Infraorbital Bones and Their Bearing on the Phylogeny and Geography of Osteoglossomorph Fishes

BY GARETH J. NELSON[1]

INTRODUCTION

Infraorbital bones of teleosts and their relevance to systematics have been considered by Smith and Bailey (1962) and Gosline (1965). Smith and Bailey dealt with the occurrence in Recent teleosts of the subocular shelf, a modification of one or a few of the infraorbitals, known so far only in notopterids, myctophids, and acanthopterygians (Greenwood, Rosen, Weitzman, and Myers, 1966; Rosen and Patterson, 1969). Gosline briefly summarized the comparative structure of the circumorbital bones in actinopterygians. In some teleosts one of the anterior infraorbital bones (the antorbital) forms part of a "pumping system which causes an incurrent flow of water over the nasal epithelia when the mouth is opened" (Gosline, 1965, p. 189). Gosline considered this pumping system a specialization unique to teleosts, one indicating a monophyletic origin for the Teleostei.

For systematic studies, the infraorbital series as a whole has been of little interest, apparently because of a prevailing belief that the infraorbital bones vary randomly in structure and number. The infraorbital bones are normally associated with the infraorbital sensory canal and

[1] Assistant Curator, Department of Ichthyology, the American Museum of Natural History.

indeed display some of the variation of dermal bones in general (see e.g., Devillers and Corsin, 1968). To be sure, the variability of dermal bones in vertebrates remains the source of considerable controversy, especially among paleontologists (see e.g., Jarvik, 1967; Parrington, 1967). But whereas the canal bones in some cases are relatively variable, in others they are relatively constant. The relative constancy in number and position of teleostean infraorbital bones has been noted on occasion (e.g., by Gregory, 1935, p. 134; Patterson, 1967, p. 221), but has never been investigated in any detail. The present paper is an attempt to deal with some aspects of the general structure of the infraorbitals of teleosts, and from this general standpoint to assess the systematic significance of the infraorbitals of a particular teleostean group, the Osteoglossomorpha.

MATERIAL AND METHODS

Most of the material is from the collection of the Department of Ichthyology, the American Museum of Natural History. In general, adult fishes were studied. The infraorbital bones were removed as a unit, usually from the right side, cleaned, usually stained in alizarin (in aqueous 2% potassium hydroxide), and photographed. Drawings were traced from the photographs. In many cases neuromasts could be demonstrated simply with the use of transmitted light. In others, they could be demonstrated after light staining with methylene blue. In still others, neuromasts could not be demonstrated at all, and neuromast number and position were inferred from the location of afferent nerve foramina.

The abbreviation A.M.N.H. refers to catalogued specimens of the American Museum of Natural History.

For the loan of specimens, the writer is indebted to Dr. P. H. Greenwood, British Museum (Natural History), Mr. R. H. Kanazawa, U. S. National Museum, Smithsonian Institution, Dr. J. C. Tyler, the Academy of Natural Sciences of Philadelphia, Mr. L. P. Woods, Field Museum of Natural History. Dr. H. Roellig allowed the writer to read his dissertation on *Phareodus*. Mrs. Norma Rothman made roentgenographs of preserved specimens and prepared the drawings for publication.

RESULTS

Aside from the reduction of the antorbital and loss of its associated canal, the infraorbital bones occur in very nearly the same pattern in generalized members of many teleostean groups: Elopomorpha (fig. 1),
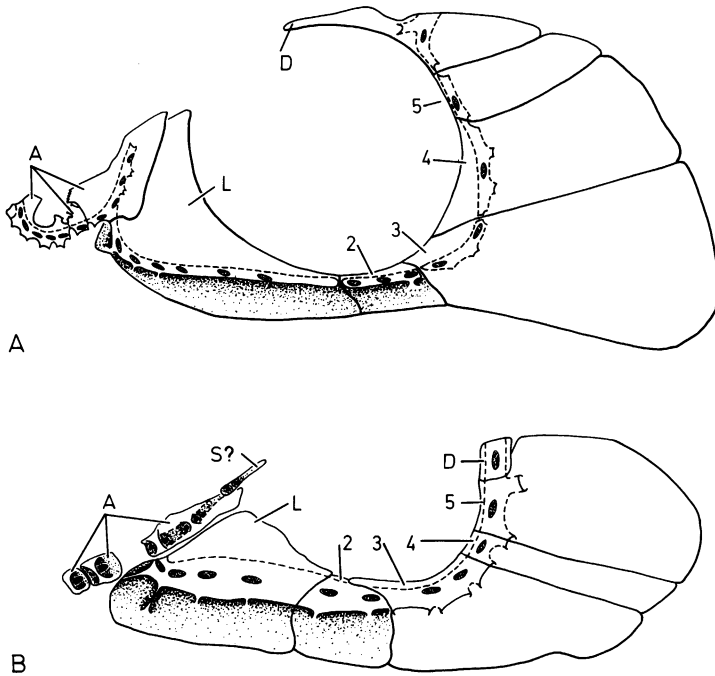
FIG. 1. A. *Elops saurus* (A.M.N.H. uncatalogued ×1½). B. *Albula vulpes* A.M.-N.H. uncatalogued ×2). Infraorbital bones, lateral view of left side.

Abbreviations: A, antorbital; D, dermosphenotic; L, lacrimal; S, supraorbital; 2–5, infraorbitals.

Clupeomorpha (figs. 2, 3), Ostariophysi (figs. 4, 5), Salmoniformes (figs. 6, 7), Myctophiformes (fig. 8B), Acanthopterygii (fig. 8A), and others. In Recent teleostean fishes, the widespread occurrence of an antorbital and lacrimal, followed by five infraorbitals, suggests that this pattern is a primitive feature of most or all of the major teleostean groups.

Not only is the bone pattern itself relatively constant, but so also is the pattern of neuromasts enclosed within the infraorbital sensory canal. Thus, at the posterior end of the series, the dermosphenotic and the two bones below it, almost invariably have but a single neuromast each. In contrast, at the anterior end of the series, the antorbital, lacrimal, and the two bones following, often have several neuromasts each, the number varying among related species.

The bones bordering the rear of the orbit are of particular interest. In their primitive condition, these bones seemingly include the dermosphenotic (D), usually recognizable by the characteristic fork of the

infraorbital canal, and three other bones (3–5). Of these four bones, the most ventral (3) generally has two (figs. 1, 2, 3, 4A, 7A, 7D, 7F) but in some cases only one (figs. 4B, 7E, 8B), and in some cases three neuromasts (figs. 7B, C).

It is therefore possible to suggest that the primitive condition for teleosts included seven canal bones from the antorbital to the dermosphenotic, with the anterior four bones having more than one neuromast each, and the posterior three bones having only one neuromast each. If such was the primitive condition, reduction both of bone and neuro-
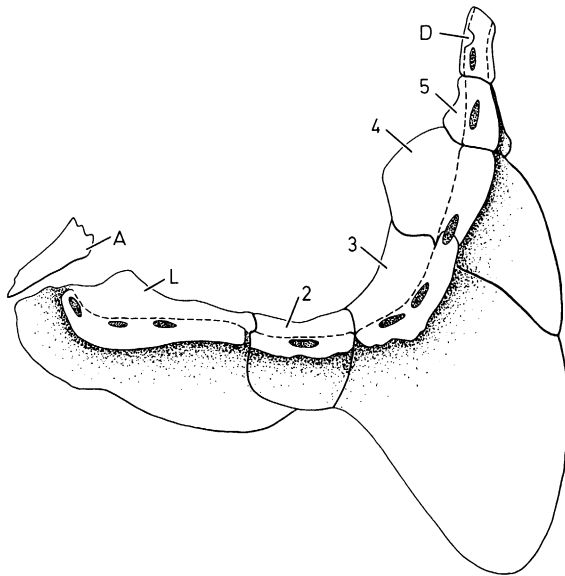

FIG. 2. *Alosa sapidissima* (A.M.N.H. uncatalogued, ×1½).
Abbreviations: A, antorbital; D, dermosphenotic; L, lacrimal; 2–5, infraorbitals.

mast numbers seems to have occurred during the evolution of most teleostean groups. Reduction of the antorbital and loss of its sensory canal seem to have been common. Among salmonids, reduction seems also to have involved loss of the dermosphenotic from the genus *Salvelinus* (figs. 7E, F). In *Chanos* and cypriniforms, reduction in bone number seems to have involved fusion between two middle members of the bone series (fig. 5). Finally, among species of the genus *Esox,* reduction seems to have involved both loss of some bones and fusion of others (fig. 9A, B).
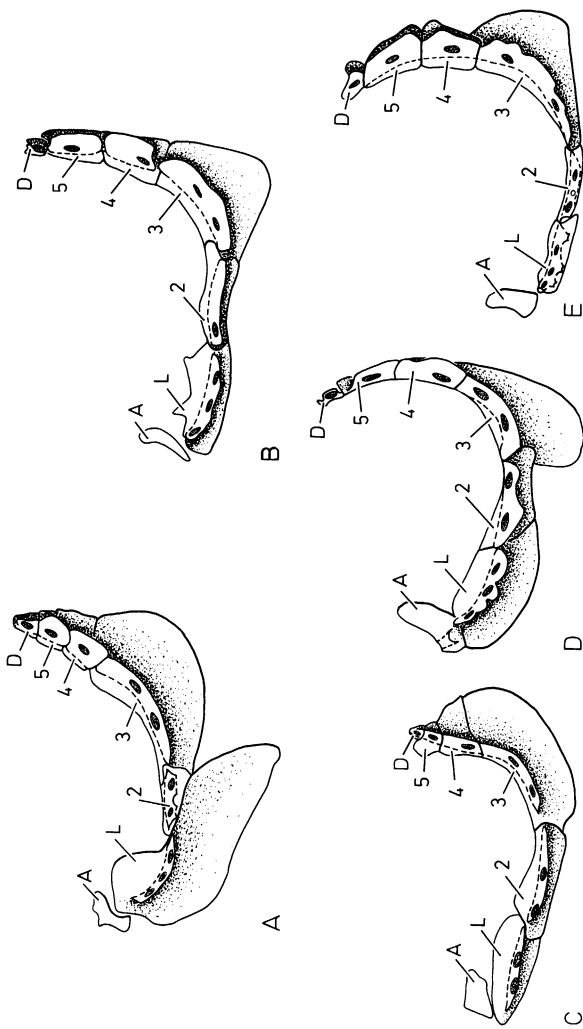
FIG. 3. A. *Chirocentrus dorab* (A.M.N.H., uncatalogued ×3). B. *Opisthonema oglinum* (A.M.N.H., uncatalogued ×2½). C. *Etrumeus teres* (A.M.N.H. 2321, ×1½). D. *Ilisha* sp. (A.M.N.H. 20759, ×3). E. *Dorosoma cepedianum* (A.M.N.H. 25843, ×2½).

Abbreviations: A, antorbital; D, dermosphenotic; L, lacrimal; 2–5, infraorbitals.

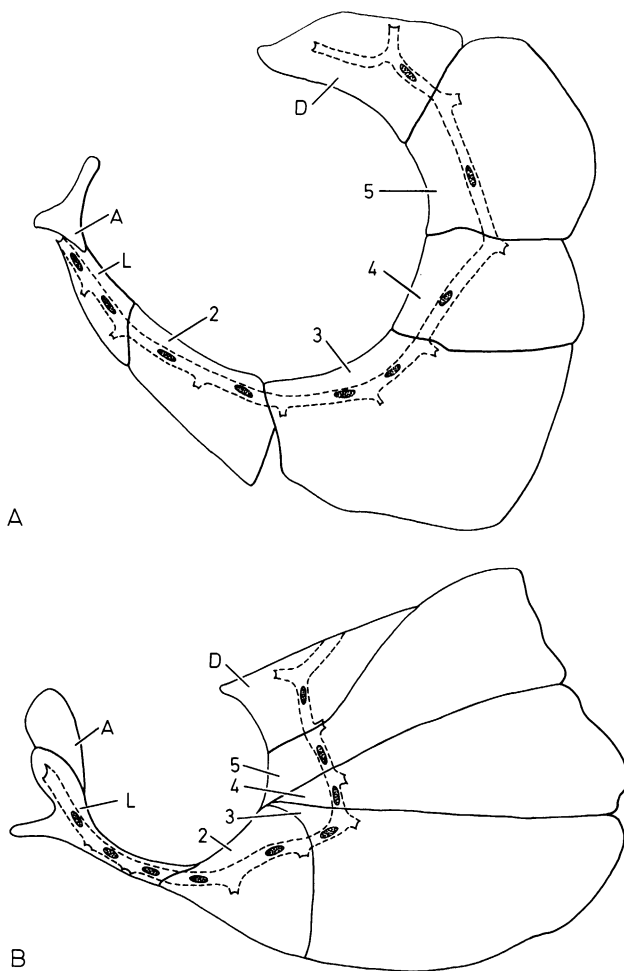FIG. 4. A. *Brycon guatemalensis* (A.M.N.H. 25395, ×3). B. *Hoplias malabaricus* (A.M.N.H. 3777, ×3½).
Abbreviations: A, antorbital; D, dermosphenotic; L, lacrimal; 2–5, infraorbitals.

With the exceptions of *Gymnarchus* (Allis, 1904, pl. 16, fig. 29; Pehrson, 1945, fig. 2; pers. obs.) and *Pantodon* (fig. 10), no osteoglosso-morph is known to have more than six separate ossifications in the infra-orbital series. *Pantodon* apparently has the lacrimal fragmented into two parts. *Hiodon* (fig. 11) is without an independent antorbital (fused with the lateral ethmoid according to Greenwood and Patterson [1967] and
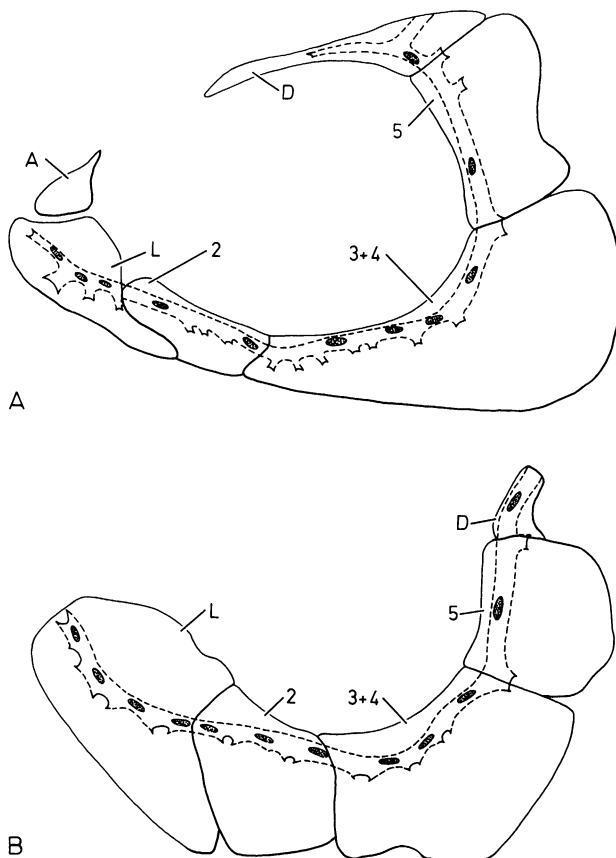
Fig. 5. A. *Chanos chanos* (A.M.N.H. 27390, ×3). B. *Opsariichthys hainanensis* (A.M.N.H. 11053, ×5).

Abbreviations: A, antorbital; D, dermosphenotic; L, lacrimal; 2–5, infraorbitals.

personal observations). *Arapaima* and *Heterotis* (fig. 12) have the ant-orbital apparently fused with the lacrimal. With the exception of a few mormyrids with four or five (fig. 13), all other examined osteoglosso-morphs have six infraorbitals (figs. 14–16). Most of the bones have a single neuromast, but the lacrimal has two in nearly all osteo-glossomorphs examined (the fused antorbital-lacrimal of *Arapaima* and *Heterotis* has three neuromasts), and the antorbital has two in most or all species of notopterids (the small, upper neuromast could not always be demonstrated in the available material (see e.g., fig. 16D; Omarkhan, 1949, fig. 1; Kapoor, 1964, fig. 2; cf. Sharma, 1964, fig. 1).

DISCUSSION

Osteoglossomorph Infraorbital Bones

Between the lacrimal and dermosphenotic of osteoglossomorphs, there generally are only three bones, whereas four occur in most other generalized teleosts. It is possible to imagine the number of bones in osteoglossomorphs to have become secondarily reduced through fusion between two middle members of the infraorbital series. In *Hiodon*, the occurrence of three neuromasts in a bone with a postorbital position supports this interpretation (however, the intraspecific variation of this
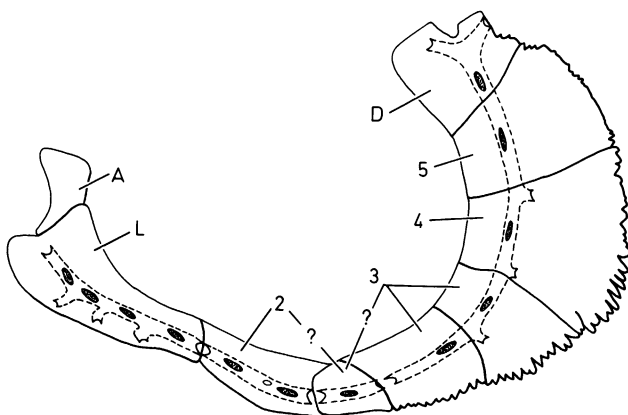

Fig. 6. *Thymallus arcticus* (A.M.N.H. 10320, ×3).
Abbreviations: A, antorbital; D, dermosphenotic; L, lacrimal; 2–5, infraorbitals.

character was not investigated). Thus, the three neuromasts primitively might have been enclosed within two bones, and through fusion, have become enclosed in only one. Indeed, the reduced number of infraorbitals in osteoglossomorphs, *Chanos*, and cypriniforms might have arisen by fusion of the same two bones (3 + 4). That fusion of primitively separate infraorbitals (the antorbital and lacrimal of *Arapaima* and *Heterotis*), each adding their own neuromast complement to the compound bone, has occurred among osteoglossomorphs further increases the probability of this interpretation.

The writer is aware of the continuing controversy regarding the possibilities of fusion between canal bones (see e.g., Devillers and Corsin, 1968). If it can be agreed, however, that where two bones occurred in an ancestor, there is only one in a descendant, then it matters little, as
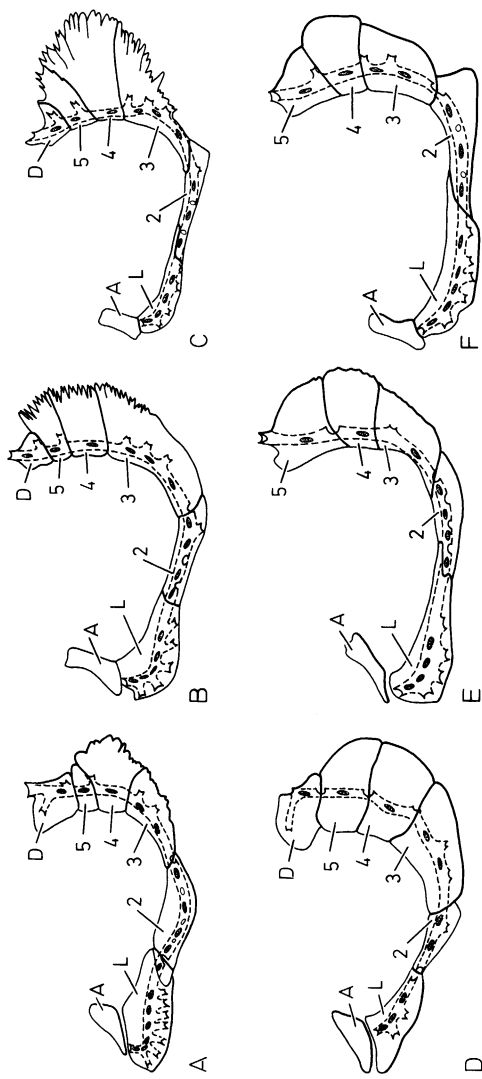
FIG. 7. A. *Brachymystax lenok* (A.M.N.H. 10431, ×1½). B. *Salmo trutta* (A.M.N.H. 26348, ×2). C. *Oncorhynchus nerka* (A.M.N.H. 3292, ×1½). D. *Coregonus artedi* (A.M.N.H. 232, ×1). E. *Salvelinus namaycush* (A.M.N.H. 27276, ×2). F. *Salvelinus fontinalis* (A.M.N.H. 12093, ×2½). *Abbreviations*: A, antorbital; D, dermosphenotic; L, lacrimal; 2–5, infraorbitals.
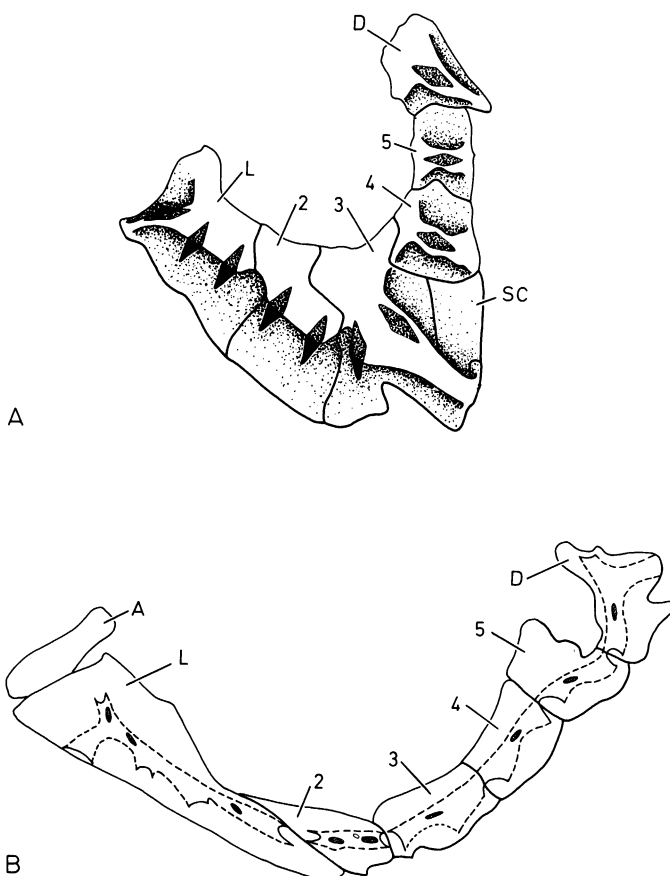
FIG. 8. A. *Monocentris japonicus* (A.M.N.H. 26765, ×2). B. *Synodus intermedius* (A.M.N.H. 18913, ×4).

Abbreviations: A, antorbital; D, dermosphenotic; L, lacrimal; SC, scale bone; 2–5, infraorbitals.

Ørvig (1962, p. 59) has pointed out, whether the two bones fused into one, or one bone "invaded" the territory of the other, "conquered" it completely, and "captured" all of its neuromasts and nerves. Whatever the details of the phylogenetic process, which are not demonstrable, the over-all result is called fusion here, for want of a better word.

It can be suggested here, but not argued very convincingly, that osteoglossomorphs really have reduced the infraorbital number from seven to six. Thus, the possibility remains that the osteoglossomorph condition of six bones is primitive relative to that of other teleosts.
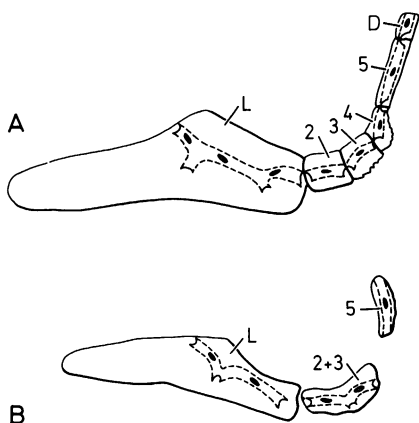
FIG. 9. A. *Esox lucius* (A.M.N.H. 27280, ×1). B. *Esox americanus* (A.M.N.H. 13278, ×2½).
    Abbreviations: D, dermosphenotic; L, lacrimal; 2-5, infraorbitals.

Indeed, infraorbital structure might be interpretable as evidence that the nearest relatives of the Osteoglossomorpha are all other teleosts combined. But the closest Recent relatives of the Osteoglossomorpha are unknown, and there is some belief that the group as here conceived is not monophyletic. The relationships of *Hiodon,* because of its many primitive characters, are the most difficult to assess. The infraorbitals of *Hiodon,* despite their reduced number, are highly peculiar and do not closely resemble those of any other Recent osteoglossomorph, or apparently of any other Recent teleost.

FIG. 10. *Pantodon buchholtzi* (A.M.N.H., uncatalogued ×8).
Abbreviations: A, antorbital; D, dermosphenotic; L, lacrimal; 2-5, infraorbitals.

Advanced characters indicating a monophyletic origin for the Osteo-glossomorpha as here conceived are few. The most striking peculiarities found among osteo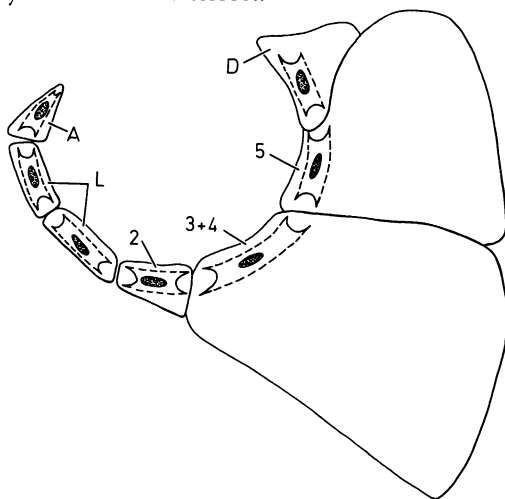glossomorphs generally do not occur in *Hiodon:* fusion between the upper hypurals and second ural centrum, development of full spines on the ural centra, reduction of "hypohyals," epurals, and uroneurals, development of tendon bones or hypobranchial processes
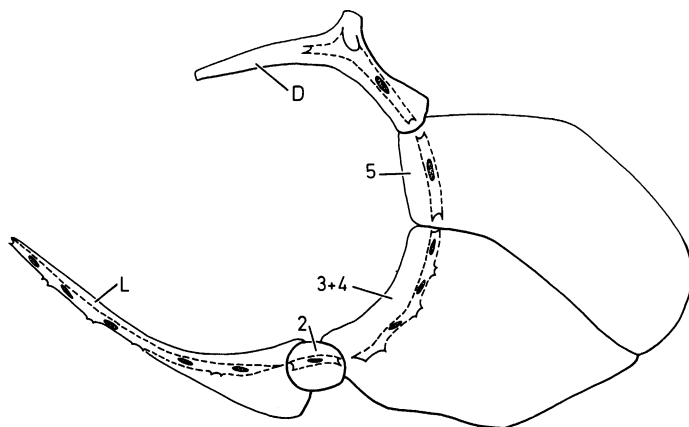
FIG. 11. *Hiodon alosoides* (A.M.N.H. 23755, ×2).
Abbreviations: D, dermosphenotic; L, lacrimal; 2–5, infraorbitals.

(Gosline, 1960; Greenwood and others, 1966; Greenwood, 1967; Patterson, 1967; McAllister, 1968; Nelson, 1968). It is possible that most osteoglossomorphs have secondarily acquired a full spine on the first preural and first ural centra (Patterson, 1968b, pp. 84, 85), but these spines are not constant features of *Hiodon,* which in some cases has a full spine on preural centrum 1, but apparently rarely, if ever, on ural centrum 1 (Cavender, 1966, p. 316; pers. obs.). Gosline (1960), Green-wood (1967), and Patterson (1967) are of the opinion that most osteo-glossomorphs are without independent uroneurals, but it is difficult to see how the paired bones present apparently in all osteoglossids (fig. 17A; the "epural" of Gosline, 1960, figs. 13, 14; Greenwood, 1967, figs. 1–6, 9–12), *Pantodon* (the "epural" of Greenwood, 1967, figs. 7, 8; Taverne, 1967, fig. 9), and mormyrids (figs. 17B, C; the "epural" of Gosline, 1960, fig. 15) can be called anything but uroneurals (Taverne, 1967, figs. 2, 3; 1968, fig. 16; Monod, 1968, pp. 325–350, figs. 397–400, 430–438). Gosline (1965) has noted the absence of a supraorbital-antorbital pumping sys-
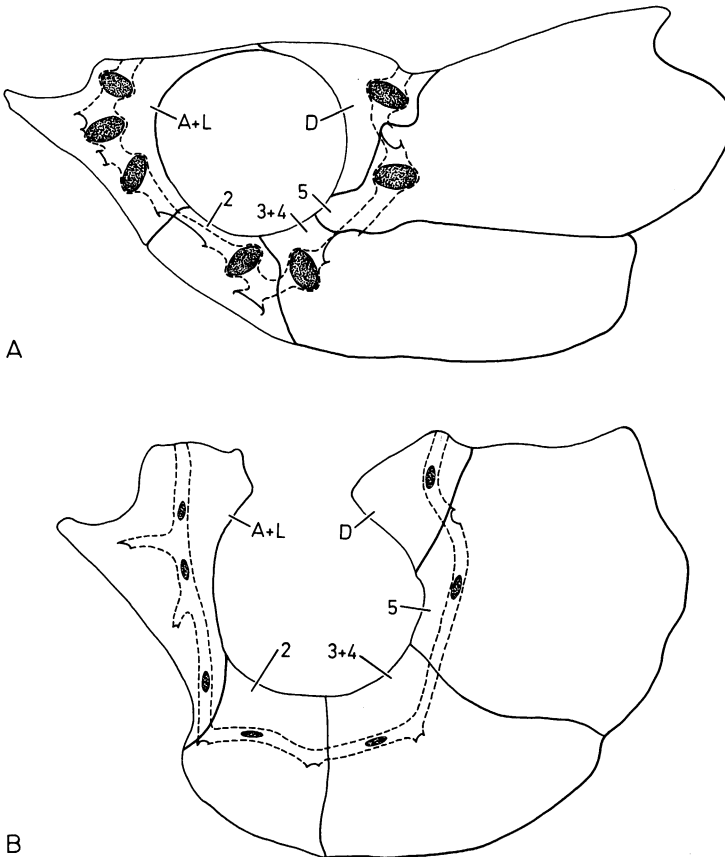
FIG. 12. A. *Arapaima gigas* (A.M.N.H. 26089, ×1½). B. *Heterotis niloticus* (A.M.-N.H. 9808, ×1½).

Abbreviations: A, antorbital; D, dermosphenotic; L, lacrimal; 2–5, infraorbitals.

tem in all osteoglossomorphs, but there is no direct evidence suggesting that this absence is anything but a primitive condition. Some characters, probably advanced, are shared by *Hiodon* and most or all osteoglosso-morphs: a reduced number (16 or fewer) of branched caudal rays, para-pophyses fused with the centra, and no supramaxillaries nor lower intermuscular bones. To these might be added the reduced number of infraorbitals. Those advanced characters occurring only in *Hiodon* and the Notopteridae (a similar type of swimbladder-ear connection, a spe-cialized basihyal tooth plate, and the absence of oviducts [Berg, 1947; Greenwood, 1963; Nelson, 1968]) increase the probability that *Hiodon* is
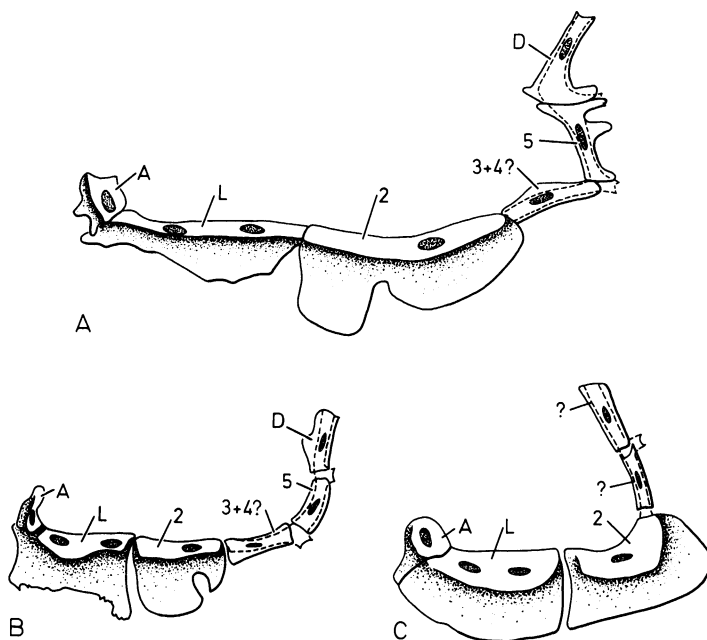
FIG. 13. A. *Mormyrops anguilloides* (A.M.N.H. 18629, ×2). B. *Mormyrus macrops* (A.M.N.H. 12393, ×4). C. *Stomatorhinus humilior* (A.M.N.H. 6716, ×4).

Abbreviations: A, antorbital; D, dermosphenotic; L, lacrimal; 2–5, infraorbitals.

an osteoglossomorph and that the Osteoglossomorpha are a monophyletic group. Finally, the similar and highly distinctive brain structure of the notopterids, osteoglossids, and mormyrids (Nieuwenhuys, 1962a, 1962b, 1963) should be mentioned; if this condition were found also in *Hiodon*, the position of *Hiodon* within the Osteoglossomorpha would be better substantiated.

INTERRELATIONSHIPS AMONG OSTEOGLOSSOMORPHS

NOTOPTEROIDEI-MORMYROIDEI: Mormyrids traditionally have been regarded as close relatives of notopterids and hiodontids (see e.g., Ridewood, 1904, p. 212; Omarkhan, 1949; Greenwood, 1963, p. 409), but Nelson (1968) was unable to find any supporting evidence in the gill-arch structure, and such evidence as was found suggested a relationship of mormyrids (and *Gymnarchus*) with osteoglossids (and *Pantodon*) rather than with notopterids or hiodontids. The infraorbital evidence adds little to clarify the interrelationships of these fishes, for the bones of *Hiodon*,
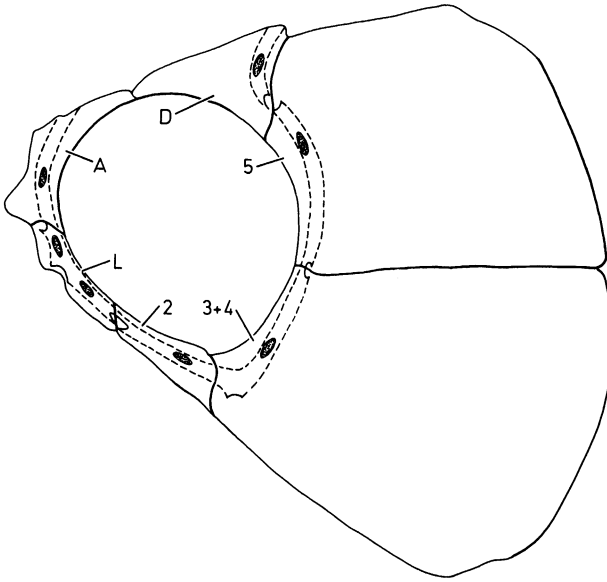
FIG. 14. *Scleropages leichardti* (A.M.N.H. 13977, ×2).
Abbreviations: A, antorbital; D, dermosphenotic; L, lacrimal; 2–5, infraorbitals.

notopterids, and mormyrids for the most part are peculiar each in their own way. It is true that the anterior infraorbitals of notopterids and mormyrids do not completely enclose in bone the anterior part of the enlarged infraorbital canal. But the tendency toward a cavernous head-canal system has been repeated many times in teleostean phylogeny, and in itself is of secondary value as an indication of relationships.

It might be added that even in some osteoglossids, which have the infraorbital canal completely bone enclosed, the primary tubes (in the sense of Allis, 1889, p. 467) have been modified into large sinuses. In osteoglossoids there is an opening in the infraorbital canal between each two neuromasts. In most genera the opening communicates with a short primary tube or small sinus, and this tube or sinus communicates with the exterior by means of a single or in some cases a double pore. In *Heterotis* (fig. 18) the tubes are somewhat enlarged. In *Arapaima* (fig. 19) they form large sinuses that open to the exterior by means of two or more pores (see also Lüling, 1964, p. 492).

It is generally agreed that the notopterids and mormyrids are groups that are distinctive in different ways. The infraorbital peculiarities of each group support this view. Notopterids have an unenclosed canal in
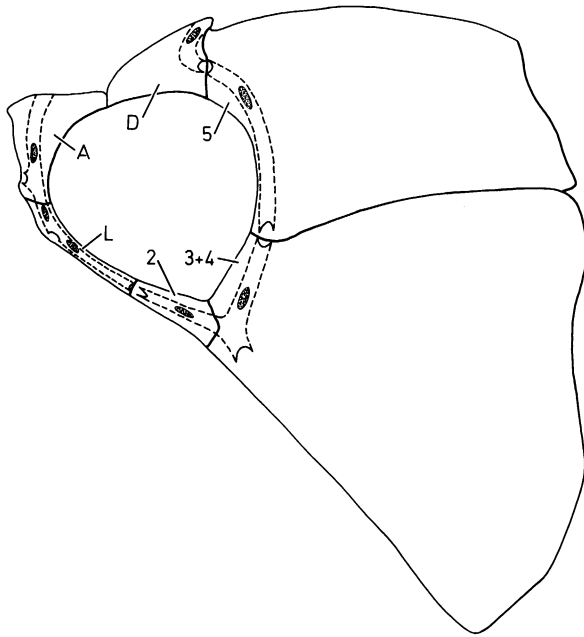
FIG. 15. *Osteoglossum bicirrhosum* (A.M.N.H. 1126, ×1).
Abbreviations: A, antorbital; D, dermosphenotic; L, lacrimal; 2–5, infraorbitals.

all of the bones except the dermosphenotic, and apparently have no primary tubes. In fact the sensory canals of the head are said not to communicate with the exterior by canals or pores of any kind. In mormyrids only three anterior infraorbitals do not enclose the canal and primary tubes are present, but are few in number and apparently end blindly. Antorbital neuromasts occur in both groups, but there are generally two in notopterids and only one in mormyrids.

Any supposed relationship between the notopterids and mormyrids is unsupported by the structures of the caudal skeletons. The caudal skeletons of both groups are widely different, with that of the notopterids by far the more advanced, having a reduced number of caudal rays, full spines on all centra except the last, no uroneurals nor epurals, and hypurals consolidated into two compound elements (fig. 20). Mormyrids in contrast have a primitive complement of caudal rays, a rudimentary arch but no full spine on ural centrum 1, one uroneural, but no epurals, and the hypurals only partly consolidated, but present in two groups. The caudal skeleton of the osteoglossids in certain respects is inter-
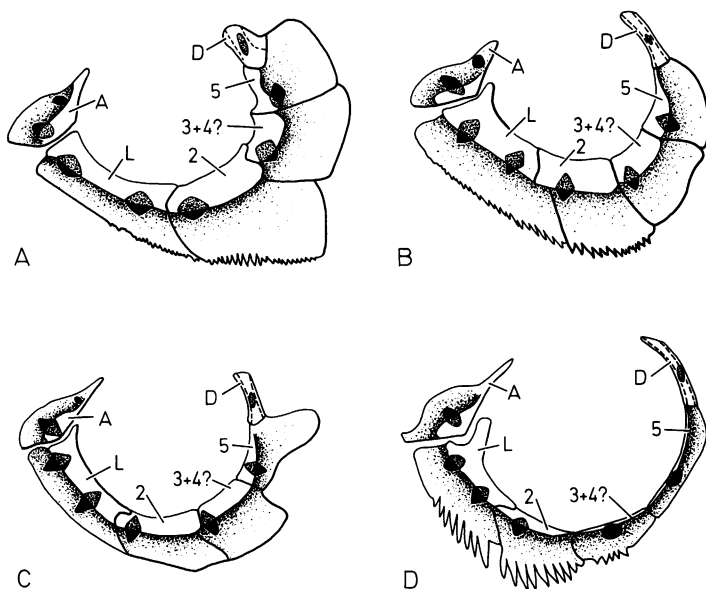
FIG. 16. A. *Notopterus chitala* (A.M.N.H. 9522, ×1½). B. *Notopterus notopterus* (A.M.N.H. 9537, ×2). C. *Papyrocranus afer* (A.M.N.H. 11706, ×2½). D. *Xenomystus nigri* (A.M.N.H. 6583, ×4).

Abbreviations: A, antorbital; D, dermosphenotic; L, lacrimal; 2–5, infraorbitals.

mediate, having a reduced number of caudal rays, a full spine on ural centrum 1, a single uroneural, but no epurals, and about the same amount of hypural consolidation as the mormyrids. Clearly there is similarity between the caudal skeleton of mormyrids and osteoglossids, but relative to the notopterids, this similarity is due to the common occurrence of primitive characters.

In view of the common occurrence of prominent ventral processes of the second hypobranchial of osteoglossids and mormyrids, an investigation was made of the branchial musculature. Here, too, there is better agreement in advanced features between the osteoglossids and mormyrids, than between those of the mormyrids and notopterids. In fact the development dorsally of inferior obliques, with which some of the external levators seem to be fused, is doubtless an advanced condition suggesting a relationship between the osteoglossids and mormyrids. But the significance of this resemblance is offset slightly by the development ventrally of a rectus communis in notopterids and in mormyrids, but not in osteoglossids (see Nelson, 1967 for a general summary of branchial

TABLE 1
Summary of Ventral Branchial Muscles[a] in Selected Osteoglossomorph Species

	O_1	O_2	O_3	R_4	RC	AT	PT	ECB	ICB	A4	A5	S
Hiodon alosoides	x	x	x	—	x	x	x	x	x	x	x	x
Notopterus chitala	x	x	x	—	x	x	x	x	x	x	x	x
Scleropages leichardti	x	x	x	x	—	x	x	x	x	x	x	x
Osteoglossum bicirrhosum	x	x	x	x	—	x	x	x	x	x	x	x
Arapaima gigas	x	x	x	x	—	x	x	x	x	x	x	x
Mormyrus ovis	x	x	x	—	x	x	x	x	x	x	x	x

[a] A4, 5, adductores 4, 5; AT, transversus anterior; ECB, coracobranchialis externus; ICB, coracobranchialis internus; O1–3, obliqui 1–3; PT, transversus posterior; R4, rectus 4; RC, rectus communis; S, sphincter oesophagi; x, muscle present; —, muscle absent.

TABLE 2
Summary of Dorsal Branchial Muscles[a] in Selected Osteoglossomorph Species

	EL				IL			ASO	PSO	PO	AT	PT	DR	IO		
	1	2	3	4	1	2	3							1	2	3
Hiodon alosoides	x	x	x	x	x	x	—	x	x	x	—	—	—	—	—	x
Notopterus chitala	x	x	x	x	x	x	—	x	x	—	—	—	—	—	—	—
Scleropages leichardti	x	x	x	x	x	x	—	x	x	—	—	—	—	—	x	x
Osteoglossum bicirrhosum	x	x	—	x	x	x	—	x	x	—	—	—	—	—	x	x
Arapaima gigas	x	—	—	x	x	x	—	x	—	—	—	—	—	—	x	x
Mormyrus ovis	x	x	x	—	x	—	—	x	—	—	—	—	—	—	x	—

[a] ASO, obliquus superior anterior; AT, transversus anterior; DR, retractor dorsalis; EL1–4, levatores externi 1–4; IL1–3, levatores interni 1–3; IO, obliquus inferior; PO, obliquus posterior; PSO, obliquus superior posterior; PT, transversus posterior.
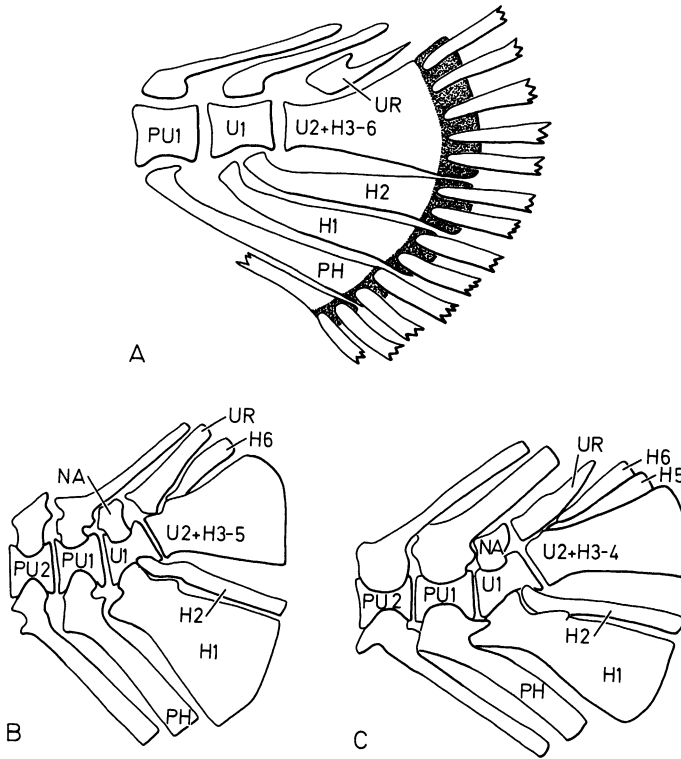
Fig. 17. A. *Osteoglossum ferreirai* (A.M.N.H. 27679, ×20). B. *Mormyrops deliciosus* (A.M.N.H. 6892, ×7). C. *Gnathonemus elephas* (A.M.N.H. 6822, ×6). Caudal skeletons, lateral view of left side.

Abbreviations: H1-6, hypurals 1-6; NA, neural arch; PH, parhypural; PU1, PU2, preural centra 1, 2; U1, U2, ural centra 1, 2; UR, uroneural.

musculature in teleosts; Bishai, 1967, has described the branchial muscles of *Mormyrus caschive*).

HIODONTIDAE: That the two, Recent, North American species of *Hiodon* are more closely related to each other than to any other Recent species has never been doubted (for distribution see Trautman, 1957, maps 16, 17). The fossil record (Eocene) of the Hiodontidae is confined to North America, and is represented only by *Eohiodon*, of which the exact relationships with Recent species are obscure (Cavender, 1966).

NOTOPTERIDAE: This family contains about six species, *Papyrocranus afer* and *Xenomystus nigri* of Africa (for distribution, see Poll, 1957, pp. 25, 26; Blache, 1964, pp. 24-26; Daget and Iltis, 1965, pp. 19-21) and

Notopterus notopterus, N. chitala, N. blanci, and *N. borneensis* of Asia and
Indonesia (for distribution, see Fowler, 1941, pp. 544–547; Smith, 1945,
pp. 56–60; d'Aubenton, 1965). The systematics of the family as a whole
have not been reviewed since Günther (1868), and of the Asian species
not since Fowler (1941).

Greenwood (1963) in a study of the African Notopteridae placed
Xenomystus in a monotypic subfamily (Xenomystinae), leaving the other
two genera in the Notopterinae. There is no doubt that *Xenomystus* is
highly peculiar, but many of its peculiarities (a reduction of branchi-
ostegal rays, reduction of pelvic fins, reduction in ray number of the
dorsal, pelvic and caudal fins, reduction in the number of upper pharyn-
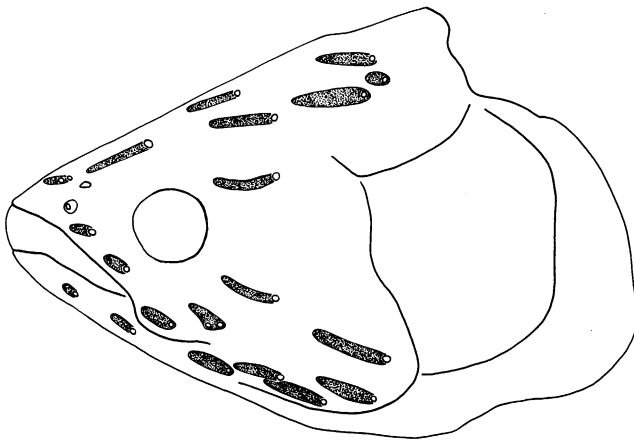
Fig. 18. *Heterotis niloticus,* lateral view, showing openings of head sensory
canals, with sinuses stippled.

geal tooth plates from two to one, an increase in the number of swim-
bladder diverticula, and intracranial penetration of the swimbladder)
are shared to varying degrees with *Papyrocranus.* It therefore would appear
that the African notopterids are more closely related to one another than
to any of the Asian species and are to be classified together. This can
be accomplished simply by placing *Papyrocranus* in the Xenomystinae.

With the scanty material at hand, the writer can contribute little to
clarify the interrelationships of Asian notopterids. However, *N. chitala,
N. borneensis,* and *N. blanci* appear to be more closely related to one an-
other than to *N. notopterus,* for they share at least a tendency toward
dorsal curvature of the anterior part of the vertebral column (confirmed
in roentgenographs of *N. chitala* and *N. borneensis;* for *N. blanci,* see

TABLE 3
SUMMARY OF SOME MERISTIC AND OTHER CHARACTERS OF RECENT OSTEOGLOSSOMORPH FISHES

	Dorsal rays	Anal rays	Caudal rays (total/branched)	Pelvic rays	Pectoral rays	Vertebrae	Lateral line scales	Ventral scutes	Branchiostegal rays	Upper Pharyngeal plates	Swimbladder diverticula	Intracranial penetration of swimbladder	Infraorbital bones	Reticulate scales
S. formosus	20	26–27	17/12[a]	6	7	60[a]	21–24	—	14–17	3[a]	—	—	6	+
S. leichardti	20[a]	31[a]	19/14[a]	6	8[a]	67[a]	35	—	14[a]	3[a]	—	—	6[a]	+
O. bicirrhosum	42–50	49–58	14/5[a]	6	7	84–92	30–37	—	10	3[a]	—	—	6	+
O. ferreirai	52–57	61–67	13/2[a]	6[a]	7	96–100	37–40	—	10	3[a]	—	—	6[a]	+[a]
A. gigas	40[a]	30–32	34/18[a]	6[a]	11[a]	81[a]	55[a]	—	11[a]	3[a]	—	—	5	+
H. niloticus	32–37	34–39	15/10[a]	6	11–12	66–70	32–39	—	7–9	0	—	—	5	+
P. buchholtzi	6	9–14	13/9	6	8	30	28–30	—	8[a]	2[a]	—	—	7	—
Mormyridae	12–91	20–70	40/16[a]	6	9–13	37–64	35–140	—	6–8	0	—	+	4–6	+
G. niloticus	183–230	—	—	—	9–10	114–120	?	—	4	0	—	+	6+	+
H. alosoides	8–10	29–32	40/16[a]	7	11–12	58–61	55[a]	—	7–10	3[a]	—	—	5	—
H. tergisus	11–12	23–29	40/16[a]	7	12–14	55–58	56[a]	—	8–9	3[a]	—	—	5	—
N. notopterus	8–9	85–95	15/8[a]	5–6	15–17	71[a]	150+	28–33	8	2[a]	14	—	6	—
N. chitala	9–10	95–120	15/8[a]	4–6	15–16	87[a]	150+	37–45	8–9	2[a]	14	—	6	—
N. blanci	9–10	119–122	13–15/?	3	15–16	?	177–181	41	8	?	?	?	?	?
N. borneensis	9–10	94–106	15/8[a]	4–5	16–17	84[a]	150+	37–41	8	2[a]	18	—	6[a]	—
P. afer	6–7	100–141	13/8[a]	—	14–15	78–84	130–178	38–45	6–9	1[a]	115–120	+	6[a]	—
X. nigri	—	99–121	9/5[a]	4[b]	11–13	70–73	120–168	25–32	3	1[a]	70–75	+	6[a]	—

[a] based on personal observations of single specimens.

[b] rudimentary rays.

Data partly from d'Aubenton, 1965; Blache, 1964; Boulenger, 1909; Cavender, 1966; Daget and Iltis, 1965; Dehadrai, 1957; Greenwood, 1963; Kanazawa, 1966; McAllister, 1968; Nelson, 1968; Smith, 1945; Trautman, 1957; Weber and de Beaufort, 1913.
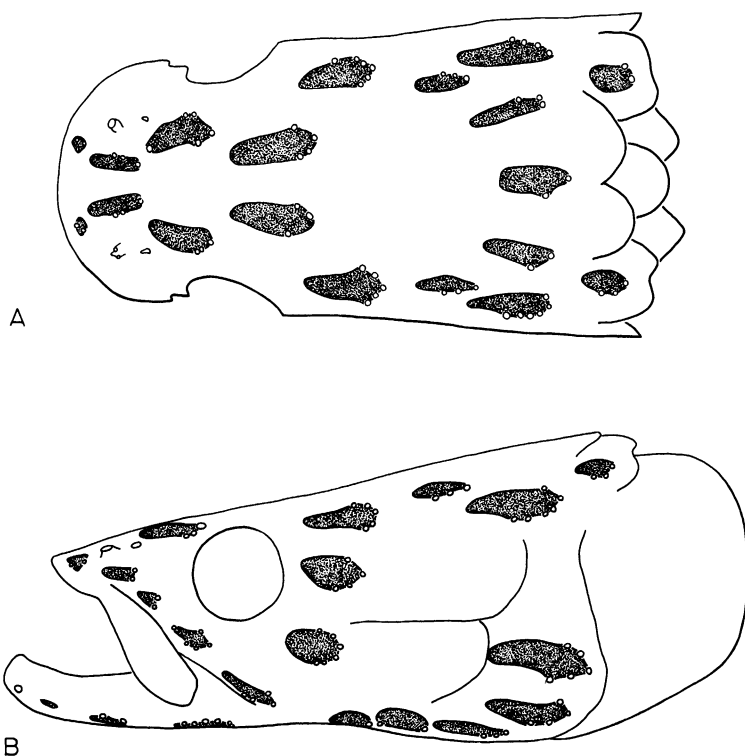
Fɪɢ. 19. *Arapaima gigas,* showing openings of head sensory canals, with sinuses stippled. A. dorsal view. B. lateral view.

d'Aubenton, 1965, fig. 1) and apparently increased numbers of anal rays, vertebrae, and paired ventral scutes. The subgenus *Chitala* (Fowler, 1934, p. 244) apparently is available for these three species. Weber and de Beaufort (1913, p. 10) listed "about 200" lateral line scales for *N. chitala,* but this probably is a high estimate.

MORMYRIDAE: This family presently contains numerous genera and species, all confined to Africa. The many specializations of this group, although strongly indicating a monophyletic origin, render difficult any assessment of the interrelationships between mormyrids and other Recent fishes. Some or all mormyrids are probably related to *Gymnarchus,* but if *Gymnarchus* is to be included in a subdivision of the Mormyridae, for example, with *Mormyrops* (see e.g., Gregory, 1933, p. 173), then some basis other than the peculiarities of *Gymnarchus* will be necessary for

Fig. 20. A. *Notopterus chitala* (A.M.N.H. 9522, ×5). B. *Notopterus notopterus* (A.M.N.H. 9537, ×6). C. *Papyrocranus afer* (A.M.N.H. 11706, ×14). D. *Xenomystus nigri* (A.M.N.H. 6583, ×12). Caudal skeletons, lateral view of left side.

Abbreviations: H1–6, hypurals 1–6; PH, parhypural; PU1, PU2, preural centra 1, 2; U1, U2, ural centra 1, 2.

subdivision of the family. No fossil record exists for the mormyrids and *Gymnarchus.*
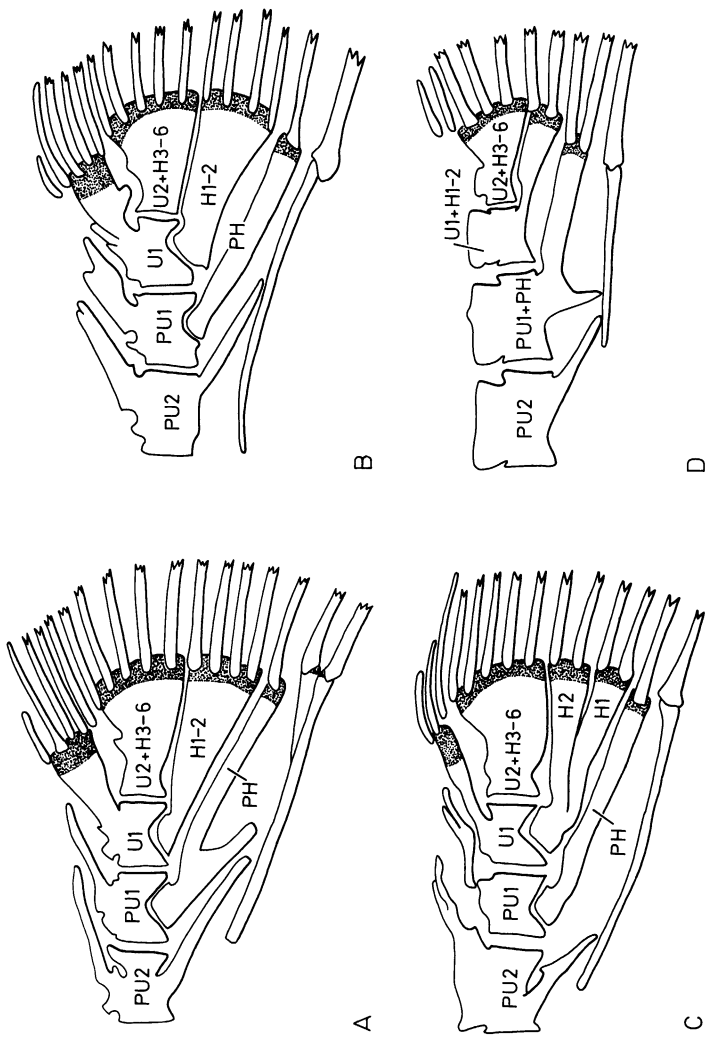
OSTEOGLOSSOIDAE: As conceived here the superfamily includes seven species in five genera: *Scleropages* (*S. formosus, S. leichardti;* Fowler, 1941, p. 535, listed a second Australian species, *S. guntheri*) in southeast Asia and Australia (for distribution, see also Blanc and d'Aubenton, 1965), *Osteoglossum* (*O. bicirrhosum, O. ferreirai*) and *Arapaima gigas* in South America, (for distribution, see Fowler, 1948, pp. 28–30; Lüling, 1964), *Heterotis niloticus* and *Pantodon buchholtzi* in West Africa (for distribution, see Blanc, 1954; d'Aubenton, 1955, fig. 2; Poll, 1957, pp. 24, 25; Blache, 1964, pp. 26, 27; Daget and Iltis, 1965, pp. 23, 26, 27). The interrelationships of these fishes are not yet thoroughly settled. *Pantodon,* because of its many distinctive characters, traditionally has been placed in a family by itself, with the other species lumped together in the family Osteoglossidae. Greenwood and Thompson (1960) and Nelson (1968) found some evidence that *Pantodon* is more closely related to *Scleropages* and *Osteoglossum* than to *Arapaima* and *Heterotis.* Circumorbital evidence is consistent with, but does not directly support, this view.

That the two species of *Osteoglossum* are closely related, and in most respects advanced relative to the species of *Scleropages,* is scarcely open to doubt. The numerous vertebrae, lateral-line scales, and dorsal and anal fin rays, reduced caudal rays (especially the branched caudal rays), and reduced branchiostegal rays all support this interpretation. The genus *Scleropages,* however, is presently defined on the basis of characters that appear to be primitive (e.g., a large number of branchiostegal rays). It is possible, therefore, that one species of *Scleropages* is really more closely related to *Osteoglossum.* At present, however, little evidence can be brought to bear on this problem. Provisionally, therefore, both *S. formosus* and *S. leichardti* can be retained in the genus *Scleropages,* and the genus can be considered monophyletic.

That *Arapaima* and *Heterotis* are more closely related to each other than to any other Recent fishes is supported by circumorbital evidence, namely the fusion of the antorbital and lacrimal. Other similarities have been noted (see e.g., Herald, 1961; Dorn, 1968; Dorn and Schaller, 1968; Nelson, 1968; Roellig, personal communication). That these genera and *Scleropages* and *Osteoglossum* form a monophyletic group has long been assumed, but supporting evidence has never been coherently summarized, and appears rather meager. Perhaps the most notable peculiarity shared by all four genera is the reticulate type of scale.

Cockerell (1910a, 1910b, 1911a, 1911b, 1911c, 1911d) found scales of a reticulate type in lungfishes, osteoglossids, mormyrids, and some other

teleosts, and concluded that the "ancestor of the teleosteans must have had reticulated scales" (1911b, p. 127). Recent authors, too, have commented on the similarity between lungfish and osteoglossid scales (Dorn, 1968; Dorn and Schaller, 1968). But notable differences exist, especially in the pattern of surface ridges (circulae). In the lungfishes (see e.g., Brien, 1962, fig. 16), coelacanths (see e.g., Schaeffer, 1952, fig. 12), and *Amia* (see e.g., Lagler, 1947, pl. 2, fig. 4), the ridges are longitudinal, whereas in most teleosts, including all osteoglossomorphs, they are circular.

Reticulate scales with well-developed dentinous and enameloid tissues are unknown. Relative to cosmoid and ganoid types, reticulate scales appear to be advanced in having reduced or lost such tissues. The fact that this reduction has occurred independently among dipnoans and neopterygians, can hardly be doubted, especially because reticulate scales are absent from known fossil sarcopterygian and neopterygian fishes (see e.g., Schultze, 1966). Therefore, the hypothesis that reticulate scales were present in ancestral teleosts is to be rejected.

The exact relationships of *Pantodon* remain to be determined. In certain respects (e.g. reduced numbers of branchiostegals and caudal rays), *Pantodon* resembles *Osteoglossum,* but in others it represents evolutionary trends probably opposite to those of *Osteoglossum* (e.g., reduction rather than increase in vertebrae and dorsal and anal fin rays). There is no evidence for a relationship between *Pantodon* and *Scleropages,* although *Pantodon* shares some peculiarities with the Osteoglossinae as a whole (Greenwood and Thomson, 1960; Nelson, 1968). In certain respects (a cellular swim-bladder) *Pantodon* resembles the Heterotinae, but there is little other evidence suggesting a relationship. *Pantodon,* without a reticulate scale, lacks one of the major features that distinguishes all of its probable relatives. The systematic position of *Pantodon* consequently is obscure.

The fossil record of the superfamily Osteoglossoidae is more significant than that of any other osteoglossomorph group. Of particular interest are the fossil genera *Phareodus* (Eocene of North America and Tertiary of Queensland), *Musperia* (Eocene? of Sumatra and possibly Tertiary of India), and *Singida* (Oligocene? of East Africa; see Hills, 1934; Sanders, 1934; Hora, 1938a, 1938b; Hora and Menon, 1953; Greenwood and Patterson, 1967; *Brychaetus* from the Tertiary of England and possibly North Africa [Casier, 1966, p. 144] and *Genartina* [otoliths] from the Tertiary of England and North America [Frizzell and Dante, 1965] are not yet identifiable as osteoglossomorphs).[1] The relationships of these

---

[1] Taverne (1969) has recently described an osteoglossomorph caudal skeleton from

fossils have never been established, although there is some agreement that *Musperia* and both the Australian and North American species of *Phareodus* are very similar to each other. *Singida,* in contrast, is different in numerous ways from other fossil osteoglossomorphs. One interesting similarity among all three genera, however, is the occurrence of 15 branched caudal rays, with seven supporting the upper lobe, and eight the lower lobe of the caudal fin (7 + 8 branched caudal rays seem to occur in *Musperia,* see Sanders, 1934, pl. 2; for *Phareodus* and *Singida,* see Greenwood and Patterson, 1967, p. 220). There probably is good reason to assume that in the ancestors of the Osteoglossomorpha the number of branched rays was higher. Most groups of lower teleosts have 17 branched caudal rays with nine supporting the upper lobe and eight the lower (Gosline, 1960, p. 333), a condition probably primitive for the Teleostei, with the Osteoglossomorpha included. Pholidophoroids have greater numbers of branched caudal rays (Lund, 1967; Patterson, 1968a), but leptolepids apparently have the teleostean number of 9 + 8 (see e.g., Nybelin, 1963). Thus, there is reason to believe that early osteoglossomorphs reduced the number of branched caudal rays, perhaps from the primitive teleostean number of 9 + 8. Recent and fossil hiodontids and most mormyrids have 8 + 8 branched caudal rays, a condition presumably derived from the loss of one upper branched ray (the only mormyrids known to deviate from this number are species of the genus *Mormyrops,* which often have one or both lobes supported by nine or more branched rays; *Gymnarchus* is without a caudal fin and has the caudal skeleton severely reduced [Taverne, 1967, fig. 4]). Fossil osteoglossoids, with 7 + 8 branched rays, would seem to represent a condition more advanced than that of the hiodontids and mormyrids, a condition presumably achieved by the loss of another upper branched ray. Further reduction apparently proceeded independently, giving rise to the condition of the Recent osteoglossids on the one hand and to that of the notopterids on the other. There is no indication that the early reduction in number of rays took place in round-tailed forms (cf. Gosline, 1960, p. 344). Secondary increases, apparent both in *Arapaima* and *Mormyrops,* are correlated with a round tail (in *Mormyrops* the tail is lobed, but the lobes are rounded).

As discussed above, *Phareodus* and *Musperia,* with reticulate scales and

---

the Paleocene of North Africa and identified it as belonging to a species of *Brychaetus.* This fact has little relevance to the present discussion, insofar as the relationships of *Brychaetus* within the Osteoglossomorpha, as well as the significance of its occurrence in marine beds, remains to be determined.

only 15 branched caudal rays are tentatively identifiable as osteoglossoids, but with present knowledge, cannot be attributed to any particular sub-division of the superfamily Osteoglossoidae. Possibly they are closely re-lated to each other and together represent an early side branch. *Singida,* in contrast, shows some of the peculiarities of *Pantodon,* such as tendencies toward reduction of dorsal and anal rays and vertebral number (Green-wood and Patterson, 1967, discussed other similarities). *Singida,* like *Pantodon,* is without a reticulate type of scale, but with the evidence at hand whether this is a primitive or an advanced condition is not determinable. In any case, *Singida,* even as a possible early representative of the lineage leading to the Recent *Pantodon,* sheds no light on the problem of the relationships between *Pantodon* and other Recent osteo-glossomorphs.

Doubtless the greatest problem in osteoglossomorph systematics is that of the relationships of *Hiodon* and the mormyrids. If *Hiodon* and the notopterids together form a monophyletic group, as suggested elsewhere by the writer (Nelson, 1968; see also Berg, 1947; Greenwood, 1963, p. 410), the peculiarities (a lateral cranial foramen, and enclosed sensory canal system) said to be common to the mormyrids and notopterids but absent from *Hiodon* (but see Greenwood, 1963, p. 405) would become of secondary importance as evidence of relationship. As it stands now, the problem is not anywhere near a final solution. For this reason, the writer in the present paper will not attempt any better classification than that already proposed (Nelson, 1968) even though the classification was written as a summary of a particular study, not of a general synthesis.

OSTEOGLOSSOMORPH GEOGRAPHY

With a scattered distribution in the southern continents, the Recent Osteoglossidae have caused some comment in relation to theories of continental stability and drift. But how these fishes might have attained their present distribution certainly cannot be resolved without the eluci-dation of the probable distributions of the past, particularly those of the species ancestral to the Recent ones.

A complete understanding of past distributions is unattainable, but only the known data concerning interrelationships and distribution of Recent and fossil osteoglossomorph fishes can directly furnish a basis for discussion. That a historical analysis of biogeography implies, logi-cally follows from, and can be no more reliable than, a prior phyletic analysis has been discussed elsewhere by the writer (Nelson, 1969). Some of the phyletic interrelationships of Recent osteoglossomorphs re-main problematical; for this reason a simple and comprehensive theory

regarding past distributions cannot be formulated. Further progress in unraveling interrelationships among Recent forms would make such a theory possible. Of greatest importance for this purpose would be clarification of the relationships of *Hiodon*, the species of *Scleropages*, *Pantodon*, and the mormyrids.

HIODONTIDAE: If the Hiodontidae and the Notopteridae together constitute a monophyletic group, each must be characterized geographically for the purpose of a historical analysis. The Hiodontidae are known only
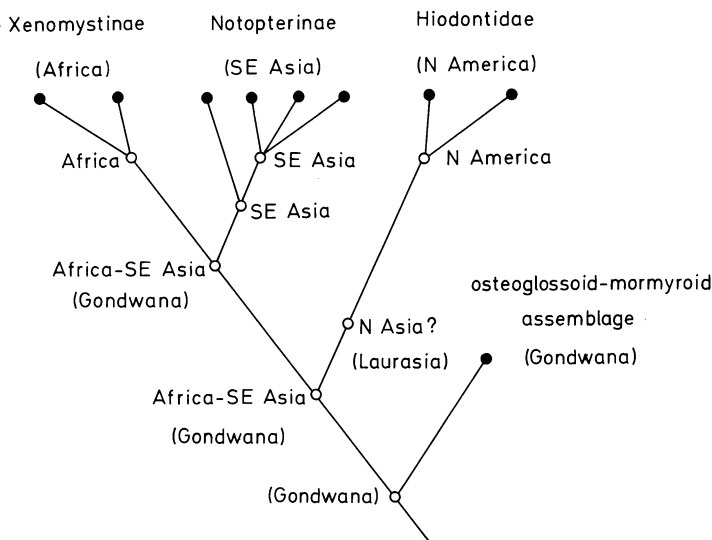
FIG. 21. Possible phyletic and geographic histories of the Recent notopteroid fishes. Recent species are represented by black circles (o), hypothetical ancestors by white circles (o), "Gondwana" and "Laurasia" are roughly synonymous with "southern continents" and "northern continents" respectively.

from North America, the Notopteridae from Africa and Asia, with an apparently monophyletic subfamily in each (the Xenomystinae in Africa and the Notopterinae in Asia). One may hypothesize that the ancestral hiodontid last occurred in North America, and that the ancestral notopterid last occurred in Asia and Africa (fig. 21). A hypothesis concerning the last occurrence of the ancestor common to both families depends upon some assumption concerning the relations between these three geographical regions. If one assumes that the Asian-African distribution of the ancestral notopterid is "Gondwanian," and the North American

distribution of the ancestral hiodontid "Laurasian," then the ancestor common to both families can be hypothesized to have occurred last in Gondwana and Laurasia. If one chooses the more traditional assumption of a faunal exchange between the Old and New World by means of a Bering land bridge, then one would have to hypothesize that either the Notopteridae or the Hiodontidae, or both, had a primary distribution in northeast Asia, for which there is no direct evidence. However, even with the Gondwana-Laurasia concept, it is necessary to admit that there must have been some region of faunal exchange, regardless of the direction of faunal movement, between the "supercontinents." It is possible that northeast Asia might have been involved (see also Darlington, 1957, fig. 18). If so, it would follow that the distribution either of the Notopteridae in Africa, or the distribution of the Hiodontidae in North America, or both, are secondary. But the Recent distribution of their relatives (the osteoglossoids and mormyroids) is Gondwanian. On this basis, the presence of osteoglossomorphs (Hiodontidae) in North America may be considered secondary and of relatively late occurrence.

Scleropages: With one species in Asia and one or two in Australia the genus *Scleropages* is a zoogeographic problem in itself: which distribution, if any, is primary and which secondary? The problem is complicated by uncertainty regarding the relationships between the species. If one species were more closely related to *Osteoglossum* than to the other, the basic zoogeographic problem might considerably be changed.

If the genus *Scleropages* is assumed to be a monophyletic group with *Osteoglossum* the Recent genus most closely related to it, an expanded zoogeographic problem results that involves three continents instead of two, and there is no indication of where the primary distribution of *Scleropages* might have been. There is little basis for favoring either faunal migration between Asia and South America independent of Australia, or faunal migration between Australia and South America independent of Asia. Examining other probable Recent relatives, such as *Pantodon,* the Heterotinae (*Arapaima* and *Heterotis*), and the Mormyridae adds to the puzzle the continent of Africa but no further clarification.

The fossil osteoglossoids *Musperia* and *Phareodus,* known from the Tertiary of Asia, Australia, and North America, suggest at most that some early osteoglossoids had a distribution not very different from the present distribution of the Notopteridae-Hiodontidae. However, the fossil species are of uncertain relationships, and there is no evidence that they themselves form a monophyletic group. Without supporting evidence, the possibilities that the fossils are early representatives of the genus *Scleropages,* of the subfamily Osteoglossinae, or of the family Osteoglos-

sidae may be dismissed here. At present, any zoogeographic analysis would have to involve some arbitrary assumption concerning even the interrelationships of the fossil species. If, for example, the North American *Phareodus* were most closely related either to the Australian species or to *Musperia*, a secondary occurrence of "phareodids" in North America would be indicated. If, as has been suggested, *Musperia* and the Australian *Phareodus* were more closely related to each other than to the North American *Phareodus*, a problem would arise similar to that of the
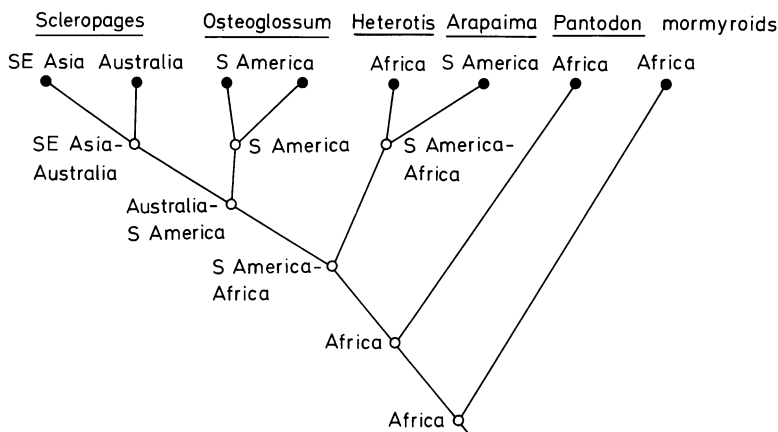

FIG. 22. One possible interpretation of the phyletic and geographic histories of the Recent osteoglossoid-mormyroid fishes.

Hiodontidae-Notopteridae. Neither of these alternatives are acceptable at the present time, without evidence that all of the phareodids themselves constitute a monophyletic group. With present uncertainties, therefore, the direction of movement of phareodids between Asia and Australia cannot be decided with a reasonable margin of probability. It follows that the present fossil evidence cannot be brought to bear on the distributional history of *Scleropages*.

That *Scleropages* is related to *Osteoglossum*, and that these genera together are related to the Heterotinae, are assumptions that reasonably can be accepted for the purpose of a zoogeographic analysis. That all of the southern continents and only one northern continent are involved in the Recent distribution of those fishes, must raise the possibility of direct faunal interchange between the southern continents, and the possibility of a secondary distribution of *Scleropages* in Asia and of *Phareodus* in North America. Clarification of the systematic position of

Pantodon might contribute to the solution of this problem.

If, as has been suggested (Greenwood and Thomson, 1960; Nelson, 1968), *Pantodon* were most closely related to the Osteoglossinae (*Scleropages* and *Osteoglossum*), its occurrence in Africa might be relatively Recent and parallel the possibly secondary distribution of the African notopterids, implicating Asia even more as a possible area of primary osteoglossoid distribution, primary at least relative to Africa. This possibility would be enhanced somewhat if *Singida* from the Tertiary of East Africa proved to be most closely related to *Pantodon*. In contrast, if *Pantodon* were most closely related to the Osteoglossidae as a whole, its occurrence in Africa might be relatively old, and would support the opposite interpretation (as in fig. 22).

Little will be said here about the Heterotinae. Arguments relating to its primary distribution either in South America, Africa, or elsewhere will depend upon clarification of the problems already touched upon.

MORMYRIDAE: The uncertainties regarding the relationships of the mormyrids render their zoogeographic significance obscure. Whatever their relationships, their origin probably goes back to the early stages in the differentiation of the lineages that led to the Recent osteoglossomorphs. That much of this early differentiation could have taken place in Africa is suggested at least by the occurrence there of representatives of all major osteoglossomorph groups. On present evidence, however, Africa as an area of origin for the Osteoglossomorpha is questionable in view of the possibly secondary distribution there of notopterids and *Pantodon*. A purely North American origin in the fashion of Matthew (1915, p. 298) is here dismissed in view of the absence of evidence in its favor, but an Asian origin remains plausible. It can be hoped that the Antarctic continent might hold one key to the Recent osteoglossomorph distribution. Discovery on the Antarctic continent of fossil Osteoglossomorpha of whatever sort would doubtless establish a primary distribution for them somewhere within the southern continents.

SUMMARY

The primitive condition of the teleostean infraorbital series probably included seven separate bones from the antorbital to the dermosphenotic. The anterior four bones probably enclosed more than one neuromast each, but the posterior three bones probably enclosed only one neuromast each. Reduction both of bone and neuromast numbers seems to have occurred during the evolution of most teleostean groups.

The primitive condition of seven infraorbital bones occurs in at least

some members of all major teleostean groups except the Osteoglosso-morpha. It is suggested that the osteoglossomorph condition, typically of six or fewer bones, has resulted from secondary fusion between two of the middle bones of the series.

Infraorbital and other evidence, primarily the structure of the caudal fin, indicate that the Recent Osteoglossomorpha constitute a monophyletic group, and suggest certain interrelationships among the members of that group. Nevertheless, some interrelationships remain problematical. For this reason a satisfactory phyletic classification of the Osteoglosso-morpha and a comprehensive theory of their geographic history are not yet attainable.

REFERENCES

ALLIS, E. P., JR.
   1889. The anatomy and development of the lateral-line system in *Amia calva*. Jour. Morph., vol. 2, pp. 463–566, pls. 30–42.
   1904. The latero-sensory canals and related bones in fishes. Internatl. Monatsschr. Anat. Physiol., vol. 21, pp. 401–502, pls. 8–20.
AUBENTON, F. D'
   1955. Etude de l'appareil branchiospinal et de l'organe suprabranchial d'*Heterotis niloticus* Ehrenberg 1827. Bull. Inst. Français Afrique Noire, sér. A, vol. 17, pp. 1179–1201, 17 figs.
   1965. *Notopterus blanci* n. sp., nouvelle espèce de poisson Notopteridae du haut MéKong Cambodgien. Bull. Mus. Natl. Hist. Nat., sér. 2, vol. 37, pp. 261–264, 1 fig.
BERG, L. S.
   1947. Classification of fishes both Recent and fossil. Ann Arbor, pp. 87–517, 190 figs.
BISHAI, R. M.
   1967. Cranial muscles of *Mormyrus caschive* (L.). Anat. Anz., vol. 121, pp. 12–25, 8 figs.
BLACHE, J.
   1964. Les poissons du bassin du Tchad et du bassin adjacent du Mayo Kebbi. Paris, 483 pp., 147 figs.
BLANC, M.
   1954. La répartition des poissons d'eau douce africains. Bull. Inst. Français Afrique Noire, sér. A, vol. 16, pp. 599–628, 13 figs.
BLANC, M., AND F. D'AUBENTON
   1965. Sur la présence de *Scleropages formosus* (Müller et Schlegel, 1844), poisson de la famille des Osteoglossidae dans les eaux douces du Cambodge. Bull. Mus. Natl. Hist. Nat., sér. 2, vol. 37, pp. 397–402, 2 figs.
BOULENGER, G. A.
   1909. Catalogue of the fresh-water fishes of Africa in the British Museum (Natural History). London, vol. 1, xi + 373 pp., 270 figs.

BRIEN, P.
1962. Etude de la formation, de la structure des écailles des dipneustes actuels et de leur comparaison avec les autres types d'écailles des poissons. Ann. Mus. Afrique Cent., sér. 8°, Sci. Zool., vol. 108, pp. 53–128, 34 figs., 7 pls.

CASIER, E.
1966. Faune ichthyologique du London Clay. London, xiv + 496 pp., 82 figs., 68 pls.

CAVENDER, T.
1966. Systematic position of the North American Eocene fish, "*Leuciscus rosei*" Hussakof. Copeia, pp. 311–320, 6 figs.

COCKERELL, T. D. A.
1910a. On the scales of some malacopterygian fishes. Proc. Biol. Soc. Washington, vol. 23, pp. 111–114.
1910b. The scales of the mormyrid fishes, with remarks on *Albula* and *Elops*. Smithsonian Misc. Coll., vol. 56, pp. 1–4, 3 figs.
1911a. The scales of the dipnoan fishes. Science, vol. 33, pp. 831–832.
1911b. Additional note on reticulated fish-scales. *Ibid.,* vol. 34, pp. 126–127.
1911c. Note on the scales of the osteoglossid fishes. Proc. Biol. Soc. Washington, vol. 24, p. 39.
1911d. The scales of freshwater fishes. Biol. Bull., vol. 20, pp. 367–386, 5 pls.

DAGET, J., AND A. ILTIS
1965. Poissons de Côte d'Ivoire (eaux douces et saumâtres). Mem. Inst. Français Afrique Noire, no. 74, xi + 385 pp., 212 figs., 4 pls.

DARLINGTON, P. J.
1957. Zoogeography: the geographical distribution of animals. New York, London and Sydney, xi + 675 pp., 80 figs.

DEHADRAI, P. V.
1957. On the swimbladder and its relation with the internal ear in genus *Notopterus* (Lacepède). Jour. Zool. Soc. India, vol. 9, pp. 50–61, 5 figs.

DEVILLERS, C., AND J. CORSIN
1968. Les os dermiques crâniens des poissons et des amphibiens; points de vues embryologiques sur les "territoires osseux" et les "fusions." *In* Ørvig, T. (ed.), Nobel Symposium 4, Current Problems of Lower Vertebrate Phylogeny. Stockholm, pp. 413–428, 4 figs.

DORN, E.
1968. Schwimmblasenbau und Lebensweise der Osteoglossiden. Zool. Anz., Suppl., vol. 31, pp. 370–380, 12 figs.

DORN, E., AND F. SCHALLER
1968. Die Knockenzüngler—eine Besonderheit unter den Fischen. Umschau, pp. 426–431, 7 figs.

FOWLER, H. W.
1934. Descriptions of new fishes obtained 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. Proc. Acad. Nat. Sci. Philadelphia, vol. 85, pp. 233–367, 117 figs.
1941. Contributions to the biology of the Philippine archipelago and

adjacent regions. Bull. U. S. Natl. Mus., no. 100, vol. 13, x + 879 pp., 30 figs.

1948. Os peixes de água doce do Brasil. Arq. Zool. Estado São Paulo, vol. 6, pp. 1–204, 237 figs.

FRIZZELL, D. L., AND J. H. DANTE
1965. Otoliths of some early Cenozoic fishes of the gulf coast. Jour. Paleont., vol. 39, pp. 687–718, 2 figs., pls. 86–88.

GOSLINE, W. A.
1960. Contributions toward a classification of modern isospondylous fishes. Bull. Brit. Mus. (Nat. Hist.), Zool., vol. 6, pp. 325–365, 15 figs.

1965. Teleostean phylogeny. Copeia, pp. 186–194, 1 fig.

GREENWOOD, P. H.
1963. The swimbladder in African Notopteridae (Pisces) and its bearing on the taxonomy of the family. Bull. Brit. Mus. (Nat. Hist.), Zool., vol. 11, pp. 377–412, 5 figs.

1967. The caudal fin skeleton in osteoglossoid fishes. Ann. Mag. Nat. Hist., ser. 13, vol. 9, pp. 581–597, 12 figs.

GREENWOOD, P. H., AND C. PATTERSON
1967. A fossil osteoglossoid fish from Tanzania. Jour. Linnean Soc. London (Zool.), vol. 47, pp. 211–223, 3 figs., 3 pls.

GREENWOOD, P. H., AND K. S. THOMSON
1960. The pectoral anatomy of Pantodon buchholzi (a freshwater flying fish) and the related Osteoglossidae. Proc. Zool. Soc. London, vol. 135, pp. 283–301, 9 figs.

GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, AND G. S. MYERS
1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Amer. Mus. Nat. Hist., vol. 131, pp. 339–456, 9 figs., pls. 21–23.

GREGORY, W. K.
1933. Fish skulls. A study of the evolution of natural mechanisms. Trans. Amer. Phil. Soc., vol. 23, vii + pp., 75–481, 302 figs.

1935. 'Williston's law' relating to the evolution of skull bones in the vertebrates. Amer. Jour. Phys. Anthrop., vol. 20, pp. 123–152, 4 figs.

GÜNTHER, A.
1868. Catalogue of the fishes in the British Museum. London, vol. 7, xx + 512 pp.

HERALD, E. S.
1961. Living fishes of the world. Garden City, 304 pp., illus.

HILLS, E. S.
1934. Tertiary fresh water fishes from southern Queensland. Mem. Queensland Mus., vol. 10, pp. 157–174, 14 figs., 8 pls.

HORA, S. L.
1938a. On the age of the Deccan Trap as evidenced by fossil fish remains. Curr. Sci., vol. 6, pp. 370–372.

1938b. On some fossil fish-scales from the inter-trappean beds at Deothan and Kheri, Central Provinces. Rec. Geol. Surv. India, vol. 73, pp. 267–294, 14 figs., pls. 17, 18.

HORA, S. L., AND A. G. K. MENON
1953. Distribution of Indian fishes of the past and their bearing on the

geography of India. 2. The extinct freshwater teleostean fishes of India. Everyday Sci., vol. 2, pp. 105–113, 5 figs.

JARVIK, E.
   1967.   The homologies of frontal and parietal bones in fishes and tetrapods. Colloques Internatl. Cent. Natl. Rech. Sci., no. 163, pp. 181–213, 12 figs., 4 pls.

KANAZAWA, R. H.
   1966.   The fishes of the genus *Osteoglossum* with a description of a new species from the Rio Negro. Ichthyologica, vol. 37, pp. 161–172, 4 figs.

KAPOOR, A. S.
   1964.   Functional morphology of latero-sensory canals in the Notopteridae (Pisces). Acta Zool., Stockholm, vol. 45, pp. 77–91, 6 figs.

LAGLER, K. F.
   1947.   Lepidological studies 1. Scale characters of the families of Great Lakes fishes. Trans. Amer. Micros. Soc., vol. 66, pp. 149–171, 7 pls.

LÜLING, K. H.
   1964.   Zur Biologie und Ökologie von *Arapaima gigas* (Pisces, Osteoglossidae). Zeitschr. Morph. Ökol. Tiere, vol. 54, pp. 436–530, 46 figs.

LUND, R.
   1967.   An analysis of the propulsive mechanisms of fishes with reference to some fossil actinopterygians. Ann. Carnegie Mus., vol. 39, pp. 195–218, 12 figs.

McALLISTER, D. E.
   1968.   The evolution of branchiostegals and associated opercular, gular and hyoid bones and the classification of teleostome fishes, living and fossil. Bull. Natl. Mus. Canada, no. 221, xiv + 239 pp., 3 figs., 21 pls.

MATTHEW, W. D.
   1915.   Climate and evolution. Ann. New York Acad. Sci., vol. 24, pp. 171–318, 33 figs.

MONOD, T.
   1968.   Le complex urophore des poissons téléostéens. Mém. Inst. Fondamental Afrique Noire, no. 81, vi + 705 pp., 989 figs.

NELSON, G. J.
   1967.   Branchial muscles in some generalized teleostean fishes. Acta Zool., Stockholm, vol. 48, pp. 277–288, 2 figs.
   1968.   Gill arches of teleostean fishes of the division Osteoglossomorpha. Jour. Linnean Soc. (Zool.), vol. 47, no. 312, pp. 261–277, figs. 1–11.
   1969.   The problem of historical biogeography. Syst. Zool., vol. 18, pp. 243–246, 5 figs.

NIEUWENHUYS, R.
   1962a. Trends in the evolution of the actinopterygian forebrain. Jour. Morph., vol. 111, pp. 69–88, 10 figs.
   1962b. Some aspects of the comparative anatomy of the forebrain. Arch. Neerlandaises Zool., vol. 14, pp. 598–601.
   1963.   The comparative anatomy of the actinopterygian forebrain. Jour. Hirnforsch., vol. 6, pp. 171–192, figs. A–J.

NYBELIN, O.
   1963.   Zur Morphologie und Terminologie des Schwanzskelettes der

Actinopterygier. Arkiv Zool., ser. 2, vol. 15, pp. 485–516, 22 figs.

ORVIG, T.
1962. Y a-t-il une relation directe entre les arthrodires ptyctodontides et les holocéphales? Colloques Internatl. Cent. Natl. Rech. Sci., no. 104, pp. 49–61, 1 pl.
1968. The dermal skeleton; general considerations. *In* Orvig, T. (ed.), Nobel Symposium 4, Current Problems of Lower Vertebrate Phylogeny. Stockholm, pp. 373–397, 5 figs.

OMARKHAN, M.
1949. The lateral sensory canals of larval *Notopterus*. Proc. Zool. Soc. London, vol. 118, pp. 938–972, 16 figs., 6 pls.

PARRINGTON, F. R.
1967. The identification of the dermal bones of the head. Jour. Linnean Soc. London, vol. 47, pp. 231–239, 5 figs.

PATTERSON, C.
1967. A second specimen of the Cretaceous teleost *Protobrama* and the relationships of the sub-order Tselfatioidei. Arkiv Zool., ser. 2, vol. 19, 215–234, 8 figs.
1968a. The caudal skeleton in Lower Liassic pholidophorid fishes. Bull. Brit. Mus. (Nat. Hist.), Geol., vol. 16, pp. 201–239, 12 figs., 5 pls.
1968b. The caudal skeleton in Mesozoic acanthopterygian fishes. *Ibid.*, vol. 17, pp. 47–102, 28 figs.

PEHRSON, T.
1945. The system of pit organ lines in *Gymnarchus niloticus*. Acta Zool., Stockholm, vol. 26, pp. 1–8, 3 figs.

POLL, M.
1957. Les genres des poissons d'eau douce de l'Afrique. Ann. Mus. Roy. Congo Belge, Sci. Zool., vol. 54, 191 pp., 49 pls.

RIDEWOOD, W. G.
1904. On the cranial osteology of the fishes of the families Mormyridae, Notopteridae, and Hyodontidae. Jour. Linnean Soc. London, vol. 29, pp. 188–217, pls. 22–25.

ROSEN, D. E., AND C. PATTERSON
1969. The structure and relationships of the paracanthopterygian fishes. Bull. Amer. Mus. Nat. Hist., vol. 141, pp. 357–474, 74 figs., pls. 52–78.

SANDERS, M.
1934. Die fossilen Fischen der altertiären Süsswasserablagerungen aus Mittel-Sumatra. Verhandl. Geol.-Mijn. Genootsch. Nederland Kolonien, geol. ser., vol. 11, pp. 1–144, 9 pls.

SCHAEFFER, B.
1952. The Triassic coelacanth fish *Diplurus*, with observations on the evolution of the Coelacanthini. Bull. Amer. Mus. Nat. Hist., vol. 99, pp. 25–78, 16 figs., pls. 5–16.

SCHULTZE, H.-P.
1966. Morphologische und histologische Untersuchungen an Schuppen mesozoischer Actinopterygier (Ubergang von Ganoid zu Rundschuppen). Abhandl. Neues Jahrb. Geol. Paläont., vol. 126, pp. 232–314, 61 figs.

SHARMA, M. S.
    1964.   The cephalic lateral-line system in *Notopterus chitala* (Ham.). Copeia,
            pp. 530–533, 3 figs.
SMITH, C. L., AND R. M. BAILEY
    1962.   The subocular shelf of fishes. Jour. Morph., vol. 110, pp. 1–18, 3 pls.
SMITH, H. M.
    1945.   The fresh-water fishes of Siam, or Thailand. Bull. U. S. Natl. Mus.,
            vol. 188, xi + 622 pp., 107 figs.
TAVERNE, L.
    1967.   Le squelette caudal des Mormyriformes et des Ostéoglossomorphes.
            Bull. Acad. Roy. Belgique, Cl. Sci., sér. 5, vol. 53, pp. 663–678, 10
            figs.
    1968.   Ostéologie du genre *Campylomormyrus* Bleeker (Pisces, Mormyriformes).
            Ann. Soc. Roy. Zool. Belgique, vol. 98, pp. 147–188, 19 figs.
    1969.   Sur un squelette caudal d'ostéoglossomorph (*Brychaetus*) dans le
            Paléocène (Montien) de Landana (Enclave de Cabínda). —Etablisse-
            ment d'une nouvelle espèce pour les restes de *Brychaetus* de Landana:
            Brychaetus caheni sp. nov. Rev. Zool. Bot. Africaines, vol. 69, pp.
            125–131, 2 figs.
TRAUTMAN, M. B.
    1957.   The fishes of Ohio with illustrated keys. Baltimore, xvii + 683 pp.,
            172 figs., 7 pls., 172 maps.
WEBER, M., AND L. F. DE BEAUFORT
    1913.   The fishes of the Indo-Australian Archipelago. II. Malacopterygii,
            Myctophoidea, Ostariophysi: I. Siluroidea. Leiden, xx + 404 pp., 151
            figs.