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The deep-sea Ophiuroidea of the North Atlantic Ocean

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Synopsis

The North Atlantic deep-sea ophiuroid fauna, comprising of approximately 120 species, is revised for the first time. Proposals for the revision of the family Ophiacanthidae are made and four sub-families are erected. The present purely taxonomic treatment relies on a series of pictorial keys aimed at the non specialist.

Introduction

The recent interest in deep-sea biology has highlighted the need for a taxonomic reappraisal in many animal groups. In all but a few our taxonomic knowledge is based on expedition reports dating back often more than 50 years. Such reports are not comprehensive, and may be difficult to obtain, so that identifications require a large library. With the modern emphasis in deep-sea studies on ecology, population biology and biological processes generally, good taxonomic information is essential.

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The aim of this study is to revise the abyssal ophiuroids of the North Atlantic portraying the species likely to occur within this area so as to fascilitate identification by the non specialist. Within the study area there are about 120 species including several new records for the North Atlantic.

The boundries of the study area are more of convenience than purely zoogeographical, because of the paucity of material from certain regions. So the area is taken to be that south of the Shetland-Iceland-Greenland ridges as far as Cap Blanc in the eastern Atlantic and the Demerara Abyssal Plain in the west. This is approximately equivalent to the abyssal provinces C1 and C2 proposed by Menzies, George & Rowe (1973) or the 2B abyssal zones proposed by Vinogradova (1979).

The upper bathymetric limit is *c.* 1000 m, following the scheme proposed by Menzies, George & Rowe (1973). This corresponds to the Archibenthic Zone of Transition in the eastern Atlantic and to the Abyssal Province in the west. The Abyssal Province begins around 2000 m in the east. Since many ophiuroids are eurybathic these bathymetric limits are only guidelines. In some families species have been included from the upper slope in the avent of overlapping bathymetric ranges. Also hydrographic factors may influence distributions: for example in the Rockall Trough the influence of Norweign Sea overspill water is thought to extend upwards the distribution of certain species commonly associated with the lower abyssal zone (Gage *et al.*, 1983). It is also noticeable that pan Atlantic species have a shallower upper bathymetric limit in the west than in the east, possibly due to the effects of the Western Boundary Current.

This paper is based on extensive collections made by three institutions: The Centre Oceanologique de Bretagne—Biogas investigations in the Bay of Biscay, Biovema in the Vema Fracture Zone, Demeraby in the Demerara Abyssal Plain and the INCAL cruise in conjunction with the IOS and SMBA in the NE Atlantic; the Institute of Oceanographic Sciences—*Discovery* Investigations off North Africa and in the Porcupine Seabight; the Scottish Marine Biological Association's investigations in the Rockall Trough. Type specimens of most species were also examined together with material in the collections of the BMNH. A list of the specimens studied, together with their register numbers, and a photograph of each species have been deposited in the Echinoderm Section, BMNH.

Biology

Our knowledge of life histories of most deep-sea ophiuroids is poor (see Tyler, 1980 for a review) although in recent years there have been several accounts of the reproductive biology of the more common species (Schoener 1968, 1972; Tyler & Gage 1979, 1980, 1982; Gage & Tyler, 1981, 1982) together with some work on the post-larval stages (Schoener 1967, 1969; Gage & Tyler 1981). Accordingly this study is limited to taxonomic aspects.

Little has been done on the ecology of deep-sea species apart from observations on certain conspicuous species such as *Ophiomusium lymani* in the course of more general studies (Barham *et al.* 1967; Rowe, 1971; Menzies, George & Rowe, 1973; Grassle *et al.* 1975 and Haedrich *et al.* 1975). Detailed treatment of the ophiuroid fauna of the Bay of Biscay has been carried out by Paterson, Lambshead & Sibuet (1985) and Gage *et al.* (1983) have discussed aspects of ophiuroid distribution in the Rockall Trough.

There are little data on the nutrition of abyssal ophiuroids (Litvinova & Sokolova 1971, Litvinova, 1980) or of their predators or parasites.

Taxonomic keys

Review. Traditionally most taxonomic works employed dichotomous keys for identification of the taxa involved. There is, however, a growing feeling amongst users that these are far from adequate in aiding quick accurate identifications and can be misleading when taxa new to the area or to science are being identified.

In recent year there have been several attempts to produce new kinds of keys. A key in this context is taken in its widest definition—an artificial system for identifying animals or plants; the term key should not be restricted to the dichotomous kind. An improvement to the basic dichotomous key is the illustration of the individual characters in the couplet: for examples see Bayer (1961) or Grasshoff (1973, 1977). Keys produced by the Field Studies Council under their AIDGAP scheme are also of this kind and have the advantage of being tested before they are published.

This sort of key is taken to an ultimate conclusion in the keys associated with the San Francisco Bay project. Instead of couplets the information is presented in the form of a pictorial flow diagram. Light (1976) highlighted the problems associated with specialist dichotomous keys and proposed this pictorial alternative.

The tabular key has also been developed as an alternative to the traditional kind. Such keys were pioneered by Newel (1953) for mites. Here a series of characters represented by letters or symbols are presented for comparison, usually arranged in tabular form. The specimen for identification is examined with regard to a series of relevant characters and the resulting list compared with the table. The advantage of this form of key is that several different characters are compared together so that if one or more is missing, closeness of fit to the list can be used to gain an identification. The other feature of these keys is that the actual characters which separate the species can easily be assessed; helping both to improve the key and assess the real difference between species. For examples of tabular keys, see Newel (1970), Monniot & Monniot (1972) on ascidians, Cherbonnier & Guille (1978) on ophiuroids, Doumenc (1979) on actinians, and A. M. Clark (1981) on asteroids.

Some workers have done away with the need to have keys to the symbols by including the phrase or picture in the body of the table (see Lambshead, 1981 and Paterson, Tyler & Gage, 1983).

For quick accurate identifications the most promising keys are totally pictorial. These have been sadly neglected by most taxonomists. Exceptions are Fische d'Identification du Zooplankton which also incorporates tabular textual keys, Russell's (1953) pictorial key to the hydromedusae and scyphomedusae, Zavodnick (1972) key to the amphiurid ophiuroids and more recently Lambshead (1981) and Platt & Warwick (1983) keys to marine free-living nematodes. However, these are still in the minority (see also Cornelius, 1982).

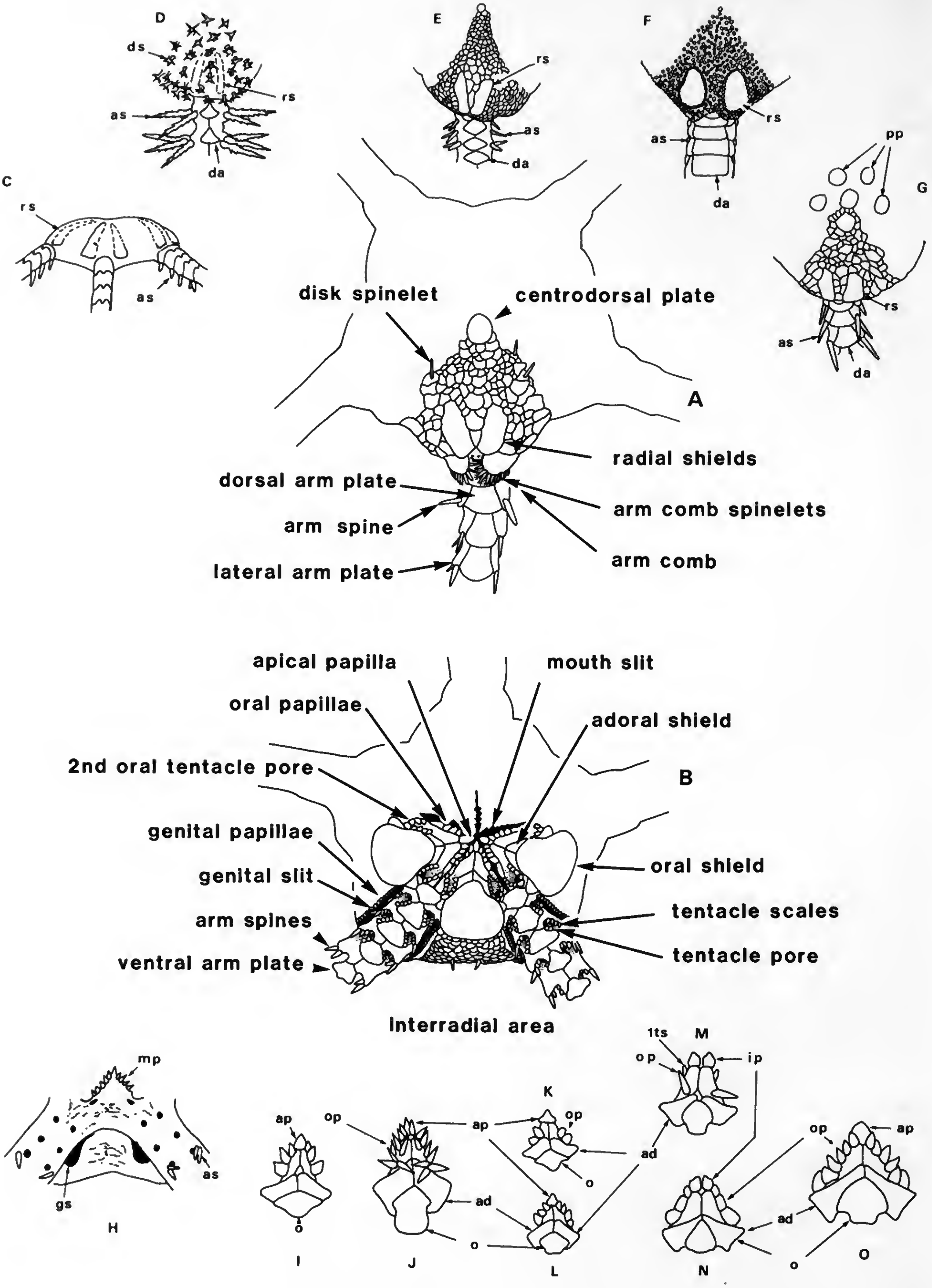
In the more popular field guides such keys have been common since the first popular guides were written by R. Tory Petersen. He arranged similar looking birds on the illustration with arrows to highlight important taxonomic features, a layout followed by most Collin's Field Guides. This easy use by non specialists is the great advantage of pictorial keys. Provided that there is some information on the basic anatomy and organisation of the animals being dealt with, it is possible to identify many animal groups without extensive knowledge of the group.

It is interesting to compare the use of pictorial aids to identification in other fields. The accurate identification of ships and aircraft during the recent world wars was of major importance. The emphasis was on good visual guides with courses on the methods used to identify these objects. Much of the experience learnt then applies equally to the biological sphere now. For example, it was found that the most effective way of comparing aircraft was to compare two aircraft at a time (C. H. Gibbs-Smith, 1942, Aircraft Recognition, **1**(2)). This can easily be done with a pictorial key. In some examples it was thought necessary to highlight important distinguishing features with arrows or emphatic shading. This was suggested for guides for the recognition of ships from the air (G. Bijur, 1943). Again highlighting drawings, as in the Petersen field guides draws attention to particular features which should be present.

Present treatment

Ophiuroids are particularly suitable for a pictorial treatment. Most of their taxonomic characters are evident in the external skeleton. So no special preparation is needed.

Basic ophiuroid morphology comprises a central disk and five (sometimes more) radiating arms; dorsally the disk is covered with calcite plates or thickened skin which may possess various spinelets or granules; ventrally there is a centrally placed mouth with angular interradial jaws. Most of the important taxonomic features are found on the ventral side particularly the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arm spine
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apical papilla
mouth slit
oral papillae
adoral shield
2nd oral tentacle pore
B
genital papillae
oral shield
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arrangement of the plates around the jaw (Fig. 1). The arms carry spines; in euryalid genera on the ventral part of the arm, while in the ophiurids they are carried laterally on the lateral arm plates. Along the ventral part of the arm the tube feet called tentacles arise in pairs, each tentacle emerging via a pore which is often armed with one or more scales (Fig. 1).

The pictorial keys presented apply to adult individuals only (disk diameter ⩾4 mm). As far as possible species which are similar are grouped together. Drawings of each species were done using a Wild M-5 stereomicroscope with drawing tube. The orientation of the drawings is as shown in Figure 1. The ventral view comprises 2–3 of the 5 jaw angles—about half the disk area; while the dorsal view covers a wedge from the centre of the disk to the base of the arms. Where necessary the ventral view is supplemented with drawings of the disk armament, arm spines and lateral views of the arms. Drawings are not in scale, being made to a convenient and similar size, so *particular attention should be paid to the accompanying bar scales.*

The only special preparation needed is for euryalid species, the thickened skin covering the arm spines must be dissolved using bleach (sodium hypochlorite) or KOH. In most North Atlantic species these spines are not crucial to the identification, but are included to help confirmation.

Usually there is only one drawing per species but supplementary ones may be included to show excessive variation. Allowances should be made for some variation but the key characters highlighted by arrows, are unlikely to vary significantly. Particular characters are high-lighted by a touching arrow whereas important regions are indicated by an arrow slightly removed. The text should be consulted both to verify identifications and to check the range of variation.

Colour of species is not dealt with partly because the information is not available for many species and also because the range of variation has not been studied. Gage *et al.* (1983) have noted the colours of the species they collected and how it may aid the identification of certain species.

Abbreviations

BMNH	British Museum (Natural History)
COB	Centre Oceanologique de Bretagne
DM	Dublin Museum
IOS	Institute of Oceanographic Sciences
MCZ	Museum of Comparative Zoology, Harvard
MNHN	Museum National d'Histoire Naturelle, Paris
MOM	Museum d'Oceanographie de Monaco
NMNH	National Museum of Natural History, Washington DC
RSM	Royal Scottish Museum, Edinburgh
SAM	South African Musuem, Cape Town
SMBA	Scottish Marine Biological Association
ZMC	Zoologisk Museum, Copenhagen
ZSM	Zoologische Staatsammlung München
AT	Aggassis Trawl
CP	Beam Trawl (Chalut a perche)
DS	Epibenthic sledge (Drague Sanders)
ES	Epibenthic Sledge

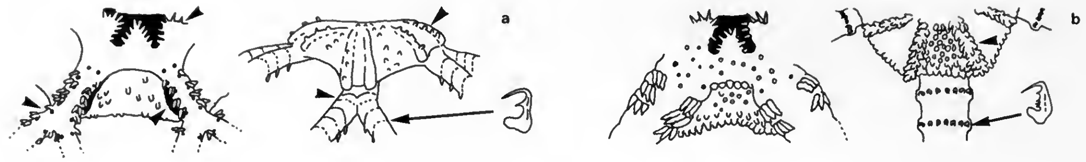
For details of the BIOGAS station localities see Laubier & Sibuet (1977).
BIOGAS stations 1–4 are in the North of the Bay of Biscay 5 & 6 are in the South.

Fig. 1 Illustrated glossary of morphological terms used in this study. A–dorsal, B–ventral view of *Ophiura ljungmani* illustrating the important features. C–O shows the range of variation of these features in the main families; C–G variation of the disk and arm morphology of: C–euryalids, D–ophiacanthids, E–amphiurids, F–ophiodermatids, G–ophiochitonids. H–O variation in jaw morphology of: H–euryalids; I–J the range of morphology within the Ophiacanthidae, I–*Ophiacantha,* J–*Ophiocamax*; K–L the range within the Ophiactidae, K–*Ophiactis,* L–*Histampica*; M–N the range within the Amphiuridae, M–*Amphiura,* N–*Amphioplus*; O–ophiochitonids. Abbreviations: a.d.–adoral shield; a.p.–apical papilla; a.s.–arm spine; d.a.–dorsal arm plate; d.s.–disk spinelets; g.s.–genital slit; i.p.–infradental papillae; m.p.–mouth papillae; o–oral shield; o.p.–oral papillae; p.p.–primary radial plates; r.s.–radial shields; 1t.s.–first oral tentacle scale.

KEY TO FAMILIES

EURYALAE

GORGONOCEPHALIDAE



ASTERONYCHIDAE

ASTEROSCHEMATIDAE

Fig. 2 Key to the Families. Gorgonocephalidae—(a) *Gorgonocephalus*, (b) *Astrochele*. Asteronychidae—(a) *Asteronyx*, (b) *Astrodia*. Asteroschematidae—(a) *Asteroschema*, (b) *Ophiocreas*.

Taxonomic section

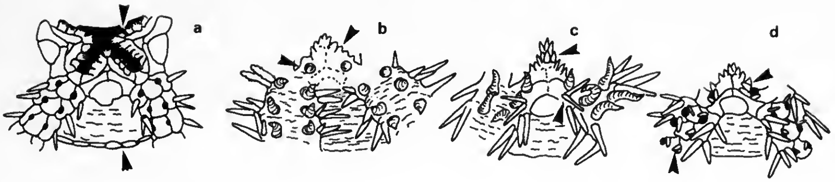
EURYALAE Müller & Troschel, 1842

GORGONOCEPHALIDAE Ljungman 1867 emended Mortensen 1933*b*

This family is characterised by a large disk often covered with granules, spinelets or sometimes with thickened skin; the bar shaped radial shields extending almost to the middle of the disk; the papillae on the jaw usually spine like; the arms may be branched or simple, covered with granules and distally with bands of minute hooks. There are two genera represented in the abyssal North Atlantic: *Gorgonocephalus* Leach, 1815 which has branching arms and *Astrochele* Verrill, 1878 which has simple arms. *Astrochele* is commonly found clinging to gorgonians, corals, etc.

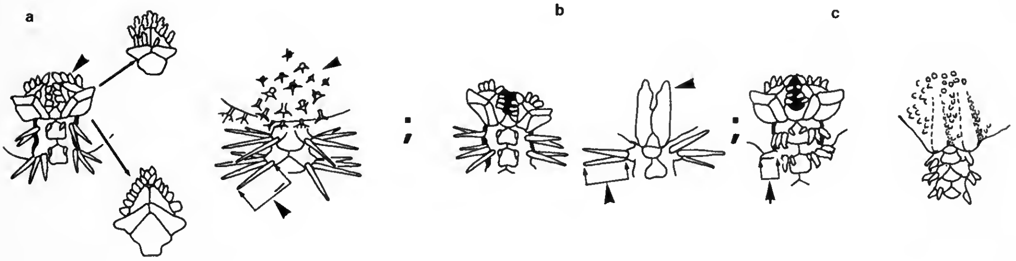
OPHIURAE

OPHIOMYXIDAE



OPHIACANTHIDAE

OPHIACANTHINAE



OPHIOTOMINAE

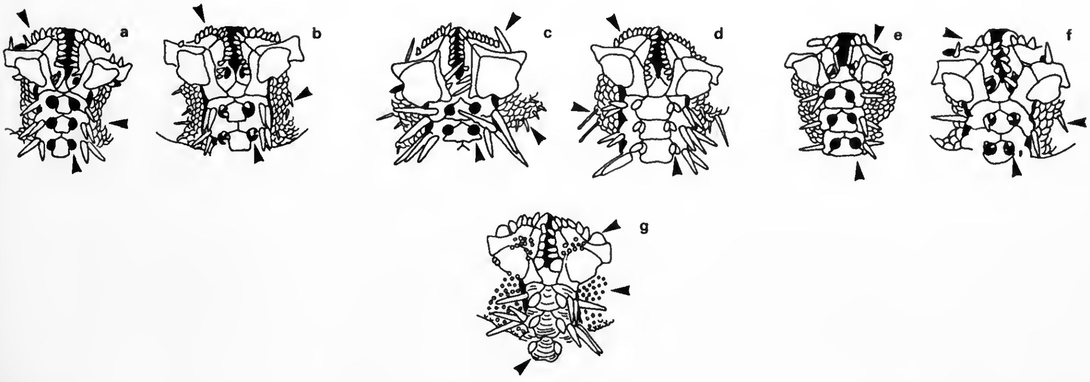


Fig. 3 Key to the Families cont. Ophiomyxidae—(a) *Ophiomyxa,* (b) *Ophiophrixus,* (c & d) *Ophioscolex.* Ophiacanthinae—(a) *Ophiacantha,* showing extremes of range, (b) *Ophiacanthella,* (c) *Ophiolebes.* Ophiotominae—(a) *Ophiotoma,* (b) *Ophiotrema,* (c) *Ophioprium,* (d) *Ophiopristis,* (e) *Ophiocymbium,* (f) *Ophiomedea,* (g) *Ophiolimna.*

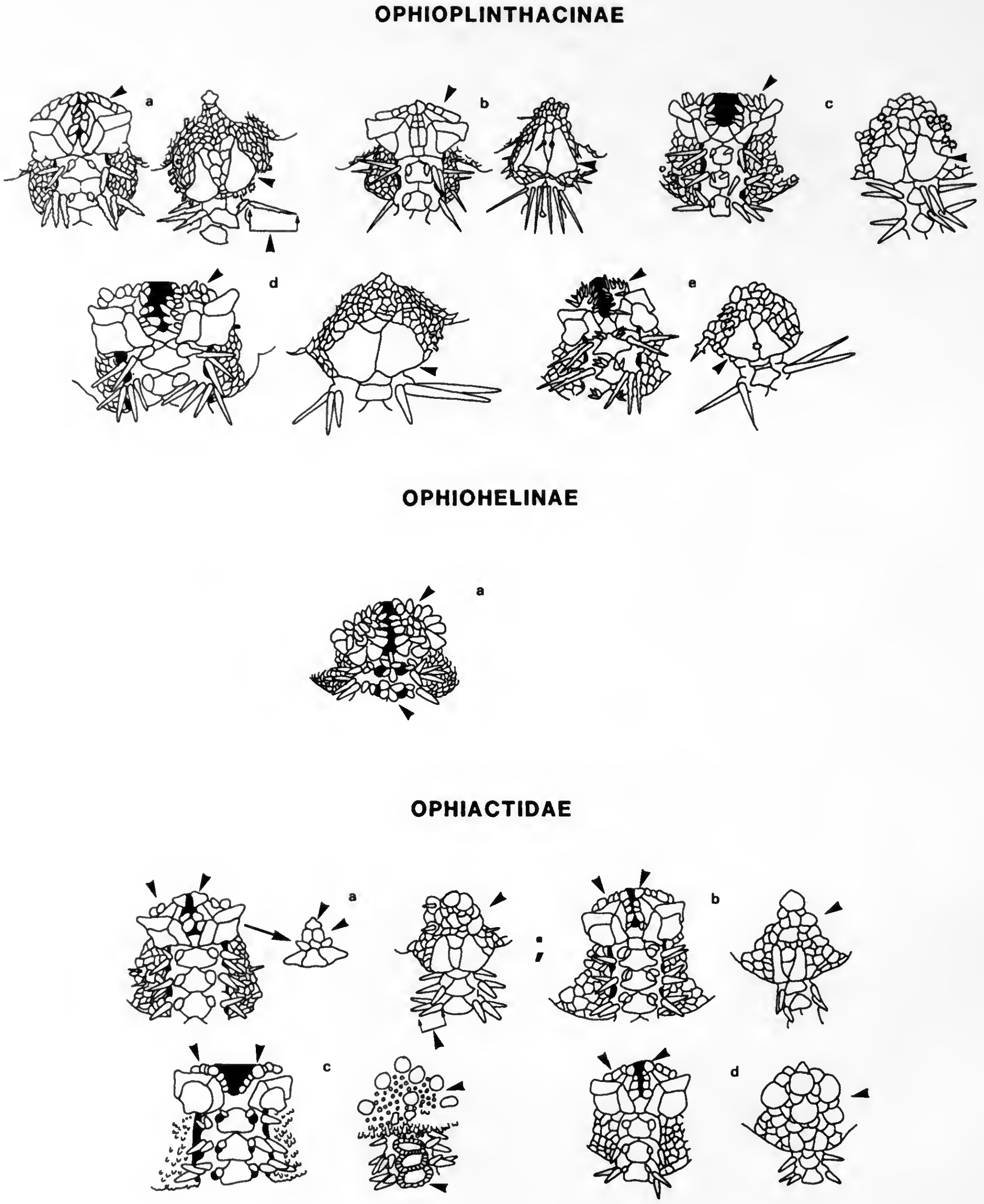
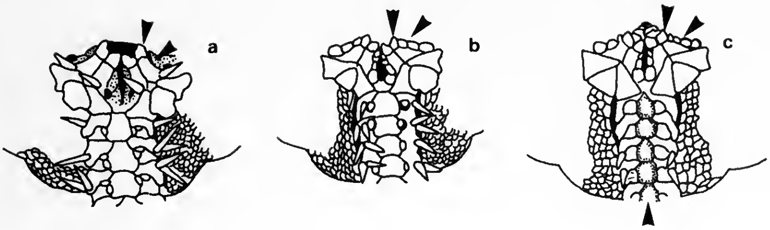
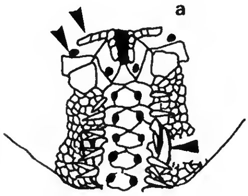


Fig. 4 Key to the Families cont. Ophioplinthacinae—(a) *Ophioplinthaca,* (b) *Ophiothamnus,* (c) *Ophiomitrella,* (d) *Ophiomitra,* (e) *Ophiocamax.* Ophiohelinae—(a) *Ophiomyces.* Ophiactidae—(a) *Ophiactis,* (b) *Histampica,* (c) *Ophiopholis,* (d) *Ophiopus.*

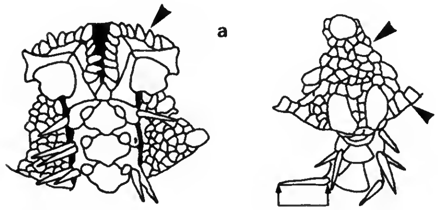
AMPHIURIDAE



AMPHILEPIDINAE



OPHIOCHITONIDAE



OPHIODERMATIDAE

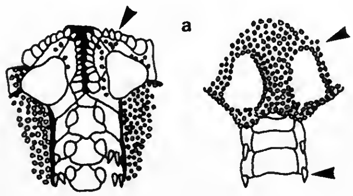


Fig. 5 Key to the Families cont. Amphiuridae—(a) *Amphiura*, (b) & (c) *Amphioplus*. Amphilepidinae—(a) *Amphilepis*. Ophiochitonidae—(a) *Ophiochiton*. Ophiodermatidae—(a) *Bathypectinura*.

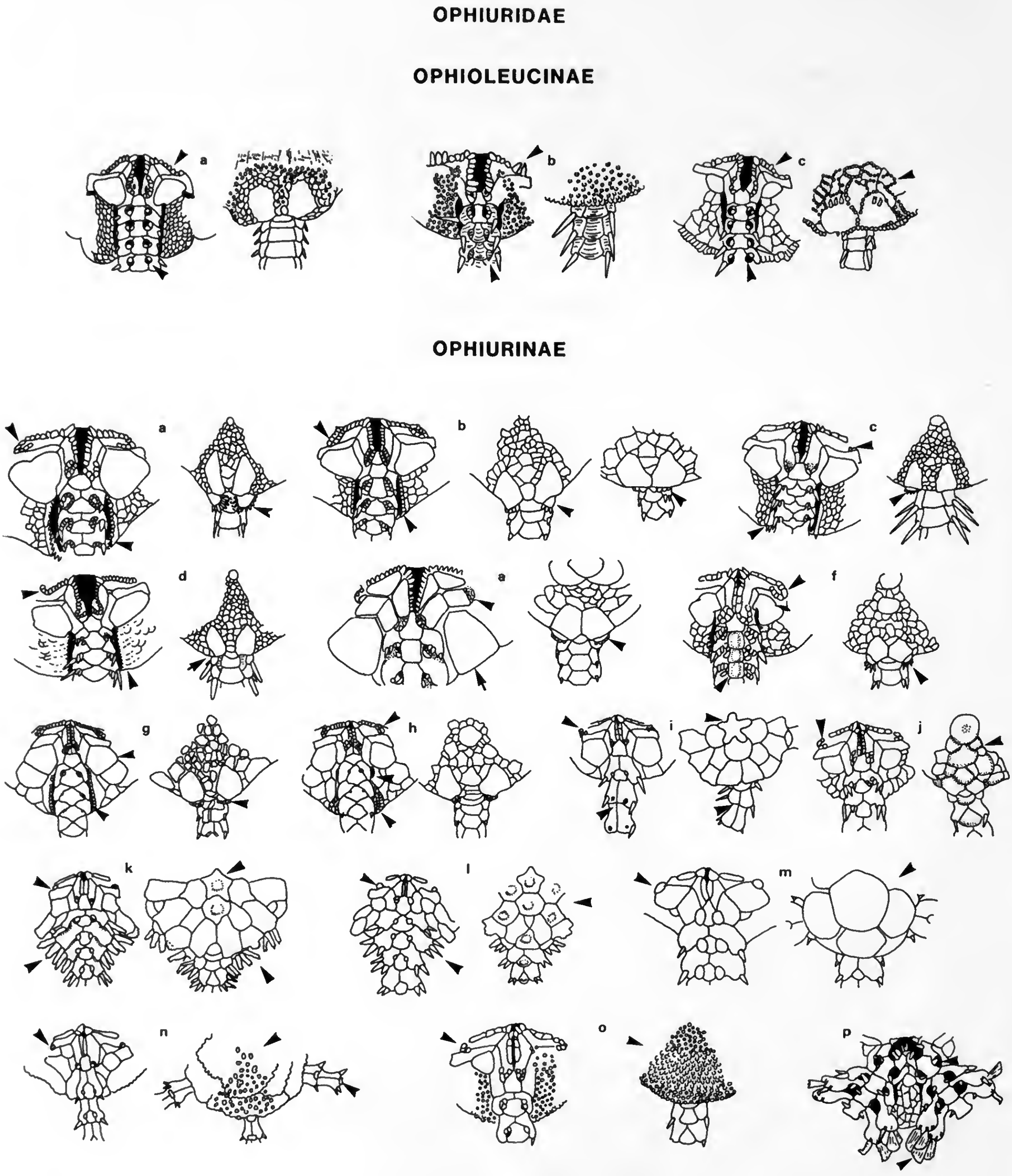


Fig. 6 Key to the Families cont. Ophioleucinae—(a) *Ophiernus,* (b) *Ophiostriatus,* (c) *Ophioleuce.* Ophiurinae—(a) & (b) *Ophiura,* (c) *Ophiocten,* (d) *Ophiopleura,* (e) *Amphiophiura,* (f) *Stegophiura,* (g) *Homophiura,* (h) *Ophiurolepis,* (i) *Anthophiura,* (j) *Ophiotjalfa,* (k) *Ophiophycis,* (l) *Ophiomisidium,* (m) *Ophiotypa,* (n) *Perlophiura,* (o) *Uriopha,* (p) *Ophiambix.*

OPHIOLEPIDINAE

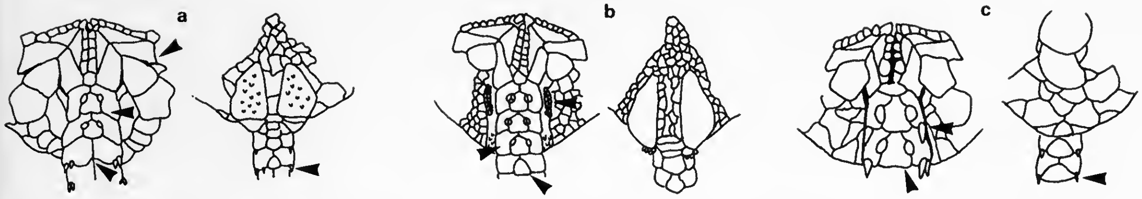


Fig. 7 Key to the Families cont. Ophiolepidinae—(a) *Ophiomusium,* (b) *Ophiosphalma,* (c) *Ophiozonella.*

Gorgonocephalus caputmedusae (Linnaeus, 1758)

Fig. 8

Asterias caputmedusae Linnaeus, 1758: 663.
Gorgonocephalus caputmedusae: Leach, 1815: 51; Mortensen, 1924: 13–16; 1927: 162–163; Blacker, 1957: 46–47; Gage *et al.* 1983: 288.
Astrophyton linckii Müller & Troschel, 1842: 122; Lyman, 1865: 190; Norman, 1865: 105.
Gorgonocephalus linckii: Lyman, 1882: 264; Hoyle, 1885: 138; Bell, 1892: 137–138; Grieg, 1902: 18; 1904: 35; 1913: 130; Farran, 1913: 49; Koehler, 1924: 223.

Material Studied. **COB:** BIOGAS HZ Stn CV21 994 m 1 specimen.
SMBA: RRS *Challenger II* Stn 8 56°23′N: 9°18′W 1010–1030 m 1 specimen.
BMNH: Lousy Bank 60°20′W: 12°40′W 183–366 m Ministry of Agriculture & Fisheries 5 specimens; Christiansund 274 m 1 specimen; Rodberg, Trondheim Fjord 457 m 2 specimens.

The disk is pentagonal, up to 90 mm in diameter and covered with small stumpy spinelets which have a multipointed crown. In small specimens of disk diameter less than 20 mm the spinelets are not well developed and resemble low hemispherical granules. Occasionally some specimens do not have such a dense covering of spinelets and the interradial areas have only a few scattered spinelets with a greater number on the radial shields. The radial shields are long and bar-like reaching almost to the middle of the disk. The ventral interradial areas are similar to the dorsal surface.

The jaws are armed with spine-like mouth papillae, otherwise covered by thick skin which obscures the associated plates. This area and the ventral parts of the arms have a coating of granules. The genital slits are relatively long extending from the edge of the disk to half way towards the oral frame.

The arms are densely granulated. The first branch is close to the edge of the disk often within the disk edge. Hooks are found on segments after the second branching but they do not form complete rings until beyond the third or fourth branch; in juvenile specimens the rings may appear after the second branch. Hooks not arranged in a complete band, are often arranged in discreet units separated from one another. The first tentacle pore on the arm has no arm spines associated with it, the second has one spine the third has two and subsequent ones have three or four.

Remarks. *G. caputmedusae* can be distinguished from the other Atlantic species of *Gorgonocephalus* by the spinelets and their arrangement. Even specimens which have a sparse covering of spinelets and therefore resemble *G. arcticus* can be distinguished by the multipointed crown of the spinelets and by the occurrence of spinelets in the interradial areas. Spinelets are confined to the radial shields in *G. arcticus* and more closely resemble large granules. *G. caputmedusae* differs from *G. lamarcki* by the density and type of disk covering. In *G. lamarcki* (Fig. 8) the disk is densely covered by small, skin-covered granules causing several authors to remark on its velvet-like appearance. In addition *G. lamarcki* does not have a dense covering of granules in the oral region and ventral part of the arms and it has a maximum of five arm spines not four as in *G. caputmedusae*. *G. eucnemus* (Fig. 8) differs from *G. caputmedusae* by the following characters: the disk is covered by hemispherical granules which occur more densely on the radial shields than interradially and in some large specimens the interradial areas look bare until examined closely.

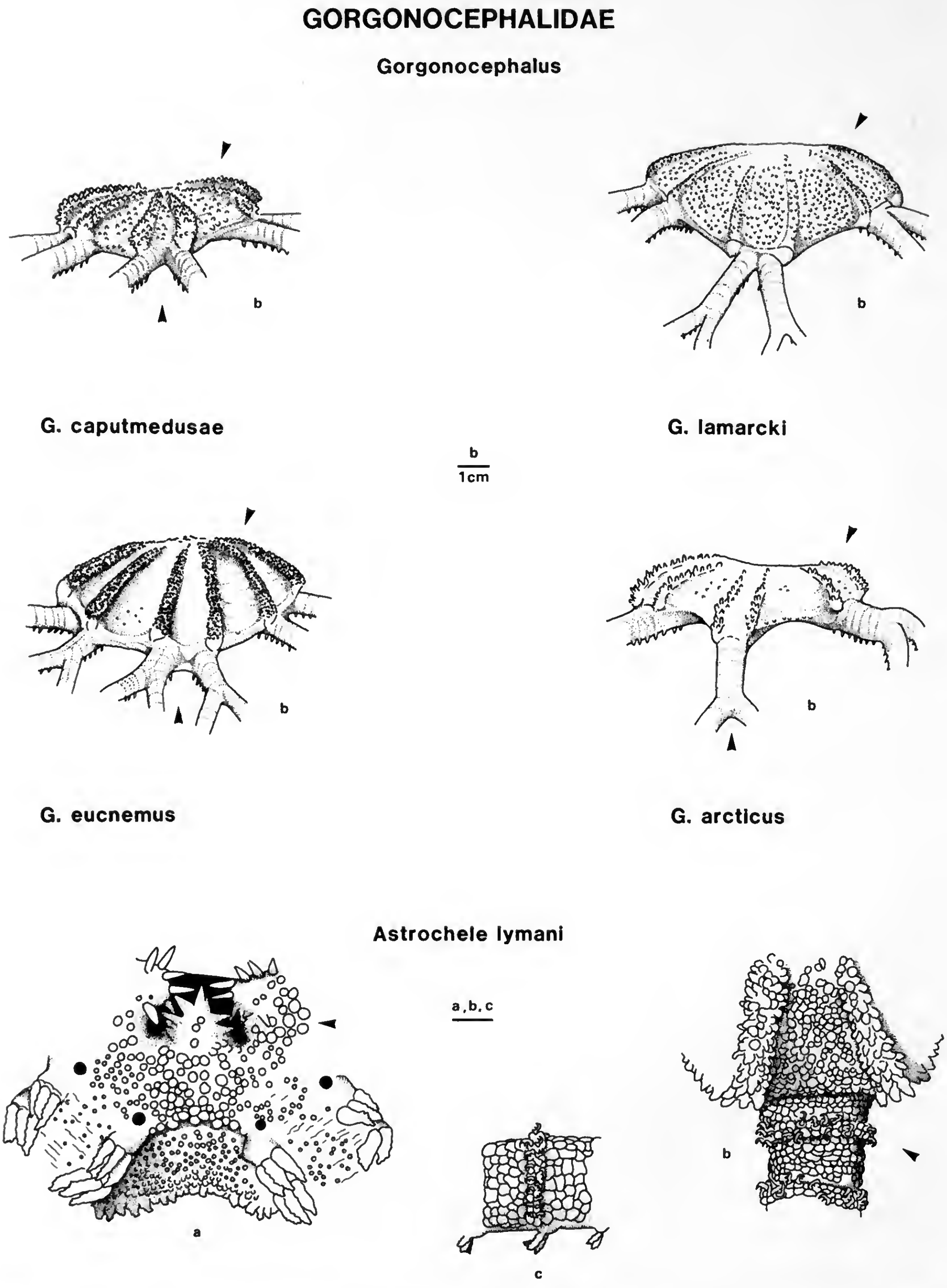


Fig. 8 Key to the Gorgonocephalidae. *Gorgonocephalus* and *Astrochele* (a) ventral; (b) dorsal view of disk; (c) lateral view of arm. NB. Bar scales associated with *Gorgonocephalus* = 1 cm; Bar scales associated with *Astrochele* = 1 mm.

The ventral part of the arms does not have the small granules found in *G. caputmedusae. G. caputmedusae* differs from *G. arcticus* (Fig. 8) as follows: the arms are densely covered in granules which are absent or sparse in *G. arcticus*; in *G. arcticus* the granules or low spinelets are confined to the radial shields with a very sparse scattering of smaller granules interradially.

DISTRIBUTION. *G. caputmedusae* is confined to the eastern Atlantic and has been recorded from Norway south to the Bay of Biscay with a bathymetric range of 150–1200 m.

Astrochele lymani Verrill, 1878
Fig. 8

Astrochele lymani Verril, 1878: 374; 1885: 264, 407. Döderlein, 1927: 89.

MATERIAL STUDIED. **COB:** BIOGAS Stn 1: CV09 2119 m 2 specimens; CV39 2350 m 4 specimens; CPO8 2177 m 2 specimens; CP26 2115 m 3 specimens; BIOGAS Stn 2: CP09 2171 m 1 specimen.
IOS: *Discovery* Investigations: Stn 9042 45°15′N: 11°22·0′W 1662–1541 m 7 specimens.

The disk is subpentagonal often slightly domed, disk diameter up to 14 mm. The radial shields are prominent, rib-like and widely separated. They and the disk are covered by a dense coating of low rugose granules which are often slightly larger on the radial shields and the distal edge of the disk. The ventral interradial areas are also covered with low rugose granules.

There is usually one spine-like apical papilla flanked by several similar spiniform oral papillae. The oral area is covered with skin, often with small granules, which extends on to the ventral surface of the arms. The genital slits extend the full length of the ventral interradial areas.

The arms are long, undivided, often coiled. The upper surface of the arms are covered with a dense coating of granules and segmental bands of hooks. Each band has two rows of hooks. The hooks are long and glassy with several supplementary points below the terminal hook. Between each band of hooks there are three bands of granules. There are usually three rugose arm spines from the first tentacle pore situated ventrally on the arm, their position corresponding with the bands of hooks. The cleaned arm spines are rugose with several long points.

REMARKS. *Astrochele lymani* can be readily identified by the bands of hooks on the undivided arms, the granular covering of the disk and the spine-like mouth papillae.

DISTRIBUTION. *A. lymani* has been recorded from both sides of the North Atlantic: in the western Atlantic it has been recorded off Nantucket in 547–1764 m while in the eastern Atlantic it has been found in the Bay of Biscay and off Portugal at depths of 1541–2350 m.

ASTERONYCHIDAE Verrill, 1899 emend Mortensen, 1933*b*

This family is characterised by a large well defined disk usually covered with thick skin or indistinct scales; the radial shields long and bar shaped; the papillae on the jaw may be spine-like or block-like; the genital slits on the proximal part of the ventral interradial areas; the arms long and covered with skin.

There are two genera represented in the abyssal North Atlantic: *Asteronyx* Muller & Troschel, 1842 which has spine-like mouth papillae, skin covered disk and 8–9 arm spines; and *Astrodia* Verrill, 1884 which has block-like mouth papillae, scales on the disk and only 3 arm spines. Species of the two genera are frequently found clinging to pennatulids and gorgonians.

Asteronyx loveni Müller & Troschel, 1842
Fig. 9

Asteronyx loveni Müller & Troschel, 1842: 199; M. Sars, 1861: 5; Norman, 1865: 98–129; Lyman, 1882: 285; 1883: 282; Verrill, 1885: 550; Grieg, 1893: 29; Koehler, 1897: 370; 1904: 167; Sussbach & Breckner, 1911: 262; H. L. Clark, 1911: 285; Döderlein, 1911: 115; Mortensen, 1912: 264–287; Matsumoto, 1917: 33; Koehler, 1922: 34; H. L. Clark, 1923: 314; Koehler, 1924: 227; May, 1924: 269; Rivera Galle, 1926: 17; Döderlein, 1927: 59; Mortensen, 1927: 158; Fedotov, 1929: 170; Koehler, 1931: 23; Baranova, 1957: 186; Chang, Liao & Wa, 1965: 61–62; Rowe, 1971: 574; Cherbonnier & Sibuet, 1972: 1364; Gage *et al.*, 1983: 287.

ASTERONYCHIDAE

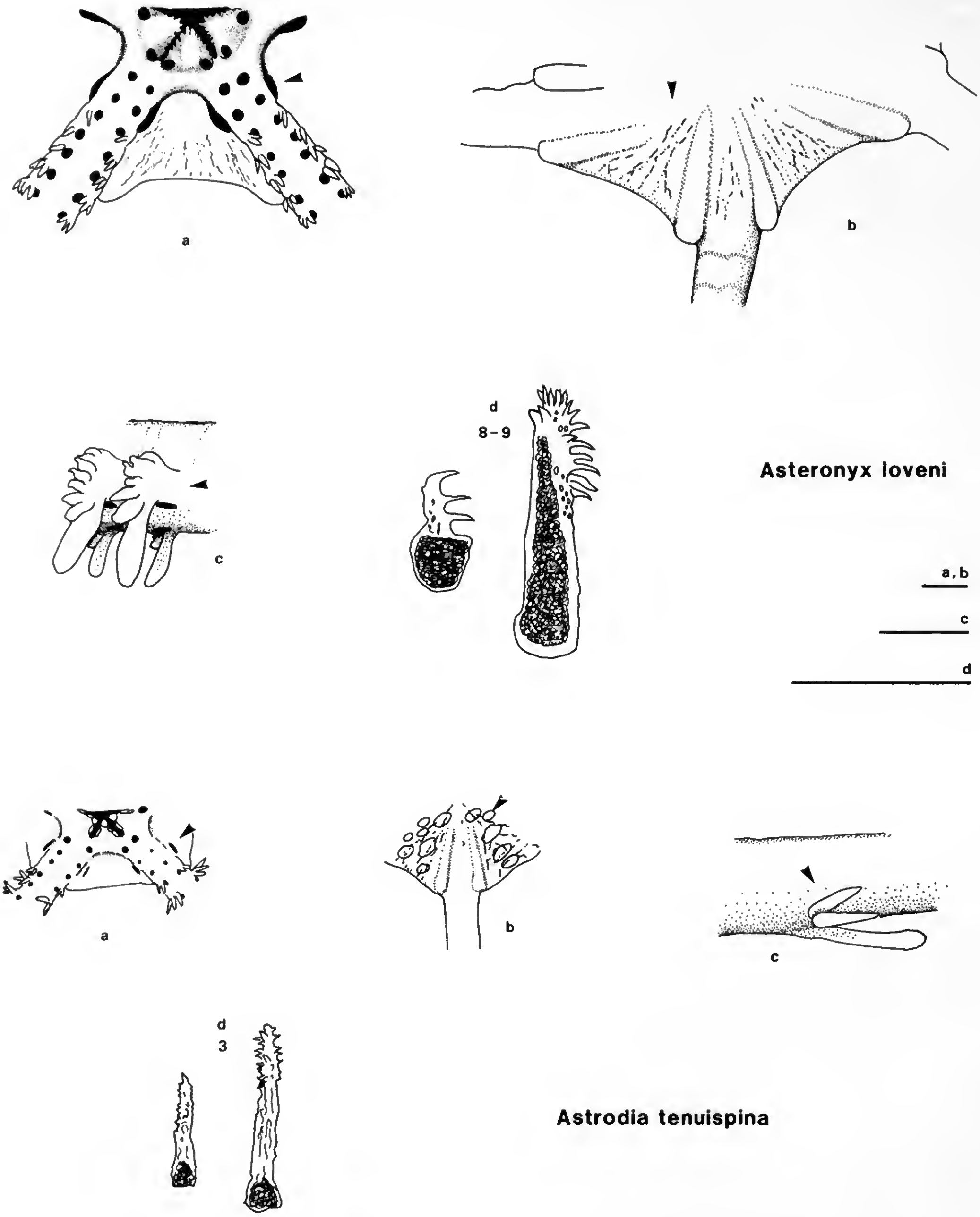


Fig. 9 Key to the Asteronychidae. *Asteronyx* and *Astrodia* (a) ventral; (b) dorsal view of disk; (c) lateral view of arm; (d) arm spines number with the spine indicates the number of arm spines on the middle segments of the arm. Bar scales = 1 mm.

Asteronyx locardi Koehler, 1896*a*: 88; 1907: 303; Grieg, 1921: 38.
Asteronyx dispar Lütken & Mortensen, 1899: 185; H. L. Clark, 1913: 219.
Asteronyx cooperi Bell, 1909: 22.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 49 off Nova Scotia 152 m 1 specimen; *Porcupine* off the Minch, Norman Collection 3 specimens.
COB: BIOGAS Stn 1: CV24 2025 m 5 specimens; CP01 2245 m 8 specimens; CP02 2174 m 4 specimens; CP03 2119 m 2 specimens; CV39 2350 m 1 specimen; CP08 2177 m 1 specimen. BIOGAS Stn 2: CV26 2822 m 1 specimen; BIOGAS Stn 4: CV35 4721 m 1 specimen; BIOGAS HZ Stn: CV11 2141 m 1 specimen.
SMBA: RRS *Challenger II*: Stn SWT 18 56°46′N: 09°42′W 1809 m 1 specimen; Stn SWT 32 56°48′N: 09°56′W 2006 m 1 specimen.

The disk is round to pentagonal, and covered in skin with occasional small plates, usually only noticeable when the specimen is dried; disk diameter up to 35 mm. The radial shields are long, bar shaped reaching almost to the centre of the disk. The ventral interradial areas are also covered with skin.

The jaws and oral area are covered by skin. The jaws appear as if recessed within the mouth. The jaws are armed with blunt papillae which are not arranged in a regular series. The second oral tentacle pore emerges superficially. The genital slits are small about one segment long and are situated beside the arm between the first and second tentacle pores.

The arms are covered with skin, and are very long with two or three longer than the others. Dorsal arm plates are absent and the ventral arm plates are obscured by skin. The arm spines are situated on the ventral side of the arms usually just proximal to the tentacle pore. There are no spines on the first arm segment, one on the second, two on the third increasing up to 8 or 9. These spines are slightly rugose and hook shaped. On the longer arms the ventralmost arm spine is elongated, about four times as long as the other spines, and is club shaped. The arm spines are usually covered with skin. When cleaned the shorter ones are revealed to be rather hook-like with a terminal hook and 2 large supplementary hooks on the shaft. The longer spines are mace-like; with a slightly rugose body and a head with multiple points.

REMARKS. *Asteronyx loveni* can be distinguished by the skin covered disk; the bar shaped radial shields which reach almost to the centre of the disk; the blunt mouth papillae; the 8 to 9 arm spines on the arm and the well developed club shaped arm spine on the longer arms.

DISTRIBUTION. *Asteronyx loveni* appears to be widespread in distribution, there being no records from the Arctic Ocean and parts of the Southern Ocean; the bathymetric range is wide; from *c.* 100–4721 m.

Astrodia tenuispina Verrill, 1884

Fig. 9

Astrodia tenuispina Verrill, 1884: 219; 1899*b*: 371; Koehler, 1906: 33–34; 1907: 304–5; Gage *et al.*, 1983: 287–288.
Hemieuryale tenuispina: Verrill, 1885: 550.

MATERIAL STUDIED. **COB:** BIOGAS Stn 1: CV10 2108 m 1 specimen; BIOGAS Stn 2: DS19 2865 m 1 specimen; DS 41 3548 m 2 specimens; DS66 3480 m 3 specimens; CV26 2822 m 1 specimen; CP28 3380 m 2 specimens. BIOGAS HZ Stn: DS 14 1560 m 1 specimen.
IOS: *Discovery* Investigations: Stn: 8511/2 41°49·6′N: 11°6·0′W 2274–2584 m 4 specimens; Stn 9640/1 50°3·2′W: 13°50·6′W 8 specimens.
SMBA: RRS *Challenger II*: Stn SWT 13 52°04′N: 16°09′W 3463 m 147 specimens.

The disk is pentagonal, disk diameter up to 10 mm; the skin covering has numerous rounded thin scales embedded in it, usually most conspicuous when the specimen is slightly dried. The radial shields are bar-like almost reaching the middle of the disk. Distally the pair of shields terminates on each side of the arm. The ventral interradial areas are similar to the dorsal surface.

The jaw bears one pointed apical papilla flanked by up to 5 block-like, contiguous oral papillae. The second oral tentacle pore arises superficial. The other plates of the jaw are often conspicuous. The adoral shields are large and broad. The oral shield is usually small, rounded, triangular except the madreporite which is usually large. The genital slits are short equal to about one arm segment, and are situated by the side of the arm between the first and second tentacle pore on the ventral interradial area.

The arms are long, with no dorsal arm plates and the ventral arm plates hidden by skin. The arm spines are situated on the ventral side of the arms proximal to the tentacle pore. There are no spines on the first arm segment, one on the second, two on the third then three on the remaining arm segments. The arm spines are thin and pointed with the ventralmost becoming elongated up to three times the length of the others and developing a rugose multipointed crown. When the arm spines are cleaned in bleach the smaller ones are seen to be thin and only slightly rugose with the area of attachment reinforced while the larger spine has an almost smooth shaft with a multipointed head.

REMARKS. *Astrodia tenuispina* can be recognised by the skin covered disk embedded with small thin plates; jaws with a pointed apical papilla and as many as 5 contiguous block like oral papillae, and 3 arm spines of which the ventral most is the longest.

DISTRIBUTION. *A tenuispina* has been recorded from both sides of the North Atlantic. In the west from off the east coast of the United States at depths of 2452–3659 m; in the east from the Rockall Trough, the Porcupine Sea Bight, the Bay of Biscay and off Portugal with a bathymetric range of 1560–3548 m.

ASTEROSCHEMATIDAE Verrill, 1899 emended Mortensen, 1933*b*

This family is characterised by the disk being ill-defined or constricted with the arms appearing to continue to the centre of the disk in some genera; the disk may be covered with skin or a dense coating of granules; the long and narrow radial shields; the reduced papillae on the jaw with only the apical papillae well developed and the oral papillae small, like enlarged granules; the genital slits situated vertically on the sides of the disk; the arms long and covered with skin or granules. There are two genera present in the North Atlantic abyssal: *Asteroschema* Orsted & Lütken, 1856, which is densely covered with granules and has a small ill-defined disk, and *Ophiocreas* Lyman, 1879, which is covered mainly by skin although the disk has a light covering of small granules and the disk is slightly larger and more distinct. Species of both genera are frequently found on gorgonians and corals.

Asteroschema inornatum Koehler, 1906

Fig. 10

Asteroschema inornatum Koehler, 1906: 30–31; 1907: 303–304; 1909: 206; A. H. Clark, 1948: 78; Gage *et al.*, 1983: 288.

MATERIAL STUDIED. **COB:** BIOGAS Stn 6 CV32 1895 m 1 specimen; CP07 2170 m 16 specimens.
IOS: *Discovery* Investigation Stn 9042 42°15′N: 11°12′W 1662–1541 m 2 specimens.
SMBA: RRS *Challenger II*: Stn ES 112 55°12′N: 15°50′W 1900 m 1 specimen.

The disk is small and ill-defined with the arms appearing to continue to the middle of the disk. The disk diameter may reach 10 mm. Both disk and arms are densely covered with granules. The radial shields are covered but can be distinguished as two long swellings at the base of the arms, reaching to the centre of the disk.

The ventral side is also densely covered with granules obscuring the underlying plates. The jaws bear one large blunt apical papilla. The oral papillae are reduced and resemble large flattened granules. The second oral tentacle pore arises superficially. The genital slits are short and situated on the vertical sides of the interradial areas of the disk.

The arms are very long, greater than seven times the disk diameter. The plates of the arms are obscured by granules. The first tentacle pore lacks an accompanying spine, the second to fourth have only one spine subsequent pores have two. The inner one of the pair becomes larger and club-like on distal arm segments.

REMARKS. *A. inornatum* can be distinguished by the small ill-defined disk, the dense covering of granules, the genital slits positioned vertically on the sides of the disk, the arrangement of the jaw and the arrangement of the arm spines.

DISTRIBUTION. *A. inornatum* has been recorded from the Rockall Trough, the Bay of Biscay, off NW. Spain and off the Azores; with a bathymetric range of 1478–2170 m.

ASTEROSCHEMATIDAE

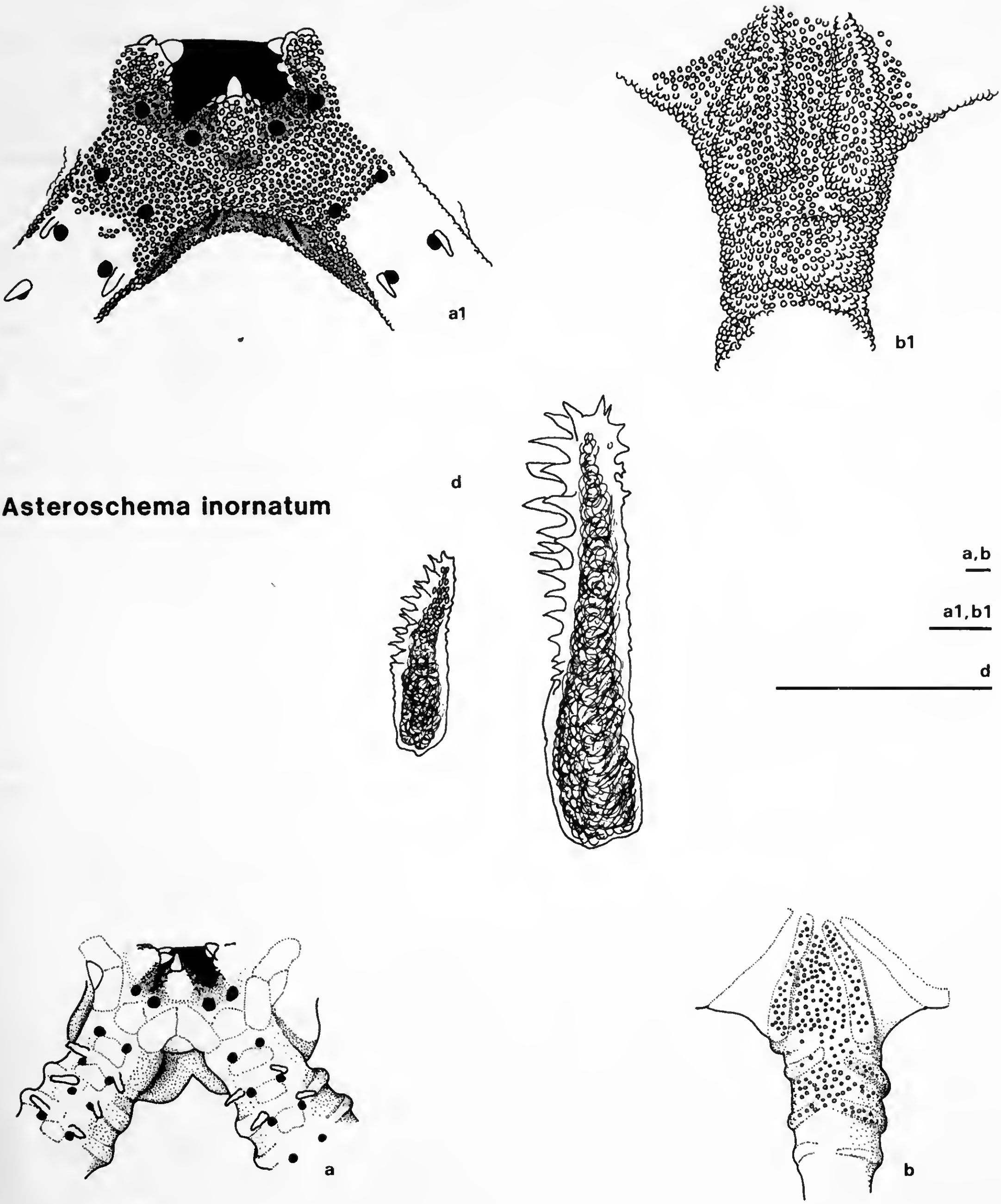


Fig. 10 Key to the Asterochematidae. *Asteroschema* and *Ophiocreas* (a) ventral; (b) dorsal view of disk; (d) arm spines. Bar scales = 1 mm.

Ophiocreas oedipus Lyman, 1878

Fig. 10

Ophiocreas oedipus Lyman, 1878: 65; 1882: 283; Koehler, 1904: 166; 1909: 206.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 344 off Ascension Island 756 m HOLOTYPE; HMS *Chalenger* Stn 343 off Ascension Island 778 m 2 PARATYPES.

DIAGNOSIS. The disk is small indented interradially; the disk diameter up to 12 mm. The arms do not appear to extend to the middle of the disk as in *Asteroschema inornatum*. Both the arms and disk appear covered with skin, but close examination of the disk reveals small granules, which covers the disk but less densely than in *Asteroschema*. Although covered the radial shields are conspicuous, bar shaped nearly extending to the middle of the disk.

The ventral side of this species is covered by skin but without any granules. The jaws bear one broad pointed apical papilla. The oral papillae are reduced resembling irregularly arranged, enlarged granules. The second oral tentacle pore arises superficially above the jaws, when viewed ventrally. The genital slits are almost vertical placed on the interradial areas of the disk.

The arms are long and thin, greater than seven times the disk diameter. In larger specimens the base of the arms may be enlarged, three or more arm segments may be effected, this is an indication of the degree of gonad development. The first tentacle pore on the arm has no spine associated, the next five or so pores have one and subsequent ones have two. The inner spine becomes enlarged and clublike on distal segments.

REMARKS. *O. oedipus* can be distinguished from *Asteroschema inornatum* by the following characters: the disk is not densely covered by granules, the disk is more developed and the ventral areas are skin covered.

DISTRIBUTION. *O. oedipus* appears to be widely distributed having been recorded from both Atlantic and Pacific Oceans. In the North Atlantic it has been recorded from off Madeira with a bathymetric range of 1500–1970.

OPHIURAE Müller & Troschel, 1842

OPHIOMYXIDAE Ljungman, 1867b

This family is characterised externally by thickened skin covering the disk and arms which conceals the reduced or fragmented plates or scales; rudimentary and inconspicuous radial shields; the jaws usually as broad as long or longer than broad armed with simple spine-like or broad scale-like rugose papillae; the second oral tentacle pore may arise within the mouth slit as in *Ophiomyxa,* or more superficially and nearly outside the mouth slit as in *Ophioscolex* and *Ophiophrixus*; oral area usually covered with skin which may obscure the underlying plates; the arm spines erect laterally placed, covered with thickened skin.

Ophiomyxa serpentaria Lyman, 1883

Fig. 11

Ophiomyxa serpentaria Lyman, 1883: 274; Bell, 1892: 136; Farran, 1913: 47–48; Mortensen, 1913*b*: 362; 1927: 168; 1933*a*: 11–14; Cumano, 1941: 1–7.
Ophiodera serpentaria Verrill, 1899*a*: 67; Koehler, 1909: 203.

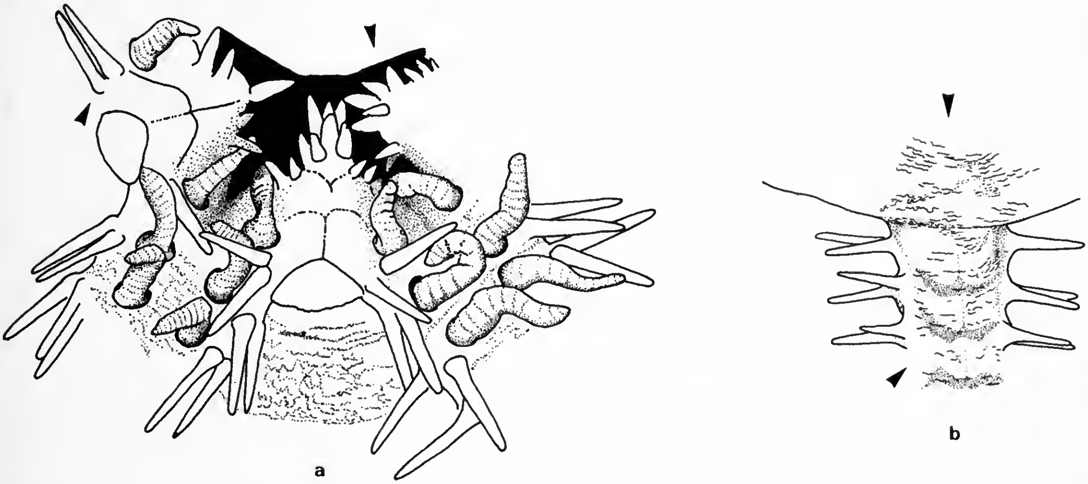
MATERIAL STUDIED. **BMNH:** *Helga* Stn CXX 53°58′N: 12°24′W 688 m 1 specimen.
IOS: *Discovery* Investigations: Stn 8966 31°21′N: 6°41·5′W–31°22′N: 10°39·2′W 686–742 m 1 specimen.

The disk is pentagonal; covered with skin in which it is possible to discern small thin transparent plates; disk diameter up to 27 mm. The radial shields are inconspicuous. Along the margin of the disk there is a series of fairly distinct plates. The ventral interradial areas are covered with skin, like the dorsal surface. Mortensen (1933*a*) mentions that the skin of the disk also contains small irregular, bone shaped spicules.

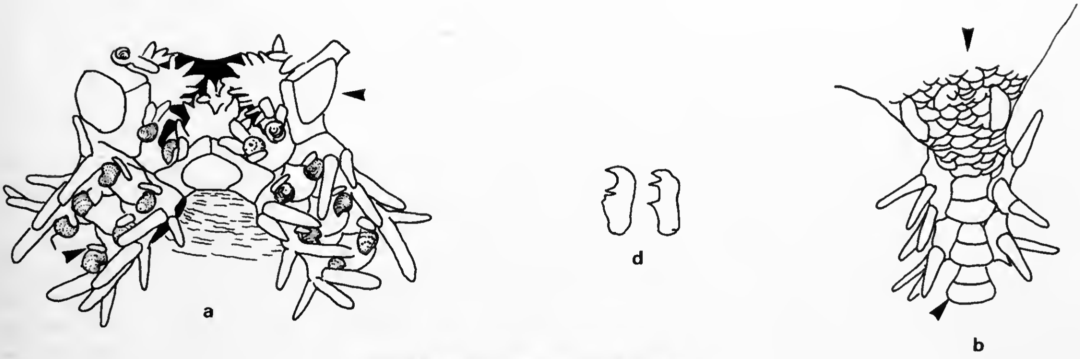
The jaw is as broad as long. There is one apical papillae flanked on each side by 3–4 oral papillae. The papillae are broad and glassy with rugose tips; webs of skin connect their bases. The adoral shields are long and slightly flared distally, separating the oral shield from the first lateral arm plate. The oral shield is large, rounded triangular in shape often with a slight distal projection.

OPHIOMYXIDAE

Ophiomyxa serpentaria



Ophioscolex glacialis



Ophioscolex purpureus

Fig. 11 Key to the Ophiomyxidae *Ophiomyxa* and *Ophioscolex* (a) ventral; (b) dorsal view of disk; (d) distal dorsal arm spine. Bar scales = 1 mm.

Ophiophrixus spinosus

Fig. 12 Ophiomyxidae *Ophiophrixus* (a) ventral; (b) dorsal view of disk. Bar scales = 1 mm.

The arms are covered by skin. The dorsal arm plates are very thin, visible only in dried specimens and often it is necessary to dissolve away the skin, nearly rectangular and contiguous or nearly so at least on proximal segments. The ventral arm plates are irregularly hexagonal, with the lateral edges extending laterally; broadly contiguous on proximal joints. The tentacle pores are large and open without tentacle scales, gradually becoming smaller on the distal segments. There are three skin covered arm spines, proximal spines are rugose but towards the end of the arm, all the spines become more hook-like.

REMARKS. *O. serpentaria* can be distinguished by the shape of the apical and oral papillae, the skin covered disk and the marginal series of plates on the disk.

DISTRIBUTION. This species has only been recorded from the eastern Atlantic from SW. Ireland, Faeroe Channel south to the Azores; with a bathymetric range of 450–2440 m.

Ophioscolex glacialis Müller & Troschel, 1842
Fig. 11

Ophioscolex glacialis Müller & Troschel, 1842: 109; Lyman, 1883: 268; Verrill, 1885: 549; Bell, 1892: 134; Grieg, 1893: 9; Pfeffer, 1894: 107–121; Grieg, 1900: 268; 1902: 16; 1903: 32; Michailovskij, 1902: 533; Mortensen, 1903: 86; Grieg, 1910: 6; Süssbach & Breckner, 1910: 259; Mortensen, 1913: 361; Koehler, 1914: 124; Hofsten, 1915: 117; Mortensen, 1927: 169; Schorygin, 1928: 60; Mortensen, 1932: 25; 1933*a*: 14; Hedling, 1934: 57; Djakanov, 1935: 82; 1954: 30; Stendall, 1967: 837.

MATERIAL STUDIED. **BMNH.** *Ernest Holt* Stn 24 off Greenland 3 specimens; Norman Coll. off Matha's Vineyard NE. America 360–464 m 3 specimens; west coast of Sweden 1 specimen.
IOS: *Discovery* Investigation Stn 7711 52°50′N: 20°02·8′W 2727 m 1 specimen.

The disk is round to pentagonal, delicate and frequently damaged so as to obscure the shape; covered with skin without any plates; disk diameter up to 25 mm. The radial shields are inconspicuous. The ventral interradial areas are also covered by naked skin.

The jaws appear longer than broad. In large specimens there are several rounded blunt or often spine-like superficial apical papillae barely distinguishable from the ventralmost teeth; in smaller specimens there are fewer papillae, often only one. There are 3–4 large irregularly arranged oral papillae; distal to these and situated within the mouth slit is a series of 3 or 4 smaller papillae. The second oral tentacle pore emerges superficially and is armed with one or two large tentacle scales, situated on the adoral shields and similar to the arm spines. The adoral shields are long and slightly curved, indented over the area of the second oral tentacle pore. The oral shield has a rounded proximal edge with an almost straight distal edge or may be rounded triangular in shape.

The arms are covered with skin which obscures the dorsal side of the arm. Dried specimens reveal a lack of dorsal arm plates. The ventral arm plates are irregularly rectangular with indented lateral edges and a rounded distal edge; they are contiguous at least proximally. The tentacle pores are large and open without tentacle scales; the tentacles themselves are long and not retractable and may obscure the plates beneath. There are 3 erect, slightly flattened, blunt arm spines, covered by thick skin.

REMARKS. *O. glacialis* can be distinguished from *O. purpureus* by the absence of tentacle scales; the shape and position of the second oral tentacle scales and by a lack of dorsal arm plates.

DISTRIBUTION. This species has been recorded on both sides of the North Atlantic and from Arctic Seas; in the east it has been recorded from the Kara Sea south to the Faeroe Channel and in the west from the Davis Strait south to off Maryland, with a bathymetric range of 50–2727 m.

Ophioscolex (Ophiolycus) purpureus Düben & Koren, 1844

Fig. 11

Ophioscolex purpureus Düben & Koren, 1844: 235; G. O. Sars, 1861: 8; Bell, 1892: 134; Grieg, 1893: 28; 1895: 10; 1902: 16; 1903: 32; Mortensen, 1903: 87; Koehler, 1907: 302; Farran, 1913: 47; Mortensen, 1913: 362; 1920: 45–48; 1927: 170; 1933*a*: 17; 1933*b*: 315; Djakanov, 1954: 30.
Ophioscolex quadrispinus Verrill, 1885: 550.

MATERIAL STUDIED. **BMNH:** *Porcupine* Stn 82 60°0′N: 5°13′W 562 m 15 specimens; *Porcupine* Stn 87 59°35′N: 9°11′W 1403 m 3 specimens; *Ernest Holt,* S. of Bear I. 4 specimens.

The disk is round to subpentagonal; covered with thickened skin; no scales but granules are scattered over the surface which are more conspicuous in dried specimens; disk diameter up to 20 mm. The radial shields are inconspicuous. The ventral interradial areas are similar to the dorsal surface.

The jaws appear to be longer than broad. The plates of the oral frame are often obscured by thickened skin. There are up to 3 flat pointed apical papillae flanked on each side by 4–5 flattened, pointed oral papillae. Distal to the oral papillae there are 2–3 large flat tentacle scales of the second oral tentacle pore, often forming a series with the oral papillae. The adoral shields are long and narrow, flared distally so that they separate the oral shield from the first lateral arm plate. The oral shield is rounded triangular.

The arms may be covered by a thin covering of skin which may obscure the plates. Distally the dorsal arm plates are well developed, rectangular and contiguous with two successive plates to each segment; at the base of the arms there is an irregular arrangement of many small plates merging into the disk, usually only distinctly seen in dried specimens. The ventral arm plates are rectangular contiguous with their lateral edges indented. The tentacle pores are large and open with one long flat tentacle scale. There are three flat, blunt, finely rugose arm spines, on the distal portion of the arm the two dorsalmost ones are transformed into hooks.

REMARKS. *O. purpureus* can be distinguished by the presence of dorsal arm plates, the arrangement of the tentacle scales of the second oral tentacle pore, the presence of one long flat tentacle scale on each arm pore and the transformation of the dorsal spines into hooks.

Mortensen (1933*b*) erected a sub-genus for those species of *Ophioscolex* with well formed dorsal arm plates and well developed hooks on the arms. In addition their jaws are better developed and similar in structure to those of the ophiacanthid subfamily Ophiotominae. However *Ophioscolex* can be distinguished from the Ophiotominae because it lacks the comma shaped arm spine articulation on the lateral arm plate, and by having the distal dorsal spines transformed into hooks.

DISTRIBUTION. *O. purpureus* has been recorded from Greenland, Norway, the Rockall Trough south to the Bay of Biscay, with a bathymetric range of 75–1480 m.

Ophiophrixus spinosus (Storm, 1881)

Fig. 12

Ophioscolex ? spinosa Storm, 1881: 88.
Ophiobyrsa hystricis Lyman, 1883: 272; Bell, 1892: 135; Kemp, 1905: 196; Koehler, 1907: 302; Farran, 1913: 48; H. L. Clark, 1915: 170.
Ophiobyrsella hystricis: Verrill, 1899*b*: 359.
Ophiophrixus spinosus: Mortensen, 1924: 3–11; 1927: 171; 1933*a*: 18–20.

Material studied. **BMNH:** HMS *Research* Stn 2 1 specimen; Ministry of Agriculture and Fisheries 60°20′N: 12°40′W 180–360 m; The Lousey Bank 1 specimen; Irish Fisheries *Helga* Stn SR 188 51°53′N: 11°59′W 576–670 m 2 specimens.

The disk is round, often indented interradially, high and covered with skin with small scattered spines attached to small plates within the skin; diameter up to 30 mm. The radial shields are short and bar-like and carry a single row or well developed spinelets along their length. The ventral interradial areas are similar to the dorsal side of the disk.

The jaws and other plates of the oral surface are obscured by skin. The jaws are as long as broad. There may be up to 3 apical papillae although it is difficult to differentiate these papillae from the teeth. There are 3 oral papillae situated within the mouth slit below the level of the second oral tentacle pore which emerges quite superficially. There are no tentacle scales associated with the second oral tentacle pore. The adoral shields are wing-like often completely separating the oral shield from the first lateral arm plate. The oral shield is rounded, rhombic in shape.

The arms are long up to 10 times the disk diameter, covered with skin which obscures the underlying plates. The dorsal arm plates of each segment consist of two separate oval plates lying side by side isolated from the proceeding and succeeding ones. The ventral arm plates are rounded pentagonal with a rounded obtuse proximal angle and with the distal edge indented and are contiguous proximally. The tentacle pores are large and open without any tentacle scales. There are 5 arm spines obscured by thick skin; when denuded they appear glossy and quite rugose with large secondary points along the shaft of the spine.

Remarks. *O. spinosus* can be distinguished by the thin bar shaped radial shields which carry a single row of spinelets, the pointed oral and apical papillae, the lack of tentacle scales on the second oral tentacle pore and the thick skin which covers the disk and arms.

Distribution. *O. spinosus* has been recorded from the Denmark Strait, off SE. Iceland and south to the Azores, with a bathymetric range of 40–1310 m.

OPHIACANTHIDAE Perrier, 1891

A family with the disk ranging from a sack-like bag covered with skin or thin scales to a more rigid structure covered with large plates, usually armed with spinelets, granules, or simple rods, the density of covering varying; the characters of the oral frame falling into broad categories: either the jaws longer than broad with many papillae or as broad as long usually with fewer papillae, rarely more than 6–7; the arms usually noded but sometimes only slightly so; arm spines usually erect, often long and rugose; the tentacle pores either large and open with small tentacle scales or none at all or small with a variety of tentacle scales.

Remarks. The diagnosis above is a very general definition of this family which is a taxonomist's nightmare defying a unified description because of the variety of generic forms. The problem is that while the species of ophiacanthids are generally well described, most of the genera and families are ill-defined. Several authors (Verrill, 1899*a*, *b* and Matsumoto 1915, 1917) have attempted to revise the family but none of the schemes have been accepted in their entirity. At the risk of adding to the confusion four sub-divisions of the Ophiacanthidae are proposed for testing. The characters upon which these subdivisions are based are as follows: the nature of the arm spine articulation surface of the lateral arm plate, the SEM has revealed that the majority of genera studied in this family have one form, a comma-shaped tubercule (Fig. 13) but one genus, *Ophiomyces*, does not. Such is the widespread occurrence of this character that its absence prompts separating *Ophiomyces* and possibly *Ophiotholia* and *Ophiohelus* into a subfamily. The second set of characters used are the nature of the covering of the disk, and the form of the radial shields. These characters fall into two broad categories, the radial shields are sometimes bar-like and long, often covered over by the disk covering which is usually small thin scales or occasionally stouter scales, or a disk covered by distinct plates with the radial shield distinct

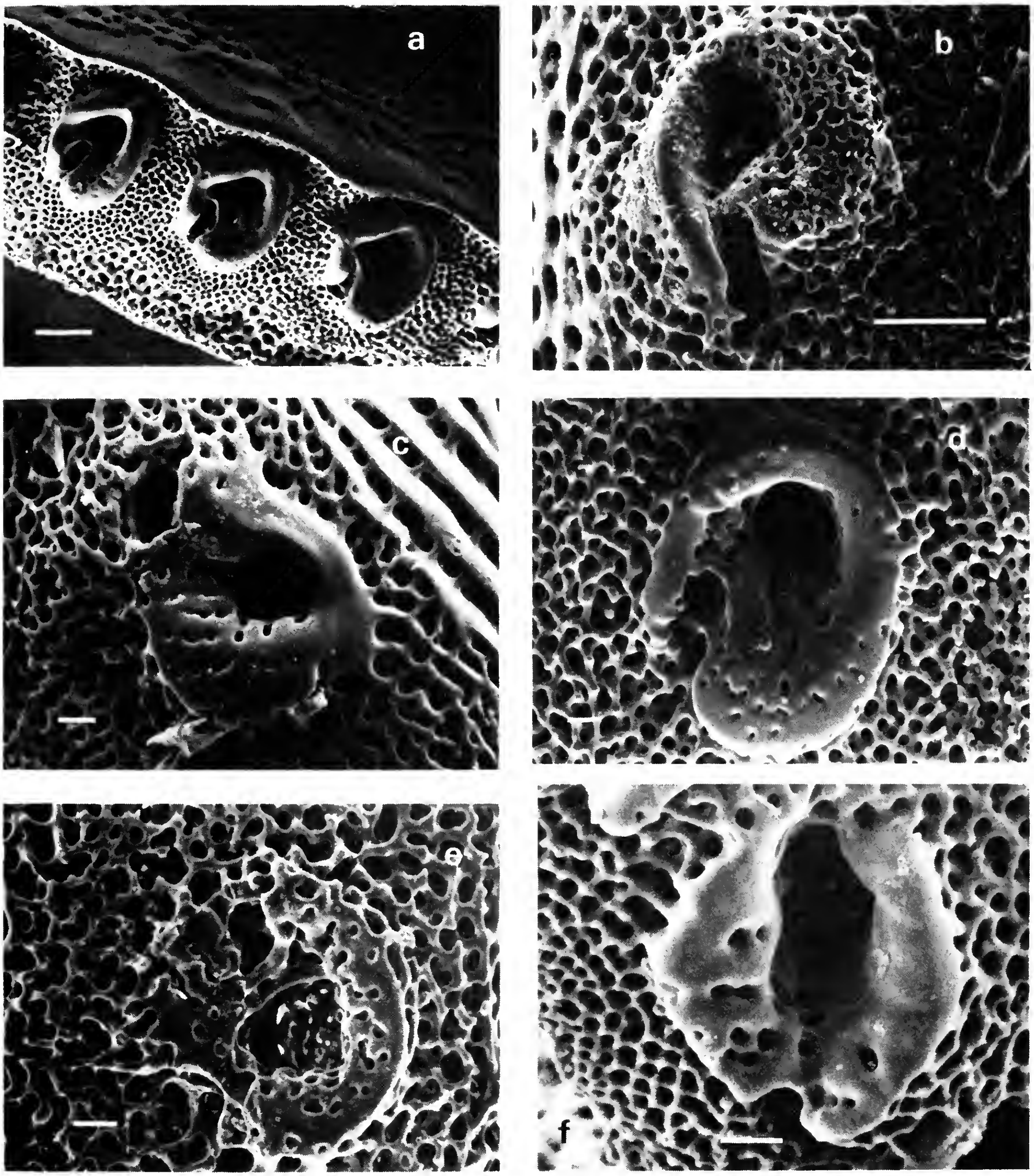


Fig. 13 Ophiacanthidae. SEM photographs of the arm spine tubercles on the lateral arm plate of: (a) *Ophiacantha aristata*, (b) *Ophiotoma coriacea*, (c) *Ophiocymbium cavernosum*, (d) *Ophioplinthaca abyssalis*, (e) *Ophiocamax dominans*, (f) *Ophiomyces frutectosus*. Bar scales a, b = 100 µ, c–f = 30 µ.

and integrated with the other plates. The final series characters used are the appearances of the jaw and the arrangement of the mouth papillae and tentacle pores. Again there are two broad categories: either the jaws appear longer than wide with many oral papillae and large open tentacle pores or the jaw appears as broad as long with few oral papillae and small tentacle pores.

The four subfamilies; Ophiacanthinae, Ophiotominae, Ophioplinthacinae and Ophiohelinae, are treated in detail under their respective headings.

Characters of taxonomic importance in the Ophiacanthidae

1. The disk (*a*) whether it is covered by small scales or by distinct plates; (*b*) most scales or plates carry one or more spinelets, the shape and density of these spinelets are important; (*c*) in some species of the subfamily Ophioplinthacinae the shape and position of radial shields is important. In the other subfamilies the radial shields are partially or totally hidden.

2. The jaw: the characters are: (*a*) the shape of the jaw; (*b*) the shape and arrangement of the apical and oral papillae; (*c*) the shape of the adoral and oral shields; (*d*) in species of the Ophiotominae the arrangement of the tentacle scales associated with the second oral tentacle pore and their alignment with the oral papillae.

3. The arms: (*a*) the form of the tentacle pore; (*b*) the number and shape of the arm spines, the degree of rugosity; (*c*) the number and shape of the tentacle scales; (*d*) whether the arm spines of the proximal joints meet midradially forming a fan when viewed transversely; (*e*) often in outline the arms amy appear to be constricted between the rows of arm spines usually because the articulation areas are elevated. The taxonomic significance of this noded shape has yet to be fully investigated.

OPHIACANTHINAE Sub Family nov

Diagnosis. A subfamily of the Ophiacanthidae with small imbricating transparent scales or skin covering the disk, the scales often armed with spinelets or granules which may obscure them; the disk sack-like, sometimes indented interradially; the radial shields not integrated with the disk but over laid by the scales or skin covering the disk with only their distal ends evident;.the jaws as broad as long; one to several apical papillae flanked by three to many oral papillae each side;. tentacle pores not conspicuously large usually armed with at least one tentacle scale; arm spines vary in length but dorsal ones usually longer than one arm segment, sometimes forming a fan on proximal arm segments.

Type genus. *Ophiacantha* with type species *O. bidentata* (Retzius)

Remarks. The genera now included in this subfamily are: *Ophiacantha* Müller & Troschel, 1842; *Ophiacanthella* Verrill, 1899; *Ophialcaea* Verrill, 1899; *Ophiogema* Koehler, 1922*a*; *Ophiolebes* Lyman, 1878 and *Ophiotreta* Verrill, 1899. The genera *Ophialcaea* and *Ophiotreta* were treated as subgenera of *Ophiacantha* by Mortensen (1936) and Fell (1960), but H. L. Clark (1915) and Koehler (1922, 1931) considered them to be of generic rank, a treatment followed here pending future study on the generic boundaries in this subfamily.

The most important characters which distinguish the Ophiacanthinae are the often long and narrow mainly internal radial shields; the small scale-like plates of the disk and the relative broad jaw coupled with a relatively simple arrangement of apical and oral papillae.

Ophiacantha anomala G.O. Sars., 1871

Fig. 14

Ophiacantha anomala G. O. Sars, 1871: 12; Verrill, 1885: 547; 1899*a*: 36; 1899: 324, 335; Grieg, 1902: 16; Mortensen, 1903: 86; 1913: 360; Koehler, 1914: 77; Mortensen, 1924: 115; 1927: 191; 1933*a*: 24–26.

Material studied. **BMNH:** Trondheim Fjord Norway 450–540 m 1 specimen; *Porcupine* Stn 64 653 m 1 specimen.

This species usually has six arms. The disk is round, covered by tall rugose spinelets with multipointed crowns; disk diameter up to 11 mm. Only the tips of the radial shields are visible but the extent of the plate beneath the disk can be distinguished. The ventral interradial areas are also covered with spinelets.

The jaws appear to be long and narrow. There is one thin spine-like apical papilla flanked by 3–5 oral papillae, occasionally there are many supernumerary papillae on the side of the jaw and over the adoral shields and jaw plates. The oral papillae are often long and the distalmost ones may be flared at the tips. The adoral shields are flared and wing-like separating or nearly separating the oral shield from the first lateral arm plate. The oral shield is a rounded pentagon with a straight distal edge and a rounded proximal one; in some specimens it may be more rounded, nearly oval.

OPHIACANTHIDAE

OPHIACANTHINAE

Ophiacantha

6 - ARMED SPECIES

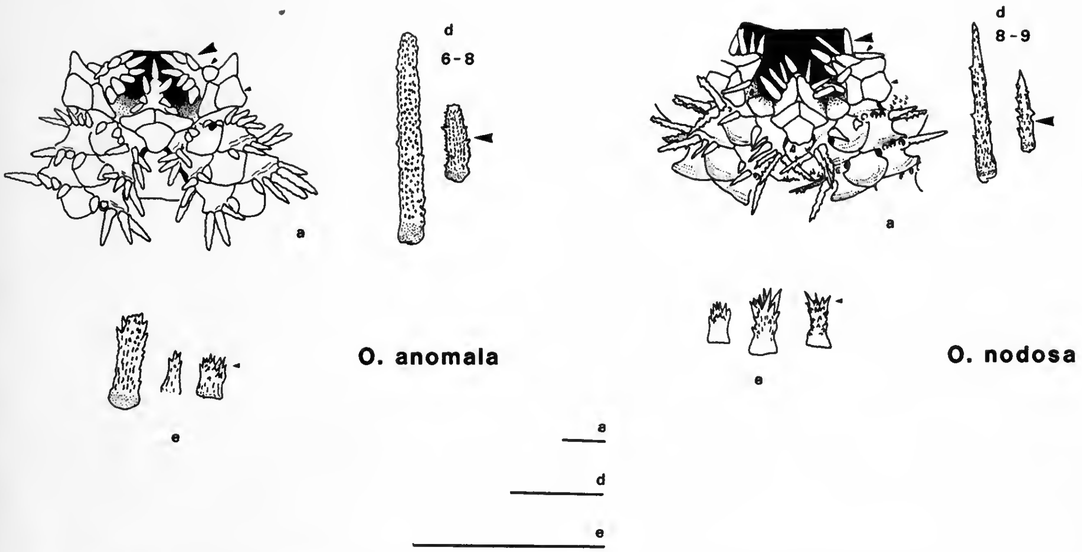
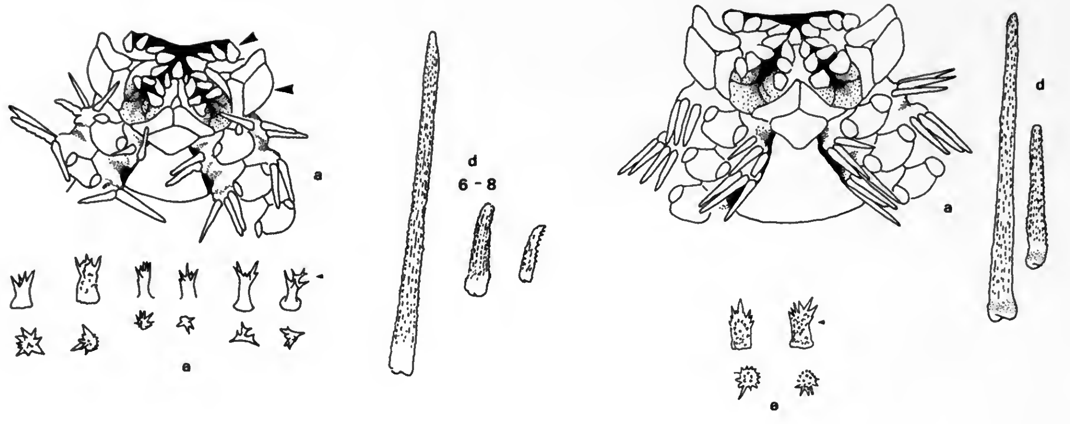


Fig. 14 Key to the Ophiacanthidae: Ophiacanthinae, *Ophiacantha* = six armed species: (a) ventral view of disk; (d) arm spines—a number with this figure indicates the number of proximal arm spines. The larger spine is the dorsalmost, the smaller a ventral spine; in figures with only one arm spine it is the dorsalmost one. A number with an arrow pointing to an arm spine signifies the number of proximal arm spines. (e) Disk spinelets. NB. The ventral interradial areas have been left blank in certain figures for clarity. Bar scales = 1 mm, letters above the bars refer to the figures.

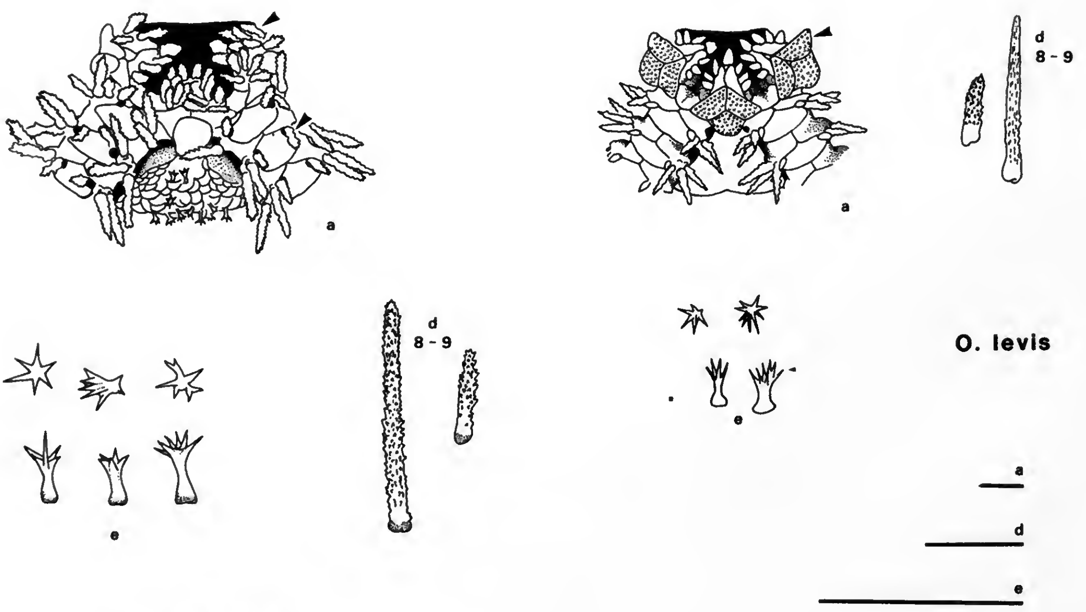
There are six slightly noded arms. The dorsal arm plates are rhombic to fan shaped and separated. The ventral arm plates are pentagonal with a rounded distal edge, which may also be slightly elevated, and are nearly contiguous. On the first tentacle pore on the arm there may be two large flat leaf shaped tentacle scales. Subsequent pores have only one. There are 6–8 arm spines proximally in large specimens, 4–5 in smaller ones. The ventralmost spines are finely rugose, the dorsal ones highly rugose. The dorsal or second dorsalmost spine is the longest. The arm spines do not form a fan across the first free joint.

REMARKS. *O. anomala* can easily be distinguished from other North Atlantic species of *Ophacantha* (except *O. nodosa* Lyman) because it has 6 arms. Although Koehler (1914) suggested that *O. nodosa* was conspecific with *O. anomala* several differences are apparent, *O. anomala differing from O. nodosa* by the following characters: **1.** the jaw appears narrower than *O. nodosa;* **2.** the apical and oral papillae do not appear to be as long nor as widely seperated from each other

5 - ARMED SPECIES



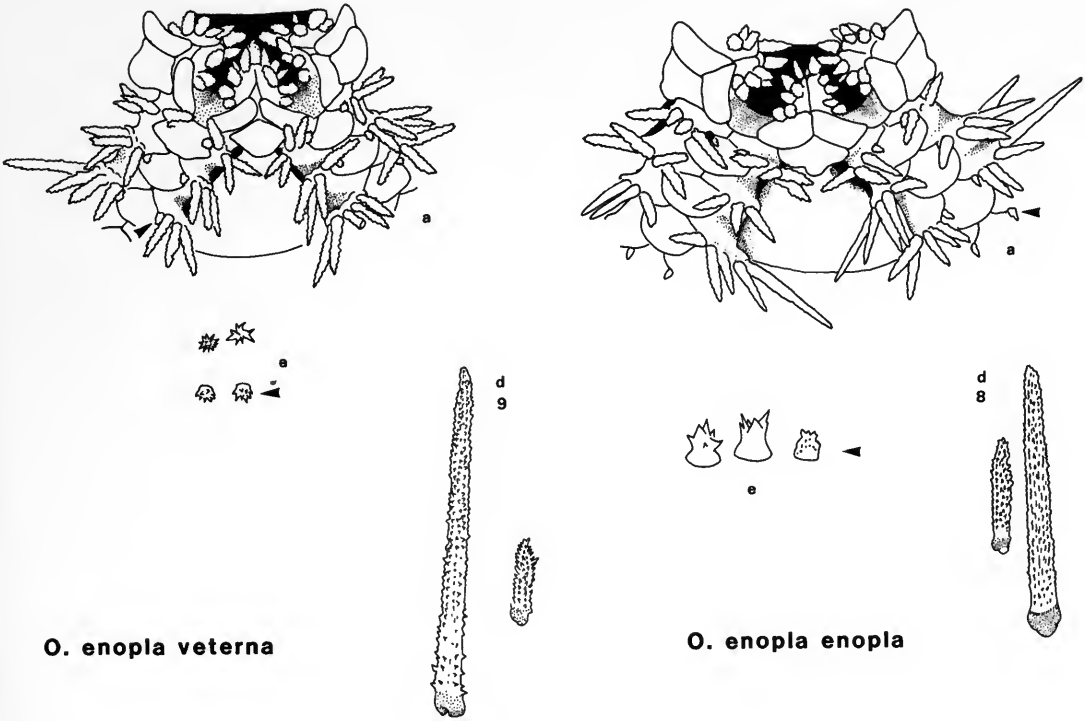
O. bidentata



O. levis

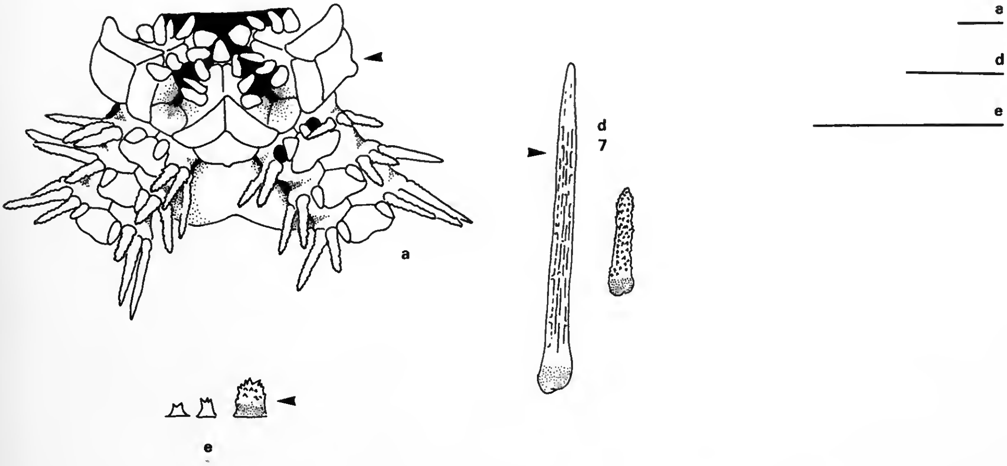
O. aristata

Fig. 15 Ophiacanthidae: Ophiacanthinae. *Ophiacantha*—five armed species. Captions as in Fig. 14.



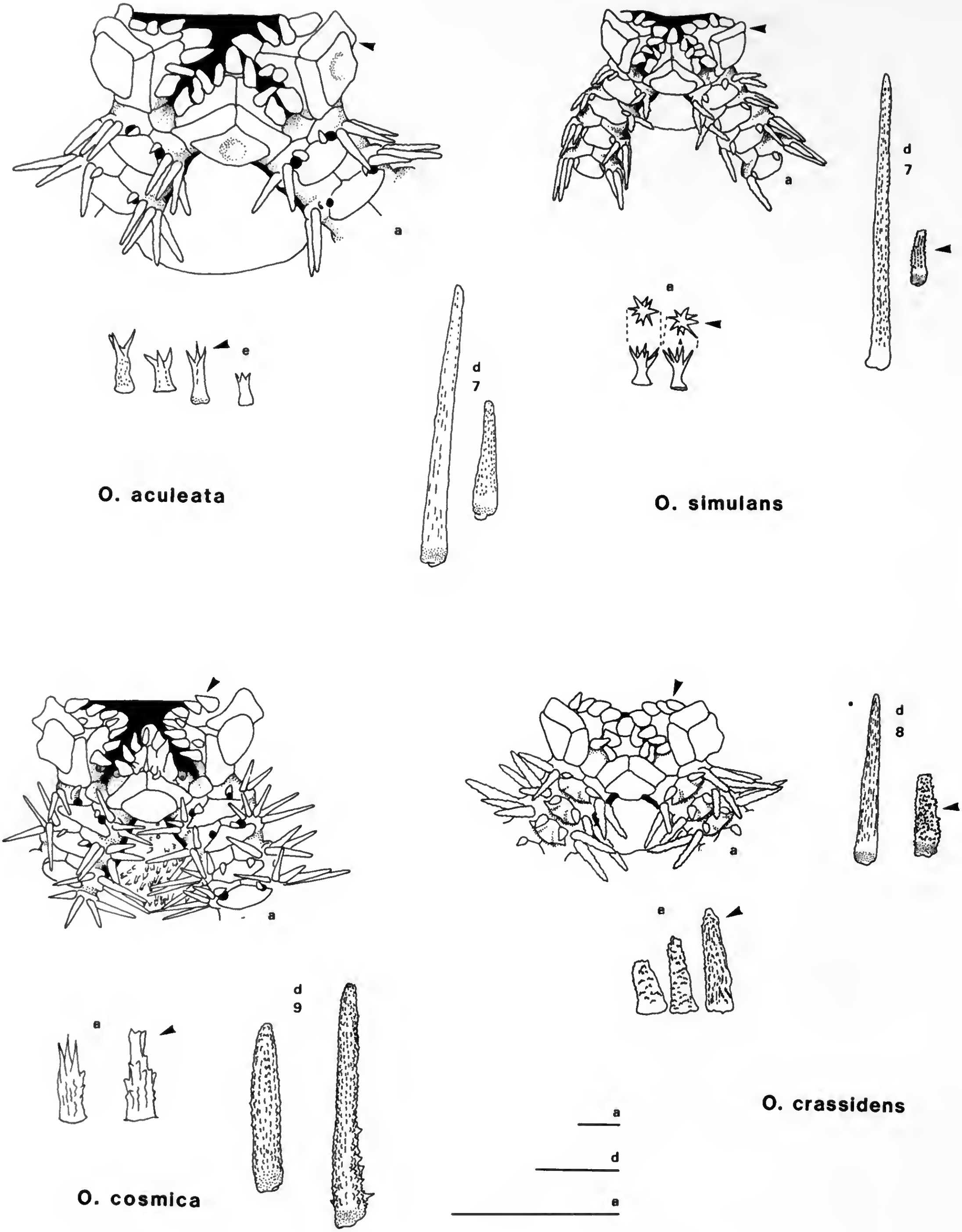
O. enopla veterna

O. enopla enopla



O. setosa

Fig. 16 Ophiacanthidae: Ophiacanthinae. *Ophiacantha*—five armed species. Captions as in Fig. 14.



O. aculeata

O. simulans

O. cosmica

O. crassidens

Fig. 17 Ophiacanthidae. Ophiacanthinae. *Ophiacantha*—five armed species. Captions as in Fig. 14.

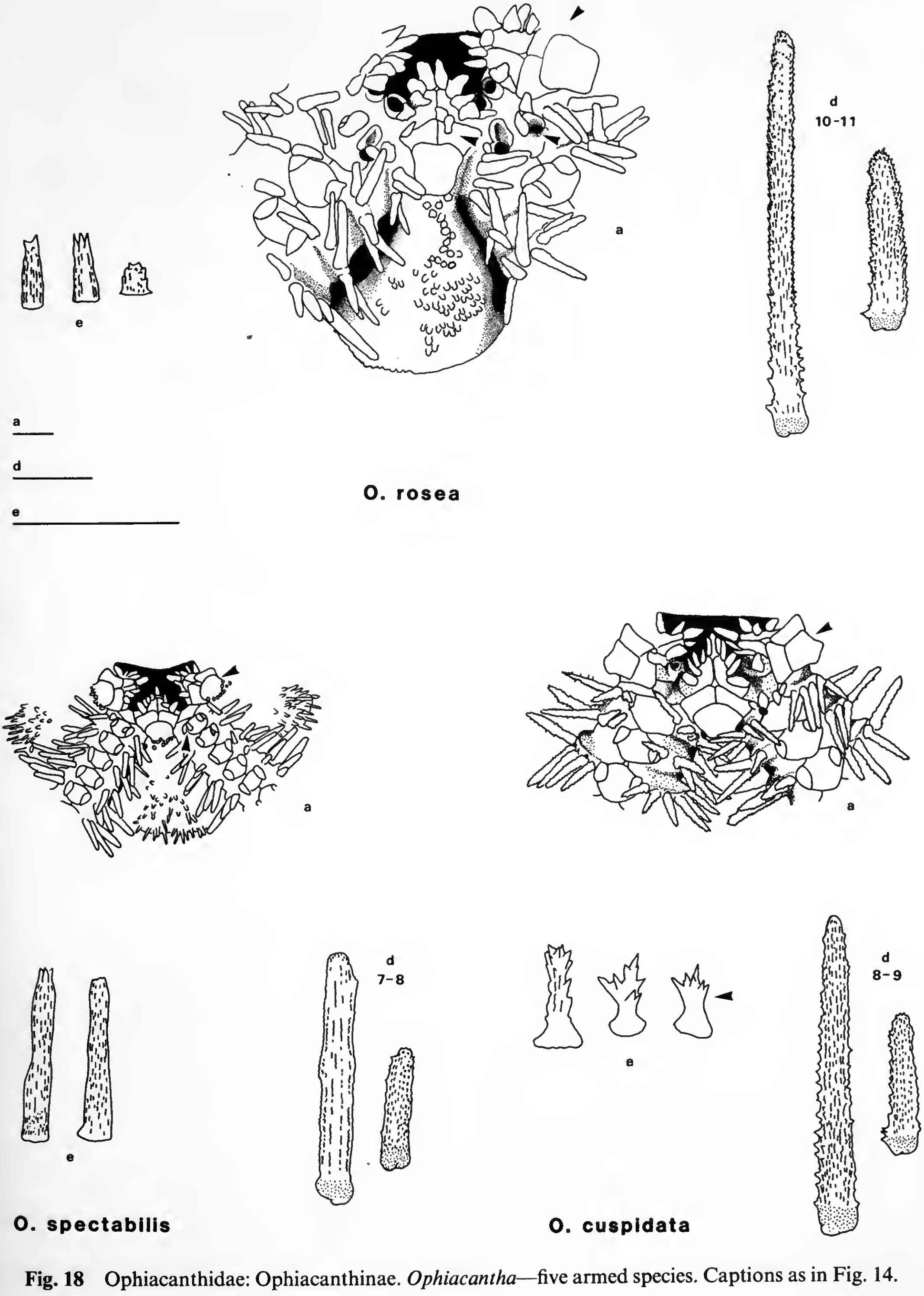
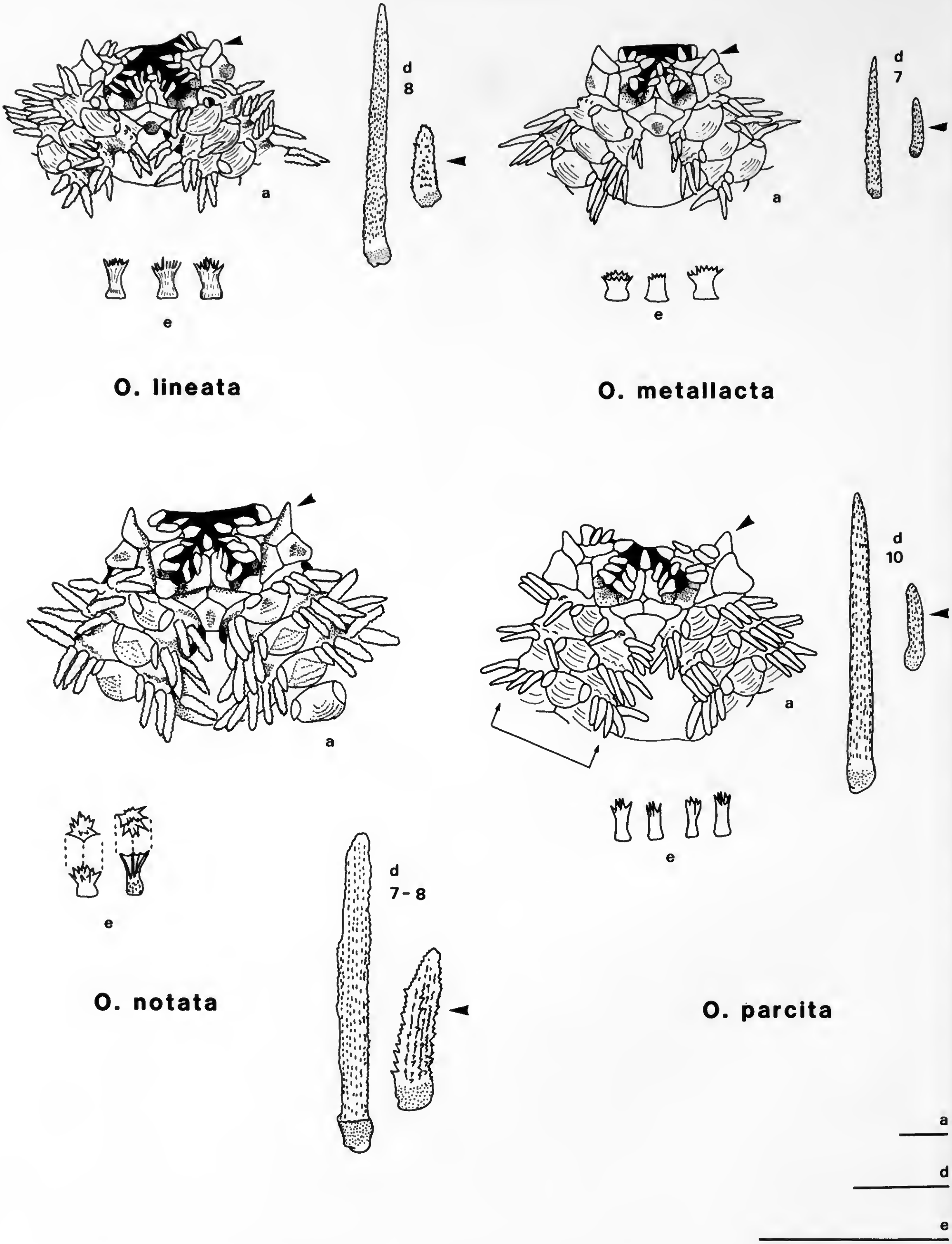


Fig. 18 Ophiacanthidae: Ophiacanthinae. *Ophiacantha*—five armed species. Captions as in Fig. 14.



O. lineata

O. metallacta

O. notata

O. parcita

Fig. 19 Ophiacanthidae: Ophiacanthinae. *Ophiacantha*—five armed species. Captions as in Fig. 14.

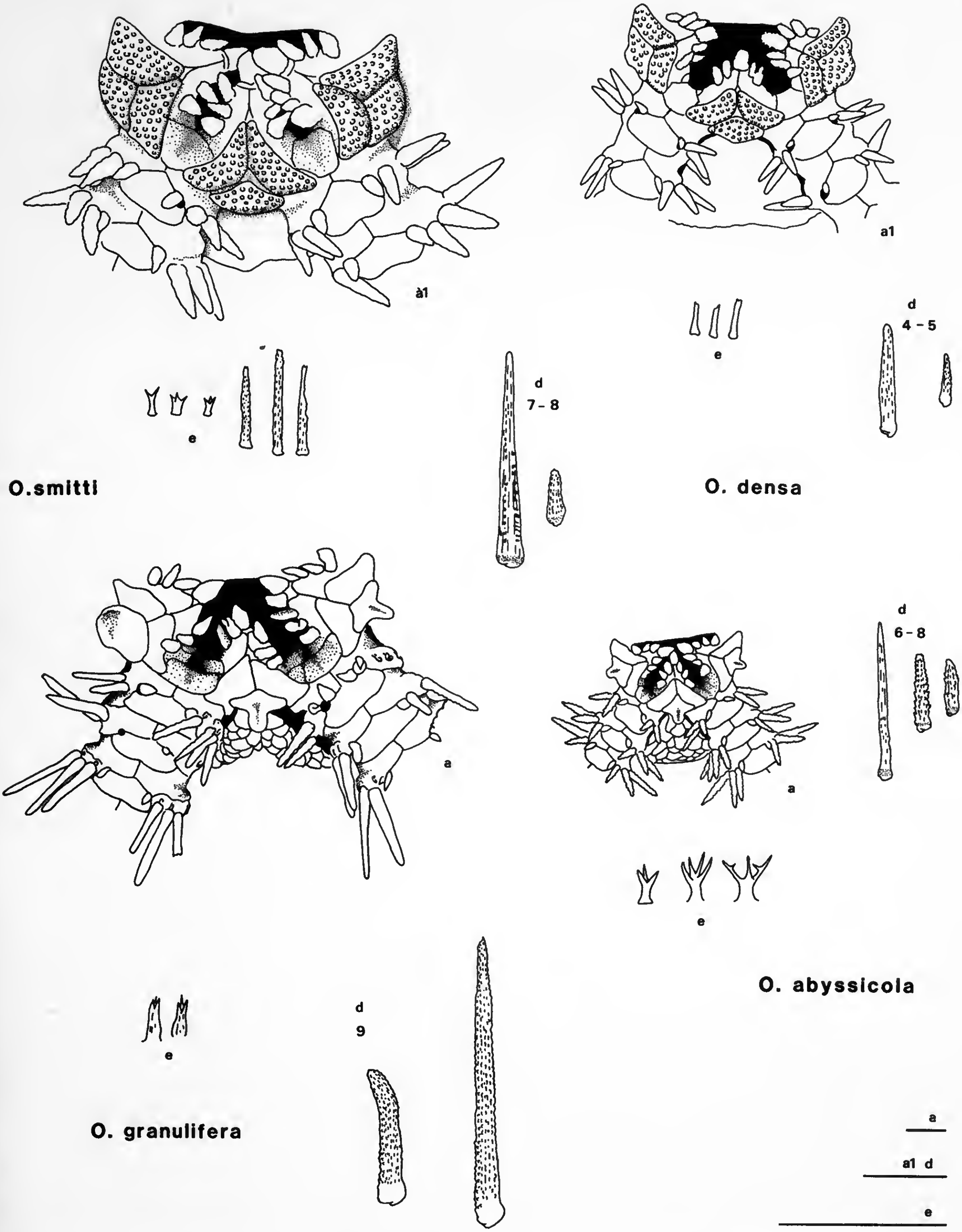
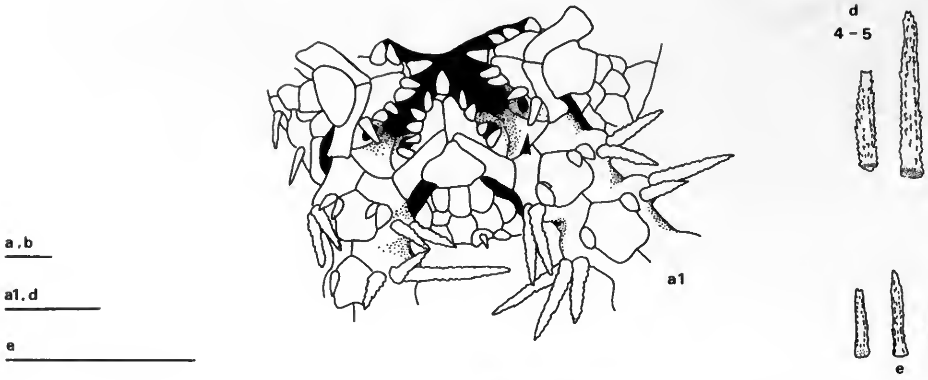
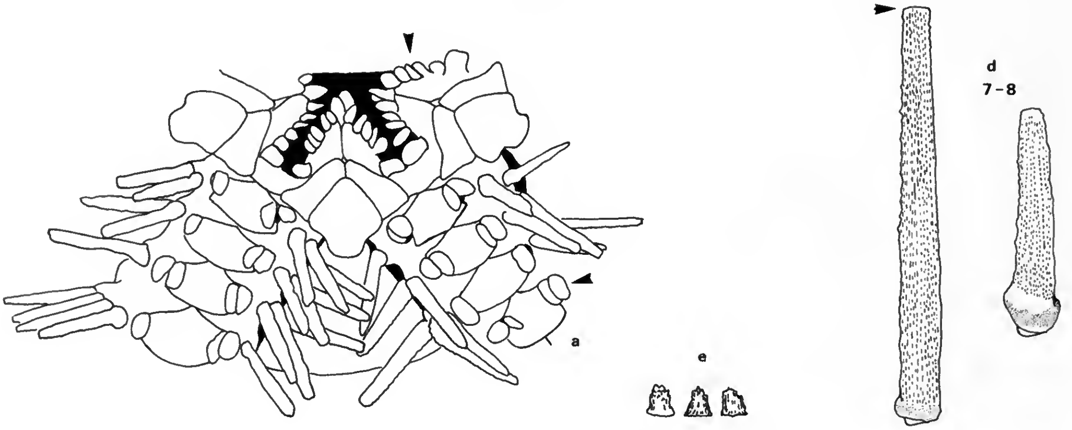


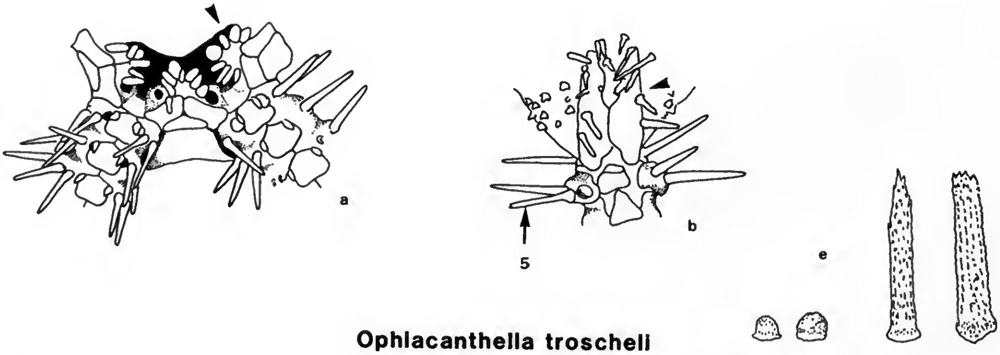
Fig. 20 Ophiacanthidae: Ophiacanthinae. *Ophiacantha*—five armed species. Captions as in Fig. 14.



O. spinosella



Ophiotreta valenciennesi rufescens



Ophiacanthella troscheli

Fig. 21 Ophiacanthidae: Ophiacanthinae. *Ophiacantha*—five armed species; *Ophiotreta* and *Ophiacanthella*. Captions as in Fig. 14.

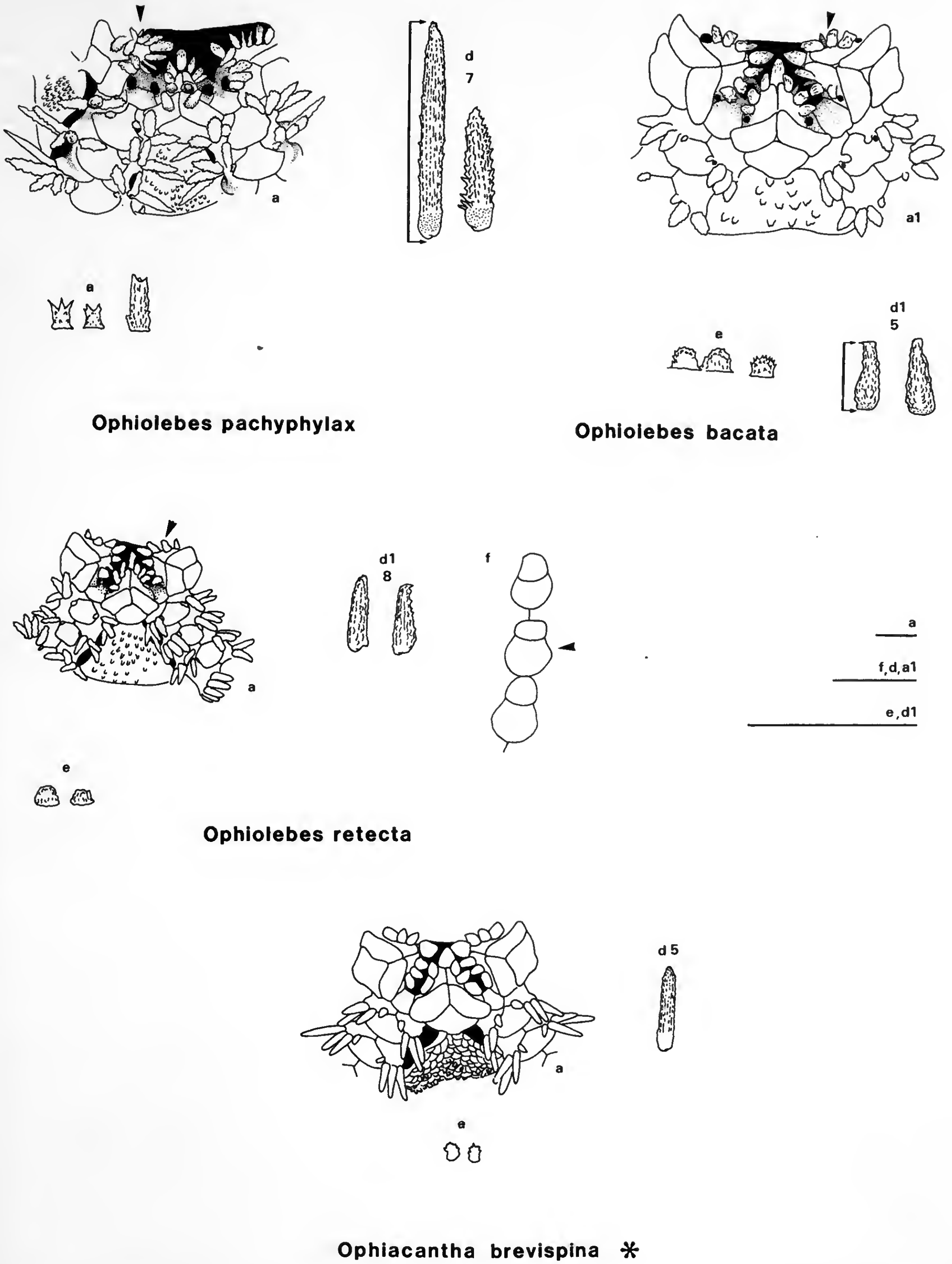


Fig. 22 Opiacanthidae: Ophiacanthinae. *Ophiolebes* and supplement to *Ophiacantha*. Captions (a)–(e) as in Fig. 14; (f) dorsal arm plates, *–not described in text.

as in *O. nodosa;* **3.** the distalmost oral papilla is often large and flap like in *O. anomala* but long and flattened like the other papillae in *O. nodosa;* **4.** the shape of the oral shields differs in *O. anomala* where it is rounded pentagonal with a rounded to obtuse proximal angle, straight lateral sides and a straight or slightly rounded distal edge, in *O. nodosa* it is a more ornate pentagonal shape with an obtuse proximal angle, slightly indented lateral sides and a rounded distal edge or one with a slight median projection; **5.** the ventral arm spines of *O. anomala* are slightly rugose with small or no secondary points doing the shaft; those of *O. nodosa* have very prominent secondary points along the shaft; **6.** the ventral arm plates of *O. anomala* appear to be narrow and less axehead shaped than *O. nodosa.* Until more material of *O. nodosa* is available it would be best to treat them as distinct specimens.

DISTRIBUTION. It has been recorded from both sides of the North Atlantic: in the west from off Florida to SW. Iceland 141–1200 m, and in the east from Iceland, Norway and the Rockall trough 140–1500 m.

Ophiacantha nodosa Lyman, 1878

Fig. 14

Ophiacantha nodosa Lyman, 1878: 144–145; Mortensen, 1933*a*: 25–26.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 3 25°45′N: 20°12′W 2789 m. HOLOTYPE.

This species has six arms: the disk is round, covered by tall rugose spinelets with a multipointed crown in many instances often abraded; disk diameter 5·5 mm. Only the tips of the radial shields are visible and even then they may carry spinelets. The ventral interradial area is covered by spinelets similar to those of the dorsal side.

The jaw appears long and narrow. There is one long pointed apical papilla flanked on either side by 3–4 similarly shaped apical papillae; the papillae have a slightly rugose texture and are well separated from one another. The adoral shields are about twice as long as broad not particularly wing-like and not separating the oral shield from the first lateral arm plate. The oral shield is rounded pentagonal but with a convex distal edge.

The arms are distinctly noded, the ridges carrying the arm spines being particularly prominent. The dorsal arm plates are fan shaped with an acute proximal angle and separated. The ventral arm plates are nearly pentagonal with a distinct convex distal edge textured with layers of calcite forming a concentric pattern. There is one large pointed slightly rugose tentacle scale on each pore. There are 8–9 arm spines. The ventral ones are slightly flattened and very rugose; the dorsal ones appear smooth or finely rugose. They do not quite meet midradically to form a fan on the proximal joints.

REMARKS. Koehler (1914) considered that *O. nodosa* was conspecific with *O. anomala* but several characters appear to separate them as detailed under *O. anomala.*

Ophiacantha bidentata (Retzius, 1805)

Fig. 15

Asterias bidentata Retzius, 1805: 33.
Ophiocoma bidentata: Müller & Troschel, 1842: 99.
Ophiacantha spinulosa Müller & Troschel, 1842: 107; Lütken, 1859: 65; Lyman, 1865: 93.
Ophiacantha grönlandica Müller & Troschel, 1842: 183.
Ophiacantha bidentata: Lyman, 1882: 186; Verrill, 1885: 545; Bell, 1892: 127; Grieg, 1893: 22; Koehler, 1896*a*: 79; 1896*b*: 212; Koehler, 1898: 55; Verrill, 1899*a*: 36; 1899*b*: 323, 335; Grieg, 1900: 267; H. L. Clark, 1901: 249; Koehler, 1901: 102; Knipovich, 1901: 1; Whiteaves, 1901: 60; Grieg, 1902: 13; 1903: 31; Michaelovskij, 1902: 533; Mortensen, 1903: 86; Michaelovskij, 1904: 174; Grieg, 1905: 159; Schmitt, 1904: 24; Koehler, 1907: 289; Kalischewskij, 1907: 19; Koehler, 1909: 184; Grieg, 1910: 5; H. L. Clark, 1911: 30; Mortensen, 1913: 358; Koehler, 1914: 80; Mortensen, 1927: 196; Grieg, 1928*a*: 10; 1928*b*: 19; Mortensen, 1932: 26; Nobre, 1931: 81; Mortensen, 1933*a*: 20–22; Heding, 1935: 58; Djakanov, 1954: 36–37; Grainger, 1955: 907; Tyler & Gage, 1982: 45–55; Gage *et al.* 1983: 289–290.
Ophiacantha fraterna Verrill, 1885: 545; Koehler, 1914: 83; H. L. Clark, 1915: 198.

MATERIALS STUDIED. **BMNH:** *Ernest Holt* Barent Sea (several localities) 24 specimens; *Porcupine* Lofoten Is Norway 37–55 m 4 specimens; *Porcupine* Stn 52 702 m 2 specimens; *Porcupine* Stn 57 805 m 2 specimens; D'Arcy Thompson Coll. off Norman's Light Labrador 1 specimen; Arctic Expedition 1875–76 Franklin Pierce Bay, N. Canada 2 specimens; *Ernest Holt* various localities around southern Greenland 24 specimens; Kara Sea 3 specimens.

COB: BIOGAS Stn 1: DS12 2180 m 1 specimen; DS15 2246 m 26 specimens; DS16 2325 m 4 specimens; DS17 2103 m 14 specimens; DS18 2138 m 14 specimens; DS35 2226 m 5 specimens; DS63 2250 m 1 specimen; DS64 2156 m 3 specimens; DS71 2194 m 1 specimen; CV09 2119 m 2 specimens; CV10 2108 m 9 specimens; CV20 2282 m 12 specimens; CV23 2034 m 4 specimens; CV24 2025 m 7 specimens; CV25 1985 m 1 specimen; CP01 2245 m 38 specimens; CP02 2177 m 23 specimens; CV39 2350 m 18 specimens; CP08 2177 m 11 specimens; CP26 2115 m 13 specimens; CP27 1920 m 12 specimens.

BIOGAS Stn 2: DS58 2775 m 1 specimen; DS74 2774 m 1 specimen CV12 2775 m 1 specimen; CV26 2822 m 1 specimen; CV40 2860 m 3 specimens; CP09 2171 m 30 specimens; CP10 2878 m 2 specimens; CP12 2925 1 specimen; CP28 3380 m 2 specimens.

BIOGAS Stn 4: DS23 4734 m 3 specimens; CV35 4721 m 4 specimens.

BIOGAS Stn 6: DS25 2096 m 4 specimens; DS26 2076 m 11 specimens; DS51 2430 m 2 specimens; DS70 2150 m 3 specimens; CV16 1909 m 1 specimen; CV32 1895 m 6 specimens; CP07 2170 m 36 specimens; CP23 1980 m 2 specimens.

BIOGAS Stn HZ: DS04 1100 m 1 specimen; DS14 1560 m 17 specimens; CV05 2305 m 2 specimens; CV06 2200 m 1 specimen; CW03 2160 m 2 specimens; CV11 2141 m 9 specimens.

INCAL: Stn WS01 50°18′N: 13°08′W 2550 m 1 specimen; Stn CP01 57°57′N: 10°55′W 2068 m 376 specimens; Stn CP02 57°58′N: 10°42′W 21 specimens; Stn CP04 56°33′N: 11°11′W 2494 m 5 specimens; Stn CP09 50°15′N: 13°16′W 2719 m 1 specimen.

IOS: *Discovery* Investigations: Stn 8512/4 42°15·2′N: 11°35·2′W 2281–2465 m 2 specimens; Stn 9041 1 specimen; Stn 9133/5 20°57·5′N: 18°13·7′W 1 specimen.

SMBA: RRS *Challenger II.* Stn ES 55 54°40′N: 12°16′W 2878 m 2 juveniles Stn ES 112 55°12′N: 15°50′W 1900 m 20 specimens; Stn AT 141 54°44′N: 12°14′W 2909 m; Stn ES 195 57°23′N: 10°27′W 2190 m 186 specimens; Stn ES 197 57°21′N: 10°29′W 104 specimens.

The disk is round, covered with an armament of spinelets or sometimes granules which obscure the scales of the disk; disk diameter up to 13 mm. The spinelets are basically trifid but may be elaborated with secondary points; in larger specimens, disk diameter greater than 7 mm, the armament has the form of rugose granules which may be abraded spinelets. The radial shields are long, thin and separated usually with only their distal ends visible. The ventral interradial areas have similar armament to the dorsal side.

The jaw is as broad as long. There is one pointed apical papilla flanked by 3–4 oral papillae, occasionally as many as 5 or 6 on each side. The oral papillae are usually pointed although distalmost ones may be slightly rectangular. The adoral shields are long and thin and barely separating, if at all, the oral shield from the first lateral arm plate. The oral shield is variable ranging from a lozenge to a flattened triangle.

The arms have a distinct noded appearance. The dorsal arm plates are fan shaped and usually separated but proximal ones may be contiguous. The ventral arm plates are pentagonal to square with a rounded or sometimes concave distal edge; they are usually separated throughout the arm. There is one scale-like scale on each tentacle pore. There are 6 to 8 finely rugose arm spines on the proximal arm segments; on distal segments the ventral spines may be flattened and have a comb-like structure along one edge.

REMARKS. *O. bidentata* can be distinguished from other *Ophiacantha* species by the form of the spinelets which are either rugose granules or trifid spinelets, the larger specimens usually having more abraded spinelets; the arrangement of the oral papillae; the shape of the oral shields which are basically rhombic although variable in shape; and the texture of the arm spines which are finely rugose.

O. bidentata is a variable species; particularly with regard to the shapes of the dorsal and ventral arm plates, the tentacle scales and the disk armament. Mortensen (1933*a*) considered *O. fraterna* to be a variety of *O. bidentata* apparently more commonly found in the cold water regions of the Atlantic. If such a geographical distribution holds good then *O. fraterna* should be treated as subspecies distinguished from *O. bidentata bidentata* by the nearly bell shaped dorsal arm plates which are sometimes contiguous on proximal arm segments and by the ventral arm plates which are notched on the distal edge.

Recent work by Tyler & Gage (1982) has shown that the deep sea populations have a different reproductive cycle to shallow high Arctic ones. As yet there is no morphological features which can distinguish them as separate species, except perhaps the features mentioned above but this needs to be investigated.

DISTRIBUTION. This is a very common Arctic and North Atlantic species. It has been recorded in the west from South Carolina north to Greenland and in the east from southern Iceland, south to the Azores and off north Africa with a bathymetric range 32–4730 m. In the Arctic it has been recorded from Baffin Bay, Barents, Kara and Siberians Seas. It has also been recorded in the northern Pacific from the Bering Sea to off Japan.

Ophiacantha aristata Koehler, 1896*a*

Fig. 15

Ophiacantha aristata Koehler, 1896*a*: 84; 1896*b*: 212; 1898: 55; Farran, 1913: 43–44; Mortensen, 1927: 193–194; Grieg, 1932: 38.

MATERIAL STUDIED. **MNHN:** *Talisman* 1883 Stn 52 28°33′N: 15°39′W 946 m 5 specimens.
IOS: *Discovery* Investigations: Stn 8519/7 24°02′N: 16°59′W 997–1037 m 2 specimens; Stn 8967 31°25·9′N: 10°53·7′W 8 specimens; Stn 9042 42°15′N: 11°22′W 1662–1541 m 5 specimens.
DM: Irish Fisheries *Helga* S.R. 477 51°15′N: 11°47′W 1272–1278 m 1 specimen.

The disk is round, covered with spinelets, disk diameter up to 8 mm. The spinelets are crowned with 9 or more points which may be subdivided into secondary points giving the crown a very irregular appearance. The radial shields are sometimes inconspicuous but in some specimens their distal ends may be distinguishable. The ventral interradial areas are covered with spinelets similar to those of the dorsal side.

The jaws are as broad as long. There is one pointed apical papilla flanked on each side by 3–4 rugose oral papillae, although in some specimens there may be more giving the appearance of a double row. The oral papillae are longer than broad and may be widened at their free end. The adoral shields are longer than broad separating the oral shield from the first lateral arm plate. The oral shield is approximately rhombic sometimes with the distal edge slightly produced.

The arms are distinctly noded. The dorsal arm plates are triangular to fan shaped and separated from one another. The ventral arm plates are pentagonal to nearly rectangular with a convex distal edge, and are separated from one another. There is one highly rugose spine-like tentacle scale on each tentacle pore. There are 8–9 highly rugose arm spines proximally, the dorsal most is the longest equal to 3 arm segments; on proximal joints the arm spines may meet in the midradial line forming a single fan.

REMARKS. *O. aristata* may be confused with *O. bidentata,* particularly juveniles. It can be separated from *O. bidentata* by the following characters; the spinelets of the disk have more points and are more irregular; the arm spines are highly rugose and the tentacle scale is also rugose and spine-like while that of *O. bidentata* is small, flat and scale-like.

DISTRIBUTION. *O. aristata* has only been recorded from the north-east Atlantic: from the Canary Islands north to SW. Ireland with a bathymetric range of 822–1700 m.

Ophiacantha enopla enopla Verrill, 1885*a*

Fig. 16

Ophiacantha enopla Verrill, 1885*a*: 153; 1899*a*: 37, 42; 1899*b*: 331.

MATERIAL STUDIED. **USNM:** *Fish Hawk* Stn 1124 40°01′N: 68°54′W off Martha's Vineyard 1152 m SYNTYPE.

The disk is round to subpentagonal, up to 11 mm in diameter; and is covered with stubby spinelets with an irregular crown of many points. The radial shields are not visible. The ventral interradial areas are also covered with spinelets which are more nearly granular than those of the dorsal side.

The jaws are as broad as long. The single spineform apical papilla is flanked by 6 or more rugose, often blunt and peg-like oral papillae which are irregularly arranged on each side. The adoral shields are large but do not separate the oral shield from the first lateral arm plate. The oral shield is rhombic often with the two proximal sides indented.

The arms are slightly noded. The dorsal arm plates are triangular to fan shaped; the first 2–3 dorsal arm plates may be contiguous. The ventral arm plates are pentagonal with a rounded distal edge, proximal plates are contiguous or nearly so. There is one small rugose tentacle scales on each tentacle pore. There are proximally 8 slightly rugose arm spines, the second dorsalmost one the largest, equal in length to 3 segments. The proximal arm spines do not form a fan.

REMARKS. The similarity of this western Atlantic subspecies to its eastern counterpart is dealt with under the REMARKS section of *O. enopla veterna.*

DISTRIBUTION. *O. enopla enopla* has so far only been recorded from SE. of Cape Cod at a depth of 1152 m.

Ophiacantha enopla veterna (Koehler, 1907*b*)
Fig. 16

Ophiacantha veterna Koehler, 1907*b:* 41; 1909: 189; Mortensen, 1927: 187.

MATERIAL STUDIED. **COB:** BIOGAS Stn 6: CP07 2170 m 1 specimen; CP23 1980 m 1 specimen. BIOGAS Stn 1: CV10 2108 m 2 specimens; CP01 2245 m 1 specimen; CP02 2177 m 4 specimens.
IOS: *Discovery* Investigations: Stn 8005 22°29'N: 17°14'W 101 m 1 specimen, Stn 9042 42°15'N: 11°22'W 1662–1541 m 48 specimens.

The disk is round to subpentagonal covered by low granules which have a rugged crown of many small points, disk diameter up to 11 mm. Often the whole length of the radial shields is visible and they may be bowed upwards in some specimens. The ventral interradial areas are also covered with granules although perhaps not as densely as the dorsal surface.

The jaws appear to be as broad as long. There is one pointed slightly rugose apical papilla usually flanked by 4 oral papillae on each side but frequently there are also irregularly arranged papillae. The oral papillae are blunt conical and rugose. The adoral shields are long and narrow and do not separate the oral shield from the first lateral arm plate. The oral shield is pentagonal to lozenge shaped, with the 2 proximal sides indented and the distal sides convex.

The arms are only slightly noded. The dorsal arm plates are fan shaped to bell shaped and separated. The ventral arm plates are pentagonal and separated. The tentacle pores are small with 'spine-like' scales on the first and second arm pores but subsequently become very much smaller and are absent on distal pores. Proximally there are 9 arm spines, distally 7. The dorsal arm spines are smooth to finely rugose with large secondary points along the shaft, the ventralmost spines are highly rugose. The proximal arm spines approach midradially but do not form a single fan.

REMARKS. *O. enopla veterna* is characterised by the many rugose oral papillae and the low rugose granules. *O. enopla veterna* differs from *O. enopla enopla* chiefly by the shapes of the disk spinelets and the tentacle scales; the spinelets appear to be larger in *O. enopla enopla* and have a better defined crown with distinct points. The tentacle scales of *O. enopla enopla* are small and rugose while those of *O. enopla veterna* are very small and missing distally. These characters are not of sufficient weight to warrant maintaining *O. enopla* as a separate species.

DISTRIBUTION: *O. enopla veterna* has been recorded only from the eastern Atlantic from the Bay of Biscay south to the Azores and Madeira, with a bathymetric range of 101–2245 m.

Ophiacantha setosa (Retzius, 1805)
Fig. 16

Asterias setosa Retzius, 1805: 30.
Ophiacantha setosa: Müller & Troschel, 1842: 106; Marenzeller, 1893: 12; Koehler, 1892: 414; 1896*b*: 212; 1898: 12; 1906: 6; 1907: 291; Gallo, 1926: 19; Nobre, 1931: 83; Cherbonnier, 1962: 5–6; Madsen, 1970: 161.

MATERIAL STUDIED. **BMNH:** Rad Nord and South of the Rion, off Marseille 60–110 m 7 specimens.

The disk is round, sometimes indented interradially, diameter up to 12 mm. The disk is covered with scales which may be obscured by thickened skin. Low granules are found sporadically over the disk, slightly larger ones in the vicinity of the radial shields. Usually only the tips of the radial shields are visible but in some specimens a large distal portion of the shield may be visible. The ventral interradial area is covered by scales slightly larger than those of the dorsal side, few bearing granules.

The jaws are as long as broad. There is a stout pointed apical papilla flanked by 3 pointed oral papillae on each side. The adoral shields are slightly convex; they do not separate the oral shield from the first lateral arm plate. The oral shield is rhombic sometimes with a distinct distal lobe.

The arms are slightly noded. The dorsal arm plates are bell shaped; all are separated. The ventral arm plates are slightly rectangular with a convex distal edge which in some specimens may have a median concave indentation. The tentacle pores are large. The basal part of the tentacle itself appears to be reinforced with calcite and resembles a tube out of which the distal part of the tentacle projects. There is one rather large rugose pointed tentacle scale on each tentacle pore. There are 7 arm spines proximally, 6 distally, forming a fan over the arms on the proximal points. The dorsal arm spines are long and glassy often with sharp secondary points on the shaft. The dorsal or second dorsalmost spine is the longest, up to 3 arm segments long. The ventral arm spines are highly rugose.

REMARKS. *O. setosa* is recognisable by the skin covering of the disk, the low density of granule-like armament, the shape of the oral shield and the glassy arm spines.

DISTRIBUTION. *O. setosa* has been recorded from the Mediterranean and the Eastern Atlantic, as far north as the Bay of Biscay, and south to Angola. Most records come from shelf or bathyal depths, 50–1480 m.

Ophiacantha cosmica Lyman, 1878
Fig. 17

Ophiacantha cosmica Lyman, 1878: 146; 1882: 194–195; Koehler, 1909; 611; Clark, 1939: 42; Tommasi, 1970: 17.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 157 53°55′S: 108°35′E 3566 m HOLOTYPE & 2 PARATYPES.

The disk is round, diameter up to 19·5 mm; covered by a dense coating of long rugose spinelets with basically a trifid crown. The radial shields are usually covered although in some specimens it is possible to see the outline of distal end. The ventral interradial areas are also covered by spinelets which are slightly smaller than those of the dorsal side.

The jaws appear wider than long. There is one large broad apical papilla which sometimes lies within the mouth slit. Several papillae may lie above it. It is flanked by 3–4 large pointed oral papillae each side, of which the distalmost is the largest. In addition to these papillae there may be several supernumerary papillae situated on the edge of the jaw and on the edge of the adoral shields, but they are less common in smaller specimens. The adoral shields are wide and distinctly wing-like, separating the oral shield from the first lateral arm plate. The oral shield is somewhat variable in shape but is basically a rounded rhombic or triangular shape, the distal edge being more or less flattened or convex.

The arms are not distinctly noded proximally. The dorsal arm plates are fan shaped not or only just contiguous proximally, separated distally. The ventral arm plates are wider than long, pengatonal or nearly triangular with a wide distal edge which may be slightly indented; all are separated. There is one small pointed tentacle scale on each pore. There are 9 arm spines proximally, 7–8 distally in large specimens, 6–8 on smaller ones. The arm spines are finely rugose with occasional larger points, the second or third dorsalmost ones which are often up to 2 arm segments long. In some specimens the arm spines form a fan on the proximal arm segment.

REMARKS. This species may be recognised by the long rugose disk spinelets, the large apical and oral papillae, and the large adoral shields.

DISTRIBUTION. *O. cosmica* has a widespread distribution being recorded from the Atlantic, Indian and Pacific Oceans. In the North Atlantic it has only been recorded from south of Martha's Vineyard in 2509 m.

Ophiacantha aculeata Verrill, 1885*a*
Fig. 17

Ophiacantha aculeata Verrill, 1885*a*: 153; 1899*a*: 32; 1899*b*: 323, 335; Mortensen, 1933*a*: 28–29; Gage *et al.* 1983: 291.

MATERIAL STUDIED. **COB:** BIOGAS Stn 2: DS41 3548 m 7 specimens; CP11 3056 m 35 specimens; CP28 3380 m 80 specimens.
IOS: *Discovery* Investigations: Stn 7711/8 53°09·8′N: 20°14·7′W 2425–2430 m 3 specimens. 'Knorr' cruise Stn 35 39°10′N: 71°35′W 2 specimens.
SMBA: RRS *Challenger II*: Stn SWT 13 52°04′N: 16°09′W 3463 m 1 specimen.

The disk is round, to slightly pentagonal, diameter up to 13 mm; covered by trifid spinelets, rarely the spinelets may be more elaborate but often the crown is indistinct and the spinelets appear to be rugose. Only the tips of the radial shields are visible although the extent of the shield can be discerned beneath the scales of the disk. The ventral interradial areas are also covered with spinelets.

The jaw appears broader than long. There is one large often blunt apical papilla flanked by 3 oral papillae on each side, the two proximal ones are large and pointed, the distalmost one is block-like. The adoral shields are large with lateral projections making them appear wing-like; they separate or appear to separate the oral shield from the first lateral arm plate. The oral shield is basically rhombic but in some specimens the distal lobe is produced and the plate becomes arrow shaped. There may be a slight depression in the centre of the shield.

The arms are slightly noded becoming distinctly so distally. The dorsal arm plates are fan to bell shaped and separated. The ventral arm plates are pentagonal with a wide distal edge and are separated from one another. In some specimens there are indications of transverse ridges on the edge of these plates and also on the lateral arm plates. The tentacle scale is pointed and spine-like; on a few specimens there are two tentacle scales on the first arm segment. There are 7 finely rugose arm spines proximally, 4–5 distally; there are large secondary points on the shaft of some spines. The arm spines form a fan on the proximal arm joint.

REMARKS. This species is very similar to *O. simulans* but differs in the following respects: it appears to reach a much larger size; the spinelets of the disk are less elaborate and have fewer points to the crown; the shape of the oral shield differs and is depressed in *O. aculeata*; the adoral shields are more wing-like and separate the oral shield from the first lateral arm plate; the arm spines are less rugose particularly the proximal ventral spines; and finally the ventral most arm spine is not so distinctly sabre shaped as in *O. simulans*.

DISTRIBUTIONS. *O. aculeata* has been recorded in the west Atlantic from off Virginia at depths of 2500–2539 m and in the east from the Rockall Trough, the Bay of Biscay and the Iberian Basin at depths of 3425–3584 m.

Ophiacantha simulans Koehler, 1896*a*

Fig. 17

Ophiacantha simulans Koehler, 1896*a*: 82; Mortensen, 1933*a*: 26–29; Gage *et al.* 1983: 291.
Ophiacantha composita: Koehler, 1907: 289–290; Mortensen, 1927: 191; (non *O. composita* Koehler, 1904).

MATERIAL STUDIED. **MNHN:** *Travailleur & Talisman* 1882 Stn 13 44°7′N: 10°16′W 2030 m 5 specimens.
COB: BIOGAS Stn 1: DS11 2205 m 1 specimen; DS15 2246 m 13 specimens; DS17 2103 m 6 specimens; DS18 2138 m 8 specimens; DS17 2103 m 6 specimens; DS65 2360 m 2 specimens; CV08 2180 m 6 specimens; CV09 2119 m 4 specimens; CV10 2108 m 2 specimens; CV23 2034 m 2 specimens; CV24 2025 m 1 specimen; CV25 1985 m 2 specimen; CV01 2245 m 9 specimens; CP02 2177 m 22 specimens; CV39 2350 m 4 specimens; CP09 2171 m 11 specimens; CP10 2878 m 3 specimens. BIOGAS Stn 3: CV28 4032 m 1 specimen. BIOGAS Stn 6: CV32 1895 m 1 specimen; CP07 2170 m 3 specimens; CP23 1980 m 1 specimen. BIOGAS Stn HZ: CW03 2160 m 1 specimen; CV11 2141 m 5 specimens.
IOS: *Discovery* Investigations: Stn 8512/4 42°15·2′N: 11°35·2′W 2281–2465 m 1 specimen.
SMBA: RRS *Challenger II:* Stn ES 112 55°12′N: 15°50′W 1900 m 26 specimens.

The disk is round, diameter up to 10 mm, covered with a dense coating of spinelets each crowned with 7–8 points. The radial shields are long and narrow with only their distal ends visible. Only the distal part of each ventral interradial area is covered with spinelets.

The jaws are as long as broad. There is a single pointed apical papilla flanked on each side by 3 sometimes 4 oral papillae; the distalmost of which is distinctly block-like. The proximal corner of this papilla may be produced into a point. In a few specimens this papillae may be partially divided giving the appearance of being two papillae. The adoral shields are large prominent about twice as long as broad and only just separating the oral shield from the first lateral arm plate. The oral shield is rhombic with a convex distal edge.

The arms are slightly noded. The dorsal arm plates are fan shaped and separated. The ventral arm plates are pentagonal, broader than long and separated. The tentacle scale is small and scale-like. There are 7 rugose arm spines proximally, 5 distally; the dorsalmost is the longest often up to 3 arm segments long on proximal segments. On the proximal arm segment the arm spines meet midradially forming a single fan. The ventralmost arm spine may be curved or sabre shaped.

REMARKS. *O. simulans* is similar to *O. aculeata* Verrill and the West Indian species *O. mesembria* H. L. Clark. The differences between *O. simulans* and *O. aculeata* are dealt with under *O. aculeata*. *O. simulans* differs from *O. mesembria* in the form of the disk spinelets which have more points to the crown than those of *O. mesembria*; shorter more rounded tentacle scales; and stout, often curved lower arm spines, those of *O. mesembria* being long and quite rugose but not curved.

DISRTRIBUTION. This species has been recorded from both sides of the Atlantic: in the west from off the Carolinas and in the east from Iceland south of the Azores in depths of 1575–3018 m.

Ophiacantha levis comb nov.

Fig. 15

Ophiomitrella levis Koehler, 1914: 105.

MATERIAL STUDIED. **MCZ:** *Albatross* Stn 2666 30°47′N: 79°49′W off Fernandina, Florida 486 m HOLOTYPE.

The disk is round, diameter up to 5 mm; covered by a dense coating of spinelets with widened multipointed crowns. Only the distal edge of the radial shields are visible. The ventral interradial area are also coated with multipointed spinelets like those of the dorsal surface.

The jaws appear as wide as long. There is usually one large blunt apical papilla, flanked on each side by 3 spine-like oral papillae. The adoral shields are large, slightly convex and situated totally proximal to the oral shield not separating it from the first lateral arm plate. The adoral shields have glassy concretions embedded within the matrix of the plate. The oral shield is slightly pentagonal with an acute proximal angle and a slightly convex distal edge.

The arms appear noded. The dorsal arm plates are fan shaped to bell shaped and not contiguous. The ventral arm plates are wide, pentagonal, with an obtuse proximal angle and convex distal edge, which may sometimes be medianly indented; they are separated from one another. The tentacle pores are small, each is armed with a small slightly pointed tentacle scale. There are 8–9 arm spines on proximal arm segments, 6 on distal ones; dorsal arm spines are quite smooth while ventral ones are flattened and slightly sabre shaped with a toothed proximal edge. The second dorsalmost spine is the longest, up to 2 arm segments long. The arm spines form a fan on proximal arm segments.

REMARKS. *O. levis* is now transferred to *Ophiacantha* from *Ophiomitrella* because the radial shields are thin and rib-like not integrating with the plates of the disk like *Ophiomitrella* species and the disk is covered with fine scales. *O. levis* can be distinguished from other *Ophiacantha* species by the shape of the disk spinelets, large curved adoral shields, small pentagonal oral shield, wide ventral arm plates, and the shape of the ventral arm spines.

DISTRIBUTION. This species has only been recorded from the tropical western Atlantic off Fernandina, Florida 486 m.

Ophiacantha crassidens Verrill, 1885

Fig. 17

Ophiacantha crassidens Verrill, 1885: 152; 1899*a*: 38; 1899*b*: 325; Farran, 1913: 42; Grieg, 1932: 38; Mortensen, 1927: 192–193; Gage *et al.* 1983: 291.
Ophiacantha decipiens Koehler, 1906: 22; 1907: 283–284.

MATERIAL STUDIED. **BMNH:** 'Knorr' cruise 35 stn 311 39°19′N: 72°00′W 1 specimen.
MNHN: *Travailleur & Talisman* Stn 127 15 août 1883 38°38′N: 30°41′W 1257 m HOLOTYPE of *O. decipiens*.
COB: BIOGAS Stn 1: DS16 2325 m 1 specimen; CV10 2108 m 1 specimen; CV23 2034 m 1 specimen; CP27 2115 m 2 specimens; CV34 1970 m 16 specimens. BIOGAS Stn 6: CV16 1909 m 1 specimen. BIOGAS Stn HZ: CV11 2141 m 1 specimen.
SMBA: RRS *Challenger II:* Stn AT 192 57°21′N: 12°02′W 1862 m 6 specimens.

The disk is round, diameter up to 14 mm, covered by small imbricating scales, each of which may carry a single rod-like spinelet, the tip of which may be multifid or simply abraided. Only the tips of the radial shields are visible. The ventral interradial areas are covered by scales and spinelets similar to those of the dorsal surface.

The jaws appear to be slightly wider than long. The apical papilla is large, flattened and leaf shaped, flanked on either side by 3 similarly shaped oral papillae. The adoral shields are large, not separating the oral shield from the first arm plate. The oral shield is rounded, triangular often with the lateral sides indented.

The arms are not distinctly noded. The dorsal arm plates are small, triangular and separated along the length of the arm. The ventral arm plates are pentagonal to broadly triangular with a convex distal edge which is often raised up in proximal segments. They are nearly contiguous proximally and separated distally. The tentacle scale is stout, spine-like with a blunt tip. There are 8 arm spines proximally, 6 distally, the dorsalmost of which are smooth and rounded while the ventral ones are flattened with a comb-like proximal edge.

REMARKS. *O. crassidens* is easily distinguished by the shape of the mouth and oral papillae, the low density of the rod-like spinelets and the two forms of the arm spines. The author has compared the type of *O. decipiens* with the other specimens of *O. crassidens* and could find no significant differences, and concludes that they are conspecific.

DISTRIBUTION. This species is recorded on both sides of the North Atlantic; in the west off Cape Hatteras at a depth of 1570 m, and in the east from SW. Ireland south to the Azores in depths of 980–3120 m.

Ophiacantha spectabilis G. O. Sars
Fig. 18

Ophiacantha spectabilis G. O. Sars, 1871: 10; Verrill, 1885*a*: 152; Bell, 1892: 128; Grieg, 1893: 24; Koehler, 1896*a*: 80–81; Verrill, 1899*a*: 38; 1899*b*: 335; Grieg, 1902: 14; 1905: 159; 239–740; Koehler, 1924: 246; Mortensen, 1927: 191; 1933*a*: 33–34; Djakanov, 1954: 40.

MATERIAL STUDIED. **BMNH:** Bodo, Lofoten Is 184 m 1 specimen; *Triton* West of Wyville-Thompson Ridge 789–515 m 2 specimens; Rodberg, Trondheim Fjord 450–710 m 1 specimen.

The disk is round, slightly indented over the arms, diameter up to 14 mm, covered by rod-like spinelets which are slightly rugose often with a narrow trifid crown. The spinelets are largest in the centre of the disk becoming shorter and more rugose towards the edge. The radial shields are not distinct. The ventral interradial areas are also covered with spinelets although the extent and density of covering varies.

The jaws have the appearance of being short and wide. There is one pointed apical papilla flanked on each side by 4 pointed slightly rugose oral papillae; Mortensen (1927) reports that there may be as many as 8 each side. The adoral shields are nearly rectangular and situated almost entirely proximal to the oral shield not separating it from the first lateral arm plate. The oral shield is oval to rounded pentagonal with the distal edge fringed by granules or low spinelets.

The dorsal arm plates are fan to bell shaped not contiguous sometimes with a finely rugose distal edge. The ventral arm plates are pentagonal with a convex distal edge and an obtuse proximal angle, separated or only just contiguous; in some specimens the plate boundaries are obscured by skin but this is not a constant feature. The tentacle pores are large; the tentacle scales are large leaf shaped and there are two on the first arm pore and sometimes also on the second. There are 7–8 finely rugose and flattened arm spines proximally 5–6 distally; not forming a fan on the proximal arm joints. The dorsal or second dorsalmost spine is the longest often up to three arm segments in length.

REMARKS. *O. spectabilis* appears to have a close affinity with *O. rosea*. Both have a similar jaw structure, position of the adoral shields, and shape of the ventral arm plates and tentacle scales. They differ in the shape of the oral shield which is nearly rectangular in *O. rosea* but more pentagonal in *O. spectabilis*, also the distal edge of the oral shield in *O. spectabilis* is fringed with papillae. *O. rosea* commonly has supernumerary papillae on the jaw which are rare or absent in *O. spectabilis*. Finally the tentacle pores are usually larger in *O. rosea* and the first arm pore may have 3 tentacle scales.

DISTRIBUTION. *O. spectabilis* is found on both sides of the North Atlantic: in the west it has been recorded from off Nova Scotia at the depth of 238 m, while in the east it has been found south of Iceland, Norway, SW. Ireland south to the Bay of Biscay in the depths of 145–1700 m.

Ophiacantha cuspidata Lyman, 1878
Fig. 18

Ophiacantha cuspidata Lyman, 1878: 143; 1882: 191; Verrill, 1899*a*: 42; Koehler, 1909: 186; Mortensen, 1927: 189; 1933*a* 31–33; Gage *et al.*, 1983: 291.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 344 off Ascension Island 768 m HOLOTYPE & 3 PARATYPES.

COB: *Cymor* 47°44′N: 8°21′W 2420 m 2 specimens.
IOS: *Discovery* Investigations: Stn 9042 42°15′N: 11°22′W 1662–1541 m 5 specimens.
SMBA: RRS *Challenger II*: Stn ES 112 55°12′N: 15°50′W 1900 m 2 specimens.

The disk is round, diameter up to 10 mm, covered by large rugose spinelets often with elaborate multipointed crowns. The tips of the radial shields are sometimes visible and it is usually possible to see the extent of the shields beneath the disk scales. The ventral interradial areas are covered by spinelets similar to the dorsal side although they are usually smaller and in some specimens they may resemble rugose granules.

The jaws appear to be slightly longer than wide. There is one long pointed apical papilla flanked on each side by 3–5 long thin oral papillae the distalmost of which may have the free end enlarged. The adoral shields are short, rectangular in shape, they do not or only just separate the oral shield from the first lateral arm plate. The oral shield is a rounded pentagonal with an obtuse or slightly rounded proximal angle. The distal part of the shield may be indented.

The arms are not markedly noded. The dorsal arm plates are triangular with a convex distal edge and separated. In some specimens the distal edge may be raised up often with many small spikes. The ventral arm plates are rounded pentagonal with a rounded, nearly pointed, distal edge and are contiguous. There are two, occasionally three, large flat tentacle scales on the first tentacle pore subsequent pores have only one. There are 8–9 slightly rugose arm spines of which the ventral spines are the most rugose. The second or third dorsalmost spine is the longest, up to 3 arm segments long. On the proximal arm segment the arm spines form a fan.

REMARKS. *O. cuspidata* appears to have an affinity with *O. lineata, O. metallacta* and *O. parcita*. It can be distinguished by the form of the disk armament, the shape of the oral shield and the lack of transverse striations on the ventral and lateral arm plates (see Table 1).

DISTRIBUTION. *O. cuspidata* has been recorded in the eastern Atlantic from Iceland as far south as Ascension Island with a bathymetric range of 768–2460 m.

Ophiacantha lineata Koehler, 1896*c*

Fig. 19

Ophiacantha lineata Koehler, 1896*c*: 247; 1909: 187–188; 1914: 87; 1921: 4; Cherbonnier & Sibuet, 1972: 1366.

MATERIAL STUDIED. **MOM:** *Princesse Alice* Stn 578 1895 38°26′N: 26°30′45″W 1165 m 3 SYNTYPES.
MNHN: *Princesse Alice* Stn 3140 37°38′N: 26°01′W 1378 m. 1 specimen.
COB: *Cymor* 2 DR 29 48°19′N: 11°57′W 1470 m. 1 specimen.

The disk is round, up to 6 mm diameter covered by spinelets with a crown of many points, 9 or more, the spinelets may extend on to the dorsal part of the arm. Only the distal ends of the radial shields are visible. The ventral interradial areas are covered by spinelets similar to the dorsal side.

The jaws are as wide as long. The oral plates are often distinctly bowed meeting only at their proximal ends. There is one pointed apical papilla flanked on each side by 3–5 oral papillae, the distalmost of which is long and rectangular. The adoral shields are about 2–3 times as long as broad, wing-like, not separating the oral shield from the first lateral arm plate. The oral shield is irregular in shape, the proximal edge is rounded and the distal edge may be produced and this region may be depressed; in some specimens the oral shield looks pentagonal, again with the distal portion depressed.

The arms are distinctly noded. The dorsal arm plates are triangular and nearly contiguous. The ventral arm plates are pentagonal with the distal edge rounded and contiguous at least proximally. The tentacle scale is rugose and pointed. The lateral and ventral arm plates have distinctive transverse ridges most noticeable in dry or nearly dry specimens. There are 8 rugose arm spines, many are distinctly curved. The dorsalmost arm spines are the longest up to 4 arm segments in length.

REMARKS. The transverse ridges are a distinctive feature which separates this species from many other North Atlantic species, other species with this feature are *O. parcita, O. metallacta, O. notata* (see Table 1) and *Ophiolimna bairdi* (Lyman). *Ophiolimna bairdi* can easily be distinguished from *O. lineata* by a number of features: the disk is covered with granules, not spinelets; which extend on to the oral frame; the oral shield is a large triangle and the oral papillae have a different shape and arrangement (see p. 60)

Table 1 Comparison of *Ophiacantha cuspidata*, *O. lineata*, *O. metallacta*, *O. notata* and *O. parcita*

CHARACTERS	SPECIES *O. cuspidata*	*O. lineata*	*O. metallacta*	*O. notata*	*O. parcita*
Disk spinelets	elongated rugose shank, elaborated trifid crown	smooth shank, wide multipointed crown	smooth shank, wide crown with elaborated points	smooth shank, wide crown with elaborated points	smooth shank, narrow multipointed crown
Adoral shields	nearly rectangular	curved winglike	curved winglike	angular winglike	rounded, nearly straight proximally
Oral shields	rounded pentagonal	irregularly shaped rounded with a distal projection	rounded rhombic, nearly pentagonal	angular pentagonal	rounded, light-bulb shape
Arms outline shape	not noded	distinctly noded	slightly noded	distinctly noded	flattened, not noded
Transverse ridges on VAP & LAP	No	Yes	Yes	Yes	Yes
Arm spine no.	8–9	8	7	7–8	10
Arm spine; texture	dorsally finely rugose; ventrally distinctly rugose	curved; rugose	finely rugose	dorsally finely rugose; ventrally very rugose	short; finely rugose

Distribution. *O. lineata* has been recorded from both sides of the Atlantic; in the west it has been recorded off Florida 511–792 m and in the east off the Azores and in the Bay of Biscay 1165–1378 m.

Ophiacantha metallacta H. L. Clark, 1915
Fig. 19

Ophiacantha metallacta H. L. Clark, 1915: 202.

Material studied. **MCZ:** *Blake* Stn 320 off S. Carolina 463 m PARATYPE.

The disk is round, diameter up to 7 mm, covered by multipointed spinelets which have a very wide crown, approximately round in the top view with many irregular points, often 10 or more. The radial shields are inconspicuous. The ventral interradial areas are covered by similar spinelets to the dorsal side but they become less dense nearer the proximal part of the disk.

The jaws appear as broad as long. There is one pointed apical papilla flanked on each side by 3 oral papillae, the distalmost of which is leaf shaped with a rounded outer edge. The adoral shields are large, wing-like, and do not separate the oral shield from the first lateral arm plate. The oral shield is rhombic almost pentagonal, the centre of the shield may be slightly depressed.

The arms are slightly noded. The dorsal arm plates are triangular and separated although proximally they may be nearly contiguous. The ventral arm plates are nearly pentagonal with a rounded distal edge. They are contiguous proximally. The distal portion of the plate has transverse striations which are also present on the lateral arm plates. The tentacle pores are armed with one flat leaf shaped tentacle scale. There are 7 slightly rugose arm spines, often with larger points along the shaft of the spine. The spines on proximal segments nearly meet midradially forming a fan.

Remarks. *O. metallacta* bears a close resemblance to *O. notata* but differs in the shape of the oral and adoral shield (see Table 1).

Distribution. This species has been recorded from the western Atlantic where it has been found from the West Indies as far north as South Carolina 295–763 m.

Ophiacantha notata Koehler, 1906
Fig. 19

Ophiacantha notata Koehler, 1906: 23; 1907: 284.

Material studied. **MNHN:** *Travailleur & Talisman* 1881 Stn 39 44°5′N: 9°20′40″W 1226 m HOLOTYPE.

The disk is round and densely covered by spinelets with a multipointed crown; disk diameter is 8 mm. The tips of the radial shields are visible and the extent of the shields can be seen beneath the disk scales. The ventral interradial areas are also covered with spinelets.

The jaws appear slightly angular and pointed. There is one pointed, slightly angular, apical papilla flanked on each side by 3 to 4 irregularly arranged long pointed oral papillae, some of which are slightly flattened. The adoral shields are extremely wing-like with the lateral edges acutely pointed. They lie proximal to the oral shield and not separating it from the first lateral arm plate. The oral shield is distinctly pentagonal, with an obtuse proximal angle and a convex distal edge. There may be a slight depression in the plate.

The arms are noded. The dorsal arm plates are fan to bell shaped and separated. The ventral arm plates are slightly pentagonal with a nearly straight proximal edge and convex distal edge. The distal segment is strongly striated. Striations also occur on the lateral arm plates. The tentacle pores are small, each armed with one large flap-like tentacle scale, which is pointed on proximal pores but becomes rugose on distal ones. There are 7 to 8 arm spines, the dorsalmost of which are finely rugose while the ventral are highly rugose and are slightly curved and club shaped. The arm spines do not form a fan on the proximal joints.

Remarks. *O. notata* appears to be similar to *O. parcita, O. lineata,* and *O. metallacta*, see Table 1. *O. notata* can be distinguished by its angular wing-like adoral shields and the shape of the oral shield.

Distribution. This species has only been recorded from the Bay of Biscay at a depth of 1226 m.

Ophiacantha parcita Koehler, 1906
Fig. 19

Ophiacantha parcita Koehler, 1906: 25; 1907: 286.

Material studied. **MNHN:** *Traivailleur & Talisman* 30 Juillet 1883 Stn 114 16°51′N: 27°30′W 633–598 m 1 specimen.

The disk is round, up to 9 mm in diameter, covered by spinelets with a narrow crown of up to 8 points. The radial shields are visible in some specimens but in others they are partially or totally obscured by the spinelets. The ventral interradial areas are also covered with spinelets.

The jaws appear slightly longer than broad. There is one pointed apical papilla flanked on each side by 3 oral papillae, the distalmost of which is long with its free and widened and squared off. The adoral shields are short slightly larger than wide with the proximal edge at nearly right angles to the jaw; they do not separate the oral shields from the first lateral arm plate. The oral shield is very distinctive with a rounded proximal edge and the distal edge produced resembling a deformed light bulb in profile.

The arms appear to be wide and slightly flattened. The dorsal arm plates are triangular and almost contiguous proximally. The lateral arm plates are wide and the area where the spines articulate is not raised up as much as in species like *O. bidentata* but is flatter. The ventral arm plates are short almost as wide as long pentagonal with the distal edge curved and are contiguous or nearly contiguous proximally. The lateral and ventral arm plates have distinctive transverse ridges most noticeable in dry specimens. The tentacle scale is flat and scale-like, rounded not pointed. There are up to 10 short only slightly rugose arm spines.

Remarks. *O. parcita* can be distinguished from the other species which have striations on the ventral and lateral arm plates by the shape of the adoral and oral shield and the arm (see Table 1).

Distribution. *O. parcita* has been recorded once—from the Cape Verde Island, 633–598 m. It is included in the present study because it may possibly occur in deeper water elsewhere in the North Atlantic.

Ophiacantha rosea Lyman 1878
Fig. 18

Ophiacantha rosea Lyman, 1878: 139; 1882: 184; Verrill, 1899*a*: 42; 1899*b*: 331; Koehler, 1897*a*: 81–82; Mortensen, 1927: 189–190.
Ophioprium rosea: Baker & Devaney, 1981: 173–174.

Material studied. **BMNH:** HMS *Challenger* Stn 308 50°10′S: 74°42′W 320 m HOLOTYPE & 1 PARATYPE.

The disk is round, disk diameter up to 15·5 mm, covered by long spinelets. Some of these longer spinelets end in only a few points, others are shorter more rugose with a multipointed crown. In the holotype the radial shields are visible as a thin area devoid of spinelets, this is not so distinct in the paratype. The ventral interradial area is covered by similar spinelets to the dorsal side.

The jaw appears short and wide. There are up to 3 broad pointed apical papilla flanked on either side by 3 broad flap-like oral papillae. Several pointed supernumerary papillae are present on the edge of the jaw and often on the proximal edge of the adoral shields. The adoral shields are just longer than broad and positioned almost totally proximal to the oral shield. The oral shield is a rounded rectangular shape slightly longer than broad.

The arms are quite broad, not particularly noded. The dorsal arm plates are fan shaped, contiguous proximal, but well separated distally. The ventral arm plates are roughly pentagonal with a convex almost angular distal edge, and are separated. The tentacle pores are quite large often the proximal ones are built up. On the first tentacle pore of the arm there 2 often 3 large broad flap-like tentacle scales, subsequent pores have one broad flap-like scale with sometimes a smaller pointed more spine-like scale. There are 10–11 arm spines on the proximal joints 7–8 on distal ones. The second dorsalmost arm spine is the longest and maybe nearly 3 arm segments long. The arm spines are finely rugose. They do not form a fan on proximal segment.

Remarks. *O. rosea* can be distinguished from the other species of *Ophiacantha* by the following characters: the arrangement of the papillae on the jaw the shape and arrangement of the adoral and oral shields; the large tentacle scales and their number on the proximal pores. Baker & Devaney (1981) consider *O. rosea* to be a species of *Ophioprium* because the oral papillae are of two sizes which are located on different parts of the jaw and the tentacle pores are large armed with large tentacle scales. However there are several reasons which suggest that *O. rosea* should be retained in *Ophiacantha*: firstly in all specimens examined the jaws are short, broader than long not longer than broad as in *Ophioprium*. Secondly, although larger specimens of *O. rosea* examined often have many smaller thinner supernumerary papillae such papillae are not distributed in a similar way to other species of *Ophioprium*. They appear to be quite randomly arranged on the distal portion of the jaw although sometimes they appear to cluster in the region of the second oral tentacle pore. In *Ophioprium cervicornis* the two types of papillae are distributed in a regular way; the smaller papillae are situated on the proximal part of the jaw and can be regarded as the oral papillae. Distal to them there are several longer more spine-like papillae usually associated with the second oral tentacle pore; these papillae can be regarded as tentacle scales. As discussed under the subfamily Ophiotominae this is a common arrangement amongst its genera. Smaller specimens of *Ophiacantha rosea* have an arrangement of 3–4 oral papillae much like other species of *Ophiacantha*. Lastly in *Ophioprium cervicornis, O. permixtum* the pores are open with small spine-like tentacle scales or none at all. In *O. rosea* the tentacle pores are relatively large but are armed with a large tentacle scale.

DISTRIBUTION. *O. rosea* has a wide distribution being found in the Pacific off Japan, southern Chile; South Africa, Marion Island; and in the Atlantic from the Bay of Biscay. In the Atlantic it has a bathymetric distribution of 1410–1700 m.

Ophiacantha densa Farran, 1913

Fig. 20

Ophiacantha densa Farran, 1913: 40; Cherbonnier, 1970: 1272.

MATERIAL STUDIED. **BMNH:** Irish Fisheries *Helga* Stn SR 504 50°42′N: 11°18′W 1128–1310 m HOLOTYPE & PARATYPE.
COB: BIOGAS Stn HZ: CM01 1100 m 1 specimen.

The disk is round, diameter up to 5–6 mm covered with a dense coating of spinelets, which are rod-like with bifid tips and in some specimens may be covered with skin. The radial shields are inconspicuous. The ventral interradial areas are also covered with spinelets like those of the dorsal surface.

The jaws appear to be as broad as long. There is one pointed apical papilla flanked on either side by 3 conical, pointed oral papillae. The adoral shields are larger about twice as long as broad, slightly curved, and do not separate the oral shield from the first lateral arm plate. The oral shield is small rhombic to triangular in shape. The oral and adoral shields, and to some extent the lateral arm plates and the ventral arm plates, have very conspicuous glassy tubercles embedded in the plates.

The arms are distinctly noded. The dorsal arm plates are bell shaped or triangular with a convex distal edge and are separated. The ventral arm plates are pentagonal often with a rounded distal edge, and are separated. Each tentacle pore has one small pointed tentacle scale. There are 4–5 smooth arm spines, the proximal ones well separated midradially, not forming a fan.

REMARKS. *O. densa* has an affinity with *O. smitti* Ljungman; both have a similar arrangement of the oral frame and the adoral and oral shields have glassy tubercles. *O. densa* has fewer arm spines, 4–5 as opposed to 7–8, the oral frame is not raised away from the ventral portion disk, there are no trifid spinelets amongst the rods of the disk as there commonly are in *O. smitti* and the arm spines do not form a fan on proximal arm segments.

DISTRIBUTION. *O. densa* has been recorded from the eastern Atlantic off SW. Ireland and in the Bay of Biscay; 300–1324 m.

Ophiacantha smitti Ljungman, 1872

Fig. 20

Ophiacantha smitti Ljungman, 1872: 615; Lyman, 1882: 179; Koehler, 1926: 25; Nobre, 1931: 81; Cherbonnier & Sibuet, 1972: 76.
Ophiacantha segesta Lyman, 1878: 141–142.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 56 off Bermuda 1996 m HOLOTYPE of *O. segesta.*
COB: BIOGAS Stn HZ: DS04 1100 m 4 specimens; CM01 13 specimens; CV21 994 m 2 specimens. BIOGAS Stn 1: CV20 2282 m 46 specimens.
IOS: *Discovery* Investigations: Stn 8967 31°25·9′N: 10°25·9′W 2 specimens.

The disk is round, diameter up to 8 mm, sometimes with a domed appearance due to the arched radial shields but this may be an artifact of preservation. The disk is covered by a dense coating of simple rods and trifid and bifid spinelets which are sometimes reduced resembling small granules, the proportions of each varies some specimens having nearly all rods. Generally the spinelets are situated periferally extending onto the ventral interradial areas whereas the rods are found in the middle of the disk. The rods and spinelets may be covered with a coating of skin.

The jaws appear to be as broad as long. The oral frame has the appearance of standing out from the disk. There is one large pointed apical papilla flanked on each side by 3 rounded spinelike oral papillae. The adoral shields are large, swollen, slightly curved and not separating the oral shield from the first lateral arm plate. The oral shield is small and triangular. The adorals and oral shields, ventral and lateral arm plates have conspicuous glassy tubercles embedded in the matrix of the plate.

The arms are distinctly noded. The dorsal arm plates are triangular or slightly bell shaped with a convex distal edge and are separated. The ventral arm plates are pentagonal and in some specimens the distal edge may be indented. The tentacle scale is small and pointed. There are 7–8 smooth arm spines, the first 3–4 dorsal spines are the longest and on proximal segments are smoother and thinner than the ventral ones. On the proximal arm segment the arm spines almost meet midventrally forming a fan.

REMARKS. *O. smitti* is a variable species with the covering of the disk varying from being densely covered with rods and spinelets to being quite open. Also the proportion of rods to spinelets varies to the exclusion of spinelets which would lead to confusion with *O. densa* were it not for the different number of arm spines, the proximal spines forming a fan and the raised oral frame.

O. segesta Lyman from off Bermuda was thought to differ from *O. smitti* in having longer, thinner spinelets and rods sparsely distributed over the surface of the disk and the arm spines, particularly the ventral ones, were more rugose. However, a large sample of *O. smitti* shows so much variation in these characters that the type material of *O. segesta* cannot be considered other than conspecific with *O. densa.*

DISTRIBUTION. This species has been recorded from both sides of the North Atlantic: in the east from the Bay of Biscay south to off North Africa in depths of 994–2282 m, and in the west off Bermuda 1996 m.

Ophiacantha abyssicola G. O. Sars, 1871

Fig. 20

Ophiacantha abyssicola G. O. Sars, 1871: 8; Bell, 1892: 128; Nordgaard, 1893: 5; Grieg, 1893: 24; 1895: 10; Koehler, 1895: 463; 1896*a*: 79; 1896*b*: 213; 1898: 55; Grieg, 1903: 31; Kemp, 1905: 183; 195: Koehler, 1906: 42; 1907: 287; 1909: 182; Farran, 1913: 38; Mortensen, 1913: 356; Grieg, 1921: 73; Koehler, 1924: 247; Mortensen, 1925: 180; 1927: 194; Grieg, 1932: 37; Mortensen, 1933a: 23–24; Djakanov, 1935: 86; 1954: 38; Madsen, 1970: 15; Gage *et al.*, 1983: 289.
Ophiacantha millespina Verrill, 1879: 203; 1899*b*: 324; H. L. Clark, 1915: 203.

MATERIAL STUDIED. **BMNH:** *Porcupine* Stn 74 W. of Shetlands 365 m 9 specimens; *Knight Errant* NW of Rona 927 m 3 specimens; Norman Collection Rödburg, Norway 2 specimens.
COB: BIOGAS Stn HZ: DS04 1100 m 4 specimens; DS05 2210 m 1 specimen; DS07 2170 m 1 specimen.
IOS: *Discovery* Investigations: Stn 7844 23° 43·27′N: 16°56·66′W 485–479 m 5 specimens; Stn 48°48′N: 11°49·7′W 955 m.
SMBA: RRS *Challenger II*: Stn: ES 23 56°37′N: 09°10′W 704 m 4 specimens; Stn ES 115 56°29′N: 10°22′W 1000 m 4 specimens.

The disk is round, up to 8 mm in diameter, covered with glassy spinelets, which are basically elongated trifids often elaborated with secondary points, sometimes one of the points may be greatly enlarged resembling a rod. The plates of the interradial region are usually large and conspicuous.

The jaws appear to be as broad as long. There is one pointed apical papilla flanked on either side by 3–4 oral papillae; the free end of the distalmost one may be widened. The adoral shields are large, about twice as long as broad, and do not separate the oral shield from the first lateral arm plate. The oral shield varies from being roughly pentagonal to distinctly arrow shaped. There is a distinct groove or depression in the distal part of the plate.

The arms are noded. The dorsal arm plates vary from fan shaped to bell shaped, and are separated. The ventral arm plates are distinctly wider than long, pentagonal in shape and separated. Each tentacle pore is armed with one pointed tentacle scale. There are 6–8 slightly rugose arm spines, the dorsalmost arm spines are the longest up to 2 arm segments long, the ventral most are usually the most rugose. On distal segments of the arm the ventralmost arm spines may be flattened and have a comblike structure along one edge. The spines on the proximal joints may join midradially forming a fan.

Remarks. *O. abyssicola* is easily recognised by the arrow shaped oral shield, the very wide and separated ventral arm plates and the elaborated trifid disk spinelets. *O. abyssicola* closely resembles the holotype and only known specimen of *O. granulifera* Verrill: both have similarly shaped oral shields and ventral arm plates. Indeed certain specimens of *O. abyssicola* studied showed intermediate characters between the two. However, *O. abyssicola* differs from *O. granulifera* by the following characters: the arm spines only form a fan on the first free arm joint while in *O. granulifera* the fans extend along at least half the arm; the spinelets of the disk differ, those of *O. abyssicola* are trifid and glassy while those of *O. granulifera* are low and resemble granules; *O. abyssicola* has a rounded disk whereas *O. granulifera's* disk is indented interradially, although this could be an artifact of preservation.

Several features of *O. abyssicola* and *O. granulifera* distinguish them from most species of *Ophiacantha*: the high often indented disk, the arm spines of *O. granulifera* forming a fan on most proximal arm segments, large conspicuous disk plates and the very wide ventral arm plates are all reminiscent of the Ophioplinthacinae. But most members of that subfamily have large conspicuous radial shields and a slightly different arrangement of the jaw.

Distribution. This is a predominantly bathyal species recorded from both sides of the North Atlantic: in the west from Cape Hatteras north to southern Greenland of depths of 561–1048 m; in the east from SE. Iceland, northern Norway (the Lofoten Islands) south to the Canary Islands at depths of 260–2300 m.

Ophiacantha granulifera Verrill, 1885*a*

Fig. 20

Ophiacantha granulifera Verrill, 1885*a*: 153; 1899*a*: 38; 1899*b*: 326; Koehler, 1914: 86–87; Wheateaves, 1901: 61.

Material studied. **MCZ:** Off Georges Bank 181 m HOLOTYPE.

The disk is high and indented interradially, disk diameter 9 mm. It is covered by low multipointed granules. The radial shields are inconspicuous amongst the plates of the disk. The ventral interradial area is devoid (in this specimen) of any granules and the plates of this area are large and conspicuous.

The jaw appears to be wider than long. There is one large, broad, pointed apical papilla flanked on either side by 3–4 large slightly blunt oral papillae. The adoral shields are about twice as broad as long and are wing-like separating the oral shield from the first lateral arm plate. The oral shield is arrow shaped with the distal projection slightly depressed.

The arms are noded flattened ventrally. The dorsal arm plates are triangular and separated. The ventral arm plates are much wider than long with an obtuse proximal angle and a straight distal edge rounded at the corners and indented midradially. There are two flattened rounded tentacle scales on the most proximal arm segment, subsequent pores have only one and distally the tentacle scale becoming quite small. There are 9 finely rugose arm spines. The longest is the second dorsalmost spine which is up to two arm segments in length. Ventral arm spins may be slightly flattened and in some the arm spine may be curved. The arm spines form a fan on the proximal arm segments. The matrix of the arm joints, the subsequent plates ventral plates and jaw plates appears coarse.

Remarks. See under *O. abyssicola*.

Distribution. This species has only been recorded from the western Atlantic off the Georges Bank, off Cape cod 184 m.

Ophiacantha spinosella Mortensen, 1933*a*
Fig. 21

Ophiacantha spinosella Mortensen, 1933*a*: 29–30.

MATERIAL STUDIED. **ZMC:** *Thor* Stn 57 63°21′N: 16°27′W 500–560 m HOLOTYPE.

The disk is round, diameter of holotype 2 mm, covered by imbricating scales many of which carry a rugose rodlike spinelet. The radial shields are not visible. The ventral interradial area is covered by scales like those of the dorsal side but with fewer shorter spinelets.

The jaws appear slightly longer than broad. There is a pointed slightly rugose apical papilla flanked on either side by 3–4 pointed oral papillae which form a continuous series with 2–3 tentacle scales of the second oral tentacle pore. The adoral shields are long and narrow, separating the oral shield from the first lateral arm plate. The oral shield is rounded, triangular, sometimes with a slight distal lobe.

The arms are noded. The dorsal arm plates are fan shaped and separated. The ventral arm plates are pentagonal and separated. The tentacle pores are relatively large with two flat pointed tentacle scales on the first arm pore and one on subsequent pores. There are 4–5 rugose arm spines, the dorsalmost one is longest, up to 2 segments long. They do not form a fan on the proximal joints.

REMARKS. The arrangement of the oral papillae and tentacle scales of the second oral tentacle scales are reminiscent of the subfamily Ophiotominae. These characters coupled with the relatively large tentacle pores suggest that this species is not an *Ophiacantha* but perhaps a young stage of a species of the Ophotominae. This must remain uncertain until more specimens are found.

DISTRIBUTION. *O. spinosella* has been recorded once, off Iceland at a depth of 500–560 m.

Ophiotreta valenciennesi rufescens Koehler, 1896*c*
Fig. 21

Ophiacantha rufescens Koehler, 1896*c*: 249–250.
Ophiacantha valenciennesi: Koehler, 1909: 188–189.
Ophiotreta valenciennesi: Koehler, 1914: 102.
Ophiacantha valenciennesi var *rufescens*: Mortensen, 1933*a*: 36–37; Cherbonnier, 1962: 7–9.

MATERIAL STUDIED. **MNHN:** *Princesse Alice* Stn 584 38°31′N: 29°9′3″W 845 m 10 specimens; *Travailleur* et *Talisman* No. 70 1883 25°39′N: 18°18′W 698 m 10 specimens.
IOS: *Discovery* Investigations: Stn 8966 31°21′N: 10°41·5′W–31°22′N: 10°39·2′W 686–742 m 10 specimens.

The disk is round, diameter up to 15 mm, densely covered with low granules or spinelets which are very rugose and do not form a crown. Only the tips of the radial shields are visible. The ventral interradial areas are also covered by spinelets although the extent of covering varies; in some specimens only the distal portion has spinelets, in others it is totally covered.

The jaws appear to be elongated, distinctly longer than broad. In some specimens the apical papilla may not be distinct while in others there are 1 or 2 large, pointed papillae; these are flanked by up to 6 flat, pointed or sometimes scale-like oral papillae. The distalmost one is larger than the others and is scale-like. The adoral shields are slightly wing-like, not or just separating the oral shield from the first lateral arm plate. The oral shields are large and arrow shaped but in some specimens the shield may be more rounded.

The arms are only slightly noded. The dorsal arm plates are bell shaped sometimes with a distinct lobe on the distal edge, and contiguous. The ventral arm plates are wider than long, pentagonal with an obtuse proximal angle and a slightly convex distal edge. The tentacle pores are relatively large armed with 2 flat scale-like tentacle scales, and occasionally the first arm pore may have 3, the third may lie hidden beneath the other two. There are 7–8 distinctly flattened, finely rugose arm spines, with the tips squared off. The arm spines do not form a fan on the proximal joints.

REMARKS. *O. valenciennesi rufescens* differs from *O. valenciennesi* Lyman (Challenger Stn 192 off Kei Is 236 m) in the following respects: the disk spinelets are not as rugose as those of *O. valenciennesi* and the adoral shields do not or only just separate the oral shield from the first lateral arm plate, those of *O. valenciennesi* are more wing-like and extend to the genital slits. However, these are minor differences insufficient to warrant more than an infraspecific distinction, supporting Mortensen's (1933) evaluation.

The complex jaw arrangement and the relatively large tentacle pores of *O. valenciennesi* suggest an affinity with the subfamily Ophiotominae particularly with the genus *Ophiopristis*.

DISTRIBUTION. This species has been recorded from off Madeira south to Angola from 640–1440 m.

Ophiacanthella troscheli (Lyman, 1878)
Fig. 21

Ophiacantha troscheli Lyman, 1878: 142; 1882: 190.
Ophiacanthella troscheli: Verrill, 1899*a*: 39; Matsumoto, 1915: 62.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 33 Bermuda 796 m HOLOTYPE.

The disk is pentagonal, diameter up to 6 mm, covered by very small fine scales; the holotype has a slightly transparent appearance. The scales are armed with low granules and simple spines. The radial shields are visible, distinctly longer than wide the distal portion of the shield bulges and touches or overlaps the opposite shield, the distal ends are separated. The ventral interradial areas are also covered by low granules.

The jaw appears as wide as long. There is usually one pointed apical papilla sometimes two or three flanked on each side by 3–4 pointed oral papillae. Distal to the oral papillae the second oral tentacle pore is particularly prominent. The adoral shields are large wing-like and separate the oral shield from the first lateral arm plate. The oral shield is oblong to rhombic.

The arms are slightly noded. The dorsal arm plates are fan shaped and contiguous on proximal segments. The ventral arm plates are pentagonal and separated from one another. The tentacle pores are not enclosed by the lateral arm plates but are open. The tentacle scale is small and pointed. There are 5 finely rugose and slightly flattened arm spines, of which the dorsalmost is the largest extending about 2 arm segments in length. The arm spines do not form a fan across the midradial on proximal arm segments.

REMARKS. *O. troscheli* is characterised by the contiguous radial shields and the two kinds of disk spinelets—low rugose granules and spines.

DISTRIBUTION. *O. troscheli* has only been recorded from the western Atlantic; from Bermuda 796 m.

Ophiolebes pachyphylax H. L. Clark, 1915
Fig. 22

Ophiacantha anomala?: Lyman, 1883: 260.
Ophiolebes pachyphylax H. L. Clark, 1915: 194.

MATERIAL STUDIED. **MCZ:** *Blake* Stn 306 41°32′50″N: 65°55′W 943 m HOLOTYPE.

The disk is round to sub pentagonal, diameter up to 8 mm; covered with small umbricating scales, in the dried holotype there is no indication of a covering of skin, many carrying a low spinelet with a multipointed crown. The radial shields are bar shaped separated, often covered over by the disk scales; and extended slightly less than half the disk radius. The ventral interradial areas are covered by scales and spinelets similar to those of the dorsal side.

The jaws are as wide as long. There is one long, finely rugose, club-like apical papilla flanked on each side by 4 oral papillae similar in shape and size to the apical papilla. In addition there may be one or two smaller papillae lying slightly below the oral papillae series between the first and second or the second and third oral papillae. The adoral shields are slightly curved large and occupying a large portion of the jaw proximal to the oral shield. The oral shield is rhombic often with the distal edge slightly produced.

The arms are noded. The dorsal arm plates are scallop shaped and separated from one another. The proximal ventral arm plates are approximately trapezoidal with a wide convex distal edge, they are contiguous with one another at least proximally. The distal ventral arm plates are more pentagonal with an obtuse proximal angle and a wide convex distal edge. The tentacle pores are small armed with a small, rugose, pointed tentacle scale. There are 7 arm spines proximally. The dorsal spines are long, pointed and finely rugose while the ventral ones are shorter, club shaped and often highly rugose with large secondary points on the shaft of the arm spine. The second dorsalmost spine is the longest, nearly 2 arm segments long, proximal arm spines do not form a fan.

REMARKS. *O. pachyphylax* disagrees in two characters with the descriptions of other species of *Ophiolebes,* including the type species *O. scorteus* Lyman, 1878. Firstly, the arm spines are long, up to 2 segments long while in the other species they tend to equal only one arm segment and secondly the skin of the disk is not thickened obscuring the plates beneath, although this may be an artefact due to the dried condition of the holotype there is usually some indication of a skin covering even in dried specimens. Other species of *Ophiolebes* species have a thickened skin covering the disk and to a certain extent the arm spines.

O. pachyphylax differs from *O. bucata* in having 7 long dorsal arm spines as opposed to 5 short ones in *O. bucata,* and in the disk armament.

Lyman (1883) was unsure of the identity of this species and assigned it to *Ophiacantha* thinking that it might be a juvenile *O. anomala.* H. L. Clark (1915) compiling his catalogue of specimens in the MCZ recognised it as a new species of Ophiolebes.

DISTRIBUTION. *O. pachyphylax* has only been recorded from off Nantucket 943 m.

Ophiolebes bacata Koehler, 1921

Fig. 22

Ophiolebes bacata Koehler, 1921: 5–8.

MATERIAL STUDIED. **MOM:** *Princesse Alice* Stn 3113 1911 32°34′45″N: 17°05′30″W 1700 m HOLOTYPE. **COB:** BIOGAS Stn 1 CV23 2034 m 1 specimen.

The disk is subpentagonal, slightly indented interradially, diameter up to 4·5 mm; densely covered by small rugose granules. The radial shields are aslo covered with rugose granules but it is possible to distinguish their position on the disk. The ventral interradial areas are also covered by low granules.

The jaws appear to be as wide as long. There is one pointed apical papilla flanked on either side by 3–4 blunter oral papillae. There is a small spine-like papilla lying within the mouth slit which is probably the first oral tentacle scale. The adoral shields are large and are restricted to the proximal sides of the oral shield, not separating it from the first lateral arm plate. The oral shield is rhombic, often with a slight distal projection. The adoral and oral shields and the arm plates are textured with glassy granules embedded in the matrix of the plate.

The arms are not noded. They are long and are capable of coiling vertically. The dorsal arm plates are fan shaped and not contiguous. The ventral arm plates are pentagonal with an acute proximal angle, a slightly indented distal edge, and separated from one another. The tentacle pores are quite small each armed with a very small tentacle scale. There are 5 short arm spines, the longest is scarcely equal in length to one segment. Ventral arm spines have a distally directed, hooked tip or at least conspicuous secondary points at the tip. This feature becomes more conspicuous on distal arm segments.

REMARKS. *O. bacata* is distinguished from *O. pachyphylax* under the REMARKS section of that species.

DISTRIBUTION. This species has been recorded from the eastern Atlantic from the Bay of Biscay and off Madeira 1300–2034 m.

Ophiolebes retecta (Koehler, 1895)

Fig. 22

Ophioscolex retectus Koehler, 1895: 462; 1896*a*: 78–79.
Ophiolebes retecta Mortensen, 1927: 183, 185.

MATERIAL STUDIED. **MNHN:** *Caudan* 1895 45°57′N: 6°21′W 1410 HOLOTYPE.
COB: BIOGAS Stn 1: CV20 2282 m 1 specimen.

The disk is pentagonal up to 7 mm; covered with thin skin covering a coating of imbricating scales many carrying a low granule. The radial shields are visible through the skin of some preserved specimens and are long bar shaped widely separated from one another. The ventral interradial areas are skin covered with a coating of granules.

The jaws are as broad as long. There is one long pointed apical papilla with 2–3 oral papillae on each side of the jaw. The oral papillae are small and pointed, irregularly arranged either along the edge of the jaw or slightly more superficial. The jaw, oral and adoral shields and the underside of the arms are covered with thick skin, which in wet specimens almost obscures the outlines of the plates beneath. The adoral shields are short, slightly curved and situated proximal to the oral shield, not separating it from the first lateral arm plate. The oral shield is rhombic but often with an obtuse proximal angle and a convex distal edge.

The arms are capable of coiling vertically. The dorsal arm plates are divided transversely into two; the proximal part is small rounded or rectangular and the outer one is rounded trapezoidal with a convex distal edge. The double plates of consecutive segments, are not contiguous with the next pair. The ventral arm plates are approximately pentagonal with an obtuse proximal indented in the middle and are separated from one another. The tentacle pores are small and are absent on arm segments beyond the second or third segment. Tentacle scales are either absent or inconspicuous. There are up to 8 rugose arm spines which are invested with thickened skin.

Remarks. In the characters of the divided dorsal arm plates and the oral papillae *O. retecta* bears a closer resemblance to *Ophiochondrus armatus* than to any of the other species of *Ophiolebes*. The only characters which appears to separate them are the scaling of the disk, which is formed of imbricating plates in *O. retecta* but non-imbricating plates in *Ophiochondrus*, and the covering of thick skin over the jaws and ventral part of the arm in *O. retecta* which is absent in *Ophiochondrus*. It is possible that *O. retecta* is referable to *Ophiochondrus* but inadequate material prevents a satisfactory assessment of this problem. In addition Mortensen (1927) has called attention to the fact that *Ophiochondrus armatus* may not be congeneric with *Ophiochondrus convolutus* Lyman, 1869, the type species. It seems best at present to leave *Ophiolebes retecta* in *Ophiolebes* until *Ophiochondrus* and its allies can be properly revised.

The above remarks also apply to the Japanese species *Ophiolebes tuberosa* Matsumoto, 1917 which closely resembles *O. retecta*. It too has divided dorsal arm plates and its inclusion in *Ophiolebes* is also suspect.

Distribution. *Ophiolebes retecta* has only been recorded from the Bay of Biscay at depths of 1410–2282 m.

OPHIOTOMINAE Subfamily nov.

Diagnosis. A subfamily of the Ophiacanthidae with a sack-like disk covered with thickened skin or thin scales which often carry spinelets or granules; radial shields variable in shape, either rib-like with only the distal ends not covered by scales or short with most of the plate visible; the jaws distinctly longer than broad; one or sometimes as many as three large blunt apical papillae flanked on each side by three to many oral papillae; in most genera the second oral tentacle pore arising superficially or nearly so and the associated tentacle scales often forming a continuous series with the oral papillae; the oral tentacle scales often spine-like and larger than the oral papillae, except in *Ophiolimna* where the second oral tentacle pore is obscured by a large opercular distal oral papillae; nearly all genera with well developed elongated adoral shields and a large oral shield; the tentacle pores of the arm mostly large and often with small spine-like tentacle scales although some genera with smaller pores armed with well developed tentacle scales; the arm spines relatively short usually only slightly longer than one arm segment.

Type Genus *Ophiotoma* Lyman, 1883 with type species *O. coriacea* Lyman, 1883.

Remarks. Genera included in this subfamily are *Amphilimna* Verrill, 1899*a*, *Ophiocymbium* Lyman, 1880, *Ophiodaces* Koehler, 1922*b*; *Ophiodelos* Koehler, 1930; *Ophiolimna* Verrill, 1899*a*; *Ophiologimus* H. L. Clark, 1911; *Ophiomedea* Koehler, 1906; *Ophiophiura* H. L. Clark, 1911; *Ophiopristis* Verrill, 1899*a*; *Ophioprium* Verrill, 1899*a*; *Ophiosparte* Koehler, 1922*b*; *Ophiotoma* Lyman, 1883; *Ophiotrema* Koehler, 1896*c*.

H. L. Clark (1915) considered *Ophiopristis* to be congeneric with *Ophiacantha* but as outlined on p. 53 I believe that *Ophiopristis* is not only a valid genus but also referable to a separate subfamily.

The most important features of this subfamily are found in the mouth parts and the tentacle pores.

Commonly the second oral tentacle pore is quite superficial situated adjacent to the proximal edge of the adoral shield. The various arrangements of the tentacle scales associated with this pore provide useful generic characters. They may form a continuous series with the oral papillae as in the genus *Ophiopristis*. This may also be true for *Ophiodelos* and *Ophiologimus* judging from original figures and descriptions.

The tentacle scales may be distinct from the oral papillae being either separated by a gap or placed at a higher level as viewed from the ventral side as in the genera *Ophiotoma* and *Ophioblenna*. In these two genera the tentacle pores on the arm are open and do not usually have tentacle scales. The tentacle scales may also be distinguished by their size or shape as well as position, as in the genera *Ophiotrema, Ophioprium, Ophiophiura, Ophiosparte* and *Ophiodaces*. Here the oral tentacle scales tend to be larger than the oral papillae as well as being separated above them. There is however a graduation between these five genera and genera like *Ophiotoma*. For instance, *Ophiotoma affinis* Koehler, 1921, unlike *Ophiotoma coriacea* has an arrangement of oral papillae and tentacle scales similar to *Ophiotrema alberti* Koehler, 1896*c*. The tentacle pores of this latter group are open and often armed with small spine-like tentacle scales except in *Ophiosparte* which has open tentacle pores but a well developed tentacle scale which forms a continuous series with the arm spines.

In *Ophiomedea* and *Ophiocymbium* the second oral tentacle pore becomes increasingly superficial and the oral tentacle scales can easily be distinguished. The tentacle pores on the arms of these two genera are open and large with only small spine-like tentacle scales being present if at all.

The exception to the kinds of oral arrangements mentioned is *Ophiolimna*. Here the oral pore although quite superficial is hidden by an opercular papillae, the distalmost in the oral series. Whether this is a true oral papillae or a modified tentacle scale is uncertain. *Ophiolimna* is included in this subfamily because it has elongated jaws, a similar arrangement of the oral and adoral shields to the other genera in the Ophiotominae. The tentacle pores of the arms are not as open as in other members of this subfamily and are armed with one large tentacle scale, resembling the arrangement of *Ophiopristis*, and may be intermediate between the Ophiotominae and Ophiacanthinae but pending further study should remain in the Ophiotominae.

There appears to be some confusion concerning the genera *Ophioprium* and *Ophiopristis*. H. L. Clark (1915) did not consider *Ophiopristis* to be a distinct genus and transferred the type species *O. hirsuta* to *Ophiacantha* the remaining species *O. cervicornis, O. permixta* and *O. axiologia* together with a new species *O. imperfectum* he transferred to a new genus *Ophioprium* with the type species *O. cervicornis*. *Ophioprium* was defined as follows: hidden radial shields; large tentacle pores armed by two or more tentacle scales one attached to the lateral arm plate the other to the ventral arm plate; numerous oral papillae forming a continuous series with long slender spinelets which are associated with the second oral tentacle pore. Clark added that he was uncertain that *O. axiologia* and *O. imperfectum* did belong in *Ophioprium*.

Baker (1979) added two more species *O. larissae* and *O. kalalae* and Baker & Devaney (1981) proposed to transfer *Ophiacantha rosea* Lyman to *Ophioprium* (see under *Ophiacantha rosea*).

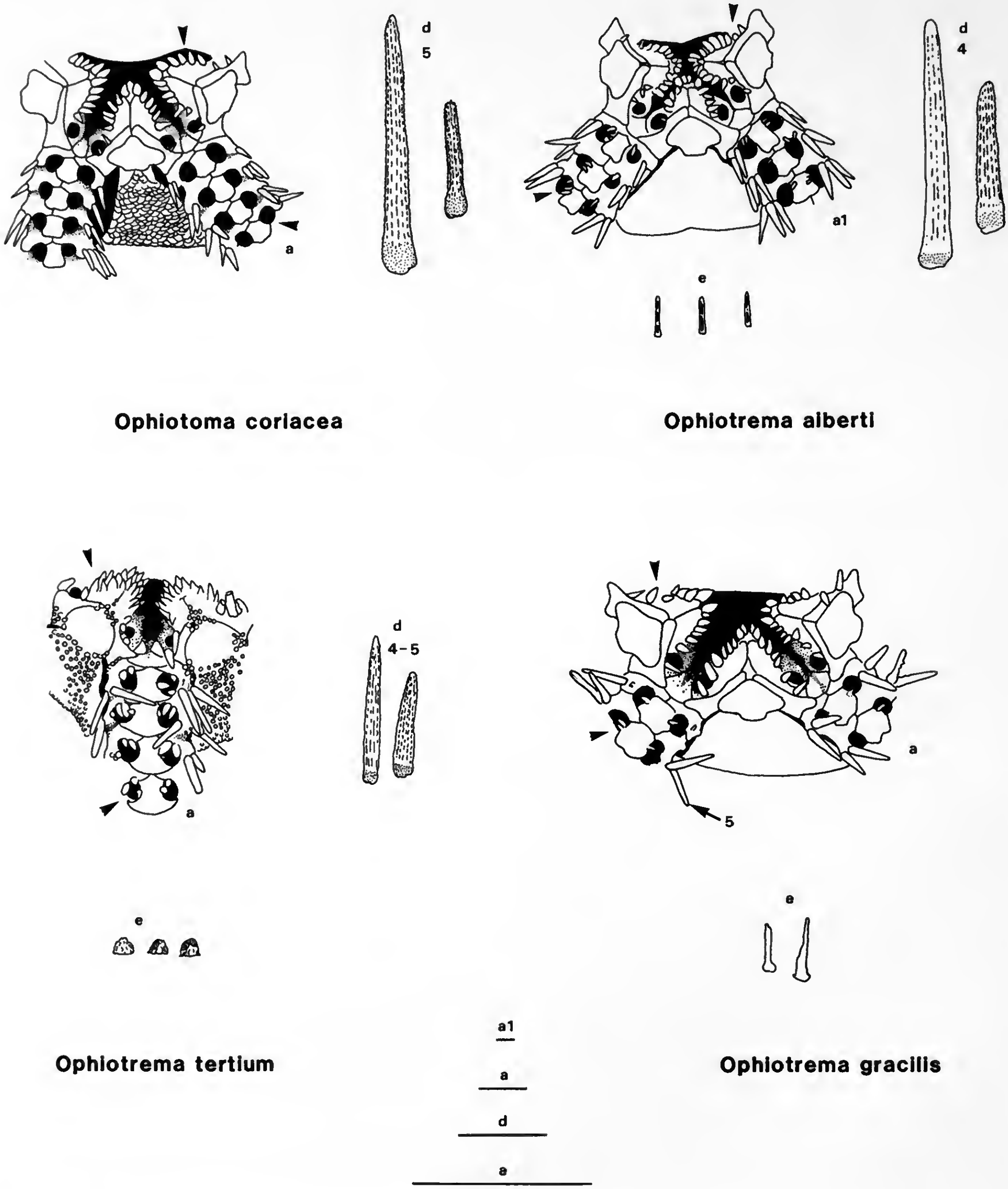
In transferring *O. hirsuta* H. L. Clark confused two distinct genera. *O. hirsuta* is distinctly a Ophiotominid not an *Ophiacantha* and I therefore propose to re-establish the genus *Ophiopristis*.

Ophiopristis may be defined as follows: the jaw longer than broad with one or two apical papillae flanked on each side by 4 or more rounded or slightly pointed oral papillae which form a continuous series with 2–4 slightly larger tentacle scales associated with the second oral tentacle pore, these scales may arise on the adoral shields, in some species there may also be papillae on the inner edge of the first ventral arm plate, the adoral shields long and narrow separating the oral shield from the first lateral arm plate; disk covered by small scales each bearing a spinelet; radial shields covered and inconspicuous; tentacle pores of the arm not open but armed with one or two leaf-like or scale-like tentacle scales. Species included are: *Ophiopristis hirsuta*-type, (Fig. 24) *Ophioprium axiologus* H. L. Clark, 1909.

Ophiopristis differs from *Ophioprium* as follows the oral tentacle scales are not markedly different from the oral papillae—those of *Ophioprium* are much more elongate and slightly separated; the tentacle pores are smaller and armed with 1–2 large tentacle scales whereas the pores in *Ophioprium* are open and armed with small thin tentacle scales.

Ophiopristis does seem to be similar in appearance to *Ophiologimus* H. L. Clark, 1911 but differs mainly in the form of the tentacle pore which is slightly smaller with larger tentacle scales than *Ophiologimus*. The relationship between *Ophiopristis* and some species assigned to *Ophiotreta* needs to be investigated.

OPHIACANTHIDAE : OPHIOTOMINAE



Ophiotoma coriacea

Ophiotrema alberti

Ophiotrema tertium

Ophiotrema gracilis

Fig. 23 Key to the Ophiacanthidae: Ophiotominae. *Ophiotoma* and *Ophiotrema*: (a) ventral view of disk; (d) arm spines. A number with this figure indicates the number of proximal arm spines. The larger spine is a dorsal spine; the smaller a ventral spine; in figures with only one spine it is the dorsal one. (e) Disk spinelets. NB. In some figures the ventral interradial area has been left blank for clarity. Bar scales = 1 mm, letters above the bars refer to the figures.

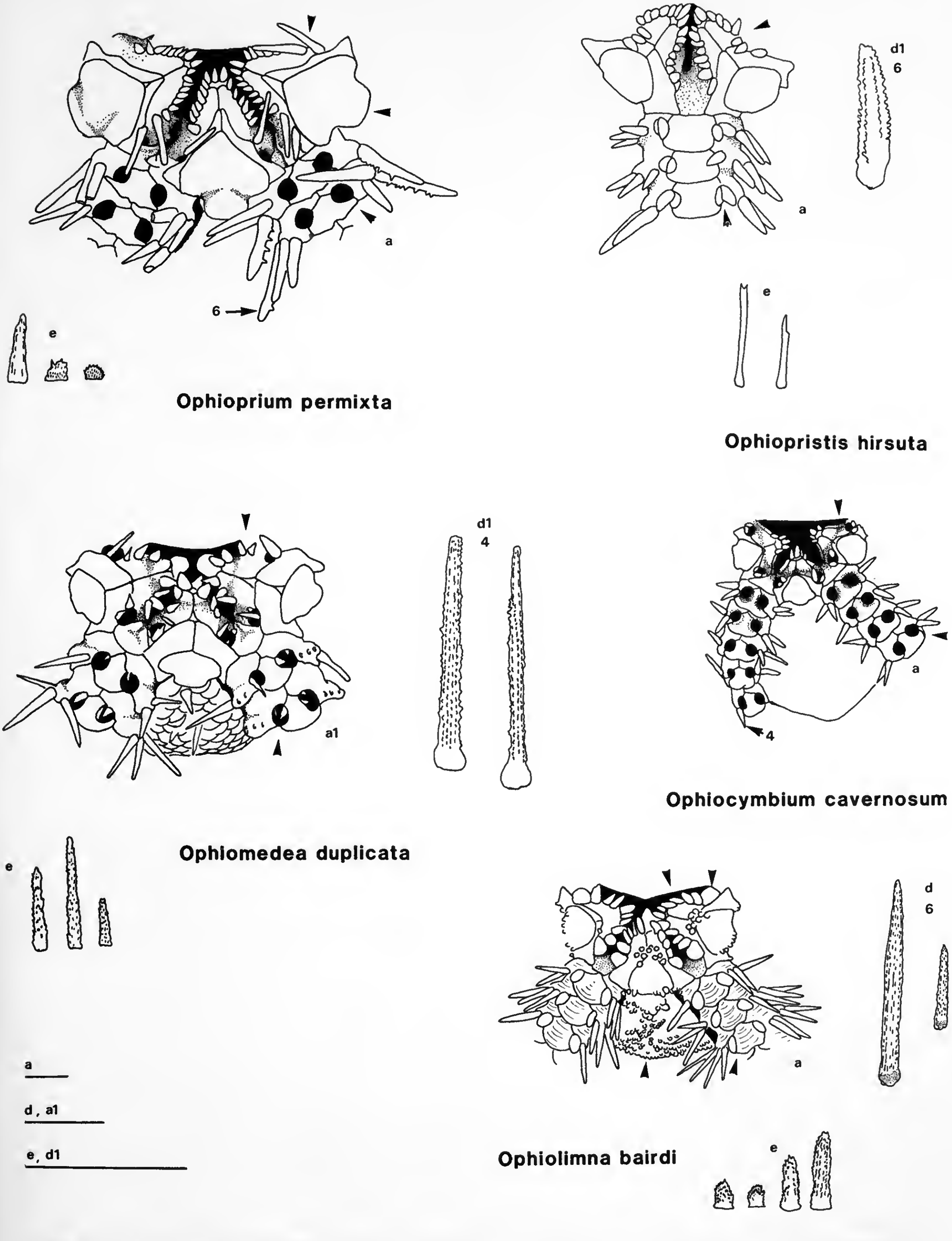


Fig. 24 Ophiacanthidae: Ophiotominae. *Ophioprium*, *Ophiopristis*, *Ophiomedea*, *Ophiocymbium* and *Ophiolimna*. Captions as in Fig. 23.

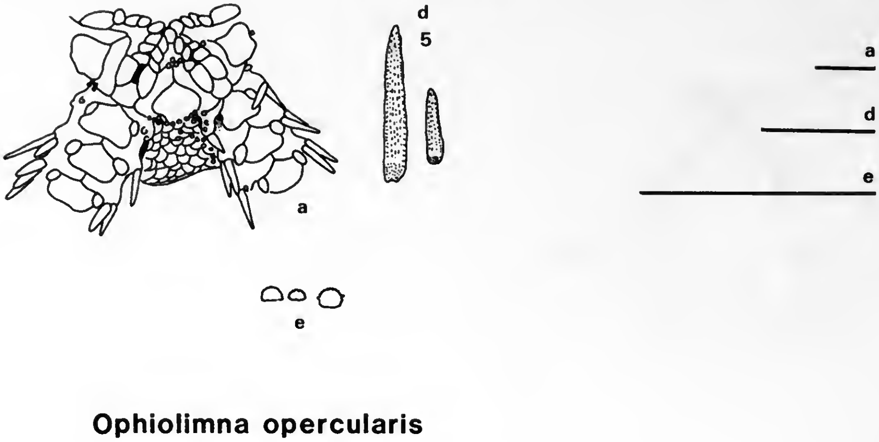


Fig. 25 Ophiacanthidae: Ophiotominae. *Ophiolimna*. Captions as in Fig. 23.

Ophioprium is now defined as follows: the jaws longer than wide with one or two large apical papillae flanked on each side by 4–6 pointed oral papillae distal to which up to 4 elongated spine-like tentacle scales associated with the second oral tentacle pore, the distal scales markedly distinct from the oral papillae; the adoral shields long narrow often partially overlain by the large oral shield; disk covered by scales obscured by dense covering of spinelets and or granules; radial shields covered and inconspicuous; tentacle pores of the arm open armed with 1–2 long thin tentacle scales.

Species included are: *Ophioprium cervicornis* (Lyman 1883)—type species, *Ophiopristis permixta* Koehler, 1914 (Fig. 24), and *Ophioprium imperfectum* H. L. Clark, 1915.

The reasons for excluding *Ophiacantha rosea* Lyman are dealt with under that species. The species described by Baker (1979) do not appear to belong in this genus. They lack the elongated jaw, the two sets of papillae i.e. the oral papillae and markedly different oral tentacle scales and while the tentacle pores are relatively large, they are not open but are armed with 1–2 large tentacle scales. The figures and description suggest affinities with *Ophiotreta* or possibly *Ophiopristis*.

The genus *Ophioprium* shares several characters with *Ophiophiura, Ophiotrema* and possibly *Ophiotoma* and *Ophioblenna*. In particular the two distinct forms of papillae on the jaw, open tentacle pores and small tentacle scales. Differences between them centre on the covering of the disk, numbers of tentacle scales, arm spine number and shape. It is likely that in several instances such differences will be specific not generic.

Summary of proposed changes

Usage as in H. L. Clark (1915), Baker (1979) and Baker & Devaney (1981)	Proposed usage
Ophioprium cervicornis	*Ophioprium cervicornis*
Ophioprium permixta	*Ophioprium permixta*
Ophioprium imperfectum	*Ophioprium imperfectum*
Ophioprium axiologia	*Ophiopristis axiologia*
Ophiacantha hirsuta	*Ophiopristis hirsuta*
Ophioprium larissae	*Ophiotreta? larissae* or *Ophiopristis?*
Ophioprium kalalae	*Ophiotreta? kalalae* or *Ophiopristis*
Ophioprium rosea	*Ophiacantha rosea*

Ophiotoma coriacea Lyman, 1883
Fig. 23

Ophiotoma coriacea Lyman, 1883: 227–287; Farran, 1913: 45; Mortensen, 1927: 187; 1933*a*: 39–41.

Material studied. **MCZ:** *Blake* Stn 308 E. off Cape Cod 1242 m HOLOTYPE.
COB: BIOGAS HZ CV06 2200 m 1 specimen; BIOGAS Stn 1 CP27 1920 m 1 specimen; BIOGAS Stn 3 DS 30 4106 m 1 specimen.

The disk is round up to 17 mm disk diameter, and appears to be covered with skin but in dry specimens small scales can be seen through this covering. Small granules are scattered over the surface some developed into low spinelets. Only the distal tips of the radial shields are visible. The ventral interradial areas are similar to those of the dorsal side but the scales are usually more conspicuous.

The jaws appear to be longer than wide. There are up to three rounded blunt apical papillae flanked on either side by 6–7 oral papillae, the proximal ones are blunt but the distal ones are more spine-like. The series of oral papillae is separated from the 2–3 small blunt oral tentacle scales situated on the proximal edge of the adoral shields—these scales are much smaller than the oral papillae. The adoral shields are long with a straight proximal edge and widening distally so that they separate the oral shield from the first lateral arm plate. The oral shield is a large, rounded arrow shape.

The arms do not appear to be noded. The dorsal arm plates are slightly fan shaped, and contiguous on at least in the proximal segments; in some specimens the most proximal plates are slightly irregular and may be smaller than those on the rest of the arm. The ventral arm plates are irregularly pentagonal; with an obtuse proximal angle, indented lateral sides and a curved or indented distal edge; they are separated. The tentacle pores are large and open without tentacle scales. There are 5 simple arm spines proximally, 4 distally.

Remarks. *O. coriacea* superficially resembles *Ophiotrema alberti* from which it differs by the lack of distinct spinelets on the disk; the shape of the adoral shields which are straight and do not have an indented proximal edge while those of *Ophiotrema alberti* are more wing-like and indented over the second oral tentacle pore; the shape of the oral shields which are arrow shaped not round and almost hemispherical as in some specimens of *Ophiotrema* and by the absence of tentacle scales in *Ophiotoma*. *Ophiotoma coriacea* bears a close resemblance to the ophiomyxid *Ophioscolex purpureus*. It differs from *Ophiotoma* in having one distinct tentacle scale, only 3 as opposed to 4–5 arm spines the proximal arm spines are transformed into hooks, the ventral arm plates are more rounded and pentagonal, and are contiguous at least proximally.

H. L. Clark (1915) considered that *O. coriacea* is conspecific with *O. bartletti* Lyman, 1883. As all that remains of the type specimen in the MCZ Harvard are fragments of the arms this cannot be confirmed. Accordingly it is proposed to retain the name *Ophiotoma coriacea* for this species.

Distribution. It has been recorded from both sides of the North Atlantic: in the west off Cape Cod at a depth of 1242 m and in the east off Iceland south to the Azores in depths of 1765–4106 m.

Ophiotrema alberti Koehler 1896*c*
Fig. 23

Ophiotrema alberti Koehler, 1896*c*: 251; 1906: 6; 1907: 295; 1907*b*: 142; 1908: 612; 1909: 196–198; Matsumoto, 1915: 67; Gage *et al.* 1983: 288.

Material studied. **MNHN:** *Travailleur & Talisman* 1883 Stn 134 38°9′N: 25°36′W 4010 m SYNTYPE.
COB: BIOGAS Stn 3: CV13 4252 m 2 specimens. CYMOR-2 DR29 2 specimens. INCAL: WS08 4287 m 2 specimens; WS10 4354 m 1 specimen; CP01 2068 m 2 specimens; CP16 4262 m 2 specimens; ØS05 4297 m 1 specimen.
SMBA: RRS *Challenger II*: Stn AT 192 57°21′N: 12°02′W 1862 m 2 specimens.

The disk is subpentagonal and covered with small thin scales many of which carry a simple glassy spinelet or rod, disk diameter up to 15 mm. The tips of the radial shields are sometimes visible and are rounded pear drop shaped. The disk is very delicate and often damaged particularly in the centre. The ventral interradial areas are covered with small plates armed with simple rods like those of the dorsal surface.

The jaw appears longer than broad. There may be one or more apical papillae flanked on each side by 4 or 5 oral papillae on the jaw edge. These papillae form an almost continuous series with 4 or 5 similar papillae associated with the second oral tentacle pore. In some specimens the latter papillae are much more developed forming a line among the proximal edge of the adoral shields. The second tentacle pore arises superficially. The adoral shields are wing-like with the proximal edge indented opposite the second oral tentacle pore and separate the oral shield from the first lateral arm plate. The oral shield is large, nearly hemispherical, with a rounded proximal edge and a slight distal lobe.

The arms are not particularly noded. The dorsal arm plates are triangular to bell shaped, and separated from one another. The ventral arm plates are nearly rectangular with a very obtuse proximal angle and a slight indent in the distal edge; they are nearly contiguous on proximal arm segments. The tentacle pores are large and the tube feet appear to be unretractable. The tentacle scales are small and variable, numbering from 0–5, some are needle-like while others resemble small granules. There are 4 glassy, smooth arm spines, slightly flattened with a rounded tip. The dorsalmost arm spine appears to be the longest up to 2 arm segments long.

REMARKS. *O. alberti* is similar to *O. gracilis* Koehler, 1914 (Fig. 23) from the West Indies (*Albatross* Stn 2751 16°54′N: 63°12′W 1236 m) the main differences appear to be the arrangement of the oral papillae and tentacle scales which are more regularly arranged in *O. gracilis* not forming an irregular line along the edge of the adoral shields. The oral shield is distinctly arrow shaped in *O. gracilis*. However, these differences may be just infraspecific but until more specimens are recovered from the western Atlantic it is better to recognise both.

DISTRIBUTION. This species has been recorded from the Rockall Trough, the Bay of Biscay and off the Azores with a bathymetric range of 1862–4252 m.

Ophiotrema tertium Koehler, 1922*a*

Fig. 23

Ophiotrema tertium Koehler, 1922*a*: 88–91.

MATERIAL STUDIED. **COB:** BIOVEMA CP03 10°47′13N: 42°41′01W 5127 m 1 specimen.

The disk is pentagonal; often very damaged; covered with granules and sometimes lanceolate spinelets; disk diameter up to 15 mm. The ventral interradial area is also covered with granules, if spinelets are present they are usually confined to the distal edge.

The jaws appear to be longer than broad. There are 1–4 pointed apical papillae flanked on each side by 4–5 pointed oral papillae; there are 2, sometimes more larger tentacle scales associated with the second oral tentacle pore, distal to be oral papillae. The adoral shields are partially overlaid by the oral shield, flared distally, and often obscured by thickened skin and scattered granules. The oral shield is large, rounded triangular.

The arms are not particularly noded. The dorsal arm plates are fan-shaped, sometimes contiguous. The ventral arm plates are axe shaped and sometimes contiguous. The tentacle pores are large armed with 5 or more tentacle scales whose shape varies from thin and pointed to scale-like. There are 4–5 finely rugose arm spines; the second dorsalmost spine is the longest up to 2 arm segments long.

REMARKS. *O. tertium* can easily be distinguished from the other two species of *Ophiotrema* by the covering of the disk and the shape of the ventral arm plates.

The Biovema specimen differs from the type description in that the disk covering is comprised only of granules and in the shape of some of the tentacle scales. However, a lack of material prevents a study of the variation of such characters and as there is an overall similarity it is best not to describe this specimen as a new species.

DISTRIBUTION. *O. tertium* has been recorded from the Pacific off the Philippine Islands at a depth of 1335 m, and from the North Atlantic from the Vema Fracture zone at 5127 m.

Ophiomedea duplicata Koehler, 1906

Fig. 24

Ophiomedea duplicata Koehler, 1906: 19–21; 1907: 280; 1922: 97.

MATERIAL STUDIED. **MNHN:** *Travialleur & Talisman* 25 Juin 1883 No. 43 29°52′N: 14°4′W 2075 m 1 specimen HOLOTYPE.

The disk is rounded to pentagonal, diameter up to 5 mm covered with thin overlapping scales many of which carry a simple rodlike spinelet. The spinelets are finely rugose. The radial shields may be visible, they are small irregular in shape and are as wide as long. The ventral interradial areas are covered by scales similar to those of the dorsal side, these scales also carry rod like spinelets.

The jaws appear to be wide as long. The surface of the jaw is indented about a third from the tip. There is one large blunt apical papilla flanked by 3–4 oral papillae irregularly arranged on each side; those nearest the apical papillae are conical the distalmost ones may be more spine-like. Sometimes the oral papillae form a continuous series with the tentacle scales of the second oral tentacle pore. Alternatively the tentacle scales may lie above the distal oral papillae. The second oral tentacle pore is superficial and is armed with 2–3 tentacle scales, the distalmost of these is large and spine-like. The adoral shields are large occupying a large portion of the jaw proximal to the oral shields. They are not particularly wing-like but separate the oral shield from the first lateral arm plate. The oral shield is rounded, rhombic but sometimes with a slight distal projection; the proximal edge is often complete rounded and not angular.

The arms are distinctly noded. The dorsal arm plates are triangular and separated. The first ventral arm plate is pentagonal with the lateral edges raised forming a boundary lip to the second oral tentacle pores. The subsequent ventral arm plates are pentagonal to bell shaped, separated with a wide curved distal edge and indented lateral edges. The tentacle pores are large and open, each is armed usually with two spine-like tentacle scales, the inner one of the two is the larger. There are 5–6 simple, finely rugose arm spines, the dorsalmost spine is the largest.

REMARKS. *Ophiomedea duplicata* may be mistaken for a juvenile *Ophiotrema alberti,* it differs from that species by the following characters: the jaw shape is as wide as long not longer than wide as in *O. alberti;* there are fewer oral papillae and oral tentacle scales than in *O. alberti,* the ventral arm plates are bell shaped with a distinctly widened distal edge, the ventral arm plates of *O. alberti* being more pentagonal or rectangular with rounded edges and the distal edge indented but not widened. *O. duplicata* also resembles *Ophiocymbium cavernosum* but differs by having spine-like not block-like oral papillae, differently shaped oral and adoral shields.

DISTRIBUTION. *Ophiomedia duplicata* has been rarely encountered, recorded only from the type locality off the Canary Islands at a depth of 2075 m.

Ophiocymbium cavernosum Lyman, 1880

Fig. 24

Ophiocymbium cavernosum Lyman, 1880: 7; 1882: 162–163.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 157 53°55′S: 108°35′E 3566 m HOLOTYPE.
COB: BIOGAS Stn 4: CP15 4715 m 1 specimen; DS79 4715 m 1 specimen. INCAL: WS05 4796 m 3 specimens; WS9 4277 m 2 specimens; WS10 4354 m 5 specimens; CP08 2644 m 1 specimen; CP13 4800 m 4 specimens; DS16 4262 m 6 specimens; ØS 04 4796 m 4 specimens; ØS 05 4296 m 1 specimen; ØS 07 4249 m 2 specimens; ØS 08 4327 m 4 specimens.

The disk is round flexible, rather bag-like, diameter up to 9 mm; covered by small thin semi-transparent scales some of which carry low granules. The radial shields are indistinct. The ventral interradial areas are similar to the dorsal surface.

The jaws are slightly wider than long. There are 3 prominent spine-like papillae on the oral plate with 2 rudimentary block like papillae on each side of the jaw. The second oral tentacle pore emerges superficially and is armed with 2 flat, blunt, spine-like papillae arising on the adoral shields and 1 small block-like papillae arising at the junction of the first ventral arm plate and the adoral shield. The adoral shields are partially overlayn by the oral shield obscuring their proximal suture, distally the adoral shields are slightly flared and separate the oral shield from the first lateral arm plate. The oral shield is large, triangular in shape with a slight distal projection.

The arms are only slightly noded. The dorsal arm plates are triangular and separated from one another. The ventral arm plates are axe shaped; thin proximally but flaring out with a wide convex distal edge and only contiguous on the first few arm segments. The tentacle pores are large, open, only the first few may have tentacle scales which are usually thin and spine-like. There are 4 simple glassy spines of which the dorsalmost is the largest, nearly a segment long.

REMARKS. *O. cavernosum* is characterised by the structure and armament of the jaw, the open tentacle pores and the simple arm spines. Only *Ophiomedea duplicata* bears any resemblance to it but *O. duplicata* can be distinguished by the spine-like oral papillae not block-like papillae as in *Ophiocymbium;* the adoral and oral shields differ in shape while the arm spines are rugose not smooth and glassy as in *Ophiocymbium.*

DISTRIBUTION. *Ophiocymbium cavernosum* is a little known ophiuroid previously only recorded from east of Kerguelen Islands, Southern Ocean, its discovery in the Bay of Biscay marks an exciting extension of range perhaps accountable to the considerable depth at which this species is found.

Ophiolimna bairdi (Lyman, 1883)

Fig. 24

Ophiacantha bairdi Lyman, 1883: 70–72; Lütken & Mortensen, 1899: 9–13; Koehler, 1907: 289; H. L. Clark, 1911: 230; 1915: 106; Mortensen, 1927: 188, 190; 1932: 27; 1933*a*: 30–31.

Ophiolimna bairdi: Verrill, 1899*a*: 40,–44; 1899*b*: 346; Matsumoto, 1917: 101–102 Djakanov, 1954: 32–33; Baranova, 1957: 189; Fell, 1960: 17.

MATERIAL STUDIED. **MCZ:** *Blake* Stn 308 Off Cape Cod 2235 m PARATYPE.
COB: BIOGAS Stn 1: CV10 2108 m 1 specimen; 1 CP02 2177 m 1 specimen; CV39 2350 m 1 specimen; CP26 2115 m 1 specimen; DS16 2325 m 1 specimen; DS18 2138 m 2 specimens; DS32 2138 m 1 specimen. BIOGAS Stn 2: CP09 1 specimen. BIOGAS Stn 6: CV16 1909 m 1 specimen; CP25 1985 m 5 specimens; DS26 2076 m 4 specimens. INCAL: DS03 609 m 1 specimen.
IOS: *Discovery* Investigations: Stn 8511/2 41°49·6′N: 11°6·0′W 2574–2584 m 2 specimens.
SMBA: RRS *Challenger II:* Stn ES 118 54°39′N: 12°14′W 2910 m 1 specimen.

The disk is round to sub pentagonal, diameter up to 11 mm, covered with elongated granules and spines. The disk is often damaged with the central portion of the disk missing. Only the tips of the radial shields are sometimes visible. The ventral interradial areas are covered with granules like those of the dorsal surface.

The jaws appear large, slightly longer than wide. There is one, sometimes two, pointed apical papilla flanked on each side by 5–6 oral papillae, the proximal ones are pointed similar in shape to the apical papilla but distally they become rounded, and the distalmost one is large and opercular. The adoral shields are very wing-like and separate the oral shield from the first lateral arm plate. At the proximal suture of the shields there is often a cluster of granules. The oral shield is large and is approximately triangular in shape.

The arms are noded. The dorsal arm plate are bell shaped and contiguous. The ventral arm plates are approximately pentagonal, the lateral sides are indented with the distal edge convex, and are contiguous. The tentacle pores are quite large each is armed with a rounded or slightly pointed scale-like tentacle scale. The lateral arm plates, ventral arm plates and tentacle scales are distinctly striated. There are 6 arm spines. They do not form a fan on proximal arm segments.

REMARKS. *Ophiolimna bairdi* can be easily recognised by its large triangular oral shields, granules and simple spines on the disk, granules on the adoral shields, striations on the lateral and ventral arm plates.

DISTRIBUTION. This species is perhaps of Arctic origin which is also found in bathyal and abyssal depths of both sides of the North Atlantic: south to Martha's Vineyard in the west and from the Rockall Trough south to Portugal in the east.

Ophiolimna opercularis Koehler, 1907*b*

Fig. 25

Ophiolimna opercularis Koehler, 1907*b*: 43; 1909: 191–192.

Ophiacantha opercularis: Mortensen, 1927: 190.

MATERIAL STUDIED. **MOM:** *Princesse Alice* 1901 Stn 1173 12°7′N: 33°33′W 6035 m HOLOTYPE.

The disk is round covered with a dense coating of low hemispherical granules which extend on to the ventral interradial area; disk diameter is 4 mm.

The jaws appear to be longer than broad. There is one rounded apical papilla flanked on each side by up to 5 oral papillae, the distalmost of which is large, rectangular and opercular. The adoral shields are large, slightly flared distally and separating the oral shield from the first lateral arm plate. Scattered granules are often present on the jaw plates and on parts of the adoral shields. The oral shield is approximately rounded triangular, often with an acute proximal angle and a distal projection.

The arms are not particularly noded. The dorsal arm plates are slightly bell shaped or fan shaped, they approach but are not quite contiguous. The first ventral arm plate is pentagonal, subsequent ones are rounded pentagonal with an obtuse proximal angle and a convex distal edge, only the first and second ventral arm plates are contiguous. The tentacle pores are relatively large armed with one rounded tentacle scale. There are 5 finely rugose arm spines, distally only 3; the spines approach but do not form a fan on the proximal arm segments. The dorsal, lateral, and ventral arm plates are distinctly striated.

REMARKS. *O. opercularis* is very similar to *O. bairdi* suggesting that any differences may be due to infraspecific variation. However, until more specimens of *O. opercularis* are available it is best to regard them as distinct.

O. opercularis can be distinguished from *O. bairdi* by the disk bearing only low granules, the shape of the oral shield which is more rounded, the shape of the proximal oral papillae which are more rounded than those of *O. bairdi,* finally the tentacle pore is smaller—although this may be due to the small size of the specimen.

DISTRIBUTION. One specimen of this species has been recorded, from the Cape Verde Basin, SW. of the Cape Verde Is at 6035 m.

OPHIOPLINTHACINAE Subfamily Nov.

DIAGNOSIS. A subfamily of the Ophiacanthidae with well developed disk plates or enlarged disk scales; the disk sometimes indented interradially and often high; the radial shields forming part of the disk, often quite long but not bar-like and hidden by the disk plates; jaws as broad as long; one apical papilla flanked on each side by up to six oral papillae found in most genera except *Ophiocamax* and *Ophiomitra* which have multiple apical and oral papillae; oral tentacle pore not superficial and without conspicuously modified tentacle scales; oral shield small to medium in size; the tentacle pores of the arm not conspicuously large and always armed with at least one tentacle scale; arm spines usually long, the longest equal in length to at least 2 arm segments.

TYPE GENUS. *Ophioplinthaca* Verrill, 1899*a* with type species *O. dipsacos* (Lyman, 1878).

REMARKS. Genera included in this subfamily are: *Microphiura* Mortensen, 1911; *Ophiocamax* Lyman, 1878; *Ophiocopa* Lyman, 1883; *Ophiodictys* Koehler, 1922*a*; *Ophiomitra* Lyman, 1869; *Ophiomitrella* Verrill, 1899*a; Ophiomytis* Koehler, 1904 *'Ophiophthalmus'* Matsumoto, 1917, an invalid junior homonym of *Ophiophthalmus* Fitzinger, 1843, a Reptile; *Ophioplinthaca* Verrill, 1899*a*; *Ophioripa* Koehler, 1922*a*; *Ophiothamnus* Lyman, 1869; *Ophiurithamnus* Matsumoto, 1917.

Ophioplinthaca has been chosen as type genus because it shows the greatest and therefore most unambiguous development of the characters which separate this subfamily from the others but from the Ophiacanthinae in particular. These characters: the large size of the disk plates and the integration of the whole radial shield in the plating of the disk, appears to be constant throughout the group. There does not appear to be a graduation from the small semi-transparent scales of the Ophiacanthinae to the larger, well developed, plates of the Ophioplinthacinae.

Within the Ophioplinthacinae the characters used to distinguish the genera are the shape and position of the radial shields, the shape of the disk whether or not it is indented and the form and number of both the apical and oral papillae, the arrangement of the adoral and oral shields and the degree of development of the dorsal arm plates. While the Ophioplinthacinae as a whole apparently forms a well-differentiated subfamily group many of the genera included appear ill-defined. *Ophiomitrella, Ophioripa, 'Ophiophthalmus'* and *Ophiomelina* are distinguished on characters which elsewhere in the Ophiacanthidae would be used as specific characters. For example, the differences cited by Matsumoto (1917) to distinguish '*Ophiophthalmus*' from *Ophiomitrella* were the contiguous proximal dorsal arm plates and the absence of a fan arrangement of arm spines on the proximal arm segments. Koehler (1922) distinguished these two also by the character of the imbricating disk plates and round naked radial shields. However, two species of *Ophiomitrella, O. clavigera* and *O. globifera* show most of the features of '*Ophiophthalmus*' except for having contiguous dorsal arm plates. In species like '*Ophiophthalmus*' *granifera* Koehler, 1922 and *O. cataleimmoida* (H. L. Clark, 1911) the proximal dorsal arm plates are only just contiguous. Even within this genus Koehler (1922) was able to distinguish three groupings. If doubt is caste on the taxonomic validity of the generic grouping called '*Ophiophthalmus*' then *Ophiomitrella, Ophioripa* and *Ophiomelina* must also be suspect. Other nominal genera which should be investigated include *Ophiothamnus-Ophiurothamnus* and *Ophioplinthaca-Ophiomytis.*

No new generic name has been proposed for '*Ophiophthalmus*' partly because there has been no opportunity to look at all the material but mainly because it remains to be demonstrated that it is distinct from the genus *Ophiomitrella* as stated before. Hopefully this problem will be solved when the group is thoroughly revised.

Ophioplinthaca chelys (Wyville Thomson, 1877)
Fig. 26

Ophiacantha chelys Wyville Thompson, 1877: 64.
Ophiomitra chelys: Lyman, 1878: 64; 1882: 205.
Ophioplinthaca chelys: Verrill, 1889*b*: 352; Koehler, 1904: 131; 1906: 6; 1907: 294; 1909: 194.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 84 30°38′N: 18°5′W 2056 m HOLOTYPE & PARATYPE. HMS *Challenger* Stn 3 25°45′N: 20°12′W 2789 m 3 specimens; HMS *Challenger* Stn 33 off Bermuda 796 m 2 specimens.

The disk is high and appears round but the interradial areas are deeply indented, diameter up to 10 mm; covered with large and conspicuous plates amongst which the centrodorsal plate can usually be distinguished. The disk has large granular spinelets, some of which are just rounded others with a crown of 3 or 4 points, scattered over the dorsal and ventral surfaces. The radial shields are long and thin, about 3–4 times as long as broad, separated from one another and recessed into the disk. They are slightly longer than half the disk radius. The ventral interradial areas are covered with large plates sometimes bearing a spinelet.

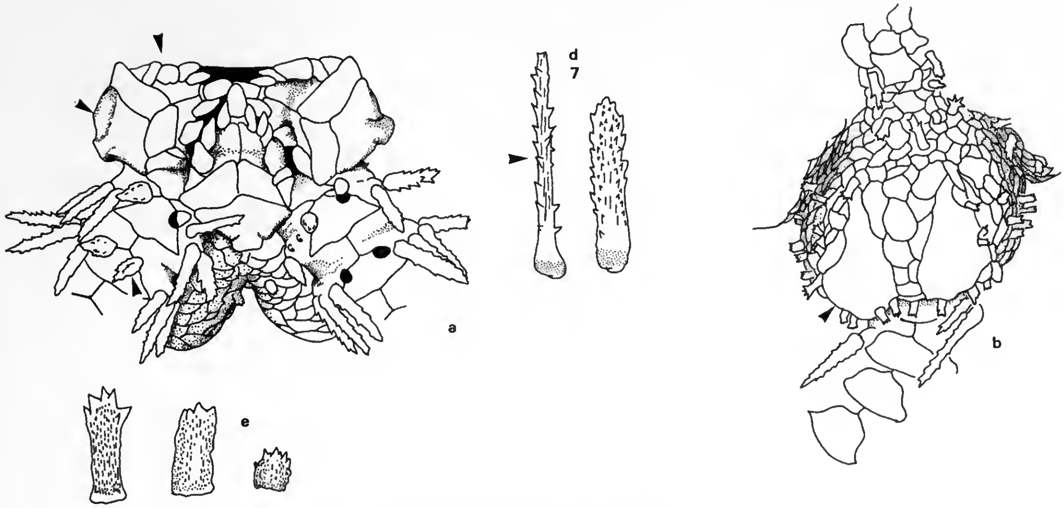
The jaws appear to be as long as broad or slightly longer. The apical papilla is large and blunt with 4 or 5 contiguous oral papillae. The proximal oral papillae are pointed and roughly leaf shaped, the distalmost papillae is distinctly triangular. The adoral shields are slightly convex occupy a large portion of the jaw proximal to the oral shield, not separating it from the first lateral arm plate. The oral shield is large and distinctly pentagonal, the proximal angle is often very acute.

The arms are distinctly noded. The dorsal arm plates are swollen, fan shaped and separated from one another. The ventral arm plates are wider than long broadly pentagonal in shape and separated from one another. The tentacle pores are relatively large, each is armed with a pointed tentacle scale. There are 6 arm spines on proximal arm segments, 4 on distal ones. The arm spines appear rugose due to very large secondary points on the shaft; the dorsalmost spines are the longest often 2 or more arm segments long; the ventralmost spines become sabre shaped distally. The arm spines do not form a fan on proximal arm segments.

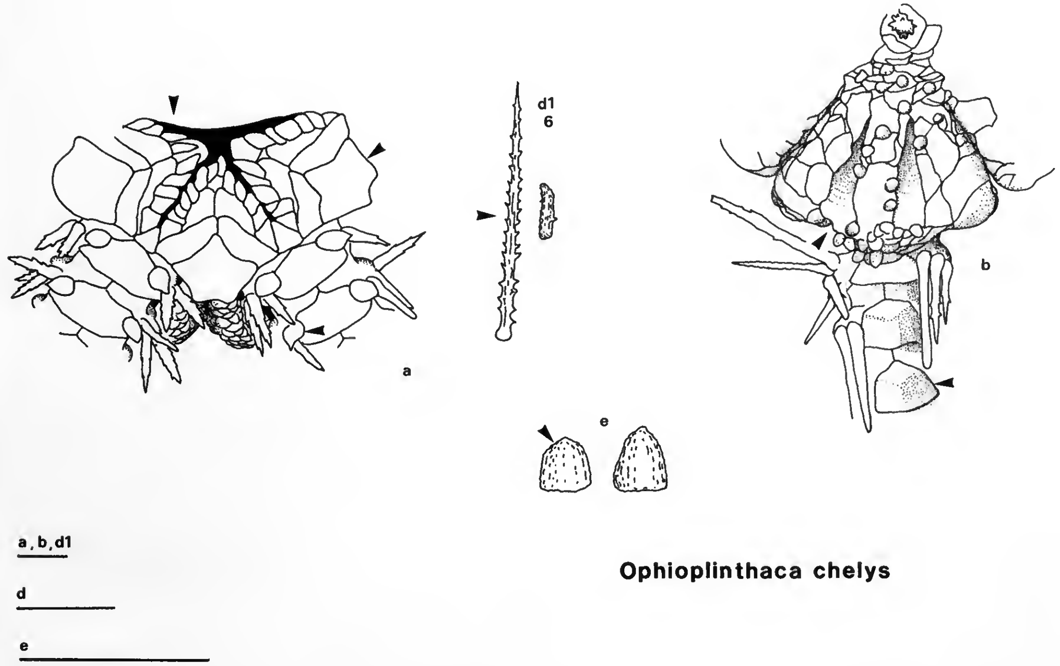
REMARKS. *Ophioplinthaca chelys* can be distinguished from *O. carduus* by its recessed radial shields lower more granule-like disk spinelets, more angular oral shields, contiguous oral papillae and smooth leaf-like tentacle scales. *O. chelys* differs from *O. abyssalis* in the following ways: the radial shields are separated and recessed into the disk while those of *O. abyssalis* are contiguous and not recessed; the oral papillae are contiguous and slightly angular; those of *O. abyssalis* are longer and more spinelike; the oral shield is pentagonal as opposed to slightly arrow shaped in *O. abyssalis.*

DISTRIBUTION. *O. chelys* has been recorded from both sides of the North Atlantic, in the west off Bermuda 796 m and in the east off Portugal south to the Canaries, with a bathymetric range of 2056–3307 m. Outside the Atlantic Koehler (1922*a*) records it from off the Philippines with a bathymetric range of 1165–2081 m.

OPHIACANTHIDAE : OPHIOPLINTHACINAE



Ophioplinthaca carduus



Ophioplinthaca chelys

Fig. 26 Key to the Ophiacanthidae: Ophioplinthacinae. *Ophioplinthaca*: (a) ventral; (b) dorsal view of disk; (d) arm spines—a number with this figure indicates the number of proximal arm spines. The larger spine is a dorsal spine, the small a ventral spine; in figures with only one spine it is the dorsal one. (e) Disk spinelets. NB. The ventral interradial area has been left blank in some figures for clarity. Bar scales = 1 mm, letters above the bars refer to the figures.

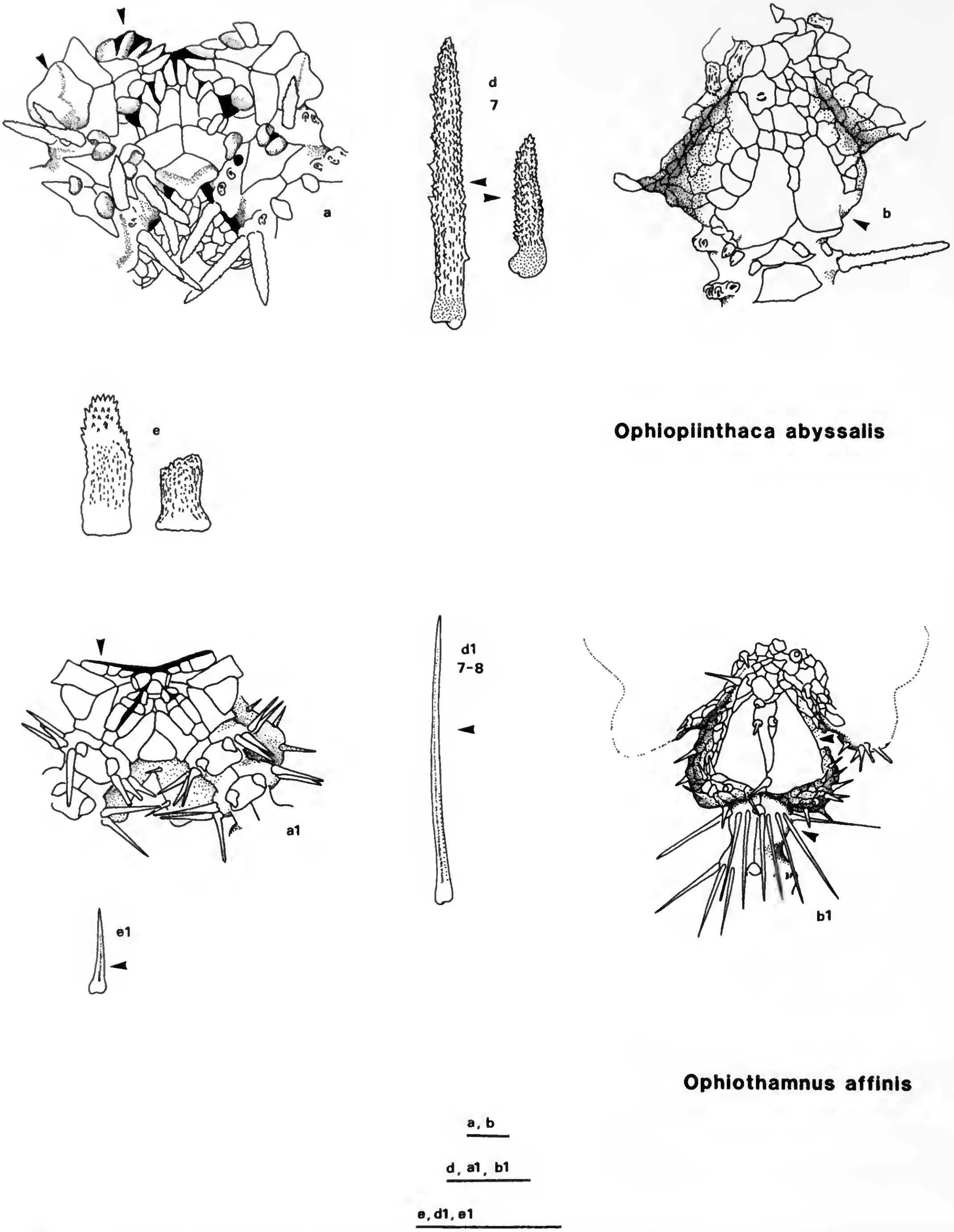
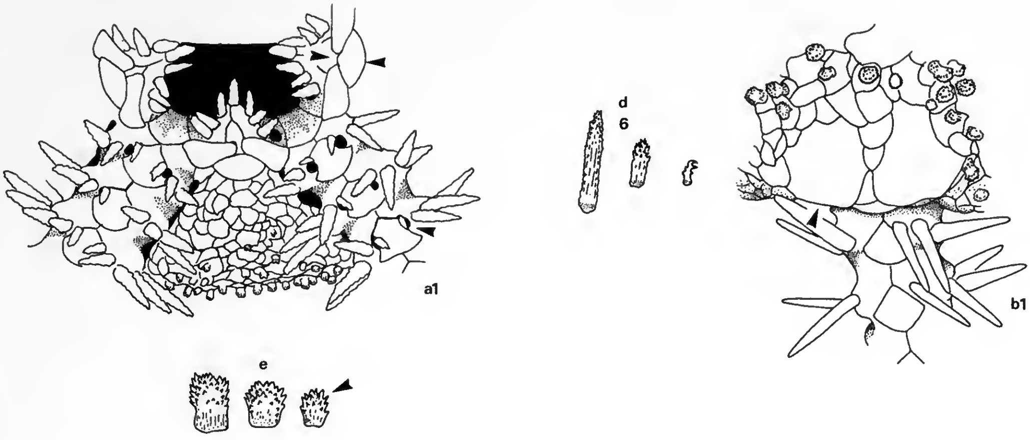
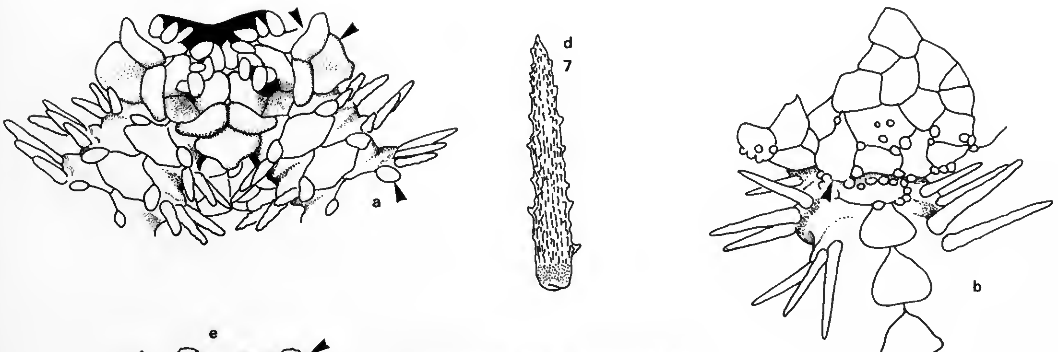


Fig. 27 Ophiacanthidae: Ophioplinthacinae. *Ophioplinthaca, Ophiothamnus.* Captions as in Fig. 26.



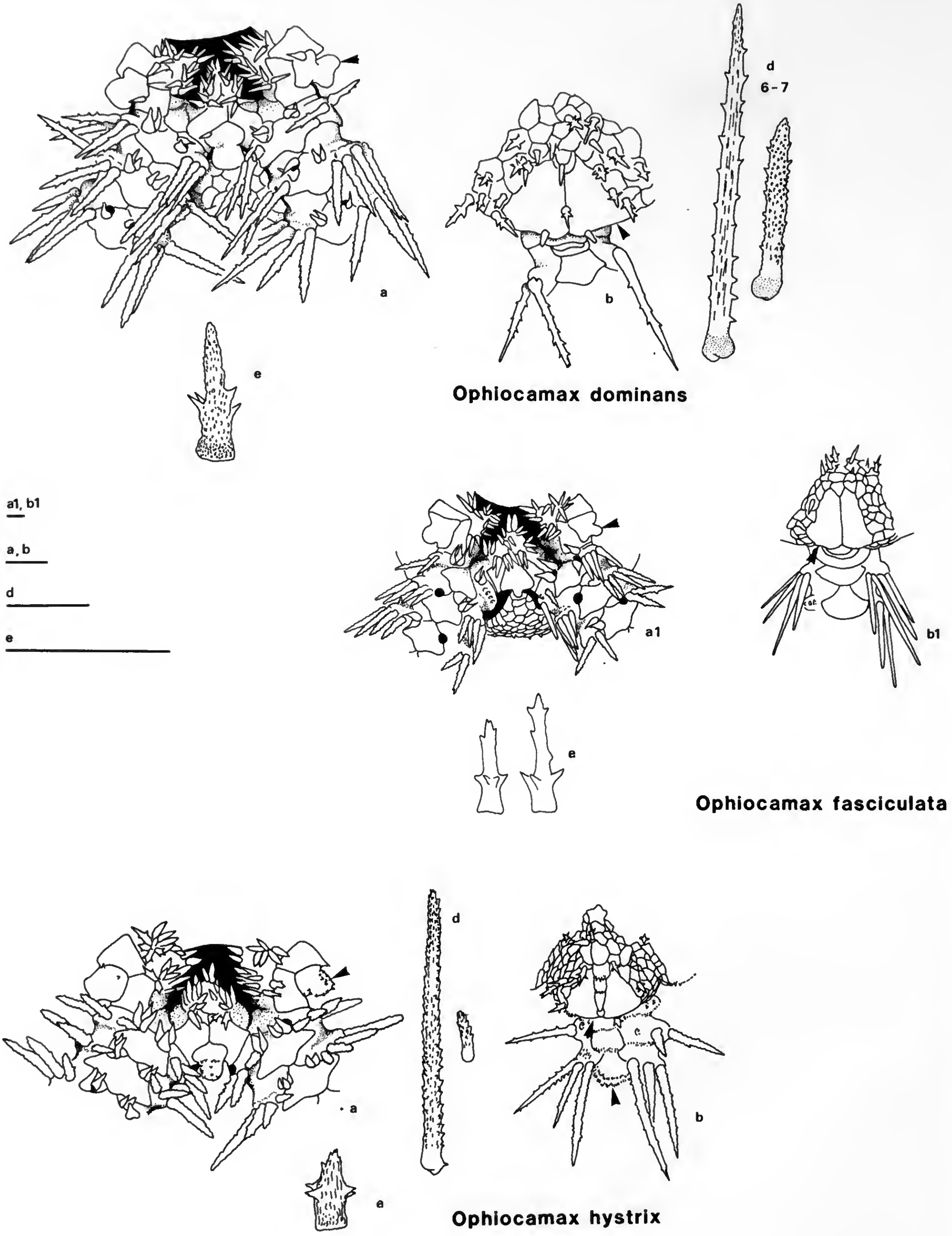
Ophiomitrella clavigera

Ophiomitrella cordifera



Ophiomitrella globifera

Fig. 28 Ophiacanthidae: Ophioplinthacinae. *Ophiomitrella*. Captions as in Fig. 26.

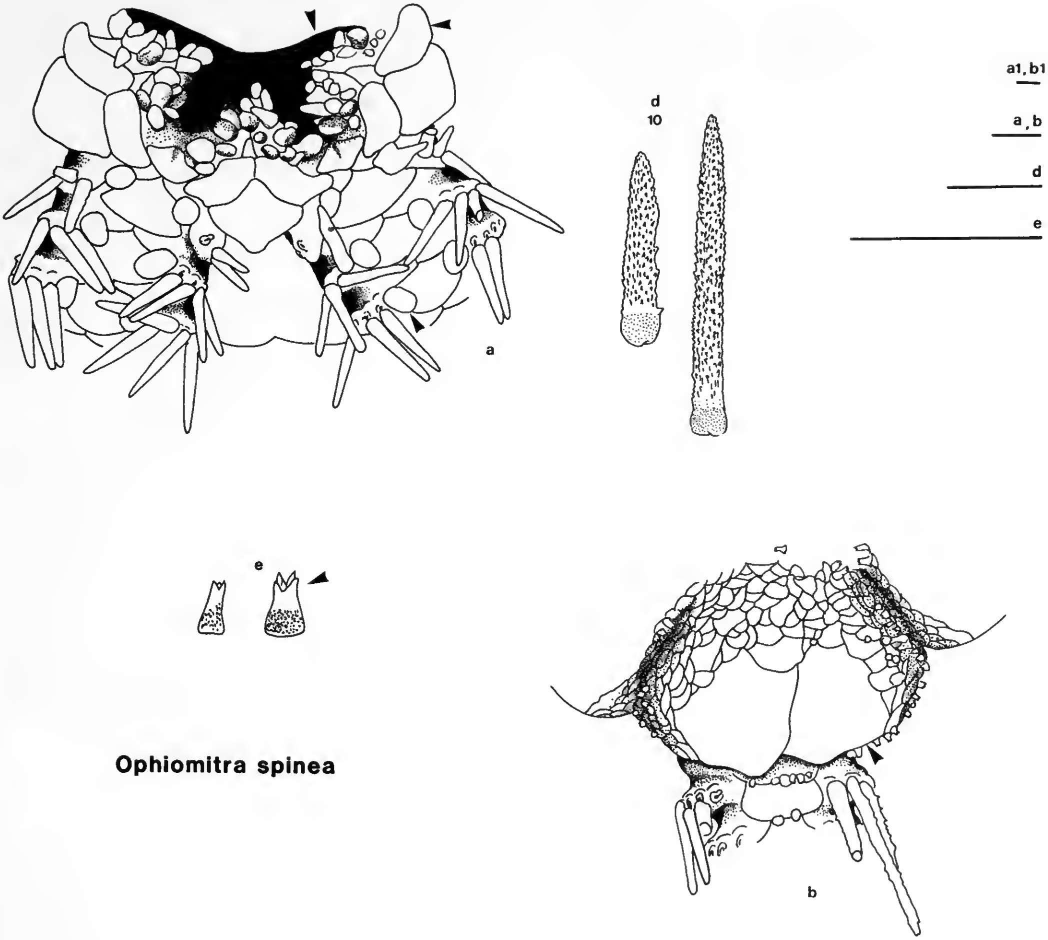


Ophiocamax dominans

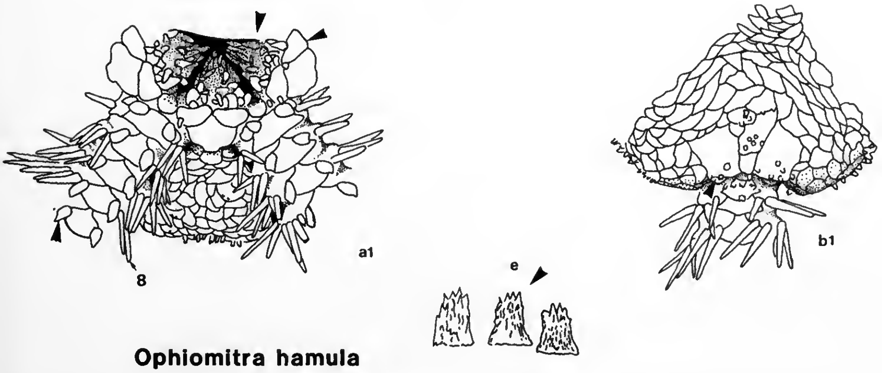
Ophiocamax fasciculata

Ophiocamax hystrix

Fig. 29 Ophiacanthidae: Ophioplinthacinae. *Ophiocamax*. Captions as in Fig. 26.



Ophiomitra spinea



Ophiomitra hamula

Fig. 30 Ophiacanthidae: Ophioplinthacinae. *Ophiomitra*. Captions as in Fig. 26.

Ophioplinthaca carduus (Lyman, 1878)

Fig. 26

Ophiomitra carduus Lyman, 1878: 154.
Ophioplinthaca carduus: Verrill, 1899*b*: 35; Koehler, 1906: 6; 1907: 294.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 33 off Bermuda 796 m HOLOTYPE.

The disk is strongly indented interradially diameter up to 16·5 mm; covered by plates amongst which the centrodorsal is usually conspicuous. Many of the plates carry a spinelet which usually have multipointed tips, the shaft is usually straight but occasionally there are secondary points. The radial shields are irregularly tear drop shaped about twice as long as broad and separated along their entire length. The radial shields are slightly longer than half disk radius. The ventral interradial areas are covered with plates similar to those of the dorsal side, many of them carry spinelets.

The jaw appears to be as wide as long. There is one large, wide, blunt or slightly pointed apical papilla flanked on each side by 4–5 oral papillae, which are pointed with the distalmost one being the largest. The adoral shields are curved and situated proximal to the oral shield, not separating it from the first lateral arm plate. The oral shield is pentagonal to arrow head shaped. In pentagonally shaped plates there is often a distal tongue or lobe slightly lower than the rest of the plate.

The arms are distinctly noded. The dorsal arm plates are fan shaped, domed and are separated from one another. The ventral arm plates are basically triangular and separated from one another, the mid portion of the distal edge is raised up, sometimes quite acutely, forming a small hillock. The tentacle pores appear to be medium sized each is armed with a large, leaf shaped tentacle scale which becomes highly rugose on many pores. There are 7 arm spines proximally 4–5 on distal segments. The spines appear to be quite rugose with large secondary points on the shaft of the spine. The dorsalmost or second dorsalmost spine is usually the largest up to 2 arm segments long. The ventral arm spines are usually straight. The proximal arm spines do not form a fan.

REMARKS. Comparisons with the other North Atlantic species are given under *O. chelys*. *O. carduus* may be distinguished by the shape and position of the radial shields, the shape of the oral shield, the tentacle scale shape, the domed shaped dorsal arm plate and the rugose arm spines.

DISTRIBUTION. *O. carduus* has been recorded from off Bermuda 796 m in the Western Atlantic and from 30°17'N: 43°7'W 3500 m, on the Mid-Atlantic Ridge SW. of the Azores.

Ophioplinthaca abyssalis Cherbonnier & Sibuet, 1972

Fig. 27

Ophioplinthaca abyssalis Cherbonnier & Sibuet, 1972: 1368–1370

MATERIAL STUDIED. **MNHN:** Noraltlante 132–D.12 47°41'07"N: 08°30'06"W 3100 m HOLOTYPE.
IOS: *Discovery* Investigations Stn 9042 42°15'N: 11°22'W 1662–1541 m 4 specimens.

The disk is high indented interradially, diameter up to 10 mm, covered with large irregularly shaped plates many of which are armed with finely rugose, large simple spinelets. The spinelets are largest in the centre of the disk. The radial shields are basically triangular in shape, pairs of shields are usually contiguous, at least distally. The radial shields are slightly less than half disk radius in length. The ventral interradial areas are covered with large plates like those of the dorsal surface, spinelets may be present.

The jaws are wider than long. There are one or two pointed or spine like apical papillae flanked by 3–5 oral papillae on each side. The proximal oral papillae are flattened and lanceolate while the distal ones are large rounded and slightly club shaped. Occasionally there are one or two supranumerary papillae, on the proximal edge of the adoral shield. The adoral shields are large, not particularly wing-like, restricted to the proximal sides of the oral shield, not separating it from the first lateral arm plate. The oral shield is slightly arrow shaped with an obtuse proximal angle and with a slight projection of the distal edge; the distal part of the plate is distinctly swollen in most specimens but in some the plate is flat.

The arms are noded. The dorsal arm plates are bell shaped and contiguous on the proximal arm joints. The ventral arm plates are pentagonal nearly triangular with a very wide distal edge; the distal edge may project slightly midradially. The ventral arm plates are separated. The tentacle pores are small; those of the first and sometimes the second arm segment armed with two large, rounded tentacle scales, the others only have one. There are 7 rugose arm spines on proximal segments 6 distally; the dorsal or second dorsalmost spine is usually the longest up to 2 arm segments in length. The ventral arm spines are more rugose than the dorsal ones and slightly curved or sabre shaped. The arm spines do not form a fan on proximal arm segments.

REMARKS. *O. abyssalis* may be distinguished from the other North Atlantic species by the shape of the radial shields, the disk spinelets, the arrangement of the apical and oral papillae, the swollen oral shield, the flat dorsal arm plates and the shape of the tentacle scales.

DISTRIBUTION. *O. abyssalis* has been recorded from the Bay of Biscay and off NW. Spain in 1541–3100 m.

Ophiomitra spinea Verrill, 1885*a*

Fig. 30

Ophiomitra spinea Verrill, 1885*a*: 153; 1885*b*: 544; Mortensen, 1933*a*: 43–44.

MATERIAL STUDIED. **USNM:** *Albatross* Stn 2035 off Nantucket Shoals 2479 m HOLOTYPE.
COB: CYMOR DR 13 47°44′N: 8°35′14″W 3150 m 1 specimen.

The disk is round, indented interradially, high and the area of the radial shields is raised up, in diameter up to 13·5 mm. The disk is covered by small overlapping plates which are partially obscured by the dense covering of spinelets. The spinelets are low with a wide base and a trifid or rugose crown. The radial shields are naked. They are large nearly as wide as long, contiguous distally or just separated by a wedge of plates. The ventral interradial areas are covered with small plates and spinelets similar to those of the dorsal side.

The jaws appear short, wider than long. There are several apical papillae flanked on each side by many oral papillae, it is difficult to distinguish the oral from the apical papillae. The oral papillae appear to be arranged in two series: a superficial series edging the side of the jaw and a series within the mouth slit which might be oral tentacle scales associated with the first and second oral tentacle pores. The adoral shields are convex, restricted to the proximal sides of the oral shield and not separating it from the first lateral arm plate. The oral shield is approximately rhombic with the centre of the plate slightly depressed.

The arms are slightly noded. The dorsal arm plates are fan shaped and contiguous proximally. The ventral arm plates are pentagonal, nearly triangular with a wide convex distal edge, and nearly contiguous on proximal segments. The tentacle pores are small, each is armed with one large flat leaf-like tentacle scale. There are 10 slightly rugose arm spines on proximal arm segments, 6–7 on distal ones. The spines approach but do not form a fan on proximal arm segments.

REMARKS. Mortensen (1933*a*) remarked that *O. spinea* was similar to *O. hamula* but as few specimens of either had been collected it was not possible to judge if they were conspecific. An examination of the type specimens together with those from the CYMOR suggest several differences which can be tested when more specimens are collected. *O. spinea* appears to differ from *O. hamula* in the following characters:

1. The disk is high, indented interradially whereas that of *O. hamula* is neither indented nor as high especially in the region of the radial shields.
2. The radial shields are large and contiguous or nearly so in *spinea* while they are quite small, usually separated and confined to the edge of the disk in *hamula*.
3. The granules of *spinea* have broad base and a trifid or slightly rugose crown, those of *hamula* have a narrower base and the crown is more rugose.
4. The jaw of *spinea* has rounded stubby oral papillae, those of *hamula* are more spinelike and the jaw itself appears to be sunken into the disk, not on the same level as the adoral shields. There is a slight indication of this in *spinea* but it is not as marked as in *hamula*.
5. The adoral shields are not as wing-like in *hamula* as those of *spinea*.

DISTRIBUTION. *O. spinea* has been recorded from both sides of the Atlantic, in the west from off Martha's Vineyard at a depth of 2479 m and in the east from the Bay of Biscay at a depth of 3150 m.

Ophiomitra hamula Mortensen, 1933*a*

Fig. 30

Ophiomitra hamula Mortensen, 1933*a*: 41–44.

MATERIAL STUDIED. **ZMC:** *Ingolf* Stn 64 62°06′N: 19°00′W 1874 m HOLOTYPE.

The disk is round to subpentagonal not deeply indented interventrally, disk diameter up to 8 mm. The disk is covered by conspicuous overlapping plates which in turn are covered by granule-like spinelets that appear quite rugose on close examination. The radial shields are quite small, nearly as wide as long, usually separated by a wedge of three or four plates but some shields may be contiguous at their distal ends. The ventral interradial areas are covered by plates and granules like those of the dorsal side.

The jaws appear to be wider than long. There are several spine-like papillae at the apex of the jaw, distal to these papillae the jaw appears to be covered by irregularly spaced oral papillae which are smaller and more rounded than those at the apex. The jaw proximal to the adoral shields appears to be recessed into the mouth. The adoral shields are small slightly convex but not particularly wing-like, and restricted to the proximal edges of the oral shield, not separating it from the first lateral arm plate. The oral shield is rhombic with a slight distal lobe.

The arms are slightly noded. The dorsal arm plates are fan shaped to bell shaped and contiguous on proximal arm segments. The ventral arm plates are pentagonal with a wide distal edge, and contiguous on proximal arm segments. The tentacle pores are quite small each is armed with one flat leaf-like tentacle scale. On the first arm tentacle pores there are sometimes two scales. There are 8 arm spines on proximal segments, 7 on distal ones, the dorsal arm spines are finely rugose becoming rugose ventrally. They do not form a fan on proximal arm segments.

Remarks. The differences between *O. hamula* and *O. spinea* are described under the Remarks section of *O. spinea*.

Distribution. *O. hamula* has been recorded once from the south of Iceland, at a depth of 1874 m.

Ophiocamax dominans Koehler, 1906
Fig. 29

Ophiocamax dominans Koehler, 1906: 21; 1907: 281.

Material studied. **MNHN:** *Talisman* off Sahara 822 m HOLOTYPE & PARATYPE.
IOS: *Discovery* Investigations: Stn 8967 31°25·9′N: 10°53·7′W 1220–1140 6 specimens; Stn 9028 31°26′1 N: 10°52·8′W 1229–1166 m 3 specimens.
COB: CYMOR-2 DR2 47°47′N: 08°49′W 2600 m 1 specimen.

The disk is round or slightly indented interradially and domed; diameter up to 15 mm; covered by large plates each plate carrying at least one stout disk spine. In some specimens these spines may have been rubbed off but the area of attachment is usually visible. The disk spine may be simple or sometimes there is a collar of secondary points about a third of the way up the shaft. The radial shields are large, contiguous and extend half to three-quarters the radius of the disk. The ventral interradial areas are similar to the dorsal side with larger plates but not all carry spinelets.

The jaw is typical of the genus with multiple spine-like apical papillae and oral papillae along its edge. The oral papillae appear to be arranged in three tiers. This is because the tentacle scales of the first and second oral tentacle pores are also spinelike, resembling the oral and apical papillae. The adoral shields are prominent and wing-like distinctly separating the oral shield from the first lateral arm plate. The oral shield has an irregular shape, although it may sometimes be hourglass shaped, and extends from the oral frame on to the interradial area. In some specimens the distal portion may carry a spine.

The arms are distinctly noded. The dorsal arm plates are bell shaped, the proximal ones contiguous. The ventral arm plates are triangular with the mid portion of plate raised up. The tentacles are large, each is armed with up to 3 long spine-like tentacle scales, sometimes missing. There are 6–7 rugose arm spines. They do not form a fan on contiguous segments. The second to fourth dorsalmost spines are the longest, up to 3 arm segments long.

Remarks. In the Atlantic *O. dominans* bears closest affinity with *O. fasciculata* Lyman, 1883, found off St. Kitts, Leeward Is (Fig. 29) but differs by the following characters: the plates of the disk are much larger and fewer in number than in *O. fasciculata*; the oral shield is irregular or hourglass in shape, not arrowhead shaped as in *O. fasciculata,* finally the shape of the tentacle scales simple and spine-like in *O. dominans* but leaf-like or with a broad base and an acute tip in *O. fasciculata*.

Another species likely to be found in the North Atlantic is *O. hystrix* Lyman, 1878, found off Havana, Cuba. (Fig. 29) *O. hystrix* may be identified by the very rugose nature of the dorsal arm plates distal portion of the hourglass shaped oral shield and arm spines. The radial shields are often separated unlike those of the previous two species which are usually contiguous.

DISTRIBUTION. *O. dominans* has been recorded from off North Africa in 822–1229 m.

Ophiomitrella clavigera (Ljungman, 1864)

Fig. 28

Ophiactis clavigera Ljungman, 1864: 365.
Ophiolebes clavigera: Lyman, 1882: 201; Farran, 1913: 44; Mortensen, 1913: 361; H. L. Clark, 1915: 193; Grieg, 1921: 37.
Ophiolebes acanellae Verrill, 1885*b*: 548.
Ophiomitrella clavigera: Mortensen, 1920: 48–50; 1927: 186, 1933*a*: 40.

MATERIAL STUDIED. **BMNH:** Norman Collection, Norway. 1 specimen; Irish Fisheries Stn 483 51°37′N: 11°56′W 1098–1952 m 2 specimens; North Sea 1 specimen.

The disk is round to pentagonal, sometimes high, this feature may vary according to the position of the arms whether they are coiled under the disk; diameter is up to 6–7 mm usually smaller. The disk is covered with imbricating plates each carrying a club-like spinelet, the enlarged tip of which is rugose; in some specimens there are roughly two sizes of spinelet; the larger club-like spinelet and a smaller more granule-like spinelet. The radial shields are distinct separated or just touching at their distal ends, and irregularly triangular nearly as wide as broad. The ventral interradial areas are covered with plates similar to those of the dorsal surface except they tend to be smaller, many also carry rugose spinelets.

The jaws are as wide as long or slightly wider, the oral plates are bowed only meeting at their proximal tips. There is one blunt apical papilla flanked on either side by 3–4 long, spine-like, rugose papillae. The adoral shields are approximately triangular and restricted to the proximal sides of oral shields, not separating it from the first lateral arm plate; they often do not meet in the midline proximal to the oral shields. The oral shield is an irregular oblong to a round rhombic shape, sometimes with a distal projection.

The arms are distinctly noded, short, about 3–4 times the disk diameter. The dorsal arm plates are fan shaped and separated. The ventral arm plates are small, pentagonal with a rounded distal edge, sometimes the distal edge is indented. The tentacle pores are small, each is armed with a small pointed tentacle scale. There are 6 rugose arm spines proximally, 4–5 distally. The dorsal most or second dorsal most arm spines are the longest about 1½ arm segments long, the ventral ones usually less than an arm segment in length.

REMARKS. Mortensen (1933*a*) considered that *O. clavigera* is possibly distinct from *Ophiomitrella cordifera,* pointing out that the difference in shapes of the oral shield and disk spinelets could warrant specific distinction. However, *O. cordifera* appears to be a valid species which can distinguish from *O. clavigera* by the following characters: the shape of oral shield which is rounded slightly irregular in *O. clavigera* but pentagonal to rhombic often with an acute proximal angle in *O. cordifera,* the adoral shields are not separated as in *O. clavigera* but meet in the midline, proximal to the oral shield in *O. cordifera* and the larger size of the granules of the disk in *O. cordifera.*

O. clavigera can easily be distinguished from *O. globifera* by the following characters: the plates of the dorsal side are thin not as well developed as in *O. globifera*; the spinelets of *O. clavigera* often have an enlarged rugose tip, those of *O. globifera* are all of one kind, low and rugose, nearly granuliform; the apical and oral papillae of *O. globifera* are shorter and not as rugose as those of *O. clavigera*; the oral shield is more regularly rhombic in *O. globifera* than *O. clavigera* and the tentacles scales of *O. globifera* are large rounded while those of *O. clavigera* are small and spine-like.

DISTRIBUTION. *O. clavigera* has been recorded from both sides of the Atlantic; from Nova Scotia north to the Davis Strait and W. Greenland in the western Atlantic with a bathymetric range of 166–1100 m; in the eastern Atlantic it has been recorded from SE. Iceland, off the Faroes, SW. Ireland and the Azores with a bathymetric range of 170–1348 m.

Ophiomitrella globifera (Koehler, 1896*a*)

Fig. 28

Ophiomitra globifera Koehler, 1896*a*: 86–88.
Ophiomitrella globifera: Verrill, 1899*b*: 352; Koehler, 1907: 295.

Material studied: **MNHN:** *Travailleur & Talisman* 30th Aout 1883 No. 83 22°57′N: 19°51′W 930 m 2 specimens; *Travailleur & Talisman* 3 Juillet 1883 No. 73 25°39′N: 18°30′W 1475 m 1 specimen.

The disk is pentagonal, up to 9 mm in diameter; covered by large plates each carrying from 1–4 slightly rugose granules. The radial shields are small, slightly less than a quarter of the disk diameter in length, triangular to irregularly rectangular in shape. Their distal edges may be fringed with granules. The ventral interradial areas are covered with plates like those of the dorsal side, some are also armed with granules.

The jaws are as wide as long. There is one large, blunt apical papilla flanked on either side by 3 oral papillae. The oral papillae are slightly flattened and the distalmost papillae may be widened at the free end or in some specimens larger than the others almost opercular. The adoral shields are curved slightly wing-like, with glassy beads embedded in the matrix. The adoral shields do not separate the oral shield from the first lateral arm plate. The oral shields are rounded slightly pentagonal to almost rhombic often there is a distal projection.

The arms are noded. The dorsal arm plates are fan shaped nearly contiguous. The ventral arm plates are pentagonal often with a broad distal edge, the plates on proximal segments are contiguous or nearly so, but separated on distal ones. The tentacle pores are relatively large each is armed with a large flat tentacle scale. There are 7 finely rugose arm spines, with large secondary points on the shaft giving the arm spine a more rugose appearance. The dorsal or second dorsalmost spines is the longest, up to 2 arm segments in length, the ventral arm spines are short often less than an arm segment in length. The arm spines do not form a fan on the proximal arm segments.

Remarks. *O. globifera* can be distinguished from the other Atlantic species of *Ophiomitrella* by the shape of the disk granules which are much less rugose than those of *O. clavigera*. The papillae of the jaw are more regular in shape, arrangement, and are not long, spine-like like those of *O. clavigera* and *O. cordifera*; adoral shields have glassy tubercles in the plate matrix which appears to be absent in the other species, the ventral arm plates are broader than those of *O. clavigera* and *O. cordifera*.

Distribution. *O. globifera* has only been recorded from the eastern Atlantic from the Bay of Biscay, Off NW. Africa and off the Canaries with a bathymetric range of 930–1700 m.

Ophiomitrella cordifera (Koehler, 1896*c*)
Fig. 28

Ophiomitra cordifera Koehler, 1896*c*: 250–251.
Ophiomitrella cordifera: Koehler, 1909: 192.
Ophiomitrella clavigera: Mortensen 1927: 186 (non *Ophiomitrella clavigera* Ljungman, 1864).

Material studied. **MNHN:** *Princesse Alice* 1st Aout 1895 Stn 618 38°25′15N: 28°52′45W 1143 m SYNTYPE.

The disk is round to pentagonal up to 4 mm disk diameter; covered with large, imbricating plates often armed with low globular granules, many specimens have the granules rubbed off. The radial shields are roughly triangular in shape often contiguous for up to half their length; extending to just about half the radius of the disk. The ventral interradial areas are covered with large plates like those of the dorsal surface, they may also be armed with granule-like spinelets.

The jaws are as wide as long. There is one large pointed apical papilla flanked on either side by 3 flattened, slightly rugose, oral papillae. The adoral shields are rectangular to wing-like just or not quite separating the oral shield from the first lateral arm plate. The oral shield is a rounded rhombic to pentagonal shape; often the proximal angle is acute and produced so that it almost separates the adoral shields.

The arms are slightly noded. The dorsal arm plates are fan shaped and separate. The ventral arm plates are pentagonal, the distal edge is convex but indented in the middle. The ventral arm plates are not contiguous. The tentacle pores are small, each is armed with a small pointed tentacle scale. There are 6–7 slightly rugose arm spines, the shaft of the spines has large secondary points. The dorsal arm spines are the longest nearly two arm segments in length, the ventral arm spines are much shorter. They do not form a fan on proximal arm segments.

Remarks. *O. cordifera* can be distinguished from other species by the contiguous radial shields, the pentagonal shape of the oral shield often with an acute proximal edge and the small pointed tentacle scale. The similarity between *O. cordifera* and *O. clavigera* has already been commented on under *O. clavigera*.

DISTRIBUTION. This species has been recorded off the Canaries and Azores at depths of 1143–1530 m.

Ophiothamnus affinis Ljungman, 1872

Fig. 27

Ophiothamnus affinis Ljungman, 1872: 622.
Ophioleda minima Koehler, 1906: 26; 1907*a*: 292–294; 1914: 111; 1921: 4.
Ophioplinthaca occlusa: Koehler, 1907*b*: 4; 1909: 194–195.
Ophiothamnus minima: Matsumoto, 1917: 123–126.

MATERIAL STUDIED. **MNHN:** *Travailleur & Talisman.* 1st Aout 1881 No. 39 44°6'N: 9°25'40"W 1220 m (about 20 specimens from a large sample SYNTYPES); *Travailleur & Talisman* 19th Juillet 1882 No. 19 41°32'N: 11°41'W 1350 m SYNTYPES of *Ophioleda minima.*

The disk is indented interradially and the centre is often depressed, while the area of the radial shields is commonly raised up often swollen, in some specimens the disk distal to the tips of the radial shields bulges out overlying the arm. The disk diameter is up to 5 mm. The disk is covered by small imbricating plates many bearing a simple glassy rod-like spinelet. The radial shields are large extending over half the radius of the disk in length. They are triangular in shape with their distal ends in contact, sometimes they are contiguous for slightly more than half their length. The ventral interradial areas are also covered with plates some bearing smaller glassy spinelets.

The jaws are as wide as long. There is one large blunt tricuspid or occasionally heart-shaped apical papilla flanked on either side by 3 oral papillae; the proximal papillae are pointed spiniform but the distalmost is large and block-like nearly opercular. The adoral shields are large becoming slightly flared distally, they separate the oral shield from the first lateral arm plate. The oral shield is a rounded triangular shape.

The arms are distinctly noded. The dorsal arm plates are wider than long, approximately triangular in shape and separated from one another. The ventral arm plates are pentagonal with the distal edge slightly indented. The tentacle pores are relatively large, each is armed with a lanceolate tentacle scale which becomes more spiniform on distal pores. The arm spines articulation area does not have a proximal ridge. There are 7–8 simple glassy arm spines of which the second dorsalmost is the longest, up to 3 arm segments long. The arm spines form a fan on the proximal arm segments.

REMARKS. *O. affinis* is similar to *O. vicarius* Lyman, 1869, from the West Indies but differs in the shape of the apical papilla which is simple blunt or slightly pointed in *O. affinis* as opposed to heart shaped in *O. vicarius,* though the occasional occurrence of heart shaped apical papillae in *O. affinis* throws doubt on the validity of this character, the degree to which the disk is constricted interradially, which is very pronounced in most specimens of *O. affinis* but not noticeably so in *O. vicarius;* and the number of arm spines, 7–8 in *O. affinis* but as many as 10–12 *O. vicarius.*

DISTRIBUTION. *O. affinis* has been recorded from both sides of the North Atlantic; in the western Atlantic from off Florida in 229–491 m and in the eastern Atlantic from the Bay of Biscay, off the Canaries and from the Josephina Bank with a bathymetric range of 1425–1935 m.

OPHIOHELINAE (Perrier, 1891 amended)

DIAGNOSIS. A subfamily of the Ophiacanthidae with simple arm spine articulation surfaces on the lateral arm plates, not forming a comma-shaped surface; disk delicate, sack-like covered with small thin semitransparent scales; radial shields absent or internally concealed; jaws as broad as long often with numerous flattened distally projecting papillae arranged in two or more rows covering the surface of the jaw; arms noded, often standing vertically around the disk position found in preserved specimens; tentacle pores large open with up to five tentacle scales; arm spines often numerous varying in length.

TYPE GENUS. *Ophiomyces* Lyman, 1869 with type species *O. frutectosus* Lyman, 1869.

REMARKS. The genera included are: *Ophiohelus* Lyman, 1878; *Ophiomyces* Lyman, 1869; *Ophiothauma* H. L. Clark, 1938 and *Ophiotholia* Lyman, 1880. Verrill (1899) proposed that *Ophiomyces* and *Ophiotholia* be segregated as a separate family and Fell (1960) suggested that if Verrill's proposal is valid then *Ophiothauma* should be included. *Ophiohelus* is considered to be closely allied to these three genera. It is not possible at present to assess the taxonomic weight of the character of the arm spine articulation surface on the lateral arm plates, whether of familial or

OPHIACANTHIDAE : OPHIOHELINAE

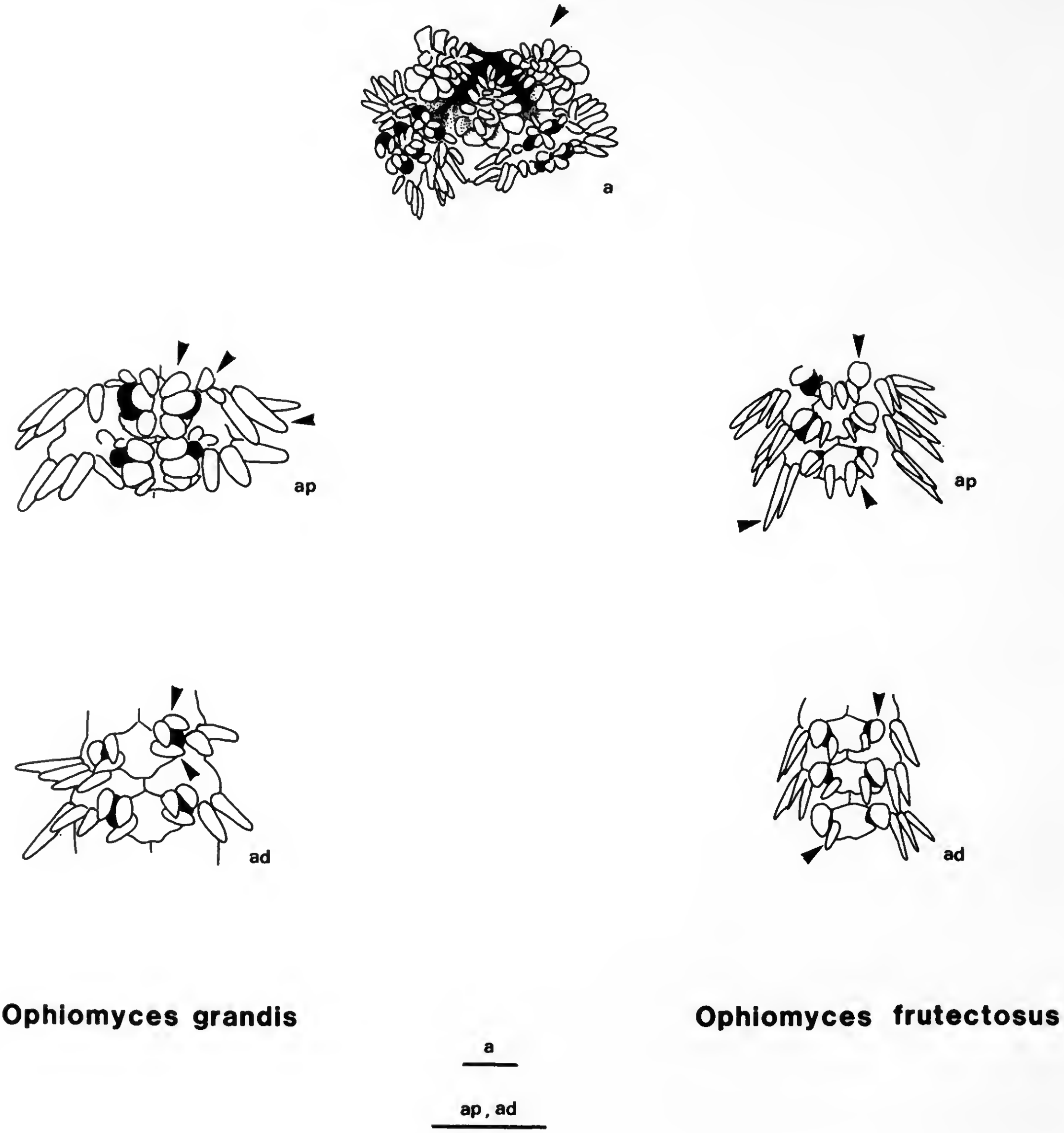


Fig. 31 Key to the Ophiacanthidae: Ophiohelinae. *Ophiomyces*: (a) ventral view of *Ophiomyces*; (ap) detail of ventral side of the proximal arm segments showing the arrangement of tentacle scales; (ad) detail of the ventral side of the distal arm segments to show the tentacle scales. Bar scales = 1 mm.

subfamilial worth as only a few species have yet been examined. Most Ophiacanthids so far examined possess a comma shaped surface except for *Ophiomyces*, the possession of similar articulation surfaces in *Ophiohelus, Ophiothauma* and *Ophiotholia* is inferred pending future study, so an absence of this form of socket would support Verrill's proposal.

Ophiomyces frutectosus Lyman, 1869
Fig. 31

Ophiomyces frutectosus Lyman, 1869: 343; 1882: 243; Ljungman, 1871: 615–657; Mortensen, 1927: 185; Tommasi, 1970: 18–19.

MATERIAL STUDIED. **BMNH:** *Explorer* 24°53′N: 80°04′W 365–375 m 5 specimens.

The disk is round, sack-like, often raised up; diameter up to 9 mm; covered with thin semi-transparent scales often carrying a simple rod. The radial shields are not visible, probably absent. The ventral interradial areas are covered by scales like those of the dorsal surface but the rod-like spinelets are usually smaller.

The jaws are as wide as long. The surface of the oral plates adoral and oral shields is obscured by superficial, wide, flat papillae. There is one flat, broad, apical papillae flanked by two rows of each of about 5 papillae flanking on each side, the row situated on the surface of the oral plates are considered to be supplementary. The proximal papillae of each series are flat and slightly spiniform but the distal ones become wider especially the free edge with the distalmost papillae being very large, almost triangular. The adoral shields are small wing-like almost separating the oral shield from the first lateral arm plate. The oral shield is small, arrow shaped. These shields are obscured by the supplementary papillae and by papillae arising on the shields themselves.

The arms are flattened. The lateral arm plates on the proximal part of the arm are slightly enlarged. The dorsal arm plates are fan shaped, much wider than long and separated from one another. The ventral arm plates are longer than wide with the lateral edges distinctly convex and the distal edge indented, they are contiguous on proximal segments, separated on distal ones. The tentacle pores are large, the proximal ones are armed with 3 flat, elongated, tentacle scales, one on the lateral arm plate the other two arising on the ventral arm plate. The first may be difficult to distinguish from the ventral arm spines but may be recognised because it usually lies between the preceding arm spine row and the row of the arm segment with the pore. On distal tentacle pores there are only two tentacle scales, a large rounded one arising on the lateral arm plate and a smaller more spine-like one on the ventral arm plate. There are 8–10 arm spines, the dorsalmost 3–4 are small, thin and spine-like the remaining gradually become larger towards the ventral side with the largest spines being in the middle of the series. These larger spines are slightly flattened and on proximal joints may have blunt tips. On proximal joints the dorsal arm spines from one side of the arm form a continuous series with those from the other, but this cannot be called a fan in the sense used in other genera of the Ophiacanthidae.

REMARKS. *Ophiomyces frutectosus* may be distinguished from the second N. Atlantic species, *O. grandis,* by the arrangement of the tentacle scales on the proximal pores; *O. grandis* having up to 5 tentacle scales, two on the lateral arm plate and three on the ventral arm plate. Distally *O. grandis* has three spine-like scales, two on the lateral arm plates and one on the ventral arm plates. Near the tip of the arm *O. grandis* may have just one large rounded scale on the ventral arm plate.

DISTRIBUTION. This species has been recorded primarily from the Caribbean and off Florida but Ljungman (1871) records it from the Josephina Bank, W. of Portugal in 210–410 m. Bathymetric records suggest that it is a bathyal species with its lower limit in the upper abyssal zone.

Ophiomyces grandis Lyman, 1878
Fig. 31

Ophiomyces grandis Lyman, 1878: 383–385; 1882: 241–242; Koehler, 1907: 295; Mortensen, 1927: 185; Cherbonnier, 1966: 846; Cherbonnier, 1970: 346–348; Cherbonnier & Sibuet, 1972: 1366; Gage *et al.*, 1983: 288–289.
Ophiomyces peresi Reys, 1961: 154–155.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Tristan d'Acunha 1800 m HOLOTYPE.
SMBA: RRS *Challenger* II: Stn 62 57°28′N: 11°00′W 610 m 2 specimens.
IOS: *Discovery* Investigations: Stn 7857 3 36°44′N: 14°18′W 277–271 m 1 specimen.

The disk is round, sack-like and often raised up, diameter up to 9 mm; covered with small semi-transparent scales, many of them are armed with large simple rods. The radial shields are not visible, probably absent. The ventral interradial areas are similar to the dorsal side but the rods are not as long.

The jaw is as wide as long. The surface of the jaw, adoral and oral shields are obscured by papillae. There is one apical oral papilla flanked on each side by two rows of papillae. The series of oral papillae line the free edge of the jaw while the supplementary papillae lie on the surface. There are 5–6 oral papillae and 5 or more supplementary papillae. The proximal papillae of both rows are spine-like but distally they become flatter and wider with the distalmost papillae of each series being nearly triangular. The adoral shields are wing shaped, with very angular lateral projections and separate or just fail to separate the oral shield from the first lateral arm plate. The oral shield is quite large and arrow shaped. These plates are usually obscured by papillae.

The arms are flattened. The dorsal arm plates are wider than long and separated from one another. The ventral arm plates are longer than wide with concave lateral edges and an indented distal edge, they are almost contiguous proximally but widely separated distally. The tentacle pores are large and open on proximal arm segments. These proximal tentacle pores are armed with 5 blunt club shaped tentacle scales, but on distal segments there are usually only three tentacle scales, two on the lateral arm plate and one on the ventral arm plate; often one of the tentacle scale is larger and more rounded than the others. Near the tip of the arm there is usually only one rounded tentacle scale. There are 9 arm spines proximally. The dorsalmost 3–4 are small, thin with subsequent spines gradually becoming larger, the largest being those in the middle of the series. These spines are flattened and pointed.

REMARKS. A comparison of *O. grandis* with the other N. Atlantic species *O. frutectosus* is dealt with under that species.

DISTRIBUTION. This species has been recorded from the Rockall Trough south to Gibraltar, with a bathymetric range of 230–800 m, in the North Atlantic. It has also been recorded from Tristan d'Acunha in 1800 m, the type locality.

OPHIACTIDAE Matsumoto, 1915

This family is characterised by the disk covered with plates often carrying spinelets or granules which do not conceal them, except in *Ophiopholis* where the granules obscure the plates; radial shields usually conspicuous; one apical papilla flanked with rounded oral papillae often separated from it by a diastema and not forming a contiguous series with it, except in *Histampica*; the second oral tentacle pore opening within the oral slit; arm spines short, pointed and erect, not appressed to the side of the arm.

Ophiactis abyssicola (M. Sars 1861)

Fig. 32

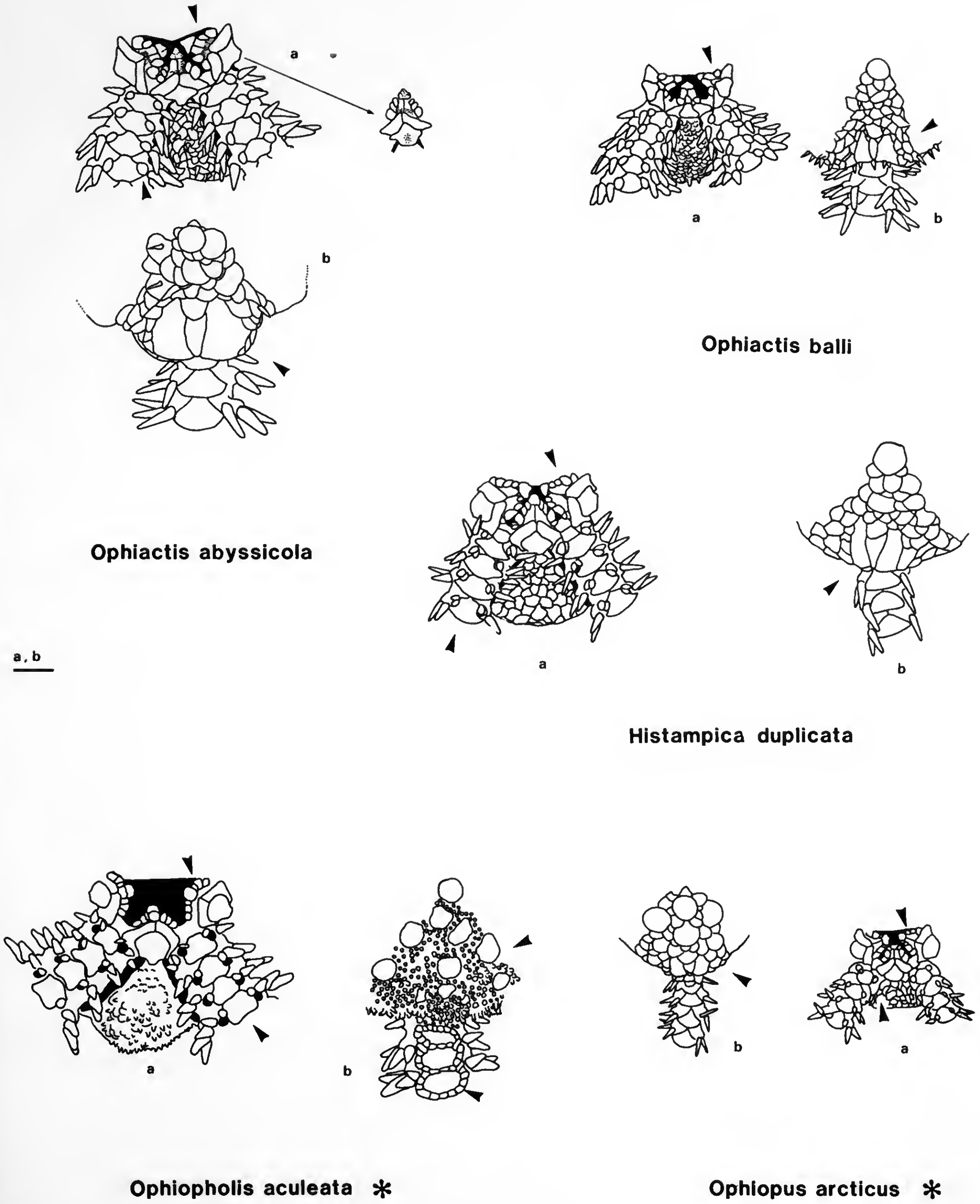
Amphiura abyssicola M. Sars, 1861: 18.
Ophiocnida abyssicola: Lyman, 1865: 12.
Ophiactis abyssicola: Ljungman, 1867*b*: 324; Lütken, 1872: 98; Lyman, 1882: 122; Hoyle, 1884: 710, 715, 718; Bell, 1892: 123; Koehler, 1898: 46; Grieg, 1903: 29; Koehler, 1909: 169; Mortensen, 1913: 356; Farran, 1913: 35; Grieg, 1921: 36; H. L. Clark, 1923: 334; Koehler, 1924: 293; Mortensen, 1927: 202; 1933*a*: 47–50; John & Clark, 1954: 154; Cherbonnier & Sibuet, 1972: 1370; Gage *et al.*, 1983: 292.
Ophiactis poa Lyman, 1882: 119.
Ophiactis echinata Koehler, 1898: 48; Mortensen, 1927: 199; Cherbonnier & Sibuet, 1972: 1370.
Ophiactis corallicola Koehler, 1896*a*: 75; 1907: 272; 1909: 170.

MATERIAL STUDIED. **COB:** BIOGAS Stn 1: DS15 2246 m 16 specimens; DS16 2325 m 34 specimens; DS17 2103 m 40 specimens; DS18 2138 m 30 specimens; DS32 2138 m 1 specimen; DS35 2226 m 1 specimen; DS61 2250 m 2 specimens; DS63 2126 m 2 specimens; DS65 2360 m 4 specimens; CV08 2180 m 2 specimens; CV09 2119 m 27 specimens; CV10 2108 m 29 specimens; CV20 2282 m 2 specimens; CV23 2034 m 6 specimens; CV24 2025 m 9 specimens; CV25 1985 m 2 specimens; CP01 2245 m 25 specimens; CP02 2177 m 22 specimens; CV39 2350 m 16 specimens; CP08 2177 m 13 specimens; CP26 2115 m 6 specimens; CP27 1920 m 31 specimens.

BIOGAS Stn 2: DS60 3742 m 2 specimens; DS66 3480 m 1 specimen; CV41 3800 m 1 specimen; CP09 2171 m 50 specimens; CP28 3380 m 2 specimens.

BIOGAS Stn 4: CV35 4721 m 1 specimen.

OPHIACTIDAE



Ophiactis abyssicola

Ophiactis balli

Histampica duplicata

Ophiopholis aculeata ✻

Ophiopus arcticus ✻

Fig. 32 Key to the Ophiactidae. *Ophiactis, Histampica, Ophiopholis* and *Ophiopus*: (a) ventral; (b) dorsal view of disk. Bar scales = 1 mm, *–not described in text.

BIOGAS Stn 6: DS52 2006 m 1 specimen; DS70 2150 m 1 specimen; CV16 1909 m 18 specimens; CV32 1895 m 2 specimens; CP07 2170 m 89 specimens; CP23 1980 m 15 specimens; CP25 1894 m 1 specimen.

BIOGAS Stn HZ: DS04 1100 m 6 specimens; DS33 2338 m 28 specimens; CM01 1100 m 1 specimen; CV06 2200 m 5 specimens; CW03 2160 m 8 specimens; CV11 2141 m 7 specimens; CV22 1331 m 68 specimens.

IOS: *Discovery* Investigations Stn 8511/2 41°49′N: 11°06′W 2574–2585 m 1 specimen; Stn 8967 31°25·9′N: 10°53′7″W–31°26·3N: 10°50·8′W 11 specimens; Stn 8970 31°30·4′N: 11°4·4′W–31°30·0′N: 11°3·8′W 5 specimens; Stn 9029 32°14·3′N: 11°28′W–32°14·1′N: 11°2·5′W 1886–1835 m 1 specimen; Stn 9042 42°15·0′N: 11°22·0′W 1662–1541 m 20 specimens; Stn 9753/4 50°54·9′N: 12°12′W–50°56·5′N: 12°14·8′W 1942–1947 m 1 specimen; Stn 9753/7 60°54·5′N: 12°10·9′W–50°59·8′N: 12°11·4′W 1942 m 3 specimens; Stn 9754/3 51°8·4′N: 12°1·5′W–51°9·5′N: 12°1·8′W 1484 m 2 specimens.

The disk may be round or indented; covered by large plates amongst which the centrodorsal plate and usually the primary plates are distinct; disk diameter up to 9 mm. There are often conical spinelets on both the dorsal and the ventral interradial plates, however, they may be absent from one or other side or even completely missing. The radial shields are large, longer than broad, sometimes contiguous but usually separated by a single row of plates. The plates of the ventral interradial areas are not as coarse as those on the dorsal surface.

There is a tricuspid or heart shaped apical papilla flanked on each side by two distal oral papillae, which arise on the adoral shields occasionally the more distal one is divided making it appear as two papillae. The adoral shields are large, longer than broad, not separating the oral shield from the first lateral arm plate. The oral shield is lozenge shaped or rhombic.

The dorsal arm plates are fan shaped and contiguous at least proximally. The ventral arm plates are pentagonal with a rounded distal edge and contiguous at least on proximal arm segments. There is one round tentacle scale on each tentacle pore. There are 4 conical arm spines on the proximal arm segments 3 further out.

REMARKS. *Ophiactis abyssicola* is a variable species, a fact which has misled authors in the past. Mortensen (1933*a*) concluded that the characters of the disk are subject to a number of variations, especially occurrence of spines, differences in scaling, but that features of the oral frame are sufficiently constant to easily identify this species.

DISTRIBUTION. *O. abyssicola* has been recorded from the Davis Strait, off Iceland, the Faeroes and Norway south to southern Africa, with a bathymetric range of 125–4721 m.

Ophiactis balli (Thompson, 1840)
Fig. 32

Ophiocoma balli Thompson, 1840: 99; Forbes, 1840: 35; Thompson, 1856: 437.
Ophiocoma goodsira Forbes, 1840: 57.
Ophiactis balli: Lütken, 1859: 126; Lyman, 1882: 121; Hoyle, 1884: 718; 1885: 143.
Ophiolepis ballii: Müller & Troschel, 1842: 97.
Ophiolepis goodsira: Müller & Troschel, 1842: 97.
Ophiopholis ballii: Gray, 1848: 25.
Ophiopholis goodsira: Gray, 1848: 25.
Amphiura balli: Sars, 1859: 42; 1861: 17; Norman, 1865: 109.
Ophiocnida balli: Lyman, 1865: 12.
Ophiactis balli: Koehler, 1896*a*: 77; Bell, 1892: 123–124; Grieg, 1903: 29; Koehler, 1909: 169; Süssbach & Brecker, 1911: 252; Farran, 1913: 37; Koehler, 1921: 83; 1924: 292; Mortensen, 1925: 181; 1927: 200; 1933*a*: 51–52; Gage *et al.*, 1983: 292.

MATERIAL STUDIED. **COB:** BIOGAS Stn HZ D01 400 m 2 specimens.
BMNH: D'Arcy Thompson Coll. Moray Firth c.25 specimens.

The disk is round, covered with small plates amongst which the primary plates are inconspicuous; disk diameter up to 5 mm. The radial shields are small and longer than broad. The ventral interradial area has smaller plates than the dorsal surface. There are often small spinelets on the ventral side on the edge of the disk, and occasionally on the dorsal side.

There is a pointed or heart shaped apical papilla with one pointed oral papilla on each side usually arising on the oral plates. The adoral shields are large, flared distally and often not meeting proximally. The oral shield is rounded triangular often with the lateral edges slightly concave.

Table 2 Comparison of North Atlantic Ophiactidae species. l = length, b = breadth, dr = disk radius, A.P. = apical papillae, O.P. = oral papillae

SPECIES	DISK PLATING	RADIAL SHIELDS	MOUTH PAPILLAE	ORAL SHIELD SHAPE	GENITAL SLITS	DORSAL ARM PLATE	ARM SPINE NO
Ophiactis abyssicola (Fig. 32)	large plates often with spinelets	large, $l \geqslant \frac{1}{2}$ dr; $l > b$	1 A.P., 2/3 O.P. O.P. separated	rhombic $l < b$	present	fan-shaped contiguous	4–3
Ophiactis balli (Fig. 32)	small plates spinelets usually confined to disk edge	small $l \leqslant \frac{1}{4}$ dr; large $l \geqslant \frac{1}{2}$ dr; $l > b$	1 A.P., 1 O.P. O.P. separated	rounded triangular $l = b$	present	rounded contiguous	5–3
Histampica duplicata (Fig. 32)	large plates	small $l = \frac{1}{4}$ dr; $l > b$	1 A.P., 5–6 O.P. O.P. contiguous	pointed triangular $l > b$	present	fan-shaped contiguous	3
Ophiopholis aculeata (Fig. 32)	only CD & PP visible rest covered with granules spinelets	not usually visible	1 A.P., 3 O.P. O.P. contiguous	oval $l < b$	present	oblong surrounded by small plates	4–3
Ophiopus arcticus (Fig. 32)	large plates	small $l = \frac{1}{4}$ dr; $l \geqslant b$	1 A.P., 2 O.P. O.P. contiguous	pointed triangular $l > b$	absent	fan-shaped contiguous	7–6

The dorsal arm plates are rounded triangular to fan shaped and contiguous. The ventral arm plates are pentagonal to almost rectangular, the distal edge may be slightly concave. The tentacle pores have one broad tentacle scale. There are 5 conical arm spines proximally, the middle ones usually the largest; distally there are only 4.

REMARKS. *Ophiactis balli* differs from *O. abyssicola* in the following characters: it only has one distal oral papilla, which arises on the oral plate, it has fewer arm spines and the shape of the ventral arm plates which are almost square compared to the distinctly pentagonal plates of *O. abyssicola*.

DISTRIBUTION. *Ophiactis balli* is more commonly found in shallower depths (between 60–400). It is confined to the eastern Atlantic.

Histampica duplicata (Lyman, 1875)

Fig. 32

Amphiura duplicata Lyman, 1875: 19; 1879: 31; 1882: 136; 1883: 251; Koehler, 1896: 74; 1898: 49.
Ophiactis duplicata: Lütken & Mortensen, 1899: 142–143; Koehler, 1909: 171; 1914: 40.
Amphiactis duplicata: Matsumoto, 1915: 66–67; 1917: 146–147; Mortensen, 1927: 198.
Histampica duplicata: A. M. Clark, 1970: 73–74.

MATERIAL STUDIED. **COB:** BIOGAS Stn 1: DS15 2246 m 5 specimens; DS17 2103 m 6 specimens; CV09 2119 m 1 specimen; CV10 2108 m 4 specimens; CV20 2282 m 1 specimen; CP01 2245 m 8 specimens; CP02 2177 m 4 specimens; CV39 2350 m 1 specimen; CP27 1920 m 2 specimens. BIOGAS Stn 6: DS25 2096 m 1 specimen; DS26 2076 m 1 specimen; CP07 2170 m 72 specimens. BIOGAS Stn HZ: CW03 2160 m 1 specimen.
IOS: *Discovery* Investigations Stn 9042 42°15′N: 11°22·0′W 1662–1541 m 4 specimens.

The disk is round; covered with many large plates amongst which the centrodorsal and usually the primary plates are distinct, often these plates have a knob in the centre; disk diameter up to 9 mm. The radial shields are about twice as long as broad, separated by a wedge of plates, nearly half the disk radius in length. The ventral interradial areas covered by plates slightly smaller than those of the dorsal side.

There is one large tricuspid papilla flanked on each side by 3–5 rounded oral papillae. The first oral tentacle scale which usually lies below these papillae, often becomes superficial and joins the oral papillae series. The adoral shields are large, becoming slightly flared distally, separating the oral shield from the first lateral arm plates. The oral shield is triangular to rounded pentagonal in shape with an obtuse proximal angle and a rounded distal edge.

The arms are relatively long and capable of vertical coiling. The dorsal arm plates are fan shaped, contiguous at least on proximal segments. The ventral arm plates are axe shaped; with an obtuse proximal angle, indented lateral edges and a convex distal edge, and are contiguous, at least proximally. The tentacle pores are large and armed with two rounded or slightly elliptical tentacle scales. There are 3 slightly flattened pointed conical arm spines, of which the middle one is the largest.

REMARKS. *H. duplicata* can be recognised from other ophiactids by the arrangement of the oral papillae; the form of the ventral arm plates, the number of tentacle scales, the scaling of the disk and the number of arm spines.

DISTRIBUTION. *H. duplicata* is a widespread species recorded from the West Indies, Bay of Biscay to off North Africa, and from the East Pacific off Colombia and Equador with a bathymetric range of 125–2870 m.

AMPHIURIDAE Ljungman, 1867

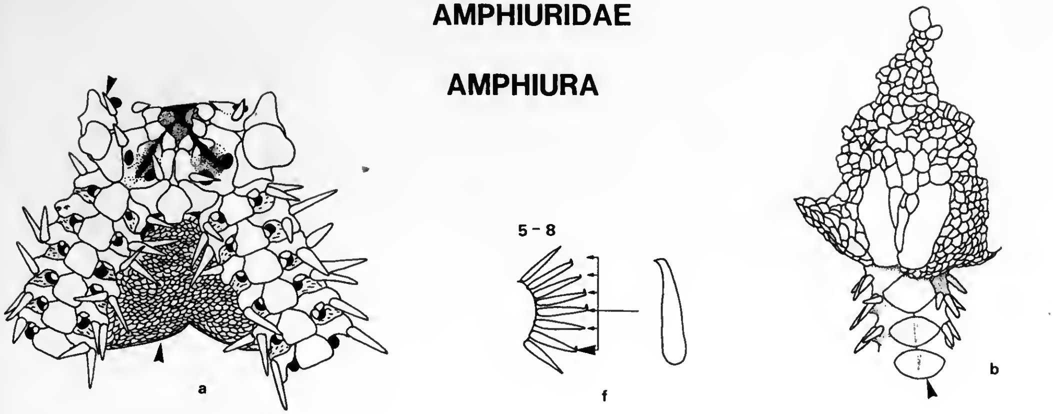
This family is characterised by the paired infradental papillae at the apex of the jaw. The disk is usually scaled, the arms are very long and the arm spines are short and erect. There is a single series of square or in the case of *Amphioplus* sometimes tricuspid teeth.

The disk in this family is delicate and prone to damage and it is common to find deep sea specimens without their disks. However, it should be possible to identify such specimens to genus and often to species from the remaining characters.

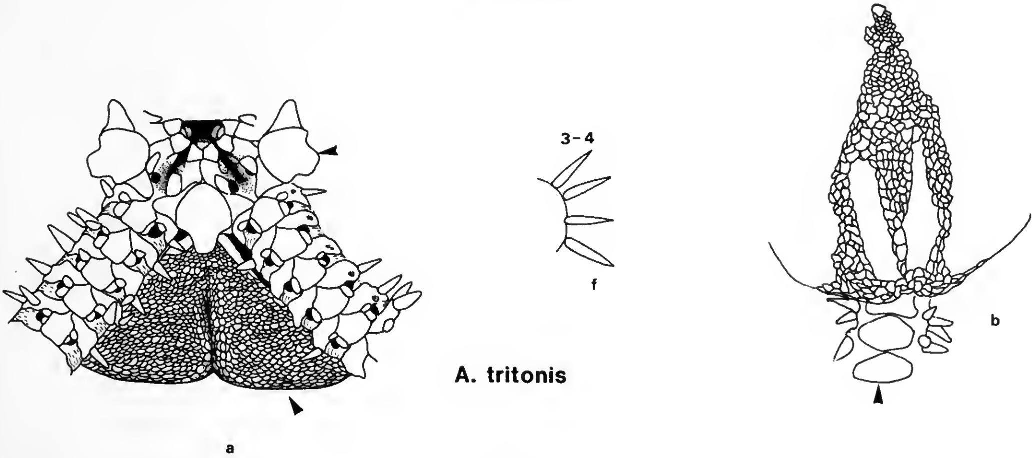
The genera of this family are characterised chiefly by the arrangement and number of oral papillae. A. M. Clark (1970), reviewing the genera using these characters, proposed a linear

AMPHIURIDAE

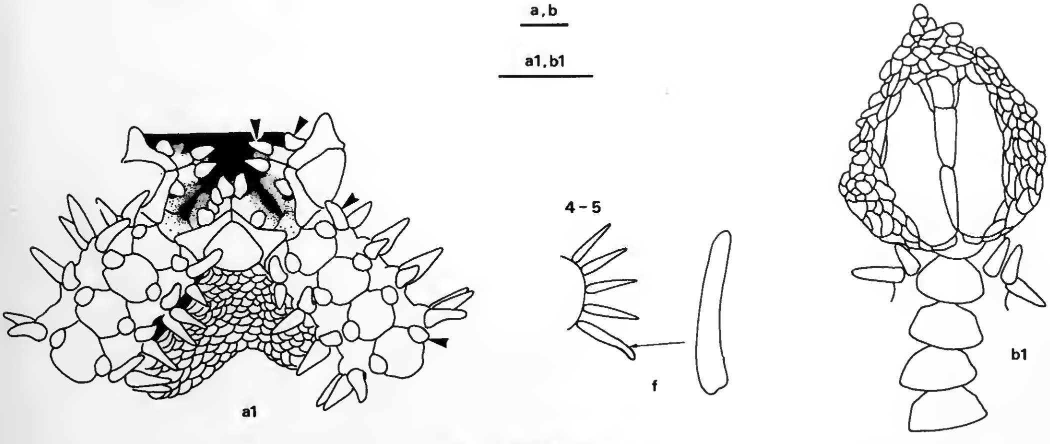
AMPHIURA



A. otteri

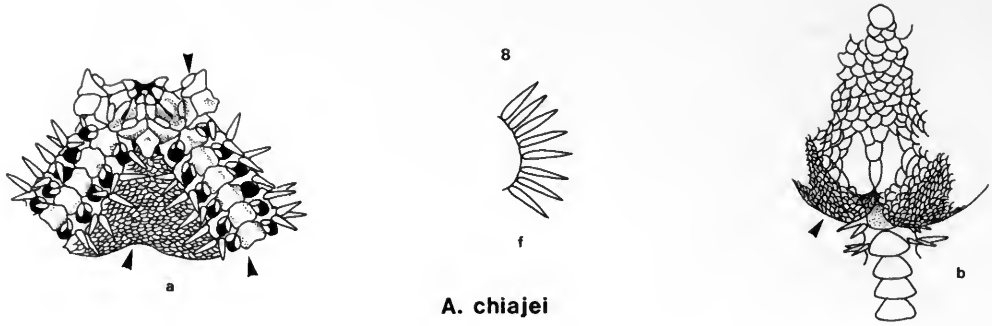


A. tritonis

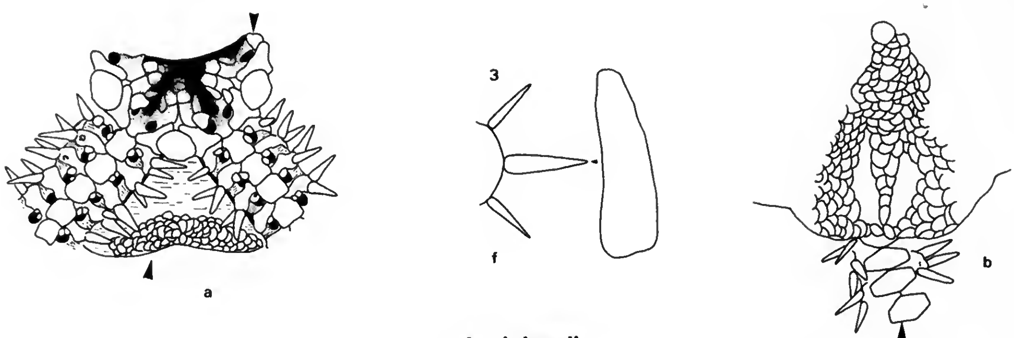


A. grandisquama

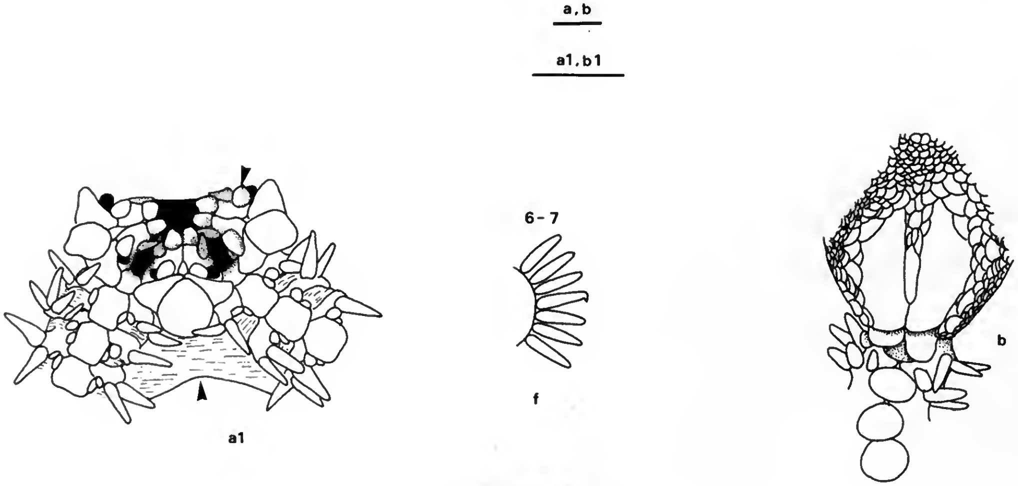
Fig. 33 Key to the Amphiuridae. *Amphiura*: (a) ventral; (b) dorsal views of disk; (f) diagrammatic representation of arm spine number and position of modified arm spines. The number represents the number of proximal arm spines. Modified arm spines are drawn enlarged and their position on the lateral arm plate indicated by an arrowed line. Bar scales = 1 mm.



A. chiajei



A. richardi



A. griegi

Fig. 34 Amphiuridae. *Amphiura*. Captions as in Fig. 33.

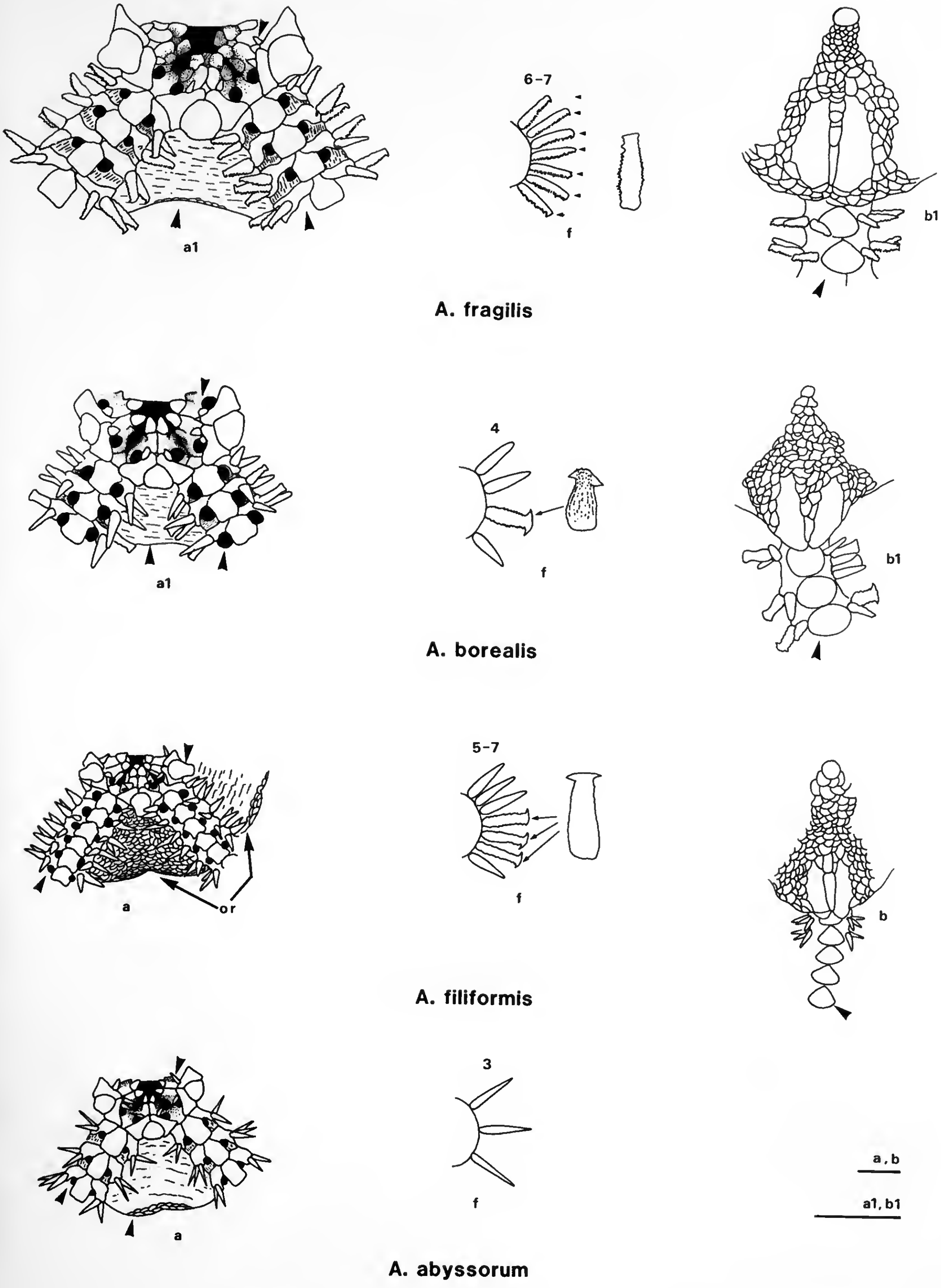


Fig. 35 Amphiuridae. *Amphiura*. Captions as in Fig. 33.

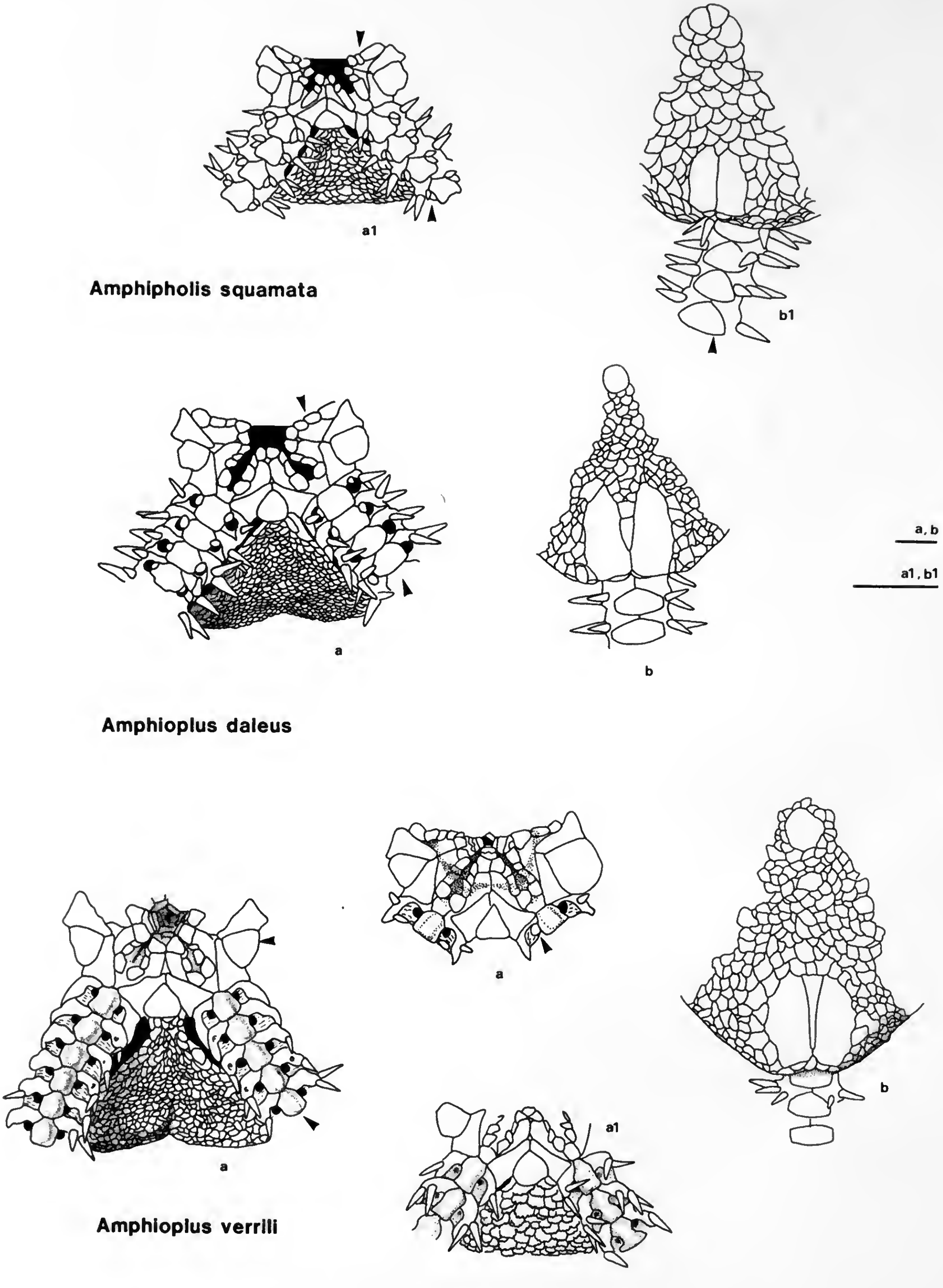


Fig. 36 Amphiuridae. *Amphipholis* and *Amphioplus*. Captions as in Fig. 33.

formula to express the occurrence of the oral papillae. The formula is given below and her conclusions where applicable are followed here.

1. The three main areas of the jaw, the apex below the dental plate, the side of the oral plate and the edge of the adoral shields, are delimited from one another by commas.
2. Each papilla arising entirely from a single area is represented by the letter m.
3. In cases where a papilla arises on two adjacent areas the m is split into 2n's with a comma between them and a linking bar above them.
4. A significant gap between papillae is indicated by an o.
5. The presence or absence of the first oral tentacle scale is denoted by + or −t. In most genera the oral tentacle scales arise deep within the mouth slit and not on the same level as the other papillae. However, in *Amphioplus* there is a more or less superficial second papilla next to the infradental papilla which is homologous with the first oral tentacle scale. This relationship is indicated by equating it with the first m of the oral plate is the second area.
6. If a papilla is particularly enlarged it may be shown by the use of capitals i.e. M or N, N.

The formulae together with a brief diagnosis is given of the genera found in the abyssal North Atlantic.

Amphiura Forbes 1843: m, o m, o+t. A single distal oral papillae, very occasionally two as in *A. filiformis* and *A. otteri,* separated from the infradental papillae by a space or diastema. The first oral tentacle scale arises deeper within the mouth slit and therefore not contiguous with the infradental papillae. The radial shields are usually separated or contiguous only distally. The ventral arm plates are flat or at most weakly arched.

Ten species have been recorded from the bathyal and abyssal North Atlantic: *A. abyssorum* Norman, 1876; *A. borealis* (G. O. Sars, 1871); *A. chiajei* Forbes, 1843; *A. filiformis* (O. F. Muller, 1776); *A fragilis* Verrill, 1885; *A. grandisquama* Lyman, 1869; *A. greigi* Mortensen, 1920; *A. otteri* Ljungman, 1871; *A. richardi* Koehler, 1896; *A. tritonis* Hoyle, 1884.
The key to these species is given in figs. 33–36.

Amphiopholis Ljungman, 1867: m, m N, N–t. The two oral papillae contiguous with the infradental papillae. The distal most papilla is enlarged and block-like. The radial shields are usually widely contiguous. The ventral arm plates are usually flat. Only one species has been recorded below 1000 m.

A. squamata (D. Chiaje, 1829) page 91.

Amphioplus Verrill, 1889*a* subgenus *Unioplus* Fell, 1962: m (m = t) m, M; m, (m = t) m, N, N; or m, om, N, N(+t). The oral papillae form a continuous series, there are no significant gaps between the papillae. The second oral papilla is in fact the superficial first oral tentacle scale. The ventral arm plates are flat or arched. There is one rounded tentacle scale on each tentacle pore. Only two species have so far been recorded in the deep N. Atlantic; *A. daleus* (Lyman, 1879) page 92. *A. verrilli* (Lyman, 1879) page 92.

Amphiura tritonis Hoyle, 1884

Fig. 33

Amphiura bellis var. *tritonis* Hoyle, 1884: 716; Mortensen, 1927: 213; Nobre, 1931: 85.
Amphiura bellis: Koehler, 1907: 277. (non *Amphiura bellis* Lyman, 1879).

MATERIAL STUDIED. **BMNH:** *Triton* Faeroe Channel, 930 m HOLOTYPE.

The disk diameter is up to 12 mm, pentagonal, indented interradially. The disk plates are small, imbricating, the centrodorsal plate is distinct but the primary plates are inconspicuous. The radial shields are 3–4 times as long as broad, extending to just over half the radius of the disk. The ventral interradial areas are covered with small scales.

The infradental papillae are block-like and contiguous. The distal oral papillae are large and scale-like. The adoral shields are wing-like but do not separate the oral shield from the first lateral arm plate. The oral shield is triangular but with a very prominent distal lobe giving the plate an arrow shape.

The dorsal arm plates are roundly hexagonal and contiguous proximally. The ventral arm plates are distinctly pentagonal. The tentacle pores are large with two large tentacle scales. There are three or four conical pointed arm spines.

REMARKS. Although both Hoyle (1884) and Mortensen (1927) consider that this species might be conspecific with *Amphiura bellis* Lyman, however, the shape of the oral shield and the distal oral papillae are sufficient to warrant specific distinction for *A. tritonis*. The oral shield of *A. bellis* is slightly rounded triangular while in *A. tritonis* it is distinctly arrowhead-shaped and this disparity cannot be attributed to differences in size. Koehler's (1907) description of *A. bellis* closely resembles *A. tritonis,* particularly in the well developed distal lobe to the oral shield.

DISTRIBUTION. This is a rare species with only three known records all in the Eastern Atlantic the Faeroe Channel, 930 m (Hoyle, 1884), Bay of Biscay 627 m and 1290 m (Koehler, 1907: *Travailleur & Talisman* under the name of *A. bellis*).

Amphiura otteri Ljungman, 1872
Fig. 33

Amphiura otteri Ljungman, 1872: 631; Lütken, 1872: 98–101; Lyman, 1878: 32; 1882: 128; 1883: 252; Verrill, 1885*b*: 548; Koehler, 1907: 302; 1914: 61; Mortensen, 1927: 210; Nobre, 1931: 85; Gage *et al.*, 1983: 292–293.

Amphiura grandis Koehler, 1896*c*: 246; 1907: 277; 1909: 175–177; Mortensen, 1927: 210.

Amphiura palmeri Koehler, 1907: 279 (part); Mortensen, 1927: 209; 1933*a*: 59–61 (non *A. palmeri* Lyman, 1875).

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 45, 32°34'N: 72°10'N, 2268 m 1 specimen; HMS *Challenger* Stn 50, off Nova Scotia, 2286 m 1 specimen; HMS *Challenger* Stn 76, off the Azores, 1646 m 1 specimen; US Fisheries Commission. Stn 2042, off Martha's Vineyard, 1799 m 1 specimen; *Dana* Stn 2346 Davis Strait 450 m 1 specimen; *Manahine* Stn 5, SW Ireland, 729–819 m 2 specimens.
MNHN: *Talisman* drag. 101, 16°38'N: 20°44'W, 3200 m. 16 specimens.
IOS: *Discovery* Investigations: Stn 8521/6 20°48'N: 18°53'W 3070–3064 m.
COB: BIOGAS Stn 1: DS65 2360 m 1 specimen; CP01 2245 m 2 specimens. BIOGAS Stn 6: DS6 2090 m 6 specimens; DS26 W 2076 m 13 specimens; DS49 1845 m 6 specimens; DS50 2124 m 6 specimens; DS52 2006 m 18 specimens; DS86 1950 m 9 specimens; DS87 1913 m 14 specimens; DS88 1894 m. BIOGAS Stn HZ: DS34 1031 m 1 specimen.

The disk is pentagonal, indented interradially and covered by small scales amongst which the centrodorsal and primary plates are conspicuous, disk diameter up to 8–10 mm. The radial shields are equal to or less than half the disk radius, about twice as long as broad and contiguous only distally. The ventral interradial areas are covered with small scales.

The infradental papillae are block-like often contiguous. The first oral tentacle scale is distinctly spine-like occurring within the mouth slit. The distal oral papillae are also spine-like and arise on the adoral shields, in some specimens they may be absent. The oral shield may be rounded and triangular or distally lobed and like a blunt flattened arrow head.

The dorsal arm plates are hexagonal and the proximal ones are almost contiguous. The ventral arm plates are pentagonal, contiguous becoming square distally. The tentacle pores are large with two small tentacles although in some specimens one or both scales may be missing on some of the pores. There are 5–8 pointed arm spines; the second ventralmost spine and some of those dorsal to it may have a small distally directed terminal hook.

REMARKS. Mortensen (1927) remarked that *A. otteri, A. grandis* and *A. bellis var. tritonis* are not easily distinguished. In his key he differentiates them on the number of arm spines and suggested that *A. grandis* could be separated from *A. otteri* by its ridged proximal ventral arm plates and by a lower number of arm spines. However, a study of specimens of *A. grandis* identified by Koehler shows that the ridged ventral arm plates do not appear to be constant feature and that differences in arm spine number are within the normal range found in *A. otteri.* In the absence of any other constant characters it may be concluded that these two species are conspecific. Mortensen's (1933*a*) confusion over the identity of the *Ingolf* specimens from Iceland can be attributed to the form of the second arm spine. Mortensen described it as having a hooked tip and identified his specimens as *A. palmeri,* type locality: Key Biscayne, Florida because that species has a prominent hook on the second arm spine. He evidently forgot that *A. otteri* also has a hooked tip to this arm spine. The arm spines of *A. palmeri* are very different from Mortensen's specimen;

they are thick with a very distinct hook, the arm spines of *A. otteri* are slender with only a small hook, like those of the *Ingolf* specimens.

The specimens identified by Koehler (1907) as *A. palmeri* proved on re-examination to be wrongly identified, some of them are *A. filiformis* and some *A. grandis*. *A. palmeri* has only been found in the tropical western Atlantic in comparatively shallow water.

DISTRIBUTION. *A. otteri* has been recorded from both sides of the North Atlantic. In the west from the West Indies 325–1036 m and as far north as the Labrador basin 198–2888 m; in the east Atlantic it has been recorded from Southern Iceland, Rockall Trough, south to the Cape Verde Islands with a bathymetric range of 729–3200 m.

Amphiura grandisquama Lyman, 1869

Fig. 33

Amphiura grandisquama Lyman, 1869: 334; Verrill, 1899*a*: 26; Koehler, 1907: 301; Mortensen, 1927: 211; Madsen, 1970: 177.
Amphiura josephinae Ljungman, 1871: 631.
Amphiura iris Lyman, 1879: 23; 1882: 132.
Amphiura longispina Koehler, 1896*a*: 74–75; 1897*b*: 211; 1898: 52; 1907: 279.
Amphiura grandisquama guineensis Mortensen, 1936: 269.
Amphiura apicula Cherbonnier, 1957: 200.

MATERIAL STUDIED. **MCZ:** Tennesse Reef, 313 m HOLOTYPE.
IOS: *Discovery* Investigations: Stn 8966 31°21′N: 10°41·5′W 686–742 m 6 specimens; Stn 9015 28°46·8′N: 12°47·4′W, 610–637 m 10 specimens; Stn 9016 28°55·7′N: 12°37·1′W, 873–898 m.
BMNH: HMS *Challenger* Stn 236 34°58′N: 139°30′E 756–1395 HOLOTYPE of *A. iris*.

The disk is round, indented over the arms, covered with small scales, disk diameter up to 7 mm. The centrodorsal and primary plates usually indistinct. The radial shields are about 3 times as long as broad and fully separated. They extend for about half the radius of the disk. The ventral interradial areas are covered by small scales.

The infradental papillae are conical often contiguous. The distal oral papillae are large and scale-like but in some specimens may be missing altogether. The adoral shields are wing-like often not separating the oral shield from the first lateral arm plate. The oral shield is rounded triangular with a slight distal lobe.

The dorsal arm plates are oval or slightly fan shaped, at least the proximal ones are usually contiguous. The ventral arm plates are hexagonal, almost pentagonal with the proximal angle square off, and contiguous. The tentacle pores are large with a round tentacle scale. There are 4–5 arm spines of which the ventralmost is usually the longest and often sabre shaped.

REMARKS. This species is characterised by the long ventralmost arm spine, the shape of the distal oral papillae and having one tentacle scale on each pore. Mortensen (1927) first speculated on the possibility that *A. iris* and *A. josephinae* were conspecific at least in the Atlantic. A comparison of the type of *A. grandisquama* and *A. iris* does not reveal any distinguishing characters and it is concluded that they are conspecific.

DISTRIBUTION. This species has been recorded from the Atlantic, Indian and Pacific Oceans. In the western Atlantic it has been described from the West Indies (325 m), from various localities off North America at depths of between 425–818 m; in the eastern Atlantic it has been recorded from Iceland south to the Azores and Cape Verde Islands at depths of 861–1635 m. It was recorded in shallow water (20–55 m) from the Gulf of Guinea (Madsen, 1970) while in the South Atlantic from Gough I. In the Indian Ocean it has been collected from the Gulf of Aden at depths of 655–732 m and from the Philippine area of the West Pacific.

Amphiura chiajei Forbes, 1843

Fig. 34

Amphiura chiajei Forbes, 1843: 151; Bell, 1892: 119; Mortensen, 1927: 212; Madsen, 1970: 167–168.

MATERIAL STUDIED. **BMNH:** Off Marseille 40–60 m 11 individuals.

The disk is covered with scales which become smaller towards edge, disk diameter up to 10–11 mm. The centrodorsal and primary plates are generally distinct. The radial shields are about 1·5–2 times as long as broad, separated for their whole length. The ventral interradial areas are covered with small plates.

The infradental papillae are square and usually contiguous in larger specimens more conical in smaller ones. The first oral tentacle scales are not very calcified having a slightly membranous appearance, and well within the mouth slit. The distal oral papillae are broad and scale-like. The adoral shields are wing-like usually separating the oral shield from the first lateral arm plate. The oral shield may be rhombic or rounded triangular with only a slight distal projection.

The dorsal arm plates are fan shaped and at least the proximal ones are usually contiguous. The ventral arm plates are an irregular pentagonal or hexagonal shape, often keeled, with the distal edge sometimes indented. The tentacle pores are large with two large tentacle scales. There are up to 8 straight pointed arm spines.

DISTRIBUTION. This species has been recorded from the eastern Atlantic, and Mediterranean, and from West Africa. It is usually a shelf species but has been recorded from a depth of 1200 m so is included in this study.

Amphiura richardi Koehler, 1896*c*

Fig. 34

Amphiura richardi Koehler, 1896*c*: 245; 1907: 279–280; 1909: 178–179; Mortensen, 1927: 210; Nobre, 1931: 86; Cherbonnier, 1970: 1267, 1270.

MATERIAL STUDIED. **MNHN:** *Talisman* 1881 drg. 39, 33°5′N: 9°25′40″W, 1225 m 1 specimen.

The disk is pentagonal, indented interradially, covered with quite large overlapping or contiguous scales amongst which the centrodorsal plate is usually distinct, disk diameter up to 8 m. The radial shields are slightly less than half the disk radius and about three times longer than broad. Only the distal half of the ventral interradial area has scales, it is naked proximally.

The infradental papillae are block-like and contiguous. The first oral tentacle scale, situated within the mouth slit, is distinctly spine-like. The distal oral papillae are large scale-like with a pointed free end and arising on the adoral shield and oral plate. The oral shield is rounded with an acute proximal angle, it is separated from the first lateral arm plate by the wing-like adoral shields.

The dorsal arm plates are hexagonal and contiguous at least proximally, distally they become fan shaped. The ventral arm plates are hexagonal, approaching a pentagonal shape, and contiguous. The tentacle pores are large with two tentacle scales. There are 3 arm spines of which the middle one is distinctly enlarged and may be laterally compressed.

REMARKS. This species is characterised by the number and shape of the arm spines and by the large distal oral papillae.

DISTRIBUTION: This rare species has been recorded from the Bay of Biscay, off northern Spain and the Canary Islands. It has a bathymetric range of 850–1494 m.

Amphiura griegi Mortensen, 1920

Fig. 34

Amphiura griegi Mortensen, 1920: 58–60; 1927: 210; Cherbonnier, 1970: 344–347; 1970: 1267; Gage *et al.*, 1983: 293.

MATERIAL STUDIED. **SMBA:** RRS *Challenger II* ABD Stn 24 56°36′N: 09°13′W 810 m 1 specimen.

The disk is deeply indented interradially, diameter up to 5·5 mm; it is covered with small scales which are slightly larger around the radial shields. The centrodorsal and primary plates are inconspicuous. The radial shields extend over half the radius of the disk and are about 3 times as long as broad. They are contiguous only distally, and separated proximally by a wedge of small scales. The scales on the disk extend just to the dorsal edge of the disk, the ventral interradial areas are naked except for a few scales next to the genital slit.

The infradental papillae are block-like sometimes contiguous. The first oral tentacle scale, situated within the mouth slit, is distinctly spine-like. The distal oral papillae are large, triangular in shape with a broad base and a blunt tip. They arise on the border of the oral plate and the adoral shield. The adoral shields are wing-like separating the oral shield from the first lateral arm plate. The oral shield is rounded with a distinct distal lobe.

The dorsal arm plates are rounded and the proximal ones are contiguous. The ventral arm plates are hexagonal to nearly rectangular and the proximal ones are contiguous. The tentacle pores are large with 2 thin tentacle scales. There are 6–7 arm spines. They are broad and slightly flattened with blunt tips, some may have a small distal directed hook at the tip.

Remarks. *A. griegi* can be recognised by the following characters: the lack of scales on the ventral interradial area, the spine-like first oral tentacle scale and oral papillae, the tentacle pores with two scales and the shape of the arm spines. Superficially this species could be confused with *A. fragilis, A. borealis* or *A. abyssorum. A. griegi* differs from all three because it has 2 tentacle scales on each pore, by the shape of the oral papillae and the shape of the arm spines. *A. griegi* has broad triangular distal papillae whereas *A. fragilis* and *A. abyssorum* have spine-like papillae and *A. borealis* has small scale-like papillae. The arm spines of *A. griegi* are broad, slightly flattened and blunt; those of *A. fragilis* are often rugose and have a serrated distal edge; the second ventralmost arm spines of *A. borealis* are widened at the tip and the arm spines are long and pointed in *A. abyssorum.*

A. griegi and *A. otteri* may be confused if the specimens lack a disk as the features of the oral frame are similar. However, *A. griegi* can be distinguished by the following characters: the oral papillae tend to be more triangular with a broader base, the arm spines are thicker, broader at the base, the dorsalmost become flattened and have a blunt rounded tip, those of *A. otteri* are thin and pointed.

Distribution. This species has been recorded from Hardanger Fjord, Rockall Trough and Bay of Biscay, with a bathymetric range of 70–810 m.

Amphiura fragilis Verrill, 1885

Fig. 35

Amphiura fragilis Verrill, 1885: 549; Mortensen, 1933*a*: 58–59; Gage *et al.*, 1983: 293.
Amphiura denticulata Koehler, 1898: 50; Grieg, 1903: 27; Mortensen, 1913: 358; 1927: 214.

Material studied. **USNM:** *Albatross* Stn 952. Martha's Vineyard 663 m SYNTYPE; *Albatross* Stn 2025, Martha's Vineyard 430 m SYNTYPE; *Albatross* Stn 2043, off Nantucket Shoals 2640 m SYNTYPE.
SMBA: RRS *Challenger II.* Stn ABD 24 56°36′N: 9°13′W 810 m 2 specimens.

The disk is pentagonal to round not indented interradially, diameter up to 5 mm. It is covered by scales; in small specimens, disk diameter *c.* 2·5 m, it is possible to distinguish the centrodorsal and primary plates but in larger specimens they become inconspicuous. The radial shields are about 3 times as long as broad and separated even in smaller specimens. The ventral interradial areas are completely naked.

The infradental papillae are conical in small specimens, block-like in larger ones. The distal oral papillae are small and pointed or scale-like, arising on the adoral shield. The oral shield is rounded triangular, often with a very slight distal lobe. The oral shield is separated from the first lateral arm plate by the wing-like adoral shields.

The dorsal arm plates are rounded in smaller specimens becoming hexagonal in the larger ones; they are not contiguous. The ventral arm plates are hexagonal nearly pentagonal and contiguous. The tentacle pores are large without tentacle scales. There are 6–7 arm spines proximally 4 distally. The arm spines are rugose with a serrated distal edge, often the whole arm spine may be covered with fine points. There is often a terminal distally directed hook to the spine.

Remarks. This species can be recognised by the shape and number of the arm spines, the lack of tentacle scales on the tentacle pores and the lack of scales on the ventral interradial area. Mortensen (1933*a*) pointed out that the oral frame was subject to variation, particularly the shape and relative positions of the infradental papillae to one another.

Distribution. *A. fragilis* has been found on both sides of the Atlantic: in the west it has been recorded off Martha's Vineyard north to the Davis Strait and W. Greenland at depths of 430–2640 m; in the eastern side it has been recorded from the Faeroe Channel in 750 m.

Amphiura borealis (G. O. Sars, 1871)

Fig. 35

Ophiopeltis borealis G. O. Sars, 1871: 16.
Amphiura borealis: Ljungman, 1871: 643; Hoyle, 1885: 139; Bell 1892: 121; Grieg, 1893: 15; Mortensen, 1920: 54; Koehler, 1924: 288; Mortensen, 1927: 215; 1933*a*: 57; Djakanov, 1954: 85; 1967: 75.

MATERIAL STUDIED. **BMNH:** *Porcupine* Stn 23a 56°13′N: 14°18′W 768 m 1 specimen; Rev. A. M. Norman Collection, Norway, 3 specimens; Rev. A. M. Norman Collection, Hardanger Fjord 3 Specimens; Rev. A. M. Norman Collection, Trondheim Fjord 276–552 m 7 specimens; J. Murray Collections, Lofoten Is 110–184 m.

The disk is round to subpentagonal, disk diameter up to 6 mm; covered by small scales amongst which the centrodorsal and primary plates are inconspicuous. In some specimens the disk plates are very thin making the disk slightly transparent. The radial shields are roughly three times longer than broad, however in some specimens the extent of the radial shields is difficult to see. They are contiguous only distally and separated proximally by a wedge of scales. The ventral interradial areas are covered with thick skin.

The infradental papillae are block-like or conical sometimes contiguous. The first oral tentacle scale, situated in the mouth slit, is small and spine-like. The distal oral papillae are small and low sometimes slightly block-like. Often there are two papillae on each side. The adoral shield are wing-like and separate the oral shield from the first lateral arm plate. The oral shield is rounded, triangular. In some specimens the adoral and oral shields may be obscured by a layer of skin.

The dorsal arm plates are rounded and nearly contiguous. The ventral arm plates are hexagonal, nearly pentagonal, to rectangular and contiguous or nearly so. The tentacle pores are large. There are no tentacle scales. There are 4 arm spines on the proximal arm segments, 3 on distal segments. The second ventralmost arm spine is flattened with widened tip which may be axe shaped on some segments.

REMARKS. *A. borealis* is similar to *A. fragilis* but may be distinguished from it by the following characters: the shape of the modified arm spines which are flattened often with an axe shaped tip in *borealis*, while those of *fragilis* have a serrated edge; the number of arm spines; *borealis* has 3–4, *fragilis* has 5–7 arm spines; the distal oral papillae, which in *borealis* are small and low, often two on each side of the jaw, in *fragilis* they are slightly larger and more spine-like, with usually only one on each side of the jaw.

DISTRIBUTION. *A. borealis* has been recorded from Norway, Iceland, the Faeroe Channel and the Rockall Trough. It has a bathymetric distribution of 150–800 m.

Amphiura filiformis (O. F. Müller, 1776)

Fig. 35

Asterias filiformis O. F. Müller, 1776: 285.
Amphiura filiformis: Lütken, 1855: 56; Bell, 1892: 117, 119; Mortensen, 1927: 214; 1933*a*: 57; Madsen, 1970: 179–181.
Amphiodia ascia Mortensen, 1936: 290.

MATERIAL STUDIED. **BMNH:** Oxwich Bay, South Wales 6 specimens; off Marseille, France 40–60 m 80 specimens.

The disk is round to pentagonal, diameter up to 10 mm. The centrodorsal and primary plates are conspicuous. The radial shields are just over twice as long as broad, separated except at their distal ends. They extend for half the disk radius. The ventral interradial areas are partially naked, but in some large specimens often covered with overlapping plates.

The infradental papillae are square or sometimes conical in smaller specimens. The first oral tentacle scales are not very calcified and have a membranous appearance. They lie within the mouth slit. There are two distal oral papillae on each side of the jaw; a conspicuous spine-like one on the oral plate and a smaller scale-like one on the adoral plate which may be missing in some specimens (see Madsen, 1970: 179–181 for a discussion of this character). The oral shield has a rounded proximal edge with a slight distal lobe. It is separated from the first lateral arm plate by the wing-like adoral shields.

The dorsal arm plates are oval or weakly fan shaped contiguous only proximally. The ventral arm plates are pentagonal with the distal edge indented. The tentacle pores are large and lack tentacle scales. There are usually 5–7 arm spines proximally. The second, often third and fourth have a compressed axe-shaped tip.

Distribution. Like *A. chiajei* this is a common NE. Atlantic species found from Norway to West Africa and in the Mediterranean. It is usually a shelf species but has been recorded from 1665 m.

Amphiura abyssorum Norman, 1876
Fig. 35

Amphiura abyssorum Norman, 1876: 215; Mortensen, 1927: 211; 1933*a*: 62.
Amphiura digna Koehler, 1907: 274; Mortensen, 1927: 211.

Description. In the absence of any material for study this diagnosis is based on Mortensen's (1933*a*) and Koehler's (1907) description.

The disk is covered with coarse imbricating plates amongst which the centrodorsal and primary plates are conspicuous, diameter up to 8 mm. The radial shields are about twice as long as broad, small triangular. The ventral interradial area is partly naked.

The infradental papillae are block-like and contiguous or small and conical. The distal oral papillae are spine-like arising on the adoral shields, occasionally there is a supplementary papilla on the oral plate (see Mortensen, 1933*a*, Fig. 36). The adoral shields are wing-like separating the oral shield from the first lateral arm plate. The oral shield is rounded triangular with a slight distal lobe.

The dorsal arm plates are large, fan shaped to rounded hexagonal and contiguous. The ventral arm plates are hexagonal and contiguous. There are 3 or 4 conical, pointed arm spines on proximal plates, 3 on distal ones. The tentacle pores do not have tentacle scales.

Remarks. The features of the jaw resemble *A. otteri* and if the disk is missing *A. abyssorum* could be mistaken for it. *A. abyssorum* differs from *A. otteri* in the arm spine number, the lack of any terminal hook to these spines and a lack of tentacle scales on the tentacle pore, although in some specimens of *A. otteri* tentacle scales may be insignificant or absent from many pores. If the disk is preserved *A. abyssorum* differs further in the naked ventral interradial area and in the coarser scaling of the disk. This latter character may not be particularly useful as pointed out by Clark (1970).

Distribution. *A. abyssorum* has only been recorded from the Eastern Atlantic and Davis Strait. It has a bathymetric range of 915–3210 m (Mortensen, 1933*a*).

Amphipholis squamata (D. Chiaje, 1829)
Fig. 36

See A. M. Clark 1970: 28–29 for discussion and synonymy of this genus and species.

Material studied. **COB:** BIOGAS. Stn HZ: DS01 47°56′N: 7°40′W 400 m. 2 specimens.
SMBA: RRS *Challenger II* SBC 66 56°39′N: 09°23′W 1200 m 5 specimens.
BMNH: C. E. Halben coll, N. Ireland 6 specimens.

The disk is round covered by coarse scales amongst which the centrodorsal and primary plates are indistinguishable except in small individuals; diameter up to 5 mm, usually smaller. The radial shields extend about one third to half the radius of the disk. They are usually slightly longer than broad and contiguous throughout their length. The ventral interradial plates are slightly smaller than the dorsal plates and there is usually a distinct boundary between them.

The two infradental papillae are usually block-like in larger specimens, conical in the smaller, often contiguous. There are two distal oral papillae on each side of the jaw forming a continuous series with the infradental papillae. The distalmost one is broad and opercular. The oral shield is rounded triangular in small specimens almost rhombic in larger ones.

The dorsal arm plates are fan shaped, contiguous proximally, separated distally. The ventral arm plates are pentagonal to nearly triangular contiguous. The tentacle pores are small with two tentacle scales. There are 4 arm spines proximally, 3 distally.

Distribution. This is a widespread species found in warm and temperate areas. It has previously been recorded from depths of 0–740 m but recent investigations in the Rockall Trough by the SMBA have recorded it from 1200 m.

Amphioplus (Unioplus) daleus (Lyman, 1879)
Fig. 36

Amphiura dalea Lyman, 1879: 27; 1882: 137–138; Lütken & Mortensen, 1899: 154.
Amphioplus daleus: Verrill, 1899*b*: 315.
Amphichilus daleus: Matsumoto, 1917: 177; Mortensen, 1933*a*: 63.
Unioplus daleus: Fell, 1962: 16.
Amphioplus (Unioplus) daleus: A. M. Clark, 1970: 45; Tommasi, 1976: 285–286.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 325 36°44′S: 46°16′W 4929 m. HOLOTYPE.
COB: BIOGAS Stn 1: CP01 2245 m 1 specimen. BIOGAS Stn 2: DS40 3345 m 2 specimens. BIOGAS Stn 6: DS52 1 specimen. BIOVEMA: DS03 10°47′10″N: 42°41′01″W 5150 m 1 specimen.

The disk is indented interradially, diameter up to 10 mm. The disk scales are small imbricating becoming slightly larger towards the edge of the disk. The centrodorsal plate is usually conspicuous but not the primary plates. The radial shields are about twice as long as broad and contiguous only distally.

The infradental papillae are block-like usually contiguous. The first oral tentacle scale is superficial and together with the distal oral papillae forms a continuous series with the infradental papillae. The two distal oral papillae are block-like, the distalmost one is the largest and arises on the adoral shield and/or the oral plate. The oral shield is rounded triangular sometimes with a slight distal lobe. It is separated from the first lateral arm plate by the wing-like adoral shields.

The dorsal arm plates are slightly hexagonal or nearly rectangular and separated. The ventral arm plates are hexagonal, almost pentagonal but with the proximal angle squared off, to nearly square and contiguous. The tentacle pores have one large rounded tentacle scale. There are 3 conical arm spines; the middle one may be thicker and longer than the others.

REMARKS. This species looks superficially like *Amphioplus verrilli* but differs from that species by the following characters: the tentacle pores usually have a rounded tentacle scale whereas *verrilli* has no tentacle scales and the ventral arm plates are flat not ridge as in *verrilli*.

DISTRIBUTION. *A. daleus* appears to be a widespread abyssal species. In the North Atlantic it has been recorded from Iceland (2418 m) and the Bay of Biscay (2006–3345 m). It has also been found in the South Atlantic, off Patagonia (4929 m. Type locality) and in the eastern Pacific, off southern California and Mexico (2736–4151 m).

Amphioplus verrilli (Lyman, 1879)
Fig. 36

Amphiura verrilli Lyman, 1879: 29–30; 1882: 139–140.
Silax verrilli: Fell, 1962: 16; Clark, 1970: 36–37.
Silax pulvinus Cherbonnier & Sibuet, 1972: 1372–1375.
Amphioplus verrilli: Bartsch, 1983*b*: 14–15.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 54 34°51′N: 63°59′W 4846 m HOLOTYPE.
MNHN: *Jean Charrot* 52°06′03″N: 45°33′01″W 4165 m HOLOTYPE of *Silax pulvinus*
COB: BIOGAS Stn 3: CV14 4252 m 1 specimen. BIOGAS Stn 4: CP15 4715 m 2 specimens; CP16 4825 m 1 specimen; CP17 4706 m 1 specimen. BIOVEMA CP02 10°59′N: 45°15′W 5073 m 5 specimens; 10°46′23N: 42°40′4W 5100 m 4 specimens; DS05 10°45′97N: 42°40′29W 5100 m 1 specimen.

The disk is pentagonal, often indented interradially particularly in larger specimens, diameter up to 13·5 mm. The disk is covered with many small imbricating or contiguous scales amongst which the centrodorsal plate and sometimes the primary plates are distinct. The radial shields are about twice as long as broad; in small specimens they may be contiguous along their whole length, in larger specimens they become separated by a single triangular plate or by a wedge of plates. The ventral interradial areas are covered by plates similar to those on the dorsal surface.

The infradental papillae are block-like usually contiguous lying above the broad rectangular teeth, but in smaller specimens these papillae may lie on the same level as the first tooth and be separated by it. The first oral tentacle scale is superficial and arises just distal to the infradental papillae and the two block-like distal papillae form a continuous series with the infradental papilla. The distalmost papillae are usually enlarged. The adoral shields are flared distally and separate the oral shields from the first lateral arm plate. The oral shields range from rounded triangular, particularly in small individuals, to distinctly triangular, almost a regular isosceles triangle, in some larger specimens.

The dorsal arm plates are hexagonal, with angular pointed proximal and distal edges and straight lateral sides, sometimes becoming nearly rectangular. The lateral arm plates appear to have a more open calcite skeleton giving the plate a spongy appearance. The ventral arm plates are keeled rounded pentagonal to nearly square in shape and contiguous. The tentacle pores are large and lack tentacle scales. There are 4–5 short conical arm spines proximally, 3 distally.

REMARKS. Cherbonnnier & Sibuet (1972) consider *S. pulvinus* to be distinct from *S. verrilli* because the infradental papillae lie above the teeth and are contiguous, not lying on the same level as and separated by the ventral most tooth as in Lyman's holotype, and the ventralmost tooth, i.e. the one next to the infradental papillae is block-like whereas in the holotype of *S. verrilli* it is tricuspid. However material from the Biogas reveals, as pointed out by Bartsch (1983*b*), that such differences are partly attributable to size and that the tooth shape is not constant. Several specimens have contiguous block-like infradental papillae with tricuspid teeth.

DISTRIBUTION. *A. verrilli* has been recorded from both sides of the Atlantic: in the west from St Vincent (763 m), off N. Carolina and the Labrador Basin (4165–4864 m), in the east it has been recorded from the Bay of Biscay and the Iberian Basin (4252–5315 m). Apart from the record from St Vincent *verrilli* appears to be a member of the lower abyssal zone fauna.

AMPHILIPIDINAE

Amphilepis ingolfiana Mortensen, 1933*a*

Fig. 37

Amphilepis ingolfiana Mortensen, 1933*a:* 54–56; Schoener, 1967: 655–658; Gage *et al.*, 1983: 293–294.
Amphilepis norvegica? Ljungman, 1872: 632; ?Lyman, 1882: 149; ?Koehler, 1914: 42; ?Cherbonnier & Sibuet, 1972: 1375 [non *A. norvegica* (Ljungman, 1867)].

MATERIAL STUDIED. **COB:** BIOGAS Stn 1: DS18 2325 m 5 specimens; DS17 2103 m 1 specimen; DS62 2175 m 4 specimens. Stn 2: CP11 3056 m 2 specimens. Stn 3: DS76 4228 m 2 specimens; CV12 4252 m 1 specimen. Stn 4: CP16 4825 m 1 specimen. Stn 6: DS51 2430 m 3 specimens; DS52 2006 m 6 specimens. DS70 2150 m 1 specimen; CP07 2170 m 1 specimen; CP24 1995 m 3 specimens.

INCAL: DS01 57°59′7N: 10°39′8W 2091 m 31 specimens; DS02 57°58′8N: 10°48′5W 2081 m 53 specimens; DS05 56°28′1N: 11°11′7W 2494 m 12 specimens; DS06 56°26′6N: 11°10′5W 2494 m 1 specimen; DS09 55°07′7N: 12°53′6W 2897 m 1 specimen; DS10 50°12′7N: 13°16′6W 2719 m 6 specimens; DS13 46°01′9N: 10°17′9W 4822 m 1 specimen; DS16 47°30′9N: 9°35′3W 4182 m 11 specimens. CP01 57°57′7N: 10°55′W 2068 m 4 specimens; CP02 57°58′4N: 10°42′8W 2091 m 1 specimen; CP03 56°38′N: 11°06′4W 2466 m 3 specimens; CP04 56°33′2N: 11°11′3W 2483 m 1 specimen; CP05 55°00′4N: 12°29′4W 2884 m 1 specimen; CP06 55°02′3N: 12°40′3W 2888 m 4 specimens; CP07 55°03′4N: 12°46′2W 2 specimens; CP08 50°14′7N: 13°13′5W 2644 m 84 specimens; CP09 50°15′4N: 13°15′8W 2659 m 37 specimens; CP12 46°00′5N: 10°18′3W 4796 m 1 specimen; CP13 46°02′1N: 10°14′8W 4800 m 3 specimens. WS01 50°19′4: 13°08′1W 2550 m 76 specimens; WS02 50°19′3N: 12°55′8W 2498 m 95 specimens; WS05 46°03′0N: 10°15′7W 4804 m 1 specimen. ØS01 50°19′4N: 13°10′9W 2634 m 18 specimens; ØS02 48°19′2N: 15°15′9W 4929 m 1 specimen; ØS04 46°03′9N: 10°12′8W 4796 m 46 specimens; ØS07 47°31′8N: 9°34′3W 4249 m 10 specimens; ØS08 47°29′8N: 9°39′2W 4327 m 1 specimen.

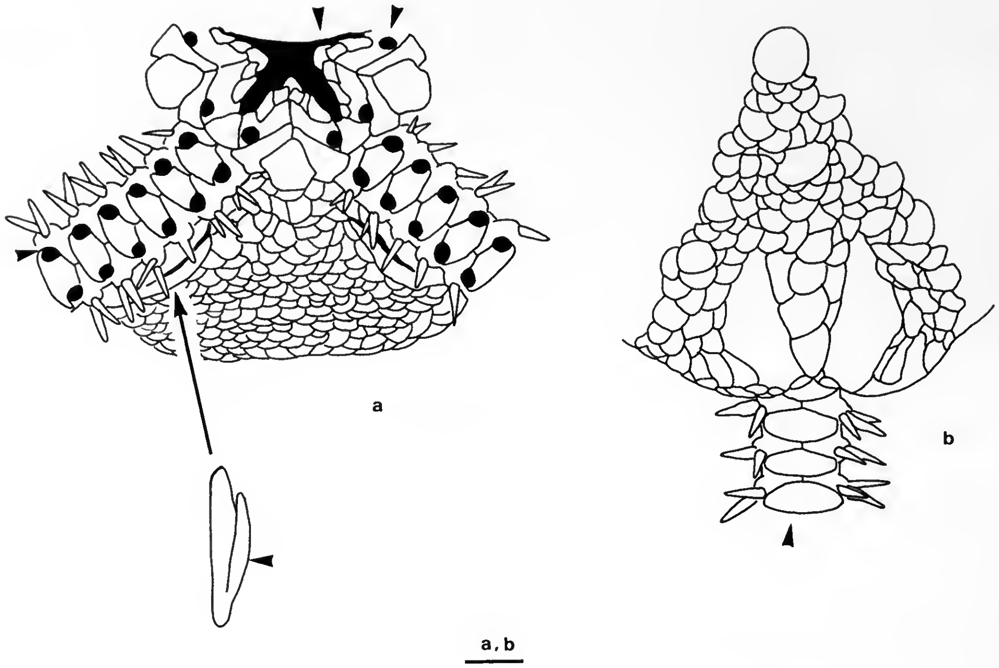
IOS: *Discovery* Investigations Stn 7709/73 60°7·1′N: 19°30·3′W 2649–2663 m 1 specimen; Stn 8519/7 24°02′N: 16°59′W 997–1037 m 4 specimens; Stn 8521/6 20°48′N: 18°53′W 3064–3070 m 3 specimens.

SMBA: RRS *Challenger II* Stn ES8 54°45′N: 12°10′W 2900 m 1 specimen; Stn ES10 56°37′N: 10°04′W 2540 m 19 specimens; Stn 56 54°40′N: 12°16′W 2886 m 2 specimens.

The disk is round, flat covered with overlapping plates amongst which primary plates, certainly the centrodorsal plate, are generally distinct. The radial shields are long, about a half the disk radius in length, longer than broad, rounded proximally and separated by a wedge of plates.

At the apex of the jaw the ventralmost tooth may be superficial, separating, the infradental papillae so that it appears to be an apical papilla; in other specimens the infradental papillae lie closer together; they are followed on each side by two block-like oral papillae. The second oral tentacle pore arises superficially outside the mouth and is open without a tentacle scale, except in juveniles where there is one pointed spine-like scale arising on the adoral shield. The adoral shields are longer than broad, flared distally. The oral shield is triangular. There are no genital slits but the genital plate has two branches: a long one lying adjacent to the arm and a slightly shorter one lying adjacent to that with only a small slit between them.

AMPHILEPIDINAE



Amphilepis ingolfiana

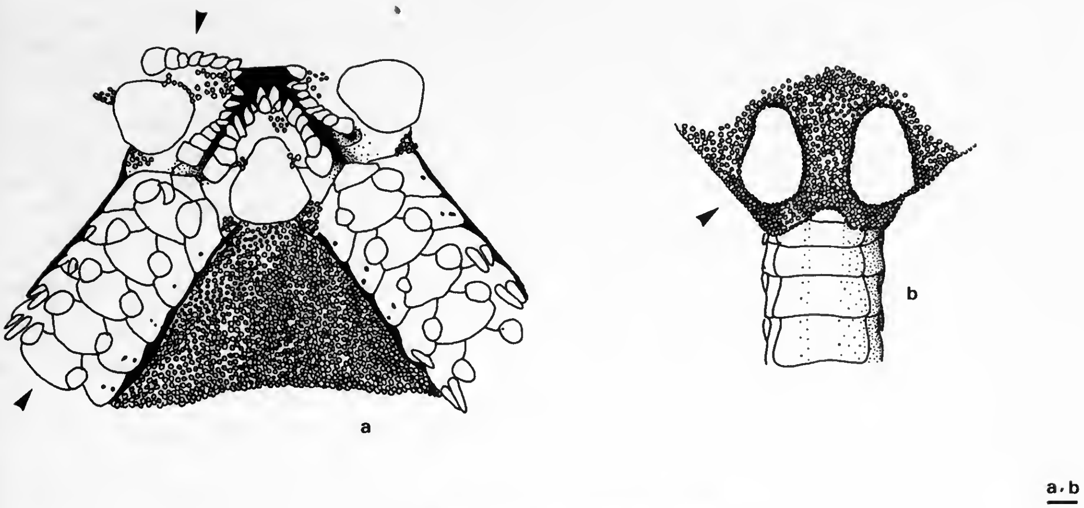
Fig. 37 Key to the Amphiuridae: Amphilepidinae. *Amphilepis*: (a) ventral; (b) dorsal view of disk. Bar scales = 1 mm.

The arms are about 5–6 times the disk diameter in length. The dorsal arm plates are oblong, wider than long and separated from one another. The ventral arm plates are pentagonal in juveniles becoming more rectangular in larger specimens, and are separated from one another. The tentacle pores are open without tentacle scales. There are three pointed arm spines.

Remarks. *A. ingolfiana* can be distinguished from other amphiurid genera and certain ophiurinids, to which it bears a superficial resemblance because of the superficial second oral tentacle pore, by the scaling of the disk, the arrangement of the oral plates, the lack of tentacle scales and the erect arm spines. Mortensen (1933*a*) noted that *A. ingolfiana* and *A. norvegica* were very similar and could only be distinguished from one another by the following characters: the shape of the genital plate which has two branches in *A. ingolfiana* but in *A. norvegica* the abradial branch—the one on the ventral interradial side of the genital plate is reduced and broadened, while the radial shields which are more rounded on the proximal abradial—outer side in *A. ingolfiana* while in *A. norvegica* this side is more angular. Mortensen also noted that *A. ingolfiana* was bigger than *A. norvegica* and had coarser arms.

Distribution. It has been recorded from both sides of the North Atlantic, in the west from Cape Hatteras north to the Davis Strait and SW. Iceland and in the east from the Rockall Trough south to off North Africa, with a bathymetric range of 957–4829 m.

OPHIODERMATIDAE



Bathypectinura heros

Fig. 38 Key to the Ophiodermatidae. *Bathypectinura*: (a) ventral; (b) dorsal view of the disk. Bar scale = 1 mm.

OPHIODERMATIDAE Ljungman, 1867

A family characterised by the disk covered with small plates usually completely concealed by a dense coating of granules in adult specimens; the radial shields usually visible; the oral papillae forming a continuous series with the apical papillae; the second oral tentacle scale opens within the mouth slit; the arm spines short may be numerous, and appressed to the side of the arm.

Bathypectinura heros (Lyman, 1879)
Fig. 38

Pectinura heros Lyman, 1879: 48; 1882: 16; Koehler, 1897: 325; 1904: 9.
Pectinura tessellata Lyman, 1883: 230.
Pectinura lacertosa Lyman, 1883: 231.
Pectinura conspicua Koehler, 1897: 322; 1899: 37; 1904: 9.
Pectinura modesta Koehler, 1904: 7.
Ophiocrates lenta Koehler, 1904: 19.
Pectinura elata Koehler, 1906: 7; 1907: 249; Grieg, 1921: 32.
Ophiocrates secunda Koehler, 1906: 1; 1907: 253; H. L. Clark, 1939: 132.
Bathypectinura lacertosa: H. L. Clark, 1909: 129–130; 1915: 306; 1941: 90.
Bathypectinura elata: H. L. Clark, 1909: 129–130; 1915: 306; Mortensen, 1927: 226.
Bathypectinura modesta: H. L. Clark, 1909: 129–130; 1915: 306.
Bathypectinura conspicua: H. L. Clark, 1909: 129–130; 1915: 306; Koehler, 1922: 342; H. L. Clark, 1939: 96.
Bathypectinura tessellata: H. L. Clark, 1909: 129–130; 1915: 306.
Bathypectinura heros: H. L. Clark, 1909: 129–130; 1915: 306; Hertz, 1927: 116; Shoener, 1967: 77; Rowe & Menzies, 1969: 533; Madsen, 1973: 133–143.
Bathypectinura gotoi Matsumoto, 1915: 87; 1917: 320.
Ophiozonella brachyactis H. L. Clark, 1939: 129.
Ophiocrates intervallus Madsen, 1947: 9.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 191 5°41′S: 134°4′E 1440 m HOLOTYPE. *Investigator* Godavery Detta 16°01′N: 81°25′E 738 m SYNTYPES of *Bathypectinura conspicua* (Koehler, 1897).
IOS: *Discovery* Investigations Stn 8968 31°35′N: 11°02′W 1 specimen; Stn 8971 31°47·5′N: 11°10·2′W 2432 m 16 specimens.

The disk is pentagonal; diameter up to 53 mm. Small specimens have large disk plates exposed, being only fringed with granules while in larger specimens, d.d. > c.15 mm the plates are smaller and usually completely hidden by granules. The radial shields are oval, usually naked in all but the largest specimens. The ventral interradial areas are at first naked but become granule covered.

There are from 1 to as many as 10 (Madsen, 1973) apical oral papillae flanked on each side by 7–10 oral papillae, depending on the size of the specimen, with the distalmost becoming flat and widened. The adoral shields are overlain proximally by the oral shield but distally slightly widened, and in large specimens separate the oral shield from the first lateral arm plate. The oral shield is variable in shape from a rounded triangular to slightly pentagonal; it lies proximal to the genital slits not spanning them. The oral plates and adoral shields often have scattered granules which become more numerous in larger specimens.

The arms are up to 7 times the disk diameter. The dorsal arm plates, nearly square in small specimens, become broader than long in larger ones; the arms become increasingly ridged with size. The ventral arm plates are axe shaped to irregularly hexagonal and broadly contiguous except on the tips of the arms. The tentacle pores are large armed with one, or occasionally two, round or slightly egg shaped tentacle scales. There are 2 to 4 pointed appressed arm spines the longest may be up to one segment in length.

REMARKS. Madsen (1973) has dealt in detail with the range of variation in this species.

DISTRIBUTION. *B. heros* is a widespread species recorded in most oceans except the Arctic and Southern Oceans. In the Atlantic it has been recorded in the west from North Carolina 1920–2050 m, and in the east from the Bay of Biscay to the Azores 2100–2580 m.

OPHIOCHITONIDAE Matsumoto, 1915

A family with a rounded flat disk covered by small imbricating plates amongst which the centrodorsal and primary plates usually distinct; the radial shields small, length less than half the radius of the disk, well separated from one another; the jaw broader or as broad as long; usually one sometimes two apical papillae flanked by 5–7 oral papillae on each side the distalmost slightly curved and extending beneath the largest oral papilla just proximal to it, it is possible that this distalmost papillae is part of the second oral tentacle pore; the adoral shields large and wing-like; the oral shield large, rounded triangular or arrow shaped, usually longer than broad; the arms long and slender; the dorsal and ventral arm plates well developed and contiguous at least proximally; the tentacle pores moderately large each armed with one or two flat leaf-like tentacle scales; usually three times long, erect arm spines, equal in length to two arm segments.

Ophiochiton ternispinus Lyman, 1883
Fig. 39

Ophiochiton ternispinus Lyman, 1883: 255; Hoyle, 1884: 144; Bell, 1892: 114; Mortensen, 1913: 354; H. L. Clark, 1915: 287; Grieg, 1921: 33; Mortensen, 1927: 224; 1933*a*: 67–69; Gage *et al.*, 1983: 294–295; Bartsch, 1983*b*: 15–16.
Ophiochiton grandis Verrill, 1884: 383; Koehler, 1914: 116.
Ophiochiton solutus Koehler, 1906: 16–17; 1907*a*: 269–271.
Ophiozona tjalfiana Mortensen, 1913*a*: 38; 1913*b*: 353.
Ophiozonella tjalfiana: Matsumoto, 1915: 294; H. L. Clark, 1915: 340; Mortensen, 1933*a*: 71.

MATERIAL STUDIED. **BMNH:** *Porcupine* Stn 42 49°12′N: 12°52′W 1572 m HOLOTYPE.
IOS: *Discovery* Investigations Stn 8519/7 24°02′N: 16°59′W 997–1037 m 1 specimen.
MNHN: *Travailleur & Talisman* 4 Juillet 1883 Stn 80 23°50′N: 19°37′W 1113 m HOLOTYPE of *O. solutus* Koehler.
SMBA: RRS *Challenger II*: Stn AT 157 49°31′N: 13°11′W 1752 m 2 specimens; Stn AT 177 57°18′N: 10°16′W 2220 m 1 specimen; Stn AT 191 56°00′N: 13°58′W 2190 m 1 specimen; Stn AT 192 57°22′N: 12°02′W 1862 m 1 specimen.

The disk is round and flat, diameter up to 20 mm; covered with many small imbricating plates in large specimens or by fewer larger plates in smaller ones; the centrodorsal and primary plates are distinct and

OPHIOCHITONIDAE

Ophiochiton ternispinus

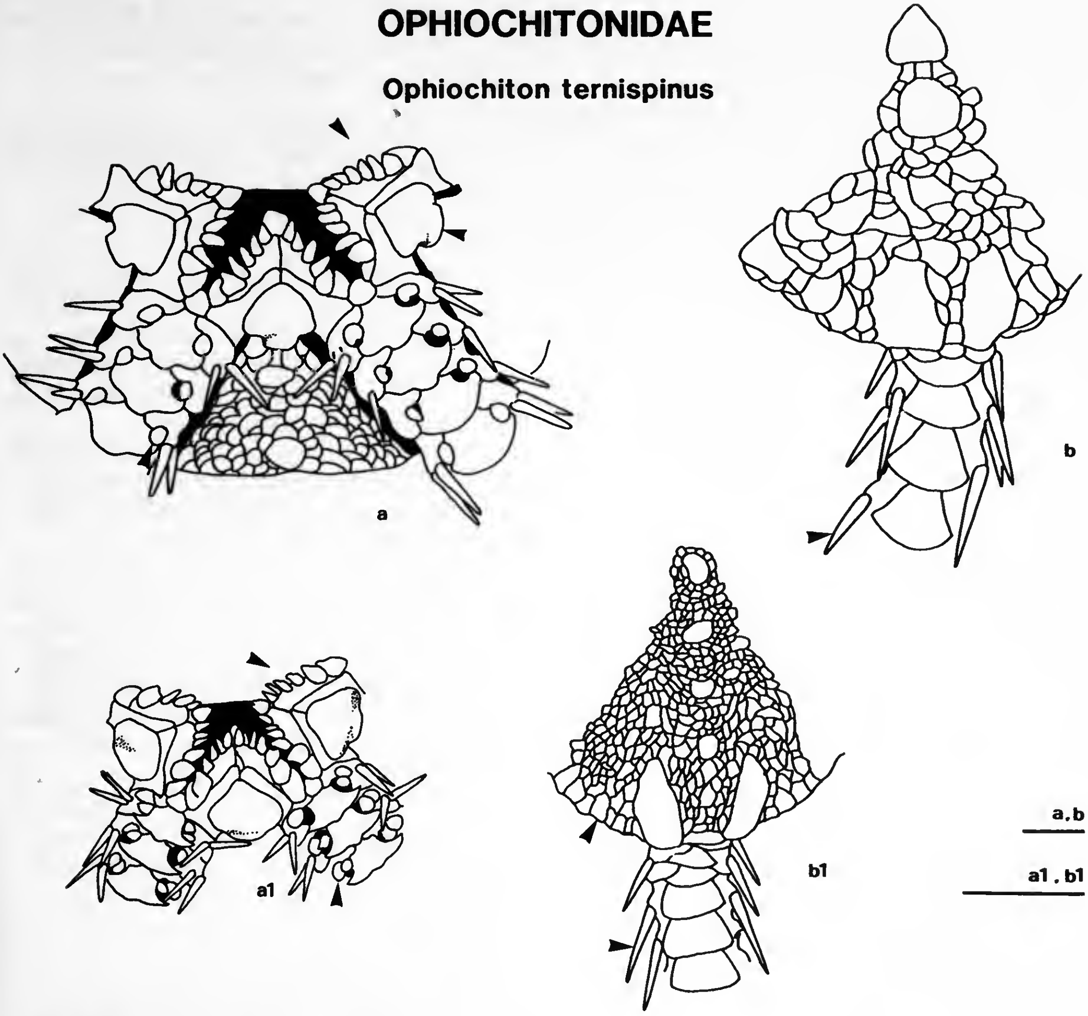


Fig. 39 Key to the Ophiochitonidae. *Ophiochiton:* (a) ventral; (b) dorsal view of the disk. Bar scales = 1 mm.

larger than the surrounding plates. The radial shields are small, well separated from one another; they are usually longer than broad, slightly teardrop shaped. The ventral interradial areas are covered with small plates similar to those of the dorsal surface.

The jaws are as broad or broader than long. There is usually one, or sometimes two, blunt apical papilla flanked on each side by 6–7 oral papillae; the proximal oral papillae are pointed and spine-like becoming broader more triangular distally. The second distalmost papillae is the largest and partly overlies the distalmost papillae when viewed from the ventral side. The distalmost papillae may appear to be slightly curved. The adoral shields are long wing-like and flared distally separating or only just separating the oral shield from the first lateral arm plate. The oral shield varies from rounded triangular to arrow shaped.

The dorsal arm plates are broader than long, contiguous at least on proximal arm segments, with a slightly convex and, in some specimens, carinate distal edge. The first ventral arm plate is small and round, the subsequent plates roughly pentagonal with a convex distal edge which may be produced in the midline; they are contiguous at least on the proximal arm segments. The tentacle pores are not conspicuously large each is armed with two sometimes only one large flat tentacle scales. There are three pointed, slightly flattened, minutely rugose arm spines of which the dorsalmost one appears to be the longest reaching nearly two arm segments in length.

REMARKS. *Ophiochiton ternispinus* can be distinguished by the shape and scaling of the disk, the structure of the jaw particularly the arrangement of the two distalmost oral papillae, the shape of the dorsal and ventral arm plates and the limited number of arm spines.

DISTRIBUTION. It has been recorded from both sides of the Atlantic; in the west from the Gulf of Mexico north to the Davis Strait with a bathymetric range of 425–1244 m and in the east from off SE. Iceland south to Azores with a bathymetric range of 1577–2220 m.

OPHIURIDAE

The family is comprised of three subfamilies Ophiurinae, Ophiolepidinae and Ophioleucinae, reduced by Madsen (1983) from full familial rank. The features which appear to unite them are: the arm spines are short and usually appressed; the arm spine articulation is usually simple, very rudimentary; oral papillae forming a continuous series and usually either spine-like proximally becoming block-like or block-like throughout; internally the peristomal plates are double and the genital plate articulates upon the radial shield by means of two condyles and one pit.

However, the subfamilies possess characters which suggest that they should be considered as full families. The family Ophiolepidinae can be distinguished by: both oral tentacle pores arising within the mouth; the plating of the disk is usually conspicuous with large plates; and the shape of the dental plates which is twice as long as broad and rounded at both ends (Murakami, 1963).

The remaining subfamilies would appear to be more closely related from the characters of the oral and dental plates shown by Murakami (1963). The dental plates and the position of the sockets for the teeth are particularly similar. It had previously been considered that the feature of the second oral tentacle pore arising outside the mouth was distinctive enough to warrant raising the Ophiurinae to familial rank (Paterson, 1980). However, within certain species of the Ophioleucinae, e.g. *Ophiernus vallinicola,* the structure and position of the second oral tentacle pore and its tentacle scales superficially resembles the arrangement found in some species of the Ophiurinae i.e. *Ophiogona döderleini.* While examination of these features reveals that the resemblance is no more than superficial there is a need to investigate the form and arrangement of both the hard skeletal structure and the soft tissues such as the tentacle and water vascular system associated with the second oral tentacle pore. Therefore, these subfamilies have not been raised to full familial rank, until more evidence is available.

OPHIOLEUCINAE Matsumoto, 1915

A subfamily of the Ophiuridae characterised by the disk comprising scales completely or partially covered with a coat of granules sometimes also covering the radial, adoral and oral shields; the teeth are papilla-form and arranged in a single series; the second oral tentacle pore opens within the mouth slit; the adoral shields are usually long and flared distally; the oral shields are small, triangular or arrow shaped; the arms are long, often flat and wide, tapering slowly to the end of the arm; the dorsal and ventral arm plates are large and successive ones may be contiguous; the tentacle pores are variable in size, sometimes enlarged, armed with one to several scales.

Ophiernus vallincola Lyman, 1878

Fig. 40

Ophiernus vallincola Lyman, 1878: 122; H. L. Clark, 1923: 365; Hertz, 1927*a*: 114; H. L. Clark, 1939: 134.
Ophiernus abyssalis Koehler, 1896*c*: 242; 1909: 143.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 78 37°44′N: 25°13′W 1830 m HOLOTYPE.
IOS: *Discovery* Investigations Stn 8968 31°35′N: 11°2·0′W 12 specimens; Stn 9042 42°15′N: 11°22′W 1662–1541 m 4 specimens.
COB: BIOGAS: Stn CP34 6 specimens. INCAL: DS04 57°23·2′N: 11°06·5′W 1035 m 53 juvenile specimens.

The disk is round, sack-like being thin walled and flexible, slightly indented over the arms; covered by small imbricating scales except for the central area of the disk which is covered by a thickened wrinkled skin; diameter up to 20 mm. The scales of the disk carry a light covering of granules which never form a dense coating. The radial shields are round, naked, about a quarter of the disk radius in length.

The jaws appear long and thin. There is one long pointed apical papilla flanked by 7–10 rounded or slightly pointed oral papillae. The distal papillae appear to form a continuous series with the superficial tentacle scales of the second oral tentacle pore. This pore lies close to the surface of the jaw but within the mouth slit and has 2–3 tentacle scales. The adoral shields are flared distally separating the oral shield from the first lateral arm plate. The oral shield is rounded triangular in shape often with a slight distal projection.

The arms are long up to seven times the disk diameter, flat, and evenly taper from the base of the disk. The dorsal arm plates wider than long, rectangular and contiguous proximally. The tentacle pores are large and open proximally becoming less conspicuous distally; the first four are armed with 2–3 rounded tentacle scales, the subsequent pores usually with two pointed tentacle scales. There are two, occasionally three or four, small, appressed arm spines. The lateral arm plates also carry a series of bristle-like spines dorsal to the arm spines which are usually more noticeable in slightly dried specimens.

REMARKS. *O. vallincola* can be distinguished from *O. adspersus* by 1. The skin covered central portion of the disk; 2. the shape of the oral shield; 3. the evenly tapering arms and 4. the shape of the radial shields.

DISTRIBUTION. This is a widespread species recorded from the Pacific, Indian and Atlantic Oceans with a bathymetric range of 840–4065 m. In the North Atlantic it has been recorded from SW. Ireland, the Bay of Biscay and the Azores.

Ophiernus adspersus adspersus Lyman, 1883

Fig. 40

Ophiernus adspersus Lyman, 1883: 236; Koehler, 1897: 316; 1899: 32; 1904: 20; 1907: 251; H. L. Clark, 1911: 95; Koehler, 1914: 151; H. L. Clark, 1915: 95; Koehler, 1922: 440; Mortensen, 1927: 228; Hertz, 1927*b*: 112; Koehler, 1930: 280; H. L. Clark, 1939: 133; 1941: 107; John & A. M. Clark, 1954: 159.
Ophiernus adspersus adspersus: Madsen, 1977: 114–116.

MATERIAL STUDIED. **BMNH:** *Blake* Stn 185 off Dominique 599 m PARATYPE.

The disk is round, slightly indented over the arms; covered with small imbricating scales which may be obscured by a dense covering of granules; diameter up to 25 mm. The radial shields are triangular to tear-drop shaped, just over a quarter the disk radius in length.

The jaws appear to be long and narrow. There is one, occasionally two, pointed apical papilla flanked by 7–9 rounded oral papillae which form a continuous series with the superficial oral tentacle scales. As in *O. vallinicola*, the second oral tentacle pore lies close to the surface of the jaw but within the mouth slit. The adoral shields are flared distally, separating the oral shield from the first lateral arm plate. The oral shield is triangular often with a distinct distal projection giving the shield an arrow shaped.

The arms are about 8 times the disk diameter, flat, and widening outside the disk. The dorsal arm plates are wider than long, rectangular and contiguous. The ventral arm plates are subpentagonal and contiguous. The tentacle pores are open proximally, the first three armed with up to three rounded tentacle scales, subsequent pores have two pointed scales. There are two occasionally three short, pointed arm spines of which the dorsal most one is the longest. The lateral arm plates also carry a series of long bristle-like spines, dorsal to the arm spines.

REMARKS. *O. adspersus adspersus* can be distinguished by 1. the shape of the radial shields; 2. the granulation of the entire disk except for the radial shields; 3. the widening of the arm beyond the disk.

DISTRIBUTION. This species is known from the West Indies, Cape Verde Is also from the Indian and Pacific Oceans; bathymetric distribution of 291–3650 m.

Ophioleuce oxycraspedon ?Baranova, 1954

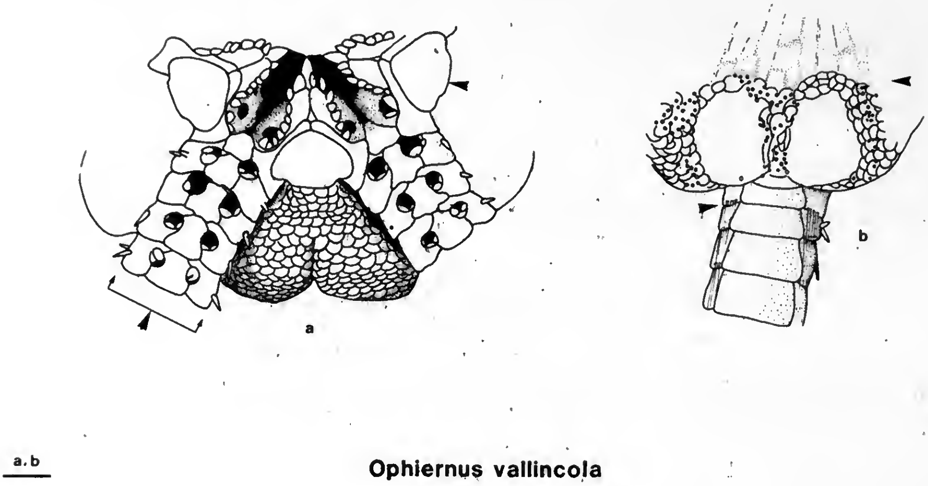
Fig. 41

Ophioleuce oxycraspedon Baranova, 1954: 339; Djakanov, 1954: 128–129; Madsen, 1983: 49.

MATERIAL STUDIED. **COB:** BIOGAS Stn HZ: CV22 1331 m 1 specimen.

The disk is round, covered with plates which on the dorsal side of the disk are surrounded by a single row of rounded granules. Occasionally a row of larger, more elongated granules occur on the plates themselves, particularly the radial shields. Larger granules form a continuous fringe around the perifery of the disk.

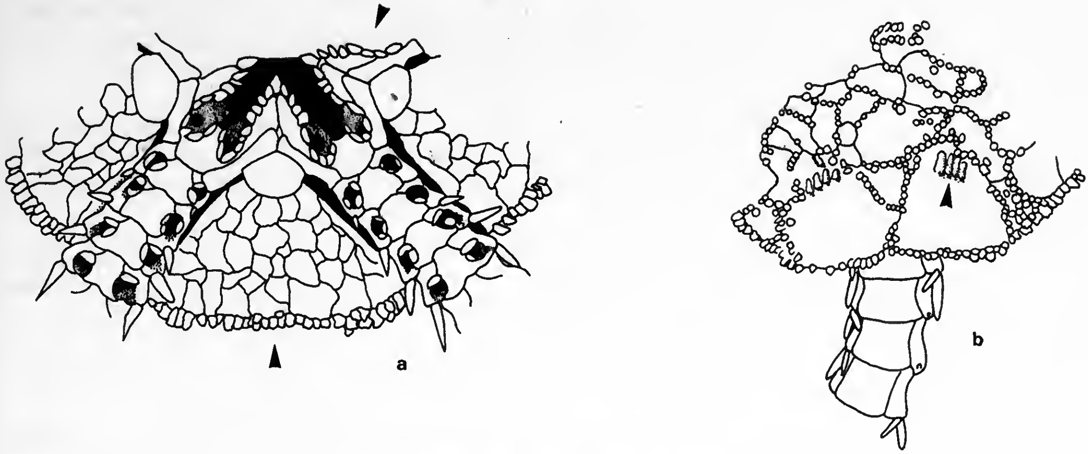
OPHIURIDAE : OPHIOLEUCINAE



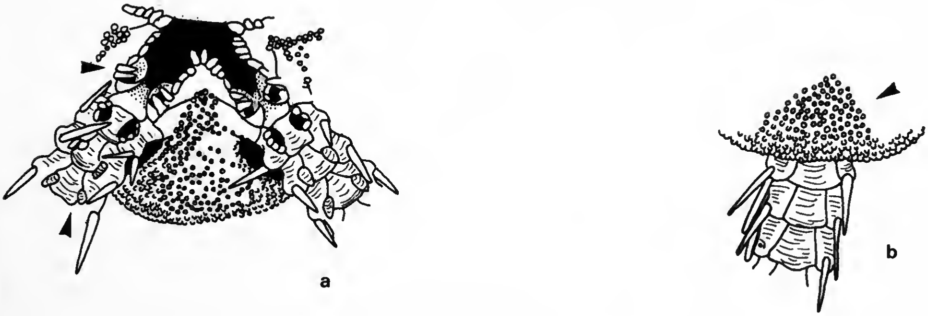
Ophiernus vallincola

Ophiernus adspersus adspersus

Fig. 40 Key to the Ophiuridae: Ophioleucinae. *Ophiernus*: (a) ventral; (b) dorsal view of disk. Bar scales = 1 mm.



Ophioleuce oxycraspedon



Ophiostriatus striatus ✻

Fig. 41 Ophiuridae: Ophioleucinae. *Ophioleuce* and *Ophiostriatus*. Captions and scale as in Fig. 40, *–not described in text.

Disk diameter is up to 12 mm. The radial shields are rounded triangular to teardrop shaped, slightly greater than a quarter of the disk diameter in length, distally contiguous except for a row of granules which runs along the suture. Ventral interradial areas are covered by many quite small plates but granules are not present.

The jaws appear longer than wide. There is one large pointed apical papilla flanked on each side by 4 rounded or slightly pointed oral papillae which merge with tentacle scales associated with the nearly superficial second tentacle pore. There are 3–6 elongated tentacle scales on each side of this pore. The adoral shields are long, narrow and slightly flared distally. The oral shields are rounded, pentagonal, occasionally arrow shaped. The genital slits are large.

The arms are about 3 times the disk diameter, slightly flattened, all the plates of the arm are striated. The dorsal arm plates are rectangular, slightly longer than broad, contiguous over much of the arm. The ventral arm plates are also contiguous with a wide distal edge, which may also be slightly indented, and sloping lateral sides. The proximal tentacle pores are large; the first two are armed with 2–3 broad flap-like scales, the next two pores with 2 then only one. There are 2 arm spines situated close together, a large ventral one and a small dorsal spine.

REMARKS. The Biogas specimen appears to bear closest resemblance to *O. oxycraspedon* particularly in the granulation of the disk and the shape of the arm spines. The main differences are the number of oral papillae: up to 6 or 7 in *O. oxycraspedon* and only 4 perhaps 5 oral papillae in the Biogas specimen.

This specimen also resembles *O. gracilis* Belyaev & Litvinova, 1976 which has a similar range of enlarged granules around the perifery of the disk and arrangement of oral papillae. It differs from the Biogas specimen in the shape of the dorsal arm spines, which appear to be equal and nearly an arm segment long.

DISTRIBUTION. *O. oxycraspedon* has been recorded from north of the Commander Islands in the Northern Pacific at 2440 m, its occurrence in the North Atlantic marks a considerable extension of range.

OPHIURINAE

A subfamily of the Ophiuridae characterised by the disk usually covered by plates sometimes with thickened skin; radial shield usually conspicuous; arm combs sometimes present; one to many apical papillae flanked by a continuous series of oral papillae; second oral tentacle pore opening outside the mouth slit or opening outside but entering the mouth slit via a furrow; oral shield variable in shape and size; arms varying size; arm spines usually less than an arm segment in length and usually appressed.

Characters of taxonomic importance in the Ophiurinae

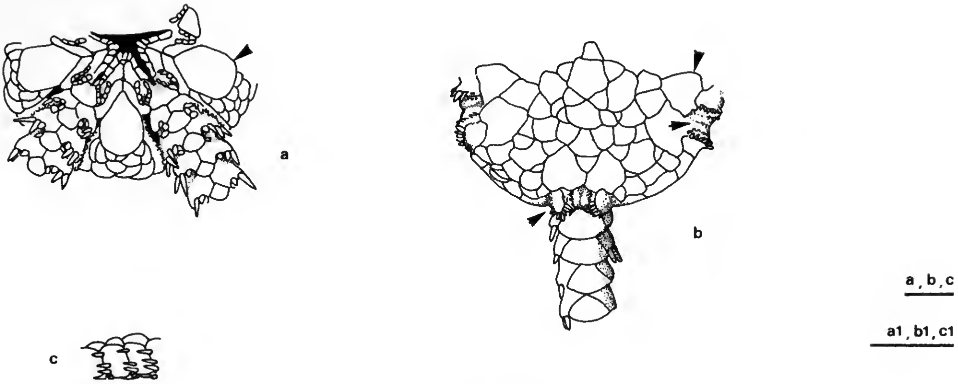
1. Disk:
- (*a*) The overall plating and texture.
- (*b*) The size and arrangement of the radial shields.
- (*c*) The presence of arm combs, the form of the spinelets and their arrangement—particularly important in the genus *Ophiura*.
- (*d*) The arrangement of the second oral tentacle pore—whether opening superficially outside the mouth slit or opening outside but entering the mouth slit via a furrow. This character, first proposed by Koehler (1904), could also be important in separating groups within *Ophiura*. Species such as *Ophiopleura borealis* have a oral tentacle pore which superficially resembles the arrangement in some species of Ophioleucinae.
- (*e*) The form of the apical and other oral papillae: whether pointed or block-like, separated or contiguous.
- (*f*) The length of the genital slits and form of the genital papillae.

2. Arms:
- (*a*) The shape and length of the arm—important, particularly in separating *Amphiophiura* and *Stegophiura* from other genera.
- (*b*) The form of the dorsal arm plates, whether or not contiguous or carinate.
- (*c*) The shape and arrangement of the ventral arm plates—important in separating species of many genera such as *Ophiura* and *Ophiocten*.
- (*d*) The form of the tentacle pores and the arrangement of the tentacle series—both useful at the generic level as in *Amphiophiura* and *Stegophiura* and the species level as in the genus *Ophiura*.

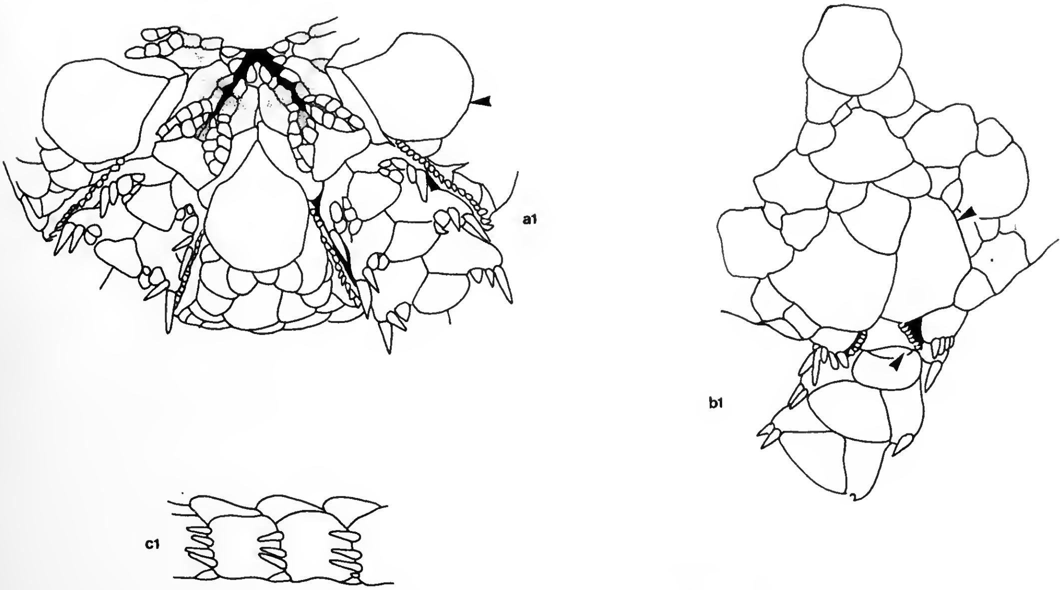
  A short-hand formula is now proposed to indicate the number of tentacle scales on each arm pore on the proximal portion of the arm. Each pore is given a number starting with the proximal pores i.e. A.P. 1 = the first arm pore. The tentacle scales which arise on the lateral arm plate or on the abradial part portion of the pore furthest from the mid-line of the arm are counted, i.e. L4–5. Then those which arise on the ventral arm plate on the abradial portion of the pore nearest the mid-line of the arm i.e. V4–5.
- (*e*) The number, form and arrangement of the arm spines on the lateral arm plate—generally a specific character.

OPHIURIDAE : OPHIURINAE

OPHIURA

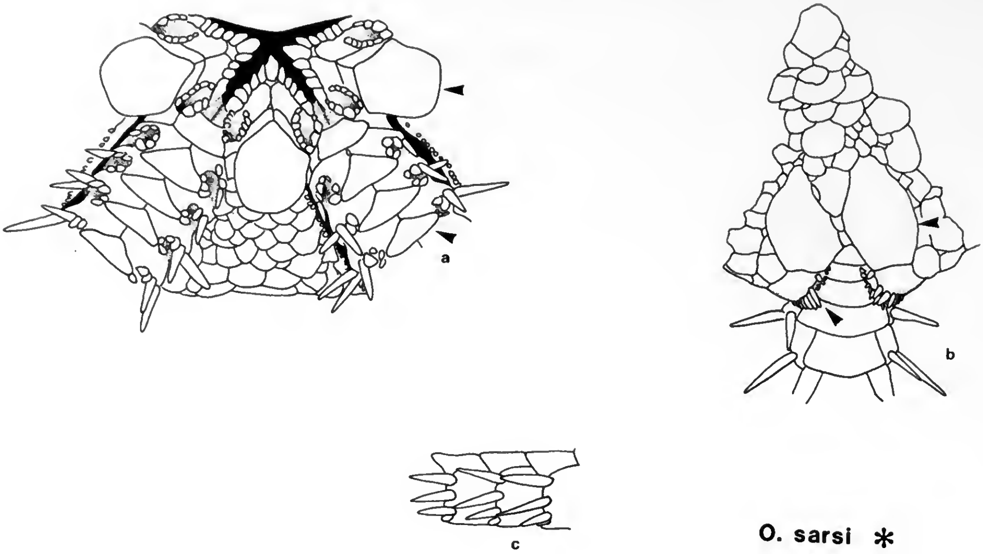


O. carnea

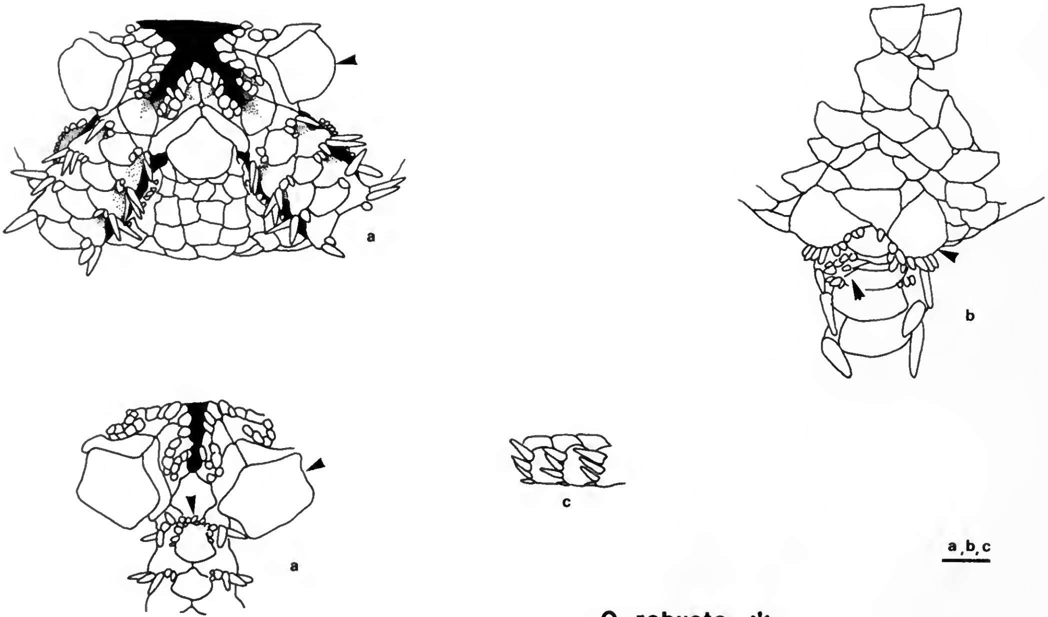


O. imprudens

Fig. 42 Key to the Ophiuridae: Ophiurinae. *Ophiura*: (a) ventral; (b) dorsal view of disk; (c) lateral view of arm. Bar scales = 1 mm.

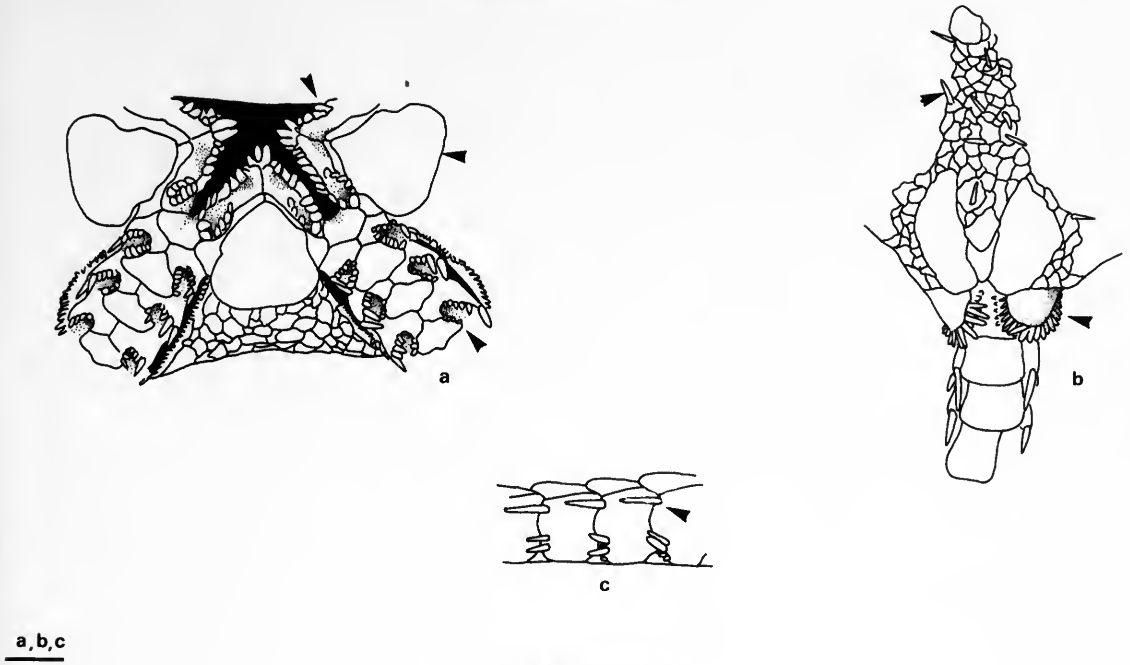


O. sarsi *



O. robusta *

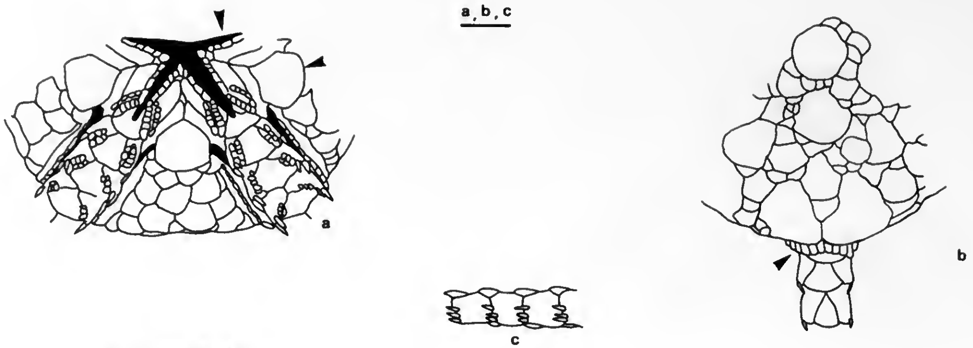
Fig. 43 Ophiuridae: Ophiurinae. *Ophiura*. Captions as in Fig. 42. *–not described in text.



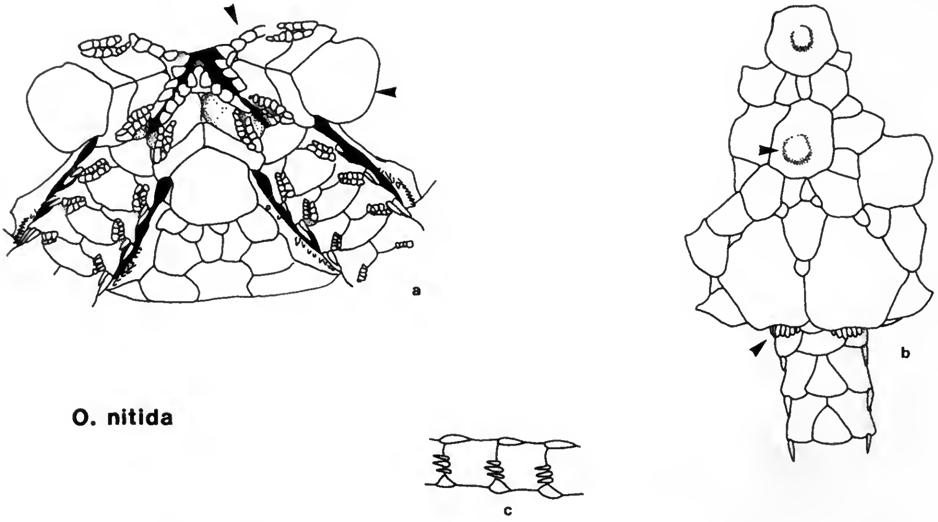
O. ljungmani

O. flagellata

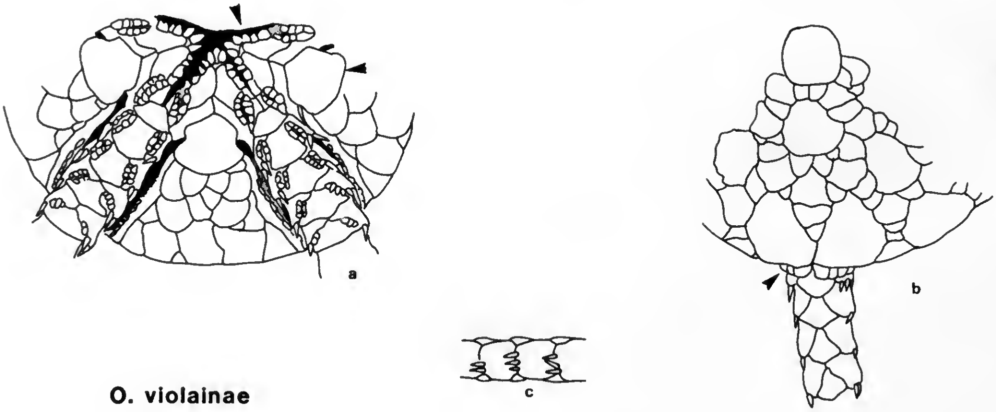
Fig. 44 Ophiuridae: Ophiurinae. *Ophiura*. Captions as in Fig. 42.



O. clemens

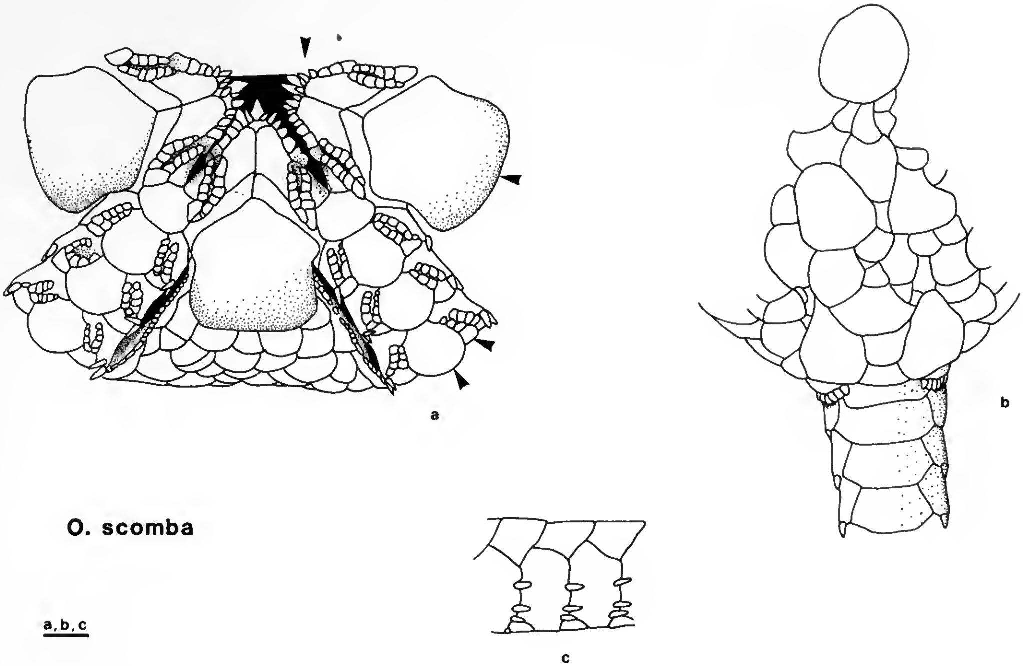


O. nitida

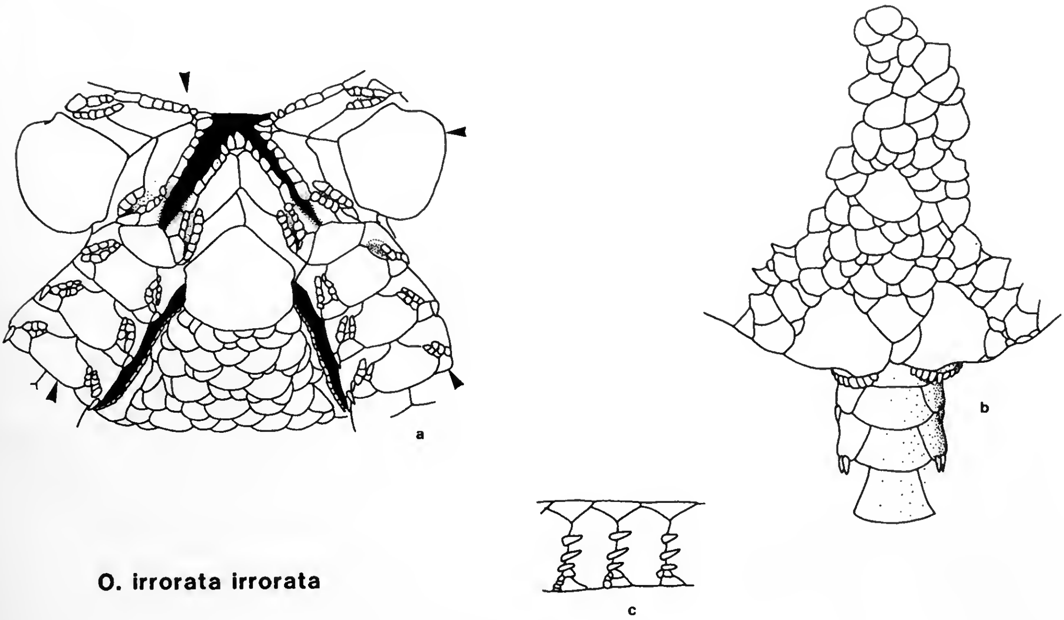


O. violainae

Fig. 45 Ophiuridae: Ophiurinae. *Ophiura*. Captions as in Fig. 42.



O. scomba



O. irrorata irrorata

Fig. 46 Ophiuridae: Ophiurinae. *Ophiura*. Captions as in Fig. 42.

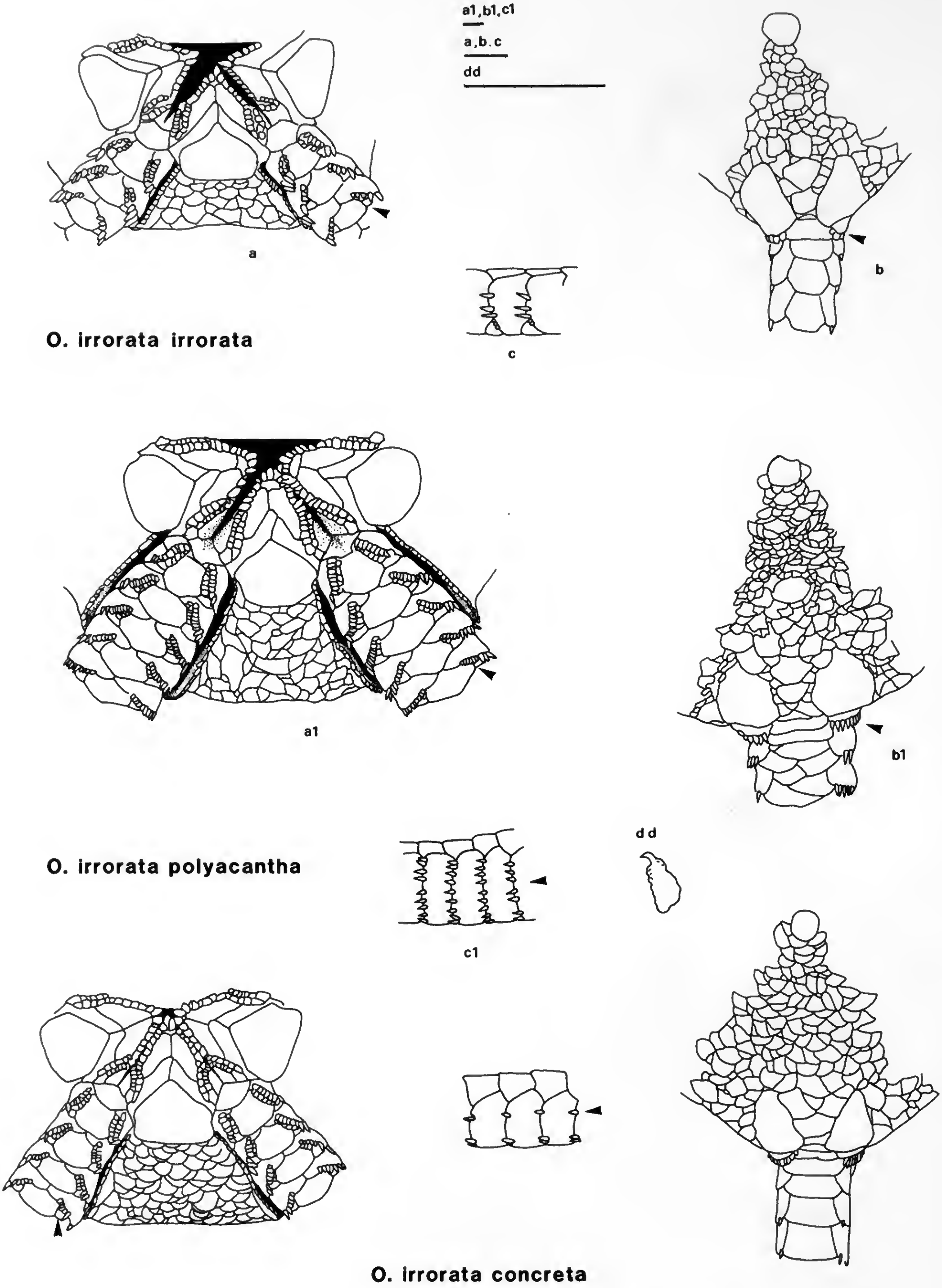
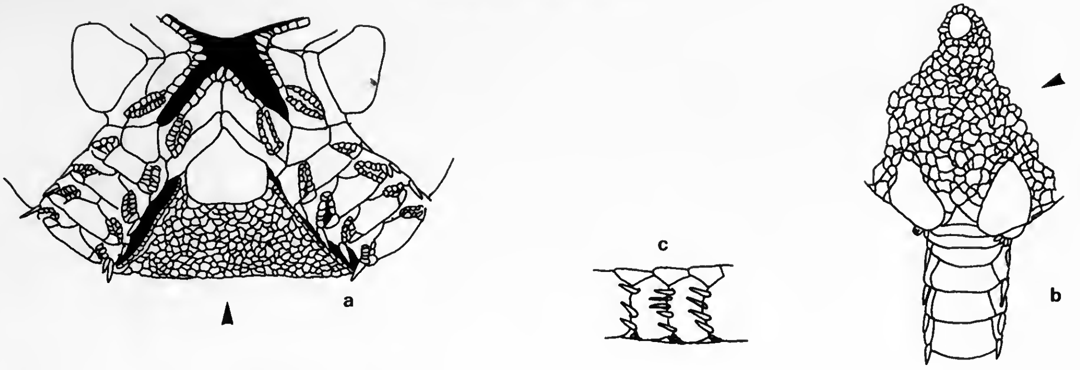
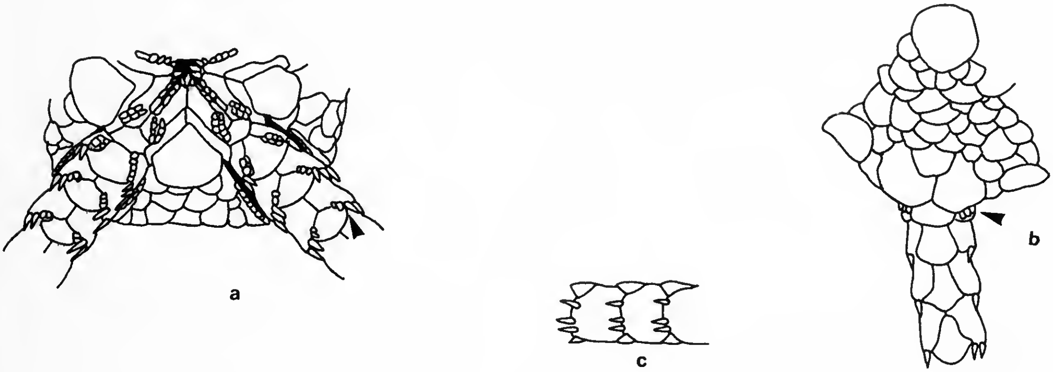


Fig. 47 Ophiuridae: Ophiurinae. *Ophiura*. Captions a–c as in Fig. 42; d.d–distal arm spine.



O.irrorata loveni *



O. mundata

Ophiopleura inermis

Fig. 48 Ophiuridae: Ophiurinae. *Ophiura* and *Ophiopleura*. *Not described in text. Captions as in Fig. 42.

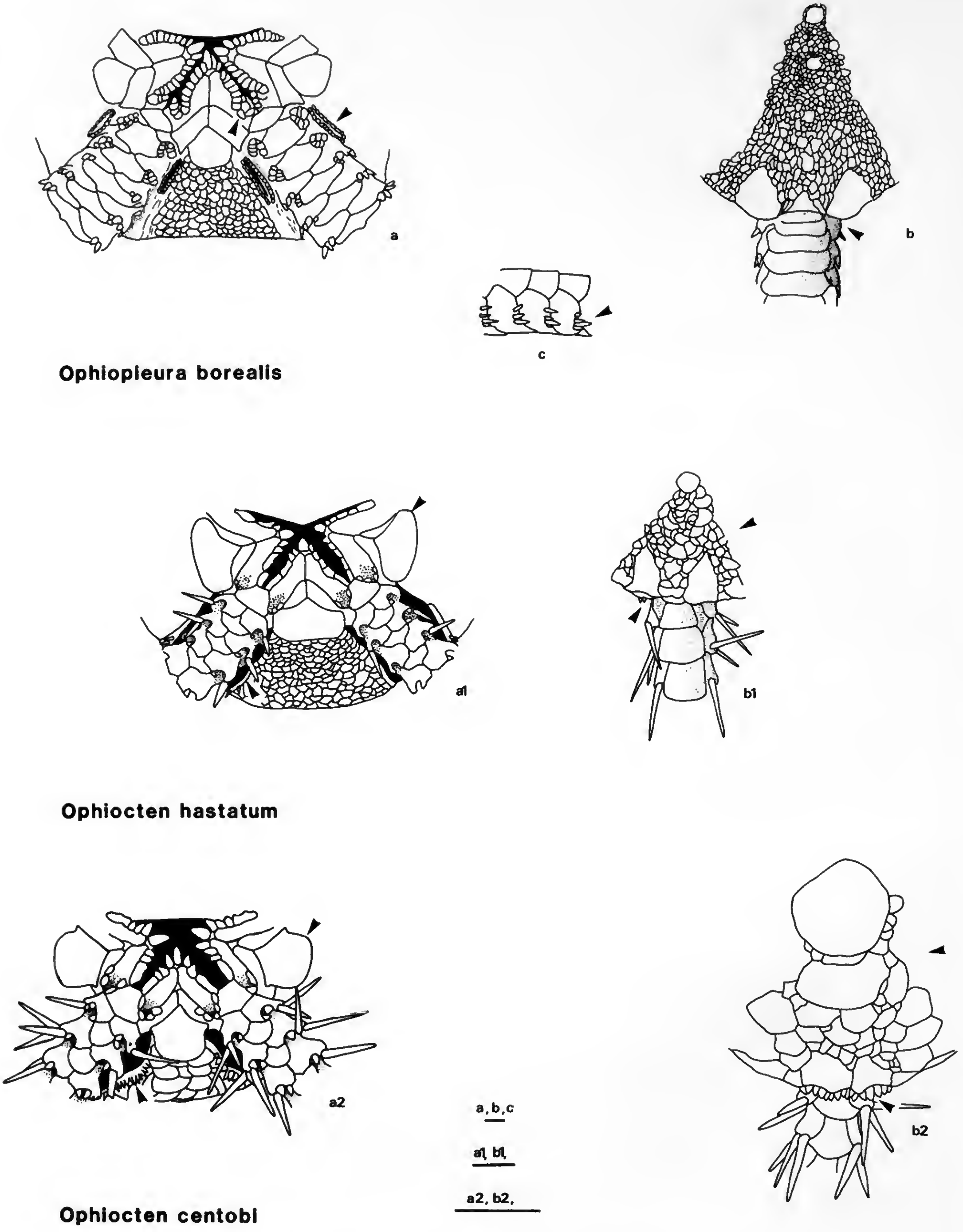
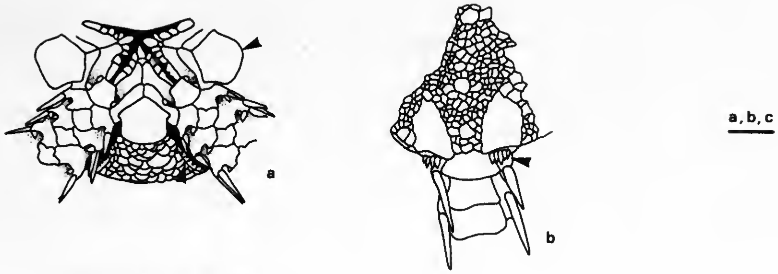
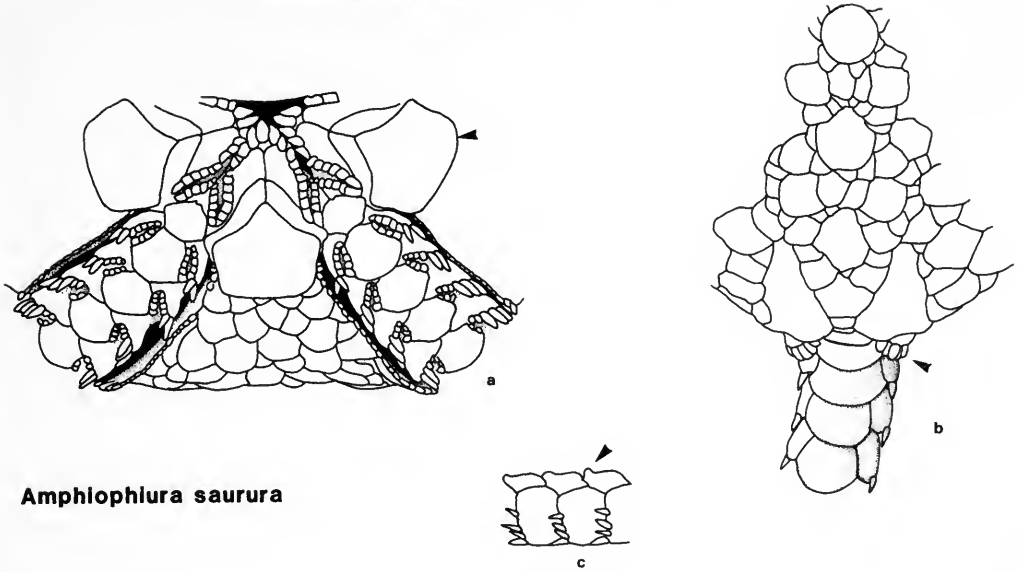


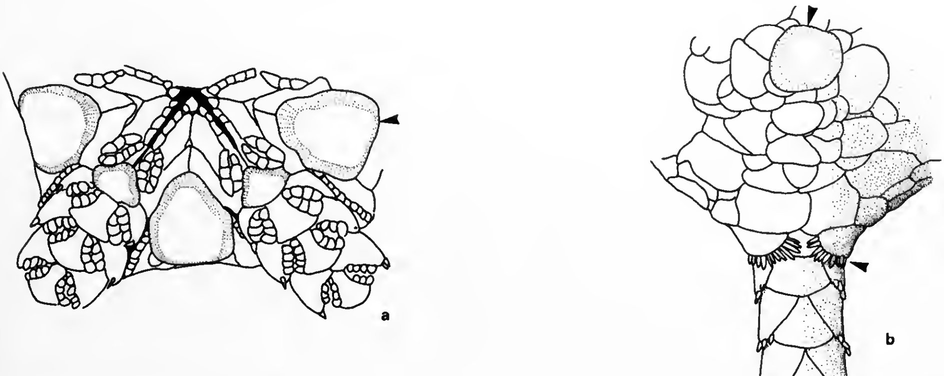
Fig. 49 Ophiuridae: Ophiurinae. *Ophiopleura* and *Ophiocten*. Captions as in Fig. 42.



Ophiocten gracilis



Amphiophiura saurura



Amphiophiura metabula

Fig. 50 Ophiuridae: Ophiurinae. *Ophiocten* and *Amphiophiura*. Captions as in Fig. 42.

Amphiophiura bullata complex

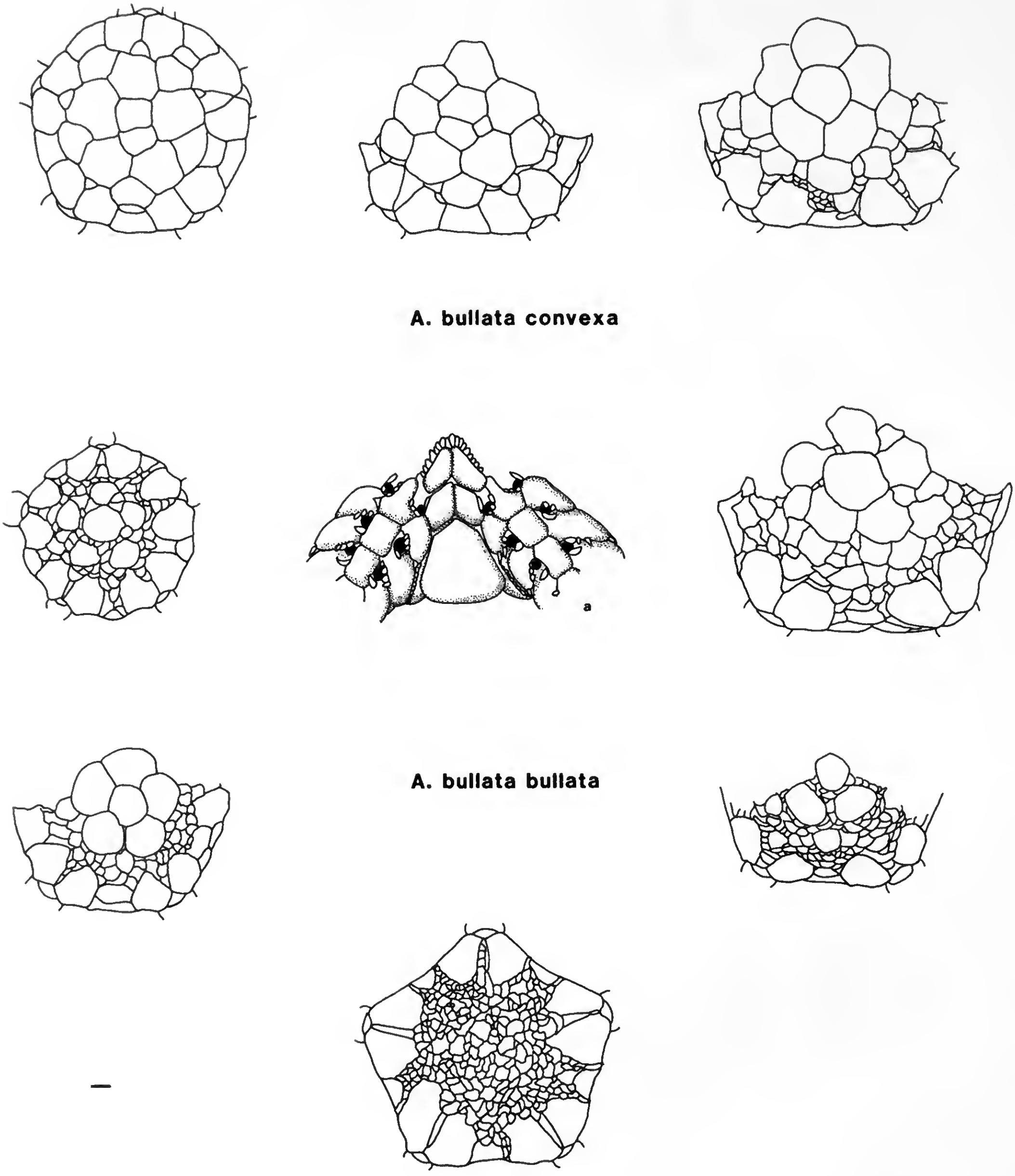


Fig. 51 Ophiuridae: Ophiurinae. *Amphiophiura bullata* complex: (a) ventral view of disk; all other figures are dorsal views of disk.

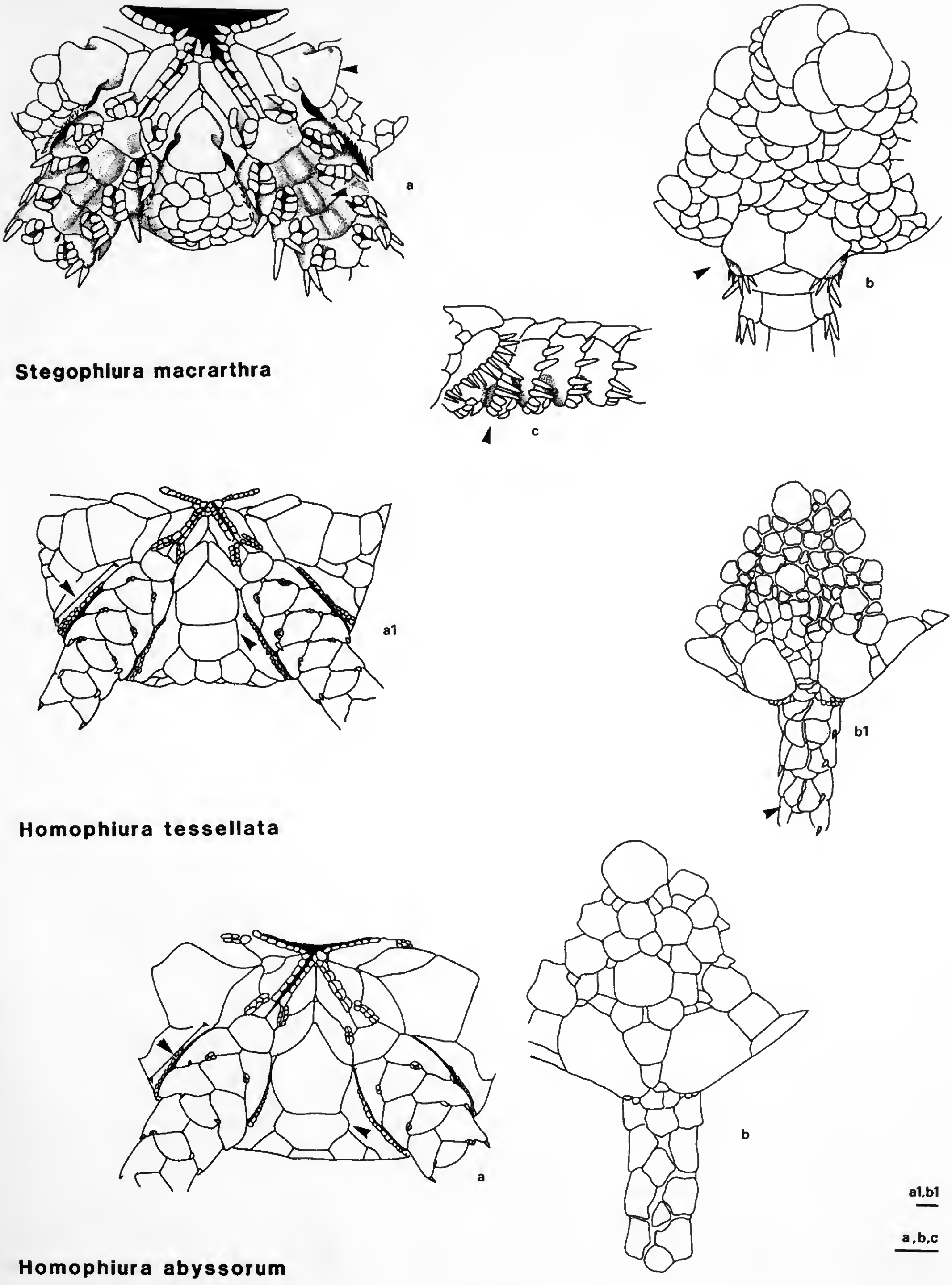
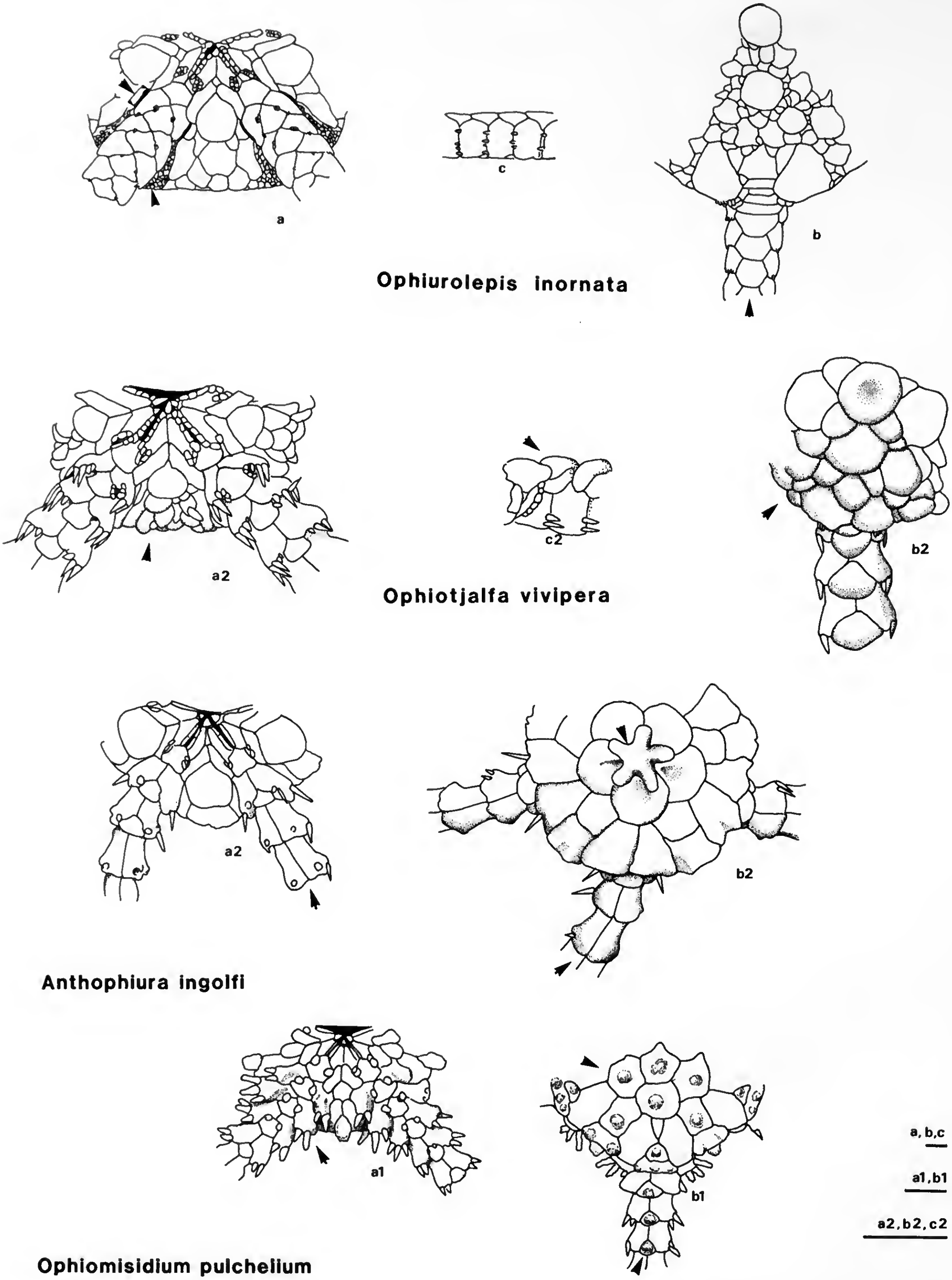


Fig. 52 Ophiuridae: Ophiurinae. *Stegophiura* and *Homophiura*. Captions as in Fig. 42.



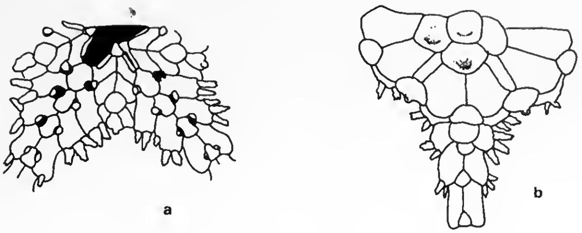
Ophiurolepis inornata

Ophiotjalfa vivipera

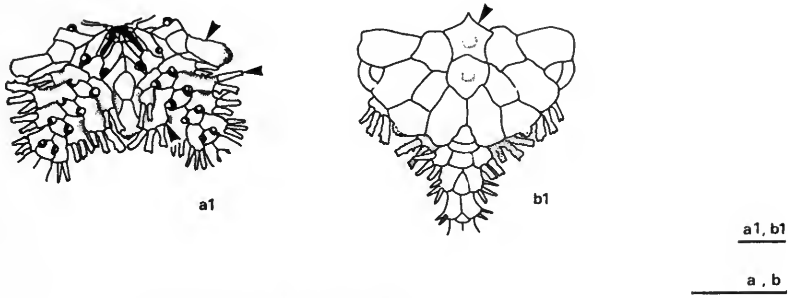
Anthophiura ingolfi

Ophiomisidium pulchellum

Fig. 53 Ophiuridae: Ophiurinae. *Ophiurolepis*, *Ophiotjalfa*, *Anthophiura* and *Ophiomisidium*. Captions as in Fig. 42.



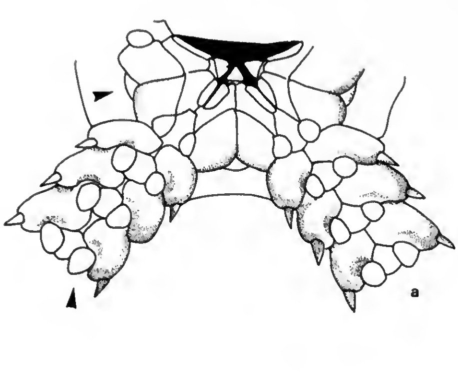
Ophiomisidium speciosum



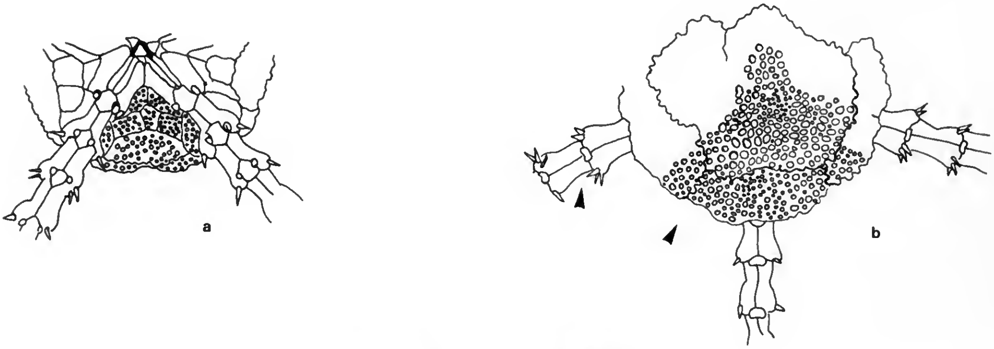
Ophiophycis mirabilis

Ophiambix meteoris **Ophiambix devaneyi**

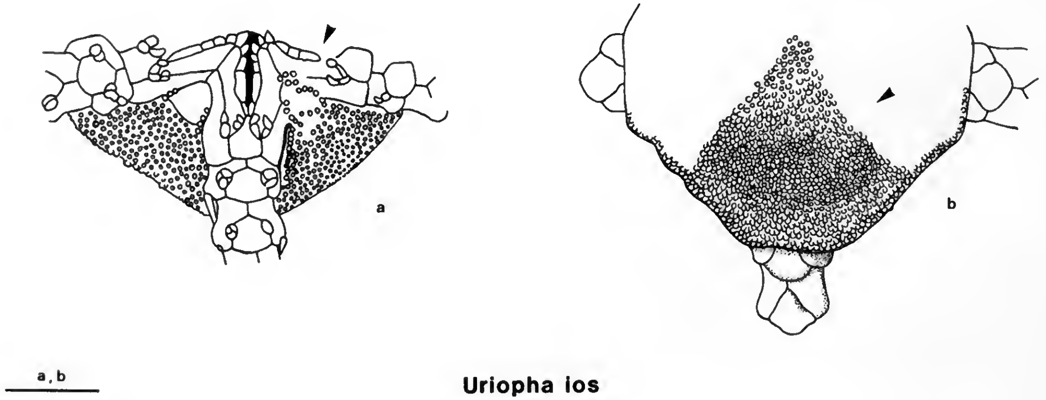
Fig. 54 Ophiuridae: Ophiurinae. *Ophiomisidium, Ophiophycis* and *Ophiambix*. Captions as in Fig. 42.



Ophiotypa simplex



Perlophiura profundissima



Uriopha ios

Fig. 55 Ophiuridae: Ophiurinae. *Ophiotypa, Perlophiura* and *Uriopha*. Captions as in Fig. 42.

Ophiura (Dictenophiura) carnea Lütken, 1858
Fig. 42

Ophiura carnea Lütken, 1858: 41; M. Sars, 1861: 24; Farran, 1913: 29; Mortensen, 1927: 243; Hertz, 1927*a*: 69; Gage *et al.*, 1983: 297.
Ophioglypha carnea: Lyman, 1865: 10; Grieg, 1893: 6; Marenzeller, 1893: 15; Koehler, 1896: 203; 1896: 241; 1898: 35; Grieg, 1902: 10; Grieg, 1905: 159; Koehler, 1906: 6; 1907: 260; Grieg, 1912: 8.
Dictenophiura carnea: H. L. Clark, 1923: 361.
Ophiura (Dictenophiura) carnea: Mortensen, 1933*a*: 81–82; Madsen, 1947: 13–14; 1970: 234.

MATERIAL STUDIED. **SMBA:** RRS *Challenger II* Stn ES2 55°04′N: 12°33′W 2857 m 1 specimen; AT 194 57°21′N: 11°10′W 630 m 1 specimen.
BMNH: *Sarsia* Bjornfjord Norway 120 m 1 specimen.

The disk is round to subpentagonal, high with almost vertical sides; covered with many plates amongst which the centrodorsal and primary plates are usually distinct; diameter up to 8 mm. The radial shields are rounded to teardrop shaped, contiguous distally about equal to a quarter of the disk radius in length, often relative smaller in larger specimens. The arm combs are prominent, extending up toward the dorsal surface of the disk; both the inner and outer comb are visible, the outer comb spinelets are conical and slightly rounded, the inner ones short and pointed. Within the notch of the arm combs are several arm plates, the innermost one sometimes indented medially or occasionally divided into two halves by a suture.

There is one pointed apical papilla flanked by one spine-like and two block-like oral papillae. The second oral tentacle pore opens outside the mouth slit and is armed with 4–5 rounded tentacle scales on each side. The adoral shields are thin, slightly bowed in appearance due to an indentation opposite the oral tentacle pore. The oral shield is approximately pentagonal with an obtuse proximal angle and a straight or convex distal edge, the shield is long extending just over half-way to the edge of the disk. The genital papillae are small, pointed, merging distally with the arm comb spinelets.

The arms are short, 2–4 times the disk diameter. The arm plates are textured with small fine inclusions in the matrix of the plate. The dorsal arm plates are fan shaped and contiguous only on the first 2–3 arm segments, the plates in profile appear to be slightly swollen. The first ventral arm plate appears trapezoidal or slightly pentagonal while the subsequent plates become more rounded with an obtuse proximal angle and a rounded distal edge; they are separated from one another. The proximal tentacle pores are large with rounded tentacle scales becoming scale-like on the proximal edge of the pore and number as follows: AP1: L2–3, V2; AP2: L1, V1; AP3+: L1, V0. There are three small, pointed arm spines; one towards the dorsal surface and the other two adjacent to the tentacle pores.

REMARKS. H. L. Clark (1923) erected *Dictenophiura* as a genus primarily characterised by the median division of the most proximal dorsal arm plate. As noted by other authors (Mortensen, 1933*a*; Madsen, 1970) this is not a consistent character, but Madsen considered that *Dictenophiura* should be retained as a subgenus a view shared here. *O. carnea* is compared with other bathyal species of *Ophiura* in Table 3.

DISTRIBUTION. *O. carnea* has been recorded from the Faeroes and Norway south to the Cape Verde Islands and the Mediterranean with a bathymetric range of 40–2857 m.

Ophiura (Ophiura) imprudens (Koehler, 1906)
Fig. 42

Ophioglypha imprudens Koehler, 1906: 8–10; 1907: 256.
Ophiura imprudens: Gage *et al.*, 1983: 298.

MATERIAL STUDIED. **MNHN:** *Travailleur & Talisman* 13 Aout 1883 Stn 123 38°23′N: 31°10′W 560 m HOLOTYPE.
SMBA: RRS *Challenger II*: Stn ES 113 57°18′N: 14°07′W 168 m 6 specimens.

The disk is round, flat, covered with relatively large plates amongst which the centrodorsal and primary radial plates are distinct; diameter up to 7 mm. The radial shields are large, just over half the disk radius in length, longer than broad; contiguous or sometimes overlapping. The outer arm comb consists of stout spinelets, the inner comb of smaller ones. The dorsal arm plate upon which the inner comb arises, is nearly vertical on the side of the disk.

Table 3 Comparison of bathyal species of *Ophiura*. l = length, b = breadth, dr = disk radius

	RADIAL SHIELDS	ARM COMBS	VENTRAL ARM PLATE SHAPE	ORAL SHIELD
O. albida	large, $l > b$; contiguous distally	outer & inner present; 10–12 spinelets in outer comb	rounded triangular, contiguous	rounded pentagonal $l > b$; $l \geqslant \frac{1}{4}$ dr
O. sarsi (Fig. 43)	large, $l > b$; just contiguous distally	outer & inner comb present; 9–10 spinelets in outer comb	wide triangular, contiguous	rounded pentagonal, $l > b$; $l > \frac{1}{4}$ dr
O. imprudens (Fig. 42)	large, $l > b$; contiguous over most their length	outer & inner comb present	rounded triangular, separated	rounded pentagonal, $l > b$; $l = \frac{1}{2}$ dr
O. robusta (Fig. 43)	small, $l = b$; separated	irregularly arranged; 8–10 spinelets with supplementary spinelets on DAP & R.S.	slightly rectangular only 1–3 contiguous	pentagonal—arrow shaped $l \simeq b$; $l < \frac{1}{4}$ dr.
O. carnea (Fig. 42)	small, $l \geqslant b$; contiguous	comb almost vertical; 12 spinelets in outer comb	rounded triangular separated	rounded elongated pentagonal, $l > b$; $l \geqslant \frac{1}{2}$ dr.

The jaw appears to be depressed just distal to the apex. There is one pointed apical papilla flanked on each side by 3 oral papillae, broadening progressively from spine-like to block-like. The second oral tentacle pore is large with 4–5 rounded tentacle scales on each side. The adoral shields are about 3 times longer than broad and indented in the region of the second oral tentacle pore. The oral shield is rounded with an acute proximal angle. The genital slits are lined with relatively large pointed papillae.

The arm length is about three times the disk diameter. The dorsal arm plates are fan shaped to rounded triangular and contiguous proximally. The first ventral arm plate is triangular, subsequent ones pentagonal with the distal edge becoming more convex distally, separated along the length of the arm; the proximal ones appear to be slightly swollen. The proximal tentacle pores are large and armed with rounded tentacle scales which number as follows: A.P.1: L2–3, V2–3; A.P.2: L2, V1–2; A.P.3: L1, V1; A.P.4+: L1, V0; the distal pores appear to lack scales. There are three equally spaced pointed arm spines on the proximal segments, but they are lacking on the distalmost segments.

REMARKS. *O. imprudens* is included because it has not been figured satisfactorily and as bathyal species its distribution may extend to 1000 m. It is compared with other bathyal species of *Ophiura* in Table 3. *O. carnea* most closely resembles it and they may be conspecific.

DISTRIBUTION. This species has been recorded from the Rockall Trough and off the Azores with a bathymetric range of 168–560 m.

Ophiura (Ophiura) ljungmani (Lyman, 1878)

Fig. 44

Ophioglypha ljungmani Lyman, 1878: 71; 1882: 44–45; 1883: 241; Verrill, 1885: 544; Koehler, 1896*a*: 71; H. L. Clark, 1901: 243; Koehler, 1907: 263; 1909: 152; 1914: 21.

Ophioglypha lepida Lyman, 1878: 70; 1882: 43–44; Koehler, 1914: 20.

Ophioglypha ljungmani var. spinulosa Verrill, 1885*b*: 543.

Ophioglypha thouleti Koehler, 1896*a*: 69; 1909: 158.

Ophiura lepida: Meissner, 1901: 925.

Ophiura ljungmani: Farran, 1913: 31; Mortensen, 1927: 240–242; 1932: 33; Schoener, 1967*a*: 647–650; Tommasi, 1970: 79–80; Lightfoot, Tyler & Gage, 1979: 970–971; Gage & Tyler, 1981: 153–161; Gage *et al.*, 1983: 298–299; Bartsch, 1983*b*: 17–18.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 122 9°5′S: 34°49′W 630 m PARATYPE; HMS *Challenger* Stn 46 40°17′N: 66°48′W 2469 m HOLOTYPE of *O. lepida;* HMS *Challenger* Stn 76 38°11′N: 27°9′W 1646 m.

COB: BIOGAS Stn 1: DS10 2240 m 11 specimens; DS11 2205 m 6 specimens; DS13 2165 m 30 specimens; DS15 2246 m 45 specimens; DS16 2325 m 36 specimens; DS17 2103 m 9 specimens; DS18 2138 m 15 specimens; DS32 2138 m 41 specimens; DS35 2226 m 6 specimens; DS36 2147 m 15 specimens; DS37 2110 m 13 specimens; DS38 2138 m 10 specimens; DS61 2250 m 2 specimens; DS62 2175 m 47 specimens; DS63 2126 m 35 specimens; Ds64 2156 m 52 specimens; DS71 2194 m 11 specimens; CV8 2180 m 6 specimens; CV09 2119 m 4 specimens; CV10 2108 m 45 specimens; CV20 2282 m 1 specimen; CV23 2034 m 11 specimens; CV24 2025 m 8 specimens; CV25 1985 m 13 specimens; CP01 2245 m 403 specimens; CP02 2177 m 2 specimens; CV39 2350 m 15 specimens; CP08 2177 m 244 specimens; CP26 2115 m 90 specimens; CP27 1920 m 1 specimen.

BIOGAS Stn 2: DS19 2865 m 73 specimens; DS41 3548 m 1737 specimens; DS57 2906 m 13 specimens; DS58 2775 m 21 specimens; DS59 2790 m 3 specimens; DS60 3742 m 2 specimens; DS66 3480 m 1 specimen; DS73 2805 m 4 specimens; DS74 2777 m 11 specimens; DS75 3250 m 6 specimens; CV37 3000 m 6 specimens; CV38 2695 m 2 specimens; CV40 2860 m 2 specimens; CP09 2171 m 56 specimens; CP10 2878 m 13 specimens; CP11 3056 m 5 specimens; CP12 2925 m 2 specimens; CP28 3380 m 3 specimens.

BIOGAS Stn 3: DS22 4144 m 2 specimens; DS67 4150 m 5 specimens.

BIOGAS Stn 6: DS25 2096 m 29 specimens; DS26 2076 m 216 specimens; DS49 1845 m 23 specimens; DS50 2124 m 43 specimens; DS51 2430 m 218 specimens; DS52 2006 m 177 specimens; DS70 2150 m 7 specimens; DS86 1950 m 81 specimens; DS87 1913 m 112 specimens; DS88 1894 m 2 specimens; CV16 1909 m 16 specimens; CV32 1895 m 2 specimens; CV33 1913 m 7 specimens; CP07 2170 m 112 specimens; CP23 1980 m 18 specimens; CP24 1995 m 10 specimens; CP25 1894 m 12 specimens.

BIOGAS Stn HZ: DS04 1100 m 2 specimens; DS05 2210 m 6 specimens; DS07 2170 m 6 specimens; DS09 2130 8 specimens; DS14 1560 m 24 specimens; CW03 2160 m 21 specimens; CV11 2141 m 8 specimens; CV22 1331 m 9 specimens.

IOS: *Discovery* Investigations Stn 8511/1 41°55′N: 11°15′W 2384–2399 m 1 specimen; Stn 8970 31°30·4′N: 11°4·4′W–31°30·0′N: 11°3·8′W 12 specimens; Stn 9021 30°04·2′N: 11°51·7′W 2122–2173 10 specimens; Stn 9029 32°14·3′N: 11°2·8′W–32°14·1′N: 11°2·5′W 1886–1835 m 13 specimens; Stn 9042 45°15·0′N: 11°22·0′W 1662–1541 m 5 specimens; Stn 9640/1 50°3·2′N: 13°50·6′W 34 specimens.

SMBA: RRS *Challenger II:* Stn ES8 54°45′N: 12°10′W 2900 m 10 specimens; Stn ES10 56°37′N: 10°04′W 2540 m 6120 juvenile specimens; Stn SBC46 55°04′N: 12°06′W 2875 m 3 specimens; Stn ES56 54°40′N: 12°16′W 2886 m 688 specimens; Stn SBC68 58°42′N: 09°43′W 1800 m 1 juvenile specimen.

The disk is pentagonal, box-like with steep sides; covered by small plates amongst which it is possible to distinguish the centrodorsal plate but not usually the primary radial plates; disk diameter up to 10 mm. There are simple spinelets scattered over the dorsal surface of the disk although they are often rubbed off in preserved specimens. The radial shields are longer than broad, extending up to half the radius of the disk in length; each pair separated by a wedge of plates. The arm combs are distinct, extending on to the dorsal side of the arm; the outer comb spinelets are thin and pointed, the inner ones small and pointed.

There are one or two pointed apical papillae at the apex of the jaw flanked on each side by 6–7 pointed oral papillae. The second oral tentacle pore is large, opening superficially away from the mouth, and is armed with 4 rounded tentacle scales on the outer edge, 6 on the inner. The adoral shields are long, narrow and slightly flared distally. The oral shield has an obtuse proximal angle, indented lateral sides and a convex distal edge; the distal portion of the shield appears enlarged, extending approximately half-way to the disk edge. The genital slits are edged with rounded papillae proximally which become more elongated and spine-like until they merge at the edge with the arm comb-spinelets.

The arms are about 3–5 times the disk diameter, and high slightly compressed laterally. The dorsal arm plates are longer than broad, rectangular proximally becoming fan shaped, and contiguous over most of the arm. The ventral arm plates are approximately rounded pentagonal in shape becoming broader than long and rectangular on distal segments and separated except occasionally for the second and third ventral plates. The tentacle pores are large and open proximally becoming smaller distally armed with rounded slightly elongated tentacle scales; they number as follows: A.P.1: L2–4, V3–5; A.P.2: L2–4, V4; A.P.3: L2–3, V0–3; A.P.4: L1–3, V0–2; A.P.5: L2, V0–1; A.P.6+: L+2, V0. Small specimens usually have tentacle scale numbers in the lower part of the range. There are three pointed arm spines, the longest one located dorsally and nearly equal in length to segment, the other two much shorter and located on the ventral portion of the arm adjacent to the tentacle pores.

REMARKS. *O. ljungmani* can be distinguished by the shape of the disk, the possession of disk spinelets, the form of the arm comb, the large tentacle pores, the shape of the oral shields and the arrangement of the arm spines. See Schoener (1967) and Gage & Tyler (1981) for a discussion of the recognition of juvenile stages.

DISTRIBUTION. *O. ljungmani* is a common species found on both sides of the North Atlantic often in large numbers. In the west it has been recorded from off Florida north to the Labrador Basin with a bathymetric range of 101–2750 m and in the east from SE. Iceland to North Africa with a bathymetric range of 777–4150 m. It has also been recorded off Pernambuco, Brazil, 736 m, and southern Africa.

Ophiura flagellata (Lyman, 1878)

Fig. 44

Ophioglypha flagellata Lyman, 1878: 69; 1882: 42; Koehler, 1904: 56; 1907: 261.
Ophiura flagellata: H. L. Clark, 1911: 60; 1913: 208; Matsumoto, 1915: 81; H. L. Clark, 1915: 320; Koehler, 1922: 375–377.
Gymnophiura coerulescens Lütken & Mortensen, 1899: 114.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 232 Sagami Bay, Japan 636 m HOLOTYPE; *Albatross* Stn 3431 23°59′N: 108°40′W 1791 m SYNTYPE of *Gymnophiura coerulescens* Lütken & Mortensen, 1899.

The disk is round to subpentagonal, lacking calcareous plates in the centre and often with poorly developed plates around the periphery; in some preserved specimens there appears to be interradial rays of thickened skin; diameter up to 24 mm. The radial shields are small, rounded often with only the tips visible. The arm combs are well developed; consisting of long pointed spinelets. The ventral interradial area is covered with distinct plates.

There is one rounded apical papilla, sometimes two, flanked on each side by 4–5 rounded or pointed apical papillae. The second oral tentacle pore is large lined on each side by 4–6 long rounded tentacle scales which sometimes nearly form a continuous series with the oral papillae. The adoral shields are longer than broad slightly flared distally. The oral shield is arrow shaped or light-bulb shaped and is about a quarter of the disk radius in length. The genital papillae are thin and spiniform.

The arms are 3–4 times as long as the disk diameter. The dorsal arm plates are wider than long, slightly rectangular, and contiguous. The first ventral arm plate is irregularly hexagonal, the second slightly trapezoidal with a convex distal edge, subsequent plates are wider than long axe shaped or squat bell shaped; the proximal plates are contiguous. The proximal tentacle pores are large armed with long rounded scales of which those on the lateral plate are the larger; they number as follows: A.P. 1–2: L4, V3–4; A.P. 3–4: L3, V2–3; A.P.5+: L3, V0–1. There are 3–4 flat, distally widened, pointed arm spines of which the dorsalmost one is the largest, often equal in length to 2 segments.

REMARKS. *O. flagellata* can be recognised by the poorly calcified disk plates, the well developed arm combs, and the shape of the oral shield.

DISTRIBUTION. In the North Atlantic this species has only been recorded from south of the Canaries at depths of 932–2330 m. It is also known from South Africa and the Pacific Ocean off Mexico.

Ophiura (Ophiuroglypha) clemens (Koehler, 1904)

Fig. 45

Ophioglypha clemens Koehler, 1904: 51; 1907: 291.
Ophiura clemens: H. L. Clark, 1915: 319; Matsumoto, 1917: 268; Koehler, 1922: 374–375.

MATERIAL STUDIED. **MNHN:** *Travailleur & Talisman* 14th Aout 1881 Stn 38 41°11′N: 10°38′W, 4 specimens.

The disk is round, slightly domed, covered in large plates amongst which it is possible to distinguish the centrodorsal and primary radial plates; diameter up to 8 mm. The radial shields are approximately triangular, longer than broad just under half the disk radius in length, and are contiguous only distally. The arm comb comprises a single row of rounded block-like spinelets which form a continuous fringe over the base of the arms.

There is one pointed apical papilla flanked on each side by 4–5 block-like oral papillae. The second oral tentacle pore is relatively large and extends almost to the mouth slit, with 5–6 rounded block-like tentacle scales on each edge. The adoral shields are longer than broad not flared distally. The oral shield is rounded

Table 4 Comparison of *Ophiura clemens, O. violainae* and *O. nitida*

SPECIES	ARM COMB	ORAL PAPILLAE	ORAL SHIELDS	ARM SPINES	PRIMARY PLATES
O. clemens	continuous fringe of block-like spinelets	blocklike, contiguous	rounded pentagonal	evenly spaced	no sculpting
O. violainae	continuous fringe of block-like spinelets	pointed, blocklike only distally	obtuse proximal angle, enlarged distal portion	evenly spaced	no sculpting
O. nitida	continuous fringe of conical spinelets	blocklike, contiguous	slightly arrow shaped	bunched on ventral portion of the arm	with a raised boss in centre of plate

pentagonal with an obtuse nearly acute proximal angle and a rounded distal edge, it extends less than halfway to the disk edge. The genital slits are edged with contiguous block-like papillae which merge with the arm comb spinelets.

The arms are 3–4 times the disk diameter. The dorsal arm plates are fan shaped with only the first 3 contiguous. Ventrally the proximal part of the arm appears flat. The first ventral arm plate is triangular or pentagonal with a slightly convex distal edge, the second is nearly rectangular and is longer than broad; subsequent plates are broadly pentagonal with a wide convex distal edge. Only the first three plates are contiguous. The tentacle pores are relatively large proximally, and armed with rounded block-like papillae, which number as follows: A.P.1: L4, V4; A.P.2: L3, V3; A.P.3: L3, V3; A.P.4: L2–3, V0; A.P.5: L1, V0; A.P.6+: L0, V0.

Occasionally on the second arm segment the distalmost inner tentacle scale may be enlarged to resemble a supplementary ventral arm plate. There are 3 short pointed arm spines positioned towards the ventral side of the lateral arm plate. Distally one of the arm spines is transformed into a hook.

REMARKS. *O. clemens* closely resembles *O. nitida* and *O. violainae*; see Table 4 for a comparison of these species.

DISTRIBUTION. Within the North Atlantic this species has been recorded from the Bay of Biscay at a depth of 1916 m. It has also been found in the Indo-West Pacific off the Philippines and East Indies.

Ophiura (Ophiura) nitida Mortensen, 1933*a*
Fig. 45

Ophiura nitida Mortensen 1933*a*: 84–86.

MATERIAL STUDIED. **ZMC:** *Ingolf* Stn 18, 61°44′N: 30°29′W, 2065 m. HOLOTYPE and PARATYPE.

The disk is round, slightly indented interradially, flat, covered with large plates amongst which the centrodorsal and primary radial plates are distinct each with a raised boss in the centre; diameter up to 13 mm. The radial shields are slightly longer than broad, up to a quarter the disk radius in length, contiguous along the distal portion. The arm combs just protruding from beneath the radial shields form a continuous fringe over the base of the arms; there is only a single row of conical, sometimes blunt arm comb spinelets.

There is one, sometimes two, blunt apical papilla at the apex of the jaw, flanked by 3–4 pointed, block-like oral papillae. The adoral shields are long and broad. The second oral tentacle pore opens outside the mouth and is armed with 5–7 block-like scales on the inner side and 5 on the outer, the distalmost of which is broad and flap-like. The oral shield is approximately arrow shaped with an obtuse proximal angle and a convex edge. The genital papillae are small and blunt.

The arms are 2–3 times the disk diameter, the ventral side is nearly flat. The dorsal arm plates are fan shaped with only the first two plates being contiguous. The first two ventral arm plates are trapezoidal and contiguous the subsequent plates are pentagonal with an obtuse proximal angle and a gently convex distal edge. Proximal tentacle pores are large; armed with round block-like papillae which number as follows: A.P.1: L4–5, V5; A.P.2: L4, V4; A.P.3: L4, V3; A.P.4: L4, V3; A.P.5–6: L3, V2; A.P.7+: L1, V0; A.P.12+: L0, V0. There are three conical arm spines situated close together towards the ventral part of the arm.

REMARKS. *O. nitida* can be recognised by the form of the primary disk plates, the form of the arm comb, and the arrangement of the arm spines. See Table 4 for comparison with *O. clemens* and *O. nitida*.

DISTRIBUTION. This species has only been recorded from the type locality on the Rekjanes Ridge, SW of Iceland at 2065 m.

Ophiura (Ophiura) violainae (Cherbonnier & Sibuet, 1972)

Fig. 45

Homalophiura violainae Cherbonnier & Sibuet, 1972: 1378.

MATERIAL STUDIED. **MNHN:** 'Noratlante' Stn 124, 47°29.6'N: 8°22.6'W, 2210 m. HOLOTYPE.
IOS: *Discovery* Investigations Stn 8511/1, 41°55'N: 11°15'W, 2384–2399 m. 1 specimen.

The disk is round, flat and covered by relatively large plates; the centrodorsal and the primary radial plates are conspicuous being larger than the other plates; diameter 9·5 mm. The radial shields are longer than broad, separated or contiguous only distally and extending just over a quarter of the disk radius in length. The arm comb consists of a single row of block-like spinelets which form a continuous fringe over the base of the arm.

There is one pointed apical papilla flanked on each side by 5–6 pointed oral papillae which become slightly block-like distally. The second oral tentacle pore is large and extends towards the mouth slit with 4–5 rounded tentacle scales on each side. The adoral shields are long and narrow slightly flared distally. The oral shield has an obtuse proximal angle and a convex distal edge, the distal portion is enlarged; the shield is about one-third of the disk radius in length. The genital papillae are low and block-like.

The arms are about 2–3 times the disk diameter. The dorsal arm plates are fan shaped with only the first three contiguous. The first three ventral arm plates are trapezoidal slightly longer than broad subsequent plates are more axe-shaped or slightly rectangular and are broader than long. Only the first four arm segments have distinct tentacle pores, which are armed with rounded tentacles and number as follows: A.P.1–2: L3–4, V3–4; A.P.3: L3, V3; A.P.4: L2–3, V0–2; A.P.5+: L1, V0. There are 3 closely spaced short pointed arm spines.

REMARKS. *O. violainae* resembles *O. clemens* and *O. nitida*, the 3 are compared in Table 4. *O. violainae* is transferred from *Homalophiura* for the reasons given on p. 136.

DISTRIBUTION. This species has been recorded from the northern Bay of Biscay and off Portugal at depths of 2210–2399 m.

The *Ophiura irrorata* Group

This group of species and subspecies all share the character of an enlarged distal tentacle scale on the proximal tentacle pores, which resembles a supplementary ventral arm plate. Clark (1911), Koehler (1914) and Madsen (1956) commented that the species *Ophiura irrorata* appeared to be variable particularly in the degree of scaling of the disk and dimensions of the oral shield. This has led to many species being regarded as conspecific with *O. irrorata*, i.e. *O. grandis* (Verrill, 1894), *O. involuta* (Koehler, 1898), *O. orbiculata* (Lyman, 1878) and *O. tumulosa* (Lütken & Mtsn, 1899). In view of this degree of variation it was necessary to examine other species with this character to determine their status. The species in question are *O. concreta* (Koehler, 1901*b*), *O. loveni* (Lyman, 1878), *Ophiuroglypha lymani* Studer, *O. ossiculata* Koehler, 1922 and *O. plana* (Lükten & Mtsn, 1899).

The last three species appear to be distinct; they differ in the type of disk plates—usually swollen and not flat.

The other two species, however, differ only by the arrangement or number of arm spines, in all other respects they appear to be very similar to *O. irrorata*. I propose to reduce them to subspecies of *O. irrorata*, because number of arm spines or their arrangement on its own does not appear to be a specific character.

O. irrorata concreta can be recognised by the arrangement of the arm spines: the dorsalmost spine is well separated from the two ventrally placed ones. This feature appears to be constant over a wide range of sizes and geographical areas.

O. irrorata loveni is characterised by having 5— arm spines, also the disk is covered with small plates and the primary plates are well separated. Madsen (1956) pointed out that this latter character appeared to be just one extreme of variation found in *O. irrorata*. Certainly some of the specimens identified by Lyman (1878, 1882) as *O. loveni* are *O. irrorata irrorata* having small disk plates but only 3 arm spines.

O. irrorata polyacantha Mortensen, 1933*a* is maintained as a subspecies characterised by having 8–9 arm spines.

O. irrorata irrorata can be distinguished by having only 3 arm spines which are equally spaced and situated on the ventral part of the arm or the dorsalmost one is slightly separated and situated more dorsally.

An examination of the Atlantic specimens nominally referred to *O. irrorata* revealed that there were in fact two species *O. irrorata irrorata* and a new species *Ophiura scomba*. The latter can be distinguished by its swollen oral shield, the rounded proximal ventral arm plates and pointed proximal oral papillae. *O. scomba* also appears to be found at slightly shallower depths in the NE Atlantic 1595–2240 m although there is one record of it from 4406 m in the Bay of Biscay.

Ophiura (Ophiuroglypha) irrorata irrorata (Lyman, 1878)
Figs 46, 47

Ophioglypha irrorata Lyman, 1878: 73; 1882: 47; Koehler, 1896*a*: 67; 1896*c*: 241; Koehler, 1914: 18.
Ophioglypha grandis Verrill, 1894: 293.
Ophioglypha involuta Koehler, 1898: 61–63.
Ophioglypha tumulosa Lütken & Mortensen, 1899: 120.
Ophioglypha integra Koehler, 1908: 248.
Ophioglypha figurata Koehler, 1908: 251.
Ophiura irrorata: H. L. CLark, 1911: 62; 1915: 320; Matsumoto, 1917: 227; Grieg, 1921: 32; Koehler, 1922: 380; H. L. Clark, 1923: 358–359; Mortensen, 1927: 235; Hertz, 1927*a*: 86; Grieg, 1932: 32–33; Madsen, 1955: 11; 1956: 26; Baranova, 1957: 207; Belyaev, 1972: 5–20.
Homalophiura irrorata: Koehler, 1922*b*: 55.
Ophiuroglypha irrorata: Hertz, 1927: 86–87; Pawson, 1969: 52–54.
Ophiura (Ophiuroglypha) irrorata: Mortensen, 1933*a*: 86–87; A. M. Clark & Courtman-Stock, 1976: 197.

MATERIAL STUDIED. **BMNH:** HMS *Challenger*. Stn 143, 36°48′S: 19°24′E. 3475 m. HOLOTYPE; HMS *Challenger*. Stn 164, 34°13′S: 151°38′E. 738 m; HMS *Challenger*, Stn 160, 42°42′S: 134°10′E. 4680 m (as *O. loveni*); John Murray Expedition: Stn 62, Northern Arabian Sea, 1893 m, 5 specimens; Stn 135, Maldive Area, 2727 m, 1 specimen; Stn 26, Gulf of Aden, 2312 m, 35 specimens.
COB: BIOGAS, Stn 3: CP04, 3850 m, 1 specimen. BIOGAS, Stn 5: CV34, 4406 m.
IOS: *Discovery* Investigations: Stn 8511/1, 41°54.9′N: 11°15.7′W, 2384–2399 m, 1 specimen; Stn 8521/6, 20°47.9′N: 18°23.4′W, 3064–3070 m, 1 specimen; Stn 9042, 45°15.0′N: 11°22.0′W, 1660–1541 m, 2 specimens.
RSM: 1921 143/1233, *Scotia* Stn 313, 62°10′S: 41°20′W, 3195 m. HOLOTYPE of *Ophioglypha figurata* Koehler, 1908; 1921 143/1231, *Scotia* Stn 313, 62°10′S: 41°20′W, 3195 m. 2 SYNTYPES of *Ophioglypha integra*; 1921 143/1231, Stn 313, 2 SYNTYPES of *O. integra*.

The disk is pentagonal, flat and covered with small plates amongst which the centrodorsal and primary plates are often conspicuous; diameter up to 30 mm. The radial shields are small, longer than broad, triangular or teardrop shaped, less than a quarter of the disk radius in length. The arm combs are just visible, below the radial shields; arm comb spinelets block-like and only an outer comb appears to be present.

There are 1–4 apical papillae flanked on either side by up to 6–7 continuous block-like oral papillae, often, particularly in larger specimens, there are supernumerary papillae which lie dorsal the oral papillae, when looking at the ventral side. The second oral tentacle pore is large and long not opening into the mouth slit, with up to 8 or 9 block-like tentacle scales on each edge. The adoral shields are long and narrow about 4 times as long as broad. The oral shield is approximately pentagonal, extending less than half way to the disk edge. The genital slits are edged with contiguous block-like papillae.

The arms are 4–6 times the disk diameter, rounded and not high. The dorsal arm plates are fan shaped in small specimens becoming broad and rectangular in large ones, and contiguous at least on proximal joints. The first two ventral arm plates are approximately hexagonal the subsequent plates are more pentagonal with an obtuse proximal angle, distally diverging lateral edges and a convex distal edge, further out on the arm they become broader than long and more rectangular; only the first three plates are contiguous. The proximal tentacle pores are large, armed with up to 8 rounded tentacle scales on each edge, the distalmost scale of the inner edge is enlarged blocking off the pore, it reaches such a size that it can be mistaken for a supplementary ventral arm plate. This enlarged tentacle scale is found on most pores except perhaps the distalmost ones. There are three short, pointed arm spines situated on the ventral part of the arm or with one slightly separated and situated more dorsally than the others; on distal arm segments the middle spine may be transformed into a small hook.

Remarks. *O. irrorata* closely resembles *O. mundata* and *O. irrorata loveni* (Fig. 48). It can be distinguished from the former by the enlarged distal tentacle scale. The only feature which appears to separate it from *O. loveni* is the scaling of the disk, *O. irrorata loveni* having a disk covered with smaller plates than *O. irrorata* of the same size. Otherwise they appear to be very similar, a fact which Madsen (1956) noted suggesting that they may be conspecific. Mortensen (1933*a*) described a new variety of *O. irrorata*; *O. irrorata polyacantha* for two specimens collected by the *Ingolf* which had 9 arm spines evenly spaced on the lateral arm plate instead of the normal 3 arm spines.

Distribution. *O. irrorata irrorata* has been recorded from the Caribbean Sea, Atlantic, Indian, Southern and Pacific Oceans with a bathymetric range of 403–5870 m. In the North Atlantic it has been recorded from off Cape Cod and SW Iceland in the west and from the Bay of Biscay south to off North Africa, in the east.

Ophiura (Ophiuroglypha) irrorata polyacantha Mortensen, 1933*a*

Fig. 47

Ophiura (Ophiuroglypha) irrorata var. polyacantha Mortensen, 1933*a*: 87–88.
Homalophiura multispina Cherbonnier & Sibuet, 1972: 1379–1382.

Material studied. **MNHN:** Noratlante P43–B7 106, 58°30′N: 53°04.2′W, 3365 m. HOLOTYPE of *Homalophiura multispina*.
BMNH: HMS *Challenger*, Stn 158, SE Indian Ocean, 3290 m, 1 specimen originally described as *O. loveni?*

The disk is round to subpentagonal, covered with relatively large plates amongst which the larger primary plates are usually distinct although separated from one another by numerous smaller plates; diameter up to 23·5 mm. The radial shields are rounded, longer than or as long as broad, well separated, length less than a quarter the disk radius. The arm combs are just visible below the radial shields and comprise a single row of block-like spinelets.

There are 1–3 apical papillae flanked on either side by 6 or more contiguous block-like oral papillae which are often irregularly arranged. The second oral tentacle pore is large and runs to the edge of the mouth slit where it usually lies above the distal oral papilla although it can appear that the tentacle scales form a continuous series with the oral papillae. There are 7–8 rounded tentacle scales on each side with the distalmost tentacle scale much larger than the others. The adoral shields are narrow; indented in the region of the oral tentacle pore. The oral shield is rounded with an obtuse proximal angle. The genital papillae are block-like merging with the arm comb spinelets.

The arms are slightly high. The dorsal arm plates are wider than long, rectangular to trapezoidal, contiguous proximally; the proximal plates are irregular in shape and overlap each other obliquely. The first ventral arm plate is pentagonal or rhombic, the next 4–5 plates are rounded hexagonal and contiguous becoming slightly rhombic and separated. The tentacle pores are well developed proximally and armed with rounded tentacle scales the distalmost of which is the largest, resembling a supplementary ventral arm plate; the scales number as follows; A.P.1: L8–9, V6; A.P.2: L8–9, V5; A.P.3: L7, V4; A.P.4: L5, V3; A.P.5: L2–3, V1; A.P.6: 2–3, L1; A.P.7–8: L1, V1; A.P.8+: L0, V0. There are 9 short pointed arm spines proximally, 4–5 distally of which the middle one is transformed into a small hook.

Remarks. In many characters, with the main exception of the number of arm spines, *H. multispina* was similar to specimens of *Ophiura irrorata polyacantha*. The holotype of *H.*

multispina closely resembles the description and figures given by Mortensen (19332a) for *O. irrorata polyacantha* and, therefore, it was concluded that they are consubspecific.

DISTRIBUTION. *O. irrorata polyacantha* has been recorded from the Labrador Basin in the NW Atlantic at depths of 3051–3366 m.

Ophiura (Ophiuroglypha) irrorata concreta (Koehler, 1901*b*)

Fig. 47

Ophioglypha concreta Koehler, 1901*b*: 228; 1906: 7; 1907: 261; 1909: 148–149.
Ophiura concreta: H. L. CLark, 1915: 324; Mortensen, 1927: 235; Madsen, 1951: 116.

MATERIAL STUDIED. **MOM:** *Princesse Alice* 1901, Stn 1182, 14°47′N: 24°31′45″W, 2478 m, HOLOTYPE.
BMNH: C.S. *Monarch,* 47°32′N: 8°43′W, 2250 m, 1 specimen.
SAM: No. 22036 A 193, 33°49′S: 16°30′E, 2743 m, 4 specimens, 2096 19317, 33°50′S: 16°30′E, 2617 m, 2 specimens.

The disk is pentagonal, covered with relatively large plates amongst which the centrodorsal and primary radial plates are usually distinct although in some large specimens only the centrodorsal can be distinguished; disk diameter up to 20 mm. The radial shields are small, teardrop shaped, longer than broad and usually separated from one another by a row of large plates; they extend to about a third of the disk radius in length. The arm comb consists of a single row of contiguous block-like spinelets.

There are one to two pointed apical papillae flanked on each side by 6–7 oral papillae which are pointed proximally becoming rectangular and block-like distally. The second oral tentacle pore is large and opens into the mouth slit via a furrow. It is flanked on each side by 7 block-like tentacle scales which in some specimens form a continuous series with the oral papillae, while in others it lies above the distalmost oral papillae. The adoral shields are long and narrow indented distally adjacent to the second oral tentacle pore. The oral shield is pentagonal and as broad as long. The genital slits are edged with contiguous block-like papillae.

The arms are slightly ridged, about 3–4 times the disk diameter. The dorsal arm plates are approximately hexagonal, broader than long proximally becoming rectangular and longer than broad distally; they are contiguous along most of the arm. The first ventral arm plate is rounded, pentagonal, the second more rectangular with subsequent ones axe shaped; only the first 3–4 are contiguous. Proximal tentacle pores are large and armed with block-like tentacle scales; the distalmost scale on the inner edge is enlarged and blocking off the pore, it resembles a supplementary ventral arm plate. The tentacle scales number as follows: A.P.1: L5–6, V7; A.P.2: L6, V5–6; A.P.3: L5, V4; A.P.4: L5, V2–3; A.P.5: L3–4, V1–2; A.P.6: L3–4, V0–1; A.P.7: L3, V0–1; A.P.8–10: L3, V0; A.P.11+: L1, V0 (for large specimen dd$\geq$15 mm). There are 3 short rounded arm spines; the dorsalmost one is distinctly separated from the other two.

REMARKS. The character which distinguishes *O. irrorata concreta* is the arrangement of the arm spines. This feature is remarkably consistent over a wide geographical range.

DISTRIBUTION. *O. concreta* has been recorded from the Bay of Biscay, off the Cape Verde Is, and off South Africa at depths of 2250–2743 m.

Ophiura (Ophiura) scomba sp. nov

Figs 46 & 56a–d

Ophiura irrorata: Gage *et al.*, 1983: 297–298 [non *O. irrorata* Lyman, 1878].

MATERIAL STUDIED. HOLOTYPE: **SMBA:** RRS *Challenger II* AT 254, 58°26′N: 12°35′W, 1595 m.
PARATYPES: **SMBA:** AT 151, 57°21′N: 10°22′W, 2175 m, 2 specimens; AT 175, 57°19′N: 10°16′W, 2220 m, 1 specimen, AT 191, 56°00′N: 13°58′W, 2190 m, 59 specimens; AT 192, 57°21′N; 12°02′W, 1862 m, 220 specimens.
COB: BIOGAS Stn 1: CP01, 2245 m, 4 specimens; CP27, 1920 m, 1 specimen.
BIOGAS Stn 5: CV34, 4406 m, 1 specimen.
BIOGAS Stn 6: DS49, 1845 m, 1 specimen; CV16, 1909 m, 7 specimens; CP24, 1995 m, 1 specimen; CP25, 1894 m, 5 specimens.
IOS: *Discovery* Investigations, Stn 9029, 31°33.4′N: 11°04.8′W, 1886–1835 m.

The disk is pentagonal, flat and covered with large plates amongst which the centrodorsal and primary plates are usually distinctive; diameter up to 17 mm, the holotype has a d.d. of 13 mm. The radial shields are

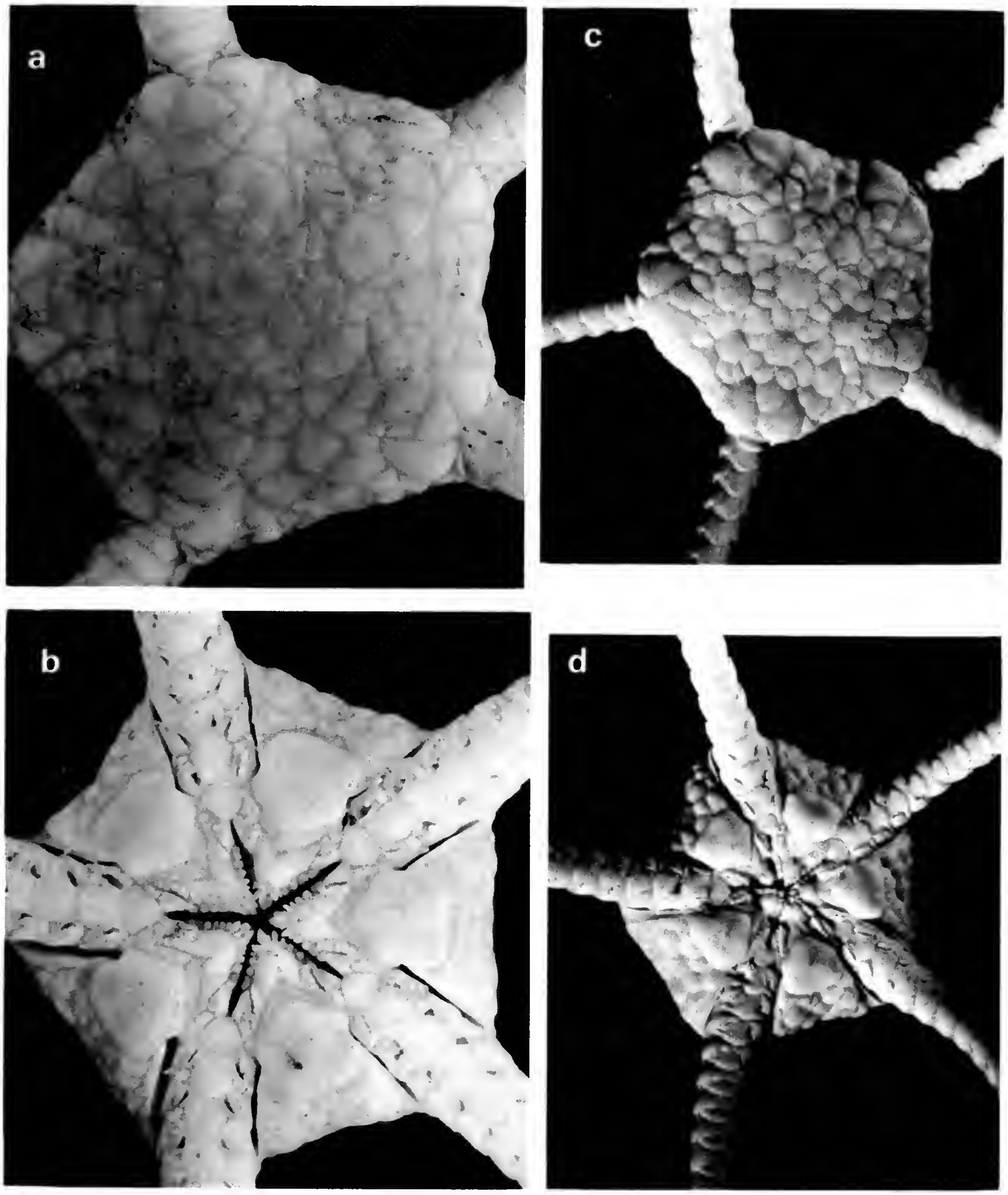


Fig. 56 Ophiuridae: Ophiurinae. a–d *Ophiura scomba* sp. nov.: (a) dorsal; (b) ventral view of holotype, d.d = 13 mm; (c) dorsal; (d) ventral view of paratype, d.d = 8·5 mm.

small, pear-shaped longer than broad, less than a quarter of the disk radius in length. The arm combs lie below the radial shields; the spinelets are block-like, contiguous and only an outer comb appears to be present.

There are 1–3 pointed apical papillae, usually one in smaller specimens, flanked by 5–6 oral papillae. The proximal oral papillae are pointed, distally they become block-like. The second oral tentacle pore arises outside the mouth slit; it is large with up to 7 contiguous block-like tentacle scales on each edge. The adoral shields are long and partially overlaid by the oral shield. The oral shield is usually pentagonal and as broad as long or slightly longer, swollen and stands out conspicuously.

The arms are 2–3 times the disk diameter. The dorsal arm plates proximally are broader than long and contiguous, distally they are longer than broad and fan shaped usually separated. The first ventral arm plate is approximately pentagonal with an indented proximal angle. Subsequent plates are trapezoidal with a very distinct convex distal edge. The first 2–5 ventral arm plates are contiguous, the number depends on the size of the specimen. The proximal tentacle pores are large and armed with rounded block-like tentacle scales, there is a large tentacle scale distally which blocks off the pore and resembles a supplementary ventral arm plate; the tentacle scales number as follows: A.P.1: L3–5, V3–4; A.P.2: L5–6, V2–5; A.P.3: L3–4, V1–3; A.P.4: L2–4, V1–3; A.P.5: L2–3, V0–2; A.P.6–7: L1–3, V0–1. There are 3 arm spines situated towards the ventral portion of the lateral arm plate.

REMARKS. For comparison with *O. irrorata* see the opening remarks.

DISTRIBUTION. *O. scomba* has been recorded from the NE Atlantic from the Rockall Trough south to off North Africa Morocco) at depths of 1595–4406 m.

The holotype and paratype material is deposited in the BMNH and paratype material is deposited in the Dunstaffnage Marine Research Laboratory, Oban; COB, Brest; IOS, Wormley and the MNHN Paris.

DERIVATION OF NAME. The specific name *scomba* is derived from the initials of the *SCO*ttish *M*arine *B*iological *A*ssociation.

Ophiura (Ophiura) mundata (Koehler, 1906)

Fig. 48

Ophioglypha mundata Koehler, 1906: 10–11; 1907: 257; 1909: 153.
Ophiura mundata Mortensen, 1933*a*: 88–89.
Ophiura irrorata Mortensen, 1927: 237. [non *Ophiura irrorata* (Lyman, 1878)].

MATERIAL STUDIED. **COB:** BIOGAS Stn 2, CV40, 2860 m, 1 specimen.
IOS: *Discovery* Investigations: Stn 8511/1, 41°55′N: 11°15′W, 2399–2384 m, 2 specimens; Stn 8512/4, 42°15′N: 11°36′W, 2281–2245 m, 1 specimen.

The disk is round to subpentagonal, covered with large plates amongst which the centrodorsal and sometimes the primary radial plates are distinguishable by their larger size; disk diameter up to 8 mm. The radial shields are longer than broad, just over a quarter the disk radius in length, contiguous distally. There is a single row of block-like contiguous arm comb spinelets opposite each side of the arms.

There is one, sometimes two, pointed apical papillae flanked on each side by 4–6 oral papillae, the proximal ones are pointed but the rest are block-like and contiguous. The second oral tentacle pore opens away from the mouth slit and is flanked by 3–5 block-like papillae on each side. The adoral shields are long and narrow. The oral shields are pentagonal, as long as broad, extending over about half of the interradial area in length. The genital papillae are block-like and contiguous, merging with the arm comb spinelets.

The arms are approximately 4 times the disk diameter and round. The dorsal arm plates are slightly fan shaped, often indented laterally; only the first 3–5 are contiguous. The first ventral arm plate is hexagonal, subsequent plates are wider than long and have an obtuse proximal angle and a convex distal edge; only the first two, sometimes the third and fourth depending on the size of the specimen, are contiguous. The tentacle pores are large and conspicuous only on the first 3–4 arm segments, and are armed with rounded tentacle scales and number as follows: A.P.1: L3–5, V3–5; A.P.2: L2–4, V1–4; A.P.3: L2–4, V0–2; A.P.4: L2–3, V0–1; A.P.5+: L1–2, V0.

There is no enlarged distal tentacle scale as in *O. irrorata*. There are three short pointed arm spines equally spaced or sometimes the dorsalmost spine is closer to the dorsal side and slightly distanced from the other spines.

Remarks. This species resembles *O. irrorata* but differs primarily because it lacks the enlarged distal tentacle scale. The dorsal scaling of the disk is coarser than in *O. irrorata. O. concreta* could also be confused with *O. mundata*; here the main difference lies in arrangement of the arm spines—in *O. mundata* the spines are equally spaced while in *O. concreta* they are grouped together towards the ventral side of the arm. It also closely resembles *Amphiophiura saurura* and further study is needed to determine their status.

Distribution. *O. mundata* has been recorded from the Labrador Basin, SW of Iceland, from the Bay of Biscay, off Portugal south to the Azores with a bathymetric range of 2043–4315 m.

Ophiopleura inermis (Lyman, 1878)

Fig. 48

Ophioglypha inermis Lyman, 1878: 95–96; 1882: 71–72; Koehler, 1909: 142.
Ophioglypha aurantiaca Verrill, 1882: 141; Lyman, 1883: 240; Hoyle, 1884: 717.
Ophiopleura aurantiaca Verrill, 1882; 248; Mortensen, 1927: 251–252; 1933*a*: 93–94.
Ophiura inermis H. L. Clark, 1915: 319.
Ophiopleura inermis Gage *et al.*, 1983: 295.

Material studied. **BMNH:** HMS *Challenger* Stn off Tristan d'Acunha, HOLOTYPE & 2 PARATYPES; *Triton* Faroe Channel, 944 m, 2 specimens; *Triton* Wyville Thomson Ridge, 1015 m, 5 specimens.
SMBA: RRS *Challenger II:* Stn ES20, 56°46′N: 09°17′W, 1271 m, 1 specimen; Stn ES99, 60°00′N: 05°57′W, 1040m, 1 specimen.

The disk is round to subpentagonal, covered with small thin imbricating plates, often partially obscured by thickened skin; disk diameter usually up to 18 mm, although Koehler (1909) reports a specimen with disk diameter of 40 mm. The radial shields are small, rounded and separated from one another. Arm combs are not present.

The jaws are wider than long. There is one large, rounded apical papilla flanked on each side by 6–7 small rounded or sometimes pointed oral papillae which often form a continuous series with the tentacle scales of the second oral tentacle pore. The second oral tentacle pore emerges via a furrow into the mouth slit and is armed with 4–5 small rounded tentacle scales. The adoral shields are often large, longer than broad and slightly flared distally. The oral shield is wider than long, arrow shaped to rounded pentagonal. The genital slits reach to the edge of the disk and are lined with rounded papillae.

The arms are about 3–4 times the disk diameter. The dorsal arm plates are wider than long, rectangular and contiguous over most of the arm; proximally the first four may not meet and there is a conspicuous naked area. The first ventral arm plate is round pentagonal in shape, the second hexagonal and subsequent plates have a produced proximal angle and a convex distal edge; only the first four are contiguous. Only the tentacle pores of the first two segments are conspicuous and armed with 2–3 tentacle scales; the following pores are armed with 2, reducing distally to one large rounded scale. There are 3 arm spines, the dorsalmost one is the largest approximately equal in length to 1–2 arm segments, and flat with a rounded tip; the ventralmost spine is quite small resembling an enlarged tentacle scale.

Remarks. *O. inermis* can be distinguished from *O. borealis* by the following characters: 1. lack of distinct primary plates on the disk; 2. the shape of the jaw and the oral papillae; 3. genital slits which extend to the edge of the disk; 4. long and quite narrow adoral shields; 5. the shape of the arm spines particularly the long dorsalmost one.

Distribution. This species has been recorded from both sides of the N. Atlantic; in the west off Martha's Vineyard, New England north to western Greenland at depths of 150–1100 m, and in the east from the Faeroes south to the Azores at depths of 800–1740 m.

Ophiopleura borealis Danielssen & Koren, 1877

Fig. 49

Ophiopleura borealis Danielssen & Koren, 1877: 77; Levinsen, 1886: 23; Grieg, 1893: 3; Knipovitsch, 1901; Grieg, 1903: 15; Michailovskij, 1903: 530; Mortensen, 1903: 84; Koehler, 1909: 142; Grieg, 1910: 2;

Mortensen, 1913: 352; Koehler, 1924: 328; Mortensen, 1927: 249; Schorygin, 1928: 50; Grieg, 1932: 32; Mortensen, 1932: 35; 1933*a*: 95–96; Djakanov, 1954: 124–125; Blackler, 1957: 26–47; Stendall, 1967: 839; Gage *et al.*, 1983: 295.
Lutkenia arctica Duncan, 1878: 188.
Ophiopleura arctica: Duncan & Sladen, 1881: 55; Koehler, 1901: 101.

MATERIAL STUDIED. **BMNH:** *Ernest Holt* Barents Sea, 16 specimens; Dr A. Shorygin, Kara Sea, 3 specimens; Arctic Expedition 1875, Discovery Bay, 128 m. HOLOTYPE of *L. arctica* Duncan.
SMBA: RRS *Challenger II*, Stn ES87, 61°13′N: 01°59′W, 1050 m, 4 specimens.

The disk is subpentagonal, covered with small plates which are obscured by thickened skin and only seen in dried specimens, the primary plates can often be distinguished in such specimens; diameter up to 45 mm. The radial shields are small, rounded to teardrop shaped, longer than broad, and widely separated from one another. There are no arm combs.

The jaws appear to be as long as broad. There are 1–3 apical papillae flanked on either side by 6–8 rounded oral papillae which merge with the tentacle scales of the second oral tentacle pore. This pore emerges via a furrow into the mouth slit and is armed with 3–5 rounded tentacle scales on each side. The adoral shields are large about twice as long as broad. The oral shield is triangular to rounded pentagonal in shape. The genital slits are short about 2–3 arm segments in length and not extending to the edge of the disk; lined on both sides by small rounded papillae.

The arms are about 4–5 times the disk diameter. The dorsal arm plates are wider than long, rectangular, contiguous and arched. The first ventral arm plate is nearly rhombic the next one or two are hexagonal or nearly rectangular, subsequent plates become much longer than broad and more triangular in shape; only the first 2–3 ventral arm plates are contiguous. The proximal pores within the disk are large armed with rounded tentacles and number as follows: A.P.1–3: L3–6, V3–4; A.P.4: L2–3, V2; A.P.5: L1–2, V0; A.P.6+: L1–2, V = 0. There are three short pointed arm spines.

REMARKS. The differences between *O. borealis* and *O. inermis* are dealt with under the latter.

DISTRIBUTION. *O. borealis* is an Arctic species found only in negative temperature water. It has been recorded from the Norwegian Sea as far south as the Faeroe Channel, east to the Barents, Kara and White Seas, with a bathymetric range of 10–1400 m.

Ophiocten hastatum Lyman, 1878
Fig. 49

(For full synonymy and material studied see Paterson, Tyler & Gage, 1982.)

The disk is round covered with small imbricating plates amongst which the primary plates are sometimes distinct, the plates when dried are matt; diameter up to 12 mm. The radial shields are longer than broad, approximately half the disk radius in length, separated from one another. The arm combs are reduced, confined to the distal end of the genital plate, sometimes absent altogether.

There is one, sometimes two, apical papilla flanked on each side by 3–5 oral papillae, which are pointed proximally becoming contiguous and block-like distally. The second oral tentacle pore opens superficially away from mouth slit and is armed with 1 or 2 small, rounded tentacle scales on each side. The adoral shields are longer than broad. The oral shields are broader than long and pentagonal. The genital slits are conspicuous without genital papillae except sometimes at the distal end of the genital plate.

The arms are about 4–5 times the disk diameter. The dorsal arm plates are often strongly arched with a convex distal edge, contiguous at least proximally. The first ventral arm plate is pentagonal to trapezoidal, the second arm plate is broader than long sometimes contiguous with the third; subsequent plates have an obtuse proximal angle and a rounded distal edge, and are separated. The tentacle pores are open armed only with one or two small tentacle scales. There are three pointed arm spines of which the dorsalmost is the longest up to 1·5 arm segments long and twice as long as the other two arm spines.

REMARKS. *O. hastatum* can be distinguished from other deep water *Ophiocten* species by the reduced or absent arm combs and genital papillae and by the long dorsal arm spines.

DISTRIBUTION. This species has been found in the Atlantic, Southern and Pacific Oceans. In the North Atlantic it has mainly been recorded from the east from the Rockall Trough south to the Azores at depths of 1970–4700 m, but it has been recorded only from the Labrador Basin in the west at 2340–2750 m.

Ophiocten gracilis (G. O. Sars, 1871)
Fig. 50

(See Paterson, Tyler & Gage, 1982 for full synonymy and material studies.)

The disk is round with distinct primary plates, dorsal surface matt when dried, diameter up to 12 mm. The radial shields are longer than broad, just under half the disk radius in length, separated from one another. The arm combs are moderately well developed consisting of pointed spinelets confined to each side of the arm sometimes with one or two spinelets on the first dorsal arm plate.

There is one pointed apical papilla flanked on each side by 3–4 oral papillae which are pointed proximally becoming block-like distally; often these distal ones have secondary points. The second oral tentacle pore opens away from the mouth and is armed with 1–2 small tentacle scales. The adoral shields are longer than broad. The oral shields are broader than long pentagonal or squat arrow shaped. Only the distal portion of the genital slit is edged with spine-like papillae.

The arms are about 3–5 times the disk diameter. The dorsal arm plates are broader than long, contiguous and usually strongly arched. The first ventral arm plate is pentagonal, the second has an acute proximal angle and a convex distal edge, in subsequent plates the distal edge is also indented; all are separated. There are 3 arm spines the dorsal one is often the longest. The tentacle pores are open, armed with 1–2 small often pointed tentacle scales.

REMARKS. The confusion surrounding this species has been discussed by Paterson, Tyler & Gage (1982). *O. gracilis* can be distinguished by the shape of the oral shield, presence of genital papillae only on the distal portion of the genital plate and an arm comb of pointed spinelets at the base of the arms, not forming a fringe over the base of the arm.

DISTRIBUTION. *O. gracilis* has been recorded on both sides of the North Atlantic in the west from off the east coast of North America to Iceland and in the east from the Norwegian Sea south to the Rockall Trough. It is a bathyal species found at depths of 600–1200 m.

Ophiocten centobi Paterson, Tyler & Gage, 1982
Fig. 49

Ophiocten centobi Paterson, Tyler & Gage, 1982: 119–121.

MATERIAL STUDIED. **COB:** *Cymor* drague 15, 47°44′N: 8°21′W, 2420 m. HOLOTYPE & 2 PARATYPES.

The disk is round with very large conspicuous plates which are nearly contiguous but are separated by a ring of much smaller plates; diameter up to 4·5 mm. The radial shields are small less than a quarter of the disk radius, nearly twice as broad as long and contiguous for most of their length. The arm combs form a continuous fringe over the arm base and consist of stout, pointed spinelets.

There is one pointed apical papilla flanked on each side by 3–4 oral papillae, the proximal ones are pointed, the distalmost ones block-like. The second oral tentacle pore arises superficially away from the mouth slit and is armed with 2–3 tentacle scales on each side. The adoral shields are long and narrow. The oral shield is as broad as or broader than long, pentagonal or squat arrow shaped. The genital slits are conspicuous and lined along their entire length by stout, pointed papillae.

The arms are about 3 times the disk diameter. The dorsal arm plates are fan shaped and contiguous, not strongly arched. The first ventral arm plate is pentagonal subsequent plates have an acute proximal angle and a convex distal edge; all are separated. The tentacle pores are open, each is armed with 2 relatively large tentacle scales. There are 3 long, pointed arm spines, the dorsalmost is usually the largest.

REMARKS. *O. centobi* can be distinguished by the continuous fringe of stout pointed arm comb spinelets across the base of the arms, similar genital papillae which extent the full length of the slit the large disk plates and the small contiguous radial shields.

DISTRIBUTION. This species has been recorded only from the type locality in the Bay of Biscay at 2420 m.

The ***Amphiophiura bullata*** complex

This complex comprises the species *A. bullata bullata, A. bullata pacifica, A. convexa* and *A. vitjazi,* taxa which have the same organisation of the ventral and oral plates but which differ mainly in the plating of the dorsal surface of the disk. A review of other *Amphiophiura* species suggests that a character such as disk plating is often subject to considerable variation.

A study of the species in question, using type specimens in the BMNH and other specimens from the Vema and Demeraby collections, shows that they appear to lie on a cline of variation. *A. convexa* has a disk dominated by the primaries with few secondary plates; in *A. bullata bullata* the primaries are smaller and usually separate often by many small plates. *A. bullata pacifica* appears to have a disk with more secondary plates and finally *A. vitjazi* has a disk of small plates, often slightly obscured by thickened skin, and the primaries least conspicuous. The thickening of skin could be the result of decreasing plate size.

A. bullata and *A. convexa* have been considered to be conspecific by several authors (e.g. Cherbonnier & Sibuet, 1972, Gage *et al.*, 1983 and A. M. Clark personal communication). But small specimens of *A. convexa* generally have fewer plates on the disk, large contiguous primary plates with few small supplementary ones whereas a comparison of type specimens of *A. bullata* of similar size, dd *c.* 5 mm reveals that the primary plates are not always contiguous and there are often many supplementary plates even by a disk diameter of 7 mm. In larger specimens (dd. of 15 mm) it becomes difficult to separate the two as *A. convexa* may have many supplementary plates and the primaries are not always contiguous.

The range of variation described by Litvinova (1972) for *A. bullata pacifica* appears to encompass the range of disk plate patterns described for *A. bullata bullata* to *A. vitjazi.* This suggests that the character of the disk plating could be polymorphic. I therefore propose to reduce *A. convexa* and *A. vitjazi* to the rank of subspecies of *A. bullata* together with *A. bullata pacifica.*

Amphiophiura bullata bullata (Wyville Thomson, 1877)
Fig. 51

Ophioglypha bullata Wyville Thomson, 1877: 399; Lyman, 1878: 83–84; 1882: 57–58; Verrill, 1885*b*: 543; 1894: 295; Koehler, 1906: 6; 1907: 259; 1908: 598.
Ophioglypha abdita Koehler, 1901*b*: 225; 1909: 145–147.
Amphiophiura bullata Matsumoto, 1915: 77; Mortensen, 1927: 231; Madsen, 1951: 107–108; Schoener, 1967: 653–655; Litvinova, 1971: 305; Cherbonnier & Sibuet, 1972: 1376.

MATERIAL STUDIED. **BMNH:** HMS *Challenger,* Stn 61, 34°54′N: 56°38′W, 5212 m. HOLOTYPE & PARATYPES; Stn 45, 38°34′N: 72°10′W, 2268 m, specimen; Stn 54, 34°51′N: 63°59′W 4846 m, specimens.
COB: BIOGAS Stn, CP05, 3850 m, 2 specimens.

The disk is round to subpentagonal, high, sometimes domed; covered with two sizes of plate, large primaries and often numerous smaller plates. The primaries may be contiguous and separated from the radial shields and disk edge by the smaller plates or they may be separated and encircled by these smaller plates. The disk diameter reaches 16 mm. The radial shields are usually longer than broad but sometimes as broad as long, just over a quarter of the disk diameter in length, often contiguous. The arm combs are comprised of distinct rounded squarish spinelets, the comb is situated opposite the base of the arms. The plates of the disk and arms are textured by what appears to be small glassy beads or crystal bodies in the matrix of the plates.

There are 1–3 large pointed papillae at the apex of the jaw which are sometimes difficult to distinguish from the teeth and the first oral papillae; flanking them on each side are up to 8 small rounded or slightly pointed oral papillae, which decrease in size distally. The second oral tentacle pore opens superficially away from the mouth slit and is armed with 3–4 scales on the outer-first ventral plate-edge, 1–3 on the adoral shield edge. The adoral shields are short, broader than or as broad as long. The oral shield is large occupying most of the interradial space, approximately pentagonal with an obtuse proximal angle and lateral edges which diverge towards the straight or slightly convex distal edge. The genital slits extend to the edge of the disk and are lined by contiguous block-like papillae.

The arms are short, only about twice the disk diameter in length, and high. The dorsal arm plates are domed and hexagonal, usually wider than long but sometimes as long as broad, contiguous along the proximal arm. The first ventral arm plate is pentagonal, subsequent plate square, contiguous along the proximal part of the arm. Tentacle pores are large proximally, armed with rounded or elongated scales which number as follows: A.P.1–5; L3–5, V1–2; A.P.5+: L2–3, V0–1. There are 3 very short, pointed, equally spaced arm spines.

REMARKS. *A. bullata bullata* has variable disk plating patterns, ranging from the disk dominated by the contiguous primaries which are usually surrounded by many smaller plates although the number of small plates varies to the primary plates being separated from one another with the disk comprising of mostly small plates. This degree of variability may well encompass *A. bullata pacifica* but not having examined any material from the Pacific, it is not possible to comment further.

Schoener (1967) and Litvinova (1971) both comment that it is difficult to separate juvenile individuals of *A. bullata bullata* and *A. bullata convexa.*

DISTRIBUTION. This subspecies has only been recorded from the North Atlantic; in west from off Delaware, Bermuda and near the Mid-Atlantic Ridge at depths of 2268–5320 m, in the east from the Bay of Biscay to off Sierra Leone at depths of 4165–5600 m.

Amphiophiura bullata convexa (Lyman, 1878)

Fig. 51

Ophioglypha convexa Lyman, 1878: 84; 1882: 58; Koehler, 1907: 293; 1908: 149; 1909: 142; 1914: 12.

Amphiophiura convexa Matsumoto, 1915: 77; 1917: 263; Hertz, 1927*a*: 75; H. L. Clark, 1939: 107; Litvinova, 1971: 302–303; Litvinova & Sokolova, 1971: 284; Cherbonnier & Sibuet, 1972: 1376; Gage *et al.,* 1983: 295–296; Bartsch, 1983: 16.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 241, E of Japan, 4206 m. HOLOTYPE & PARATYPE; HMS *Challenger* Stn 246, Hawaii, 3749 m, 2 specimens; HMS *Challenger* Stn 346, 2°42′S: 178°E, 3770 m, 1 specimen; U.S. Fish Comm. 68°53′N: 89°23′W off Martha's Vineyard, 3116 m, 1 specimen; J. Murray Exped. Stn 171, Central part of Arabian Sea, 2 specimens.

COB: BIOGAS Stn 4, CV30, 4518 m, 2 specimens; CV35, 4721 m, 3 specimens; CP15, 4715 m, 2 specimens; CP16, 4825 m, 14 specimens; CP17, 4706 m, 21 specimens; CP18, 4721 m, 2 specimens. BIOGAS Stn 6, DS86, 1950 m, 1 specimen.

INCAL: CP12, 46°00′5N: 10°18′3W, 4796 m, 14 specimens; CP13, 46°02′1N: 10°14′8W, 4800 m, 17 specimens; DS13, 46°01′9N: 10°17′9W, 4822 m, 2 specimens; 0S03, 46°02′5N: 10°19′5W, 4798 m, 1 specimen; 0S04, 46°03′9N: 10°12′8W, 4796 m; WS05, 46°03N: 10°15′7W, 4804 m, 5 specimens; WS09, 47°28′8N: 9°34′0W, 4277 m, 2 specimens.

BIOVEMA: CP01, 10°58′3N: 45°14′3W, 10°58′3N: 45°13′W, 5100 m, 1 specimen; CP02, 10°59′0N: 45°15′0W—11°00′3N: 45°12′9W, 5073 m, 5 specimens; CP04, 10°45′97N: 42°40′25W—10°45′90N: 42°39′35W, 5100 m, 1 specimen; CP05, 10°46′23N: 42°40′41W—10°46′36N: 42°39′75W, 5100 m, 2 specimens.

DEMERABY, Stn 12: CP07 10°23.17′N: 46°45.34′W—10°23.53′N: 46°46.13′W, 4850 m, 2 specimens; CP08, 10°25.13′N: 46°55.93′W—10°25.66′N: 46°45.93′W, 4850 m, 5 specimens; CP09, 10°23.65′N: 46°47.22′W—10°23.86′N: 46°48.12′W, 4850 m, 11 specimens; CP10, 10°24.36′N: 46°44.68′W—10°24.93′N: 46°45.28′W, 4850 m, 5 specimens; CP11, 10°23.16′N: 46°46.23′W—10°23.83′N: 46°47.08′W, 4850 m, 2 specimens; CP12, 10°21.11′N: 46°47.71′W—10°21.63′N: 46°48.13′W, 4830 m, 3 specimens; CP13, 10°24.16′N: 46°45.10′W—10°24.74′N: 46°45.68′W, 4830 m, 3 specimens; CP14, 10°24.32′N: 46°46.02′W—10°25.14′N: 46°46.26′W, 4830 m, 2 specimens.

The disk is round to subpentagonal, high sometimes domed covered with a few large plates, usually the primary plates and large secondaries; diameter up to 15 mm. The primary plates nearly always contiguous, the secondary plates are only slightly smaller than the primaries. Only in larger specimens are smaller plates developed, usually around the periphery of the primaries and associated secondary plates. Such specimens are often difficult to tell apart from *A. bullata bullata.* The radial shields are slightly longer than broad, just over a quarter the disk radius in length; usually contiguous over most of their length except in some of the larger specimens where they are separated distally by a wedge of plates.

Other features are as described for *A. bullata bullata.*

REMARKS. The disk plating patterns of this subspecies are quite constant in that the primary plates are usually contiguous and that the overall number of plates remains low until quite a large size is reached i.e. dd 12–13 mm. Litvinova (1971) reports that *A. bullata convexa* can be distinguished from *A. bullata bullata* in that the radial shields of *convexa* are usually contiguous irrespective of disk size while those of *bullata* are contiguous usually only in small specimens and are progressively separated with increasing size. Certainly from the specimens examined this would appear to be true but in addition separation of the radial shields can also be linked to the development of small secondary plates. Specimens of *bullata* with separated primary plates and numerous small plates covering the disk usually have the radial shields separated. But specimens with contiguous or nearly contiguous primaries usually do not have so many secondaries and the radial shields are usually contiguous or only just separated. This feature does not appear to be linked with size.

Distribution. *A. bullata convexa* has been recorded on both sides of the North Atlantic; in the west from the Labrador Basin off the coast of New England and south in the Demerara Abyssal Plain off northern South America at depths of 3126–4800 m; in the east from the Rockall Trough, Bay of Biscay, off the Azores and Vema Fracture zone at depth of 1997–5100 m. It has also been recorded from the Indian and Pacific Oceans.

Amphiophiura bullata vitjazi Litvinova, 1971

Fig. 51

Amphiophiura vitjazi Litvinova, 1971: 300–301; Litvinova & Sokolova, 1971: 287.

Material studied. **COB:** BIOVEMA DS09, 11°36′4″N: 32°51′8″W—11°37′1″N: 32°51′3″W, 5875 m, 49 specimens; DS11, 11°37′5″N: 32°53′8″W—11°37′8″N: 32°52′8″W, 5867 m, 108 specimens; CP06 11°34′2″N: 32°53′5″W—11°34′1″N: 32°52′8″W, 5880 m, 422 specimens.

The disk is round to subpentagonal, high, not usually domed, covered with many small plates amongst which the rounded primary plates are usually distinct, being slightly larger; diameter up to 11 mm. The plate edges are often indistinct and covered with thickened skin which encircles each plate. The primary plates are usually separate and in some specimens may be indistinct. The radial shields are longer than broad occasionally broader or as broad as long, contiguous only distally, if at all, separated by a wedge of plates; just over a quarter to nearly a half of the disk radius in length.

Ventral and arm characters as in *A. bullata bullata*.

Remarks. Litvinova (1971) separated this species from *A. bullata* by the disk plating, the small size of the plates and the rounded nature and small size of the primary plates, and the adoral shield being only half as wide as the oral plate.

The character of the plates of the disk was discussed earlier. Litvinova's subspecies *A. bullata pacifica* has a similar arrangement although the plates do not appear to be encircled by thickened skin. The relative sizes of the oral plate and adoral shield appear to be variable; in specimens collected by the Biovema, which agree with Litvinova's description in all other respects, the relative widths of the two plates varies from nearly twice as wide to approximately equal. In specimens of *A. bullata convexa* the proportions also vary but not as much as twice as broad as long.

Distribution. This subspecies was previously recorded from the Pacific Ocean from the Ryukyu Trench at a depth of 6810 m. Its occurrence in the North Atlantic from the Vema Fracture Zone at depths of 5100 m marks an extension of range.

Amphiophiura metabula H. L. Clark, 1915

Fig. 50

Amphiophiura metabula H. L. Clark, 1915: 311; John & A. L. Clark, 1954: 158–159.

Material studied. **BMNH:** *Blake* Stn 271, off St Vincent, 1164 m. PARATYPE; *Rosaura* Stn 26, 17°53′N: 87°44′W, 900 m, 2 specimens; Stn 34, 12°05′N: 61°49′W, 720–800 m, 2 specimens.

The disk is round to subpentagonal, only slightly domed and covered with many large plates often with smaller ones between them; the centrodorsal and primary plates distinct; diameter up to 10 mm. The disk plates are not as heavily textured as *Amphiophiura bullata bullata* and each plate is surrounded by thin lamellar border. The oral shield and proximal ventral arm plates also have this structure while the lateral arm plates have a texture resembling *A. bullata bullata*. The radial shields are rectangular to teardrop shaped, as long as or only slightly longer than broad, contiguous for at least half their length and extending to about a quarter of the disk radius. The arm comb extends beyond the edge of the disk, comprising two rows of spinelets, an inner often obscured, row of fine pointed spinelets and an outer row of thin often blunt spinelets which become more block-like ventrally.

There are one or two large triangular apical papillae flanked on each side by 4–5 oral papillae which become progressively more block-like and elongated distally. The second oral tentacle pore is large, not quite opening into the mouth; armed with large block-like tentacle scales, 4–5 on each edge. The adoral shields are longer than broad, widening slightly towards their distal edge. The oral shields are rounded triangular with indented lateral edges. The genital slits are conspicuous fringed with block-like papillae which merge with the spinelets of the arm comb.

The arms are short about two times the disk diameter; they are not conspicuously keeled. The dorsal arm plates are fan shaped only the first four or five contiguous. The first ventral arm plate is roughly hexagonal with a broad distal edge, the other ventral arm plates are axe shaped, only the first three or four contiguous. The tentacle pores are large particularly the proximal ones and armed with large block-like tentacle scales, which number as follows: A.P.1: L4–5, V3–4; A.P.2: L3–4, V3; A.P.3: L3, V2–3; A.P.4+: L1–2, V0–1. There are 3–5 short, pointed, equal arm spines.

REMARKS. *A. metabulla* can be distinguished by the texturing of the plates, the form of the arm comb, the shape of the oral shield and the large size of the second oral tentacle pore and scales.

DISTRIBUTION. It has been recorded primarily from the West Indies and Gulf of Mexico but the *Blake* took one specimen from off South Carolina in 1164 m.

Amphiophiura saurura (Verrill, 1894)
Fig. 50

Ophioglypha saurura Verrill, 1894: 288.
Ophioglypha aspera Koehler, 1898: 40.
Amphiophiura saurura H. L. Clark, 1915: 315; Mortensen, 1927: 231; 1933*a*: 89; Gage *et al.*, 1983: 296.
Amphiophiura aspera Mortensen, 1927: 231.

MATERIAL STUDIED. **COB:** BIOGAS Stn 1: CP01, 2245 m, 1 specimen; BIOGAS Stn Hz, DS14, 1560 m, 1 specimen.
SMBA: RRS *Challenger II*, ES Stn 112, 55°12′N: 15°50′W, 1900 m, 5 specimens.

The disk is round to subpentagonal; not usually high or domed; covered with many large plates amongst which the centrodorsal and primary plates are distinguishable; diameter up to 13 m. The radial shields are triangular to tear drop shaped, separated by a wedge of plates, and extend to about a quarter of the disk radius. The arm combs just project from beneath the radial shields; the arm comb spinelets are block-like.

There is one pointed apical papilla flanked on each side by 3–5 oral papillae which become progressively more block-like distally. The oral papillae appear to merge with the inner tentacle scales of the second oral tentacle pore which opens via a slit into the mouth and is armed with up to 6 contiguous block-like tentacle scales on its inner edge and 6 similarly shaped scales on its outer. The adoral shields are long and narrow slightly bowed. The oral shield is pentagonal with often an acute proximal angle, slightly convex proximal lateral edges and a straight distal edge. The genital slits run from the oral shield to the dorsal surface and are edged with block-like papillae which merge with the spinelets of the arm comb.

The arms are short, two to three times the disk diameter in length; and are rounded without a conspicuous keel so that they do not appear high. The dorsal arm plates are slightly domed, in profile the distal edge appears to be slightly raised then terminates quite abruptly, and contiguous. The first ventral arm plates is irregularly hexagonal or sometimes pentagonal, with an obtuse proximal angle and a convex distal edge, the next four plates are irregularly pentagonal with a more pronounced convex distal edge. Subsequent plates become wider than long approaching a rectangle in shape. The first three to five plates are contiguous. The proximal tentacle pores are large and conspicuous and armed with block-like tentacle scales, the number of which decreased down the arm as follows: A.P.1: L5, V4; A.P.2: L4, V4; A.P.3: L3–4, V3; A.P.4: L2–3, V3; A.P.5: L2, V2; A.P.6+: L1, V1. There are three short pointed arm spines on the ventral side of the arm.

REMARKS. *A. saurura* superficially resembles *Ophiura irrorata* or *O. mundata,* particularly smaller specimens d.d. less than 6 mm, but is distinguished by: 1. the slightly domed dorsal arm plates; 2. the shape of the oral shield; 3. the second oral tentacle pore opening into the mouth via a slit; 4. the arm spines being aligned on the ventral part of the arm.

More specifically *A. saurura* lacks the excessively developed distal tentacle scale found in *O. irrorata.*

DISTRIBUTION. *A. saurura* has been recorded from both sides of the North Atlantic Ocean; in the west from off Nantucket and Newfoundland with a bathymetric range of 844–1267 m and in the east from south of Iceland to the Bay of Biscay with a bathymetric range of 1560–2245 m.

Stegophiura macrarthra H. L. Clark, 1915
Fig. 52

Ophioglypha stuwitzii? Lyman, 1883: 242.
Ophioglypha elevata Koehler, 1914: 16–17; [non *O. elevata* (Lyman) acc. H. L. Clark 1915].
Stegophiura macrarthra H. L. Clark, 1915: 317–316.

MATERIAL STUDIED. **MCZ:** *Blake* Stn 321, 32°43′25″N: 77°20′30″W, 429 m, HOLOTYPE.
COB: BIOGAS Stn 1: DS64, 2156 m, 1 specimen; Stn HZ: DS 33, 2338 m 1 specimen.
IOS: *Discovery* Investigations: Stn 9042, 45°15′N: 11°22′W, 1662–1541 m, 23 specimens.
SMBA: RRS *Challenger II* Stn ES112, 55°12′N: 15°50′W, 1900 m, 1 specimen.

The disk is round, moderately high covered with plates amongst which the slightly larger centrodorsal and primary radial plates are distinct; diameter up to 6·5 mm. The radial shields are short, less than one quarter of the disk radius in length, broader than or as broad as long; the distal edge forms an obtuse angle; the shields are contiguous for most of their length. The arm comb consists of long pointed spinelets.

There is one, sometimes two, apical papilla flanked on each side by 4–6 contiguous, block-like papillae. The second oral tentacle pore is large, opening away from the mouth slit, armed with 2–3 large, rounded tentacle scales on each side. The adoral shields are long and narrow. The oral shields are approximately arrow shaped; the ventral portion lies above the part proximal to the genital slits. The genital slits are fringed by a row of pointed papillae.

The arms are short, at most 2–3 times the disk diameter, rounded distally. The dorsal arm plates are rectangular, slightly wider than long and contiguous, distally they become fan-shaped and separated. The first ventral arm plate is pentagonal and slightly swollen, the next four plates are contiguous and approximately rectangular, each has a distinctive keel in the midline; subsequent plates have a more convex distal edge but no keel. The proximal tentacle pores are large and distinctly swollen and armed with large rounded tentacle scales which number as follows: A.P.1: L3, V2–3; A.P.2: L3–4, V2–3; A.P.3: L2–3, V2; A.P.3–5: L3, V2–1; A.P.6+: L2, V0. There are 3–4 pointed arm spines proximally; the first three dorsalmost are evenly spaced but the fourth and ventralmost spine is situated close to the third.

REMARKS. *S. macrarthra* closely resembles *Stegophiura stuwitzii* (Lütken) it can be distinguished by the following characters: a. the shape of the oral shield which is arrow shaped with a median constriction, but more pentagonal in *S. stuwitzii*; b. the fewer and larger arm spines which are quite evenly spaced, while those of *S. stuwitzii* are smaller more number up to 6 proximally; c. the first four ventral arm plates only being swollen or keeled, while the first 10 are keeled or swollen in *S. stuwitzii*.

DISTRIBUTION. This species has been recorded from both sides of the North Atlantic; in the west off Georgia 32°43′25″N: 77°20′30″W, 419 m and in the east from the Rockall Trough south to the Bay of Biscay with a bathymetric distribution 1541–2338 m.

A review of the genus *Homalophiura* H. L. Clark, 1915

Hertz (1927*b*), Mortensen (1936) considered that *Homalophiura* could not be maintained as a genus distinct from *Ophiurolepis* Matsumoto, 1915, a view supported by Madsen (1969) who transferred the type species *H. inornata* to *Ophiurolepis* thus invalidating the generic name. However, the remaining species (see list below) are in need of review.

Ophiurolepis is characterised by poorly developed arm combs, small tentacle pores restricted to the proximal arm segments, short genital slits with rudimentary genital papillae and high more or less normally carinate arms or with sculptured dorsal arm plates. *H. inornata* and three other species which have been included in *Homalophiura* also conform to this diagnosis but the majority of *Homalophiura* species do not.

Homalophiura was characterised only by: the reduced arm combs and tentacle pores restricted to the proximal segments. However, H. L. Clark (1915) expanded the generic diagnosis to include all Ophiurinae with reduced development of the tentacle pores which did not otherwise conform with *Ophiurolepis* or *Ophioplinthus* Lyman, 1878.

This character is more widespread than H. L. Clark realised, particularly within the genus *Ophiura* where the tentacle pores become ill-defined distally in many species.

Based on specimens within the BMNH and descriptions of the other species—see list below—four groups emerge within *Homalophiura:*

A. Species with short genital slits, poorly defined arm combs, high arms and small tentacle pores restricted to the proximal 2–3 arm segments i.e. *H. inornata, H. confragosa*—referable to *Ophiurolepis*.

B. Species with genital slits extending to the disk edge, well developed arm combs, tentacle pores relatively large and armed with conspicuous tentacle scales, e.g. *H. divisa, H. nana*—referable to *Ophiura (Ophiura)* sensu lato, pending full revision of this genus.

C. Species agreeing with those in B but also having the distalmost arm spine modified to hooks, e.g. *H. glypta* and *H. schmidtotti* referable to *Ophiura* (*Ophiuroglypha*).

D. Species with long genital slits, poorly developed arm combs small tentacle pores restricted to the first 2–4 proximal arm segments and slightly enlarged proximal arm segments referable to a new genus *Homophiura,* defined below.

Assignment of species of *Homalophiura* sensu extenso

Group A—referrable to *Ophiurolepis*
+*H. brucei** (Koehler, 1907*b*); +*H. confragosa* (Lyman, 1878), +*H. inornata* (Lyman, 1878), +*H. scissa* (Koehler, 1908).

Group B—referable to *Ophiura (Ophiura)*
H. divisa (Lütken & Mortensen, 1899), *H. flexibilis* (Koehler, 1911); *H. inflata* (Koehler, 1897); *H. madseni* (Belyaev, 1972); +*H. mimaria* (Koehler, 1908); *H. nana* (Lütken & Mortensen, 1899); *H. scutellata* (Lütken & Mortensen, 1899); +*H. violainae* Cherbonnier & Sibuet, 1972.

Group C—referable to *Ophiura (Ophiuroglypha)*
+*H. euryplax* H. L. Clark, 1939; +*H. glypta* H. L. Clark, 1939; +*H. intorta* (Lyman, 1878); *H. schmidtotti* (Hertz, 1927); +*H. multispina* Cherbonnier & Sibuet is conspecific with *Ophiura (Ophiuroglypha) irrorata polyacantha,* see p. 124.

Group D—referable to *Homophiura* gen. nov.
+*H. abyssorum* (Lyman, 1883); *H. clasta* (H. L. Clark, 1911); +*H. tessellata* (Verrill, 1894);—type species.

Fell (1961) transferred *H. partita* (Koehler, 1907*b*) to his new genus *Theodoria* and noted that *H. frigida* (Koehler, 1901*a*) may also belong in this genus.

*+specimens examined.

HOMOPHIURA gen. nov.

The disk covered by rounded plates separated from one another by thickened skin; radial shields relatively large longer than broad; arm combs rudimentary comprised of one or two rows of rounded or slightly elongated granules; one block-like apical papilla flanked by contiguous oral papillae second oral tentacle pore arising outside the mouth slit; oral shields large and contiguous along the distal edge with a large accessory plate usually of equal width, genital slits extending to the edge of the disk lined the whole length or only distally by rounded or elongated granules; the arms relatively long rounded not high; dorsal arm plates not particularly high, often fragmented; tentacle pores small restricted to the first 3–5 arm segments armed with small pointed tentacle scales; arm spines short and pointed; proximal arm segments within the disk are swollen.

TYPE SPECIES. *Ophioglypha tessellata* Verrill, 1894.

REMARKS. Other species included are *Homalophiura abyssorum* (Lyman, 1883), *Homalophiura clasta* (H. L. Clark, 1911) and *Ophiurolepis martensi* (Studer, 1885).

Homophiura is related to *Ophiurolepis* and probably *Theodoria* Fell, 1961. It differs from *Ophiurolepis* mainly by the greater extent of the genital slits which reach to the edge of the disk, regular arrangement of the oral papillae, jaw plates, adoral and oral shields. The latter tend to be fragmented in *Ophiurolepis* whereas in *Homophiura* they are large undivided and abut distally a large plate. Also the dorsal arm plates of *Homophiura* are flat, or sometimes slightly elevated, but never carinate. This character is also quite variable in *Ophiurolepis* although specimens with low dorsal arm plates tend to have short genital slits and fragmented oral frame plates, i.e. *Ophiurolepis partita*.

Ophiurolepis gelida is perhaps intermediate between the two genera often having relatively long genital slits although these do not quite reach the disk edge—the length is variable. *O. gelida* has carinate dorsal arm plates, fragmented oral frame plates and no single large plate distally. The oral shield features relate it more closely to *Ophiurolepis*. However, further studies are necessary to clarify the relationships between *Homophiura, Ophiurolepis, Theodoria* and *Ophioplinthus,* a task beyond the scope of this study.

Homophiura tessellata (Verrill, 1894) n. comb
Fig. 52

Ophioglypha tessellata Verrill, 1894: 290; Koehler, 1898: 37; 1909: 156.
Homalophiura tessellata H. L. Clark, 1915: 327; Mortensen, 1927: 232; 1933*a*: 91; Gage *et al.*, 1983: 295.

MATERIAL STUDIED. **USNM:** *Albatross* Stn 2205, 39°35′N: 71°18′W, S of Block Island, 1928 m, 3 SYNTYPES.
COB: BIOGAS Stn 1: DS17, 2103 m, 1 specimen; CP26, 2115 m, 1 specimen; CP27, 1920 m, 2 specimens. BIOGAS Stn 2: CV12, 2775 m, 14 specimens; CV26, 2822 m, 2 specimens; CV38, 2695 m, 9 specimens. BIOGAS Stn 3: CV13, 4252 m, 1 specimen. BIOGAS Stn 4: CP17, 4706 m, 1 specimen.
INCAL: Stn CP04, 56°33′2N: 11°11′3W, 2483 m, 3 specimens; Stn DS14, 47°32′6N: 9°35′7W, 4254 m, 9 specimens; Stn 15, 47°33′4N: 9°39′1W, 4211 m, 1 specimen.
IOS: *Discovery* Investigations: Stn 7711/52, 52°53.3′N: 19°52.4′W, 2734–2742 m, 1 specimen; Stn 7711/78, 53°9.8′N: 20°14.7′W, 2425–2430 m, 1 specimen; Stn 8511/2, 41°49.6′N: 11°6.0′W, 2574–2584 m, 1 specimen.
SMBA: RRS *Challenger II* Stn SWT18, 56°46′N: 09°42′W, 1809 m, 1 specimen; Stn AT144, 57°13′N: 10°20′W, 2240 m, 2 specimens; Stn AT151, 57°21′N: 10°22′W, 2175 m, 1 specimen; Stn AT154, 57°00′N: 10°22′W, 2264 n, 2 specimens.

The disk is pentagonal, sometimes high, and covered with large irregularly shaped plates amongst which it is sometimes possible to distinguish the centrodorsal and primary radial plates; each plate seems to be encircled by thin layer of skin; diameter up to 30 mm. The radial shields small just over a quarter the disk radius in length, longer than broad slightly oval, and separated. There are a number of block-like papillae visible opposite the base of each arm forming a rudimentary arm comb. These may be arranged into two rows.

There is one angular apical papilla flanked on each side by up to 8 block-like contiguous oral papillae. The second oral tentacle pore is small, opening away from the mouth armed with 3–4 block-like tentacle scales on the inner edge, 3–5 on the outer. The outer scales arise on a triangular plate situated proximal to the first ventral arm plate. The adoral shields are relatively short and narrow, about 3 times as long as broad. The oral shield is pentagonal with a slightly obtuse proximal angle and a straight distal edge, often butting on to another pentagonal plate—almost the mirror image of the oral shield, occasionally there is a small supplementary plate at an inner corner or outer edge. The genital slits are not easily distinguished being obscured by skin but extend the full length of the ventral interradial area. Specimens infected with a athecate hydroid—*Hydractinia* sp.—often have fragmented, ill-defined plates.

The arms are 5 times the disk diameter, and are smooth in profile viewed from the dorsal surface. The dorsal arm plates are not particularly swollen in profile, fan shaped and contiguous at least on proximal segments, slightly longer than broad. These plates are often fragmented by an irregular suture which runs down the mid line. The first three segments of the arm within the disk appear to be slightly swollen. The first ventral arm plate is pentagonal with a straight proximal edge and an obtuse distal angle. Subsequent plates are broadly pentagonal with a very obtuse proximal angle and a convex distal edge. Only the first 2–4 plates are contiguous. The tentacle pores are small only distinct on the first 3 segments. The tentacle scales are small and spine-like with A.P.1: L2, V2; A.P.2: L2, V0–1; A.P.3: L1, V0, reducing to 1 on the fourth segment which merges with arm spines. The arm spines are short, variable in number but usually 3 or 4 and not equally spaced on the arm.

REMARKS. *H. tessellata* closely resembles *H. abyssorum* Lyman but differs from it by the following characters: 1. The arm comb is made up of irregularly arranged papillae while in *H. abyssorum* there is only one row of square papillae. 2. The oral shield is smaller and appears to be associated with a second plate of similar shape. 3. The proximal part of the arms is not as swollen as in *H. abyssorum.*

DISTRIBUTION. It is found on both sides of the North Atlantic; in the west from off New England north to the Labrador Basin with a bathymetric range of 433–3229 m and in the east from S. Iceland south to off the Azores with a bathymetric range of 1809–4706 m.

Homophiura abyssorum (Lyman, 1883)

Fig. 52

Ophioglypha abyssorum Lyman, 1883: 238.
Homalophiura abyssorum H. L. Clark, 1911: 326; 1939: 112–113.
Ophiurolepis abyssorum Hertz, 1927*a*: 93.

MATERIAL STUDIED. **MCZ:** *Blake* Stn 140, off Virgin Gorda, West Indies, 1974 m, HOLOTYPE. **BMNH:** J. Murray Expedition, Stn 135, Maldive Area, 2727 m, 1 specimen.

The disk is pentagonal, slightly elevated covered with large plates amongst which the centrodorsal and the primary radial plates are distinct; plates may be separated by thickened skin; diameter up to 10 mm. The radial shields are large, slightly less than half the disk radius in length and are longer than broad, and separated by a row of plates. The arm comb consists of a few square papillae at the base of the radial shields.

There is one small, pointed, often angular apical papilla flanked on each side by up to 6 block-like usually contiguous papillae of which the distalmost ones are the largest. The second oral tentacle pore emerges superficially outside the mouth slit and is armed with 3–5 rounded oral papillae. The adoral shields are relatively short but longer than broad. The oral shield is large extending up to half the interradial area in length; pentagonal in shape with an acute proximal angle and a straight distal edge; the shield is contiguous distally with a large plate, usually of equal width. The genital slits are long reaching to the edge of the disk and are edged with rounded or block-like papillae. The disk plates adjacent to the slits are large the same length as the slits.

The arms are about 3–4 times the disk diameter and rounded. The dorsal arm plates are tear-drop shaped although in some specimens they may be fragmented, with only the first 2–3 contiguous. The first ventral arm plate is hexagonal nearly pentagonal, truncated proximally; the second is also hexagonal then subsequent plates become more triangular, all are separated. Tentacle pores are small, conspicuous only on the first three arm segments each is armed with small rounded or slightly pointed tentacle scales as follows: A.P.1: L2–3, V1; A.P.2–3; L2, V0. The arm spines are small, pointed and peg-like, usually numbering 3 with one situated dorsally, the other two more ventral, occasionally there may be 4–5 spines.

REMARKS. *H. abyssorum* is compared with *H. tessellata* under that species. Lyman described the genital papillae as present only on the distal portion of the genital slits whereas examination of the holotype shows them to be present along the whole length of the slits on some interradii.

Dr F. J. Madsen (personal communication) considers it was perhaps unnecessary to describe *Homalophiura abyssorum africanum* Madsen, 1947, as a separate subspecies, and that it should be treated as another record of *H. abyssorum.*

DISTRIBUTION. *H. abyssorum* has been recorded from the Western tropical Atlantic off Virgin Gorda, West Indies, at a depth of 1974 m and in the east off the Straits of Gibraltar (35°43′N: 8°16′W) at a depth of 2150–2300 m. It has also been recorded from the Indian Ocean at 2727 m.

Ophiurolepis inornata (Lyman, 1878)

Fig. 53

Ophioglypha inornata Lyman, 1878: 97; 1882: 73–74; Koehler, 1904: 40; 1907: 262–263.
Homalophiura inornata H. L. Clark, 1915: 326; Mortensen, 1927: 327–328; Mortensen, 1936: 327–329; Koehler, 1922: 387.
Ophiurolepis inornata Madsen, 1969: 132.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 106, 1°47′N: 24°26′W, 3330 m, HOLOTYPE, 2 PARATYPES; *Discovery* Stn WS212, 49°22′S: 60°10′W, 242–249 m, 2 specimens; WS820, 52°53′S: 61°51′W, 351–367 m, 3 specimens; WS236, 46°55′S: 60°40′W, 272–300 m, 4 specimens.

The disk is pentagonal covered with small plates amongst which the centrodorsal and primary radial plates are conspicuous, being usually larger than the others. The radial shields are triangular to teardrop shaped, separated and longer than broad, slightly greater than a quarter the disk radius in length. The arm combs consist of rounded, slightly elongated papillae which become smaller towards the ventral side.

There is one pointed angular apical papilla flanked on each side by 5–7 contiguous block-like oral papillae, the second distalmost of which is the largest and lies between the second oral tentacle pore and the mouth slit. Often there is an accessory plate lying distal to the apical papillae. The second oral tentacle pore is relatively large, arising superficially outside the mouth slit, and armed with 3–5 tentacle scales on each side. The adoral shields are relatively short but longer than broad. The oral shield is rounded pentagonal, longer than broad, not extending beyond half the interradial area in length; in some specimens the shield may be divided longitudinally. The genital slits are short, lying adjacent to first lateral arm plates. A series of irregularly arranged, low granules continues from the distal portion of the genital slits to the edge of the disk.

The arms are about 3–4 times the disk diameter, not particularly noded in outline. The dorsal arm plates are nearly rhombic proximally becoming fan shaped, and contiguous along most of the arm; individual plates are often divided by a longitudinal furrow. The first two ventral arm plates are hexagonal, longer than broad, subsequent plates are wider than long approximately hexagonal but becoming triangular; only the first three are contiguous. Tentacle pores are visible on the first 3–4 arm plates, very small and armed with 4 then 2 very small tentacle scales. There are 4 small pointed arm spines, small accessory plates sometimes appear to lie between them.

REMARKS. *O. inornata* bears a resemblance to *Homophiura tessellata* and *H. abyssorum*; it can be distinguished from the former by the short genital slits which do not extend to the edge of the disk like those of *H. tessellata,* and by the smaller oral shield which is separated from the first lateral arm plate by the adoral shields and a supplementary plate unlike *H. tessellata* and *H. abyssorum* where the oral plate is large and appears to abut or nearly abut the lateral arm plates.

DISTRIBUTION. *O. inornata* has a wide distribution being recorded from the Pacific, Indian, Southern and North Atlantic Ocean. In the latter ocean it has been found off St Paul's Rocks, east of Trinidad, off Cap Blanc and the Azores with a bathymetric range of 640–3330 m.

Ophiotjalfa vivipara (Mortensen, 1913)

Fig. 53

Ophiotjalfa vivipara Mortensen, 1913*a*: 40; 1913*b*: 352; H. L. Clark, 1915: 344; Mortensen, 1933*a*: 71–72.

MATERIAL STUDIED. **BMNH:** *Ingolf* Stn 78, 60°37′N: 27°52′W, 1482 m, SW of Iceland, 1 specimen.

The disk is round to subpentagonal, covered with large tumid plates of which the centrodorsal and primary radial plates are the largest; diameter up to 5 mm. The radial shields are small, less than a quarter of the disk radius in length, broader than long and separated or contiguous only distally. There is an arm comb of a few block-like or slightly pointed spinelets at the base of the arm, although Mortensen (1913*a*), describing the type, recorded that there were no combs at the base of the arm.

There is one pointed apical papilla flanked on each side by 4–5 block-like contiguous papillae of which the distalmost one is the largest. The second oral tentacle pore opens superficially outside the mouth slit and is armed with 1–3 tentacle scales on each side. The adoral shields are relatively long, about three times as long as broad. The oral shields are rounded with an obtuse proximal angle. The genital slits extend the full length of the ventral interradial area and are not fringed with papillae.

The arms are three times the disk diameter and are slightly noded. The dorsal arm plates are tumid, fan shaped and separated. The first ventral arm plate is bell shaped or trapezoidal subsequent plates are approximately pentagonal with an acute proximal angle and a convex distal edge; on distal segments the ventral arm plates become triangular; all but sometimes the first two are separated. The tentacle pores are only conspicuous on the first four arm segments; the first two pores are armed with 2–3 rounded tentacle scales, the next with 1 or 2—then the rest with just one which becomes smaller distally. There are three short, pointed arm spines.

REMARKS. *O. vivipara* can be distinguished by its tumid disk and dorsal arm plates, and the lack of genital papillae.

DISTRIBUTION. This species has been recorded from the Davis Strait (no depth record) and off SW Iceland at 1438 m.

Anthophiura ingolfi Fasmer, 1930
Fig. 53

Anthophiura ingolfi Fasmer, 1930: 4; Schoener, 1969: 128–131.
Aspidophiura minuta? Koehler, 1896*a*: 72 [non *Aspidophiura minuta*, Lyman]?

MATERIAL STUDIED. **ZMC:** *Ingolf* Stn 11, 64°34′N: 31°12′W, 2430 m, HOLOTYPE.
COB: BIOGAS Stn 6, DS51, 2430 m, 2 specimens.

The disk is rounded, domed and covered with large plates, the centrodorsal plate is star shaped and partly overlies the primary radial plates; diameter up to 5 mm. The radial shields are large, nearly as broad as long, contiguous for most of their length. There are no arm combs.

There is one triangular apical papilla flanked on each side by 3 block-like contiguous oral papillae of which the dorsalmost one is the largest. The second oral tentacle pore opens superficially outside the mouth slit and is armed with one or two tentacle scales on either side. The adoral shields are about 3 times as long as broad. The oral shield is pentagonal and longer than broad. The genital slits extend from the oral shield nearly to the edge of the disk.

The arms are noded, about three times the disk diameter. There are no dorsal arm plates. The ventral arm plates are bell shaped and present only proximally. The tentacle pores are small armed with small single rudimentary tentacle scale, absent on some pores. There are only 2 pointed arm spines.

REMARKS. This is a very distinctive ophiuroid easily recognised by the star shaped centrodorsal plate, and the limited number of large disk plates, the lack of dorsal arm plate. Fasmer (1930) thought the Koehler's (1896*a*) record of *Aspidophiura minuta* from the Bay of Biscay was a mistaken identification of *Anthophiura ingolfi*. This view is plausible as the two species appear very similar varying mainly in the presence of an arm comb in *Aspidophiura*.

DISTRIBUTION. *A. ingolfi* has been recorded from both sides of the North Atlantic; in the west from off the eastern United States to the west of Iceland in the Labrador Basin and in the east from the Bay of Biscay, with a bathymetric range of 2430–2862 m.

Ophiomisidium speciosum Koehler, 1914
Fig. 54

Ophiomisidium speciosum Koehler, 1914: 34–36; Schoener, 1969: 131–133; Litvinova, 1981: 122.
Ophiophycis gracilis Mortensen, 1933*d*: 455–461; Litvinova, 1981: 122.

MATERIAL STUDIED. **USNM:** *Albatross* Stn 2415, 30°44′N: 79°26′W, 792 m, 2 SYNTYPES.

The disk is pentagonal, dominated by the pentagonal centrodorsal plate and the primary radial plates, diameter up to 5 mm. The radial shields are large about half the disk radius in length, longer than wide and separated by a large dorsal arm plate distally. Interradially each pair of radial shields is separated by a single row of two plates; the proximal one is the largest, pentagonal and longer than wide. The distal one is rectangular, wider than long.

There is one pointed apical papillae flanked on each side by one long rectangular oral papilla. The second oral tentacle pore opens outside the mouth slit and is armed with one, round, relatively large tentacle. The adoral shields are rectangular. The oral shield is rounded pentagonal. The genital slits are short equal in length to the first lateral arm plate and not edged with papillae.

The arms are short, equal in length to the disk diameter. The first four proximal lateral arm plates are distinctly enlarged. The first two dorsal arm plates are rounded distally contiguous; subsequent plates are fan shaped and separated. The first ventral arm plate is pentagonal and longer than wide, subsequent ones are axe-shaped, all are separated. The tentacle pores are relatively large armed with one rounded tentacle scale. There are 3 pointed arm spines proximally, 2 distally.

REMARKS. *O. speciosum* can be distinguished from *O. pulchellum* chiefly because it lacks the rugose, spine-like boss on the primary disk plates and dorsal arm plates.

Litvinova (1981) has commented on the similarity of this genus to *Ophiophycis*. Differences between them centre on: 1. the lateral arm plates are widened and more elongated giving the ventral side of the disk a flatter appearance in *Ophiophycis* than in *Ophiomisidium*. 2. The arm spines are pointed in *Ophiomisidium* but flattened with squared off tips in *Ophiophycis*. Further investigation may prove that such differences are specific not generic. Should this be so then *Ophiophycis* has priority as the generic name.

DISTRIBUTION. This species has been recorded from off Brazil and Florida with a depth range of 547–1472 m.

Ophiomisidium pulchellum Wyville Thomson, 1877

Fig. 53

Ophiomusium pulchellum Wyville Thomson, 1877: 67; Lyman, 1878: 118; 1882: 96; Koehler, 1907: 266.
Ophiomisidium pulchellum Koehler, 1914: 32–37; A. M. Clark & Courtman-Stock, 1976: 190–191.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 142, S of Cape Town, 35°4′S: 18°37′E, 274 m, 3 specimens.

The disk is subpentagonal, covered with a few large plates amongst which the centrodorsal and primaries are distinct; diameter up to 5 mm. Most of the disk plates, except the radial shields, and the proximal dorsal arm plates carry a rugose, central, spine-like boss. The radial shields are large, more than half the disk radius in length, longer than broad, meeting about half way down their length then diverging proximally or sometimes contiguous proximally separated distally.

There is one triangular apical papilla flanked by one or two oral papillae; the first is slightly pointed, the second long thin and block-like running the length of the mouth slit. The second oral tentacle pore arises outside the mouth slit and is armed with one rounded scale. The adoral shields are relatively large, longer than broad. The oral shield is small pentagonal with an acute proximal angle and a convex distal edge. The genital slits are short often difficult to discern.

The arms are noded, only about twice the disk diameter. The proximal lateral arm plates are distinctly enlarged. The dorsal arm plates are triangular, proximal ones with a central rugose boss, and separated. The first ventral arm plate is hexagonal subsequent ones pentagonal, the first three may be contiguous. Tentacle pores are present only on the first 4 segments, each pore is armed with one round scale. There are 3–4 irregularly shaped, slightly rugose arm spines, the middle spines usually the longest, proximally nearly one segment long reducing in size rapidly along the arm.

REMARKS. *O. pulchellum* can be distinguished from *O. speciosum* primarily by the presence of rugose bosses on the disk and dorsal arm plates.

DISTRIBUTION. This species has been recorded in the eastern Atlantic from the Bay of Biscay south to off the Cape of Good Hope with a bathymetric range of 70–3063 m and in the western Atlantic off South Carolina 440 m and off Pernambuco, Brazil 270 m.

Ophiophycis mirabilis Koehler, 1901*b*

Fig. 54

Ophiophycis mirabilis Koehler, 1901*b*: 222; 1909: 163; Cherbonnier, 1970: 348; Cherbonnier & Sibuet, 1972: 1387.

MATERIAL STUDIED. **IOS:** *Discovery* Investigations Stn 9042, 45°15′N: 11°12′W, 1662–1541 m, 1 specimen. **COB:** BIOGAS Stn 6, 23, 1980 m, 1 specimen.

The disk is pentagonal, fringed by stout squared tipped spines, which are in fact modified arm spines, diameter up to 6 mm. The disk is dominated by the large pentagonal centrodorsal and primary radial plates. The radial shields are longer than broad, greater than $\frac{1}{2}$ the disk radius in length, and contiguous along the mid-portion of the plate. Interradially pairs of radial shields are separated by a single row of two plates.

There are one or two pointed apical papillae flanked on each side by 2–3 contiguous block-like papillae. The second oral tentacle pore opens superficially away from the mouth slit, and is armed with one small, slightly pointed tentacle scale. The adoral shields are large, longer than broad. The oral shield is pentagonal and not quite half the disk radius in length. The genital slits are small partially hidden beneath the elongated first lateral arm plates.

The arms are only one or two times the disk diameter in length. The first two dorsal arm plates are triangular or trapezoidal and contiguous, the subsequent plates rounded triangular and separated. The first ventral arm plate is approximately rectangular or pentagonal subsequent plates are pentagonal with a straight proximal edge and an obtuse distal angle; all the ventral arm plates are separated. The tentacle pores on the proximal arm are large and each is armed with a small pointed tentacle scale. The lateral arm plates of the first 5 arm segments are widened and elongated. There are two or three flattened rugose arm spines.

REMARKS. *Ophiophycis mirabilis* resembles *Ophiomisidium pulchellum* and *O. speciosum*; all three have enlarged lateral arm plates, reduced disk plating and simple oral armament. *Ophiophycis mirabilis* can be distinguished by the flatter arm spines, the lack of knobs on the dorsal disk and arm plates and a different arrangement of the plates of the ventral interradial area.

DISTRIBUTION. This species has been recorded only in the eastern Atlantic from the Bay of Biscay south to the Azores with a bathymetric range of 1175–1662 m.

Ophiambix meteoris Bartsch, 1983*a*
Figs 54 & 57e, f

Ophiambix meteoris Bartsch, 1983*a*: 97–100; 1983*b*: 13–14.

MATERIAL STUDIED. **ZSM:** *Meteor* Stn M3, 30/AT3 42°55.4′N: 14°07.9′W, 5260 m, 4 PARATYPES.

The disk is round, covered with thin imbricating plates; neither centrodorsal nor primary plates distinct, plates are often obscured by a covering of pointed spinelets, which have an elaborate structure (see Fig. 57); diameter up to 5 mm. Radial shields are absent. The proximal portion of the ventral interradial area is naked without plates.

There are up to three pointed apical papillae flanked on either side by 2 to 4 pointed irregularly arranged oral papillae. The second oral tentacle pore is large and opens outside the mouthslit and is armed with up to 6 pointed tentacle scales. The adoral shields are long, thin and slightly bowed, separating the oral shield from the first lateral arm plate. The oral shield is small and rounded.

The arms are flattened about 1–3 times the diameter of the disk. Proximally, it is often difficult to distinguish the dorsal arm plates as the disk plates appear to continue to the arm so there is no distinct boundary between the disk and the arm. Distally dorsal arm plates can be recognised; they are, usually, irregularly rectangular contiguous and flanked on each side by a triangular accessory plate. At the ends of the arm the dorsal arm plates are rhombic and the accessory plates are absent. The ventral arm plates are approximately rectangular and contiguous proximally. The tentacle pores are large, open and armed with up to 8 pointed tentacle scales on proximal segments. There are 4–5 arm spines proximally reducing to three distally; the spines are rugose, flattened with an irregular open lattice work structure, slightly flared free end (see Fig. 57). Distally the ventral arm spines may be slightly hooked.

REMARKS. This species differs from the other *Ophiambix* species by the shape of the dorsal disk spinelets, the shape of the arm spines. *Ophiambix* has been transferred from the Ophiacanthidae because the second oral tentacle pore arises outside the mouth slit and the dental and oral plate characters are more consistent with this family (Paterson & Baker, in preparation).

DISTRIBUTION. *Ophiambix meteorensis* has been found off Spain in the Iberian Basin at 5315 m.

Ophiambix devaneyi sp. nov.
Figs 54 & 57a–d

MATERIAL STUDIED. *Pillsbury* Stn 931, 15°32′N: 61°13′W, 146–494 m, HOLOTYPE.

The disk is round, covered with thin imbricating plates amongst which neither the primary plates nor the radial shields are distinct; diameter 3 mm. The plates carry small but very elaborate pyrimidical spinelets (see Fig. 57b). The ventral interradial area is covered with thin plates without spinelets.

There are one to two spine-like apical papillae flanked on each side by two, spaced, spine-like oral papillae. The second oral tentacle pore is large and opens outside the mouth slit; it is armed with 4 pointed, spine-like tentacle scales, two on the first ventral arm plate and two on the adoral shield. The adoral shields are narrow, longer than broad. The oral shield is irregular in shape, sometimes rounded triangular in shape. The genital slits are adjacent to the first lateral arm plate.

The arms appear to be short about equal to the disk diameter in length. They are not clearly demarked from the disk and spinelets extend on to the arm. Dorsal arm plates are only really distinct distally and appear to be fan shaped and just contiguous; proximally they appear to be flanked by approximately triangular accessory plates but spinelets obscure the plate boundaries. The ventral arm plates are rectangular longer than broad, slightly indented laterally adjacent to the tentacle pores, and contiguous along most of the arm. The lateral arm plates are enlarged and flared at their distal ends, the second lateral

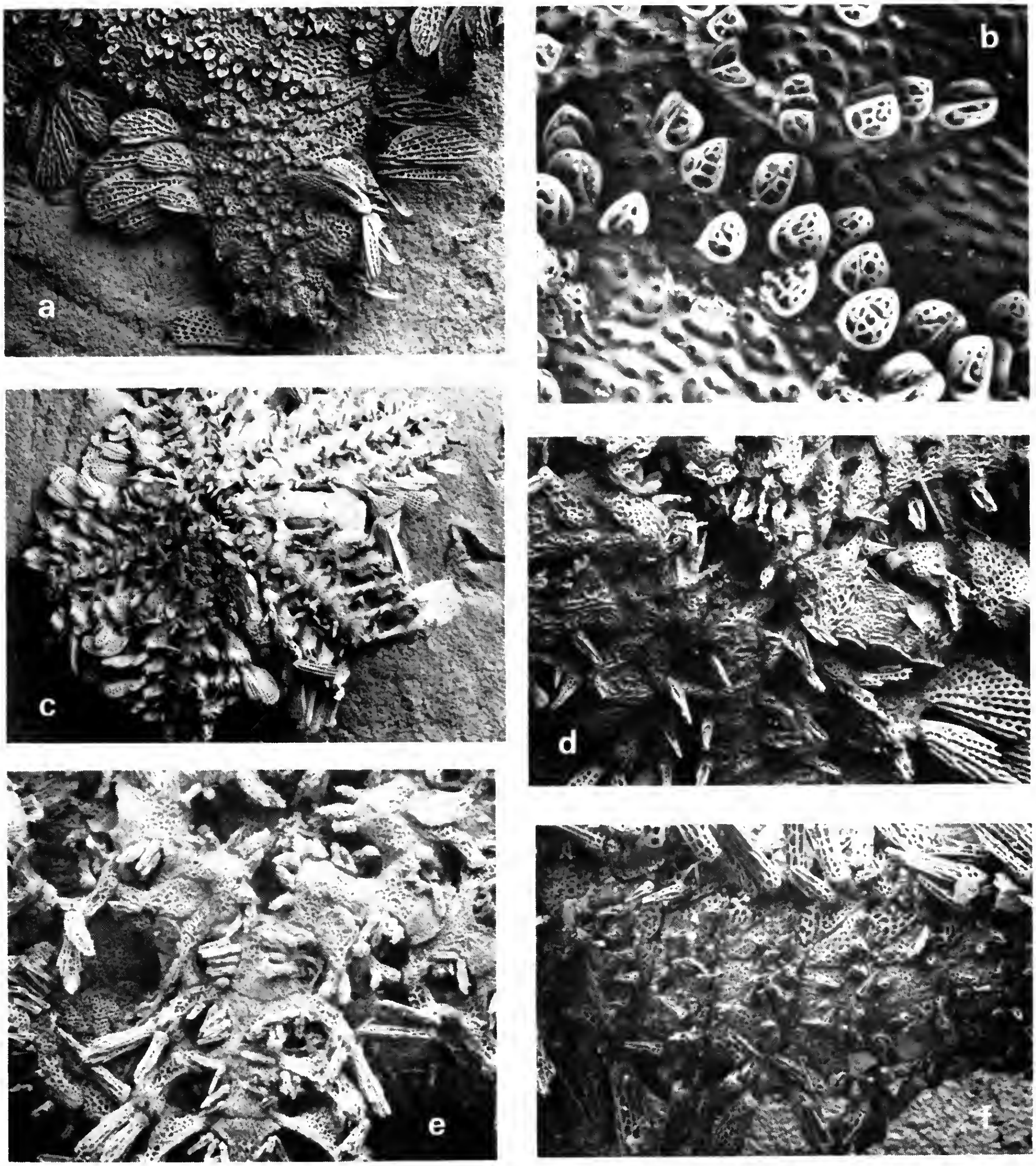


Fig. 57 Ophiuridae: Ophiurinae. a–f *Ophiambix devaneyi* holotype d.d. 3 mm: (a) Part of dorsal side; (b) detail of dorsal side of disk showing disk spinelets, (c) ventral side, (d) of jaw; e–f *Ophiambix meteoris* paratype, d.d. 3·5 mm; (e) close up of jaw; (f) showing arm spines and disk spinelets. All SEM pictures taken of an ISI 60A with environmental chamber.

arm plate is particularly enlarged and nearly reaches the edge of the disk. The tentacle pores are large and open, each is armed with two spine-like tentacle scales—one on the ventral arm plate and one on the lateral arm plate. There are 3–4 arm spines proximally; the ventralmost one is hooked then the others become progressively fan shaped towards the dorsal side; the dorsalmost or second dorsalmost spines are the largest.

TYPE LOCALITY. *Pillsbury* Stn 931, 15°32′N: 61°13′W, 146–494 m off Dominica Leeward Is. The holotype is deposited in the National Museum of Natural History, Smithsonian Institution, Washington D.C.

DERIVATION OF NAME. *O. devaneyi* is named after the late Dennis Devaney, of the Bernice P. Bishop Museum, Honolulu, Hawaii.

REMARKS. *O. devaneyi* can be distinguished from *O. meteoris* by 1. shape of the disk spinelets, 2. the enlarged, flared lateral arm plates, 3. the shape of the arm spines, 4. the number of tentacle scales.

Although the specimen is small it has sufficient developed characters to distinguish it from the other *Ophiambix* species.

Uriopha ios **Paterson, 1980**

Fig. 55

Uriopha ios Paterson, 1980: 211–213.

MATERIAL STUDIED. **IOS:** *Discovery* Investigations Stn 8524/1, 20°46′N: 22°42′W, 4412 m, HOLOTYPE and 10 PARATYPES.

The disk is round to subpentagonal, high, sometimes domed, covered by a dense coating of granules which obscure the underlying plates, the granules extend on to the ventral interradial areas and over the oral and adoral shields; diameter up to 4 mm. Arm combs are absent.

There is one pointed apical papilla flanked on each side by 3–4 oral papillae broadening progressively from peg-like to block-like. The second oral tentacle pore arises superficially away from the mouth slit and is armed with 2–3 tentacle pores each side. The adoral shields are about four times as long as broad. The oral shield is triangular situated totally proximal to the genital slits.

The arms are nearly cylindrical and fragile. The dorsal arm plates are triangular to fan shaped and separated. The ventral arm plates are pentagonal, indented laterally by the tentacle pores with a convex distal edge. The tentacle pores are relatively small armed with 3 tentacle scales on the first arm pore then one sometimes two on subsequent pores. There are two conical, pointed arm spines about half an arm segment in length.

REMARKS. This species can be readily distinguished by the granulated disk, position and armament of the second oral tentacle pore, the number and shape of arm spines and the shape of the arms.

DISTRIBUTION. *U. ios* has only been recorded from the type locality west of Cap Blanc at a depth of 4412 m.

Ophiotypa simplex **Koehler, 1897**

Fig. 55

Ophiotypa simplex Koehler, 1897: 3–6; 1907: 255; 1909: 145. Litvinova, 1975: 196–198.

MATERIAL STUDIED. **IOS:** *Discovery* Investigations Stn 8524/1, 20°46′N: 22°42′W., 4412 m, 9 specimens.

The disk is round, domed and dominated by the primary plates, only one other plate lying interradially. No radial shields or arm combs are present; diameter up to 5 mm.

There is one large triangular apical papilla, individual oral papillae are not developed instead there is a long narrow bar along the edge of the jaw. The second oral tentacle scale opens outside the mouth adjacent to the first ventral arm plate and is armed with a large round tentacle scale. The adoral shields are large swollen, just wider than long. The oral shield is small, barely distinguishable, triangular with a convex distal edge.

The arms are short noded and flattened dorsoventrally. The dorsal arm plates are small, triangular, separated, and appear to lie beneath the level of the very tumid lateral arm plates. The ventral arm plates are pentagonal, often with a convex distal edge, and separated; they too appear to lie beneath the level of the lateral arm plates. The tentacle pores are relatively large and armed with one large rounded tentacle scale. There is one short, pointed conical spine.

Remarks. *O. simplex* is easily recognised by its overall 'star shape', the domed disk dominated by the primary plates and by the swollen lateral arm plates which carry only one arm spine.

Distribution. This species has been recorded in the NE Atlantic from off the Azores and Cape Verde Is, it has also been found in the Venezuelan Basin in the Caribbean and from the Indian Ocean. It appears to be a member of the lower abyssal fauna being recorded at depths of 3595–4366 m.

Perlophiura profundissima Belyaev & Litvinova, 1972
Fig. 55

Perlophiura profundissima Belyaev & Litvinova, 1972: 7–11; Litvinova 1975: 198–199.

Material studied. **COB:** BIOGAS Stn 5: DS82, 4462 m, 1 specimen.
INCAL: Stn 0S5, 47°32′2N: 9°34′7W, 4248 m, 1 specimen; Stn WS08, 47°29′N: 9°34′1W, 4287–4301 m, 2 specimens; Stn WS09, 47°27′9N: 9°34′W, 4277 m, 1 specimen; Stn WS10, 47°27′3N: 9°39′W, 4354 m, 1 specimen.
IOS: *Discovery* Investigations Stn 8524/1, 20°46′N: 22°42′W, 4412 m, 30 specimens.

The disk is round to pentagonal, covered with only the primary plates, occasionally one of the radial plates may be divided, each plate is thin and fenestrated, diameter up to 4·8 mm. This species resembles the post metamorphosed stage of many other ophiuroids.

There is one pointed, nearly triangular, apical papillae. The oral papillae are often not developed, instead there is a long continuous, narrow plate along the edge of the jaw. However, Belyaev & Litvinova (1972) found some specimens with up to 3 rounded discrete oral papillae on each side. The second oral tentacle pore opens outside the mouth slit, adjacent to the first ventral arm plate. The adoral shields are of varying length. The oral shield is irregular in shape varying from triangular to pentagonal. In the specimens from the *Discovery* there are two rectangular plates flanking the oral shield; these plates appear to be missing in the specimen figured by Belyaev & Litvinova (1972), suggesting that the plating in this species is relatively variable.

The arms are noded, long and fragile. The dorsal arm plates are small transversely dumb-bell shaped and broader than long. The first and second ventral arm plates are hexagonal, longer than broad, subsequent plates are pentagonal becoming triangular. The lateral arm plates are long. The tentacle pores are small, each armed with one small, rounded tentacle scale. There are two or three very short pointed arm spines.

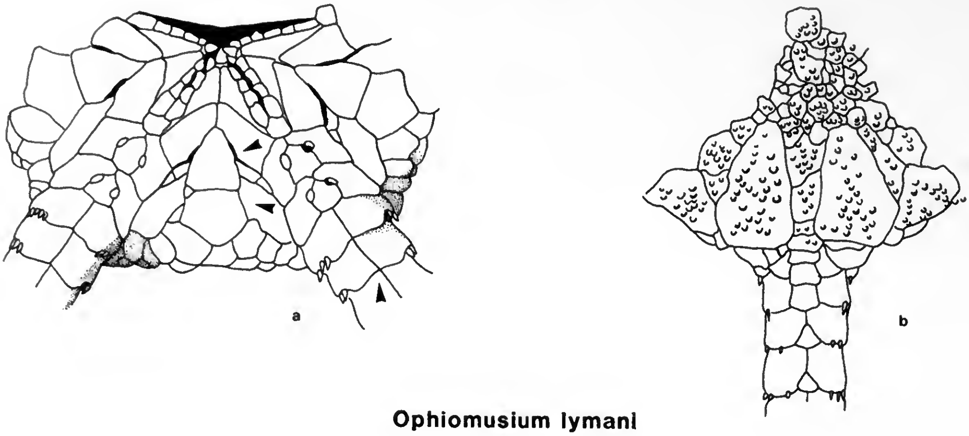
Remarks. This is a distinctive species characterised by several neotonous features: a disk comprising large primary plates which are thin and fenestrated; rudimentary apical and oral papillae with ill-defined adoral and oral shields; long lateral arm plates and rudimentary dorsal arm plates; small arm spines. The relatively small size of this species perhaps accounts for its comparatively recent discovery.

Distribution. *P. profundissima* is a member of the lower abyssal zone (sensu Menzies, George & Rowe, 1973) rarely having been recorded shallower than 4000 m. Besides the NE Atlantic it has been recorded from the Pacific and Indian Oceans and the Caribbean Sea with a bathymetric range of 2265–8135 m.

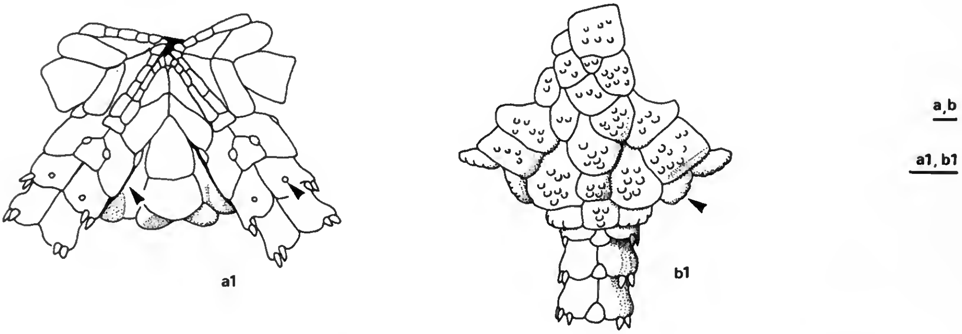
OPHIOLEPIDINAE

Diagnosis. This subfamily of the Ophiuridae is characterised by the disk covered with distinct plates amongst which the centrodorsal and primary plates are distinct; radial shields conspicuous; usually one apical papilla flanked by a series of continuous oral papillae; the second oral tentacle pore opens within the mouth; arms with distinct dorsal and ventral arm plates; arm spines short and appressed.

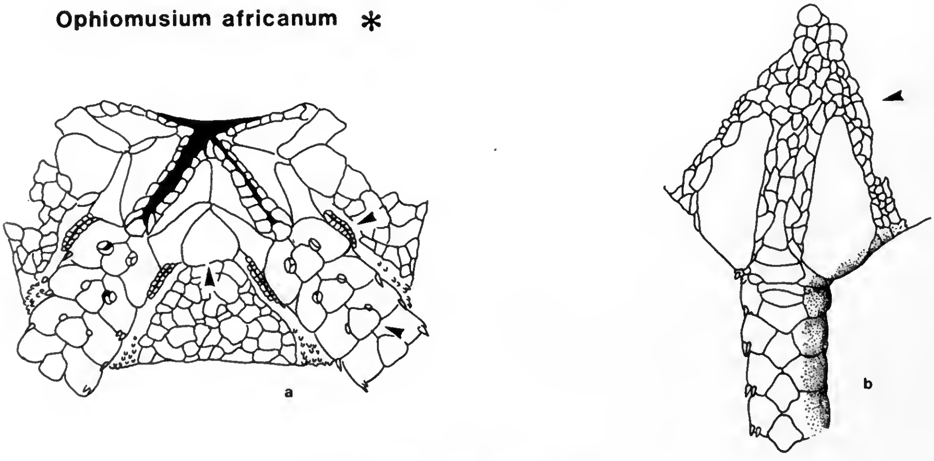
OPHIURIDAE : OPHIOLEPIDINAE



Ophiomusium lymani

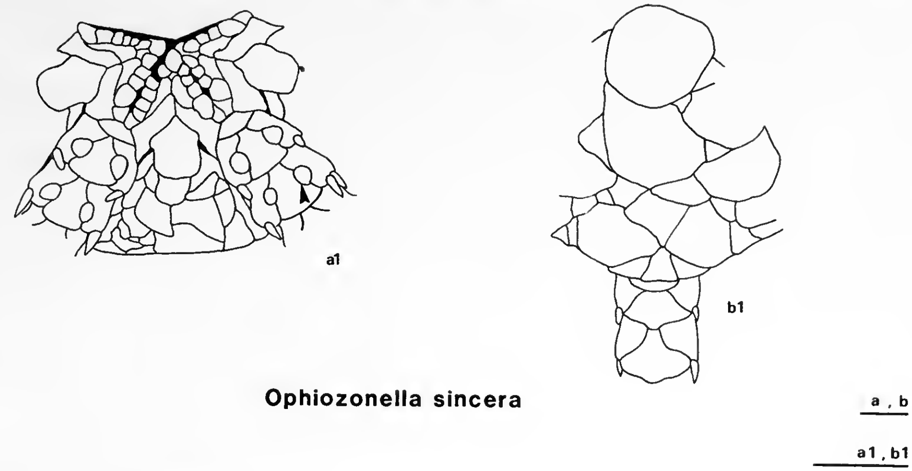


Ophiomusium africanum *

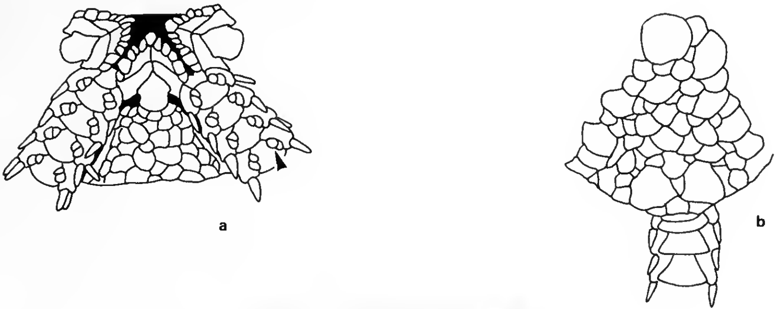


Ophiosphalma armigerum

Fig. 58 Key to the Ophiuridae: Ophiolepidinae. *Ophiomusium* and *Ophiosphalma*: (a) ventral; (b) dorsal view of disk. Bar scales = 1 mm. *–not described in text.



Ophiozonella sincera



Ophiozonella molesta

Fig. 59 Ophiuridae: Ophiolepidinae. *Ophiozonella.* Captions as in Fig. 56.

Ophiomusium lymani Wyville Thomson, 1873

Fig. 58

Ophiomusium lymani Wyville Thomson, 1873: 174; Lyman, 1878: 113; 1882: 90; 1883: 245; Koehler, 1895: 453; 1896*a*: 72; 1896*b*: 204; 1898: 42; Lütken & Mortensen, 1899: 137; Nichols, 1903: 254; Koehler, 1904: 58; Kemp, 1905: 194; Schmidt, 1904: 24; Koehler, 1907: 264; 1909: 161; Grieg, 1910: 33; H. L. Clark, 1911: 107; Mortensen, 1913*b*: 354; Farran, 1913: 34; Koehler, 1914: 26; Koehler, 1922: 411; 1924: 330; Mortensen, 1927: 253; 1933*a*: 100–102; H. L. Clark, 1939: 67; Barham *et al.*, 1967: 777; Schoener, 1967: 650–652; 1968: 84–85; Okutami, 1969: 21–22; Rowe, 1971: 569–581; Ayala & Valentine, 1971: 51–57; Doyle, 1971: 661–664; Cherbonnier & Sibuet, 1972: 1386–7; A. M. Clark & Courtman-Stock, 1976: 191; Murphy, Rowe, Haedrich, 1976: 339–348; Gage & Tyler, 1982: 73–83; Gage *et al.*, 1983: 299–300; Bartsch, 1983: 18–19.

Ophiomusa lymani Hertz, 1927: 103–105; H. L. Clark, 1939: 128.

Material studied. **BMNH:** *Porcupine*. SYNTYPES. HMS *Challenger* Stn 76, 38°11′N: 27°9′W, 1646 m, 1 specimen; HMS *Challenger* off Tristan d'Acunha, 1829 m, 2 specimens; Stn 169, 37°34′S: 179°22′E, 1280 m, 1 specimen. Irish Fisheries Stn SR944, 51°22′N: 12°41′W, 1767 m, 7 specimens.

COB: BIOGAS Stn 1: DS10, 2240 m, 4 specimens; DS11, 2205 m, 12 specimens; DS12, 2180 m, 6 specimens; DS13, 2165 m, 6 specimens; DS15, 2246 m, 33 specimens; DS16, 2325 m, 2 specimens; DS17, 2103 m, 7 specimens; DS18, 2138 m, 2 specimens; DS35, 2226 m, 1 specimen; DS36, 2147 m, 2 specimens; DS61, 2250 m, 2 specimens; DS62, 2175 m, 4 specimens; DS63, 2126 m, 7 specimens; CV08, 2180 m, 20 specimens; CV09, 2119 m, 16 specimens; CV10, 2108 m, 19 specimens; CV20, 2282 m, 2 specimens; CV23, 2034 m, 5 specimens; CV24, 2025 m, 47 specimens; CV25, 1985 m, 13 specimens; CP01, 2245 m, 32 specimens; CP02, 2177 m, 40 specimens; CP03, 2119 m, 6 specimens; CV39, 2350 m, 4 specimens; CP08, 2177 m, 25 specimens; CP26, 2115 m, 97 specimens; CP27, 1920 m, 38 specimens.

BIOGAS Stn 2: DS60, 3742 m, 2 specimens; CV12, 2775 m, 2 specimens; CV37, 3000 m, 1 specimen; CV40, 2860 m, 1 specimen; CP09, 2171 m, 94 specimens; CP12, 2925 m, 7 specimens; CP28, 3380 m, 8 specimens.
Stn 6: DS25, 2096 m, 12 specimens; DS26, 2076 m, 122 specimens; DS49, 1845 m, 3 specimens; DS50, 2124 m, 5 specimens; DS51, 2430 m, 162 specimens; DS52, 2006 m, 14 specimens; DS70, 2150 m, 3 specimens; DS86, 1950 m, 6 specimens; DS87, 1913 m, 19 specimens; CV32, 1895 m, 42 specimens; CP07, 2170 m, 1089 specimens; CP23, 1980 m, 7 specimens; CP24, 1995 m, 39 specimens; CP25, 1894 m, 4 specimens.

INCAL: DS01, 57°59′7N: 10°39′8W, 2091 m, 140 specimens; DS02, 57°58′8N: 10°48′5W, 2081 m; DS05, 56°28′1N: 11°11′7W, 2503 m, 8 specimens; DS06, 56°26′6N: 11°10′5W, 2494 m, 4 specimens; CP01, 57°57′0N: 10°55′0W, 2068 m, 95 specimens; CP03, 56°38′N: 11°06′4W, 2466 m, 82 specimens; CP04, 56°33′2N: 11°11′3W, 2483 m, 5 specimens; CP08, 50°14′7N: 13°13′5W, 2644 m, 16 specimens; CP09, 50°15′4N: 13°15′8W, 2659 m, 13 specimens; CP10, 48°25′5N: 15°10′7W, 4823 m, 1 specimen. WS01, 50°19′4N: 13°08′1W, 2550 m, 81 specimens; WS02, 50°19′3N: 12°55′8W, 2498 m, 97 specimens; WS09, 47°28′8N: 9°34′W, 4277 m, 4 specimens. 0S01, 50°14′9N: 13°10′9W, 2634 m, 2 specimens; 0S02, 48°19′2N: 15°15′9W, 4829 m, 1 specimen; 0S04, 46°03′9N: 10°12′8W, 4796 m, 2 specimens.
IOS: *Discovery* Investigations: Stn 7423, 37°51′N: 27°06′W, 2283 m, 4 juveniles; Stn 8511/1, 41°55′N: 11°15′W, 2389–2399 m, 3 specimens; Stn 8512/4, 42°15′N: 11°36′W, 2281–2245 m, 1 specimen; Stn 8521/6, 20°48′N: 18°53′W, 3064–3070 m, 2 specimens; Stn 9133/5, 20°57.5′N: 18°13.7′W, 2112–2160 m, 3 specimens; Stn 9753/4, 50°54.9′N: 12°12′W, 1942–1947 m, 20 specimens; Stn 9753/7, 50°54.5′N: 12°10.9′W, 1942 m, 5 specimens; Stn 9753/8, 50°54.6′N: 12°11.1′W, 1942 m, 9 specimens; Stn 9756/3 49°48′N: 14°14.8′W, 4080–4156 m, 2 specimens.
SMBA: RRS *Challenger II*: Stn ES4, 56°52′N: 10°01′W, 1993 m, 35 specimens; Stn ES12, 56°49′N: 10°15′W, 2076 m, 6 specimens; Stn ES10, 56°37′N: 10°04′W, 2540 m, 7 specimens; Stn ES14, 56°45′N: 9°46′W, 1770 m, 2 specimens; Stn ES18, 56°44′N: 09°20′W, 1392 m, 1 specimen.

The disk is pentagonal, high covered with relatively small plates amongst which usually only the centrodorsal plate, but sometimes the primary radial plates can be distinguished, diameter up to 30 mm. The radial shields are large, about $\frac{1}{2}$ the disk radius in length, longer than broad and slightly triangular in shape, usually separated by a single row of plates. All the dorsal disk plates are textured, with round glassy beads embedded in the matrix of the plate. There is a rudimentary arm comb of small, rounded, irregularly arranged papillae.

There is one rounded or slightly pointed apical papilla flanked on each side by 5–6 contiguous, block-like oral papillae, the distalmost one of which is the largest. The adoral shields are large, slightly longer than broad. The oral shield is pentagonal to nearly triangular with a straight distal edge. Distally the oral shield usually abuts on a plate of similar shape but almost a mirror image. The genital slits are short and lie adjacent to the oral shield and the first lateral arm plate.

The arms are cylindrical, about 4–5 times the disk diameter. The dorsal arm plates are small, the first three are rectangular and contiguous, subsequent plates triangular and well separated. Ventral arm plates are present only on the first two arm segments, and are pentagonal to irregularly hexagonal in shape. Tentacle pores are present on the first two arm segments, each is armed with one oblong tentacle scale. There are 7–12 short pointed arm spines.

REMARKS. This is a very common and easily identified member of the abyssal fauna. Schoener (1967) has described the juvenile stages, showing that at disk diameters of 2 mm they have three pairs of tentacle pores but as growth proceeds the proximal segment becomes incorporated into the mouth leaving two pairs of arm pores, Gage & Tyler (1982) have dealt with its reproductive biology. Murphy, Rowe & Haedrich (1976) investigated the genetic variability of *O. lymani* from different sample sites.

Ophiomusium africanum Koehler, 1901 (Fig. 58) differs from *O. lymani* in the heavier texturing of the dorsal disk plates, genital slits which extend from the oral shield to the edge of the disk, and the presence of only two ventral arm plates and the distal pair of tentacle pores emerging on the lateral arm plates not associated with a ventral arm plate. *O. africanum* has only been recorded from the Azores at 219 m.

DISTRIBUTION. This species is found in the Pacific, Indian and Atlantic Oceans. In the North Atlantic it has been recorded from the west from the West Indies north to the Davis Strait and SW Iceland and in the east from SE Iceland south to Cap Blanc, with a bathymetric range of 651–4829 m, more usually in the shallower end of this range.

Ophiosphalma armigerum (Lyman, 1878)

Fig. 58

Ophiomusium armigerum Lyman, 1878: 109; 1882: 86–87; Koehler, 1914: 31–32.
Ophiomusium planum Lyman, 1878: 218; 1882: 99; Koehler, 1896*c*: 242; 1899: 26; 1906: 6; 1907: 265; 1914: 26; Grieg, 1910: 36; Nobre, 1931: 94.
Ophiosphalma armigerum H. L. Clark, 1941: 97; Madsen, 1951: 109; Schoener, 1968: 136–139; Bartsch, 1983*b*: 19.
Ophiosphalma planum H. L. Clark, 1941: 98; Madsen, 1951: 108.

MATERIAL STUDIED. **BMNH:** HMS *Challenger* Stn 332, 37°29'S: 27°31'W, 4023 m, HOLOTYPE; HMS *Challenger* Stn 83, 33°13'N: 18°13'W, 3018 m, 1 specimen; HMS *Challenger* Stn 106, 1°47'N: 24°26'W, 3383 m, 2 specimens; Norman collection N. Atlantic, 5 specimens.
COB: BIOGAS Stn 2: CP12, 2925 m, 19 specimens; Stn 4: CV35, 4721 m, 1 specimen; CP05, 3850 m, 4 specimens; CP15, 4715 m, 4 specimens; CP16, 4825 m, 5 specimens; CP17, 4706 m, 1 specimen; Stn 5: CV34, 4406 m, 1 specimen; CP06, 4460 m, 3 specimens; CP19, 4434 m, 1 specimen; CP20, 4459 m, 10 specimens; CP22, 4475 m, 1 specimen.
INCAL: DS13 46°01'9N: 10°17'9W, 4822 m, 1 specimen; CP12, 46°00'5N: 10°18'3W, 4796 m, 1 specimen; CP13, 46°02'1N: 10°14'8W, 4800 m, 4 specimens; WS03, 48°19'2N: 15°23'3W, 4823 m, 8 specimens; WS07, 47°30'6N: 9°37'6W, 4296 m, 1 specimen; WS08, 47°30'5N: 9°32'9W, 4826 m, 6 specimens; WS09, 47°28'8N: 9°34'0W, 4277 m, 2 specimens; WS10, 47°27'3N: 9°30'9W, 4354 m, 3 specimens; ØS04, 46°03'9N: 10°12'8W, 4796 m, 1 specimen.
IOS: *Discovery* Investigations 27°33'N: 14°41.5'W, 2410 m, 1 specimen.

The disk is pentagonal, occasionally indented interradially, slightly raised and covered with relatively small plates amongst which the primary radial plates are usually distinct but the centrodorsal less so; in some specimens the boundaries of disk plates are obscured by thickened skin; diameter up to 25 mm. The radial shields are large, over half the radius of the disk in length, elongated, longer than broad and separated by many small disk plates. There is an irregularly arranged arm comb of small rounded papillae, in two or three rows. All disk plates are textured with small glassy beads embedded in the plate matrix.

There is one rounded or pointed apical papilla flanked on each side by 6–8 contiguous block-like papillae, the distalmost of which is sometimes curved above the next one. The adoral shields are large longer than broad and flared distally. The oral shield is rounded pentagonal to triangular. The genital slits are short, about 1 arm segment long, lined by about 9–12 block-like papillae.

The arms are cylindrical about 3–5 times the disk diameter. The first three dorsal arm plates are rectangular or pentagonal, subsequent ones are teardrop shaped often with a produced distal edge; only the first four plates are contiguous. The ventral arm plates are pentagonal proximally, triangular on distal segments, all are separated. There are three arm tentacle pores, the first is armed with 2–3 tentacle scales, the rest with 2. There are 5 short conical arm spines.

REMARKS. Examination of the material from the Biogas, together with specimens from the BMNH revealed that there are no appreciable differences between *O. armigerum* and *O. planum*. Dr Baker (National Museum of New Zealand), who is preparing a revision of *Ophiomusium* and *Ophiosphalma,* informs me that such differences which have been used to separate them in the past can be correlated with size and stage of development. The name *O. armigerum* has priority.

O. armigerum superficially resembles *Ophiomusium lymani* but differs in having ventral arm plates along most of the arm, an additional pair of tentacle pores, genital slits lined by papillae, the different scaling of the disk and shape of the oral shield. This resemblance to *O. lymani* could cause confusion in deep sea photographs. However, *O. lymani* appears to be limited to shallower depths, although recorded from 600 to 4000 m the records below 3000 m for this species need to be investigated. *O. armigerum* is mainly found from 3000–5000 m.

DISTRIBUTION. *O. armigerum* has been recorded from both sides of the North Atlantic, in the west from off the West Indies north to Nantucket and in the east from the Bay of Biscay south to Cape Verde Is with a bathymetric range of 1601–5025 m.

Ophiozonella sincera (Koehler, 1906)

Fig. 59

Ophiozona sincera Koehler, 1906: 11–12; 1907: 251–252.
Ophiozonella sincera Matsumoto, 1915: 82.

MATERIAL STUDIED. **MNHN:** *Travailleur & Talisman* 15 Aout 1881, Stn 39, 40°5′N: 9°25′40″W, 1225 m, HOLOTYPE.

The disk is round covered with large plates amongst which the large contiguous primary plates are distinct; diameter 4·5 mm. The radial shields are small less than a quarter of the disk radius in length, rounded, about as broad as long, and separated.

There is one angular or rounded apical papilla flanked on each side by 5 contiguous block-like papillae, the distalmost papilla appears to extend above the adjacent papilla which also is the largest. The adoral shields are relatively large and longer than broad. The oral shield is approximately pentagonal with an obtuse proximal angle, slightly indented lateral sides and a convex distal edge. The genital slits extend to the disk edge but are not lined with papillae.

The arms are short, about twice the diameter of the disk in length. The dorsal arm plates are fan shaped, not contiguous. The ventral arm plates are approximately pentagonal becoming axe shaped distally, contiguous at least proximally. The tentacle pores are large each armed with a rounded tentacle scale. There are two pointed arm spines about three quarters of an arm segment long.

REMARKS. *O. sincera* can be distinguished from *O. molesta* by larger disk plates—although this may be just a difference in size, and the tentacle pores being armed with one tentacle scale while *O. molesta* has two scales per pore.

DISTRIBUTION. *O. sincera* has been recorded from the Bay of Biscay at 1225–1690 m.

Ophiozonella molesta (Koehler, 1904)
Fig. 59

Ophiozona molesta Koehler, 1904: 23; 1906: 6; 1907*a*: 253.
Ophiozonella molesta Matsumoto, 1915: 82; 1917: 294; Koehler, 1922*a*: 425.

MATERIAL STUDIED. **MNHN:** *Siboga* 1 specimen.

The disk is subpentagonal, low, covered with relatively large plates amongst which the centrodorsal and primary radial plates are distinct; the latter are separated from the centrodorsal by a ring of smaller plates; diameter up to 12 mm. The radial shields are small, less than a quarter of the disk radius in length, about as long as broad, separated or just touching distally.

There is one large rounded apical papilla flanked on each side by 5–6 oral papillae which are pointed proximally becoming block-like distally; the distalmost papilla appears to curve above the adjacent one, this second distalmost oral papilla is also the largest. The adoral shields are longer than broad and flared distally. The oral shield is pentagonal or slightly arrow shaped longer than broad, with an acute proximal angle slight lateral projections and a convex distal edge. The genital slits extend to the edge of the disk.

The arms length is about 2–3 times the disk diameter. The dorsal arm plates are fan shaped, contiguous proximally. The first ventral arm plate is pentagonal, the second trapezoidal with subsequent plates nearly axe shaped; ventral arm plates are contiguous. The tentacle pores are relatively large each is armed with 2 tentacle scales, an inner small one and an outer round large one. There are two pointed arm spines, situated on the ventral portion of the lateral arm plate, they are nearly one arm segment long.

REMARKS. See *O. sincera* for a comparison with this species.

DISTRIBUTION. This species has been recorded once in the North Atlantic off the Cape Verde Islands, 30°1′N: 14°6′W, 2115 m. It has mostly been recorded from the Indo-West Pacific region at depths of 68–1407 m.

Summary of Taxonomic Proposals and Changes

1. New subfamilies and genera

(*a*) Ophiacanthidae: four new subfamilies proposed.
  (i) Ophiacanthinae, comprising the genera *Ophiacantha* Müller & Troschel 1842, *Ophiacanthella* Verrill, 1899*a*; *Ophialcaea* Verrill, 1899*a*; *Ophiogema* Koehler, 1922*a*; *Ophiolebes* Lyman, 1878 and *Ophiotetra* Verrill, 1899.

(ii) Ophiotominae, comprising the genera *Ophiotoma* Lyman, 1883; *Amphilimna,* Verrill, 1899*a*; *Ophiocymbium* Lyman, 1880; *Ophiodaces* Koehler, 1922*b*; *Ophiodelos* Koehler, 1930; *Ophiolimna* Verrill, 1899*a*; *Ophiologimus* H. L. Clark, 1911; *Ophiomedea* Koehler, 1906; *Ophiophiura* H. L. Clark, 1911; *Ophiopristis* Verrill, 1899*a*; *Ophioprium* Verrill, 1899*a*; *Ophiosparte* Koehler, 1922*b*; and *Ophiotrema* Koehler, 1896*a*.

(iii) Ophioplinthacinae, comprising the genera *Ophioplinthaca* Verrill, 1899*a*; *Microphiura* Mortensen, 1911; *Ophiocamax* Lyman, 1878; *Ophiocopa* Lyman, 1883; *Ophiodictys* Koehler, 1922*a*; *Ophiomelina* Koehler, 1922*a*; *Ophiomitra* Lyman, 1869; *Ophiomitrella* Verrill, 1899*a*; *Ophiomytis* Koehler, 1904; *'Ophiophthalmus'* Matsumoto, 1917; *Ophioripa* Koehler, 1922*a*; *Ophiothamnus* Lyman, 1869; and *Ophiurithamnus* Matsumoto, 1917.

(iv) Ophiohelinae comprising the genera *Ophiohelus* Lyman, 1878; *Ophiomyces* Lyman, 1869; *Ophiothauma* H. L. Clark, 1938; and *Ophiotholia* Lyman, 1880.

(*b*) Ophiuridae: Ophiurinae. New genus erected *Homophiura* with type species *Ophioglypha tessella,* Verrill, 1894.

2. Changes at the generic/specific level

(*a*) Ophiacanthidae

CURRENT USAGE	PROPOSED CHANGE
Ophiacantha veterna Koehler, 1906	*Ophiacantha enopla veterna*
Ophiomitrella levis Koehler, 1914	*Ophiacantha levis*
Ophioprium axiologia H. L. Clark, 1909	*Ophiopristis axiologia*
Ophiacantha hirsuta Lyman,	*Ophiopristis hirsuta*
Ophioprium rosea (Lyman, 1878)	*Ophiacantha rosea*
Ophiacantha (Ophiopristis) permixta Koehler, 1914	*Ophioprium permixtum*

(*b*) Ophiuridae

(i) Revision of the genus *Homalophiura* H. L. Clark, 1915

CURRENT USAGE	PROPOSED CHANGE
Homalophiura confragosa (Lyman, 1878)	*Ophiurolepis confragosa*
H. inorata (Lyman, 1878)	*Ophiurolepis inornata*
H. scissa (Koehler, 1908)	*Ophiurolepis scissa*
H. divisa (Lütken & Mortensen, 1899)	*Ophiura divisa*
H. flexibilis (Koehler, 1911)	*Ophiura flexibilis*
H. inflata (Koehler, 1897)	*Ophiura inflata*
H. madseni Belyaev, 1972	*Ophiura madsen*
H. mimaria (Koehler, 1908)	*Ophiura mimaria*
H. nana (Lütken & Mtsn., 1899)	*Ophiura nana*
H. scutellata (Lütken & Mtsn., 1899)	*Ophiura scutella*
H. violainae Cherbonnier & Sibuet, 1972	*Ophiura violainae*
H. euryplax H. L. Clark, 1939	*Ophiura (Ophiuroglypha) euryplax*
H. glypta H. L. Clark, 1939	*Ophiura (Ophiuroglypha) glypta*
H. intorta (Lyman, 1878)	*Ophiura (Ophiuroglypha) intorta*
H. schmidtotti (Hertz, 1927)	*Ophiura (Ophiuroglypha) schmidtotti,*
H. multispina Cherbonnier & Sibuet, 1972	*Ophiura irrorata polyacantha* Mortensen, 1933*a*
H. abyssorum (Lyman, 1883)	*Homophiura abyssorum*
H. clasta (H. L. Clark, 1911)	*Homophiura clasta*
H. tessellata (Verrill, 1894)	*Homophiura tessellata*

(ii) The *Ophiura irrorata* group

CURRENT USAGE	PROPOSED CHANGE
Ophiura irrorata (Lyman, 1878)	*O. irrorata irrorata*
Ophiura concreta (Koehler, 1901)	*O. irrorata concreta*
Ophiura loveni (Lyman, 1878)	*O. irrorata loveni*

(iii) The *Amphiophiura bullata* complex

CURRENT USAGE	PROPOSED CHANGE
Amphiophiura bullata (Wyville Thomson, 1877)	*A. bullata bullata*
A. convexa (Lyman, 1878)	*A. bullata convexa*
A. vitjazi Litvinova, 1971	*A. bullata vitjazi*

(iv) Ophiolepidinae

CURRENT USAGE	PROPOSED CHANGE
Ophiosphalma planum (Lyman, 1878)	*O. armigerum* (Lyman, 1878)

3. New species described

Ophiuridae
- (i) *Ophiura scomba*
- (ii) *Ophiambix devaneyi*

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British Museum (Natural History)

Tilapine fishes of the genera *Sarotherodon, Oreochromis* and *Danakilia*

Dr Ethelwynn Trewavas

The tilapias are cichlid fishes of Africa and the Levant that have become the subjects of fish-farming throughout the warm countries of the world. This book described 41 recognized species in which one or both parents carry the eggs and embryos in the mouth for safety. Substrate-spawning species, of the now restricted genus *Tilapia*, are not treated here.

Three genera of the mouth-brooding species are included though in one of them, *Danakilia*, the single species is too small to warrant farming. The other two, *Sarotherodon*, with nine species, and *Oreochromis*, with thirty-one, are distinguished primarily by their breeding habits and their biogeography, supported by structural features. Each species is described, with its diagnostic features emphasised and illustrated, and to this is added a summary of known ecology and behaviour. Conclusions on relationships involve assessment of parallel and convergent evolution. Dr Trewavas writes with the interests of the fish culturists, as well as those of the taxonomists, very much in mind.

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Miscellanea

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Miscellanea

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A revision of the Suctoria (Ciliphora, Kinetofragminophora) 2. An addendum to *Acineta*

Colin R. Curds
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Introduction

The important revision of suctorian taxonomy by Jankowski (1981) did not come to the author's attention until after the paper by Curds (1985) had passed the page-proof stage when a brief note was added on page 126. While many of the changes made by Jankowski (1981) were independently included by Curds (1985) several important differences, alternatives and additions made by the Russian author merit attention in detail in order to prevent any future possible taxonomic confusion.

Additional notes on the genus *Acineta* Ehrenberg, 1833

The transference of most of the *Acineta* species described by Swarczewski (1928) including *Acineta biloba, A. commensalis, A. cordiformis, A. crypturopi, A. foecunda, A. lobata, A. ovalis, A. parva, A. pulchra, A. pumila, A. pusilla, A. pugmaea, A. sphaerifera* and *A. vulgata* to the genus *Tokophrya* by Jankowski (1981) is not considered to be appropriate. The major difference between these two genera lies in the fact that while *Acineta* has a lorica *Tokophrya* does not and most of the illustrations of the above list of species clearly show the presence of lorica. Admittedly the lorica is indistinct in *A. commensalis* and *A. lobata* but even in these examples the presence of an intervening collar between stalk and zooid indicates the presence of a lorica. Thus each of the above species possesses an additional synonym in the name of *Tokophrya* attributable to Jankowski (1981).

The erection of the new genus *Tomodiscophrya* for the species *Acineta paratuberosa* Nie & Ho, 1943, erroneously omitted from Curds (1985), is considered here to be unwarranted since it lies within the known range of variation in the type species *Acineta tuberosa* Ehrenberg, 1833 to which the synonyms *Acineta paratuberosa* Nie & Ho, 1943 and *Tomodiscophrya paratuberosa* Jankowski, 1981 should be added. Similarly the new species *Acineta oceanica* Jankowski, 1981 is also thought to lie within the range of variation of *Acineta tuberosa* and this should be added to its list of synonyms.

Jankowski (1981) transferred *Acineta amphiasci* Precht, 1935 into the genus *Trematosoma* Batisse, 1972 whereas Curds (1985) transferred the same taxon into the genus *Conchacineta* Jankowski, 1978. Both authors referred to the linear arrangement of the tentacles as a major reason for their actions but it remains a matter of opinion which is accepted. However, it should be pointed out that the original generic description of *Trematosoma* states that the cytoplasm is totally covered by a thin lorica and that the tentacles emerge from a deep furrow. This is not the case in *Acineta amphiasci* Precht, 1935 where the cytoplasm is clearly depicted as protruding from the aperture of the lorica. Similarly the distinctive row of alveolar sacs which lie along the apical edge of the cytoplasm in *Trematosoma* is not present in *Acineta amphiasci.* Further differences between the two genera lie in bud morphology which has not been described in *A. amphiasci.* For these reasons, it is thought that transference of the latter taxon to the genus *Conchacineta* as suggested by Curds (1985) is the better course to take until more information becomes available.

The erection of a new genus *Vasacineta* Jankowski, 1981 with *A. cuspidata* Kellicott, 1885 as the type species coincided precisely with the ideas of the present author who erected the genus *Kellicotta* Curds, 1985 for the same taxon. This means that *Kellicotta cuspidata* Curds, 1985 becomes a junior synonym to *Vasacineta cuspidata* Jankowski, 1981. Furthermore the new

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species *Acineta talitrus* Jankowski, 1981 is considered to be distinct and needs adding to those described in Curds (1985).

The insertion of the following amendments into the key of Curds (1985) will serve to distinguish this new species from its close morphological relative *Acineta corophii* Collin, 1912.

41	Attached to crustacea	41a
	Attached to inanimate objects	***A. tuberosa***
41a	Rim of lorica distinctly curves outwards	***A. talitrus***
	Rim of lorica not curved outwards	42
42	Body confined within lorica, only tentacles protrude	***A. crater***
	Body projects out from lorica	***A. corophii***

Description of additional species

Acineta talitrus Jankowski, 1981

Description (Fig. 1). Small (40–50 µm long), marine loricate suctorian that is bell-like in outline, laterally flattened. Two small, rounded actinophores present, each bearing a fascicle of large numbers of capitate tentacles. Apical aperture dumb-bell shape at which the rim of the lorica distinctly curves outwards. Cytoplasm does not always completely fill the lorica. Stalk short, less than quarter body length, joining lorica without an intervening collar or other structure, usually with small basal disc. Attached to the gills of the crustacean amphipod *Talorchestia*. Reproduction by endogenous budding. Spherical macronucleus centrally located, with a single contractile vacuole situated apically nearby.

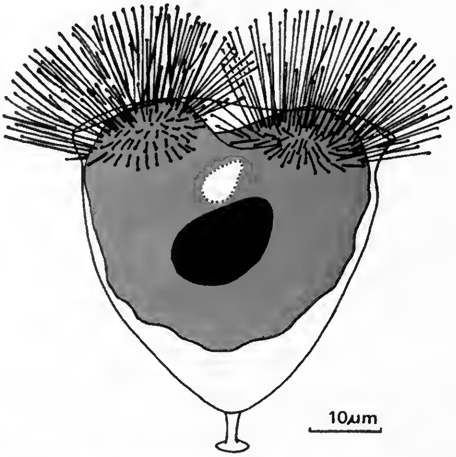

Fig. 1 *Acineta talitrus* after Jankowski (1981).

Note. Apparently closely related to *Acineta corophii* with which this may later be found synonymous. However the rather different lorica shape and greater numbers of tentacles merits its retention as a separate species until further information is obtained.

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A revision of the Suctoria (Ciliophora, Kinetofragminophora) 3. *Tokophrya* and its morphological relatives

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Contents

Introduction

The first two parts of this series (Curds, 1985*a* & *b*) dealt with *Acineta* and its relatives which are all stalked forms that possess a lorica and reproduce asexually by circum-invaginative endogenous budding. The genera included here similarly reproduce by endogenous budding but none possess a lorica, some are stalked while others attach or anchor themselves to the substrate by a body projection. The major genus included here is *Tokophyra* Butschli, 1889 a well known freshwater genus that contains a large number of nominal species. Many of these have been transferred to other genera but until recently not even a check list of those which remained was available, thus making it difficult for the taxonomist and ecologist to identify them. A brief account of the structures and modes of reproduction important in taxonomy was given in Curds (1985a) and will not be repeated here as the genera included in both parts are related.

Genus *TOKOPHRYA* Butschli, 1889

Butschli (1889) erected the genus *Tokophrya* for a wide variety of suctorians since his diagnosis included all those species which had a stalk, reproduced endogenously and were without a lorica. He divided the genus into three subgenera, including *Discophrya* and two other unnamed subgeneric groups, because of the variety of form included in the diagnosis. Collin (1912) merged the first two of these subgeneric groups into the genus *Discophyra* Lachmann, 1859 which clearly had priority and emended the diagnosis of *Tokophrya* to include only those species with a pyriform or pyramidal body shape and tentacles in 1 to 4 fascicles on the apical surface. With the one exception of *Tokophrya flexilis* Kellicott, 1887, all 8 species included by Collin (1912) were retained by Matthes & Rebhan (1983) in their recent check list of 19 species. The species included here agree, to a large extent, with those in the previously mentioned list although there are some differences that should be noted. The two loricate species *Acineta tripharetrata* and *Tokophrya muscicola* have been transferred to *Phyllacineta tripharetrata* Curds, 1985*a* and *Rondacineta muscicola* Jankowski, 1978 respectively. The stalkless *Tokophrya bathynellae* Chappuis, 1944 is transferred to *Brachyosoma bathynellae* later in this publication. Additionally 5 other species of *Tokophrya* omitted by Matthes & Rebhan (1983) and one doubtful species have been included here. Jankowski (1981) suggested the transfer of several of Swarczewsky's (1928) *Acineta* species into

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Tokophrya but these changes were not accepted by Curds (1985*b*) and are therefore omitted from this publication.

Diagnosis of *Tokophrya*

Suctorians whose outline may be oval, pyriform or triangular, not usually flattened laterally and only weaker so when they are. All species so far reported are freshwater. Lorica absent. Attached to invertebrates, aquatic plants or inanimate objects by means of a stalk. Tentacles arranged in 1 to 4 fascicles, usually situated on the apical surface. Actinophores, if present, simple rounded lobes and not ring-like. Reproduction by circum-invaginative endogenous budding resulting in ovoid larvae bearing 4 or 5 transverse ciliary rings. Macronucleus spherical to elongate.

Key to the species of *Tokophrya*

1.	Tentacles in one or two fascicles	6
	Tentacles in more than two fascicles	2
2.	All tentacles at apical end of body	3
	Most tentacles at apex but one fascicle at posterior end of body	***T. fasciculatum***
3.	Tentacles in four fascicles on actinophores	5
	Tentacles in three fascicles not on actinophores	4
4.	Not epizooic, tentacles capitate, two contractile vacuoles	***T. pyrum***
	Epizooic, tentacles not capitate, one contractile vacuole	***T. diaptomi***
5.	Actinophores in centre of apical region surrounded by rim	***T. emarginata***
	Actinophores at corners of apical region, not surrounded by rim	***T. quadripartita***
6.	Tentacles in single fascicle	7
	Tentacles in two fascicles	10
7.	Single contractile vacuole, found on peritrichs	8
	Two contractile vacuoles, found on arthropods	***T. manueli***
8.	Tentacles long, stalk thin	9
	Tentacles short but many, stalk thick	***T. pygmaea***
9.	Ovoid body, many tentacles, stalk as long as body	***T. okobojiensis***
	Pyriform or irregular body, few tentacles, stalk half body length	***T. carchesii***
10.	Gregarious, grows in colonial groups	***T. glomerata***
	Solitary	11
11.	Junction of stalk with body simple (Fig. 1a)	14
	Junction of stalk with body complex (Fig. 1b–d)	12

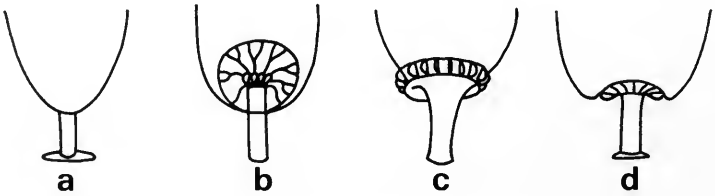

Fig. 1 Various junctions between stalk and body found in *Tokophrya*.

12.	Apical body region with circular rim	***T. wenzeli***
	Apical body region without circular rim	13
13.	Stalk joins body inside a pocket, single contractile vacuole	***T. actinostyla***
	Stalk joins body via external frilled collar, two contractile vacuoles	***T. ornata***
14.	Epizooic on crustacea or molluscs	18
	Not epizooic	15
15.	One contractile vacuole posterior, one anterior	***T. infusionum***
	All contractile vacuole lie in anterior	16

16.	Body elongate, with one or two contractile vacuoles situated laterally	***T. lemnarum***	
	Body rounded, with single contractile vacuole centrally located at apex		17
17.	Stalk thin, body small, found in sphagnum moss	***T. gracilipes***	
	Stalk wide, body medium, found in foul water	***T. bengalensis***	
18.	Body rounded	***T. stammeri***	
	Body conical to pyramidal		19
19.	Apical region strongly convex, two contractile vacuoles, situated laterally	***T. grisea***	
	Apical region concave or slightly rounded, single, usually centrally located, contractile vacuole		20
20.	Apical region strongly concave, actinophores well developed	***T. phreaticum***	
	Apical region rounded or convex, actinophores present but not well developed	***T. cyclopum***	

Species descriptions

Tokophrya quadripartita (Claparède & Lachmann, 1859) Butschli, 1889

Podophrya quadripartita Claparède & Lachmann, 1859
Acineta quadripartita Stein, 1859
Podophyra cyclopum Claparède & Lachmann, 1861 *pro parte*
Acineta quadriloba Stein, 1867
Megatricha partita Badcock, 1880
Tokophryopsis (*Epitokophrya*) *quadripartita* Jankowski, 1978

Description (Fig. 2). This, the type, is a medium to large, (60–140 µm long), freshwater species whose body shape is pyramidal and approximately square in cross section. There are 4 lobe-like prominent actinophores, one at each corner of the apical surface, each bearing a fascicle of capitate tentacles. Lorica absent. Stalk of variable length present. Attached to a variety of substrata including animals such as peritrich stalks (*Epistylis plicatilis*), mollusc shells (*Paludina* sp.), crustacea (*Cyclops*), turtle shells (*Chrysemys picta belli*), a variety of aquatic plants, to organic debris such as activated sludge and to inanimate objects. Number of contractile vacuoles varies from 1 to 3. Macronucleus spherical to ovoid, centrally placed. Endogenous budding results in an ovoid larval form with variable numbers of ciliary rows and formations. Both Collin (1912) and Kormos and Kormos (1958) clearly illustrate (see Fig. 2f, g, i, j) 5 rings of cilia while the more modern silver-line preparations of Guilcher (1951) have shown (Fig. 2d,e) that there are 4 double transverse rows of cilia encircling the body with a single short posterior row. It is not yet quite clear whether or not the ciliation is variable or if the earlier reports reflect the difficulties of examining ciliary rows without the use of staining procedures.

Note. Jankowski (1978) was of the opinion that this species should form a subgenus *Epitokophrya* of the genus *Tokophryopsis* Swarczewsky, 1928 with the major character of having 4 actinophores. However, the major distinguishing characteristic of *Tokophryopsis* is not just the presence of three actinophores but more importantly their ring or crown-like shape. No suctorian described to date, other than *Tokophryopsis gigantea,* has actinophores of that form and for this reason should be kept distinct until further evidence based on other characters suggests otherwise. Butschli (1889) did not designate a type when he erected the genus but it was one of his original nominal species. Sand (1899) did not indicate types in any way but Collin (1912) listed the species in other of the date of the original description and here this has been interpreted to indicate that the first mentioned is the type. Furthermore it is a commonly occurring species that has been figured and described on several occasions.

Tokophrya actinostyla (Collin, 1912) Penard, 1920

Tokophrya cyclopum var. *actinostyla* Collin, 1912

Description (Fig. 3). Medium to large (87–120 µm long), freshwater suctorian whose body shape is approximately cylindrical. There are 2 fascicles of capitate tentacles, one on either side of the apical surface. Lorica and actinophores absent. Attached to crustacea such as *Cyclops* by a wide short stalk that is about a quarter of the body length. Junction between stalk and suctorian a

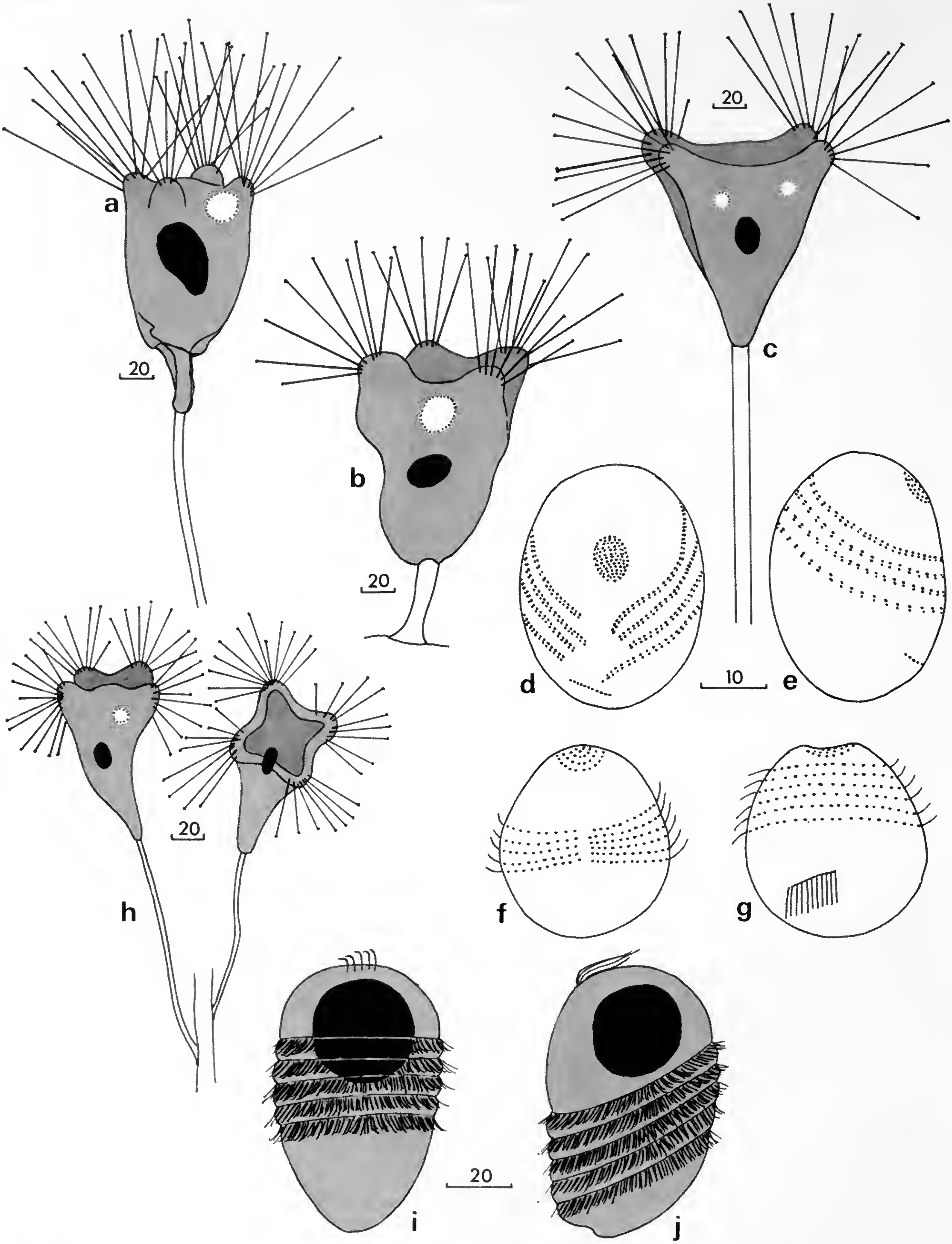

Fig. 2 *Tokophrya quadripartita*: (a) after Goodrich & Jahn, 1943; (b) after Claparède & Lachmann, 1861 (called *Podophrya quadripartita*); (c) after Holm, 1925; (d,e) embryos after Guilcher, 1951; (f,g) embryos after Kormos & Kormos, 1958; (h) after Kent, 1882 (called *Podophrya quadripartita*); (i,j) embryos after Collin, 1912.

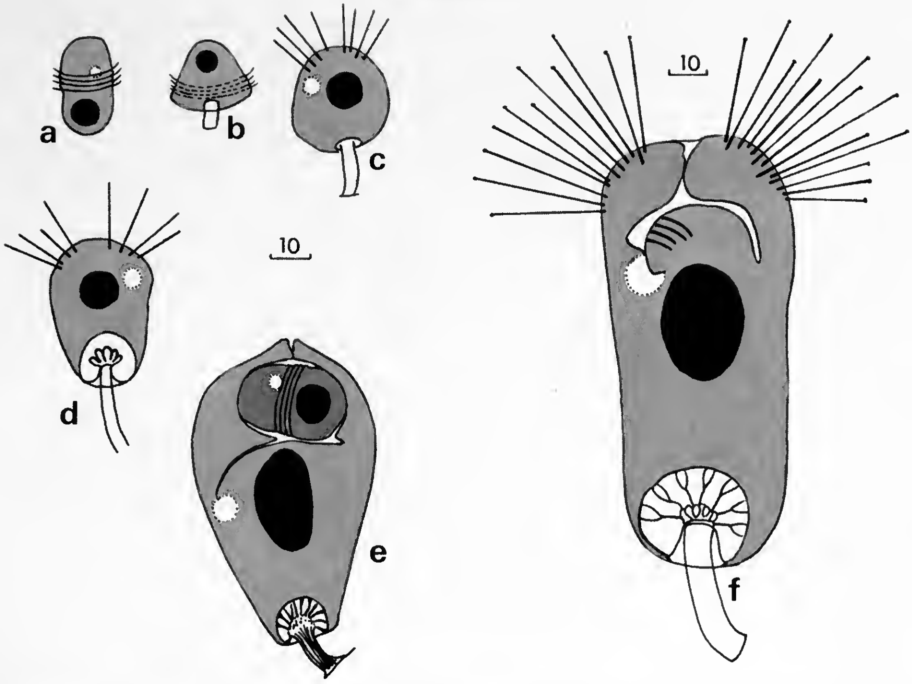

Fig. 3 *Tokophrya actinostyla*: (a–e) stages of development from bud to adult, after Collin, 1912; (f) after Penard, 1920.

prominent spherical capsule enclosed within posterior region of body. Capsule contains many rods radiating from the stalk end to its periphery (Fig. 3e,f). Single contractile vacuole situated anterio-laterally. Centrally located spherical to ovoid macronucleus. Ovoid endogenous buds with 4 or 5 ciliary rings encircling mid-region of bud.

Tokophrya bengalensis Ghosh, 1929

Tokophrya apartita Fukui & Morishita, 1962
Tokophrya conica Fukui & Morishita, 1962
Tokophrya longistyla Fukui & Morishita, 1962
Tokophrya magna Fukui & Morishita, 1962
Tokophrya oligotentaculata Fukui & Morishita, 1962
Tokophrya oviforme Fukui & Morishita, 1962
Tokophrya rotunda Fukui & Morishita, 1962

Description (Fig. 4). Small to medium (30–80 µm long), freshwater species whose body shape varies from roundly conical to ovoid or spherical. There are 2 apical fascicles of capitate tentacles, actinophores either absent or reduced. Lorica absent. Attached by a long stalk to bacterial growths and inanimate objects associated with aerobic sewage-treatment processes. Single contractile vacuole anteriorly located. Macronucleus irregularly ovoid to pyramidal. Budding not described.

Tokophrya carchesii (Claparède & Lachmann, 1859) Butschli, 1889

Podophrya carchesii Claparède & Lachmann, 1859
Tokophryella carchesii Jankowski, 1973

Description (Fig. 5). Small (25–50 µm long), freshwater suctorian whose body varies from pyriform or spherical to irregularly ovoid. Body commonly held at right angles to stalk. Attached to the stalks of peritrichous ciliates such as *Carchesium polypinum, C. aselli, Campanella*

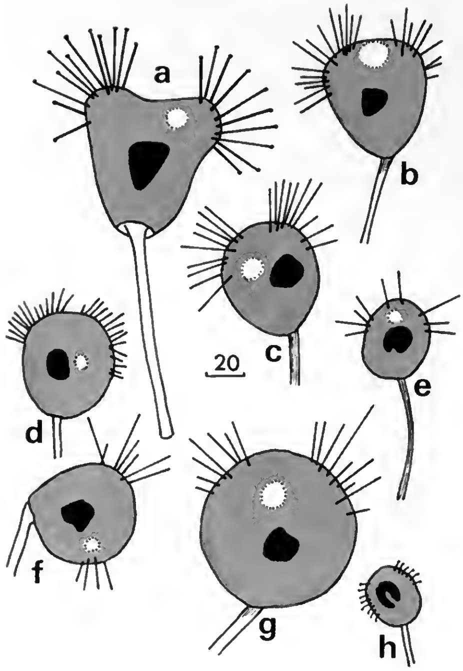

Fig. 4 *Tokophrya bengalensis*: (a) after Ghosh, 1929; (b–h) after Fukui & Morishita, 1962 (called *T. conica, T. oviforme, T. magna, T. apartita, T. oligotentaculata, T. rotunda* and *T. longistyla* respectively).

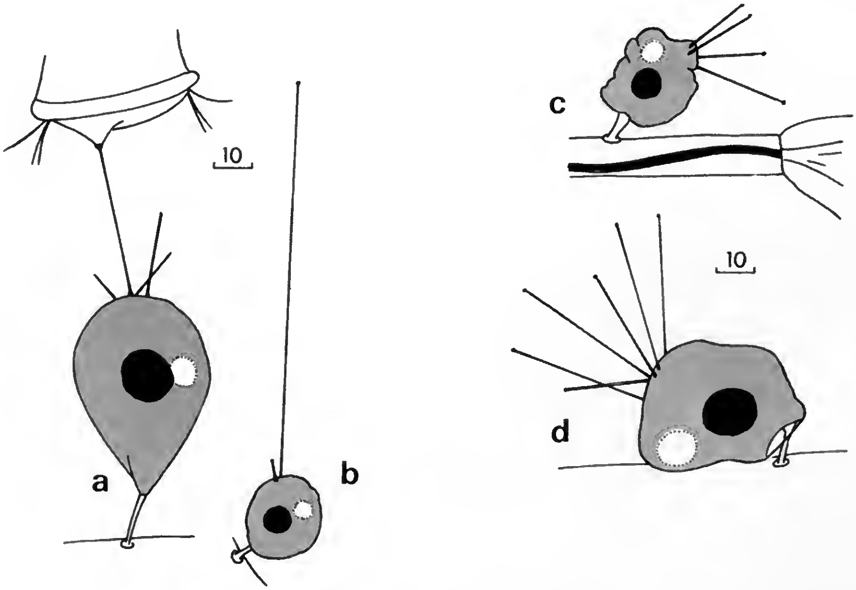

Fig. 5 *Tokophrya carchesii*: (a–d) after Matthes, 1971.

umbellaria and *Epistylis flavicans* upon which the suctorian feeds. Stalk usually less than half the body length. Single fascicle of capitate tentacles of highly variable length. Lorica and actinophores absent. Reproduction by endogenous budding. Macronucleus spherical, single contractile vacuole present.

NOTE. Jankowski (1973) erected the genus *Tokophryella* with this species as the type, however the move was ignored by more recent workers (Matthes and Rebhan, 1983).

Tokophrya cyclopum (Claparède & Lachmann, 1859) Butschli, 1889

Podophrya cyclopum Claparède & Lachmann, 1859
Acineta cyclopum Stein, 1859

DESCRIPTION (Fig. 6). Small to medium (25–80 µm long), freshwater suctorian whose body shape varies from pyriform to pyramidal. Actinophores, if present, rarely prominent. Capitate tentacles in 2 fascicles. Lorica absent. Attached to crustacea such as *Cyclops*. *Gammarus* and *Epischura,* also attached to aquatic plants such as *Lemna* and *Vallisneria* often in the presence of the peritrich *Epistylis anastatica.* Stalk short, usually less than length of the body and frequently longitudinally striated. Reproduction by formation of endogenous buds which bear 4 transverse

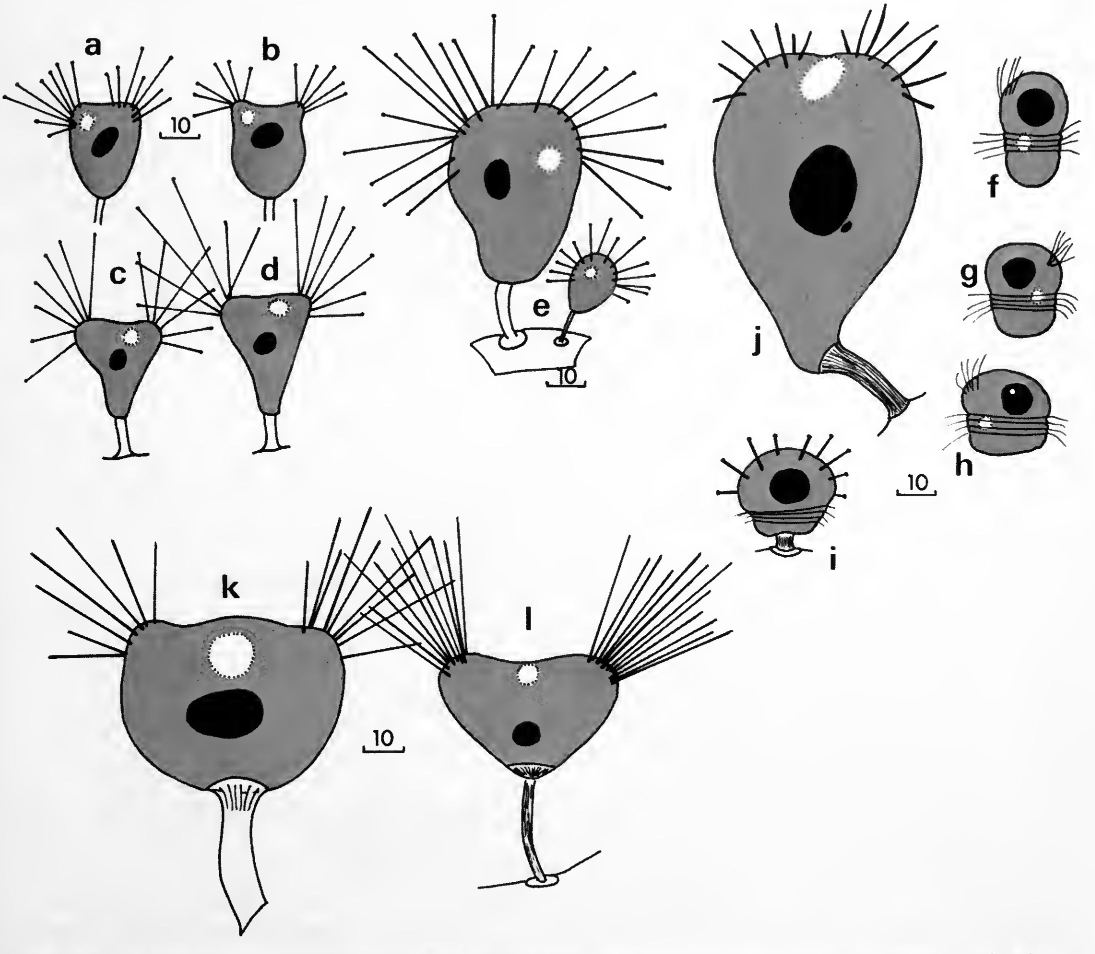

Fig. 6 *Tokophrya cyclopum*: (a,b) after Schewiakoff, 1893 (called *Podophrya cyclopum*); (c,d) after Wailes, 1928; (e) after Kent, 1882 (called *Podophrya cyclopum*); (f–j) stages in development from embryo to adult, after Collin, 1912; (k) after Penard, 1920; (1) after Gajewskaja, 1933.

girdles of cilia. Macronucleus ovoid to spherical, centrally located. Contractile vacuole in anterior body half.

Tokophrya diaptomi (Kellicott, 1885) Sand, 1900

Podophrya diaptomi Kellicott, 1885
Tokophrya diaptami Sand, 1901
Trinacineta diaptomi Jankowski, 1981

Description (Fig. 7). Medium (65 µm long), freshwater species whose pyriform body is elongate and plastic. Numerous tentacles present, not distinctly capitate, arranged in 3 fascicles on the apical body surface. Actinophores and lorica absent. Stalk length varies between half and total body length, is slightly curved and striated. Attached to the freshwater crustacean *Diaptomus*. Budding not described. Contractile vacuole situated apically, spherical macronucleus located centrally.

Note. Jankowski (1981) erected the genus *Trinacineta* with this species as the type. The presence of three fascicles is not regarded sufficient reason to erect a new genus.

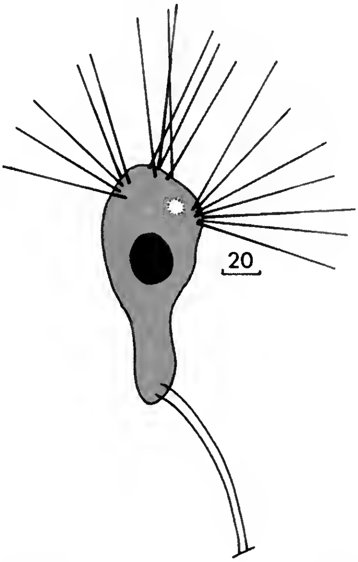

Fig. 7 *Tokophrya diaptomi,* after Kellicott, 1885 (called *Podophrya diaptomi*).

Tokophrya emarginata Swarczewsky, 1928

Tokophrya radiata Gajewskaja, 1933
Tokophryopsis emarginata Jankowski, 1981

Description (Fig. 8). Medium to large (60–150 µm long), freshwater suctorian whose body is distinctly pyramidal in shape. Number of prominent actinophores present, usually 4 but sometimes only 1 or 2. Actinophores situated on the apical surface surrounded by a rim of cytoplasm. Number of fascicles similarly vary from 1 to 4, tentacles not distinctly capitate. Lorica absent. Stalk varies in length, from 50 to 400 µm long, equipped with large basal disc. Attached to crustacean *Odonthogammarus improvisus* in Lake Baikal. Reproduction by endogenous budding. Central spherical macronucleus. Contractile vacuole usually in apical position between the actinophores.

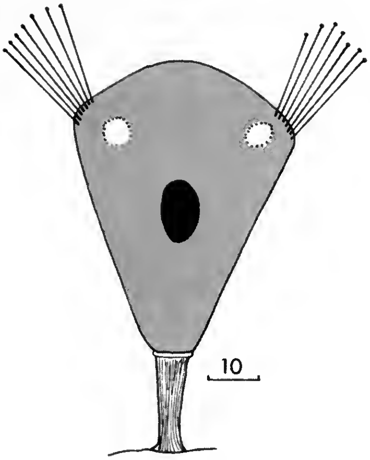

Fig. 8 *Tokophrya emarginata*: (a–c) after Gajewskaja, 1933 (called *Tokophrya radiata*); (d) after Swarczewsky, 1928.

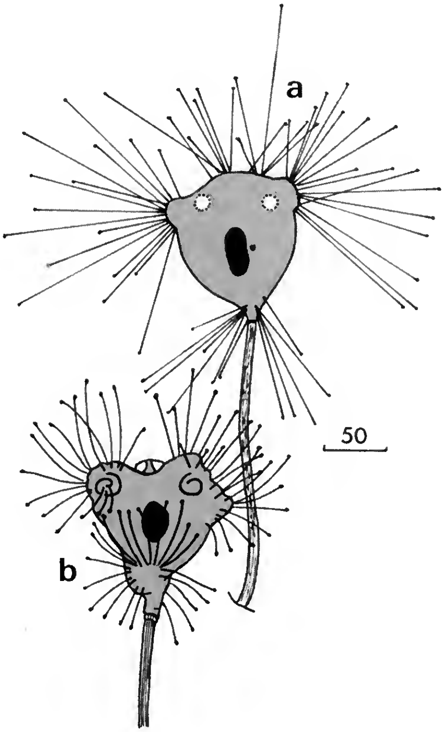

Fig. 9 *Tokophrya fasciculata*: (a) after López-Ochoterena, 1964 (called *Hypophrya fasciculata*); (b) after Entz, 1902 (called *Tokophrya cyclopum*).

Tokophrya fasciculata (López-Ochoterena, 1964) Matthes & Rebhan, 1983

Tokophrya cyclopum Entz, 1902 *pro parte*
Tokophrya cyclopum var. *patagonica* Collin, 1912
Hypophrya fasciculata López-Ochoterena, 1964
Trinacineta patagonica Jankowski, 1981.

DESCRIPTIONS (Fig. 9). Medium to large (96–126 µm long), freshwater suctorian whose body shape is pyramidal. There are 2 lobe-like actinophores but 4 fascicles of capitate tentacles, 3 fascicles are situated on the apical surface but the other is in the posterior region with the tentacles clustered around the stalk. Lorica absent. Attached to the shells of the mollusc *Limnaea attenuata* Say and *Physa osculans* Aldeman by a striated stalk that is at least twice the length of the body. There are two anterior contractile vacuoles, one either side of the body. Central macronucleus ovoid. Reproduction by endogenous budding.

NOTE. López-Ochoterena (1964) erected the genus *Hypophrya* with this as the type species, however recent authorities (Matthes & Rebhan, 1983) do not consider it to be sufficiently distinct to warrant separation from *Tokophrya*. It should be noted that the first record of this organism was that of Entz (1902) who considered it to be a variant of *Tokophrya cyclopum*.

Tokophrya glomerata Penard, 1920

DESCRIPTION (Fig. 10). Small (20 µm long), gregarious, freshwater species which form pseudocolonies of ten to twenty individuals. Each zooid is pyriform in shape and the colony is roughly hemispherical. Stalk short, attached to central mucilaginous mass. Colony floats freely in water. Actinophores greatly reduced or absent. Capitate tentacles in 2 fascicles. Lorica absent. Central macronucleus spherical. Single contractile vacuole located behind nucleus in anterior body third. Conjugation but not asexual reproduction has been described.

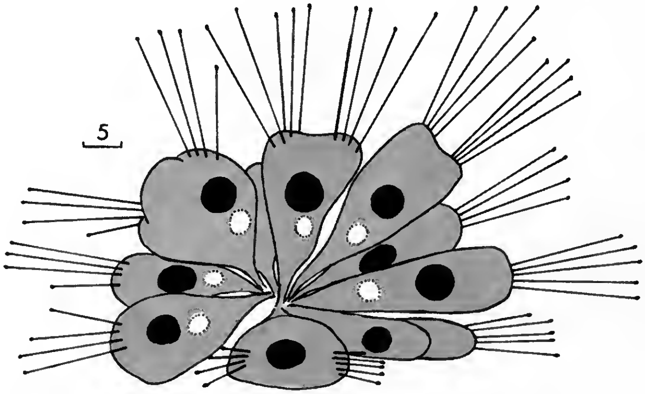

Fig. 10 *Tokophrya glomerata*, after Penard, 1920.

Tokophrya gracilipes Penard, 1920

DESCRIPTION (Fig. 11). Small (30 µm long), freshwater suctorian whose shape is ovoid to pyriform, oval in cross-section. Actinophores and lorica absent. Capitate tentacles arranged in 2 anterio-lateral fascicles. Stalk, which is just longer than the body, widens posteriorly to join a prominent basal plate. Found in sphagnum moss. Central spherical macronucleus, single apical contractile vacuole. Reproduction by endogenous budding.

Tokophrya grisea Gajewskaja, 1933

DESCRIPTION (Fig. 12). Medium (60 µm long), freshwater species whose shape is pyriform with a strongly convex apical surface. Actinophores and lorica absent. Capitate tentacles arranged in 2 anterio-lateral fascicles. Stalk less than length of body, striated and joins body via a narrow, unstriated band. Attached to gammarid crustacea in Lake Baikal. Two anterio-lateral contractile vacuoles present. Macronucleus ovoid and centrally located. Budding not described.

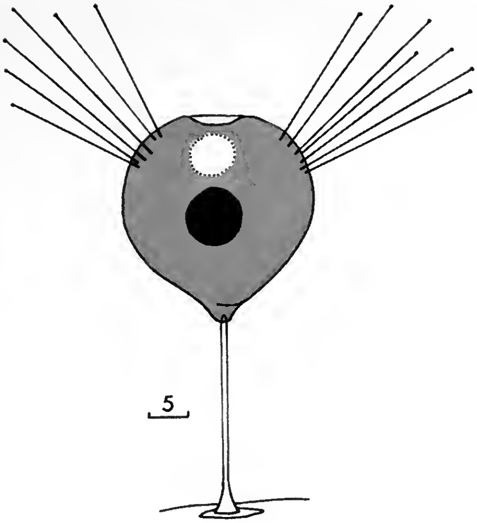

Fig. 11 *Tokophrya gracilipes*, after Penard, 1920.

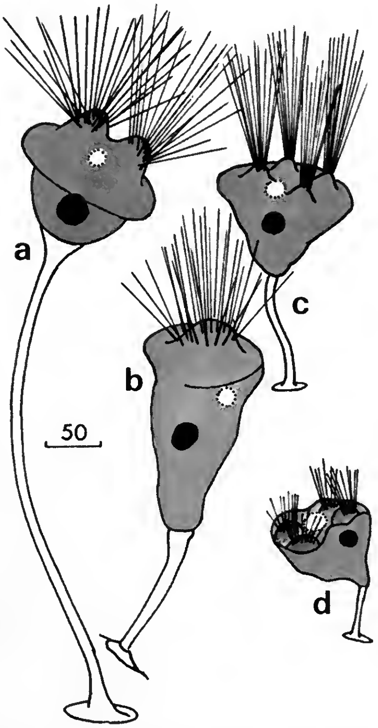

Fig. 12 *Tokophrya grisea* after Gajewskaja, 1933.

Tokophrya infusionum (Stein, 1859) Butschli, 1889

Podophrya fixa Stein, 1854 *pro parte*
Actinophrys sol Stein, 1854 *pro parte*
Acineta infusionum Stein, 1859
Podophrya infusionum Engelmann, 1862
Acineta gelatinosa Buck, 1884 *non* Swarczewsky, 1908
Podophrya fixa Dangeard, 1890
Trichophrya angulata Dangeard, 1890

DESCRIPTION (Fig. 13). Medium (60–80 µm long), freshwater suctorian whose body shape is pyramidal. Actinophores and lorica absent. Capitate tentacles arranged in 2 anterio-lateral fascicles. Stalk short, usually only 5–10 µm long with prominent basal disc, attached to inanimate objects in pond water and infusions. Two contractile vacuoles present, one each in anterior and posterior body halves. Central spherical macronucleus. Reproduction by endogenous budding producing a bud with 4 or 5 ciliary girdles. Most reports indicate the presence of 5 bands of cilia, but Guilcher (1951) illustrated the presence of 4 double bands and a short posterior ciliary row although she too illustrated an example with 5 bands.

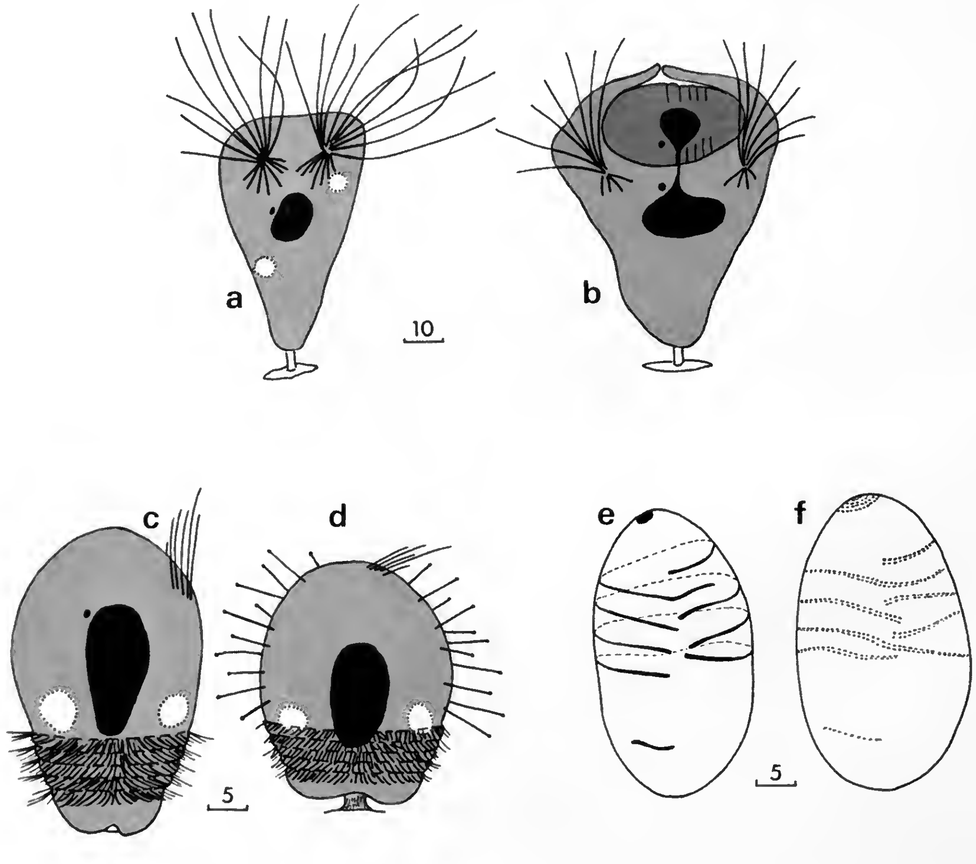

Fig. 13 *Tokophrya infusionum*: (a–d) various stages in development, after Collin, 1912; (e,f) embryos after Guilcher, 1951.

Tokophrya lemnarum (Stein, 1859) Entz, 1902

Acineta lemnarum Stein, 1859
Acineta phryganidarum Stein, 1859
Podophrya mollis Kent, 1882
Podophrya phryganidarum Kent, 1882
Tokophrya cyclopum Sand, 1901 *pro parte*

Description (Fig. 14). Small to medium (40–100 µm long), freshwater species whose body shape is pyriform to pyramidal. Lorica absent. Fascicles of capitate tentacles mounted on 2 actinophores. Stalk striated, of variable length but usually at least as long as body, attached to aquatic plants including *Lemna*. There are usually 2 anterio-lateral contractile vacuoles. Macronucleus ovoid to elongate with several micronuclei. Reproduction by endogenous budding producing buds with 4 ciliary girdles. Conjugation has been reported (Collin, 1912; Kent, 1980–82).

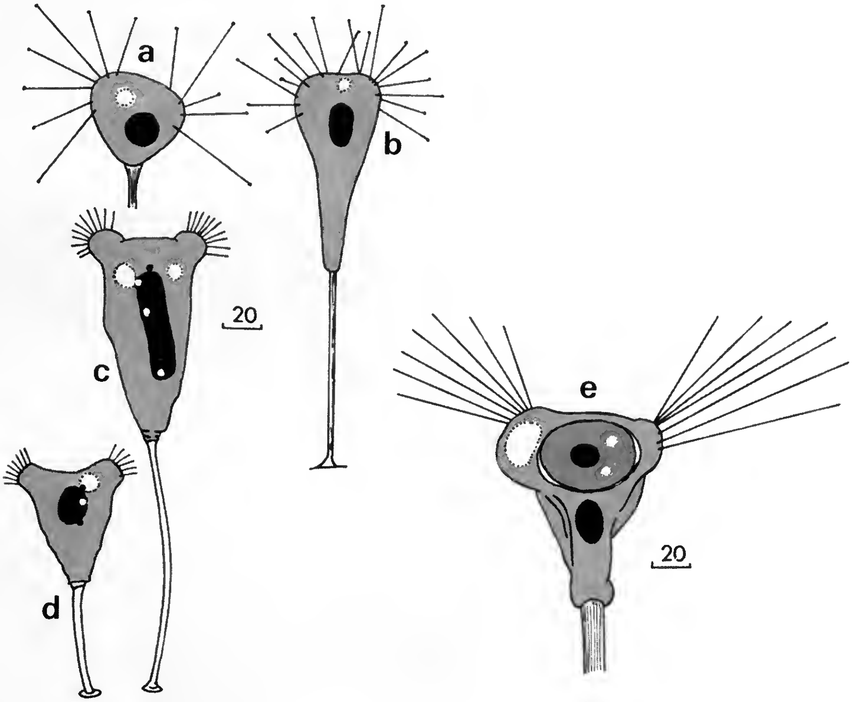

Fig. 14 *Tokophrya lemnarum*: (a,b) after Collin, 1912; (c,d) after Entz, 1902; (e) after Penard, 1920.

Tokophrya manueli Matthes & Rebhan, 1983

Description (Fig. 15). Small (20–55 µm long), freshwater suctorian whose body shape is ovoid. Actinophores and lorica absent. Capitate tentacles in single fascicle distributed over apical surface. Stalk length variable, at least the length of the body but often 2–3 times its length. Junction of stalk with body with scalloped edge. Attached to algae and to the hydrocaulus of *Cordylophora caspia*. There are 3 contractile vacuoles and a centrally located ovoid macronucleus. Reproduction by endogenous bud formation.

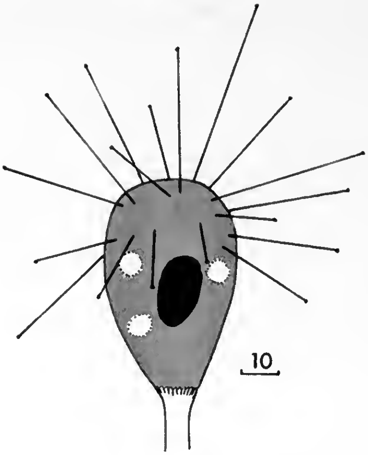

Fig. 15 *Tokophrya manueli*, after Matthes & Rebhan, 1983.

Tokophrya okobojiensis (Goodrich & Jahn, 1943) n. comb.

Podophrya okobojiensis Goodrich & Jahn, 1943
Tokophryella okobojiensis Jankowski, 1981

Description (Fig. 16). Small (35 µm long), ovoid freshwater species. Actinophores and lorica absent. Single anterior fascicle of many capitate tentacles that are at least the length of the body. Stalk about the same length as body, attached to stalks of peritrichs on freshwater turtles. Macronucleus spherical, centrally located with an adjacent contractile vacuole. Mode of reproduction undescribed.

Note. Appears to be related to *T. carchesii* and *T. pygmaea*.

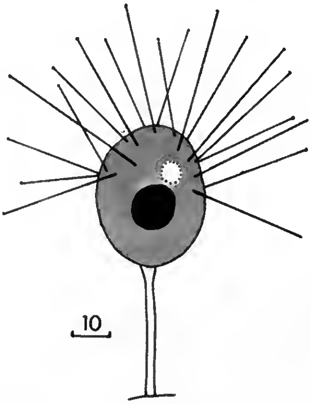

Fig. 16 *Tokophrya okobojiensis*, after Goodrich & Jahn, 1943 (called *Podophrya okobojiensis*).

Tokophrya ornata Gajewskaja, 1933

Basitokophrya Jankowski, 1982

Description (Fig. 17). Small (30–35 µm long), freshwater suctorian whose body shape is approximately ovoid. Actinophores and lorica absent. Two fascicles of tentacles, which have

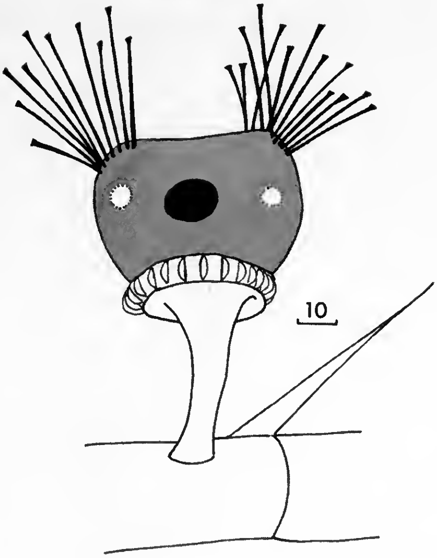

Fig. 17 *Tokophrya ornata,* after Gajewskaja, 1933.

expanded, trumpet-shaped ends, are situated on the anterio-lateral edges of the body. Stalk stout, about same length as body. Junction of stalk with body in form of a prominent frilled collar-like disc. Attached to gammarid crustacea in Lake Baikal. There are 2 contractile vacuoles situated laterally, halfway down the body. Macroneucleus spherical, located centrally. Reproduction not described.

Tokophrya phreaticum Uéno, 1962

Description (Fig. 18). Small (25 µm long), freshwater species whose body is pyramidal. Lorica absent. Two prominent actinophores each with a fascicle of capitate tentacles. Stalk short, usually only 2–4 µm long, attached to the crustacean *Bathynella inlandica* Uéno found in a Japanese well. Single large apical contractile vacuole present, located just in front of central, spherical macronucleus. Reproduction not described.

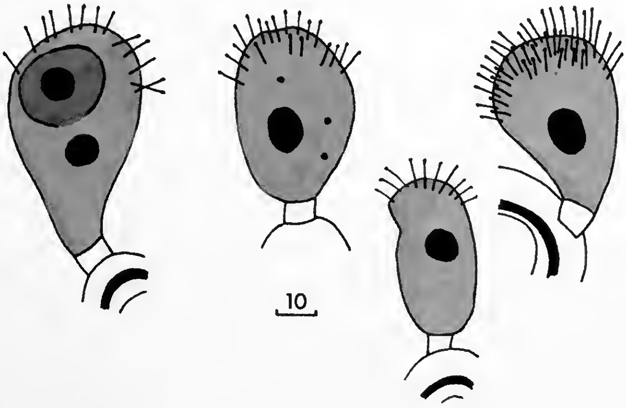

Fig. 18 *Tokophrya phreaticum.* After Uéno, 1962.

Tokophrya pygmaea (Swarczewsky, 1928) n. comb.

Discophrya pygmaea Swarczewsky, 1928
Riftus pygmaea Jankowski, 1981

Description (Fig. 19) Small (50–55 µm long), freshwater suctorian whose body shape is pyriform. Actinophores and lorica absent. Single fascicle of many, short capitate tentacles borne on the apical surface. Attached to the stalks of colonial peritrichs such as *Zoothamnium* sp. by a short but stout stalk. Reproduction by endogenous budding. Macronucleus centrally located.

Note. Originally described as a species of *Discophrya* a genus that reproduces by evaginative budding and usually has a lorica. It would appear to be related to *Tokophrya carchesii*.

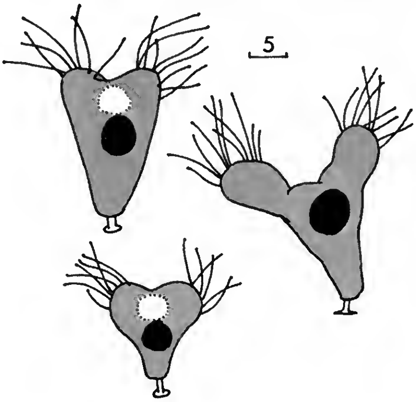

Fig. 19 *Tokophrya pygmaea*, after Swarczewsky, 1928 (called *Discophrya pygmaea*).

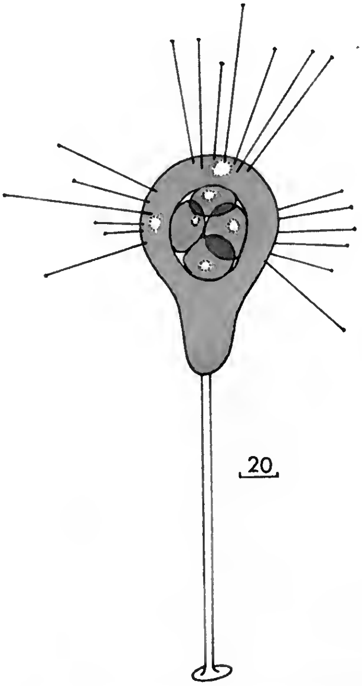

Fig. 20 *Tokophrya pyrum*, after Claparède & Lachmann, 1859 (called *Podophrya pyrum*).

Tokophrya pyrum (Claparède & Lachmann, 1859) Butschli, 1889

Podophrya pyrum Claparède & Lachmann, 1859

DESCRIPTION (Fig. 20). Large (120–170 µm long), freshwater species which is pyriform in shape. Actinophores and lorica absent. There are 3 fascicles of capitate tentacles, 1 on the apex and 2 lateral bundles. Stalk long, usually about double the body length. Attached to aquatic plants including *Lemna trisulca*. There are 2 contractile vacuoles, one apically situated the other is lateral. Spherical macronucleus centrally located. Reproduction by multiple endogenous bud formation.

Tokophrya stammeri Strouhal, 1939

DESCRIPTION (Fig. 21). Small (20 µm long), freshwater suctorian with an ovoid body. Actinophores and lorica absent. There are 2 fascicles of tentacles situated apically. Stalk almost the length of body, attached to the amphipod *Niphargus strouhali*. Single apical contractile vacuole. Spherical macronucleus located in centre of body. Reproduction not described.

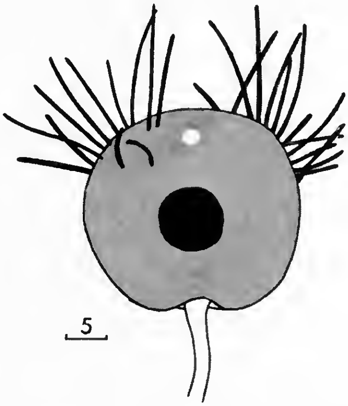

Fig. 21 *Tokophrya stammeri*, after Strouhal, 1939.

Tokophrya wenzeli Matthes & Stiebler, 1970

DESCRIPTION (Fig. 22). Small (22–55 µm long), freshwater suctorian that is pyramidal in shape. Two actinophores present, located on the apical surface and surrounded by a cytoplasmic ridge. Two fascicles of tentacles present. Stalk striated, short, usually about half the body length, joins body via a striated, prominent disc. Attached to water mites such as *Limnesia undulata*, *L. maculata*, *Piona conglobata*, *P. variabilis*, *Arrhenurus globata* and *A. stecki*. Single apical contractile vacuole. Central ovoid macronucleus. Reproduction by endogenous budding.

Species dubium

Tokophrya sp Guilcher, 1951

DESCRIPTION (Fig. 23). Adult undescribed other than it attaches itself to the shed skin of the newt *Triturus vulgaris*. Bud described with 5 girdles of cilia.

NOTE. A description of the adult is necessary before the position of this organism can be assessed.

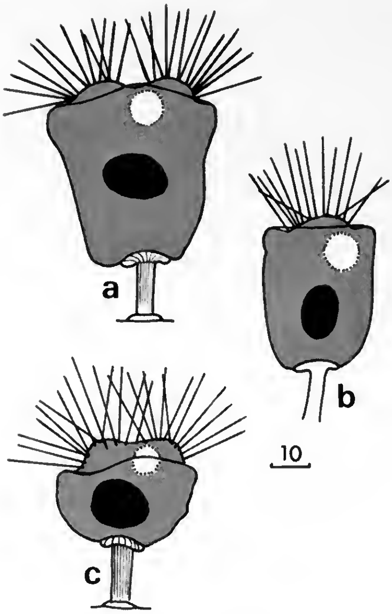

Fig. 22 *Tokophrya wenzeli*, after Matthes & Stiebler, 1970, (a,b) front aspect; (c) side view.

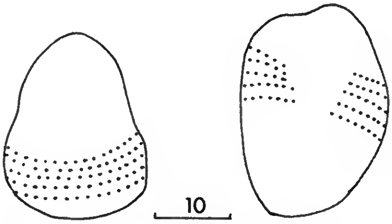

Fig. 23 *Tokophrya* sp., after Guilcher, 1951.

Genus *TOKOPHRYOPSIS* Swarczewsky, 1928

Single species genus.

Diagnosis of *Tokophryopsis*

Freshwater suctoria whose shape is pyramidal, rounded in cross-section. Lorica absent. Attached to crustacea by means of a stalk. Tentacles arranged in 3 fascicles, each arising from the centres of 3 crown or ring-like actinophores on the apical surface. Mode of reproduction undescribed. Macronucleus elongate.

Key to species of *Tokophryopsis*

Attached to gammarids in Lake Baikal . . . . ***T. gigantea***

Species description

Tokophryopsis gigantea Swarczewsky, 1928

DESCRIPTION (Fig. 24). This the type species by monotypy is a large (150–160 µm long), freshwater suctorian whose body shape is distinctly pyramidal. There are 3 crown or ring-like actinophores on the apical surface from within which the tentacles emerge. Lorica absent. Stalk about same length as body, attached to the gammarid crustacean *Poeckilogammarus sukaczewi* in Lake Baikal. Macronucleus elongate. Reproduction not described.

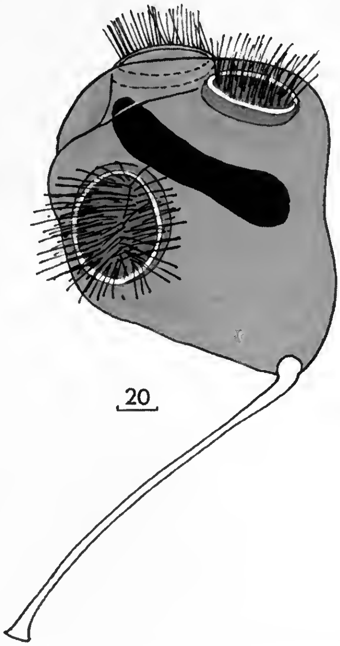

Fig. 24 *Tokophryopsis gigantea*, after Swarczewsky, 1928.

Genus *BRACHYOSOMA* Batisse, 1975

The genus *Hallezia* Sand, 1895 was erected to include those suctoria which, although without lorica and stalk, were nevertheless attached to the substratum via a simple adhesive projection that was not differentiated from the rest of the body. Tentacles were either in fascicles or distributed over the anterior end of the body and reproduction was by multiple endogenous budding. Sand (1899) included the following three species in his genus; *H. brachyopoda* Stokes, 1885, *H. buckei* Kent, 1882 and *H. oviformis* Sand, 1899. Collin (1912) removed *H. buckei* to *Periacineta buckei* because of the presence of a lorica but little more was written about the genus until Corliss (1960) pointed out that the generic name was preoccupied. Finally Batisse (1975) erected the name *Brachyosoma* for *Hallezia* to include those species attached to the substratum only by means of a basal plate and established *Brachyosoma brachyopoda* Stokes, 1885 as the type species. Over the years several species have been described as being attached by simple basal body projections and these, for the first time, have been incorporated into the genus *Brachyosoma*.

Diagnosis of *Brachyosoma*

Freshwater or marine suctorians whose outline varies from oval to triangular. Lorica and stalk absent. Attached to animals or plants by means of a basal plate that is usually situated at the end of a simple projection of the body. Tentacles may be arranged in one to four anterior fascicles or distributed over much of the anterior body surface. Actinophores sometimes present. Reproduction by endogenous budding. Macronucleus spherical to elongate.

Key to the species of *Brachyosoma*

1.	Freshwater, some epizooic on crustacea	2
	Marine, epizooic on crustacea	***B. scottocalani***
2.	Tentacles arranged in several fascicles	3
	Tentacles arranged in single fascicle or distributed all over body surface	4
3.	Epizooic on crustacea	***B. bathynellae***
	Not epizooic, attached to aquatic plants	***B. brachypoda***
4.	Tentacles with widened bases distributed over anterior body half	***B. lycoperdon***
	Tentacles in single anterior fascicle, without widened bases	***B. oviformis***

Species descriptions

Brachyosoma brachypoda, Batisse, 1975

Podophrya brachypoda Stokes, 1885
Tokophrya brachipoda Butschli, 1889
Hallezia brachypoda Sand, 1899
Trichophrya melo Penard, 1920

DESCRIPTION (Fig. 25). This the type species, is a small (40–65 µm long), freshwater suctorian that is approximately spherical to pyramidal in shape. There are two to four fascicles of tentacles sometimes borne upon small rounded actinophores. The animal is attached to debris and fragments of aquatic plants by means of a basal plate that is situated at the end of a short, 5 µm long, posterior projection of the body. There is neither stalk nor lorica. Macronucleus spherical. Reproduction is by endogenous budding. The ciliated embryo is ovoid in shape and the single observation of its ciliation by Penard (1920) suggests that it has six, or possibly five, transversal rows of cilia.

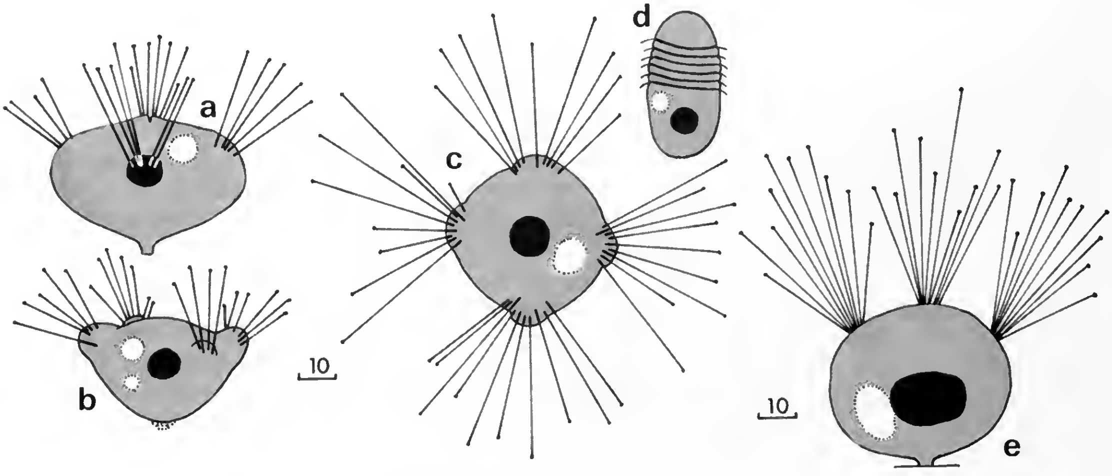

Fig. 25 *Brachyosoma brachypoda:* (a–d) after Penard, 1920 (called *Trichophrya melo*); (e) after Stokes, 1885 (called *Podophrya brachypoda*).

Brachyosoma bathynellae (Chappuis, 1944) n. comb.

Tokophrya bathynellae Chappuis, 1944

DESCRIPTION (Fig. 26). Small (15–25 µm long, freshwater epizooic suctorian whose shape is ovoid to irregular. It is approximately circular in cross section. There are usually three prominent actinophores which give it an irregular shape. Capitate tentacles in three fascicles. Attachment is by a simple basal plate that is situated at the end of a columnar extension of the body. Found attached to the syncarid crustacean *Bathynella* in subterranean lakes. Macronucleus spherical, with single adjacent contractile vacuole. Reproduction not described.

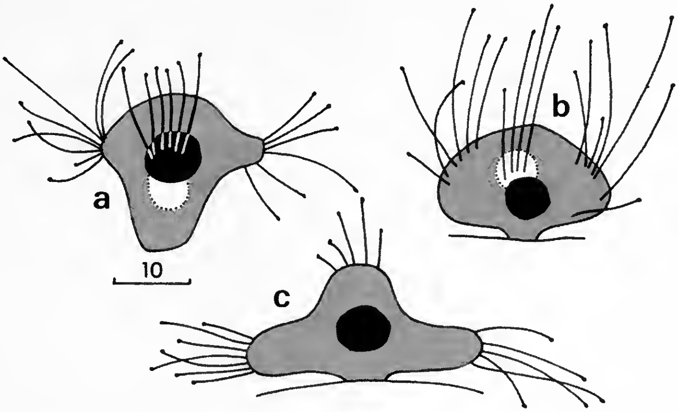

Fig. 26 *Brachyosoma bathynellae*, after Chappuis, 1944 (called *Tokophrya bathynellae*).

Brachyosoma lycoperdon (Penard, 1920) n. comb.

Trichophrya lycoperdon Penard, 1920
Muscophyra lycoperdon Jankowski, 1978

DESCRIPTION (Fig. 27). Small (22–35 µm long), freshwater, spherical suctorian whose dense pellicle is almost entirely covered with capitate tentacles. They are not arranged in fascicles but are limited to the anterior-most surfaces of the body. The tentacles are distinct in being quite wide at their bases and taper towards the tips giving the suctorian a rather ‘prickly’ appearance. Attachment is via a posterior projection of the body. Spherical macronucleus centrally located. Contractile vacuole in posterior body half. Reproduction not described. Found amongst detrital vegetation in lakes.

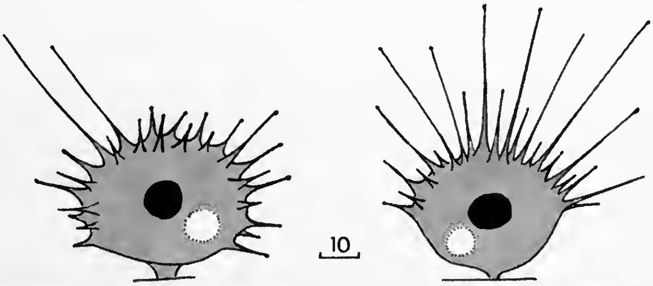

Fig. 27 *Brachyosoma lycoperdon*, after Penard, 1920 (called *Trichophrya lycoperdon*).

NOTE. Jankowski (1978) erected the genus *Muscophrya* for this species stating the major characteristic to be tentacles of the *Parapodophrya* type. Until more information becomes available this species has been transferred to *Brachyosoma* as the method of attachment is here considered to be of greater significance than the slightly different type of tentacles.

Brachyosoma oviformis (Sand, 1899) n. comb.

Hallezia oviformis Sand, 1899

DESCRIPTION (Fig. 28). Small (25–50 µm long), freshwater, ovoid suctorian with a single fascicle of capitate tentacles at the apex of the body. Attached by simple posterior body projection to aquatic plants. Neither lorica nor stalk present. Actinophores absent. Macronucleus spherical to ovoid. Contractile vacuole centrally located. Found amongst algae in rivers. Reproduction not described.

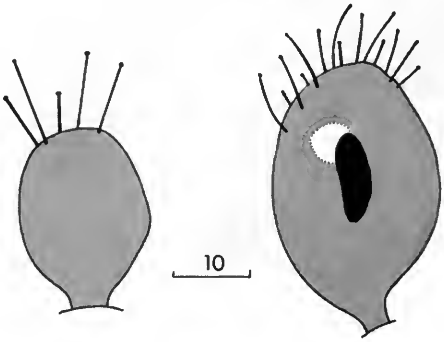

Fig. 28 *Brachyosoma oviformis*, after Sand, 1899 (called *Hallezia oviformis*).

Brachyosoma scottocalani (Sewell, 1951) n. comb.

Hallezia scottocalani Sewell, 1951

DESCRIPTION (Fig. 29). Small (10–31 µm long), marine, ovoid to pyriform suctorian. Two fascicles of capitate tentacles present situated either side of the body. Actinophores absent. Neither lorica nor stalk present. Attachment in young forms by flattened posterior region of body itself while older forms develop a body projection. Found attached to the copepod *Scottocalanus dauglishi* Sewell from the Gulf of Oman. Reproduction by endogenous bud formation. Macronucleus spherical, centrally located.

Genus *ERASTOPHRYA* Fauré-Fremiet, 1944

Until now *Erastophrya* has remained a single species genus, however, here another species *Trichophrya odontophora* Sand has been transferred into the genus because of its possession of some rather odd cytoplasmic extensions.

Diagnosis of *Erastophrya*

Freshwater or marine suctoria whose shape is pyriform, ovoid or irregularly so. Lorica and actinophores absent. Tentacles distributed all over body surface or restricted to anterior end. Posteriorly there are 2 or 3 cytoplasmic extensions that may be used as organelles of attachment. Reproduction by endogenous bud formation. Macronucleus ovoid, centrally located.

Key to species of *Eraštophrya*

Freshwater, attached to peritrichs epizooic on fish, tentacles distributed all over body	***E. chattoni***
Marine, among algae, tentacles restricted to anterior half of body . . .	***E. odontophora***

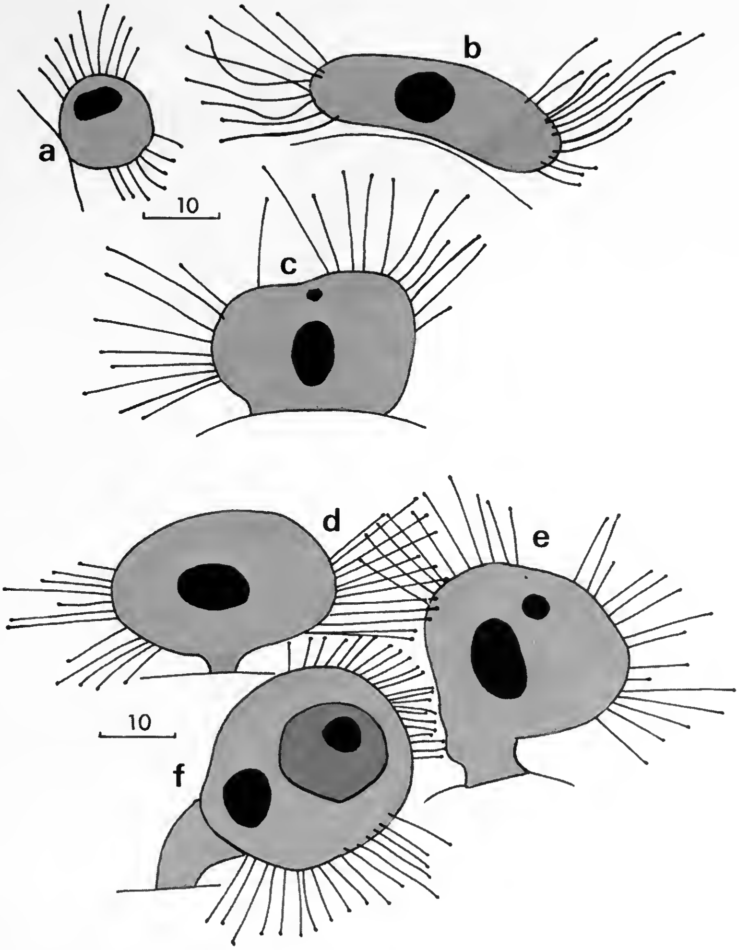

Fig. 29 *Brachyosoma scottocalani*: (a–f) after Sewell, 1951 (called *Hallezia scottocalani*).

Species descriptions

Erastophrya chattoni Fauré-Fremiet, 1944

Description (Fig. 30). This the type species is a medium to large (90–130 µm long), freshwater suctorian whose shape is pyriform to ovoid. Actinophores, lorica and stalk absent. There are a pair of posterior claspers that are used to grip the stalks of peritrichs such as *Apiosoma piscicola, A. campanulata* and *Rhabdostyla gasterostei* which are epizooic on freshwater fishes. Tentacles distributed all over body surface. Macronucleus ovoid, centrally located. Single lateral contractile vacuole. Reproduction by endogenous budding.

Note. There seems to be some disagreement on the description of the tentacles and body shape. Fauré-Fremiet (1944) and Matthes (1974) both illustrate (Fig. 28a) capitate tentacles well distributed over the pyriform body, but Banina (1973) and Jankowski (date not given) illustrate (Fig. 28b, c) (both taken from Banina, 1984) non-capitate tentacles and an ovoid body.

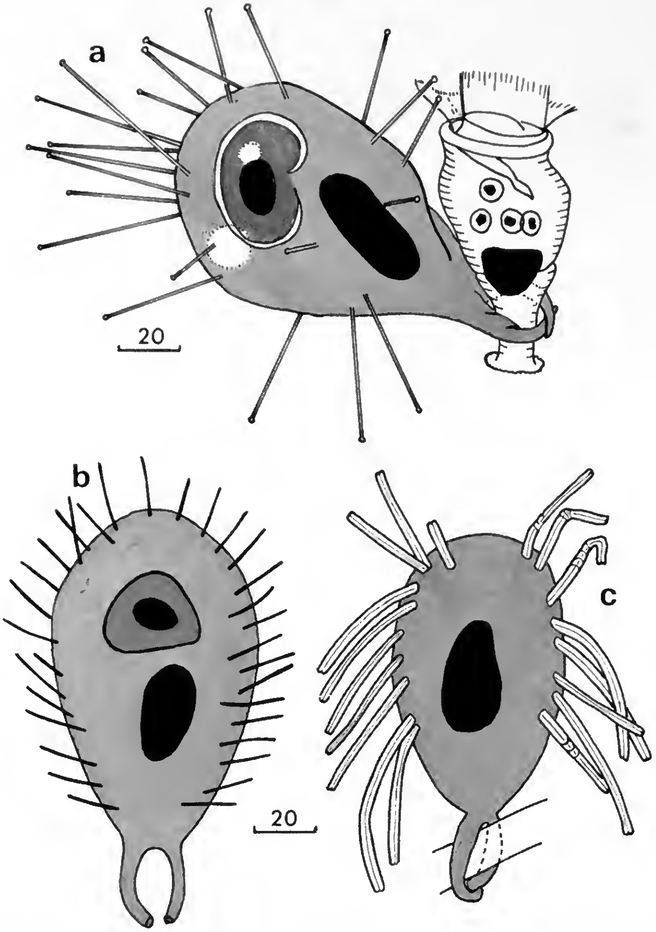

Fig. 30 *Erastophrya chattoni*: (a) after Fauré-Fremiet, 1944; (b) after Banina, 1973 *in* Banina, 1984; after Jankowski *in* Banina, 1984.

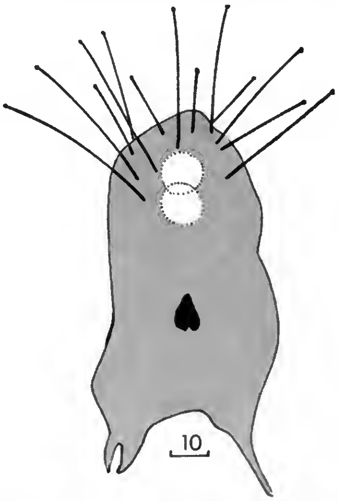

Fig. 31 *Erastophrya odontophora* after Sand, 1899 (called *Trichophrya odontophora*).

Erastophrya odontophora (Sand, 1899) n. comb.

Trichophora odontophora Sànd, 1899

DESCRIPTION (Fig. 31). Medium (80–90 µm long), marine suctorian whose shape is irregularly ovoid. Actinophores, lorica and stalk absent. There are 3 posterior cytoplasmic extensions that may be used as organelles of attachment. Capitate tentacles restricted to anterior half of the body. Macronucleus centrally located. There are 2 contractile vacuoles located in the anterior body third. Found amongst marine algae. Reproduction not described.

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Index to Species

(Names given in roman refer to synonyms)

Studies on deep-sea Protobranchia (Bivalvia); the family Malletiidae

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Contents

Synopsis

This paper redefines the deep water protobranch bivalve family Malletiidae and describes the functional morphology, growth and geographical distribution of nine species obtained from abyssal and slope depths of the Atlantic. Three new species are described, all from the Guinea Basin.

Subtle differences in the shell shape between different populations are, where possible, quantified and described. The differences are discussed in relation to reproduction and isolation, and taking into account possible slow rates of gene flow and the emergence of sibling species.

Introduction

This is the fifth paper in a series on the biology and ecology of the deep-sea protobranch bivalves of the Atlantic (Allen & Sanders, 1973, 1982; Sanders & Allen, 1975, 1977). Our interest lies in a multiplicity of aspects of the life and evolution of these molluscs, (Allen, 1978), but in particular we have endeavoured to determine the adaptations of these animals to conditions at great depths.

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Thus, much of our study concerns the functional morphology of the animal, its reproduction, the variations in population parameters and the geographical and depth distribution. In addition, because protobranchs dominate the deep sea bivalve fauna with many species present, and because of the large and comprehensive collection at our disposal containing many new species, our work has had of necessity to concern itself with the taxonomy of the group. The presentation of the work is therefore formulated in a taxonomic framework. Our samples come from a variety of sources and the data given under each species section lists these sources. In the main they come from the expeditions of the research vessels of the Woods Hole Oceanographic Institution, U.S.A., the Natural Environment Research Council, U.K., and the Centre National pour Exploitation des Océans (CNEXO), France. Thus, we are greatly indebted to the many scientists and staff of these Institutions for their various contributions.

In this paper we continue our appraisal of the Order Nuculanoidea and consider the family Malletiidae.

It has been the custom by authors of earlier papers on the protobranch Bivalvia to include those nuculanoid species possessing an external ligament within a single subfamily the Malletiinae or family Malletiidae (e.g. Dall, 1898; Verrill & Bush, 1897; Vokes, 1967; McAlester in Moore, 1969). Vokes (1967) included the following recent genera within the Malletiidae:

**Austrotindaria* Fleming, 1948; *Clencheria* (=*Malletia*) Clarke, 1961; *Ctenoconcha* (=*Malletia*) Gray, 1840; *Malletia* des Moulins, 1832; *Malletiella* Soot-Ryen, 1957; *Minormalletia* Dall, 1908; **Neilo* Adams, 1854; **Neilonella* Dall, 1881; **Nucularia* Conrad, 1869; **Protonucula* Cotton, 1930; **Pseudoglomus* Dall, 1898; *Pseudomalletia* (=*Malletia*) Fischer, 1886; *Solenella* (=*Malletia*) G.B. Sowerby, 1833; [*Tindaria* Bellardi, 1875]; **Tindariopsis* Verrill & Bush, 1897.

Our recent studies have shown that this assemblage comprises a variety of unrelated morphologies which have external ligaments as the character in common (Allen, Hannah & Sanders, in prep.). As a result the family Tindariidae was confirmed (Sanders & Allen, 1977). With the asiphonate genus *Tindaria* removed, the remaining siphonate assemblage with external ligaments can be divided into two groups: those marked with an asterisk which have thick shells with strong concentric ornamentation and are not markedly posteriorly elongate; and those without an asterisk which have thin, translucent, ovate or rectangular to ovate shells, with at most, fine concentric striations and which may be rostrate. Some of the species of the first group are probably not closely related; at least two subgroups are present, one ovate and neilonellid in form and the other more rostrate typified by *Malletia (Tindaria) aeolata* Dall as presently named (see p. 234). The second group are unified and are included within the family Malletiidae as here defined.

Family MALLETIIDAE

Nuculanoid protobranchs, shell elongate, ovate or ovate/rostrate, thin, glossy, translucent, usually without marked ornamentation, maybe slender or swollen; umbos, low, anterior, pointing inwards or slightly forward; hinge line slender or, at most moderately developed, with fewer teeth in the anterior as compared with the posterior series, edentulous space between the series; ligament predominantly external, extending beyond the umbos anteriorly and posteriorly, posterior section longer than anterior, small resilium composed of inner and outer layer set in a shallow marginal resilifer; siphonate, specialized posterior mantle feeding area ventral to siphons well developed, single tentacle on right side of siphonal embayment; hind gut in form of single anterior loop on right side, in part contiguous with the anterior adductor, but not penetrating the right mantle; gill axis parallel to anterior-posterior body axis; palps vary in size; cerebro-visceral commissure stout, pedal statocyst large; neck of foot slender, marginal pedal papillae moderately large; 'byssal' gland moderately large.

There is considerable confusion in the literature concerning the form of the malletiid ligament. Thus Verrill & Bush (1897, 1898) state that 'the resilium is wanting or else is represented by a special part of the ligament external to the teeth', while McAlester (1964) defined the family as comprising Cenozoic and Recent forms 'lacking an internal separated ligament and resilifer'. We confirm that in addition to the elongate anterior and posterior external parts of the ligament there is in all species a small internal ligament or resilium inset superficially into the hinge plate below the umbos.

The family includes species of three genera, *Malletia, Minormalletia & Malletiella.* Most species belong to the genus *Malletia.* Of the others *Malletiella* comprises two species and *Minormalletia* one species. The two latter genera are restricted to the eastern Pacific. *Minormalletia* and *Malletiella* may on further study prove to be synonymous with *Malletia.* From the existing descriptions the difference of note from *Malletia* in the case of *Minormalletia* is that the lower edge of the pallial sinus is confluent with the pallial scar and in the case of *Malletiella* the postumbonal length is extreme with 3 to 4 times the number of posterior teeth compared with the number of anterior teeth.

MALLETIA des Moulins, 1832

TYPE SPECIES. *M. chilensis* des Moulins, 1832 by monotypy

TYPE LOCALITY. Valparaiso, 100–110 m mud.

SYNONYMY. Solenella Sowerby, 1833; *Ctenoconcha* Gray, 1840; *Pseudomalletia* Fischer, 1886; *Clencheria* Clarke, 1961

The characters of the genus are those that define the family and additionally the number of posterior hinge teeth are less than three times the number of anterior hinge teeth and the pallial sinus scar is not confluent with the pallial mantle scar. There is sufficient similarity of form within the family to describe one species, *M. abyssorum*, in detail while in the case of other species only those characters that differ from those in *M. abyssorum*, or for reason of better material extend the original description need be given. Species of the genus are among the largest protobranch bivalves of the deep-sea, many exceeding 15 mm in total length.

MINORMALLETIA Dall, 1908

TYPE SPECIES. *M. arciformis* Dall, 1908 by monotypy.

TYPE LOCALITY. *Albatross* Sta 3417, off Acapulco, Mexico.

Shell small, blunt, plump; ligament amphidetic; pallial sinus large, ventrally confluent with pallial line, other shell features as given under the family diagnosis. Anatomy unknown.

MALLETIELLA Soot-Ryen, 1957

TYPE SPECIES. *Malletia pacifica* Dall, 1899.

TYPE LOCALITY. *Albatross* Sta 2791, SW Chile.

Umbones anterior; posterior hinge teeth 3–4 times more numerous than anterior; pallial sinus very short, slightly rostrate; other shell features as for family diagnosis. Anatomy unknown.

Malletia abyssorum Verrill & Bush, 1898

Malletia abyssorum Verrill & Bush, 1898: *Proc. U.S. Natl Mus.* **20:** 875, pl. 97, fig. 7. TYPE LOCALITY. U.S. Fish Comm. Sta 2566, 4791 m, Lat 37°23′N, Long 68°28′W. TYPE SPECIMEN. Holotype, U.S. Nat. Mus. No. 52159.

Tindaria (Clencheria) diaphana Clarke, 1961; *Bull. Mus. Comp. Zool. Harv.* **125:** 374, pl. 1, fig. 2. TYPE LOCALITY. *Vema* Sta 52. 2711 fms Lat 41°03′S 07°49′E. TYPE SPECIMENS. Holotype, Mus. Comp. Zool. Harvard No. 224965; paratype, Natl Mus. Canada No. 4741.

DEPTH RANGE = 2864 m to 5280 m.

Shell description

The original shell description by Verrill & Bush (1898) is both detailed and accurate and requires no enlarging, however for comparative purposes the species is figured (Figs 1, 2, 3 & 4). Maximum recorded length 7·8 mm; prodissoconch length 300 μm–325 μm.

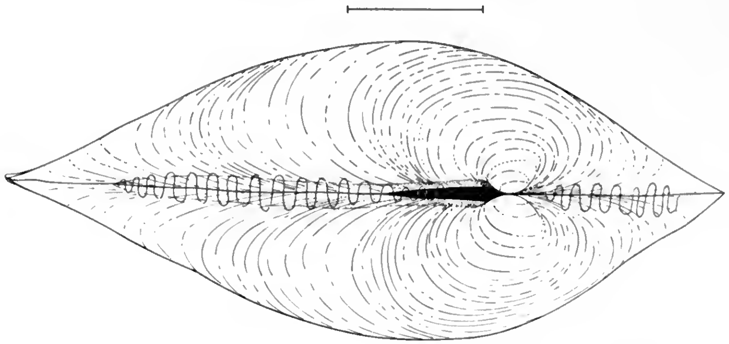

Fig. 1 *Malletia abyssorum*. Dorsal view of shell. From Station BG VI DS.79. (West European Basin). Scale 1 mm.

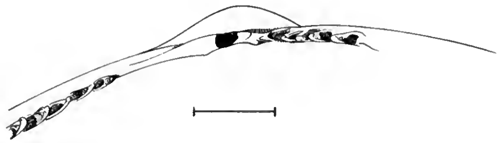

Fig. 2 *Malletia abyssorum*. Lateral view of hinge of right valve in umbonal region. From Station BG VI DS.79. Scale 0·25 mm.

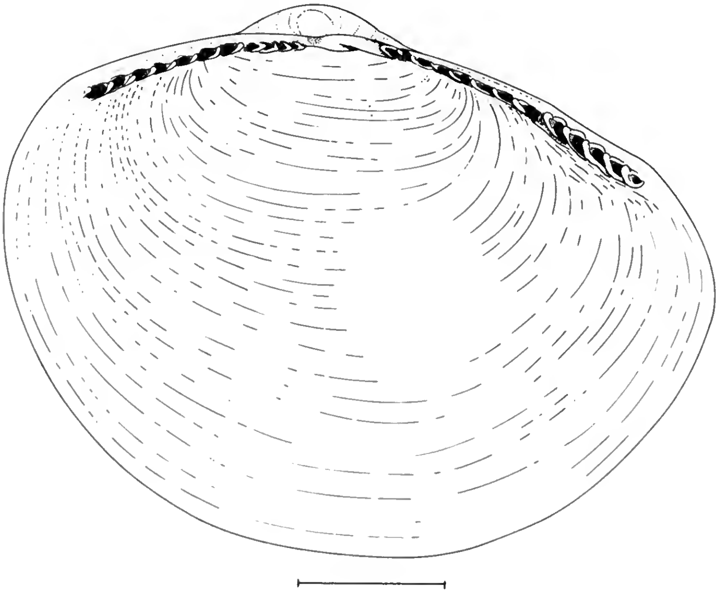

Fig. 3 *Malletia abyssorum*. Lateral internal view of left valve of shell. From Station BG VI DS.79. (West European Basin). Scale 1 mm.

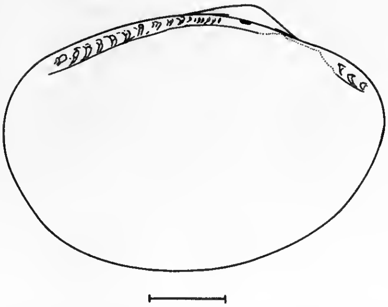

Fig. 4 *Malletia abyssorum.* Lateral internal view of left valve of type specimen. (Hinge broken since figured by Verrill & Bush, 1898), U.S. Nat. Mus. 52159. Station 2566, 4791 m off Martha's Vinyard. Scale 1 mm.

Material

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
NORTH AMERICA BASIN							
Atlantis II	64	2886	5	38°41·0′N	70°06·0′W	ES	21.8.64
	70	4680	26	36°23·0′N	67°58·0′W	ES	23.8.64
	72	2864	9	38°16·0′N	71°47·0′W	ES	24.8.64
Chain	77	3806	10	38°01·0′N	69°16·0′W	ES	30.6.65
	78	3829	144	38°01·0′N	69°19·0′W	ES	30.6.65
	80	4970	21	34°49·8′N	66°34·0′W	ES	2.7.65
Atlantis II	81	5042	19	34°41·0′N	66°28·0′W	ES	2.7.65
	83	5000	8	34°39·0′N	66°26·0′W	ES	3.7.65
Chain	84	4749	256	36°24·0′N	67°56·0′W	ES	4.7.65
	85	3835	1475	37°59·0′N	69°26·0′W	ES	5.7.75
Atlantis II	92	4694	37	36°20·0′N	67°56·0′W	ES	13.12.65
	93	5007	17	34°39·0′N	66°26·0′W	ES	14.12.65
	121	4800	178	35°50·0′N	65°11·0′W	ES	21.8.66
	122	4833	199	35°52·0′N	64°14·0′W	ES	21.8.66
	123	4853	69	37°29·0′N	64°14·0′W	ES	22.8.66
	124	4862	37	37°26·0′N	63°59·5′W	ES	22.8.66
	125	4825	284	37°24·0′N	65°54·0′W	ES	23.8.66
	126	3806	139	39°37·0′N	66°47·0′W	ES	24.8.66
	175	4693	81	36°36·0′N	68°31·0′W	ES	29.11.67
Chain	331	4793	21	41°13·2′N	41°38·7′W	ES	29.8.72
Knorr	340	3356	65	38°17·6′N	70°22·8′W	ES	24.11.73
WEST EUROPEAN BASIN							
Chain	328	4435	2	50°04·7′N	15°44·8′W	ES	23.8.73
	330	4632	10	50°43·4′N	17°52·9′W	ES	24.8.73
Polygas	DS20	4226	14	47°33·0′N	9°36·7′W	ES	24.10.72
(J. Charcot)	DS21	4190	16	47°31·5′N	9°40·7°W	ES	24.10.72
	DS22	4144	12	47°34·1′N	9°38·4′W	ES	25.10.72
	DS23	4737	163	46°32·8′N	10°21·0′W	ES	26.10.72
Biogass II	DS30	4106	4	47°38·3′N	9°33·9′W	ES	18.4.73
Biogass III	DS46	4521	12	46°28·6′N	10°23.0′W	ES	29.8.73
	CV30	4518	6	46°32·8′N	10°20.0′W	BT	29.8.73
	DS48	4203	7	44°29·0′N	4°54.0′N	ES	31.8.73

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Biogas IV	DS53	4425	25	44°30·4′N	4°56.3′W	ES	19.2.74
	DS54	4659	68	46°31·1′N	10°29·2′W	ES	21.2.74
	DS55	4125	65	47°34·9′N	9°40·9°W	ES	22.2.74
	CV36	4209	1	47°34·1′N	9°38·5′W	ES	22.2.74
Biogas V	DS67	4150	7	47°31·0′N	9°35·0′W	ES	17.6.74
(Cryos)	DS68	4550	2	46°26·7′N	10°23·9′W	ES	19.6.74
	DS69	4510	1	44°21·9′N	4°52.4′W	ES	20.6.74
Biogas VI	DS75	3250	1	47°28·1′N	9°07·8′W	ES	22.10.74
(J. Charcot)	CP13	4134	9	47°34·4′N	9°38·0′W	FT	23.10.74
	DS76	4228	8	47°34·8′N	9°33·3′W	ES	23.10.74
	DS77	4240	10	47°31·8′N	9°34·6′W	ES	24.10.74
	DS78	4706	201	46°31·2′N	10°23·8′W	ES	25.10.74
	DS79	4715	127	46°30·4′N	10°27·1′W	ES	26.10.74
	CP17	4706	9	46°30·8′N	10°29·5′W	ES	26.10.74
	DS80	4720	35	46°29·5′N	10°29·5′W	ES	27.10.74
	DS81	4715	8	46°28·3′N	10°24·6′W	ES	27.10.74
	CP19	4434	1	44°24·9′N	4°51·3′W	FT	28.10.74
	DS82	4462	94	44°25·4′N	4°52·8′W	ES	29.10.74
	DS84	4466	11	44°22·4′N	4°51·0′W	ES	29.10.74
	DS85	4462	4	44°30·0′N	4°53·9′W	ES	29.10.74
	CP21	4453	1	44°21·2′N	4°49·3′W	FT	30.10.74
	CP22	4475	21	44°22·9′N	4°54·8′W	FT	30.10.74
Guiana basin							
Knorr	288	4429	2	11°04·0′N	55°05·0′W	ES	25.2.72
Biovema	DS04	5150	5	10°47·5′N	42°40·74′W	ES	24.3.71
(J. Charcot)							
Argentine basin							
Atlantis II	243	3820	23	37°36·8′S	52°23·6′W	ES	14.3.71
	256	3917	86	37°40·0′S	52°19·0′W	ES	24.3.71
Siera leone basin							
Atlantis II	148	3828	2	10°37·0′N	18°14·0′W	ES	7.2.67
	149	3861	13	10°30·0′N	18°18·0′W	ES	7.2.67
Angola basin							
Campagne Walvis I	DS07	5157	1	27°00·0′S	1°06·4′E	ES	3.1.79
Cape basin							
Campagne	DS05	4560	9	33°20·5′S	2°34·9′E	ES	30.12.78
Walvis I	DS06	4585	13	33°24·5′S	2°32·9′E	ES	31.12.78
	DS02	5280	9	33°54·7′S	5°07·5′E	ES	25.12.78
Newfoundland basin							
Knorr	334	4400	121	40°43·3′N	46°14·2′W	ES	30.8.72
	331	4793	21	41°13·1′N	41°37·7′W	ES	29.8.72

*BT Blake Trawl. ES Epibenthic sledge. FT 'Honfleur' Trawl.
Filatova & Shileiko (1981) record four specimens of *M. abyssorum* (= *Clencheria diaphana*) from 5020 m in the South Australian Basin of the Indian Ocean. This is the only record of this species outside the Atlantic Ocean.

Morphology

No account of the anatomy has been given hitherto. The mantle is typically nuculanoid (Sanders & Allen, 1973). There is a marginal anterior sense organ developed from the middle sensory lobe which consists of two epithelial folds with a ciliated glandular region between them similar to that described for other nuculanoid species (Allen & Sanders, 1982). It is antero-ventral in position

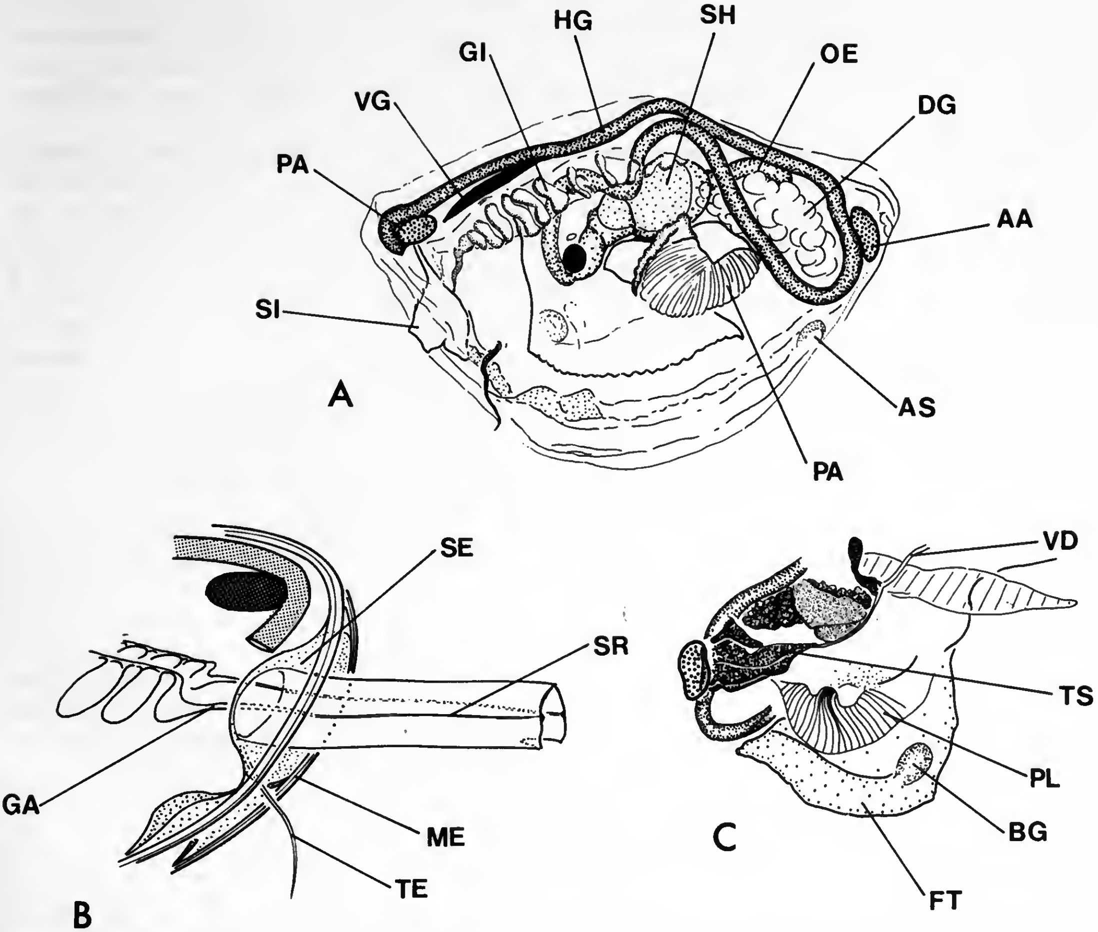

Fig. 5 *Malletia abyssorum.* (a) Lateral view of the anatomy from the right side; (b) diagrammatic lateral view of the posterior part of the body showing the relationship of the gill axis with extended siphon; (c) lateral view showing the early development of testis on the left side of the viscera. Abbreviations see Appendix.

and lies ventral to the ventral limit of the hind gut loop (Fig. 5). The posterior mantle edge is highly specialized and comprises a combined incurrent and excurrent siphon with a feeding region ventral to it. The latter is a specialized aperture created by the aposition of the mantle margins. The siphonal embayment and the feeding region do not encroach mantle space to any marked degree. Siphon formation involves fusion of the inner mantle lobes both dorsally and ventrally, however, that ventral to the inhalent siphon is not complete distally and here is limited to the adhesion of the opposing inner mantle lobes. The internal division into incurrent and excurrent lumena is not complete but the integrity of the passages is probably maintained by a pair of opposed longitudinal midlateral ridges (Fig. 5b). A single tentacle similar to that described for other nuculanoids (Allen & Sanders, 1982) is present on the right side and originates at the inner part of the siphonal embayment ventrally at the base of the siphon.

The adductor muscles are approximately equal in size and oval in shape. The 'quick' and 'catch' portions are approximately equal in size. The gill axis lies parallel to the dorsal margin of the shell and is attached posteriorly to the midlateral siphonal ridges and anteriorly to the body wall. There is no axial membrane posterior to the foot to physically separate a suprabranchial region from the rest of the mantle cavity. The gill plates number 24 in a specimen 3·0 mm total length. The palps, in preserved specimens, are relatively small. The palp ridges are slender in cross-section, lie close together and number 40 in a specimen 3 mm in length. The anterior limit of the palps, i.e. the position of the mouth, is far removed from the ventral face of the anterior adductor muscle (Fig. 5a). Judged by their small size, the palp proboscides when extended must be very slender.

The gut configuration follows the primitive protobranch form in which the hind gut makes a single loop to the right hand side of the body (Fig. 5a). The oesophagus first takes an anterior dorsal course towards the anterior adductor and just short of the muscle turns posteriorly to join the anterior face of the stomach dorsally. The stomach is elongate and not greatly inflated. The number of ciliated sorting ridges on the right side are few. The style sac is elongate penetrating the foot as far as the ventral limit of the neck. The hind gut further penetrates the foot ventral to the pedal ganglion (Fig. 5a) and, thereafter passes immediately posterior to the stomach dorsally to the umbo before taking an anterior and ventral course to the posterior face of the anterior adductor where it turns to follow the line of the dorsal shell margin, dorsal to the posterior adductor muscle to the anus which lies close to the posterior limit of the gill. Hind gut and body tissue do not penetrate mantle space as they do in *Tindaria* (Sanders & Allen, 1977). Voided faeces are guided by the gill axes and siphonal ridges. The greater part of the digestive gland is anterior to the stomach although overlapping it to some extent antero-laterally. That part on the right side is contained within the loop of the hind gut. The configuration of the section of the hind gut that lies posterior to the stomach is related to the attitude of the foot. In specimens in which the foot is fixed so that it lies in the posterior part of the mantle cavity there is a double bend in the course of the gut (Fig. 5a), when the foot is anterior the bends are pulled straight. A single typholosole that is little more than a faint ridge is present along the entire length of the hind gut. The epithelial cells of the hind gut are vacuolated. The foot is moderately large with a narrow neck, and the margins of the sole of the foot are papillate. The 'byssal' gland is well developed and spherical in outline. The pedal musculature consists of a broad band of posterior retractors attached to each valve between the posterior adductor muscle and the heart and three pairs of anterior reactors lying close together and attached to the valves between the anterior adductor and the anterior wall of the stomach. All these muscles closely flank the ventral walls of the stomach and pass into the foot (see Fig. 22). In addition there are subepithelial circular muscles and inner transverse muscles similar to those described in other protobranchs (Sanders & Allen, 1977; Allen & Sanders, 1982). The nervous system is well developed, the ganglia are stout and the cerebro-visceral commissure relatively thick. As in all malletiids the statocysts dorsal to the pedal ganglia are large and can be clearly seen in whole mounts. The sexes are separate and gonads develop peripheral to the digestive gland. Initially the gonads appear at anterior and ventral margins of the gland, but as they mature they spread laterally across its entire surface. A simple duct passes dorsal to the gill to a point directly above the posterior edge of the neck of the foot (Fig. 5c). Eggs are moderately large and measure approximately 140 μm maximum diameter as measured from sections of mature specimens. The kidneys are small, slender paired sacs that do not abut the posterior adductor but lie anterior to the visceral ganglion and extend anteriorly to the level of the hind gut posterior to the stomach.

The difference in size range of the samples is considerable (Fig. 6). The maximum length of specimens from the well sampled Gayhead-Bermuda transect is 6·5 mm and from the Bay of Biscay, also well sampled, is 7·8 mm. This difference may be but a reflection of the sampling techniques of the CNEXO compared with the Woods Hole ships. Histograms show various maxima over the size range of the samples. These may indicate discrete larval settlements and are not necessarily annual events (Fig. 6). The smallest specimen with developing gonads was 3·8 mm total length. No spent individuals were seen in any sample nor was there any evidence that brooding of the young occurs. In an analysis of specimens from Stations DS79, all specimens of 4·6 mm and above had gonads present, most of which were judged to be either half or three quarter mature. However, it was apparent that the testis was of greater volume than the ovary (Fig. 7). This is probably a reflection of the slow accumulation of egg reserves in an animal living at abyssal depths where food is limited and this may be generally true of animals living in abyssal depths. Sections indicate the eggs in individual specimens develop in unison.

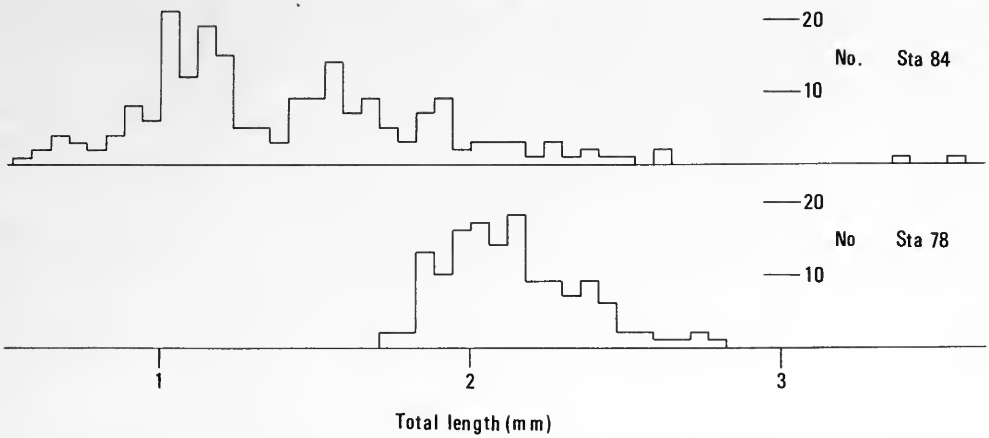

Fig. 6 *Malletia abyssorum.* Comparison of the size frequencies of samples from two Stations on the Woods Hole-Bermuda transect across the North American Basin.

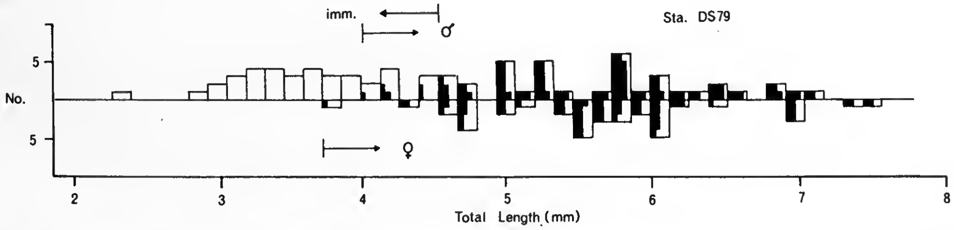

Fig. 7 *Malletia abyssorum.* Analysis of the maturity of a sample taken from Station DS.79 in the West European Basin. The degree of maturity is indicated by the proportion, blacked out on each size frequency.

The prodissoconch measures 300 µm,–325 µm. As in all species of *Malletia* the shell changes in shape with increasing size. Young specimens are oval in shape, while large specimens tend to become very slightly rostrate (Figs 8 & 9). Analysis of various populations shows that there is also a very gradual increase in shell height as reference to a plot of the height to length ratio to length shows (Fig. 9). The same figure also plots the ratio of posterior umbonal length and total length against total length and from this it is apparent that the shell is not fully rostrate until it is half grown, thereafter the rostral increase is much slower matching the increase in height length ratio. There is relatively little variation in shell shape in specimens from different geographical localities. *M. abyssorum* is one of the commoner protobranchs living at abyssal depths and therefore the number of larvae released might be expected to be relatively large. On that count alone, there should be a favourable spread of larvae for the maintenance of gene flow.

Malletia abyssorum is widely distributed throughout the abyssal depths of the Atlantic Ocean and is probably present in all its deep basins at depths in excess of 3500 m. The depth range for the entire suite of samples yielding specimens extends from 2864 m to 5280 m. In depths smaller than 3500 m, this species is a minor numerical constituent of the protobranch fauna and is often absent from well-sampled stations. At depths greater than 3500 m, however, *M. abyssorum* is a more constant element and often comprises a numerically significant percentage of the protobranch bivalves present (10-30%).

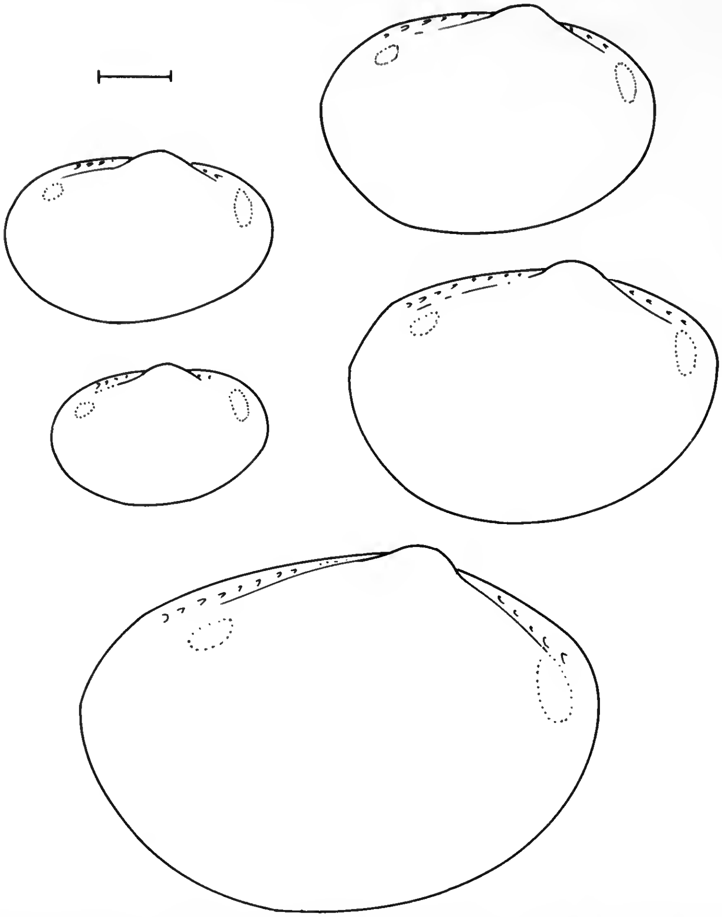

Fig. 8 *Malletia abyssorum*. Lateral outlines of specimens to show change in shape with increasing size. Scale 1 mm.

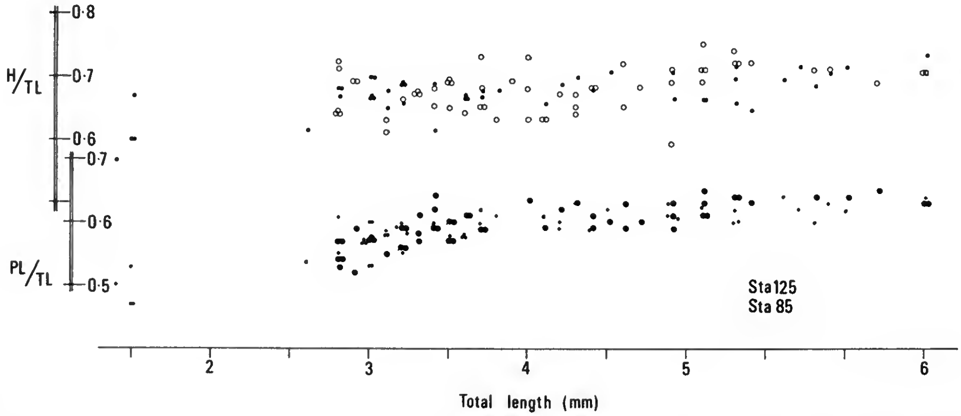

Fig. 9 *Malletia abyssorum*. Analysis of shell proportions of samples taken from Station 85, small closed circles, and Station 125, large open and closed circles, (North Atlantic Basin) showing a change in the ratio umbo-rostum length to total length PL/TL with increasing length, but little change in the ratio of height to total length H/L during growth.

The deeper depth limit of *M. abyssorum*, 5280 m, is an arbitrary boundary in the sense that it is merely the manifestation of the deepest abyssal station sampled rather than the *de facto* maximum depth occupied by this species. *M. abyssorum* has also been collected outside the Atlantic Ocean in the South Australian Basin of the Indian Ocean at a depth of 5020 m (Filatova & Shileika, 1981).

Malletia johnsoni Clarke, 1961

Malletia johnsoni Clarke, 1961: *Bull. Mus. Comp. Zool. Harv.* **125:** 370, pl. 2, fig. 6 TYPE LOCALITY. *Vema* Sta 22, Angola Basin, 175 miles W. of Banana, Zaire, 3065 m. TYPE SPECIMEN. Holotype, Mus. Comp. Zool. Harvard, 224961, paratypes Nat. Mus. Canada No. 4737.

Malletia estheriopsis Barnard, 1963: *Ann. S. Af. Mus.* **46:** 447, fig. 11b. TYPE LOCALITY. *Africana* Sta 317, Lat 33°55′S Long 16°30′E 2706 m—3036 m. TYPE SPECIMEN. Syntype, South Africa Mus. No. 9817.

DEPTH RANGE = 1100 m to 3834 m.

There has been considerable confusion between this species and *M. obtusa* G.O. Sars, 1878 (see p. 232). *M. obtusa* appears to be restricted to the biologically isolated Norwegian Basin and is found in more shallow water. The following records of *M. obtusa* are all of *M. johnsoni*: Jeffreys, 1879: 586; Verrill, 1884: 226 & 280; Smith, 1885: 245; Bush, 1893: 234; Locard, 1896: 202; Locard, 1898: 331: Verrill & Bush, 1898: 874, pl. 97, fig. 4; Thiele & Jaeckel, 1931: 49; Johnson, 1934: 19; Heath, 1937, fig. 62, 65; Clarke, 1962: 51.

Material

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
SIERRA LEONE BASIN							
Atlantis II	138	1976	3	10°36·0′N	17°52·0′W	ES	4.2.67
	141	2031	7	10°30·0′N	17°51·5′W	ES	5.2.67
	142	1796	4	10°30·0′N	17°51·5′W	ES	5.2.67
	143	2095	1	10°35·0′N	17°44·0′W	ES	5.2.67
	144	2204	3	10°36·0′N	17°49·0′W	ES	5.2.67
	145	2148	30	10°36·0′N	17°49·0′W	ES	6.2.67
	146	2867	2	10°39·5′N	17°44·5′W	ES	6.2.67
	147	2934	34	10°38·0′N	17°52·0′W	ES	6.2.67
ANGOLA BASIN							
Atlantis II	200	2754	1	9°29·0′S	11°34·0′E	ES	22.5.68
	201	2031	8	9°05·0′S	12°17·0′E	ES	23.5.68
CAPE BASIN							
Atlantis II	192	2154	3	23°02·0′S	12°19·0′E	ES	17.5.68
	194	2864	1	22°54·0′S	11°55·0′E	ES	17.5.68
Walda	DS06	2992	5	22°50·2′S	11°59·9′E	ES	11.6.71
	CY13	2044	195	12°03·7′S	12°22·3′E	T	.6.71
NORTH AMERICA BASIN							
Atlantis II	62	2496	140	39°26·0′N	70°33·0′W	ES	21.8.64
	64	2886	14	38°46·0′N	70°06·0′W	ES	21.8.64
	72	2864	53	38°16·0′N	71°47·0′W	ES	24.8.64
	73	1400	341	39°46·5′N	70°43·0′W	ES	25.8.64
Chain	76	2862	23	39°32·0′N	67°58·0′W	ES	29.6.65
	85	3834	2	37°59·0′N	69°26·0′W	ES	5.7.65
	87	1102	31	39°49·0′N	70°41·0′W	ES	6.7.65
	103	2022	185	39°44·0′N	70°37·0′W	ES	4.5.66
	115	2040	125	39°39·2′N	70°24·5′W	ES	16.8.66
Atlantis II	128	1388	19	39°46·5′N	70°45·2′W	ES	16.12.66
	131	2178	39	39°39·0′N	70°37·2′W	ES	18.12.66
Chain	210	2044	22	39°43·1′N	70°47·7′W	ES	22.2.69

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
WEST EUROPE BASIN							
Sarsia	S44	1739	14	43°41·0′N	3°35·0′W	ES	16.7.67
	S50	2379	13	43°47·0′N	3°38·0′W	ES	18.7.67
	S65	1922	50	46°15·0′N	4°50·0′W	ES	25.7.67
Chain	316	2191	109	50°58·7′N	13°01·6′W	ES	18.8.72
	318	2506	3	50°27·3′N	13°20·9′W	ES	19.8.72
Biogas I (La Perle)	DS11	2205	19	47°35·5′N	8°33·7′W	ES	8.8.72
	DS12	2180	1	47°28·5′N	8°35·5′W	ES	9.8.72
	CW03	1100	22	47°30·6′N	8°17·5′W	BT	5.8.72
	DS15	2246	8	47°35·2′N	8°40·1′W	ES	21.10.72
	DS18	2138	4	47°32·2′N	8°44·9′W	ES	22.10.72
	DS25	2096	5	44°08·2′N	4°15·7′W	ES	1.11.72
	CV09	2119	1	47°31·4′N	8°43·6′W	BT	22.6.72
Biogas II (J. Charcot)	DS32	2138	10	47°32·2′N	8°05·3′W	ES	19.8.73
Biogas III (J. Charcot)	DS35	2226	6	47°34·2′N	8°40·7′W	ES	24.8.73
	DS36	2147	2	47°32·7′N	8°36·5′W	ES	24.8.73
	DS37	2110	3	47°31·8′N	8°34·6′W	ES	24.8.73
	DS38	2138	8	47°32·5′N	8°35·8′W	ES	25.8.73
	DS49	1845	3	44°05·9′N	4°15·6′W	ES	1.9.73
Biogas IV (J. Charcot)	DS51	2430	10	44°11·3′N	4°15·4′W	ES	18.2.74
	DS52	2006	5	44°06·3′N	4°22·4′W	ES	18.2.74
	DS58	2775	1	47°34·1′N	9°08·2′W	ES	23.2.74
	DS61	2250	4	47°34·7′N	8°38·8′W	ES	25.2.74
	DS62	2175	19	47°32·8′N	8°40·9′W	ES	26.2.74
	DS64	2156	6	47°29·2′N	8°30·7′W	ES	26.2.74
	CP01	2315	1	47°34·6′N	8°38·8′W	FT	25.2.74
Biogas V (Cryos)	DS70	2150	2	44°08·8′N	4°17·4′W	ES	26.6.74
	CV39	2350	1	47°33·5′N	8°45·0′W	BT	14.6.74
	CP07	2170	8	44°09·8′N	4°16·4′W	FT	21.6.74
Biogas VI (J. Charcot)	CP08	2177	6	44°33·2′N	8°38·5′W	FT	20.10.74
	CP09	2171	2	47°33·0′N	8°44·1′W	FT	20.10.74
	DS71	2194	4	47°34·3′N	8°33·8′W	ES	20.10.74
	DS86	1950	3	44°04·8′N	4°18·7′W	ES	31.10.74

Shell description

Good descriptions of shell morphology have been given by Verrill & Bush (1898), Clarke (1961), Barnard (1963) and Knudsen (1970) and little needs to be added (Figs 10a & b). Maximum shell length 17·0 mm; prodissoconch length 410 μm.

Except for a very small resilium superficially inset onto the valves below the umbo the ligament is external and opisthodetic with a shorter component anterior to the umbo (Fig. 10a). The ligament in *M. johnsoni* is at its maximum development in terms of anterior and posterior extent both in the family and in the Order Nuculanoidea (Fig. 39). The resilium which represents the ligament of the prodissoconch or early post larva, comprises both inner and outer layers. It is extended posteriorly by both inner and outer layers with the outer layer extending posterior to the posterior limit of the inner layer. There is a further small posterior extension of the ligament by fused periostracum. Anteriorly the resilium is extended by anterior outer layer alone. As shell growth occurs the inner layer of the early resilium splits sagittally as the margins of what was the post larval valves open to 180° or more. The two halves of the inner layer are carried through the same angle, the split between them becoming filled with anterior outer layers. This was first observed in lamellibranchs (Allen, 1960) but had not been recorded in protobranchs no doubt because so few have a ligament so well developed as that in *M. johnsoni.*

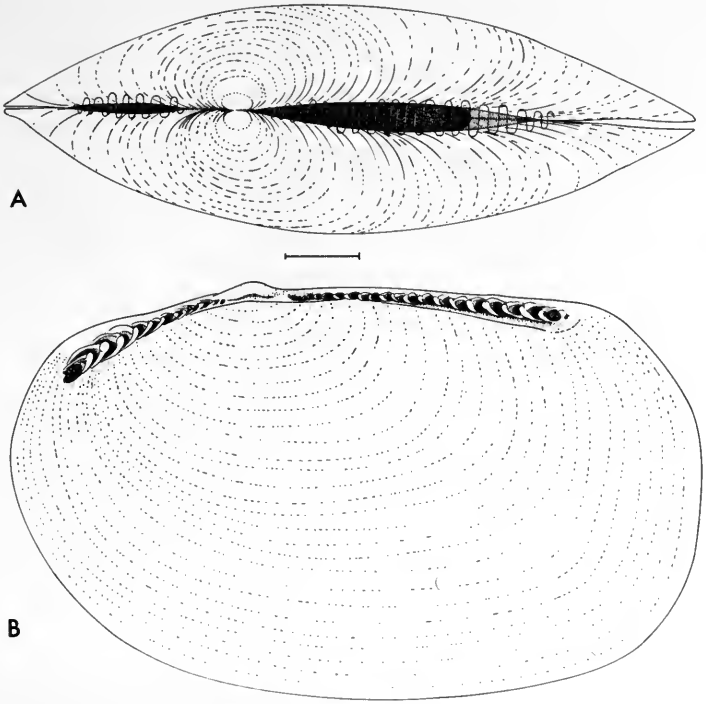

Fig. 10 *Malletia johnsoni.* (a) Dorsal view; (b) internal view of right valve of the shell of specimens from Stations 103 and 131 respectively. (North American Basin). Scale 1 mm.

Morphology

A few morphological details of *M. johnsoni* have been given by Verrill & Bush (1898) and Knudsen (1970) and some of the observations, particularly those on the siphons, are inaccurate. Verrill & Bush (1898) admit that their specimens were poorly preserved and from the small amount of detail given it must be assumed that those of Knudsen (1970) may also have been in poor condition.

Although there are relative differences the basic form of the anatomy is similar to that of *M. abyssorum* (Fig. 11). The adductor muscles are relatively large and oval in shape. The anterior sensory organ is well developed and so far anterior in position as to be slightly anterior to the anterior adductor. The feeding aperture is particularly well developed with an extensive inner glandular area (Fig. 11). The siphon is moderately long and can be completely retracted within a deep, narrow embayment. Whole mounts and sections show that the siphon is not permanently divided into inhalent and exhalent channels nor is there a pair of marked internal ridges of the type present in *M. abyssorum* which by aposition would divide the siphon into inhalent and exhalent portions (Fig. 12a). Nevertheless, there are few longitudinal muscle fibres ventrolaterally to each side of the siphon wall. These fibres connect with the gill axes but whether there is any effective division into incurrent or excurrent parts is very doubtful.

M. johnsoni is one of the few deep sea species that have been examined alive and muscular division of the siphonal aperture was not observed. Only outgoing currents, carrying faecal and pseudofaecal material were seen. The siphon was never extended far beyond the shell margins, but this may be but a reflection on the unnatural conditions under which these observations were made (in cool seawater in a glass dish at 1 atmosphere) and the inevitable lack of well-being of the animal. In contrast the single tentacle attached to the inner lower right wall of the mantle embayment was long, moderately developed, and extended some distance beyond the shell margins. The tentacle in cross section is composed of an outer epithelium tissue enclosing ten groups of longitudinal connective tissue and muscle fibres and a pair of small central longitudinal cavities.

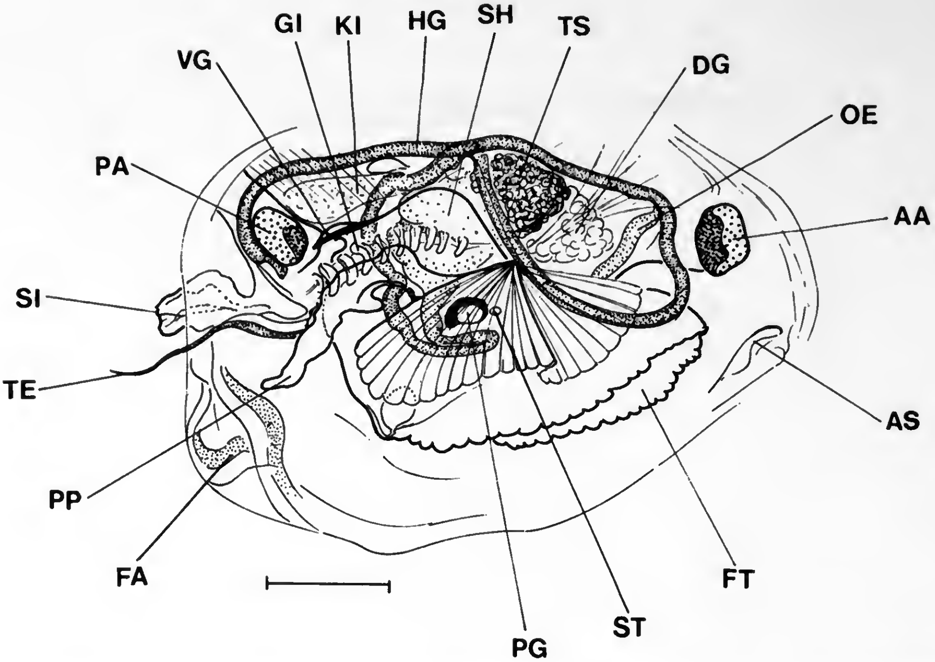

Fig. 11 *Malletia johnsoni.* Lateral view of the anatomy from the right side. For abbreviations see Appendix. Scale 1 mm.

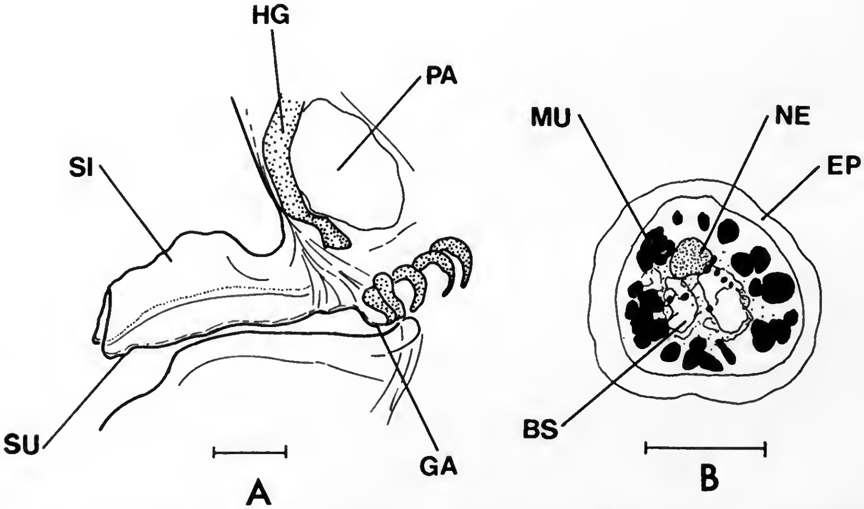

Fig. 12 *Malletia johnsoni.* (a) Lateral view of siphon (b) transverse section of siphonal tentacle. Scale 0·05 mm. Abbreviations see Appendix.

There is an acentric longitudinal nerve present (Fig. 12b). The flaps of the feeding aperture were also extended somewhat beyond the shell margins in living specimens, the palp proboscides being partially extended through the aperture. There is a main ventral rejection tract to the inside of the inner mantle fold, and particles are carried to the dorsal side of the feeding aperture. Particles on the mantle ventral and posterior to the palps are rejected via this tract.

Gills and palps are similar to those of *M. abyssorum*. The palps are moderately large with fine, numerous ridges. Rejected particles from each palp travel posteriorly to the posterior limit of the ventral palp margin from where they pass to the mantle and join the main rejection current. Observations on living gills indicate that particles on the frontal surface are passed to the ventral midline and then carried posteriorly to join either pseudofaecal material at the dorsal limit of the feeding aperture or pass through the siphon. No particles on the gills were seen to move anteriorly and be accepted by the palps or palp proboscides. Nevertheless, this has been seen to occur in some species of deep sea protobranchs.

The gut follows a similar course to that described in *M. abyssorum*. The stomach is very large taking up the posterior half of the visceral mass. Sorting areas are extensive with at least 16 ridges on the right hand wall of the stomach (Fig. 13). The gastric shield is also extensive with a large hooked tooth. Three apertures open to the digestive diverticula, the greatest proportion of which lies anterior to the stomach. The style sac is large and the gut extends ventral to the pedal ganglia. The hind gut has a single, poorly developed, typhlosole forming a fine ridge that is even less obvious than that of *M. abyssorum*.

The commissures and ganglia are large and prominent. The visceral ganglia abuts the anterior face of the posterior adductor muscle. There is a very large statocyst dorsal to each pedal ganglion.

The strong muscular, divided, foot is large with moderately fine papillae at the margins of the sole. The 'byssal' gland is large and spherical.

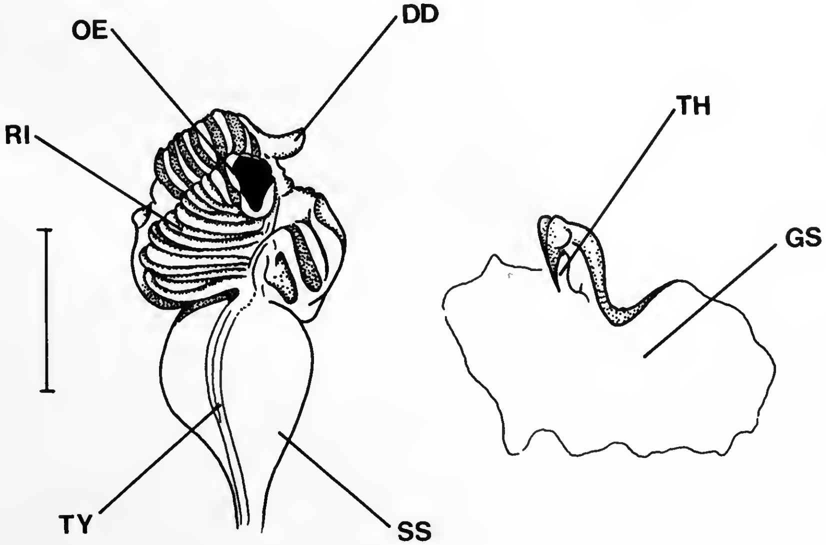

Fig. 13 *Malletia johnsoni*. Anterior view of stomach and style sac, with a gastric shield shown separately in whole mount. Scale 0·5 mm.

The gonads are similar in position to those of *M. abyssorum*. As in all deep sea protobranchs there are changes in shell shape as growth proceeds. In young specimens the umbos are posterior to the dorsal mid point of the shell (Fig. 14). The young shell is more oval in shape than it is when fully grown. With increasing size the height of the posterior part of the shell increases and in relation to length becomes more angular in outline. From the size frequency histograms which, unusually for a deep sea bivalve, are skewed markedly to the left, relatively fast growth is indicated (Fig. 15).

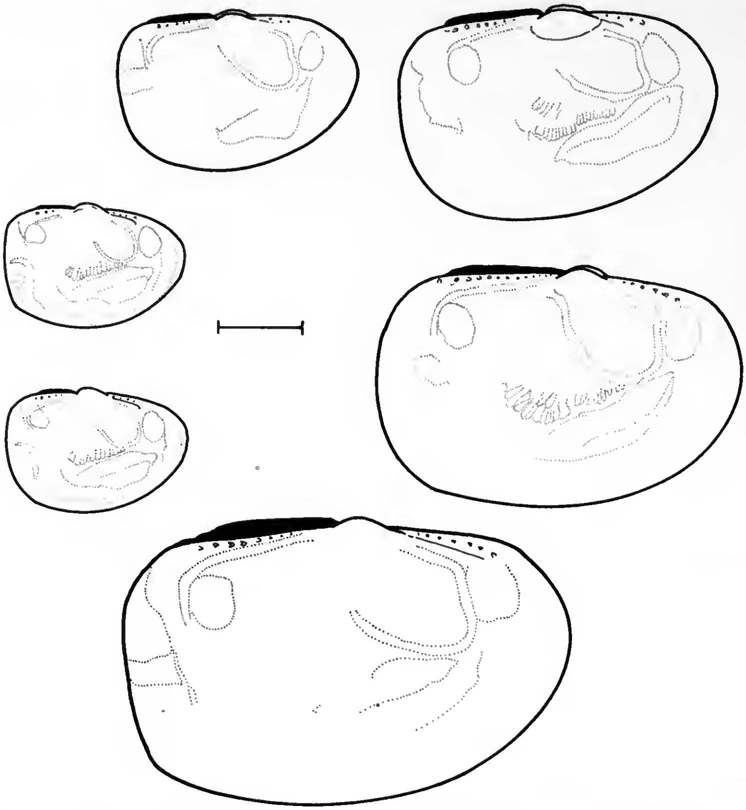

Fig. 14 *Malletia johnsoni.* Lateral view of a growth series showing variations in shape and relative positions of the umbo. Scale 1 mm.

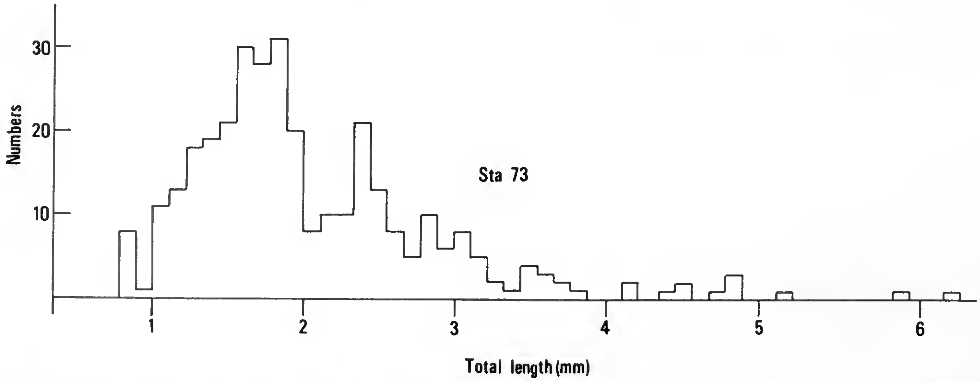

Fig. 15 *Malletia johnsoni.* Size frequency distribution of a sample from Station 73, North Atlantic Basin.

Malletia johnsoni is an inhabitant of the lower continental slope and upper abyssal rise. It has been collected from the Cape, Angola, Guinea, Sierra Leone, West Europe and North America Basins. On the assumption that *M. johnsoni* also occurs in those Eastern Atlantic Basins that were either not or superficially sampled (Cape Verde and Canaries Basins) and in the Newfoundland Basin in the Northwest Atlantic where analysed samples from the appropriate depths are lacking, we conclude that this species is continuously present at depths of from about 1000 m to 3000 m throught the entire Eastern Atlantic, across the North Atlantic and southwards in the Northwest Atlantic to at least the North America Basin. James (1972) reports an undescribed malletid similar if not identical to *Malletia johnsoni* from the Gulf of Mexico and Caribbean Basins with depth records which fall within the depth range found for *M. johnsoni.* It is occasionally collected from stations less than 1000 m and more than 3000 m but at the peripherals of its depth range where it is a minor numerical constituent of the protobranch fauna. For example, at its deepest recorded depth 3834 m (WHOI Sta 85, North America Basin), it comprised a mere 0·03% of the protobranch fauna.

Malletia grasslei (new species)

TYPE LOCALITY. *Knorr* Cruise 25, Sta 297, 523 m, Lat 7°45·3′N, Long 54°24′W, Guiana Basin.

TYPE SPECIMEN. Holotype, BM(NH) 1984058.

DEPTH RANGE = 523 m to 1022 m.

Material

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
GUIANA BASIN							
Knorr	295	1022	13	8°04·2′N	54°21·3′W	ES	28.2.72
	297	523	158	7°45·3′N	54°24·0′W	ES	28.2.72

Shell description

Shell slender, elongate, moderately fragile, fine concentric growth lines, maximum shell height at level of umbos; umbos fairly prominent, anterior to midline, anterior/posterior umbonal length ratio 5/9 in largest specimen, more central in small specimens; antero-dorsal margin gently slopes to form continuous curve with anterior margin, anterior limit of shell dorsal to horizontal midline of shell, postero-dorsal margin almost straight, slightly angled at posterior margin of hinge plate, posterior margin faintly angulate at two points dorsal to horizontal midline, ventral margin gently curved; hinge plate slender, slightly expanded posteriorly and anteriorly, numerous chevron teeth (up to 52), posterior series exceeding anterior in ratio of approximately 1·5/1, anterior and posterior series separated by edentulous space below umbos; ligament external and opisthodetic extended by fused periostracum, external except for small resilium inset at margin of edentulous space, short anterior external portion barely visible (Figs 16a, b & c). Maximum recorded shell length 17·9 mm; prodissoconch length 320 μm.

Morphology

The basic morphology of *M. grasslei* is similar to *M. johnsoni* (Fig. 17). Differences that occur can be related to the attenuated and slender form of this species. The anterior sense organ lies close to the anterior limit of the mantle margin. The posterior adductor muscle is elongate oval in shape but of similar area to the ovate anterior adductor muscle. The siphon is long. It differs from that described for *M. abyssorum* in that dorsal and ventral fusion forms an exhalent siphon but the ventral margins of the inhalent siphon are not fused but come together to form the inhalent channel. The gill axes connect with the ventrolateral edges of the exhalent siphon (Fig. 17b). The feeding aperture is relatively broad and moderately deep occupying about a third of the posterior ventral mantle margin. There is a single elongate tentacle on the right side and attached ventral to the base of the siphon. The gill axis is parallel to the antero-posterior axis. The palps are relatively short in preserved specimens and do not extend beyond the limits of the foot. There are 18 broad ridges in a specimen 5 mm in length.

In whole mount preparations a pair of small anterior palp retractor muscles can be seen attached to the shell posterior to the anterior adductor and to the palp at the point close to the mouth. The palp proboscides are very long and slender, a reflection of the small size of the palp and the posterior elongation of the body (Fig. 17a).

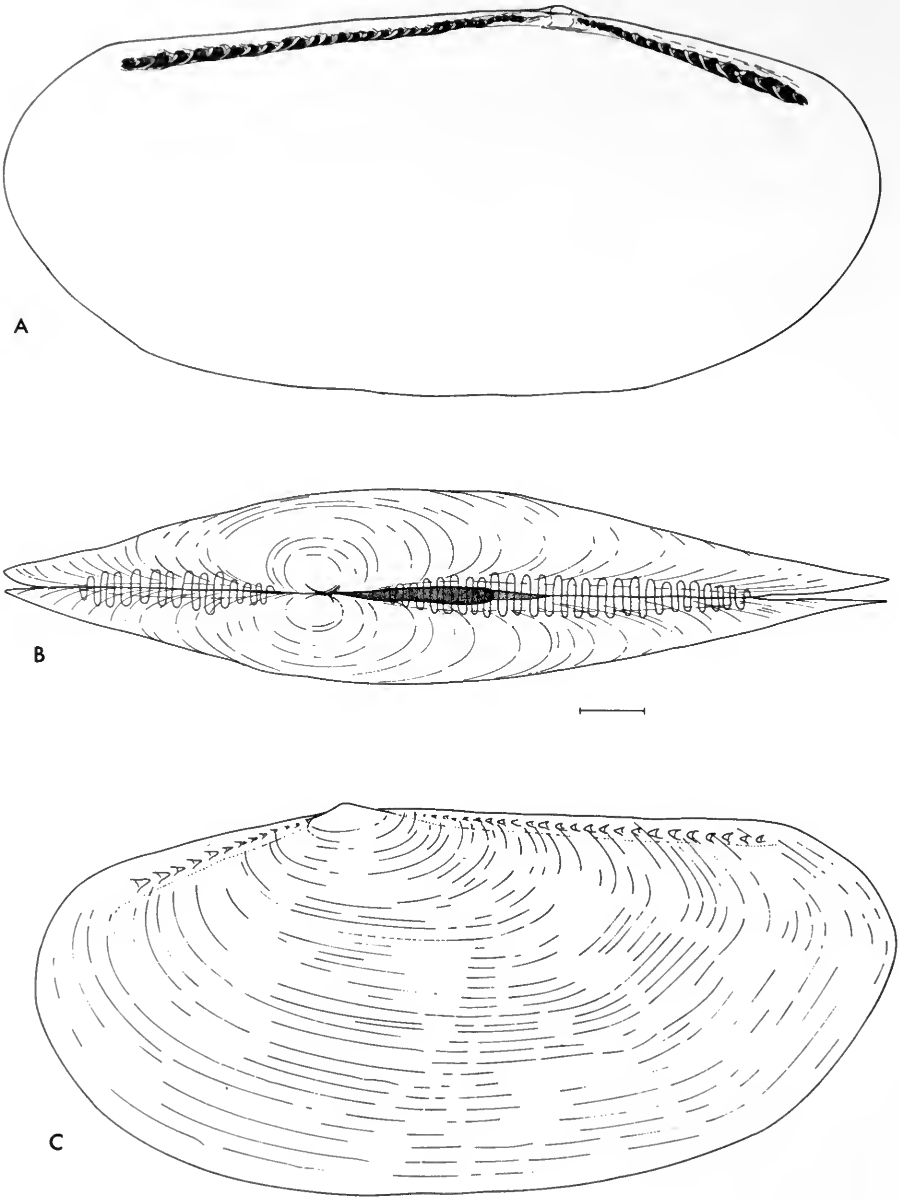

Fig. 16 *Malletia grasslei.* (a) Lateral view of left valve; (d) dorsal; (c) lateral view of the shell of the type specimen. Station 297, Guiana Basin, 7°45·3′N 54°24·0′W, 523 metres. Scale 1 mm.

Digestive and nervous systems are similar to those of *M. abyssorum* and *M. johnsoni.* The foot is elongate and points anteriorly, the margins are fringed with moderately fine papillae. The 'byssal' gland is exceptionally large. It is spherical, the sphere partially divided sagittally by an extension of the dorsal part of the peripheral epithelial cells. The cavity of the sphere appears to be filled with large cells, the contents of which cannot be made out. Peripheral nuclei can be seen only in the walls of the preparations (Allen & Chevis, in prep).

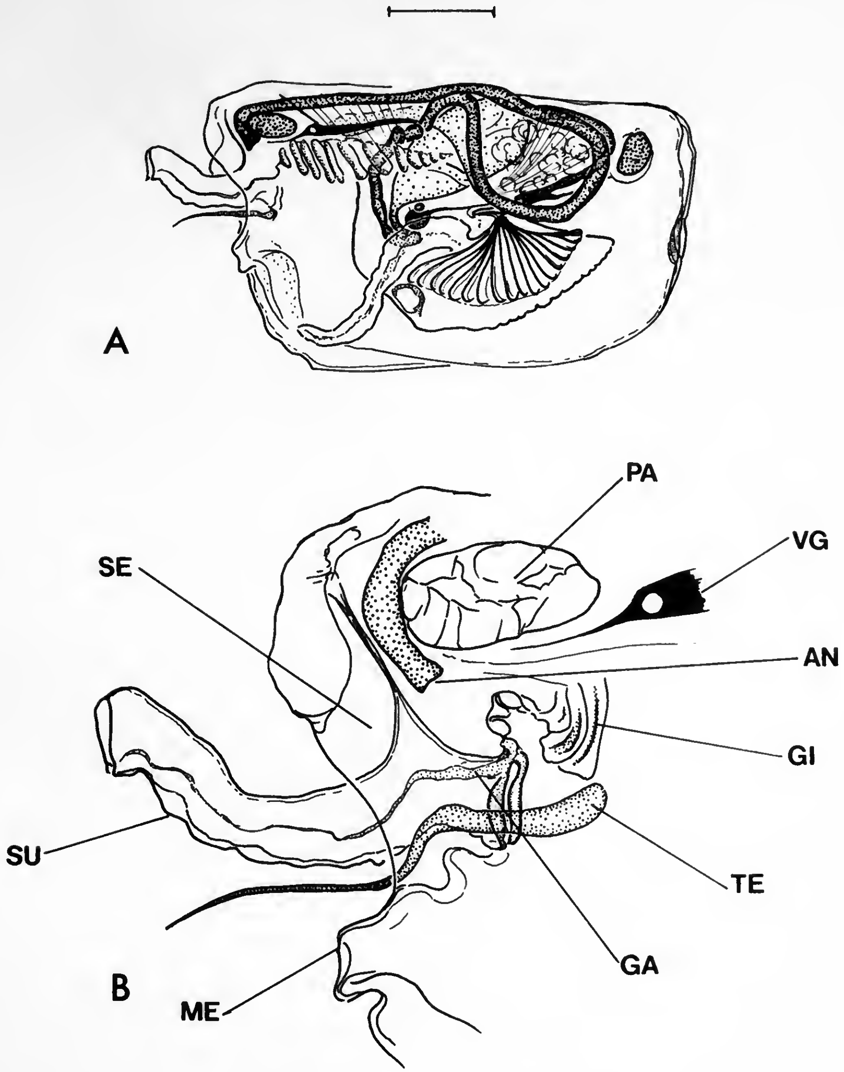

Fig. 17 *Malletia grasslei.* (a) Anatomy seen from the right side. Scale 1 mm (b) enlarged detail of siphonal region. For abbreviations see Appendix.

There is a very marked alteration in shell shape as growth proceeds. Specimens become more attenuated and there is a relative change in the height/length ratio which is accentuated by a corresponding relative increase in post umbonal shell length (Figs 18 & 19).

Malletia grasslei is present only at the two most shallow stations in the Guiana Basin from depths of 523 m and 1022 m, thus it has a remarkably narrow depth range and a very circumscribed zoogeographic distribution.

Malletia surinamensis (new species)

TYPE LOCALITY. *Knorr* Cruise 25, Sta 295, 1022 m, Lat 8°04·2′N Long 54°21·3′W, Guiana Basin.

TYPE SPECIMEN. Holotype, BM(NH) No. 1984059.

DEPTH RANGE = 523 m to 1022 m.

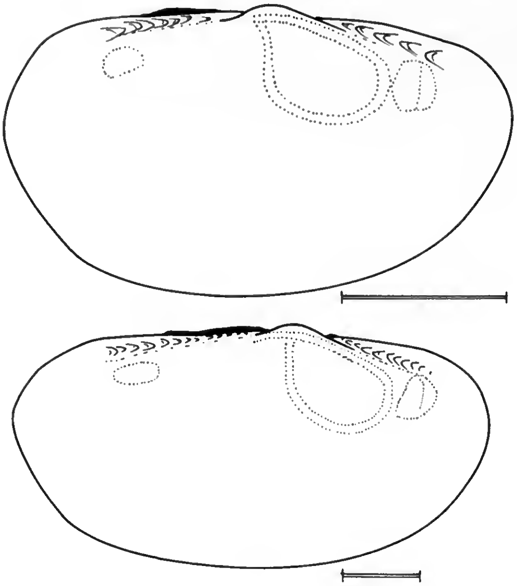

Fig. 18 *Malletia grasslei.* Comparison two shells in lateral view at different magnifications so that drawings are approximately the same overall length. Scale 1 mm. Station 295, Guiana Basin.

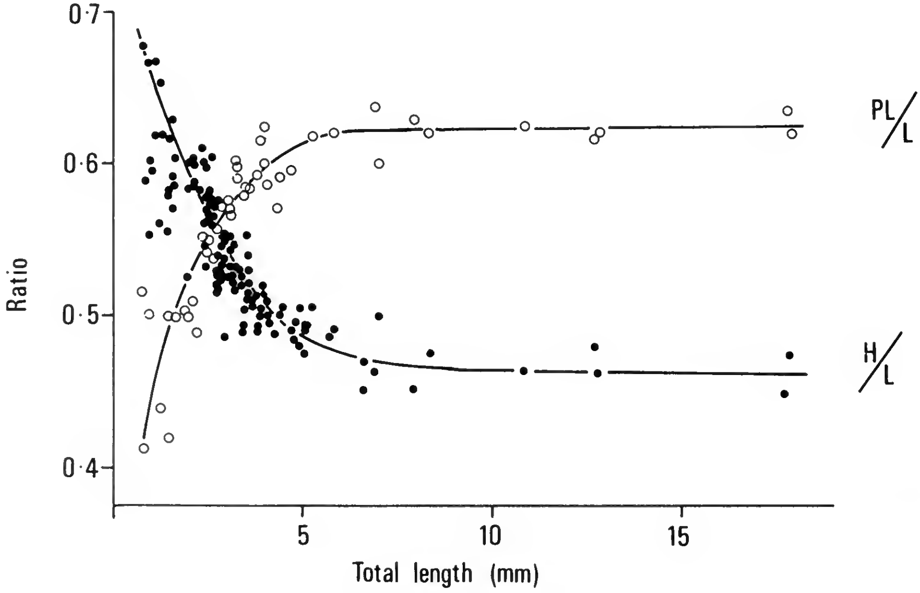

Fig. 19 *Malletia grasslei.* Analysis of shell proportions of sample taken from Station 297 showing changes with increasing size of the height/length ratio H/L and of the umbo to rostrum length/total length ratio PL/L.

Material

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
GUIANA BASIN							
Knorr	295	1022	40	8°04·2′N	54°21·3′W	ES	28.2.72
	297	523	9	7°45·3′N	54°24·0′W	ES	28.2.72

Shell description

Shell relatively short, moderately robust, with fine concentric lines, highest part of shell posterior to umbo; umbos prominent, anterior; anterior/posterior umbonal length ratio 2/3 in largest specimens, antero-dorsal margin almost straight, slopes gently to an anterior margin which it meets in a sharp curve dorsal to horizontal midline of shell, postero-dorsal margin almost

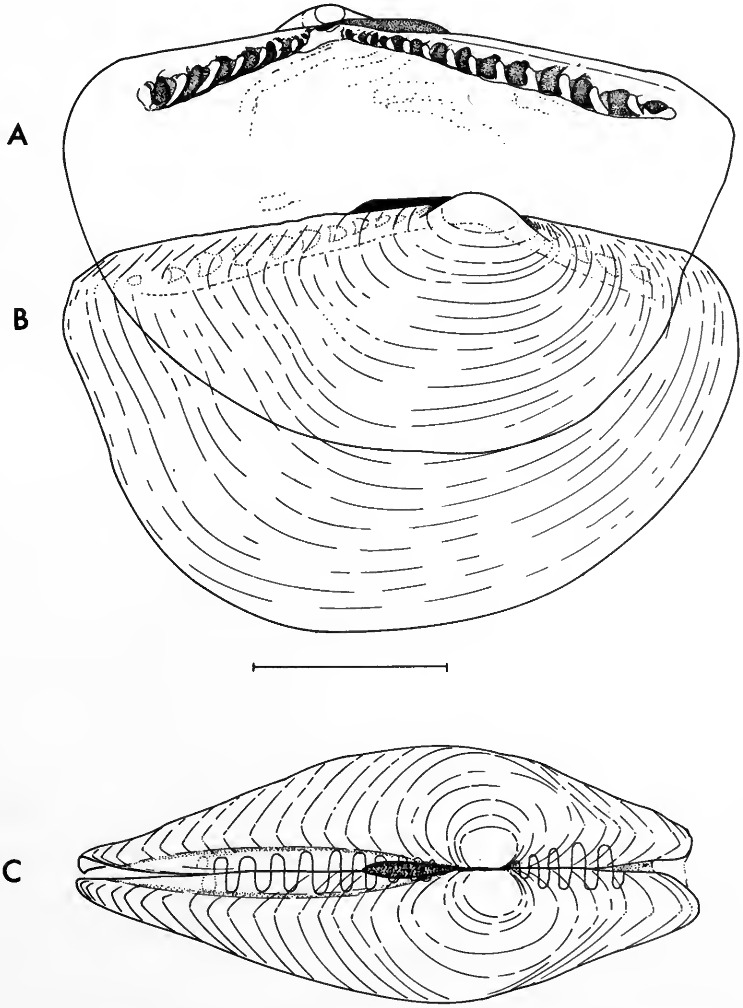

Fig. 20 *Malletia surinamensis*. (a) Lateral view of right valve; (b) lateral; (c) dorsal view of shell of type specimen from Station 295, Guiana Basin, 8°04·2′N 54°21·3′W, 1022 metres. Scale 1 mm.

straight, sharply angulate where it meets posterior margin, posterior margin deep, ventrally slightly sinuous where a very faint ridge meets margin, ventral margin moderately deeply curved; hinge plate moderately strong, well developed chevron teeth (up to 25), posterior series exceeding anterior by approximately 2/1, series separated by endentulous space below umbo; small elongate marginal resilium, relatively short opisthodetic, external, ligament, anterior outer layer very short, and due to curvature of the beaks may not be visible externally (Figs 20a, b & c; 39). Maximum shell length 4·9 mm; prodissoconch length *c.* 300 μm.

This species bears some resemblance to *Malletia dilatata* (Philippi, 1884) a specimen of which taken in 534 m off Moro Light, Havana, is illustrated in Figure 21. *M. surinamensis* does not have the upturned concave postero-dorsal margin which *M. dilatata* shares with the genus *Megayoldia*.

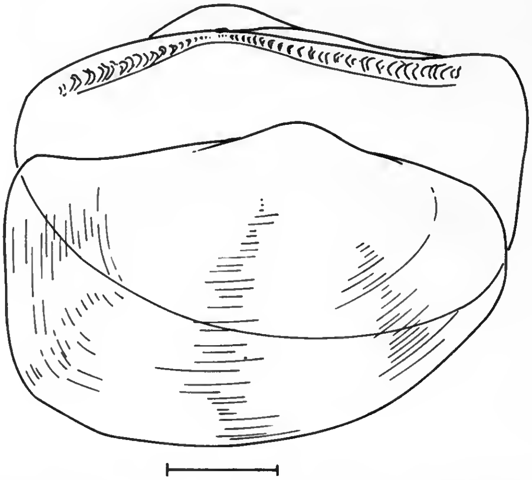

Fig. 21 *Malletia dilatata.* Internal and external lateral views of right valve of specimen, MCZ 7957, off Moro Light, Havana, 534 metres.

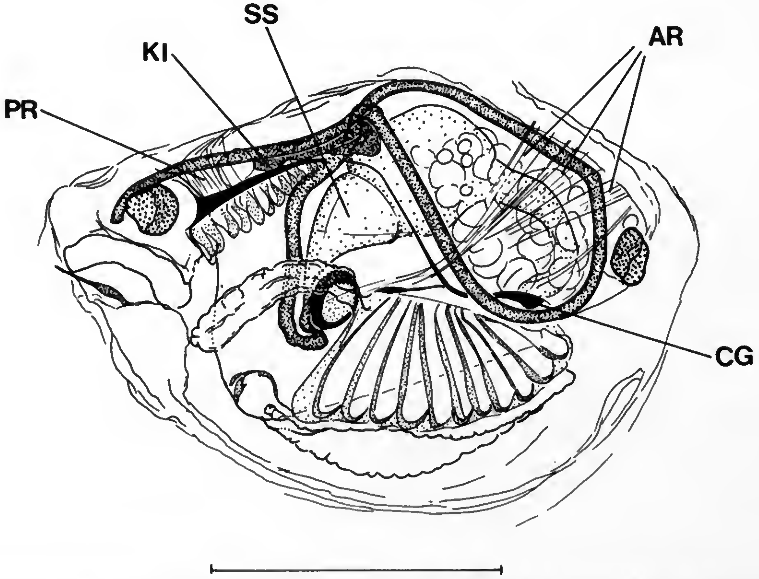

Fig. 22 *Malletia surinamensis.* Anatomy as seen from the right side. Scale 1 mm. Abbreviations see Appendix.

Although without the great development of a rostrum there is also some slight resemblance in shell shape to the genus *Spinula* (Allen & Sanders, 1982), however the ligaments is opisthodetic and not amphidetic, and the anatomy is typically malletiid in character. Thus, the hind gut is a single loop to the right of the body rather than multiple coils.

Morphology

The morphology of *M. surinamensis* is similar to that described for *M. abyssorum* (Fig. 22). The anterior mantle sense organ is situated ventral to the anterior adductor. The adductor muscles are large in comparison with other species of *Malletia.* The siphon is not permanently divided into inhalent and exhalent channels nor is there any clear internal ridging. As in *M. johnsoni* the gill axes attach ventrally and thus there is no clearly marked region that can be homologised with an inhalent siphon. The siphon is slender and ventral to it is an extensive feeding aperture. A pair of epithelial glandular ridges some seven cells deep occur to the inside of the inner mantle fold close to the siphonal embayment. The folds forming the feeding area are well supplied with mucous cells of two kinds. Glands are also present in the proximal ventral epithelium of the siphon. A tentacle is present on the right side ventral to the base of the siphon. The gill axes are at a slight angle to the anterior posterior axis of the body and in a specimen 2·0 mm total length there are 12 gill plates. The palp is relatively large with a small number of broad ridges. The palp proboscides are long and slender. The morphology of the foot and the nervous system is similar to that described for *M. abyssorum.* The hind gut is relatively slender. The digestive gland is clearly more extensive on the left side of the body but this reflects the space taken up on the right by the mid gut. The kidney extends far anterior to the level of the hind gut, posterior to the stomach. Microscopic examination of the contents of the stomach shows that there are more skeletal remains than are present in the mud trapped in the mantle, perhaps indicating that selective processes occur in the collection of food material.

Although likely, the present samples give no indication of a change in shape with the increasing size. This is because of the limited size range with 33 specimens out of 40 in the larger of the two samples under 2 mm total length and only two (3·6 mm and 4·9 mm) being larger than 3 mm.

Malletia surinamensis is limited to the same two shallow sampling sites as *M. grasslei,* i.e. depths of 523 m and 1022 m in the Guiana Basin.

Malletia malita (new species)

TYPE LOCALITY. *Knorr* Cruise 25, Sta 295, depth 1022 m, Lat 8°04·2′N, Long 54°21·3′W, Guiana Basin.

TYPE SPECIMEN. Holotype, BM(NH) No. 1984057.

DEPTH RANGE = 523 m to 1518 m.

Material

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
GUIANA BASIN							
Knorr	293	1518	2	8°58·0′N	54°04·3′W	ES	27.2.72
	295	1022	20	8°04·2′N	54°21·3′W	ES	28.2.72
	297	523	4	7°45·3′N	54°24·0′W	ES	28.2.72

Specific description

Shell ovate, moderately stout, with fine concentric growth lines, highest part of shell coincides with midline; umbos moderately prominent, slightly anterior to mid point of shell, in largest specimens posterior/anterior ratio 5/4; antero-dorsal shell margin more or less straight, inclined to form an even curve with anterior margin, postero-dorsal margin more or less straight, forms angle at posterior limits of hinge plate, posterior margin rostrate with moderately well defined ridge from umbo which meets posterior margin dorsal to horizontal midline from tip of blunt rostrum, very slight sinuosity ventral to rostrum, ventral margin smoothly and moderately deeply curved; lunule and escutcheon outlined by faint ridge; hinge plate moderately strong, expanded posteriorly and anteriorly, well-developed chevron teeth (up to 28), posterior series exceeding anterior in ratio approximately 5/3, series separated by edentulous plate below umbo, small marginal resilium; opisthodetic, external, ligament, short external anterior part (Figs 23a & b). Maximum shell length 7·8 mm; prodissoconch length 285 μm.

The form of the ligament is similar to other malletiids described here differing only in the extent of its parts. In *M. malita* the anterior outer layer extends over the proximal fifth of the anterior hinge plate while posteriorly the primary ligament extends to half the length of the hinge plate (Fig. 23a).

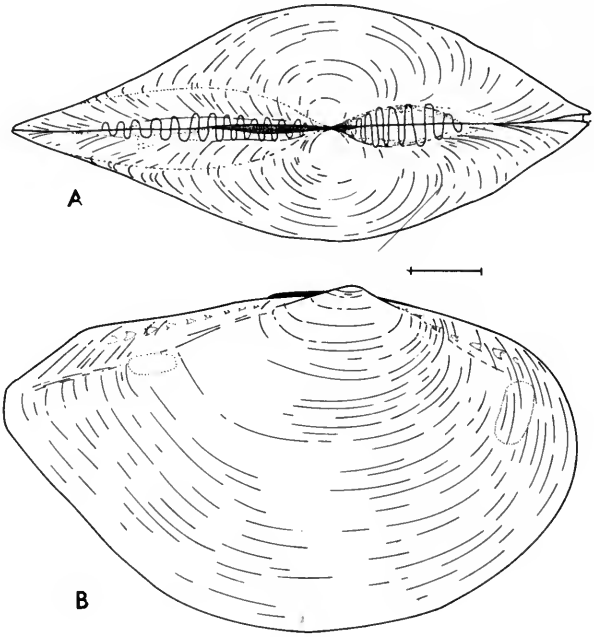

Fig. 23 *Malletia malita.* (a) Dorsal view; (b) lateral view of shell of type specimen from Station 295, Guiana Basin, 8° 04·2′N 54° 21·3′W, 1022 metres. Scale 1 mm.

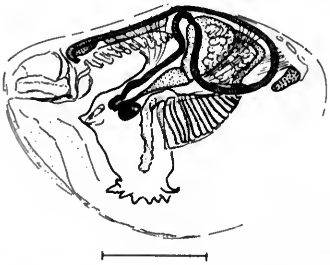

Fig. 24 *Malletia malita.* Anatomy seen from the right side. Scale 1 mm.

Morphology

The morphology of *M. malita* is essentially similar to that of other species described here (Fig. 24). The mantle differs somewhat from that of other species, in that the position of the anterior marginal sense organ is ventral and slightly anterior to the anterior adductor muscle. The adductor muscles are unequal in size, the posterior being the smaller, they also differ in shape, the anterior being broad and oval while the posterior is narrow, elongate and parallel to the dorsal shell margin. The siphons resemble those of *M. grasslei*. The feeding aperture occupies more than half of the ventro-posterior mantle margin but is relatively shallow. The gill axis lies parallel to the posterior dorsal shell margin and bears up to twelve plates. The palp is moderately large with up to eighteen ridges.

The morphology of the internal organs is similar to other malletiids described here. It may be noted that the hind gut is relatively narrow and the visceral ganglion lies short of the posterior adductor muscle. The commissures are slender. The foot is relatively small, fringing papillae being few in number. The 'byssal' gland is of moderate size.

No specimen is mature but in several, developing gonads can be seen at the anterior and ventral edge of the digestive gland.

Malletia malita is the third severely restricted malletiid species only to be found in the Guiana Basin. It co-occurs with *M. grasslei* and *M. surinamensis* at the two shallowest depths of 523 m and 1022 m but in this case is also present at the third shallowest depth of 1518 m.

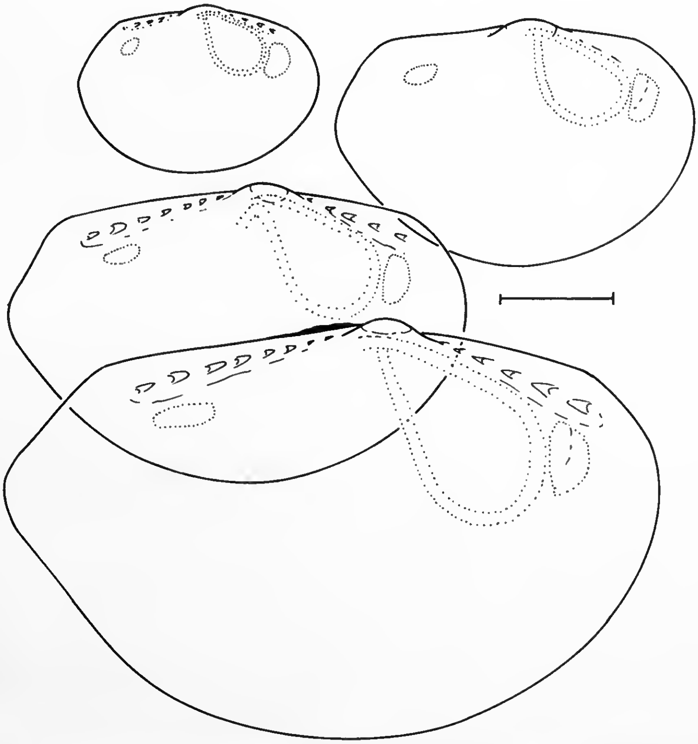

Fig. 25 *Malletia malita.* Lateral outlines of specimens to show change in shape with increasing size. Scale 1 mm.

As in the previous species, there are too few specimens to make any sure statement on change in shape with increasing size, but it is highly likely that the shell becomes more rostrate with age (Fig. 25).

Malletia pallida Smith, 1885

Malletia pallida Smith, 1885: *Chall. Rep.* **13:** 246, pl. 20, figs 8, 8a. TYPE LOCALITY. Challenger Sta 137, depth 4667 m, Lat 35°59·0'S, Long 01°34·0'E. TYPE SPECIMEN. Holotype, BM(NH) No. 1887.2.9.300 ba

Nuculana pallida Knudsen, 1970: *Galathea Rep.* **11,** figs 9 & 10.

DEPTH RANGE = 1261 m to 5280 m.

Knudsen (1970) gives no reason for transferring this species to the genus *Nuculana*. The species conforms to all the characters of genus *Malletia*.

Material

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
SIERRA LEONE BASIN							
Atlantis II	146	2891	1	10°39·5'N	17°44·5'W	ES	6.2.67
	147	2934	29	10°38·0'N	17°52·0'W	ES	6.2.67
	148	3828	6	10°37·0'N	18°14·0'W	ES	7.2.67
	149	3861	20	10°30·0'N	18°18·0'W	ES	7.2.67
GUINEA BASIN							
Walda (J. Charcot)	DS28/36	1261	4	4°21·2'N	4°35·2'E	ES	.6.71
ANGOLA BASIN							
Atlantis II	195	3797	58	14°40·0'S	9°54·0'E	ES	19.5.68
	197	4595	3	10°29·0'S	9°04·0'E	ES	21.5.68
	198	4566	7	10°24·0'S	9°09·0'E	ES	21.5.68
	199	3779	11	9°49·0'S	10°33·0'E	ES	22.5.68
	200	2754	5	9°43·5'S	10°57·0'E	ES	22.5.68
Walda (J. Charcot)	CY13/19	2044	228	12°03·7'S	12°22·3'E	T	.6.71
	DS05/06	2992	5	21°45·0'S	11°07·8'E	ES	11.6.71
CAPE BASIN							
Campagne Walvis I	DS02	5280	3	33°54·7'S	5°07·5'E	ES	25.12.78

Shell description

The original description by Smith (1885) and its later amplification by Knudsen (1970) is detailed and accurate. The species is closely related to *M. polita* of the North America Basin, to *M. polita* of the West Europe Basin and *M. cuneata* of the North Atlantic Ocean. Maximum shell length 16·5 mm; prodissoconch length 260 μm.

The morphologies of the species and varieties of the *pallida/polita/cuneata* complex are very similar. They possess the same basic malletiid form and only items of significance for identification need to be mentioned. The shell differences are subtle and not easily defined, but they are consistent and can be recognized by the experienced observer, and, thus, are best illustrated (Fig. 26a & b). In each case there is a change in shell shape with increasing size and undoubtedly the larger the specimen the more readily identifiable it becomes.

In the case of *M. pallida* the following may be mentioned: The umbos are small and anterior in position, the anterior/posterior umbonal length ratio is 5/8. The ligament is elongate, the anterior and posterior parts, not including extension by fused periostracum, occupy half the length of the dorsal shell margin (Figs 26a & 39). The shell is characteristically inflated in the central region lateral to the umbos and the maximum width coincides with the line of the maximum height measurement. A moderately strong hinge bears numerous close-set chevron teeth (50 in large specimens), the anterior and posterior series are in the ratio of 2/3.

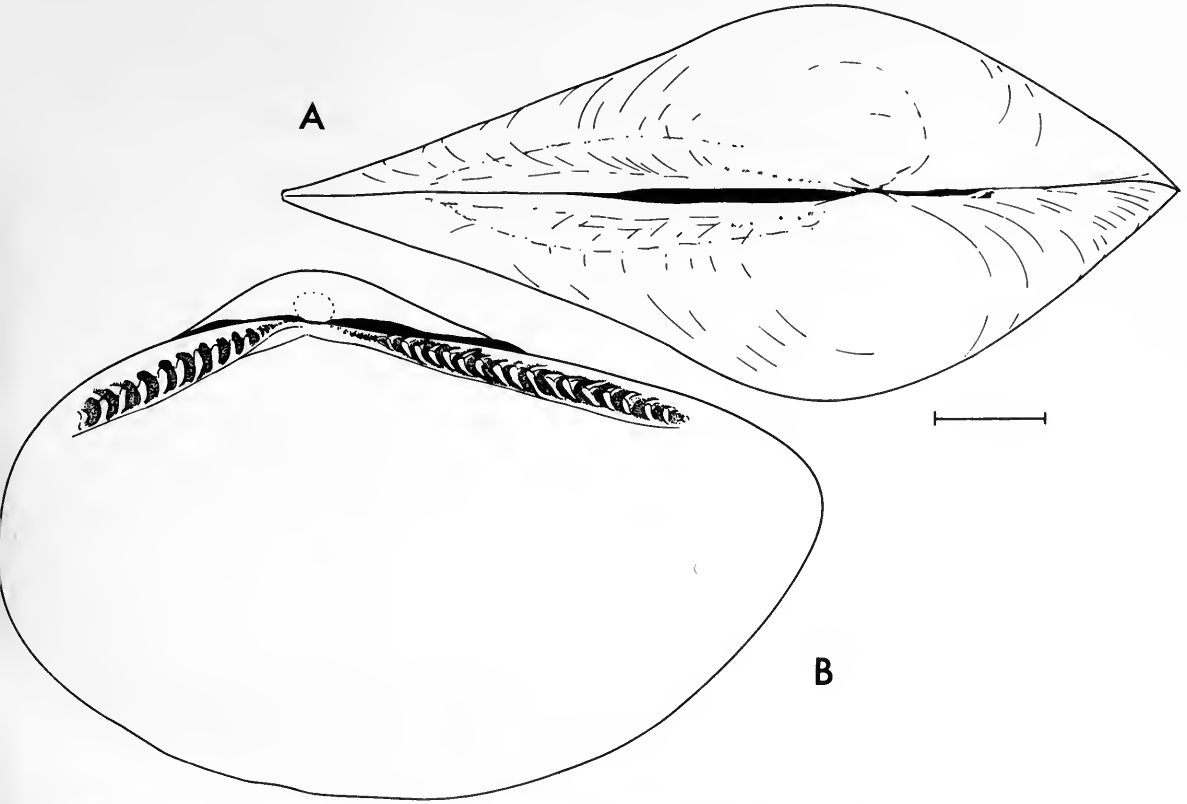

Fig. 26 *Malletia pallida.* (a) Dorsal view of shell; (b) internal lateral view of right valve from Station CY 13 Angola Basin 2044 metres. Scale 1 mm.

Morphology

The strength of the malletiid hinge is related to the size of the adductor muscles. In *M. pallida* these are relatively small and unequal in size. The posterior adductor is an elongate oval in the horizontal plane, the anterior adductor is somewhat larger in cross section and broadly oval. The siphons and feeding aperture are similar to those described for *M. grasslei.* The 'byssal' gland is very large. The cerebral and visceral ganglia and the connecting commissures are particularly stout. Other features are best compared by reference to Figures 27, 31 & 37.

Growth with age follows a similar course to that described for *M. abyssorum* with large specimens more elongate and rostrate than smaller (Fig. 28). *M. pallida* collected in the Sierra Leone, Guinea, Angola and Cape basins, is confined to tropical and southern regions of the East Atlantic. It has a remarkably wide depth distribution that extends from 1261 m to 5280 m.

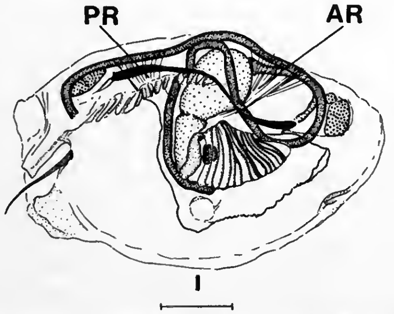

Fig. 27 *Malletia pallida.* Anatomy as seen from the right side. Scale 1 mm.

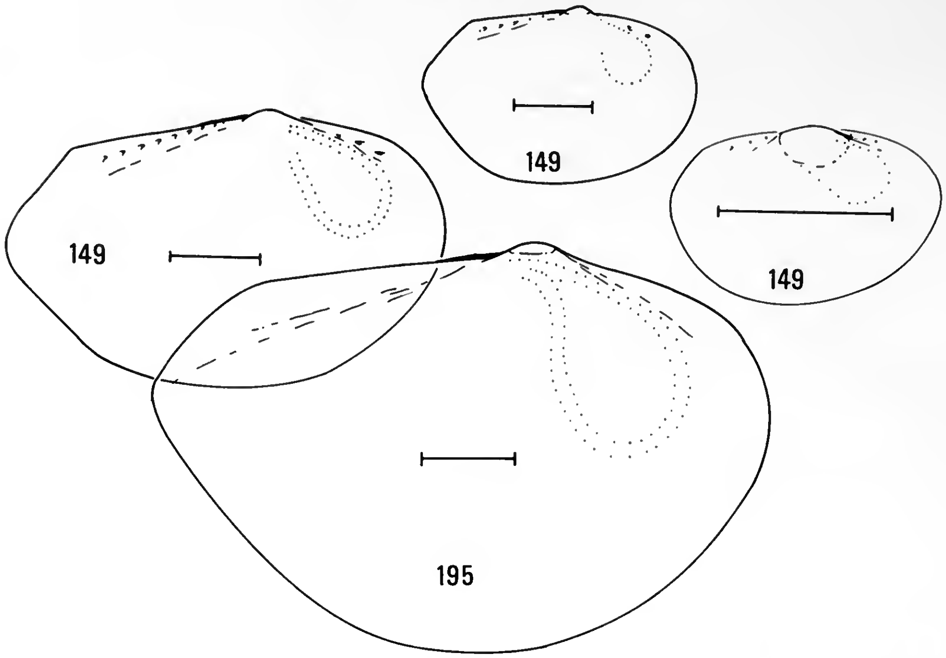

Fig. 28 *Malletia pallida.* Lateral outlines of specimens to show change in shape with increasing size. Note smallest specimen is magnified × 2 and largest specimen is from a different Station (195) to the others (149) and shows a difference in ventral curvature between the two populations. Scale 1 mm.

Malletia polita Verrill & Bush, 1898

Malletia polita Verrill & Bush, 1898: *Proc. U.S. natl. Mus.* **20:** 876, pl. 82, fig. 10. Type locality. US Fish. Commission, Sta 2718, Lat 38°24·0′N, Long 71°51·0′W. 2871 m. Type specimen. Holotype, U.S. Natl Mus. No. 78972.

Malletia bermudensis Haas, 1949; *Butl. Inst. Catalana d'Hist. Nat.* **37:** 71. Type locality. Lat 32°82.0′N, Long 64°33.0′W, 1700 fathoms deep off Bermuda coast. Type specimen. Holotype. Field Mus. Natl Hist., Chicago, No. 31658.

Depth range Variety **A** = 2871 to 5867 m.
Depth range Variety **B**—4521 to 4825 m.

Material

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Variety **A**							
North America basin							
Chain	80	4970	71	34°50·0′N	66°34·0′W	ES	2.7.65
	84	4749	6	36°24·0′N	67°56·0′W	ES	4.7.65
	85	3834	2	37°59·0′N	69°26·0′W	ES	5.7.83
Atlantis II	93	5007	51	34°39·0′N	66°26·0′W	ES	14.12.65
	121	4800	7	35°50·0′N	65°11·0′W	ES	21.8.66
	122	4833	2	35°52·0′N	64°58·0′W	ES	21.8.66
	123	4853	3	37°29·0′N	64°14·0′W	ES	22.8.66
	124	4862	3	37°58·0′N	63°58·0′W	ES	22.8.66
	125	4825	20	37°26·0′N	65°50·0′W	ES	23.8.66
	175	4693	5	36°36·0′N	68°31·0′W	ES	29.11.67
Oceanus	605	4986		35°11·0′N	67°20·0′W	ST*	27.4.76

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
GUIANA BASIN							
Knorr	287	4980	180	13°16·0′N	54°52·0′W	ES	24.2.72
	288	4429	71	11°04·0′N	58°05·0′W	ES	15.2.72
	307	3862	1	12°41·0′N	59°09·0′W	ES	3.3.72
Biovema							
(J. Charcot)							
	DS01	5097	1	10°57·2′N	45°07·6′W	ES	14.11.77
	DS03	5150	22	10°47·1′N	42°40·7′W	ES	16.11.77
	DS04	5100	49	10°46·3′N	42°41·4′W	ES	17.11.77
	DS05	5100	24	10°46·0′N	42°40·3′W	ES	18.11.77
	DS11	5867	63	11°37·5′N	32°53·8′W	ES	26.11.77
Variety **B**							
WEST EUROPE BASIN							
Polygas	CV15	4700	1	46°32·2′N	10°28·4′W	BT	27.10.72
(J. Charcot)							
	DS23	4721	3	46°32·8′N	10°21·0′W	ES	26.10.72
Biogas III	DS46	4521	1	46°28·6′N	10°23·0′W	ES	29.8.73
Biogas IV	DS59	4659	1	46°31·1′N	10°29·2′W	ES	19.2.74
Biogas VI	CP16	4706	16	46°27·3′N	10°25·8′W	FT	25.10.74
	CP17	4825	39	46°30·8′N	10°19·5′W	FT	26.10.74
	DS78	4706	8	46°31·2′N	10°23·8′W	ES	25.10.74
	DS79	4715	12	46°30·4′N	10°27·1′W	ES	26.10.74
	DS80	4720	3	46°29·5′N	10°29·5′W	ES	27.10.74
	DS81	4715	2	46°28·3′N	10°24·6′W	ES	27.10.74

*41 foot Gulf of Mexico Shrimp Trawl

Shell description

The original description (Verrill & Bush, 1898) was based on a single damaged valve, however, for the most part this description is both detailed and accurate. The description by Haas (1949) of what he thought was a new species of *Malletia* is based on three valves which are much less damaged than the type. The description is modest and in no great detail, but is supported by a photograph. Both descriptions are of shells from the Western Atlantic North America Basin and correspond to Variety **A.**

Despite the existing descriptions the following shell features should be mentioned (Figs 29a & b). Shell robust, inflated with clear concentric ornamentations; umbos prominent, anterior/posterior umbonal length ratio being 2/3; antero-dorsal, anterior and ventral margins in continuous curve, posterior margin somewhat rostrate dorsally with postero-dorsal margin angled at posterior limit of hinge plate, faint indication of a rostral ridge, no lunule, escutcheon barley visible, hinge plate moderately strong, many short chevron teeth (*c.* 40 in large specimens) anterior and posterior series in ratio 3/5, series separated by relatively short edentulous space below umbo; resilium small, inset at margin of edentulous space, external ligament prominent anterior and posterior to umbo, posterior ligament extends along half posterior hinge plate and is three times length of anterior external ligament. With increasing size, the shell becomes posteriorly elongate and more clearly rostrate (Fig. 30).

Although sample numbers are small, population histograms show a typical deep-sea pattern without a marked skew in numbers to the left, indicative of low mortality of the younger specimens. Maximum shell length 24·5 mm; prodissoconch length 340 µm.

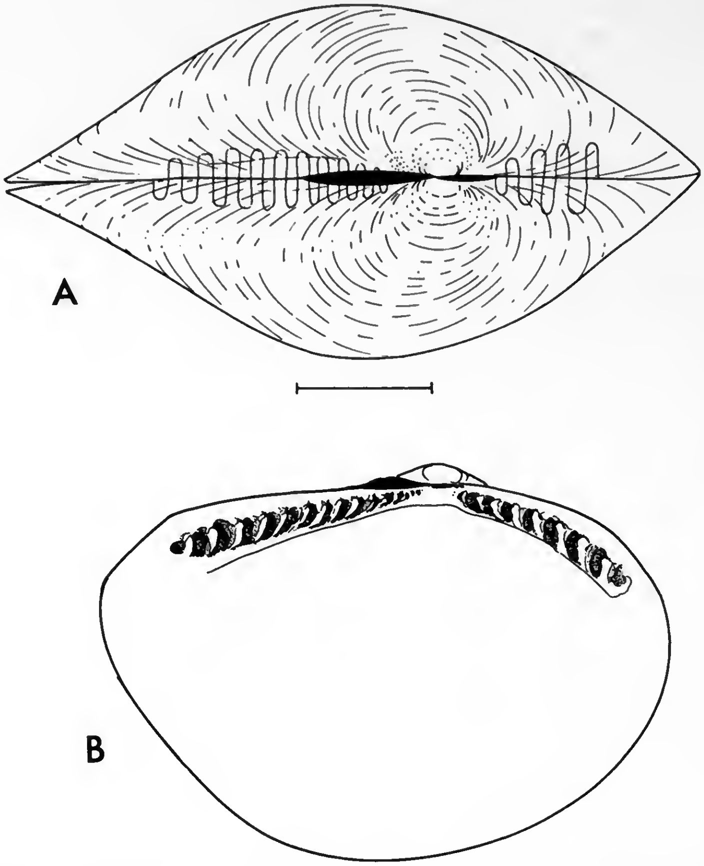

Fig. 29 *Malletia polita.* Variety A. (a) dorsal view of shell; (b) lateral view of inner left valve from Station 125, North America Basin, 4825 metres. Scale 1 mm.

Morphology

The morphology is similar to the previous species (Fig. 31a & b). The adductor muscles are elongate, oval and relatively small. The mouth lies some distance posterior to the anterior adductor, the stomach lies in the body and the hind gut is large in diameter with a well defined typhlosole. The palps are relatively large with elongate slender proboscides, the palp ridges are broad. The gills are elongate with relatively few broad plates. The gills are not joined in the midline behind the foot. The axes are connected to the fused ventral margin of the exhalent siphon. There is no clearly defined inhalent siphon although in some preserved specimens there is a suggestion of a short, ventrally open, channel, which extends about half way along the proximal ventral margin of the exhalent siphon. A narrow feeding aperture is ventral to the siphon. The centro-visceral commissures are stout. The above description relates to Variety **A** which is restricted to the Western Atlantic.

Variety **B**

Specimens from the West Europe Basin are, to the practised eye, subtly distinct and have been designated Variety **B**. The differences are not so clearly obvious as to define a different species. This is a state of affairs that is common to many species of deep sea bivalves from the Atlantic and must relate to the relative isolation of the basins as the ocean enlarged and to the slowness of gene flow, which in turn presumably is related to reproductive strategy and the extent of larval dispersion.

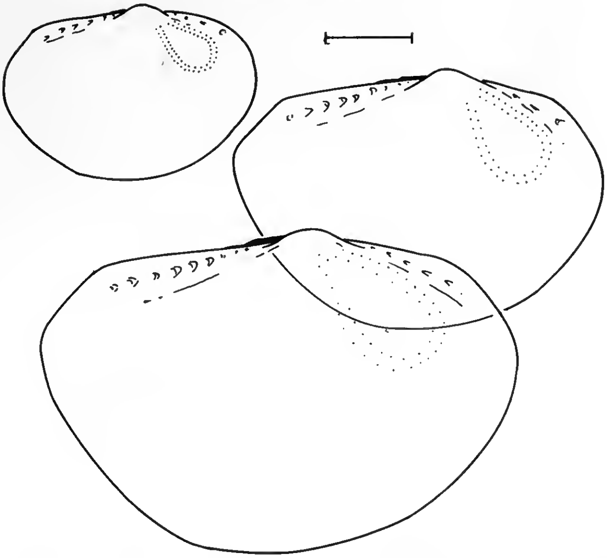

Fig. 30 *Malletia polita.* Variety A. Lateral outlines of specimens to change in shape with increasing size. Scale 1 mm.

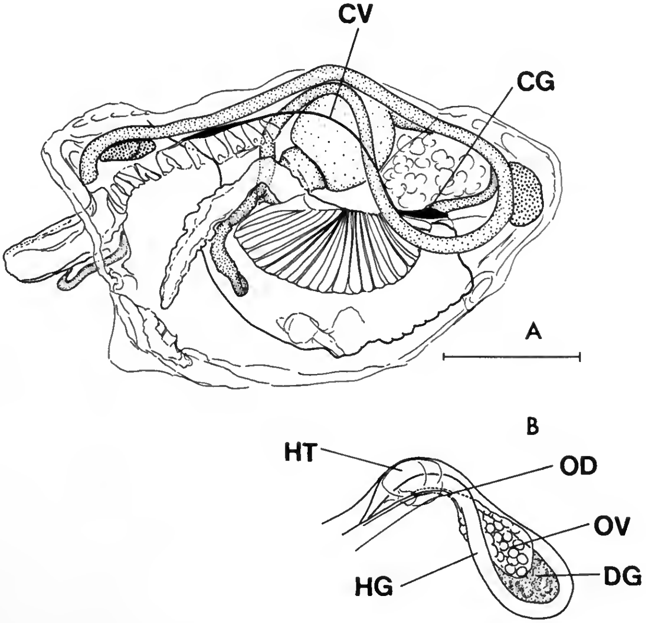

Fig. 31 *Malletia polita.* Variety A. (a) Anatomy as seen from the right side; (b) detail of developing ovary and oviduct as seen dorso-laterally. Scale 1 mm. Abbreviations see Appendix.

The shell differs from Variety **A** in that it is slightly more posteriorly elongate (Figs 32a & b) with the rostral ridge and escutcheon slightly more defined; the ventral margin is not so deep and round. The ligament of Variety **A** is longer than that of Variety **B** and extends further anterior (Fig. 39). Maximum shell length 19·0 mm; prodissoconch length 340 μm.

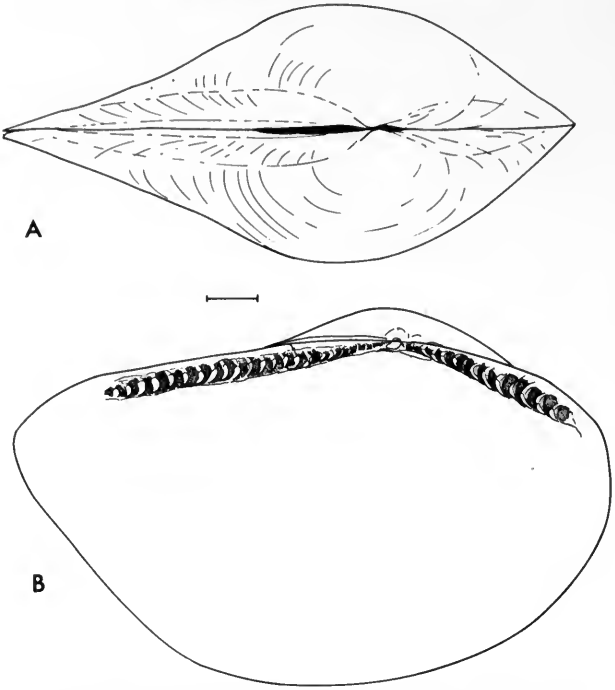

Fig. 32 *Malletia polita.* Variety B. (a) Dorsal view of shell; (b) lateral view of inner left valve from Station BG VI CP 16, West European Basin, 4825 metres. Scale 1 mm.

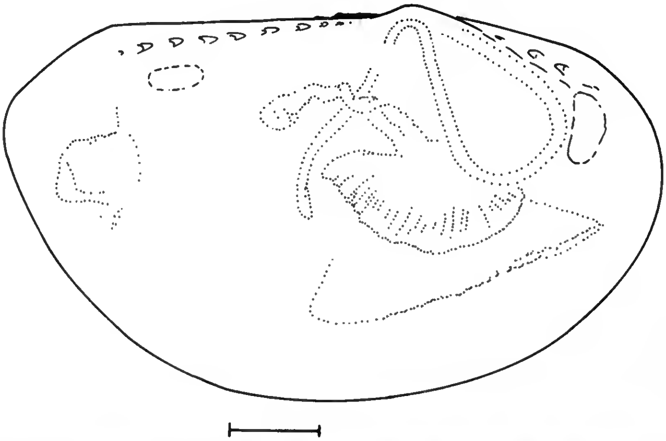

Fig. 33 *Malletia polita.* Variety B. Lateral view of shell from the right side with outline of hind gut, foot, palp and adductor muscles seen through the partially transparent shell. Scale 1 mm.

Anatomically **B** differs little from **A,** but the gut appears to be not so large in diameter and the loop of the hind gut not so deep. (*cf.* Fig. 31 & Fig. 33). The overall impression of the European specimens is that they are less robust than their West Atlantic counterparts. This is a subjective opinion, which may possibly be quantified in the future by genetical and computer analysis of larger collections. At present it rests on an almost indefinable overall comparative appreciation.

Two varieties of *Malletia polita* are found only at deeper abyssal depths. Variety **A**, the Western Atlantic form, was collected from the North America Basin and Guiana Basin. Excepting polar seas it occurs over a depth range of 3834 m to 5867 m however, if the two shallowest records are excluded and which form a mere trace of the protobranch fauna present (0·74%, 0·03%) then the depth range narrows to 4429 m to 5867 m. *M. polita* variety **B,** the Eastern Atlantic form, was taken only from the West Europe Basin, is similarly confined to great depths which range from 4521 m to 4706 m.

Malletia cuneata Jeffreys, 1876

Malletia cuneata Jeffreys, 1876: *Ann. mag. nat. Hist.* (18)**4:** 435 (*non Solenella cuneata* Jeffreys, 1874: *Rep. Brit. Ass.*, 1873, *nomen nudum*). Type locality. *Valorous* Expedition, Sta 9, 59°10.0′N, Long 50°25.0′E, 3150 m. Type specimen. Lectotype. BM(NH) No. 1877–11.28.34.

Portlandia kolthoffi Hägg, 1904: *Ark. Zool.* 2: 12, pl. 1, figs 1–3. Type locality. Swedish Zoological Polar Expedition 1900. Lat 72°1′N Long 08°33′W, 2400 m. Type specimen. Not recorded.

Malletia pellucida Thiele, 1912: *Dt. Südpol. exped.* **13:** 254, pl. 17, fig. 23. Type locality. Deutsch Südpolar Expedition. North West of Gauss-Station, 2916 and 3423 m. Type specimen. Zoological Museum Berlin.

Malletia (Neilo) fiora Dall, 1916: *Proc. U.S. natn. Mus.* **52:** 400. Type locality. U.S. Fisheries Steamer *Albatross* Sta 2859 SW of Stika Bay, Alaska, 2860 m. Type specimen. U.S. Natl Mus. No. 207251.

Neilonella kolthoffi Gurbunov, 1946: *Trudy drief. Eksped. 'G. Sedov'* 1937–40. **3:** 312, fig. 4, pl. 3, figs 2a–c.

Neilonella cuneata Soot-Ryen, 1966: *Sarsia* **24:** 3.

Katadesmia kolthoffi Bouchet & Waren, 1979; *Sarsia* 64: 214, figs 2a–c, 21 & 22.

non Malletia cuneata Smith, 1888: *Chall. Rep.* **13:** 247, pl. XX, figs 10–10a.

Material

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Variety A							
NORTH AMERICA BASIN							
Atlantis II	64	2886	6	38°46·0′N	70°06·0′W	ES	21.8.64
	70	4680	8	36°23·0′N	67°58·0′W	ES	23.8.64
	72	2864	1	38°16·0′N	71°47·0′W	ES	24.8.64
Chain	77	3806	1	38°07·0′N	69°16·0′W	ES	30.6.65
	78	3828	64	38°08·0′N	69°18·7′W	ES	30.6.65
	84	4749	3	36°24·4′N	67°56·0′W	ES	4.7.65
	85	3834	787	37°59·2′N	69°26·2′W	ES	5.7.65
Atlantis II	92	4694	2	36°20·0′N	67°56·0′W	ES	13.12.65
	175	4693	4	36°36·0′N	68°31·0′W	ES	2.12.67
Chain	340	3356	43	38°17·6′N	70°22·8′W	ES	24.11.73
WEST EUROPE BASIN							
Sarsia	50	2379	4	43°46·7′N	03°38·0′W	ES	18.7.67
Chain	321	2890	3	50°12·3′N	13°35·8′W	ES	20.8.72
	323	3356	8	50°08·3′N	13°53·7′W	ES	21.8.72
	326	3859	85	50°04·9′N	14°23·8′W	ES	22.8.72
	328	4435	1	50°04·7′N	15°44·8′W	ES	23.8.72
Polygas (J. Charcot)	DS20	4226	25	47°33·0′N	09°36·7′W	ES	24.10.72
	DS21	4190	24	47°31·5′N	09°40·7′W	ES	24.10.72
	DS22	4144	20	47°34·1′N	09°38·4′W	ES	25.10.72
	DS23	4734	6	46°32·8′N	10°21·0′W	ES	26.10.72
Biogas II (J. Charcot)	DS30	4106	1	47°38·3′N	09°33·9′W	ES	18.4.73
	CV18	4120	1	47°32·2′N	09°36·5′W	BT	18.4.73

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Biogas III	DS41	3548	2	47°28.3′N	09°07·2′W	ES	26.8.73
	DS42	4104	2	47°32·1′N	09°35·6′W	ES	27.8.73
	DS44	3992	2	47°33·2′N	09°42·0′W	ES	27.8.73
	DS45	4260	3	47°33·9′N	09°38·4′W	ES	27.8.73
	CV27	4023	4	47°34·2′N	09°32·4′W	BT	28.8.73
	CV30	4518	2	46°32·8′N	10°20·0′W	BT	29.8.73
Biogas IV	DS54	4659	7	46°31·1′N	10°29·2′W	ES	21.2.74
	DS55	4125	109	47°34·9′N	09°40·9′W	ES	22.2.74
	DS56	4050	2	47°32·7′N	09°28·2′W	ES	23.2.74
	DS57	2906	1	47°30·8′N	09°07·6′W	ES	23.2.74
	DS58	2775	3	47°34·1′N	09°08·2′W	ES	23.2.74
	DS60	3742	10	47°26·8′N	09°07·2′W	ES	24.2.74
	DS61	2250	1	47°34·7′N	08°38·8′W	ES	25.2.74
Biogas V (Cryos)	CV36	4209	1	47°34·1′N	09°38·5′W	BT	22.2.74
	DS66	3480	18	47°28·2′N	09°00·0′W	ES	16.6.74
	DS67	4150	7	47°31·0′N	09°35·0′W	ES	17.6.74
Biogas VI (J. Charcot)	CP13	4134	12	47°34·4′N	09°38·0′W	HT	23.10.74
	CP14	4237	9	47°32·0′N	09°35·9′W	HT	23.10.74
	CP15	4715	25	46°32·2′N	10°28·5′W	HT	23.10.74
	CP17	4706	2	46°30·8′N	10°19·5′W	HT	26.10.74
	DS75	3250	1	47°28·1′N	09°07·8′W	ES	22.10.74
	DS76	4228	198	47°34·8′N	09°33·3′W	ES	23.10.76
	DS77	4240	34	47°31·8′N	09°34·6′W	ES	24.10.74
	DS78	4706	21	46°31·2′N	10°23·8′W	ES	25.10.74
	DS79	4715	58	46°30·4′N	10°27·1′W	ES	26.10.74
	DS80	4720	17	46°29·5′N	10°29·5′W	ES	27.6.74
	DS82	4462	3	44°25·4′N	04°52·8′W	ES	29.10.74
	DS84	4466	1	44°30·0′N	04°53·8′W	ES	29.10.74
CANARIES BASIN							
Discovery	6696	1780	2	28°06·0′N	13°28·0′W	ES	15.3.68
	6711	2988	5	27°14·9′N	15°36·3′W	ES	19.3.68
	6714	3301	1	27°13·0′N	15°41·0′W	ES	20.3.68
GUINEA BASIN							
Walda (J. Charcot)	DS30/38	3109	7	04°04·1′N	03°42·0′E	ES	.6.71
Variety **B**							
ARGENTINE BASIN							
Atlantis II	242	4402	15	38°16·9′S	51°56·1′W	ES	13.3.71
	245	2707	62	36°55·7′S	53°01·4′W	ES	14.3.71
	256	3917	353	37°40·9′S	52°19·3′W	ES	24.3.71
	259	3317	106	37°13·3′S	52°45·0′W	ES	26.3.71
	262	2480	231	36°05·2′S	52°17·9′W	ES	27.3.71

Malletia cuneata is one of the few cosmopolitan protobranch species of the abyss. As would be expected, as we confirm, populations from the various oceans and basins show variations in shell form which, in our experience, overlap to an extent that we would be unwilling at this stage to define as species. Because it is one of the more common and larger bivalve species present in the deep sea it has been collected frequently during the past hundred years of exploration. As a result there is a long and confused literature. This is indicated by the list of synonymies. The most recent nomenclatural debate is by Bouchet & Warén (1979) when they discuss the population from the Norwegian Sea and they separate *M. cuneata* from *Katadesmia kolthoffi*. Bouchet & Warén (1979, Figs 21–24) compare, photographically, a specimen from the Norwegian Sea and one of the original specimens of *M. cuneata* taken by Jeffreys. They clearly differ in shape and in fact illustrate extremes of the range of variation that exist in the Atlantic populations. Bouchet & Warén claim that Soot-Ryen also recognised *M. kolthoffi* as differing from *M. cuneata,* in fact Soot-Ryen (1966: 3) states 'in my opinion *M. cuneata* is a northern deep water species identical to *Portlandia kolthoffi*' and then goes on to say 'the outline of *cuneata* is somewhat variable'. Soot-Ryen (1966) however does doubt whether the more southern forms from the tropics and the Mediterranean can be referred to *M. cuneata*. We confirm that specimens from the Sierra Leone Basin are distinct (see M. *pallida* p. 220). Unfortunately Soot-Ryen had so little material to consider that it is little wonder that he was perplexed by the range in form. Knudsen (1970) also covers similar ground and, with similar debate, concludes that *M. kolthoffi* and *M. cuneta* are one of the same species. In this we agree.

Shell description

There are numerous descriptions of both shell and animal, here we will emphasize only those features of Variety A that are of comparative importance.

Shell, moderately fragile, fine concentric growth lines; umbos moderately prominent, anterior, anterior/posterior umbonal length ratio *ca.* 3/5 (see below); postero-dorsal shell margin almost straight, angled at posterior limit of hinge plate, posterior margin angulate, dorsal to horizontal mid-line of shell, an ill-defined posterior umbonal ridge follows line of hinge plate, but does not meet posterior angle to form a rostral ridge, antero-dorsal and antero-ventral margins smoothly curved, ventral margin curvature varies with size and population, thus may be curved or, centrally, almost straight; hinge plate moderately broad, numerous short chevron teeth (*c.* 35 in large specimens), small edentulous space between tooth series; anterior and posterior series ratio 1/2; resilium small, relatively deep set, resilifer extending to half depth of hinge plate below umbo, external ligament, opisthodetic, shortest ligament of all species described here, less than half length of posterior hinge plate, anterior external ligament very short (Figs 34a & b; 35a & b; 39). Maximum shell length 10·0 mm; prodissoconch length 325 μm.

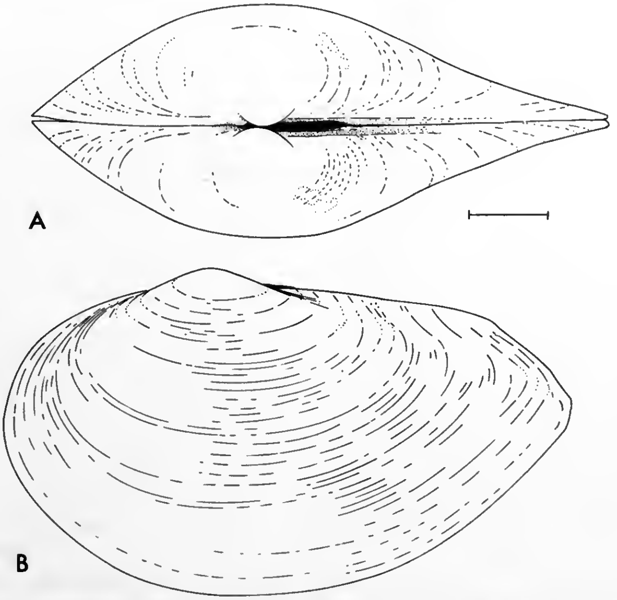

Fig. 34 *Malletia cuneata*. Variety A. (a) Dorsal; (b) lateral view of the shell of a specimen from Station 85, North America Basin, 3834 metres. Scale 1 mm.

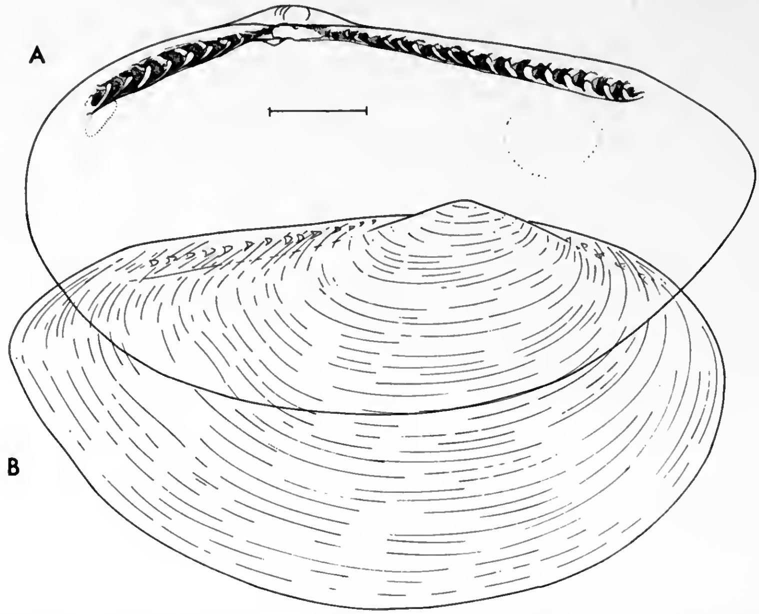

Fig. 35 *Malletia cuneata*. Variety A. (a) Internal lateral view of right valve; (b) lateral view of shell of specimen from Station BG II CV 18 West European Basin, 4120 metres. Scale 1 mm.

Morphology

With increasing size the shell becomes posteriorly more elongate and angulate. In older specimens the central portion of the ventral margin tends to become straighter (Fig. 36).

The morphology of the animal is similar to the other species described here (Fig. 37). The adductor muscles are oval, the anterior being more than twice as large as the posterior. The mouth is distant from the anterior adductor. The palps are relatively large with numerous ridges (*c*. 30), the foot and gills are large and robust in comparison with other species. The hind gut follows a similar course to other species of *Malletia* with a single loop on the right side of the body. There is a well marked typhlosole and the gut is relatively large in diameter. The ganglia and commissures are not particularly robust. Both inhalent and exhalent channels of the siphons are clearly demarcated, the exhalent siphon is entire, the ventral margins of the inhalent siphon are not fused. The feeding aperture ventral to the inhalent siphon is extensive and occupies most of the postero-ventral mantle margin, but the mantle folds themselves are not excessively well developed. The anterior mantle sense organ is well defined and lies ventral to the anterior adductor.

The above description relates to Variety **A.** Variety **B** occurring in the Argentine Basin is sufficiently consistent in its differences to warrant separate treatment, and indeed, it may be possible to erect a new species to include it. However, at our present limited state of knowledge we prefer to retain this form within *M. cuneata*.

The shell of Variety **B** differs from that of Variety **A** in that the umbo is slightly more anterior in position, anterior/posterior umbonal length ratio being 1/2, the marginal angle at the posterior limit of the hinge plate is less acute and the angle of the posterior margin relatively more distal in position (*cf*. Figs. 38a & b; 39). The proportion and numbers of anterior and posterior hinge teeth are not significantly different in the two varieties. The external ligament is significantly longer than in Variety **A,** both anteriorly and posteriorly. This is the only clear difference between the two varieties. Maximum shell length 9·5 mm; prodissoconch length 322 µm.

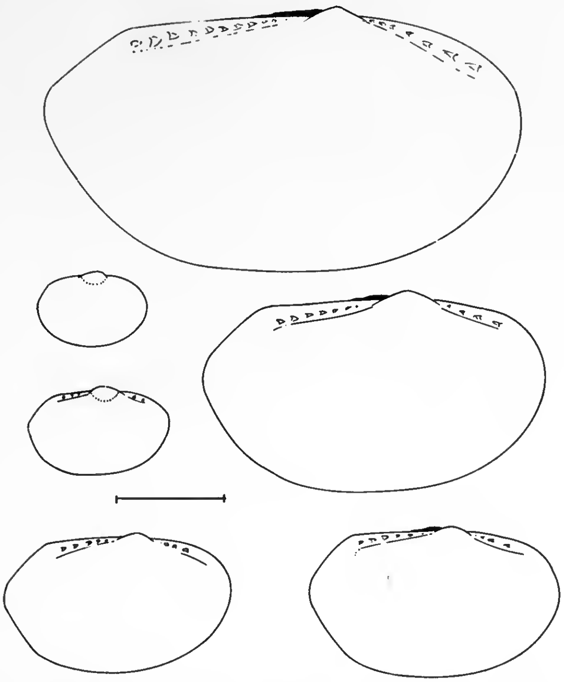

Fig. 36 *Malletia cuneata.* Variety A. Lateral outlines of specimens to show change in shape with increasing age. Station 326, West European Basin, 3859 metres. Scale 1 mm.

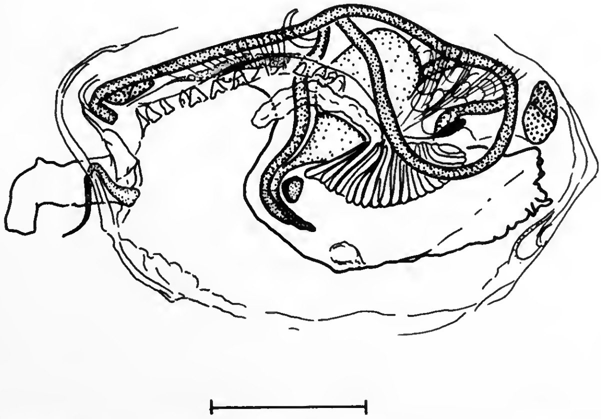

Fig. 37 *Malletia cuneata.* Variety **B**. Anatomy as seen from the right side. Scale 1 mm.

Very few differences can be seen in the morphology of the varieties. The general impression of Variety **B** is that the anatomy is less robust. For example the gut is marginally smaller in diameter, and foot, palp and gills are also smaller. Unfortunately these subjective differences are not easy to quantify in preserved material. Based entirely on those samples that we have personally examined, the depth range of *Malletia cuneata* in the Atlantic Ocean ranges from 1780 m to 4797 m. *M. cuneata* variety **A** includes all specimens collected from the North America, West Europe, Canaries and Guinea Basins and encompasses the entire depth range of 1780–4749 m. The large concentrations of *M. cuneata* variety **A** appears to be aggregated between 3000 m and

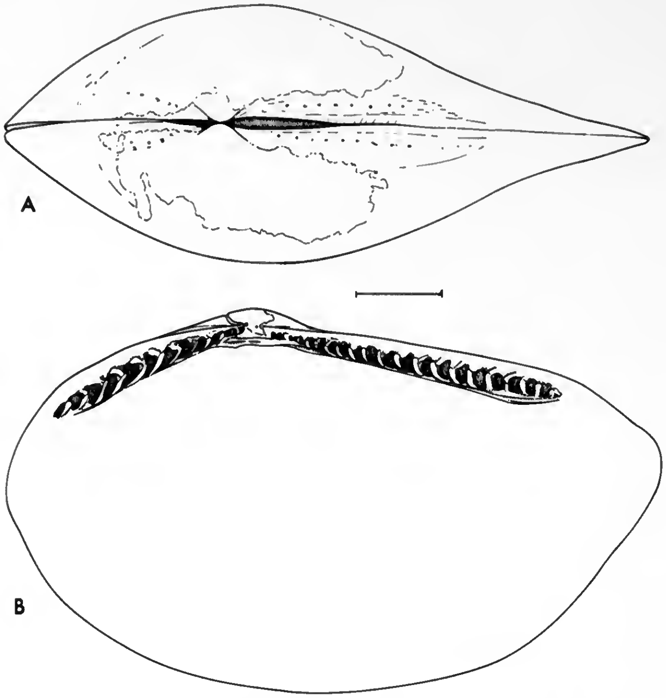

Fig. 38 *Malletia cuneata.* Variety B. (a) Dorsal view of shell; (b) internal lateral view of right valve of a specimen from Station 265, Argentine Basin, 3908 metres. Scale 1 mm.

4500 m. *M. cuneata* variety **B** was obtained from the Argentine Basin at all depths between 2480 m and 4402 m. At each of the five stations where it was recorded it was the numerically dominant constituent of the protobranch fauna.

Malletia obtusa G. O. Sars, 1878

Malletia obtusa G.O. Sars, 1878: *Moll. reg. arct. Norv.* p. 41, pl. 19, figs 3a & b. TYPE LOCALITY. Off west coast of Norway, South of Lofoten Isles, exact locality not recorded. TYPE SPECIMEN. Not recorded. DEPTH RANGE = 350 m to 2941 m.
[Although Michael Sars recorded the name of *Malletia obtusa* in 1872 in *Bidrag til Kundskab om Christiania fjordens* Fauna I–III (1868–73) he gave no adequate description of the species. An earlier species *Yoldia abyssicola* recorded by Michael Sars in 1858 is also unacceptable (Sars, G. O., 1878)]
Specimens were obtained from Korsfjorden 50 km south of Bergen, Norway.

This species appears to be restricted to the Norwegian Basin and all records of *M. obtusa* from outside this area have in all probability been mis-identified and are of *M. johnsoni* (see p. 205).

This is the best known of all species of the genus and is well described both in terms of its shell characters (Sars, 1878) and in terms of its functional morphology (Yonge, 1939).

Morphology

Although the morphology is similar to *M. johnsoni* (Figs 40 & 41) certain characters should be mentioned for comparative purposes. Thus, the anterior sense organ is far anterior, more so than any other species. The siphons are well developed, broad and elongate, and the inhalent and exhalent channels are entire. There is a single tentacle attached to the base of the inhalent siphon

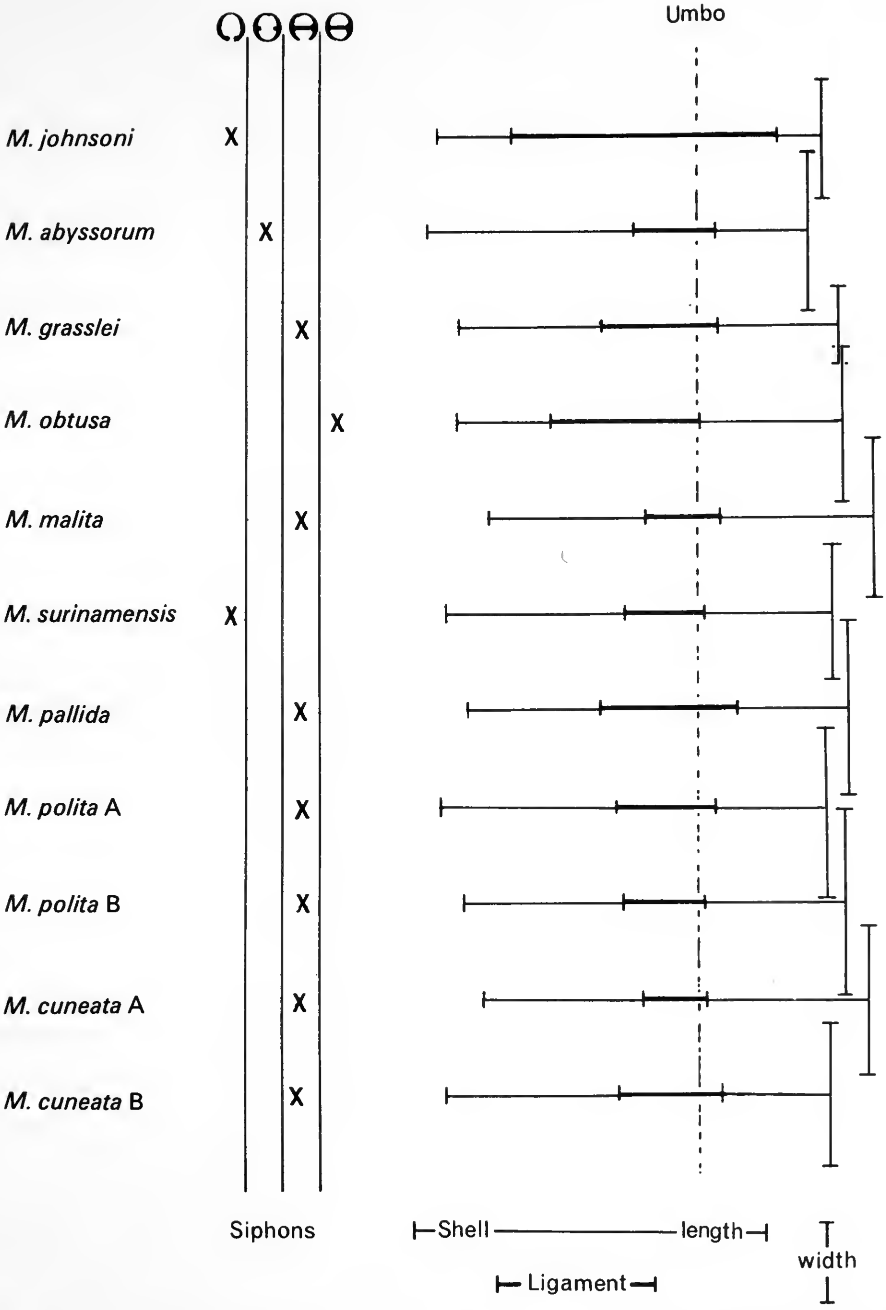

Fig. 39 The comparison of siphonal morphology, and dimensional ratios of shell features of live species of *Malletia*.

ventrally on the right hand side. The feeding aperture is relatively circumscribed, no more than 1/4 of the post mantle margin in extent. The palp is large and with numerous ridges. The foot is also large, but not the pedal ganglion, in comparison with other species. The visceral ganglion abuts the posterior adductor yet it and the commissures are not large.

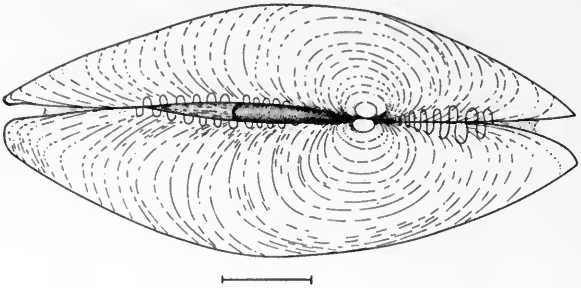

Fig. 40 *Malletia obtusa.* Dorsal view of shell, from Korsfjorden, Norway. Scale 1 mm.

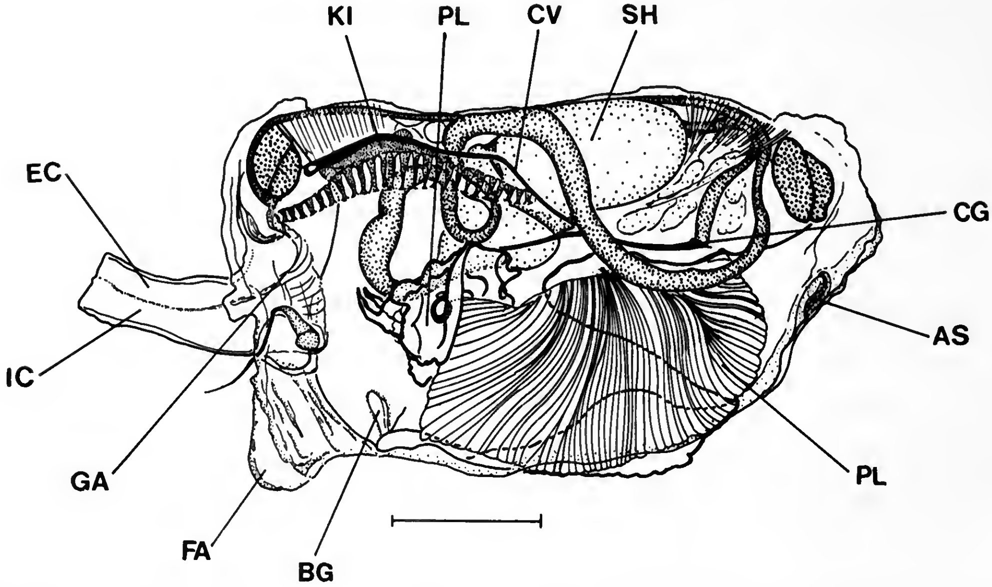

Fig. 41 *Malletia obtusa.* Anatomy as seen from the right side. Scale 1 mm. Abbreviations see Appendix.

Other species: previously identified as malletiids

In the course of these studies we have examined two species which have previously been identified as members of the family Malletiidae, namely, *M. aeoleta* Dall, 1980 and *M. agatheda* Dall, 1890. Both heavy rostrate shells with a prominent external amphidetic ligament. Their internal morphology differs greatly from the species described here, in particular both have multiple coiled hind guts. They belong to the genus *Tindariopsis* that is to be included in the subfamily Ledellinae (Allen & Hannah, in prep).

Discussion

Assessment of shell shape in terms of lateral outline, obesity and attenuation of the posterior region and of morphological features including the position of anterior sense organ and the length of siphons indicates that there are two major trends in form. On the one hand there are the elongate species with dorso-ventrally parallel shells, exceptionally long posterior external ligaments and with the mantle sense organ far anterior (eg. *M. johnsoni* and *M. obtusa*) and on the other hand there are species with cuneate, rostrate, ventrally curved shells, shorter ligaments, and with the anterior sense organ more ventral in position (eg. *M. polita, M. pallida, M. cuneata* and other species described here).

One can argue differences in probable behaviour and we speculate that the *johnsoni/obtusa* group is positioned vertical to the sediment surface and the *polita/pallida/cuneata* group at an angle to it. The latter group of species changes shape dramatically with increasing size becoming more obese centrally and posteriorly more rostrate. Although the siphons of the *polita/pallida/cuneata* group are relatively well developed, suggesting an infaunal habit at least they must appear at the surface at times because some large specimens have Foraminifera and hydroids attached to them. The more obese shape must functionally make rapid and efficient burrowing more difficult and result in a more sedentary mode of life. In contrast, the large specimens of *M. johnsoni* and *M. obtusa* do not have an attached fauna and they may well burrow deeper than the species of the other group.

The malletiid species are extremely conservative in their anatomy and shell morphology. Young specimens of the *polita/pallida/cuneata* groups in particular are extremely difficult to tell apart even though larger specimens clearly differ. The change in form of the species with increasing size presents considerable taxonomic difficulties, particularly to the observer with few specimens at hand.

The morphologies of the nine species are remarkably similar and for the most part differ only in minor ways (see Fig. 39). The most variable feature is the structure of the siphons. Within the Atlantic species of *Malletia* there are all the protobranch variations that Yonge (1939) described and two other besides. The variation involves the degree of separation of the lumena of inhalent and exhalent siphons and whether the enclosing siphonal wall is entire or not. As best developed the lumena are separate and formed by entire but conjoined siphons (*M. obtusa* and *M. cuneata*). Other morphologies are:

—separate lumena but the ventral wall of the inhalent siphon are not entire but, in life, the edges are apposed in the ventral mid-line (*M. grasslei* and *M. polita*).

—The inhalent siphon may be shorter than the exhalent siphons in which the lumena are not separate but there is a pair of mid lateral ridges, that may or may not be apposed in life to form functionally separate lumena but which certainly act as ventral guides to the extended faecal rod (*M. abyssorum*).

—Siphons in which the lumena are not separate and without mid lateral ridges marking the ventral and dorsal limits respectively of the inhalent and exhalent channels (*M. johnsoni* and *M. surinamensis*). In this case the gill axes are attached lateroventrally and therefore the inhalent siphon and ventral section must be considered to be functionally absent—although the ventral floor of the siphon may be the remnant of the wall of the inhalent siphon.

In the variety of its form the malletiid siphon differs little from some other deep water nuculanoid families and subfamilies, eg. Yoldiellidae (Allen, Hannah & Sanders, in prep). The reason for the variation lies in the fact that the nuculanoid protobranchs possess a feeding aperture from which the palp proboscides extend.

In deep water species with gills reduced in size and having specialized respiratory surfaces and mechanisms that are least developed, there is probably sufficient inflow of water in the feeding process to satisfy the animal's needs. The exhalent aperture remains functional for the passage of the faeces. If the faecal rods are large in diameter, then the use of the combined inhalent and exhalent lumena is advantageous.

Thus the picture of protobranch siphon evolution that Yonge (1939) described and which involved successive fusion of the posterior mantle to form totally enclosed apertures may have to be extended further to involve secondary loss of siphonal walls with the lumena combined that probably relate in part to reduced respiratory needs satisfied by another point of inflow and in part to accommodate an enlarged faecal rod.

Other noteworthy aspects of the morphology are the robustness of the nervous system and size of the foot and statocysts (eg. Fig. 41). The anterior sense organ and the byssal gland are also extremely well developed. All would indicate that *Malletia* is an active burrowing genus. Whether the well developed external ligament is also related to this is debatable, but the analogy with the shallow water, fast burrowing deposit feeding Tellinacea is obvious.

The malletiids have retained the primitive form of the hind gut—a single loop to the right of the body. However it is lengthened and in all species extends to the inner face of the anterior adductor. The diameter of the hind gut although varying from species to species is either large or very large. All have a typhlosole. The stomach is also very voluminous and all points to the consumption and processing of great quantities of particulate matter.

Malletiids are of unusually large size in comparison with other deep sea protobranchs and this may be a reflection of their ability to process considerable quantities of sediment with commensurate energy gain.

Observations on the digestive system indicate that selection of particles occurs. The number of skeletal remains within the gut is significantly greater than those present in the general sediment.

The recent recognition (Gooday pers. comm.) of rich infaunal populations of undescribed species of foraminifera, xenophyophores and komoki that live within frustules and other foraminiferan exoskeletions and have differing depth ranges within the substrata appear to provide answers to the ecological problem of why many nuculanoid species (→ 15) are able to live together and appear to ingest the same deposits. Niche separation, by living in different depth horizons was always postulated (Allen, 1978) but is now immeasurably strengthened by the knowledge of differing cryptic meiofaunal communities at differing depths of abyssal sediments.

A universal feature of all deep sea protobranchs is the solid packing of the gut with ingested fine deposits. However, it is not clear how this material is transported posterior to the stomach. Probably the pedal retractor muscles play a role. They lie close to all parts of the gut (eg. Figs 22, 27 & 37). Anteriorly there are four pairs of pedal retractors lying lateral to the oesophagus. The anterior retractors cradle the anterior ventral side of the stomach while the posterior retractor muscles lie close to the mid and hind gut posterior to the style sac. Since the gut wall is not muscular, it is difficult to imagine that cilia are the sole means of moving the solid rod of sediment through the hind gut, although it will play an important role in movement of the contents of oesophagus and stomach.

The Argentine and Guinea Basins both show endemism, a feature of many protobranch groups. Elsewhere the situation is one of slight east to west Atlantic population differences. This suggests some gene flow but there is insufficient evidence for us to speculate that we are seeing the first stages in emergent species. Further south on the eastern Atlantic there is clearly more discontinuity with our recognition of the sibling species *M. pallida,* from the more cosmopolitan *M. cuneata*.

Apart from holotypes of new species, specimens (including paratypes) listed in this paper presently remain in the possession of the authors. When the analysis of the protobranch bivalves of the Atlantic is completed specimens will be lodged in the British Museum, the Smithsonian Museum and the Paris Museum depending on the country origin of the collections.

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Appendix

Abbreviations to text figures

AA	Anterior adductor
AN	Anus
AR	Anterior pedal retractor muscles
AS	Anterior sense organ
BG	'Byssal' gland
BS	Blood space
CG	Cerebral ganglion
CV	Cerebro-visceral commisure
DD	Digestive duct
DG	Digestive gland
EC	Excurrent canal
EP	Epidermis
FA	Feeding aperture
FT	Foot
GA	Gill axis
GL	Gill
GS	Gastric shield
HG	Hindgut
HT	Heart
IC	Incurrent canal
KI	Kidney
ME	Mantle edge
MU	Muscle
NE	Nerve
OD	Oviduct
OE	Oesophagus
OV	Ovary
PA	Posterior adductor
PG	Pedal ganglion
PL	Palp
PP	Palp proboscis
PR	Posterior pedal retractor muscles
RI	Ridges
SE	Siphonal embayment
SH	Stomach
SI	Siphon
SR	Siphonal ridge
SS	Style sac
SR	Statocyst
SU	Unfused siphon
TE	Siphonal tentacle
TH	Tooth
TS	Testis
TY	Typhlosole
VD	Vas deferens
VG	Visceral ganglion

Larval development of the Red Swimming Crab, *Bathynectes longipes* (Risso, 1816) (Crustacea: Decapoda: Portunidae)

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Introduction

The Red Swimming Crab, *Bathynectes longipes* (Risso), has been reported from southwestern regions of the British Isles (Ingle, 1980) and may occur as far south as Madeira (see Türkay, 1976); Mediterranean records are listed by Zariquiey Alvarez (1968).

Very brief accounts of the first zoea of this species were given by Lebour (1928, 1931) and the second stage zoea described by Rice & Williamson (1977, fig. 22 e–f) as *'Bathynectes sp. B.'* may be that of *B. longipes,* otherwise the larval development has not been described and the complete larval morphology of only one other species of *Bathynectes* is known at present. Roberts (1969) described five zoeal stages attributed to *B. superba*. The female from which these larvae were obtained was collected off the Virginia coast, USA and more correctly belonged to *B. longispina* Stimpson, 1871, a species represented on the American Atlantic seaboard, whereas *B. superba* (Costa) is a synonym of *B. maravigna* (Prestandrea, 1839) (see Manning & Holthius, 1981) and is confined to the eastern Atlantic and Mediterranean.

In May 1984 a living ovigerous *B. longipes*, collected from the coast of Co. Donegal, was presented to this Museum by D. W. Connor of the Ulster Museum. The crab was maintained in the larval rearing laboratory of the BM (NH) and the larvae that hatched were successfully reared to megalopa stage. They provide material for the first complete account of the larval development of this species and have enabled comparisons to be made with the described stages of *B. longispina* and with the larvae of seven *Liocarcinus* species.

Materials and methods

The ovigerous crab was collected on 7 May 1984 in a depth not exceeding 20 m, from beneath boulders on limestone ridges at Bullockmore, St John's Point, Co. Donegal, Ireland. Rearing was carried out in temperatures of 16–18°C. The eggs hatched on 3–4. 6. 1984 and the first megalopas appeared on 24.7.1984. Drawings were made through a camera lucida attachment on an Olympus BH2 microscope and from preparations mounted in polyvinyl lactophenol. Measurements are as follows: T.T. = total length of zoea, measured between tips of dorsal and rostral spines; C.L. = carapace length, measured from between eyes to posterio-lateral carapace margins for zoeas and from rostral tip to median posterior margin of carapace for the megalopas. Proportional measurements given in Table 2 are expressed as ratios of averaged measurements of a minimum of five specimens of each stage (except for *L. arcuatus* and *L. marmoreus* where sufficient material was not available). Telson fork lengths were measured from the bases of the lateral and dorsal spines respectively, to the fork tip. The base of the antennal spinous process was determined at a line drawn across the articulation of the endopod. All material was initially fixed and stored in the preservative formulated by Steedman (1976 : 148) and later transferred to 70% ethanol alcohol.

The female and reared material are deposited in the Collections of the Zoology Department, British Museum (Natural History), registration number: 1984 : 336.

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Descriptions

Bathynectes longipes (Risso, 1816)

Bathynectes longipes: Lebour, 1928 : 515, Pl.IV, fig. 7; 1931 : 93, Pl.I, fig. 1 (coloured), 1st zoea.

FIRST ZOEA

Dimensions: T.T. 1·50 mm, C.L. 0·40 mm.
Carapace (Fig. 1a, 6a): Dorsal spine stout and curved backwards; rostral spine stout proximally and acute distally, longer than antennae; lateral spines very long; dorso-median process prominent and without setules, a pair of posterio-median setules present; posterio-lateral margin of carapace without setules.
Eyes: Partly fused to carapace.
Antennule (Fig. 3a): Unsegmented, with 3 terminal aesthetascs and one seta.
Antenna (Fig. 3f): Spinous process long, about $2\frac{3}{4}\times$ exopod length, distal $\frac{1}{2}$ with numerous spinules; exopod with 2 terminal setules, one short seta and one long seta reaching into distal $\frac{1}{3}$rd of spinous process.
Mandible (not figured): Incisor and molar processes developed, palp absent.
Maxillule (Fig. 4b): Endopod 2-segmented, with 1, 6 setae; basal endite with 5 spines; coxal endite with 7 spines/setae.
Maxilla (Fig. 4g): Endopod with lobes almost equally developed bearing 5 and 3 setae respectively; basal endite with pronounced outer and less prominent inner lobe bearing 4 and 5 setae respectively; coxal endite with broad outer and narrower inner lobe bearing 4 and 3 setae respectively; scaphognathite with 4 marginal plumose setae and a stout posterior plumose process.
First maxilliped (Fig. 5f): basis with 10 setae arranged 2, 2, 3, 3,; endopod 5-segmented, with 2, 2, 1, 2, 4+1 setae; exopod incipiently segmented, with 4 terminal plumose setae.
Second maxilliped (Fig. 5g): Basis with 4 setae; endopod 3-segmented, with 1, 1, 4+1 setae, exopod with 4 terminal plumose setae.
Third maxilliped: Not developed.
Pereiopods: Not developed.
Abdomen (Figs 2a, b, g, 3k): with 5 segments + telson, 2nd with a pair of forwardly directed dorso-lateral processes, 3rd with a smaller pair of backwardly directed dorso-lateral processes. Posterio-lateral margins of segments sub-oval, 2–5 with minute spinules. A pair of small setules near posterio-dorsal margins of segments 2–5. Telson forks stout, slightly diverging posteriorly, proximally very minutely spinulate, each with one long and one shorter lateral spine and a dorsal spine; each half of telson posterior margin with 3 setae, median part concave.

SECOND ZOEA

Dimensions: T.T. 1·60 mm, C.L. 0·60 mm.
Carapace (Fig. 1b): Lateral spines shorter than in first zoea; dorso-median process with 2 pairs of setules; posterio-lateral margin with 2–3 long setules inserted near margin.
Eyes: Now stalked.
Antennule (Fig. 3b): With 5 terminal aesthetascs and one seta.
Antenna (Fig. 3g): Second longest of the apical setae on exopod now slightly shorter than in first zoea, antenna otherwise unchanged.
Mandible (not figured): Unchanged.
Maxillule (Fig. 4c): Basal endite with 7 spines/setae; coxal endite unchanged; outer margin of basis with prominent plumose seta.
Maxilla (Fig. 4h): Endopod, basal and coxal setation unchanged; scaphognathite with 10 marginal plumose setae.
First maxilliped (not figured): Basal and endopod setation unchanged; exopod with 6 terminal plumose setae.
Second maxilliped (not figured): Basal and endopod setation unchanged; exopod with 6 terminal plumose setae.
Third maxilliped: Not developed.
Pereiopods: Just discernible as undifferentiated buds.
Abdomen (Figs 2c, h, 31): Posterio-lateral margins of segments 3–5 with small and acute processes and 2–3 spinules. Medial part of telson posterior margin with a pair of small setules.

THIRD ZOEA

Dimensions: T.T. 2·30 mm, C.L. 0·75 mm.
Carapace (Fig. 1c): Dorso-median process with 3 pairs of setules; posterio-lateral margin with 4–5 long setules.

Eyes: Unchanged.
Antennule (Fig. 3c): Unchanged except for seta that is much shorter than in second zoea.
Antenna (Fig. 3h): Exopod slightly longer (relative to spinous process) than in second zoea; endopod with an incipient bud.
Mandible (not figured): Unchanged.
Maxillule (Fig. 4d): Basal endite with 8–9 spines/setae; coxal endite unchanged.
Maxilla (Fig. 5a): Endopod setation unchanged; basal endite with 5 setae on outer lobe; coxal setation unchanged; scaphognathite with 17 long plumose setae.
First maxilliped (not figured): Basal and endopod setation unchanged; exopod with 8 terminal plumose setae.
Second maxilliped (Fig. 5h): Basal setation unchanged; distal segment of endopod with 5+1 setae; exopod with 8 terminal plumose setae.
Third maxilliped: Not developed.
Pereiopods: Undifferentiated buds slightly larger than in second zoea.
Abdomen (Figs 2d, i, 3 m): With 6 segments+telson; dorso-lateral processes on 3 smaller than in second zoea; posterio-lateral margin of 3–5 with well developed and acute processes; a small median setule on dorsal surface of first segment; median pair of setae on posterior margin of telson longer than in second zoea.

FOURTH ZOEA

Dimensions: T. T. 2·40 mm, C.L. 0·90 mm.
Carapace (Fig. 1d): Dorsal spine with 6–7 setules; posterio-lateral margin with 5–6 long setules.
Eyes: Unchanged.
Antennule (Fig. 3d): With 6 aesthetascs.
Antenna (Fig. 3i): Longest terminal seta on exopod much longer (relative to spinous process) than in third zoea; endopod bud almost as long as exopod in some specimens.
Mandible (not figured): Teeth on incisor and molar processes differentiated.
Maxillule (Fig. 4e): Basal endite with 10 spines/setae; coxal endite with 8 spines/setae.
Maxilla (Fig. 5b, d): Endopod setation unchanged; basal endite with 6 setae on inner lobe; coxal setation unchanged; scaphognathite with 20 long plumose setae.
First maxilliped (not figured): Basal and endopod setation unchanged; exopod with 10–11 terminal plumose setae.
Second maxilliped (not figured): Basal and endopod setation unchanged; exopod with 10–11 terminal plumose setae.
Third maxilliped (not figured): Now represented as an incipient bud.
Periopods (Fig. 1d): Represented as well formed undifferentiated buds.
Abdomen (Figs 2e, j): Posterio-lateral processes on segments 3–5 longer than in third zoea; dorsal surface of first segment with 2 setules; 3 median setae present on telson posterior margin; pleopod buds on segments 2–5.

FIFTH ZOEA

Dimensions: T.T. 2·80 mm, C.L. 1·15 mm.
Carapace (Fig. 1e): Dorso-median region with 5 pairs of setules; dorsal spine shorter (relative to carapace width) that in fourth zoea and with 6–8 setules; posterio-lateral margin with 8–9 long setules.
Eyes: Unchanged.
Antennule (Fig. 3e): Exopod with 7 terminal and 3 sub-terminal aesthetascs; endopod represented as a small bud.
Antenna (Fig. 3j): Distal margin of endopod with several minute spinules, shorter of the 2 setae now considerably reduce in length, only one setule now apparent; endopod but much longer than exopod.
Mandible (Fig. 4a): Palp represented as a short broad bud.
Maxillule (Fig. 4f): Basal endite with 15 spines/setae; coxal endite with 10 spines/setae.
Maxilla (Fig 5 c, e): Endopod setation unchanged; basal endite with 6–7 setae on outer and 7 on inner lobe respectively; coxa with 4 setae on each lobe; scaphognathite with 29 or 30 long plumose setae.
First maxilliped (not figured): Basal and endopod setation unchanged; exopod with 12 terminal plumose setae.
Second maxilliped (not figured): Basal and endopod setation unchanged; exopod with 12 terminal plumose setae.
Third maxilliped (not figured): Bud much longer than in fourth zoea.
Pereiopods (Fig. 1e): First pair differentiated as chelipeds, others still unsegmented.

Abdomen (Fig,. 2 f, k): First segment with 3 dorsal setae; dorso-lateral process on 3 very small; dorsal surface of telson with a pair of setules, 3 median setae on posterior margin longer than in fourth zoea; pleopod buds on segments 2–5 almost equal to lengths of segments.

MEGALOPA

Dimensions: C.L. 2·03 mm.
Carapace (Figs 6b, c): Longer than broad, narrowing anteriorly; rostrum long, directed obliquely downward and converging strongly distally to acute apex; submedian lobes rounded and raised; each protogastric and mesogastric region with raised broad carina; each epibranchial region with a short faint carina; cardiac region broadly elevated.
Eyes: Large and suboval.
Antennule (Fig. 6e): Peduncle 3-segmented, segments 2 & 3 each with setae; exopod 4-segmented, segments 2–4 with 6, 4 and 3 aesthetascs respectively, segment 3 also with 2 setae and 4 with one sub-terminal and one terminal seta; endopod 2-segmented, distal segment with 5 + 1 setae.
Antenna (Fig. 6d): Peduncle 3-segmented, segment 1 with 4 setae, 2 and 3 each with 2 setae respectively; flagellum 8-segmented, with (from proximal to distal) 0, 0, 2, 0, 5, 1, 4 and 3 setae respectively.
Mandible (Fig. 6f): Molar and incisor portions not differentiated; mandibular palp large, 3-segmented, distal segment longest and with 12 setae.
Maxillule (Fig. 6g): Endopod unsegmented, with 3–4 setae; basal endite with 25–26 spines/setae; coxal endite with 11 spines/setae.
Maxilla (Fig. 6h): Endopod reduced to a sub-acute lobe; basal endite with 9 setae on outer and 8 on inner lobe respectively; coxal endite with 3 setae on outer and 7 on inner lobe respectively; scaphognathite with 49–50 plumose setae.
First maxilliped (Fig. 7a): Coxal and basal segments differentiated, with 10–11 and 24–25 setae respectively; endopod unsegmented, with 5–6 setae on distal margin; exopod 2-segmented, outer distal margin of proximal segment with 3 setae, distal segment with 5 terminal setae; epipod with 7 long setae.
Second maxilliped (Fig. 7b): Coxal and basal segments undifferentiated with 2–4 short setae; endopod, merus with 2 inner distal setae, carpus with one outer distal seta, propodus with 6 distal setae, dactylus with 4 spines and 5 setae. Exopod 2-segmented, distal segment with 5 long setae.
Third maxilliped (Fig. 7c): Basal and coxal segments undifferentiated, with 2 setae on internal margin. Endopod, ischium with 3 teeth on inner margin 17–18 setae near inner margin and 4 on outer surface, merus with 10–11 setae, carpus and propodus with 7 and 8 setae respectively, dactylus with 10–11 setae all arranged as shown in figure. Exopod 2-segmented, distal segment with 4 terminal setae; epipod (not shown) with 14 setae.
Pereiopods (Figs 7d, e, 8a-c): Chelipeds stout, setosed as shown in figs 7d and with a prominent ischial spine; propodal inner margin with 4 obtuse teeth; dactylar inner margin with 2–3 poorly developed teeth. Pereiopods 2–5 relatively stout, setosed as shown; coxa of 2–4 with a spine and lower propodal margin with 3 thin spines and 1–2 small setae, inner lower dactyl margin with 7 spines, upper inner dactyl margin of pereiopod 2 with 5 spines, the 2nd–4th of which are very long (see inset to fig. 7e); dactyl of pereiopod 3 with similar spines of more or less equal lengths (inset to fig. 8a); fifth pereiopod (fig. 8c) shorter than pereiopods 2–4, lower propodal margin with 2 prominent setae; dactylus slightly flattened, lower margin 4 spines/setae and with 3 long hook-shaped setae on apex.
Abdomen (Figs 7f, g, 8f–g): With 6 segments + telson. Posterio-lateral margins of segments 2–4 truncate; setae on 1–6 arranged as shown in figs 7f, g. Telson slightly broader than long, dorsal surface with one pair of median setules, ventral surface with 2 pairs of median and one of laterally placed setules (fig. 7g). Five pairs of pleopods, distal segment of exopods with long plumose marginal setae numbering 18, 20, 19, 16 on pleopods 1–4 respectively; pleopod 5 (uropod) with 11 setae on distal segment and one on outer margin of proximal segment (fig. 8f). Endopods of pleopods 1–4 with 2, 3, 4 and 3 coupling hooks respectively on disto-internal margins.

Remarks

The zoeal stages of *Bathynectes longipes* differ in a number of features from those of *B. longispina* (described by Roberts, 1969 as *B. superba*). The first stage zoea of *B. longispina* apparently has 'long posterio-lateral spines' on abdominal segments 3–5. This is a feature more typical of geryonid and xanthid first stage zoeae whereas this stage in all known polybiinid zoea has the posterio-lateral margins of segments 3–5 hardly produced. *B. longispina* has also a high number

Table 1 Comparative features of zoeal stages of *Bathynectes longipes* and *B. longispina*

	Bathynectes longipes (Risso)	*Bathynectes longispina* Stimpson
Zoea I		
Antennule, setae/aesthetascs:	4	6
Antenna, spinous process/exopod:	much more than × 2 length	slightly more than × 2 length
Abdomen, posterio-lateral margin of segments 3–5:	not produced as spinous processes	produced as spinous processes
Telson, width of anterior margin:	much less than telson length (measured to posterior margin)	equal to telson length (measured to posterior margin)
first lateral spine:	not extending to dorsal spine	extending to dorsal spine
Zoea II		
Antenna, spinous process/exopod:	much more than × 2 length	slightly more than × 2 length
Maxillule, spines/setae on basis:	7	9
Maxilla, setae on basal inner lobe:	4	5
Abdomen, posterio-lateral margin of segments 3–5:	only slightly produced as spinous processes	well produced as spinous processes
Telson, width of anterior margin:	much less than telson length (measured to posterior margin)	slightly more than telson length (measured to posterior margin)
first lateral spine:	not extending to dorsal spine	extending to dorsal spine
Zoea III		
Antenna, spinous process/exopod:	more than × 2 length	slightly more than × 2 length
Maxillule, spines/setae on basis:	8–9	10
Maxilla, scaphognathite setae:	17	19
Second maxilliped, endopod distal segment:	5+1 setae	4+1 setae
Abdomen, posterio-lateral margin of segments 3–5:	much shorter than segments	almost as long as segments
dorsal surface segt. 1:	1 seta	4 setae
Telson, width of anterior margin:	about $1\frac{1}{3}$ × length (measured to posterior margin)	nearly × 2 length (measured to posterior margin)
first lateral spine:	not extending to dorsal spine	extending to dorsal spine
Zoea IV		
Antennule, setae/aesthetascs:	7	9
Maxillule, spines/setae on basis:	10	16
coxa:	8	9
Maxilla, setae on outer/inner lobes of basis:	5+6	7+7
scaphognathite:	20	27
Second maxilliped, endopod distal segment:	5+1 setae	4+1 setae
Abdomen, dorsal surface segt. 1:	2 setae	4 setae
Telson, width of anterior margin:	slightly exceeding telson length (measured to posterior margin)	nearly × 2 telson length (measured to posterior margin)
first lateral spine:	not extending to dorsal spine	extending to dorsal spine
posterior margin:	3 setules	4 setules

Table 1 Continued

	Bathynectes longipes (Risso)	*Bathynectes longispina* Stimpson
ZOEA V		
Antennule, setae/aesthetascs:	10	14
Antenna, spinous process/exopod:	more than × 2 length	less than × 2 length
Maxillule, spines/setae on basis:	15	19
coxa:	10	13
Maxilla, setae on outer/inner lobes of basis:	6–7+7	9+8
coxa:	4+4	5+5
scaphognathite:	29–30	42
Abdomen, dorsal surface segt. 1:	3 setae	4 setae
Telson, width of anterior margin:	slightly less than telson length (measured to posterior margin)	less than telson length (measured to posterior margin)
dorsal surface:	with a pair of setules	without setules
first lateral spine:	not extending beyond dorsal spine	extending beyond dorsal spine

of scaphognathite setae (42) in the fifth stage zoea. *B. longipes* has 29–30 in this stage and a similar number is found in the known fifth zoeal stages of *Liocarcinus* species, except for *L. marmoreus* which has 40 setae. Additional comparative features of *B. longipes* and *B. longispina* are given in Table 1. Collectively these indicate that there are greater differences between the zoeae of these two species of *Bathynectes* than between *B. longipes* and the *Liocarcinus* zoeae examined (see Table 2). Clark (1984) was unable to discover satisfactory meristic characters for distinguishing zoeae of *Liocarcinus* species at all stages and this present study has revealed a similar situation with respect to the zoeae of *B. longipes* and *Liocarcinus*. However, there appear to be a number of subtle differences separating zoeal stages of *B. longipes* from those of *Liocarcinus* species studied as well as fine distinctions between the zoeae of these *Liocarcinus* species themselves. These differences are expressed as combined characters in Table II. Recently it was possible to assign plankton collected *Liocarcinus* zoeae to either *L. puber* or *L. holsatus* using the combined features listed in this table. These larvae were collected in the Aran Islands region of Co. Galway where adults of both species are common (pers. comm. O. Tully, Univ. College, Galway). Further studies are needed to establish whether this Table, based on laboratory material, is satisfactory for identifying plankton caught specimens of other *Liocarcinus* species.

The megalopal stage of *B. longipes* has been compared with this stage of only five *Liocarcinus* species; megalopas of *L. marmoreus* were not available for study and this stage of *L. corrugatus* is still unknown. These comparisons are also listed in Table 2. The more important combined features that distinguish this stage of *B. longipes* are: (1) the setal formula on the antennal flagellum and uropods; (2) the number of spines on the dactyl lower margins of pereiopods 2–4; (3) the broadly rounded posterio-lateral margins of the telson. Additional, less significant features are also listed in the Table.

The zoeal stages of *B. longipes* and *Liocarcinus* thus all show considerable homogeneity and specific larval differences are recognisable only in the megalopal stage. This contrasts with the more apparent dissimilar morphology of the known young crab stages into which these respective species metamorphose (see Ingle & Rice, 1984) and the very clear specific differences of the adults (see Ingle, 1980). Indeed, within the genus *Liocarcinus* it is possible to recognise at least six 'species-groups' on adult features, viz: (i) *L. puber*; (ii) *L. holsatus, L. marmoreus;* (iii) *L. pusillus, L. maculatus, L. zariquieyi;* (iv) *L. corrugatus*; (v) *L. depurator, L. bolivari*; (vi) *L. arcuatus*. The larval morphology of this genus is still incompletely known and the available larval

Table 2 Comparative larval features of *Bathynectes longipes* and seven *Liocarcinus* species. Abbreviations: < = not extending into; ~ = extending as far as; > = just extending into; > + = extending well into. 1 from Clark (1984); 2 from Rice & Ingle, 1975; 3 from Rice & Ingle, 1978; 4 from Goldstein, 1971. For measurement details see Material and methods

Feature	*B. longipes*	*L. puber*	*L. holsatus*	*L. marmoreus*	*L. pusillus*	*L. corrugatus*	*L. arcuatus*	*L. depurator*
Zoea I								
T.T:	1·50	1·9–2·2[2]	1·1–1·3[2]	1·18–1·24[2]	1·90–2·20[2]	1·55	0·95	1·52
Antennule, aesthetascs + setae:	4	4[1]	5[1]	6[1]	5[1]	4[1]	6[1]	7[1]
Antenna, exopod length/spinous process:	2·61	3·00	2·50	2·50	2·18	2·35	2·25	2·40
Antenna exopod innermost seta/ distal ⅓ spinous process:	>	>	~	~	~	~	>	~
Maxilla, endopod setation for all stages:	5+3	usually[1] 4+3	5+3	5+3	5+3	5+3	5+3	5+3
Telson, fork length/outermost lateral spine:	3·88	6·25	4·25	4·57	3·87	3·88	5·50	5·00
Telson, fork length/dorsal spine:	4·50	5·00	3·71	3·71	3·71	5·60	6·50	4·50
Zoea II								
T.T:	1·60	2·2–2·5[2]	1·40–1·60[2]	1·40[2]	1·43–1·58[3]	1·65	1·12	1·65
Antennule, aesthetascs + setae:	6	4[1]	5[1]	5[1]	5[1]	7[1]	8[1]	7[1]
Antenna, exopod length/spinous process:	2·66	2·84	2·50	3·10[4]	2·33	2·36	3·71	3·35
Antenna, exopod innermost seta/ distal ⅓ spinous process:	>	<	~	~[4]	<	>	>	<
Maxilla, scaphognathite setae:	10	9[1]	9[1]	11[1]	9[1]	10[1]	9[1]	9[1]
Telson, fork length/outermost lateral spine:	4·70	6·80	4·04	5·16[4]	4·30	4·92	4·26	5·00
Telson, fork length/dorsal spine:	5·50	8·66	4·70	4·40[4]	4·28	5·60	6·86	5·00
Zoea III								
T.T:	2·30	3·0–3·3[2]	1·90–2·20[2]	1·70[2]	1·66–1·76[2]	2·0	1·40	2·02
Antennule, aesthetascs + setae:	6	6[1]	6[1]	5[1]	6[1]	7[1]	8[1]	5[1]
Antenna, exopod length/spinous process:	2·60	2·33	2·67	2·90[4]	2·51	2·35	3·58	2·98
Antenna exopod innermost seta/ distal ⅓ spinous process:	>	<	<	<	<	>	<	~
Maxilla, scaphognathite setae:	17	17[1]	17[1]	13[1]	15[1]	17[1]	15[1]	18[1]
Telson, fork length/outermost lateral spine:	4·73	6·60	4·53	4·50[4]	4·30	5·07	3·95	4·62
Telson, fork length/dorsal spine:	6·60	6·56	5·76	5·20	4·28	6·17	4·53	5·14
Abdominal segment 3, lateral processes:	+	–	–	——	+	+	+	+
Zoea IV								
T.T.:	2·40	3·40–3·60[2]	2·60–2·90[2]	2·0[2]	2·11–2·25[2]	2·55	1·95	2·50
Antennule, aesthetascs + setae:	6	9[1]	7[1]	7[1]	7[1]	7[1]	8[1]	5[1]
Antenna, exopod length/spinous process:	2·60	2·08	2·64	2·56[4]	2·52	2·33	3·46	2·90
Antenna exopod innermost seta/ distal ⅓ spinous process:	> +	> +	<	<	<	> +	<	> +
Maxilla, scaphognathite setae:	20	22[1]	26[1]	26[1]	22[1]	23[1]	22[1]	27[1]
Telson, fork length/outermost lateral spine:	5·00	6·50	4·41	6·30[4]	5·50	6·37	5·41	5·80
Telson, fork length/dorsal spine:	7·70	5·88	4·11	3·3[4]	4·45	6·50	5·14	6·04
Abdominal segment 3, lateral processes:	+	–	–	——	–	+	–	+

Table 2 Continued

Feature	*B. longipes*	*L. puber*	*L. holsatus*	*L. marmoreus*	*L. pusillus*	*L. corrugatus*	*L. arcuatus*	*L. depurator*
Zoea V								
T.T:	2·80	3·8–4·1^2	3·00–3·50^2	3·70^2	2·54–2·78^2	2·90	2·45	2·80
Antennule, aesthetascs + setae:	11	17^1	15^1	14^1	11^1	11^1	12^1	13^1
Antenna, exopod length/spinous process:	2·50	1·93	2·61	2·42	2·50	2·05	2·58	2·38
Antenna exopod innermost seta/ distal $\frac{1}{3}$ spinous process:	> +	> +	<	<	<	> +	<	> +
Maxilla, scaphognathite setae:	29–30	32^1	31^1	40^1	32^1	28^1	31^1	32^1
Telson, fork length/outermost lateral spine:	5·00	5·40	5·39	5·10^4	5·50	7·45	6·04	6·01
Telson, fork length/dorsal spine:	7·70	7·12	4·11	3·60^4	5·31	7·89	5·26	6·30
Abdominal segment 3, lateral processes:	+	−	−	—	−	+	−	+
Megalopa								
C.L:	2·03	1·66–2·09^2	1·86–2·16^2	2·0^2	1·67–1·93^2	—	1·25	2·01
Antennal flagellum, segmt. no:	8	7	8	6^4	7	—	8	8
Antennal setation of segmts:	0,0,2,0, 5,1,4,3	0,0,4,0, 4,4,4	0,0,2,0, 5,1,2,3	0,4,5, 4,4,4^4	0,3,0,4, 0,4,3	—	0,0,2,0, 4,0,3,5	0,0,4,0, 4,1,3,4
Pereiopods 2–4, spines on dactyl lower margin:	7,7,7	5,5,4	6,7,5	—	5,5,5	—	4,4,2	7,8,8
Pereiopods 2–3, stout spines on dactyl inner upper margin:	5,5	5,5	4,4 2nd long	—	3,3 2nd long	—	3,4 2nd long	3,4 2nd long
Pleopods 1–4, exopod setae:	18,20,19, 16	17–19,16–19,17–18, 13–15	17–20,19–20,18–19, 14–16	16^4—	14–17,14–16, 13–15,12–14	—	17,16,14 12	19,18,18 15
Uropod, exopod setae:	11	8–10	9–10	8^4	7–8	—	7–8	8–10
Telson, lateral setae:	+	+	−	—	−	—	−	+
Telson, posterio-lateral margins:	broadly rounded	subacute	subacute	—	subacute	—	subacute	subacute

evidence does not provide convincing support for these suggested species-groups. Rice (1981) however, has suggested that zoeal similarities could be the result of evolutionary convergence and the zoeal congruences demonstrated here may be examples of such convergence, particularly as the zoeal stages of polybiinids appear to show considerable plasticity in their morphology in the reduction or loss of spines and in exhibiting variations in setal numbers during their individual development.

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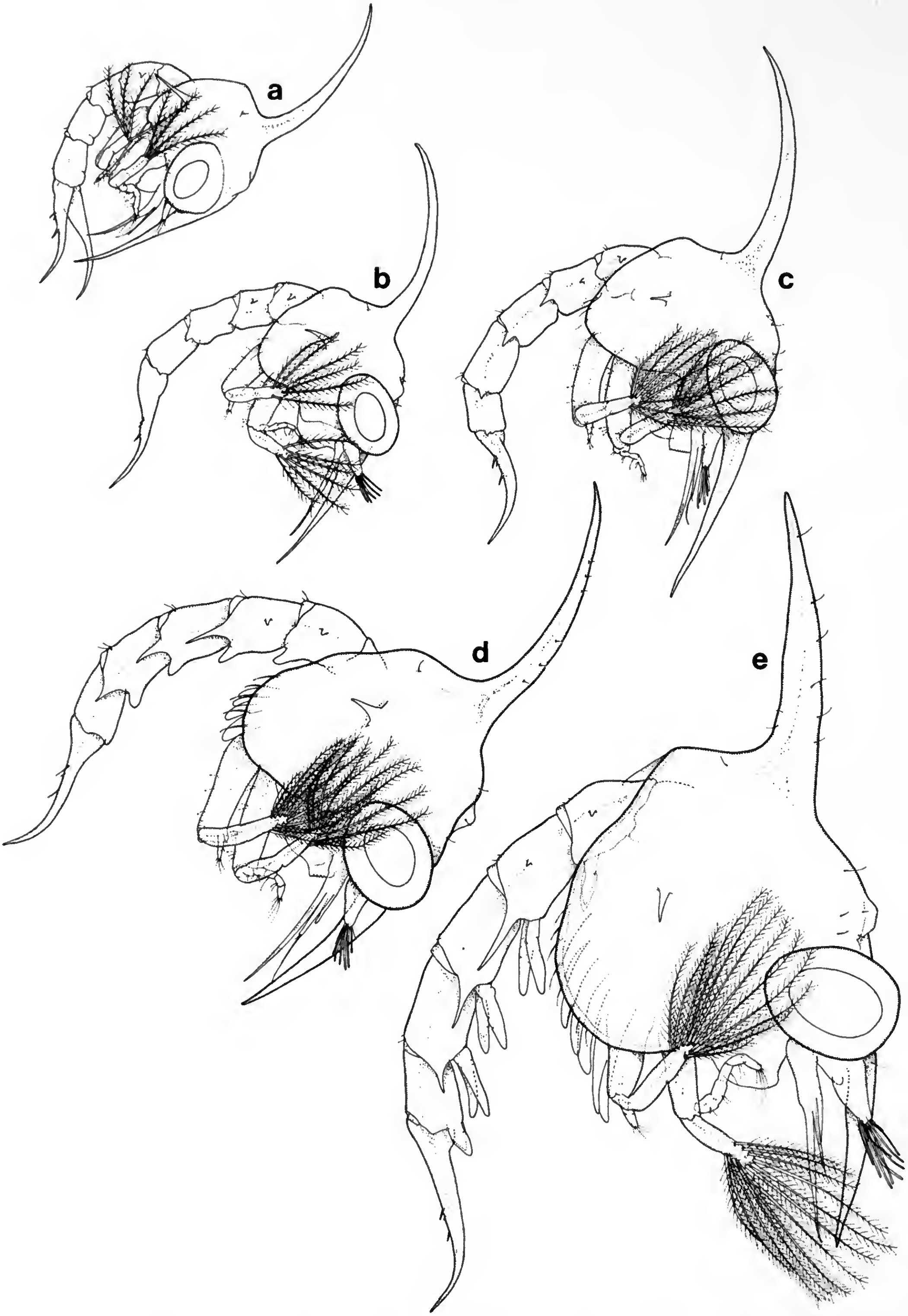

Fig. 1 *Bathynectes longipes* (Risso): a-e, zoeae I–V lateral aspects.

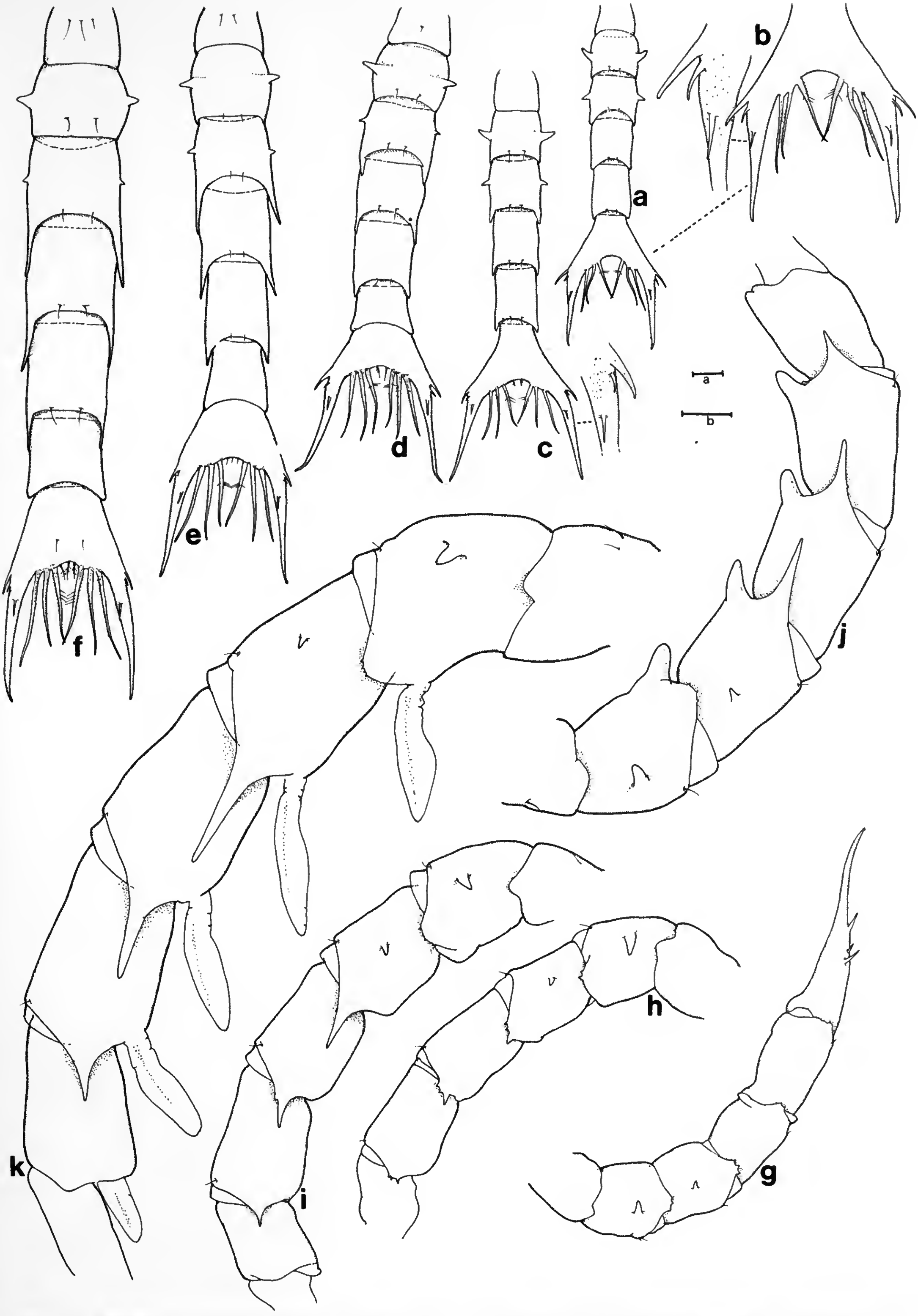

Fig. 2 *Bathynectes longipes* (Risso): abdomen, a-f dorsal and g-k lateral aspects of zoeae I-V. Scales = 0·1 mm; a, c-f to scale a; b, g-k to b.

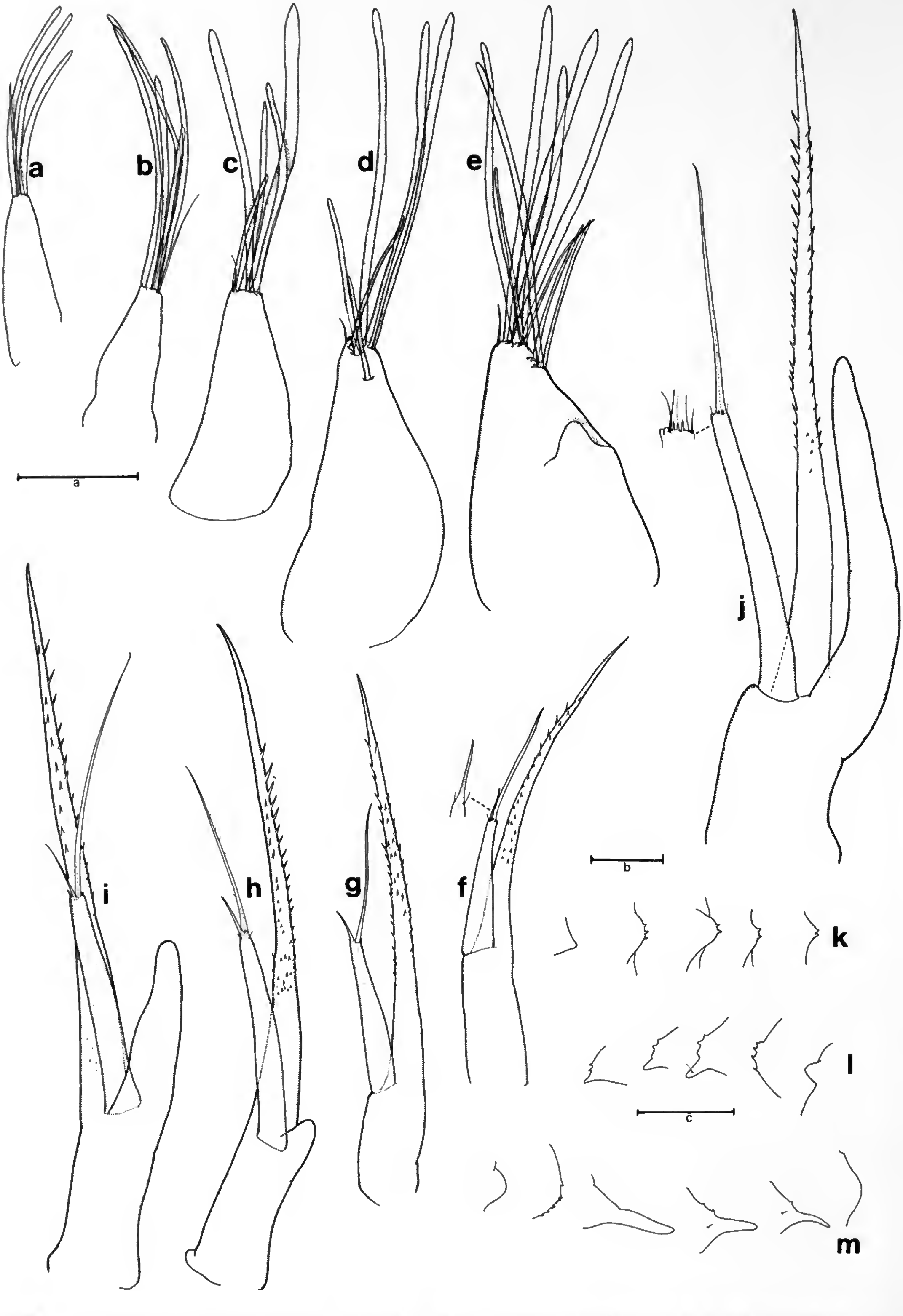

Fig. 3 *Bathynectes longipes* (Risso): a-e antennule, f-j antenna of zoeae I–V; k-m lateral processes of abdominal segments of zoeae I-III. Scale = 0·1 mm; a-j scale a; k to b; l, m to c; insets to c.

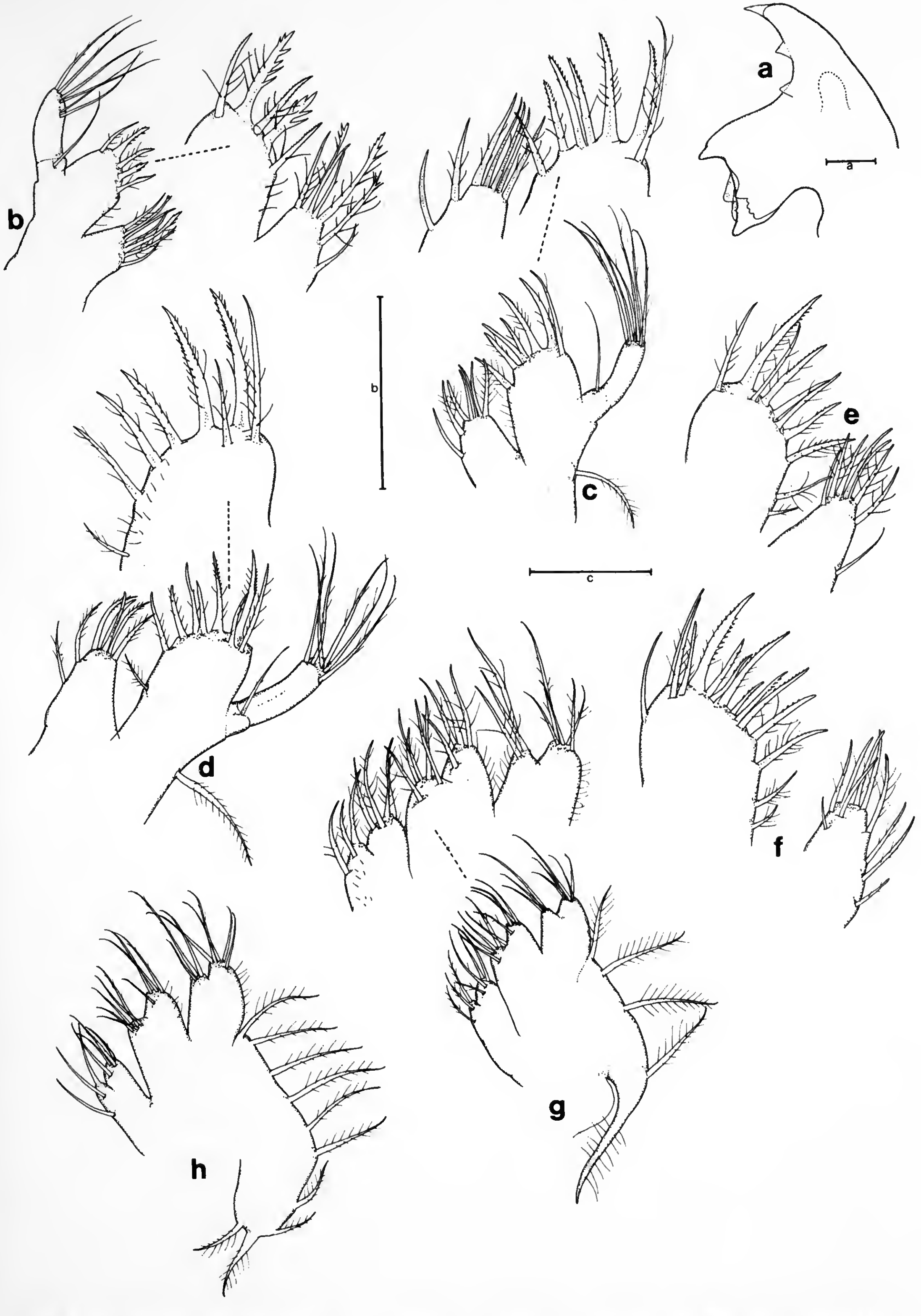

Fig. 4 *Bathynectes longipes* (Risso): a mandible of zoea V; b-f maxillule of zoeae I-V; g-h maxilla of zoeae I-II. Scale = 0·1 mm; a to scale a; b-h to c; insets to b (inset of d depicts a different specimen).

Fig. 5 *Bathynectes longipes* (Risso): a maxilla of zoea III; b maxilla basis and coxa of zoea IV; c maxilla basis and coxa of zoea V; d-e maxilla scaphognathite of zoeae IV and V; f-g first and second maxillipeds of zoeae I-II; h second maxilliped, distal endopod segment of zoea III. Scale = 0·1 mm; a, d, e, h, to scale b; b, c and inset to a; f, g to c.

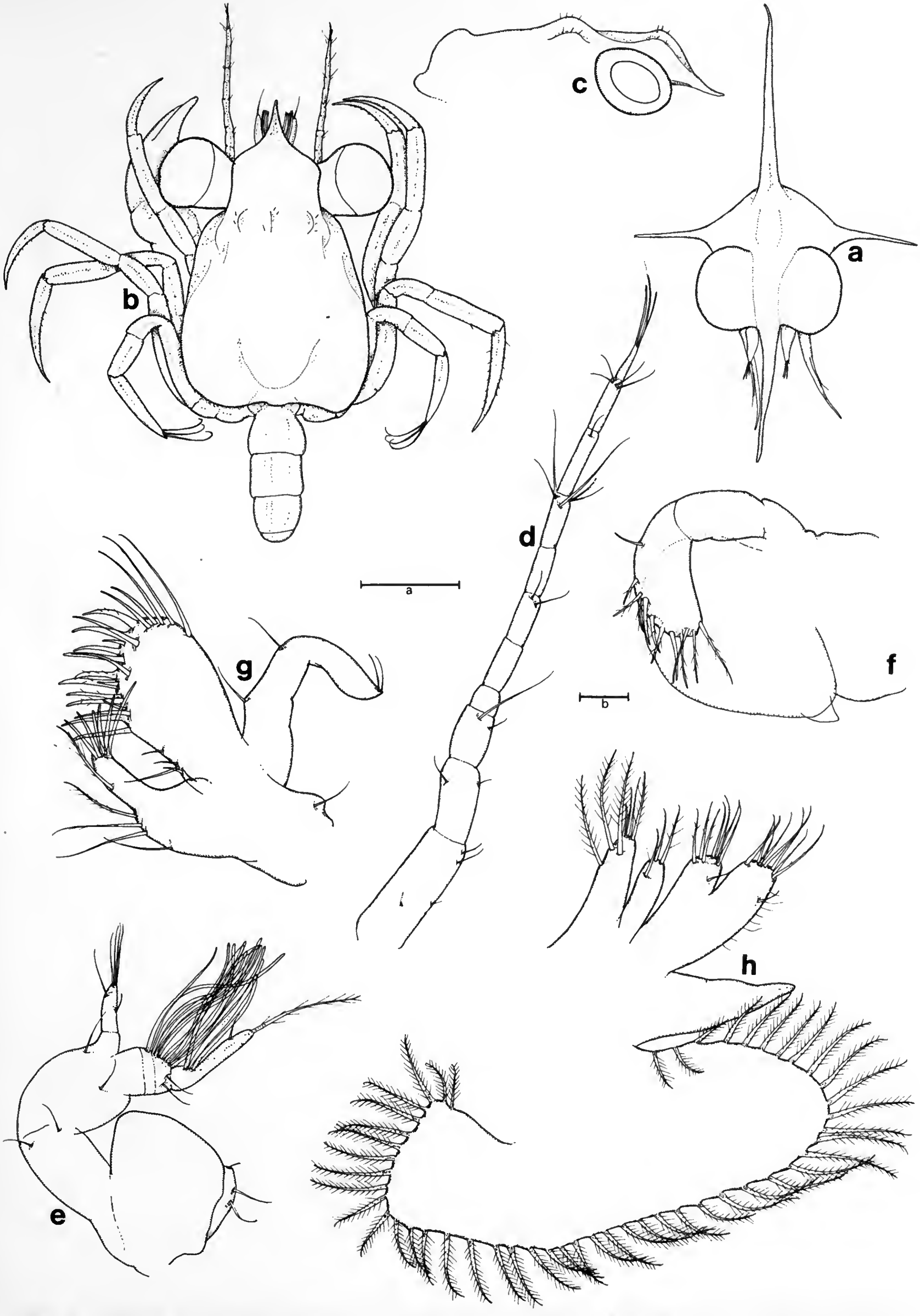

Fig. 6 *Bathynectes longipes* (Risso): a frontal aspect of zoeae I. Megalopa, b-c dorsal and lateral aspects of carapace (limb segments foreshortened); d antenna; e antennule; f mandible; g maxillule; h maxilla. Scale = 0·1 mm; f, g, h to scale a; d to b.

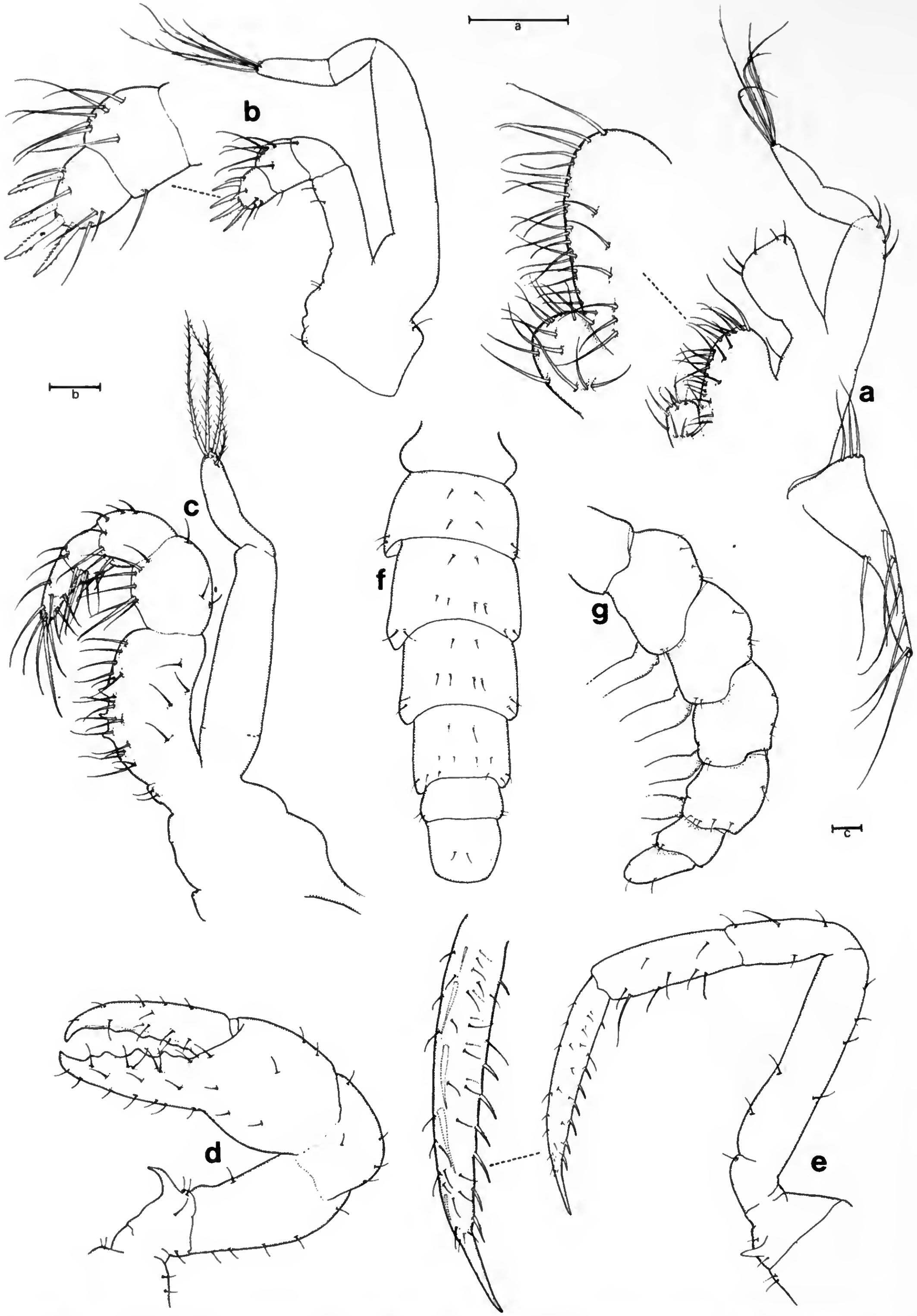

Fig. 7 *Bathynectes longipes* (Risso): megalopa, a-c first to third maxilliped; d left cheliped; e second pereiopod; f-g abdomen from dorsal and lateral aspects. Scale = 0·1 mm; a-c, e to scale b; d, f, g to c; insets to a.

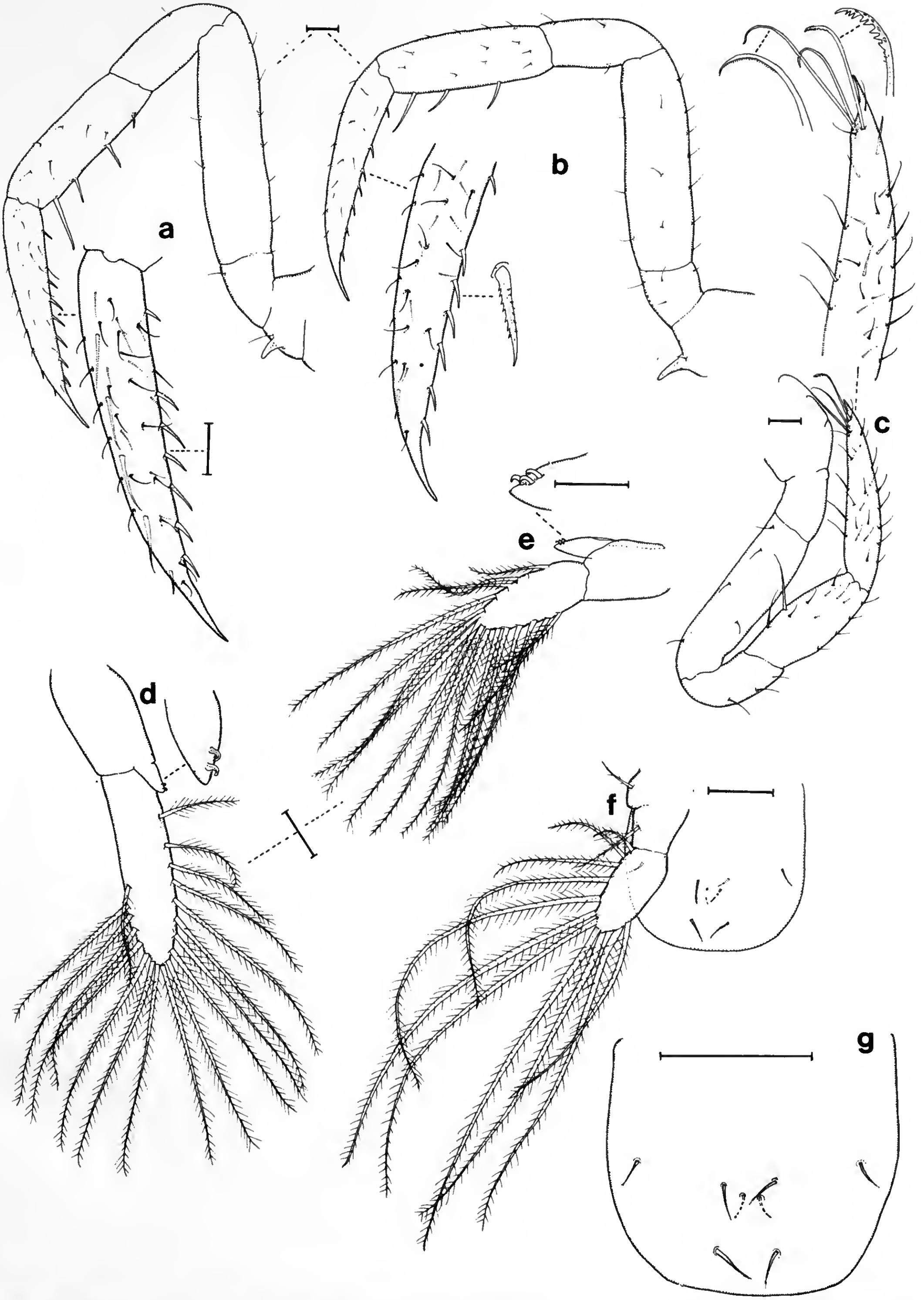

Fig. 8 *Bathynectes longipes* (Risso): megalopa, a-c third to fifth pereiopod; d-e first and fourth pleopod; f right uropod and telson from ventral aspects; g telson from ventral aspect. Scale = 0·1 mm.

The generic status and affinities of *Paratilapia thomasi* Blgr 1915 (Teleostei, Cichlidae)

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Contents

Introduction and synopsis

When originally described (Boulenger, 1915), the species *thomasi* was placed in the genus *Paratilapia* Bleeker, 1868, then a large, catch-all assemblage of African Cichlidae. The artificiality of *Paratilapia* (*sensu* Boulenger) was recognized by Regan in his classical series of papers on the generic classification of African cichlid fishes, the first explicitly 'natural' classification of the group attempted (Regan, 1920: 34).

Regan (1922: 252) considered *Paratilapia thomasi* to be a member of the genus *Pelmatochromis* Steindachner, 1894. Regan's definition of that genus was based largely on osteological and dental features, most of which were present in *P. thomasi,* but some of which could not be checked because no skeletal material was available, as for example, the nature of the apophysis on the third vertebra, and the number of vertebrae.

That Regan's concept of *Pelmatochromis* embraced a polyphyletic taxon was recognized by Thys van den Audenaerde (1968:373), who in revising it, took into account features of soft anatomy as well as osteological characters, and certain ethological and other biological features such as coloration. *Pelmatochromis thomasi,* however, proved to be something of a stumbling block since neither alone nor in combination did its various characters qualify it for inclusion in any of the informal divisions into which Thys van den Audenaerde split Regan's *Pelmatochromis.* According to Thys van den Audenaerde (1968: 382), *P. thomasi* shows greatest affinity with *Hemichromis bimaculatus.* He did not, however, transfer the species to that genus, and nomenclaturally at least it remained in *Pelmatochromis,* even after Trewavas (1973) formally redefined that genus and excluded *thomasi* from it (Trewavas, *op cit*.: 14).

Most recently, Wilson & Loiselle (1980) placed *P. thomasi* in the genus *Hemichromis.* Their reasons for so doing are that, as a result of Loiselle's (1978) revision of *Hemichromis, P. thomasi* could not be excluded on the basis of its dentition, and that its breeding biology and live coloration also argued '. . cogently for regarding this species as a specialized dwarf *Hemichromis*'.

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Regrettably, I overlooked Wilson & Loiselle's paper when preparing my account on the anatomy and phyletic relationships of *Hemichromis* (Greenwood, 1985) and so did not discuss their arguments when considering the possible relationships of the taxon. I cannot, however, support their reasons for considering *P. thomasi* as a species of *Hemichromis,* particularly since it does not share with *Hemichromis* the unique and highly derived ethmopalatine articulatory system found in all members of that genus. Instead, *P. thomasi* has the plesiomorphic double type of ethmopalatine articulation found in most African cichlids and many other percomorph groups as well (see Greenwood, 1985: 139). Furthermore, although there are some undoubted and close similarities in the ethology and coloration of the two taxa, it is impossible to assess the significance of these features in a phylogenetic context (see p. 270 below). Finally, in addition to the ethmopalatine articulation, there are several other derived features in *Hemichromis* which are not shared with *P. thomasi* (see Greenwood, 1985).

That said, however, *P. thomasi* and the *Hemichromis* species do share, and apparently share uniquely, one very unusual feature. That is, the absence of a passage through the anguloarticular bone for the mandibular-preopercular laterosensory canal (Greenwood, 1985: 150). This feature, of course, was not known to Wilson & Loiselle (1980), or to Thys van den Audenaerde (1968) or Trewavas (1973). As far as I can tell from a wide-ranging examination of African, South American and Asian cichlids, combined with a survey of the literature and an examination of many other teleost taxa, the absence of a laterosensory passage through the anguloarticular is probably a feature shared only by *Hemichromis* and *P. thomasi.*

Thus, although it is a 'loss character', its very restricted distribution (a few species within a single family) would seem to strengthen the probability of it indicating a close relationship between those species possessing it. In other words, I would moderate the opinions I expressed recently (Greenwood, 1985: 168) and would now definitely suggest that *P. thomasi* and *Hemichromis* are recognised as sister groups.

If this sister-group status be accepted, the problem of formally ranking the taxa still remains. It might be argued that the relationship of *Hemichromis* to *P. thomasi* could best be indicated by ranking *P. thomasi* as a subgenus of *Hemichromis.* Against such a decision can be ranged the several autapomorphic features of *Hemichromis* (see Greenwood, 1985), in particular its unique and highly derived ethmopalatine articulation, and the absence of all but one synapomorphy shared uniquely by members of the two sister groups. For those reasons I consider the relationship would better be indicated if *P. thomasi* is ranked as a distinct genus, and that a suprageneric group comprising it and *Hemichromis* be recognised informally. The possibility that *Hemichromis* itself may comprise two very closely related lineages (*ie* subgenera) is discussed in Greenwood (1985: 168).

Study material

The study material listed in Greenwood (1985) provided relevant background information. In addition, the following material was examined:

All preserved specimens of *Pelmatochromis thomasi* currently in the collections of the BMNH. From that material two alizarin-alcian blue transparencies were prepared (*ex* 1981.6.19:10, 105–117, 44 mm & 50 mm SL) as were two dry skeletons (*ex* 1981.6.19: 105–117, *ca* 45 mm SL, and 1981.6.19:119–121, 50 mm SL). The gill-arch and jaw musculature were dissected in a 50 mm SL specimen *ex* 1981.6.19:119–121.

Radiographs were made from the three syntypes (1914.12.9:9–11), and from lots 1915.4.13:42–43; 1971.8.13:1; 1971.8.13:17, 1981.6.19:105–124; 1981.8.17:26–41, and 1982.2.4:1–10.

One specimen, *ca* 18 mm SL, of *Hemichromis* cf *H. bimaculatus* (1984.12.17:1, from Lamborini, Gabon, collected by R. Knowles) was partly dissected and stained with alizarin. One specimen of *Tilapia joka* (1982.11.9:24) was partially dissected.

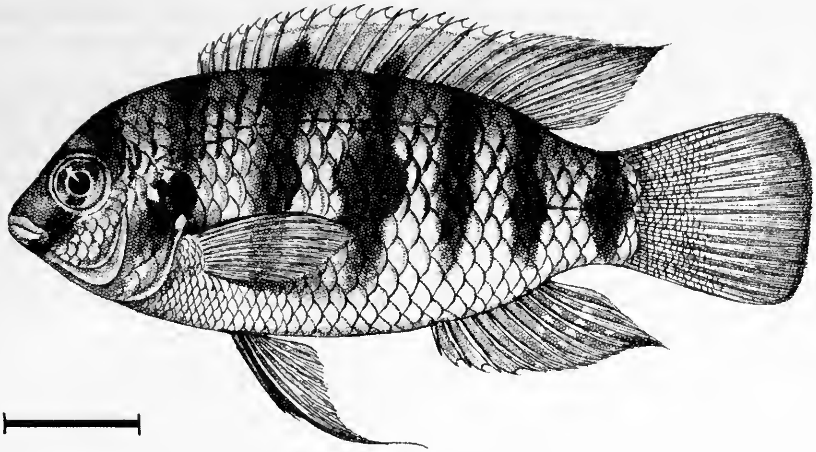

Fig. 1 *Anomalochromis thomasi.* Lectotype. 1·5 times natural size; from Boulenger, 1916.

ANOMALOCHROMIS gen. nov.
(Fig. 1)

SYNONYMY

Paratilapia (part): Boulenger (1915) *Ann. Mag. nat. Hist.* (8) **15:** 202–204; *idem.* (1916) *Cat. Afr. Fw. Fish* **4:** 331, fig. 192.

Pelmatochromis (part): Regan (1922) *Ann. Mag. nat. Hist.* (9) **10:** 252.

Hemichromis (part): Wilson & Loiselle (1980) *Cichlid Index* **4** (5): 1–2, in *Buntbarsche Bulletin* (*J. Amer. Cichlid Assn.* no. 78).

TYPE SPECIES. *Paratilapia thomasi* Blgr (1915). The original description, based on 3 syntypes only, is repeated unchanged in Boulenger (1916: 331), despite 3 additional specimens being listed there; this account is accompanied, for the first time, by a figure. On the basis of that figure, one syntype, 49·5 mm standard length (BMNH 1914.12.9:9) is now chosen as the lectotype.

ETYMOLOGY. The prefix is derived from the Greek *anomalus,* irregular, and refers to the unusual condition of the preopercular-mandibular lateral-line canal; the suffix *chromis* is a word now frequently used, in combination, for various genera of African cichlids.

DIAGNOSIS. Cichlid fishes with the articular surface of the neurocranial apophysis for the upper pharyngeal bones formed from the parasphenoid only. Vertebral column (excluding the fused PU_1 and U_1 centra) with 23–25 (mode 24) vertebrae; the apophysis for the insertion of *retractor arcuum branchialium* muscles situated on the 3rd vertebrae, its two halves not united ventrally. Palatine bone articulating with the lateral ethmoid in two places and not supported antero-ventrally by a lateral, peg-like process of the vomer. The anguloarticular bone lacks a canal for the passage of the mandibulo-preopercular lateral-line canal. Microbranchiospines present on the outer face of gill arches 2-4; 1 or 2 epibranchial gill-rakers on the first gill-arch, 5 or 6 on the ceratobranchial of that arch, and 1 at its epi- ceratobranchial articulation. Buccal tissue immediately anterior to the upper pharyngeal bones neither developed into a prominent pre-pharyngeal pad nor produced into a visor-like hanging pad. *Adductor arcus palatini* muscle with an insertion on the palatine. Scales on the body weakly ctenoid, their circuli arranged in an essentially 'gothic arch' pattern (clearly not of the 'Norman arch' type: see Trewavas, 1973:14, fig. 10); last scale of the upper lateral-line series not reaching a vertical drawn through the first scale of the lower series, there being a horizontal distance of about 2 scales between the two lines at this point; upper lateral-line, over most of its extent, separated from the base of the dorsal fin by one large and one small scale. Pelvic fins in adult males with the first and second branched rays produced and filamentous, of equal length, and extending to the middle of the anal fin base.

DISTRIBUTION. The single known species, *A. thomasi*, is restricted to coastal rivers in Guinea, Sierra Leone and Liberia. In the original description of the species, its type locality is recorded as Matca, Sierra Leone, but in Boulenger (1916) it is given as Maka. No 'Maka' is listed in any of the gazetteers consulted, but there are at least 11 places named Moka and whose coordinates range from 7°08'N, 11°24'W, to 8°25'N, 12°02'W.

Notes on the osteology and anatomy of *Anomalochromis thomasi*

Osteology

Neurocranium (Fig. 2). In its general outline and proportions the neurocranium is somewhat foreshortened and deep; the supraoccipital crest is high.

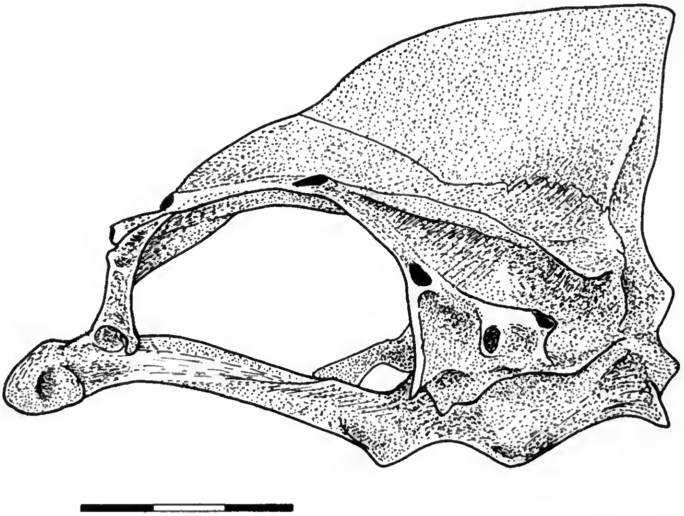

Fig. 2 *Anomalochromis thomasi.* Neurocranium in left lateral view. In this and following figures, the scale bars are in mm divisions.

The articular surface for the upper pharyngeal bones is formed entirely from the parasphenoid (*ie* of the *Tilapia*-type; Greenwood, 1978), and is carried on a low apophyseal eminence contributed to by the prootic and basioccipital of each side. The hind opening to the posterior myodome is relatively large.

The *lateral commissure* is narrow and strut-like, and there is no internal jugular bridge anterior to it. There is, however, a well-developed and prominent, dorsally directed spur from the prootic between the foramina for the 3rd and the 5th cranial nerves. This spur does not contact the upper part of the prootic, neither is it connected with that region of the bone by a ligament.

The *ethmoverine* region of the skull is relatively short, and lacks the casket-like elevation of the vomer which is so characteristic of this region in *Hemichromis* (*cf* fig. 1 in Greenwood, 1985 with Fig. 2). Judging from the condition found in two alizarin transparencies (in which the neurocranium is *ca* 11–12 mm long), the supraethmoid does not contact the vomer and, in consequence, a large area of the ethmoid cartilage is exposed. The anterior margin of the supraethmoid does, however, extend forward to a point where it is level with the anterior margin of each lateral ethmoid's medial arm. The situation in both these specimens of *A. thomasi* very closely resembles that illustrated by Trewavas (1973: 22, fig. 4) for *Sarotherodon shiranus*. The length of the *S. shiranus* skull is not given, but judging from the scale of the figure it is about 5 or 6 times longer than the *A. thomasi* skull examined.

In adult specimens of those *Hemichromis* species I have studied the vomer and supraethmoid are in close contact laterally, and are separated medially only by a small rostral fenestra (Greenwood, 1985). Recently I was able to study the neurocranium in a small *Hemichromis* cf *H. bimaculatus* of about 19 mm standard length. Here, although the vomer is produced dorsally into its typical casket-like medial crest (see above; also Greenwood, 1985) it differs from the adult condition because it is not in contact with the supraethmoid. Indeed, the two bones are widely separated and an expansive area of the ethmoid cartilage is visible, a situation contrasting markedly with that seen in specimens of 70 mm standard length.

Clearly, at least in this species of *Hemichromis*, there are marked ontogenetic changes in the spatial relationships of those bones contributing to the ethmoverine skull region. When the adult condition of *A. thomasi* is compared with the juvenile and adult conditions in *Hemichromis*, it would seem to be interpretable as a paedomorphic one. Wilson & Loiselle (1980) give the maximum adult sizes for male and female *A. thomasi* as, respectively, 80 and 70 mm standard length; no fishes of that length were available to me, so it was impossible to investigate the condition of the ethmovomerine complex in *A. thomasi* specimens in the upper part of that species' size range.

All specimens of the various *Chromidotilapia* and *Pelvicachromis* species examined (all, it should be noted, larger than the *A. thomasi* available) have the vomer and supraethmoid in contact, but, *pace* Trewavas (1973: 22), in *Pelmatochromis buettikoferi*, type species of that genus, the bones do not contact one another. The possible phyletic significance of these differences is currently under review (see also discussion in Trewavas, 1973).

Anomalochromis thomasi has a shallow *hyomandibulad shell*, a depression in the ventrolateral aspect of the neurocranium associated with the origin of the *levator externi* muscles of the gill arches (see Barel *et al*, 1976). In *Hemichromis* the shell is a deep, dorsally directed and pit-like indentation. In *A. thomasi* the lateral awning is much shallower than that of *Hemichromis*, and, like the hyomandibulad shell, conforms to the modal cichlid type (Greenwood, 1985: 142).

There are no outstanding peculiarities in the morphology of the dorsicranium, nor are there any noteworthy characteristics associated with the otic region.

Gill-arch skeleton and the lower pharyngeal bone. Unlike *Hemichromis* (see Greenwood, 1985: 150–153) the gill-arch skeleton of *A. thomasi* is, in general, of the supposedly generalized type found in such haplochromine species as *Astatotilapia elegans* (see Barel *et al*, 1976; Stiassny, 1981 & 1982).

The *epibranchials* of all four arches are relatively less elongate than those in *Hemichromis*, and epibranchial I has a long uncinate process, about three times the length of its process for articulation with the first pharyngobranchial; the angle between the uncinate and pharyngobranchial processes is small, about 10°, and the former process is directed posteriorly. As in most cichlids, no interarcual cartilage is developed.

Epibranchial II has a large, anvil-shaped cartilage associated with its anterior border. The cartilage is much larger than its counterpart in *Hemichromis*, and is comparable with that of *Pelmatochromis nigrofasciatus* figured by Trewavas (1973; fig. 11). A well-developed cartilage on this epibranchial is apparently the modal condition for cichlids (Stiassny, 1982; Greenwood, 1985: 151).

Epibranchial IV has a prominent and well-developed shank spine, and an expansive but not elongate quadrangular area. In both these features *A. thomasi* shows the generalized cichlid condition and thus differs from *Hemichromis* (Greenwood, 1985: 151: fig. 15).

The pharyngobranchial elements also conform to the generalized cichlid condition, and pharyngobranchial III is noticeably less rectangular in outline than is its counterpart in *Hemichromis*. A prominent 'frayed zone' (Stiassny, 1981) is present on the posterior border of the 4th upper pharyngeal tooth-plate.

The *ventral part* of the gill-arch skeleton, like that in *Hemichromis*, shows no peculiar or unusual features (Greenwood, 1985: 153).

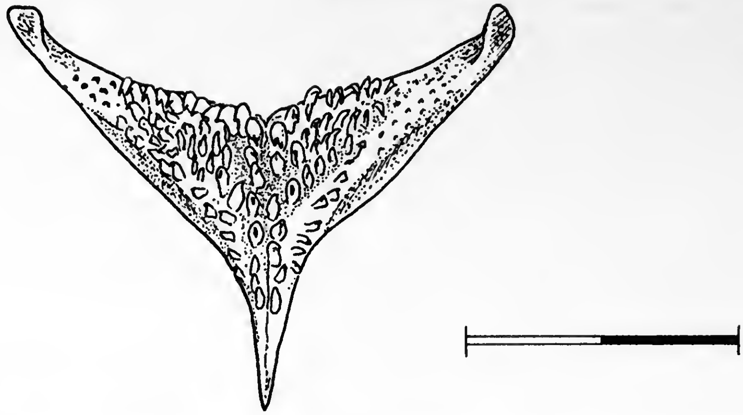

Fig. 3 *Anomalochromis thomasi.* Lower pharyngeal bone, occlusal view.

Microbranchiospines are present on the outer face of the 2nd to 4th ceratobranchials, and although small are quite obvious and consistently present.

The *lower pharyngeal bone* is illustrated in Fig. 3. Its short and broad outline resembles that in *Hemichromis* species; in *Pelvicachromis* and *Chromidotilapia* the bone has a more elongate and arrowhead-shaped outline, whilst the outline of the bone in *Pelmatochromis* is intermediate between the *Hemichromis* and *Pelvicachromis-Chromidotilapia* types.

Palatoquadrate arch and suspensorium (Figs 4a & B). There are few outstanding features in this region of the orobranchial skeleton which, in most respects, is of the plesiomorphic pattern found in many African cichlids. The *palatine bone* has a double articulation with the ethmoid region; that is: anteriorly with the lateral face of the lateral ethmoid near that bone's junction with the vomer, and posteriorly, with a low but distinct 'drum facet' on the ventro-medial face of the lateral ethmoid. In this feature *A. thomasi* differs markedly from *Hemichromis* where the articulation is a single and specialized one confined to the anterior face of the lateral ethmoid (see discussion in Greenwood, 1985: 139). Parenthetically it can be noted that in the small *Hemichromis* (19 mm SL) mentioned on page 261, the ethmopalatine articulation is exactly like that in the largest *Hemichromis* examined.

The palatine in *A. thomasi* also differs from that bone in *Hemichromis* since it has a distinct ridge developed on its lateral face, a plesiomorphic feature seemingly uncommon amongst African cichlids (Cichocki, 1976: 82 & 150; Oliver, 1984: 16).

The palatine and entopterygoid in *A. thomasi* are in contact ventrally, but dorsally their margins diverge very slightly (Fig. 4).

Together, the *hyomandibula* and *metapterygoid* bones contribute to the formation of a large *calyx*, with the metapterygoid also providing the incomplete anteroventral wall of this structure. It is thought that the calyx is a plesiomorphic feature; it is not developed in *Hemichromis* (Greenwood, 1985: 145–146).

The hyomandibular flange is relatively broad (Fig. 4) and does not contact the metapterygoid anteriorly, thus leaving a distinct anteromedial gap between the two bones. The shank of the hyomandibula is slender, its length contributing to slightly less than a third of the bone's entire length.

The *symplectic* has an unusual and somewhat sigmoidal shape (*cf* Fig. 4 with fig. 6 in Greenwood, 1985), with a noticeable gap between the ventral margin of its middle section and the rim of the preoperculum.

Hyoid arch (Fig. 5). The branchiostegal rays are fine and elongate; the greater part of each ray is cartilaginous and only its proximal quarter to third is strongly ossified. A large cartilaginous area is interposed between the ossified portions of the epi-and ceratohyal elements.

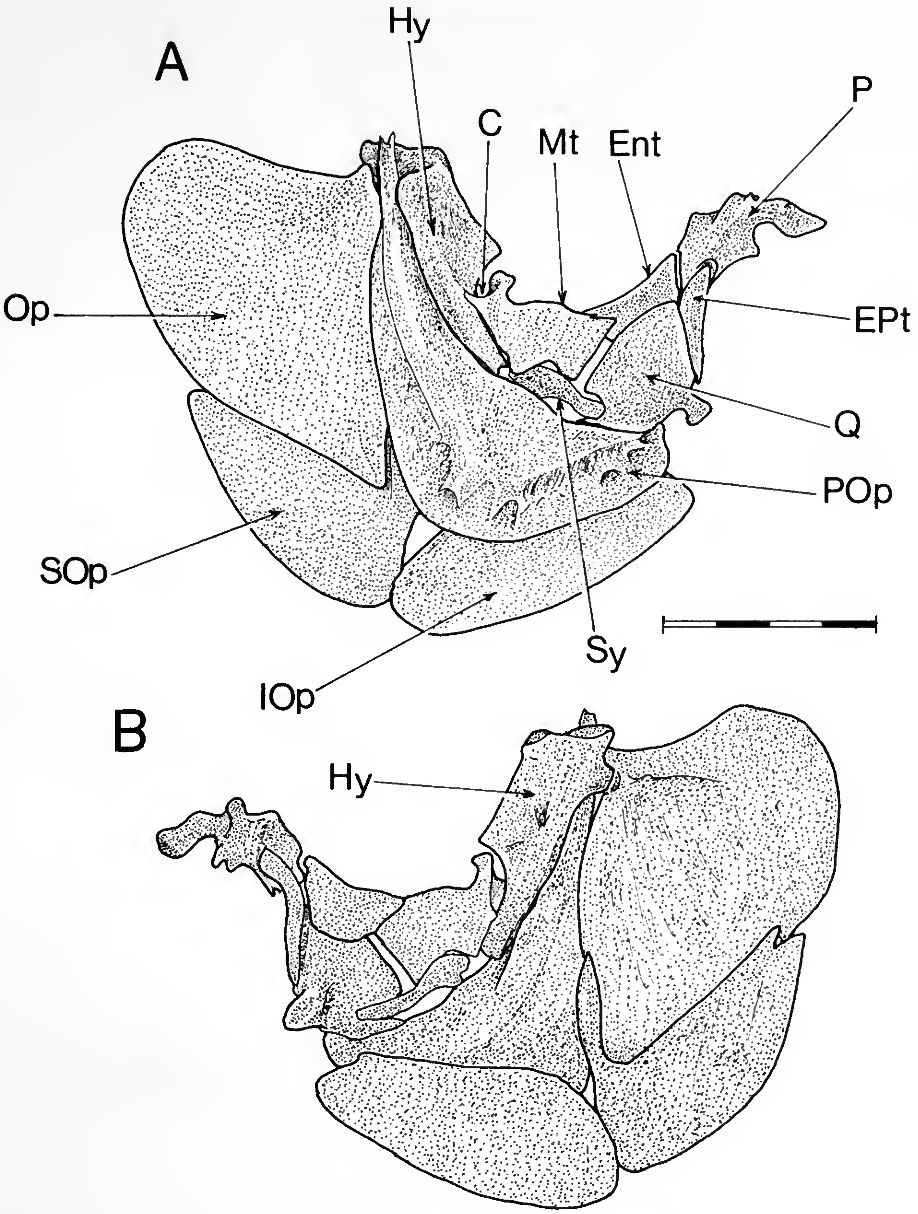

Fig. 4 *Anomalochromis thomasi*. Right palatoquadrate arch and opercular series: A, lateral view; B, medial view. C = Calyx. Ent = Entopterygoid. EPt = Ectopterygoid. Hy = Hyomandibula. IOp = Interoperculum. Mt = Metapterygoid. Op = Operculum. P = Palatine. POp = Preoperculum. Q = Quadrate. SOp = Suboperculum. Sy = Symplectic.

Jaws. The *maxilla* (Figs 6B & C) is rather foreshortened, slightly curved, and has its ventral margin incurved posteriorly where it is drawn-out into a distinct point. The mediad curvature of the bone's shank between the premaxillary saddle and the shank-ridge is much less obvious than the curvature in some *Hemichromis* species (eg *H. fasciatus* and *H. bimaculatus*) but is about equal to the curvature in *H. letourneauxi*. The outward inclination of the shank-ridge in *A. thomasi* is less pronounced than in any of the *Hemichromis* species examined (Greenwood, 1985: 148; fig. 12).

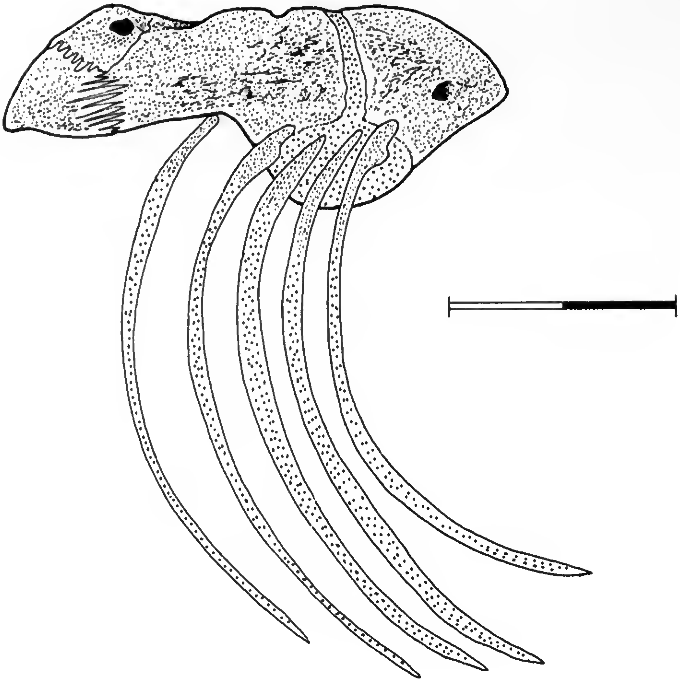

Fig. 5 *Anomalochromis thomasi.* Hyoid arch, left side, in lateral view. Stipplied areas are cartilaginous or very poorly ossified.

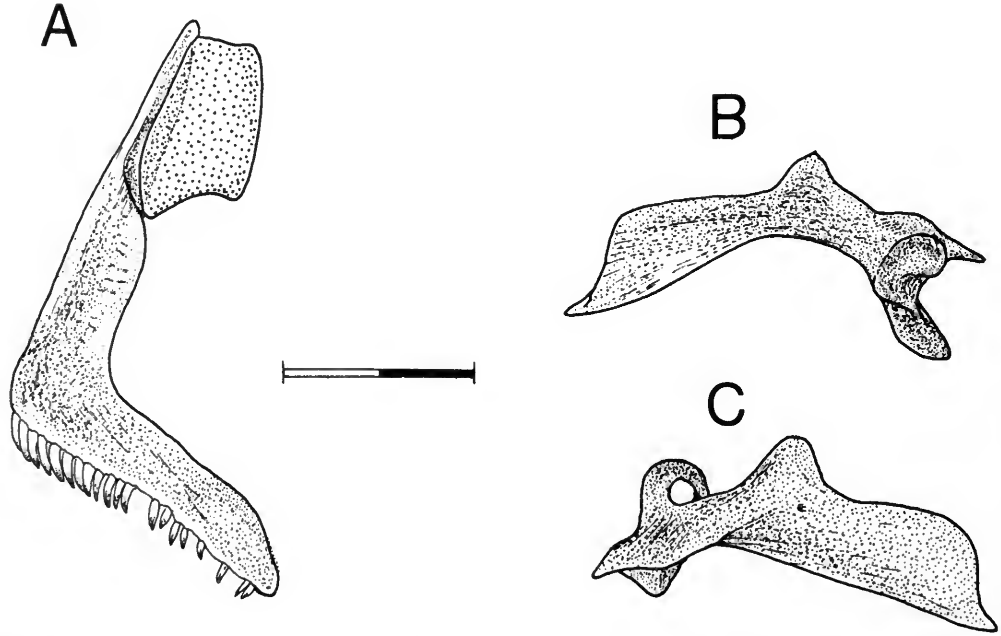

Fig. 6 *Anomalochromis thomasi.* A, Left premaxilla, in lateral view; the rostral cartilage is stippled; B & C, left maxilla in, respectively, dorsal and lateral views.

The ascending process of the *premaxilla* (as measured from its distal tip to the level where the process becomes indistinguishable from the dentigerous arm) is but slightly shorter than the dentigerous arm; the articular process extends distally to a point slightly more than half way along the ascending process. The dentigerous arm has almost no ventral curvature to its posterior tip, and the alveolar surface reaches nearly to the posterior limit of the arm.

There is a large, very thick and cushion-like *rostral cartilage,* which is oval in cross-section and is tightly applied to the ascending processes of the premaxilla (Fig. 6A).

The *dentary* (Fig. 7) has a very low coronoid process, and is a generally foreshortened and deep bone with four lateral-line sensory canal openings. Teeth in the outer series of the bone extend onto the anterior margin of the coronoid process as far as its crown.

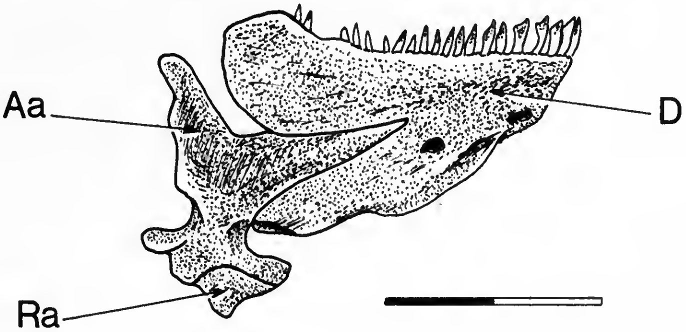

Fig. 7 *Anomalochromis thomasi.* Right mandible; viewed from a very slightly ventro-lateral aspect. Aa = Anguloarticular. D = Dentary. Ra = Retroarticular.

The *anguloarticular* (Fig. 7) is noteworthy for the complete absence of any tube, fossa or foramen for the passage of the preopercular sensory canal into the dentary. Such a condition is one apparently shared only with *Hemichromis* amongst the cichlids; if it also occurs amongst other teleosts it is of very rare occurrence and has not been recorded (see discussion, p. 258).

Infraorbital bones (Fig. 8). Apart from the relatively stout and well-ossified lachrymal (1st infraorbital) the bones in this series are very poorly ossified and delicate. For that reason, and because the available specimens were not suitably preserved for finer osteological study, it has proved difficult to give a precise account of this series.

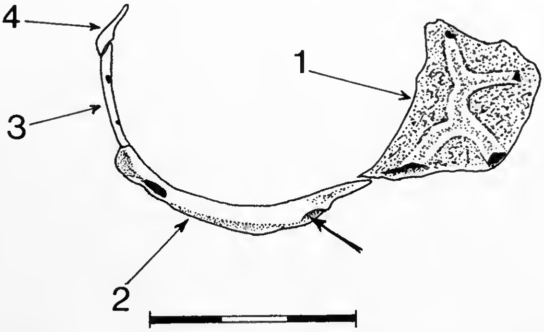

Fig. 8 *Anomalochromis thomasi.* Right infraorbital series. 1–4: First (lachrymal) to fourth infraorbital bones. Arrow indicates anterior opening of second bone.

The 1st infraorbital (lachrymal) has four laterosensory canal pores, the presumed plesiomorph condition in African cichlids (Greenwood, 1985: 165). The posterior pore lies at some distance from the anterior opening in the second bone of the series; the mouth of that opening lies in the same horizontal as the posterior pore in the lachrymal but is directed ventrally and not horizontally as it is in the lachrymal bone (see Fig. 8).

The remaining elements of the infraorbital series each consists of little more than an ossification around the sensory tubule; only the second bone is produced into a shallow flange ventrally. There are apparently only three infraorbital bones in addition to the lachrymal. The second in the series is greatly elongate, and extends along virtually the entire ventral margin of the eye. The third bone is moderately elongate but the fourth is much reduced in size, being in that respect comparable with the sixth bone in the infraorbital series of *Hemichromis* (*cf* Fig. 8 with fig. 9 in Greenwood, 1985).

It is impossible to tell from the material examined whether or not the second and third bones are compound elements, a possibility suggested by the low total number of bones and the elongation of the second and third elements.

The *supracleithrum and posttemporal bones* (Fig. 9) differ from those in *Hemichromis* only in the shorter and wider arms of the posttemporal. For comments on the possible value of these elements as indicators of phyletic relationships see Greenwood (1985: 147) where Van Couvering's (1982) ideas on that point are discussed.

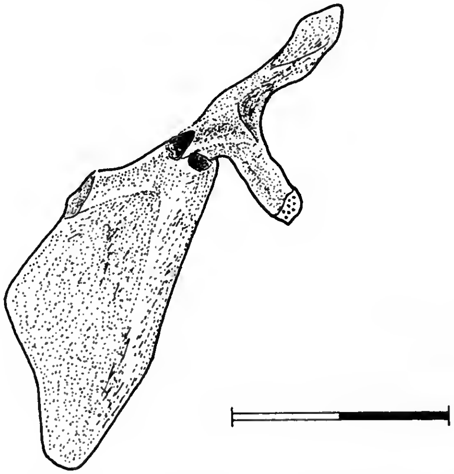

Fig. 9 *Anomalochromis thomasi.* Right supracleithrum and posttemporal.

Pectoral girdle and postcleithra (Figs 10A & B). This complex shows few noteworthy characters, except that the spine on the head of the second postcleithrum is well-developed and is much more obvious than the spine in *Hemichromis*. It was impossible to establish whether or not the spine in *Anomalochromis* is associated with a muscle sheet from the first rib (Greenwood, 1985: 154).

Axial skeleton. As in the majority of African cichlids there is only a single *predorsal bone* (see Oliver, 1984).

Excluding the fused PU_1 and U_1 centra there are 23 (f1), 24 (f35) or 25 (f3) *vertebrae*, of which 12 are abdominal in position, and 11 (f1), 12 (f35) or 13 (f3) are caudal elements. The lectotype and one paralectotype have total vertebral counts (excluding the fused PU_1 and U_1 elements) of 25 (*ie* 12+13), the second paralectotype (39·0 mm SL) has a teratologically distorted vertebral column in which the number of centra cannot be ascertained with certainty, but appears to be 25.

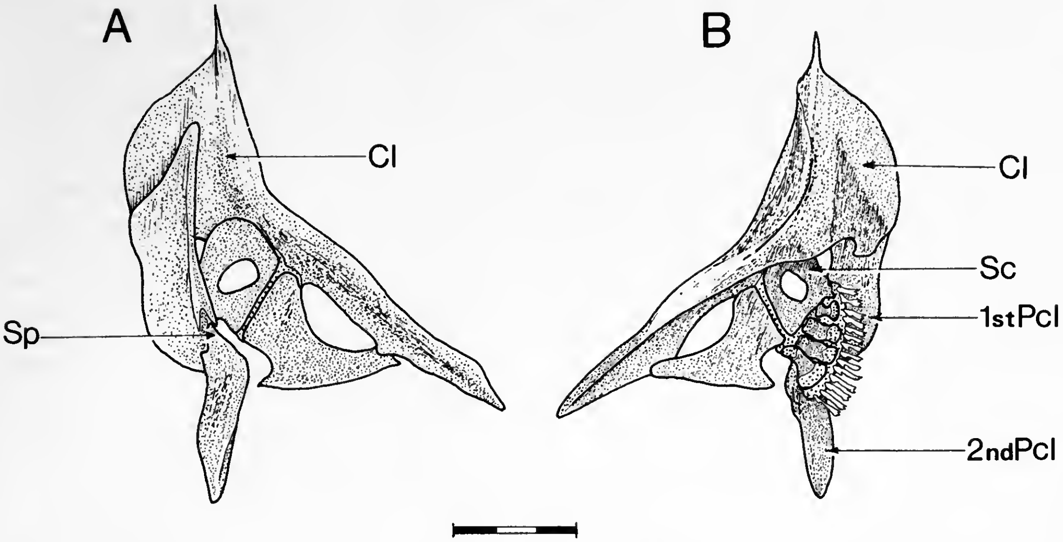

Fig. 10 *Anomalochromis thomasi.* Left pectoral girdle and postcleithra in: A, medial, and B, lateral view. Cl = Cleithrum. 1stPcl = 1st Postcleithrum. 2ndPcl = 2nd Postcleithrum. Sc = Scapula. Sp = Spine on head of 2nd Postcleithrum.

A low *apophysis* for the insertion of the *retractores arcuum branchialium* muscles is present on the third abdominal vertebrae; the two sides of the apophysis do not meet ventrally.

Epipleural bones are present on all pleural ribs in the two alizarin specimens examined; *epineurals* are present only on the first two vertebrae, which are without pleural ribs.

Caudal fin skeleton. All five hypurals are free in one of the two alizarin specimens examined, but in the other the 3rd and 4th hypurals are either fused or very closely apposed to one another. In both these specimens, and in all those specimens radiographed, the first hypural is noticeably deeper (from twice to 3 times so) than the second hypural. Further information on the condition of the hypurals, in particular the possible extent of the fusion, could not be obtained from the radiographs.

Well-developed dorsal and ventral accessory cartilages are present; both are free from the thin cartilaginous strip lying along the distal margin of the epurals, hypurals and the parhypural. This strip is not continuous across the gap separating the 2nd and 3rd hypurals, and no cartilaginous plate occupies that gap. Ventrally, a second and smaller accessory cartilage lies between the haemal spines of the 2nd and 3rd preural vertebrae; it too is free from the major ventral accessory cartilage, and it is not connected with the strip lying along the distal margins of the 1st and 2nd hypurals and the parhypural.

An unusually prominent 'stegural' plate is developed on the base of the uroneural complex. In one of the alizarin specimens there is a double neural arch and spine on the centrum of the second preural vertebra; in the other specimen there is a single but expansive arch and spine.

The parhypural is apparently without an hypurapophysis, an unusual condition in African cichlids.

Dentition (Figs 11A–C). Teeth situated anteriorly in the outer row of both jaws are of two kinds: relatively slender unicuspids with slightly incurved crowns, or relatively slender teeth with compressed, somewhat obliquely sloping crowns which sometimes have a faint indication of a much smaller minor cusp appearing as a shallow notch in the crown. Laterally and posterolaterally unicuspids in the outer tooth row are noticeably more slender than those occurring anteriorly, and their crowns are but slightly incurved.

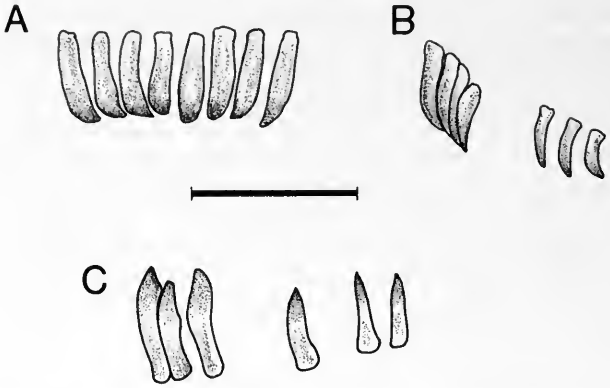

Fig. 11 *Anomalochromis thomasi.* Oral dentition; outer row. A, Anterior premaxillary teeth on either side of the premaxillary symphysis; frontal view of labial aspect. B, Premaxillary teeth from the anterior part and the extreme posterior part of the left premaxilla; labial aspect viewed laterally. C, Teeth from the anterior, middle and extreme posterior part of the left dentary; labial aspects as viewed laterally. All are from a fish ca 40 mm SL. Scale = 1 mm.

The predominant form of tooth situated anteriorly and laterally in the jaws is correlated with the fish's size. Unicuspid anterior teeth are found only in fishes more than 40 mm standard length, and even in specimens as long as 45 mm SL some weakly bicuspid teeth with expanded crowns are often present. Similarly, the proportion of slender unicuspids occurring laterally and posterolaterally increases with size. Only the posterior one or two teeth in the smallest fish examined (25 mm SL) are unicuspids.

All teeth in the inner rows are unicuspid, even in the smallest fish examined. Anteriorly and anterolaterally, the inner teeth of the upper jaw are arranged in from 1 to 3 irregular rows, but generally in 2 rows. There is a single row posteriorly, extending to a point about half-way along the alveolar surface of the premaxilla. The interspace separating the inner rows from the outer series, especially towards the midline of the jaw, is sometimes greatly reduced in size.

Inner tooth arrangement in the lower jaw is like that in the upper jaw, except that the interspace between the inner series and the outer row is more obvious, and the reduction of the inner series to a single row takes place more anteriorly in this jaw. As in the upper jaw, the inner row extends posteriorly only for about half the length of the alveolar surface.

Anatomy

The small adult size of *A. thomasi,* coupled with the generally poor preservation of most specimens in the BMNH collection, have rendered difficult any precise study of soft anatomy. For example, it has proved impossible to determine the pattern of intestinal coiling, a feature probably of some importance in assessing phylogenetic relationships amongst cichlids (see Zihler, 1982); nor was it possible to learn much about other internal organs. Some observations could, however, be made on the cranial musculature and ligaments, and on the muscles of the gill-arches.

The *jaw musculature* is essentially similar to that described for *Hemichromis* (Greenwood, 1985: 155–157), but in *A. thomasi* the tendon A_1b of the *adductor mandibulae* 1 muscle, although closely associated with the tendon of *adductor* A_w, remains discrete throughout its passage across the latter tendon before it inserts on the nipple process of the anguloarticular bone. The tendon of *adductor mandibulae* 3, which inserts on Meckel's cartilage, is long, as is that from *adductor mandibulae* 1 to the maxilla; the tendon of *adductor mandibulae* 2, inserting on the poorly defined coronoid process of the dentary, is short and deep.

A small part of the *adductor arcus palatini* muscle inserts on the palatine, a feature apparently characteristic of all African cichlids (see Greenwood, 1985: 156).

The dorsal musculature of the gill-arches is like that in *Hemichromis* and thus is of the generalized cichlid pattern (see Greenwood, 1985: 159–162). As in other species with this type of musculature, only a small slip of the *levator externus* IV muscle passes to the 4th epibranchial, the greater part inserting on the horn of the lower pharyngeal bone.

A detailed study of ventral gill-arch muscles, and the associated ligaments of the gill-arches, could not be made.

Ligaments associated with the jaw and palatoquadrate arch. Unlike *Hemichromis, A. thomasi* has a full complement of these ligaments (see Greenwood, 1985: 158–159), including a definite anteroventral palato-maxillary ligament. The broad, vertical lateral ethmoid to palatine ligament (absent in *Hemichromis*) is not subdivided and lies behind the origin of the palatopalatine ligament. The palato-maxillary ligament (also wanting in *Hemichromis*) is broad and well-defined.

That *A. thomasi* has a full complement of ethmo-palatine and palato-maxillary ligaments is probably correlated with the species having, unlike *Hemichromis,* a generalized and double articulation between the ethmoid and palatine bones (see Greenwood, 1985: 158).

Squamation. Except for those scales above the upper lateral-line, and on the thoracic and ventral abdominal regions, all other scales are weakly ctenoid. The circuli are arranged in a pattern essentially of the 'gothic arch' type (Trewavas, 1973: 14), especially towards the centre of the scale. Circuli lying more laterally are often arranged almost in parallel, but converge slightly as they approach the exposed margin of the scale.

There are from 24–26 scales in the lateral-line series, the last in the upper series not overlapping, in the vertical plane, the first scale of the lower series. The beginning and the end of each series respectively is thus separated by one, and generally two vertical scale rows. Scales in the upper lateral-line are separated from the base of the dorsal fin by one large and one much smaller scale over most of the line's course.

Gill-rakers and buccopharynx. Rakers on the epibranchial of the first arch are greatly reduced in size, and number one or two. A single raker occurs in the angle between the epibranchial and ceratobranchial of this arch, and there are 5 or 6 short rakers carried on the ceratobranchial.

Although the roof of the buccal cavity immediately in front of, and slightly medial to the upper pharyngeal bones is somewhat thickened and thrown into a number of deep folds, it cannot be described as forming a prominent prepharyngeal pad such as occurs in *Pelmatochromis* and *Thysia.* It is certainly in no way comparable with the visor-like pad found in *Chromidotilapia* and certain other genera (Trewavas, 1974: 389; Greenwood, 1983: 265).

The relationships of *Anomalochromis thomasi*

In his original description of *Paratilapia thomasi,* Boulenger (1915) suggested that the species '. . . appears to be closely related to *Paratilapia dorsalis',* but gave no substantiating evidence for his suggestion. *Paratilapia dorsalis* Pellegrin is currently treated as a synonym of *Pelmatochromis nigrofasciatus* (Pellegrin); see Thys van den Audenaerde (1968) and Trewavas (1973).

Boulenger's (1915) suggestion is clearly based on an overall and superficial similarity between the two species. From Trewavas' (1973) revision and redescription of *Pelmatochromis* Steindachner it is clear that *A. thomasi* shares no uniquely synapomorphic features with any members of that genus, and indeed Trewavas excluded it as being '. . . . not a true *Pelmatochromis*'; she did not, however, suggest where its affinities might lie, nor did she comment on Thys van den Audenaerde's (1968) alignment of the species with *Hemichromis.* On the basis of synapomorphies, *A. thomasi* cannot be considered closely related to *Chromidotilapia* or *Pelvicachromis* (pers. obs.), the two genera amongst which Trewavas distributed, either explicitly (Trewavas, 1974) or implicitly, the species which Regan (1922) had included in his concept of *Pelmatochromis.*

Thys van den Audenaerde's (1968) paper referred to above was concerned, essentially, with an attempt to unravel the phylogeny and relationships of the numerous species, including *A.*

thomasi, then placed in *Pelmatochromis*, *sensu* Regan (1922). Although several anatomical features were used in that attempt, the unique nature of the palato-ethmoidal articulation in *Hemichromis* (see Greenwood, 1985) was then unknown, as was the absence of a latero-sensory canal in the anguloarticular of both *A. thomasi* and *Hemichromis*. The discovery of the latter feature would certainly seem to strengthen Thys van den Audenaerde's (1968) idea of a close relationship between the two taxa (see p. 265). Similarities in coloration and breeding biology, characters which also influenced Thys van den Audenaerde's views, are of equivocal value (see below).

In the following year, Thys van den Audenaerde (1969) suggested, without reference to the 1968 paper, that his newly described species *Tilapia joka* was related to *A. thomasi*. *Tilapia joka*, unlike *A. thomasi*, has a fully developed latero-sensory canal in the anguloarticular and, as far as I can determine, shares no synapomorphies uniquely with *A. thomasi*. A close relationship between the two taxa is most unlikely.

It has also been thought that the genus *Thysia* Loiselle & Welcomme is related to *A. thomasi*. In their paper describing *Thysia*, Loiselle & Welcomme (1972: 53 *et seq*) took up the ideas expressed by Thys van den Audenaerde (1968) and, developing them further, postulated that *Thysia*, together with '... the *Hemichromis bimaculatus-Pelmatochromis thomasi* group within *Hemichromis* sensu lato', and the *Hemichromis fasciatus* complex within *Hemichromis*, '... can be considered an oligophyletic assemblage comparable to *Tilapia* sensu lato'. Loiselle & Welcomme's ideas are discussed fully in Greenwood (1985: 164–169), and the conclusion reached that, if synapomorphies and not just overall levels of similarity are used to determine relationships, the full Loiselle-Welcomme hypothesis could not be substantiated. That part of the hypothesis which indicates an *A. thomasi-Hemichromis* (*sensu lato*) relationship, however, does now seem to be one that can be substantiated.

In my 1985 paper I expressed reservations about using the absence of an anguloarticular sensory canal as a synapomorphy to link *Hemichromis* and *A. thomasi* on the grounds that it was a 'loss character'. Further investigation and reflection (see p. 258) has, however, led me to alter my earlier opinions. I would now argue that the absence of the canal in those taxa alone amongst the cichlids and their outgroup relatives is more parsimoniously treated as a true synapomorphy indicative of recent common ancestry. That conclusion is strengthened by there being no contra-indicative synapomorphies suggesting that either taxon has closer affinities with any other taxon or lineage. The wider-based comparative anatomical investigation which led to my changed viewpoint failed to substantiate Loiselle & Welcomme's (1972) proposed relationship of either *Hemichromis* or *A. thomasi* with *Thysia*, neither did it indicate a close relationship of *A. thomasi* with *Chromidotilapia*, *Pelvicachromis* or *Pelmatochromis*.

The only other worker to consider the relationship of *A. thomasi* is Voss (1980), who used for that purpose data obtained from his comparative studies on the ethology and coloration of *A. thomasi* and certain other African cichlids. Voss' work is, unfortunately, limited by the extent of the outgroup comparisons he could make since very few observations as detailed as his are available, even for members of the Cichlidae. As with most of those authors who used morpho-anatomical features to investigate the relationships of *A. thomasi*, Voss' approach is not a cladistic one, but is based on degrees of similarity in characters whose polarity cannot yet be determined.

Voss' (1980) conclusions derived from details of coloration and colour patterns seem rather indecisive and even contradictory. In one place (Voss, 1980: 47) he says that '... On the scheme of colored markings, *P. thomasi* and *H. bimaculatus* appear to us then rather closely related. It is the same with *T.* [*Thysia*] *ansorgii*, but in a distinctly lesser way. This species seems nearer *P. thomasi* than *H. bimaculatus* (on this scheme at the very least)'. Elsewhere (*op. cit*: 87) he comments that '... *H. bimaculatus*, *P. thomasi* and *T. ansorgii* unquestionably show a certain relationship on the basis of their colored markings (especially the first two [species] mentioned). Still, these same species can be set widely apart by these same elements. According to these criteria, it is rather then of a group in which the species are related in a rather loose manner'. In another context (*op. cit.*: 86), the presence of a silvery genito-anal spot, Voss believes that '... there is not much separation' between the *Pelvicachromis-Nanochromis-Chromidotilapia* group and the genus *Thysia;* no mention is made here of *A. thomasi,* which lacks the genito-anal spot.

Based on a study of ethological features, Voss (*op. cit.*: 118) notes that '. . . *P. thomasi, H. bimaculatus,* and *Thysia ansorgii* have numerous common points which allow placing them together, but also some important differences in their patterns which lead one to think that they are already very distant'. He concludes that remark with the seemingly contradictory statement . . . 'Moreover, the ethological data does not justify a classification of *H. bimaculatus* and *P. thomasi* in different genera'.

Obviously a lot more data on ethology and coloration are required before such information is likely to be of value in unravelling phyletic relationships. Those data, too, should be derived from a wide range of cichlid taxa, and from out-group taxa as well.

The previously most recent generic assignment of *A. thomasi,* one based mainly on similarities in ethology and coloration, was to the genus *Hemichromis* (see Wilson & Loiselle, 1980). That placement would, in my opinion, be negated by *A. thomasi* having a plesiomorphic palato-ethmoidal articulation and not the highly derived condition found, uniquely, in *Hemichromis* (Greenwood, 1985); it is also weakened by the equivocal nature of the behavioural and colour similarities on which Wilson & Loiselle place so much emphasis (see above). However, I would certainly subscribe to the idea of *A. thomasi* and *Hemichromis* being sister taxa (see p. 258, and discussion in Greenwood, 1985: 168–169).

On the information currently available it is impossible to relate a *Hemichromis-Anomalochromis* lineage to any other African cichlid species or group of species; for that reason I would propose that the lineage be given the informal status, and epithet, of the hemichromine group, but would suggest that it is more readily defined and is phylogenetically more coherent than at least two other informal groups now recognised, namely the tilapiines and the haplochromines.

Some might, and some no doubt will argue, on the basis of Regan's division of cichlids into a *Haplochromis*-group and a *Tilapia*-group, that *A. thomasi* cannot be closely related to *Hemichromis* since it has a *Tilapia*-type neurocranial apophysis whilst all *Hemichromis* species have an apophysis of the *Haplochromis*-type. The validity of this supposedly diphyletic division has been questioned by several workers (see Greenwood, 1978), an uncertainty reinforced by the *Tilapia*-type apophysis being the plesiomorphic condition and thus of no value as an indicator of close relationship amongst those species with this apophyseal type. Furthermore it has yet to be demonstrated that any unifying synapomorphy exists among the very large number of species having an apophysis of the *Haplochromis*-type.

In its ontogeny, the *Haplochromis*-type apophysis first passes through a condition comparable with the adult *Tilapia*-type (Ismail *et al.* 1982). Thus it is possible that the occurrence of *Tilapia*-type apophyses in species otherwise apparently related to taxa with a *Haplochromis*-type, could be interpreted as demonstrating paedomorphosis in this character. Such an explanation might well apply to *A. thomasi,* a species whose members reach only a small size at sexual maturity, and one apparently exhibiting, in the adult, a paedomorphic juxtaposition of certain bones in the ethmoverine complex of the neurocranium (see p. 261).

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Once again, and with no less gratitude, I must thank Gordon Howes for the varied assistance he has given me, and for his important contribution as an artist. To Bernice Brewster go my thanks for her help, especially in preparing the alizarin transparencies and in numerous other and time consuming but boring tasks she has so willingly performed.

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Cranial muscles of gonorynchiform fishes, with comments on generic relationships

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Contents

Introduction

The ostariophysan order, Gonorynchiformes comprises a small group of seven genera, totalling some 30 species of diverse morphology and habitat. Two genera, *Chanos* and *Gonorynchus* are marine and have their distribution in the coastal and shelf waters of the Indo-Pacific. The other five genera, *Kneria, Parakneria, Cromeria, Phractolaemus* and *Grasseichthys* are confined to the freshwaters of Africa. Apart from *Chanos* (see Schuster, 1960), life-history and ecological data are almost entirely lacking.

Only incidental observations are available on *Gonorynchus,* which according to Marshall (1964) feeds on crustacea by burrowing into sand. Such few data as exist on the African freshwater genera *Kneria* and *Parakneria* indicate that they are inhabitants of quiet forest pools as well as fast flowing water areas such as rapids and waterfalls (see Bell-Cross, 1976:96; Nicholson & Nicholson, 1975; Banister & Bailey, 1979:208,214) and are epilithic feeders. *Phractolaemus,* on the other hand, occurs in quiet, shaded waters and may be an epiphytic feeder. Nothing is known of the life-histories of the minute *Grasseichthys* and *Cromeria,* although Roberts (1972:144) reports the latter as spending '... much of its time buried in the sand'.

The systematic history of the gonorynchiforms has been summarised by Fink & Fink (1981) and Patterson (1984*a*). Fink & Fink (1981) provided a positive basis for further systematic research by identifying a suite of synapomorphies, later enumerated and modified by Patterson (1984*a* & *b*). In Patterson's (1984*a*) relationship scheme, the Chanoidei (Chanidae; *Chanos*) are recognised as the sister-group to the Gonorynchoidei, comprising the families Gonorynchidae (*Gonorynchus*), Kneriidae (*Kneria, Parakneria, Cromeria, Grasseichthys*) and Phractolaemidae (*Phractolaemus*). Thus, following Fink & Fink, Patterson recognised the African freshwater taxa as a monophyletic lineage on the basis of five synapomorphies involving the suspensorium, vertebral column and gill-arches.

A re-examination of those primary synapomorphies (i.e. unique to gonorynchiforms within the Ostariophysi) has failed to falisify their status. Similarly, the synapomorphies used to

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unite the Gonorynchoidei are upheld. However, within this suborder, generic relationships amongst the African freshwater taxa are at present unresolved.

Apart from osteology, anatomical studies of gonorynchiforms have dealt with visceral and pulmonary systems (see Thys van den Audenaerde, 1961 on Phractolaemidae and Lenglet, 1973 on the Kneriidae). Virtually no myological data are available for these fishes. The cranial musculature of only one gonorynchoid, *Gonorynchus gonorynchus*, has been described in detail by Le Danois (1966). It is, however, unfortunate that numerous inaccuracies, misidentifications and misinterpretations (see below under *Gonorynchus*) render this work virtually useless.

The aim of this paper is to partly fill the lacunae of descriptive myology and thereby provide another data base for assessing relationships within the Gonorynchiformes. Attention has been directed primarily to those muscles attaching to the jaw, opercular and suspensorial elements as these were thought, because of their more variable nature, to be the most rewarding indicators of phylogenetic relationship. Some of the hyoid muscles and those of the branchial arches are not treated in detail; the pattern of gonorynchiform gill-arch muscles conforms closely to those illustrated for the ostariophysan characiphysan *Brycon* by Winterbottom (1974, figs 20 & 29), apart from the reduced length and tendinous nature of the *levatores externi* in the Phractolaemidae. (Suitable material for examining branchial arch muscles by sectioning was not available for *Cromeria* and *Grasseichthys*.)

Gonorynchiform fishes are not well represented in museum collections, particularly the rarer small-sized African freshwater species. It is fortunate that the British Museum (Natural History) has representatives of all gonorynchiform genera and so it has been possible to make direct osteo-myological comparisons. The opportunity has been taken to comment, where appropriate, on the osteological observations of previous authors.

Abbreviations used in the figures
(Except when given otherwise the scale bar divisions = 1 mm)

Muscles and soft tissues:

a_1 (i, o) a_2 (i, o) a_3, a_w	divisions of *adductor mandibulae* muscle (i = inner, o = outer)
a_2L	lachrymal portion of muscle A_2
aa_2	aponeurosis of muscle A_2
aap	*adductor arcus palatini*
ad4	*adductor* of the 4th branchial arch
ah	*adductor hyomandibularis*
ao	*adductor operculi*
b	barbel
bm	body musculature
brp	lateral branchial pouch
ca	rictal cartilages
cmc	coronomeckelian cartilage
cms	cartilaginous maxillary-palatine meniscus
ctf	fatty connective tissue
do	*dilatator operculi*
ec	ethmoid cartilage
ebd	epibranchial diverticulum
edc	epidermal canal
epx	*epaxialis* muscle
hy	*hyohyoideus*
im	*intermandibularis*
lap	*levator arcus palatini*
le	*levator externus*
lep	ethmoid-palatine ligament
li	lower lip

lin	*levator internus*
lmp	maxillary-palatine ligament
lo	*levator operculi*
lpp	palatine-premaxillaryligament
lq	quadrate spine-quadrate face ligament
lri	retroarticular-interopercular ligament
lrt	coiled upper jaw ligament
mc	maxillary cartilage
nc	nasal cavity transverse canal
nt	nasal tube
od	*obliquus dorsalis*
on	olfactory nerve
pc	palatine cartilage
ph	*protractor hyoideus*
pp	*protractor pectoralis*
pqc	palato-quadrate cartilage
rm	mandibular ramus of the trigeminal nerve
rmf	dentary foramen for mandibular nerve
rs	*rectus superior*
sh	*sternohyoideus*
tA	tendon of muscle A_2o to antorbital
ta_1	insertion tendon of muscle A_1
ta_2a_1i	tendon from A_2 to A_1 inner muscle
ta_2	insertion tendons of muscle A_2
ta_2Q	tendon from A_2 aponeurosis to quadrate
tvd	*transversus dorsalis*

Bones

AA	anguloarticular
AH	anterohyal
BA4	4th branchial arch
BB	basibranchial
BR	branchiostegal ray
CB1–5	ceratobranchials
CM	coronomeckelian bone
D	dentary
DF	dilatator fossa
EB1–5	epibranchials
ECT	ectopterygoid
ENT	entopterygoid
EP	epioccipital
ETH	ethmoid bloc
FR	frontal
HB1–3	hypobranchial
HY	hyomandibula
IO1–5	infraorbitals
IOP	interoperculum
LAC	lachrymal (1st infraorbital)
LE	lateral ethmoid
ME	mesethmoid
MET	metapterygoid
MX	maxilla
N	nasal
OA	opercular aperture
OF	olfactory foramen in the frontal
OP	operculum
P1–4	dentary processes
PA	parietal
PAL (A,D)	palatine (auto-, dermo-)
PB1–4	pharyngobranchials
PHY	posterohyal
PM	premaxilla
PO	preoperculum
PS	parasphenoid
PTO	pterotic
PTS	pterosphenoid
Q	quadrate
QS	quadrate spine
RA	retroarticular
RE	rostrodermethmoid
SO	suboperculum
SP	sphenotic
SY	symplectic
UH	urohyal
V	vomer

Descriptive myology

Definitions

For the most part, the muscle nomenclature follows that of Winterbottom (1974), including the use of *protractor hyoideus* rather than *geniohyoideus* for the ventral head muscle (see Lauder & Liem, 1980:373 for discussion).

The outer, ventral portion of the *adductor mandibulae* musculature is regarded as division A_1. The definition and homology of this element has been the subject of much discussion (see below, for various authors), and further comments are added below although no solution to the problem is offered.

Winterbottom (1974) defines muscle A_1 as an element having a dorsal position on the cheek musculature and inserting on the maxilla. However, Winterbottom noted that the position and insertion were not constant and thus he recognised A_1 as a muscle of variable topography. Following examples given by Edgeworth (1935:53) Winterbottom considered that because the mandibularis branch of the fifth cranial nerve was variable in its path it could not be taken as a reference point for identifying a particular muscle. I would contest this, however, on the grounds that Edgeworth had probably mistaken the homology of the elements he identified as A_1 (in siluroids for example, Edgeworth's A_1 is the *retractor tentaculi,* which originates from the medial face of the adductor complex; see Howes, 1983*a*:11 for discussion of homology). Furthermore, nerves do not alter their courses randomly but become displaced according to the shift of the muscle element with which they are associated (see below, p. 299 and Howes, 1983*b*:328).

By defining A_1 as the element inserting on the maxilla and lying *exterior* to mandibular V, a more precise identification may be possible. On this basis the ventral, outer element in ostariophysans is clearly A_1. In elopoids (*Elops*), alepocephalids (*Alepocephalus*), clupeids (*Clupea*) and most 'salmoniforms' (*Salmo, Coregonus, Esox*), even though the outer muscle element may have a maxillary insertion, it is clearly not A_1 since the mandibular V lies external to it. Furthermore, the outer element in these groups most often inserts on the lower jaw and is continuous with an intramandibularis section (A_w) and so must be considered A_2 $(+A_3)$, as identified by Winterbottom (1974:figs 1 & 2).

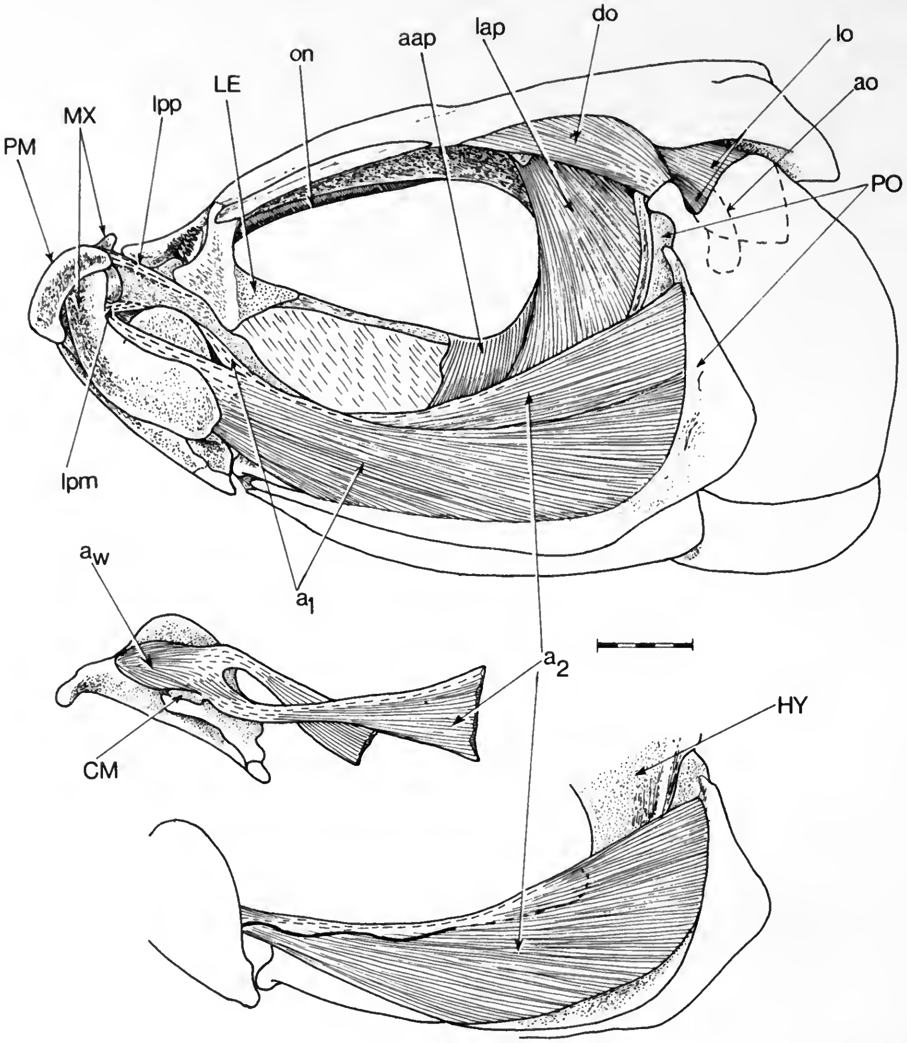

Fig. 1 *Chanos chanos*. Above: lateral view of cranial muscles. Dashed lines on operculum indicate the extent of the *levator* and *adductor operculares* insertions. Centre: medial view of lower jaw muscle insertions. Below: lateral view of inner adductor muscle; dashed line indicates medial path of the mandibularis nerve, shown in solid black laterally.

In Gadiformes (*Gadus, Melanogrammus, Nezumia*), the mandibular ramus of V lies medial to A_1 and external to A_2. In Stomiiformes (*Astronesthes*), the mandibular ramus passes lateral to the outer adductor element, but there is an insertion to the upper jaw of a medial division of the adductor, often referred to as A_1b. Fink & Weitzman (1982:72) have argued that A_1 and A_1b are not homologues. I agree with this conclusion, but the problem still remains whether muscle A_1 in neoteleosts is equivalent to A_1 in ostariophysans. Fink & Weitzman (1982:72) claim that A_1 is a 'eurypterygian character' (i.e. is present in groups above and including Aulopiformes). This statement suggests that their concept of A_1 differs from that given here, since by regarding the muscle as characterising eurypterygians they exclude ostariophysans. It is noted that these authors refer to A_1 as a *dorso*-lateral division of the adductor mandibulae.

Amongst some 'salmoniforms' *viz*: *Galaxias, Prototroctes, Brachygalaxias* and *Aplochiton* there is a partial ventro-lateral division of the *adductor mandibulae* and the mandibularis V nerve

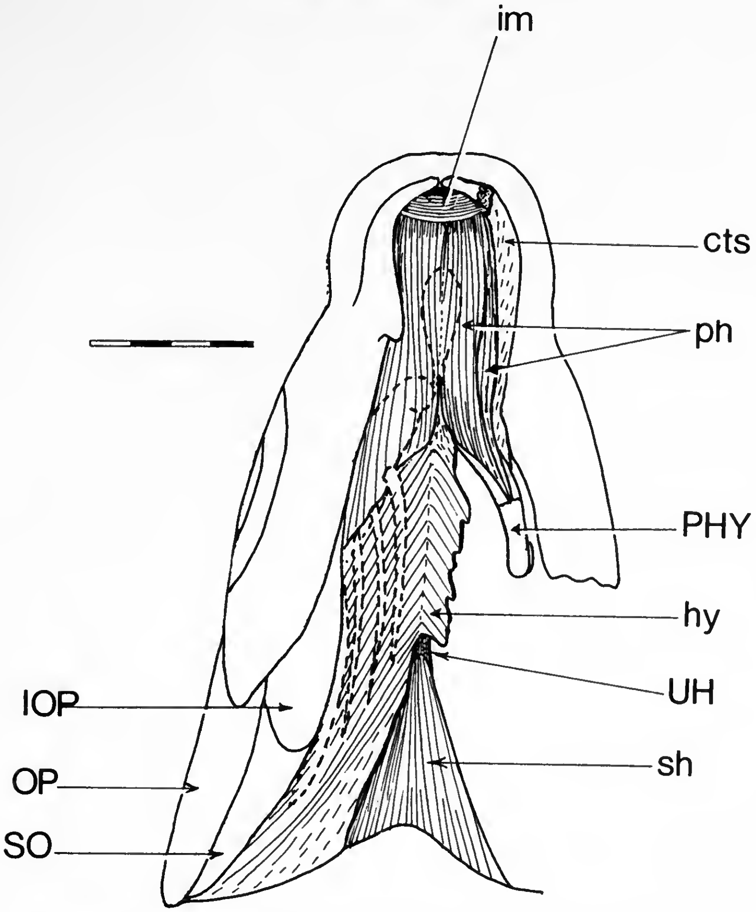

Fig. 2 *Chanos chanos*. Ventral head musculature. Outlines of hyoid elements are indicated by dashed lines.

passes lateral to A_2. The nerve courses across the inner muscle close to its insertion tendon and passes into the body of the outer element. In other words, these taxa possess a muscle segment topographically identical with that defined as A_1 in ostariophysans. Whether indeed it is homologous or homoplasious is a matter that needs further investigation.

One other problem must be mentioned, and this concerns the plesiomorphic nature of insertion of muscle A_1 in ostariophysans. Fink & Fink (1981:343) contended that a maxillary insertion of the element is plesiomorphic. Howes (1983*a*:14) argued the reverse, believing that a lower jaw insertion was the primitive condition. No conclusive evidence has emerged from the present study that would support either one or other of these hypotheses; either assumption of primitiveness recognises a reversal if one acknowledges each ostariophysan subgroup as being monophyletic.

CHANOS Lacepède, 1803

Chanos is a monotypic genus represented by *Chanos chanos* (Forsskål, 1775) found in tropical and subtropical areas of the Indian and Pacific oceans. The species inhabits mainly coastal, and often brackish waters and is an epipelic feeder.

SPECIMENS EXAMINED: *Chanos chanos:* BMNH 1948.10.15:1–2 (185, 220, 290 mm SL); uncatalogued (8 alcian-alizarin preparations, 23–47 mm SL); 1898.9.13:1 (dry skeleton, neurocranial length 70 mm).

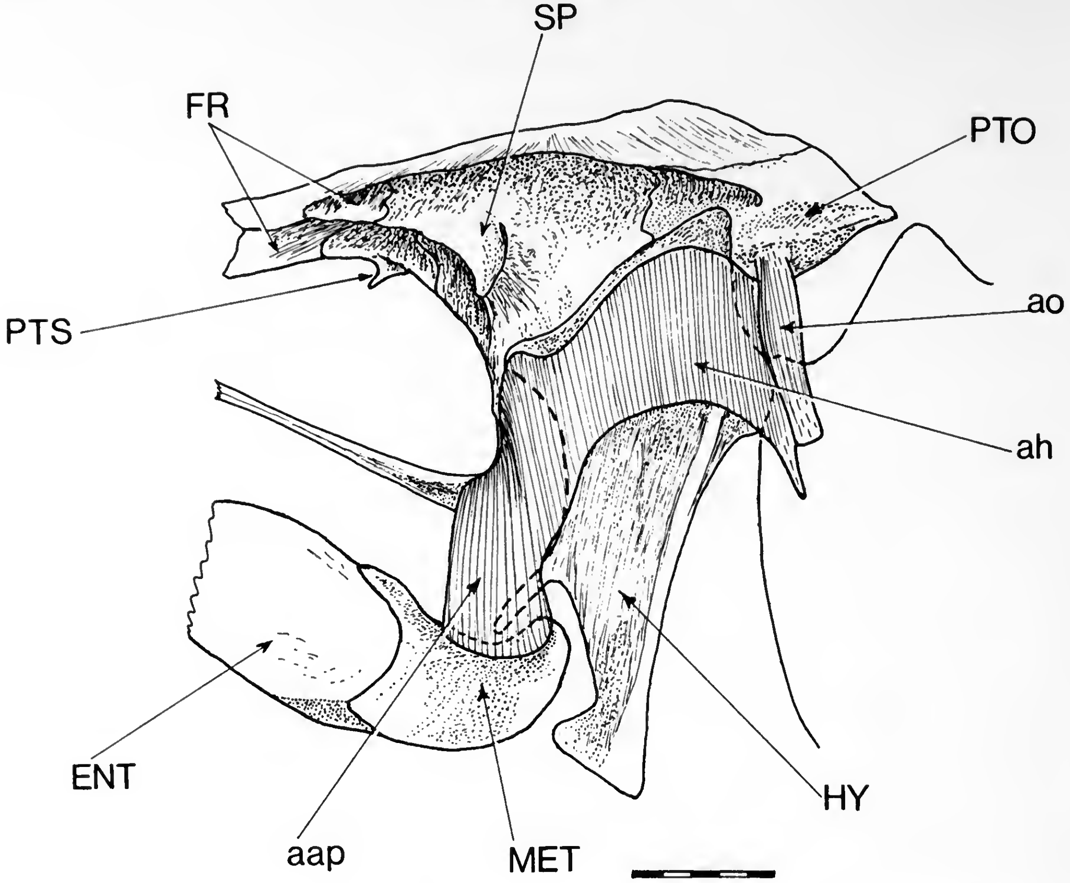

Fig. 3 *Chanos chanos.* Lateral view of suspensorial musculature. Dashed lines indicate *overlying* bony elements.

Muscles attaching to the jaws (Figs 1–3). The *adductor mandibulae* is a thin, elongate muscle with a markedly concave, tendinous orbital border; its origin is from the skin covering the cheek, the face of the preoperculum, the posterior border of the hyomandibular and the posterior extension of the quadrate. Posterodorsally the muscle is divided, the inner element, A_2, inserting *via* a long and deep tendon on to the coronomeckelian bone in the lower jaw. A slip of fibres branches dorsally from A_2 tendon to become continuous with the fibres of the intramandibularis division of the muscle (A_w).

The outer element, A_1, has a double insertion, the outer fibres terminating *via* a deep tendon on the connective tissue fascia of the medial face of the maxilla, at its midpoint; another tendon branches off from the dorsal face of the muscle to join an aponeurosis from which extends A_w. Prior to its branching this tendon is tightly bound to the quadrate by connective tissue.

The *protractor hyoideus* (Fig. 2) is a thick, wide element running from the dorso-, ventral- and anterohyals of each side. Laterally, a narrow bundle of fibres detaches from the main element and has a separate, tendinous attachment to the anterohyal. Anteriorly, at the midpoint of the lower jaw, the *protractor* divides, each segment inserting on its respective dentary at the point of that bone's greatest curvature. A thin, wide *intermandibularis* muscle joins the mandibles, having its points of attachment above and below those of the arms of the *protractor hyoidei.*

Suspensorial and opercular muscles (Figs 1 & 3). The *levator arcus palatini* is a large pyramidal muscle extending between the sphenotic and lateral face of the hyomandibula. The *adductor* *arcus palatini* is a large, bolster-like element confined to the posterior portion of the parasphenoid and its ascending process. Insertion is on the metapterygoid. There is a distinct division between the *adductor arcus palatini* and the *adductor hyomandibularis,* the latter muscle extending from the upper part of the prootic to the dorsal, medial face of the hyomandibula. Posteriorly, the *adductor hyomandibularis* inserts on the operculum together with fibres of the *levator operculi.* The *dilatator operculi* occupies a deep cranial fossa comprising the frontal, sphenotic and pterotic bones, the sphenotic being the major contributor. The fossa is roofed by the frontal, although the sphenotic process and its associated part of the dilatator muscle project laterally from beneath the frontal roof.

There are two sections of the *levator operculi,* one stemming from the pterotic border, the other from the slightly recessed ventral surface of the pterotic. Both sections insert together over a triangular area of the medial face of the operculum. The *adductor operculi* originates anteriorly and somewhat medially to the *levator* and has its insertion anteroventral to that muscle.

Comments

Chanos has a double insertion of muscle A_1, to the upper and lower jaws. In *Albula,* a muscle identified as A_1b by Greenwood (1977:71) inserts both on the maxilla and joins the aponeurosis of A_w. However, as discussed above (p. 275) this element would not seem to be homologous with A_1 in *Chanos* since it lies medial to the mandibularis ramus of nerve V.

Other anatomical features. Features of the ethmoid region of *Chanos* were commented upon and figured by Fink & Fink (1981). My observations on double-stained specimens agree for the most part with their figures. I would disagree, however, with their interpretation of the cartilaginous body lying between the palatine and ethmoid. According to Fink & Fink (1981) this is an ethmopalatine cartilage. In none of the specimens I have examined does this nodule contact, or closely approach the ethmoid cartilage (cms Fig. 4) and, indeed in Fink & Fink's figure (1981, fig. 3A), there is no contact between these elements. Furthermore, whereas Fink & Fink show the element with convex faces I find that in all the specimens to hand, it is a thin disc with markedly concave faces (Fig. 4). In fact, the element has the appearance of a simple meniscus between the cartilaginous medial process of the maxilla and the palatine cartilage.

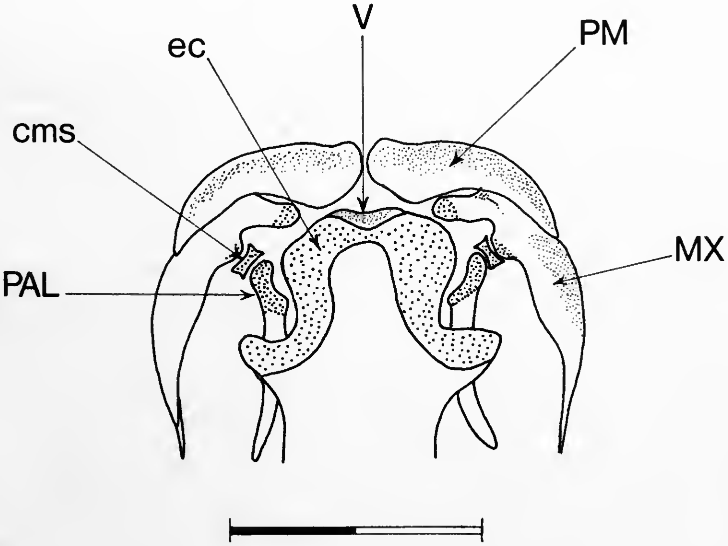

Fig. 4 *Chanos chanos.* Dorsal view of ethmoid region of a specimen 45 mm SL.

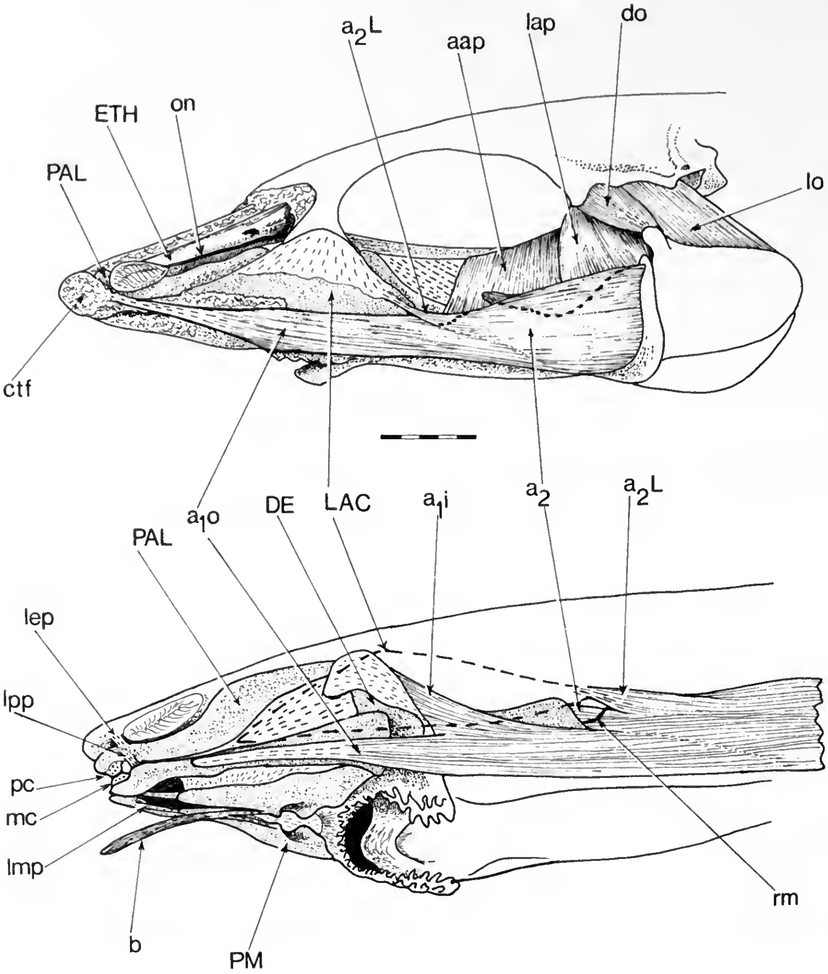

Fig. 5 *Gonorynchus gonorynchus*. Upper: lateral view of cranial muscles. Heavy dashed lines indicates medial path of mandibularis nerve. Lower: ventro-lateral view of jaw musculature lachrymal bone is indicated by dashed outline.

GONORYNCHUS Scopoli, 1777

According to Fowler (1936) and Nelson (1984:122) there is probably only a single species *G. gonorynchus* (Linn., 1766) having an Indo-Pacific and southern Atlantic continental shelf distribution. However, Ferraris (pers. comm.) has evidence to suggest that there are seven species.

SPECIMENS EXAMINED: *Gonorynchus gonorynchus* Uncat. 203 & 290 mm SL; 1914.2.18:25 (alizarin prep.); *G. greyi* 1875.11.12:27; 1885.3.3:16 (both dry skulls), 1914.8.20.34 (204 mm SL).

Muscles attaching to the jaws (Figs 5–7). Superficially there appears to be a single, elongate muscle originating from the preoperculum; about halfway along a medial portion separates from the main bundle to insert, principally, on the lower jaw. Its points of insertion, and the position of the mandibularis nerve, which is interlaced within its fibres, suggest that the element is A_2. The outer part of the muscle continues forward to insert on the upper and lower jaws and is designated as A_1.

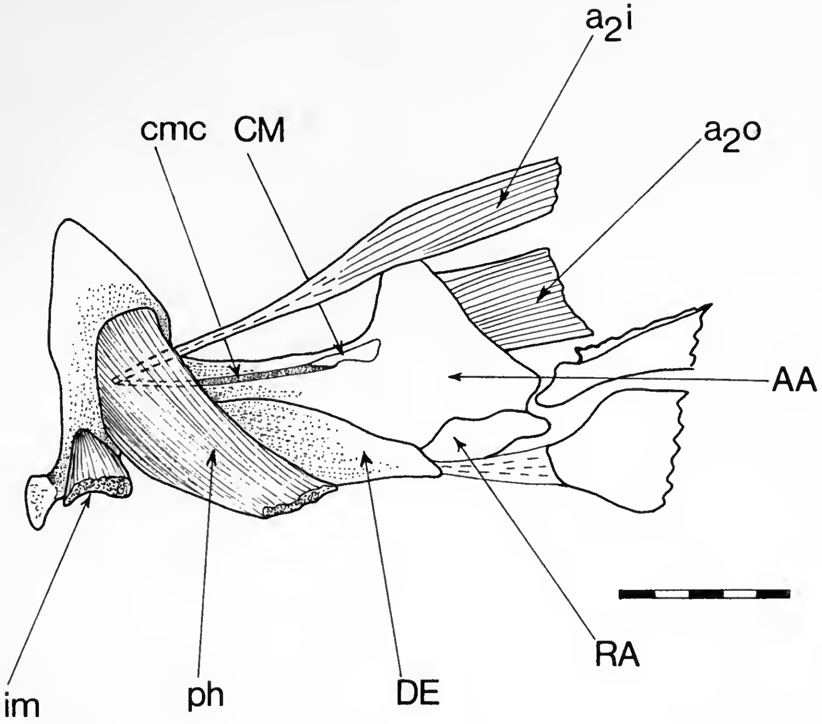

Fig. 6 *Gonorynchus gonorynchus*. Medial view of lower jaw muscle attachments.

Muscle A_1 separates from the main adductor mass at a point posterior to the coronoid process of the dentary; a broad medial bundle of fibres inserts into the thick connective tissue surrounding the coronoid process (a_1o, Fig. 5), whilst the outer, elongate segment runs forward to insert via a narrow tendon about half-way along the maxilla (a_1i, Fig. 5).

Muscle A_2 has three insertions (Figs 5 & 6); 1, an outer (a_2o), to the rim of the anguloarticular; 2, an inner (a_2i) *via* a long tendon to the anterior tip of the coronomeckelian cartilage; 3, a lateral (a_2L) to the posterior tip of the lachrymal. There is no intramandibularis (A_w) section of the adductor muscle.

The *protractor hyoideus* (Figs 6 & 7) stems from each hyoid bar, the two halves joining at an aponeurosis below the anterohyals and extending forward joined in the midline by connective tissue fascia. Anteriorly, the halves separate, diverge dorsally and insert on their respective dentaries at a point almost level with the rim of the coronoid process (Fig. 6).

Laterally, the *protractor hyoidei* are firmly attached to tendinous connective tissue that extends upward to line the inner side of the suspensoria. A large *intermandibularis* muscle connects the two dentaries and lies anteroventral to the insertion of the *protractor hyoidei.*

Suspensorial and opercular muscles (Figs 5 & 8). The *adductor arcus palatini* is a well-developed muscle originating from the prootic and the posterior part of the parasphenoid, its ventral insertion is on the quadrate and the dorsal margin of the preoperculum. A medial bundle of fibres inserts on the rod-like metapterygoid. Where the *adductor* joins the preoperculum, a long segment of fibres separates off from the body of the muscle to attach to the sclerotic covering of the eyeball. Ventro-posteriorly, the fibres of the *adductor* intergrade with those of the *levator arcus palatini.* A posterior portion of the *adductor* stems from the pterotic and inserts on the medial face of the hyomandibula; this segment is considered to be the *adductor hyomandibularis.*

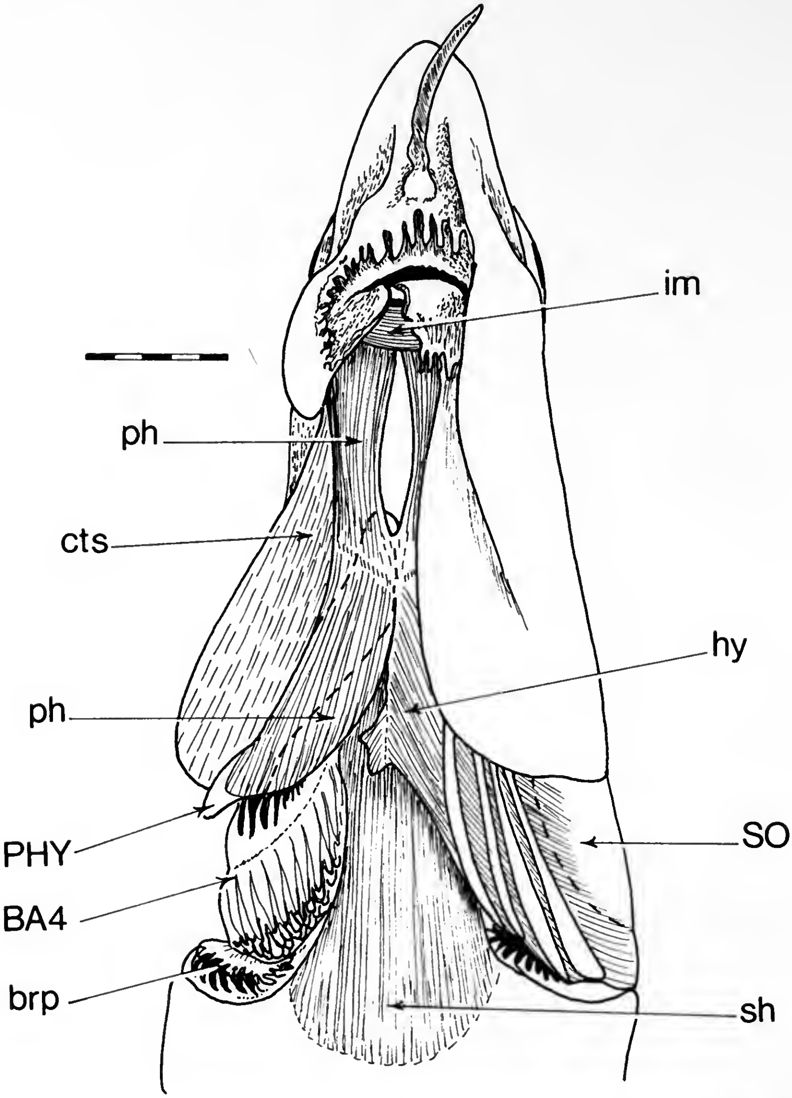

Fig. 7 *Gonorynchus gonorynchus*. Ventral head musculature. Outlines of hyoid and opercular elements indicated by dashed lines. The *protractor hyoidei* have been pulled apart in the midline.

The *levator arcus palatini* extends from the sphenotic process to insert on the lower half of the hyomandibula and the upright limb of the preoperculum. At its origin, the fibres are continuous with those of the *dilatator operculi*.

The dilatator operculi originates partly from the posterior rim of the sphenotic process and partly from a shallow sphenotic-pterotic fossa. Insertion is on the long anterior process of the operculum. The *levator operculi* has two origins, an outer one from the deeply concave posterior face of the hyomandibula and an inner one from that area of the pterotic medial to the hyomandibular fossa. At this site, the fibres of the *levator operculi* are contiguous with those of the *adductor hyomandibularis*. The *levator* inserts along the upper medial face of the operculum. The *adductor operculi* is a cone-shaped muscle originating posterior to the hyomandibular fossa, and inserting on the postero-medial area of the operculum.

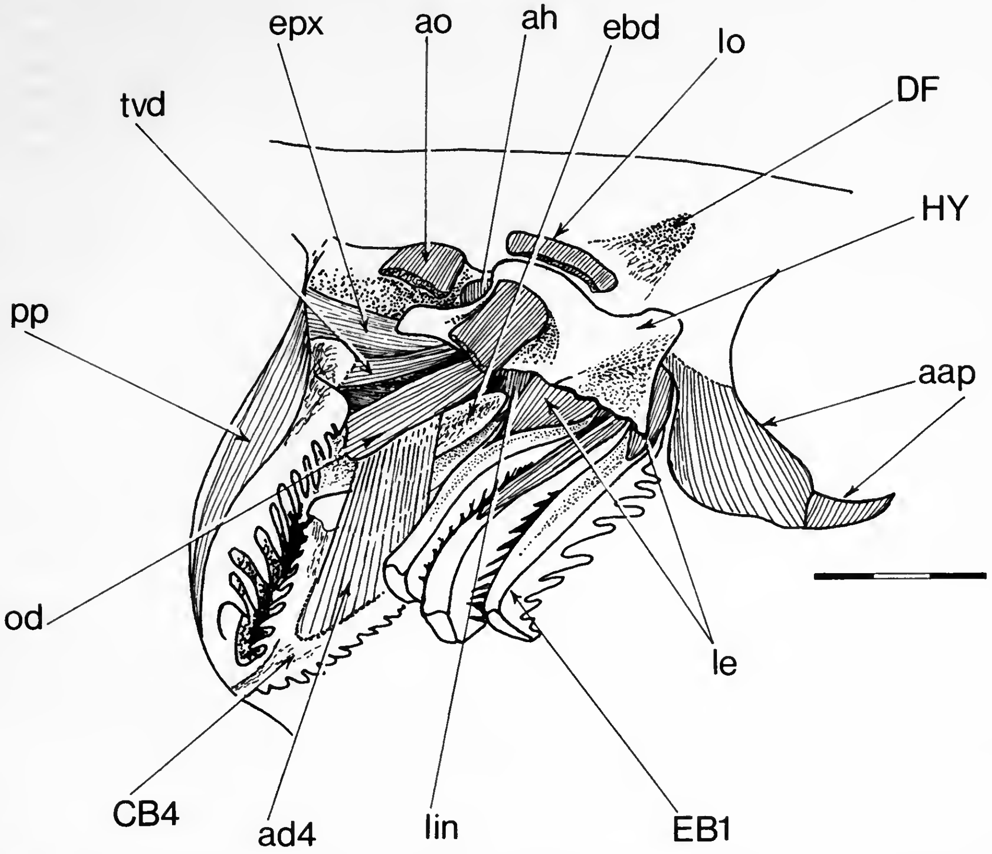

Fig. 8 *Gonorynchus gonorynchus.* Suspensorial, opercular and branchial arch musculature. The opercular muscles and hyomandibula have been cut through to expose the upper gill-arch muscles. The small ventral segment of the aap inserts on the eyeball covering.

Comments

Le Danois (1963; 1966) described the jaw and hyoid musculature of *Gonorynchus*. However, her descriptions and those presented above have few points in common. It would be unproductive to detail every difference between my interpretation and that of Le Danois of *Gonorynchus* musculature; the following examples are the most disparate.

Le Danois (1966) recognises three distinct divisions of the adductor musculature, labelled as 'muscle preorbitaire externe', 'A_1' and 'muscle quadrato-mandibulare interne'. These correspond respectively to my A_1 outer, A_1 inner and A_2 divisions. Several muscles she illustrates such as 'muscle labial sous cutane', 'muscles labio-rostraux' and 'labio-premaxillaire' simply do not exist in any specimens I have examined and I can only conclude that Le Danois has mistaken the thick, fibrous connective tissue occurring in those areas as muscle fibres.

Compared with other ostariophysans the jaw and suspensorial muscles of *Gonorynchus* display certain derived features. As in *Chanos*, muscle A_1 has a double insertion with part of the muscle inserting on the lower jaw (? a plesiomorphy). Muscle A_2 has a tripartite insertion, with an outer segment inserting on to the lachrymal. The insertion of the *protractor hyoideus* high on the dentary coronoid process is an autapomorphic feature. The quadrate and preopercular attachments of the *adductor arcus palatini* are possibly unique amongst ostariophysans. Absence of A_w is a feature shared with other gonorynchoids.

Other anatomical features. *Jaw bones and their ligaments:* The premaxillae are long triangular bones lying almost horizontally (Fig. 5). In shape and alignment they are strongly reminiscent of the premaxillae of some notacanthids (see Greenwood, 1977). Each premaxilla is attached to its respective maxilla by a ligament extending from its anterior tip. A ligament attaches the tip of the maxilla to the palatine. The maxillary tip also articulates with a ventral cartilaginous process of the palatine *via* a cartilaginous meniscus (as in *Chanos*). The single, symphysial barbel is connected to each premaxilla by a bifurcated ligament.

Nasal sac: Derscheid (1924:160) described the nasal sac in *Gonorynchus,* but due to paucity of material was unable to delimit '. . . the shape, the extent and the relationships' of the caudal extremity of the sac. According to Gosline (1961:28), the nasal sac extends '. . . back in the flesh external to the large lacrimal'. This is an error; the area above the lachrymal is covered with dense fatty tissue and no portion of the sac intrudes there. Monod (1963) although in disagreement with Gosline (1961) regarding the lateral position of the sac, was none the less of the opinion that the terminal caecum of the sac extended well posteriorly and may even be linked to a 'muscle particulier'. In fact, the nasal sac, whilst relatively large, has no peculiar feature. It lies above the palatine and is bordered ventro-posteriorly by the lachrymal and dorsally by the nasal bone. The thick olfactory nerve courses inward, alongside the borders of the vomer and parasphenoid, passing through a frontal foramen, lying above the lateral ethmoid, and thence into the cranial cavity (Fig. 9). Thus, the notable feature concerning the gonorynchid nasal organ is the frontal foramen through which the olfactory nerve passes, and which must be regarded as an autapomorphy for the genus.

Ethmo-vomerine region (Fig. 10): Some comments seem appropriate on the peculiar nature of the ethmoid and vomer which appears to have escaped the attention of previous authors. The dorsal surface of the ethmoid (? rostrodermethmoid) is seen as somewhat spatulate with a semicircular anterior border. Underlying it is a tube-like central portion (mesethmoid) the opening of which is exposed anterior to the ethmoid border. The anterior, lamellate border of the mesethmoid has a medial notch. The elongate vomer terminates anteriorly beneath the tubular portion of the mesethmoid.

Infraorbital bones (Fig. 10): The anterior circumorbital bone was identified by Woodward (1896:503) and Ridewood (1905:364) as a preorbital and by Gosline (1961:28) as a lachrymal. Monod (1963:258) discussed the identification of the bone and concluded that it was '. . . en fait, quadripartite', illustrating it as an antorbital overlying a series of three infraorbitals.

In alizarin stained preparations it is clear that there are a total of five infraorbitals, *contra* Ridewood (1905) who claimed infraorbitals were lacking. The 1st infraorbital (lachrymal) is a large, triangular, lamellate bone with a narrow canal along its ventral border containing two or three ventrally facing pores. The bony canal is preceded by a short epidermal canal opening terminally at the tip of the snout (Fig. 10). The posterior portion of the lachrymal canal overlies the anterior part of the 2nd infraorbital, which, like the remainder of the infraorbitals, is reduced to the bony sensory canal; the third is sometimes fragmented (Fig. 10).

Gill arches (Fig. 9): Monod (1963, fig. 40) shows the 4th epibranchial comprised of two portions, a cartilaginous element separated by a space from the epibranchial proper. I find no such separation, the 4th epibranchial having a noticeable cartilaginous process apposing the tip of the bow-like 5th epibranchial.

The 4th gill-arch is served by a particularly well-developed *adductores* muscle (ad4, Fig. 8) which attaches to a fascia extending from the *obliquus dorsalis* (elevateurs internes 5 of Le Danois, 1966:313, fig. 18).

Le Danois (1966:313, fig. 25) erroneously refers to, and illustrates the median part of the epaxialis muscle as a *retractor dorsalis.* Her justification for so naming the muscle is its attachment to the pharyngeal tooth plate. Pharyngeal tooth plates are absent in *Gonorynchus,* and the extension of the muscle to what appears to be a 'metapterygoid' tooth patch in her figure is non-existent.

Other derived features such as the lateral and median buccal cavity processes and pectoral and pelvic fin appendages do not occur in other gonorynchiforms and are considered as autapomorphies for *Gonorynchus* (see Le Danois, 1966 and Monod, 1963 for descriptions).

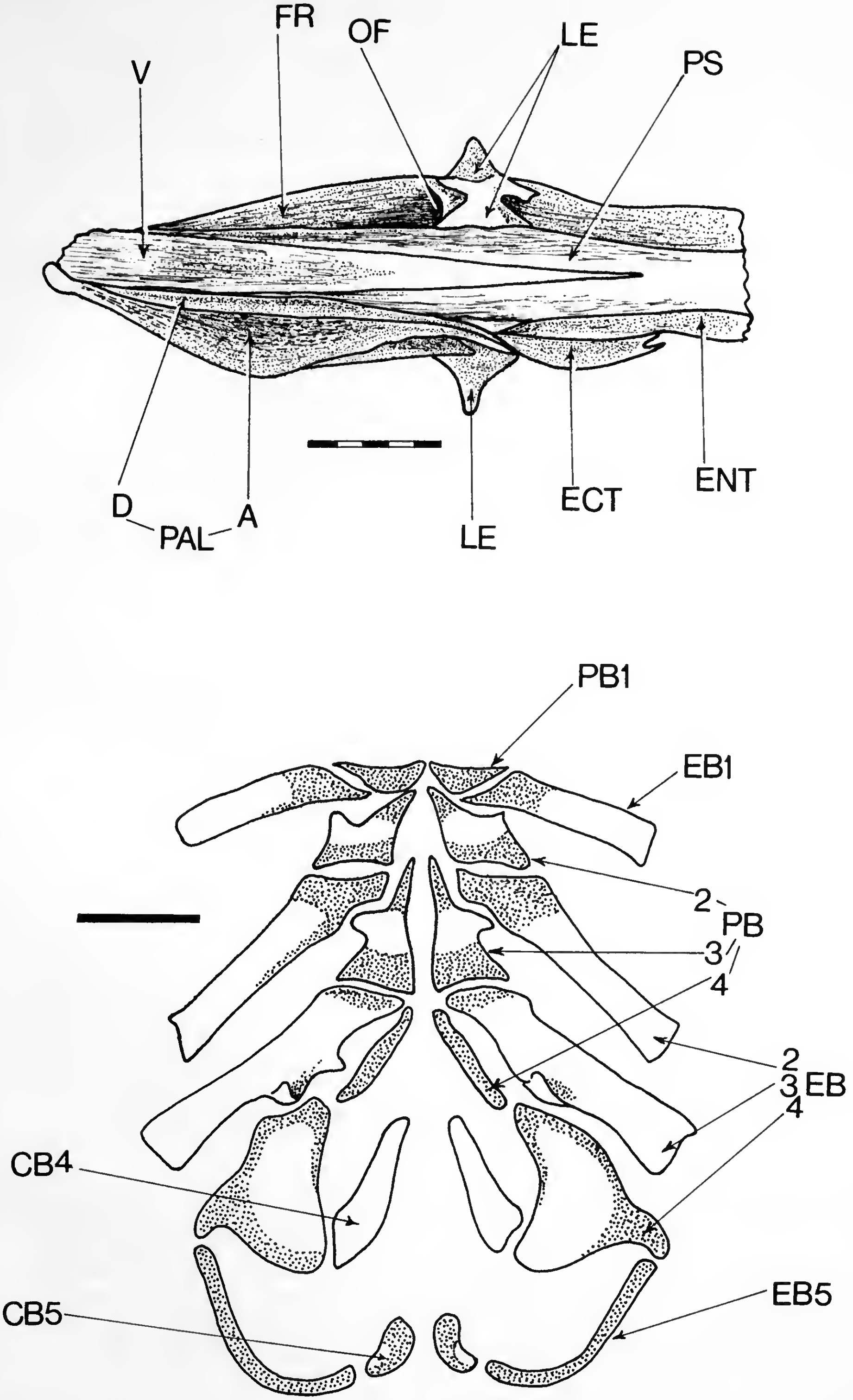

Fig. 9 *Gonorynchus gonorynchus*. Above: ventral view of anterior region of neurocranium and suspensorium. Below: dorsal view of branchial arch elements. Of the lower elements, only ceratobranchials 4 and 5 are shown.

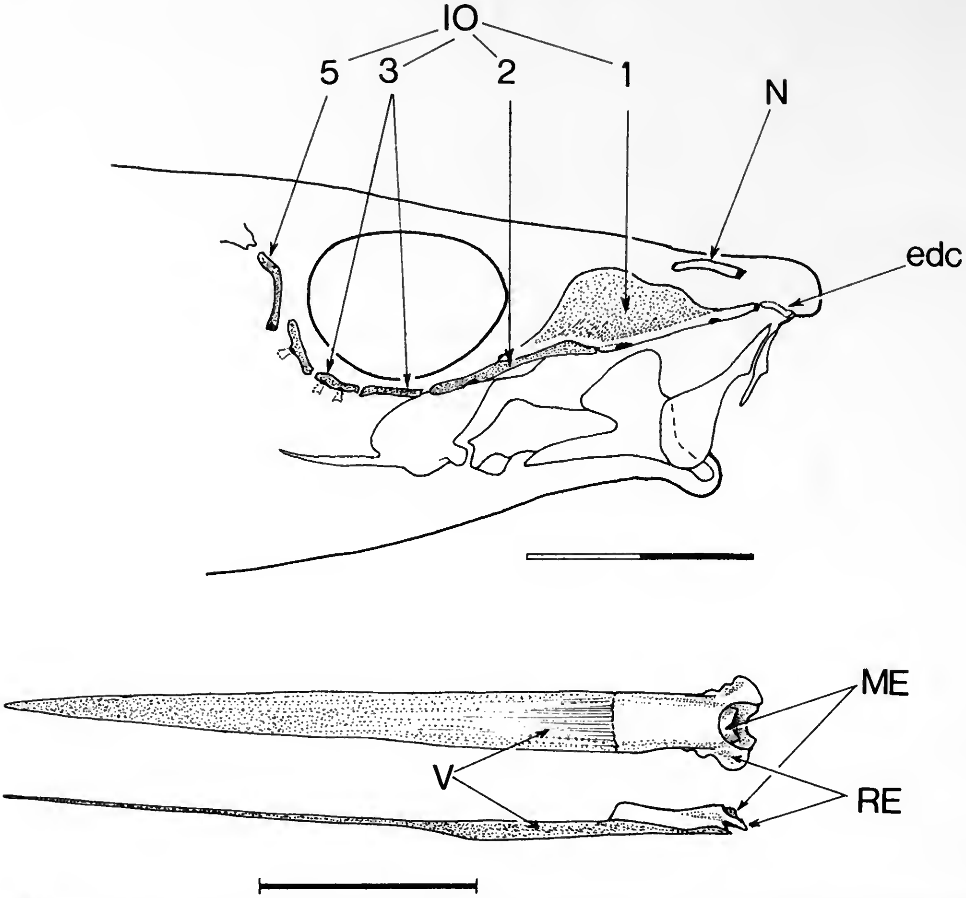

Fig. 10 *Gonorynchus gonorynchus*. Above: lateral view of head showing infraorbital bones and jaw elements. Below: dorsal and lateral views of ethmo-vomerine elements.

KNERIA Steindachner, 1866

PARAKNERIA Poll, 1965

These two genera are considered together since their myology is virtually identical (see remarks on p. 299 concerning generic status). There are *ca* 24 species in both genera combined, distributed in east, west and central Africa (see Poll, 1965 and Roberts, 1975 for detailed distributions).

SPECIMENS EXAMINED: *Kneria auriculata* BMNH 1967.5.2:1–4;8–15; *K. katangae* 1976.10.20:116–137; *K. wittei* 1976.10.20:142–160; 1953.1.26:1–6 (alizarin preps); uncatalogued (alcian-alizarin prep.); *Parakneria tanzaniae* 1976.10.21:163–172 (including alizarin specimen).

Muscles attaching to the jaws (Figs 11–12). The *adductor mandibulae* comprises three distinct elements; 1, an outer cone-shaped muscle (a_1o, Fig. 11) originating from the horizontal limb of the preoperculum and inserting on the medial face of the broadly expanded maxilla (the maxilla lies in an almost transverse plane and so its medial face is positioned posteriorly); 2, a short, stout muscle (a_1i, Fig. 11) originating from the leading edge of the quadrate and extending dorsolaterally at an angle of 45° to insert on the inner face of the maxilla, medial to A_1o; 3, an inner muscle (a_2, Fig. 11) originating from the preoperculum and running virtually horizontally with insertion *via* a long tendon on to the coronomeckelian bone. There is no intramandibularis section (A_w) of the adductor.

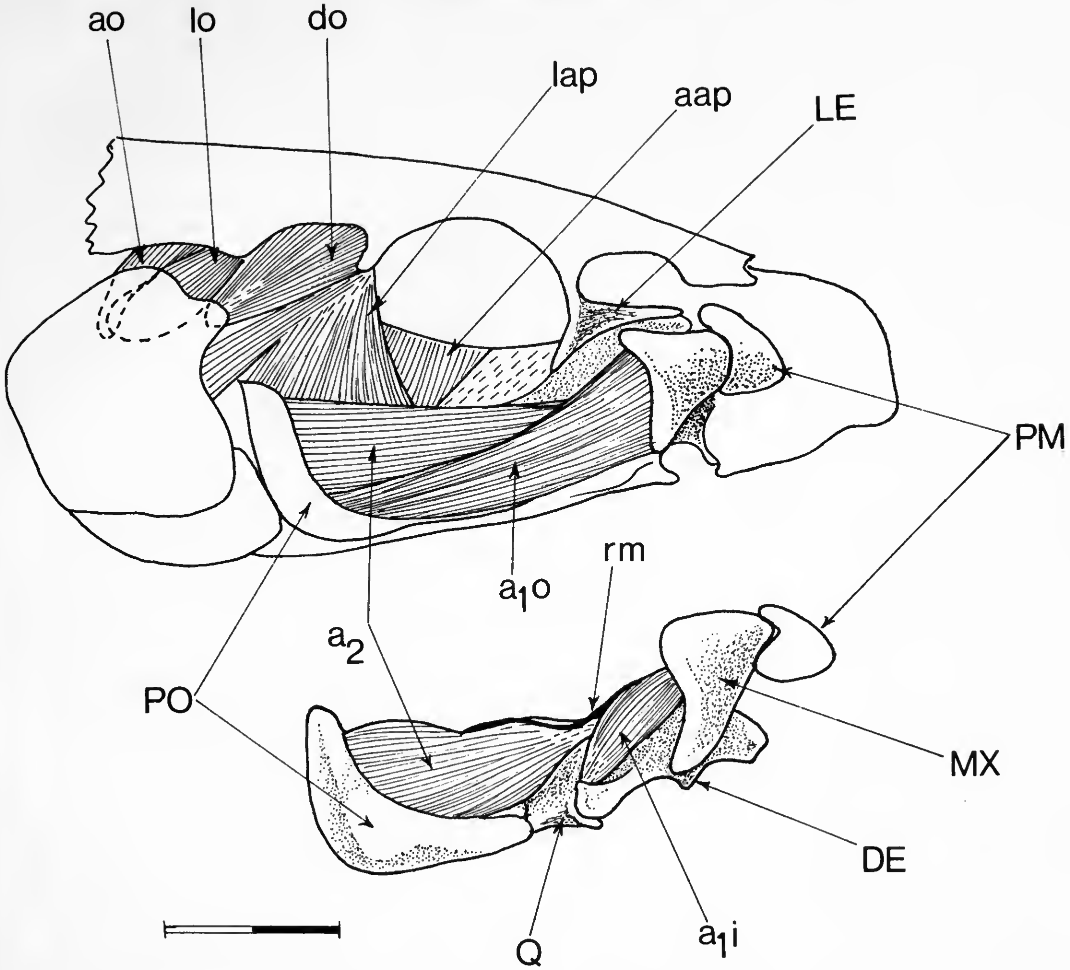

Fig. 11 *Parakneria tanzaniae*. Above: lateral view of cranial muscles. Below: lateral view of inner jaw muscles.

Each portion of the *protractor hyoideus* (Fig. 12) extends from its respective hyoid bar to meet its antimere in the midline prior to separating, diverging and inserting on to the ventral process of the dentary (P3, Fig. 13). the *intermandibularis* connects the anterior portions of the divergent dentaries and passes above the protractor hyoideus.

Suspensorial and opercular muscles. The *adductor arcus palatini* runs from the posterior part of the parasphenoid and inserts along the entire medial face of the hyomandibula. The *levator arcus palatini* originates from the sphenotic process and inserts on the borders of the hyomandibula and operculum.

The *dilatator operculi* extends from a rudimentary sphenotic fossa to the dilatator process of the operculum. The *levator* and *adductor operculares* originate respectively from the pterotic fossa, their overlapping insertions being on the upper medial face of the operculum.

Comments

The jaw muscles of *Kneria* and *Parakneria* display a derived state in that the inner element of A_1 has its origin from the quadrate border and runs obliquely lateral. Such a feature has not been

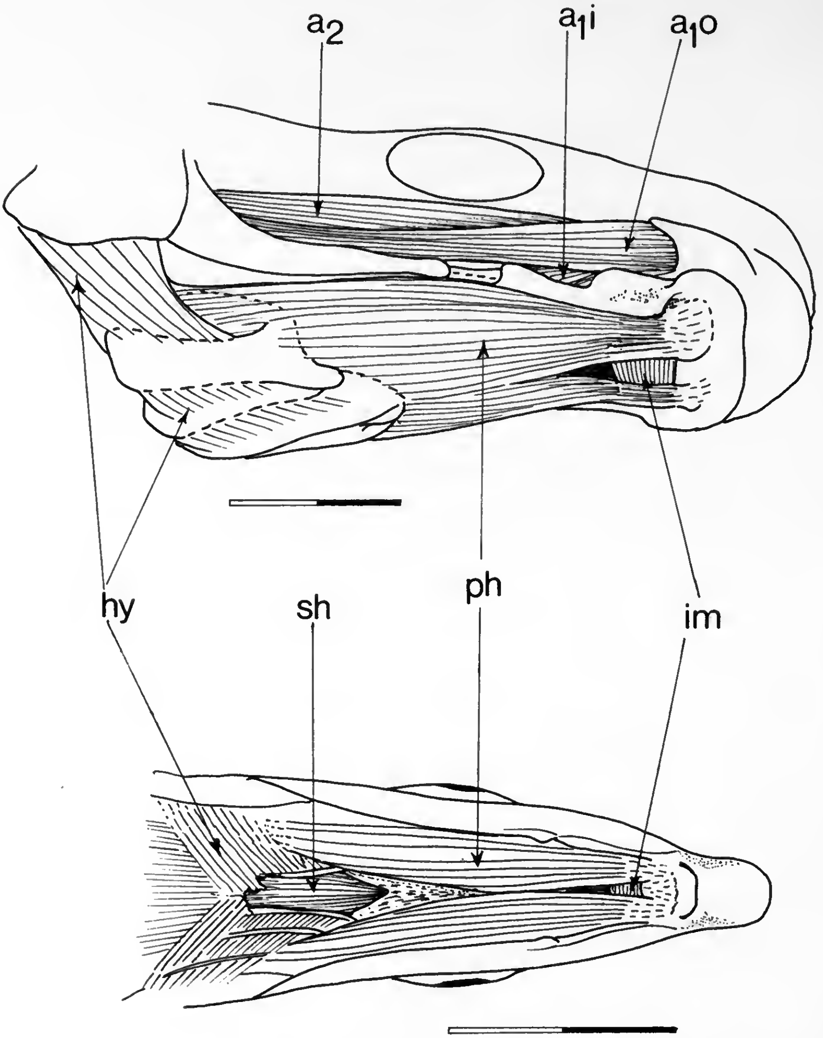

Fig. 12 Ventral head of muscles of: above, *Parakneria tanzaniae*; below, *Cromeria nilotica*.

reported in other ostariophysans and appears similarly only in *Cromeria* (see below) and in a more derived form in *Phractolaemus* (see below).

Other anatomical features: *Lower jaw* (Fig. 13). The lower jaw is complex and was not adequately described in Lenglet's (1974) treatment of kneriid osteology. In both *Kneria* and *Parakneria* the dentary curves laterally at almost a right angle; its lateral flange is notched medially and produced into a process (P3) on to which the *protractor hyoideus* inserts.

Because of the outward curvature of the dentary, the coronoid process has a posteriorly concave face which bears two processes, one lateral (P1) and one medial (P4). These processes provide insertion points for, respectively, muscles A_1o and A_1i. A broad shelf-like process (P2) extends posteriorly and this cups the anterior tip of muscle A_1o. The coronomeckelian protrudes above the dorsal margin of the dentary (see also Lenglet, 1974, figs 12 & 13) and provides the point of insertion for muscle A_2. *Ethmo-vomerine region* (Fig. 14). The vomer in *Kneria* and *Parakneria* extends beyond the ethmoid bloc and its head is inclined ventrad at a sharp angle.

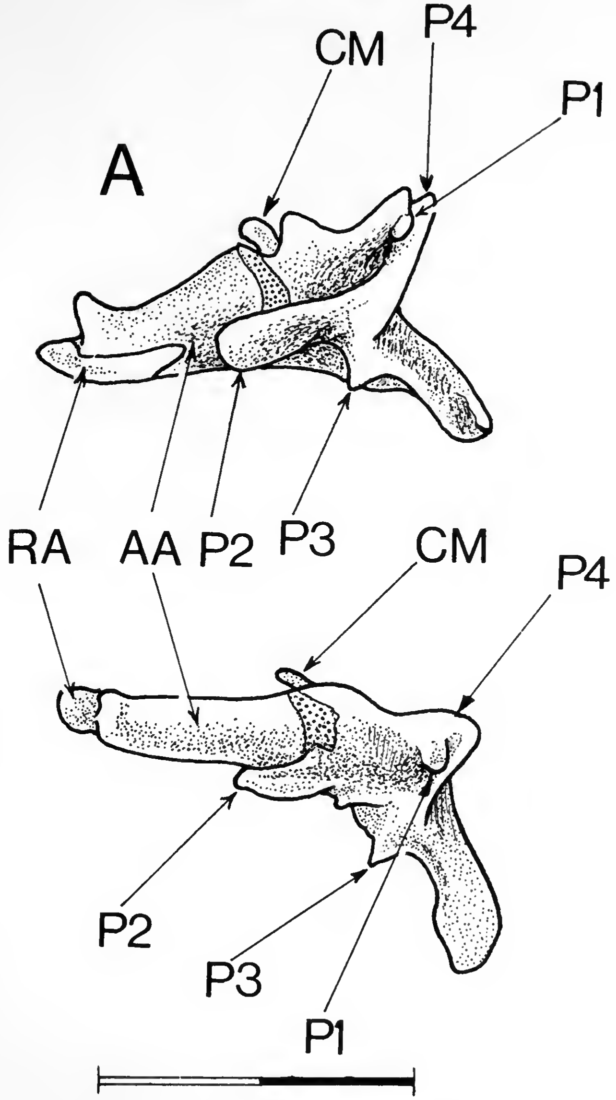

Fig. 13 *Kneria wittei.* Lower jaw in lateral (above) and dorsal (below) views.

The vomer is joined synchondrally to the overlying mesethmoid which bears a short rostral process and spatulate wings. The lateral ethmoid curves forward sharply and extends anteriorly (Fig. 11) and is covered laterally by the antorbital. *Pterosphenoids* (Fig. 14). Lenglet (1974) stated that pterosphenoids are absent in kneriids. They are, however, present, and like those of other gonorynchiforms are small and widely separated.

CROMERIA Boulenger, 1901

A monotypic genus represented by *C. niloticus* Blgr, 1901 from the Nile, Niger, Volta and Tchad basin.

SPECIMENS EXAMINED: BMNH 1969.11.14:124–135 (including 4 alcian-alizarin preparations).

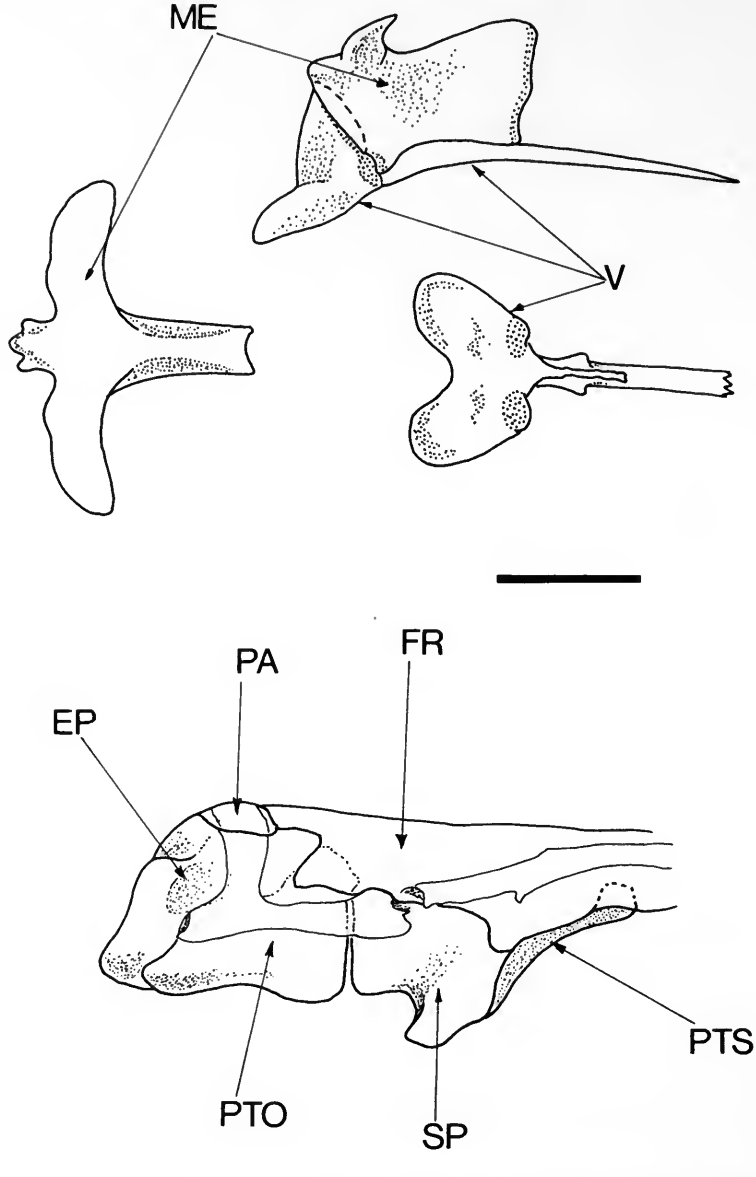

Fig. 14 *Parakneria tanzaniae*. Above: ethmo-vomerine region in lateral view; dorsal views of mesethmoid (left) and vomer (right). Below: lateral view of the upper bones of the cranial wall. Scale = 0·5 mm.

Muscles attaching to the jaws (Figs 16 & 12). The *adductor mandibulae* comprises 1, an elongate, horizontal muscle, A_1o which originates from the preoperculum and quadrate and inserts *via* a broad tendon on to the maxilla and the connective tissue covering the upper jaw bones; 2, a medial muscle, A_1i that originates from the leading edge of the quadrate, runs somewhat laterally, and inserts on the rim of the maxilla; and 3, muscle A_2 which originates from the preoperculum. Below the centre of the orbit A_2 becomes aponeurotically constricted and linked to the quadrate by a tendinous band which runs mesad from the aponeurosis. From the point of

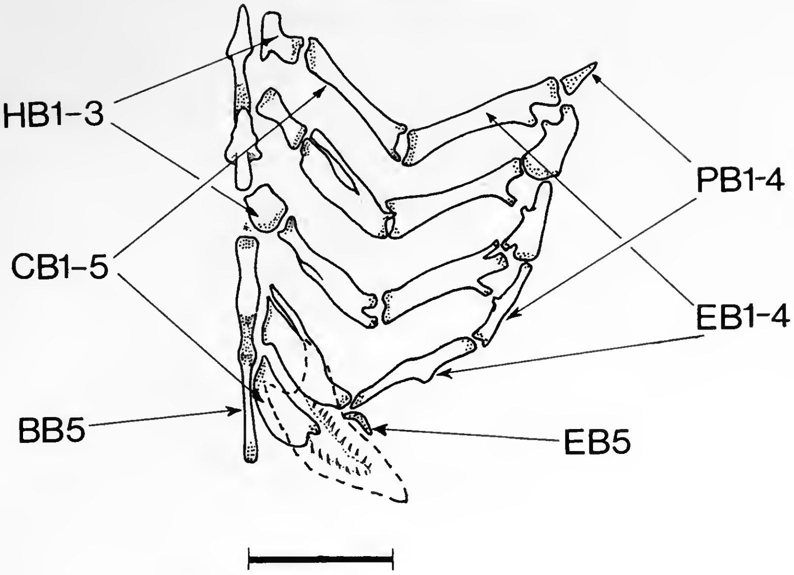

Fig. 15 *Kneria wittei.* Branchial arch elements (right side). Dashed lines indicate extent of epibranchial diverticulum; gill-rakers are also indicated.

its constriction to its insertion, the muscle is represented by a tendinous sheet which fans out to form tripartite attachments with the palatine, the coronomeckelian (see d'Aubenton, 1961:148), and the connective tissue covering the medial face of the maxilla. There is no intramandibularis (A_w) section of the *adductor mandibulae.*

Each part of the *protractor hyoideus* extends from its respective hyoid bar to meet its antimere in the plane of the lower jaw articulation (Fig. 12). Anteriorly, the halves of the muscle diverge to insert into a tendinous sheet extending along the length of the lower jaw. The *intermandibularis* runs dorsad to the *protractor hyoideus,* attaching beneath a medial flange on each dentary.

Suspensorial and opercular muscles (Fig. 16). The *levator arcus palatini* originates from the sphenotic and inserts across the lower, anteriorly extended, portion of the hyomandibula. The *dilatator operculi* is barely discernible from the *levator arcus palatini* as a separate muscle since their fibres are contiguous at their sphenotic origin. Insertion in on the dilatator process of the operculum. The posterior suspensorial muscle appears to be an *adductor hyomandibularis* since it originates from the prootic and pterotic. The anterior fibres run on to the fascia of the suspensorium, whilst the posterior, and majority, of its fibres insert on the dorso-medial face of the hyomandiubla. The *levator operculi* is an extensive muscle, stemming from the pterotic and inserting along the medial edge of the long opercular border. The tubular *adductor operculi* also originates from the pterotic and inserts on to the medial face of the operculum below that of the *levator.*

Comments

The configuration of the jaw muscles most closely resembles that of *Kneria* and *Parakneria,* both in the almost horizontal arrangement of muscle A_1 and in the presence of a medial muscle A_1i having its origin from the quadrate border. The *levator operculi* is more extensive than in *Kneria* and *Parakneria* and indeed, most closely resembles that of *Gonorynchus,* except that in the latter genus the *levator operculi* also has its origin from the hyomandibula.

In *Cromeria* the opercular margin is sealed to the body wall leaving only a small ventral opening above the pectoral fin base. The posterior opercular borders of *Kneria, Parakneria* and

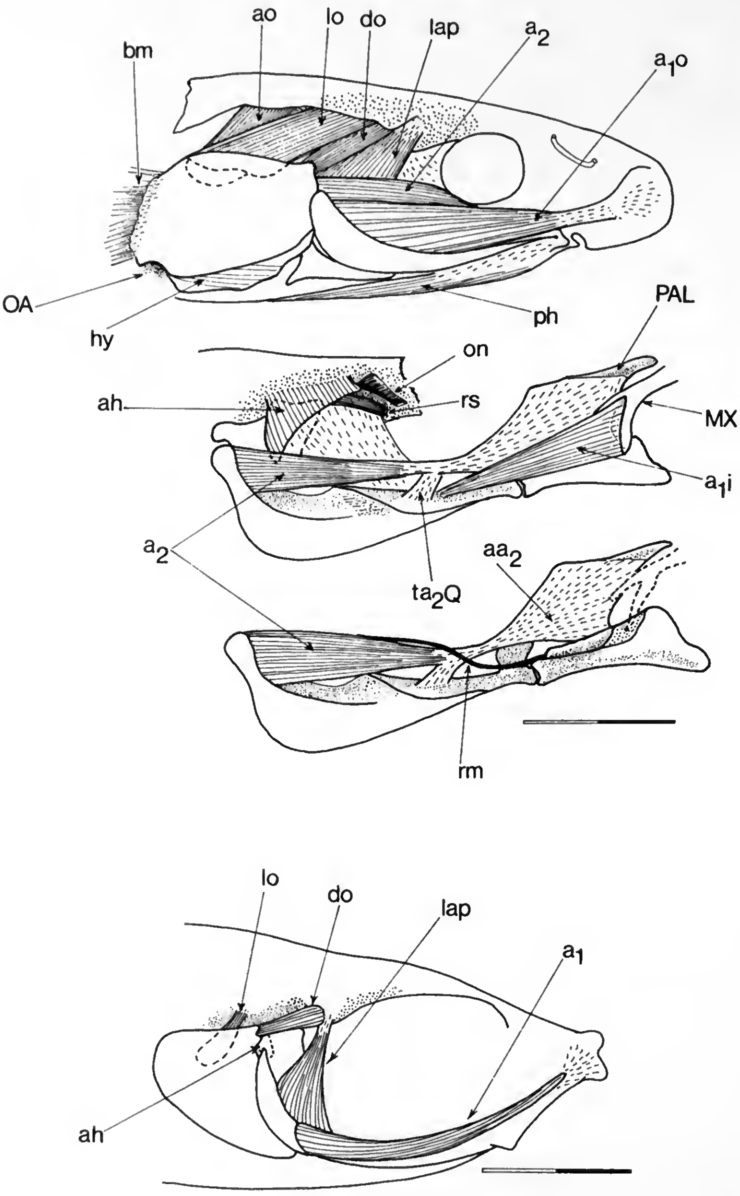

Fig. 16 *Cromeria nilotica* (above), three lateral views showing cranial and superficial jaw muscles; inner jaw and suspensorial muscles (dashed line indicates *overlying* hyomandibula) and innermost jaw muscle and its tendinous connections.

Grasseichthys gabonensis (below), lateral view of cranial muscles. The *adductor hyomandibularis* is shown in outline by a closely-dashed line.

Grasseichthys (see below) are partially sealed, that of *Grasseichthys* having a condition midway between *Cromeria* and the kneriid genera. In *Phractolaemus* only the dorsal border of the operculum is sealed to the body wall.

Other anatomical features: *Ethmoid region* (Figs 17A & B). The osteology of *Cromeria* has been adequately dealt with by Swinnerton (1903) and d'Aubenton (1961). It is clear from these works

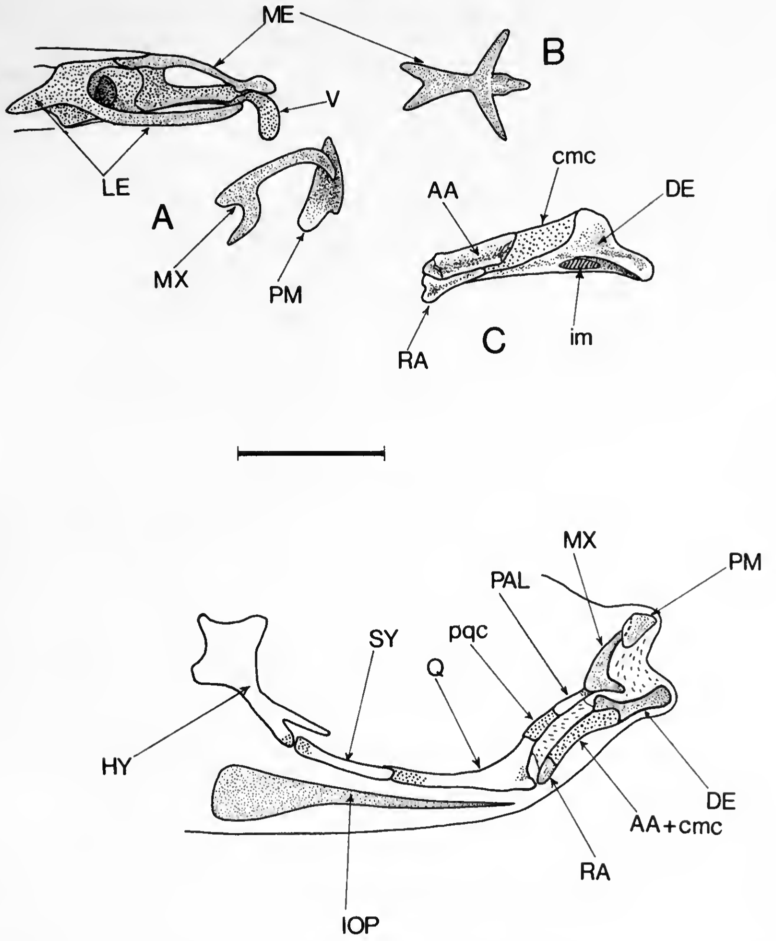

Fig. 17 Above: A, *Cromeria nilotica,* lateral view of ethmoid region and medial view of upper jaw; B, dorsal view of mesethmoid; C, medial view of lower jaw. Below: *Grasseichthys gabonensis,* lateral view of jaw and suspensorial bones.

and personal observations that four derived features are shared with *Kneria* and *Parakneria,* namely, the rostral extension and ventral inclination of the vomer, the long mesethmoid lateral wings, and the anterior curvature and anterior extension of the lateral ethmoids. In specimens examined the curvature of the lateral ethmoids is so great that their anterior tips fall in the same transverse plane as that of the mesethmoid lateral wings. (Fig. 17A).

GRASSEICHTHYS Géry, 1964

A monotypic genus represented by *G. gabonensis* Géry, 1964, from the Ivindo basin, Gabon, and the cuvette centrale, Zaire (see Roberts, 1972:134).

Specimens examined: BMNH 1966.10.20:1–10; 1984.9.12:62 (alcian-alizarin preparation).

Muscles attaching to the jaws (Fig. 16). There is a single adductor muscle (?A_1) comprised of a narrow band of fibres, originating laterally from the inner face of the infraorbital series and posteriorly from the lower limb of the preoperculum. Insertion of the muscle is tendinously to the connective tissue investing the rictus of the jaws, with the majority of fibres appearing to insert into the tissue covering the maxilla. There is, apparently, no inner muscle (A_2) or intramandibularis, (A_w) attaching to the lower jaw (but see below with regard to A_2).

The *protractor hyoideus* is thin and narrow, resembling that of *Cromeria*; each segment inserts *via* a narrow tendon on to its respective dentary. The *intermandibularis* is a mere layer of fibres passing between the dentaries above the *protractor hyoideus*.

Suspensorial and opercular muscles. The *levator arcus palatini* is a thin, band-like element originating from the sphenotic. Its fibres run almost vertically to their insertion on the preoperculum. The *dilatator operculi* originates from the postero-ventral portion of the sphenotic, a typical dilatator fossa being absent. The *adductor operculi* is a thin, tubular element inserting mid-dorsally on the medial face of the operculum. I am unable to ascertain the presence of an *adductor arcus palatini* or a *levator operculi* in the material to hand. However, the *levator* is possibly such a thin element that it has been destroyed in removing the connective tissue layer. There is a small *adductor hyomandibularis* running from the prootic to the postero-medial face of the hyomandibula.

Comments

The jaw and suspensorial muscles of *Grasseichthys* are greatly reduced in comparison with those of other gonorynchiforms and indeed, most teleosts. The *adductor mandibulae* is reduced to a mere slip of fibres which would seem to activate, principally, the upper jaw, but whose insertions are not at all definite. Neither is it definite that this muscle represents A_1; it could, conceivably, be homologous with the dorsal branch of A_2 in *Phractolaemus* (see below) which also attaches to the rictal tissue covering the upper jaw. Unfortunately, I am unable to trace the path of the mandibularis V nerve in the specimen available, the course of which would establish the identity of the element.

The lower jaw, which is merely a slender curved rod with a slight coronoid process (Fig. 17), would thus seem to be adducted passively *via* a connective tissue-ligamentous linkage with the lower.

Other anatomical features. The mesethmoid bears a rostral process and long lateral wings and greatly resembles that of *Cromeria*. The lateral ethmoid, however, lacks the anteriorly directed lateral processes present in other kneriids. No ectopterygoid could be detected in the specimen examined. *Grasseichthys* has an elongate, spine-like interoperculum (Fig. 17), a feature shared with *Phractolaemus* (see p. 297).

PHRACTOLAEMUS Boulenger, 1901

A monotypic genus represented by *P. ansorgei* Blgr, 1901. Two subspecies are recognised (see Thys van den Audenaerde, 1961:113, *P. a. ansorgei* Blgr, 1901 from the Niger drainage and *P. a. spinosus* Pellegrin, 1925 from the central Zaire basin.

SPECIMENS EXAMINED: BMNH 1979.3.5:217–219 (104 & 110 mm SL); 1984.9.27:3–12 (130,120, 120 mm SL, 115 mm SL alizarin prep.).

Muscles attaching to the jaws (Figs 18–21). The lateral cheek muscles are readily distinguished as two elongate elements. The ventral muscle (A_1) narrows into a thin tendon as it approaches the jaw articulation; the tendon passes beneath a bridge formed by a short, thick ligament attached from the outer quadrate spine to the lateral face of the quadrate (1q), and across the base of muscle a_1i (see below). Exiting from the bridge, the tendon turns through 90° whereupon it joins a broad aponeurosis from which extend two muscle segments. The ventral segment (a_1o, Figs 16 & 18) is a thin sheet of fibres, a bundle of which inserts on the distal cavity of the maxilla (Fig. 19B), whilst the remainder cover the rictal cartilages that lie ventrally and between the dentaries and insert on the connective tissue extending between the maxilla and the small premaxilla.

The dorsal segment (a_1i, Figs 18 & 19A & B) of the muscle originates ventrally from the quadrate spine, covers the outer face of the lower jaw and inserts on the posterior process of the curved maxilla.

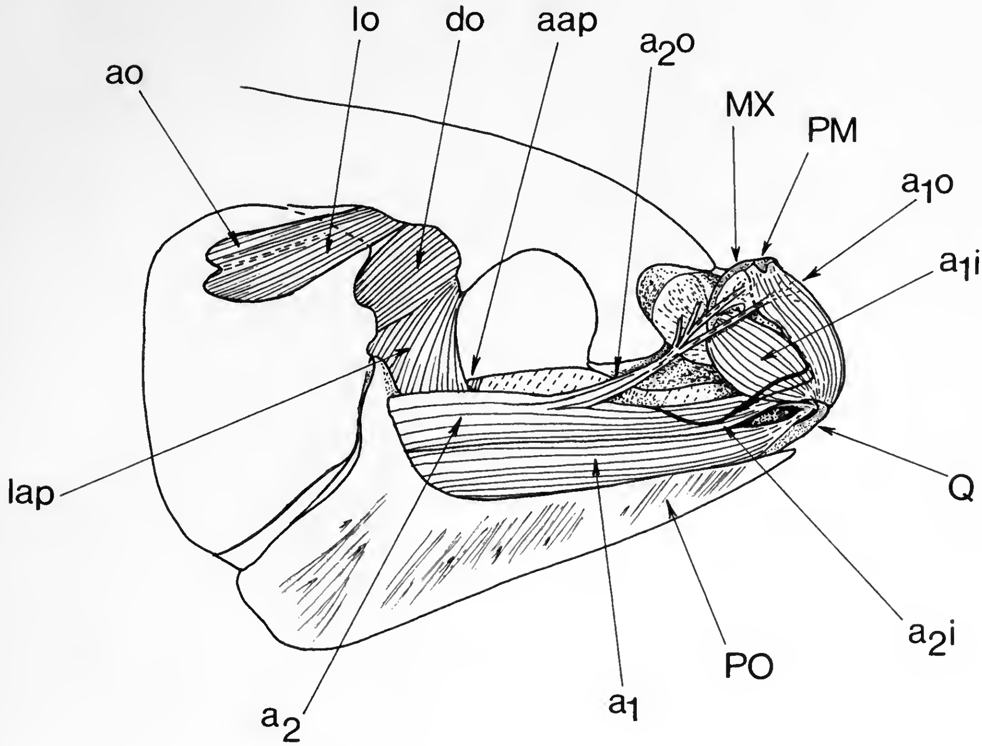

Fig. 18 *Phractolaemus ansorgei.* Lateral view of cranial muscles.

The dorsal adductor muscle (A_2) originates from the preoperculum and hyomandibula. Below the lateral ethmoid a segment of fibres (a_2o, Figs 18 & 19A) branches off from the main body of the muscle and inserts *via* two long, dorsal and ventral, tendons into the connective tissue covering the rictal cartilages. At least three small tendons branch off from the long dorsal tendon and insert on the innner face of the antorbital. The body of A_2 (a_2i, Fig. 19C) continues forward, its insertion tendon divides, the inner inserting on the coronomeckelian bone, and the outer branch making an aponeurotic connection with element A_1i. There is no intramandibularis (A_w) section of the *adductor mandibulae.*

Each part of the *protractor hyoideus* extends forward from the hyoid bar to meet its antimere along a median raphe (Fig. 20). At the jaw articulation each half separates and inclines dorsad to insert *via* its respective tendon on to the anguloarticular. The insertion point of the *protractor* is ventral to the origin of the *intermandibularis,* which, contrary to the known condition in other teleosts, runs between the anguloarticulars rather than the dentaries (Fig. 21).

Suspensorial and opercular muscles. The *levator arcus palatini* originates from the sphenotic and inserts on the broad anterior extension of the hyomandibula. The *adductor arcus palatini* and *adductor hyomandibularis* are contiguous, the anterior part of the muscle (*aap*) originating from the posterior portion of the parasphenoid and the prootic. Insertion is on the dorsal rim of the metapterygoid. The posterior part of the muscle originates from the prootic and pterotic and inserts on the hyomandibular medial face.

The *levator operculi* extends from the junction of the pterotic-prootic with some dorsal fibres stemming from the connective tissue surrounding the *adductor hyomandibularis*; insertion is on the anterior inner face of the operculum. The *adductor operculi* originates from the posterior region of the pterotic and joins the *levator* along a medial aponeurosis, both muscles insert on to

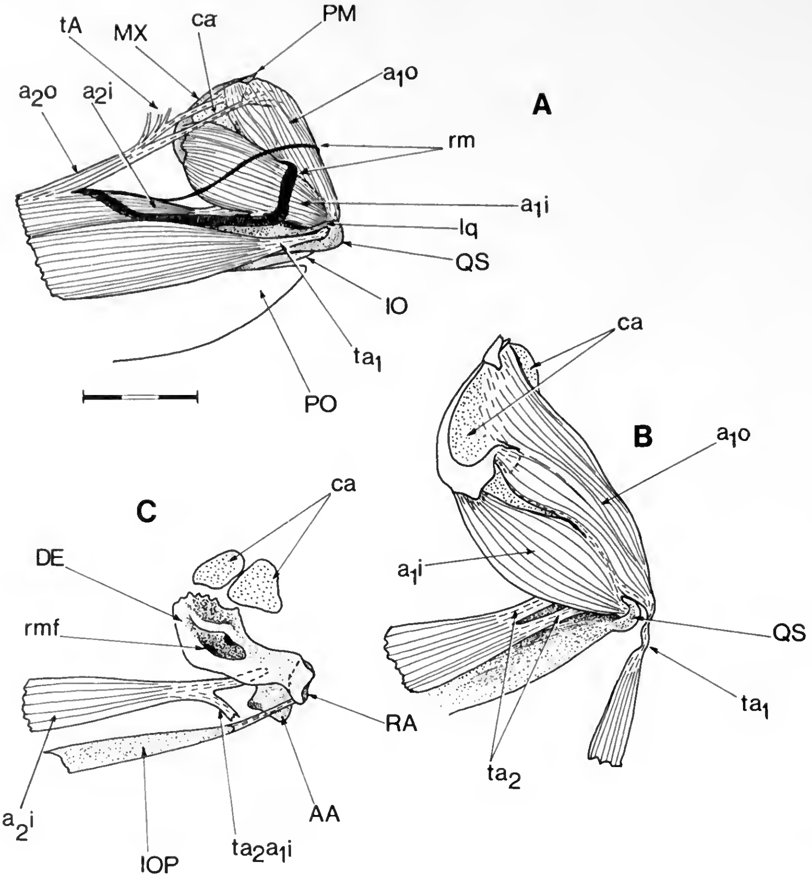

Fig. 19 *Phractolaemus ansorgei.* Anterior jaw musculature in: A, lateral view; B, dorso-lateral view, muscle A_1 has been cut posteriorly and moved laterally to the quadrate spine to expose the lower portion of A_1i; the ligament joining the quadrate spine to the quadrate face (1q) has been removed, as has muscle A_2o; C, lateral view of the lower jaw with the various parts of A_1 and A_2o removed. The upper tendon (dashed line) of A_1i inserts on the coronomeckelian bone.

the concave medial face of the operculum above the levator ledge. The *dilatator operculi* originates from the sphenotic process and pterotic ventral border, there being no dilatator fossa; the muscle inserts on the thick anterior process of the operculum.

Comments

Phractolaemus resembles other non-chanoid gonorynchiforms in the elongate, almost tubular adductor musculature. The curious arrangement of muscle A_1 with its anterior division is reckoned to be the counterpart of the situation in *Kneria, Parakneria* and *Cromeria* (see above). As in those taxa, the dorso-anterior element in *Phractolaemus* originates from the quadrate and inserts on the posterior margin of the maxilla. *Phractolaemus* shares with *Cromeria* a divided insertion tendon of muscle A_2, one segment of which runs to the quadrate origin of muscle A_1i.

Both Géry (1962) and Thys van den Audenaerde (1961) describe the possible mechanism of jaw protrusion in *Phractolaemus.* Poll (1957) and Géry (1962) figure the snout in a protruded position, it appearing proboscis-like with the mouth rotated from its dorsal, retracted position to a ventral feeding position. The mechanics of jaw adduction and abduction cannot be readily ascertained from the morbid anatomy and any functional hypotheses are beyond the scope of

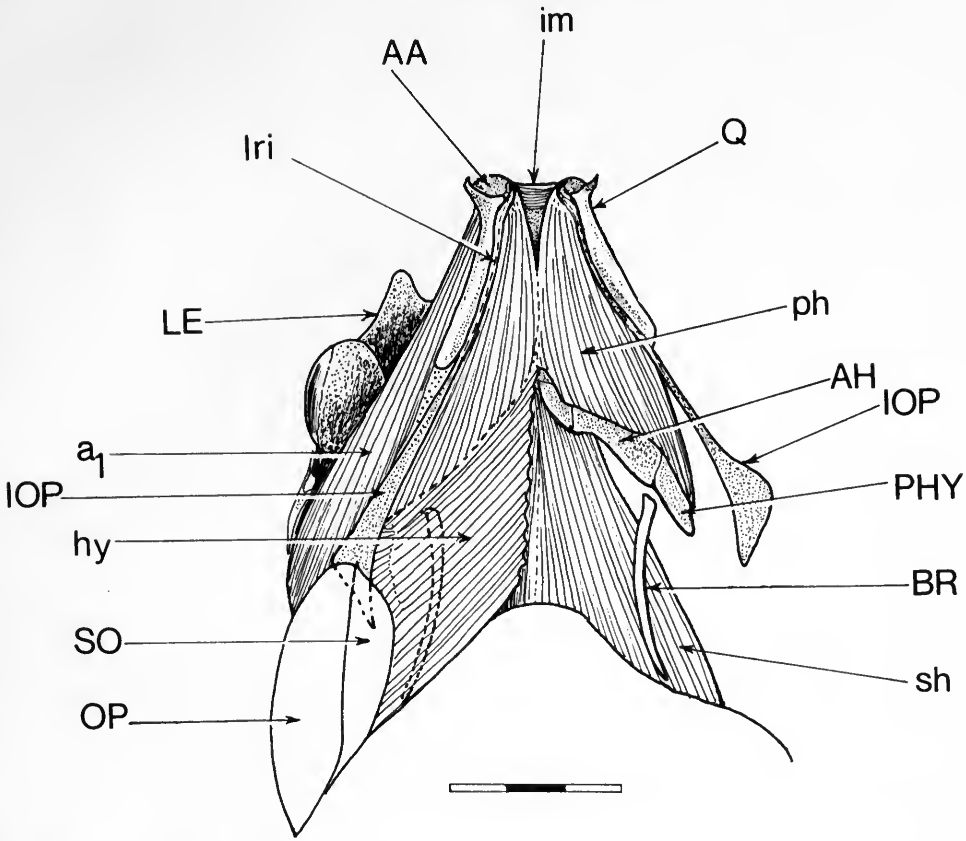

Fig. 20 *Phractolaemus ansorgei.* Ventral head musculature. The *hyohyoideus* is cut away from the specimen's left side to expose the hyoid bar and the single branchiostegal ray; the left interoperculum has been separated from the *hyohyoideus* and hyoid bar to which it is tightly bound.

this work. However, Sara Fink has pointed out to me that a mandibulohyoid ligament is apparently absent in *Phractolaemus* and that the hyoid bar is tightly bound to the interoperculum; observations with which I concur. In this case the abduction mechanism involving the *sternohyoideus* acting *via* the hyoid and mandibulohyoid ligament (Lauder, 1982) is absent. The extensive (?elastin) X-shaped ligaments attached to the upper jaws (ligament pseudocartilagineaux of Thys van den Audenaerde, 1961) seemingly recoil against the protruding vomer (lrt, Fig. 21) and muscle A_2, the outer section of whose tendinous insertions run to the antorbital and skin covering the underside of the lower jaw, must be considerably tensed during jaw abduction and exert a strong contracting force. The unique shift of the *intermandibularis* from the anterior to the posterior regions of the jaws is concomittant with the development of the circular, tube-like mouth involving symphysial separation of the dentaries.

Other anatomical features. Thys van den Audenaerde (1961) described the anatomy (minus the myology) of *Phractolaemus ansorgei* and drew attention to its many peculiarities. Amongst the osteological features are the excessively broad frontals; deep infraorbitals; extensive development of the preopercular bones which overlap in the ventral midline; reduced suspensorial elements, including absence of a symplectic, and an elongate spine-like interoperculum. The vomer is an almost square bone with an anterior notch; it projects anteriorly from beneath the mesethmoid, its anterior border curving upward. To the vomer is attached the central ligament (see above),

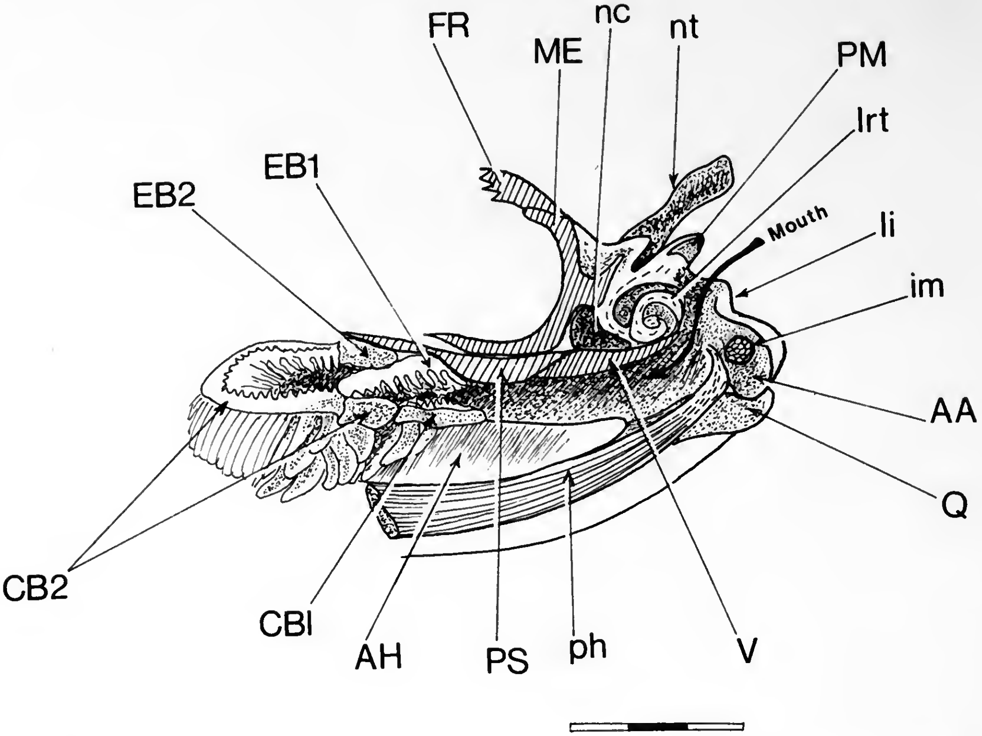

Fig. 21 *Phractolaemus ansorgei.* Sagittal section through the anterior cranium and buccal cavity. The branchial arches and hyoid bar are those of the left side.

from which branches extend laterally to the palatines and anteriorly to the maxillae (see Thys van den Audenaerde, 1961, Fig. 19). When the ligament is recoiled it lies on the vomerine shelf and in this sense resembles the coiled kinethmoid ligament of some cyprinoids. The vomer also floors a transverse canal, backed and partially roofed by the mesethmoid (nc Fig. 21), that connects the nasal tubes. The nasal bone lies at the medial base of the tube.

The statement in Nelson (1984:123) that *Phractolaemus* possesses teeth is erroneous.

Discussion

The hope of a conclusive pattern of relationships of the gonorynchid genera emerging from an anlaysis of jaw and suspensorial muscles has not been realised. Most of the taxa display many autapomorphic myological features and their resemblances are symplesiomorphic. Nevertheless a few specific points can be made.

Adductor musculature

Muscle A_1 is present in all gonorynchiforms, and in all genera, apart from *Chanos,* is an elongate, almost tubular element. The muscle has a double insertion in all genera, although the insertion points are variable; in *Chanos* and *Gonorynchus* part of A_1 inserts on the lower jaw whereas in *Kneria, Parakneria, Cromeria* and *Phractolaemus* A_1 is completely divided, the inner section derived in whole or part from the anterior border of the quadrate. In the kneriid genera the mandibularis ramus of nerve V runs medial to and along the dorsal border of the inner segment of muscle A_1 (a_1i). In *Phractolaemus,* when the jaw is adducted, the nerve crosses the lower face of the muscle (Fig. 18); when abducted, however, the nerve lies horizontally, although laterad to the muscle. It is hypothesised that the unusual position of the nerve is due to the reorientation of muscle A_1i to the outer face of the lower jaw. I thus consider that the inner element of A_1 having its origin from the quadrate is homologous in the Kneriidae and Phractolaemidae.

Within the Kneriidae, muscle A_1i originates from the mid-lateral ledge or the quadrate (*Cromeria*) or its lateral anterior face (*Kneria* and *Parakneria*). In the Phractolaemidae the origin of the muscle is from a lateral quadrate spine. The lateral quadrate origin of muscle A_1i in kneriid genera is taken to be synapomorphic and is supported by other synapomorphies noted above, *viz*: laterally extended mesethmoid wings, nodular mesethmoid rostral process, ventrally inclined and rostrally extended vomer, and reduction of branchiostegal ray number (to 3). The characters listed by Lenglet (1974:95) as separating the genera *Kneria* and *Parakneria* appear ones of degree and on the basis of synapomorphies of the skeleton and jaw musculature, the two genera should probably be considered as a single genus, *Kneria,* which forms the sister-group to *Cromeria.*

Grasseichthys is characterised myologically by reduced adductor and suspensorial muscles. Only a single *adductor mandibulae* element has been identified whilst an *adductor arcus palatini* muscle appears to be absent. *Grasseichthys* was considered by Géry (1964) to belong to a separate family, but was included in the Kneriidae by Greenwood *et al.* (1966). Such a placement appears to be the correct procedure since *Grasseichthys* shares with other kneriids a reduced opercular aperture (see p. 291) and similar ethmoid morphology (laterally extended mesethmoid wings and nodular rostral process). Both an ectopterygoid and metapterygoid appear to be lacking in the specimen of *Grasseichthys* to hand; the sympletic is elongate rather than short as in other kneriids. Branchiostegal rays are reduced to two.

No myological characters support Patterson's (1984*a*) placement of the Gonorynchidae as the sister-group to the Kneriidae. A single 'loss' character, *viz.* absence of muscle A_w, is shared by the Gonorynchidae, Kneriidae and Phractolaemidae (the muscle is also absent in various otophysan taxa and its absence can hardly be considered a 'strong' synapomorphy). The Gonorynchidae and Phractolaemidae share a divided A_2 muscle where in *Phractolaemus* the dorsal division inserts on the antorbital and in *Gonorynchus* on the lachrymal. In both taxa the ramus mandibularis of the V nerve runs anterior to the division of A_2.

In addition to the derived adductor musculature, the Phractolaemidae shares with the Kneriidae (including *Grasseichthys*) anteriorly extended lateral ethmoid wings (see Thys van den Audenaerde, 1961, fig. 15), reduction of branchiostegal ray number to a single element, *cf* 2 or 3 in kneriids, 4 or 5 in *Gonorynchus* and *Chanos* and partial sealing of the opercular border to the body wall.

Scale morphology

Fink & Fink (1981) suggest a close relationship between *Kneria* and *Gonorynchus* based on a derived scale pattern, this pattern being one of parallel longitudinal striae, and with circuli restricted to the scale margins. In fact the scale morphology of *Chanos, Gonorynchus, Kneria-Parakneria* and *Phractolaemus* differs quite markedly. Whilst circuli are restricted to the borders of the scales in *Gonorynchus* and kneriids, the longuitudinal striae display different patterns. In *Gonorynchus* the striae are divergent, but both parallel and divergent in the kneriids. This latter feature varies too according to the part of the body on which the scales are situated. Moreover, the scales of the kneriids bear more deeply incised striae which have a wavy appearance (Fig. 22D). The scales of *Gonorynchus* have markedly ctenoid anterior and posterior margins (Fig. 22A and Le Danois, 1966: 286 & fig. 2). In overall shape the scales of *Phractolaemus* and *Chanos* resemble one another closely, but this is in a symplesiomorphic sense, the scales being typically rounded with close-set concentric circuli on the posterior field and many radial striae on the anterior field (Figs 22B & C). Both *Cromeria* and *Grasseichthys* lack scales. The variance in scale morphology within the gonorynchiforms appears to make it an unrewarding character for assessing phylogenetic relationships.

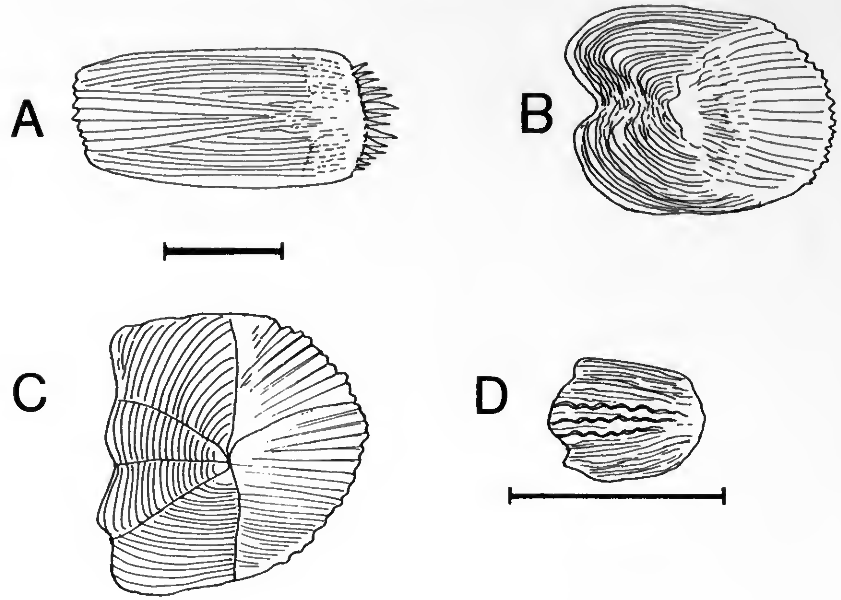

Fig. 22 Body scales of gonorynchiform genera: A, *Gonorynchus gonorynchus*; B, *Chanos chanos*; C, *Phractolaemus ansorgei*; D, *Kneria auriculatus*. All taken from the mid-flank below the lateral line. Scale = 1 mm.

Epibranchial organ

The structure of the epibranchial organ in gonorynchiforms deserves some comment. Nelson (1967) has claimed that epibranchial organs in various groups of lower euteleosts (Osteoglossiformes, Cypriniformes, Clupeiformes, Gonorynchiformes and argentinoids) have been independently derived in those lineages. That this is so, appears to be evident from the nature of the involvement of various elements of the posterior upper and lower gill-arches, and in the overall structure of the organ itself (see Nelson, 1967). In gonorynchiforms both the 4th and 5th epibranchials are supporting elements of the investing diverticulum. The 5th epibranchial is a well-developed cartilaginous element in all gonorynchiform taxa and bears gill-rakers. In *Chanos,* the epibranchial organ is a highly developed structure with each diverticulum in the form of a medially recurved, finger-like sac (see Kapoor, 1954). The 4th epibranchial is a stick-like bone with a high dorsal process; the 5th epibranchial is a broad, bifurcated element (Nelson, 1967, fig. 1j).

In other gonorynchiform genera, the epibranchial diverticulum is not recurved as in *Chanos,* but is a straight, finger-like sac projecting antero-medially. In *Gonorynchus* the 4th epibranchial is a massive element and the 5th a slender curved, rod-like cartilage (Fig. 9).

In *Kneria* and *Parakneria* there is, posterior to the junction of the 4th epi- and ceratobranchials, a curved cartilaginous element that I take to be the 5th epibranchial. The diverticulum is cone-shaped and invests the 4th and 5th ceratobranchials, but not the 5th epibranchials (Fig. 15).

In *Cromeria* there is a 5th epibranchial (labelled by d'Aubenton, 1961, as an accessory epibranchial). It is not clear from my specimens as to which elements the epibranchial pouch covers, but the situation appears like that in *Kneria* with the 4th epibranchial providing little contribution to the support of the diverticulum. There is an ossified 5th basibranchial, a feature shared with other kneriids.

In *Grasseichthys* the diverticulum of the organ is not well-developed and only a few gill-rakers are present in the pouch. Greenwood *et al.* (1966) figured the gill-arches of *Grasseichthys* but they did not show a 5th epibranchial, which occurs as a small cartilage postero-dorsal to the 4th epibranchial. The 4th epibranchial has an elongate dorsal process and the bone appears to contribute to the support of the diverticulum.

In *Phractolaemus* the cartilaginous tips of the 4th and 5th ceratobranchials are in contact; the diverticulum involves only the 4th and 5th ceratobranchials.

In all taxa the epibranchial diverticula communicate directly with the oesophagus and appear to incorporate fibres of the *sphincter oesophagi* muscle (see d'Aubenton, 1961; Thys van den Audenaerde, 1961). Also, the diverticula appear attached to the *posterior transversi dorsales* muscles.

In summary, the epibranchial organ seems most highly developed in *Chanos* (see Kapoor, 1954); amongst gonorynchoids, the Kneriidae and Phractolaemidae differ from the Gonorynchidae in the degree of association of the epibranchial diverticulum with the posterior gill-arch elements; the 4th epibranchial contributing no or little support to that structure in the former two families.

To summarise the results of this study:

1. *Chanos* has a basically plesiomorphic jaw, hyoid and suspensorial muscle arrangement. It shares with *Gonorynchus* a divided A_1 muscle where part inserts on the lower jaw. This is probably a plesiomorphic condition for gonorynchiforms.
2. *Gonorynchus* has several jaw and suspensorial muscle autapomorphies (p. 283). Regrettably, no conclusive synapomorphies have been identified that would corroborate the pattern of relationships hypothesised by Fink & Fink (1981) and Patterson (1984*a*), that *Gonorynchus* is the sister-group to the Kneriidae.
3. *Phractolaemus* has several jaw muscle apomorphies one of which, a divided A_2 it shares with *Gonorynchus* (see p. 299). With *Cromeria, Kneria* and *Parakneria* it shares a divided A_1 of which part originates from the quadrate; anteriorly extended lateral ethmoid wings and reduced number of branchiostegal rays. *Phractolaemus* has a specialised swimbladder and pulmonary system enabling it to utilise atmospheric air (see Thys van den Audenaerde, 1961). *Kneria,* also, is apparently capable of atmospheric respiration (see discussion in Lenglet, 1973 and observations of Bell-Cross 1976:97) and this may represent another synapomorphy.
4. *Kneria, Parakneria* and *Cromeria* possess a synapomorphic arrangement of *adductor mandibulae* muscles (p. 291) in addition to sharing derived ethmo-vomerine morphologies (p. 293). There seems little doubt that they represent a monophyletic unit.
5. *Grasseichthys* has a autapomorphically reduced jaw muscle system. It shares with *Kneria, Parakneria* and *Cromeria* a derived ethmo-vomerine morphology, reduced number of branchiostegal rays and partially sealed operculum (the two latter characters shared also with *Phractolaemus,* see p. 299). *Grasseichthys* shares with *Phractolaemus* an elongate, spine-like interoperculum, and with *Cromeria,* the absence of body scales.

From these data the Phractolaemidae and Kneriidae appear to be related as sister groups (this is on the assumption that, in the light of other synapomorphies listed here and given in Fink & Fink, 1981 and Patterson, 1984*a*, that the divided A_2 muscle present in the Phractolaemidae and Gonorynchidae is homoplasious).

Grasseichthys which is currently assigned to the Kneriidae, lacks those myological features identified as synapomorphic for the other kneriids, although it shares derived osteological features with them (see above). There is, however, a character conflict in that *Grasseichthys* shares with *Phractolaemus* a derived interopercular morphology (p. 294), and it may also be that the single adductor muscle is homologous with the dorsolateral division (A_2o) of *Phractolaemus* (p. 295). It is not therefore possible on present evidence to determine whether it is more closely related to the kneriid or phractolaemid lineage.

Both *Cromeria* and *Grasseichthys* have been regarded by some authors as neotenic, or paedomorphic (see D'Aubenton, 1961; Lenglet, 1974), presumably because of a general lack of skeletal ossification, 'larval appearance' and miniature size (see Roberts, 1984 for a list of neotenic features pertaining to salangoids, but common to other groups). If indeed these taxa are paedomorphic, then *Grasseichthys* might well be viewed as representing an ontogenetic stage where the adductor musculature, rather than being 'reduced' is merely retarded in its development, as might also be the 'loss' of scales in both *Grasseichthys* and *Cromeria.*

Whether paedomorphosis (by retardation) alone is the mechanism responsible for dwarfed lineages is discussed by Hanken (1984). Hanken argues that 'Parallel morphological evolution in related groups may be explained as a consequence of their sharing common developmental pathways which are truncated in an analagous manner, albeit independently. In the case of closely related taxa, parallelism may even be *expected'.* However, if two groups are known to be closely related, presumably on the basis of shared homologies (synapomorphies) then why should 'parallel morphological evolution' be evoked? The 'common developmental pathways' must also be synapomorphic. Should the epigenetic cause(s) of truncation in related taxa be the same, then, presumably the resulting paedomorphosis must be regarded as synapomorphic.

Another of Hanken's assertions is that decreased body size is associated with 'morphological novelty'. Granted, truncation of development will be at different stages in each group but these terminal stages will simply be autapomorphic, characterising each taxon. Thus, it is difficult to see how paedomorphic taxa are susceptible to any greater degree of 'morphological novelty' than those taxa whose ontogeny has 'deviated' in some other way from the plesiomorphic pattern of development.

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Tilapine fishes of the genera *Sarotherodon, Oreochromis* and *Danakilia*

Dr Ethelwynn Trewavas

The tilapias are cichlid fishes of Africa and the Levant that have become the subjects of fish-farming throughout the warm countries of the world. This book described 41 recognized species in which one or both parents carry the eggs and embryos in the mouth for safety. Substrate-spawning species, of the now restricted genus *Tilapia*, are not treated here.

Three genera of the mouth-brooding species are included though in one of them, *Danakilia*, the single species is too small to warrant farming. The other two, *Sarotherodon*, with nine species, and *Oreochromis*, with thirty-one, are distinguished primarily by their breeding habits and their biogeography, supported by structural features. Each species is described, with its diagnostic features emphasised and illustrated, and to this is added a summary of known ecology and behaviour. Conclusions on relationships involve assessment of parallel and convergent evolution. Dr Trewavas writes with the interests of the fish culturists, as well as those of the taxonomists, very much in mind.

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