Zitteliana 96, 2022, 51–67 | DOI 10.3897/zitteliana.96.81737

SNSB Bayerische Staatssammlung für Paläontologie und Geologie

ZITTELIANA
An International Journal of Paleontology and Geobiology

# Early teleost otolith morphogenesis observed in the Jurassic of Franconia, Bavaria, southern Germany

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*http://zoobank.org/CD8C70BA-0253-4540-8EFC-D430A12F6B35*

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Academic editor: Oliver Rauhut ♦ **Received** 6 February 2022 ♦ **Accepted** 28 March 2022 ♦ **Published** 12 April 2022

## Abstract

The otoliths described in this study are from the late Pliensbachian of the Buttenheim clay pit near Bamberg, Franconia, northern Bavaria, and represent one of the earliest teleost otolith assemblages known so far. A total of 351 otoliths have been recovered, many of which are well-preserved and of sizes that indicate they originated from adult specimens and can be considered morphologically mature. The assemblage contains seven species, four of them stem teleosts of the genus *Leptolepis* and three from the enigmatic otolith-based genus *Archaeotolithus*, which cannot be attributed to a firm systematic position. We describe three species as new: *Leptolepis buttenheimensis* **sp. nov.**, *Leptolepis steberae* **sp. nov.** and *Archaeotolithus doppelsteini* **sp. nov.** In addition, we review 49 otoliths from the original material of Schröder's (1956) publication that were uncovered at the University of Erlangen. This material stems from the late Toarcian/early Aalenian and early Callovian of Franconia. In this review, we accept only a few of the species described by Schröder as valid. The otolith associations from the Early and Middle Jurassic of Franconia, in combination with previously published material, allow for an assessment of the morphogenesis of early teleost otoliths. Early Jurassic teleost otoliths are represented by a few common and long-ranging species. A sudden burst in otolith diversity seems to have occurred during the Middle Jurassic and is first evident in the Bathonian.

## Keywords

Early Jurassic, Middle Jurassic, Leptolepididae, *Leptolepis*, *Archaeotolithus*, review

## 1. Introduction

Jurassic otoliths have rarely been studied. Frost (1924, 1926) and Stinton (in Stinton and Torrens 1968) described otoliths from southern England, Weiler (Neth and Weiler 1953; Martin and Weiler 1954 and 1965) described them from wells drilled in northern Germany, Hesse (2014) described them from a clay pit in northern Germany, and Schröder (1956) described them from Jurassic outcrops in Franconia. Delsate (1997) later described otoliths found *in situ* from *Leptolepis normandica*, which allowed for the first-time allocation of a large proportion of these Jurassic otoliths in a systematic context. A further case of an otolith *in situ* was documented by Hesse (2014). Malling and Grønwall (1909) described a peculiar group of otoliths of unknown relationships from the early Jurassic of Bornholm, and Stolley (1912) described them from the middle Jurassic of Bad Harzburg, northern Germany. Stolley later established the otolith-based genus (which he called "typus") *Archaeotolithus* for this group.

The taxonomic identification of Jurassic otoliths meets certain problems besides a lack of comparability with otoliths of crown teleosts. One of the principal problems is their low level of morphological diversity. Other problems

concern uncertainties in the level of inter- and intraspecific variations expected in the otoliths of these early bony fishes. Weiler (1954) noted that the interspecific diversity might have been rather low in such "primitive" otolith morphologies and established a plethora of otolith-based species based on vague, minute morphological differences. Schwarzhans et al. (2019) recent study of many otoliths, both *in situ* and in isolated otolith specimens from the late Jurassic *Cavenderichthys talbragarensis*, has indeed confirmed a low level of morphological diversity when compared with otoliths of the early Jurassic *Leptolepis normandica*; however, indications have also shown a "normal" level of intraspecific variability. In conclusion, these observations do not support the excessive number of species described by Weiler. In fact, Nolf (1985: p. 111) considers Weiler's works on Mesozoic otoliths as "constituting the most problematic part of the whole otolith literature." Revisions of Jurassic and early Cretaceous otoliths embedded in the handbooks of Nolf (1985 and 2013), and more specifically by Schwarzhans (2018), have recognized only a small fraction of Weiler's otolith-based taxa as valid but considered most of them synonymies of other taxa or of doubtful nature. Two studies of Jurassic otoliths—Neth and Weiler (1953) and Schröder (1956)—remain unreviewed because the type-material was not recovered.

Here we describe a large collection from the Early and Middle Jurassic of Franconia composed from two sources. The first is a collection of 351 otoliths of the latest Pliensbachian from the Buttenheim clay pit. The other contains 86 otoliths from the type-material of Schröder (1956) that stem from the late Toarcian/early Aalenian and from the early Callovian, both of which were located in the Geological Institute of the University of Erlangen. Schröder mentioned that he had 147 otoliths for study. Among the 86 recovered otoliths, 49 come from teleosts, and 37 are putative coleoid statoliths. The latter are not reviewed here. The collection of teleost otoliths contains 16 of the 18 nominal species described by Schröder, including 14 holotypes. The purpose of our study is to describe the early teleost otoliths stemming from probably the largest collection of early to middle Jurassic otoliths, thereby revising Schröder's work, which has rarely been cited because of the difficulties of interpreting his documentation and descriptions (see Nolf 2013 and Schwarzhans 2018).

# 2. Materials and methods

## 2.1. Localities and stratigraphic positions of the studied otoliths

The otoliths described in this study were collected in Upper Franconia, northern Bavaria, Germany, in a clay pit near Buttenheim, southeast of Bamberg. Specimens described by Schröder (1956) were collected from five locations near Bamberg and Nürnberg (Fig. 1). The otoliths from Buttenheim come from the clay pit of the Liapor Company at Altendorf, south of Buttenheim. Exposed in this clay pit are the Lower Jurassic Amaltheenton Formation (upper Pliensbachian) and the Posidonia Shale (lower and middle Toarcian). All studied otoliths were obtained from the upper Pliensbachian Amaltheenton Formation, which consists of about 35 m thick homogenous grey claystone with intercalations of calcareous concretions.


**Figure 1.** Location plate, Bavaria, southern Germany. The red star indicates the Buttenheim clay pit from which late Pliensbachian otoliths have been obtained. The yellow stars refer to locations sampled by Schröder (1956).

The section is divided by four thin beds representing short phases of reworking by high water energy resulting from low-stand sea levels that caused winnowing of small grain sizes and enrichment of the reworked concretions (see Keupp and Schobert 2015; Keupp et al. 2016a, 2016b) (Fig. 2). The stratigraphic boundary between the top of the *Margaritatus* ammonite zone (*Gibbosus* subzone) and the basal *Spinatum* ammonite zone (*Apyrenum* subzone) is marked by the "pyrite-bed" that contains large ammonites of *Amaltheus margaritatus* up to 60 cm in size as well as the first *Amaltheus salebrosus* and *Pleuroceras solare*. This horizon is further characterized by an enrichment of small calcareous nodules of 1–4 cm in diameter that exhibit bioerosive scratch marks on the surface. The second reworking horizon, the "Quellhorizont" (spring horizon), marks the stratigraphic boundary between the *Apyrenum* subzone and the *Hawskerense* subzone, and bears the first *Pleuroceras spinatum*. The third reworking horizon, the so-called echinid-pectinid-bed (EPH), is characterized by a pebbly coquina and large reworked calcareous nodules that are extensively settled by a diverse association of hardground settlers (fungi, sessile foraminifers, serpulids, brachiopods, bryozoans, phoronids, cirripeds, rhabdopleurids, etc.; Keupp 2021a, c). The top of the Amaltheenton facies is marked by a fourth distinct reworking horizon, the "Bollernbank," which contains mass occurrences of belemnite rostra and reworked nodules

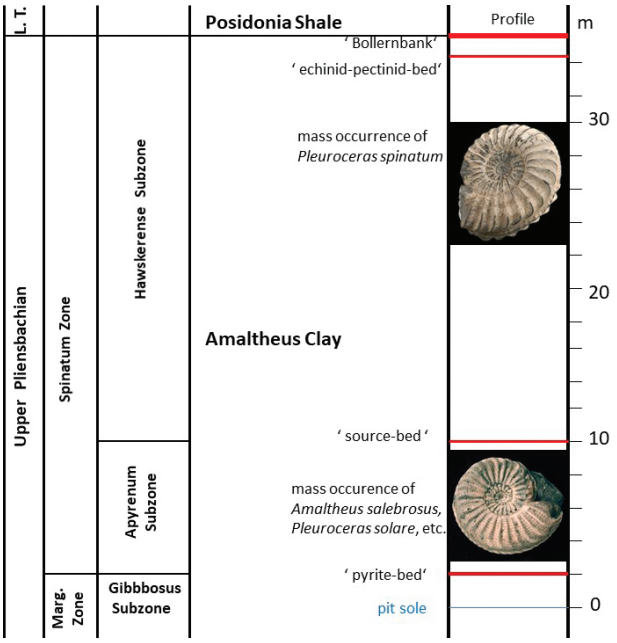


**Figure 2.** Stratigraphic scheme for the Buttenheim clay pit after Keupp (2021a). Otolith bearing sampled intervals are the 'echinid-pectinid-bed' (EPH), the 'source-bed' (Quellhorizont) and the *Apyrenum* subzone.

with endolithic borings of bivalves. Some of the nodules ("Hiatus-Konkretionen" sensu Voigt 1968) continued to aggregate during the onset of the bituminous shale formation of the Toarcian Oceanic Anoxic Event following a sedimentation gap of about 150 ky (Keupp 2021a).

The condensed sections between the first three reworking horizons are fossil rich and comprise mass occurrences of ammonites and other fossils. They represent sea level highstands with reduced sedimentation rates and some faunal immigration from the Tethyan Ocean in the south (see Keupp and Schweigert 2017). The section above the pyrite-bed of about 6 m thickness corresponds with the *Apyrenum* subzone and contains aragonitic shells of a diverse ammonite assemblages with *Amaltheus laevigatus*, *A. margaritatus*, *A. salebrosus*, *Pleuroceras transiens*, *P. solare*, *P. apyrenum*, and *Amauroceras ferrugineum*, which are often preserved with color patterns. Above the "Quellhorizont" the increasing fossil enrichment culminates in a mass occurrence of *Pleuroceras spinatum*. Most of the otoliths were obtained from the highest Pliensbachian level, where the EPH was about 2 m below the "Bollernbank" (333 out of 351 studied specimens); two are from the "Quellhorizont" and 14 were collected in the *Apyrenum* subzone. The otoliths are neomorphed in calcite from their presumed original composition in aragonite. The calcification has resulted in a more stable nature of the otoliths, even those with delicate and thin features, and has made them more resistant to mechanical recovery. Sometimes, healed fractures can be observed. On the downside, however, the calcite neoformation has sometimes resulted in incrustations on the surface of the otolith or creation of surface rugosity that partly obliterates morphological features.

Most of the material described by Schröder (1956) was collected from temporary outcrops in the vicinity of Scheßlitz, northeast of Bamberg. The transitional section of uppermost Toarcian and lowermost Aalenian was temporarily excavated along the riverbank of the small Leithenbach stream to the southeast of the village Kremmeldorf. Two additional localities of a similar stratigraphic position were mentioned without further details: Peulendorf near Scheßlitz (lower Aalenian) and Freiahorn, which is about 8 km north of Pottenstein (upper Toarcian). A landslide along the steep Middle Jurassic sandstone slopes of the Deisterbach valley, southeast of Pünzendorf and about 15 km east of Bamberg temporarily exposed lower Callovian clay containing pyritized ammonite molds (the so called "Goldschnecken") that are iridescent due to a thin limonitic skin. The stratigraphic position of the exposed strata was based on the occurrence of *Macrocephalites* and *Hecticoceras* (Schröder 1956). A single otolith (*Otolithus kolbi*) has been described from the Amaltheenton facies (*Spinatum* zone) from Teufelsgraben near Forth, east of Erlangen, at the banks of the small Schwabach river.

A good proportion of Schröder's type-material was recovered from the collection of the Geological Institute of the University of Erlangen, mostly from Kremmeldorf and Pünzendorf. The type specimens, including holotypes, were recovered from 14 out of 16 species described by Schröder and from otoliths he placed in *Otolithus* cf. *ornatus* Weiler, 1953. Not accounted for are the specimens pertaining to *Otolithus liasicus* and *Otolithus kolbi*. Most of Schröder's otoliths are rather small (< 1.5 to 1 mm in length) and, therefore, pose problems for reliable identification, as we discuss in the descriptive section. Other specimens are incomplete, have encrusted surfaces, or are otherwise damaged; thus, we found that only a relatively small fraction of otolith specimens was preserved well enough to serve as type specimens. The registration numbers on the recovered microslides do not match the numbers assigned in Schröder's publication. However, a comparison of the specimens with his drawings allowed for reliable correlation. In addition, Schröder apparently colored in red the labels of the specimens that are denoted in his work as holotypes. Thus, now only the Jurassic otoliths described by Weiler (1953) and two species described by Schröder (1956) remain unreviewed.

## 2.2. Characterization of early Jurassic otoliths and methodology

The otolith terminology follows Koken (1884), with amendments by Chaine and Duvergier (1934) and Schwarzhans (1978). Three patterns of otolith morphologies have been observed in the early Jurassic: the *Leptolepis*-pattern, the *Xenoleptolepis*-pattern and the *Archaeotolithus*-pattern. Two of these patterns are observed in the Jurassic sediments of Franconia, namely the *Leptolepis*- and *Archaeotolithus*-patterns. The *Xenoleptolepis*-pattern has only been found in the early Jurassic of England. The two

patterns identified in Franconia differ significantly, and each requires specific methods for their characterization.

The *Leptolepis*-pattern is characterized by a straight sulcus with a widened ostium, which is poorly defined against the cauda, and a vague, undifferentiated, and often poorly discernable colliculum. The rostrum is massive and long while the antirostrum is minute. The ostium opens to the anterior-dorsal rim along the entire stretch of the rostrum, but its colliculum is often separated from the predorsal rim of the otolith by a shallow ridge, which Schröder (1956) termed "crista anterior". Morphometric measurements are made for otolith length (OL), otolith height (OH), and otolith thickness (OT). The true length of the rostrum is measured from its tip to the tip of the antirostrum/termination of the upper margin of the ostium and is projected along the axis of the otolith. Due to their poorly defined ostium and cauda, their length cannot be measured, but their maximal height (OsH and CaH respectively) and the total length of the sulcus (SuL) is measurable.

The *Archaeotolithus*-pattern differs considerably and is characterized by a triangular otolith shape and an eccentrically positioned, dorsally shifted sulcus with vague margins and unclear distinction into ostium and cauda. The sulcus is often curved anteriorly and posteriorly in a manner that makes measuring difficult. Furthermore, the sulcus is open anteriorly and posteriorly it reaches very close to the posterior tip of the otolith; therefore, measurements of the length of the sulcus do not contain diagnostic value and are omitted. The length of the ostium and cauda (OsL and CaL) can be measured but is not very accurate, so the absolute values should be regarded with some caution. This leaves only OL, OH and OT as reliable measurements in these otoliths.

All otoliths were studied with a reflected-light microscope. Photographs were taken remotely controlled from a computer with a Canon EOS 1000 mounted on the phototube of a Wild M400 photomacroscope, and were captured at regular field-of-depth levels for each view. The individual photographs of each view were stacked using Helicon Soft's Helicon Focus software. The continuously focused pictures were digitally processed with Adobe Photoshop to enhance contrast, balance exposition, or retouch small inconsistencies, such as sand grains, incrustations, or pigmentation spots, insofar as doing so without altering the otolith morphology was possible.

## 2.3. Depository

Types, other photographed specimens, along with a selection of additional specimens, are deposited in the Staatliche Naturwissenschaftliche Sammlungen Bayerns, Bayrische Staatssammlung für Paläontologie und Geologie in München. Schröder's collection is cataloged under SNSB-BSPG 2022 III 1–62, and the Buttenheim collection is cataloged under SNSB-BSPG 2022 IV 1–18. Other specimens are kept in the private collection of B. Doppelstein, Berlin, B.Steber, Leibersdorf and in the collection of the senior author.

# 3. Results

## 3.1. Systematics

**Remarks.** The description of fossil otolith-based taxa principally represents a parataxonomy with taxa established by articulated skeletons. The risks of parataxonomy actually occurring varies greatly in the fossil record. For instance it is low for many young Cenozoic strata, for regions such as New Zealand where there is an abundance of otolith data but very few articulated skeletons, and for certain systematic groups such as the Ophidiiformes where fossil otolith data significantly prevail over skeletal material. In the case of Jurassic teleosts, however, there is a considerable wealth of skeletal data and relatively limited data of otoliths. The cause for this discrepancy may be the adverse effects of diagenesis over a long period of geological time for aragonitic fossils such as otoliths.

One aspect hampering the identifications of Jurassic otoliths is the fact that only a single case exists in which otoliths of fishes where were found *in situ*, namely in *Leptolepis normandica* (see Delsate 1997). This is the only otolith-based taxa from the early Jurassic that can be related to a skeletal record. Hesse (2014) figured another case of an otolith *in situ* in a fish identified as *Leptolepis* sp. from the lower Toarcian of the clay pit Klein Lehmhagen near Grimmen, western Pomerania. Unfortunately, this specimen is exposed only from the outside, but its outline suggests that it also represents *L. normandica*. The low level of morphological diversity of the early teleost otoliths also does not allow for a comparable level of phylogenetical evaluation such as skeletal material (see, e.g., Arratia 1996, 1997, 2004; López-Arbarello et al. 2008; Guinot and Cavin 2015).

The following section complements the review of Jurassic to early Cretaceous otoliths by Schwarzhans (2018). Species contained in that review are not described in detail and are only characterized by differential diagnoses. Only new species are described in full. Due to the relatively imprecise documentation in the publications of Weiler (1953) and Schröder (1956), we recommend not using names of not revised species. A specific consequence is the (temporary) suppression of *Leptolepis ornatus* (Weiler, 1953) as used in Schwarzhans (2018) and its replacement with *Leptolepis curvisulcatus* (Schröder, 1956) following our current review below.

**Class Osteichthyes Huxley, 1880**
**Subclass Actinopterygii sensu Goodrich, 1930**
**Division Teleostei Müller, 1885**
**Order Leptolepidiformes s.l. Nicholson & Lydekker, 1889**
**Family Leptolepididae s.l. Nicholson & Lydekker, 1889**
**Genus *Leptolepis* Agassiz, 1832**

### *Leptolepis normandica* Nybelin, 1962

Plate 1, figs 1–15

1956 *Otolithus* cf. *ornatus* Weiler, 1953 - Schröder: pl. 6, figs 1–3.
1956 *Otolithus opalini* - Schröder: pl. 6, fig. 9 (non figs 7–8).

1956 *Otolithus cristatus* - Schröder: pl. 6, figs 13–14.
1956 *Otolithus vastus* - Schröder: pl. 7, figs 36–38.
1956 *Otolithus* (*Lycopteridarum*?) *brevis* - Weiler: pl. 3, figs 16–19.
1965 *Otolithus* (*Lycoperidarum*?) *brevirostris* - Weiler: pl. 3, figs 20–23.
?1965 *Otolithus* (*Lycopteridarum*?) *elegans* - Weiler: pl. 3, figs 24, 25, pl. 4, fig. 26.
1965 *Otolithus* (*Lycopteridarum*?) *similis* - Weiler: pl. 2, figs 10–13, pl. 3, figs 14–15.
1997 *Leptolepis normandica* Nybelin, 1962 - Delsate: figs 1–5, pl. 1, fig. 4, pl. 2, figs 5–9 (otoliths *in situ*).
2013 *Leptolepis normandica* Nybelin, 1962 - Nolf: pl. 6.
2014 *Otolithus* (*Lycopteroidarum*?) *similis* Weiler, 1965 - Hesse: fig. 18A–G.
2014 *Otolithus* (*Lycopteroidarum*?) *brevis* Weiler, 1965 - Hesse: fig. 19A–F.
2014 *Otolithus* (*Lycopteroidarum*?) *ornatus* Weiler, 1953 - Hesse: fig. 20A–D.
2014 *Otolithus* (inc. sed.) sp. 1 - Hesse: fig. 21A–C.
?2014 *Otolithus* (inc. sed.) sp. 2 - Hesse: fig. 22A–B.
2014 *Otolithus* (inc.sed.) sp. 3 - Hesse: fig. 23A.
2014 *Otolithus* (inc. sed.) sp. 5 - Hesse: fig. 25A.
?2014 *Leptolepis* sp. - Hesse: fig. 32 (otolith *in situ*).
2018 *Leptolepis normandica* Nybelin, 1962 - Schwarzhans: fig. 1C–H.
2021b *Leptolepis normandica* Nybelin, 1962 – Keupp: fig. 9.3 B.

**Material.** 264 specimens: 251 specimens from the late Pliensbachian of Buttenheim: 8 specimens *Apyrenum* subzone (figured specimen SNSB-BSPG 2022 IV 1, Plate 1, fig. 10), 1 specimen "Quellhorizon" (figured specimen SNSB-BSPG 2022 IV 2, Plate 1, fig. 9), 242 specimens *Hawkerense* subzone (figured specimen SNSB-BSPG 2022 IV 3, Plate 1, figs 1–8, 11); 13 specimens from Schröder's collection from the late Toarcian to early Aalenian: paratype of *Ot. cristatus* from Kremmeldorf (SNSB-BSPG 2022 III 5, Plate 1, fig. 12), 4 specimens designated as *Ot.* cf. *ornatus* with 3 from Kremmeldorf and 1 from Peulendorf (SNSB-BSPG 2022 III 11–13), 3 paratypes of *Ot. opalini* from Kremmeldorf (SNSB-BSPG 2022 III 20–22, Plate 1, fig. 13), holotype of *Ot. vastus* from Peulendorf (SNSB-BSPG 2022 III 30, Plate 1, fig. 15), 4 paratypes of *Ot. vastus* from Kremmelsdorf (SNSB-BSPG 2022 III 31–34, Plate 1, fig. 14).

**Differential diagnosis.** Otoliths of *Leptolepis normandica* are more compressed than other coeval species of *Leptolepis* with an OL:OH ratio of 1.25–1.45 (vs. >.1.5), but less compressed than that of *L. steberae* sp. nov. (1.1–1.25). The rostrum is shorter than that of *L. buttenheimensis* sp. nov. ranging from about 30 to 36% of OL (vs. 37–45%), but longer that those of *L. steberae* sp. nov. (12–25%). The short postdorsal rim is higher than that of *L. curvisulcatus* and *L. kremmeldorfensis* and longer than that of *L. kremmeldorfensis*. The ostium tends to be wider in *L. normandica* than in coeval *Leptolepis* species except of *L. steberae* sp. nov. (OsH:CaH = 1.5–2.2 vs 1.25–1.6).

**Discussion.** *Leptolepis normandica* is the most common otolith-based species so far recognized in the Early Jurassic and the early Middle Jurassic (Pliensbachian to Aalenian). Its distinction from coeval species is not always easy to determine, particularly regarding *L. curvisulcatus*, and transitional forms exist. The type specimens of the synonymized species of Weiler (1965) and Schröder (1956) are mostly small and sometimes not very well-preserved; nevertheless, they bear the pertinent diagnostic characteristics. The specimens of this species exhibit a considerable variability, which may have led Weiler and Schröder to establish many species that can no longer be maintained after review. The variability encompasses primarily the shape of the postdorsal rim, width of the cauda and to a lesser degree its curvature, and ornamentation of the rims. Due to the large degree of variability, we have figured many specimens from Buttenheim in comparison to selected refigured specimens of Schröder. The largest specimen from Buttenheim is 2.85 mm in length; the largest specimen from Schröder's collection is 2.4 mm. Otoliths attributable to *L. normandica* have been found in Pliensbachian to Aalenian strata in Belgium (Nolf 2013), Luxemburg (Delsate 1997), England, and Germany.

### *Leptolepis curvisulcatus* (Schröder, 1956)

Plate 1, figs 15–19

1956 *Otolithus curvisulcatus* - Schröder: pl. 7, figs 25–27.
1956 *Otolithus opalini* - Schröder: pl. 6, figs 7–8 (non fig. 9).
1956 *Otolithus schattenbergi* - Schröder: pl. 6, figs 10–12.
2018 *Leptolepis ornatus* (Weiler, 1953) - Schwarzhans: fig. 1I–J, ?K.

**Material.** 15 specimens from Schröder's collection from the late Toarcian to early Aalenian: holotype of *Ot. curvisulcatus* from Kremmeldorf (SNSB-BSPG 2022 III 42, Plate 1, fig. 16) and 3 paratypes of *Ot. curvisulcatus*, thereof 2 from Kremmeldorf and 1 from Freiahorn (SNSB-BSPG 2022 III 43–45), holotype of *Ot. opalini* from Kremmeldorf (SNSB-BSPG 2022 III 16, Plate 1, fig. 19) and 3 paratypes of *Ot. opalini* from Kremmeldorf (SNSB-BSPG 2022 III 17–19, Plate 1, fig. 15), holotype of *Ot. schattenbergi* from Kremmelsdorf (SNSB-BSPG 2022 III 2, Plate 1, fig. 17), 6 paratypes of *Ot. schattenbergi* with 5 from Kremmelsdorf (SNSB-BSPG 2022 III 3–5, 47–48, Plate 1, fig. 18) and 1 from Peulendorf (SNSB-BSPG 2022 III 46).

**Differential diagnosis.** *Leptolepis curvisulcatus* is slightly more elongate than *L. normandica* with an OL:OH ratio of 1.4–1.6 (vs. 1.25–1.45), which is mainly caused by a relatively low postdorsal rim, which is also more rounded. Other proportions and characteristics are shared with *L. normandica*. *Leptolepis curvisulcatus* also differs from *L. normandica* in its longer ostium as compared to the length of its cauda, but because of the gradual transition from ostium to cauda, this feature cannot be measured unequivocally. The rounded and short postdorsal rim distinguishes *L. curvisulcatus* from the coeval *L. kremmeldorfensis*.

**Discussion.** The distinctions among the three nominal late Toarcian to Aalenian species *L. normandica*,

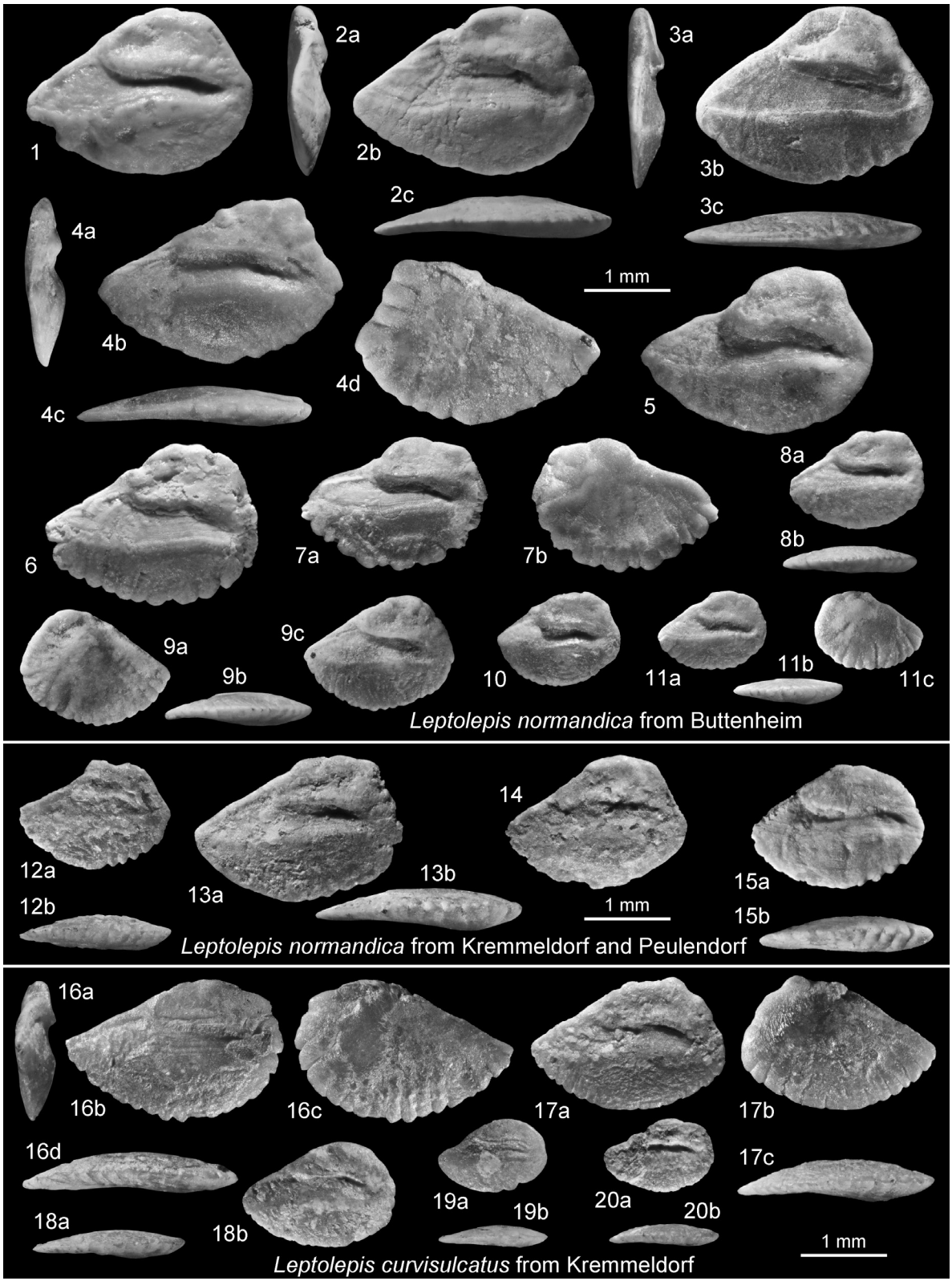


**Plate 1.** Otoliths of *Leptolepis normandica* and *L. curvisulcatus*. **figs 1–15:** *Leptolepis normandica* Nybelin, 1962; **1–11:** From late Pliensbachian of Buttenheim, **1–8, 11:** EPH horizon (SNSB-BSPG 2022 IV 3); **9:** "Quellhorizon" (SNSB-BSPG 2022 IV 2); **10:** *Apyrenum* subzone (SNSB-BSPG 2022 IV 1); **12:** paratype of *Ot. cristatus* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 5); **13:** paratype of *Ot. opalini* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 20); **14:** paratype of *Ot. vastus* Schröder, 1956 from Kremmelsdorf (SNSB-BSPG 2022 III 34); **15:** holotype of *Ot. vastus* from Peulendorf (SNSB-BSPG 2022 III 30). **figs 15–19** *Leptolepis curvisulcatus* (Schröder, 1956); **15:** paratype of *Ot. opalini* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 17); **16:** holotype of *Ot. curvisulcatus* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 42); **17:** holotype of *Ot. schattenbergi* Schröder, 1956 from Kremmelsdorf (SNSB-BSPG 2022 III 2); **18:** paratype of *Ot. schattenbergi* Schröder, 1956 from Kremmelsdorf (SNSB-BSPG 2022 III 47); **19:** holotype of *Ot. opalini* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 16).

*L. curvisulcatus*, and *L. kremmeldorfensis* are all very subtle and it is possible that with more material becoming available from this time interval their nature and validity may have to be revised again. This is also because most specimens so far known from *L. curvisulcatus* and *L. kremmeldorfensis* are smaller than 1.5 mm in length and, therefore, cannot be considered morphologically mature. Schröder (1956) mentioned that the slightly curved shape of the sulcus (cauda) is a distinctive character of the species (hence the name curvisulcatus). However, this character does not seem to be reliable for its distinction from otoliths of *L. normandica*, and we therefore consider it to reflect a degree of variability.

The best-preserved and largest specimen that we attribute to *L. curvisulcatus* is a paratype of Schröder's *Otolithus opalini* of 2.55 mm in length (Plate 1, fig. 16), while the specimen selected as holotype represents a small and poorly preserved otolith of 1.25 mm in length (Plate 1, fig. 19). The holotype of *L. curvisulcatus* is the next best-preserved specimen of 2.25 mm in length, and we have thus chosen this name to represent this nominal species. Schwarzhans (2018) could not review Schröder's specimens and attributed similar specimens from the same stratigraphic interval to *L. ornatus* (Weiler, 1953). Unfortunately, Weiler's type-material has not been located and is not available for revision. His documentation is rather indistinct, so we therefore propose no longer using this name and instead refer to *L. curvisulcatus*.

### *Leptolepis buttenheimensis* sp. nov.

http://zoobank.org/A335ABA4-315F-49F6-B9D7-11CD0F8CED66

Plate 2, figs 1–7

2021b *Leptolepis ornatus* (Weiler, 1953) – Keupp: fig. 9.3 A,C.

**Etymology.** Named after the type-locality Buttenheim near Bamberg, Franconia.

**Holotype.** SNSB-BSPG 2022 IV 4 (Plate 2, fig. 1), Clay pit near Buttenheim, upper Pliensbachian, *Hawkerense* subzone, EPH horizon.

**Paratypes.** 11 specimens: 10 specimens same data as holotype (SNSB-BSPG 2022 IV 5, Plate 2, figs 2–5, 7), 1 specimen same location, *Apyrenum* subzone (SNSB-BSPG 2022 IV 6, Plate 2, fig. 6).

**Additional material.** 48 specimens: same location as holotype, 45 specimens from the EPH horizon, 3 specimens from the *Apyrenum* subzone.

**Diagnosis.** OL:OH = 1.55–1.75; OH:OT = 4.0–5.0. Rostrum length 37–45% of OL. Ventral rim of ostium shallow and fading, and ostium relatively narrow; OsH:CaH = 1.25–1.6.

**Description.** Slender, thin otoliths up to 3.25 mm in length (holotype 2.65 mm). Ventral rim relatively shallow, regularly curved, deepest at or behind middle, and smooth to irregularly undulating. Rostrum very long, nearly half of otolith length. Dorsal rim behind ostial opening short, moderately elevated, broad and irregularly undulating. Posterior rim broadly rounded.

Inner face very slightly bent with distinctly supramedian sulcus. Ostium long, not expanding backward from rostrum and antirostral notch, about as long as cauda but separation poorly defined. Ventral margin of ostium indistinct, gradual, and shallow, resulting in relatively narrow ostium. Cauda very slightly flexed, terminating close to posterior tip of otolith. Dorsal depression very small, restricted to position above anterior part of cauda. No ventral furrow. Outer face flat to slightly concave with particularly thin and delicate rostrum, smooth dorsally and few indistinct furrows ventrally. Shallow umbo positioned near dorsal rim opposite to dorsal field of inner face.

**Discussion.** *Leptolepis buttenheimensis* is readily recognized by its elongated shape, extremely long rostrum, and very thin and delicate structure. However, a few morphologically transitional specimens exist with *L. normandica* in specimens smaller than about 2.2 mm in length, which are not considered to be fully morphologically developed. Another distinctive feature is the shallow and fading lower margin of the ostium as seen in figures 1a, 2, 3a, 4a, 5 and 7a on Plate 2. This development somewhat resembles otoliths of *Leptoelops rhenanus* (see below) where the lower margin of the ostium has become completely flattened and is level with the ventral margin of the cauda.

*Leptolepis buttenheimensis* is known only from the upper Pliensbachian of the type locality where it represents the second most common species.

### *Leptolepis steberae* sp. nov.

http://zoobank.org/35891115-EFFB-42C3-A196-CA22CEF8799D

Plate 2, figs 8–12

**Etymology.** Named after Birgit Steber (Leibersdorf), who has intensely collected from the Buttenheim clay pit and provided specimens of this species which were instrumental for its recognition.

**Holotype.** SNSB-BSPG 2022 IV 13 (Plate 2, fig. 8), Clay pit near Buttenheim, upper Pliensbachian, *Hawkerense* subzone, EPH horizon.

**Paratypes.** 9 specimens same data as holotype (SNSB-BSPG 2022 IV 14, Plate 2, figs 9–12).

**Diagnosis.** OL:OH = 1.1–1.25. Rostrum short, its length 12–25% of OL. Ventral and dorsal rims regularly curving. Ventral rim of ostium shallow, often fading, no or very weak distinction of ostium and cauda.

**Description.** Nearly round, thin otoliths up to 2.5 mm in length (holotype 2.2 mm); OH:OT = 3.5–4.5. Ventral rim deeply and regularly curved, and smooth or intensely and finely crenulated. Rostrum short, blunt. Dorsal rim behind ostial relatively long, elevated, rounded, broad and irregularly undulating. Posterior rim broadly rounded.

Inner face distinctly bent with slightly supramedian sulcus. Ostium short, indistinctly separated from cauda, slightly expanding backward from rostrum and antirostral notch, about as long as cauda. Ventral margin of sulcus often indistinct, gradual, relatively straight with no or very feeble

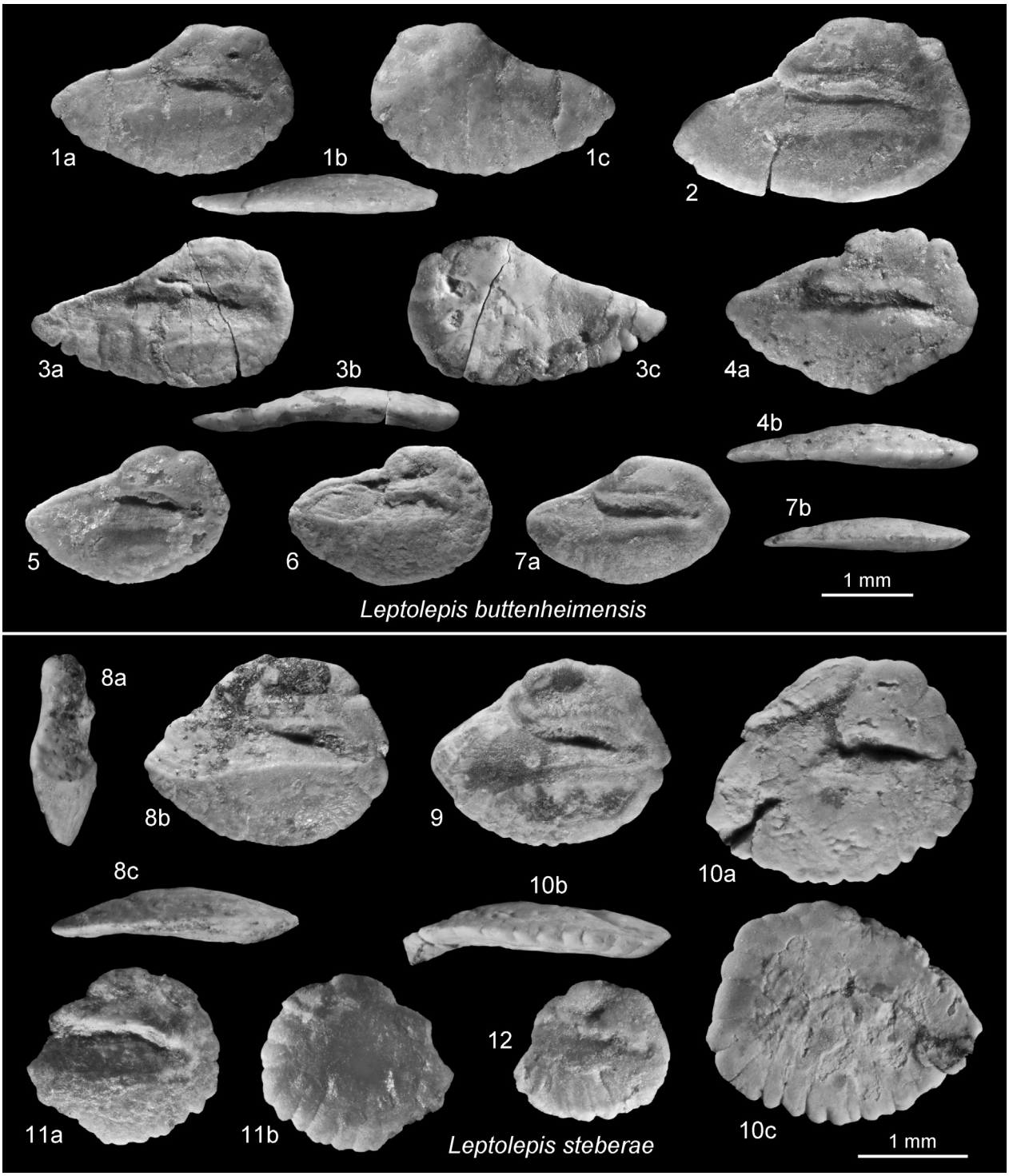


**Plate 2.** Otoliths of *Leptolepis buttenheimensis* and *L. steberae*. **figs 1–7** *Leptolepis buttenheimensis* sp. nov. from the late Pliensbachian of Buttenheim; **1:** holotype SNSB-BSPG 2022 IV 4, EPH horizon; **2–7:** paratypes SNSB-BSPG 2022 IV 5–6; **2–5, 7:** EPH horizon; **6:** *Apyrenum* subzone. **figs 8–12:** *Leptolepis steberae* sp. nov. from the Pliensbachian of Buttenheim, EPH horizon; **8:** holotype SNSB-BSPG 2022 IV 13; **9–12:** paratypes SNSB-BSPG 2022 IV 14.

indication of differentiation into ostium and cauda. Cauda straight, terminating close to posterior tip of otolith. Dorsal depression very small, restricted to position above anterior part of cauda. No ventral furrow. Outer face flat to slightly concave, with many short radial furrows particularly along ventral margin of otolith. No or very feeble postcentral umbo.

**Discussion.** *Leptolepis steberae* is a relatively rare and small species in the late Pliensbachian of Buttenheim. It is recognized by its compressed, rounded outline with only a moderately projecting and rather blunt rostrum. Its OL:OH ratio is less than in contemporaneous congeners (1.1–1.25 vs. 1.25–175). The rostrum is shorter than in coeval *Leptolepis* species (12–25% of OL vs. 30–45%). Another typical characteristic is the nearly straight ventral margin of the sulcus, which is also often rather gradational.

### *Leptolepis kremmeldorfensis* (Schröder, 1956)

Plate 3, figs 1–8

1956 *Otolithus kremmeldorfensis* - Schröder: pl. 7, figs 34–35.
1956 *Otolithus amygdalinus* - Schröder: pl. 6, figs 4–6.
?1956 *Otolithus bambergensis* - Schröder: pl. 6, fig. 19, pl. 7, fig. 20.
?1956 *Otolithus franconicus* - Schröder: pl. 7, figs 31–33.

**Material.** 11 specimens from Schröder's collection from the late Toarcian to early Aalenian: holotype of *Ot. kremmeldorfensis* from Kremmeldorf (SNSB-BSPG 2022 III 35, Plate 3, fig. 1) and 1 paratype from Kremmeldorf (SNSB-BSPG 2022 III 36, Plate 3, fig. 2), holotype of *Ot. amygdalinus* from Kremmeldorf (SNSB-BSPG 2022 III 14, Plate 3, fig. 3) and 1 paratype from Kremmeldorf (SNSB-BSPG 2022 III 15), 1 paratype of *Ot. bambergensis* from Freiahorn (SNSB-BSPG 2022 III 10, Plate 3, fig. 4), holotype of *Ot. franconicus* from Kremmeldorf (SNSB-BSPG 2022 III 24, Plate 3, fig. 5) and 5 paratypes, with 4 from Kremmeldorf (SNSB-BSPG 2022 III 25, 27–29, Plate 3, fig. 6) and 1 from Freiahorn (SNSB-BSPG 2022 III 26).

**Tentatively assigned specimens.** 2 poorly preserved specimens from the late Pliensbachian of Buttenheim (SNSB-BSPG 2022 IV 15, Plate 3, figs 7–8).

**Differential diagnosis.** *Leptolepis kremmeldorfensis* shares its otolith and sulcus proportions with the coeval *L. curvisulcatus* and differs in its flat, low, and relatively long postdorsal rim. However, small specimens below 1 mm in length, which have been described as *Ot. bambergensis* and *Ot. franconcius*, mostly show a more rounded postdorsal rim similar to the status in *L. normandica*. Therefore, they are only tentatively attributed and could in fact represent juveniles of any other *Leptolepis* species.

**Discussion.** As with *L. curvisulcatus*, the validity of *L. kremmeldorfensis* should be regarded as provisional until larger otoliths have become available from the region and stratigraphic interval. Although a single larger otolith of nearly 3 mm in length, designated as *Ot. amygdalinus* by Schröder (1956), shares the characteristic shape of the postdorsal rim, it is otherwise too eroded to make a firm identification. Two poorly preserved specimens from the late Pliensbachian of Buttenheim are tentatively accounted for in *L. kremmeldorfensis* because of their relatively shallow and long postdorsal rim. If verified, it would extend the stratigraphic reach of the species significantly.

### *Leptolepis inaequalis* (Weiler, 1954)

Plate 3, figs 9–11

1954 *Otolithus* (inc.sed.) *inaequalis* - Weiler: pl. 4, fig. 170.
1956 *Otolithus calloviensis* - Schröder: pl. 6, figs 17–18.
1956 *Otolithus pünzendorfensis* - Schröder: pl. 7, fig. 39.
2018 *Leptolepis inaequalis* (Weiler, 1954) - Schwarzhans: fig. 2E.

**Material.** 4 specimens: Weiler's holotype of *Ot. inaequalis* from the Callovian to Oxfordian of Kandern, Baden-Würtemberg (SMF P.3067, refigured in Plate 3, fig. 11); 3 specimens from Schröder's collection from the early Callovian: holotype of *Ot. calloviensis* from Pünzendorf (SNSB-BSPG 2022 III 8, Plate 3, fig. 10) and 1 paratype from Pünzendorf (SNSB-BSPG 2022 III 9), holotype of *Ot. puenzendorfensis* (emended spelling, SNSB-BSPG 2022 III 39, Plate 3, fig. 9).

**Differential diagnosis.** *Leptolepis inaequalis* is characterized by being very thin with nearly flat inner and outer faces. It shares these features only with *L. macrocephalus* (see below), from which it differs in its slightly slenderer shape (OL:OH = 1.5 vs. 1.35–1.4) and its shallow and rather long postdorsal rim (vs. rounded and expanded).

**Discussion.** Due to the fragile nature of these thin and delicate otoliths, only one complete specimen of *L. inaequalis* is known: the holotype from Weiler. All three specimens from Schröder, which we synonymized with *L. inaequalis*, are incomplete because they lack the rostrum, but they do show the typical flat inner face in combination with the shallow and long postdorsal rim. Schröder's drawing of the holotype of *Ot. calloviensis* indicates a complete specimen, but the one found in his collection is slightly damaged, which possibly happened after the drawing was made.

### *Leptolepis macrocephalus* (Schröder, 1956)

Plate 3, figs 12–13

1956 *Otolithus macrocephali* - Schröder: pl. 7, fig. 40.
1956 *Otolithus guttaeformis* - Schröder: pl. 6, figs 15–16.

**Material.** 3 specimens from Schröder's collection from the early Callovian of Pünzendorf: holotype of *Ot. macrocephalus* (emended spelling, SNSB-BSPG 2022 III 1, Plate 3, fig. 13), holotype of *Ot. guttaeformis* (SNSB-BSPG 2022 III 6, Plate 3, fig. 12) and 1 paratype (SNSB-BSPG 2022 III 7).

**Differential diagnosis.** *Leptolepis macrocephalus* differs from the coeval *L. inaequalis* in its more compressed shape, which is exhibited by a deeper ventral rim and a more expanded postdorsal rim and is expressed in the OL:OH ratio of 1.35–1.4 (vs. 1.5). It shares with *L. inaequalis* completely flat inner and outer faces, features that distinguish both species from all other known *Leptolepis* otoliths.

**Discussion.** *Leptolepis macrocephalus* and *L. inaequalis* form a small group of otoliths with a special trait of having flat inner and outer faces. They occur during the Callovian and possibly the early Oxfordian. Their attribution to the genus is therefore less certain than that of *Leptolepis* otoliths from the Early Jurassic (see above).

## Order Elopiformes Jordan, 1923
## Family indet.
## Genus *Leptoelops* Schwarzhans, 2018

### *Leptoelops rhenanus* (Weiler, 1954)

Plate 3, figs 14–16

1954 *Otolithus* (*Lycopteridarum*?) *rhenanus* - Weiler: pl. 1, fig. 18.
1956 *Otolithus rectisulcatus* - Schröder: pl. 6, fig. 21.
?1956 *Otolithus scissus* - Schröder: pl. 7, figs 29–30.
2018 *Leptoelops rhenanus* (Weiler, 1954) - Schwarzhans: fig. 5O.

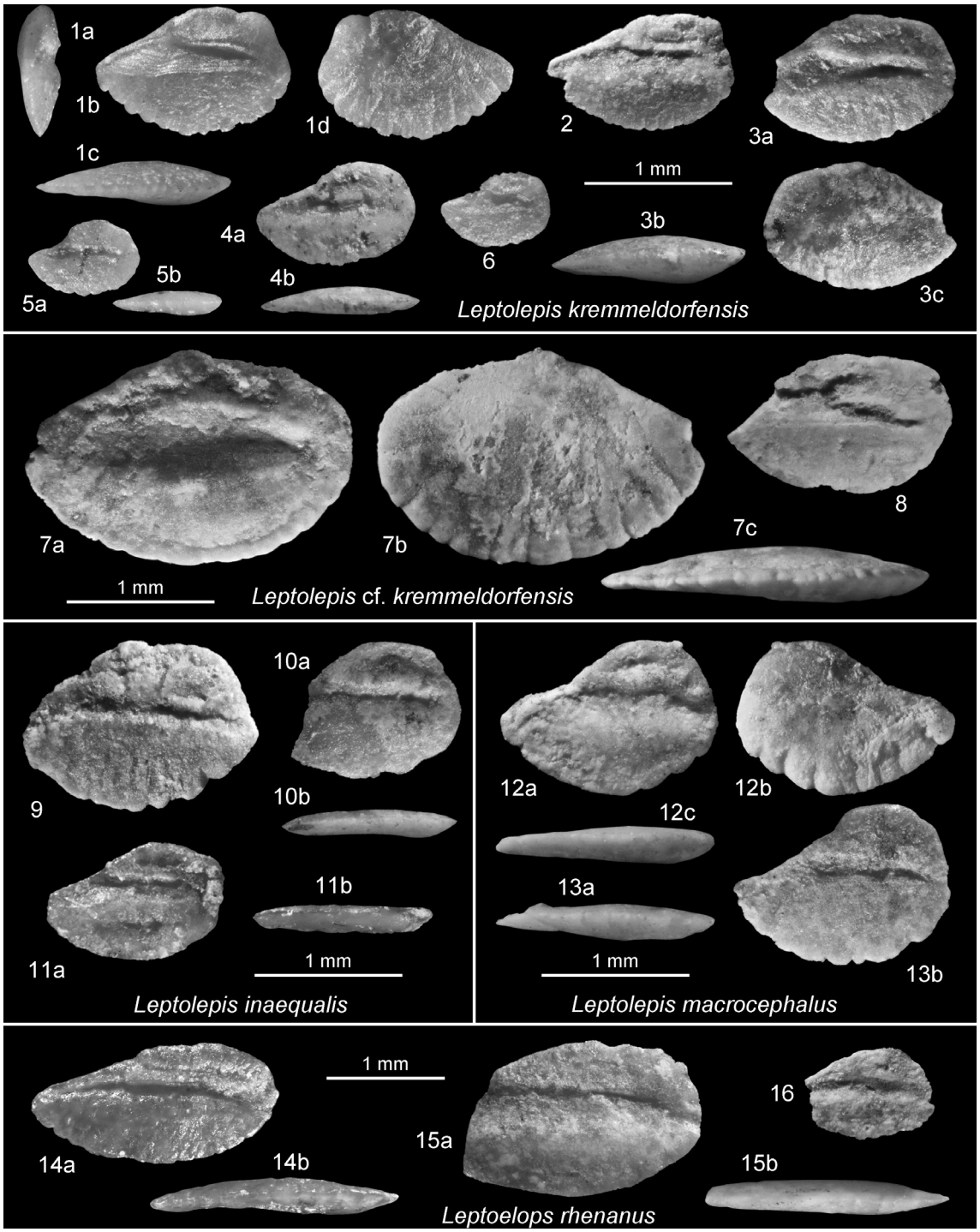


**Plate 3.** Otoliths of *Leptolepis kremmeldorfensis*, *L. inaequalis*, *L. macrocephalus*, and *Leptoelops rhenanus*. **figs 1–6:** *Leptolepis kremmeldorfensis* (Schröder, 1956); **1:** holotype of *Ot. kremmeldorfensis* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 35); **2:** paratype of *Ot. kremmeldorfensis* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 36); **3:** holotype of *Ot. amygdalinus* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 14); **4:** paratype of *Ot. bambergensis* Schröder, 1956 from Freiahorn (SNSB-BSPG 2022 III 10); **5:** holotype of *Ot. franconicus* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 24); **6:** paratype of *Ot. franconicus* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 27). **figs 7, 8:** *Leptolepis* cf. *kremmeldorfensis* (Schröder, 1956), from the late Pliensbachian of Buttenheim, SNSB-BSPG 2022 IV 15. **figs 9–11:** *Leptolepis inaequalis* (Weiler, 1954); **9:** holotype of *Ot. puenzendorfensis* Schröder, 1956 from Pünzendorf (SNSB-BSPG 2022 III 39); **10:** holotype of *Ot. calloviensis* Schröder, 1956 from Pünzendorf (SNSB-BSPG 2022 III 8); **11:** holotype of *Ot. inaequalis* Weiler, 1954 from the Callovian to Oxfordian of Kandern, Baden-Würtemberg (SMF P.3067). **figs 12–13:** *Leptolepis macrocephalus* (Schröder, 1956); **12:** holotype of *Ot. guttaeformis* Schröder, 1956 from Pünzendorf (SNSB-BSPG 2022 III 6); **13:** holotype of *Ot. macrocephalus* Schröder, 1956 from Pünzendorf (SNSB-BSPG 2022 III 1). **figs 14–16:** *Leptoelops rhenanus* (Weiler, 1954); **14:** holotype of *Ot. rhenanus* Weiler, 1954 from the Callovian of well Bruchsal D 205 (core from 482 to 487 m) near Weingarten, Baden-Württemberg (SMF P.2953); **15:** holotype of *Ot. rectisulcatus* Schröder, 1956 from Pünzendorf (SNSB-BSPG 2022 III 37); **16:** holotype of *Ot. scissus* Schröder, 1956 from Pünzendorf (SNSB-BSPG 2022 III 40).

**Material.** 5 specimens: Weiler's holotype of *Ot. rhenanus* from the Callovian of well Bruchsal D 205 (core from 482 to 487 m) near Weingarten, Baden-Würtemberg (SMF P.2953, refigured in Plate 3, fig. 14); 4 specimens from Schröder's collection from the early Callovian of Pünzendorf: holotype of *Ot. rectisulcatus* (SNSB-BSPG 2022 III 37, Plate 3, fig. 15) and 1 paratype (SNSB-BSPG 2022 III 38), holotype of *Ot. scissus* (SNSB-BSPG 2022 III 40, Plate 3, fig. 16) and 1 paratype (SNSB-BSPG 2022 III 41).

**Diagnosis (from Schwarzhans 2018).** Thin, elongate otolith with an OL:OH ratio of 2.1. Rostrum about 40% of OL. Ostium dorsally open, its ventral margin level with the ventral margin of its cauda. Outer face with radial furrows near ventral rim.

**Discussion.** *Leptoelops rhenanus* is a very characteristic otolith that differs readily from *Leptolepis* otoliths in both its very slender shape and its absence of a ventrally widened ostium. Schröder's holotype of *Ot. rectisulcatus* lacks the rostrum, but otherwise it largely resembles Weiler's holotype of *L. rhenanus*. The specimens of *Ot. scissus* are also fragmentary, less well-preserved, and much smaller in size. They differ somewhat in the posteriorly elevated dorsal rim and a slight bend in the cauda. We consider these features aspects of an ontogenetical allometry, but we are aware that they could also indicate the presence of another species in the Callovian. We have therefore only tentatively attributed *Ot. scissus* to *L. rhenanus*, subject to finding additional and better-preserved specimens in the future.

## Actinopterygii indet.
## Family indet.

### Genus *Archaeotolithus* Stolley, 1912

**Type-species.** Designated here as *Archaeotolithus trigonalis* Stolley, 1912. Stolley (1912) established *Archaeotolithus* as an otolith-based genus, or, in his words, as a new "typus" (typ. nov.). He may have been considering *Archaeotolithus* to represent a collective group genus comparable to *Otolithus* as introduced by Koken (1884; see Schwarzhans 2012 in Addendum). However, we are of the opinion that the otoliths Stolley attributed to *Archaeotolithus* indeed represent a very specific and unique morphology, and, therefore, a formal otolith-based genus for this pattern is well-justified. This point also generates the need to select a type-species for the redefined otolith-based genus of Stolley (1912), which we represent here.

**Diagnosis.** Otoliths with a triangular shape that can reach about 7 mm in length. The three corners are the preventral, postventral and middorsal angles. Inner face convex; outer face flat, often with fine radial furrows starting from the middorsal angle. Otolith nucleus distinctly eccentric, visible on the outer face at the middorsal angle. Inner face with distinctly supramedian sulcus with often vague margins, particularly its ventral margin. Ostium and cauda intergrading and poorly distinguished. Ostium open anteriorly, its ventral margin deeply expanding downward. Cauda narrower, slightly downward-oriented toward posterior, and terminating close to posterior tip of otolith. No dorsal depression or ventral furrow.

**Species, distribution and stratigraphic ranges.** Three species are referred here to *Archaeotolithus*: *A. bornholmiensis* (Malling & Grønwall, 1909) from the Pliensbachian of the isle of Bornholm, Denmark, and Franconia; *A. doppelsteini* sp. nov. from the late Pliensbachian of Franconia; and *A. trigonalis* Stolley, 1912 from the late Pliensbachian of Franconia and the Bajocian of northern Germany. Malling and Grønwall (1909) also reported two additional, presumably *Archaeotolithus*, otoliths from the Pliensbachian of Bornholm in open nomenclature, which cannot be identified from their documentation.

**Relationships.** The relationships of *Archaeotolithus* are obscure. We are not entirely certain whether it represents a sagittal otolith, although this appears likely because of the presence of a sulcus on what is perceived as the inner face of the otoliths, or a lapillus. In any case its peculiar and highly characteristic morphology does not relate to that of any known teleost.

Three kinds of vaguely similar otoliths have also been reported from the Late Jurassic freshwater sediments of eastern Australia (Schwarzhans et al. 2019). This Lagerstätte is of interest because it bears four taxa of pholidophoriforms, one macrosemiiform and one chondrostean in addition to the most common fish, *Cavenderichthys talbragarensis* (Woodward, 1895), a "primitve" teleost. Otoliths *in situ* are only known from the latter, probably due to a function of its overwhelming abundance (Schwarzhans et al. 2019). It thus appears likely that the three Australian *Archaeotolithus* look-alike morphotypes belong to pholidophoriforms instead of chondrosteans (palaeonisciforms) as suggested by Schwarzhans (2018). Indeed, the *Archaeotolithus* morphotype best resembles the otoliths of extant lepisosteiforms (for figures, see Nolf 2013 and Schwarzhans et al. 2019). Therefore, the most likely candidates for relationships with *Archaeotolithus* may be expected in Ginglymodi or very basal Teleostei below the Leptolepidiformes level. We hope that otoliths will eventually be found *in situ* and this enigmatic otolith morphology can be reliably related to a systematic context.

### *Archaeotolithus bornholmiensis* (Malling & Grønwall, 1909)

Plate 4, fig. 1

1909 *Otolithus bornholmiensis* - Malling & Grønwall: pl. 11, figs 14–16.

1912 *Arcaeotolithus bornholmiensis* (Malling & Grønwall, 1909) - Stolley: pl. 7, figs 4–5.

?2014 archaeotoliths group 1 - Hesse: fig. 28A–B.

**Material.** 1 specimen from the late Pliensbachian, *Hawkerense* subzone, of Buttenheim (SNSB-BSPG 2022 IV 7, Plate 4, fig. 1).

**Differential diagnosis.** *Archaeotolithus bornholmiensis* is the only species in the genus with almost no indication of a sulcus and further differs from its congeners in the

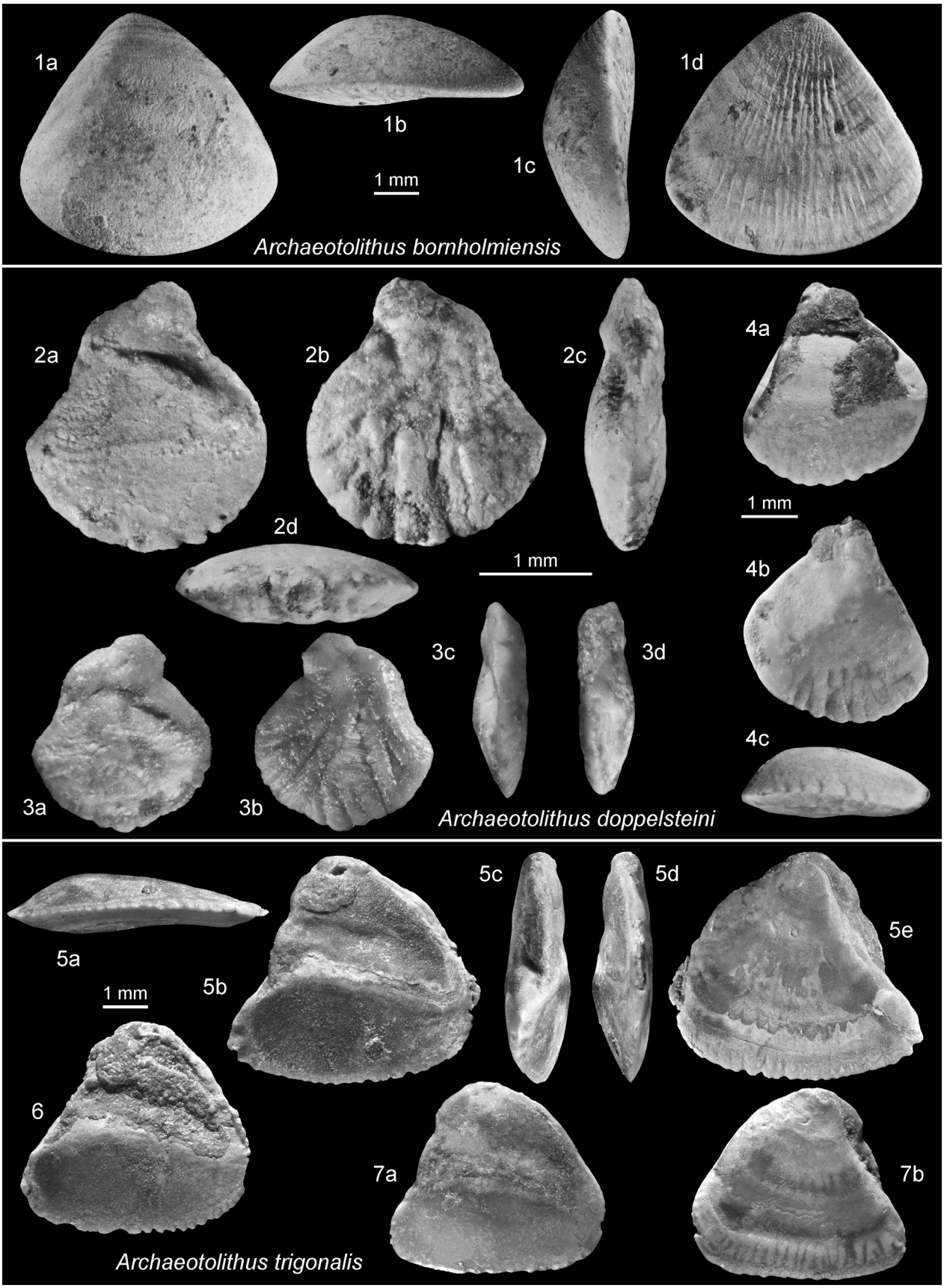


**Plate 4.** Otoliths of *Archaeotolithus*. **fig. 1:** *Achaeotolithus bornholmiensis* (Malling & Grønwall, 1909), from the late Pliensbachian of Buttenheim, holotype SNSB-BSPG 2022 IV 7, EPH horizon. **figs 2–4:** *Archaeotolithus doppelsteini* sp. nov., from the late Pliensbachian of Buttenheim, EPH horizon; **2:** holotype SNSB-BSPG 2022 IV 8; **3–4:** paratypes SNSB-BSPG 2022 IV 9. **figs 5–7:** *Archaeotolithus trigonalis* Stolley, 1912, from the late Pliensbachian of Buttenheim, EPH horizon, figured specimens SNSB-BSPG 2022 IV 12.

more strongly convex inner face. It is thus also the one most resembling the characteristics of a lapillus.

### *Archaeotolithus doppelsteini* sp. nov.

http://zoobank.org/6CF0B3D2-345A-4225-BC1E-769F8444169F
Plate 4, figs 2–4

2021b *Lapillus unbekannter* Zuordnung – Keupp: fig. 9.3 D.

**Etymology.** Named after Bernd Doppelstein (Berlin), who has intensely collected from the Buttenheim clay pit and provided the largest specimen of this species.

**Holotype.** SNSB-BSPG 2022 IV 8 (Plate 4, fig. 2), Clay pit near Buttenheim, upper Pliensbachian, *Hawkerense* subzone, EPH horizon.

**Paratypes.** 4 specimens same data as holotype (SNSB-BSPG 2022 IV 9, Plate 4, figs 3–4).

**Diagnosis.** OL:OH = 0.9–0.93; OH:OT = 2.8–3.6. Ventral rim deeply curved, middorsal angle with small process. Outer face with complex pattern of subvertical furrows.

**Description.** Very high-bodied otoliths up to 3.25 mm in length (holotype 2.2 mm) with rounded ventral rim and rounded postventral angle. Middorsal angle with small projection. Anterior and posterior rims smooth, ventral rim regularly and coarsely crenulated.

Inner face moderately convex with distinct supramedian positioned sulcus. Dorsal margin of sulcus relatively well-defined, ventral margin gradational and indistinct. Sulcus anteriorly open and ventrally widened, posteriorly curved slightly downward and terminating close to rounded postventral angle. Distinction in ostium and cauda indistinct or with broad shallow ventral bend at junction; OsL:CaL notably variable, ranging from 0.7 to 1.2. Outer face flat, with set of opposing subvertical furrows on pre- and postventral fields, diminishing in intensity with size.

**Discussion.** The relatively small holotype is well preserved whereas the large figured paratype (Plate 4, fig. 4) has severe incrustations across much of the sulcus that obliterate part of its morphology. *Archaeotolithus doppelsteini* is readily distinguished from its congeners by its deep ventral rim, rounded postventral angle, and process of the middorsal angle. It differs from *A. trigonalis* in its higher body shape, expressed in the lower OL:OH ratio (0.9–0.93 vs. 1.05–1.12) and the different proportions of the ratio OsL:CaL (0.7–1.2 vs. 0.3–0.4). Furthermore, the ornamentation of the outer face differs from that observed in its congeners.

### *Archaeotolithus trigonalis* Stolley, 1912

Plate 4, figs 5–7

1912 *Archaeotolithus trigonalis* - Stolley: pl. 7, figs 1–3.
2014 archaeotoliths group 2 - Hesse: fig. 29A–E.
2018 *Archaeotolithus trigonalis* Stolley, 1912 - Schwarzhans: fig. 8K.

**Material.** 25 specimens from the late Pliensbachian of Buttenheim: 2 specimens *Apyrenum* subzone (SNSB-BSPG 2022 IV 10), 1 specimen "Quellhorizon" (SNSB-BSPG 2022 IV 11), 22 specimens *Hawkerense* subzone (figured specimens SNSB-BSPG 2022 IV 12, Plate 4, figs 5–7).

**Differential diagnosis.** Otoliths with nearly equilateral triangular shape similar to *A. bornholmiensis* but distinctly less high-bodied than *A. doppelsteini*. *Archaeotolithus trigonalis* differs from *A. bornholmiensis* in being thinner, having a smooth outer face with exposed growth rings (vs with fine radial furrows starting from the middorsal angle), and showing a clear sulcus. It differs from *A. doppelsteini* not only in the otolith proportions and shape but also in the very short and strongly ventrally extended ostium and the rather straight, inclined cauda.

**Discussion.** *Archaeotolithus trigonalis* is the most common species of the genus in Buttenheim. It almost always shows some kind of incrustation on the inner face, which often obliterates the sulcus morphology. However, in some instances, such as the figured specimens, it can still be reliably identified. A similar incrustation is also seen on the large paratype of *A. doppelsteini*, which could have been caused by organic material that was attached to it during the early process of fossilization and mineralization.

## 3.2 Early teleost otolith morphogenesis

The earliest teleost otoliths are known from the late Sinemurian (Weiler 1965; Schwarzhans 2018), which is consistent with the first occurrence of leptolepidid skeletons in the fossil record (Arratia 1997). Only three otolith morphologies are known from the entire Liassic (early Jurassic): the *Leptolepis*-pattern, the *Xenoleptolepis*-pattern and the *Archaeotolithus*-pattern. Of these three, only the *Leptolepis* and the *Archaeotolithus* morphotypes have been found in Franconia. Liassic otoliths have so far only been found in England, Denmark, Belgium, Luxemburg, and Germany (Fig. 3). These occurrences reflect data from a rather restricted region and mostly comparable environments. Therefore, it is not surprising that the individual faunal assemblages are relatively similar, except for *Xenoleptolepis* that is absent in the southern German localities and *Archaeotolithus* that is absent in England.

The stratigraphic ranges and speciation levels vary considerably among the three morphotypes. *Xenoleptolepis* is known from two species: *X. withersi* from the Sinemurian and early Pliensbachian (Fig. 4) and a second species known from the single holotype, *X. oncorhynchoides* (Weiler, 1954), from the basal Cretaceous (Berriasian) of northern Germany. *Archaeotolithus* comprises three species ranging from the Pliensbachian to the Bajocian (Fig. 4), which all occur in parallel during the late Pliensbachian of Franconia. We don't know if similar morphologies found in freshwater otoliths from the Late Jurassic of Australia may represent a related group of fishes or not. Both the *Xenoleptolepis* and *Archaeotolithus* otolith morphologies have so far not been found *in situ*; therefore, their systematic position is unresolved. *Xenoleptolepis* most likely represents a stem teleost related to the Leptolepididae. The

**Figure 3.** Paleogeographic map of Europe at 175 Ma based on Blakey (2021). Stars indicate locations with otoliths from the Early to Middle Jurassic. The big violet star indicates the finding of otoliths *in situ* in skeletons of *Leptolepis normandica* from Delsate (1997). The red stars indicate localities from which otoliths have been studied for this article. Each star can represent more than one locality.

relationships of *Archaeotolithus* are completely obscure (see above). In any case, it is obvious that both morphotypes existed only across a restricted time period and do not exhibit any substantial degree of diversification.

The situation is somewhat different for the *Leptolepis* morphotype. Initially, it occurs more or less in parallel with the two other morphotypes. During the early Jurassic it also shows limited diversity (Fig. 4). The early Jurassic speciation level is low, with a maximum of five *Leptolepis* species occurring simultaneously (Nybelin 1974). Some of those nominal species are currently considered only tentatively valid, such as *Leptolepis kremmeldorfensis* or *L. curvisulcatus*. Another aspect is the relatively long stratigraphic range of the key species *L. normandica*, which is based on both skeletal and otolith material. Once otoliths have been found *in situ*, it is likely that one of the other Early Jurassic otolith-based *Leptolepis* species will represent the iconic skeleton-based *L. coryphaenoides* (Bronn, 1830). The situation changes drastically during the Middle Jurassic. Otolith finds in the Aalenian and Bajocian are relatively sparse, but in the Bathonian the number of species with a *Leptolepis*-type otolith morphology increase rapidly to 11 species that occur more or less simultaneously (Fig. 4). This increase brings with it some variations in the morphological pattern that Schwarzhans (2018) attributed to a set of different extinct otolith-based genera. However, the disparity in morphological diversity is still relatively low compared to the taxonomic diversity. Obviously, diversity spread faster than disparity.

Unfortunately, we do not know how the beginning disparity during the Bathonian matches with the early separation of clades seen in the skeletal record (Nybelin 1975; Arratia 1996, 1997; López-Arbarello et al. 2008; Guinot and Cavin 2015) because there is virtually no linkage with otoliths *in situ* during that time interval. The only exception is an otolith recovered "quasi" *in situ* in the phosphatized solution residue of a leptolepid head carved out from the stomach of a pholidophorid predator in a rock of Callovian age (Patterson 1975). Stinton (cited by Nolf 1985) considered this otolith to represent *L. coryphaenoides* and his rather schematic drawing was first published by Nolf (1985 and 2013). The otolith resembles the otolith-based

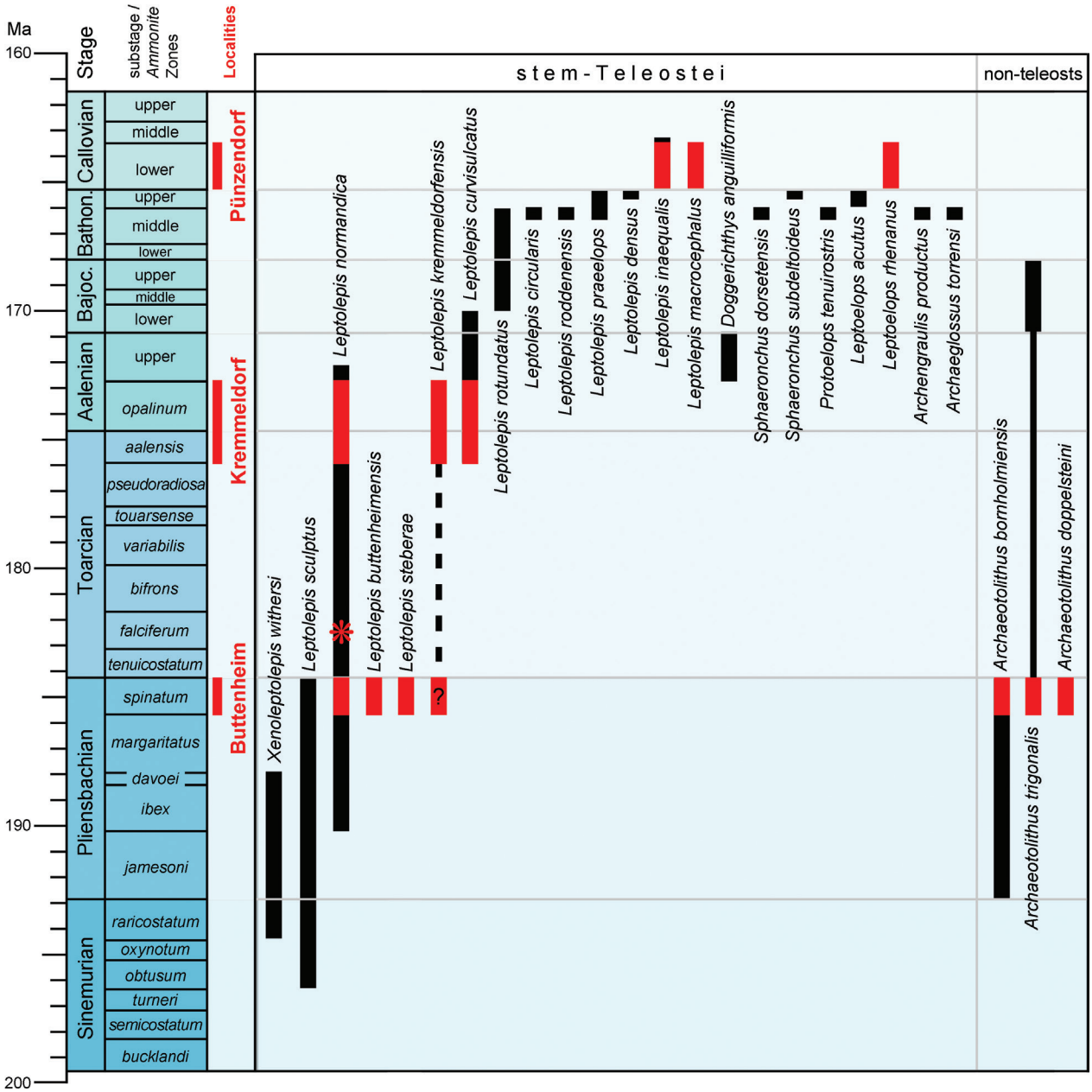


**Figure 4.** Stratigraphic chart depicting ranges of Early to Middle Jurassic otolith-based fish species. Red bars reflect ranges of localities from which otoliths have been studied for this article. The red asterisk indicates the stratigraphic position of the fishes with otoliths *in situ* described by Delsate (1997). Chronostratigraphy and ammonite zonation after Gradstein et al. (2020).

species *L. praeelops* (Stinton, 1968) from the Bathonian. It is unlikely to represent *L. coryphaenoides*, which does not extend so far up into the Middle Jurassic as Delsate (1997) noted. Schwarzhans (2018) has tentatively related some of the otolith morphologies found in the Bathonian to stem elopiforms (*Protoelops*, *Leptoelops*) and stem osteoglossiforms (*Archaeglossus*). Others, such as *Doggerichthys* and *Sphaeronchus* cannot be associated with any degree of likelihood.

Another question is whether the observed explosive burst of diversity associated with some degree of increase in disparity in the Bathonian otoliths represents a real evolutionary signal or is the result of a Lagerstätten effect. Guinot and Cavin (2015) analyzed a similar rapid increase in diversity observed in skeletal teleost remains of the Late Jurassic (based on Arratia 1997). They concluded that this apparent burst would in all likelihood represent a Lagerstätten effect. The rapid increase of otolith-based teleost species during the Bathonian relates to two specific localities in England described by Stinton (in Stinton and Torrens 1968). Stinton counted 368 otoliths, which have been reviewed and refigured by Schwarzhans (2018) and are of exceptionally good preservation. These finds are definitely apt to suspect a Lagerstätten effect. However, about as many otoliths (351) have been retrieved from the late Pliensbachian of Buttenheim that are predominantly also of good preservation quality and which only represent three *Leptolepis* and three *Archaeotolithus* species.

Therefore, when comparing the Bathonian assemblage described by Stinton and the Pliensbachian from Buttenheim described here, it becomes clear that the increase of teleost otolith-based species observed in the Bathonian must represent a real phylogenetic signal.

The question is when the evolutionary event took place. Otolith data from the Toarcian, Aalenian and Bajocian are sparse. The largest otolith assemblage studied in this interval is probably the one from the latest Toarcian to early Aalenian that was originally available to Schröder and amounted to 55 specimens. Most of the specimens are relatively small and poorly preserved; nevertheless, they seem to represent only three teleost species. Therefore, it seems that the burst of diversity happened between the early Aalenian and the late Bathonian, over a time interval of about 7 mya. This observation would also indicate that the Bathonian speciation level actually represents a window into early teleost evolution from an otolith perspective. Conversely, the teleost otolith associations of the Pliensbachian and Toarcian are characterized by few common and long ranging species as would typically be expected during an early evolutionary phase. Combined, the now known otolith record from the early and middle Jurassic represents a first view into the early teleost otolith morphogenesis.

## 4. Conclusions and outlook

The knowledge of Mesozoic otoliths has steadily increased in recent years and the data of older works have been reviewed (Nolf 2013; Schwarzhans 2018), although the data from the Early Jurassic were still sparse. The newly collected otoliths from the late Pliensbachian of Buttenheim and the review of Schröder's specimens from the late Toarcian/early Aalenian and early Callovian filled a gap in the stratigraphic sequence and helps to better understand the otolith morphogenesis of early teleosts and associates. The main results are as follows:

- Early Jurassic stem teleost otoliths are represented by few, common and long ranging species of the genus *Leptolepis*. The most common one pertains to *L. normandica*, which was calibrated by otoliths *in situ* (Delsate 1997; Nolf 2013).
- Other groups of uncertain relationships such as *Xenoleptolepis*, another putative stem teleost, and *Archaeotolithus* (a "pre-leptolepidid" fish) occur simultaneously but are much less common.
- Teleost otolith diversity has dramatically increased in the late Middle Jurassic (Bathonian) and may have gotten its initial boost in the relatively short time interval between the Aalenian and Bathonian.
- The disparity in morphological diversity of early teleost otoliths during the Early to Middle Jurassic trails their taxonomic diversity and is thus not comparable to the disparity observed in fish skeletons of the Late Jurassic.

The key to a better understanding of Jurassic otoliths is the calibration of their morphology through finds of otoliths *in situ*, particularly as more otolith assemblages emerge and a denser stratigraphic and wider morphological spectrum becomes available. Unfortunately, only otoliths of *Leptolepis* and *Cavenderichthys* have so far been found *in situ* of any Jurassic fishes. We would therefore hope that our colleagues will be mindful of prospects for finding otoliths *in situ* so that more of the enigmatic otolith morphologies can in the future be tied to the skeleton-based record.

## Acknowledgements

We are indebted to the private collectors Johann Schobert, Hirschaid, Bernd Doppelstein, Berlin, and Birgit Steber, Leibersdorf, for providing their material of otoliths from Buttenheim, and to Christian Schulbert and Axel Munnecke for providing the original material of Gert Schröder (1956), which was hosted in the paleontological collection of the Friedrich Alexander University of Erlangen. We thank Giorgio Carnevale (Torino) and Gary Stringer (West Monroe, Louisiana) for their constructive reviews of the manuscript.

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