

THE SYSTEMATICS AND BIOLOGY OF *BATHYPTEROIS* (PISCES, CHLOROPHTHALMIDAE)

WITH A REVISED CLASSIFICATION OF BENTHIC MYCTOPHIFORM FISHES

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ABSTRACT

The deep benthic fish genus *Bathypterois* (Pisces: Myctophiformes) is revised on a worldwide basis. A descriptive synopsis of each of the 18 species is provided. A key to these species is presented. Two new species, *B. perceptor* and *B. oddi*, are described. Based on comparative osteology relationships among recent benthic myctophiform genera are revised. These genera are placed in three families: Aulopidae (*Aulopus*), Synodontidae (*Synodus*, *Saurida*, *Trachinocephalus*, *Harpadon*, *Bathysaurus*), and Chlorophthalmidae (*Chlorophthalmus*, *Parasudis*, *Bathysauropsis*, *Ipnows*, *Bathypterois*, *Bathytyphlops*, *Bathymicrops*).

The biology of *Bathypterois* is discussed. The latitudinal limits of the genus are found to coincide with the poleward limits of central oceanic water. Bottom

temperatures and interspecific competitive exclusion appear to determine the distributions of individual species. Among dominant fish groups of deep Bahamian basins, the ipnopsine genera *Ipnows* and *Bathypterois* rank third in numerical abundance. In this same region at least two species pertaining to these genera exhibit seasonally synchronized reproductive cycles. Histological examination of the specialized pectoral fin rays reveals innervation by enlarged spinal nerves and suggests a sensory function for these rays. The stiff elongate pelvic and caudal fin rays are found to be poorly innervated. They appear to function like stilts to raise the fish into the water column. The food of *Bathypterois* is found to consist primarily of very small planktonic crustaceans.

CONTENTS

I. Introduction	50	Systematics of the genus <i>Bathypterois</i> Günther, 1878	74
Institutional abbreviations	51	Key to subgenera and species of <i>Bathypterois</i>	75
Osteological abbreviations	51	Subgenus <i>Benthosaurus</i> Goode & Bean, 1886	76
Acknowledgments	52	<i>Bathypterois</i> (<i>Benthosaurus</i>) <i>grallator</i>	
Material and methods	52	(Goode & Bean, 1886)	77
II. Systematic part	53	<i>Bathypterois</i> (<i>Benthosaurus</i>) <i>viridensis</i> (Roule, 1916) ...	80
Relationships among benthic myctophiform taxa	53	<i>Bathypterois</i> (<i>Benthosaurus</i>) <i>guentheri</i> Alcock, 1889 ...	82
Relationships within the subfamily Ipnopinae	64	Subgenus <i>Bathypterois</i> Günther, 1878	83
Key to genera of the subfamily Ipnopinae	64	<i>Bathypterois</i> (<i>Bathypterois</i>) <i>longifilis</i> Günther, 1878	83

<i>Bathypterois</i> (<i>Bathypterois</i>) <i>perceptor</i> n. sp.	86	<i>Bathypterois</i> (<i>Bathycygnus</i>) <i>insularum</i> Alcock, 1892	97
<i>Bathypterois</i> (<i>Bathypterois</i>) <i>ventralis</i> Garman, 1899	87	<i>Bathypterois</i> (<i>Bathycygnus</i>) <i>longipes</i> Günther, 1878	97
<i>Bathypterois</i> (<i>Bathypterois</i>) <i>atricolor</i> Alcock, 1896	87	<i>Bathypterois</i> (<i>Bathycygnus</i>) <i>longicauda</i> Günther, 1878	98
<i>Bathypterois</i> (<i>Bathypterois</i>) <i>dubius</i> Vaillant, 1888	89	<i>Bathypterois</i> (<i>Bathycygnus</i>) <i>oddi</i> n. sp.	99
<i>Bathypterois</i> (<i>Bathypterois</i>) <i>phenax</i> Parr, 1928	90	III. Biology	100
<i>Bathypterois</i> (<i>Bathypterois</i>) <i>mediterraneus</i>		Distribution	100
Bauchot, 1962	91	Abundance	102
<i>Bathypterois</i> (<i>Bathypterois</i>) <i>quadrifilis</i> Günther, 1878 ..	92	Fin ray specializations	102
<i>Bathypterois</i> (<i>Bathypterois</i>) <i>pectinatus</i> Mead, 1959	93	Aspects of reproduction	104
Subgenus <i>Bathycygnus</i> n. subgen.	94	IV. Summary	105
<i>Bathypterois</i> (<i>Bathycygnus</i>) <i>bigelowi</i> Mead, 1959	94	V. References	106
<i>Bathypterois</i> (<i>Bathycygnus</i>) <i>filiferus</i> Gilchrist, 1908	96		

I. INTRODUCTION

The genus *Bathypterois* Günther, 1878 comprises a small group of benthic myctophiform species adapted for life in the deep sea. The genus is circumglobal beneath temperate and tropical seas (Fig. 1), and archibenthic to abyssobenthic in habit. In terms of numerical abundance the genus appears to be a constant and important component of the benthic fish fauna at depths of 250-6000 m. Recent extensive quantitative trawling by the R/V "Columbus Iselin" in deep basins of the Bahamas has revealed that in this region at least *Bathypterois* and *Ipnots* combined rank third in abundance (behind synbranchids and brotulids, ahead of alepocephalids, halosaurs, and macrourids). There is evidence (Nybelin 1957) that *Bathypterois* is also important at abyssal depths in the northeastern Atlantic.

In the 104 years that have passed since the first recorded capture of *Bathypterois* by the Challenger Expedition, approximately 27 nominal species and subspecies of that genus (*Benthosaurus* inclusive) have been described. As is more generally true of deep benthic fish species than previously indicated (Briggs 1960), several species of *Bathypterois* are very widely distributed. Thus attempts to summarize the genus on a regional basis (Alcock 1899, Barnard 1925, Mead 1966c) have proven inadequate in testing the validity of the various nominal forms. Previous attempts to treat the genus on a wider basis (Goode & Bean 1896, Parr 1928, Bauchot 1962) have also left many species-level problems unresolved. At higher taxonomic levels relationships to other taxa of benthic myctophiform

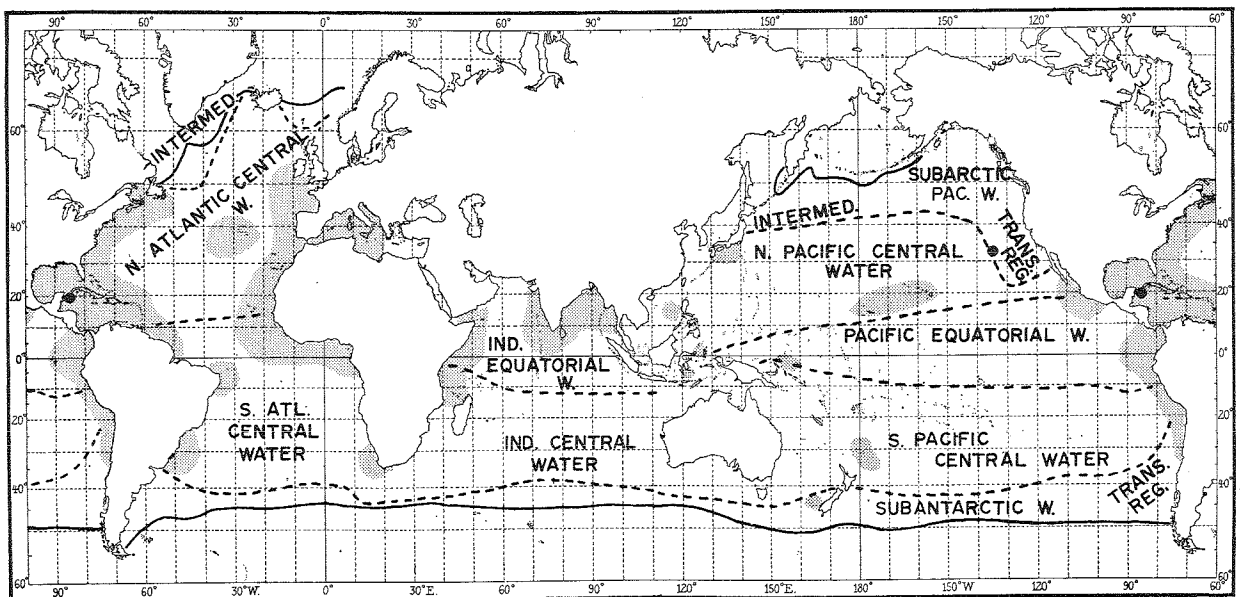


Fig. 1. Distribution of the genus *Bathypterois* in relation to oceanic watermasses. Shaded area: known distribution of adults; solid circles: known localities for juveniles; broken line: approximate upper boundaries of major oceanic watermasses (after Sverdrup et al. 1942); solid line: poleward limits of the 10°C surface isotherm (after Sverdrup et al. 1942).

fishes have not been critically evaluated from the standpoint of comparative osteology.

The genus *Bathypterois* as herein constituted incorporates the monotypic *Benthosaurus*, and is thus equivalent to the family Bathypteroidae sensu Mead (1966c) and the subfamily Bathypteroinae sensu Marshall & Staiger (1975). The present investigation has considered the osteology of *Bathypterois*, along with that of *Bathymicrops*, *Bathytyphlops*, and *Ipnops*, in an effort to define natural relationships among these genera, which together are taken to constitute a redefined subfamilial unit, the Ipnopinae. Additionally, representatives of all remaining benthic myctophiform genera have been examined osteologically. A comprehensive comparative study of these genera has not previously been attempted. Such a study was undertaken here as a logical and necessary prerequisite to understanding the systematic position of the subfamily Ipnopinae within the larger framework of related taxa. Based on this comparative study, a revised classification of benthic myctophiform taxa has been formulated. Finally, relationships among the species of *Bathypterois* have been considered, resulting in a revision of the genus on a worldwide basis. Observations on the poorly known natural history of the genus have also been presented.

Institutional abbreviations

AMNH:	American Museum of Natural History, New York
BM:	British Museum (Natural History), London
CAS-SU:	Stanford University Collection, maintained at California Academy of Sciences, San Francisco
CNHM:	Field Museum of Natural History, Chicago
CSU:	California State University, San Francisco
IOSR:	Institute of Oceanology, Academy of Sciences of the USSR, Moscow
ISH:	Institut für Seefischerei, Hamburg
LACM:	Los Angeles County Museum
MCZ:	Museum of Comparative Zoology, Harvard University
MNHN:	Museum National d'Histoire Naturelle, Paris
NHMB:	Natural History Museum »Grigore Antipa«, Bucharest, Rumania

ORI:	Ocean Research Institute, University of Tokyo
RUSI:	J.L.B. Smith Institute of Ichthyology, Rhodes University, Grahamstown, S.A.
SAM:	South African Museum, Capetown
SIO:	Scripps Institution of Oceanography, La Jolla, California
SOSC:	Smithsonian Oceanographic Sorting Center, Washington, D.C.
TABL:	U.S. National Marine Fisheries Service, Tropical Atlantic Biological Laboratory (collection now maintained at UMML)
UMML:	Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida
USNM:	United States National Museum of Natural History, Washington, D.C.
VIMS:	Virginia Institute of Marine Science, Gloucester Point, Virginia
WHOI:	Woods Hole Oceanographic Institution, Massachusetts
ZMUC:	Zoological Museum, University of Copenhagen

Osteological abbreviations

a-mx:	anterior portion of maxilla
an:	angular
ar:	articular
bb:	basibranchial
bh:	basihyal
c:	cartilage
cb:	ceratobranchial
cc:	coracoid
ch:	ceratohyal
cl:	cleithrum
d:	dentary
dbb:	dermal basibranchial
dbh:	dorsal basihyal
dpcl:	dorsal postcleithrum
ds:	dermosphenotic
e:	epural
eb:	epibranchial
ec:	ectopterygoid
eh:	epihyal
en:	endopterygoid
fs:	fucral scale (caudal scute)
h ₁₋₆ :	hypurals
hb:	hypobranchial
hs:	haemal spine
hy:	hyomandibular

ih:	interhyal
io:	interopercle
mt:	metapterygoid
mx:	maxilla
na:	neural arch
np:	neural plate
ns:	neural spine
o:	circumorbital
op:	opercle
or:	orbit
pb:	pharyngobranchial
ph:	parhypural
pl:	palatine
pm:	premaxilla
p-mx:	posterior portion of maxilla
po:	preopercle
pu ₁ u ₁ :	fused first preural and first ural centra
pu:	preural centrum
q:	quadrate
r:	pectoral fin radial
scl:	supracleithrum
sm ₁ :	posterior supramaxilla
sm ₂ :	anterior supramaxilla
so:	subopercle
sp:	scapula
sy:	symplectic
tp:	tooth patch
u ₂ :	second ural centrum
un:	uroneural
v:	vomer
vhh:	ventral hypohyal
vpcl _{1,2} :	ventral postcleithra
vpcl ₁₋₂ :	fused ventral postcleithra

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Material and methods

Bathypterois material examined is listed under individual species headings in the systematic part of this report. Comparative material of related genera is listed below. Detailed locality data for all specimens examined are on deposit at UMML. Additionally, a list of locality data for all known captures of *Bathypterois* is also available at UMML and ZMUC.

Aulopidae:

Aulopus cadenati (2 specimens) TABL

Aulopus nanae (1) UMML

Aulopus purpurissatus (2) USNM

Ipnopinae:

Bathymicrops regis (3) UMML

Bathytyphlops azorensis (1) UMML

Bathytyphlops marionae (3) UMML

Ipnops agassizi (5) UMML

Ipnops murrayi (17) UMML

Chlorothalminae¹:

Bathysauropsis gracilis (1) RUSI

Bathysauropsis malayanus (1) USNM

*Chlorothalmus*¹ *agassizi* (7) TABL, (27) UMML

Parasudis truculentis (5) UMML

Synodontidae:

Bathysaurus ferox (2) UMML

Bathysaurus mollis (1) UMML

Harpadon microchir (2) USNM

Harpadon nehereus (2) USNM

1. This spelling has been used throughout by the author. - Ed.

Saurida brasiliensis (5) UMML
Saurida normani (1) UMML
Synodus scituliceps (15) UMML
Synodus synodus (6) UMML
Trachinocephalus myops (9) UMML

Conventional meristic and morphometric characters were used in evaluating relationships among the species of *Bathypterois* examined. Counts and measurements were determined in accordance with the standards set forth in Hubbs & Lagler (1958). The comparative osteology of the cranial, caudal, and pectoral regions was more extensively utilized

in evaluating systematic relationships beyond the species level. Specimens were prepared for osteological examination by trypsin clearing and alizarin staining, supplemented by gross dissection of alcohol preserved specimens. Extensive use was made of radiographs as well.

Nerves supplying the produced fin rays were traced by gross dissection and by use of the modified Sihler nerve staining technique (Freihofer 1963). Histological sections of fin rays were prepared from material fixed in Bouin's fluid, embedded in paraffin, cut to 6 μ thickness, and stained with Gomori's one-step trichrome stain.

II. SYSTEMATIC PART

RELATIONSHIPS AMONG BENTHIC MYCTOPHIFORM TAXA

The following revised scheme of classification for benthic myctophiform fishes is advanced as discussed below.

- Family Aulopidae Bonaparte, 1841, 7 spp.
 Genus *Aulopus* Cloquet, 1816 (incl. *Hime* Starks, 1924, and *Latropiscus* Whitley, 1931), 7 spp.
- Family Synodontidae Gill, 1862, ca. 39 spp.
 Subfamily Harpadontinae Jordan, 1923
 Genus *Harpadon* Lesueur, 1825 (incl. *Peltharpadon* Fowler, 1934), 3 spp. (secondarily pelagic in habit)
 Genus *Saurida* Valenciennes, 1849, 9 spp.
- Subfamily Bathysaurinae
 Genus *Bathysaurus* Günther, 1878 (incl. *Macristium* Regan, 1911), 2 spp.
- Subfamily Synodontinae Gill, 1862
 Genus *Synodus* Gronow, 1763 (incl. *Xystodus* Ogilby, 1910), 24 spp.
 Genus *Trachinocephalus* Gill, 1862, 1 sp.
- Family Chlorophthalmidae Jordan, 1923, 38 spp.
 Subfamily Chlorophthalminae Jordan, 1923
 Genus *Chlorophthalmus* Bonaparte, 1840, 7 spp.
 Genus *Parasudis* Regan, 1911, 2 spp. (secondarily pelagic in habit)
 Genus *Bathysauropsis* Regan, 1911 (incl. *Bathysaurops* Fowler, 1938), 3 spp.
- Subfamily Ipnopinae Gill, 1884
 Tribe Ipnopini
 Genus *Ipnops* Günther, 1878 (incl. *Ipnoceps* Fowler, 1943), 3 spp.

Tribe Bathypteroini

Genus *Bathypterois* Günther, 1878 (incl. *Benthosaurus* Goode & Bean, 1886), 18 spp.

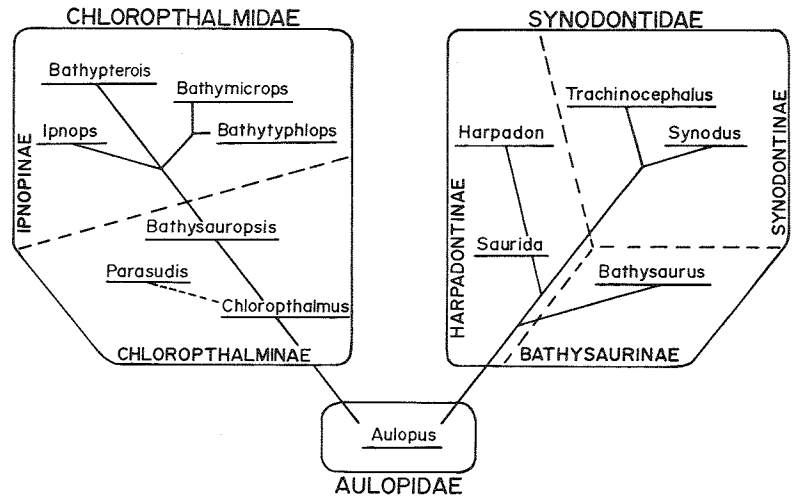
Tribe Bathymicropini

Genus *Bathymicrops* Hjort & Koefoed, 1912, 2 spp.

Genus *Bathytyphlops* Nybelin, 1957 (incl. *Macristiella* Berry & Robins, 1967), 3 spp.

Three natural groupings of benthic fishes are evident in the Myctophiformes (Fig. 2). A conservative basal group is represented by the Aulopidae, an inshore family with a single genus and seven recent species worldwide (Mead 1966a). *Aulopus* is rather generalized in body form (Regan 1911) and primitive with respect to other benthic myctophiform fishes in possessing two supramaxillae (Fig. 3a), an orbitosphenoid (Regan 1911), a completely roofed post-temporal fossa, parietals that meet on the skull midline (Rosen & Patterson 1969), ectopterygoid and endopterygoid dentition, caudal fulcra (Gosline 1961), and perhaps a complex second ural centrum. The degree of osteological stability of *Aulopus* is apparent in its very close correspondence to the Cretaceous genus *Nematonotus* (Rosen & Patterson 1969). From the Aulopidae in one direction has evolved the synodontid lineage. Fishes of this lineage are characterized structurally by an upper jaw dominated by a strong premaxilla with the maxilla reduced and variously modified (usually partially or wholly adherent to the premaxilla), and the supramaxillae extremely reduced or absent; gill rakers modified into clusters of short gill teeth; a pointed snout (in dorsal profile); a hyomandibular

Fig. 2. Phylogenetic relationships among the benthic Myctophiformes.



enlarged and strengthened antero-ventrally by a broad flange (Figs 3 b-c, 6 b-e); and a high number of branchiostegal rays (12-26, except in the neotenous *Bathysaurus mollis*, which has but eight). Synodontids, with the possible exception of *Bathysaurus* (Mead 1960, 1966b), are further characterized by a dioecious mode of reproduction.

From the Aulopidae in a second direction has evolved the chlorophthalmid lineage with fishes characterized by an upper jaw having a prominent maxilla that is dilated and free posteriorly, and a single elongate supramaxilla; a short, weakly-toothed palatine; small to minute conical teeth, usually in multiple rows on each jaw; bladelike gill rakers; a broad, rounded to spatulate snout; a low number of branchiostegal rays (8-13); an unossified gap between the cranium and the first vertebra (Gosline et al. 1966, Rosen & Patterson 1969); and a characteristic elaboration of superficial lateralis organs on the scales of the trunk lateral line (Marshall & Staiger 1975). In contrast to both the basal aulopids and the synodontids, chlorophthalmids have a monoecious mode of reproduction (Mead et al. 1964).

The synodontid line is herein considered to comprise a single family, the Synodontidae. Five genera are recognized (see scheme of classification above) including *Bathysaurus* and *Harpadon*.

Saurida is the most primitive generalized member of the family, being in many respects transitional between the aulopid and synodontid structural levels. Alone among the synodontid genera, but in common with *Aulopus*, *Saurida* possesses caudal fulcra (Fig. 4a) and two (albeit rudimentary) supra-maxillae (Fig. 3b, inset). Moreover, *Saurida* has an *Aulopus*-like vomer, a toothed endopterygoid, nine

pelvic fin rays, a rounded snout (dorsal aspect), and 49-52 vertebrae - features more consistent with the Aulopidae than the Synodontidae. Additionally *Saurida* retains two epurals (Fig. 4a), while the advanced genera *Synodus* and *Trachinocephalus* have but one (Fig. 4b). However, *Saurida* agrees with these in its prominent and strongly-toothed premaxilla, its long well-toothed palatine, its patches of gill teeth, its reduced and upturned second ural centrum (Fig. 4a), its more posteriorly placed (cf. *Aulopus*, Table 1) dorsal fin, and other characters typical of the Synodontidae. A peculiarity of *Saurida* (and the related *Harpadon*) is the separation of the maxilla into anterior and posterior portions (Fig. 3b,c). The posterior portion is reduced to a thin lamina adherent to the premaxilla along the posterior half of that bone. The anterior portion consists of the isolated head of the maxilla. It lies between the head of the palatine and the head of the premaxilla and retains its original articulating function with respect to these bones.

Closely allied to (and perhaps derived from) *Saurida* is the genus *Harpadon*. It has formerly been variously included in the Synodontidae (Goode & Bean 1896, Regan 1911, Norman 1935), united with *Bathysaurus* in a rather artificial family, Harpadontidae (sensu Harry 1952), or placed in its own monogeneric family Harpadontidae (Jordan 1923, Gosline et al. 1966, Greenwood et al. 1966). However, an adequate basis for differentiation of *Harpadon* from the Synodontidae has not been demonstrated. Indeed, despite its specialized appearance and pelagic habit, *Harpadon* exhibits an osteology that is characteristically synodontid. Particularly instructive in this regard is the condition of the upper jaw (Fig. 3c). It is dominated by the

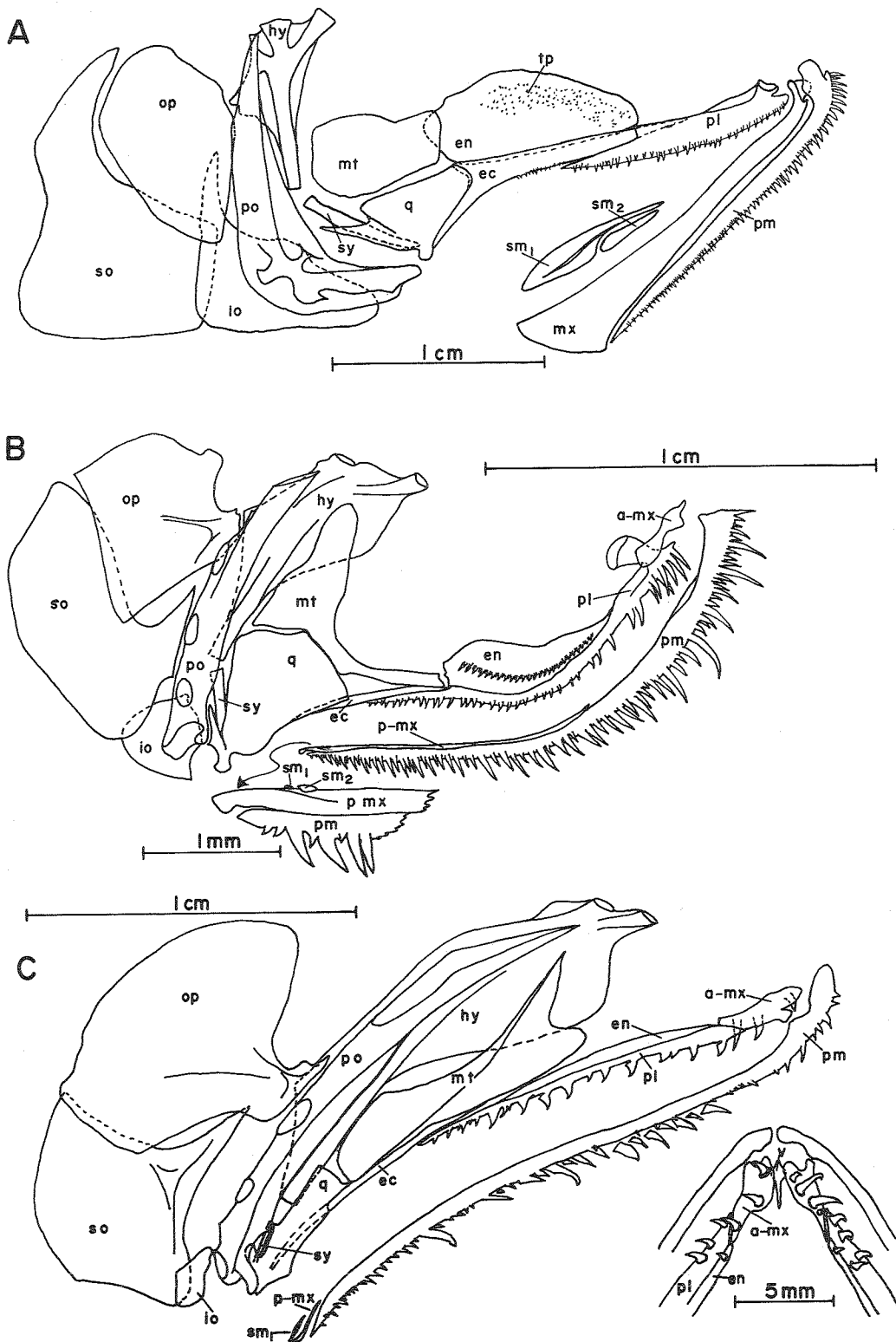


Fig. 3. Lateral facing bones of the skull. A, *Aulopus cadenati*, TABL 100967; B, *Saurida brasiliensis*, UMML 21327; C, *Harpodon nehereus*, USNM 93238.

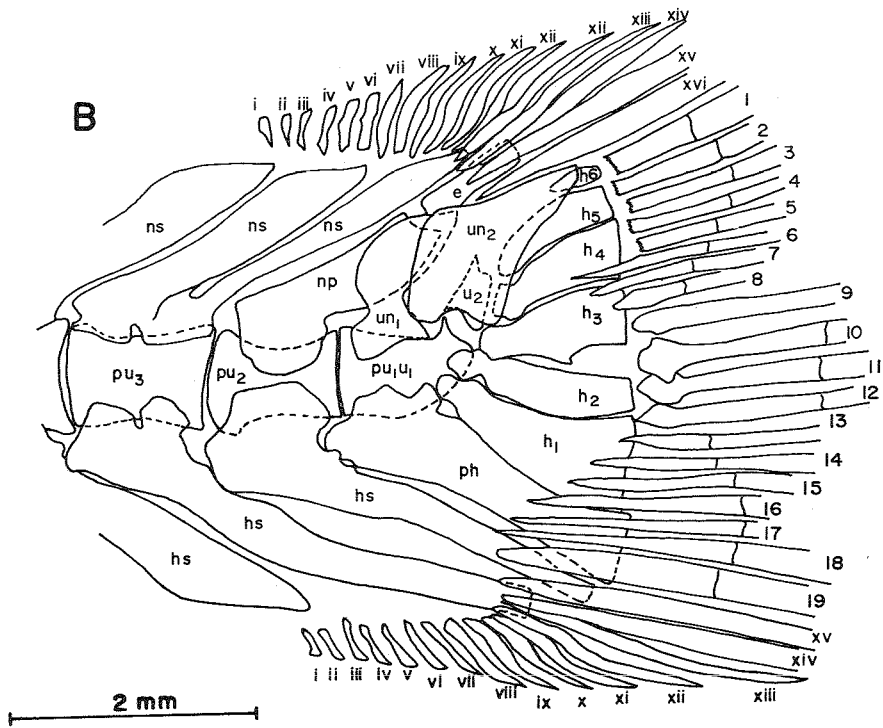
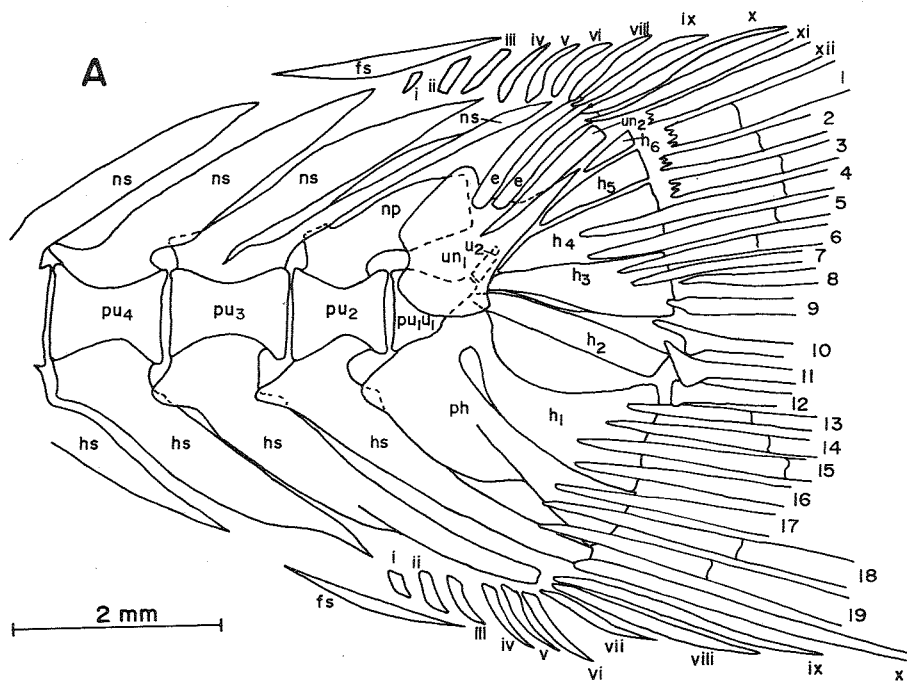


Fig. 4. Caudal skeleton. A, *Saurida brasiliensis*, UMML 21327;
 B, *Synodus synodus*, UMML 19328.

Table 1. A comparison of selected characters of *Aulopus* and the synodontid genera (based only on those species examined herein, see text).

Character	<i>Aulopus</i>	<i>Saurida</i>	<i>Harpadon</i>	<i>Bathysaurus</i>	<i>Synodus</i>	<i>Trachinoceph.</i>
pelvic fin rays	9	9	9	8	8	8
supramaxillae	2	2	1	0	0	0
caudal epurals	3	2	2	3	1	1
caudal procurrent rays (dorsal + ventral)	9-10+7-8	11-13+10-12	12+10-11	6-8+6	12-17+11-15	14+14
facral scales	present	present	absent	absent	absent	absent
branchiostegal rays	14-17	13	17	8-12	15-18	12
postcleithra	3	3	1	3	2	2
vertebrae (incl. urostyle)	48-51	49-52	54-56	52	56-61	56-57
vertebra under dorsal-fin origin	9	16	21-23	14	15-20	16
vomer	present	present	present	present	absent	absent
vomerine teeth	present	present	absent	present	—	—
ectopterygoid teeth	present	present	absent	absent	absent	absent
endopterygoid teeth	present	present	present	absent	absent	absent

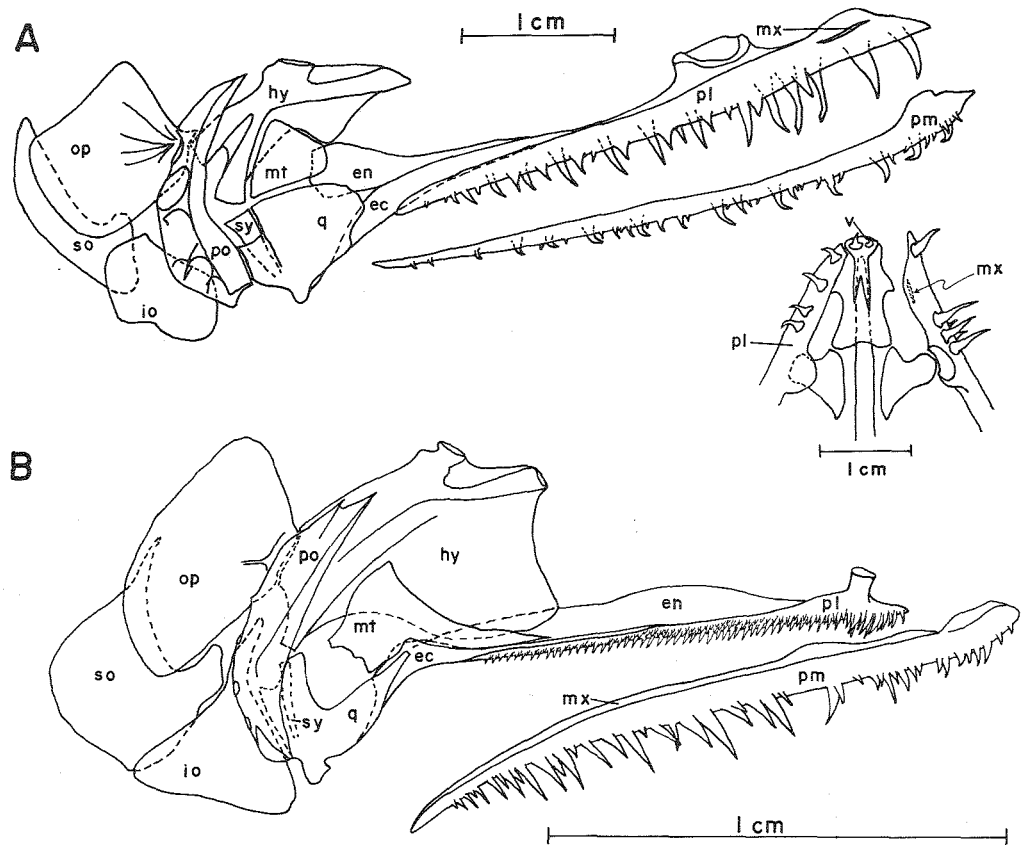
premaxilla and the palatine, which are aligned in parallel with each other. Both are armed with numerous large, strong, depressible teeth. Externally the maxilla, as in other synodontid fishes, is not evident. Again, typically synodontid gill rakers, in the form of clustered gill teeth, are present. A high number of branchiostegal rays are also present. The hyomandibular shows strong development of the antero-ventral flange characteristic of all synodontids (Fig. 3c). *Harpadon* demonstrates a particular affinity with *Saurida* in a number of characters. Most significant among these is the differentiation of the maxilla into separate anterior and posterior portions. The posterior portion is extremely reduced, but betrays its origin by its position and a dilation distally (Fig. 3c). A vestigial supramaxilla lies above it. The anterior portion of the maxilla, as in *Saurida*, consists of the head of that bone only. It still articulates on its outer surface with the premaxilla, but is immovably joined (not truly fused) on its inner surface with the head of the palatine (Fig. 3c, inset). These two bones appear continuous, an impression reinforced by the presence on the maxillary portion of three or four strong teeth identical to those of the palatine portion. Clearing and staining is necessary to elucidate the dual origin of this *de novo* palato-maxillary unit. As the maxillary portion provides the effective anterior point of support and movable articulation of this unit, the typical palatine-lateral ethmoid articulation has become obsolete and has been lost. The palatine-

lateral ethmoid communication is a consistent feature of all other benthic myctophiform genera. The unusual condition of the anterior elements of the upper jaw in *Harpadon* is nonetheless presaged in *Saurida*. Upper jaw modifications in both genera are influenced by the caudad elongation of jaw elements, at the same time as the cranium is undergoing a reduction in size. A second character unique to *Harpadon* and *Saurida* is the presence of endopterygoid tooth rows in parallel with the long palatine tooth rows (Fig. 3b,c). Further agreement between these genera is evident in the narrow lower jaw which closes so that the dentary tooth row lies between the premaxillary and palatine tooth rows. Again the interopercle in both genera is reduced in association with an increased moment arm extension of the articular, caudad of the quadrate pivot point. Reduction of the interopercle and elongation of the articular undoubtedly facilitate manipulation of the disproportionately long lower jaw, particularly in *Harpadon*. Despite its specializations, *Harpadon* also retains a number of primitive features which tend to reaffirm its affinity with *Saurida*. Like *Saurida*, *Harpadon* has nine pelvic rays (the remaining synodontid genera have but eight), a vomer (absent in *Synodus* and *Trachinocephalus*), endopterygoid dentition, two caudal epurals, and one vestigial supramaxilla (two supramaxillae in *Saurida*, none in the other genera).

A close association between *Harpadon* and another specialized genus, *Bathysaurus*, has been

Fig. 5. Lateral facing bones of the skull.

A, *Bathysaurus ferox*, UMMML 32437;
 B, *Synodus synodus*, UMMML 19328.



advanced (Harry 1952). However, the two fishes differ substantially not only in habit but in structure as well. Both do have a large gape, but the resemblance is superficial. The extremely short-snouted *Harpadon* achieves a large gape by rearward elongation of the jaws coupled with rotation dorsad and caudad of the elongate hyomandibular - preopercle (Fig. 3c). In the very long-snouted *Bathysaurus*, on the other hand, a large gape is achieved almost entirely by forward prolongation of the jaws, with the hyomandibular and preopercle being little modified (Fig. 5a). Moreover, the palatine of *Bathysaurus* exhibits the best developed articulation with the lateral ethmoid (Fig. 5a, inset) to be found among members of the family, a strong contrast to the situation obtaining in *Harpadon*. *Bathysaurus* and *Harpadon* also differ in body form, the former being depressed, the latter compressed. Additionally, in *Bathysaurus* the maxilla is not joined to the palatine anteriorly; it is present only as a slender rudiment lying between the palatine and the premaxillary head (Fig. 5a).

In terms of cranial osteology *Bathysaurus* resembles *Synodus* somewhat (Fig. 5a,b), but the two have achieved similar levels independently. The possibility that *Bathysaurus* is derived from *Synodus* or that it

represents a final stage along the main line of synodontid evolution (Gregory & Conrad 1936) is precluded by its retention of characters more primitive than those of *Synodus*. These include the presence of a toothed vomer (Fig. 5a, inset), three postcleithra (one dorsal and two ventral postcleithra are present primitively in *Aulopus*; the dorsal element is lost in *Synodus* and *Trachinocephalus*: compare Fig. 6a-d), three caudal epurals, a dorsal fin with a far anterior origin (over vertebra 9, see Table 1), and a hyomandibular with only moderate development of the antero-ventral flange. Thus the morphological evidence indicates that, despite certain obvious specializations, *Bathysaurus* is a very basal and rather distinct entity within the Synodontidae. The affinity of its "Macristium" juvenile with the juveniles of fishes of the chloropthalmid line (Berry & Robins 1967, Rosen 1971) would tend to support the same conclusion. The other synodontid genera have a more advanced type of juvenile. Nonetheless, *Bathysaurus* is certainly in close agreement with the other synodontid genera osteologically. A strong premaxilla dominates the upper jaw, the maxilla being reduced to a mere vestige, and the supra-maxillae being lost. Flanking the premaxilla is a long straight heavy palatine comparable to that found in

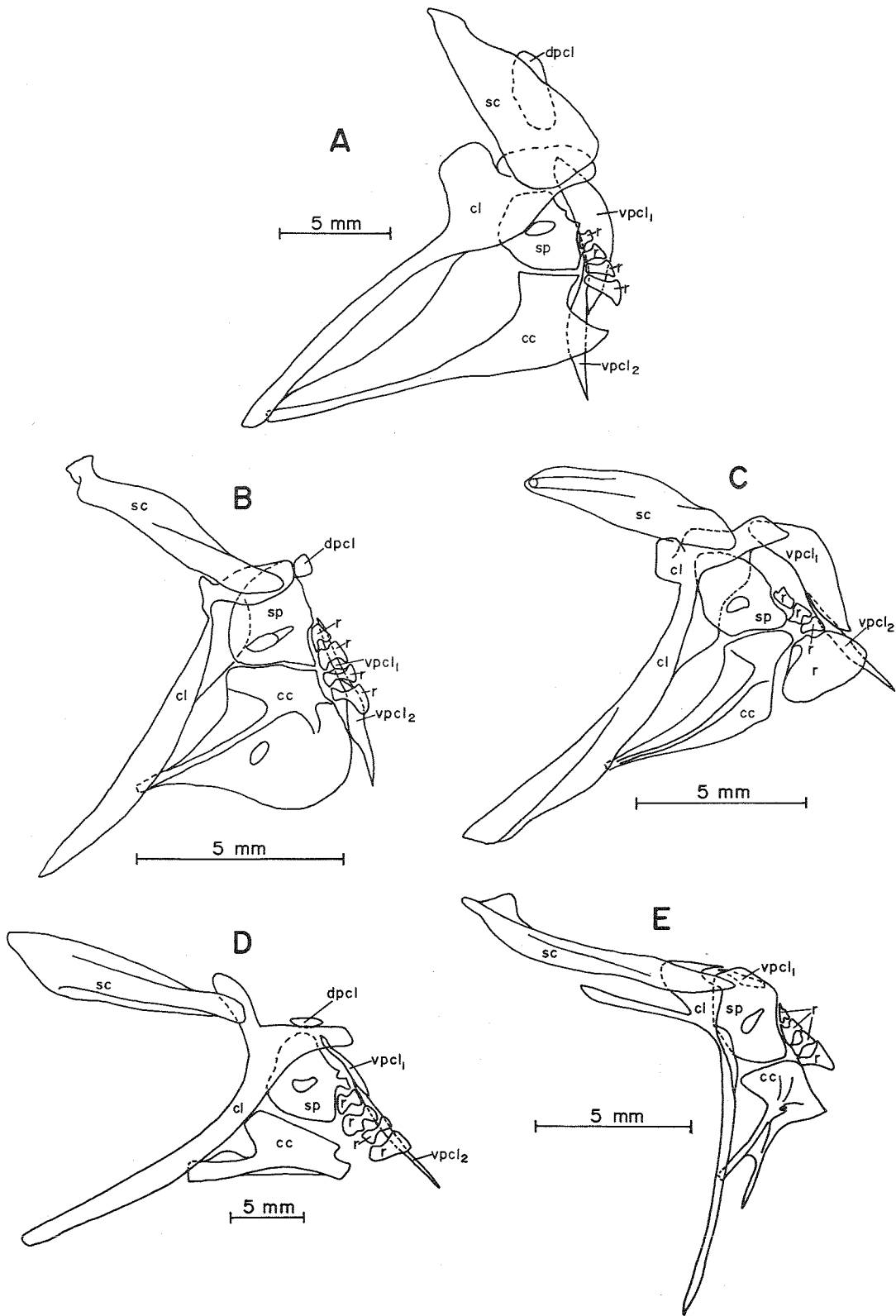


Fig. 6. Pectoral girdle. A, *Aulopus cadenati*, TABL 100967; B, *Saurida brasiliensis*, UMML 21327; C, *Synodus scituliceps*, UMML 25091; D, *Bathysaurus ferox*, UMML 32437; E, *Harpadon nehereus*, USNM 93238.

other synodontids. These two bones are provided with long needlelike depressible teeth (Fig. 5a). As in other synodontids also, the gill rakers are modified into clusters of short gill teeth. The snout is pointed in dorsal profile, three large supraneurals are present, and the hyomandibular has the characteristic antero-ventral flange.

The remaining synodontid genera, *Synodus* and *Trachinocephalus*, are closely allied and rather advanced with respect to the more primitive genera already discussed. Trends characteristic of the family achieve their best expression in *Synodus* and *Trachinocephalus*. The vomer and supramaxillae are now completely absent; dentition on the pterygoid series bones is lacking. The maxilla is reduced to a simple lamina adherent to the premaxilla, without a free articulating head anteriorly or a dilation posteriorly. A single caudal epural remains of the primitive three. An advanced condition with respect to *Saurida* is evident in the increase in vertebral number and in caudal procurrent rays (Table 1), as well as the great expansion of the lower pectoral fin radial (cf. Fig. 6b,c).

As the synodontid genera fall into three natural groups morphologically, as discussed above, a tripartite subdivision of the Synodontidae is appropriate (cf. scheme of classification above). The degree of differentiation of the three groups is certainly consistent with their recognition at the subfamily level. Thus the following arrangement of the family is advanced:

1) Subfamily Harpadontinae¹ Jordan, 1923, presently constituted to include the two genera *Harpadon* and *Saurida*; type genus, *Harpadon* Lesueur, 1825; type species by monotypy, *Osmerus nehereus* Hamilton Buchanan, 1822 (= *Harpadon nehereus*); subfamilial synonyms: Synodontidae (partim) Gill, 1862, Harpadontidae (partim): Harry 1952, Harpadonticae: Fowler 1959.

2) Subfamily Bathysaurinae Mead, 1960, including the single genus *Bathysaurus*; type genus, *Bathysaurus* Günther, 1878; type species by subsequent designation (Norman 1966), *Bathysaurus ferox* Günther, 1878; subfamilial synonyms: Macristiidae Regan, 1911, Harpadontidae (partim): Harry 1952.

3) Subfamily Synodontinae Gill, 1862, presently constituted to include the two genera *Synodus* and

Trachinocephalus; type genus, *Synodus* Gronow, 1763; type species by absolute tautonymy, *Esox synodus* Linnaeus, 1758 (= *Synodus synodus*); subfamilial synonyms: Saurina² (partim) Günther, 1864, Synodontidae (partim) Berg, 1940, Synodontidae (partim): Anderson et al. 1966.

The chloropthalmid line of benthic myctophiform fishes is herein considered to comprise a single family, the Chloropthalmidae. Two subfamilies are recognized as follows:

1) Subfamily Chloropthalminae Jordan, 1923; type genus, *Chloropthalmus* Bonaparte, 1840; type species by monotypy, *Chloropthalmus agassizi* Bonaparte, 1840; subfamilial synonyms: Aulopidae (partim): Goode & Bean 1896, Chloropthalmini: Parr 1928.

2) Subfamily Ipnopinae³ Gill, 1884; type genus, *Ipnops* Günther, 1878; type species by monotypy, *Ipnops murrayi* Günther, 1878; subfamilial synonyms: Bathypteroidae Gill, 1888, Benthosauridae Gill, 1892, Bathyptéroidés: Roule 1916, Bathypterini: Parr 1928, Macristiidae (partim): Berry & Robins 1967, Bathypteroidae + Ipnopidae: Mead 1966c,d, Bathypteroinae + Ipnopinae + Bathytyphlopinae + Bathymicropinae: Marshall & Staiger 1975.

The two subfamilies can be distinguished as follows: Subfamily Chloropthalminae. Eyes large, normal; pseudobranch present; dorsal postcleithrum present, ventral postcleithra broad and unfused; a high number (15-26, see Table 1) of caudal procurrent rays; endopterygoid discoidal and forming a concave subocular shield (Fig. 7a,b); pyloric caeca present; gape moderate, not extending beyond the posterior margin of the orbit. - Subfamily Ipnopinae. Eyes reduced or otherwise peculiarly modified (*Ipnops*); pseudobranch absent in adult (present in juvenile); dorsal postcleithrum usually absent, ventral postcleithra narrow and fused in adult (broad and unfused in juvenile, Fig. 21b); procurrent rays reduced in number (2-12); endocleithrum elongate-triangular and not forming a subocular shield (Figs 7, 11, 12, 13); pyloric caeca absent; gape large, usually extending well beyond the

2. The family-group name Saurina Günther, 1864, is based on the genus *Saurus* (a junior synonym of *Synodus*), not on *Saurida*. It would therefore be incorrect to construe Saurina as a prior name for the subfamily uniting *Saurida* and *Harpadon* (the Harpadontinae above).

3. The first adequate definition of Gill's Ipnopidae, Bathypteroidae, and Benthosauridae is found in Goode & Bean (1896) who clearly attribute definition of these families to Gill.

1. Jordan's original spelling of the family name, Harpodontidae, perpetuates an erroneous spelling (*Harpodon* instead of *Harpadon*) first used by Cuvier (1829).

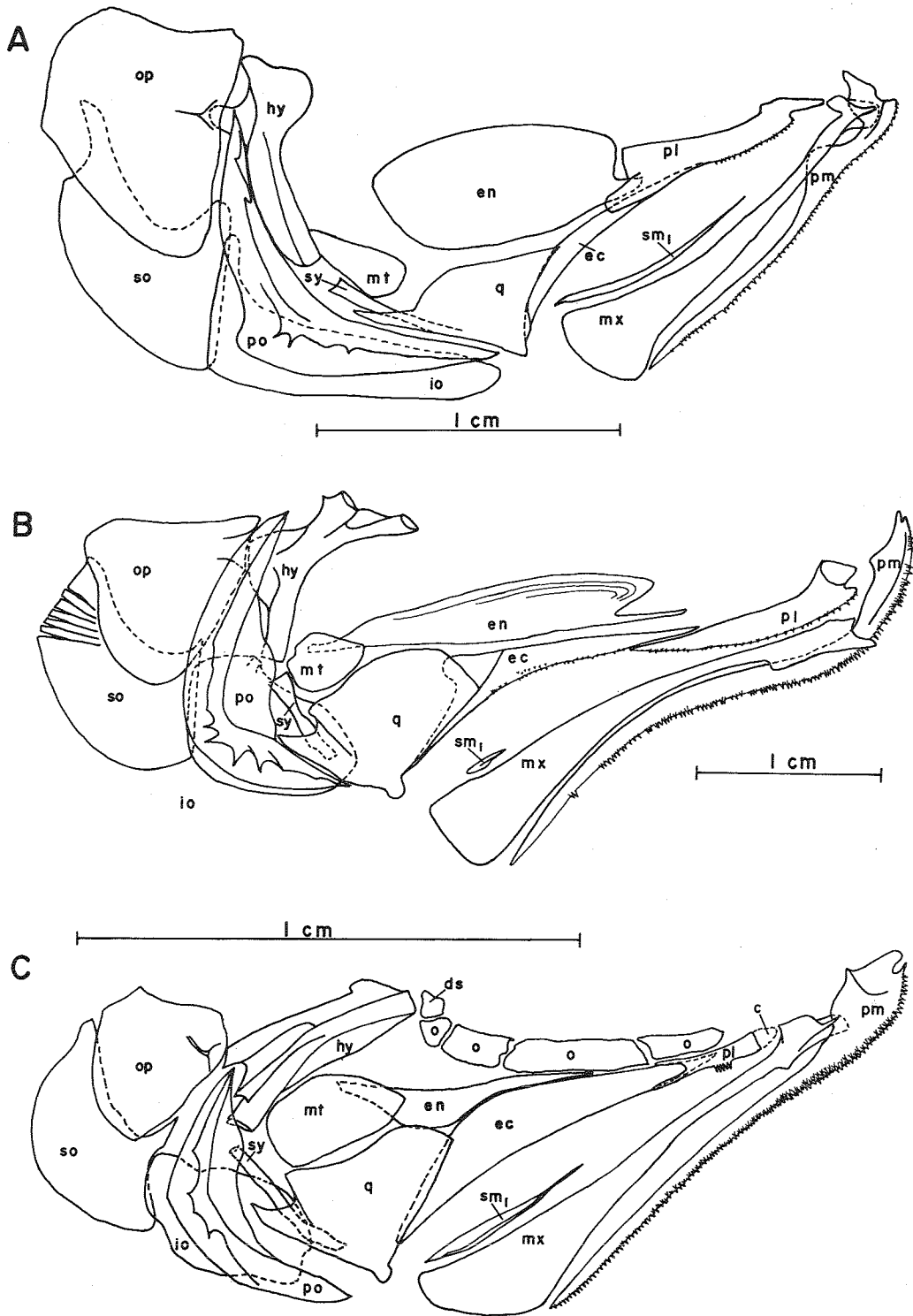


Fig. 7. Lateral facing bones of the skull. A, *Chlorophthalmus agassizi*, UMML 31496; B, *Bathysauropsis gracilis*, RUSI; C, *Ipnops murrayi*, UMML 30814.

posterior margin of the orbit; frontals expanded antero-laterally above the eyes.

Many of the characters which differentiate the Ipnopinae from the Chlorophthalminae represent the results of reduction, fusion, and loss associated with the stringent economy of a deep-sea mode of existence. Others, such as specialization of the feeding apparatus for a diet of very small invertebrates (mostly pelagic crustaceans), represent the culmination of a trend in this direction already apparent in the Chlorophthalminae (especially in *Bathysauropsis*). Thus, the family Chlorophthalmidae can be understood, as herein construed, as a structural and behavioral continuum proceeding from *Chlorophthalmus*, through *Bathysauropsis*, to the deep benthic radiation represented by the four ipnopine genera. However, the genus *Parasudis* represents an offshoot in a different direction. It is close to *Chlorophthalmus* but is adapted for a more active off-bottom existence in pursuit of large active prey (Mead 1966e) - as is evident in its shortened trunk, produced jaws, enlarged teeth, and reduced gill rakers.

Chlorophthalmus is the basal member of this continuum, being the most generalized member of the family. It resembles *Aulopus* in body form, fin placement, and vertebral number (Tables 1, 2). The lateral facing bones of the skull and bones of the upper jaw in *Chlorophthalmus* (Fig. 7a) are nearly identical in development to those of *Aulopus* (Fig. 3a). A simi-

larity in caudal osteology is suggested by the shape and orientation of the first dorsal and first ventral procurrent rays in the juvenile of *Chlorophthalmus*. From their position with respect to adjacent procurrent rays (Fig. 8a), it seems probable that these two elements derive ontogenetically from fucral scales like those of *Aulopus* and *Saurida* (Fig. 4a). The single row of teeth along the anterior edge of the vomer and the basihyal of the juvenile of *Chlorophthalmus* (Rosen 1971) are further particularly instructive points of agreement with the juvenile of *Aulopus*. Like *Aulopus*, *Chlorophthalmus* has three large unfused postcleithra (Fig. 9a).

Occupying a clearly intermediate position between the predominantly shallow benthic *Chlorophthalmus* and the deep benthic ipnopine genera is the genus *Bathysauropsis*. The transitional position of this genus has long been recognized (Regan 1911, Parr 1928, Mead 1966e). Like *Chlorophthalmus*, *Bathysauropsis* has a large normal eye, a well-developed pseudobranch, a very posteriorly-placed anal fin, three supraneurals (vs. one or two in the Ipnopinae), and a moderate gape. Moreover, in the shapes and configurations of the opercular series and palato-ptyergoid series bones (Fig. 7b), *Bathysauropsis* conforms very closely with *Chlorophthalmus* (Fig. 7a). On the other hand, the deep-dwelling *Bathysauropsis* approximates the ipnopine level of specialization in having a high number of pectoral fin rays (Table 2), narrow (but unfused) ventral

Table 2. A comparison of selected characters of the chlorophthalmid genera (excluding *Parasudis*)

Character	<i>Chlorophthalmus</i>	<i>Bathysauropsis</i>	<i>Ipnops</i>	<i>Bathypterois</i>	<i>Bathytyphlops</i>	<i>Bathymicrops</i>
eyes	large, normal	large, normal	peculiarly modified	minute	minute	minute
pyloric caeca	5, long	1-2, short	absent	absent	absent	absent
pseudobranch	present	present	absent	absent	absent	absent
vertebrae (incl. urostyle)	47-48	58	55-61	49-61	64-67	65-69
vertebra under dorsal-fin origin	9	15	15-19	20-26	20-22	26-27
caudal procurrent rays (dorsal + ventral)	13-14+11-12	8+7	2+1	4-7+3-5	6+5	1-2+1
caudal epurals	3	3	2	3	3	1
pectoral fin rays (incl. rudiments)	16-18	23-24	18	13-21	13-16	10-11
dorsal fin rays	10-12	11	8-10	12-16	12-13	8-9
anal fin rays	8	11	13-19	7-13	13-17	12
branchiostegal rays	10	9	11	11-14	14	10-12
gill rakers (total, anterior arch)	23	26	21-23	34-49	20-21	15-16
supraneurals	3	3	1	1	2	1

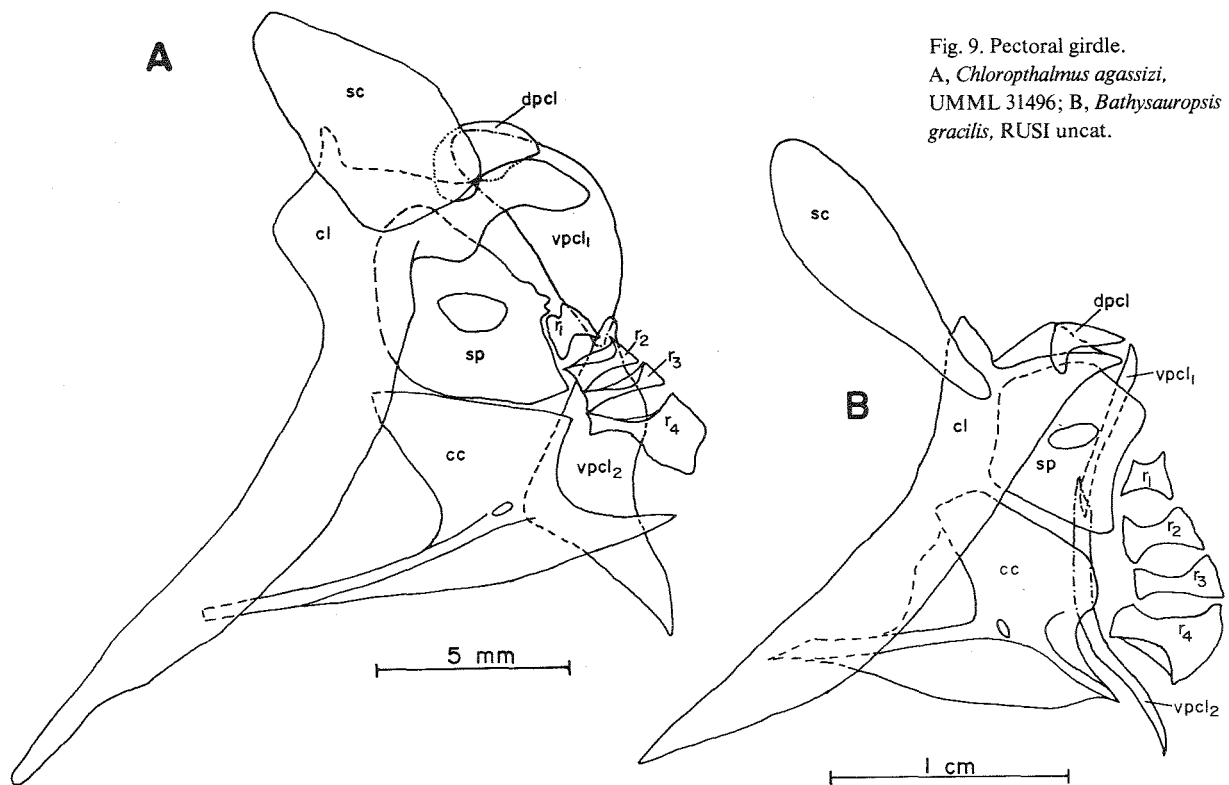


Fig. 9. Pectoral girdle.
 A, *Chloropthalmus agassizi*,
 UMML 31496; B, *Bathysauropsis*
gracilis, RUSI uncat.

postcleithra (Fig. 9b), a broad spatulate snout, an increased vertebral number (Table 2), one or two short pyloric caeca (vs. two-five long caeca in *Chloropthalmus* and *Parasudis*, and none in the ipnopine genera), an intermediate placement of the dorsal fin with respect to the vertebral column (Table 2), and an endopterygoid that still forms an enlarged elliptical shield beneath the eye - but is elongate on its outer margin as in *Bathypterois* or *Ipnops*. Thus *Bathysauropsis* exhibits a level of specialization that places it at the base of the ipnopine radiation. The very intermediate condition of this genus is the primary basis of the present incorporation of the ipnopine genera into the Chloropthalmidae.

**RELATIONSHIPS WITHIN THE
 SUBFAMILY IPNOPINAE**

The ipnopine radiation is essentially tripartite in nature (Fig. 2); the three directions of specialization

can be considered to represent three tribes: the Ipnopini (*Ipnops*), the Bathypteroiini (*Bathypterois*), and the Bathymicropini (*Bathymicrops* and *Bathytyphlops*). Despite a resemblance in body plan of a conservative nature, the genus *Ipnops* and the bathymicropin genera occupy opposite poles within the subfamily in terms of cranial osteology. Thus a family Ipnopidae (sensu Nybelin 1957, Mead 1966d, Nielsen 1966) uniting *Ipnops*, *Bathymicrops*, and *Bathytyphlops*, to the exclusion of *Bathypterois*, is a rather artificial assemblage. I concur with Marshall & Staiger (1975) in concluding that all four genera should be placed in a single unit of family-group rank. Their opinion is based on similarities in the development of the lateral-line system, while the present opinion is based on osteological evidence. Taxonomic categories within the subfamily Ipnopinae, as herein understood, can be distinguished as follows:

Key to genera of the subfamily Ipnopinae

- 1 a. Ectopterygoid untoothed; endopterygoid elongate, joining palatine anteriorly; palatine short, weakly toothed; opercle normal or somewhat elongate; hyomandibular wide and heavy, short or moderately elongate; teeth in jaws of the simple conical type; 49-61 vertebrae 2
- 1 b. Ectopterygoid long, straight, and well toothed; endopterygoid reduced, not joining palatine anteriorly; palatine elongate and well toothed; opercle an elongate crescent rotated to a posi-

- tion above and parallel to the hyomandibular; hyomandibular narrow, greatly elongate; teeth in jaws bladelike and either blunt or curiously pointed; 64-80 vertebrae Tribe Bathymicropini
- 2 a. Eyes transformed into flattened, dorsally-directed plaques; pectoral, pelvic, and caudal fins without stiffened produced rays; 3-4 rakers on the upper limb of the anterior gill arch Tribe Ipnopini, Genus *Ipnops* Günther, 1878
- 2 b. Eyes minute but otherwise normal; pectoral, pelvic, and caudal fins with stiffened produced rays; 8-14 rakers on the upper limb of the anterior gill arch Tribe Bathypteroiini, Genus *Bathypterois* Günther, 1878
- 3 a. Rakers of the anterior arch modified into low spinulose knobs or plaques, except for a single elongate element at the angle; 19 principal caudal rays; 12-14 pectoral fin rays visible externally; HL 21-23% SL Genus *Bathytyphlops* Nybelin, 1957
- 3 b. Rakers of the anterior arch of the typical bladelike form; 15-18 principal caudal rays; 7-9 pectoral fin rays visible externally; HL 12-17% SL Genus *Bathymicrops* Hjort & Koefoed, 1912

While each of the three ipnopine subgroups exhibits some conservative features, the genus *Ipnops* most closely approximates *Bathysauropsis*, especially in terms of cranial osteology. Regions of the skull not directly involved with the transformed eye maintain the most primitive condition to be found in the Ipnopinae. The opercular series in particular (Fig. 7c) is little modified over the condition in *Bathysauropsis* or *Chlorophthalmus* (Fig. 7b, a). Similarly, with the exception of the endopterygoid, the pterygoid series bones are comparable in shape to those of *Bathysauropsis*. As it no longer guards the ventrum of a large spherical eye, the endopterygoid is not elaborated into a suborbital shield. The hyomandibular of *Ipnops* is short and heavy. Correspondingly, the gape is moderate, not extending beyond the posterior margin of the orbit (Fig. 7c). In *Bathypterois* and the bathymicropine genera, where the hyomandibular is moderately to greatly elongate, the gape extends well beyond the eye. Another conservative region in *Ipnops* is the pectoral fin (Fig. 10a). It departs from that of *Bathysauropsis* only in the reduction of certain elements (coracoid, outer fin rays) and the fusion of others (ventral postcleithra). The fin radials are somewhat expanded, but ray specialization of the type seen in *Bathypterois* is absent. A final conservative feature of *Ipnops* is the far posterior placement of the anal fin. In fact, the overall body plan of *Ipnops* is quite comparable to that of *Bathysauropsis*.

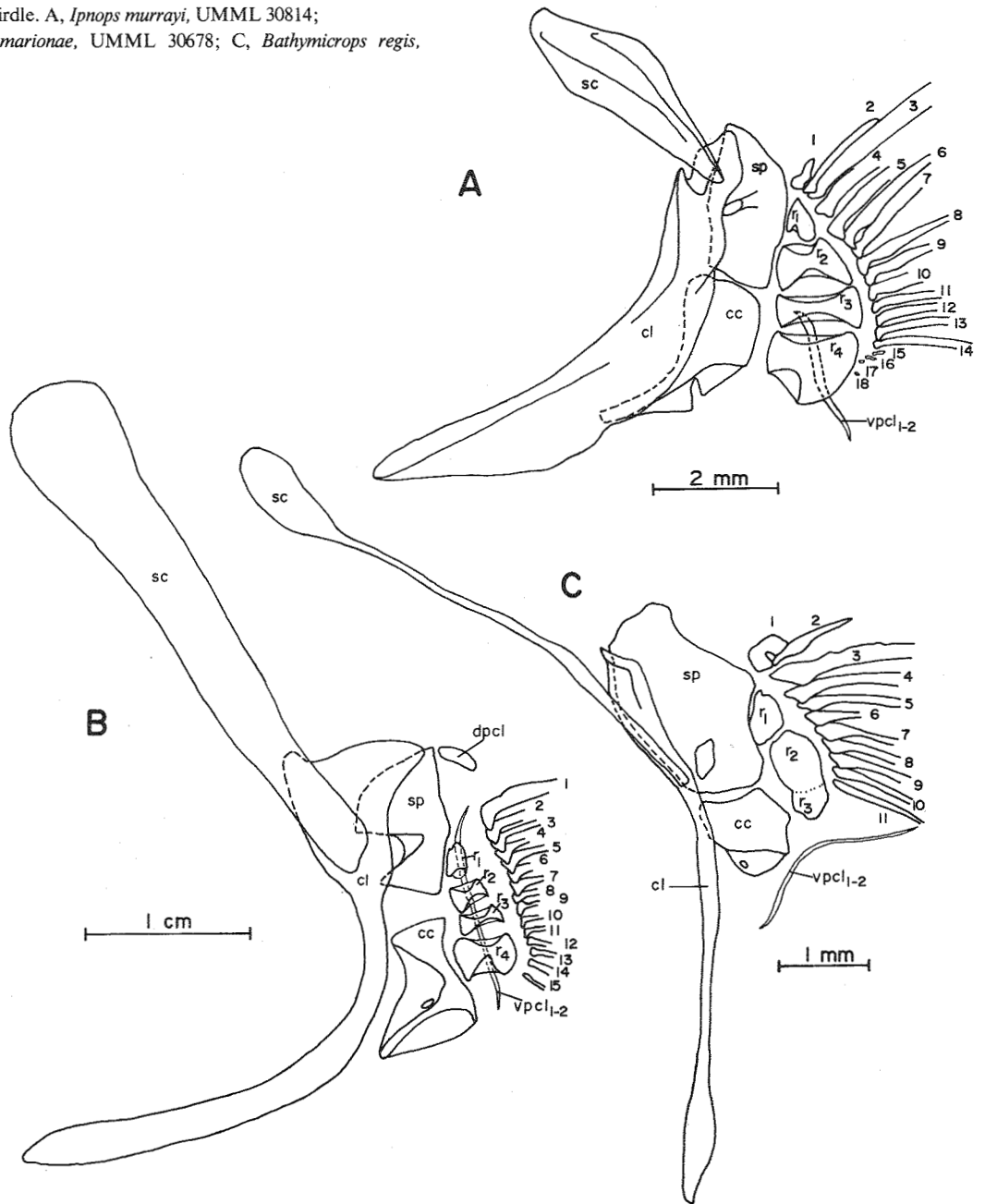
Ipnops does, of course, exhibit specialization in the area of the dorsicranium in association with the peculiarly modified eye (Günther 1887, Theisen 1966). Beyond this, structural modifications are

mainly reductional in nature. Reduction characterizes not only the pectoral fin, but also the caudal fin, which retains but two epurals and three caudal procurrent rays (dorsal + ventral). The adipose fin has also been lost. But loss of caudal elements and the adipose fin is a recurring theme in the Myctophiformes. This type of reduction occurs in parallel in each of the three ipnopine tribes and is not generally instructive taxonomically beyond the species level.

The second ipnopine subgroup is the tribe Bathymicropini, comprising the genera *Bathymicrops* and *Bathytyphlops*. These fishes undoubtedly differ in their modes of feeding as reflected in differences in body size and gill raker form. Nevertheless, they are much closer to one another osteologically than either is to *Ipnops* or *Bathypterois*. A suprageneric taxon uniting *Bathymicrops* and *Bathytyphlops* has been established herein to clarify the particular affinity of these two genera, and in turn, their mutual distance from *Ipnops* and from *Bathypterois*.

Of the two genera, *Bathytyphlops* is the more conservative. Its pectoral fin (Fig. 10b) agrees with that of *Bathysauropsis*, especially in the retention of the dorsal postcleithrum. However, the supracleithrum is greatly elongated in conjunction with rearward elongation of the jaws. The caudal region retains the primitive three epurals and a high number of procurrent rays (six dorsal + three-five ventral). The anal fin maintains a primitive position well behind the dorsal fin. In the cervical region *Bathytyphlops* is the only member of the Ipnopinae to retain two supraneurals (three is the primitive myctophiform number). Finally, close agreement with *Bathysauropsis* is evident in the presence of a

Fig. 10. Pectoral girdle. A, *Ipnops murrayi*, UMML 30814; B, *Bathytyphlops marionae*, UMML 30678; C, *Bathymicrops regis*, UMML 31265.



vomer with two large elliptical tooth patches, as well as a long toothed palatine and a toothed ectopterygoid.

However, *Bathytyphlops* is much advanced osteologically over *Bathysauropsis* and *Ipnops*, having attained a high level of cranial specialization. The gape is greatly lengthened by rearward elongation of the hyomandibular and ectopterygoid. To accommodate this elongation the hyomandibular is canted caudad, coming to lie nearly parallel to the long axis of the body (Fig. 11a). Correspondingly, the opercle

is rotated 90° out of normal position. As a result, this bone now lies entirely above the hyomandibular. At the same time the endopterygoid is reduced, having nearly lost to the ectopterygoid alone the function of bridging the metapterygoid-palatine interspace.

Cranial specialization following an exactly comparable plan, but carried to a further extreme, is displayed by *Bathymicrops* (Fig. 11b). The jaws extend back even farther than in *Bathytyphlops*; the hyomandibular and ectopterygoid are thinner and

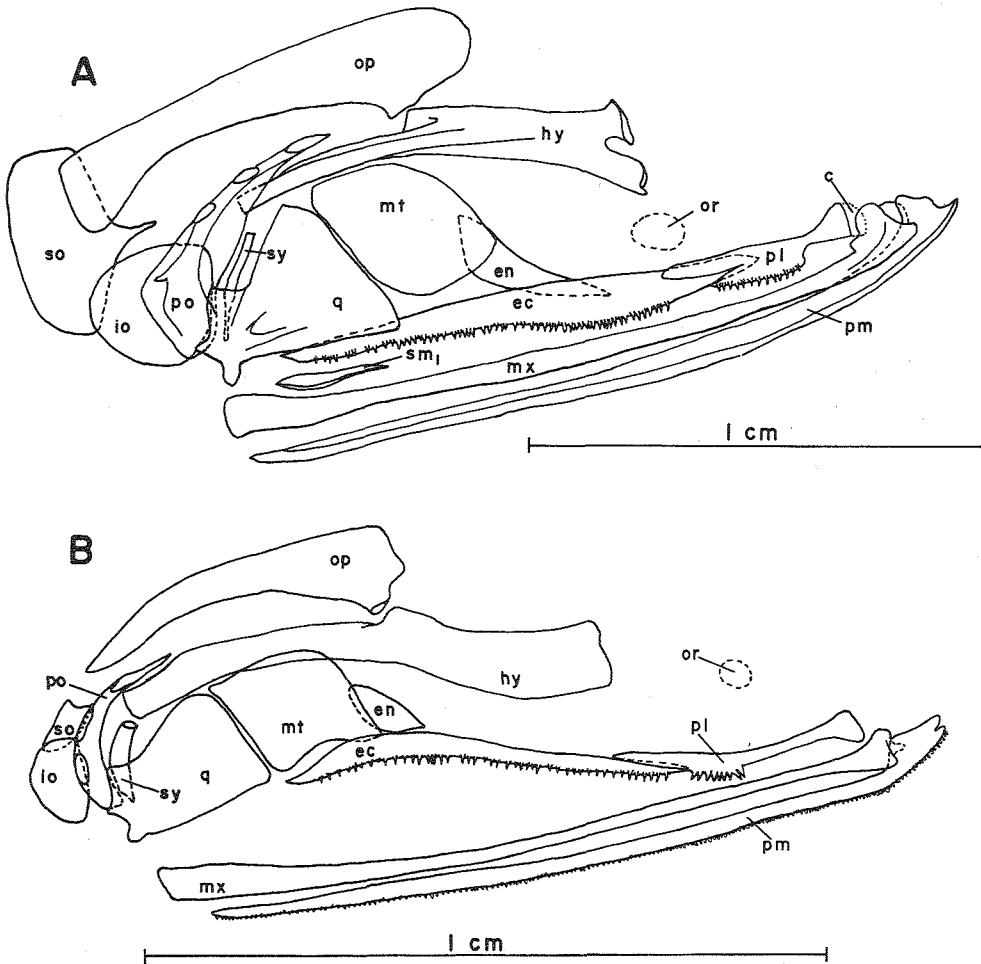


Fig. 11. Lateral facing bones of the skull.

A, *Bathytyphlops marionae*, UMML 30700

(premaxillary dentition omitted);

B, *Bathymicrops regis*, UMML 31265.

more attenuate, and the endopterygoid is greatly reduced. Moreover, the trend in *Bathymicrops* toward reduction and simplification of elements tends to emphasize rather than obscure the similarity in specialization between the genus and *Bathytyphlops*. Like *Bathytyphlops*, *Bathymicrops* has a greatly elongated supracleithrum (Fig. 10c) and a long well-toothed ectopterygoid. Furthermore both genera have a peculiar type of dentition on the premaxilla and the dentary. As in the other ipnopine genera a broad band made up of numerous small teeth is present in each jaw. However, in the *Bathymicropini* the teeth are smaller, much more numerous, compressed, and either blunted (*Bathytyphlops*) or provided with a unique type of tip (*Bathymicrops* (Pl. 4 Fig. 1). In contrast, the more typical teeth of *Ipnops* and *Bathypterois* (Pl. 4 Fig. 2) are larger, less numerous, circular in cross section, and conical - tapering to a simple point.

Bathytyphlops departs from *Bathymicrops* and the other ipnopine genera in having the gill rakers

modified into low spinulose knobs or plaques (Sulak 1974) instead of the typical bladlike rakers. This modification apparently results from specialization toward a diet of larger bottom invertebrates, rather than one of small pelagic crustaceans as in the related genera. Consequently, the form of the gill rakers is an adaptation of a positive nature and should not be viewed as the result of degeneracy as previously suggested (Mead 1959a, 1966d; Okiyama 1972). On the other hand *Bathymicrops* does display a measure of degenerative reduction and loss. Especially notable is the absence of a supramaxilla and the presence of fewer than 19 principal caudal rays (15-18), both being unique conditions for a chloropthalmid fish.

The third and most successful ipnopine subgroup is the genus *Bathypterois*. This genus accounts for more than twice as many species as the other three genera combined. Its success is undoubtedly related to the evolution of specialized fins which serve diverse and important functions (see below). In terms

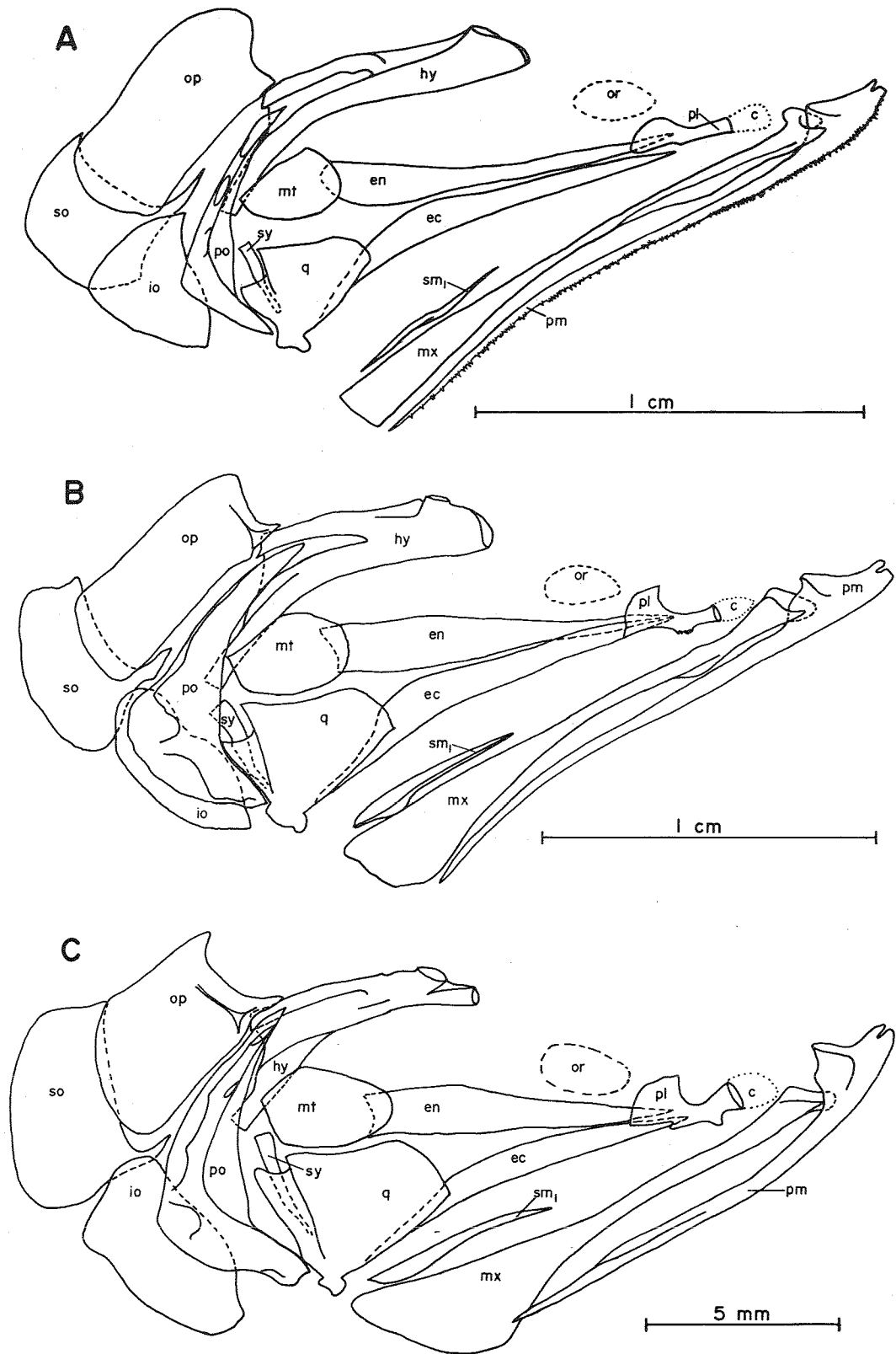


Fig. 12. Lateral facing bones of the skull. A, *Bathypterois grallator*, UMML 30759; B, *B. viridensis*, UMML 30831; C, *B. bigelowi*, UMML 28173 (premaxillary dentition omitted in B and C).

of cranial osteology, *Bathypterois* occupies a level of specialization intermediate between *Ipnops* on the one hand, and *Bathytyphlops* and *Bathymicrops* on the other. The gape in *Bathypterois* is longer than in *Ipnops*, but shorter than in the Bathymicropini. Correspondingly, attenuation of the hyomandibular is moderate (Figs 12, 13). The opercle varies from a nearly normal shape (Fig. 12c) to an elongate shape (12a, b). The degree of rotation of this bone in a caudad direction is accordingly variable. At the same time, the endopterygoid and ectopterygoid of *Bathypterois* agree in shape and development with those of *Ipnops*, the former bone being unreduced and the latter untoothed. The palatine also compares to that of *Ipnops*, being rather short and poorly toothed.

The pectoral fin of *Bathypterois* is a highly adapted structure of rather singular appearance externally. Nonetheless, internal changes are slight,

consisting mainly of expansion of the fin radials, and also the coracoid and scapula (Figs 14, 15). However, some degree of expansion of the fin radials is already apparent in *Bathysauropsis* (Fig. 9b) and *Ipnops* (Fig. 10a). In *Bathypterois* the lowermost radial is greatly expanded to support the long fin rays of the lower portion of the pectoral fin, while the uppermost radial is fused with the scapula. This fused unit invariably supports the first five fin rays of the upper portion of the pectoral fin, including the produced rays (rays 3 and 4) of most species (Figs 14, 15). Of course the most striking aspect of the pectoral fin of *Bathypterois* is the specialization of the individual rays. This type of adaptation is not presaged in related genera. However, the probable antecedent of the pectoral fin of *Bathypterois* (which has as many as 22 variously developed fin rays) is present in *Bathysauropsis* (which has 22-24 undifferentiated pectoral fin rays).

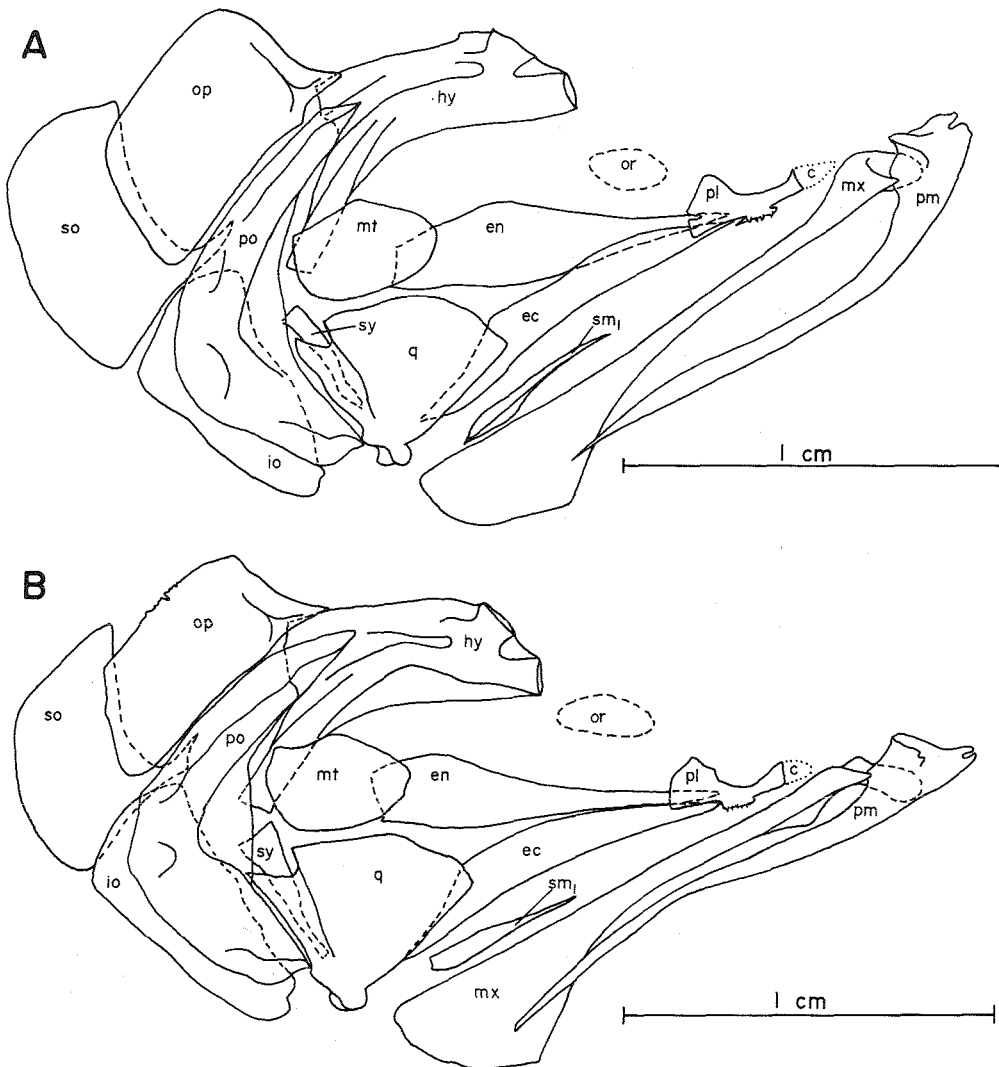


Fig. 13. Lateral facing bones of the skull. A, *Bathypterois ventralis*, ZMUC, "Galathea" St. 739; B, *B. pectinatus*, ZMUC, "Galathea" St. 739 (premaxillary dentition omitted).

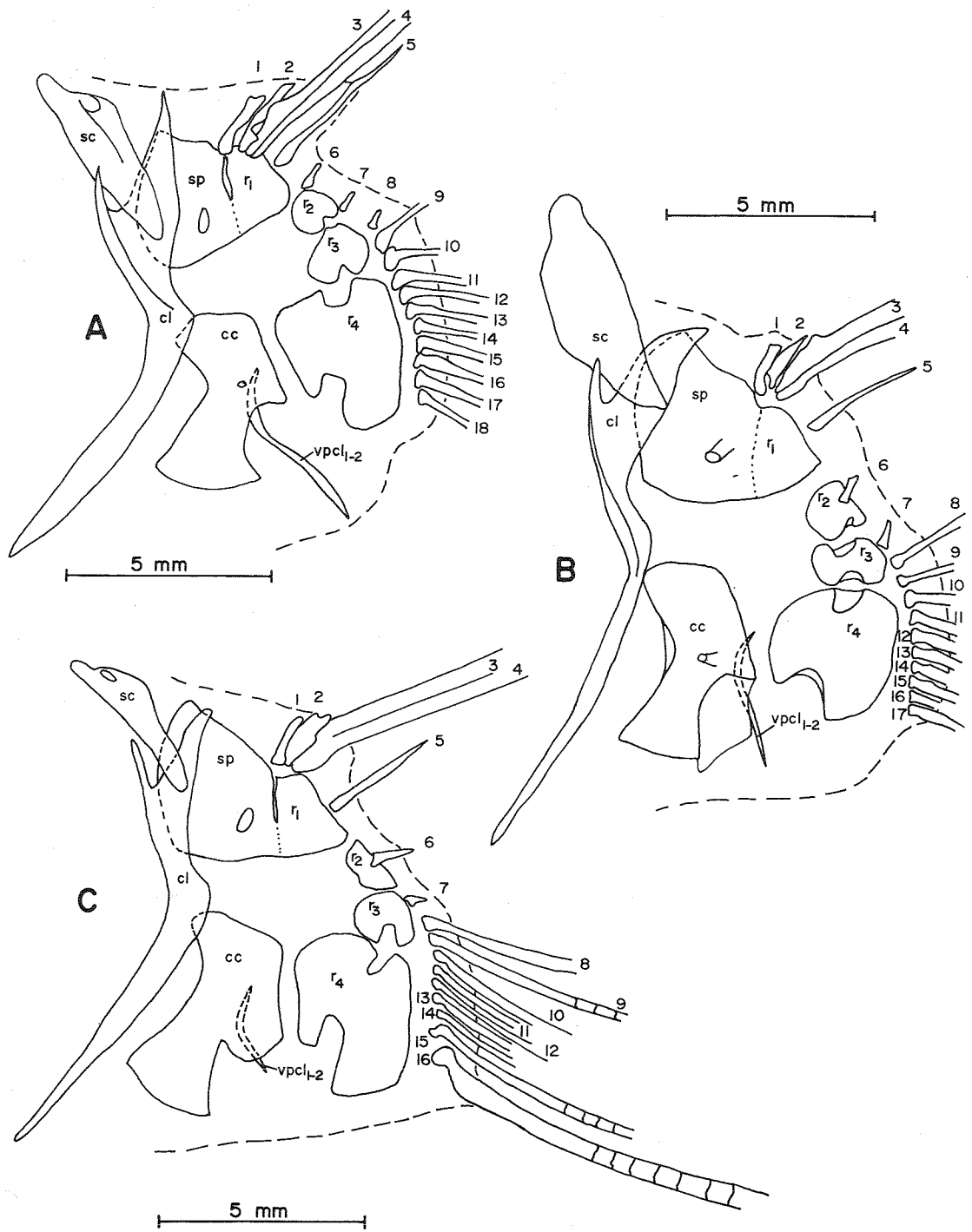


Fig. 14. Pectoral fin. A, *Bathypterois atricolor*, UMML 21683; B, *B. longipes*, UMML 24515; C, *B. quadrifilis*, UMML 30540.

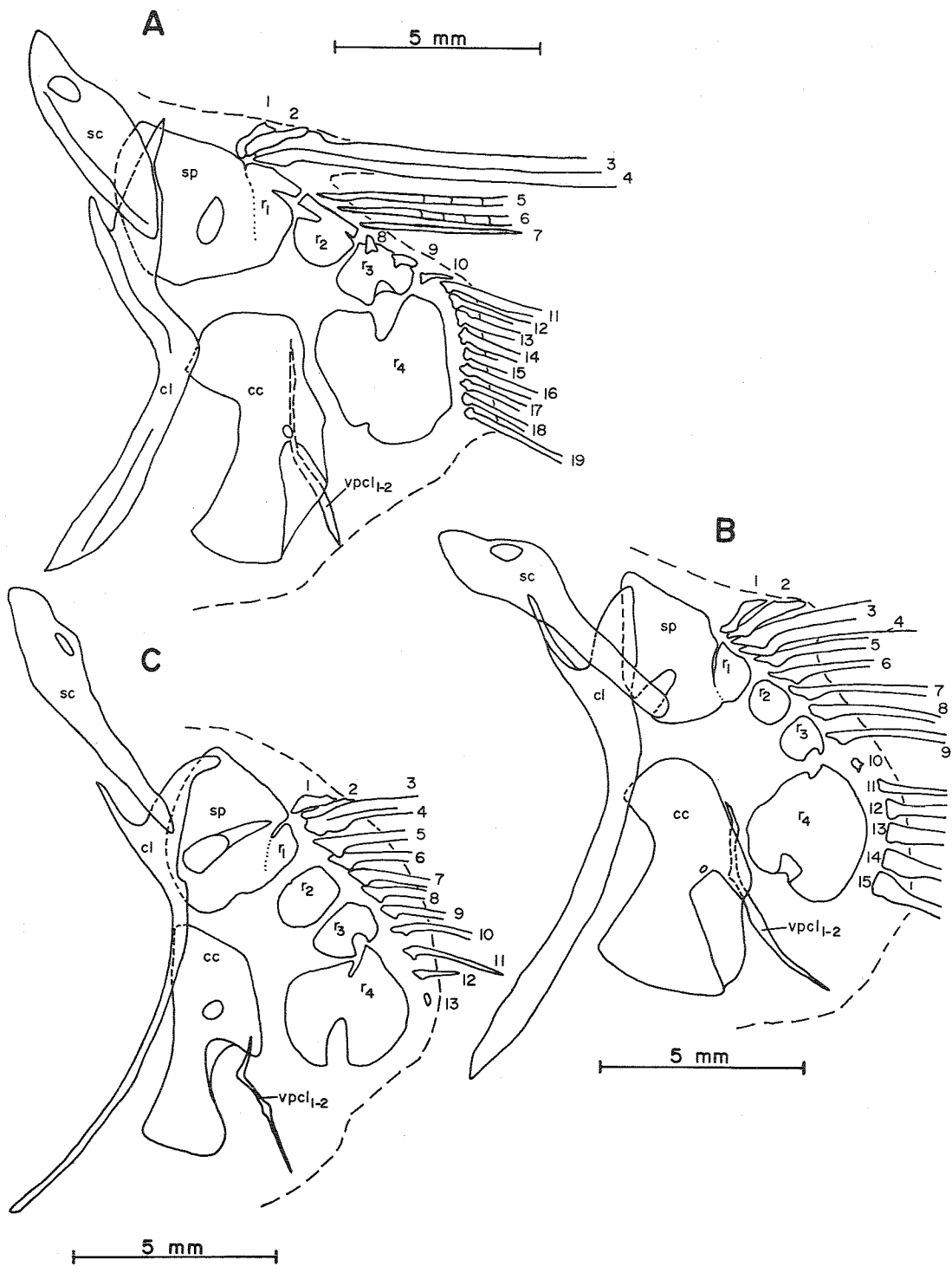


Fig. 15. Pectoral fin. A, *Bathypetris bigelowi*, UMML 28173; B, *B. viridensis*, UMML 30831; C, *B. grillator*, UMML 21637.

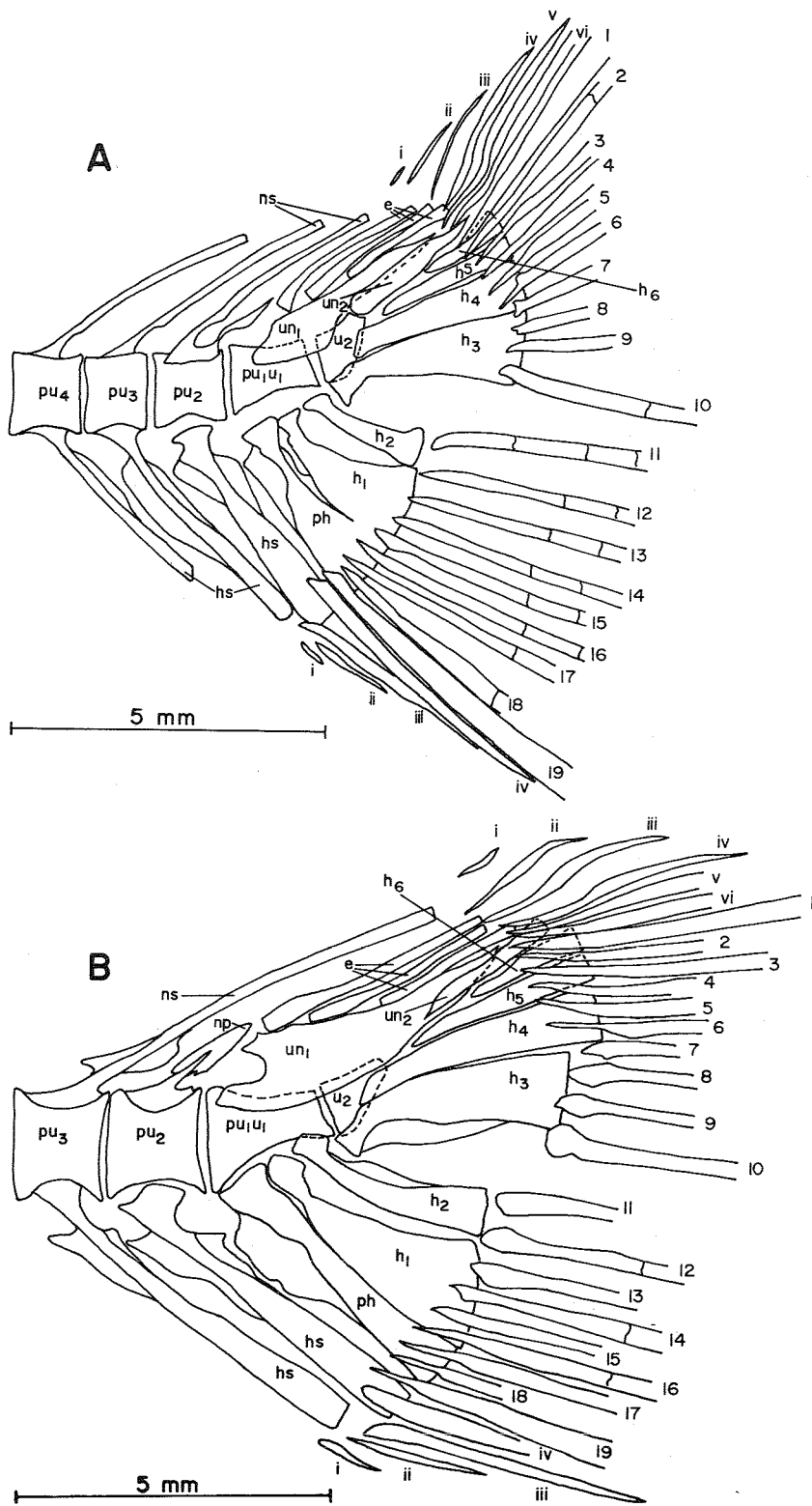


Fig. 16. Caudal fin. A, *Bathypterois grillator*, UMML 30759;
 B, *B. viridensis*, UMML 30831.

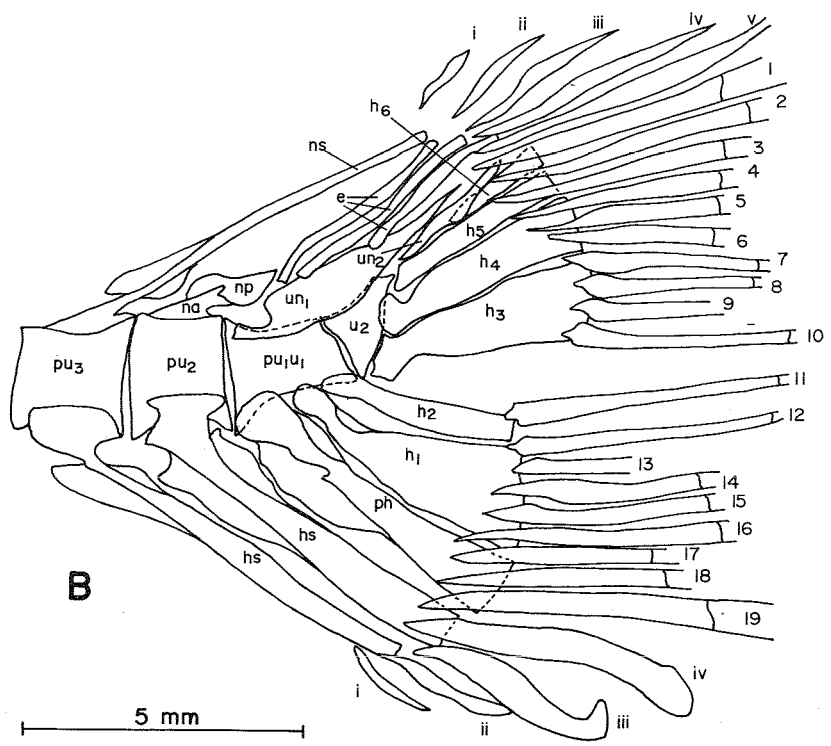
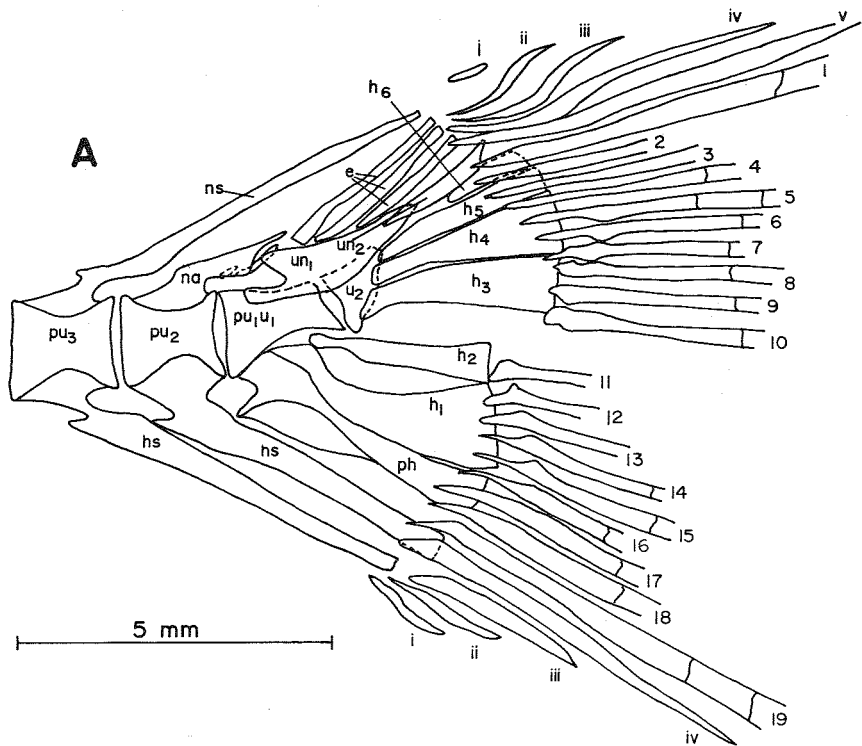


Fig. 17. Caudal fin. A, *Bathypterois bigelowi*, UMML 30759;
 B, *B. phenax*, UMML 30837.

Bathypterois employs its caudal and pelvic fins to elevate itself above the substrate. Accordingly, the lower caudal and outer pelvic fin rays are thickened, stiffened, and elongated. The underlying bones, however, are little modified. For example, the caudal skeleton is quite conservative (Figs 16, 17), comparing nearly exactly with that of *Chloropthalmus* (Fig. 8). The greatest change associated with its support function is a simple shift of the ventral hypurals to a more anterior position relative to the dorsal hypurals. There is also a reduction in the number of caudal procurrent rays (cf. *Chloropthalmus*). But a trend in this direction is characteristic of all ipnopsine genera, and is in fact already apparent in *Bathysauropsis*.

Aside from fin ray specialization, further expression of the advanced condition of *Bathypterois* is found in the abandonment of the primitive far posterior placement of the anal fin and the increase in the number of gill rakers. A singular primitive feature characteristic of the genus (*B. grallator* excepted) is the retention of the adipose fin.

SYSTEMATICS OF THE GENUS *BATHYPTEROIS* GÜNTHER, 1878

Distinctive characters:

Pectoral fin. Total fin rays including rudiments 13-22; upper two rays always rudimentary and embedded in the axil of the next two rays, which are usually thickened, stiffened, and greatly produced (28-183% SL); the two produced pectoral rays united over a substantial portion of their lengths, giving the appearance of a single bifid ray; the upper five fin rays always associated internally with the fused upper fin radial-scapula; one to four rudimentary rays usually present in the middle of the fin, giving it a divided appearance; the remaining several rays usually long, equal, and associated with the expanded lower fin radial. - *Pelvic fin.* Outermost ray or two rays modified into stiff elongate (19-144% SL) stiltlike appendages terminating in thick epidermal pads; these produced rays usually united along most of their lengths, their segments being very short and thick. - *Caudal fin.* Lowermost fin ray or fin rays modified in a similar fashion and

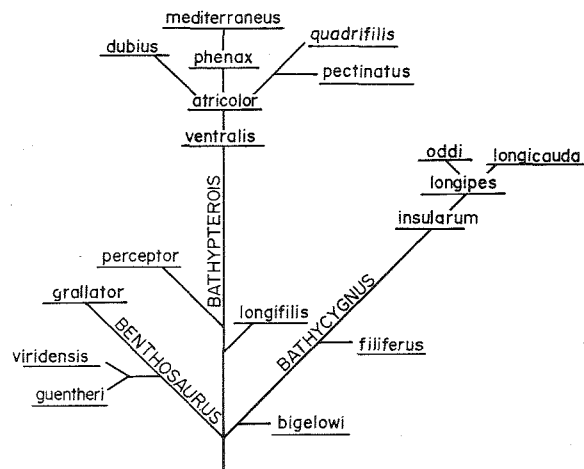


Fig. 18. Phylogenetic relationships within the genus *Bathypterois*.

elongated to a similar extent (15-134% SL) as the outer pelvic fin rays; four to seven dorsal and three to five ventral procurrent rays; always ten dorsal plus nine ventral principal rays. - *Anal fin.* Inserted opposite the middle to the end of the dorsal fin. - *Adipose fin.* Present in most species; always very small. - *Gill rakers.* Long, numerous, bladelike; anterior arch provided with 8-14 rakers on the upper limb, one at the angle, and 21-34 on the lower limb. - *Dentition.* Premaxilla and dentary each provided with a band of small conical pointed teeth; vomer with a patch of similar teeth on each knob; palatine usually with a few small teeth; ectopterygoid and endopterygoid untoothed (except rarely in the former). - *Vertebrae.* 49-61 including the ural centra; first ural and first preural centra fused. - *Lateral-line scales.* 48-65, each provided with a vertical row of superficial lateral line organs. - *Eyes.* Minute, but otherwise normal in appearance.

With the incorporation of *B. grallator*, the resurrection of *B. longicauda*, and the description herein of two new species, the genus *Bathypterois* comprises 18 species worldwide. These species can be arranged into three natural groupings (Fig. 18); the subgenera *Benthosaurus*, *Bathypterois*, and *Bathycygnus* (with three, nine, and six species, respectively). The subgenera and species of *Bathypterois* can be distinguished according to the following key.

Key to subgenera and species of *Bathypterois*

- 1a. Gular fold scaled; 10-13 anal fin rays; 13-15 pectoral fin rays (incl. rudiments), rays 3 and 4 closely applied but unfused, rays 5 through 9 never rudimentary; first pelvic fin ray strengthened and greatly elongated (58-144% SL), second fin ray thin, half as long as the first, and closely applied to it; lower caudal ray(s) greatly produced (38-134% SL); vomer with two large elliptical tooth patches; basibranchial 3-4 with dentigerous dermal plates; 34-37 rakers on the anterior gill arch Subgenus *Benthosaurus* Good & Bean, 1886 2
- 1b. Gular fold unscaled; 8-10 anal rays; 15-22 pectoral rays (incl. rudiments), rays 3 and 4 (the produced rays) united or fused over a substantial portion of their lengths, rays 5 through 7-10 reduced or rudimentary; first and second pelvic fin rays equally strengthened and produced (19-56% SL), usually united or fused; vomer usually with only a few teeth on each knob; basibranchial 3-4 usually without dentigerous dermal plates; 38-49 rakers on the anterior gill arch 4
- 2a. Color uniform black; 58-60 lateral-line scales; 53-54 vertebrae; produced pelvic rays greater than 100% SL *B. (Benthosaurus) grallator* (Goode & Bean, 1886)
- 2b. Color white with wide brown bands; 51-56 lateral-line scales; 50-52 vertebrae; produced pelvic rays less than 100% SL 3
- 3a. Area under the dorsal fin white; caudal fin dark; dorsal fin colorless *B. (Benthosaurus) viridensis* (Roule, 1916)
- 3b. Area under the dorsal fin dark; caudal fin white; dorsal fin dark *B. (Benthosaurus) guentheri* Alcock, 1889
- 4a. Ventral procurrent rays modified to form a subcaudal notch Subgenus *Bathypterois* Günther, 1878 5
- 4b. Ventral procurrent rays not modified to form a subcaudal notch Subgenus *Bathycygnus*, n. subgen. 10
- 5a. Scales beneath and immediately posterior to pectoral not pectinate; produced pectoral fin rays separate caudad of dorsal fin 6
- 5b. Scales beneath and immediately posterior to pectoral strongly pectinate; produced pectoral fin rays separate cephalad of dorsal fin 9
- 6a. Color green; scales adherent; 12-13 long rays in the lower portion of the pectoral fin *B. (Bathypterois) longifilis* Günther, 1878
- 6b. Color pinkish-white with dark pigment specks on each scale pocket; scales deciduous; 13 long rays in the lower portion of the pectoral fin; 61 lateral-line scales; 59 vertebrae; produced pelvic fin rays equal 19% SL *B. (Bathypterois) perceptor* n. sp.
- 6c. Color uniform brown to black; scales deciduous; ten or more long rays in the lower portion of the pectoral fin 7
- 6d. Color uniform brown to black; scales deciduous; fewer than ten long rays in the lower portion of the pectoral fin 8
- 7a. 12-14 long rays in the lower portion of the pectoral fin; 57-59 lateral-line scales; 52-56 vertebrae; produced pelvic fin rays equal 29-72% SL. *B. (Bathypterois) ventralis* Garman, 1899
- 7b. 10-11 (rarely 9) long rays in the lower portion of the pectoral fin; 9 pelvic fin rays; 56-62 lateral-line scales; 54-57 vertebrae *B. (Bathypterois) atricolor* Alcock, 1897
- 7c. 10-11 (rarely 9) long rays in the lower portion of the pectoral fin; 8 pelvic fin rays; 61-65 lateral-line scales; 59-61 vertebrae *B. (Bathypterois) dubius* Vaillant, 1888
- 8a. 7-8 long rays in the lower portion of the pectoral fin; 9 pelvic fin rays *B. (Bathypterois) phenax* Parr, 1928
- 8b. 7-8 long rays in the lower portion of the pectoral fin; 8 pelvic fin rays *B. (Bathypterois) mediterraneus* Bauchot, 1962
- 9a. Lowermost pectoral fin ray thicker and longer than that above it; 6 lateral-line pores along the ventral surface of the dentary; always 9 pelvic fin rays *B. (Bathypterois) quadrifilis* Günther, 1878

- 9b. Lowermost pectoral fin ray equal in thickness and length to that above it; 7-9 dentary lateral-line pores; 8 or 9 pelvic fin rays *B. (Bathypterois) pectinatus* Mead, 1959
- 10a. Color under preservation whitish below, darker above; base of each caudal lobe with a dark spot; basibranchial 3-4 with dentigerous dermal plates; pectoral fin rays 5, 6, and 7 never rudimentary; 8-10 long rays in the lower portion of the pectoral fin
..... *B. (Bathycygnus) bigelowi* Mead, 1959
- 10b. Color under preservation uniform green to black; basibranchial 3-4 without dentigerous dermal plates; pectoral fin ray 5 very reduced, fin rays 6 and 7 rudimentary and embedded 11
- 11a. Color green or brown; scales adherent in well-preserved specimens; 11-14 long rays in the lower portion of the pectoral fin; 8 pelvic fin rays
..... *B. (Bathycygnus) filiferus* Gilchrist, 1908
- 11b. Color brown to black; scales deciduous 12
- 12a. 12-14 long rays in the lower portion of the pectoral fin; 9 pelvic fin rays
..... *B. (Bathycygnus) insularum* Alcock, 1892
- 12b. 9-11 long rays in the lower portion of the pectoral fin; 1-3 rudimentary rays in the middle of the pectoral fin; 8 or 9 pelvic fin rays; dentary lateral-line pores smaller than eye; HL equals 21-26% SL; predorsal length equals 42-47% SL
..... *B. (Bathycygnus) longipes* Günther, 1878
- 12c. 8-10 long rays in the lower portion of the pectoral fin; 4 rudimentary rays in the middle of the pectoral fin; always 8 pelvic fin rays; dentary lateral-line pores larger than eye; HL equals 25-29% SL; predorsal length equals 46-51% SL; 54-56 lateral-line scales; 53-55 vertebrae; longest produced caudal ray equals 25-39% SL; body emaciated in appearance
..... *B. (Bathycygnus) longicauda* Günther, 1878
- 12d. 8 long rays in the lower portion of the pectoral fin; 8 pelvic fin rays; 60-62 lateral-line scales; 57-58 vertebrae; longest produced caudal ray equals 38-46% SL; body robust in appearance
..... *B. (Bathycygnus) oddi* n. sp.

Subgenus *Benthosaurus* Goode & Bean, 1886

Skagerakia Nybelin, 1947; type by monotypy or by original designation, *Skagerakia nilssoni* Nybelin, 1947 (= *Benthosaurus grillator* Goode & Bean, 1886).

Hemipterois Regan, 1911; type by original designation, *Bathypterois guentheri* Alcock, 1889.

Belonepterois Roule, 1916; type by original designation, *Belonepterois viridensis* Roule, 1916.

Type species: *Bathypterois (Benthosaurus) grillator* (Goode & Bean, 1886), type by monotypy.

Diagnostic characters: Those given in step 1a of the key above.

Remarks: The subgenus comprises three species: *Bathypterois grillator*, *B. guentheri*, and *B. viridensis*. *B. grillator* was formerly placed in a separate monotypic genus, *Benthosaurus*, differentiated from the remaining species of *Bathypterois* as follows (Mead 1966c): "Pectoral fin not divided into two parts and without greatly produced rays, none

extending beyond origin of anal fin; outer ventral and lower caudal rays longer than standard length; no adipose fin". However, while these characters are useful at the species level, they are somewhat arbitrarily applied in differentiating *B. grillator* from the other species of *Bathypterois* at a generic level.

The divided appearance of the pectoral fin in species of *Bathypterois* is due to the presence of rudimentary rays in the middle of the fin. However, while the pectoral fin appears to be divided in all species of the genus except *B. grillator*, the point of division differs in different species. In fact, a complete spectrum of variation is evident in development and configuration of the pectoral fin rays. Commonly, division of the fin is rather marked (Fig. 15a) since rays 3 and 4 of the upper portion of the fin are greatly produced and followed by a very short ray 5 and three to four rudimentary rays (rays 6 through 8-9), in turn followed by seven to fourteen long rays in the lower portion of the fin. But in some of these species only one or two embedded rudimentary rays (rays 6 or 6 and 7) separate the

upper and lower portions of the fin (Fig. 14b). In the basal species, *B. bigelowi*, division of the pectoral fin occurs lower in the fin (Fig. 15a). Here ray 5 is not reduced, but is quite long, while rays 6 and 7 are not rudimentary, but moderate in length. Instead, rays 8-9 through 10 are rudimentary and are followed by only eight or nine long rays in the lower pectoral. Division of the pectoral occurs at a lower point in the fin and is even less marked in *B. viridensis* (Fig. 15b). In this species the produced upper rays are variably developed, often being only slightly elongated beyond adjacent lower rays. Below the two produced rays (rays 3 and 4), rays 5 through 10-11 gradually decrease in length with only a single element (ray 11 or 12) being rudimentary. Below this only five long rays are present. Finally, in *B. grallator*, a division of the pectoral is no longer evident (Fig. 15c). However, arrangement of the fin rays is very similar to that in *B. viridensis*, except that no long lower pectoral rays remain. In *B. grallator* also, rays 3 and 4 are rarely produced beyond the adjacent lower rays. Instead rays 3 through 10-12 form a continuous series of gradually shorter rays, terminating in one to three (rays 11-13) rudimentary rays. What remains of the lower pectoral is occasionally present as one or two very short rays below these rudimentary rays. In view of the particular closeness of *B. grallator* and *B. viridensis* with regard to pectoral configuration, and of the fact that the configuration in *B. grallator* merely represents a variation on the basic *Bathypterois* theme, the segregation of *B. grallator* from the other species of *Bathypterois* is unwarranted.

Much the same can be said concerning a differentiation of *B. grallator* based on length of the produced pelvic and caudal fin rays, and on the absence of the adipose fin. Elongation of the outer pelvic and usually the lower caudal fin rays is a characteristic of all species of *Bathypterois*. *B. grallator* merely exhibits the extreme in this respect, commonly having these rays produced in excess of 100% SL. However, the closely related *B. viridensis* approaches *B. grallator* in this character, having the produced caudal ray(s) as long as 80% SL and the produced pelvic rays as long as 91% SL. And in turn several species approach or overlap *B. viridensis* in extent of fin ray elongation. The length of the produced caudal and pelvic fin rays is sometimes a useful specific character, but is a poor generic determinant. Likewise the absence of the adipose fin in *B. grallator* can be viewed with little significance beyond the species level. The adipose fin is clearly on

its way out at this level of chlorophthalmid evolution (e.g., it is absent in *Ipnops* and the Bathymicropini). While it is present in all species of *Bathypterois* except *B. grallator*, it is always very small and in some species (e.g., *B. longicauda*) minute.

B. grallator, *B. guentheri*, and *B. viridensis* share many characters. Together they make up the most distinctive subunit of the genus. With respect to the remaining species of the genus this group shows the greatest attenuation of the hyomandibular and the opercle. The elongate opercle is rotated to a position above the hyomandibular, a configuration paralleling that achieved in the Bathymicropini (above). Also unique to species of the subgenus *Benthosaurus* is the presence of a wide scaled gular fold and a second pelvic fin ray that is only half as long as and firmly adherent to the outer pelvic fin ray. Other distinctive features include a vomer with two large elliptical tooth patches (as in *Bathysauropsis*) and the presence of ossified dermal tooth plates on the third and fourth basibranchials. Species of the subgenus also have fewer gill rakers than other species of *Bathypterois*, although the discontinuity here is not striking (34-37 rakers on the anterior arch in *Benthosaurus* vs. 38-49 in species of the other two subgenera).

Bathypterois (Benthosaurus) grallator

(Goode & Bean, 1886)

(Figs 12a, 15c, 16a, 19, 20a-c; Pl. 5 Fig. 1)

Benthosaurus grallator Goode & Bean, 1886; type localities: 39°03.25'N, 70°50.75'W, 2811 m, "Albatross" St. 2222; 24°33'N, 84°23'W, 3383 m, "Blake" St. 31, 1887 or 1888.

Skagerakia nilssoni Nybelin, 1947; type locality: 35°43'N, 08°16'W, 2300 m, "Skagerak".

Benthosaurus amblyops Bernard, 1958; type locality: Mediterranean Sea, off Toulon, 9 mi south of Cape Sicié, 2290 m, FNRS Bathyscaphe "Trieste".

Material:

2 syntypes (SL 240-275 mm); MCZ (1), USNM (1).

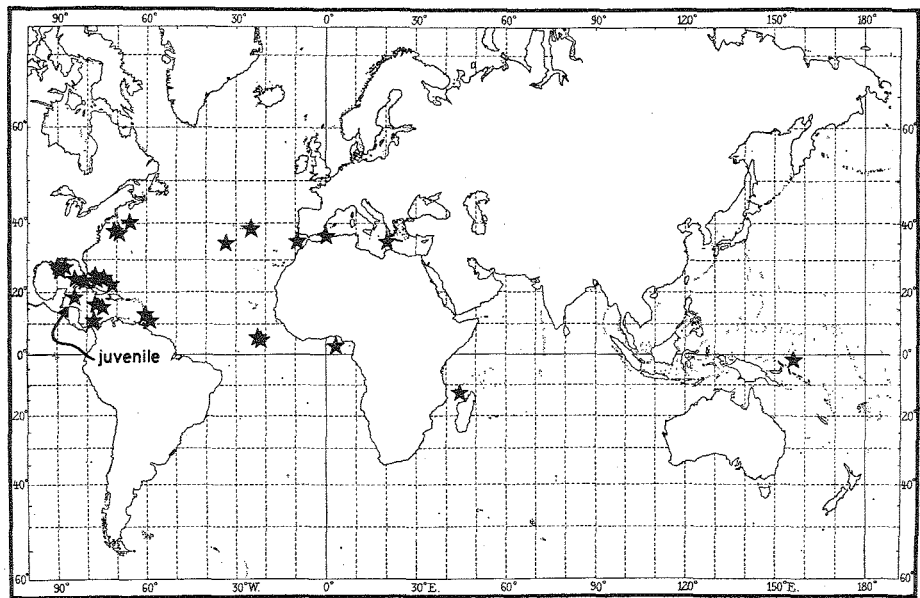
10 specimens (SL 85-268 mm); UMML.

1 juvenile specimen (SL 43 mm); UMML.

Description:

Counts. Dorsal rays 12-13; anal rays 12-13; pelvic rays 8; pectoral rays 7-10 visible externally, 13-15

Fig. 19. The known distribution of *B. grallator*.



total, formulae¹: (ii)7(ii)ii, (ii)8(ii)i, (ii)9(iii)i, or (ii)10(i-ii); caudal rays (dorsal + ventral) vi-vii 10+9 iv-v; gill rakers (anterior arch) 9-10+1+24-26; branchiostegal rays 12; lateral-line scales 58-60; dentary lateral-line pores 7-8, small; vertebrae (incl. urostyle) 53-54; dorsal-fin origin over vertebra 21-23; anal-fin origin under vertebra 28-30.

Morphometry (values in % SL). HL 23.9-29.9; predorsal length 46.0-48.2; preanal length 50.4-57.8; prepelvic length 35.4-41.2; length of produced pelvic ray 104-144; length of produced caudal ray 97-134; length of longest upper pectoral ray 35.5-36.9.

Dentition. A broad band of small conical teeth on the dentary and the maxilla; vomer with two large elliptical patches of similar teeth; palatine untoothed; endopterygoid and ectopterygoid untoothed (except rarely in the latter); upper pharyngeals (epibranchials 3 and 4, pharyngobranchials 3 and 4) and lower pharyngeal (ceratobranchial 5) toothed, basibranchial cartilages 3 and 4 with dentigerous dermal plates (cf. Fig. 28).

Color. Head and body entirely black; scale pockets outlined in white; lateral-line pores white.

Size. SL range of known adult specimens is 71-368 mm.

Distinctive characters: Pelvic and caudal fins with produced rays commonly equal to or exceeding

1. *Bathypterois* pectoral formulae are to be interpreted as follows: I = a stiffened produced ray, l = a long normal ray, i = a very short ray, (i) = an embedded rudimentary ray.

SL; pectoral fin with a characteristic configuration of fin rays (above), without two especially produced rays; no adipose fin; no teeth on the palatines; SL commonly exceeding 200 mm, often exceeding 300 mm; maxilla squared off abruptly posteriorly (Fig. 13a), only slightly longer than the premaxilla.

Distribution: *B. grallator* is extremely eurybathic, known from depths of 878-3492 m. Adults are benthic in habit, but the single known juvenile was taken in a midwater trawl (IKMT) working from the surface to 3000 m, over 4407 m bottom depth. No more than four adults have ever been taken in a single bottom trawl. Its much larger size, and hence greater food requirements compared to other species of *Bathypterois*, make it probable that *B. grallator* is generally less abundant than its smaller congeners. A temperature range of 2.7°C to 4.5°C has been reported for *B. grallator* from four localities with depths of 1860-2865 m. However, photographic records of the species at 2132-4720 m in the Mediterranean extend its temperature tolerance to at least 13.5°C.

B. grallator has been obtained at numerous localities in the Atlantic, from a single locality in the Indian Ocean ("Galathea" St. 217), and from a single western Pacific locality ("Hakuho-Maru" St. 67-5-19). The species has also been recorded in the Mediterranean by submersible photographs (Mac Leish 1954, Edgerton 1955, Houot & Willm 1955, Piccard 1968). Given the dearth of deep-sea bottom trawls in the Indian and Pacific Oceans, it seems probable that *B. grallator* is somewhat more com-

mon in these regions than the few available records suggest. It appears to be circumglobal in distribution (Fig. 19), but may be absent from the eastern Pacific.

Development: Okiyama (1973) presented a figure and brief description of a juvenile fish referable to *Bathypterois*. Aside from this single specimen, no other juveniles of *Bathypterois* have ever been described, although several juveniles of the related genus *Bathytrophops* have been reported (Berry & Robins 1967, Okiyama 1972). A juvenile fish attributed to *Bathypterois* by Roule & Angel (1921) probably pertains to the young stage of a stomiatoid species (Mead 1966c).

A 43 mm SL juvenile of *B. grallator* from the UMML collection has been studied, radiographed (Pl. 5 Fig. 1), and cleared and stained with alizarin. The skeleton was incompletely ossified and became partially disarticulated during staining. It remained sufficiently intact to permit camera lucida drawings

to be made of the caudal and pectoral fins and the lateral skull bones (Fig. 20a-c). In overall appearance this juvenile of *B. grallator* is very similar to that of *Bathytrophops* ("*Macristiella*") as figured by Okiyama (1972). It agrees closely in meristic and morphometric values (Table 3) and in other details with the adult of *B. grallator*. These include a pectoral fin having the two uppermost rays already reduced (rudimentary in the adult) and set closely together (Fig. 20a), a pelvic fin having the outer fin ray already approximately twice as thick as the remaining rays, and a caudal having the lower hypurals shifted forward (as in the adult, Fig. 16a) with respect to the upper hypurals (Fig. 20b). An anal papilla is also present as in the adult; the vent is placed near the origin of the anal fin; the gill rakers are of the usual blade-like form. However, the juvenile differs from its adult counterpart in several details attributable to its stage of development and the phylogenetic history of the genus. The young of *B. grallator* has a relatively large eye, a short upper

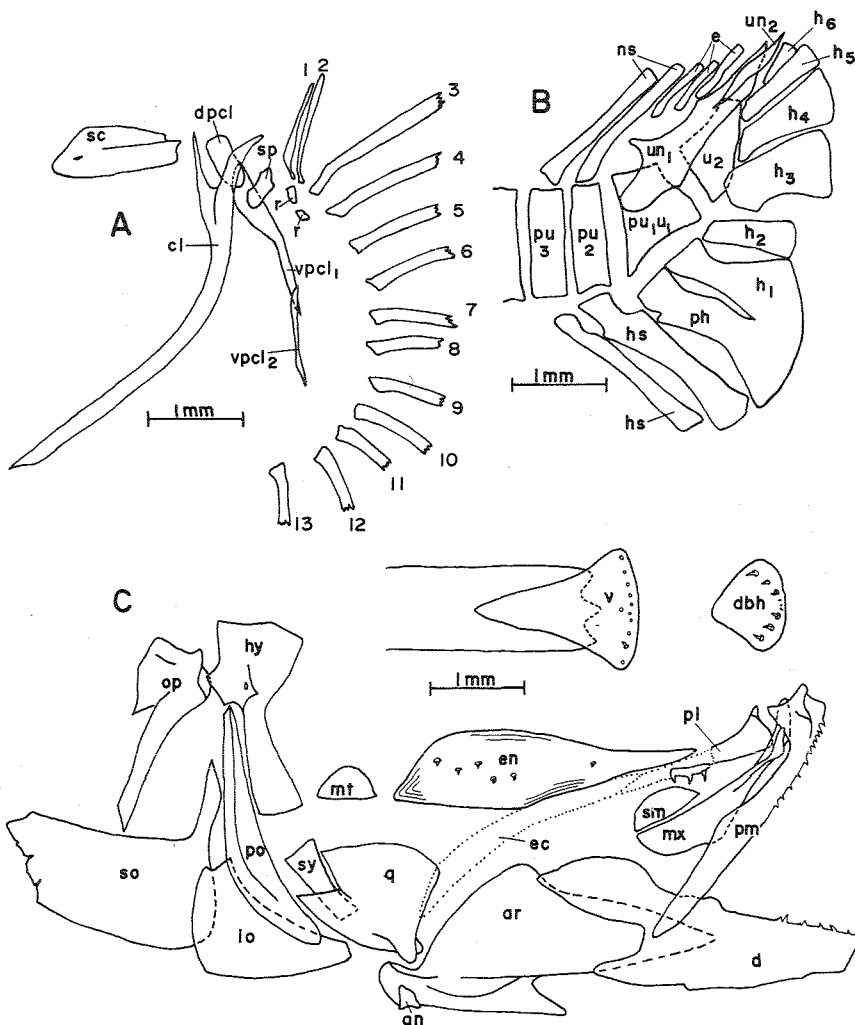


Fig. 20. Osteology of a juvenile (SL 43 mm) of *B. grallator*, UMML 24437. A, pectoral fin; B, caudal skeleton; C, lateral facing bones of the skull (ectopterygoid and portion of the palatine hypothetical).

Table 3. A comparison of the juvenile and the adult of *Bathypterois grillator* and *Bathytyphlops marionae*.

Character	<i>Bathypterois</i> juvenile	<i>grillator</i> adult	<i>Bathytyphlops</i> juvenile ¹	<i>marionae</i> adult
dorsal fin rays	13	12-13	12-13	12-13
anal fin rays	13	12-13	12-15	13-14
pelvic fin rays	8	8	8	8
pectoral fin rays ²	13	13-15	13-15	15-16
caudal procurent rays (dorsal + ventral)	6+4	6-7+4-5	1-6+2-5	6+5
branchiostegal rays	13	12	10-17	15-17
gill rakers (anterior arch) ³	8+1+21	9-10+1+24-26	7-8+0-1+13-16	7+1+13
vertebrae (incl. urostyle)	53	53-54	62-69	64-66
vertebra under dorsal-fin origin	22	21-23	20	20-22
vertebra over anal-fin origin	28	28-30	...	43-45
predorsal length (in % SL)	51.2	46.0-48.2	36.9-44.5	38.5
preanal length (in % SL)	60.5	50.2-57.8	64.9-69.3	68.9
prepelvic length (in % SL)	39.5	35.4-41.2	35.6-40.9	36.1
HL (in % SL)	18.6	23.9-29.9	21.0-25.6	21.6
eye diameter (in % SL)	4.0	1.0	3.3-5.1	1.0
pseudobranch	present	absent	present	absent
adipose fin	present	absent	present	absent
dorsal postcleithrum	present	absent	?	present
ventral postcleithra	unfused	fused	unfused	fused

1. Data from Okiyama (1972), based on the five known specimens (SL 13-39 mm) of juvenile *Bathytyphlops* (= "*Macristiella*").

2. Pectoral ray count includes rudimentary rays.

3. Gill raker count = rakers of the upper limb + rakers at the angle + rakers of the lower limb.

jaw and gape, an unattenuated and unrotated hyomandibular, a broad dentigerous endopterygoid, three unfused postcleithra, and a pseudobranch. In these details it approaches the condition of adults of *Chlorophthalmus* and *Aulopus*. A close affinity with the "*Macristiella*" juvenile of *Bathytyphlops* is also evident (Table 3). In turn, the juveniles of both *Bathypterois* and *Bathytyphlops* show an affinity with that of *Chlorophthalmus* (see Rosen 1971). Particularly instructive in this regard is the common presence in these three chlorophthalmid genera of a peculiar type of juvenile dentition on the vomer and dermal basihyal. The two bones oppose each other and each is provided with a single row of strong teeth along the anterior margin (Fig. 20c). This condition appears to be unique to the juvenile stages of basal myctophiform fishes (Rosen 1971). The endopterygoid, dermal basihyal, and palatine teeth of the juvenile of *B. grillator* are lost in the adult. The row of large vomerine teeth is replaced by two separated patches of small teeth. The adipose fin and pseudobranch of the juvenile are also lost in the adult.

Bathypterois (Benthosaurus) viridensis
(Roule, 1916)

(Figs 12b, 15b, 16b, 21; Pls 4 Fig. 2,
5 Fig. 2, 7 Fig. 1)

Belonepterois viridensis Roule, 1916; type locality:
16°34'N, 23°03.25'W, 1477 m, "Princesse Alice"
St. 1209.

Bathypterois (Hemipterois) viridensis, Parr 1928,
Mead 1966c.

Bathypterois (Hemipterois) nigrescens Parr, 1934;
type locality: 25°39'N, 77°18'W, 1050-1100 m,
"Atlantis" St. 1478.

Bathypterois viridensis, Fowler 1944.

Material:

20 specimens (SL 71-187 mm); UMML (18), VIMS
(2).

Description:

Counts. Dorsal rays 12-13; anal rays 10-12; pelvic rays 8; pectoral rays 12-13 visible externally, 15-17 total, formulae: (ii)7(i)5 or rarely (ii)7(i)6; caudal rays (dorsal + ventral) v-vi 10+9 iii-iv; gill rakers

(anterior arch) 11+1+27-28; branchiostegal rays 12-13; lateral-line scales 51-56; dentary lateral-line pores 7-8, small; vertebrae (incl. urostyle) 50-52; dorsal-fin origin over vertebra 21-22; anal-fin origin under vertebra 28-29.

Morphometry (values in % SL). HL 24.2-28.0; predorsal length 44.5-47.9; preanal length 56.0-58.4; prepelvic length 38.0-46.1; length of produced pelvic ray 57.6-90.6; length of produced caudal ray 38.3-80.0; length of longest upper pectoral ray 28.2-78.1.

Dentition. As in *B. grallator* except for the palatine, which bears a few small teeth, and the ectopterygoid, which is always untoothed.

Color. In young specimens (subadults, SL less than 75-80 mm) the head and body are uniformly black with the scale pockets outlined in white. In larger preserved specimens the background color of the body is largely white, but interrupted by three dark brown to black bands (Pl. 5 Fig. 2). The first of these begins behind the gill cover and ends just in advance of the dorsal and pelvic fin origins. A small dark area just behind the pelvic fins is sometimes continuous with this first dark band. A second dark band occupies the middle of the body, beginning just under or at the end of the dorsal fin and ending ahead of the adipose fin. The first and second dark bands are connected by a narrow horizontal stripe lying midway between the lateral line and the dorsal-fin base, and by another stripe along the base of the dorsal fin. A third dark band begins at the caudal peduncle and extends onto the caudal-fin base. The remainder of the caudal fin is also dark in well-preserved specimens. The other fins are commonly transparent with traces of black. The head is pale above, darker below and laterally. The cheek is bluish-white with scattered dark specks. The gill cover and branchiostegal membrane are black. On the white areas of the body each scale pocket bears a central brown pigment spot, a vertical row of spots, numerous pigment specks, or a vertical pigment bar. A submersible photograph (Church 1971) of a live specimen of *B. viridensis* reveals that the darkly pigmented areas of the body are more extensive in life. Nevertheless, the basic color pattern is the same as described above. Differences in the degree of pigmentation of live versus freshly trawled (Mead 1966c) or preserved specimens are probably due to abrasion and stress-induced melanophore contraction during trawling.

Size. The numerous available specimens range in SL from 61 mm to 222 mm.

Distinctive characters: Among species of the genus only *B. viridensis* and its closely related counterpart *B. guentheri* display color patterns consisting of alternating light and dark bands along the body. But the relative positions of the dark bands differ in the two species. *B. viridensis* has three dark bands, the white area between the first and second of these underlying the dorsal fin (Pl. 5 Fig. 2). In *B. guentheri* there are also three dark bands, but the second of these underlies the dorsal fin (Pl. 5 Fig. 3). *B. viridensis* also differs from *B. guentheri* in having only seven (vs. eight in *B. guentheri*) fin rays above the midpectoral rudimentary ray (Fig. 15b).

As discussed above several rather distinctive characters unite *B. viridensis*, *B. grallator*, and *B. guentheri* in opposition to the other members of the genus.

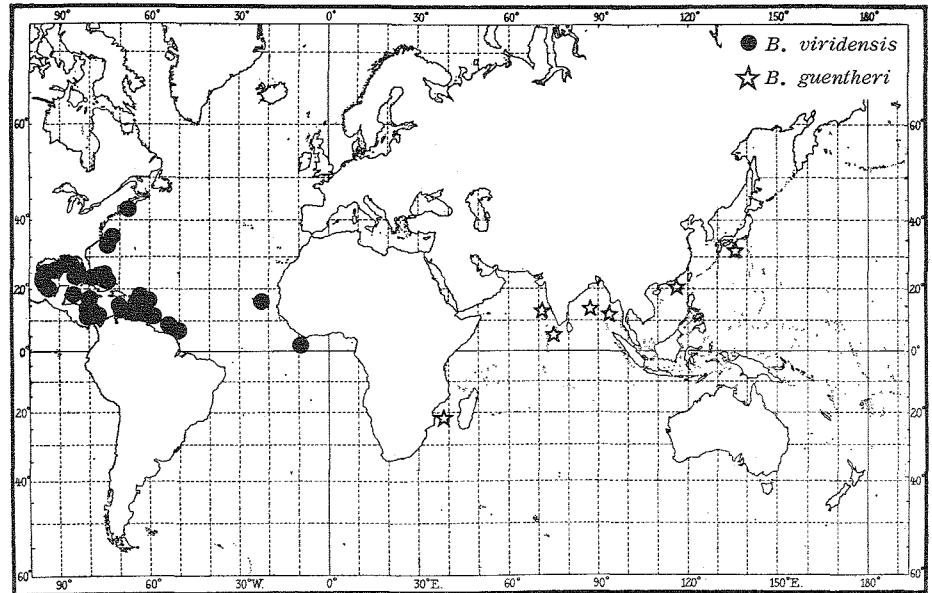
Distribution: Recorded at depths of 476-1477 m. Most captures of the species have been of single specimens; however, as many as 24 individuals have been taken in a single trawl. Bottom temperatures for 14 localities range between 6.0°C and 11.1°C. Bullis & Rivas (1972) report a temperature range of 5.6°C to 7.8°C in the Gulf of Mexico and the Caribbean.

B. viridensis is reported from numerous Atlantic localities between 04°N and 44°N (Fig. 21) but not from the South Atlantic or the Mediterranean, although it seems probable that this eurybathic species ranges into both areas.

Remarks: Some differences are apparent between the type as described by Roule (1916, 1919) and the 19 eastern and western Atlantic specimens examined herein. Roule's caudal-ray count of 18 is almost certainly incorrect, since 19 principal rays are present not only in the specimens of *B. viridensis*, but in all specimens of *Bathypterois* examined. The upper pectoral and anal-fin counts, respectively 6 and 9, given by Roule may also be erroneous. In 59 specimens of *B. viridensis* examined with respect to pectoral-ray configuration, the number of upper pectoral rays counted was invariably 7. The number of anal rays for 19 specimens ranged between 10 and 12. Roule's pelvic-ray count of 7 (vs. 8 typically) may be explained by the fact that the second pelvic ray is difficult to detect, being reduced in length and thickness, and adhering closely to the thickened outer ray.

Mead (1966c) tentatively equated *B. nigrescens*

Fig. 21. The known distributions of *B. viridensis* and *B. guentheri*.



Parr, 1934, with *B. viridensis*, noting that Parr's type was perhaps a teratological specimen with an abnormally shortened vertebral column. This would explain the morphometric differences between *B. nigrescens* and *B. viridensis* detailed by Mead. It seems likely, however, that these morphometric disparities are merely due to the stage of development of Parr's specimen, this specimen being undoubtedly a subadult, as is evident from its small size (SL 61 mm) and its dark color (Parr 1934). Several small specimens (SL 65-80 mm) have been obtained by the R/V "Columbus Iselin" in the Tongue-of-the-Ocean. These subadults of the species agree with Parr's specimen in having a uniform black color and exhibiting some morphometric differences with respect to larger specimens.

Bathypterois (Benthosaurus) guentheri

Alcock, 1889

(Fig. 21; Pl. 5 Fig. 3)

Bathypterois guentheri Alcock, 1889, 1899; type locality: Indian Ocean, 7.5 mi east of North Cinque Island, "Investigator" St. 10.

— (*Synapteretmus guentheri*, Goode & Bean 1896.

Hemipterois guentheri, Regan 1911.

Belonepterois guentheri, Roule 1919.

Bathypterois (Hemipterois) guentheri, Parr 1928, Mead 1966c.

Material:

1 specimen (SL 121 mm); USNM.

Description:

Counts. Dorsal rays 13; anal rays 11; pelvic rays 8; pectoral rays 13 visible externally, 15-16 total, formula: (ii)8(i)5; caudal rays (dorsal + ventral) v 10+9 iii; gill rakers (anterior arch) 11+1+27; branchiostegal rays 11-13; lateral-line scales ca. 48-50; dentary lateral-line pores 7-8, moderate in size; vertebrae (incl. urostyle) 50; dorsal-fin origin over vertebra 22; anal-fin origin under vertebra 28.

Morphometry (values in % SL). HL 26.0; pre-dorsal length 46.4; preanal length 56.2; prepelvic length 40.7; length of produced pelvic ray 75.5; length of produced caudal ray 53.6 (incomplete); length of longest upper pectoral ray 41.5.

Dentition. As in *B. viridensis*.

Color. The few known specimens are all large adults. The coloration is basically comparable to that of *B. viridensis*, but the position of the dark bands is different. Anteriorly, the dark pigmentation of the head continues onto the body to a point just behind the pectoral fin. A second dark band lies between the dorsal and pelvic fins. A third dark body band begins in advance of the caudal peduncle, but extends only a short distance onto the base of the caudal fin. The remainder of the caudal fin is white (brown to black in *B. viridensis*). According to Alcock (1889, 1899) the fins, except for the caudal, are covered with a deciduous velvety-black integument. By way of comparison, the "Deepstar" photograph (Church 1971) of *B. viridensis* shows the fins to be black, including the caudal, except for the dorsal fin which is colorless. The head of *B.*

guentheri is dark ventrally, paler dorsally. The gill cover and branchiostegal membrane are black. As in *B. viridensis* each scale pocket in white areas of the body bears dark pigment specks of variable shape and size.

Size. SL range of the few recorded specimens is 121 mm to ca. 180 mm.

Distinctive characters: The single dark band underlying the dorsal, the black dorsal fin, and the white caudal fin are characteristic details. The pectoral formula, (ii)8(i)5, is unique, although close to that of *B. viridensis*. In other characters it agrees exactly with *B. viridensis*.

Distribution: Known from five Indian Ocean localities and two sites in the West Pacific (Fig. 21). Depth range for the seven localities is 720-1163 m; temperature range for three localities is 4.3-7.2°C. The species has been obtained on gray, green, and brownish-green mud, and on fine coral sand.

Remarks: Alcock did not specify a type specimen in his original description (1889) or in a subsequent account (1899). However, of the four »Investigator« localities at which the species was obtained, only one, »Investigator« St. 10, predates Alcock's original description. The single specimen obtained at St. 10, IMC 11770, is herein designated the lectotype of *B. guentheri*.

Subgenus *Bathypterois* Günther, 1878

Synapteretmus (partim) Goode & Bean, 1896; type by subsequent designation (Jordan & Evermann 1896), *B. quadrifilis* Günther, 1878.

Type species: *Bathypterois longifilis* Günther, 1878; type by subsequent designation (Jordan & Evermann 1896).

Diagnostic characters: Those given in steps 1b and 4a of the key (p. 75).

Remarks: The type species, *B. longifilis*, has a subcaudal notch. Eight more species also have a subcaudal notch, the exact function of which is unknown. Together the nine species form a natural subunit of the genus, the subgenus *Bathypterois*. Other species formerly included in the subgenus lack a subcaudal notch and are herein placed in a new subgenus (below).

The subcaudal notch forms as a gap between two of the ventral procurent rays. In basal members of the subgenus (e.g., *B. longifilis*, *B. perceptor*, and *B. ventralis*) the notch is very simple, the two procurent rays being but slightly curved and never hooked (Fig. 22a-c). In intermediate species (e.g., *B. dubius* and *B. atricolor*) the anterior procurent ray of the notch is usually curved upward or hooked terminally (Fig. 22d, e), while the posterior element is bent medially and swollen distally. In advanced species (e.g., *B. quadrifilis* and *B. phenax*) the anterior procurent ray is always strongly hooked terminally (Fig. 22f, g). Thus a trend toward more elaborate development of the subcaudal notch is apparent in species of the subgenus.

Concurrently, a trend toward reduction in the number of pectoral fin rays is also apparent. More primitive species have nearly as many pectoral fin rays as *Bathysauropsis* (22-24). Thus *B. longifilis* has 20-21, *B. ventralis* 19-21, and *B. perceptor* 19. The intermediate level species, *B. dubius* and *B. atricolor*, have 18-19 and 16-18 total pectoral fin rays, respectively. Advanced species have the fewest pectoral fin rays: *B. phenax* has 15-16, *B. mediterraneus* and *B. quadrifilis* 15-17. Reduction in pectoral fin ray number usually results from loss of long rays from the lower portion of the fin. A similar trend is evident in the other two subgenera of the genus.

Bathypterois (Bathypterois) longifilis

Günther, 1878

(Figs 22a, 23)

Bathypterois longifilis Günther, 1878, 1887; type localities: ca. 30°00'S, 178°15'W, 951 m, »Challenger« St. 170; ca. 29°40'S, 178°05'W, 1152 m, »Challenger« St. 170a.

– (*Bathypterois*) *longifilis*, Goode & Bean 1896, Parr 1928.

Material:

1 syntype (SL 278 mm); BM.

Description:

Counts. Dorsal rays 13; anal rays 9; pelvic rays 8 or 9; pectoral rays 16-17 visible externally, 20-21 total, formula: (ii)III(ii)12-13; caudal rays (dorsal + ventral) v 10+9 iv; gill rakers (anterior arch) 12+1+27-28; branchiostegal rays 11-12; lateral-line scales 58-62; dentary lateral-line pores 6, moderate in size; vertebrae (incl. uro-

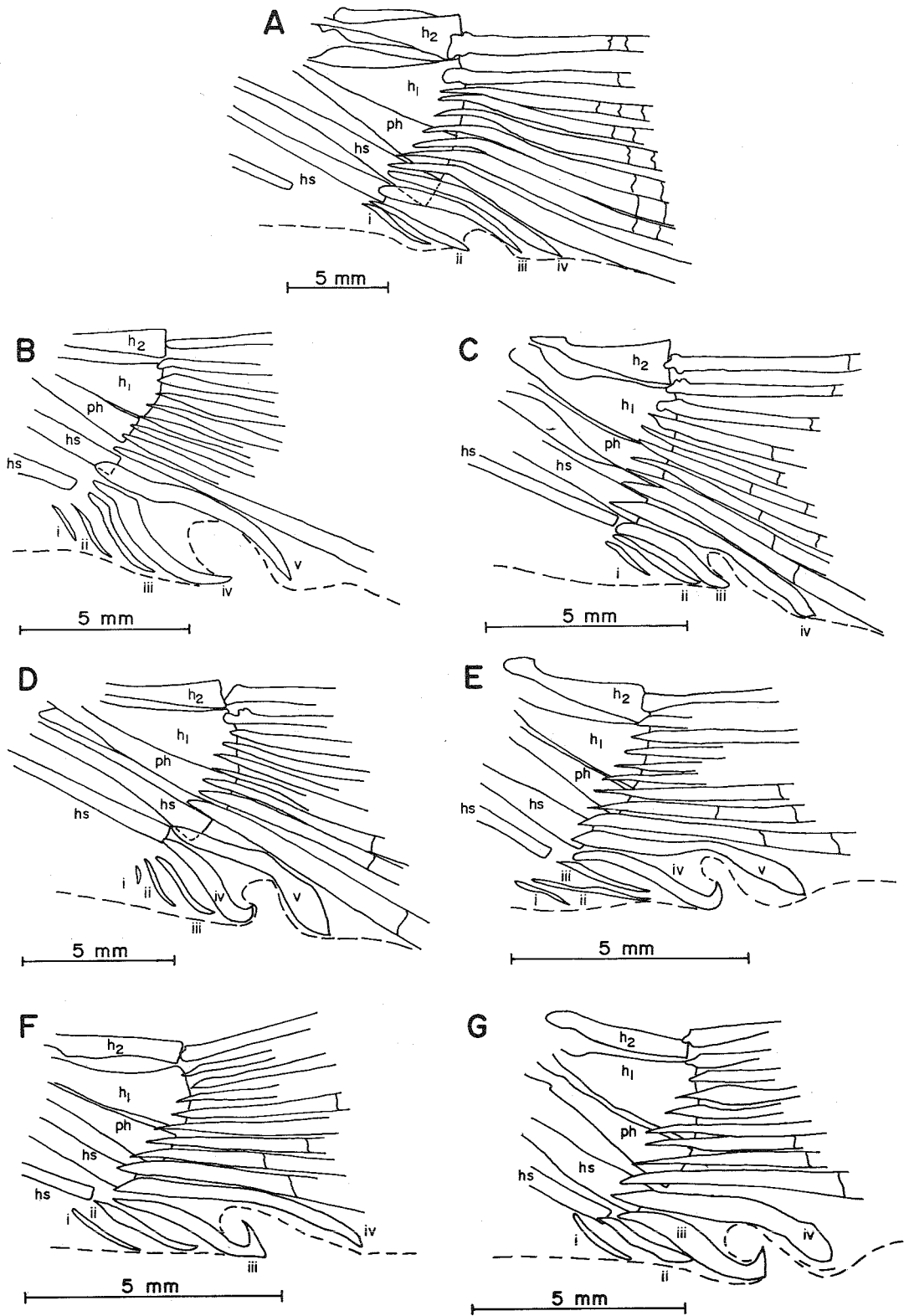


Fig. 22. A comparison of the subcaudal notches. A, *B. longifilis*, BM 1887.12.7. 194.5; B, *B. perceptor*, ISH 2006/68; C, *B. ventralis*, ZMUC, "Galathea" St. 739; D, *B. dubius*, ZMUC, "Thor" St. 75; E, *B. atricolor*, UMML 21676; F, *B. quadrifilis*, UMML 22571; G, *B. phenax*, UMML 30837.

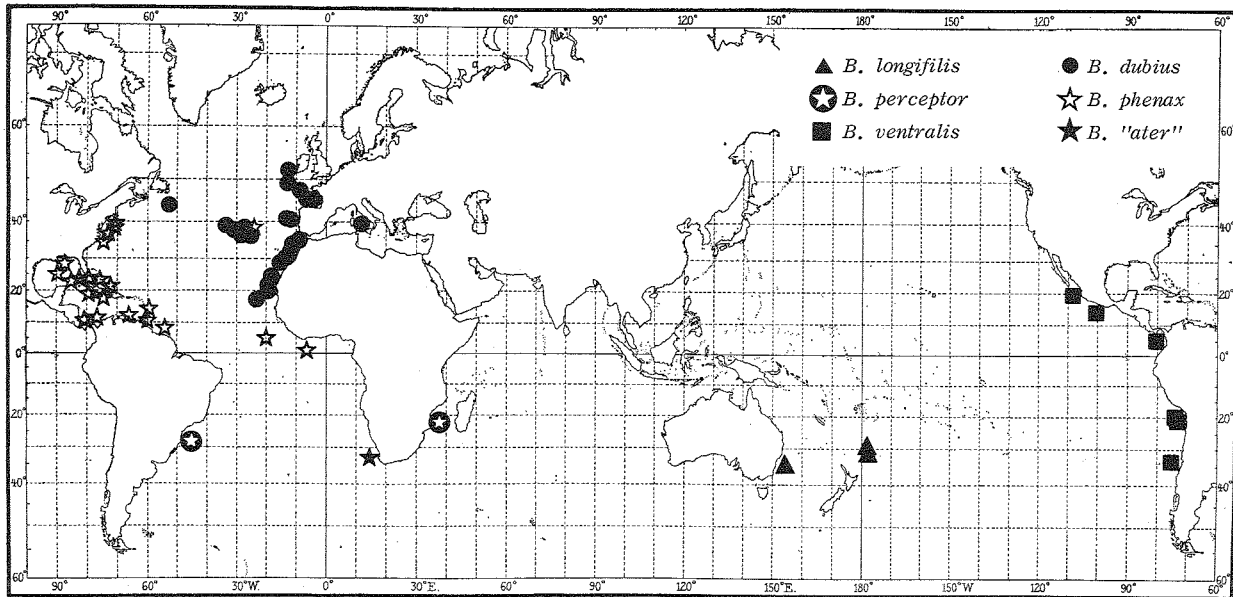


Fig. 23. The known distributions of *B. longifilis*, *B. perceptor*, *B. ventralis*, *B. dubius*, *B. phenax*, and *B. "ater"*.

style) 58; dorsal-fin origin over vertebra 24, anal-fin origin under vertebra 36.

Morphometry (values in % SL). HL 24.8-25.6; predorsal length 46.1; preanal length 64.0; pre-pelvic length 39.6; length of longest produced pelvic ray 31.8-34.2; length of longest lower caudal ray 14-18 (incomplete in both syntypes); length of longest produced pectoral ray 84.5 (incomplete).

Dentition. The usual bands of small cardiform teeth present on the premaxilla and the dentary; vomer with two elliptical tooth patches, each with numerous small teeth; pterygoid series bones untoothed; palatine with a few small teeth; a tooth patch present on pharyngobranchial 2, in addition to those normally present on the pharyngeals (pharyngobranchials 3 and 4, epibranchials 3 and 4, ceratobranchial 5) of *Bathypterois* (see Fig. 28); basibranchial 3-4 untoothed.

Color. The single specimen examined has apparently lost much of its original color during its 100 years of preservation in ethanol. Günther (1887) provides the following color notes: »Colour light greenish with narrow black margins to the scales; sides of the head, the abdomen, and the buccal and abdominal cavities black. Vertical and ventral fins black, with lighter margins; pectoral fins without colour«.

Size. SL of the two specimens, 278 and 270 mm.

Distinctive characters: The large tooth patch on pharyngobranchial 2 is a feature unique to *B.*

longifilis among species of the genus. Within the subgenus *Bathypterois*, *B. longifilis* is distinctive in having a green coloration and very large adherent scales (smaller and deciduous in the other species), and in achieving a very large size (270-278 mm SL). It is also unique in having the fifth pectoral ray long and well-developed. In the remaining species of the subgenus this ray, which lies immediately below the two produced rays of the upper part of the pectoral fin, is very short and weak. Otherwise, the pectoral fin configuration of *B. longifilis* is very similar (formula = (ii)IIIi(ii)12-13) to those of *B. ventralis* (formula = (ii)IIi(ii)12-14) and *B. perceptor* (formula = (ii)IIi(i)13). However, these three species differ in other characters and are geographically distinct as well.

Distribution: The two »Challenger« specimens were obtained in the western South Pacific (Fig. 23) at 951 and 1152 m, and 6.11°C and 4.17°C, respectively. John Paxton of the Australian Museum has recently reported (pers. comm.) additional specimens obtained at 777 m off Sydney, Australia.

Remarks: *B. longifilis* is the most primitive member of the subgenus. It has a very high number of pectoral rays and, despite its large size, a very small and simple subcaudal notch (Fig. 22a). In its un-reduced fifth pectoral fin ray, its large size, and most particularly its large elliptical vomerine tooth patches, it displays a closeness to species of the

subgenus *Benthosaurus*. On the other hand, an affinity with the subgenus *Bathycygnus* is evident in the close correspondence to *B. filiferus*, a basal species in *Bathycygnus*. Both are large species with adherent scales, a green coloration, and very similar pectoral fin formulae (in *B. longifilis* (ii)III(ii)12-13, in *B. filiferus* (ii)III(iii)12-13 typically).

***Bathypterois (Bathypterois) perceptor* n. sp.**

(Figs 22b, 23; Pl. 6 Fig. 1)

Material:

Holotype (SL 165 mm); ISH 2006/68; type locality: 28°34'S, 46°53'W, 1200 m, "Walther Herwig" St. 120/1968.

1 specimen (SL 160 mm); SOSC undesignated; 21°18'S, 36°18'E, 1510-1600 m, "Anton Bruun" St. 8-399B.

Diagnosis: A *Bathypterois* with a subcaudal notch, a white coloration, very short produced outer pelvic and lower caudal fin rays, a high vertebral number (59, total), and a pectoral formula of (ii)III(i)13.

Etymology: Specific name, *perceptor*, with reference to the sensory function of the specialized pectoral fin.

Description (holotype):

Counts. Dorsal rays 14; anal rays 9; pelvic rays 9; pectoral rays 15 visible externally, 19 total, formula: (ii)III(i)13; caudal rays (dorsal + ventral) v 10+9 v; gill rakers (anterior arch) 12+1+28; branchiostegal rays 13; lateral-line scales 61; dentary lateral-line pores 7, moderate in size; vertebrae (incl. urostyle) 59; dorsal-fin origin over vertebra 25; anal-fin origin under vertebra 35.

Morphometry (values in % SL). HL 19.4; predorsal length 42.4; preanal length 54.6; prepelvic length 36.4; length of longest produced pelvic ray 18.8; length of longest lower caudal ray 21.2; length of longest produced pectoral rays 93.4-100; depth at shoulder 12.7; depth at peduncle 7.8; preadipose length 77.6.

Dentition. Typical *Bathypterois* tooth bands present in each jaw; vomer untoothed; palatine with a few very small teeth; ectopterygoid with a row of minute teeth; upper and lower pharyngeals with the usual patches of teeth; dermal ossifications present but untoothed on basibranchial 3-4 cartilage.

Color. The body is a uniform silvery, pinkish-white. Each scale pocket is outlined in minute black specks. Additional pigment specks are present on the center of each scale pocket; they grow in size cephalad of the dorsal fin. The head is the same color as the body except for the eye, gill cover, and branchiostegal membrane - all of which are bluish-black to black.

Other features. Scales deciduous; produced rays of the pectoral fin united as far caudad as the adipose fin; gular area narrow and unscaled; gill rakers bladelike; subcaudal notch large but simple in design, the two procurrent rays smoothly and oppositely curved and without hooks or dilations distally (Fig. 22b).

Distinctive characters: The coloration of the new species is distinctive, since the remaining species of the subgenus are green or brown to black. Only *B. bigelowi* of the subgenus *Bathycygnus* approaches its nearly uniform pale coloration. The stiffened outer pelvic fin rays in the holotype are shorter than in any other species of the genus (Pl. 6 Fig. 1), but pelvic fin ray length is a highly variable character in most species of *Bathypterois*. Therefore, a differentiation of *B. perceptor* based on this character must be tentative until additional specimens become available. The new species also has a shorter head and upper jaw than any other species except for *B. pectinatus* and *B. quadrifilis*. Within the subgenus the new species and *B. longifilis* and *B. ventralis* all have a similar number (12-14) of long fin rays in the lower part of the pectoral fin. But *B. perceptor* is distinct in having only a single rudimentary ray in the middle of the pectoral fin; *B. longifilis* has two, *B. ventralis* has two or three. The three species differ as well in terms of development of the subcaudal notch. In the new species the notch is proportionately very wide and deep (Fig. 22b); the two procurrent rays involved are long and smoothly curved. In *B. longifilis* the notch is quite small, considering the large size of the species; the procurrent rays are only slightly curved (Fig. 22a). In *B. ventralis* both procurrent rays are nearly straight; the gap between them is shallow and small (Fig. 22c). A final character peculiar to *B. perceptor* among species of the subgenus is its minutely dentigerous ectopterygoid.

Additional record: Subsequent to determination of the new species based on the holotype, an additional specimen of *B. perceptor* was located at SOSC.

It agrees well with the holotype; counts and proportional measurements (in % SL) are as follows: Dorsal rays 14; anal rays 9; pelvic rays 8; pectoral rays (ii)III(0)14; lateral line scales 57; HL 19.4; predorsal length 43.2; preanal length 58.1; length of longest produced pelvic ray 23.8; length of longest lower caudal ray 16.9; length of longest produced pectoral ray 138.

Distribution: Known from the SW Atlantic at 1200 m depth and the Mozambique Channel in the SW Indian Ocean at 1510-1600 m (Fig. 23). Thus, it seems likely that *B. perceptor* is quite broadly distributed in the southern hemisphere. The two most closely related species, *B. longifilis* and *B. ventralis*, are known only from the southwestern and the eastern Pacific, respectively.

Bathypterois (Bathypterois) ventralis

Garman, 1899

(Figs 13a, 22c, 23)

Bathypterois ventralis Garman, 1899; type localities: 16°33'N, 99°51.5'W, 1207 m, "Albatross" St. 3418; 21°19'N, 106°24'W, 1244 m, "Albatross" St. 3425.

— (*Bathypterois atricolor ventralis*, Parr 1928.

Material:

9 syntypes (SL 85-126 mm); MCZ (8), USNM (1). 25 specimens (SL 92-150 mm); MCZ (1), SIO (11), ZMUC (13).

Description:

Counts. Dorsal rays 12-14; anal rays 9-10; pelvic rays 9 (rarely 10); pectoral rays 14-16 visible externally, 19-21 total, formula: (ii)III(ii-iii)12-14; caudal rays (dorsal + ventral) v-vi 10+9 iv-v; gill rakers (anterior arch) 12-14+1+30-32; branchiostegal rays 13; lateral-line scales 57-59; dentary lateral-line pores 7-9, moderate in size; vertebrae (incl. urostyle) 52-56; dorsal-fin origin over vertebra 21-23; anal-fin origin under vertebra 31-34.

Morphometry (values in % SL). HL 20.6-24.4; predorsal length 42.8-46.8; preanal length 54.2-62.9; prepelvic length 35.2-39.6; length of longest produced pelvic ray 39.1-59.4; length of longest lower caudal ray 32.7-44.6; length of longest produced pectoral ray 101-103.

Dentition. The usual tooth bands present on the dentary and the premaxilla; vomer toothed or un-

toothed; palatine with a few small teeth; ectopterygoid untoothed; tooth patches present on the upper and lower pharyngeals; dermal basibranchials 3 and 4 unossified and untoothed.

Color. Body a uniform black (fading to brown in preserved material); scale pockets outlined in white; lateral-line pores white; head black; fins dusky to black in preserved specimens, probably covered with black membrane in life.

Size. Range in SL for the 34 known specimens is 85-150 mm. The species apparently does not attain a very large size.

Distinctive characters: Taken together its black color, small size, simple unhooked subcaudal notch, nine-rayed pelvic fins, and pectoral formula separate *B. ventralis* from other members of the subgenus. Its nine-rayed pelvic fins readily differentiate the species from *B. dubius*, *B. mediterraneus*, and *B. quadrifilis* — all of which have eight-rayed pelvic fins. The remaining black species having nine-rayed pelvic fins, *B. atricolor* and *B. phenax*, differ from *B. ventralis* in possessing 10-11 and 7-8 long rays, respectively, in the lower portion of the pectoral fin. *B. pectinatus*, a species with variably 8 or 9 fin rays in the pelvic fin, has 8-10 long rays in the lower portion of the pectoral fin and pectinate scales behind the base of the pectoral fin.

Distribution: Obtained at six localities in the eastern Pacific between 21°N and 33°S (Fig. 23), at depths between 768 m and 1510 m. If this depth range indicates the approximate limits of the species, it appears likely that *B. ventralis* is restricted in horizontal distribution to a narrow strip paralleling the coastline of the Americas. Bottom temperatures (three localities) range from 3.3°C to 5.0°C. *B. ventralis* has been taken concurrently with *B. pectinatus* at three of the six known localities. Both species appear to co-occur in similar abundance at similar depths. »Galathea« St. 739, for example, yielded 13 specimens of *B. ventralis* and 11 of *B. pectinatus*.

Bathypterois (Bathypterois) atricolor

Alcock, 1896

(Figs 14a, 22e, 24; Pl. 7 Figs 3, 4)

Bathypterois atricolor Alcock, 1896, 1899; type locality: 13°47'N, 72°03.75'E, 1630 m, "Investigator" St. 194.

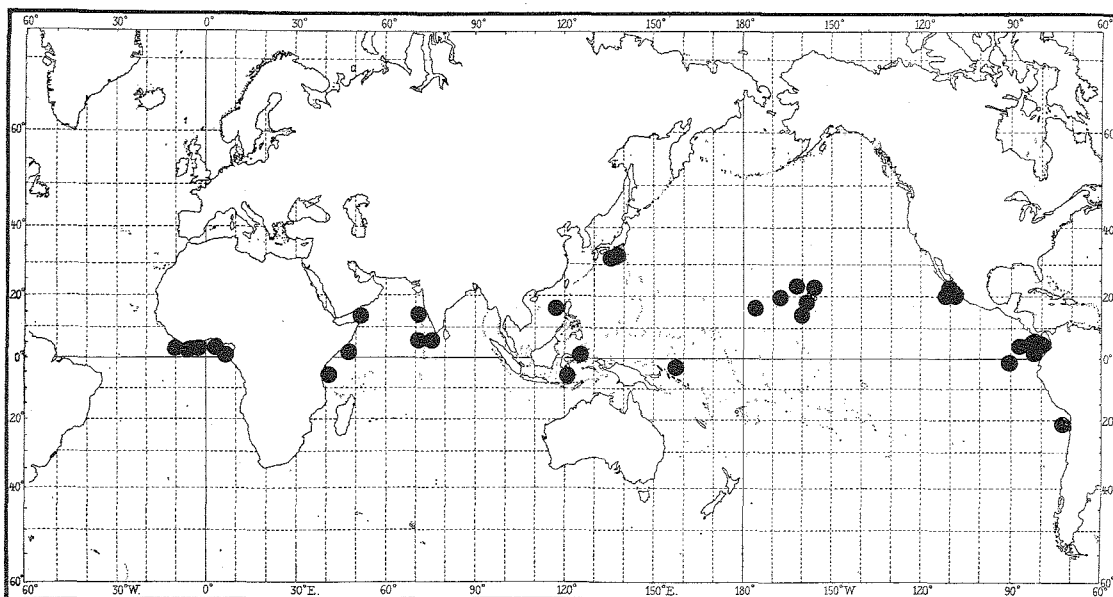


Fig. 24. The known distribution of *B. atricolor*.

- *pectoralis* Garman, 1899; type localities: 03°09'N, 82°08'W, 2036 m, "Albatross" St. 3376; 07°15'N, 79°36'W, 1866 m, "Albatross" St. 3393; 00°04'S, 90°24.5'W, 1618 m, "Albatross" St. 3407; 23°59'N, 108°40'W, 1819 m, "Albatross" St. 3431.
- *antennatus* Gilbert, 1905; type locality: Pacific Ocean, vicinity of Bird Island, Hawaii, 573-1463 m, "Albatross" St. 4151.
- *atricolor indicus* Brauer, 1906; type locality: 01°48.03'N, 45°42.08'E, 1644 m, "Valdivia" St. 257.
- (*Bathypterois*) *atricolor atricolor*, Parr 1928.
- (*Bathypterois*) *atricolor antennatus*, Parr 1928, Matsubara 1954.

Material:

- B. antennatus*: holotype (SL 134 mm); USNM.
- B. pectoralis*: 7 syntypes (SL 123-201 mm); MCZ (6), USNM (1).
- B. atricolor*: 31 specimens (SL 75-204 mm); BM (1), CAS-SU (2), UMML (23), USNM (4), ZMUC (1).

Description:

Counts. Dorsal rays 13-16; anal rays 8-10; pelvic rays 9; pectoral rays 12-13 visible externally, 16-19 total, formula: (ii)IIi(ii-iii)10-11, occasionally (ii)III(ii-iii)9, once (ii)II(iv)11; caudal rays (dorsal + ventral) iv-v 10+9 iv-v; gill rakers (anterior arch) 11-14+1+27-33; branchiostegal rays 12-14; lateral-line scales 57-62; dentary lateral-line pores 6-8,

moderate to large; vertebrae (incl. urostyle) 54-57; dorsal-fin origin over vertebra 21-25; anal-fin origin under vertebra 32-35.

Morphometry (values in % SL). HL 20.0-25.2; predorsal length 40.5-46.3; preanal length 56.7-63.6; prepelvic length 35.4-42.2; length of longest produced pelvic ray 24.5-57.8; length of longest lower caudal ray 14.8-33.3; length of longest produced pectoral ray 81.4-189.

Dentition. Teeth present in bands on each jaw; vomer toothed or untoothed; palatine with a few teeth; upper and lower pharyngeals toothed; basi-branchials untoothed.

Color. As in *B. ventralis*.

Size. Range in SL of the known material, 69-204 mm.

Distinctive characters: With its black color, small to moderate size, and nine-rayed pelvic fins, *B. atricolor* can be confused only with *B. ventralis*, *B. phenax*, or *B. pectinatus*. The presence of 10-11 long rays in the lower part of the pectoral fin distinguishes *B. atricolor* from the first two of these species; the absence of pectinate scales separates it from *B. pectinatus*.

Distribution: Nearly circumglobal in distribution (Fig. 24), but unknown in the northeastern and western Atlantic, where it is apparently replaced by *B. dubius* and *B. phenax*, respectively (Fig. 23). *B. atricolor* is extremely eurybathic and eurythermal:

258-5150 m and 2.5°C to 10.2°C (14 localities). It has been taken on a variety of bottom types including ooze, clay, mud, coral sand, manganese sand, and gravel.

Remarks: Alcock (1896) did not indicate that his description of *B. atricolor* was based on a single specimen, nor did he designate a type specimen in his original description. However, in a subsequent report (1898), he states: "This species was described and figured from a single injured specimen". And in the same report he compares subsequently obtained material of *B. atricolor* with "the type specimen". The depth and locality given in the original description of *B. atricolor* correspond with "Investigator" St. 194 (Alcock 1902, appendix). Thus the single specimen of *B. atricolor* obtained at "Investigator" St. 194 (IMC reg. No. 62/1) should be considered the lectotype of the species.

In his original description of *B. atricolor*, Alcock (1896) gives a pectoral-fin formula of 2/10, indicating a fin with two produced rays in the upper portion plus ten long rays in the lower portion. This formula agrees with the material examined herein. But in later accounts of the species (1898, 1899) Alcock gives a pectoral formula of 2/12. I have examined a specimen of *B. atricolor* from "Investigator" St. 230 (BM 1898.7.13.10, originally IMC 316/1) reported in Alcock's 1898 paper, and I find only ten rays in the lower part of the pectoral fin. Thus, the pectoral-fin formula of 2/12 given in the 1898 and 1899 accounts is apparently incorrect. This clarification is important, since the closely related *B. ventralis* from the eastern Pacific has 12 long rays in the lower portion of its pectoral fin.

Bathypterois (Bathypterois) dubius

Vaillant, 1888)
(Figs 22d, 23)

Bathypterois dubius Vaillant, 1888; type locality:

38°38'N, 28°21'W, 1257 m, "Talisman" St. 127 as per Vaillant 1888 (St. 139 as per Smith 1889).

— (*Bathypterois) dubius* Goode & Bean 1896.

— *dubius*, Bini 1970 (with color fig.).

Material:

2 paratypes (SL 131-137 mm); MCZ (1),
USNM (1).

5 specimens (SL 134-180 mm); MNHN (1),
ZMUC (4).

Description:

Counts (those in parentheses and all morphometric data from Bauchot 1963). Dorsal rays 15-16 (14-16); anal rays 9 (8-10); pelvic rays 8 (8); pectoral rays 11-13 visible externally, 18-19 total, formula: (ii)III(iii-iv)9-11 [(ii)III(iii)10-11]; caudal rays (dorsal + ventral) v-vi 10+9 v; gill rakers (anterior arch) 12-14+1+28-30; branchiostegal rays 13; lateral-line scales 59-61 (60-63); dentary lateral-line pores 6-7, small to large; vertebrae (incl. urostyle) 61-65 (61); dorsal-fin origin over vertebra 25-26; anal-fin origin under vertebra 37-39.

Morphometry (values in % SL). HL 18.0-21.9; predorsal length 40.4-45.7; preanal length 60.4-65.5; prepelvic length 37.6-42.4; length of longest produced pelvic ray 19.2-54.6; length of longest lower caudal ray 14.6-29.2; length of longest produced pectoral ray 70.2-98.5.

Dentition. As in *B. atricolor*.

Color. Head and body entirely black; scale pockets outlined in white; except for a black caudal, the fins transparent to dusky in preserved material, but possibly black in life.

Size. Known material ranges between 70 mm and 205 mm in SL.

Distinctive characters: A pectoral with 3-4 embedded rudimentary rays above 9-11 long lower rays; a pelvic fin with 8 fin rays; a high number of lateral-line scales (61-65) and vertebrae (59-61).

Distribution: Obtained at depths of 750-1941 m and bottom temperatures of 3.99°C-11.5°C (15 localities). A record in the Mediterranean extends the upper limit of its temperature range to at least 12.5°C. *B. dubius* is apparently restricted to the northern Atlantic Ocean (Fig. 23). It has been recorded from 42 localities in the eastern N. Atlantic, one in the western N. Atlantic (Templeman 1966), and one in the Mediterranean (Bauchot 1963).¹ Up to 15 specimens have been obtained in a single bottom tow.

Remarks: Mead (1966c) stated that the status of *B. dubius* was uncertain. Nevertheless, Bauchot (1963) had earlier established that the species was valid and well-defined. She described a new species, *B. mediterraneus*, from Mediterranean material previously confused with *B. dubius*. Templeman (1966) has also demonstrated that *B. dubius* is a valid entity.

1. This specimen (= *B. "longipes"*: Giglioli 1880) may represent a waif transported into the Mediterranean as a juvenile.

Vaillant (1888) did not specify a holotype. But he did indicate that his description was based on the best developed of the 70 available "Talisman" specimens, especially the specimen identified as MNHN 1885-121. This specimen has been referred to (by Bauchot 1963) as the holotype of *B. dubius*; the remaining "Talisman" specimens have been considered to be paratypes (e.g., "Talisman" specimens in the MCZ and USNM collections bear the designations "cotype" or "paratype"). Bertin & Estève (1951) have given "Talisman" St. 128 as the type locality. However, as Grey (1956) has pointed out, St. 128 was not listed in Vaillant's account of the species (1888). Bauchot has indicated (pers. comm.) that St. 127 (as per Vaillant 1888) pertains to specimen 1885-121; this station is the correct type locality for the species. Vaillant (1888) does include St. 127 in his list of stations for *B. dubius*. His St. 127 corresponds to St. 139 of Smith (1889) as explained in Bauchot et al. (1971).

Bathypterois (Bathypterois) phenax

Parr, 1928

(Figs 17b, 22g, 23, 26c; Pl. 4 Fig. 3)

Bathypterois (Bathypterois) atricolor phenax Parr, 1928; type locality: 21°16'N, 71°18'W, 1646-1728 m, "Pawnee" St. 54.

— *atricolor*, Fowler 1944.

— (*Bathypterois phenax*, Mead 1966c.

Possible senior synonym: *Bathypterois ater* Gilchrist, 1908; type locality: off Cape Point, South Africa, NE by E, ½ E, 43 mi, 1646 m, "Pieter Faure" St. 16983.

Material:

23 specimens (SL 54-165 mm); MCZ (1), UMML (22).

Description:

Counts. Dorsal rays 13-15; anal rays 8-10; pelvic rays 9; pectoral rays 9-11 visible externally, 15-17 total, formula: (ii)III(ii-iii)7-8, once (ii)III(iii)9; caudal rays (dorsal + ventral) iv-vi 10+9 iii-iv; gill rakers (anterior arch) 10-12+1+27-28; branchiostegal rays 12-13; lateral-line scales 55-60; dentary lateral-line pores 5-6, small to large; vertebrae (incl. urostyle) 53-56; dorsal-fin origin over vertebra 21-24; anal-fin origin under vertebra 32-34.

Morphometry (values in % SL). HL 20.0-24.1; predorsal length 42.4-48.4; preanal length 57.4-

62.8; prepelvic length 35.3-40.3; length of longest produced pelvic ray 27.2-38.7; length of longest lower caudal ray 20.6-29.8; length of longest produced pectoral ray 111-131.

Dentition. Small conical teeth on the palatine, sometimes on the vomer, and in bands on the dentary and premaxilla. In young specimens a row of larger arrowhead-shaped, outwardly directed teeth is present along the edge of the dentary (Pl. 4 Fig. 3) and the premaxilla. These peculiar teeth have been found in small adults of several other species of *Bathypterois*. They may be a feature of metamorphosing subadults or a retention of juvenile dentition.

Color. Head and body black; scale pocket outlines and lateral-line pores white; fins, including adipose, black in fresh specimens (fading to dusky brown or colorless in preserved material).

Size. Ca. 400 specimens of *B. phenax* have been obtained in the Pan-Caribbean region; none exceeds 165 mm SL. Farther north the species attains a larger size; five of the eight known specimens taken above 30°N latitude exceed 165 mm SL, the largest being 180 mm in SL. The smallest specimen is a 54 mm SL individual (MCZ 45918), which has not achieved a fully adult condition. It retains a remnant of a pseudobranch on the underside of the gill cover; its subcaudal notch is just beginning to form. The upper jaw is shorter than in the fully developed adult (11% vs. 14% SL), and the nasal rosettes appear proportionally much larger than in the adult. Otherwise, however, it is identical to the adult of the species.

Distinctive characters: The presence of a subcaudal notch in combination with nine-rayed pelvic fins and a pectoral fin with only 7 or 8 long rays in the lower portion distinguishes *B. phenax* from all other species.

Distribution: Off the American coast from latitude 39°N to 09°N (Fig. 23); it is the common small black species obtained there between 1200 m and 2000 m (known depth limits 827-2651 m). It has also been recorded twice off the central western coast of Africa at 2523 m and 2784 m. In this region it is probably replaced at shallower depths by the closely related *B. atricolor* (five records off W. Africa at 914-2332 m). Additional trawling off southwestern Africa may prove *B. phenax* to be continuous with *B. ater* from off South Africa. Rannou & Gaborit-Rezzouk (1976) have reported a single example of *B. phenax* from the Azores region. With

this single exception *B. phenax* is unknown in the northeastern Atlantic where the closely-related *B. dubius* prevails at bathyal depths. Bottom temperatures of 3.6°C to 4.4°C are available (three *B. phenax* localities). However, Tongue-of-the-Ocean records extend the upper limit of its temperature range to approx. 6.0°C.

Remarks: *B. ater* (Gilchrist 1908) may be a senior synonym of *B. phenax*. The description of the former was based on a single specimen obtained off South Africa by the "Pieter Faure". This sole representative has subsequently been lost (Barnard 1925), and no additional examples have been obtained off South Africa. Gilchrist's inadequate original description precludes a satisfactory comparison of *B. ater* and *B. phenax*. However, *B. ater* is described as possessing a subcaudal notch, a black coloration, and a pectoral with eight rays in the lower portion of the fin. This description identifies *B. ater* most closely with either *B. phenax* or *B. mediterraneus*, of which only the former choice is probable since *B. phenax* ranges into waters off western Africa, while *B. mediterraneus* is restricted to the Mediterranean. Additional material from the southwestern coastal waters of Africa must become available before the status of *B. ater* can be resolved with certainty.

Bathypterois (Bathypterois) mediterraneus

Bauchot, 1962

(Fig. 25)

- Bathypterois mediterraneus* Bauchot, 1962, 1963;
type locality: Mediterranean Sea, Gulf of Lion, Costa Brava, off Rosas, Spain, > 600 m.
– *mediterraneus*, Tortonese & Orsi 1970, Bini 1970 (with color fig.), Geistdoerfer & Rannou 1972, Rannou & Gaborit-Rezzouk 1976.
– *mediterraneus algeriensis* Bauchot, 1962, 1963;
type locality: Mediterranean Sea, off Pointe Chenoua, Algeria, 260 m.

Material:

None, description below based on Bauchot (1963).

Description:

Counts. Dorsal rays 15; anal rays 8-9; pelvic rays 8; pectoral rays 9-11 visible externally, 16-18 total, formula: (ii)III(iii)7-9; lateral-line scales 54-57; vertebrae (incl. urostyle) 53-55.

Morphometry (values in % SL). HL 20.6-25.8; predorsal length 42.7-45.9; preanal length 61.2-65.5; prepelvic length 28.5-41.9; length of longest produced pelvic ray 24.4-86.1; length of longest lower caudal ray 23.6-69.6; length of longest produced pectoral ray 74.2-120.

Color. As in *B. ventralis*.

Size. Range in SL of available specimens is 87-186 mm.

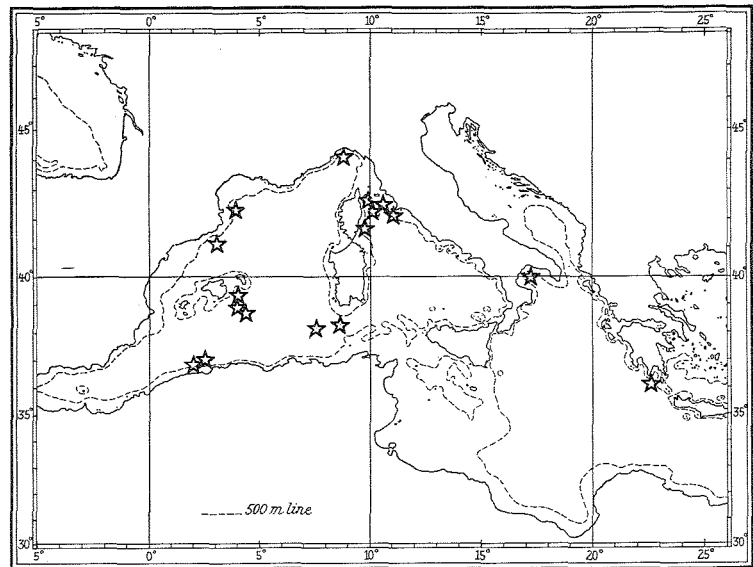
Distinctive characters: A pelvic fin with only 8 rays distinguishes *B. mediterraneus* from *B. phenax* and *B. atricolor*. A pectoral fin with 9-11 long rays in the lower portion further differentiates it from *B. atricolor* and from *B. dubius* as well. It has fewer lateral-line scales (54-57 vs. 61-65) and vertebrae (53-55 vs. 59-61) than *B. dubius*.

Distribution: Appears to be endemic to the Mediterranean Sea (Fig. 25). It is known from both the western and eastern basins (15 localities) at depths of 260-2830 m (Bauchot 1963, Tortonese & Orsi 1970, Geistdoerfer & Rannou 1972, Rannou & Gaborit-Rezzouk 1976). Bottom temperature data are unavailable, but a range of 12.5°C to 13.5°C can be estimated within the known depth range. *B. mediterraneus* is very closely allied to *B. phenax*, with which it agrees in every respect except pelvic-ray count; these two species are, however, geographically distinct. Aside from submersible records of *B. grillator*, *B. mediterraneus* and *B. dubius* are the only species so far obtained in the Mediterranean. However, *B. dubius* has been obtained there only once (p. 89).

Remarks: Bauchot (1962, 1963) named the subspecies *B. mediterraneus algeriensis* for a specimen of *B. mediterraneus* having exceptionally long produced pelvic and caudal rays. However, the degree of elongation of the outer pelvic and lower caudal rays is quite variable in many species of the genus and is not by itself a reliable taxonomic character. In fact, selection appears to have favored individual variation in length of the pelvic and caudal fin rays in relation to feeding success. Great variability in length of the supporting fins is to be expected in a species like *B. mediterraneus* which lacks congeneric competitors within its depth range.

The holotype of *B. mediterraneus* is MNHN 1962-551, a SL 124 mm specimen taken off Rosas, Spain.

Fig. 25. The known distribution of *B. mediterraneus*.



Bathypterois (Bathypterois) quadrifilis

Günther, 1878

(Figs 14c, 22f, 26a, 27, 37)

Bathypterois quadrifilis Günther, 1878, 1887; type locality: 10°46'S, 36°08'W, 1408 m, "Challenger" St. 126.

- (*Synapteretmus*) *quadrifilis*, Goode & Bean 1896.
- (*Bathypterois*) *quadrifilis*, Parr 1928, Mead 1966c.

Material:

15 specimens (SL 112-145 mm); MCZ (1), UMML (14).

Description:

Counts. Dorsal rays 12-15; anal rays 8-9; pelvic rays 9; pectoral rays 10-12 visible externally, 15-17 total, formula: (ii)III(ii-iii)7I-9I; caudal rays (dorsal + ventral) iv-v 10+9 iv-v; gill rakers (anterior arch) 11-12+1+28-30; branchiostegal rays 11-12; lateral-line scales 57-63; dentary lateral-line pores 6, small to moderate in size; vertebra (incl. urostyle) 54-59; dorsal-fin origin over vertebra 23-25; anal-fin origin under vertebra 33-36.

Morphometry (values in % SL). HL 18.6-21.9; predorsal length 42.2-45.0; preanal length 57.7-60.7; prepelvic length 37.4-40.8; length of longest produced pelvic ray 22.3-28.4; length of longest lower caudal ray 17.3-24.2; length of longest produced upper pectoral ray 70.5-87.6; length of produced lower pectoral ray 28.1-85.0.

Dentition. As in *B. atricolor*.

Color. Ground color black; outlines of scale pockets and lateral-line pores white; caudal fin black; adipose fin colorless; remaining fins dusky to black.

Size. SL range of the known material is 54-180 mm.

Distinctive characters: *B. quadrifilis* is the only species of the genus to have the lowermost ray of the lower pectoral fin singularly thickened and produced (Fig. 14c). Two additional characters are peculiar to this and the closely related species *B. pectinatus*. One is the presence of strongly pectinate scales immediately behind the base of the pectoral fin. The other is the unusual condition of the two produced upper pectoral rays. In contrast to all other species of the subgenus, *B. quadrifilis* and *B. pectinatus* have these rays separating in advance of the dorsal-fin origin. Also in the two species these produced rays are largely unsegmented, except for a specialized section of the upper ray at the point of separation (Fig. 26a, b). In other species of *Bathypterois* and *Bathycygnus* the produced pectoral rays divide at or caudad of the end of the dorsal fin; both rays display typical segmentation (Fig. 26c, d) at the point of separation. Also characteristic of *B. quadrifilis* is a strongly developed hook on the anterior procurrent ray of the subcaudal notch (Fig. 22f).

Distribution: Depth range is from 402 m to 1408 m. In the western Atlantic the species occurs in deep offshore waters from North Carolina south

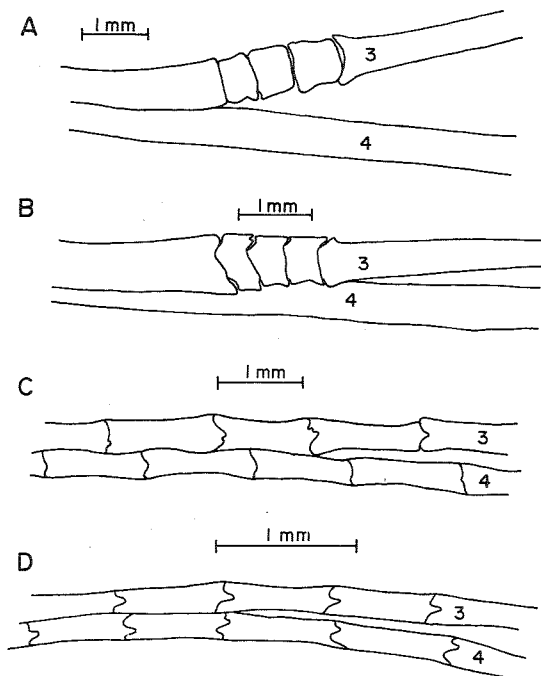


Fig. 26. Fin-ray segmentation at the point of separation of the produced upper pectoral fin rays. A, *B. quadrifilis*, UMML 30693; B, *B. pectinatus*, ZMUC, "Galathea" St. 739; C, *B. phenax*, UMML 31599; D, *B. insularum*, ZMUC, "Galathea" St. 314.

to Recife, Brazil. In the eastern Atlantic it has been obtained in the Gulf of Guinea region (Fig. 27). Bullis & Rivas (1972) report a temperature range of 5.0°C to 7.8°C in the Gulf of Mexico and Caribbean. Temperature range of four additional localities is 4.3°C-4.7°C.

Remarks: Günther's original description (1878) of *B. quadrifilis* was based on two specimens from

"Challenger" St. 126; these (BM 1887.12.7.199-200) are the syntypes of the species.

Bathypterois (Bathypterois) pectinatus

Mead, 1959

(Figs 13b, 26b, 27)

Bathypterois (Bathypterois) pectinatus Mead, 1959b; type locality: 05°46'S, 81°32'W, 2388 m, "Albatross" St. 4654.

— *quadrifilis peruanus* Nalbant, 1971; type locality: Pacific Ocean, Peru-Chile Trench between 03° 40'S and 12°40'S, 77°49'W and 82°17'W, R/V "Anton Bruun", 11th cruise.

Material:

Holotype (SL 143 mm); USNM.

20 specimens (SL 80-126 mm); CSU (7), USNM (1).

Description:

Counts. Dorsal rays 13-14; anal rays 7-9; pelvic rays 8-9; pectoral rays 10-12 visible externally, 15-18 total, formula: (ii)III(ii-iii)8-10; caudal rays (dorsal + ventral) iv-v 10+9 iii-iv; gill rakers (anterior arch) 12-13+1+30; branchiostegal rays 13; lateral-line scales 60-65; dentary lateral-line pores 7-9, large; vertebrae (incl. urostyle) 57-60; dorsal-fin origin over vertebra 23-25; anal-fin origin under vertebra 34-35.

Morphometry (values in % SL). HL 18.7-22.8; predorsal length 39.7-40.6; preanal length 54.5-54.8; prepelvic length 34.2-35.7; length of longest pectoral pelvic ray 22.0-32.2; length of longest lower caudal ray 17.4-21.1; length of longest produced upper pectoral ray 96.8-111.

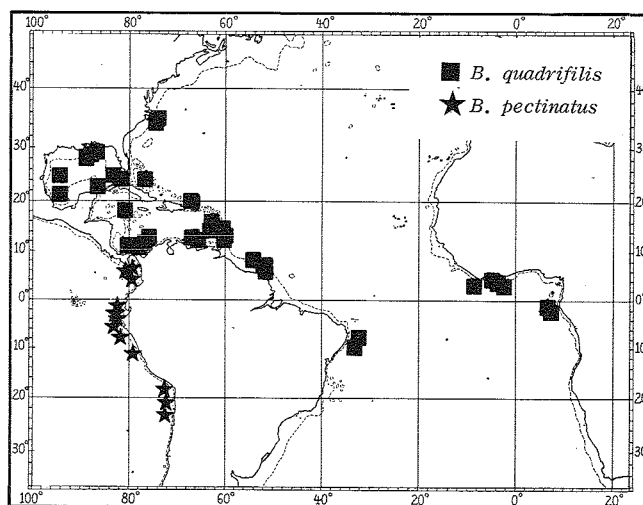


Fig. 27. The known distributions of *B. quadrifilis* and *B. pectinatus*.

Dentition. As in *B. atricolor*.

Color. Head and body black; scale pockets outlined in white; lateral-line pores white; caudal and adipose fins colorless; remaining fins colorless to dusky.

Size. Range in SL of the known material is 71-143 mm.

Distinctive characters: The presence of produced pectoral fin rays that separate at a specialized junction (Fig. 26b) in advance of the dorsal fin and of pectinate scales behind the pectoral fin base distinguishes *B. pectinatus* from all other species of the genus. *B. pectinatus* lacks the thickened produced lowermost pectoral ray of *B. quadrifilis* and has the caudal fin colorless (vs. black), 8 or 9 pelvic fin rays (vs. 9 invariably), and 7-9 large pores piercing the ventral surface of the dentary (vs. 6 small pores in *B. quadrifilis*).

Distribution: Obtained from a narrow zone paralleling the western coast of South America (Fig. 27), at depths of 700-2100 m. Temperatures for two of the 16 known localities are 2.9°C and 3.73°C.

Subgenus *Bathycygnus* n. subgen.

Bathypterois (partim) Günther, 1878; type by subsequent designation (Jordan & Evermann 1896), *B. longifilis* Günther, 1878.

Synapteremus (partim) Goode & Bean, 1896; type by subsequent designation (Jordan & Evermann 1896), *B. quadrifilis* Günther, 1878.

Type species: *Bathypterois longipes* Günther, 1878.

Etymology: From the Greek *bathys* = deep + *kyknos* = swan, the spelling latinized: *cygnus*.

Diagnostic characters: Those given in steps 1b and 4b of the key (p. 75).

Remarks: The six species of *Bathycygnus* lack a subcaudal notch, but they are otherwise closely related to the members of *Bathypterois*. The two subgenera represent natural species groups that have evolved along similar lines. Parallelism is evident in common trends toward adoption of an overall black coloration and reduction in the number of long rays in the lower part of the pectoral fin. These subgenera display similar cranial osteologies compared with that of the more specialized subgenus

Benthosaurus. In *Bathycygnus* (Fig. 12c) and *Bathypterois* (Fig. 13a, b) attenuation and rotation of the opercular series bones and the hyomandibular is slight (in the more primitive species) to moderate (in advanced species). Correspondingly, the gape in these subgenera is moderate. Species of *Benthosaurus* exhibit the largest gape relative to body size and the most extensively modified cranial osteology.

Bathypterois (Bathycygnus) bigelowi

Mead, 1959

(Figs 12c, 15a, 17a, 28, 29)

Bathypterois (Bathypterois) bigelowi Mead 1959a; type locality: 13°13'N, 82°13'W, 640 m, "Oregon" St. 1915.

Material:

8 paratypes (SL 79-130 mm); MCZ (1), UMML (7). 2 specimens (SL 109-112 mm); UMML (2).

Description (with gill raker count, lateral-line scale count, and morphometric values from Mead 1959a, based on 66 specimens):

Counts. Dorsal rays 12-13; anal rays 8-9; pelvic rays 8; pectoral rays 13-15 visible externally, 18-19 total, formula: (ii)IIiii(ii)10 or (ii)IIiii(iii)8-9; caudal rays (dorsal + ventral) v 10+9 iv; gill rakers (anterior arch) 10-12+1+22-28; branchiostegal rays 10-12; lateral-line scales 48-55; dentary lateral-line pores 6-7, small to moderate in size; vertebrae (incl. urostyle) 49-51; dorsal-fin origin over vertebra 20; anal-fin origin under vertebra 29-30.

Morphometry (values in % SL). HL 20.9-24.1; predorsal length 40.0-45.0; preanal length 57.6-62.0; prepelvic length 37.3-42.1; length of longest produced pelvic ray 29.1-37.2; length of longest lower caudal ray 22.7-27.7; length of longest produced pectoral ray 78.1-98.3.

Dentition. The typical bands of cardiform teeth in each jaw; vomer and palatine each with a few small teeth; ectopterygoid either untoothed or provided with a single row of very small teeth; upper pharyngeals (epibranchials 3 and 4, pharyngobranchials 3 and 4) and lower pharyngeal (ceratobranchial 5) toothed (Fig. 28); dentigerous dermal ossifications present above basibranchial cartilage 3-4 (Fig. 31).

Color. Ground color of body white, occasionally irregularly mottled with pale red-violet, yellow, and blue; fresh specimens greenish (Mead 1966c); each

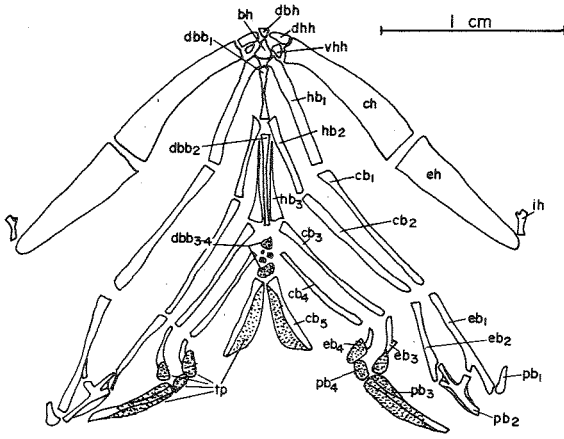


Fig. 28. The visceral arches and associated dentition in *B. bigelowi*, UMML 28173.

saurus it is the only species to have several non-rudimentary fin rays (rays 5 through 7) immediately below the produced rays of the pectoral fin. In other species of *Bathycygnus* and *Bathypterois* these rays are typically very short (ray 5) or rudimentary (rays 6 and 7). *B. bigelowi* is also the only species outside of *Benthosaurus* to have dentigerous dermal plates capping basibranchial cartilage 3-4 (Fig. 28).

scale pocket provided with one or more dark pigment specks – developing on the dorsal half of the body into larger triangular or diamond-shaped pigment fields on each pocket; a large dark spot at the base of each lobe of the caudal fin; fins generally colorless with traces of black, especially at the bases of the dorsal and anal fins and on central rays of the caudal fin. Branchial region, roof of the mouth, and lining of the abdominal cavity dark.

Size. The species appears to mature at a rather small size. Known SL range of adults is 45-144 mm.

Distinctive characters: The color pattern is quite distinctive. Aside from members of *Bentho-*

Distribution: Appears to be endemic to the Gulf of Mexico and Caribbean region (Fig. 29). Its known range extends up the eastern coast of Florida as far as 29°N and southwards to French Guiana. A specimen from the eastern Atlantic, MNHN 1961-81, reported by Roux & Hureau (1969) as *B. bigelowi*, proved to be *B. dubius*. *B. bigelowi* has one of the shallowest bathymetric ranges, 377-986 m, of any species of the genus. Most captures are between 550 m and 700 m. Bottom temperatures (15 localities) vary between 4.2°C and 11.1°C. *B. bigelowi* appears to occur in greater densities than other species of *Bathypterois*; as many as 53 individuals have been taken in a single bottom tow and captures of 10-20 specimens per tow are frequent.

Remarks: *B. bigelowi* exhibits the most generalized cranial osteology (Fig. 12c) of all species and may be considered basal in this respect. The shapes and relative positions of the opercular series bones in particular are very similar to those of *Ipnops*.

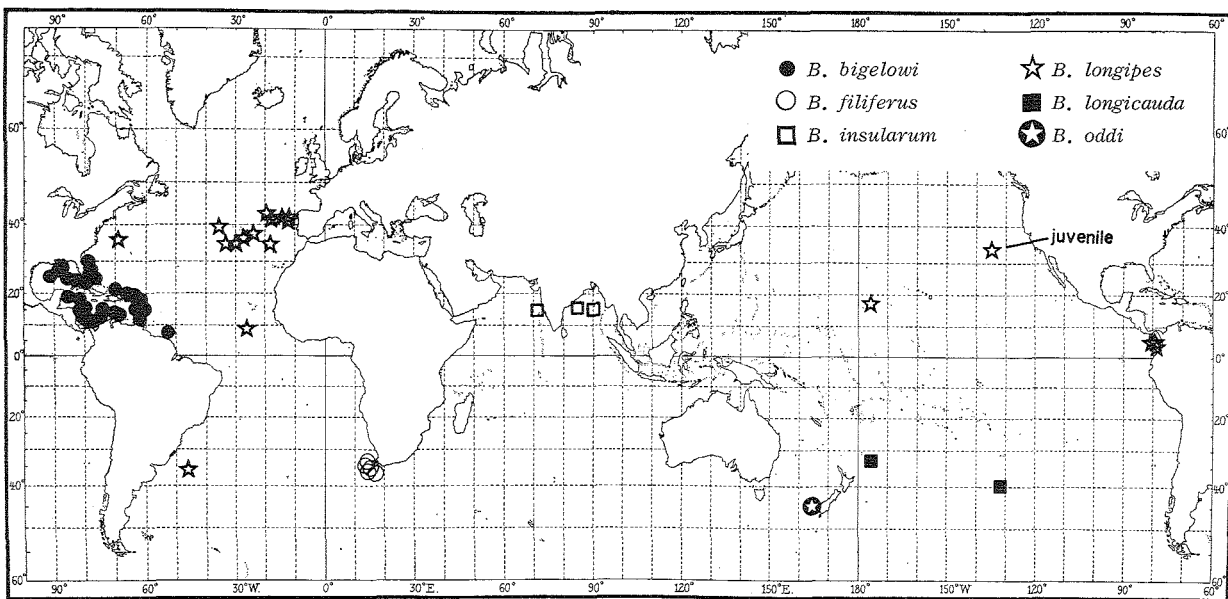


Fig. 29. The known distributions of *B. bigelowi*, *B. filiferus*, *B. insularum*, *B. longipes*, *B. longicauda*, and *B. oddi*.

Bathypterois (Bathycygnus) filiferus

Gilchrist, 1908

(Fig. 29)

Bathypterois filiferus Gilchrist, 1908; type locality:

Atlantic Ocean, off Cape Point, South Africa, NE, 3/4E, 36 mi, 1097 m, "Pieter Faure" St. 16659.

Belonepterois filiferus, Roule 1919.

Bathypterois capensis Gilchrist & von Bonde, 1924;

type locality: 33°30-31'S, 16°39-40'E, 2232 m, "Pickle" St. 524.

— (*Bathypterois*) *filiferus*, Parr 1928.

Material:

B. filiferus: 8 specimens (SL 144-200 mm); CAS-SU (1), SAM (7).

B. capensis: 1 specimen from the type series (SL 159 mm); RUSI.

Description:

Counts. Dorsal rays 14-16; anal rays 9-10; pelvic rays 8; pectoral rays 13-16 visible externally, 18-22 total, formula: usually (ii)III(iii-iv)12-13, rarely (ii)II(iii)11 or (ii)III(ii)12-14; caudal rays (dorsal + ventral) v-vii 10+9 iv-v; gill rakers (anterior arch) 12-13+1+28-30; branchiostegal rays 12; lateral-line scales 57-60; dentary lateral-line pores 7, small to moderate; vertebrae (incl. urostyle) 52-55; dorsal-fin origin over vertebra 21-25; anal-fin origin under vertebra 30-34.

Morphometry (values in % SL). HL 23.2-26.6; predorsal length 45.9-48.0; preanal length 58.6-64.1; prepelvic length 36.5-40.3; length of longest produced pelvic ray 41.4-54.5; length of longest lower caudal ray 31.8-36.1; length of longest produced pectoral ray 122-168.

Dentition. Bands of small conical teeth present on the dentary and the premaxilla; a few small teeth on the vomer and palatine; the usual tooth patches present on the upper and lower pharyngeals; ectopterygoid untoothed; dermal basibranchial 3-4 apparently ossified but untoothed.

Color. No details of coloration were given in the original descriptions. Barnard (1925) has given the color of *B. filiferus* as brownish. The examined specimens are generally faded to a pale brown, but those retaining scales have a greenish tone. The fins in preserved specimens are transparent or brownish.

Size. SL available for known specimens is 144-260 mm.

Distinctive characters: *B. filiferus* can be differentiated from other species of *Bathycygnus* by its greenish color, thick scales, large size, extremely elongate produced pectoral rays, and its pectoral-ray formula (above). Only *B. insularum* has a comparable number of long rays (12-14) in the lower part of the pectoral fin; but the two species are easily distinguished. *B. filiferus* has eight pelvic fin rays and 14-16 dorsal fin rays; the much smaller *B. insularum* has nine pelvic fin rays and only 12-13 dorsal fin rays. *B. filiferus* corresponds closely to *B. longifilis* of the subgenus *Bathypterois* in color, large size, pectoral-ray formula, and the possession of thick adherent scales. However, *B. filiferus* has no subcaudal notch and has much longer produced pectoral rays, in addition to differences in vertebral number and lateral-line scale count. Both species are near the bases of their respective evolutionary lines. A peculiarity of *B. filiferus* is the condition of its produced pelvic and caudal rays. Most species of *Bathypterois* have the two or three produced outer pelvic fin rays closely adherent over most of their lengths. In *B. filiferus*, however, the two stiffened equally produced outer pelvic rays are invariably independent of each other in the material examined.

Distribution: Known from a rather restricted area off Cape Point, South Africa (Fig. 29). Seventeen capture localities range in depth from 1055 m to 2835 m. No bottom temperatures are available, but a range of 2.3°C-3.7°C can be estimated, based on the depth range.

Remarks: The nominal species *B. capensis* Gilchrist & von Bonde, 1924, agrees in every respect with its senior synonym *B. filiferus* Gilchrist, 1908. A supposed difference in pelvic-ray length (Barnard 1925) does not exist. In nine specimens of *B. filiferus* examined, pelvic length equals 42.4-54.5 % SL (57.1 % SL in the specimen figured in Gilchrist 1908); in two specimens of *B. capensis* pelvic-ray length equals 41.4-45.3 % SL (39.5 % in the 200 mm specimen of Gilchrist & von Bonde's original description). Differences between the available specimens are due to individual variation, the total extent of which (39.1-57.1 % SL) is well within the normal range of variation for a species of *Bathypterois*. A differentiation of *B. filiferus* and *B. capensis* with respect to dorsal-ray count (Smith 1949) is fallacious, since it is based on an erroneous count (12 instead of 16) reported for *B. filiferus* by Barnard (1925). Finally, Gilchrist (1908) describes the scales

of *B. filiferus* as deciduous, whereas those of *B. capensis* are adherent. However, I found adherent scales present in at least two specimens of *B. filiferus*. The character is somewhat variable and undoubtedly partially dependent on conditions endured in the trawl and upon subsequent handling.

Bathypterois (Bathycygnus) insularum

Alcock, 1892

(Figs 26, 29)

Bathypterois insularum Alcock, 1892, 1899; type locality: 14°35.25'N, 72°02.62'E, 2085 m, "Investigator" St. 121.

— (*Synapteretmus*) *insularum*, Goode & Bean 1896.

— (*Bathypterois*) *insularum*, Parr 1928.

Material:

13 specimens (SL 78-133 mm); ZMUC.

Description:

Counts. Dorsal rays 13; anal rays 8-10; pelvic rays 9; pectoral rays 14-16 visible externally, 19-21 total, formula: (ii)III(ii)12-14; caudal rays (dorsal + ventral) v 10+9 iv-v; gill rakers (anterior arch) 12-13+1+30-31; branchiostegal rays 12-13; lateral-line scales 52-56; dentary lateral-line pores 6, large; vertebrae (incl. urostyle) 50-53; dorsal-fin origin over vertebra 21-23; anal-fin origin under vertebra 29-32.

Morphometry (values in % SL). HL 23.0-25.8; predorsal length 45.7-51.2; preanal length 58.7-62.5; prepelvic length 36.7-39.8; length of longest produced pelvic ray 37.5-48.8; length of longest lower caudal ray 24.6-35.8; length of longest produced pectoral ray 73.4-79.8.

Dentition. The typical *Bathypterois* tooth bands present in each jaw; vomer with a few or no small conical teeth; palatine with a few small teeth; basi-branchial cartilage 3-4 without ossified tooth plates.

Color. Body and head probably black in life (faded brown in preserved material); scale pocket outlines and lateral-line pores along the trunk white; adipose fin colorless; other fins transparent to dusky.

Size. The 15 known specimens vary between 78 mm and 140 mm in SL.

Distinctive characters: With 12-14 long rays in the lower portion of the pectoral fin, *B. insularum* can be confused with *B. filiferus*. However, as dis-

cussed above, the two species differ in pelvic-ray count, dorsal-ray count, length of the produced pectoral rays and other characters. *B. insularum* is closely related to *B. longipes*, which has 9-11 long rays in the lower portion of the pectoral fin and variably 8 or 9 pelvic fin rays. In other respects, including a low dorsal-ray count (12-14), they agree closely, but are distinct geographically (Fig. 29).

Distribution: Known from three localities only: one in the Arabian Sea, two in the Bay of Bengal (Fig. 29). Like the related *B. longipes*, it is a deep-dwelling species; depths vary from 2085 m to 2820 m. A bottom temperature of 3.1°C is available for the shallowest locality.

Bathypterois (Bathycygnus) longipes

Günther, 1878

(Figs 14b, 29)

Bathypterois longipes Günther, 1878, 1887; type locality: 36°44'S, 46°16'W, 4846 m, "Challenger" St. 325.

— (*Synapteretmus*) *longipes*, Goode & Bean 1896.

— sp., Roule 1919.

— (*Bathypterois*) *longipes*, Parr 1928, Mead 1966c.

Material:

8 specimens (SL 92-206 mm); ISH (2), MCZ (1), UMML (3), USNM (1), ZMUC (1).

Description:

Counts. Dorsal rays 12-14; anal rays 9-10; pelvic rays 8-9; pectoral rays 11-13 visible externally, 16-19 total, formula: usually (ii)III(ii-iii)9-10, occasionally (ii)III(iii)11, rarely (ii)III(i)10; caudal rays (dorsal + ventral) v-vi 10+9 iv-v; gill rakers (anterior arch) 12+1+27-29; branchiostegal rays 11-13; lateral-line scales 54-58; dentary lateral-line pores 6-7, small to moderate in size; vertebrae (incl. urostyle) 52-55; dorsal-fin origin over vertebra 21-23; anal-fin origin under vertebra 30-31.

Morphometry (values in % SL). HL 20.7-25.6; predorsal length 40.8-46.6; preanal length 56.5-59.7; prepelvic length 35.8-38.4; length of longest produced pelvic ray 30.4-54.4; length of longest lower caudal ray 27.2-30.4; length of longest produced pectoral ray 89.9-107.

Dentition. Palatine with five to nine small teeth in a row anteriorly, instead of the more typical cluster of small teeth; ectopterygoid occasionally with a few

very small but well-ossified teeth; dentition otherwise as in *B. insularum*.

Color. As in *B. insularum*.

Size. Known SL range for the available specimens is 66-249 mm.

Distinctive characters: A pectoral fin with 9-11 long rays in the lower portion; a variable number of pelvic fin rays (8 or 9); a low number of dorsal fin rays (12-14).

Distribution: A deep-dwelling species, ranging between 2615 and 5610 m in depth (19 captures). Bottom temperatures from 0.39°C to 4.49°C (7 localities). According to Nybelin (1957), *B. longipes* is the commonest deep benthic fish in the north-eastern Atlantic. The species is wide-ranging geographically, having also been recorded off Cape Hattaras, off extreme southern Brazil, in the Gulf of Panama, and in the mid-Pacific (Fig. 29). Considering that relatively very few bottom trawls have been accomplished between 3000 m and 6000 m, the widely-scattered records of *B. longipes* make it probable that the species is circumglobal. Bullis & Rivas' (1972) statement that it does not occur in the central Atlantic region (between latitudes 35°N and 35°S) must again be tempered by the paucity of trawlings within the depth range of the species. But, in fact, *B. longipes* had earlier been obtained in the central eastern Atlantic by the Swedish Deep-Sea Expedition (Nybelin 1954, 1957).

Development: A 14 mm SL juvenile described by Okiyama (1973) agrees most closely with *B. longipes* meristically and may pertain to the species.

Bathypterois (Bathycygnus) longicauda

Günther, 1878

(Fig. 29; Pl. 6 Fig. 2)

Bathypterois longicauda Günther, 1878, 1887; type locality: 39°41'S, 131°23'W, 4663 m, "Challenger" St. 289.

— (*Synapteretmus*) *longicauda*, Goode & Bean 1896.

Material:

5 specimens (SL 97-122 mm); ZMUC.

Description:

Counts. Dorsal rays 12-13; anal rays 9-10; pelvic rays 8; pectoral rays 10-12 visible externally, 17-19

total, formula: (ii)III(iv)8-10; caudal rays (dorsal + ventral) v 10+9 iv; gill rakers (anterior arch) 10-12+1+31; branchiostegal rays 12; lateral-line scales 54-56; dentary lateral-line pores 6-7, very large (greater than horizontal diameter of the orbit); vertebrae (incl. urostyle) 53-55; dorsal-fin origin over vertebra 22-24; anal-fin origin under vertebra 29-32.

Morphometry (values in % SL). HL 24.8-28.8; predorsal length 46.4-50.9; preanal length 56.7-64.4; prepelvic length 34.1-40.1; length of longest produced pelvic ray 33.6-56.7; length of longest lower caudal ray 24.8-38.6; length of longest produced pectoral ray 94.7-95.4.

Dentition. As in *B. longipes*.

Color. The specimens examined are considerably faded to a light tan; the fins are transparent. Günther (1887) describes the type specimen as follows: "Sides of the head and lower part of the abdomen black; tail and fins transparent".

Size. The six known specimens vary between 59 mm and 122 mm in SL. It seems unlikely that the species attains a much larger size.

Other features. A very small adipose fin. *B. longicauda* has a peculiarly emaciated appearance (Pl. 6 Fig. 2). The dorsal profile of the body behind the shoulder is concave, the body tapering rapidly in the caudad direction.

Distinctive characters: Closely related to *B. longipes* with which it agrees in many characters. Distinguishing characters are as follows (with values for *B. longipes* in parentheses); 4 mid-pectoral rudimentary rays (1-3 rudimentary rays); 8 pelvic rays (8 or 9 pelvic rays); HL 24.8-28.8 % SL (20.7-25.6 % SL); predorsal length 46.4-50.9 % SL (40.8-46.6 % SL); diameter of dentary lateral-line pores greater than horizontal diameter of eye (less than diameter of eye); body thin, emaciated (body stout, robust); a small species, maximum known SL 122 mm (a much larger species, maximum known SL 249 mm); adipose fin minute (adipose fin normal).

Distribution: Obtained twice in the Pacific between latitudes 30°S and 40°S (Fig. 29) at 4663 m and 5850-5900 m, making *B. longicauda* the deepest-dwelling species of the genus. Bottom temperatures are 1.56°C and 1.2°C, respectively.

Remarks: Parr (1928) considered *B. longicauda* to be a synonym of *B. longipes*. However, Nybelin

(1957) noted differences between *B. longipes* and *B. longicauda*, and considered the latter a "species inquirenda", suggesting that Günther's type specimen was perhaps malnourished or possessed of an abnormally shortened vertebral column. But a radiograph of the type reveals 53 vertebrae, comparing favorably with the 52-55 vertebrae of *B. longipes*. The radiograph also reveals that the type specimen is a subadult, the centra being uncontracted and the two uppermost pectoral fin rays being incompletely reduced (rudimentary in the adult). However, the type specimen of *B. longicauda* is not a young example of *B. longipes*. The five specimens of *Bathypterois* obtained at "Galathea" St. 654 agree closely with Günther's 59 mm SL type and confirm that it is not a teratological specimen. The "Galathea" specimens have the same thin, emaciated appearance (Pl. 6 Fig. 2) as the type specimen.

Bathypterois (Bathycygnus) oddi n. sp.

(Fig. 29; Pl. 6 Fig. 3)

Material:

Holotype (SL 200 mm); ZMUC P 2334534; type locality: 45°51'S, 164°32'E, 4400 m, "Galathea" St. 601.

Paratype (SL 153 mm); ZMUC P 2334535, collected with the holotype.

Diagnosis: A *Bathypterois* without a subcaudal notch, and with 8 pelvic fin rays, 60-62 lateral-line scales, 57-58 vertebrae, a pectoral-ray formula of (ii)IIi(iii)8, and a robust body.

Etymology: The new species is named in honor of the legendary Icelandic hero of Bandamanna Saga, Odd, symbol of good fortune and of the Scandinavian seafaring spirit.

Description (of the holotype with values for the paratype in parentheses):

Counts. Dorsal rays 14 (14); anal rays 11 (10); pelvic rays 8 (8); pectoral rays 10 visible externally, 16 total, formula: (ii)IIi(iii)8 (same in the paratype); caudal rays (dorsal + ventral) vi 10+9 iv (vi 10+9 iv); gill rakers (anterior arch) 12+1+28 (12+1+28); branchiostegal rays 12 (12); lateral-line scales 60 (61-62); dentary lateral-line pores 7 (7), moderate in

size; vertebrae (incl. urostyle) 58 (57); dorsal-fin origin over vertebra 24 (24); anal-fin origin under vertebra 33 (33).

Morphometry (values in % SL). HL 24.1 (22.8); predorsal length 47.0 (45.8); preanal length 58.0 (56.2); prepelvic length 36.0 (34.7); length of longest produced pelvic ray 57.5 (41.9); length of longest lower caudal ray 46.0 (38.2); length of longest produced pectoral ray 100 (not intact in paratype); depth at shoulder 13.0 (11.8); depth at caudal peduncle 7.0 (7.2); preadipose length 81.0 (79.1).

Dentition. Premaxilla with a band of small conical teeth; dentary with a similar but narrower band; palatine with a linear row of small teeth anteriorly (as in *B. longipes* and *B. longicauda*); vomer with a few small teeth on each knob; ectopterygoid and basibranchial 3-4 untoothed; upper pharyngeals (epibranchials 3 and 4, pharyngobranchials 3 and 4) and lower pharyngeal (ceratobranchial 5) toothed.

Color. The holotype and paratype are a uniform faded brown with clear outlines around the scale pockets. This type of coloration in preserved specimens is usually indicative of an overall black coloration in fresh *Bathypterois* material. The fins of the two specimens are colorless, but may have been dark originally.

Size. The standard lengths (200 mm and 153 mm) and stout body form of the two known specimens suggest that *B. oddi* may attain a fairly large size.

Other features. Scales deciduous; produced fin rays of the pectoral fin (rays 3 and 4) united to a point midway between the adipose fin and the base of the caudal fin; gular area unscaled; gill rakers bladellike.

Distinctive characters: *B. oddi* is closely related to *B. longipes* and *B. longicauda*. The following characters in combination distinguish *B. oddi* from these species: a pectoral with 8 long rays in the lower portion of the fin, a pelvic fin with 8 fin rays, 60-62 lateral-line scales, 57-58 vertebrae, a produced lower caudal ray equal to 38-46 % SL, and a robust body.

Distribution: Known only from the type locality in the Tasman Sea off the southern tip of New Zealand (Fig. 29), at 4400 m depth and 1.15°C. Like its congeners, *B. longipes* and *B. longicauda*, *B. oddi* would appear to be a very deep-dwelling species.

III. BIOLOGY

DISTRIBUTION

The known distribution of *Bathypterois* is displayed in Fig. 1 (p. 50) which shows that the genus is somewhat closely tied to continental and major insular landmasses. It is true that eight species are known to occur only between 250 m and 1500 m, and are consequently generally restricted to areas adjacent to landmasses. However, the picture in Fig. 1 is heavily biased in favor of these shallower-dwelling species, since trawling effort has tended for a number of reasons to be concentrated on the continental shelf and slope and immediately off major island groups. Records from deep ocean basins are few despite the occurrence of half of the 18 species in depths exceeding 2000 m, with at least three species in depths exceeding 5000 m (Fig. 30). As recently as 1957 Nybelin could list only 23 trawls yielding benthic fishes from depths greater than 3660 m in the North Atlantic, the most thoroughly studied region of the world's oceans. Yet, of these, six yielded specimens of *Bathypterois*. With several eurythermal and eurybathic species, and with species dwelling as deeply as 5900 m, it seems probable that the genus will prove ubiquitous at bathyal and abyssal depths within its own latitudinal limits.

In general the genus is confined between latitudes 55°N and 45°S. The factors determining these lati-

tudinal limits are unknown. However, the 10°C surface isotherm (Fig. 1) corresponds as a first approximation with the limits of the genus. But, if surface temperature alone were the limiting factor, then the genus should range much farther northward in the North Pacific than it is known to. In the eastern North Pacific *Bathypterois* is unknown (except for a single juvenile specimen) above the southern extreme of Baja California, despite the large number of trawlings off the west coast of the U.S. A similar situation prevails in the western North Pacific where *Bathypterois* is unknown above the southern tip of Japan. A finer approximation to the observed horizontal limits of the genus is provided by the upper boundaries between subpolar (subarctic, subantarctic, intermediate, and transitional) and central oceanic watermasses in both hemispheres (Fig. 1). With minor exceptions (e.g., along the southwestern coast of South America) records of *Bathypterois* are confined within the area subtended at the surface by the poleward limits of central oceanic water. Such a correlation for a benthic fish group would make sense only if the ultimate distribution of adults were dependent on near-surface processes. The logical mediator of such a surface-dependent distribution in *Bathypterois* is the larval or juvenile stage which may exist mesopelagically. Paxton (1967) has demonstrated that the hori-

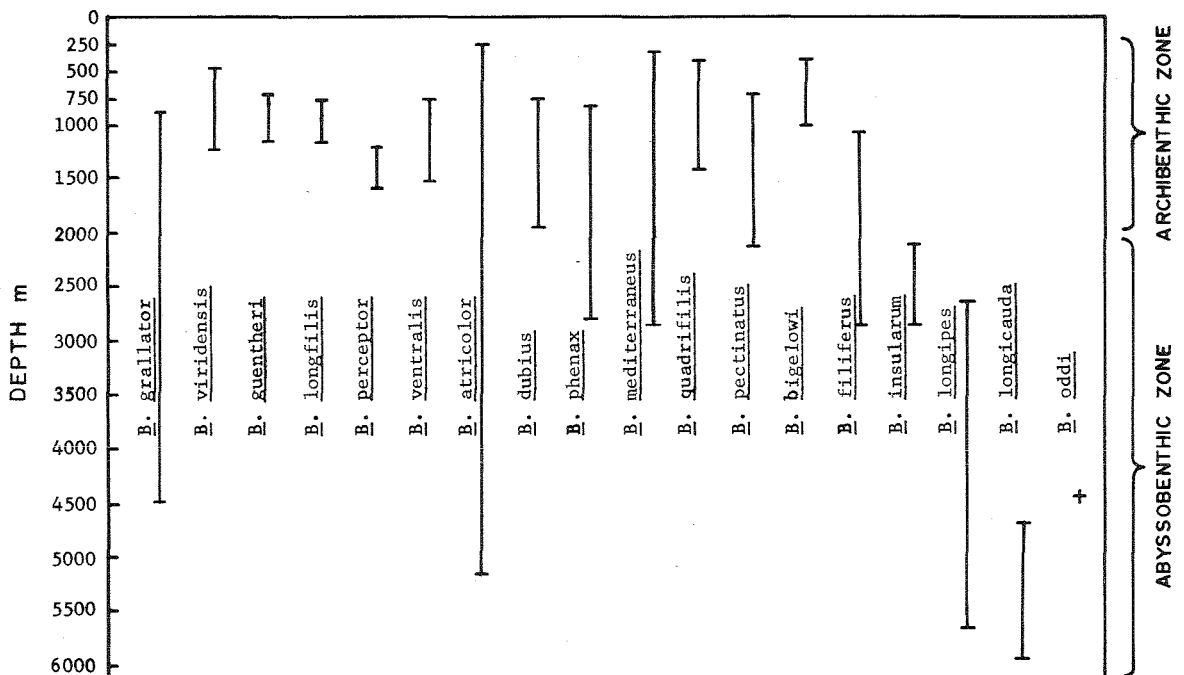


Fig. 30. A comparison of the known depth ranges of species of *Bathypterois*.

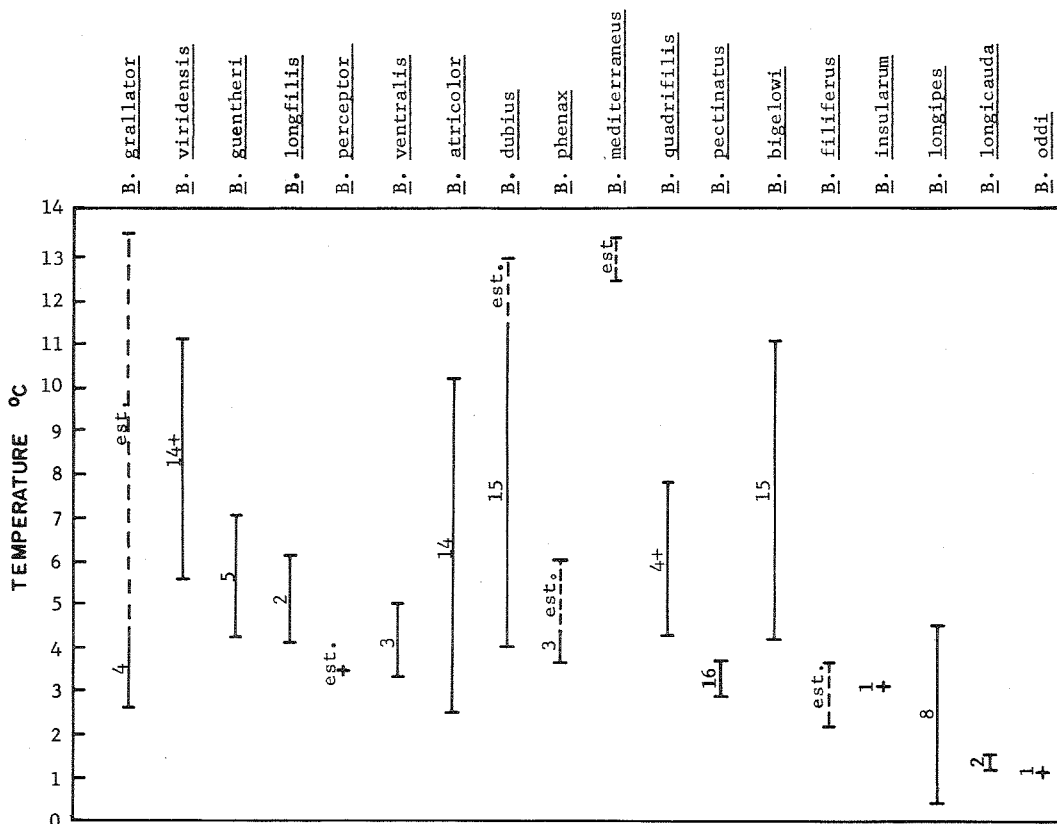


Fig. 31. A comparison of the known temperature ranges of species of *Bathypterois*, with the number of temperature records available for each species indicated. In some cases temperature limits have been estimated by correspondence of capture locality with independent temperature data.

zonal distributions of certain myctophids coincide with the limits of particular watermasses. The same may be true of the juvenile stages of *Bathypterois*.

Although *Bathypterois* is a benthic fish, it takes its food from the water column rather than from the substrate. Therefore, it is largely independent of particular bottom types or particular associations of bottom-feeding invertebrates. For example, *B. atricolor* has been obtained on various substrates including green, brown, and gray muds, globigerina and foraminifer oozes, coral sand, fine gray sand, stones, and gravel. However, *Bathypterois* would seem to require a suitable substrate upon which to rest with its produced stiltlike fin rays. Thus areas of very rough bottom may be unsuitable for members of the genus.

Bottom temperature appears to be the primary factor controlling the vertical distribution of individual species of *Bathypterois*. It may also effectively determine the horizontal ranges of certain species. The limits of e.g., *B. bigelowi*, a species endemic to the Pan-Caribbean region, are basically coincidental with the geographic limits of 4-10°C bottom water in the central western Atlantic. Thus, although the

species is quite eurythermal (between 4°C and 11°C), it is limited bathymetrically and geographically by its apparent inability to tolerate water colder than 4°C. At the opposite extreme is *B. longipes* with a broad - perhaps circumglobal - distribution, apparently made possible by a tolerance to cold bottom water (temperature range: 0.4°C to 4.5°C). It is the upper end of the temperature tolerance range that tends to determine its bathymetric and geographic occurrence; the species has not been found above 2600 m, nor has it been found in areas of the Caribbean that are deeper but relatively warm (temperatures greater than 4°C).

A second factor controlling the distribution of individual species of *Bathypterois* may be competitive exclusion. Thus, *B. atricolor* is extremely eurythermal (2.5°C to 10°C) and eurybathic (250-5100 m). Consequently this well-known species is nearly circumglobal (Fig. 24) but is curiously absent from the western Atlantic and from most of the northeastern Atlantic where it is replaced by *B. phenax* and *B. dubius*, respectively. The three species are closely related members of the same subgenus and have overlapping temperature (Fig.

31) and depth (Fig. 30) ranges. They are similar in size and, more importantly, degree of elongation of the stiltlike pelvic and caudal fin rays. This morphological similarity means that the three species stand the same height off the bottom, making them potential competitors for the same near-bottom layer of zooplankton. *B. phenax* and *B. dubius* have more restricted bathymetric ranges than *B. atricolor* and may in other ways be more specifically adapted than is the wide-ranging *B. atricolor* to conditions within their own geographic areas. They are apparently successful in outcompeting *B. atricolor*, preventing it from invading their respective areas. In the limited area where *B. phenax* and *B. atricolor* do overlap geographically off central western Africa, they apparently remain separate ecologically by adjusting their bathymetric ranges in opposite directions. Off Africa *B. phenax* is known from 2523 m and 2784 m, *B. atricolor* from 914-2332 m. By way of comparison *B. phenax* occurs over a much broader bathymetric range (827-2651 m) in the western Atlantic; *B. atricolor* also exhibits a broader range (258-5150 m) elsewhere. Thus it seems that the potential for interspecific competition plays a role in determining the horizontal and vertical distributions of some species of *Bathypterois*.

ABUNDANCE

In the Tongue-of-the-Ocean and Exuma Sound in the Bahamas, where an assessment of the deep benthic fish population is underway, a quantitative measure of the importance of *Bathypterois* and its allies to the deep-sea community is possible for the first time. Based on limited records of deep benthic fishes, Nybelin (1957) had indicated that *B. longipes* was possibly the most abundant abyssobenthic species in the northeastern Atlantic, thus suggesting an important role in general for *Bathypterois* as a deep-sea fish. In the deep Bahamian basins the three common species of *Bathypterois* combined with the allied *Ipnots* rank third in abundance behind synphobranchid eels and brotulids. The four ipnotine species represent approximately 15% of all benthic fishes obtained by the R/V "Columbus Iselin" in the Bahamian basins. However, they account for just 3% of the total benthic fish biomass. For the Tongue-of-the-Ocean alone preliminary estimates of population density and biomass per unit area have been determined for the four common ipnotine species as follows:

Species	Density, individuals/km ²	Biomass, g/km ²
<i>B. phenax</i>	87.9	1493
<i>B. viridensis</i>	13.7	322
<i>B. grillator</i>	3.5	565
<i>I. murrayi</i>	69.8	320

These estimates of population density and biomass may not be generally applicable to other geographic areas, even for these same species of *Bathypterois* and *Ipnots*. However, as the first such estimates for deep benthic fish species, they do provide a basis for order of magnitude estimates on a larger geographic scale.

FIN RAY SPECIALIZATIONS

Function of the specialized pectoral fin rays
The elaborate pectoral fins of *Bathypterois* are undoubtedly employed as sensory devices to detect the presence of its planktonic prey. Submersible-obtained photographs (Church 1971) of *B. viridensis* reveal that the long pectoral fin rays are spread and arched forward to encircle the head. The exact sensory function of these rays is unknown, as is the exact mode of feeding in *Bathypterois*. The extremely large gape, reduced dentition, and numerous long closely-set spinulose gill rakers suggest it is a filter feeder, as does its habit of facing into a current. The outspread pectoral fins may serve as tactile receptors, simply assaying the impinging current with the delicate fin membranes for the presence or absence of zooplankton. However, *Bathypterois* has never been observed to hold its mouth open in the fashion of a filter feeder, even when the pectorals are outspread. An alternative mode of feeding could be the sucking in of prey by dropping the lower jaw at the appropriate moment. This type of feeding would depend on the reception of particular distant stimuli, and would imply a more discriminatory sensory role for the pectorals. Perhaps the antennalike array of pectoral rays encircling the head is capable of detecting delicate nearby movements or of sensing chemical stimuli emanating from its prey.

It seems unlikely that the specialized fin rays are actually employed to dig in or to raise food items from the substrate. Their very delicate tips and the delicate interradial membrane are ill-equipped for

such a function. Also, the muscles supplying the pectoral fin rays are better suited for an arching outward, upward, forward movement than for a downward type of movement necessary for probing and feeding in a bottom fish standing on stilts. Moreover, in some species of *Bathypterois* the pectoral fin rays are insufficiently elongate to reach the substrate while the fish is standing upon it.

Nerve tracing reveals that the long pectoral rays are innervated by unusually enlarged spinal nerves which bear large extravertebral ganglia proximally (Pl. 7 Figs 3, 4). A comparable arrangement exists in *Prionotus*, where a chemical sensibility has been demonstrated for the spinally innervated specialized fin rays (Scharrer et al. 1947). Additionally in *Bathypterois*, regions of the medulla usually associated with the coordination of somatic responses to the chemical sense of taste are enlarged. These are the vagal and facial lobes (Pl. 7 Fig. 4). However, the somatic branch of the facial nerve (the ramus lateralis accessorius) does not supply the pectoral fin in *Bathypterois*. Nevertheless, these enlarged lobes deserve further investigation, since similar medullar enlargements have been shown to be associated with the spinal nerves supplying the specialized fin rays in *Bregmaceros* (Okamura 1966).

The spinal nerves in *Bathypterois* course directly to the fin rays of the pectoral fin without detectable branching or interconnection, implying a discrete flow of sensory input along each of the three nerves. The nerves divide along the bases of the fin rays to supply each long ray of the pectoral. The pattern of fin-ray innervation seen in *B. quadrifilis* (Fig. 32) is generally applicable to the other species of the genus. Spinal nerve 1 supplies the two produced rays (rays 3 and 4) in the upper part of the pectoral fin; spinal nerve 2 innervates several long rays (rays 8 through 13 in Fig. 32) in the upper half of the lower part of the pectoral fin; spinal nerve 3 innervates the remaining long rays (rays 14 through 17) in the lower part of the pectoral fin. The rudimentary rays of the pectoral fin (rays 1, 2, 5, 6, and 7) do not appear to be innervated. The spinal nerves send a process up the center of each of the long pectoral fin rays. The fate of these processes distally is unknown, since the delicate tips of the rays and the associated interradiol membrane are invariably damaged during trawling. Material suitable for histological examination with respect to the structure of nerve endings in the pectoral fin of *Bathypterois* could probably only be obtained with a research submersible. Until such material be-

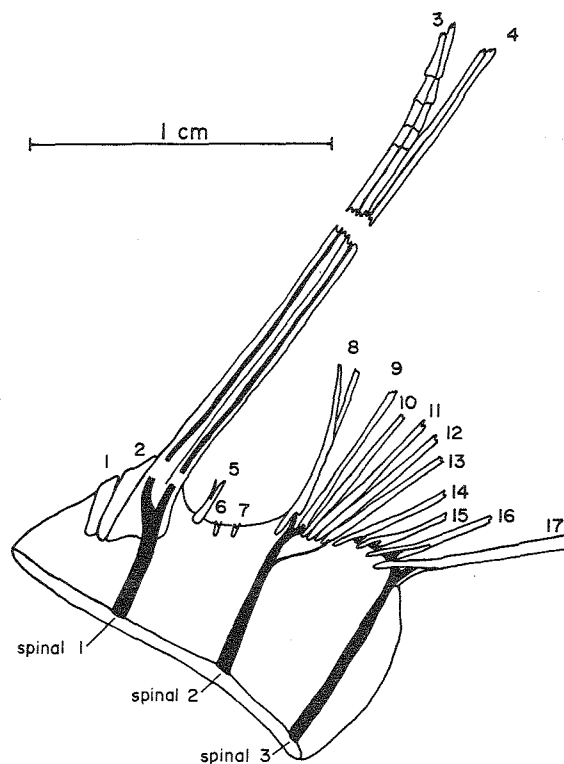


Fig. 32. The pattern of spinal nerve innervation of the pectoral fin rays in *B. quadrifilis*, MCZ 44235 (semi-diagrammatic).

comes available it may remain impossible to determine the precise sensory function of the pectoral fin of *Bathypterois*.

Function of pelvic and caudal fin ray pads

The curious fleshy pads at the ends of the produced pelvic and caudal fin rays probably serve as no more than abrasion surfaces to protect the tips of the rays where they contact the substrate. Histological sections of these structures show that they consist of epithelial tissue (Pl. 7 Figs 1, 2). A sensory function for these structures or the rays themselves seems unlikely. In contrast to the well-innervated produced rays of the pectoral fins the produced rays of the pelvic and caudal fins are poorly innervated.

The stiff elongate pelvic and caudal fin rays seem to serve simply to elevate the fish above the substrate. It seems quite unlikely that the pelvic rays are ever employed directly in raising food from the substrate to the mouth. These specialized fin rays do bear an important relation to feeding, however, since they elevate the fish into the water column where feeding occurs.

ASPECTS OF REPRODUCTION

Seasonality

The deep-sea realm has often been characterized as one of unusual environmental stability, largely devoid of temporal fluctuations in physical parameters. As a consequence of the absence of temporal cues, it has been assumed that reproduction in deep-sea organisms must not be synchronized in a seasonal sense. That is, one would always expect to find a certain percentage of ripe individuals in a population at any given time. However, preliminary analysis of ovaries in large numbers of *Bathypterois phenax* and *Ipnops murrayi* from the Bahamas (Tongue-of-the-Ocean and Exuma Sound) shows that reproduction in these deep benthic ipnopsine fishes is strongly seasonal. The specimens studied were obtained during three cruises in 1973 and 1974 of the R/V "Columbus Iselin" as part of the benthic fish population program at this institution. Depths of captures ranged between 1155 m and 1895 m.

Four arbitrary categories, IM, ER, R1, and R2, were established to describe progressive levels of ovarian maturity. Definition of these categories as applied to *B. phenax* and *I. murrayi* is as follows: IM - ovaries very small, eggs discernible with magnification, but very small and unpigmented; ER - ovaries small to moderate in size, eggs small and yellow to cream-colored; R1 - ovaries large and full, but eggs mostly small, uniform in size, and yellow to cream-colored; R2 - ovaries filling the body cavity, eggs variable in size, a high percentage large (approaching 1 mm in diameter), color tending

toward white, some eggs clear. The distribution of individuals among the four categories is summarized for each cruise in Table 4. Since *Bathypterois* and *Ipnops* are hermaphroditic (Mead 1960, Mead et al. 1964), percentages based on ovary evaluation alone reflect actual percentages of the whole sample population.

A comparison of category R2 (very mature ovaries) for the three cruises reveals marked reproductive seasonality in both species (Table 4). Curiously, however, the sexual cycles do not peak at the same time. *B. phenax* achieves gonad maturity in the fall, *I. murrayi* in the spring. Thus the reproductive cycles of the two species are exactly 180° out of synchrony. The significance of this fact is unknown, but it may represent an adaptive mechanism to reduce feeding competition among newly metamorphosed adults. How these species cue their reproductive cycles is also unknown. However, if the adult life span is short (one or two breeding cycles), then the reproductive cycle could simply be initiated and the reproductive clock set by the event of metamorphosis in the juvenile. One can assume that metamorphosis of pelagic juveniles to the adult stage is cued by seasonal events near the surface. In turn sexual development may begin immediately upon metamorphosis, so that the event itself may function as a sort of secondary cue to synchronize seasonality in the resulting adult population.

Development

Little is known concerning the developmental stages of *Bathypterois*. Only two juvenile specimens have

Table 4. The distribution of individuals in various stages of gonad maturity in three sample populations of *B. phenax* and *I. murrayi* obtained in the Bahamas (Tongue-of-the-Ocean and Exuma Sound) by the "Columbus Iselin".

Cruise	Period	Total n	% of Sample			
			IM	ER	R1	R2
<i>B. phenax:</i>						
CI-7305	Feb.-Mar. 1973	117	29.9	36.8	33.3	0
CI-7315	Sep. 1973	106	36.8	6.6	27.4	29.2
CI-7402	Feb. 1974	96	26.0	39.6	34.4	0
<i>I. murrayi:</i>						
CI-7305	Feb.-Mar. 1973	165	21.8	10.9	13.9	53.3
CI-7315	Sep. 1973	67	20.9	17.9	61.2	0
CI-7402	Feb. 1974	192	9.4	8.3	13.5	68.8

so far been obtained, both in poor condition. With regard to related ipnopine fishes only five juvenile specimens are known (Okiyama 1972), all pertaining to the genus *Bathytyphlops*.

The smallest known adults of 16 species of *Bathypterois* range between 42 and 96 mm in SL (the remaining species are poorly known), giving an estimate of the length range within which metamorphosis is completed. This is a reasonable estimate, since specimens at the lower end of this range retain certain larval features absent in the adult, and could be termed subadults. For example, a 54 mm SL specimen of *B. phenax* (MCZ 45918), the smallest known for the species, was obtained in a bottom trawl and has the general appearance of an adult. But this specimen retains an incompletely resorbed pseudobranch, has only an indication of the incipient subcaudal notch, and has rays 1 and 2 of the pectoral fin reduced but not fully rudimentary as in the adult. A second example is a 42 mm SL specimen of *Ipnops murrayi* (UMML 30798), also the smallest known example of its species. It too has the appearance of an adult, but the eye plaques are elliptical (vs. the normal angular shape in adults) and not yet fully expanded anteriorly and laterally.

Considering the widespread occurrence and relative abundance of adults of *Bathypterois* and related ipnopine fishes, it seems remarkable that so few juvenile specimens are known. It is possible that the few examples obtained near the surface were distressed individuals, and that larval development in ipnopine fishes normally takes place at mesopelagic depths or even deeper. In this respect, the available

evidence (Mead et al. 1964) concerning several other major deep benthic fish groups (Alepocephalidae, Brotulidae, Macrouridae, Liparidae, and Zoarcidae) also indicates deep development.

Mature eggs stripped from freshly-trawled specimens of *I. murrayi* sink in sea water samples with salinities adjusted to range between 33‰ and 37‰ (at 20°C). This suggests that their density is such that they do not ascend in the water column immediately upon release. It does not, of course, preclude the possibility of water uptake - with subsequent density alteration - prior to or following release of eggs. However, there are additional indications that the eggs at least remain near the bottom after release. First of all, the number of eggs produced is low (Mead et al. 1964). Secondly, the population densities of adults of ipnopine species suggest a wide spacing of individuals on the bottom. Thus, barring regular spawning aggregation or self-fertilization, the eggs must remain on the bottom for some length of time to insure fertilization. Self-fertilization is a possibility, since ipnopine species, like all other chlorophthalmids, are synchronous hermaphrodites (Mead 1960). However, it is unlikely that self-fertilization is the normal mode of reproduction in ipnopine fishes. If it were, one would expect a broadly distributed species (e.g., *B. atricolor*) to fragment into regional clonelike populations, with resulting character discontinuities between individual populations. But to the contrary, even the most broadly distributed species of *Bathypterois* display comparable character variability from region to region.

IV. SUMMARY

Relationships among the taxa of benthic myctophiform fishes are re-evaluated on the basis of comparative osteology. The benthic genera are placed in the three families Aulopidae, Synodontidae, and Chlorophthalmidae. The Synodontidae is resolved into the subfamilies Harpadontinae (*Harpadon* and *Saurida*), Bathysaurinae (*Bathysaurus*), and Synodontinae (*Synodus* and *Trachinocephalus*). The four deep benthic genera, *Bathypterois*, *Bathymicrops*, *Bathytyphlops*, and *Ipnops*, are united in a single subfamily, the Ipnopinae, of the Chlorophthalmidae. *Chlorophthalmus*, *Parasudis*, and *Bathysauropsis* comprise a second subfamily, the Chlorophthalminae, of the Chlorophthalmidae. The ipnopine genus *Bathy-*

pterois is subdivided into three subgenera: *Benthosaurus* (three species), *Bathypterois* (nine species), and a new subgenus *Bathycygnus* (six species).

The genus *Bathypterois* is revised on a worldwide basis. The previously described nominal species and subspecies are resolved into 16 species; two new species are described.

The horizontal and vertical distribution of *Bathypterois* is discussed in relation to physical and biological factors. The latitudinal limits of the genus are found to coincide with the poleward limits of central oceanic water. The vertical and horizontal distributions of individual species appear to be controlled by bottom temperature. Interspecific competition

also appears to influence the distributions of species of *Bathypterois*.

Estimates of population density and biomass per unit area are determined for the four common ipnopine species of the Bahamas (Tongue-of-the-Ocean), including three species of *Bathypterois*. Population densities range from 3.5 to 87.9 individuals/km²; wet biomasses range from 320 to 1493 g/km². These are the first such quantitative estimates for ipnopine fishes. Together the ipnopine species comprise the third most abundant benthic fish group of deep Bahamian basins.

The fin rays of the specialized pectoral fins of *Bathypterois* are found to be innervated by enlarged spinal nerves with enlarged proximal ganglia. A sensory function related to feeding is implied for the pectoral fins. The produced outer pelvic and lower caudal fin rays are found to be poorly innervated

and encased distally by a pad of epithelial tissue. These specialized rays appear to serve as stilts to elevate *Bathypterois* into the near bottom layer of zooplankton upon which it feeds.

Reproduction in two ipnopine species, *B. phenax* and *Ipnots murrayi*, is shown to be strongly seasonal, contrary to the general supposition of non-seasonality in deep-sea organisms. The smallest adults of 16 species of *Bathypterois* range between 42 and 96 mm in standard length, giving an estimate of the length range within which metamorphosis is completed. Individuals near the low end of this range are found to retain certain larval characters. The paucity of larval examples of *Bathypterois* and the negative buoyancy of freshly stripped eggs suggest the possibility of deep development in this genus and other deep dwelling ipnopine fishes.

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PLATE 4

- Fig. 1. Dentary teeth of *Bathymicrops regis*, UMML 31265.
- Fig. 2. Dentary teeth of *Bathypterois viridensis*, UMML 31445.
- Fig. 3. Dentary teeth of a young adult (SL 72 mm) of *Bathypterois phenax*, UMML uncat., "Columbus Iselin" St. 154, to show the large outwardly-directed arrowhead-shaped teeth.