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Leptolepid otoliths from the Hauterivian (Lower Cretaceous) Lower Weald Clay (southern England)

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ABSTRACT

Teleostean saccular otoliths from the upper part of the late Hauterivian Lower Weald Clay Formation of the Wealden Supergroup exposed at Langhurstwood Quarry, West Sussex, UK, and Clockhouse Brickworks, Surrey, UK are described for the first time. Two new species of the genus *Leptolepis*, *L. wealdensis* and *L. toyei* are described. Many of the specimens are densely packed on individual bedding planes and they are interpreted as coprocoenotic accumulations. Additional mechanisms of deposition and concentration are discussed, in particular wave action. Ontogenetic series show isometric growth of the otoliths, and some specimens show growth rings on two orders of magnitude.

Keywords: Hauterivian, teleost, coprocoenosis, Wealden, leptolepid, otolith

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1. Introduction

The Early Cretaceous was a time of transition in vertebrate evolution. This was a result of protracted upheavals spanning the Jurassic–Cretaceous boundary, when short-term catastrophic events, large-scale tectonic processes, and environmental perturbations drove dramatic faunal and ecological turnovers in the oceans and on land (Tennant et al., 2016). The Early Cretaceous record of marine teleosts is well documented from sites around the globe, but non-marine assemblages are infrequent by comparison (Martill and Sweetman, 2011).

The Barremian Wealden Group (here and below, stratigraphic terminology follows Batten, 2011) of the Isle of Wight, southern England, and the Jehol Group of China are among the best examples of fossiliferous Early Cretaceous non-marine strata. Their similar age has allowed for detailed comparisons of their biotas between continents (Sweetman, 2016); a greater diversity of freshwater teleosts is known from the Jehol Group, but the rich microvertebrate assemblages from the Wealden Supergroup have the potential to yield new taxa (Sweetman, 2011, 2013). Dominant finds among these are bones and teeth of chondrichthyans and osteichthyans (Duffin and Sweetman, 2011; Sweetman, 2013; Sweetman et al., 2014), lissamphibians (Sweetman and Evans 2011a), and reptiles (Sweetman 2011; Sweetman and Evans, 2011b). Otoliths are currently unknown from the Wealden Group of the Isle of Wight, but recently saccular otoliths have been recovered from Wealden Supergroup strata exposed in southeast England.

Otoliths are mineralised nodules within the stato-acoustic sensory system in the teleost skull (Duffin, 2007). Typically three different pairs of otoliths are secreted by the membranous labyrinths of the teleost inner ear (Fig. 1). The otic vesicle, attached by ampullae to the three semi-circular canals of the inner ear, has a large dorsal chamber (utricle), and a smaller ventral chamber (sacculus), which also possesses a diverticulum

(lagenae); otoliths are secreted in each of these locations (Fig. 1). Saccular otoliths (sacculiths) are larger than either the utricular otoliths (utriculiths) or lagenar otoliths (lagenaliths) and so are more common as fossils. Thus there is a well-developed descriptive terminology (Fig. 2) for their morphology (Chaine and Duvergier, 1934). The form of the otolith is species-specific and provides a means of identifying and diagnosing taxa, and of reconstructing faunal assemblages in the absence of skeletal remains (Woydack and Morales-Nin, 2001; Reichenbacher, 2004). One study (Patterson, 1993) showed that at the time 24% of extant teleost families were represented in the fossil record only by otoliths rather than skeletal remains. In addition to their use in systematics, otoliths can provide invaluable geochemical data for palaeoecological and palaeoclimatic reconstructions (Agiadi et al., 2010). In combination with microstructural analyses, they may also provide a powerful means of examining life histories, for example the identification of migration patterns (Carpenter et al., 2003).

Fossil otoliths are known from British localities spanning the Jurassic (Rundle, 1967; Simms and Jeram, 2007; Stinton and Torrens, 1968), Cretaceous (Stinton, 1973), Eocene (Stinton, 1975-1984) and Pleistocene (Stinton, 1985). Two are known from the Lower Cretaceous (Speeton Clay) and one from the Upper Cenomanian (Lower Chalk), while a greater number have been recovered from the Albian Gault Formation of Kent (Stinton, 1973); these have not received extensive study. Furthermore, they all come from marine lithofacies, and so the Wealden Supergroup otoliths described here provide a novel record of Early Cretaceous teleosts from a freshwater environment. In view of variable salinities represented by other Wealden Supergroup strata, future finds may permit study of taxa living in brackish and quasi-marine environments (Radley and Allen, 2012).

Otoliths were recorded from the Wealden Supergroup at Small Dole, West Sussex in the 1970s (Austen, 2007), but never formally documented. The first formal records of

Wealden otoliths were in 2005 from the Lower Weald Clay Formation at Langhurstwood Quarry, Warnham, West Sussex (Anon, 2005) and from the Lower Weald Clay Formation at Clockhouse Brickworks, Capel, Surrey (Toye et al., 2005). Subsequent excursions to both localities (Fig. 3) by the Geologists' Association and Horsham Geological Field Club located in situ beds yielding otoliths (Jarzembowski et al., 2006, 2010) and ex situ specimens in different lithologies.

This paper records abundant otoliths from the Wealden Supergroup of southeast England and presents two new species of freshwater teleost named from them. The materials come from Langhurstwood Quarry and Clockhouse Brickworks (Austen, 2011).

Institutional and other abbreviations below are: BGS (British Geological Survey), NGR (UK National Grid Reference), NHMUK (UK Natural History Museum, London).

2. Geological Setting

2.1 Langhurstwood Quarry, Warnham, West Sussex

Langhurstwood Quarry (NGR TQ 179352–TQ 182354) is the active pit at Warnham Brickworks (Fig. 3). It has not been logged, but stratigraphic schemes exist for worked-out pits 750 m to the west (Gallois and Worssam, 1993) and the Greylands Borehole 700 m to the south-west. These are used here as a proxy for the active pit (Fig. 4). Langhurstwood Quarry exposes late Hauterivian shaly ostracodal mudstones and silty mudstones with occasional thin limestones, siltstones, sandstones and pebbly horizons from the upper part of the Lower Weald Clay Formation (Fig. 4). BGS Bed 2a (Batten, 2011) is bounded 4.5 m from the base of the exposure by a lower, slightly pyritic limestone horizon bearing the euryhaline bivalve *Filosina gregaria*, and an upper limestone horizon bearing the freshwater to lower oligohaline gastropod *Viviparus infracretacicus* 1.7 m above this (Radley and Allen, 2012).

Lower shaly and fossiliferous beds were deposited in a marginal lagoonal environment periodically inundated by barometric tides and infrequent, powerful storm surges. The whole succession records generally freshwater to oligohaline salinity fluctuations (Radley and Allen, 2012).

2.2 Clockhouse Brickworks, Capel, Surrey

Clockhouse Brickworks (NGR TQ 176387–TQ 177387) exposes a more varied lithological sequence (Figs. 3, 4) stratigraphically above the exposure at Langhurstwood Quarry (Gallois and Worssam, 1993). The lower beds comprise mudstones and silty bioturbated mudstones containing frequent fish debris and *Cypridea marina*, and the bioturbated mudstones yielding multiple plant and arthropod species (Jarzembowski, 1991; Batten, 1998). Overlying this is a 1 m thick bed, the Clockhouse Sandstone (BGS Bed 3), then the base of the Upper Weald Clay Formation (Fig. 4) and the Hauterivian-Barremian boundary a further 8.3 m above (Radley and Allen, 2012).

The Clockhouse exposure records a transition from offshore lake and lagoonal environments to lake shoreline settings. The basal mudstones are lagoonal, with silt derived from temporarily increased runoff. Beds with abundant *Viviparus infracretacicus* record periods of slightly oligohaline to freshwater salinities. The Clockhouse Sandstone and the bed marking the base of the Barremian represent proximal overbank deposits, while 3 m of intercalated grey mudstone represents a brief return to brachyhaline conditions (Radley and Allen, 2012).

3. Materials and Methods

An extensive collection of several hundred lithological specimens, most containing multiple otoliths, was assembled by Peter and Joyce Austen over a period of ten years. In situ

lithological specimens of Clockhouse mudstone were collected in July 2006, while unstratified samples from the same locality were collected between 2005 and 2007. In situ lithological specimens of Langhurstwood sandstone and limestone were collected between 2010 and 2012. Loose specimens below the level of BGS Bed 2a (Fig. 4) were collected between 2011 and 2014, and unstratified specimens found loose or in spoil heaps between 2005 and 2015. Unstratified shaly mudstones mostly from alongside vehicle trackways in the main quarry were collected in July 2015. All Langhurstwood specimens were collected from the recent quarry workings on the east side of the Langhurstwood Road (NGR TQ 180352).

Otoliths for description were selected using a Nikon SMZ460 stereomicroscope, photographed at approximately 40x magnification using a Leica M205 C photomicroscope and digitally isolated from the matrix in GIMP 2 (The Gimp Team, version 2.8).

Several specimens were separated from the matrix using a scalpel. These were then embedded in Epofix™ epoxy resin, cured at room temperature and sectioned using an IsoMet® Low Speed Saw. The sections were polished using progressively finer wetted grit papers, three micron, one micron, and then 0.25 micron diamond paste.

Raman spectroscopy to determine aragonite preservation was conducted on one of the polished sections using a DXR™ 2xi Raman Imaging Microscope, yielding peaks within a few cm^{-1} of the characteristic calcite signatures at 713, 283 and 156 cm^{-1} (Edwards et al., 2005).

Preliminary scans of otolith microstructure were performed on the surfaces of uncoated specimens using a Hitachi TM3030 scanning electron microscope at 15 kV. Polished, uncoated sections were analysed using a variable pressure Hitachi S-3500 scanning electron microscope at 50 Pa and 20 kV, and employing backscattered electrons.

4. Palaeontological Background

A significant discrepancy exists between the theoretical Triassic date of origin for crown Teleostei and the oldest fossils of the primitive extant teleost lineages Elopomorpha, Osteoglossomorpha, Clupeomorpha, Ostariophysii, and stem-group Euteleostei, all of which appear, partly for taphonomic reasons, in a short interval between the Late Jurassic and Early Cretaceous (Benton et al., 2015). Present also through the Early Cretaceous are stem group halecostomes († = extinct): Holostei, Pycnodontiformes†, Amiidae, Pholidophoridae†, Leptolepidae†, Pachycormidae†, Aspidorhynchidae† and Ichthyodectidae† (Benton, 2015). The majority of English Mesozoic otoliths have been assigned to the Pycnodontiformes (Stinton and Torrens, 1968), Pholidophoridae (Harte et al., 2009; Stinton and Torrens, 1968), Leptolepidae (Frost, 1924, 1926; Harte et al., 2006; Stinton and Torrens, 1968), Elopomorpha (Harte et al., 2006; Stinton, 1973), and Amiidae (Harte et al., 2006; Rundle, 1967), a smaller number to Euteleostei (Stinton and Torrens, 1968) and one to the non-teleost clade Chondrostei (Stinton and Torrens, 1968).

Two saccular otolith-based species from the Wealden Supergroup are identifiable, both of which are leptolepids. The first (Fig. 5A-E) is abundantly represented by the specimens recovered from the calcareous sandstone exposed at Langhurstwood Quarry. This form is most similar to “*Teleostus*” *similis* (Nolf, 2013) from the Lower Jurassic of Germany (Fig. 6G). There is also a strong resemblance to *Leptolepis circularis* (Stinton and Torrens, 1968) from the Bathonian of southern England (Fig. 6F). This Bathonian taxon lacks the dorsal curving of the dorsal rim seen in the Wealden Supergroup specimens and no data exists regarding the lateral face of otoliths of this species. As a result, direct comparison cannot be made. “*Teleostus*” *similis* and *L. circularis* are similar to each other in general morphology, suggesting that the former may also represent a leptolepid. Morphological similarity of the Wealden Supergroup otoliths suggests that the Wealden taxa may also be leptolepids. The Jurassic taxa, however, come from marine lithofacies and have a substantial

temporal separation from the Early Cretaceous English Wealden species recovered from freshwater lithofacies. Again this suggests that the latter represent separate species. Large numbers of otoliths have been reported from the Wealden of Germany (Martin and Weiler, 1954), some of which are similar to those from Langhurstwood Quarry (Fig. 6H). The German specimens, however, have a less ventrally convex ventral rim and the ventral edge of the sulcus is anteriorly straight, rather in contrast to the curved anterior end observed in the English specimens. Despite these differences, the German specimens have been tentatively assigned to the Leptolepidae (Martin and Weiler, 1954), further suggesting that the Langhurstwood specimens are also attributable to this family.

While the first species is represented by multiple specimens, the second is known from only a single otolith (Fig. 5F) from the calcareous sandstone horizon at Langhurstwood Quarry (Fig. 4). It is most similar to “*Teleostus*” *roddenensis* (Nolf, 2013) from the Bathonian of southern England (Fig. 6B), a species that was originally assigned to *Leptolepis* (Stinton and Torrens, 1968). In view of its general morphological similarity to leptolepid otoliths from the Wealden of Germany, and now Britain, and despite some differences, the original interpretation appears to be more parsimonious. “*Teleostus*” *roddenensis* lacks the shallow dorsal depression and strongly incised ostial colliculum seen in the English Wealden specimen, but the latter bears similarities to otoliths from the Wealden of Germany (Fig. 6C-D). The sulci of the German specimens, however, are anteroposteriorly straighter than that seen in the English Wealden specimen, and they have crenulate rather than denticulate ventral rims. Additionally, all specimens figured in Martin and Weiler (1954) were named using the invalid and generic tripartite nomenclature developed by Koken (1884) for fossil otoliths of uncertain taxonomic affiliation.

Leptolepid remains from the Wealden Supergroup of England are known from several mass mortality assemblages (Austen, 2007) collected from the Upper Weald Clay Formation

at Smokejacks Brickworks. A single complete specimen of *Leptolepis brodiei* has also been recovered from the Lower Weald Clay Formation at Hamsey Brickworks, East Sussex (Forey and Sweetman, 2011). These skeletal records of leptolepids from the Weald Clay Group are consistent with the otolith record reported here. Given the stratigraphic and geographical proximity of Hamsey Brickworks and Smokejacks Brickworks to Clockhouse Brickworks and Langhurstwood Quarry, there is the possibility that one of the otolith morphotypes is attributable to *Leptolepis brodiei*. The specimens from Hamsey Brickworks and Smokejacks Brickworks could not be obtained for study. Instead specimens of *Leptolepis brodiei* from the Middle Purbeck Formation at Dinton, Wiltshire, England were examined (Fig. 7A; NHMUK PV P7635, P34036, P42725). Only one specimen (NHMUK PV P7635, a syntype) preserved anything resembling an otolith (Fig. 7B). The structure is partially exposed, but bears a groove that may correspond to the sulcus. The position of the structure, however, is not consistent with the locations of the sacculiths in the teleost skull and so it may instead be a displaced part of the frontal bone. The groove may therefore be one of the large slime canals observable on the external surface of skull bones in *Leptolepis brodiei* (Woodward, 1916). As study of the specimens proved inconclusive, neither otolith morphotype can be positively assigned to *Leptolepis brodiei*, although the possibility remains. Given that the morphotypes are very different from one another, however, at least one represents a taxon separate from *Leptolepis brodiei*.

In view of this, both species from Langhurstwood Quarry cannot be assigned to any pre-existing taxon for either morphological and/or nomenclatural reasons, and new species are erected for them. These are *Leptolepis wealdensis* and *Leptolepis toyei*.

5. Systematic Palaeontology

Infraclass Teleostei Müller, 1845

Family Leptolepididae *sensu* Nicholson and Lydekker, 1889

Genus *Leptolepis* Agassiz, 1832

Leptolepis wealdensis sp. nov

Holotype. NHMUK PV P 74947 (Fig. 5A): a left sacculith

Paratypes. NHMUK PV P 74953 (Fig. 5D), NHMUK PV P 74954 (Fig. 8D), NHMUK PV P 74955 (Fig. 9A), NHMUK PV P 74956 (Fig. 9D): left sacculiths; NHMUK PV P 74948 (Fig. 5B), NHMUK PV P 74949 (Fig. 5C, 8A, 9C), NHMUK PV P 74950 (Fig. 5E), NHMUK PV P 74951 (Fig. 8B-C), NHMUK PV P 74952 (Fig. 9B): right sacculiths

Etymology. The specific epithet ‘wealdensis’ was chosen in reference to the region where otoliths of the species were found.

Type stratum. Just below the top of the *Viviparus infracretacicus* limestone marking the top of BGS Bed 2a (Fig. 4).

Type locality. Langhurstwood Quarry, Warnham, West Sussex, UK (TQ 179352 – TQ 182354) (Figs. 3, 4).

Range and other localities. Worssam’s Bed 21 (Worssam, 1978) at Clockhouse Brickworks, Capel, Surrey, UK (TQ 176387–TQ 177387) (Figs. 3, 4); unidentified horizons at both Clockhouse Brickworks and Langhurstwood Quarry.

Diagnosis. Otoliths from an Early Cretaceous (Hauterivian) freshwater setting with narrow, straight cauda; gently curved ostium; small, distinct posterodorsal depression; smooth ventral and dorsal rims

Differential diagnosis. Differs from leptolepid otoliths from the Wealden of Germany in curved ventral margin of the sulcus and wider ventral rim. Differs from the marine, Jurassic “*Teleostus*” *similis* and *Leptolepis circularis*, which lack the outward bowing of the dorsal rim, as well as in age (Early Cretaceous) and palaeoenvironment (freshwater).

Description. In medial view (Fig. 5D, E), the ventral rim is smooth and evenly curved throughout its length. A small but distinct posterodorsal depression separates the posterior rim from the posterodorsal angle. The dorsal rim is initially straight before curving dorsally to the anterodorsal angle. There is a shallow dorsal depression. The cauda is dorsoventrally narrow and anteroposteriorly straight, in comparison to other Wealden Supergroup leptolepid otoliths, while the ostium widens and curves towards the ventral rim before terminating at the rostrum. The rostrum is gently pointed and the antirostrum and excisura are absent. In lateral view, the otolith bears regularly spaced striations that run radially from the ventral rim and terminate approximately level with the ventral edge of the sulcus. Small specimens, presumably representing juveniles, have more rounded profiles and less clearly defined sulci than the largest specimens, which presumably represent old individuals. The majority are from an intermediate stage of development and show greater angularity in their profiles and more sharply defined sulci than the putative juveniles. In a few specimens, the posterior end of the crista curves very gently towards the ventral rim. Specimens are typically 2 mm in length as measured from the posterior rim to the anterior tip of the rostrum and 1.5 mm in height as measured from the anterodorsal angle to the ventral rim. The observed length range was 1.34 – 2.87 mm.

Species *Leptolepis toyei* sp. nov

Holotype. NHMUK PV P 74957, an isolated left sacculith (Fig. 5F)

Etymology. The specific epithet ‘toyei’ in honour of Mr Geoff Toye, the first to discover English Wealden otoliths, and in recognition of his outstanding contribution to Wealden Supergroup palaeontology (Austen, 2012).

Type stratum. Just below the top of the *Viviparus infracretacicus* limestone marking the top of BGS Bed 2a (Fig. 4).

Type locality. Langhurstwood Quarry, Warnham, West Sussex, UK (TQ 179352 – TQ 182354) (Figs. 3, 4).

Diagnosis. Distinct ostial colliculum; tapered rostrum; small denticles on anterior portion of the ventral rim; ostium gently curved towards dorsal rim.

Differential diagnosis. Slight dorsal depression and strongly incised ostial colliculum are absent in “*Teleostus*” *roddenensis*; specimens from the Wealden of Germany have dorsoventrally straighter sulci and lack the denticles of the anterior ventral rim seen in this species.

Description. On the medial face, the ventral rim is slightly curved throughout its length and its anterior portion bears a series of small, regularly placed denticles. The posterior rim transitions smoothly into the dorsal rim, and the dorsal rim is straight throughout its length. There is a slight dorsal depression. The anterodorsal angle meets the dorsal edge of the ostium at a sharp angle. The cauda is wide and straight while the ostium gently curves towards the dorsal edge before terminating at a more sharply pointed rostrum. The antirostrum and excisura are absent. There is a distinct ostial colliculum. The holotype of this species is a left sacculith. It is 2.1 mm in length and 1.2 mm in height using the previous points of reference

Remarks. Decalcification of Clockhouse mudstone otoliths makes confident identification problematic. Nevertheless, these specimens are of generally of similar morphology to those of *Leptolepis wealdensis* from Langhurstwood Quarry. Those from the Clockhouse limestone and the other otolith-bearing lithologies at Langhurstwood Quarry are also attributable to *Leptolepis wealdensis*.

The family Leptolepididae, as erected by Nicholson and Lydekker (1889), has been used as a dustbin taxon to include various stem group teleosts. Revisions made by Arratia

(2013) restrict the genus to the monotypic *Leptolepis coryphaenoides* from the Middle Jurassic of France (Bronn, 1830). Basal teleostean phylogeny, however, has yet to be fully resolved. Furthermore, *Leptolepis wealdensis* bears strong similarities to the otoliths of *Leptolepis coryphaenoides*, in particular the form of the sulcus and ventral rim, and the striations of the lateral face. This suggests that the two share a close evolutionary relationship, despite the paraphyletic nature of the group. Nevertheless, they must be separated owing to their distinct ages and the marine lithofacies of the French species versus the freshwater lithofacies of the English Wealden species. Thus the classification as leptolepid *sensu* Nicholson and Lydekker has been chosen to reflect this.

6. Taphonomy

In situ otoliths from Langhurstwood Quarry were collected from thinly bedded, fine-grained, calcareous grey sandstone rich in *Viviparus infracretacicus* from just below top of BGS Bed 2a (Fig. 4). Some ex situ lithological specimens show different lithologies: pale grey limestone bearing procerithiid gastropods, *Mantelliana* sp and *Cypridea aculeata*; and shelly yellow limestones and grey mudstones with *Viviparus infracretacicus*. All three lithologies contain fish bones, teeth and scales. Otoliths were recorded by Toye et al. (2005) in ex situ fragments collected above the level of BGS Bed 2a, suggesting that they come from an overlying bed. We tentatively identify the source horizon for the otoliths as a thin limestone bed with *Procerithium*, lying 10.5 m above the base of the exposed succession. Our evidence is that this gastropod occurs in the matrix associated with some of the ex situ otoliths that we describe here. Mudstones with *Viviparus infracretacicus* occur at all levels and so the mudstone-hosted otoliths could be derived from any of these.

The Langhurstwood Quarry otoliths have a relatively uniform colouration, ranging from brown to beige, and they are composed of calcite, presumably from diagenetic alteration

of the original aragonite. Some have a thin coating of black phosphate (Fig. 8A). Most have been mildly abraded as a result of wave and/or current action. One specimen (Fig. 9B) has a pale colouration and the central body has been decalcified; it is anomalous compared to the other otoliths from this locality.

In situ otoliths from Clockhouse Brickworks are preserved in shaly mudstone collected from Worssam's (1978) Bed 21, which outcrops in the floor of the quarry (Fig. 4). This bed contains fish debris, *Mantelliana* sp. and *Cypridea aculeata*. The otoliths are pale and have been partly decalcified and flattened into thin, densely packed clusters on the bedding planes (Fig. 8B–C). A number of ex situ specimens from Clockhouse Brickworks come from thinly bedded, fine grained, grey, shelly limestone horizons with ostracod valves and occasional fish remains. These also have a pale colouration but without the compression or dense packing seen in the mudstone (Fig. 8D). Overall, the matrix lithology and morphology of these otoliths is very similar to the Langhurstwood specimens.

Individual sedimentary horizons with otoliths may contain thousands of otoliths, so representing accumulations from thousands of source fishes. Otoliths are not shed during life and so large otolith concentrations could indicate the mass death of fishes, often of a single species. However, fish bones in the mudstone are far less abundant than the otoliths, making it unlikely that the bed records mass mortality events. Instead the concentrations could be either sedimentological by a process of winnowing, or alimentary by a process of ingestion and expulsion by the predator. Most researchers (Nolf, 1985, 1995) have favoured the latter explanation because of the near absence of other bony elements of the source fish and because of the evidence from modern fish-eating predators in the oceans. Predatory fish today (Clarke et al., 1995) can dissolve all the soft tissues and bones of their prey, leaving nothing but the otoliths. Why aragonitic otoliths can survive and accumulate in the acidic environment of the gut is still unclear. Current evidence, however, simply shows that pH

variation due to taxonomy, metabolism and ecology facilitate otolith survival and accumulation in a wide range of species (Jobling and Breiby, 1986). In a further dramatic example, Fitch and Brownell (1968) found more than 18,000 otoliths in the guts of 17 whales, evidence of massive concentration by ingestion. In palaeontological examples, otoliths are known from coprolites, demonstrating that they can survive passage through the alimentary canal (Martini, 1965). A coprocoenotic explanation has been proposed for large accumulations of otoliths relative to bones and teeth at the boundary between the Jason and Coronatum Zones of the Lower Oxford Clay at Peterborough (Martill, 1985) and in sieved clay samples from Eocene localities of England (Stinton, 1975–1985). As outlined above, fish bones are generally rare components among English Wealden otolith accumulations. Here we propose that the sacculiths accumulated within the digestive tract of predators largely unharmed by gastric acids before their mass egestion (Nolf, 1985) as coprocoenotic accumulations *sensu* Mellett (1974). Likewise, the utriculiths and lagenaliths may also have been concentrated, but we did not identify any, which is to be expected since they are typically much smaller than sacculiths and morphologically nondescript.

The mudstone-hosted otoliths from Clockhouse Brickworks accumulated in calm conditions, as indicated by the composition of the matrix. Their rugose surface texture and the hollowing of the central body are comparable to post-depositionally decalcified otoliths from sands and clays reported from other localities (Nolf, 1985, 1995). Post-depositional decalcification therefore explains why the otoliths were not destroyed prior to burial and provides a mechanism for their compaction into thin, fragile concentrates.

In the mudstone-hosted specimens from Langhurstwood Quarry, otolith abundance is lower and specimens are less clustered than at Clockhouse, but their concentration is still considered to represent a coprocoenosis. As well as being less numerous, they are less decalcified and have a colouration and state of preservation more comparable to other

specimens from Langhurstwood, indicating differing depositional and diagenetic conditions between the two mudstones.

In the sandstone-hosted samples from Langhurstwood Quarry, bones are more frequent and the otoliths, while numerous, are less clustered, with typically between one and ten specimens in a hand-sized sample of Langhurstwood sandstone compared to the several tens of specimens in even a small piece of Clockhouse mudstone (Fig. 8C). The greater degree of abrasion seen in the otoliths and the coarser matrix grain size indicate deposition under higher energy conditions. The otolith and shell debris may therefore represent lag deposits formed under wave and storm influence in the shallow lagoonal environment. Viviparid shell beds formed by wave and storm winnowing are known throughout the Wealden succession (Radley, 2009). One might expect a greater taxonomic diversity if the beds were strongly time averaged. The fluctuating salinities indicated by the abundant *Viviparus infracretacicus* (Radley and Allen 2012), however, may have favoured the development of the monospecific invertebrate fauna seen in the sandstone. Similar monospecific assemblages of viviparid gastropods in storm-influenced lagoons are known from the Berriasian–Valanginian Jydegård Formation of Denmark (Noe-Nygaard et al., 1987). As the vertebrate remains are primarily fragmentary, a greater diversity of fish species may nevertheless be represented despite not being identifiable.

The grey limestone-hosted specimens from Clockhouse Brickworks are similar in their lithology to the Langhurstwood specimens and so may also have formed as lag deposits. This interpretation is uncertain, however, as the specimens are unstratified and may have come from fluvially dominated lithofacies rather than the more basal lagoonal lithofacies.

The yellow, *Viviparus infracretacicus* limestone-hosted otoliths from Langhurstwood are strongly abraded. Shelly limestones within the Langhurstwood succession were generated by phases of weak wave and/or current winnowing (Radley and Allen, 2012) and so the

presence of otoliths and teeth in this lithology could also be attributed to processes of transport concentrating and abrading biogenic fragments.

The specimens in grey, ostracodal limestone from Langhurstwood Quarry display frequent stacking and nesting of valves (Fig. 10). These resemble a coquina resulting from reworking during storm events (Fürsich and Kirkland, 1986; Wakefield, 1995), during which otoliths and bone fragments may also have settled. The procerithiid gastropods in the specimens indicate salinity excursions into the mesohaline and brachyhaline range (Radley and Allen, 2012). Thus a storm origin is fitting, providing a mechanism for the formation of shell debris and the rise in salinity by inundation of the lagoonal environment with seawater. High concentrations of otoliths within shell beds in the Lower Oxford Clay at Peterborough have also been partly attributed to storm activity, as well as coprocoenotic accumulation (Martill, 1985).

7. Ecology and Ontogeny

Ecological and ontogenetic interpretations are restricted to *Leptolepis wealdensis* as only a single specimen representing *Leptolepis toyei* is currently available. All studied specimens are from the Langhurstwood calcareous sandstone, collected in situ from the horizon just below the top of BGS Bed 2a (Fig. 4). This approach was adopted to select an instant in time and a single biotic and physical environment of accumulation of otoliths. Thus the sample is an accurate representation of sacculith morphology for *Leptolepis wealdensis* at this instant.

Sample measurements of otolith length using the same previous points of reference show a normal distribution. This combines aspects of normal trait distribution within a population structure with biasing effects resulting from the mode of otolith accumulation and preservation. Assuming linear circumferential otolith growth in *Leptolepis wealdensis*, as

seen in extant species (Hobbs et al., 2007), the most common size class of otoliths (1.81 to 2.20 mm) are from sub-adults. The low number of large otoliths is likely a reflection of the lower abundance of large individuals relating to the decrease in probability of survival with age in natural populations. The low frequency of otoliths from hatchlings and fry, and the greater proportion of those from sub-adults, is harder to relate to natural population structure and so may arise from bias. These could be biological, for example the well-known impact of juvenile mortality on populations (Sogard, 1997), or sampling as a result of predation, or sedimentological by the winnowing processes that acted during deposition of the sandstone. Certainly it is likely we missed tiny specimens when picking over the sandstone samples. Currently, however, there is not enough data to distinguish which of these biases prevailed.

The mode of accumulation shown by the otoliths indicates that English Wealden leptolepids occupied an intermediate position in their food web. Emplacement of the accumulations alongside *Cypridea aculeata* and *Viviparus infracretacicus* indicates freshwater to oligohaline salinity tolerances for English Wealden leptolepids. Stratigraphic megacyclicity in the Weald sub-basin resulted from rapid uplift of the Cornubian and American massifs, producing an arenaceous phase from enhanced stream flow, then erosion and down-faulting of the massifs, producing an argillaceous phase in freshwater to brackish lakes, lagoons and mudswamps (Radley and Allen, 2012). The identified otolith-bearing horizons at Langhurstwood Quarry and Clockhouse Brickworks both come from the argillaceous phase at the end of megacycle I. The mass mortality assemblages from Smokejacks Brickworks were localised to a bed yielding fish and insect remains, and the primitive plant *Belhavstia pebja* (Austen, 2007). This corresponds to the argillaceous mudstones below the level of the Alfold Sand, BGS Bed 5c (Radley and Allen, 2012), which marks the beginning of megacycle III. Thus the mass mortality assemblages come from the argillaceous phase at the end of megacycle II. Given the depositional setting for the end of

the Wealden megacycles and the available fossil evidence, English Wealden leptolepids occupied freshwater to oligohaline lagoons and lakes close to the coast. This provides an indication for where English Wealden leptolepid otoliths may be located in the future.

Under a linear growth model, otolith size is an accurate reflection of the age of the individual to which it belonged. The otoliths of juveniles typically have more rounded profiles and less clearly defined sulci than adults, while in older individuals ornamentation becomes smoother (Nolf, 1985). These differences can be seen between the smallest and largest otoliths in our collection, allowing the reconstruction of an ontogenetic sequence (Fig. 10), which shows a simple increase in size with a corresponding enhancement of the features of the medial face and subsequent smoothing during senescence.

Otoliths grow by the circumferential deposition of aragonite in a proteinaceous matrix to form concentric rings (Gauldie and Nelson, 1990). Ring deposition can record daily growth and larger scale banding can represent longer periodic growth (Pannella, 1971). Concentric banding on a 100 μm scale was observable on the lateral faces of a small number of the Langhurstwood sandstone otoliths (NHMUK PV P 74958, NHMUK PV P 74959; Fig. 11). Scanning electron microscopy revealed smaller intercalated bands on a 10 μm scale. These two size classes could therefore correspond to diurnal and longer periodic banding. Sectioned specimens showed dark blotches with elevated iron, manganese and magnesium (Fig. 12) and no internal preservation of growth rings. The specimens have recrystallized and so are highly unlikely to yield any additional ontogenetic data on a microstructural scale. Incremental growth lines in unionid bivalves from the Wealden Supergroup are often best preserved on external surfaces after recrystallisation of aragonite (Allen, 1998), a situation reflected by the otoliths. Why the growth rings are apparent is unclear. Frequent pyrite crystals within the calcareous sandstone are a potential indicator of acidic conditions in the sediment during deposition, offering the possibility that they were syndepositionally etched.

8. Conclusions

Otoliths collected from Langhurstwood Quarry and Clockhouse Brickworks show a greater diversity of English Wealden leptolepids than previously documented and provide materials for the erection of two new species, *Leptolepis toyei* and *Leptolepis wealdensis*. One of these may prove to be a junior synonym of *Leptolepis brodiei* pending future finds. *Leptolepis wealdensis* occupied an intermediate ecological position within early Cretaceous non-marine food webs, within freshwater to oligohaline lakes and lagoons. The good preservation of its otoliths allows the reconstruction of ontogeny. The trajectory shows a simple increase in size, along with enhancement and then smoothing of the sulcus. Otolith growth is assumed to be linear for *Leptolepis wealdensis* as there is no evidence to the contrary, and linear otolith growth is also common in many recent fish species. The presence of growth rings further highlights the excellent degree of preservation observable in some Wealden microvertebrate fossils and points to the possibility of extracting further ontogenetic data not just from the other known fossils of Wealden leptolepids, but also from species in other clades. Given the span of time represented by the Wealden Supergroup, further species of freshwater teleost may be found in its microvertebrate assemblages, which would give a still wider view of the diversity and ecology of early Cretaceous freshwater teleosts.

9. Acknowledgements

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Fig. 1. The teleost vestibular system. A. brain; B. membranous labyrinth of the inner ear; C. semicircular canals; D. utricle; E. utriculith; F. sacculus; G. lagenalith; H. lagena; I. sacculith. After Duffin (2007).

Fig. 2. General features of a teleost sacculith. A. rostrum; B. ventral rim; C. posterior rim; D. sulcus; E. ostium; F. cauda; G. ostial colliculum; H. anterodorsal angle; I. dorsal rim; J. dorsal depression; K. posterodorsal angle; L. posterodorsal depression.

Fig. 3. Geological map of the area north of Horsham, showing the locations of Clockhouse Brickworks (1), the now worked-out Warnham Brickworks (2) and the more recent Langhurstwood Quarry (3). Pits are shown as red hatched areas. © Crown Copyright and Database Right, 2015. Ordnance Survey (Digimap Licence).

Fig. 4. The relative stratigraphic positions of the exposures at Clockhouse and Warnham Brickworks. The Warnham Brickworks section is taken from the older worked-out pit 750 m west of Langhurstwood Quarry, although the lithology is similar in both pits. A. otolith-bearing horizon at Clockhouse Brickworks; B. otolith-bearing horizon corresponding to the succession at Warnham Brickworks. After Gallois and Worssam (1993).

Fig. 5. A. Medial face of a left sacculith of *Leptolepis wealdensis* (NHMUK PV P 74947); B, C. medial faces of right sacculiths of *Leptolepis wealdensis* (NHMUK PV P 74948, NHMUK PV P 74949); D, E. lateral faces of left and right sacculiths respectively of *Leptolepis wealdensis*, showing striations of the ventral edge (NHMUK PV P 74953, NHMUK PV P 74950); F. medial face of the left sacculith of *Leptolepis toyei* (NHMUK PV P 74957). All specimens are from Langhurstwood Quarry. Scale bar represents 1 mm.

Fig. 6. Comparison of saccular otoliths, all figured in medial view, aside from G where the lateral view is also shown. A. *Leptolepis toyei*; B. “*Teleostus*” *roddenensis*; C, D. German Wealden leptolepids similar to *Leptolepis toyei*; E. *Leptolepis wealdensis*; F. *Leptolepis circularis*; G. “*Teleostus*” *similis*; H. German Wealden leptolepid similar to *Leptolepis*

wealdensis. Dashed lines indicate inferred portions of specimens. The scale bar is 1 mm, but is not applicable to the German specimens as scale information was unavailable. After Martin and Weiler (1954) and Nolf (2013).

Fig. 7. Syntype of *Leptolepis brodiei* from the Lower Purbeck of Dinton, Wiltshire (Brodie Collection, NHMUK PV P7635). A. Whole specimen in left lateral view; B. skull in left lateral view. Note the displaced frontal bone just dorsal to the posterodorsal corner of the orbit, which bears a similarity to a sacculith. The scale bars are 5 mm.

Fig. 8. A. well preserved right sacculith with a phosphate coating in medial view, collected in situ from the calcareous sandstone bed at Langhurstwood Quarry (NHMUK PV P 74949); B. well preserved, decalcified right sacculith in medial view, collected in situ from the mudstone at Clockhouse Brickworks (NHMUK PV P 74951); C. coprocoenotic cluster of decalcified left and right sacculiths in medial and lateral views, collected in situ from the mudstone at Clockhouse Brickworks (NHMK PV P 74951); D. a worn left sacculith in medial view, collected ex situ from the grey shelly limestone at Clockhouse Brickworks (NHMUK PV P 74954). All specimens are from *Leptolepis wealdensis*. Scale bars represent 1 mm.

Fig. 9. Ontogenetic sequence for *Leptolepis wealdensis*. A and D are left sacculiths which have been rotated for aid of comparison (NHMUK PV P 74955, NHMUK PV P 74956). B and C are right sacculiths (NHMUK PV P 74952, NHMUK PV P 74949). The dashed line shows the inferred margins in chipped specimens. Scale bar represents 1 mm.

Fig. 10. Nested ostracodal debris from Langhurstwood, here interpreted as a storm coquina (NHMUK PV P 74954). Scale bar represents 5 mm.

Fig. 11. SEM images of the growth rings preserved on the lateral faces *Leptolepis wealdensis* otoliths from Langhurstwood Quarry. A, C and D are from the same otolith (NHMUK PV P 74958) while B is a different specimen (NHMUK PV P 74959). Clockwise from top left, the scale bars represent 1 mm, 1 mm, 100 μ m and 500 μ m.

Fig. 12. Backscatter SEM image of a polished transverse section through a sacculith of *Leptolepis wealdensis*, showing dark blotches indicative of recrystallisation and no evidence for preserved growth rings. The dark blotches contain elevated levels of iron, manganese and magnesium. Scale bar represents 200 μm .

Figure 1
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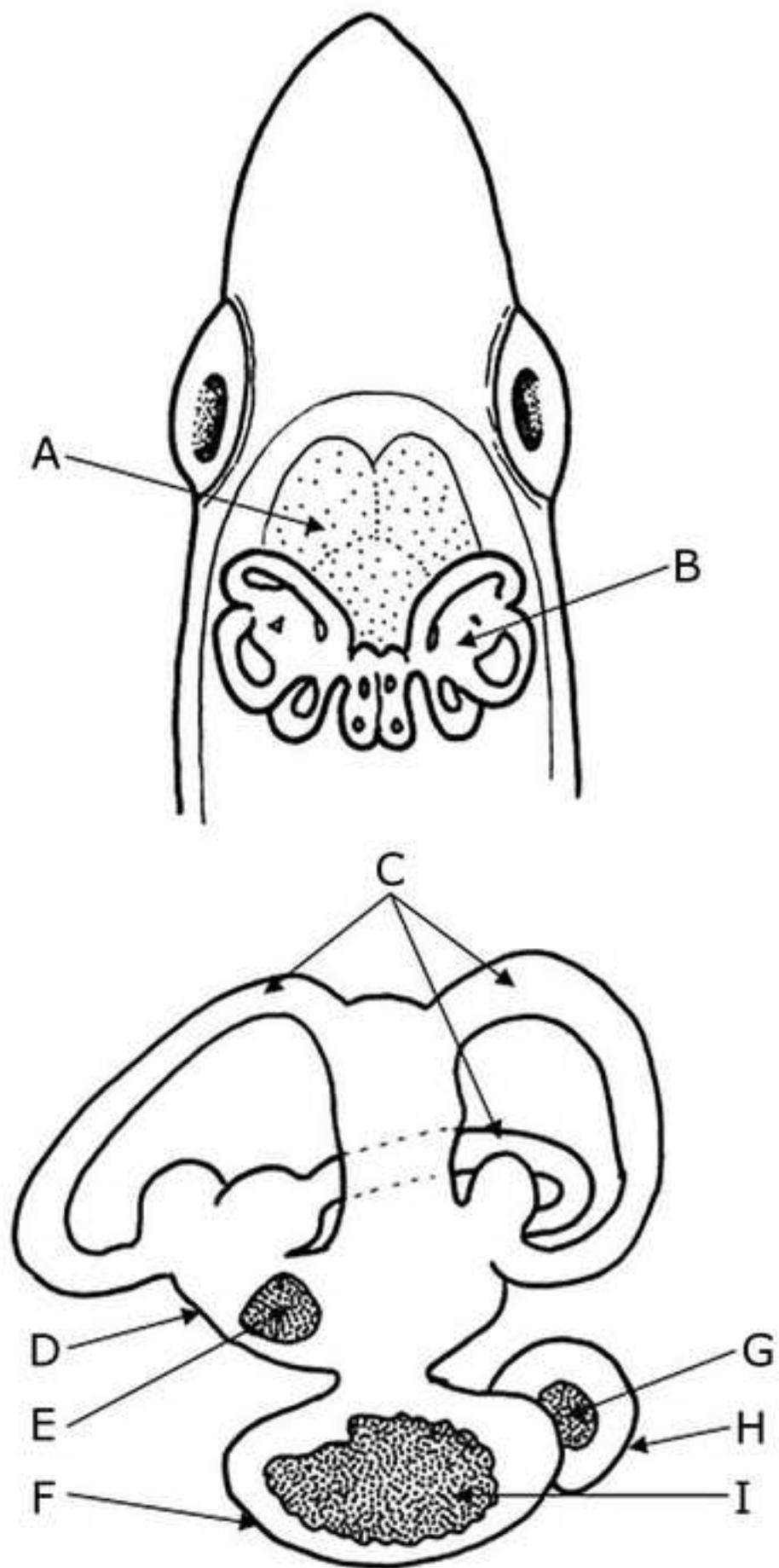


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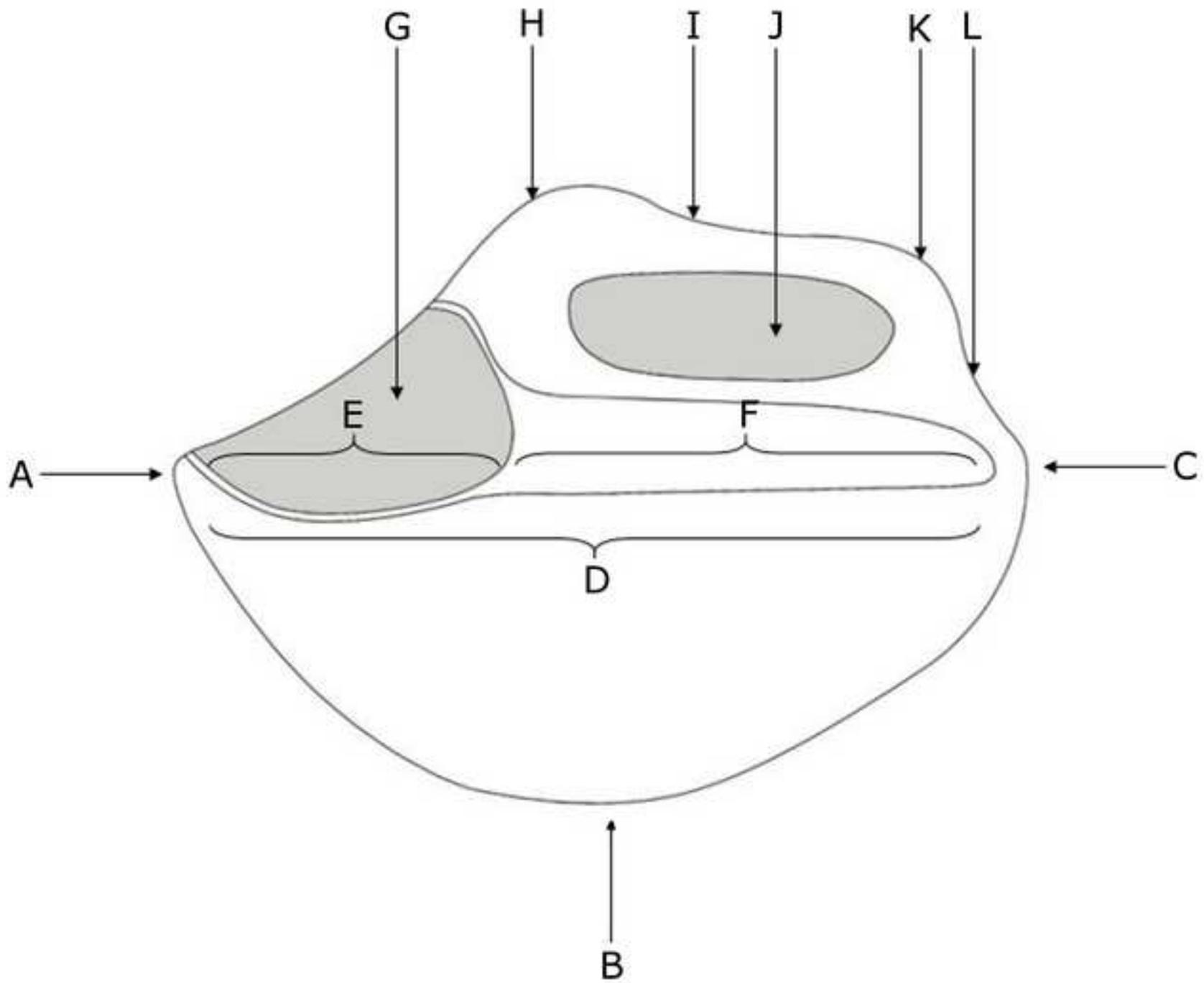


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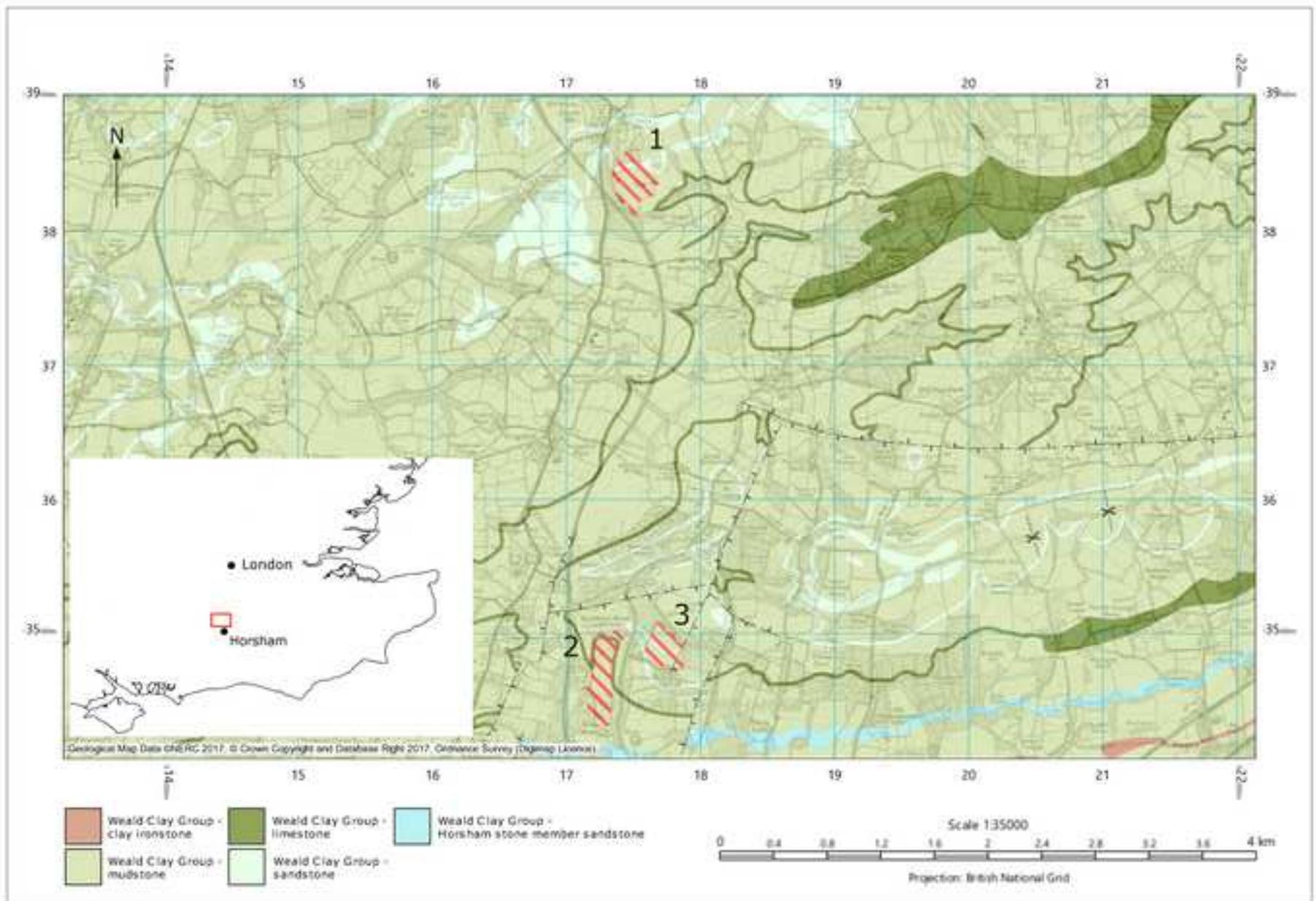


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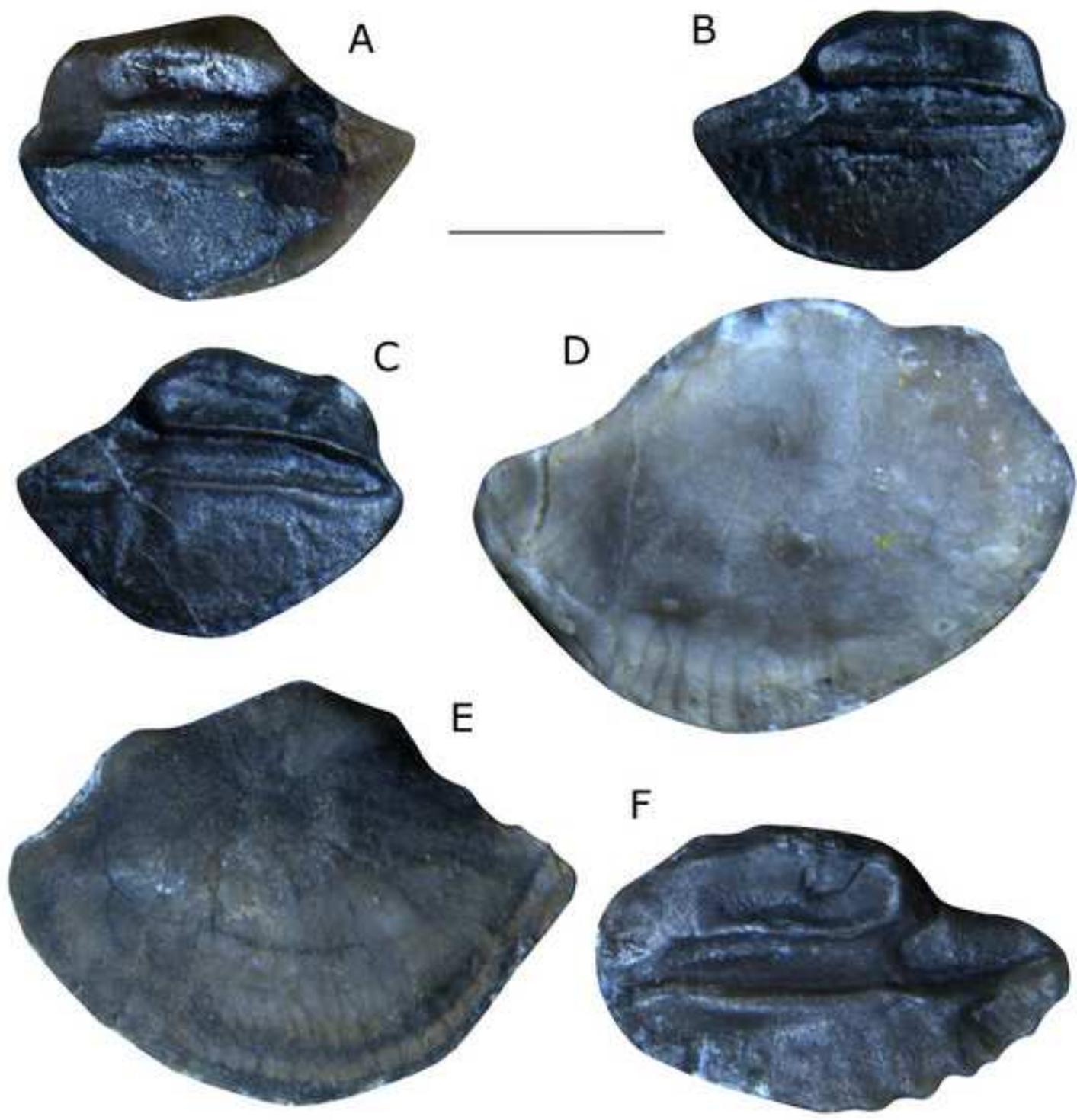


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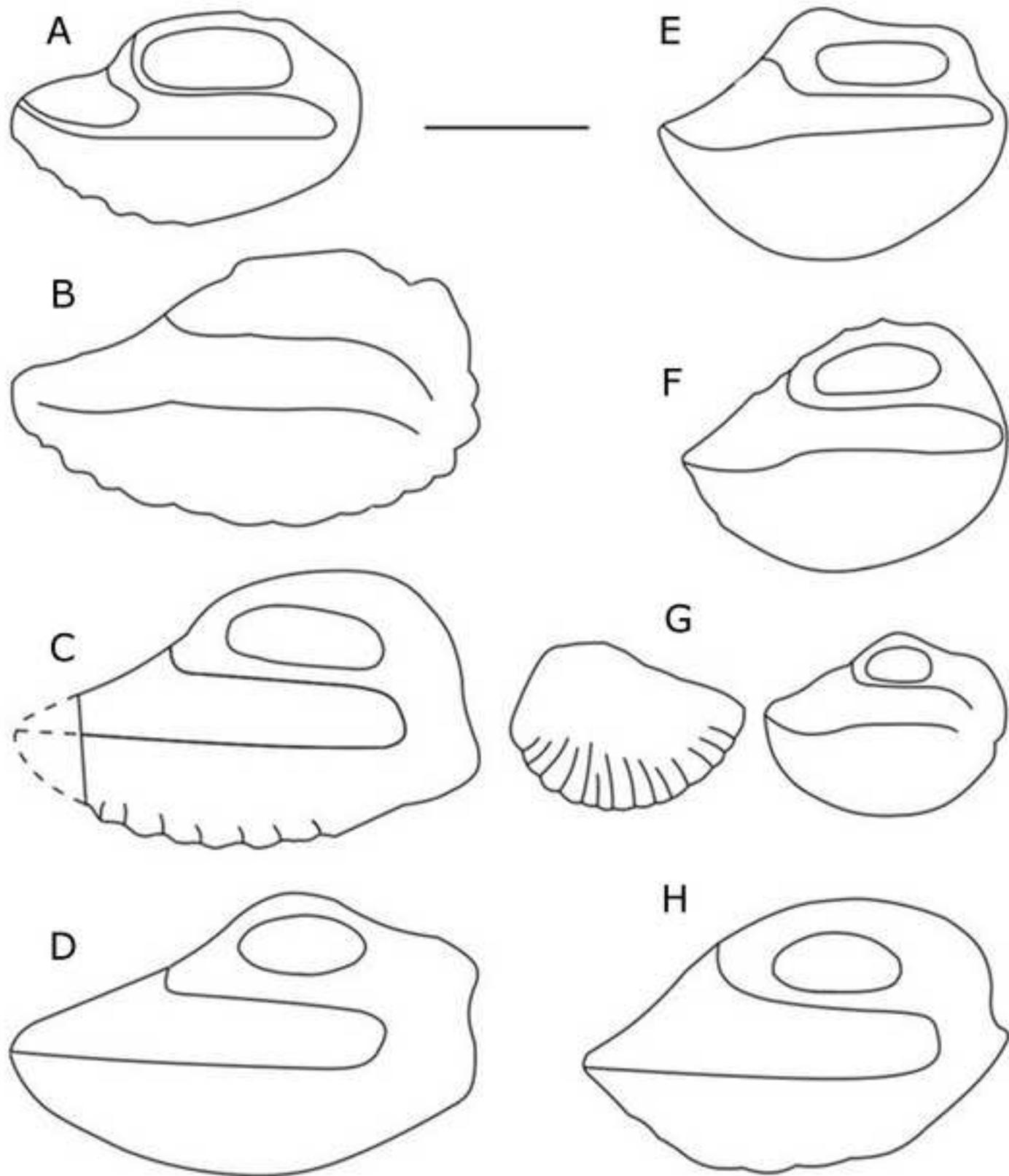


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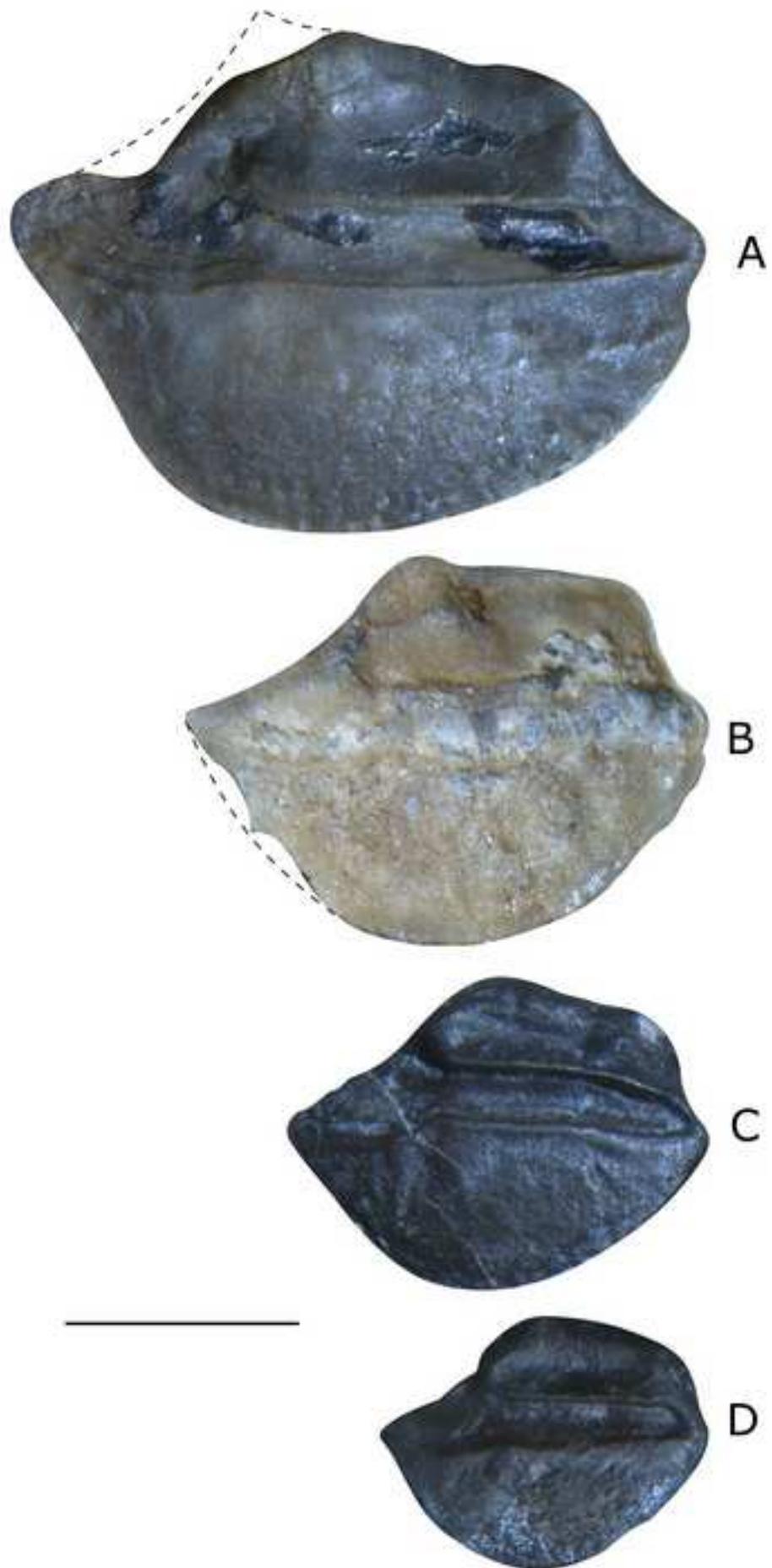


Figure 10
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Figure 11
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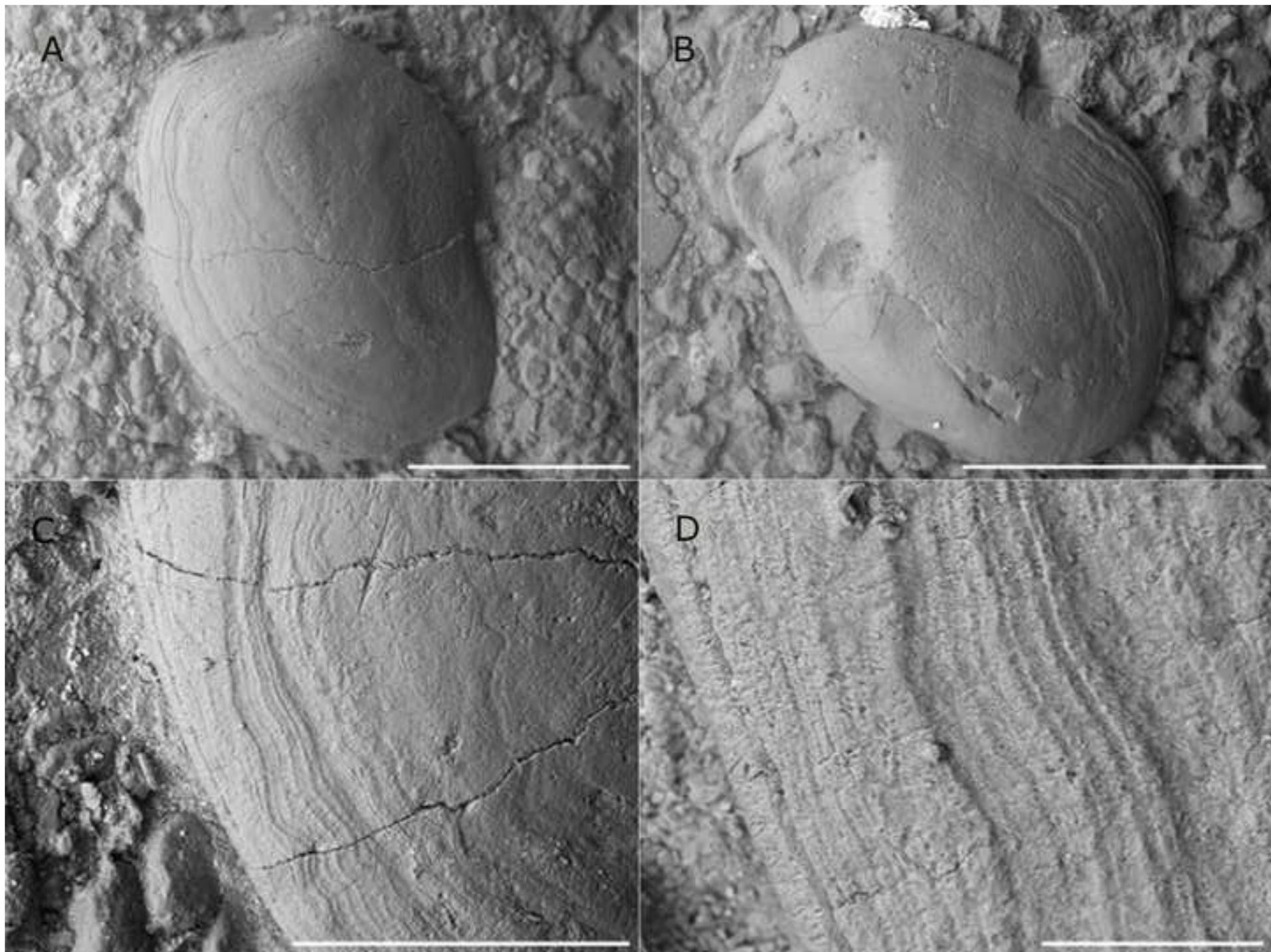


Figure 12
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