

A Review of the Bathygadidae (Teleostei: Gadiformes)

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SYNOPSIS. The taxonomic status and relationships of the gadiform genera *Bathygadus* Günther, 1878 and *Gadomus* Regan, 1903 are reviewed in the light of characters shared with macrouroids and gadoids. The genera are recognised as sister-taxa which constitute the family Bathygadidae. Relationships of the family are ambiguous since it exhibits only gadiform symplesiomorphies, and might therefore represent the sister-lineage to all gadiforms.

The osteology and soft anatomical features of *Bathygadus* are described. The taxonomy of *Bathygadus* and *Gadomus* is reviewed; 10 species of the former and 12 of the latter are recognised. Bathygadid distribution is centred above the Equator in both Atlantic and Indo-Pacific oceans; no bathygadids are recorded from the eastern Pacific.

INTRODUCTION

The taxonomic status and relationships of 'bathygadines'

Traditionally, *Bathygadus* and *Gadomus* have constituted the subfamily Bathygadinae of the family Macrouridae. Regan (1903) gave as characters for the Bathygadinae:

First vertebra articulating with the skull, its neural spine not directly attached to the occipital crest. First dorsal ray not spinous. First gill-arch entirely free anteriorly.

Regan also included in the Bathygadinae the genera *Melanonus*, *Lyconus* and *Trachyrincus*. Subsequent removal of these taxa (see below) left only *Bathygadus* and *Gadomus* in the subfamily. The revised diagnosis of that group (Okamura, 1970a; Marshall & Cohen, 1973) relies on characters plesiomorphic for Gadiformes (and for 'paracanthopterygians') ie. mouth wide, terminal; rows of small or minute jaw teeth; premaxillae with relatively short pedicels, slightly protractile; seven branchiostegal rays; olfactory bulbs close to the fore-brain; first gill-arch unrestricted; gill-rakers on 1st arch long and numerous; abdominal vertebrae 11–13; pelvic fin with 8 or 9 rays; scales without spinules; swimbladder with 2 or 4 retia, no drumming muscles; no light organs (Marshall & Cohen, 1973). Nasal bones small, separated; lachrymal without medial ventral bony plate; symplectic slender; hyomandibular without lateral ridge; ethmoid not enlarged into plate dorsally; interosseus spaces between symplectic and preoperculum and between preoperculum and operculum (Okamura, 1970a).

If these characters are plesiomorphic among gadiforms what are the derived characters which define 'bathygadines' and what

justification is there for considering *Bathygadus* and *Gadomus* as macrouroids or gadoids? To consider these questions the diagnostic features of those two groups are examined.

MACROUROIDEI

Regan (1903) listed characters for the Macrouridae and Gadidae, concluding that 'The Macruridae (*sic*) . . . in the two essential characters of the more posterior ventrals and absent caudal, are less specialized than the Gadidae . . .' Other macrouroid characters listed by Regan are, apart from 'vertebrae numerous' not confined to that group but nevertheless form the bases of subsequent diagnoses by Okamura (1970a, b) and Marshall & Cohen (1973). Regan's concept of the Macrouroidei included *Bathygadus* and *Gadomus* and other genera (*Lyconus*, *Macruronus* and *Steindachneria*) which Marshall (1966) included in the Gadoidei. Marshall (1966) also detailed certain characters as gadoid and others as macrouroid (see below). Okamura (1970a, b) followed Regan's diagnosis of macrouroids, incorporating features identified by Marshall (1966) and others of his own, concluding (1970a) that the absence of a caudal fin is '... the only constant characters by which the macrouroids can be separated from other gadiforms.' Marshall & Cohen (1973) also utilized Regan's character of the 1st vertebra not being closely joined to the skull and recognised as specializations: absence of caudal fin and presence of broad lateralis canals, light organ, and spine-like element in the 1st dorsal fin. All authors cited agree on the absence of a caudal fin (as a correlate, the caudal skeleton) as diagnostic for macrouroids. However, the gadoid *Steindachneria* also lacks a caudal fin and skeleton, and the 'macrouroid' *Trachyrincus* has a modified fin and skeleton (Howes, 1989). Okamura (1970a, b), Marshall (1973a) and Marshall & Cohen (1973) list

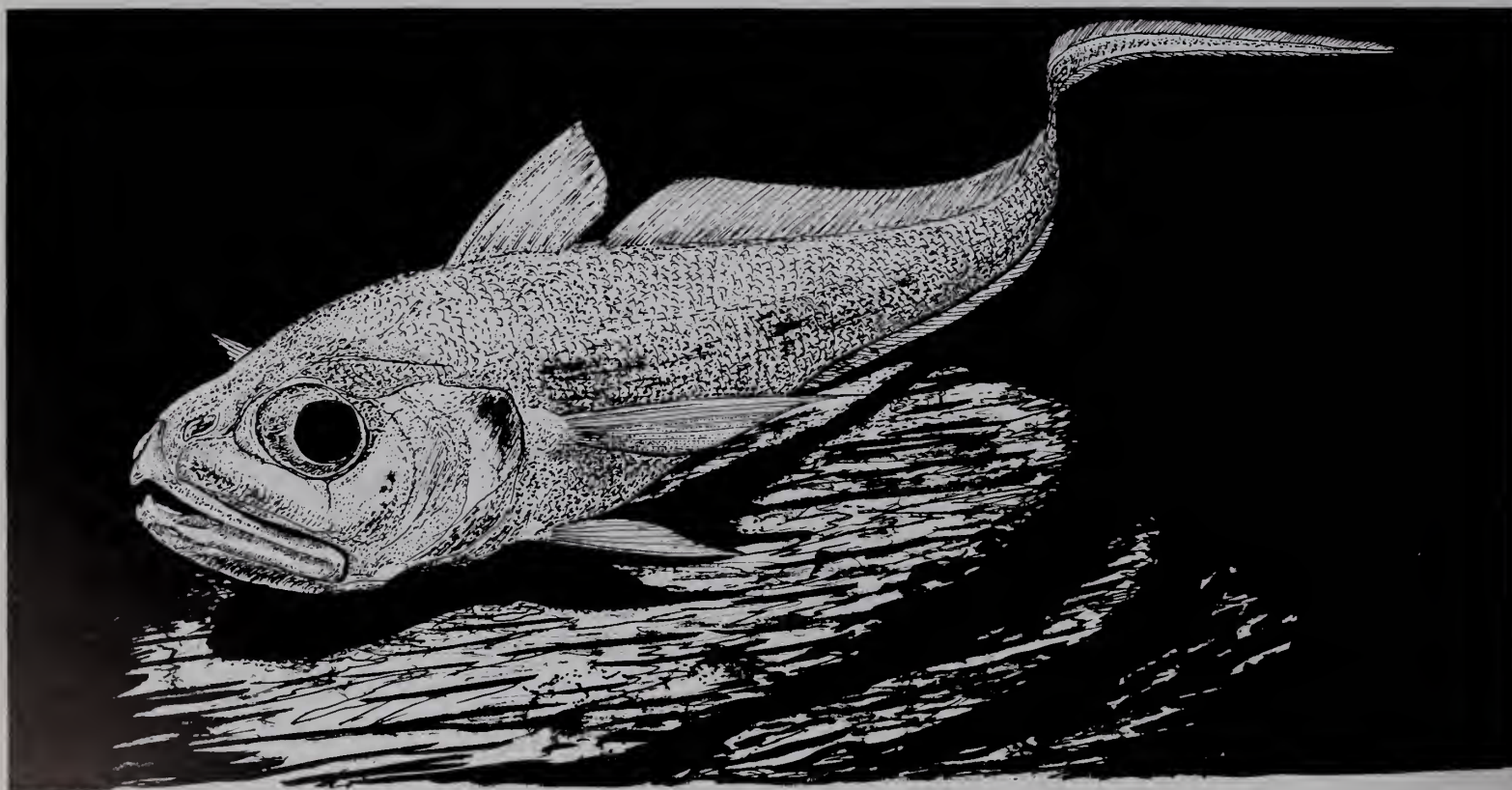


Fig. 1 A bathygadid in assumed swimming mode. Reconstruction based on photograph taken by remote controlled camera (Pl.2) in Marshall & Bourne, 1964); drawn from a specimen of *Bathygadus melanobranchus* ca 280mm TL.

characters apparently synapomorphic for macroroids if one excludes *Bathygadus* and *Gadomus*; these characters are as follows:

Scales keeled or spinigerous

Okamura (1970a, b) recognised that *Bathygadus* and *Gadomus* differed from other macroroids in possessing cycloid scales with a reticulate pattern on the exposed surface. The scales of macroroids (including *Trachyrincus*) are often keeled and bear spiniferous processes on their exposed area.

Infraorbitals

Okamura (1970b:38) noted that the lachrymal of macroroids is divided by a ventral longitudinal plate, absent in *Bathygadus*, *Gadomus* and gadoids.

Palatine bone

Okamura (1970b:46) recognised different palatine morphotypes between *Bathygadus*, *Gadomus* and macroroids, being deep with a shallow lateral depression in the former and shallow with a medial lateral ridge in the latter. Howes (1988) noted that macroroids have a loose ligamentous connection between the palatine and ventral and lateral surfaces of the lateral ethmoid. Unlike *Bathygadus* and *Gadomus* and gadoids there is no contact with the ethmovomerine bloc or mesethmoidal part of the lateral ethmoid.

Expansion of the symplectic

The symplectic is deep and posteriorly expanded to contact the leading edge of the preoperculum (Okamura, 1970b).

Upper jaw accommodation

Okamura (1970b:55) noted in macroroids 'With the exception of *Gadomus* and *Bathygadus*, a large space or cavity, into or out of which the premaxillary pedicel slides, is formed between the nasal and ethmoid'. This 'cavity' results from an anteriorly truncated ethmoid bloc and a medially and anteriorly extended nasal and is a character complex unique to macroroids.

Nasals joined in midline

Okamura (1970b:55) and Marshall (1973a:498) recognised that expanded nasals, joined in the midline and bearing a median crest are diagnostic for macroroids. The nasals in *Bathygadus* and *Gadomus* although large and cavernous remain medially separated or in contact only posteriorly.

Ethmoid produced into a high vertical plate

Okamura (1970a, b) noted that the ethmoid forms a vertical plate with a posterior extension in macroroid taxa other than *Bathygadus* and *Gadomus* (see also p. 162).

Macroroid subfamilies

Characters recognised by Regan (1903) and subsequent authors as diagnostic for the subfamily Macrouroidinae, *viz*: 1st gill-slit restricted by membraneous fold; short, denticulate

gill-rakers on 1st arch; drumming muscles connected to swimbladder and light organs are synapomorphic as are ligaments connecting the nasal bone to the maxilla and the attachment of the maxillary-premaxillary ligament to the rostral cartilage (Howes, 1989). The subfamily Macrouroidinae is characterized by cranial and other anatomical specializations (see Okamura, 1970a, b; Marshall, 1973a; Howes, 1989).

GADOIDEI

Gadoids have been defined ambiguously by the presence of a homocercal caudal fin skeleton. Regan's (1903) Gadidae, corresponding to most later authors' Gadoidei, differed from the macroroids '... only in the more anterior ventrals, which have 1-9 rays, and in having a separate caudal fin'. Reliance on the derived absence of the caudal fin in macroroids leaves gadoids characterized by symplesiomorphies.

Svetovidov (1948) noted an osseous canal formed from ventral laminae of the frontal which provides a channel for the olfactory tracts in gadoids. Usually, the tracts lie adjacent to one another, but in macroroids they are separated for much of their length by the interorbital septum.

Rosen & Patterson (1969) recognised a 'gadoid caudal skeleton', being homocercal and having a particular fusion pattern of hypurals, involving procurrent rays and often the presence of superior and inferior elements (termed X and Y bones).

Howes (1989) recognised the Gadoidei by a ligament connecting the interoperculum to the preoperculum and hyomandibular; reduction (including loss) of *obliqui ventrales* muscles on the laterally compressed 1st and 2nd gill-arches, and indirect attachment (*via* the *rectus communis* muscle) of the *sternohyoideus* muscle to the urohyal.

Markle (1989) outlines a concept of the Gadoidei based on loss of an interarcual cartilage, position of the scapular-coracoid foramen, high number of pre-caudal vertebrae and two separate hypural plates. Patterson & Rosen (1989) consider the first two of these characters as synapomorphies for the Gadiformes but they do not remark on the monophyly of the Gadoidei.

Characters shared by *Bathygadus* and *Gadomus* with macroroids

Specialized characters shared by *Bathygadus*, *Gadomus* and macroroids are:

1. Two spinous rays in the 1st dorsal fin (Okamura, 1970a, b; Marshall, 1973a)
2. Supraoccipital crest separated from 1st neural spine (Regan, 1903; Marshall, 1973a).

Spinous dorsal rays have a restricted disjunct distribution among gadiforms. In the Macrouroidei, the two genera *Macrouroides* and *Squalogadus* in the subfamily Macrouroidinae lack the feature. In the Gadoidei, Moridae and Merlucciidae possess a single spine (reduced in the former and in *Macruronus* of the latter). In Okamura's (1970b) opinion, not backed by evidence, spinous rays were not remnants of a former primitive condition but a neomorph. This question may be resolved by observing, in those taxa lacking dorsal spines, their presence during ontogeny.

Separation of the supraoccipital crest from the 1st neural spine is a plesiomorphic feature; a high crest separated

from the spine is present in the Lower Eocene gadoid *Rhinocephalus* (Rosen & Patterson, 1969:431) and is widespread among 'paracanthopterygians' and acanthopterygians. In *Gadomus*, however, homology of the supraoccipital crest is doubtful since the supraoccipital bone is 'overlain' by a separate element which forms the crest (Figs 7, 8). The overlapping margin of the crest covers the medial border of the exoccipital and the crest may represent the 1st neural spine. The possibility that the 'exoccipital' condyles represent that bone or are the fused facets of the 1st neural spine has been discussed by Rosen & Patterson (1969), Patterson (1975) and Rosen (1985).

There are no identified synapomorphies which relate *Bathygadus* and *Gadomus* to macrouroids. Okamura (1970b) listed 25 osteological and 3 soft anatomical differences between 'bathygadines' and macrouroid taxa (Table 1). Only differences pertinent to questions of homology are included in the anatomical descriptions of this text.

Table 1 Contrasting characters in Bathygadidae and Macrouroidei. Compiled from data given in Okamura (1970b).

Character	Bathygadidae	Macrouroidei
1 Scales	reticulate	spiniferous
2 Outer gill-arch	unrestricted	restricted by fold of skin
3 Outer gill-rakers	slender	short and spinous
4 Premaxillary teeth	villiform	larger; various
5 Maxilla	slender with posterior notch	deep, notched
6 Premaxilla	ventrally situated	posteriorly situated
postmaxillary process		
7 Retroarticular	J-shaped	L-shaped
8 Mouth	terminal, protrusibility limited	inferior, protrusile
9 Lachrymal with ventral lamina	absent	present
10 Palatine	deep	shallow
11 Quadrate-preopercular space	present	absent
12 Symplectic	expanded dorso-posteriorly	expanded ventro-posteriorly
13 Hyomandibula	flat	with ventral flange
14 Preopercular width	more than 3 in its length	less than 3
15 Preopercular-symplectic space	present	absent
16 Operculum-preoperculum	separated	operculum overlaps preoperculum
17 Interoperculum, sickle-shaped	in <i>Bathygadus</i>	variously shaped
18 Nasal-premaxillary cavity	absent	present
19 Nasals	separated	meet
20 Ethmoid lamina	low	high
21 Frontal	unelaborated	many ridges
22 Hypohyal	oblong	rounded
23 Cleithrum	narrow	broad
24 Rib	on last abdominal vertebra	lacking on last or penultimate vertebra
25 Anal pterygiophores	normal	anteriorly placed, arc-like
26 Swimbladder	thin-walled, few retia	thick-walled, many retia
27 Intestine	simple, S-shaped	elaborate coiling
28 Luminous organs	absent	present in some genera

Characters shared by *Bathygadus* and *Gadomus* with gadoids

Most character states listed in Table I for *Bathygadus* and *Gadomus* are shared with gadoids but these correspondences are mainly plesiomorphic; of the three features Howes (1989) considered synapomorphic, two are found in other gadiforms. The ligamentous attachment of the interoperculum with hyomandibular occurs in some 'ophidiiforms' (see above) and indirect connection of *sternohyoideus* muscle with urohyal occurs in some macrouroids (Howes, 1988). The other character, reduction of *obliqui ventrales* muscles is unique to some Gadoidei.

In summary, there are no features that suggest a close relationship with either macrouroids or gadoids. Gadoids are ambiguously diagnosed (see above). Howes (1990) recognises upper and lower fused hypural plates as diagnostic for a subgroup of 'higher' gadoids, but 'lower' gadoids, including Bathygadidae, Steindachneriidae and Moridae remain a paraphyletic assemblage. The Bathygadidae conform to Stiassny's (1986) dictum of a 'morphologically and phylogenetically primitive lineage' and may eventually be regarded as the plesiomorphic lineage to other gadiforms.

Integrity of Bathygadidae

Howes (1988; 1989) united *Bathygadus* and *Gadomus* on a single synapomorphy (occasional absence of *obliqui ventrales* muscles on 1st gill-arch); other synapomorphies support this relationship and justify recognition of a monophyletic lineage, these are;

1. Development of anterior body muscles where *infracarinalis anterior* markedly tendinous and well-separated from *hypaxialis* (p. 181);
2. Modified nerve pathway serving pectoral fin rays (p. 182);
3. Reduced gill-filaments (p. 181).

One character shared by *Bathygadus* and *Gadomus* (recognised by Gilbert & Hubbs, 1916 as diagnostic for the Bathygadinae) is that the 2nd dorsal fin rays are longer than those of the anal fin. This feature is not restricted to bathygadids, however, but occurs in *Trachyrincus* (included by Gilbert & Hubbs, 1916 in Bathygadinae). In *Steindachneria* (a 'gadoid'; Fahay, 1989) only the first 10–12 anal rays are lengthened, the remainder reduced; in *Macruronus* (Merlucciidae) and Eulichthyidae anterior anal rays are lengthened; in Moridae, 2nd dorsal has longer rays than anal in *Antimora*, *Physiculus*, *Auchenoceros*, *Mora* and *Tripterophycis*. The feature is not therefore diagnostic for Bathygadidae.

As noted above, it is impossible at present to determine the sister-group of Bathygadidae, but there seems little justification for letting it remain as a macrouroid sub-group (see above). Iwamoto (1989) prefers to recognise 'Bathygadinae' as the plesiomorphic sister-lineage to macrouroids, but he identifies no synapomorphy that unites them with macrouroids. Iwamoto's (1989) reference to Howes' (1989) inclusion of *Gadomus* in Melanonidae was based on a statement in an early draft of that paper and one subsequently revised as published.

METHODS AND MATERIALS

Osteological study was based primarily on cleared and alcian-alizarin stained preparations of *Bathygadus melanobranchus*

and *B. macrops* with observations on *Gadomus longifilis* and dry skeletal preparations of these taxa and *Bathygadus favosus*, *B. furvescens* and *Gadomus arcuatus*.

Parameters used are fewer than those of previous authors as most were of little utility. Gilbert & Hubbs (1920) give meristics and counts of up to 27 parameters and features, but the preserved state of their material limits the accuracy of their measurements to at least ± 2 mm. Use of total length measurement is discarded as the posterior part of the tail is often broken off and the 'caudal' is merely a regeneration (see p. 179). As the 1st anal fin ray nearly always lies below the 13th vertebra the distance from the snout to this point has been taken as the principal dividend for proportional measurements (s-a).

Body depth (**bd**), expressed as % of s-a distance is an unreliable measurement and of limited use as a species-specific character. Head length (**hl**), expressed as % of s-a distance and interorbital width (**io**), expressed as % of head length, are useful indications of specific differences as this part of the fish is little affected by preservation and usually undamaged. Orbital diameter (**od**), expressed as % of head length is taken horizontally from the inner edge of the lateral ethmoid to the inner rim of the posterior infraorbital.

Premaxillary length (**pml**), expressed as % of head length, is measured from the anterior surface of the bone to its distal tip. The length (or height) of the premaxillary ascending process (**pma**), expressed as % of premaxillary length, is measured along its symphyseal margin. The distance across the midline between the premaxillary dentigerous surfaces (**pms**) is expressed as % of premaxillary length.

Dorsal and anal fin rays are often broken and measurements of their lengths are of little value and as the tail is often missing, counts have been limited to the first dorsal fin (**D**) and denote the first two spinous rays thus: II. Pectoral fin length (**pl**) expressed as % of s-a distance; as the outer (usually, prolonged) ray is often broken. Barbel length (**bl**) is given as % of head length. It is unreliable as a specific character (Gilbert & Hubbs, 1920).

Scale counts are not given; Gilbert & Hubbs (1916; 1920) used numbers in transverse rows but differences of two or three scales in these series can occur intraspecifically. Gill-rakers (**GR**) are counted on the 1st arch as those on the epibranchial + those on the ceratobranchial (the raker sometimes overlapping the elements is counted with those on the ceratobranchial). Pyloric caeca (**PC**) have been counted where possible.

Specimens examined for anatomy

Material is listed in alphabetical order of genera and species. D=dissected; A=cleared and stained; S=dry skeleton.

GADIFORMES: *Antimora rostrata* 1986.4.22:10–11(A); *Bathygadus favosus* 1963.2.25:26–27 (S); 28–30 (D); *B. furvescens* 1939.5.24:670–672 (D); *B. macrops* 1973.3.5:3–6 (A); *B. melanobranchus* 1969.6.26:3227–31 (A, D); 1963.2.3:31–35 (D); 1934.12.19:26–27(A, tail only); *Bregmaceros atripinnis* 1889.2.1:3988–91 (D); *Brosme brosmes* (two skulls uncat.); *Coelorinchus caribbaeus* 1963.2.25:244–250 (A); *C. coelorinchus* 1905.2.2:18(S); *Euclichthys polynemus* 1986.5.14:1–3(D); *Gadomus arcuatus* Uncat. (A, tail only); *G. longifilis* 1963.2.25:7–17(D); 1890.6.16:43(S); 1965.2.25:7–17 (S, A); *Gadus morhua* 1971.2.16:628–633(A); *Gaidropsarus mediterraneus* uncat.(A); uncat.(S); *Halargyreus johnsonii* 1981.3.16:

406–7(D); 1973.10.29:384–440(D, A); 1968.5.13:1(A); *Lepidion eques* 1981.3.16:437–44(A); 1902.10.30:4(S); *Lota lota* 168.6(S, two skulls); 1953.6.26:15–18(D); *Lotella marginata* 1976.9.28:6–7(A); *Macruronus magellanicus* 1936.8.26:342–51(D); *M. novaezelandicus* Uncat.(S); *Malacocephalus laevis* 104.11.30:33(S); *Melanonus zugmayeri* 1981.3.16:377(D); *Merluccius merluccius* 1971.7.21:44–57 (D, A); *M. productus* 1896.9.25:6(S); *Merlangius aeglefinis* Uncat.(S); *Microgadus proximus* 1984.12.5:45–48(D); *Molva molva* Uncat. (S, skull); *Mora moro* Uncat. (S); *Muraenolepis microps* 1937.7.13:24–29(D, S); 1937.7.12:11–17(A); *Nezumia aequalis* 1973.3.5:60–4(A); *Phycis blennoides* 1972.2.22:73–6(D); 1898.4.30:14 (S); Uncat. (14 skulls); *Physiculus marginatus* 1936.8.26:424–431(A); *Raniceps raninus* 1967.1.1:4(D); 1893.7.6:2(A); 1884.8.26:3(S); *Salilota australis* 1936.8.26:394–404(A); *Steindachneria argentea* 1963.2.25:325–9(D); 344–54(A); *Trachonurus villosus* 1963.2.25:226–8(D); *Trachyrincus trachyrincus* 1976.7.30:42–53 (D, A); 1888.6.15:7(S); *Trisopterus luscus* Uncat. (S, 8 skulls); *Urophycis regia* 1985.6.6:109–119(A); *Ventrifossa occidentalis* 1965.2.25:61–71(D, A).

OPHIDIIFORMES: *Acanthonus armatus* 1887.12.7:55, 56 (syn-types); *Bassosetus compressiceps* 1887.13.7:47–8(D); *Brotula jayakari* 1891.2.9:30(S); *Carapus bermudensis* 1985.6.6:138–83(A); *Cataetix messieri* 1936.8.26:1060–1(D); *Dicrolene introniger* 1939.5.24:1441–4(D); *Echiodon drummondi* 1967.5.4:3–5(D); *Genypterus blacodes* 1896.6.17:73(S); *Glyptophtidium macropus* 1986.10.6:49–50(D); *Hypopleura caninum* 1986.10.6:63–5(D); *Lamprogrammus exutus* Uncat. Discovery Colln.; *L. fragilis* 1939.5.24:1493–96(D); *L. nigricans* 1939.5.26:1483–7(D); *Monomitopus metriostoma* 1964.8.6:47–54; *Neobythites steaticus* 1910.1.31:11(S); *Ophidion rochei* 1971.12.17:6–8(D); *Sirembo armatus* 1938.6.23:27–8(D); *Thalassobathia pelagica* 1967.11.8:1(D);

OTHER TAXA: Gadopsiidae *Gadopsis marmoratus* 1914.8.20:228–233(A); Lipariidae *Careproctus longipinnis* 1956.5.1:6–8(D).

Institutional abbreviations

Material examined for the anatomical study is from the collections of the Natural History Museum, London (BMNH); specimens used in the taxonomic review are also from BMNH and from the J. L. B. Smith Institute of Ichthyology, Rhodes University (RUSI), the United States National Museum of Natural History (USNM) and the Zoologisch Museum of Amsterdam University (ZMA).

Abbreviations used in the figures

Bones and ligaments

aa	anguloarticular
aap	articular process of premaxilla
ac	actinost
ahy	anterohyal
ap	ascending process of premaxilla
apr	articular process of radial
ar	anal fin ray
ard	anal fin radial
asc	'accessory' supraoccipital crest
bb	basibranchial
bh	basihyal
bo	basioccipital

ANATOMY OF BATHYGADUS

Osteology

In dorsal view cranium is broadly triangular; in *B. melanobranchus* pterotic region 80% of cranial length; steep dorsal profile and orbital depth of 30% of its length. Crania of *Gadomus* species narrower than *Bathygadus* (see diagnoses). High supraoccipital crest, depth of occipital part of cranium exceeding length. Skull bones of both *Bathygadus* and *Gadomus* papery, fragile and lateral borders of cranial roofing bones irregular.

Olfactory region (Figs 2 & 3)

Ethmoid bloc: Dorsal profile cruciform, dorsal surface and posterior lamina fully ossified; unity with underlying ethmoid cartilage suggests it is a *rostromediosupraethmoid* (*sensu* Patterson, 1975); ossified portion and underlying part of ethmoid cartilage is a compressed plate. Ethmoid cartilage slopes forward anteriorly and expands laterally and is trowel-shaped (Fig. 2A, re & me). *Lateral ethmoid* (le, Figs 2B, 3) contacts ethmoid cartilage ventromedially; thin lamellate lateral wing; dorsomedial lamina of bone contacts frontal. *Vomer* (v, Fig. 2) short, narrowly triangular with thick, convex anterior border; extends level with lateral ethmoid posteriorly; ventral surface deeply concave and edentulous (Fig. 2C).

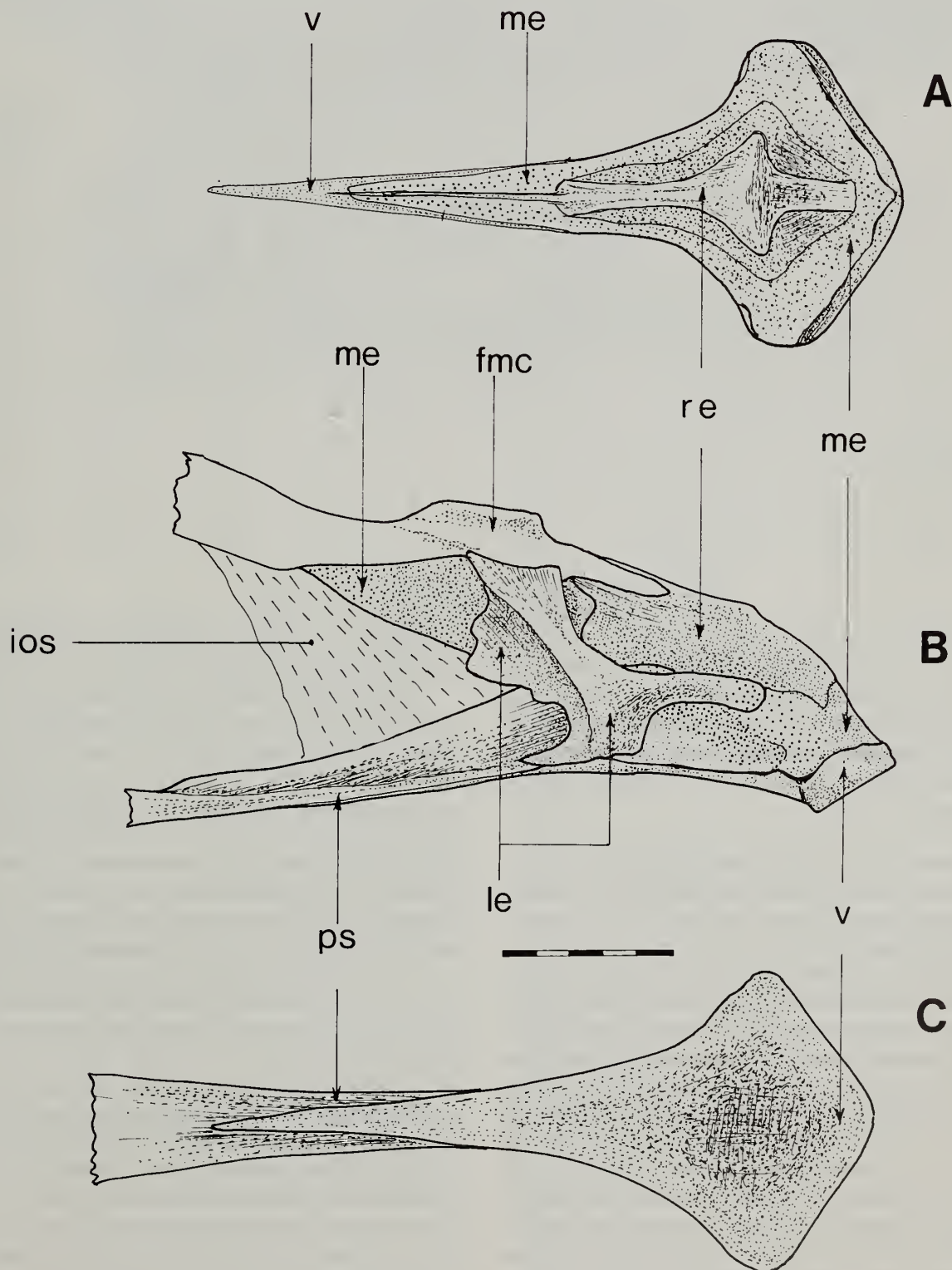


Fig. 2 *Bathygadus favosus* (BMNH 1963.2.25:26-7 and following figures). Ethmovomerine region in A, dorsal; B, lateral, and C, ventral views. In A, the parasphenoid and frontals have been removed to show the dorsal surface of the vomer.

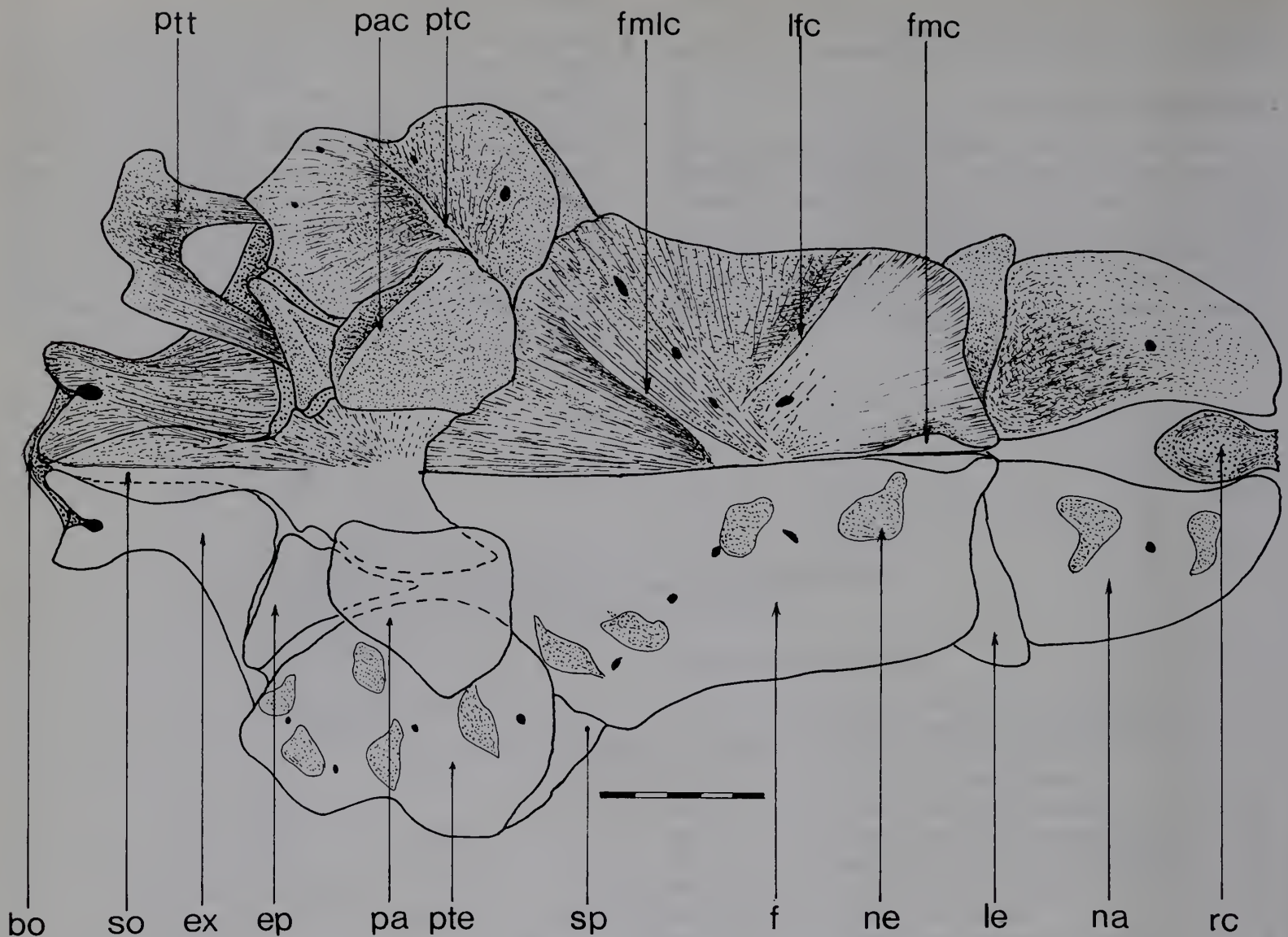


Fig. 3 *Bathygadus favosus*. Dorsal view of cranium.

Nasals large, trough-like, bluntly triangular separated anteriorly by rostral cartilage and ascending premaxillary processes; posteriorly joined in midline by strong connective tissue. Posterior border covers lateral ethmoid, overlapped medially by frontal (Fig. 3). Contains two neuromasts, roofed by skin. In *Gadomus* nasals narrower, broadly separated for their entire length (Okamura, 1970b).

COMMENTS. In other gadoids ethmoid region similar to *Bathygadus* being compressed, ossified plate capping flared, medially elevated cartilaginous base. Ethmoid ossification is taxonomically variable; in Moridae, Merlucciidae, Bregmacerotidae and Muraenolepididae, ossified part of ethmoid separated from vomer by narrower area of cartilage than in other groups. Slope of ethmoid variable; in *Melanonus* (Melanonidae) and *Merluccius* (Merlucciidae) ossified part of ethmoid acutely sloped and confluent with anterior surface of ethmoid cartilage but in *Macruronus* and *Lyconus*, also referred to Merlucciidae, ethmoid is gently sloped as in Bathygadidae. In Gadidae, Lotidae, Muraenolepididae and Ranicipitidae, ethmoid profile almost vertical; concave in Bregmacerotidae. Macrouroid ethmoid morphology similar to that of Gadidae etc, except that ossified portion of ethmoid cartilage is thin vertical lamina bearing anterior and posterior extensions (Okamura, 1970b:59; fig. 35) a feature synapomorphic for macrouroids (see p. 157). *Trachyrincus* has compressed ethmoid but lacks laminar extensions.

Okamura (1970b, fig. 20) incorrectly identified in *Bathygadus* the mesethmoid cartilage as the rostral cartilage.

Among gadoids edentulous vomers occur in Bathygadidae, Eulichthyidae and Muraenolepididae and throughout macrouroids, including *Trachyrincus*. Vomerine teeth variously developed in other gadoids; in Steindachneriidae and Melanonidae single row of small recurved teeth and patch of lateral teeth respectively, outer row teeth in *Melanonus* firmly fixed but larger inner teeth depressible. Vomerine teeth occur biserially in Merlucciidae; in Gadidae, Ranicipitidae and Phycidae teeth more numerous in bands or patches on either side of vomerine head. In Bregmacerotidae, teeth in single row of 3 or 4 along edge of vomerine head, which has prominent anterior extension (D'Ancona & Cavinato, 1965; fig. 18). Patches of vomerine teeth in some genera of Moridae (eg. *Mora*).

Lateral ethmoid in Bathygadidae has single, ventromedial contact point with ethmoid cartilage, as in Melanonidae, but in Steindachneriidae and most other gadoids lateral ethmoid wing contacts parasphenoid medially. Mujib (1967:1361) notes that in *Merluccius* and *Lota* lateral ethmoid has '... the anterior and dorsal processes; the ventral process, which is very prominent in *Gadus*, is entirely lacking'. This is not so, although in Merlucciidae (*Merluccius*) and Lotidae lateral ethmoid extends further posteriorly, greater area of contact with parasphenoid, and more horizontal lateral wing but

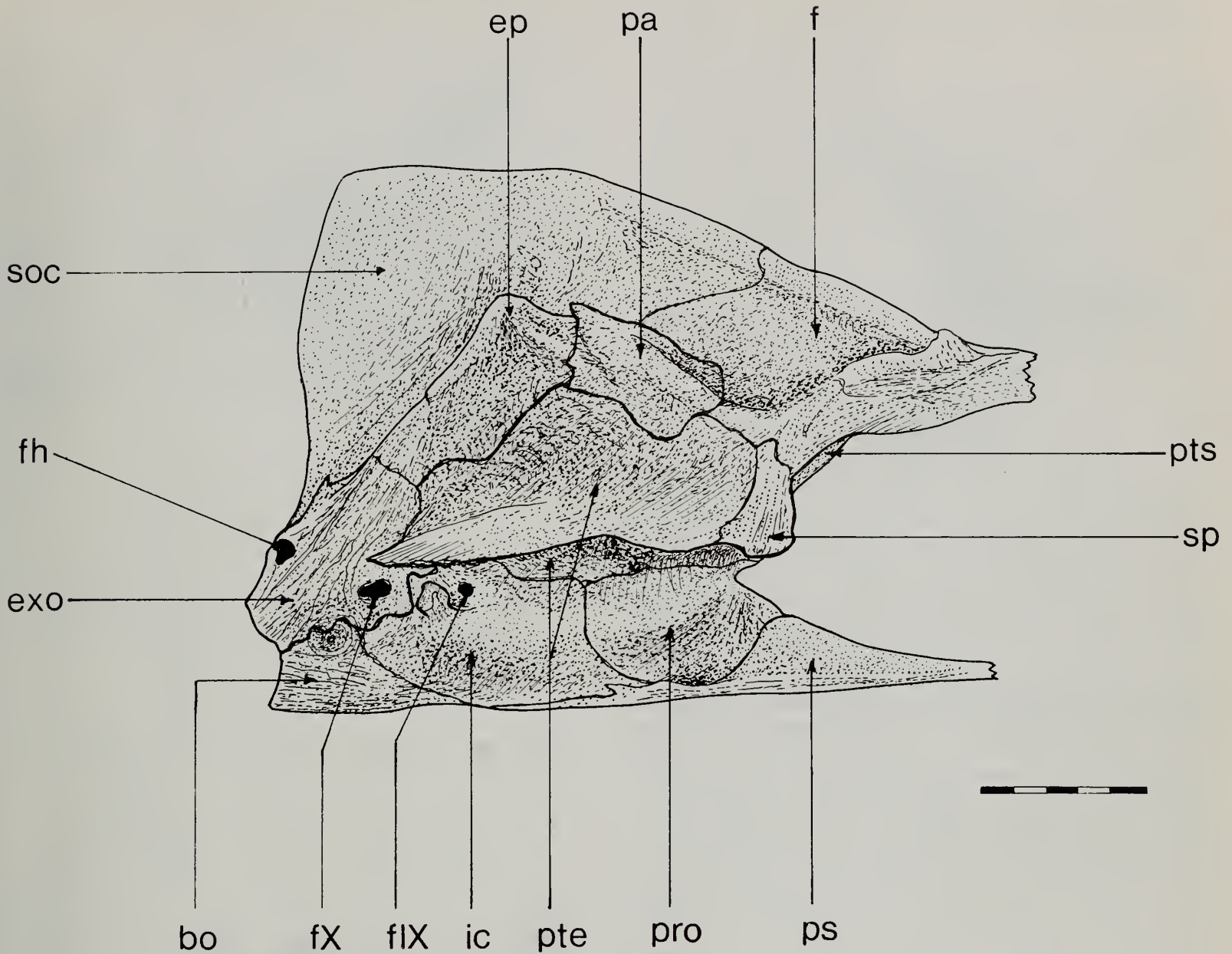


Fig. 4 *Bathygadus favosus*. Lateral view of occipital and otic cranial regions.

retain ventral curvature of wing (called 'ventral process' by Mujib *op. cit.*).

Orbital region (Figs 4, 5)

Pterosphenoids widely separated by optic foramen, each narrowly triangular, lamellate plate overlapping sphenotic posteriorly and contacting medial border of prootic; dorsally, contact with descending lamina of frontal. Anterior border of pterosphenoid contributes to optic fenestra (Fig. 5).

Parasphenoid with flat underside, grooved anteriorly for reception of vomer; dorsally lateral ridges rise anteriorly to meet ethmoid cartilage. Posteriorly shallow ascending process overlaps lower part of prootic; deep ventral indentation between parasphenoid and prootic. At junction of prootic and intercalary parasphenoid widens and overlapped by anteroventral edge of intercalary; narrows posteriorly, forks and sutures to basioccipital; no parasphenoid foramina.

Frontal (f, Fig. 3) broad with slightly concave lateral border above orbit; slight anteromedial crest with right-angled dorsal surface. Diagonal crest extends from lateral point of contact with parietal to midline at centre of frontal. 'Supraorbital' crest anteriorly runs from lateral border of frontal toward

centre. Four foramina in each frontal from which exit branches of supraorbital nerve supplying respective neuromasts. Thin lamina extends from ventral surfaces of each frontal in orbital region.

Interorbital septum (ios, Fig. 2B) extends from posterior lamina of ethmoid cartilage to form medial wall to orbital cavity. Septum of thick membranous tissue extends from lamina of each frontal bone, joining above parasphenoid and forming enclosed channel for olfactory tract. Septum joins prootic, sphenotic and pterosphenoid posteriorly, enclosing rear of orbital cavity. Posterior eye muscles originate from thickened part of septum in midline, anterior to where septum is perforated by optic nerve (Fig. 22C). Where prootic border indented, septal membrane parts from bone leaving opening for trochlear, trigeminal and facial nerve trunks and internal carotid artery.

COMMENTS. Small, widely separated pterosphenoids are commonly encountered in gadoids. Exceptionally, Moridae and some Merlucciidae (*Merluccius*) possess large pterosphenoids forming anterior border to a common trigeminal and facial nerve foramen.

In frontal morphology, bathygadids are plesiomorphic, *viz.*

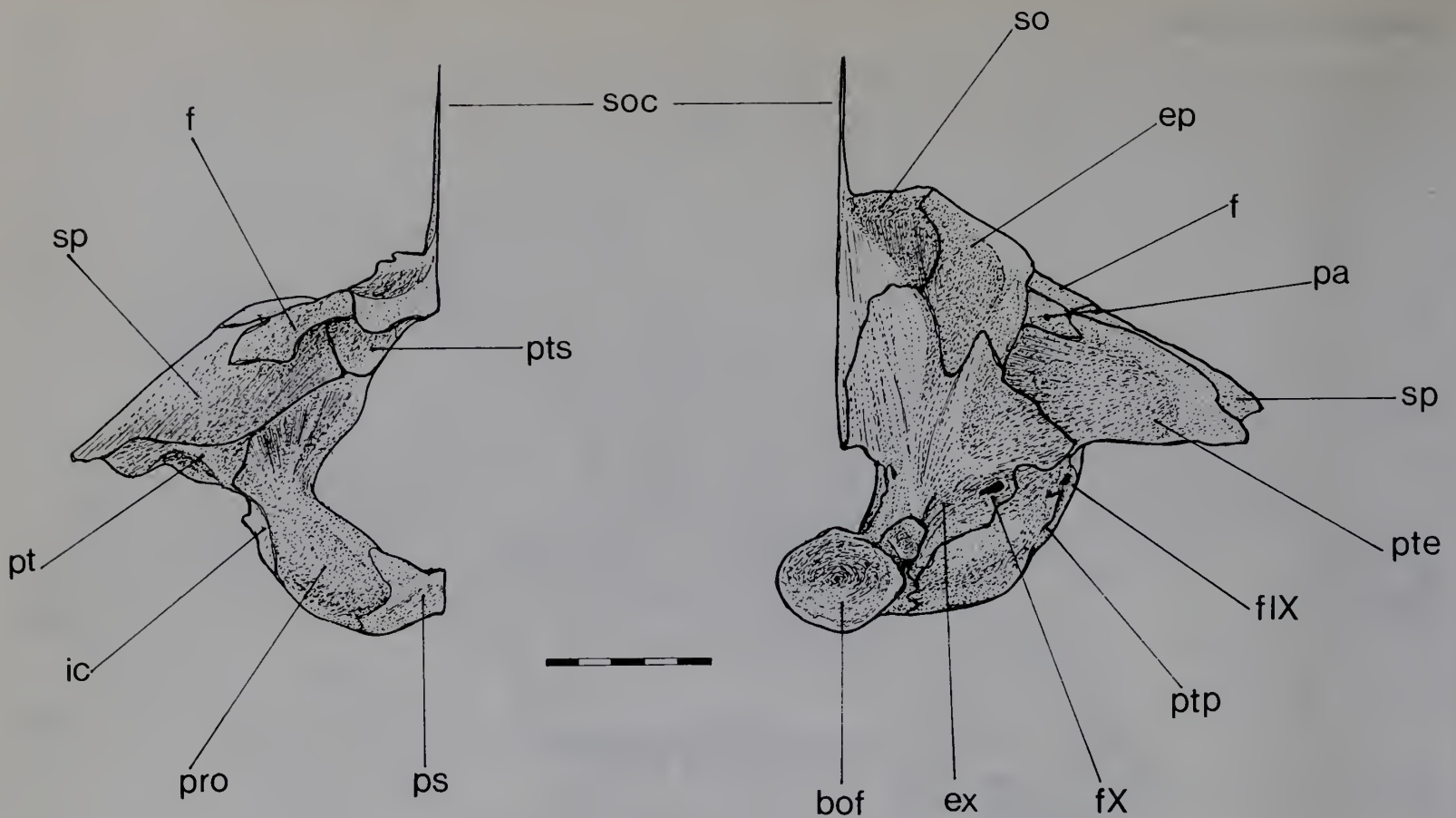


Fig. 5 *Bathygadus favosus*. Cranium in A, anterior, and B, posterior views.

bones broad, bearing simple, X-shaped pattern of ridges and lacking high lateral crest; mucosal cavity absent or wide and open anteriorly. Frontals in gadoids are diverse; in some Gadidae they are narrow interorbitally, fused medially into single plate and have a high lateral ridge; in others mucosal cavity is closed anteriorly (Svetovidov, 1948 illustrations). In Merlucciidae (*Merluccius*) frontal crests in V-formation; in some Phycidae lateral crest uninterrupted and dorsal surface of frontal flat. Development of ventral lamina enclosing olfactory tracts highly variable; lamina may be deep and narrowly separated (*Merluccius*), shallow and narrowly separated (*Molva*, *Phycis*, *Trisopterus*), shallow and broadly separated (*Lota*, *Raniceps*), or deep and narrowly separated anteriorly but shallow and broadly separated posteriorly (*Gaidropsarus*). In Moridae olfactory tracts totally enclosed in osseus canal and interorbital septum usually completely ossified (Svetovidov, 1948; Paulin, 1983), conditions accepted as synapomorphic for the family. Anterior frontal crest variously developed and in some Gadidae (eg. *Trisopterus*) forms medial wall to frontal sensory canal.

Occipital region (Figs 4–6)

The single, median *supraoccipital* is almost square, overlain anteriorly by frontals and laterally by parietals; synchondrally contacts posteriorly epioccipital and laterally pterotic. Supraoccipital crest long and high with a near vertical posterior border. Thin wedge of supraoccipital ventroposterior border forms upper margin of foramen magnum (cf. *Gadomus* where most of foramen's dorsal rim formed by 'supraoccipital' (p. 158; Figs 7, 8). Posteriorly crest narrowly separated from 1st neural spine, a plesiomorphic feature for gadiforms (p. 157).

Posterior cranial wall formed by large *exoccipital* which contacts anterodorsally, supraoccipital and epioccipital *via* synchondral joints, anterolaterally sutured to pterotic and ventrally to intercalar and basioccipital. Posteromedially

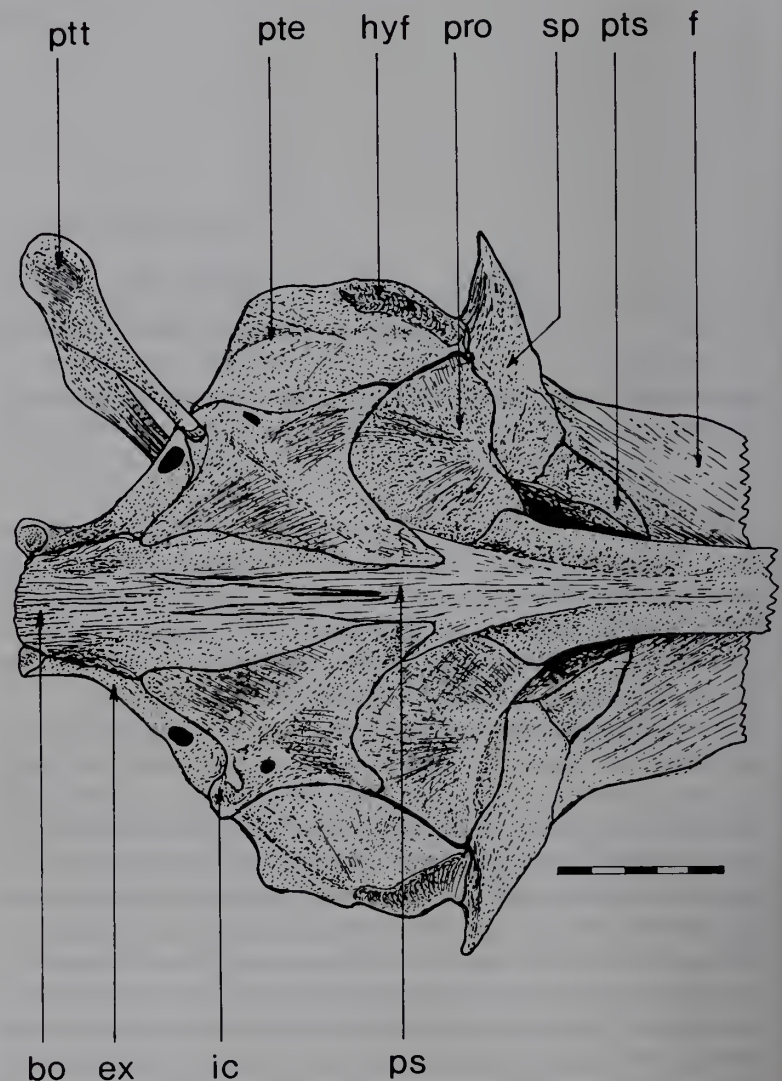


Fig. 6 *Bathygadus favosus*. Basicranium.

exoccipital contributes to border of foramen magnum and posteriorly extends a process whose distal surface forms a fossa for articulation with prezygapophysis of 1st vertebra. Foramen for vagus (X) nerve pierces exoccipital anterolaterally, that for accessory and hypobranchial nerves, posterodorsally.

Basioccipital; single, median bone flooring posterior part of neurocranium (Fig. 6); ventral surface overlain for half its length by parasphenoid; laterally contacts exoccipitals and intercalars; occipital condyle oblate.

Epioccipital; small, pyramidal bone capping posterodorsal corner of cranium, anterodorsal surface overlapped by parietal, medially bordered by supraoccipital, posteroventrally by exoccipital and laterally by pterotic; dorsal surface forms lamboidal crest, contacted by upper limb of posttemporal.

Paired *parietals* small, covering union between pterotic, supraoccipital and epioccipital bones; shallow diagonal crest runs close to parietal posterior border.

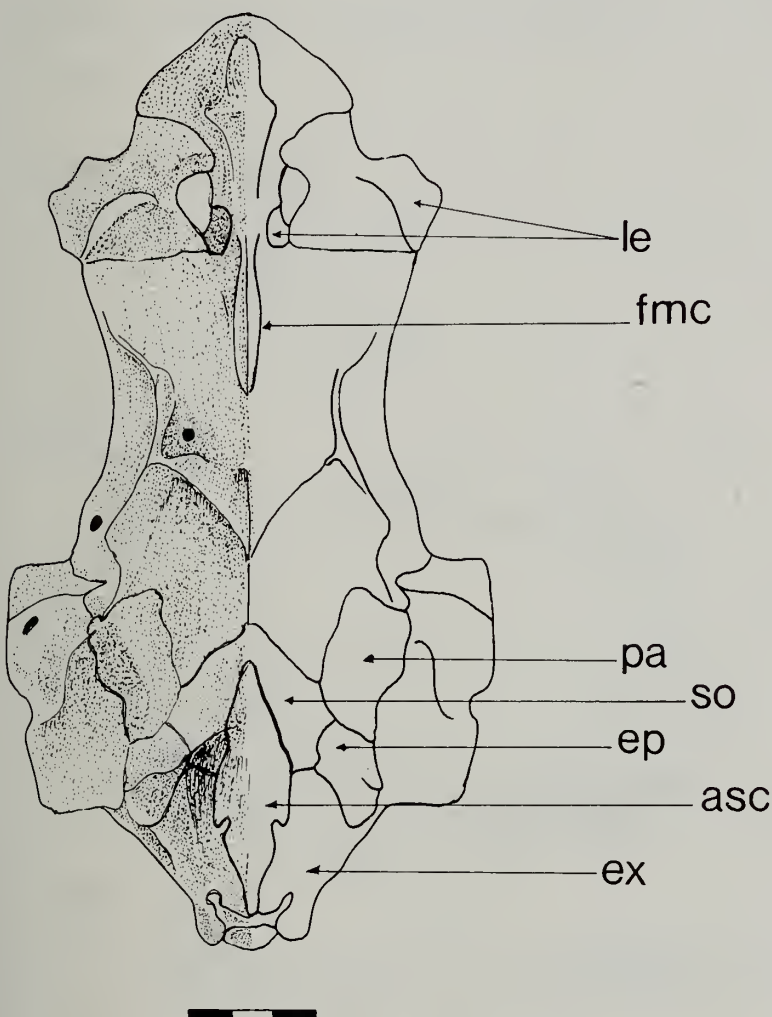


Fig. 7 *Gadomus longifilis* (BMNH 1963.2.25:7-17). Cranium in dorsal view.

Otic region (Fig. 4)

Sphenotic, triangular in dorsal view, overlapped medially by frontal and posteriorly by pterotic leaving narrow area exposed dorsally; anterior, vertical surface lamellar, contacting, anterodorsally, pterosphenoid and ventrally, dorsal rim of prootic.

Pterotic extensive, flaring laterally and roofing nearly entire occipital region; concave dorsal surface receives fan-shaped segment of *epaxialis* muscle (p. 181). Anteriorly, pterotic overlies sphenotic, medially meets both supraoccipital and

epioccipital synchondrally, and anteromedially overlain by parietal; ventral margin contacts both intercalar and prootic and posteriorly, exoccipital; ventrally indented by hyomandibular articulatory fossa.

Posterior region of otic bulla formed by *intercalar* which overlaps posteroventral part of pterotic dorsally and anteriorly, posterior third of prootic; ventrally contacts basioccipital and posteriorly exoccipital. Posterolateral face of intercalar bears small protruberance to which attaches lower limb of posttemporal; anterior to protruberance lies glossopharyngeal (IX) nerve foramen.

Prootic forms border of optic fenestra; anterodorsally contacts pterosphenoid and sphenotic, anteroventrally overlapped by ascending wing of parasphenoid; ventral contact with parasphenoid marked by deep unperforated cavity. Posteriorly, prootic overlapped by intercalar and dorsally by pterotic.

Otolith and inner ear. Saccular otolith (Fig. 22) rather elongate with undulating dorsal border; ventral border rounded and smooth; rostrum pointed, posterior margin broadly rounded. Outer surface bears central prominence with two or three indentations close to dorsal border; inner surface smooth, apart from small ostial and caudal colliculi. Otolith nearly spans entire longitudinal opening between saccular and brain cavities. Horizontal canal runs laterally, then posteriorly along wall of prootic-pterotic junction, passing medially to intercalar wall and upward to posterior vertical canal; latter rises into posterior recess of epioccipital; anterior canal lies beneath parietal and pterotic, and runs along mesial wall of prootic.

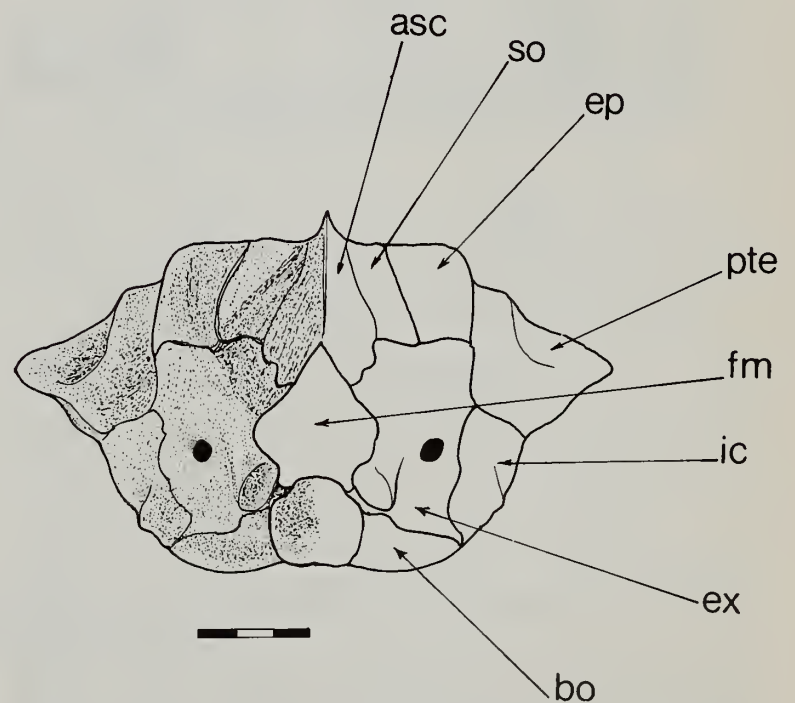


Fig. 8 *Gadomus longifilis* (BMNH 1963.2.25:7-17). Cranium in posterior view.

Circumorbital series (Fig. 9)

First infraorbital (lachrymal) extends from tip of premaxilla to posterior border of eye; sensory canal roofed by outward convexity of bone, lower part of canal covered by skin. Strong, anteriorly situated dorsal process connects infraorbital with ventral surface of lateral ethmoid wing. Contains

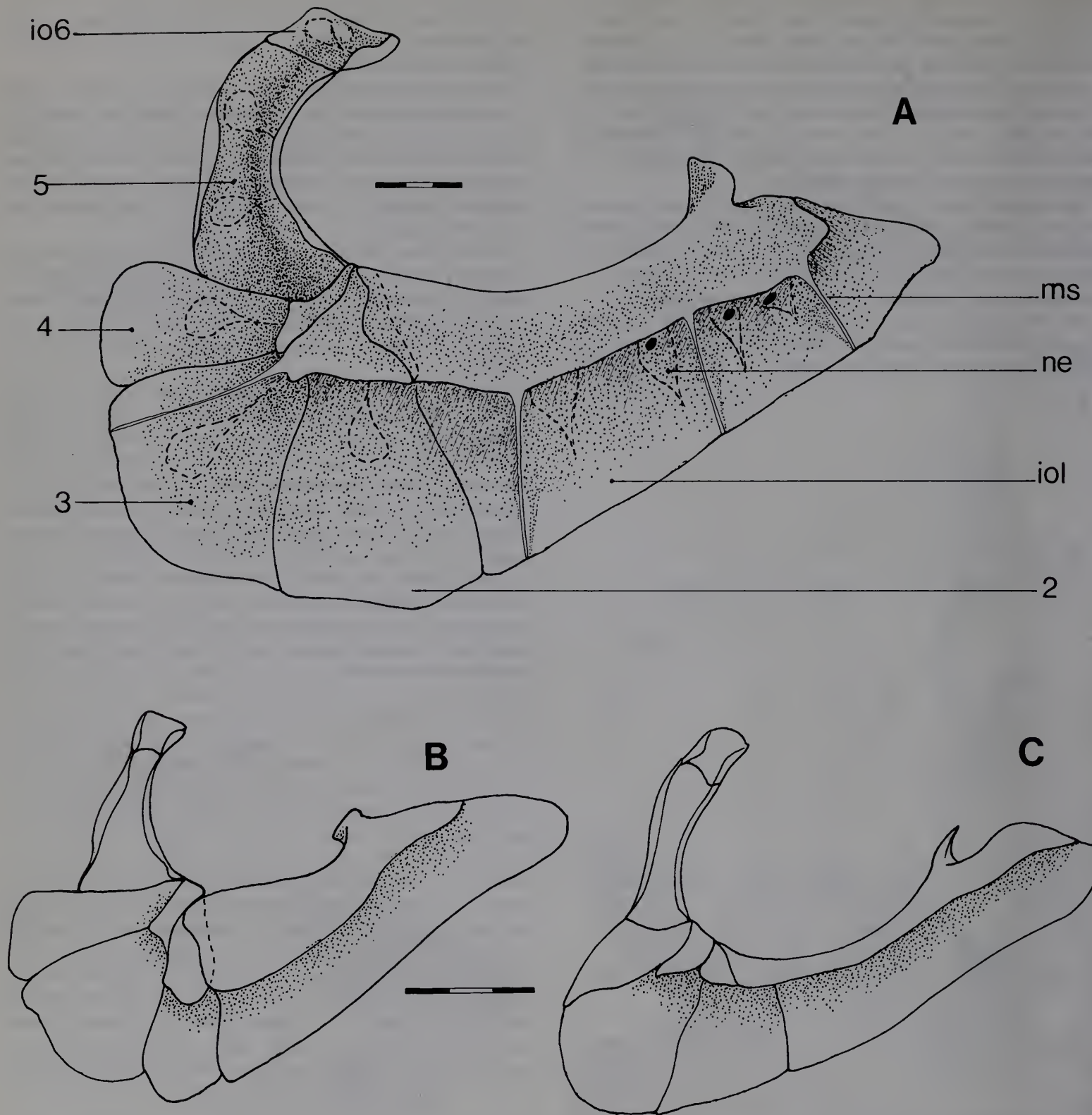


Fig. 9 Circumorbital bones of A, *Bathygadus melanobranchus* (1969.6.26:3227); B, *B. cottoides* (syntype, BMNH 1887.12.7:140.3; C, *Gadamus longifilis* (BMNH 1963.2.25:7-17).

5 neuromasts, two anterior ones close together. *Second infraorbital* as deep as first but only third of its length; orbital border short, bone expanding ventrally. This and subsequent infraorbitals with single neuromast. *Third infraorbital* triangular, forming posteroventral corner of orbit; small portion of bone contributes to orbital rim and marginally forms roof to sensory canal, greater part of canal being covered by skin. *Fourth infraorbital* same length as third, but fifth and sixth half as deep, sixth (dermosphenotic) reduced in length. No antorbital or supraorbital bones.

COMMENTS. Okamura (1970b, fig. 21b) shows a marked

forward inclination of infraorbitals five and six in *Bathygadus antrodes*; this was not found in any *Bathygadus* examined and it is assumed that Okamura's observation is the result of infraorbital displacement in his specimen. Okamura (1970b:38) noted presence in macrouroids of a ventral plate dividing first infraorbital longitudinally; this plate is absent in Bathygadidae and other gadoids but slightly developed in *Trachyrincus*.

Jaw bones (Figs 10, 11)

Maxillaries with strong medial curvature, forming near perfect arc. Each bone thin, narrow and edentulous with

slight posterodorsal process at central point of medial curvature (to which attaches muscle A1B); head of bone comprises raised transverse process which contacts ascending process of premaxilla, and an anteriorly directed medial process whose tip is notched to receive ligament connecting with premaxilla (Figs 10A, B). *Premaxillaries* broadly curved toward symphysis; each with tall mid-lateral process bifurcated ascending process and broadly triangular mid-lateral process (postmaxillary process of Rosen & Patterson, 1969; Fig. 10B). Ventral symphyseal border of anterior ascending process deeply indented, dentigerous surfaces of two bones widely separated across midline; base of ascending process with deep fossa. Ventral surface toothed, teeth closely and irregularly arranged giving granular appearance to dentigerous surface; teeth unicuspid with flat, inwardly curved tips. Along posterodorsal margin of dentigerous area occur more regularly arranged rows (3 or 4) of smaller teeth, their tips pointing upward.

Rostral cartilage wedge-shaped, held firmly in midline between premaxillary ascending processes (Fig. 10A).

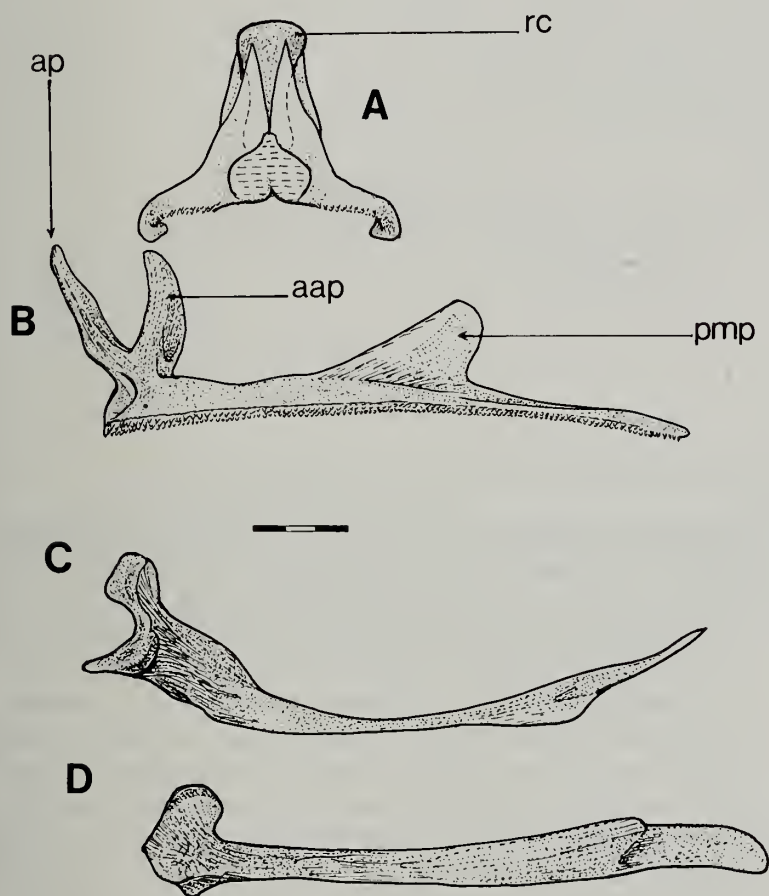


Fig. 10 *Bathygadus melanobranchus* (BMNH 1969.6.26:3227 and following figures). Upper jaw bones: A, symphyseal attachment of the premaxillae; B, premaxilla in lateral view; C, maxilla in dorsal view, and D, in lateral view.

Dentaries (d, Fig. 11) angled toward midline and begin to curve anteriorly; bones have strong syndesmotical symphyseal connection; coronoid process shallow, rising gently to meet anguloarticular. Posteriorly dentary forked, posterior border of lower branch with long vertical surface abutting anguloarticular. Underside of dentary deeply channeled, medial wall of channel deepening posteriorly, its lateral, open part covered by skin containing five neuromasts. Dentigerous surface narrow, more so on rise of coronoid process; teeth

small, conical with inwardly curved tips similar to those of premaxilla arranged irregularly with 4 or 5 in transverse series. Narrow, triangular anterior portion of *anguloarticular* (aa, Fig. 11) articulates between posterior forks of dentary to end in deep articular fossa that receives quadrate condyle; lower part of bone almost square, medially with indentation in which lies posterior part of Meckelian cartilage together with minute *coronomeckelian* bone (cm, Fig. 11). Three ligaments link anguloarticular with quadrate, one lateral and two medial. Of the latter, one attaches to anterior, the other to posterior surfaces of quadrate condyle. *Retroarticular* (ra, Fig. 11), J-shaped, occupying posteromedial corner of anguloarticular. *Labial ligament* surrounds the border of lower jaw attaching to distal margin of upper jaw (see Howes, 1988 for detailed description).

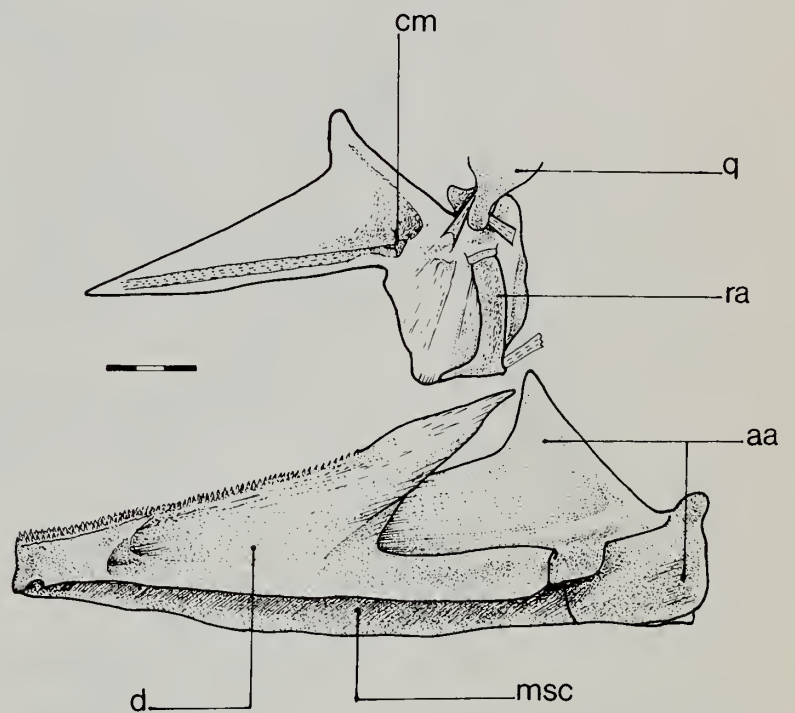


Fig. 11 *Bathygadus melanobranchus*. Lower jaw bones; above, medial view of anguloarticular and retroarticular and their ligamentous connections; below, lateral view of entire jaw.

COMMENTS. Marshall (1966) and Okamura (1970b) considered protractile premaxillaries diagnostic for macrouroids. However, 'protractile' is ambiguous. Marshall, comparing the gadoids *Macruronus*, *Lyconus* and *Steindachneria* with macrouroids, noted premaxilla in those taxa to be '... no more than slightly protractile' and '... with rather short pedicels'. For Macrouroidei Okamura gives 'Premaxillary more or less protractile' and for Bathygadinae, 'premaxillary pedicel lower than one-third the length of the premaxillary ramus'; in bathygadids measured the premaxillary ascending process, which is slightly larger than the articular, has variable length (*Bathygadus*, 20.6–31.6%; *Gadomus* 17.8–22.7% pmx ramus). Ascending and articular processes in other gadoids are less than 30% length of ramus. Fahay (1989) noted length of premaxillary ascending process in *Steindachneriidae* approached that in macrouroids; we measure length as 25% of ramus, which lies within the gadoid range.

Okamura (1970a) recognised bathygadids differ from macrouroids in a centrally situated, triangular postmaxillary process of the premaxilla. In macrouroids the process is situated close to, or at the posterior extremity of the ramus

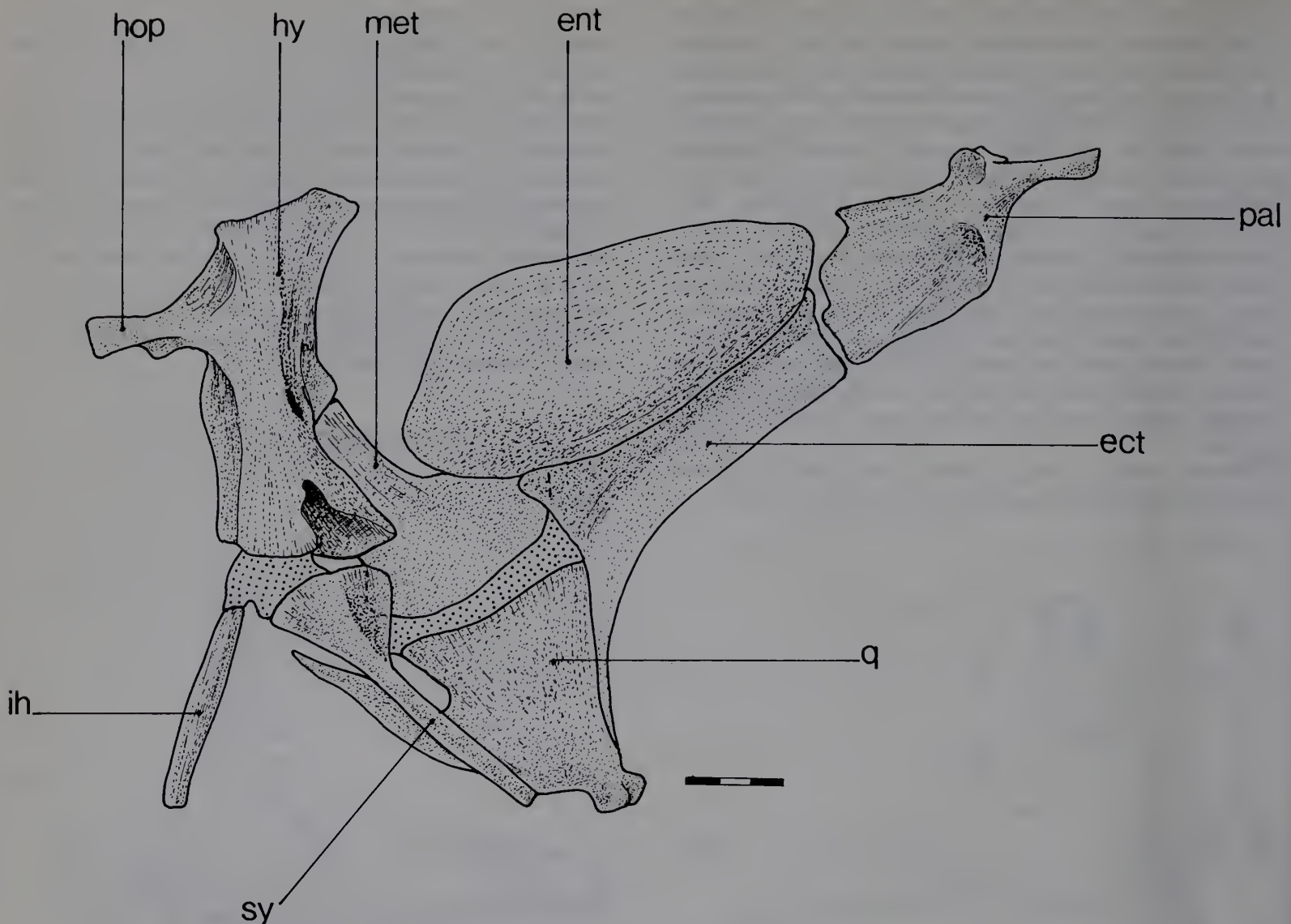


Fig. 12 *Bathygadus melanobranchus*. Palatoquadrate and suspensorial bones in medial view.

and is either blunt or deeply bifurcate posteriorly. In gadoids, position and degree of development of postmaxillary process is variable. Most Moridae possess a broad and posteriorly directed process as in Bathygadidae. In Steindachneriidae the anterodorsal border of the process is rounded and situated centrally on the ramus. The process is small in most Gadidae lacking a marked indentation (gadoid notch of Rosen & Patterson, 1969:401) of its posteroventral border. In Merlucciidae (*Merluccius*) the process is sharply angled posteriorly with a broad and deep notch; in Phycidae it is situated at posterior extremity of premaxilla and may be separated from the ramus by a long shallow notch.

Okamura (1970b) recognised a difference between bathygadids and macrouroids where the former has a slender, straight and posteriorly stepped maxilla with a simple articular head. The macrouroid maxilla is convex with an enlarged, complex head and truncated or sloped posterior margin. The general maxillary shape in gadoids is uniformly slender and straight but there is variability in the shape of its distal portion, viz. rounded in Moridae, many Gadidae; subtriangular in Merlucciidae, expanded ventrally into a rectangular flange (Phycidae); spade-like (Muraenolepididae). The 'stepped' distal portion of the maxilla of bathygadids is present in Steindachneriidae and Melanonidae. In all these taxa is a well-developed labial ligament (Howes, 1988) with complex fastenings to upper and lower jaws; the posterior portion of

the maxilla is anchored by a thickened stump (supramaxillary ligament of Howes, 1988) which fills the 'tread' of the step between the maxillary process and ramus.

In summary, little evidence from jaw morphology supports a relationship between Bathygadidae and Macrouroidei, apart from long premaxillary ascending and articular processes. It is presumably this feature which caused Marshall (1966) and Marshall & Cohen (1973) to list jaw protractibility as one of the characters embracing *Bathygadus* and *Gadomus* with macrouroids. Contrariwise, there are many more resemblances with upper jaws of gadoids, particularly, the large, centrally situated triangular postmaxillary process on the premaxilla.

Palatoquadrate (Figs 12, 13)

Orientation of the palatoquadrate bones is such that anterior articulation with the skull lies at the same level as that of the hyomandibular articulation; dorsal border of palatine and pterygoid bones forms an angle of 45° to horizontal.

Palatine edentulous with almost square, lamellate body (dermopalatine) bearing slight lateral ridge; posterior border is near vertical and articulates with ectopterygoid. Anteriorly, a long process (rostropalatine articulation) extends to overlie maxilla, its base raised into a boss whose medial surface abuts ethmoid cartilage; palatine-premaxillary ligament attaches to anterior surface of boss.

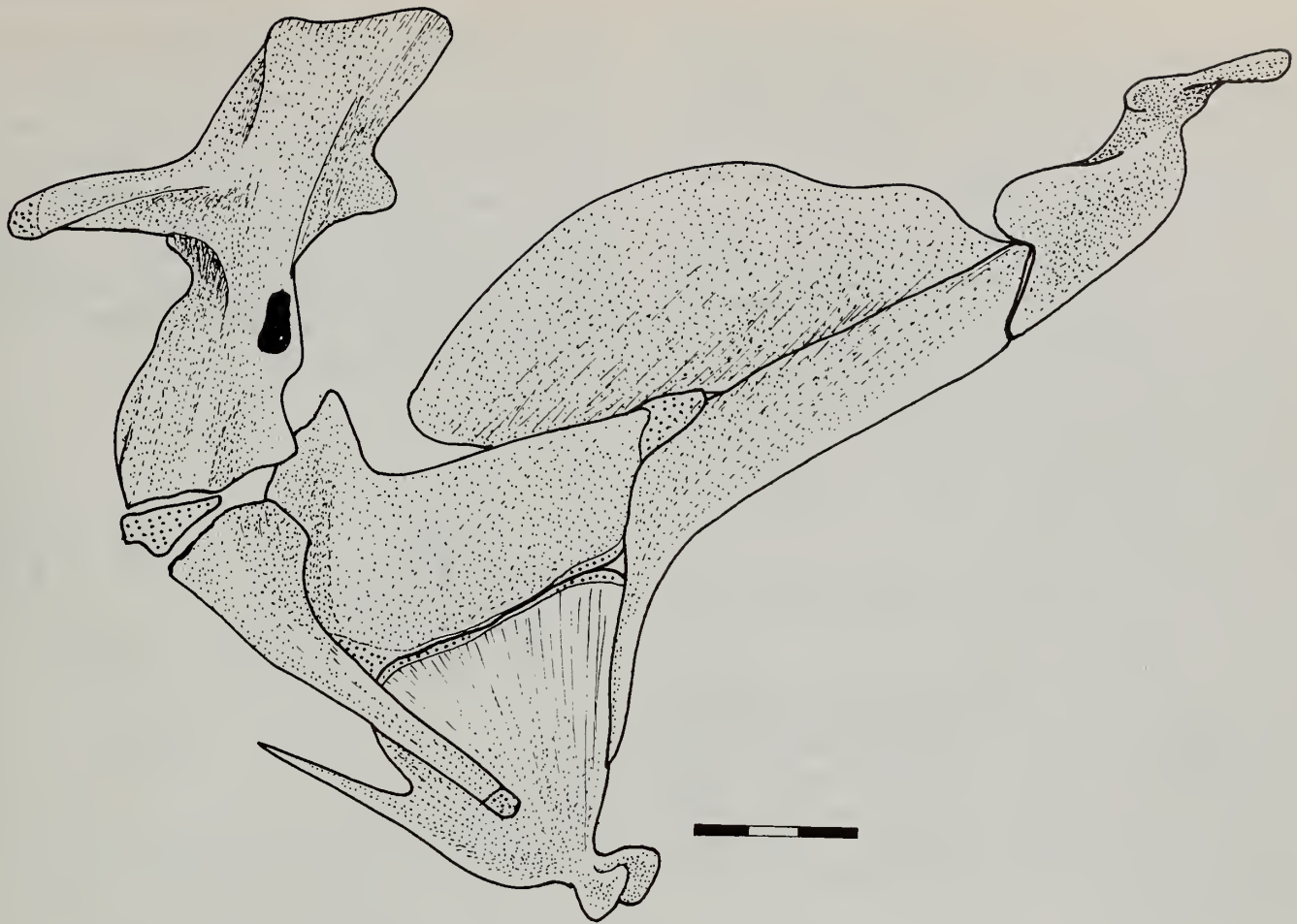


Fig. 13 *Gadomus longifilis* (BMNH 1963.2.25:7-17). Palatoquadrate and suspensorial bones in medial view.

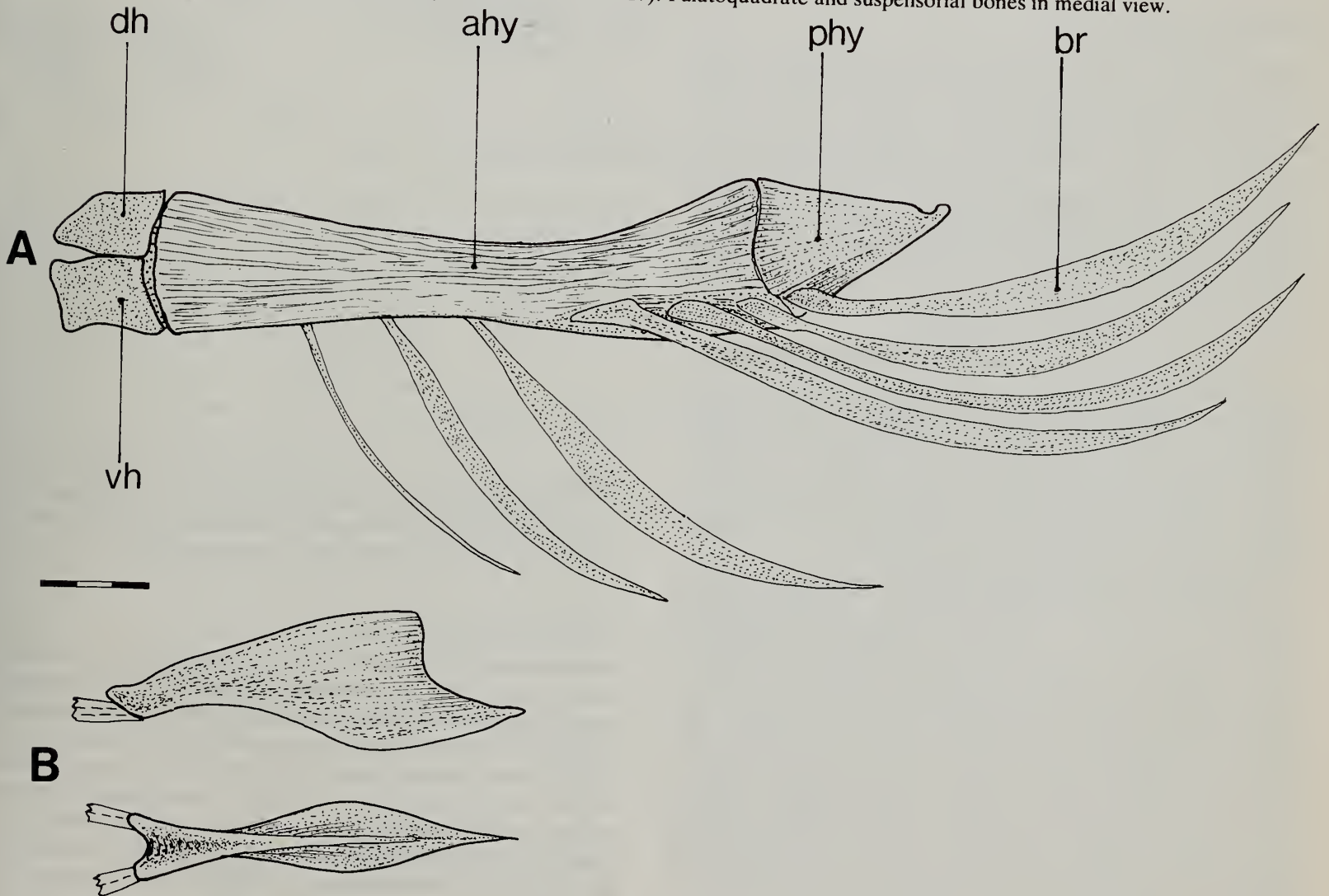


Fig. 14 *Bathygadus melanobranchus*. A, hyoid bar in medial view; B, urohyal in lateral (above) and dorsal (below) views.

Ectopterygoid deep, anterior border meets palatine in vertical synchondral joint; body of bone slopes mesiad at steep angle, posterodorsal tip lying beneath metapterygoid (Fig. 12). Posteroventral stem lies in anterior groove of quadrate. Ventral borders of palatine and ectopterygoid connected to maxilla by broad skin fold.

Quadrate large, trapezoidal; anterior grooved surface articulates with ectopterygoid for almost its entire length; articular condyle broad, deeply indented. Quadrate posterior border contacts metapterygoid *via* strip of cartilage; posteroventral border notched, produced into acuminate strut.

Entopterygoid large, nearly rectangular, sloped mesiad with dorsal border underlying lateral edge of parasphenoid. Posterior border slightly angled, widely separated from hyomandibular. Ventrally, meets meta- and ectopterygoid dorsal borders *via* connective tissue.

Metapterygoid small, axe-shaped having weak attachment to outer flange of hyomandibular and meeting dorsal border of quadrate *via* cartilaginous strip.

COMMENTS. In *Gadomus* the palatine has a strong medial flange and is smaller than in *Bathygadus* (Fig. 13). Gilchrist & Von Bonde (1924) were in error in reporting palatine teeth in *Gadomus capensis* (see Iwamoto, 1986). Among gadoids palatine teeth occur only in Melanonidae. *Gadomus* differs from *Bathygadus* in having a prominent dorsoposterior metapterygoid process and a metapterygoid-hyomandibular space (*cf.* Figs 12 & 13).

Hyoid arch (Figs 12–15)

Hyomandibular with flat outer surface and vertically ridged medial surface; slight depression on dorsolateral face (Fig. 12); anterior border slightly concave, lower part meets metapterygoid; posterior border nearly straight with, dorsally, long, flat posteriorly directed process articulating with operculum. Dorsal articular surface short with slight anterior rise; medial shaft forming body of bone perforated anteriorly and posteriorly for hyoid and mandibular branches of ramus hyomandibularis of facial (VII) nerve. Hyomandibular shaft hollow, allowing passage of mandibular branch of facial which exits from indented medial border.

Symplectic with expanded dorsoposterior surface lying medial to posteroventral edge of metapterygoid contacting, synchondrally, ventral border of hyomandibular. Anterior part of symplectic rod-like, lying medial to ventral surface of quadrate.

Interhyal long, rod-shaped with same length as symplectic shaft. Dorsally articulates with cartilage intervening between ventral border of hyomandibular and symplectic; ventrally articulates with posterior tip of posterohyal.

Dorsohyal and *ventrohyal* small, cone-shaped bones synchondrally joined to one another and to anterior border of anterohyal (Fig. 14); ventrohyals attached ligamentously across midline; dorsohyals separated by basihyal. Anterohyal long, slender with vertical anterior and posterior borders. Posterior part almost rectangular; three *branchiostegal* rays attach to ventral surface and three to ventrolateral face (Fig. 14A). *Posterohyal* slender, triangular with extended posterior vertex articulating with interhyal; anterior border vertical, joining synchondrally with anterohyal. Posterior branchiostegal ray articulates within ventrolateral groove. *Urohyal* (Fig. 14B) small with shallow medial crest whose dorsal surface is produced into triangular plate; ventrally, arrow-shaped.

COMMENTS. Okamura (1970*b*) drew attention to the condition

of the dorsohyal in macrouroids where it lies horizontally, making firm midline attachment with its partner. This is not a feature unique to macrouroids; among gadoids a range of conditions is present; almost vertical in Steindachneriidae (Fig. 15A), slightly inturned in Muraenolepididae, Eulichthyidae, Merlucciidae (Figs 15C, E). In Bregmacerotidae, the ventrohyals also contribute to a flat dorsal surface formed by the dorsohyals and are in midline contact so preventing basihyal from extending forward (Fig. 15B); horizontally aligned dorsohyals also occur in Lotidae, Ranicipitidae, Moridae, Phycidae and Trachyrincidae.

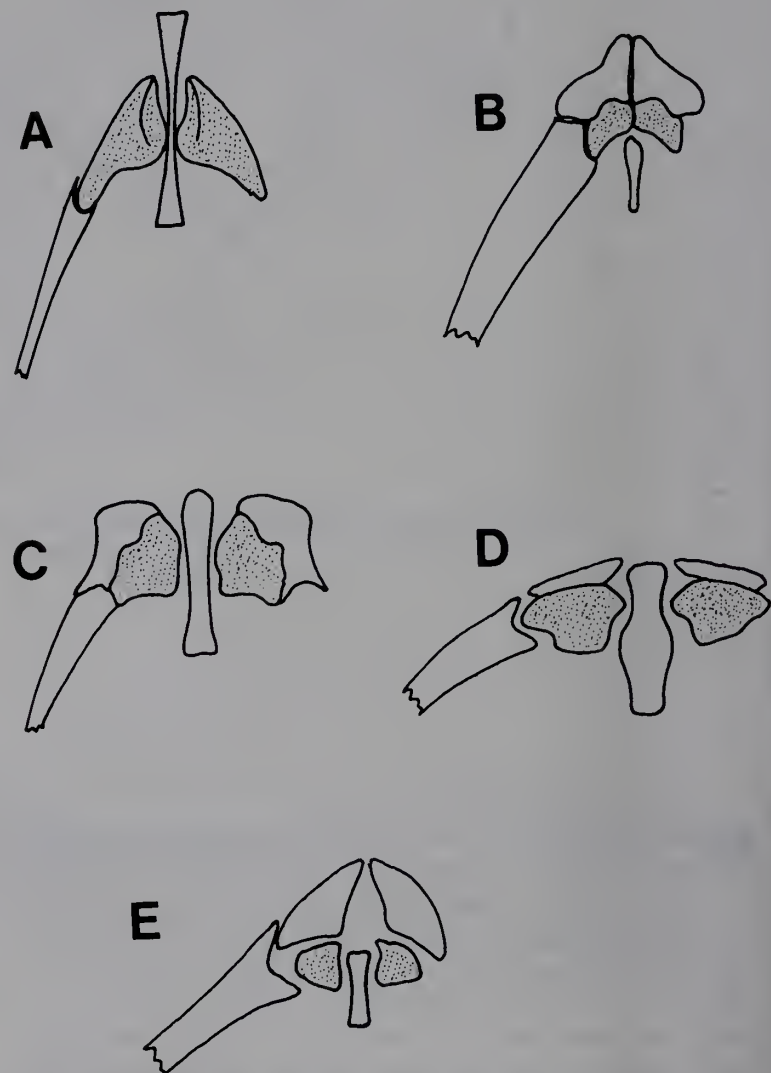


Fig. 15 The relationships of the basihyal to the dorsohyals in A, Steindachneriidae; B, Bregmacerotidae; C, Merlucciidae (*Macruronus*); D, Eulichthyidae; E, Merlucciidae (*Merluccius*). Dorsohyals are shaded, ventrohyals blank.

Opercular series (Figs 16, 17)

Preoperculum large with irregular anterior margin bearing flange along outer border, forming partial roof to sensory canal which contains four neuromasts, two ventrally, one at curvature of bone and one at posterior limb. Ventral part of bone curved mesiad, both posterior and ventral borders fretted. *Suboperculum* flat, ovoid, lying along posteroventral margin of operculum and contacting posterior edge of preoperculum. *Interoperculum* long, shallow, crook-shaped lying medial to preoperculum, its highest point attached to both preoperculum and hyomandibular by dorsally bifurcated ligament (Howes, 1988; 1989). *Operculum* small, triangular

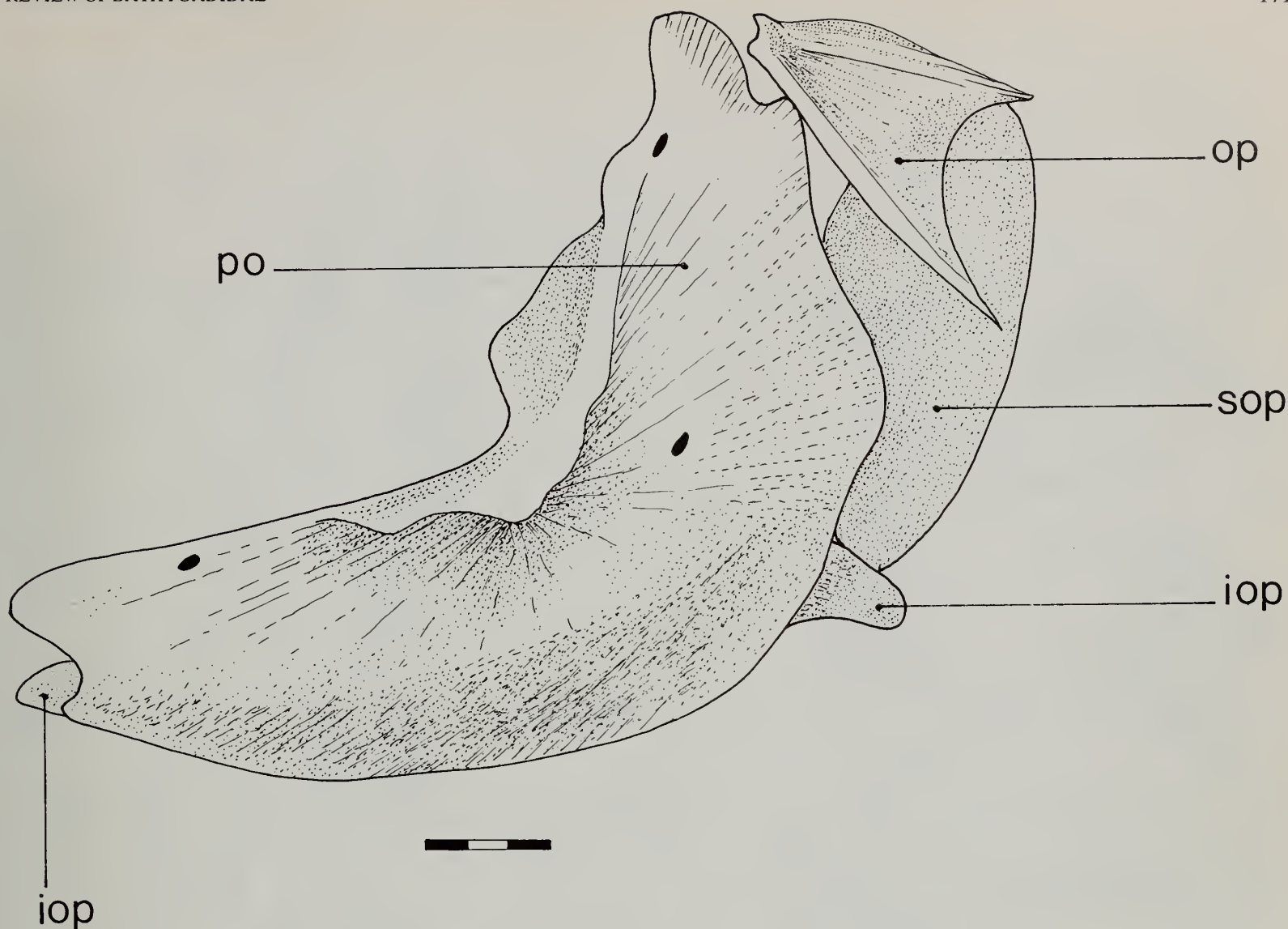


Fig. 16 *Bathygadus melanobranchus*. Opercular series in lateral view.

with markedly concave border, small condyle articulates with hyomandibular opercular process. Two well-developed ridges radiate from condylar part, lower ridge forming preopercular border of bone. Anterodorsal part of operculum lies beneath overhanging posterior pterotic border and restricts maximum elevation of operculum.

COMMENTS. Okamura (1970b:51) noted two interopercular morphotypes, one common to *Bathygadus* and some macrouroid genera, the other to *Gadomus* and some other macrouroids. There is a basic difference in shape between the interoperculum of the two genera, that of *Bathygadus* being shallow with a concave ventral margin, that of the latter being deep and more rectangular. However, within *Bathygadus* there is much variation in shape from that of the *Gadomus*-type to the crook-shaped form which Okamura regarded as *Bathygadus*-type (Figs 17, 8–11). Wide variability is not so evident in *Gadomus* (Fig. 17, a-k). As well as occurring in some macrouroids, the *Bathygadus* interopercular morphotype is present in the bythitoid *Lamprogrammus* (Fig. 171), so it seems that similar interopercular shapes may not be reliable as indicators of phylogenetic relationship, but rather reflect functional demands.

In *Bathygadus* a wide space occurs between the preoperculum and operculum covered by the black membrane lining the bones' inner surfaces. In common with gadoids the operculum is separated from the preopercular border whereas in macrouroids it is overlapped by the preoperculum

(Okamura, 1970b). An interosseous space occurs between symplectic and preoperculum, a feature common to gadoids; in macrouroids the area is occluded by symplectic expansion.

Branchial arches (Fig. 18)

Medial, basal branchial arch elements comprise a narrow-waisted, ossified *basihyal*, posteriorly overlapped by arrow-shaped 1st *basibranchial* comprising ossified plate overlying thin cartilaginous rod; fully ossified large pyriform 2nd *basibranchial*, and a medial cartilage lying between 4th *hypobranchials*. The latter are long, 1st *hypobranchial* with four slender gill-rakers along outer margin and six, club-shaped rakers along inner; 2nd *hypobranchial* with six outer and five inner (denticulate) rakers; 3rd short, with two or three large denticulate outer rakers.

Ceratobranchials elongate, 1st with 16–17 long, spear-like outer rakers, 12–14 club-shaped, denticulate inner rakers; 2nd, 3rd and 4th each with 10–12 large club-shaped outer and inner rakers; 5th narrowly triangular with concave underside, toothed surface bears numerous, short, conical teeth with slightly posteriorly curved tips. First *epibranchial* with 6–7 long, slender outer rakers, 3–4 club-shaped, denticulate inner rakers; 2nd with 3 outer and 3 inner; 3rd and 4th each with 2 outer and 1 inner raker. Each epibranchial bears an uncinat process. Epibranchial 3 bears a long, near rectangular tooth plate along its medial surface. *Pharyngobranchials* number

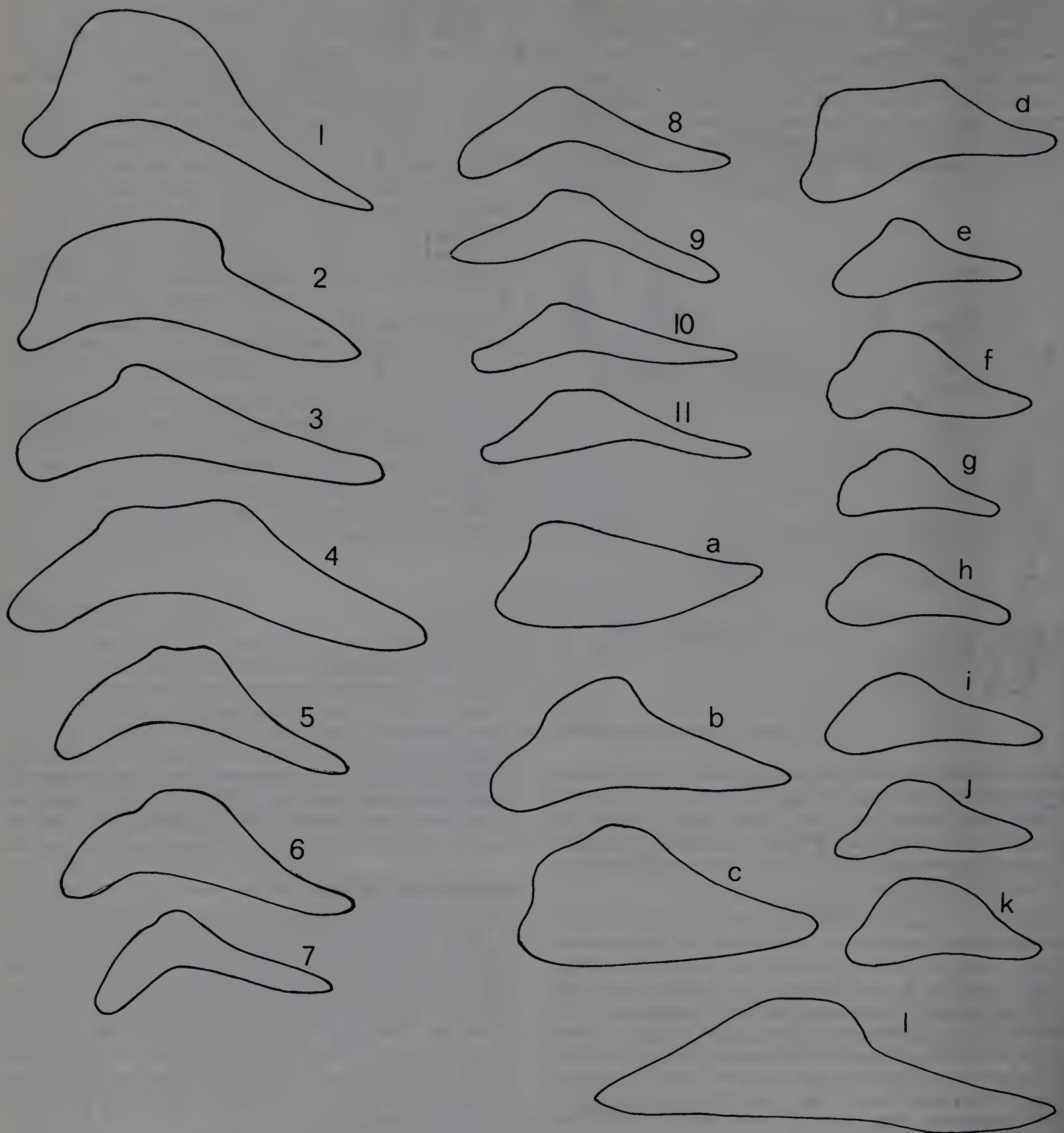


Fig. 17 Interopercular shapes in *Bathygadus* (1–11), *Gadomus* (a–k) and the ophidiiform *Lamprogrammus niger* (1). 1, *B. cottoides*, 2, *macrops*, 3, *favosus* 4, *melanobranchus* 5, *sulcatus*, 6, *nipponicus*, 7, *bowersi*, 8, *spongiceps*, 9, *entomelas*, 10, *filamentosus*, 11, *antrodes*; a, *G. multifilis*, b, *capensis*, c, *arcuatus*, d, *furvescens*, e, *longifilis*, f, *colletti*, g, *melanopterus*, h, *micronema* (type; = *melanopterus*), i, *introniger*, j, *denticulatus*, k, *magnifilis*.

three; 1st small, cartilaginous and lunate; 2nd and 3rd large, ossified each bearing tooth-plates (two plates on 3), teeth moderately developed, conical, curved mesiad. *Interarcual cartilage* small, lying in collagenous strand linking 1st and 2nd pharyngobranchials (Travers, 1981).

Gill-rakers (Fig. 18B–D) on outer margin of 1st ceratobranchial, thin, blade-like, forward facing margin of raker bearing irregular rows of conical denticles. Almost always a single, dorsally directed denticle at tip of raker (Fig. 18B), no denticles on raker's posterior margin. Club-shaped rakers

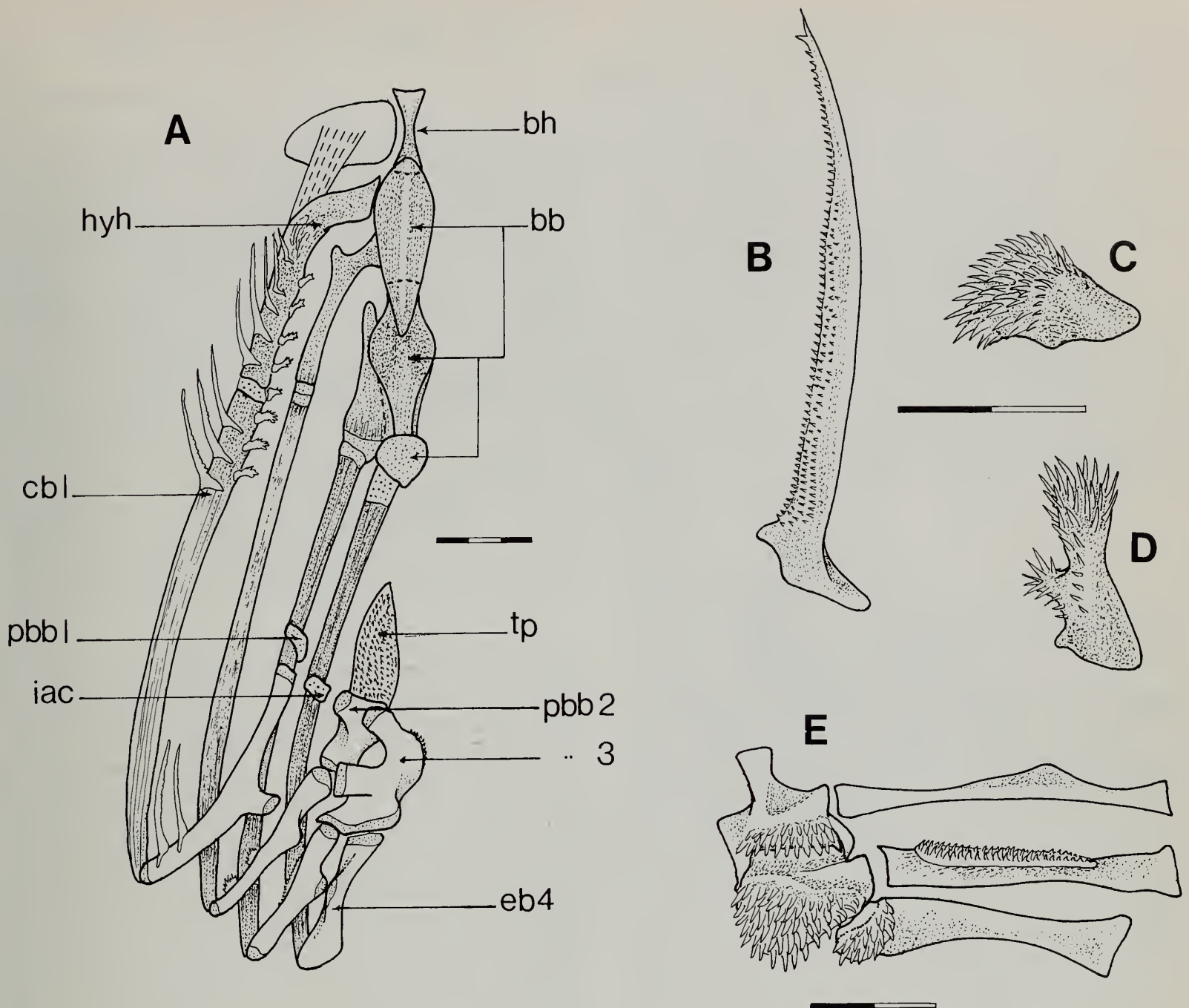


Fig. 18 *Bathygadus melanobranchus*. A, branchial arch in dorsal view. B, gill-raker on outer surface of 1st cerato-branchial. C, ephibranchial gill-raker. D, gill-raker of inner ceratobranchials. E, ventral view of epibranchials 2-4 and pharyngobranchials 2 and 3, showing tooth-patch along epibranchial 3.

which occur on inner surfaces of 1st gill-arch and outer and inner margins of 2nd, 3rd and 4th arches are; 1) tall, often bifurcate armed with long pointed denticles arranged along anterior and lateral margins, and situated at tip of each bifurcation, confined to ceratobranchials; (Fig. 18D); 2) short, wide with sloped outer and rounded inner margin, armed with cluster of pointed denticles, confined to epibranchials (Fig. 18C).

Pectoral girdle (Fig. 19)

Supracleithrum splint-like, slightly expanded distally with smooth rounded surface articulating with distal depression of posttemporal; lies at 45° angle to cleithral limb. *Cleithrum* with short, upright upper limb and long narrowly pointed lower limb angled at 55° to horizontal. Posterior lamina of upper part broadly triangular with ventromedial cleft from whose base a narrow lamina extends horizontally (scapular

articular process) to contact narrow *scapula* along its posterior surface and *coracoid* along its ventral edge. *Coracoid* trowel-shaped, contacting *scapula* and *cleithrum* posteriorly; anterior blade extends forward to almost contact medial lamina of lower cleithral limb leaving wide coracoid-cleithral aperture.

Baudelot's ligament runs from upper medial surface of *supracleithrum* to turn immediately posteriorly, loop around dorsal tip of cleithral limb then pass anteromedially and downward beneath epaxial muscle mass to attach to 1st centrum (Figs 19 & 25).

A single *postcleithrum* extends ventroposteriorly, firmly attached to hypaxial musculature (Fig. 25). *Actinosts* number 5 in *Bathygadus melanobranchus* and *B. favosus* (3 in *B. antrodes*, (Okamura, 1970b) and *B. melanobranchus*; 14-17 fin rays articulate with actinosts.

COMMENTS. Okamura (1970b:93) noted variability among

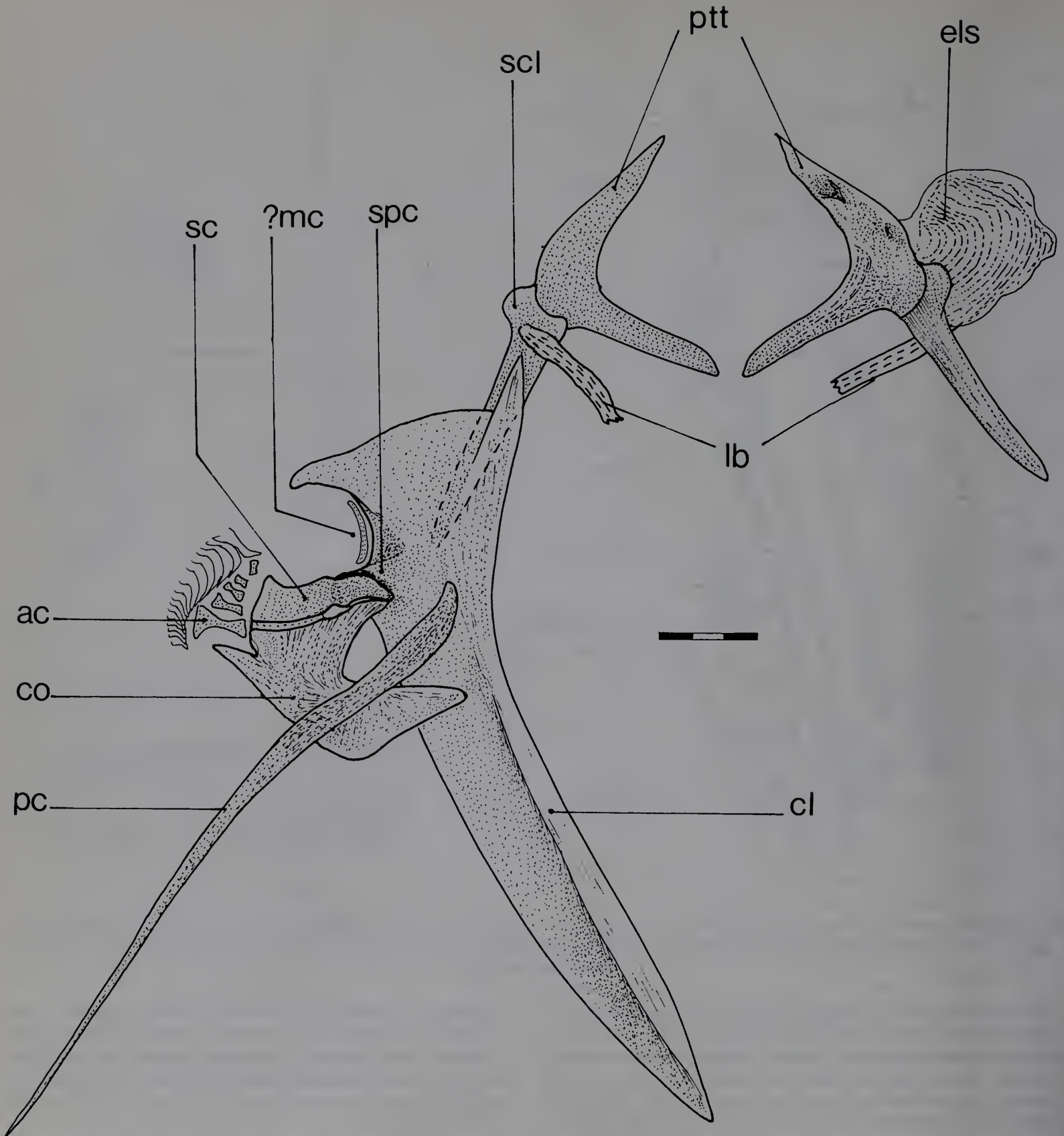


Fig. 19 *Bathygadus favosus*. Pectoral girdle and posttemporal in medial view and (above right) lateral view of posttemporal with enlarged lateral line scale.

gadoids of the placement of the scapular foramen. In macrouroids and most gadoids it lies between the scapula and coracoid as in *Bathygadus melanobranchus*, *B. favosus* and *Gadomus longifilis*; in *B. sulcatus*, *B. filamentosus* and *G. melanopterus* it lies within the scapula (Gilbert & Hubbs, 1916) and in *B. antrodes* almost entirely within the scapula (Smith & Radcliffe, 1912). A brief survey among gadoids shows the foramen lies between the scapula and coracoid in

all families, although in the two examined morid genera *Lepidion* and *Physiculus* it lies within the scapula (see also Regan, 1903:463). The size of the medial cleithral lamina which contacts the scapula may have classificatory relevance being well-developed in Bathygadidae, Moridae and Trachyrincidae; in most gadoids it is usually absent and only slightly developed in Lotidae, Merlucciidae and Gadidae. In *Bathygadus melanobranchus* an oblong cartilage lies along the

cleithral border of the scapula (?mc Fig. 19) which may represent a mesocoracoid, otherwise lacking in gadoids.

Posttemporal (Figs 3, 6, 19)

Posttemporal is boomerang-shaped, its dorsal limb attaching to epioccipital summit, its narrow ventral limb ligamentously to lateral process of intercalar. Passing between the limbs is a broad segment of *epaxialis* muscle which inserts on pterotic (Fig. 25). A small V-shaped opening occurs near junction with supracleithrum and is narrowly separated from wide aperture extending across width of limb. Running along anterior border of posttemporal is main branch of *ramus lateralis accessorius* (RLA) nerve; pectoral-pelvic branch of nerve detaches from main trunk, crosses dorsal face of posttemporal and runs down posteromedial border. Ventrally, posttemporal attaches to rounded upper part of supracleithrum *via* cartilaginous meniscus.

Anterolateral to posttemporal lie one or two thin, gutter-like elements containing neuromasts which provide a posterior continuation of pterotic sensory canal linking it with the enlarged scale (see below) of the lateral line. These elements are identified as *extrascapulars*; their large, open canal appears to have no connection with the small posttemporal canal.

COMMENTS. Association between the posttemporal and lateral cranial wall is variable in gadiforms. In all macrouroids examined and *Trachyrincus* the lower limb of the bone is broad, flat articulating firmly and broadly with the intercalar. The pterotic extends backwards to contact the lower limb (sometimes leaving only a small ventral gap) thus forming a solid wall. This type of contact is present in some gadoids, eg. *Molva*, *Lota*, *Brosme* (all Lotidae), there is only partial contact of pterotic with posttemporal limb, the *extrascapulars* intervening laterally between the pterotic and posttemporal. Posttemporal morphology in Merlucciidae, Moridae, Ranicipitidae, Melanonidae and Steindachneriidae resembles the (presumed plesiomorphic) condition of Bathygadidae where the lower limb is slender, cylindrical and contacts the intercalar cartilaginously. *Trachyrincus* possesses a unique condition, *viz.* posttemporal bears extensive medial lamina contacting exoccipital (Regan, 1903:462).

An *enlarged scale* (els, Fig. 19) attaches to the posterior border of the posttemporal with often, a smaller scale lying partly beneath it. The enlarged scale has a single neuromast served by a branch of the lateral line nerve which passes medial to its lower border. Okamura (1970b:16) considered similar scales in macrouroids as being so modified as not to be regarded as scales. There is no evidence which suggests they are not merely enlarged lateral line scales. Such scales occur in (? all) taxa belonging to the macrouroid subfamily Macrourinae and some ophidiiforms (p. 185).

Pelvic girdle (Fig. 24B)

Pelvic girdle comprises two V-shaped *pelvic bones*, each with strongly developed, medially directed postpelvic process; the right always slightly overlaps the left, both are connected by thick ligament. Anteriorly bones are separated from one another and from cleithral symphysis of pectoral girdle by median cartilage. Halfway along each pelvic bone a ligament connects its lateral face with medial border of lower cleithral limb. Outer edge of pelvic bone bears up-turned spine-like

process which attaches to tendinous *hypaxialis* muscle. Posterior corner of pelvic base with long facet for articulation with eight or nine pelvic fin rays; all rays have triangular 'hammer-head' proximal articular surfaces; outer ray thickened and short; 2nd ray thickened, filamentous in *Gadomus*.

In *Bathygadus* the 'pelvic spine' is a solid bony process not to be confused with 'pelvic splint' or 'spinelet' common in other teleosts. Okamura (1970b:98) noted the 'spine' in *Gadomus* which he considered homologous with the 'mid-pelvic process' of macrouroids. A lateral pelvic process is widespread in gadoids and macrouroids but never so prominently anterodorsally directed as in Bathygadidae.

The tendinous connections between pelvic girdle and cleithrum are more complex than depicted by Okamura (1970b:95); a wide, medial tendinous band extends backward from the cleithral symphysis to join a diagonal, cylindrical tendon running from the ventromedial cleithral surface to the anterodorsal surface of the pelvic bone. Thick, darkly pigmented connective tissue covers the triangular space between the tendons; hypaxial and pelvic muscles insert on medial tendinous band.

Vertebral column (Fig. 20)

Bathygadus has 12–14 (rarely 13 or 14) abdominal and *ca* 70 caudal vertebrae, *ie.* those with closed haemal arches. *Gadomus* has 12–13 abdominal and always more than 80 caudal vertebrae.

In *Bathygadus* the first three centra bear stout, blunt neural spines whose tips are widely divergent from one another; the first narrowly separated from supraoccipital crest, its anterior surface grooved (doubtless due to contraction of longitudinal body musculature, the supraoccipital is forced back into this groove). A pair of neural zygapophysis on 1st centrum articulate with paired exoccipital condyles. Each successive neural spine with more finely pointed tip until from 7th or 8th they become slender, needle-like. Pre- and postzygapophyses present posteriorly from 17th–18th vertebrae; 5th–11th vertebrae bear broad, lateral parapophyses each bearing a rib, 6th–10th parapophyses successively broader, diminishing in width from 11th–14th and replaced by haemal spine on 14th. *Epipleural ribs* 4–8 from 3rd to 10th vertebrae. Caudal vertebrae elongate, narrow-waisted with low-angled neural and haemal arches and spines; spines of more caudal elements with marked posterior curvature causing them to lie almost horizontally.

COMMENTS. Okamura (1970b:110) noted in macrouroids the absence of neural and haemal spines from the last four vertebrae. In all bathygadids examined, neural and haemal spines are present on all caudal centra.

Dorsal and anal fins and supports (Fig. 20)

Bathygadus and *Gadomus* have two *dorsal fins*, 1st with 2 spines, 6–12 soft rays; 2nd with *ca* 100+ soft rays. First dorsal fin spine small, lying adnate to anterior base of long 2nd dorsal spine, spines supported by single narrow radial; following *ca* 13 radials diminish in length and stoutness, numbers 2–10 support fin rays, the following three or four radials do not support rays; 14th or so radial followed by another much stouter of nearly same length as 2nd supporting 1st ray of second dorsal fin. *Anal fin* lacks stout spine, composed of soft rays supported by slender radials with cartilaginous proximal tips. There are no supraneurals.

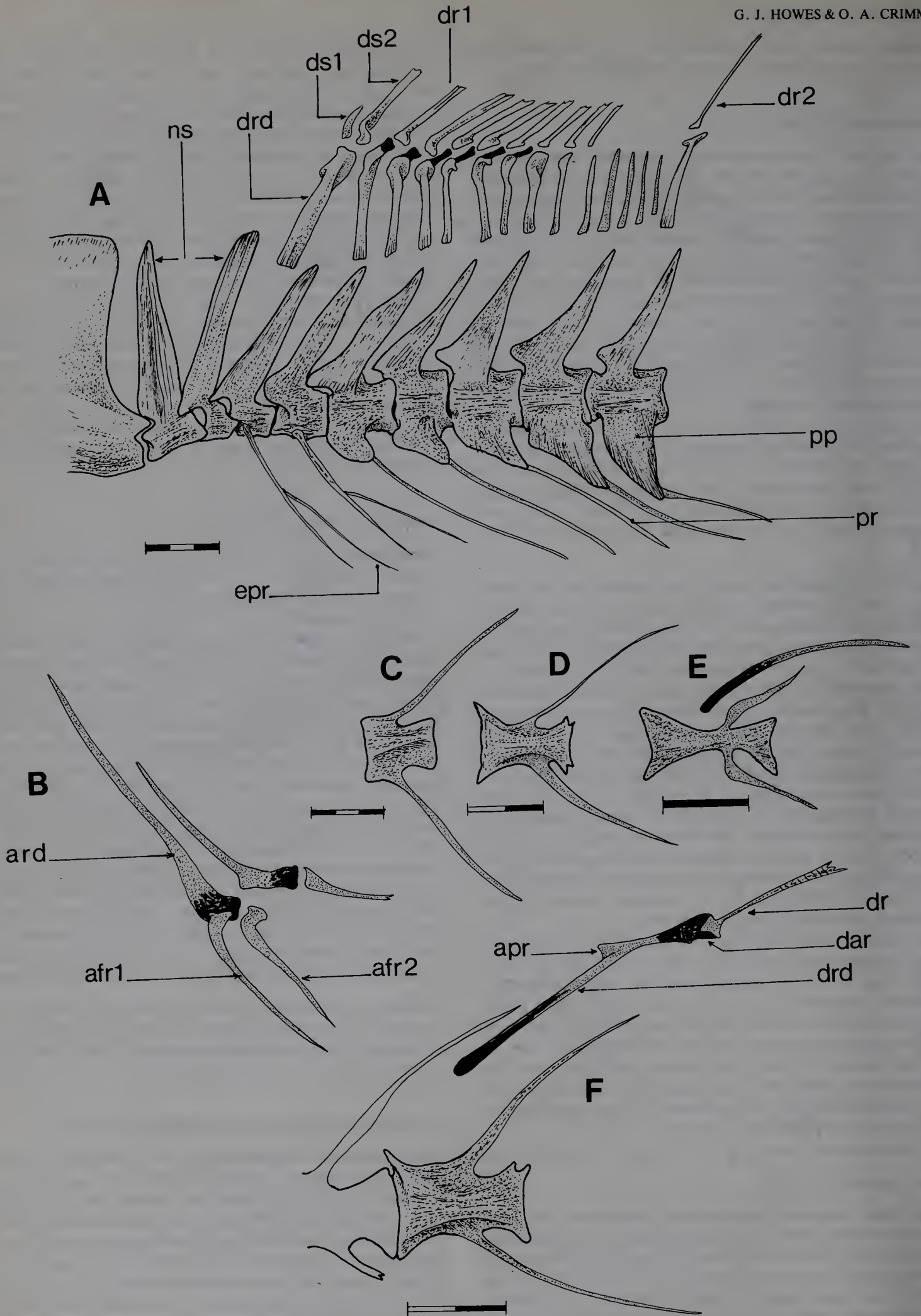


Fig. 20 *Bathygadus melanobranchus*. Anterior region of vertebral column with dorsal fin supports *in situ*. B, anterior supports of the anal fin. C-F, vertebrae; C=19th, D=39th, E=60th and with associated radial, F=35th with associated dorsal radial. Cartilage shown as solid black.

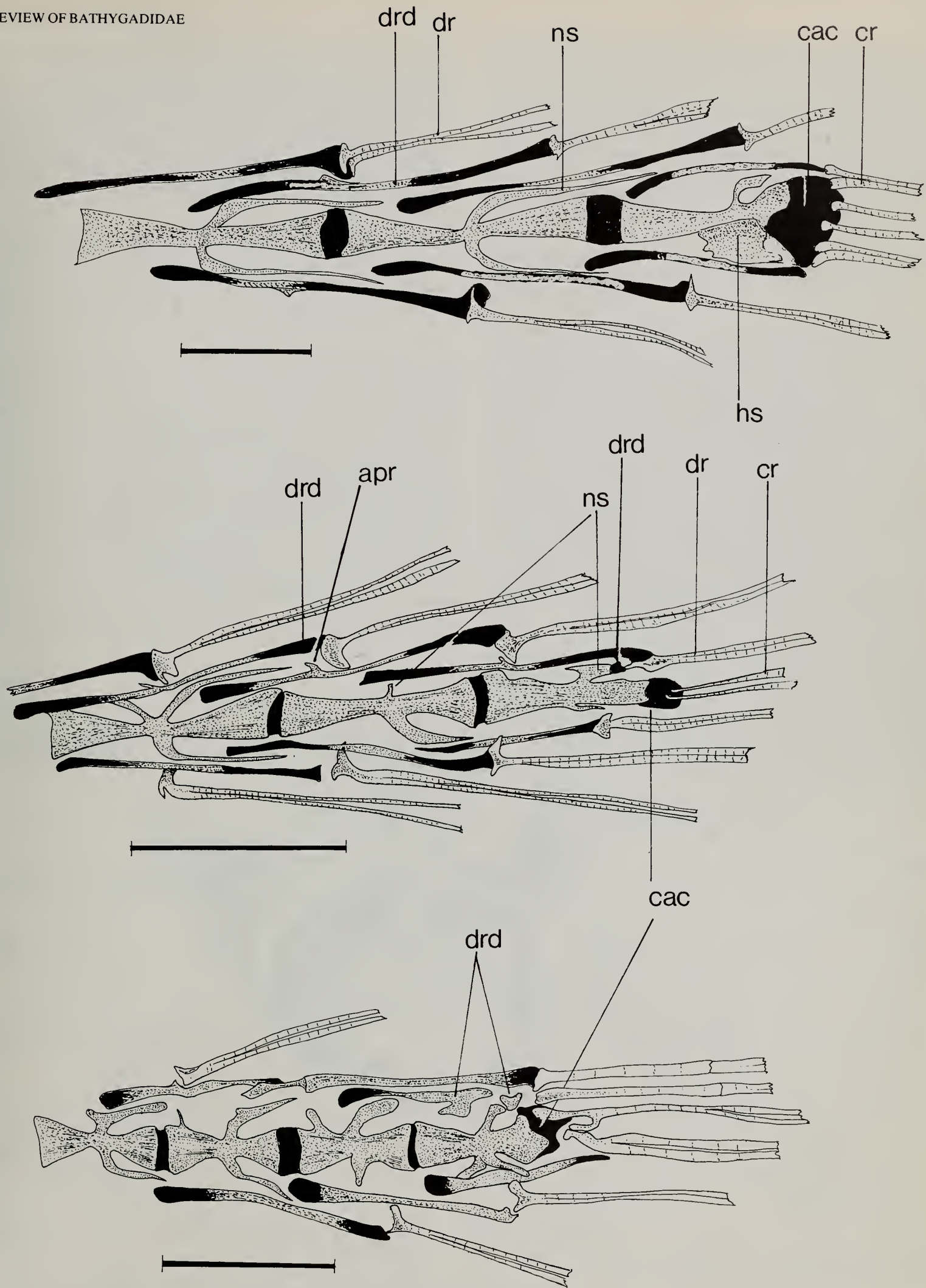


Fig. 21 Caudal fin region of; A, *Bathygadus melanobranchus*, B, *B. macrops*; C, *Gadomus arcuatus*. Cartilage is shown as solid black. Scale bars=1mm.

Fahay & Markle (1984, table 75) give 8–13 1st dorsal rays for *Bathygadus* and 11–14 for *Gadomus*. In specimens examined there are no more than a total of 12 rays in the former and 13 in the latter. Both posterior dorsal and anal fin radials bear, posterodorsally, a spine-like process which articulates with the distal cartilaginous radial supporting the preceding fin ray.

In macrouroids the first few radials of the anal fin lie well

forward, below the 9th or 10th abdominal vertebrae rather than the posterior abdominal or 1st caudal as in the Bathygadidae and other gadoids; the exception among macrouroids is *Hymenocephalus* which retains the plesiomorphic gadoid condition (Okamura, 1970b:108). In *Trachyrincus* three or four anal radials lie beneath the last abdominal and 1st caudal vertebrae and do not form the anteroventral arc arrangement characteristic of macrouroid anal radials.

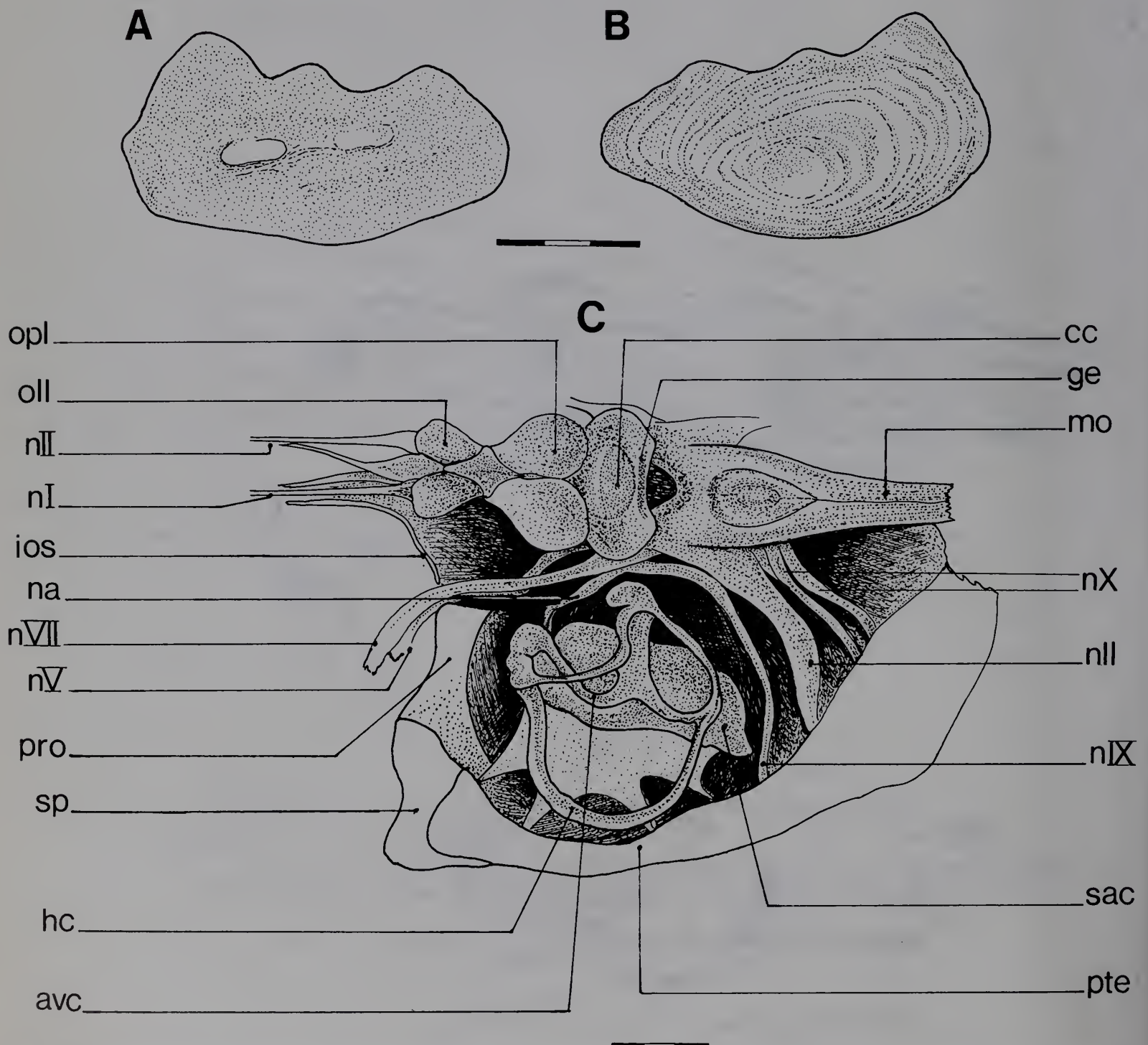


Fig. 22 *Bathygadus favosus*. The inner ear and brain. Above, otolith showing A, inner, and B, outer surfaces; C, dorsal view of inner ear and brain.

Caudal 'skeleton' (Fig. 21)

Like macrouroids, bathygadids display no distinct caudal fin, the tail terminating in 4 or 5 long filamentous rays. The internal structure of the tail is simple although there is some variability with regard to neural and haemal spines and radials (see below). There is no true caudal skeleton and the 'caudal' rays seem derived either from dorsal and/or anal rays which surround the terminal centrum. The last centrum is never complete, its posterior part terminating in a flat cartilaginous plate supporting 2-4 rays. The neural spine of the last vertebra may be normal shape (Fig. 21A), elongate and lamellate (Fig. 21B) or shortened (Fig. 21C); the haemal spine is similarly modified. The last radial may be posteriorly expanded as in *Gadomus arcuatus* (Fig. 21C).

COMMENTS. Okamura (1970b) considered a normal macrouroid caudal skeleton one in which each ray is supported by a radial (interneural of Okamura), and a regenerated caudal (or pseudocaudal) one in which a large cartilaginous plate, derived from intervertebral cartilage, supports caudal rays. All bathygadids examined fall into this latter category and since there are no obvious breaks in the radials or other distortions which suggest breakage it is difficult to ascertain which is normal and which is regenerated caudal skeleton. Presumably, when the tail is broken off in life, breakage occurs intervertebrally so a 'caudal' cartilage will develop from the intervertebral one. Compared with *Melanonus*, *Steindachneria* and *Trachyrincus* in which caudal elements are identifiable (see respectively, Paulin, 1983; Fahay, 1989; Howes, 1989) the caudal fin of bathygadids is reductive, in which it resembles macrouroids.

Brain
Fig. 22

The bathygadid brain is elongate and shallow, filling central area of cranial cavity; olfactory bulbs lie midway between

lateral ethmoid and olfactory lobes being situated within paired cavities formed by frontal ventral laminae and extensions of medial septum (p. 163). Olfactory tracts thin, narrowly separated from one another posterior to olfactory sac. Olfactory lobes ovoid, separated from optic lobes by shallow fissure. Optic nerves thin, feeble, crossing one another anterior to olfactory lobes. High cerebellar corpus bordered by ovoid granular eminences. Inferior lobes prominent, hypophysis large, almost spherical. High posterior cerebellar crests. Trigeminal and facial trunk emanates from below cerebellar corpus; acoustic nerve stems from above root of trigeminal trunk, turns dorsad, branching into two rami serving anterior ampullae of inner ear canal.

COMMENTS. Okamura (1970b:73) noted olfactory lobes in macrouroids are 'spherical or ovoid in shape and considerably well developed'. Observations on at least one taxon of each gadoid family indicate that gadoid olfactory lobes are larger than macrouroid, as they are in bathygadids. Anterior placement of olfactory bulbs has been considered diagnostic of Gadiformes (Svetovidov, 1948). Olfactory bulb position is, however, variable; in *Bathygadus* they occur between fore-brain lobes and olfactory sacs, in *Gadomus* they lie close to the brain. In macrouroids, the bulbs lie within the nasal cavity in Macrourinae but in Macrouroidinae are close to the brain (this is considered the plesiomorphic position since it is the condition of most teleosts). Among gadoids the bulbs lie close to the brain in Melanonidae, Eulichthyidae and Ranicipitidae; occupy an intermediate position in *Lyconus* (Merlucciidae); lie close to nasal sac, but posterior to lateral ethmoid in Moridae, Gadidae, Phycidae (? all) and Muraenolepididae; and within nasal cavity in other merlucciid genera *Merluccius* and *Macruronus* (condition in *Lyconodes* unknown). In Steindachneriidae and Merlucciidae the olfactory bulbs migrate forward during ontogeny (Inada, 1981; Fahay, 1989) which suggests that an ontogenetic shift has occurred independently

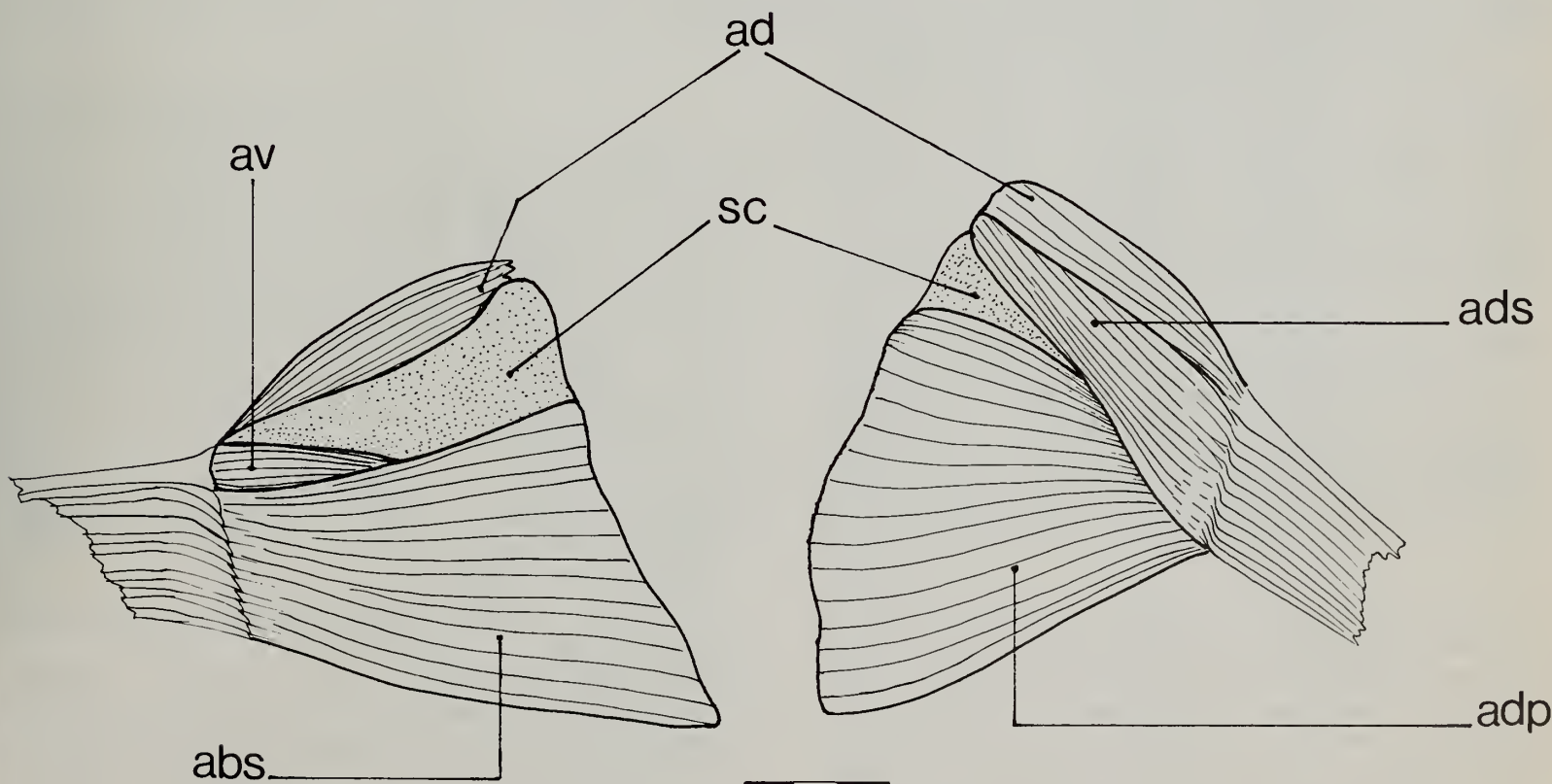


Fig. 23 *Bathygadus favosus*. Muscles of the pectoral girdle; left, lateral; right, medial view.

in various gadoid and macrouroid lineages (Howes, 1989). According to Fahay (1989), in *Steindachneria*, the olfactory lobes migrate forward to become olfactory bulbs; this is perplexing since in all specimens we have examined, olfactory bulbs and lobes are distinct entities. In Bathygadidae the olfactory tract is simple and undivided whereas in macrouroids and many gadoids it comprises two or more strands. The optic lobes are relatively small compared with those of other gadoids.

Swimbladder

Swimbladder; simple, elongate sac extending to above anus containing 2 retia mirabilia in *Bathygadus*, 4 in *Gadomus*; no drumming muscles.

COMMENTS. Okamura (1970b:115-7) describes a pair of muscle bands extending from the auditory bullae (intercalar) to between 4th and 7th vertebrae. No muscles in this position have been found in any bathygadid, macrouroid or gadoid examined and it appears Okamura has misinterpreted as drumming muscles the *retractor dorsalis* which run from those vertebrae to the pharyngobranchials (Howes, 1988).

Intestine

Intestine S-shaped coil in *Bathygadus* and *Gadomus*. Okamura (1970b) recognised this pattern as primitive for macrouroids; more derived patterns involve 4-6 loops or spirals (eg. *Squalogadus* (Macrouroidinae)).

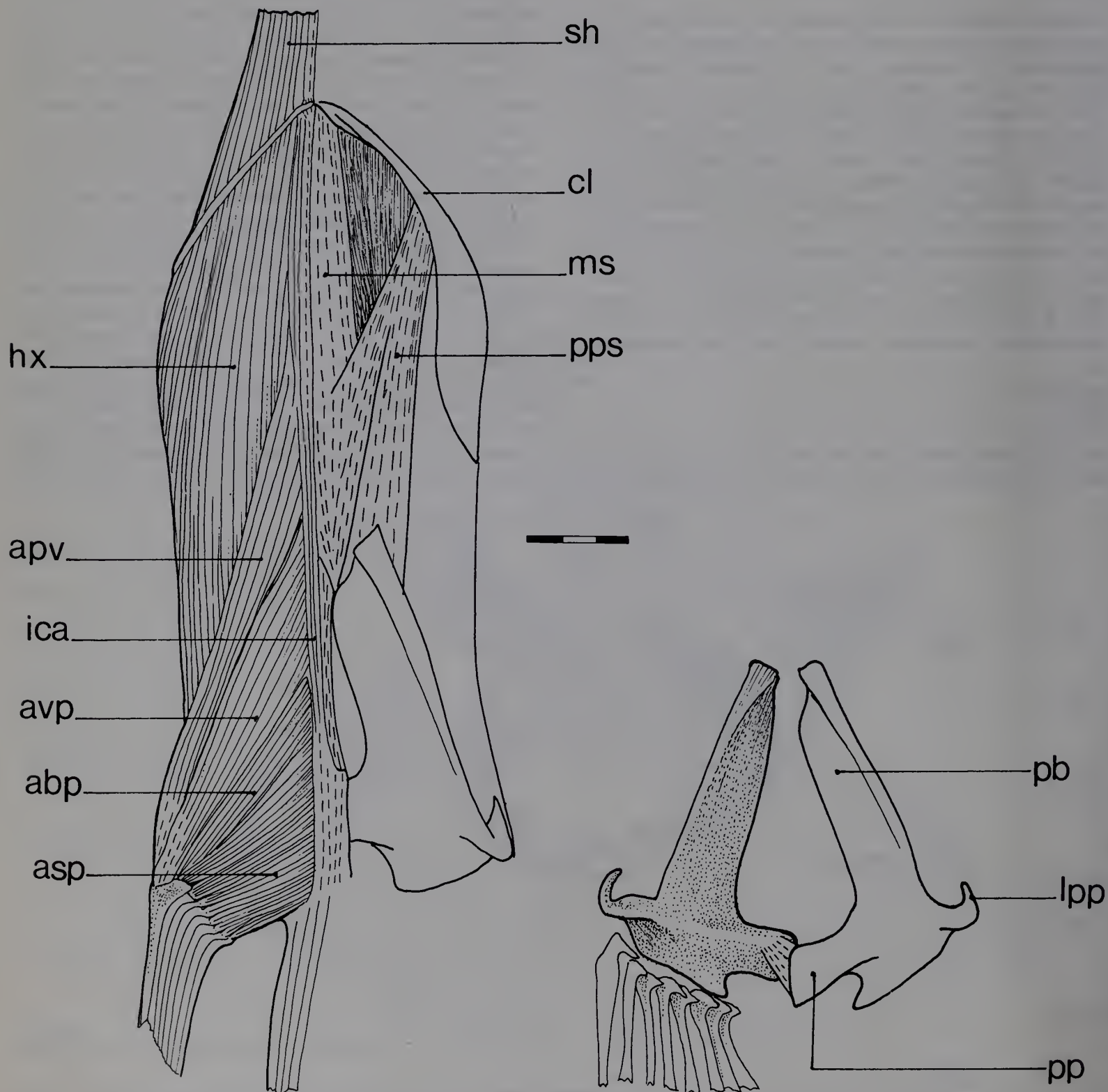


Fig. 24 *Bathygadus favosus*. A, muscles of the pelvic girdle; B, bones of the pelvic girdle in dorsal view.

Gill-filaments

Gill-filaments of *Bathygadus* and *Gadomus* are short, 20–25% of outer gill-raker length (measured against longest raker on ceratobranchial); exceptionally, *B. macrops* has filaments of equal length to rakers.

COMMENTS. Among gadoids short gill-filaments occur only in Merlucciidae (*Merluccius*); Inada (1981, fig. 47L) illustrates this example in *M. australis*, even so the filaments of this species are short compared with other *Merluccius* (equal to gill-raker length, those in other species longer than rakers) and still longer than those of bathygadids. Short gill-filaments have not been found in macrouroids but occur in some Bythitoidei, viz. *Abyssobrotula*, *Acanthonus*, *Bassogigas*, *Bassozetus*, *Glyptophidium* and *Lamprogrammus*. In these taxa it is usually only the outer arch filaments that are reduced, those on the inner arches being twice as long. In bathygadids reduction of filaments on all gill-arches is considered to be a derived feature for the family.

Myology

Muscles and ligaments of the head have been described by Howes (1988); here is given a more complete description of branchial arch muscles together with descriptions of pectoral and pelvic girdles and axial skeleton.

Branchial arch muscles

Obliquus ventralis muscles of 1st and 2nd gill-arches were referred to by Howes (1988; 1989) as 'reduced'. This ambiguous term means that the muscle is almost entirely tendinous, in some taxa comprising only a tendon without muscle fibres. Attachment to ceratobranchial is at its articulatory (with hypobranchial) margin, rather than a distance along it as in other teleosts. *Bathygadus melanobranchus* lacks muscle and tendon from 1st arch, 2nd bears reduced muscle body; a similar condition occurs in *Gadomus 'multifilis'* and *G. longifilis*.

Pectoral girdle muscles (Fig. 23)

Abductor superficialis spans proximal part of scapula and coracoid, originates from dorsomedial rim of cleithrum; insertion on each fin ray, other than 1st, via tendon. *Arrector ventralis* originates from lateral face of coracoid, and ventromedial area of cleithral rim; mostly covered by abductor, inserts tendinously on dorsomedial aspect of 1st pectoral ray. *Adductor profundus* originates from coracoid, inserts tendinously on pectoral rays. Dorsally and partially medial to profundus lies *arrector dorsalis*, and *adductor superficialis*, both originating from medial posteromedial border of cleithrum, barely separable from one another, the latter identified by its insertion to the medial aspect of the 1st pectoral ray; the latter inserting on bases of all other rays.

Pelvic girdle muscles (Fig. 24)

Abductor superficialis pelvica originates from midline septum, inserts on all pelvic rays. *Arrector ventralis pelvica*, narrow, tendinous and continuous medially with *infracarinalis anterior*, inserts on ventrolateral aspect of 1st pelvic ray. *Adductor profundus pelvica* runs from midline septum, inserts on outer pelvic ray. *Arrector dorsalis pelvica* extends

from midline septum of *hypaxialis*, inserts tendinously on anteriorly directed lateral pelvic process (p. 175). *Abductor profundus pelvica* stems from midline raphe, loosely attached to pelvic girdle by connective tissue, inserts on bases of all but 1st pelvic ray.

Dorsal pelvic musculature comprises *adductor superficialis pelvica*, extends from midline raphe inserts tendinously on all rays; *adductor profundus pelvica*, narrow, tendinous, originating with former muscle, its more posterior fibres stem from ventrolateral margin of pelvic bone, inserts on 1st ray and heads of the three outer soft rays.

Anterior body muscles (Fig. 25)

Supracarinalis anterior runs from anterolateral face of 1st radial to supraoccipital crest; muscle deepens at attachment to dorsal radial and immediately joins an aponeurosis with fibres stretching mesiad from the upper element of *epaxialis*. Anteriorly, *supracarinalis* becomes tendinous, joining its antimere in midline before inserting on supraoccipital crest.

Epaxialis comprises dorsal and ventral segments. Dorsal segment has helically arranged fibres between anterodorsally directed myocommata. Anteriorly segment inserts on posterior area of supraoccipital; medially loosely attached by connective tissue to neural arches and ventrally free from underlying segment. Ventral segment has fibre direction varying from parallel, between posterior myocommata, to anteroventral, between anterior myocommata. Anteriorly, segment trifurcates, upper, principal portion inserts on epioccipital, together with middle portion, lower passes between forked posttemporal limbs to insert on pterotic. Posterior to where middle and lower portions divide, muscle is tendinously attached to tip of cleithrum. Medially, ventral segment is loosely attached to horizontal septum which marks vertebral lateral processes. Laterally, ventral *epaxialis* joins *hypaxialis*. Connection between the muscles effected via aponeuroses formed from expansion of ventral margins of anterior (7–8th) epaxial myocommata. Lateral boundary between *epaxialis* and *hypaxialis* marked by wavy course of lateral line nerve.

Hypaxialis single, thin sheet anteriorly comprising seven or eight broad bands of fibres each connected to respective epaxial myocommata (vex, Fig. 25). Anteroventrally, *hypaxialis* attaches to cleithrum, ventromedially to thick, tendinous sheet stretching from pelvic girdle to cleithrum (p. 175). Ventrally, *hypaxialis* joins *infracarinalis anterior*. Post-cleithrum runs diagonally across lateral surface of *hypaxialis* to which it is firmly attached. *Lateralis superficialis* (ls, Fig. 25) becomes apparent only at the point where fibres of *epaxialis* and *hypaxialis* become horizontally aligned.

Infracarinalis anterior stretches from medial margin of pelvic bone to symphyseal tip of cleithrum. Posteriorly, muscle undifferentiated from *arrector ventralis pelvica* (see above) and anteriorly from *hypaxialis*. *Infracarinalis medius* is a short segment which immediately passes into the fascia of *hypaxialis*.

COMMENTS. The loose attachments of *epaxialis* segments both medially to the vertebral column and laterally to the *hypaxialis* suggest they are significant functional attributes toward elevating the head. Manipulation of preserved bathygadids show the lower epaxial border capable of sinking below the upper level of the *hypaxialis* and is 'cradled' by the horizontal septum. The position of the lateral line nerve is maintained by its connective tissue adhesion to the *hypaxialis*.

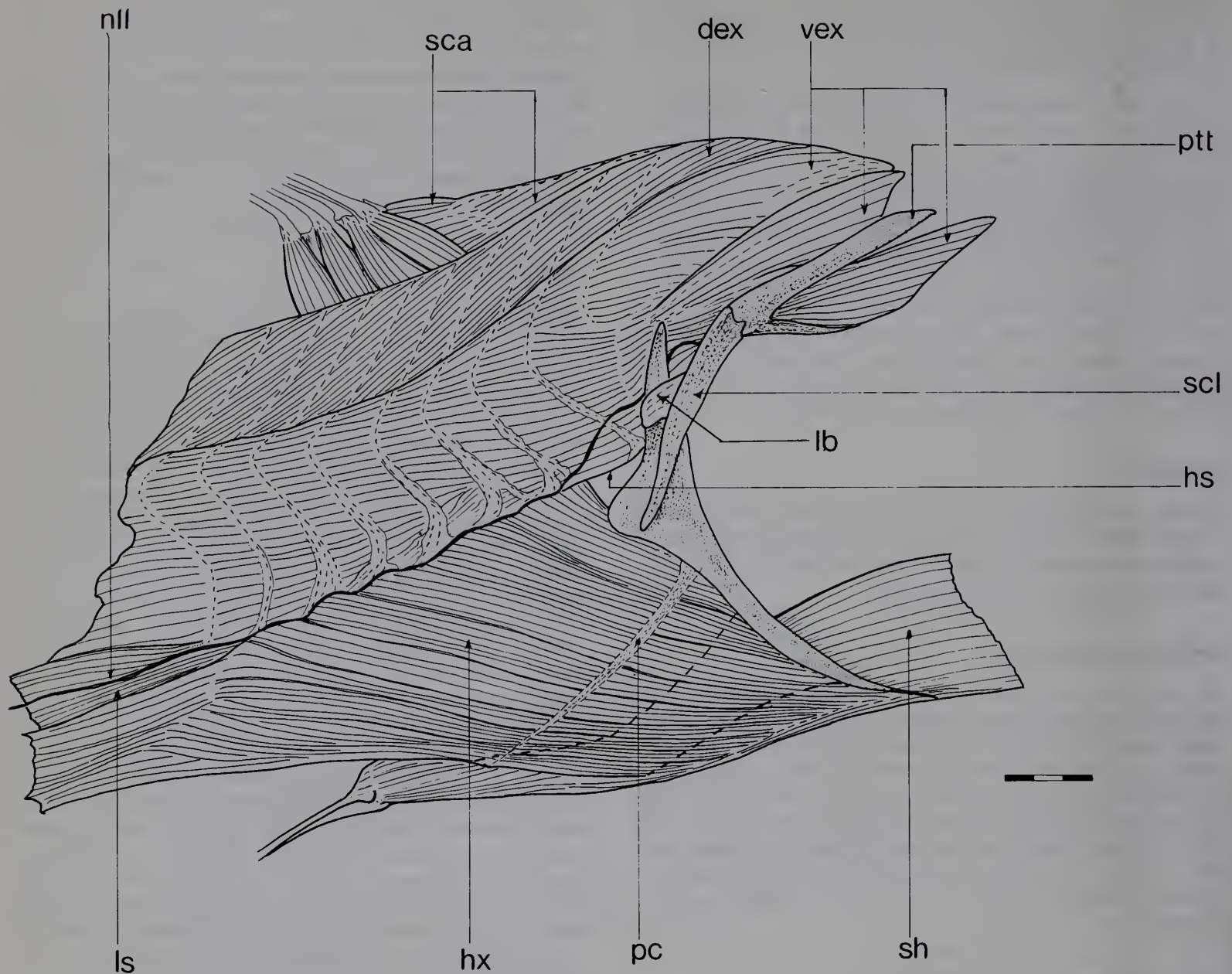


Fig. 25 *Bathygadus favosus*. Anterior body musculature; dashed outline indicates the pelvic-cleithral tendinous sheet; the pectoral girdle and its muscles have been removed.

The tripartite articulation of the cranium with the vertebral column possessed by bathygadids might seem to limit the degree of vertical cranial rotation, but as noted by Rosen & Patterson (1969), the near horizontal arrangement of basioccipital and exoccipital condyles would alleviate such limitation. Although in bathygadids, the exoccipital condyles are reduced in size it appears that the principal factor in achieving cranial elevation is modification of the *epaxialis* which allows greater flexure in the vertical plane. There is striking similarity in anterior body muscle arrangement between bathygadids and stomiatoids, exemplified by *Chauliodus* (Tchernavin, 1953), a fish which also flexes the vertebral column in cranial elevation.

Reduction of epipleural ribs and diminution of regular myotomes in bathygadids also suggests a considerable degree of freedom in anterior body muscle movement, present elsewhere in gadiforms only in Bregmacerotidae.

Pelvic musculature of macrouroids and most gadoids is more extensively developed than in bathygadids and extends well forward to the pectoral girdle where it meets the median

septum supporting hypaxial musculature. The entire pelvic girdle of bathygadids is loosely arranged and its tendinous connections with the *sternohyoideus* (in *Gadomus*) and with the *hypaxialis* (see above) supports the idea that a specialized functional sequence is involved in feeding.

We suggest that future attention should be directed toward elucidating the arrangement of anterior body musculature in 'paracanthopterygian' fishes. A brief survey of 'para' and acanthopterygian taxa suggests that loss of the outer hypaxial layer (*obliquus superioris*) has occurred among 'paracanthopterygians'.

Ramus lateralis accessorius nerve (RLA)

Fig. 26

The outstanding feature of the RLA in Bathygadidae is the hypertrophy and pathway of its pectoralis branch (RLA-P). The usual gadoid condition (Freihofer, 1970) is for the pectoral branch to diverge from the main vertical pectoral-pelvic trunk (RLA-PP) and loop around the pectoral fin base,

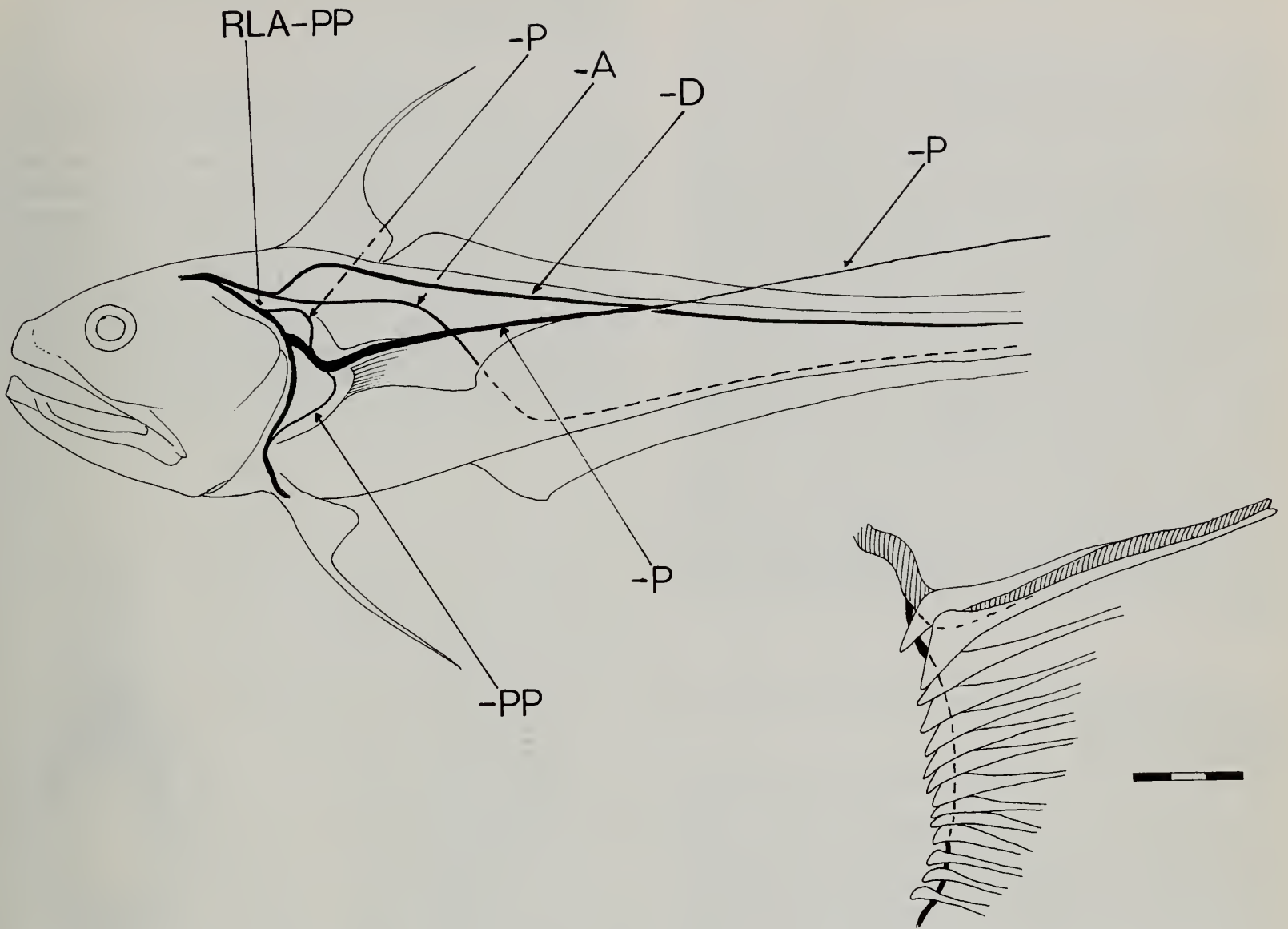


Fig. 26 Pathway of the RLA nerve in a bathygadid (*Gadomus longifilis*, BMNH 1963.2.25:7-17). The pathway of the anal branch has not been detected with certainty, the assumed course is indicated as a dashed line. The enlarged drawing shows in detail the ramification of the pectoral branch, running between the first and second anal fin rays.

with sub-branches of the outer loop innervating fin rays. In *Bathygadus* and *Gadomus* RLA-P branches twice from RLA-PP, first *via* a thin nerve, secondly along the dorsal rim of the pectoral base *via* a thickened branch. The first meets the second some distance before the origin of the 1st fin ray, together they pass between the ray halves, the thickened branch extending between the shortened 1st, and prolonged 2nd rays, eventually lying exposed along outer border of 2nd ray. The first branch passes between bases of fin ray halves, turns caudad and joins main RLA-PP trunk.

COMMENTS. The bathygadid branching pattern, hypertrophy and pectoral ray extension of RLA-P appears unique to that group. Extension of the nerve along 2nd pectoral ray is more pronounced in *Gadomus* since the ray is more attenuated than in *Bathygadus*. Some hypertrophy of RLA-P occurs in Steindachneriidae and it extends slightly between 1st and 2nd pectoral rays. Freihofner (1970, fig. 4) described and illustrated a small branch of RLA-P in *Physiculus* (Moridae). In overall pattern, the anterior ramification of the bathygadid RLA more closely resembles that of Moridae than Gadidae. However, we have been unable to trace fully the

connections between the anal fin (RLA-A) and dorsal (RLA-D) branches. The branching pattern of the dorsal ramus (RLA-D) differs, however, from that in both Moridae and Gadidae as illustrated by Freihofner (1970), there being an additional lateral branch diverging from RLA-PP trunk (RLA-L, Fig. 26).

Functional significance of an exposed nerve along the pectoral fin might be that bathygadids extend their pectorals for prey detection. Bardack & Case (1965) recorded how the phycid *Urophycis* samples the environment by extending forward its modified, prolonged pelvic fins and the high degree of sensitivity that these fins have to chemical and mechanical stimulation. Sulak (1977:102) described similar nerve configuration to that of bathygadids in the pectoral fins of the chlorophthalmid *Bathypterois*. Here, however, innervation is from the 1st and 3rd spinal nerves; the 1st sends branches along the length of the extended 1st pectoral ray, analogous to the situation in *Gadomus*. Sulak (1977) supposes a 'discriminating sensory role' for the pectoral fins in *Bathypterois*, perhaps capable of sensory stimuli. A similar role is hypothesised for the elongated bathygadid pectoral fins. Of interest is Freihofner's (1970) observation of

hypertrophy and exposure of RLA-D serving the 1st dorsal fin spine in the macrouroid *Lionurus*.

JUVENILE BATHYGADIDS

Only one pelagic juvenile bathygadid has been recorded previously (Fahay & Markle, 1984:267) of ca 30mm TL, identified as *Gadomus*. Three others are recorded here identified as *Bathygadus* sp. (USMN 288422), 68.5, 70.5 and 74mm TL, head lengths are, respectively, 12, 12 and 12.7mm; pectoral fin rays 15–16, pelvic rays 8, fin rays of both pectoral and pelvics filamentous, those of dorsal fins too damaged to ascertain their filamentous nature. Gill-rakers 2(n1)–3(n2) + 10. Mental barbel lacking. Guts distended and full of calanid copepods (Euchaetidae, including *Euchaeta spinosa* and Augaptilidae). Specimens were recovered from stomach of an *Alepisaurus ferox* from Gulf of Mexico (30° 28'S, 89° 31'W; 24.11.1966). The species to which these juveniles belong is uncertain as they exhibit no characters diagnostic for adults (Merrett, 1986). It is assumed that gill-raker number increases throughout growth. At these stages, denticles, found on rakers of adults are lacking.

MODE OF LIFE

(Fig. 1)

Marshall (1979:276) noted that swimming action of bathygadids is unlike that of macrouroids which swim nose-down and undulating tail up. Bathygadids, on the contrary, swim steadily, parallel to the sea-floor (Marshall & Bourne, 1964). Differences in swimming modes are due to the reverse pattern of dorsal and anal fin enlargement, in bathygadids, the dorsal rays being longer than the anal and so making for a headlifting, tail down mode.

The food of bathygadids, viz. copepods, amphipods, euphausiids, mysids and decapods, suggests the fish chase moving prey (Marshall, 1979). The large, pectoral RLA nerve exposed along the outer extended pectoral ray indicates a high sensitivity of the fin-rays to external movement. Perhaps, like some bathypteroids, the rays contain gustatory cells that enable distant detection of prey (p. 183). Bathygadids possibly maintain a near stationary level above the substrate, punctuated by rapid prey-capture swimming sequences. Rapid flexure of body musculature probably elevates the head during prey-capture (p. 181). The photograph of what appears to be *Bathygadus furvescens* in Marshall & Bourne (1964, pl. 2) clearly demonstrates the lateral attitude of pectoral and pelvic fins as the fish maintains position in the water column and undoubtedly pursues a somewhat leisurely swimming action, as do other gadoids (eg. *Gadus*).

The short gill-filaments of bathygadids suggest they live either in well-oxygenated water or they expend little energy. Their depth range suggests they encounter oxygen-poor levels and it is more likely they have a low VO₂ achieved by reduced activity. Their thin scales suggest oxygen exchange across the skin may even occur.

HOMOPLASY BETWEEN GADIFORMS AND OPHIDIIFORMS

During the course of out-group comparisons, we were struck by the similarity of the ophidiiform neobythitine *Lamprogrammus nigricans* to bathygadid species. This taxon shares with *Bathygadus* and *Gadomus* five supposedly derived characters, namely: 1) body scales with reticulate pattern of circular and transverse ridges, 2) wide separation between premaxillary dentigerous areas, 3) reduced gill-filaments, those on 1st arch less than half the length of outer gill-rakers, 4) broad nasal bones, in midline contact posteriorly and separated anteriorly by rostral cartilage (shared with *Bathygadus*), 5) narrow and elongate interoperculum with dorsally humped margin (shared with some *Bathygadus* species; Fig. 17).

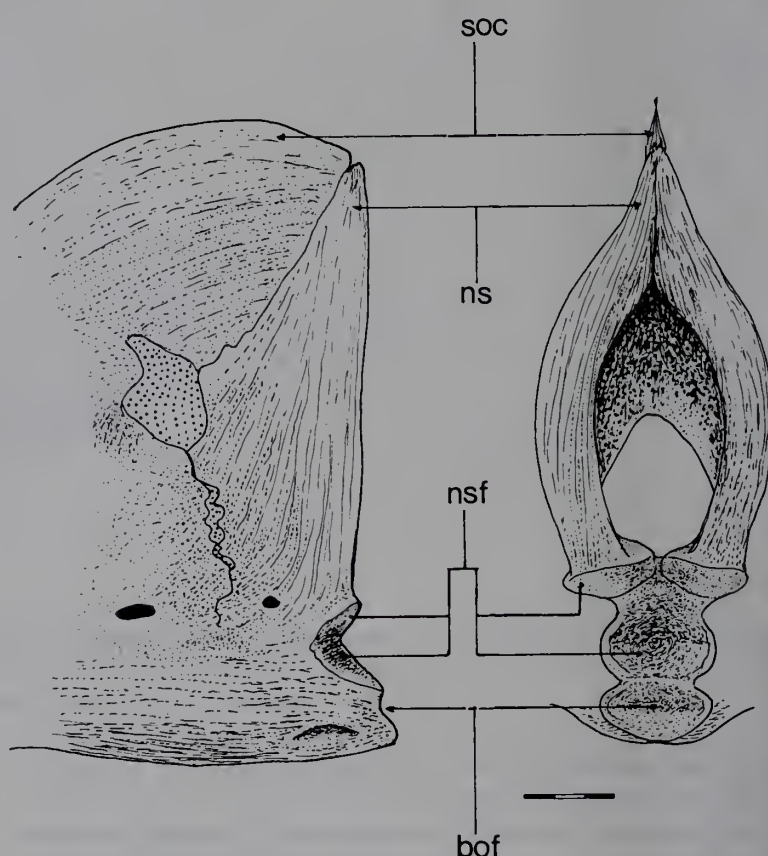


Fig. 27 *Lamprogrammus nigricans* (BMNH 1939.5.26:1483–7). Posterior region of the cranium in lateral and posterior views to show fused neural spine.

In contrast to bathygadids, *Lamprogrammus nigricans* possesses a trigemino-facialis foramen in the lateral face of the braincase, a feature lacking in Gadiformes and one synapomorphic for that group (Howes, 1989). In view of the number of homologies shared with bathygadids, the presence of a trigemino-facialis chamber might be regarded as secondarily derived in *Lamprogrammus*. This assumption is anatomically unsound, however, since to 'regain' this feature would require associated reorganization of attendant nerves and vessels and it is more parsimonious to assume that the 'synapomorphies' are homoplasies.

Lamprogrammus has a strong ligament connecting the inter-operculum and hyomandibular, a feature found in other bythitoid ophidiiforms examined. Previously considered

synapomorphic for gadoids (Howes, 1988; 1989) one must now consider the possibility that its presence might indicate sister-group relationship of at least some 'ophidiiforms' with gadiforms. Alternatively, accepting Patterson & Rosen's (1989) revised view of paracanthopterygian relationships, the ligamentous connections would be viewed as lost in batrachoidiforms, lophiiforms and macrouroids.

In common with other *Lamprogrammus* species, *L. nigricans* possesses vomerine and palatine teeth, both are absent in bathygadids (p. 162). *Lamprogrammus* has a sensory canal running along the dorsum of the body. The canal comprises ca 30 evenly-spaced neuromasts each mounted on a large scale, covered laterally by a hemitube of scale-bearing skin. The canal is not a lateral line canal as previously reported by Cohen & Nielsen (1978:34) but a dorsal branch of nerve RLA-D (p. 183); the lateral line nerve follows the more usual course along the midlateral line of body.

It is noted that the posterior cranial region of *Lamprogrammus* shows evidence of occipital fusion with the 1st (or

an accessory) vertebra (Fig. 27). In *L. nigricans* there is a marked posterior suture between the supraoccipital crest and vertical lamella of what is apparently a neural arch. Anteriorly a large area of cartilage separates the 'neural arch' from the supraoccipital and a synchondrosis extends ventrally from this area to disappear in the exoccipital region. Situated posteriorly to the ventral margin of the suture is the 1st spinal nerve foramen which indicates the basal region of the fused neural arch. The posterior lateral cranial facets are elliptical and ventrally directed, the medial facet is double, the upper circular with a steep downward slope, the lower oblate and vertical. A similar arrangement of facets is illustrated by Rosen & Patterson (1969, fig. 10E) for the bythitoid *Dinematichthys*, a morphology which also occurs in *Genypterus*, *Brotula* and *Neobythites*. The lateral and upper medial facets possibly represent those of the fused neural arch and the lower, vertical facet that of the basioccipital.

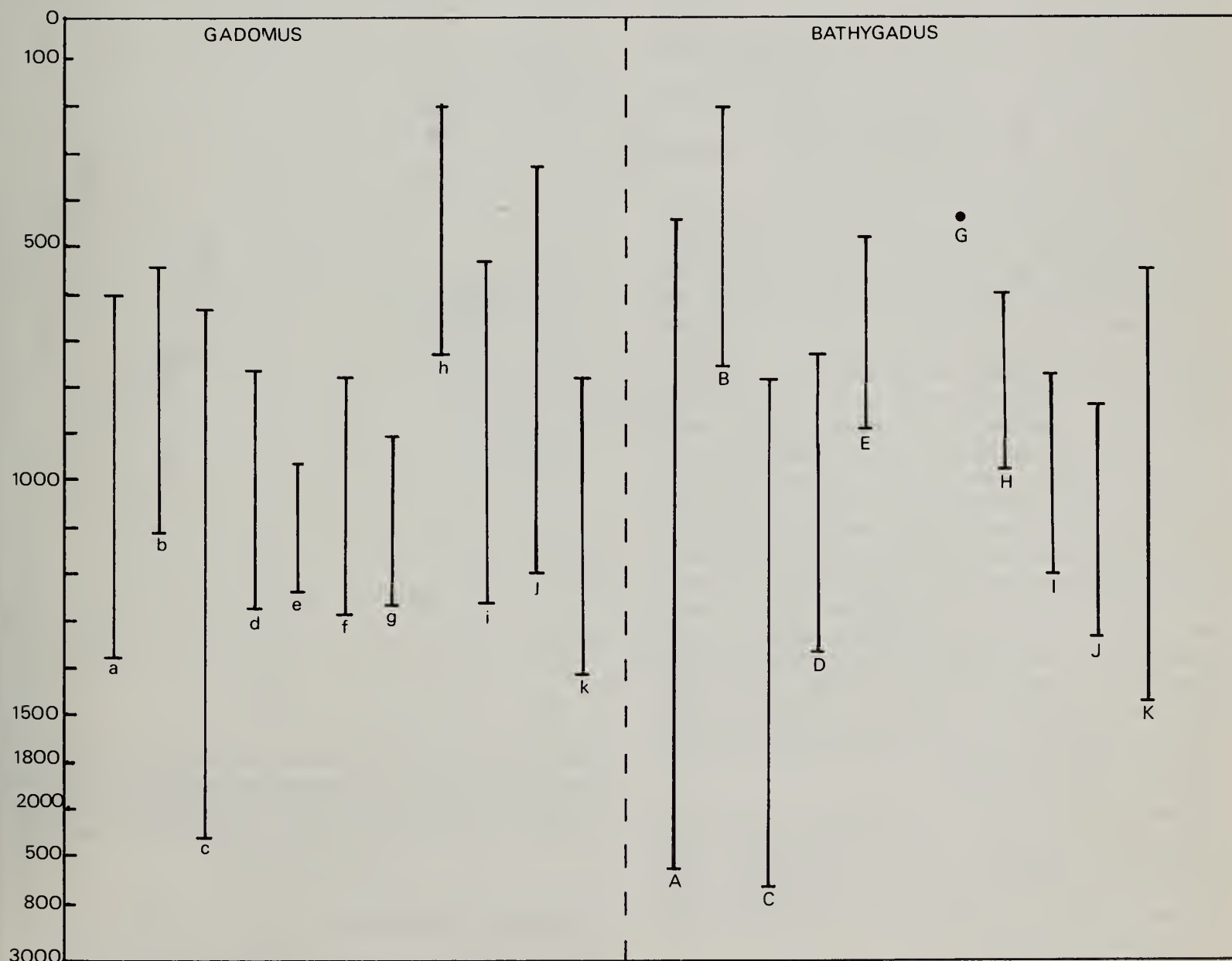


Fig. 28 Depth distribution (in metres) of *Gadomus* and *Bathygadus*. *Gadomus* species are indicated as; a=*arcuatus*, b=*dispar*, c=*longifilis*, d=*multifilis*, e=*aoteanus*, f=*furvescens*, g=*magnifilis*, h=*denticulatus*, i=*introniger*, j=*colletti*, k=*melanopterus*. *Bathygadus* species are indicated as; A=*melanobranchus*, B=*macrops*, C=*favosus*, D=*cottoides*, E=*spongiceps*, G=*entomelas* (type only), H=*sulcatus*, I=*antrodes*, J=*nipponicus*, K=*bowersi*.

TAXONOMY

BATHYGADIDAE

Bathygadinae Jordan & Evermann, 1898:2562.

DIAGNOSIS. Family of gadoid fishes distinguished from others in: specialised nature of anterior body musculature, where *infracarinalis anterior* well-separated from *hypaxialis* and markedly tendinous; in modified nerve pathway of *ramus lateralis accessorius* serving pectoral fin, where branch supplying first and second ray is hypertrophied and extends along second ray; in reduced gill-filaments which are (with one exception) always less than half the length of the gill-rakers, and in absence of caudal fin skeleton.

Included genera: *Bathygadus* Günther, 1878

Gadomus Regan, 1903

In the following species accounts, only principal taxonomic references listed in synonymies.

Bathygadus Günther, 1878

Bathygadus Günther, 1878:23 (type, *B. cottoides* Günther, 1878 by monotypy).

Melanobranchnus Regan, 1903:459 (type, *Bathygadus melanobranchnus* Vaillant, 1888 by original designation).

Regania Jordan & Gilbert 1904:602; 604 (type *R. nipponicus* Jordan & Gilbert, 1904 by original designation).

DIAGNOSIS. (Features distinguishing *Bathygadus* from *Gadomus* are italicised). Head and body compressed, tail slender, without caudal fin; two dorsal fins, the first with two spiny rays, first ray reduced. Rays of second dorsal fin longer than those of anal fin. *Dorsal, pectoral and pelvic rays rarely attenuated and if so, not extending beyond centre of body.* Snout blunt, mouth large and terminal; *teeth minute to moderate* in size, villiform; *dentigerous areas of premaxillae usually widely separated across midline.* *Palatine contacts lateral ethmoid and mesethmoid.* *Barbel rarely present and when so, minute and often concealed beneath skin.* *Interoperculum variable in shape, but shallow and sometimes crook-shaped, with angular posterior border; not visible below border of preoperculum.* Gill-opening wide; gill-rakers on first arch slender and denticulate; gill-filaments reduced, at most 25% length of rakers (except in one species); pseudo-branch present. *Nasal bones broad and may be narrowly separated, or even meet, posteriorly, in the midline.* Skull with generally broad interorbital width, rarely <25% of head length, orbit often >25% of head length. *Number of vertebrae < 100.* Scales small, bearing fine reticulate pattern. *Olfactory bulbs midway between olfactory lobes of brain and the nasal cavity.* *Two retia in swimbladder.*

Gilbert & Hubbs (1920) and subsequent authors are followed in recognising *Melanobranchnus* and *Regania* as synonyms of *Bathygadus*. Weber & de Beaufort (1929) considered *Bathygadus* as comprising the subgenera *Bathygadus* and *Gadomus*. The present anatomical findings point to a more distinct dichotomy.

Atlantic species

Adequate keys to Atlantic Ocean species of *Bathygadus* have been produced by Iwamoto (1970) and Marshall (1973a). The

following are additional data and comments on the three species.

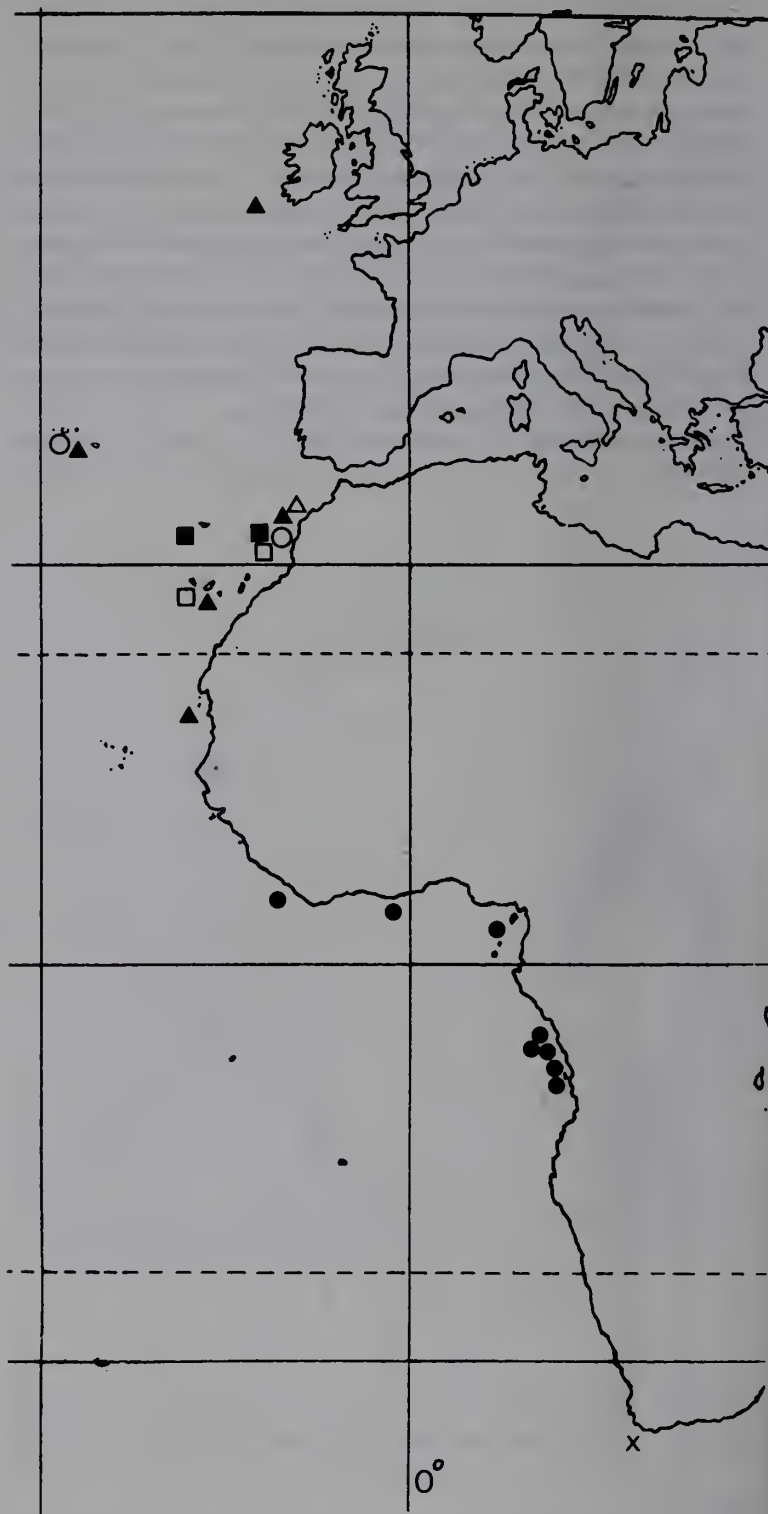


Fig. 29 Eastern Atlantic distribution of *Bathygadus* and *Gadomus* species. ■ = *B. favosus*, ▲ = *B. melanobranchnus*, ● = *B. macrops*, ○ = *G. longifilis*, △ = *G. dispar*, X = *G. capensis*. Records mainly from Poll (1953) and Marshall (1973a). Each symbol may represent more than one collecting station.

Bathygadus melanobranchnus Vaillant, 1888

Bathygadus melanobranchnus Vaillant, 1888:206 (description).

Melanobranchnus melanobranchnus; Regan, 1903:459.

Bathygadus vaillanti Roule & Angel, 1933:63.

Iwamoto (1970) and Marshall (1973a) give complete synonymies and Marshall (1973b) gives additional references.

Iwamoto (1986:332) comments on southern African records and Arai (1983) provides descriptions of Surinam-shelf specimens.

Marshall (1973a) distinguished *B. melanobranchus* from *B. macrops* not only on interorbital width and absence of barbel (see under *B. macrops*) but also on darkly pigmented gill-filaments of the first arch. Although preservation tends to obscure this feature, pigmentation is present in all the specimens examined in this study. The number of gill-rakers in *melanobranchus* is mostly higher than in other Atlantic species, being 21–24, cf. 18–22, such a high number is present only in the Indo-Pacific species *B. antrodes* and *B. bowersi*.

As noted by Marshall (1973a), specimens examined show an allometric relationship between head length and interorbital width, the latter decreasing with increasing head length. In relation to increasing body length, however, head length remains proportionately constant. All our proportional measurements are within the ranges given for those parameters by Iwamoto (1970) and Marshall (1973a).

The assumption by Iwamoto (1970:342) that *melanobranchus* is closely related to *B. nipponicus*, *entomelas* and *furvescens* is unsupported by any revealed synapomorphies, although we

agree that *melanobranchus* does not closely resemble the other two Atlantic species.

DISTRIBUTION. Western and eastern Atlantic and mid-Atlantic ridge (off Azores), ? south to the Cape, South Africa. According to Iwamoto (1986:332) the specimens on which South African records of this species have been based cannot be traced, neither have we been successful in locating this material and thus this extension of the species' range cannot be verified (but see p. 195).

DEPTH RANGE. 450–2560m (Marshall, 1973a). Merrett & Marshall (1981) found *B. melanobranchus* to be one of the most numerous species of fishes collected off north-west Africa, occupying a depth range of 734–1017m.

MATERIAL EXAMINED. BMNH 1890.6.16:35–6, (syntypes) off Arguin Bank, Mauritania; 1934.12.19:26–7, 96.0, 99.8mm s-a, 37° 37'N, 25° 20'W; 1963.2.25:31–35, 131–150mm s-a, 'Oregon' Stn 3586; USNM 202777, off Zaire coast; Uncat. 147mm s-a, off Panama. USNM 74342 (from paratype series of *B. favosus*; see p. 189), NE Gulf of Mexico, 'Albatross' Stn 2394.



Fig. 30 Western Atlantic distribution of *Bathygadus* and *Gadomus* species. Symbols as in previous figure. Records from Iwamoto (1970), Marshall (1973a) and Arai (1983). Each symbol may represent more than one collecting station.

Bathygadus macrops* Goode & Bean, 1885Bathygadus macrops* Goode & Bean, 1885:598.*Bathygadus goethemi* Poll, 1953:219.

Iwamoto (1970) and Marshall (1973a) give complete synonymies and Iwamoto (1986:331) provides descriptions of South African forms.

Bathygadus macrops distinguished from other Atlantic species by presence of small barbel, narrower interorbital width (18.0–27.0% of head length, cf. 24.1–39.0%), and from other species by length of gill-filaments which equal or exceed that of gill-rakers. Size of eye distinguishes *macrops* from *favosus* (26.0–34.0% of head length, cf. 19.0–24.0%) but not from *melanobranchus* (24.7–34.2% of head length). Teeth arranged in definite parallel rows on premaxilla. Only a single tooth band on dentary. Second pectoral ray somewhat filamentous, at least in juveniles.

Pyloric caeca could be counted in only two specimens of 94 and 100mm s-a length and number, respectively, 22 and 40. Three specimens of 106, 111 and 128mm s-a length possess ripe testes.

According to Marshall (1973a) *B. macrops* is most closely related to *B. sulcatus* of the Philippine Islands but differs in having fewer pelvic rays (8, cf. 9–10), larger eyes and shorter snout. Such differences occur between *macrops* and other species and we can find no evidence to support such a close relationship.

DISTRIBUTION. Western and eastern Atlantic.

DEPTH RANGE. 200–770m (Marshall, 1973a).

MATERIAL EXAMINED. USNM 37339 (Holotype), 103mm s-a; 53047 (Paratypes) 70, 74mm s-a, 28° 34'N, 86° 48'W; USNM

(un-numbered), 80, 96, 106, 111, 126, 134, 145mm s-a, 03° 65'S, 09° 15'E; BMNH 1973.3.5:3–6, 73.5, 81.5, 86mm s-a, 9° 10'N, 15° 99'W.

Bathygadus favosus* Goode & Bean, 1885Bathygadus favosus* Goode & Bean, 1885:160.

Iwamoto (1970) and Marshall (1973a) give complete synonymies; Marshall (1973b) gives additional references and Iwamoto (1986:331) provides descriptions of South African forms.

Bathygadus favosus distinguished from other Atlantic species by higher number of pelvic fin rays, viz. 9 (rarely 10) vs 7–8 in others, and broader interorbital width (29.6–39.4% of head length, cf. 24.1–27%). As in *B. melanobranchus*, a barbel is lacking. Pyloric caeca were counted in only four specimens but fewer in number than in the other two species; counts are 15(150), 15(91), 16(60), 23(113) (numbers in parentheses refer to the s-a length in mm).

Marshall (1973a) related *B. favosus* to the broad-headed species of the Philippine-Indonesian area. Elsewhere (p. 200) we indicate that there is a continuum of cranial width in *Bathygadus* and on this basis alone we are unable to support Marshall's contention.

DISTRIBUTION. Given as western and eastern Atlantic by Marshall (1973a, b), but recorded from the mid-Atlantic Ridge by Pakhurov (1980).

DEPTH RANGE. 770–2745m.

MATERIAL EXAMINED. USNM 74342 (Paratypes) 156, 146mm s-a, and four others too damaged to measure (the two

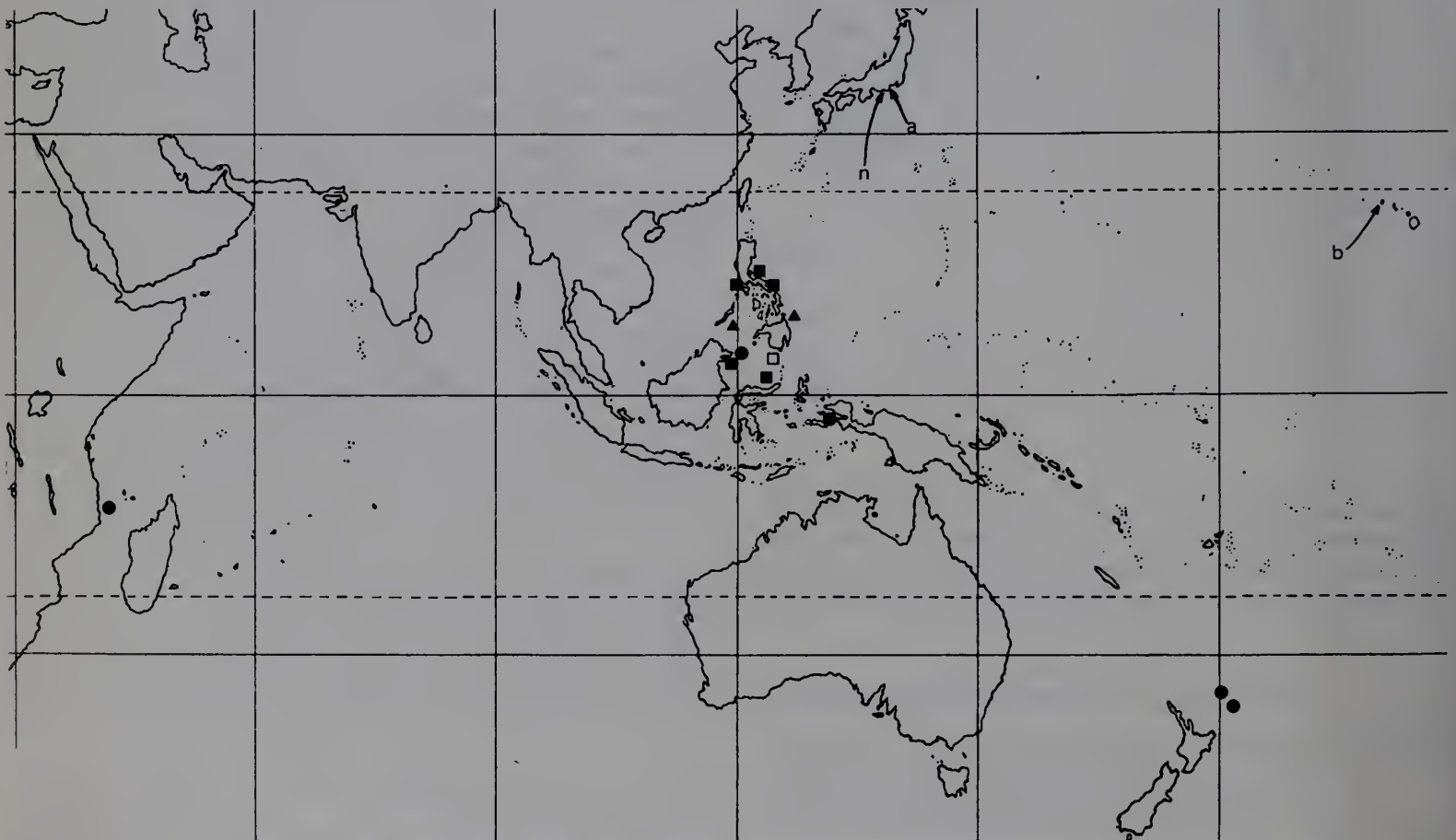


Fig. 31 Indo-Pacific distribution of *Bathygadus* species. □=*B. entomelas*, ■=*B. spongiceps*, ●=*B. cottoides*, ▲=*B. sulcatus*, a=*B. antrodes*, n=*B. nipponicus*, b=*B. bowersi* (Hawaii).

smallest specimens in this lot are re-determined as *B. melanobranchus*), NE Gulf of Mexico 'Albatross' Stn 2394; 34918, 34910 (Paratypes) 113, 157mm s-a, Lesser Antilles; BMNH 1903.2.25.20–25, 116.5mm s-a, off Panama 'Oregon' Stn 3586.

Indo-pacific species

Bathygadus cottoides Günther, 1878

Bathygadus cottoides Günther, 1878:23 (brief descr.); 1887:154 (detailed descr.).

Regania filamentosa Smith & Radcliffe, 1912:149 (listed).

Bathygadus melanobranchus; Weber, 1913 (*non* Vaillant):172 (descr.).

Bathygadus dubiosus Weber, 1913:173 (descr.).

Bathygadus filamentosus; Gilbert & Hubbs, 1916:149 (listed).

Bathygadus filamentosus; Gilbert & Hubbs, 1920:384 (descr.).

Bathygadus furvescens; Gilbert & Hubbs, 1920 (*non* Alcock):388 (Philippines).

Bathygadus (Gadomus) filamentosus; Weber & de Beaufort, 1929:16 (synonymy; descr.).

?*Bathygadus spongiceps*; Norman, 1939 (*non* Gilbert & Hubbs): 48 (descr.).

?*Bathygadus* sp. Iwamoto, 1986:93 (descr.).

Described by Günther from fourteen specimens, all apparently in poor condition. There are now six syntypes in the BMNH, from five of which we have made our measurements (one specimen being too badly damaged to include). In all but one specimen the pectoral fins are broken off at their bases so that it is impossible to count the rays. In the exceptional specimen only the bases of the rays remain. Günther records 10 pectoral rays for the species, but we count 14 in this specimen. We also count II, 6–7 dorsal rays, whereas Günther gives a total of 8, presumably having overlooked the first, reduced ray.

Gilbert & Hubbs (1920) synonymised *B. dubiosus* Weber, 1913 with *B. filamentosus*. An examination of the holotypes of these species reveals almost identical morphometric and meristic features (Table 3). The present study revealed no morphometric, meristic or other differences that distinguish *B. filamentosus* from *B. cottoides* and so those species are treated as synonymous.

The specimens described by Gilbert & Hubbs (1920:388) as *B. furvescens* Alcock, 1894 are certainly not that species and are possibly *B. cottoides*. Only one of their specimens was located (USNM 99450 from between Siquijor and Bohol Island, Philippines) and a close correlation between all parameters was found (Table 2).

Norman (1939) reported a specimen, possibly of *B. spongiceps*, from the Zanzibar area: This appears to be close to, if not conspecific with *B. cottoides*. The Zanzibar specimen matches *B. cottoides* in almost every respect with the exception of having 9 instead of 8 pelvic rays, a shorter head (50.7 *cf.* 52.9–57.6% of s-a length) and a broader interorbital width. The midline premaxillary tooth-patch separation is narrower, being 11.6 of the premaxillary length, *cf.* 14.2–20.0% in *B. cottoides*. This specimen also closely resembles the *Bathygadus* sp. recorded by Iwamoto (1986) except that Iwamoto records 9–12 pyloric caeca whereas in the Zanzibar specimen there are 23.

McCann & McKnight (1980) recorded *B. cottoides* from the eastern New Zealand slope, but measurements they give differ from ours in several respects. There are fewer pectoral and pelvic fin rays, fewer gill-rakers, a longer head and shorter upper jaws in their specimens (see Table 2). We are

Table 2 Counts and proportional measurements for six syntypes of *Bathygadus cottoides*, a specimen from near Zanzibar and a specimen from New Zealand (data taken from McCann & McKnight, 1980).

	Syntypes	Mean	Zanzibar spec.	From McCann & McKnight, 1980.
D	II6–8		II7	II6
Pe	14–15		15	10–11
Pl	9		9	8
GR	5–6+18–22		6+20	5+15
PC	?		23	?
s-a	26.0–63.3mm		97.5mm	102mm
bd	35.3–48.1	40.4	45.1	46.0
pl	broken		broken	14.7
hl	52.9–57.6	55.1	50.7	60.7
od	16.7–20.8	19.0	24.2	20.9
io	26.8–33.8	30.7	40.3	35.4
pml	56.4–61.5	58.5	60.6	53.2
pma	22.8–26.8	24.9	24.0	?
pms	14.2–20.0	16.8	11.6	?

Table 3 Counts and proportional measurements for the holotype and paratype of *Bathygadus filamentosus* and for the holotype of *Bathygadus dubiosus* (considered synonyms of *B. cottoides*).

	Holotype	Paratype	<i>B. dubiosus</i>
D	II8	II8	II8
Pe	13	14	14
Pl	8	8	8
GR	6+20	6+20	6+19
PC	12	?	?
s-a	73mm	54mm	80mm
bd	43.1	42.5	42.5
pl	50.0	broken	77.5
hl	57.5	55.5	56.2
od	23.8	20.0	24.4
io	36.1	31.3	35.5
pml	59.9	61.6	56.6
pma	22.0	16.2	23.5
pms	12.0	7.0	9.7

unable to say whether their specimens are *B. cottoides*, the differences in proportions may merely reflect the larger size of their specimens.

DISTRIBUTION. Off Kermadec Islands, Indonesia (? and east coast of Africa).

DEPTH RANGE. 700–1400m.

MATERIAL EXAMINED. BMNH 1887.12.7.139 (Syntype) 56.5mm s-a, N.E. of New Zealand; 1887.12.7:140–3 (Syntypes) 63.3–33m s-a; 144–5 (Syntypes), 26mm s-a, all from near Kermadec Islands; 1939.5.24:677, 97.5mm s-a, Zanzibar area; USNM 72924 (Holotype of *B. filamentosus*), 73mm s-a, near Sipadan Island, east coast of Borneo; 148990 (Paratype of *B. filamentosus*), 54mm s-a, Molucca Passage; ZMA 114.896 (Holotype of *B. dubiosus*), 80mm s-a, 03° 37'S, 131° 26'E.

Bathygadus spongiceps Gilbert & Hubbs, 1920

Bathygadus spongiceps Gilbert & Hubbs, 1920:381 (descr.).

Known from the types (seven specimens).

In their key, Gilbert & Hubbs (1920) separate *B. spongiceps*

from *B. cottoides* on the number of gill-rakers (6+19–22, cf. 6+17) and on the larger diameter of the eye of the former. In fact, the gill-raker count for *B. cottoides* is 5–6+18–22 cf. 5–6+19–22 in *B. spongiceps*, and the orbital diameters (measured as percentages of the head lengths in both species), almost completely overlap. The interopercular shapes of the two species are also virtually identical (Fig. 17, cf. 1 & 8). Only in the upper jaw is there a marked discrepancy between the species; the length of the premaxilla in *B. cottoides* is 56.4–61.5% of the head length, while that of *B. spongiceps* is 52.3–55.0%; the height of the ascending process is greater in the latter species, viz. 26.1–31.6% cf. 22.8–26.8% of the premaxillary length. There is also a greater midline separation of the premaxillary dentigerous surfaces in *B. cottoides*: 14.2–20.0% cf. 7.6–12.9% of the premaxillary length. In *B. spongiceps* there are 15–16 pectoral fin rays, cf. 12–15 in *B. cottoides*.

These differences may simply represent clinal variation within a single species. However, without the benefit of material from intermediate geographical areas *B. spongiceps* is here regarded as specifically distinct from *B. cottoides*.

Counts and measurements for the holotype and three paratypes (four others are too poorly preserved to make accurate measurements) are given in Table 4.

Table 4 Counts and proportional measurements for the types of *Bathygadus spongiceps* and *B. entomelas*

	holotype	<i>spongiceps</i> paratypes (3)	<i>entomelas</i> holotype
D	II9	II8	II8
Pe	16	15	16
Pl	9	9	10
GR	6+22	5–6+19	5+21
PC	?	6 & 12	37*
s-a	115mm	73, 94, 97mm	87mm
bd	40.0	41.2–45.2	41.3
pl	24.0	27.0 (1 spec.)	broken
hl	51.3	51.5–58.9	55.0
od	20.6	17.4–21.6	27.0
io	36.4	25.5; 30.9; 40.0	32.2
pml	52.5	52.3–55.0	48.9
pma	27.4	26.1–31.6	23.4
pms	12.9	7.6, 11.0	10.6

* 35, according to Gilbert & Hubbs, 1920.

DISTRIBUTION. China and Celebes Seas.

DEPTH RANGE. 864–1600m.

MATERIAL EXAMINED. USNM 78210 (Holotype), 115mm s-a, Derval Bay, Borneo, northeastern coast; USNM 220978 (paratype), 73mm s-a, off south Luzon, China Sea; USNM 220979 (paratype), 94mm s-a, North Island, Celebes; USNM 078235 (paratype), 97mm s-a, Atulayan Island, Philippines (13° 35'N, 123° 37'E). Three other paratypes, USNM 220980 from the southeast coast of Luzon are too badly damaged to derive any accurate measurements and counts.

***Bathygadus entomelas* Gilbert & Hubbs, 1920**

Bathygadus entomelas Gilbert & Hubbs, 1920:386 (descr.).

Bathygadus (Bathygadus) entomelas; Weber & de Beaufort, 1929:18 (descr. after Gilbert & Hubbs).

The species is known only from the type specimen collected in the Molucca Passage. It strongly resembles specimens of *B. spongiceps* and was distinguished from that species by Gilbert & Hubbs (1920) on the basis of its larger orbit. *Bathygadus entomelas* also differs from *B. spongiceps* (and other species) in possessing 10 pelvic fin rays and a large number of pyloric caeca (37, cf. 6–12). In its dentition and overall morphology, *entomelas* most closely resembles *B. spongiceps*.

In their key, Gilbert & Hubbs (1920) separated *B. entomelas* from *B. sulcatus* in the supposed absence of a barbel. However, like *sulcatus*, *B. entomelas* has a minute barbel hidden beneath the skin at the lower jaw symphysis.

B. entomelas might be recognised as a synonym of *B. spongiceps* if those differences that do exist are regarded as intraspecific variability. However, in view of the lack of specimens it is impracticable to assess such variability and so the species is here retained.

DISTRIBUTION. Philippines.

DEPTH RANGE. 780m.

MATERIAL EXAMINED. USNM 78211 (Holotype and only known specimen), 87mm s-a, Molucca Passage, Philippines. Meristic and morphometric data are given in Table 4.

***Bathygadus sulcatus* (Smith & Radcliffe, 1912)**

Regania sulcata Smith & Radcliffe, 1912:108 (descr.).

Bathygadus sulcatus; Gilbert & Hubbs, 1916:142 (listed).

Bathygadus sulcatus; Gilbert & Hubbs, 1920:390 (descr.).

Smith & Radcliffe (1912) noted the close resemblance of *B. sulcatus* to *B. nipponicus*, but distinguished their species by its higher arched dorsal profile, narrower interorbital width and larger eye. Certainly, *B. sulcatus* has a deeper body than *B. nipponicus*, but is no deeper than that of the types of *B. garretti*, which name we consider to be synonymous with *B. nipponicus*. In its interorbital width, however, *B. sulcatus* does differ, both from *B. nipponicus* and *B. garretti*, the range being below that of other Indo-Pacific species. viz. 23.5–26.4, cf. 26.8–37.5% of head length. The diameter of the orbit, although only slightly greater than that of the type

Table 5 Counts and proportional measurements for *Bathygadus sulcatus*. Data from the holotype are included in the Mean.

	Holotype	4 other specimens (USNM149276–82, 192598)	Mean
D	II9	II9–10	
Pe	17*	16–17	
Pl	10**	9–10	
GR	5+18	6+17–18	
PC	30	?	
s-a	161mm	49.0–176.5mm	
bd	41.6	36.0–42.1	39.0
pl	37.2	24.4–30.7	30.7
hl	52.1	50.5–57.1	54.1
od	27.9	26.9–29.8	28.9
io	23.8	23.5–26.4	25.2
pml	57.7	49.6–57.1	55.5
pma	20.6	21.8–26.0	23.2
pms	10.3	4.7–9.5	8.0
bl	concealed	0.2 (1 measured)	

* given as 16 by Smith & Radcliffe (1912)

** given as 9 by Smith & Radcliffe (1912)

of *B. nipponicus*, is embraced by that of the two types of *B. garretti*. Smith & Radcliffe (1912) note the interpremaxillary symphyseal space as being 75% of the diameter of the pupil. Although the maximum premaxillary separation in *B. sulcatus* is 10.3% of the premaxillary length, there is a wide variation in the five specimens measured (see Table 5).

Gilbert & Hubbs (1920:391) consider the interoperculum to differ in shape from that of other Philippine species in that its posterior half, and posterior border are almost straight. The present study reveals that in common with other *Bathygadus* species, the posterior margin of the bone is rounded (Fig. 17, 5). Like *B. nipponicus* (the types of *B. garretti*) a minute barbel is concealed beneath the skin at the mandibular symphysis. Only in one specimen is it exposed and it measures 0.6mm.

Although there is apparently only one major morphometric difference between *B. sulcatus* and *B. nipponicus*, viz. the width of the interorbital space, *B. sulcatus* is nonetheless regarded here as a separate species. This is simply because the presently recognised distribution of the two taxa is allopatric, but the Japanese and Philippine 'species' might well exhibit a population difference within a more widely distributed species.

DISTRIBUTION. Sulu sea, Philippines.

DEPTH RANGE. 600–954m.

MATERIAL EXAMINED. ISNM 72925 (Holotype), 161mm s-a, Cagayan Island, Sulu Sea, 9° 37' 35"N, 121° 12' 37"E; USNM 192598, 176.5mm s-a, from near Cagayan Island; USNM 149176–82, 49, 57, 75mm s-a, off northern Mindanao; between Marinduque and Luzon; between Siquigor and Bohol, and near Cagayan Island. Although noted as paratypes in the USNM collection, none was designated in the original description, nor subsequently by Gilbert & Hubbs (1920). There is no evidence to suggest that these specimens were used in compiling the original description which appears to be based solely on the holotype.

Bathygadus antrodes (Jordan & Gilbert, 1904)

Melanobranchus antrodes Jordan & Gilbert (1902) 1904:606 (descr.).

Bathygadus antrodes; Gilbert & Hubbs, 1916:149 (descr.).

Bathygadus antrodes; Okamura, 1970a:30 (descr.).

Table 6 Counts and proportional measurements for *Bathygadus antrodes*. Data from the holotype are included in the Mean.

	Holotype	8 other specimens (see material examined)	Mean
D	II8	II8	
Pe	13	12–15	
Pl	9	8	
GR	6+21	5–7+20–24	
PC	?	10, 13, 14 & 15	
s-a	95mm	65–129mm	
bd	41.0	38.5–54.8	42.7
pl	broken	26.3–41.2	30.3
hl	55.2	51.8–58.4	54.3
od	22.8	19.8–23.4	21.6
io	32.3	32.2–37.1	34.4
plm	53.3	51.4–55.9	53.3
pma	23.2	23.6–26.5	24.8
pms	14.6	10.0–12.5	10.2

Bathygadus antrodes is separated from the other Japanese species, *B. nipponicus* by its broader head, smaller eye and wider midline separation of the premaxillary tooth bands (Table 6). There is also a lower number of pectoral fin rays, 14–16 cf. 16–19, and pyloric caeca, 10–18, cf. 30 to >50. The teeth, although small, are prominent, particularly in small specimens, and have a strong inner curvature. The interoperculum is shallow with an expanded posterior tip (Fig. 17, 11).

According to Okamura (1970a:33) *B. antrodes* appears to be closely related to *B. cottoides*. Certainly both share a low number of pectoral fin rays (14–16 and 12–14 respectively) and both have a wide interorbital (32.2–37.1% of head length, cf. 26.8–33.8%), but these are also features shared with *B. spongiceps* (see Tables 2 & 3).

DISTRIBUTION. Southern Japan.

DEPTH RANGE. 792–1200m.

MATERIAL EXAMINED. USNM 50932 (Holotype), 95mm s-a, Sagami Bay; USNM 51442 (Paratype), 134mm s-a and one juvenile, ca 140mm TL, Sagami Bay, 99246, 83mm s-a, off Shio Misaki; 77242 & 77245, 113, 126mm s-a, off Omi Saki; 77243, 129mm s-a, 77244, 80, 65mm s-a.

Bathygadus nipponicus (Jordan & Gilbert, 1904)

Regania nipponica Jordan & Gilbert, (1902) 1904:605 (descr.).

Bathygadus garretti Gilbert & Hubbs, 1916:151 (descr.).

Gilbert & Hubbs (1916:151) separated *B. garretti* from *B. nipponicus* on the presence in the former species of a small barbel, greater number of gill-rakers, fewer dorsal fin rays, greater number of pelvic rays, narrower interorbital and small orbit.

Table 7 Counts and proportional measurements for *Bathygadus nipponicus*.

	Holotype of <i>nipponicus</i>	Types of <i>B. garretti</i> holotype	paratype
D	II10	II9	II9
Pe	17	16	19
Pl	10	10	11
GR	5+16	5+18	5+18
PC	?	?	54
s-a	217mm	180mm	156.5mm
bd	32.7	38.3	42.8
pl	28.5	broken	broken
hl	48.8	52.7	63.8
od	26.4	24.2	30.1
IO	30.6	29.4	33.3
pml	54.2	72.4	66.6
pma	26.0	26.0	23.8
pms	6.4	5.0	8.3
bl	absent	1.0	1.5

Although a barbel is present in *B. garretti* it is often hidden below the skin (see Okamura, 1984) and the development of a barbel in *Bathygadus* appears to be a primitive feature of little significance in discriminating between species. Gill-rakers on the lower arch differ by two (18 in *B. garretti*, cf. 16 in *B. nipponicus*), within the range of variation of other species. Again, the dorsal fin ray count differs by only one. Jordan & Gilbert (1904) miscounted the pelvic

rays in *B. nipponicus* (see also Okamura, 1984:357) and both species have 10 (sometimes 11 in *garretti*). Both the orbital diameter and interorbital width of *B. nipponicus* are encompassed by the ranges of those parameters in *garretti* (see Table 7).

Okamura (1984:357) notes that *B. garretti* is separable from *B. nipponicus* in a single character, namely the presence of a mandibular barbel. Since, as detailed above, this feature does not reliably indicate specific identity, *B. garretti* is treated as a synonym of *B. nipponicus*.

DISTRIBUTION. Suruga Bay; Okinawa Trough.

DEPTH RANGE. 840–1348m.

MATERIAL EXAMINED. USNM 50931 (Holotype) 217mm s-a, Suruga Bay; 76863 & 135351 (Holotype and paratype of *B. garretti*) 180, 156.5mm s-a, Suruga Bay (35° 05' 30"N, 138° 39' 50"E).

***Bathygadus bowersi* (Gilbert, 1905)**

Gadomus bowersi Gilbert (1903) 1905:659 (descr.).

Bathygadus bowersi; Gilbert & Hubbs, 1916:142 (listed).

Bathygadus bowersi; Gilbert & Hubbs, 1920:379 (in key).

The features given by Gilbert (1905) to distinguish *B. bowersi* from *B. antrodes* are lightness of colour, firmer consistency of cranial bones, differing proportions of the operculum and preoperculum, greater development of the opercular ridge and somewhat smaller scales.

Table 8 Counts and measurements for the types of *Bathygadus bowersi*.

	Holotype		Paratypes	
D	II8	II8	II8	II8
Pe	17	17	17	17
Pl	9	9	9	9
GR	8+24*	8+21	8+21	8+21
PC	?	?	?	?
s-a	139.5mm	130mm	65mm	55mm
bd	53.0	53.0	46.1	49.6
pl	30.1	broken	16.9	18.1
hl	57.3	58.4	58.4	61.8
od	33.0	21.7	23.6	23.5
io	37.5	36.0	36.8	33.6
pml	56.2	48.6	57.8	54.0
pma	24.4	25.6	29.0	27.0
pms	17.7	12.1	11.0	10.0

* given by Gilbert (1903) as 6+22 in the holotype and 6–7+22–24 in the paratypes

In their key, Gilbert & Hubbs (1920) distinguished *B. bowersi* from other species by its lack of filamentous extensions of the outer pectoral and pelvic fin rays, its wide interorbital space and dark colouration. Most of these characters are subjective and not easily quantifiable. Severe damage to the pectoral and pelvic fins of the types has made it impossible to determine whether they were filamentous. The interorbital width of *B. bowersi* has an almost co-incident ratio with that of *B. antrodes*, viz. 33.6–37.5% cf. 32.2–37.1% of the head length. Also, like *B. antrodes*, *B. bowersi* has a broad midline separation of the premaxillary dentigerous surfaces, 10.0–17.7% cf. 10.0–14.6% of the premaxillary

length, a feature in which these species also resemble *B. cottooides* (14.2–20.0%). At its maximum, the orbital diameter (as a percentage of the head length) of *B. bowersi* exceeds that of any Indo-Pacific species, being 21.7–33.0%, cf. 16.7–30.1%. *Bathygadus bowersi* also has a relatively high number of gill-rakers on the first ceratobranchial (21–24), matched only by *B. antrodes* (20–24) and *B. melanobranchus* of the Atlantic (21–24). Counts and measurements for four of the types are given in Table 8.

On the basis of the six specimens which represent this species it is impossible to comment further on the variability of morphometric characters and, in view of its 'isolated' geographical position *B. bowersi* is here recognised as a distinct species.

DISTRIBUTION. Hawaiian Islands, near Bird Island and Kauai;

DEPTH RANGE. 550–1460mm.

MATERIAL EXAMINED. USNM 51658 (Holotype), 139.5mm s-a, near Bird Island, Hawaii; 51695 (paratype), 130mm s-a, 65, 55mm s-a, near Bird Island.

Key to the Atlantic species of *Bathygadus*

- 1 Pelvic rays 9, rarely 10 *B. favosus* 2
- Pelvic rays 7, rarely 8 2
- 2 Gill-rakers 5–6/19–21; interorbital width 19.7–25.0% of head length *B. macrops*
- Gill-rakers 5–7/21–24; interorbital width 24.5–33.9% of head length *B. melanobranchus*

Key to the Indo-Pacific species of *Bathygadus*

- 1 Gill-rakers 5–6+16–18* 2
- Gill-rakers 5–6+19–24 3
- 2 Interorbital width 23.5–24.4% of head length *B. sulcatus* (Philippines)
- Interorbital width 29.4–32.3% of head length *B. nipponicus* (Japan)
- 3 Gill-rakers 5–6+19–21 4
- Gill-rakers 5–8+21–24 6
- 4 Orbital diameter 16.0–24.5% of head length 5
- Orbital diameter 30% or more of head length *B. entomelas* (Philippines)
- 5 Premaxillary length 56.4–61.6% of head length *B. cottooides* (Kermadec area, Indonesia, ?Indian Ocean)
- Premaxillary length 52.3–55.0% of head length *B. spongiceps* (Indonesia)
- 6 Pectoral rays, 17 *B. bowersi* (Hawaiian-Islands)
- Pectoral rays 12–15 *B. antrodes* (Japan)

* 18 occurs rarely also in *B. cottooides*.

***Gadomus* Regan, 1903**

Gadomus Regan, 1903:459 (orthotype, *Bathygadus longifilis* Goode & Bean, 1885).

DIAGNOSIS. (Features distinguishing *Gadomus* from *Bathygadus* italicised). Head and body compressed, tail slender, without caudal fin; two dorsal fins, the first with two spiny rays, first ray reduced. Anterior dorsal and outer pectoral and pelvic fin rays attenuated; pectoral fin with exposed nerve tract

bordering second ray. Rays of second dorsal fin longer than those of anal fin. Snout blunt; mouth large and terminal; *teeth minute*, villiform, sometimes arranged in bands on both premaxilla and dentary; *dentigerous area of premaxillae usually narrowly separated across midline*. Palatine contacts only the lateral ethmoid. Barbel present. Interoperculum deep, trapezoidal or triangular, usually with convex posterior border. Gill opening wide, gill-rakers on first arch slender and denticulate; gill-filaments reduced, at most half the length of the rakers (except one species); pseudobranchiae present. Nasal bones slender and widely separated at midline. Skull with generally narrow interorbital width, always <25% of head length; orbit always <30% of head length. Vertebral count greater than 100. Scales small, bearing fine reticulate pattern. Olfactory bulbs close to olfactory lobes of brain. Four retia in swimbladder.

Atlantic species

Iwamoto (1970) and Marshall (1973a) provided keys with descriptions, distributional ranges, synonymies and complete references. The following are additional data and comments.

Gadomus arcuatus (Goode & Bean), 1886

Bathygadus arcuatus Goode & Bean, 1886:158 (descr.).
Gadomus arcuatus; Gilbert & Hubbs, 1916:142 (listed).

The most obvious feature distinguishing this from other Atlantic, and indeed all other *Gadomus* species are the prolongation of the two outer pelvic rays rather than only the outer (second) ray, and the higher number of pectoral rays (20–25, cf. 13–20). In our sample, there is a higher number of gill-rakers on the first ceratobranchial than that recorded by Marshall (1973a), viz. 4–5+19–33, cf. 4–6+18–21. In other proportional measurements, ours correspond with the ranges given by Iwamoto (1970) and Marshall (1973a).

Another feature distinguishing *G. arcuatus* from the other Atlantic species is the length of the premaxillary ascending process, which is 24.3–28.0% of the premaxillary length. This contrasts with the shorter processes in *G. dispar* (19.6–24.1) and *G. longifilis* (21.0–23.6).

The gill-filaments are exceedingly short, being only 25% of the gill-raker length.

Marshall (1973a) drew attention to the similarity in dentition between *G. arcuatus* and *G. denticulatus* (Indonesia). This similarity lies in an upward expansion of the premaxillary dentigerous area onto the medial ascending process. However, this is not uncommon in *Gadomus* species, particularly in large individuals. The rows of premaxillary teeth in *G. arcuatus* appear to be more regularly arranged than in other species.

We have found no specimens from localities that alter the distribution given by Marshall (1973a) namely between the Equator and 30°N.

DEPTH RANGE. 610–137m (Marshall, 1973a).

MATERIAL EXAMINED. BMNH 1969.6.26:3264, 160mm s-a (ca 347mm TL), off Honduras; 1963.2.25:2–3, 57.5 & 68mm s-a, Caribbean; USNM 212158, 83mm s-a, off Nicaragua; 212160, 99mm s-a, Gulf of Mexico; 3658, 175mm s-a (ca 485mm TL), 126mm s-a, 179mm s-a; Uncat. 133mm s-a, off Mississippi delta.

Counts and measurements for a sample of ten specimens are given in Table 9.

Table 9 Counts and proportional measurements for ten specimens of *Gadomus arcuatus*. Ranges in square brackets are those given by Marshall (1973a).

	Range	Mean	
D	11–11		
Pe	20–22		
Pl	8		
GR	4–5+19–23		
Pc	25–30		
s-a	83–179mm		
bd	40.9–51.1	46.5	
pl	32.4–53.0	43.4	
hl	50.0–55.5	52.1	
od	20.6–27.0	23.4	[17.8–26.7]
io	17.0–21.8	17.1	[16.7–20.0]
pml	58.0–51.6	55.7	[52.0–57.3]
pma	24.3–28.0	24.2	
pms	4.6–7.8	4.9	
bl	67.1–94.8	80.1	[65.6–87.3]

Gadomus dispar (Vaillant, 1888)

Hymenocephalus dispar Vaillant, 1888:221 (descr.).
Gadomus dispar; Gilbert & Hubbs, 1916:142 (listed).

In Marshall's (1973a) key, *G. dispar* is separated from *G. longifilis* by its fewer gill-rakers (20–21, cf. 27–31) and higher number of pectoral rays (18–20, cf. 14–16). The other feature given by Marshall to separate the two species is the interorbital width, given as 15–17% of the head length in *G. dispar* and 21–25% in *longifilis*. In our sample of *dispar*, the proportion is 18.6–19.1% and in *longifilis* 19.7–24.8%. Thus there is very nearly a continuum rather than a wide gap in this parameter. Nevertheless, it is sufficiently distinct to separate the two species.

Two other parameters that separate *dispar* from the other Atlantic species are length of the head and diameter of the orbit. The head length of *dispar* is the shortest of the three species, being 47.0–49.5% of the snout to anal fin distance, cf. 50–55.5% in *arcuatus*, and 52.5–55.6% in *longifilis*. The horizontal diameter of the orbit is the longest of the three species, viz. 27.6–29.5% of the head length (given by Marshall as 26.8–31.6%), cf. 20.6–27.0% in *arcuatus* and 23.5–27.7% in *longifilis*.

In only one specimen examined is the pectoral fin complete, measuring 91.0% of the snout-anal fin distance. It is thus longer than the pectoral fin of the other two species, viz. 32.4–53.0% in *arcuatus* and 57.8–63.2% in *longifilis*.

We are unable to corroborate Marshall's (1973a) opinion that *G. dispar* is closely related to *G. denticulatus* of the Philippines.

Comparisons between *G. dispar* and *G. longifilis* are given in Table 10.

MATERIAL EXAMINED. USNM 216159, two specimens 100 & 108mm s-a, off Honduras, 14° 10'N, 81° 50'W; USNM Uncat., 112mm s-a, off Nicaragua, 12° 25'N, 82° 15'W.

DISTRIBUTION. Western and eastern Atlantic, Caribbean Sea, and off Morocco.

DEPTH RANGE. 548–1105mm (see Marshall, 1973a).

Gadomus longifilis (Goode & Bean, 1885)*Bathygadus longifilis* Goode & Bean, 1885:599 (descr.).*Hymenocephalus longifilis*; Vaillant, 1888:218 (descr.).*Gadomus longifilis*; Regan, 1903:459 (type species designation).

Apart from the higher number of gill-rakers on the first ceratobranchial (27–31, cf. 20–21 in *dispar* and 18–23 in *arcuatus*), the lower number of pectoral fin rays (13–16, cf. 17–22 in the other two species), and the modally wider interorbital (22.7% of head length, cf. 17.1% in *arcuatus* and 18.8% in *dispar*), *G. longifilis* can also be distinguished from the other Atlantic species by the shorter barbel, which is only 40.0–50.0% of the head length, cf. 67.1–94.8% in *G. arcuatus* and 75.4–90.0% in *dispar*. The gill-filaments are, at the centre of the ceratobranchial, only 20% of the length of the gill-rakers; the shortest of any *Gadomus* species.

Pyloric caeca are few, varying from 5 in a specimen of 37.3mm s-a, and 9 in one of 49.0mm, to 12 in larger specimens. This is the lowest number of caeca possessed by any of the Atlantic species.

The premaxillary teeth are relatively well-developed, in common with the other Atlantic species, and arranged in a narrow band; teeth on the dentary are reduced to a single row posteriorly.

Table 10 Counts and proportional measurements for three specimens of *Gadomus dispar* and fifteen specimens of *G. longifilis*. Ranges in square brackets are those given by Marshall (1973a).

<i>G. dispar</i>			
	Range	Mean	
D	II9–11		
Pe	17–18		
Pl	8		
GR	4+20–21		
Pc	35+		
s-a	100–112mm		
bd	40.1–41.6	40.3	
pl	91.0 (others broken)		
od	27.6–29.5	28.3	[26.8–31.0]
io	18.6–19.1	18.8	[15.2–17.1]
pml	52.2–54.7	53.7	[51.6–56.3]
pma	19.6–24.1	22.0	
pms	5.0–5.8	(two only measured)	
bl	75.4–90.0	84.2	
<i>G. longifilis</i>			
D	II9–10		
Pe	17–18		
Pl	8		
GR	6–8+27–29		
PC	12–15		
s-a	37.3–75.5mm		
bd	35.3–45.2	39.7	
pl	57.8–63.2	60.5	
hl	52.5–55.6	53.6	
od	23.5–27.7	26.2	[23.1–28.0]
io	19.7 24.8	22.7	[21.1–25.0]
pml	52.7 56.8	55.1	
pma	21.0–23.6	22.0	
pms	4.7–5.2	4.9	
bl	40.0–50.0	43.8	[31.6–40.0]

According to Marshall (1973a), *G. longifilis* is most closely related to the Indo-Pacific *G. multifilis*, although we have found no evidence to support this assumption.

Gilbert & Hubbs (1920:406) note that records of *G. longifilis* from the Indian Ocean are probably misidentifications. Marshall (1973a) supported this view by citing a specimen of Alcock, from off the Maldives, which Marshall identified as *G. multifilis*. Regardless of the correct identity of the Indian Ocean species (p. 196) our findings support those of previous authors in failing to locate any specimen of *longifilis* from an Indo-Pacific locality.

DISTRIBUTION. Gulf of Mexico, Caribbean, Straits of Florida, Azores, Canary Islands and off Mauritania, west coast of Africa.

DEPTH RANGE. 630–2165m (see Marshall, 1973a).

MATERIAL EXAMINED. BMNH 1963.2.25:7–17, ten specimens, 37.3–75.5mm s-a (largest specimen ca 230mm TL) 'Oregon' Stn 3562; 1963.2.25:18–19, 61.0, 62.5mm s-a, 'Oregon' Stn 3586; USNM 37338 (syntypes), 67.4 & 68.0mm s-a, 28°N 87°W; USNM Uncat. 65.5mm s-a, 'Oregon' Stn 4040.

Gadomus capensis (Gilchrist & von Bonde) 1924*Bathygadus capensis* Gilchrist & von Bonde, 1924:13 (descr.).*Bathygadus fumosus* Barnard, 1925a:500 (published April); 1925b:333 (published June) (descriptions).*Gadomus capensis*; Marshall, 1973a:519 (in key).*Gadomus fumosus*; Marshall, 1973a:519 (in key).*Gadomus capensis*; Iwamoto, 1986:335 (synonymisation).

Iwamoto (1986) states that Heemstra's examination (reported in litt.) of the types of *B. capensis* and *B. fumosus* reveal no differences other than the rudimentary barbel of the former (said by Gilchrist & von Bonde to have been absent). Further examination of types of both specimens supports Heemstra's findings and Iwamoto's synonymy (Table 11).

Gadomus capensis is undoubtedly closely related to the species recognised here as *G. 'multifilis'* from the east African coastal waters and other Indian Ocean localities. It differs, however, in a greater body depth (46.4–48.2%, cf. 33.8–43.6% of s-a length), longer premaxilla (57.1–60.4%, cf. 55.2–58.4% head length), narrower midline separation of the premaxillary dentigerous surfaces (3.5–6.8%, cf. 8.2–13.1% premaxillary length) and shorter barbel. The length of the pectoral fin is virtually the same, which distinguishes *capensis* and '*multifilis*' from other Atlantic species. With *G. longifilis* and *G. multifilis*, *G. capensis* shares a high number of gill-rakers (6–7+25–7), a feature which also sets it apart from *G. furvescens* which has 6–7+20–22 rakers. There is no trace of any dark pigmentation on the dorsal and pectoral fins which appears to be a characteristic of the Indian Ocean *G. multifilis* (see p. 196).

Also identified as *G. capensis* is a specimen from off Cape Point, previously determined by Gilchrist as *Bathygadus (Gadomus) furvescens*. This misidentification draws attention to the possibility that those specimens listed by Gilchrist & von Bonde (1924) under *Bathygadus melanobranchus (B. furvescens)* was treated by those authors as a synonym of that species) may well include *Gadomus capensis*. Pakhurov (1980) records *G. capensis* (cited as *G. fumosus*) from the mid-Atlantic ridge. If these specimens have been correctly identified then the species' distribution encompasses both Atlantic and Indian Oceans.

DISTRIBUTION. Table Bay to Mozambique (Iwamoto, 1986); Atlantic (Pakhurov, 1980).

DEPTH RANGE. 750–1450m.

MATERIAL EXAMINED. RUSI 36 (Holotype), 94mm s-a, off Cape, Stn 450; BMNH 1927.12.6:14 (syntype of *G. fumosus*), 84mm s-a, off Cape Point; 1904.5.28:11, 74.2mm s-a, 34 miles north-east of Cape Point.

Table 11 Counts and proportional measurements for the types of *Gadomus capensis* and *G. fumosus*.

	<i>capensis</i>	<i>fumosus</i>
D	II9	II8
Pe	17	18
Pl	8	8
GR	7+25	6+25
PC	?	19
s-a	94mm	84mm
bd	48.2	46.4
pl	123.9	84.5 (broken)
hl	52.1	51.1
od	25.5	23.2
io	23.4	23.2
pml	57.5	60.4
pma	21.4	21.1
pms	3.5	5.7
bl	1.8	6.9

Indo-Pacific species

Gadomus furvescens (Alcock, 1894)

Bathygadus furvescens Alcock, 1894:128 (descr.); 1895:pl.16, fig.1.

Bathygadus furvescens; Norman, 1939:47 (synonymy; comments).

?*Bathygadus melanobranchus*; Brauer, 1906 (*non*-Vaillant): 272 (descr.); Barnard, 1925b:334 (descr.).

This species is here referred to the genus *Gadomus* on the basis of its long filamentous dorsal, pectoral and pelvic fin rays; a barbel (albeit reduced); a well-developed branch of the RLA-P nerve passing along the second pectoral fin ray; narrow midline separation of the premaxillary dentigerous surfaces and deep, nearly square interoperculum.

Alcock (1894:199) was incorrect in stating that a barbel was lacking in *G. furvescens*; a small barbel is present in the syntype we have examined. Of the other twelve specimens examined, eight have small or minute barbels, but in the other four, a barbel is totally lacking. There is apparently no correlation between barbel length and head length, nor between interorbital width and head length, or orbital diameter and head length.

The teeth of *G. furvescens* are coarse and rather large and are not arranged in regular rows on the premaxilla. The separation between the dentigerous tips of the premaxillae is variable (3.7–6.5% of premaxillary length) but is one of the narrowest (3.7%) of all *Gadomus* species. The length of the premaxilla is also variable (46.2–60.0% of head length) and the higher figure is the maximum premaxillary-head length ratio recorded in *Gadomus*.

The gill-filaments are long, compared with those of other species, being 50–93% of the length of the gill-raker. In this feature, *G. furvescens* differs from other *Gadomus* species.

The membranes of the dorsal fins are noticeably black and in this respect resemble those of the Indian Ocean *G. multifilis*. *Gadomus furvescens* differs from *G. multifilis* and

G. capensis, however, in having fewer gill-rakers on the ceratobranchial (20–22, *cf.* 25–27), shallower body depth and shorter pectoral fin (see Table 12 for proportional measurements).

It seems likely that most of the references to Indian Ocean *Bathygadus melanobranchus* refer to *G. furvescens* (but see also p. 194 under *Gadomus capensis*). Specimens identified as *Bathygadus furvescens* by Gilbert & Hubbs (1920:338) from the Philippines do not belong to this species and should be referred to *Bathygadus cottoides* along with the *B. melanobranchus* of Weber, 1913.

DISTRIBUTION. Gulf of Aden, Maldives, Andaman Sea, Bay of Bengal.

DEPTH RANGE. 790–1295m.

MATERIAL EXAMINED. BMNH 1896.9.11:2 (Syntype), 150.0mm s-a, Arabian Sea, 9° 34'N, 73° 36'E; 1939.5.24:675-6, 35.5 & 122.5mm s-a, plus one specimen of 64mm TL, 13mm hl, (tail broken), too damaged to measure, Gulf of Aden; 1939.5.24: 673–74, 84.5 & 53mm s-a, Maldivian area; 1939.5.24:669, *ca* 275mm TL (not measured), Gulf of Aden; 1939.5.24:670–72, 88mm s-a and three other specimens not measured but used in counts, one badly disintegrated, one *ca* 140mm TL, 35.5mm hl, one *ca* 255mm TL, *ca* 63mm hl, Gulf of Aden.

Table 12 Counts and proportional measurements for a syntype of and five other specimens of *Gadomus furvescens*.

	Syntype	5 specimens, BMNH 1939,5,24:699; ex:670–76	Mean
D	II10	II9–10	
Pe	15	14–15	
Pl	8	8	
GR	6+22	6–7+20–21	
PC	*	20–28(n3)	
s-a	150mm	35.5–122.5mm	
bd	38.5	29.6–40.8	31.6
Pl	32.0	49.7–53.2(n3)	45.0
hl	50.5	53.8–61.9	55.6
od	23.2	21.6–27.3	24.4
io	20.9	19.6–27.3	22.5
pml	55.4	46.2–60.0	57.4
pma	22.6	20.5–26.8	22.6
pms	6.5	3.7–9.3	6.2
bl	5.4	0.7–3.0(n3)	2.7

* Gut removed, but given as 20 by Alcock (1894).

Gadomus multifilis (Günther, 1887)

Bathygadus multifilis Günther, 1887:155 (descr.).

Bathygadus longifilis; Alcock, 1890 (*non* Goode & Bean):302; 1891:123 (descr.); Chun, 1900:504 (descr.); Brauer, 1906: 270 (descr.).

?*Gadomus* sp. Gilbert & Hubbs 1916:153 (descr. Japan).

Gadomus multifilis; Gilbert & Hubbs, 1920:406 (descr.).

Bathygadus (Gadomus) multifilis; Weber & de Beaufort, 1929:23 (descr.).

Gadomus multifilis; Norman, 1939:48 (partial descr.).

Gadomus multifilis; Okamura, 1970a:27 (descr. of Philippine specimen).



Fig. 32 Indo-Pacific distribution of *Gadomus* species. □=*G. denticulatus*, ○=*G. aoteanus*, △=*G. colletti* (Japan), ●=*G. furvescens*, ■=*G. multifilis*, ▲=*G. magnifilis*, X=*G. introniger*, m=*G. melanopterus* (Hawaii).

The type specimen is recorded from south of the Philippines; it is a juvenile of 123.5mm TL (tail missing). According to Gilbert & Hubbs (1920:406) the species identified as *G. longifilis* by Alcock, Brauer and Chun from the Indian Ocean is probably *G. multifilis*. Marshall (1973a) agreed with this view, in identifying one of Alcock's specimens from the Maldive area as *multifilis*.

The present study confirms that the Indian Ocean species differs from *G. longifilis* and on the basis of corresponding meristic and morphometric features it would appear to be *multifilis*. However, the type and other *multifilis* specimens examined, have, compared with all other species, a longer head (53.2–60.4% s-a, cf. 46.6–55.6% in others); the width separating the dentigerous areas of the premaxillae is also greater (8.2–13.1% cf. 3.9–6.0% in others). In this latter feature *G. multifilis* approaches the condition observed in *Bathygadus*. Counts and measurements are given in Table 13.

The Indian Ocean specimens assigned to *G. multifilis* have a very dark anterior area on the dorsal fin membrane and black pelvic rays. The branchiostegal membrane is also black with a white proximal region. Such a pigmentation pattern is lacking in the type specimen, although this may simply be due to its long period of preservation. The specimen recorded from Japan by Gilbert & Hubbs (1916) as *Gadomus* sp. and later (1920) referred by them to *multifilis* cannot now be traced, although their (1920) specimen reported from the Philippines certainly belongs to that species and it is upon this that Okamura (1970a:26–29) based his description. Okamura noted (presumably referring to Gilbert & Hubbs, 1916), that only one specimen is known from Japanese waters. It is doubtful, however, that it represented *multifilis* since according to Gilbert & Hubbs it had a higher number of gill-rakers and

a narrower interorbital width. The record of *G. multifilis* from the Emperor sea mount chain (Novikov *et al.*, 1980) is also doubtful; this (these) specimens probably represent the northward extension of the Hawaiian species, *G. melanopterus*.

Gilbert & Hubbs (1920:406) thought that *G. melanopterus* might be synonymous with *G. multifilis*. However, *melanopterus* differs in its higher number of pelvic rays (9, cf. 8), a narrower midline separation of the dentigerous areas of the premaxillae, shorter head and greater number of gill-rakers (7+27, cf. 6+25).

Table 13 Counts and proportional measurements of the holotype of *Gadomus multifilis* and eight other specimens.

	holotype (Philippines)	7 specimens from Indian Ocean localities	1 specimen from Molucca Sea (USNM 99447)
D	II8	II8	II9
Pe	15	16	16
Pl	8	8	8
GR	6+25	6+25 6+25	6+25
PC	?	25 (1 spec.)	15
s-a	42mm	43–71.5mm	63mm
bd	36.9	33.8–43.6	43.6
pl	broken	109.6–123.0	broken
hl	57.1	53.2–60.4	60.3
od	25.0	25.8–27.3	24.2
io	20.8	19.0–25.0	22.3
pml	52.0	57.1–58.4	55.2
pma	21.6	20.6–22.1	19.0
pms	10.4	8.2–13.1	14.2
bl	47.9	63.0–68.8	63.0

DISTRIBUTION. Indian Ocean, Philippines.

DEPTH RANGE. 760–1170m.

MATERIAL EXAMINED. BMNH 1887.12.7:146 (Holotype), 42mm s-a, south of Philippines; 1939.5.24:682, 43mm s-a, Zanzibar area; 681, 74mm s-a, Maldive area; 683, 24mm s-a, Gulf of Aden; 1898.7.13:16, 71.5mm s-a, Maldives; USNM 99447, 63mm s-a, 0° 04'S, 121° 36'E, East Philippines; BMNH 1939.5.24:678–80, 62, 66, 71mm s-a, Maldive area.

Gadomus aoteanus McCann & McKnight 1980

Gadomus aoteanus McCann & McKnight, 1980:21 (descr.).
Bathygadus longifilis; McCann, 1972 (*non* Goode & Bean, 1886):620

Described from three specimens, the meristics and morphometrics of two of which were published in the description. These measurements have here been converted to proportional values (Table 14).

According to McCann & McKnight, *G. aoteanus* is related to the Philippine species *G. introniger* from which it supposedly differs in having a longer head and upper jaw, fewer pectoral fin rays and one more pelvic ray. In fact only one specimen of *G. aoteanus* has a head length greater than *G. introniger* and the upper jaw (taken as premaxillary length) is shorter than that of *introniger* (51.8–50.8%, cf. 52.3–56.1% of head length). *Gadomus aoteanus* differs from all the Philippine species in having a shorter upper jaw, a broader interorbital (width recorded from only one specimen by McCann & McKnight; viz. 25.0% of head length cf. 15.5–11.5% in Philippine species and 23.1% in the Hawaiian species, *G. melanopterus*) and in having a higher number of gill-rakers (7+25 cf. 4–6+20–23). As in *G. melanopterus*, *G. aoteanus* has 9 pelvic fin rays. It differs from other Indo-Pacific *Gadomus* in having a relatively short barbel (16.6–18.6% of head length, cf. 22.1–83.3%).

At present, this species is recorded only from the southern Norfolk Ridge off the North Island of New Zealand at a depth range of 970–1232m.

No material was available for this study.

Table 14 Counts and proportional measurements for *Gadomus aoteanus* compiled from data given by McCann & McKnight (1980)

	102mm	106mm
D III0; Pe 14–15; Pl 9; GR 7+25; PC 14–100+		
s-a	102mm	106mm
bd	42.1	47.1
pl	107.8	132.0
hl	52.9	55.6
od	22.2	22.7
io	25.0	?
pml	51.8	50.8
bl	16.6	18.6

Gadomus magnifilis Gilbert & Hubbs, 1920

Gadomus magnifilis Gilbert & Hubbs, 1920:398 (descr.).

Known only from the holotype and two paratypes taken off northern Mindanao.

Gilbert & Hubbs (1920) considered this species to be most closely related to *G. denticulatus* from which, according to those authors, it is distinguished by 'marked differences'.

There is, however, an overlap in all our measurements and counts between the two species (with the exception of the head length). In *G. magnifilis*, the head is 51.7–55.2% of the snout-anal fin distance, in contrast to a range for *G. denticulatus* of 46.6–48.9% and *G. introniger* of 48.0–53.2%. *Gadomus magnifilis* resembles *G. introniger* in the broad midline separation of the dentigerous surfaces of the premaxillae (5.0% of premaxillary length, cf. 6.0%). The most striking distinguishing feature of *G. magnifilis* is the length of its second pectoral fin ray, which is 141–142.8% of the snout-anal fin distance compared with a maximal measurement of 126.0% in *G. denticulatus*.

Both *G. magnifilis* and *G. denticulatus* possess similar dentition. The teeth are minute, giving an almost smooth appearance to the premaxillary and dentary dentigerous surfaces and both share the same degree of expansion of the premaxillary dentigerous surface near to the symphysis. Both species also possess a short, deep interoperculum with a shallowly concave posterior border (Fig. 17g,j).

With the collection of more material it may become apparent that *G. magnifilis* and *G. denticulatus* are conspecific. However, on the basis of the differences given above *magnifilis* is here recognised as a distinct species.

DISTRIBUTION. Off Mindanao, Philippines.

DEPTH RANGE. 914–1260m.

MATERIAL EXAMINED. USNM 78208 (Holotype), 112mm s-a, off northern Mindanao, Philippines; 221089 (paratype), 75.5mm s-a southern Leyte Island; 078234, Sulu Sea (too damaged to record measurements). Meristic and morphometric data are given in Table 15.

Table 15 Counts and proportional measurements of the holotype (USNM 78208) and paratype (USNM 221089) of *Gadomus magnifilis*.

	Holotype	Paratype
D	II10	II9
Pe	17	17
Pl	8	8
GR	5+22	6+21
PC	?	22
s-a	112mm	75.5
bd	42.8	45.0
pl	142.8	141.0
hl	51.7	51.6
od	19.8	25.6
io	17.2	17.9
pml	57.7	56.4
pma	22.5	22.7
pms	5.9	5.0
bl	60.3	79.4

Gadomus denticulatus Gilbert & Hubbs, 1920

Gadomus denticulatus Gilbert & Hubbs, 1920:393 (descr.).

Bathygadus (Gadomus) denticulatus; Weber & de Beaufort, 1929:21 (descr. after Gilbert & Hubbs).

?*Bathygadus longifilis*; Weber, 1913:173 (descr.).

Known from the holotype and ten paratypes from the Philippines and off Borneo.

Gilbert & Hubbs (1920:392–3) distinguish *denticulatus* from *G. colletti* on the basis of differences in the posterior

expansion of the premaxillary tooth bands. 'Expanded posteriorly' is here understood to mean where the dentigerous surface expands somewhat dorsad onto the postmaxillary process of the premaxilla. This is not, however, a valid diagnostic feature, since it appears to be phenotypically variable. The anterior region of the dentigerous surfaces of both the premaxilla and dentary are broadly expanded in *G. denticulatus* whereas in other species they remain constantly narrow or are only slightly broadened.

The number of pyloric caeca is also given by Gilbert & Hubbs (1920) as a distinguishing feature of *denticulatus* and *colletti*. For the former species they give 61–75 and for the latter, 95. However, the number of caeca in *denticulatus* appears to be more variable, ranging from 30 to over 70.

In most morphometric parameters, *denticulatus* shows overlap with other species; the exceptions being the head length and interorbital width. The head is 46.6–48.9% of the snout and anal fin distance, *cf.* 48.0–55.2% in other Philippine species, (but 47.9–49.1% in *G. colletti*; see Table 16). The interorbital width is narrow, being 15.5–17.1% of the head length, *cf.* 17.2–22.5% in Philippine species and 17.7–19.1% in *G. colletti*.

As noted under *G. magnifilis*, the interopercular morphology of the two species is virtually identical and in this respect differs from that of *G. colletti* where the interoperculum is more extended anteriorly and rounded posteriorly (*cf.* Figs 17f,j).

Gilbert & Hubbs (1920) synonymised Weber's (1913) *G. longifilis* with *G. denticulatus*, an action followed by Weber & de Beaufort (1929). We are less certain, however, of the correct identity of Weber's material since Weber & de Beaufort (1929) give a gill-raker range of 17–26. Only in *G. melanopterus*, from Hawaii is there such a high number of rakers and certainly such a broad range has not been recorded in other *Gadomus* species.

Table 16 Counts and proportional measurements for the holotype, and nine paratypes of *Gadomus denticulatus*

	Holotype	Paratypes	Mean
D	II9	II9–11	
Pe	17	16–18	
Pl	8	8	
GR	5+17	4–5+17–20	
PC	?	30–70+	
s-a	120mm	70.5–114mm	
bd	41.6	33.9–41.4	38.4
pl	126.0	96.4–126.0	115.6
hl	46.6	46.9–48.9	47.7
od	25.0	26.3–29.1	26.8
io	15.5	16.4–17.1	16.4
pml	53.5	50.4–57.1	53.5
pma	26.6	20.0–27.7	24.7
pms	4.0	2.0–3.0	3.0
bl	69.9	70.0–83.3	77.5

DISTRIBUTION. Between the Philippine islands and the Sulu Sea.

DEPTH RANGE. 194–747m (the North Bornean depth distribution for 'longifilis' given by Weber & de Beaufort is 475–759m).

MATERIAL EXAMINED. USNM 078207 (Holotype), 120mm s-a, off northern Mindanao; 148985 (paratypes), 70.5 & 73.5mm

s-a; 148977–83 (paratypes), 72–114mm s-a, Sulu and Mindanao Seas, off North Borneo, vicinities of Bohol, Leyte, Gollololo and Makyan Islands, Luzon, Mindoro and between Cebu and Leyte.

Gadomus introniger Gilbert & Hubbs, 1920

Gadomus multifilis; Radcliffe, 1912 (*non* Günther, 1867):106 (part).

Gadomus introniger Gilbert & Hubbs, 1920:401 (descr.).

Bathygadus Gadomus introniger; Weber & de Beaufort, 1929:21 (descr. after Gilbert & Hubbs).

Known from the holotype and twelve paratypes, the type locality Buton Strait, near Celebes (see Table 17).

According to Gilbert & Hubbs (1920) *G. introniger* differs from *G. denticulatus* and *G. colletti* in its coarser dentition. The 'coarseness' of the dentition is, if judged by the number of teeth occurring on any particular area of the premaxilla or dentary, phenotypically variable and some specimens of *introniger* have the same 'coarseness' as those of *denticulatus*. In some individuals the teeth on both the premaxilla and dentary may be longer and more pronounced along the outer margin of the bones.

In most meristics and morphometric parameters *G. introniger* overlaps with those of other Philippine species. However, in the width of the interorbital, *introniger* is distinct, (22.0–22.5% of the head length, *cf.* 15.5–21.1% in the other three Philippine species, *magnifilis*, *denticulatus* and *multifilis*). *Gadomus introniger* also has a wider midline separation of the premaxillary dentigerous surfaces than *G. denticulatus* and *G. colletti* (6.0–6.1% of premaxillary length, *cf.* 3.1–4.4%). The interoperculum is also longer than in other species and has a rounded posteroventral margin (Fig. 17i).

Twenty pyloric caeca were counted in one specimen.

Table 17 Counts and proportional measurements for the holotype and three paratypes of *Gadomus introniger*

	Holotype	Paratypes	Mean
D	II9	II10	
Pe	18	17	
Pl	8	8	
GR	5+22	5–6+21–23	
PC	?	20 (1 spec.)	
s-a	124mm	57–102mm	
bd	31.4	34.2–44.9	37.1
pl	100.8	108.0 (1 spec., others broken)	
hl	50.8	48.0–53.2	50.9
od	23.8	22.0–27.1	23.9
io	22.2	22.0–22.5	23.0
pml	52.3	55.1–56.1	54.6
pma	18.1	20.0–24.0	21.6
pms	6.0	not measured	
bl	15.8 (broken)	51.6–69.0	60.5

DISTRIBUTION. Philippine Sea.

DEPTH RANGE. 540–1260m.

MATERIAL EXAMINED. USNM 78209 (Holotype), 124mm s-a, Buton Strait, near Celebes; 99484 (paratype), 83.5mm s-a, Malavantuan Island; 99485 (paratype), 57mm s-a, North Island; 99486 (paratype), 102mm s-a. The other paratypes are in too poor a condition to provide accurate measurements but

have been used for fin-ray and gill-raker counts. Only in specimen 99485 could pyloric caeca be counted, as it had been dissected to expose the everted stomach; in other specimens the caeca are obscured by eversion.

Gadomus colletti Jordan & Gilbert, 1904

Gadomus colletti Jordan & Gilbert, (1902) 1904:603 (descr.).
Bathygadus colletti; Weber, 1913:172 (listed).

Known from the holotype collected in Suruga Bay, Japan and from several other specimens collected subsequently from around southern Japan (see Okamura, 1970a; 1982; 1984). According to Gilbert & Hubbs' (1920) key, *G. colletti* can be separated from other *Gadomus* species on the posterior expansion of the premaxillary teeth, 'colour lighter', 'head firmer' and pyloric caeca numbering 95.

The variability of the posterior width of the premaxillary dentigerous surface has been remarked above, under *G. denticulatus*. Insufficient data were available in the present study to judge 'lightness of colour' as a diagnostic feature, although from Okamura's (1984) description of fresh material, the body is purplish-pink or pinkish, being lighter on its ventral surface. The firmness of the head is too imprecise a character to be diagnostic. Okamura (1970a:23), in his key separating *G. colletti* from *G. multifilis*, modified this feature to that of sensory canals being less developed in *colletti* than in *multifilis*.

The number of pyloric caeca is higher than in other species; it has not been possible to confirm Gilbert & Hubbs (1920) count since the stomach of the type of *G. colletti* has been removed, as has that of the other two specimens examined.

Table 18 Counts and proportional measurements for the holotype and two other specimens of *Gadomus colletti*. Ranges in square brackets indicate those figures given by Okamura (1982; 1984) for a total of 15 specimens of 148–420mm TL.

	Holotype	USNM135352	USNM150253	
D	II10	II9	II10	
Pe	21	19	19	[18–22]
Pl	8	8	8	
GR	4+20	5+20	4+20	[3–5+20–22]
PC	*	?	?	
s-a	120mm	116.3mm	66.0mm	
bd	36.2	39.6	43.3	
pl	89.1	89.7	75.7	
hl	49.1	44.8	50.0	
od	23.7	22.4	30.3	[22.2–32.8]
io	17.7	20.1	19.6	
pml	54.4	50.0	52.1	[50.0–58.8]
pma	26.5	19.2	17.4	
pms	3.1	5.7	?	
bl	76.2	88.4	81.8	[75.0–90.6]

* given as 90 by Jordan & Gilbert (1902).

The most significant characters separating *G. colletti* from other Indo-Pacific species appear to be the higher number of pectoral fin rays, viz. 18–22, cf. 16–18; the second pectoral ray is not as attenuated as in other species (75.0–89.1%, \bar{x} 85.3% of snout to anal fin distance, cf. 96.4–142.8% \bar{x} 115.0% in other species). The length of the barbel is also longer than in other species, being 75.0–90.6% of the head length, cf. 16.6–83.3%. The interoperculum is deep with a

broadly rounded posterior border (Fig. 17f). Counts and proportional measurements for the holotype and two other specimens are given in Table 18.

DISTRIBUTION. confined to the Pacific coast of Japan and along the Kyushu-Palau Ridge.

DEPTH RANGE. 335–1200m (Okamura, 1982; 1984).

MATERIAL EXAMINED. USNM 50930 (Holotype), 120mm s-a (ca 330mm TL), Suruga Bay, Japan; 135352, 116.3mm s-a (ca 300mm TL), Suruga Gulf; 150253, 66mm s-a (ca 190mm TL), Suruga Gulf.

Gadomus melanopterus Gilbert 1905

Gadomus melanopterus Gilbert, (1903) 1905:23 (descr.).

Melanobranchus micronema Gilbert, *ibid.*:661 (descr.).

Bathygadus melanopterus; Weber, 1913:172 (listed).

Gadomus melanopterus; Gilbert & Hubbs, 1916:142 (listed).

Known from two specimens from the Hawaiian Islands.

Separated by Gilbert & Hubbs (1920) from *G. multifilis* by 9, vs 8 pelvic fin rays, absence of pseudobranchiae, and the scapular foramen being entirely within the coracoid. The variability of the latter feature is discussed on p. 174, and, in fact, pseudobranchiae are present in the type specimen. The presence of 9 pelvic rays is, however, unusual and occurs elsewhere only in *G. aoteanus* (but see below).

We refer *Melanobranchus micronema* Gilbert to the synonymy of this species. Gilbert & Hubbs (1916) listed *micronema* as a species of *Bathygadus*, which they later included (1920) in the subgenus *Melanobranchus*, separating the species from *B. filamentosus* on the basis of its higher number of gill-rakers, presence of a barbel and longer orbit. The present investigation concludes that *micronema* belongs to *Gadomus* since it possesses a barbel (albeit reduced), has prolonged fin rays, narrow midline separation of the premaxillary dentigerous surfaces, and the interopercular shape characteristic of that taxon (Fig. 17h). It differs from *G. melanopterus* in having 8 rather than 9 pelvic rays; 6+29, cf. 7+27 gill-rakers on the first arch and a reduced barbel. Otherwise its proportional measurements agree with those of *melanopterus*, particularly in the equivalent sizes of the orbital diameters and interorbital widths (see Table 19).

Like *G. multifilis* and *G. aoteanus*, *G. melanopterus* has a high number of gill-rakers (6–7+27–29, cf. 6+25 in *multifilis* and *aoteanus* and 4–6+17–23 in other species). The jaw teeth are well-developed in comparison with the minute teeth of the Philippine species and the dentigerous area of the dentary is narrower than in those species. The interpremaxillary dentigerous space is narrow (3.0–3.5% of the premaxillary length). The interorbital width is also narrow (23.1–25.6% of head length), although not as narrow as in some individuals of *G. magnifilis* and *G. inroniger* (see Tables 15 & 17). Likewise, the premaxillary ascending process is short, 17.8–19.6% of the premaxillary length, cf. 20.0–24.0% in other species, and is as short in only one specimen of *G. inroniger* (18.1%). The length of the barbel is also shorter than that of most other Indo-Pacific species and approaches that of *G. multifilis* (58.9% of head length in holotype, only 2.5% in type of *micronema*, cf. \bar{x} 59.9% for *G. multifilis*). The interoperculum is deep and nearly an equilateral triangle with only a slightly convex posterior border (Fig. 17h).

The absence of other specimens of *Gadomus* from Hawaii (apart from one listed by Gilbert, 1903:659, also from near

Kauai, but which we have been unable to locate), or from between Hawaii and the east Indies makes it impossible to tell whether the meristic and morphometric parameters overlapping those of *G. magnifilis* and *G. denticulatus* indicate inter- or intraspecific variability. On the basis of those differences that are apparent, and from its isolated locality we recognise *G. melanopterus* as a distinct species.

Table 19 Counts and measurements for the holotypes of *Gadomus melanopterus* and *G. micronema*

	<i>melanopterus</i>	<i>micronema</i>
D	II9	II10
Pe	18	18
Pl	9	8
GR	7+27	6+29
PC	15	12*
s-a	91.0mm	75.5mm
bd	44.5	45.6
pl	98.9	72.8 (broken)
hl	52.1	51.6
od	23.1	25.6
io	23.1	25.6
pml	58.9	60.2
pma	19.6	17.8
pms	3.5	5.0
bl	58.9	2.5**

* 9 given by Gilbert (1905)

** the length of the barbel shown in Gilbert's figure is either exaggerated or part of the barbel has since been broken off.

DISTRIBUTION. Hawaiian Islands.

DEPTH RANGE. 799–1416m.

MATERIAL EXAMINED. USNM 51606 (holotype), 91mm s-a (ca 270mm TL), near Kauai Island; 51643 (holotype of *Melanobranchnus micronema*), 75.5mm s-a (ca 235mm TL) Pailolo Channel between Kauai and Molokai Islands.

Key to the Atlantic species of *Gadomus*

- 1 Outer two rays of pelvics elongated; pectoral rays 22–25..... *G. arcuatus*
Outer ray only of pelvic elongated; pectoral rays 18–21 .. 2
- 2 Gill-rakers on 1st ceratobranchial, 20–21 *G. dispar*
Gill-rakers on 1st ceratobranchial above 25 3
- 3 Gill-rakers on 1st ceratobranchial 25–27; pectoral fin length greater than 80% of s-a distance *G. capensis*
Gill-rakers on 1st ceratobranchial 27–31; pectoral fin length less than 65% of s-a distance *G. longifilis*

Key to the Indo-Pacific species of *Gadomus*

- 1 Gill-rakers on 1st ceratobranchial 17–23 2
Gill-rakers on 1st ceratobranchial 25–29 5
- 2 Pectoral rays, 16–18 3
Pectoral rays, 19–21 *G. colletti* (Japan)
- 3 Interorbital width 15.5–18.0 of head length 4
Interorbital width 22.0–23.0% of head length
G. introniger (Philippines)
- 4 Gill-rakers: 5–6+21–23; orbital diameter 19.8–25.6% of head length; body depth 42.0–45.0% of s-a head length *G. magnifilis* (Philippines)

- Gill-rakers 4–5+17–20; orbital diameter 25.0–29.1% of head length, body depth 31.9–41.6% s-a length
G. denticulatus (Philippines)
- 5 Gill-rakers 25 6
Gill rakers 27–29 ... *G. melanopterus* (Hawaiian Islands)
- 6 Barbel length 1.8–18.6% of head length; body depth 42.0–48.2% of s-a length 7
Barbel length 47.9–68.8% of head length; body depth 33.8–43.6% of s-a length .. *G. multifilis* (Indian Ocean)
- 7 Barbel length 1.8–6.9% of head length; premaxillary length 57.8–60.4% of head length *G. capensis* (Atlantic ? and Indian Ocean)
Barbel length 16.6–18.6% of head length; premaxillary length 50.8–51.8% of head length *G. aoteanus* (Kermadec region)

Interspecific relationships

Interrelationships of *Bathygadus* and *Gadomus* species have not been resolved due to the paucity of osteological material. Morphometric and meristic parameters are of little use in determining such relationships, as often there is overlap. Polarity of osteological features examined such as dentition and interopercular shape are also difficult to assess. No characters suggest that the Atlantic species of either *Bathygadus* or *Gadomus* are monophyletic groups.

Among *Bathygadus* species, relatively longer jaws characterise the Japanese species (*antrodes*, *nipponicus*), being 51.1–72.4% head length cf. 48.9–61.5% in others. Interorbital width, which, in the past, has been used as an indicator of subgeneric rank is continuously variable (23.5–37.5% head length). Interopercular shape, unlike that of *Gadomus* is more varied and one group of species (*entomelas*, *filamentosus*, *antrodes*, *spongiceps*, *bowersi*) share a crook-shaped morphotype (p. 171). *Bathygadus sulcatus* and *nipponicus* also share a particular interopercular morphotype (Fig. 17, 5 & 6); these morphotypes may be indicators of relationship, but it is not possible to determine which is the derived.

Bathygadid relationships formulated by Gilbert & Hubbs (1920), and largely followed by Iwamoto (1970) and Marshall (1973a) are based on superficial resemblances to which polarity cannot be ascribed.

Distribution

The distributions of *Bathygadus* and *Gadomus* species coincide, both in areas occupied and numbers of species in those areas (Figs 29–32). *Bathygadid* specimens are few compared with other continental slope groups, eg. macrouroids, and one must guard against making too many assumptions on the basis of what are, after all, distributional plots of collecting stations. However, despite several collections from the eastern and southern Pacific and Indian Oceans (eg. Pearcy *et al.* 1982), none have yielded bathygadids suggesting that their absence from these regions is real rather than artefactual. The most significant feature of bathygadid distribution is their association with continental slopes and with 'enclosed' seas whose topography is dominated by sea-floor trenches and ridges, eg. South China, Philippine and Caribbean Seas.

Indo-west Pacific

The largest clusters of *Bathygadus* and *Gadomus* species occur in the Philippine region. Gilbert & Hubbs (1920)

ascribed the large proportion of species in this area as being due to the nearly complete isolation of the Sulu Sea. This sea has particular environmental conditions, viz. consistently high temperature, relatively large salinity variation and lower oxygen saturation than surrounding seas. *Bathygadus* species in this region are *spongiceps* (China and Celebes Seas); *cottoides*, *entomelas* (Philippine Sea); *sulcatus* (Sulu Sea); *multifilis* (Celebes Sea); all at depths between 700–1600m. *Gadomus* species are *magnifilis*, *denticulatus* and *introniger*, all in the Philippine region at depths between 194–1260m.

Species from off Japan (south-east coast) are *Bathygadus antrodes* and *B. nipponicus* from depths between 792–1348m; *Gadomus colletti* from 335–1200m.

There is only one record for *Bathygadus* from the Indian Ocean; cf. *cottoides* from near Zanzibar. *Gadomus* is represented by *multifilis*, *furvescens* and *capensis*. *Gadomus furvescens* is recorded only from above the Equator (Arabian Sea and Bay of Bengal); only *G. capensis* occurs in the western Indian Ocean at lat. 40°S and along eastern Africa.

A species of each genus occurs in the Hawaiian Islands, viz. *Bathygadus bowersi* and *Gadomus melanopterus*, both from depths between 563–1440m. The occurrence of bathygadids in the Southern Ocean is also marked by a single species of each genus, viz. *Bathygadus* cf. *cottoides* and *Gadomus aoteanus*; both occur on Lord Howe Rise, the former also from along the Kermadec trench.

Atlantic

Six of the seven bathygadid species occurring here (*Bathygadus melanobranchus*, *B. favosus*, *B. macrops*, *Gadomus longifilis*, *G. arcuatus*, *G. dispar*) are present on both sides of the mid-Atlantic ridge. Their distribution is, however, limited to above the Equator (most northerly record, for *Bathygadus melanobranchus*, 51° 46'N; Holt & Byrne, 1908); only one species, *Gadomus capensis* occurs in the southern Atlantic. The only records for the mid-Atlantic ridge are for *Bathygadus melanobranchus*, *Gadomus longifilis* and *G. capensis* (respectively, Collett, 1896; Roule, 1919; Pakhurov, 1980). Records for the two former species are from off the Azores, and the latter from the equatorial Whale Ridge. From the western Atlantic most specimens are from the Caribbean Sea, particularly the Gulf of Mexico and from the eastern Atlantic from the Gulf of Guinea.

Merrett & Marshall (1981) commented on the narrow depth range of *Bathygadus melanobranchus* off the north-western African shelf from between 734–1017m. The depth range for Atlantic *Bathygadus* species given by Marshall (1973a) is 200–2743m and for *Gadomus* 548–2165m; only two *Bathygadus* and one *Gadomus* species are recorded from below 2000m (Fig. 28).

As noted above bathygadids appear to be absent from the eastern Pacific, an absence which may be due to a variety of factors, single or in concert such as unsuitable topography, temperature, salinity, currents affecting larval dispersal or the result of historical biogeographic events which have tied bathygadids to particular areas. Concerning the latter it is noted that a common distributional pattern occurs among other abyssal fishes, involving west-east Atlantic, high Indian Ocean, Philippines and Kermadec region (eg. Ipnopidae, various Brotulidae and Aphyonidae; Nielsen, 1965; 1966; 1969; 1977).

Discussion of bathygadid biogeography is limited by our

lacking a scheme of phylogenetic relationships (p. 200), a necessary prerequisite to understanding distributional patterns.

ACKNOWLEDGEMENTS. The first author is indebted to Dr Richard Vari and the staff of the Division of Fishes, United States National Museum for their assistance and hospitality during the period of his visit which was generously funded by the Smithsonian Institution's Office of Fellowships and Grants.

We are most grateful to Dr. I. Isbrücker (Institut voor Taxonomische Zoologie, Amsterdam) and E. G. Ranchod (J. L. B. Smith Institute, Grahamstown) for loans of type specimens; to our colleagues Dr. G. Boxshall for identifying crustaceans and Ms M. Holloway for providing radiographs.

We especially thank Nigel Merrett for his advice and tolerance of our ignorance, P. Humphry Greenwood, A. Wheeler and an anonymous reviewer for their critical and helpful readings of the manuscript and to Drs Jeff Graham (Scripps Institute) and Ian Harrison (Parma University) for their helpful and stimulating discussions regarding respiration.

Finally, we express our thanks to Jennie Cummings for her word-processing and editing skills.

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Manuscript accepted for publication 30 October 1989