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Review article

A review of the systematic biology of fossil and living bony-tongue fishes, Osteoglossomorpha (Actinopterygii: Teleostei)

Eric J. Hilton¹ and Sébastien Lavoué^{2,3}

The bony-tongue fishes, Osteoglossomorpha, have been the focus of a great deal of morphological, systematic, and evolutionary study, due in part to their basal position among extant teleostean fishes. This group includes the mooneyes (Hiodontidae), knifefishes (Notopteridae), the abu (Gymnarchidae), elephantfishes (Mormyridae), aruanas and pirarucu (Osteoglossidae), and the African butterfly fish (Pantodontidae). This morphologically heterogeneous group also has a long and diverse fossil record, including taxa from all continents and both freshwater and marine deposits. The phylogenetic relationships among most extant osteoglossomorph families are widely agreed upon. However, there is still much to discover about the systematic biology of these fishes, particularly with regard to the phylogenetic affinities of several fossil taxa, within Mormyridae, and the position of *Pantodon*. In this paper we review the state of knowledge for osteoglossomorph fishes. We first provide an overview of the diversity of Osteoglossomorpha, and then discuss studies of the phylogeny of Osteoglossomorpha from both morphological and molecular perspectives, as well as biogeographic analyses of the group. Finally, we offer our perspectives on future needs for research on the systematic biology of Osteoglossomorpha.

Keywords: Biogeography, Osteoglossidae, Paleontology, Phylogeny, Taxonomy.

Os peixes da Superordem Osteoglossomorpha têm sido foco de inúmeros estudos sobre a morfologia, sistemática e evolução, particularmente devido à sua posição basal dentre os peixes teleosteos. Fazem parte deste grupo os “mooneyes” (Hiodontidae), “knifefishes” (Notopteridae), o “abu” (Gymnarchidae), peixes-elefante (Mormyridae), aruanãs e pirarucu (Osteoglossidae), e o peixe-borboleta africano (Pantodontidae). Esse grupo de morfologia heterogênea possui um longo e diverso registro fóssil, incluindo táxons de todos os continentes, oriundos tanto de depósitos de água doce quanto marinhos. As relações filogenéticas dentre a maioria das famílias de osteoglossomorfos é amplamente aceita. Entretanto, há muito a ser descoberto sobre a sistemática biológica desses peixes, particularmente com relação às afinidades filogenéticas de inúmeros fósseis, relações dentro de Mormyridae, e a posição filogenética de *Pantodon*. Neste manuscrito nós revisamos o atual estado de conhecimento dos peixes osteoglossomorfos. Nós primeiramente provemos uma abordagem geral da diversidade de Osteoglossomorpha, e então discutimos os estudos filogenéticos sobre Osteoglossomorpha sob a perspectiva morfológica e molecular, assim como uma análise biogeográfica do grupo. Finalmente, oferecemos nossas perspectivas sobre os futuros passos para pesquisa sobre a sistemática biológica de Osteoglossomorpha.

Palavras-chave: Biogeografia, Filogenia, Osteoglossidae, Paleontologia, Taxonomia.

Introduction

Osteoglossomorpha – the bony-tongue fishes – have been the focus of a great deal of morphological, systematic, and evolutionary study, due in part to their basal position among extant teleostean fishes (e.g., Greenwood *et al.*, 1966; Nelson, 1969; Greenwood, 1973; Taverne, 1979, 1998; Li, Wilson, 1996a; Hilton, 2003; Wilson, Murray, 2008). Among the world’s extant ichthyofaunal, this is a widespread group of primary freshwater fishes, including the neotropical genera *Arapaima* and *Osteoglossum*, the North American genus

Hiodon, and several Old-World groups, including the Mormyridae, *Gymnarchus*, *Pantodon*, *Heterotis* (Africa), Notopteridae (Africa and Southeast Asia), and the Australasian genus *Scleropages*. In addition, this morphologically heterogeneous group has a long and diverse fossil record, including taxa from all continents and both freshwater and marine deposits (Forey, Hilton, 2010). In their pivotal classification, Greenwood *et al.* (1966) formally established the modern conceptualization of crown-group Osteoglossomorpha, although all families had been more or less associated with one another by ichthyologists for some time (e.g., Ridewood, 1904, 1905;

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Garstang, 1931; Gosline, 1960). Two characters were offered to support this grouping: the presence of a so-called “paraphenoid-tongue bite” and the presence of “paired, usually ossified, rods at the base of the second gill arch” (Greenwood *et al.*, 1966:361). Although both of these characters have been shown to be complex characters, with different aspects of each defining different subgroups within Osteoglossomorpha (Hilton, 2001), the monophyly of the group has been well established and accepted (see discussion by Hilton, 2003).

The importance of Osteoglossomorpha for understanding early teleostean evolution has been long appreciated (e.g., Greenwood, 1973; Patterson, Rosen, 1977; Patterson, 1977; Arratia, 1997). Osteoglossomorpha was among the first vertebrate taxa to have their relationships analyzed in a cladistic framework (e.g., Nelson, 1968), and have also been used to exemplify general patterns, for instance, of biogeography (Nelson, 1969; Patterson, 1981). Based on a series of osteological descriptions (e.g., Taverne, 1972, 1977, 1978), Taverne (1979) first proposed the general pattern of relationships among extant taxa that is widely adopted today, namely that Hiodontidae is the sister group of all other extant osteoglossomorphs, Notopteridae and Mormyroidea (Gymnarchidae + Mormyridae) are each other’s closest relatives, and Osteoglossidae has two subfamilies (*Arapaima* + *Heterotis* and *Osteoglossum* + *Scleropages*, with *Pantodon* more closely related to the latter). This set of relationships was maintained by Li, Wilson (1996a), the first published computer-assisted cladistic analysis of Osteoglossomorpha. In the last 25 years there have been several studies of the relationships within Osteoglossomorpha, with broad congruence (with only a few exceptions) regarding their relationships, at least among extant taxa. However, there is still much to discover about these fishes, particularly with regard to the phylogenetic affinities of several fossil taxa and the position of *Pantodon*. The most recent review of the Osteoglossomorpha was conducted by Wilson, Murray (2008). Since that review, there have been numerous new data published on their morphology, many new fossil taxa described or redescribed, as well as renewed study of their biogeogra-

phy and their phylogeny based on genetic data. Osteoglossomorpha is at the same time both a well-studied taxon and one in need of new and focused study at all levels.

In this paper we review the state of knowledge for osteoglossomorph fishes, emphasizing studies published since Wilson, Murray (2008). We first provide an overview of the diversity of Osteoglossomorpha, using the family-level taxonomy presented by Nelson *et al.* (2016) as a framework for this discussion. We then discuss studies of the phylogeny of Osteoglossomorpha from both morphological and molecular perspectives, as well as biogeographical analyses of the group, with a particular emphasis on recent studies; the earlier history of the study of this group is described in more detail by Greenwood *et al.* (1966), Hilton (2003) and Wilson, Murray (2008). Finally, we offer our perspectives on future needs for research on the systematic biology of Osteoglossomorpha.

Diversity of Osteoglossomorpha

†**Lycoperidae and other Stem-Group Osteoglossomorpha.** †Ichthyodectiformes, a group of predatory Jurassic and Cretaceous fishes (Cavin *et al.*, 2013), had been closely associated with Osteoglossomorpha (e.g., potentially within Osteoglossomorpha by Greenwood *et al.*, 1966; Taverne, 1979), due in part to general body form and superficial similarity. It was shown by Patterson, Rosen (1977), however, that †Ichthyodectiformes was best interpreted as a stem-group Teleostei, phylogenetically separate from Osteoglossomorpha, and this has been supported in recent analyses of relationships among basal teleostean fishes (e.g., Arratia 1997, 1999, 2008).

Members of †Lycoperidae (Fig. 1) are a group of generalized, plesiomorphic osteoglossomorph fishes. According to Nelson *et al.* (2016), three genera are included in the family (†*Lycoptera*, †*Jiuquanichthys*, and †*Kuyangichthys*), although Zhang (2006) found the relationships of all of these basal genera to be largely unresolved along the stem of Osteoglossomorpha. The recently described monotypic genus †*Kokuraichthys* from the Early Cretaceous of Japan was in-



Fig. 1. †Lycoperidae. *Lycoptera davidi*, Early Cretaceous, China (UMA F10652; 110 mm SL). Scale bar = 2 cm.

terpreted to be either a member of †Lycopteriformes (co-extensive with †Lycopteridae) or Hiodontiformes (Yabumoto, 2013). A number of possible stem-group osteoglossomorphs have been identified, but not assigned to a specific family (including some taxa included within †Lycopteridae). Without exception, these fishes come from Early Cretaceous deposits in Asia, primarily China. Included among these

taxa are †*Jinanichthys*, †*Tongxinichthys* (Fig. 2a; see Zhang, Jin, 1999), and †*Xixiaichthys*.

The group †*Huashia* + †*Kuntulunia* (Fig. 2b) has been interpreted as both a stem-group (*e.g.*, unresolved node with Hiodontiformes and all other osteoglossomorphs; Zhang, 2006), sister to Notopteroidei + Osteoglossidae (Zhang, 1998), or as more closely related to Arapaiminae (*e.g.*, ba-

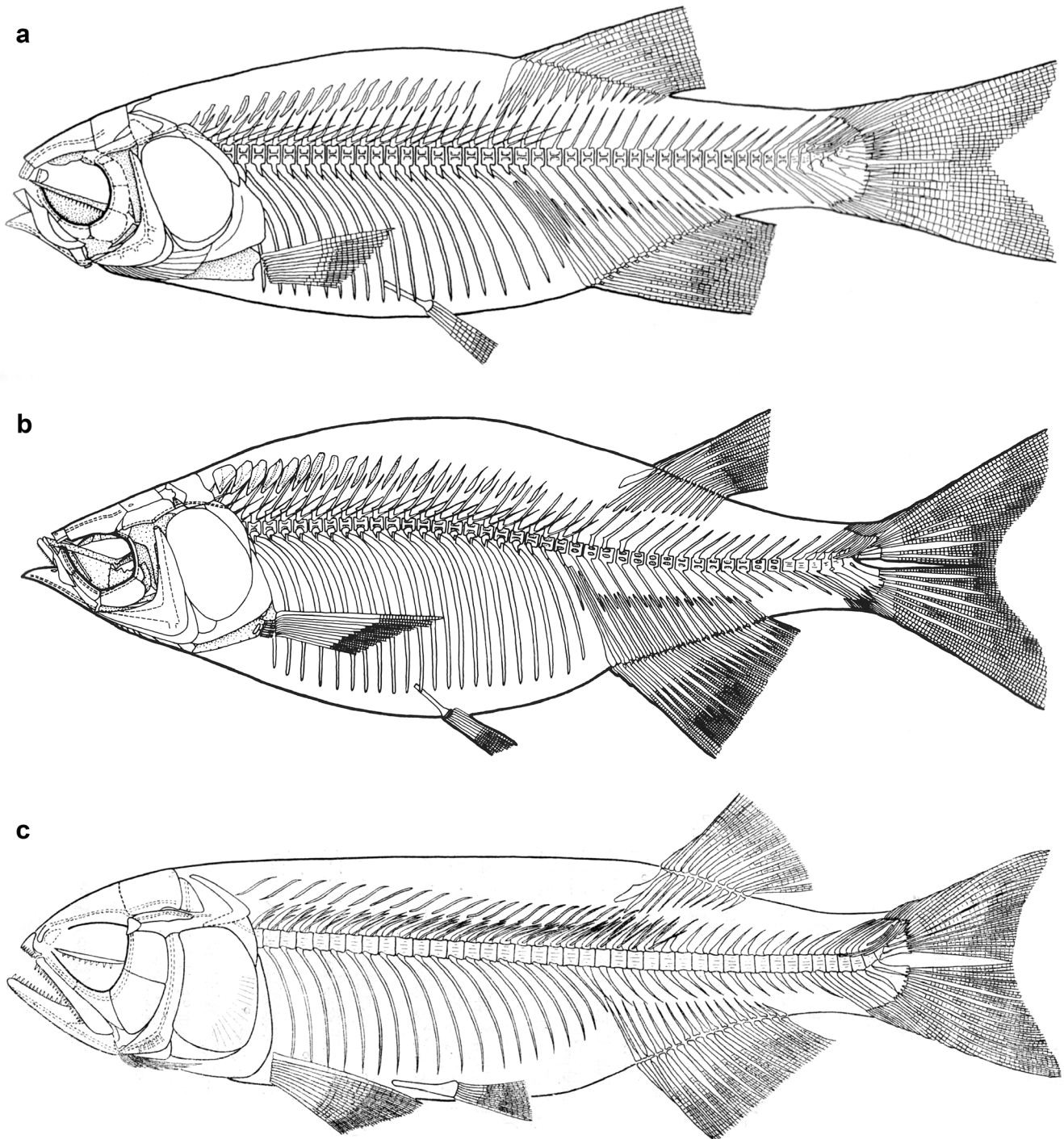


Fig. 2. Stem-group Osteoglossomorpha. Reconstructions of **a.** †*Tongxinichthys microdus* (modified from Zhang, Jin, 1999: fig. 2), **b.** †*Kuntulunia longipterus* (modified from Zhang, 1998: fig. 11), and **c.** †*Tanolepis ningjiagouensis* (modified from Jin, 1991: fig. 1; note that †*Tanolepis* has been suggested to be a synonym of †*Paralycoptera*).

sed in part on preopercular and opercular shape; Li, Wilson, 1999). Similarly, †*Paralycoptera*, from the Early Cretaceous (or possibly Late Jurassic as well; Tse *et al.*, 2015) of China, was initially described as a member of †Lycoperiformes (Chang, Chou, 1977); †*Tanolepis* (Fig. 2c; Jin, 1991) is either a synonym (Jin *et al.*, 1995; Xu, Chang, 2009) or sister-group (Li, Wilson, 1999) of †*Paralycoptera*. Ma, Sun (1988) and Jin *et al.* (1995) suggested that it possessed reticulate scales, indicating an affinity to Osteoglossidae (although concluding that †*Paralycoptera* was within crown Osteoglossidae, Zhang, 2006 noted differences in the details of the pattern of reticulation between the two groups). However, Xu, Chang (2009: figs. 8c,d) studied and illustrated very well preserved specimens that preserved the details of the scales, and show that these do not bear any furrows, but rather are large cycloid scales with fine circuli and a few radii (and are similar in overall form to the scales of *Pantodon*; Hilton, 2003: fig. 39d). Li, Wilson (1999) recovered it as sister to Osteoglossoidei (sharing similarities in the position and angle of the jaw and six hypurals), Zhang (2006) found it to be within crown-group Osteoglossidae (sister to Osteoglossinae + †Phareodontinae; supported only by homoplasies), and Xu, Chang (2009), who found this genus to be intercalated between Mormyroidea and all fossil and living Osteoglossidae (sharing with the latter the condition of having the entire post- and suborbital region of the palatoquadrate covered by the infraorbitals). Wilson, Murray (2008; also Murray *et al.*, 2010, 2018), in contrast, recovered †*Paralycoptera* + †*Tanolepis* as a stem group osteoglossomorph, just above the level of †*Lycoptera*. For details on the history of phylogenetic hypotheses for these and other stem-group osteoglossomorphs, including synapomorphies supporting the various hypotheses, the reader is referred to Shen (1996), Li, Wilson (1999), Zhang (2006), and Xu, Chang (2009). A full taxonomic and phylogenetic review, however, of many of these fishes, including those that were historically included in †Lycoperidae, is needed.

Hiodontidae. Hiodontidae (Fig. 3), which is regarded as the living sister group of all other extant Osteoglossomorpha (Taverne, 1979; Li, Wilson, 1996a; Hilton, 2003; Zhang, 2006; Wilson Murray, 2008), with one or two genera (*Hiodon* and †*Eohiodon*); the fossil taxa †*Yanbiania* and †*Jiaohichthys* from the Early Cretaceous of China and †*Plesiolycoptera* from the Mid Cretaceous of China are stem group Hiodontiformes. *Hiodon* comprises two extant species (*H. alosoides* and *H. tergisus*), both found exclusively in the freshwater rivers and lakes throughout much of North America east of the Rocky Mountains. These fishes have a generalized, laterally compressed body, with large eyes, a forked caudal fin, and a silvery body with cycloid scales (Hilton *et al.*, 2014). The parasphenoid and basihyal toothplate are armed with large, caniniform teeth that serve the so-called “parasphenoid-tongue bite apparatus” (Hilton, 2001). The osteology of *Hiodon* has been described by Taverne (1977) and Hilton (2002), with specific aspects of its

skeleton described by others (*e.g.*, caudal skeleton, Schultze, Arratia, 1988) due in part to its overall plesiomorphic morphology, which has led to its use as a representative basal teleost in broad based systematic analyses (see discussion and references by Hilton, 2002).

The three species of †*Eohiodon* from the Early Eocene of western North America have been regarded as close relatives of the extant genus *Hiodon* (Li *et al.*, 1997a; Hilton, Grande, 2008; Fig. 3b). Indeed, because of the absence of any synapomorphies distinguishing the species of †*Eohiodon* from those of *Hiodon*, Hilton, Grande (2008) regarded it as a synonym of *Hiodon*. The two extant species of *Hiodon* possess a post-pelvic bone, and this is considered a synapomorphy of the extant taxa (Hilton, 2003), although the condition in most fossil taxa, including †*H. consteniorum* and the species of †*Eohiodon*, is unknown (Hilton, 2003). Murray *et al.* (2010: fig. 10) illustrated a fragmentary bone that they interpreted as a postpelvic bone in †*Schuleichthys brachypteryx*, a species from the Early Cretaceous of China that was left as *incertae sedis* at the base of Osteoglossomorpha. These authors suggested that the presence of a postpelvic bone in †*Schuleichthys* was a character of a broader group and therefore resurrected the genus †*Eohiodon* (see also Murray *et al.*, 2018). However, we find the published photograph documenting the postpelvic bone in †*Schuleichthys* to be unconvincing, and maintain that until this element is clearly seen in taxa outside of the extant taxa, it should be considered to be a synapomorphy of these two extant taxa. Regardless, there has yet to be any synapomorphies identified that group the taxa previously included in the genus †*Eohiodon* (*i.e.*, all diagnostic characters cited for the genus, such as low vertebral and fin ray counts, are plesiomorphic, being similar to stem group Hiodontiformes and †Lycoperidae). We therefore support the interpretation that those taxa previously included in †*Eohiodon* should be regarded as stem group *Hiodon* (Hilton, Grande, 2008).

Notopteridae. The featherbacks, or Old World knife-fishes, of the family Notopteridae comprise ten species in four genera distributed in the freshwaters of south and southeast Asia (*Chitala*, six species; *Notopterus*, one species; Fig. 4) and Africa (*Papyrocranus*, two species; *Xenomystus*, one species; Fig. 5) (Kottelat, 2013). The taxonomy of this family was revised by Roberts (1992), who noted that more material is needed to be examined from across the ranges of *Notopterus* and *Xenomystus* to better investigate the monospecific nature of these two genera. A single whole body fossil taxon (†*Notopterus primaevus*, from the Tertiary of Sumatra; Sanders, 1934) is known, but is in need of preparation and redescription. †*Palaeonotopterus greenwoodi*, from the Early Cretaceous of Morocco, was initially described based on isolated braincase and fragmentary skull bones (Forey, 1997, Taverne, Maisey, 1999) as a member of Notopteridae based on the presence of a supraorbital branch of the otic sensory canal, although this character was since identified in mormyroids (Cavin, Forey, 2001). Cavin, Forey (2001) con-

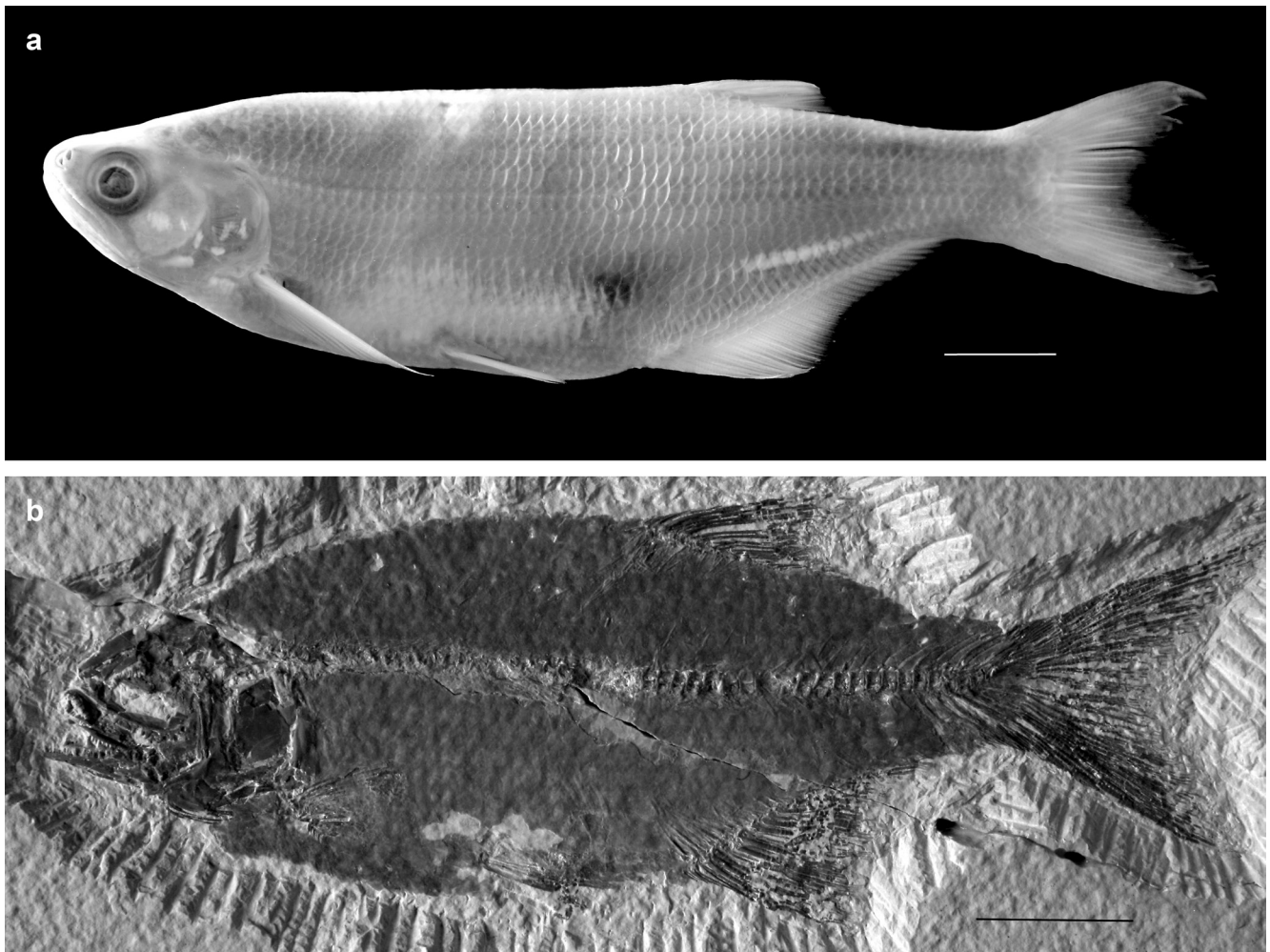


Fig. 3. Hiodontidae. **a.** *Hiodon alosoides* (VIMS 12099). **b.** †*Hiodon falcatus*, Eocene, Wyoming, USA (UMA F10651). Scale bars = 2 cm.

sidered †*Palaeonotopterus greenwoodi* to be either a stem notopterid or a stem mormyroid, and in subsequent phylogenetic analysis, it has been recovered as a stem group mormyroid (Hilton, 2003; Wilson, Murray, 2008). As noted by Cavin, Forey (2001), however, its anatomy is largely unknown and prevents confident phylogenetic interpretations.

All notopterids are extremely laterally compressed with an elongate anal fin that is confluent with the rounded caudal fin. The dorsal fin (absent in *Xenomystus*) has a short base but is tall and rounded. The body profile particularly that of *Chitala*, undergoes a dramatic ontogenetic change, in which there is a substantial dorsal concavity above the head in adult fishes (not evident in *Notopterus* or *Xenomystus*, and only slightly developed in *Papyrocranus*). All species have a series of small abdominal scutes formed by paired elements (Hilton, 2003: fig. 34). The species of *Xenomystus* and *Papyrocranus* are electroreceptive, whereas those of *Notopterus* and *Chitala* are not (Bradford, 1982).

Notopteridae is widely regarded as the sister group of Mormyroidea (= Mormyridae + Gymnarchidae) based on both morphological (Ridewood, 1904, 1905; Taverne, 1979;

Lauder, Liem, 1983; Li, Wilson, 1996a) and molecular data (Lavoué, Sullivan, 2004). Hilton's (2003) analysis resulted in a Notopteridae + Osteoglossidae clade, but he allowed that there were several characters that were not included in that analysis that supported the conventional grouping, as found in more recent phylogenetic analyses (Bonde, 2008; Wilson, Murray, 2008; Murray *et al.*, 2010, 2018).

Mormyridae. By far Mormyridae is the largest family of Osteoglossomorpha. It has about 21 genera and well over 200 species (Fricke *et al.*, 2018); the rate of new species descriptions in recent years suggests that there are far more to be discovered (*e.g.*, a new genus, *Cryptomyrus*, was described recently from Gabon, suggesting that there are significant gaps in our knowledge of mormyrid diversity; Sullivan *et al.*, 2016). All members of the family are found throughout Africa (except the Saharan, northern Maghreb, and southern Cape regions), and are particularly diverse in Central and West Africa (Stiassny *et al.*, 2007). The earliest fossil remains of the family, comprising fragmentary skull bones, teeth, and isolated vertebrae, are Middle Pliocene

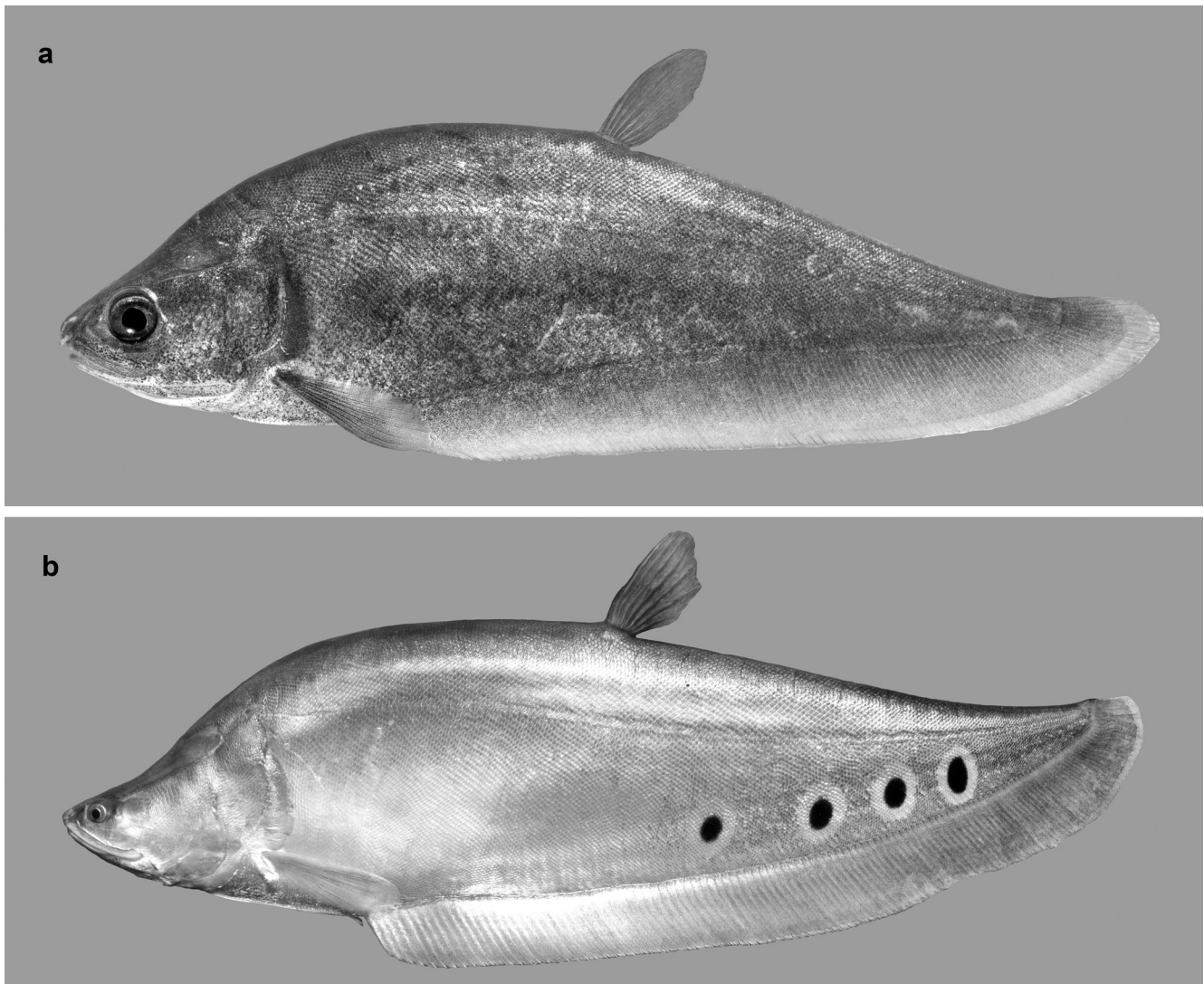


Fig. 4. Notopterinae. **a.** *Notopterus notopterus* (UF 237410; 167 mm SL). **b.** *Chitala ornata* (UF 237959; 498 mm SL). Photos by Z. Randall.

(Greenwood, 1972), although the family is very poorly represented in the fossil record. Hilton (2003) noted the irony of this, as this family is the most species rich in the extant fauna, but most other families have a much more temporally and taxonomically extensive fossil record. The diversity of the family, established in part by fast evolution of reproductive isolation caused by selection in mate recognition signals (*i.e.*, electric organ discharges), is pronounced and the family has been cited as the only example of a freshwater species flock in a riverine (*vs.* lacustrine) system (Sullivan *et al.*, 2002). All members of the family are weakly electric fishes, having both electroreceptors, and producing species-specific electric organ discharges for communication and localization purposes. There is great morphological diversity within this family in body form, but especially of their head shape, which ranges from blunt and rounded (*e.g.*, *Petrocephalus*, Fig. 6a; *Pollimyrus*), to elongate, with a long snout and jaws (*e.g.*, *Gnathonemus* and *Campylomormyrus*;

Figs. 6b,c). The cranial diversity of certain taxa within the family, such as *Campylomormyrus*, has been suggested to reflect adaptive radiation driven by variation in diet (Feulner *et al.*, 2007). Mormyridae (inclusive of Gymnarchidae; see below) all share an enlarged cerebellum, electric organs, electroreceptors, opercular bones covered by a thick fleshy flap, an intracranial diverticulum of the swim bladder, loss of the ventral hypohyal, absence of the basihyal and its toothplate, and features of the caudal skeleton (Boulenger, 1898; Taverne, 1972, 1979; Hilton, 2003).

The systematics of Mormyridae has not been investigated recently from a morphological perspective (see Future Research Needs, below). The most taxonomically rich data set to be analyzed to date is that of Sullivan *et al.* (2000), who investigated relationships among representatives of 18 genera and 41 species using mitochondrial (12S and 16S rRNAs, Cytochrome *b*) and nuclear (RAG2) loci. The results of this analysis are largely congruent with those of Taverne (1972)



Fig. 5. Xenomystinae. **a.** *Xenomystus nigri* (CU 91453). **b.** *Papyrocranus afer* (CU 97661). Scale bars = 2 cm.

at the higher taxonomical-levels, in that Gymnarchidae is its sister group, and the family can be divided into the Petrocephalinae (with only *Petrocephalus*) and Mormyrinae (all other genera). Within Mormyrinae, *Myomyrus macrops*, and *Mormyrops* spp. were recovered as successive sister groups to all other members of the subfamily. Notable results also included the non-monophyly of *Brienomyrus*, *Pollimyrus*, *Marcusenius*, and *Hippopotamyrus*. Based on this topology, the authors conclude that electrocytes with penetrating stalks is a derived conditions but they evolved early in the evolution of Mormyrinae; the electrocytes of *Gymnarchus* are stalkless (hypothesized to be the larval form of electrocytes found in Mormyridae) and those of *Petrocephalus* have non-penetrating stalks. There are several occurrences, presumably homoplastic, of reversal to the non-penetrating condition (e.g., within *Brienomyrus*, *Paramormyrops*, *Marcusenius*, and *Campylomormyrus*), although the taxon sampling in these genera was insufficient to draw firm conclusions of the number of reversals within Mormyrinae. Other previous phylogenetic studies, reviewed by Sullivan *et al.* (2000), include Agnèse, Bigorne (1992), Van der Bank, Kramer (1996), Alves-Gomes, Hopkins (1997), Alves-Gomes (1999), and Lavoué *et al.* (2000). Recent molecular phylogenetic studies of relationships of Mormyrinae include those

of Sullivan *et al.* (2016) and Levin, Golubtsov (2018), and provide further evidence that the taxonomy and phylogeny of Mormyridae is far from settled.

Gymnarchidae. A single species, *Gymnarchus niloticus*, is included in this family (Fig. 7), and is found distributed throughout tropical Africa from Senegal to Ethiopia in the Ghazal and Jebel systems, White Nile, and Nile River to Lake Nasser (Sudan) in northeast Africa, and in the Gambia, Senegal, Niger, Volta, Ouémé and Chad rivers of western Africa (Azeroual *et al.*, 2010). It has an elongate, cylindrical body with a broadly rounded head and a dorsal fin that runs most of the length of its body; anal, caudal, and pelvic fins are lacking. It reaches 1.67 m in length and 18.5 kg (Bigorne, 1990). Its osteology has been described by Taverne (1972), and aspects of its skeleton are illustrated by Benveniste (1994). Fossil remains identified as *Gymnarchus* are known from several localities throughout central and northern Africa (e.g., Pliocene deposits of Chad, Otero *et al.*, 2009), including the Late Eocene Birket Qarun Formation in Egypt (Murray *et al.*, 2010), which is the oldest record of the family.

Gymnarchidae is broadly considered to be the sister group of Mormyridae (Taverne, 1979, 1998; Bonde, 2008; classified as a subfamily of Mormyridae in some classifica-

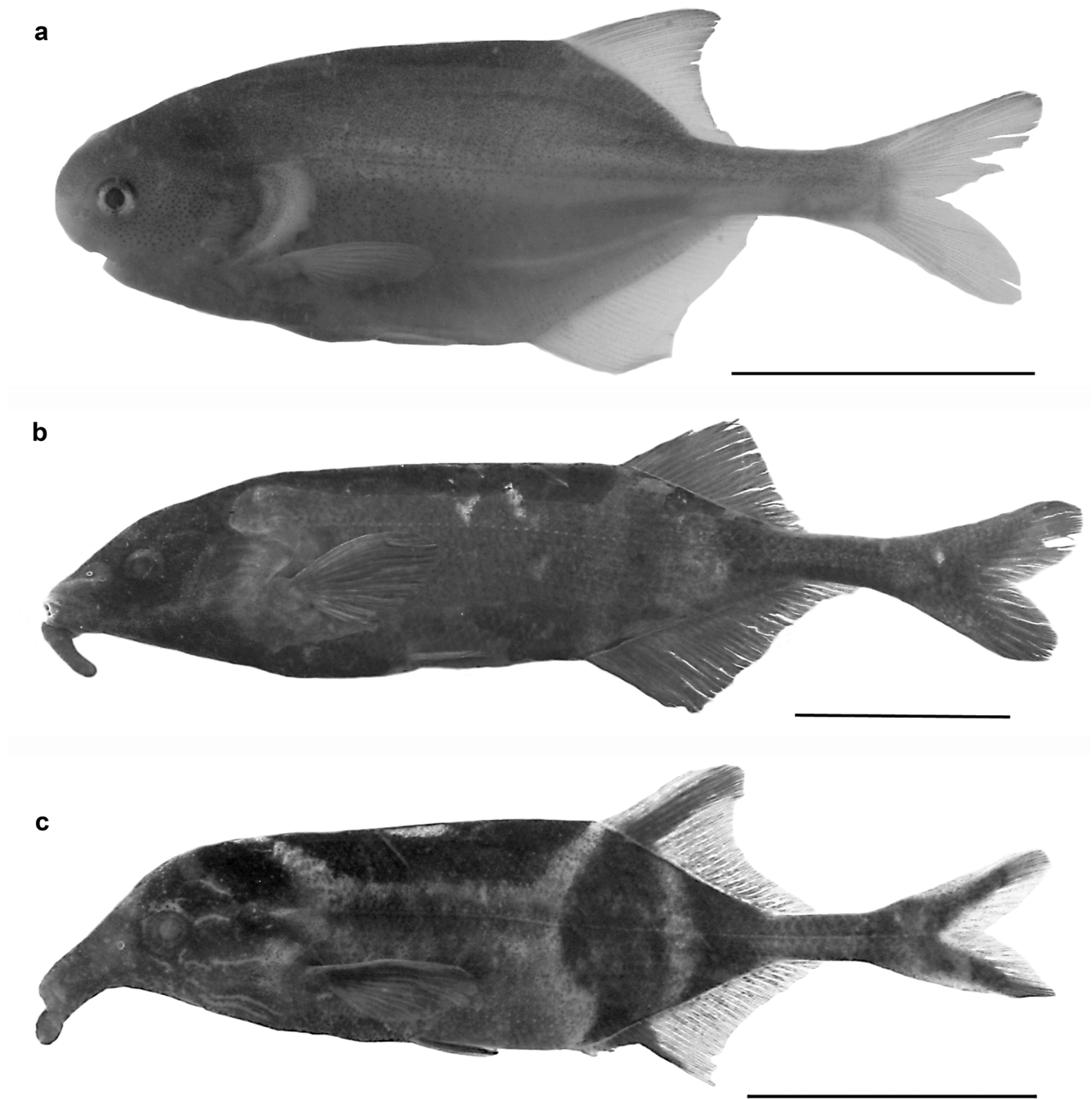


Fig. 6. Mormyridae. **a.** *Petrocephalus bovei* (CU 94594). **b.** *Gnathonemus petersii* (CU 91805). **c.** *Campylomormyrus tamandua* (CU 91801). Scale bars = 2 cm.

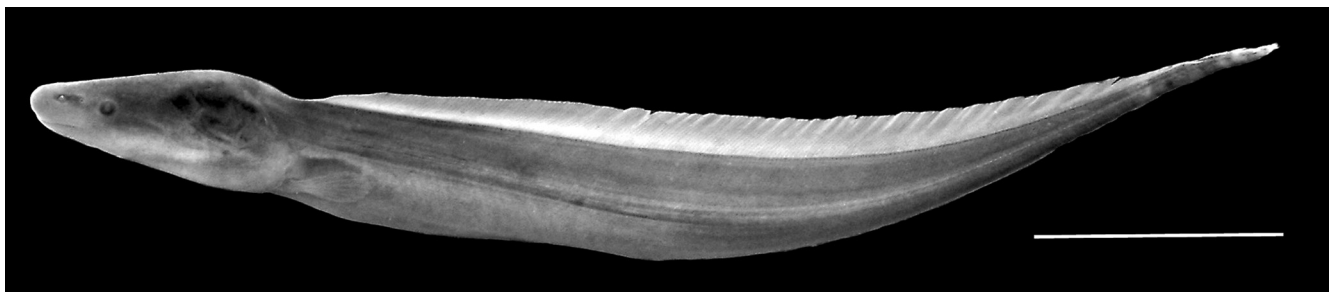


Fig. 7. Gymnarchidae. *Gymnarchus niloticus* (VIMS 22064). Scale bar = 2 cm.

tions, e.g., Greenwood, 1971; Lauder, Liem, 1983), although in most analyses and classifications it is not explicitly coded for, being subsumed into the supraspecific terminal group Mormyroidea (e.g., Li, Wilson, 1996a; Wilson, Murray 2008) or left uncoded (e.g., Hilton, 2003; Zhang, 2006). Although she did not designate it as a monotypic family, Benveniste (1994) recovered *Gymnarchus* as the sister-group of *Petrocephalus* + Mormyriinae. In this study, several unambiguous autapomorphies were identified distinguishing *Gymnarchus* from other mormyroids (absence of a supraoccipital crest, absence of basibranchial toothplates, absence of the first pharyngobranchial, absence of supraneurals, absence of the caudal fin, a dorsal fin with more than 100 fin rays, absence of an anal fin, a small posttemporal bone formed primarily by the ventral limb, the condition of having the *m. posterior intermandibularis* absent and the *m. interhyoideus* present); *Gymnarchus* also has an edentulous parasphenoid, although this is homoplastically found within Osteoglossomorpha in *Heterotis* and some mormyrids (Benveniste, 1994).

Osteoglossidae. Outside of Mormyridae, Osteoglossidae is the most diverse family of Osteoglossomorpha, with four extant genera, classified in two subfamilies (Osteoglossinae, including *Osteoglossum* from South America and *Scleropages* from Southeast Asia and Australia, and Arapaiminae (= Heterotidinae) including *Heterotis* from Africa and *Arapaima* from South America). In all osteoglossids, the large, cycloid scales are reticulate, with a network of furrows across the entire surface of the scales (mormyroids have reticulate furrows on just the posterior field of the scale, with well-developed radii on the anterior field; see Hilton, 2003: fig. 39). These furrows define so-called squamules, which have been recovered in the fossil record (Gayet, Meunier, 1983; Taverne *et al.*, 2007). The crown-group osteoglossids have elongate, posteriorly positioned dorsal and anal fins (these are longer in *Osteoglossum* than in *Scleropages*), a short caudal peduncle, and a large rounded caudal fin.

Osteoglossinae (Fig. 8) have laterally compressed bodies and large, dorsally directed mouths with elongate lower jaws. Two barbels extend from the anterior tip of the lower jaws, and in life these are held horizontally in the water column. Most remarkably are the large pectoral fins that have a long, very robust leading pectoral fin ray. These fin rays support the strong pectoral fins that contribute to the ability of these fishes to float at the surface while hunting prey and leap from the water to capture terrestrial invertebrate and vertebrate prey items above the water line (Goulding, 1980; Verba *et al.*, 2018). Adults of the two species of *Osteoglossum* are silver (*O. bicirrhosum*) or greyish-steel (*O. ferreirai*) colored, the yolk-sac larvae of *O. bicirrhosum* are silver whereas those of *O. ferreirai*, which is restricted to the Rio Negro, are black with a distinct yellow lateral stripe on the body. The species of *Osteoglossum* are largely allopatric: *O. bicirrhosum* is found throughout the Amazon and the Branco river basins, and *O. ferreirai* is found in the Rio

Negro basin, including the Branco, and the Orinoco River, which was likely the result of an introduction (Escobar *et al.*, 2013). Using a ~1,000 base-pair fragment of the mitochondrial genome, Escobar *et al.* (2013) calculated a genetic distance of 8.9% between the two species. *Scleropages* comprises four species, two from Southeast Asia (*S. formosus* from Vietnam, Cambodia, Thailand, the Malay Peninsula, Sumatra, and Borneo, and *S. inscriptus* from Myanmar) and two from Australia (*S. jardinii* from the coastal river systems of northern Australia and Papua New Guinea, and *S. leichardti* from the Fitzroy River basin). Roberts (2012) suggested the subgenus name *Delsmania* Fowler, 1933 could usefully be applied to the group containing *S. formosus* and *S. inscriptus*, with the two Australian species being in the subgenus *Scleropages*. The four species of *Scleropages* have dramatic coloration and, at least in the case of *S. inscriptus*, patterning. Color variants of *S. formosus* have been suggested to be distinct species (Pouyaud *et al.*, 2003), although these are not regarded as valid (Kottelat, Widjanarti, 2005; Roberts, 2012). A fossil species of *Scleropages*, †*S. sinensis*, has been recently described from the Early Eocene Xiwanpu and Yangxi formations of China (Zhang, Wilson, 2017). Several additional fossil taxa have been interpreted as being close to Osteoglossinae, if not within the subfamily itself, including †*Opsithrissops*, †*Brychaetus*, †*Foreyichthys*, †*Heterosteoglossum* (see Taverne, 1998; Bonde, 2008; and Forey, Hilton, 2010 for discussion of these and other fossil osteoglossid taxa). Although it bears an elongate lower jaw similar to that of osteoglossids, †*Furichthys*, from the Early Eocene of Denmark, has been interpreted as stem-group Osteoglossi (= Osteoglossiformes + Mormyriiformes; Bonde, 2008).

Arapaiminae comprises two genera of extant fishes (*Arapaima* and *Heterotis*; Fig. 9) and putatively several fossil taxa, including †*Joffrichthys* from the Paleocene of Canada (Li, Wilson, 1996b), †*Trissopterus*, from the Eocene of Italy, and †*Sinoglossus* from the Eocene of China (although see Murray *et al.*, 2018, who found †*Joffrichthys* to be a potential stem osteoglossiform). *Arapaima*, because of the unique configuration of its occipital region (Hilton *et al.*, 2007), has been identified in the fossil record based on isolated basioccipital/vertebral elements (Lundberg, Chernoff, 1992; Gayet, Meunier, 1998). *Arapaima* has long been considered to be a widespread monotypic genus, with only *A. gigas* found throughout the Amazon basin. Stewart (2013a,b) argued that four nominal species and a new species should be recognized (*A. arapaima*, *A. agassizi*, *A. mapae*, *A. gigas*, and *A. leptosoma*). Stewart (2013a) further suggested that *A. agassizi* had no known specimens and had not been collected for 190 years, and that *A. mapae* and *A. gigas* were only known from their holotypes. Several studies have found moderate to low population genetic structure across the range of the genus at various scales (Ararape *et al.*, 2013; Watson *et al.*, 2013). Most range-wide structure appears to be associated with distance between populations (Hrbek *et al.*, 2005), and low genetic diversity within smaller portions of its range is sugges-

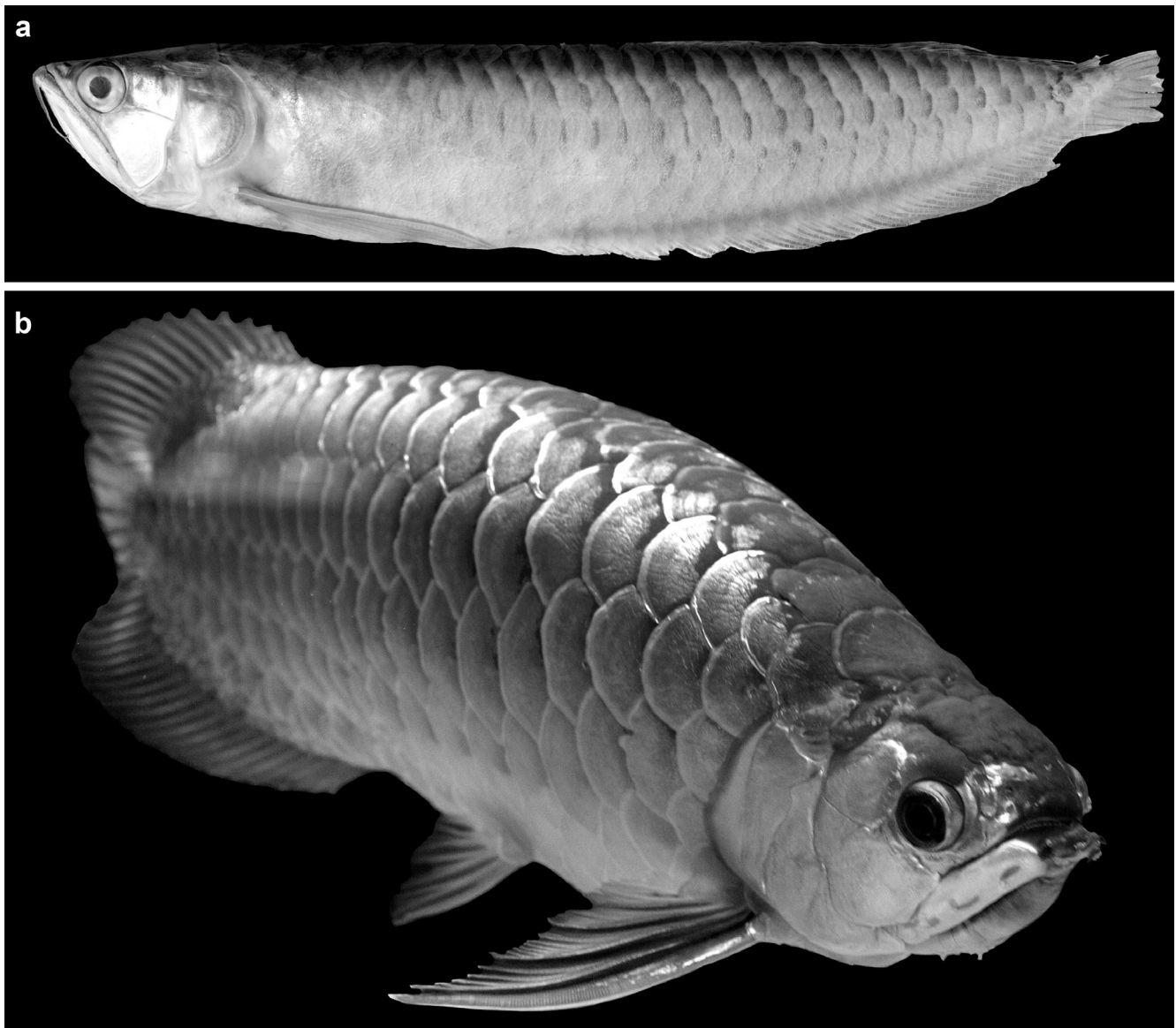


Fig. 8. Osteoglossinae. **a.** *Osteoglossum bicirrhosum* (UF 189007; 260 mm SL; photo by Z. Randall). **b.** *Scleropages formosus* (aquarium specimen; photo by Z. Randall).

tive of overfishing (e.g., Araguaia-Tocantins basin; Vitorino *et al.*, 2017). *Heterotis niloticus* is distributed throughout the Nilo-Sudanese region of Africa from Ethiopia to Senegal, the Chad basin, and Lake Turkana; it has been widely introduced in central and western Africa and is regionally extinct in the upper Egyptian Nile (Akinyi *et al.*, 2010). In contrast to *Arapaima*, there is genetic structure of *Heterotis*, even within relatively small portions of their range (e.g., Hurtado *et al.*, 2013, found significant genetic differentiation between three river basins in Benin). *Arapaima* and *Heterotis* are broadly regarded as sister taxa, supported by genetics and several morphological characters (enlarged first infraorbital bone, divided first infrapharyngobranchial, and having the angular, articular, and retroarticular all unfused in the adult [otherwise seen only in †*Phareodus*]; Hilton, 2003).

As a taxonomic aside, Taverne (1979) named two sub-

families of Osteoglossidae: †Phareodontinae (including †*Phareodus*, †*Brychaetus*, †*Musperia*, and †*Phareoides*) and Osteoglossinae (including *Osteoglossum* and *Scleropages*), with Pantodontidae (only *Pantodon*) and Arapaimidae as separate families, and the latter containing the subfamilies Heterotinae (= *Heterotis* + †*Paradercetus*) and Arapaiminae (= *Arapaima*). Two family group names for the clade including *Arapaima* and *Heterotis* have been used in the literature, Arapaimini Bonaparte, 1846 and Heterotidae Cope, 1871. Although the former has priority, the latter is in broad current usage, as Heterotidinae (e.g., Nelson, 1994, 2006; Li, Wilson, 1996a; Hilton, 2003; Nelson *et al.*, 2016). However, the ICZN's (1999) criteria for reversal of precedence (Article 23.9) are not satisfied, as both family-group names have been used since 1899, and indeed Arapaimidae is also used in current literature (e.g., Taverne, 1998; Bonde,



Fig. 9. Arapaiminae. **a.** *Arapaima* sp. (VIMS 38993; 120 mm SL). **b.** *Heterotis niloticus* (CU 95903); Scale bar = 2 cm.

2008; Akinyi *et al.*, 2010). Therefore, the principle of priority should prevail, and Arapaiminae is the correct name for this family-group taxon (van der Laan *et al.*, 2014).

The genus-level diversity among the extant Osteoglossidae is dwarfed by the number of fossil genera included in or allied closely to the family (Forey, Hilton, 2010). Some of these taxa are *insertae sedis*, but several can be referred to the subfamily †Phareodontinae (Fig. 10), which was erected by Taverne (1979) to encompass †*Phareodus* (Eocene, North America, Australia, including †*Phareoides*), †*Brychaetus*, (Eocene, Europe, Africa, south Asia, and possibly North America), and †*Musperia* (Eocene, Sumatra). To this group can be added †*Cretophareodus*, †*Taverneichthys*, and †*Ridewoodichthys* (*e.g.*, see Kumar *et al.*, 2005; Taverne, 2009a,b; Taverne *et al.*, 2009; Forey, Hilton, 2010). Other taxa that are referable to the subfamily, or otherwise near its base (*e.g.*, interpreted to branch off from the stem of the family, or crownward from the phareodontines) include †*Brychaetoides*, †*Phareodusichthys*, †*Monopteros*, †*Xosteoglossid*, †*Magnigena*, and several unnamed taxa (Bonde, 2008; Forey, Hilton, 2010). Two Eocene osteoglossomorphs from Africa, †*Singida* (Fig. 11) and †*Chauliopareion*, are frequently considered to be related to Osteoglossidae, primarily either as stem-groups (Murray, Wilson, 2005; Xu, Chang, 2009; Murray *et al.*, 2018), or as sister-group to *Pantodon* (Hilton, 2003), although other positions have been supported (*e.g.*, stem Osteoglossine, Zhang, 2006; stem Osteoglossi, Bonde, 2008). †*Chanopsis* (Aptian, Democratic Republic of the Congo) has also been considered to be an osteoglossid (Bonde, 1996; Taverne, 1998), although Forey, Hilton (2010) questioned this assessment.

A remarkable aspect of the fossil record of Osteoglos-

sidae is that several forms are known from undisputedly marine deposits (Taverne, 1998; Bonde, 1996, 2008; Forey, Hilton, 2010). This is remarkable because all extant osteoglossomorphs are entirely freshwater forms, and their distribution has been held as a text-book example of vicariance biogeography. However, the occurrence of marine fossil taxa suggests that at least portions of the evolutionary history of Osteoglossomorpha took place in the marine realm (Taverne, 1998; Bonde, 2008; Forey, Hilton, 2010). Bonde (2008) in fact concluded a marine origin of Osteoglossomorpha, with two or three freshwater invasions, although as many as nine possible invasions into marine habitats was offered as an alternative hypothesis [this latter hypothesis was regrettably miscited as Bonde's primary conclusion by Forey, Hilton, 2010]]. Among the marine forms are †*Magnigena* (Paleocene, Saudi Arabia), †*Brychaetus* (Eocene, Europe, Africa, south Asia, and possibly North America), †*Heterosteoglossum*, †*Furichthys*, †*Xosteoglossid*, †*Brychaetoides*, and an unnamed osteoglossiform (Early Eocene, Denmark), †*Monopteros*, †*Thrissopterus*, and †*Foreyichthys* (Eocene, Monte Bolca, Italy), as well as several unnamed taxa (*e.g.*, a particularly osteoglossid-like partial braincase from the Eocene London Clay; Forey, Hilton, 2010).

Pantodontidae. A single species comprising genetically differentiated allopatric populations, *Pantodon buchholzi*, the African butterfly fish, is classified in the family Pantodontidae (Nelson *et al.*, 2016), although it is frequently included within the family Osteoglossidae (*e.g.*, Taverne, 1979; Li, Wilson, 1996a; Hilton, 2003). This is a relatively small fish, with a strongly upturned mouth, flattened head,

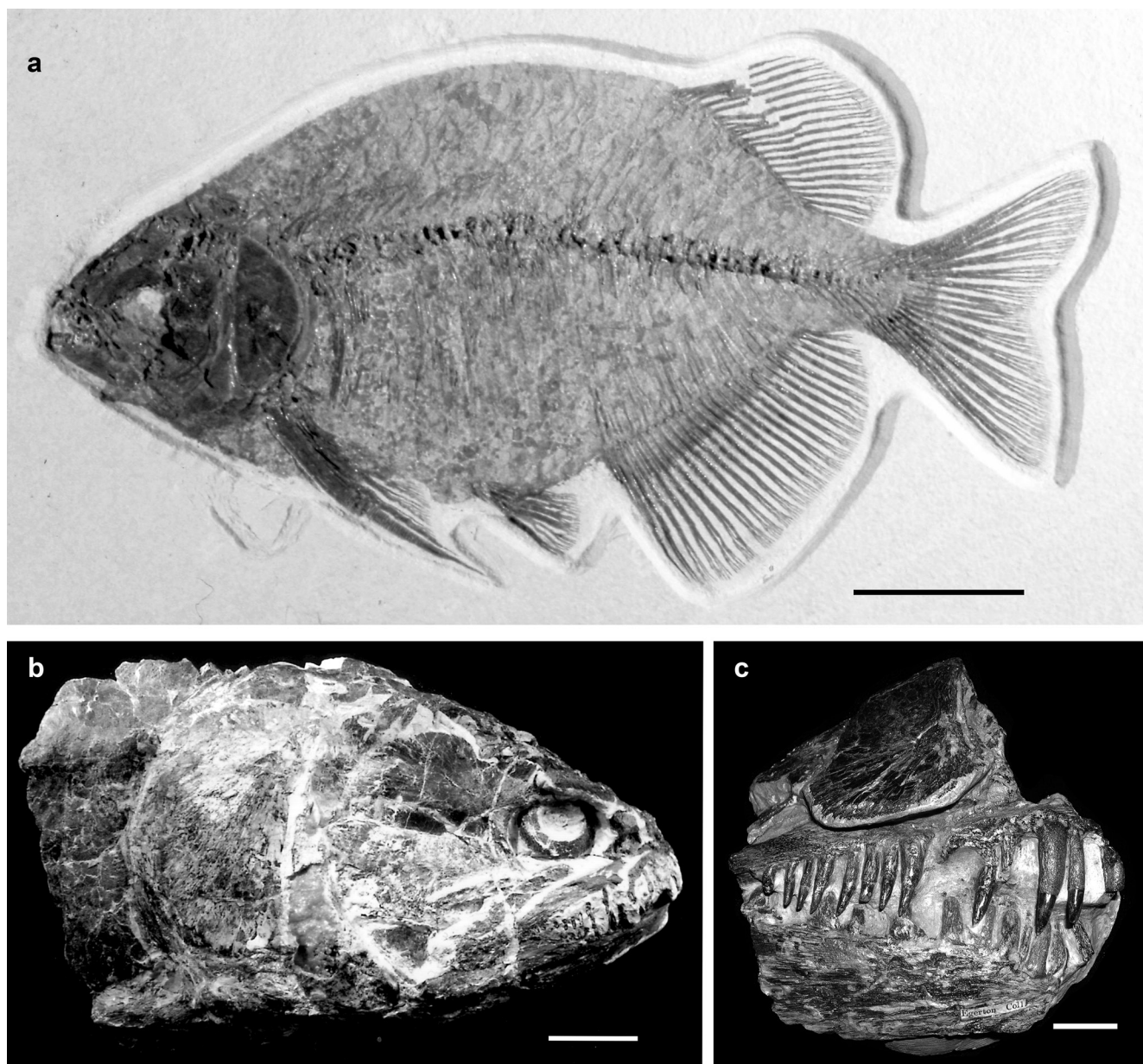


Fig. 10. †Phareodontinae. **a.** †*Phareodus testis*, Eocene, Wyoming, USA. (UMA F11332; scale bar = 2 cm). **b.** †*Brychaetus muelleri* (BMNH P3898; holotype; scale bar = 5 cm) and **c.** †*Brychaetus muelleri* (BMNH 1748; scale bar = 2 cm), Eocene, England.

short dorsal and anal fins positioned far back on its body, a rounded caudal fin, large wing-like pectoral fins, and pelvic fins with an elongate fin rays (Fig. 12). The head and pectoral fin has a superficial similarity to that of osteoglossines. Despite its similarity in some respects (e.g., infraorbital bones) to Osteoglossinae, Nelson (1969: 25) observed that “the systematic position of *Pantodon* consequently is obscure.” This remains to be the case (see below). Part of the issue with the systematic placement of *Pantodon* is that it is a highly derived taxon, with numerous autapomorphies as well as significant character conflict with other osteoglossomorphs. For instance, the absence of a symplectic is shared with Mormyroidea, whereas the absence of an autopalatine

is shared with Osteoglossidae (Moritz, Britz, 2005). However, unlike those of osteoglossid conditions, the scales of *Pantodon* lack reticulations (e.g., Hilton, 2003: fig. 39) and *Pantodon* has two gonads (*versus* one) (Britz, 2004).

The skeletal anatomy of *Pantodon* has been described and illustrated by Taverne (1978), and portions of its skeleton was illustrated and described by Hilton (2003) and Hilton, Britz (2010). In a study of its development, Moritz, Britz (2005) showed that the single dermal bone of the palatoquadrate in the adult of *Pantodon* is an ontogenetic fusion of the dermopalatine and ectopterygoid. They further conclude that the basiptyerygoid articulation found in *Pantodon* and Osteoglossidae is structurally homologous to that found

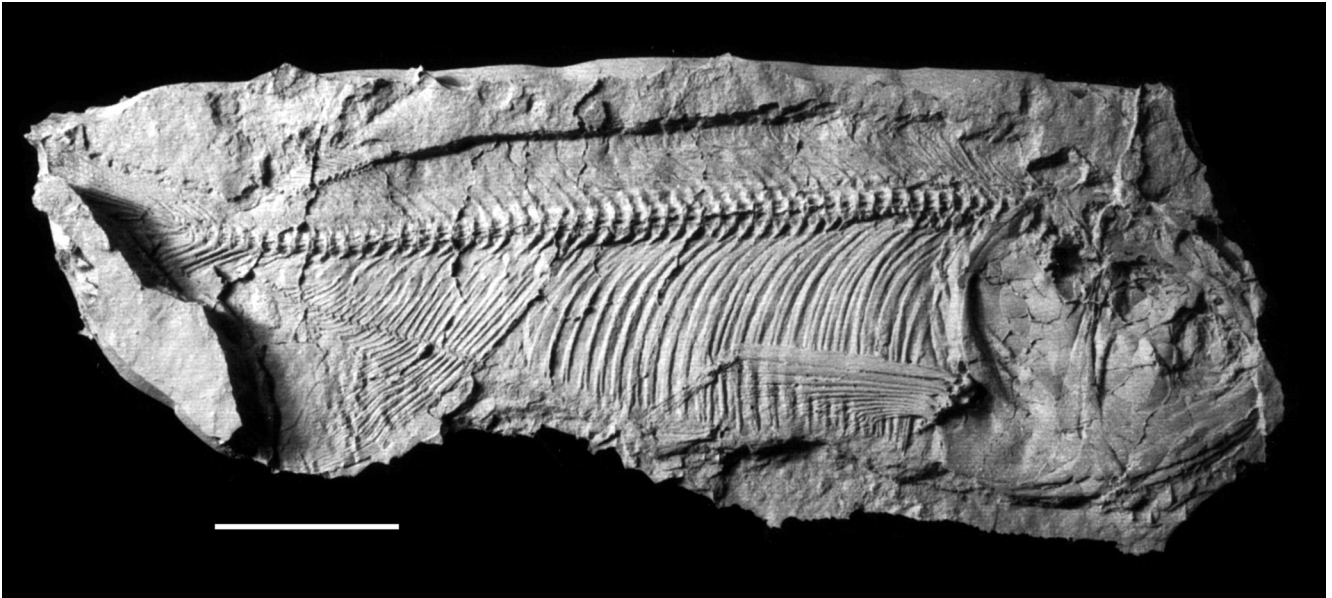


Fig. 11. †*Singida jacksonoides* (BMNH P63333, latex peel of holotype). Scale bar = 2 cm.



Fig. 12. Pantodontidae. *Pantodon buchholzi* (CU 87447). Scale bar = 2 cm.

in non-teleosts and a basal clupeomorph, and therefore is a character at a broader level of phylogeny than uniting a subgroup of osteoglossomorphs (e.g., Greenwood *et al.*, 1966; Lauder, Liem, 1983; Arratia, Schultze, 1991).

Systematic Biology of Osteoglossomorpha

Morphological systematics of osteoglossomorph fishes.

Although there is broad agreement that there are three primary groups at the base of crown-group Teleostei (*i.e.*, Osteoglossomorpha, Elopomorpha and Clupeocephala), their interrelationships have been debated. The two primary hypotheses based on morphological data are alternatively that Osteoglossomorpha or Elopomorpha holds the basal position, with the other resolved as sister group to Clupeocephala. The hypothesis that Osteoglossomorpha is the sister group of all other living Teleostei is supported by elopomorphs and clu-

peocephalans having a reduced number of uroneurals that extend anteriorly beyond the second ural centrum (two versus three or four, as found in *Hiodon*), and in having epipleural bones throughout the abdominal region (Patterson (1977; also Patterson, Rosen 1977). In contrast, basal members of Elopomorpha retain a broad suite of plesiomorphies (e.g., a gular plate, a suprpharyngobranchial bone, mandibular sensory canal that open posteriorly or medially, and the antorbital bone carry the infraorbital canal) such that the alternate state of these characters resolve as synapomorphies for Osteoglossomorpha + Clupeocephala (e.g., Arratia, 1991, 1997, 1999; Li, Wilson, 1996a; Shen, 1996).

Taverne's (1979) analysis of osteoglossomorph relationships set the stage for all subsequent studies of the interrelationships of the group. The topology of extant taxa reflects that which is recovered in most other studies (with

the exception of the position of *Pantodon* in molecular analyses; see below), with Hiodontidae as sister group of all other osteoglossomorphs, Notopteridae and Mormyroidea as sister groups, and three lineages within Osteoglossidae (*Osteoglossum* + *Scleropages*, *Arapaima* + *Heterotis*, and *Pantodon*). Notable in this analysis was the inclusion of many fossil taxa, particularly those from Africa and Monte Bolca (Italy), which have been rarely included in more recent analyses (e.g., †*Chetungichthys*, †*Kipalaichthys*, †*Paradercetis*, †*Foreyichthys*, †*Opsithrissops*, †*Monopterios*, and †*Musperia*). Some of these are represented by few, fragmentary or poorly preserved specimens, and their systematic affinities have been discussed by other authors. Taverne (1998; Fig. 13a) revisited the systematics of Osteoglossomorpha following his redescription of several osteoglossomorph taxa from Monte Bolca. This new analysis defined 333 characters (some of which appear at multiple times or as reversals at different levels of phylogeny), and expanded the taxon sampling, in part by evaluating individual species (e.g., species of †*Phareodus*). Unsurprisingly, the position of many of the fossil taxa moved around compared to his 1979 analysis (which had left several relationships ambiguous), including dissolution of †Phareodontinae, the members of which spread out along the backbone of the tree within Osteoglossiformes. In the context of analyzing the systematic affinities of new marine fossil osteoglossomorphs from the Eocene of Denmark, Bonde (2008) critically examined the phylogeny of Osteoglossomorpha as a whole. The discussion, which weighed character data from Taverne (1998) and Hilton (2003), with the resulting classification (Fig. 13b) largely consistent with the phylogeny proposed by Taverne (1998), with differences among some fossil taxa (e.g., †*Foreyichthys*).

In a series of studies on fossil and living osteoglossomorphs, Li and colleagues (Li, Wilson, 1996a,b, 1999; Li *et al.*, 1997a,b; Fig. 14a) made the first attempts to incorporate data for osteoglossomorphs into a global, computer-assisted parsimony analysis, and this data matrix has served as the basis for all subsequent study of the group. In particular, these studies included data for an expanded taxon sampling, which included several of the fossil taxa from the Cretaceous of China (e.g., †*Tongxinichthys*, †*Yanbiania*, †*Plesioleptocheilus*, †*Paraleptocheilus*, †*Kuntulumia*, etc.). The basic framework of the topology is similar to that presented by Taverne (1979) for the extant taxa. Hilton (2003; Fig. 14b) reevaluated the characters used in Li's analyses and discovered errors of coding and criticized aspects of their character definition. In Hilton's (2003) results, the major difference was in the position of Notopteridae (as sister group of Osteoglossidae + Mormyroidea, instead of sister to Mormyroidea). Although Osteoglossidae + Mormyroidea was supported by several uniquely derived characters (e.g., extrascapular reduced and irregularly shaped, fifteen or fewer branched caudal fin rays, and one neural spine on ural centrum 1), several characters that support Notopteridae + Mormyroidea could not be fully evaluated in that study. Zhang (2006) and Xu, Chang (2009)

further examined the systematic relationships of Osteoglossomorpha, based in part on a new study of several of the early osteoglossomorphs from the Early Cretaceous of China. Both are consistent with relationships among extant taxa, with the exception of the position of *Pantodon*, which Zhang (2006) found to be the sister group of Osteoglossinae (*vs.* sister to Osteoglossidae).

Wilson, Murray (2008) also reviewed the relationships within Osteoglossomorpha, accepting some of Hilton's (2003) characters and interpretations, and rejecting others to return to Li *et al.* (1997b; the most recent of data sets, despite publication dates). The resulting topology again, provided consistent results regarding the relationships of extant taxa (including return of the traditional Notopteridae + Mormyroidea clade, contra the results of Hilton, 2003). This data matrix has been expanded by coding of newly described fossil taxa (e.g., †*Chauliopareion*, †*Wilsonichthys*, †*Shuleichthys*, †*Lopadichthys*), and the most recent iteration appears in Murray *et al.* (2018; Fig. 14). That study described a new species of †*Joffrichthys* (†*J. tanyourus*), a new genus and species (†*Lopadichthys colwellae*) and reviewed the fossil record of osteoglossomorphs in North America. Notable among its results is the exclusion of †*Joffrichthys* from the Osteoglossidae. The authors also convincingly justified removal of †*Ostariostoma wilseyi*, a monotypic genus from the Late Cretaceous or Early Paleocene of Montana, from Osteoglossomorpha, where it had been assigned since Grande, Cavender's (1991) redescription. †*Ostariostoma* has long been regarded as a problematic taxon, of unstable relationships, and Murray *et al.* (2018) suggest that it might be allied to Gonorynchiformes, citing similarities of the vertebral column of these fishes. A further result of this study is the demonstration of just how sensitive the data matrix is to changes in coding, as with both changes in taxon sampling (e.g., expansion of outgroups to include *Amia* and taxa from Clupeomorpha, and removal of †*Ostariostoma*) and slight changes to homology assessment (e.g., identification of epurals and uroneurals in fossil taxa) and the resulting coding changes, produce very different phylogenies, including the non-monophyly of Osteoglossomorpha. This suggests that many of the nodes are weakly supported and/or that many taxa contain substantial suites of conflicting characters.

Molecular systematics of osteoglossomorph fishes.

The molecular systematics of osteoglossomorph fishes have focused primarily on three main questions relative to its monophyly, its phylogenetic position within Teleostei, and the inter-familial relationships within the order Osteoglossiformes (*i.e.*, Osteoglossomorpha excluding the order Hiodontiformes). In addition to these higher-taxonomic level studies, several molecular studies have inferred the phylogeny of each osteoglossomorph family, often to examine either the evolution of some of their most remarkable traits or their geographical distribution or their evolutionary processes. The molecular systematics of Osteoglossomorpha is slowly

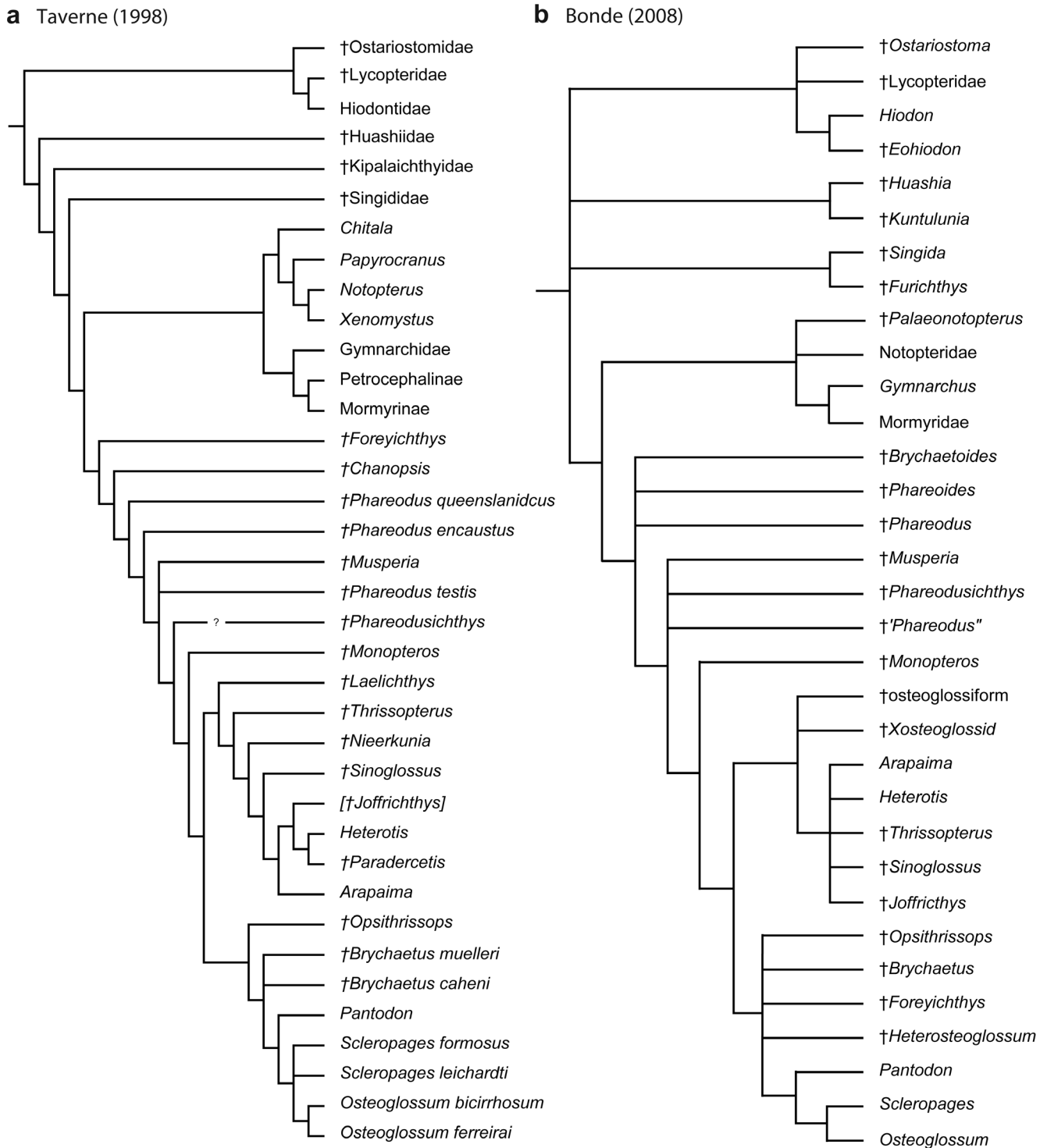
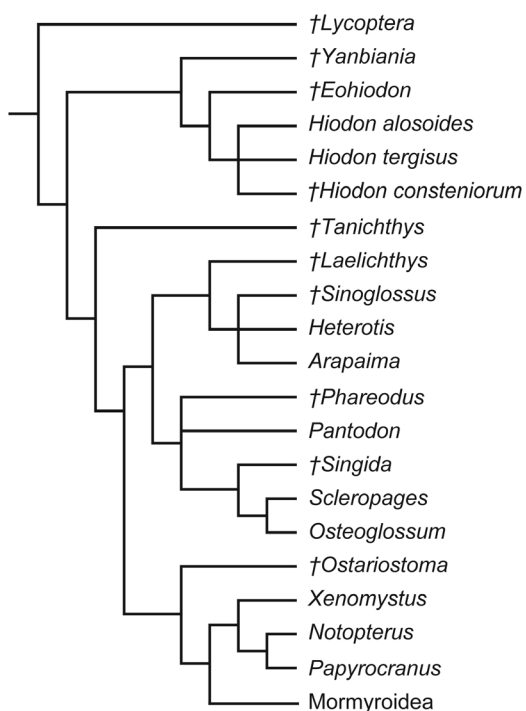


Fig. 13. Morphological systematics of Osteoglossomorpha. Phylogenies redrawn from **a.** Taverne (1998) and **b.** inferred phylogeny based on classification presented by Bonde (2008).

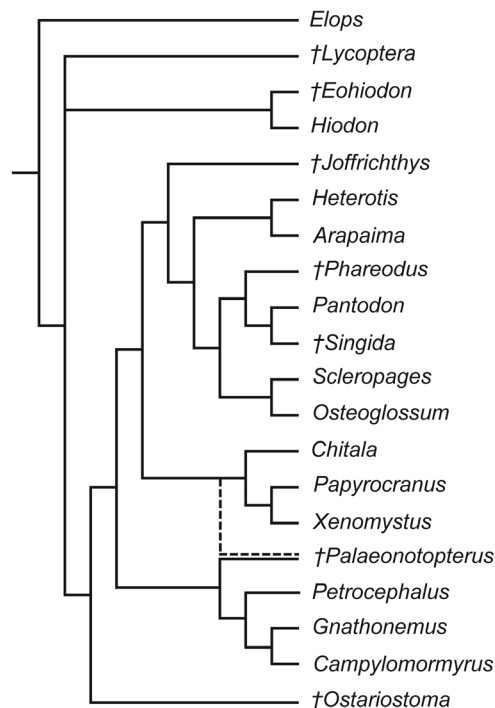
entering in a new area, the “genomic area”, thanks to the development of molecular biology technology making it possible to sequence complete genomes at a reasonable cost and the progresses in computer sciences making possible to compare such large genomic data. In this section, we review these aspects of the systematics of Osteoglossomorpha.

Monophyly of Osteoglossomorpha. The monophyly of living Osteoglossomorpha is strongly supported by several morphological synapomorphies (see above), and this hypothesis therefore represented a good test to evaluate the value of molecules in systematics of Osteoglossomorpha. Only few molecular studies comprehensively tested the monophyly

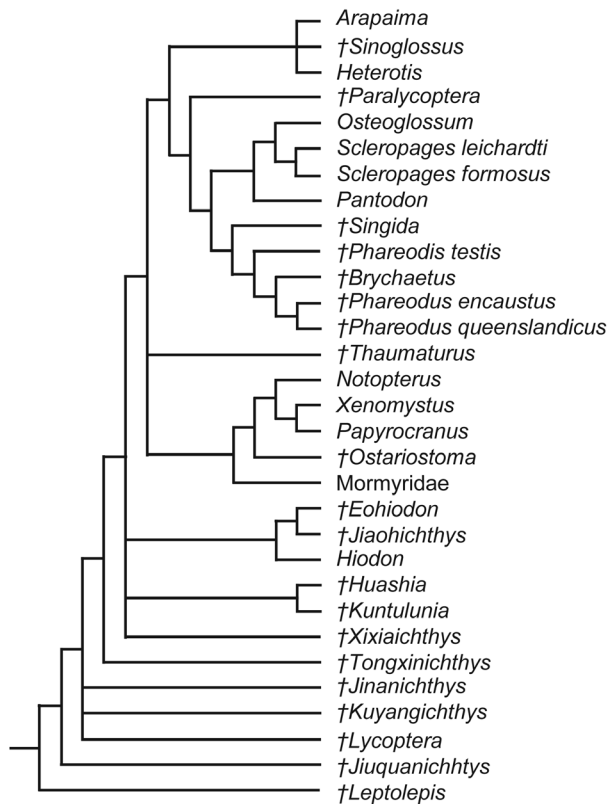
a Li & Wilson (1996a)



b Hilton (2003)



c Zhang (2006)



d Murray et al. (2018)

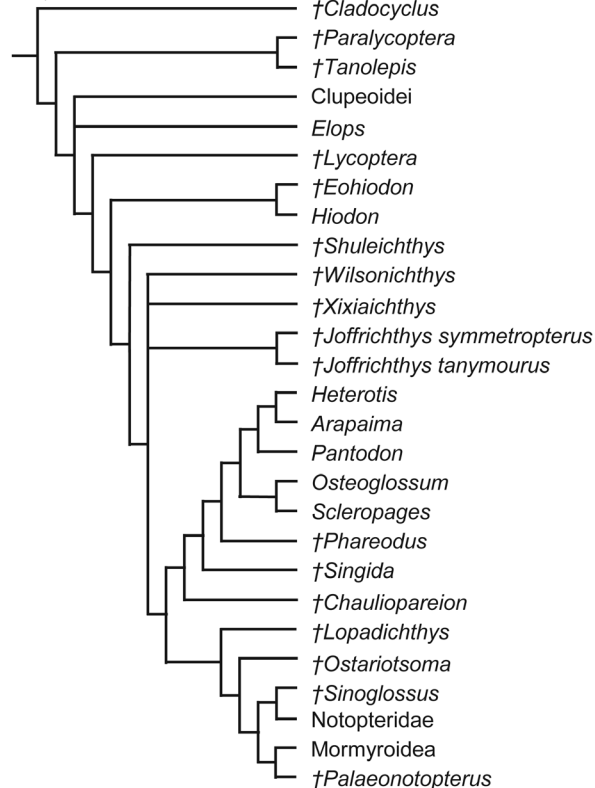


Fig. 14. Morphological systematics of Osteoglossomorpha. Phylogenies redrawn from **a.** Li, Wilson (1996a), **b.** Hilton (2003), **c.** Zhang (2006), and **d.** Murray *et al.* (2018).

of Osteoglossomorpha by including at least one species of *Hiodon* and one species of Osteoglossiformes, along with at least one representative of Elopomorpha, one representative of Clupeocephala and one non-teleost ray-finned fish (such as *Amia calva*) to root the tree. All these studies recovered a monophyletic Osteoglossomorpha with strong statistical support, using either complete mitogenomes (e.g., Inoue *et al.*, 2003; Lavoué *et al.*, 2012) or large selections of nuclear genes (Near *et al.*, 2012; Betancur-R *et al.*, 2013).

Phylogenetic position of Osteoglossomorpha. Since the first (*i.e.*, early 1990s) nucleotide sequence-based studies aiming to investigate the relationships among main teleost lineages, Osteoglossomorpha, Elopomorpha (eels and relatives), Clupeomorpha (sardines, anchovies and relatives), Ostariophysi (milkfish, carps, catfishes, and relatives) and Euteleostei (salmons, pikes, spiny-fishes and relatives) (*i.e.*, Normark *et al.*, 1991; Le *et al.*, 1993), several molecular studies have addressed the question of the phylogenetic position of Osteoglossomorpha relative to other teleosts using larger molecular datasets and denser taxonomic samplings. The topologies of the phylogenetic trees of Normark *et al.* (1991) and Le *et al.* (1993) were different from each other and also contained some unconventional groupings that were likely the consequence of sparse taxon samplings and short molecular sequences used in these two exploratory molecular studies. However, despite these limitations, both studies confirmed the Osteoglossomorpha as one of the primary basal teleostean lineages.

Most subsequent molecular studies identified three main monophyletic teleostean groups, as do morphological studies: Elopomorpha, Osteoglossomorpha, and Clupeocephala (comprising Clupeomorpha, Ostariophysi and Euteleostei) (Fig. 15a). However, molecular data provide unclear results regarding to the phylogenetic position of Osteoglossomorpha relative to the two other lineages (Elopomorpha and Clupeocephala) because of the unresolved position of the root (Fig. 15a). There is a tendency in recent molecular studies using large taxonomic samplings and sets of several genes to identify Elopomorpha as the sister group of the rest of Teleostei with the consequence that Osteoglossomorpha and Clupeocephala form a monophyletic group (Near *et al.*, 2012; Betancur-R *et al.*, 2013; Chen *et al.*, 2014). This phylogenetic arrangement is at best moderately supported by statistics (such as Bootstrap values) and often alternative arrangements cannot be rejected statistically. Other molecular studies present different hypotheses such as the sister relationship between Osteoglossomorpha and Elopomorpha (Le *et al.*, 1993) or the sister relationship between Elopomorpha and Clupeocephala (Inoue *et al.*, 2003; Johnson *et al.*, 2012) (Fig. 15a) or a polytomy among the three groups (Li *et al.*, 2008).

Four recent genomic studies, each based on several thousand molecular characters (sampled across the whole genome) but few taxa found conflicting results: Chen *et al.* (2014) and Bian *et al.* (2016) supported the hypothesis of a

sister group relationship between Elopomorpha and Osteoglossomorpha, whereas Austin *et al.* (2015) recovered Osteoglossomorpha as the sister group of all other Teleostei and Faircloth *et al.* (2013) recovered Elopomorpha in this position (Fig. 15a). Shen *et al.* (2017) examined the distribution of the phylogenetic signal in the dataset of Chen *et al.* (2014) and found that only a small subset of genes provides support for Elopomorpha + Osteoglossomorpha over Elopomorpha + Clupeocephala; Shen *et al.* (2017) did not evaluate the third hypothesis (*i.e.*, Elopomorpha is the sister group of the rest of Teleostei). Therefore, molecular data, so far, has not provided unambiguous phylogenetic signal to resolve the question of the phylogenetic position of Osteoglossomorpha within Teleostei. We note that the two most recent studies that examined this question (*i.e.*, Hughes *et al.*, 2018; Vialle *et al.*, 2018) also provided contrasting results.

Molecular phylogeny of Osteoglossomorpha. The higher-level (*i.e.*, inter-familial level) relationships of Osteoglossomorpha have been addressed in a few molecular studies. Among these studies, those based on a single gene (such as cytochrome *b* or 18S rDNA) have been shown to produce unreliable phylogenetic results (relative to the phylogeny of Osteoglossomorpha) because of weak resolution, weak support, and variable or unexpected tree topologies (e.g., Kumazawa, Nishida, 2000; Santini *et al.*, 2009; Mu *et al.*, 2012, 2013). This is likely the consequence of the limited and low quality (*i.e.*, high-level of homoplasy content) of phylogenetic signal when using such single gene. Contrary to the single-gene approach, the multi-gene phylogenetic studies tend to produce highly similar (often identical) topological hypotheses (see below).

At higher-levels, Lavoué, Sullivan (2004) was the first molecular phylogenetic study of Osteoglossomorpha in which *Hiodon* (Hiodontiformes) and at least one representative of each osteoglossiform family were examined together. Their most-parsimonious phylogenetic tree of Osteoglossomorpha based on the analysis of five genes (Fig. 15b) shows Hiodontiformes (*Hiodon alosoides*) to be the sister group of Osteoglossiformes. Within the Osteoglossiformes, *Pantodon buchholzi* is the sister group of the rest of the taxa and Osteoglossidae (minus *P. buchholzi*) is the sister group of Notopteroidei (= Notopteridae (Gymnarchidae + Mormyridae)). Within Osteoglossidae, two lineages were identified, one including *Arapaima gigas* and *Heterotis niloticus* and another comprising *Scleropages* sp. and *Osteoglossum bicirrhosum*. The main difference between this molecular tree and previous morphological hypotheses is the position of *Pantodon*. While the overall topology of this tree (Fig. 15b) is well supported, the branch supporting *Pantodon* is significantly longer than the other branches, which could indicate a difficulty for reliably inferring the placement of *Pantodon* (*i.e.*, potentially a case of long branch attraction; Bergsten, 2005). Several subsequent studies that addressed the phylogenetic position of *Pantodon* within Osteoglossomorpha using different characters and taxonomic sampling found si-

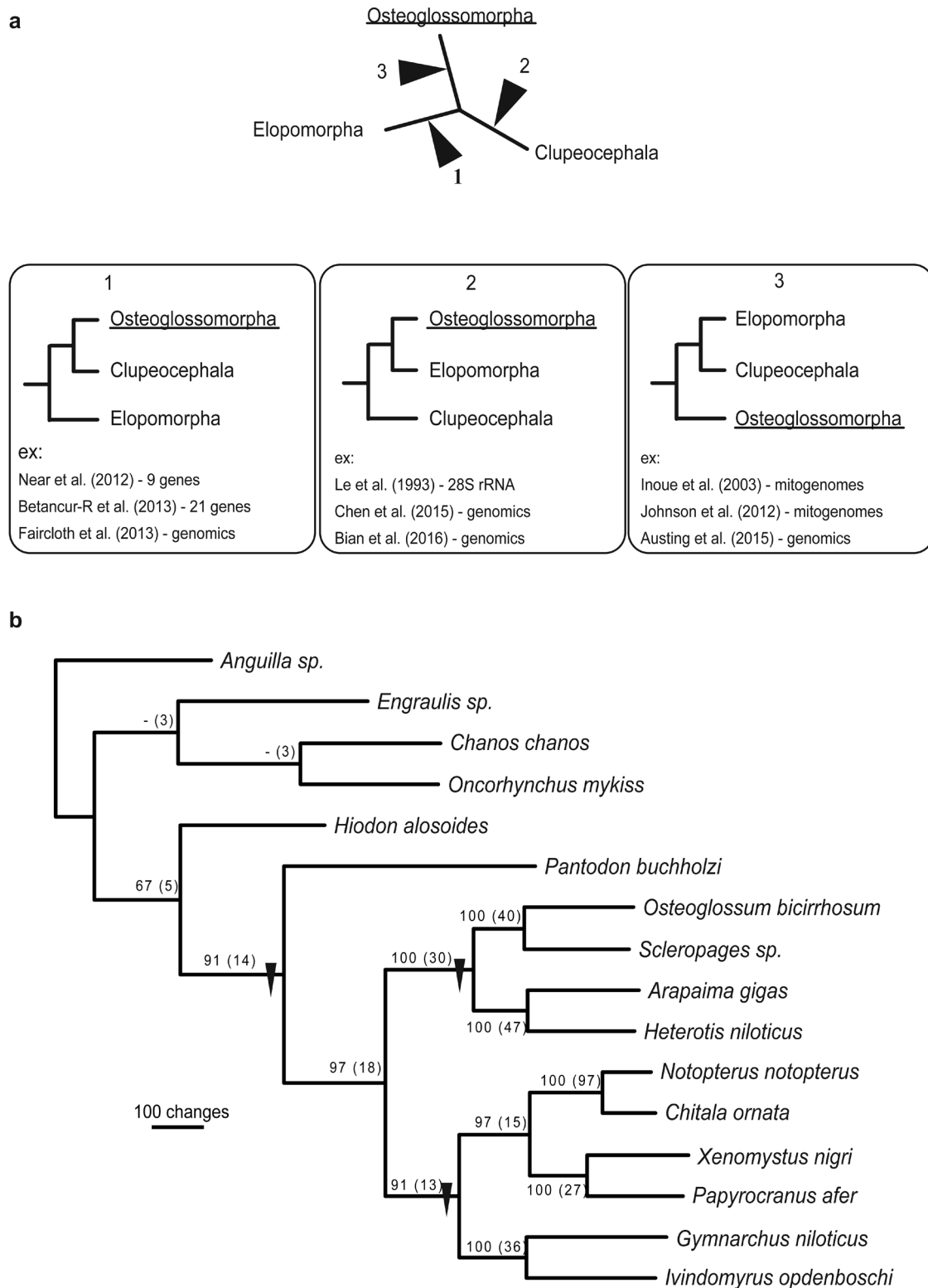


Fig. 15. Molecular systematics of Osteoglossomorpha. **a.** The phylogenetic positions of Osteoglossomorpha relative to Elopomorpha and Clupeocephala as inferred from molecules. Each arrow-head indicates a root position on the same unrooted topology providing three different hypotheses (1 to 3). For each rooted topology, three references are given. **b.** A molecular phylogenetic tree of Osteoglossomorpha (modified from Lavoué, Sullivan, 2004). This is the single most-parsimonious tree recovered from a dataset of five molecular markers (12S and 16S rRNA, cytochrome b, RAG2, and MLL). Bootstrap proportions (>50%) and Bremer support indices (in parentheses) are indicated at nodes. Synapomorphic molecular insertions from 12S rRNA are shown by inverted triangles.

milar results as Lavoué, Sullivan (2004). In particular, Inoue *et al.* (2009), Lavoué *et al.* (2011) and Lavoué *et al.* (2012) examined the phylogeny of Osteoglossomorpha using complete mitogenomic sequences but different taxonomic samplings; all inferred the same tree topology.

Near *et al.* (2012) reconstructed the phylogeny of more than 230 ray-finned fish species (including nine osteoglossomorph species but, noticeably, not *Pantodon*) using a nine-nuclear-gene dataset also found the same topology as previous analyses. Betancur-R *et al.* (2013) examined a larger dataset (more than 1400 teleost species and 20 nuclear genes along with one mitochondrial gene, 16S rRNA). Both studies found similar results to Lavoué, Sullivan (2004) except for the position of *Pantodon* in Betancur-R *et al.* (2013), which was recovered as the sister group to the rest of osteoglossids examined (*i.e.*, *Arapaima gigas*, *Heterotis niloticus* and *Osteoglossum bicirrhosum*). However, the dataset of Osteoglossomorpha of Betancur-R *et al.* (2013) contains more than 50% missing data and a recent re-analysis of this dataset placed *Pantodon* as the sister group of the rest of Osteoglossiformes (Betancur-R *et al.*, 2017). Lavoué (2016) combined the morphological dataset of Hilton (2003), as modified by Wilson, Murray (2008), with the mitogenomic dataset of Lavoué *et al.* (2012) and the nuclear gene datasets of Near *et al.* (2012) and Betancur-R *et al.* (2013) to reconstruct the phylogeny of Osteoglossomorpha. Analytical results provided a tree topology identical to that of Lavoué, Sullivan (2004) in which *Pantodon* is the sister group of the rest of Osteoglossiformes. Bian *et al.* (2016) is the first genomic study in which the phylogenetic position of *Pantodon*, relative to Notopteroidei (only *Papyrocranus afer* sampled) and Osteoglossidae (only *Scleropages formosus* sampled) could be investigated. The authors found *Pantodon* sister group of *S. formosus*, keeping open the question of the position of *Pantodon* in molecular systematics. Finally, in the most recent genomic study to date, Hughes *et al.* (2018) found *Pantodon* sister group of the rest of Osteoglossiformes (Hiodontiformes was not sampled).

Molecular systematics at or below the family level. At lower-level (*i.e.*, intra-familial levels), molecular phylogenetic analyses of several osteoglossiform families have been conducted to produce frameworks to explore the evolution of some remarkable traits in these fishes. For example, based on topologies generated by novel molecular data, Sullivan *et al.* (2000) studied the evolution of the cell-anatomy of the electric organs of African weakly electric fishes (Mormyridae and Gymnarchidae), based on a new phylogenetic hypothesis, Carlson *et al.* (2011) studied the evolution of their brain, and Lavoué *et al.* (2012) studied the origins and timing of the electric sense in Osteoglossomorpha and Teleostei.

Molecular-based phylogenies have also served as the basis for biogeographical analyses, radiation, and conservation. Inoue *et al.* (2009) examined the phylogeny of Notopteridae to test biogeographical hypotheses relative to

their distribution. Lavoué (2015) specifically tested some biogeographical hypotheses relative to the distribution of the trans-Wallace's Line distributed genus *Scleropages* in reconstructing the phylogeny of this genus within the Osteoglossidae. Feulner *et al.* (2007), Sullivan *et al.* (2004) and Arnegard *et al.* (2010) examined the speciation process within genera of African weakly electric fishes. Finally, the genetic population structure of osteoglossomorph species listed in the "IUCN Red List of Threatened Species" was recently reported for conservation purpose, including *Arapaima gigas* (Hrbek *et al.*, 2005; Araripe *et al.*, 2013) and *Scleropages formosus* (Yue *et al.*, 2000, 2003, 2006; Mohd-Shamsudin *et al.*, 2011).

Biogeography of Osteoglossomorpha. Osteoglossomorpha has attracted much attention from biogeographers studying trans-oceanic distributions of non-marine taxa (Cracraft, 1974; Darlington, 1957; Nelson, 1969) because they are charismatic, easy to identify, their systematics was studied in early cladistic frameworks, and they are distributed on all continents except Antarctica, thereby exhibiting several inter-continental allopatric taxa pairs (*i.e.*, Neotropical *Arapaima*/Afrotropical *Heterotis*; Oriental *Scleropages*/Australian *Scleropages*; Oriental Notopterinae/Afrotropical Xenomystinae; Nearctic Hiodontiformes/Gondwanan Osteoglossiformes, etc.). Further, they have a rich fossil record (including several marine forms) dating back to the Late Jurassic or Early Cretaceous (†*Paralycoptera*, Tse *et al.*, 2015) and, therefore, they are considered to be one of the oldest living freshwater teleost lineages. The distribution of Osteoglossomorpha was either discussed as a whole (Nelson, 1969; Taverne, 1979; Li, 1997; Wilson, Murray, 2008) or in part: *e.g.*, *Arapaima*/*Heterotis* (Lundberg, Chernoff, 1992), Notopteridae (Inoue *et al.*, 2009), Osteoglossidae (Bonde, 1996; Forey, Hilton, 2010), Oriental *Scleropages*/Australian *Scleropages* (Darlington, 1957; de Beaufort, 1964; Lavoué, 2015). Sometimes, the distribution of Osteoglossomorpha was part of a more general discussion on the biogeographical relationships of continental regions, such as Neotropics versus Afrotropics (Cracraft, 1974; Lundberg, 1993), Neotropics versus Australia (Cracraft, 1974) or the Gondwanan breakup (Cavin, 2008; Lavoué, 2016; Nelson, Ladiges, 2001; Patterson, 1975).

The work of Nelson (1969) marked a radical methodological change in the study on the biogeography of Osteoglossomorpha because this author was the first to use a synapomorphy-based phylogeny to reconstruct the ancestral regions at nodes within the context of plate tectonics (Fig. 16). Nelson, however, limited his analysis to extant taxa with little consideration for the information that osteoglossomorph fossils can bring (such as minimum age or past range extension or past ecological associations). Patterson (1975) based his analysis on a modified version of Nelson's (1969) tree, in which mormyrids are transferred as the sister group of notopterids (Greenwood, 1971; Fig. 16). Importantly, he added two fossils in the tree: †*Lycoptera* as the sister group of Hio-

dontidae and †*Brychaetus* as the sister of Osteoglossidae plus Pantodontidae. Doing this, Patterson (1975) provided a strict minimum age for the base of the Osteoglossomorpha tree corresponding to the age of the oldest fossil, †*Lycoptera*. He also discussed the evidence of possible marine dispersal in the Osteoglossidae-Pantodontidae lineage because †*Brychaetus* is a marine taxon. Taverner (1979) published a fully dated phylogeny of Osteoglossomorpha in including many fossils. Taverner (1979) used this tree to discuss the biogeography of these fishes but without explicitly reconstructing ancestral areas at nodes. Li (1997) briefly reviewed the knowledge on the biogeography of Osteoglossomorpha at that time and he provided his own hypothesis based on his phylogenetic results (Li, Wilson, 1996a). Wilson, Murray (2008) reviewed more extensively the fossil record and biogeography of Osteoglossomorpha and Forey, Hilton (2010) provided the most complete critical account, to date, on the significance of the many fossils that have been related to Osteoglossidae and their value to study the biogeography of Osteoglossidae.

Below, we review recent hypotheses of the historical biogeography of Osteoglossomorpha, specifically addressing splits between *Arapaima* and *Heterotis*, *Osteoglossum* and *Scleropages*, and within Notopteridae. We emphasize the importance of timing (to test vicariance hypothesis) and habitat constrains (relative to temperature and salinity) in the biogeography of trans-oceanic pair taxa that are regularly discussed.

Biogeography of *Arapaima* and *Heterotis*. Neotropical freshwater fishes has attracted attention of biogeographers because, in particular, of the similarity of this fauna and that of the Afrotropics, which was noticed more than 100 years ago (Eigenmann, 1912; Regan, 1922), well before the theory of continental drift of Wegener (1915) radically transformed the field of biogeography (Gosline, 1975; Hallam, 1967; Patterson, 1975). In this context, the trans-Atlantic distribution of (*Arapaima*, *Heterotis*) has been discussed (Cavin *et al.*, 2008; Cracraft, 1974; Lundberg, 1993; Lundberg, Chernoff, 1992); yet there is no consensus to explain their distribution because of the uncertain phylogenetic position of some “stem or crown arapaimin” fossils (Forey, Hilton, 2010; Lundberg, Chernoff, 1992) and the age of the divergence between *Arapaima* and *Heterotis*. Three hypotheses are commonly proposed to explain the Neotropical-Afrotropical distribution of *Arapaima* and *Heterotis*: 1) the previcariance hypothesis, which postulates that the divergence between *Arapaima* and *Heterotis* predated the fragmentation of South America and Africa (Lundberg, Chernoff, 1992; Fig. 16); 2) the tectonic-mediated vicariance hypothesis, which postulates that the divergence *Arapaima* and *Heterotis* was the consequence of the separation of Africa and South America (Nelson, 1969; Fig. 16); and the post-fragmentation dispersal (marine or geodispersal) hypothesis, which postulates that the divergence between *Arapaima* and *Heterotis* postdated the final fragmentation between Africa and South America (Bonde, 1996, 2008). In theory and under some circumstances (such as rates of regional extinction), each of these three hypotheses

can generate a sister group relationship between *Arapaima* and *Heterotis*. However, timing is critical as it provides a strong test of the vicariance hypothesis: the vicariance hypothesis is not rejected if the time divergence between *Arapaima* and *Heterotis* overlapped the time of the final separation of Africa and South America (about 105 Ma).

Nelson (1969; Fig. 16) and Nelson, Ladiges (2001) hypothesized that the ancestral region of the clade (*Arapaima*, *Heterotis*) was “Africa plus South America”; these authors did not include any timescale although Nelson, Ladiges (2001) mentioned the molecular work of Kumazawa, Nishida (2000) in which a timescale is provided. Lundberg, Chernoff (1992) hypothesized that the divergence between *Arapaima* and *Heterotis* predated the fragmentation of South America and Africa because they considered the Neotropical fossil †*Laeliichthys* (Aptian, about 110 Ma) more closely related to *Heterotis* (plus †*Paradercetus*) than to *Arapaima* (Taverner, 1979; Fig. 16). Therefore, the divergence between *Arapaima* and the *Heterotis* lineage must have predated the separation of Africa and South America. However, the phylogenetic placement of †*Laeliichthys* (and †*Paradercetus*) was criticized by several researchers (see Bonde, 1996; Forey, Hilton, 2010). In particular, Bonde (1996) produced a dated phylogenetic tree in which the divergence between *Arapaima* and *Heterotis* is Eocene, therefore *de facto* rejecting the vicariance hypothesis and favoring a post-fragmentation (likely marine; see indirect evidence in Bonde, 2008) dispersal hypothesis. Recent molecular works favored the post-fragmentation divergence in estimating the time of divergence between *Heterotis* and *Arapaima*, which is strictly younger (105 Ma) than the breakup of South America and Africa (Lavoué, 2016),

Beside †*Laeliichthys* and †*Paradercetus*, the paleontological evidence to date the divergence of *Arapaima* and *Heterotis* is scarce. Otero, Gayet (2001) assigned very fragmentary fossils from the Oligocene or Miocene (about 31-23 Ma) to *Heterotis* that make them the earliest record of this lineage. Some Paleocene remains of *Arapaima*-like specimens represent the earliest record of the lineage *Arapaima* in South America (Forey, Hilton, 2010; Gayet, Meunier, 1983; Lundberg, Chernoff, 1992); fossils of *Arapaima* and *Heterotis* have never been found outside their current continental regions. A strict interpretation of the fossil record, therefore provide a strict minimum age of about 56 Ma for the divergence between *Heterotis* and *Arapaima*. The Eocene †*Sinoglossus lushanensis* (Su, 1986) is closely related to this clade, either as its sister group (Forey, Hilton, 2010; Li, Wilson, 1996b) or in an unresolved position relative to *Heterotis* and *Arapaima* (Li, Wilson, 1996a; Lavoué, 2016; Wilson, Murray, 2008). The uncertainty in the phylogenetic position of †*Sinoglossus* from China adds difficulties to resolve the biogeography of *Arapaima* and *Heterotis* but it does not modify the current evidence that the divergence postdated the separation between Africa and South America. Other Paleocene and Eocene fossils may represent stem representatives of the clade (*Arapaima*, *Heterotis*) such as †*Joffrichthys* (Nearctic,

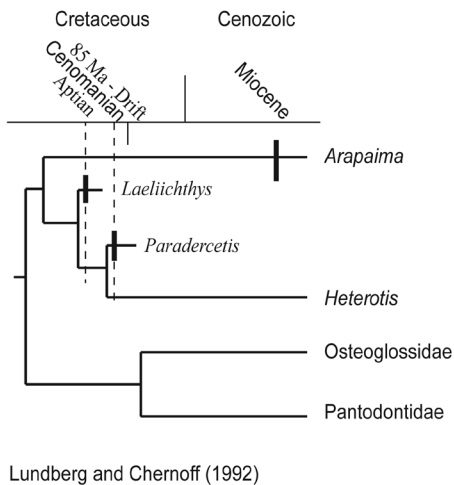
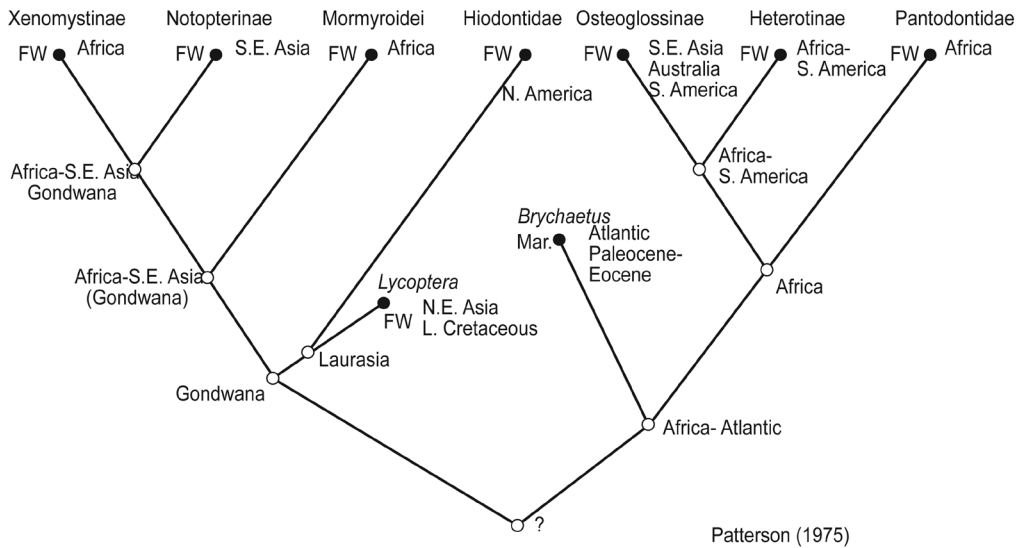
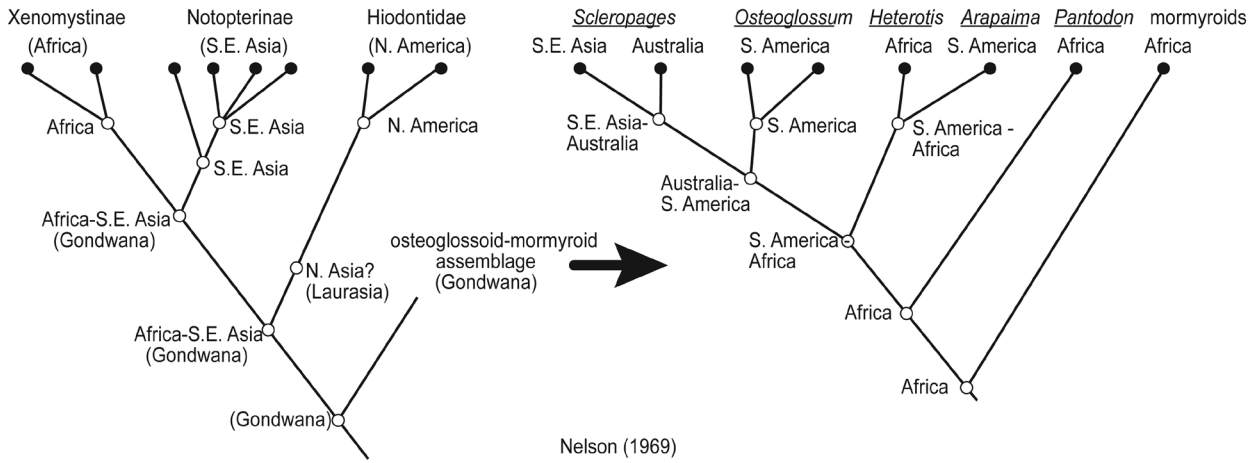


Fig. 16. Phylogeny-based biogeographic hypotheses. Nelson (1969), Patterson (1975), Lundberg, Chernoff (1992).

Paleocene, freshwater; Li, Wilson, 1996b, though see Murray *et al.*, 2018) and †*Trissopterus* (West Palearctic, Eocene, marine; Bonde, 2008; Taverne, 1998).

Evidence related to timing is growing to support trans-Atlantic dispersal during the Cenozoic not just for *Arapaima* and *Heterotis* but also for several trans-Atlantic groups of

fishes (including Cichlidae, Polycentridae, and Siluroidei), well after the separation of Africa and South America (Lundberg *et al.*, 2007; Near *et al.*, 2012; Friedman *et al.*, 2013; Lavoué, 2016; Matschiner *et al.*, 2017). However, the mechanism(s) of these dispersal events is still not known. Often, direct marine dispersals were proposed as *ad hoc* hypotheses to explain these post-drifting faunistic exchanges (Briggs, 2003; Matschiner *et al.*, 2017). However, in the case of *Arapaima* and *Heterotis*, there is no convincing evidence that the most recent common ancestors were marine adapted (Lavoué, 2016; Sparks, Smith, 2005; but see Bonde, 2008; Taverne, 1998). Moreover, although in theory it is possible, the marine dispersal hypothesis explaining the distribution of *Arapaima* and *Heterotis* seems highly unlikely because it necessitates the combination of four rare evolutionary events (Fig. 17): one “freshwater-to-marine” transition, one long-distance marine dispersal, one “marine-to-freshwater” transition and, finally, the selective extinction of marine organisms on each side of the marine environment. Recent habitat preference reconstructions using phylogenetic trees show that environmental transitions are rare events in Teleostei (Bloom, Lovejoy, 2012; Davis *et al.*, 2012; Lavoué *et al.*, 2012; Conway *et al.*, 2017).

While direct trans-oceanic dispersals seem unlikely, other dispersal processes must be hypothesized to account for such trans-Atlantic faunistic exchanges during the Cenozoic. The geodispersal hypothesis between Africa and South America (or vice versa) through the Holarctic route “North America (= Nearctic) -Greenland region-West Europe (West Palearctic)” represents an alternative to the direct marine dispersal to explain the inter-continental exchanges of freshwater fishes from the end of the Cretaceous to the Eocene (Fig. 17). At first glance, geodispersal through Northern hemisphere may also seem unlikely for tropical freshwater fish because 1) the current climatic conditions in the northern hemisphere (above 30 degree latitude) are, at the best, temperate during summer and often cold during winter; this is unsuitable for warm-adapted organisms such as tropical fishes and 2) three trans-continental land bridges, supporting continuous freshwater systems, must have existed synchronously or repetitively between South-America and North America, North America and Europe and Europe and Africa during the Late Cretaceous-early Cenozoic interval.

Biogeography of *Osteoglossum* and *Scleropages*. The distribution of the lineage including *Osteoglossum* and *Scleropages* is unique among recent fishes in spanning the following three continental regions: Neotropics (two species of *Osteoglossum*), Australia (two species of *Scleropages*) and Orient (two species of *Scleropages*). Because of that, the region where the most recent common ancestor of this lineage lived is still mostly unknown. The fossil record documents the presence of *Scleropages* in Orient and in Australia in the early Eocene and Oligocene, respectively (Hills, 1934, 1943; Zhang, Wilson, 2017). Very incomplete fossils from

India (Maastrichtian), Europe (Palaeocene), Sumatra (Eocene) and Africa (Palaeocene) have also been assigned to *Scleropages* (Kumar *et al.*, 2005; Taverne *et al.*, 2007; Nolf *et al.*, 2008; Sanders, 1934; Taverne, 2009c). These fossils are all freshwater forms. Bonde (2008) described several marine fossils as stem to the clade *Scleropages* + *Osteoglossum*, but none as crown. There is no fossil of *Osteoglossum*. The extant species of *Scleropages* form a putatively monophyletic group that is the sister group of *Osteoglossum*.

Some studies postulated that “South America + Australia + East Antarctica” was the region where lived the ancestor of the clade *Osteoglossum* + *Scleropages* during the Eocene/Oligocene followed by one vicariant event between South America and “Australia plus East Antarctica” (and extinction in East Antarctica), then followed by a marine dispersal event between Australia and Orient (which explains the presence of extant *Scleropages* in Orient) (Cracraft, 1974; Nelson, 1969). The recent discovery of the Eocene †*S. sinensis* in the Orient refutes in part this scenario because it forced the divergence between *Scleropages* and *Osteoglossum* to predate the final separation of South America and “East Antarctica-Australia”. Lavoué (2016) dated the divergence between *Scleropages* and *Osteoglossum* broadly between 80-45 Ma but without considering †*S. sinensis*, which was described later (Zhang, Wilson, 2017).

Given the current evidence, the most likely hypothesis to explain the trans-marine distribution of *Scleropages* is a marine dispersal between Australia and Orient across Wallace’s Line; the ancestral region where the most recent common ancestors of *Osteoglossum* and *Scleropages* lived is unresolved.

Biogeography of Notopteridae. It is only recently that the biogeography of Notopteridae has been investigated. Phylogenetic and paleontological evidence strongly support the hypothesis that the monophyletic Asian Notopterinae originated from Afrotropics. The oldest notopteroid fossil known is †*Palaeonotopterus greenwoodi* from the Cenomanian of Morocco (Forey, 1997). This fossil provides a strict minimum age of 94 Ma for the presence of the Notopteroidei in Africa. Notopterid otoliths (“genus *Notopteridarum*” Nolf *et al.*, 2008) from the Deccan Intertrappean Beds (India), dated to the Late Cretaceous (66 Ma), mark the earliest presence of Notopteridae in Asia. However, these otoliths do not share the modification present in recent species, leading Nolf *et al.* (2008) to suggest that they should belong to some stem notopterid species. Another Asian fossil Notopteridae was described from the Eocene of Sumatra (56.0-33.9 Ma) (Sanders, 1934). This fossil is very similar to the living *Notopterus* and it provides a strict minimum age for the presence of the crown group Notopterinae in Asia.

Two biogeographical hypotheses have been proposed to explain the distribution of the Asian Notopteridae: 1) the tectonic mediated vicariance hypothesis caused by the separation of Africa and India (the “Indian ferry” hypothesis) (Inoue *et al.*, 2009), and 2) the Miocene geodispersal

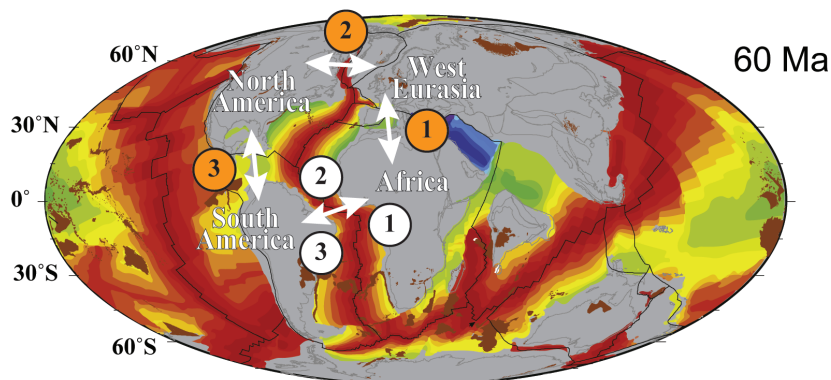
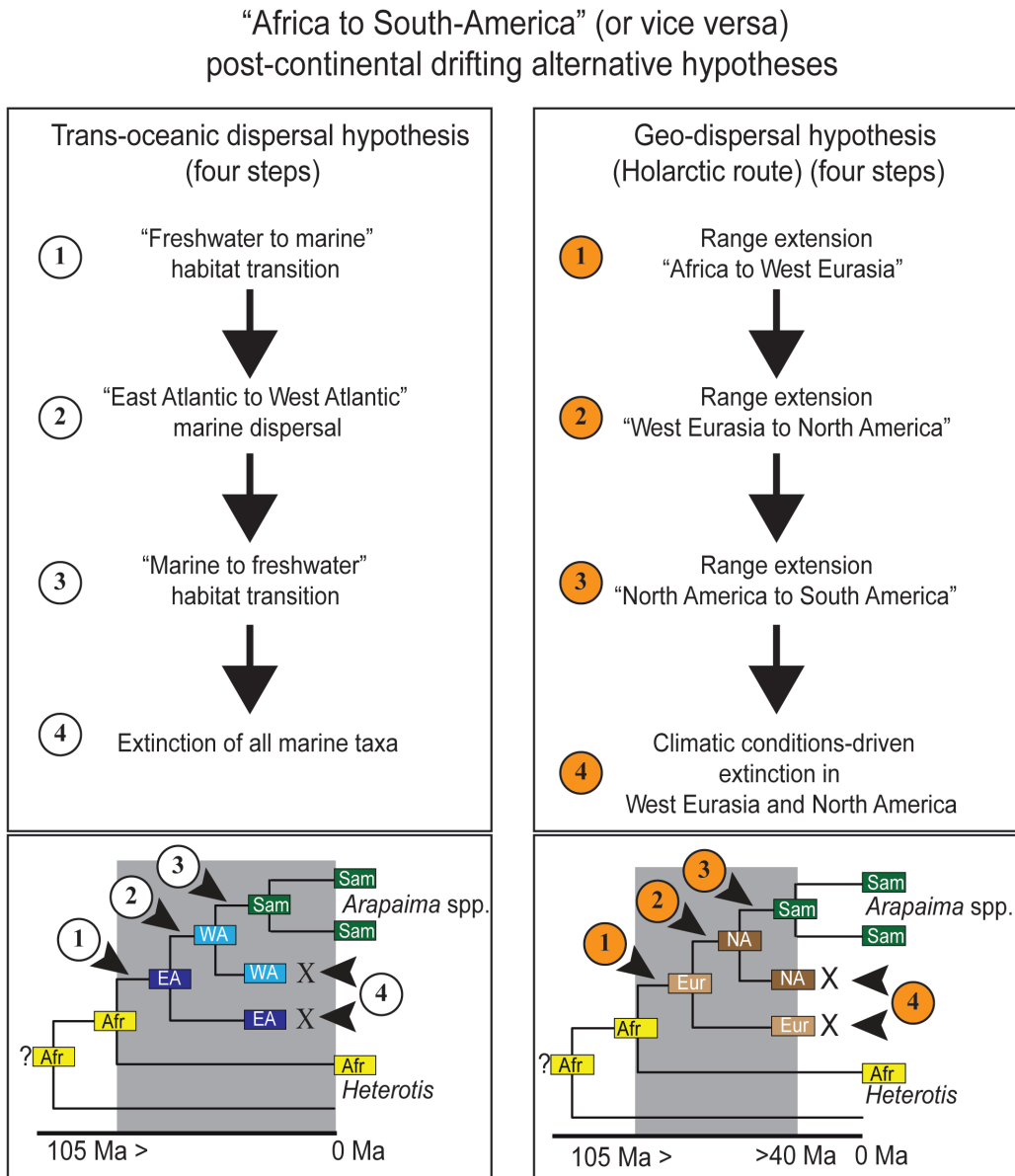


Fig. 17. Evolutionary events supporting the marine and geodispersal dispersal hypotheses to explain the distributions of *Arapaima* and *Heterotis*. Each dispersal hypothesis requires four main evolutionary events (that are mapped on time calibrated phylogenetic trees and a 60 Ma paleomap reconstruction). Paleomap modified from Seton *et al.* (2012). Timescale in million years ago (Ma). For each hypothesis, possible ancestral areas at nodes shown on phylogenies (Abbreviations: Afr, Africa (Afrotropics); Sam, South America (Neotropics); NA, North America (Nearctics); Eur, West Eurasia (West Palearctics); EA, East Atlantic; WA, West Atlantic. “X” means extinction). Grey rectangles indicated time limit for each hypothesis.

hypothesis, which is linked to the collision between Africa and Eurasia (Bănărescu, 1991). Inoue *et al.* (2009) estimated the divergence between Notopterinae and Xenomystinae broadly between 160 Ma and 110 Ma. These authors did not reject the vicariance hypothesis but the age of the Teleostei was overestimated to 300 Ma. Within the hypothesis that Teleostei is about 200 Ma, Lavoué (2016) re-estimated the time divergence between Notopterinae and Xenomystinae to 83.2 Ma (95% CI: 105-60 Ma) with the conclusion that the tectonic mediated vicariance hypothesis should be rejected. In the same study, the age of the crown group Xenomystinae was roughly estimated to 50 Ma. In agreement with this molecular dating (Lavoué, 2016), the presence of the *Notopterus*-like fossil in Sumatra (Sanders, 1934) rejects the second hypothesis.

Therefore, a third dispersal hypothesis (marine?) should be considered in which the dispersal event would have occurred between a maximum of 100 Ma and a minimum of 50 Ma (maybe 66 Ma if the fossil otoliths found in India are related to Notopterinae). Lavoué, Sullivan (2004) noted that Asian notopterids lose the electroreception sense, and they speculated this could be the result of a marine dispersal event between Africa and Asia. Future investigations should consider the following two points: 1) this spatio-temporal pattern is similar to the distribution of other groups of freshwater fish (*e.g.*, cichlids, cyprinodontiforms, and possibly †*Sinoglossus* and *Heterotis*); 2) The Indian subcontinent during the Late Cretaceous-Early Cenozoic does not look biogeographically isolated from Africa (reviewed in Verma *et al.*, 2016 and Vêrard *et al.*, 2017, including freshwater fishes, Nolf *et al.*, 2008), as the current paleogeological reconstructions would suggest (Ali, Aitchison, 2008; Chatterjee *et al.*, 2013; Gaina *et al.*, 2015). Recent studies, such as Torsvik *et al.* (2013), improve the paleogeological reconstruction of the Indian Ocean region during the Cretaceous-Early Cenozoic and show that this region was more complex than previously thought. Further study is needed to better understand the biogeography of this region.

Future research needs

Reassessment of the morphology and systematics of fossil and living osteoglossomorphs. The morphology of osteoglossomorph fishes has been intensively studied for a long time. Many of the preeminent ichthyologists of the 19th century (*e.g.*, Cuvier, Agassiz, Cope, and others) offered much of the early taxonomic descriptions and a lot of anatomical characters and broad comparisons, many of which persist now. These studies culminated in Ridewood's (1904, 1905) papers on the skull of osteoglossomorphs and other basal teleostean fishes (his underlying approach foreshadowing cladistic phylogenetic analysis; Hilton, Forey, 2005). Throughout much of the 20th century, the morphology of individual taxa were explored in varying levels of detail, but it was not until Taverne's monographic treatments of osteological data that Osteoglossomorpha was treated in

a comprehensive, systematic manner. Since these studies there have been many studies focused on individual aspects of osteoglossomorph anatomy and descriptions of many new fossil taxa. Given the abundant newly described taxa, new data matrices, and new definitions and discussions of morphological characters related to Osteoglossomorpha that have been published recently (*e.g.*, Hilton, 2003; Murray, Wilson, 2005; Zhang, 2006; Leal, Brito, 2007; Wilson, Murray, 2008; Bonde, 2008; Xu, Chang, 2009; Taverne, 2009a,b,c; Taverne *et al.*, 2009; Hilton, Britz, 2010; Forey, Hilton, 2010; Murray *et al.*, 2010, 2016, 2018), the time seems good for a complete reassessment of characters and new study of relationships among all taxa. Further, many of the recently described fossil taxa need to be reexamined and incorporated into an expanded comparative data set. Given the technological advances that have been developed for the study of anatomy, including the comparative study of soft tissues and ontogeny (Hilton *et al.*, 2015), which are virtually unstudied for osteoglossomorphs, there remain, even in this well studied group, many unknown aspects of their comparative anatomy that will undoubtedly prove useful for understanding their phylogenetic relationships.

Morphology of Mormyridae and intrafamilial relationships. In an extensive series of papers, Taverne (1967, 1968a, b, 1969, 1970, 1971, 1972) established a taxonomically robust source of osteological data for mormyroid fishes. Since that time, significant variation within the family continues to be documented (*e.g.*, in the caudal skeleton and its development; Hilton, Britz, 2010). Within Mormyridae, the hypotheses of relationships among genera that were proposed by Taverne (1972) have been largely untested by morphological data (*e.g.*, through collection of new data, by different approaches for character conceptualization, etc.), and the time seems ripe to revisit the relationships among mormyrid genera based on new morphological observations. Further, several genera have been recovered as non-monophyletic by genetic analyses (*e.g.*, Sullivan *et al.*, 2000), and these now must be reconsidered and redefined.

Embryology and early ontogeny of *Hiodon* As putatively the basal most extant osteoglossomorph genus, *Hiodon* is considered to be of great systematic importance, and is often used as a representative osteoglossomorph in broad phylogenetic analyses (*e.g.*, Arratia, 2001; Hurley *et al.*, 2007). Hiodontids have semi-buoyant eggs, and this is among the earliest occurrence of such an egg type found in Teleostei. Among the smallest larval specimens of *H. tergisus* described in the literature is a 7.1 mm specimen (Snyder, Douglas, 1978). Battle, Sprules (1960) described the embryology and larval development of *H. alosoides*, based on specimens prehatching stages, as well as 7.27 mm larvae. Both studies focus on external features and larval identification (see also Wallus, 1986). Two morphological

studies have focused on the osteology of this taxon (Taverne, 1977; Hilton, 2002), yet there is still a poor understanding of the early developmental stages of *Hiodon*. For example, the smallest stages available to Hilton (2002) for his osteological study was 21 mm SL, and the smallest specimens used by Schultze, Arratia (1988) in their study of the development of its caudal skeleton was 22 mm SL. By these stages, many of the skeletal elements are already present, particularly in the cranial skeleton, and therefore there is no data, for instance, on the relative timing of skull bones. Ontogenetic data can be important for homology assessment, for example, and as character data in systematic studies (Leis *et al.*, 1997; Hilton *et al.*, 2015).

Species limits among classically monotypic taxa. With the suggestion that there is more than a single extant species of *Arapaima* (Stewart 2013a,b), the question arises whether there remains cryptic species within other traditionally held monotypic genera. Certainly, population-level structure for wide-ranging, monotypic osteoglossomorph taxa can be informative (*e.g.*, for biodiversity and conservation purposes), whether or not variation (morphological or genetic) is determined to be at the level of distinct species. Other monotypic taxa for that are good candidates for reconsideration are *Scleropages formosus*, *Heterotis niloticus*, *Xenomystus nigri*, *Notopterus notopterus*, and *Gymnarchus niloticus* (*e.g.*, Roberts, 1992). *Pantodon buchholzi* would appear also to be a good candidate for testing its monotypic status, being distributed with two widely disjunct populations in the Niger and Congo basins. Lavoué *et al.* (2011) found very little morphometric divergence between these two populations, despite finding genetic divergence that was suggestive of more than 50 million years of separation. New morphological data, including internal anatomy, should now be assessed for *Pantodon*.

Phylogenetic affinities of *Pantodon*. *Pantodon* has long been recognized to be a problematic taxon in the context of understanding the phylogeny of Osteoglossomorpha. Although generally recovered as close, if not within Osteoglossidae, the relationships of *Pantodon* to other osteoglossomorphs is problematic (*e.g.*, Nelson 1968, 1969 discussed the conflicting nature of gill arches, infraorbital bones, and other aspects of its anatomy, which suggested either a sister group relationship to either Osteoglossidae or Osteoglossinae). This phylogenetic difficulty was further discussed by Hilton (2003) in an analysis that removed all fossil taxa included in his matrix. The resulting strict consensus tree had a topology that was largely consistent with that of the full analysis, with the exception that *Pantodon* was recovered in a polytomy with Notopteridae and Osteoglossidae (*i.e.*, in the fundamental trees it was interpreted as either the sister group of Notopteridae or Osteoglossidae, or nested within Osteoglossidae). This was offered as an example of the use of fossils as arbiters between competing hypotheses of relationships. The characters supporting each of these alternati-

ve hypotheses were not fully explored in this analysis, and the character conflict within Osteoglossomorpha as related to the affinities of *Pantodon* need to be more fully understood. Based on molecular data, Lavoué, Sullivan (2004; also Lavoué, 2016) found *Pantodon* to be the sister group of the rest of Osteoglossiformes (but see Betancur-R *et al.*, 2013; Bian *et al.*, 2016, and discussion above). At this point, new morphological and molecular analyses are needed to further address the phylogenetic position of *Pantodon* within Osteoglossomorpha.

Systematic biology, taxonomy, and monophyly of *Scleropages*. Traditionally, three species have been recognized in the genus *Scleropages*: *S. jardinii* and *S. leichardti* from tropical Australia, and the widespread species *S. formosus*, found from the Mekong basin, Thailand, Myanmar, the Malay Peninsula, Borneo, and Sumatra in Southeast Asia. Several recent studies have increased the diversity of fossil and living taxa described in the genus *Scleropages*. Pouyaud *et al.* (2003) named several new species of *Scleropages* based on coloration, slight meristic and morphometric differences, and slight mitochondrial variation; as noted above, these are widely held to be color variants of *S. formosus* and not accepted as valid (*e.g.*, Kottelat, Widjanarti, 2005; Mohd-Shamsudin *et al.*, 2011; Roberts, 2012; Kottelat, 2013). *Scleropages inscriptus* was described by Roberts (2012) from Myanmar, and diagnosed based on the presence of maze-like markings on the head and body, unlike the even coloration of *S. formosus*; it differs also in meristic and morphometric characters from the Australian *Scleropages*. There are significant taxonomic concerns regarding the Australian species of *Scleropages* as well, in that evidence suggests that *S. leichardti* was that the relatively general description provided by Günther (1864) was based on a specimen that is of unclear provenance but likely originated outside of its known range (*i.e.*, the Fitzroy River basin) and has inconsistencies with current descriptions of *S. leichardti* (Pusey *et al.*, 2016). Pusey *et al.* (2016) further suggest that close examination of the disjunct populations of *S. jardinii* are warranted to determine degree of separation and whether or not there is species-level distinction and structure within this species. Zhang, Wilson (2017) recently described †*S. sinensis* from the Early Eocene Xiwanpu and Yangxi formations of China based on well-preserved whole body fossils. This taxon was assigned to *Scleropages* based on overall similarities of the skull, caudal skeleton, fins, and scales to modern species of the genus. We do not dispute these similarities, but note that the cited characteristics (*e.g.*, shape of fins and reticulate scales) are all plesiomorphic, at least to the level of Osteoglossidae. Indeed, no synapomorphies have yet been offered to support the genus *Scleropages* as a monophyletic group, and at least two studies (Taverne, 1998; Xu, Chang, 2009) have failed to recover its monophyly. Renewed study of the genus, including all taxa provisionally included, as well as robust outgroup sampling, is necessary to robustly define the genus *Scleropages*.

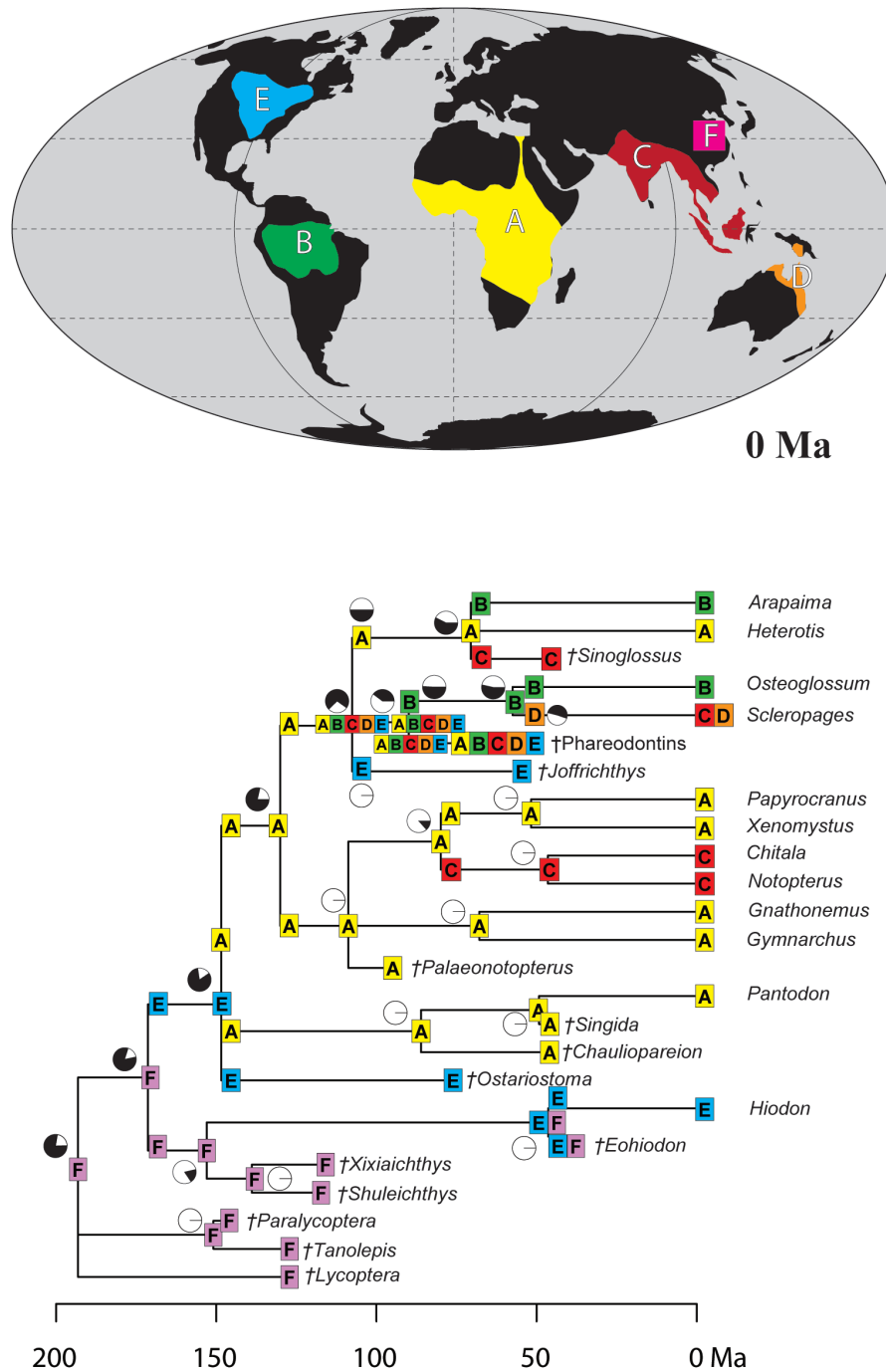
Future directions for molecular systematics of Osteoglossomorpha. With the development of high throughput sequencing technology and the near-future possibility to sequence whole genome at reasonable cost (and the concomitant progresses in computer-based comparative methods), we are entering in a new area in fish systematics which will complete traditional approaches (morphological examination and low efficiency sequencing technology) and refine our understanding of the phylogeny (and evolution) of Osteoglossomorpha (Braasch *et al.*, 2015). Three draft genomes of Osteoglossomorpha are already available, *Scleropages formosus* (Austin *et al.*, 2015; Bian *et al.*, 2016), *Paramomyrops kingsleyae* (Gallant *et al.*, 2017) and *Arapaima gigas* (Vialle *et al.*, 2018) and there are plans to sequence additional ones, such as that of *Hiodon* and *Pantodon* (Bernardi *et al.*, 2012). Although as promising as each (including this one) new technological step can be with the comparison of extremely large genetic datasets, it is not expected this will be the “panacea” as already evidenced by the incongruent results presented by several genomic studies on the phylogenetic position of the Osteoglossomorpha (Austin *et al.*, 2015; Faircloth *et al.*, 2013; Chen *et al.*, 2015; Bian *et al.*, 2016; Hughes *et al.*, 2018; Vialle *et al.*, 2018). We anticipate that this overwhelming amount of genetic data will make more sense when they will be analyzed with existing and new phenotypic data (especially morphological data) from both extant and fossil taxa. In combining all the evidence, more reliable phylogenies will be produced.

Historical biogeography of Osteoglossomorpha. Phylogenetically based reconstruction of the evolution, including both pattern and process, of the distribution of the living Osteoglossomorpha within a changing paleo-geological and paleo-climatic context requires the combination of several lines of evidence – which are sometimes ambiguous or even in conflict – relative to their past geographical distribution (direct evidence from the fossil record plus inference), their past habitat preference relative to salinity and temperature (direct evidence from the fossil record plus inference) and the timing of diversification (direct evidence from the fossil record plus inference). As discussed above, there have been several attempts made to address these factors, both individually and in combination. However, there are numerous methods available that have not been employed for analyzing the historical biogeographic patterns exhibited by Osteoglossomorpha, including comparative, or cladistic, biogeography (*e.g.*, Parenti, Ebach, 2009) and ancestral area analysis (Ree, Smith, 2008).

To illustrate one of possible directions for future investigation of the historical biogeography of the Osteoglossomorpha, we explored the potential of using a likelihood model, the dispersal-extinction-cladogenesis +J (DEC+J) model (Matzke, 2013; Ree, Smith, 2008), to infer the evolution of geographic ranges within the Osteoglossomorpha. For this analysis we used the BioGeoBEARS v.0.2 R-package (Matzke, 2013) and the phylogenetic timetree of osteoglossomorpha obtained in

Lavoué (2016) (this work was published before the systematic reevaluation of †*Joffrichthys* and †*Ostariostoma* in Murray *et al.*, 2018), which includes molecular and morphological characters and extant and extinct taxa. We consider a possible founder speciation event (J) that allowed dispersal without range expansion at nodes (Matzke, 2013). We deleted the outgroup *Elops*. Six different geographical areas were considered in this analysis, each of them being delimited based on the continental distribution of the tip (extant and extinct) taxa of the tree (Fig. 18). The regions are: A – Afrotropics (= Africa), B – Neotropics (= South America), C – Orient (= Southeast Asia), D – Oceania (Australia and Papua-New Guinea), E – Nearctics (= North America), and F – East Palearctics (= East Asia). No combination of areas was *a priori* excluded from the analysis. The maximum number of areas was set to five, corresponding to the maximum range occupied by the fossil †*Phareodus* and its closely allied forms of the extinct †Phareodontinae (Li, Wilson, 1996a) (= “†Phareodontins” in the tree). All other taxa were restricted to one (or two for *Scleropages* and †*Eohiodon*) pre-defined areas.

Results show that the (DEC+J) model provided low support for ancestral area inference at the deepest nodes of the tree and within the family Osteoglossidae (Fig. 18). An ancestral area comprising only East Asia (“F”) was inferred as the main place where the early diversification of the Osteoglossomorpha took place (including the most recent common ancestor, mrca) of the crown group Osteoglossomorpha, which lived during the Jurassic (about 190-150 Ma), though there is low support for this node. This reconstruction is in agreement with the hypothesis of Li (1997) and Greenwood (1970), who suggested that the most recent common ancestor of Osteoglossomorpha lived only in East Asia because the most ancient and morphologically primitive osteoglossomorphs known, such as †*Lycoptera*, came from this region. Hiodontidae (*Hiodon* plus †*Eohiodon*) experienced a first range extension from East Asia to Nearctics. Then two regional shifts are inferred with low support: a first shift from East Asia to Nearctics leading to the stem Osteoglossiformes, and a second shift from Nearctics to Africa (again with low support) leading to the crown Osteoglossiformes (excluding †*Ostariostoma*). After that, the central region of diversification of the Osteoglossiformes was Africa from where successive and independent events of dispersal to other regions occurred which were followed by intra-regional diversification (Notopterinae, †*Joffrichthys*, *Arapaima*, etc.). The model inferred rapid dispersal events with high likelihood between Africa and Southeast Asia to explain the distribution of notopterins. Finally, within the early osteoglossids, the model inferred large areas mostly driven by the condition coded for the “†phareodontins”, with most of the ancestral area reconstructions at nodes receiving low likelihood support. Obviously, this attempt is far from complete, and we only present it to demonstrate the possibility of using a model-based approach to explore the biogeographic history of these fishes. This type of parametric approach may represent one direction for future studies of the historical biogeography of Osteoglossomorpha.



BioGeoBEARS model DEC+J

(ancstates: global optim, 5 areas max. $d=6e-04$; $e=0$; $j=0.0403$; $\text{LnL}=-51.93$)

Fig. 18. Historical biogeography of Osteoglossomorpha based on ancestral area analysis (AAA). Ancestral area estimates under the unconstrained model DEC+J using the time-calibrated Bayesian phylogeny of Osteoglossomorpha of Lavoué (2016) that combines molecular and morphological characters and extant and extinct taxa. Letters from A to F represent the regions (see above map) used for the biogeographical reconstruction: A (yellow), Afrotropics; B (green) Neotropics; C (red) Orient; D (orange) Australia; E (blue) Nearctics, F (pink) North-Eastern Palearctics (Cretaceous period). The geographical distributions of extant and extinct taxa are indicated. The most likely ancestral range is provided: ancestral ranges at nodes indicate the inferred ancestral distributions before speciation and ancestral ranges at corner positions represent geographical ranges immediately after speciation. Black and white pie charts above specific ancestral area reconstruction show the probability (white) of the corresponding reconstruction.

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