



WHY OSTEOGLOSSOMORPHA IS ONE OF THE MOST PECULIAR GROUPS OF FISH – A REVIEW

Anna M. Dymek¹, Jakub Dymek^{2*}, Przemysław Pol¹

¹Department of Small Livestock Breeding, National Research Institute of Animal Production, 32-083 Balice n. Kraków, Poland

²Department of Cell Biology and Imaging, Institute of Zoology and Biomedical Research, Jagiellonian University, Gronostajowa 9, 30-387 Kraków, Poland

*Corresponding author: kuba.dymek@uj.edu.pl

Abstract

Osteoglossomorpha is a significant taxon for studies of evolution and various aspects of fish biology as an evolutionarily old group of fish. The taxon exhibits anatomical, morphological and physiological diversity and various adaptations such as air breathing or electroreception as well as modifications visible in sight and olfactory organs. A peculiarity of this group is the presence of four types of spermatozoa, namely complex introsperm and uni-, bi-, and aflagellate aquasperm. Given the unique morphology and large dimensions of some species, osteoglossomorphs are popular in aquaristics as ornamental fish, and in fisheries because they are an important source of food in many countries. The aim of this paper is to focus on some aspects of the biology and unique features as well as the importance for humans of this unusual group of fish.

Key words: bony-tongue fishes, biogeography, electroreception, air breathing, reproductive biology

The taxon of bony-tongue fishes (Osteoglossomorpha) is one of the most diverse groups among teleosts. Early divergence during the Jurassic period as well as a long separate evolution of each family seem to be the main causes of the observed diversity within this taxon (Betancur et al., 2017; Hilton and Lavoué, 2018; Lavoué, 2016). Representatives of the bony-tongue fishes exhibit numerous modifications visible in anatomy, morphology, physiology and behaviour, therefore this group is significant for studies of evolution and various aspects of fish biology (Braford Jr, 1986; A.M. Dymek et al., 2021 a, b, 2021; Dymek and Pecio, 2019; J. Dymek et al., 2021; J. Dymek, 2021; Greenwood et al., 1966; Hilton, 2003; Hopkins, 1980, 1986, 1999; Hopkins and Bass, 1981; Nelson, 1969; Sullivan et al., 2000; Taverne, 1979, 1998; Wilson and Murray, 2008). Osteoglossomorphs exhibit a morphological diversity visible e.g., in body size. The smallest species, *Petrocephalus catostoma*, is a 4-cm-long fish, whereas the biggest one, *Arapaima gigas*, can reach up to 300 cm in length (Froese and Pauly, 2019). Thanks to the morphological variation and large sizes reached by mature specimens of some species, they are also popular among aquarists and in aquaculture (Hossain and Mohsin, 2021; Monentcham et al., 2009; Oladimeji et al., 2021; Sarkar et al., 2008; Tavares-Dias et al., 2007). The aim of this review is to focus on some aspects of the biology and unique features as well as the significance for humans of this unusual group of fish.

Phylogeny, taxonomy and biogeography

The late Jurassic and early Cretaceous fossil records including species of the family †Lycoperidae found in Asia are closely associated with Osteoglossomorpha and this family seems to be a stem group of the bony-tongue fishes (Figure 1) (Hilton and Lavoué, 2018; Nelson et al., 2016; Tse et al., 2015).

Extant osteoglossomorphs are divided into two orders, Hiodontiformes and Osteoglossiformes (Figure 1) (Betancur et al., 2017). They are only freshwater fish, however extinct species were also marine (Forey and Hilton, 2010).

Within Hiodontiformes, there is one family, Hiodontidae, in which extinct †*Eohiodon* and two species of *Hiodon* (*H. alosoides* and *H. tergisus*) are classified. They are the only extant osteoglossomorphs that live in North America (Berra, 2001). Stem groups of Hiodontiformes (†*Yanbiania*, †*Jiaohichthys*, †*Plesiolycoper*) from the Cretaceous were found in China (Hilton and Lavoué, 2018).

The order Osteoglossiformes includes five families: Pantodontidae, Osteoglossidae, Notopteridae, Gymnarchidae and Mormyridae (Figure 1), the divergence of which occurred 100–150 Mya (Hilton and Lavoué, 2018). They occupy mostly tropical regions of Africa, Asia, Australia and South America (Berra, 2001).

Pantodontidae comprise only one species, *Pantodon buchholzi* living in Africa (Nelson et al., 2016). The late Cretaceous fossils of closely related †*Prognathogloss-*

sum kalassyi found in the Lebanon may indicate early divergence of this family from other osteoglossiforms (Taverne and Capasso, 2012). As a result of numerous apomorphies observed in *P. buchholzi*, its phylogenetical position within Osteoglossiformes evokes extensive discussions among scientists, however, it is often described as a sister group to Osteoglossidae (Hilton, 2003; Nelson, 1969; Taverne, 1979).

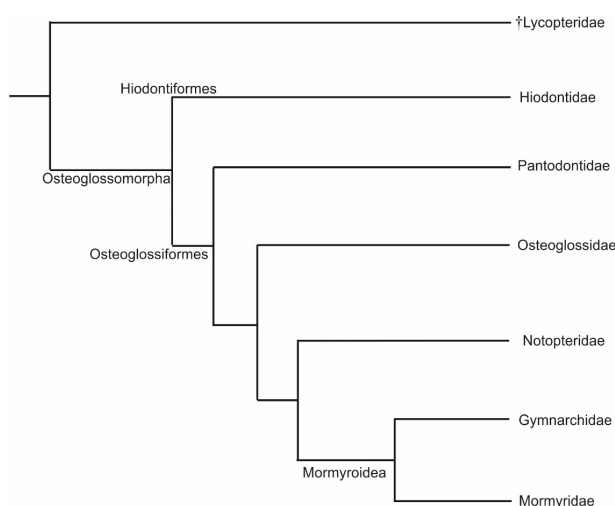


Figure 1. Phylogenetic tree of Osteoglossomorpha and its stem groups. Based on Lavoué (2016) with modifications

The family Osteoglossidae is divided into two subfamilies, Osteoglossinae (two species of *Osteoglossum* and four species of *Scleropages*) and Arapaiminae (four species of *Arapaima* and *Heterotis niloticus*) (Betancur et al., 2017), however some authors (see Hilton, 2003) distinguished these two lineages as two sister families, namely Osteoglossidae and Arapaimidae. Besides the above-mentioned extant species, numerous Paleogene fossil taxa are also included in this family (Hilton and Lavoué, 2018). Species classified within Osteoglossidae exhibit a peculiar trans-oceanic distribution: *Osteoglossum* and *Arapaima* live in South America, *Heterotis* in Africa, whereas *Scleropages* in Asia and Australia (Cracraft, 1974; Nelson, 1969).

Notopteridae include ten extant species in four genera: *Chitala*, *Notopterus* living in Asia as well as *Papyrocranus* and *Xenomystus* from Africa (Moyle and Cech, 2004). The earlier fossil classified in this family is Cretaceous †*Palaeonotopterus greenwoodi* from Maroko (Forey, 1997; Taverne and Maisey, 1999). Nelson (1969) proposed that osteoglossiforms' trans-oceanic dispersal is correlated with plate tectonics and continents fragmentation, whereas Patterson (1975) and Taverne (1979) included also marine fossils in their analysis and indicated possible marine dispersion in some cases.

Gymnarchidae, with only a single species, *Gymnarchus niloticus*, and Mormyridae, which include more than 200 species in 21 genera, together are classified as

Mormyroidea, a sister taxon to Notopteridae, and the youngest group of Osteoglossomorpha (Guo-Qing and Wilson, 1996; Lavoué and Sullivan, 2004; Sullivan et al., 2000; Taverne, 1979). All members occur in Africa (Stiassny et al., 2007). The earliest fossils of this taxon are Pliocene; however, this group is poorly documented in the fossil record (Greenwood, 1972).

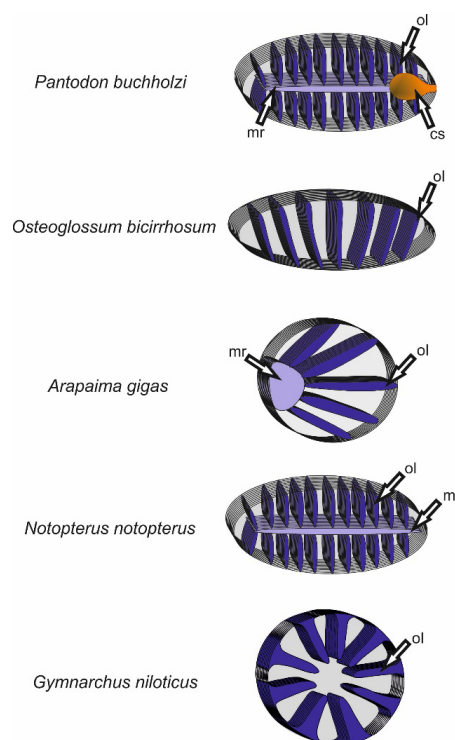


Figure 2. Schemes of olfactory rosettes of osteoglossiforms. Based on J. Dymek et al. (2021) and Patle (2014) with modifications. Abbreviations: cs – cudgel shaped structure; mr – median raphe; ol – olfactory lamellae

Sense organs and electroreception

Olfaction

All the osteoglossiforms investigated so far possess an olfactory rosette within an olfactory chamber, however the morphology of this structure varies even across closely related species (Figure 2). Only *P. buchholzi* and *N. notopterus* possess a typical, multilamellar olfactory rosette with an elongate, centrally located median raphe and two rows of olfactory lamellae (J. Dymek et al., 2021; Patle, 2014). Moreover, in the olfactory chamber of *P. buchholzi*, there is a peculiar cudgel-shaped structure, which can slow down the water passing through the olfactory chamber when the fish jumps out of water (J. Dymek et al., 2021). In *O. bicirrhosum*, the olfactory rosette consists of one row of nearly parallel organized olfactory lamellae, whereas *A. gigas* possesses semicircularly arranged olfactory lamellae merged to a small median raphe. In the olfactory rosette of *G. niloticus*, olfactory lamellae are organized circularly (J. Dymek et al., 2021). Among the species investigated to date, only members of the family Osteoglossidae possess a folded olfactory

epithelium with a sensory area placed in concavities. In *P. buchholzi* and *N. notopterus*, the sensory region covers proximal parts of olfactory lamellae, whereas in *G. niloticus*, it lines the bottom of the olfactory chamber and basal parts of olfactory lamellae (J. Dymek et al., 2021; Patle, 2014). A comparison of morphometrical data on the olfactory organs of osteoglossiforms indicated that *P. buchholzi* possesses a nearly ten times larger total area of the sensory epithelium than other species of this taxon (J. Dymek et al., 2021).

Sight

An analysis of the sense of vision allowed identifying some differences in the eye morphology among osteoglossomorphs (Saidel and Braford Jr, 1985). The embryonic fissure is present in Hiodontidae, Pantodontidae and Osteoglossidae, whereas a lack of this structure was noted in Notopteridae and Mormyroidea. The existence of the falciform process has been described only in Pantodontidae and Osteoglossidae. In the subfamily Arapaiminae this structure is of the usual length (from the optic disc to the *ora terminalis*), while in the rest of species the process is placed across the entire retina (Saidel and Braford Jr, 1985). A horizontal (or nearly horizontal as in Arapaiminae) arrangement of the falciform process in these taxa is probably an adaptation to the subsurface visual environment (Saidel, 2000).

Electroreception

Electroreceptors (ampullary organs) are present in the African notopterids, *Xenomystus* and *Papyrocranus*, as well as Mormyroidea, in which there are also electric organs made of electrocytes (Braford Jr, 1986; Bullock and Northcutt, 1982; Carlson and Arnegard, 2011; Hopkins, 1999, 1980; Hopkins and Bass, 1981; Kirschbaum, 1995, 1987; Sullivan et al., 2000). Electric organs differ between Gymnarchidae and Mormyridae because *G. niloticus* possesses stalkless electrocytes, whereas mormyrids exhibit the presence of two main types of stalked electrocytes: with or without stalks penetrating the electrocytes

(Figure 3) (Sullivan et al., 2000). Additionally, Orlov et al. (2015) indicated that despite the lack of any data on the presence of the electrogenic tissue in Osteoglossidae, both *O. bicirrhosum* and *H. niloticus* can produce weak electric discharges. Therefore, Orlov et al. (2015) postulated that in these fish there might be a primitive electric organ and suggested further investigation of weak sporadic discharges in other osteoglossomorphs.

Air breathing

The gas bladder of a few osteoglossiforms is adapted to aerial respiration as well as buoyancy regulation, sound production and reception (Graham, 1997). The ability of breathing air is seen in representatives of each family (Graham, 1997; Graham and Wegner, 2010; Moritz and Linsenmair, 2007). To breathe, *A. gigas* and *H. niloticus* use a voluminous alveolate gas bladder, whereas *G. niloticus* possesses a highly developed, lung-like gas bladder (Figure 4) (Graham, 1997; Liem, 1989). *P. buchholzi* uses its bladder with numerous extensions (Figure 4) pneumatizing the skeleton also to detect sounds. Such a specialized organ, as found in this species, allows maximizing both respiratory and buoyancy functions (Graham, 1997; Liem, 1989; Poll and Nysten, 1962; Schwartz, 1969). In *Notopterus* spp., a highly specialized, voluminous gas bladder with caudal extension and finger-like projections (Figure 4) plays an additional role in sound production and detection (Graham, 1997; Greenwood, 1963; Liem, 1989). *B. niger* does not have a specialized gas bladder, however observations of the air-gulping manoeuvre (Moritz and Linsenmair, 2007) and long-term surviving in drying ponds (Benech and Lek, 1981) may indicate that this species is air-breathing.

Reproductive biology

The bony-tongue fishes reveal great diversity in terms of reproduction. With the exception of inseminating *P. buchholzi*, all osteoglossomorphs are externally fertilizing.

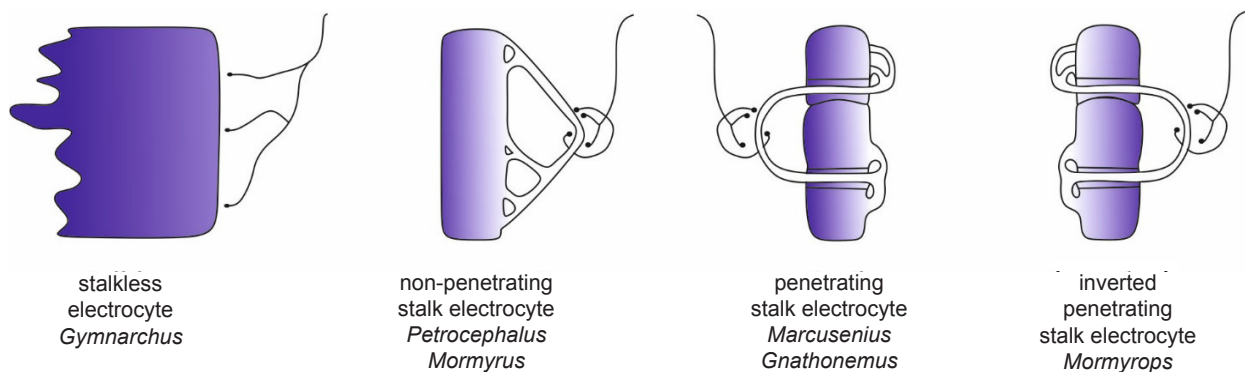


Figure 3. Drawings of electrocytes found in representatives of Gymnarchidae and Mormyridae. Based on Hopkins (1995) with modifications

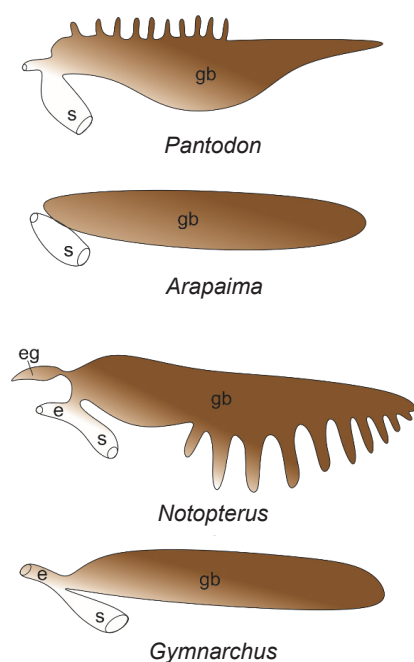


Figure 4. Schemes of gas bladders found in osteoglossiforms. Based on Liem (1989) with modifications. Abbreviations: e – esophagus; eg – extension of gas bladder; gb – gas bladder; s – stomach

Species classified in Osteoglossidae, Notopteridae, Mormyridae and Gymnarchidae exhibit parental care. Males of *N. notopterus* as well as *Chitala* spp. guard eggs, whereas *A. gigas*, *H. niloticus* and *G. niloticus* guard nests with eggs and juveniles (Axelrod and Burgess, 1981; Daget, 1957; Johnels, 1954; Pinxteren, 1974). In *Osteoglossum* and *Scleropages* (with the exception of *S. leichardtii* whose females exhibit parental care) males are mouthbrooders (Merrick and Green, 1982).

Only Hiodontidae and Pantodontidae possess typical paired gonads. In other osteoglossiforms, there is atrophy of the right gonad, therefore only the left one is functional (A.M. Dymek, 2021, A.M. Dymek et al., 2021 b; Dymek and Pecio, 2019; Godinho et al., 2005; Opadokun and Ajani, 2015; Pankhurst et al., 1986; Talajic, 1980).

Males possess tubular testes, which consist of numerous anastomosing tubules (A.M. Dymek, 2021; Dymek and Pecio, 2019). This type is characteristic for evolutionarily older fish taxa, because in Neoteleostei testes are lobular (Billard, 1970; Pecio, 2020). In *P. buchholzi*, testes are divided into the anterior spermatogenic part, in which cysts with cells at different stages of spermatogenesis are located, and the posterior aspermatogenic part functioning as a reservoir of sperm packets and as a testicular gland. The testicular gland has so far been described only in externally fertilizing species, and *P. buchholzi* is the first known inseminating species in which this structure is present (Dymek and Pecio, 2019). A laterally placed testicular gland was observed in *N. notopterus*, whereas it was absent in *X. nigri* and *C. alces* (A.M. Dymek, 2021). The testicular gland in teleosts is a place of steroidogenesis and sperm maturation. Its secretion may nourish sperm (Lahnsteiner et al., 1990; Mansour et al., 2004).

Given the occurrence of four sperm types in osteoglossiforms, this taxon is one of the most diverse among vertebrates in terms of sperm morphology (Figure 5). Only in *P. buchholzi* can one find complex introsperm (Figure 5), defined by Jamieson (1991) as a one of the most compound gametes among all vertebrates. It consists of a conical head, an extremely long (~ 60% of the total sperm length) midpiece with 9 helical mitochondrial derivatives, a fenestrated sheath with vesicles present just under the membrane and a free flagellum (Dymek and Pecio, 2020; van Deurs, 1973; van Deurs and Lastein, 1973).

Other osteoglossiforms possess aquasperm with a round head and a short midpiece with a few mitochondria (Figure 5). An unflagellate spermatozoon was described in *P. afer*, whereas a biflagellate one was found in *H. niloticus* (Mattei, 1970; Mattei et al., 2019). Unique among vertebrates, an aflagellate spermatozoon was reported in *G. niloticus* as well as in five mormyrids, *B. niger*, *M. senegalensis*, *H. bebe*, *M. rume* and *P. bovei* (Mattei, 1991; Mattei et al., 1967, 1972).

As in most teleosts, females of the bony-tongue fishes

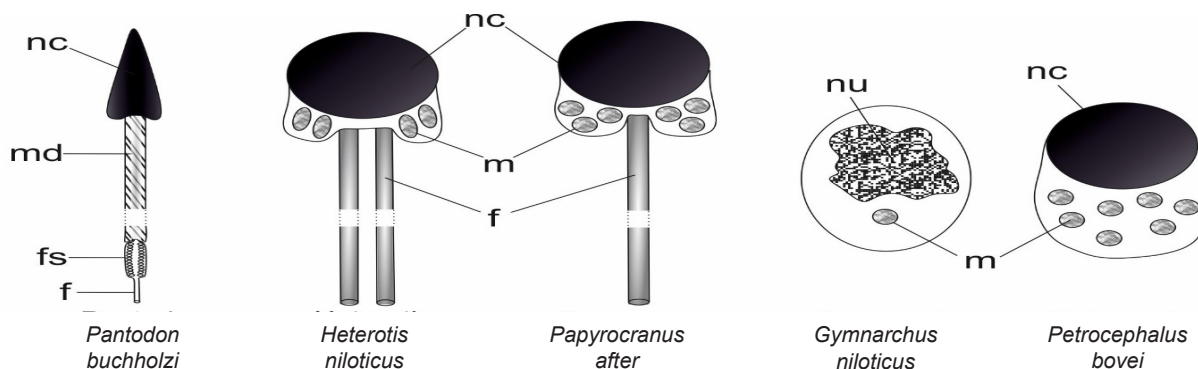


Figure 5. Drawings of spermatozoa that occur in osteoglossiform representatives. Based on Mattei et al. (1967; 2019) with modifications. Abbreviations: f – flagellum; fs – fenestrated sheath; m – mitochondrion; md – midpiece with mitochondrial derivatives; nc – nucleus with condensed chromatin; nu – nucleus with uncondensed chromatin

have cystovaries with a centrally located lumen (A.M. Dymek et al., 2021 b). In ovaries of many inseminating species, there are some modifications related to this type of reproduction (Koya, 1995; Koya et al., 1997; Muñoz et al., 2002, 2000, 1999; Potter and Kramer, 2000; Uribe et al., 2010). In *P. buchholzi*, epithelial invaginations as well as secretory activity and apical specializations of the cells (cilia and microvilli) have been observed (A.M. Dymek et al., 2021 b).

An analysis of the oocyte development in a few osteoglossiforms revealed a great variation of cell composition and the Balbiani body formation even across closely related species (A.M. Dymek et al., 2021 a, b). In previtellogenic oocytes of *P. buchholzi*, there are three types of ooplasm with different electron densities, whereas in *O. bicirrhosum*, *M. cyprinoides* and *B. niger*, two types – centrally located homogenous and peripheral granular ooplasm (A.M. Dymek et al., 2021 b). Cytoplasmatic inclusions also appear in different manners. Cortical alveoli appear before oil droplets in *P. buchholzi*, *G. petersii* and *M. rume*, whereas in *O. bicirrhosum* and *M. cyprinoides* both structures are present at the same time in ooplasm (A.M. Dymek et al., 2021 b).

Importance for humans

Some species of osteoglossiforms are popular in aquaristics as ornamental fish, namely, animals used to beautify aquariums. *P. buchholzi* is one of the most favoured species by aquarists given its large pectoral fins as well as unusual way of feeding – this species can capture prey above the water level (Ibim and Ike, 2019).

The Asian arowana, *S. formosus*, is a common fish in aquaria, especially in Asia, because of its colours (three main varieties of green, gold and red) (Medipally et al., 2016). Additionally, as a result of the presence of two barbels on the jaw, this fish resembles the oriental dragon, the symbol of good luck in Asian culture (Ng and Tan, 1997).

Osteoglossiforms are also important in inland fisheries of some countries. *H. niloticus* is one of the most highly valued species in African fisheries. In aquaculture, it exhibits great growth performances (Adite et al., 2006; Ezekiel and Abowei, 2013; Moreau, 1982; Odo et al., 2009). However, the lack of sexual dimorphism makes its breeding in captivity difficult (Carreiro et al., 2011; Monentcham et al., 2009; Núñez-Rodríguez et al., 2020; Obi, 2010).

Closely related South American *A. gigas*, one of the biggest freshwater species, has been utilized by people as an important source of food (Goulding, 1980; Hrbek et al., 2007; Sánchez, 1960; Van Damme et al., 2015). Unfortunately, it had been the main cause of the dramatic decline of this species in the Amazon by the 1980s, which resulted in a ban for fishing of *A. gigas* for a few years in Brazil (Castello et al., 2009). In the 21st century, this species has begun to be common in the Amazon (Farrel and Azurdry, 2006; Van Damme et al., 2015).

Members of the family Mormyridae are of high importance in African fisheries. They occur in many top riv-

ers (e.g., the Nile, the Niger, the Zambezi, etc.) as well as in streams (Adjibade et al., 2019). Adjibade et al. (2019) indicated that in the Niger River the most common species are *Marcusenius senegalensis*, *Mormyrus macrophthalmus*, *Hyperopisus bebe*, *Petrocephalus bovei*, *Mormyrus rume* and *Hippopotamyrus psittacus*.

Summary

Osteoglossomorpha, an ancient lineage of Teleostei, is a very diverse taxon, which probably results from the early divergence of this group. Numerous adaptations observed in some families or species allow for an analysis of the evolution of different aspects of fish biology. Additionally, the bony-tongue fishes are of great importance for humans as a significant source of food and aquarium attractions (some species). However, the level of the human impact on the populations of these fishes should be balanced to protect them for further generations.

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