

A FOURTH NEOTROPICAL SPECIES  
OF SYNBRANCHID EEL AND THE  
PHYLOGENY AND SYSTEMATICS  
OF SYNBRANCHIFORM FISHES

DONN ERIC ROSEN AND P. HUMPHRY GREENWOOD

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## ABSTRACT

The discovery of an undescribed species of synbranchiform eel, with populations in the Atlantic slope of Mexico, Guatemala, Honduras, Cuba, and northeastern South America, presented problems in its taxonomic assignment that required a review of the genera and higher groups within the order. Analyses of superficial anatomy, skull, and vertebral column, but particularly of the detailed structure of the hyoid, gill arch, and branchial vascular systems indicated that some of the groups of synbranchiform species are paraphyletic and others polyphyletic, and that the Alabetidae, long associated with the swamp eels, should be excluded from the assemblage. A phylogenetic hypothesis is put forward that divides all synbranchiforms (treated here as the single family Synbranchidae) into two line-

ages: the Macrotreminae (containing only *Macrotrema caligans*) and the Synbranchinae [including three genera: *Ophisternon* (containing the species *bengalense*, *gutturale*, *candidum*, *afrum*, *infernale*, and the new neotropical form *aenigmaticum*), *Synbranchus* (containing *mar-moratus* and *madeirae*), *Monopterus* (containing *albus*, *boueti*, *cuchia*, *fossorius*, and two forms originally described under the name *indicus*)]. The generic names *Furmastix* and *Anomatophasma* are placed in the synonymy of *Ophisternon*, and *Typhlosynbranchus* and *Amphipnous* are placed in the synonymy of *Monopterus*. The nomenclatural histories of the genera and some species are discussed and an analytical key to the subfamilies, genera, and species is provided.

## INTRODUCTION

The Synbranchidae, or swamp eels, a family of eel-like percomorph fishes, are widely distributed in tropical and subtropical regions of the New World and Old World, and are especially well represented in Asia and Australasia. Their eel-like appearance is enhanced by lack of paired fins (at least in postlarval stages; see Derjugin, 1912; Taylor, 1913; Wu and Liu, 1942; Rangarajan and Jacob, 1960), the reduction of the long dorsal and anal fins to low, rayless skin folds generally confluent with the much reduced caudal fin, and the absence or great reduction of the squamation.

Synbranchids occur in a variety of habitats, both freshwater and estuarine. Many species live in swamps or marshy areas, where burrowing and amphibious habits are commonly displayed, although the same species may be found in streams, rivers, ponds, or lakes (Day, 1889; Das, 1927, 1946; Hora, 1935; Nayar, 1952; Lüling, 1958).

Two Old World and one New World species are cavernicoles (Hubbs, 1938; Mees, 1962; Eapen, 1963); all show considerable atrophy of the eye tissues. A trend toward eye reduction is also apparent in several epigeal taxa, especially among those with burrowing habits (Nayar,

1952). Even when the eye is fully developed it is small and lies below a thickened covering of skin.

Many, and probably most, synbranchids are capable of some form of aerial respiration and at least three species possess paired, lunglike suprapharyngeal diverticula that have a respiratory function (Taylor, 1831; Müller, 1839; Das, 1927; Hora, 1935; Nayar, 1952; Lüling, 1958; Liem, 1961; Samuel, 1963; Johansen, 1966, 1970; Datta Munshi and Singh, 1968; Lomholt and Johansen, 1974).

In this work 15 synbranchid species (including the new taxon described below) are recognized, four from the New World and 11 from the Old. We are of the opinion that this number will be increased when more material is available for meristic and detailed anatomical studies. The zoogeographical problems raised by the distribution of the Synbranchidae are dealt with in a separate publication (Rosen, In press).

Major general classifications treating the Synbranchidae are those of Regan, 1912; Berg, 1940, 1947; Norman, 1966; Greenwood, Rosen, Weitzman, and Myers, 1966; McAllister, 1968; Gosline, 1971; and Lindberg, 1971. However, like Gill (1906), Liem (1968), and Gosline (1971) before us, we do not consider the Alabe-



tidae to be synbranchid fishes; an alternative placement of the Alabetidae is suggested below.

We are unable to offer any evidence of the relationships of the Synbranchidae to any particular group of percomorph fishes, although we have found new evidence that is consistent with their placement in the Percomorpha. We cannot, however, agree with the reasons advanced by McAllister (1968) for relating the synbranchids with the mastacembelids (see discussion below on hyoid structure).

Few groups of teleostean fishes have had so long and obscure a taxonomic history as the swamp eels. Their scientific description dates back to Zuiew (1793) and Bloch (1795). Nevertheless, their nomenclatural status, the number of species to be recognized, and their inter- and intra-relationships have been little understood. So great is the confusion surrounding swamp eel nomenclature that some authors have attempted to contrast the characters of specimens identified in collections by the different names that are objective synonyms of a single taxon. Genuine biological difficulties in the taxonomic allocation of demonstrably distinct taxa have resulted from attempts to arrange species on the basis of their similarities and differences in external morphology—difficulties that should not surprise us considering that these fishes have a virtually featureless superficial anatomy and are rather variable in the very few external characters that can be measured or described precisely. The literature contains only scattered and incomplete accounts of the internal anatomy, especially that of the skull and branchiovascular apparatus. The few striking specializations uncovered by anatomical investigations have been applied according to that uncritical dictum of evolutionary taxonomy that hierarchically separates species with respect to the magnitude of their differences but without regard to their genealogical relationships. Hence, the Indian *Amphipnous cuchia* was placed in a separate family (Amphipnoidae) because it possesses paired suprabanchial sacs, whereas the other swamp eels (without sacs) were relegated to the Synbranchidae (Regan, 1912). One other Old World form, *Monopterus albus*, was separated briefly from the Synbranchidae in a family of its own (see Jordan, 1923). Prior to our own study 13 species of swamp eels were arranged in

seven genera and two families included in one of two suborders of the order Synbranchiformes.

The research reported here was undertaken as a result of the chance discovery that a large number of specimens from the New World previously assigned to *Synbranchus marmoratus* represent a distinct form unrelated to that species. The suspicion that the taxon *marmoratus* includes another species arose during a recent reexamination of radiographs that had been made to obtain vertebral counts for the report of a second Amazonian species of *Synbranchus* (Rosen and Rumney, 1972). In connection with current studies of Guatemalan fishes by Rosen, the radiographs of Pacific and Atlantic slope Guatemalan synbranchids were compared and it was discovered that in some Atlantic slope specimens the shoulder girdle appeared to be less remote from the skull than in examples of Pacific slope material. The difference in relative position of the cleithrum was subsequently confirmed by dissection. A detailed study of the original, and many new, radiographs showed that all specimens from the Atlantic slope of Guatemala, all but a single specimen from Mexico, all from Cuba, and five specimens from northeastern South America (Marajo Island at the Amazonian mouth, French Guiana, and Trinidad) showed the less remote shoulder girdle position. All of these specimens are considered to represent a distinct synbranchid species, which is described herein.

Detailed comparisons of the head anatomy of the newly recognized form with that of other synbranchids indicate that the new form may be more closely related to the cavernicolous *Furmastix infernalis* from Yucatan, and to certain Old World species, than it is to the widespread neotropical *Synbranchus marmoratus* and the Amazonian *S. madeirae*. These studies also revealed unsuspected interrelationships among Old World and New World swamp eels. In fact, it is our conclusion that without first having resolved some of the confusion concerning the phylogeny of synbranchiforms generally, a reasonable generic allocation of the previously unrecognized New World species would not have been possible.

We acknowledge with pleasure loans and gifts of specimens from Drs. Reeve M. Bailey and Robert R. Miller (University of Michigan, Museum of Zoology; UMMZ), Stanley H. Weitzman

and Ralph Taylor (National Museum of Natural History, Smithsonian Institution; USNM), Karel Liem and Tyson Roberts (Museum of Comparative Zoology, Harvard; MCZ), William Eschemeyer (California Academy of Sciences, CAS), and James Reddell (specimens as gifts, assigned American Museum of Natural History numbers; AMNH). Additional material was available from the collections of the American Museum of Natural History and the British Museum (Natural History); BMNH. We especially thank Dr. Reeve M. Bailey for various kinds of nomenclatural assistance and Richard Vari and Lynn Hirsch, both of the Department of Ichthyology, the American Museum of Natural History, for technical help. We are also very pleased to acknowledge that most of the material of the new synbranchid described below was collected with financial support from Mr. James C. Greenway, Jr.

#### Abbreviations Used in Figures

a, afferent branchial artery  
 ach, anterior ceratohyal  
 ae I-IV, continuous affero-efferent artery, gill arches I-IV  
 an, anterior naris  
 art, articular  
 bb, basibranchial  
 bb-1(f), first basibranchial ankylosed with basihyal  
 bh, basihyal  
 bo, basioccipital  
 bsph, basisphenoid  
 cb, ceratobranchial  
 ce, combined efferent artery from gill arches III and IV  
 Da, dorsal aorta  
 deth, dermal ethmoid  
 dhh, dorsal hypohyal  
 dn, dentary  
 e, efferent branchial artery  
 ect, ectopterygoid  
 end, endopterygoid  
 epb, epibranchial  
 epo, epiotic  
 exo, exoccipital  
 fr, frontal  
 hb, hypobranchial  
 Hyd, hyoidean artery  
 hyo, hyomandibular  
 iab, interarcual bone  
 Ic, internal carotid artery

ih, interhyal  
 io, interopercle  
 lat, lateral ethmoid  
 latp, lateral process  
 meta, metapterygoid  
 mx, maxilla  
 na, nasal  
 nsp, neural arch and spine  
 op, opercle  
 pal, palatine  
 pas, parasphenoid  
 pch, posterior ceratohyal  
 phb, pharyngobranchial  
 phb+tp, pharyngobranchial with fused, dermal, toothed component  
 Pla, paired lateral aorta (radix aorta)  
 plg, articular plug of first vertebra  
 pmx, premaxilla  
 pn, posterior naris  
 pop, preopercle  
 prb, pleural rib  
 pro, prootic  
 pto, pterotic  
 ptsph, pterospheoid  
 pzyg, postzygapophysis  
 qu, quadrate  
 rab, M. retractores arcuum branchialium  
 ret, retroarticular  
 se I-II, secondary efferent artery from first or second gill arch  
 ses, sesamoid bone  
 Sinus, vascular sinus in buccopharyngeal epithelium  
 sop, subopercle  
 spho, sphenotic  
 sym, symplectic  
 tp, tooth patch; dermal toothed component of pharyngobranchial  
 t-rab, tendon of M. retractores arcuum branchialium  
 trp, transverse process  
 unc, uncinat process  
 up, upper pharyngeal tooth plate  
 Va, ventral aorta  
 vhh, ventral hypohyal  
 vo, vomer

#### PRELIMINARY NOMENCLATURAL NOTE

The results of this investigation cause us to recommend numerous taxonomic and nomenclatural changes. Because nomenclatural details have been such a persistent source of confusion in

prior discussions of synbranchiforms, we have elected to introduce our nomenclatural recommendations at the outset (table 1), and to employ the new and revised usages throughout the body of the present paper. In addition, we call to the reader's attention that the orthography of some of the specific names has been altered to make them conform in gender with new generic assignments. For example, six specific names are now assigned to the genus *Ophisternon* M'Clelland.

This generic name is formed from the Greek roots *ophis* (=serpent) and the neuter suffix *sternon* (=chest). Accordingly, trivial adjectival names placed in *Ophisternon* must agree in gender as follows (earlier usage given in parentheses): *bengalense* (=bengalensis), *afrum* (=afer), *infernale* (=infernalis), *candidum* (=candidum), *aenigmaticum* (newly described below), *gutturale* (=gutturalis).

GENERAL SYNBRANCHOID ANATOMY AND INITIAL  
PHYLOGENETIC HYPOTHESES

The 15 species of synbranchoids recognized in this study are presently arranged in seven genera (table 1). We have seen material of all but *Monopterus* "*indicus*" Eapen (1963). On superficial comparison the species are divisible into two main groups. *Macrotrema caligans* is distinguished from all others in the extensive gill opening, the position of the posterior nares antero-dorsal to the eye (fig. 1), and the presence of a small but distinct caudal fin supported by as many as 14 bony rays (fig. 2). All other species have the gill opening confined to the ventral body wall, the posterior nares dorsomedial to the eye, and the caudal fin further reduced or absent.

What remains of the caudal fin is a membrane continuous with the dorsal and anal fin folds and having seven or fewer slightly ossified rays or un-ossified filaments. In having derived conditions of the gill slit, narial position, and caudal fin relative to those of *Macrotrema*, other synbranchoids are inferred to be more closely interrelated than is any one of them to *Macrotrema*. It is therefore proposed that all synbranchoids be placed in a single family, the Synbranchidae, divided into two subfamilies, the Macrotreminae and Synbranchinae.

The Synbranchinae can be subdivided on some relatively simple criteria. A group of Old

TABLE 1  
Current Taxonomic Assignments of the Species of Synbranchoids  
and Those Proposed in This Study

Species and Author	Current	Proposed
<i>caligans</i> Cantor	<i>Macrotrema</i>	<i>Macrotrema</i>
<i>bengalense</i> M'Clelland	<i>Synbranchus</i>	<i>Ophisternon</i>
<i>afrum</i> Boulenger	<i>Synbranchus</i>	<i>Ophisternon</i>
<i>infernale</i> Hubbs	<i>Furmastix</i>	<i>Ophisternon</i>
<i>candidum</i> Mees	<i>Anomatophasma</i>	<i>Ophisternon</i>
<i>aenigmaticum</i> , new species	<i>Synbranchus marmoratus</i> (part)	<i>Ophisternon</i>
<i>gutturale</i> Richardson	<i>Synbranchus bengalensis</i> (part)	<i>Ophisternon</i>
<i>marmoratus</i> Bloch	<i>Synbranchus</i>	<i>Synbranchus</i>
<i>madeirae</i> Rosen and Rumney	<i>Synbranchus</i>	<i>Synbranchus</i>
<i>albus</i> Zuiew	<i>Monopterus</i>	<i>Monopterus</i>
<i>boueti</i> Pellegrin	<i>Typholsynbranchus</i>	<i>Monopterus</i>
<i>cuchia</i> Hamilton	<i>Amphipnous</i>	<i>Monopterus</i>
<i>fossorius</i> Nayar	<i>Amphipnous</i>	<i>Monopterus</i>
" <i>indicus</i> " Eapen	<i>Monopterus</i>	<i>Monopterus</i>
<i>indicus</i> Silas and Dawson	<i>Amphipnous</i>	<i>Monopterus</i>



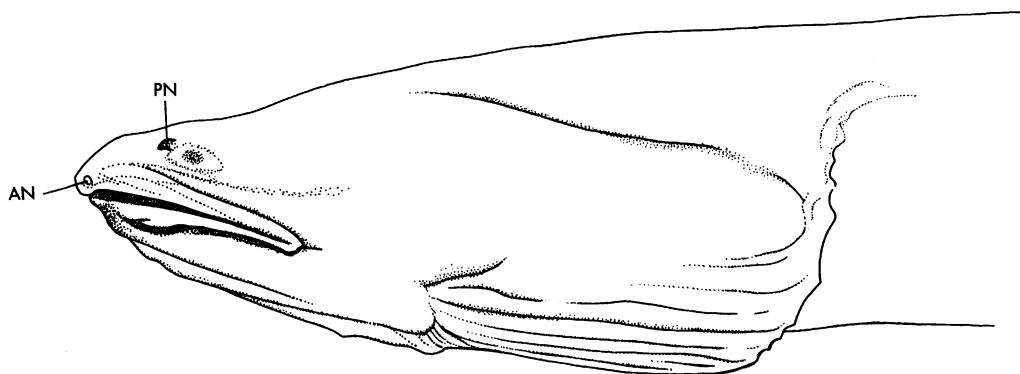


FIG. 1. Head of *Macrotrema caligans*. MCZ 47107; Thailand. Note position of posterior naris anterior to eye.

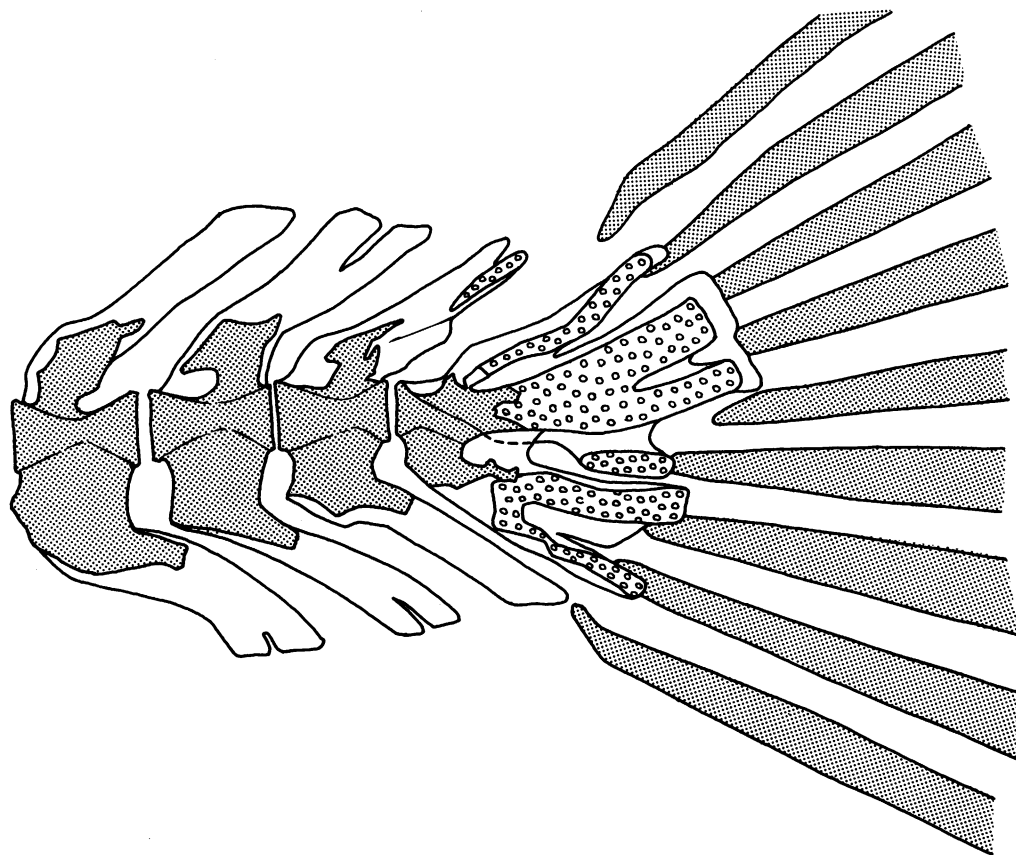


FIG. 2. Caudal skeleton and caudal fin ray bases in *Macrotrema caligans*. BMNH 1908.7.13:1; Singapore. Nine caudal rays are shown, but as many as 14 may be present. Hypural elements are better developed in this species than in any other synbranchoid.

TABLE 2  
Vertebral Number in the Synbranchidae  
Total Number and Range of Abdominal + Caudal Elements (in Parentheses)

	100	106	112	118	124	130	136	142	148	154	160	166	172	178	184	190
<i>Macrotrema caligans</i>	1 <sup>a</sup>	1 (79 + 24)														
<i>Ophisternon bengalense</i>				1	1	2	1	2	1 (71 - 92 + 49 - 61) <sup>b</sup>							
<i>gutturale</i>	1	1	3	7	1	(80 - 90 + 30 - 40)										
<i>candidum</i>													2 <sup>c</sup> (51, 54 + 109, 111)			
<i>afrum</i>							1 (80 + 50)									
<i>infernale</i>								1 (67 + 72)								
<i>aenigmaticum</i>	1	2	1	2	3	4	5	5	4	3	5	3	1 (70 - 82 + 25 - 58)			
<i>Synbranchus marmoratus</i>																
<i>maderiae</i>				1	1	3	13	7	14	57	49	17	4 (68 - 99 + 37 - 73) <sup>d</sup>			
<i>Monopterus albus</i>													1	1	4	1 (86 - 91 + 65 - 73)
<i>boueti</i>								1	1	3	5	4	16	13	8 (88 - 102 + 45 - 74) <sup>e</sup>	
<i>cuchia</i>													1	1	1	1 (140 - 144 + 39 - 45)
<i>fossorius</i>													1	1	1	1 <sup>f</sup> (99 - 112 + 55 - 70)
<i>indicus</i>				1			1 <sup>g</sup> (73, 76 + 45, 56)									
"indicus" Eapen							1	1	1 (total = 137 - 144; 93 - 99 + 42 - 45) <sup>h</sup>							1 <sup>i</sup> (135 + 24)

<sup>a</sup>Count of 100 from Günther (1870).

<sup>b</sup>Counts taken from specimens collected in India, Shri Lanka (Ceylon), Philippines, Thailand.

<sup>c</sup>Counts from Mees (1962).

<sup>d</sup>Counts taken from specimens collected from Argentina north to Pacific slope Guatemala; a single count, not shown, of 172; counts from Laguna Atescatempa, Guatemala = 128 - 139 (80 - 83 + 47 - 56).

<sup>e</sup>Counts taken from specimens collected in China, Japan, Burma, Java.

<sup>f</sup>Count of 188 from Günther (1870).

<sup>g</sup>Count of 129 from Nayar (1952).

<sup>h</sup>Counts from Silas and Dawson (1961); the ranges given representing 32 specimens are greater than the two for which exact figures were presented: 95 and 99 abdominal and 42 caudal.

<sup>i</sup>Count of 159 from Eapen (1963).

World species including *albus*, *boueti*, *cuchia*, *fosorius* "indicus" Eapen, and *indicus* (Silas and Dawson), and making up the genus *Monopterus*, are characterized by having the soft tissue surrounding the upper jaw forming a kind of jowl that slightly overhangs or extends beyond parts of the lower jaw; as a consequence, these species lack the distinct, swollen upper lip fold of all other Synbranchidae (figs. 3-23). The two species of *Synbranchus*, *marmoratus*, and *madeirae*, are distinguished by having the ventral gill opening reduced to a tiny flap or pore bounded on the right and left by deep folds of tissue that are continuous with the branchiostegal membrane, by having the shoulder girdle displaced posteriorly to the level of the fifth or sixth abdominal vertebra, and the posttemporal bone reduced to a simple rod unconnected with the supracleithrum.

The two groups, *Monopterus* and *Synbranchus*, are similar to each other in having members

generally with high precaudal vertebral counts as compared with those of other synbranchids (table 2).

There are two apparent exceptions to the divisions of the Synbranchidae thus far outlined. The largely Indian species, *cuchia*, and the African *boueti*, also have the shoulder girdle remote from the skull and the posttemporal reduced or absent, but other characters analyzed below support their inclusion in a group with *albus* (based on the structure of the upper lip).

The recently described *Monopterus* "indicus" Eapen (1963) is said by its describer to have a vertebral count that would be aberrant in this group (135 abdominal and 24 caudal) and to have the posterior nares anterior to the eye. We cannot comment on the vertebral count until material is available for study, but we conclude from Eapen's (1963) depiction of the head of "indicus" that the characteristic *Monopterus*

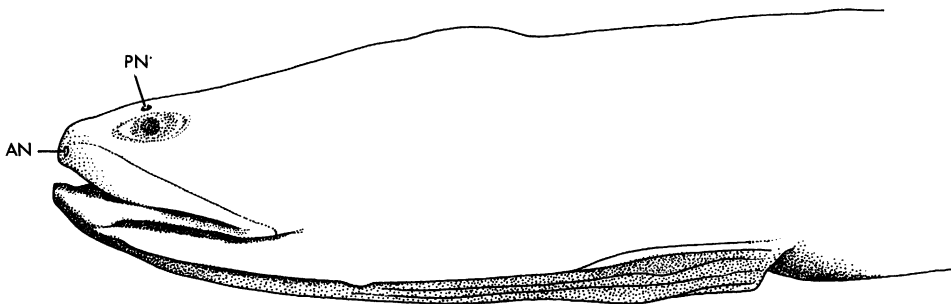


FIG. 3. Head of *Ophisternon bengalense*. BMNH 1860-3.19:365-375. Specimen from type series, India.

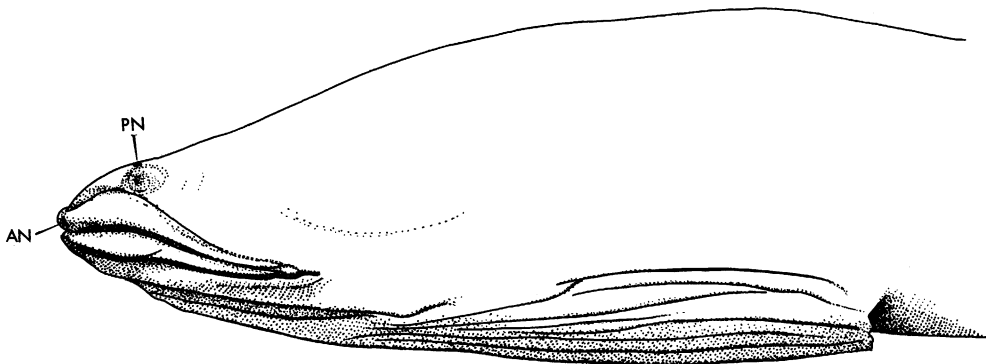


FIG. 4. Head of *Ophisternon bengalense*. MCZ 26377, Philippines.



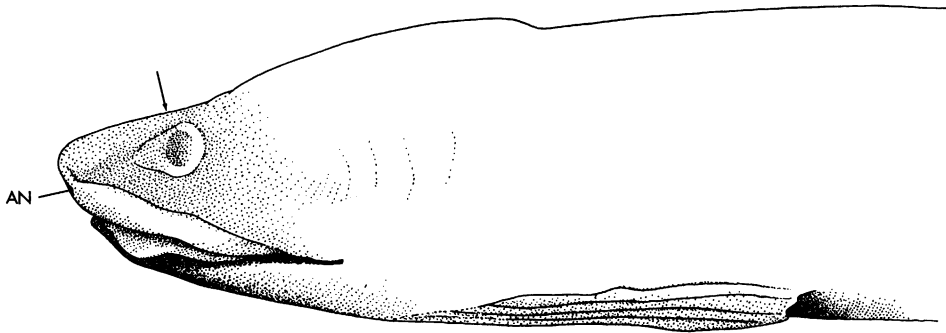


FIG. 5. Head of *Ophisternon gutturale*. AMNH 30893; Northern Territory, Australia. Arrow indicates position of posterior nares medial to eyes.

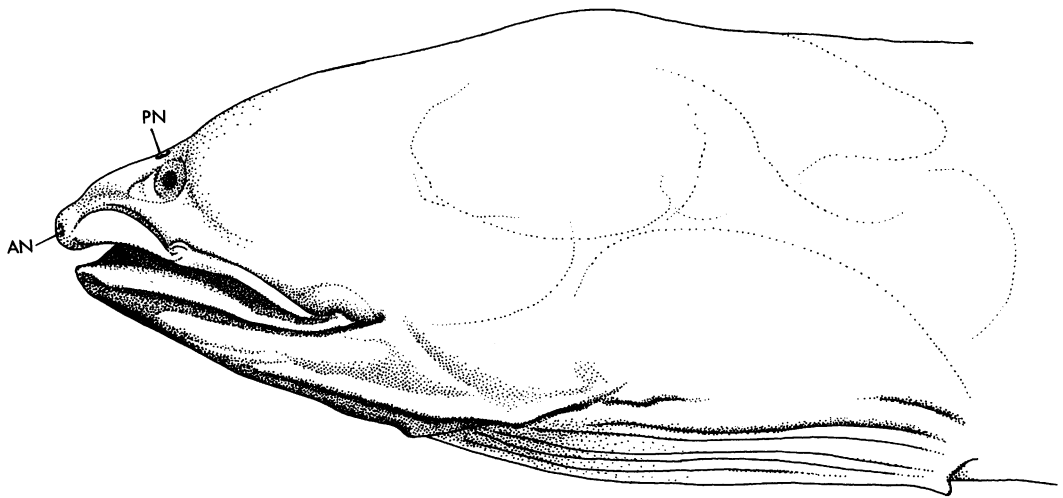


FIG. 6. Head of *Ophisternon afrum*. BMNH 1909-10.29:114. Lectotype. Portuguese Guinea.

upper lip jawl is present, that what he identifies as the posterior naris is the cephalic lateral line pore normally present in front of the eye in synbranchids, and that the rather large, lunate or subtriangular, ventral gill opening is typical of that found in *cuchia* and *fossorius*. The characteristics of this gill opening (fig. 22) are that a series of sharply incised grooves extend backward in the ventral midline from about the level of the eye to a point just short of the margin of the gill opening, and that the membrane of the large, lunate gill opening extends the width of the ventral surface of the body and merges smoothly with the ventrolateral body wall.

The nominal species *indicus* of Silas and Dawson (1961), is assigned by them to the genus *Amphipnous* because the presence in their specimens of a suprapharyngeal pouch, and the presence of minute scales in a peculiar pattern on the caudal region, are characters held in common with *cuchia* and *fossorius*. Thus far, only *cuchia*, *fossorius*, and *indicus* (Silas and Dawson) have been found to possess scales, among the species of Synbranchidae. Both *indicus* (Silas and Dawson) and *cuchia* have scales present around the caudal peduncle that extend slightly forward of the anus along the dorsum, whereas *fossorius* was described by Nayar (1952) as having scales

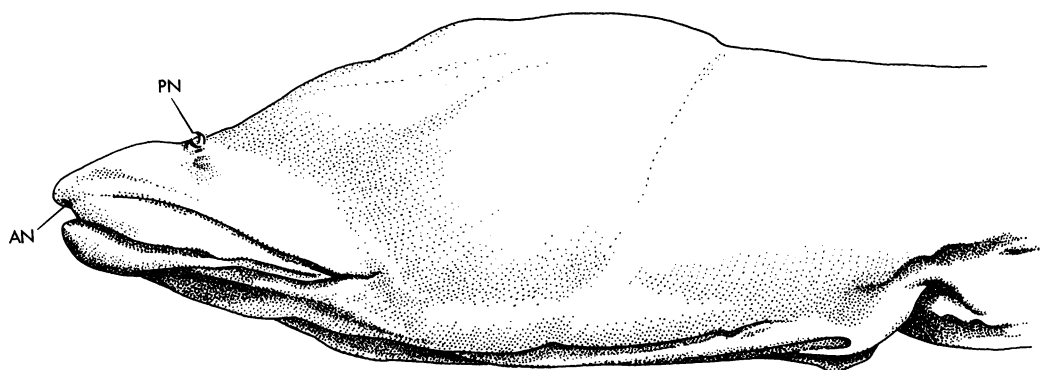


FIG. 7. Head of *Ophisternon infernale*. UMMZ M74-20; Yucatan, Mexico. Reduced, sunken eye appears as small spot below posterior naris.



FIG. 8. Ventral view of head of *Ophisternon infernale*, showing form of gill opening. Specimen as in figure 7.



FIG. 9. Head of *Ophisternon aenigmaticum*. AMNH 31508; Alta Verapaz, Guatemala. Arrow indicates position of posterior naris medial to eye.

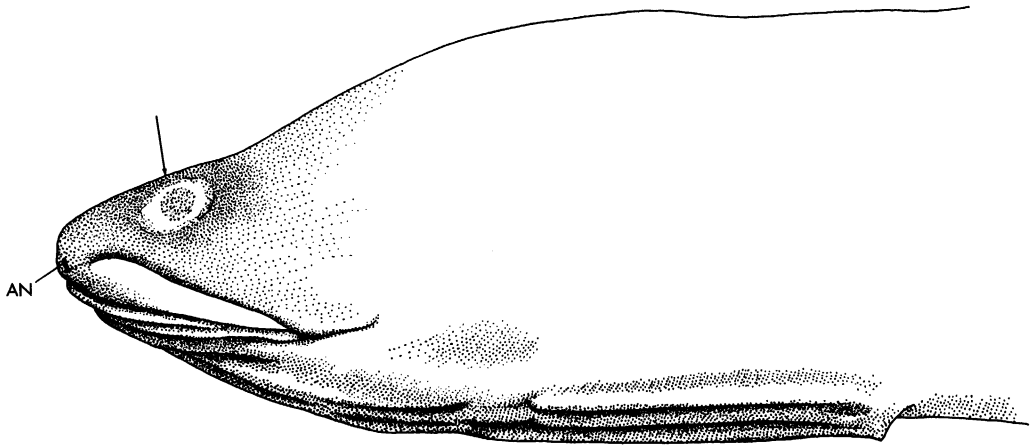


FIG. 10. Head of *Ophisternon aenigmaticum*. AMNH 26271, Oaxaca, Mexico. Arrow indicates position of posterior naris medial to eye.

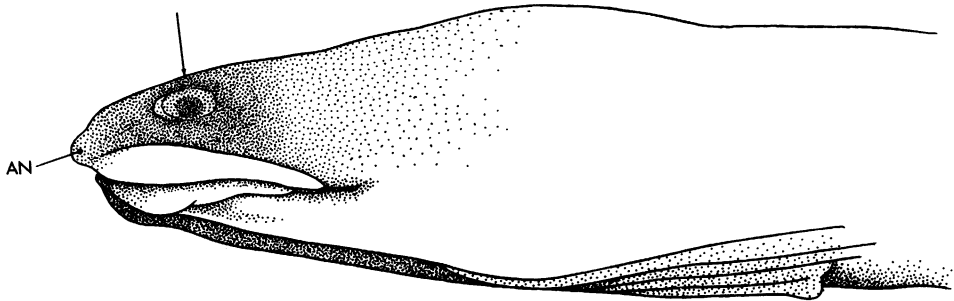


FIG. 11. Head of *Ophisternon aenigmaticum*. AMNH 18683, Cuba. Arrow indicates position of posterior naris relative to eye.

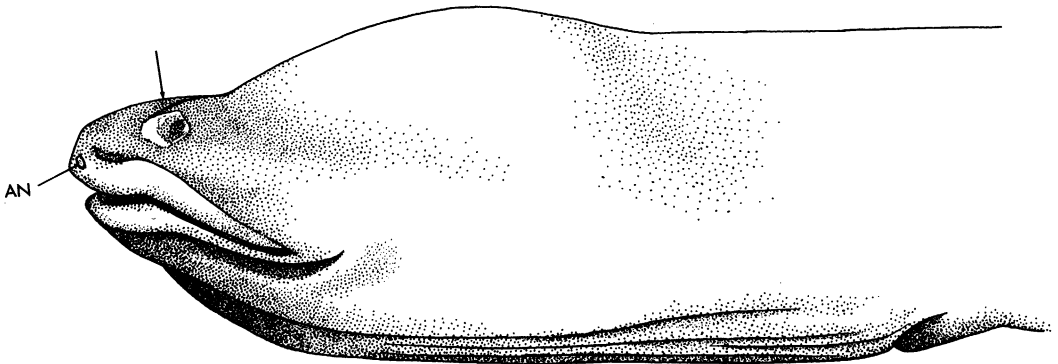


FIG. 12. Head of *Ophisternon aenigmaticum*. BMNH 1923-8.11:44-45; Marajo Island, Brazil. Arrow indicates position of posterior naris medial to eye.



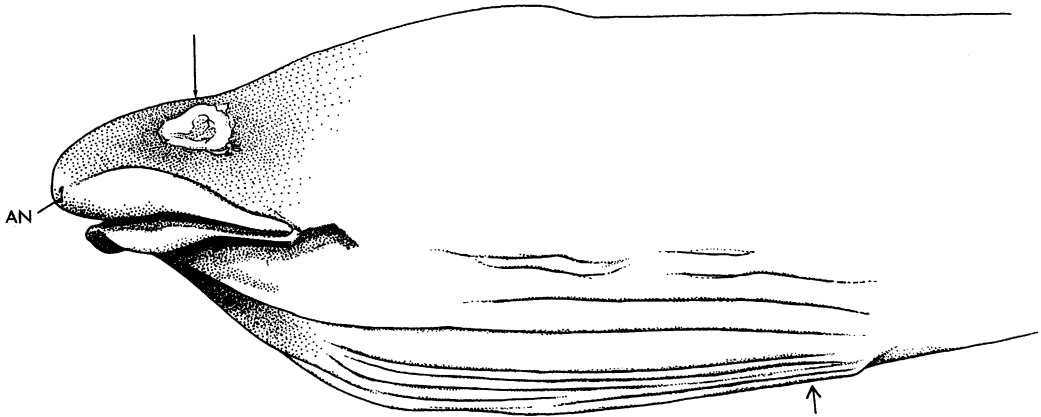


FIG. 13. Head of *Synbranchus marmoratus*. AMNH 30215, Panama. Arrow above eye points to position of posterior nares, that below and behind head to position of gill opening.

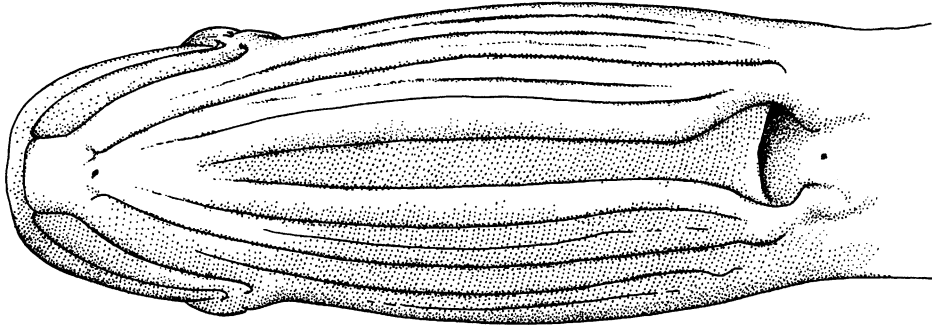


FIG. 14. Ventral view of head of *Synbranchus marmoratus*, specimen as in figure 13, showing form of gill opening.

along the entire trunk as well. Of the several specimens of *cuchia* and *fossorius* available to us none has had scales forward of the position described for them in *indicus* (Silas and Dawson), but we imagine that the regular rows of glandular elevations in the skin of *cuchia* and *fossorius* might be misinterpreted as embedded scales or empty scale pockets. Silas and Dawson have illustrated such glandular tissue in their material of *indicus*. Exactly what to conclude about the validity of these various nominal forms of *Monopteris* is difficult to decide because we have seen no material of "*indicus*" Eapen (1963).

The nominal species *fossorius* is diagnosed as different from *cuchia* in having more than one

row of teeth on the jaws and palatine and a much lower vertebral count, two differences that we have confirmed in our specimens. Silas and Dawson's *indicus* also has more than one row of jaw and palatine teeth, but it has a vertebral number intermediate between those of *fossorius* and *cuchia* (table 2). In addition Silas and Dawson's photographs and drawings of *indicus* show the gill opening to be distinctly triangular like that of *M. albus*, but our single specimen of *indicus* (Silas and Dawson) does not support that depiction (see Key, below, section CC, cc, in which the gill opening is identified as crescentic and like that of *cuchia* and *fossorius*). Eapen's "*indicus*" is also described as having more than

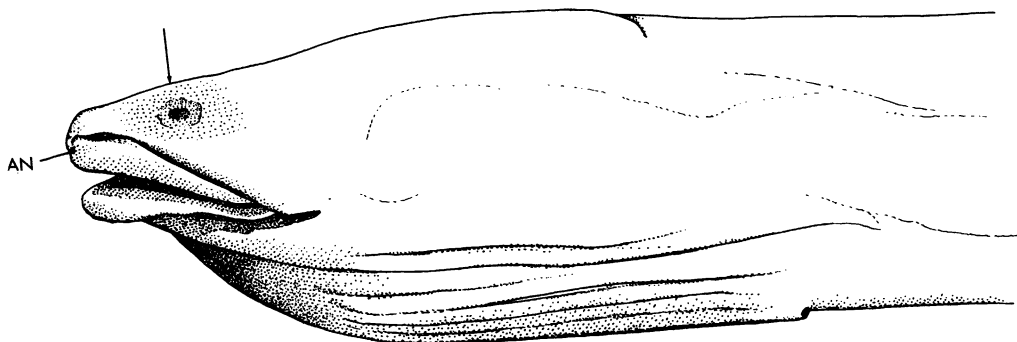


FIG. 15. Head of *Synbranchus marmoratus*. AMNH 20636, Bolivia. Arrow above eye points to position of posterior nares.

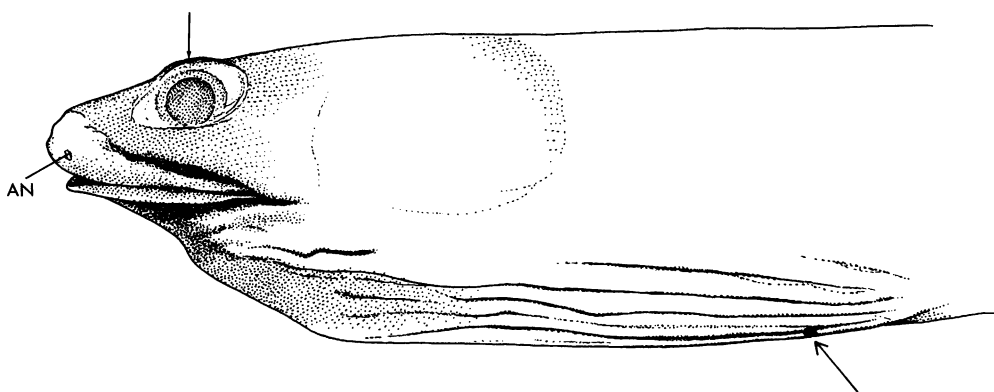


FIG. 16. Head of *Synbranchus marmoratus*, small juvenile (110 mm. total length). AMNH 32429, Peru (Río Tamaya, upper Amazon). Arrow above eye points to position of posterior nares, that below and behind head to position of gill opening.

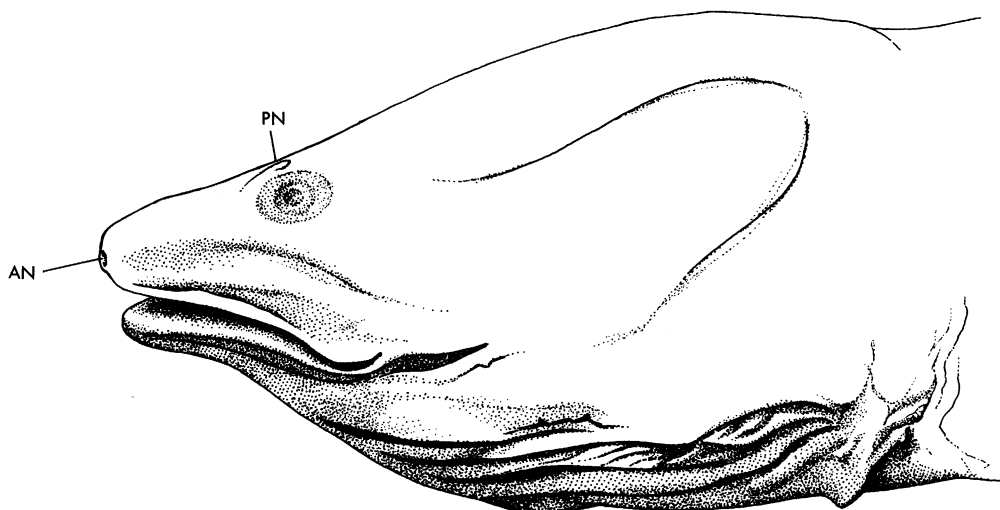


FIG. 17. Head of *Monopterus albus*. AMNH 7033, Fukien Province, China.

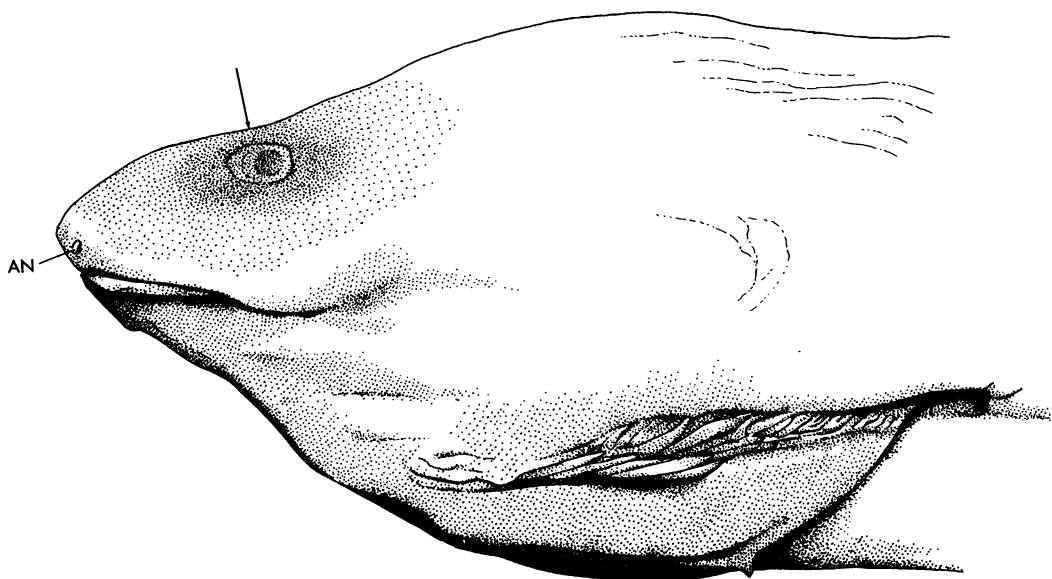


FIG. 18. Head of *Monopterus albus*. AMNH 8935, Lombok, Indonesia.

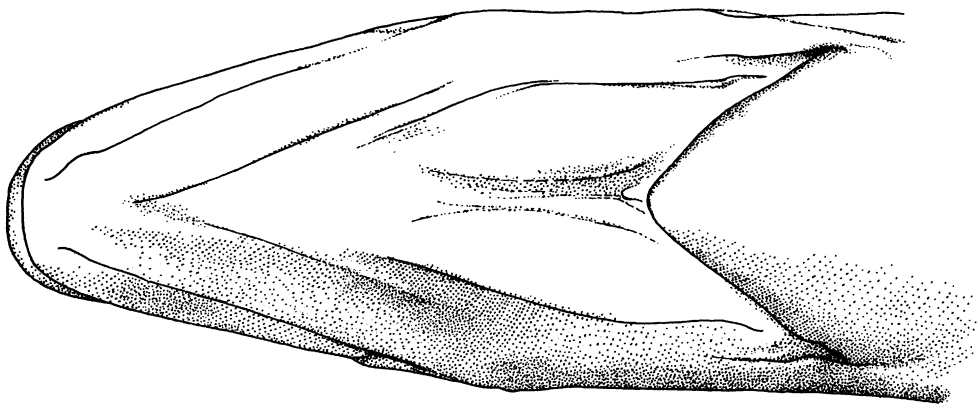


FIG. 19. Ventral view of head of *Monopterus albus*, specimen as figure 18, showing form of gill opening.

one row of teeth, at least anteriorly on the mandible, and it is illustrated as having a gill opening like that of *cuchia* and *fossorius* (subtriangular or crescentic and preceded by longitudinal grooves in the branchiostegal membrane). The "*indicus*" of Eapen, however, is devoid of scales, is a subterranean form, and has an exceedingly slender, whiplike body as in other subterranean synbranchids (*candidum* and *infernale*). Vertebral num-

ber in "*indicus*" Eapen is intermediate between that of *indicus* (Silas and Dawson) and *cuchia* (table 2), but significantly the precaudal count is considerably higher than in *cuchia*, *fossorius*, or *indicus* (Silas and Dawson). Such high precaudal counts occur elsewhere in *Monopterus* only in *boueti* and *albus*, the latter also having two rows of mandibular teeth. There is, thus, a reasonable likelihood that all of these nominal forms are

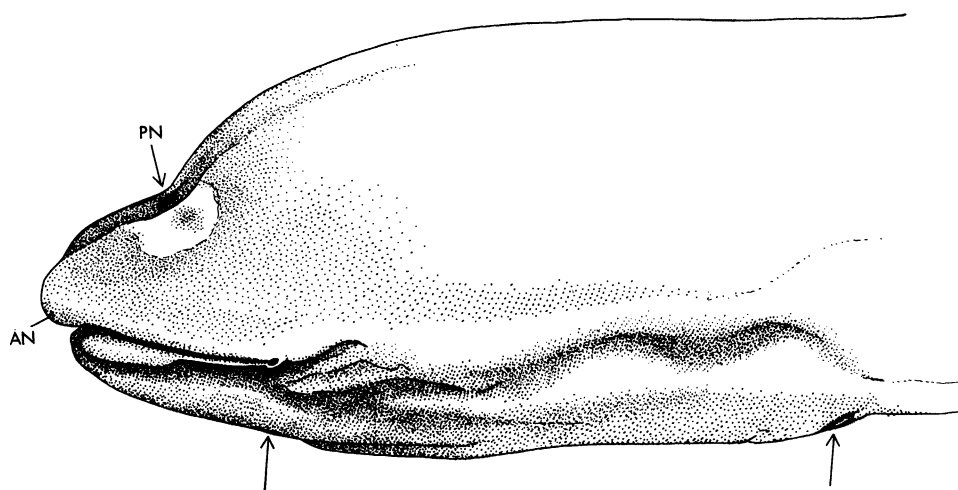


FIG. 20. Head of *Monopterus boueti*. USNM 208875, Sierra Leone. Arrows mark level of corner of gape (anteriorly) and position of gill opening (posteriorly).

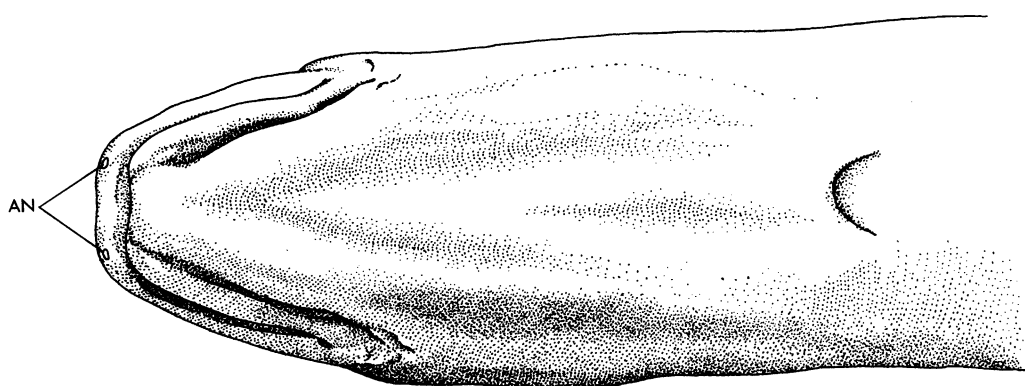


FIG. 21. Ventral view of head of *Monopterus boueti*, specimen as in figure 20, showing form of gill opening.

valid taxa, and it is clear that if even one of the forms named *indicus* is to be recognized a case of homonymy will have to be resolved by renaming the last described fish, that of Eapen (1963). Until we have available for study specimens of Eapen's material, we prefer to take no formal action.

The species remaining in the Synbranchidae are from both worlds, the New and the Old; *ben-galense* (Indo-Australia), *afrum* (Africa), *candidum* (Australia), *infernale* (Yucatán, Mexico),

and the species *aenigmaticum* (northern South America, Atlantic slope of Guatemala and Mexico, and Cuba) to be described below. These fishes are the most generalized of the Synbranchinae. The shoulder girdle is close behind the skull and firmly attached to the latter by a strong, forked posttemporal. Vertebral number is as low as for any member of the family Synbranchidae, ranging from 98 to 139. In general and with respect to larger individuals (200 mm. and more) the eye position is farther forward on the

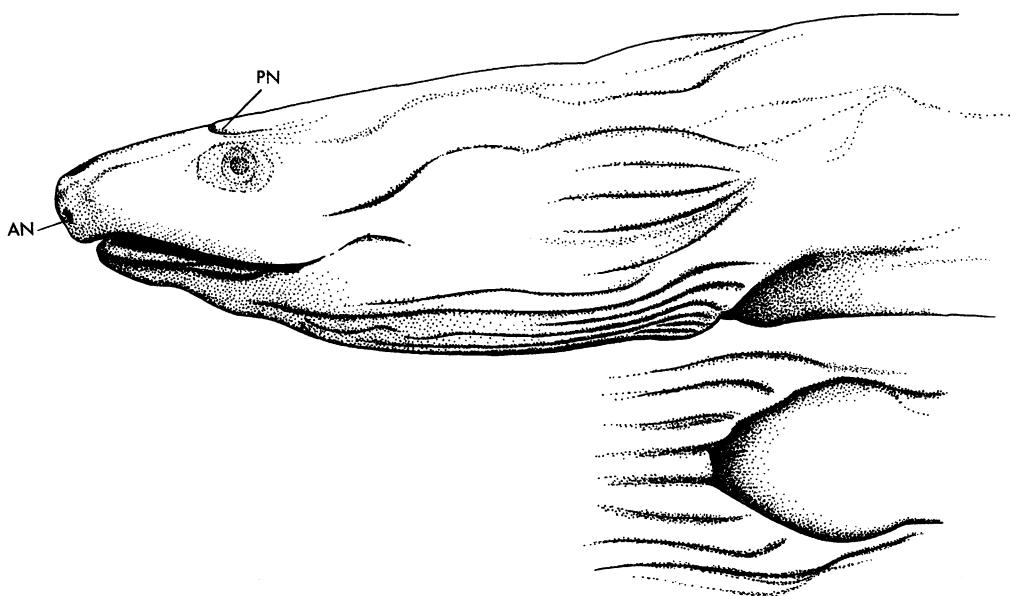


FIG. 22. Head of *Monopterus fossorius*. BMNH 1962-2.14:6-7 (above) and ventral view of gill opening (below).

snout than in all other synbranchids (on or anterior to a vertical through the midpoint of the upper lip fold, as compared with on, or posterior to, a vertical from that point in other synbranchids). The gill opening is slitlike or indented and lunate (figs. 8, 24), never so small, or enclosed laterally by heavy folds of tissue, as in *Synbranchus* (fig. 24), or as large as in *Monopterus albus* (fig. 19). It occupies a third to a half of the ventral body wall. Size variation, however, strongly influences relative eye size and position, and body size and degree of contraction of the buccopharyngeal chamber at time of preservation influences the shape and extent of the gill opening. There is, in addition, considerable individual variation in the development of the dorsal lip fold and position of the eye within an eye socket that is almost always much larger than the eyeball. At the smallest sizes (150 mm. and less) differences in eye-snout distance and upper lip development are difficult, and in some cases, impossible to use in separating these forms from the species of *Synbranchus*. Nevertheless, the lunate to nearly straight gill opening, being neither as small and porelike and enclosed laterally by folds

of the branchiostegal membrane as in *Synbranchus*, nor as large as that of *Macrotrema*, nor formed from such relatively thick unfolded membrane along its posterior edge, and not joined to the isthmus internally as it is in *Monopterus*, serves to distinguish these species from other synbranchids.

The question naturally arises whether the anterior eye position and form of the gill opening are derived characters justifying an initial hypothesis that all of these remaining species are more closely interrelated than is any one of them related to *Synbranchus* or *Monopterus* singly or together. Inferring the relative position of the posterior naris in front of the eye in *Macrotrema* to be primitive, since this is its position in most other teleosts, two simple evolutionary sequences can be envisioned to account for the modally more posterior position of the eye and naris in *Synbranchus* and *Monopterus* as compared with their modally more anterior position in other Synbranchinae. One is that the posterior naris migrated to a position dorsomedial to the eye and that the eye and nares subsequently migrated forward or backward on the snout region or not

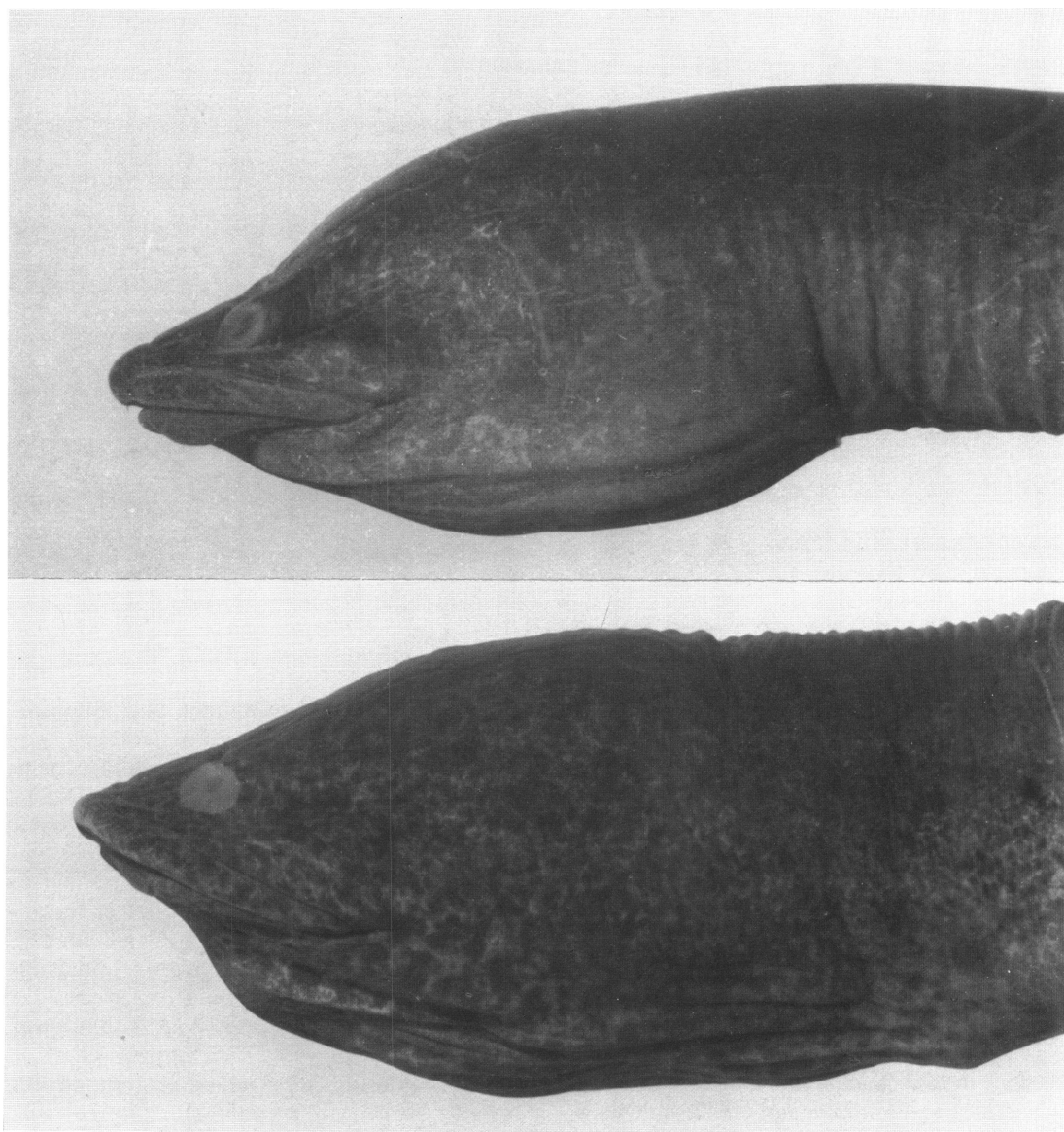


FIG. 23. Head of holotype of *Ophisternon aenigmaticum*, 350 mm. total length, AMNH 32410, from Department of Alta Verapaz, Guatemala (above) and of *Synbranchus marmoratus*, 425 mm. total length, from Department of Esquintla, Guatemala, AMNH 24465 (below).

at all in the cases of species in which the eye is in about the same relative position over the mouth as in *Macrotrema*. The second sequence involves the eye migrating forward under the naris (to place both in an anterior position) and then both

eye and naris moving posteriorly together (thus bringing them into a more posterior position). Once the eye and naris became aligned in the same vertical plane, subsequent changes in their position relative to the snout might, of course,

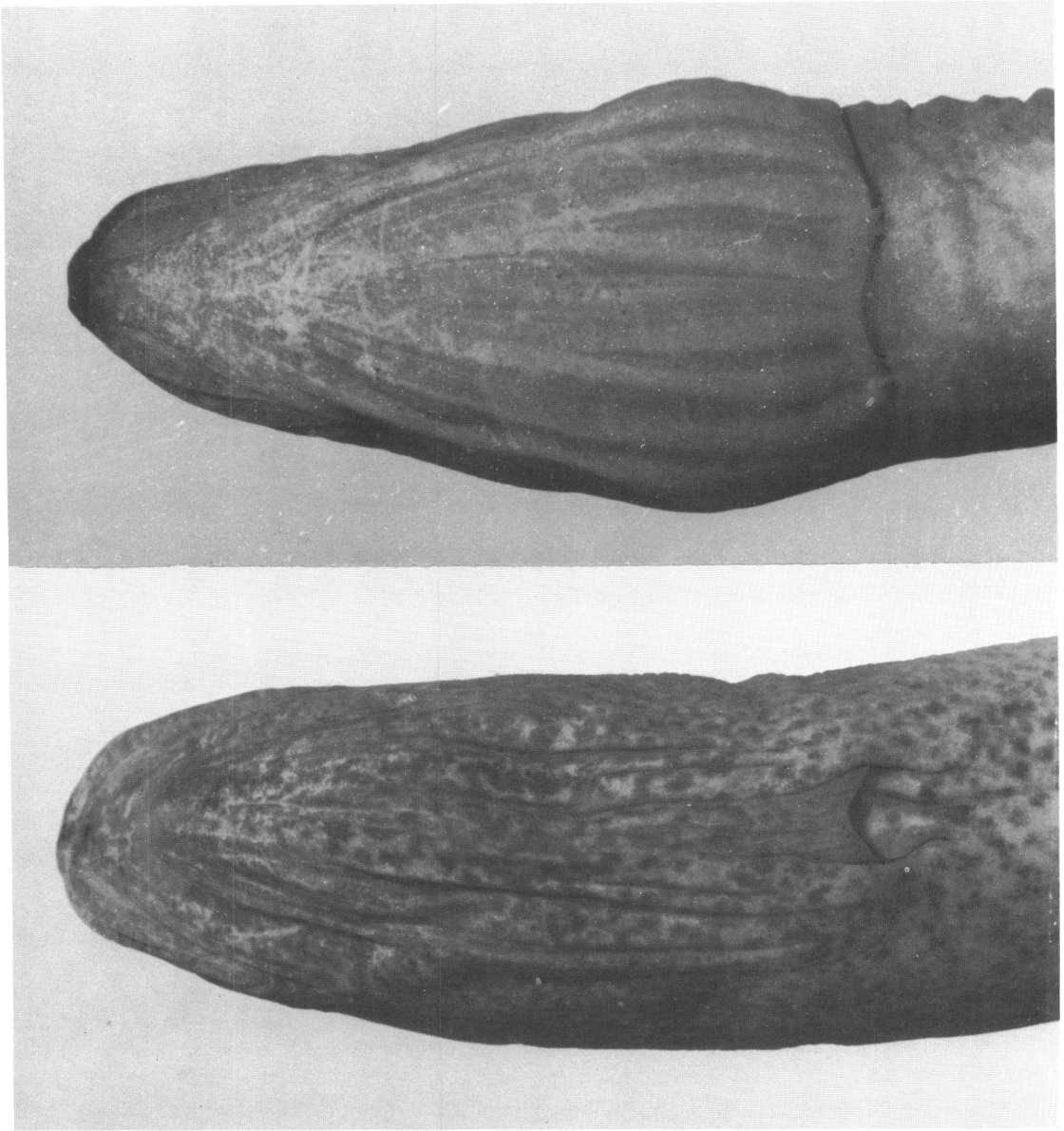


FIG. 24. Ventral view of head of specimens as in figure 23, showing form of gill opening. *Ophisternon aenigmaticum*, holotype (above) and *Synbranchus marmoratus* (below).

have been equally the result of changes in relative snout length as in a shift in the size or position of the orbit and nasal bone. Because we know of no way at present of choosing among the alternatives, and because the differences in relative eye

position are rather small ones that, with size and populational variation, cause a certain amount of overlap between groups (see, e.g., the comparison in fig. 23), we may reject at this point the position of the eye as evidence that the non-



*Synbranchus* and non-*Monopterus* Synbranchinae form a third monophyletic group.

When the form of the gill opening is used in this context similar problems arise. In *bengalense*, *candidum*, *afrum*, *infernale*, and *aenigmaticum* the gill opening is generally a shallow crescent of branchiostegal membrane confined to one-half or one-third of the ventral body wall; it has a simple confluence with the body skin laterally and is not attached to the isthmus internally. The restriction of this type of gill opening to the ventral surface is certainly derived relative to the condition in *Macrotrema*, but we can find no compelling reason to consider it derived for the Synbranchinae. In other words, the *Synbranchus* condition might be a further reduction of a *bengalense* pattern and the *Monopterus* condition might also have arisen from such a pattern by the reinforcement of the margin of the fold and the attachment of the branchiostegal membrane internally to the isthmus.

All synbranchid species, except those of the genus *Monopterus*, have the conjoined branchiostegal membranes free from the overlying isthmus. In *Monopterus* species there is a moderately dense connective tissue association between the ventral and ventrolateral aspects of the isthmus and the branchiostegal membrane over the whole length of the former; the connection is weakest in *M. boueti* which species, it may be noted, has the smallest opening to the branchial chamber of all *Monopterus* species. Posteriorly in all *Monopterus*, the connection is continued to the dorsal and dorsolateral aspects of the isthmus by a sheet of thicker tissue. In this way, the opening to the gill chamber is effectively divided into left and right entrances.

Of the gill opening in the species of *Monopterus*, that of *albus* is the most generalized. It is relatively large, extending the width of the head, it has a relatively narrow connection with the isthmus internally, and the membrane is indented posteriorly in a way that suggests a fusion of once separate right and left branchiostegal membranes. If the common ancestor of today's synbranchids had an opercular and branchiostegal apparatus somewhat like that of some tropical blennies, i.e., a single continuous membrane attaching dorsolaterally to the body wall above

the horizontal septum, indented postero-ventrally, and attached to the isthmus (e.g., in *Blennius* or *Centronotus*), then the gill opening of *Macrotrema* could be explained by the loss of the isthmian connection, and that of *Monopterus*, by the restriction of the opening to the ventral body surface. In this hypothesis the gill openings of *Macrotrema* and *Monopterus* represent alternate modifications of a more primitive condition and the gill openings of species such as *bengalense* a further modification of either the *Macrotrema* or *Monopterus* condition. Arising from the *Macrotrema* condition, that of *bengalense* would require only the restriction of the gill opening, and from the *Monopterus* condition, the further restriction of the opening and the loss of an isthmian connection. The gill opening of *Synbranchus* would then most parsimoniously be interpreted as a further reduction of the derived condition seen in *bengalense*, and *Synbranchus* and the group including *bengalense* would then share different states of the same derived character and could be inferred to be sister taxa. Based on the rather substantial evidence given above for dividing the synbranchids into the Macrotreminae and Synbranchinae, the wide gill opening of *Monopterus albus* is most parsimoniously interpreted as plesiomorphous to the less wide conditions seen in *Synbranchus* and the group including *bengalense*. This argument would be far simpler if it could be shown that the connection of the branchiostegal membranes with the isthmus in *Monopterus* is secondary rather than primary, a demonstration that would require knowing the condition of the gill opening in the sister group of all Synbranchidae. Regrettably, we have no insight into the problem of synbranchid relationships and, for reasons discussed below, cannot accept their relationships to the masticembeliforms as proposed by McAllister (1968), Gosline (1971), and others.

It is clear, however, that regardless of which hypothesis is accepted (the *bengalense* type of gill opening being plesiomorphous to both the *Synbranchus* and *Monopterus* type, or only to the *Synbranchus* type and being apomorphous to that of *Monopterus*), *bengalense* and similar species cannot be considered to constitute a monophyletic group on the basis of the nature of their

gill opening since that type of gill opening would be judged primitive in relation to those of the members of one or both the other two groups of synbranchines.

The taxonomic problems posed by that conclusion are several. At the present time *bengalense* and *afrum* are assigned to the genus *Synbranchus*, *afrum* having been described in that genus and *bengalense* having been transferred to it from *Ophisternon* M'Clelland (previously regarded as a synonym of *Synbranchus*). The Old World subterranean form, *candidum*, is placed in its own genus *Anomatophasma*, as is the New World troglobyte, *infernale*, in *Furmastix*. Although *candidum* and *infernale* can be retained in their present genera, *bengalense* and *afrum* cannot be left in *Synbranchus* (type species *S. marmoratus*), the defining characters of which they do not have and to which, in our opinion, they apparently have no close relationship. Clearly the name *Ophisternon* can be resurrected for *bengalense*; but where shall *afrum* be assigned and in which genus shall *aenigmaticum* be described? The alternatives are 1) represent each of these taxa as the type of a monotypic genus (creating two new generic names for *afrum* and *aenigmaticum*), 2) leave *candidum* and *infernale* in their present generic positions, and assign the other three species to *Ophisternon*, or 3) assign all five to the oldest available name, *Ophisternon*, until their relationships to each other and to other synbranchines are worked out. We reject the first solution as a multiplication of names unwarranted by specific phylogenetic inferences. The second solution is rejected because its application would imply to the unwary that *bengalense*, *afrum*, and *aenigmaticum* are more closely interrelated than is any one of them related to *candidum* or *infernale*. The third solution

appears to us as the most practical, serving notice, as it were, of an unresolved series of phylogenetic questions involving all five taxa at the species level and higher. There is a possibility that some of these species are divisible into two or more recognizable taxa, but these and many other important taxonomic issues cannot be decided until additional material is available.

Finally, the position of the Alabetidae, long associated with synbranchids can now be resolved, in part, according to evidence discussed below.

In summary, 13 nominal species of synbranchoids can be separated from *Macrotrema caligans* on the basis of three major shared derived features (synapomorphies) involving the position of the posterior nares, the form of the gill opening, and the development of the caudal fin. The swamp eels are, therefore, considered to constitute a single family, the Synbranchidae, including the Macrotreminae and Synbranchinae. Within the Synbranchinae numerous synapomorphies of general anatomy are shown to describe *albus*, *boueti*, *cuchia*, *fossorius*, "*indicus*" of Eapen (1963) and *indicus* of Silas and Dawson (1961) as one monophyletic group, *Monopterus*; and *marmoratus* and *madeirae* as another, *Synbranchus*. The remaining forms, *bengalense*, *afrum*, *candidum*, *infernale*, and *aenigmaticum* (described below), although similar, show specific resemblances to one another only in primitive characters (symplesiomorphies), and cannot be defined as a monophyletic group. For reasons given above, they are provisionally assigned to the genus *Ophisternon*. The taxonomic propositions herein summarized will be examined in more detail, with reference to studies of the internal anatomy of the species, in the following sections.

## HYOBRANCHIAL ANATOMY

### HYOID ELEMENTS

The hyoid bar of synbranchoids (fig. 25) consists of an upper and lower hypohyal, the former fenestrated for passage of the hyoidean artery. This artery is greatly swollen where it lies along

the dorsal surface of the anterior and posterior ceratohyals. The anterior and posterior ceratohyals are suturally united dorsally, in some cases completely ankylosed. The posterior ceratohyal bears a lateral facet for the interoperculum and a dorsal facet for the lower end of the

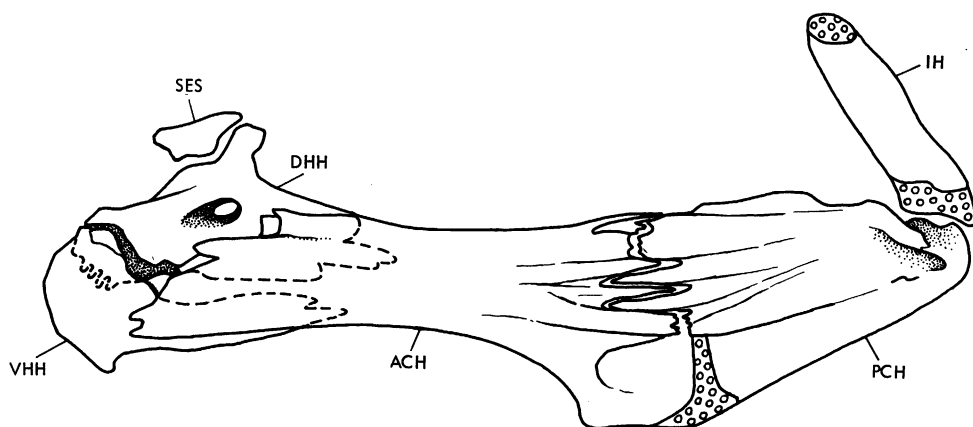


FIG. 25. Lateral view of left hyoid bar of *Macrotrema caligans*. Anterior to left.

ossified interhyal. Branchiostegal rays are six, rarely four or seven, with two, rarely three, slender elements attaching to the medial or ventral surface of the shallow anterior part of the anterior ceratohyal, and four robust rays attaching laterally on the deeper posterior part of the anterior ceratohyal and anterior part of the posterior ceratohyal. The arrangement is typical of acanthopterygians generally except for the existence of a foramen for the hyoidean artery in the dorsal hypohyal. A perforated dorsal hypohyal is spottily distributed among "higher" teleosts.

Branchiostegal rays in synbranchoids are of two types. In the species of *Macrotrema* and *Ophisternon* all the rays are long, slender, and gradually taper to filamentous tips. The rays terminate posteriorly below or beyond the level of the cleithrum where they support part of the membrane of the gill opening. In *Macrotrema* all elements support a large gill opening that consists of the ventrally fused right and left branchiostegal membranes. This membrane extends upward along the side, enveloping the opercle, and merges with the body wall above the horizontal septum. In *Ophisternon* the tips of only the anterior (or medial) branchiostegals support the free margin of the gill opening, which is constricted and confined to the ventral body wall as a lunate or nearly straight membranous flap. In *Synbranchus* the ossification of the branchiostegals is abruptly reduced halfway along their lengths between their origin on the hyoid bar and the clei-

thrum. Posterior to their main anterior ossification, the rays are unossified in the smallest specimens and poorly ossified or simply very slender and delicately ossified in larger individuals. The tips of only the innermost, anterior branchiostegals, whether ossified or present only as hyaline (collagenous) extensions of the rays, support the free margin of the small, ventral, often porelike gill opening. In *Monopterus* the branchiostegals are abruptly terminated and are bluntly pointed posteriorly about halfway between the hyoid bar and the cleithrum—ending where the main ossification stops in *Synbranchus*. Some specimens of *M. albus* have fine, ossified, hairlike extensions of the posterior tips of the rays, further suggesting that the branchiostegal modifications in *Monopterus* represent a reductional state of the *Synbranchus* pattern. In *M. boueti* the first two rays are absent. McAllister (1962) illustrated the hyoid apparatus of a Guatemalan synbranchid identified as *S. marmoratus*, but judging from the unconstricted, gradually tapering character of the branchiostegals, his specimen was an example of the previously undescribed Atlantic slope *Ophisternon* diagnosed below.

The structure of the urohyal (fig. 26) supports the separation of the species of *Monopterus* from other synbranchids. In *Monopterus* this bone, as seen in ventral view, has the posterior part reduced in length and the anterior part expanded. Within *Monopterus*, the urohyal is shortest and

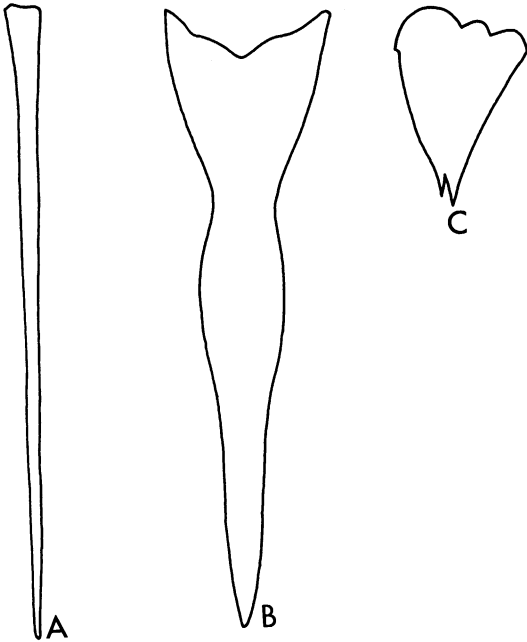


FIG. 26. Urohyal patterns in synbranchids as seen in ventral view, anterior at top. A. *Synbranchus marmoratus* (pattern also present in *Ophisternon* and *Macrotrema*). B. *Monopterus albus*. C. *Monopterus cuchia*. B and C to same scale. The relatively much longer urohyal of the A type reduced to the same size as B for comparison of shape.

widest in *cuchia*, *fossorius*, and *boueti*. Other synbranchids have a long, slender urohyal only little enlarged anteriorly where it is joined by strong ligaments to the hypohyals.

The basihyal bone of synbranchoids (see below, figs. 44-52) is untoothed and, except in *Ophisternon infernale*, is fused with the first ossified basibranchial element. The unfused condition (see below, fig. 47) was seen in two specimens of *infernale*, and it may well be a species-specific secondary failure of ankylosis during early ontogeny if other suites of derived characters accurately align this cavernicolous species in *Ophisternon*. Hence, the compound basibranchial-basihyal element may be regarded as a probably primary, derived, diagnostic feature of synbranchoids.

Branchiostegal anatomy, on the other hand,

divides the synbranchoids into three groups: 1) *Macrotrema* and *Ophisternon*, which have a primitive pattern, and for which, therefore, branchiostegal anatomy provides no evidence of relationship; 2) *Synbranchus* and 3) *Monopterus* each of which has a different, but clearly related, derived pattern of the branchiostegals, evidence that these two groups of species are more closely related to each other than is either to *Macrotrema* or *Ophisternon*. Urohyal anatomy supports the inference that *Monopterus* is a monophyletic group, and identifies a subgroup within *Monopterus* including *cuchia*, *fossorius*, and *boueti*.

### DORSAL GILL ARCH ELEMENTS

The dorsal gill arch skeleton of synbranchoids (figs. 27-43) has distinctive modifications of the first two arches. There is no first pharyngobranchial and the second is greatly reduced or even absent in some cases. The first epibranchial is rotated forward and its posteromedial edge is connected to what remains of the second pharyngobranchial or to the tips of the second epibranchial and third pharyngobranchial by a long interarcual cartilage. An interarcual cartilage is a synapomorphy of the perciform dorsal gill arch skeleton, thereby indicating the relationships of synbranchoids with these fishes, but the significant aspect of this cartilage is that uniquely among fishes possessing this structure, it is ossified as an interarcual bone in synbranchoids. The distribution and characteristics of this structure in acanthopterygians is discussed in a forthcoming paper by Rosen.

The relationships between the first epibranchial and the interarcual bone are of two types in synbranchoids. In *Macrotrema* and *Ophisternon* (figs. 27-35) the proximal end of this epibranchial has a deep excavation and an acute process or rounded flange at the anterodorsal edge of the excavation. The lateral end of the interarcual bone is seated in this excavation and held in place there by dense connective tissue. The medial end of the interarcual bone is joined via connective tissue with the lateral end of the second pharyngobranchial. The second pharyngobranchial in the species of these two genera is an irregularly oval or rodlike ossicle that lies

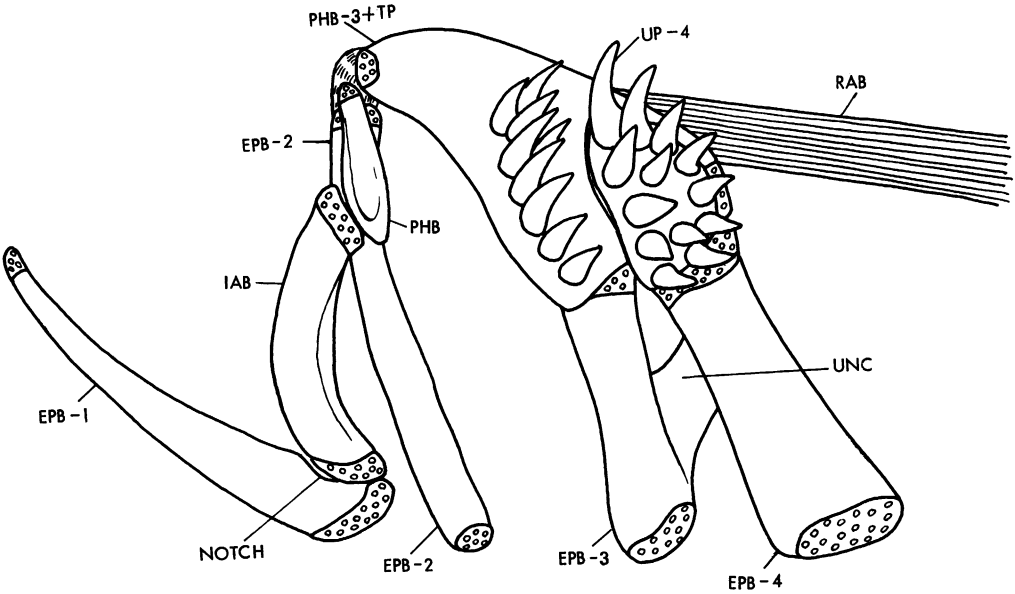


FIG. 27. Dorsal gill arch skeleton of *Macrotrema caligans* BMNH 1908.7.13:1; Singapore. Ventral view, right side.

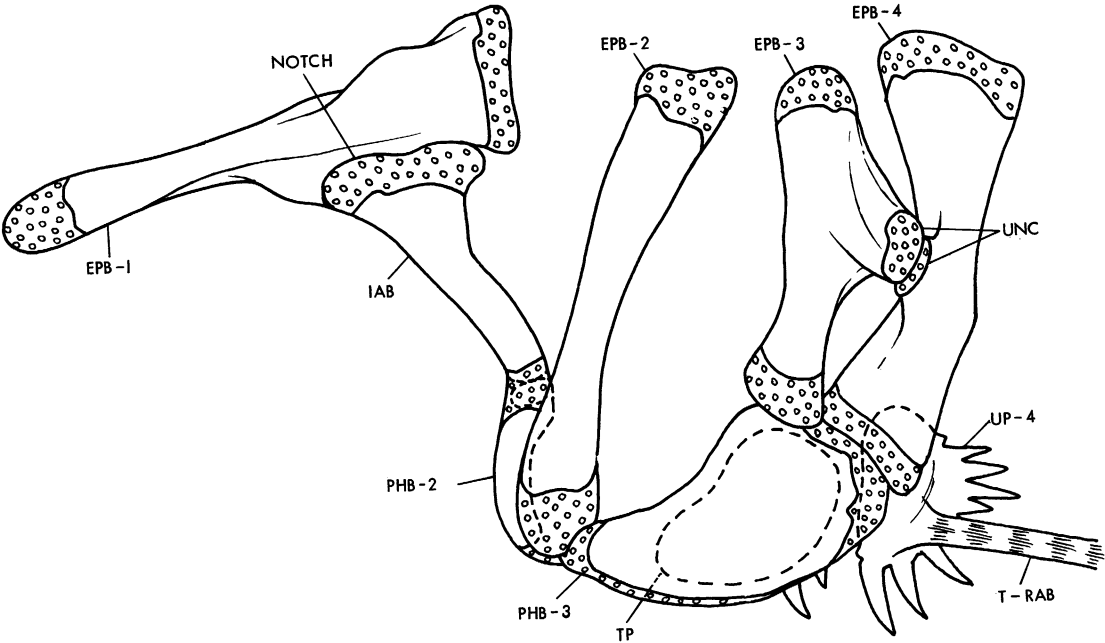


FIG. 28. Dorsal gill arch skeleton of *Ophisternon bengalense* AMNH 32403, Ceylon. Dorsal view, right side.

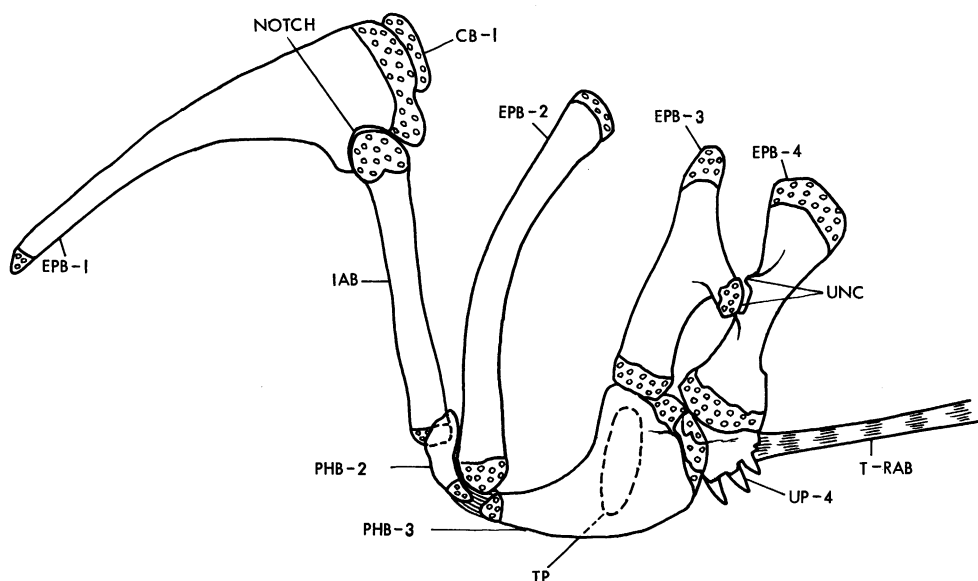


FIG. 29. Dorsal gill arch skeleton of *Ophisternon candidum* AMNH 32404, Western Australia. Dorsal view, right side.

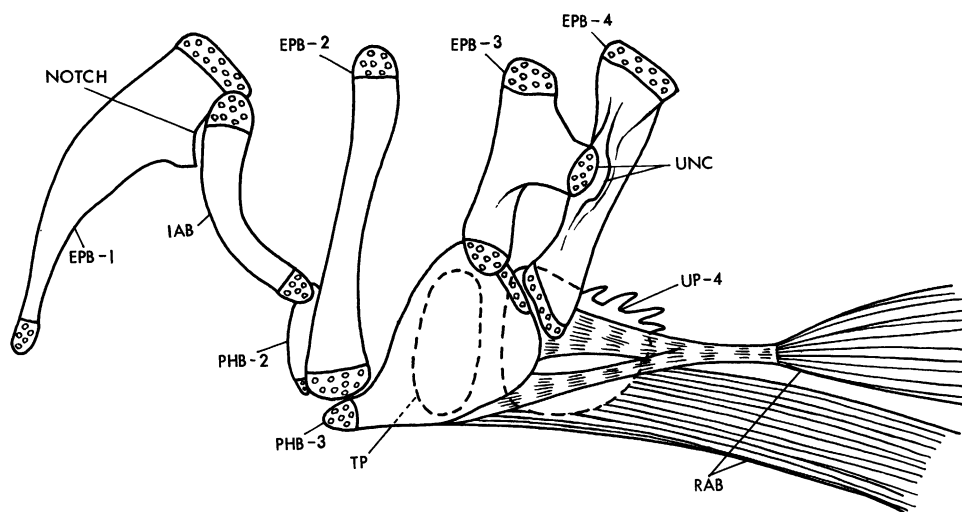


FIG. 30. Dorsal gill arch skeleton of *Ophisternon afrom* BMNH 1909.10.29:113; Portuguese Guinea. Dorsal view, right side.

anteroventral to the distal end of the second epibranchial and parallel with the long axis of that bone. The third pharyngobranchial is a simple triangular bone.

In *Synbranchus* (figs. 36, 37) the excavation and associated process near the base of the first epibranchial is lost or only the slightest trace of a process remains. The interarcual element is

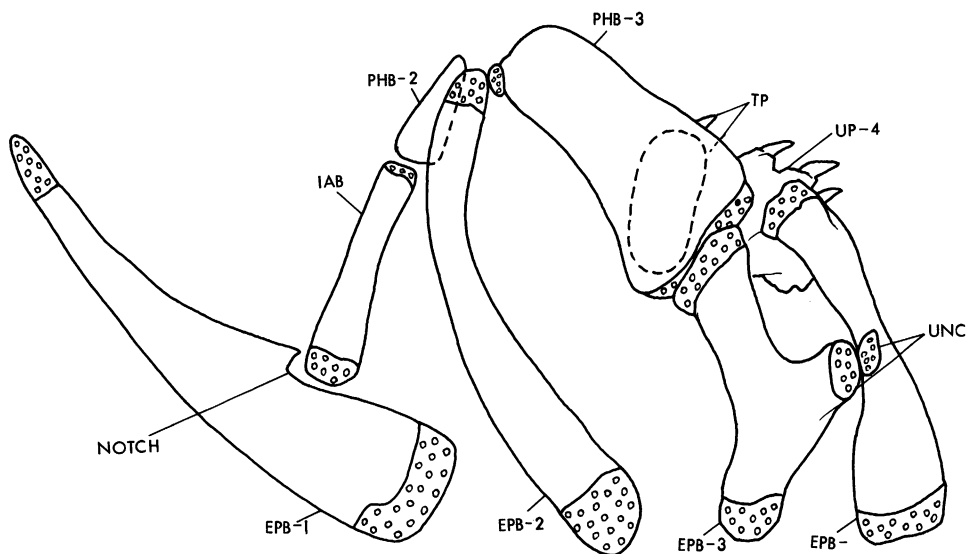


FIG. 31. Dorsal gill arch skeleton of *Ophisternon infernale* AMNH 32405; Yucatan, Mexico. Dorsal view, left side.

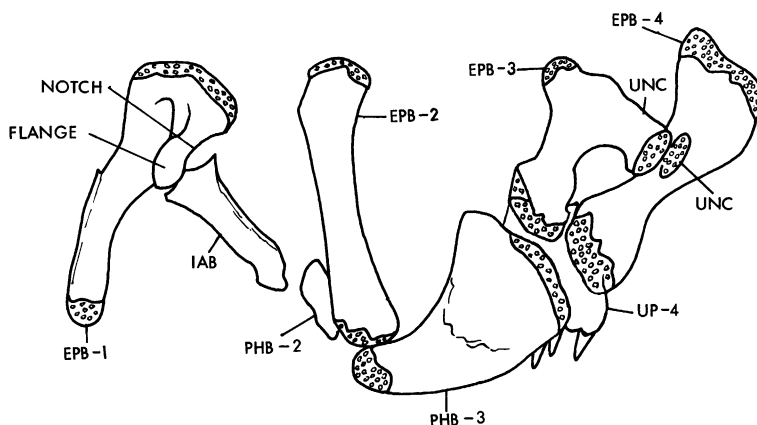


FIG. 32. Dorsal gill arch skeleton of *Ophisternon aenigmaticum*, AMNH 31687, Department of Alta Verapaz, Guatemala. Dorsal view, right side.

loosely associated with the proximal third of the shaft of this epibranchial. The medial end of the interarcual bone is loosely attached to a small second pharyngobranchial, or, when the second pharyngobranchial is absent in many instances, it is attached to the second epibranchial and third pharyngobranchial. When present in *Synbranchus* the second pharyngobranchial ossicle lies at a de-

cided angle to the long axis of the second epibranchial, extending forward and medially away from that bone. The third pharyngobranchial often has a decidedly bent appearance, rather than being simply triangular as in *Macrotrema* and *Ophisternon*.

In *Monopterus cuchia* the dorsal components of the first gill arch are lost (cf. figs. 38-41), an



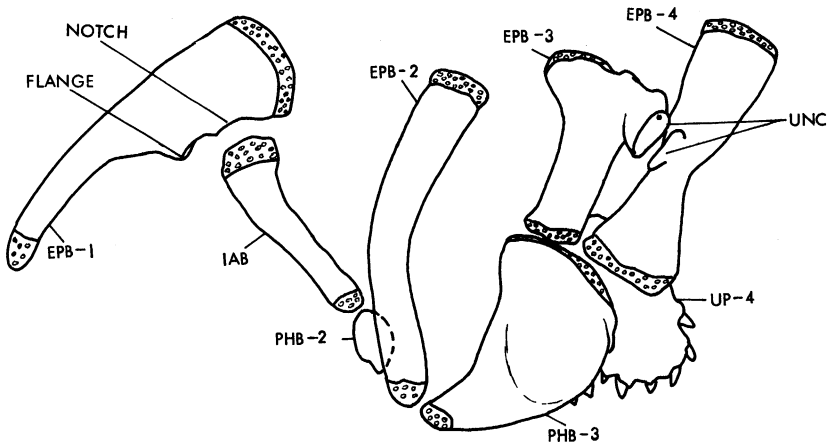


FIG. 33. Dorsal gill arch skeleton of *Ophisternon aenigmaticum*, AMNH 8817, Cuba. Dorsal view, right side.

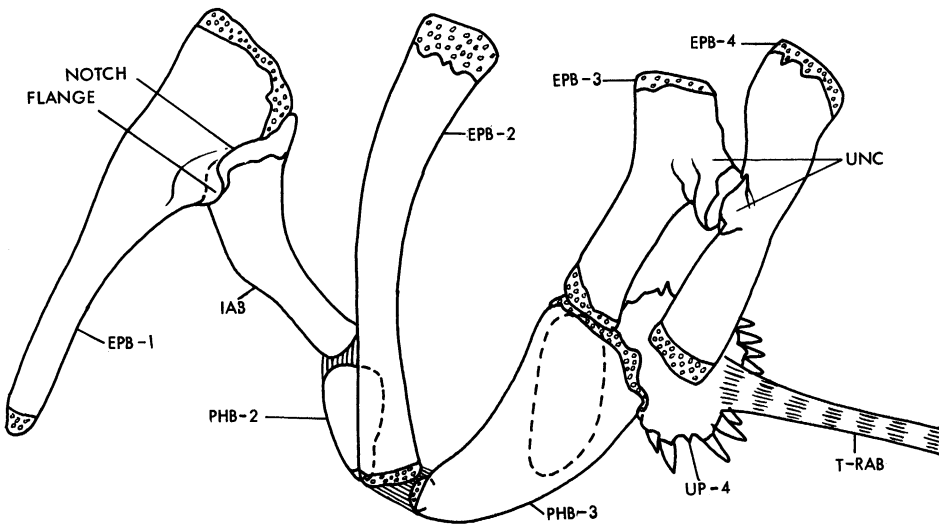


FIG. 34. Dorsal gill arch skeleton of *Ophisternon aenigmaticum*, BMNH 1866.4.25:9, Trinidad. Dorsal view, right side.

absence perhaps associated with the unique development in this synbranchoid species of a suprabranchial respiratory organ (see below). The second epibranchial in *cuchia* is expanded proximally and greatly foreshortened and is remote from the third pharyngobranchial. In *Monopteris albus* and *M. boueti*, however, the dorsal arch elements are present. In *boueti* (fig. 40) the

first epibranchial also has lost all signs of the proximal excavation except for a low peak on the posterior margin of the bone. The interarcual bone is loosely attached with connective tissue near this peak at the midpoint of the epibranchial. Medially the interarcual element joins a long, slender, rodlike second pharyngobranchial and the tip of the second epibranchial, both of

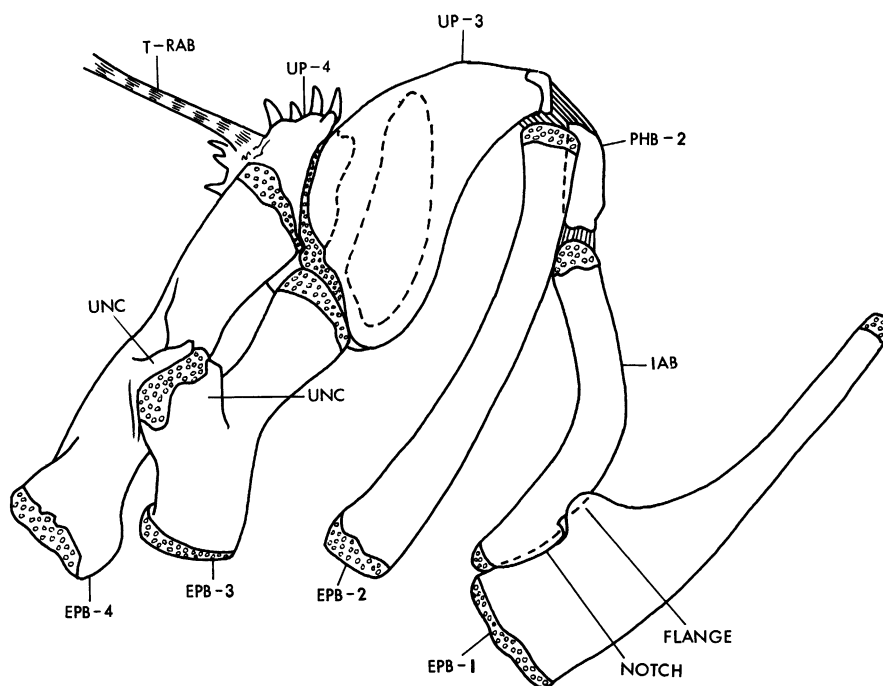


FIG. 35. Dorsal gill arch skeleton of *Ophisternon aenigmaticum*, BMNH 1846.2.16-129, Cayenne, French Guiana. Dorsal view, right side.

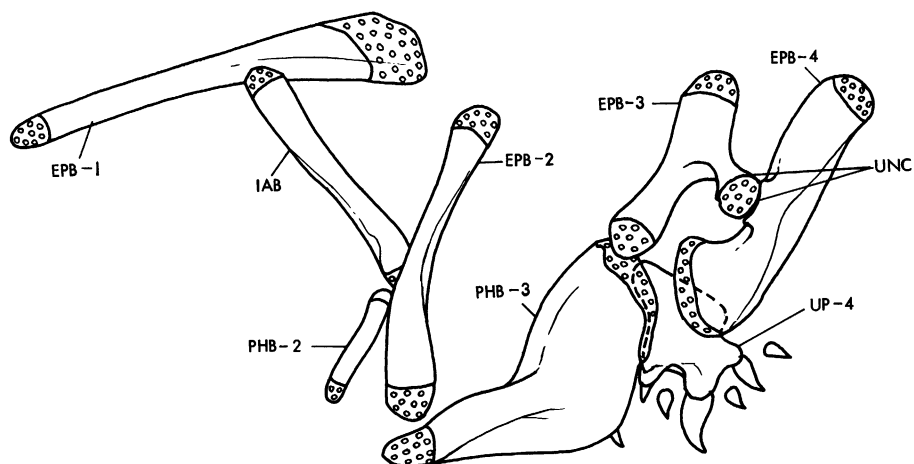


FIG. 36. Dorsal gill arch skeleton of *Synbranchus marmoratus*, BMNH 1935.6-4:474-492, Paraguay. Dorsal view, right side.

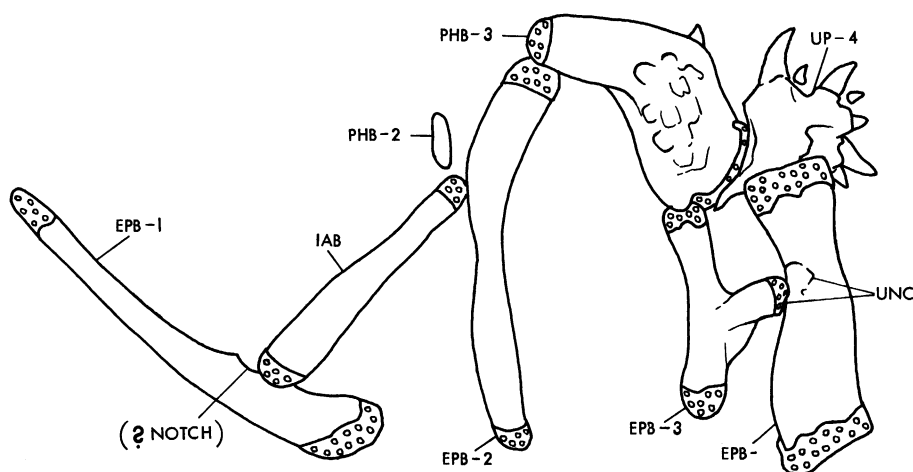


FIG. 37. Dorsal gill arch skeleton of *Synbranchus madeirae*, AMNH 30219, Bolivia. Dorsal view, left side.

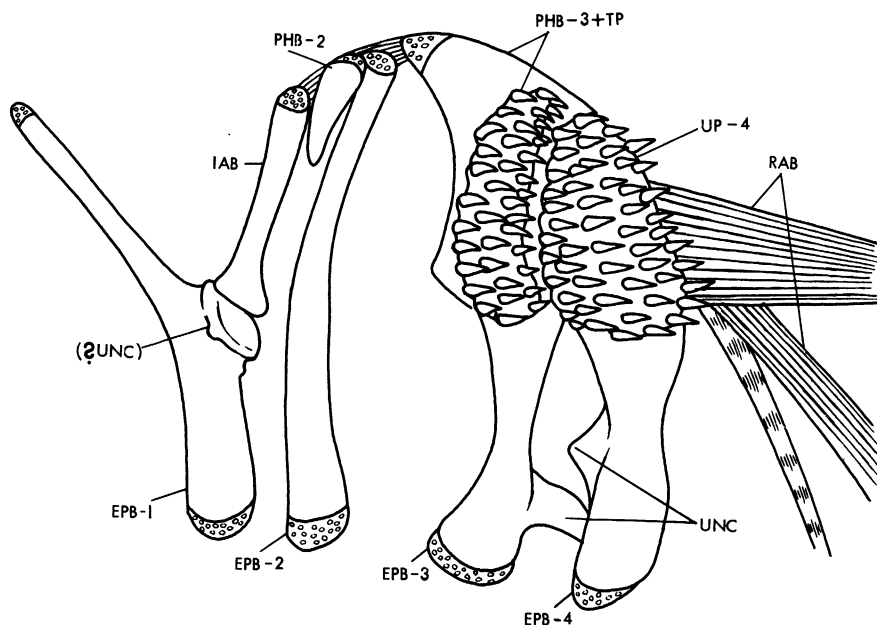


FIG. 38. Dorsal gill arch skeleton of *Monopterus albus*, AMNH 7033, Fukien Province, China. Ventral view, right side.

which are remote from the third pharyngobranchial. This last positional similarity between the second epibranchial and the third pharyngobranchial in *boueti* (fig. 40) and *cuchia* (fig. 41) is

accentuated by the distinctively squared off and bent appearance of the latter bone, and by the fact that both species lack uncinate processes on their third and fourth epibranchials.

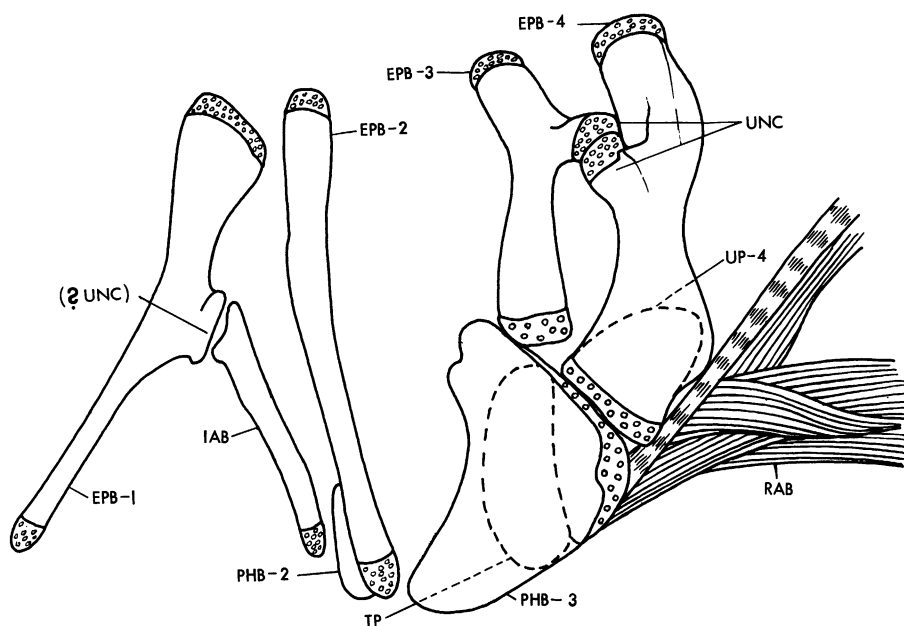


FIG. 39. Dorsal gill arch skeleton of *Monopterus albus*, AMNH 10240, Hainan Province, China. Dorsal view, right side.

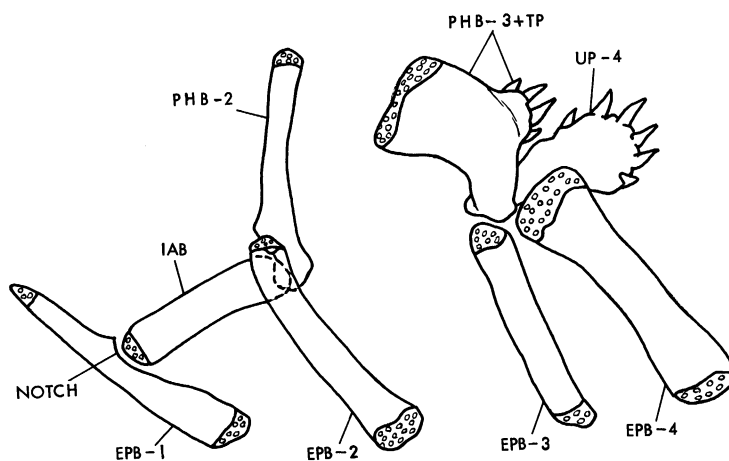


FIG. 40. Dorsal gill arch skeleton of *Monopterus boueti*, AMNH 32411, Sierra Leone. Dorsal view, left side.

In *Monopterus albus* (figs. 38, 39) a proximal excavation on the first epibranchial also is lacking and is replaced instead by a simple elevation or nubbin on top of which the interarcual bone attaches. The point of attachment is also fairly

high on the epibranchial, generally at or somewhat proximal to the midpoint. The medial attachment of the interarcual bone and the second pharyngobranchial have a more generalized aspect as in *Macropterna* and *Ophisternon*.

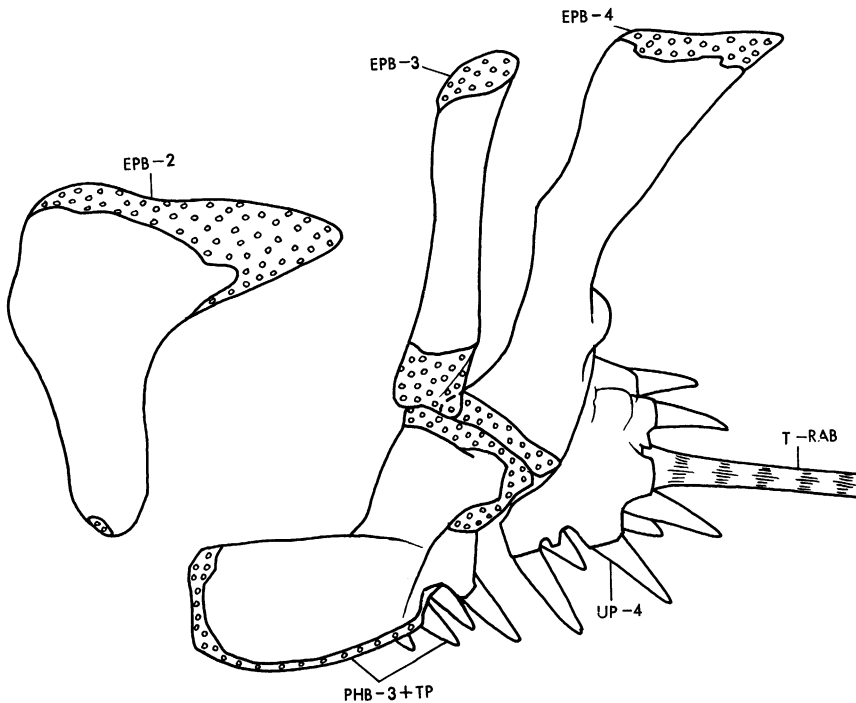


FIG. 41. Dorsal gill arch skeleton of *Monopterus cuchia*, BMNH 1889-2.1:2723, India. Dorsal view, right side.

The third pharyngobranchial in *M. albus* is roughly triangular or somewhat bent, the latter feature recalling the structure of this element in some examples of *Synbranchus* species and the more decidedly bent elements in *M. boueti* and *M. cuchia*.

The conclusion to be reached from these comparisons is that the species of *Synbranchus* and *Monopterus* resemble one another in the loss of the excavation on the first epibranchial, the outward migration of the point of attachment of the interarcual element to that bone, and the tendency for the third pharyngobranchial to bend forward near its midpoint. Each of these features, either in their reductional aspects or departures from structural patterns common to other synbranchoids and various generalized acanthopterygians (e.g., the bent third pharyngobranchial), are derived relative to comparable traits in *Macrotrema* and *Ophisternon*, and constitute evidence that *Synbranchus* and *Monopterus* are sister taxa more closely related to each other than

to other synbranchoids. This conclusion is consistent with the suggested relationships of these genera based on study of the hyoid apparatus. Dorsal gill arch evidence also indicates that within *Monopterus*, *boueti*, *fossorius*, and *cuchia* are more closely related than is either to *albus*.

#### VENTRAL GILL ARCH ELEMENTS

Ventral gill arch elements in the species of *Macrotrema*, *Ophisternon*, and *Synbranchus* (figs. 42-47) are more or less typical for advanced teleosts. In these groups the ventral elements differ from those of other teleosts in the fusion of the first basibranchial with the basihyal (discussed above) and the relative forward displacement of the joint between the hypobranchial and ceratobranchial of the first arch so that this joint is no longer aligned with the comparable flexure points on the second to fourth arches. Further specializations along these same lines serve to characterize the species of *Monopterus* (figs.

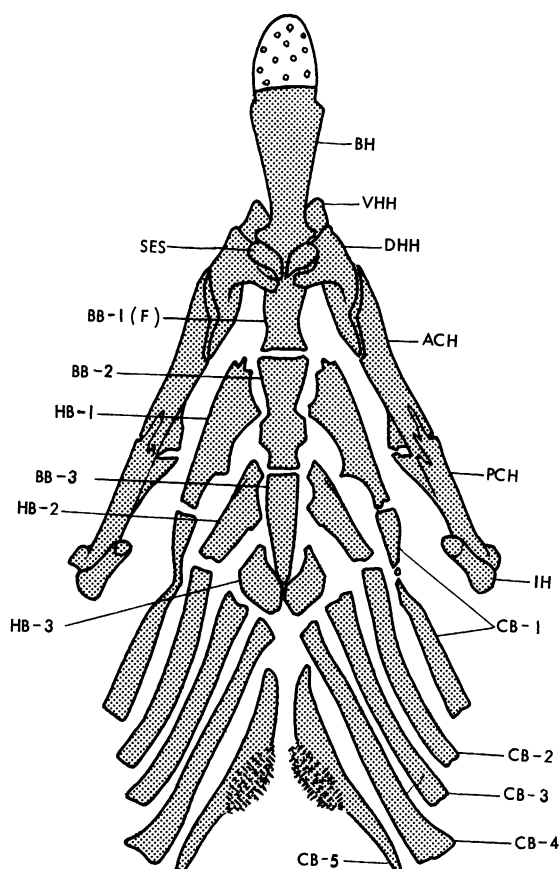


FIG. 42. Ventral gill arch skeleton of *Macrotrema caligans*, MCZ 47107, Thailand. Dorsal view.

48-50), as discussed below. In a single specimen of *Ophisternon infernale* and of *O. afrum*, and in one of three specimens examined of *Macrotrema caligans* (figs. 42, 44, 45), the first ceratobranchial is slightly to very constricted near its anterior end (interrupted on one side in the specimen of *M. caligans*), and in a single specimen of each of these species there is a small sesamoid ossicle above the dorsal hypohyal (see figs. 42, 45). Other specimens of these taxa are known not to have this ossicle.

*Monopterus* is distinguished from other synbranchids in the reduction or loss of the second and third basibranchials, and increase in distance between the hypobranchials of the first and second arches, and the medial displacement of the ceratobranchial of the first arch so that it no

longer articulates with its hypobranchial. Within *Monopterus*, *cuchia*, *fossorius*, and *boueti* are united by having the displaced first ceratobranchial more closely associated with the second than with the first arch and by having the reduced second basibranchial acuminate posteriorly and articulating with the ankylosed first basibranchial by an interlocking joint. *Monopterus albus* completely lacks a second and third basibranchial in most cases; one *M. albus* was found with tiny ossicles in the positions these basibranchials would normally occupy in other synbranchids. In *cuchia*, *fossorius*, and *boueti* the third basibranchial is absent, but a tiny ossicle was found in one specimen of *cuchia* in the position the third would otherwise occupy. Both *cuchia* and *fossorius* are further set apart by

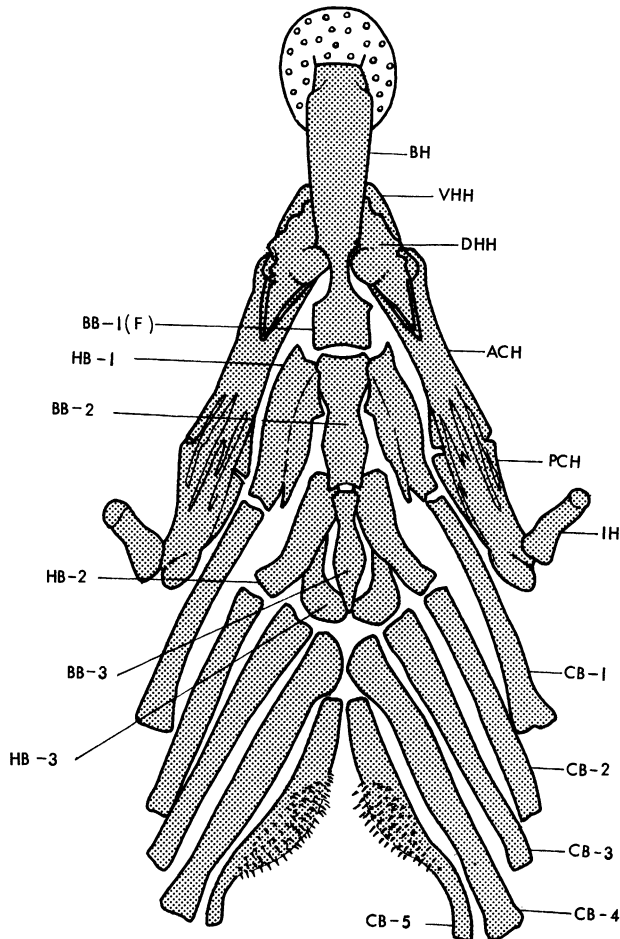


FIG. 43. Ventral gill arch skeleton of *Ophisternon bengalense*, BMNH 1962-2.14:4, India. Dorsal view.

having both ends of the first ceratobranchial closed over and noncartilaginous and the second ceratobranchial foreshortened and noticeably expanded dorsally for articulation with the modified second epibranchial (see above).

Complete holobranchs are absent in *Monopterus* but are present in other synbranchids. The details of holobranch anatomy are given in the following section.

The evidence provided by the ventral gill arch skeleton, therefore, supports the conclusion that *Monopterus* as here defined is a monophyletic group, but it is neither consistent with, nor

refutes, the proposed alignments of other synbranchid species.

#### BRANCHIAL VASCULAR SYSTEM, GILLS AND SUPRAPHARYNGEAL POUCH

To date the only Synbranchidae in which the blood-vascular system has been described are *Monopterusuchia*, *M. albus*, and *M. fossorius* (Taylor, 1831; Müller, 1839; Liem, 1961; and Samuel, 1963. See Liem, 1961, for other references). All three species have a specialized branchial vascular system that deviates markedly

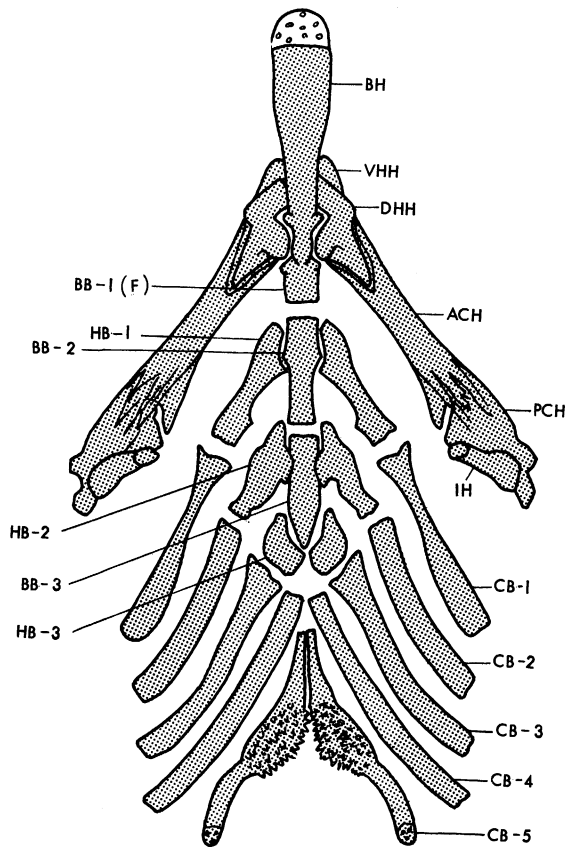


FIG. 44. Ventral gill arch skeleton of *Ophisternon afrom*, BMNH 1909.10.29:113, Portuguese Guinea. Dorsal view.

from the basic teleost condition (see below, also Liem, 1961).

Most other synbranchid species, in contrast, have a branchial vascular arrangement that is essentially of the general teleost type. All Synbranchidae do, however, share the following derived characters: an elongate heart situated well behind the cleithra and branchial arches, with a consequent elongation of the ventral aorta (which originates at a point between the ninth and twentieth vertebrae); hypertrophied auriculæ cordis; and thirdly, the hyoidean artery originating from the first afferent branchial artery (rather than from the efferent vessel of that arch).

The branchial vascular anatomy of *Synbranchus marmoratus* may be taken as representative of the generalized synbranchid condition

(fig. 51). There are distinct afferent and efferent vessels associated with the first to fourth gill arches. All the efferent arteries empty into the paired lateral aortae, although the third and fourth efferents join the lateral aorta through a common vessel. The internal carotid artery originates from a point near the confluence of the first efferent branchial artery with the lateral aorta, and a voluminous hyoidean artery arises near the base of the first afferent branchial.

A similar arrangement of branchial blood vessels, lateral aortae, internal carotids, and hyoidean arteries is found in *Macropterus caligans*, *Ophisternon aenigmaticum*, *O. bengalense* (at least in specimens from India and Sri Lanka), and in *O. infernale*.

A specimen, identified as *O. bengalense*, from



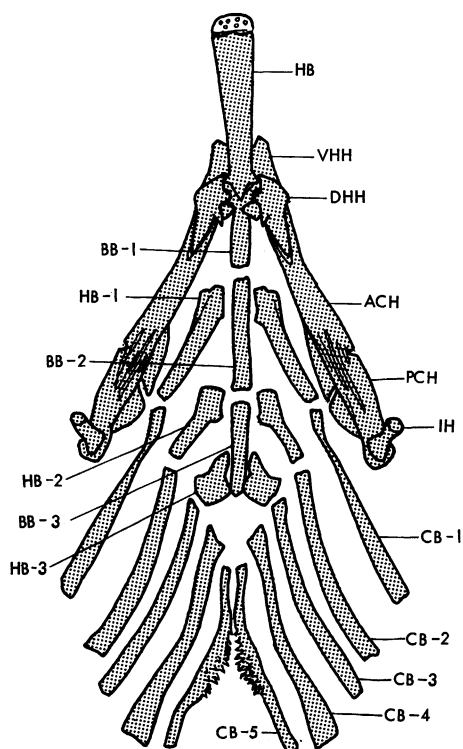


FIG. 45. Ventral gill arch skeleton of *Ophisternon infernale*, AMNH 32405, Yucatan, Mexico. Dorsal view.

Bangkok has the first efferent branchial not connected with the paired aorta of its side. Instead, the efferent vessel terminates in a large median sinus lying within the buccopharyngeal epithelium; the sinuses of each side apparently are separate.

Some departure from the generalized arrangement is also found in *Ophisternon afrum* and in *Synbranchus madeirae*.

In the latter species (fig. 52) the branchial vascular system is basically of the generalized type. However, from the upper face of the second arch a distinct and stout vessel forms a dorsally directed loop that passes lateral to the paired aorta before swinging inward to join an unpaired median sinus in the buccopharyngeal epithelium. As far as we can determine from the single specimen available for dissection, this vessel is not confluent with the second efferent branchial

artery at any point; the two vessels do, however, run parallel with one another over the dorso-lateral aspect of the arch and we cannot discount the possibility of fine interconnections occurring in this region. Another, and also seemingly independent efferent artery is associated with the first gill arch. It is visible on that arch in the same position as the supernumerary vessel of the second arch. However, the artery of the first arch passes inwards medial to the paired aorta of its side before it too joins the sinus. Unfortunately, the condition of our specimen precludes a de-

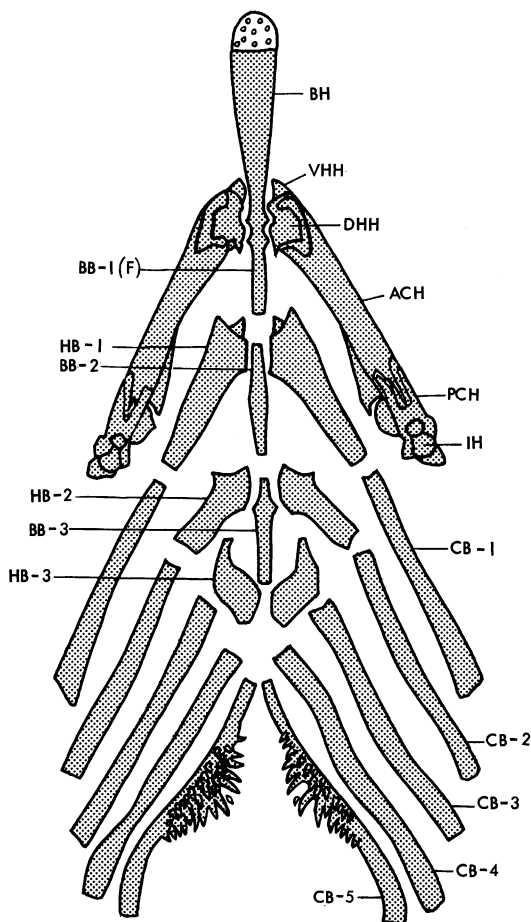


FIG. 46. Ventral gill arch skeleton of *Synbranchus marmoratus*, AMNH 30213, Bolivia. Dorsal view.

tailed investigation of the extent and ramifications of the sinus.

*Ophisternon afrom* (fig. 53) also has a median vascular sinus in the buccopharyngeal epithelium. Here, however, the sinus is supplied by the primary efferent arteries of the first and third gill arches, the artery of the third arch looping forward and upward lateral to the efferent artery of the second arch. Thus, in *O. afrom* only the second and fourth efferent branchial arteries join the paired aortae to discharge, ultimately, into the dorsal aorta. Again our dissections were confined to a single specimen and it was impossible to determine fully the extent and interconnections of the buccopharyngeal sinus.

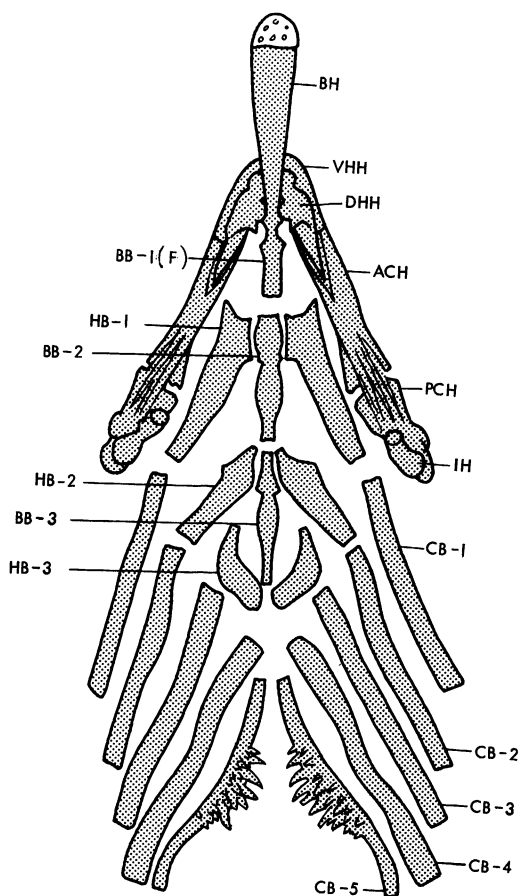


FIG. 47. Ventral gill arch skeleton of *Synbranchus madeirae*, AMNH 30219, Bolivia. Dorsal view.

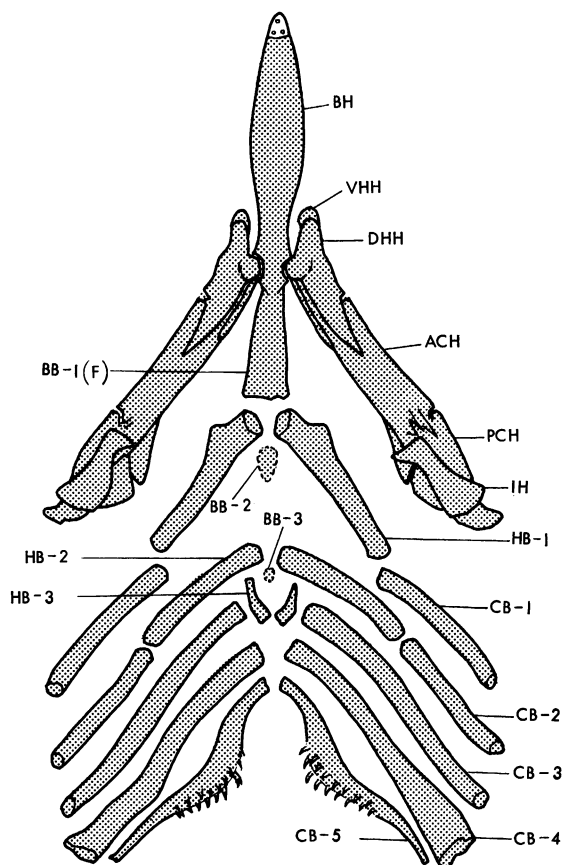


FIG. 48. Ventral gill arch skeleton of *Monopterus albus*, AMNH 7033, Fukien Province, China. Dorsal view.

Both *Synbranchus madeirae* and *Ophisternon afrom* have the same arrangement of afferent branchial arteries as is found in other taxa of these genera and also in *Macropterus caligans*.

Every species with a generalized type of branchial vascular system (including *O. afrom* and *S. madeirae*) has well-developed holobranchs on all four gill arches, and none shows any indication of a suprapharyngeal pouch such as occurs in three out of the six *Monopterus* species. It may be noted here that *Ophisternon candidum* (which could not be dissected) also has well-developed holobranchs on the first four gill arches.

In complete contrast, no species of *Monopterus* has visible gill tissue on the fourth arch [but see below with reference to *M. indicus* (Silas

and Dawson)], and all *Monopterus* species have reduced or much modified branchial tissues on the other three gill arches.

*Monopterus albus* has short but free and closely spaced filaments, arranged in a single row, on the second and third arches and on the lower two-thirds of the first arch; the upper third of that arch has the filaments replaced by a plate of highly vascularized tissue. Eapen (1963) described the gill lamellae of *Monopterus*

"*indicus*" Eapen as rudimentary, but gave no further details. *Monopterusuchia* has, invariably, a low flange of tissue on the first arch and a deeper flange on the third arch, but on the second arch there is a variable amount of true filamentous tissue combined with some flange-like tissue; as much as the lower two-thirds of the arch can carry filaments. The gills of *Monopterus fossorius*, according to our observations, are like those of *M.uchia*, but Samuel (1963) stated

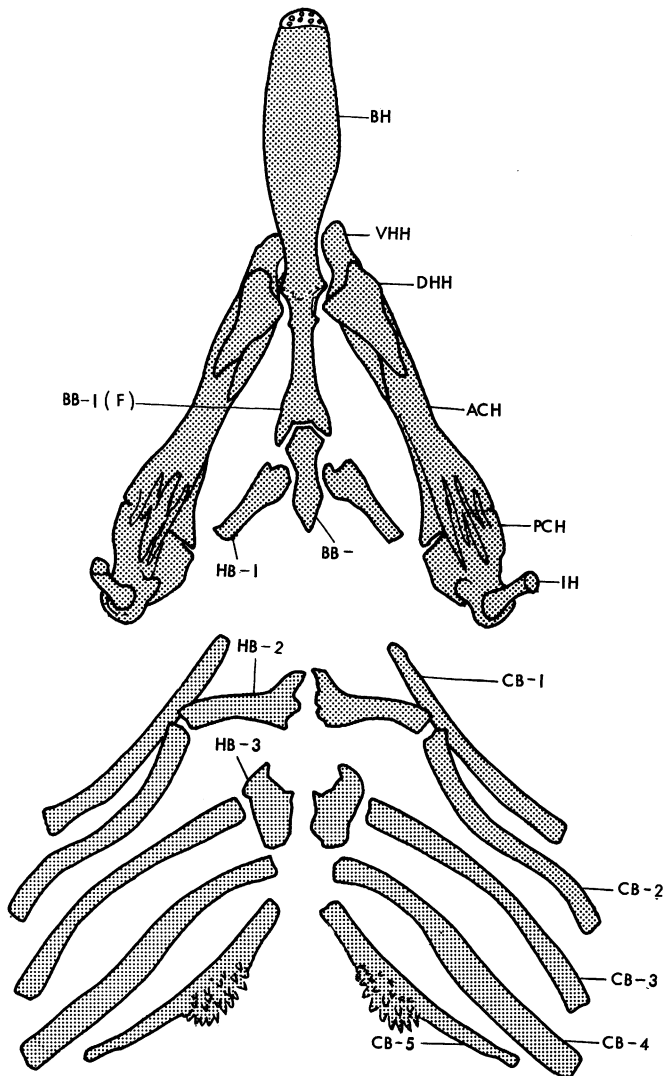


FIG. 49. Ventral gill arch skeleton of *Monopterus boueti*, AMNH 32411, Sierra Leone. Dorsal view.

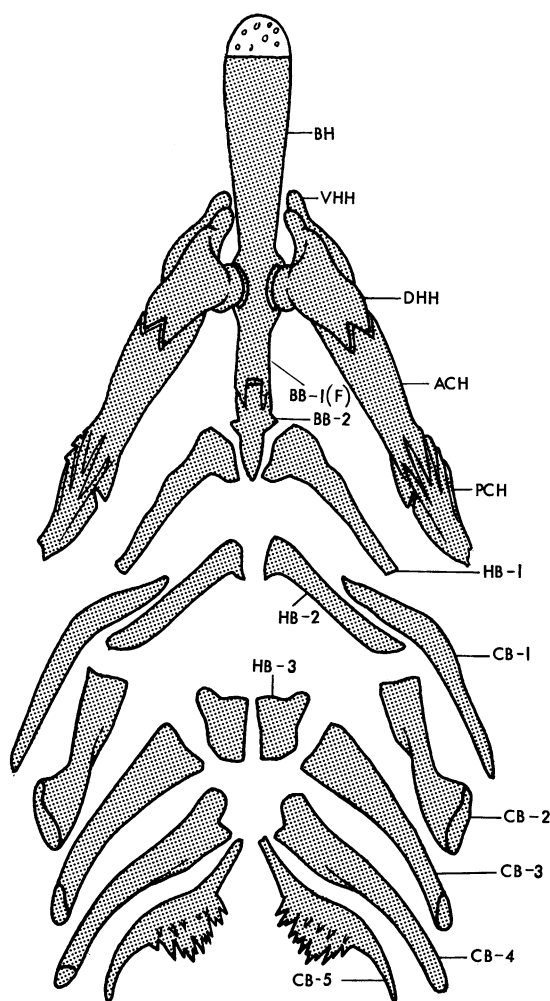


FIG. 50. Ventral gill arch skeleton of *Monopterusuchia*, BMNH 1889-2.1:2723, India. Dorsal view.

that "all four gill arches are devoid of gill filaments," and Nayar (1952) in the original description of the taxon noted that "None of the branchial arches carry well-developed gill filaments."

*Monopterus indicus* (Silas and Dawson) is described (Silas and Dawson, 1961) as having a plate of tissue on the third and fourth gill arches, but nothing on the first two arches. If this is so, then this species is quite unlike any other *Mon-*

*opterus* (or, for that matter, any other synbranchid). However, a careful examination of Silas and Dawson's figures (plate 1, fig. 7) and description strongly suggests that these authors have made two errors of observation. Firstly, they seem to have misidentified the first gill slit (which is described as a blind pouch; in other species the slit, although reduced in size is open). Secondly, they appear to have overlooked the small fifth arch (which is visible in their figure 7 of plate 1); thus, their gill-less fifth arch is, in fact, the fourth arch. If these corrections are made, it is the first and fourth arches that are gill-less, and the platelike branchial tissue is carried on the second and third arches, a less unusual condition than that described by Silas and Dawson, but one nonetheless unique among the species of *Monopterus*.

*Monopterus boueti* has no free gill filaments on any arch; the first to third arches each carrying a narrow flange of tissue, the flange on the first arch being the smallest.

Suprapharyngeal pouches are present in *M. cuchia*, *M. fossorius*, and *M. indicus* (Silas and Dawson) (Taylor, 1831; Nayar, 1952; Silas and Dawson, 1961) but are wanting in *M. albus* and, at least by implication because none is described by Eapen (1963), in *M. "indicus"* Eapen. We have been able to confirm the absence of the pouches in *M. boueti*.

The branchial vascular system has yet to be described in *Monopterus "indicus"* Eapen and in *M. indicus* (Silas and Dawson). In all other *Monopterus* species (including *M. boueti*) the system is known to differ markedly both from the usual teleost type and from the condition found in all

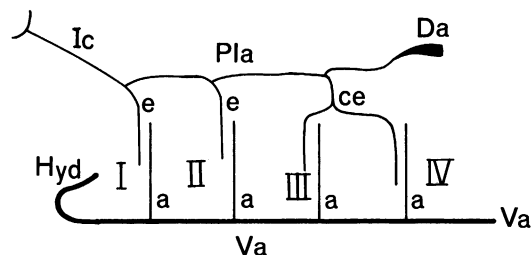


FIG. 51. Pattern of branchial blood-vascular system and associated vessels (left side) in *Synbranchus marmoratus*.

FIG. 53. Pattern of branchial blood-vascular system and associated vessels (left side) in *Ophisternon afrom*.



branchial (or the upper part of an affero-efferent vessel) from the paired aortae (or the dorsal aorta if paired aortae are absent).

Synapomorphous characters shared only by *M. cuchia*, *M. fossorius* and *M. boueti*<sup>1</sup> are the presence of a single (i.e., affero-efferent) artery in each of the first three gill arches, and the loss of contact between these vessels and the paired lateral aortae (and, that is, ultimately with the dorsal aorta).

*Monopterus cuchia* and *M. boueti* share one apomorphous character, namely the origin of the internal carotid artery from the second branchial

artery. From Samuel's (1963) account of *M. fossorius* it seems that in this species the internal carotids arise as anterior extensions of the small, persistent lateral aortae (in other words a plesiomorphous condition comparable with that in *Monopterus albus*).

The development of a suprapharyngeal pouch is to be considered a derived condition shared by *M. cuchia*, *M. indicus* (Silas and Dawson), and *M. fossorius* (Silas and Dawson, 1961; Nayar, 1952). No traces of pouches were found in *M. boueti*, and the organs are apparently absent in *M. "indicus"* Eapen (Eapen, 1963).

## OTHER VASCULAR CHARACTERS, SKULL AND JAWS, AND VERTEBRAE

*Vascular characters.* We have not made a detailed study of the entire blood-vascular system in all the species available to us, but some observations on the arrangement of the internal jugular veins are pertinent.

Both left and right internal jugulars are present in specimens identified as *Ophisternon bengalense*, and in *O. afrum*, *O. infernale*, *Synbranchus marmoratus*, and *S. madeirae*. In all these fishes the left vein is the larger of the pair. Five of the six *Ophisternon aenigmaticum* dissected have both internal jugulars present (again with the left the larger vein), but in the sixth specimen the right vessel is absent.

The left internal jugular alone is present in *Macrotrema caligans*, and it is closely applied to the overlying anterior cardinal vein with which it is almost equal in diameter. So closely applied are these veins that at first sight the internal jugular was thought to be absent.

The left internal jugular is also the only one present in *Monopterus albus*, *M. boueti*, and *M. cuchia* but is quite separate from the anterior cardinal vein in these species. For *M. fossorius*, Samuel (1963) described and figured paired internal jugulars. We suspect that examination of other specimens will show that Samuel's material is exceptional in having both veins present and of apparently equal size (Samuel, 1968, fig. 2). No

information is available for *M. "indicus"* Eapen or *M. indicus* (Silas and Dawson).

On the basis of the condition in other teleost groups, we conclude that the suppression of the right internal jugular vein is an apomorphous condition (as is the close apposition of internal jugular and anterior cardinal veins in *Macrotrema caligans*).

In summary, the evidence derived from the blood-vascular system shows: 1) that all synbranchids share the derived characters of an elongate and posteriorly displaced heart, extended ventral aorta, hypertrophied auriculae cordis, a hyoidean artery originating from the first afferent branchial artery, and a reduction or loss of the right internal jugular vein; 2) that all species of *Monopterus* examined or described have a single affero-efferent artery on the fourth gill arch, no holobranch on that arch and greatly modified branchial tissue (also reduced in area) on the other three arches, and that the third efferent branchial artery is functionally dissociated from the dorsal aorta, supplying instead the buccopharyngeal epithelium.

The vascular system in other synbranchids is of a generalized type and primitive for the group or is autapomorphous and therefore provides no evidence of relationship.

*Skull and Jaws.* All synbranchids have an elongate skull with the orbit placed far forward in the anterior third or fourth of the neurocranium, and the manner in which this elongation is accom-

<sup>1</sup>No specimens of *M. "indicus"* Eapen were available for study.

plished appears to us to be unique. In other fishes with elongate syncrania, such as mastacembelids and ammodytids, most or all the membrane and endochondral bones are strongly, if not always proportionally, involved in the lengthening process. In mastacembelids, for example, the vomer, nasals, palatine, ethmoids, frontals, parasphenoid, sphenotics, and prootics are all greatly attenuated (fig. 57). In synbranchids, on the other hand, the otic region, and to

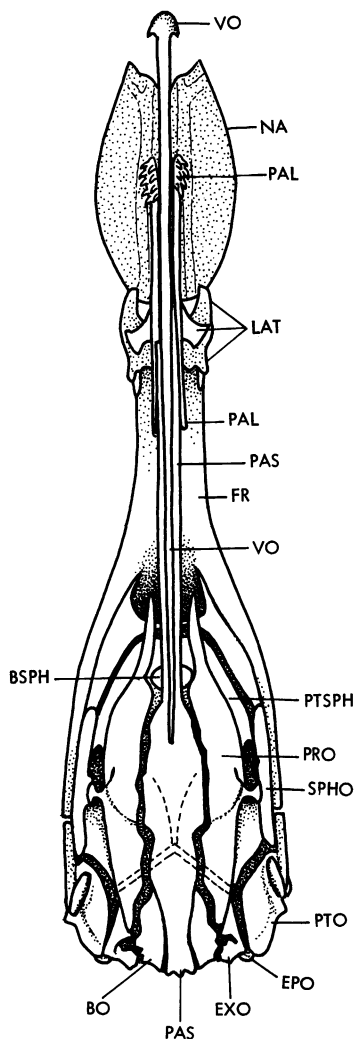


FIG. 57. Basicranium of *Mastacembelus congicus*, AMNH 6042.

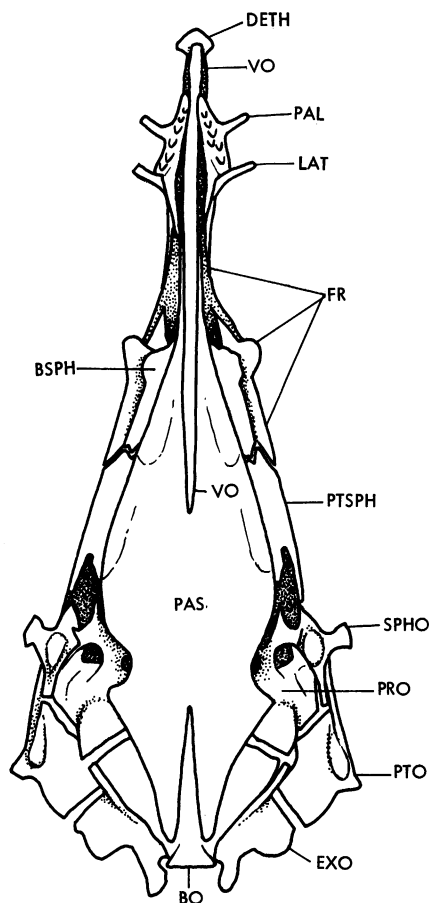


FIG. 58. Basicranium of *Synbranchus marmoratus*, AMNH 30213.

a lesser extent the ethmoid region, retain rather normal proportions (figs. 58, 59). Dorsally, however, the frontals are greatly attenuated, and ventrally, accommodative growth takes place between the anterior margin of the prootic and the posterior wall of the orbit. Consequently the pterospheneids and basisphenoid are massive bones occupying somewhat less than half the total length of the neurocranium. The vomer and parasphenoid are also elongate below these sphenoid elements. The massive development and forward extension of the basisphenoid is associated with its function of supporting an anterodorsal, but subdistal, boss or process of the toothed ectopterygoid, although the ectopterygoid also



has a more usual distal articulation with the palatine. The palatines are small crescentic bones, each with a lateral wing, and are closely applied and strongly adherent to the vomerine shaft. The vomer is a simple untoothed rod. It is evident that what previous workers with synbranchids have identified as vomerine and palatine teeth are, respectively, the palatine and ectopterygoid teeth. In the occipital region, each exoccipital has a posteriorly directed, horizontal facet on the underside of which attach corresponding processes of the first vertebra. The basioccipital facet is hollowed out to receive the pluglike,

central, articular part of that vertebra. In ventral outline, the neurocranium may be either narrowly triangular or very slender and almost tubular. Tubular neurocrania appear to be associated with eye reduction in *Ophisternon* (*infernale* and *candidum*) and *Monopterus* (*boueti*), although in the latter genus the relatively small-eyed *cuchia* and *fossorius* have more broadly triangular skulls than the larger-eyed *albus*. We have not found neurocranial characters particularly illuminating to phylogenetic questions, although a number of species-specific features have been identified, and these and other general cranial characters are given below in the group synopsis and key.

The jaws, jaw suspension and opercular apparatus (figs. 60, 61) also show numerous uncorrelated characteristics that, singly and in combination, are species-specific. They too are given below in the synopsis and key. The special attributes of all synbranchids, however, are 1) massive and elongate toothed ectopterygoids, and 2) narrow, strutlike, and anteriorly simplified, maxillae and premaxillae. Among the species of *Monopterus*, *cuchia*, *fossorius*, and *boueti* all appear to have reduced secondarily the alveolar premaxillary arms, so that the entire bone is only slightly more than half the length of the maxilla. All other synbranchids have a maxilla and premaxilla of nearly equal length.

One feature of the lower jaw, the coronoid elevation of the articular bone, is of some phylogenetic interest. In *Macrotrrema*, the coronoid elevation of the articular is present only as a low, gently rounded hump, as it is also in *Synbranchus* (fig. 60). In one specimen of *S. madeirae* and one of *S. marmoratus* the center of the hump is slightly peaked, that is, very low and obtusely triangular. In *Monopterus*, *cuchia*, *fossorius*, and *boueti* also have a low, gently rounded coronoid elevation, but in some *albus* there is a high, narrow-based, coronoid process with an expanded distal end that is sharply demarcated from the dorsal margin of the articular and inclined forward toward the coronoid elevation of the dentary (fig. 61). In *Ophisternon* all species possess a large, high, broad-based coronoid process in the form of an equilateral triangle. Such coronoid prominences on the articular of teleosts are common, although in

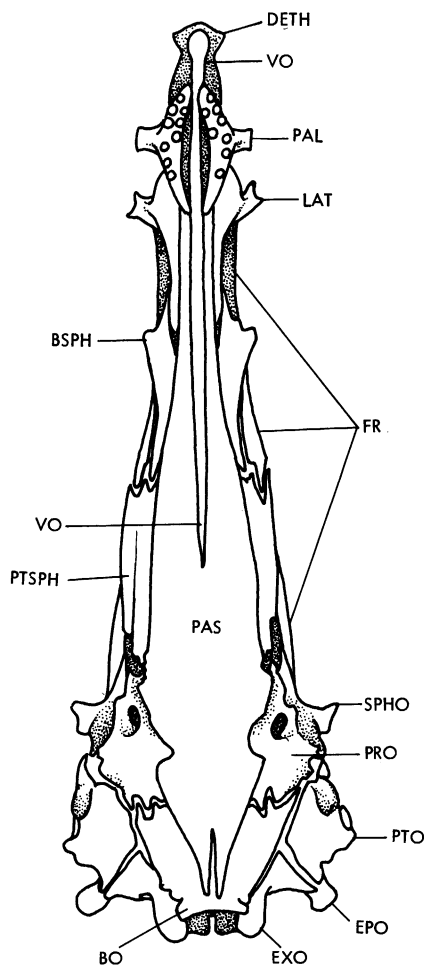


FIG. 59. Basicranium of *Monopterus albus*, AMNH 7033.

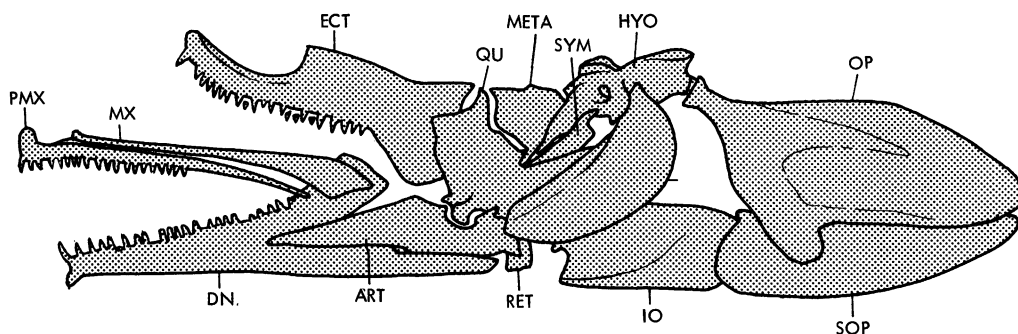


FIG. 60. Jaws, jaw suspension, and opercular apparatus in *Synbranchus marmoratus*, AMNH 30213.

many unrelated fishes with elongate crania and jaws the process is absent. For the moment we can only assume that its absence is either primitive or advanced in synbranchids, and consider the alternative hypotheses that each assumption will generate. For reason of the abundant contradictions discussed in earlier sections, we can rule out the possibility that the presence of a coronoid process relates *Monopterus albus* most closely to the *Ophisternon* group, or that its absence relates *cuchia*, *fossorius*, and *boueti* more closely to *Synbranchus* than to *Monopterus albus*. If we allow those conclusions, there are four possible theories to explain the distribution of this character, two assuming its presence in the common ancestor of all synbranchids, and two assuming its absence. Each theory initially involves a phylogeny in which *M. albus* is the sister group of other *Monopterus* species, *Synbranchus* the sister group of *Monopterus*, *Ophisternon* (or one of its species) the sister group of *Synbranchus* plus *Monopterus*, and *Macrotrrema* the sister group of all other synbranchids. If we assume the coronoid process to have been present in the ancestral synbranchid, then in case one it would have been lost in *Macrotrrema*, lost again independently in *Synbranchus*, changed into the specialized process of *albus* (or alternatively retained in a primitive form in *albus* and altered in *Ophisternon*), and lost a third time independently in the ancestor of *cuchia*, *fossorius*, and *boueti* (four evolutionary steps). In case two, the process would have been lost in *Macrotrrema*, lost in the common ancestor of the species of *Monopterus* and *Synbranchus*, and regained in a differ-

ent form in *M. albus* (three evolutionary steps). In case one involving the assumption that the process was absent in the ancestral synbranchid, the process would be gained in the common ancestor of *Ophisternon*, *Synbranchus*, and *Monopterus*, lost in *Synbranchus*, changed in *M. albus*, and lost in the ancestor of *cuchia*, *fossorius*, and *boueti* (four steps). In case two, the process would be gained in *Ophisternon* and gained again in a different form in *Monopterus albus* (two steps). A phylogeny in which *Ophisternon*, rather than *Synbranchus*, is the sister group of *Monopterus* requires three or four steps if the process were ancestrally present, and if ancestrally absent two or three steps. In the last two instances, in which the process is ancestrally absent, the process would be acquired in the ancestor of *Ophisternon* and *Monopterus*, further changed in *M. albus*, and then lost in the ancestor of *cuchia*, *fossorius*, and *boueti* (three steps), or gained independently by *Ophisternon* and by *M. albus* in a somewhat different form (two steps). It is evident from these considerations that the most economical interpretation of the data, that involving the fewest historical assumptions, regardless of which of the alternative theories of relationship is applied, is that *Ophisternon* and *M. albus* acquired their coronoid processes independently—an interpretation that is consistent with the very different character of the process in the two groups. This conclusion specifies that the coronoid process in *albus* is a distinctive autapomorphy of that species, and that the process in *Ophisternon* is evidence of the monophyletic origin of that genus, evidence that is

consistent with the less certain indications of monophyly provided by the structure of the first epibranchial as discussed above.

In summary, the skull anatomy of synbranchids has many distinctive features, some of which serve to define the whole group as monophyletic, are consistent with the interrelationships of some of the species of *Monopterus* based on many other lines of evidence, and provide the first bit of solid evidence that *Ophisternon* is a natural and not a grade group.

**Vertebrae.** Using alizarin preparations and radiographs, we have examined vertebral morphology in, and obtained vertebral counts for, all species except *Monopterus* "indicus" Eapen and *M. indicus* (Silas and Dawson).

Within the plan of general vertebral morphology common to all synbranchids, slight intergeneric and interspecific differences can be recognized in vertebral proportions, in the shape of neural and haemal spines, and in the shape and size of the zygapophyses (see, for example, fig. 21 in Rosen and Rumney, 1972). We have not, however, found any characteristics of vertebral morphology that are of value for indicating intra-familial relationships.

A consistent morphological feature in all synbranchid vertebrae is the long neural arch, almost rectangular in profile and which extends virtually the whole length of the centrum. Such arches are found on both abdominal and caudal vertebrae; similarly formed haemal arches occur on all but the first few caudal centra.

When viewed from above, the neural arches resemble parallel-sided gutters, open except in those regions covered by the base of the neural spine and, in some species, by the tips of the medially directed prezygapophyses that fuse or are closely apposed in the midline. Except in *Macropterna caligans* (where the tips of the prezygapophyses are fused into a crestlike prominence on all vertebrae save the first), those species with fused zygapophyses have these structures widely separated on the first 14 to 20 centra (e.g., in *Synbranchus marmoratus*, *S. madeirae*, *Ophisternon infernale*, *O. candidum*, and *Monopterus boueti*). The prezygapophyses are not fused medially (on either abdominal or caudal vertebrae) in *Ophisternon aenigmaticum*, *O. bengalense*, and *Monopterus albus*. Such may also be the condition in small individuals of species otherwise having fused prezygapophyses; for example, the prezygapophyses are separated throughout the column in a specimen of *S. marmoratus* 65 mm. long, but are fused medially (posteriorly to the sixteenth centrum) in a fish 136 mm. long.

The characteristic first vertebra of synbranchids was described in the section dealing with the neurocranium above.

There is considerable interspecific and intra-specific variation in the shape of the ultimate caudal vertebra. In many species (except *Macropterna caligans*) this vertebra is reduced to a small nubbin of bone. Several specimens we examined appear, on the basis of the small, irregular

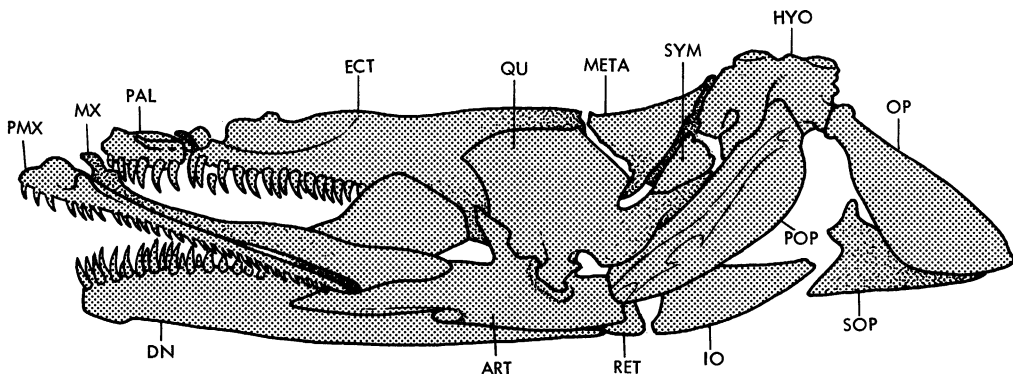


FIG. 61. Jaws, jaw suspension, and opercular apparatus in *Monopterus albus*, AMNH 7033. Palatine shown in positional relationship to ectopterygoid.

vertebrae in that region, to have suffered loss or damage to the caudal tip, which had then regenerated.

In *Macrotrema caligans* (the only species with an externally distinct caudal fin) the ultimate caudal vertebra articulates with five cartilaginous

hypural-like and one parhypural-like plates (fig. 2), the latter associated with from 9 to 14 barely ossified fin rays. Occasional specimens of *Ophisternon* and *Synbranchus* species have from three to seven unossified rays still present, but no hypural-like structures can be detected.

## RELATIONSHIPS OF THE ALABETIDAE

The reasons for including *Alabes* with the synbranchoids were never very clear or precisely formulated. Chiefly *Alabes* appears to have been so placed because it is eel-like, lacks fin spines, has the dorsal, caudal, and anal fins continuous, the caudal fin reduced and with few rays, has no pectoral fin or radials, and has the branchial openings joined in a single, transverse, ventral slit. The published literature also records that *Alabes* has well-developed dorsal and anal fins, ventral fins and girdle, a parasphenoid not united with the frontals and only 75 vertebrae (compare diagnosis of the Synbranchidae, below). The latter features are all primitive with respect to comparable details in synbranchids, leaving the derived reductional features of the body, fins, and gill opening as the only evidence of their proposed relationship. Certain details of the in-

ternal anatomy, however, can be used to reject the alignment of *Alabes* and synbranchids by showing that *Alabes* shares more numerous, and more specific, derived features with other acanthopterygians than with synbranchids. For example, with tropical blennies *Alabes* shares an elongate body, a reduction in fin spination, long dorsal and anal fins that are confluent or associated by a membranous fold with the caudal, a reduced caudal ray count, and branchial openings joined in the ventral midline and in some cases restricted laterally to the region below the horizontal septum. In the upper jaw *Alabes* shares with some blennioids a premaxilla with a short alveolar process and an indistinct articular process that merges with the base of a very high and robust ascending process (compare the upper jaw bones in synbranchids, figs. 60, 61). In the dorsal

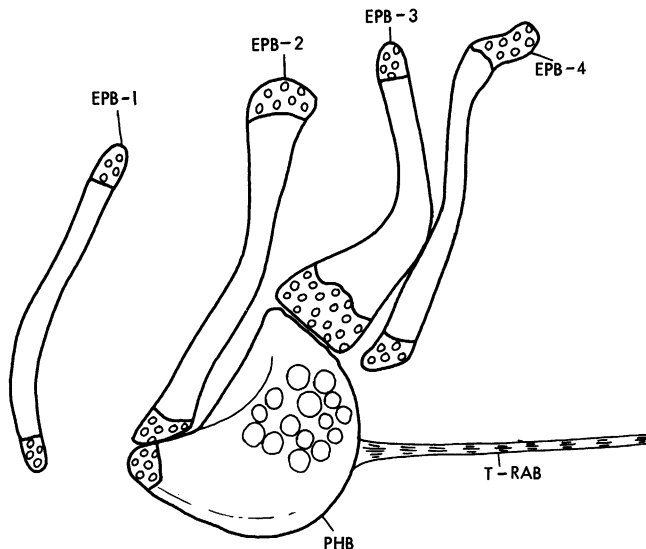


FIG. 62. Dorsal gill arch skeleton of *Alabes rufa*, AMNH 32447. Dorsal view, right side.

gill arch skeleton, *Alabes* (fig. 62) has a single, toothed, comma-shaped pharyngobranchial to which the second, third, and fourth epibranchials attach (a second pharyngobranchial is not present and no interarcual cartilage arising from the base of the first epibranchial. Synbranchids, in contrast, have a more generalized pattern in which there is a separate third and fourth upper pharyngeal tooth patch, primitively a small second pharyngobranchial, and an interarcual cartilage (enlarged and ossified in all synbranchids). Whatever the precise relationships of *Alabes* may

be, it seems reasonably clear that it has closer affinities with blenny-like fishes than with synbranchids (a conclusion reached independently by Dr. V. Springer, *in litt.*, and which will be discussed more fully by him). Gosline (1971) had also previously voiced suspicion about the position of alabetids among synbranchoids, a suspicion that now appears fully justified. Hence, the alabetids are considered here as irrelevant to questions concerning synbranchid phylogeny and are not discussed.

## ANNOTATED ACCOUNT OF GROUPS AND SPECIES OF THE SYNBRANCHIDAE

### FAMILY SYNBRANCHIDAE SWAINSON (1838)

*Diagnosis.* Eel-like fishes of small to moderate size (to more than 70 cm.), without pectoral fins (except in larval stages), pelvic fins or girdles or dorsal and anal fins (except as the fins are represented by median folds), and with caudal fin reduced or absent. Gill membranes united and continuous around isthmus. Eyes small, well forward in skull, near a vertical from the midpoint of upper lip, and covered by dense skin. With anterior and posterior nares. Scales, when present (in a few species), small, oval and confined largely to caudal region. Neurocranium elongate, region between prootic and posterior wall of orbit greatly expanded (figs. 58, 59). Frontals, pterosphenoid, basisphenoid, vomer, and parasphenoid attenuated, the last bone also much widened and with two prongs posteriorly. Palatines joined firmly to vomer in midline. Vomer a long, thin strut, edentulous. Frontal turned down and sutured to basisphenoid. Parietals large, meeting in midline. Infraorbital bones reduced to a single preorbital. Palatoquadrate articulating with a prominence on the basisphenoid, frontal, or both, and with the vomer and lateral ethmoids. Maxilla and premaxilla long and strut-like, with their symphyseal processes reduced and simplified (figs. 60, 61). Teeth present on the premaxilla, dentary, palatine, and ectopterygoid. First vertebra with a central plug and pair of lateral flanges for articulation with occipital region (fig. 63). Basihyal edentulous, ankylosed

with first basibranchial (secondarily unfused in one species). Branchiostegals four to six (rarely seven) in number. Dorsal gill arch skeleton with an ossified interarcual cartilage connecting first epibranchial with medial part of second arch. No first pharyngobranchial; second pharyngobranchial reduced or absent. A small tooth patch below third pharyngobranchial and another in position of missing fourth. Scapulocoracoid absent; cleithrum well developed and turned sharply forward ventrally. Heart posterior, behind shoulder girdle; ventral aorta originating from level of ninth to twentieth vertebrae. Atrium of heart with large ventral outpocketings (auriculae cordis). Right internal jugular vein reduced or absent. Vertebrae numerous, 98 to 188, never having fewer than 51 abdominal elements (table 2). Pantropical fishes from fresh water at high and low elevations; individuals of some species reported from brackish water. Fifteen species.

### SUBFAMILY MACROTREMINAE, NEW

*Diagnosis.* Small synbranchids (of not more than 20 cm.) with the eye greatly reduced and sunken well below the surface skin, without a right internal jugular vein and with remaining left internal jugular hypertrophied and applied closely to anterior cardinal vein. With many attributes primitive for the family, including: large gill opening, extending up along the side above horizontal septum; with a small caudal fin of nine to 14 unsegmented and unbranched ossified rays

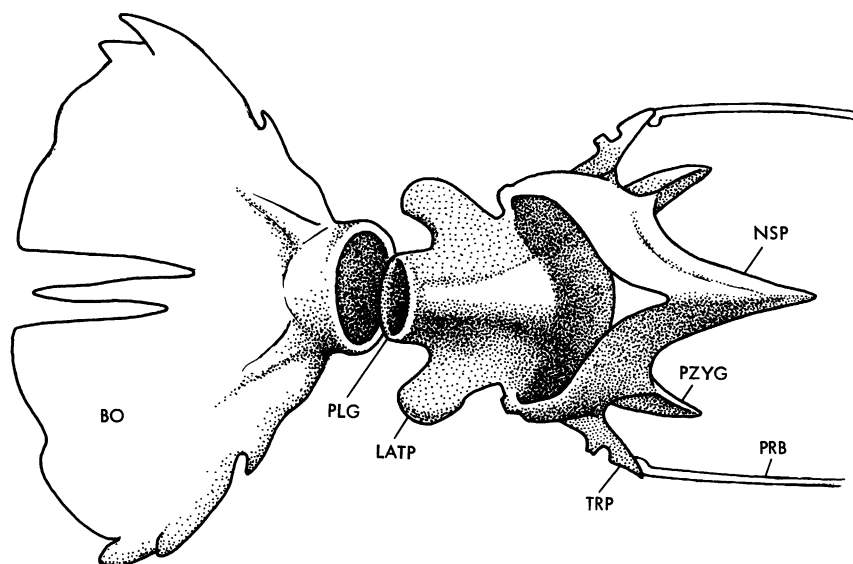


FIG. 63. Basioccipital bone and first vertebra of *Synbranchus marmoratus*, AMNH 30213. Dorsal view.

distinct from the dorsal and anal fin folds; posterior nares anterior to orbit; vertebrae 100 to 103. A single species from the Malayan Archipelago.

#### GENUS *MACROTREMA* REGAN

*Macrotrema* Regan, 1906 (type species by original designation *Synbranchus caligans* Cantor, 1849).

#### *Macrotrema caligans* (Cantor)

*Synbranchus caligans* Cantor, 1849 (Penang, Malaysia).

**Remarks.** Four specimens were available: the holotype, from Penang (BMNH 1860.3.19:943), one from Singapore (BMNH 1908.7.13:1), and two from Thailand (MCZ 47107), one of which, our largest, was 184 mm.

**Range.** Thailand and the Malay Peninsula.

#### SUBFAMILY SYNBRANCHINAE SWAINSON

**Diagnosis.** Synbranchids in which gill opening is reduced to a ventral slit or pore, posterior nares are dorsomedial to eye, and caudal fin is greatly reduced (without ossified rays) and con-

tinuous with dorsal and anal fin folds or absent. Fourteen species. Pantropical.

#### GENUS *OPHISTERNON* M'CLELLAND

*Ophisternon* M'Clelland, 1845 (type species by monotypy, *O. bengalensis*).

*Tetrabanchus* Bleeker, 1851 (type species by original designation *T. microphthalmus*).

*Pluto* Hubbs, 1938 (type species by original designation, *P. infernalis*).

*Furmastix* Whitley, 1951 (as a replacement for *Pluto*, preoccupied in Insecta, Hymenoptera).

*Anomatophasma* Mees, 1962 (type species by original designation, *A. candidum*).

The name *Unipertura* of Duméril (1856) was designed as a replacement name for *Unibranchapertura* Lacépède (1803). The type of Duméril's name was designated as *Unibranchapertura laevis* Lacépède (1803). The trivial name *laevis* was assigned by Cantor (1849) to the synonymy of *Monopterus javanicus* (Monoptère javanais) of Lacépède (1800), the latter being presently in the synonymy of *Monopterus albus*. Since it would be manifestly impossible to determine from any relevant descriptions by Lacépède exactly which synbranchid truly is involved, one

can only assume that, coming from the Old World tropics, the fish referred to as *laevis* might be either a *Monopterus* or an *Ophisternon*. Hence, *Unibranchapertura laevis* will forever remain in taxonomic limbo and should be formally suppressed.

In addition to the second neotropical species of *Ophisternon* described below, there may be another as yet uncollected in Cuba. Hubbs (1938, p. 270) cited Poey's account of a subterranean "eel" from Cartagena with its eyes hidden beneath the skin, with pores on the side of the head, and with a series of parallel vertical folds on the side of the neck bordered by scalelets like short, white hairs.

*Ophisternon bengalense* M'Clelland

*Ophisternon bengalensis* M'Clelland, 1845 (original description p. 197; pl. XI, fig. 1).

?*Ophisternon hepaticus* M'Clelland, 1845 (Burma).  
*Tetrabanchus microphthalmus* Bleeker, 1851 (Borneo).

**Remarks.** The taxon recognized here as *bengalense* excludes specimens from northern Australia. The latter are separated as a distinct species bearing Richardson's name *gutturale* (see below). Even after the exclusion of Australian material, *bengalense* remains a variable form. Differences between specimens from widely separated areas involve eye position and relative size and shape of mouth and head (see figs. 3 and 4). Detailed anatomical investigations of large samples may show that some populations are recognizably distinct. We are unable to identify *O. hepaticus* M'Clelland (1845) from the description although from the figure it would certainly seem to be a member of the genus *Ophisternon*, either identical with or closely related to *O. bengalense*.

**Material.** From India, the syntypic series from the Hooghly River, BMNH 1860.3.19:765-775; and those recorded as simply from India, BMNH 1858.3.15:71, and South India, BMNH 1962.2.14:4; from Ceylon, AMNH 32403; Bangkok, MCZ 9158; and Philippines, MCZ 26377. A lectotype is designated from the syntypic series, as follows: Lectotype (BMNH 1860.3.19.765): Total length 480 mm. Head length 49 mm. Caudal length 123 mm. Snout to eye center 5.8 mm. Dorsum of head and body

except for ventral surface, light brown. Lips, ventral surface of head, operculum, branchiostegal membrane, yellowish. Under low-power magnification, evenly scattered melanophores over entire body.

**Range.** Indo-Malaysian region and Philippine Islands.

*Ophisternon gutturale* (Richardson)

*Synbranchus gutturalis* Richardson, 1844 (Dampier's Archipelago, Australia).

**Remarks.** Whitley (1948) was, without stated reasons, the first to resurrect Richardson's name for Australian material of what was formerly, and subsequently (Mees, 1962), identified as *bengalense*. The material we examined from northern Australia is markedly different from more northern samples of *bengalense* and is easily separated from them (see Key and figs. 3-5). Although we have seen no examples from New Guinea, and cannot specify the range of this type of *Ophisternon* with precision, use of the name *gutturale* we hope will serve to emphasize the need for more detailed analysis of the Old World *Ophisternon*. It seems clear to us that *bengalense* and *gutturale* are closely related on the basis of a shared, derived maxillary character (section B, cc of the Key). Material examined is from Northern Territory, Australia, AMNH 30893 and USNM 174019.

**Range.** Northern Australia.

*Ophisternon candidum* (Mees)

*Anomatophasma candidum* Mees, 1962 (North West Cape, Western Australia).

**Remarks.** We have examined only a single specimen of *candidum* from the North West Cape, Western Australia (the known range of the species), AMNH 32404.

*Ophisternon afrum* (Boulenger)

*Synbranchus afer* Boulenger, 1909 (Portuguese Guinea, west Africa).

**Remarks.** We have examined the two syntypes from BMNH 1909.10.29: 113-114, and herewith designate the larger one as lectotype: Lectotype

(BMNH 1909.10.29:114): Total length 310 mm. Head length 31 mm. Caudal length 85.5 mm. Snout to eye center 4 mm. Gape length 7.5 mm. Body pale, uniform, except for darker dorsum and dorsal fin fold on both of which small melanophores are visible. Upper half of head uniform with body, lower half, including lips and branchiostegal membrane, lighter. See figure 6.

*Range.* Point Mansoa, Portuguese Guinea, the type locality. Boulenger (1915) also reported this species from the Niger delta.

*Ophisternon infernale* (Hubbs)

*Pluto infernalis* Hubbs, 1938 (Hoctun Cave, Hoctun, Yucatan, Mexico).

*Remarks.* Material, two specimens, the larger 231.5 mm. in total length (UMMZ M74-20; AMNH 32405).

*Range.* Caves of Yucatan, Mexico.

*Ophisternon aenigmaticum*, new species

Figures 23, 24; tables 2-4

*Synbranchus marmoratus*: Rosen and Rumney, 1972 (specimens from locality nos. 36, 47, 60 [BMNH 1866-4-25:9], 92-95, 98-103, 105, 107-110, 112-116 representing material from South America, Guatemala, Mexico, and Cuba). Probably all other earlier references to material of *S. marmoratus* from Atlantic slope Guatemala and Mexico, and Cuba, are based on this species.

*Material.* Holotype, a presumed adult 350 mm. in total length, AMNH 32410, from a woodland pool about 13 km. southwest of Sebol in the valley of the Río Chajmaic, Alta Verapaz, Guatemala. Taken with the holotype are four other specimens 130 to 500 mm. in total length, AMNH 32071. Paratypes include some materials listed by Rosen and Rumney (see synonymy above) and the following:

Northern South America (locality not otherwise specified), AMNH 17269 (1);

Honduras (Copán), UMMZ 104117 (1);

Belize, UMMZ 97883 (1), UMMZ 158397 (1), UMMZ 167700 (1);

Guatemala (Río Motagua system), AMNH 31554 (1), AMNH 31573 (3), AMNH 32096 (2), UMMZ 190581 (2), UMMZ 190711 (3), UMMZ 190810 (2), UMMZ 193885 (2);

Guatemala (Río Polochic system), AMNH 31619 (1), AMNH 32408 (3), AMNH 32411 (1), UMMZ 190755 (2);

Guatemala (Río Sarstún system), AMNH 31594 (3), UMMZ 190611 (2);

Guatemala (Río Usumacinta system), AMNH 31502 (1), AMNH 31504 (4), AMNH 31508 (1), AMNH 31701 (1), AMNH 31723 (2), AMNH 32002 (2), UMMZ 131144 (1), UMMZ 144164 (3), UMMZ 144167 (1), UMMZ 144169 (5), UMMZ 144170 (1), UMMZ 144305 (1), UMMZ 146110 (2), UMMZ 146114 (3), UMMZ 187943 (3), UMMZ 190502 (4);

Guatemala (Petén lake district), AMNH 32017 (3), UMMZ 138234 (1), UMMZ 144160 (2), UMMZ 144161 (1), UMMZ 144162 (1), UMMZ 144163 (4), UMMZ 144165 (7), UMMZ 144166 (2), UMMZ 144168 (2), UMMZ 144306 (1);

Mexico (Campeche), UMMZ 104682 (1);

Mexico (Tabasco), UMMZ 194846 (1), UMMZ 194864 (1);

Mexico (Chiapas), UMMZ 191718 (3);

Mexico (Oaxaca), UMMZ 124202 (1), UMMZ 124287 (1);

Mexico (Veracruz), UMMZ 183899 (1), UMMZ 184558 (1), UMMZ 187757 (1), UMMZ 187801 (1), UMMZ 187818 (4), UMMZ 194839 (1);

Cuba, UMMZ 171891 (2).

*Diagnosis.* A species of *Ophisternon* reaching more than 700 mm. in total length, and differing from other members of the genus in the wider skull (greatest width across otic region 40 percent of length of neurocranium, as compared with 30 percent or less) and absence of an angulate prominence on posterodorsal aspect of maxilla.

*Description.* Meristic and morphometric data are given in tables 2 to 4. The background color of the dorsum and sides varies from almost black to medium gray. Individuals may be speckled, blotched, or uniform but the blotches never form large, discrete spots as in *Synbranchus marmoratus*. The ventral region of the body is dusky, pale, brownish, or reddish in life and dusky or pale in preservative. One or two dusky streaks behind the eye are present in some cases. The eye is always visible through a dense but translucent layer of skin, and is directly over or in front of a



line drawn through the midpoint of snout to corner-of-gape length. The lips are swollen laterally and merge anteriorly with the tissues of the snout and dental symphysis. The anterior naris on the snout tip often is directed somewhat ventrally; the posterior naris is anteromedial to the eye. Mandibular, preorbital, preopercular, and opercular cephalic lateral line pores are present. The branchiostegal membrane is drawn into long folds ventrally; the gill opening is irregular or crescentic and occupies a third to a half of the width of the ventral body surface just behind the head.

Among the northern samples of this form, Cuban material can be separated from Middle American specimens on an average difference in relative length of caudal peduncle (22 versus 29 percent of total length; range of values 19 to 26 percent versus 24 to 32 percent of total length; see table 3). The relatively short peduncle of Cuban specimens is reflected also in their relatively few caudal vertebrae (table 4). Cuban material is scarce, however, and also extremely variable in most attributes, including vertebral number.

In spite of the possible existence of features to separate Cuban from Middle American specimens, both of these northern populations may be more closely interrelated than is either to South American populations. The suggestion is tentative because the South American material is represented by only five specimens, one of which is unaccompanied by an exact locality. Nevertheless, on the basis of radiographs and dissections of material on hand, the northern and southern samples of *aenigmaticum* may be characterized with respect to cranial anatomy, as follows:

*Middle American and Cuban specimens.* In the pharyngobranchial apparatus (figs. 32, 33), the interarcual bone is usually straight and the basal articular flange on the first epibranchial is not large enough to overlap the base of the interarcual bone. In the neurocranium the saccular bullae are widely separated in the midline by the posterior arm of the parasphenoid, the outline of the skull in dorsal or ventral view is somewhat convex and gently tapering in front of the pterotic, and the anterior part of the braincase is a little wider than the orbital region.

*South American specimens.* In the pharyngo-

branchial apparatus (figs. 34, 35) the interarcual bone is strongly curved posteriorly and the basal articular flange of the first epibranchial is larger and overlaps the base of the interarcual bone. The saccular bullae and sagittae are massive and are only narrowly separated by the posterior parasphenoid arm, the outline of the skull tapers more abruptly anterior to the pterotic and is straight rather than convex, and the anterior part of the braincase is only about as wide as the orbital region.

When more Cuban and South American material becomes available, study may show that the Cuban, South American, and Middle American populations should be recognized as distinct taxa.

Like other synbranchids, *O. aenigmaticum* occurs in a variety of habitats from standing water in small muddy pools to clear running water in streams. It has even been taken in large bodies of water, e.g., in weed beds along the margin of El Golfete (Río Dulce, Río Polochic basin), in the department of Izabal, Guatemala, and in Lake Petén.

*Etymology.* The trivial name is from the Latin *aenigma*, something obscure, and agrees in gender with the name *Ophisternon* [suffix *sternon* (neuter) from the Greek word for chest].

#### GENUS *SYNBRANCHUS* BLOCH

*Synbranchus* Bloch, 1795 (type species by subsequent designation, *S. marmoratus*).

*Typhlobranchus* Bloch and Schneider, 1801 (type by monotypy *T. spurius*).

*Unibranchapertura* Lacépède, 1803 (replacement name for *Synbranchus*, type by original designation, *S. marmoratus*).

#### *Synbranchus marmoratus* Bloch

*Synbranchus marmoratus* Bloch, 1795 (Surinam).

*Synbranchus immaculatus* Bloch, 1795 (type locality given as Surinam or Tranquebar, India. Bloch's figure shows the gill opening typical of *marmoratus* so that the Tranquebar locality is undoubtedly erroneous).

*Unibranchapertura lineata* Lacépède, 1803 (Surinam).

*Synbranchus fuliginosus* Ranzani, 1840 (Brazil).

*Synbranchus pardalis* Valenciennes, 1847 (Buenos Aires, Argentina).

TABLE 3  
Morphometric Comparisons of the Epigean Species of *Ophisternon*  
(Ratios expressed as percentages.)

	L e n g t h s				
	<u>Caudal</u> Total	<u>Head</u> Total	<u>Snout</u> Head	<u>Snout</u> Gape	<u>Gape</u> Head
<i>Ophisternon aenigmaticum</i>					
Mexico					
No. specimens	16	16	16	16	16
Mean	29.88	11.71	14.24	42.41	33.13
Standard deviation	1.76	0.69	1.15	3.95	2.16
Min.-max. values	27-33	11-13	12-16	36-51	28-36
Size (total length) range in mm. = 116-579					
Guatemala					
No. specimens	23	23	25	25	25
Mean	29.17	11.13	15.68	47.48	32.96
Standard deviation	1.97	0.87	2.10	3.50	4.08
Min.-max values	24-32	10-13	(9) <sup>a</sup> 12-18	43-53	(20) <sup>a</sup> 27-38
Size (total length) range in mm. = 124-735					
Honduras					
No. specimens	1	1	1	1	1
Ratios	28.68	11.29	16.08	39.68	40.51
Size (total length) in mm. = 276					
Cuba					
No. specimens	7	7	7	7	7
Mean	22.49	12.00	12.76	41.00	31.52
Standard deviation	2.18	0.00	1.01	6.10	3.56
Min.-max. values	19-26	12-12	11-14	35-52	24-34
Size (total length) range in mm. = 318-491					
South America					
No. Specimens	4	4	4	4	4
Mean	28.25	10.00	13.50	40.50	33.25
Standard deviation	1.71	0.00	2.38	3.70	3.77
Min.-max. values	26-30	10-10	12-17	37-45	29-38
Size (total length) range in mm. = 97-436					
<i>Ophisternon afrum</i> (lectotype)					
No. specimens	1	1	1	1	1
Ratios	27.42	9.90	12.05	38.95	30.95
Size (total length) in mm. = 310					
<i>Ophisternon bengalense</i> (from type series)					
No. specimens	8	8	8	8	8

TABLE 3—(Continued)

	Lengths				
	Caudal Total	Head Total	Snout Head	Snout Gape	Gape Head
Mean	27.50	10.13	11.63	35.13	32.50
Standard deviation	1.20	0.35	4.10	7.77	4.17
Min-max. values	25-29	10-11	8-12(21) <sup>a</sup>	25-49	29-42
Size (total length) range in mm. = 186-611					
<i>Ophisternon gutturale</i> (Arnhem Land)					
No. specimens	5	5	5	5	5
Mean	26.60	11.20	14.00	42.80	33.00
Standard deviation	0.55	0.45	0.71	3.56	2.45
Min.-max. values	26-27	11-12	13-15	38-48	31-37
Size (total length) range in mm. = 132-282					

<sup>a</sup>Single exceptional value.

*Synbranchus vittata* Castelnau, 1855 (Rio de Janeiro, Brazil).

*Synbranchus hieronymi* Weyenbergh, 1877 (Argentina).

*Synbranchus doringii* Weyenbergh, 1877 (Argentina).

*Synbranchus tigrinus* Weyenbergh, 1877 (Argentina).

*Synbranchus mercedarius* Weyenbergh, 1877 (Argentina).

**Remarks.** *Synbranchus transversalis* Bloch and Schneider (1801), *Unibranchapertura grisea* Lacépède (1803), *U. cinerea* Lacépède (1803) and *Muraena lumbricus* (Gronow (1854), although previously included in the synonymies of *Synbranchus marmoratus*, are either clearly stated by their authors, or interpreted by us from reading of the original descriptions, to have come from the Gulf of Guinea region of west Africa. Hence, these nominal forms, now unrepresented or in some cases never represented by type material, may have referred to *Ophisternon afrum* or to *Monopterus boueti* (see below). Moreover, because *Synbranchus marmoratus* and *Ophisternon aenigmaticum* (described above) are sympatric over a wide area of South America from which *marmoratus* and other nominal forms synonymized with it have come, and because these two

species are superficially so similar (fig. 23), a certain likelihood exists that some of the names given above may have referred to *aenigmaticum*. There unfortunately are no types available to eliminate this uncertainty.

**Material.** (Includes specimens examined and cited by Rosen and Rumney (1972).) Only two specimens from Mexico are identified as *marmoratus* (all others are *Ophisternon aenigmaticum*), as follows: Rosen and Rumney's locality no. 104, Oaxaca, Río Coatzacoalcos drainage, AMNH 20305; and their locality no. 106, Tabasco, in the Río Teapa at Teapa, BMNH 1913.6.21:225. In Guatemala, *Synbranchus marmoratus* apparently is confined to the Pacific coast (Rosen and Rumney locality nos. 96 and 97). In northeastern South America, Rosen and

TABLE 4  
Vertebral Variation in *Ophisternon aenigmaticum*

	Precaudal	Caudal	Total
Mexico (N = 19)	70-81	45-57	118-136
Guatemala (N = 9)	71-79	43-58	114-137
Cuba (N = 13)	70-82	25-49	98-128
South America (N = 2) Cayenne-Brazil	75-76	48-54	123-130

Rumney locality no. 36, Marajo Island at the Amazonian mouth, Pará, Brazil (BMNH 1923.8.11:44-45), locality no. 47 Cayenne River, Cayenne, Guayane (French Guiana) (BMNH 1846.2.16), and one of three lots from locality no. 60, Trinidad (BMNH 1866.4.25:9), represent specimens of *Ophisternon aenigmaticum*. All other localities cited in South America north to and including Honduras represent *S. marmoratus*. All other Guatemalan, Mexican, and Cuban localities represent *Ophisternon aenigmaticum*. It is apparent therefore that the two species occur together in Atlantic drainages of southern Mexico (Oaxaca and Tabasco), and in north-eastern South America.

*Range.* Argentina north in Atlantic drainages of South America, and on both slopes of Central America to Pacific slope Guatemala and Oaxaca and Tabasco, Mexico.

*Synbranchus madeirae* Rosen and Rumney

*Synbranchus madeirae* Rosen and Rumney, 1972 (Río Madeira, Bolivian Amazon).

*Remarks.* All specimens except the holotype cited in Rosen and Rumney (1972) have been restudied.

*Range.* Río Madeira, Bolivian Amazon.

#### GENUS *MONOPTERUS* LACÉPÈDE

*Monopterus* Lacépède, 1800 (type species by subsequent designation, *Muraena alba* Zuiew).

*Fluta* Bloch and Schneider, 1801 (type species by monotypy *Monopterus javanensis* Lacépède).

*Ophichthys* Swainson, 1839 (type species by monotypy, *Unibranchapertura cuchia* Hamilton; used as a replacement name in the combination *O. punctata* Swainson).

*Amphipnous* Müller, 1841 (type species by monotypy, *Unibranchapertura cuchia* Hamilton).

*Ophiocardia* M'Clelland, 1845 (type species by monotypy, *O. phyariana* M'Clelland).

*Pneumabanchus* M'Clelland, 1845 (type species by monotypy, *P. striatus* M'Clelland).

*Apterigia* Basilewski, 1855 (type species by original designation, *A. saccogularis* Basilewski).

*Typhlosynbranchus* Pellegrin, 1922 (type species by original designation, *T. boueti* Pellegrin).

Considerable uncertainty exists regarding the correct generic and trivial names for the species we are calling *Monopterus albus*. The binomina *Fluta alba* (Zuiew), *Monopterus albus* (Zuiew), *Monopterus javanensis* Lacépède, *Monopterus javanicus* Lacépède, and even *Monopterus fluta* (no authority cited) have all been used by various workers for what was generally accepted by ichthyologists as the same taxon. This problem is further complicated because we now suspect that two taxa, one occurring in China, the other with a more southerly distribution (including Java, the locality of Lacépède's *Monopterus javanensis*), may be represented among material assigned to *M. alba*.

The confusion over the correct generic name stems partly from a widely held belief (see for example Cantor, 1849; Jordan, 1917) that Lacépède (1800) used only the vernacular name "monoptère javanais" when first describing *Monopterus*, and that Duméril's (1806) latinization of this name (that is, its validation) was predated by Bloch and Schneider's (1801) description of *Fluta javanensis*, a species based on Lacépède's taxon. Further confusion arose from Jordan's (1919) contention that *Monopterus* was a junior homonym of *Monopteros* Volta, 1796 and "is thus preoccupied and must give way to FLUTA Bloch and Schneider (1801)."

Our resolution of this problem is as follows. Although Lacépède (1800) does refer to his fish as "monoptère javanais" he also used the latinized version *Monopterus javanensis* on two occasions in the same work, once on page 138 and again on page 139. Thus, Lacépède (1800) is clearly the author of the name *Monopterus*, and Bloch and Schneider's (1801) name *Fluta* is a junior objective synonym. Jordan's (1919) rejection of *Monopterus* as a junior homonym of Volta's *Monopteros* is not acceptable under Rule 56 (a), (one-letter difference), of the current International Code of Zoological Nomenclature. We therefore accept *Monopterus* Lacépède, 1800 as the valid name for this genus.

The question of what species constitutes the type species of *Monopterus* is also somewhat confused.

It is clear from the literature that both *Monopterus javanensis* Lacépède, and *Muraena alba* Zuiew (1793) are thought to have this status.

However, Jordan (1919) designated Zuiew's *Muraena alba* as the type of *Fluta* Bloch and Schneider (a replacement name for *Monopterus* Lacépède, see above), and we can see no reason for not accepting his decision. Zuiew's figure and description of *Muraena alba* clearly show the fish to be a synbranchid, although it is not possible to tell whether it is a species of *Monopterus* or one of *Ophistemon* (nor, for that matter, can one be certain about the generic identity of Lacépède's *javanensis*). Since the type specimens of neither *alba* nor *javanensis* are still in existence, we consider it in the best interests of nomenclatural stability to accept that Zuiew's *alba* is a member of the genus currently recognized as *Monopterus*. It seems likely that Zuiew's specimen came from Asiatic Russia (Nichols, 1943).

The generic name *Amphipnous* of Müller (1841) is usually associated with the taxon we recognize as *Monopterus cuchia* (type *Unibranchapertura cuchia* Hamilton, 1822). Norman (1966), however, purported to show that the current name should be *Cuchia*, citing for this change Taylor, 1831. We do not agree with Norman because in our opinion Taylor uses the term "Cuchia" as a vernacular name (as indeed does Hamilton, on occasion, in the original description of the taxon). Throughout his account of the species, Taylor always prefixes the word "Cuchia" with the definitive article (and nowhere uses "Cuchia" in binomial combination). Since "Cuchia" is, according to Hamilton, a native name for the fish in question and because Taylor worked in India, this usage would be natural to him.

Müller's (1841) definition of *Amphipnous* for *Unibranchapertura cuchia* is precise and his reasons for separating this species from *Unibranchapertura* are unequivocal.

Unfortunately the matter does not rest here. Swainson (1839) created without explanation the genus *Ophichthys* for Hamilton's *U. cuchia*, at the same time replacing *cuchia* by *punctatus* (presumably because, as Swainson makes clear in the introduction to his book, he found Hamilton's barbaric names offensive). We can find no technical reason why Swainson's name should not have been used, although to do so would have created considerable confusion because the name *Ophichthys* (an emendation of *Ophichtus*

Ahl, 1789; see Jordan, 1923 and Norman, 1966) is widely used for a genus of true eels (*Anguilliformes*).

Thus, pending the outcome of any necessary application to the International Commission for Zoological Nomenclature requesting the suppression of *Ophichthys* Swainson, 1839, on these grounds, the name *Amphipnous* Müller, 1841, should be used for any future subdivision of the group recognized here as *Monopterus*, which includes *cuchia* and its related species.

#### *Monopterus albus* (Zuiew)

*Muraena alba* Zuiew, 1793 (type locality presumed to be Asiatic Russia).

*Monopterus javanensis* Lacépède, 1800 (Islands of Java).

*Monopterus javanicus* Shaw, 1803 (lapsus for *javanensis*).

*Unibranchapertura laevis* Lacépède, 1803 (China).

*Synbranchus grammicus* Cantor, 1842 (Chusan, China).

*Monopterus xanthognathus* Richardson, 1845 (Canton, China).

*Monopterus cinereus* Richardson, 1845 (Woo-sung, China).

*Ophiocardia phyariana* M'Clelland, 1845 (Bengal).

*Monopterus helvolus* Richardson, 1846 (name based on Chinese paintings from Canton).

*Monopterus marmoratus* Richardson, 1846 (Chusan, China).

*Apterigia saccogularis* Basilewski, 1855 (North China).

*Apterigia nigromaculata* Basilewski, 1855 (Peking, China).

*Apterigia immaculata* Basilewski, 1855 (North China).

**Remarks.** See above, nomenclatural notes under the synonymy of *Monopterus*.

Among the abundant samples examined, three from Yunnan, China (AMNH 7039, 7050, 10248), include four specimens (326 mm. and 340 mm. in length) which have a distinctive combination of lower jaw and dorsal gill arch characters: the coronoid process on the articular bone is very low, almost absent, the first epibranchial bone is wider and more robust than in other samples, and the interarcual bone is reduced and of variable shape (cf. figs. 64, 65 and 38, 39).

These four specimens, along with other northern Chinese samples, were assigned by Nichols (1943) to Richardson's *cinereus* (as a subspecies of *albus*), and separated from members of more southerly Chinese populations on the basis of average differences in tail length, eye size, coloration, and head shape. A comparison of AMNH 7039, 7050, and 10248 with other lots assigned by Nichols to *cinereus* failed to uncover the peculiar lower jaw and gill arch features elsewhere. The possibility, therefore, exists that the Yunnan sample represents a distinct form, and that other identifiable populations may exist within the extensive range of this taxon. It is probable, however, that neither of Richardson's names *cinereus* and *xanthognathus*, nor Cantor's *grammicus*, apply to the Yunnan specimens since all of Richardson's and Cantor's material came from more easterly localities, and because all of the specimens examined by us from east of Yunnan have dorsal gill arch and lower jaw structures typical of *albus* from throughout its range.

**Material.** China, Fukien (AMNH 7033, 10246,

10251, 32406, 32407), Anhwei (AMNH 10239), Shansi (AMNH 10245), Hainan (AMNH 10240), Yunnan (AMNH 7039, 7050, 10248); Burma (AMNH 13758); Vietnam (USNM uncatalogued); Java (AMNH 8934, 8935 and several lots of uncatalogued specimens from BMNH); Okinawa (AMNH 17299).

**Range.** East Indies, Indo-Malayan Archipelago, eastern Asia north to Japan. *Monopterus albus* is not reported from the Philippines or New Guinea, but does occur in Sulawesi (Celebes). Its westernmost limits are in northeastern India. Lake (1971) remarked that *M. albus* was probably introduced into Australia where it was taken in Queensland but it may be native there.

*Monopterus "indicus" Eapen*

*Monopterus indicus* Eapen, 1963 (Kottayam, Kerala State, India).

**Remarks.** No material seen.

**Range.** Kerala State, India.

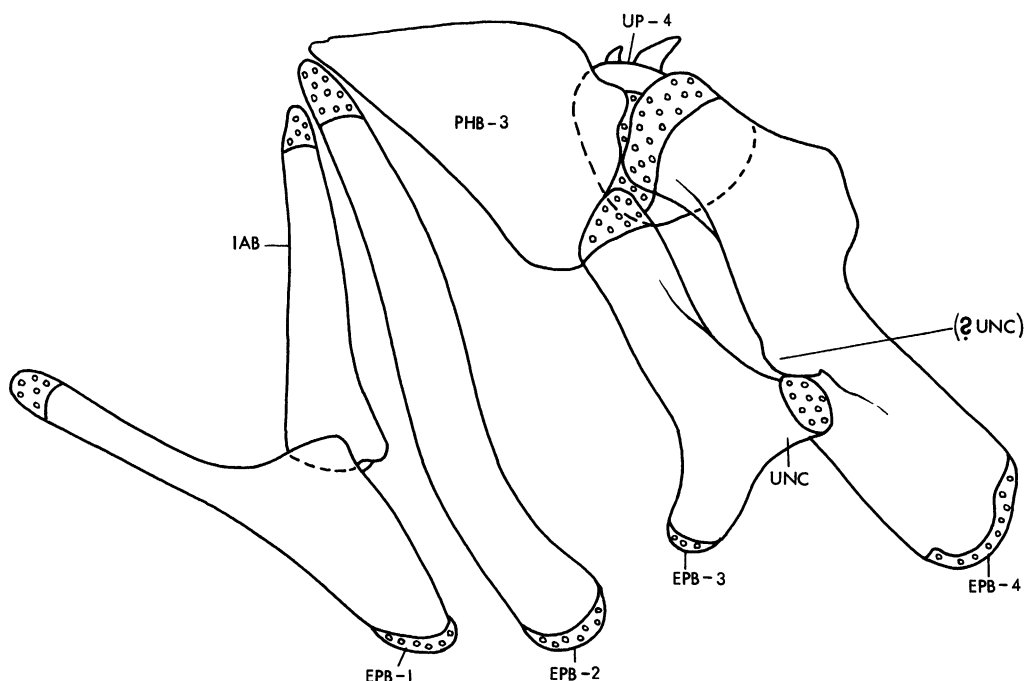


FIG. 64. Dorsal gill arch skeleton of *Monopterus "albus,"* AMNH 7039, from Yunnan Province, China. Dorsal view, left side. Note absence of second pharyngobranchial.

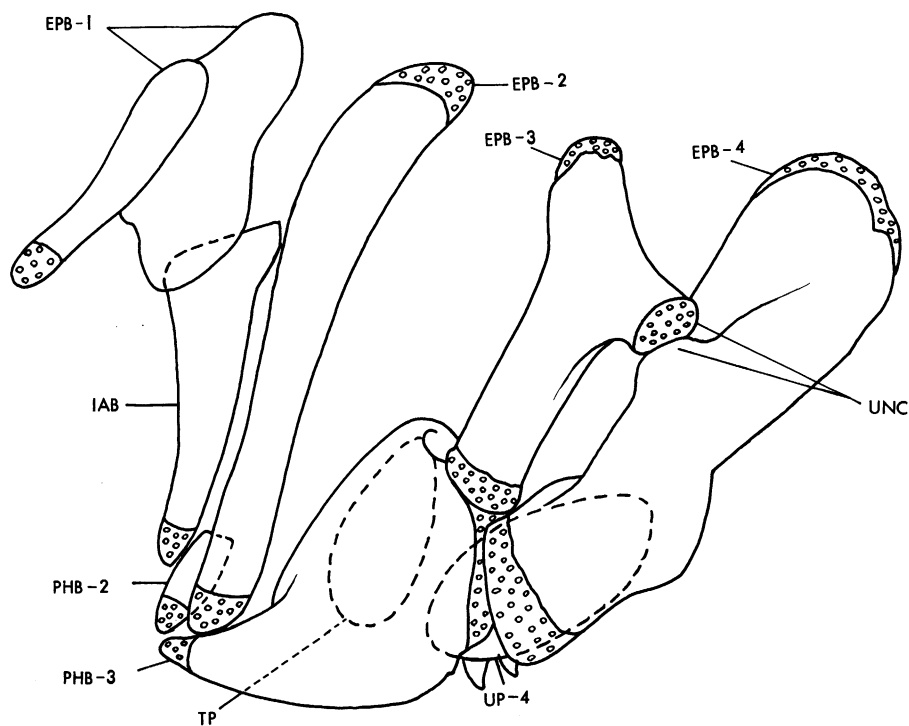


FIG. 65. Dorsal gill arch skeleton of *Monopterus* "albus," specimen as in figure 64. Dorsal view, right side. Note presence of second pharyngobranchial and form of first epibranchial. The first epibranchial in Yunnan specimens tends to be of irregular shape and the second pharyngobranchial is unilaterally or bilaterally absent.

*Monopterus boueti* (Pellegrin)

*Typhlosynbranchus boueti* Pellegrin, 1922 (Monrovia, Liberia).

**Remarks.** Material examined, seven specimens from Sierra Leone, 5 miles east of Bo, USNM 240702-F77 (208875) and AMNH 32411. Although virtually eyeless and pale in color, this species apparently lives in mud holes in swamps, not in caves, according to ecological data accompanying our specimens.

**Range.** Sierra Leone and Monrovia, Liberia (the type locality).

*Monopterus cuchia* (Hamilton)

*Unibranchapertura cuchia* Hamilton, 1822 (southeast parts of Bengal).

**Remarks.** Silas and Dawson (1961) gave a very complete and annotated synonymy of this spe-

cies, to which we have nothing to add, except to note their misspelling of *Pneumabbranchus* (misspelled *Pneumobranchus*). See also comments above under the synonymy of *Monopterus*, and footnote, page 1320, of Cantor (1842).

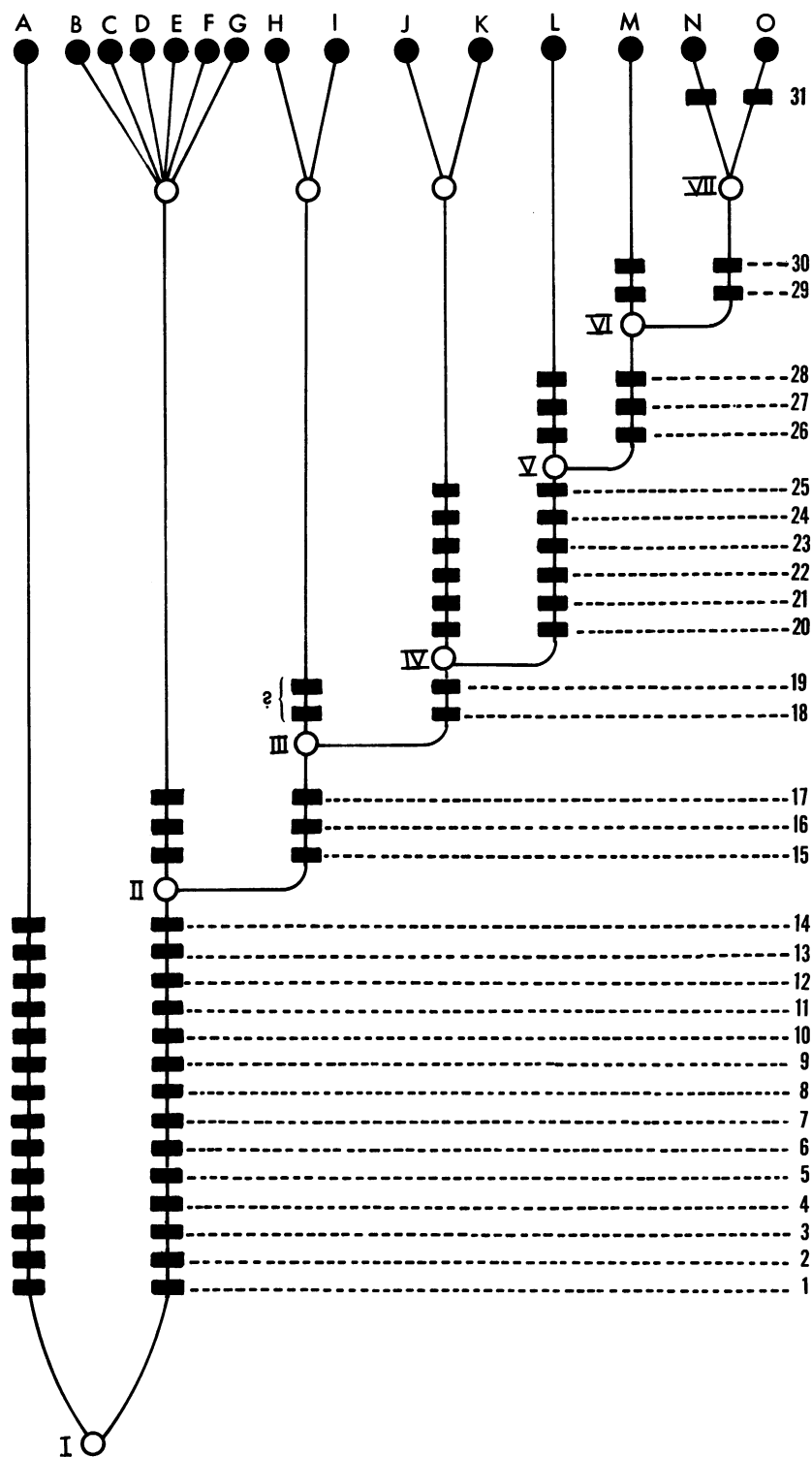
Five specimens were examined, all from India (AMNH 33000; BMNH 1858.8.15:115; BMNH 1859.5.7:50; BMNH 1889.2.1:2723; MCZ 25694), and ranging in size from about 20 cm. to over 50 cm.

**Range.** Northern and northeastern India, Pakistan, Nepal, and Burma.

*Monopterus fossorius* (Nayar)

*Amphipnous fossorius* Nayar, 1952 (near Karamanai River, Trivandrum, Travancore State, India).

**Remarks.** Two small specimens were available, 7 and 13 cm. (BMNH 1962.2.14:6-7).





*Range.* Travancore State, extreme south-western India.

*Monopterus indicus* (Silas and Dawson)

*Amphipnous indicus* Silas and Dawson, 1961 (Robbers Cave, Mahableshwar, Satara District, Maharashtra State, India).

*Remarks.* Material seen: a single specimen from the type series.

*Range.* Maharashtra (Bombay) State, western India.

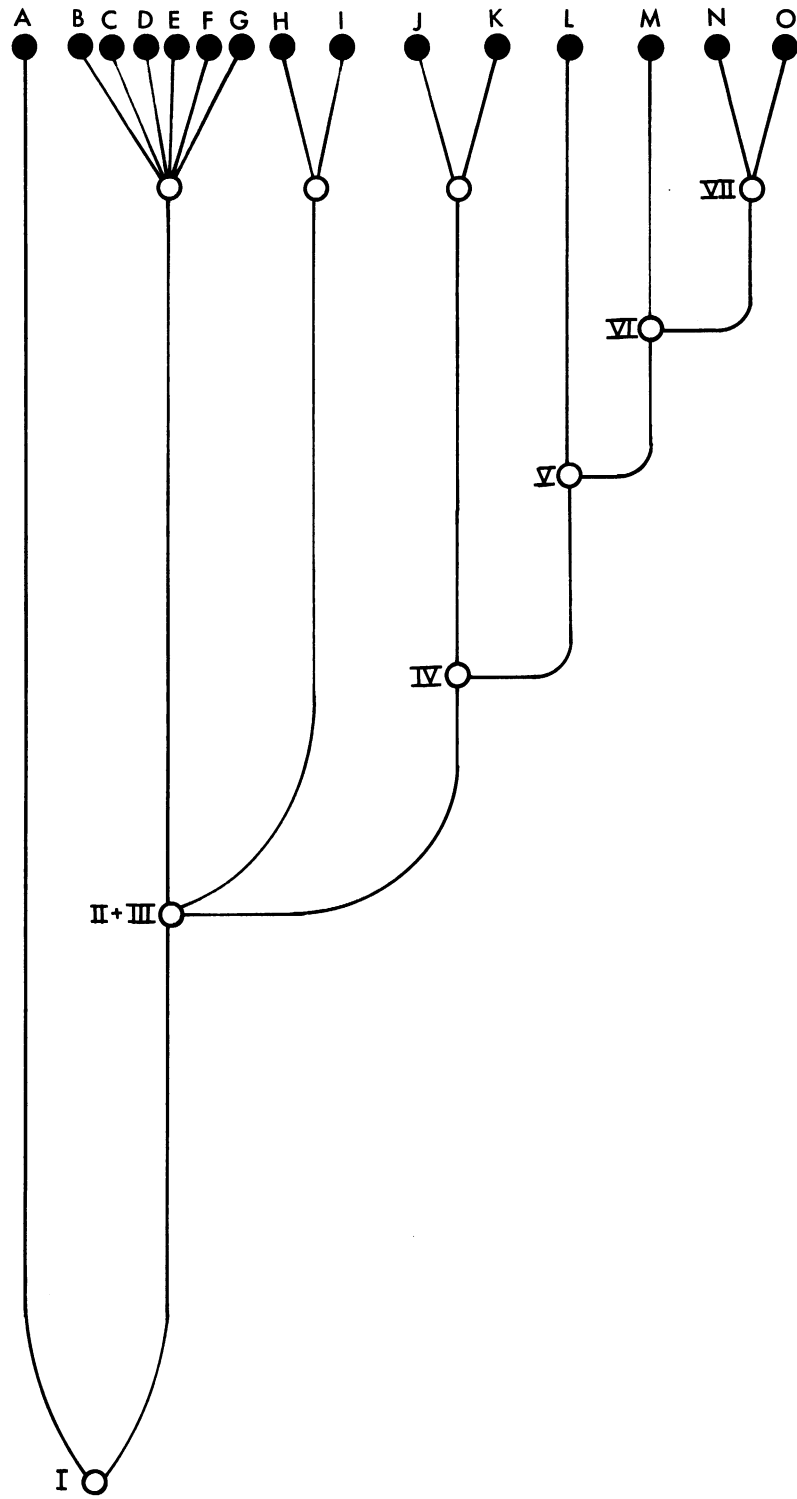
### KEY TO GENERA AND SPECIES

The reader will find many parts of the following key difficult to use because we have included anatomical characters that require elaborate dissections to uncover. We can only assure the reader that the effort needed to find these features is worthwhile in the interests of accu-

rate identification. We, ourselves, continued to experience a measure of uncertainty in identification of species during the work that was only removed completely after detailed anatomical study. Diagnostic external characters, as noted above, are few indeed, and these exhibit a confusing variability between individuals of different, and in some cases, even the same, populations. Small individuals especially are difficult to assign when two or more species are known to be in the same region. Radiographs will frequently serve in place of elaborate dissections for discerning the larger bony features such as the position of the shoulder girdle and its relation to the skull.

The key provides in condensed form what we have learned about the anatomy of synbranchid fishes. The shared derived characters (synapomorphies) that provide the basis of all but the first dichotomy (between the Macrotreminæ and Synbranchinæ) form the basis of the cladogram of relationships shown in figures 66 and 67. The

FIG. 66. Phylogeny of the Synbranchidae based on 31 principal synapomorphies. Main branch points indicated by Roman numerals. Derived characters defining individual taxa (A, L, M) or groups (B-G; H,I; J,K) are given in text and key. The questionable nature of characters 18 and 19 is discussed in text, and see figure 67. Taxa (solid circles): A, *Macrotréma caligans*; B, *Ophisternon afrum*; C, *O. aenigmaticum*; D, *O. bengalense*; E, *O. gutturale*; F, *O. candidum*; G, *O. infernale*; H, *Synbranchus madeirae*; I, *S. marmoratus*; J, *Monopterus albus*; K, *M. "indicus"*; L, *M. boueti*; M, *M. indicus*; N, *M. fossorius*; O, *M. cuchia*. Synapomorphies: 1, body eel-like with numerous vertebrae (never fewer than 98 total and 51 abdominal); 2, no paired fins in adults and no pelvic girdle or scapulocoracoid; 3, dorsal and anal fins represented by rayless folds and caudal fin greatly reduced or absent; 4, gill membranes united and continuous around isthmus; 5, scales absent, or reduced and confined to caudal region; 6, region between prootic and posterior wall of orbit greatly expanded anteroposteriorly; 7, frontal and basisphenoid united and forming posterior articulation for palatoquadrate; 8, first vertebra with articular plug and lateral flanges; 9, basihyal ankylosed with first basibranchial; 10, enlarged and ossified interarcual cartilage between first epibranchial and second pharyngobranchial; 11, first pharyngobranchial absent and second pharyngobranchial reduced to tiny rod or ossicle, or absent; 12, heart posterior, ventral aorta originating from level of ninth to twentieth vertebra; 13, atrium of heart with large auriculæ cordis; 14, right internal jugular vein reduced or absent; 15, gill opening confined to ventral surface of head; 16, caudal fin, when present, with fewer than 7 rays and not separated by a notch from the dorsal and anal fin folds; 17, posterior nares medial to eyes; 18, branchiostegals with distal half poorly ossified or absent; 19, first epibranchial without a deep notch for ossified interarcual cartilage; 20, upper lip jowl-like, not swollen and separated from snout region by a groove; 21, gills, when present, reduced to single row of filaments or to thin ridge of tissue on first to third arches; 22, efferent and afferent arteries of fourth gill arch together forming a single continuous vessel; 23, second and third basibranchials greatly reduced or absent; 24, first ceratobranchial not articulating with first hypobranchial; 25, tissue of gill opening internally attached to isthmus; 26, second basibranchial present but reduced, posteriorly acuminate, and interlocked with first basibranchial+basihyal; 27, first ceratobranchial more closely associated with second than with first arch; 28, efferent and afferent arteries of first three gill arches continuous, not joining radix aortae, third and fourth branchial vessels with common stem from ventral aorta, and internal carotid arising from second rather than first gill arch; 29, first epibranchial, interarcual cartilage, and second pharyngobranchial absent; 30, paired suprabranchial pouches (respiratory organs) present; 31, skin of branchial region on ventral side of head drawn into longitudinal folds.



derived characters uniting the two subfamilies are given in the family diagnosis, above, and are noted in the figure caption. All other groups of synapomorphous features are identified by the appropriate code letters, or combination of code letters, that make up the hierarchical structure of the key.

The key is dichotomized along phylogenetic lines, except within the genus *Ophisternon* where the interrelationships of most of the species are unknown. Characters primitive for the family are italicized.

- A. Gill membrane extending up along side of head to above horizontal septum; small caudal fin with nine to 14 rays present and separated by notch from dorsal and anal fin folds; posterior nares anterior to eye; hypertrophied left internal jugular vein closely applied to anterior cardinal vein . . . . . Macrotreminae, with a single species, *Macrotrema caligans* from Malaysia . . . . .
- AA. Gill opening confined to the ventral surface of the head as a slit or pore; caudal fin greatly reduced or absent, when present with seven or fewer rays and not separated from dorsal and anal fin folds by a notch; posterior nares medial to eye; left internal jugular vein not hypertrophied or applied to anterior cardinal. . . . . Synbranchinae
- B. Gill opening a simple crescentic transverse fold free from the isthmus and occupying one-half to one-third of ventral surface of head; eye on or anterior to a vertical through upper lip; six or seven branchiostegals, well ossified to their tips at all sizes, and extending backward beyond ventral tip of cleithrum; first epibranchial wide-based and with a deep notch posteriorly for an interarcual bone connecting the first and second dorsal gill arch elements; shoulder girdle connected to skull by forked posttemporal bone; articular bone of lower jaw with a dorsal coronoid prominence in the form of an equilateral triangle. . . *Ophisternon*
  - a. Body well pigmented; eyes visible through skin; vent in posterior part of body; abdominal vertebrae more numerous than caudal vertebrae; body robust, not whiplike; epigeal . . . . . b.
  - b. Efferent (dorsal) branchial arteries of the first and third gill arches not joining paired lateral aortae, but emptying into median sinus in buccopharyngeal epithelium; west Africa . . . . . *Ophisternon afrum*
  - bb. Efferent (dorsal) branchial arteries of gill arches one to four joining paired lateral aortae (as in basic teleost condition) . . . . . c.
  - c. Neurocranium relatively broad, its greatest width across the otic region 40 percent of its length from supraoccipital to dermal ethmoid; posterodorsal aspect of maxilla without an angulate prominence; northeastern South America, Atlantic slope of Guatemala and Mexico, and Cuba . . . . . *Ophisternon aenigmaticum*
  - cc. Neurocranium relatively narrow, its greatest width across the otic region about 30 percent of its length from supraoccipital to dermal ethmoid; posterodorsal aspect of maxilla with a distinctly angulate prominence. . . . . d.
  - d. Distance from center of eye to bony snout 37 to 50 percent of distance from bony snout to corner of gape of mouth; caudal vertebrae 49 to 61; Indo-Malayan. . . . . *Ophisternon bengalense*
  - dd. Distance from center of eye to bony snout 59 to 67 percent of distance from bony snout to corner of gape of mouth; caudal vertebrae 30 to 40; northern Australia . . . . . *Ophisternon gutturale*
  - aa. Body with little or no visible surface pigment, white or amber in color; eyes reduced, barely visible through skin; vent near center, or in anterior half of body; abdominal vertebrae equal in number to, or less numerous than, caudal vertebrae; body whiplike; cavernicolous . . . . . e.
  - e. Abdominal vertebrae 51 to 54, caudal vertebrae 109 to

FIG. 67. Alternative phylogeny of the Synbranchidae in which branch points II and III are joined and considered to form parts of an unresolved trichotomy. This construction considers characters 18 and 19 in figure 66 to be unacceptable. Both constructions show taxa B-G (*Ophisternon*) forming an unresolved polychotomy.

- 111; *basihyal fused with first basibranchial*; North West Cape, Western Australia . . . . .  
 . . . *Ophisternon candidum*  
 ee. Abdominal vertebrae about 67, caudal vertebrae about 72; *basihyal not fused with first basibranchial*; Yucatan Peninsula, Mexico . . . . .  
 . . . *Ophisternon infernale*
- BB. Gill opening porelike and flanked by deep folds, or of variable size, obtusely triangular or crescentic and internally attached to isthmus; eye on or posterior to a vertical through upper lip; branchiostegals four to six, not extending back to cleithral symphysis or, when extending back to cleithra, with the distal half of each ray much less well ossified than proximal part in specimens over 150 mm. and little if at all ossified in specimens under 150 mm. in total length; first epibranchial without a deep notch for interarcual bone; *shoulder girdle connected to skull or not; articular bone of lower jaw without a distinct coronoid prominence* or with a specialized coronoid process that is wider at the tip than at the base, set off sharply from the dorsal edge of the articular, and sloped forward. . . . . C
- C. Gill opening porelike and flanked by deep folds and *free from isthmus; a distinct, somewhat swollen upper lip fold present; holobranchs well developed on four arches; branchial vascular system normal, with the efferent arteries joining paired lateral aortae*; in the ventral gill arch skeleton, *basibranchials two and three present and well developed, and first ceratobranchials in the same plane as and articulating with the first hypobranchials*; in the dorsal gill arch skeleton, second pharyngobranchials, when present (in most cases), directed anteromedially and not parallel with the long axis of the second epibranchial; neotropical . . . . . *Synbranchus*
- a. Body coloration gray or clouded, with a broad, pale band middorsally bordered by slender dark lines and a series of whitish spots; caudal peduncle 35 to 37 percent of total length; neural spines of abdominal region long and slender, longer than the distance between any two succeeding spines; parietal bones rounded anteriorly; supernumerary efferent (dorsal) branchial arteries on first two gill arches emptying into a median sinus within the buccopharyngeal epithelium; Río Madeira, Bolivia. . . . .  
 . . . . . *Synbranchus madeirae*
- aa. Body coloration speckled or blotched; caudal peduncle 23 to 34 percent of total length; neural spines of abdominal region short and stout, not longer than the distance between any two succeeding spines; parietal bones rectangular anteriorly or distinctly squared off in examples more than 200 mm.; *branchial arteries normal, without supernumerary elements, the efferent vessels emptying into paired lateral aortae*; Argentina north to Pacific slope of Guatemala. . . . .  
 . . . . . *Synbranchus marmoratus*
- CC. Gill opening triangular or crescentic, without lateral folds, and internally attached to isthmus; upper lip jowl-like, without a separate or swollen fold; gills, when present, reduced to single row of filaments on arches one to three, or represented by a thin ridge of tissue; branchial vascular system with efferent and afferent arteries of the fourth gill arch joined to form single continuous vessel that merges dorsomedially with its counterpart to form an unpaired dorsal aorta; in ventral gill arch skeleton basibranchials greatly reduced or absent in most cases, and first ceratobranchials displaced medially and not articulating with the first hypobranchials; in dorsal gill arch skeleton, *second pharyngobranchial, when present, not directed anteromedially*; Old World . . . . . *Monopterus*
- a. In ventral gill arch skeleton, basibranchials two and three reduced to tiny nodules or absent (in most cases), the medially displaced first ceratobranchial more closely associated with first than with second branchial arch; in

- dorsal gill arch skeleton, interarcual bone between first and second arches articulating anterolaterally with a raised process at midpoint on first epibranchial, *and uncinat processes present and well developed on epibranchials three and four*; in branchial vascular system, efferent and afferent vessels of first three gill arches separate and with efferent vessels joining radix aortae, third and fourth branchial vessels arising separately from ventral aorta, and internal carotid artery arising from first arch; coronoid process of articular bone slender, narrow-based, of angular form in most cases (squared off dorsally), and of variable height. . . . . b.
- b. *Body robust, not whiplike*; ventral gill opening triangular; 88 to 102 abdominal and 45 to 74 caudal vertebrae; *epigean*; Indo-Australian archipelago, China and Japan . . . . . *Monopterus albus*
- bb.<sup>1</sup> *Body slender and whiplike*; gill opening crescentic; about 135 abdominal and 24 caudal vertebrae; *cavernicolous*; extreme southwestern India *Monopterus "indicus"* Eapen
- aa. In ventral gill arch skeleton, basibranchial two reduced and acuminate posteriorly, basibranchial three reduced to a tiny nodule or absent (in most cases), and medially displaced first ceratobranchial more closely associated with second than with first branchial arch; in dorsal gill arch skeleton, first epibranchial, when present, with only a vestige of a notch for articulation with the interarcual bone, and without a bony process or prominence, and uncinat processes absent on epibranchials three and four; in branchial vascular system, efferent and afferent vessels of first three gill arches continuous and not joining radix aortae, third and fourth branchial vessels with common stem from ventral aorta, and internal carotid artery arising from second arch; *without a coronoid prominence on articular bone*. . . . . c.
- c. Gill opening minute and triangular, occupying only a fourth to a third of the ventral surface behind the head; eyes greatly reduced and sunken below surface skin; head gibbous; in dorsal gill arch skeleton, *first epibranchial, interarcual bone, and second pharyngobranchial present*, the latter element long and tubular and directed posteromedially; *no supra-branchial pouches*; branchiostegals four; body slender and whiplike, without scales; with 140 to 144 abdominal and 39 to 45 caudal vertebrae; swamp dwelling; west African . . . . . *Monopterus boueti*
- cc. Gill opening crescentic, occupying most of ventral region behind head, and divided into a pair of porelike lateral apertures by a broad, midventral fusion between the branchiostegal membrane and the isthmus; head not gibbous; in dorsal gill arch skeleton, first epibranchial, the interarcual bone, and second pharyngobranchial absent; large and paired supra-branchial pouches (respiratory organs) present; branchiostegals five or six; body robust, not whiplike, *with scales present posteriorly*; with 73 to 112 abdominal and 42 to 70 caudal vertebrae; swamp and stream fishes. . . . . d.
- d. Skin of branchial region of ventral side of head

<sup>1</sup>We have not seen specimens of "*indicus*" Eapen for comparison with other forms of *Monopterus*, but we are predicting that, if valid, it will be most closely related to *albus* and will, of course, require a replacement name as a junior homonym of *indicus* (Silas and Dawson).

- drawn into shallow longitudinal folds; in gill arch skeleton, epibranchials two and three delicate, rod-like; near Bombay, India. *Monopterus indicus* (Silas and Dawson)
- dd. Skin of branchial region of ventral side of head drawn into deep longitudinal folds; in gill arch skeleton, epibranchial two short and wide-based, broadly triangular, epibranchial three a stout rod as robust as that of fourth arch. . . . e. Teeth on palate and laterally on jaws uniserial; with 99 to 112 abdominal and 55 to 70 caudal vertebrae; northern and northeastern India, Pakistan, Nepal, Burma . . . . .  
 . . . *Monopterus cuchia*
- ee. Teeth on palate and laterally on jaws biserial; with 73 to 76 abdominal and 45 to 56 caudal vertebrae; extreme southwestern India . . . . .  
 . *Monopterus fossorius*

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