RESEARCH & KNOWLEDGE

Review Article

The origination and rise of teleost otolith diversity during the Mesozoic

Werner Schwarzhans[1,*], Tanja Schulz-Mirbach[2], Antoni Lombarte[3] and Victor M. Tuset[3]

[1] Natural History Museum of Denmark, Universitätsparken 15, 2100 Copenhagen, Denmark
[2] Ludwig-Maximilians-University, Department Biology II, Großhaderner Strasse 2, 82152 Planegg-Martinsried, Germany
[3] Institut de Ciències del Mar-CSIC, Passeig Marítim 37-49, Barcelona 08003, Catalonia, Spain

Abstract - The development of an improved hearing sense in teleosts as expressed in fossil otoliths may have been one important element in the success of their evolution. Hence, fossil otoliths add valuable information to paleoichthyology. Teleost otolith morphology, however, has initially diversified very slowly during the Jurassic and Early Cretaceous and accelerated only during major phases of teleost radiation in Late Cretaceous and Paleogene times.

Keywords: Otolith, macula sacculi, morphological disparity

1. Introduction

Otoliths are solid calcium carbonate aggregates in the ear of actinopterygian fishes, while most other vertebrates have numerous tiny crystals, so-called otoconia (Carlström, 1963). Teleosts possess three sets of otoliths, namely the lapillus in the utricle, the sagitta in the saccule, and the asteriscus in the lagena, which are mostly composed of aragonite (sagitta, lapillus) or vaterite (asteriscus) (Carlström, 1963). Each otolith overlies the respective sensory epithelium (= macula). The macula sacculi is characterized by sensory hair cells that are arranged into different orientation groups (Platt and Popper, 1981). The orientation of a sensory hair cell and thus its morphological and physiological polarization is based on the position of its eccentrically placed kinocilium within the ciliary bundle (Platt and Popper, 1981). Relative motion between otolith acting as inertial mass and ciliary bundles leads to (maximum) stimulation of the sensory hair cells, if the bundle is deflected towards the kinocilium (Hudspeth, 1985). The saccule together with the lagena is hypothesized to play an important role for the acoustic sense.

The sagitta is usually the largest and commonly referred to as the "otolith". It has developed a particularly diverse morphology in teleosts, which is generally found to be diagnostic at the species level and often at higher taxonomic ranks as well; this variation in otolith morphology is extensively used in the fossil record for the reconstruction of non-skeleton-based fossil fish faunas (Nolf, 2013). Isolated otoliths are much more abundant than articulated and identifiable fossil fish skeletons. Therefore, they allow a more continuous tracking of the fossil record of actinopterygian fishes through space and time, especially in sediments which are devoid of articulated skeletons. In addition, isolated otoliths tend to represent assemblages of small fish having lived in well oxygenated shallow waters and in offshore environments, thereby partly complementing articulated skeletons which are often found in carbonatic rocks or in sediments indicating anoxic environments (Schwarzhans, 2012). However, the identification of fossil species or higher taxa using isolated otoliths depends very much on the comparison with Recent taxa or (rare) fossil fishes displaying otoliths *in situ*. Moreover, otoliths cannot provide the level of "evolutionary" detail as articulated skeletons do and they become increasingly rare with geological age because of their composition of metastable aragonite.

2. Methods

Here, we present and discuss the early phases in the evolution of Mesozoic teleost otolith morphology and the rise of new sulcus patterns that may be correlated with the orientation patterns of ciliary bundles on the macula sacculi (Schulz-Mirbach and Ladich, 2016). A geometric morphological analysis of the contour and sulcus has been used to describe the evolution (Tuset *et al*., 2016) and diversification of the otolith morphology. Morphological disparity is calculated as the sum of the diagonal elements of the group covariance matrix of the Procrusted Variance using the Geomorph package (Adams *et al*., 2014) in R. In contrast to other measures of disparity, multivariate variance has the desirable property of being relatively insensitive to variations in sample size.

3. Results

Teleost (sagitta) otoliths are readily recognized by the presence of a structured and diversified sulcus in an axial position on the inner face of the otolith, corresponding to a diversified macula sacculi, which attaches to the sulcus (Fig. 1). The macula sacculi in teleost fishes displays five principle orientation patterns of ciliary bundles including

*Author for correspondence: wwschwarz@aol.com

sub-patterns and some specializations thereof (Popper and Coombs, 1982; Schulz-Mirbach and Ladich, 2016). The functional advantage of teleost otoliths remains widely elusive; however, the morphological diversification of otoliths clearly flourished with the explosive radiation of teleosts and is therefore suggestive of an important role in teleost evolution.

The earliest true teleost otoliths are known from the Sinemurian, synchronous with the earliest leptolepiform skeletons of the genus *Proleptolepis*. These "leptolepid"-type otoliths are calibrated by *in situ* finds in *Leptolepis normandica* and *Cavenderichthys talbraganensis* (Delsate, 1997 and unpublished data), with the caveat, that no otoliths are known from extinct stem Teleostei such as the Pholidophoridae (Arratia, 2013). "Leptolepid"-type otoliths represent an "archaetypical" teleost otolith morphology, for which the term "archaesulcoid" had been coined (Schwarzhans, 1978) (Fig. 1). Extant teleosts displaying a similar otolith morphology are predominantly found associated with the widespread "standard" macula pattern (Popper and Coombs, 1982). All known teleost otoliths from the Jurassic and many from the Early Cretaceous show the same otolith pattern. As a result, the otolith morphospace was rather restricted throughout this time period (Fig. 2).
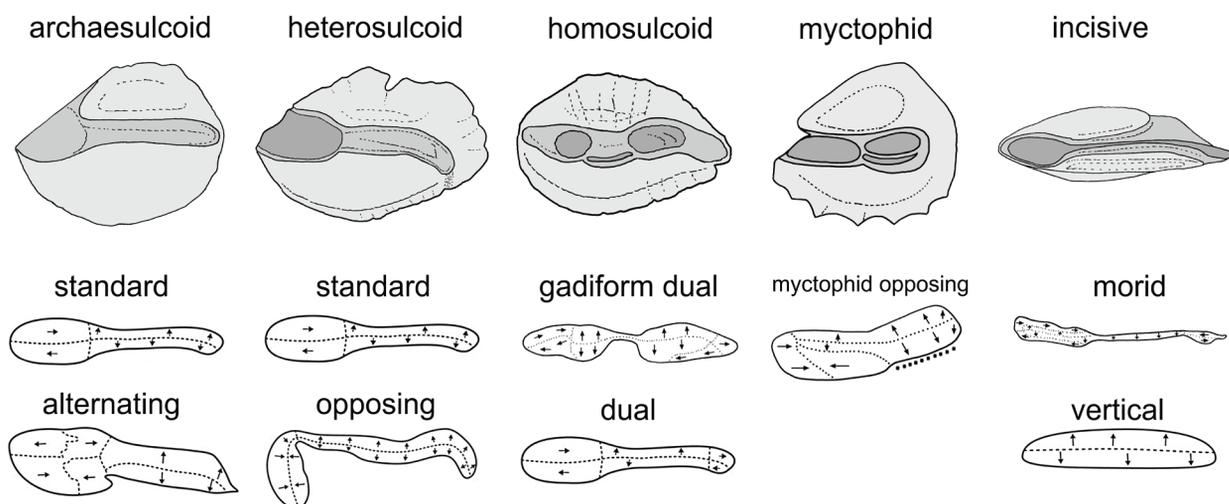

Figure 1. Principle sulcus morphologies of sagitta otoliths (upper row) and associated macula patterns (lower row) (after Schwarzhans, 1978; Schulz-Mirbach and Ladich, 2016).

During Late Jurassic, the earliest putative elopomorph and osteoglossomorph otoliths however, recorded (Nolf, 2013). Their occurrence is more or less in accordance with skeletal findings (Patterson, 1993). The Elopomorpha and also one osteoglossiform family appear to have a potentially synapomorphic "alternating" macula pattern (Schulz-Mirbach and Ladich, 2016). During the Early Cretaceous, increasing diversity in elopiform and albuliform otoliths is observed, slightly predating the earliest skeletal finds. These are the first otolith morphologies that can be linked to extant teleost groups at family level.

The Aptian to Turonian time interval has yielded few otolith associations (Nolf, 2004; 2016) and even fewer otoliths *in situ* (revealed by microCT imaging; Schwar- zhans, Beckett, Schein and Friedman, ms.). The diversity of otolith morphology has slightly increased. "Leptolepid"-type otoliths are still present and elopomorph and possibly protacanthopterygian otoliths become more common and diverse (Fig. 2). A few more modern otolith morphologies are emerging as well, but without adequate linking to *in situ* finds; thus, their interpretation is controversial. The postulated occurrence of acanthomorph otoliths in the Aptian (Nolf, 2004) and of "perciform" otoliths in the Cenomanian (Nolf, 2016) remains to be verified. This contrasts with the first skeleton-based acanthomorphs in the Cenomanian (Patterson, 1993) and of perciforms in the Late Cretaceous to Paleocene (Carnevale and Johnson, 2015).
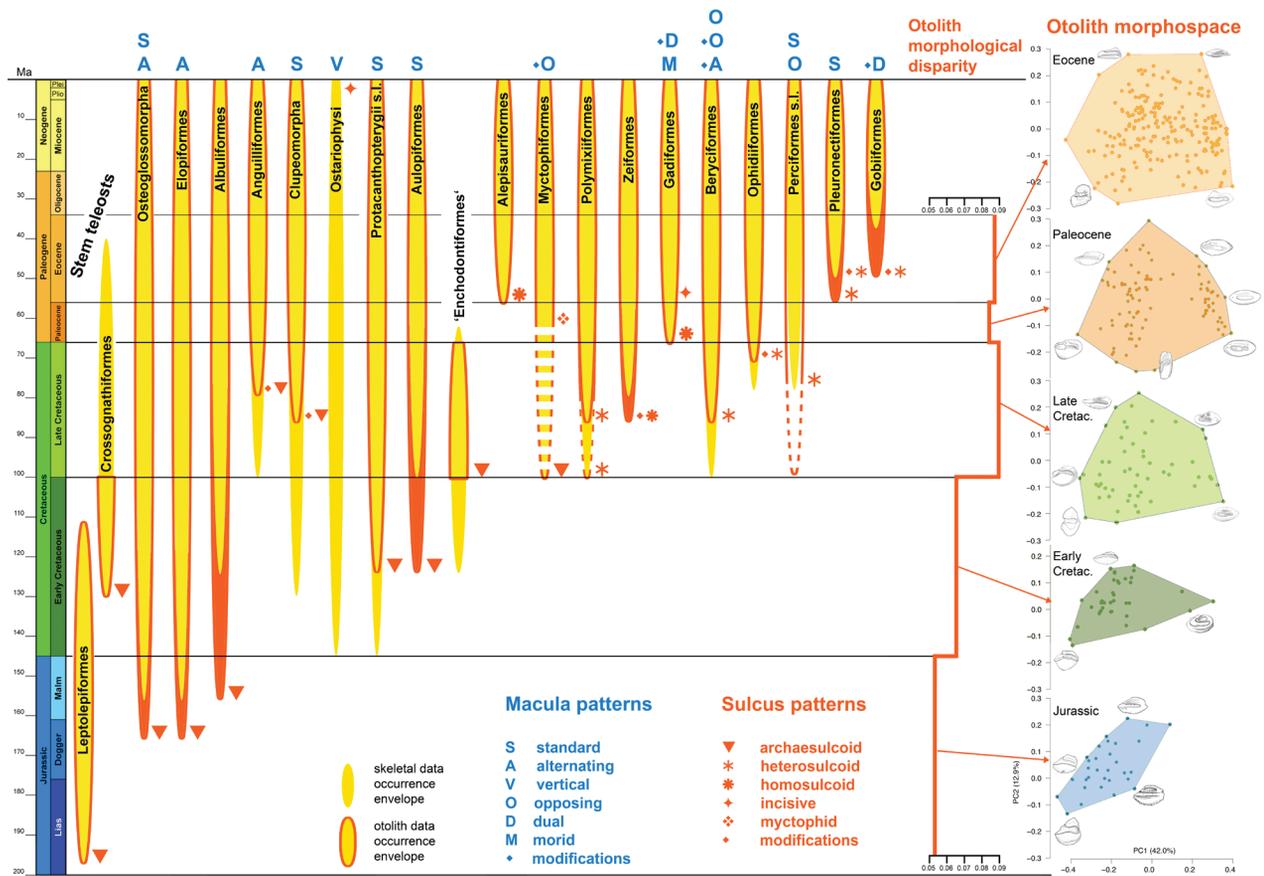
Figure 2. The fossil record of skeleton- and sagitta otolith-based data of selected teleost groups through time, and the evolution of the morphological diversity of otoliths.

The Late Cretaceous (Senonian) marks the onset of a significant increase in otolith diversity (Fig. 2). At that time, several different morphological types emerge such as the acanthomorph (mostly beryciforms and holocentriforms, but also first unambiguous perciforms), anguilliform, stomiiform, aulopiform, zeiform, polymixiiform, ophidiiform, and potentially myctophiform. Most of these otolith-based records are consistent with respective skeleton finds (Patterson, 1993). Presence of *Myripristis*-type otoliths point to a unique specialization of the macula sacculi at this time; *Sargocentron*-type otoliths are characterized by a posterior-ventrally bent cauda (heterosulcoid sulcus). The Myctophiformes have a unique "opposing" macula pattern with the rear vertical section extending over the anterior opposing section and a line of large cells below the posterior part of the macula sacculi (Popper, 1977). The latter feature may relate to the unique caudal pseudocolliculum found in myctophid otoliths (Schwarzhans, 1978), and is first observed in the Late Paleocene. Many otolith morphologies found in the Late Cretaceous are highly specialized belonging to extinct taxa and therefore pose a severe problem for taxonomic allocation due to the paucity of fossils with otoliths *in situ* (Schwarzhans, 2010; 2012).

After the K/Pg-boundary, a new composition and diversification of otolith morphologies is observed during the Paleogene, most notably with the advent of gadiforms during Paleocene, perciforms and pleuronectiforms during Paleocene and Eocene or gobiiforms during Eocene to Oligocene (Fig. 2). Again, these otolith finds are consistent with skeleton-based records (Patterson, 1993). The Gadiformes are characterized by a symmetrical otolith morphology (homosulcoid sulcus) and a "gadiform dual" macula pattern (Lombarte and Popper, 2004), but also include the family Moridae with a highly specialized morphology of the otolith and its macula (Deng *et al*., 2011) possibly triggered by specific extensions of the swimbladder contacting the ears. The gobies also developed a specific otolith morphology along with a specific "dual" macula pattern. In conclusion, the otolith morphospace has increased significantly during the Late Cretaceous, and has reached its current complexity and diversity during the Paleogene with the advent of gadiforms and gobiiforms and their specific otolith and macula developments.

4. Discussions and conclusions
The emergence of the diversity of sulcus morphology may be connected with major evolutionary events in teleosts and extrinsic factors; however future studies have to test this assumption. We further emphasize the urgency for studies of otoliths *in situ* in order to overcome persisting obstacles in their taxonomic interpretation. The results of the analysis of the otolith morphospace show a noticeable increase of the disparity (MD) from Jurassic (MD=0.053) to Late Cretaceous (MD=0.090). The greatest expansion occurred during Late Cretaceous with the advent of fusiform and tall otoliths with a heterosulcoid sulcus, and with mesial sulcus positions. During the Palaeocene (MD=0.083) the gadiform homosulcoid sulcus occurred,

and mesial sulci increased noticeably. Finally, in the Eocene (MD=0.087) the complete morphospace was filled with a wide variety of otolith outlines and sulcus shapes (Fig. 2).

Our understanding has increased regarding the interplay between otoliths and the corresponding maculae, but we still lack some basic knowledge about the effects of sulcus morphology and otolith shape on ear function. Further progress will depend primarily on two fields of research:

- We need a wider array of investigations of the macula sacculi covering a broader range of the enormous diversity of Recent actinopterygian fishes. These data should be integrated into studies on otolith morphology, with special focus on the sulcus acusticus.

- An intense search for otoliths *in situ* is strongly promoted, either by physical observation or application of novel techniques such as microCT imaging. Particular emphasis should be on fishes from crucial time periods in the evolution of teleosts such as the Aptian-Albian and the Late Cretaceous.

References
Adams, D. C., Otárola-Castillo, E. and Sherratt, E. 2014. Geomorph: software for geometric morphometric analyses. R package version 2.0. (http://CRAN.R-project.orgpackage=geomorph).

Arratia, G. 2013. Morphology, taxonomy, and phylogeny of Triassic pholidophorid fishes (Actinopterygii, Teleostei). Journal of Vertebrate Paleontology 33, (suppl. 1), 1-138.

Carlström, D. 1963. A crystallographic study of vertebrate otoliths. Biological Bulletin 125 (3), 441-463.

Carnevale, G. and Johnson, G.D. 2015. A Cretaceous cusk-eel (Teleostei, Ophidiiformes) from Italy and the Mesozoic diversification of percomorph fishes. Copeia 103 (4), 771-791.

Delsate, D. 1997. Actinoptérygiens du Toarcien inférieur du Grand Duché de Luxembourg: présence de *Leptolepis normandica* NYBELIN 1962 (Téléostéen) avec otolithes *in situ*. - Travaux scientifiques du Musée national d'histoire naturelle de Luxembourg 27, 105-129.

Deng, X. H., Wagner, H.-J. and Popper, A. N. 2011. The inner ear and its coupling to the swim bladder in the deep-sea fish *Antimora rostrata* (Teleostei: Moridae). Deep-Sea Research I 58, 27-37.

Hudspeth, A. J. 1985. The cellular basis of hearing: The biophysics of hair cells. Science 230, 745-752.

Lombarte, A. and Popper, A. N. 2004. Quantitative changes in the otolithic organs of the inner ear during the settlement period in European hake *Merluccius merluccius*. Marine Ecology Progress Series 267, 233-240.

Nolf, D. 2004. Otolithes des poissons aptiens du Maestrazgo (province de Castellon, Espagne Orientale). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 74, 101-120.

Nolf, D. 2013. The diversity of fish otoliths, past and present. Royal Belgian Institute of Natural Sciences, pp. 222.

Nolf, D. 2016. Otoliths of Cenomanian fishes in the Ballon Marl (France), the earliest fossil record of perciform fishes. Bulletin d'information des Géologues du Bassin de Paris 53, 14-20.

Patterson, C. 1993. Osteichthyes: Teleostei. In: Benton, M. J. (Ed.), The fossil record 2. Chapman & Hall, 621-656.

Platt, C. and Popper, A. N. 1981. Fine structure and function of the ear. In: Tavolga, W. N., Popper, A. N. & Fay, R. R. (Eds.), Hearing and Sound Communication in Fishes. Springer, New York, 3-38.

Popper, A. N and Coombs, S. 1982. The morphology and evolution of the ear in Acanthopterygian fishes. American Zoologist 22, 311-328.

Schulz-Mirbach, T. and Ladich, F. 2016. Diversity of inner ears in fishes: Possible contribution towards hearing improvements and evolutionary considerations. In: Sisneros, J. A.(Ed.), Fish Hearing and Bioacustics. Advances in Experimental Medicine and Biology, 341-391.

Schwarzhans, W. 1978. Otolith-morphology and its usage for higher systematical units, with special reference to the Myctophiformes s.l. Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie 15, 167-185.

Schwarzhans, W. 2010. Otolithen aus den Gerhartsreiter Schichten (Oberkreide, Maastricht) des Gerhartsreiter Grabens (Oberbayern). Palaeo Ichthyologica 4, pp.100.

Schwarzhans, W. 2012. Fish otoliths from the Paleocene of Bavaria (Kressenberg) and Austria (Kroisbach and Oiching-Graben). Palaeo Ichthyologica 12, pp. 88.

Tuset, V. M., Farré, M., Otero-Ferrer, J. L., Vilar, J. A., Morales-Nin, B. and Lombarte, A. 2016. Testing otolith morphology for measuring marine fish biodiversity. Marine and Freshwater Research 67, 1037-1048.