2}$ m off N.E. Jazirat al Fuṭaysi.	Intertidal zone, mid-lagoon, rocky island.
102	$\frac{1}{4}$ m off Batin fishing village, S.W. Abu Dhabi I.	Sub-tidal zone, outer lagoon, oolite sand shoal.
103	Inner lagoon, 2 m S. Jazirat al Fuṭaysi.	Low water mark, muddy sand, some <i>Thalassia</i> .
104	1 m S.W. of Halat al Bahrani.	Limestone from surface of oolite shoal, sub-tidal.
105	Abu Dhabi—Jazirat as Sa'diyat lagoon.	Shallow water.

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PLATE I

FIG. 1. Algal flat in intertidal zone with low bushes of *Anthrocnemum glaucum* at the back of Abu Dhabi—Es Sadyyat Lagoon.

FIG. 2. Mangrove Swamp (*Avicenna marina*) on a small Island in the Abu Dhabi—Es-Sadyyat Lagoon.

FIG. 3. Undercut Quaternary (Aeolian) limestone with fossil rootlet structures at back of Abu Dhabi—Es Sadyyat Lagoon. High water washes over the top of the platform shown in the photograph and reaches the base of the cliff in the background. A rocky floor with a thin cover of sandy carbonate occurs at the base of the cliff.

FIG. 4. Dunes of carbonate sand with low deflated surface behind on the south west shoreline of Es Sadyyat I.



PLATE 2

- FIGS 1, 2 *Emarginula planulata* N. Adams  
Lectotype L. 1.54 mm, H. 4.4 mm, W. 0.1 mm
- FIGS 3, 4 *Phenecolepas evansi* n. sp.  
Holotype L. 5.6 mm, H. 2.6 mm, W. 4.7 mm
- FIGS 5, 6 *Phenecolepas omanensis* n. sp.  
Holotype L. 8.2 mm, H. 2.8 mm, W. 7.6 mm

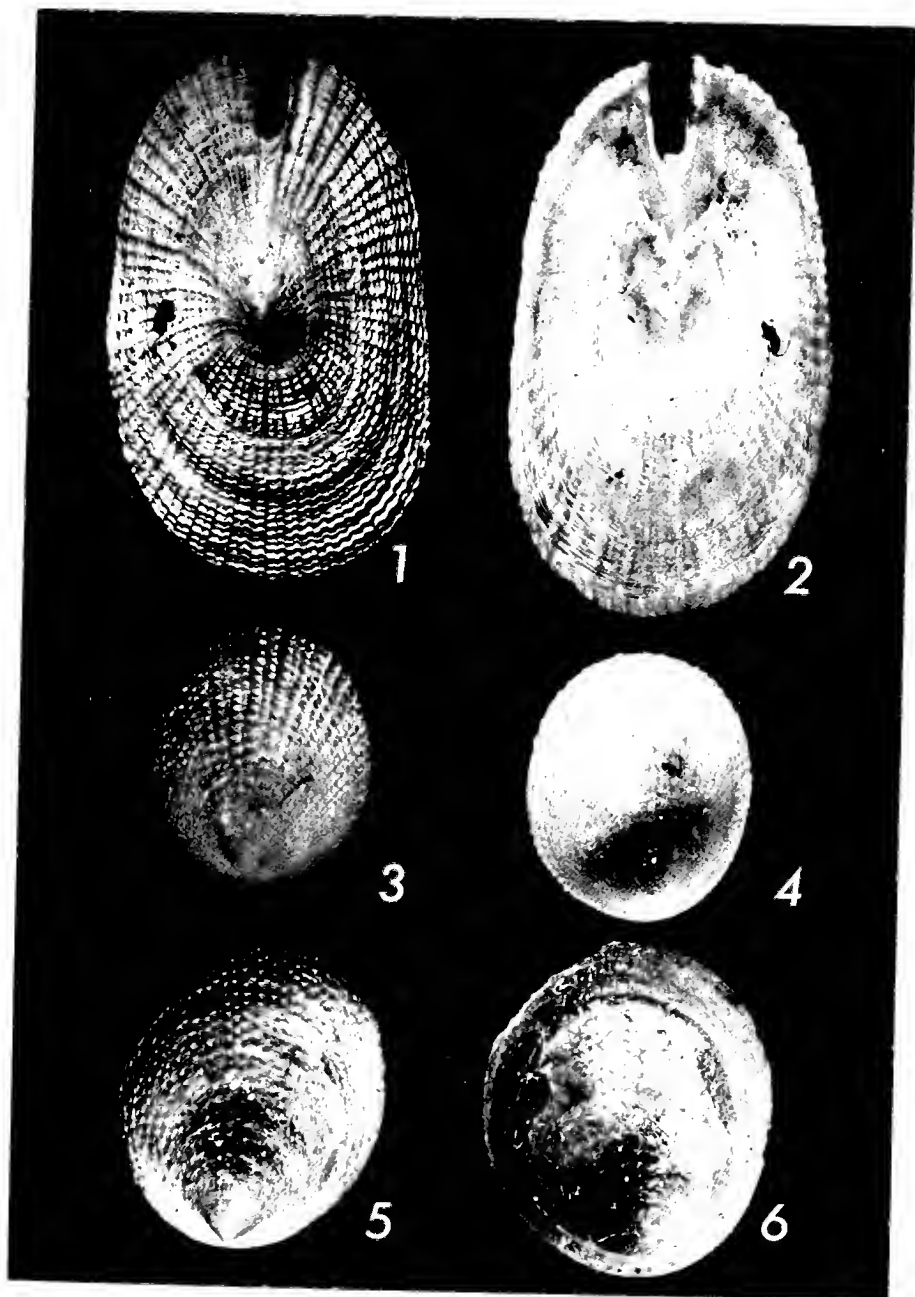


PLATE 3

- FIGS 1, 2 *Mitrella (Mitrella) blanda* (Sowerby)  
Lectotype. H 13.7 mm, W 5.6 mm
- FIGS 3, 4 *Mitrella (Mitrella) blanda* (Sowerby)  
Trucial Coast specimen. H 18.3 mm, W 7.2 mm

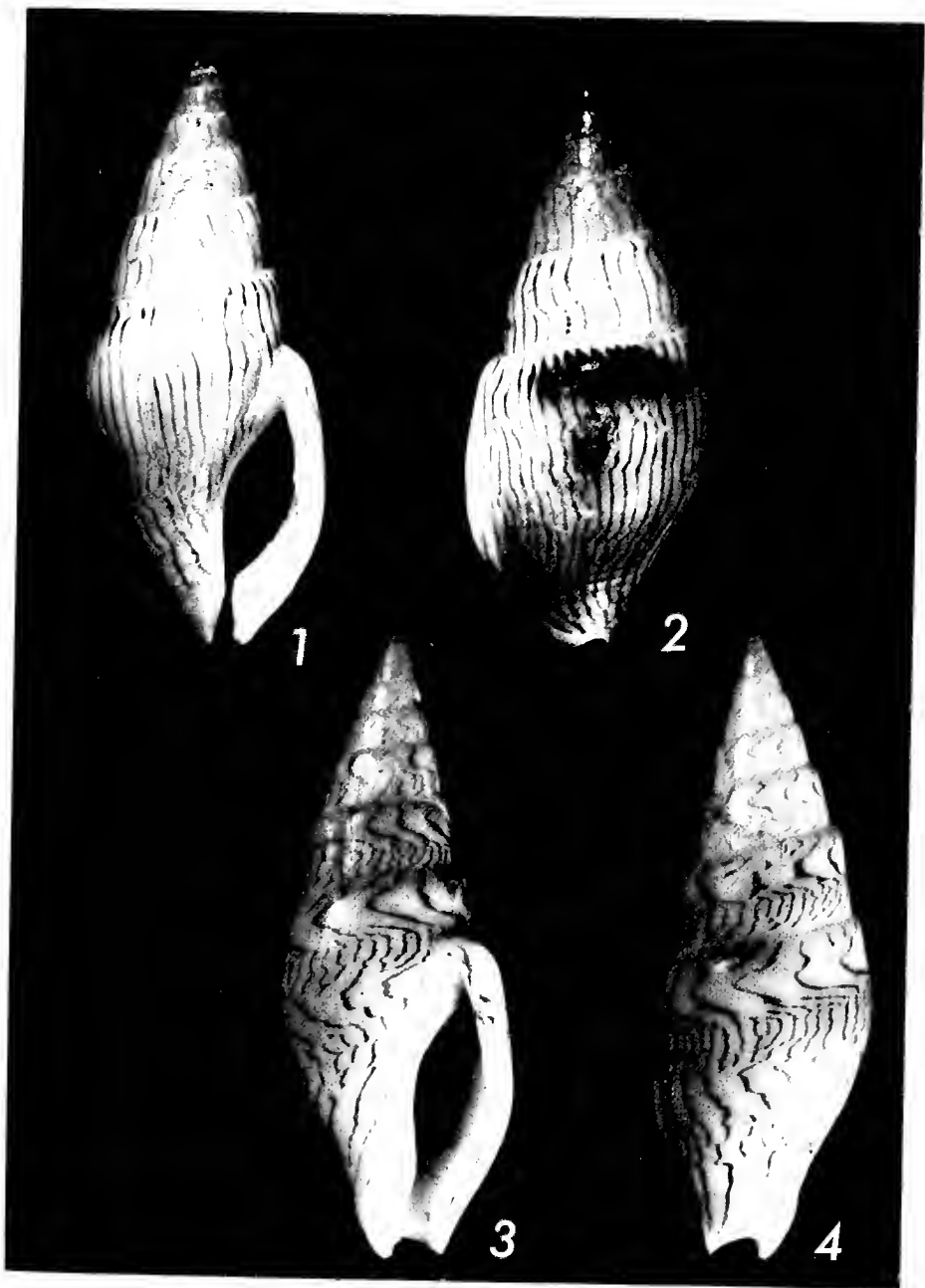


PLATE 4

- FIGS 1, 2 *Mitella (Mitella) cartwrighti* (Melvill)  
Syntype H 7.6 mm, W 3.5 mm
- FIG. 3 *Mitella (Mitella) cartwrighti* (Melvill)  
Lectotype H 8.0 mm., W 3.0 mm.
- FIGS 4, 5 *Triphora* sp.  
Trical Cost H 6.6 mm, W 2.1 mm



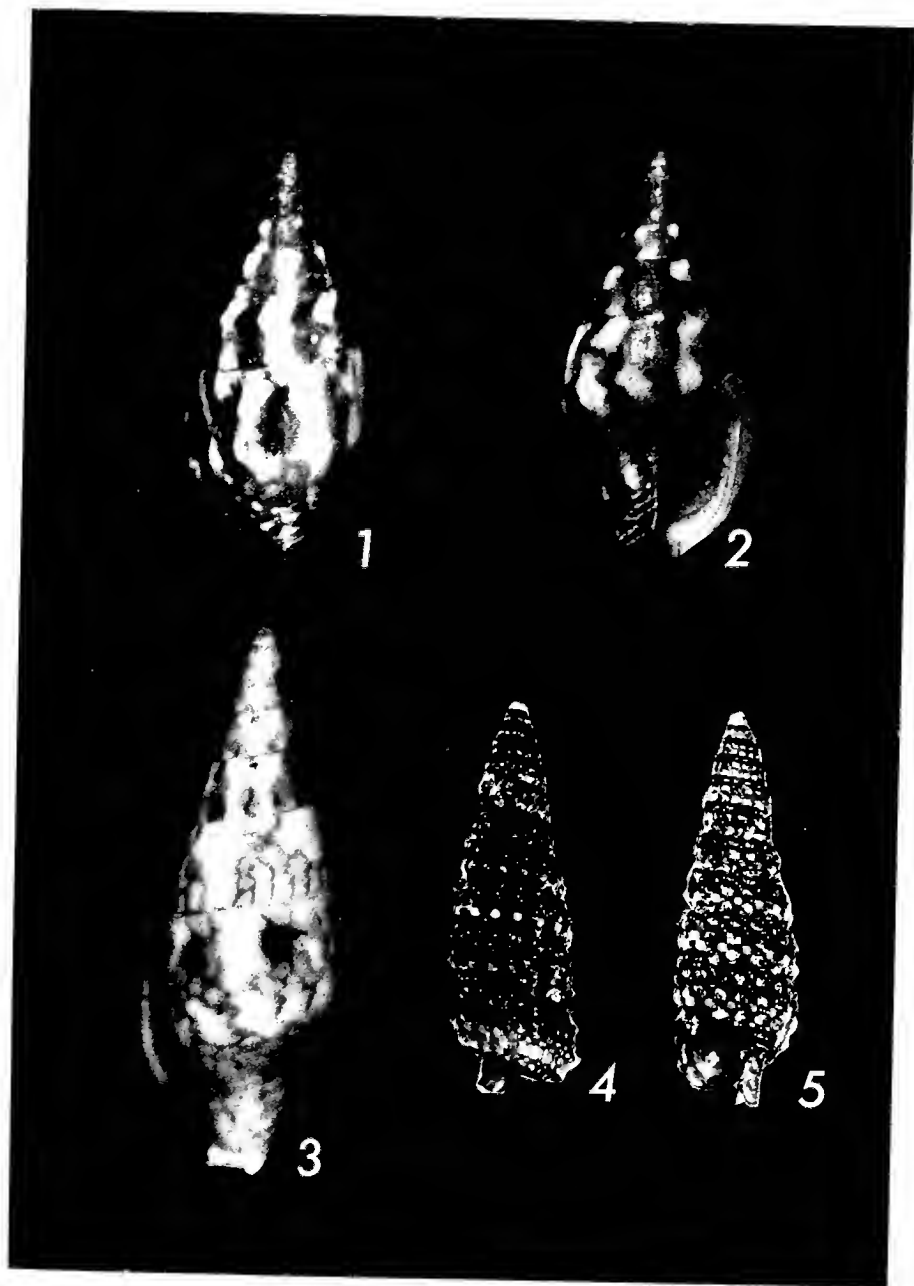


PLATE 5

- Figs 1, 2. *Murex spinosus* Adams  
Holotype. H 60.4 mm., W 50.4 mm.
- Fig. 3. *Murex küsterianus* Tapparone Canefri  
Type figure
- Figs 4, 5. *Murex küsterianus* Tapparone Canefri  
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- Figs 8, 9. *Murex küsterianus* Tapparone Canefri  
Trucial Coast specimen. H 38.7 mm., W 31.1 mm.

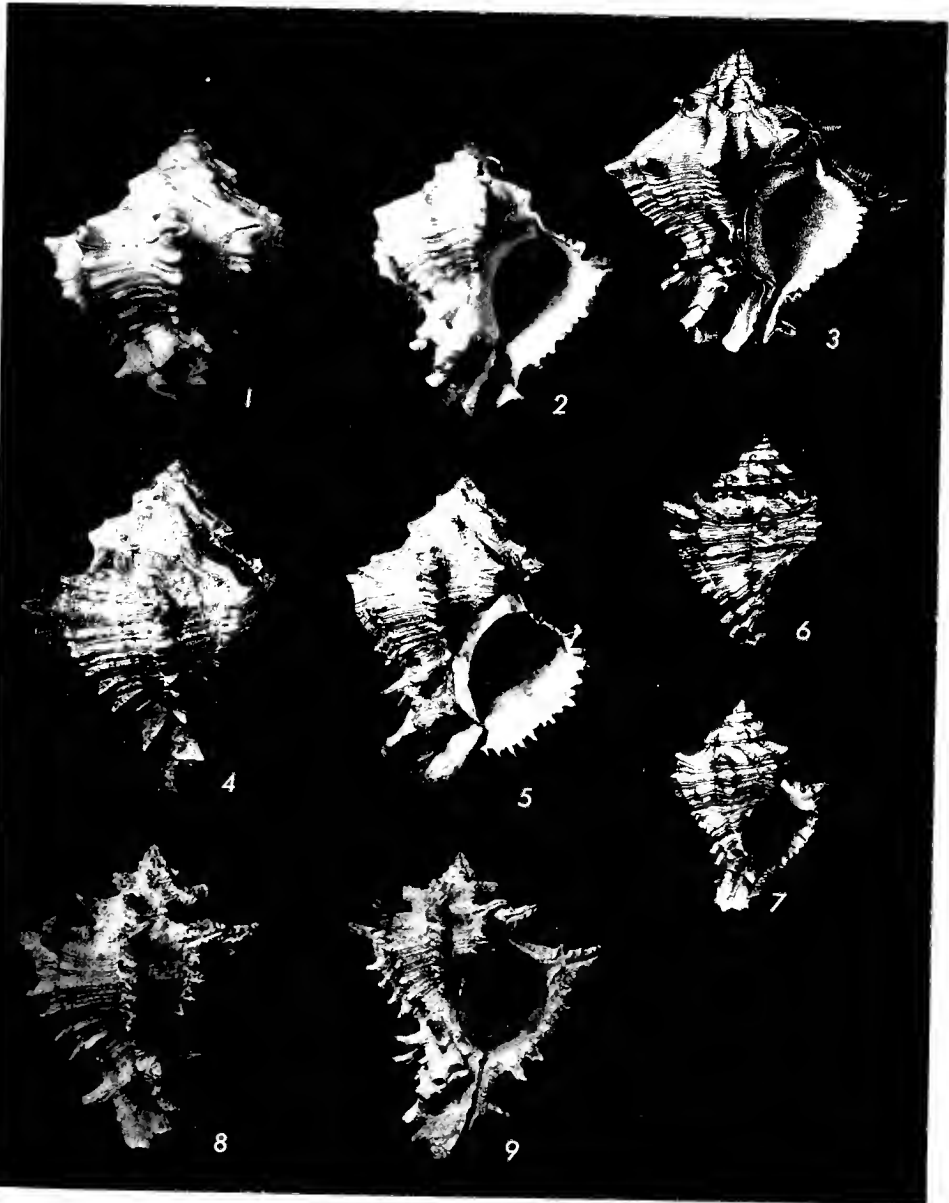
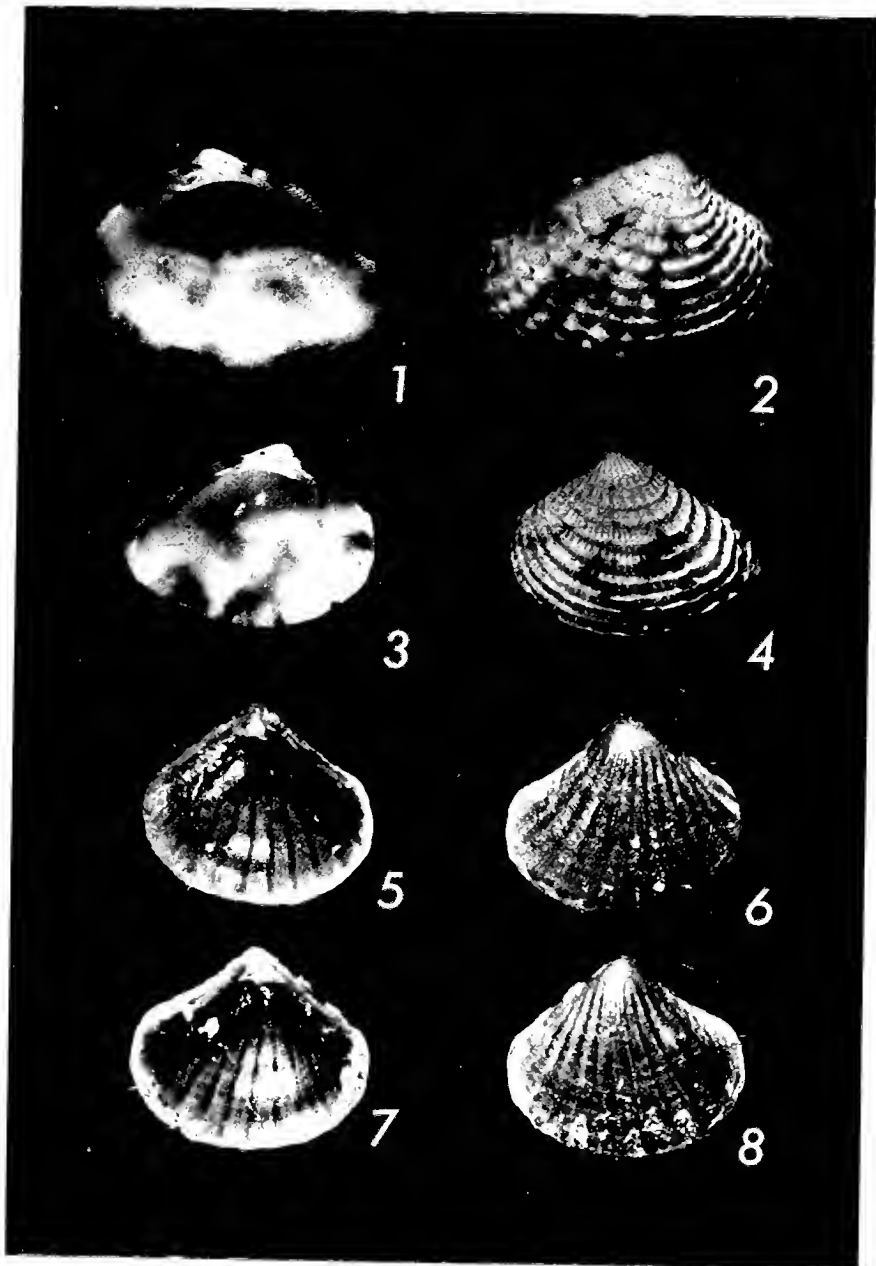


PLATE 6

- Figs 1, 2 *Timolea jaisiana* n. sp.  
Holotype. L. 6.3 mm., W 4.6 mm
- Figs 3, 4 *Timolea jaisiana* n. sp.  
Paratype. L. 5.4 mm., H 4.0 mm
- Figs 5-8 *Cina mayeda* n. sp.  
Holotype. L. 1.6 mm., H 1.4 mm







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# REVISION OF SOME SERPULIDAE (ANNELIDA POLYCHAETA) FROM ABYSSAL DEPTHS IN THE ATLANTIC AND PACIFIC, COLLECTED BY THE "CHALLENGER" AND PRINCE OF MONACO EXPEDITIONS

By HELMUT ZIBROWIUS

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## INTRODUCTION

IN connection with a study of little-known species of abyssal serpulids collected by some early deep-sea expeditions, it was found that two species, described under *Placostegus ornatus* by McIntosh (1885) and collected by the "Challenger" expedition in the abyssal depths of the North and South Pacific, and *Vermiliopsis langerhansi* by Fauvel (1909), collected by the Prince of Monaco expeditions in the deep parts of the North Atlantic, show some common characters which set them apart from *Vermiliopsis*, *sensu stricto*, as well as from *Placostegus*. Both species are herein redescribed in detail and referred to *Bathyvermilia* gen. nov. The present review is the second in a series of revisionary studies on the former genus *Vermiliopsis*, *sensu lato*. The first one dealt with the genus *Metavermilia* Bush (Zibrowius, 1971).

Additional comments are made on two incompletely known serpulids of doubtful generic status, *Placostegus benthalianus* and *Placostegus moerchii*, both collected by the "Challenger" from abyssal depths in the North and South Pacific and described by McIntosh (1885) from rather incomplete and damaged specimens.

This study is based on material in the collections of the British Museum (Natural History), London (BMNH), Marine Biological Association U.K., Plymouth (MBAP), Naturhistoriska Museet, Göteborg (NHMG), Muséum National d'Histoire Naturelle, Paris (MNHN), Musée Océanographique de Monaco (MOM).

## SYSTEMATIC DESCRIPTIONS AND NOTES

**BATHYVERMILIA** gen. nov.

TYPE-SPECIES: *Bathyvermilia challengerii* sp. nov.

[=*Placostegus ornatus*: McIntosh, 1885]. Gender: feminine.

DIAGNOSIS. Tube white, opaque (not vitreous), with more or less distinct sculpturing, subtriangular or subquadrangular in cross-section. 7 thoracic segments, 6 of them uncinigerous. First thoracic segment with setae similar to those of the following segments (no special setae); thoracic sickle setae ("*Apomatus* setae") present, abdominal setae geniculate. Thoracic uncini saw-shaped, with few teeth (about 6 to 10), anterior tooth simple (not bifurcate); abdominal uncini saw-shaped, similar to thoracic uncini, except in a few far posterior segments with rasp-shaped uncini. Thoracic membranes short, ending at about the second or third segment. Gill tuft without gill membranes uniting bases of filaments and without pseudo-operculum; basal lobes rather elongate. Second dorsal filament transformed into a cylindrical smooth opercular stalk, without pinnules or wings. Operculum with simple, entire horny cap encrusted by calcareous deposit.

The following species are herein referred to *Bathyvermilia*: *B. challengerii* sp. nov. [= *Placostegus ornatus*: McIntosh, 1885], Central North and South Pacific, abyssal depths.

*B. langerhansii* (Fauvel, 1909) [= *Vermiliopsis langerhansii* Fauvel, 1909], Central North Atlantic, abyssal depths.

NOTES. While in *Vermiliopsis*, *sensu stricto*, the opercular stalk is formed by the first dorsal filament on one side, it is formed by the second dorsal filament in *Pseudovermilia* Bush (emend. Zibrowius, 1970), *Metavermilia* Bush (emend. Zibrowius, 1971) and *Bathyvermilia*. Tubes flaring out in successive wide peristomes are typical of all known true species of *Vermiliopsis*, *sensu stricto*, but are not found in the other genera. *Bathyvermilia* is distinguished from *Metavermilia* chiefly by its cylindrical (not ribbon-like) opercular stalk, and from *Pseudovermilia* by its uncini (anterior tooth simple, not bifurcate).

The accompanying table summarises the principal differences of the four genera previously united by various authors under *Vermiliopsis*.

***Bathyvermilia challengerii*** sp. nov.

(Fig. 1a-d)

*Placostegus ornatus*: McIntosh, 1885, pp. 522-524, pl. 55, fig. 5-6, pl. 30A, fig. 25-27. NOT  
*Placostegus ornatus* (Sowerby MS) Mörch, 1863.

MATERIAL STUDIED. Mid-Pacific, "Challenger" expedition, station 244, 28 June 1875, 35°22' N, 169°53' E, 5307 m, bottom temperature 1.83°C, red clay (PARATYPE: fragment of one specimen without gill tuft or operculum, tube fragment, BMNH. 1885.12.1.411). Station 253, 14 July 1875, 38°09' N, 156°25' W, 5719 m, bottom temperature 1.72°C (PARATYPE: tube fragment, BMNH. 1885.12.1.412). Station 285, 14 October 1875, 32°36' S, 137°43' W, 4346 m, bottom temperature 1.66°C



	<i>Vermithopsis</i> Saint Joseph [emend. Zibrowius, 1970]	<i>Bathyeremia</i> gen. nov.	<i>Metaeremia</i> Bush [emend. Zibrowius, 1971]	<i>Pseudoveremia</i> Bush [emend. Zibrowius, 1970]
type-species	<i>V. multivariata</i> Mörch, 1863 [= <i>V. infundibulum</i> : (Philippi, 1844)]	<i>B. challengeri</i> sp. nov.	<i>M. multicristata</i> (Philippi, 1844)	<i>P. occidentalis</i> (McIntosh, 1885)
anterior tooth of uncini	simple	simple	simple	bifurcate
Opercular stalk	1st filament cylindrical	2nd filament cylindrical	2nd filament ribbon-like, flat	2nd filament cylindrical
a. position	subcircular or sub- quadrangular in cross-section, flaring out in successive wide peristomes, often with several smooth longitudinal keels	subtriangular or sub- quadrangular in cross-section, with- out peristomes, sometimes with transverse sculpturing	not flaring out in suc- cessive wide peri- stomes, otherwise variable, generally with longitudinal keels	subtriangular in cross- section, often with transverse sculpturing
b. shape				
tube				

(HOLOTYPE: fragment of one specimen with gill tuft, operculum and tube fragment; PARATYPE: fragment without gill tuft, BMNH. 1885.12.1.413).

DESCRIPTION. Diameter of tube up to 2 mm. Tube white, thick and hard, with bright surface, subquadrangular in cross-section, with slightly dilated basal attachment; numerous, close, well marked, crest like, smooth transverse ridges encircling tube; transverse ridges directed slightly forward in midline; no longitudinal keels; longitudinal groove cutting transverse ridges into isolated lower bars near base and continuous upper bars.

Length of specimens up to 19 mm, length of gill tuft up to 7 mm. 7 thoracic setigerous segments, 6 of them uncinigerous. Number of abdominal segments unknown. Details of collar structure unknown. Thoracic membranes very short, ending at about second setigerous segment.

Gill tuft of about 12 filaments on each side; basal lobes long and slender; no gill membranes. Second filament on left side transformed into smooth opercular stalk, without pinnules or wings, slightly enlarged at base of operculum.

Operculum subglobular, somewhat higher than wide, with slightly convex simple distal plate; opercular plate smooth, thin, with white calcareous deposit and two indistinct concentric zones.

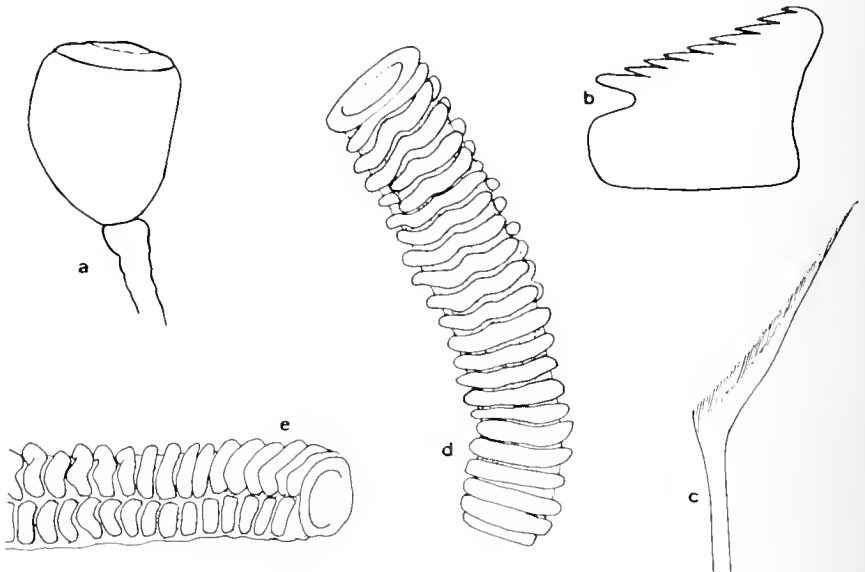


FIG. 1. *Bathyvermilia challengeri*. a: operculum; b: thoracic uncinus; c: abdominal seta; d, e: tube, upper side and side view.

First thoracic setigerous segment with two types of setae: uniformly simple limbate and thin capillary. Similar setae in segments 2 to 7. Additional thoracic setae with short proximal limbate zone ("*Apomatus* setae") present in segments 3 to 7. Abdominal setae geniculate, with rather broad triangular blade. Thoracic uncini saw-shaped with about 7 to 10 teeth; anterior tooth simple (not bifurcate). Anterior abdominal uncini similar to thoracic uncini; uncini of far posterior segments rasp-shaped.

NOTES. McIntosh (1885) erroneously referred his specimens from the "Challenger" stations to *Placostegus ornatus* (Sowerby MS) Mörch, 1863, a littoral serpulid from the Philippine Islands and described from the tube only. The sculpturing of the tube of McIntosh's deep-water species is characteristic and the tube fragments from the three "Challenger" stations in the North and South Pacific (halfway between Hawaii and Japan, Hawaii and Alaska, and South of Touamotou archipelago) are similar.

As Mörch had studied various shell collections in search of serpulids, he had probably seen Sowerby's original material of *Serpula ornata* (manuscript name or unpublished name found on a museum specimen?). He then described (Mörch, 1863, p. 420) two "varieties" of *Placostegus ornatus*, both observed in Cuming's collection on shells from the Philippine Islands (rather detailed but not illustrated descriptions of the tubes only): var. *articulata* (on *Arca obliquata* Reeve) and var. *pennata* (on *Ostrea hyotis*). The types of Mörch's var. *articulata* have been rediscovered recently (BMNH. 1965.31.14-16). These tubes are similar to other serpulids such as *Spirobranchus*, *Pomatoceros*, *Pomatoleios*, and *Galeolaria*. A preserved operculum was extracted from one of these tubes; it is a massive calcareous operculum similar to that of *Pomatoleios kraussii* (Baird).

***Bathyvermilia langerhansi* (Fauvel, 1909) comb. nov.**

(Fig. 2a-k)

*Vermiliopsis langerhansi* Fauvel, 1909, pp. 61-62, fig. 6a-d.

[part.] *Vermiliopsis langerhansi*: Fauvel, 1914, pp. 334-346, pl. 29, fig. 22-32. Fauvel 1927, pp. 363-365, fig. 124h-g.

*Vermiliopsis* sp.: Eliason, 1951, p. 142, pl. 1, fig. 7-8.

[?] *Vermiliopsis* ? *langerhansi*: Hartman & Fauchald, 1971, p. 181.

Not *Vermiliopsis langerhansi*: Bellan, 1960, p. 289, 1963, p. 264 [= *Vermiliopsis agglutinata* (Marenzeller)].

Not *Vermiliopsis langerhansi*: Southward, 1963, p. 584 [= *Vermiliopsis eliasoni* Zibrowius].

Not *Vermiliopsis langerhansi*: Bellan, 1964, p. 175.—Cabiocch, L'Hardy & Rullier, 1968, p. 73.—Chapman & Dales, 1954, p. 682.—Nelson-Smith, 1967, p. 33, fig. 20.—Tenerelli, 1961, 1962 [all: *Vermiliopsis* sp.].

MATERIAL STUDIED. North Atlantic, Prince of Monaco expeditions, station 527, 25 June 1895, east of Azores, 38°08' N, 23°18'45" W to 38°09' N, 23°15'45" W, 4020 m (4 SYNTYPES: specimens or fragments, 3 of them without abdominal region, tube fragments, MOM.—2 SYNTYPES: anterior fragments without abdominal region, tube fragments, MNHN).

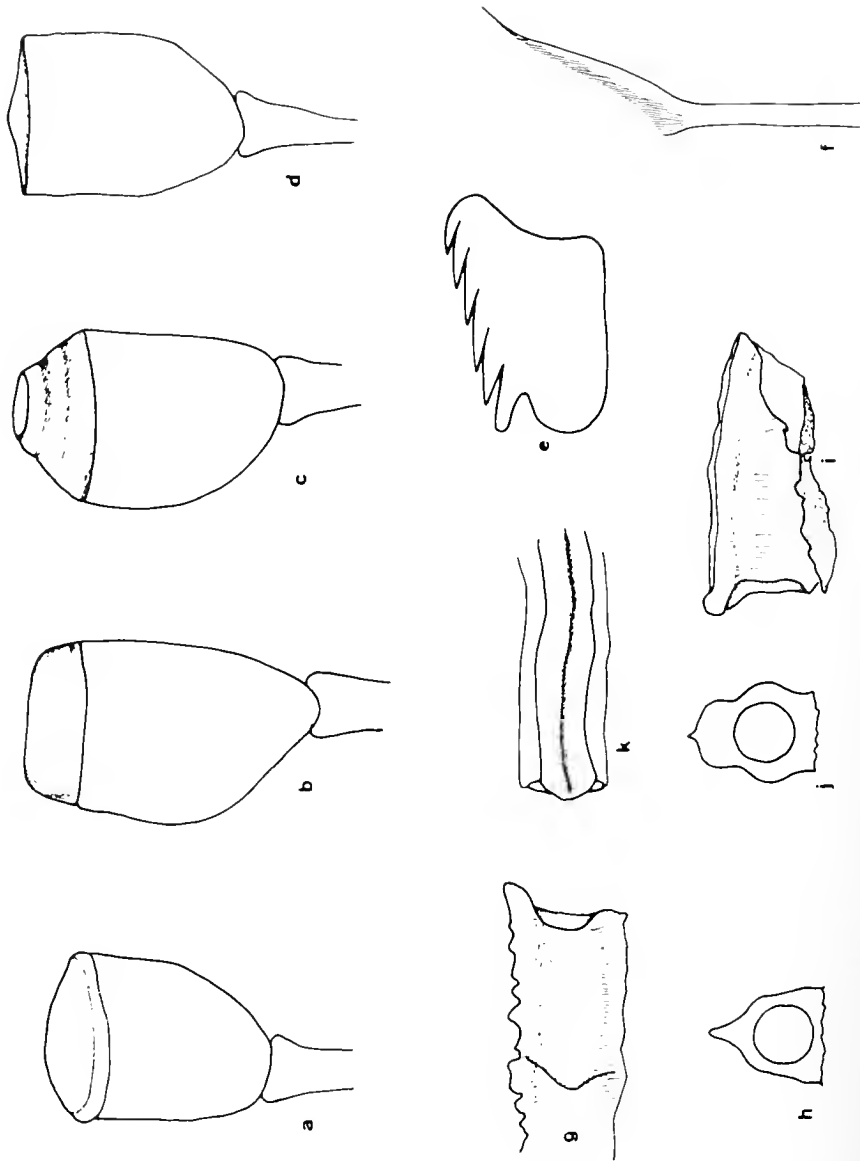


FIG. 2. *Bathynermitea langerhansii*. (a-h): from type locality, d labelled "Nacqueville 8.7.1911"; i-k: from Swedish Deep Sea Exped. station 373) a-d: opercula; e: thoracic uncus; f: abdominal seta; g, h: tube, side view and cross section; i, j, k: tube, side view, upper side, and cross section

North Atlantic, Swedish Deep Sea Expedition, station 373, 23-24 August 1948, south-east of Bermuda, 28°25' N, 61°05' W to 28°05' N, 60°49' W, 5500-5987 m (1 specimen: anterior fragment, tube fragment, NMG. 11015).

DESCRIPTION. Diameter of tube about 2 mm. Tube white, smooth, thick and hard, with bright surface, subtriangular in cross-section, as high as wide, not encrusting substratum. Tubes of syntypes with median keel irregularly denticulate and forming prominent tooth over orifice; no well-marked lateral keels or ridges; some transverse ridges across the tube. Tube of specimen collected by the Swedish Deep-Sea Expedition with upper face rather flat and wide, with median keel.

Larger specimens all incomplete: anterior region including gill tuft and thoracic segments, about 10 mm long; operculum up to 1.2 mm in diameter. The single complete, smaller specimen with about 50 abdominal segments. 7 thoracic setigerous segments, 6 of them uncinigerous. Thoracic membranes rather short, extending to about segment 3. Gill tuft composed of about 15 filaments on each side, forming single row on slightly elongate basal lobes; without gill membrane or pseudo-operculum. Second dorsal filament on either side transformed into smooth stalk, cylindrical, slightly enlarged at base of operculum.

Operculum vesicular, slightly elongate, higher than wide, with distal brown horny cap encrusted by calcareous white deposit (calcareous deposit sometimes lost). Opercular plate generally flat or slightly convex, but sometimes forming short cylinder or section of cone (simple, not subdivided into transverse layers).

First thoracic setigerous segment with two kinds of setae: stouter limbate with narrow uniform wing and smaller capillary; similar setae in following thoracic segments but more numerous. Additional sickle setae with short proximal limbate zone ("*Apomatus* setae") present in some posterior thoracic segments. Abdominal setae geniculate, with denticulate wing; posterior segments with long capillary setae.

Thoracic uncini saw-shaped, with 6 teeth; anterior tooth simple, not bifurcate. Uncini of anterior abdominal segments similar to those of thoracic region (saw-shaped, 6 or 7 teeth); uncini of posterior abdominal segments rasp-shaped and with more teeth when seen in profile.

NOTES. In former publications (Zibrowius, 1968a : 124-125; 1968b : 8, footnote), it was pointed out that there was some confusion regarding *Vermiliopsis langerhansi* Fauvel, especially as Fauvel himself confused the abyssal species with a shallow water form.

The original description of *Vermiliopsis langerhansi* by Fauvel (1909) was based on specimens from abyssal depths east of the Azores. All specimens examined by Fauvel consisted only of anterior fragments (a supplementary complete specimen was extracted from its tube when the original material was recently studied again).

Fauvel (1909) questionably included in the synonymy of his abyssal new species the record of *Vermilia clavigera* by Langerhans (1884) from shallow water around Madeira. Based on a study of Langerhans' specimens, Marenzeller (1892) referred this record to a quite different species, *Vermilia multicristata* Philippi, 1844, better known under the name *Vermiliopsis multicristata* and recently transferred to the genus *Metaveremia* Bush (Zibrowius, 1971). Taking for granted the identity of his

fragmentary abyssal specimens with those described by Langerhans (1884) from Madeira, Fauvel apparently combined his own observations with those by Langerhans on the other species. He further misunderstood Marenzeller's remarks, and believing that Langerhans' *Vermilia clavigera* should not be referred to *Vermiliopsis multicristata* (Philippi) and that the name *clavigera* was preoccupied (by Philippi, 1844), he named the abyssal new species *Vermiliopsis langerhansi*.

In the original description of the abyssal species by Fauvel (1909), the calcareous deposit found on some opercula (lost on other opercula) was not mentioned. The tube was not correctly described; it is not encrusting and wide but subtriangular in cross-section and lacking well-marked smooth lateral keels; thus it does not resemble the tube of *Vermiliopsis agglutinata* (Marenzeller) as erroneously stated by Fauvel.

Later Fauvel (1914) redescribed the same specimens from east of the Azores without any further details. He only added the remark that in 1911 he had found the same species in the English Channel (near Cherbourg); the description (otherwise the same as in 1909) was now more abundantly illustrated, including a figure of the geniculate abdominal setae (apparently from specimens other than the truncate ones from abyssal depths).

Finally, Fauvel (1927) included *Vermiliopsis langerhansi* in the "Faune de France" because of its supposed occurrence in the English Channel (intertidal zone). The description was now modified by the remark that the distal horny plate (rather flat or hemispherical) was encrusted by a calcareous deposit. As this detail had not been mentioned in the earlier descriptions (though it can be now confirmed after the syntypes were re-examined), the calcareous deposit was probably observed by Fauvel on the intertidal specimens from the English Channel.

Undoubtedly Fauvel's littoral form is a form close to *Vermiliopsis infundibulum* (Philippi, 1844) characterized by a short horny operculum encrusted by a calcareous deposit. Analogous forms are quite widespread along the Mediterranean and Atlantic coasts. The passing remark by Fauvel (1919) that *Vermiliopsis langerhansi*, as well as *Vermiliopsis glandigera* Gravier, may be nothing but a juvenile form or a "variety" of *Vermiliopsis infundibulum* (Philippi), was probably made in regard to the littoral form, rather than to the abyssal species.

In the collection of the Muséum National d'Histoire Naturelle (Paris), an anterior fragment was found labelled "*Vermiliopsis langerhansi* F., Nacqueville, 8.7.1911" (in Fauvel's own handwriting). By all observable details (operculum, position of opercular stalk, uncini) this specimen is identical to the syntypes from the type locality in the Central Atlantic (Prince of Monaco expeditions, station 527) and does not belong to a form close to *Vermiliopsis infundibulum* (Philippi). In spite of its label, the specimen in question does not appear to be Fauvel's littoral form but a specimen from the type locality of the abyssal species. It would appear that labels had been mixed up (similar label errors concerning other species have been detected in Fauvel's collection).

Since Fauvel (1914, 1927) had apparently confused a shallow water species with an abyssal species under the name *Vermiliopsis langerhansi*, other authors subsequently reported serpulids under that name from shallow water as well as from great depths (however, the records from bathyal and abyssal depths were less

numerous than those from shallow water). Only one or two of all these records are referable to the abyssal species *Bathyvermilia langerhansi*, as revised herein.

Eliason (1951) described a small serpulid as *Vermiliopsis* sp. ("perhaps *V. langerhansi*") collected off Bermuda (depth about 5500 m). This specimen was re-examined (NMG. 11075) and it proved to be the same species.

Some deep water serpulids from the continental slope south of Martha's Vineyard (39°43,6' N, 70°37,4' W, 2022 m) and briefly characterized by Hartman and Fauchald (1971 : 181—operculum consisting of a simple, cylindrical stalk topped by a translucent ampule with a flat top, circular in full view and calcareous) possibly belonged to the same species.

Southward (1963 : 584, species list) reported *Vermiliopsis langerhansi* from the continental slope off Western Europe (depth 1590–1775 m). This record is referable to *Vermiliopsis eliasoni* Zibrowius, 1970, as well as another record from the same area (1464–1555 m) (material studied, MBAP).

Bellan (1960 : 289; 1963 : 264) referred an empty tube dredged in the Mediterranean off Corsica (depth 565–610 m) to *Vermiliopsis langerhansi*; as indicated previously (Zibrowius, 1968a : 124–125) this was probably a tube of *Vermiliopsis agglutinata* (Marenzeller), a widespread species in the bathyal depths of the Mediterranean.

Chapman & Dales (1954 : 682) reported *Vermiliopsis langerhansi* from shallow water at Faial (Azores), Tenerelli (1961, 1962) from shallow water at Sicily, Bellan (1964 : 175) from shallow water algal communities in the Marseille area, Nelson-Smith (1967 : 33) from shallow water at Cap Ferrat (Mediterranean coast of France), Cabioch, l'Hardy and Rullier (1968 : 73) from the intertidal zone of Brittany. The operculum figured by Nelson-Smith (1967 : 33, fig. 20) showing a short horny operculum with calcareous deposit and longitudinal grooves, may be representative of what has generally, and erroneously, been considered as *V. langerhansi* in shallow water. All these shallow water forms are closely related to *Vermiliopsis infundibulum*: (Philippi, 1844), and had even been referred, tentatively, to that species (Zibrowius, 1968a). This group should be revised in detail.

INDETERMINABLE SERPULIDAE FROM ABYSSAL DEPTHS  
PREVIOUSLY REFERRED TO *PLACOSTEGUS*

*Placostegus benthalianus* McIntosh, 1885

*Placostegus benthalianus* McIntosh, 1885, p. 524, pl. 55, fig. 7, pl. 30A, fig. 28.

MATERIAL STUDIED. North Pacific, "Challenger" Expedition: station 253, 14 July 1875, 38°09' N, 156°25' W, 5719 m, bottom temperature 1.72°C (type material: several fragments from abdominal region extracted from tube fragments, probably of two specimens, not one as indicated by McIntosh, BMNH. 1885.12.1.414).

NOTES. The original description, based on a fragmentary specimen, is deficient in many respects. Based on the remaining fragments of the holotype, the following may be added.

Tube white, solid, subquadrangular in cross-section, not pentagonal as indicated by McIntosh; with three slightly rugose ridges in oldest part of tube, more prominent and bluntly denticulate on rather flat upper face in the younger part of the tube.

Number of thoracic and abdominal segments unknown. Details of gill tuft, collar and thoracic membranes unknown. According to McIntosh opercular stalk cylindrical, without pinnules or wings, slightly enlarged at base of operculum. Operculum vesicular, higher than wide, with horny distal plate slightly concave and yellowish brown at the rim. Thoracic setae and uncini insufficiently known. Thoracic uncini saw-shaped, with probably about 7 teeth (not 4 or 5 as mentioned by McIntosh), anterior tooth simple, not bifurcate (by analogy with abdominal uncini). Uncini of anterior abdominal segments saw-shaped, with about 7 teeth; anterior tooth simple, not bifurcate. Uncini of posterior abdominal segments rasp-shaped. Abdominal setae geniculate.

The species is too poorly known to be placed into a genus. However, it is evident that it does not belong to the genus *Placostegus*. The abdominal setae and uncini rather closely resemble those of *Bathyrermilia challengerii* (see above).

### *Placostegus moerchii* McIntosh, 1885

*Placostegus moerchii* McIntosh, 1885, pp. 524-525, pl. 55, fig. 8, pl. 30A, fig. 29-30.  
*Protoplacostegus mörchii*: Bush, 1904, pp. 179, 226; 287-288.

MATERIAL STUDIED. South Pacific, "Challenger" Expedition: station 285, 14 October 1875, 32°36' S, 137°43' W, 4336 m, bottom temperature 1.66°C, red clay (holotype: damaged specimen in poor condition, without tube, BMNH. 1885. 12.I.415).

NOTES. It is not possible to give an adequate description for the species. Based on the damaged holotype, the following may be added to the original description (no remnants of the opaque, white tube remain). Length about 12 mm (5 mm for gill tuft). 7 thoracic setigerous segments, 6 of them uncinigerous. Details of collar and thoracic membranes unknown; the latter probably short. Gill tuft in poor condition, about 7 filaments on each side. Second (?) dorsal filament on right side with pinnules (not differing from other filaments) with vesicular operculum. Operculum higher than wide, with bilateral symmetry. Distal face of operculum convex, slightly different from side wall, thicker, whitish but not encrusted with calcareous deposit. Second (?) dorsal filament on left side with pinnules and small globular (not differentiated) terminal knob or pseudo-operculum.

First thoracic setigerous segment with two types of setae: thicker (broken distally; limbate ? special setae ?) and thinner capillary setae; these fascicles of setae not less developed than those of the following segments. Sickle setae with short proximal limbate zone ("Apomatus setae") present in segments 2 to 7. Abdominal setae geniculate, with triangular blade. Thoracic uncini saw-shaped (about 10 teeth ?); anterior tooth simple, not bifurcate. Uncini of abdominal segments rasp-shaped.



The species is characterized by an opercular stalk with pinnules, not differing from the other gill filaments. This detail should be confirmed from additional specimens, since exceptional specimens of species, characterized by smooth opercular stalks, have been found bearing pinnules as in *Filogranula* (Zibrowius, 1968a: *Omphalopoma*). Vesicular opercula on opercula stalks bearing pinnules, not differing from the other filaments, are known in the genus *Protula* Risso [= *Apomatus* Philippi]. *Protula*, however, is characterized by a quite different type of uncini than those found on McIntosh's species, which are rather of the type found in *Vermiliopsis*, *sensu stricto*, and *Bathyvermilia*.

The genus *Protoplacostegus* was established by Bush (1904) for *Placostegus moerchii* as the type-species. The latter species, however, is too poorly known at present to give a satisfactory diagnosis.

#### SUMMARY

The genus *Bathyvermilia* gen. nov. is established for two abyssal serpulid species originally described under *Placostegus ornatus* by McIntosh (1885), and *Vermiliopsis langerhansi* by Fauvel (1909), the name emphasizing their morphological affinities to *Vermiliopsis*, *sensu stricto*, as well as their deep-sea distribution. Since the name *Placostegus ornatus* is preoccupied by a littoral species described by Mörch (1863), McIntosh's deep-sea species from the Central North and South Pacific is renamed *Bathyvermilia challengerii* sp. nov.

It is pointed out that *Bathyvermilia langerhansi*, a deep-sea species from the Central Atlantic, had been confused with littoral forms of *Vermiliopsis*, *sensu stricto*, from the Mediterranean, Brittany and the Azores.

Additional comments are made on two other Central Pacific abyssal serpulid species of doubtful generic status, *Placostegus benthalianus* and *Placostegus moerchii*, both incompletely described by McIntosh (1885).

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# FOSSIL AND RECENT COMATULID CRINOIDS WITH COELOMIC EXTENSIONS PENETRATING THE CENTRODORSAL

By AILSA M. CLARK

IN 1877 Ludwig published an anatomical study of the dorsal or chambered organ and associated structures of *Antedon rosacea* (i.e. *A. mediterranea* (Lamarck)) made on sections of decalcified material. He showed that there are five blind radial coelomic sacs extending from the coelom a short distance downwards (aborally) outside the chambered organ (see fig. 3j). On the oral (upper or ventral) face of intact centrodorsals of *Antedon* there are five radial depressions to house the ends of these sacs, which depressions are lacking in the majority of recent comatulids.

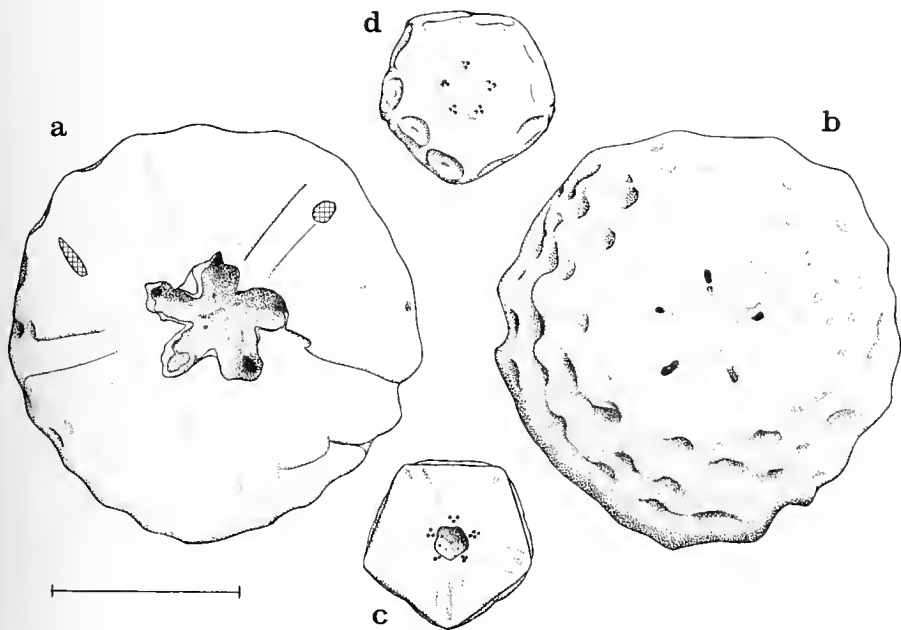


FIG. 1. a, b. †*Glenotremites paradoxus* Goldfuss. B.M. Palaeontological Department reg. no. E.297, Upper Chalk, Gravesend, Kent, centrodorsal after ultrasonic cleaning in ventral (a) and dorsal (b) views. c, d. The same of *Pterometra pulcherrima* (A. H. Clark). B.M. Zoological Department reg. no. 1972. 8.21.100, 'Anton Bruun' st. 18A, 07°34'N: 98°00'E (between Malaya and the Nicobar Islands), 77 metres. The scale measures 5 mm.

However, subsequent studies on some fossil comatulids and on recent members of the families Notocrinidae and Asterometridae, especially by Gislén (1924), have shown the presence in them of blind-ending radial pits in the centrodorsals housing similar but more extensive prolongations of the coelom. These pits open on the ventral face of the centrodorsal outside the cavity for the chambered organ unless that cavity is markedly lobate, when the perforations emerge at the extremities of the lobes, their much larger size differentiating them from the small apertures of the axial cords connecting the cirri to the chambered organ. The latter condition is found in the Cretaceous *Glenotremites paradoxus* Goldfuss (fig. 1a), which also has aboral radial openings situated in the lobes of a stellate hollow on the dorsal pole. Ultrasonic cleaning of a large centrodorsal of *G. paradoxus*, mentioned by Rasmussen (1961 : 292, no. 36) and by Gislén (1925 : 9, as *G. batheri*) has shown that these two sets of holes are the opposite ends of the same cavities. However, in none of the recent species so far sectioned, including *Notocrinus virilis* Mortensen, 1917, *Pterometra trichopoda* (A. H. Clark, 1908) and *Asterometra anthus* (A. H. Clark, 1907) have the cavities yet been shown to perforate the centrodorsal completely. It is possible that such a condition does exist in smaller specimens of *Notocrinus virilis*. Mortensen (1918) observed that a 'half grown' individual of this species showed a central pore on the dorsal pole ringed by five radially-placed pores, which he assumed did not fully penetrate the centrodorsal. Gislén (1924 : 129, fig. 196) illustrates the centrodorsal of Mortensen's specimen in dorsal view showing five additional inter-radial indentations on the small cirrus-free dorsal pole; his caption says 'the five black dots are radially arranged, nearly perforate the Cd, and are the continuations of the chambered organ, the five interradial rings are small pits only'. This assumption that the radial aboral openings are connected to the chambered organ is surprising in view of the fact that he also shows (fig. 199) a vertical section through a centrodorsal with a conical radial pit opening on the upper side but (apparently) ending further aborally than the chambered organ, while the angle of alignment of the pit points directly at the dorsal pole.

To check this point, serial horizontal sections were made through the decalcified calyx of a specimen of *Notocrinus virilis* with the centrodorsal c. 3.5 mm in diameter and therefore probably comparable in size with Mortensen's (the largest individuals have centrodorsal c. 10 mm across). The aboralmost of the sections show a complete absence of cavities except for a few of the small double axial cords leading to the more apical cirri (fig. 2a). As the central mass of nervous tissue forming the aboral 'floor' of the chambered organ appears in successive sections, so also do apertures in two radii representing the extremities of the longest radial pits but these are well spaced from the nervous capsule. In the centre of the capsule an opaque spot of tissue resolves itself into five small cavities (see fig. 2b), which are radial in position and represent the uppermost end of the atrophied connection between the chambers of the chambered organ and the larval stalk. As these open out into the chambers upwardly, the three other radial pits appear in the matrix of the centrodorsal. Towards the upper end of the chambered organ, the central core of it becomes more opaque and enlarged; this is the base of the axial organ which emerges on the ventral side of the chambered organ into the much divided coelom. The chambers contract

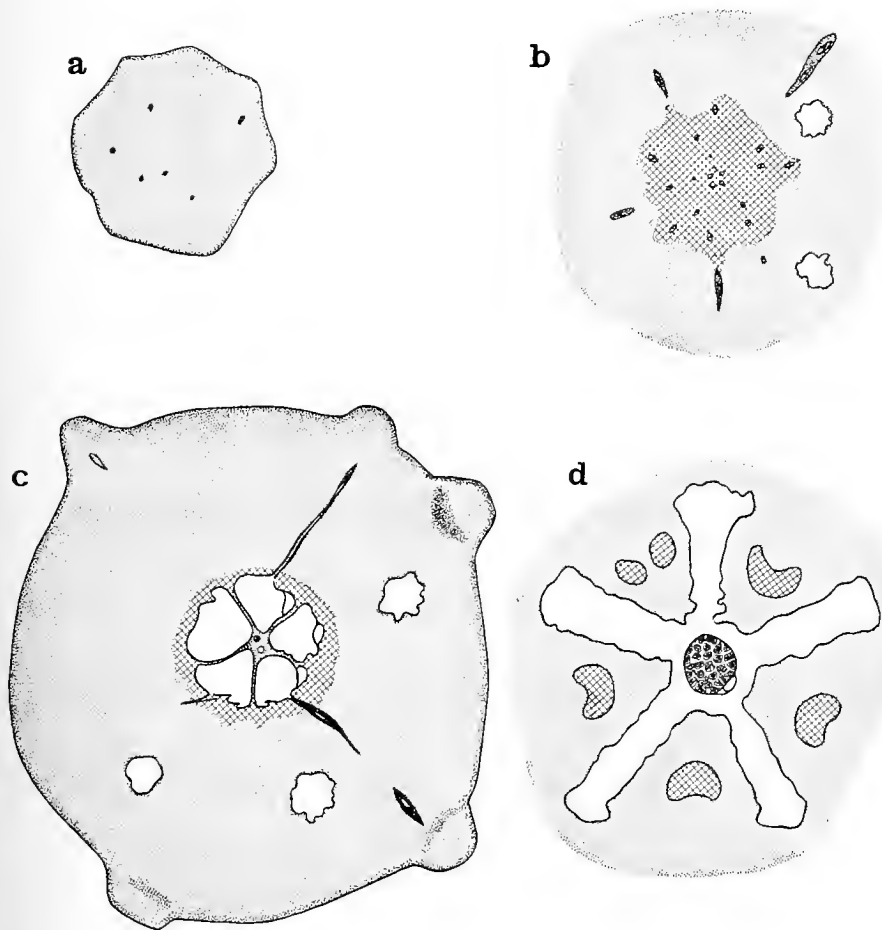


FIG. 2. *Notocrinus virilis* Mortensen. 1948.1.7.121, B.A.N.Z.A.R. Expedition st. 107, off MacRobertson Land, Antarctica, 219 metres, horizontal sections of decalcified calyx, original diameter of centrodorsal 3.5 mm. a. Section close to dorsal (aboral) extremity with only some obsolete axial cords to the more apical cirrus sockets interrupting the collagenous matrix (stippled); b. Nervous tissue (cross-hatched) forming the floor of the chambered organ showing the five small aboral extremities of the chambers centrally, with coelomic pits in two radii and oblique sections of axial cords; c. Lower part of chambered organ showing origin of two axial cords, a third radial pit having appeared; d. Axial organ in the centre, having emerged from the top of the chambered organ, with coelomic spaces around it linking horizontally to the upper ends of the radial pits in the centrodorsal. [In b and d the peripheral parts are omitted.]

sharply and the nervous tissue diverges obliquely ventro-laterally from them, dividing into five interradiar tracts which themselves soon split into two parts at the same time as the vertical radial pits give way abruptly to horizontal canals leading into the coelomic spaces around the axial organ (fig. 2d). The paired interradiar nerve tracts rapidly diverge and reunite radially, then are linked together horizontally by commissures forming the nerve ring, this in turn giving way to the five radial nerves leading to the arms. The whole arrangement of this aboral nervous system is very similar to that of *Antedon*, as illustrated by Hamann (1889, fig. on p. 65); the five circumscribed areas interrupting the direct link between the capsule of the chambered organ and the radial nerves leading to the arms serving to accommodate the radial coelomic sacs in *Antedon* and the comparable canals to the radial pits of the centrodorsal in *Notocrinus*.

A smaller centrodorsal (diameter 2.5 mm) of *N. virilis* decalcified and sectioned shows essentially the same limited extent of the radial pits. Also the untreated centrodorsal of another small specimen shows a somewhat pitted dorsal pole to the centrodorsal but without any particular regularity. I think that the apertures described by Gislén and supposed to connect with the larval stalk may have been due to similar erosion at the dorsal pole. Their existence needs to be checked by further sectioning of material at early ontogenetic stages.

This anatomical study of *Notocrinus* was in fact prompted by a large sample of *Pterometra pulcherrima* (A. H. Clark, 1909) taken off the coast of Burma at 'Anton Bruun' station 18A, which allowed several specimens to be sacrificed for anatomical study. This showed that, not only are the centrodorsals perforated on the ventral face in each radius, but also dorsally on five, radially-aligned, convexities on the dorsal pole, there being complete radial canals penetrating the centrodorsal (fig. 1c, d; also A.M.C., 1972, fig. 14). In this species, compared with *Notocrinus virilis*, the canals are not only more extensive but also multiple, with a cluster of up to four openings in each radius, though horizontal sections of decalcified specimens show that the divisions are irregular and incomplete, anastomosing at some levels into a single lobed canal only to separate again into separate parts, adding considerably to the surface area of the walls of the canals.

Although perforating the skeleton of the centrodorsal, these canals do not appear to open on the dorsal pole, the body wall being continuous across the mouth of each one. However, in a series of horizontal sections the cavities appear almost immediately within the five convexities of the dorsal pole and continue vertically to the level of the top of the chambered organ but outside it, though closer to it than the radial pits of *Notocrinus virilis*, causing the axial cords to the cirri to deviate more sharply around the radial canals.

The function of these coelomic extensions in the families Asterometridae and Notocrinidae (the Notocrinida of Gislén) remains to be determined. Professor Nichols (personal communication) has suggested that they are the probable sites of coelomocyte production. My thanks are due to him for this comment, also to Dr Jefferies of our Palaeontology Department, who suggested and carried out the ultrasonic treatment of the *Glenotremites*, and to Mr Cooper of the histological section of the Zoology Department, who made the sections.



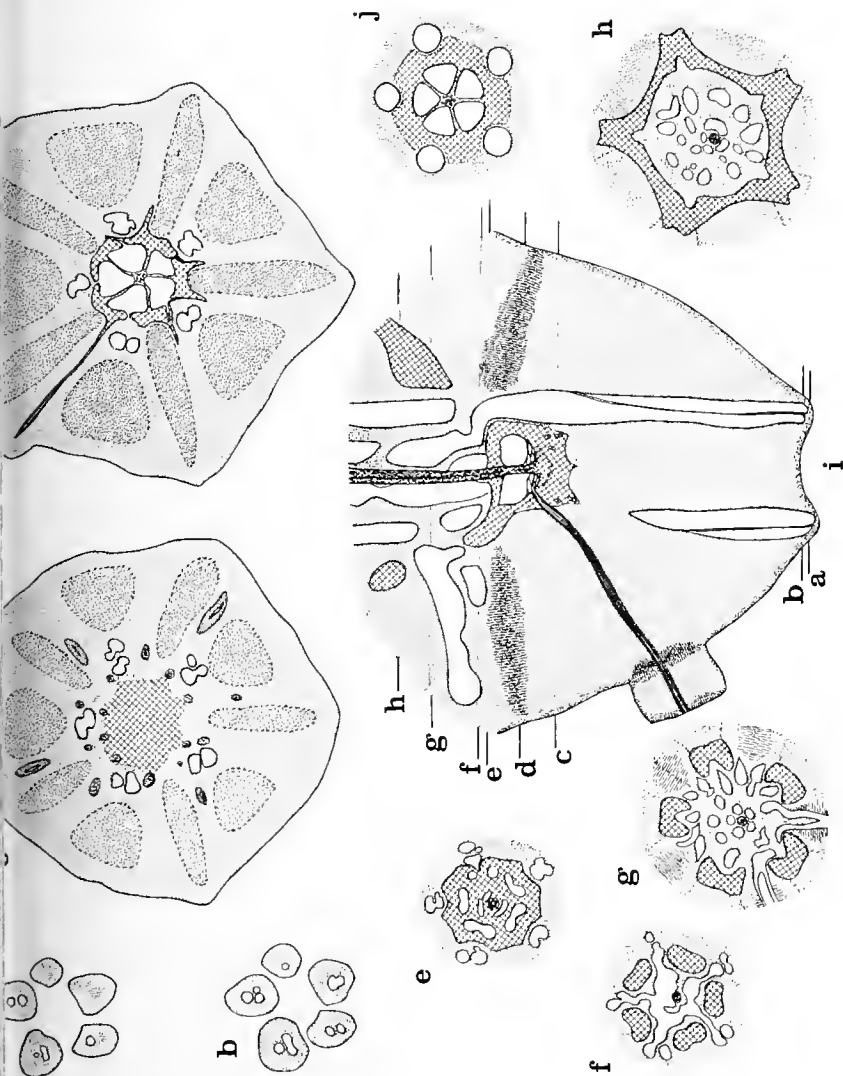


FIG. 3. a-i, *Pterometra pulcherrima* (A. H. Clark). [Details as in fig. 1, c, d]. Sections of decalcified calyces, original diameter of centrodorsal c. 4.5 mm., the levels of the horizontal sections (a-h) indicated on the vertical section (i), showing radial coelomic canals penetrating the centrodorsal to the convexities on the dorsal pole. In e, the base of the axial organ has appeared centrally with small coelomic pockets around it indenting the roof of the chambered organ; outside these the uppermost ends of the chambers are also visible while in one radius a coelomic canal is beginning its inward course to join up with the others around the

axial organ, as shown in f. In g and h, the coelom is further subdivided and the intraradial nerve trunks arising obliquely from the chambered organ have split and reunited radially and then become linked horizontally by commissures before giving off the five primary radial nerves. Compare the vertical section i with fig. 54 (p. 42) of Cuénot (1948) showing a similar section of *Antedon*. j, *Antedon mediterranea* (Lamarck), a decalcified horizontal section through the chambered organ [after Ludwig, 1877, pl. xiv, fig. 20.]

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# THE AFFINITIES OF *PIPISTRELLUS RIDLEYI* THOMAS, 1898 AND *GLISCHROPUS ROSSETI* OEY, 1951 (CHIROPTERA: VESPERTILIONIDAE)

By J. E. HILL & G. TOPÁL

## INTRODUCTION

IN a recent study Hill (1969) examined four further specimens of *Glischropus rosseti* Oey, 1951, hitherto known in the literature only from the holotype and paratype from Cambodia, and concluded that the species should be transferred to *Pipistrellus*, being allied to the equally poorly known *P. ridleyi*, described from Malaya by Oldfield Thomas many years before. Four additional specimens of *rosseti* have now been found in the collections of the Hungarian Natural History Museum, obtained at Bangkok nearly one hundred years ago by the traveller J. Xantus. Not immediately recognized as *rosseti*, their external features in particular suggested to one of us (G.T.) that they might represent the genus *Myotis*, and one skull was sent to London where its identity with *rosseti* was established. There seemed sufficient grounds, however, to justify a further examination of the generic affinities of the two species, Hill (1969 : 138) having considered their features distinctive enough to warrant the establishment of a separate group (the *ridleyi* group) within *Pipistrellus*.

## SYSTEMATIC SECTION

For many years it remained customary to separate the genera *Myotis*, *Pipistrellus* and *Eptesicus* on the basis (in part) of the premolar dentition, the premolar formula of *Myotis* being  $pm\frac{3}{3}-\frac{3}{3}$ , of *Pipistrellus*  $pm\frac{2}{2}-\frac{2}{2}$  and of *Eptesicus*  $pm\frac{1}{2}-\frac{1}{2}$ . In *Myotis* the central teeth ( $pm\frac{3}{3}$ ) are small and sometimes displaced from the tooththrows: in *Pipistrellus* they are presumed to have disappeared and the anterior premolars ( $pm\frac{2}{2}$ ) are frequently much reduced, the upper tooth often displaced. The extent of reduction and degree of displacement has been and is used as a diagnostic feature at the specific level in both *Myotis* and *Pipistrellus*, and some authors such as Tate (1942) employ these features as indicators of "primitive" or "specialised" species, a greater degree of reduction and displacement being presumed to indicate greater specialisation, reflecting as it does the extent of shortening of the rostrum from a "primitive" long-nosed condition.

### Premolar dentition of *Pipistrellus* and *Eptesicus*

In the last three decades much doubt has been cast on the adequacy of the premolar dentition in *Pipistrellus* and *Eptesicus* as a diagnostic generic feature, although many years ago Leche (1875 : 34) mentioned a specimen of *Pipistrellus maurus* (= *P. savii*) in which  $pm^2$  was rudimentary and barely pierced the gum, and its occasional absence in this species was noted by Miller (1912 : 221). More recently, *Bull. Br. Mus. nat. Hist.*(Zool.)**24**, 9

Tate (1942 : 232, 271) questioned the validity of a distinction based on the presence or absence of an obsolescent, disappearing structure, bearing in mind that  $pm^2$  may be present or absent in another vespertilionid genus, *Scotococcus*, but nevertheless retained the conventional distinction between *Pipistrellus* and *Eptesicus*. Kuz'yakin (1944 : 101, 1950 : 388 et seq., 1965 : 103) and Topál (1959 : 91) noted and discussed the occasional absence of  $pm^2$  from the toothrows of *Pipistrellus savii*: Kuz'yakin referred the Russian species of *Pipistrellus* and *Eptesicus* to the related genus *Vespertilio*, but Topál (1958) described and illustrated differences in the baculum or os penis of their European species. The occasional presence of  $pm^2$  in *Eptesicus capensis* was noted by Hayman (1954 : 289, 290) and in *E. pumilus* by Hill (1966 : 303) who also (1972 : 33) has described a specimen of *Pipistrellus javanicus* from Malaya which has a small supernumerary premolar in the right upper toothrow, situated in a recess or shallow angle between the postero-internal face of the canine and the antero-internal face of the usual anterior premolar. It is clear that the presence or absence of  $pm^2$  can have no universal validity in defining *Pipistrellus* or *Eptesicus*, but most authors, e.g. Miller (1912 : 303), Ellerman & Morrison-Scott (1951 : 152) or Rosevear (1965 : 243), who have discussed the point retain them as distinct on grounds of convenience.

#### Premolar dentition of *Myotis*

The absence from one or both sides of the jaw of the "diagnostic" second upper premolar ( $pm^3$ ) in *Myotis* has been reported on a number of occasions and the loss of the corresponding lower tooth ( $pm_3$ ) less frequently so: occasionally the anterior upper tooth ( $pm^2$ ) may be absent. Allen (1908 : 45) recorded a specimen of *M. nigricans* which lacked the right  $pm^3$  and another lacking the left  $pm_3$ . Ärnback-Christie-Linde (1909 : 578) discussed dental variation in the same species, noting a specimen without the left  $pm^3$  and a second example lacking  $pm^3_3$  from both sides of the jaw. This author also (p. 579) drew attention to specimens of *M. muricola* with  $pm^3$  so reduced and displaced as to be quite functionless: the right  $pm^3$  is lacking from a specimen (B.M. 10.4.6.24) of *muricola* in the collections of the British Museum (Natural History).

Miller & Allen (1928 : 7, 99) found  $pm^3$  frequently absent from the toothrows of *M. occultus* (= *M. lucifugus occultus*) and  $pm_3$  occasionally so: in *M. lucifugus carissima* these authors reported (p. 53) a specimen without the right  $pm_3$  and with (pp. 8, 53) the left  $pm^{2-3}$  coalesced, while in *M. thysanodes* they recorded (p. 124) a specimen lacking the left  $pm^{2-3}$  and with only  $pm^2$  present in the right toothrow, another specimen (pp. 8, 124) having  $pm^{2-3}$  on one side coalesced. Findley & Jones (1967 : 432, fig. 3) indicated a geographical variation in the number of small premolars ( $pm^{2-\frac{2}{3}}$ ) in *M. lucifugus* and showed that in *M. fortidens* from Mexico the normal condition is the presence of but one small upper and lower premolar in each side of the jaw: in the holotype (B.M. 88.8.8.18)  $pm^3_3$  are lacking from both sides. A specimen referred to *fortidens* by Miller & Allen (1928 : 8, 55) had on each side in addition to the two small upper premolars ( $pm^{2-3}$ ) common in *Myotis* a third small supernumerary tooth crowded beneath the inner anterior border of the large premolar ( $pm^4$ ).

Status and records of *Pipistrellus annectans* Dobson, 1871

Topál (1970) has shown from an examination of the holotype that *Pipistrellus annectans* Dobson, 1871 from Assam (Nagaland), north eastern India is in fact synonymous with *Myotis primula* Thomas, 1920, from the northern part of the nearby province of West Bengal, the small pm $\frac{2}{3}$  being absent from both sides of the jaw in the holotype. This finding has been confirmed by Hill & Thonglongya (1972 : 188) who reported a further specimen (from Thailand) referable to *annectans* and who were able to compare it directly with the holotype of *Myotis primula*.

The existence of a species sharing some features of *Myotis* and of *Pipistrellus* was first indicated by Dobson (1871 : 214), who wrote of *Pipistrellus annectans* (= *Myotis annectans*): "This species unites the external form of a *Vespertilio* to the dentition of a *Pipistrellus*; the form of the ear and tragus is almost precisely similar to those of the next species which is a true *Vespertilio*". The next species described by Dobson is *Vespertilio nipalensis*, nowadays (Ellerman & Morrison-Scott, 1951 : 139) listed as a subspecies of *Myotis mystacinus*. Subsequently, Dobson (1876 : 117) reiterated this conclusion, transferring *annectans* to *Vesperugo*: "This species unites the external appearance of a *Vespertilio* to the dentition of a *Vesperugo*. In the form of the ear and tragus, and elevation of the roof of the skull above the face, it very closely resembles some species of the former genus".

Schneider (1905 : 80) reported three specimens from the Upper Langkat, Sumatra in the Zoological Institute of the University of Stockholm (now apparently transferred to the National Museum of Natural Sciences, Stockholm) identified by Leche as *Pipistrellus annectans*, but gave no diagnostic details. Subsequently, Ärnäck-Christie-Linde (1909 : 574) gave a detailed description of these examples, noting (p. 575) that in the shape of the muzzle, ear and tragus, the absence of a post-calcarial lobe and height of braincase they corresponded with *Myotis* but in dental formula with *Pipistrellus*. A comparison (p. 575) of the length of the tibia with the length of the head and body led Ärnäck-Christie-Linde to conclude that the tibia is relatively longer in *Myotis* than in *Pipistrellus*, the holotype of *Pipistrellus annectans* being close to *Myotis* in this respect while in the specimens from Sumatra referred to *annectans* the tibia proved longer than in any *Pipistrellus* examined, although not as long as in the holotype. Furthermore, Ärnäck-Christie-Linde demonstrated (p. 577) that in the Sumatran examples the coracoid is not bifurcated at the tip so that in this respect they resemble *Myotis* rather than *Pipistrellus*, although this author also reported (pp. 578, 581) a specimen of *Myotis nigricans* with the coracoid showing a tendency to bifurcation but with the dental formula of *Pipistrellus*.

Ärnäck-Christie-Linde concluded (pp. 578, 581) from the description of the holotype and from the Sumatran specimens referred to *annectans* that this species represented an example of transition between forms referred to different genera. However, the Sumatran specimens are much too small (length of forearm 29.9 mm) to represent *Myotis annectans* (length of forearm 45-47 mm) of which Ärnäck-Christie-Linde (pp. 576, 580, 582) considered them to be a small form. From the size and description these specimens seem likely to represent the species known as *Pipistrellus ridleyi*, hitherto reported only from Malaya.

Generic affinities of *Pipistrellus ridleyi* and *P. rosseti*

Except in dental formula, there is no doubt that many of the features of *Pipistrellus ridleyi* and *P. rosseti* are those of *Myotis* rather than of *Pipistrellus*, to which Hill (1969 : 138) transferred *rosseti* from *Glischropus* where originally it had been placed. Both have long, rather narrow, slightly funnel-shaped ears with the tragus one half or almost one half as long as the ear, its outline narrowed distally to a blunt, anteriorly directed point. There is no post-calcarial lobe in *ridleyi* but a narrow lobe is present in *rosseti*. So far as can be determined from specimens in alcohol, the tibia in both *ridleyi* and *rosseti* is approximately one third of the length of the head and body, as in the specimens of "*Pipistrellus annectans*" from Sumatra described by Årnäck-Christie-Linde (1909 : 574). In both species the braincase is high and inflated, rising above the facial line in a smooth but sharp curve. The rostrum is narrow and low, especially in *ridleyi*, medianly slightly flattened, with a shallow median depression, and agrees more closely with that of *Myotis* than with the more elevated, wider rostrum of *Pipistrellus* which as a rule does not lie markedly lower than the braincase. The toothrows are parallel posteriorly but converge at the level of the front face of  $pm^4$  to give the anterior palate a slightly "pinched-in" look very like the anterior palate of *Myotis*.

The peculiarities of the incisive dentition of both *ridleyi* and *rosseti* provide perhaps the most convincing indication of their affinity to *Myotis*. These features were commented upon by both Thomas (1898) and Oey (1951) in their descriptions of the two species. Thomas (p. 362) in particular noted of *ridleyi* that "This little Pipistrelle is readily distinguishable from all others by its short and peculiarly shaped incisors, for all the ordinary members of the genus have long styliform incisors, which may or may not have a small supplementary cusp near their tips, but which are never short, broad, and separated into two almost subequal cusps, as is the case in *P. ridleyi*". Oey (p. 3) noted that the upper dentition of *rosseti* differed from that of *Pipistrellus* in the position and size of  $i^2$  (in fact the outer incisor, usually considered to be  $i^3$ ). These anomalies are immediately explained if the incisive dentition is compared with *Myotis* rather than with *Pipistrellus*.

The inner upper incisor ( $i^2$ ) of both *ridleyi* and *rosseti* is short and broad, anteriorly rather narrow, wider posteriorly, with a strong anterior cusp and small posterior cusp about one half the height of the anterior cusp: the base of the tooth is expanded posteriorly to form a low, cusp-like labial extension. The tooth is hollowed posteriorly through engagement with  $i_3$  and in profile the anterior cusp is slightly hooked. It thus corresponds with  $i^2$  of *Myotis*: in *Pipistrellus*  $i^2$  is more linear, its base not expanded posteriorly but in fact often narrower posteriorly than anteriorly. In *ridleyi* and *rosseti* the principal cusp of  $i^3$  is equal to or exceeds that of  $i^2$  in height and is hooked so that its tip points very slightly posteriorly to give the tooth in profile the appearance of a reduced canine, again a condition corresponding more closely with *Myotis* than with *Pipistrellus* in which  $i^3$  is usually much lower in height than  $i^2$  and, like  $i^2$ , points forward rather than having a hooked appearance. The lower incisors in *ridleyi* and *rosseti* resemble those of *Myotis*, especially in the wide disparity in size between  $i_3$  and  $i_{1-2}$ , the former being much larger, its bulk twice that of the latter teeth.

Apart from the absence of  $pm_3^2$  the premolar dentition of *ridleyi* and *rosseti* presents few diagnostic features: the anterior tooth ( $pm^2$ ) is more or less circular in basal outline, with a narrow cingulum and central cusp. It is in the toothrow, in contact with the canine but separated from  $pm^4$  by a short diastema. The anterior lower premolar ( $pm_2$ ) is oval or sub-circular in basal outline, in the toothrow but not at all compressed between the canine and  $pm_4$ , in close agreement with  $pm_2$  in *Myotis*: in *Pipistrellus*  $pm_2$  is usually more angular in outline and is usually compressed in the toothrow.

Some emphasis is placed by Ärnäck-Christie-Linde (1909 : 577, 581) on the structure of the coracoid as a diagnostic feature between *Myotis* and *Pipistrellus*. It has been possible to examine the coracoid of the paratype of *ridleyi* and of three specimens of *rosseti*: in all it is a plain, narrow shaft, not bifurcated or even expanded distally, and strongly curved. It thus satisfies the criteria set by Miller (1907 : 205) for the coracoid of *Myotis*.

It is our conclusion, therefore, that properly to reflect the evident similarities of *ridleyi* and *rosseti* to *Myotis* they must be transferred to that genus and that the dental formula must be disregarded in this instance for the purposes of generic classification. The only real features by which the two species may be allied to *Pipistrellus* are those concomitant with a shortening of the rostrum, a tendency already apparent in *Myotis*, which in *ridleyi* and *rosseti* has proceeded sufficiently far as to involve the disappearance of  $pm_3^2$ . These teeth in some species of *Myotis* such as *nigricans*, *muricola* or *annectans* are greatly reduced or in some specimens completely lacking and in one species, *fortidens*, their absence is apparently a normal condition. In all of the recorded examples of *ridleyi* (six, if the specimens from Sumatra reported as "*Pipistrellus annectans*" by Ärnäck-Christie-Linde (1909 : 574) represent this species) and of *rosseti* (ten, including two juveniles) these teeth are absent in both upper and lower jaws. The remaining  $pm_3^2$  are not at all compressed in the toothrows, and, indeed,  $pm^2$  is separated from  $pm^4$  by a small diastema.

Divisions within *Myotis* are uncertain, the most recent reviewer of the Asiatic species, Tate (1941), recognizing a number of weakly defined subgenera, some of which may not prove valid. *Myotis ridleyi* and *M. rosseti* are referable to the division to which Tate allocates *Selysius* as a subgeneric name. This subgenus includes a number of species such as *frater* and *siligorenstis* with elevated, rounded braincase and also species in which reduction and displacement of  $pm_3^2$  has begun as it has in *nigricans* and *muricola*, also referred to *Selysius* by Tate. Both *ridleyi* and *rosseti* stand rather apart in *Selysius* by virtue of their shortened rostra: their nearest approach in the subgenus appears to be *muricola* which has a longer, slightly lower rostrum and in which  $pm_3^2$  are reduced and often displaced, the canines and remaining cheekteeth being more massive than in either *ridleyi* or *rosseti*.

The two species may be diagnosed:

### *Myotis ridleyi* (Thomas, 1898)

*Pipistrellus ridleyi* Thomas, 1898 : 361 (Selangor, States of Malaya); Kloss, 1908 : 158 (listed, type locality given as Kepong); Chasen, 1940 : 51 (listed); Tate, 1942 : 240, 291 (notes, measurements of holotype); Medway, 1969 : 39 (description, measurements, Malayan

records); Hill, 1969 : 136 (notes, measurements of holotype, paratype and further example, allied to *rosseti*); Hill (1972:33) (incisive dentition, measurements of Malayan specimens repeated).  
 ?*Pipistrellus annectans*, Schneider, 1905 : 80 (specimens from Sumatra); Årnäck-Christie-Linde, 1909 : 574 (description, measurements of Sumatran specimens).

Similar to *Myotis muricola* but smaller (length of forearm 28–30 mm) with slightly shorter ear; skull with similarly expanded braincase but with the frontal region more elevated; rostrum shorter and deeper, generally a little more massive; dentition less massive, the canines short,  $c^1$  barely exceeding  $pm^4$  in height and  $c_1$  equal in height to  $pm^4$ . There is some resemblance to *M. siligorensis* which has similarly reduced canines but in which the braincase rises more abruptly from the rostrum, this itself lower, narrower and less massive than in *ridleyi*. There is no trace of  $pm^3$  in either side of the jaw in any of the three Malayan specimens examined, nor is it to be found in the specimens from Sumatra reported as "*Pipistrellus annectans*" by Årnäck-Christie-Linde, if correctly these should be referred to *ridleyi*. The species has been reported from lowland localities in the Malayan States of Perak, Pahang and Selangor (Medway, 1969 : 39) and possibly occurs also in Sumatra.

#### *Myotis rosseti* (Oey, 1951)

*Glischropus rosseti* Oey, 1951 : 4 (Cambodia).

*Pipistrellus rosseti*, Hill, 1969 : 133 (description, measurements of further specimens, transferred to *Pipistrellus*).

Externally like *ridleyi* but ears slightly longer, the base of the thumb expanded to form a fleshy, wrinkled pad, the soles of the feet similarly swollen to form a broad concave pad, and with a narrow post-calcarial lobe. Skull similar to that of *ridleyi* but braincase a little more swollen frontally; interorbital region shorter; rostrum slightly shorter and wider, its median depression shallower and less clearly defined; narial emargination more nearly U-shaped rather than V-shaped as in *ridleyi*, not extending as far posteriorly; basal depressions more pronounced. Lower canine ( $c_1$ ) slightly exceeding  $pm^4$  in height, the latter tooth a little less reduced than in *ridleyi*: no evidence of the presence of  $pm^3$  has been found in any of the ten known specimens. *Myotis rosseti* has been recorded so far only from Cambodia and Thailand (specimens in Hungarian Natural History Museum, Budapest).

*Myotis ridleyi* and *M. rosseti* may be readily recognised among *Myotis* by their expanded braincases and shortened, rather massive rostra, *rosseti* being the only described species of the genus to have enlarged basal thumb pads or to have the soles of the feet similarly swollen. The occurrence of pads on the thumbs and feet in the Vespertilionidae was discussed by Hill (1969 : 135). Such pads occur incipiently in *Pipistrellus* and characterize the related genus *Glischropus*, the genera *Eudiscopus* and *Tylonycteris*, and occur in one species of *Hesperoptenus*. All of these, however, are removed from any affinity with *rosseti* by a variety of features of the skull and dentition.



## SUMMARY

The discovery of additional specimens of *Glischropus rosseti* Oey, 1951 has prompted a further examination of the generic affinities of this and the related species *Pipistrellus ridleyi* Thomas, 1898. Variations in the premolar dentition of *Myotis*, *Pipistrellus* and *Eptesicus* are reviewed and it is concluded that the numerical premolar formula is not always an adequate guide to the allocation of species within these genera. As a result of an examination of alternative features in both *ridleyi* and *rosseti*, both species are transferred to *Myotis* as components of the subgenus *Selysius*. Specimens from Sumatra first reported by Schneider (1905 : 80) as *Pipistrellus annectans* Dobson, 1871 (= *Myotis annectans*) and later described in detail under this name by Årnäck-Christie-Linde (1909 : 574) are thought in fact to represent *Myotis ridleyi*, known otherwise only from Malaya.

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BUDAPEST VIII.

# A NEW ACANTHOCEPHALAN FROM AN EAST AFRICAN GALLIFORM BIRD

By M. T. HARRIS

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### 1. SYNOPSIS

A new species of acanthocephalan, *Mediorhynchus selengensis*, is described from the yellow-necked spurfowl (*Pternistes leucoscepus*) in Kenya, and its relationship to other species of *Mediorhynchus* discussed. A brief discussion on the relationship between the genera *Empodius*, *Empodisma* and *Mediorhynchus* is also given.

### 2. INTRODUCTION

THE worms to be described in this paper were amongst a collection of helminths submitted for identification by Mr. John E. Cooper of the Veterinary Research Laboratory, Kabete, Kenya. Thirty-two specimens were obtained from the intestine of yellow-necked spurfowl (*Pternistes leucoscepus*) at Selengai in Kenya. The worms belong to the family Gigantorhynchidae Hamann, 1892, the members of which occur in birds and mammals.

### 3. DESCRIPTION

#### *Mediorhynchus selengensis*, sp. n.

(Figs 1-4)

The male worm measures 11.6-43.0 mm in length and 0.80-2.24 mm in maximum width; females, 11.3-91.5 mm and 0.70-2.75 mm, respectively. The body is fairly long, pseudosegmented in mature specimens, with the anterior portion slightly thinner than the remainder of the body.

The proboscis is cylindrical and composed of an anterior region bearing hooks and a posterior part armed with spines (fig. 1). It was found extruded in only 7 of the specimens, and in these it measures 0.41-0.86 mm in length and 0.35-0.59 mm wide at the base. The hooks are stout and strong with a sharply-curved point, those on the anterior surface of the proboscis being slightly smaller than the remainder (fig. 2). There are 20-22 longitudinal rows of 4-5 hooks. The blades of the hooks measure 0.04-0.07 mm from their base to uppermost point. The base is distinctively winged

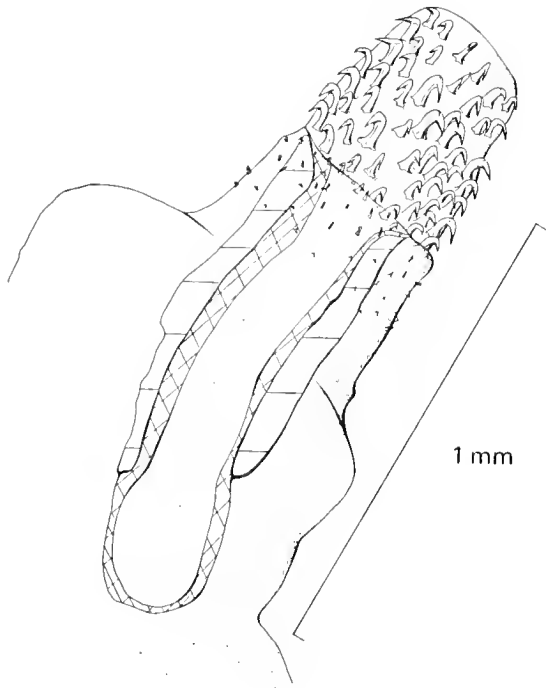


FIG. 1. Anterior region of *Mediorhynchus selengensis*

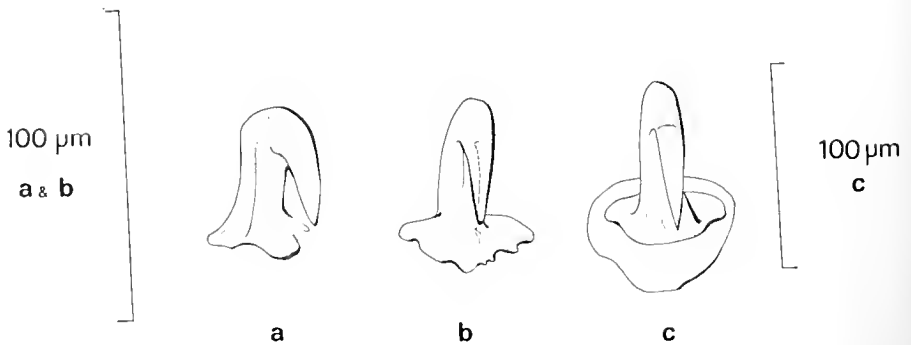


FIG. 2. a, b, c. Large hooks from the anterior part of the proboscis of *Mediorhynchus selengensis*

and surrounded by a strengthening basal-plate on the surface of the proboscis (fig. 2, b and c). The spines form 26-30 longitudinal rows of 2-3 each and their length from base to tip varies between 0.014-0.033 mm. There is a fairly rapid gradation in the size and the shape of the spines, those in the anterior rows being similar in shape to a bill-hook, but more slender, and the form of the posterior spines being almost mere pointed stumps.

The proboscis-sheath is sac-like, but divided into two parts; the anterior portion consisting of a thin, inner layer of longitudinal muscle and a thick outer wall of circular muscle, while the posterior portion has no such outer wall (fig. 1). The entire sheath measures 0.64-1.8 mm in length and 0.11-0.35 mm at its widest point. The nerve-ganglion lies very near to the centre of the sheath. The lemnisci are

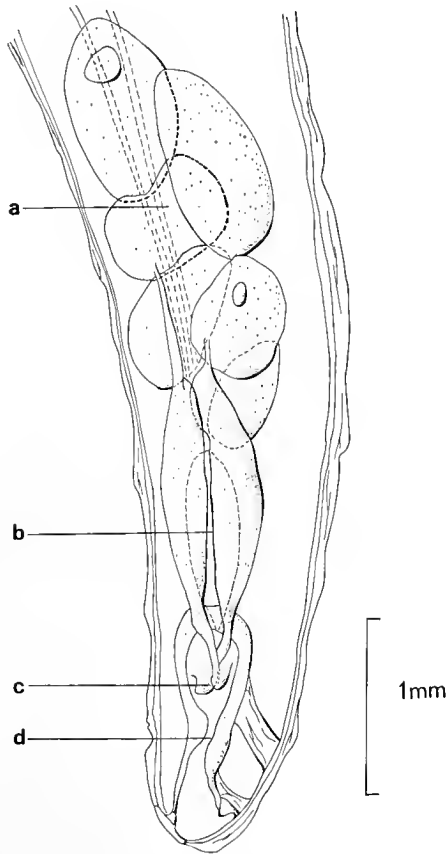


FIG. 3. The male reproductive system of *Mediorhynchus selengensis*. a, cement glands; b, Saeftigen's pouch; c, penis papilla; d, bursa.

slender and often slightly coiled around each other, occupying  $1/7-1/18$  of the length of the body and measuring 1.6-4.9 mm in length and 0.30-0.32 mm wide.

In the male there are two elongate-oval testes situated in the posterior third of the body, measuring 0.9-4.1 mm in length and 0.30-0.97 mm in width. Just posterior to the testes are 8 cement-glands, irregularly disposed and varying in size and shape. The remainder of the male reproductive system and the layout of the female system is typical of the genus (figs 3 and 4). Mature eggs within the uterus measure  $65-75 \mu\text{m} \times 39-48 \mu\text{m}$  and possess a compact granular shell which surrounds the embryonic membrane.

These specimens are deposited in the British Museum (Natural History): B.M. (N.H.) Reg. No. 1972. 1-32.

#### 4. DISCUSSION

The history of the genus *Mediorhynchus* Van Cleave, 1916, was discussed at length by Van Cleave (1947), who regarded the genus *Empodius* Travassos, 1916, as a synonym of *Mediorhynchus*; the four species of *Empodius* described by Meyer (1932) being transferred to *Mediorhynchus*. Yamaguti (1963) appears not to have con-

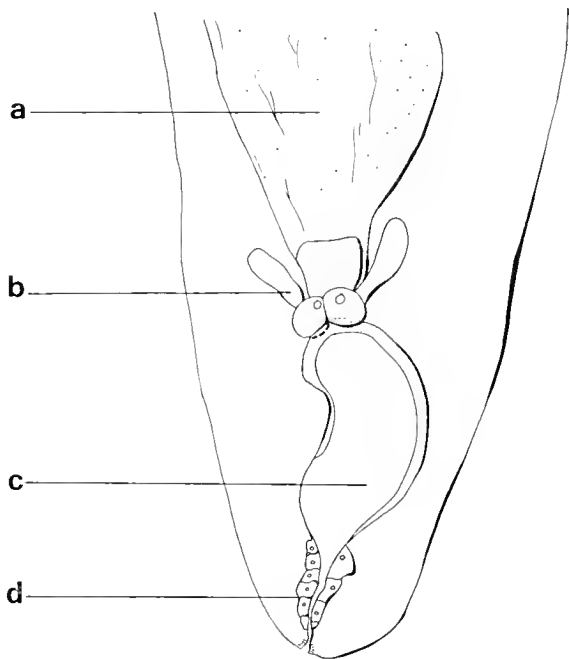


FIG. 4. Diagram of the female reproductive system of *Mediorhynchus selengensis*. a, uterine bell; b, lateral uterine pouch; c, uterus; d, vagina.

sidered the views of Van Cleave and assigned Meyer's species to the genus *Empodisma*, a new name for *Empodius*, except *E. taeniatus* (V. Linstow, 1901) which he listed under *Mediorhynchus*.

More recent authors Bullock (1969) and Byrd and Kellogg (1971) agree with Van Cleave and consider *Empodius* (= *Empodisma*) as a synonym of *Mediorhynchus*. The present writer accepts this conclusion and assigns the above-described specimens to *Mediorhynchus*.

With the exception of *Mediorhynchus garruli* Yamaguti, 1939, from *Garrulus glandarius japonicus* in Japan, the species described above may be readily differentiated from other species of the genus *Mediorhynchus* by the number and arrangement of the proboscis-hooks and spines. In *M. garruli* there are 28-30 rows of 4-5 proboscis-spines, whereas *M. selengensis* has 26-30 rows of 2-3 spines. This feature is constant in all the specimens of the latter species in which the spines are clearly visible. This difference as well as the geographical isolation of the two forms from each other, gives sufficient grounds for considering *Mediorhynchus selengensis* as a new species.

Table 1 shows some of the morphological differences to be found in species of *Mediorhynchus* recorded from African hosts.

The present material came from the intestine of *Pternistes leucoscepus*, but two specimens recovered from *Numida* sp. were also examined and these bear a marked resemblance to *M. selengensis*. In both cases, however, the proboscis is withdrawn and so positive identification is not possible without examination of further material in better condition from the same host-species and locality.

#### 5. ACKNOWLEDGMENTS

I should like to thank Mr S. Prudhoe for his helpful advice and encouragement throughout the course of this study. Thanks are also due to Mr John E. Cooper of the Veterinary Research Laboratory, Kabete, Kenya, for providing the material.

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Species	<i>M. gig</i> (Meyer)	<i>M. leptis</i> Ward, 1966	<i>M. selengensis</i> sp. n.
Length of ♂	35		
Length of ♀	110	6-8	11.6-43.0
Width of ♂	—	6.0	11.3-91.5
Width of ♀	2.5	0.52-0.65	0.80-2.24
Proboscis	anterior 0.35	0.7 0.57-0.77 × 0.5-0.75	0.70-2 0.41-0.86 × 0.35-0.59
Proboscis-hook arrangement	8 S*	18 S* × 6	20-22 × 4-5
Spine arrangement	20	26 S* × 11	26-30 × 2-3
Proboscis-sheath	length 0.3	0.62-0.72 × 0.34	0.64-1.80 × 0.11-0.35
Eggs	66 × m	—	69-75 × 39-48 μm
Locality	East Africa	Egypt	Kenya
Order of avian hosts	Galliformes	Falconiformes	Galliformes

It is notable that the spines have been included with the anterior region of the proboscis is the only part of the species from their descriptions rather difficult.

In the above table

S\* = spiral rows of

TABLE I

Measurements and hook arrangement in some African species of *Mediorhynchus*

Species	<i>M. giganteus</i> (Meyer, 1931)	<i>M. numidae</i> (Baer, 1925)	<i>M. tenuis</i> Meyer, 1931	<i>M. taeniatus</i> (v. Linstow, 1901)	<i>M. huntzi</i> Ward, 1960	<i>M. meiringi</i> Bisseru, 1960	<i>M. wardi</i> Schmidt and Canaris, 1967	<i>M. leptis</i> Ward, 1966	<i>M. selengensis</i> sp. n.
Length of ♂	35.0	17.0	12.0	} 90-115	15-18	74	11-15	6-8	11.6-43.0
Length of ♀	110.0	—	30-33		16-20	124	25-37	6.0	11.3-91.5
Width of ♂	—	1.10	0.5	} 2.5-3.0	0.7	1.56	1.0	0.52-0.65	0.80-2.24
Width of ♀	2.0	—	0.50-0.75		1.0	3.2	1.5	0.7	0.70-2
Proboscis	anterior only 0.35 × 0.4	0.6 × 0.4	0.65 × 0.35	0.86 × 0.4	0.6-0.7 × 0.4	♂ 0.72 ♀ 0.96 length	♂ 655 × 360 ♀ 720 × 515-545 μm	0.57-0.77 × 0.5-0.75	0.41-0.86 × 0.35-0.59
Proboscis-hook arrangement	8 S* × 9	12 × 3	12-14 S* × 9	6 × 5	12-14 S* × 6-8	14-15 d × 12-13	24-26 × 6-8	18 S* × 6	20-22 × 4-5
Spine arrangement	20 × 7	32 × 3-4	25 × 10	12 × 16	20-22 S* × 9-10	—	40 × 4-5	26 S* × 11	26-30 × 2-3
Proboscis-sheath	length 1.0	0.99 × 0.32	—	2.6 × 0.22	0.7-0.9 × 0.2-0.25	♂ 0.97 ♀ 1.75 length	1.0-1.3 × 0.25-0.3	0.62-0.72 × 0.34	0.64-1.80 × 0.11-0.35
Eggs	66 × 34 μm	—	60 × 37 μm	100 × 40 μm (80-106 × 40-52 μm)	—	67 × 41 μm	52 × 29-33 μm	—	69-75 × 39-48 μm
Locality	East Africa	South West Africa	Egypt	South East Africa	Egypt	South Africa	Kenya	Egypt	Kenya
Order of avian hosts	Galliformes	Galliformes	Passeriformes	Galliformes, Gruiformes, Charadriiformes	Charadriiformes	Passeriformes	Passeriformes	Falconiformes	Galliformes

It is notable that certain authors have not delimited and standardised the points between which their measurements were taken. It is evident in some descriptions that the spines have been included with the hooks in working out the proboscis armature, instead of being considered separately. Furthermore, in other descriptions the anterior, hook-bearing, region of the proboscis is the only part of this attachment organ that has been measured, the spiny region having been neglected. These variations of approach make comparison of species from their descriptions rather difficult.

In the above table all measurements given in mm unless otherwise stated.

S\* = spiral rows of hooks

d = diagonal rows of hooks

# SOME ULTRASTRUCTURAL STUDIES ON THE EXCRETORY BLADDER OF *PODOCOTYLE STAFFORDI* MILLER, 1941, (DIGENEA)

By D. I. GIBSON

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## 1. SYNOPSIS

The ultrastructure of the excretory bladder of *Podocotyle staffordi* Miller, 1941, a digenean parasitic in the gut of the flounder *Platichthys flesus* (L.), is described. Crystalline 'excretory corpuscles', not previously recorded in adult digeneans, are shown to be associated with the bladder epithelium. An attempt is made to explain their formation by suggesting that they might have an osmo-regulatory function. This is related to the location of this parasite in the gut of a marine teleost, a region of variable osmolarity.

## 2. INTRODUCTION

VERY few papers have been written on the ultrastructure of the excretory bladder of adult digeneans. Pantelouris and Threadgold (1963) studied the excretory system of *Fasciola hepatica* L. and Erasmus (1967) the reserve bladder of *Cyathocotyle bushiensis* Khan. The reserve bladder of the latter is a modified excretory bladder, and therefore does not conform to the normal digenean morphology. No research appears to have been done on the excretory bladder of digeneans parasitic in the gut of marine teleosts. This group is of special interest because these parasites encounter an environment of varying osmolarity, and thus may have an osmoregulatory problem lacking in the gut-parasites of other vertebrates. The ultrastructure of the excretory bladder of *Podocotyle staffordi* Miller, 1941, from the flounder *Platichthys flesus* (L.) has therefore been examined in an attempt to compare it with that of digeneans from other vertebrates reported on by other workers, and to see if such a study could shed any light on the ability of these parasites to withstand such variations in the osmolarity of their environment.

## 3. MATERIAL AND METHODS

Specimens of *P. staffordi* were obtained from flounders from the Ythan estuary, Aberdeenshire. These specimens were fixed, immediately after removal from the host, in 1 per cent osmic acid in sodium phosphate buffer at pH 7.2 for 1 hour. They

were dehydrated in ethanol, embedded in Epon 812 (Luft, 1961), and polymerised at 60°C for 48 hours. Transverse sections of the whole worms were cut on a Huxley ultra-microtome and mounted on uncoated grids. The sections were then stained for 30 minutes in a 5 per cent solution of uranyl-acetate in 50 per cent ethanol, followed by lead citrate (Reynolds, 1963) for 10 minutes. They were then examined under an A.E.I. E.M. 6B electron microscope at 60 kV.

#### 4. OBSERVATIONS

The bladder-wall of *P. staffordi* consists of a single layer of epithelial cells. These cells are about 0.6  $\mu\text{m}$  in thickness, except in the region of the nucleus where they reached 2  $\mu\text{m}$ . The cells contain a large nucleus, rough endoplasmic reticulum, free ribosomes, mitochondria and three types of possible secretory granule. The endoplasmic reticulum and mitochondria are especially preponderate in the region of the nucleus (plate 1B). The three types of possible secretory granule (plates 1A & E) are as follows: type A, very granular, electron dense, about 150 nm in diameter, surrounded by a membrane and may be discoid; type B, round, slightly or non-staining, 50 nm in diameter, and occur close together in large numbers, often appearing to join and form long parallel canals (plate 1A); and type C, osmophobic or containing a slightly granular material, 200–300 nm in diameter, and occasionally appearing to release their contents into superficial vacuoles (plate 1C). Occasionally tubular or sheet-like invaginations of the inner plasma-membrane can be seen to pass deep into the cell (plate 1B): these are similar to the structures recorded by Davis *et al.* (1968) in the gastrodermal cells of *Haematoloechus medioplexus* Stafford, 1902. From the luminal surface of these cells project microrugae (leaf-like processes similar to those found in the gastrodermis of digeneans) which have bent over and anastomosed either with each other or with the outer plasma-membrane to form superficial vacuoles (plates A, B, D & E). Inside many of the superficial vacuoles are large crystalline corpuscles formed in concentric layers (plate 1A). These 'excretory corpuscles' vary in size to as much as 7  $\mu\text{m}$  in diameter. Much of the luminal surface of the bladder is covered by superficial vacuoles.

Beneath the basal plasma-membrane is a basement membrane and a wide region of interstitial matrix (plates 1 A, B, D & E). Beneath these are layers of circular and longitudinal muscle (plate 1B), which are frequently interspersed with what appear to be cytoplasmic connections between the bladder epithelium and the sub-epithelial cells. Type B and C secretory granules can be seen passing along these connections (plates 1 A, D & E).

The bladder epithelium does not give a positive reaction to the modified coupling azo dye method of Pearse (1960) for alkaline phosphatase activity, but the excretory ducts do.

#### 5. DISCUSSION

The presence of 'excretory corpuscles' in the excretory bladder of digeneans has been noted by Erasmus (1967) in the metacercariae of *Cyathocotyle bushiensis* and by Martin and Bills (1964) in the metacercariae of *Acanthoparyphium spinulosum*

Johnston, but were not mentioned by Pantelouris and Threadgold (1963) in their study of the excretory system of *Fasciola hepatica*. Erasmus (1967) noted that these corpuscles were soon lost when the metacercariae entered the definitive host. Their presence, therefore, in adult Digenea does not appear to have been recorded previously. Their suggested function in metacercariae, according to Erasmus (1967), is for carbon dioxide fixation and the storage of phosphates. This is similar to some of the suggested functions of calcareous corpuscles in cestodes (von Brand *et al.*, 1965). The ultrastructure and formation of the corpuscles from the metacercariae of *A. spinulosum* was described by Martin and Bills (1964). The presence of these corpuscles in adult *P. staffordi* is not unique, as I have also found them similarly positioned in *Hemiuirus ocreatus* (Rud.), a totally unrelated digenean from the gut of the flounder.

The question therefore arises, why, in respect of the 'excretory corpuscles', are *P. staffordi* and *H. ocreatus* different from the species studied by other authors? In adult *C. bushiensis* the bladder-epithelium is associated with lipid excretion, but there was no evidence for the presence of lipids in the bladder-epithelium of *P. staffordi*. According to Erasmus (1967) lipid excretion was not necessarily associated with the microrugae; but he did not attempt to postulate a function for these structures, though at the electron microscope level he did show that they possessed alkaline and acid phosphatase activity. The apparent lack of alkaline phosphatase activity in the bladder-epithelium of *P. staffordi* could be due to a less sensitive technique. With regard to the 'excretory corpuscles', the difference, if carbon dioxide fixation is a function, between the aerobic conditions in the gut of the flounder and those in the gut of a duck, the definitive host of *C. bushiensis*, must be very small, as in both cases the oxygen tension is very low (my own preliminary experiments; Crompton *et al.*, 1965). This cannot be directly responsible for the corpuscles therefore. As mentioned above, one significant difference is that digeneans parasitic in the gut of marine teleosts are subject to an environment of varying osmolarity. This variation is caused by the need of marine teleosts to swallow sea-water. The osmolarity of the body-fluids of *P. staffordi* are probably hypotonic to that of the gut, as when food is not present in the gut it moves back to the regions of the gut with the lowest osmolarity (MacKenzie and Gibson, 1970), and it appears to survive longest *in vitro* in an environment with a lower osmolarity than is normally found in the flounder gut (unpublished results). The parasites may, therefore, have to absorb water or actively lose salts in order to keep the osmolarity of its body-fluids down. These corpuscles may be a means to that end, in addition to having a carbon dioxide fixing function. It is possible to imagine the mixing of two salts in the superficial vacuole in such a way that the solubility product of one of the salts produced in the mixture is exceeded, especially when, as shown by MacKenzie and Gibson (1970), the concentrations of magnesium and calcium ions in the flounder gut are built up to a high level as water and the monovalent ions are absorbed from the swallowed sea-water (crystals free in the lumen of the flounder gut have often been observed). That such a mechanism could occur is supported by an analysis of the chemical composition of the 'excretory corpuscles' of the metacercariae of *A. spinulosum* by Martin and Bills (1964), which showed a high calcium

carbonate content, and of the calcareous corpuscles of cestodes (von Brand *et al.*, 1967), which have a high magnesium, calcium, carbonate and phosphate content. In addition, it is difficult to imagine how else these corpuscles could be formed without postulating the active uptake of water. It is therefore possible to postulate, on the above evidence, that these 'excretory corpuscles' might be formed thus:

- (1) vacuoles containing salts such as sodium carbonate (fixed carbon dioxide) are formed in the sub-epithelial cells, and are passed to the bladder epithelial cells via the cytoplasmic connections (suitable vacuoles, such as the type C secretory granules, are visible in these cells);
- (2) the superficial vacuoles are formed by anastomosis of the microrugae with the outer plasma-membrane of the cell and with each other, thus entrapping fluid from the lumen which may contain calcium and magnesium ions;
- (3) the contents of the secretory vacuoles are released into the superficial vacuoles (what appear to be type C secretory granules releasing their contents are shown in plate 1C);
- (4) the salts in the superficial vacuoles mix, and, as the solubility products of salts such as magnesium and calcium carbonate are soon reached, they crystallize out of solution;
- (5) further growth of the corpuscles could be obtained by the release of more secretory vacuoles into the superficial vacuoles and by anastomosis of further microrugae with the wall of the superficial vacuole (this, and variations in the solubility products in different salts, might account for the concentric nature of the corpuscles);
- (6) once these salts have precipitated the osmolarity in the superficial vacuole will fall and water can be re-absorbed by the cell via the outer plasma-membrane and microrugae by osmosis (at the base of the bladder epithelial cells vacuoles, perhaps type B secretory granules, might transport this water to the sub-epithelial cells);
- (7) eventually the microruga around the corpuscle breaks away from the epithelial cell, and the corpuscle passes through the excretory pore.

The parasite, therefore, may be able to use these corpuscles to lose fixed carbon dioxide and unwanted ions and, at the same time, reclaim water from the lumen of the excretory bladder. If such a mechanism is involved, it is probably evolved from the carbon dioxide fixing corpuscles of the metacercariae, which, due to the presence of high concentrations of calcium and magnesium ions in the gut of marine teleosts, have been retained in these adult digeneans.

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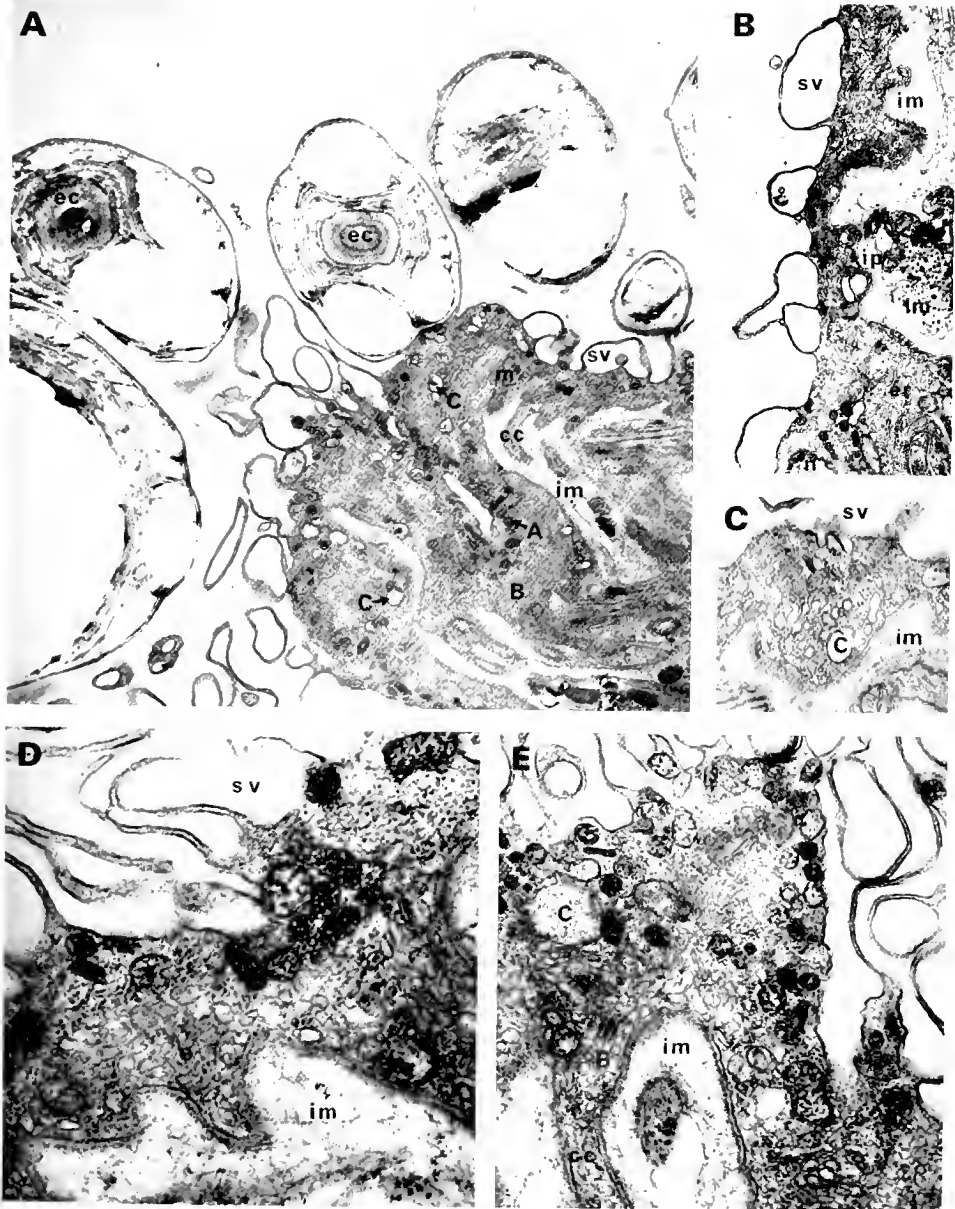
PLATE 1

The ultrastructure of the excretory bladder of the adult *Podocotyle staffordi*.

- A. Section of bladder epithelium showing 'excretory corpuscles'. ( $\times 8000$ ).
- B. Section of bladder epithelium showing that the cells are thicker in the region of the nucleus. ( $\times 10\ 000$ ).
- C. Possible release of secretions from bladder epithelial cells. ( $\times 17\ 000$ ).
- D. & E. Projections of bladder epithelial cells possibly connecting sub-epithelial cells. ( $\times 31\ 000$ ).

(A, secretory granule; B, secretory granules; C, secretory granule; cc, cytoplasmic connection; ec, 'excretory corpuscle'; er, endoplasmic reticulum; im, interstitial matrix; ip, invaginations of plasma-membrane; lm, longitudinal muscle; m, mitochondrion; n, nucleus; sv, superficial vacuole).







# SHELL ULTRASTRUCTURE IN ALLOGROMIID FORAMINIFERA (PROTOZOA)

By R. H. HEDLEY C. G. OGDEN and J. Sr J. WAKEFIELD

## INTRODUCTION

THE form and structure of calcified or agglutinated foraminiferal shells are important in the classification of Foraminiferida and, as a consequence, have been the subject of extensive studies. In contrast, the structure of tectinous or purely organic foraminiferal shells has received relatively less attention. Since the subject was reviewed by Hedley (1964) a number of morphological studies of tectinous forms, using transmission electron microscopy, have been published which include brief descriptions of shell-structure: for example, *Shepherdella taeniformis* (Hedley *et al.*, 1967), *Allogromia laticollaris* (Lengsfeld, 1969; Schwab, 1970) and *Myxotheca arenilega* (Schwab, 1969; Angell, 1971).

The present account describes the shell-structure of six additional tectinous foraminiferans and attempts to relate some aspects of the fine structure to the functioning of the shell in the living animal.

## PREVIOUS WORK

The ability of some tectinous foraminifera to alter their shape appears to have been initially reported by Cushman (1920), after examining *Iridia diaphana*. Morphological variants of *Allogromia laticollaris* are described by Arnold (1954a), who reported that young animals appear to be more flexible than older individuals. Recently freed schizonts, for example, are characterised by erratic distension and contraction at localised points at the periphery of the shell. Similar movements have been observed in an unnamed *Allogromia* sp., which varied in shape from ovoid to elongate, bioral, 'Shepherdella-like' forms (Lee & Pierce, 1963). These authors note that such irregular forms are very plastic and continually change shape. *Shepherdella taeniformis* and *Boderia turneri* are capable of great and rapid change in form (Hedley, 1964 and Hedley *et al.*, 1968).

Wohlfarth-Bottermann (1961) in an account of the fine-structure of *Allogromia laticollaris* comments on the occurrence of fine pores in the shell with cytoplasmic threads running through them. He does not, however, comment on the nature or structure of the shell wall material itself. Lengsfeld (1969) describes the shell of *A. laticollaris* as being composed of filament-like elements embedded in a glue-like substance; the filaments being arranged parallel to the surface of the cell with the outermost layer appearing to be coarsely granular. Schwab (1969) describes the shell of both young and adult specimens of *Myxotheca arenilega* as being composed of fibrous-like material. In adult specimens the wall is divided into two layers of unequal thickness, the outer layer being thin and osmophilic, whilst the inner layer

is thick and composed of fibrous material lying parallel to the cell surface. He further suggests that this material is formed in the Golgi apparatus. A report by Angell (1971) describes the test of *Myxotheca* sp. as being composed of fibrous material, of undetermined chemical composition, but having a 'herring-bone' pattern. He also suggests that these fibres originate from vacuoles at the inner edge of the test wall. The shell of *Shepherdella taeniformis* is described by Hedley *et al.* (1967) as having a fibrous component which is not recognised as being orientated in any way. In a detailed study of the fine structure of *Gromia oviformis*, which occupies a rather enigmatic position in the classification of the Protozoa, the organic shell consists of three distinct regions (Hedley & Wakefield, 1969). These are an outer region composed of fine fibres with an electron-dense outer layer, a middle region of complex honeycombed membranes and an inner region of fibrillar material. The fine fibrillar elements of both the inner and outer regions appear to be morphologically similar.

Numerous workers (Moss, 1963; Hedley, 1962, 1963; Pierce *et al.*, 1968; Angell, 1967 and Hedley & Wakefield, 1969) recognise the organic wall of the tectinose foraminifera as being composed of protein and acid mucopolysaccharides. Attempts have been made to define the composition of some of these organic shells using cytochemical methods (Angell, 1967, and Pierce *et al.*, 1968) and amino-acid analysis (Hedley & Wakefield, 1969). Nevertheless, the precise composition remains obscure because of the technical difficulties in isolating this material from the cytoplasm of the animal, and because of the limited value of the cytochemical and other methods employed so far.

#### MATERIALS AND METHODS

The animals used and discussed in this paper are as follows:

*Allogromia laticollaris* Arnold, 1948

—maintained in this laboratory for several years from cultures established from collections from Panama City, Florida, U.S.A. by Professor Z. M. Arnold.

*Allogromia* sp. A and B

—isolated from tufts of the inter-tidal calcareous alga *Corallina officinalis* at Plymouth, England

*Allogromia* sp. C

—isolated from tufts of *Corallina officinalis* from Wellington, New Zealand.

*Iridia diaphana* Heron-Allen & Earland, 1914

—isolated from sandy sediment, 5 fm, from Plymouth, England.

*Boderia turneri* (Wright, 1867)

—isolated from tufts of *Corallina officinalis* from Plymouth, England.

The cultures are kept at room temperature, 18–20°C, in small plastic containers and maintained on Foyn's Erdschreiber medium (Arnold, 1954b). The animals are sub-cultured regularly every five or six weeks and are fed weekly on freshly killed *Tetraselmis chui*. Under these conditions the animals appear to feed and reproduce readily, with the exception of *Allogromia* sp. A, *Boderia turneri* and *Iridia diaphana* which remain alive and active for about four months, but do not appear to grow or

reproduce under these laboratory conditions. We are unable to distinguish specifically between the three forms A, B and C of *Allogromia* but the characters which appear to be significant are detailed in Table 1.

### Electron Microscopy

The standard fixation and embedding used for these species is as follows. Specimens are fixed in 4 per cent glutaraldehyde in 0.1 M cacodylic acid buffer with 0.25 M sucrose for 3 h at pH 7.0. After several washes in buffer, they are post-fixed in Caulfield's osmium tetroxide followed by rapid ethanol dehydration and finally embedded in Epon 812. One naked specimen of *Iridia diaphana* which had left its 'tent' and was observed to become an elongate form (Text-fig. 1), was fixed *in situ* in the plastic culture vessel with 4 per cent glutaraldehyde in equal parts of 0.1 M cacodylic acid buffer with 0.25 M sucrose and sea-water, pH 7.4, for forty-five minutes, washed with several changes of equal parts of buffer and sea-water, post-fixed with 1 per cent osmium tetroxide in 0.1 M cacodylic acid buffer, followed by rapid ethanol dehydration and embedded in Epon. Sections were cut with a diamond knife (Du Pont) on a Porter-Blum Mt 2 ultramicrotome, stained with a saturated alcoholic solution of uranyl acetate followed by Reynold's lead citrate. All the micrographs were obtained from an AEI EM 6B microscope operating at 60 kV and recorded on either Ilford's N50 or 'special lantern contrasty' plates.

## RESULTS

### *Allogromia laticollaris*

The shell appears to be divided into two distinct regions: an outer, thin, electron-dense region 0.4 to 1.0  $\mu\text{m}$  thick and an inner fibrillar region 1.8 to 3.0  $\mu\text{m}$  thick (Pl. 1, fig. A). In those animals examined the shell varies in thickness from 2 to 4  $\mu\text{m}$ , but it can vary between 4 and 38  $\mu\text{m}$  in thickness, according to Pierce *et al.* (1968). The outer region is composed of concentrations of electron-dense material with a fine fibrillar network interspersed. The inner region is composed of a mass of fine fibrillar material which appears to be organized into layers. In cross-sections of the wall the fibrils appear to be aligned parallel to the cell surface, and occasionally they are arranged to produce a 'herring-bone' pattern (Pl. 1, fig. A). In tangential section the fibrils appear to be arranged at random. The fibrils are approximately 4 nm thick and the electron-dense points are approximately 14 nm in diameter. The diameter of these points is similar to that found in the electron-dense region.

### *Allogromia* sp. A.

The shell is divided into three distinct regions, an outer, intense, electron-dense region 0.01 to 0.04  $\mu\text{m}$  thick, and two inner regions both composed of fibrillar material (Pl. 1, fig. B). The outermost fibrillar region is 0.1 to 0.5  $\mu\text{m}$  thick and is composed of closely packed fibrils which are randomly orientated, whilst the inner region is 1.0 to 3.5  $\mu\text{m}$  thick and composed of fine fibrils which usually lie parallel to the shell surface, but are occasionally arranged to produce a 'herring-bone' pattern such as is found in *A. laticollaris*. The electron-dense points in the fibrillar material

have a similar diameter to the fibrils seen in longitudinal cross-section and are probably cross-sections of them.

The pronounced corrugated appearance of the shell (Pl. 1, fig. C), is not seen in any other species of *Allogromia* which we have examined.

#### *Allogromia* sp. B.

The fine structure of the shell is similar to that found in *A. laticollaris* with the exception of some slight corrugations of the external electron-dense layer. In young schizonts of these animals the fibrillar material and the electron-dense material appear to be distributed at random (Pl. 1, fig. D). As the young schizonts mature, however, the electron-dense particles are arranged in a thin, clearly defined outer layer, that appears to delimit the shell of the animal. The fibrils of the fibrillar layer are then arranged parallel to the surface. The shell of the parent surrounding the schizonts appears to become less compact with the components of both shell layers being dispersed. At this time degeneration of the parent shell is apparent.

#### *Allogromia* sp. C.

The fine structure of the shell is similar to that of *A. laticollaris*.

#### *Iridia diaphana*

This species is unusual in having two organic shells, one adjacent to the plasma membrane, and the other a tent-like covering at some distance from the animal (Le Calvez, 1936). This latter covering is only associated with sessile forms and is left behind when the animal moves away. It consists mainly of diatoms and other siliceous elements held together by a network of fibrils which are of a similar nature to those found in the main shell.

The true shell of *I. diaphana*, comparable with that of *Allogromia*, is composed of only one fibrillar layer (Pl. 2, fig. A). It varies between 0.8 and 3.3  $\mu\text{m}$  in thickness, with the fibrils usually lying parallel to the shell surface, but occasionally appearing to be swept together to form the 'herring-bone' type of pattern (Pl. 2, fig. B). The electron-dense points seen amongst the fibrils, are probably cross-sections of fibrils, as they have a similar diameter.

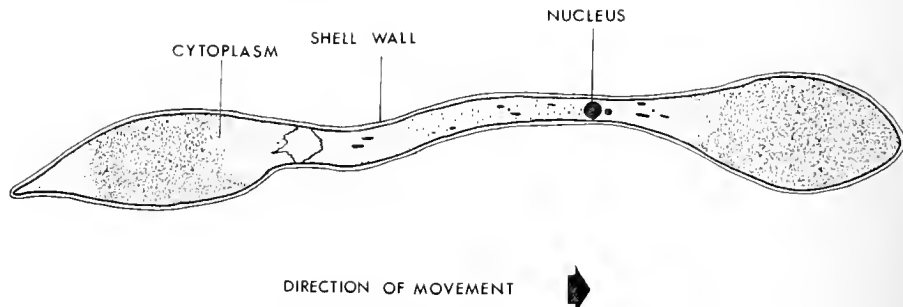


FIG. 1. Diagram of the elongated specimen of *Iridia diaphana*, referred to in the text at the time of fixation.

A specimen of this species was fixed in gluteraldehyde whilst it was moving and changing shape (Text-fig. 1). The structure of the shell in this animal consists of one fibrillar layer (Pl. 2, fig. C) which differs from those in other animals previously discussed here in that constituent fibrils are smaller. These fibrils are arranged at random in both cross and tangential sections.

#### *Boderia turneri*

The shell varies between 0.4 and 1.0  $\mu\text{m}$  in thickness. It is composed of only one layer, a fibrillar layer composed of small fibril elements (Pl. 2, fig. D), similar to those seen in the moving specimen of *Iridia diaphana*.

### DISCUSSION

The observations reported here throw light on two aspects of shell structure in tectinuous foraminifera. Firstly, the evidence suggests that differences exist between the ultrastructural organisation within the shell of actively moving as compared with inactive individuals and secondly, clear differences exist in the ultrastructure of shells of animals which are very similar when examined by optical microscopy alone.

For the purpose of this discussion, the animals examined can be divided into three groups on the basis of their gross shape. Animals belonging to the first group have a relatively constant shape and a fixed aperture position, and include *Allogromia laticollaris*, *Allogromia* sp. A, *Allogromia* sp. B, and *Allogromia* sp. C. In these animals the wall is composed of long thin fibrils arranged parallel to the shell surface and often organized into a herring-bone pattern (Pl. 1, figs A & B). A thin electron-dense layer is usually present at the periphery of the shell. It is worthy of note that adult specimens of *Gromia oviformis*, although not necessarily related to the forms under discussion, also have this type of organic wall (Hedley & Wakefield, 1969).

Animals belonging to the second group usually have a constant shape and aperture position, but under certain conditions they change both. Such a change can take place very rapidly and is typical of *Shepherdella taeniformis* and *Iridia diaphana*. When the shell of these animals is similar to that of the constant shape forms they have a similar ultrastructural organization to them except that the electron-dense peripheral region is either reduced, as in *Shepherdella taeniformis* (Hedley *et al.*, 1967, fig. 3) where it has a minimal thickness, or is absent as in *Iridia diaphana* (Pl. 2, fig. A). When the shell undergoes change in shape as in *Iridia diaphana* the wall has a variable thickness with the fibrils being short, thick, and arranged at random (Pl. 2, fig. C).

Animals belonging to the third group have a constantly changing shape, no apparent aperture and pseudopodia arise from any position of the body surface. A representative of this group is *Boderia turneri* (Pl. 2, fig. D), in which the ultrastructure of the shell resembles that of the moving form of *Iridia diaphana*.

It appears from these observations that differences in the fibrous element of the shells may be correlated with the state of movement in these allogromiids. The short, thick, fibrils in the shell being the form that is associated or correlated with

animals undergoing rapid movement and change in form, whilst the thin, long fibrils are associated with the stable or non-changing state of the shell. In the case of animals capable of changing their shape, for example, *Iridia diaphana*, the short fibrils present in the shells of active animals are presumably transformed into the long fibrils characteristic of inactive forms. These ultrastructural differences between the shells of inactive and active animals of the same species emphasize the need for careful observation of the physical state of the animal at the time of fixation.

The four forms of *Allogromia* studied here appear to be similar in many respects (Table 1). The greatest similarity at the optical level is between *Allogromia latcollaris* and *Allogromia* sp. A. Nevertheless, the fine structure of the shell of *Allogromia* sp. A is seen (Text-fig. 2b, Pl. 1, fig. B) to differ from the other three forms (Text-fig. 2a, Pl. 1, fig. A), by having a compact electron-dense outer region, whilst the remainder of the shell ultrastructure is basically similar (compare Text-figs 2a & b) in all four forms. This feature alone is not sufficient to enable one to differentiate between the forms. However, it would appear to indicate that such details of fine structure of the shell wall (Table 2), could be used as specific characters. A combination of the type of detail listed in Tables 1 & 2 could possibly provide the basis for future identifications.

As the tectinous shell of allogromiid foraminifera lies outside the plasmalemma but remains attached to its outer surface, we regard it as representing a modified glycocalyx as defined by Bennett (1969). He has reviewed the structure and function of various glycocalyxes associated with numerous cell types, including protozoa.

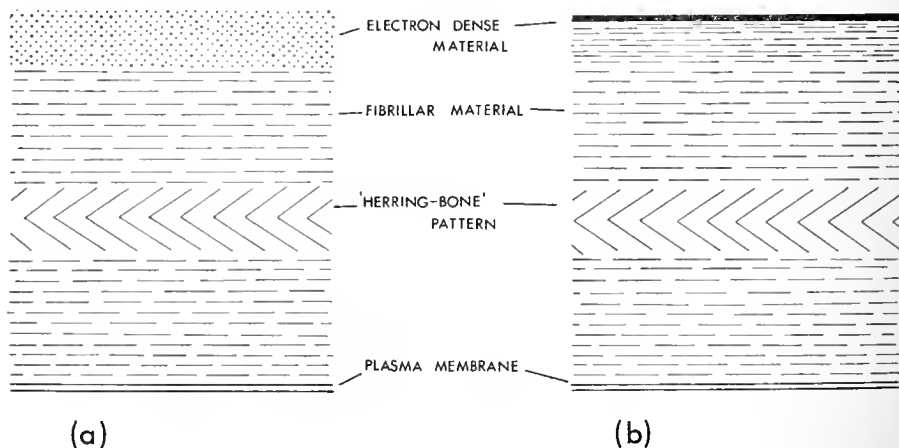


FIG. 2. Diagram of the different arrangements of shell material in forms of *Allogromia*—(a) shell with diffuse electron-dense region; (b) shell with thin compact electron-dense region overlying a region of concentrated fibrillar material. Note that the main fibrillar region is similar in both examples.



From this it would appear that the allogromiid glycocalyx has some affinities with the mucous coat glycocalyces in amoeba.

The permeable nature of such glycocalyces not only allows them to act as effective filters (Bennett, 1963), but in addition they can serve as molecular sieves. For instance, various organic materials can be bound to the strongly anionic polysaccharides of the glycocalyx and they can also be impregnated with inorganic crystals. This property of the glycocalyx, may explain the selective retention of organically bound ferric iron found by Hedley (1960) in the shell of *Gromia oviformis*, and possibly the electron-dense region of the forms described here. Moreover, it also allows the retention of enzymes in the space between the cell and the glycocalyx, which could enable enzymatic changes to occur at the cell surface. This would perhaps facilitate the transformation of the shell ultrastructure in those animals which change rapidly from sessile to active forms.

TABLE I

Observed differences of four forms of *Allogromia* based on specimens maintained under culture conditions

	<i>Allogromia laticollaris</i> U.S.A.	<i>Allogromia</i> sp. A Plymouth England	<i>Allogromia</i> sp. B Plymouth England	<i>Allogromia</i> sp. C New Zealand
Maximum size (in $\mu\text{m}$ )	400	450	1000	200
General colour	orange-pink	orange-pink	green-yellow	orange-brown
General shape	spherical	pear-like	spherical to elongate <i>Boderia</i> -like	spherical
Maturing time*—in weeks	3-4	No information	8	4
Number of schizonts	30-40	No information	50-500	30-50

\* Time taken by young schizont to mature

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TABLE 2

Details of the ultrastructure of shells of several tectinous foraminifera

Reference	<i>Allogromia</i> <i>laticollaris</i>	<i>Allogromia</i> sp. A	<i>Allogromia</i> sp. B		<i>Allogromia</i> sp. C	<i>Myxotheca</i> <i>arenilega</i>		<i>Shepherdella</i> <i>taeniformis</i>	<i>Iridia</i> <i>diaphana</i>	<i>Boderia</i> <i>turneri</i>	<i>Gromia</i> <i>oviformis</i>			
	Lengsfeld, 1969 Schwab, 1970 present work	present work	present work	schizont	adult	present work	Schwab, 1969 Angell, 1971	schizont	adult	Hedley <i>et al</i> , 1967	present work sessile	present work active	present work	Hedley & Wakefield, 1969
Electron-dense material—diffuse	+	-	-	+	+	-	+	+	-	-	-	-	-	-
Electron-dense material—intense	-	+	-	-	-	N.A.	N.A.	-	-	-	-	-	-	+
Long fibril structure	+	+	+	+	+	+	+	+	+	-	-	-	-	+
Short fibril structure	-	-	-	-	-	-	N.A.	N.A.	-	-	+	+	+	-

N.A. = information not available  
 + = structure present  
 - = structure absent

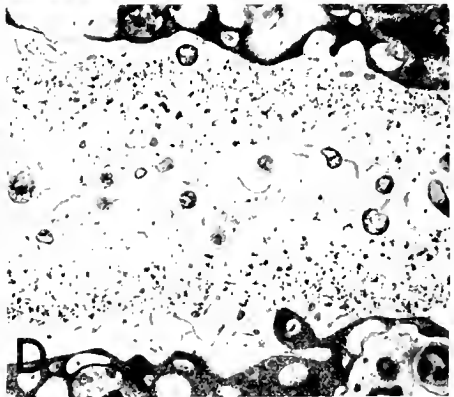
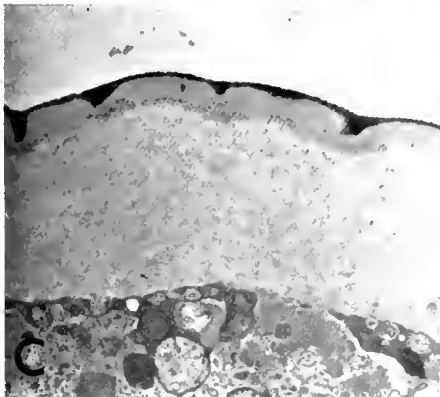
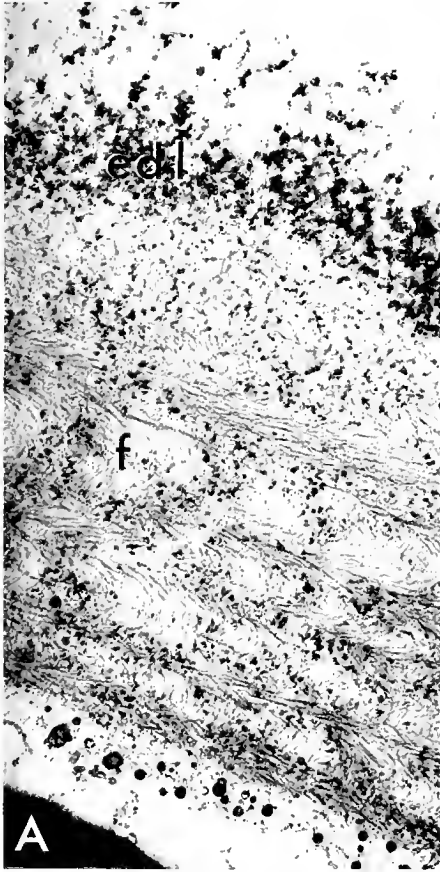
PLATE I

FIG. A. Cross-section of the shell of *Allogromia laticollaris*, showing outer electron-dense layer EDL and inner fibrillar layer F.  $\times 31\ 300$

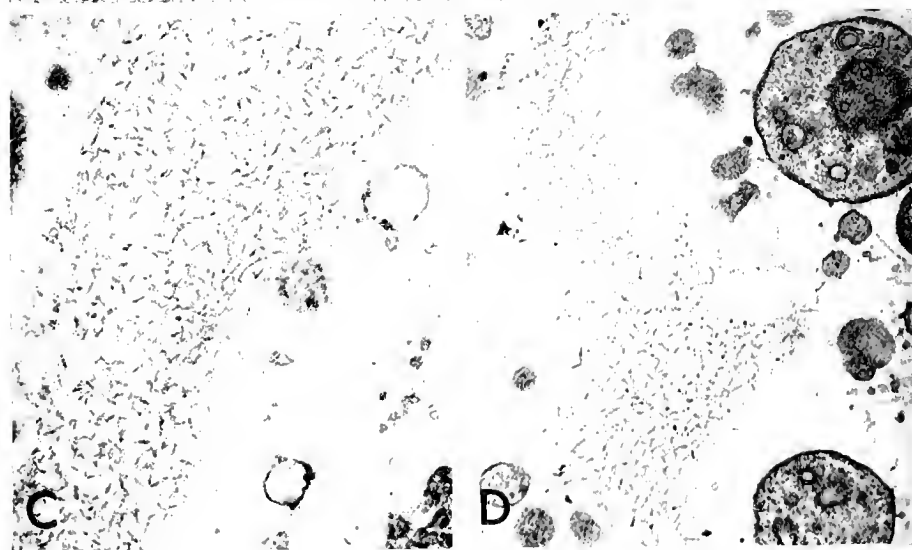
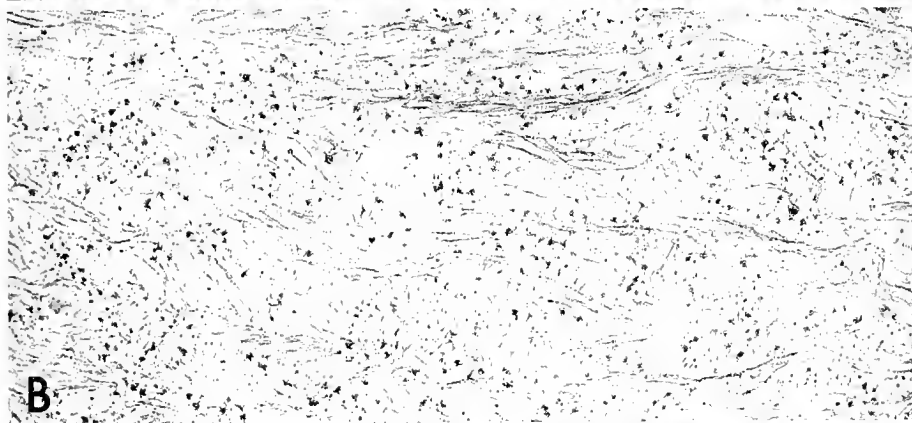
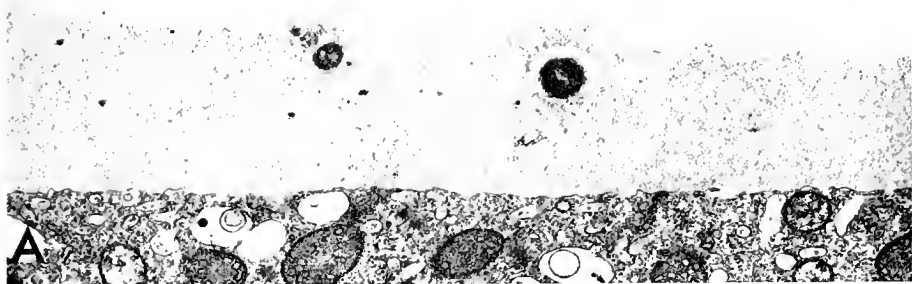
FIG. B. Section of the shell of *Allogromia* sp. A. Note the intense electron-dense layer, EDL, and the two fibrillar layers F<sub>1</sub> & F<sub>11</sub>.  $\times 51\ 200$

FIG. C. General view of shell of *Allogromia* sp. A., showing corrugated appearance of outer layers.  $\times 10\ 000$

FIG. D. Cross-section through the shell walls of two adjacent schizonts within the parent shell of *Allogromia* sp. B.  $\times 17\ 200$









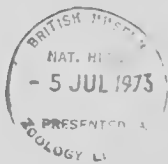




A LIST OF SUPPLEMENTS  
TO THE ZOOLOGICAL SERIES  
OF THE BULLETIN OF  
THE BRITISH MUSEUM (NATURAL HISTORY)

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1. KAY, E. ALISON. Marine Molluscs in the Cuming Collection British Museum (Natural History) described by William Harper Pease. Pp. 96; 14 Plates. 1965. (Out of Print.) £3.75.
2. WHITEHEAD, P. J. P. The Clupeoid Fishes described by Lacepede, Cuvier and Valenciennes. Pp. 180; 11 Plates, 15 Text-figures. 1967. £4.
3. TAYLOR, J. D., KENNEDY, W. J. & HALL, A. The Shell Structure and Mineralogy of the Bivalvia. Introduction. Nuculacea-Trigonacea. Pp. 125; 29 Plates, 77 Text-figures. 1969. £4.50.
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