

Comparative osteology and phylogenetic systematics of fossil and living bony-tongue fishes (Actinopterygii, Teleostei, Osteoglossomorpha)

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Several recent studies using analyses of morphological characters have addressed the interrelationships of Osteoglossomorpha, a group that sometimes is considered the living sister group of all other living teleosts. Many characters used in these studies were found to be poorly defined, to be coded incorrectly or illogically, or to display more variation than was described. The goal of this study is to address these concerns and contribute generally to knowledge of the morphology and systematic relationships of osteoglossomorphs. Analysis of 72 characters (65 informative) scored for 20 genera resulted in two most parsimonious cladograms (171 steps, CI = 0.6433, CI = 0.6139 excluding uninformative characters, HI = 0.3977, HI = 0.3861 excluding uninformative characters; RI = 0.7782; RC = 0.5006). Osteoglossomorpha is supported by both synapomorphies and homoplasies, although its monophyly was not truly tested in this analysis (only a single outgroup, *Elops*, was included in the analysis). The only difference in the topologies of these cladograms is in the position of †*Lycoptera* (recovered as either the sister group of all other osteoglossomorphs sampled or of †*Eohiodon* + *Hiodon*). †*Ostariostoma* is recovered as the sister group of all non-hiodontiform osteoglossomorphs. Mormyrids are the sister group of notopterids + osteoglossids. This clade has not been found in other recent analyses. Mormyrids and notopterids usually are considered more closely related to each other than to any other group; characters not included here support this relationship and future consideration of these characters must be made. Although almost completely dichotomous, many nodes of the resulting trees lack rigorous support. For example, †*Palaeonotopterus* is interpreted as the sister group of all mormyrids sampled, although for this taxon only 22% of characters could be scored. © 2003 The Linnean Society of London. *Zoological Journal of the Linnean Society*, 2003, 137, 1–100.

ADDITIONAL KEYWORDS: – Gymnarchidae – Hiodontidae – Heterotinae – †Lycopteridae – Mormyridae – Notopteridae – Osteoglossidae – Osteoglossinae – *Pantodon*.

INTRODUCTION

'And whereas Sense and Memory are but knowledge of Fact, which is a thing of past, and irrevocable; Science is the knowledge of Consequences, and dependance [sic] of one fact upon another . . .'

Hobbes (1651), Chapter V of the First Part of *Leviathan* (Of Reason, and Science)

Osteoglossomorpha is a radiation of teleostean fishes that sometimes is considered to be the living sister group of all other living teleostean fishes (e.g. Patterson & Rosen, 1977; Lauder & Liem, 1983; Patterson, 1994; Inoue *et al.*, 2001), although this has

been challenged (e.g. Lê, Lecointre & Perasson, 1993; Arratia, 1991, 1996, 1997, 1999; Filleul & Lavoué, 2001). Most living osteoglossomorph fishes, commonly known as 'bony tongue' fishes, are primary freshwater fishes (*sensu* Myers, 1949) although some may enter brackish water, and only a few fossil taxa come from marine deposits (e.g. †*Brychaetus* Woodward, 1901) – telolimnic in the terms of Patterson (1975a). For this reason, as well as their geographical and geological distributions, the osteoglossomorphs have been of particular interest from a biogeographical standpoint (e.g. Nelson, 1969; Cracraft, 1974; Patterson, 1975a, 1981; Wilson & Williams, 1992; Lundberg, 1993; Li, 1994a; Maisey, 2000). With approximately 240 living and fossil species (Nelson, 1994), this is a relatively small group of teleostean fishes, yet they are very diverse morphologically.

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The only two extant species of North American osteoglossomorphs belong to the genus *Hiodon* Lesueur, 1818, and inhabit the rivers and lakes of much of central North America. Osteoglossomorpha also includes many popular aquarium fishes such as the arowanas of the family Osteoglossidae (*Osteoglossum* [Vandelli in Cuvier, 1829]: two species, South America; *Scleropages* Günther, 1864: three species, Asia and Australia), the heterotines (*Arapaima* Müller, 1843: South America, and *Heterotis* (Cuvier, 1829): Africa, both genera monotypic), the African butterfly fish (*Pantodon* Peters, 1877: one species, Africa), the Old World knifefishes of the family Notopteridae (*Chitala* Fowler, 1934: four species, Asia; *Notopterus* Lacépède, 1800: one species, Asia; *Xenomystus* Günther, 1868: one species, Africa; *Papyrocranus* Greenwood, 1963: two species, Africa; see Roberts, 1992 for a revision of the family), and the elephant-nose mormyrid fish (19 genera, 200+ species, Africa; see Hopkins, 1986; Sullivan, Lavoué & Hopkins, 2000).

Osteoglossomorpha is unusual among living groups of teleostean fishes in that there is greater generic diversity of fossil than of living forms (Patterson, 1994). Known fossil osteoglossomorphs range from largely incomplete taxa (e.g. †*Osteoglossidarum* Stinton, 1977, which is the only otolith-based fossil genus of osteoglossomorphs, see Nolf, 1985: 38–39; fragments of scales from the Eocene of Pakistan, the Cretaceous of Niger and the Cretaceous of Bolivia, Gayet & Meunier, 1983), to relatively well known taxa, such as †*Phareodus* Leidy, 1873, an osteoglossid from the Eocene of western North America, Australia and Europe (Li, Grande & Wilson, 1997a). Ironically, Mormyriiformes, the most speciose distinct subgroup of Osteoglossomorpha, is very poorly known from the fossil record. Some very fragmentary fossil material (isolated vertebrae, teeth and fragments of the parasphenoid) have been assigned to the genus *Hyperopisus* and another mormyrid (Greenwood, 1972). These specimens, which were collected from the Middle Pliocene Wadi el Natrum fauna of Egypt, 'suggest that by the Pliocene the family [Mormyridae] had undergone quite extensive differentiation [sic], because *Hyperopisus* has a specialized interbuccal dentition of a kind not found in any other mormyrid' (Greenwood, 1974: 216). There are also two isolated teeth from the Lower Miocene of Kenya, Africa that were identified as *Gymnarchus* sp. in the collection of the Natural History Museum (London; BMNH P.59692 & P.59693). Cavin & Forey (2001) recently described several mormyrid-like characters of the skeleton of †*Palaeonotopterus* Forey, 1997 from the Early Cretaceous of Morocco. This suggested to the authors that †*Palaeonotopterus* is either the sister group of Notopteridae or the sister group of Mormyroidea; the former

hypothesis was preferred (also see Forey, 1997; Taverne & Maisey, 1999; Taverne, 2000a). In addition to the fossil record of the various subgroups within the crown-group, several putative stem-group osteoglossomorph fishes have been described from the Late Jurassic and Early Cretaceous of China (see reviews in Chang & Chou, 1977; Jin, Zhang & Zhou, 1995; Chang & Jin, 1996; Chang, 1999); these are among the earliest known of all Osteoglossomorpha.

The purpose of this paper is two-fold. First, I review the history of classification and systematic analyses of the fishes that are currently recognized as osteoglossomorphs. Second, I present the results of a new phylogenetic analysis following a critical review of characters that have been used in recent computer analyses of their interrelationships. There have been several recent morphological systematic studies of Osteoglossomorpha (e.g. Shen, 1996; Bonde, 1996; Taverne, 1998). In particular, papers by Li and colleagues (Li & Wilson, 1994, 1996a,b, 1999; Li, 1994a,b, 1996; Li, Grande & Wilson, 1997a; Li, Wilson & Grande, 1997b) will serve as the starting point for the present study. As observed by Cavin & Forey (2001: 43), the 'overlapping authorship of these papers reflects overlapping data sets and similar phylogenetic conclusions.' Therefore, the papers by Li & Wilson (1996a, 1999), which represent the broadest taxonomic sampling within osteoglossomorphs and include the most complete character information of any of these papers, will serve as the basis for much of my review.

Over the course of previous study (Hilton, 2001, 2002), as well as a current study of †*Eohiodon* Cavender, 1966 (Hilton & Grande, unpublished), I found that several characters in the literature on osteoglossomorph systematics have been vaguely defined, in that they are poorly written, coded incorrectly or illogically, or display more variation than was described in the character state definitions. Many characters have not been illustrated, so the exact intent of the authors for certain characters is unclear. It is hoped that the present study can help to correct these shortcomings, and contribute to the knowledge of the morphology and systematic relationships of osteoglossomorph fishes generally.

HISTORY OF THE CLASSIFICATION OF OSTEOGLOSSOMORPHA

In this section, I provide a brief history of the classification and systematic study of the osteoglossomorph fishes. Greenwood *et al.* (1966) is a pivotal study in the history of the study of osteoglossomorphs for two reasons. First, it is the paper in which the name Osteoglossomorpha was coined. Second, since it was published, discussion in the literature has centred

around relationships within a monophyletic Osteoglossomorpha (although not exclusively) rather than of its content. Therefore, I use this publication as a turning point for my discussion of osteoglossomorph classifications. In the third subsection, I offer a brief overview of the debate on the position of Osteoglossomorpha within Teleostei.

ANALYSES OF OSTEOGLOSSOMORPHA UP TO AND INCLUDING GREENWOOD *ET AL.* (1966)

The history of classification of osteoglossomorph fishes dates from the tenth edition of *Systema Naturae* (Linnaeus, 1758), when the genus *Mormyrus* was first described as a member of Linnaeus' 'Branchiostegi', a group that also included the tetraodontiform genera *Balistes*, *Ostracion*, *Tetraodon* and *Diodon* and the gasterosteiform genera *Centriscus*, *Sygnathus* and *Pegasus* [Taxonomic names surrounded by quotation marks indicate that the group is currently considered to be non-monophyletic]. Additional osteoglossomorphs were described in the late 1700s and early 1800s (e.g. the genus *Notopterus* by Lacépède, 1800), and many important classifications of fishes were published (e.g. Agassiz; 1833–1844; Müller, 1844, 1846), but I use the ideas formalized in *Histoire Naturelle des Poissons* (Cuvier & Valenciennes, 1846, 1848) as the starting point for my discussion of classifications. I then discuss, roughly in chronological order, various classifications of fishes with respect to ideas of osteoglossomorph inter- and intrarelationships, although this discussion is by no means exhaustive.

A relationship of *Hiodon* with other osteoglossomorph fishes was suggested by Cuvier & Valenciennes (1846: 287), who saw similarities between *Osteoglossum* and *Hiodon* in terms of 'le corps comprimé, le ventre comprimé sans dentelures, et des cœcums au pylore', [the compressed body, the compressed belly without scutes, and the pyloric caeca]. In the introduction to this chapter, the relationships of the two genera to other fishes, however, were somewhat uncertain: 'La forme comprimée du corp des Ostéoglossum et des Hyodon rappelle celle des Chirocentres; mais les deux cœcums de l'Ostéoglossum et la ressemblance des autres viscères nous conduit vers les Mormyres, en même temps que la forme de la bouche et la grandeur des sous-orbitaires cuirassant la joue, rappellent Érythrins' [The compressed body form of *Osteoglossum* and *Hiodon* is similar to that of *Chirocentrus*, but the two pyloric caeca of *Osteoglossum*, as well as the resemblance of other internal organs, recalls the mormyrids, although the shape of the mouth and the size of the suborbital armouring of the cheek are similar to erythrins] (Cuvier & Valenciennes, 1846: 148). *Osteoglossum* and *Hiodon* were therefore grouped together in an assemblage that included

Chirocentrus, *Alepocephalus*, *Chanos*, *Gonorynchus*, *Mormyrus*, *Albula*, *Elops*, *Megalops*, *Amia*, *Arapaima*, *Heterotis*, *Erythrinus*, *Hoplias*, *Lebiasina*, *Pyrrhulina*, and *Umbra*, which were discussed in the volume describing 'de quelques familles de malacoptérygiens, intermédiaires entre les brochets et les clupes' [some families of 'malacopterygians', intermediate between esocids and clupeids] (Cuvier & Valenciennes, 1846: 145). The mormyrids were considered to form 'une petite famille séparée, qui se groupe cependant à côté des Butirins; ceux-ci ont de grandes affinités avec les Élopes et Mégalopes, qui ramènent à eux les Amia' [a small, separate family, which groups with *Albula*; these have great affinities with *Elops* and *Megalops*, which recall *Amia*] (Cuvier & Valenciennes, 1846: 148).

Of the relationships of the notopterids, which were discussed in a later volume (following the clupeids), Cuvier & Valenciennes (1848: 129) commented:

'Tels sont les caractères généraux des Notoptères. Qu'on les compare avec ceux déjà observés dans les différentes familles d'une classe aussi nombreuse que celle des poissons, et l'on trouvera des répétitions de caractères que la nature nous a déjà offertes dans les familles les plus éloignées les unes des autres. Ainsi les dentelures des sous-orbitaires, du sous-opercule, de la mâchoire inférieure, et les crêtes qui surmontent le crâne, sont empruntées aux diverses familles des Acanthoptérygiens. Il n'est pas jusqu'à la réunion des très-petites ventrales qui ne reproduise un des singuliers caractères de la famille des Gobioides. La dentition, et surtout celle du sphénoïde, nous ramène vers les Butyrins, en même temps que le caractère de la langue nous rapproche des Hyodons ou des Mormyres. Les Notoptères ont encore avec ces poissons une affinité notable par les grandes trous latéraux du crâne. Ce résumé me paraît justifier ce que j'ai dit tout à l'heure sur la nécessité de considérer les Notoptères comme une famille très distincte . . .'

[Such are the general characters of the notopterids. When these are compared with those observed in the various families of a group as large as that of 'fishes', one will find the repetition of characters in families that are very distantly related to each other. The serration of the suborbitals, of the subopercle and of the lower jaw, and the supraoccipital crest are similar to those of various families of acanthopterygians. It is the junction of the very small pelvic fins that mirrors one of the unique characters of the family of Gobiidae. The dentition, and especially that of the parasphenoid, recall the albulids, at the same time the form of the 'tongue' is closer to that of *Hiodon* or the mormyrids. Notopterids also have a notable affinity with these fish in the presence of a large fenestra in the side of the skull. This appears me to justify the need for regarding Notopteridae as a very distinct family . . .]

Günther (1868: v) discussed the hiodontids, osteoglossids and notopterids in a volume describing 'the Cyprinoid and Clupeoid Fishes and several other small families formerly associated with them, but already more or less distinctly separated by Valenciennes.' The hiodontids (including only *Hiodon*) and the osteoglossids (including *Arapaima*, *Heterotis* and *Osteoglossum*, which included the species of *Scleropages*) were described sequentially, following Gonorynchidae and preceding Clupeidae. The notopterids (a single recognized genus, *Notopterus*, with two subgenera, *Notopterus* and *Xenomystus*) were described following Alepocephalidae. Mormyrids and gymnarchids also were included within 'Physostomi', but were described in an earlier volume of the *Catalogue of Fishes of the British Museum* (Günther, 1866).

Cope (1871a,b, 1890) placed *Hiodon* in a group with albulids and elopids as part of his 'Isospondyli' (Fig. 1A). The other families of Osteoglossomorpha were also included in 'Isospondyli' (although heterotines were linked more closely to Galaxiidae than with Osteoglossidae, Cope, 1871a, b), with the exception of Mormyridae and Gymnarchidae, which were the sole constituents of Scyphophori (Fig. 1A), a separate order within Actinopteri. This separation was based in part on the structure of the pterotic ('Pterotic annular, including a cavity closed by a special bone', Cope, 1871a: 588).

In Gill's (1872) classification of fishes, Hiodontidae were placed between Gonorynchidae and Albulidae. Osteoglossidae and Notopteridae were sequential families placed earlier in his succession of 'isospondylous' fishes. Gill (1872) followed Cope (1871a, b) in separating out the mormyroids as the group Scyphophori, although he grouped them with catfishes, gymnotiformes, and eels. Gill (1893), in his later classification, again separated Hiodontidae and placed it in a unique suborder, Hiodontoidea, as an early group of 'malacopterygian' fishes, between Osteoglossoidea (= Osteoglossidae) and Albuloidea (= Albulidae). Gill also put the notopteroids (= Notopteridae) in 'Malacopterygii', but separated them from the hiodontoids and osteoglossoids. Gill (1893) again followed Cope's (1871a,b, 1890) separation of the mormyrids and gymnarchids in Scyphophori, and placed them between the catfishes and the synbranchiforms.

A possible relationship of *Hiodon* and notopterids was suggested by Bridge (1900), based on his and Stannius' (1854) observations on the swimbladders of *Notopterus* & *Hiodon*. Ridewood (1904a: 212, 1905) was among the first to critically examine the cranial osteology of osteoglossomorph fishes in a systematic manner. He concluded that the 'families Mormyridae, Notopteridae, and Hyodontidae [sic], though more closely related *inter se* than is either family with any

other family of Malacopterygian fishes, are not more intimately related with one another than was previously assumed to be the case.' Ridewood (1904a: 213) declined to hypothesize on the relationship of this grouping to other teleosts, stating that '[t]he three families must remain, as hitherto, the terminals of a radiating system.' He discussed at length and rejected the characters suggested by Boulenger (1898) to unite the mormyrids with *Albula* (e.g. presence of the orbitosphenoid bone), as well as other characters that 'do not point to any closer resemblance between the Mormyridae and the Albulidae than with any other primitive family' (Ridewood, 1904a: 213). Just one year later, Ridewood (1905: 272) stated: 'I should be disposed to associate the Osteoglossidae with the Pantodontidae . . . and to regard the next nearest family to be the Albulidae. The conclusion is arrived at by a consideration of the craniological features mainly, but the characters of the other parts of the skeleton and of the soft parts of the body, so far as they are known to me, do not militate against the suggestion that the Osteoglossidae and Albulidae have descended from a common stock.' Also, within Osteoglossidae, Ridewood (1905) suggested that *Osteoglossum* (including species of *Scleropages*) and *Arapaima* were more closely related to each other than either is to *Heterotis*; this view has not been supported in subsequent analyses. The relationships of *Hiodon*, however, seemed to be more problematic to him: 'I am disposed to doubt whether any close affinity exists between the Hyodontidae on the one hand and the Pantodontidae and Osteoglossidae on the other; but the results of the present investigation fully justify the action taken by the ichthyologists named [e.g. Boulenger, Peters, etc.] in closely associating the Pantodontidae with the Osteoglossidae' (Ridewood, 1905: 277). [Ridewood, like many other comparative anatomists of that time, seemed to have a well-developed concept of 'primitive' vs. 'derived' characters and the inability of 'primitive' (i.e. plesiomorphic) features to rigorously define taxa. For instance, he remarked on the difficulty of expressing relationships, and how 'the necessity of treating families [or any taxonomic level] in linear series when writing about them tends to obscure many natural relationships of which the author is fully cognizant [sic]' (Ridewood, 1905: 272). Likewise, Cope (1875: 9), in describing his 'law of persistence of type' and the science of palaeontology, although not using the word 'derived', seemed to approach classification with this concept in mind (i.e. in a hierarchical framework with natural groups defined by unique, derived characteristics). For example, he formed the following analogy: 'Thus, to illustrate, certain parts are common to all stoves, and distinguish them from all other articles of furniture; but certain other parts not only belong to a stove, but mark a given pattern of stove, since they

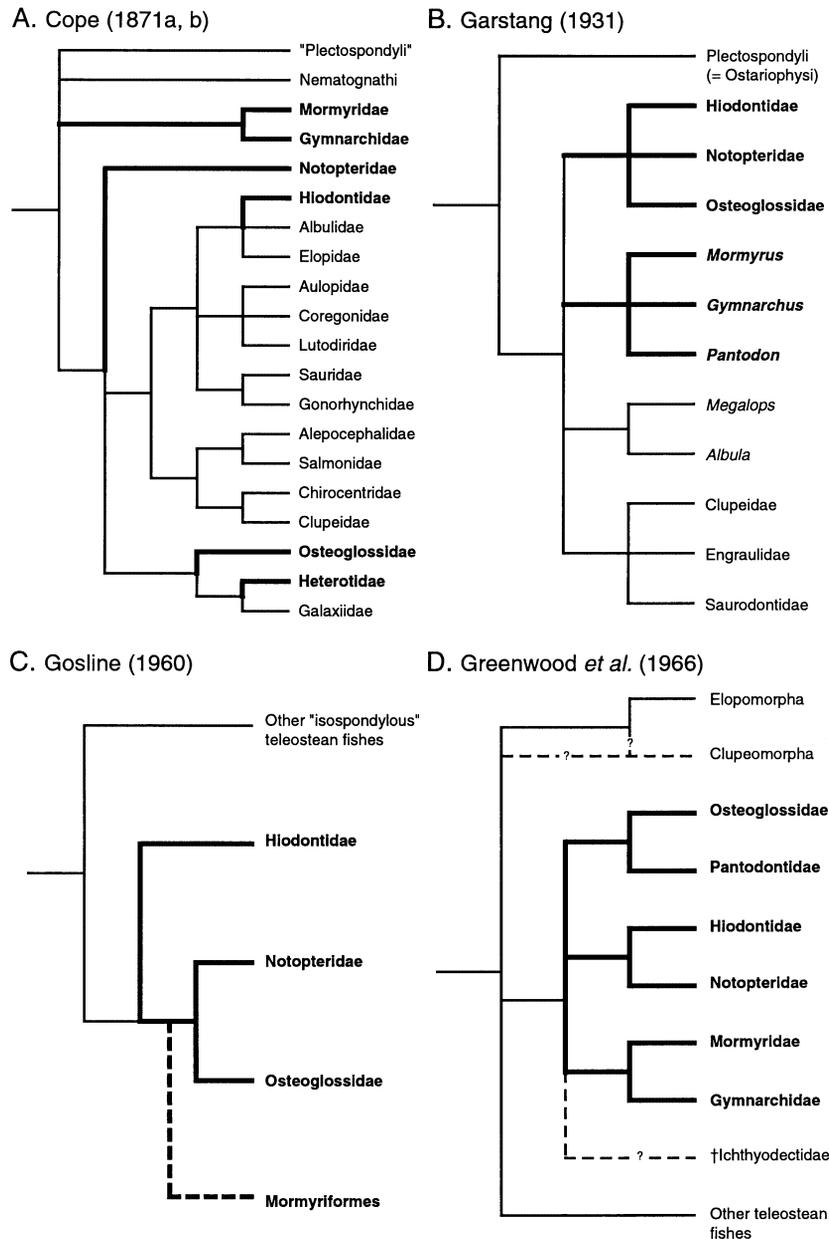


Figure 1. Schemes of interrelationships among 'lower' teleostean fishes, drawn after: A, Cope (1871a,b); B, Garstang (1931); C, Gosline (1961); and D, Greenwood *et al.* (1966). Bold-face indicates taxa considered here to belong in Osteoglossomorpha. Question marks and dashed lines indicate the author's doubt concerning the exact placement of a taxon. These diagrams were translated from textual classifications (with the exception of Greenwood *et al.*'s, which is partly redrawn from their fig. 1), and therefore are somewhat extrapolated (i.e. some of these authors indicated ancestors, which have been redrawn as sister groups).

belong only to it. A still more minute range of appearances is found only in one man's make of stoves, and others in that of another man. Hence, a person acquainted with stoves, sewing-machines, &c., can readily determine the origin of a very small part by referring to its proper kind and make.' In other words, 'certain other parts' (i.e. derived characters) that 'dis-

tinguish' one taxon from another should serve as the basis of classification (i.e. classifications should reflect phylogeny). Whereas Cope and others often were influenced by other ideals (e.g. special creation or Lamarckian evolution), comparative anatomy, including palaeontology, can be viewed as the direct predecessor of phylogenetic systematics.]

Regan (1909) included hiodontids within his 'Notopteroidei', a group of 'Isospondyli' of equal rank to the other members, which included the clupeoids, stomiatoids, osteoglossoids, mormyroids, phractolaemoids, gonorynchoids, and cromerioids. This hypothesis of relationships was influenced by the work of Bridge, Ridewood and others, and was based on 'notopteroids' possessing a 'lateral foramen or cartilaginous area superiorly and a vesicular diverticulum of the air-bladder inferiorly' (Regan, 1909: 77).

Gregory (1933: 168) clearly was influenced by the work of Ridewood (1904a, 1905), although he was confident in the relationship between *Hiodon* and other osteoglossomorphs, stating 'At first sight the skull of *Hyodon* [sic] suggests relationships with that of *Osteoglossum*', and cited similarities, although none specifically, in the pectoral girdle of *Hiodon* and *Osteoglossum*, writing, 'Notwithstanding these and other differences [in the skull] noted by Ridewood, the construction of the pectoral girdle in *Hyodon* [sic] shows the most unmistakable marks of affinity with that of *Osteoglossum*.' Gregory (1933: 167) kept the 'Osteoglossoidae' and 'Mormyroidea' (= *Hiodon* + *Notopterus* + mormyrids) as separate taxa in his 'Isospondyli' and referred to *Hiodon* as 'the least aberrant' member of Mormyroidea.

Jordan (1923) again separated Hiodontidae (including only *Hiodon*) from his 'Osteoglossoidae' (which included all other extant groups currently considered to belong in Osteoglossomorpha, including notopterids and mormyrids), and placed it within 'Clupeoidei', a suborder of 'Isospondyli.' No characters, however, were given to support this grouping. Jordan's (1923) 'Isospondyli' included the families Chanidae, Ancylostylidae, Chirocentridae, †Erythrinolepidae, Pterothrissidae, †Ichthyodectidae, †Saurodontidae, Gonorynchidae, †Notegonidae, Hiodontidae, Clupeidae, Dussumieriidae, Dorosomidae, Engraulidae, Alepocephalidae, Macristiidae, Phractolaemidae, Kneriidae, and Cromeriidae. In his classification, in which families were placed 'in as natural sequence as is possible' (Jordan, 1923: 79), Hiodontidae is listed between †Notogonidae and Clupeidae.

Garstang (1931) defined several new taxonomic groupings (e.g. 'Archicranioti') in his evaluation of teleostean interrelationships (Fig. 1B). Relevant to this discussion is his 'Osteoglossi', which included the 'Hyodontoidae' (= Hiodontidae, Notopteridae and Osteoglossidae), 'Mormyroidei' (= *Mormyrus*, *Gymnarchus* and *Pantodon*), 'Elopoidei' (= *Megalops* and *Albula*) and 'Clupeoidei' (= Clupeidae, Engraulidae, Saurodontidae). 'Osteoglossi' was defined in part based on the presence of teeth on the parasphenoid and gill arches and the presence of 'temporal fossae – often containing air-vesicles' (Garstang, 1931: 256–257).

Berg (1940) grouped Hiodontidae and Notopteridae in the 'Notopteroidei', a suborder of his 'Clupeiformes' on the basis of several primitive and derived characters, such as the possession of a swim bladder–inner ear connection, the absence of supramaxillae, the presence of orbitosphenoid, intercalar, basisphenoid, symplectic and entopterygoid bones, and the fusion of the parapophyses with the vertebral centra. Berg's (1940) 'Clupeiformes' included †Lycopteroidei, †Leptolepoidei, 'Clupeoidei' (including Elopidae, Megalopidae, and Albulidae), †Centrothrissoidei, 'Chirocentroidei' (including †Ichthyodectidae), †Saurodontoidae, 'Chanoidei', 'Phractolaemoidei', 'Cromeroidei', 'Salmoidei', 'Esocoidei', 'Stomatoidei', 'Echondontoidei', 'Opisthoproctoidei', 'Gonorynchoidei', 'Notopteroidei', 'Osteoglossoidae', 'Pantodontoidei' & Anopteroidei. Berg (1940 [1947: 417]) realized, however, that his 'Clupeiformes' was 'an artificial assemblage . . . [that] will be, doubtlessly, divided in many orders.'

Gosline (1960, 1961, 1965) largely followed Berg's classification, and proposed a group that included hiodontids, notopterids, and osteoglossids (Fig. 1C) under Garstang's (1931) name 'Osteoglossi', one of two divisions of his 'Clupeiformes' (= 'Isospondyli'). Gosline's (1960: 361) 'Osteoglossi' was based on the following characters: 'Parasphenoid terminating well short of the posterior end of the basioccipital. Parasphenoid sometimes with lateral processes for articulation with the mesopterygoid; anterior ribs either articulating directly with centra or with strong parapophyses that are fused to the centra; branched caudal rays 16 or fewer.' Gosline (1960, 1961: diagram 4) also commented on the probable relationship between 'Osteoglossi' and Mormyriiformes (Fig. 1C), citing similarities of the caudal skeleton of osteoglossids (e.g. *Heterotis*) and *Mormyrus* and stating 'The gymnarchid-mormyrid stock can be traced back with considerable certainty into the osteoglossid-notopterid group of isospondylous fishes' (Gosline, 1960: 357); the extremely derived nature of the mormyrids, however, was deemed sufficient to separate them (although see Gosline, 1971, which followed the inclusive concept of Greenwood *et al.*, 1966; see below).

McAllister (1968: 45) considered *Hiodon* to belong to a unique group of his 'Clupeiformes', which included the groups †Lycopteroidei, Elopoidei, Albuloidae, 'Clupeoidei', Bathylaconoidei, †Tselfatoidei, †Saurodontoidae, Hiodontoidei, 'Gonorynchoidei', 'Chanoidei', Stomiatoidae, Enchondontoidei, 'Salmonoidei' and Esocoidei. However, no specific relationships were proposed beyond the suggestion that 'the origin of the Hiodontidae appears to lie with the elopoids, albuloids, or clupeoids.' Some of the characters cited by McAllister (1968) are primitive at the level of Teleostei.

Greenwood *et al.* (1966; also see 1967) broke up 'Isospondyli' (roughly equivalent to 'Clupeiformes' of Berg and others) and defined the group Osteoglossomorpha (Fig. 1D) on the basis of two derived characters: the primary parasphenoid tongue bite and 'tendon bones' associated with the ventral portion of the second gill arch skeleton (see discussion of these characters in Hilton, 2001). Greenwood *et al.* (1966) included the fossil group †Ichthyodectiformes within Osteoglossomorpha (Fig. 1D), as did Taverne (1979; see below); †Ichthyodectiformes is currently interpreted by most systematists working on teleosts as a stem-group within Teleostei (e.g. Patterson & Rosen, 1977; Arratia, 1997, 2001; Taverne, 1998). However, all other groups currently recognized as belonging to Osteoglossomorpha were included in this group by Greenwood *et al.* (1966). Although not cladistic in their analysis (e.g. their fig. 1 shows groups derived from other groups), Greenwood *et al.* (1966: 346) did strive to have their classification reflect an hypothesis of phylogeny: 'However, unless one wishes to abandon the principal that taxonomic classification should reflect what can be determined of phylogeny (as some people do), taxa that are obviously polyphyletic [i.e. 'Isospondyli'] must be broken up and a new classification adopted.'

ANALYSES OF OSTEOGLOSSOMORPHA SINCE GREENWOOD *ET AL.* (1966)

Following the English translation and update in 1966 of Hennig's (1950, 1966) *Grundzüge einer Theorie der phylogenetischen Systematik*, the systematic ichthyological community was quick to embrace the logic of his methods for hypothesizing phylogenetic patterns (i.e. cladistics), and the interrelationships of osteoglossomorph fishes were among the first to be analysed using this philosophy (e.g. Nelson, 1968, 1969; see also the preface of Greenwood, Miles & Patterson, 1973, and papers therein). Since Greenwood *et al.* (1966), a monophyletic Osteoglossomorpha has been recognized in nearly all studies (McAllister, 1968 and Shen, 1996 are notable exceptions). Therefore, in this section I will focus on cladistic studies of the interrelationships among the various subgroups within Osteoglossomorpha.

Nelson (1968, 1969: 12), although certainly supporting the inclusion of *Hiodon* within Osteoglossomorpha, conceded that 'Advanced characters [i.e. synapomorphies] indicating a monophyletic origin for the Osteoglossomorpha as here conceived are few. The most striking peculiarities found among osteoglossomorphs generally do not occur in *Hiodon*.' Nelson (1969: 13) listed several characters taken from the literature for Osteoglossomorpha, which included 16 or fewer branched caudal fin rays, absence of supramaxillae, and absence of 'lower intermuscular bones' (= the

epipleural series, because all osteoglossomorphs lack this series, at least as ossifications, except *Heterotis*, see Patterson & Johnson, 1995: 20–21). Based on a study of the gill arches of osteoglossomorphs, Nelson (1968) recognized two major subgroups: 'Notopteroidi' and 'Mormyroidei' (Fig. 2A). His 'Notopteroidi' (= Notopteridae + Hiodontidae) shared the presence of a basihyal toothplate that surrounds the basihyal laterally and possesses posteroventral processes. Nelson's 'Mormyroidei' [= (Osteoglossidae) + (Mormyroidea)] was found to share processes of the second ventral gill arch (Nelson did not accept Greenwood *et al.*'s, (1966) statement of homology of these processes and the 'tendon bones' of notopterids; see Hilton, 2001 and Character 45). Nelson (1968) further recognized two clades within Osteoglossidae (Fig. 2A): Osteoglossinae (= *Scleropages* + *Osteoglossum*; these possess an enlarged basibranchial toothplate) and Heterotinae (= *Arapaima* + *Heterotis*; these possess segmentation of the third infrapharyngobranchial). Nelson (1968) was careful to stress that these hypotheses of relationships were based only on the structure of the gill arches, citing the lack of information available for other anatomical systems. However, he reached similar systematic conclusions in a later study that encompassed anatomical evidence from other components of the skeleton (Nelson, 1969).

In contrast to Nelson, Greenwood (1973) proposed that notopterids and mormyrids + gymnarhids were sister groups (= his 'Notopteroidea', Fig. 2B), based on characters of the cephalic sensory canal system (e.g. without pores and gutter-like, temporal lateral-line opens into lateral cranial fenestrae), inner ear morphology (utricle completely separate from the sacculus and lagena) and ventral gill arch musculature (also see Greenwood, 1963, 1970, 1971). His 'Notopteroidea', in turn, was considered to be the sister group to 'Hiodontoidea' (= Hiodontidae + †Lycoperidae; Fig. 2B) based on characters shared by, in particular, hiodontids and notopterids (e.g. intercalar contributes to the hyomandibular facet and the form of basihyal toothplate), as well as the vaguely defined 'osteoglossomorph-type' otophysic connection.

Greenwood's phylogeny was adopted by Lauder & Liem (1983), who also cited the presence of a posterior intermandibularis muscle separate from the interhyoideus muscle as a character uniting notopterids, mormyrids and hiodontids. Greenwood (1971, 1973: 310), however, did not describe this similarity, and stated that '[c]ontrasting with the osteoglossid condition on the one hand and the notopterid-mormyrid condition on the other is that of *Hiodon*. Here the muscle arrangement is little different from that in *Amia* or *Elops*'. Greenwood was referring to the presence of partially fused posterior intermandibularis and interhyoideus muscles (the 'protractor hyoideus complex')

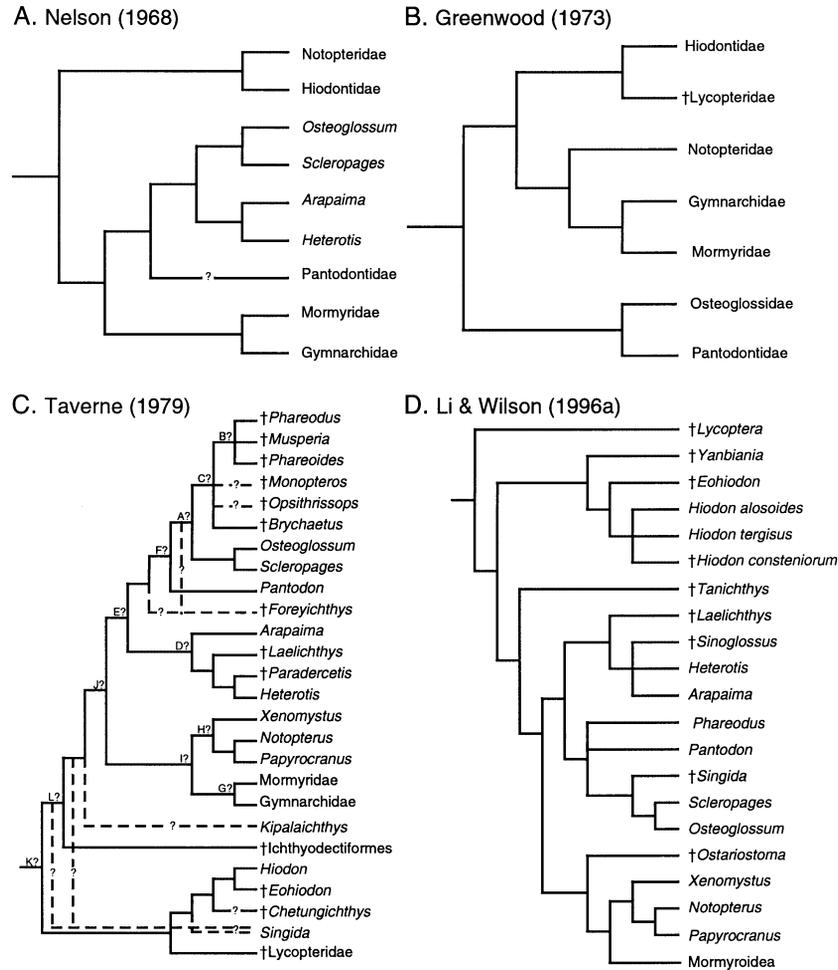


Figure 2. Hypotheses of osteoglossomorph interrelationships, redrawn from: A, Nelson (1968); B, Greenwood (1973); C, Taverne (1979); and D, Li & Wilson (1996a). The letters in Taverne's phylogeny are the ancestral 'forms' that Taverne described in his text. Question marks and dashed lines indicate the author's doubt concerning the placement of a taxon.

found in *Hiodon*, which may become increasingly fused during ontogeny (Hilton, 2001). Therefore, separate posterior intermandibularis and interhyoideus muscles may support the group Notopteridae + Mormyridae (Fig. 2B).

Greenwood (1973) further proposed a possible relationship between Osteoglossomorpha and Clupeomorpha, with this group as the sister group of all other extant teleosts. This interpretation has been rejected by several authors (e.g. Patterson & Rosen, 1977; Arratia, 1997) although the interrelationships of 'lower' teleostean groups remains controversial (see below).

Following a study of the osteology and myology of the head, Kershaw (1976) presented an hypothesis of relationships among the living genera of Osteoglossidae and *Pantodon*. Based on her own work, as well as that of others, she recognized the well accepted group-

ings, namely (*Scleropages* + *Osteoglossum* = Osteoglossinae) and (*Arapaima* + *Heterotis* = Heterotinae). She found the relationships of *Pantodon* to be more difficult to establish, and discussed several similarities that *Pantodon* shares with both Osteoglossinae (e.g. upturned jaws, feeding behaviour, and aspects of cranial musculature) and Heterotinae (e.g. reduced subtemporal fossa, an aveolate swim bladder, and other aspects of cranial musculature). However, she concluded that 'the similarities between the cranial anatomy of *Pantodon* and that of *Osteoglossum* and *Scleropages* point to a closer relationship between *Pantodon* and the Osteoglossinae than between *Pantodon* and the Heterotinae.'

The hypothesis of relationships within Osteoglossomorpha presented by Taverne (1979), although not cladistic (Fig. 2C), followed from the most comprehensive monographic analyses of the skeletal anatomy of

all osteoglossomorph genera presented to date (e.g. Taverne, 1968a,b, 1969, 1971, 1972, 1977, 1978, among many other smaller papers). Taverne's (1979) hypothesis of relationships supported a group that corresponds to Greenwood's (1973) 'Hiodontoidea' (a group that included *Hiodon*, †*Eohiodon*, †*Chetungichthys* and †*Lycoperidae*) as the sister group of all other osteoglossomorph fishes (Fig. 2C). He also found evidence to support the sister-group relationship between notopteroids and mormyroids (Fig. 2C), which he included in the group 'Mormyriformes', and *Arapaima* + *Heterotis* (among living fishes; he placed two fossil taxa – †*Paradercetes kipalaensis* Casier, 1965 and †*Laeliichthys ancestralis* da Silva Santos, 1985 – as more closely related to *Heterotis* than to *Arapaima*; Fig. 2C; see also Taverne, 1979). [The published description of †*Laeliichthys* evidently reports several features that cannot be confirmed on the known specimens (P. Brito, pers. comm., 2001)]. Taverne (1979) found that *Pantodon*, the only member of the family Pantodontidae, was the sister group to Osteoglossidae (Fig. 2C), which included most other osteoglossomorphs. He divided the family Osteoglossidae into two subfamilies (Fig. 2C): Osteoglossinae (= *Scleropages* + *Osteoglossum*) and †Phareodontinae (including genera such as †*Phareodus*, †*Brychaetus* and †*Musperia*).

Taverne (1979) had difficulty placing five extinct genera: †*Singida*, †*Kipalaichthys*, †*Foreyichthys*, †*Monopteros* and †*Opsithrissops*. In particular, I will discuss his problem placing †*Singida jacksonoides* Greenwood & Patterson, 1967, an edentulous fossil osteoglossomorph from the Eocene of Tanzania. [Wilson & Murray (2001), in an abstract for a presentation at the 2001 meeting of the Society of Vertebrate Palaeontology, reported the discovery of new specimens of †*Singida* from Mahenge, Tanzania.] Taverne (1979) thought that †*Singida* may be related to Hiodontiformes (Fig. 2C), based in part on the structure of its caudal skeleton, which he believed to be derived from the condition of *Hiodon* (see his fig. 6). Alternatively, he thought that †*Singida* could be the sister group of 'Mormyriformes' + 'Osteoglossiformes' (Fig. 2C). Taverne (1979) also included †Ichthyodectiformes nested within osteoglossomorphs, above the level of Hiodontiformes; by 1998, Taverne (1998) agreed with Patterson & Rosen (1977) and others (e.g. Arratia, 1997, 1999) that †Ichthyodectiformes constitute a stem-group of Teleostei. For a complete discussion of this work, including characters supporting each node, see Taverne's (1979: 72–98) summary of his interpretations.

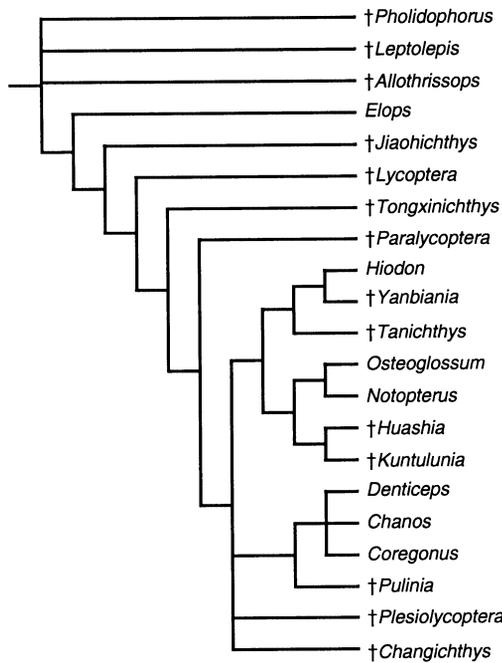
Li & Wilson (1996a) broke new ground with the publication of the first computer analysis of osteoglossomorph interrelationships (Fig. 2D). Several other papers by these authors and colleagues were also published (Li & Wilson, 1994, 1996a,b; Li, 1994a,b, 1996;

Li *et al.*, 1997a,b). The phylogeny proposed by Li & Wilson (1996a) places †*Lycoptera* Müller, 1848 as the sister group of all other osteoglossomorphs (Fig. 2D). This placement differs from the hypothesis that †*Lycoptera* is the sister group of Hiodontidae (e.g. Greenwood, 1970, 1973; Taverne, 1979, 1998; see Fig. 2B, C). Li & Wilson (1996a) also suggested that Hiodontiformes is the sister group of all other living osteoglossomorph fishes, as first suggested by Taverne (1979; see Fig. 2C). Another phylogenetic interpretation that resulted from Li & Wilson's (1996a) analysis was the hypothesis of a sister-group relationship between †*Ostariostoma* Schaeffer, 1949 and Notopteridae + Mormyridae. Grande & Cavender (1991) redescribed †*Ostariostoma*, a small fossil known from a single specimen from the Upper Cretaceous of Montana, and suggested that it was an osteoglossomorph possibly related to Hiodontidae, rather than the clupeoid as it was originally described (Schaeffer, 1949). Because †*Ostariostoma* was interpreted as the only North American representative of an otherwise Old World group (African and Asian), Li & Wilson's (1996a) placement of this taxon has great implications for the analysis of osteoglossomorph biogeography.

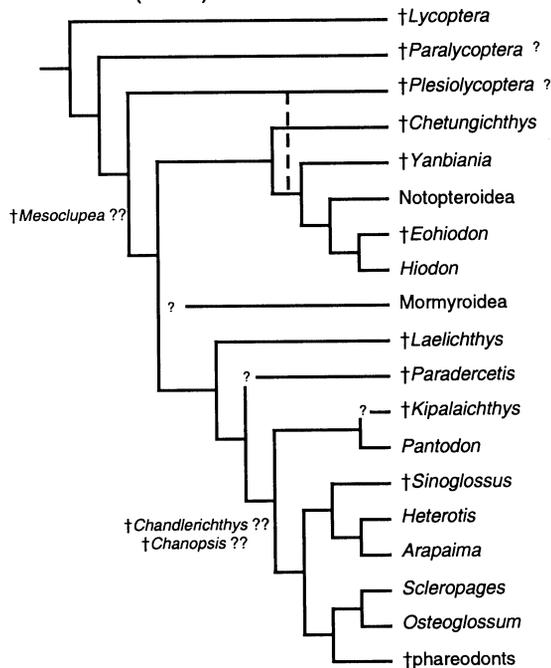
Two other analyses of osteoglossomorph interrelationships were published in 1996. Bonde (1996) examined the relationships and temporal distribution of osteoglossids. Although he offered no data matrix or specific characters supporting his hypothesis (Fig. 3B), he presented a phylogeny (Bonde, 1996: fig. 4) that showed: (1) †*Lycoptera* forming the sister-group of all other osteoglossomorphs; (2) a group containing Notopteridae + *Hiodon*; (3) the position of Mormyridae uncertain; and (4) *Pantodon* forming the sister group to Osteoglossidae. Shen (1996), who examined the characters of Osteoglossomorpha proposed by Patterson & Rosen (1977) and provided an original data matrix, concluded that †*Plesiolycoptera*, †*Toxinichthys*, †*Lycoptera*, and †*Jiaohichthys*, which are typically regarded as osteoglossomorphs (e.g. Chang, 1999), were basal teleosts outside of Osteoglossomorpha (Fig. 3A).

Recently, Taverne (1998) revisited the interrelationships of Osteoglossomorpha in his review of the morphology of the fossil osteoglossomorphs from the Eocene deposits of Monte Bolca, Italy. His conclusions largely agree with Li & Wilson (1996a) in terms of relative relationships of living groups (i.e. the relationships of families of living osteoglossomorphs are consistent between the two analyses), but the position of nearly every fossil taxon is different (Fig. 3C). Taverne (1998) described 344 characters in his analysis (which was not computer-based), although, as Cavin & Forey (2001) pointed out, some of these characters are in fact reversals of characters that he used

A. Shen (1996)



B. Bonde (1996)



C. Taverne (1998)

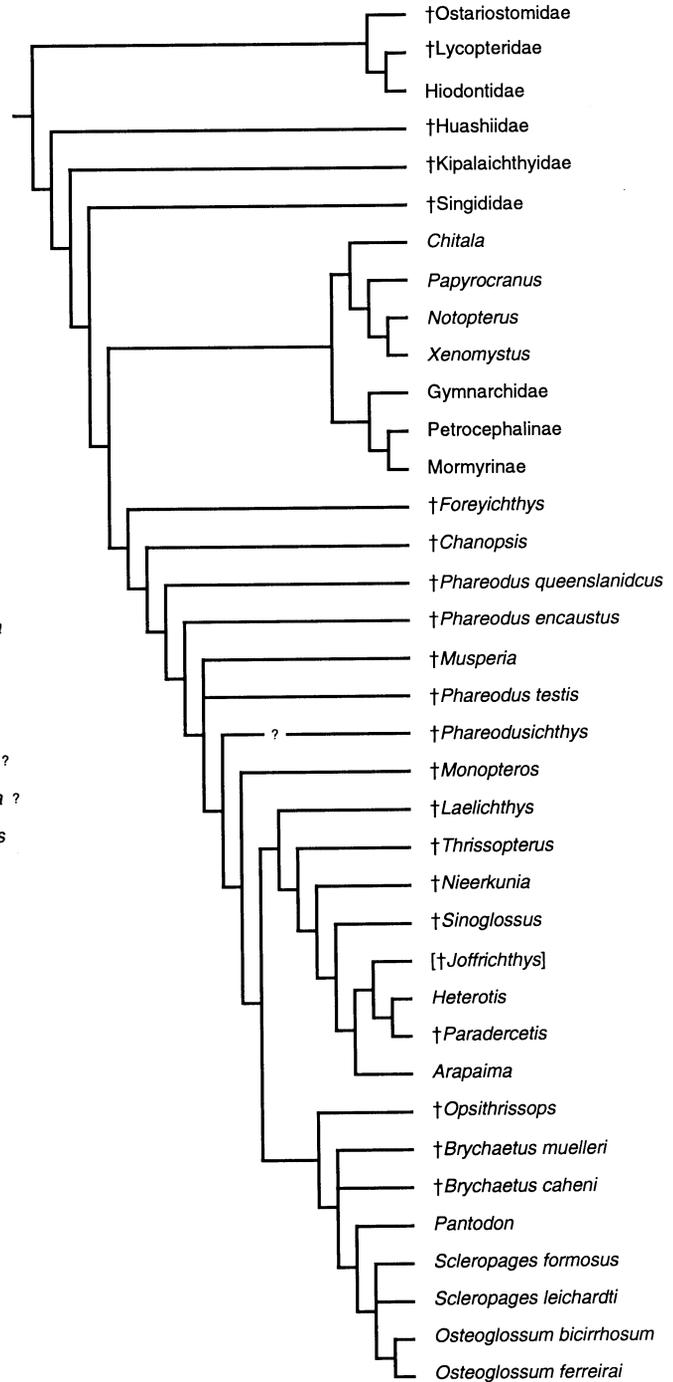


Figure 3. Hypotheses of osteoglossomorph interrelationships, redrawn from: A, Shen (1996); B, Bonde (1996); C, Taverne (1998). Question marks and dashed lines indicate doubt concerning the placement of a taxon. Note that Shen's (1996) hypothesis places several fossil taxa that are commonly regarded as osteoglossomorphs outside the group (e.g. †*Jiaohichthys*, †*Lycoptera*, †*Tongxinichthys* & †*Plesiolycoptera*). Taverne's (1998) hypothesis resulted from analysis of 344 characters, although these were presented as a list rather than in the form of a data matrix, and some characters were reversals of others (see Cavin & Forey, 2001). Note that Taverne (1998) considered †*Brychaetus* to be distantly related to †*Phareodus* (contrary to Li *et al.*, 1997a), and he considered both genera to be paraphyletic. Contrary to Li & Wilson (1996a), Taverne (1998) considered †*Ostariostoma* and †*Lycoptera* to be closely related to the hiodontids, †*Singida* to be relatively basal, and the monophyly of *Scleropages* to be uncertain.

to define other groups. A full review of Taverne's (1998) characters is beyond the scope of the present paper, although it will be important to incorporate his observations into future analyses of osteoglossomorph interrelationships.

Cavin & Forey (2001) also recently reviewed the skeletal anatomy of osteoglossomorphs in a description of new specimens of †*Palaeonotopterus greenwoodi* Forey, 1997) from the Early Cretaceous Kem Kem Beds of Morocco (see also Taverne & Maisey, 1999; Taverne, 2000a). Both Forey (1997) and Taverne & Maisey (1999) concluded that †*Palaeonotopterus* was the sister group of all other notoapterids. Based on this new material, Cavin & Forey (2001) described several mormyroid-like characters of the skull and pectoral girdle (the only portions of the skeleton of †*Palaeonotopterus* that are known). In doing so, these authors provided a detailed review of cranial and pectoral girdle anatomy of osteoglossomorphs, clarified the definition and distribution of several characters used by both Li & Wilson (1996a) and Taverne (1998), and described several new characters of notoapterids and mormyrids; some of these will be discussed below in the character analysis. Cavin & Forey (2001) and Taverne (2000a) both suggested that the parasphenoid dentition of †*Palaeonotopterus* resembles that of some species of †*Plethodus* (e.g. †*Plethodus libycus*, which Taverne, 2000a synonymized with †*Palaeonotopterus*), whereas other species of †*Plethodus* are not as similar (e.g. †*Plethodus oblongus*, which is known from cranial material as well as toothplates); the genus †*Plethodus* was recently revised by Taverne (2000b).

A molecular-based phylogeny of all living osteoglossomorphs has yet to be published. In an analysis of elopomorph phylogeny using both morphological and molecular data (both mitochondrial – 16S and 12S rRNA – and nuclear – 18S rRNA – data were analysed), Forey *et al.* (1996) included three osteoglossomorphs (*Hiodon alosoides*, *Osteoglossum ferreirai*, and *Petrocephalus* sp.) in their study. They found Hiodontiformes (*Hiodon*) to be the sister group of Osteoglossidae (*Osteoglossum*) + Mormyridae (*Petrocephalus*), which is consistent with the results of Li & Wilson's (1996a) morphological analysis. Several morphological (e.g. Benveniste, 1994) and molecular (e.g. Alves-Gomes & Hopkins, 1997; Alves-Gomes, 1999; Sullivan *et al.*, 2000) analyses have focused on the phylogenetic relationships within Mormyriiformes, a systematic problem that had not been critically addressed since Taverne (1972). Although some of the groups and relationships proposed by Taverne (1972) are upheld by the molecular evidence (e.g. that *Gymnarchus* is the sister group to Mormyridae and that Mormyridae can be divided into two monophyletic subfamilies: Petrocephalinae and Mormyrinae), several of Taverne's genera within Mormyrinae are not monophyletic as

currently constituted (Sullivan *et al.*, 2000). The phylogenetic relationships of these fishes are among the most problematic of any subgroup within Osteoglossomorpha, and most authors of morphologically based cladistic analyses (e.g. Li & Wilson, 1996a) have sidestepped the issue and coded for a supraspecific taxon 'Mormyroidea', merely assuming the monophyly of this group. Alves-Gomes (1999) suggested the need for more study of the possible paraphyly of Notopteriiformes, citing evidence from Braford (1982, 1986) and Benveniste (1994) that the African notoapterids (*Xenomystus* and *Papyrocranus*) are more closely related to the mormyroids than they are to the Asian notoapterids (*Chitala* and *Notopterus*). There is little compelling evidence for this hypothesis. Braford (1986: fig. 7), for example, merely offered the paraphyly of Notopteriidae to be one possible explanation for the distribution of electroreception within mormyroid and notoapteroid osteoglossomorphs, rather than argue that this was the most plausible phylogeny in conjunction with other available data. *Xenomystus* and *Papyrocranus* share the presence of ampullary electroreceptors with mormyroids, but these organs are absent in the Asian notoapterids. Although a detailed morphological study of mormyrid systematics is beyond the scope of the present study, I include three mormyrid genera in my analysis, with the caveat that future work on the anatomy and systematics of Mormyridae is necessary.

Kumazawa & Nishida (2000) recently analysed the complete sequence of two genes (ND2 and cytochrome *b*) for representatives of most clades of Osteoglossomorpha (*Hiodon* is a very noticeable and surprising absence and it is unfortunate that only two genera of Mormyriiformes were included in their study). Their tree suggests that mormyroids and osteoglossoids are sister groups, and that *Pantodon* is sister group of the notoapterids, a pattern not found in any morphological analyses (although when all fossils are removed from the present analysis, the clade *Pantodon* + Notopteriidae is recovered in some of the most parsimonious trees; see below). It is interesting that Patterson (1994: 75) stated 'the problematic Recent member of the group is not *Hiodon*, but the African butterfly fish, *Pantodon*, which can be placed either with the osteoglossoids (Gondwanan), with the notoapteroids (Africa + S. E. Asia) or as the sister group of both in parsimony trees that differ in length by no more than 1%.' Only a Neighbour-joining tree was presented by Kumazawa & Nishida (2000), although maximum parsimony, Neighbour-joining and maximum likelihood analyses were performed. These authors noted that the results of the three methods largely agreed, with the exception of relative position of the mormyroids, notoapteroids and osteoglossoids, although it is unclear which of the other methods (par-

simony and likelihood) produced which result. Kumazawa & Nishida (2000) had a specific agenda in mind with their analysis (i.e. they sought to establish a molecular clock in order to propose a biogeographical model to explain the distribution of the genus *Scleropages*, which crosses Wallace's line), and examining the relationships among osteoglossomorphs was only one part of their study. Their conclusions included the suggestions that: (1) the divergence of osteoglossids, mormyrids and notopterids occurred during the Permian or Triassic; (2) that the split between *S. formosus* (Asian arowana) and *S. leichardti* + *S. jardini* (Australian arowanas) occurred during the Early Cretaceous, which was 'much deeper than [they] expected from the fact that they were classified within the same genus', in contrast to 'the divergence between two *Osteoglossum* species [which] is reasonably shallow in light of their classificatory status' (Kumazawa & Nishida, 2000: 1872–1873). This led the authors to comment on 'the exceptionally high morphological conservatism among the *Scleropages* species' (Kumazawa & Nishida, 2000: 1873). Although these authors do allow that 'taxonomic ranks should not be determined from molecular divergence values only', they miss a more fundamental issue, namely that *differences*, molecular or morphological, should have no bearing on whether or not taxa are classified in a single genus, but rather this must be supported by shared *similarity*.

Using the observation that all osteoglossomorphs they studied (*Pantodon*, *Xenomystus*, *Gnathonemus*, *Chitala* and *Osteoglossum*) except for *Pantodon* have the 'salmon' form of gonadotropin releasing hormone (sGnRH), O'Neill *et al.* (1998) suggested the paraphyly of osteoglossomorphs (see their fig. 6), in that all osteoglossomorphs except for *Pantodon* were considered to be more closely related to other teleosts than to *Pantodon*. There are problems with their conclusions. Their cladogram, described as an 'hypothetical cladogram' is said to be based on de Pinna (1996) and Lauder & Liem (1983), except for the position of eels and *Pantodon*, which were modified to fit their data. This is unacceptable, as it amounts to the creation of a phylogenetic hypothesis based on this single character (i.e. the form of GnRH). In their 'cladogram' they depicted Hiodontidae and Gymnarchidae (not included in their analysis of GnRH) to be sister groups, although none of the sources they cite show such an arrangement. Furthermore, Nelson (1994) and de Pinna (1996: fig. 1) made no attempt to resolve the relative position of elopomorphs and osteoglossomorphs, despite being cited by O'Neill *et al.* (1998: 423) as having placed eels 'both after (Lauder and Liem *et al.* [sic], 1983b [1983]; Nelson, 1994) and before (de Pinna, 1996) the bony tongue fishes.' These authors justified their claim of osteoglossomorph paraphyly in their text (p. 424), contending that 'analysis of

anatomical characteristics (Li & Wilson, 1996[a]) and spermatozoal morphology (Jamieson, 1991) has [also] placed the butterfly fish [*Pantodon*] as an outlying member of the bonytongue fishes', concluding that 'the presence of mGnRH ['mammalian' GnRH – the plesiomorphic condition] in the butterfly fish is consistent with a unique status.' *Pantodon* is indeed a highly derived taxon (Patterson, 1994). However, it should be noted that Li & Wilson (1996a) have *Pantodon* nested deeply within Osteoglossomorpha (as have all authors), and it is more parsimonious to interpret the presence of mGnRH as a secondary condition (i.e. a reversal). The finding that Osteoglossomorpha (except *Pantodon*) possesses the same form of GnRH as other teleosts studied to date except for Elopomorphs (or at least eels) is interesting and may be informative in resolving higher taxonomic questions (see below). However, this character must be evaluated in analyses with other data.

Al-Mahrouki *et al.* (2001) also used molecular techniques to approach relationships within Osteoglossomorpha. As in O'Neill *et al.* (1998), there are several misrepresentations of the literature. For example, they claim that Arratia (1991) suggested that osteoglossomorphs and elopomorphs were sister groups (this is incorrect; see Arratia's fig. 29) and that O'Neill *et al.* (1998) supported a close relationship between an eel and an osteoglossomorph (*Pantodon*) – no mention is made of the other osteoglossomorphs included in their analysis or that the only relationship between *Anguilla* and *Pantodon* was based on symplesiomorphy. Al-Mahrouki *et al.*'s (2001) analysis of the sequences of preproinsulin cDNAs from five osteoglossomorphs (*Osteoglossum*, *Pantodon*, *Hiodon*, *Chitala* and *Gnathonemus*), however, seems more straightforward, although no discussion beyond 'maximum parsimony' was made of their methods of phylogenetic analysis. Of the taxa analysed, they concluded that *Chitala* and *Gnathonemus* are sister groups, and that *Osteoglossum* is the sister group of *Pantodon* + *Hiodon*. The close relationship between *Pantodon* and *Hiodon* has little or no compelling support from any other morphological or molecular analysis performed to date. Their monophyletic Osteoglossomorpha was the sister group of the group (chum salmon (angler fish + Nile tilapia)). This larger group was in turn the sister group of (zebrafish (common carp + white sucker)). Although I am not discounting the value of this data being applied to phylogenetic questions, I am skeptical about Al-Mahrouki *et al.*'s (2001: 57) suggestion that their data have helped in 'resolving the debate over the position of osteoglossomorphs within teleosts', for two reasons. First, they did not include any elopomorph ('key-players' in the debate over basal teleost relationships) in their analysis, and second, this debate is far from being resolved (see below).

PHYLOGENETIC POSITION OF OSTEOGLOSSOMORPHA
WITHIN TELEOSTEI

Much has been written in the last 30 years regarding the interrelationships of the basal radiations of teleostean fishes (see, for example, the exchange between Arratia, 1998 and Patterson, 1998). Although a thorough analysis of the position of Osteoglossomorpha within Teleostei is beyond the scope of this paper, it is important to at least mention some aspects of the current debate and note some references.

In their study of the relationships among teleosts, Greenwood *et al.* (1966) identified four major lineages at the base of teleostean phylogeny: the elopomorphs, clupeomorphs, osteoglossomorphs, and a group formed by all other teleosts. Elopomorphs and clupeomorphs were combined (although not without strong doubt) within their 'Division I' (= 'Taeniopaedia' of Greenwood *et al.*, 1967), osteoglossomorphs (including †Ichthyodectiformes) formed 'Division II' (= 'Archaeophylaces' of Greenwood *et al.*, 1967), and all other living teleosts were grouped in 'Division III' (= 'Euteleostei' of Greenwood *et al.*, 1967). 'Divisions I and II' were both described as being '[f]ishes of ancestry at or near the holostean level of organization' (Greenwood *et al.*, 1966: 350), whereas 'Division III' were described as '[f]ishes mostly of distinctively teleostean level ancestry, only a single basal group [Salmonidae] having obviously holostean affinities' (Greenwood *et al.*, 1966: 351). Greenwood *et al.* (1966: 348) also noted:

'Among the various living primitive groups of teleosteans, only elopids (Division I) and salmonids (Division III) are sufficiently generalized to be suitable morphologically as basal types for the major teleostean radiations. Other primitive groups, for example, the clupeiforms and osteoglossiforms, are too specialized for this role. We realize that elopids, of all teleosts, possess the greatest assemblage of holostean characters. At the same time, we recognize that their larval and other specializations, and the absences of certain snout and jaw structures . . . put at least the living elopids off the main course of teleostean evolution.'

Although noting the plesiomorphic nature of elopids, it is unclear if these authors regarded at least the elopomorph part of their 'Division I' to be basal to all other teleosts because their ideas were presented in an evolutionary diagram showing all groups radiating from a group of 'pholidophoroid holosteans' (Greenwood *et al.*, 1966: fig. 1). The monophyly of all three of Greenwood *et al.*'s (1966) divisions has been cladistically tested. Osteoglossomorphs are no longer thought to include †Ichthyodectiformes (Patterson & Rosen, 1977). Elopomorpha has been suggested to be non-monophyletic (Filleul & Lavoué, 2001). Clupeomorpha has been interpreted as the sister group of

ostariophysan 'euteleosteans' (e.g. Lecointre & Nelson, 1996). Clearly much work remains regarding the systematics within individual subgroups of teleosts, as well as the interrelationships among the subgroups. However, with these groups identified, Greenwood *et al.* (1966) set the stage for future broad-based cladistic studies and discussion of interrelationships among basal teleostean fishes.

Two hypotheses of interrelationships among groups of basal teleosts can be found in *Interrelationships of Fishes* (Greenwood *et al.*, 1973). As noted above, Greenwood (1973) presented the hypothesis that Osteoglossomorpha and Clupeomorpha are sister groups, which in turn forms the sister group to Elopomorpha + Euteleostei. The hypothesis that Elopomorpha and Euteleostei are sister groups was also supported by Forey (1973a) in that he noted similarities between elopids and salmonids, particularly in regards to the ossifications and ligaments of the snout and the caudal skeleton. Nelson (1973a), however, concluded that Clupeomorpha and Euteleostei were sister groups on the basis of lower jaw morphology.

In 1977, Patterson & Rosen published a cladistic analysis combining data from fossil and living teleostean fishes. This study focused on †Ichthyodectiformes, but also included a cladistic treatment of the interrelationships among the groups of 'basal' Teleostei. A major phylogenetic result of this paper was the hypothesis that Osteoglossomorpha is the most basal of any group of teleosts with living representatives, and that Elopomorpha and Clupeomorpha were sequential sister groups to Euteleostei. This hypothesis was quickly adopted and used in widely cited review works (e.g. Lauder & Liem, 1983).

In 1991, Arratia published a cladistic analysis of 67 characters derived from study of the caudal skeleton of 25 fossil and living teleosts (all but three were fossils). This was a significant study because the results suggested that elopomorphs (represented by *Elops*) are more basal than osteoglossomorphs (represented by *Hiodon*, †*Lycopera* and †*Pingolepis*) within Teleostei (although other than *Elops*, non-osteoglossomorph teleosts were represented in her study by only *Salmo* and †*Diplomystus*). In later studies (e.g. Arratia, 1996, 1997, 1999), she increased both the number of taxa and characters (e.g. by 1999, her matrix included 48 taxa and 196 characters), and she still reached the same conclusion. Although these analyses are not error free (e.g. some miscodings and illogical codings; pers. observ.), several other recent studies (e.g. Shen, 1996; Li & Wilson, 1999) also have recovered elopomorphs as the most basal group of living teleosts (i.e. the living sister group of all other living teleosts). In other recent studies, however, Patterson & Rosen's (1977) hypothesis has been upheld (e.g. Forey *et al.*, 1996; Taverne, 1998; Inoue

et al., 2001) or even new hypotheses presented (e.g. Elopomorpha + Osteoglossomorpha; L   *et al.* 1993).

Most studies have focused primarily on interrelationships within one of the subgroups of teleosts, and therefore the characters used to establish relationships outside of the in-group are not well sampled. For example, in his study Taverne (1998: fig. 21) concluded that osteoglossomorphs are more basal than elopomorphs, although there are no characters indicated on his cladogram to support this interpretation. Also, often these studies included one or at most a few taxa as exemplars of the subgroups, thereby falling victim to poor taxon sampling (e.g. L   *et al.*, 1993 used only *Anguilla* as a representative elopomorph). Studies of the interrelationships of 'basal' groups of teleosts likely will always be plagued by issues of taxon sampling and character incorporation. Also, one of the difficulties surrounding, in particular, the placement of Osteoglossomorpha within the phylogeny of teleostean fishes may lie in the fact that the skeleton of the majority of osteoglossomorphs (including that of most well preserved fossils) is extremely derived, thereby masking characters that are useful in resolving this polytomy. Similar situations can be found in broad-scale studies of other groups in which the living members are highly derived (e.g. position of lungfishes within Sarcopterygii; see Rosen *et al.*, 1981; Forey, Gardiner & Patterson, 1991).

MATERIAL AND METHODS

SPECIMEN PREPARATION AND STUDY

Specimens examined during this study consisted of museum specimens that were already prepared, newly prepared material, and newly acquired specimens. Some specimens stored in alcohol were cleared-and-stained for bone and cartilage following a protocol modified from Dingerkus & Uhler (1977) and Hanken & Wassersug (1981). Skeletons studied also included dry specimens prepared with dermestid beetles. Fossils were either prepared mechanically, as latex peels or with acid (e.g. see Toombs & Rixon, 1959; Grande & Bemis, 1998). Specimens examined for scoring the data matrix are listed below (Specimens Examined).

All illustrations are of the left side, with anterior facing left, unless otherwise noted in the figure or figure caption. Most illustrations are based on camera lucida sketches and were generated electronically using Adobe Illustrator. Photographs were taken digitally using a Nikon Cool-Pix 990 camera, either with its built-in lens or mounted on a Wild M400 Photomakroskop dissection microscope equipped with both substage illumination and fibre optic lights. Some photographs were taken with 4 × 5 inch black and white

Polaroid film, and were scanned and contrast and brightness were adjusted using Adobe Photoshop.

SYSTEMATIC METHODS

All characters included in the data matrix (Appendix 1) were scored from first-hand observation of specimens. In my discussion of characters, which are listed in Appendix 2, I include published information on taxa that were not included in my analysis. If a particular character for a particular taxon is not illustrated in the character discussion, then a reference to an illustration from the literature is provided (whenever possible). If a figure from the literature was used to illustrate a taxon scored in my matrix, I checked my own specimens to determine the accuracy of the illustration. If there was a discrepancy, I coded the character as polymorphic.

Of the 72 characters analysed, 43 are binary and 24 are multistate. Much has been written on how multistate characters should best be dealt with in phylogenetic analyses (e.g. Lipscomb, 1992; Wilkinson, 1995; Hawkins, Hughes & Scotland, 1997; Strong & Lipscomb, 1999; Forey & Kitching, 2000). For the present study, however, no special methods were used to incorporate multistate characters into the analysis (i.e. I used the pure multistate method of Forey & Kitching, 2000). Forey & Kitching (2000: 62–63) noted numerous disadvantages to this method, ranging from philosophical (e.g. 'Linking together different observations [into a single character] denies the possibility of testing propositions of homology between the states because the test of homology involves comparing one row of data with another') to the practical (e.g. in the cost of steps in tree reconstruction). As noted at the beginning of this paper, my main purpose is to illustrate and describe the variation among osteoglossomorph fishes for those morphological characters that have been extensively cited but never fully explored in all taxa. Ease and clarity of discussion of characters related to specific anatomical elements, in my opinion, is best achieved by defining and describing pure multistate characters. However, I also coded the data matrix in both binary (absent/present) and contingent coding (Forey & Kitching, 2000) and found the same trees in the case of contingent coding, or, in the case of binary coding, similar trees of which the strict consensus is consistent with that of my multistate trees. Future manipulation of the data matrix, however, including employing different coding strategies for multistate characters, will be important. In addition to potentially changing the topology or number of trees obtained (although not a result for this data set), the type of character coding that is employed also will have dramatic effect on the optimization of characters and, ultimately, on theories of character evolution;

these also must be considerations in future work. All characters were run unordered and of equal weight.

When I detected intrataxonomic variation (e.g. individual variations or generic-level polymorphism), these so-called polymorphic characters were scored as such (indicated in my matrix with a 'P'). Other methods for dealing with polymorphic data have been proposed (e.g. Campbell & Frost, 1993; Mabee & Humphries, 1993; Kornet & Turner, 1999; Wiens, 1999, 2000, 2001). The method employed here is not perfect (see criticisms in the papers cited above), but it does not presume that polymorphisms observed in two groups are homologous, as is the case in coding strategies that score polymorphisms as a distinct character state (e.g. 'scaled' and 'unscaled' methods of Campbell & Frost, 1993). 'Frequency' methods (e.g. Wiens, 1999, 2000), although superior in some regards (e.g. a variation found in only 5% of a sample of specimens is not treated the same as a variation found in 95% of specimens), are very sensitive to the sample size of specimens examined, which may not capture the actual level of variation that occurs in a taxon (which is a theoretical concern for any character that is scored). For example, if, after study of a sample of 10 specimens of a taxon, an investigator discovered that one of those specimens possessed a variation, then this would be scored as a polymorphism with a 10% frequency. If a second sample of the same taxon was examined, this time of 100 specimens, and again only a single individual of the sample possessed the variation, it would now be treated as a polymorphism with a 1% frequency, which, given sufficient sample sizes, may be better treated as an anomaly (as in Grande & Bemis, 1998: character 48). Coding characters as polymorphic only recognizes the presence of the polymorphism, and does not assign a level of 'meaning' (i.e. weight) to that variation.

For analyses of the data matrix I used PAUP* 4.0b10 (Swofford, 1998). For creation of the data matrix and postanalytical study of character distribution, I used MacClade 4 (Maddison & Maddison, 2000). Trees were generated using the heuristic search option of PAUP* with the initial tree obtained through stepwise addition and *Elops* used as the reference taxon. Tree-bisection-reconnection (TBR) was employed as the branch-swapping algorithm. In Results (Character Optimization and Node Support), I present the character support for nodes of my resulting two trees under accelerated transformation (ACCTRAN) optimization (as opposed to delayed transformation, or DELTRAN). I favour this optimization because it favours loss of complex structures, rather than independent gains (Kitching *et al.*, 1998), although I made note of the characters that support a node no matter which optimization method (ACCTRAN or DELTRAN) is employed.

SPECIMENS EXAMINED

The focus of this study is the morphology and interrelationships of osteoglossomorphs, rather than the position of osteoglossomorphs within teleosts. In other words, I am not testing the monophyly of Osteoglossomorpha; rather, I am concerned with the character evidence for the various hierarchical levels within Osteoglossomorpha. I scored the data matrix for 19 genera (several are monotypic) of fossil and living osteoglossomorphs. All extant genera are represented except for *Notopterus* (the only extant notopterid genus excluded), the gymnarchid (a monotypic family) *Gymnarchus*, and the mormyrids *Boulengeromyrus*, *Brienomyrus*, *Genyomyrus*, *Hippopotamyris*, *Hyperopisus*, *Isichthys*, *Ivindomyrus*, *Marcusenius*, *Mormyrops*, *Mormyrus*, *Myomyrus*, *Paramormyrops*, *Pollimyrus*, and *Stomatorhinus*. Elopomorpha, represented by *Elops saurus*, was used as the outgroup. Information for *Elops* was based on study largely of UMA F10255 (425 mm SL), although many other dry skeletons and cleared and stained specimens of *Elops* in the collections at UMass were examined as well. Other outgroup taxa are figured (e.g. the clupeomorph *Alosa*) or discussed, but are included only to allow discussion of various characters (e.g. the temporal fossae); they are not included in the formal analysis.

Below, I list the osteoglossomorph specimens used during the course of this study; references to specimens of taxa outside Osteoglossomorpha are given in the text when relevant. The type of specimen for extant taxa is indicated as an alcohol-stored specimen (a), a dry skeleton (ds) or a cleared and double stained skeleton (c & s). A dagger (†) precedes taxa known exclusively as fossils.

†*Lycoperidae*

†*Lycoptera davidi*: FMNH PF14046; FMNH PF14225; FMNH PF14049; MNHN 1927-13-06 (mass mortality); UMA F10652; UMA F11260 (mass mortality).

†*Lycoptera middendorffi*: BMNH P. 1841; BMNH P.12122; BMNH P.20930.

†*Lycoptera sinensis*: BMNH P.7357; BMNH P.7358; BMNH P.28848.

†*Lycoptera wangi*: BMNH P.28847.

Hiodontidae

Specimens listed in Hilton (2002).

†*Ostariostomidae*

†*Ostariostoma wilseyi*: PU 14728 (latex peel of holotype and only known specimen). Note: The single taxon in this monotypic family is treated as a plesion within Osteoglossiformes in my classification.

Mormyridae

Campylomormyrus rhynchophorus: MCZ 50166 (2 c & s), MCZ 50492 (1 c & s).

Campylomormyrus tamandua: FMNH 55300 a & b (2 c & s); FMNH 51337 (1 ds).

Gnathonemus petersii: UMA F11267 (1 ds); UMA F11327 (1 c & s).

Myomyrus macrodon: MCZ 50218 (19 a, 2 c & s).

Petrocephalus simus: MCZ 50113 (17 a, 2 c & s).

Notopteridae

Chitala sp. UMA F10341 (1 c & s); UMA F10342 (1 c & s); UMA F10359 (1 ds); MCZ 156815 (5 a).

Notopterus notopterus: MCZ 52370 (19 a, 3 c & s).

†*Notopterus primaevus*: BMNH P.47512 (holotype).

†*Palaeonotopterus greenwoodi*: BMNH P.64799; BMNH P.65643. Note: The only known specimens of †*P. greenwoodi* consist of the braincase, portions of the pectoral girdle and fragments of the anterior vertebral column. Therefore, many characters (i.e. almost all post cranial characters) are coded as unknown due to lack of preservation for this taxon.

Papyrocranus sp. MCZ 54925 (1 c & s).

Xenomystus nigri: FMNH 69494 (1 c & s); UMA F11326 (1 c & s).

Osteoglossidae

Arapaima gigas: FMNH 85741 (1 ds); FMNH 97450 (5 c & s); FMNH 99286 (1 ds); FMNH 72733 (1 ds); MCZ 153736 (1 partial ds – branchial arches and ventral hyoid arch); MCZ 88951 (1 a); MCZ 156812 (1 a); UMA F10355 (1 partial ds, neurocranium); UMA F10349 (1 ds); UMA F11261 (1 c & s) UMA F11263 (1 ds).

†*Brychaetus muelleri*: BMNH P.3893 (holotype, head and anterior body); BMNH P.28424; BMNH P.39699 (oral jaws only).

Heterotis niloticus: MCZ 50959 (1 partial ds – skull and pectoral girdle); UMA F10653 (1 c & s).

†*Joffrichthys* sp. FMNH PF12171a & b (latex peels of head and pectoral girdle).

†*Joffrichthys symmetropterus*: UALVP 23705 (holotype).

Osteoglossum bicirrhosum: FMNH 109232 (6 a, 2 c & s); UMA F10335 (1 ds); UMA F10336 (1 c & s); UMA F10160 (1 ds).

Osteoglossum sp. MCZ 99472 (1 a), MCZ 12861 (1 a), MCZ 156813 (2 a).

Pantodon buchholzi: FMNH 63752 (3 c & s); MCZ 156814 (3 a); UMA 11264 (1 c & s); UMA F11265 (1 ds).

†*Phareodus encaustus*: UMA F10155.

†*Phareodus testis*: BMNH P.64636; FMNH PF12411; FMNH PF11943; FMNH PF10627; FMNH PF25014; UMA F11332.

Scleropages formosus: FMNH uncatalogued specimen (1 c & s; in Department of Geology); UMA F11266 (1 ds).

Scleropages jardini: UMA F11325 (1 c & s).

Scleropages leichardti: BMNH 6780 (1 partial ds – skull only).

†*Singida jacksonoides*: BMNH P.42623 (holotype); BMNH P.63333 (referred to as PJK in Greenwood & Patterson, 1967).

ABBREVIATIONS USED IN FIGURES AND TEXT

ANATOMICAL ABBREVIATIONS

abtp	anterior basibranchial toothplate
af	auditory fenestra
ah	anterior head of the hyomandibula
ahp	anterior process of the hyomandibula
ang	angular
ang-rar	fused angular and retroarticular
ao	antorbital
ap	autopalatine
ar	articular
arp	ascending ramus of the parasphenoid
ascu	anal 'scutes'
aupr	autogenous process associated with basibranchial2
bb	basibranchial
bh	basihyal
bhtp	basihyal toothplate
bo	basioccipital
bop	basioccipital process of the parasphenoid
br	branchiostegal
c	vertebral centrum
cb	ceratobranchial
cb5-acc	accessory gill arch cartilage (possible subdivision of cb 5)
cha	anterior ceratohyal
cl	cleithrum
cm	coronomeckelian
co	coracoid
d	dentary
dcr	distal caudal radial
dpl	dermopalatine
dsp	dermosphenotic
eb	epibranchial
ecp	ectopterygoid
enp	entopterygoid
enptp	entopterygoid tooth patch
ep	epural
epbo	epibranchial organ
epbof	foramen in the epibranchial organ
epo	epioccipital
es	extrascapular
exo	exoccipital

fmc	Meckelian fossa
fr	frontal
g	gular
gr	gill raker
h	hyomandibula
hb	hypobranchial
hh	hypohyal
hmf	foramen in the hyomandibula for the anteroventral lateral line nerve
hp	opercular process of the hyomandibula
hy	hypural
ic	intercalar
io	infraorbital
iocn	infraorbital sensory canal
iop	interopercle
iph	infrapharyngobranchial
iph3-md	medial division of infrapharyngobranchial3
lptp	lower pharyngeal toothplate(s)
mcp	opening of the mandibular sensory canal
met	mesethmoid
mpt	metapterygoid
mx	maxilla
n	nasal
nacn	nasal sensory canal
nau	neural arch of ural centrum
nspu	neural spine of preural centrum
nsu	neural spine of ural centrum
obs	orbitosphenoid
op	opercle
otcn	otic sensory canal
pa	parietal
pas	parasphenoid
pastp	parasphenoid tooth patch
pb	pelvic bone (basipterygium)
pbbtp	posterior basibranchial toothplate
pbpt	basipterygoid process of the parasphenoid
pcf	pectoral fin
ph	posterior head of the hyomandibula
phy	parhypural
plf	pelvic fin
pmx	premaxilla
pop	preopercle
popc	opening of preopercular sensory canal
pr	proximal radial of pterygiophore of dorsal or anal fin
prhb2	bony process of basibranchial 2
pro	prootic
ptfr	postfrontal
pto	pterotoc
pts	pterosphenoid
pu	preural centrum
q	quadrate
rar	retroarticular
scu	abdominal scutes
set	supraethmoid
SL	standard length

smx	supramaxilla
soc	supraoccipital
socn	supraorbital sensory canal
sop	subopercle
sor	supraorbital
spo	sphenotic
stcn	supratemporal sensory canal
sym	symplectic
tf	temporal fenestra
u	ural centrum
uh	urohyal
un	uroneural
uptp	upper pharyngeal toothplate
vo	vomer
votp	vomerine tooth patch

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York, NY
BMNH	The Natural History Museum, London
FMNH	Field Museum of Natural History, Chicago, IL
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA
MNHN	Museum Nationale d'Histoire Naturelle, Paris
PU	Princeton University (now deposited at Peabody Museum, Yale University)
TU	Tulane University Fish Collection, Belle Chase, LA
UALVP	University of Alberta (Edmonton) Laboratory for Vertebrate Palaeontology
UMA	University of Massachusetts, Amherst, MA

RESULTS

Analysis of 72 characters (65 parsimony informative) scored in a matrix for 20 taxa (Appendix 1) resulted in two most parsimonious trees, each of 171 steps (Fig. 4); the strict consensus of these two trees is shown in Figure 5. The two fundamental trees differ only in the position of †*Lycoptera*, which is interpreted as either the sister group of all other osteoglossomorphs (consistent with the results of Li & Wilson) or the sister group of †*Eohiodon* + *Hiodon* (consistent with the results of Greenwood and others); the strict consensus tree therefore shows a polytomy between †*Lycoptera*, (†*Eohiodon* + *Hiodon*), and all other osteoglossomorphs (Fig. 5).

The monophyly of Osteoglossomorpha is supported in both fundamental trees (Fig. 4) by three synapomorphies (16 principal branched caudal fin rays, 65[1]; one epural, 68[1]; and a complete neural spine on the first preural centrum, 69[0]). Several homoplastic characters also support the monophyly of Osteoglossomorpha (see below). Two additional characters were

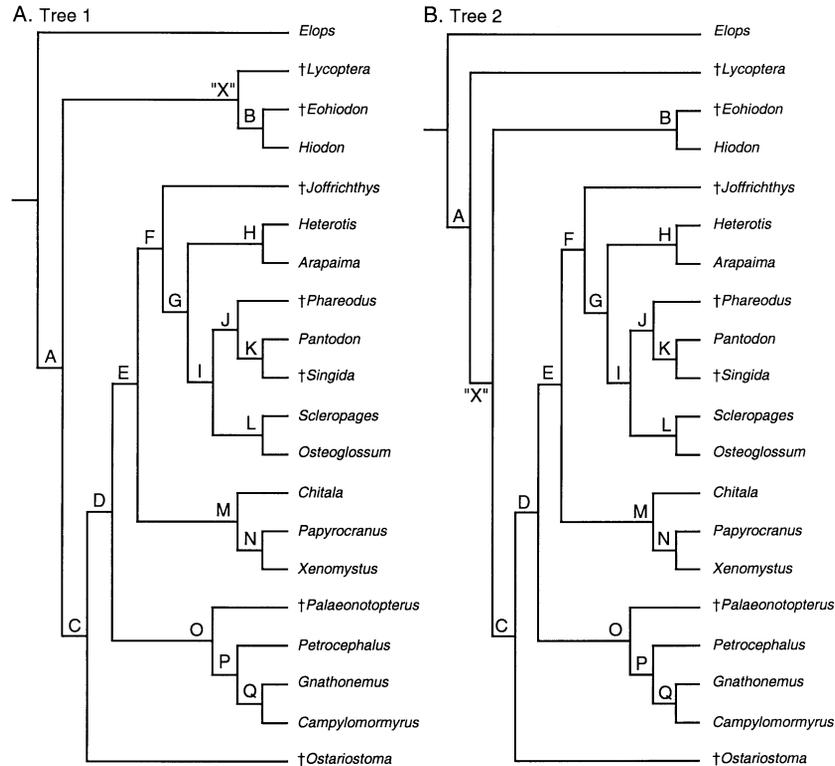


Figure 4. The two fundamental most parsimonious trees resulting from analysis of the data matrix provided in Appendix 1; characters and character states described in text are listed in Appendix 2. The strict consensus is provided in Fig. 5. These trees both have a length of 171 steps, a consistency index (CI) of 0.6433 (0.6139 excluding uninformative characters), a homoplasy index (HI) of 0.3977 (0.3861 excluding uninformative characters), a retention index (RI) of 0.7782 and a rescaled consistency index (RC) of 0.5006. Letters above the nodes correspond to those listed in the text under the heading Character Optimization and Node Support.

recovered as synapomorphies of Osteoglossomorpha (supraorbital bones absent, 20[1]; supramaxilla bone absent, 40[1]) in both trees, but were coded as unknown in †*Lycoptera*.

Although almost completely dichotomous, many nodes of the resulting trees lack much rigorous support. For example, the group †*Lycoptera* (†*Eohiodon* + *Hiodon*), shown in Figure 4A, is supported by eight characters (see Character Optimization and Node Support, below), two of which are synapomorphies (i.e. CI = 1.00; see Table 1). However, both of these characters (posterior fossa of the neurocranium for the hyomandibula formed of the pterotic and intercalar, 27[1]; and postpelvic bone present, 62[1]) are unknown in both †*Lycoptera* and †*Eohiodon*. Also, only three of the homoplastic characters supporting this node (frontal bone less than twice the length of the parietal, 5[1]; nasal bones separated by only the ethmoid bones, 6[1]; medial wall of the Meckelian fossa of the lower jaw absent, 44[1]) could be scored for these two taxa. Therefore, this node, which superficially seems to be

well supported, has over half of that support derived from inference and not from observed data. This situation is common in this study, where a fossil is interpreted as the sister group of a larger clade (e.g. nodes C, F & O of Fig. 4A, B).

The nodes uniting †*Phareodus* (†*Singida* + *Pantodon*) (Node J) and †*Singida* + *Pantodon* (Node K) are also very poorly supported. All characters supporting these nodes are homoplasies (see Character Optimization and Node Support). Additionally, there are many missing data for the two fossil taxa. For instance, three of the six characters supporting Node J could not be scored for both †*Phareodus* and †*Singida*, and the other three could not be scored for one or the other. Additionally, five of the six characters supporting †*Singida* and *Pantodon* (Node K) were scored as unknown for †*Singida*. This emphasizes the need for careful examination of character support and the distribution of missing data given a particular topology, and cautious interpretation of relationships.

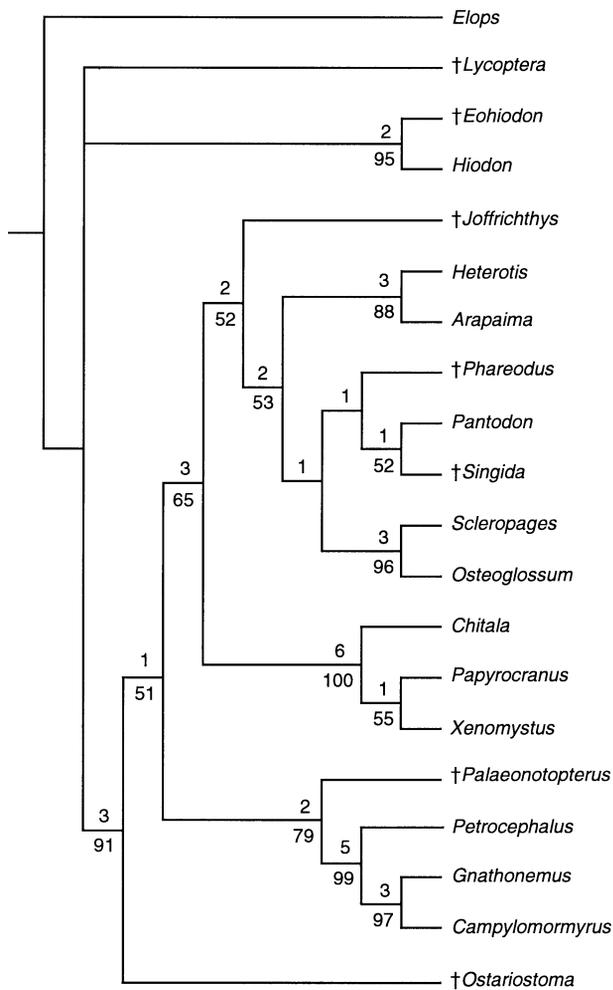


Figure 5. The strict consensus of the two equally parsimonious cladograms shown in Fig. 4. Numbers above the nodes are the Bremer support; numbers below the nodes are bootstrap values (5000 replicates).

Some clades recovered in these trees have never been suggested in previous morphological cladistic analyses. One such example is the sister-group relationship between notopterids and osteoglossids, which is supported by both uniquely derived characters (e.g. extrascapular reduced and irregularly shaped, 2[1], although this is further derived in all osteoglossids; 15 or fewer branched caudal fin rays, 65[2]; one neural spine on preural 1, 67[1]) and homoplastic characters (e.g. nasal bones meet each other in the midline, 6[2]; supratemporal commissure within the parietals, 10[1]; preopercular sensory canal opens through pores dorsally and a groove ventrally, 32[2]; the ascending process of the premaxilla is well developed, 37[0]).

Other nodes, such as the sister-group relationship between †*Palaeonotopterus* and the mormyrids,

although not without support from other analyses (e.g. Cavin & Forey, 2001), are also undoubtedly influenced by the high degree of missing data (e.g. 78% of characters were coded as unknown for †*Palaeonotopterus*). †*Palaeonotopterus*, in fact, may better be treated as an 'inserted' taxon (*sensu* Grande & Bemis, 1998). However, analysis of the data matrix with the exclusion of this taxon had no effect on either the topology or number of trees recovered, so I therefore present its position as recovered in my full analysis.

When all fossils are deleted from the analysis, five most parsimonious trees (154 steps) were recovered (Fig. 6A–E). As in the full analysis, mormyrids are recovered as the sister group of Osteoglossidae + Notopteridae. It is the position of *Pantodon* that changes most dramatically in the trees. In one tree (Fig. 6A), *Pantodon* is the sister group of *Scleropages* + *Osteoglossum*, supported by three synapomorphies (opercle depth to width ratio about two or greater than two, 33[1]; first pectoral fin ray greatly enlarged and extremely long, 61[1]; pelvic bone possesses a thin deep lamella in dorsoventral plane, 63[1]). In two other trees (Fig. 6B, E), *Pantodon* is the sister group of all other osteoglossids, supported by four synapomorphies (shape of extrascapular reduced and tubular, 2[2]; nasal bones flat and broad, 7[3]; palatoquadrate area behind and below the orbit is completely covered by the infraorbitals, 25[1]; basibranchial toothplate and basihyal toothplate are continuous, 49[1]). In the other two trees (Fig. 6C, D), however, *Pantodon* is the sister group of Notopteridae. This grouping is supported by two synapomorphies (median basioccipital process of the parasphenoid, 14[1]; subopercle absent, 35[2]). The strict consensus of the five trees (Fig. 6F) therefore shows a polytomy between *Arapaima* + *Heterotis*, *Scleropages* + *Osteoglossum*, *Pantodon* and Notopteridae. The trees found in the full analysis are consistent with this strict consensus, suggesting that the fossils are not affecting the topology, but rather helping to 'choose' among competing phylogenetic hypotheses.

Figure 7 shows a summary hypothesis of the interrelationships of osteoglossomorph fishes based on the results of this analysis. In this figure, I have collapsed any node that is not supported by at least one synapomorphy (i.e. nodes that are only supported by homoplasy). I show the position of †*Palaeonotopterus* as unresolved because the synapomorphies that support its mormyrid relationship (as recovered in my analysis) were not based on observed data, but rather scored as missing for this taxon. The characters supporting this node that could be scored for †*Palaeonotopterus* were all homoplasies (see next section). The unresolved nodes presented in this tree should be viewed as the source of future areas of research.

Table 1. Summary of the consistency indices for the characters (ch.) supporting the nodes of the trees shown in Figure 4

Node	Tree One (Fig. 4A)			Tree Two (Fig. 4B)		
	No. of ch. with CI = 1.00	No. of ch. with CI < 1.00	No. of ch. with CI < 0.50	No. of ch. with CI = 1.00	No. of ch. with CI < 1.00	No. of ch. with CI < 0.50
A	6	9	2	6	9	3
B	2	0	0	3	3	0
C	6	8	3	6	11	5
D	1	4	2	1	4	2
E	3	4	1	3	4	1
F	4	6	2	4	6	2
G	1	2	0	1	2	0
H	2	8	3	2	8	3
I	2	2	1	2	2	1
J	0	6	3	0	6	3
K	0	8	4	0	8	4
L	1	4	1	1	4	1
M	5	6	3	5	6	3
N	0	2	0	0	2	0
O	2	10	1	2	10	1
P	2	3	2	2	3	2
Q	1	3	1	1	3	2
X'	2	6	1	3	1	1

CHARACTER OPTIMIZATION AND NODE SUPPORT

In this section, I have listed the character changes under ACCTRAN optimization for the two fundamental trees (Fig. 4) resulting from analysis of the data matrix presented in Appendix 1. The letters of the nodes in these lists correspond to those in Figure 4 and the names correspond to those used in Figure 7. Apomorphies for terminal taxa (= genera) are not listed. Characters in bold-face type have a consistency index (CI) of 1.00, which indicates that character is uniquely derived for that node. Characters preceded by an asterisk (*) are unambiguous, in that they support that node no matter which optimization, ACCTRAN or DELTRAN, is employed. In parentheses is the number of the character with its state following in brackets (see Appendix 2). In some instances, there is missing data in a basal taxon for that node, and the interpretation that I present is an artifact of the way in which the computer algorithm treats missing data (i.e. the computer fills in a value for that cell). In such instances, I note this following the character. If the missing data is due to inapplicability or uncertain homology, this is noted as well. Above Node D (i.e. Node D–Q), the character support for the two trees is exactly the same, but it is repeated for completeness. These lists were adapted from the output of the PAUP*

analysis, using the 'list of apomorphies' option under the 'Describe Trees . . .' command.

Tree One (Fig. 4A)

Node A: OSTEOGLOSSOMORPHA

*Temporal fossae present – bordered by the epio-cipital, pterotic, and parietal (1[2]). Unknown in †*Lycoptera*.

*Parasphenoid teeth large and found along the length of the parasphenoid (8[2]).

Supraorbital sensory canal ending in frontal (11[1]).

***Supraorbital bone absent (20[1])**. Unknown in †*Lycoptera*.

*Four bones in the infraorbital series, not including the dermosphenotic or the antorbital, if present (22[1]). Unknown in †*Lycoptera*.

One neurocranial head of the hyomandibula or two heads but they are continuous (28[0]). Unknown in †*Lycoptera*.

*Autopalatine bone absent (31[1]). Unknown in †*Lycoptera*.

Gular bone absent (36[1]).

Ascending process of the premaxilla only slightly developed, if at all (37[1]).

***Supramaxillae absent (40[1])**. Unknown in †*Lycoptera*.

***Epipleural bones absent (56[0])**.

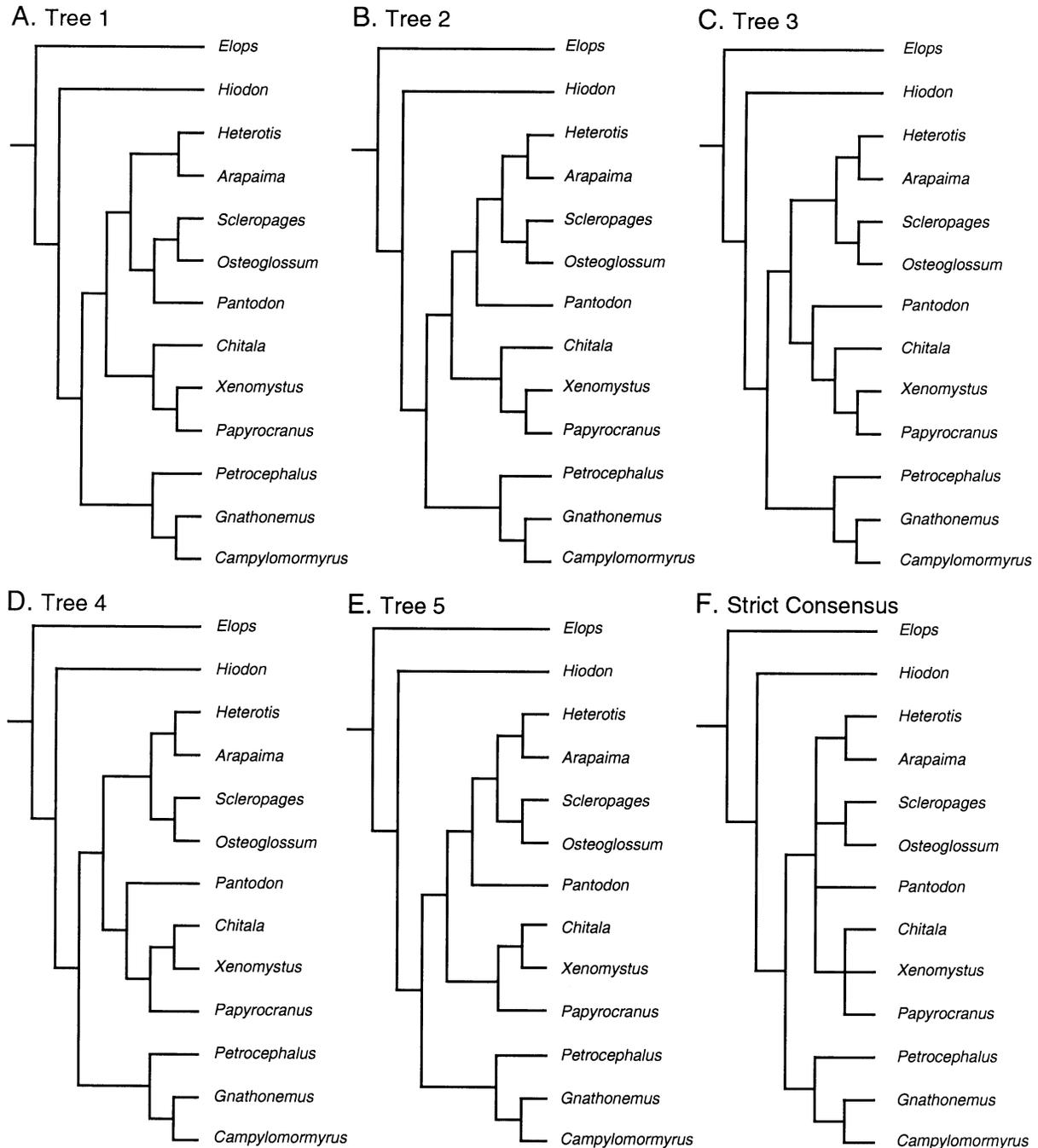


Figure 6. A–E, the five most parsimonious cladograms and F, their strict consensus resulting from analysis of the data matrix in Appendix 1 with the exclusion of all fossil taxa. Note that the strict consensus of these trees (F) is consistent with that for the full analysis (Fig. 5).

*Dorsal arm of the post-temporal bone more than twice as long as the ventral arm (57[1]).

*Sixteen principal branched caudal fin rays (65[1]).

*One epural (68[1]).

*Neural spine on the first preural centrum complete (69[0]).

NODE 'X': †LYCOPTERA + HIODONTIDAE

*Frontal bone less than twice as long as parietal (5[1]).

*Nasal bones separated only by ethmoid bones (6[1]).

Dermosphenotic triradiate (26[1]). Unknown in †*Lycoptera*.

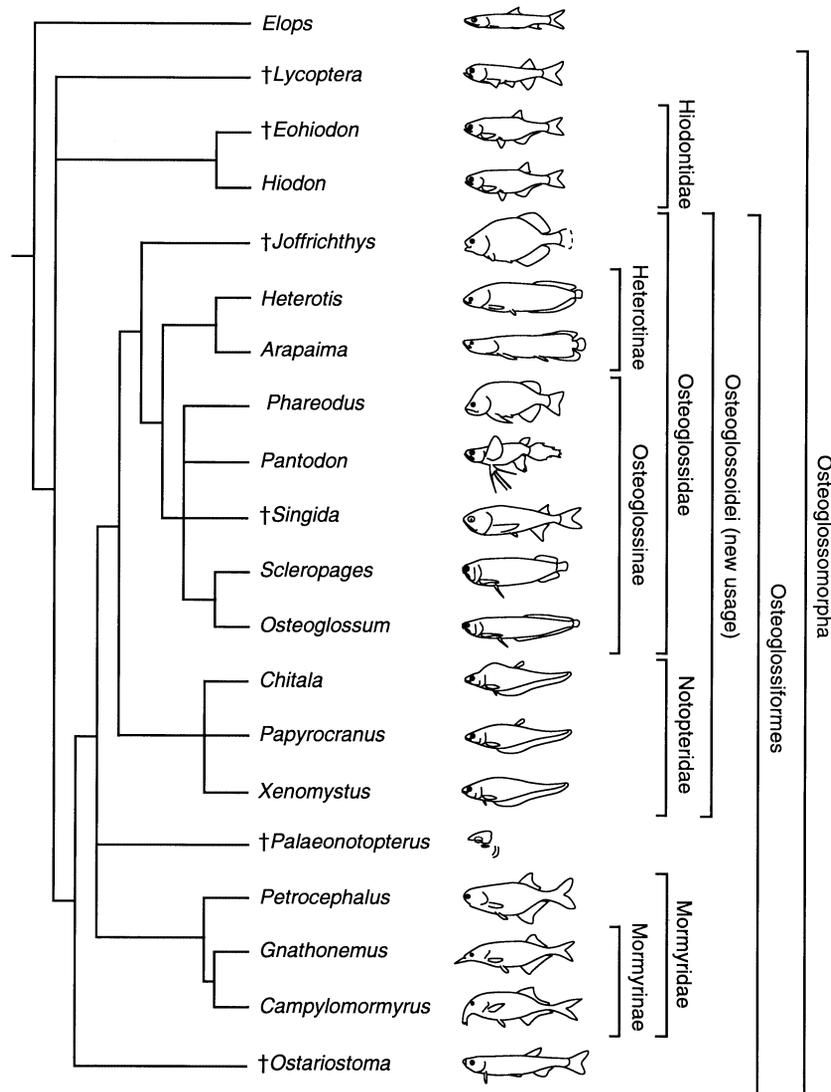


Figure 7. A hypothesis of the interrelationships of the osteoglossomorph fishes based on the results of this analysis (see Figs 4 and 5). In this figure, I collapsed all nodes of the strict consensus tree shown in Fig. 5 that have no synapomorphies or are not supported by observed data (see Character Optimization and Node Support). Some more prominent characters (although not necessarily uniquely derived) supporting the various nodes are provided here. **Osteoglossomorpha:** parasphenoid teeth large and found along the length of the parasphenoid; supraorbital bone absent; four bones in the infraorbital series; supramaxillae absent. **Hiodontidae:** nasal bones tubular and strongly curved; posterodorsal spine on the opercle. **Osteoglossiformes:** bony process on the second hypobranchial; one ossified pair of hypohyals; six or fewer hypurals. **Osteoglossoidae (= Osteoglossidae + Notopteridae):** nasal bones meet each other in the midline; supratemporal commissure passing through the parietals; 15 or fewer branched caudal fin rays; one neural spine on ural centrum 1. **Osteoglossidae:** nasal bones flat and broad; palatoquadrate area behind and below the orbit completely covered by infraorbitals; scales with reticulate furrows over the entire scale. **Heterotinae:** enlarged first infraorbital; posterior bones of the lower jaw all separate; infrapharyngobranchial 3 divided into two elements. **Osteoglossinae:** opercle depth to width ratio about two or greater than two; first pectoral fin ray greatly enlarged and extremely long. **Notopteridae:** autogenous bony elements associated with the second ventral gill arch; abdominal scutes present as paired structures; posterior end of anal fin continuous with caudal fin. **Mormyridae:** proximal tip of infrapharyngobranchial 1 posteriorly directed; cleithrum with a broad medial lamina; scales with both radial and reticulate furrows. **Mormyrinae:** hypohyal greatly reduced in size; basihyal toothplate absent.

Posterior region of the fossa on the neurocranium for the hyomandibula formed of pterotic and intercalar (27[1]). Unknown in †*Lycoptera* and †*Eohiodon*.

Two neurocranial heads of the hyomandibula, bridged (28[2]). Unknown in †*Lycoptera*.

*Medial wall of the Meckelian fossa of the lower jaw absent (44[1]).

Basihyal toothplate with ventrally directed processes (48[1]). Unknown in †*Lycoptera* due to uncertain homology.

Post-pelvic bone present (62[1]). Unknown in †*Lycoptera* and †*Eohiodon*.

NODE B: HIODONTIDAE

***Nasal bones tubular and strongly curved (7[1]).**

***Posterodorsal spine on the opercle present (34[1]).**

NODE C: OSTEOGLOSSIFORMES

Nasal bones gutter-like (7[2]). Unknown in †*Ostariostoma* due to uncertain homology.

Cranial nerve foramen/foramina straddling the suture between the prootic and pterospheneid (17[1]). Unknown in †*Ostariostoma*.

*Infraorbital sensory canal open in a gutter in at least some infraorbitals (24[1]).

One lateral dermal element in palatoquadrate (30[1]). Unknown in †*Ostariostoma*.

*Angular and articular bones fused (42[1]).

Retroarticular bone excluded from the articulation with the quadrate (43[1]).

Bony elements associated with the second ventral gill arch present as a bony process on the second hypobranchial (45[2]). Unknown in †*Ostariostoma*.

Toothplate(s) associated with basibranchial 4 absent (46[1]). Unknown in †*Ostariostoma*.

Basihyal present and cartilaginous (50[1]). Unknown in †*Ostariostoma*.

One ossified pair hypohyals present (51[1]). Unknown in †*Ostariostoma*.

Lateral line does not pierce the supracleithrum (58[1]).

Coracoid fenestra present (60[1]). Unknown in †*Ostariostoma*.

***Uroneurals two or one (66[1]).**

***Six or fewer hypurals (71[1]).**

NODE D: UNNAMED GROUP

*Temporal fossae bordered by the epioccipital, exoccipital, and pterotic (1[1]).

Otic and supraorbital sensory canal partially or completely in grooves (21[1]).

Mandibular canal open in a groove (41[1]).

Dorsal arm of the post-temporal bone less than 1.5 times as long as the ventral arm (57[0]).

***Epurals absent (68[2]).**

NODE E: OSTEOGLOSSOIDEI (NEW USAGE) (= OSTEOGLOSSIDAE + NOTOPTERIDAE)

Extrascapular reduced and irregularly shaped (2[1]).

*Nasal bones meet each other in midline (6[2]).

*Supratemporal commissure passing through the parietals (10[1]).

*Preopercular sensory canal opens by pores dorsally and a groove ventrally (32[2]).

Ascending process of the premaxilla well-developed (37[0]).

***Fifteen or fewer branched caudal fin rays (65[2]).**

***One neural spine on ural centrum 1 (67[1]).**

NODE F: OSTEOGLOSSIDAE

Temporal fossae bordered by the epioccipital and pterotic (1[3]). Unknown in †*Joffrichthys*.

Extrascapular reduced and tubular (2[2]). Unknown in †*Joffrichthys*.

***Nasal bones flat and broad (7[3]).**

Basisphenoid absent (13[1]). Unknown in †*Joffrichthys*.

Otic and supraorbital sensory canal in bony canals (21[0]).

*Infraorbital sensory canal enclosed in a bony canal (24[0]).

***Palatoquadrate area behind and below the orbit completely covered by infraorbitals (25[1]).**

Anterior process (wing) of the hyomandibula present (29[1]). Unknown in †*Joffrichthys*.

Mandibular canal enclosed in a bony tube (41[0]).

Basibranchial toothplate and basihyal toothplate continuous (49[1]). Unknown in †*Joffrichthys* due to uncertain homology.

NODE G: UNNAMED GROUP

*Basipterygoid process present (9[0]).

***Subopercle small and anterior of the opercle (35[1]).**

*Scales with reticulate furrows only present over entire scale (72[2]).

NODE H: HETEROTINAE

*Frontal bone less than twice as long as parietal (5[1]).

*Ventral occipital groove absent (15[1]).

***Enlarged first infraorbital (23[1]).**

*Two separate neurocranial heads of the hyomandibula (28[1]).

*Preopercular sensory canal opens by pores the entire length of the canal (32[0]).

*Posterior portion of the maxilla lies on dentary (39[1]).

*Posterior bones of the lower jaw all separate (42[2]).

Retroarticular bone included in the articulation with the quadrate (43[0]).

*Basihyal toothplate absent (47[1]).

***Infrapharyngobranchial 3 divided into two elements (52[1]).**

NODE I: OSTEOGLOSSINAE

*Anterior margin of frontal bones about equal in width to posterior margin (3[1]).

***Opercle depth to width ratio about two or greater than two (33[1]).**

***First pectoral fin ray greatly enlarged and extremely long (61[1]).**

Pelvic bone possesses a thin deep lamella in dorsoventral plane (63[1]).

NODE J: UNNAMED GROUP

Temporal fossae bordered by the epioccipital, pterotic, and parietal (1[2]). Unknown in †*Singida* and †*Phareodus*.

*Supratemporal commissure passing through the parietals absent (10[0]). Unknown in †*Singida*.

*Basioccipital process of the parasphenoid median (14[1]). Unknown in †*Singida*.

Toothplate(s) associated with basibranchial 4 present (46[0]). Unknown in †*Singida* and †*Phareodus*.

Infrapharyngobranchial 1 absent (53[1]). Unknown in †*Singida* and †*Phareodus*.

Lateral line pierces the supracleithrum (58[0]). Unknown in †*Phareodus*.

NODE K: UNNAMED GROUP

Frontal bone less than twice as long as parietal (5[1]). Unknown in †*Singida*.

Nasal bones separated only by ethmoid bones (6[1]). Unknown in †*Singida*.

Ventral occipital groove absent (15[1]). Unknown in †*Singida*.

*Otic and supraorbital sensory canal partially or completely in grooves (21[1]).

Anterior process (wing) of the hyomandibula absent (29[0]). Unknown in †*Singida*.

Median premaxilla (38[1]). Unknown in †*Singida* due to inapplicability (see text).

Retroarticular bone included in the articulation with the quadrate (43[0]). Unknown in †*Singida*.

Scales with both radial and reticulate furrows present (72[1]). Unknown in †*Singida*.

NODE L: UNNAMED GROUP

*Parasphenoid teeth large and restricted to the basal portion of the parasphenoid (8[3]).

***Orbitosphenoid absent (12[1]).**

*Cranial nerve foramen/foramina in the prootic (17[0]).

*Suture between the parasphenoid and sphenotic present (18[1]).

*Ascending process of the premaxilla only slightly developed, if at all (37[1]).

NODE M: NOTOPTERIDAE

Anterior margin of frontal bones about equal in width to posterior margin (3[1]).

*Basioccipital process of the parasphenoid median (14[1]).

*Foramen for cranial nerve VI opens anterior to the prootic bridge (19[1]).

***Posterior region of the fossa on the neurocranium for the hyomandibula formed of exoccipital and intercalar (27[3]).**

*Subopercle bone absent (35[2]).

***Bony elements associated with the second ventral gill arch present as autogenous elements (45[1]).**

*Basihyal toothplate with ventrally directed processes (48[1]).

Infrapharyngobranchial 1 absent (53[1]).

***Abdominal scutes present as paired structures (55[1]).**

***Posterior end of anal fin continuous with caudal fin (64[1]).**

***Uroneurals absent (66[2]).**

NODE N: UNNAMED GROUP (= Xenomystinae of Greenwood, 1963)

*Temporal fossae bordered by the exoccipital and the pterotic (1[4]).

*Dermosphenotic tubular (26[2]).

NODE O: UNNAMED GROUP

Basipterygoid process present (9[0]). Unknown in †*Palaeonotopterus*.

*Suture between the parasphenoid and sphenotic present (18[1]). Unknown in †*Palaeonotopterus*.

Dermosphenotic tubular (26[2]). Unknown in †*Palaeonotopterus*.

One dermal element in palatoquadrate (30[2]). Unknown in †*Palaeonotopterus*.

Median premaxilla (38[1]). Unknown in †*Palaeonotopterus*.

Posterior portion of the maxilla lies on dentary (39[1]). Unknown in †*Palaeonotopterus*.

Posterior bones of the lower jaw are all fused (42[3]). Unknown in †*Palaeonotopterus*.

Basihyal absent (50[2]). Unknown in †*Palaeonotopterus*.

Proximal tip of infrapharyngobranchial 1 posteriorly directed (54[1]). Unknown in †*Palaeonotopterus*.

Lateral line does pierce the supracleithrum (58[0]). Unknown in †*Palaeonotopterus*.

*Cleithrum with a broad medial lamina (59[1]).

Scales with both radial and reticulate furrows (72[1]). Unknown in †*Palaeonotopterus*.

NODE P: MORMYRIDAE

*Ventral occipital groove absent (15[1]).

***Intercalar absent (16[1]).**

*Cranial nerve foramen/foramina straddling the suture between the sphenotic and pterospheoid (17[2]).

*Foramen for cranial nerve VI opens anterior to the prootic bridge (19[1]).

***Posterior region of the fossa on the neurocranium for the hyomandibula formed of pterotic and exoccipital (27[2]).**

NODE Q: MORMYRINAE

*Basisphenoid absent (13[1]).

*Medial wall of the Meckelian fossa of the lower jaw absent (44[1]).

*Basihyal toothplate absent (47[1]).

***One pair of hypohyals greatly reduced in size (51[2]).**

Tree Two (Fig. 4B)

NODE A: OSTEOGLOSSOMORPHA

Temporal fossae present – bordered by the epioccipital, pterotic, and parietal (1[2]). Unknown in *Lycoptera*.

Frontal bone less than twice as long as parietal (5[1]).

Nasal bones separated only by ethmoid bones (6[1]).

*Parasphenoid teeth large and found along the length of the parasphenoid (8[2]).

***Supraorbital bone absent (20[1]).** Unknown in †*Lycoptera*.

Four bones in the infraorbital series, not including the dermosphenotic or the antorbital, if present (22[1]). Unknown in †*Lycoptera*.

One neurocranial head of the hyomandibula or two heads, although they are continuous (28[0]). Unknown in †*Lycoptera*.

Autopalatine bone absent (31[1]). Unknown in †*Lycoptera*.

***Supramaxillae absent (40[1]).** Unknown in †*Lycoptera*.

Medial wall of the Meckelian fossa of the lower jaw absent (44[1]).

***Epipleural bones absent (56[0]).**

*Dorsal arm of the post-temporal bone more than twice as long as the ventral arm (57[1]).

***Sixteen principal branched caudal fin rays (65[1]).**

***One epural (68[1]).**

***Neural spine on the first preural centrum complete (69[0]).**

NODE X: OSTEOGLOSSOMORPHA, TO THE EXCLUSION OF †LYCOPTERA

***Nasal bones tubular and strongly curved (7[1]).**

***Supraorbital sensory canal ending in frontal (11[1]).**

***Gular bone absent (36[1]).**

*Ascending process of the premaxilla only slightly developed, if at all (37[1]).

NODE B: HIODONTIDAE

*Dermosphenotic triradiate (26[1]). Unknown in †*Lycoptera*.

***Posterior region of the fossa on the neurocranium for the hyomandibula formed of pterotic and intercalar (27[1]).** Unknown in †*Lycoptera* and †*Eohiodon*.

Two neurocranial heads of the hyomandibula, bridged (28[2]). Unknown in †*Lycoptera*.

***Posterodorsal spine on the opercle present (34[1]).**

*Basihyal toothplate with ventrally directed processes (48[1]). Unknown in †*Lycoptera* due to uncertain homology.

***Post-pelvic bone present (62[1]).** Unknown in †*Lycoptera* and †*Eohiodon*.

NODE C: OSTEOGLOSSIFORMES

Frontal bone over twice as long as parietal (5[0]).

Some part of nasal bones separated by anterior portion of frontals (6[0]). Unknown in †*Ostariostoma* due to uncertain homology.

***Nasal bones gutter-like (7[2]).** Unknown in †*Ostariostoma* due to uncertain homology.

Cranial nerve foramen/foramina straddling the suture between the prootic and pterospheoid (17[1]). Unknown in †*Ostariostoma*.

*Infraorbital sensory canal open in a gutter in at least some infraorbitals (24[1]).

***One lateral dermal element in palatoquadrate (30[1]).** Unknown in †*Ostariostoma*.

*Angular and articular bones fused (42[1]).

Retroarticular bone excluded from the articulation with the quadrate (43[1]).

Medial wall of the Meckelian fossa of the lower jaw present (44[0]). Unknown in †*Ostariostoma*.

***Bony elements associated with the second ventral gill arch present as a bony process on the second hypobranchial (45[2]).** Unknown in †*Ostariostoma*.

Toothplate(s) associated with basibranchial 4 absent (46[1]). Unknown in †*Ostariostoma*.

Basihyal present and cartilaginous (50[1]). Unknown in †*Ostariostoma*.

***One ossified pair hypohyals present (51[1]).** Unknown in †*Ostariostoma*.

Lateral line does not pierce the supracleithrum (58[1]).

Coracoid fenestra present (60[1]). Unknown in †*Ostariostoma*.

***Uroneurals two or one (66[1]).**

***Six or fewer hypurals (71[2]).**

NODE D: UNNAMED GROUP

*Temporal fossae bordered by the epioccipital, exoccipital, and pterotic (1[1]).

Otic and supraorbital sensory canal partially or completely in grooves (21[1]).

Mandibular canal open in a groove (41[1]).

Dorsal arm of the post-temporal bone less than 1.5 times as long as the ventral arm (57[0]).

***Epurals absent (68[2]).**

NODE E: OSTEOGLOSSOIDEI (NEW USAGE) (= OSTEOGLOSSIDAE + NOTOPTERIDAE)

Extrascapular reduced and irregularly shaped (2[1]).

Nasal bones meet each other in midline (6[2]).

*Supratemporal commissure passing through the parietals (10[1]).

*Preopercular sensory canal opens by pores dorsally and a groove ventrally (32[2]).

*Ascending process of the premaxilla well-developed (37[0]).

***Fifteen or fewer principal branched caudal fin ray (65[2]).**

***One neural spine on ural centrum 1 (67[1]).**

NODE F: OSTEOGLOSSIDAE

Temporal fossae bordered by the epioccipital and pterotic (1[3]). Unknown in †*Joffrichthys*.

Extrascapular reduced and tubular (2[2]). Unknown in †*Joffrichthys*.

***Flat and broad nasal bones (7[3]).**

Basisphenoid absent (13[1]). Unknown in †*Joffrichthys*.

Otic and supraorbital sensory canal in bony canals (21[0]).

*Infraorbital sensory canal enclosed in a bony canal (24[0]).

***Palatoquadrate area behind and below the orbit completely covered by infraorbitals (25[1]).**

Anterior process (wing) of the hyomandibula present (29[1]). Unknown in †*Joffrichthys*.

Mandibular canal enclosed in a bony tube (41[0]).

Basibranchial toothplate and basihyal toothplate continuous (49[1]). Unknown in †*Joffrichthys* due to uncertain homology.

NODE G: UNNAMED GROUP

*Basipterygoid process present (9[0]).

***Subopercle small and anterior of the opercle (35[1]).**

*Scales with reticulate furrows only present over entire scale (72[2]).

NODE H: HETEROTINAE

*Frontal bone less than twice as long as parietal (5[1]).

*Ventral occipital groove absent (15[1]);

Enlarged first infraorbital (23[1]).

*Two separate neurocranial heads of the hyomandibula (28[1]).

*Preopercular sensory canal opens by pores the entire length of the canal (32[0]).

*Posterior portion of the maxilla lies on dentary (39[1]).

*Posterior bones of the lower jaw all separate (42[2]).

Retroarticular bone included in the articulation with the quadrate (43[0]).

*Basihyal toothplate absent (47[1]).

***Infrapharyngobranchial 3 divided into two elements (52[1]).**

NODE I: OSTEOGLOSSINAE

*Anterior margin of frontal bones about equal in width to posterior margin (3[1]).

***Opercle depth to width ratio about two or greater than two (33[1]).**

***First pectoral fin ray greatly enlarged and extremely long (61[1]).**

Pelvic bone possesses a thin deep lamella in dorsoventral plane (63[1]).

NODE J: UNNAMED GROUP

Temporal fossae bordered by the epioccipital, pterotic, and parietal (1[2]). Unknown in †*Singida* and †*Phareodus*.

*Supratemporal commissure passing through the parietals absent (10[0]). Unknown in †*Singida*.

*Median basioccipital process of the parasphenoid (14[1]). Unknown in †*Singida*.

Toothplate(s) associated with basibranchial 4 present (46[0]). Unknown in †*Singida* and †*Phareodus*.

Infrapharyngobranchial 1 absent (53[1]). Unknown in †*Singida* and †*Phareodus*.

Lateral line pierces the supracleithrum (58[0]). Unknown in †*Phareodus*.

NODE K: UNNAMED GROUP

Frontal bone less than twice as long as parietal (5[1]). Unknown in †*Singida*.

Nasal bones separated only by ethmoid bones (6[1]). Unknown in †*Singida*.

Ventral occipital groove absent (15[1]). Unknown in †*Singida*.

*Otic and supraorbital sensory canal partially or completely in grooves (21[1]).

Anterior process (wing) of the hyomandibula absent (29[0]). Unknown in †*Singida*.

Median premaxilla (38[1]). Unknown in †*Singida* due to inapplicability (see text).

Retroarticular bone included in the articulation with the quadrate (43[0]). Unknown in †*Singida*.

Scales with both radial and reticulate furrows present (72[1]). Unknown in †*Singida*.

NODE L: UNNAMED GROUP

*Parasphenoid teeth large and restricted to the basal portion of the parasphenoid (8[3]).

***Orbitosphenoid absent (12[1]).**

*Cranial nerve foramen/foramina in the prootic (17[0]).

*Suture between the parasphenoid and sphenotic present (18[1]).

*Ascending process of the premaxilla only slightly developed, if at all (37[1]).

NODE M: NOTOPTERIDAE

Anterior margin of frontal bones about equal in width to posterior margin (3[1]).

*Basioccipital process of the parasphenoid median (14[1]).

*Foramen for cranial nerve VI opens anterior to the prootic bridge (19[1]).

***Posterior region of the fossa on the neurocranium for the hyomandibula formed of exoccipital and intercalar (27[3]).**

*Subopercle bone absent (35[2]).

***Bony elements associated with the second ventral gill arch present as autogenous elements (45[1]).**

*Basihyal toothplate with ventrally directed processes (48[1]).

Infrapharyngobranchial 1 absent (53[1]).

***Abdominal scutes present as paired structures (55[1]).**

***Posterior end of anal fin continuous with caudal fin (64[1]).**

***Uroneurals absent (66[2]).**

NODE N: UNNAMED GROUP (= Xenomystinae of Greenwood, 1963)

*Temporal fossae bordered by the exoccipital and the pterotic (1[4]).

*Dermosphenotic tubular (26[2]).

NODE O: UNNAMED GROUP

Basipterygoid process present (9[0]). Unknown in †*Palaeonotopterus*.

*Suture between the parasphenoid and sphenotic present (18[1]). Unknown in †*Palaeonotopterus*.

Dermosphenotic tubular (26[2]). Unknown in †*Palaeonotopterus*.

One dermal element in palatoquadrate (30[2]).

Unknown in †*Palaeonotopterus*.

Median premaxillae (38[1]). Unknown in †*Palaeonotopterus*.

Posterior portion of the maxilla lies on dentary (39[1]). Unknown in †*Palaeonotopterus*.

Posterior bones of the lower jaw are all fused (42[3]). Unknown in †*Palaeonotopterus*.

Basihyal absent (50[2]). Unknown in †*Palaeonotopterus*.

Proximal tip of infrapharyngobranchial 1 posteriorly directed (54[1]). Unknown in †*Palaeonotopterus*.

Lateral line pierces the supracleithrum (58[0]). Unknown in †*Palaeonotopterus*.

*Cleithrum with a broad medial lamina (59[1]).

Scales with both radial and reticulate furrows (72[1]). Unknown in †*Palaeonotopterus*.

NODE P: MORMYRIDAE

*Ventral occipital groove absent (15[1]).

***Intercalar absent (16[1]).**

*Cranial nerve foramen/foramina straddling the suture between the sphenotic and pterosphenoid (17[2]).

*Foramen for cranial nerve VI opens anterior to the prootic bridge (19[1]).

***Posterior region of the fossa on the neurocranium for the hyomandibula formed of pterotic and exoccipital (27[2]).**

NODE Q: MORMYRINAE

*Basisphenoid absent (13[1]).

*Medial wall of the Meckelian fossa of the lower jaw absent (44[1]).

*Basihyal toothplate absent (47[1]).

***One pair of hypohyals greatly reduced in size (51[2]).**

CHARACTER ANALYSIS

In this section, I discuss the characters that were used in the phylogenetic analysis. These are discussed according to anatomical region so that there can be logical flow with the figures (e.g. all the neurocranial characters are discussed together). Following the name of the character and the list of its states, I indicate (through abbreviation) if this character was taken from a previous analyses. LW, for example, stands for Li & Wilson, and this is followed by the last two numbers of the year of the publication and their character number in brackets (e.g. LW96[6] means this was character 6 of Li & Wilson, 1996a). Other papers that were the source of characters are Li & Wilson (1999; abbreviated LW99), Taverne (1998; abbreviated T98), Cavin & Forey (2001; abbreviated CF01), and Arratia, 1997; abbreviated A97). A discussion of the character as interpreted in my analysis follows.

SKULL ROOF AND BRAINCASE

(1) *Temporal fossae*: Absent [0]; present – bordered by the epioccipital, exoccipital, and pterotic [1]; Present – bordered by the epioccipital, pterotic, and parietal [2]; Present – bordered by the epioccipital and pterotic [3]; Present – bordered by the exoccipital and the pterotic [4]; Present – bordered by the exoccipital, epioccipital,

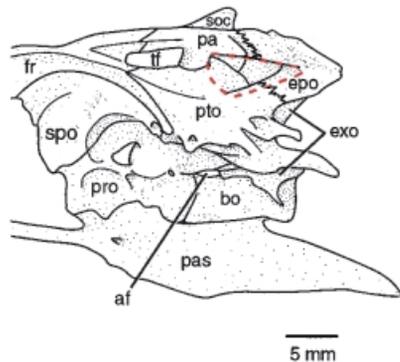
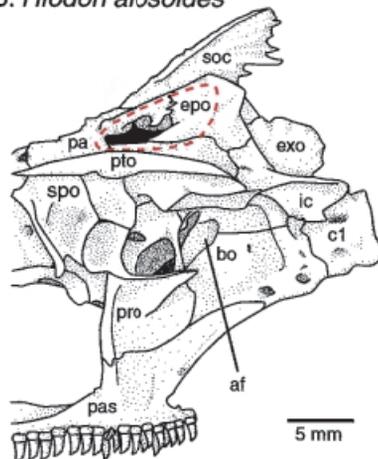
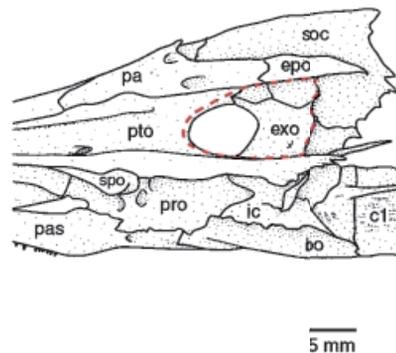
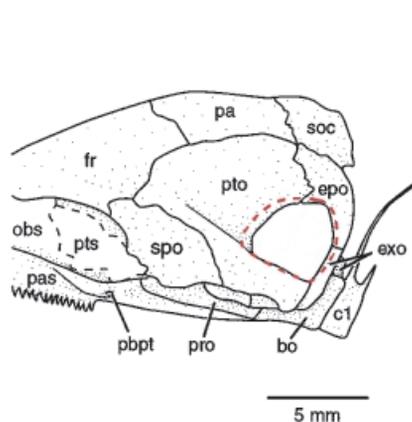
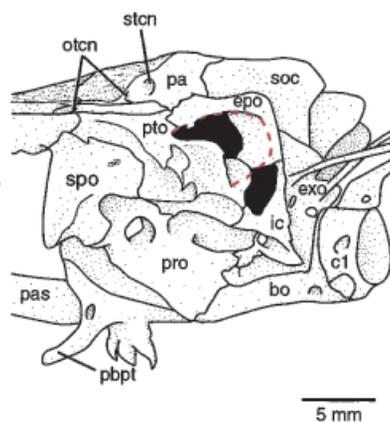
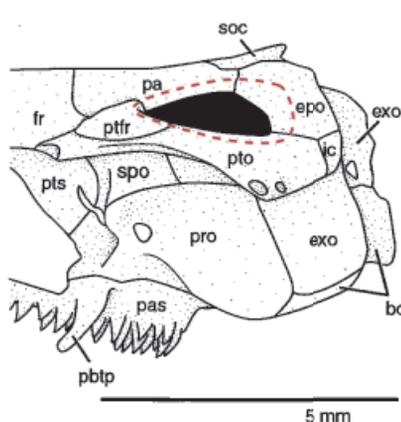
A. *Alosa sapidissima*B. *Hiodon alosoides*C. *Chitala chitala*D. *Campylomormyrus tamandua*E. *Osteoglossum bicirrhosum*F. *Pantodon buchholzi*

Figure 8. Otic and occipital region in lateral or posterolateral view. A, *Alosa sapidissima* (UMA F10359, 390 mm SL). B, *Hiodon alosoides* (UMA F10581, 315 mm SL). C, *Chitala chitala* (UMA F10349, 437 mm SL). D, *Campylomormyrus tamandua* (FMNH 51337, 145 mm SL). E, *Osteoglossum bicirrhosum* (UMA F10160, 365 mm SL). F, *Pantodon buchholzi* (UMA F11265, approx. 50 mm SL). Dashed red line indicates the outline of the temporal fossa. Illustration of *Hiodon* modified from Hilton (2002: fig. 21). Anterior facing left.

parietal and pterotic [5]. Modified from LW99[8]. Descriptions of the temporal fossae of various osteoglossomorph fishes can be found in Ridewood (1904a, 1905), Greenwood (1970, 1973), Li & Wilson (1996a), Taverne (1977, 1978, 1998), Cavin & Forey (2001), and Hilton (2002). Although they discussed the temporal fossae in osteoglossomorphs and other basal teleostean groups, Li & Wilson (1996a) did not include it as a character in their analysis. The main point of their discussion concerned the hiodontid affinities of the †Lycoperidae that was suggested by Greenwood (1970) and others. Li & Wilson (1996a: 166) concluded that, because a similar structure is also present in other 'basal' teleosts (e.g. clupeids, salmonids and osmerids; see below), the shared presence 'does not

support a special relationship between [†]lycopterids and hiodontids.' In their 1999 paper, Li & Wilson included the temporal fossae as a dichotomous, present-absent character in their analysis (their character 8). As discussed by Cavin & Forey (2001) and Hilton (2002), the morphology of the temporal fossae varies within taxa that possess it. Therefore, several derived states are recognized here, and differ by the bones that border or surround the fossae.

In *Pantodon* (Fig. 8F), †*Ostariostoma* (Grande & Cavender, 1991: fig. 2), *Hiodon* (Fig. 8B) and †*Eohiodon*, the temporal fossa is bordered by the epioccipital, pterotic and parietal (state 2); in *Pantodon*, a unique bone, the postfrontal, is also included. I found the condition of the temporal fossa in *Hiodon* and

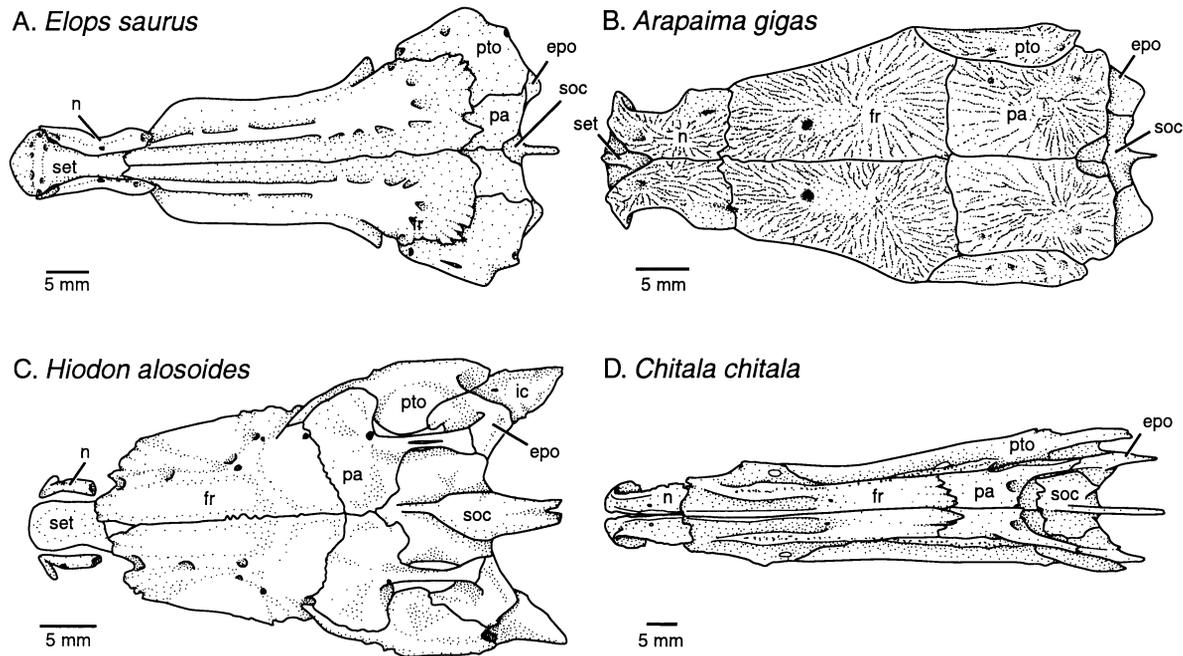


Figure 9. Skull roof in dorsal view. A, *Elops saurus* (UMA F10255, 425 mm SL). B, *Arapaima gigas* (UMA F11262, approx. 240 mm SL). C, *Hiodon alosoides* (UMA F10581, 315 mm SL). D, *Chitala chitala* (UMA F10349, 437 mm SL). Anterior facing left. Illustration of *Hiodon* modified from Hilton (2002: fig. 9).

†*Eohiodon* to be nearly indistinguishable, although this was inferred from the form of disarticulated skull elements found in specimens of †*Eohiodon* (articulated specimens are typically crushed in the posterior region of the skull, making details very hard to distinguish). As discussed further below, the condition of †*Lycoptera* has been reconstructed to be very similar to that of *Hiodon* (e.g. Gaudant, 1968; Greenwood, 1970). However, the skull of †*Lycoptera* is nearly always poorly preserved, and the sort of detail needed to reliably code this character for this taxon is lacking ('?' in my matrix). However, one specimen of †*L. davidi* that I examined (MNHN 1927-13-06 a'; see Gaudant, 1968: plate 3, figs 3 and 4) consisted of an isolated skull roof comprised of the nasals, frontals, parietals and supraoccipital. The posterolateral edge of the parietals curved smoothly posteriorly, suggesting a morphology similar to that of *Hiodon* (Fig. 9C), although the posterior extension of the parietal is neither as narrow nor as elongate as that found in *Hiodon*. This may suggest that in †*Lycoptera* the parietal bordered the anterior edge of a temporal fossa, as in *Hiodon*, although this must await confirmation from more and better preserved specimens. This character was coded as unknown due to preservation also in †*Joffrichthys*, †*Phareodus*, and †*Singida*.

For †*Palaeonotopterus*, Cavin & Forey (2001) describe the temporal fossa as being surrounded by

the pterotic, exoccipital and epioccipital (pers. observ.; state 1), as in *Gymnarchus* (Benveniste, 1994), and mormyrids (e.g. *Campylomormyrus*, Fig. 8D). *Xenomystus* and *Papyrocranus* share the condition of having only the exoccipital and pterotic border the temporal fossa (state 4). As pointed out by Cavin & Forey (2001: 35), *Notopterus* is polymorphic, as Taverne (1978: fig. 62) figured a specimen of *N. notopterus* with a small epioccipital contribution to the fossa, whereas Cavin & Forey (2001) described a large skull with no epioccipital contribution, which they suggested may be a function of ontogeny. In *Chitala* (Fig. 8C), the epioccipital is included in the temporal fossa, but, as in mormyrids (e.g. *Campylomormyrus*, Fig. 8D), it is not included in the cranial fenestra in the side of the skull.

Cavin & Forey (2001) suggested the possibility that the deep fossae found in taxa such as *Osteoglossum* (Fig. 8E) was also homologous to the temporal fossae of other osteoglossomorphs (e.g. *Hiodon*, Fig. 8B), and only differed in that it is roofed by the parietal. This hypothesis was also suggested by Taverne (1977, 1978), who labelled this structure as a temporal fossae ('fosse temporale') in *Osteoglossum* (Taverne, 1977: figs 44, 46), as well as *Scleropages* (Taverne, 1977: figs 72, 75, 80), *Heterotis* (Taverne, 1977: figs 94, 95, 97) and *Arapaima* (Taverne, 1977: figs 125, 128). Ridewood (1905: 254) also called this structure the temporal fossa, although he remarked (for at least

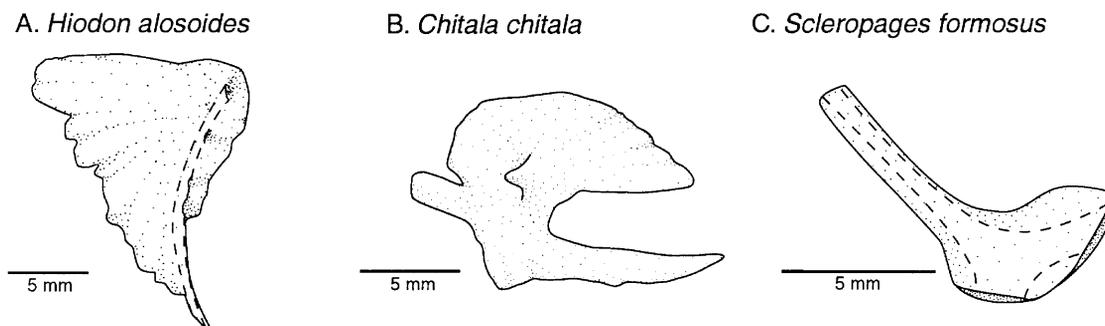


Figure 10. Extrascapular bones in dorsal view. A, *Hiodon alosoides* (UMA F10586, 273 mm SL). B, *Chitala chitala* (UMA F10349, 437 mm SL). C, *Scleropages formosus* (UMA F11266, approx. 320 mm SL). Dashed lines indicate path of the supratemporal sensory canal; note that this sensory canal is not enclosed in the extrascapular in *Chitala*. Anterior facing left. Illustration of *Hiodon* modified from Hilton (2002: fig. 28).

Osteoglossum and *Scleropages*) that [t]his aperture appears at first glance to correspond with the 'temporal foramen' of the Clupeoids; but it must be remembered that the latter foramen leads directly into the cranial cavity, and is bounded by the parietal and frontal bones' (as opposed to the pterotic and epioccipital – state 3 – in *Osteoglossum* and *Scleropages*). It is, however, unlikely that the temporal fossa is homologous with the temporal foramen of clupeomorphs (Fig. 8A). For most osteoglossids (except *Pantodon*), the temporal fossa is roofed by the parietal (Cavin & Forey, 2001). For example, for *Arapaima*, Ridewood (1905: 264–265) remarked that the '[t]he posterior temporal fossa is completely roofed; its aperture is triangular in the small specimen, but rounded in the large one; it is bounded by the epiotic [= epioccipital], opisthotic [= intercalar] and squamosal [= pterotic]. Its anterior blind end is limited by the supraoccipital, parietal, and squamosal [= pterotic] bones.' The condition of having the temporal fenestra bordered by the exoccipital, epioccipital, parietal and pterotic (state 5) was only found in *Heterotis* (e.g. Taverne, 1978: fig. 94).

Li & Wilson (1996a), following Ridewood (1904a), homologized the temporal fossa of *Hiodon* with the pre-epioccipital fossa (= pre-epiotic fossa of Grande, 1985 and others; see Hilton, 2002) of clupeomorphs in that both are bordered by the parietal, epioccipital, and pterotic; this topographical correspondence is recognized here (e.g. *Alosa*, Fig. 8A). Taverne (1998) suggested that the temporal fossa of osteoglossomorphs was homologous with the post-temporal fossa of other basal teleosts. Cavin & Forey (2001: 45), however, noted that 'it is unlikely that the temporal fenestra [fossa] is homologous with, or a transformation from, the post-temporal fossa since osteoglossids would have both.'

(2) *Shape of extrascapular*: Expanded [0]; reduced and irregularly shaped [1]; Reduced and tubular [2].

Modified from LW9[27]; based in part on discussion of Cavin & Forey (2001: 36). This character was defined as a binary character (expanded – plesiomorphic – vs. slender and distinctly angular – apomorphic) by Li & Wilson (1996a), and subsequently by Li *et al.* (1997a: character 33) and Li & Wilson (1999: character 9), with the derived condition interpreted as a synapomorphy of the genus †*Phareodus* (including †*Brychatus*). However, many of the taxa Li & Wilson (1996a) scored as possessing an expanded extrascapular (state 0), as exemplified here by *Hiodon* (Fig. 10A), have a much reduced extrascapular, which may be one of two forms. In many taxa (e.g. *Scleropages*, Fig. 10C), the extrascapular is a bony angular tube that surrounds the supratemporal sensory canal (state 2; see also Fig. 11). In notopterids, the extrascapulars are somewhat reduced (although they may come close to completely covering the temporal fossa in *Notopterus*, Taverne, 1979: fig. 61), but are irregularly shaped (e.g. *Chitala*, Fig. 10B; state 1). In these fishes, the extrascapular may (e.g. *Xenomystus* and *Papyrocranus*, pers. observ., Taverne, 1978: figs 90 and 115, respectively) or may not (e.g. *Chitala*, pers. observ., *Notopterus*, Taverne, 1979: fig. 61) retain an association with the supratemporal sensory canal. Mormyrids have large extrascapulars (see figures in Taverne, 1968a, 1969, 1971, 1972) and the supratemporal sensory canal is enclosed in this bone as it crosses the back of the skull. This is the condition found also in †*Palaeonotopterus* (Cavin & Forey, 2001: fig. 6). The extrascapulars of osteoglossomorphs generally were also discussed by Cavin & Forey (2001; see their fig. 8). The form of the extrascapulars is unknown for †*Lycoptera*, †*Joffrichthys*, †*Singida* and †*Ostariostoma*.

(3) *Shape of frontal bones*: Anterior margin narrower than posterior margin [0]; Anterior margin about equal in width to posterior margin [1]; Anterior margin wider than posterior margin [2]. Modified from

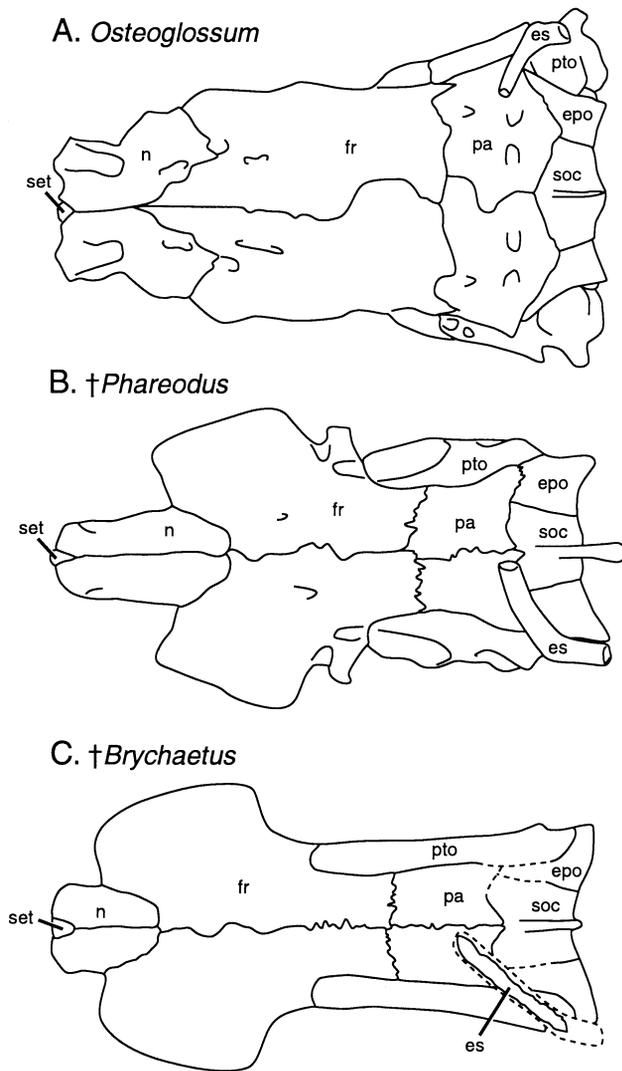


Figure 11. Some elements of the skull roof of osteoglossids in dorsal view. A, *Osteoglossum bicirrhosum* (190 mm SL; drawn after Taverne, 1977: fig. 44). B, †*Phareodus testis* (composite, drawn after Taverne, 1978: fig. 4). C, †*Brychaetus muelleri* (composite, drawn after Taverne, 1978: fig. 22). Note the distinctive anterior supraorbital shelf present in †*Phareodus* and †*Brychaetus*. This character is described by Li & Wilson (1996a: character 25) as the condition of having the anterior portion of the frontal at least as twice as wide as the posterior portion (see also discussion in Li *et al.*, 1997a). It is proposed here, however, that the 'supraorbital shelf' is recognizable as a distinct structure. Anterior facing left.

LW99[5]. As described by Li & Wilson (1999), this character is a modification of one they defined earlier (Li & Wilson, 1996a: character 25), which had three states (i.e. character state 0 and 1 were combined into a single state in Li & Wilson, 1999). I modified this

character: Li & Wilson's (1999: 382) state 2 reads 'anteriorly about 1.5 times as broad as posteriorly' and their state 3 reads 'anteriorly at least twice as broad as posteriorly.' The two states share in common that the anterior margin of the frontal is wider than the posterior margin. However, their state 3 (anteriorly two or more times as wide as posteriorly), which they identified as a synapomorphy of the genus †*Phareodus*, reflects a wide portion of the frontal that extends laterally over the orbit. This 'supraorbital shelf' is recognizable as a distinct character (Fig. 11), and is analysed separately (see below, Character 4).

I also found discrepancies in the coding of this character by Li & Wilson (1999). For example, several taxa that Li & Wilson (1999) coded as state 1 (anterior only slightly narrower), in fact have frontals that taper substantially anteriorly, better fitting their description of state 0 (e.g. *Arapaima*, Fig. 9B; †*Joffrichthys*, Fig. 12). Also, *Heterotis* was coded by Li & Wilson (1999) as having the frontals that are narrower anteriorly, whereas my adult specimen (Fig. 13; MCZ 50959) has frontals that are clearly wider anteriorly (state 2; see also Daget & d'Aubenton, 1957: fig. 26). Taverne (1977: fig. 95) illustrated a small specimen (62 mm SL) in which the frontals taper anteriorly (i.e. the anterior margin is narrower than posterior margin) as in my small specimen (Fig. 14; UMA F10653, 75 mm SL), although in my specimen the taper is shallower. This indicates that there is significant ontogenetic shape change in the shape of the frontal in *Heterotis*.

Osteoglossum (Taverne, 1977: fig. 44), *Scleropages* (Taverne, 1977: fig. 73) and *Pantodon* (Taverne, 1978: fig. 32) have frontals that are about equal in width anteriorly and posteriorly, as was coded by Li & Wilson (1999). I coded this character as unknown for †*Singida*.

Li & Wilson (1999) coded Notopteridae and Mormyroidae as terminal taxa, thereby masking potential lower level variation. For instance, the frontals of *Notopterus*, *Xenomystus* and *Papyrocranus* are approximately the same width, or only slightly narrower anteriorly (state 1; e.g. see Taverne, 1978: figs 63, 92 and 115, respectively). In *Chitala*, on the other hand, the anterior and posterior edges of the frontal are about equal in width, or even narrower posteriorly (Fig. 9D; Taverne, 1978: fig. 84 illustrated the neurocranium from a species of this genus, then known as *N. chitala*, but only in lateral view, so it is impossible to see the shape of the frontal in this specimen). Mormyrids generally have frontals that taper very strongly anteriorly, likely as a consequence of the extreme modifications of the snouts typical of the group as a whole; all mormyrids sampled here are coded as state 0. In *Gymnarchus*, the frontals are of relatively even width along their entire length,

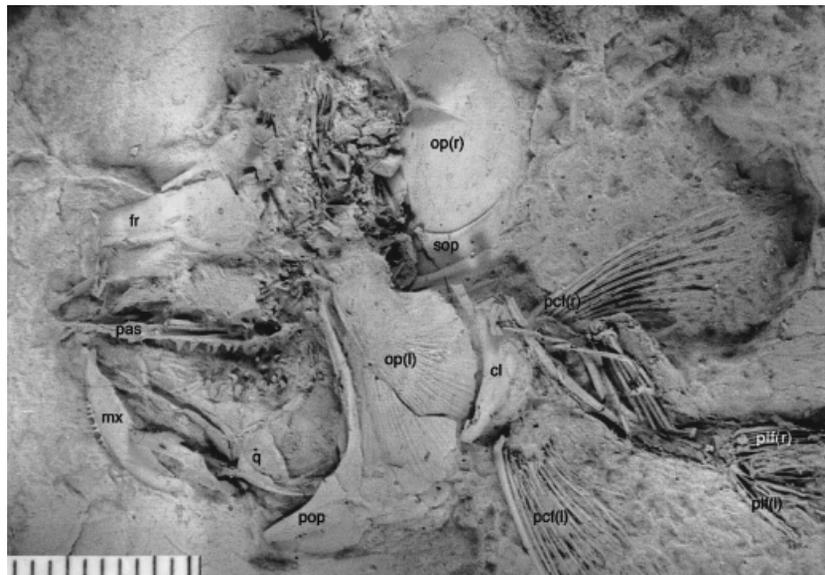


Figure 12. A specimen identified as †*Joffrichthys* sp. (FMNH PF12171b). This specimen is a black latex peel dusted with ammonium chloride made from a natural mould of one half of the specimen. This specimen was collected from the Sentinel Butte Formation, North Dakota – the same locality as †*J. triangulopterus* Newbrey & Bozek, 2000. The type species of the genus, †*J. symmetropterus* Li & Wilson, 1996b, is known from the Paskapoo Formation of Alberta, Canada. Although this specimen consists of only a disarticulated skull, pectoral girdle, pectoral fin and pelvic fin, much detail of the morphology is visible. The specimen was identified as †*Joffrichthys* based on the combination of the shape of the opercle and preopercle and the morphology of the parasphenoid and maxilla. Note that the subopercle is large, extending along the entire ventral edge of the opercle. Scale in millimeters. Anterior facing left.

although there is a sharp taper very far anteriorly, and the parietals separate the posterior 25% of the frontals (Taverne, 1972: fig. 92).

(4) *Supraorbital shelf of frontal bone*: Absent [0]; Present [1]. I interpret the presence of a supraorbital shelf formed from the anterior part of the frontal as a synapomorphy of †*Phareodus*. Li & Wilson (1996a) defined this character as part of another character describing the relative width of the anterior and posterior margins of the frontal (see discussion under Character 3). This character reflects the presence of what I term the ‘supraorbital shelf’, which is the drastic broadening of the frontal over the orbital region that is characteristic of †*Phareodus* (Fig. 11; see also illustrations of †*Phareodus* in Taverne, 1978: fig. 4 and Li *et al.*, 1997a: fig. 2, and that of †*Brychaetus* by Taverne, 1978: fig. 22). Taverne (1998: character 214) considered this a synapomorphy of Osteoglossidae + *Pantodon*, secondarily lost in the living forms (Cavin & Forey, 2001). As suggested by Cavin & Forey (2001), this character is better interpreted as a synapomorphy of †*Phareodus* + †*Brychaetus* (or of the genus †*Phareodus* if †*Brychaetus* is considered to be synonymous with it; e.g. Li *et al.*, 1997a). I coded this as absent in †*Singida*. Although the exact width of the anterior portion of the frontal is poorly known for this taxon

(see Character 3), there is no trace of a broad supraorbital shelf.

A shallow anterolateral expansion of the frontal is also found in *Chitala* (Fig. 9D; see also Character 3). However, the condition differs from that of †*Phareodus* and †*Brychaetus* (Fig. 11) in that the anterolateral expansion does not extend from the lateral margin of the skull roof (i.e. there is a straight lateral edge to the skull roof).

(5) *Length of frontal bone*: Over twice as long as parietal [0]; Less than twice as long as parietal [1]. LW99[7]. This character was used by Li & Wilson (1999; also see Li *et al.*, 1997b: character 10), and the condition of having the frontal less than twice as long as the parietal was found to support the groups (†*Eohiodon* + *Hiodon*), (†*Kuntulunia* + †*Huashia*), and (*Heterotis* + *Arapaima*). It was also coded as present in *Pantodon*.

In my study, I also found this condition in a specimen of †*Lycoptera davidi* (Fig. 15A) and in *Gnathone-mus* (see Taverne, 1968: fig. 6); these taxa were either coded as 0 by Li & Wilson (1999) or not included (as such) in their analysis. Based on the figures of Jin *et al.* (1995: figs 5, 6), †*L. muroii* also displays this condition, although further study of the skull roof of †*Lycoptera* is needed. Because the skull roof is incom-

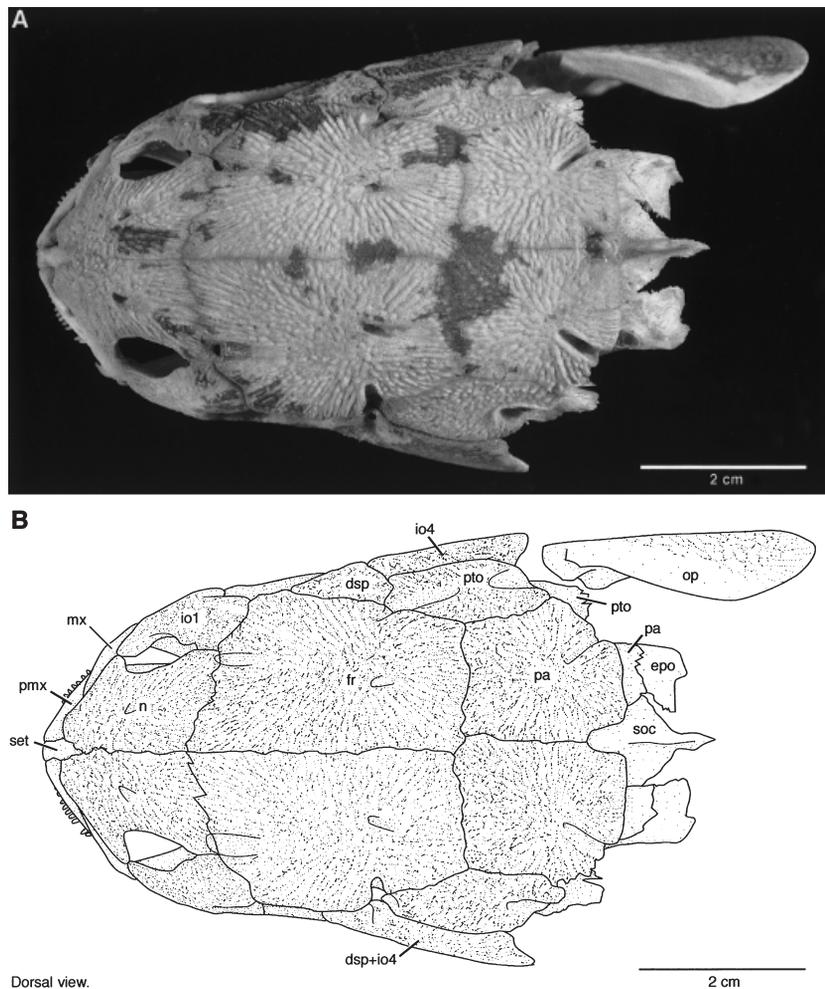


Figure 13. Skull roof of an adult specimen of *Heterotis niloticus* (MCZ 50959, adult, unknown SL) in dorsal view. A, photograph. B, line drawing. Note that the left opercle was removed, the exoccipitals are missing, and the dermosphenotic and infraorbital 4 of the left side are fused in this specimen. Anterior facing left.

plete anteriorly in known specimens (pers. observ., also see Forey, 1997: fig. 1), I scored †*Palaeonotopterus* as unknown. I also scored †*Singida* and †*Joffrichthys* as unknown (scored as 0 by Li & Wilson, 1999) because I was not confident in the extent of either the frontal or the parietal. Li & Wilson (1996b: fig. 3) illustrated a large frontal in comparison with a small parietal in †*J. symmetropterus*, although Newbrey & Bozek (2000: fig. 4A) showed a relatively large parietal in †*J. triangularpterus*. In the specimens of †*Singida* that have been described, there are 'no recognizable traces of the parietals' (Greenwood & Patterson, 1967: 214), a conclusion with which I agree (pers. observ.).

(6) *Relationship of nasal bones:* Some part separated by anterior portion of frontals [0]; Separated only by ethmoid bones [1]; Meet each other in midline [2].

Modified from LW99[3]. Li & Wilson (1999) found that having nasals separated by the mesethmoid (more accurately the dermal supraethmoid) was plesiomorphic for the osteoglossomorphs, clupeomorphs and euteleosts, and the condition of having the nasal bones contacting each other along their midline was derived independently three times within Osteoglossomorpha: (1) in (†*Laeliichthys* (†*Joffrichthys* (†*Sinoglossus* (*Heterotis* + *Arapaima*))))); (2) in Notopteridae; and (3) in (†*Singida* (*Scleropages* + *Osteoglossum*)). A minor point of criticism, which is reflected in my definition of the character states, is that the nasals in some elopiforms (e.g. *Elops saurus*; Fig. 9A) have the nasals separated by both the anterior part of the frontals and the ethmoid bones. Li & Wilson (1999: 382) defined state 1 as having the nasals 'separated *mainly* by the mesethmoid' (my emphasis). As such, many Elopiformes

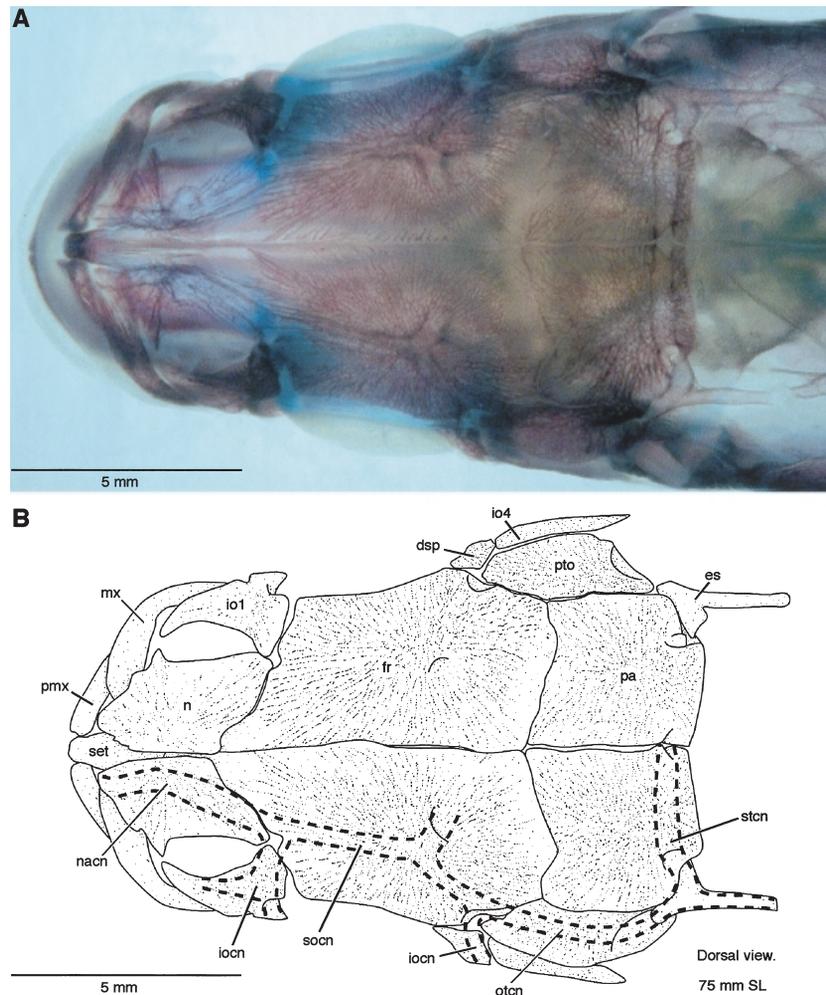


Figure 14. Skull roof of a juvenile specimen of *Heterotis niloticus* (UMA F10653, 75 mm SL) in dorsal view. A, photograph. B, line drawing. Note that some skull elements are not included in line drawing (e.g. posterior flanges of the parietals, see Fig. 13). The course of the sensory canals is outlined on the left side. At this stage, the frontals are still tapered slightly anteriorly, so that the anterior margin is narrower than the posterior margin (although this is not as extreme as in the 62 mm SL specimen illustrated by Taverne, 1977: fig. 95).

should better be coded as 1 (e.g. *Elops saurus*, Fig. 9A; *Megalops atlanticus*, UMA F10251, pers. observ., see also Forey, 1973b: fig. 20), as most of the length of the nasals is separated by the ethmoid bones rather than the frontals. The nasals of elopomorphs do appear to be further posterior than those of osteoglossomorphs (i.e. they overlap more with the frontals than in any osteoglossomorph except mormyroids; see below). *Elops* is therefore coded as state 0.

In mormyroids, the nasal bones vary in shape, although those examined here are all gutter like (see Character 7). In blunt snouted forms, such as *Petrocephalus*, the nasals are separated by both the elements of the ethmoid region and the anterior portion of the frontals (for an extreme example of this, see Taverne's, 1969: fig. 29 illustration of *P. bane*). In my

specimens of *P. simus*, I noticed that posteriorly the nasals come close to contacting each other in the midline, although they remain separated by the frontals. In long snouted forms, on the other hand, the nasals lie immediately lateral to the anterior portion of the frontals, which are telescoped to form the skeletal support of the characteristic rostrum (e.g. *Campylomormyrus*, Taverne, 1968b: fig. 1). In *Gymnarchus*, the nasals lie anterior to the frontals (Taverne, 1972: fig. 90).

The left and right nasals of †*Lycoptera* (Fig. 15A), *Hiodon* (Fig. 9C), †*Eohiodon*, and *Pantodon* lie lateral to the supraethmoid (state 1). In all other osteoglossomorphs (except the mormyroids; see above) for which this character could be coded the left and right nasals contact one another (state 2; e.g. *Arapaima*, Fig. 9B; *Chitala*, Fig. 9D).

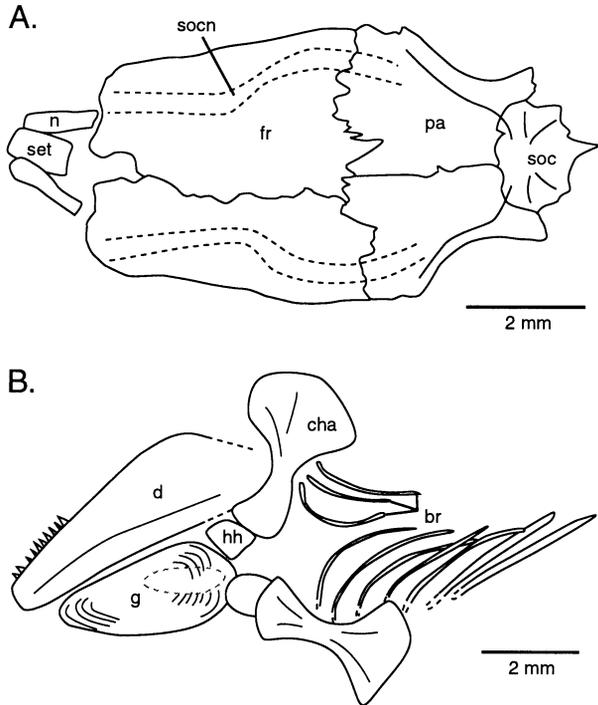


Figure 15. †*Lycoptera davidi*. A, isolated skull roof from a small specimen (MNHN 1927-13-06 a'). This specimen is preserved as an impression in ventral view. Note the small length of the frontals relative to the parietals. B, isolated elements of the lower jaw and hyoid arch (MNHN 1927-13-06 e'). This partial specimen, which is preserved in dorsal view (right lower jaw in medial view), clearly shows the presence of a gular plate. The impression left by what is possibly the basihyal toothplate (visible on the counterpart of this specimen) is marked by a dashed grey line. Anterior facing left.

The state for this character in †*Ostariostoma* is ambiguous. When Grande & Cavender (1991) re-described the only known specimen, they identified a large first infraorbital (io1) followed by four infraorbital bones (including the dermosphenotic, see their fig. 2). Another relatively large element was described as lying lateral to the posterior portion of the nasal capsule, in slight contact with the frontal. This bone, which Grande & Cavender (1991) identified as the antorbital, appears to carry a portion of a sensory canal. A small, poorly preserved bone was identified possibly as a nasal. Li & Wilson (1996a: fig. 3), on the other hand, interpreted the large element that Grande & Cavender (1991) identified as io1 as being a separate antorbital and io1, the antorbital as a nasal, and the questionable nasal as a mesethmoid. Given that many of these features are very subtly preserved on this unique specimen (e.g. I could not identify the suture that Li & Wilson, 1996a described between

their 'antorbital' and 'io1'), I coded †*Ostariostoma* as unknown for this character (as I do for the other characters of the nasal bones below).

The condition in †*Singida* is also unclear (pers. observ.) and is coded here as unknown (coded as state 2 by Li & Wilson, 1999). As Greenwood & Patterson (1967: 215) described it, the nasal of †*Singida* is a 'poorly preserved bone which has a large pore at each end, the upper pore lying close to the groove for the supraorbital sensory canal at the anterior tip of the frontal; this bone appears to be a nasal which was not firmly sutured to the frontals as are the nasals of osteoglossoids, and is intermediate in size between the large nasals of osteoglossoids and the small, tubular nasal of *Hiodon*.' †*Palaeonotopterus* was coded as unknown because the nasals are not preserved at all.

(7) *Nasal bones*: Tubular but not curved [0]; Tubular and strongly curved [1]; Gutter-like [2]; Flat and broad [3]. Modified from LW96[12]. This character was originally identified by Li & Wilson (1994) when they concluded that a strongly curved, tubular nasal bone is diagnostic of the genus *Hiodon* (see Hilton, 2002: fig. 13). However, an identical shaped nasal bone (state 1) has been discovered in all species of †*Eohiodon* as well (Hilton & Grande, unpublished data) and is therefore considered a synapomorphy of *Hiodon* + †*Eohiodon*. In order to better describe the variation in the shape of the nasal bones, I divided Li & Wilson's (1996a) character state 2 into two states (my states 2 and 3). The nasals of notopterids are strongly gutter-like (e.g. *Chitala*, Fig. 9D). Within mormyroids, which Li & Wilson (1999) coded as 'gutter-like or irregularly subrectangular', there is significant variation in the overall shape of the nasal bones, although all of those studied here are, indeed, gutter-like. Much of this shape variation may be associated with the skeletal rearrangements due to the elongation of the snout in some mormyroids. For instance, in the short-snouted genus *Petrocephalus*, the nasals are very much gutter-like, closely resembling those found in notopterids. However, in mormyroids with very elongate snouts (e.g. *Gnathonemus*, see Taverne, 1968a: fig. 4; *Campylomormyrus*, Taverne, 1968b: fig. 1), the nasals are slender straight bones that lie lateral to the anterior extensions of the frontals (see Character 6). All other osteoglossomorphs for which this character could be scored have nasals that are flat and broad (state 3; e.g. *Arapaima*, Fig. 9B).

An associated character concerning the shape of the posterior edge of the nasal bone (although only when this bone is gutter-like) was defined by Li & Wilson (1996a: character 22; also 1999: character 4), and was used to support their Osteoglossoidae (= Osteoglossidae). Many of the taxa that they have coded as '0', however, logically cannot be coded for this character

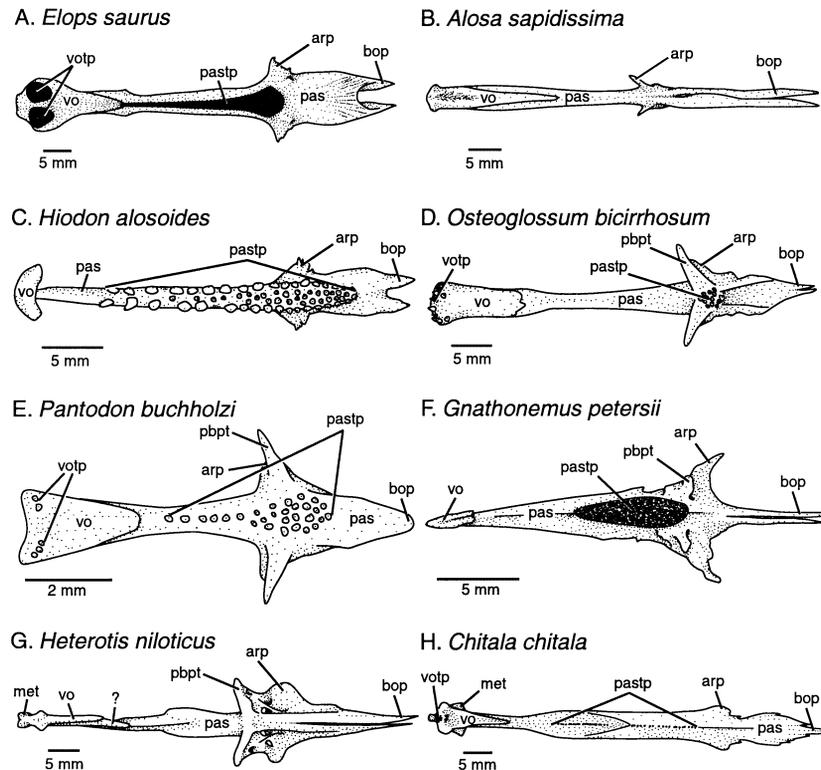


Figure 16. Parasphenoid and vomer in ventral view. A, *Elops saurus* (UMA F10255, 425 mm SL). B, *Alosa sapidissima* (UMA F10359, 390 mm SL). C, *Hiodon alosoides* (UMA F10586, 273 mm SL). D, *Osteoglossum bicirrhosum* (UMA F10160, 365 mm SL). E, *Pantodon buchholzi* (UMA F11265, approx. 50 mm SL). F, *Gnathonemus petersii* (UMA F11267, approx. 140 mm SL). G, *Heterotis niloticus* (MCZ 50959, adult, unknown SL). H, *Chitala chitala* (UMA F10349, 437 mm SL). Note that the mesethmoid is fused to the vomer in *Chitala* and *Heterotis*. Anterior facing left. Illustration of *Hiodon* modified from Hilton (2002: fig. 31).

because they do not possess a gutter-like nasal bone (e.g. *Hiodon*). This character therefore should have been coded as inapplicable for several taxa.

(8) *Parasphenoid teeth*: Absent [0]; Small [1]; Large and found along the length of the parasphenoid [2]; Large and restricted to the basal portion of the parasphenoid [3]. Modified from A99[12]; see also Shen (1996: character 9). Many early groups of teleosts have small teeth on the parasphenoid, as in *Elops* (Fig. 16A); this is plesiomorphic for Neopterygii (Patterson, 1975b; Arratia, 1999). Absence of parasphenoid teeth (e.g. in *Alosa*, Fig. 16B) characterizes more derived teleosts (Arratia, 1999). Within Osteoglossomorpha, there is wide diversity of form and position of these teeth. I consider the presence of teeth on the parasphenoid to be one component of the so-called parasphenoid tongue bite apparatus (Hilton, 2001; see Characters Not Used in Analysis).

Most osteoglossomorphs have well developed, enlarged teeth on most of the ventral surface of the parasphenoid (state 2; e.g. *Hiodon*, *Pantodon*, and

Gnathonemus; Fig. 16C, E, F, respectively), and this condition supports the monophyly of Osteoglossomorpha as a whole. †*Joffrichthys* and †*Lycoptera* also have large teeth (Figs 12 and 17, respectively) on the parasphenoid. †*Palaeonotopterus* has a large tooth patch that appears to be formed of fused teeth (Cavin & Forey, 2001). That these taxa are coded similarly does not imply that the teeth are of similar overall form, but only that the teeth are enlarged. Further study may reveal a pattern to the variation in the form of these teeth (e.g. the form of the parasphenoid teeth in *Hiodon* and †*Palaeonotopterus* are quite different, although both are enlarged).

Some osteoglossomorphs (e.g. *Chitala*, Fig. 16H) have parasphenoid dentition that is secondarily reduced in size (state 1), although this reduction is only particularly noticeable in adults. In some osteoglossomorphs, the dentition has been lost completely (state 0; e.g. *Heterotis*, Fig. 16G). I have added an additional character state (state 3) to distinguish the conditions found in *Osteoglossum* and *Scleropages* from those found in other osteoglossomorphs with large

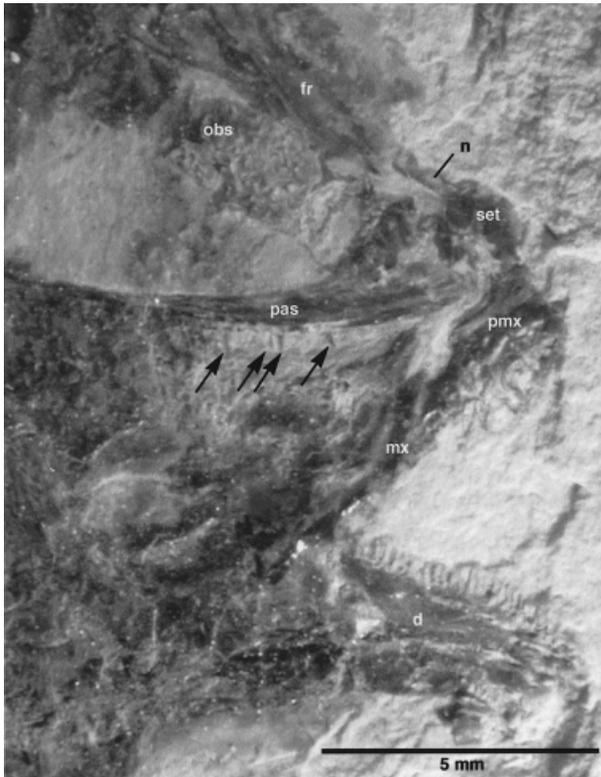


Figure 17. Head of †*Lycoptera cf. davidi* (UMA F10652, 110 mm SL) in lateral view. Arrows indicate well-developed parasphenoid teeth. Anterior facing right.

parasphenoid teeth. In these taxa, the parasphenoid tooth patch, which is composed of large teeth, is restricted to a small area posterior of the basipterygoid processes and ventral of the ascending processes (e.g. *Osteoglossum*, Fig. 16D).

†*Singida* is coded as unknown because, although no teeth are visible, the posterior portion of the parasphenoid is obscured by overlying bones. Greenwood & Patterson (1967: 215) suggested that 'it is probable that the bone was toothless', based on the observation that its oral jaws are edentulous. †*Ostariostoma* is another taxon that is difficult to interpret due to preservation. Grande & Cavender (1991) could not say whether or not the parasphenoid had teeth (i.e. none were visible to these authors but they could not rule out absence due to lack of preservation by being obscured by more superficial bones). Li & Wilson (1996a), however, illustrated the parasphenoid with two teeth in the orbital region of the bone. I could not find these teeth in examining this specimen and therefore code this character as unknown for this taxon. Available specimens of †*Phareodus* did not show the ventral structure of the parasphenoid clearly, so I coded this character as unknown. Taverne (1978)

and Li *et al.* (1997a), however, described a few teeth in a position similar to those of *Osteoglossum* and *Scleropages*.

(9) *Basipterygoid process*: Absent [0]; Present [1]. Modified from LW99[13]. The basipterygoid process is an enlarged projection from the parasphenoid that articulates with the suspensorium. Several groups of teleosts (e.g. †*Humbertia*, Patterson, 1970: fig. 17; †pholidophorids and †leptolepids; Patterson, 1975b: figs 62 and 92; †paraclupeids, Grande, 1982: fig. 6 and Chang & Grande, 1997: 14; †*Chanoides*, Patterson, 1984: fig. 4), including several osteoglossomorphs (see below), possess well developed basipterygoid processes. As pointed out by Patterson (1984: 432), however, this is 'a structure that is rarely retained in Recent teleosts' (e.g. *Elops* lacks a basipterygoid process, Fig. 16A, as does the clupeomorph *Alosa*, Fig. 16B). There is also an extremely well developed basipterygoid process in Lepisosteidae, but it consists of two bones broadly sutured together (the prootic and the parasphenoid) and thus does not completely correspond with the basipterygoid process of teleosts (L. Grande, pers. comm., 2002). Arratia & Schultze (1991) concluded that the basipterygoid process found in some members of Osteoglossomorpha were not homologous to those of other fishes because they articulate with the endopterygoid rather than the metapterygoid, because of its position on the parasphenoid, and because of its distribution among basal teleosts (i.e. parsimony demands that these elements are derived independently in osteoglossomorphs). Thus, these authors termed the processes in osteoglossomorphs 'ventrolateral processes' to reflect this independent evolution. Shen (1996) accepted this homology statement, and coded *Osteoglossum* as lacking a basipterygoid process. Given that Arratia & Schultze's homology statement was at least in part based on character distribution, Shen's coding for *Osteoglossum* is logically circular. The presence of a basipterygoid process in osteoglossomorphs must be considered independently derived from the plesiomorphic condition, as was suggested by Arratia & Schultze (1991), although I do not see the necessity for a new term.

There is no basipterygoid process in hiodontids (e.g. *Hiodon*, Fig. 16C) or in notopterids (e.g. *Chitala*, Fig. 16H). The presence of a basipterygoid process in †*Palaeonotopterus* is uncertain (Cavin & Forey, 2001: 45). I found no trace of a basipterygoid process in †*Lycoptera*, which is how it was coded for by Li & Wilson (1999), but Gaudant (1968) indicated the presence of one. †*Joffrichthys* was coded as lacking a basipterygoid process by Li & Wilson (1999), which is supported by the FMNH specimen from North Dakota (Fig. 12).

Well developed basipterygoid processes that articulate with the bones of the suspensorium are found in

members of Osteoglossiformes (e.g. *Osteoglossum*, Fig. 16D; *Pantodon*, Fig. 16E; and *Heterotis*, Fig. 16G). There is a moderate basiptyergoid process in some mormyroids (e.g. see Taverne, 1968a, b, 1969, 1971, 1972). Mormyroidea (= *Gymnarchus* + Mormyridae) was coded by Li & Wilson (1999: 382) as not having a process, although this may be because the authors specified that the basiptyergoid process must articulate 'mainly with the postero-dorsal end of [the] endopterygoid and the dorsal process of [the] metapterygoid' (the process of mormyrids is typically reduced so that contact with the suspensorium is lost; pers. observ.). *Gymnarchus* lacks a basiptyergoid process (Taverne, 1972: fig. 93), and there is significant variation in the size of the basiptyergoid process within the family Mormyridae. In some taxa, the process may be absent altogether (e.g. *Mormyrus*, Taverne, 1972: fig. 4), to moderate in size (e.g. *Gnathonemus*, Fig. 16F), to very well developed (e.g. *Hyperopisus*, Taverne, 1968a: fig. 24). Taverne (1972: 61) wrote 'Le processus basiptyergoïde du parasphénoïde est beaucoup plus développé que chez les autres Mormyridae et s'articule sur le métapterygoidé' [The basiptyergoid process of the parasphenoid is much more developed [in some mormyrids] than in other Mormyridae and this structure articulates with the metapterygoid]. Therefore, at the very least, Mormyroidea should have been coded as polymorphic.

†*Ostariostoma* is coded here as '?' (coded as absent by Li & Wilson, 1999), because, although there is no evidence that a basiptyergoid process exists in this taxon (e.g. a process is broken through the more superficial bones, as in †*Singida* and †*Phareodus*), the parasphenoid is covered posteriorly, so that the region where a basiptyergoid process would be cannot be seen (Grande & Cavender, 1991: fig. 2). Li & Wilson (1999) also describe a basiptyergoid process as present in †*Kuyangichthys*, which was one of the characters they cited as differing between this genus and †*Lycoptera*.

(10) *Supratemporal commissure passing through the parietals*: Absent [0]; Present [1]. LW99[10]. This character was described by Li & Wilson (1999; see also Li *et al.* 1997) and they coded it as present in Mormyroidea, Notopteridae and Clupeoidea; all other taxa were coded as absent or unknown. As pointed out by Cavin & Forey (2001), they made an error in the coded distribution of this character. In mormyroids, †*Palaeonotopterus* and †*Phareodus*, the only portion of the supratemporal canal that is enclosed in bone is surrounded by the extrascapular.

In notopterids, the supratemporal canal does cross the back of the skull within the parietals. A supratemporal canal passing through the parietals also is found in Osteoglossidae (e.g. *Heterotis*, Figs 13, 14; *Osteoglossum*, Fig. 8E). In †*Joffrichthys*, the parietal appears

to have a canal crossing it posteriorly, although this was not described by Li & Wilson (1996b). The supratemporal canal also passes through the parietals in a number of nonosteoglossomorph teleosts (e.g. Clupeomorpha, Grande, 1985).

The parietals in †*Ostariostoma* are not very well preserved, although Grande & Cavender (1991: fig. 2) found no trace of a canal in these bones; I agree with this interpretation. †*Singida* could not be coded due to lack of preservation as well.

(11) *Supraorbital sensory canal*: Ending in parietal [0]; Ending in frontal [1]. LW99[12]. This character also was included in Li *et al.* (1997b: character 7). My only comment on this character is that the condition in *Hiidon* is polymorphic (Hilton, 2002). In †*Lycoptera*, the supraorbital canal ends in the parietal (Fig. 15A). This was also seen in a large, relatively well-preserved specimen (UMA F10652), in which the supraorbital canal clearly extends into the parietal; this condition has been reported for other species of †*Lycoptera* as well (e.g. Jin *et al.*, 1995). I coded this character as unknown for †*Singida* and †*Joffrichthys*. The parietals are incompletely known in †*Singida*, although Greenwood & Patterson (1967: 214) remark that the frontal bone possesses a 'long posterior branch of the [supraorbital] canal, in the holotype running back almost to the hind end of the frontal in an open groove; a similar but shorter groove occurs in *Scleropages* & *Heterotis*.' Li & Wilson (1999) coded †*Joffrichthys* as having the supraorbital canal ending in the parietal. This is not evident in their illustration (Li & Wilson, 1996b: fig. 3) and I could not definitively tell in specimens that I examined. Newbrey & Bozek (2000), however, in their description of †*J. triangulpterus*, remarked that the supraorbital canal ends in the frontal.

(12) *Orbitosphenoid*: Present [0]; Absent [1]. LW96[44]. Absence of the orbitosphenoid in *Scleropages* and *Osteoglossum* was described by Ridewood (1905) and Taverne (1979: 28), and was identified by Li & Wilson (1996a, 1999: character 24) as a character uniting these two genera (also Taverne, 1998: character 277). This is supported by my analysis (see Character Optimization and Node Support).

(13) *Basisphenoid*: Present [0]; Absent [1]. The basisphenoid has been lost in several osteoglossomorphs, apparently independently. The absence of a basisphenoid in several osteoglossomorphs (some mormyrids and osteoglossids) was noted by Ridewood (1904a, 1905). Taverne (1979: 29) described the condition in *Heterotis* as follows: 'la territoire du cartilage basisphénoïdien est envahi, au stade adulte, d'une part, par les ptérosphénoïdes qui se répandent dans la zone méningostes et, d'autre part, par un processus

médio-dorsal du parasphénoïdes qui vient occuper la région du bélophragme' [In the adult, the 'basisphenoid' region of cartilage is invaded, in part by the pterosphenoids, which occupy the region of the meningost, and, in part by a middorsal process of the parasphenoid, which occupies the area of the belophragm]. In *Arapaima*, however, the parasphenoid is flat and broad, and does not bear any dorsal process, although the basisphenoid is absent. As observed by Taverne (1979), the basisphenoid is somewhat reduced in size in *Xenomystus* and absent in *Papyrocranus*, and well-developed in other notopterids (*Chitala*, pers. observ.). Of the mormyrids examined here, only *Petrocephalus* has a basisphenoid. This also was the only mormyrid genus found by Taverne (1979) to possess a basisphenoid, although he identified a basisphenoid that is fused to the surface of parasphenoid in *Gymnarchus* (Taverne, 1972: fig. 91, 1979); this was also observed by Ridewood (1904a: 210) and Benveniste (1994: 17).

(14) *Basioccipital process of the parasphenoid*: Divided [0]; Median [1]. The basioccipital process (Fig. 16) of the parasphenoid is defined as the portion of the parasphenoid that lies ventral to the occipital region of the neurocranium (this is equivalent to what Grande & Bemis, 1998 termed the posterior flanges of the parasphenoid for *Amia calva*). Within osteoglossomorphs, there are two distinct forms for this structure: either divided (state 0), in which there the process is distinctly paired (e.g. *Hiodon*, *Osteoglossum*, *Arapaima* and *Gnathonemus*, Fig. 18B–E, respectively; *Heterotis*, Fig. 16G); or median (state 1), in which the process tapers to a point (e.g. *Chitala* and *Pantodon*, Fig. 18F, G, respectively). In *Osteoglossum* (Fig. 16D), the divided basioccipital processes converge onto the midline, but are still clearly paired (see also Taverne, 1977: fig. 45). The parasphenoid of †*Phareodus* ends posteriorly in a rounded tip (Li *et al.*, 1997a: fig. 2B or a series of very dense interdigitations (Taverne, 1978: fig. 5), but it is not divided into a distinct pair of processes.

In notopterids, the overall form of the basioccipital process is variable, although none of the taxa within the family I examined possess a distinctly divided basioccipital process. In *Papyrocranus*, for instance, there are several interdigitations in the basioccipital process (see Taverne, 1978: fig. 116) although taken together, they form a triangular median process, and in *Xenomystus* (Taverne, 1978: fig. 93) it is broadly rounded. *Chitala* (Figs 16H, 18F) and *Notopterus* (Taverne, 1978: fig. 64), clearly have a median basioccipital process. The mormyroids examined are similar to *Gnathonemus* (i.e. they have slender elongate divided basioccipital processes Figs 16F, 18E), as well as those illustrated in the various works of Taverne,

including *Gymnarchus* (Taverne, 1972: fig. 93). The condition is unknown in †*Lycoptera*, †*Eohiodon*, †*Joffrichthys*, †*Singida*, †*Ostariostoma* and †*Palaeonotopterus*.

(15) *Ventral occipital groove*: Present [0]; Absent [1]. The ventral surface of the occipital region of the skull (i.e. the basioccipital and parasphenoid) in osteoglossomorphs may (e.g. *Hiodon*, *Osteoglossum*, *Chitala*) or may not (e.g. *Arapaima*, *Pantodon*, *Gnathonemus*) possess a well defined groove for the anterior portion of the dorsal aorta (see Fig. 18). This aortal groove appears to be independently absent in different groups of osteoglossomorphs. In *Arapaima*, this region of the neurocranium is extremely flattened (Fig. 18D). Interestingly, this condition is also seen in an undescribed *Osteoglossum*-like species from the Eocene London Clay (pers. observ. & P. L. Forey, pers. comm., 2001). In *Heterotis* (Taverne, 1977: fig. 96) and the mormyrids examined (e.g. *Gnathonemus*, Fig. 18E), there is no distinct groove, although the occipital region of these taxa is not flattened as in *Arapaima*. In *Pantodon*, the occipital region is inflated and there is no distinct aortal groove (Fig. 18G); the groove illustrated by Taverne (1978: fig. 33) is apparently due to this ventral inflation of the prootics, and basioccipital rather than a groove in the basioccipital. An aortal groove is present in †*Palaeonotopterus* (Forey, 1999: fig. 2) and in †*Eohiodon* (FMNH 9881), in which the basioccipital is shown to have a morphology exactly like that of the extant *Hiodon* (see Hilton, 2002: figs 12C, D and 22). The condition is unknown in †*Lycoptera*, †*Joffrichthys*, †*Singida*, and †*Ostariostoma*.

(16) *Intercalar*: Present [0]; Absent [1]. T98[157]. Taverne (1998) identified the absence of the intercalar as a synapomorphy of Mormyroidea, and this was supported by Cavin & Forey (2001: fig. 13, character 12), as it is in my analysis. Benveniste (1994: 16), citing evidence from Orts (1967), suggested that the intercalar was present in mormyroids as a slender rod of bone in which the 'posterior extremity is enlarged and flattened, and is fixed dorsally to the basioccipital ([her] pers. observ.). The anterior extremity, free and pointed, lies against the ventral side of the auditory vesicle, slightly behind and more interiorly to the diverticulum.' I could not confirm the presence of the element that Benveniste described, but at the very least, the intercalar is absent in mormyroids as an autogenous element.

(17) *Cranial nerve foramen/foramina*: In the prootic [0]; Straddling the suture between the prootic and pterosphenoid [1]; Foramen straddling the suture between the sphenotic and pterosphenoid [2]; Foramina are separate from one another, one straddling the

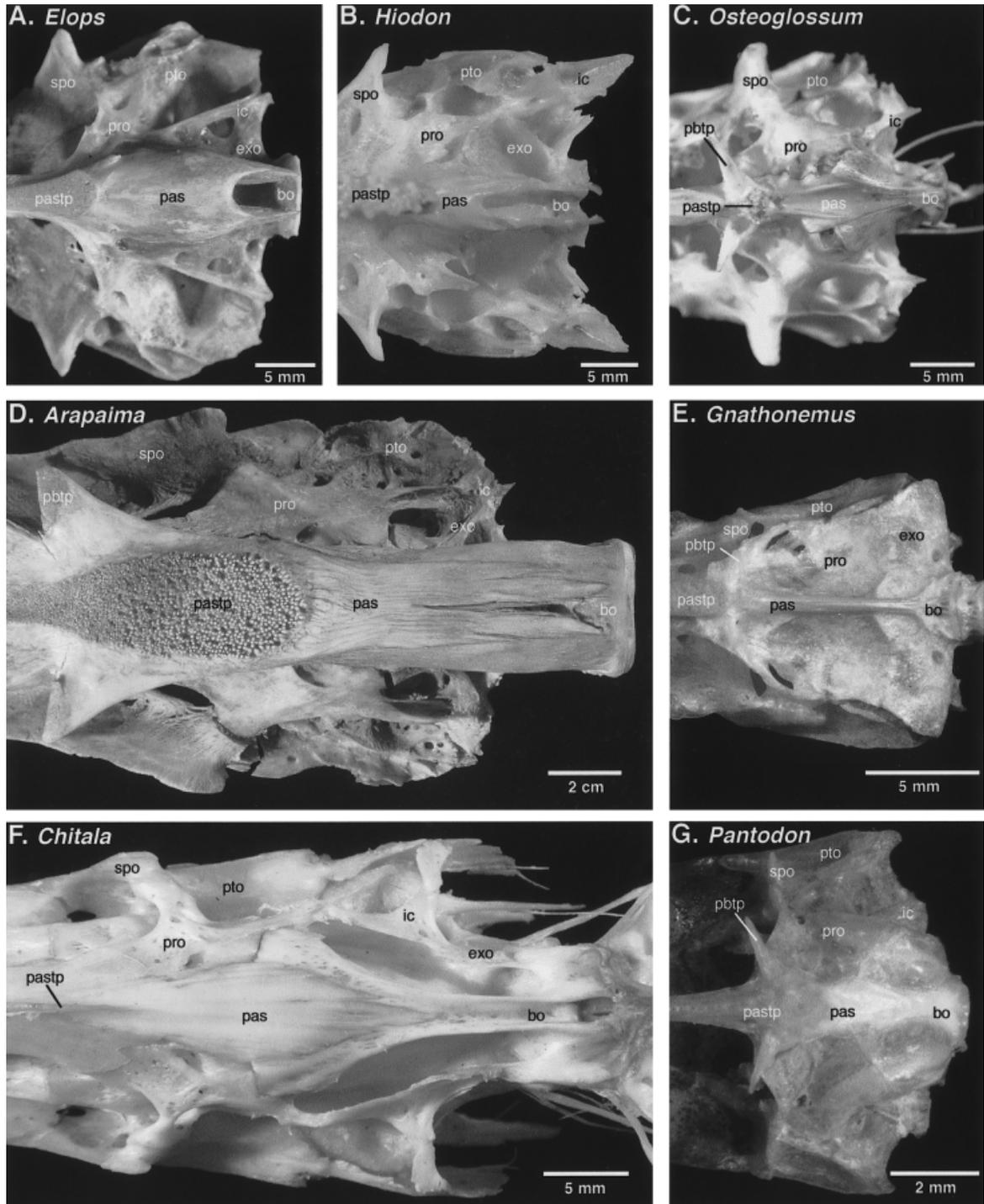


Figure 18. Occipital region in ventral view. A, *Elops saurus* (UMA F10255, 425 mm SL). B, *Hiodon alosoides* (UMA F10581, 315 mm SL). C, *Osteoglossum bicirrhosum* (UMA F10160, 365 mm SL). D, *Arapaima gigas* (UMA F10355, est. 1500 + mm TL). E, *Gnathonemus petersii* (UMA F11267, approx. 140 mm SL). F, *Chitala chitala* (UMA F10349, 437 mm SL). G, *Pantodon buchholzi* (UMA F11265, approx. 50 mm SL). Anterior facing left.

suture between the prootic, sphenotic and the pterosphe-noid (dorsally) and one straddling the suture between the prootic, pterosphe-noid and parasphenoid (ventrally) [3]. Modified from CF01[5]. This character refers to the foramen for the nerve that historically was called the combined cranial nerves V and VII; this nerve actually consists mostly of the anteroventral lateral line nerve as well as V (VII is no longer regarded as carrying lateralis fibres; see Northcutt & Bemis, 1993). This is not to be confused with the foramen for the so-called hyomandibular trunk of nerves V and VII (as far as I know, the hyomandibular trunk foramen is always fully in the prootic in osteoglossomorphs). Regardless of the exact identification of the nerve passing through the foramen, however, correspondence of that foramen between taxa can still be established based on position, although future confirmation through comparative neuroanatomy would be ideal.

Primitively for teleosts, the prootic completely surrounds this foramen anterodorsal to the anterior entrance for the jugular canal (Patterson, 1975b) and is exemplified in this analysis (state 0) by *Elops*, *Hiodon* (Fig. 19A), *Heterotis*, *Scleropages* and *Osteoglossum*.

Cavin & Forey (2001: fig. 5) identified the condition in which this foramen is within the suture between the prootic and the pterosphe-noid as a synapomorphy of †*Palaenopterus* and all other noto-pterids (e.g. Fig. 19B; Cavin & Forey, 2001: fig. 13A). A similar condition also is present in *Pantodon* (Fig. 19C), although the foramen is confluent with the anterior opening of the jugular canal. This may represent a different condition than that of noto-pterids, but in that the nerve likely passes through the anterior part of this foramen, which does straddle this suture, I coded it the same state as seen in noto-pterids. In *Arapaima*, a large foramen positioned between the prootic, sphenotic, pterosphe-noid and parasphenoid (pers. observ.; see Taverne, 1978: fig. 125) encloses cranial nerve III, V, VI, and VII, the jugular vein and the external carotid artery. Because this foramen encloses cranial nerves V and VII, and is positioned (in part) between the prootic and pterosphe-noid, *Arapaima* is also coded here as state 1. However, given the morphological specializations of this foramen (e.g. the parasphenoid and the sphenotic also being involved), it is not surprising that it is interpreted in my results as having evolved independently in *Arapaima*.

The condition in mormyroids is somewhat more complicated. In some mormyroids, this foramen is positioned between the sphenotic and the pterosphe-noid (state 2). In this analysis, *Campylomormyrus* (pers. observ.; Taverne, 1972b: fig. 2) and *Petrocephalus* (pers. observ.; see Taverne, 1969: fig. 30) display this condition. Other mormyroids that possess this state

include *Boulengeromyrus* (Taverne, 1969: fig. 2), *Genyomyrus* (Taverne, 1969: fig. 19), *Marcusenius* (Taverne, 1971: fig. 2), *Cyphomyrus* (Taverne, 1971: fig. 42), *Mormyrus* (Taverne, 1972: fig. 2), *Mormyrops* (Taverne, 1972: figs 16, 28), *Hyperopisus* (Taverne, 1972: fig. 33), *Isichthys* (Taverne, 1972: fig. 47), *Myomyrus* (Taverne, 1972: fig. 62), *Stomatorhinus* (Taverne, 1972: fig. 76) and *Gymnarchus* (Taverne, 1972: fig. 91). In some of these taxa (e.g. *Isichthys*), the parasphenoid may also be involved in this foramen, possibly because it also encloses the palatine ramus of nerve VII, nerves III and VI, and the orbitonasal artery (Taverne, 1972). In other mormyroids (e.g. *Gnathonemus*, Fig. 19D; see Taverne, 1968a: figs 5, 20), there are two separate foramina. The dorsal of these foramina, for nerve V (Taverne, 1968a), straddles the suture between the prootic, sphenotic and pterosphe-noid; the ventral, for nerve VII (Taverne, 1968a), straddles the suture between the prootic, pterosphe-noid and parasphenoid. To describe this condition, I defined character state 3, which is recovered here as an autapomorphy of *Gnathonemus*. Further analysis of this character within mormyroids, however, is warranted.

(18) *Suture between the parasphenoid and sphenotic*: Absent [0]; Present [1]. CF01[15]. Contact between the parasphenoid and the sphenotic (termed the autosphenotic by Cavin & Forey, 2001) lateral to the jugular canal was identified as a synapomorphy of mormyroids, as well as being present in †*Palaenopterus*. A suture between these two bones is also found in *Osteoglossum* (Taverne, 1977: fig. 43) and *Scleropages* (Taverne, 1977: fig. 72), which is, as Cavin & Forey (2001: 46) described: 'situated anteriorly to the anterior opening of the jugular canal and is thus not homologous with the pattern observed in [†] *P. greenwoodi* and mormyroids.' Parsimony also dictates that the condition in the two groups was independently evolved, further supporting the proposed non-homology. Taverne (1978: fig. 5) illustrated a specimen of †*Phareodus testis* in which the ascending process of the parasphenoid is shown in contact with the sphenotic. Li *et al.* (1997a: fig. 2), however, illustrated a specimen of †*P. encaustus* that shows the prootic in between the sphenotic and parasphenoid. This region of the skull was not clearly visible on specimens available for this study, and I therefore code †*Phareodus* as unknown. Also scored as unknown are †*Lycoptera*, †*Eohiodon*, †*Joffrichthys*, †*Singida* and †*Ostariostoma*. Because the ascending process of the parasphenoid is relatively low in some of these fishes (e.g. †*Joffrichthys*, pers. observ.), it is unlikely that there is contact with the sphenotic, but the condition must be confirmed on better preserved specimens.

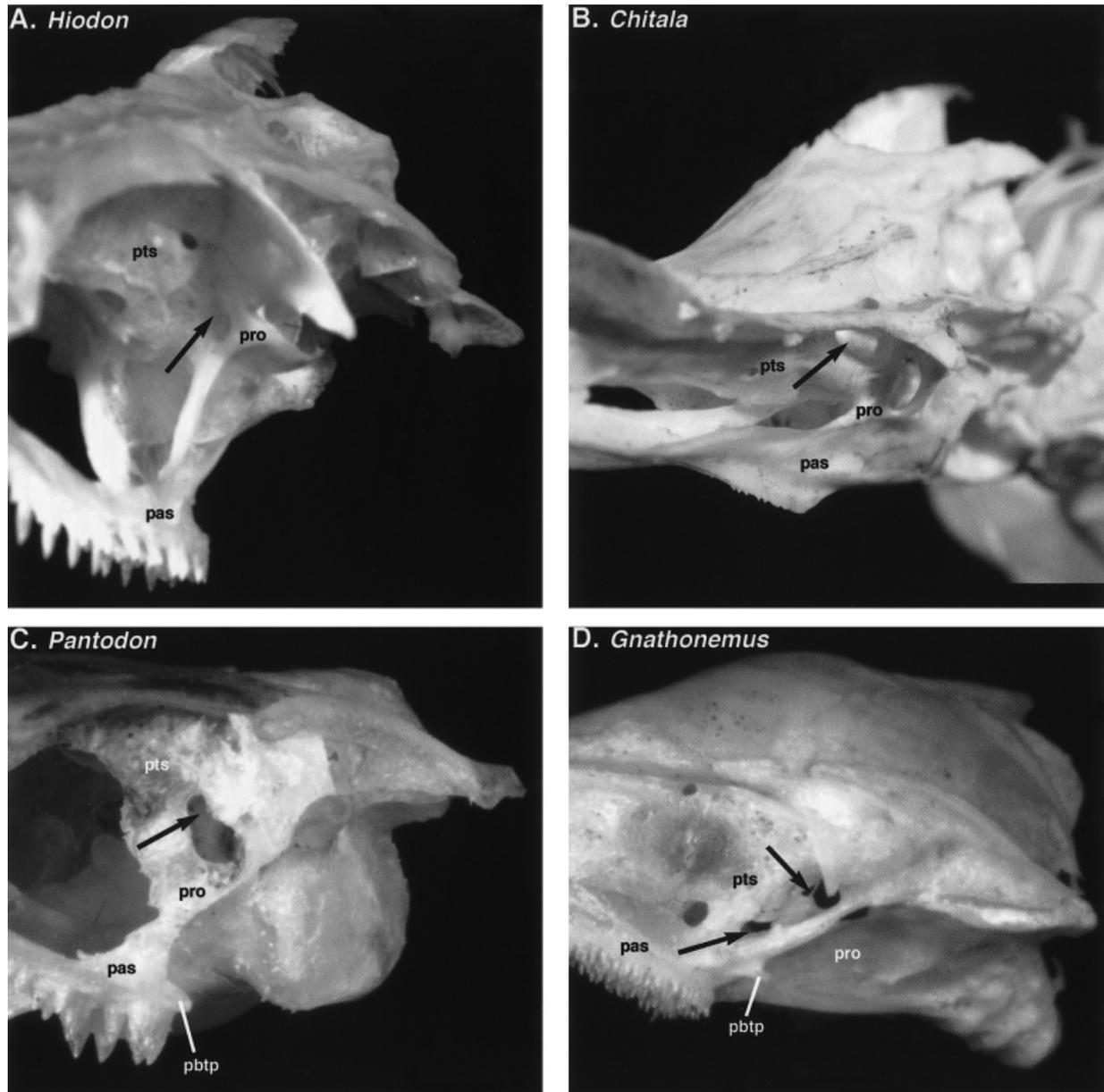


Figure 19. Photographs of neurocrania in anterolateral view showing aspects of the trigeminofacialis chamber in four osteoglossomorphs. A, *Hiodon alosoides* (UMA F10581, 315 mm SL). B, *Chitala chitala* (UMA F10349, 437 mm SL). C, *Pantodon buchholzi* (UMA F11265, approx. 50 mm SL). D, *Gnathonemus petersii* (UMA F11267, approx. 140 mm SL). Arrows indicate position of the foramen for the nerve historically called the combined cranial nerves V and VII; this nerve likely contains a portion of the anteroventral lateral line nerve as well. In *Gnathonemus*, as in some other mormyroids, there are two separate foramina (i.e. one for V and one for VII).

(19) *Foramen for cranial nerve VI*: CF01[17]. Opens within the prootic bridge [0]; Opens anterior to the prootic bridge [1]. Cavin & Forey (2001: 47) wrote that '[t]he opening for the VI in front of the prootic bridge, instead of through the prootic bridge, is a synapomorphy of notopterids + mormyroids and is absent in [†]*Palaeonotopterus*.' In *Arapaima*, VI passes through

an enlarged opening that also encloses several other nerves and blood vessels (see Character 17) that is anterior to the prootic bridge as well, but this condition is likely not homologous with the condition in notopterids and mormyroids. In *Pantodon*, VI exits the braincase, although within the prootic bridge, more ventrally than in the primitive condition (e.g. *Hiodon*,

Hilton, 2002: fig. 34D), and shares a foramen with the palatine ramus of VII ('Plus ventralement encore, un foramen s'ouvre entre la paroi du prootique et la membrane orbito-ptéro-basisphénoïdienne et sort à l'émergence hors du crâne du ramus palatinus du facial (VII) et du nerf oculomoteur externe (VI); [Further ventrally, a foramen opens between the prootic and the sphenoid region of the neurocranium, and is where the palatine ramus of the facial (VII) and the external oculomotor nerve (VI) exit the cranium]; Taverne (1978: 63, fig. 38).

(20) *Supraorbital bone*: Present [0]; Absent [1]. LW96[5]. Absence of a supraorbital was cited as a synapomorphy of Osteoglossomorpha by Li & Wilson (1996a, 1999). Ma (1987: fig. 1) figured †*Lycoptera* with a supraorbital, although more recent interpretations (e.g. Jin *et al.*, 1995) maintain that the supraorbital is absent in †*Lycoptera*. The specimens of †*Lycoptera* available for this study are not adequately preserved for me to tell if a supraorbital is present or not, and therefore I scored it as unknown. I also scored †*Palaeonotopterus* as unknown, although it is unlikely that a supraorbital was present. Li & Wilson (1999) coded a supraorbital as present in †*Kuyangichthys* and †*Jiuquanichthys*, and these taxa, along with †*Tongxinichthys*, were interpreted as the sister group of all other osteoglossomorphs. Li & Wilson (1999) interpreted the absence of a supraorbital as a synapomorphy of all osteoglossomorphs above this level (i.e. †*Lycoptera* + Hiodontiformes + Osteoglossiformes; node 70 of their fig. 3). Specimens of †*Kuyangichthys* and †*Jiuquanichthys* were not available for study. The absence of a supraorbital is interpreted here as a synapomorphy of Osteoglossomorpha (see Character Optimization and Node Support).

(21) *Otic and supraorbital sensory canal*: In bony canals [0]; Partially or completely in grooves [1]. CF01[1]. Greenwood (1973: 312) wrote that '[i]n notoapterids the cranial canals lie immediately below the skin in open bony gutters; in *Xenomystus* a small part of the temporal canal (immediately anterior to the lateral cranial fenestra) is tubular. Mormyrids, on the other hand, have much of the system carried in enclosed tubes, but the temporal part, throughout its pterotic extent, lies in a broad gutter-like fold of that bone (see Taverne, 1968[a], 1969).' As with the open infraorbital canal found in notoapterids and mormyrids (see Character 24), Nelson (1969) thought that this character was likely subject to convergence. Cavin & Forey (2001: fig. 13), however, adopted the presence of the otic and supraorbital canals at least partially in open gutters as a synapomorphy of mormyroids and notoapteroids, and noted that this condition is independently found in †*Singida*.

In most notoapterids (e.g. *Chitala*, Fig. 9D; *Papycranus*, Taverne, 1978: fig. 113), both the supraorbital and otic sensory canals are fully open and gutter-like. In fact, *Xenomystus* (Taverne, 1978: fig. 91) appears to be unique within the family in having any part of these canals enclosed in a tube (the portion just anterior of the temporal fossa is enclosed in a tube within the pterotic; pers. observ., also see Greenwood, 1973).

In mormyroids, the otic and supraorbital canals are also largely open and gutter-like, although the enclosed canal is the frontal portion of the supraorbital canal instead of the otic canal within the pterotic bone, as in *Xenomystus*. †*Palaeonotopterus* bears an open otic sensory canal on the pterotic and a posteriorly roofed supraorbital canal on the frontal (Forey, 1997: fig. 1), a condition resembling that of mormyroids. The amount of the supraorbital canal that is open appears variable within mormyroids ranging from less than half its length (e.g. *Mormyrops*, Taverne, 1972: fig. 16; *Hyperopisus*, Taverne, 1972: fig. 34; *Isichthys*, Taverne, 1972: fig. 48; *Myomyrus*, Taverne, 1972: fig. 63; *Stomatorhinus*, Taverne, 1972: fig. 77; *Gymnarchus*, Taverne, 1972: fig. 92; *Marcusenius* Taverne, 1971: fig. 3; *Petrocephalus* Taverne, 1969: fig. 31) to almost completely enclosed in a bony tube within the frontal (e.g. *Mormyrus*, Taverne, 1972: fig. 3; *Hippopotamyrus* Taverne, 1971: fig. 35; *Cyphomyrus* Taverne, 1971: fig. 43; *Boulengeromyrus* Taverne, 1969: fig. 3; *Genyomyrus* Taverne, 1969: fig. 20; *Gnathonemus*, Taverne, 1968a: fig. 6; *Campylomormyrus*, Taverne, 1968b: fig. 3). The variation in the extent of the enclosed portion of the canal may have some phylogenetic significance within mormyrids, and should be studied further in future analyses.

†*Singida* was said to have open sensory canals on the skull roof by Greenwood & Patterson (1967). Although the possibility exists that the cephalic sensory system had thin bony canals that were broken during fossilization, it does appear that the canals are open in well defined grooves in this taxon as well, and it is therefore coded as derived (following Cavin & Forey, 2001); new specimens, however, may be able to clarify the condition.

Pantodon has a similar arrangement of cephalic sensory canals (in some respects, at least) to that of *Xenomystus*, in that the otic canal is contained in a bony tube within the pterotic bone and the supraorbital canal is completely open on the frontal (Kershaw, 1970: fig. 1), although it is not contained in a well defined groove, as it is in other notoapterids and †*Singida*. Kershaw (1970: 10) wrote: 'The part of the supraorbital canal associated with the frontals is not enclosed in a bony tube but lies superficially on the frontal. In some specimens examined the skin covering the canal is supported by two or three small bony arches' (see Taverne, 1978: figs 31, 32). The difference

in morphology between the condition in *Pantodon*, on the one hand, and notopterids and †*Singida* on the other, may suggest independence of origin. However, given that the supraorbital canal is not enclosed by a bony tube but is open, I coded *Pantodon* as derived for this character in this analysis.

All other osteoglossomorphs examined have the plesiomorphic condition, with both the supraorbital and the otic canals housed in bony tubes (e.g. *Heterotis*, see Fig. 14). It should be noted that the derived state for this character may be related to the infraorbital sensory canal being open in a groove (see Character 24) and the nasal being gutter-like (Character 7), and its inclusion may be redundant (i.e. a single character describing the bones associated with the canal as gutter-like or not might be more appropriate). It also may be better in future analyses to separate this into two characters, one each to describe the condition of the supraorbital and otic canal.

INFRAORBITAL BONES

(22) *Number of bones in the infraorbital series, not including the dermosphenotic or the antorbital, if present*: Five [0]; Four [1]. Modified from LW96[11]. The reduction of the number of bones in the infraorbital series in Osteoglossomorpha is well known (Nelson, 1969; Li & Wilson, 1996a; Arratia, 1999). The reduction has always been expressed as a function of fusion of two of bones. However, all ontogenetic studies of osteoglossomorphs to date (e.g. Daget & d'Aubenton, 1957; Hilton, 2002) have failed to find any evidence for this hypothesis (see Discussion of so-called phylogenetic fusion in Hilton, 2002). Therefore, I follow the numbering of individual elements of the infraorbital series from anterior to posterior (Fig. 20), as discussed for *Hiodon* in Hilton (2002).

Although they interpreted the reduction of infraorbitals (termed as fusion of io4 and io5) as a synapomorphy of Osteoglossomorpha (Li & Wilson, 1996a), remarked that †*Lycoptera* and †*Laeliichthys* are exceptions and that the two infraorbitals are separate in these two taxa. Ma (1987: fig. 1) also showed five independent infraorbital bones anterior to the dermosphenotic. Jin *et al.* (1995) illustrated four elements for †*L. muroii* (modified here in Fig. 21). Li & Wilson (1996a), however, indicated on their cladogram that this character is a synapomorphy of Osteoglossomorphs above the level of †*Lycoptera* (Li & Wilson, 1996a: fig. 2). The specimens of †*Lycoptera* examined for my study are too poorly preserved to study the details of the infraorbital series. Specimens of †*Laeliichthys* were not available for this study.

The infraorbital bones of †*Joffrichthys* are also poorly preserved and coded as unknown. Li & Wilson

(1996b: fig. 3) and Newbrey & Bozek (2000: fig. 4A) both illustrated the infraorbital series with four elements, as in other osteoglossomorphs (except *Pantodon*, see below). However, the edges of all elements, as figured by these authors, are indeterminable (indicated in their figures by dashed lines) and I could not find convincing infraorbital bones on the specimens of †*J. symmetropterus*, let alone separations between individual infraorbital bones. The infraorbital bones of †*Ostariostoma* are also ambiguous (see discussion of identification of infraorbitals and nasals in the description of Character 7). The infraorbitals of †*Palaeonotopterus* are completely unknown (Forey, 1997). In contrast, the infraorbital bones of †*Singida* are well preserved on BMNH P.42623a (see Greenwood & Patterson, 1967: fig. 2A), and resemble those of *Scleropages*, although the second infraorbital is slightly broader.

Pantodon is unique among living osteoglossomorphs by having five infraorbital bones between the antorbital and the dermosphenotic (Fig. 20H). Nelson (1969) considered the first two elements of the series to be homologous to the first infraorbital of other osteoglossomorphs. This hypothesis was based on correlation with the number of neuromast organs (i.e. the first infraorbital of other osteoglossomorphs typically have two neuromasts, and the first two of *Pantodon* have one each; see Fig. 21). Li & Wilson (1996a, and elsewhere) presumably accepted this hypothesis, although no explicit mention was made of the condition in *Pantodon* in these studies.

(23) *First infraorbital*: Ventral to orbit [0]; Anterior and ventral to orbit [1]. Modified from LW96[41]. I recognize two forms of the first infraorbital bone: the 'normal' condition, in which the first infraorbital lies ventral to the orbit, or is only positioned in the ventral portion of the anterior margin of the orbit (state 0); and the derived condition, in which the first infraorbital is greatly enlarged and is the only element that is present along the anterior margin of the orbit (state 1). *Arapaima* (Fig. 20F) and *Heterotis* are the only taxa in my analysis to have the derived condition, and is a synapomorphy of the two genera (Fig. 5). This condition was also reported for †*Sinoglossus* by Su (1986), a fossil from the Eocene of China, and was one of the characters used by Li & Wilson (1996b) in support of their hypothesis that †*Sinoglossus* was the sister group of *Arapaima* + *Heterotis*, and that †*Joffrichthys* was in turn the sister group of all other Heterotinae. Because specimens of †*Sinoglossus* were unavailable for this study, I cannot comment on this character beyond the fact that the presence of a large io1 supports the group *Arapaima* + *Heterotis*. The state of †*Joffrichthys* is coded as unknown due to lack of preservation.

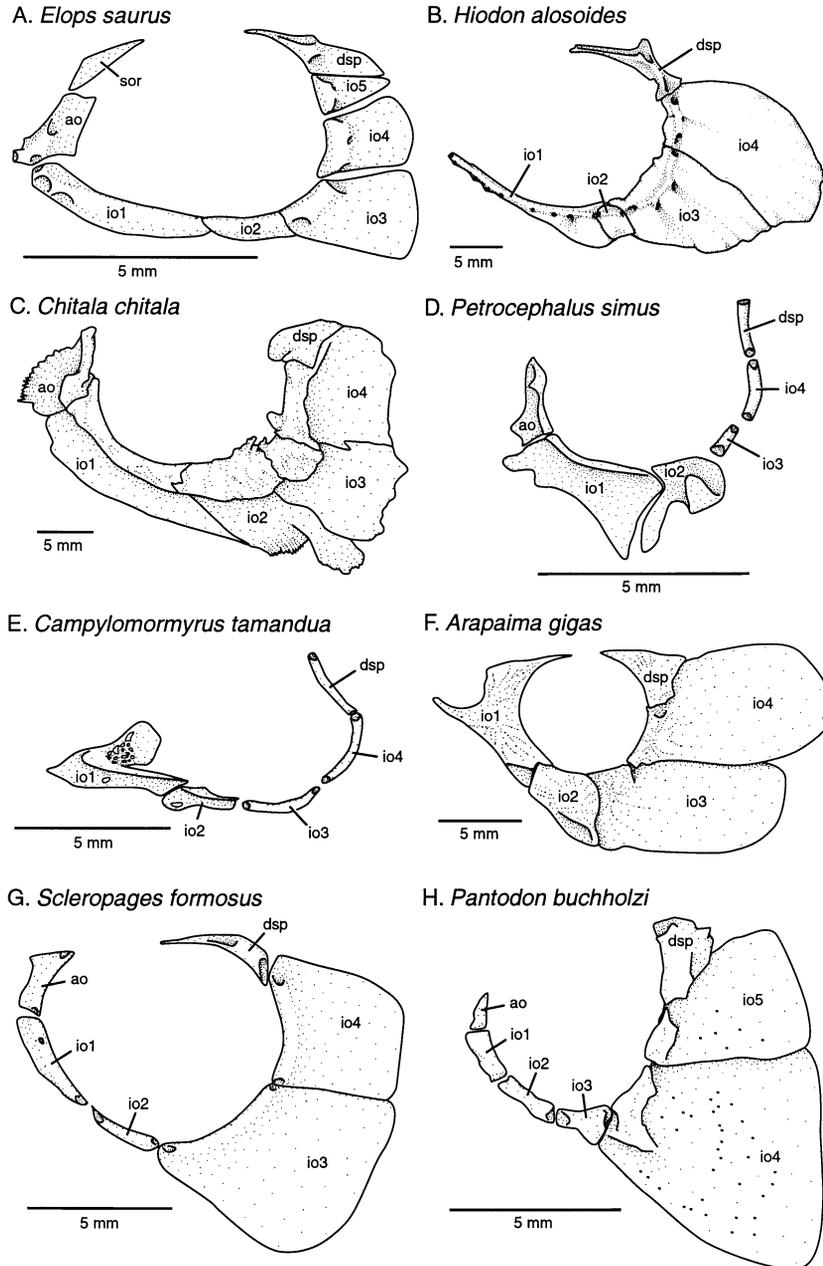


Figure 20. Infraorbital bones in lateral view. A, *Elops saurus* (UMA F11258, 62 mm SL). B, *Hiodon alosoides* (UMA F10150, 293 mm SL). C, *Chitala chitala* (UMA F10349, 437 mm SL). D, *Petrocephalus simus* (MCZ 50113, 54 mm SL). E, *Campylomormyrus tamandua* (FMNH 55300B, 84 mm SL). F, *Arapaima gigas* (UMA F11261, 145 mm SL). G, *Scleropages formosus* (FMNH uncatalogued in Geology Department, 67 mm SL). H, *Pantodon buchholzi* (UMA F11264, 70 mm SL). Anterior facing left. Illustration of *Hiodon* modified from Hilton (2002: fig. 36). Illustrations of *Arapaima*, *Petrocephalus* and *Campylomormyrus* are of right side; images reversed so anterior facing left.

This character was coined in terms of fusion between the antorbital and io1 by Li & Wilson (1996a), and stemmed from the work of Nelson (1969). Nelson (1969) suggested that the large anterior infraorbital bone found in *Arapaima* (Figs 20F, 21) and *Heterotis*

(Fig. 21) was the product of fusion between io1 and the antorbital (e.g. Fig. 20F) based on correlation with neuromast organs (the antorbital of most other osteoglossomorphs has one neuromast and io1 has two – the large bone in *Arapaima* and *Heterotis* has three;

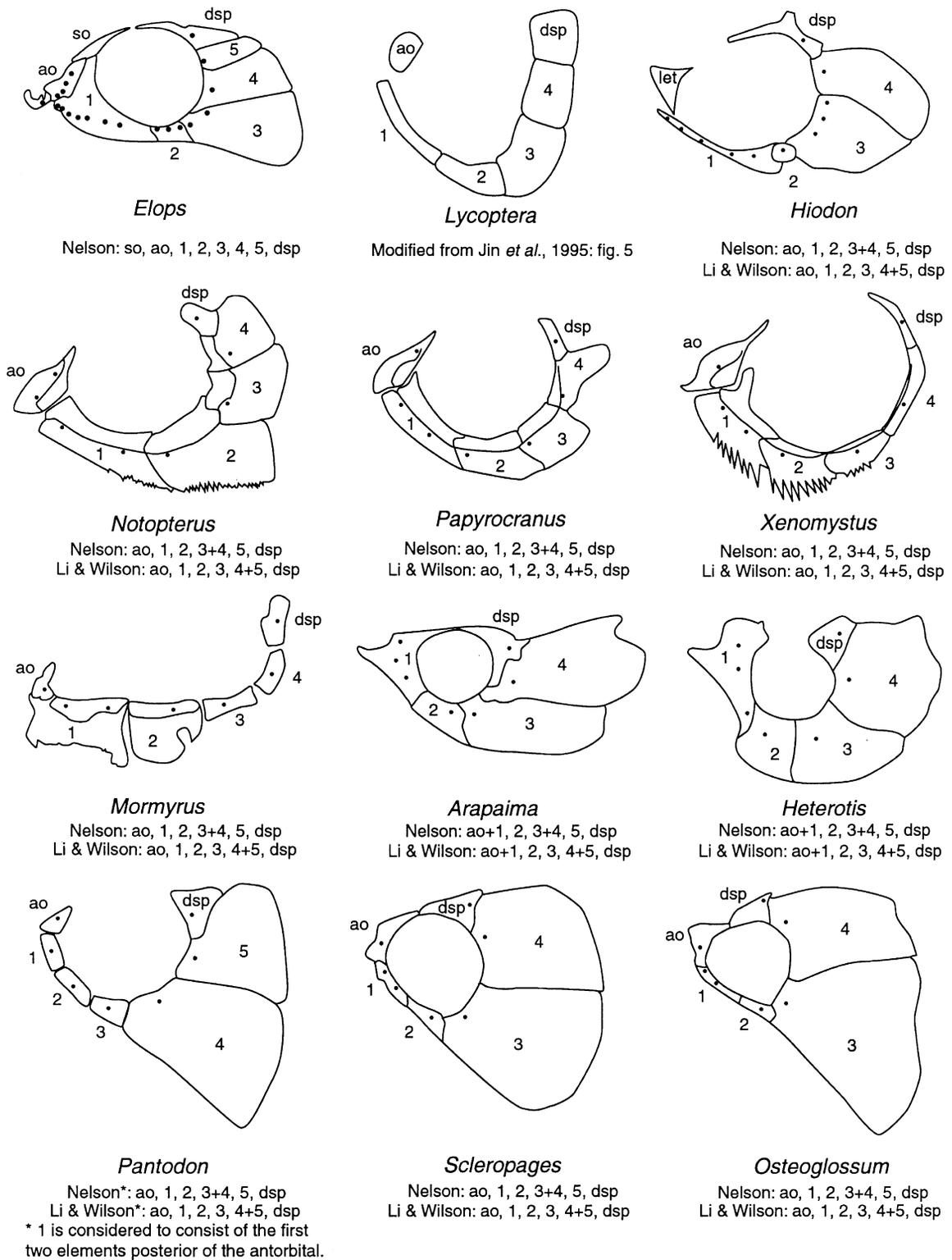


Figure 21. Infraorbital bones of *Elops* and osteoglossomorphs showing different numbering strategies employed by Nelson (1969), Li & Wilson (1996a), and the present study. Nelson's and Li & Wilson's numbering systems are given anterior to posterior, and distinct elements are separated by commas. All are redrawn from those illustrated by Nelson (1969) except for †*Lycoptera*, which is from Jin *et al.* (1995) (Nelson did not illustrate †*Lycoptera* in his study). Black dots indicate position of the neuromast organ(s) associated with each element.

see Fig. 21). No ontogenetic data are known to support this hypothesis. For example, Daget & d'Aubenton (1957) noted that the antorbital is the first ossification of the infraorbital bones of *Heterotis*, but did not find a second ossification that becomes fused with the antorbital. My small specimens of *Arapaima* (FMNH 97450; approx. 55 mm SL) already show a single element, although the infraorbital bones are relatively well developed by this stage of development. Further study of the ontogeny of this bone in both *Arapaima* and *Heterotis*, however, is warranted.

Elops is coded as having the normal condition, even though in the adult (Fig. 21) a dorsal extension of io1 separates the antorbital from the anterior margin of the orbit (Forey, 1973a). This is best considered to be secondary, because in small specimens (e.g. Fig. 20A), io lacks this dorsal extension. Other taxa (†*Lycoptera*, †*Singida* and †*Palaeonotopterus*) are coded as unknown due to preservation. Antorbitals separate from io1 have been described for †*Lycoptera* (e.g. Jin *et al.*, 1995) and †*Singida* (Greenwood & Patterson, 1967), although I could not convincingly see this bone in these taxa. †*Ostariostoma* is coded as unknown for the same reasons as Characters 7 and 22 (i.e. unclear topographic correspondence).

(24) *Condition of the infraorbital sensory canal in at least some infraorbitals*: Enclosed in a bony canal [0]; Open in a gutter [1]. Modified from LW96[32]. This character, originally discussed by Nelson (1969), was used by Li & Wilson (1996a; also 1999: character 23) in support of the group (†*Ostariostoma* (Mormyroidea + Notopteroidea)). These authors specified the gutter to be in io1–3. However, in mormyroids (at least those examined here), io3 is not open in a gutter, but rather is enclosed in an elongate slender tube of bone, as are the more posterior infraorbitals (e.g. *Petrocephalus* & *Campylomormyrus*, Fig. 20D, E, respectively). In notopterids (e.g. *Chitala*, Fig. 20C) and †*Ostariostoma* (Grande & Cavender, 1991: fig. 2), all of the bones of the infraorbital series except for the dermosphenotic have the sensory canal open and gutter-like. All other taxa for which the infraorbital bones are known are enclosed in a tube (for all taxa except †*Palaeonotopterus*, in which the infraorbital bones are completely unknown, I could at least tell that the infraorbital canal is enclosed in a tube, even though details of the infraorbital series may be lacking).

Of this character, Nelson (1969: 15) wrote that '[i]t 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.' Nelson (1969) went on to comment on

the enlarged, sinus-like openings in the bony canal of taxa such as *Arapaima* and *Heterotis*, suggesting (although not explicitly stating) that this is somehow related to the gutter-like infraorbital canals of notopterids and mormyrids. Greenwood (1973: 313) countered Nelson's idea that the gutter-like canal in notopterids and mormyrids was the result of convergence, and wrote '[t]he resemblances are too detailed, and involve rather extensive anatomical modification of structures other than the lateral-line canal system.' In my analysis, this character supports the group Osteoglossiformes.

(25) *Palatoquadrate area behind and below the orbit*: Not completely covered by the infraorbitals [0]; Completely covered by infraorbitals [1]. LW96[16]. This character was coded by Li & Wilson (1996a; also 1999: character 47) as derived for taxa corresponding to their Osteoglossidae. A second, seemingly similar character (Li & Wilson, 1996a: character 20; 1999: character 21) also was defined: 'Cheek wall formed by enlargement of 1st to 3rd infraorbitals: [0] absent; [1] present' (Li & Wilson, 1999: 382). This character was defined and coded as derived in Heterotinae (= †*Laeliichthys*, †*Sinoglossus*, †*Joffrichthys*, *Arapaima* and *Heterotis*) by Li & Wilson (1996a; also 1999: character 21). Although it is true that in some of osteoglossoid taxa (e.g. *Scleropages* and *Pantodon*, Fig. 20G & H, respectively) it is the more posterior infraorbitals that form much of the 'cheek wall' that covers the palatoquadrate region, these two characters are very closely related, if not synonymous (neither character was illustrated by Li & Wilson, and both were only briefly defined, so their exact meaning is unclear). Both characters seem to refer to the enlarged and heavily ossified nature of the posterior infraorbitals that is best exemplified by taxa such as *Arapaima*, *Scleropages* and *Pantodon* (Fig. 20F–H, respectively). This is the way in which I interpret these characters, which results in coding that is consistent with the more general character coded as derived in osteoglossoid taxa by Li & Wilson (1996a, 1999).

(26) *Dermosphenotic*: Triangular [0]; Triradiate [1]; Tubular [2]; Modified from LW96[19]. Li & Wilson (1996a, 1999: character 20) defined this character as a dichotomy between the condition of a triangular and triradiate dermosphenotic. However, in some taxa coded as possessing a triangular dermosphenotic (e.g. *Petrocephalus*, Fig. 20D; as part of the terminal taxon Mormyroidea), the dermosphenotic is not triangular, but rather is a tubular bone. Therefore I define a third character state (state 2) to describe this condition, and found it present in all mormyrids included in my analysis (*Petrocephalus*, *Gnathonemus* and *Campylomormyrus*). Taverne (1998: 123, character 121)

considered this character to be a synapomorphy of the mormyroids ('le dermosphénotique est réduit à son tube neurodermique' [the dermosphenotic is reduced to a dermal bony tube associated with the sensory canal]). This is also the condition in the notopterids *Xenomystus* (Taverne, 1978: fig. 90) and *Papyrocranus* (Taverne, 1978: fig. 113), although that of *Papyrocranus* is much shorter than in the other taxa (*Chitala* retains the primitive triangular shaped dermosphenotic, Fig. 20C). The dermosphenotic illustrated for *Scleropages* in Figure 20G also is tubular, but this is due to the early ontogenetic stage of the specimen (the adult condition was illustrated by Nelson, 1969: fig. 14; see Fig. 21 and Taverne, 1977: fig. 71; also pers. observ.). †*Ostariostoma* is coded as triangular; although it is slightly displaced and possibly damaged (see Grande & Cavender, 1991: fig. 2), it is clearly not tubular as in mormyroids, *Xenomystus* or *Papyrocranus*.

Li & Wilson (1996a, 1999) found that a triradiate dermosphenotic (state 1) is diagnostic of Hiodontiformes (Fig. 20B). My analysis supports this conclusion, although it should be pointed out that the exact shape of the dermosphenotic in †*Plesiolycoptera* is uncertain (see Li & Wilson, 1999: fig. 5, in which the infraorbital series of †*Plesiolycoptera* is illustrated and the dorsal border of the dermosphenotic, i.e. the edge that makes the triradiate shape, is completed in a dashed line, presumably indicating uncertainty in the shape of the bone). †*Lycoptera* is coded as unknown because my specimens do not clearly show the dermosphenotic, although Ma (1987: fig. 1) and others show the dermosphenotic as somewhat triangular.

SUSPENSORIUM

(27) *Posterior extent of the fossa on the neurocranium for the hyomandibula*: Formed of pterotic [0]; Formed of pterotic and intercalar [1]; Formed of pterotic and exoccipital [2]; Formed of exoccipital and intercalar [3]. The inclusion of the intercalar in the posterior portion of the fossa for the hyomandibula was discussed by Greenwood (1973), who suggested that it might be evidence of relationship between *Hiodon* and notopterids, as this condition was only otherwise known in †Ichthyodectiformes (see Bardack, 1965; Patterson & Rosen, 1977). However, Although the intercalar is included in this fossa in both *Hiodon* and notopterids, the pattern of bones that form the fossa is different. In *Hiodon* (Fig. 18B), the posterior portion of the fossa (in fact the fossa for the posterior head of the hyomandibula; see Character 28) is formed anteriorly by the pterotic and posteriorly by the intercalar, both of which contribute equally to the fossa (state 1; see Hilton, 2002: fig. 22). In notopterids (e.g. *Chitala*, Fig. 18F), on the other hand, the posterior portion of

the fossa (there is a single long head of the hyomandibula in these fishes), the majority of the fossa is formed by the exoccipital, and the intercalar is limited to the medial and posterior edges of the fossa (state 3; Fig. 18F). In *Xenomystus*, the intercalar is very large (state 0; Taverne, 1978: fig. 91), but only comprises the posteromedial portion of the fossae for the hyomandibula. In *Papyrocranus*, the intercalar is involved in the medial margin of the hyomandibular fossa. In †*Palaeonotopterus*, the posterior hyomandibular fossa is entirely within the pterotic (see Taverne & Maisey, 1999: fig. 3; note that the pterotic is incomplete in this specimen, but the exoccipital is far medial to the fossa; see also Forey, 1997: fig. 2 and Cavin & Forey, 2001: fig. 6) and the intercalar is separated from the fossa (Forey, 1997). The posterior portion of the fossa for the hyomandibula in the mormyroids examined here (e.g. *Gnathonemus*, Fig. 18E) is formed laterally by the pterotic and medially by the exoccipital (state 2). The contribution, if any, of the exoccipital is slight in *Gymnarchus* (Taverne, 1972: fig. 93).

Osteoglossum and *Scleropages* both have a deep fossa on the ventral portion of the pterotic for articulation of the posterior part of the hyomandibular head. The intercalar in both taxa wraps around and almost makes contact with this fossa, although the contribution, if any, is insignificant (Fig. 18C). In a large cleared and stained specimen of *O. bicirrhosum* (FMNH 109232b, 320 mm SL), I observed the intercalar in close contact with a cartilaginous pad separating the intercalar from the fossa part of the pterotic, although it is unclear whether this cartilage actually contributes to the fossa or not.

The posterior portion of the fossae for the hyomandibula in *Arapaima* is formed entirely within the pterotic (Fig. 18D). Taverne's (1977: fig. 127, f. hyom.) illustration is mislabelled because the fossa is more laterally located on the skull (as labelled, it appears as if the intercalar is in contact with the posterior portion of the fossa). In my adult specimen of *Heterotis* (which is partially disarticulated and could not be examined for this character) the pterotic fully surrounds the posterior portion of the fossa. Taverne (1977: fig. 96) showed the intercalar close to the posterior margin of the fossa, whereas in my small specimen it is more removed, as it is in the specimen illustrated by Kershaw (1976: fig. 15).

(28) *Neurocranial heads of the hyomandibula*: One head or two heads but continuous [0]; Two heads, separate [1]; Two heads, bridged [2]. Modified from LW96[18]. Li & Wilson (1996a; also 1999: character 50) used the two derived states of this character (states 1 and 2) to define various groups of Hiodontiformes. These authors concluded that two separate neurocranial heads was diagnostic of †*Eohiodon* (see

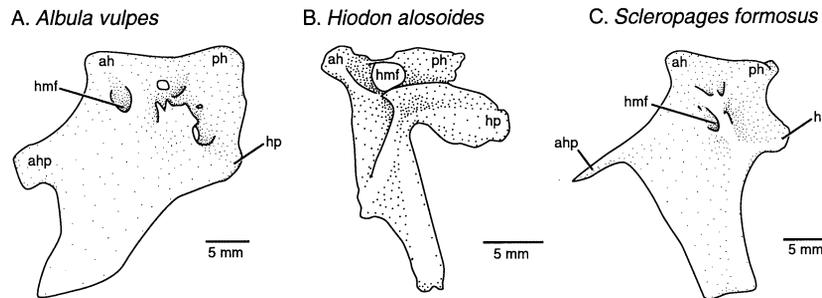


Figure 22. Hyomandibula in medial view. A, *Albula vulpes* (AMNH 93356SD, approx. 390 mm SL). B, *Hiodon alosoides* (UMA F10177, 267 mm SL). C, *Scleropages formosus* (UMA F11266, approx. 320 mm SL). Anterior facing left. Illustration of *Hiodon* modified from Hilton (2002: fig. 48), is of the right side, and is reversed so that anterior is facing left.

also Li *et al.*, 1997b). The Early Cretaceous genus †*Yanbiania* Li, 1987 (not considered in my analysis) and *Hiodon* were found to have these two heads bridged by a thin strut of bone (see Fig. 22B). All other taxa considered by Li & Wilson were coded as plesiomorphic (one neurocranial head) or unknown.

In a new study of its osteology (Hilton & Grande, unpublished data), †*Eohiodon* was also shown to have a thin strut of bone bridging the two neurocranial heads (state 2), forming a greatly enlarged foramen for the hyomandibular trunk. Therefore, this state may be better interpreted as a character of Hiodontiformes (although the condition in †*Yanbiania* should be double checked and that of †*Plesioleptocheilus* remains unknown).

Although all of the taxa considered in this study can be seen to have more or less well-defined anterior and posterior neurocranial heads of the hyomandibula, in some taxa these heads are less obvious in lateral view and in all practicality can be interpreted as having a single head (state 0). For instance, *Osteoglossum*, *Scleropages* (Fig. 22C), *Pantodon*, notopterids and mormyrids all have two neurocranial heads that are more or less combined into a single continuous articulatory surface. A single head of the hyomandibula was one of the characters cited by Greenwood & Thompson (1970) in support of their speculation on the close relationships between *Pantodon* and *Osteoglossum* and *Scleropages*. In notopterids (e.g. Figs 23A, 24A) and mormyrids, the continuity is extremely well developed (more so than in any other taxa examined), and may in fact represent another character state.

The condition is coded as unknown in †*Phareodus*, as the neurocranial head of the hyomandibula is typically covered by the heavy infraorbital bones and parts of the skull. The condition is also coded as unknown for †*Joffrichthys*, †*Singida*, †*Palaeonotopterus* and †*Ostariostoma* because the hyomandibula of these taxa are incompletely known. †*Lycoptera* has been reported to have a hyomandibula with a

single neurocranial head (e.g. Gaudant, 1968: fig. 11A, B), but it was not well enough preserved on my specimens to score with confidence, and is thus left as unknown.

This single headed condition of most osteoglossids contrasts with that found in *Heterotis* (Figs 25, 26), in which the two heads are very much independent of one another (state 1). Although to a somewhat lesser degree, the two cranial heads of the hyomandibula in *Arapaima* also are distinct (Kershaw, 1976; see Taverne, 1977: fig. 134). This condition is best interpreted as a synapomorphy of *Arapaima* and *Heterotis*. This is seen in *Elops saurus* as well, although Forey (1973b: 17) noted that *E. hawaiiensis* differs from *E. saurus* in having 'a single broad articulatory head' (the elopomorph *Albula vulpes* also has the anterior and posterior heads more or less continuous; Fig. 22A).

(29) *Anterior process (wing) of the hyomandibula that contacts the entopterygoid*: Absent [0]; Present [1]. Modified from LW96[29]. Li & Wilson (1996a, also 1999: 383, character 49) concluded that the presence of a 'greatly extended subtriangular anterior wing' of the hyomandibula (vs. the absence of an anterior extension) is a synapomorphy of some of the members of the genus †*Phareodus* (also see discussion in Li *et al.*, 1997a: character 35). However, an anterior extension of the hyomandibula is found in many teleosts (e.g. *Albula*; Fig. 22A), and more specifically, in several osteoglossomorphs, with some approximating the 'subtriangular' shape described by Li & Wilson (e.g. *Scleropages*, Fig. 22C). These authors used this character to resolve the relationships among the species of †*Phareodus* (i.e. all species of †*Phareodus* except †*P. testis* were scored as having an anterior process). Although it is agreed that there is variation in the shape of the anterior extension within this genus (†*P. encaustus*, †*P. testis*; pers. observ.), the presence of an anterior extension of the hyomandibula is a more general character, and it is difficult to understand how

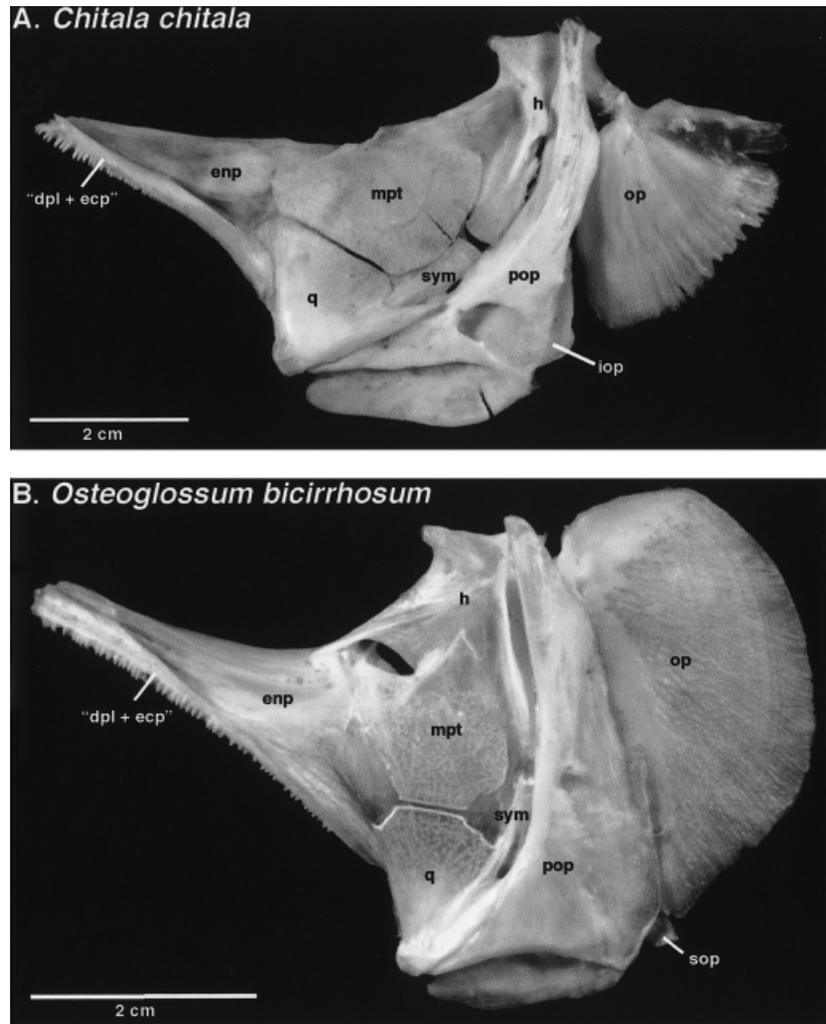


Figure 23. Suspensorium and opercular bones in lateral view. A, *Chitala chitala* (UMA F10349, 437 mm SL). B, *Osteoglossum bicirrhosum* (UMA F10160, 365 mm SL). Note the groove-like opening in the ventral portion of the preopercular sensory canal. Also notice that in *Chitala* there is no distinct horizontal and vertical limbs of the preopercle (see Discussion in Characters Not Used in Analysis). The element labelled 'dpl + ecp' has been suggested in the past to be a fusion of the dermopalatine and the ectopterygoid, although no ontogenetic evidence supports this (see Character 30). Anterior facing left.

the anterior extension of the hyomandibula in taxa such as *Scleropages* (Fig. 22C), or even *Heterotis* (Figs 25, 26), could be coded as lacking a 'subtriangular anterior wing.' Therefore, I have modified the intent of this character state to include any taxon that possesses an extension of the hyomandibula that forms a bridge that contacts the endopterygoid (e.g. as in *Osteoglossum*; Figs 23B, 24B). The plesiomorphic condition is to have the anterior margin of the hyomandibula contact the metapterygoid (e.g. *Hiodon*; Hilton, 2002: fig. 45; *Chitala*, Figs 23A, 24A). In some fishes, such as *Elops* (pers. observ.), the anterior portion of the hyomandibula may be slightly expanded

and approach the endopterygoid, but it always fails to contact any bone anterior to the metapterygoid.

(30) *Bones of palatoquadrate*: Two lateral elements [0]; One lateral element [1]; One element, laterally and medially [2]. Modified from LW99[48]. There are generally three dermal bones in the palatoquadrate of generalized lower teleosts (e.g. *Elops*, Ridewood, 1904b: fig. 10): an anterolateral dermopalatine (= palatine of Ridewood, 1904b), a posterolateral ectopterygoid, and a medial entopterygoid. Two distinct patterns of reduction in the number of dermal elements are recognizable within Osteoglossomorpha,

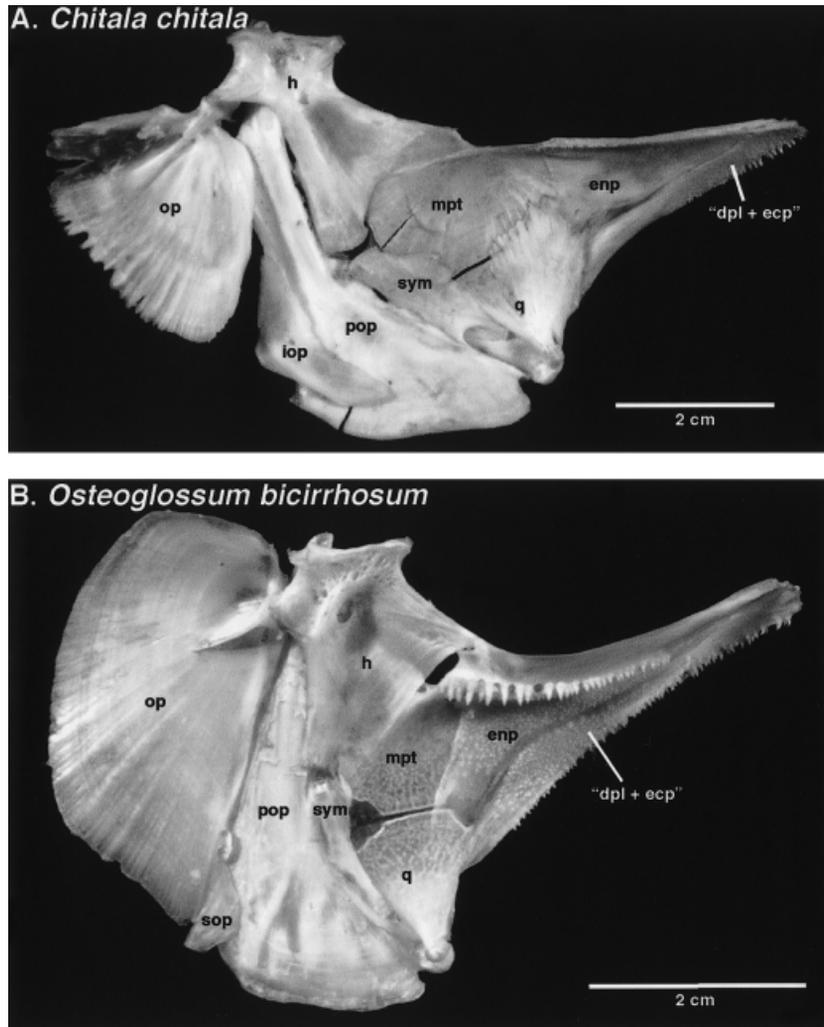


Figure 24. Suspensorium and opercular bones in medial view. A, *Chitala chitala* (UMA F10349, 437 mm SL). B, *Osteoglossum bicirrhosum* (UMA F10160, 365 mm SL). Note that the subopercle is absent in *Chitala* (as it is in all notopterids) and is reduced and positioned along the anteroventral margin of the opercle in *Osteoglossum*. The interopercle is missing in this specimen of *Osteoglossum*. The element labelled 'dpl + ecp' has been suggested in the past to be a fusion of the dermopalatine and the ectopterygoid, although no ontogenetic evidence supports this (see Character 30). Anterior facing right.

with the exception of †*Eohiodon* and *Hiodon* (Hilton, 2002: fig. 45) which retain all three bones as separate elements (the condition in †*Lycoptera* is unknown).

The first derived condition that I recognize is the presence of a single dermal element along the lateral margin of the palatoquadrate and a separate entopterygoid (e.g. *Heterotis*, Figs 25, 26). In my analysis, this condition was found to be a synapomorphy of Osteoglossiformes, although the condition in †*Ostariostoma* is unknown due to preservation (Grande & Cavender, 1991: fig. 2). This lateral element of the

palatoquadrate has been interpreted as a fused ectopterygoid and dermopalatine. Fusion of the dermopalatine and ectopterygoid was defined by Li & Wilson (1999) as a synapomorphy of Osteoglossinae (e.g. *Osteoglossum*; Figs 23B, 24B), and was found to be also independently present in *Arapaima* and notopterids (e.g. *Chitala*; Figs 23A, 24A). Taverne (1998: character 59), on the other hand, considered it a synapomorphy of Osteoglossiformes and his Mormyriiformes (= Notopteridae + Mormyroidea). There is, however, also a single lateral bone in *Heterotis* (Figs 25, 26; coded as separate by Li & Wilson, and

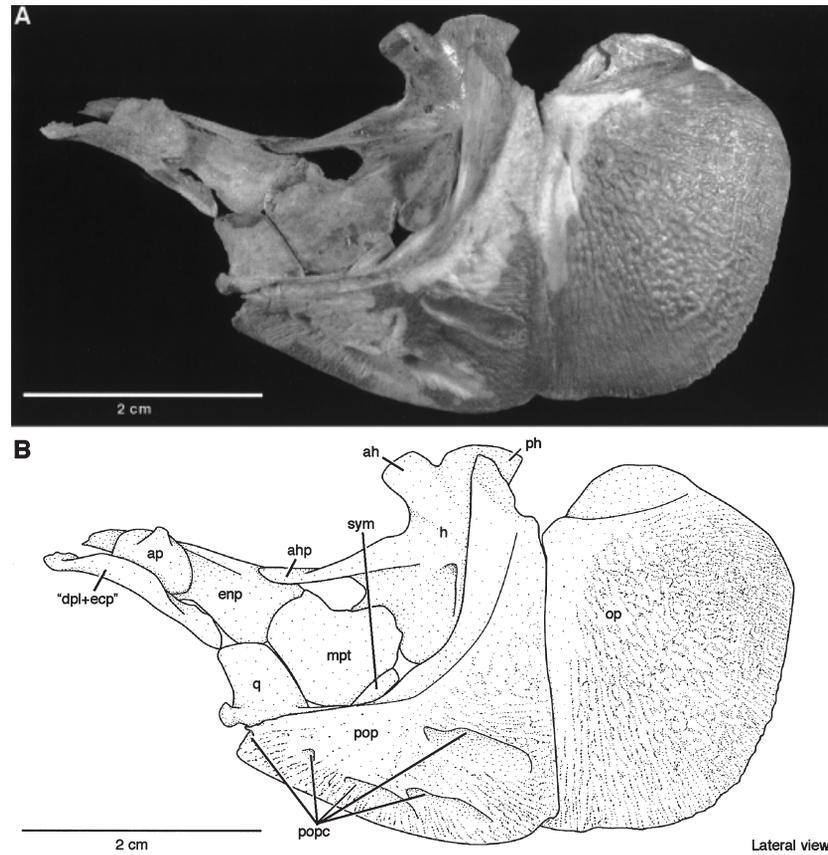


Figure 25. Suspensorium and opercular bones of *Heterotis niloticus* (MCZ 50959, adult, unknown SL) in lateral view. A, photograph. B, line drawing. Note the large pores for the preopercular sensory canal and the ossified autopalatine. The element labelled 'dpl + ecp' has been suggested in the past to be a fusion of the dermopalatine and the ectopterygoid, although no ontogenetic evidence supports this (see Character 30). Anterior facing left.

labelled as just the ectopterygoid by Taverne, 1977: fig. 107). Arratia & Schultze (1991: 53) wrote: 'In osteoglossomorphs, the dermopalatine lies ventral to the rudimentary *pars autopalatina* and to an elongate, narrow cartilaginous remnant of the palatoquadrate. In other teleosts, the dermopalatine is ventrolateral to the autopalatine (e.g. perciforms: percichthyids and *Polyprion*).' Because the bone in *Heterotis* lies ventrolateral of the autopalatine (Fig. 25; see Character 31), and occupies the space of the ectopterygoid as well, there is as much justification for calling this bone a fused dermopalatine and ectopterygoid as there is for any other osteoglossomorph that displays this condition. Daget & d'Aubenton (1957) noted that the ectopterygoid of *Heterotis* begins to ossify at 12.5 mm, but made no mention of a second lateral ossification of the palatoquadrate. To the best of my knowledge, no other study exists that examines the development of this bone within Osteoglossomorpha, so ontogenetic evi-

dence suggesting that two bones are incorporated into this single element is lacking and should be the subject of future research.

The second derived condition (state 2) that I recognize is the presence of a single dermal element in the palatoquadrate. This single bone was only observed in mormyrids. Taverne (1998: character 151) considered this bone to be a fusion of the ectopterygoid and entopterygoid. Although no specific mention was made of the dermopalatine, from reviewing his figures (e.g. those in Taverne, 1968a,b, 1969, 1972) it is clear that he considered the dermopalatine as absent in mormyrids, and I found no element that corresponds to an autogenous dermopalatine. Following the definition provided by Arratia & Schultze (1991; quoted above), the 'dermopalatine' portion of this bone is absent (pers. observ.). Benveniste (1994) considered the dermopalatine and entopterygoid both to be absent in mormyrids, following Taverne's (1972) interpretation.

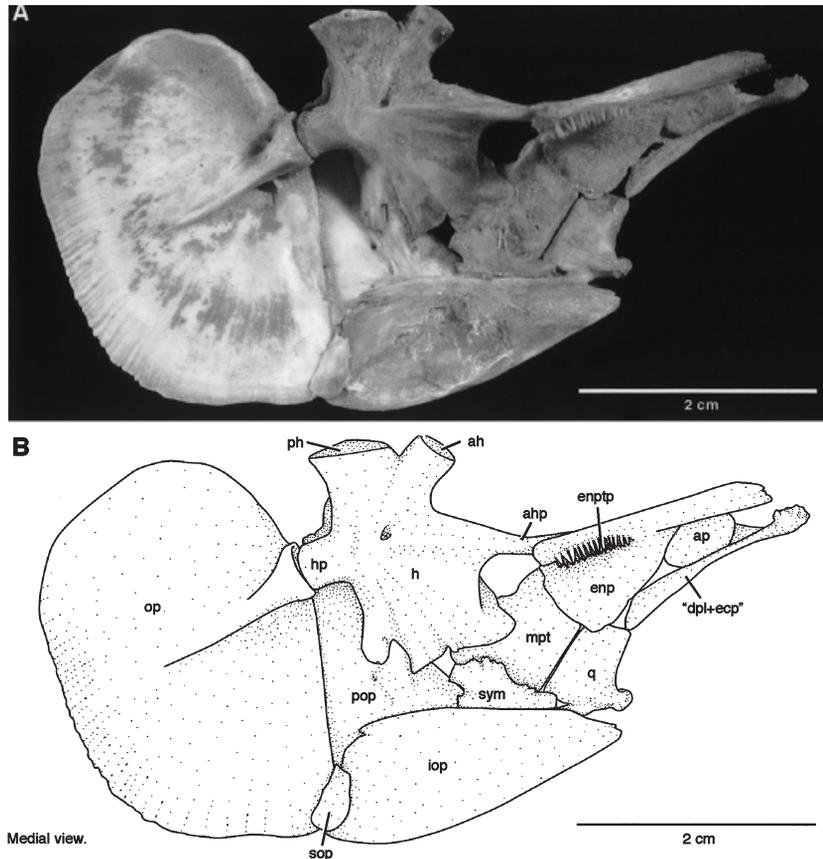


Figure 26. Suspensorium and opercular bones of *Heterotis niloticus* (MCZ 50959, adult, unknown SL) in medial view. A, photograph. B, line drawing. Note the reduced subopercle. The element labelled 'dpl + ecp' has been suggested in the past to be a fusion of the dermopalatine and the ectopterygoid, although no ontogenetic evidence supports this (see Character 30). Anterior facing right.

(31) *Autopalatine bone*: Present [0]; Absent [1]. Arratia & Schultze (1991) considered the absence of an autopalatine bone (i.e. the presence of a fully cartilaginous *pars autopalatina*) to define Osteoglossomorpha. This bone, however, is present in *Heterotis* (Figs 25, 26) and *Scleropages leichardti* (Ridewood, 1905; Taverne, 1998; pers. observ.). Other species of *Scleropages* lack an ossified autopalatine; the genus is therefore coded as polymorphic in this analysis. Based on the results of my analysis, these two cases of presence of an autopalatine are best interpreted as independent evolution.

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(32) *Preopercular sensory canal*: Opens by pores the entire length of the canal [0]; Opens by pores ventrally and by a groove dorsally [1]; Opens by pores dorsally and a groove ventrally [2]; Opens by a groove the

entire length of the canal [3]. Modified from LW96[13] and LW99[33 & 34]. This character was described by Li & Wilson (1999) as two characters, one describing the disposition of the canal on the horizontal limb (their character 33) and one describing the disposition of the canal on the vertical limb (their character 34). However, given that I could not reliably identify what these authors were calling the landmark between the horizontal and vertical limbs (particularly in taxa such as *Chitala*, in which there really is no distinction; see Characters Not Used in Analysis), I combined the two characters, giving each of the four possibilities its own character state.

†*Lycoptera*, †*Eohiodon*, *Hiodon* (e.g. Hilton, 2002: fig. 45), *Heterotis* (Figs 25, 26), *Arapaima*, *Pantodon* and the mormyroids that were examined all show the plesiomorphic condition, in which the canal opens the entire length of the bone through pores (in actuality, most of the pores are located on or near the ventral

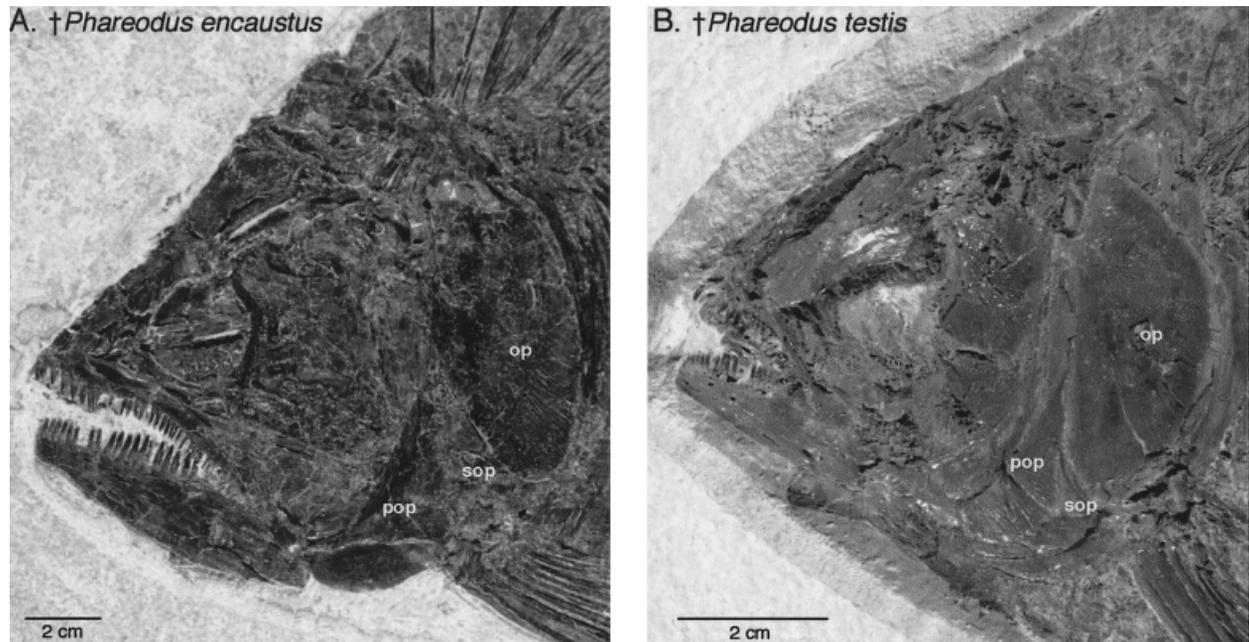


Figure 27. Skulls of †*Phareodus* in lateral view. A, †*Phareodus encaustus* (UMA F10155; 480 mm SL). B, †*Phareodus testis* (UMA F11332, 260 mm SL). Note that there is not much difference in the shape of the preopercle between these two species (see Characters Not Used in Analysis). Also note that the subopercle, although not quite as reduced as in other taxa (e.g. *Osteoglossum*), is relatively small and is positioned along the anteroventral margin of the opercle. The specimen of †*P. encaustus* (UMA F10155) is the same as the one labelled as LG 6.1 by Grande (1984: fig. II.31). Anterior facing left.

portion of the canal, but where it is open dorsally, it is through pores rather than a groove). Li & Wilson (1999) miscoded Mormyroidea as having the canal open through a groove on the ventral limb; see the figures in the descriptions of their osteology by Taverne (1968a,b, 1969, 1971, 1972). In *Pantodon*, these pores are larger than in other taxa examined, and give the impression of an intermediate state between having discrete pores and pores that are confluent in a groove (see below).

No taxa examined had character state 1 (pores ventrally and groove dorsally), but it is included as it is theoretically possible given the combination of Li & Wilson's two characters.

Most osteoglossids (all examined here, with the above noted exceptions of *Arapaima* and *Heterotis*, and †*Ostariostoma*; see below) and notoapterids possess character state 2, in which the canal opens dorsally through pores, whereas the pores ventrally become confluent into what appears to be a groove in lateral view (e.g. *Osteoglossum*, Fig. 23B). The pores actually are separated by a thin wall of bone, although there is a slight overlapping lamina of bone that obscures these walls in lateral view (see also †*Phareodus*, Fig. 27). All notoapterids possess a single large

pore near the greatest extent of the curve of the preopercle (e.g. Fig. 23A); ventral to this pore is the groove. No walls of bone separate individual pores within the groove in notoapterids, as there are in osteoglossids, so the condition may not be homologous between the two groups. †*Ostariostoma* alone bears the preopercular canal in a groove the entire length of the preopercle (state 3).

(33) *Opercle depth to width ratio*: Less than two [0]; About two or greater than two [1]. Modified from LW96[26]. Essentially, this character distinguishes between those taxa with a short, relatively broad opercle and those with a tall, relatively slender opercle. Li & Wilson (1999: character 26) redefined this character by adding a third character state (less than two [0]; about two [1]; greater than two [2]). In that analysis, Li & Wilson considered a ratio approximately equal to two to be a synapomorphy of the group †*Paralycoptera* + †*Tanolepis* (not considered in this analysis) and (†*Singida* (*Scleropages* + *Osteoglossum*)) (with a reversal in *Scleropages*, although this is merely an artifact of optimization; i.e. there is equal number of changes if independent evolution occurred in †*Singida* and *Osteoglossum*), and independently evolved in †*Hua-*

shia (not examined). The condition in which the ratio is much greater than two was found to be a synapomorphy of Osteoglossinae (with the noted exceptions of †*Singida* and *Osteoglossum*, although again, it is the same number of steps to hypothesize independent evolutions in †*Cretophareodus* + †*Phareodus*, *Pantodon* and *Scleropages*). Because there was no indication of how much greater than two the ratio had to be before it changed codings, I merged the 'about two' and 'greater than two' conditions into a single state. Additionally, the difference between the ratios in my specimens of *Osteoglossum* and *Scleropages* was not impressive. †*Phareodus* also has a very tall opercle (Fig. 27). For more discussion of characters related to the opercle in osteoglossomorphs, see Characters Not Used in Analysis.

(34) *Posterodorsal spine on the opercle*: Absent [0]; Present [1]. LW96[36] Li & Wilson (1994: character 16) first described this character (the presence of a posterodorsal spine or 'projection' on the opercle; see also Li & Wilson (1999: character 27) as a synapomorphy of the genus *Hiodon*, citing its presence in †*H. consteniorum* and its absence in †*Eohiodon* and other hiodontiform fishes. In Li & Wilson's (1994: fig. 6) illustration of the opercles of various hiodontiforms, it should be noted that the posterodorsal portion of the specimen of †*Eohiodon* they figured is missing and its outline is completed with a dashed line. This portion of the opercle is almost always damaged in specimens of †*Eohiodon*. However, a new study (Hilton & Grande, unpublished data), based in part on acid-prepared specimens, has revealed the presence of this spine in all three North American species of †*Eohiodon*. Also, Cavender (1966: 315), in his description of the genus, remarked that the 'shape [of the opercle] is like that of *Hiodon* with the distinctive notch present in the posterior border and the posterodorsal corner of drawn out dorsally to a point.' Here, this spine is interpreted as a synapomorphy of *Hiodon* and †*Eohiodon*. The dorsal margin of the opercle of †*Ostariostoma* is not clearly preserved (Grande & Cavender, 1991: fig. 2), and is coded as unknown.

(35) *Subopercle bone*: Large and ventral to the opercle [0]; Small and anterior to the opercle [1]; Absent [2]. Modified from LW99[35 & 36]. The condition of having a small subopercle that is positioned far anteriorly relative to the opercle was considered a synapomorphy of (†*Singida* (*Osteoglossum* + *Scleropages*) by Li & Wilson (1999; also see Li *et al.*, 1997a,b); all other taxa were coded as having a large subopercle positioned ventral to the opercle (e.g. as in *Hiodon*, Hilton, 2002: figs 45, 47). However, there are at least two taxa that are consistently (across papers) miscoded, as both *Arapaima* and *Heterotis* (Fig. 26) clearly have a

subopercle that is reduced in size and positioned far anteriorly. Also, †*Phareodus* has a small, anteriorly positioned subopercle (Fig. 27) that Taverne (1978: 20) described as 'un petit os qui s'aperçoit chez certain exemplaires, entre les bases de l'operculaire et du préoperculaire' [a small bone that is clearly seen in specimens between the bases of the opercle and the preopercle] (although see interpretation by Li *et al.*, 1997a). Additionally, those taxa that lack a subopercle (*Pantodon* and notoapterids, see below) are miscoded by Li and colleagues (i.e. *Pantodon* was coded as having a subopercle that is 'relatively large and ventral to [the] opercle'; Li & Wilson, 1999: 383 & fig. 2). My analysis suggests that having a small subopercle positioned anteriorly is a synapomorphy of all Osteoglossidae except for †*Joffrichthys* (Node G of Fig. 4; see Fig. 12 for condition in †*Joffrichthys*), and that this bone is secondarily lost in *Pantodon*.

The absence of a subopercle was interpreted as a synapomorphy of Notopteridae by Li & Wilson (1999; also see Li *et al.*, 1997a,b; also Taverne, 1979, 1998: character 89) and independently absent in *Pantodon* (also Taverne, 1979, 1998). Of the taxa examined here that can be reliably scored (e.g. †*Lycoptera* is scored as unknown, because specimens do not permit confident observation), notoapterids and *Pantodon* are the only ones to lack a subopercle and my results indicate that this is due to homoplasy.

(36) *Gular bone*: Present [0]; Absent [1]. LW99[52]. Among living teleosts, a gular bone is only found in Elopiformes (Forey, 1973b). Within osteoglossomorphs, †*Lycoptera* has been interpreted as possessing a gular (Gaudant, 1968; Ma, 1987), a point that Li & Wilson (1996a: 165) denied, calling it a 'misidentified structure' (although Li & Wilson, 1996a did not define a character for the gular plate). This was changed in Li & Wilson (1999), where they coded the character as present in †*Lycoptera* and †*Kuyangichthys*, among osteoglossomorphs, and presumably interpreted this as independent evolution (or retention?) of the gular in these two taxa. After examining the specimen of †*L. davidi* that served as the basis of Gaudant's (1968: fig. 10) claim (MNHN 1927-13-06 e & e'), I accept that this taxon does possess a gular plate (Fig. 15B), and that it is the only osteoglossomorph included in my analysis that possesses this structure. †*Joffrichthys*, †*Singida* and †*Ostariostoma* are coded as unknown due to lack of preservation, although it is likely that a gular was absent in these taxa as well. The possibility exists that the absence of the gular may be a character at some higher level of phylogeny (e.g. Arratia, 1997, 1999; who used this as evidence that elopomorphs are the basal lineage of living teleosts; i.e. absence of a gular is a synapomorphy of osteoglossomorphs + other 'higher' teleosts).

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(37) *Ascending process of the premaxilla*: Well developed [0]; Only slightly developed, if at all [1]. Modified from LW96[35]. Li & Wilson (1996a; also 1999: character 41) defined this character describing three states of the 'anterior portion of the premaxilla' (i.e. raised, not raised, or lower than posterior portion). The only taxon coded as having the 'not raised' condition was †*Eohiodon woodruffi*, and the only taxa to be coded as having the 'lower than posterior' condition were those of the genus *Hiodon* (see also Li *et al.* 1997b). Although I agree that the anterior portion of the premaxilla in hiodontids is narrower relative to its posterior portion than in other osteoglossomorphs (e.g. †*Lycoptera*, Fig. 17), the differences between †*Eohiodon* and *Hiodon* are difficult to interpret and this character may better be defined as the development of the medial ascending process of the premaxilla (see also discussion of the 'mid-dorsal concavity' in Characters Not Used in Analysis).

The coding of this character by Li & Wilson is somewhat problematic, as some taxa (e.g. *Heterotis*) have a very low anterior portion (at the very least the 'not raised' condition) but were coded as having a condition similar to taxa that have a very high anterior ascending process (e.g. †*Phareodus*). Also, the snout of the specimens of †*Singida* is not well preserved (if at all), although it was suggested that the premaxillae are absent in this taxon, or are at least very reduced (Greenwood & Patterson, 1967); all characters of the premaxillae for †*Singida* therefore must be coded as '?' (not so in Li & Wilson's coding). †*Ostariostoma* also is coded incorrectly by Li & Wilson, as Grande & Cavender (1991: fig. 2) illustrated and described the premaxilla as lacking any sort of ascending process (Li & Wilson, 1996a: fig. 3A illustrated a small bump on the dorsal surface of the premaxilla; after examining the specimen, I agree with Grande & Cavender's, 1991 illustration of this bone). The premaxillae of *Osteoglossum* and *Scleropages* also bear only slight ascending processes. The premaxillae of both *Pantodon* and mormyrids are substantially modified (see Character 38); however, in *Pantodon*, there is a well developed, median ascending process (Taverne, 1978: fig. 36), whereas in mormyrids there is no process at all.

(38) *Premaxillae*: Paired [0]; Median [1]. Modified from T98[199]. Primitively, the left and right premaxillae are separate elements, and this is the condition in most osteoglossomorphs included in this analysis. However, a median premaxilla is found in mormyrids and *Pantodon*. Taverne (1998: 133) considered this character to have evolved independently in the two taxa, as I recovered in my analysis. Ridewood (1905: 273) described the premaxilla of *Pantodon* as follows: 'The right and left premaxillae are fused into a single

bone and the suture is obliterated; the bone bears a row of about 14 small, pointed teeth, and is immovably united with the anterior edges of the nasal bones and mesethmoid. The premaxilla lies in a broad depression in the front edge of the roof of the cranium, with the teeth pointing directly forward; the anterior ends of the maxillary and dentary bones extend in advance of the premaxilla.' Ridewood (1904a: 199) similarly described the premaxillae of the mormyrids he examined to be fused in the midline, but noted that the premaxillae of *Gymnarchus* were 'rigidly united by an interlocking suture' (see Taverne, 1972: fig. 97).

(39) *Posterior portion of the maxilla*: Lies on angular [0]; Lies on dentary [1]. LW96[40]. Li & Wilson (1996a, 1999: character 43) found shortening of the maxilla so that it lies on the dentary to be a synapomorphy of Heterotinae (with the exception of †*Laeliichthys* and †*Chandlerichthys*; see Li *et al.*, 1997a). Here I note that this condition is also present in both the short-snouted (e.g. *Petrocephalus*, see Taverne, 1969: fig. 29) and long-snouted (e.g. *Campylomormyrus*, see Taverne, 1968b: fig. 1) mormyrids that I examined during this study. This is surely not homologous to that found in heterotines and is likely associated with the radical restructuring of the snout of these fishes. Although the individual bones of the jaws are relatively well preserved on the single known specimen of †*Ostariostoma*, the jaws look as if they were disturbed from their natural position during fossilization, and therefore this character is coded as unknown. I also coded †*Joffrichthys* as unknown for similar reasons (see Li & Wilson, 1996b: fig. 2b); the phylogenetic extent of this character state will be clarified with new specimens (although Newbrey & Bozek, 2000 agreed with Li & Wilson's interpretation in their description of †*J. triangulpterus*).

(40) *Supramaxillae*: Present [0]; Absent [1]. LW96[3]. Absence of a supramaxilla in osteoglossomorph fishes has been known since at least the works of Ridewood (1904, 1905) and was considered to be a synapomorphy of Osteoglossomorpha by Li & Wilson (1996a). Number of supramaxillae in teleosts varies between two (e.g. *Elops*, Fig. 28A) and one (e.g. *Coregonus*, Fig. 28B), but all living and most fossil osteoglossomorphs lack any supramaxilla at all (e.g. *Hiodon*, Fig. 28C).

†*Lycoptera* supposedly possesses a single supramaxilla (e.g. Gaudant, 1968: fig. 3; it was coded as absent by Li & Wilson, 1996a; although this was changed in Li & Wilson, 1999: character 45). I was unable to identify unambiguously a supramaxilla on my material of †*Lycoptera*, although there was a possible fragment of a supramaxilla in a specimen of †*L. sinensis* (BMNH P.7357); this character is coded as unknown for †*Lycoptera*.

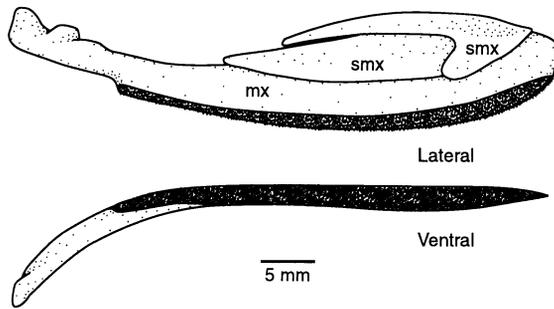
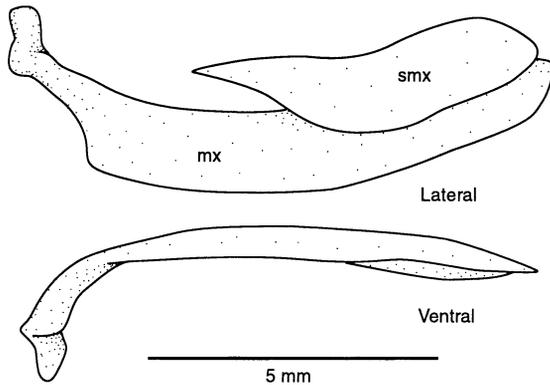
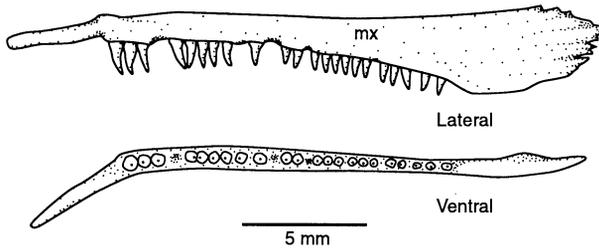
A. *Elops saurus*B. *Coregonus hoyi*C. *Hiodon alosoides*

Figure 28. Maxilla and supramaxilla in lateral and ventral (= oral) views. A, *Elops saurus* (UMA F10255, 425 mm SL). B, *Coregonus hoyi* (FMNH 94848, 115 mm SL). C, *Hiodon alosoides* (UMA F10587, 272 mm SL). Anterior facing left. Illustrations of *Hiodon* modified from Hilton (2002: figs 38, 39).

Li & Wilson (1999) also identified †*Tongxinichthys* (Zhang & Jin, 1999: fig. 3), †*Kuyangichthys*, †*Tanolepis* and †*Paralycoptera* (Chang & Chou, 1977: fig. 6) as possessing a supramaxilla (none of these taxa are considered in this analysis). This was not illustrated in the original description of †*Tanolepis* by Jin (1991: fig. 2). However, Jin *et al.* (1995) synonymized this taxon with †*Paralycoptera changae*, which supposedly possesses a supramaxilla; this synonymy was not sup-

ported by Li *et al.* (1997b) and Li & Wilson (1999). This correlates on Li & Wilson's cladogram to the absence of a supramaxilla above the level of †*Lycoptera*, with an independent loss in †*Jiuquanichthys*, and a reversal in the clade †*Paralycoptera* + †*Tanolepis*. Additionally, Taverne (1998: 137) considered 'la présence d'un petit supramaxillaire' [the presence of a small supramaxilla] to be an autapomorphy of the fossil taxon †*Nieerkunia liae* Su (1992) (Lower Cretaceous, China), which he considered closely related to *Arapaima* and *Heterotis*. However, as Chang (1999: 475–476) noted, 'the incomplete preservation as well as inadequate study of the materials [of fossil osteoglossomorphs from China] caused divergence in observation of the characters in fossil materials. A restudy of the Chinese materials is necessary to better understand the phylogenetic relationships of the Chinese osteoglossomorphs.' Because my analysis did not include the fossils that were interpreted as stem-groups by Li & Wilson, I cannot comment on the exact distribution of this character, except that it is interpreted as a synapomorphy of all osteoglossomorphs sampled here (see Character Optimization and Node Support), with the possible exception of †*Lycoptera*, which, again, was coded as unknown.

One other point must be mentioned before leaving the topic of supramaxillae. Both Roellig (1974: fig. 1) and Taverne (1978: fig. 20) illustrated a supramaxilla in †*Brychaetus*. In examining skulls of this taxon, I agree that there are elements preserved that could indicate the presence of a supramaxilla. For example, in specimen BMNH P.39699 (this specimen served as part of Taverne's reconstruction), which consists of a jumble of cranial bones, there are distinct lateral depressions on the dorsal posterior margin of both the left and right maxillae that appear to have formed fossae for the supramaxillae, which were displaced dorsally in this specimen. †*Brychaetus*, however, was coded as lacking a supramaxilla by Li & Wilson (1996a) and synonymized with †*Phareodus* by Li *et al.* (1997a), with no mention of the potential presence of a supramaxilla. Taverne (1998: 132) maintained that there was a supramaxilla in †*B. muelleri*, noting also '[o]n a déjà rencontré cette réversion vers un état plésiomorphe chez deux autre Osteoglossidae. On ignore si ell existait aussi chez [†] *Brychaetus caheni*' [I already described this reversal to the plesiomorphic state in two other osteoglossids {†*P. queenslandicus* & †*Opsithrissops*}. I am unaware if this condition also existed in †*B. caheni*]. Although I did examine specimens of †*B. muelleri*, I scored my matrix using †*P. encaustus* and †*P. testis* as exemplars of the genus †*Phareodus*, and therefore coded this character as supramaxilla absent. Although Li *et al.* (1997a) offered compelling evidence for close relationship and possible synonymy of †*Brychaetus* and †*Phareodus*, the posi-

tion of †*Brychaetus* relative to the members of the genus †*Phareodus* needs to be reexamined.

(41) *Mandibular canal*: Enclosed in a bony tube [0]; Open in a groove [1]. LW96[46]. The derived state of this character (i.e. to have the mandibular canal open in a groove rather than enclosed within the bone of the dentary) was found to be a synapomorphy of Mormyroidae + Notopteridae by Li & Wilson (1996a). In my analysis, an open groove for the mandibular canal supports Osteoglossiformes, with a reversal in Osteoglossidae (see Character Optimization and Node Support), although this is a matter of optimization. Li & Wilson (1999: character 46) also used this character, and included in their matrix †*Thaumaturus* (not included in my analysis), which they also coded as having the mandibular canal in a groove. Because of their resulting topology, this character could alternatively have been interpreted as a more inclusive synapomorphy, with a loss in †*Ostariostoma* (see Grande & Cavender, 1991: fig. 2). However, I will not comment on the presence of this condition in †*Thaumaturus* (see Micklich, 1992), because I did not have suitable specimens available for this study and its morphology is currently under study (N. Micklich, pers. comm., 1998).

There is some variation in this feature in mormyroids, although all examined in this study have at least part of the canal open. In *Petrocephalus* (see Taverne, 1969: fig. 39) the mandibular canal is within a groove that is entirely open ventrally. In *Gnathone-mus* and *Campylomormyrus*, the mandibular canal is completely open laterally, contrary to Taverne's interpretation, in which it is enclosed in a tube anteriorly (see Taverne, 1968a: fig. 9 and Taverne, 1968b: fig. 1, respectively). This character is coded as open (state 1) for these two taxa, although it is not closed dorsally and may in fact represent an additional derived state. Taverne (1972) remarked that the canal was open in *Gymnarchus*. The mandibular sensory canal is open (as a homoplasy) in *Albula vulpes* (pers. observ., AMNH 88678SD).

As an aside, I will comment briefly on the posterior opening of the mandibular sensory canal in the lower jaw. Nelson (1973a,b) extensively discussed the course of the mandibular sensory canal of teleosts, which in some groups opens lateral to the postarticular process (e.g. *Hiodon* and *Heterotis*; Fig. 29B & C, respectively). In *Elops*, the canal opens on the medial posterior surface (Fig. 29A; see Nelson, 1973a,b, who noted this condition for both *Elops* and *Megalops*). In the albuliform *Albula vulpes* (pers. observ., AMNH 88678SD) the mandibular canal opens somewhat laterally, although as Nelson (1973b: 6) remarked '[s]tudy of the lower jaw of *Albula* (and other non-elopoid taeniopae-dians [= elopomorphs]) has thus far been inconclusive,

because of secondary modifications obscuring the primitive jaw structure in them (in *Albula*, e.g. the postarticular process is reduced, and the sensory canal much enlarged; the opening of the sensory canal is, nevertheless, visible in medial view ([Nelson's] fig. 4B), but so is it, presumably secondarily, also in *Chirocentrus* ([Nelson's] fig. 9D), also with a reduced postarticular process).' The mandibular sensory canal is not visible in medial view in either *Anguilla rostrata* (UMA F10248) or *Ophichthus rex* (UMA F10995), although this may be a secondary condition as well, as no postarticular process is developed. There is another prominent opening in the medial side of the lower jaw of these eels that is not the continuation of the sensory canal, but rather is the opening, presumably, for the nerve and blood supply to the lower jaw. A medial opening for the sensory canal is also found in †ichthyodectiforms and †bananogmiids (Nelson, 1973b) and other more basal groups of teleosts (e.g. †*Leptolepis*; see Patterson & Rosen, 1977; Arratia, 1997, 1999), which led Patterson & Rosen (1977: 101) to consider it as 'a synapomorphy of post[†]*Proleptolepis* teleosts that has been lost in most modern forms' (contrary to Nelson's hypothesis that it indicated relationship between †ichthyodectiforms and elopomorphs). Arratia (1997) likewise considered it to be plesiomorphic for teleosts and considered the lateral opening of the canal to be a synapomorphy of Osteoglossomorpha plus more derived (i.e. non-elopomorph) teleosts.

(42) *Posterior bones of the lower jaw*: Angular and retroarticular bones fused [0]; Angular and articular bones fused [1]; All separate [2]; All fused [3]. The bones of the posterior lower jaw in teleosts show various patterns of fusion between the various constituent elements (Nelson, 1973a, b). As Nelson (1973a: 339, 345) wrote, '[i]n almost all teleosts, the angular is fused either the articular or with the retroarticular; in many teleosts the angular is fused with both articu-lars' and that, 'the osteoglossomorphs, of course, exemplify this entire concept, for they exhibit all three patterns. They demonstrate, also that each fusion pattern has developed at least twice within the evolution of Teleostei.' The lower jaw of teleosts served as part of the basis of Patterson's (1977a) discussion of phylogenetic fusion. Because both dermal and chondral elements are involved, the hypothesis of 'fusion' is especially compelling. Future study, however, should be made of the ontogeny of the bones involved.

In some osteoglossomorphs, the angular is fused with the retroarticular (state 0), forming a compound anguloretroarticular (e.g. as in *Hiodon*, Fig. 29B); this is the case in *Elops* as well (Fig. 29A). This fusion was shown to be during ontogeny for *Hiodon* by Hilton, 2002: fig. 44), although ontogenetic evidence for most osteoglossomorphs is lacking.

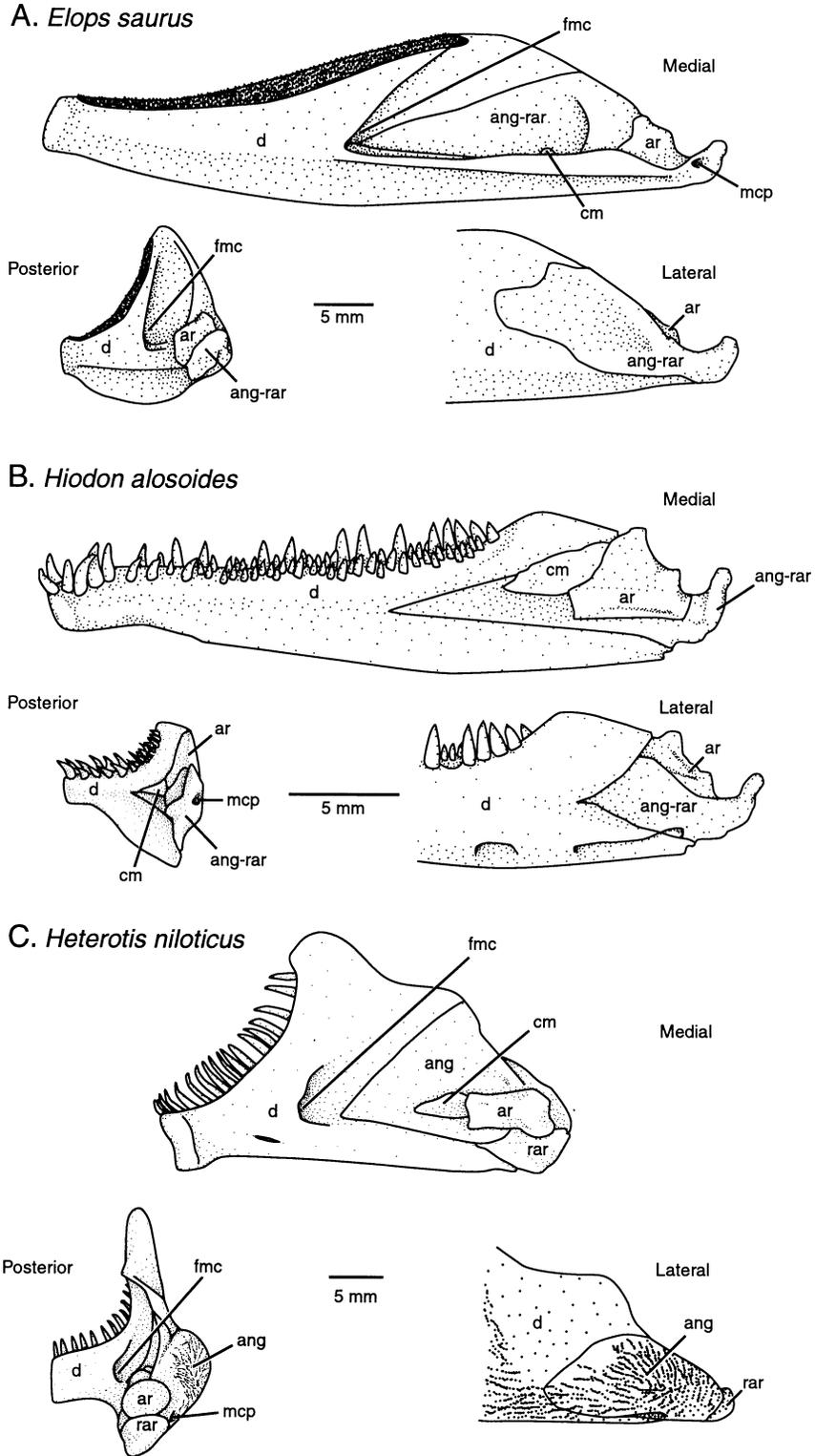


Figure 29. Lower jaw in medial, lateral (posterior portion only) and posterior views. A, *Elops saurus* (UMA F10255, 425 mm SL). B, *Hiodon alosoides* (UMA F10587, 272 mm SL). C, *Heterotis niloticus* (MCZ 50959, adult, unknown SL). Anterior facing left. Lateral and medial illustrations of *Hiodon* are modified from Hilton (2002: fig. 38); medial view has been reversed so that anterior is facing left. Lateral images of *Elops* and *Heterotis* have been reversed so that anterior is facing left.

In many osteoglossomorphs (e.g. most osteoglossids, *Pantodon* and notopterids) examined here, the angular and articular are fused (state 1), forming an anguloarticular (for various taxa, see illustrations in Nelson, 1973a: figs 2, 3). The condition is unknown in †*Singida* (Greenwood & Patterson, 1967).

Mormyrids have a single bone at the back of the lower jaw, which Nelson (1973a) interpreted as a fusion of all three bones (the angular, retroarticular and articular). This is the interpretation I am following here (state 3), and was also accepted by Benveniste (1994). However, it must be stressed again that the ontogeny of this bone is unknown in mormyrids (as it is in most of osteoglossomorphs), and so the character may need to be redefined in the future to better reflect the observable morphology (i.e. rather than include hypotheses of phylogenetic fusion, an unobservable process; Hilton, 2002). The lower jaw of *Gymnarchus*, however, has a free articular (Taverne, 1972: fig. 105; Nelson, 1973a: fig. 3) and it is presumed that the retroarticular is fused with the angular (Nelson, 1973a; although Taverne, 1972 labelled this bone as only an angular).

All of the bones of the lower jaw are free from one another in *Arapaima* and *Heterotis* (Fig. 29C), which, according to Nelson (1973a,b), are the only living teleosts to have this condition (state 2). †*Phareodus* also was noted by Nelson (1973a: 345; 1973b: fig. 1) as having all three bones separate; this was accepted by Taverne (1978: fig. 9) and Li *et al.* (1997a: fig. 4). Nelson (1973a: 345) suggested that '[i]t is reasonable to hypothesize that the unfused condition in these three forms is a primitive condition (the alternative hypothesis is that they are secondarily unfused, and this hypothesis is demonstrably unparsimonious within the context of actinopterygian relationships assumed here)'. The condition in †*Joffrichthys* is unclear: in UALVP 34770 there may be a faint suture between the angular and articular (pers. observ.), although study of new specimens is needed to confirm this observation. Li & Wilson (1996b) suggested that the angular and the articular were fused and the retroarticular remained autogenous.

(43) *Retroarticular bone*: Included in the articulation with the quadrate [0]; Excluded from the articulation with the quadrate [1]. Nelson (1973a: 340) wrote that '[t]he condition that both articulators [the articular and retroarticular] form the [jaw] joint is doubtless primitive relative to the condition where the retroarticular is excluded from the joint, as it is in all teleosts except some osteoglossomorphs and elopomorphs'. In her analysis, Arratia (1999: character 52) found this character to be uniquely derived (i.e. the retroarticular excluded from the jaw joint) in all teleosts above the level of osteoglossomorphs (in her topology, this

includes all other extant groups of teleosts except for elopomorphs). However, because there is variation within the osteoglossomorphs, I have included this character in my analysis (in Arratia's taxon sampling of osteoglossomorphs – †*Lycoptera*, *Hiodon* & *Heterotis* – there is no variation and they all have the primitive condition). Within Osteoglossomorpha, the retroarticular is excluded from the jaw joint in notopterids, †*Phareodus*, *Scleropages* & *Osteoglossum*. Nelson (1973a) also listed *Pantodon* as having the retroarticular excluded from the jaw joint, although I disagree with this (see Taverne, 1978: fig. 41). Nelson (1973a: 340) did not consider the conditions to be homologous between Notopteridae, on one hand, and the osteoglossids on the other, owing to the 'overall form of the jaw [between the two groups] is different because of the fairly high coronoid process [in notopterids]'. Of the notopterids examined here, in *Xenomystus* the retroarticular comes closest to being in contact with the jaw joint, and in *Papyrocranus*, it is furthest removed.

†*Lycoptera*, †*Joffrichthys* and †*Singida* are coded here as missing because of lack of adequate preservation. Arratia (1999) coded †*Lycoptera* as having the plesiomorphic state (i.e. retroarticular included), but this could not be determined in my specimens. Although Grande & Cavender (1991: fig. 2) showed the retroarticular to be well separated from the lower jaw joint, †*Ostariostoma* is coded as missing because the medial surface of the posterior lower jaw is completely unknown.

All mormyrids sampled here are coded as missing due to uncertain homology. Although it is hypothesized in the coding of Character 42 that all bones of the lower jaw are present and fused into a single element, it is unknown which portion or portions of this compound element contributes to the articular facet in mormyrids (this amounts to a case of unknown data due to uncertain homology; Grande & Bemis, 1998). It is, however, worth noting that both the retroarticular and the articular portion of the anguloarticular contribute to the facet in *Gymnarchus* (Taverne, 1972; Nelson, 1973a).

(44) *Medial wall of the Meckelian fossa of the lower jaw*: Present [0]; Absent [1]. The medial wall of the Meckelian fossa is the lamina of bone on the medial surface of the dentary that entirely surrounds Meckel's cartilage in bone (e.g. as in *Elops*; Fig. 29A). In *Hiodon* (Fig. 29B; Hilton, 2002), †*Eohiodon* and †*Lycoptera* (e.g. †*L. wangi*, BMNH P28847; †*L. sinensis*, BMNH P7357; and possibly in †*L. cf. davidi*, UMA F10652), there is no medial wall, so that Meckel's cartilage (or the surface where it would have been in the fossils) is completely exposed medially. In most other osteoglossomorphs examined (for which the medial

surface of the lower jaw is known), the wall was well developed (e.g. *Heterotis*, Fig. 29C). Within the mormyrids, I only found a medial wall of Meckel's fossa in *Petrocephalus*, in which the extent of this wall is restricted very far anteriorly (i.e. only the very anterior portion of Meckel's cartilage is covered medially by bone). In *Gnathonemus* and *Campylomormyrus*, the medial wall of Meckel's fossa is completely absent. This is presumably independent of the condition found in *Hiodon* and †*Lycoptera* and possibly related to the extreme modification of the lower jaw in conjunction with the elongation of the snout.

Outside of Osteoglossomorpha, there is also variation in the presence of this medial wall. Nelson (1973a: 347) wrote that '[c]lupeomorphs have reduced the medial wall of the meckelian fossa, and all of those examined, except *Denticeps*, have at least an indication of a new fossa within the dentary bone on its lateral surface.' For example, in *Alosa* there is a small notch on the medial surface of the dentary at the anterior most extent of Meckel's cartilage, although no true fossa is formed (e.g. UMA F10359, pers. observ.).

GILL ARCHES AND VENTRAL HYOID ARCH

(45) *Bony elements associated with the second ventral gill arch*: Absent [0]; Present as autogenous elements [1]; Present as a bony process on the second hypobranchial [2]. Modified from LW96[8]. Greenwood *et al.* (1966: 361) first formally defined Osteoglossomorpha in part based on the 'development of paired, usually ossified, rods at the base of the second gill arch in all Osteoglossomorpha. These tendon bones develop in association with the second hypobranchial ([their] Osteoglossoidae and Mormyriiformes) or the second basibranchial ([their] Notopteroidei; they are uncalcified in *Hiodon*): This was one of four characters taken from the literature that Li & Wilson (1996a) accepted as evidence of the monophyly of Osteoglossomorpha. However, this character needs to be reconsidered. The bony elements are absent in *Hiodon* (Fig. 30A; 'uncalcified' according to Greenwood *et al.* (1966). In *Hiodon*, there is instead a pair of tendons that arise from the sternohyoideus and insert on the proximal portions of hypobranchial 2 (hb2) and the posterior portion of basibranchial 2 (bb2) (Greenwood, 1971; Hilton, 2001; fig. 4A); it is these tendons that have been suggested to be homologous with the bony elements (see below) of other osteoglossomorphs (e.g. by Greenwood, 1971, 1973 and apparently by Li & Wilson, 1996a).

In other osteoglossomorphs, these elements occur in two distinct forms and the morphological correspondence implied by Li & Wilson and others who have coded them similarly has never been established satisfactorily (Nelson, 1968; Hilton, 2001); I therefore have separated them into two character states. In

notopterids (e.g. *Xenomystus*, Fig. 30B), there is a pair of autogenous bony elements associated with the ventral elements of the second gill arches (state 1). These elements, which lie on the lateral surface of the sternohyoideus, are completely free from any other elements of the gill arches and were called 'tendon bones' by Ridewood (1904a) and others, although their development has never been studied (i.e. it is unclear if they truly ossify in tendon). Their proximal ends lie at the junction of hb2 and bb2 (see Hilton, 2001: fig. 4B). This is a similar position as the tendon found in *Hiodon*, which was the reason for the homology statement by Greenwood *et al.* (1966).

In osteoglossids and mormyrids, there is a ventromedial (i.e. proximal) process of hb2. This process is never known to be an autogenous element during ontogeny, although Greenwood (1973) described a 'line of fusion' in various taxa; this, however, has never been illustrated, and I regard it as ambiguous. In all of the small, postlarval specimens available, these processes are relatively well developed. The degree of development of this process is extremely variable in adults. For instance, *Arapaima* (Fig. 30C), has a very small process that barely makes contact with the sternohyoideus muscle (Greenwood, 1971). In other taxa, such as *Pantodon* (Fig. 30D), *Osteoglossum* (Hilton, 2001: fig. 4C), and mormyrids (Fig. 31A, B), these processes are well developed and tightly associated with the sternohyoideus (Greenwood, 1971).

Benveniste (1994) further divided the presence of a continuous hb2 process into two character states. In her view, 'the bones [of mormyrids] seem to have retained and developed the process to a highly pronounced degree, Although severely reducing the hypobranchial component. I suggest, based on these observations, that the tendency is for the loss of the second hypobranchial in mormyrids' (Benveniste, 1994: 26). The second hypobranchial of mormyrids (Fig. 31) is indeed much smaller than that of osteoglossids (e.g. *Arapaima*, Fig. 30C). However, as far as the presence of a process goes, my analysis suggests that the elements in mormyrids and osteoglossids are homologous, and that the condition in notopterids is further derived. A bony process of hb2 is considered here to be a synapomorphy of Osteoglossiformes (see Character Optimization and Node Support). The condition in all fossil osteoglossomorphs for this and most gill arch characters is unknown due to lack of preservation.

(46) *Toothplate(s) associated with basibranchial 4*: Present [0]; Absent [1]. Nelson (1968) defined this character (i.e. the absence of a posterior toothplate) in support of the family Notopteridae (e.g. *Xenomystus*; Fig. 30B). However, this character shows more variation than suggested in Nelson's familial-level key

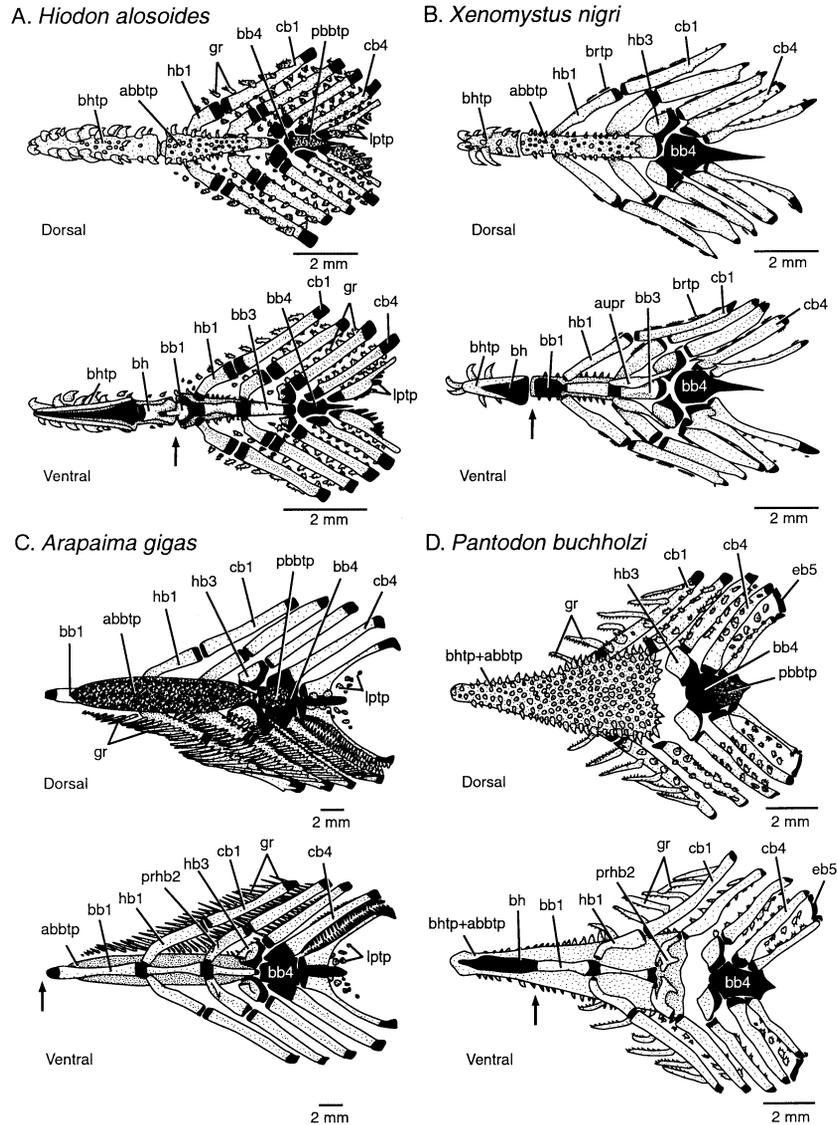


Figure 30. Ventral elements of the gill arches and the basihyal shown in dorsal (= oral) and ventral views. A, *Hiodon alosoides* (UMA F10597, 62 mm SL). B, *Xenomystus nigri* (FMNH 69494, approx. 90 mm SL). C, *Arapaima gigas* (UMA F11261, 145 mm SL), gill rakers omitted from the right side. D, *Pantodon buchholzi* (FMNH 63752, 74 mm SL). Cartilage shown in black. Anterior facing left. Arrow indicates the position at which the hypohyals meet the basihyal/basibranchial skeleton. Illustration of ventral view of *Hiodon* modified from Hilton (2002: fig. 56).

(although he is correct in that, of his 'Notopteroidei' [= Hiodontidae + Notopteridae], only the notopterids lack this toothplate). In some osteoglossomorphs (e.g. *Hiodon*, Fig. 30A; *Arapaima*, Fig. 30C; *Pantodon*, Fig. 30D) and outgroups (e.g. *Elops*, see Forey, 1973b: fig. 8), there is at least one posterior toothplate that is associated with basibranchial 4, and this is considered to be the plesiomorphic condition (state 0). In at least some specimens of *Hiodon*, this toothplate is comprised of several smaller toothplates (Taverne, 1977; Hilton, 2002); the specimen illustrated in Figure 30A

has only a single posterior basibranchial toothplate. The mormyrids I examined lack this posterior toothplate (Fig. 31A, B). It is also absent in *Osteoglossum* (see Taverne, 1977: fig. 56), *Scleropages* (see Taverne, 1977: fig. 85) and *Heterotis* (see Taverne, 1977: fig. 109).

(47) *Basihyal toothplate*: Present [0]; Absent [1]. LW96[42]. The basihyal toothplate is a toothed dermal element that lies on the dorsal surface of the basihyal element. The plesiomorphic condition for teleosts is to

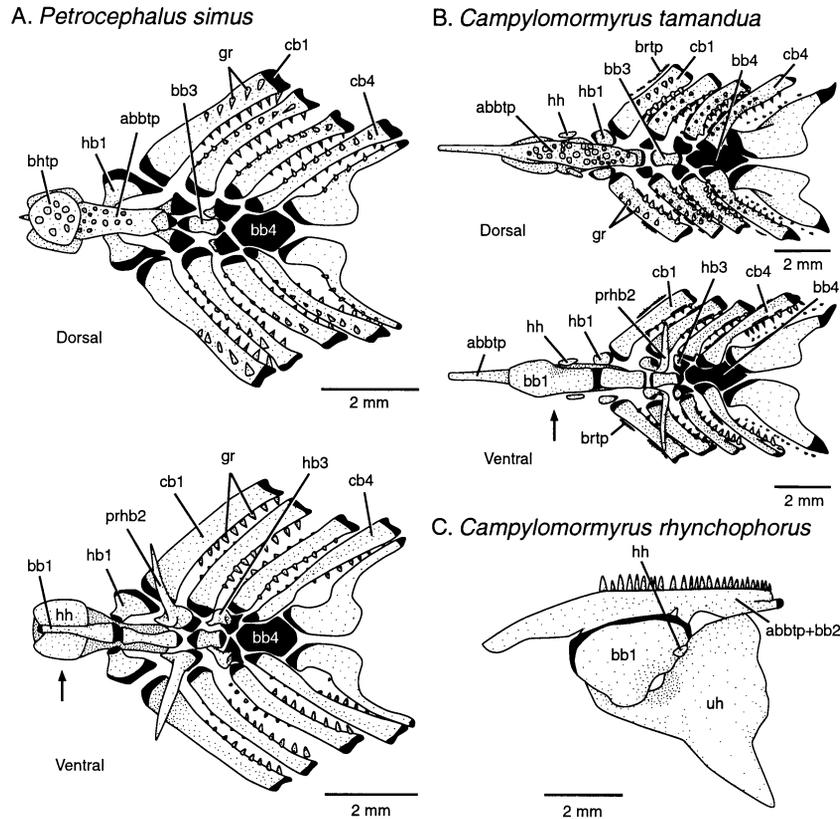


Figure 31. Ventral elements of the gill arches and basihyal of mormyrids. A, *Petrocephalus simus* (MCZ 50113, 55 mm SL). B, *Campylomormyrus tamandua* (FMNH 55300B, 84 mm SL). C, basibranchial toothplate, basibranchial 1 and urohyal of *C. rhynchophorus* (MCZ 50166, 97 mm SL). A & B shown in dorsal and ventral views; C shown in lateral view. Arrow in A & B indicates the position at which the hypohyals and ceratohyals meet the basihyal/basibranchial skeleton. Cartilage shown in black. Anterior facing left.

have an autogenous basihyal toothplate (e.g. *Hiodon*, Fig. 30A; *Elops*, Forey, 1973b: fig. 8, pers. observ.). Absence of a basihyal toothplate was regarded as a synapomorphy of *Heterotis* and *Arapaima* by Li & Wilson (1996a; also 1999: character 51). In several osteoglossomorphs (e.g. *Pantodon*; Fig. 30D), the anterior toothplate extends far anteriorly to also cover the basihyal (see Character 49), and is thus said to also be comprised in part of the basihyal toothplate.

Both *Heterotis* and *Arapaima* (Fig. 30C) have no basihyal toothplate (also see Taverne, 1977: figs 109, 136, respectively). In *Arapaima*, no discrete element can be identified as a basihyal (see Character 50), whereas in *Heterotis*, the anterior lateral edges of the anterior basibranchial toothplate extend forward to contact the cartilaginous basihyal. However, it is difficult to imagine that this is anything but a secondary anterior growth of the basibranchial toothplate and there is no separate toothplate over the basihyal.

For †*Joffrichthys*, Li & Wilson (1996b: 203) reported that the basihyal toothplate 'closely resembles that of

Arapaima', although they coded *Arapaima* as lacking a basihyal toothplate. Presumably these authors were referring to the toothplate that covers the basibranchial series in *Arapaima*. †*Joffrichthys* (e.g. UALVP 23705; FMNH PF12171b) has a well preserved toothplate in the region of the ventral gill arches, but I was unable to establish its exact relationship with elements of the basihyal/basibranchial series; I therefore code this character as unknown for †*Joffrichthys*. Also, this toothplate bears greatly enlarged caniniform teeth that bear little resemblance to those found in even juvenile (i.e. 150 mm SL) specimens of *Arapaima* (although smaller specimens of *Arapaima*, i.e. approximately 55 mm SL, do bear larger teeth than found in specimens 150 mm SL; pers. observ.).

There is an impression of a toothplate in a specimen of †*Lycoptera davidi* that I examined (Fig. 15B; MNHN 1927-13-06 e'), and it is anterior to the hypohyals (preserved as an impression overlain by the gular). However, because this partial specimen is disarticulated (this element could be the basibranchial toothplate) and no other specimen available has any

element of the gill arches preserved at all, I coded this character as unknown in †*Lycoptera* (although see Ma, 1987: fig. 8, which shows a well developed basihyal toothplate).

Among the mormyrids examined here, *Gnathonemus* and *Campylomormyrus* have no basihyal toothplate (Fig. 31). *Petrocephalus* (Fig. 31A) has an autogenous toothplate that lies dorsal to the hypohyals, which I follow Nelson (1968) in calling a basihyal toothplate. Nelson (1968: 271) considered the enlarged toothplate of derived (i.e. non-petrocephaline) mormyrids to incorporate the basihyal toothplate as well, writing '[t]hat this [presence of a single toothplate] was accomplished by a fusion of the two [toothplates] present in *Petrocephalus* is suggested by the occurrence of paired hypohyals, partially tucked under the anterior part of the tooth plate in *Mormyrus* ([Nelson's] fig. 9[A]) whose gill-arch structure otherwise is very similar to that of *Mormyrops*.' In *Campylomormyrus* (Fig. 31B, C) and other mormyrines, the hypohyals (= bone X of Taverne, 1968a, and elsewhere) are far posterior, which gives the appearance that the toothplate extends far anterior. If it is accepted that the large anterior endochondral element present in mormyrines corresponds with the first element of the basibranchial series (= basihyal of Taverne, 1968a, and elsewhere) and that the basihyal is absent, as Nelson (1968) suggested (and is followed here), then the toothplate that is present is supported mostly by the basibranchial series (although there is an anterior elongation, which likely is a secondary development). Therefore, I interpret this toothplate in mormyrines as representing only an anterior basibranchial toothplate. The gill arches of *Gymnarchus* lack all dermal elements, including all toothplates (Nelson, 1968; Taverne, 1972; Benveniste, 1994).

(48) *Basihyal toothplate*: Flat [0]; With ventrally directed processes [1]. In most groups examined here, the basihyal toothplate (if present) is a flat dentigerous bone. Nelson (1968: 272) used the similarity in shape of the basihyal toothplates of *Hiodon* (Fig. 30A) and notopterids (e.g. Fig. 30B; 'basihyal tooth plate an enlarged separate element, extending ventrally down the sides of the basihyal; a row of enlarged teeth on either side of the tooth plate') in support of the hypothesis that the two were sister groups. This similarity is not supported as homology based on the topology of my cladogram. This character is coded as unknown for *Arapaima*, *Heterotis*, *Gnathonemus* and *Campylomormyrus* because these taxa lack a basihyal toothplate, and for †*Lycoptera* and †*Joffrichthys* due to uncertain homology (see Character 47).

(49) *Basibranchial toothplate and basihyal toothplate*: Separate [0]; Continuous [1]. LW96[21]. Ridewood (1905: 257) described the gill arches of *Scleropages*

leichardti as possessing 'a large dentigerous bone overlies the glossohyal [= basihyal] cartilage, the first and second basibranchial bones, and the anterior half of the third.' This was also found to be the condition of *Osteoglossum biccirhosum* and *S. formosum* (at that time, all of these fishes were classified in the genus *Osteoglossum*). Of *Pantodon*, Ridewood (1905: 275) noted that '[a]bove the glossohyal [= basihyal] cartilage and the basibranchials is a large, triangular, dentigerous bony plate, concave on its upper surface, recalling the similarly placed lingual bone of *Osteoglossum*, except that the width of the hinder part is greater, and that the largest teeth occur in the median of the plate.' Basibranchial 3 (bb3) is not developed in *Pantodon* (Fig. 30D; also see Nelson, 1968: fig. 8), but the toothplate does extend posteriorly about half the distance between bb2 and bb4. Nelson (1968), citing a mixture of plesiomorphy and apomorphy, also noted that '[o]n the basis of the large basibranchial tooth plate, *Pantodon* more closely resembles the *Scleropages*-*Osteoglossum* division of the Osteoglossidae than that including *Arapaima* and *Heterotis*. Yet the highly specialized condition of the gill arches of *Pantodon* obscures the relationships of this fish, and its systematic position based on these features is relatively uncertain.' Li & Wilson (1996a) used the similarly shaped toothplate in support of the Osteoglossinae (= †*Phareodus* + *Pantodon* + (*Osteoglossum* + *Scleropages*)). The condition in †*Phareodus* could not be determined in my specimens, and is therefore coded here as unknown, although it was noted by Li *et al.* (1997a: 492) that 'it appears to have the same pattern as that in the Recent *Osteoglossum* and *Scleropages*, in which the basihyal tooth plate is fused with the basibranchial tooth plate.'

No other osteoglossomorph has a large basihyal/basibranchial toothplate (e.g. see Fig. 30), except for possibly the mormyrines, as proposed by Nelson (1968), although see discussion under Character 47 for my differing interpretation. This character is coded as unknown for *Arapaima*, *Heterotis*, *Gnathonemus* and *Campylomormyrus* because these taxa lack a basihyal toothplate, and for †*Lycoptera* and †*Joffrichthys* due to uncertain homology (see Character 47).

(50) *Basihyal*: Present and ossified [0]; Present and cartilaginous [1]; Absent [2]. The presence of an ossified basihyal, as seen in *Hiodon* (Fig. 30A) is considered plesiomorphic. In elopomorphs (e.g. *Elops* & *Megalops*; pers. observ.), only the very posterior portion of the basihyal is ossified (e.g. see Taverne, 1974: fig. 22).

In several groups of osteoglossomorphs, the basihyal remains cartilaginous throughout ontogeny. For instance, the basihyal of notopterids is entirely cartilaginous, and is autogenous from the anterior

basibranchial copula (e.g. *Xenomystus*, Fig. 30B). In *Pantodon*, *Osteoglossum* and *Scleropages*, the basihyal is also cartilaginous, although it is continuous with the copula in which the basibranchials ossify (e.g. Fig. 30D), and therefore may represent a condition that is not homologous with that of notopterids. In *Heterotis*, the basibranchial is also entirely cartilaginous (pers. observ.; Nelson, 1968). Nelson (1968: fig. 6) illustrated the gill arches of a specimen of *Heterotis*, but did not figure a separate basihyal, and commented that 'because neither the basihyal nor first basibranchial are ossified, it is not possible in a precise way to distinguish between them', suggesting that he considered the anterior unossified portion of the basibranchial copula to be the basihyal. However, in my small specimen of *Heterotis* (UMA F10653, 75 mm SL; the only specimen available for which this character could be studied), the basihyal is a distinct cartilage that lies anterior to the point at which the hypohyals articulate with the basihyal/basibranchial series. Nelson (1968: fig. 5) also considered the basihyal of *Arapaima* to be continuous with the first basibranchial. There is indeed a small anterior cartilaginous tip to the anterior basibranchial copula (Fig. 30C), but this is more likely an unossified portion of the anterior basibranchial copula rather than a basihyal element, and it lies completely posterior to the hypohyals. I was unable to find a distinct cartilage anterior of the hypohyals, although a diffuse mass of connective tissue, which does pick up some alcian stain, is located in the expected position, and may represent the basihyal (this hypothesis is tenuous at best); I consider the basihyal to be absent in *Arapaima*.

Nelson (1968) considered the absence of the basihyal as characteristic of mormyrids. Taverne (in his various works on mormyroid osteology) considered the basihyal to be present and represented by the large, ventrally deflected element that Nelson (1968) called bb1, which is the hypothesis that I followed here. Ridewood (1904a) suggested that the anterior element of the gill arches of the mormyroids represents the basihyal, or perhaps both the basihyal and bb1. I agree with Nelson and consider the basihyal to be absent from the mormyrids examined here. In *Gymnarchus*, there is an element that has been interpreted as a basihyal (Taverne, 1972), a urohyal (Nelson, 1968) or both (Ridewood, 1904a; Benveniste, 1994); but because no specimens were available, I cannot comment on this homology statement.

(51) *Hypohyals*: Two ossified pairs present [0]; One ossified pair present [1]; One ossified pair present, but greatly reduced in size [2]. Two pairs of ossified hypohyals is considered a synapomorphy for teleosts (Arratia & Schultze, 1990). This is the condition seen in *Hiodon* (Hilton, 2002: fig. 57).

Notopterids, osteoglossids and *Pantodon* have only a single ossified hypohyal. For some taxa, Taverne identified this element as the dorsal hypohyal (e.g. *Osteoglossum*, Taverne, 1977: fig. 55), whereas for others (e.g. *Notopterus*, Taverne, 1978: fig. 70) he declined to label this as either the dorsal or ventral hypohyal. That this single hypohyal is the dorsal element was also suggested by Arratia & Schultze (1990: 254), who wrote:

'Osteoglossomorphs and siluroids offer variability in the presence, size and position of the hypohyals. In *Hiodon* two hypohyals are present; the ventral one is slightly larger than the dorsal one; a ligament connects the urohyal with the ventral hypohyal. In all other osteoglossomorphs the ventral hypohyal is missing; the Jurassic [\dagger]*Lycoptera* possesses also only one hypohyal, the dorsal one, supposedly. The ligamentous connection has moved to anterior ceratohyal therefore it is argued that the ventral hypohyal has been lost. In *Pantodon*, a cartilaginous nodule lies at the anteroventral part of the ceratohyal; it functionally replaces the ventral hypohyal because it connects to the small urohyal by a short ligament.'

If, as Arratia & Schultze (1990) suggested, the ventral hypohyal can be identified across taxa as the element that receives a ligament from the urohyal, and if that element is missing in osteoglossomorphs, then it is reasonable to hypothesize that the single bone found in osteoglossomorphs is the dorsal hypohyal. The attachment of this ligament was not examined in this study, but because there is no evidence to the contrary, I regard the single hypohyal as an equivalent structure across taxa (i.e. I coded them all as state 1). In theory, this could change if there is evidence that in some taxa the ligament is attached to the hypohyal (indicating that it is the ventral hypohyal), whereas in others it is not (indicating that it is the dorsal hypohyal that remains).

I coded \dagger *Lycoptera* as unknown due to preservation, with the acknowledgement that it supposedly has a single hypohyal (Ma, 1987: fig. 8; Arratia & Schultze, 1990), although McAllister (1968) reported two hypohyals. I also coded as unknown due to preservation \dagger *Joffrichthys*, \dagger *Phareodus*, \dagger *Singida* and \dagger *Ostariostoma*. \dagger *Phareodus* supposedly has a single hypohyal (Taverne, 1978: fig. 11; note this specimen is \dagger *P. acutus*, which is a synonym of \dagger *P. encaustus*; Grande, 1984), although in their review, Li *et al.* (1997a) did not describe the hypohyals for either \dagger *P. encaustus* or \dagger *P. testis* at all.

Mormyroids show variation in the size of the hypohyal. *Petrocephalus*, for instance, has a single pair of hypohyals that support the basihyal toothplate (Fig. 31A; Nelson, 1968), whereas those of other mormyrids are significantly reduced in size (or absent) and are positioned adjacent to the posterior portion of

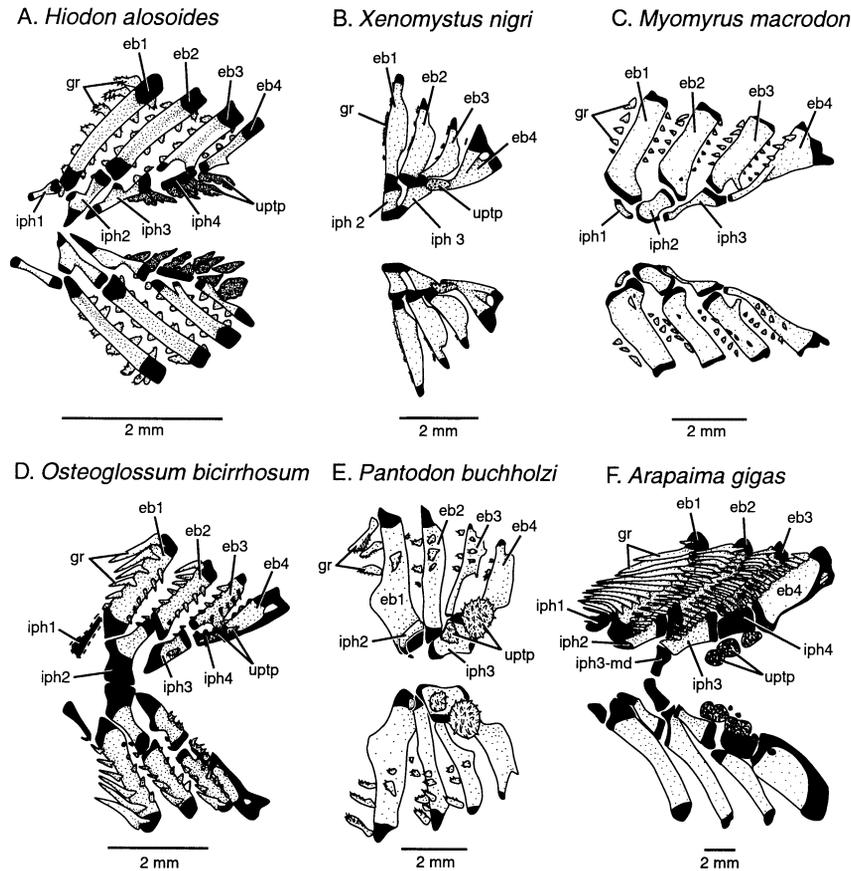


Figure 32. Dorsal gill arches. A, *Hiodon alosoides* (UMA F10597, 62 mm SL). B, *Xenomystus nigri* (FMNH 69494, approx. 90 mm SL). C, *Myomyrus macrodon* (MCZ 50218, 102 mm SL). D, *Osteoglossum bicirrhosum* (UMA F10336, approx. 55 mm SL); iph1 of the left side is missing from this specimen and is indicated by dashed line. E, *Pantodon buchholzi* (FMNH 63752, 74 mm SL); iph2 of right side is abnormally small. F, *Arapaima gigas* (UMA F11261, 145 mm SL); gill rakers omitted from the left side. All in ventral (= oral) view except *Hiodon*, which is in dorsal view. Cartilage shown in black. Anterior facing left. Illustration of *Hiodon* modified from Hilton (2002: fig. 56).

bb1 (e.g. Fig. 31B, C). This reduced hypohyal (state 2) is the element that Taverne (e.g. 1968a,b, 1969, 1971, 1972) labelled as bone 'X' and hesitantly homologized with the hypohyal of other osteoglossomorphs. As this element is a chondral bone positioned medial to the anterior ceratohyal, it seems to me that this element must correspond to the hypohyal. A potential conflict to this homology statement is that Taverne (1969: fig. 73) illustrated his element 'X' far posterior and reduced in size in *P. bane*, although he did not illustrate or describe the chondral element that supports the basihyal toothplate described by Nelson (1968) and herein (Fig. 31A). I follow Nelson, and have coded *Petrocephalus* as having a non-reduced single hypohyal (state 1). A single pair of ossified hypohyals is present in *Gymnarchus* (Nelson, 1968; Taverne, 1972).

(52) *Infrapharyngobranchial 3*: Undivided [0]; Divided into two elements [1]. Nelson (1968: 268) described the third infrapharyngobranchials (iph) of *Arapaima* (Fig. 32F) and *Heterotis* (Fig. 33A) as having medial divisions that are entirely cartilaginous, and further noted that 'this feature, which so far as known, occurs in no other teleostean fish[es]'. This interpretation is accepted here and it is interpreted as a synapomorphy of *Heterotis* and *Arapaima*, although the condition in fossils, of course, is unknown.

(53) *Infrapharyngobranchial 1*: Present [0]; Absent [1]. Nelson (1968) described the absence of iph1 in notopterids (small and cartilaginous in *Papyrocranus*; Nelson, 1968: fig. 3C), *Pantodon* (also missing iph4) and *Gymnarchus* (also missing iph4; see Benveniste, 1994). Of the taxa sampled here, there is no iph1

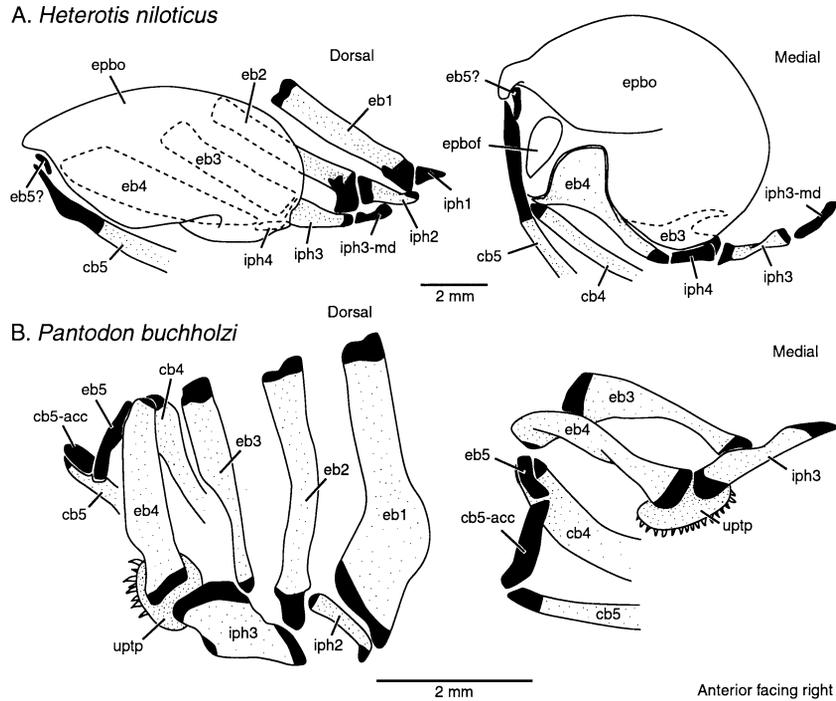


Figure 33. Some elements of the left branchial arches of A, *Heterotis niloticus* (UMA F10653, 75 mm SL) and B, *Pantodon buchholzi* (FMNH 63752, 74 mm SL) in dorsal and medial views showing position of the accessory cartilages associated with the fourth and fifth branchial arches. Gill rakers omitted. Cartilage shown in black. Anterior facing right.

(state 1) in *Pantodon* (Fig. 32E), *Chitala* and *Xenomystus* (Fig. 32B). I did confirm the presence of a very small cartilaginous iph1 in *Papyrocranus*, although the available specimen is far from ideal for the study of cartilages because it is not very well stained.

The arrangement of elements of the dorsal gill arches in *Xenomystus* deserves further comment. There are two elements in the infrapharyngobranchial series, here identified as iph2 and iph3, following Nelson (1968: table 1). These two elements contact each other proximally (Fig. 32B). The anterior element (iph2) contacts both epibranchial 1 (eb1) and eb2 at its distal end. In the specimen illustrated in Figure 32B, iph2 is in line with eb1, and the contact with eb2 is less intimate, thereby suggesting that this element is better identified as iph1. However, in the other specimen I examined (UMA F11326), this element is positioned further posteriorly, so that there is an equal degree of contact with eb1 and eb2 (see also Taverne, 1977: fig. 106); the main axis of the element in UMA F11326 is therefore between eb1 and eb2. The element identified as iph3 is triangular (Fig. 32B) and contacts eb2, eb3 and eb4, although the main axis of the element is in line with eb3. Because of the multiple distal articulations of both of these elements, it is possible that they are the product of fusion between two or more elements. For the present analysis, however, I

follow Nelson (1968) in the identification of these elements as iph2 and iph3 in *Xenomystus*.

(54) *Orientation of infrapharyngobranchial 1*: Proximal tip anteriorly directed [0]; Proximal tip posteriorly directed [1]. Typically in teleosts, iph1 is, in dorsal view, obliquely positioned and its proximal (= medial) tip is anterior to its distal tip (e.g. see Fig. 32). In *Hiodon*, iph1 extends dorsally to meet the neurocranium (Hilton, 2001: fig. 1A); this character is coded as [0] because it has a slight anterior orientation if the dorsal gill arches are viewed from above (Fig. 32A). *Pantodon*, *Chitala* and *Xenomystus* are coded as unknown for this character because iph1 is missing (see Character 53).

The three mormyrids examined here all have the derived condition, in which the proximal (= medial) tip of iph1 is posterior of the distal tip (e.g. *Myomyrus*; Fig. 32C; note that *Myomyrus* was not scored in my matrix, although the morphology of the dorsal gill arches is very conserved within mormyrids and the condition of the scored taxa is virtually identical with that shown for *Myomyrus*). This condition is also seen in *Mormyrus* (Nelson, 1968: fig. 9C). Because of the way in which the gill arches were illustrated by Taverne (i.e. in dorsal view with the dorsal arches from one side reflected to expose the oral view), it is difficult to inter-

pret this character from his drawings. *Gymnarchus* lacks iph1 (Nelson, 1968: fig. 10C; Taverne, 1972).

The gill arch skeleton of *Pantodon* is quite derived ('among the most advanced of those of osteoglossomorph fishes'; Nelson, 1968: 269) and some of these specializations, including newly discovered or unillustrated qualities, are deserving of further description. For instance, there are only two elements of the infrapharyngobranchial series, which is seen elsewhere among osteoglossomorphs only in *Xenomystus* (Fig. 32B). The anterior infrapharyngobranchial is a slender element positioned obliquely between eb1 and eb2 that articulates distally with a slight depression in the anterior margin of eb2, and corresponds to iph2 of other teleosts (Fig. 32E; Nelson, 1968; Taverne, 1977). The posterior element is a large block of bone that articulates with the proximal edges of both eb3 and eb4 (Fig. 32E). Nelson (1968) interpreted this element as an enlarged iph3. However, the association of this element and eb4 is unquestionable, and led Taverne (1978) to interpret it as a fused iph3 + iph4. However, because there is so far no ontogenetic evidence to support this interpretation, I follow Nelson (1968) in calling this element iph3 and consider iph4 to have been lost. There are four ossified epibranchials (*contra* Kershaw, 1970; who described only two ossified epibranchials), and a cartilaginous eb5 (Fig. 33B). Epibranchial 5 is a medially directed element that contacts the fourth branchial arch at the distal point where eb4 and ceratobranchial (cb) 4 meet. An additional cartilaginous element associated with the posterior gill arch skeleton (Fig. 33B) has not been described in any previous accounts of the osteology of *Pantodon* (e.g. Le Danois, 1967; Nelson, 1968; Kershaw, 1970, 1976; Taverne, 1977). This element bridges the gap between the proximal point of eb5 and the distal point of cb5 (Fig. 33B). I interpret this element as a distal subdivision of cb5 (following Nelson, 1967: 75–76 & fig. 1h for *Alepocephalus*; indicated by a question mark in his illustration) and analogous to the 'accessory cartilage' described by Greenwood & Rosen (1971) for certain alepocephaloids (e.g. compare their figs 1–5 with the condition illustrated here for *Pantodon*; Fig. 33B) and Johnson & Patterson (1997: fig. 2b) for *Gonorynchus*.

The posterior gill arches of *Heterotis* are also highly derived, due in part to the development of an epibranchial organ (Fig. 33A; see also Daget & d'Aubenton, 1957: fig. 25; Nelson, 1967; Bauchot, Ridet & Diagne, 1993). Of note here is a small cartilaginous element, possibly eb5, that was found in the single available cleared and stained specimen of *Heterotis* (UMA F10653; Fig. 33A). This differs from other descriptions of the gill arch morphology of *Heterotis* (e.g. Nelson, 1967: fig. 1G; 1968: fig. 6C; Taverne, 1977: fig. 109) and should be confirmed on more specimens.

VERTEBRAL COLUMN

(55) *Abdominal scutes*: Absent [0]; Present as paired structures [1]. Modified from LW99[75]. Li & Wilson (1999) coded this character as a dichotomous present/absent character, with only notopteroids and clupeoids coded as 'present' and resulting in a homoplasious distribution of abdominal scutes. However, the condition in these two groups is morphologically distinct (Grande, 1985: 252), which is not indicated in Li & Wilson's (1999) coding. The abdominal scutes found in clupeoids are formed as single median elements, whereas those of notopterids are paired (Fig. 34B), and therefore do not pass the test of similarity (Patterson, 1982) in the establishment of homology. This is not meant to suggest that Li & Wilson (1999) considered the two conditions to correspond to one another, but merely that this is how it is interpreted based on their coding strategy. In my analysis, this is a moot point, as no clupeomorph was scored for analysis, and therefore the only taxa scored with a derived state are notopterids. The presence of scutes is a synapomorphy of Notopteridae.

I will comment briefly on other aspects of the notopterid osteology that may be related to the development of the ventral scutes. The anterior ribs are elongate in *Chitala* (Fig. 34A). More posteriorly, the ribs are much shorter, although there is a ventral series of bones that lies in series with the ribs. These elements, which I term abdominal ribs, are preformed in cartilage like true ribs, and their dorsal and ventral tips remain cartilaginous (in the specimen shown in Fig. 34A, the posterior-most element is entirely cartilaginous and very small). These elements contact the medial surface of the ventral scutes. It is likely that the anterior elongate ribs are actually the product of fusion between the true ribs and the abdominal ribs. Taverne (1978: figs 108 and 129, respectively) illustrated the abdominal ribs as independent elements in *Xenomystus* and *Papyrocranus*, although he only showed elongate ribs in *Notopterus* (Taverne, 1978: fig. 75). Therefore, there may be some phylogenetic or individual variation in their structure within Notopteridae. In *Xenomystus* and *Papyrocranus* the abdominal ribs are much more stout along their entire length than they are in *Chitala* (pers. observ., cf. Taverne, 1978: figs 108 and 129 with Fig. 34A) and are not in line with the true ribs, but rather overlap the anterior distal surface of the true ribs. Similar morphology of *Chitala* to that shown in Figure 34A was also observed in adult specimens (e.g. UMA F10349). This distinctive morphology of the ribs in *Xenomystus* and *Papyrocranus*, although not included in my analysis, further supports a closer relationship between the two African genera relative to the Asian *Chitala* and *Notopterus* (as suggested also by Forey, 1997 and this analysis, and contrary to Li & Wilson, 1996a).

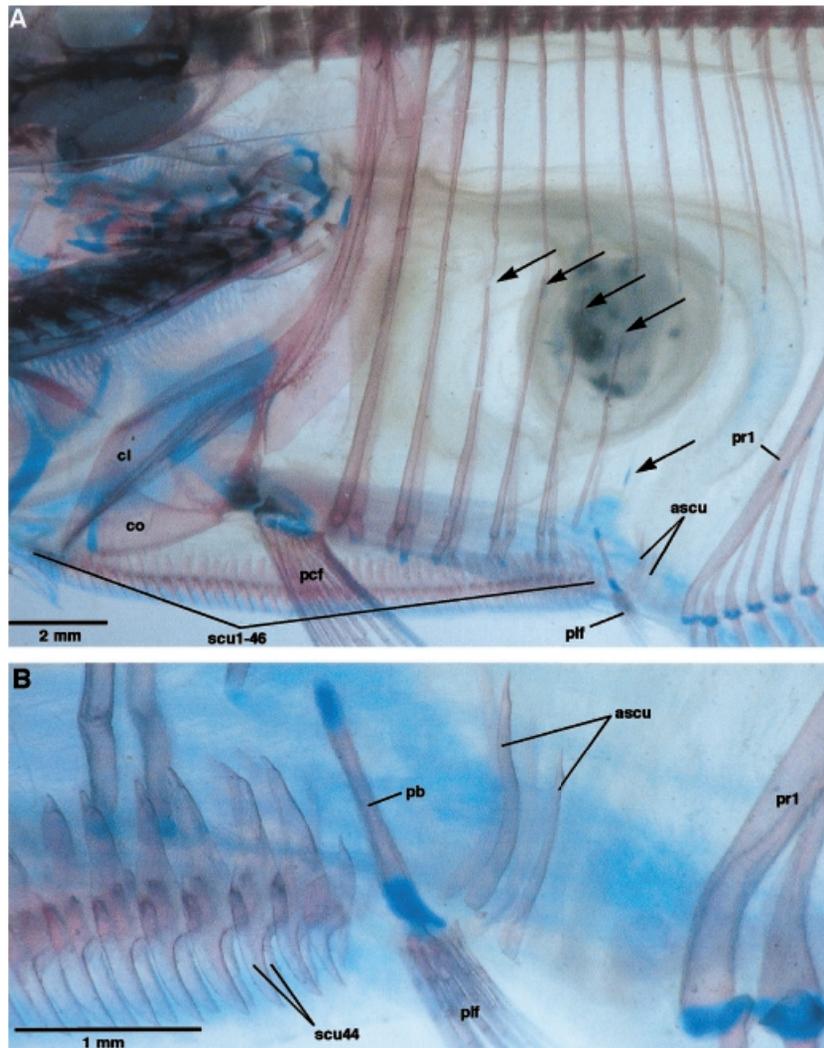


Figure 34. Abdominal region of Notopteridae. A, Abdominal region of *Chitala* sp. (UMA F10341, 75 mm SL), showing several features characteristic of the family Notopteridae. Note particularly the abdominal scutes, abdominal ribs, elongate second and third true ribs (perhaps abdominal ribs and true ribs that have fused), anal scutes and an enlarged proximal radial of the first anal pterygiophore. The abdominal ribs develop like true ribs and may fuse to the true ribs; the autogenous abdominal ribs are marked with arrows. There is a small cartilaginous element that is developed posterior to the last ossified abdominal rib, which likely is the fifth autogenous abdominal rib. B, close-up of pelvic fin region showing details of the pelvic girdle, abdominal scutes and the proximal radial of the first anal pterygiophore. Note that the abdominal and anal scutes are both paired structures.

In 'typical' clupeomorphs (e.g. *Alosa*), the lateral arms of the abdominal scutes extend far dorsally, so that they overlap superficially with the ribs, and possibly function in an analogous manner to the abdominal ribs of notopterids. In the genus *Sundasalanx*, determined to be a clupeiform by Siebert (1997: fig. 1), there are two chondral so-called 'parapelvic' bones that lie lateral to the pelvic girdle. These also may be analogous to the abdominal ribs of notopterids.

Also present in *Chitala* are two pairs of bones that I term the anal scutes (Fig. 34), although their serial

homology with the abdominal scutes is uncertain. These bones lie lateral to the opening of the anus, and do not meet in the midline. Taverne (1978: 126–127) described these bones as follows: 'À l'arrière, une ou deux paires d'écailles transformées, qui devaient primitivement appartenir à la serrature ventrale, dépassent la ceinture pelvienne, migrent plus en profondeur dans les chairs et viennent encadrer le rectum' [Further posteriorly, one or two pairs of modified scales, which originally belonged to the series of ventral scutes, are larger than the pelvic girdle, posi-

tioned deeper in the body wall and surround the anus]. Taverne (1978: fig. 75, unlabelled) figured these elements in *Notopterus notopterus*, although they were not illustrated for either *Xenomystus* or *Papyrocranus*. I did not find them in my specimens of these two taxa either, although this should be checked on more specimens.

(56) *Epipleural bones*: Absent [0]; Only a few bones in anterior caudal region [1]; Present throughout abdominal and caudal region [2]. A97[67]. Patterson & Rosen (1977: 126) regarded the condition of having 'epipleural bones well developed' to be a synapomorphy of the group including elopomorphs and euteleosts. Alternatively, the fishes they considered more basal (i.e. osteoglossomorphs and more basal teleosts) lacked well developed epipleural bones (see also Patterson, 1977b). Arratia (1997: 128) considered this character in her analysis (also see Arratia, 1999: character 89), reporting that 'the parsimony analysis . . . interprets the presence of a series of many epipleural bones developed throughout the abdominal and anterior caudal region as a homoplastic feature among advanced teleosts which is absent in teleosts such as osteoglossomorphs and some esocoids. Young and juvenile salmonids do not have epipleurals; however, very thin, hair-like bones are present in large salmonids.' *Hiodon* and †*Lycoptera* were, however, the only osteoglossomorph taxa that were coded in Arratia, 1997) analysis. In her 1999 analysis, she also included *Heterotis*, which she coded as lacking epipleural bones. However, *Heterotis* is the only living osteoglossomorph with epipleural bones, as was noted by Patterson & Johnson (1995). My cleared and stained specimen of *Heterotis* (UMA F10653, 75 mm SL) has 14 ossified epipleural bones beginning at the first vertebrae with a full haemal arch, and progressing posteriorly. The specimen studied by Patterson & Johnson (1995: table 3; BMNH uncat., 68 mm SL) had only seven epipleurals, all of which were ossified and recorded as attached to the haemal arch. Whether the ligamentous part of the epipleural was attached to the haemal arch could not be determined on my specimen, although the ossification is separate from the haemal arch. Taverne (1976) reported epipleural bones in †*Kipalaichthys sekirskyi* Casier, 1965, a Cretaceous taxon from Africa that he considered basal to all non-hiodontiform osteoglossomorphs (Taverne, 1979, 1998). There are no epipleural bones in *Arapaima*, or any other osteoglossomorph examined in this study, and therefore, their presence in *Heterotis* is interpreted here as an autapomorphy.

Some notopterids also have been reported to have epipleurals (e.g. = 'arrête ventrale' of Taverne, 1978: figs 79 and 80), although according to Patterson & Johnson (1995: 16), these are better interpreted as

ventral myorhabdoi. Myorhabdoi are defined as 'one or two extra series of unattached intermuscular bones, developed, respectively, in the uppermost and lowermost forward flexures of the myosepta.' In describing the myorhabdoi of *Xenomystus* and *Papyrocranus*, Johnson & Patterson. (1995: 20) wrote that 'the 'epipleural bones' [of Taverne] have the same relationships as the unattached 'epineural bones' above them. Because the 'epipleural bones' do not resemble the epipleurals in any other teleosts [by being lath-like, rather than slender and rod-like], and because we know of no other teleost in which there is an abrupt transition from an attached epineural on one vertebrae to a superficial, lath-like epineural on the next, we believe that both series of bones are myorhabdoi . . . , which is autapomorphous for notopterids.' *Xenomystus* and *Papyrocranus* have two sets of myorhabdoi (one dorsal, one ventral), whereas *Notopterus* has six (Patterson & Johnson, 1995). †*Palaeonotopterus* is reported to have epineurals (Cavin & Forey, 2001), as in other osteoglossomorphs, but because almost nothing is known of the postcranial skeleton, this taxon is coded as unknown for the presence of epipleurals.

PECTORAL GIRDLE AND FIN

(57) *Dorsal arm of the post-temporal bone*: Less than 1.5 times as long as the ventral arm [0]; More than twice as long as the ventral arm [1]. LW96[17]. Li & Wilson (1994: character 2) considered the presence of a post-temporal with the dorsal arm more than twice as long as the ventral arm to be a synapomorphy of the Hiodontiformes (see also Li & Wilson, 1996a, 1999; Li *et al.*, 1997b). In *Hiodon*, the ventral arm of the post-temporal is forked (Hilton, 2002: fig. 86), but the longer of these two forks (the medial branch) is about half the length (or less) of the dorsal arm, which extends dorsally and is tightly connected to the epioccipital by a stout ligament (Hilton, 2002: fig. 24). All species of †*Eohiodon* bear a post-temporal similar in form to that of the extant species of *Hiodon* (pers. observ.). Based on descriptions in the literature (specimens were not available for this study), this is the condition also seen in †*Yanbiania* (e.g. Li, 1987: fig. 3; Chang, 1999; Li & Wilson, 1999; Chang, 1999: table 3). Chang (1999: 474) suggested the possible synonymy of †*Yanbiania* with †*Jiaohichthys*, in both of which the dorsal arm is 'much longer than the ventral.' †*Plesioleptocheilus* also supposedly shows this condition (Li & Wilson, 1999). The illustration in the original description by Chang & Chou (1976: fig. 1) is not very detailed, however, and Chang (1999: 475) remarked that 'the preservation of the specimens is insufficient to allow interpretation of several character states'. Although no specific mention was made in this

account of the state of the post-temporal bone, the accompanying photograph bears witness to the poor preservation of the specimens; therefore, I cannot comment on this state in †*Plesiolycoptera*.

Li & Wilson (1996a: 167), citing personal observation, remarked that '[i]n [†]lycopterids and all out-group taxa the dorsal arm [of the post-temporal] may be longer than the ventral arm, but it is not twice as long.' The illustrations available in the literature of †*Lycoptera* are, again, lacking in detail, likely because of the poor preservation of the specimens themselves. In one specimen available for this study in which the morphology of the post-temporal could clearly be seen (UMA F10652) the dorsal arm (4.3 mm long) is just over twice as long as the ventral one (2.1 mm long); I therefore coded †*Lycoptera* as sharing the derived condition, contrary to the studies by Li and colleagues. However, this should be confirmed in additional specimens.

†*Ostariostoma* is coded as derived for this character in this study. Li & Wilson (1996a: fig. 3A) described and coded the post-temporal as having a dorsal arm less than twice as long as the ventral one, although in their figure they showed this element with a dorsal arm that is much more than twice as long. Measurements taken from the photograph published by Grande & Cavender (1991: fig. 2A) support the observation that it is more than twice as long.

Other taxa studied in this analysis have the plesiomorphic condition of having the dorsal arm of the post-temporal less than twice as long as the ventral one (e.g. *Elops*, Forey, 1973b: fig. 9; *Scleropages*, Taverne, 1977: fig. 86). However, some taxa studied in this analysis were either problematic to code for this character, or possess a post-temporal bone in which it is more than twice as long (all of which were coded as plesiomorphic by Li and colleagues). For instance, *Pantodon* clearly shows this condition (pers. observ.; see also Taverne, 1978: fig. 44). The mormyrids examined in this study are problematic in that there are no discrete dorsal and ventral arms of the post-temporal. Instead, this bone is straight, with the lateral line running nearly dorsoventrally in the ventral portion of the bone. If it is accepted that the portion of the post-temporal that carries the lateral line is the 'ventral' arm and the remaining dorsal portion is the 'dorsal' arm in such taxa, then these taxa are either approaching (e.g. *Campylomormyrus*) or surpassing (e.g. *Petrocephalus*) the derived condition (i.e. the dorsal arm is at least twice as long as the ventral one). However, there is substantial variation in the morphology of the post-temporal among mormyroids. For instance, in *Hyperopisus* (Taverne, 1972: fig. 32), there is a post-temporal with very well defined dorsal and ventral arms (which are approximately equal in length), although the lateral line only crosses the very ventral

portion of the ventral arm. In *Gymnarchus* (Taverne, 1972: fig. 90), the post-temporal is little more than a bony tube surrounding the lateral line, with small dorsal extension that possibly represents the dorsal arm. I coded the mormyrids that I sampled as missing due to unclear homology of the dorsal and ventral arms.

†*Joffrichthys* and †*Palaeonotopterus* are coded as unknown due to lack of preservation. Other osteoglossomorphs are all coded as plesiomorphic (i.e. the dorsal arm is not twice the length of the ventral one). My analysis suggests that the derived condition supports the monophyly of Osteoglossomorpha (see Character Optimization and Node Support), although there was a reversal in Osteoglossiformes minus †*Ostariostoma* (Node D of Fig. 4).

(58) *Lateral line that pierces the supracleithrum*: Present [0]; Absent [1]. T98[103]. The association of the lateral line with the supracleithrum is presumably plesiomorphic for teleosts, based on its presence in more basal actinopterygians (e.g. see Grande & Bemis, 1991: figs 13 and 20 for Acipenseriformes; Grande & Bemis, 1998: figs 17 and 87 for Amiiformes). This association is present in †*Lycoptera*, *Hiodon* (e.g. Hilton, 2002: fig. 82), *Pantodon*, †*Singida* and the mormyrids examined here. Taverne (1998: 126), who defined this character supporting his Osteoglossiformes (= Osteoglossidae) and convergently occurring in Notopteridae, wrote that 'Hypercleithrum est dépourvu du tube osseux pour le canal sensoriel de la ligne latérale, comme chez les Notopteridae. Seuls les Pantodontidae font exception, ce qui doit être considéré comme une réversion si on applique la règle de la parcimonie' [(In Osteoglossidae) the supracleithrum lacks the bony tube for the lateral line sensory canal, as in Notopteridae. Only *Pantodon* is an exception, which must be regarded as a reversal, if the rule of parsimony is observed]. The absence of the lateral line within the supracleithrum is also found in †*Ostariostoma* (Grande & Cavender, 1991: fig. 2). The condition reported for †*Phareodus* in the literature is ambiguous, in that Taverne (1978: 20) reported the absence of the lateral line in the supracleithrum, whereas Li *et al.* (1997a: 493) suggest that it is present. Because the supracleithrum is not well preserved (typically covered by the opercle), I coded this character as unknown. †*Joffrichthys* and †*Palaeonotopterus* are also coded as unknown due to lack of preservation.

(59) *Cleithrum*: With no or only a slight medial lamina [0]; With a broad medial lamina [1]. CF01[14]. A broad medial lamina of bone on the anteroventral portion of the cleithrum (generally the horizontal arm of the cleithrum) was suggested by Cavin & Forey (2001) to be a character of mormyroids. They also considered the possibility of this character being present in

†*Palaeonotopterus* and being a synapomorphy of †*Palaeonotopterus* + mormyroids (Cavin & Forey, 2001: fig. 13B). The pectoral girdle of †*Palaeonotopterus* is known from one partial girdle (BMNH P.65643II); the dorsal and ventral portions of this girdle are broken away. Even though the anterior portion of the cleithrum and the coracoid are missing, this specimen shows part of a well developed medial lamina that sutures with the scapula posteriorly (pers. observ.; Cavin & Forey, 2001: fig. 11). As Cavin & Forey (2001: 41) wrote, '[d]espite the fact that this medial flange is incomplete the relative width agrees with conditions in mormyroids examined here . . . but differs from other osteoglossomorphs, including notopterids, where a medial flange is either absent (notopterids) or relatively narrow (*Hiodon*, Osteoglossiformes, *Pantodon*).' In general, I agree with the distribution of this character as proposed by Cavin & Forey (2001), although I also consider *Arapaima* to possess a broad medial lamina (see Taverne, 1977: fig. 137) that is analogous to the medial lamina in mormyroids and †*Palaeonotopterus*. This character, although not uniquely derived, is the only character that supports †*Palaeonotopterus* + Mormyridae (Fig. 4) that could be scored for †*Palaeonotopterus* (i.e. all other characters supporting this node were scored as missing and their states inferred by the computer algorithms during tree construction; see Character Optimization and Node Support).

(60) *Coracoid fenestra*: Absent [0]; Present [1]. Cavin & Forey (2001: 43) suggested the presence of a coracoid fenestra in all Recent osteoglossomorphs with the exception of *Hiodon*, and noted that 'the polarity of this character is unclear [but] we are tempted to propose that a synapomorphy of a group osteoglossiforms + mormyriiforms.' As for Character 59, I generally agree with the distribution of this character as proposed by Cavin & Forey (2001), but will note an apparent case of reversal to the 'unfenestrated' condition. The coracoid of *Arapaima* is a broad, flat bone that bears no coracoid fenestra, although there is a foramen on its lateral surface, ventral to the suture with the mesocoracoid and anterior to its contact with the scapula (not illustrated by Taverne, 1977: fig. 137). It is unclear if this foramen is homologous with the fenestra of other osteoglossomorphs, although no foramen is present in *Heterotis*, which does have a well developed coracoid fenestra (it is interesting to note that on my adult specimen of *Heterotis* [MCZ 50959], the posterior margin of the fenestra is formed by two arms from the coracoid that contact each other but do not fuse). In *Chitala* (UMA F10349), there is a small foramen in a similar position as that of *Arapaima*, as well as a coracoid fenestra. If the two foramina are homologous between *Chitala* and *Arapaima*, then the

foramen in *Arapaima* cannot be homologous with the coracoid fenestra, as *Chitala* would have both.

(61) *First pectoral fin ray*: Normal [0]; Greatly enlarged and extremely long [1]. LW96[23]. The elongation of the first pectoral fin ray was considered by Li & Wilson (1996a; also 1999: character 68) to be a synapomorphy of Osteoglossinae (all osteoglossids, including *Pantodon*, with the exception of heterotines, including †*Joffrichthys*). This character is also coded as derived in †*Paralycoptera* by Li & Wilson (1999), and was listed as one of the characters separating †*Paralycoptera* from †*Tanolepis* (in countering Jin *et al.*'s, 1995 suggestion that the two were synonymous). Chang & Chou's (1977: e.g. fig. 5) description of this taxon, however, does not indicate a particularly enlarged first pectoral fin ray. I interpret this as a synapomorphy of Osteoglossinae (Node I of Fig. 4).

PELVIC GIRDLE AND FIN

(62) *Post-pelvic bone*: Absent [0]; Present [1]. In a previous study (Hilton, in press: fig. 90), I identified a postpelvic bone as the only known unique diagnostic character for the genus *Hiodon* (although it is unknown in †*H. consteniorum*). This thin, blade-like median bone extends posteriorly from the suture between the left and right pelvic bones. In this analysis, a postpelvic bone is a synapomorphy of †*Lycoptera* + Hiodontidae (Fig. 4A) or Hiodontidae (Fig. 4B). The condition, however, is unknown in †*Lycoptera* and †*Eohiodon*, as well as other fossil osteoglossomorphs. These fossils typically are preserved flat, and the fin rays of the pelvic fin typically cover the region where this bone would be positioned, thereby obscuring the presence or absence of a postpelvic bone. It is merely an artifact of missing data that the presence of postpelvic bones is interpreted as a synapomorphy at these nodes.

(63) *Pelvic bone*: Slender [0]; Possesses a thin deep lamella in dorsoventral plane [1]. The pelvic bone of most osteoglossomorphs, as well as other basal teleostean fishes, is a slender, rod-like element (e.g. *Hiodon*; Hilton, 2002: fig. 90). However, in *Pantodon*, †*Singida*, *Scleropages* and *Osteoglossum*, there is a moderately developed (e.g. *Pantodon*; Taverne, 1978: fig. 46) or well developed (e.g. *Osteoglossum*; Taverne, 1977: fig. 59) lamella of bone extending dorsally from the main structural portion of the pelvic girdle. The condition in †*Singida* is similar to that of *Scleropages* and *Osteoglossum* (Greenwood & Patterson, 1967). In this analysis, this lamella is interpreted as support of Osteoglossinae. *Papycrocranus* is coded as unknown because it lacks a pelvic fin and girdle.

MEDIAN FINS

(64) *Posterior end of anal fin*: Separate from caudal fin [0]; Continuous with caudal fin [1]. LW96[34]. The continuity between the anal fin and the caudal fin was identified by Li & Wilson (1996a; also 1999: character 73) as a synapomorphy of the family Notopteridae, as it is in this analysis. The extreme elongation of the anal fin in notopterids was noted by Taverne (1979) and was again used in his 1998 analysis (character 107; p. 120) in support of notopterid monophyly ('allongement considérable de la nageoire anale qui s'étend sur toute la région abdominale et rejoint la nageoire caudale' [the great elongation of the anal fin, which extends from the entire abdominal region and joins the caudal fin]). This character is unknown in †*Palaeonotopterus*. The mormyroid *Gymnarchus* lacks an anal fin (e.g. Taverne, 1970, 1972; Benveniste, 1994). Mormyroidea therefore technically should have been coded as polymorphic, with one state being not applicable (i.e. '0/?'), which is an impossible entry in a cell in MacClade (see also the discussion of characters related to dorsal fin shape in Characters Not Used In Analysis for a similar problematic situation for coding non-monomorphic higher-level taxa).

CAUDAL FIN AND SKELETON

(65) *Number of principal branched caudal fin rays*: 17 or more [0]; 16 [1]; 15 or fewer [2]. LW96[7]. The presence of 18 principal rays in the caudal fin (equivalent to 16 branched rays + 2 unbranched principal rays) was identified as a synapomorphy of Osteoglossomorpha by Patterson & Rosen (1977), and was one of four synapomorphies that were both considered and retained from the literature by Li & Wilson (1996a; also 1999: character 74). Patterson & Rosen (1977: 113) wrote '[t]he number of principal caudal fin rays of [†]ichthyodectiforms is that characteristic of all plesiomorph groups of modern teleosts except osteoglossomorphs, that is, one simple and nine branched in the upper lobe and eight branched and one simple in the lower lobe.' This is the pattern observed in outgroups here (e.g. *Elops saurus*, UMA F10255; *Alosa sapidissima*, UMA F10359). Li & Wilson (1996a) recognized two states of reduction in the number of principal branched fin rays. A combination of the two (i.e. any number of principal branched caudal rays less than 17) was considered the synapomorphy of Osteoglossomorpha, even though on their tree (Li & Wilson, 1996a: fig. 2), 16 fin rays is actually the synapomorphy of the group as a whole. Fewer than 16 is best interpreted as a synapomorphy of the Osteoglossiformes (= Osteoglossidae + Notopteridae + Mormyroidea). In my analysis, however, this is a synapomorphy of Osteoglossidae + Notopteridae.

Sixteen branched fin rays are present in the caudal fin of †*Lycoptera*, *Hiodon* (Hilton, 2002: fig. 71), †*Eohiodon*, †*Ostariostoma* and the mormyrids examined here. All other taxa included in this analysis for which this character could be scored (all except †*Palaeonotopterus*) have fewer than 16 branched caudal fin rays. †*Ostariostoma* was coded as having 15 or fewer by Li & Wilson; I, however, agree with the count of Grande & Cavender (1991: Table 1), who recorded 16 for this taxon. *Gymnarchus* has no caudal fin rays (Taverne, 1972) and was one of the autapomorphies for the monotypic family Gymnarchidae identified by Taverne (1998: character 197). As for Character 64, the terminal taxon Mormyroidea (e.g. as in Li & Wilson's, 1999 analysis) technically should have been coded as polymorphic for all characters related to the caudal skeleton, with one state being coded not applicable, as the caudal skeleton of *Gymnarchus* is extremely reduced (Taverne, 1972: fig. 112), so that many of the elements present are impossible to homologize with other taxa (Benveniste, 1994). Li & Wilson (1999: fig. 2) coded †*Jiuquanichthys*, †*Tanolepis* (although see Jin, 1991: table 1) and †*Huashia* as polymorphic, although it is not clear which states were included in the polymorphism.

(66) *Uroneurals*: Three or more [0]; Two or one [1]; Absent [2]. Modified from LW96[50]. Li & Wilson (1996a) cited this character as derived (i.e. two or fewer, their 1996 character state 1) and indicative of the monophyly of Osteoglossiformes. Li & Wilson (1999: character 53) further divided the derived states they coded for, with different states for more than four uroneurals (found only in the outgroup †*Leptolepis*), three or four uroneurals (found in the elopomorphs and clupeoids considered and non-osteoglossiform osteoglossomorphs with an independent occurrence in †*Tanolepis* + †*Paralycoptera*), one or two uroneurals (in †*Singida*, †*Thaumaturus*, †*Ostariostoma*), and uroneurals absent (found in all other Osteoglossiformes).

This character is problematic in that there is an element in many Osteoglossiformes that may correspond to the uroneurals of other teleosts (e.g. Taverne, 1977, 1978). Nelson (1968) even went so far as to write '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 (fig. 17B, C; the 'epural' of Gosline, 1960; fig. 15) can be called anything but uroneurals (Taverne, 1967; figs. 2, 3; 1968[a], fig. 16; Monod, 1968; pp. 325–350, figs. 397–400, 430–438).' Schultze & Arratia (1988: 299) noted the dispute regarding the identification of this element, and suggested that 'it may represent the compound neural arch of ural centrum 3 + 4 + 5, a

possibility that can be checked when ontogenetic series are available.' This element develops as a paired structure that fuses dorsally in the midline relatively early in ontogeny (pers. observ. for *Arapaima* [Figs 35, 36], although this should be studied in more detail using sectioned specimens of a wider sample of taxa). These elements have no cartilaginous precursors (e.g. *Arapaima*, Fig. 35A, B; *Pantodon*, R. Britz, pers. comm., 2002). Patterson (1968) noted that uroneurals ossify as membrane bone or endochondral bone. Schultze & Arratia (1989: 210) however, suggested that 'the uroneurals are usually preformed in cartilage', citing ontogenetic evidence from their studies of certain osteoglossomorphs, elopomorphs, salmonids, ostariophysans and neoteleosts (e.g. Schultze & Arratia, 1988, 1989; Arratia & Schultze, 1992). However, because some teleosts possibly show development of uroneurals without cartilaginous precursors (e.g. *Megalops atlanticus*, Hollister, 1939; although these observations must be repeated with alcian stained or histological specimens), and epurals, to my knowledge, always preform in cartilage, I accept the identification of these elements in Osteoglossiformes as uroneurals that are secondarily fused in the mid line. In adult specimens of *Arapaima*, this element becomes completely fused with the dorsal-most hypural, and the line of fusion is almost completely obscured (Figs 35, 36).

†*Joffrichthys* and †*Phareodus* have an element that could be interpreted either as an epural (e.g. Li *et al.*, 1997a for †*Phareodus*) or an uroneural (e.g. Taverne, 1978 for †*Phareodus*) and the correspondence is not satisfactorily established; I therefore coded these taxa as unknown. †*Joffrichthys* was described as having a single epural and no uroneural by Li & Wilson (1996b), although this followed from their interpretation that a similarly placed bone in other osteoglossomorphs was an epural. All notopterids examined lack uroneurals (state 2; e.g. *Chitala*, Fig. 37D) and epurals (see Character 68).

Accepting the identification of this element as an uroneural, however, means that this character, as presented by Li & Wilson (1996a: 168), needs to be clarified. Although the coding of this character by these authors remains accurate, because they defined the derived state as 2 or fewer, their interpretation that 'all other osteoglossiformes [all except for †*Singida*, †*Thaumaturus*, †*Ostariostoma*] lack uroneurals' is incorrect.

(67) *Neural spine on ural centrum 1*: Absent or rudimentary [0]; One [1], Two [2]. LW96[14]. The presence of either one or two fully developed neural spines on the first ural centrum (u1) was considered by Li & Wilson (1996a) to be a synapomorphy of their Osteoglossoidei, and convergently derived in Notopteridae (all taxa with derived states were scored as having one

ural neural arch, i.e. state 1, except for the species of †*Phareodus*, which were scored as having two ural neural arches, i.e. state 2).

In general, I agree with their coding of this character. However, in a specimen of †*Lycoptera davidi* examined here, I discovered two full ural neural arches on u1 (Fig. 37B). In another specimen (UMA F10652), I could not find any trace of a neural spine on u1. Ma (1987: fig. 11) illustrated a specimen of †*L. davidi* with a single, very reduced neural arch on u1, whereas Jin *et al.* (1995: fig. 4) illustrated three ural neural arches on u1 in another specimen of †*L. davidi*, the first one full, and the second two reduced. Because all states defined here were either observed in my available specimens or have been reported in the literature, I have coded this character as unknown for †*Lycoptera* and suggest that further study of the morphology and variation in this genus is needed (the alternative, i.e. to code it as polymorphic with all possible states, would yield the same results).

In mormyroids (e.g. *Petrocephalus*, Fig. 37C), a well developed neural arch is present on u1, but this arch lacks a neural spine. The form of this arch is remarkably similar among the mormyrid taxa that I included in this study (see also caudal skeleton figures in Taverne, 1968a,b, 1969, 1971, 1972); all are therefore coded as rudimentary (state 0). Again, the caudal skeleton of *Gymnarchus* is extremely reduced and there is no element identifiable as a ural centrum, much less a ural neural arch (Taverne, 1972: fig. 112).

Other osteoglossomorphs have a more or less full neural arch on u1 (e.g. Fig. 38). In one specimen of *Chitala* that I examined (UMA F10342), there are two small neural spines on this centrum, although the 'typical' condition is to have a single full neural spine (e.g. Fig. 37D; Taverne, 1978: figs 87, 88). The caudal skeleton of *Xenomystus* is very reduced, but the neural arch and spine on u1 is as well developed as those of the more anterior vertebrae (Taverne, 1978: fig. 110), so I therefore have coded it as a single neural spine (with the caveat that it could well be considered rudimentary).

(68) *Epurals*: Two or three [0]; One [1]; Absent [2]. LW96[2]. The condition of having only a single epural or no epural altogether (either state 1 or 2) was considered to be a synapomorphy of Osteoglossomorpha by Li & Wilson (1996a; also 1999: character 55). Again, as was the case for Character 65 (number of principal branched fin rays), character state 1 (a single epural) was the synapomorphy for Osteoglossomorpha, whereas state 2 (no epural) defined more restrictive subgroups (independently arose three times in †*Tanolepis* + †*Paralycoptera*, †*Huashia* and Notopteridae). Li & Wilson (1996a, 1999) coded all other osteoglossomorphs for which the state was known as possessing a

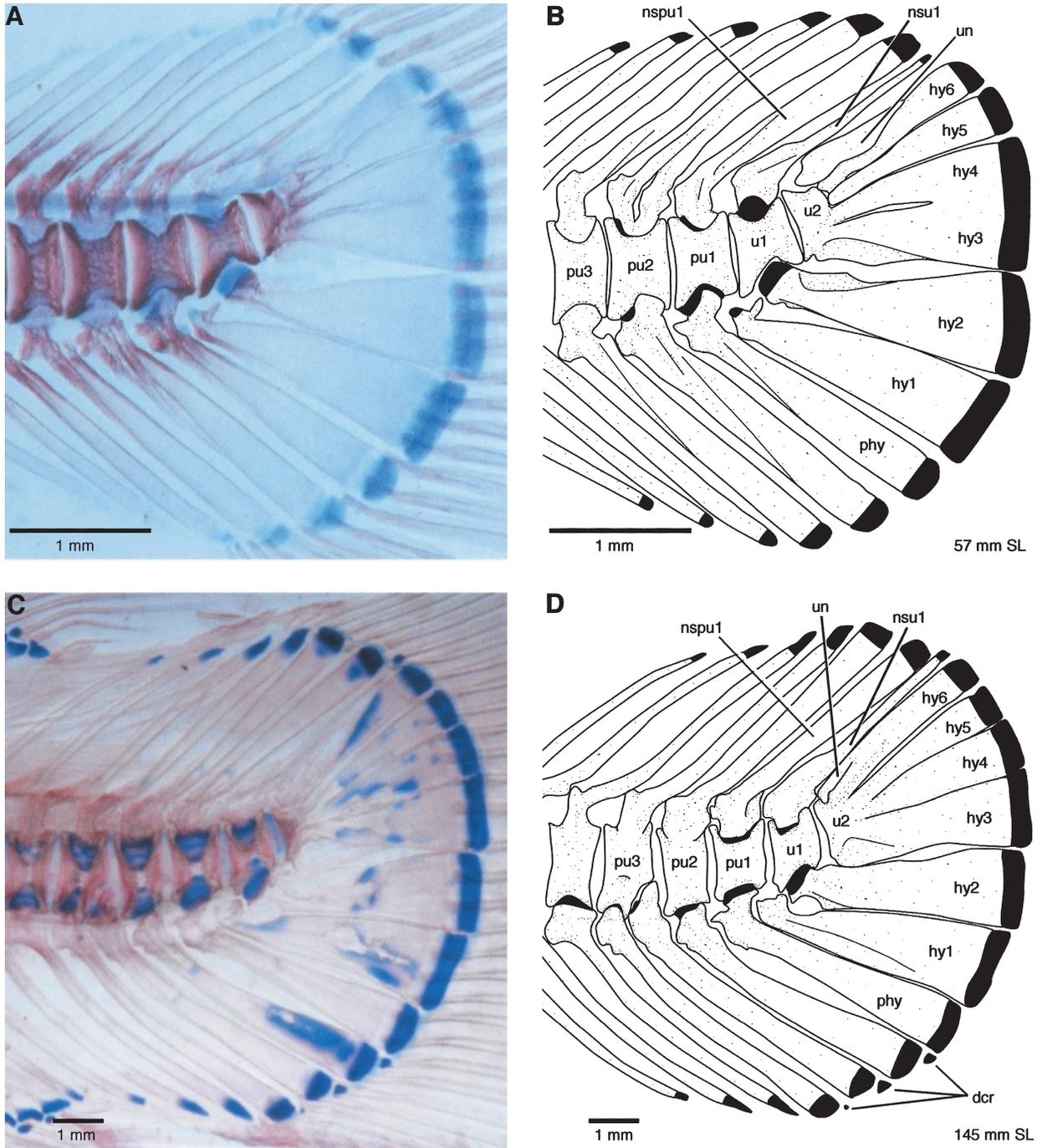


Figure 35. Caudal skeleton of two small juveniles of *Arapaima gigas*. A, photograph and B, line drawing of a 57-mm SL specimen (FMNH 97450a). C, photograph and D, line drawing of an 145 SL specimen (UMA F11261). Fin rays omitted from drawings. Note the two fused neural arches and spines on pu2 in FMNH 97450a (A & B). Note also the teratological nature of pu3 in UMA F11261 (C & D). In FMNH 97450a, the only elements of the caudal skeleton that have fused are hypurals 3 and 4, which have partially fused to each other as well as firmly fused to the second ural centrum (A & B). By 145 mm SL (UMA F11261; C & D), hypurals 3 through 6 have all fused to u2, and the uroneural is partially fused to hypural 6. Anterior facing left.

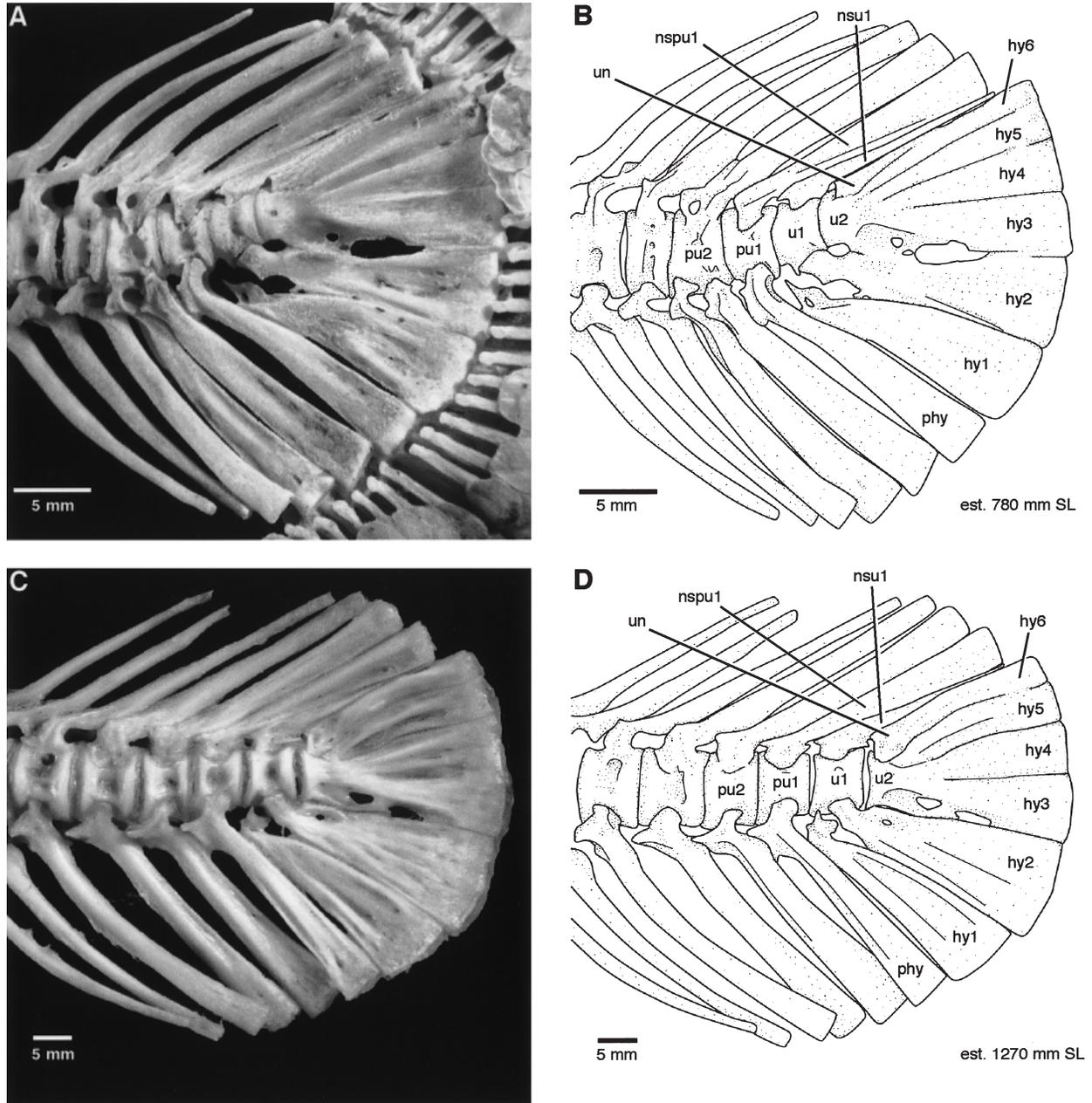


Figure 36. Caudal skeleton of a large juvenile and an adult *Arapaima gigas*. A, photograph and B, line drawing of an estimated 780 mm SL specimen (FMNH 85741). C, photograph and D, line drawing of an estimated 1270 mm SL specimen (UMA F11263). Fin rays dissected away in C & D; fin rays omitted from drawings. Note that in FMNH 85741 (A & B), the fusion of the uroneural to hypural 6 is very nearly complete; these elements are completely fused in UMA F11263 (C & D). Also note the double haemal arches and likely double (although fused) neural arches on pu2 in FMNH 85741 (A & B). Anterior facing left.

single epural. However, given the different interpretation of the elements of the caudal skeleton that I follow here, there are drastic differences in the coding of this character between my analysis and that presented by Li & Wilson.

Following my interpretation of the element referred to as an epural by Li & Wilson and others as an uroneural that has fused in the midline (see Character 66), the number of taxa coded as possessing a single epural has changed significantly between my analysis

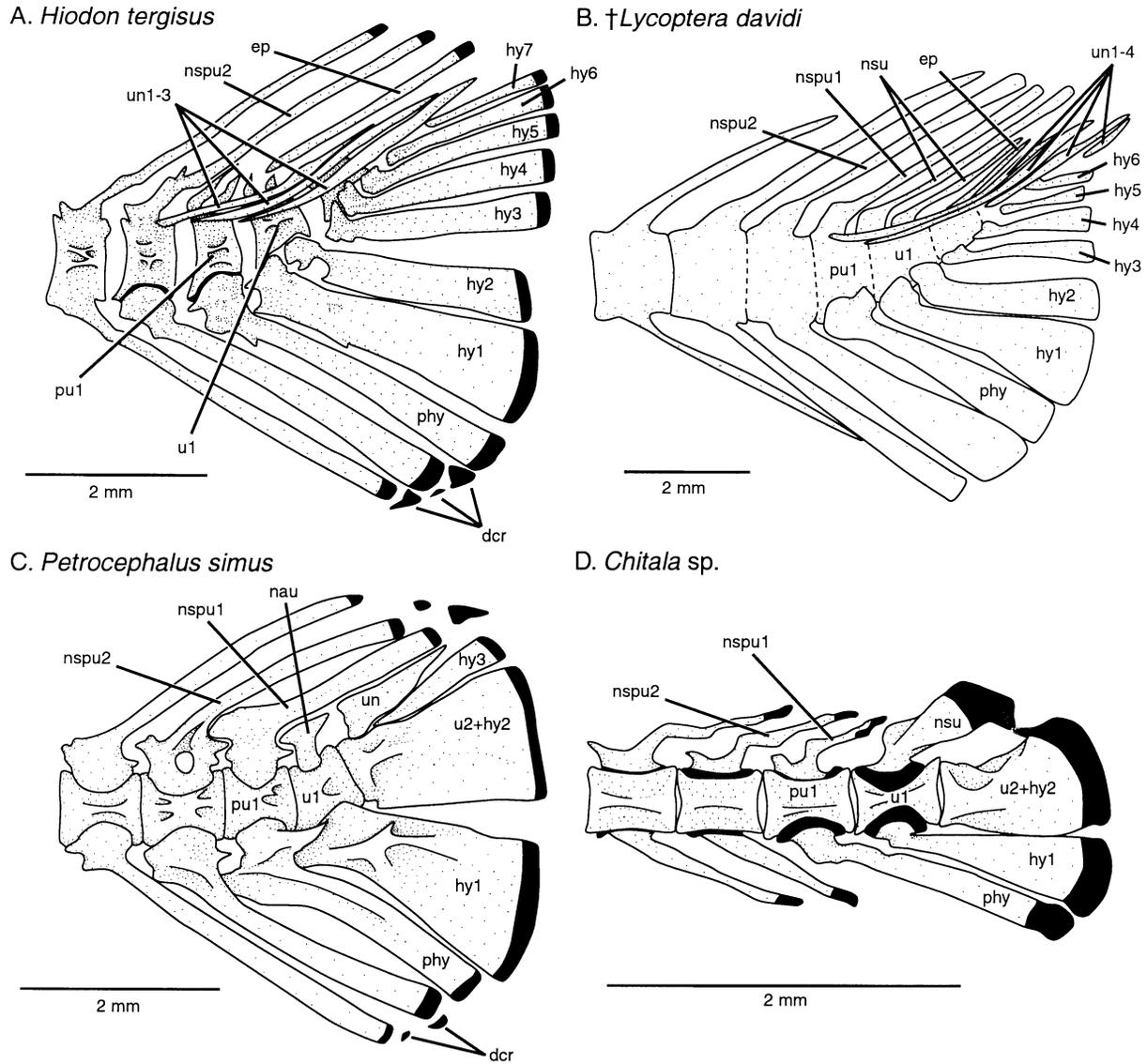


Figure 37. Caudal skeleton. A, *Hiodon tergisus* (TU 108166 A, 52 mm SL). B, †*Lycoptera davidi* (UMA F11260a, 75 mm SL). C, *Petrocephalus simus* (MCZ 50113, 55 mm SL). D, *Chitala* sp. (UMA F10341, 75 mm SL). Anterior facing left. Illustration of *Hiodon* modified from Hilton (2002: fig. 74D). Illustration of †*Lycoptera* is of right side and image reversed so anterior facing left.

and those of Li & Wilson. Within my sample of taxa, *Hiodon*, †*Eohiodon*, †*Lycoptera*, and †*Ostariostoma* have a single epural (state 1), although all other osteoglossomorphs for which this character can be coded have no element that can be unambiguously identified as an epural (state 2; see Figs 37, 38). The element that I identify as the dorsal most hypural in *Pantodon* (Fig. 38C; hypural 6 of Greenwood, 1967: figs 7, 8) may also be interpreted as an epural because it develops well after the other hypurals during ontogeny (R. Britz, pers. comm., 2002). However, I have

coded *Pantodon* as lacking an epural following my interpretation of this element as an uroneural. Because the homology of the element that could be interpreted as either an epural (e.g. Li *et al.*, 1997a) or an uroneural (e.g. Taverne, 1978) in †*Phareodus* is not satisfactorily established, I coded this taxon as unknown. †*Joffrichthys* also is coded as unknown for similar reasons. The state in †*Singida* is unclear (coded as unknown), although Greenwood & Patterson (1967: 219 & fig. 3) reported ‘indistinct traces’ of an epural.

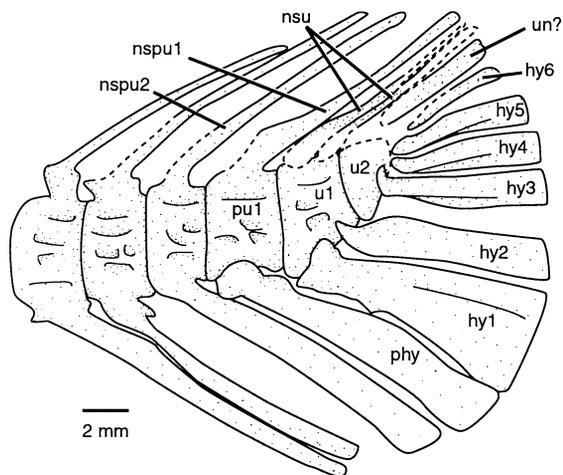
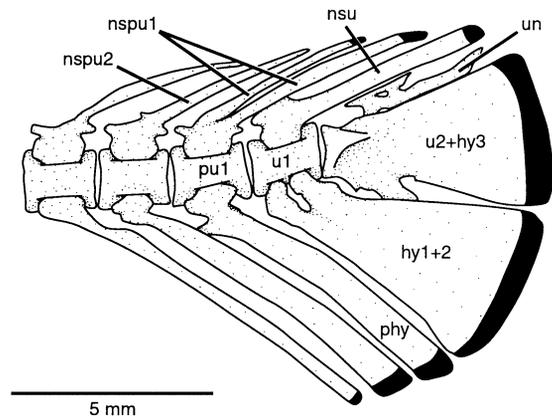
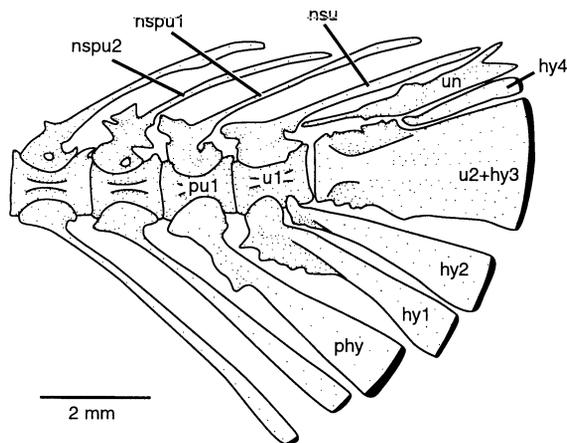
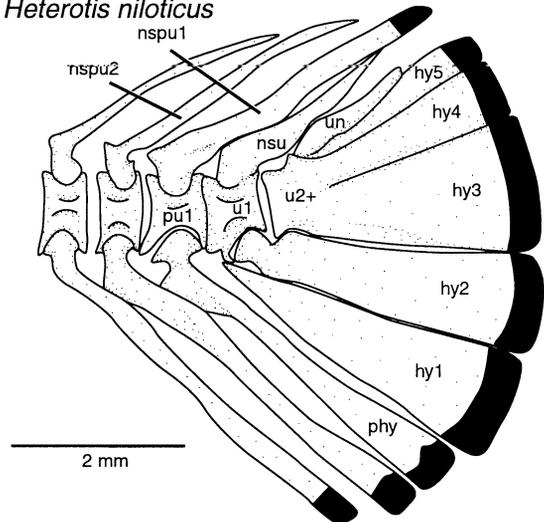
A. †*Phareodus testis*B. *Osteoglossum bicirrhosum*C. *Pantodon buchholzi*D. *Heterotis niloticus*

Figure 38. Caudal skeleton. A, †*Phareodus testis* (UMA F11332, 260 mm SL). B, *Osteoglossum bicirrhosum* (FMNH 109232a, 270 mm SL). C, *Pantodon buchholzi* (FMNH 63752, 62 mm SL). D, *Heterotis niloticus* (UMA F10653, 75 mm SL). Anterior facing left.

(69) *Neural spine on the first preural centrum*: Complete [0]; Rudimentary [1]; Absent [2]. Modified from LW96[39]. Patterson & Rosen (1977) considered a full neural spine on the first preural centrum (pu1) to be a synapomorphy of Osteoglossomorpha. Schultze & Arratia (1988) however, only found this condition in 6% of the specimens of *Hiodon* that they studied (see also Hilton, 2002), and argued that this therefore could not be a synapomorphy of Osteoglossomorpha as a whole, but rather of some more exclusive group. Most basal groups of teleosts (i.e. †ichthyodectiforms, †leptolepids, etc.) have a reduced neural spine on pu1, if it is developed at all (e.g. see figures of such taxa in Patterson & Rosen, 1977; Arratia, 1991). Arratia (1991: 288) wrote:

'[t]he length of the neural spine ([her] Character 20) and presence or absence of the neural arch ([her] Character 21) in preural vertebrae 1 seem to be significant features of the evolution of some clades. A short rudimentary neural spine on preural 1 (e.g. in †pholidophorids ([her] Figs 15a and 17), †*Leptolepis talbragarensis*, †*Tharsis* ([her] figs. 13 and 14), †*Daitingichthys* ([her] Fig. 22)) is the condition commonly found within Jurassic teleosts. A fully developed neural spine on preural centrum 1 is present in the fossil osteoglossomorph †*Lycoptera* but the length of the spine is intraspecifically variable in other lycopterids (Chang & Chou, 1977; fig. 24) and in the extant osteoglossomorph *Hiodon* (Schultze & Arratia, 1988).'

Li & Wilson (1996a, 1999: character 59) used this character in their analysis, and interpreted a rudimentary or absent first preural neural spine as a synapomorphy of the genus *Hiodon*. Most outgroups included in their analyses were coded as having a full neural spine on pu1 (e.g. †*Leptolepis*, †*Anaethalion*, Elopoidei, Clupeoidea, *Chanos*), as were all non-*Hiodon* osteoglossomorphs. However, at least some of these taxa possess a rudimentary neural arch on pu1. For example, the elopomorphs *Elops saurus* (e.g. UMA F10359) and *Albula vulpes* (e.g. AMNH 88678SD) have small neural spines on pu1 (in comparison with other preural neural spines) and *Megalops atlanticus* (pers. observ.; e.g. UMA F10251) has little or no spine associated with the neural arch of pu1. The basal teleost †*Tharsis dubia* (MCZ 7084) was also observed to have a reduced neural spine on pu1 (see also Patterson & Rosen, 1977: fig. 35). This is therefore considered the plesiomorphic condition.

As mentioned above, the presence of a reduced neural spine on pu1 in *Hiodon* is variable, although it is the typical condition (see discussion in Hilton, 2002: figs 75, 76). The presence of a full neural spine is found in less than 10% of specimens of *Hiodon*; this genus is however, coded as polymorphic. In a new study of †*Eohiodon* (Hilton & Grande, unpublished data), specimens have been discovered that also bear a reduced neural spine on this centrum, although the frequency of this condition is very low (i.e. the typical condition, found in nearly all specimens, is to have a full neural spine on pu1). †*Eohiodon* therefore is coded as polymorphic as well. In †*Lycoptera*, I observed a full neural spine on pu1 (Fig. 37B; also see Ma, 1987: fig. 11; Jin *et al.*, 1995: figs 4, 8). The 'lycopterid' referred to by Arratia (1991; quoted above) that was illustrated by Chang & Chou (1977: fig. 24) is †*Chetungichthys*, a Lower Cretaceous taxon from China which is of uncertain affinities (possibly close to hiodontiform fishes; Chang & Chou, 1977; Taverne, 1979; Bonde, 1996).

The condition in the one known specimen of †*Ostarionostoma* is ambiguous (coded here as unknown). Grande & Cavender (1991: fig. 3) interpreted this taxon as having a rudimentary neural spine on pu1, as in *Hiodon* and †*Eohiodon*, whereas Li & Wilson (1996a: 169) considered that 'the epural (epu) designated by Grande and Cavender may be the distal part of the broken neural spine of the first preural' and that 'the bone labelled as "?" in their [Grande & Cavender's] paper is here thought to be the epural.' After study of this specimen, I cannot decide if the neural spine on pu1 is complete, as suggested by Grande & Cavender (1991), or if it has been broken, as argued by Li & Wilson (1996a), and this must await the discovery of new specimens.

All other osteoglossomorphs for which this character could be scored were coded as possessing a full neu-

ral spine on pu1 (state 0). A full neural spine on pu1 is here considered a synapomorphy of Osteoglossomorpha, with a reversal in some specimens of *Hiodon*, †*Eohiodon* and possibly †*Lycoptera*.

(70) *Number of neural spines on the second preural centrum*: One [0]; Two [1]. Modified from LW99[60]. Li & Wilson (1994: character 21) regarded the presence of two neural spines on the second preural centrum (pu2) as a synapomorphy of the genus *Hiodon*. Although they recognized the variation of this character within this genus (they illustrated specimens with both one and two neural spines on this centrum; Li & Wilson, 1994: figs 3, 4), they did not code this character as polymorphic in their data matrix. The second preural with two neural spines has been figured in several other illustrations of the caudal skeletons of *Hiodon* (e.g. Monod, 1968: fig. 108 *bis*; Schultze & Arratia, 1988: fig. 11). I did not find this double neural spine in my specimens of *Hiodon* (Hilton, 2002); the frequency of this variation is still unclear. The definition of this character state changed in later analysis (e.g. Li *et al.*, 1997b; Li & Wilson, 1999), perhaps to account for this variation, as the derived state was changed to two neural spines, at least 'potentially', on pu2. However, the definition and scoring of any character state based on *potential* presence of the state in a taxon is highly suspect and I consider it to be poor systematic practice. It is both technically and philosophically more rigorous to code such characters as polymorphic, which is the strategy employed here for *Hiodon*.

Li & Wilson (1999) also coded †*Joffrichthys* and †*Phareodus testis* as having two neural spines on pu2. In †*J. symmetropterus*, Li & Wilson (1996b: 203) describe a pu2 that 'bears double, fully developed neural spines that are slightly weaker than those on other preurals', yet in their illustration (their fig. 5) they show the second neural spine as only about half the length of the other neural spines. In examining the specimen upon which the drawing was based, I agree with their illustration regarding the presence, position and form of this second neural spine, and I coded †*Joffrichthys* as possessing two neural spines. I note, however, that this is the only specimen that shows an interpretable caudal skeleton, although Newbrey & Bozek (2000: fig. 5) described a similar condition for †*J. triangulpterus*, except the second neural spine is indeed fully developed.

The condition for †*Phareodus* is more problematic. Li *et al.* (1997a: 497) noted that one difference between †*P. testis* and †*P. encaustus* was that the 'neural spines on pu1 and pu2 may be double in †*P. testis*, rather than single as in †*P. encaustus*.' No reference to a museum number was provided for a specimen of †*P. testis* that possesses two neural spines on pu2, and the specimen they illustrated (their fig. 5B) has two

neural spines on pu1, but only a single spine on pu2. Taverne (1978: fig. 13), however, earlier illustrated a specimen of †*P. testis* with two fully developed neural spines on pu2. Of this, Taverne (1978: 22–23) remarked, ‘Chez plusieurs exemplaires, on remarque un doublement de l’arc neural et de la neurépine, au niveau de cette vertèbre. L’hémépine de la vertèbre préurale II est déjà quelque peu élargie par rapport aux hémépines précédentes’ [On some specimens, one notices a double neural arch and spine on pu2. The haemal spine of the second preural centrum is also somewhat widened compared with the preceding haemal spines]. Some specimens of †*P. testis* that I examined possessed a single neural spine on pu1 (e.g. Fig. 38A; also see Cavender, 1966: fig. 5A), so I therefore regard this condition as polymorphic for this genus (and in particular for †*P. testis*). I further suggest that the condition in †*P. encaustus* should be investigated to examine the possibility of individual variation in this species as well.

I also found two neural spines on a specimen of the notopterid *Papyrocranus* (MCZ 54925), although Taverne (1978: fig. 130) illustrated a specimen with a single neural spine. Although it is possibly a teratological variation, I coded this taxon as polymorphic. The other notopterids and mormyrids examined here had a single neural spine on pu2 (e.g. Fig. 37C, D).

I suspect that given sufficiently large sample sizes the condition of having two neural spines on pu2 (or perhaps any particular centrum) would be discovered for most osteoglossomorph taxa, although the frequency of specimens showing this condition will undoubtedly be different in different taxa (i.e. it will be an anomaly in some but not others). Specimens of several taxa examined during this study support this hypothesis. For instance, in the specimen of *Petrocephalus* illustrated in Figure 37C, the neural arch of pu2 bears a large foramen in its most proximal portion and a deep groove dorsally from this foramen. This suggests that this single neural spine is the product of fusion between two independent spines. Similar observations were made for specimens of *Arapaima* (e.g. Figs 35A, B, 36A, B).

(71) *Number of hypurals*: Seven [0]; Six or fewer [1]. Modified from LW99[54]. Seven hypurals was considered by Li & Wilson (1999) to be a synapomorphy of all taxa in their analysis except for †*Leptolepis* (i.e. all extant groups of teleosts); six was considered a synapomorphy of clupeomorphs plus euteleosts (not considered in the present analysis). The condition of five or fewer was considered to be a synapomorphy of †*Ostariostoma* + (Mormyroidea + Notopteroidea).

As with other elements of the caudal skeleton of osteoglossomorph fishes, the identification of the elements of the hypural series is debatable, and different

morphological interpretations will lead to different coding of this character. Because of this uncertainty, I combined Li & Wilson’s character states 2 and 3 (six and five or fewer hypurals, respectively) into a single state (here state 2: six hypurals or fewer). There is significant ontogenetic fusion among elements of the caudal skeleton of osteoglossomorph fishes (e.g. see the growth series of *Arapaima* illustrated in Figs 35 and 36), although direct study of the ontogeny of the caudal skeleton has rarely been done. However, there never appears to be more than six hypurals incorporated into the hypural ‘fan’ of osteoglossomorph fishes that display this high degree of fusion. I am not convinced that this coding accurately captures topographic correspondence between taxa (i.e. several morphological conditions are similarly coded as state 2; cf. *Chitala*, Fig. 37D and *Heterotis*, Fig. 38D). This character should be studied further using ontogenetic evidence of fusion patterns as they become available.

Elops, the outgroup, has seven hypurals; no taxon in my sample has more than seven. Of the osteoglossomorphs, I found seven in †*Lycoptera* (although see below), *Hiodon* (Fig. 37A) and †*Eohiodon*. Schultze & Arratia (1988) described eight in small specimens of *Hiodon*, with the eighth, which is entirely cartilaginous, being resorbed during ontogeny. Gosline (1960: fig. 4) illustrated a specimen of *H. alosoides* with eight as well; I never found an eighth in my specimens of *Hiodon* (Hilton, 2002). I found only six in the specimen of †*Lycoptera* illustrated in Figure 37B, although this may be due to lack of preservation. Other specimens that I examined, as well as all other accounts (e.g. Gaudant, 1968; Greenwood, 1970; Ma, 1987; Jin *et al.*, 1995), show that †*Lycoptera* has seven.

All non-hiodontiform osteoglossomorphs have six or fewer hypurals (state 1), although one specimen of *Scleropages* (UMA F11325, *S. jardini*; 152 mm SL) has seven in various states of fusion. In this specimen, the element that corresponds to hypural 1 illustrated by Greenwood (1967: figs 1, 2) for *S. formosus* is almost completely divided, and is interpreted here as two independent hypurals that are fused proximally (i.e. there are three hypurals supported by ural centrum 1); study of more specimens is needed to confirm if this is due to ontogeny (i.e. if hypural 1 typically is composed of two elements) or is an individual variation (no adult specimens of *S. jardini* were available for study). My small specimen of *Heterotis* appears to have only five hypurals, the last three of which are fused to u1 (Fig. 38D), whereas that illustrated by Taverne (1977: fig. 120) has six. The caudal skeleton of *Arapaima* clearly has six ontogenetically fused into the hypural fan (Figs 35, 36). More extreme reduction is found in *Pantodon* (Fig. 38C), which has only four (as interpreted here). The third hypural is fused with u2 and is the largest of the series. This element was

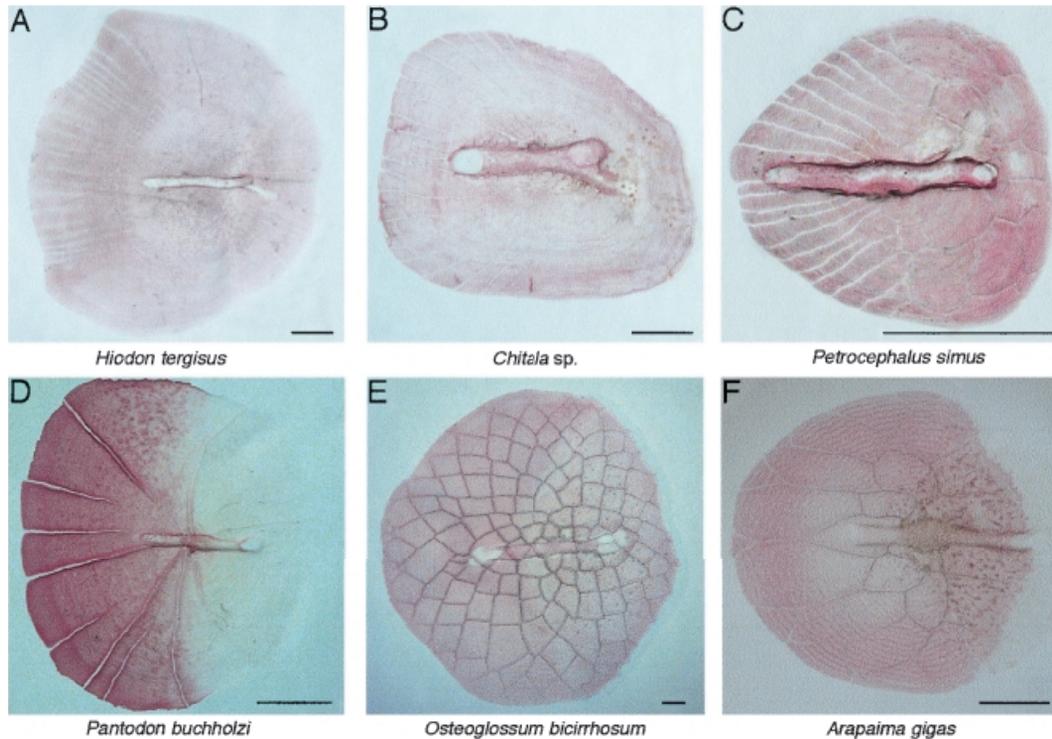


Figure 39. Lateral line scales of osteoglossomorph fishes, taken from mid-body. A, *Hiodon tergisus* (UMA F10610, 100 mm SL). B, *Chitala* sp. (MCZ 156815, 420 mm SL). C, *Petrocephalus simus* (MCZ 50113, 70 mm SL). D, *Pantodon buchholzi* (MCZ 156814, 60 mm SL). E, *Osteoglossum bicirrhosum* (FMNH 109232a, 270 mm SL). F, *Arapaima gigas* (MCZ 156812, 160 mm SL). Anterior facing left. Scale bars = 1 mm.

suggested by Greenwood (1967) to be homologous with hypurals 3, 4 and 5 of other osteoglossomorphs (also Taverne, 1978). However, it develops as a single cartilage (R. Britz, pers. comm., 2002), so there is no direct ontogenetic evidence to suggest that more than a single, albeit expanded, hypural forms this 'hypural plate' (Greenwood, 1967).

The most extreme reduction of the caudal skeleton (in terms of discrete numbers of elements in the hypural series) is found in notopterids and mormyrids (Fig. 37C, D, respectively), in which there are only two (notopterids) or three (mormyrids) separate hypural elements. The first hypural in these taxa is associated with the first ural centrum (considered by other authors to be hypural 1 and 2 fused together), and is enlarged in mormyrids in comparison to that of notopterids. There is no sign of ontogenetic fusion in a series of three specimens of *Notopterus notopterus* (MCZ 52370; 28, 35 & 56 mm SL), although this should be confirmed with still smaller specimens. The two hypurals are present in the 28 mm SL specimen as largely cartilaginous blocks with a shape similar to that of larger specimens (e.g. Taverne, 1978: fig. 81; 165 mm SL), suggesting direct development (i.e. no ontogenetic fusion of elements).

SCALES

(72) *Scales*: No reticulate furrows [0]; Both radial and reticulate furrows present [1]; Reticulate furrows only present over entire scale [2]. Modified from LW99[76]. Li & Wilson (1999) considered the distribution of two derived states describing the reticulation patterns present in some osteoglossomorph fishes. That some osteoglossomorphs (e.g. *Osteoglossum* and *Arapaima*, Fig. 39E & F, respectively; †*Phareodus* Grande, 1984: fig. II.32b) bear reticulate furrows over their entire surface has long been known (e.g. *Heterotis*, Cuvier & Valenciennes, 1846: plate 583, fig. 1). The plesiomorphic condition (state 0), found in taxa such as *Hiodon* (Fig. 39A) and notopterids (e.g. *Chitala*; Fig. 39B) among osteoglossomorphs, is to have fine circuli and radial furrows (Arratia, 1997). †*Joffrichthys* has no reticulate furrows on its scales, and possesses a series of radial furrows on the posterior field of its scales. I scored †*Singida* as unknown due to preservation, although Greenwood & Patterson (1967) suggested that there were no reticulate furrows.

Li & Wilson (1999) defined a second derived state of only having reticulate furrows over the basal part of the scale, and used this as a character separating

†*Tanolepis* (the only taxon to be coded for this state) from †*Paralycoptera*. This coding followed from Jin *et al.*'s (1995: 192) observation that the scales of †*Tanolepis* were 'slightly reticulated and sparsely granulated on the apical region' and their own observations of †*Paralycoptera*. Because specimens of these taxa were not available to me for study, and the published photographs are not very convincing (e.g. Jin *et al.*, 1995: plate 3: fig. 4), I will not comment on them.

There is additional variation in the form of the scales that was not described by Li & Wilson (1999). For instance, the scales of mormyrids (e.g. *Petrocephalus*; Fig. 39C) and *Pantodon* (Fig. 39D) have radial furrows present on their anterior field, whereas the furrows form a reticulating network in their posterior field (state 2). Cockerell (1910: 1) said of the scales of five genera of mormyrids and *Gymnarchus*: 'These fishes all have scales of the same general type; cycloid with well-developed circuli and with strong basal [anterior] radii. The truly remarkable feature is found in the apical [posterior] radii, which are greatly modified and join irregularly, forming a network . . .' (see also his figs 1 and 2). These two instances of this condition (state 1), *Pantodon* and mormyrids, is interpreted as homoplastic (see Character Optimization and Node Support).

DISCUSSION

In this section I discuss additional characters that have been used in recent analyses of osteoglossomorph fishes that were not included in my analysis. I will provide justification for their exclusion as well as comment on more general problems of character definition and coding. This section is by no means an exhaustive review of characters that have been considered for osteoglossomorphs (e.g. many more have been used by Taverne, 1998; these will be considered in future work), but rather is meant to serve as a starting point for discussion of problems of specific character definitions.

Some, but not all, soft tissue characters available in the literature are considered in this section (e.g. I do not discuss Li & Wilson's, 1996a character citing the presence of mandibular barbels as a synapomorphy of *Scleropages* + *Osteoglossum*, a character that is highly unlikely to be scorable for fossils – although it is curious that all taxa, living and fossil, were coded for this character by Li & Wilson). Some characters used by Li & Wilson (1996a, 1999) and not included in my analysis showed no variation within Osteoglossomorpha because they only are derived in outgroups that were not coded here (e.g. the presence of the pleurostyle as a synapomorphy of clupeomorphs + euteleosts); such characters will not be discussed below.

CHARACTERS NOT USED IN ANALYSIS

Primary bite between parasphenoid and tongue: Absent [0]; Present [1]. LW96[6]. This 'character' was one of the two described by Greenwood *et al.* (1966) when they first defined the group Osteoglossomorpha, and has since been cited by most authors as indicative of its monophyly. However, as I have pointed out elsewhere (Hilton, 2001), this character complex is a mixture of plesiomorphic and apomorphic character states of several different characters that belong at different levels of generality or nodes on the cladogram. I therefore did not use this character in the present analysis, but rather used some of its individual component characters (e.g. Characters 8 & 45). For descriptions of the functional aspect of this character complex (the so-called 'tongue bite apparatus') in some osteoglossomorphs, see Sanford & Lauder (1989, 1990), Frost & Sanford (1999) and Sanford (2001).

Tendonous connection of the sternohyoideus to the ventral gill arch skeleton: Absent [0]; Present [1]. I identified this character (Hilton, 2001) as a potential component of the so-called parasphenoid tongue bite apparatus. Because it is a soft tissue character, it is impossible to score for any fossil taxa. The only taxa known to have a tendon arising from the sternohyoideus and inserting on the ventral gill arch skeleton are the two living species of *Hiodon*. Greenwood (1970) suggested that these tendons were homologous to the 'tendon bones' of other osteoglossomorphs; there is no morphological evidence for this statement of homology (see discussion of Character 45).

Intestine: Coils to the right of the stomach [0]; Coils to the left of the stomach [1]. LW96[9]. Nelson (1972) identified the condition of having the intestine pass to the left of the stomach as a synapomorphy of Osteoglossomorpha, although the condition is, of course, unknown in fossil taxa. Li & Wilson (1996a) supported this as a character defining Osteoglossomorpha. I have no reason to suspect otherwise, although I have not confirmed the state in many of the taxa included in my analysis.

Ethmoid commissure passing through a bone: Present [0]; Absent [1]. LW99[1]. The ethmoid commissure is defined as the portion of the rostral sensory canal that crosses the midline of the snout (see Grande & Bemis, 1998: fig. 20). Among taxa surveyed here, an ethmoid commissure is only found in *Elops*. In *Elops*, the commissure is located in the dermethmoid (Forey, 1973b: fig. 1), whereas in non-teleostean fishes, the commissure is found in the rostral bone; whether this is merely a semantic disparity remains unclear. Li & Wilson (1999) reported an ethmoid commissure in †*Tongxinichthys*, but did not say in which bone the commissure is located. This observation may be based

on that of Ma (1980), who described a rostral bone anterior to the nasals in this taxon; Zhang & Jin (1999), however, were unable to find a rostral in any of their specimens.

Supraorbital branch of the otic sensory canal: Absent [0]; Present [1]. This character was defined by Cavin & Forey (2001: 40) as a synapomorphy of notopterids and the mormyrid *Petrocephalus* (i.e. of notopterids + mormyrids, with a loss in Mormyridae). It is not included in this analysis because appropriate material (alcohol preserved specimens) were not available for all taxa scored and because the proper study for this character (e.g. ink injection of the cephalic sensory canal system, *sensu* Cavin & Forey, 2001) was not carried out in taxa for which material was available. Future study should expand the taxon sampling for this character, including additional mormyroids.

Supraorbital and otic sensory canals: Separate [0]; Continuous [1]. Taverne (1998: character 57) used this character to support the group Osteoglossiformes + Mormyridae (Taverne's Mormyridae includes the families Notopteridae, Gymnarchidae and Mormyridae). Cavin & Forey (2001) however, found no connection of the lumen of the two sensory canals in two species of *Mormyrops* through injection of the sensory canal system with methylene blue. As for the character of the supraorbital branch of the otic canal discussed above, this character is not included in this analysis because appropriate material was not available for all taxa scored and because the proper study for this character (e.g. ink injection of the cephalic sensory canal system, *sensu* Cavin & Forey, 2001) was not carried out in taxa for which material was available. Future study should expand the taxon sampling for this character, including additional mormyroids.

Utriculus: Continuous with sacculus and lagena [0]; Completely separate from the sacculus [1]. LW96[33]. The separation of the utriculus from the sacculus and lagaena was originally cited by Greenwood (1973) as a character supporting the hypothesis that Notopteridae and Mormyroidae formed a monophyletic group (also Li & Wilson, 1999: character 78). Greenwood (1973: 310) wrote:

'Orts (1967), through a series of extremely elegant dissections on eight mormyrid species (and *Gymnarchus*) was able to confirm an earlier and generally neglected discovery of Stipetic (1939). That is, in the Mormyridae the sacculus and lagena are completely independent of the labyrinthic portion of the ear. There is no connection whatsoever between the utriculus and sacculus . . . To my knowledge such a complete physical separation of labyrinthic and vesicular portions of the ear is otherwise found only in the Notopteridae. Dissections of the inner ear in *Xenom-*

ystus, *Notopterus* and *Papyrocranus* all show a condition like that in the mormyrids.'

I was unable to confirm these observations in my specimens of notopterids and mormyrids (although specimens currently being prepared for histological sectioning may be informative). Also, I was not able to score the plesiomorphic (i.e. continuity between the labyrinthic and vesicular portions of the ear) for most other taxa in my matrix through first hand observation. Therefore, I did not include this character in my analysis, but will note that this character may support the group Notopteridae + Mormyroidae (not recovered in my analysis).

Size and shape of infraorbital 2: Slender and small [0]; Rectangular and moderate [1]; Trapezoidal and large [2]; LW96[15]. *Shape of infraorbital 3:* Short, posteriorly deep and fan-like [0]; Subrectangular [1]; Long, posteriorly shallow and fan-like [2]; LW96[30]. *Infraorbital ledge formed by lateral extension of infraorbitals 1 and 2:* Absent [0]; Present [1]; LW96[31]. Li & Wilson (1996a) described two characters associated with the shape of the infraorbital bones, with derived conditions defining their Notopteroidei (= †*Ostariostoma*, Notopteridae, and Mormyroidae). The first of these concerned the shape of io2, which was described as being slender and small, rectangular and moderate, or trapezoidal and large. The plesiomorphic condition (slender and small) was considered present in most osteoglossomorphs (e.g. *Hiodon*, *Scleropages* and *Pantodon*; see Fig. 20). Even within taxa coded with this state by Li & Wilson, there are significant differences in shape (cf. *Hiodon* & *Scleropages*; Fig. 20). Heterotines (i.e. *Arapaima*, *Heterotis*, †*Joffrichthys* & †*Sinoglossus*) were all coded as having a large trapezoidal io2. *Heterotis* and *Arapaima* (Fig. 20F) do indeed have a similar shaped io2 (see Fig. 21; pers. observ.), but I cannot comment on the shape of this element in †*Sinoglossus*, and the details of the infraorbital bones of †*Joffrichthys* are difficult to interpret (Li & Wilson, 1996b).

Further difficulty comes in Li & Wilson's (1996a: 168) coding of this character for their notopteroid taxa, all of which were said to have a 'subrectangular and medium-sized io2.' I find this description hard to interpret for those 'notopteroids' examined here (compare, for instance, io2 of *Chitala*, *Petrocephalus* and *Campylomormyrus* illustrated in Fig. 20C, D & E, respectively), for which I see little similarity in their overall shape. For this reason, I have not included this character in my analysis.

I have found similar difficulties in interpreting Li & Wilson's (1996a: 168) character describing the shape of io3, of which they said is 'subrectangular . . . in all notopteroids except *Notopterus*' (although *Notopterus* was coded the same as all other members of their

Notopteroidei). All osteoglossomorphs (and outgroups) were coded as having io3 short, posteriorly deep and fan-like, except for †*Phareodus encaustus* and †*P. queenslandicus* (coded as subrectangular) and †*Ostariostoma*, notoapterids and Mormyroidea (coded as long, posteriorly shallow and fan-like). I have difficulty interpreting io3 in †*P. encaustus* as significantly different in shape from that found in †*P. testis* (although that of †*P. testis* might be slightly broader anteriorly than that of †*P. encaustus*; pers. observ.). Again, the main problem with this character comes in their coding of the notoapterids, and in particular, referring to the shape of io3 in mormyrids, which is a tubular element (Fig. 20D, E; Taverne, 1998: character 152), as the same shape as that of notoapterids (e.g. *Chitala*, Fig. 20C) or †*Ostariostoma* (Li & Wilson, 1996a: fig. 3A).

The third of Li & Wilson's (1996a: 168) infraorbital bone characters that was not included in this analysis also was defined in support of their 'notoapteroid' clade, and concerned the presence of a 'prominent lateral extension of the orbital margin of io1 and io2 (e.g. †*Ostariostoma* and *Notopterus*). This structure, which differs from the 'subocular shelf' traditionally used to define the inwards extension of the bony lamina from infraorbitals (see Rojo, 1991), is absent in all the out group taxa.' In available specimens of notoapterids, mormyrids and †*Ostariostoma*, I have failed to find any 'prominent lateral extension' from the anterior-most infraorbitals (e.g. Fig. 20). Because these taxa have a ventrally open sensory canal, the bone that wraps around the dorsal portion of the sensory canal is broad relative to other taxa (e.g. *Osteoglossum*), but it is not a discrete lamina of bone, as implied by Li & Wilson's (1996a) discussion of this character. This broad dorsal portion is possibly what was being described as a 'ledge' by Li & Wilson (1996a), but is considered here to be related to the condition of the sensory canal (Character 24) rather than the presence of some distinct structure. This character was never illustrated by the authors, so it is unclear what it was intended to describe; I have therefore chosen to exclude it from my analysis.

Two additional characters of the infraorbital bones were cited by Taverne (1998) as synapomorphies of the family Notopteridae. In these fishes, there is a medial subocular shelf formed by io2 and io3 (pers. observ.; Taverne, 1998: character 96). Taverne (1998: character 95) also described the development of a process extending medially from the very anterior-most portion of the first infraorbital that rests against the lateral ethmoid or antorbital. I checked both of these characters against available specimens and found that they appear to further support the monophyly of Notopteridae, as they are were found to be well developed in *Chitala*, *Papyrocranus*, and *Xenomystus*, and

absent in mormyrids and all other osteoglossomorphs. The infraorbitals of †*Palaeonotopterus* are completely unknown, and the state for these characters in †*Ostariostoma* is unknown, because they relate to medial structures, and the infraorbitals of this taxon are preserved in lateral view only.

Mid-dorsal concavity of the premaxilla: Absent [0]; Present [1]. LW96[37]. This character was first described by Li & Wilson (1994: character 18), who used the presence of the mid-dorsal concavity on the premaxilla as a synapomorphy of the genus *Hiodon*. It is agreed that there is significant variation between the shape of the premaxillae of *Hiodon* (and †*Eohiodon*; see Character 37) and other osteoglossomorphs. However, I have had difficulty in identifying what, in particular, is meant by the 'mid-dorsal concavity' of Li & Wilson. For instance, I agree that in the two extant species of *Hiodon* (Fig. 40E, F), there is a very shallow depression on the dorsal surface of the premaxilla (also †*E. falcatus*, Fig. 40C). However, there is drastic variation between the two known specimens of †*H. consteniorum* (cf. the premaxilla illustrated in Fig. 40D with that of the holotype illustrated by Li & Wilson, 1994: fig. 2). In the holotype, the premaxilla bears a well defined dorsal notch, similar (although deeper) to the condition I observed on a specimen of †*E. rosei* (Fig. 40A). In the paratype of †*H. consteniorum*, the posterior end of the premaxilla is much narrower than the anterior portion (Fig. 40D), and the 'notch' is open posteriorly (also in the specimen of †*E. woodruffi* illustrated in Fig. 40B). Although the possibility exists that the posterior end of the premaxilla of the paratype was folded or otherwise remodelled during fossilization and the posterior edge of the anterior portion in fact represents the notch found in the holotype, the two would differ dramatically in terms of depth to length ratio (the anterior and posterior ends of the premaxilla on the paratype appear to be complete and unbroken). The question then becomes whether the notch found in the holotype of †*H. consteniorum* is equivalent to the mid dorsal concavity of extant *Hiodon*, and if so, how best we are to interpret the various similarities in shape between certain specimens of †*Eohiodon* with the different taxa of *Hiodon*. Additionally, the premaxillae on most specimens of †*Eohiodon* that I have examined are somehow obviously damaged or partially hidden by overlying elements, so that the true morphology of this element in the three species is still poorly known. Given such uncertainties of this morphology, I have removed this character from my analysis.

Angle of the jaw: Anterior to mid-orbit [0]; Between mid-orbit and posterior edge of orbit [1]; Posterior to the orbit [2]. LW96[24]. This character was coded by Li & Wilson (1996a) as derived for †*Phareodus testis*

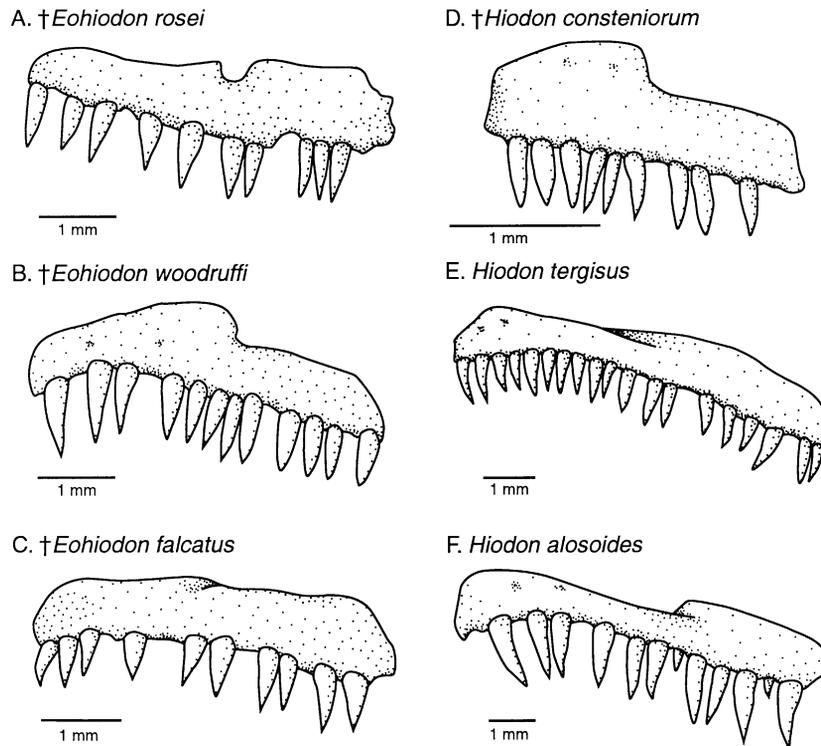


Figure 40. Premaxillae of †*Eohiodon* and *Hiodon*. A, †*Eohiodon rosei* (AMNH 2905a; unknown SL). B, †*E. woodruffi* (UALVP 22905a; 127 mm SL). C, †*E. falcatus* (UMA F10651; 125 mm SL). D, †*Hiodon consteniorum* (UALVP 24200; 60 mm SL). E, *H. tergisus* (UMA F10635; 155 mm SL). F, *H. alosoides* (UMA F10647; 258 mm SL). Anterior facing left.

(state 1; see Fig. 27B) and other species of †*Phareodus* (e.g. †*P. encaustus*; see Fig. 27A), *Pantodon*, †*Singida*, *Scleropages* and *Osteoglossum* (state 2). The angle of the jaw that was presumably being described is the angle formed by the upper and lower jaws rather than the placement of the jaw joint itself, as this point is almost always at least posterior of the midline of the orbit, if not fully behind the orbit. This character is logically dependant (at least partially) with the length of the maxilla, which is in part captured by Character 39, which describes the length of the maxilla as a function of which bone of the lower jaw it lies laterally to. For example, that character is derived in *Heterotis* (i.e. the posterior portion of the maxilla lies on dentary rather than on angular), meaning that the angle of the jaw is necessarily going to be very far forward (i.e. possibly anterior of the midline of the orbit). Fair enough – there are several taxa with a maxilla that reaches the angular that also have a relatively anterior position of the jaw angle; some taxa that are coded as having the angle of the jaw posterior of the midline of the orbit also have a maxilla that lies on the angular. Therefore, dependence between the characters is not complete. However, it seems to me that the position of the angle of the lower jaw is an interaction between the length of the maxilla, length of the lower jaw, and

the obliqueness of the hyomandibula (which is tightly correlated with the position of the joint of the lower jaw). Therefore, until this character is dissected and more critically examined, I have chosen not to include it in my analysis.

Mouth cleft: Anteriorly directed or slightly upturned [0]; Strongly upturned [1]. LW99[39]. This character, also included in analyses by Li & Wilson in other papers (e.g. 1996b: character 16), has long been cited as evidence of relationship between *Pantodon* and *Osteoglossum* and *Scleropages* (e.g. Greenwood & Thompson, 1970; Kershaw, 1976). As in other characters in which the states are largely separated by shades of grey, this character is somewhat problematic. Although it is intuitively obvious what these authors are trying to describe in the definition of the derived state (strongly upturned), the morphological reason for this upturning is unclear, and whether this corresponds (i.e. is similar) across the taxa that are similarly coded is also unclear.

The distinction between slightly and strongly upturned is ambiguous. For instance, the mouth of *Arapaima* is upturned, presumably only slightly according to the definition followed by Li and colleagues. However, this upturning is significant rela-

tive to the condition seen in other taxa, such as *Hiodon*. I would suggest that until this character is defined so that it is not based on overall similarity of morphology (ultimately an observation that is difficult to repeat from researcher to researcher), that it, and those of a similar nature, be approached with caution; for this reason I have not included it in this analysis.

Distinct horizontal limb of the preopercle: Present [0]; Absent [1]. LW96[28]. *Angle formed by the vertical and horizontal arm of the preopercle*: 90° [0]; $< 90^\circ$ [1]. LW99[31]. *Length of vertical limb of preopercular*: Longer than horizontal arm [0]; About equal to horizontal arm [1]. LW99[32]. Li & Wilson (1996a, also 1999: character 30) coded the lack of distinction between the horizontal and vertical limbs of the preopercle in †*Tanolepis* and three species of †*Phareodus* (†*P. encaustus*, †*P. queenslandicus* and †*P. muelleri*; see also Li *et al.*, 1997a); I could find no appreciable difference between condition in †*P. testis* and †*P. encaustus* (see Fig. 27). Additionally, there is an even slighter degree of curvature of the preopercle (resulting in an even less distinct horizontal limb) in notopterids (e.g. *Chitala*; Figs 23A, 24A) than is found in either species of †*Phareodus*; Li & Wilson coded Notopteridae as possessing a distinct horizontal limb. Because of the discrepancies between the way I would code this character, and the vagueness of the character itself (i.e. in some taxa there is a fine line between having and not having a horizontal limb), I excluded it from my analysis. It should be noted that characters 31, 32 and 33 of Li & Wilson (1999) refer to characteristics of the structures of the horizontal limb, and were coded for the three species of †*Phareodus* that supposedly do not possess a distinct horizontal limb (see below).

The other two characters of the preopercle listed above depend on the state of the first character. In those taxa that lack a distinct horizontal limb of the preopercle, the portion of the preopercle homologous to the horizontal limb of the preopercle of other taxa (i.e. the ventral portion of this bone) still can be said to 'exist', and it therefore may be possible to code for the angle between the horizontal and vertical limbs (although see below). However, with this accepted, the problem then becomes one of redundant characters, in that those taxa which lack a horizontal limb of the preopercle will necessarily have a greater angle between the two. A more striking problem of these characters is that inherent in conditional characters. Characters which describe condition of the horizontal limb (i.e. angle between the horizontal and vertical limbs) cannot logically be coded for those taxa that lack a horizontal limb (although see above for a possible justification for coding of this character). Similarly,

taxa that lack a horizontal limb cannot be coded for the length of the vertical limb, given that the character states are defined in relation to the length of the former (there is also the more fundamental issue: if there is no horizontal limb, does a vertical limb exist?). If used in an analysis, these conditional characters should be coded as unknown in a matrix.

Opercular shape: More or less irregularly trapezoidal [0]; Irregular parallelogram [1]; Kidney-shaped [2]; Oval [3]; Subsemicircular [4]; Fan-shaped [5]; LW96[10] & LW99[25]. *Anteroventral corner of the opercle*: $>70^\circ$ [0]; $= 70^\circ$ [1]; LW99[28]. *Posteroventral margin of the opercle*: Rounded [0]; Nearly straight [1]; Distinctly concave [2]. LW99[29]. The shape of the opercle was a source for many characters of Li & Wilson (1996a, 1999). One of these described the overall shape of the opercle. Although there is indeed a great degree of variation in the shape of the opercle of different osteoglossomorphs (Fig. 41), this character highlights the need for clear illustration or description of the condition intended for each character state of a character, particularly in characters in which there is inherently a greater deal of subjectivity than presence-absence sort of characters. For instance, the opercle of *Arapaima* was coded as 'oval' by Li & Wilson, but easily could be described as 'subsemicircular' by another investigator (Fig. 41D). Additionally, both elopoids and mormyroids were coded as having 'irregularly trapezoidal' opercles, although these two taxa have very different shaped opercles (cf. Fig. 41A, I).

The other two characters listed above describe various qualities of the opercle that ultimately will be influenced by the overall shape of the opercle, and therefore dependent on how that character is coded. Also, as I interpret these characters, there are several taxa which are miscoded. For instance, the opercle of *Scleropages* does not possess a distinctly concave posteroventral margin (Fig. 41G, as coded by Li & Wilson) like that found in *Osteoglossum* (Fig. 41H) and †*Singida* (pers. observ.). Also, the posteroventral margin of the opercle in many mormyroids is straight, but was coded as 'rounded' (e.g. *Gnathonemus*; Fig. 41I).

The necessity of using such words as 'irregularly' and 'more or less' in describing character states is indicative of definitions that potentially may be loosely interpreted and therefore are problematic for future reanalysis by different researchers. This is not to say that there is no use in characters describing the shape of structures (e.g. the shape of the opercles of taxa such as †*Phareodus*, *Pantodon*, *Scleropages*, *Osteoglossum* and †*Singida* are undeniably similar, and this similarity is likely due to common ancestry, i.e. a synapomorphy at some level). However, care must be taken in clearly illustrating what is meant by the definition of each character state.

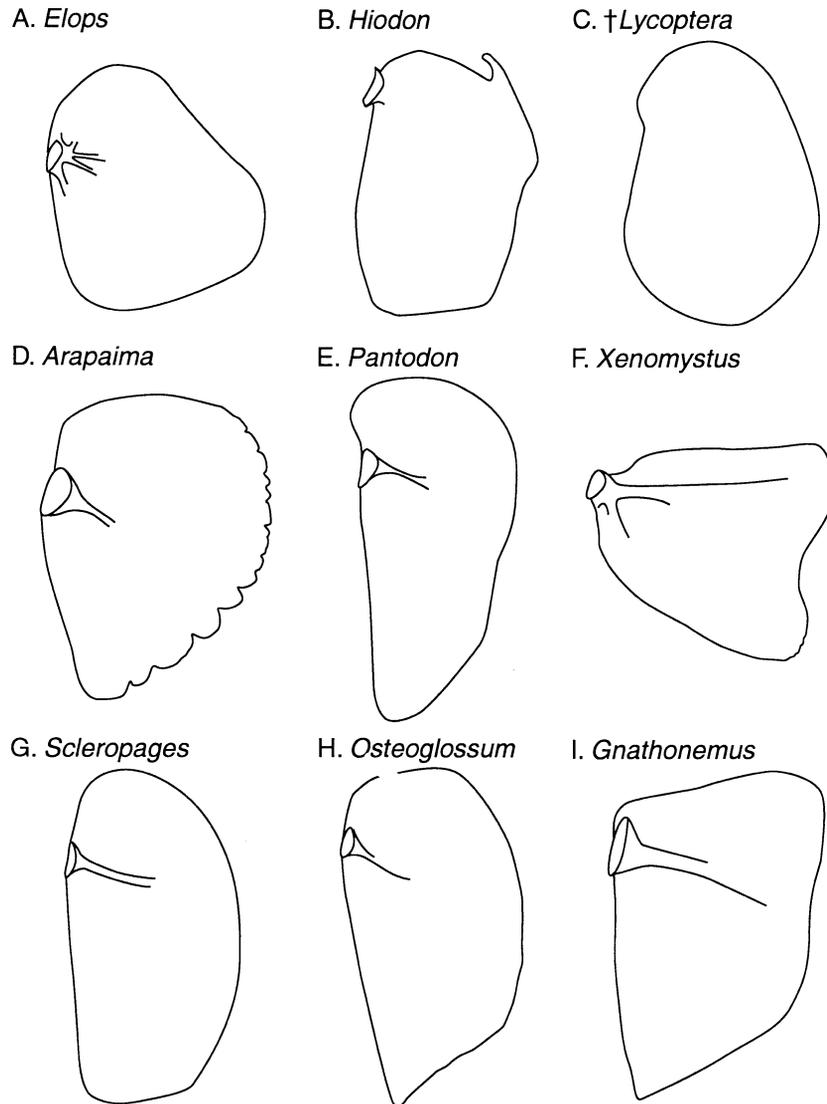


Figure 41. Semi-schematic illustrations of right opercles in medial view (except C, which is left opercle in lateral view). A, *Elops* (UMA F10255; 425 mm SL). B, *Hiodon* (UMA F10177; 267 mm SL). C, †*Lycoptera* (Modified from Jin *et al.*, 1995: fig. 6). D, *Arapaima* (UMA F11263; est. 1270 mm SL). E, *Pantodon* (UMA F11264; 70 mm SL). F, *Xenomystus* (FMNH 69494; approx. 90 mm SL). G, *Scleropages* (UMA F11266, approx. 320 mm SL). H, *Osteoglossum* (UMA F10160, 365 mm SL). I, *Gnathonemus* (UMA F11267, approx. 140 mm SL). Anterior facing left.

Belly keel: Absent [0]; Present [1]. LW96[38]. Li & Wilson (1996a) interpreted the presence of a 'belly keel' to be a synapomorphy of the two extant species of *Hiodon*; all other taxa included in their analysis were coded as having a keel absent. This character was removed from other analyses (e.g. Li *et al.*, 1997b; Li & Wilson, 1999). This character is not used here for two reasons. First, most fossils included in this analysis (as were those analysed by Li & Wilson, 1996a) are preserved as flattened specimens and in lateral view, and thus the possibility of determining the presence of a 'keel' with any degree of objectivity is compromised.

Second, several taxa that were coded as lacking a 'keel', I would have coded as possessing one; this is fundamentally due to the absence of a clear illustration or description of what the authors intended as constituting a 'keel'. For instance, the ventral body margin of notopterids is keel-like due to the development of the ventral body scutes (Character 55). Although it may be intuitively obvious that the formation of the 'keel' in notopterids vs. that of *Hiodon*, which is formed of a sharp ridge of soft tissue, is not homologous, this is not captured in the definition of this character.

Supraneurals: Present [0]; Absent [1]. LW99[66]. This character was identified by Li & Wilson (1999) as an autapomorphy of †*Ostariostoma* that was convergently present in an outgroup (*Hypomesus*). The presence of supraneurals in †*Ostariostoma* was reported by Grande & Cavender (1991: fig. 1), who illustrated seven slender elements intercalated between neural arches of the anterior abdominal vertebrae. I regard the presence of supraneurals as ambiguous in this taxon because of the size of the specimen (40 mm SL), the mode of preservation (as a natural mould, which has been studied by making a peel), and the nature of the supraneurals in other fishes (thin and slender elements that may not be well preserved as impressions).

Anterior supraneurals (when present): Same shaped and as slender as posterior ones [0]; Dorsally moderately broader and leaf-shaped [1]; Dorsally greatly broader and plate-shaped [2]. LW99[67]. Li & Wilson (1999) found that the two derived states defined for this character (states 1 and 2) characterized two different groups. State 1, in which the anterior supraneurals are leaf shaped and moderately broad dorsally, was the one synapomorphy of the stem-group osteoglossomorph clade containing †*Tongxinichthys*, †*Jiuquanichthys* and †*Kuyangichthys*. Zhang & Jin (1999: 391) described the supraneurals of †*Tongxinichthys* as 'slightly broader anteriorly than posteriorly' and their photograph (their fig. 1B) and reconstruction (their fig. 2) illustrates a smooth gradation between the 'slightly broader' anterior elements and the more slender posterior ones (no specimens were examined for this study). Li & Wilson (1999: 376) conceded that 'the evidence for this clade is admittedly weak.'

State 2 (anterior supraneurals greatly broader dorsally) was found to be a synapomorphy of the clade †*Huashia* + †*Kuntulunia*, which was far removed from the group defined by state 1, although Li & Wilson (1999: 376) suggested that this state might be a 'more derived condition' of state 1 (however, based on their tree topology, there is no reason to suspect that state 2 is a transformation of state 1). Based on the illustrations by Zhang (1998), †*Kuntulunia* does possess enlarged anterior supraneurals that are very distinctive.

Because specimens of the taxa involved with these characters (i.e. coded by Li & Wilson, 1999 as having either derived state) were not available for this study, I did not include this character in my analysis. Also, as pointed out elsewhere (Hilton, 2002), other taxa coded as plesiomorphic by Li & Wilson (1999) also possess anterior supraneurals that could be regarded as 'leaf-shaped' (or at least not similar to the posterior ones in shape) with slender posterior supraneurals (e.g.

Hiodon; Hilton, 2002: fig. 62; *Elops*, pers. observ., Forey, 1973b).

Pelvic fin rays: More than seven [0]; Seven [1]; Six or fewer [2]. LW99[69]. Li & Wilson (1994: character 8) originally identified the presence of a pelvic fin with seven fin rays as a synapomorphy of Hiodontidae. They later (Li & Wilson, 1999) showed that all outgroups except for clupeoids (e.g. †*Leptolepis*, elopomorphs and salmonoids) have a pelvic fin with more than seven. All non-hiodontiform osteoglossomorphs (including †*Lycoptera*) were coded as having less than seven. Although this is certainly true for all extant taxa included in my analysis (pers. observ.), the fossils are more problematic. For instance, I have found it difficult to confidently get reliable counts of fin rays for even relatively well preserved taxa such as †*Eohiodon*. For this reason, I did not include this character, although I was able to confirm seven in *Hiodon* (Hilton, 2002) and less than seven in all other living osteoglossomorphs that were examined.

Shape of dorsal fin: Triangular [0]; Rounded [1]; LW99[70]. *Posterior rays of dorsal and anal fins*: Shorter than anterior ones [1]; Longer than anterior ones [2]; LW99[71]. These two characters were coded by Li & Wilson (1999) with almost exactly the same distribution (i.e. those taxa that were coded as having a rounded dorsal fin were also coded as having fin rays of the median fins with posterior fin rays longer than the anterior ones), and both characters show a mosaic distribution on the topology of their cladogram. The only difference in coding of the two characters was for *Pantodon*, which was coded as having a dorsal fin that is rounded (which it is, roughly) but with posterior fin rays of the median fins shorter than the anterior ones. The anal fin has shorter fin rays in the posterior portion of the fin. However, the fin rays of the middle portion of the dorsal fin of *Pantodon* are the longest and are shorter both anteriorly and posteriorly.

It seems to me that the near redundant coding between these two characters is not coincidental. For example, if the dorsal fin is triangular it necessarily follows that the posterior fin rays of this fin will be shorter than the anterior ones. Also, the condition of having 'rounded' dorsal fins may encompass different underlying morphological sources of this 'roundness' (i.e. does not represent homologous conditions). For these reasons, I have not included these characters in my analysis.

An additional problem of how to code these characters arises in the use of the family level taxon Notopteridae. Within the family there is variation in the presence of the dorsal fin; the monotypic genus *Xenomystus* lacks a dorsal fin. Therefore, the condition of the dorsal fin (triangular or rounded) must be coded as polymorphic for Notopteridae, with one of the two

entries a question mark to code for *Xenomystus* (i.e. 1/?) because the condition of the dorsal fin must be coded as 'inapplicable' for this taxon. MacClade does not permit this to be entered into a cell of a data matrix, and it is unclear how phylogenetic programs like PAUP* would treat this type of data. This may be further justification for using species-level taxa, monotypic higher taxa, or at least monomorphic (and monophyletic) subgroups as terminal taxa in phylogenetic analyses (see Bininda-Emonds, Bryant & Russell, 1998; Kornet & Turner, 1999; Simmons, 2001; for discussion of coding polymorphic higher-taxa).

Shape of anal fin: Same in both sexes [0]; Sexually dimorphic [1]. LW96[34]. The presence of a sexually dimorphic anal fin has long been recognized in *Hiodon* (e.g. Kirtland, 1847), as well as in †*Eohiodon* (e.g. Cavender, 1966; Wilson, 1978; Wilson & Williams, 1992; Li *et al.*, 1997b). This was first interpreted as a synapomorphy of the two genera by Li & Wilson (1994: character 15). †*Plesioleptocephala* and †*Brychaetus* were the only two taxa coded as unknown for this character in Li & Wilson's (1999) analysis. Philosophically, this character is problematic for all fossil taxa. In some taxa, such as †*Eohiodon*, for which unquestioned close relatives (i.e. *Hiodon*) have sexually dimorphic fins, and there appears to be a similar condition in the fossil taxon, it is reasonable to hypothesize sexual dimorphism in the fossil as well. However, such hypotheses become circular if this character is used to help establish relationships in the first place.

Additionally, there comes the question of how many specimens of a fossil taxon that show a single morphology are needed to be certain that sexual dimorphism does not exist. For instance, if the fossil is only known from one specimen, as is the case for †*Ostariostoma* (coded as lacking a sexually dimorphic anal fin by Li & Wilson, 1999; although see Grande & Cavender, 1991: fig. 4), or even a few specimens, what is to say that both male and female specimens are included in the sample.

On a more fundamental note, some mormyroids coded by Li & Wilson (1999) as not having sexually dimorphic anal fins do in fact have them, superficially similar in external morphology to the condition found in *Hiodon* (e.g. Iles, 1960; Okedi, 1969; Brown, Benveniste & Moller, 1996). Therefore, Mormyroidea should be coded as polymorphic for this character.

CONCLUSIONS

'... good judgement proceeds from clear understanding, and a clear understanding comes from reason derived from sound rules, and sound rules are the daughters of sound experience – the common mother of all the sciences and arts.'

Leonardo da Vinci, *Codex Atlanticus*, verso 221.

GENERAL COMMENTS

Through the publication of computer-based phylogenetic analyses, Li and colleagues have brought much to the study of the systematics of osteoglossomorph fishes. Most importantly, perhaps, they have produced testable hypotheses of relationships in the form of character-by-taxon data matrices. In fact, all recent studies of osteoglossomorph systematics use, at least in part, characters that were generated by or assimilated into their studies.

As noted above, however, several of their characters were found to be problematic, either in definition or in coding. The tree presented in Figure 5 is the strict consensus of the most parsimonious interpretation for the distribution of characters in the data matrix. Trees consistent with their hypotheses of relationships are within four additional steps of my tree. However, the present analysis of osteoglossomorph relationships cannot be viewed as a 'test', in the strictest sense, of the relationships they have hypothesized. In addition to a completely different set of characters used for analysis (and refinement of many of these characters), a different set of taxa was scored. The purpose of the present study has been simply to critique the morphological basis of some of the characters currently in use, and present the results of my analysis, which, as with any phylogenetic hypothesis, should be viewed merely as a contribution to the study of osteoglossomorph interrelationships.

Many of the taxa included in Li & Wilson's analyses were not available for my direct examination (e.g. many of the fossil osteoglossomorphs from China), and were therefore not included here. Inclusion of these taxa may have a significant effect on the distribution of some characters that were included in my analysis, and therefore on the patterns of inferred relationships. However, I hesitate to take much information from the literature for many of these taxa, in particular some of the fossils, for which there is a great deal of misinformation and over-interpretation (e.g. see Chang's, 1999 warnings for some of the fossil osteoglossomorphs from the Mesozoic of China). This caution is best exemplified by the high level of missing data (in particular due to 'lack of preservation') in my data matrix in comparison with those published by Li and colleagues. For instance, my coding of †*Lycoptera* is rife with missing data (52% of characters scored as unknown), whereas Li & Wilson (1999) scored †*Lycoptera* as unknown for only four characters (only 5%). Many of the characters that I scored as unknown were scored as a known state by these authors, although I acknowledge that some of the former may in fact be observable given different specimens.

The material of extant taxa used in my study is also an issue. Although I scored the matrix from direct

observations of specimens, more often than not there was only a single or at most very few specimens available for study. Such a study cannot control for individual variation (e.g. Hilton & Bemis, 1999), and observations made here, particularly those that conflict with, or are unknown in, the literature, must be confirmed on different specimens.

In most recent analyses of osteoglossomorph relationships (including this one), emphasis has been placed on characters of the skull and caudal skeleton (e.g. 85% of those used in the present study). This may be an historical artifact, as these are the regions generally held to be of systematic importance and have received the vast majority of attention from comparative anatomists. There are, however, many more comparative morphological data available for osteoglossomorph fishes (e.g. through the works of P. H. Greenwood, G. J. Nelson, L. Taverne and others), including aspects of the postcranial skeleton and soft tissue anatomy. Many of these data have not been included here for various reasons (e.g. soft anatomical characters that I could not confirm with the specimens available to me), but future studies on the systematics of osteoglossomorph fishes must evaluate them.

CLASSIFICATION OF OSTEOGLOSSOMORPHA

I here provide a provisional classification of osteoglossomorph fishes based on the results of this analysis. Only the genera included in my analysis as terminal taxa are included in this classification (i.e. taxa such as *Gymnarchus* are not included), so there are some potential 'levels' that are missing. I use the terms 'plesion' and 'incertae sedis' in the sense of Patterson & Rosen (1977). I use the suborder name Osteoglossoidei to refer to the clade Notopteridae + Osteoglossidae.

Superorder Osteoglossomorpha

Osteoglossomorpha *incertae sedis* Family †Lycoperidae

†*Lycoptera*

Order Hiodontiformes

Family Hiodontidae

†*Eohiodon*

Hiodon

Order Osteoglossiformes

plesion †*Ostariostoma*

Osteoglossiformes *incertae sedis* †*Palaeonotopterus*

Family Mormyridae

Petrocephalus

Gnathonemus

Campylomormyrus

Suborder Osteoglossoidei (new usage)

Family Notopteridae

Chitala

Papyrocranus

Xenomystus

Family Osteoglossidae

plesion †*Joffrichthys*

Subfamily Heterotinae

Heterotis

Arapaima

Subfamily Osteoglossinae

Osteoglossinae *incertae sedis* †*Phareodus*

Osteoglossinae *incertae sedis* *Pantodon*

Osteoglossinae *incertae sedis* †*Singida*

Scleropages

Osteoglossum

CONCLUDING REMARKS

I conclude with words borrowed from Patterson & Johnson (1997: 360–361): 'With general acceptance of the cladistic approach, it is now commonplace for systematists to publish a matrix, with only a brief list of characters, and to concentrate on the results of manipulating the matrix with parsimony or other programs. In other words, the emphasis has shifted from observation, the source of the matrix, to whatever message may be extracted from the matrix . . . This change of emphasis replaces our pernicious old black box, evolutionary systematics, with a new one, the matrix.' The result of an analysis of a data matrix is not the stand-alone answer to a hypothesis (Grande & Bemis, 1998), but is rather the sum of the observations that comprise that matrix; it is the ability to justify and convey those observations (by means of description or illustration) that will ultimately advance systematic hypotheses regarding a particular group. When character states are subjectively defined and not explicitly illustrated, the result will be coding and analysing overall similarity disguised in the form of rigorous character analysis.

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APPENDIX 1: DATA MATRIX

In addition to the numerical codes for the character states (0–5), the following codes are used in this data matrix: N = Unknown due to inapplicability; H = Unknown due to uncertain homology; P = Polymorphic

Taxon	1–5	6–10	11–15	16–20	21–25
<i>Elops</i>	00000	00110	00000	00000	00000
† <i>Lycoptera</i>	??001	1021?	00???	?????	0??00
† <i>Eohiodon</i>	20001	11210	10???	0???	01000
<i>Hiodon</i>	20001	11210	P0000	00001	01000
† <i>Joffrichthys</i>	??00?	23211	?0???	?????	0??01
<i>Heterotis</i>	52201	23001	10101	00001	01101
<i>Arapaima</i>	32001	23201	10101	01011	01101
† <i>Phareodus</i>	?2210	23?00	10010	?????	01001
<i>Pantodon</i>	22101	13200	10111	01001	10001
† <i>Singida</i>	???0?	???0?	?0???	?????	11?01
<i>Scleropages</i>	32100	23301	11100	00101	01001
<i>Osteoglossum</i>	32100	23301	11100	00101	01001
† <i>Ostariostoma</i>	2?000	HH???	1????	?????	0HH10
<i>Petrocephalus</i>	10000	02200	10001	12111	11010
<i>Gnathonemus</i>	10001	02200	10101	13111	11010
<i>Campylomormyrus</i>	10000	02200	10101	12111	11010
<i>Chitala</i>	11200	22111	10010	01011	11010
<i>Xenomystus</i>	41100	22211	10010	01011	11010
<i>Papyrocranus</i>	41100	22211	10110	01011	11010
† <i>Palaeonotopterus</i>	1000?	??2?0	100?0	0110?	1????

Taxon	26–30	31–35	36–40	41–45	46–50
<i>Elops</i>	00100	00000	00000	00000	00000
† <i>Lycoptera</i>	?????	?000?	000??	0??1?	?HHH?
† <i>Eohiodon</i>	1?200	?0010	11001	0001?	?010?
<i>Hiodon</i>	11200	10010	11001	00010	00100
† <i>Joffrichthys</i>	0????	?2000	?00?1	0????	?HHH?
<i>Heterotis</i>	00111	00001	11011	02002	11NN1
<i>Arapaima</i>	00111	10001	10011	02002	01NN2
† <i>Phareodus</i>	00?1?	?2101	10001	0210?	?????
<i>Pantodon</i>	00001	10102	10101	01002	00011
† <i>Singida</i>	0????	?2101	?NN?1	0????	?????
<i>Scleropages</i>	00011	P2101	11001	01102	10011
<i>Osteoglossum</i>	00011	12101	11001	01102	10011
† <i>Ostariostoma</i>	0????	?30?0	?1???	01???	?????
<i>Petrocephalus</i>	22002	10000	11111	13H02	10002
<i>Gnathonemus</i>	22002	10000	11111	13H12	11NN2
<i>Campylomormyrus</i>	22002	10000	11111	13H12	11NN2
<i>Chitala</i>	03001	12002	10001	11101	10101
<i>Xenomystus</i>	23001	12002	10001	11101	10101
<i>Papyrocranus</i>	23001	12002	10001	11101	10101
† <i>Palaeonotopterus</i>	?0???	?????	?????	?????	?????

Appendix 1 (Continued)

Taxon	51–55	56–60	61–65	66–70	71–72
<i>Elops</i>	00000	20000	00000	00010	00
† <i>Lycoptera</i>	????0	010??	0?001	0?100	00
† <i>Eohiodon</i>	0????	01000	0?001	001P0	00
<i>Hiodon</i>	00000	01000	01001	001PP	00
† <i>Joffrichthys</i>	????0	0????	0??02	H1H01	10
<i>Heterotis</i>	11000	10101	00002	11200	12
<i>Arapaima</i>	11000	00110	00002	11200	12
† <i>Phareodus</i>	????0	00??1	1?002	H2H0P	12
<i>Pantodon</i>	101N0	01001	10102	11200	11
† <i>Singida</i>	????0	000?1	1?102	11?00	1?
<i>Scleropages</i>	10000	00101	10102	11200	12
<i>Osteoglossum</i>	10000	00101	10102	11200	12
† <i>Ostariostoma</i>	????0	011??	0?001	101H0	1?
<i>Petrocephalus</i>	10010	0H011	00001	10200	11
<i>Gnathonemus</i>	20010	0H011	00001	10200	11
<i>Campylomormyrus</i>	20010	0H011	00001	10200	11
<i>Chitala</i>	101N1	00101	00012	21200	10
<i>Xenomystus</i>	101N1	00101	00012	21200	10
<i>Papyrocranus</i>	10001	00101	00N12	2120P	10
† <i>Palaeonotopterus</i>	?????	???1?	?????	?????	??

APPENDIX 2: CHARACTERS USED
IN ANALYSIS

- Temporal fossae*: Absent (0); Present – bordered by the epioccipital, exoccipital, and pterotic (1); Present – bordered by the epioccipital, pterotic, and parietal (2); Present – bordered by the epioccipital and pterotic (3); Present – bordered by the exoccipital and the pterotic (4); Present – bordered by the exoccipital, epioccipital, parietal and pterotic (5).
- Shape of extrascapular*: Expanded (0); Reduced and irregularly shaped (1); Reduced and tubular (2).
- Shape of frontal bones*: Anterior margin narrower than posterior margin (0); Anterior margin about equal in width to posterior margin (1); Anterior margin wider than posterior margin (2).
- Supraorbital shelf of frontal bone*: Absent (0); Present (1).
- Length of frontal bone*: Over twice as long as parietal (0); Less than twice as long as parietal (1).
- Relationship of nasal bones*: Some part separated by anterior portion of frontals (0); Separated only by ethmoid bones (1); Meet each other in midline (2).
- Nasal bones*: Tubular but not curved (0); Tubular and strongly curved (1); Gutter-like (2); Flat and broad (3).
- Parasphenoid teeth*: Absent (0); Small (1); Large and found along the length of the parasphenoid (2); Large and restricted to the basal portion of the parasphenoid (3).
- Basipterygoid process*: Present (0); Absent (1).
- Supratemporal commissure passing through the parietals*: Absent (0); Present (1).
- Supraorbital sensory canal*: Ending in parietal (0); Ending in frontal (1).
- Orbitosphenoid*: Present (0); Absent (1).
- Basisphenoid*: Present (0); Absent (1).
- Basioccipital process of the parasphenoid*: Divided (0); Median (1).
- Ventral occipital groove*: Present (0); Absent (1).
- Intercalar*: Present (0); Absent (1).
- Cranial nerve foramen/foramina*: In the prootic (0); Straddling the suture between the prootic and pterosphenoid (1); Foramen straddling the suture between the sphenotic and pterosphenoid (2); Foramina are separate from one another, one straddling the suture between the prootic, sphenotic and the pterosphenoid (dorsally) and one straddling the suture between the prootic, pterosphenoid and parasphenoid (ventrally) (3).
- Suture between the parasphenoid and sphenotic*: Absent (0); Present (1).
- Foramen for cranial nerve VI*: Opens within the prootic bridge (0); Opens anterior to the prootic bridge (1).
- Supraorbital bone*: Present (0); Absent (1).
- Otic and supraorbital sensory canal*: In bony canals (0); Partially or completely in grooves (1).
- Number of bones in the infraorbital series, not including the dermosphenotic or the antorbital, if present*: Five (0); Four (1).

23. *First infraorbital*: Ventral of orbit (0); Enlarged and anterior of orbit (1).
24. *Condition of the infraorbital sensory canal in at least some infraorbitals*: Enclosed in a bony canal (0); Open in a gutter (1).
25. *Palatoquadrate area behind and below the orbit*: Not completely covered by the infraorbitals (0); Completely covered by infraorbitals (1).
26. *Dermosphenotic*: Triangular (0); Triradiate (1); Tubular (2).
27. *Posterior region of the fossa on the neurocranium for the hyomandibula*: Formed of pterotic (0); Formed of pterotic and intercalar (1); Formed of pterotic and exoccipital (2); Formed of exoccipital and intercalar (3).
28. *Neurocranial heads of the hyomandibula*: One head or two heads but continuous (0); Two heads, separate (1); Two heads, bridged (2).
29. *Anterior process (wing) of the hyomandibula that contacts entopterygoid*: Absent (0); Present (1).
30. *Dermal bones of the palatoquadrate*: Two lateral elements (0); One lateral element and one medial element (1); One element (2).
31. *Autopalatine bone*: Present (0); Absent (1).
32. *Preopercular sensory canal*: Opens by pores the entire length of the canal (0); Opens by pores ventrally and by a groove dorsally (1); Opens by pores dorsally and a groove ventrally (2); Opens by a groove the entire length of the canal (3).
33. *Opercle depth to width ratio*: Less than two (0); About two or greater than two (1).
34. *Posterodorsal spine on the opercle*: Absent (0); Present (1).
35. *Size and position of the subopercle*: Large and ventral of the opercle (0); Small and anterior of the opercle (1); Absent (2).
36. *Gular bone*: Present (0); Absent (1).
37. *Ascending process of the premaxilla*: Well developed (0); Only slightly developed, if at all (1).
38. *Premaxillae*: Paired (0); Median (1).
39. *Posterior portion of the maxilla*: Lies on angular (0); Lies on dentary (1).
40. *Supramaxillae*: Present (0); Absent (1).
41. *Mandibular canal*: Enclosed in a bony tube (0); Open in a groove (1).
42. *Posterior bones of the lower jaw*: Angular and retroarticular bones fused (0); Angular and articular bones fused (1); All separate (2); All fused (3).
43. *Retroarticular bone*: Included in the articulation with the quadrate (0); Excluded from the articulation with the quadrate (1).
44. *Medial wall of the Meckelian fossa of the lower jaw*: Present (0); Absent (1).
45. *Bony elements associated with the second ventral gill arch*: Absent (0); Present as autogenous elements (1); Present as a bony process on the second hypobranchial (2).
46. *Toothplate(s) associated with basibranchial 4*: Present (0); Absent (1).
47. *Basihyal toothplate*: Present (0); Absent (1).
48. *Basihyal toothplate*: Flat (0); With ventrally directed processes (1).
49. *Basibranchial toothplate and basihyal toothplate*: Separate (0); Continuous (1).
50. *Basihyal*: Present and ossified (0); Present and cartilaginous (1); Absent (2).
51. *Hypohyals*: Two ossified pairs present (0); One ossified pair present (1); One pair, greatly reduced in size (2).
52. *Infrapharyngobranchial 3*: Undivided (0); Divided into two elements (1).
53. *Infrapharyngobranchial 1*: Present (0); Absent (1).
54. *Orientation of infrapharyngobranchial 1*: Proximal tip anteriorly directed (0); Proximal tip posteriorly directed (1).
55. *Abdominal scutes*: Absent (0); Present as paired structures (1).
56. *Epipleural bones*: Absent (0); Only a few bones in anterior caudal region (1); Present throughout abdominal and caudal region (2).
57. *Dorsal arm of the post-temporal bone*: Less than 1.5 times as long as the ventral arm (0); More than twice as long as the ventral arm (1).
58. *Lateral line that pierces the supracleithrum*: Present (0); Absent (1).
59. *Cleithrum*: With no or only a slight medial lamina (0); With a broad medial lamina (1).
60. *Coracoid fenestra*: Absent (0); Present (1).
61. *First pectoral fin ray*: Normal (0); Greatly enlarged and extremely long (1).
62. *Post-pelvic bone*: Absent (0); Present (1).
63. *Pelvic bone*: Slender (0); Possesses a thin deep lamella in dorsoventral plane (1).
64. *Posterior end of anal fin*: Separate from caudal fin (0); Continuous with caudal fin (1).
65. *Number of principal branched caudal fin rays*: 17 or more (0); 16 (1); 15 or fewer (2).
66. *Uroneurals*: Three or more (0); Two or one (1); Absent (2).
67. *Neural spine on first ural centrum*: Absent or rudimentary (0); One (1); Two (2).
68. *Epurals*: Two or three (0); One (1); Absent (2).
69. *Neural spine on the first preural centrum*: Complete (0); Rudimentary (1).
70. *Number of neural spines on the second preural centrum*: One (0); Two (1).
71. *Number of hypurals*: Seven (0); Six or fewer (1).
72. *Scales*: No reticulate furrows (0); Both radial and reticulate furrows present (1); Reticulate furrows only present over entire scale (2).