

Origin and diversification of the Otophysi clade during the Mesozoic: a case of mosaic evolution?

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Abstract - Almost all distributed today in freshwater, except by few taxa that inhabited coastal marine waters, the Otophysi clade is a group of teleostean with a formerly worldwide distribution in all continents. The Otophysi fossil record is well known by complete species since the Paleocene. However the description of some species in marine sediments from the Cretaceous of Europe, Africa and South America led to a heated debate since the 80's years about the origin and diversification of the Otophysi clade. The aim of this work is to compare the typical outline of the Weberian Apparatus of extant species, which display the transformation series in the first four occipital vertebrae, with some fossil species otophysan-like. Its presence is an otophysan character, but its morphology and anatomy vary depending on the taxa. The observed species present some modifications in the first four vertebrae.

Keywords: Otophysi, anatomy, mosaic evolution, Weberian Apparatus

1. Introduction

Almost all distributed today in freshwater, except by few taxa that inhabited coastal marine waters, the Otophysi clade is a group of teleostean with a formerly worldwide distribution in all continents (Kailola, 2000; Berra, 2001; Ferraris, 2007; L veque *et al.*, 2008). The *Otophysi sensu* Fink and Fink (1981; 1996) and Wiley and Johnson (2010), had been classified into four monophyletic orders (cf. Characiformes (piranhas and tetras) present in South America and Africa, Siluriformes (catfishes), Gymnotiformes (electric eels) and Cypriniformes (minnows and carps)), based on a high quantity of anatomic characters and no longer exclusively shared within them, specially the complex structure so called Weberian Apparatus. Notwithstanding, other papers based on a molecular approach also corroborated such monophyletic condition for the group (Dimmick and Larson, 1996; Orti and Meyer, 1997; Lavou  *et al.*, 2005).

The Otophysi fossil record is well known by complete species since the Paleocene (e.g., Gaudant, 1980; Patterson, 1984; Albert and Fink, 2007; Conway *et al.*, 2010; Malabarba and Malabarba, 2010; Mayrinck *et al.*, 2014), from which the characteristic anatomy of the group was already established. However the description of some species in marine sediments from the Cretaceous of Europe, Africa and South America (cf. †*Lusitanichthys*, †*Salminops*, †*Santanichthys*, †*Clupavus*, †*Sorbinicharax* and

†*Nardonoides*) led to a heated debate since the 80's years about the origin and diversification of the Otophysi clade (e.g., Fink and Fink, 1981; 1996; Fink *et al.*, 1984; Gayet, 1981; 1985; 1986; Patterson, 1970; 1984; Taverne, 1977; 1995; 2003; 2005). Most of the discussions dealt with the primary environment of the early diversification of the clade as well as the erection of possibly missing link in this history. Despite the publication of numerous articles related to the evolutionary origin of the Otophysi based on the molecular data (e.g., Calcagnotto *et al.*, 2005; Hardman, 2005; Peng *et al.*, 2006; Sullivan *et al.*, 2006; Maiden *et al.*, 2008; Saitoh *et al.*, 2011; Nakatani *et al.*, 2011; Chen *et al.*, 2013) and no longer the enhance of the knowledge of certain osteological key characters specially based on ontogenetic studies (e.g., Rosen and Greenwood, 1970; Gayet and Chardon, 1987; Coburn and Futey, 1996; Chardon and Vandevale, 1997; Bird and Mabee, 2003; Grande and de Pinna, 2004; Grande and Young, 2004; Britz and Hoffman, 2006; Hoffman and Britz, 2006; Britz and Moritz, 2007), the known mesozoic fossil record was never reviewed or even observed by the neontologists. This becomes a huge problem, since these fossils are frequently used to calibrate the molecular clock and to infer early biogeographical theories for the group, until nowadays (Saitoh *et al.*, 2003; Briggs, 2005; Peng *et al.*, 2006; Diogo *et al.*, 2008). Recently, we started to review these fossils and surprisingly none of them correspond to a crown

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taxon Otophysi (Mayrinck *et al.*, 2014; 2015; 2017 *in preparation*) and the most close relation to this clade that we were able to propose was to the renamed taxon †*Nardonoides chardoni* as an “Ostariophysi incertae sedis and consider it as a pre-otophysan ostariophysan fish” (Mayrinck *et al.*, 2014, p.417).

It seems quite obviously that the biogeographical history of the Otophysi clade as a whole and its subgroups (Novacek and Marshal, 1976; Briggs, 2005; Gayet, 1982; Lundberg, 1993; Diogo, 2004; Saitoh *et al.*, 2003; Nakatani *et al.*, 2011; Chen *et al.*, 2013) is complex. And moreover, the comprehension of the acquisition of certain key characters, especially the Weberian Apparatus, remains obscure.

The aim of this work is to compare the typical outline of the Weberian Apparatus of extant species, which display the transformation series in the first four occipital vertebrae, with some fossil species otophysan-like. The preliminary results here presented suggest that the rise of the Weberian ossicles or loss of some components (e.g. 1° supraneural) may be independent and that such transformation/arrangement cannot be treated as an unique complex structure.

2. Material

The specimens here observed are housed in the Instituto Superior Técnico (IST), Lisboa, Portugal (†*Lusitanichthys characiformis*); Muséum national d’Histoire naturelle (MNHN), Paris (†*Hakeliosomus hakelensis*; †*Clupavus maroccanus*); Paleontological Collection of the Departamento Nacional de Produção Mineral (DGM), Rio de Janeiro (†*Clupavus brasiliensis*); Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México (UNAM) (new species); Natural History Museum in Boulogne-sur-Mer (BHN) (†*Lusitanichthys africanus*), France; and Museo cívico di Storia Naturale de Verona (MCSNV), Italy (†*Nardonoides chardoni*).

2.1. List of observed specimens

†*Lusitanichthys characiformis*. *Holotype*: IST-575, near-complete skeleton. *Syntypes*: IST-529; IST-532; IST-556; IST-573; IST-574; IST-577; IST-589. *Other material*: IST-DT-575-1 to IST-DT-575-19.

†*Lusitanichthys africanus*. *Holotype*: BHN 2P40. *Paratypes*: BHN 2P41, BHN 2P42 and BHN 2P43.

†*Clupavus maroccanus*. The material of †*Clupavus maroccanus* studied comprises thirty-three specimens housed in the Muséum national d’Histoire naturelle, Paris, Arambourg Collection (MNHN-F DTS). The exemplars belong to two different outcrops; fifteen from Ain-el-Kerma (MNHN-F DTS 75; DTS 78; DTS 82; DTS 83; DTS 98; DTS 109; DTS 111; DTS 113; DTS 132; DTS 140D, G; DTS 142D, G; DTS 145; DTS 146; DTS 256D, G; DTS 258D, G); and sixteen from Sigda (MNHN-F DTS 88D, G; DTS 93; DTS 121; DTS 151; DTS 245D, G; DTS 246D, G; DTS 247D, G; DTS 248D, G; DTS 249; DTS 250; DTS 253; DTS 254; DTS 255; DTS 257D, G; DTS 361; DTS 362). However there is no established holotype, only a lectotype numbered MNHN-F DTS 243D, G, and

all other specimens are considered as syntypes.

†*Clupavus brasiliensis*. *Holotype* DGM 1018. *Paratypes* DGM 1019; 1020, 1021, 1022). None of these specimens have been prepared by the transfer method. We observed the exemplars DGM 1018-1020, based on casts of silicone.

†*Nardonoides chardoni*. *Holotype* MCSNV Na 500. *Paratypes* MCSNV Na 62, MCSNV Na 108, MCSNV Na 109, MCSNV Na 173, MCSNV Na 174, MCSNV Na 175, MCSNV Na 214. *Others specimens* MCSNV Na 8, MCSNV Na 176, MCSNV Na 197, MCSNV 204, MCSNV 205, MCSNV 213, MCSNV 215, MCSNV Na 216, MCSNV Na 217, MCSNV Na 219, MCSNV Na 246, MCSNV Na 517, MCSNV Na 523, MCSNV Na 525.

†*Hakeliosomus hakelensis*. *Paratypes* MNHN-HAK-100, 111, 112, 113, 114d and 116.

3. Results and conclusive discussion

The Weberian Apparatus is a complex structure compounded of soft and bony elements including the modified anteriormost vertebrae. It includes the modified peri- and endolymphatic spaces of the inner ear, the modified anteriormost centra, spines and arches, the resulting Weberian ossicles, and the swimbladder divided into two chambers Text formatting (e.g., Weber, 1820; Sagemehl, 1885; Chardon and Vandevallé, 1997; Britz and Hoffman, 2006). It includes two series of small bony elements (claustrum, scaphium, intercalarium, tripus) linked by the interossicular ligament (e.g., Rosen and Greenwood, 1970). Its presence is an otophysan character, but its morphology and anatomy vary depending on the taxa. Moreover, the homology of certain ossicles is still debated in modern taxa (e.g., Britz and Hoffman, 2006; Hoffman and Britz, 2006). In the fossil species, only the bony elements (centra and ossicles) are preserved and their homology with structures observed in modern fish is hard to establish when the Weberian apparatus does not correspond to a modern type. Except by Grande and de Pinna (2004) in a publication concerning the phylogenetic perspective about the evolution of the Weberian Apparatus (without observing most of the fossils), no one else has worked on this structure and even treated together extant and the controversial taxa from the Cretaceous. The presumed presence of this structure on these fossil taxa was used as an argument to considered them as primitive Otophysi and the probable responsible for the first radiation of the group.

The observed species present some modifications in the first four vertebrae. Generally they show some structures related to the third vertebral centrum which is, by shape and position, very similar to a tripus. The supraneurals seem to be otophysan-like, with the third one expanded and the second one inclined posteriorly. The presence of a tripus-like ossicle and the supraneural pattern together with the absence of intermuscular bones on these first vertebral centra denote a peculiar Weberian structure. Conversely, these species present some structure that cannot be in any case associated to a Weberian Apparatus, and in this it stands out the presence of the first supraneur-

ral, and concomitantly the absence of all other concerning structures/processes/ossicles.

These fossils show a mixture of characters whose acquisition seems to follow a pattern of mosaic evolution. The appearance of a tripus-like and the transformation of the second and third supraneurals are always associated with the presence of the first supraneural. In species in which the first supraneural is absent, the tripus-like is also absent, and other weberian structures are present, such as the transformator process of the second vertebral centrum. This work is a preliminary study of all known Mesozoic fossil taxa attributed to Otophysi and takes part of our project concerning the origin and diversification of this clade.

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