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Research Article

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; Léveque *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; Lavoué *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 Vandevalle, 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 (Novaceck 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. 1º 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 Museum national d'Histoire naturelle, Paris, Arambourg Collection (MNHN-F DTS). The exemplars belong to two differents outcrops; fifteen from Aïn-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 Vandevalle, 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 supraneural, 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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References
Albert, J. S. and Fink, W. L. 2007. Phylogenetic relationships of fossil neotropical electric fishes (Osteichthyes: Gymnotiformes) from the Upper Miocene of Bolivia. Journal of Vertebrate Paleontology 27(1), 17-25.

Berra, T. M. 2001. Freshwater Fish Distribution. Academic Press, San Diego, pp. 605.

Bird, N. C. and Mabee, P. M. 2003. Developmental morphology of the axial skeleton of the zebrafish, *Danio rerio* (Ostariophysi: Cyprinidae). Developmental Dynamics 228, 337-357.

Briggs, J. C. 2005. The biogeography of otophysan fishes (Ostariophysi, Otophysi): a new appraisal. Journal of Biogeography 35, 287-294.

Britz, R. and Hoffman, M. 2006. Ontogeny and homology of the claustra in otophysan Ostariophysi (Teleostei). Journal of Morphology 267, 909-923.

Britz, R. and Moritz, T. 2007. Reinvestigation of the osteology of the miniature African freshwater fishes *Cromeria* and *Grasseichthys* (Teleostei, Gonorynchiformes, Kneriidae), with comments on Kneriidae relationships. Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe 83(1), 3-42.

Calcagnotto, D., Schaefer, S. A. and DeSalle, R. 2005. Relationships among characiform fishes inferred from analysis of nuclear and mitochondrial gene sequences. Molecular Phylogenetics and Evolution 36, 135-153.

Chardon, M. and Vandevalle, P. 1997. Evolutionary trends and possible origin of the Weberian Apparatus. Netherlands Journal of Zoology 47(4), 383-403.

Chen, W.-J., Lavoué, S. and Mayden, R. 2013. Evolutionary origin and early biogeography of otophysan fishes (Ostariophyi: Teleostei). Evolution 67(8), 2218-2239.

Coburn, M. M. and Futey, L. M. 1996. The ontogeny of supraneurals and neural arches in the cypriniforms Weberian Apparatus (Teleostei: Ostariophysi). Zoological Journal of the Linnean Society 116, 333-346.

Conway, K. W., Hirt, M. V., Yang, L., Mayden, R. L. and Simons, A. M. 2010. Cypriniformes: systematics and paleontology. In: Nelson, J. S., Schultze, H.-P. and M. V. H. Wilson (Eds.), Origin and Phylogenetic Interrelationships of Teleosts. Verlag Dr. Friedrich Pfeil, München, pp. 295-316.

Dimmick, W. W. and Larson, A. 1996. A molecular and morphological perspective on the phylogenetic relationships of the otophysan fishes. Molecular Phylogenetics and Evolution 6, 120-133.

Diogo, R. 2004. Phylogeny, origin and biogeography of catfishes: support for a Pangean origin of modern teleosts and reexamination of some Mesozoic Pangean connections between the Gondwana and Laurasian supercontinents. Animal Biology 54, 331-351.

Diogo, R., Doadrio, I. and Vandewalle, P. 2008. Teleostean phylogeny based on Osteological and Myological Characters. International Journal of Morphology 26(3), 463-522.

Fink, S. V. and Fink, W. L. 1981. Interrelationships of the ostariophysan fishes (Teleostei). Zoological Journal of the Linnean Society of London 72, 297-353.

Fink, S. V., Greenwood, P. H. and Fink, W. L. 1984. A critique of recent work on fossil ostariophysan fishes. Copeia 4, 1033-1041.

Fink, S. V. and Fink, W. L. 1996. Interrelationships of Ostariophysan Fishes. In: Stiassny, M. L. J., Parenti, L. R. and Johnson, G. D. (Eds.), Interrelationships of Fishes. Academic Press, San Diego, pp. 209-249.

Ferraris, C. J. 2007. Checklist of catfishes, recent and fossil (Osteichthyes: Siluriformes), and catalogue of Siluriform primary types. Zootaxa 1418, 4 – 300.

Gaudant, J. 1980. *Eurocharax touraini* nov. gen. nov. sp. (poisson, téléostéen, Ostariophysi), nouveau Characidae fossile des «Calcaires à Bithynies» du Var. Géobios 13, 683-703.

Gayet, M. 1981. Contribution à l'étude anatomique et systématique de l'ichthyofaune cénomanienne du Portugal. Deuxiéme partie: Les ostariophysaires. Comunicações dos Serviços Geológicos de Portugal 67(2), 173-190.

Gayet, M. 1982. Considération sur la phylogénie et la paléobiogéographie des ostariophysaires. Géobios 6, 39-52.

Gayet, M. 1985. Contribution à l'Étude Anatomique et Systématique de l'Ichthyofaune Cénomanienne du Portugal. Comunicações do Serviço Geológico de Portugal 71, 91-118.

Gayet, M. 1986. About ostariophysan fishes: a reply to S. V. Fink, P. H. Greenwood and W. L. Fink's criticisms. Bulletin du Muséum National d'Histoire Naturelle 8, 393-409.

Gayet, M. and Chardon, M. 1987. Possible otophysic connections in some fossil and living ostariophysan fishes. Proceedings of the V Congress of European Ichthyology, Stockholm, 31-42.

Grande, T. and de Pinna, M. 2004. The evolution of the Weberian Apparatus: A phylogenetic perspective. In: Arratia, G. and Tintori, A. (Eds.), Mesozoic fishes 3: Systematics, Paleoenvironments, and Biodiversity. Verlag Dr. Friedrich Pfeil, München, pp. 429-448.

Grande, T. and Young, B. 2004. The ontogeny of the Weberian Apparatus in the zebrafish *Danio rerio* (Ostariophysi: Cypriniformes) with comments on the homology of Weberian ossicles. Zoological Journal of Linnean Society 140, 241-254.

Hardman, M. 2005. The phylogenetic relationships among non-diplomystid catfishes as inferred from mitochondrial cytochrome *b* sequences; the search for the ictalurid sister taxon (Otophysi: Siluriformes). Molecular Phylogenetics and Evolution 37, 700-720.

Hoffmann, M. and Britz, R. 2006. Ontogeny and homology of the neural complex of otophysan Ostariophysi. Zoological Journal of the Linnean Society 175, 301-330.

Kailola, P. J. 2000. Six new species of fork-tailed catfishes (Pisces, Teleostei, Ariidae) from Australia and New Guinea. The Beagle, Records of the Museums and Art Galleries of the Northern Territory 16, 127-144.

Lavoué, S., Miya, M., Inoue, J. G., Saitoh, K., Ishiguro, N. B. and Nishida, M. 2005. Molecular systematics of gonorynchiform fishes (Teleostei) based on whole mitogenetic sequences: Implications for higher-level relationships within otocephala. Molecular Phylogenetics and Evolution 37, 165-177.

Lévêque, C., Oberdoff, T., Paugy, D., Stiassny, M. L. J. and Tedesco, P. A. 2008. Global diversity of fish (Pisces) in freshwater. Hydrobiologia 595, 545-567.

Lundberg, J. G. 1993. African-South American freshwater fish clades and continental drift: problemswith a paradigm. In: Goldblatt, P. (Ed.), Biological relationships between Africa and South America. Yale University Press, New Haven, pp. 156-199

Malabarba, M. C. and Malabarba, L. R. 2010. Biogeography of Characiformes: an evaluation of the available information of fossil and extant taxa. In: Nelson J. S., Schultze, H. - P. and Wilson, M. V. H. (Eds.), Origin and Phylogenetic Interrelationships of Teleosts. Verlag Dr. Friedrich Pfeil, München, pp. 317-336.

Maiden, R., Tang, K. L., Wood, R. M., Chen, W. -J., Agnew, M. K., Conway, K. W., Yang, L., Simons, A. M., Bart, H. L., Harris, P. M., Li, J., Wang, X., Saitoh, K., He, S., Liu, H., Chen, Y., Nishida, M. and Miya, M. 2008. Inferring the Tree of Life of the order Cypriniformes, the earth's most diverse clade of freshwater fishes: Implications of varied taxon and character sampling. Journal of Systematics and Evolution 46(3), 424-438.

Mayrinck, D., Brito P. M. and Otero, O. 2014. Review of the osteology of the fossil fish formerly attributed to the genus †*Chanoides*, systematic and implications for the definition of otophysan bony characters. Journal of Systematic Palaeontology 13(5), 397-420.

Mayrinck, D., Brito, P. M. and Otero, O. 2015. Anatomical review of †*Salminops ibericus*, a Teleostei *incertae sedis* from the Cenomanian of Portugal, anciently assigned to Characiformes and possibly related to crossognathiform fishes. Cretaceous Research 56, 66-75.

Nakatani, M., M. Miya, K. Mabuchi, K. Saitoh, and M. Nishida. 2011. Evolutionary history of Otophysi (Teleostei), a major clade of the modern freshwater fishes: Pangaean origin and Mesozoic radiation. BMC Evolutionary Biology 11, e177.

Novachek, M. J. and Marshall, L. G. 1976. Early biogeography history of Ostariophysan fishes. Copeia 1976, 1-12.

Orti, G. and Meyer, A. 1997. The radiation of characiform fishes and the limits of resolution of mitochondrial ribosomal DNA sequences. Systematic Biology 46, 75-100.

Patterson, C. 1970. Two Upper Cretaceous salmoniform fishes from the Lebanon. Bulletin of the British Museum (Natural History), Geology 19, 205-296.

Patterson, C. 1984. *Chanoides*, a marine Eocene otophysan fish (Teleostei: Ostariophysi). Journal of Vertebrate Paleontology 4, 430-456.

Peng, Z., He, S., Wang, J., Wang, W. and Diogo, R. 2006. Mitochondrial molecular clocks and the origin of the major Otocephalan clades (Pisces: Teleostei): A new insight. Gene 360, 113-124.

Rosen, D. E. and Greenwood, P. H. 1970. Origin of the Weberian apparatus and the relationships of the ostariophysan and gonorynchiform fishes. American Museum Novitates 2428, 1-25.

Sagemehl, M. 1885. Beiträge zur vergleichenden Anatomie der Fische. III. Das Cranium der Characinidien nebst allgemeinen Bemerkungen über die mit einem Weber'schen Apparat versehenen Physostomenfamilien. Morphologisches Jahrebücher 10, 1-19.

Saitoh, K., Miya, M., Inoue, J. G., Ishiguro, N. B. and Nishida, M. 2003. Mitochondrial genomics of ostariophysan fishes: perspectives on phylogeny and biogeography. Journal of Molecular Evolution 56, 464-472.

Saitoh, K., Sado, T., Doosey, M. H., Bart, H. L., Inoue, J. G., Nishida, M., Mayden, R. and Miya, M. 2011. Evidence from mitochondrial genomics supports the lower Mesozoic of South Asia as the time and place of basal divergence of cypriniform fishes (Actinopterygii: Ostariophysi). Zoological Journal of Linnean Society 161, 633-662.

Sullivan, J. P., Lundberg, J. G. and Hardman, M. 2006. A phylogenetic analysis of the major groups of catfishes (Teleostei: Siluriformes) using *rag*1 and *rag2* nuclear gene sequences. Molecular Phylogenetics

and Evolution 41, 636-662.
Taverne, L. 1977. Ostéologie de *Clupavus maroccanus* (Crétacé supérieur du Maroc) et considérations sur la position systématique et les relations des Clupavidae au sein de l'ordre des Clupéiformes *sensu stricto* (Pisces, Teleostei). Géobios 10(5), 697-722.
Taverne, L. 1995. Description de l'Appareil de Weber du téléostéen Crétacé marin *Clupavus maroccanus* et ses implications phylogénétiques. Belgian Journal of Zoology 125(2), 267-282.
Taverne, L. 2003. Les poissons crétacés de Nardò. 16º. *Sorbinicharax verraesi* gen. et sp. nov. (Teleostei, Ostariophysi, Otophysi, Characiformes). Bolletino del Museo Civico di Storia Naturale di Verona 27, 29-45.
Taverne, L. 2005. Les poissons crétacés de Nardò. 20º. *Chanoides chardoni* sp. nov. (Teleostei, Ostariophysi, Otophysi). Bolletino del Museo Civico di Storia Naturale di Verona 29, 39-54.
Weber, E. H. 1820. De aure et auditu hominis et animalium. Pars I. De aure animalium aquatilium. Lipsia (Leipzig), Gerhard Fleischer.
Wiley, E. O. and Johnson, G. D. 2010. Teleost classification based on monophyletic groups. In: Nelson J. S., Schultze, H.- P. and Wilson, M. V. H. (Eds.), Origin and Phylogenetic Interrelationships of Teleosts. Verlag Dr. Friedrich Pfeil, München, pp. 123-182.