Otoliths in Situ in the Stem Teleost Cavenderichthys talbragarensis (Woodward, 1895), Otoliths in Coprolites, and Isolated Otoliths from the Upper Jurassic of Talbragar, New South Wales, Australia

Authors: Schwarzhans, Werner W., Murphy, Timothy D., and Frese, Michael

Source: Journal of Vertebrate Paleontology, 38(6)

Published By: The Society of Vertebrate Paleontology

URL: https://doi.org/10.1080/02724634.2018.1539740

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Journal-of-Vertebrate-Paleontology on 01 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

Journal of Vertebrate Paleontology e1539740 (14 pages)
© Published with license by the Society of Vertebrate Paleontology
DOI: 10.1080/02724634.2018.1539740

ARTICLE

OTOLITHS IN SITU IN THE STEM TELEOST *CAVENDERICHTHYS TALBRAGARENSIS* (WOODWARD, 1895), OTOLITHS IN COPROLITES, AND ISOLATED OTOLITHS FROM THE UPPER JURASSIC OF TALBRAGAR, NEW SOUTH WALES, AUSTRALIA

WERNER W. SCHWARZHANS, *,[1,2] TIMOTHY D. MURPHY, [3] and MICHAEL FRESE [4,5]
[1]Zoological Museum, Natural History Museum of Denmark, Universitetsparken 15, 2100 København, Denmark;
[2]Ahrensburger Weg 103, 22359 Hamburg, Germany, wwschwarz@aol.com;
[3]Macquarie University, North Ryde 2109, Sydney, New South Wales, Australia, timothy.d.murphy@mq.edu.au;
[4]Faculty of Science and Technology and Institute for Applied Ecology, University of Canberra, Bruce 2601, Canberra, Australian Capital Territory, Australia;
[5]Australian Museum, 1 William Street, Sydney, New South Wales 2010, Australia, michael.frese@canberra.edu.au

ABSTRACT—*Cavenderichthys talbragarensis* (Woodward, 1895) is a common signature freshwater stem teleost in the Upper Jurassic of Australia. Our discovery of numerous otoliths in the Talbragar Fish Bed establishes *Cavenderichthys* as only the second known Jurassic teleost and the third known stem teleost with otoliths in situ and provides an important calibration point for the interpretation of isolated Mesozoic otoliths. It corroborates the low degree of morphological diversification of stem teleost otoliths. The abundance of otoliths (isolated, in coprolites and in situ) allows the mapping of ontogenetic effects and of intraspecific variability for the first time in attributable stem teleost otoliths. Here, we describe 284 otoliths, mostly from *Cavenderichthys*. Otoliths in situ in *Cavenderichthys* document the presence of sagitta, lapillus, and asteriscus. Three other, much rarer otolith types were also found that have a teleost otolith pattern more primitive than that of Leptolepidiformes; the origin of these is unknown, but it is likely that they stem from pholidophoriform fishes of the family Archaeomenidae. If confirmed, this otolith pattern would provide a further highly diagnostic and synapomorphic character to define teleosts at the level of the Leptolepidiformes and above. Different mineral replacement processes in fossils from the Talbragar Fish Bed aided us in finding many otoliths, particularly otoliths in situ. Given their abundance and distinct preservation, it is surprising that otoliths in the Talbragar Fish Bed have not been recognized before.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

Citation for this article: Schwarzhans, W. W., T. D. Murphy, and M. Frese. 2019. Otoliths in situ in the stem teleost *Cavenderichthys talbragarensis* (Woodward, 1895), otoliths in coprolites, and isolated otoliths from the Upper Jurassic of Talbragar, New South Wales, Australia. Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2018.1539740.

INTRODUCTION

Articulated fish fossils with otoliths in situ are considered to be rare. Nolf (2013) listed 93 species of extinct fish with known otoliths in situ but stated that in several of those, the otoliths are too poorly preserved to be of taxonomic value. This contrasts with several thousand fossil fish species established by osteological means or based on isolated otoliths. Recent studies by Bannikov and Kotlyar (2015), Baykina and Schwarzhans (2017a, 2017b), Přikryl et al. (2017), and Schwarzhans et al. (2017a, 2017b, 2017c, 2017d, 2017e, 2017f), however, have shown that otoliths in situ may be more common than generally perceived. Within a short time, 28 further species have been added to Nolf's (2013) count. The discovery of otoliths in situ depends largely on the lucky splitting of the fossiliferous rock to expose the otolith, or at least part of it, on the surface of the slab without damaging its fragile composition. Invasive preparation techniques are avoided as much as possible, but applications of non-invasive methods (casting from voids: Schwarzhans, 2007; micro-computed tomography [CT] scanning: Schwarzhans et al., 2018; X-ray fluorescence [XRF] spectrometry: this study) have yielded promising results.

Otoliths in situ of fossil Teleostei have mostly been found in Cenozoic rocks and recently also by micro-CT scanning of Cretaceous and Paleogene fish fossils (Schwarzhans et al., 2018). In Jurassic stem teleosts, however, they are exceedingly rare, reported only for *Leptolepis normandica* Nybelin, 1962 (in Delsate, 1997), and from a 'quasi in situ' find of an otolith in the phosphatized solution residue of a leptolepidid head carved out from the stomach of a pholidophorid predator (Patterson, 1975; otolith drawn by Stinton and first published by Nolf, 1985). Thus, the otoliths of *Cavenderichthys talbragarensis* (Woodward, 1895) described here represent only the second (or third when considering Patterson, 1975) in situ otolith of a Jurassic stem teleost.

The Talbragar Fish Bed has been extensively collected for more than 100 years and has probably yielded thousands of specimens of *C. talbragarensis*, the most common fish in this lagerstätte. However, the presence of isolated otoliths was only recently recognized by one of us (M.F.) in 2016, during preparations for a publication featuring a dragonfly specimen from Talbragar

---

*Corresponding author.

Color versions of one or more of the figures in the article can be found online at www.tandfonline.com/ujvp.

(Nel et al., 2017) that showed two otoliths adjacent to the insect wing (Nel et al., 2017:fig. 1a; AM F.141097 and AM F.141098). A subsequent systematic review of a large collection of material from Talbragar has yielded 282 further otoliths, 43 of them from 29 articulated fishes with otoliths in situ. All but 19 otoliths can be ascribed to *C. talbragarensis* (i.e., 218 sagittae, 44 lapilli, and three asterisci, which include all otoliths in situ). The 19 other otoliths are either too poorly preserved to be ascribed to a particular taxon (12 otoliths) or belong to three different species of basal holosteans or pholidophoriforms (7 otoliths). The latter could not be related to skeleton-based taxa due to the lack of respective in situ finds. As it now turns out, otoliths are common in the Talbragar Fish Bed but have been overlooked for more than a century. We hope that this amazing result will inspire colleagues to search for otoliths in other lagerstätten of fish fossils.

Cavenderichthys talbragarensis was originally described as a representative of the genus *Leptolepis*, which then acted as a basket for various 'primitive' Jurassic teleosts. Woodward (1895) described three species of *Leptolepis* from the Talbragar Fish Bed, but Wade (1941) considered them to be conspecific and recognized only a single species, *Leptolepis talbragarensis*. Arratia (1997), in a comprehensive study of Jurassic stem teleosts aimed toward unraveling the basal teleostean phylogeny, established the genus *Cavenderichthys* Arratia, 1997, to accommodate the Australian Late Jurassic freshwater teleosts but could not assign the genus to any family and treated it as Teleostei incertae sedis. She concluded that *Cavenderichthys* represents a primitive teleost, more advanced than *Leptolepis coryphaenoides* (Bronn, 1830), but more primitive than members of the varasichthyid teleost stem group. Sferco et al. (2015) confirmed Arratia's phylogenetic assessment, retrieving a clade of Gondwanan freshwater fishes comprising the genera *Luisiella* Bocchino, 1967, from South America and *Cavenderichthys* and *Waldmanichthys* Sferco, López-Arbarello, and Báez, 2015, from Australia, and established a new family, Luisiellidae, for these three genera as a member of a teleost stem group immediately above the level of *Leptolepis coryphaenoides* and below the dichotomy that gave rise to the Varasichthyidae.

Institutional Abbreviations—**AM**, Australian Museum, Sydney, New South Wales, Australia; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **MM**, Palaeontological Reference Collection, Geological Survey of New South Wales, W. B. Clarke Geoscience Centre, Londonderry, New South Wales, Australia.

Anatomical Abbreviations—**CaL**, length of cauda of otolith; **HL**, head length of fish; **OH**, otolith height; **OL**, otolith length; **OsL**, length of ostium of otolith; **OT**, otolith thickness; **SL**, standard length of fish.

HISTORY, GEOLOGICAL SETTING, AND PRESERVATION OF FOSSILS

The Talbragar Fish Bed near Gulgong in New South Wales (NSW), Australia, is of Late Jurassic age (Kimmeridgian–Tithonian), ca. 151.55 ± 4.27 Ma, as determined by radiometric dating of zircon crystal inclusions (Bean, 2006). This highly fossiliferous lagerstätte was discovered in 1889 (older Aboriginal knowledge of the site—if ever existent—has not survived), and fishes from the site were first described by Arthur Smith Woodward, the then assistant keeper of the Department of Geology at the British Museum (Natural History) in London (Woodward, 1895). Subsequent excavations yielded large numbers of often exquisitely preserved fish fossils, predominantly of *Cavenderichthys talbragarensis*, but also of other teleost fishes, namely, *Aphnelepis australis* (Woodward, 1895), *A. mirabilis* (Woodward, 1895), *Archaeomene tenuis* (Woodward, 1895) and *Madariscus robustus* (Woodward, 1895), the chondrostean *Coccolepis australis* (Woodward, 1891), and the macrosemiiform *Uarbryichthys latus* (Wade, 1953). Furthermore, the partial remains of an undetermined nonmarine chondrichthyan (Turner and Avery, 2017) and a coelacanth (Woodward, 1895) were described. The sediments also contain abundant plant material (e.g., leaves and small twigs of the broad-leaved conifer *Agathis jurassica* White, 1981). The presence of terrestrial plants and the absence of marine organisms such as ammonites, belemnites, and brachiopods indicate a lacustrine environment, probably a large freshwater lake surrounded by humid, high-latitude, lush vegetation. The recent discovery of numerous fossils of aquatic and terrestrial insect species (>600 specimens since 2006; for the most recent insect paper, see Oberprieler et al., 2016) further suggests that the Talbragar Fish Bed was deposited close to the shoreline of this lake.

The thickness of the Talbragar Fish Bed varies but does not exceed 1.5 m (Beattie and Avery, 2012). Fossils are preserved as compressions embedded in ferruginous tuffaceous siltstone, indicating nearby volcanic activity during deposition. A typical *C. talbragarensis* fossil from the Talbragar Fish Bed is of medium size (i.e., 40–80 mm long), with a complete, fully articulated skeleton and its scales still in place (although partly decomposed fish remains were also found). Many fish fossils show signs of tetany, a severe postmortem muscular contraction that leads to open mouths, erect fins, and arched backs. Because tetany is indicative of a lack of oxygen as the cause of death (Smith and Elder, 1985; Elder, 1985), it has been suggested that the fish at Talbragar succumbed to mass-killing events under hypoxic or anoxic conditions and that the bodies were quickly buried, possibly as a consequence of a large influx of volcanic ash (Bean, 2006; Beattie and Avery, 2012). Bean (2006) considered two such volcanic ash shower events that overwhelmed the fish. Elemental and mineralogical analyses of the Talbragar fish fossils revealed that bones were silicified by early diagenetic events associated with volcanic ash input and consist predominantly of quartz (SiO_2), with trace amounts of kaolinite ($Al_2Si_2O_5(OH)_4$) (Frese et al., 2017). Fish and plant fossils have similar elevated levels of Si in comparison with the matrix, but only fish bones are rich in Al, a consequence of different diagenetic pathways in plant and fish fossils (Frese et al., 2017). Otoliths were not previously studied, but their different color suggests that their mineralization differs from that of fish bones, and this was confirmed by X-ray fluorescence (XRF) spectrometry (see below).

MATERIALS AND METHODS

Locality and Fossils

Otoliths were recovered by visual inspection of hundreds of fish specimens in the search for otoliths in situ, and hundreds of coprolites and numerous slab surfaces in the search for isolated otoliths. If not indicated otherwise, all material originated from the 'South site' of the Talbragar Fish Bed that is located in the Central Tablelands of New South Wales, ca. 25 km northeast of the town of Gulgong. The 'South site' consists of an area that is demarcated by the following Universal Transverse Mercator (UTM) coordinates in zone 55H (easting, northings): (1) 753140, 6437890; (2) 753165, 6437890; (3) 753160, 6437870; and (4) 643745, 6437870. Although the Talbragar Fish Bed is on private land, most of it lies in a reserve administered by the National Parks and Wildlife Service Office in Mudgee, New South Wales.

A total of 284 otoliths were identified, including 280 otoliths collected since 2016, of which 265 (93.3%) can be attributed to *C. talbragarensis*, including 43 otoliths in situ (fish skeletons with up to four exposed otoliths, including sagittae, lapilli, and asterici, were found); seven otoliths belong to three species of either non-teleosts or basal teleosts, i.e., Pholidophoriformes; the remaining 12 specimens are unidentifiable. All new specimens were deposited at the AM under the following catalog numbers: F.143452–143571 and F.143573–143655 (for details, see Supplemental Data, Table S1).

In addition to the 280 newly found otoliths, inspection of Woodward's type specimens at the AM has revealed the presence of an otolith (sagitta) in situ in one of the paratypes of *Leptolepis gregarius* (now *Cavenderichthys talbragarensis*) (AM F.120511; Fig. S1). Woodward's (1895) drawing of the specimen (pl. IV, fig. 9), however, did not indicate the presence of an otolith in situ. Another three otoliths (two sagittae and one lapillus) were identified in a historic *C. talbragarensis* specimen (MM F.37517) from the MM.

Our study focuses on description of the otoliths found isolated or in connection with osteological material (in situ). The articulated fish skeletons themselves are not described here; for morphological details of *C. talbragarensis*, see Bean (2006). Otolith descriptions follow the terminology established by Koken (1884), with amendments by Weiler (1942) and Schwarzhans (1978).

Specimen Preparation

The otoliths show iron oxide mineralization, which has produced a variety of colors ranging from red-rust to charcoal gray. This makes it relatively easy to spot otoliths against the yellow background of the sediment, the light gray of coprolites, or the white of the bones in a fish head. The otoliths have a compact surface but are internally fragile, thus cleaning and preparation of the specimens was kept to the minimum necessary for morphometric measurements. Complete extraction of otolith bodies was achieved in only eight instances, with the otoliths remaining intact and suitable for documentation in four of these.

Imaging

Photographs were taken with a Canon EOS 5D Mark II camera mounted on a BK Plus imaging system (Visionary Digital) or with a Canon EOS I camera mounted on a Wild M400 photomacroscope. In the latter case, photographs taken of objects at different fields of depth were stitched with Helicon-Focus. Images were edited and enhanced in Adobe Illustrator, Photoshop, and PowerPoint.

X-ray fluorescence (XRF) spectrometry was used for selected samples to study the elemental composition of otoliths and to image otoliths that were partly covered by a thin layer of sediment or silicified bone. Selected samples were examined using a Bruker M4 Tornado micro-XRF spectrometer. The instrument was equipped with an Rh anode tube, operated at 50 kV and 200 µA for quantification, and imaging data were collected with a resolution of 25 µm and in 30-µm steps. For elemental compositions, a fundamental parameters routine was modified, with major elements being expressed as oxides (following the mineralogy in Frese et al., 2017) and oxygen being set as the balance element. The following elements—aluminum (Al), silicon (Si), phosphorus (P), potassium (K), calcium (Ca), titanium (Ti), manganese (Mn), and iron (Fe) are reported with a limit of reporting of 0.001 wt%.

To aid comparisons, all figures show otoliths from the right side and fishes from the left side; mirrored photographs are marked accordingly in the captions. Otolith photographs are accompanied by a schematic interpretative drawing for each species/morphotype.

DESCRIPTIONS OF OTOLITHS IN SITU AND ASSOCIATED OTOLITHS

TELEOSTEI Müller, 1846
LEPTOLEPIDIFORMES s.l. Nicholson and Lydekker, 1889
Family LUISIELLIDAE Sferco, López-Arbarello, and Báez, 2015
Genus *CAVENDERICHTHYS* Arratia, 1997

CAVENDERICHTHYS TALBRAGARENSIS (Woodward, 1895)
(Figs. 1, 2, 3A–C)

Material—A total of 261 otoliths were newly discovered (since 2016), comprising 215 sagittae, 43 lapilli, and three asterisci; included are 27 fish skeletons with 39 otoliths in situ (AM F.143479–143490, F.143555–143565, F.143619–143622, F.143639–143643, and F.143591; specimens figured in Fig. 1: AM F.143484, F.143487, F.143559, F.143639, and F.143641) and 222 otoliths ex vivo (either in coprolites, 150 otoliths in 84 coprolites, or unassociated, 72 otoliths; specimens figured in Fig. 2: AM F.143454, F.143469, F.143470, F.143495, F.143499, F.143501–143503, F.143507, F.143513, F.143520, F.143548, F.143550, F.143568, F.143569, F.143584, and F.143616; specimens figured in Fig. 3: AM F.143455, F. 143501, F.143522, and F.143579). In addition, one sagittal otolith in situ was identified in a paratype of *Leptolepis gregarius* Woodward, 1895 (syn. *Cavenderichthys talbragarensis*) (AM F.120511; Fig. S1), and three more otoliths (three sagittae and one lapillus) were identified in a historic *C. talbragarensis* specimen (MM F.37517).

Description—Sagittal otolith sizes range from 1.1 to 6.1 mm in length, with only a single specimen longer than 3.85 mm. The OL:OH ratio ranges from 1.45 to 1.83; the median is 1.6, and 75% of all values fall between 1.5 and 1.7. Extreme values above 1.7 and below 1.5 most likely result from somewhat imperfect preservation, distortion of the exposed proportions, or incomplete exposure. In fact, the rostrum in particular is rarely completely exposed or preserved, which results in some uncertainty of the measurement of the OL. We assume that the 75% range represents a value close to the true range of the index. We were able to isolate very few specimens as body fossils; hence, the OH:OT ratio was only calculated for three specimens, giving a range of 2.7–2.9. Otolith length ranges from 15% to 19% of the head length, which is toward the larger end of such relations observed in Recent fishes and above the 12% calculated for the only other Jurassic find of an otolith in situ, *Leptolepis normandica* Nybelin, 1962 (Delsate, 1997; Schwarzhans, 2018).

The outline of the otolith is spatulate, with a long and pointed rostrum (38–45% of OL). There is no excisura or antirostrum, but the otolith rim sometimes shows a broad concavity where the rear dorsal termination of the rostrum meets the anterior tip of the dorsal rim. The dorsal rim is relatively high, often undulating, with an angular or rounded posterior angle and a broadly rounded mediodorsal angle representing the highest point of the dorsal rim. The posterior rim is broadly and irregularly rounded. The ventral rim is gently curved, deepest at about its middle part, smooth or slightly denticulate, particularly at its rear part (Fig. 2A–R).

The inner face is distinctly convex and bears a somewhat supramedially positioned, long, and moderately deep sulcus (Fig. 2A–L). The sulcus is vaguely subdivided into an ostium and a cauda of about equal length. The ostium is ventrally widened, and its dorsal margin turns upward to meet the dorsal rim at the joint with the posterior-dorsal termination of the rostrum. The cauda is straight and very faintly flexed toward its rounded termination, which closely approaches the posterior rim of the otolith. The sulcus bears no discernible colliculum, and, instead, the ostium often shows parallel growth lines along its shallowing ventral margin. A small indentation or flexure at the ventral margin of the ostial-caudal joint serves as the best definition for the morphometric measurements of OsL and CaL. The OsL:CaL ratio ranges from 0.75 to 1.25, averaging 1.0, but as with the OL:OH ratio, the extreme values are likely distorted by

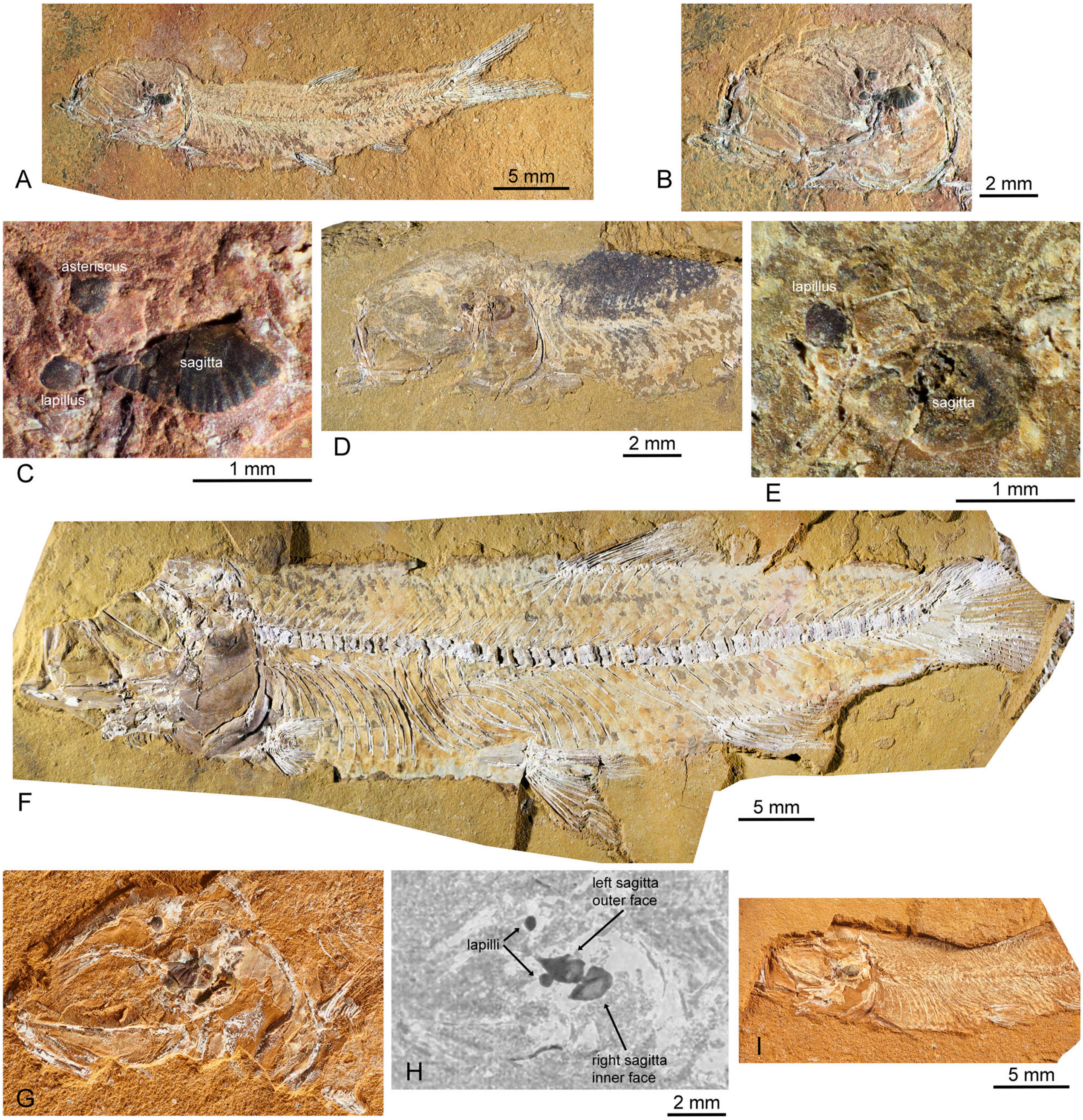

FIGURE 1. *Cavenderichthys talbragarensis* skeletons with otoliths in situ. **A**–**C**, AM F.143559: **A**, entire fish; **B**, close-up of head; **C**, close-up of otoliths in situ. **D**, **E**, AM F.143484 (mirrored): **D**, head; **E**, close-up of otoliths in situ, note that the sagittal otolith is covered by a thin veneer of sediment. **F**, AM F.143487 (mirrored), the largest specimen with otoliths in situ, note that the sagittal otolith is covered by a thin veneer of sediment. **G**, **H**, AM F.143639: **G**, head under normal light photography, note incomplete exposure of sagittal otoliths; **H**, XRF-generated image (cumulative overlay of a photograph and several elemental maps) showing the otoliths' outline more clearly. **I**, AM F.143641 (mirrored), incomplete fish with otoliths in situ.

preservation effects and therefore the true range probably falls within approximately 0.85–1.2. The dorsal field shows a small, ventrally often well-marked depression above the anterior part of the cauda. The ventral field is smooth, without a ventral furrow. The outer face is flat to slightly concave, with some radial furrows on its ventral part and a moderate umbo close to the mid-dorsal angle, or is nearly smooth.

Ontogeny—The otoliths of *C. talbragarensis* show few ontogenetic effects. The OL:OH relationship appears to be stable across all sizes (Fig. 4A); however, the ratio of otolith length to head length appears to increase slightly with fish size (Fig. 4A, B). Likewise, the length of the ostium increases with fish size, possibly caused by the development of a longer (and sharper) rostrum. This effect is, however, faint and only indicated in the comparison of the ostium length (OL) with the OsL:CaL ratio (Fig. 4C), whereas the trend appears to be linear in the cross-plot of OsL vs. CaL (Fig. 4D). The strongest ontogenetic change is manifested in the change of ornamentation of the otolith rims and the outer face, which are smooth in small specimens up to about 1.5–1.7 mm in length. In larger specimens, the

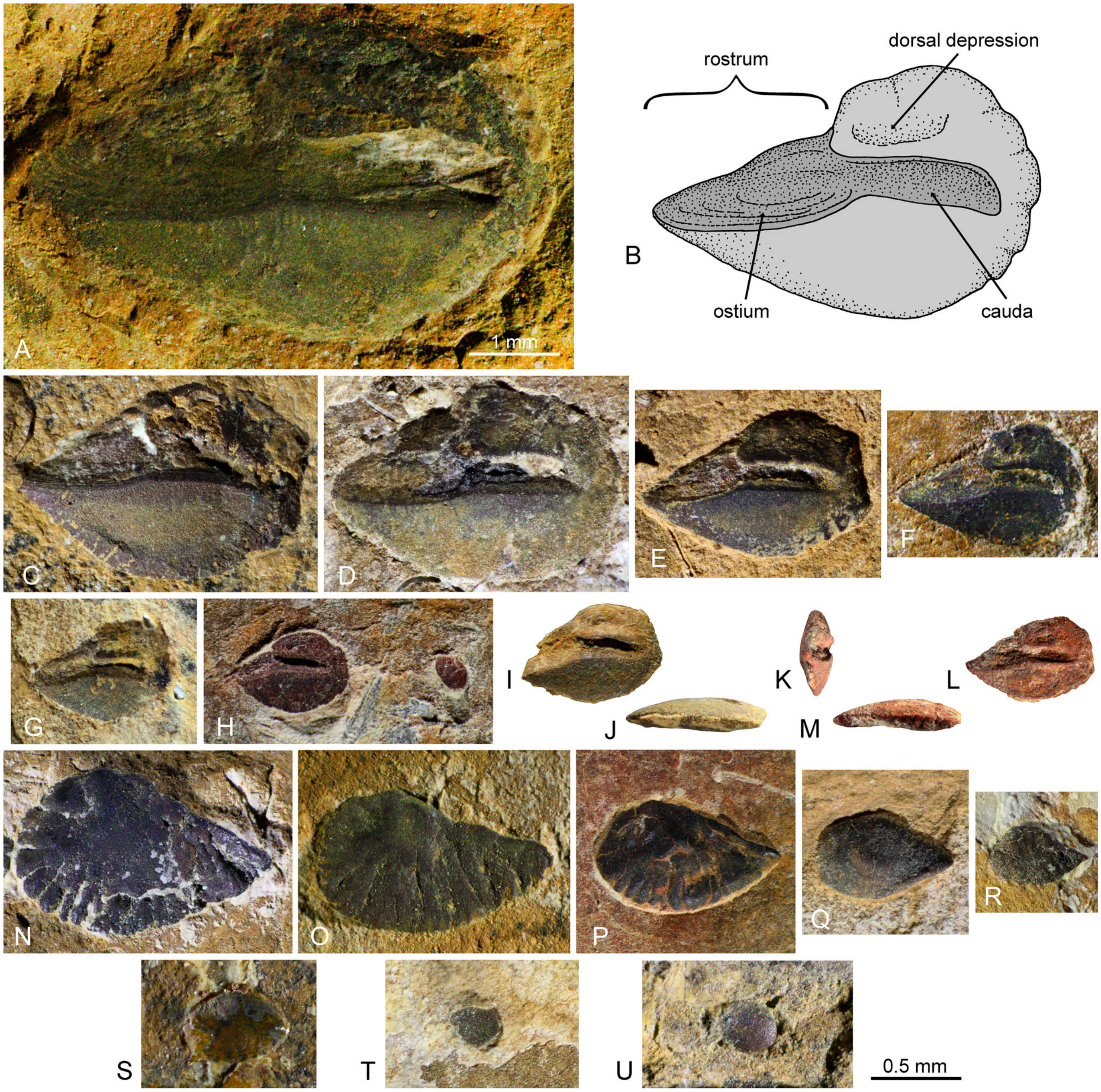

FIGURE 2. *Cavenderichthys talbragarensis* otoliths. **A**–**H**, sagittae, inner faces: **A**, AM F.143568, the largest specimen of 6.1 mm in length; **B**, interpretative drawing based on AM F.143569, not to scale; **C**, AM F.143495 (mirrored); **D**, AM F.143520; **E**, AM F.143550 (mirrored); **F**, AM F.143569; **G**, AM F.143548; **H**, AM F.143503 (mirrored), note lapillus on right side of picture. **I**–**L**, sagittae, extracted otoliths: **I**, **J**, AM F.143616: **I**, inner face; **J**, ventral view. **K**–**M**, AM F.143502: **K**, anterior view; **L**, inner face; **M**, ventral view. **N**–**R**, sagittae, outer faces: **N**, AM F.143454 (mirrored); **O**, AM F.143584 (mirrored); **P**, AM F.143469; **Q**, AM F.143513; **R**, AM F.143501 (mirrored). **S**–**U**, lapilli: **S**, AM F.143507; **T**, AM F.143499; **U**, AM F.143470. 1-mm scale bar for **A**,**C**–**R** and 0.5-mm scale bar for **S**–**U**.

outer face is rather extensively ornamented in the way described above and the ventral rim is often finely crenellate (Figs 2N–R). This ontogenetic change is opposite to that commonly observed in extant otoliths, in which small specimens of a given species are usually more strongly ornamented than large ones of the same species.

Variability—Some variation is observed in the OL:OH and OsL:CaL ratios. Even though the range of variation may be exaggerated in our calculations due to varying exposure, preservation, or distortion in the plane of observation, these inconsistencies, when adjusted, still allow for a sizeable variation, i.e., OL:OH of 1.5–1.7 and OsL:CaL of 0.85–1.2, which is a greater ratio than that observed in most Cenozoic or Recent otoliths. Nevertheless, we consider the observed level of variation not unusual for a single species, which is consistent with the current recognition of a single species of the genus *Cavenderichthys* in the Talbragar Fish Bed.

Other Otoliths—Forty-four lapilli of *C. talbragarensis* were observed in situ and isolated, the latter mostly in coprolites. Sagittae are 3.5–4.5 times larger than lapilli. The lapilli have an oval shape, are gently rounded along the ventral rim, and have a broadly rounded and very slight protrusion at the middle of the dorsal rim (Figs. 2S–U, 3A, C). Three asterisci about the same size as the lapilli were found; one in situ (AM F.143559; Fig. 1C)

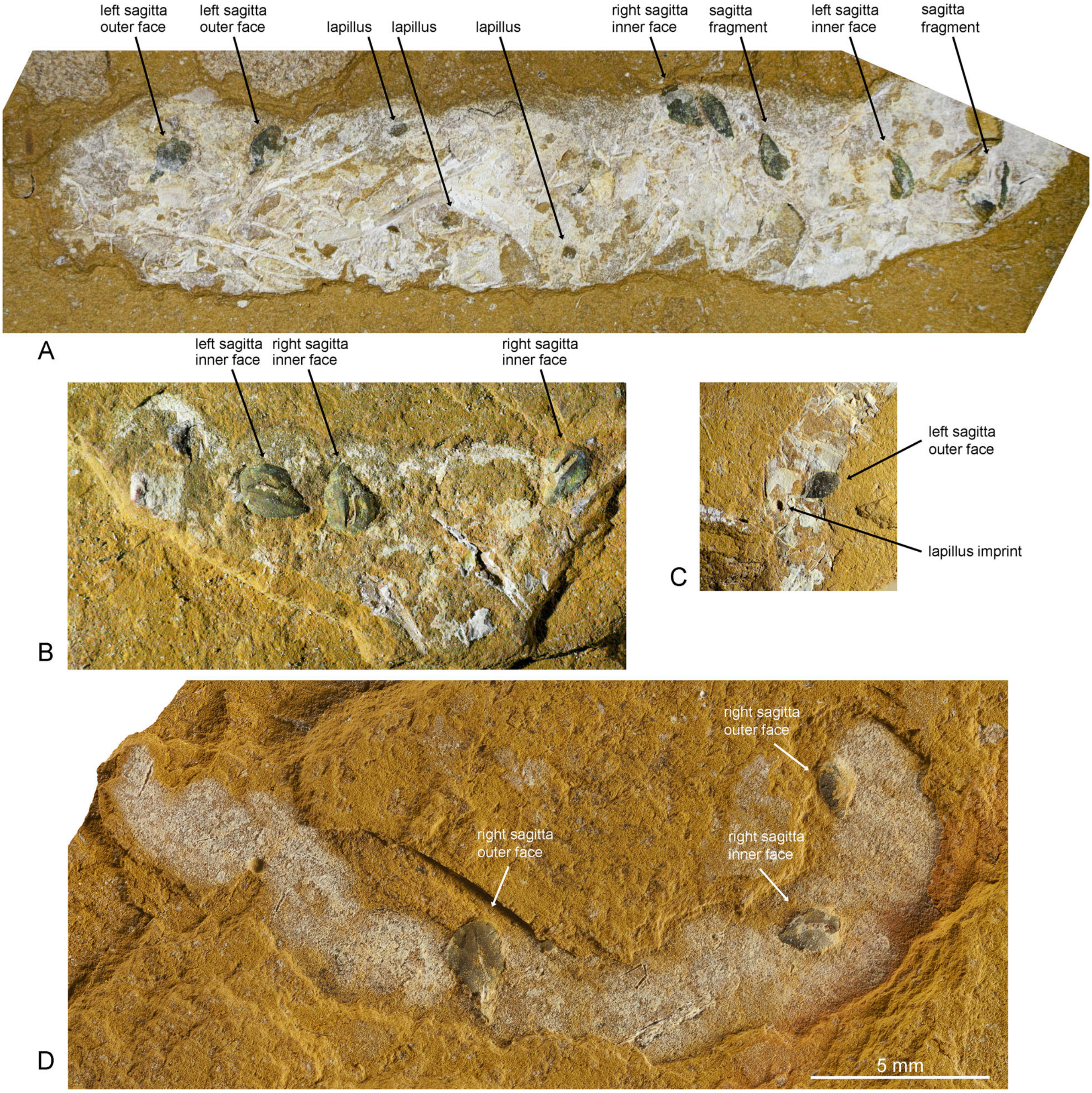

FIGURE 3. Coprolites with otoliths (mostly *Cavenderichthys talbragarensis* sagittae). **A**, AM F.143522; **B**, AM F.143579; **C**, AM F.143501; **D**, AM F.143455.

and the other two isolated (AM F. 143570 and F.143625, respectively). All three asterisci are exposed from the outer face and are near perfectly round with some faint radial ornamentation. Asterisci are extremely rare in the fossil record; hence, these three finds are rather extraordinary and prove that stem teleosts did indeed have the complete set of three pairs of otoliths. The reason asterisci are so rarely fossilized is, however, not fully understood.

DESCRIPTIONS OF ISOLATED NON-*CAVENDERICHTHYS* OTOLITHS

Teleostei or Ginglymodi indet.—Seven isolated seemingly sagittal otoliths (indicated by the presence of a sulcus acusticus) found in the Talbragar Fish Bed do not represent *C. talbragarensis* but most likely three different species of one or more extinct basal teleostean or holostean group(s), of which otoliths in situ are not yet known. They all share a rounded triangular outline, although of different proportions and with different surface features; a nearly flat outer face; a convex, smooth inner face; and a wide, faintly delimited (particularly ventrally), and poorly structured sulcus along the dorsal margin of the otolith. In extant ginglymodians, vaguely similar sagittal otoliths are only known for *Lepisosteus* (see *L. osseus*; Fig. 5A–D). So far, the Talbragar Fish Bed has not yielded any otoliths in situ from Pholidophoriformes, a basal fossil stem teleost group, which are locally represented by several genera and species of the family Archaeomenidae.

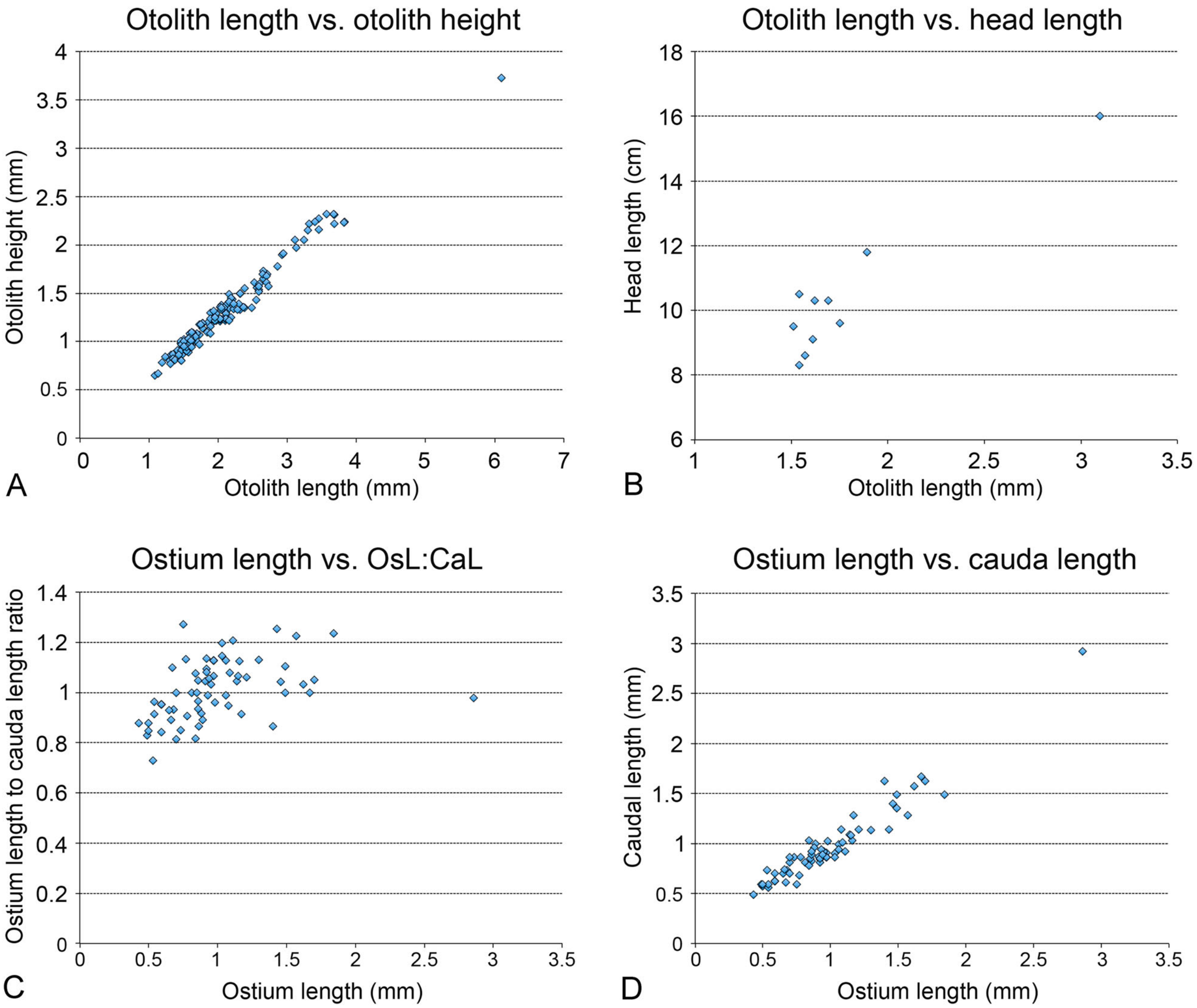

FIGURE 4. Scatter plots of various otolith measurements. Relationships between **A**, otolith length and otolith height; **B**, otolith length and head length; **C**, ostium length and the ratio of ostium length (OsL):caudal length (CaL); **D**, ostium length and cauda length.

MORPHOTYPE A
(Fig. 5E–I)

Material—Three otoliths: AM F.143464, F.143465, and F.143566 (part) and F.143567 (counterpart) (figured specimens: AM F.143464 and F.143566). All originally exposed on the outer face, but one was carefully extracted to facilitate study of its inner face (AM F.143566). However, the inner face still shows some attached sediment, which could not be fully removed.

Description—The otoliths are rounded triangular in shape and almost symmetrical. They are 1.9–2.1 mm long; OL:OH = 1.0–1.15 and OH:OT = 3.0. The ventral rim is deeply and regularly curved. The dorsal tip is narrow and moderately pointed. The mirrored symmetrical anterior and posterior rims are only slightly bent and inclined at 45–50°.

The inner face is convex, much more so than the outer face, smooth and thickest at about its middle. The ventral half of the inner face is completely smooth. The dorsal half shows a poorly defined, very wide, anteriorly and posteriorly open sulcus. Its ventral margin is expressed as a faint kink line toward the ventral region and is slightly inclined backward and downward bent anteriorly. The dorsal margin of the sulcus is developed only across a very short distance, clipping the mid-dorsal projection. It is slightly better expressed than the ventral margin due to the sulcus being slightly deepened just below its dorsal margin. The sulcus otherwise shows no internal structure, except for a few faint parallel growth lines near the ventral margin. The small dorsal area above the sulcus is slightly bulging.

The outer face is almost flat and shows a number of distinct radial furrows on the ventral area that extend and merge toward the middle of the otolith.

Comparison—The otoliths of morphotype A are best recognized by their intense ornamentation of the outer face. The inner face is much less structured than in morphotypes B and C.

MORPHOTYPE B
(Fig. 5J–L)

Material—Two otoliths: AM F.143516 and F.143576 (both figured), exposed from the outer face and the inner face, respectively.

Description—The otoliths are rounded high triangular in shape, 1.1–1.8 mm long; OL:OH = 0.95–1.05 and OH:OT could

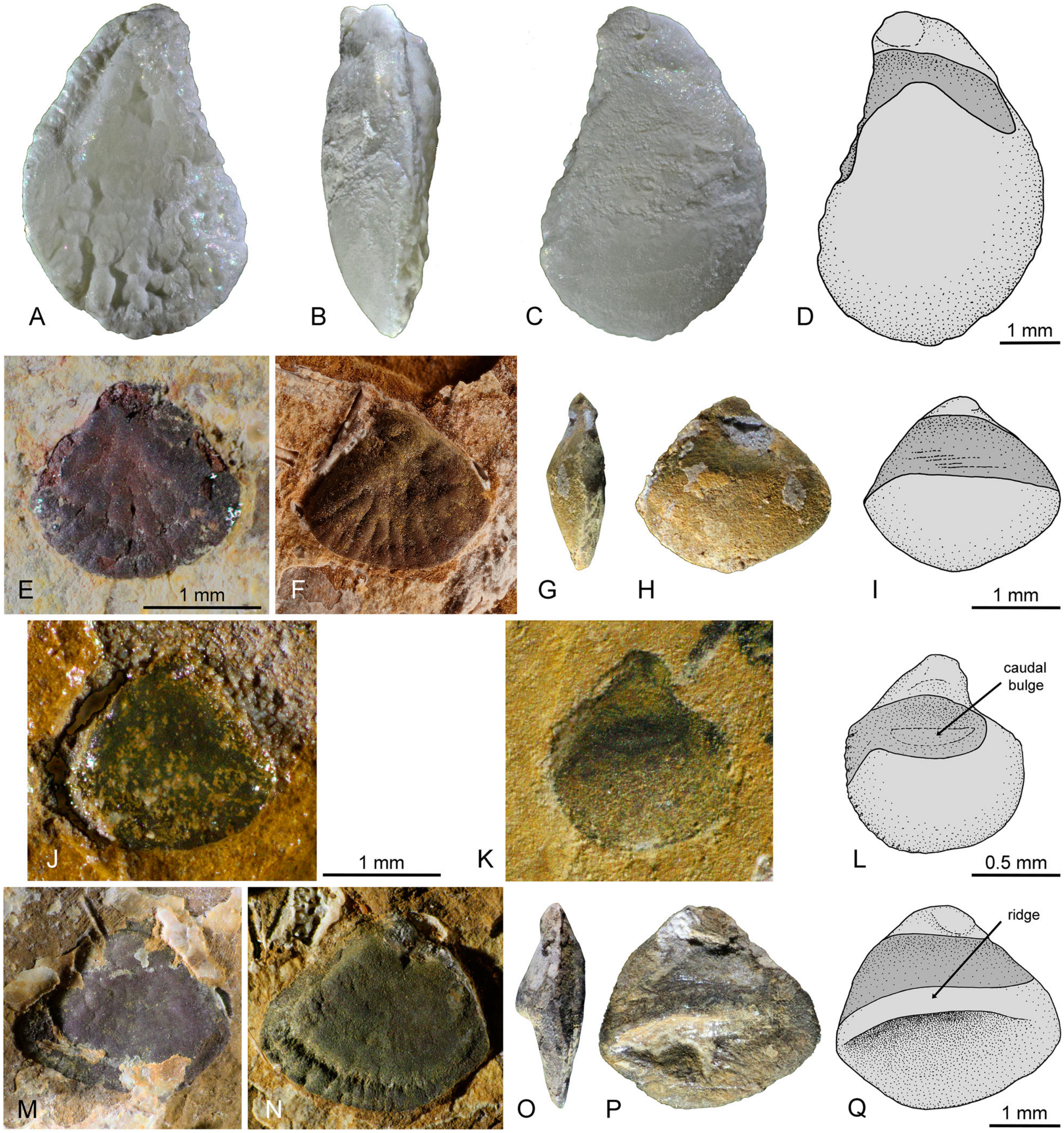

FIGURE 5. Non-*Cavenderichthys* otoliths (presumed sagittae of Ginglymodi or Pholidophoriformes). **A–D**, Recent otolith of *Lepsosteus osseus* (collection W.S.): **A**, outer face; **B**, lateral view; **C**, inner face; **D**, interpretative drawing of inner face with sulcus in dark shading. **E–I**, morphotype A: **E**, AM F.143464, outer face; **F–I**, AM F. 143566 (mirrored); **F**, outer face; **G**, lateral view after extraction; **H**, inner face after extraction; **I**, interpretative drawing of inner face with sulcus in dark shading. **J–L**, morphotype B: **J**, AM F.143516, outer face; **K**, **L**, AM F.143576, inner face; **K**, photograph; **L**, interpretative drawing with sulcus in dark shading. **M–Q**, morphotype C: **M**, AM F.143471, outer face; **N–Q**, AM F.143474 (mirrored); **N**, outer face; **O**, lateral view after extraction; **P**, inner face after extraction; **Q**, interpretative drawing of inner face with sulcus in dark shading.

not be measured. The ventral rim is deeply and regularly curved, nearly semicircular. The dorsal tip is narrow, slightly projecting, moderately pointed, and slightly set off posteriorly by a broad concavity, which is variably developed. The anterior and posterior rims are only slightly bent and inclined at 45–50°.

The inner face is convex, much more so than the outer face, smooth and thickest at about its middle. The ventral half of the inner face is completely smooth. The dorsal half shows a poorly defined, very wide sulcus, which is anteriorly open and terminates posteriorly very close to the dorsal region of the posterior rim. Its ventral margin is expressed as a faint curved line, which anteriorly bends down sharply in a distinct inflection point. The curved part stretches across more than two-thirds of the inner face and may represent the cauda, whereas the downturned part is very short.

The caudal part contains a distinct but transition-free bulge in its ventral area. The dorsal margin of the sulcus is convex, with the sulcus being slightly deepened just below. The small dorsal area above the sulcus is slightly bulged. The outer face is nearly flat and perfectly smooth.

Comparison—The otoliths of morphotype B are characterized by their more compressed shape, the completely smooth outer face, and the very distinctive development of the sulcus on the inner face, with its bulging feature in the ventral part of the cauda.

MORPHOTYPE C
(Fig. 5M–Q)

Material—Two otoliths, AM F.143474 and F.143471 (both figured); both otoliths originally exposed from the outer face, but one was carefully extracted to facilitate study of its inner face (AM F.143474). However, the inner face still shows some attached sediment, which could not be fully removed.

Description—These otoliths are rounded triangular in shape but not as symmetrical as the other two morphotypes and also somewhat more elongate. They also represent the largest otoliths among these morphotypes, with lengths of 3.1–3.5 mm; OL:OH = 1.2–1.3 and OH:OT = 3.0. The ventral rim is deeply and regularly curved. The dorsal tip is narrowed, rounded, and somewhat broader than in the other two morphotypes. The anterior and posterior rims are only slightly bent and also not perfectly symmetrical; the anterior rim is inclined at about 50–55°, the posterior rim at 40–45°.

The inner face is convex but shows a distinct depression on its ventral area, which is sharply offset against a narrow ridge running longitudinally across the center of the inner face, separating the ventral depression from the sulcus. The ventral depression resembles a collapsed structure, but it is difficult to envisage an otolith organization that would facilitate such an effect during sedimentary compression. The sulcus is relatively well marked, crossing the dorsal region of the inner face above the central ridge and appearing to be open anteriorly and posteriorly. The ventral margin of the sulcus is expressed as a moderately well-defined edge; its dorsal margin is affected by slight damage during preservation but apparently is short, close to the dorsal rim of the otolith, and marked by the sulcus being slightly deepened just below. The sulcus otherwise shows no discernible internal structure. The small dorsal area above the sulcus is slightly bulged.

The outer face is relatively flat and slightly convex in the dorsal region. It is smooth for the larger part but shows a distinct furrow close and parallel to the ventral rim and to part of the posterior rim and some irregular ornamentation in the narrow band between the furrow and the otolith rim.

Comparison—The otoliths of morphotype C are characterized by the slightly more elongate shape with a larger OL:OH ratio, the slight asymmetry of anterior and posterior rims, and the ornamentation of the outer face with the distinct furrow close to the ventral rim, and on the inner face by the very characteristic broad and deep depression of the ventral region, which is sharply offset against a central longitudinal ridge.

ELEMENTAL COMPOSITION OF OTOLITHS AND FISH BONES

Otoliths from the Talbragar Fish Bed show distinctive colors (mostly dark gray to anthracite on the surface, orange-red in the interior), suggesting that the mineral replacement process in the otoliths differs significantly from that of the usually white bones. XRF spot measurements of the elemental composition of otoliths found in situ, in coprolites, or isolated suggests that they consist predominantly of the iron oxide mineral goethite (Table S2). In contrast, the bones of a fish skeleton with otoliths is situ (AM F.143639) was found to be rich in Si (Table S2), confirming earlier reports that fish bones in the Talbragar Fish Bed are at least partly silicified (Frese et al., 2017). We also determined the elemental composition of several mollusk shells found in the Talbragar Fish Bed because snails and bivalves build shells that consist largely of the calcium carbonate mineral aragonite ($CaCO_3$), the very mineral that is used by fish to grow otoliths. We found that otoliths and shell fossils from the Talbragar Fish Bed not only look similar in color and luster, they also have a similar elemental composition (Table S2), suggesting a similar diagenesis from aragonite to goethite.

DISCUSSION

The fossil record of teleost fishes is primarily based on two data sets: articulated skeletons and isolated otoliths. It has been argued that these two records partly complement each other due to mineralogical differences and fossilization potentials (Nolf, 1985, 2013; Schwarzhans and Carnevale, 2017). It is, however, also true that the systematic interpretation of isolated otoliths largely depends on correlation with extant otoliths, a situation that becomes particularly complex in Mesozoic rocks with the predominance of extinct teleost groups from which otoliths are unknown (Schwarzhans, 2018; Schwarzhans et al., 2018). Articulated identifiable fossil fish skeletons with otoliths in situ thus represent the only means of linking these two rich and mostly separate records of extinct fishes and provide vital calibration points for the interpretation of isolated otoliths.

Cavenderichthys talbragarensis fossils with in situ otoliths from the Talbragar Fish Bed not only serve as an important calibration point but also allow statistical observations because of the sheer abundance of specimens. The sagittal otoliths of *C. talbragarensis* represent the leptolepid (or 'primitive' teleost) pattern (Schwarzhans, 2018) (see also 'archaesulcoid' sulcus pattern of Schwarzhans, 1978) that is characterized by inner and outer faces not strongly bent, sulcus straight and cauda not inclined, ostium and cauda poorly defined and with a single undivided vague colliculum (or no discernible colliculum), a strong rostrum but no excisura or antirostrum (Martin and Weiler, 1954), and outer face with radial furrows along the ventral margin and converging at a focal point in a shallow umbo at the mid-dorsal rim. The otolith outline and sulcus, as well as the absence of a discernible colliculum and the presence of growth lines along the ventral margin of the ostium, resemble the pattern recently described from isolated otoliths from Early Cretaceous freshwater deposits of Brazil (Schwarzhans, 2018), which have been interpreted as otoliths from possible representatives of the genus *Luisiella*. The fossil stem teleost family Luisiellidae was recently introduced for three exclusive Gondwanan freshwater genera of Late Jurassic to Early Cretaceous times, i.e., *Luisiella, Cavenderichthys*, and *Waldmanichthys* (Sferco et al., 2015). The otoliths of *C. talbragarensis* closely resemble those of *Leptolepis normandica*, the only other Jurassic teleost from which otoliths in situ have been described (Delsate, 1997; Nolf, 2013). This finding is consistent with the observation that the stem teleost otolith morphology indeed shows a very low degree of diversity (Schwarzhans, 2018).

Cavenderichthys talbragarensis otoliths are relatively large in comparison with the head length (15–19% of HL; see above), a percentage that is slightly larger than that found in *Leptolepis normandica* (about 12%) and well within the range of otolith length to head length ratios observed in modern teleosts (Schwarzhans, 2018). Ten specimens of fishes with otoliths in situ are completely preserved and facilitated the measurement of fish lengths, which range from 15.0 to 57.7 mm SL. The corresponding otolith lengths range from about 1.0 to 3.1 mm. Bean (2006) provided a graph of fish lengths vs. depths of 86 specimens ranging in length from 30 to 130 mm TL. We measured 'standard length' (SL) instead of 'total length' (TL) because the tips of the caudal fin are rarely well preserved and therefore SL is a more reliable measurement of body size. Standard length appears to be on average 17.5% less than TL, which would result in lengths of about 25–110 mm SL for the specimens measured by Bean (2006). Of the 10 specimens with otoliths in situ, nine are from fishes of 27.0–57.7 mm SL, i.e., toward the lower end of the range measured by Bean (2006), and one is distinctly smaller (15 mm SL). This one is also noticeable for its weak ossification, possibly indicative of a postlarval fish. Thus, otoliths from 1.0 to 1.5 mm in length likely represent juveniles and those up to about 2.5 mm represent still-immature fish. According to the correlation of OL with SL and the deduced linear trend from the fishes with otoliths in situ, the largest isolated otolith with a length of 6.1 mm would stem from a fish of about 100–110 mm SL, i.e., corresponding to the largest fish specimens measured by Bean (2006). However, only a single otolith of this size was found, and none 3.9–6.1 mm long. The cause of this size gap in otoliths is not known and does not match the skeletal record reported by Bean (2006).

We consider otoliths of *C. talbragarensis* to be morphologically diagnostic from about a length of 1.5 mm OL. This corresponds favorably with the sizes of most isolated otolith-based Jurassic teleost species with a leptolepid pattern, which are generally 1.5–3.5 mm long (Schwarzhans, 2018). Larger specimens occasionally found in Middle–Upper Jurassic strata belong to more advanced patterns than the leptolepid pattern and probably to larger fishes. However, there is also an abundance of very small otoliths, mostly <1.5 mm OL and often <1.0 mm, that have been described from paralic environments of the Jurassic/Cretaceous transition in northern Germany. A plethora of poorly defined otolith-based species has been described from these rocks (Martin and Weiler, 1954, 1957), which in recent literature have been regarded as problematic and were recommended not to be used (Nolf, 1985, 2013; Schwarzhans, 2018). The apparent morphological plasticity of these small otoliths was hypothesized to stem from juvenile fishes and was considered not to be diagnostically mature for identification (Nolf, 1985; Schwarzhans, 2018). Observations made from in situ otoliths of *C. talbragarensis* and *L. normandica* (Delsate, 1997) suggest that these otoliths stem from fishes of 10–25 mm SL and thus indeed most likely from juveniles or immature fishes.

By far, the most isolated otoliths were found in coprolites of unknown predator(s). The Talbragar Fish Bed contains different types of coprolites (Beattie and Avery, 2012), but probably only one type contains obvious fish remains and otoliths (Fig. 3A–C). Otoliths of *C. talbragarensis* occur regularly in these coprolites. In many instances, they contain one or two otoliths, but coprolites containing up to 12 otoliths have been found as well (AM F.143651). Sagittae are more often found than lapilli, but this may be due to their easier identification even as imprints. The sizes of sagittal otoliths of *C. talbragarensis* range from 1.0 to 3.5 mm long, but the dominant length is 1.5 mm, and with decreasing abundance, to 2.0–2.5 mm (Fig. 6). Thus, the range of otolith sizes in coprolites correlates well with those retrieved in situ. These otolith sizes correspond to a standard length of the fishes in the range of 25–60 mm (for calculation see above) and are consistent with the size distribution graph in Bean (2006).

The identity of the predator(s) feasting on small *C. talbragarensis* specimens is as yet unknown, but Bean (2017) suggested *Coccolepis* Agassiz, 1843, a chondrostean known from the Talbragar Fish Bed. Nevertheless, given that the numerous fish fossils in the Talbragar Fish Bed are considered to have resulted from a mass mortality event, probably caused by volcanic activity, it appears reasonable to assume that the predator producing these coprolites may not have been an aquatic animal and was perhaps benefiting from drifting dead fish in the freshwater lake after a mass mortality event. Interestingly, the coprolites also contain four of the seven recognized non-*Cavenderichthys* otoliths, which indicates that the predator probably fed indiscriminately on different fish species of a certain size. The relationship of the abundance of *Cavenderichthys* otoliths to other types probably represents the relative abundance of the respective fish species.

The number of isolated otoliths found unassociated with coprolites is smaller than the number found in coprolites (82 vs. 159), but it is possible that a substantial number of those seemingly unassociated otoliths stem from disintegrated coprolites or coprolites that are no longer recognizable because of poor preservation. It is also noticeable that the unassociated *Cavenderichthys* otoliths have a slightly larger maximum size than otoliths found in coprolites, i.e., 2 vs. 1.5 mm (Fig. 7). Also, otoliths more than 3.5 mm long were only found unassociated with coprolites, including the single largest otolith of 6.1 mm length. This suggests that the lack of large *Cavenderichthys* otoliths could be the result of a predator's preference for smaller fish.

The Talbragar Fish Bed has also yielded three otolith morphotypes different from that of *Cavenderichthys*. These rare otoliths resemble those of the extant ginglymodian *Lepisosteus osseus* (Linnaeus, 1758) (Fig. 5A–D) but also the strange triangular otoliths of unknown non-teleostean relationships described from Lower and Middle Jurassic deposits of Europe as *Archaeotolithus* Stolley, 1912 (Schwarzhans, 2018). It is likely that these otoliths originated from fishes of which articulated skeletons are already known from the Talbragar Fish Bed, but specimens with otoliths in situ have not yet been discovered, i.e., *Coccolepis australis* Woodward, 1891 (a chondrostean), *Uarbryichthys latus* Wade, 1941 (a macrosemiiform) (Bean, 2017), or *Archaeomaene tenuis* Woodward 1895, *Madariscus robustus* (Woodward, 1895), *Aphnelepis australis* Woodward, 1895, and *Aetheolepis mirabilis* (Woodward, 1895), originally placed in semionotids (Semionotiformes) by Woodward (1895) but later considered to be pholidophoriforms (Wade, 1941; Patterson, 1993; Arratia, 2013).

Coccolepis australis is relatively common in the Talbragar Fish Bed (Cavin, 2017). In a reinvestigation of the type species of *Coccolepis*, *C. bucklandi* Agassiz, 1843, Hilton et al. (2004) did not mention anything that could point to otoliths, but the photographs of the specimen MCZ 5293F (Hilton et al., 2004:figs. 3A, 4) indicate a suspicious 'blank spot' at the location where an otolith might be expected. Nielsen (1949) and Coates (1998) published figures of sagittal otoliths in situ from Paleozoic palaeonisciforms. These otoliths do not show any discernible sulcus, whereas extant chondrosteans (Nolf, 2013; Schwarzhans, 2018) show a poorly defined sulcus unlike any teleosteans. It is therefore unlikely that any otoliths found so far in the Talbragar Fish Bed represent *Coccolepis*. The Macrosemiiformes and Semionotiformes represent extinct sister taxa of the Lepisosteiformes within Ginglymodi. An allocation of our otolith morphotypes to such taxa would be consistent with their apparent similarity with extant otoliths of *Lepisosteus*. However, there is only a single, very rare macrosemiiform known from the Talbragar Fish Bed. The Archaeomenidae, originally regarded as semionotids by Woodward, are currently considered to represent pholidophoriforms of an exclusive freshwater family. Thus, the most plausible assumption appears to be that the three other otolith types from the Talbragar Fish Bed stem from archaeomenids.

In a recent study of the origin of teleost otolith diversity, Schwarzhans et al. (2017c:6) concluded that "teleost (sagitta) otoliths are readily recognized by the presence of a structured and diversified sulcus in an axial position on the inner face of the otolith, corresponding to a diversified macula sacculi, which attaches to the sulcus." This highly diagnostic otolith type was first identified in the late Sinemurian (Early Jurassic) (Schwarzhans, 2018) and coincides with the first occurrence of leptolepid skeletons in the fossil record. The Pholidophoriformes, which are considered to represent the most primitive teleosts (Patterson, 1975; Arratia, 1999, 2013), are known since the Middle Triassic (Ladinian) (Tintori et al., 2015), predating

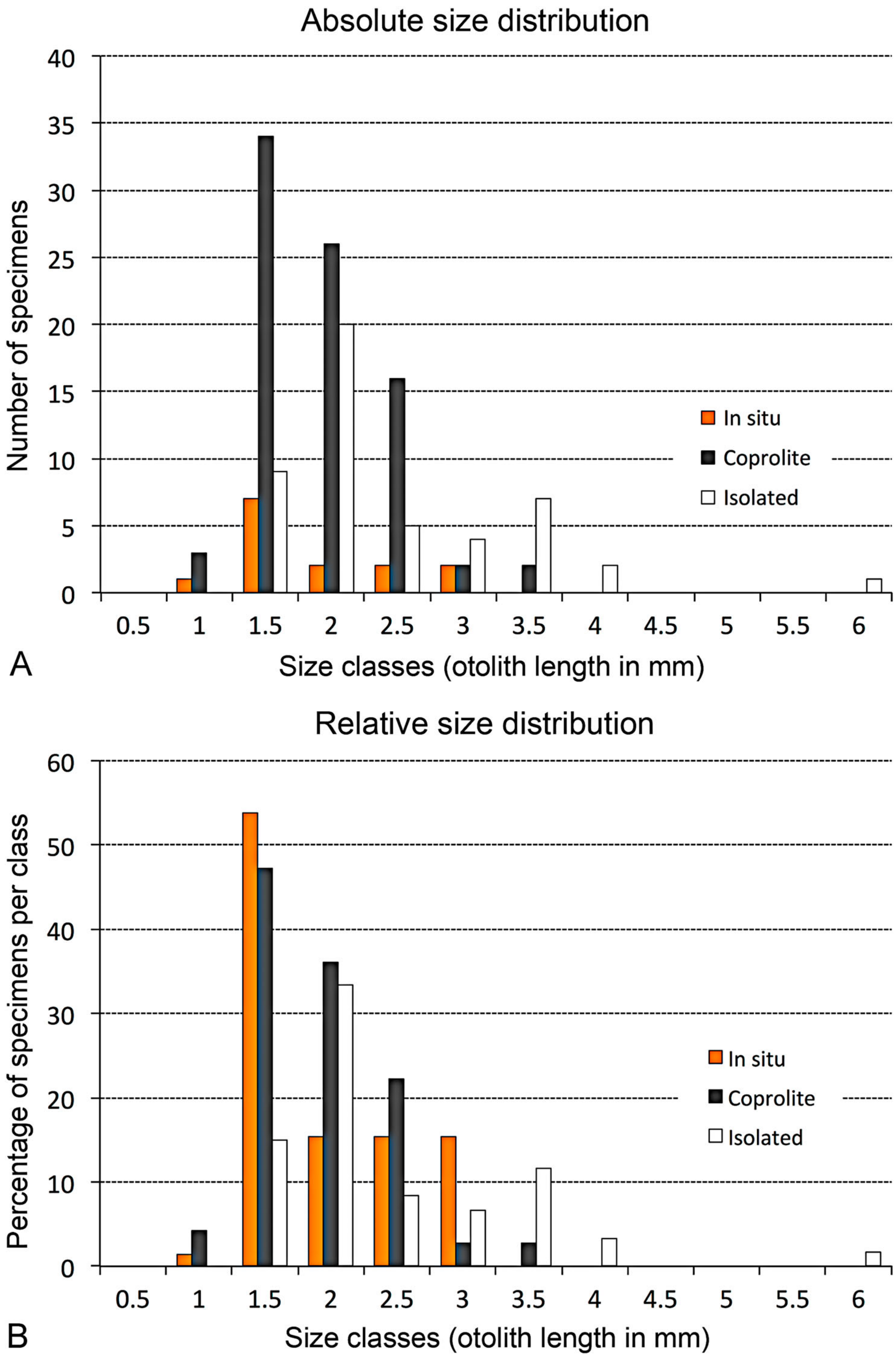

FIGURE 6. Otolith sizes (*Cavenderichthys* sagittae) found within fish skeletons (in situ, orange columns), coprolites (charcoal columns), and isolated (white columns). **A**, absolute number of otolith specimens per size class; **B**, frequency (%) of otoliths per size class.

the Leptolepidiformes by ca. 40 Ma. As per current status, no pholidophoriform skeleton with otoliths in situ has been described, nor are any 'teleostean otoliths' known from comparable time intervals when pholidophoriforms already existed but leptolepidiforms did not. Arratia (2001) listed five characters occurring at the level of *Leptolepis coryphaenoides* that represent an important landmark in the evolution of the Teleostei. Should the otoliths described here be confirmed as pholidophoriform representatives, it would add another novel and highly diagnostic character separating Leptolepidiformes and derived Teleostei from Pholidophoriformes.

Diagenetic Alterations

Elemental analyses show clear distinctions between samples with hydroxyapatite vs. calcium carbonate precursors, with the

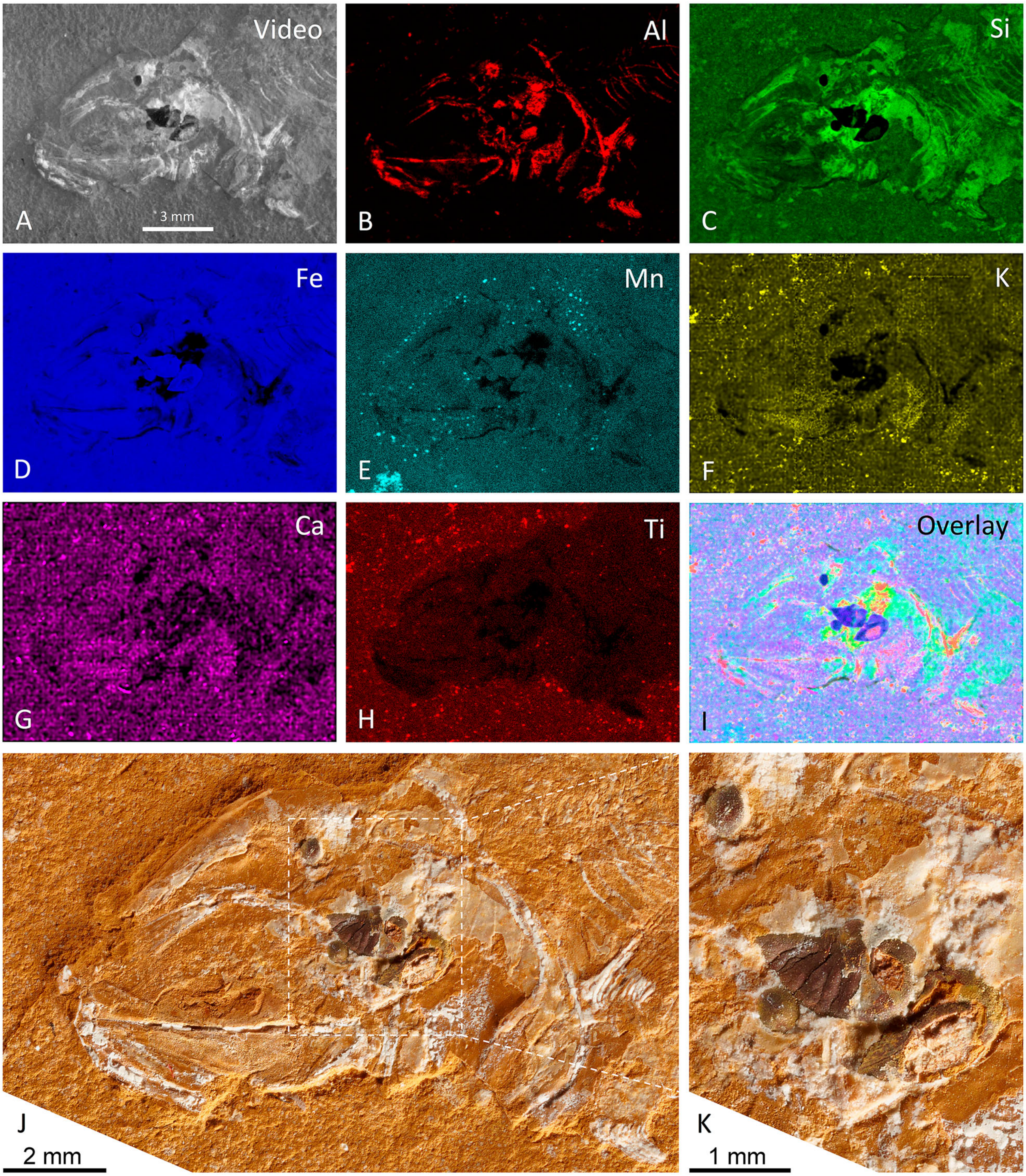

FIGURE 7. Elemental maps of a *Cavenderichthys* head with otolith in situ (AM F.143639). **A**, video image of the measured area; **B**–**H**, elemental maps for aluminum (Al), silicon (Si), iron (Fe), manganese (Mn), potassium (K), calcium (Ca), and titanium (Ti), respectively; **I**, video image overlain with elemental maps for Al, Si, Fe, Mn, K, Ca, and Ti; **J**, **K**, conventional photographs.

former richer in most elements, except in phosphorus (Table S2). Phosphorus could be expected to be found in greater concentrations in fish bones, but during diagenesis the element has been substituted for other elements, including aluminum, allowing kaolinite to form (Frese et al., 2017). In general, fossilized bone (originally made of hydroxyapatite) shows a greater elemental similarity to the surrounding rock matrix than fossilized otoliths or shells from snails and bivalves (all originally made of calcium carbonate). Therefore, elemental maps or images generated by overlaying conventional photographs with elemental maps (Figs. 1, 7; Fig. S2) are useful for the photographic documentation of otoliths, especially in cases where the otolith surface has been damaged (AM F.143639) or in which a thin layer of silicified bone obscures the view in standard photographic images (AM F.14341). The present resolution of XRF elemental maps, however, is generally too low for a detailed description on a stand-alone basis. Nevertheless, XRF elemental mapping is useful for morphometric measurements and for correlation with isolated otoliths.

CONCLUSIONS AND OUTLOOK

Cavenderichthys talbragarensis is only the second Jurassic teleost species known with otoliths in situ, the other being *Leptolepis normandica* (see Delsate, 1997; Nolf, 2013), and the third stem teleost with otoliths in situ (including the Early Cretaceous *Apsopelix anglicus* in Schwarzhans et al., 2018). It confirms the low degree of morphological diversification of stem teleost otoliths as suggested by Schwarzhans (2018). The abundance of otoliths from *Cavenderichthys* for the first time allows the mapping of ontogenetic effects and of intraspecific variability in stem teleost fishes and the calibration of otolith vs. fish sizes, which are all important for the calibration of interpretation of Jurassic and Early Cretaceous isolated otoliths.

Three different albeit interrelated otolith types found among isolated otoliths do not represent the 'teleost otolith morphology' as described by Schwarzhans et al. (2017c). Their most plausible association appears to be with Archaeomenidae, which are known from four different species and genera in the Talbragar Fish Bed. If confirmed, this teleost otolith pattern would provide a further highly diagnostic and synapomorphic character to define teleosts at the level of the Leptolepidiformes and above.

We expect that other, non-*Cavenderichthys*, fish skeletons found in the Talbragar Fish Bed will also contain otoliths in situ and that their discovery can be aided by visualization techniques such as XRF, X-ray imaging, and CT scanning, or by careful preparation of promising fish specimen. The specific diagenetic mineral replacement in otoliths that is characterized by goethite incrustation has not only positively affected their preservation but also can aid their physical recovery and enable their recognition by noninvasive techniques. We hope that the results presented in this study will encourage and inspire colleagues to search for otoliths in situ in other fishes from the Talbragar Fish Bed and from other lagerstätten with a similar preservation history.

ACKNOWLEDGMENTS

We thank N. McGrath (landholder) and M. Sharp (Head Ranger, National Parks and Wildlife Services, Mudgee, New South Wales) for access to the site; R. Beattie for organizing field work; R. Pogson, M. McCurry (both Australian Museum, Sydney, New South Wales), and Y.-Y. Zhen (Geological Survey of New South Wales, Londonderry, New South Wales) for providing access to specimens in their care and help with the registration and export of newly discovered specimens (M. McCurry also discovered an interesting in situ otolith); S. McClusky (Australian National University, Canberra, Australian Capital Territory) for aerial maps of the site; J. Long (Flinders University, Adelaide, South Australia) for helpful comments and encouragement; R. Oberprieler (Commonwealth Scientific and Industrial Research Organisation, Canberra, Australian Capital Territory) for helpful discussions and a critical reading of the manuscript; and K. Mills (University of Canberra, Canberra, Australian Capital Territory) for finding many of the otoliths that are featured in this publication. We thank A. Tintori (University of Milan, Milan, Italy) and an anonymous reviewer for their constructive criticism on an earlier version of the manuscript.

ORCID

Werner W. Schwarzhans http://orcid.org/0000-0003-4842-7989
Timothy D. Murphy http://orcid.org/0000-0002-4539-3667
Michael Frese http://orcid.org/0000-0002-1059-2375

LITERATURE CITED

Agassiz, L. 1833–1844. Recherches sur les Poissons fossiles, 5 vols. Petitpierre, Neuchâtel, 248 pp.

Arratia, G. 1997. Basal teleosts and teleostean phylogeny. Palaeo Ichthyologica 7:1–168.

Arratia, G. 1999. The monophyly of Teleostei and stem-group teleosts. Consensus and disagreements; pp. 265–334 in G. Arratia and H.-P. Schultze (eds.), Mesozoic Fishes 2: Systematics and Fossil Record. Verlag Dr Friedrich Pfeil, Munich, Germany.

Arratia, G. 2001. The sister-group of Teleostei: consensus and disagreements. Journal of Vertebrate Paleontology 21:767–773.

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

Bannikov, A. F., and A. N. Kotlyar. 2015. A new genus and species of early Sarmatian porgies (Perciformes, Sparidae) from the Krasnodar region. Paleontological Journal 49:627–635.

Baykina, E. M., and W. Schwarzhans. 2017a. Description of *Karaganops* n. gen. *perrata* (Daniltshenko, 1970) with otoliths in situ, an endemic Karaganian (Middle Miocene) hering (Clupeidae) in the Eastern Paratethys. Swiss Journal of Palaeontology 136:129–140.

Baykina, E. M., and W. Schwarzhans. 2017b. Review of "*Clupea humilis*" from the Sarmatian of Moldova and description of *Moldavichthys switshenskae* gen. et sp. nov. Swiss Journal of Palaeontology 136:141–150.

Bean, L. B. 2006. The leptolepid fish *Cavenderichthys talbragarensis* (Woodward, 1895) from the Talbragar Fish Bed (Late Jurassic) near Gulgong, New South Wales. Records of the Western Australian Museum 23:43–76.

Bean, L. B. 2017. Reappraisal of Mesozoic fishes and associated invertebrates and flora from Talbragar and Koonwarra, eastern Australia. The Royal Society of Victoria 129:7–20.

Beattie, R. G., and S. Avery. 2012. Palaeoecology and palaeoenvironment of the Jurassic Talbragar Fossil Fish Bed, Gulgong, New South Wales, Australia. Alcheringa 36:453–468.

Bocchino, A. 1967. *Luisiella inexcutata* gen. et sp. nov. (Pisces, Clupeiformes, Dussumieridae) del Jurásico superior de la Provincia de Chubut, Argentina. Ameghiniana 4:91–100.

Bronn, H. 1830. Über zwei fossile Fischarten: *Cyprinus coryphaenoides* und *Tetragonolepis semicinctus* aus dem Gryphitenkalke bei Donaueschingen. Jahrbuch für Mineralogie, Geognosie und Petrefaktenkunde l:13–40.

Cavin, L. 2017. Freshwater Fishes: 250 Million Years of Evolutionary History. Elsevier, Dordrecht, The Netherlands, 200 pp.

Coates, M. I. 1998. Actinopterygians from the Namurian of Bearsden, Scotland, with comments on early actinopterygian neurocrania; pp. 27–59 in D. B. Norman, A. R. Milner, and A. C. Milner (eds.), A Study of Fossil Vertebrates. Linnean Society of London, London.

Delsate, D. 1997. Actinoptérygiens du Toarcien inférieur du Grande Duchée de Luxembourg: présence de *Leptolepis normandica* Nybelin 1962 (Teleostéens) avec otolithes *in situ*. Travaux scientifiques du Musée national d'Histoire naturelle de Luxembourg 27:105–129.

Elder, R. L. 1985. Principles of aquatic taphonomy with examples from the fossil record. Ph.D. dissertation, University of Michigan, Ann Arbor, Michigan, 336 pp.

Frese, M., G. Gloy, R. G. Oberprieler, and D. B. Gore. 2017. Imaging of Jurassic fossils from the Talbragar Fish Bed using fluorescence, photoluminescence, and elemental and mineralogical mapping. PLoS ONE 12:e0179029.

Hilton, E. J., L. Grande, and W. E. Bemis. 2004. Morphology of †*Coccolepis bucklandi* Agassiz, 1843 (Actinopterygii, †Coccolepidae) from the Solnhofen lithographic limestone deposits (Upper Jurassic, Germany); pp. 209–238 in G. Arratia and A. Tintori (eds.), Mesozoic Fishes 3: Systematics, Paleoenvironments and Biodiversity. Verlag Dr Friedrich Pfeil, Munich, Germany.

Koken, E. 1884. Über Fisch-Otolithen, insbesondere über diejenigen der norddeutschen Oligocän-Ablagerungen. Zeitschrift der Deutschen Geologischen Gesellschaft 36:500–565.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordinus, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Impensis Direct. Laurentii Salvii, Stockholm, 824 pp.

Martin, G. P. R., and W. Weiler. 1954. Fisch-Otolithen aus dem deutschen Mesozoikum (Dogger bis Wealden). Senckenbergeana lethaea 35:131–192.

Martin, G. P. R., and W. Weiler. 1957. Das Aldorfer Otolithen-„Pflaster“ und seine Fauna (Mittlerer Münder Mergel, Malm). Senckenbergeana lethaea 38:211–250.

Müller, J. 1846. Über den Bau und die Grenzen der Ganoiden und über das natürliche System der Fische. Archiv für Naturgeschichte 11:91–141.

Nel, A., M. Frese, G. McLean, and R. Beattie. 2017. A forewing of the Jurassic dragonfly *Austroprotolindenia jurassica* Beattie & Nel (Odonata: Anisoptera) from the Talbragar Fish Bed, New South Wales, Australia. Alcheringa 41:532–535.

Nicholson, H. A., and R. Lydekker. 1889. A Manual of Palaeontology for the Use of Students, with a General Introduction on the Principles of Palaeontology, third edition. William Blackwood and Sons, Edinburgh, 735 pp.

Nielsen, E. 1949. Studies on Triassic fishes II. Meddelelser om Grønland 146:1–309.

Nolf, D. 1985. Otolithi piscium; in H.-P. Schultze (ed.), Handbook of Paleoichthyology, Volume 10, Gustav Fischer Verlag, Stuttgart, Germany, 145 pp.

Nolf, D. 2013. The Diversity of Fish Otoliths, Past and Present. Royal Belgian Institute of Natural Sciences, Brussels, Belgium, 222 pp.

Nybelin, O. 1962. Preliminary note on two species previously named *Leptolepis bronni* Agassiz. Arkiv för Zoologi 15:303–306.

Oberprieler, R. G., L. G. Ashman, M. Frese, and A. Slipinski. 2016. The first elateroid beetles (Coleoptera: Polyphaga: Elateroidea) from the Upper Jurassic of Australia. Zootaxa 4147:177–191.

Patterson, C. 1975. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. Philosophical Transactions of the Royal Society, London 289:275–579.

Patterson, C. 1993. Osteichthyes: Teleostei; pp. 621–663 in M. J. Benton (ed.), The Fossil Record 2. Chapman and Hall, London.

Přikryl, T., W. Schwarzhans, and O. Kovalchuk. 2017. Lanternfishes (Myctophidae) with otoliths in situ from the Early Oligocene of the Eastern Paratethys (western Ukraine). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 285:213–225.

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

Schwarzhans, W. 2007. Otoliths from casts from the Eocene Lillebælt Clay Formation of Trelda Næs near Fredericia (Denmark), with remarks on the diet of stomatopods. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 246:69–81.

Schwarzhans, W. 2018. A review of Jurassic and Early Cretaceous otoliths and the development of early morphological diversity in otoliths. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 287:75–121.

Schwarzhans, W., and G. Carnevale. 2017. Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Preface: a first attempt to fill the gap between the otolith and skeletal records of teleost fishes. Swiss Journal of Palaeontology 136:1–6.

Schwarzhans, W., H. Beckett, J. Schein, and M. Friedman. 2018. Computed tomography as a tool for linking the skeleton- and the otolith-based fossil records of teleost fishes. Palaeontology. doi: 10.1111/pala.12349.

Schwarzhans, W., G. Carnevale, S. Japundžić, and K. Bradić. 2017a. Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part IV: Scorpaenidae, Labridae and Gobiesocidae. Swiss Journal of Palaeontology 136:93–108.

Schwarzhans, W., G. Carnevale, S. Japundžić, and K. Bradić. 2017b. Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part V: Bothidae and Soleidae. Swiss Journal of Palaeontology 136:109–128.

Schwarzhans, W., T. Schulz-Mirbach, A. Lombarte, and V. M. Tuset. 2017c. The origination and rise of teleost otolith diversity during the Mesozoic. Research & Knowledge 3:5–8.

Schwarzhans, W., G. Carnevale, A. F. Bannikov, S. Japundžić, and K. Bradić. 2017d. Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part I: *Atherina suchovi* Switchenska, 1973. Swiss Journal of Palaeontology 136:7–18.

Schwarzhans, W., G. Carnevale, A. Bratishko, S. Japundžić, and K. Bradić. 2017e. Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part II: Gadidae and Lotidae. Swiss Journal of Palaeontology 136:19–44.

Schwarzhans, W., H. Ahnelt, G. Carnevale, S. Japundžić, K. Bradić, and A. Bratishko. 2017f. Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part III: tales from the cradle of the Ponto-Caspian gobies. Swiss Journal of Palaeontology 136:45–92.

Sferco, E., A. López-Arbarello, and A. M. Báez. 2015. Phylogenetic relationships of †*Luisiella feruglioi* (Bordas) and the recognition of a new clade of freshwater teleosts from the Jurassic of Gondwana. BMC Evolutionary Biology 15:268. doi: 10.1186/s12862-015-0551-6.

Smith, G. R., and R. L. Elder. 1985. Environmental interpretation of burial and preservation of Clarkia fishes; pp. 85–93 in Late Cenozoic History of the Pacific Northwest. American Association for the Advancement of Science, San Francisco, California.

Tintori, A., S. Zuoyu, N. Peipang, C. Lombardo, J. Dayong and R. Motani. 2015. Oldest stem teleostei from the late Ladinian (Middle Triassic) of Southern China. Rivista Italiana di Paleontologia e Stratigrafia 121:285–296.

Turner, S., and S. Avery. 2017. A Jurassic non-marine chondrichthyan in Australia and its palaeogeographic significance. Paleoworld 26:268–293.

Wade, R. T. 1941. The Jurassic fishes of New South Wales. Journal and Proceedings of the Royal Society of New South Wales 75:71–84.

Wade, R. T. 1953. The Jurassic fishes of New South Wales (Macrosemiidae) with a note on the Triassic genus *Promecosomina*. Journal and Proceedings of the Royal Society of New South Wales 87:63–72.

Weiler, W. 1942. Die Otolithen des rheinischen und nordwestdeutschen Tertiärs. Abhandlungen des Reichsamt für Bodenforschung, Berlin, Neue Folge 206:1–140.

White, M. E. 1981. Revision of the Talbragar fish bed flora (Jurassic) of New South Wales. Records of the Australian Museum 33:695–721.

Woodward, A. 1891. Catalogue of the fossil fishes in the British Museum (Natural History); Part II containing Elasmobranchii (Acanthodii), Holocephali, Ichthyodorulites, Ostracodermi, Dipnoi, and Teleostomi (Crossopterygii and Chondrostean Actinopterygii). British Museum (Natural History), London, 567 pp.

Woodward, A. 1895. The fossil fishes of the Talbragar Beds (Jurassic?). Memoirs of the Geological Society of New South Wales, Palaeontology 9:1–21.

Submitted April 28, 2018; revisions received September 8, 2018;
accepted September 10, 2018.
Handling editor: Martin Brazeau.