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Article type : Original Article

Handling Editor: Dr. Imran Rahman

Running head: CT reveals otoliths in situ

Computed tomography scanning as a tool for linking the skeletal and otolith-based fossil records  
of teleost fishes

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This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/pala.12349](https://doi.org/10.1111/pala.12349)

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**Abstract:** Micro-computed tomography scanning ( $\mu$ CT scanning) now represents a standard tool for non-destructive study of internal or concealed structure in fossils. Here we report on otoliths found *in situ* during routine  $\mu$ CT scanning of three-dimensionally preserved skulls of Palaeogene and Cretaceous fishes. Comparisons are made with isolated otolith-based taxa in order to attempt correlations between the body fossil and otolith fossil records. *In situ* otoliths previously extracted mechanically from specimens of *Apogon macrolepis* and *Dentex laekeniensis* match our  $\mu$ CT models. In some cases, we find a high degree of congruence between previously independent taxonomic placements for otolith and skeletal remains (*Rhinocephalus*, *Osmeroides*, *Hoplopteryx*). Unexpectedly, *in situ* otoliths of the aulopiform *Apateodus* match isolated otoliths of Late Cretaceous age previously interpreted as belonging to gempylids, a group of percomorph fishes that do not appear in the body fossil record until the Palaeogene. This striking example of convergence suggests constraints on otolith geometry in pelagic predators. The otoliths of *Apateodus* show a primitive geometry for aulopiforms and lack the derived features of Alepisauroidea, the lizardfish clade to which the genus is often attributed. *In situ* otoliths of Early Cretaceous fishes (*Apsopelix*) are not well preserved, and we are unable to identify clear correlations with isolated otolith morphologies. We conclude that the preservation of otoliths suitable for  $\mu$ CT scanning appears intimately connected with the taphonomic history, lithological characteristics of surrounding matrix, and syn- and postdepositional diagenetic effects.

**Key words:** Teleostei,  $\mu$ CT scanning, otolith, *Apateodus*, *Osmeroides*, *Rhinocephalus*,

With a diversity of species challenging that of all tetrapod radiations combined, teleost fishes are critical component of modern vertebrate biodiversity. Extant teleosts occupy aquatic settings ranging from ocean trenches to alpine streams, and show a striking range of anatomical innovations reflecting a broad range of ecologies (Nelson *et al.* 2016). Diversity in the modern fauna is complemented by a rich fossil record, which, for the teleost total-group, is well established since the Early Jurassic and extends deep into the Triassic (Friedman 2015; Tintori *et al.* 2015).

Teleosts, and indeed fishes generally, are unusual among vertebrates in having a fossil record characterized by a relative abundance of articulated, effectively complete skeletons. The bulk of our understanding of the relationships and diversification of extinct fishes, from the seminal work of Agassiz (1833-1844) onward, derives from this remarkable anatomical archive. Such intact fossils can yield osteological data comparable to that available for extant species, and can be critical for illuminating patterns of character evolution (Friedman 2008) or resolving phylogenetic relationships (Grande 2010). Articulated specimens also provide the substrate for functional and palaeobiological analysis, ranging from individual anatomical systems (e.g. jaws: Bellwood *et al.* 2015) to overall geometry of the body and fins (e.g. Friedman 2010). Despite these clear strengths, the body fossil record of teleosts suffers from conspicuous deficiencies. The preservation of articulated fishes requires particular taphonomic conditions, with the consequence that horizons yielding complete skeletons are generally restricted to specific facies such as laminated limestones and anoxic shales. The result is a highly heterogenous, gap-filled stratigraphic distribution of exceptional deposits (e.g. apparent abundance during sea-level highstands: Guinot & Cavin 2015) that, combined with the less informative nature of isolated fish bones, has led to repeated suggestions that the fish fossil record is particularly prone to bias arising from so-called *Lagerstätten* effects (Patterson & Smith 1987, 1989; Patterson 1993a, b; but see Lloyd & Friedman 2013).

Skeletal fossils are not the only palaeontological line of evidence bearing on past patterns of fish diversity; they are joined by a rich record of isolated otoliths. Informally known as ‘ear stones’, otoliths are consolidated aragonitic bodies housed within the labyrinth organ of fishes, and involved in hearing and balance. Living actinopterygians have three pairs of otoliths, with the largest typically located in the sacculus. First systematically described by Koken (1884), otoliths are often diagnostic for species, genera and higher taxa. They are abundant in the fossil

record where aragonite is preserved and sediments are unconsolidated. The otolith record is, as a consequence, denser both stratigraphically and geographically than the spottier archive of skeletal remains. The ubiquity of fossil otoliths led Patterson (1977: p. 580) to conclude that the fossil records of teleosts and mammals were comparable in terms of quality and density: “whereas mammals have teeth, teleosts have otoliths.”

The otolith record is not without problems. Facies biases aside, otoliths are relatively uncommon in Mesozoic rocks, a probable consequence of ‘calcite sea’ chemistry that favoured the dissolution of aragonite during this interval (Nolf 1995; similar patterns apply to aragonitic fossils in other intervals characterized by comparable marine chemistry: Cherns & Wright 2000; Palmer *et al.* 1988). Reports of Palaeozoic otoliths are sparse, reflecting little research effort and rarity of unconsolidated sediments of this age. These taphonomic and research biases are minor in comparison to the greatest challenge of isolated fossil otoliths: their allocation to genera is almost exclusively based on correlation with extant otoliths, rather than association with diagnostic fossil skeletal remains. This phenetic exercise becomes more problematic for otoliths from increasingly ancient strata. The taphocoenoses of otoliths and articulated skeletons diverge as a consequence of mineralogical differences, a restrictive range of sedimentary settings conducive to the preservation of articulated skeletons and otoliths, and difficulties in retrieving *in situ* otoliths from articulated skeletons. Because few otoliths are known *in situ* from body fossils, the taxonomy of fossil otoliths has developed largely parallel to that of articulated material. Patterson’s claimed equivalence between mammal teeth and teleost otoliths is thus false. To put the teleost record in perspective, it is as if extinct mammals were known from abundant isolated teeth combined with rarer skeletons almost always lacking preserved dentition.

The identification and characterization of otoliths preserved in association with skeletons provides the key to marrying these two complementary teleost fossil records. The most recent census suggests that fewer than 100 skeleton-based fossil species bear otoliths (Nolf 2013). In many of these taxa otoliths are mentioned rather than described in detail (but see: Fedotov 1976; Schwarzhans 2014; Schwarzhans *et al.* 2017a-e; Prikryl *et al.* 2017), and most of those *in situ* finds are from Oligocene or younger deposits. So far few are recorded from the Eocene, and none from the Paleocene and Late Cretaceous (Fig. 1). The Late Cretaceous-Palaeogene represents a crucial interval in the evolution of modern teleosts, associated with the origin of many extant lineages, especially within the species-rich percomorph radiation (Near *et al.* 2013).

In addition, multiple skeleton-based lineages of teleost fishes became extinct at or near the Cretaceous-Palaeogene boundary (Friedman 2009). Otoliths are virtually unknown for these once abundant extinct groups, posing a substantial problem for the interpretation of isolated otoliths from the Cretaceous.

Heavily compressed skeletons are the most common articulated remains in the fish record, and it is from such specimens that the vast majority of *in situ* otoliths have been described. However, the geometry of such specimens is often a challenge for standard tomographic studies (although laminography might represent a productive alternative in the future: Sutton 2009). There are a handful of cases of otoliths reported from three-dimensionally preserved fish fossils (e.g. the Eocene ophidiiform *Ampheristus*: Stinton 1966; Schwarzhans 2007a), and while three-dimensional preservation is often associated with famous *Lagerstätten* (Maisey 1991; Long & Trinajstić 2010), horizons yielding fully inflated fish crania are distributed throughout the nearly 450 million year fossil history of jawed vertebrates (e.g. Zhu *et al.* 2013; Friedman & Giles 2017). Here we report on the efficacy of high-resolution computed tomography scanning ( $\mu$ CT) for isolating otoliths from three-dimensionally preserved fossil fish crania. Our survey focuses on the Cretaceous-Eocene interval, and examines material from a variety of host lithologies including sands, chalks and clays. Although the quality of preservation varies considerably between specimens, sufficient detail is provided to allow us to make comparisons with previously described otoliths and to test their past taxonomic assignment using character data preserved in the host crania.

## **MATERIAL AND METHODS**

### *Tomographic procedures*

*In situ* otoliths described here were incidental discoveries made as part of a broader initiative to study three-dimensional fossil fish crania of Cretaceous-Palaeogene age, emphasizing material from the English Chalk Group and London Clay Formation but considering other deposits with similar modes of preservation (e.g. Beckett & Friedman 2016; Friedman *et al.* 2016; Close *et al.* 2016; Beckett *et al.* in press). The specimens were scanned with a Metris X-Tek HMX ST CT scanner in the Imaging and Analysis Centre of the Natural History Museum, London. The

scan parameters (filters, beam intensity and beam energy) are given in Table 1 and Schwarzhans *et al.* (2018).

Tomogram stacks were segmented using Mimics Materialise v.16.0-18.0 x64 (<http://biomedical.materialise.com/mimics>). Renderings of resulting models were created using Blender ([www.blender.org](http://www.blender.org)). Figure 2 shows an example of a CT scan of a head of the Eocene apogonid *Apogon macrolepis* Storms, 1896 with the position of the otoliths inside the otic capsule highlighted. Photographs of specimens for which we report *in situ* otoliths in this paper are shown in Figure 3. Following best practices in studies of digital morphology (Davies *et al.* 2017), source files are available for download from Schwarzhans *et al.* (2018).

### *Abbreviations*

*Institutional.* BMNH, The Natural History Museum, Life Sciences, London, UK (see also NHMUK for materials housed in the Earth Sciences division); FBH, Fischerrei-Biologie Hamburg, Germany (now ZMH); IRSNB, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; LACM, Los Angeles County Museum of Natural History, Los Angeles, California, USA; MNHN, Museum national d'Histoire naturelle, Paris, France; NHMUK, The Natural History Museum, Earth Sciences, London, UK (see also BMNH); NJSM, New Jersey State Museum, Trenton, New Jersey, USA; NSMT, National Science Museum, Department of Zoology, Tokyo, Japan; RGM, Naturalis Biodiversity Center, Leiden, The Netherlands; SMF, Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; WAM, Western Australian Museum, Perth, Western Australia, Australia; ZMH, Universität Hamburg, Zoologisches Institut und Museum, Hamburg, Germany; ZMUC, Københavns Universitets Zoologisk Museum, Copenhagen, Denmark.

*Anatomical.* CaL, cauda length; OH, otolith height; OL, otolith length; OsL, ostium length; OT, otolith thickness.

## **RESULTS**

Because there are likely strong depositional influences on the relative preservation of otoliths, we discuss in the following lagerstätten aspects and preservation of the otoliths found *in situ* in the stratigraphic sequence of the respective geological units separated from the Systematic Palaeontology section.

### *Palaeogene*

The early Palaeogene is an important interval in the history of fish evolution, marked by the first appearance of many modern teleost families. This pattern is reflected by both skeleton and otolith-based datasets (Patterson 1993a, b). However, these two archives show little overlap: only 10 skeleton-based species are known with *in situ* otoliths from the Paleocene and Eocene (Nolf 2013 and this study), which is remarkable given the exceptional fish *Lagerstätten* known from this interval (Fig. 1: Patterson 1993a; Friedman *et al.* 2016). Here we are able to corroborate three previous reports of *in situ* otoliths obtained via breakage or potentially damaging mechanical preparation for the late Eocene (Bartonian) Wemmel Sands Member of the Maldegem Formation of Belgium (the apogonid *Apogon* and sparid *Dentex*). To these, we add several novel examples from all from the early Eocene (Ypresian) London Clay Formation of the UK: the *incertae sedis* acanthomorphs ‘*Brachygnathus*’ and *Sciaenuropsis*, and the gadiform *Rhinocephalus*. We also report *in situ* otoliths from an undescribed holocentroid from the earliest Paleocene (Danian) or latest Late Cretaceous (Maastrichtian) Hornerstown Formation of New Jersey, USA.

*Wemmel Sands Member, Maldegem Formation, Belgium.* The Wemmel Sands Member outcrops around Asse and Wemmel, northwest of Brussels, Belgium. Lithologically, it is composed of grey, glauconitic sands with an increasing clay component toward the top. The member can reach 10 m in thickness, but averages 4 to 5 m. It is classically assigned to the regional Wemmelian stage, which corresponds to the Bartonian stage of the international timescale (De Geyter *et al.* 2006). It yields a modest fauna of teleosts known from skeletal remains: an ophichthyid eel, a sparid, an apogonid and a putative serranid (but see below; Storms 1896). We examined type material of the final two taxa.

*London Clay Formation, United Kingdom*

The London Clay Formation is 90-130 m thick sequence of argillaceous to slightly calcareous marine clays of early Ypresian age. The best known outcrops are found in southern England, although deposits in continental Europe correlative with the London Clay Formation are known from Holland, Denmark, Germany and France, with extensive exposures of the Belgian Ieper Formation (Friedman *et al.* 2016). Fossil fishes occur in calcareous concretions that formed around the decaying fossil during an early diagenetic phase shortly after deposition, resulting in common three-dimensional preservation. Exposures on the Isle of Sheppey have yielded most articulated fish crania from the London Clay Formation (Casier 1966). A majority of historical specimens derive from this locality, with continued collecting yielding new material (Clouter *et al.* 2000; Rayner *et al.* 2009). The depositional setting for the London Clay Formation on the Isle of Sheppey is interpreted as being 80 km from the shoreline (Collinson 1983).

*Hornerstown Formation, New Jersey, United States.* The Hornerstown Formation is a 3 m thick unit of bioturbated, green glauconitic sands, deposited in a marine setting (Sugarman *et al.* 1995). It includes a main fossil-bearing layer roughly 10 cm thick and only a few centimetres above contact with the Cretaceous (Maastrichtian) Navesink Formation. It contains Late Cretaceous faunal elements, including ammonites and mosasaurs, and is regarded either as a lag deposit reworking underlying fossils (Kennedy & Cobban 1996) or a condensed section (Staron *et al.* 2001). This layer includes delicate and semi-articulated fossils (including the fishes described below) that seem unlikely to have been reworked. Above this fossil-bearing layer, the Hornerstown Formation is clearly early Paleocene (Danian) in age based on microfossil biostratigraphy (Koch & Olsson 1977). The age of the fossil-bearing layer remains ambiguous, and we treat it here as latest Maastrichtian-earliest Danian.

#### *Cretaceous*

The Late Cretaceous is a time of high global sea levels, and is characterized by a rich body fossil record of fishes (Patterson 1993a, b; Friedman *et al.* 2016). Marine faunas of this age consist of a variety of members of extant clades, including elopomorphs, aulopiforms, and early-diverging acanthomorph groups (e.g. lampridiforms, trachichthyoids). These are joined by a variety of extinct groups, including a range of stem teleost clades like ichthyodectiforms and pachycormids, as well as late-surviving marine holosteans. Late Cretaceous otoliths are less common and more



poorly known than those from younger strata. In particular, the correspondence of otoliths of this age to those of modern fishes is less clear than for Cenozoic examples. Consequently, there is some debate about the interpretation of Late Cretaceous otoliths and whether or not they represent crown percomorphs (Nolf & Stringer 1996; Nolf, 2013, 2016; Schwarzhans 2010, 2012), a group represented in rocks of this age by a handful of body fossils (e.g. Carnevale & Johnson 2015). The record of Early Cretaceous marine fishes is poor relative to that of the Late Cretaceous, with the most diverse assemblages from late in the Early Cretaceous: the Aptian Gault Clay Formation of the UK (Forey & Longbottom 2010), Toolebuc Formation of Australia (Clode 2015), and Tlayúa Formation of Mexico (Applegate 1996). The best-studied fish in earlier parts of the Early Cretaceous derive overwhelmingly from continental settings, including the Wealden of the UK and Belgium (Traquair 1911; Woodward 1916, 1918, 1919), and exceptional lacustrine *Lagerstätten* in Spain (Poyato-Ariza & Martín-Abad 2016) and China (Chang & Jin 1996).

We report *in situ* otoliths of Late Cretaceous age for three taxa from two deposits: the aulopiform *Apateodus corneti*, from the Maastricht Formation of the Netherlands; and the albuloid *Osmeroides* sp. and trachichthyoid *Hoplopteryx lewesiensis* from the English Chalk Group of the UK. All three derive from chalks, with the otoliths themselves preserved either as a void following the dissolution of the original aragonite (*Apateodus*) or as a partial (*Osmeroides*) or complete (*Hoplopteryx*) infilling of such a void. Early Cretaceous examples are from the Gault Clay Formation of the UK, and include a possible eurypterygian and the crossognathiform *Apsopelix anglicus*. Isolated otoliths from this deposit are often preserved in primary aragonite, but *in situ* otoliths appear to have been replaced and overgrown with a dense mineral. This is likely pyrite, which is visible externally on some fish remains from the Gault Clay Formation.

*Maastricht Formation, the Netherlands.* The specimen of *Apateodus* described here was collected near Valkenburg aan de Guel, a village to the east of Maastricht, the Netherlands (Kruizinga 1924). Here classic members of the Maastricht Formation interdigitate with the Kunrade Limestone facies (J. Jagt, pers. comm., December 2016). These deposits are shallow marine in origin (Schioler et al. 1997; Vandenberghe *et al.* 2004), and are constrained to the late Maastrichtian on the basis of cephalopod biostratigraphy (Jagt & Jagt-Yazykova 2012).

Although some articulated fish remains are known from these Maastrichtian deposits in the

southern Netherlands (Kruizinga 1924; Friedman 2012), they are rare, with most material consisting of isolated fragments. Three-dimensionally preserved material includes the skulls of *Apateodus*, including the one described here (Kruizinga 1924, 1927; Friedman 2012), as well as a cranium of *Enchodus* that was acid prepared (Goody 1969), obliterating any possible evidence of *in situ* otoliths. We have not detected any otoliths in a CT scan of a large specimen of *Hoplopteryx* from the roughly coeval Ciply-Malogne Phosphatic Chalk of Belgium (Friedman 2012: fig. 8B).

#### *English Chalk Group, United Kingdom*

The English Chalk Group is divided into the Grey Chalk and White Chalk subgroups (Gale & Kennedy 2002). It spans much of the Late Cretaceous, and although fossils are found throughout, articulated fishes are largely, but not exclusively, restricted to the Cenomanian and Turonian parts of the succession (Friedman *et al.* 2016). The best fish fossils from these deposits were collected when chalk pits were worked by hand, and the stratigraphic control on these old specimens is often poor (Patterson 1964; Longbottom & Patterson 2002; e.g. *Osmeroides* below). It is therefore impossible at present to determine which levels within the English Chalk Group might be most conducive for the preservation of otoliths. In any case, *in situ* otoliths are dissolved in these rocks and the voids often infilled by secondary mineralization. The dissolution of aragonite in the Chalk succession is well documented, with aragonite-biomineralizing taxa becoming increasingly uncommon finds upsection (Gale & Kennedy 2002). Out of over nearly 30 genera of fishes scanned from the Chalk, we have only recognized two reasonably well-preserved examples described below, plus an additional specimen of *Trachichthyoides* (NHMUK PV OR39076) with fragments of otoliths that are too poorly preserved to describe in any detail.

#### *Gault Clay Formation*

The Gault Clay Formation of the United Kingdom underlies the English Chalk Group and comprises a 20-50 m sequence of dark clay deposited in an open marine setting (Gale & Owen 2010). The Gault Clay Formation is middle to late Albian in age, and shares many bony fish genera in common with the Chalk. Articulated fish remains from the Gault are rare, and are often pyritized to some degree (Forey & Longbottom 2010). In addition to skeletal remains, isolated otoliths in original aragonitic composition are known from this deposit (Stinton 1973),

representing a modest fauna of three species recognized as valid by Nolf (2010). None of these otoliths known from isolated remains appear to match the *in situ* examples described below.

## DISCUSSION AND CONCLUSIONS

### *Preservation of in situ otoliths as a function of depositional setting and diagenesis: a prospectus for future studies*

Our survey of three-dimensionally preserved fossil fish skulls sampled a variety of lithologies, all representing marine depositional environments: chalks (English Chalk Group, Maastricht Formation), clays or marls (Gault Clay Formation), phosphatic or carbonate concretions (London Clay Formation), and sandstones (Hornerstown Formation, Wemmel Sands Member). While otoliths can be preserved in all of these settings, it is clear—as in the case of isolated otoliths—that some lithologies and diagenetic histories are more conducive to the preservation and recovery of *in situ* examples in three-dimensionally preserved specimens. Glauconitic sands appear to hold high potential for preservation of *in situ* otoliths, in terms of the percentage of specimens yielding otoliths as well as the anatomical fidelity of those examples, although we acknowledge the limited sample size of our surveys. All specimens studied from the Hornerstown Formation (Maastrichtian to Danian) and Wemmel Sands Member (Bartonian) yield intact otoliths showing fine anatomical details, and which are directly comparable to modern examples. However, the modes of preservation in these units is distinctly different, with otoliths from the Wemmel Sands Member being original aragonitic material (as shown from physically extracted specimens) and those from the Hornerstown Formation preserved as partially infilled void spaces. Indeed, our scans of the otoliths of *Apogon macrolepis* and *Dentex laekeniensis* provide clear evidence that our non-invasive approach yields anatomical detail comparable to physical *in situ* otolith finds previously reported for these species (Taverne & Nolf, 1979; Nolf, 2013).

Clays and marls are more variable in their preservation of otoliths. Both the London Clay Formation (Ypresian) and Gault Clay Formation (Albian) yield three-dimensional skulls with *in situ* otoliths, but there are differences in the nature and frequency of preservation. Both Gault specimens examined show *in situ* otoliths, but in both cases they have been subject to partial dissolution and replacement/overgrowth with a dense mineral, likely pyrite. Paradoxically, the

Gault Clay Formation is also known for superb preservation of isolated otoliths in original aragonite material (Stinton 1973; Nolf 2010). In cases where otoliths are not partially replaced, they might be difficult to distinguish from surrounding clay matrix using  $\mu$ CT. A study of a body fish fossil from an unconsolidated marl from the Miocene of New Zealand revealed no otolith in tomograms, while a perfectly preserved specimens in original aragonitic composition was retrieved during physical preparation (Schwarzahns *et al.* 2012). Unfortunately, clays and marls are well-suited for preservation of aragonite, and mechanical extraction of otoliths might be necessary in cases where  $\mu$ CT provides insufficient contrast.

Visible otoliths are much rarer in the concretions bearing fishes from the London Clay, although they can be better preserved than examples from the Gault Clay. As part of a broader project (Friedman *et al.* 2016), we have scanned three-dimensionally preserved skulls of over 42 genera of London Clay fishes, from which we were able to identify *in situ* otoliths in the three taxa described above plus *Ampheristus* (NHMUK PV P4540e; not described here), a genus for which *in situ* otoliths has been reported in the past through physical exposure (Casier 1966; Stinton 1966). Modes of preservation range from apparently unmodified (*Brachygnathus*) to completely or partially replaced by pyrite (*Rhinocephalus*, *Sciaenuropsis*). The relative rarity of *in situ* otoliths in the London Clay is likely a joint function of taphonomy, diagenesis and taxonomy. The specimen of *Rhinocephalus* reported here is the only individual of the genus that we have examined with  $\mu$ CT that bears *in situ* otoliths, strongly implicating individual taphonomic and diagenetic histories (and specific geological horizons) as being significant in the preservation of these structures. With respect to taxonomy, scombroid or scombroid-like fishes make up a substantial fraction of well-preserved London Clay fishes, both in terms of taxonomic diversity and absolute abundance (Monsch 2005; Friedman *et al.* 2016). Otoliths of modern scombroids are small and delicate, suggesting that their retrieval in  $\mu$ CT scans is unlikely even in ideal cases. We have not detected any otoliths in the numerous scombroids scanned from the London Clay Formation (e.g. Beckett & Friedman 2016).

Chalks appear to very rarely yield otoliths in an unaltered state. The only records of isolated otoliths from such lithologies derived from the “næse” chalk of Faxe, Denmark, where they are recrystallized in calcite (Schwarzahns 2003). As a general rule, most or all aragonitic matter including otoliths are dissolved in chalk. Where otoliths *in situ* were found in the CT scans, they are either preserved as voids (*Apateodus*) or voids infilled in part or whole by

secondary mineralization (*Hoplopteryx*, *Osmeroides*). We only scanned one specimen from the Maastricht Formation, so cannot comment on the relative rarity of *in situ* otoliths from that deposit. However, we have examined nearly 30 genera from the English Chalk Group using  $\mu$ CT and have only found the two examples described here plus a poorly preserved example in the trachichthyoid *Trachichthyoides* (NHMUK PV OR39076). Preservation of otolith voids in such deposits therefore seems to depend primarily on diagenetic alterations after dissolution of the aragonitic otolith. When preserved as a void in a fine-grained matrix, CT results can be excellent, as in *Apateodus*. However, infilling and subsequent growth of diagenetic minerals can substantially disrupt preserved structure and result in lower fidelity models as appears to be the case in *Hoplopteryx*.

Collectively, these results suggest particular depositional settings and diagenetic events likely and unlikely to yield otoliths. Three-dimensional skulls from marine sandstones appear to have considerable potential for preserving *in situ* otoliths, but intact fossils in such deposits are relatively rare. As examples for further investigation, we note a three-dimensionally preserved ‘elopid’ from the Codell Member of the Late Cretaceous (Turonian) Carslile Formation of Kansas (Miller 1958) and the intact skull of the trachichthyoid *Antarctiberyx* from the Late Cretaceous Lopez de Bertodano Formation (Campanian-Maastrichtian) of Seymour Island, Antarctica (Grande and Chatterjee 1987)

Several marine clays yield three-dimensionally preserved fish material, mostly in calcareous concretions, with potential to preserve otoliths *in situ*: the early Oligocene (Rupelian) Boom Clay formation of Belgium (Taverne *et al.* 2006), the middle Eocene (Lutetian) Lillebælt Clay Formation of Denmark (Schwarzahns 2007a), the early Eocene (Ypresian) Flanders Clay of Belgium (Casier 1949, 1966), and the Early Cretaceous (Albian) deposits of Aube, France (Wenz 1965). Schwarzahns (2007a) describes *in situ* otoliths from the Lillebælt Clay, but  $\mu$ CT investigation of other specimens have thus far not yielded any additional examples, perhaps reflecting minimal differences in X-ray attenuation between aragonitic otoliths and surrounding matrix. We have also made preliminary investigations of specimens from the Iepers Formation of Belgium and Albian of Aube, France, with contrasting results. None of the samples examined to date from the Iepers Formation preserve otoliths. However, the similarity of fossil preservation between the London Clay Formation and Iepers Formation leads us to believe that otoliths might be present in some specimens from the latter, but that these might be comparatively rare, as they

are in the British deposit. By contrast, the single specimen of the megalopid *Elopoides* from Aube (MNHN CTE 14) shows otolith-like structures in its saccular chambers, although the resolution of our data was insufficient to yield interpretable results. We therefore view fossils from this site as being particularly promising for *in situ* otoliths, and note that well-preserved material of *Apsopelix* from Aube (Wenz 1965) could help to constrain our poor models of otoliths in this genus from the approximately coeval Gault Clay Formation. Although Gault otoliths that we have studied are limited in terms of detail, the apparently high yield of *in situ* otoliths suggests that additional remains from this deposit should be targeted by future studies. Particularly significant would be examples of *in situ* otoliths from extinct teleost groups like pachyrhizodontids and ichthyodectiforms, both of which are known from the Gault Clay Formation (Forey & Longbottom 2010).

Although they are a common matrix for three-dimensionally preserved fish skulls, chalks and other carbonates are promising candidates for the recovery of *in situ* otoliths only when no destructive mineralization or other diagenetic effects followed the ubiquitous dissolution of the aragonitic otoliths. The early diagenetic dissolution of aragonitic otoliths is exacerbated by low or no density contrast between any preserved otolith material and the surrounding matrix. Thus the best conditions for otolith preservation in such settings is as voids like that seen in the Maastricht Formation, or with complete subsequent infillings like in the Cretaceous examples from the English Chalk Group. Thus, while abundant three-dimensionally preserved or only slightly crushed remains of extinct groups (e.g. pycnodonts, pachycormids, crossognathiforms, ichthyodectiforms) are known from deposits not sampled in this study (e.g. Smoky Hill Member of the Niobrara Formation: Shimada & Fielitz 2006), the strong bias against aragonitic fossils in such sites (Carpenter 2008) leads us to suspect that *in situ* otoliths will unfortunately be rare.

#### *μCT and the potential for linking the otolith and body fossil records*

One of the most exciting prospects of the study of *in situ* otoliths is the reconciliation of the parallel systems of nomenclature. Here we are able to correlate skeleton- and otolith-based taxonomies in several instances (Table 2). In terms of fossils of Palaeogene age, we find that *in situ* otoliths closely match the structure of isolated otoliths assigned to the same taxonomic groups. Indeed, the otoliths of the gadiform *Rhinocephalus* and the unnamed holocentrid from the Hornerstown Formation closely match what would be expected in such taxa, while the

otoliths of the apogonid *Apogon* match previously described physical (rather than tomographically reconstructed) examples studied *in situ*. This broadly validates the approach used to identify isolated otoliths of this age, which show a reasonably close correspondence with those from extant fishes. However, it is apparent that the study of *in situ* otoliths is more than simply a corroborative exercise. In fact, several of the otoliths examined using  $\mu$ CT provide help to illuminate the taxonomic identities of the containing cranial skeletons, some of which have been the subject of remarkably little anatomical study and have been of ambiguous taxonomic placement. For example, we find that the putative serranid *Plesioserranus wemmeliensis* is a small specimen of the co-occurring sparid *Dentex laekeniensis*.

Our findings relating to Cretaceous otoliths are arguably more significant than those from the Palaeogene, despite representing a more limited taxonomic sample. Scant records of *in situ* otoliths from Mesozoic teleosts include Middle and Early Jurassic examples from *Leptolepis* cf. *coryphaenoides* (Bronn, 1830) (see Nolf, 2013), *Leptolepis normandicus* Nybelin, 1962 (see Delsate, 1997), *Cavenderichthys talbragarensis* (Woodward 1895) (Schwarzahns & Frese, in prep.) and one record from the freshwater *Lycoptera middendorfi* (Müller, 1861) from the Early Cretaceous of 'Transbaikalien' in Russia (Reis 1909). To this modest list we add a further five from the Cretaceous: *Apsopelix anglicus* (Dixon, 1850) (Cenomanian-Turonian), *Osmeroides* sp. (Cenomanian-Turonian), *Apateodus corneti* (Forir, 1887) (Maastrichtian), *Hoplopteryx lewesiensis* (Mantell, 1822) (Cenomanian-Turonian), and an undetermined form from the Gault Clay Formation (Albian). In the case of *Osmeroides* and *Hoplopteryx*, the taxonomic identifications of the otolith-based species show clear correspondance with skeleton-based taxonomy. This is not surprising, as both belong to clades persistent until today and from which many fossil otolith-based taxa are known more-or-less continuously since the Late Cretaceous times. *Apsopelix anglicus* and *Apateodus corneti* belong to extinct clades, the first as a crossognathiform of debated position just outside or just within the teleost crown group, and the second, *Apateodus*, to the enigmatic aulopiform group Ichthyotringoidei (Fig. 4). While there is no clear correlation of *in situ* otoliths of *Apsopelix* with otolith-based taxa yet, it does appear to show a generalized morphology broadly consistent with the inferred phylogenetic position of this crossognathiforms. Significantly, *Apateodus* does show a clear correlation with isolated Cretaceous otoliths previously attributed to Gempylidae, which is highly nested within acanthomorph phylogeny. Our re-identification of such otoliths as those of aulopiforms

reconciles a conspicuous discrepancy between the otolith and body fossil record of gempylids, the first skeletal remains of which are early Palaeogene in age (Prokofiev 2002; Monsch & Bannikov 2011). We would therefore advise caution in relating Late Cretaceous otoliths with extant clades, particularly when these associations strongly conflict with first appearances of groups based on skeletal records.

Surprisingly, one of the limitations to the study of *in situ* otoliths comes not from the perspective of ambiguity surrounding the otoliths themselves, but rather from inadequate documentation of the anatomy and relationships of the skeletal remains that yield them. While some of the skulls examined by us belong to well-described, well-circumscribed taxa of clear affinities (e.g. Patterson 1964; Goody 1969; Teller-Marshall & Bardack 1978; Young 1993), others like *Sciaenuropsis*, '*Brachygnathus*', and the undetermined Gault teleost have poorly constrained phylogenetic positions due to a combination of limited historical study or deficient skeletal remains, coupled with a past emphasis on complete but flattened fish body fossils preserving articulated postcrania.  $\mu$ CT has only begun to be applied to fossil teleosts in a systematic way. It is obviously a promising, non-invasive technology for linking of skeleton- and otolith-based data and it is our hope that this approach will yield significant new data on both skeletal and otolith anatomy that will advance our understanding of these two important kinds of fossil data with a bearing on the evolutionary history of fishes.

*Acknowledgements.* The authors thank Farah Ahmed, Emma Bernard, Zerina Johanson, Rebecca Summerfield, and Dan Sykes for access to the collections and assistance with scanning at the Natural History Museum, London. Donald Davense provided photographs of the holocentrid from the Hornerstown Formation. We are thankful to Dirk Nolf for allowing to use certain drawings of his. Giorgio Carnevale, Jürgen Kriwet and Chien-Hsiang Lin provided helpful reviews that, along with editorial assistance from Sally Thomas, substantially improved this contribution. This research was supported by a NERC studentship to HB on the DTP Environmental Research (NE/L0021612/1), a Leverhulme Project Grant (RPG-2012-658) and Leverhulme Prize (PLP-2012-130), both to MF.

## **SYSTEMATIC PALAEOLOGY**

Teleost systematics following Nelson *et al.* (2016).



Order CROSSOGNATHIFORMES Taverne, 1989

Family CROSSOGNATHIDAE Woodward, 1901

Genus APSOPELIX Cope, 1871

*Diagnosis (otolith).* Thin, flat, elongate otolith with deep ventral rim and shallow, flat, horizontal dorsal rim above rear part of otolith only. Rostrum massive, about 50% of otolith length, its dorsal margin flat, horizontal. Ostium wide, long, voluminous; cauda short, straight, narrow.

*Remarks.* The relationships of *Apsopelix* and other crossognathiforms is currently debated, with formal phylogenetic analyses placing the group either as crownward members of the teleost stem lineage (Patterson & Rosen 1977; Arratia & Tischlinger 2010) or early diverging members of the teleost crown group (Sferco & Lopez-Arbarello 2015). The otolith morphology of *Apsopelix* is indeed very plesiomorphic and resembles, as far as discernible, that of even earlier diverging lineages like *Leptolepis* (i.e. *Leptolepis normandica* Nybelin, 1962), the earliest teleosts from which *in situ* otoliths are known (Nolf 2013). Otoliths of stem teleosts are rather similar in appearance, with limited morphological disparity. In the case of *Apsopelix*, the thin, flat otolith seems to be characteristic with its large ostium, short dorsal rim and the horizontal dorsal margin of the rostrum.

*Apsopelix anglicus* (Dixon, 1850)

Figures 3J, 5A-C

*Material.* NHMUK PV P9890, Gault Clay Formation, Folkestone, United Kingdom. Both otoliths preserved *in situ*, partially as void and partially as replacement with a dense mineral, likely pyrite.

*Description.* A rather small, delicate otolith of about 6.5 mm length with poorly resolved surface structures due to a strongly rugose surface and edged margins. The following description is therefore reduced to relatively few discernible features. OL:OH = 2.0; OH:OT probably >4. Otolith shape elongate, with long, projecting, pointed rostrum and angular posterior tip. Dorsal rim very short, only about half of the length of the otolith, shallow, nearly straight, joined to posterior rim in nearly rectangular postdorsal angle. Dorsal rim with feeble indications of

excisura and antirostrum. Dorsal rim of rostrum straight. Ventral rim deeply curved with rounded mid-ventral angle.

Inner face rather flat with a poorly resolved sulcus in a slightly supramedian position. Ostium large, wide, particularly ventrally widened, occupying most of rostrum and short stretch behind. Cauda barely discernible, short, straight, narrow. No dorsal depression or ventral furrow apparent.

*Remarks.* The rather poorly resolved otolith model limits correlation with otolith-based taxa from the Cretaceous. There are, however, some isolated examples that show some resemblance in outline and proportions of otolith and sulcus, particularly in respect to the short dorsal rim and the voluminous ostium. The best example is '*Argentinida bergantinus* Nolf, 2004 from the Aptian of northeastern Spain, which differs in the more compressed shape (OL:OH = 1.5-1.6 vs 2.0) and the inclined instead of horizontal dorsal margin of the rostrum. If indeed a crossognathiform, it would represent a different genus and possibly family. A small number of otolith-based species have been described from the Gault of Folkestone by Stinton (1973) and Nolf (2010). Amongst them is one, *Argentina? lobata* Stinton, 1973, which resembles *Apsopelix anglicus* in outline and the thin and fragile appearance, but it does not show such a wide ostium and long rostrum. Even when considering the incomplete preservation of all isolated otoliths of *Argentina? lobata* so far obtained and the relatively poor model retrieved from the *in situ* otolith of *Apsopelix anglicus*, it appears unlikely at the current state that the two species would be synonymous.

Order ALBULIFORMES Jordan, 1923

Family OSMEROIDIDAE Forey, 1973

Genus OSMEROIDES Agassiz, 1837

[= *Preabula* Frizzell, 1965; = *Archaelbula* Frizzell, 1965]

*Diagnosis (otolith).* Oval otolith with strongly convex inner face and flat outer face. Ostium wide, about 35% of total sulcus length; cauda inclined at about 25°, straight to slightly curved.

*Remarks.* In a combined analysis of morphological, molecular, and palaeontological data, Dornburg *et al.* (2015) place *Osmeroides* outside the clade containing both Albulidae and Pterothrissidae. The otolith morphology of *Osmeroides* supports this assessment, since it does

indeed exhibit a combination of characters of the Albulidae (strongly convex inner face, open ostium) and Pterothrissidae (inclined position of cauda and cauda not bent ventrally).

The otolith-based genera *Prealbula* and *Archaealbula* are synonymized with *Osmeroides* based primarily on the inclined but unbent cauda, which differs from otoliths of the extant genus *Albula*. Frizzell (1965) noted the angle of the cauda, the expansion of the posterior rim, and the curvature of the inner face as diagnostic differences between *Prealbula* and *Archaealbula*. With many more specimens now available, we regard such variation as significant for specific rather than generic differentiation.

*Osmeroides* sp.

Figures 3H, 6A-D

*Material.* NHMUK PV 39433. Locality information as given on the specimen label is limited to “Chalk, England.” Both otoliths preserved *in situ* as voids with a dense mineral precipitated around the margins.

*Description.* A large otolith of about 12.8 mm length with a low surface rugosity. OL:OH = 1.7; OH=OT = 2.3. Otolith shape elongate, oval. Anterior rim broadly rounded; posterior rim with inferior angle. Dorsal rim moderately high, anteriorly depressed, posterodorsally with broad expanded lobe followed by steeply inclined section. Ventral rim very regularly curved, smooth.

Inner face distinctly convex. Sulcus way suprmedian positioned with ostium opening on anterior-dorsal rim. CaL:OsL = 1.6. Ostium moderately wide, dorsally more widened than ventrally, shallow. Cauda narrow, deeper than ostium, almost straight, inclined at about 25° against ostium, terminating rather close to posterior rim of otolith. Dorsal depression broad, separated from cauda by distinctly elevated crista superior. Ventral field smooth without ventral furrow. Outer face slightly concave, smooth.

*Remarks.* This otolith morphology has always been recognized as representing an albulid or pterothrissid. There are a number of otolith-based species, which share the diagnostic characters with the *in situ* example described for *Osmeroides*. The closest match with our specimen is *O. weileri* (Frizzell, 1965) (Fig. 6G-I) from the Santonian of the Gulf Coast, which differs merely in the shallower postdorsal region and the somewhat less inclined and slightly bent cauda.

*Osmeroides griffini* (Nolf & Dockery, 1990) (Fig. 6E-F) from the Campanian of Mississippi is

more compressed than both *Osmeroides* sp. and *O. weileri* from the late Santonian of Alabama, and *O. alabamiae* (Frizzell, 1965) from the Paleocene of Alabama finally is the most elongate form. *Osmeroides* apparently is common in otolith associations of the Late Cretaceous.

Order AULOPIFORMES Rosen, 1973

Suborder ICHTHYOTRINGOIDEI Jordan, 1905

Family ICHTHYOTRINGIDAE Jordan, 1905

Genus APATEODUS Woodward, 1901

*Diagnosis (otolith).* Thin, slender otolith with a long, pointed rostrum about the length of the remainder of the otolith. Ostium wide, though ventrally only moderately widened, shallow; cauda deep, narrow, slightly flexed towards rear, terminating very close to posterior rim of otolith.

*Apateodus corneti* (Forir, 1887)

Figures 3G, 7A-C

*Material.* RGM 446950, Maastricht Formation, Valkenburg aan de Guel, the Netherlands. Both otoliths preserved as voids, slightly displaced from life position.

*Description.* A large, thin and delicate otolith of about 13.8 mm length with a low surface rugosity. OL:OH = 1.85; OH:OT = 6.0. Otolith shape elongate, with rounded posterior portion and sharply pointed and exceptionally long rostrum. Dorsal rim high, deeply lobate, but without any prominent angles, its extend limited to area behind ostial opening. Dorsal rim of ostium straight, ascending, symmetrical to ventral rim along rostrum. Ventral rim almost straight anteriorly and ascending to rostral tip, more regularly and deeply curved posteriorly. Posterior rim with obtuse inferior angle below tip of cauda.

Inner face slightly convex. Sulcus positioned along axis of otolith, with ostium opening on anterior-dorsal rim. CaL:OsL = 1.3. Ostium wide, ventrally less widened than dorsally, shallow. Its dorsal margin curving upwards right at ostial-caudal joint to meet dorsal rim. Cauda moderately wide and deep, rather straight, but slightly inclined towards tip and slightly widened dorsally before tip. Caudal tip reaching very close to posterior rim of otolith. Dorsal depression

not clearly developed. Ventral field smooth without ventral furrow. Outer face slightly concave, smooth. Otolith very thin in lateral view, particularly its rostrum.

*Remarks.* Nolf & Stringer (1996) report a number of fragmented otoliths from Santonian, Campanian and Maastrichtian rocks of Mississippi and Alabama that they interpret as belonging to gempylids, a group of percomorph fishes. This substantially predates the body fossil record of this group, which begins near the Paleocene-Eocene boundary (Prokofiev 2002). In fact, these Cretaceous otoliths show a striking correspondence with the *in situ* otolith of *Apateodus corneti* including: shape and depth of cauda, proportions of the rear part of the otolith, the caudal tip extending to the posterior rim, and the overall thinness of the otoliths themselves. The rostrum is not preserved in any of the isolated specimens so far obtained, which is easy to understand given how delicate this structure appears in our *in situ* examples for *A. corneti*. We interpret these Cretaceous otoliths of putative gempylids instead representing *Apateodus* or a closely related aulopiform. The isolated otoliths differ from those of *A. corneti* in the longer dorsal section, the shallower ventral rim (at least in large specimens), and the presence of an antirostrum and excisura immediately before the area where the rostrum has broken off in most instances (Fig. 7D-G). *Apateodus* first appears in the late Early Cretaceous (Albian) and extends to the end of the Late Cretaceous, and is known from several localities throughout that interval (Newbrey & Konishi 2015). Our reinterpretation of these Late Cretaceous otoliths as belonging to that genus is thus more consistent with the body fossil record than past identifications. Otoliths of fast swimming, epipelagic predators often converge on a common morphology: slender, thin, richly sculptured and with a deep cauda and a long, pointed rostrum. Superficially similar otoliths are hence found in a number of other epipelagic fishes such as Elopidae (otoliths thicker and differing shape of ostium and rostrum) or Carangidae (strongly curved cauda and bent inner and outer faces). For instance Nolf (1993) documented that an endemic epipelagic predator in Lake Tanganyika (*Lates stappersii*; Boulenger, 1914) thought to have derived from the Nile perch (*Lates niloticus*) evolved an otolith morphology very similar to unrelated carangids and scombrids, suggestive of anatomical convergence as a consequence of shared ecology.

The phylogenetic position of *Apateodus* within Aulopiformes is unclear, being considered a representative of the Ichthyotringoidei a basal aulopiform suborder (Davis & Fielitz, 2010). However, it has also been routinely aligned with the Alepisauroidae (Rosen 1973; Newbrey & Konishi 2015; Beckett *et al.* in press). We have studied otoliths of all extant aulopiform families

and figure specimens representing all families of Alepisauroidae for comparison: Notosudidae: *Scopelosaurus lepidus* (Krefft & Maul 1955)(Fig. 7H); Chlorophthalmidae: *Chlorophthalmus acutifrons* Hiyama 1940 (Fig. 7I); Bathysauropsidae: *Bathysaurus ferox* Günther 1878 (Fig. 7J); Bathypteroideae: *Bathypterois bigelowi* Mead 1958 (Fig. 7K); Giganturidae: *Gigantura vorax* Regan 1925 (Fig. 7L); Ipnopidae: *Ipnops murrayi* Günther 1878 (Fig. 7M); Scopelarchidae: *Scopelarchus candelops* Rofen 1963 (Fig. 7N); Sudidae: *Sudis hyalina* Rafinesque 1810 (Fig. 7O); Paralepididae: *Lestidiops similis* (Ege 1933)(Fig. 7P) and *Magnisudis atlanticus* (Krøyer 1868)(Fig. 7Q); Evermannellidae: *Coccorella atlantica* (Parr 1928)(Fig. 9R); Alepisauridae: *Omosudis lowei* Günther 1887 (Fig. 7S) and *Alepisaurus ferox* Lowe 1833 (Fig. 7T). Our observations highlight two contrasting otolith morphologies within species of Alepisauroidae, with implications for the phylogenetic placement of *Apateodus*. The first of these is distinguished by a narrow, deepened cauda and a short, variably wide ostium, both without elevated colliculi. This arrangement characterizes all constituent families of the suprafamilies Ipnopoidea, Chlorophthalmoidea and Notosudoidea. There are individual variations that are likely autapomorphic traits of particular families: notosudid otoliths are remarkable for their long and pointed rostrum and the ostium being narrower than the cauda, giganturid otoliths exhibit a distinct groove below the ostium, and ipnopid otoliths show no clear division of ostium and cauda. However, the general morphologies of these otoliths corresponds broadly to those of the more deeply branching aulopoids and paraulopoids, indicating that this overall geometry is primitive for Aulopiformes.

By contrast, the pattern found in species of Alepisauroidae is highly specialized and characterized by several clear-cut synapomorphies. The sulcus bears distinctly elevated and prominent ostial and caudal colliculi (except in Alepisauridae, where they are flat), which are widely separated from each other. The collum in between the colliculi occasionally shows a ventral pseudocolliculum (Scopelarchidae, Paralepididae) and the colliculi sometimes project beyond the otolith margins anteriorly and posteriorly (Sudidae, Paralepididae, Evermannellidae). A similarly bizarre sulcus morphology otherwise is only found in certain gadiforms and zeiforms (see Nolf 2013), but in Alepisauroidae a strongly projecting and pointed preventral angle and much reduced dorsal and ventral otolith margins further contribute to a distinctive otolith morphology (except in Alepisauridae). Parsimony suggests that the unusually small and round otoliths of Alepisauridae represents a secondary reduction.

Otoliths of *Apateodus* show distinctive characters including a long and sharp rostrum, a relatively wide cauda, and an abbreviated but high dorsal rim, but these appear to be general features of aulopiforms. The genus lacks any of the derived otolith features of Alepisauroidae, the group to which most fang-bearing Cretaceous aulopiforms have been attributed (Rosen 1973). Recent analysis of gill-arch anatomy in *Apateodus* provides some support for a relationship with paralepidids, but the genus also shows features conflicting with this interpretation (Beckett *et al.* in press). Contrasting phylogenetic signals between different anatomical systems point to the need for a synoptic reappraisal of *Apateodus* and other ichthyotringids, which are among the oldest fossil aulopiform lineages.

Order GADIFORMES Goodrich, 1909

Suborder GADOIDEI Goodrich, 1909

INCERTAE FAMILIAE

Genus RHINOCEPHALUS Casier, 1966

*Rhinocephalus planiceps* Casier, 1966

Figures 3C, 8A-F

1966 *Rhinocephalus planiceps* Casier; Casier, pl. 55, figs 1-3, pl. 56, figs 1-3.

1977 *Merluccius nodosus* Stinton; Stinton, pl. 6, figs 14-15. [otolith-based species]

*Material and locality.* NHMUK PV P65195, London Clay Formation, Isle of Sheppey, United Kingdom. Both otoliths preserved *in situ*, and completely replaced with a dense material, likely pyrite.

*Description.* Each otolith is large, approximately 12.5 mm in length, with moderately rugose surface. OL:OH = 2.5; OH:OT = 2.7. Otolith elongated, with a pointed, projecting, posterior tip and a rounded anterior tip, both along median axis of otolith. Dorsal rim with broad, rounded, rather low predorsal lobe and low postdorsal angle positioned at about 30% from posterior tip. Short stretch of dorsal rim between predorsal lobe and postdorsal angle mildly concave. Ventral rim shallow, anteriorly and posteriorly regularly curved, nearly straight at its central portion.

Inner face distinctly convex with slightly supramedian sulcus reaching close to anterior-dorsal and posterior-dorsal rims of otolith. Ostium somewhat shorter than cauda, with shallow dorsal and deep ventral margin. Ostial-caudal joint (collum) narrow, incised from ventral,

probably without pseudocolliculum. Cauda slightly larger than ostium with dorsally and ventrally widened rims. Colliculi well marked in right otolith specimen, large, oval in shape and somewhat deepened. Dorsal depression narrow, only above central part of sulcus. Ventral furrow distinct and close to ventral rim of otolith. Outer face distinctly concave.

*Remarks.* The overall shape of the right otolith is preserved, but the sulcus morphology is not clear (Fig. 8A-B, shown reversed). However, the left otolith reveals more detail of the sulcus (Fig. 8C).

*Discussion and correlation with isolated otoliths.* Casier (1966) described *Rhinocephalus* as close to the extant *Merluccius*, a view reiterated by Fedotov (1976) and Fedotov & Bannikov (1989). We were unable to identify morphological features of the otoliths that would distinguish them from those of *Merluccius*. However, Endo (2002: 134) noted clear osteological differences between the supensoria of *Merluccius* and *Rhinocephalus*, and regarded the latter as the probable sister lineage of a clade comprising Merlucciidae plus seven other gadiform families. Stinton (1977) described *Merluccius nodosus* from otoliths up to 6.7 mm length from the middle Eocene (Lutetian) Brackelsham Group of the UK (Fig. 8D-F). These resemble the *in situ* otoliths of *R. planiceps* in all aspects so well that we have little doubt in synonymizing the two species, despite the stratigraphic difference and the fact that comparable otoliths so far have not been obtained from the London Clay Formation. *Palaeogadus serratus* Stinton 1966 from the London Clay Formation appears to be a typical representative of the genus *Palaeogadus*, a taxon for which *in situ* otoliths have been described by Novitskaya (1961) and Fedotov (1976). Otoliths of *Palaeogadus* resemble those of *Merluccius* and *Rhinocephalus* to a large extent, but differing in having the ostium that is much narrower and shorter than the cauda, the absence of a postdorsal angle, and the anterior tip being more strongly pointed than the posterior tip. Another species of *Palaeogadus* (*P. shepherdii* Schubert, 1916) is known from the Bartonian. Other similar, but more compressed otoliths include *Merluccius? papillosus* (Stinton 1966) from the Lutetian, *M.? antiquus* Schwarzhan & Bratishko 2011 from the Selandian of Ukraine and *Euclichthys lawsoni* Nolf & Rundle 2013 (in Nolf 2013) from the Ypresian of southern England. They most likely represent another genus of merlucciid-like gadiform. Extending from middle Paleocene (Selandian) to middle Eocene (Lutetian), these are among the oldest gadiforms outside the informally described Danian ‘*Protocodus*’ from West Greenland (Rosen & Patterson 1989).



Order HOLOCENTRIFORMES Patterson, 1993

Family HOLOCENTRIDAE Bonaparte, 1833

Genus INDET.

Figures 3F, 9A-C

*Material.* NJSM GP12145, Hornerstown Formation, Inversand Quarry, Sewell, New Jersey, USA. Both otoliths preserved as a void partially infilled with a dense mineral. We also examined NJSM GP12381, which preserves otoliths in a less satisfactory state. These fossils are mentioned, but not described, by Stewart (1996).

*Description.* A large otolith, 17.4 mm in length. OL:OH = 1.65-1.8; OH:OT = 3.5. Otolith shape elongate, with very long and pointed, but not very thin rostrum. Dorsal rim mostly low, anteriorly depressed behind distinct antirostrum, then expanded above middle section of cauda and finally deeply depressed again and concave leading to the angular posterior tip. Dorsal rim of rostrum straight, nearly horizontal and reaching into a sharp and moderately deep excisura. Ventral rim moderately deep, regularly curved, deepest at its middle. Anterior half of ventral rim intensely and regularly serrated.

Inner face distinctly convex. Sulcus distinctly supramedian, with ostium opening on anterior-dorsal rim. CaL:OsL = 1.3. Ostium wide, ventrally strongly widened, dorsally flat, slightly bent upwards to tip of antirostrum, rather deep. Cauda long, deep, anteriorly slightly upwards directed, posteriorly with a distinct downward bent at an angle of about 25-30°, terminating very close to posterior tip of otolith. Dorsal depression narrow, distinct, ventrally well marked by crista superior above cauda and dorsally by a kink-step against inclined uppermost portion of expanded median part of dorsal field. Ventral field smooth, seemingly without ventral furrow. Outer face distinctly concave, with short furrows originating vertically from serration of anterior ventral rim, otherwise smooth. Otolith moderately thin in lateral view; anterior and posterior views show distinct incision of cauda.

*Remarks.* This otolith derives from an undescribed holocentrid skull, previously interpreted as intermediate between Cretaceous stem holocentrids and members of the two modern subfamilies, the earliest definitive members of which are Maastrichtian and early Eocene for otolith and skeletal data, respectively (Stewart 1989, 1996; Schwarzhans 2010). The otolith differs from that of extant holocentrid genera only in the lesser angle of the caudal bend (70° to nearly 90° in

*Sargocentron* and 45-75° in *Neoniphon*; Rivaton & Bourret 1999; Schwarzhans 2010). Figured Recent otoliths for comparison are: *Sargocentron violaceum* (Bleeker 1853) (Fig. 9D-E) and *Neoniphon argenteus* (Valenciennes 1831) (Fig. 9F-G). Similar otolith-based fossil species have been referred to the otolith-based genus *Holocentronotus*: *H. percomorphus* Schwarzhans, 2010 from the Maastrichtian of Bavaria, *H. ryabchuni* Schwarzhans & Bratishko, 2011 from the Paleocene of Ukraine, *H. blandus* Schwarzhans, 2012 from the Paleocene of Bavaria, and *H. amplus* (Schwarzhans, 1980), *H. palasulcatus* (Schwarzhans, 1980) and *H. ventricosus* (Schwarzhans, 1980) all from the Eocene of New Zealand. None of them reach the size of the scanned otolith from the New Jersey Greensand and none show the reduced dorsal rim. Nevertheless, the pattern is sufficiently similar to assume that it could belong to the same or a closely related genus.

It should be noted that holocentrin otoliths can be easily confused with a number of percomorph otoliths with which they share the advanced heterosulcoid sulcus pattern (large ostium, narrow cauda which is bent ventrally at its rear part; by contrast myripristin otoliths are highly specialized: Schwarzhans 2010). There are few subtle differences, which may help for distinguishing in most instances, such as the lack of a ventral furrow in holocentroids or the dorsally not widened ostium. However, this might not be reliable in all cases.

Order BERYCIFORMES Regan, 1909

Suborder BERYCOIDEI Regan, 1909

Family BERYCIDAE Lowe, 1839

Genus SCIAENUROPSIS Casier, 1966

*Diagnosis (otolith)*. High bodied otolith with deep ventral rim and shallow dorsal rim. Ostium ventrally much widened and about as long as cauda; cauda distinctly upwards bent and very slightly flexed at tip close to posterior rim of otolith.

*Sciaenuropsis lerichei* (Schubert, 1916)

[= *Sciaenuropsis turneri* Casier, 1966]

Figures 3D, 10A-E

1916 *Monocentris? lerichei* Schubert; Schubert, pl. 7, figs 7-8. [otolith-based species]

1966 *Sciaenuropsis turneri* Casier; Casier: pl. 30.

1978 *Beryx lerichei* (Schubert, 1916); Stinton: pl. 10, figs 10-11.

1978 *Beryx nova* Stinton, 1977; Stinton, pl. 10, fig. 9. [otolith-based species]

?1980 *Pristigenys bella* Stinton; Stinton: pl. 13, figs 27-28. [otolith-based species]

2007b genus *Epogonidarum lerichei* (Schubert, 1916); Schwarzhans: figs 29A-E.

*Material.* NHMUK PV P6444a, London Clay Formation, Sheppey, United Kingdom. Both otoliths preserved *in situ* as original bone, partially enclosed in pyrite.

*Description.* Each otolith is large, with a length of about 14.2 mm. The surface is moderately rugose, which might reflect preservation. OL:OH = 1.15; OH:OT = 3.7. Otolith shape high bodied, compact. Anterior rim with short, supramedian positioned rostrum, small and narrow excisura and broad, indistinct antirostrum. Dorsal rim high, with broad predorsal angle and pronounced, projecting, nearly rectangular postdorsal angle positioned far backwards at junction with nearly vertically cut posterior rim. Dorsal rim apparently broadly crenulated or undulating. Ventral rim very deep, with distinct angle at deepest point below rear end of ostium and slightly in front of vertical axis of otolith, and with distinct angle at junction with posterior rim located below level of rostrum.

Inner face moderately convex with slightly supramedian sulcus. Ostium very wide with much expanded ventral rim but no expanded dorsal rim, nearly as long as cauda, slightly bent upwards towards anterior opening. Cauda narrow, deeper than ostium and slightly longer, distinctly bent upwards. Caudal tip slightly bent, terminating close to posterior rim of otolith. Dorsal depression well marked, wide and deep, extending above entire sulcus. Ventral field smooth without discernable furrow. Outer face flat.

*Remarks.* The fossil named as *Sciaenuropsis turneri* has been subjected to two principal taxonomic interpretations. Agassiz (1845) and Woodward (1901) regarded it as similar to the holocentroid *Myripristis*, a view subsequently rejected by Casier (1966) on proportional grounds. Instead, he was struck by apparent similarities with the sparid *Sparnodus* and erected the new genus *Sciaenuropsis* (Casier 1966: 218). Friedman *et al.* (2016) list *Sciaenuropsis* as a holocentroid in their faunal list of the London Clay, reviving the 'classical' interpretation of this fossil, although this placement was proposed without any supporting evidence.

The otolith model retrieved from the specimen provides some evidence bearing on phylogenetic affinities. The otolith of *Sciaenuropsis* is inconsistent with those of both sparids

and holocentroids. The wide ostium, upward turned and nearly straight cauda and the pentagonal outline with the deep ventral rim correspond broadly with otoliths of some berycids and trachichthyoids, but also certain percomorph families, notably the Priacanthidae (see Taverne & Nolf 2010) and Epigonidae. It is in these two distantly related acanthopterygian groups that isolated otoliths of this kind have also been placed at times (Taverne & Nolf 2010; Schwarzhans 2007b). It is clear that the features used to identify these taxa are homoplastic or primitive. However, there are two subtle—but seemingly consistent differences—between percomorph and non-percomorph examples. First, berycid and trachichthyoid otoliths show only a ventrally, not dorsally widened ostium, while the ostium is also somewhat expanded dorsally in Priacanthidae. Second, the ostium and cauda are nearly equally long in beryciforms while the ostium is distinctly shorter than the cauda in Priacanthidae and Epigonidae. We do not feel confident making a systematic placement of *Sciaenuropsis* on the basis of otolith anatomy alone. Although skeletal anatomy of the genus is not well known, there are two relevant features visible externally: the well-developed ridges extending the length of the frontals and converging anteriorly as a ‘V’; and sclerotic ossicles. Neither is present in priacanthids (Starnes 1988) or epigonids (Fraser 1972), but both are typical of berycids (Zehren 1979).

There are many similar looking otolith morphologies reported from isolated otoliths in the northern European Eocene. Several of them are interpreted as priacanthids like *Pristigenys rutoti* (Leriche, 1905), *P. rhombicus* (Schubert, 1906) or *P. hermani* Taverne & Nolf, 2010 (based on articulated skeletons with associated otoliths). However, their placement with *Pristigenys* has recently been rejected by Carnevale *et al.* (2017). Others, which lack the dorsally expanded ostium and which have an ostium nearly as long as the cauda are here placed in *Sciaenuropsis*, all from the North Sea Basin i.e. *S. lerichei* (Schubert, 1916) (Fig. 6C-E), *S. selsiensis* (Stinton, 1978) (Fig. 10F-H) and *S. bella* (Stinton, 1980). None of these otoliths are known from similar large specimens as the *in situ* find in *S. turneri*. However, specimens of *S. lerichei* to about 5 mm length match nearly perfectly the morphology of *S. turneri* including sulcus shape and proportions and otolith outline including the distinctive expanded backward located postdorsal angle. We have little doubt that these two nominal species, the one based on skeletal remains (*S. turneri*) the other otolith-based (*S. lerichei*) represent the same species in which case *S. lerichei* (Schubert, 1916) gains priority. It must be noted though that Taverne & Nolf (2010) figured otoliths as genus *Priacanthidarum lerichei* that are much more elongate with

a much narrower sulcus and which probably represent a different, unrelated species. *Sciaenuropsis lerichei* is known from the middle Eocene (Lutetian and Bartonian). Another species from the Ypresian of the London Clay, *S. bella*, is tentatively placed in synonymy, differing somewhat in the narrower and shorter ostium. *Sciaenuropsis selsiensis* from the Lutetian appears to be a small species and differs first of all in the distinctly narrower ostium.

Suborder TRACHICHTHYOIDEI Bleeker, 1856

Family TRACHICHTHYIDAE Bleeker, 1856

Genus HOPLOPTERYX Agassiz, 1838

*Diagnosis (otolith).* Thin, high bodied otolith with flat inner face, an apparently short, massive rostrum, a deep preventral angle and a strongly expanded postdorsal lobe. Ostium moderately wide, dorsally not widened; cauda deep, narrow, distinctly turned upwards towards posterior.

*Remarks.* Otoliths of *Hoplopteryx* resemble those of many trachichthyoids and berycoids, characterized by the combination of a high-bodied profile, a ventrally widened ostium and an upwardly bent cauda. There is a particularly close correspondence to the extant trachichthyids *Trachichthys* Shaw, 1799 and *Hoplostethus* Cuvier, 1829 (see Stinton 1966; Kotlyar 1996; Schwarzhans 2010, 2012; Nolf 2013). *Hoplopteryx* shares with *Trachichthys* the compressed shape and the deep ventral rim, but differs in the totally flat inner face and the ostium not being as much ventrally expanded. Otoliths of *Hoplostethus* are characterized by distinct and nearly equally developed pre- and post-ventral angles, the anterior-dorsal rim being much reduced and the ostium being very wide. Otoliths of other extant trachichthyoid families differ in their specific development of the sulcus with fused colliculi (Anoplogasteridae, Anomalopidae), or the very high, compressed shape of the otolith as a whole (Diretmidae, Monocentridae) (see Nolf 2013).

While a trachichthyoid affinity for *Hoplopteryx* matches past interpretations (Patterson 1964, 1993a; Gayet 1982; Moore 1993), the close correspondence of otolith shape between this genus and trachichthyids specifically is surprising. Despite their generalized appearance in comparison to other, anatomically divergent trachichthyoid lineages, trachichthyids nest highly within Trachichthyoidei in both molecular and morphological phylogenies (although exact patterns of relationships differ: Moore 1993; Dornburg *et al.* 2017), rather than as the sister-

group of all remaining members of the group. *Hoplopteryx* lacks all three derived characters reported by Moore (1993) as shared by extant trachichthyoids, and is regarded by him and other authors (Gayet 1982; Patterson 1993a) as a stem trachichthyoid. Additionally, *Hoplopteryx* lacks the single osteological synapomorphy of Trachichthyidae recognized by Moore (1993): a posteriorly pointing spine on the posttemporal. If *Hoplopteryx* is a trachichthyid, as suggested by otolith morphology, then we must invoke considerable homoplasy in these skeletal features. On the other hand, if *Hoplopteryx* is a stem trachichthyoid, it implies either the persistence of a primitive otolith morphology in trachichthyids or a reversal to a plesiomorphic geometry in that group.

*Hoplopteryx* was a widespread taxon in shallow marine deposits during the Late Cretaceous (Patterson 1964; Friedman 2012; Grandstaff & Parris 2016). The first otolith-based records of *Trachichthys* date back to the early Paleocene (Schwarzahns 2012) and those of *Hoplostethus* to the middle Paleocene (Schwarzahns 2003, 2004). It appears that the separation of the two principal extant genera of the Trachichthyidae (*Trachichthys* and *Hoplostethus*) occurred near the Cretaceous-Palaeogene boundary. While *Trachichthys* remained as a secondary endemic to the shelf seas of temperate Australia, *Hoplostethus* probably expanded into the deep sea at around the Eocene-Oligocene boundary (Schwarzahns 1985) and the establishment of a psychrosphere in the deep oceans, which has since become its principal habitat (Kotlyar 1996).

*Hoplopteryx lewesiensis* (Mantell, 1822)

Figures 3I, 11A-D

*Material.* NHMUK OR41105, Grey Chalk Subgroup, English Chalk Group, Halling, Kent, United Kingdom. Both otoliths preserved in situ, completely replaced by a dense mineral.

*Description.* A moderately large, thin and apparently fragile otolith of about 11.2 mm length with a moderate surface rugosity and some erosion along the rims. OL:OH = 0.85; OH:OT about 8.0. Otolith shape high bodied, distinctly higher than long, with incompletely preserved but apparently blunt anterior rim. Dorsal rim high, probably lobate, with prominent postdorsal lobe and somewhat anteriorly depressed. Ventral rim very deep, with prominent preventral angle located below rear margin of ostium; no postventral angle. Posterior rim slightly bent, nearly

straight, distinctly inclined at an angle of about 60° connecting rear angle of postdorsal lobe with deep preventral angle.

Inner face almost perfectly flat. Sulcus distinctly supramedian, with ostium opening on anterior rim. CaL:OsL about 1.0 or slightly less. Ostium moderately wide, ventrally distinctly widened, dorsally not widened but gently bending upwards towards opening, somewhat deepened. Cauda narrow and deep, distinctly turning upwards towards posterior. The resolution / preservation does not allow recognition of the collicular crest of the lower margin of the caudal colliculum, which otherwise is very typical for many berycoid otoliths. Dorsal depression large. Ventral field poorly preserved and no ventral furrow discernable. Outer face slightly concave. Otolith very thin in lateral view, particularly its dorsal and ventral rims.

*Remarks.* The somewhat rugose surface and erosion along the otolith edges precludes correlation of the scanned *in situ* otolith of *Hoplopteryx lewesiensis* with otolith-based Cretaceous taxa on the species level. However, there are significant characters available that warrant a definition of the otoliths at the genus level (see above). This pattern is indeed shared by a number of otolith-based taxa, which were mostly identified as *Trachichthyoidei incertae sedis*. We now refer these species to *Hoplopteryx*: *Hoplopteryx causae* (Nolf, 2003) from the late Santonian of Spain (Fig. 11E-G), *H. coffeesandensis* (Nolf & Dockery, 1990) from the Campanian of Mississippi, *H. oscitans* (Nolf & Stringer, 1996) from the Maastrichtian of Mississippi (Fig. 11H), and *H. supracretacea* (Koken, 1891) from the Maastrichtian of Bavaria. The otoliths of two Recent *Trachichthyidae* are figured here for comparative purposes: *Hoplostethus crassispinus* Kotlyar, 1980 (Fig. 11I-J) and *Trachichthys australis* Shaw, 1799 (Fig. 11K).

Order KURTIFORMES Betancur-R. *et al.* 2013

Family APOGONIDAE Günther, 1859

Genus APOGON Lacepède, 1801

*Apogon macrolepis* Storms, 1896

Figures 3A, 12A-E

*Material.* IRSNB 647, cotype, Neder-over-Hembeek, Belgium. Both otoliths preserved *in situ*, with no obvious replacement or dissolution.

*Remarks.* Otoliths *in situ* were described from *Apogon macrolepis* Storms, 1896 from the Lutetian of Belgium by Taverne & Nolf (1979) (Figs 12D-E). Our scans of an intact specimen show identical structure to these mechanically isolated examples, and represents proof-of-concept for the tomographic approach. The otoliths of *A. macrolepis* are characterized by an oval outline with a regularly and deeply curved ventral rim, a low dorsal rim without postdorsal angle, a projecting, well-rounded rostrum, and on the convex inner face a sulcus with a large, oval shaped, widened and shallow ostium and a short, somewhat deepened and straight cauda with a rounded tip.

Order SPARIFORMES Betancur-R. *et al.* 2013

Family SPARIDAE Rafinesque, 1810

Genus DENTEX Cuvier, 1814

*Dentex laekeniensis* van Benden, 1872

Figures 3B, 12F-J

1896 *Serranus wemmeliensis* Storms; Storms, fig. 2.

1966 *Plesioserranus wemmeliensis* (Storms, 1898); Casier, fig. 36B.

*Material.* IRSNB 645, type of *Plesioserranus wemmeliensis* (Storms, 1896), Neder-over-Hembeek, Belgium. Both otoliths preserved *in situ*, with no obvious replacement or dissolution.

*Remarks.* On the basis of general aspects of skeletal morphology, this specimen was named as the type of *Serranus wemmeliensis* by Storms (1896). Casier (1966) subsequently assigned it to his new genus *Plesioserranus*. However, we find that the otoliths of this specimen closely match otoliths described *in situ* by Taverne & Nolf (1979) (Fig. 12I-J) for the serranid *Dentex laekeniensis*, which also derives from the Wemmel Member. We conclude that *Plesioserranus wemmeliensis* is a junior synonym of *Dentex laekeniensis*. Otoliths of this species are characterized by a rather regular oval outline without prominent angles but a distinctly projecting rostrum, no excisura or antirostrum, a distinctly convex inner face with a long sulcus composed of a broad, rather short and somewhat deepened ostium and a long, narrow, moderately deep cauda, which is slightly flexed towards its tip which reaches close to the posterior rim of the otolith.



Series PERCOMORPHA Rosen, 1973

Order & Family INDET.

Genus 'BRACHYGNATHUS' Agassiz, 1844

*Remarks.* *Nomen nudum* according to Casier, 1966; preoccupied by *Brachygnathus* Perty, 1830 in Coleoptera. *Brachygnathus tenuiceps* Agassiz, 1844 was considered a *nomen nudum* in Casier's monograph of fishes of the London Clay (1966). In any case, he considered the 'type' specimen too poorly preserved to be identifiable even to generic level. A second specimen classified as *B. tenuiceps* was selected by Casier as holotype of *Serranopsis londinensis* Casier, 1966, which is regarded by Friedman *et al.* (2016) as *Acanthomorpha incertae sedis*. *Brachygnathus* Agassiz, 1844, if validated, would be preoccupied by *Brachygnathus* Perty, 1830 in Coleoptera. We therefore leave the generic assignment in quotation marks until the nomenclatural situation has been resolved.

'*Brachygnathus tenuiceps*' Agassiz, 1844

Figures 3E, 13A-C

?1957 *Caesio bogneriensis* Stinton; Stinton, pl. 2, fig. 15. [otolith-based species]

?1977 *Sebastodes bogneriensis* (Stinton, 1957); Stinton, pl. 10, figs 24-26.

*Material.* NHMUK PV P643, London Clay Formation, Sheppey, United Kingdom. Only the left otolith is preserved *in situ*.

*Description.* In contrast to most other examples from the London Clay Formation described here, the otolith of '*Brachygnathus*' has not been replaced with a dense material. The otolith is about 13.2 mm length with strongly rugose surface and edged margins. The following description is therefore reduced to relatively few discernable features. OL:OH = 2.1; OH:OT = 2.8. Otolith shape elongate, with projecting, inferior rostrum and angular posterior tip. Dorsal and ventral rims shallow, irregularly bent. Anterior rim possibly with excisura.

Inner face distinctly convex with sulcus positioned along axis and not inclined. Ostium somewhat shorter than cauda, but considerably wider and anteriorly open. Cauda very narrow, perfectly straight, moderately deep and terminating at considerable distance from posterior tip of otolith. No further details visible on inner face.

*Remarks.* The general outline of the otolith of ‘*Brachygnathus*’, combined with proportions of the sulcus, and the short, narrow and completely straight cauda suggest a correspondence with the London Clay otolith taxon originally described as *Caesio bognoriensis* Stinton, 1957, and later revised to *Sebastodes bognoriensis* (Stinton, 1977). Nolf (2013) rejected the species based on the strongly eroded holotype, but Stinton (1977) figured some well-preserved specimens, which undoubtedly represent the same species (Fig. 13D). These otoliths are smaller than the *in situ* otolith (up to 5 mm length) and exhibit very similar otolith and sulcus proportions and outline, but however also show a dorsally slightly widened caudal tip. Because of this and the rather poor model of the *in situ* otolith, we refrain from a definite correlation of the skeleton and the otolith-based taxon. Unfortunately, the skeletal remains of ‘*Brachygnathus*’ are very poorly preserved, not allowing us to comment further on its possible systematic placement based on osteological features.

?EURYPTERYGII Rosen, 1973

INCERTAE SEDIS

Figure 3K

*Material.* NHMUK PV P52492, Gault Clay Formation, Naccolt, Kent, United Kingdom.

*Description.* A small otolith of about 2.5 mm length with a poorly discernible surface morphology and severe erosion along the edges, probably a result of crystallization or other precipitation of minerals in the void of the dissolved otolith. OL:OH about 1.5; OH:OT about 2.5. The otolith is oval in outline and rather robust, but no further details are apparent due to the severe erosion along its margins. Likewise, very little surface detail is visible except for a large, slightly upward-oriented shallow depression connecting to the anterior-dorsal rim of the otoliths, which could represent the ostium. Therefore, unfortunately, this otolith morphology cannot be tied to any isolated otoliths. It should be mentioned, however, that similar small, robust, oval otoliths are known from isolated Late Cretaceous examples interpreted as apogonid percomorphs by Nolf & Stringer (1996) and Myctophiformes *incertae sedis* by Schwarzhans (2010).

*Remarks.* Both otoliths preserved *in situ*, partially as void and partially as replacement with a dense mineral, likely pyrite. The specimen studied here has not been subjected to detailed anatomical description, and has not formally been assigned to a named taxon. The specimen

label identifies it as *Ctenothrissa*, but this attribution is questioned based on the presence of roofed posttemporal fossae (see also note accompanying specimen left by Niels Bonde and dated January 1975, who made comparisons with the aulopiform *Aulopus*). Additionally, the specimen has ossified sclerotics and narrow, unornamented frontals, neither of which are present in *Ctenothrissa*. In the absence of more detailed information on the specimen, we instead choose to leave it in open nomenclature as a possible eurypterygian.

## DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository:

<https://doi.org/10.5061/dryad.72rh2>

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## Captions to figures and tables

**Fig. 1.** Patterns of teleost diversity from the Jurassic to the present as gauged from the otolith fossil records.

**Fig. 2.** Models of the Eocene cardinalfish *Apogon macrolepis* based on  $\mu$ CT and highlighting the encased otolith. A, model of skull and encasing matrix; B, model of fossil only with matrix remove, bone opaque and otoliths shown in red; C, model of fossil only with matrix removed, bone rendered semitransparent and otoliths shown in red.

**Fig. 3.** Photographs of fossil fish skulls studied using  $\mu$ CT in order to examine *in situ* otoliths. A, *Apogon macrolepis* IRSNB 647 (cotype), Eocene (Bartonian), Wemmel Sands Member, Maldegem Formation, Belgium; B, *Dentex laekeniensis* IRSNB 645 (holotype of *Plesioserranus wemmeliensis*), Wemmel Sands Member, Maldegem Formation, Belgium; C, *Rhinocephalus planiceps* NHMUK PV P65195, Eocene (Ypresian), London Clay Formation, UK; D, *Sciaenuropsis lerichei* NHMUK PV P6444a (holotype of *Sciaenuropsis turneri*), Eocene (Ypresian), London Clay Formation, UK; E, '*Brachygnathus*' *tenuiceps* NHMUK PV P643, Eocene (Ypresian), London Clay Formation, UK; F, Holocentridae indet. NJSM GP12145, Late Cretaceous-Paleocene (Maastrichtian-Danian), Hornerstown Formation, New Jersey, USA (photograph by D. Davense, University of Oxford); G, *Apateodus corneti* RGM 446950, Late Cretaceous (Maastrichtian), Maastricht Formation, the Netherlands (specimen image reversed); H, *Osmeroides* sp. NHMUK PV 39433, Late Cretaceous (probably Cenomanian), English Chalk Group, UK (specimen image reversed); I, *Hoplopteryx lewesiensis* NHMUK OR41105, Late Cretaceous (Cenomanian), Grey Chalk Group, UK; J, *Apsopelix anglicus* NHMUK PV P9890, Early Cretaceous (Albian), Gault Clay Formation, UK; K, ?*Eurypterygii* indet. NHMUK PV P52492, Early Cretaceous (Albian), Gault Clay Formation, UK. Scale bars = 10 mm.

**Fig. 4.** Cladogram showing systematic position of Mesozoic otoliths *in situ* so far retrieved. Vertical axis without time scale; position of stars reflecting relative time scale. Cladogram composed after Nelson *et al.* (2016).

**Fig. 5.** Scanned otolith in situ of *Apsopelix anglicus* (Dixon, 1850), Cenomanian-Turonian, English Chalk, NHMUK P9890, mirror imaged. A, schematized reconstruction of inner face from CT-scan; B, inner face; C, ventral view. Scale bar = 1 mm.

**Fig. 6.** A-D, scanned otolith in situ of *Osmeroides* sp., Cenomanian-Turonian, English Chalk, NHMUK P39433; A, inner face; B, ventral view; C, posterior view; D, left and right otolith in vivo position from above (mirror imaged). E-F, *Osmeroides griffini* (Nolf & Dockery, 1990), Maastrichtian, Mississippi, USA, holotype, IRSNB P 5683 (refigured from Nolf & Dockery, 1990); E, inner face; F ventral view. G-I, *Osmeroides weileri* (Frizzell, 1965), Santonian, Alabama, USA, LACM 58469-3; G-I inner faces; H, ventral view. Scale bar = 1 mm.

**Fig. 7.** A-C, scanned otolith in situ of *Apteodus corneti* (Forir, 1887), Maastrichtian, Maastricht, Netherlands, RGM 446950 (left otolith, mirror imaged); A, inner face; B, posterior view; C, ventral view. D-G *Apteodus* sp., Santonian, Alabama, USA, LACM 58469-20; D-E, inner face; F, posterior view; G, ventral view. H, *Scopelosaurus lepidus* (Krefft & Maul, 1955), Recent, coll. Schwarzhans. I, *Chlorophthalmus acutifrons* Hiyama, 1940, Recent, Indonesia, BMNH 1986.8.21.1. J, *Bathysaurus ferox* Günther, 1878, Recent, 44°N, 03°W, coll. Schwarzhans (leg. FBH). K, *Bathypterois bigelowi* Mead, 1958, Recent, 17°37'N, 62°48'W, coll. Schwarzhans (leg. FBH). L, *Gigantura vorax* Regan, 1925, Recent, 07°N, 20°W, coll. Schwarzhans (leg. FBH). M, *Ipnops murrayi* Günther, 1878, Recent, 28°33'N, 88°21'W, ZMUC P23449-50. N, *Scopelarchus candelops* Rofen, 1963, Recent, 11°N, 26°W, coll. Schwarzhans (leg. FBH). O, *Sudis hyalina* Rafinesque, 1810, Recent, 27°N, 52°W, coll. Schwarzhans (leg. FBH). P, *Lestidiops similis* (Ege, 1933), 33°N, 39°W, coll. Schwarzhans (leg. FBH). Q, *Magnisudis atlanticus* (Krøyer, 1868), Recent, coll. Schwarzhans (leg. Fitch). R, *Coccorella atlantica* (Parr, 1928), Recent, 30°N, 66°W, coll. Schwarzhans (leg. FBH). S, *Omosudis lowei* Günther, 1887, Recent, Anton Dohrn st. 301-79, coll. Schwarzhans (leg. ZMUC). T, *Alepisaurius ferox* Lowe, 1833, Recent, New Caledonia, from Lombarte *et al.* (2006). H-T inner faces. Scale bar = 1 mm.

**Fig. 8.** A-C, Scanned otolith *in situ* of *Rhinocephalus planiceps* Casier, 1966, Eocene (Ypresian), London Clay Formation, NHMUK P65195; A-B, left otolith, mirror imaged, A, inner face, B, ventral view; C, right otolith, drawing of scanned inner face; D-F, otolith-based species *Merluccius nodosus* Stinton, 1977 [syn. *Rhinocephalus planiceps*], Eocene, Lutetian, southern England, holotype, NHMUK PV P56371, mirror imaged; D, inner face (refigured from Stinton 1977); E, inner face; F, ventral view (E-F refigured from Nolf 2013). Scale bar = 1 mm.

**Fig. 9.** A-C, Scanned otolith *in situ* of an unspecified holocentrid, Maastrichtian-Danian, Hornerstown Formation, NJSM GP12145; A, inner face; B, outer face; C, ventral view. D-E, *Sargocentron violaceum* (Bleeker, 1853), Recent, Samoa, coll. Schwarzhans (leg. ZMH); D, inner face; E, ventral view. F-G, *Neoniphon argenteus* (Valenciennes, 1831), Recent, Samoa, coll. Schwarzhans (leg. ZMH); F, inner face; G, ventral view. Scale bar = 1 mm.

**Fig. 10.** A-E, *Sciaenuropsis lerichei* (Schubert, 1916) [syn. *Sciaenuropsis turneri* Casier, 1966]; A-B, scanned otolith *in situ*, Eocene, Ypresian, London Clay, NHMUK P6444a; A, inner face; B, ventral view. C-E, isolated otolith specimens of *S. lerichei*, Eocene, Lutetian, northern Germany, SMF P64510; C, D, inner faces; E, ventral view; F-H, otolith-based species *Sciaenuropsis selsiensis* (Stinton, 1978), Eocene, Lutetian, northern Germany, SMF P64511; F-H, inner faces; G, ventral view. Scale bar = 1 mm.

**Fig. 11.** A-D, Scanned otolith *in situ* of *Hoplopteryx lewesiensis* (Mantell, 1822), Cenomanian-Turonian, English Chalk, NHMUK OR41105, A schematized reconstruction of inner face from CT-scan; B, inner face of right otolith; C, inner face of left otolith (mirror imaged); D dorsal view. E-G, *Hoplopteryx causae* (Nolf, 2003), Santonian, Spain, holotype, IRSNB P 6865 (refigured from Nolf 2003); E, inner face; F, anterior view; G, ventral view. H, *Hoplopteryx oscitans* (Nolf & Stringer, 1996), Maastrichtian, Mississippi, USA, paratype IRSNB P 6157 (refigured from Nolf & Stringer 1996), inner face. I-J, *Hoplostethus crassispinus* Kotlyar, 1980,

Recent, 26°27'N, 127°36'E, NSMT-P 114295; I, inner face; J, anterior view. K, *Trachichthys australis* Shaw, 1799, Recent, off Western Australia, coll. Schwarzhans (leg. WAM), inner face. Scale bar = 1 mm.

**Fig. 12.** A-E, *Apogon macrolepis* Storms, 1896, Eocene, Lutetian, Belgium; A-C (left otolith, mirror imaged) scanned otolith *in situ*, IRSNB 647; A, outer face; B, inner face; C, ventral view; D-E (mirror imaged, refigured from depiction of mechanically isolated example in Nolf (2013)); D inner face; E ventral view. F-J *Dentex laekeniensis* van Beneden, 1872, Eocene, Lutetian, Belgium, IRSNB 645 (left otolith, mirror imaged); F-H, scanned otolith *in situ*; F, outer face; G, inner face; H, ventral view; I-J (mirror imaged, refigured from Nolf (2013)), I inner face, J ventral view. Scale bar = 1 mm.

**Fig. 13.** A-C, Scanned otolith *in situ* of '*Brachygnathus*' *tenuiceps*, Eocene, Ypresian, London Clay, NHMUK PV P643 (left otolith, mirror imaged); A, inner face; B, ventral view; C, schematized reconstruction of inner face from CT-scan; D, otolith-based species '*Brachygnathus*' *bognoriensis* (Stinton, 1957) [originally described as *Caesio bognoriensis*], Eocene, Ypresian, London Clay, NHMUK PV P58608 (mirror imaged; refigured from Stinton (1978), © The Palaeontographical Society, reproduced with permission).

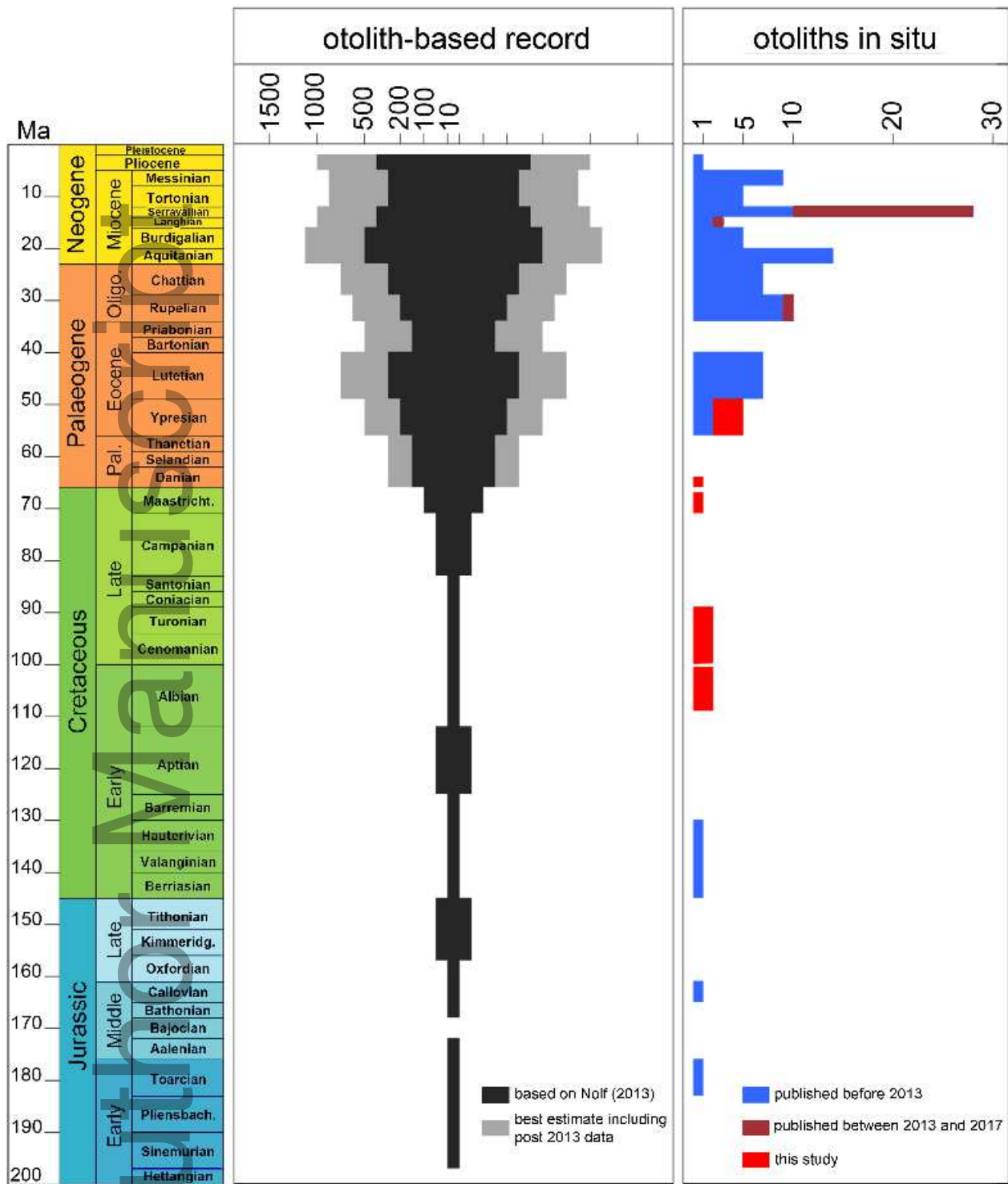
**Table 1.** Scan parameters (filters, beam intensity and beam energy).

**Table 2.** Correlations between isolated otolith and body fossil data following *in situ* otolith finds of this study.

Taxon	Specimen	Otoliths	Otolith preservation	kV, uA, filter	Scan resolution	Downsampled resolution
<i>Apogon macrolepis</i>	IRSNB 647	Both	Original	200 kV, 200 uA, 0.5 mm Cu	0.018	0.0225
<i>Dentex laekeniensis</i>	IRSNB 645	Both	Original	200 kV, 200 uA, 0.5 mm Cu	0.0261	0.0348
<i>Rhinocephalus planiceps</i>	NHMUK PV P65195	Both	Paritial void+ partial infilling + partial original material	210 kV, 200 uA, 2 mm Cu	0.056	n/a
<i>Sciaenuroopsis turneri</i>	NHMUK PV P6444a	Both	Original material + partial pyritization	200 kV, 200 uA, 2.75 mm Cu	0.0481	n/a
' <i>Brachygnathus tenuiceps</i>	NHMUK PV P643	One (left)	Original material + partial pyritization	210 kV, 190 uA, 2.0 mm Cu	0.0523	n/a
Holocentridae indet.	NJSM GP12145	Both	Void + partial infilling	195 kV, 182 uA, 0.5 mm Cu	0.0556	n/a
<i>Apateodus corneti</i>	RGM 446950	Both	Void	200 kV, 196 uA, 2.0 mm Cu	0.1059	n/a
<i>Osmeroides sp</i>	NHMUK PV 39433	Both	Void + partial infilling	205 kV, 195 uA, 2.0 mm Cu	0.0601	n/a
<i>Hoplopteryx lewesiensis</i>	NHMUK OR41105	Both	Infilled void	200 kV, 175 uA, 2.5 mm Cu	0.0461	n/a
<i>Apsopelix sp.</i>	NHMUK PV P9890	Both	Infilled void	200 kV, 170 uA, 0.5 mm Cu	0.0352	n/a

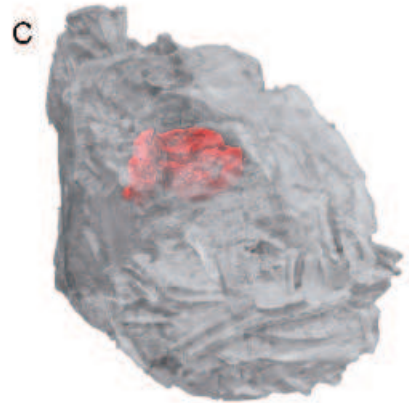
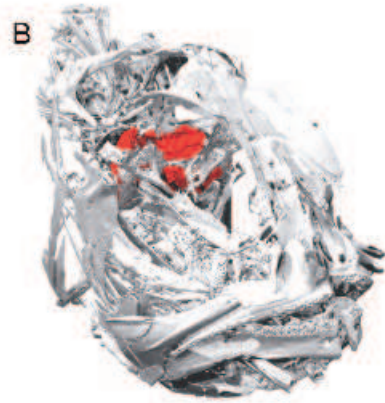
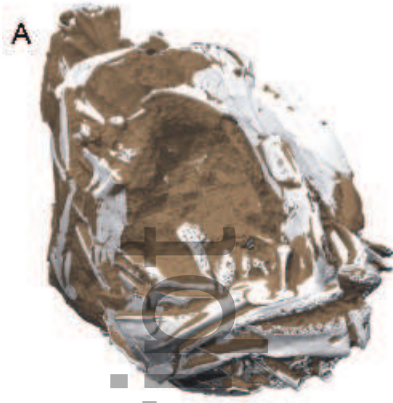
Eurypterygii indet.	NHMUK PV P52492	Both	Partial replacement	165 kV, 120 uA, 0.1 Cu	0.008	n/a
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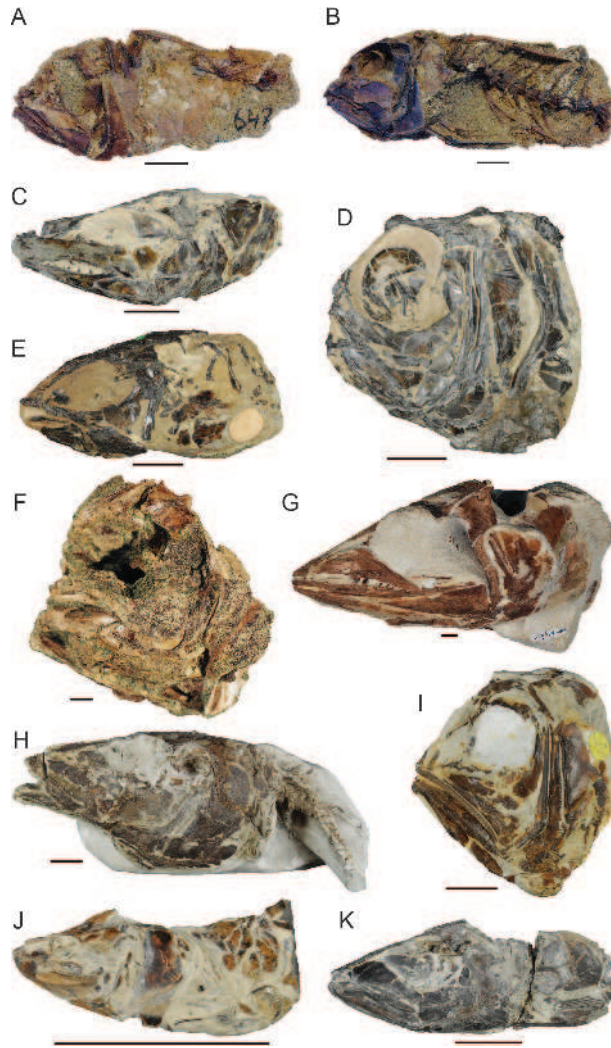
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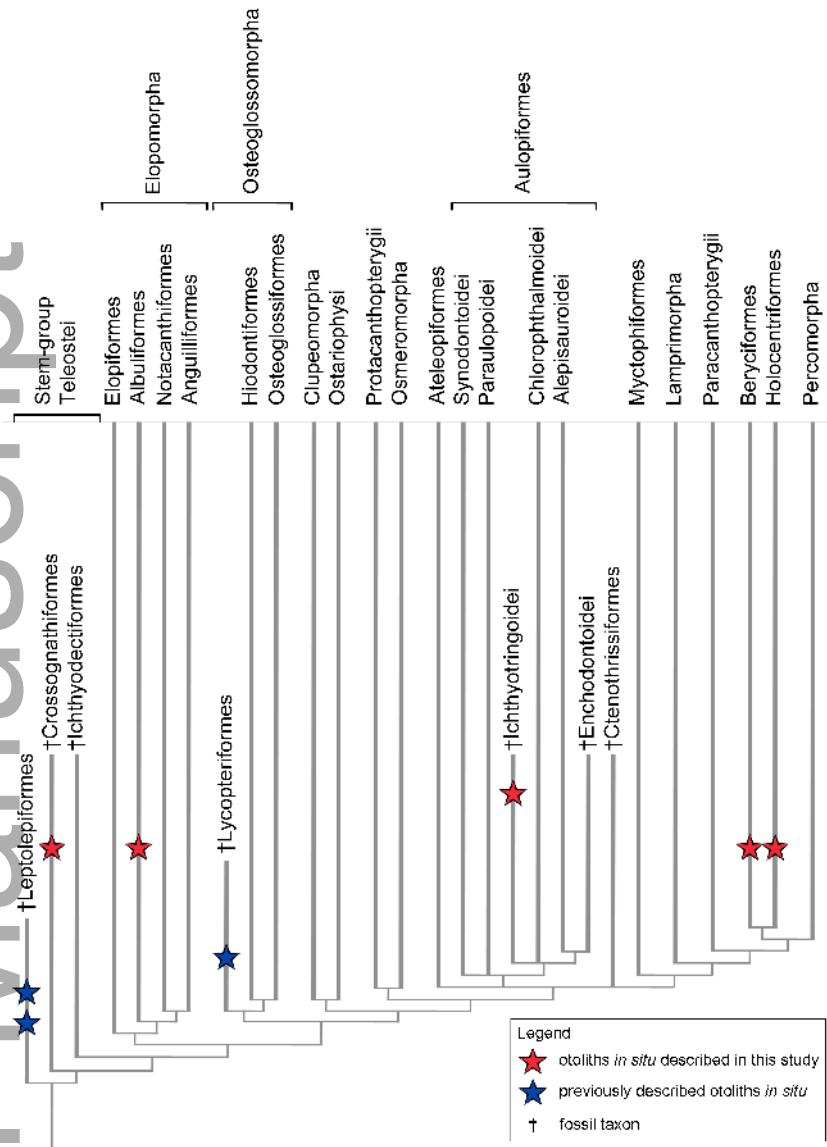


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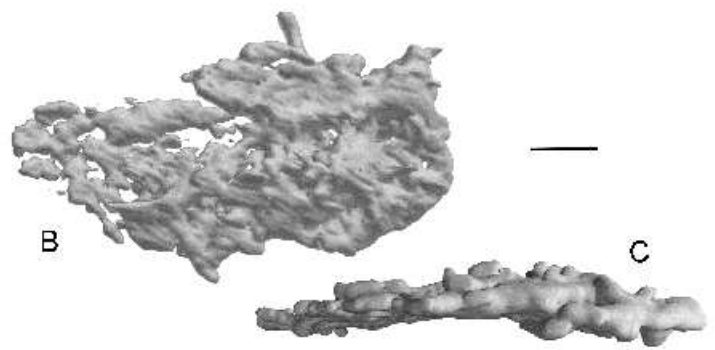
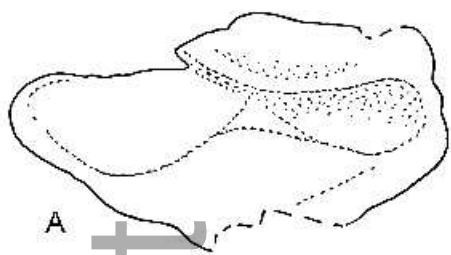
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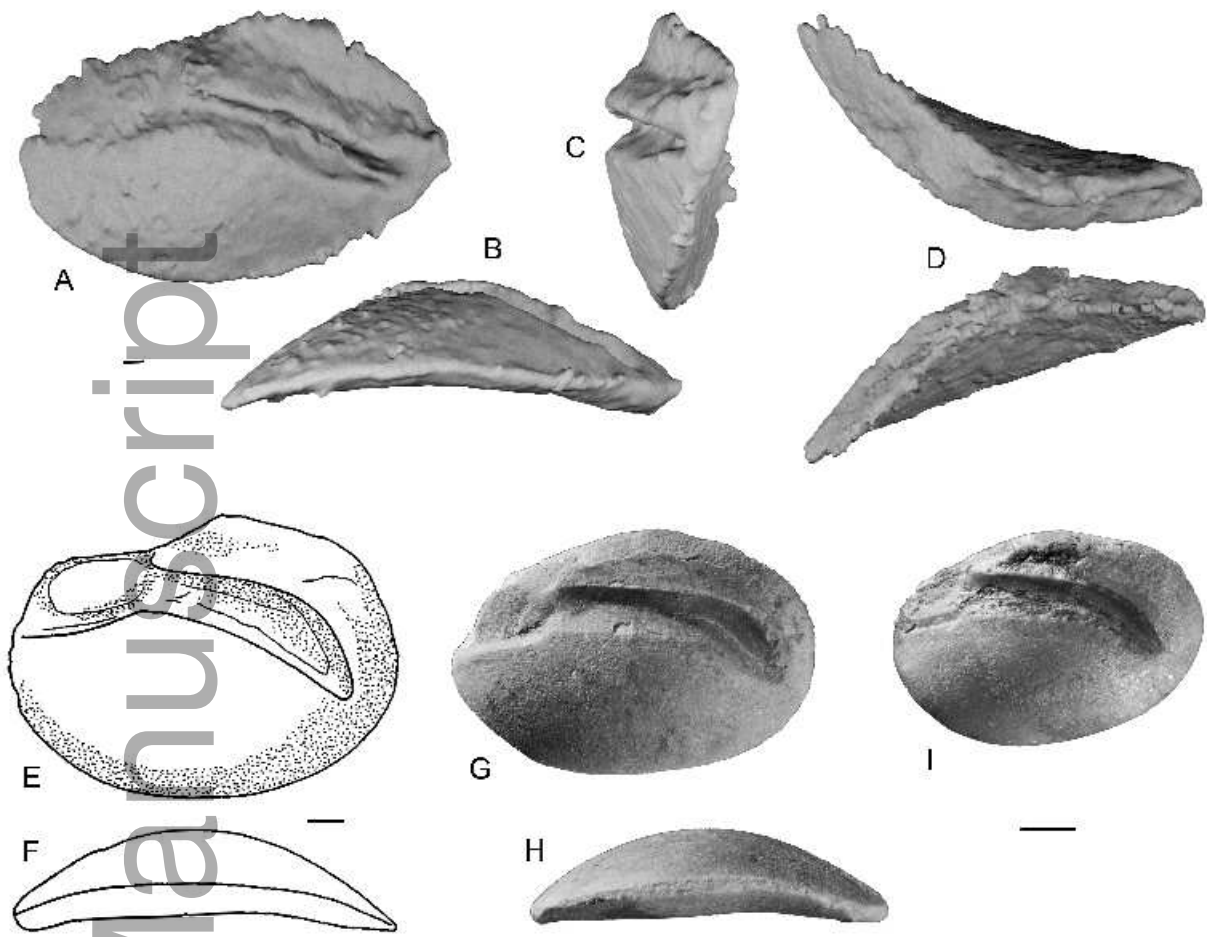


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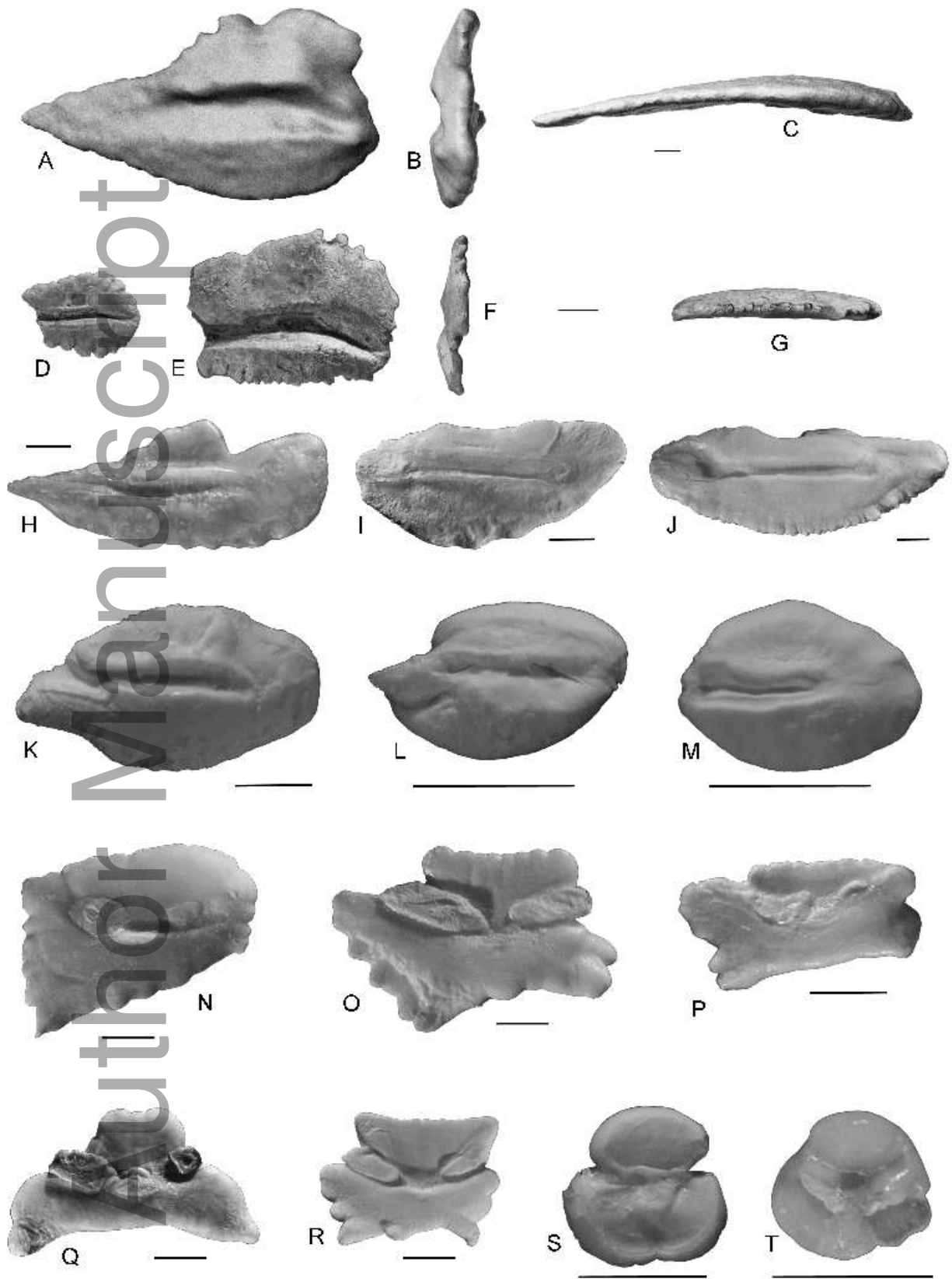


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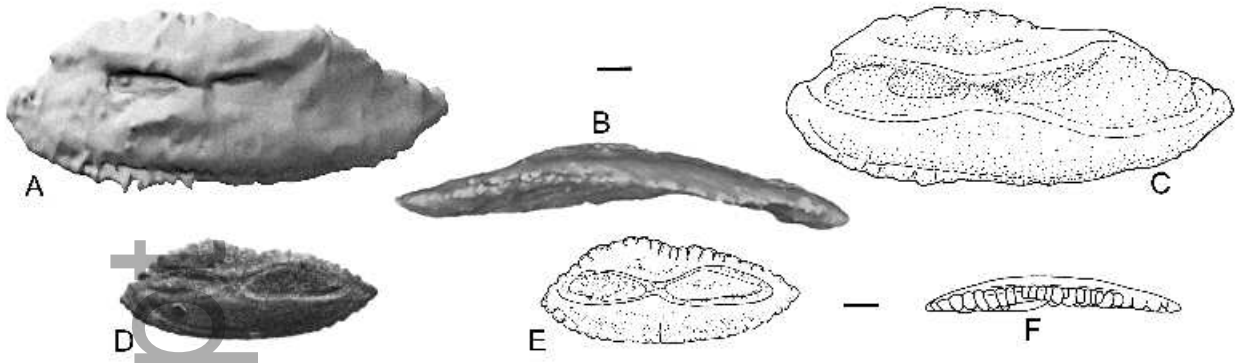
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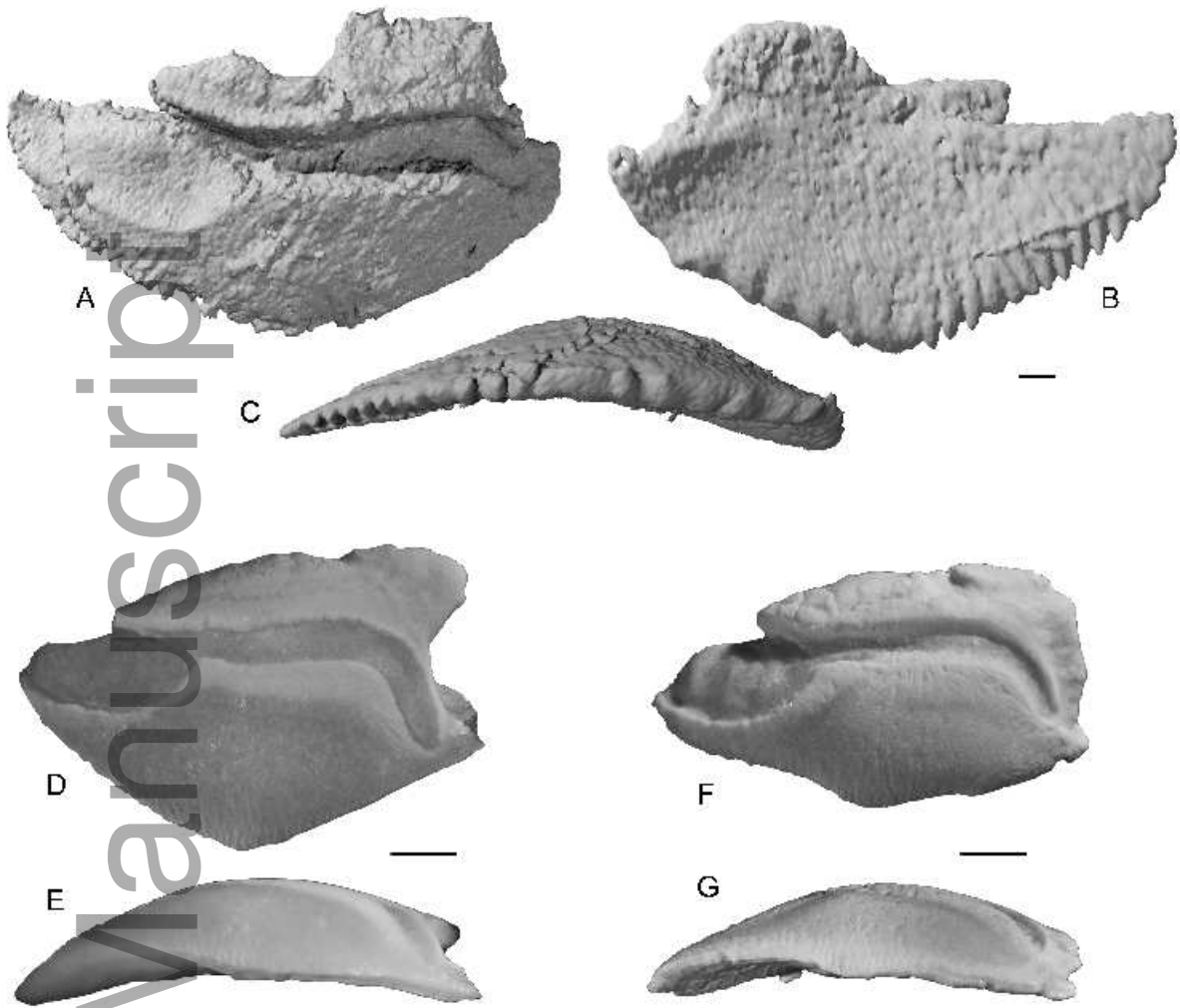


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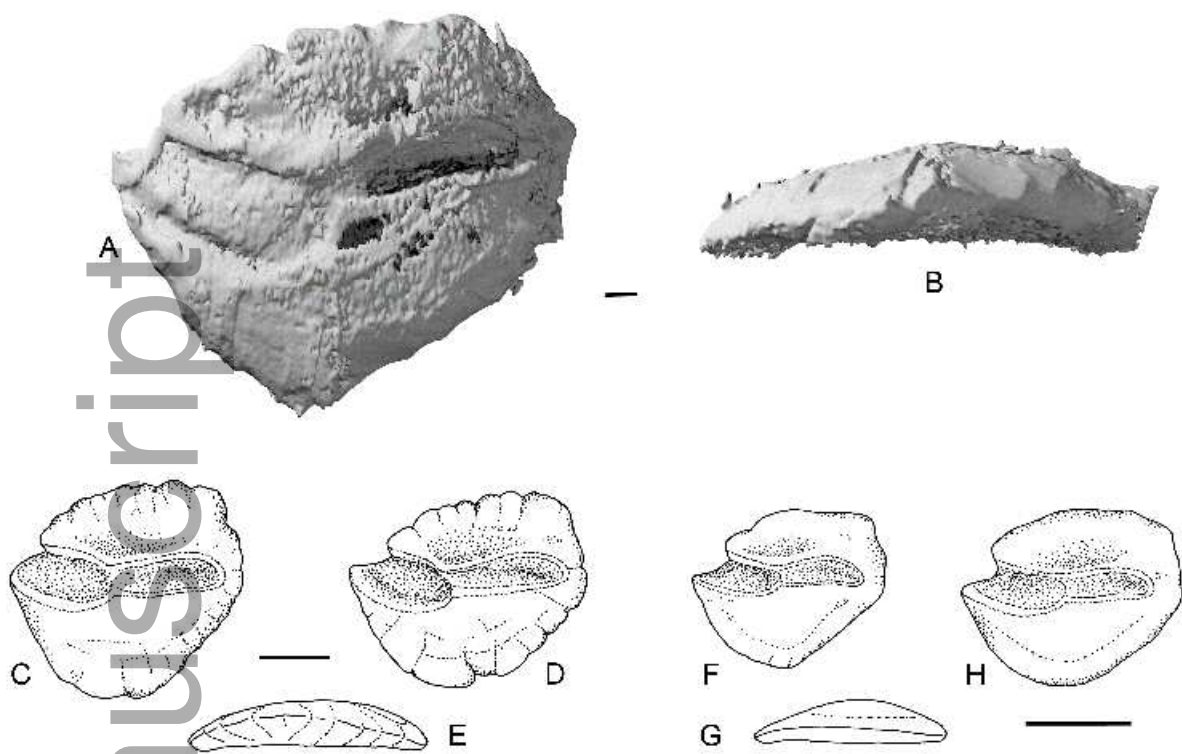
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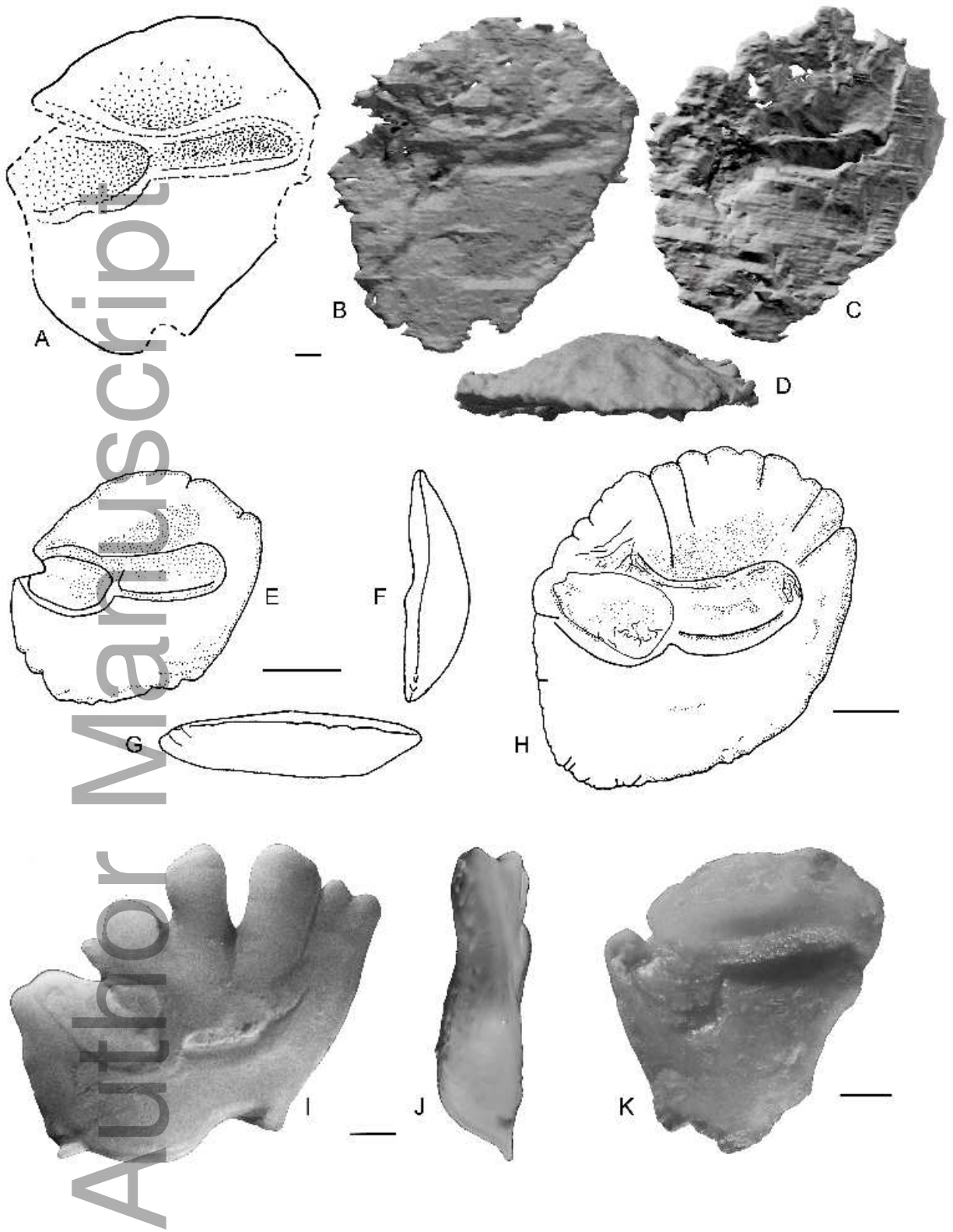


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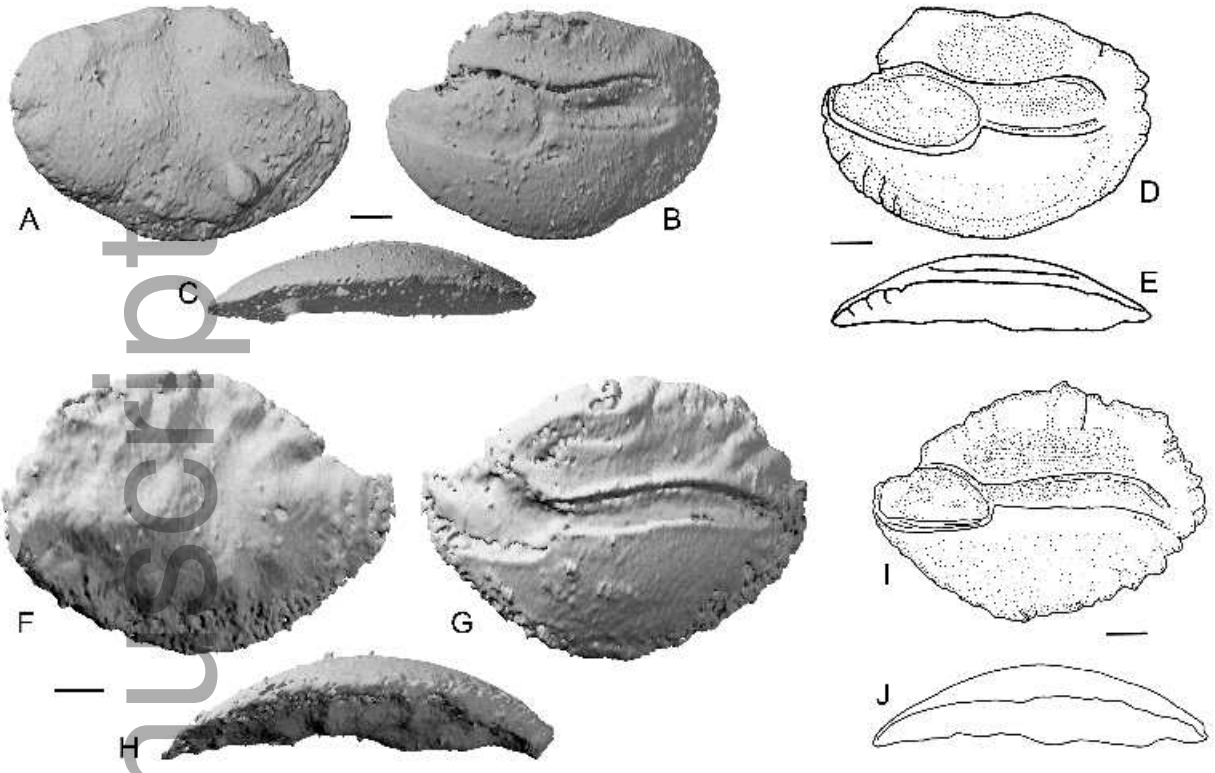




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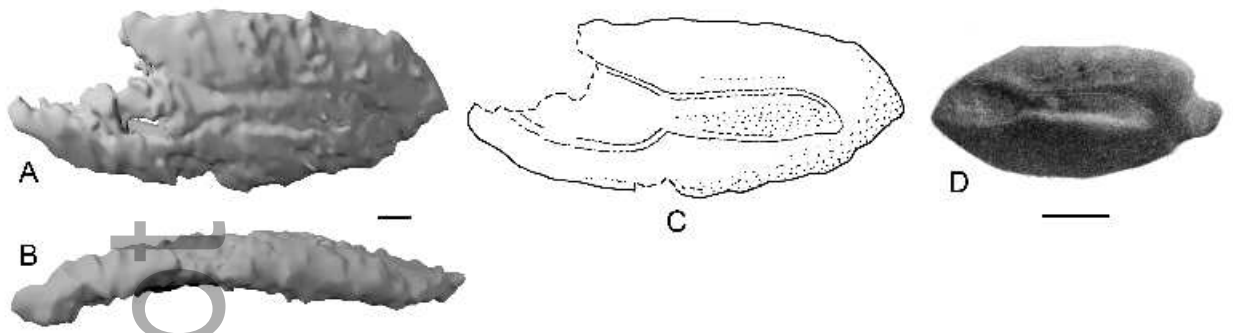


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