Instytut Paleobiologii Polskiej Akademii Nauk

Fish otoliths and statoliths of Mesozoic cephalopods: their phylogenetic and environmental significance

(Otolity ryb i statolity głowonogów mezozoicznych: ich znaczenie filogenetyczne i środowiskowe)

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Streszczenie

Otolity i statolity to głównie aragonitowe kamyki słuchowe rosnące wewnątrz ucha środkowego zwierzęcia. Otolity ryb doskonałokostnych (teleostów) jak i statolity głowonogów pomagają w orientacji w przestrzeni i wspomagają zmysły słuchu i równowagi podczas poruszania się. Otolity dzielą się na trzy pary znane jako kamyczki (lapilli), strzałki (sagittae) i gwiazdki (asterisci) a które razem tworzą układ otolitowy. W tym układzie, zawsze otolity jednej z trzech par są największe i najbardziej złożone morfologicznie. Najczęściej jest to strzałka lub kamyczek. Ich cechy morfologiczne są najczęściej charakterystyczne dla każdego gatunku. Otolity, tak jak i statolity kopalne, dobrze zachowują się w drobnoziarnistych osadach silikoklastycznych, takich jak iły, muły, łupki, a w niektórych przypadkach, również i w piaskach. Pierwszy artykuł jest poświęcony pierwszym znalezionym statolitom głowonogów z kredy. Wcześniej były znajdowane w dużych ilościach tylko w osadach jury, i mniej powszechnie, kenozoiku. W tym artykule opisujemy cztery kredowe statolity głowonogów: jeden z Wąwału w Polsce (walanżyn) i trzy ze Speeton Clays w Wielkiej Brytanii (apt). Porównując mezozoiczne statolity z ich współczesnymi odpowiednikami, zwłaszcza do mątewki pigmejki (*Idiosepius pygmaeus*) okazuje się, że należały one najprawdopodobniej do bazalnych dziesięciornic lub do blisko z nimi spokrewnionych belemnoidów. Drugi artykuł skupia się na wczesnokredowym (walanżyn), zespole otolitowym z Wąwału koło Tomaszowa Mazowieckiego. Najwięcej otolitów należy do albuliformów i najstarszych znanych argentiniformes. W wąwalskim zespole otolitowym znaleziono również reliktowego *Archeotolithus* (przypuszczalnie holostei), oraz elopiformes i osteoglossiformes. Większość opisanych albuliformów była znana z młodszych stanowisk w Wielkiej Brytanii. Zespół otolitowy z wczesnej kredy Polski nie tylko potwierdza, że radiacja teleostów nastąpiła wcześniej ale też pokazuje, że była procesem stopniowym. W tym samym zespole, na ponad pół tysiąca otolitów, został znaleziony tylko jeden statolit mezozoicznego głowonoga. Trzeci artykuł poświęcony jest otolitom ryb z późnego triasu. Najstarszy taki zespół pochodzi z dolnego karniku północnych Włoch, z formacji Cassian. W tym zespole, zostały znalezione cztery pary otolitów Neopterygii, dziewięć otolitów ryb całokostnych oraz zidentyfikowana para otolitów, należąca do najstarszych znanych z zapisu kopalnego teleostów. Otolity zostały znalezione razem z innymi mikroszczątkami ryb (zębami, łuskami, kolcami hybodontów i fragmentami szczęk ryby kostnoszkieletowej). Otolity Neopterygii zostały podzielone na dwa morfotypy, zaś otolity holostei na cztery morfotypy. Czwarty, ostatni artykuł poświęcony jest jurajskim zespołom statolitowo-otolitowym z Polski, Litwy, Wielkiej Brytanii i Rosji. Przez cały okres jurajski główną dominującą grupą zwierząt nektonicznych i nekto-bentonicznych są głowonogi, reprezentowane przez statolity morfotypu A sensu Clarke (2003). Zapis kopalny *Archaeotolithus* posiada lukę stratygraficzną pomiędzy środkową jurą (kelowej), a wczesną kredą (walanżyn). Na podstawie analizy różnorodności morfologicznej zidentyfikowanych otolitów ryb zauważyliśmy, że od wczesnej jury dominującą grupą teleostów były leptolepiformy, zaś od środkowej jury różnorodność teleostów się zwiększa. Od batonu pojawiają się pierwsze albuliformes(*Pteralbula jurassica*). W później jurze można zaobserwować płynne zastępowanie leptolepiformów przez albuliformes, elopiformes i osteoglossiformes. Ich otolity w iłach późnej jury występują niemalże równie często co statolity głowonogów. Na przełomie jury i kredy, jednakże doszło do ogromnej przemiany w składzie nektonu.
W podsumowaniu łączę wszystkie zebrane informacje o mezozoicznych kamykach

słuchowych i na tym tle przestawiam moje osiągnięcia uzyskane w tej rozprawie, przedstawiam zwięzłą historię ewolucyjną mezozoicznych ryb kostnoszkieletowych i głowonogów, oraz ich paleoekologię i rozprzestrzenienie w czasie.

Abstract

Otoliths and statoliths are predominantly aragonite auditory stones that grow inside the middle ear of an animal. Otoliths of teleosts fishes as well as cephalopod statoliths help with the spatial orientation, hearing and sense of balance during animal movement. Otoliths are divided into three pairs: lapilli, sagittae, and asterisci, from which they form an otolith system. In this system, one of the three pairs is always the largest, most complex and best identifiable. Most commonly those largest otoliths are sagittae or lapilli. In most cases the morphological features of the ear stones are species specific for both actinopterygians and cephalopods. Otoliths and statoliths, are best preserved in fine-grained siliclastic sediments i.e., clays, silts, and shales and in some cases also in sands. The first article in this dissertation reports on the first-known Cretaceous statoliths of cephalopods. Previously, they were known to occur abundantly in the Jurassic and less commonly in the Cenozoic. In this article we fill this gap describing four cephalopod statoliths from the Early Cretaceous: one from Wąwał, Poland (Valanginian) and three from Speeton Clays, United Kingdom (Aptian). Our comparison of the Mesozoic statoliths with their modern counterparts has shown their close similarity to the statoliths of recent pygmy cuttlefish (*Idiosepius pygmaeus*), what suggest that they most likely belonged to basal decabrachians or to belemnoids, which are closely related to them. The second article focuses on the Early Cretaceous (Valanginian) otolith assemblage from Wąwał near Tomaszów Mazowiecki. Most otoliths belong to albuliforms and the earliest argentiniforms. We found also otoliths of the youngest known *Archeotolithus* (alleged holostean), as well as elopiforms and osteoglossiforms. Most of the described albuliforms were already known from younger sites in the United Kingdom. The otolith assemblage from the Early Cretaceous of Poland confirms not only that the radiation of teleost fishes occurred earlier, but was also more gradual, and the new groups of teleosts appeared and differentiated gradually over time. In the same assemblage, only one Mesozoic cephalopod statolith was found for more than half a thousand otoliths. The third article focuses on otoliths from the Cassian Formation, lower Carnian, Upper Triassic of Northern Italy. In this assemblage we found four pairs of otoliths of neopterygian, nine otoliths of holostean fishes and an unidentified pair of teleost otoliths, which constitute the oldest known occurrence in the fossil record so far. Otoliths were associated by other microichthyoliths (i.e., hybodont teeth, scales, and spines and jaw fragments of an actinopterygian). The otoliths of neopterygians have been divided into two morphotypes, and the otoliths of holostean fishes into four morphotypes. The fourth and final article is devoted to the Jurassic statolith-otolith assemblages from Poland, Lithuania, Great Britain and Russia. The dominant group of nekton and nekto-benthos throughout the Jurassic period were cephalopods, represented by morphoptype A statoliths sensu Clarke (2003). The fossil record of *Archaeotolithus* have a gap between Middle Jurassic (Callovian) and the Early Cretaceous (Valanginian). On the basis of the morphological diversity of the identified otoliths, we found out that leptolepiforms were the dominant group of teleost in the Early Jurassic, and from the Middle Jurassic the diversity of some other teleosts started to build up. The oldest albuliforms (*Pteroalbula jurassica*) appeared in the Bathonian. In the Late Jurassic, leptolepiforms were smoothly replaced by albuliformes, elopiforms and osteoglossiforms. The fish otoliths in the Upper Jurassic clays became nearly as common as cephalopod statoliths. The turn of the Jurassic and Cretaceous brought large scale transformation in the nekton related. In the conclusions chapter, I summarized all published information on Mesozoic ear stones assemblages and merged it with the new data resulting from this dissertation showing the diversification pattern and an outline of the complex evolutionary history of teleosts and decabrachians as well some insights in their palaeoecology during the Mesozoic times.

The Supplementary Materials for Chapter I, II and IV are located on the CD attached to the printed version of this thesis.

Introduction

Ear stones are paired, mostly aragonitic structures growing inside of the animal’s inner ear. In most animals they are rather poorly developed in form of protein-augmented small grains of calcium carbonate (aragonite or vaterite) or occur as rounded granules collected in sacks, called statocysts. However, in some cases the ear stones are especially well-developed. The best examples are from nektonic animals, and they are known as statoliths in cephalopods and otoliths in fishes (Fig.1). They participate in enhanced sense of balance and hearing. Both statoliths and otoliths are formed by continuous incrustation of calcareous substance during animal’s growth, and possess growth lines, and thus can be used for age identification of host animal. Statoliths and otoliths have species specific morphology, and can be used for taxonomic identification. Additionally both statoliths and otoliths can be used for reconstructing an evolutional history of cephalopods and fishes. Since the prevailing mineralogy is aragonite, statoliths and otoliths preserve well mostly in claystones and siltstones. Both otoliths and statoliths are arranged in three pairs inside of the inner ear and each pair is usually characterized by different size. In fishes, these pairs are known as lapilli (utricular otolith), sagittae (saccular otolith), and asteriscii (lagenar otolith). In each species of fish, one of the three morphotypes is larger and more morphologically complex than the remaining two. In most cases this pair comprise sagittae (though lapilli may be the largest in ostariophysian fishes) in teleosts while, in chondrichthyans and basal actinopterygians most advanced pair of otoliths are lapilli.

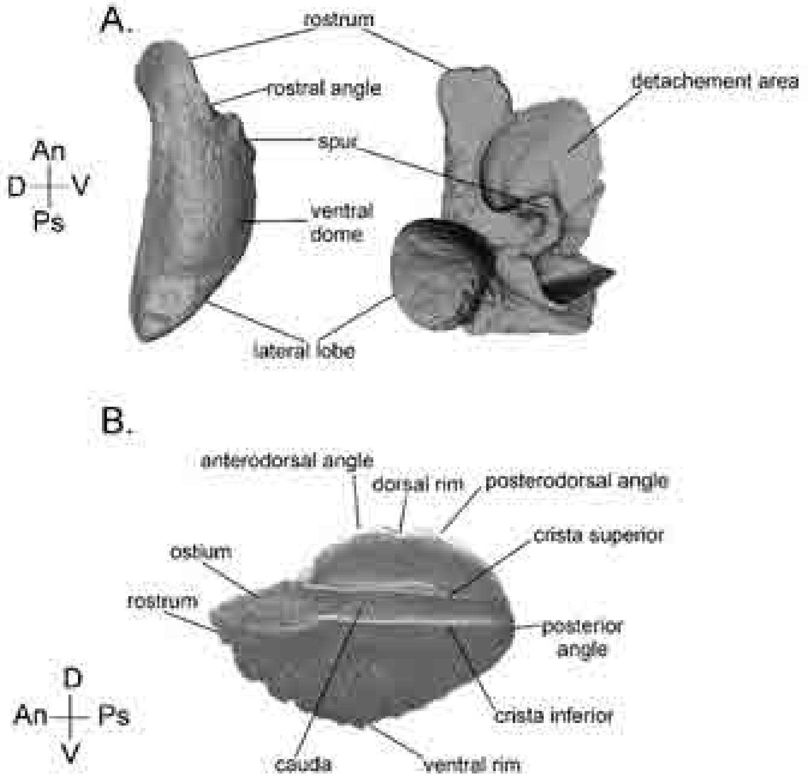

Fig. 1. Comparison of morphological features between **A**. statoliths of Cretaceous Morphotype A sensu Clarke (2003) (on the left) and *Sepia pharaonis* Ehrenberg, 1831 (on the right), and **B**. otolith of *Paleoargentina plicata* Pindakiewicz, Hryniewicz and Kaim, 2023. Abbreviations: D, dorsal, V, ventral, An, anterior, Ps, posterior. Not to scale.

The milestone works on otolith identification and taxonomy are the monographs by Nolf (1978, 2013) in which he presents detailed pictures of modern and fossil otoliths (mostly sagittae) of teleosts, neopterygians and some samples of other groups of fishes. More detailed works on lagenar and utricular otoliths of teleosts and their usefulness for species identification were published by Assis (2003, 2005). The bulk published information on otoliths and statoliths comes from Cenozoic and Recent fishes and cephalopods (Friedberg 1924, Clarke and Fitch 1979, Radwańska 1984, 1992, Schwarzhans 1986, 1994, 2004, Nolf 1991, 2013, Nolf et al. 2006, Arkhipkin 1993, 1997, Girone et al. 2006, Brzobohatý et al. 2007, 2016, 2022, Stringer 2016, Brzobohatý and Bubik 2019 Schwarzhans et al. 2020, Stringer and Hulbert Jr, 2020, Schwarzhans and Radwańska 2022), while their Mesozoic counterparts went into focus only very recently. Crucial work, that reinforced taxonomy and showed importance of Mesozoic otoliths has been published by Werner Schwarzhans in 2018. He reviewed all previously known otolith-based taxa of Jurassic–Early Cretaceous age, and added more details simultaneously showing relationships of extinct and Recent teleost families. Werner Schwarzhans became a leader expert of Mesozoic and Paleogene otoliths, and his collaboration with numerous researchers worldwide resulted in several important publications on fossil otoliths (Schwarzhans, 2004, 2010, Schwarzhans et al. 2019, 2022, Schwarzhans and Mironenko 2020, Schwarzhans and Keupp 2022).

The first account on Mesozoic statoliths came from Jurassic by Clarke (1978) who subsequently divided his material into a few morphotypes (Clarke 2003) without giving them formal names, the practice followed by the researchers until today (Clarke Hart 2019, Hart et al. 2015, 2016, Schwarzhans 2018). He noted that statoliths were much more abundant than teleost otoliths in Jurassic sediments, a statement that has been robustly supported in this dissertation (Pindakiewicz et al. in press). Mesozoic otoliths and statoliths are mostly neglected in large scale paleoecological and evolutionary research of teleosts and cephalopods (Cavin and Forey 2007, Cavin et al. 2007, Hart et al. 2013, Kröger et al. 2011).

The aim of this dissertation is to show that Mesozoic cephalopod statoliths and teleost otoliths not only can be useful for taxonomy and paleoecology (like their Cenozoic counterparts), but also they can fill the gaps in understanding of evolutionary history of both cephalopods and teleosts. The information thus provided help to understand the faunal dynamics of two major groups of nektonic and nekto-benthic animals (i.e., fishes and cephalopods) in the Mesozoic times.

Summary

My dissertation is composed of four main chapters and each of them consists of a single published (or accepted) paper.

In the first paper (Chapter I) I described first Early Cretacous statoliths and compared them to their Jurassic and modern counterparts. The statoliths in question are most similar to those of basal decabrachians today represented by idiosepiids (Pindakiewicz et al. 2022). They Cretaceous statoliths are excessively rare in comparison to very abundant Jurassic statoliths. The good illustration of this phenomenon is just a single cephalopod statolith for almost six-hundred otoliths from the Lower Cretaceous (Valanginian) deposits from Wąwał, central Poland (Pindakiewicz et al. 2022, 2023).

Second paper (Chapter II) reports the otolith assemblage from Wąwał. In this paper I described one new otolith-based genus (*Palaeoargentina* gen. nov.) and six new otolith-based species (*Pteralbula polonica* sp. nov., *Protalbula pentangularis* sp. nov., *Kokenichtys kuteki* sp. nov., *Protoelops gracilis* sp. nov., *Palaeoargentina plicata* sp. nov., *Archaeotolithus aptychoides* sp. nov.). I compared Wąwał ear stone assemblage with other otolith assemblages from the Cretaceous. I suggested that the Mesozoic teleost radiation happened earlier and it was more gradual process, than previously assumed (e.g., Cavin and Forey 2007, Cavin et al. 2007). I also illustrate a shift in the abundance of fish otoliths vs cephalopod statoliths in marine deposits with teleost otoliths being much more abundant than statoliths in the Valanginian to younger deposits in contrast to the Jurassic counterparts (Pindakiewicz et al. 2023).

In third paper (Chapter III) I reported the oldest-known Mesozoic otolith assemblage from the Cassian Fm. (early Carnian, Late Triassic age) of Dolomites Mountains (Italy). I described two morphotypes of stem-neopterygian, four of holostean and the oldest teleost otoliths (Pindakiewicz et al. 2024).

In the fourth paper (Chapter IV) I described a collection of otoliths from various Jurassic localities in Europe (Poland, Lithuania, Russia, and the United Kingdom). Based on this material I described two new otolith-based genera (*Juraelops* gen. nov., and *Vodyanoi* gen. nov.), and eight new species (*Pteralbula jurassica* sp. nov., *Protalbula dorsetensis* sp. nov., *Palealbula ventai* sp. nov., *Palealbula crenulata* sp. nov., *Juraelops prodigiosum* sp. nov., *Vodyanoi schwarzhansi* gen. et sp. nov., *Vodyanoi stringeri* gen. et sp. nov., and *Archaeotolithus solidus* sp. nov.). Simultaneously I identified and counted the cephalopod statoliths from samples collected in all investigated localities. I compared the newly described material with otolith assemblages from other Jurassic localities known already from the literature. Based on these data I concluded, that cephalopods were most common nektonic animals through most of the Jurassic, and they mostly represented by basal decabrachians, whilst teleosts were less abundant and diverse. I found out that teleosts diversification started as early as in the Middle Jurassic and accelerated in the Late Jurassic when albuliforms and elopiforms slowly replaced leptolepiforms and marine holosteans. I suggested that final turnover in abundance and diversity of cephalopod statoliths vs teleost otoliths took place between Late Jurassic (late Kimmeridgian) and Early Cretaceous (early Valanginian), and is related to gradually growing diversity of teleosts (Pindakiewicz et al. in press).

In the concluding chapter I summarise the fossil record of body fossils and ear stones of Mesozoic cephalopods and actinopterygians known from the literature and from my own data. This summary clearly shows that otolith fossil record fills the gaps and refines stratigraphic ranges of different teleost groups. I also revealed that during Mesozoic, there were three major changes in nektonic communities. I suggested three main otolith-based assemblages, that dominated nektonic and nekton-benthic environments. This dissertation shows that describing new otolith and statolith assemblages increases knowledge on evolution an ecology of these two major nektonic groups of animals.

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Chapter I

First Cretaceous cephalopod statoliths fill the gap between Jurassic and Cenozoic forms.

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ABSTRACT— We report the first cephalopod statoliths from the Early Cretaceous. These unique microfossils fill the gap in the fossil record between Jurassic and Cenozoic forms, and are more similar to the former. We compare the morphology of the Mesozoic forms with the statoliths from Recent and Cenozoic decabrachians. This comparison shows the closest resemblance to the Recent Idiosepiidae. We suggest that Mesozoic cephalopod statoliths belong to the basal decabrachians and they are related to the idiosepiids. The belemnitid identity of these forms can be neither confirmed nor rejected though some positive correlation in the investigated materials between findings of belemnitid rostra and statoliths. These finds support also some previous suggestions that decabrachians and vampyropods Statolith, diverged earlier than in the Early Jurassic. We discuss the absence of the wing in the Mesozoic statoliths and suggest that the robustly developed spur could play a similar role to the wing in Cenozoic and Recent decabrachian statoliths. We suggest that the statolith morphology might be a useful tool to interpret cephalopod evolution. We also note an evident shift in the abundance ratio of statoliths vs fish otoliths, the former being dominant in the Jurassic while declining in abundance in the Cretaceous. This supports a Cretaceous turnover in several groups of marine organisms.

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INTRODUCTION

Statoliths are paired, mostly calcareous earstones of variable sizes and morphologies but of broadly similar function, which are located within braincase cavities or statocysts of cephalopods. Similar structures are known from several other groups of metazoans (Budelmann 1992). In most groups, statoliths are minute, rounded “stones” inside the organs covered by gelatinous membrane, called statoconia, but in cephalopods (particularly in decabrachians, and octopods), the statoliths are more complicated structures, reminiscent of otoliths in teleosts (Hamlyn-Harris 1903). Main functions of the statoliths are the detection of pressure and host animal movement changes in three-dimensional environment (Arkhipkin & Bizikov 2000). Statoliths are tiny, fragile and mostly aragonitic structures, therefore they easily dissolve in weak acids (Kear *et al.* 1995). Most likely, this is the reason for their rarity in the fossil record in contrast to the other hard elements of cephalopods (Hart *et al.* 2016).

Fossil statoliths of cephalopods are known so far from the Hettangian, Lower Jurassic (Clarke 2003), Callovian, Middle Jurassic (Clarke *et al.* 1980b; Hart 2019; Hart *et al.* 2013, 2016), lower Eocene (Neige *et al.* 2016), and Pleistocene (Clarke & Fitch 1979). The morphology of the Cenozoic statoliths is relatively similar to their counterparts among Recent cephalopods, allowing direct comparisons to squids in North America (Clarke & Fitch 1979). On the other hand, the Mesozoic statoliths display a morphology that differs considerably from the ones in Recent cephalopods and therefore their phylogenetic position among cephalopods remains unclear (Hart 2019). A meaningful taxonomy of such statoliths is also challenging because of the significant stratigraphic gap between the Lower/Middle Jurassic and Cenozoic statolith occurrences (cf. Clarke 2003; Neige *et al.* 2016; Hart 2019). Despite various efforts, statoliths of Cretaceous cephalopods have not been found and identified so far (Clarke & Maddock 1988b; Clarke 2003; Hart 2019).

In this contribution, we present the first description of cephalopod statoliths from the Lower Cretaceous of Poland and Great Britain. We also compare their morphology to other statoliths, both fossil and Recent – in particular the little known statoliths of pygmy squids (Idiosepiidae). Finally, we discuss the significance of fossil statoliths for the phylogeny and evolution of cephalopods.

HISTORICAL BACKGROUND

Fossil statoliths of cephalopods for many years were misidentified as otoliths of teleosts (Frost 1926; Martin & Weiler 1954; Rundle 1967) or neglected (Hart *et al.* 2013), mostly because there was not much information about statoliths to begin with (Hamlyn-Harris 1903). Later, research on cephalopod statoliths focused mostly on growth patterns (Lipiński 1980, 1986, 2001 and Jackson 1993, 1995). More information on biological and geological aspects of cephalopod statoliths came from Clarke (1966, 2003; Clarke & Fitch 1975, 1979; Clarke *et al.* 1980a, b; Clarke & Maddock 1988a, b), and Arkhipkin (1997, 2003, 2005; Arkhipkin *et al.* 1988; Arkhipkin & Bizikov 2000). Later, the information and terminology used for Recent statoliths was adapted for description of the Mesozoic statoliths from the Jurassic of Great Britain (Clarke 2003). Most recently Hart *et al.* (2013, 2016; Hart 2019) described statoliths from the Callovian (Middle Jurassic) Christian Malford Formation and discussed the possible relationships of the Jurassic statoliths to the Mesozoic cephalopods (Hart *et al.* 2013; Hart 2019). Based on co-occurrence of the statoliths and hooks, Hart *et al.* (2016) suggested a relationship of Jurassic statoliths to the belemnitids. There are examples of poorly preserved statoliths *in situ* within belemnitid (Klug *et al.* 2016) and belemnoteuthid body fossils (Wilby *et al.* 2004), but their morphology is too diagenetically altered to allow meaningful comparisons with other known Jurassic statoliths

GEOLOGICAL SETTINGS

The Cretaceous statoliths reported in this study were recovered by wet sieving (mesh size 0.375 mm) of clay/silt bulk samples collected at two localities outcropping from the Lower Cretaceous siliciclastic formations: Wąwał in central Poland and Speeton in Yorkshire, northeast England.

The locality at Wąwał is an abandoned claypit, located near the village of Wąwał approximately 2 km east of Tomaszów Mazowiecki in central Poland. At the time of quarrying it exposed a section of Valanginian siliclastics (e.g. Kaim 2001). The lowest levels of the succession cropping out at Wąwał are clays with embedded calcareous pebbles, followed by clayish sand, siltstones and claystones, and finally sandy siltstones and limestone concretions. Samples were taken from the middle and upper parts of the succession, mostly from clays and silts with phosphate nodules (Kaim 2001). The statolith described in this paper comes from a sample F3 of Kaim (2001, 2002) belonging to the upper part of the *Saynoceras verrucosum* Zone in the Tethyan zonation scheme (or the *Dichotomites* Zone in the Boreal scheme) based on the ammonite stratigraphy of Kutek *et al.* (1989). The locality is recultivated and flooded now and inaccessible to further sampling.

A section of the Speeton Clays Formation is exposed at the sea coast of Yorkshire (north-east England) near the village of Speeton in the cliffs of the southeast part of Reighton Sands Beach. It exposes a succession of AptianAlbian siliclastic sediments (Mitchell & Underwood 1999), starting with black marls and sandy clays with concretions, followed by black clays with phosphate nodules, and terminates with pale marls (Underwood 2004). Samples were collected in front of the *SS Laura* wreck resting site, from calcareous black shales, under the phosphate zone and marls, most likely belonging to the Aptian. The stratigraphy of the section is based on belemnites and ammonites (Lamplugh 1896, 1924; Ennis 1937), but it is generally difficult to follow in the cliff due to intermingled landslides in this area.

MATERIAL AND METHODS

The wet sieving of collected samples resulted in five statoliths: one from the Wąwał (out of 52 samples approx. 2.5 kg each), and four from Speeton (out of ten samples approx. 5 kg each). Specimens were first photographed under scanning microscopy at the Laboratory of SEM Microphotography in the Institute of Paleobiology PAS. The Wąwał statolith (Appendix 1) and another statolith specimen (Appendix 2) from the Jurassic locality of Gnaszyn in Central Poland (see e.g. Gedl *et al.* 2012) were scanned in a micro-CT scanner at the Laboratory of Microtomography, Institute of Paleobiology PAS. For comparisons we also studied statoliths of Recent decabrachians; *Idiosepius pygmaeus* Steenstrup, 1881 (Appendix 3) from the Sea of Japan and *Sepia pharaonis* Ehrenberg, 1831, from the northern Indian Ocean (Appendix 4). Both Recent specimens were conserved in alcohol and scanned in the micro-CT scanner in the wet state.

SYSTEMATIC PALAEONTOLOGY

Wąwał statolith

(Fig. 2; Appendix 1)

MATERIAL. — Single (ZPAL B.II/1) well preserved specimen from the Valanginian, Lower Cretaceous of Wąwał, central Poland. Its surface is brown and shiny and similar in this respect to otoliths from the same locality.

DESCRIPTION

The general shape is close to minor arc in right lateral view. Lateral lobe is slightly wider on one end than the rostrum on the other end. Rostrum is triangular, flattened on two sides with anterior part narrow, acute on its edge. The surfaces of rostrum are inclined to the rest of statolith with rostral angle of approximately 140°. Lateral lobe triangular, pointed posteriorly, edges blunt. Clearly delimited from lateral dome on the right side with well-developed subjugation. On the left side, the lateral lobe passes continuously into flat left side of the statolith's mid part. Lateral dome located on the right side merged with ventral dome, delimited only by weakly expressed border line. Ventral margin, narrow, acute and uninterrupted from rostrum to lateral lobe. The lateral dome is moderately convex and passes continuously into ventral dome. The edge of ventral dome (ventral margin) is narrow and acute. The anterior part of ventral margin is equipped with well-developed bilobate spur which overhangs slightly to the left. Posterior lobe is wider and blunter while the anterior lobe is smaller and knob-like. The ventral edge of the spur is narrow and acute. The left side of the statolith is moderately convex and bears no recognizable features.

REMARKS

The statolith described above is the only one found in the locality of Wąwał in spite of an extensive collecting effort (Kaim 2001). Morphology of the left side of the statolith resembles the Jurassic morphotype A of Clarke & Fitch (1975), while the right side of the statolith displays unique characteristics unknown from any other statoliths to date. The lateral lobe bears no subsidiary lobes and it is small in comparison to all the other morphotypes of Mesozoic statoliths known to date. The subjugation described in Wąwał statolith occurs also in the specimens of the Jurassic morphotype A of Clarke & Fitch (1975), and it is interpreted as a feature of subadult specimens (Clarke 1978). The morphology of the spur is well developed and more complex than in other statoliths. Row of furrows on the right side of the rostrum is probably of taphonomic origin. The morphology of the posterior part of the Wąwał statolith is similar to subadult specimens of the Jurassic morphotype A of Clarke & Fitch (1975), and suggests that this morphotype belongs to a not fully grown cephalopod. However, the spur of the statolith is too well developed for a subadult decabrachian. Lack of other specimens from Wąwał renders it impossible to argue about its ontogeny any further. Judging from the morphological distinctiveness of this specimen and the gap in occurrence between the last Jurassic and the first Cretaceous statoliths, it is most plausible to argue that the Wąwał statolith most likely represents a different species and genus of a cephalopod and it is only remotely related to the species represented by the Jurassic statoliths of Clarke (1978).

Speeton statolith 1 (SS1)

(Fig. 3A)

MATERIAL. — A single well preserved specimen (ZPAL B.II/2) from the Aptian, Lower Cretaceous of Speeton, Yorkshire, United Kingdom. Its surface is cream-white, brighter than in otoliths from the same locality.

DESCRIPTION

The general shape is close to an eggplant in right lateral view, with small pointed rostrum on the anterior, and large wide lateral lobe on the posterior side. The lateral lobe is wide and blunt on the edge. The lateral lobe passes continuously on both sides into flat lateral and ventral domes. The rostrum is thin, small, flattened on the left side, and acute on the edge. The axis of the rostrum is inclined to the rest of the statolith with the rostral angle approximately 155°. The dorsal margin is sigmoidal in dorsal view, with a flattened edge, and uninterrupted from the lateral lobe to the rostrum. The lateral and ventral lobes are slightly convex, narrower towards the rostrum. The ventral margin is narrow and blunt, equipped on the edge with a minor arc-shaped, thin and narrow spur.

REMARKS

The morphology of this statolith is very similar to the Jurassic morphotype C of Hart *et al.* (2015) from the Oxford Clay Formation of southern England. It differs in having a smooth lateral lobe, while the one reported by Hart *et al.* (2015) bears a leaf-like ornamentation. Inner side of the SS1 statolith is flattened, while in the Jurassic morphotype C it is rounded. An additional difference between SS1 and the Jurassic morphotype C is the presence of a spur on the former, and its absence on the latter. The star-shaped structure located under the rostrum on the right side of SS1 is most likely of taphonomic or diagenetic origin. Overall the similarity of SS1 to the Jurassic morphotype C of Hart *et al.* (2015) suggests a close taxonomic relationship of both statolith-bearing cephalopods or a convergent evolution of this structure.

Speeton statolith 2 (SS2)

(Fig. 3B)

MATERIAL. — Three specimens (ZPAL B.II/3-5), all with broken rostral edges, from the Aptian, Lower Cretaceous of Speeton, Yorkshire, United Kingdom. The surface in all specimens is cream-white, lighter than in otoliths from the same locality.

DESCRIPTION

The shape of the preserved parts is close to an eggplant, with a lateral lobe on the posterior side. The statolith is strongly convex on the right side. The lateral lobe is round on the ventral side, narrow on the dorsal side, and equipped with a multilobate edge that overhangs slightly to the right. The lobes are located on the edge in decreasing order from the dorsal to the ventral side. The lobes are merged with lateral and ventral domes on the right view of SS2. The dorsal and ventral margins are narrow and acute. The left side of the statolith is moderately flat and bears no recognizable features. Rostra are missing in all available specimens.

REMARKS

There are no complete statoliths of this morphotype at our disposal. The damage most likely occurred during wet sieving of the sediment. The morphology of the lateral lobe is similar to the Jurassic morphotype B of Clarke & Fitch (1975). The subjugation on the SS2 is located between the multilobate edge of the lobe margin and the lateral lobe, while in the statolith reported by Clarke & Fitch (1975) this feature is absent. The lack of the spur and rostrum renders it impossible to provide a full description, but the general shape and the time gap between the last Jurassic morphotypes of Clarke & Fitch (1975) and Hart *et al.* (2015) and SS2 suggests that the latter belongs to a separate, though closely related taxon.

Statolith of *Idiosepius pygmaeus* Steenstrup, 1881

(Fig. 4A; Appendix 3)

MATERIAL. — Two paired statoliths in an undissected Recent specimen (ZPAL B.II/6) from Tsukumo Bay, Sea of Japan, scanned in a micro-CT scanner.

DESCRIPTION

The general shape is reniform in right lateral view with a strongly widened lateral lobe on one end and a thin rostrum on the other end. The rostrum is rectangular, flattened on the right side, and with an acute edge. The rostrum axis is inclined to the rest of the statolith with a rostral angle of approximately 139°. The lateral lobe is oval, rounded, and posteriorly convex on both sides. The lateral dome is convex, clearly overhanging to the right. On the right side of the statolith, the lateral dome is delimited from the ventral dome by a weakly developed subjugation. Both sides of the lateral dome pass continuously into the ventral margin. The spur is convex, triangular, with an elongated lobe, and its edge is rounded and blunt. The left side of the statolith is strongly convex and bears no recognizable features.

REMARKS

The morphology of the statoliths in the Idiosepiidae Appellöf, 1898, has been poorly known so far (Jackson 1989). Therefore, we investigated a pair of statoliths in a two-toned pygmy squid (*Idiosepius pygmaeus* Steenstrup, 1881) collected from sea grass in Tsukumo Bay, Sea of Japan, in order to get details of the statolith morphology in this group. It appears that the morphology of idiosepiid statoliths is unique among Recent cephalopods. Its lack of a wing and the concave spur is reminiscent of statoliths in Mesozoic cephalopods. The main difference is that the spur is small and not visible from the left side of the statolith, unlike in the Mesozoic statoliths, where it is well developed and visible from both sides. The lateral lobe is simple as in the Wąwał statolith and smaller than in other Recent cephalopods. The rostrum of the *I. pygmaeus* statolith is larger than the ones in any other known cephalopods. On the other hand, the rostrum is straight rather than twisted as it is known from the Mesozoic statoliths. The morphology of the *I. pygmaeus* statoliths displays a mixture of characteristics of statoliths known from Mesozoic and Recent cephalopods, but in gross morphology they are more similar to the Mesozoic forms. This may suggest that idiosepiids are more closely related to Mesozoic stem cephalopods than to the Recent crown decabrachians.

DISCUSSION

We present the first report of cephalopod statoliths from the Cretaceous, a period that so far has constituted a significant gap in their fossil record (Clarke *et al.* 1980a, b; Clarke 2003; Hart 2019). Cephalopod statoliths appear to be excessively rare microfossils in the Cretaceous. The best example of this phenomenon is the collection from the Wąwał locality, which provided almost six hundred otoliths, but only one statolith. In the Speeton Clay samples we found only four statoliths among dozens of otoliths. We have also collected signal samples from several other localities, which yielded many otoliths, but we found no statoliths so far. In contrast, marine deposits from the Jurassic that we sampled (Bathonian and Callovian clays in Poland) contained hundreds of statoliths, while otoliths were much fewer. According to Clarke (2003), this abundance of statoliths in the Jurassic results from sampling method and/ or possibility that the sample spot was a spawning place of cephalopods. Clarke (2003) also mentioned that Jurassic was a period of cephalopod dominance over the teleosts on the continental sea shelves. The ratio of cephalopod statoliths to teleosts otoliths (showing the dominance of statoliths) from several European localities supports the latter hypothesis. Conversely, the rarity of the cephalopod statoliths in Cretaceous sediments could be explained by The Great Teleost Radiation (Cavin 2008; Giersch *et al.* 2008) on one hand, and the demise of some open sea decabrachians on the other. However, the teleost radiation is dated to Cenomanian/Turonian (Late Cretaceous), while already in some localities yielding Early Cretaceous materials (in the Valanginian at Wawał or in the Aptian at Speeton), this disproportion is already visible quite clearly (Fig. 5). The dominance of statoliths vs otoliths in the Jurassic should be confronted with data on the occurrence of shells and soft tissue imprints of cephalopods vs fish skeletons, but such a study is pending. Cephalopod statoliths, although rare in the Lower Cretaceous strata, still remain a source of valuable information on the evolution of this group.

The Cretaceous cephalopod statoliths we report here constitute a missing link between Jurassic and Cenozoic occurrences. Most likely the statoliths we described above belong to two different lineages of cephalopods. Statoliths from the Speeton Clays are strikingly similar to the earlier forms described from the Jurassic by Clarke (1978), and most likely represent the same group of cephalopods. The Wąwał statolith is unique, and displays different characteristics both in comparison to the Jurassic forms (to some extent) but most of all to the Cenozoic statoliths (Clarke & Fitch1979). Morphological differences between Wąwał statolith and the other statoliths suggest that this specimen represents a separate lineage of cephalopods. Unfortunately we found only one specimen in the samples from Wąwał, and this locality is currently unavailable for further sampling. This paucity of the specimens hinders any discussion on the ontogeny and intrapopulational variation of this form.

Mesozoic statoliths are poorly explored fossils in the taxonomy and evolution of cephalopods. Their morphology recalls that of statoliths of Recent decabrachians, and their occurrences could augment the credibility of the molecular clock estimates of the Cretaceous diversification of Recent decabrachians (Kröger *et al.* 2011 and Fig. 6 herein). The major obstacle in this approach is the significant differences between Mesozoic and Recent statoliths and the lack of the wing in the latter in particular. A plausible explanation claims that the Jurassic statoliths could be derived from belemnitids and/or other related extinct decabrachians, e.g. *Belemnoteuthis*-related cephalopods (Clarke 2003; Hart 2019). This explanation is supported by the co-occurrence of statoliths and belemnitid macrofossils in Jurassic strata (Table 1). In the Callovian (Middle Jurassic) locality of Łuków-Gołaszyn we found statoliths in layers where belemnitids and aragonic rostra of *Belemnoteuthis polonica* were reported by Makowski (1952). Similarly, in the Bathonian (Middle Jurassic) locality of Gnaszyn, the belemnitids are relatively common (Wierzbowski 2013) in statolith-bearing strata. Statoliths from Łuków-Gołaszyn and Gnaszyn are very similar morphologically (unpublished data) to the forms described by Hart *et al.* (2015, 2016) from the Callovian of England (his Morphotype A). The paucity of statoliths in the Valanginian, Lower Cretaceous of Wąwał is, on the other hand, correlated with the absence of belemnitids and belemnitoids in this locality (Kutek & Marcinowski 1996; Kaim 2001). In the Aptian (Lower Cretaceous) Speeton Clay, rare statoliths co-occur with relatively abundant belemnites (Rawson & Mutterlose 1983). Although there are two examples of statoliths *in situ* in belemnitid (Klug *et al.* 2016) and belemnoteuthid (Wilby *et al.* 2004) body fossils, their preservation is so poor that no morphological information can be recovered from these specimens. Numerous statoliths occur in the layers with abundant hooks and rostra of belemnoteuthiids in the Callovian, Middle Jurassic of England (Wilby *et al.* 2004; Hart *et al.* 2016). Therefore, neither belemnitids nor belemnoteuthiids can be excluded as producers of Jurassic morphotypes of statoliths. Most likely, the statoliths from Speeton derive from these groups while the question of identity of the specimen from Wąwał remains open.

The common feature of all known Mesozoic statoliths is a lack of the wing. The wing is a relatively large, long feature with opaque structure and anchored to the concave spur (Clarke 1978). It is well developed in every Recent decabrachian, with the exception of idiosepiids (see below). Main function of the wing is to attach the statolith to the macula of the statocyst, and its morphology is characteristic enough to be helpful in taxonomy (Arkhipkin & Bizikov 2000). There is also a correlation between the length of the wing of the statolith and the bathymetry of waters characteristic of the given cephalopod. The statoliths with larger and longer wings occur in open ocean and deep-water cephalopods, and the statoliths with shorter wings occur in shallow water, mostly in cuttlefishes (Arkhipkin & Bizikov 2000). Noteworthy, the shortest wings are known from the statoliths of sepioids (Clarke & Fitch1979). So far no wings have been observed in Mesozoic statoliths. Their absence could potentially be explained by taphonomy: the wings are delicate and could detach before lithification or could be too fragile to be fossilized. This, however, is rather untenable due to the preservation of wings in other fossil statoliths, e.g. from the Eocene of North America (Clarke & Fitch 1979). Another possibility is that the wings of the Mesozoic statoliths were made of vaterite – an unstable polymorph of calcium carbonate, which easily decompose or recrystallize in the fossil record. However, the wings in Recent statoliths are made exclusively of aragonite with only a trace of proteins (Clarke 1978). Furthermore, there is no morphological evidence that Mesozoic statoliths ever had wings that could have either detached or dissolved due to taphonomy or preparation. Therefore, the most plausible explanation is that the wings have not yet developed in the statoliths prior to the Late Cretaceous, and are a younger feature. In contrast, the Mesozoic statoliths possess well developed spurs, which are convex and situated more anteriorly than in their Recent and Cenozoic counterparts. This may suggest that spurs acted as wings in statoliths of ancient decabrachians. As mentioned before, only idiosepiids among Recent decabrachians did not evolve wings and preserve convex spurs. The species of *Idiosepius* Steenstrup, 1881, are small, diurnal cephalopods, living in shallow waters and clinging to marine plants (Moynihan 1983). The statoliths of *Idiosepius* were known before, but only their daily growth pattern has been investigated. Because of their small size, their morphology has neither been properly described nor illustrated (Jackson 1989). The phylogenetic position of idiosepiids remains obscure. They were placed within Sepiidae or Sepiolida in the phylogeny of cephalopods based on fossils, molecular data, and shell development presented by Kröger *et al.* (2011). The resemblance in statolith morphology of Idiosepius to Mesozoic cephalopods rather than to the other Recent decabrachians is striking. The morphology of the Idiosepius pygmaeus statoliths displays a mixture of characteristics of Mesozoic and Recent statoliths of cephalopods, but in gross morphology they are more similar to the former. Therefore, it seems plausible to assume that idiosepiids are more closely related to Mesozoic stem cephalopods than to crown Recent decabrachians. This possibility is supported by the molecular data of Bonnaud *et al.* (2002), who calibrated their divergence as early as in the Permian. This makes them the most ancient living decabrachian cephalopod group (Strugnell *et al.* 2006).

CONCLUSIONS

The Cretaceous cephalopod statoliths described herein filled the gap between Jurassic and Cenozoic occurrences. The morphology of Cretaceous morphotypes is similar to Jurassic forms described by Clarke (1978), with the exception of the Wąwał statolith, which displays some unique characteristics. The rarity of Cretaceous statoliths is in contrast to the ubiquity of Jurassic forms, which highlights changes in the nektonic ecosystem of Mesozoic marine environments. Their number in Mesozoic siliciclastic sequences roughly correlates with co-occurrences of belemnitoids. Although being a rarity, the Cretaceous forms are significant in elucidating decabrachian evolution. Comparison of Mesozoic forms to statoliths of Recent cephalopods shows a similarity only to Idiosepiidae. Idiosepiids seem to be the closest relatives of Mesozoic cephalopods, supporting their position as basal decabrachians. Therefore, it is plausible to assume that the divergence between decabrachians and vampyropods was earlier than the Early Jurassic. This discovery fills the gap in cephalopod evolution and puts Mesozoic cephalopod statoliths in a more accurate place in the cephalopod evolutionary tree.

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AUTHOR CONTRIBUTIONS

MKP designed the project, analysed data, and drafted the manuscript. KH supervised the project. KJ prepared supplement data. AK performed fieldwork and collected materials, conceived and supervised the project. All authors edited the manuscript.

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FIGURE CAPTIONS

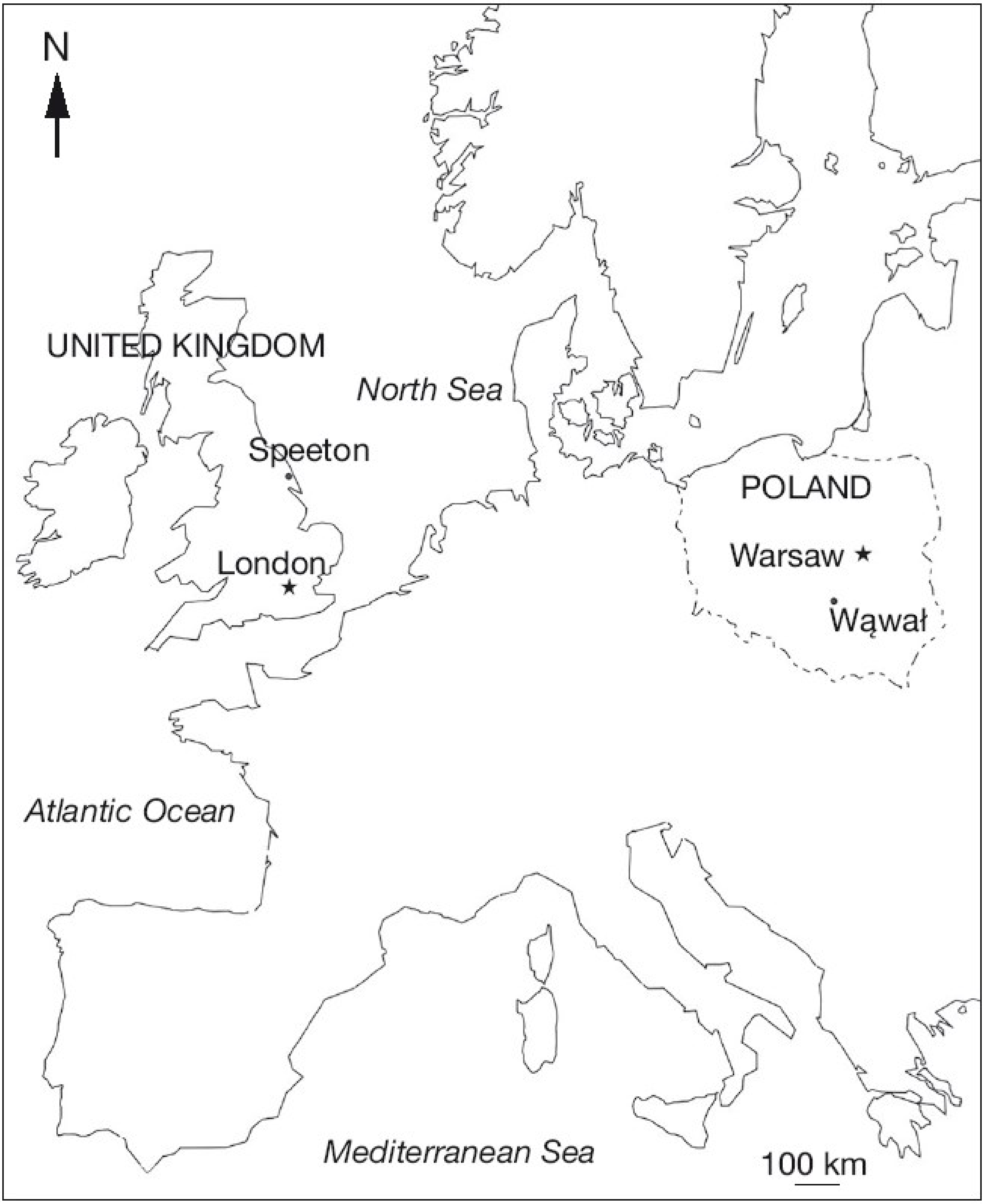

FIGURE 1. Map showing Cretaceous statholith-bearing localities discussed in this paper.

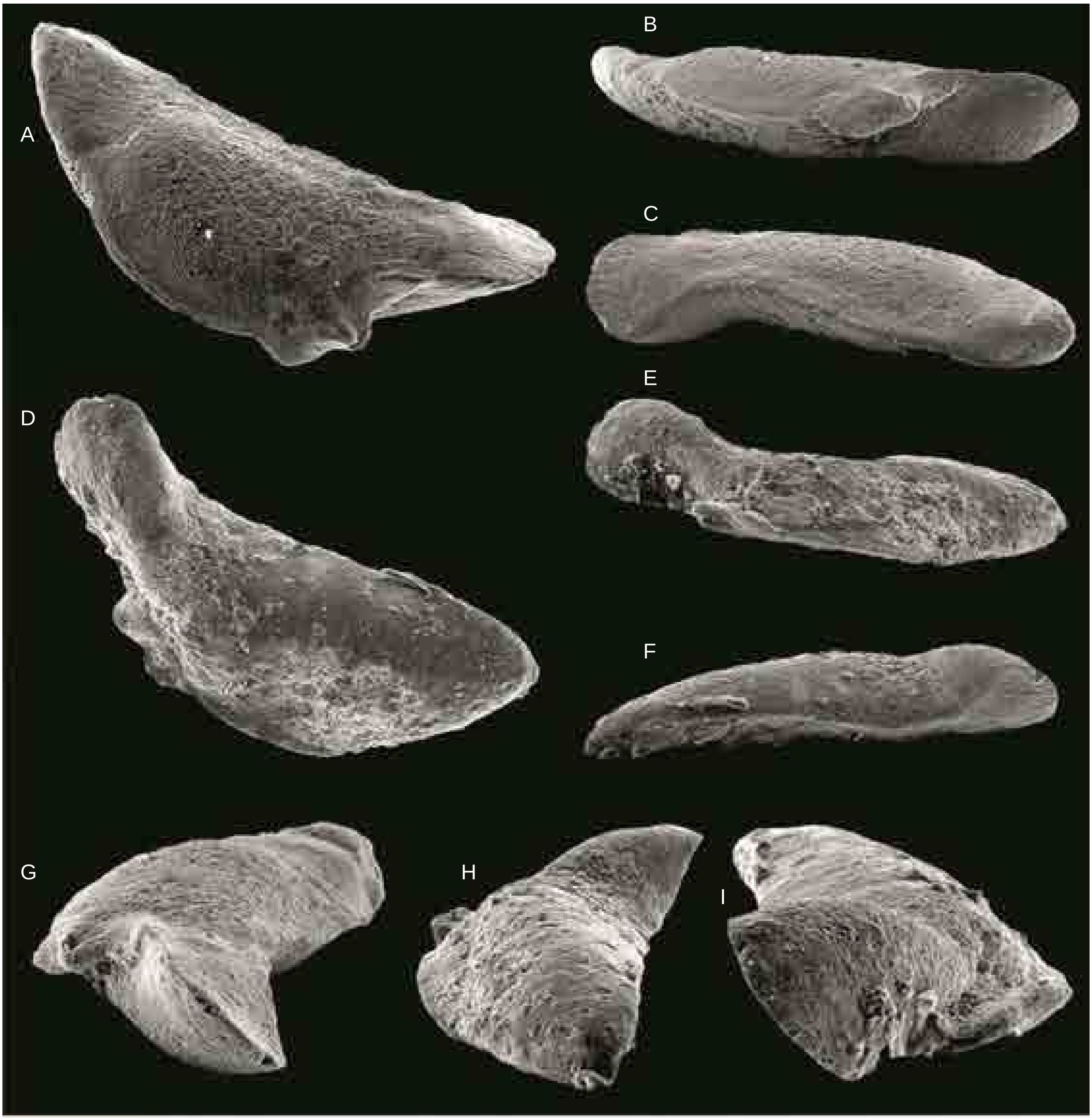

FIGURE 2. Early Cretaceous (Valanginian) cephalopod statolith from Wąwał, central Poland, left statolith ZPAL B.II/1: **A**, inner view; **B**, ventral view; **C**, dorsal view; **D**, anterio-dorsal view; **E**, outer view; **F**, anterio-ventral view; **G**, anterior view; **H**, antero-dorsal view; **I**, dorsal view. Scale bars: 200 µm. See also Appendix 1..

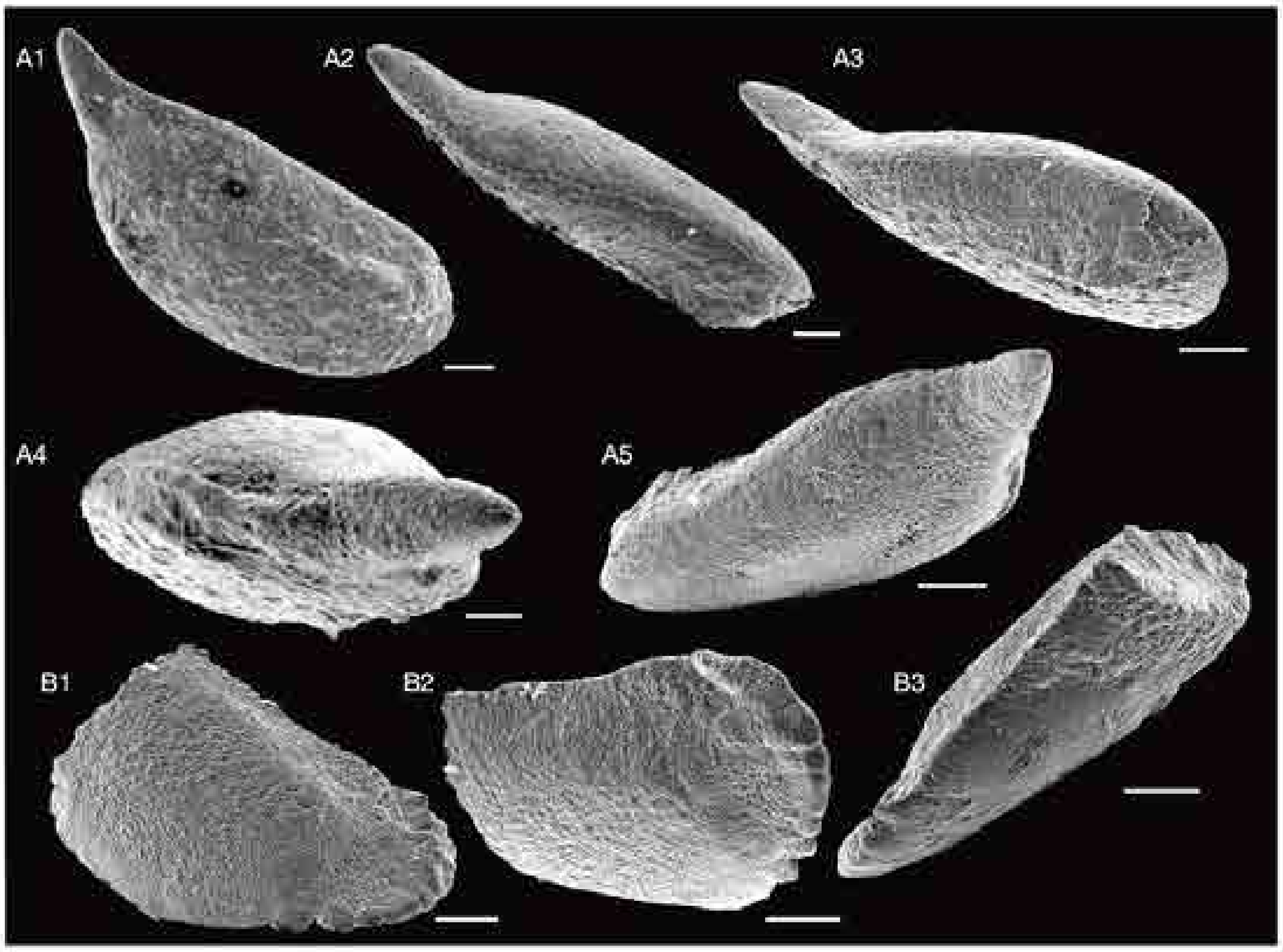

FIGURE 3. Early Cretaceous (Aptian) statoliths from Speeton, Yorkshire, United Kingdom. **A**, Speeton Statolith 1 (SS1), right statolith ZPAL B.II/2-3, Aptian, views: **A1**, outer; **A2**, dorsal; **A3**, anterior; **A4**, posterio-dorsal; **A5**, anterio-dorsal; **B,** Speeton Statolith 2 (SS2), left statolith views: **B1**, outer; **B2**, inner; **B3**, dorsal. Scale bars: 200 µm.

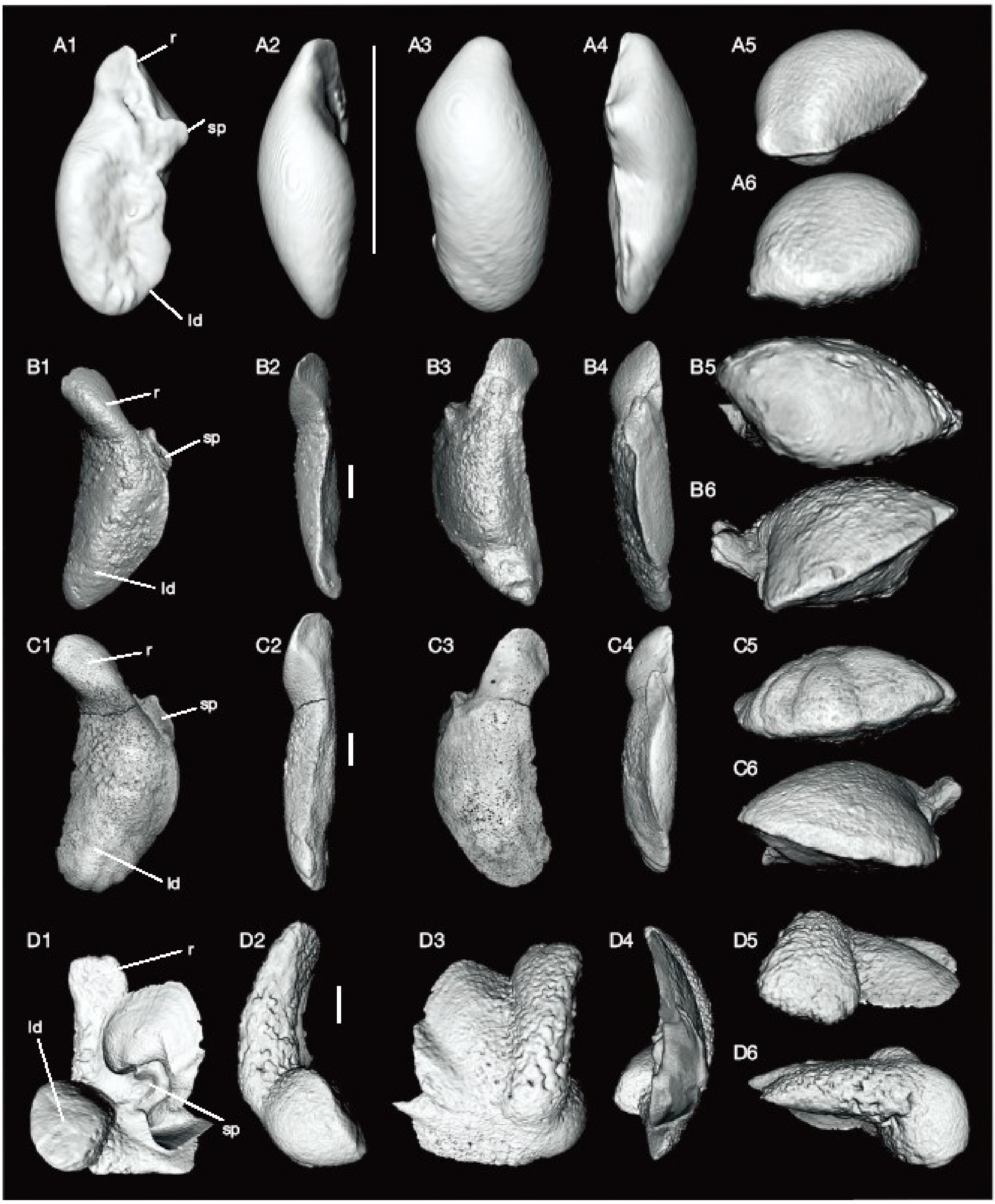

FIGURE 4. Comparison between left statoliths of *Idiosepius pygmaeus* Steenstrup, 1881, ZPAL B.II/6. **A**: Recent, Sea of Japan; **B**: Early Cretaceous (Valanginian) statolith (ZPAL B.II/1) from Wąwał, Poland; **C**: Middle Jurassic (Callovian) statolith (ZPAL B.II/7) from Gołaszyn, Poland; **D**: right reversed statolith of *Sepia pharaonis* Ehrenberg, 1831, ZPAL B.II/8, Recent, Indian Ocean. **A1**, inner side; **A2**, dorsal view; **A3**, outer side; **A4**, ventral view; **A5**, anterior view; **A6**, posterior view; **B1**, inner side; **B2**, dorsal view; **B3**, outer side; **B4**, ventral view; **B5**, anterior view; **B6**, posterior view; **C1**, inner side; **C2**, dorsal view; **C3**, outer side; **C4**, ventral view; **C5**, anterior view; **C6**, posterior view; **D1**, inner side; **D2**, dorsal view; **D3**, outer side; **D4**, ventral view; **D5**, anterior view; **D6**, posterior view. Abbreviations: **ld**, lateral dome; **r**, rostrum; **sp**, spur. Scale bars: 200 μm..

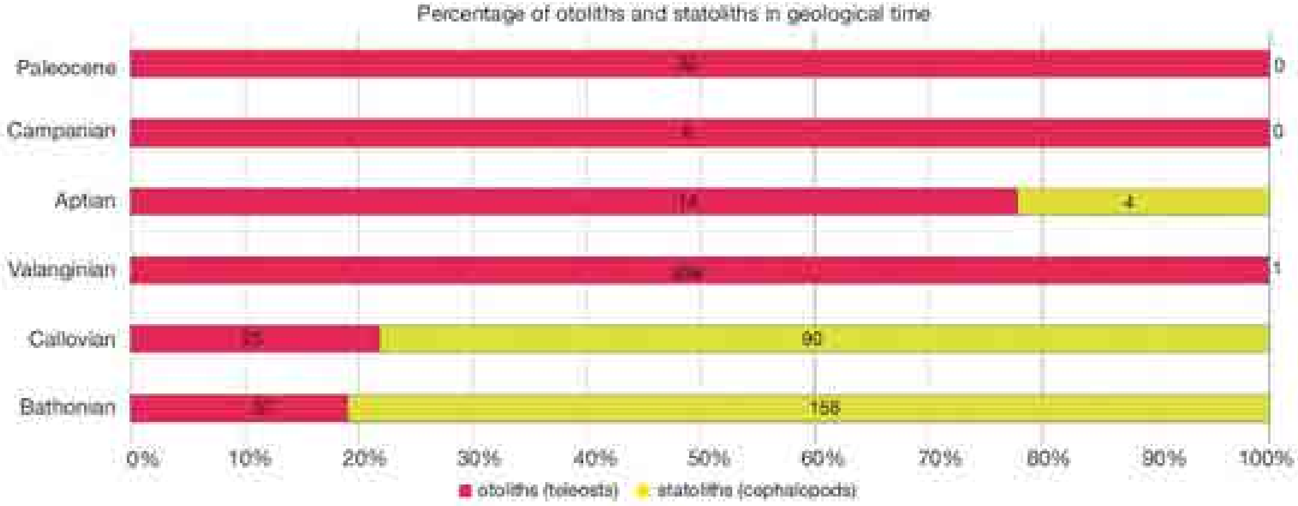

FIGURE 5. Abundance of cephalopod statoliths and fish otoliths in investigated localities (data for Coon Creek are from pilot samples only). Data compilated from the following localities: Gnaszyn (Bathonian), Gołaszyn (Callovian), Wąwał (Valanginian), Speeton Clays (Aptian), Coon Creek (Campanian), Babica (Paleocene); all own data.

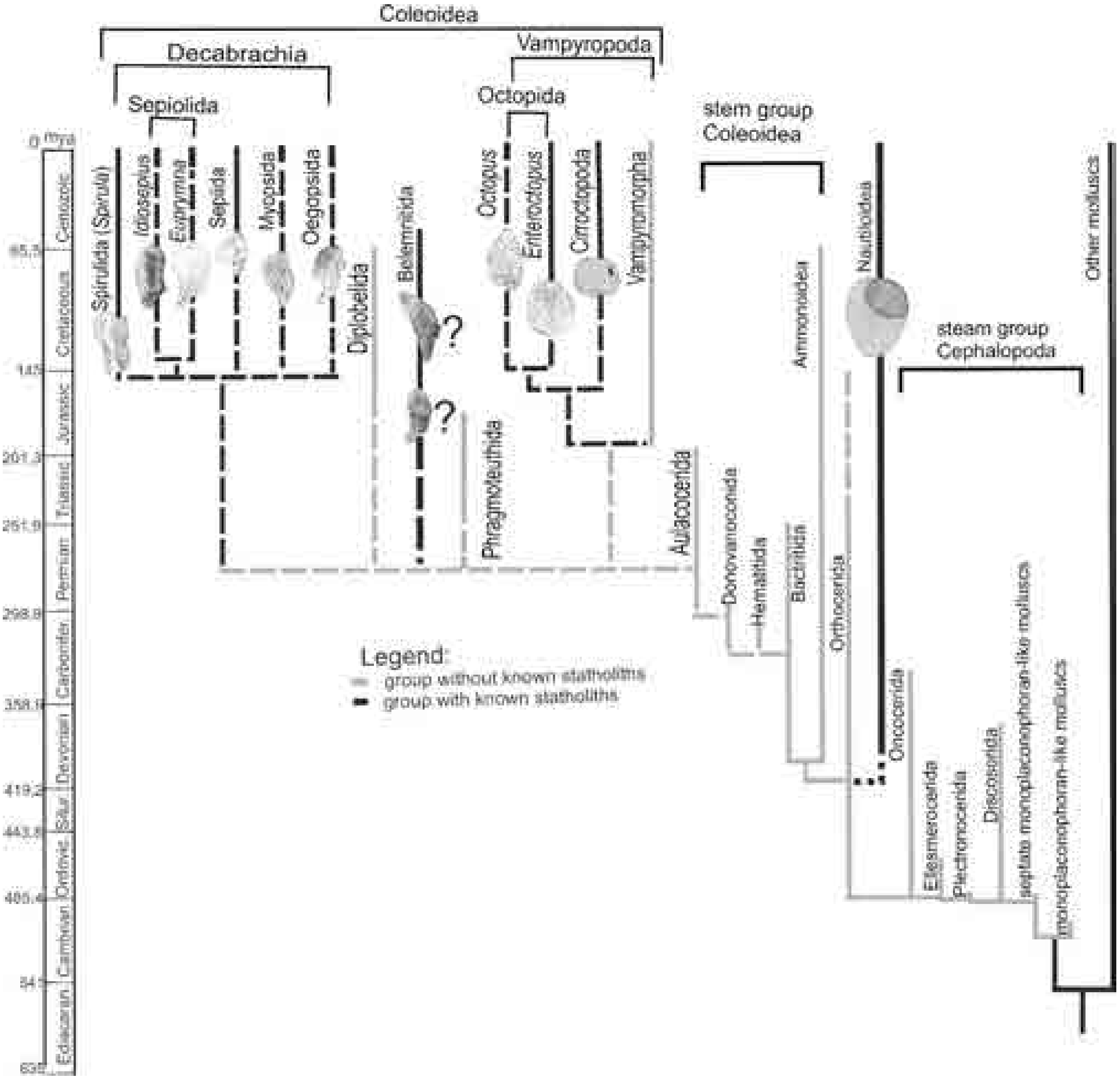

FIGURE 6. Evolutionary tree of cephalopods based on Kröger *et al*. (2011), with illustrations of typical morphology of statoliths in each group (if known).

TABLES

Locality (Age)	**Abundance of cephalopod statoliths**	**Abundance of belemnitid rostra**
Coon Creek, United States (Campanian)	Absent	Absent
Speeton, United Kingdom (Aptian)	Rare	Common
Wąwał, Poland (Valanginian)	Very rare	Absent
Christian Malfrod, United Kingdom (Callovian)	Common	Common
Łuków-Gołaszyn, Poland (Callovian)	Common	Common
Gnaszyn, Poland (Bathonian)	Common	Common

TABLE 1. Comparison between abundance of cephalopod statoliths and belemnitid rostra in seleceted localities. Own data on statoliths apart from Christian Malford (evaluated from Hart *et al*. 2016). Data on abundance of belemnitid rostra from Makowski 1952 (Łuków-Gołaszyn); Wierzbowski 2013 (Gnaszyn); Hart *et al*. 2016 (Christian Malford); Kutek & Marcinowski 1996 (Wąwał); Rawson & Mutterlose 1983 (Speeton) and Larson 2012 (Coon Creek).

APPENDICES

APPENDIX 1. — The three-dimensional model based on the micro-CT scan of Early Cretaceous (Valanginian), cephalopod statolith from Wąwał, central Poland, ZPAL B.II/1, left statolith. The length of the specimen is 1.329 mm. The interactive 3D-mode can be activated by clicking on the image, allowing the user to rotate, move and magnify the model.

APPENDIX 2. — The three-dimensional model based on the micro-CT scan of Middle Jurassic (Callovian) statolith from Gołaszyn, Poland, ZPAL B.II/7, left statolith. The length of the specimen is 1.503 mm. The interactive 3D-mode can be activated by clicking on the image, allowing the user to rotate, move and magnify the model.

APPENDIX 3. — The three-dimensional model based on the micro-CT scan view of *Idiosepius pygmaeus* Steenstrup, 1881, ZPAL B.II/6, Recent, Tsukumo Bay, Sea of Japan, left statolith. The length of the specimen is 268 μm. The interactive 3D-mode can be activated by clicking on the image, allowing the user to rotate, move and magnify the model.

APPENDIX 4. — The three-dimensional model based on the micro-CT scan view of *Sepia pharaonis* Ehrenberg, 1831, ZPAL B.II/8, Recent, Indian Ocean, right statolith. The length of the specimen is 1.414 mm. The interactive 3D-mode can be activated by clicking on the image, allowing the user to rotate, move and magnify the model.

Chapter II

Early Cretaceous radiation of teleosts recorded by the otolith-based ichthyofauna from the Valanginian of Wąwał, central Poland.

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ABSTRACT—We report a Valanginian (Early Cretaceous) otolith-based ichthyofauna from a section at Wąwał in central Poland. We describe one new genus (*Palaeoargentina gen. nov.*), six new otolith-based species (*Pteralbula polonica* sp. nov., *Protalbula pentangularis* sp. nov., *Kokenichthys kuteki* sp. nov., *Protoelops gracilis* sp. nov., *Palaeoargentina plicata* sp. nov., *Archaeotolithus aptychoides* sp. nov.) from Wąwał and compare them to species known from similar assemblages elsewhere. The comparison of teleost diversity shows similarity to the Aptian (late Early Cretaceous) and less distinctly to the Maastrichtian (latest Cretaceous) assemblages, rather than to its coeval equivalents from Germany and southern England, and indicates that a considerable teleost diversity already existed before the mid-Cretaceous. The

vertical succession of otolith taxa in the Wąwał section is in concordance to the pattern already revealed from the succession of bivalves and other benthic invertebrates and it is attributed to sea level and temperature variations. Previously identified causes of benthic invertebrate succession in the Wąwał section are used to infer paleoenvironmental factors governing fish distribution in the Valanginian marine environment recorded at this site. The new findings suggest that the radiation of teleosts started before the Valanginian, and it was a relatively long and apparently gradual process. This fossil association also reveals a significant shift in the abundance ratio of fish otoliths vs. cephalopod statoliths in fully marine deposits, with otoliths much more abundant than the statoliths in Valanginian and younger sediments while it is otherwise in the Jurassic deposits.

INTRODUCTION

Otoliths of teleost fishes are paired, calcareous ear stones consisting mostly of aragonite (or vaterite in some species) and proteins. The formation of otoliths is dependent on various biological (diet, health) and environmental (temperature, depth, salinity) factors, which leave structural and geochemical fingerprints in daily growth increments forming the structure of an otolith. For example, ^{87}Sr/^{86}Sr isotope ratios may differentiate the place of origin of a fish in archeological sites (e.g., Baltic vs. North Seas; Glykou et al., 2021). During the past 50 years, fossilized otolith assemblages gained more interest and have been the subject of a number of studies (Agiadi et al., 2022; Aguilera et al., 2014; Lin et al., 2015; Nolf, 2003, 2004, 2013; Reichenbacher, 1998; Schwarzhans, 1986, 1994, 2010, 2018).

The fossil record of fish otoliths dates back to the Middle Devonian (Nolf, 2013), but generally the occurrences are uneven and their richness is heavily skewed towards younger deposits (Nolf, 2013; Schwarzhans et al., 2017; Schwarzhans and Nielsen, 2021). Therefore, relatively much is known on otoliths of the Cenozoic fishes but the knowledge on their older counterparts is far less complete (Nolf, 2013). Increasing numbers of otolith specimens associated with skeletal fossils allow the attribution of numerous form taxa to the respective fish families, genera and even species, successively increasing the knowledge on Mesozoic teleosts (Schwarzhans, 2018). In addition, comparison of isolated otoliths to those already known from fossilized skeletons help to integrate the form taxa with the biological systematics (Schwarzhans et al., 2017). This in turn helps to fill the gaps in the knowledge on evolution and ecology of fishes whose skeletal remains are uncommon. This concerns the crucial time periods for the teleost radiation during Mesozoic times.

The teleost otoliths recovered from the Jurassic sediments so far indicate relatively low generic diversity of the group (Schwarzhans, 2018; Schwarzhans et al., 2019; Schwarzhans and Keupp, 2022) while it increases rapidly in the mid-to-Late Cretaceous, indicating an accelerating teleost radiation (Nolf, 2003;

Nolf & Stringer, 1996; Schwarzhans, 2010; Stringer et al., 2016). However, localities preserving Early Cretaceous otolith-based ichthyofaunas are in general rare rendering the onset of the teleost radiation somewhat poorly constrained. For example, the Aptian–Albian (Lower Cretaceous) of Weald and Gault clays provided fauna of lower diversity than its Late Cretaceous counterparts, and is composed mostly of Albuliformes, Elopiformes, and Argentiniformes (Stinton, 1973). The appearance and diversification of these groups was attributed to a major teleost radiation by Cavin and Forey (2007). However, the groups such as Beryciformes, Perciformes, and other acanthomorph teleosts have not appeared earlier than the Late Cretaceous–early Paleocene (Stringer et al., 2020), suggesting that in the mid-

Cretaceous the modern teleost fauna had not yet been fully developed. In this contribution, we present a rich Early Cretaceous (Valanginian) otolith association from Wawą ł (Poland) to fill the gap between the mid- to Late Cretaceous and preceding Jurassic faunas. Thanks to previous data on benthic invertebrates (Kaim, 2001) we can also furthermore interpret the environment where this teleost fauna thrived.

GEOLOGICAL SETTINGS

During the Valanginian, central Poland was covered by a shallow seaway connecting marine basins of the Northern European Platform (Kutek & Marcinowski, 1996), and temporarily during the early late Valanginian, also to the Tethys (Mutterlose, 1992). Invertebrate fauna from most of the profile in Wawą ł displays a Boreal influence with Tethyan elements present in the lower upper Valanginian due to the early late Valanginian highstand (Kaim, 2001; Kutek & Marcinowski, 1996). However, a few Tethyan elements have also been found in the upper Valanginian rocks in Poland, indicating that some intermittent connection to Tethys during the late Valanginian could also have existed (Mutterlose, 1992).

The study site is a claypit (currently recultivated and flooded) located near the village of Wawął (Fig. 1A), approximately 2 km east of Tomaszów Mazowiecki (central Poland). When active, the claypit exposed marine argillaceous deposits of the lower and upper Valanginian and their Upper Jurassic bedrock (Kutek & Marcinowski, 1996). The exposed clay profile at Wawął measured12 minthickness,withthelowermost3metersavailable to study only in the 1960s. Estimates of thickness of the clay succession at Wawą ł based on outcrop and shallow drill core data indicate that it reaches up to 23 m (Kujau et al., 2013; Morales et al., 2015; Ploch, 2018).

The studied Valanginian section at Wawą ł starts with conglomerates composed of calcareous pebbles resting disconformably on Upper Jurassic limestones (Kutek & Marcinowski, 1996). Above, the section consists of clayey sand, and subsequent siltstones and claystones, higher up replaced by sandy siltstones with limestone concretions (Kaim, 2001; Ploch, 2018) and topped by glauconitic siltstones of possible early Hauterivian age (Fig. 2). Fully exposed deposits show that the lower and upper parts of the section were deposited in a shallow-water environment, probably within the littoral zone (Kaim, 2001, 2002; Rees, 2005), while the middle part was deposited much below the littoral zone (Kaim, 2001). Seawater paleotemperature estimates indicate 13.5–16.5°C (Kaim, 2001; Rees, 2005). The Valanginian part of the section yielded well-preserved marine invertebrate fossils including ammonites (Dzik, 1990; Lewiński, 1932; Kokoszyńska, 1956; Ploch, 2007, 2018), gastropods (Kaim, 2001, 2002, 2004; Schröder, 1995), oysters (Pugaczewska, 1975), ostracods (Sztejn, 1957), decapod crustaceans (Collins, 1969), bryozoans (Dzik, 1975), holothurian sclerites (Kubiatowicz & Matyja, 1977), and nannofossils (Mutterlose, 1993). The sole cephalopod statolith has been described recently by Pindakiewicz et al. (2022). The faunistic composition of fossil assemblages from the clays at Wawą ł has been presented by Kaim (2001).

MATERIAL AND METHODS

The otoliths studied herein come from excavations performed between 1995 and 1999 (Kaim, 2001, 2004). The samples were wet sieved (0.375 mm mesh size) and handpicked from the residues under a binocular microscope. Previous studies of this collection focused on gastropods (Kaim, 2001, 2002, 2004), shark teeth (Rees, 2005), and general paleoecology (Kaim, 2001).

The core material was collected in five sets of samples (Fig. 1B). Samples S1–A1 come from the lower part of the section and encompass the upper part of the lower Valanginian (Platylenticeras involutum and lower Prodichotomites hollwedensis zones), which is interpreted as influenced by Boreal faunas. The samples F2–A2 come from the middle part of the section in the lower part of the upper Valanginian (upper Prodichotomites hollwedensis zone) and is interpreted as a highstand influenced by Tethyan faunas. The remaining sample sets (D5–A3, J10–B10, and A11–N11) are all from the upper part of the section and represent the regressive cycle in the upper part of the upper Valanginian (Dichotomites zone). The material from other samples from different works was added for this research, after correlating it with the main section (Fig. 2).

Institutional Abbreviation—ZPAL, Institute of Paleobiology, Polish Academy of Science, Warsaw, Poland.

Anatomical Abbreviations—CaL, cauda length, OH, otolith height, OL, otolith length; OsH, ostium height, OsL, ostium length.

SYSTEMATIC PALAEONTOLOGY

The systematics are based on the revision of Jurassic and Early Cretaceous fish otoliths provided by Schwarzhans (2018). The class Actinopterygii and its authorship is used and understood as in Schwarzhans et al. (2020) and references therein.

Class ACTINOPTERYGII sensu Goodrich, 1930

Subclass NEOPTERYGII Regan, 1923

Infraclass TELEOSTEI J. P. Müller, 1845

Order ALBULIFORMES Jordan, 1923

Family PTEROTHRISSIDAE Gill, 1893

Genus *PTERALBULA* Stinton, 1973

Type Species—*Otolithus* (*Atherina*) *cantiana* (Shepherd, 1916); Gault Clay, Aptian, Lower Cretaceous from Folkestone, Kent, U.K.

PTERALBULA POLONICA, sp. nov.

(Fig. 3A–C)

Etymology—Named after the country of origin.

Holotype—ZPAL P. 11/1 (Fig. 3A), from sample S1.

Type Locality—Wawął, central Poland.

Type Horizon—lower Valanginian, *Platylenticeras involutum* zone.

Material—89 specimens, mostly well preserved, and a few broken specimens: S1 (10 specimens), R1 (10 specimens), Q1 (11 specimens), P1 (7 specimens), O1 (7 specimens), N1 (6 specimens), M1 (2 specimens), L1 (5 specimens), K1 (3 specimens), J1 (3 specimens), I1 (5 specimens), H1 (2 specimens), G1 (3 specimens), D1 (2 specimens), C1 (2 specimens), B1 (5 specimens), F2 (1 specimen), E2 (4 specimens), B2 (1 specimen).

Diagnosis—Indistinctive, pseudostial sulcus opening. Shallow dorsal depression. Dorsal rim with small angles on anterior and posterior sides. Smooth, ventral rim.

Description—Small- to medium-size sagittal otoliths (OL_{max}: 7.92 mm; OH_{max}: 5.14 mm; $OL_{holotype}$: 1.45 mm, $OH_{holotype}$: 0.94 mm, $CaL_{holotype}$: 0.85 mm, $OsL_{holotype}$: 0.68 mm). Oval otoliths. Very short or absent rostrum. Straight cauda opened to the anterior side in smaller specimens, closed with small anterodorsal rim in larger specimens. Growth marks on ventral rim in smaller specimens, absent in larger specimens. Growth marks on ostial collicullum and cauda in smaller specimens.

Discussion—*Pteralbula polonica* sp. nov. is less elongated than similar otolith species Pteralbula galtina (Koken, 1891) (OL:OH = 1.52–1.54 for *Pteralbula polonica* sp. nov. vs

1.55–1.7 in P. galtina). Ostium of *Pteralbula polonica* sp. nov. is slightly longer than in P. galtina (CaL:OsL = 1.25–2.1 in *Pteralbula polonica* sp. nov. vs 1.9–2.3 in *P. galtina*). *Pteralbula polonica* sp. nov. differs from *P. galtina* with the smooth, oval-shaped ventral rim. Smaller otoliths look similar to leptolepid forms, like younger specimens of *P. galtina* (Schwarzhans, 2018). The ontogeny of *Pteralbula polonica* sp. nov. is similar to *P. galtina*. Largest specimens of *P. polonica* sp. nov. are approximately 8 mm long and show characteristics typical to adult specimens of *Pteralbula cantiana* (Shepherd, 1916), *P. galtina* (Koken, 1891), and *P. todolellana* (Nolf, 2004) such as pseudostial sulcus opening without antirostrum (Schwarzhans, 2018).

Pteralbula polonica sp. nov. and *P. galtina* do not co-occur in Wawął section. Specimens of *P. polonica* sp. nov. were found only in the lower part of the section and decreased in abundance towards the top of the profile.

Stratigraphic and Geographic Range—Lower Valanginian of Wawął, central Poland.

PTERALBULA GALTINA (Koken, 1891)
(Fig. 3D)

Otolithus (incertae sedis) *galtinus* Koken, 1891: fig. 27 (original description).

Pterothrissus galtinus (Koken, 1891) Stinton, 1973:pl. 31, fig. 8 (new combination).

Megalops bicrenulatus Stinton, 1973:pl. 31, figs. 1–3 (new combination).

Pterothrissus galtinus (Koken, 1891) Nolf, 2004:pl. 2, figs. 7–10.

Pteralbula galtina (Koken, 1891) Schwarzhans, 2018:figs. 7C–G (new combination).

Material—37 well-preserved specimens: B5 (1 specimen), A5 (1 specimen), H3 (7 specimens), G3 (10 specimens), F3 (5 specimens), E3 (4 specimens), D3 (2 specimens), B3 (2 specimens), A3 (5 specimens).

Remarks—Elongated shape of smaller specimens differentiate P. galtina from P. polonica sp. nov., both with indistinctive, pseudostial sulcus opening, and inclined cauda closed with posterior rim. Found only in upper part of Wąwał section. The material from B5–A5 samples (lower part of upper Valanginian) comprises mostly small specimens, with more rounded shape of the ventral rim, than in bigger specimens, from H3–A3 samples. The higher part also contains larger specimens with short ostium and long, straight cauda. Known previously from middle to upper Albian (Lower Cretaceous) Gault Clay of Folkestone, Kent, south England (Schwarzhans, 2018; Stinton, 1973) and Pawpaw Formation, Texas, U.S.A. (Schwarzhans et al., 2022). The specimens from Wąwał locality constitute the oldest record of Pteralbula galtina.

Stratigraphic and Geographic Range—Lower Cretaceous (upper Valanginian—upper Albian) of Poland, England, and U.S.A.

Family uncertain
Genus *PROTALBULA* Frizzell, 1965

Type Species—*Protalbula sohli* Frizzell, 1965; Campanian, Georgia, U.S.A.

PROTALBULA VENTRALIS (Weiler, 1971)
(Fig. 3E, F)

Palealbula ventralis—Weiler, 1971:figs. 1–3 (original description).

Palealbula ventralis (Weiler, 1971)—Weiler, 1972:fig. 3. Protalbula ventralis (Weiler, 1971)—Schwarzhans, 2018:fig. 6G (new combination).

Material—14 specimens: J1 (1 specimen), I1 (4 specimens), G1 (1 specimen), B1 (1 specimen), D5 (1 specimen), C5 (1 specimen), A5 (1 specimen), H3 (2 specimens), F3 (1 specimen), E3 (1 specimen).

Remarks—In many specimens, the tip of the rostrum and dorsal rim are eroded, but the location and shape of cauda and deeply curved ventral rim are preserved sufficiently well for identification. Cauda is straight in the medial part of the otolith and strongly curved towards venter posteriorly. Like most other albulids, the species is absent from the middle part of the Wawął section.

Stratigraphic and Geographic Range—Lower Cretaceous (upper Valanginian–lower Hauterivian) of central Poland (Wawął) and northern Germany.

PROTALBULA PENTANGULARIS, sp. nov.

(Fig. 4A)

Etymology—From Latin pentangularis, after the pentagonal shape of the otolith.

Holotype—ZPAL P. 11/7 (Fig. 4A), from sample N1.

Type Locality—Wawął, central Poland.

Type Horizon—lower Valanginian, *Platylenticeras involutum* zone.

Material—18 specimens, all well preserved: Q1 (1 specimen), O1 (1 specimen), N1 (3 specimens), M1 (1 specimen), G1 (2 specimens), F1 (1 specimen), C1 (1 specimen), B1 (2 specimens), A1 (1 specimen), E2 (2 specimens), D2 (2 specimens).

Diagnosis—The tip of the ostium with faint ornamentation. No clear division between ostium and cauda. The cauda close to and parallel to the dorsal rim, posteriorly strongly curved towards the posterior rim, and wide. The posterodorsal angle more developed than the anterodorsal angle. Ventral margin deeply convex. Convex inner side of the otolith. The outer side of the otolith slightly undulated with thicker anterodorsal part.

Description—Massive, dorsoventrally, laterally compressed pentagonal otolith, with dimensions $\mathrm{OL}_{\mathrm{holotype}}$ ($\mathrm{OL}_{\mathrm{max}}$): 4.18 mm; $\mathrm{OH}_{\mathrm{holotype}}$ ($\mathrm{OH}_{\mathrm{max}}$): 3.67 mm; $\mathrm{CaL}_{\mathrm{holotype}}$ ($\mathrm{CaL}_{\mathrm{max}}$): 2.36 mm; $\mathrm{OsL}_{\mathrm{holotype}}$ ($\mathrm{OsL}_{\mathrm{max}}$): 2.55 mm; $\mathrm{OsH}_{\mathrm{holotype}}$ ($\mathrm{OsH}_{\mathrm{max}}$): 0.48 mm. Long, narrow ostium. Short cauda. Visible anterodorsal and posterodorsal angles, with straight dorsal rim. Smooth posterior rim. The outer side of the otolith with faint ornamentation on the ventral part.

Discussion—The gross morphology of *Protalbula pentangularis* sp. nov. is similar to the other species of *Protalbula*. The index (OL:OH) of *P. pentangularis* is very similar to that of *P. ventralis* (1.2–1.3 in *P. pentangularis* sp. nov. vs 1.3–1.4 in *P. ventralis* based on type materials of *P. pentangularis* and topotypes of *P. ventralis* studied herein) but the shape of cauda of *Protalbula pentangularis* sp. nov. is strongly curved. The ostium of *P. pentangularis* sp. nov. is longer and narrower (OsL:OsH) than in *P. ventralis* (5.6 in *P. pentagularis* sp. nov vs 2.5 in *P. ventralis*). Shape of the rostrum in *P. pentangularis* sp. nov. is more triangular than in *P. ventralis*. Dorsal angles are more developed, and ventral rim is deeper in *P. pentangularis* sp. nov. than in *P. ventralis*.

The stratigraphic range of *Protalbula pentangularis* sp. nov. in Wawął section partially overlaps with *P. ventralis* in the lower part of the section.

Stratigraphic and Geographic Range—Lower Valanginian of Wawął, central Poland.

Genus *PALEALBULA* Frizzel, 1965

Type Species—*Otolithus* (*Clupeidarum*) *neocomiensis* (Priem, 1908); Hauterivian, Paris Basin, France.

PALEALBULA NEOCOMIENSIS (Priem, 1908)

(Fig. 4B)

Otolithus (*Clupeidarum*) *neocomiensis*—Priem, 1908: figs. 11– 14 (original description).

Otolithus neocomiensis—Stolley, 1912:pl. 7, figs. 6–9 (modified description).

Otolithus ahlumensis—Stolley, 1913, replacement name for *Otolithus neocomiensis* Stolley, 1912:pl. 7, figs. 6–9, preoccupied by *Otolithus* (*Clupeidarum*) *neocomiensis* Priem, 1908 (new combination).

Palealbula neocomiensis (Priem, 1908)—Frizzell, 1965:pl. 4, fig. 8 (new combination).

Palealbula neocomiensis (Priem, 1908)—Weiler, 1969: figs. 2, 3, 5, 7, 8.

Palealbula neocomiensis (Priem, 1908)—Weiler, 1972:fig. 2.

'Elops' neocomiensis (Priem, 1908)—Stinton, 1973:pl. 31, figs. 4, 5 (new combination).

Palealbula neocomiensis (Priem, 1908)—Schwarzhans, 2018: fig. 6E, F.

Material—49 specimens, most of the specimens broken and eroded with visible ventral part and cauda: C5 (1 specimen), B5 (1 specimen), A5 (1 specimen), H3 (11 specimens), G3 (10 specimens), F3 (5 specimens), E3 (5 specimens), D3 (2 specimens), B3 (11 specimens), A3 (2 specimens).

Discussion—Some of the specimens at our disposal are wellpreserved and can be unequivocally identified as *Palealbula neocomiensis* (Priem, 1908). Most of the specimens have only ventral parts and cauda preserved, probably because of breakage due to taphonomy or sample processing. *Palealbula neocomiensis* is very similar to *P. depressidorsalis* (Schwarzhans, 2018), although the massive ventral part of the statolithand straight cauda differentiates *P. neocomiensis* from *P. depressidorsalis*. *Palealbula neocomiensis* co-occurs with *P. depressidorsalis* in the upper part of the Wawął section.

Stratigraphic and Geographic Range—Lower Cretaceous (lower Valanginian–Hauterivian) of central Poland, France, northern Germany, and U.K.

PALEALBULA DEPRESSIDORSALIS Schwarzhans, 2018

(Fig. 4C)

Palealbula depressidorsalis (Schwarzhans, 2018)—Schwarzhans, 2018:fig. 6C, D.

Material—122 specimens, mostly broken and eroded but with visible features: Q1 (2 specimens), O1 (1 specimen), I1 (6 specimens), H1 (1 specimen), B1 (1 specimen), D2 (1 specimen), C2 (2 specimens), B2 (1 specimen), D5 (2 specimens), C5 (1 specimen), B5 (3 specimens), A5 (2 specimens), H3 (30 specimens), G3 (11 specimens), F3 (17 specimens), E3 (13 specimens), D3 (5 specimens), B3 (15 specimens), A3 (8 specimens).

Discussion—*Palealbula depressidorsalis* specimens from Wawął are less elongated than holotype and paratypes (OL:OH for Wawął population: 1.71–2.12 vs. 2.05–2.55 for Gault

Clay population) (Schwarzhans, 2018). However, other features, such as fusiform shape, shallow dorsal rim, curved cauda, dorsally opened ostium with pointed tip, smooth rims, and rounded ventral rim are very similar in otoliths from both outcrops and at present do not warrant species-level distinction. The reason behind the difference in elongation might have resulted from ontogeny (there are more juvenile or subadult otoliths in Wawął), or evolutionary changes (otoliths from Wawął represent an older population of *Palealbula depressidorsalis* than otoliths from Gault Clay). For instance, there is a considerable size distinction between *Pteralbula galtina* from Wawął, and their conspecifics from Gault Clay, with the latter being larger (medium OL:OH in Wawął population is 1.6 with L_{max} 3.63 mm, while in Gault's population medium OL: OH is 1.6 with L_{max} 15.73 mm). Thus, a similar trend might also be true for *P. depressidorsalis*.

This species is the second most abundant otolith species in the Wawął assemblage, after *Palaeoargentina plicata* sp. nov. *Palealbula depressidorsalis* was initially reported from the Gault Clay (Lower Cretaceous, Albian) of Folkestone in Kent, U.K. Our findings suggest that *P. depressidorsalis* has a much longer stratigraphic and wider geographic range. This species appears throughout the entire section in Wawął, increasing in abundance towards the top of the section. *Palealbula depressidorsalis* differs from *P. neocomiensis*, by its slender ventral part and presence of straight supramedial cauda, without widening in the medial part of the cauda. Smaller specimens of *P. depressidorsalis* have an ostium shorter than in *P. neocomiensis*, although ontogeny of that feature is similar in both species (Schwarzhans, 2018).

Stratigraphic and Geographic Range—Lower Cretaceous (Valanginian–Albian) of Poland and England.

Order OSTEOGLOSSIFORMES Regan, 1909

Family uncertain

Genus KOKENICHTHYS Schwarzhans, 2010

Type Species—“?*Albulida*” *ensis* Nolf & Dockery, 1990, Campanian (Upper Cretaceous), Alabama, U.S.A.

KOKENICHTHYS KUTEKI, sp. nov.

(Fig. 4E, F)

Etymology—Named after the late Professor Jan R. Kutek (1935–2013) for his important works on Wawął locality and its surroundings.

Holotype—ZPAL P. 11/10 (Fig. 4E), from sample S1.

Type Locality—Wawął, central Poland.

Type Horizon—Lower Valanginian (*Platylenticeras involutum* zone).

Material—16 well preserved specimens: S1 (1 specimen), Q1 (1 specimen), N1 (1 specimen), L1 (2 specimens), I1 (2 specimens), G1 (1 specimen), C1 (2 specimens), B1 (2 specimens), D5 (1 specimen), C5 (1 specimen), A5 (1 specimen), G3 (1 specimen).

Diagnosis—Shallow, highly ornamented sulcus without discernible collicullum. Elongated rostrum, with widened sulcus. Smooth, straight dorsal rim, with one large posterodorsal angle. Shallow posterodorsal depression connected with small posterior rim. Ventral rim ornamented, widened under the rostrum.

Description—Pentagonal, elongated otolith. Rostrum well developed. Dorsal and posterior part of otolith well developed. The inner side of otolith convex. The outer side of the otolith slightly undulating. Posterodorsal angle hinge-like. Holotype vs maximal measurements: $OL_{holotype}$: 2.16 mm; OL_{max}: 3.46 mm; $OH_{holotype}$: 1.12 mm OH_{max} 1.58 mm.

Discussion—Species of *Kokenichthys* were found mostly in the Campanian and Maastrichtian (Schwarzhans, 2010). From three nominal species of *Kokenichthys*, only *K. ensis*

(Nolf & Dockery, 1990) is similar to *Kokenichthys kuteki* sp. nov.—it shares very similar sulcus and small dorsal rim. Like in *K. ensis*, outer side of *K. kuteki* sp. nov. is undulated, but the ventral rim is more similar to *K. atavus* (Nolf, 2004) and *K. ripleyensis* (Nolf & Stinger, 1996). *K. kuteki* sp. nov. has three diagnostic characteristics: (I) inflated posterodorsal angle, (II) ornamented sulcus that covers only rostrum and dorsal part of the otolith, and (III) pleated ornamentation of the ventral rim. *Kokenichthys ripleyensis*, *K. atavus*, and *K. ensis* have flattened posterodorsal angle, sulcus covering almost 50% of the inner face otolith and smooth ventral rim. *Kokenichthys kuteki* sp. nov. is the oldest and the most plesiomorphic known species of *Kokenichthys*.

Stratigraphic and Geographic Range—Lower Valanginian, Wawął, central Poland

.

Order CROSSOGNATHIFORMES Taverne, 1989

Family CROSSOGNATHIDAE Woodward, 1901

Genus *APSOPELIX* Cope, 1871

Type Species—*Calamopleurus anglicus* Dixon, 1850; Cenomanian (Lower Cretaceous), southern England.

APSOPELIX? *BERLINENSIS* Schwarzhans, 2018

(Fig. 5A)

Apsopelix? *berlinensis* (Schwarzhans, 2018)—Schwarzhans, 2018:fig. 4I–L.

Material—36 well preserved specimens: R1 (1 specimen), Q1 (1 specimen), P1 (1 specimen), O1 (1 specimen), J1 (1 specimen), I1 (4 specimens), H1 (1 specimen), G1 (1 specimen), F1 (1 specimen), C1 (1 specimen), D2 (1 specimen), C5 (1 specimen), B5 (1 specimen), A5 (1 specimen), H3 (3 specimens), G3 (8 specimens), E3 (3 specimens), D3 (2 specimens), B3 (1 specimen).

Description—Oval, slender otolith with pointed rostrum. Well-developed posterior tip, with slightly developed dorsal cusp. Oval ventral rim. Straight cauda, with open terminated sulcus, and widened posteriorly ostium.

Remarks—*Apsopelix*? *berlinensis* resembles species of *Protoelops*, however rounded posterior tip, oval ventral rim, and dorsally closed ostium are different between otoliths of both genera. Morphological simplicity, small size, and co-occurrence with *Protoelops gracilis* sp. nov. could be interpreted as evidence for juvenile origin of the current materials. After a careful consideration, however, we concur that these belong to a separate species based on their similarity to *Apsopelix*? *berlinensis* (Schwarzhans, 2018). *Apsopelix*? *berlinensis* appears throughout the whole section at Wawął, but is more abundant it its upper part.

Stratigraphic and Geographic Range—Berriasian–Valanginian of Gross-Lichtenfelde well, east Germany, and Haletz, Israel, and Valanginian of Wawął, central Poland.

Order ELOPIFORMES Jordan, 1923

Family ELOPIDAE Bonaparte, 1832

Genus *PROTOELOPS* Schwarzhans, 2018

Type Species—*Otolithus* (*Leptolepidarum*) *cuneiformis* (Frost, 1924); Tithonian (Upper Jurassic), southern England.

PROTOELOPS GRACILIS, sp. nov.

(Fig. 5B, C)

Etymology—From Latin gracilis (slender) after the general shape of the otolith.

Holotype—ZPAL P. 11/13 (Fig. 5B), from sample J1.

Type Locality—Wawął, Central Poland.

Type Horizon—Lower Valanginian, *Platylenticeras involutum* zone.

Material—64 specimens, mostly well preserved, or halved, broken parts: R1 (2 specimens), Q1 (1 specimen), P1 (1 specimen), N1 (1 specimen), M1 (1 specimen), K1 (1 specimen), J1 (1 specimen), I1 (4 specimens), H1 (2 specimens), G1 (2 specimens), F1 (1 specimens), C1 (1 specimen), B1 (3 specimens), E2 (6 specimens), C5 (2 specimens), B5 (2 specimens), H3 (9 specimens), G3 (11 specimens), F3 (7 specimens), E3 (4 specimens), D3 (1 specimen), A3 (1 specimen).

Diagnosis—Elongated otolith with ostial opening. The cauda bordered by large crista superior and crista inferior in its straight part, and its posterior tip slightly curved ventrally. The dorsal rim of the otolith smooth, with one cusp, close to the ostium. The ventral rim smooth, longer, and larger than the dorsal rim. The anterior angle rounded, smooth. Description—Elongated otolith, with antirostrum and margins of ostial colliculum. The rostrum and ostium tip not preserved in holotype and paratypes. Cauda mostly straight, with slightly curved posterior tip. Dorsal part smooth with single cusp, and small, narrow depression. Well-developed crista superior and crista inferior in larger specimens. Ventral rim smooth and almost straight, and much more massive than the dorsal rim. The outer face of the otolith undulated only in the dorsal part. Dimensions of holotype which is the largest available specimen: $OH_{holotype}$ (OH_{max}): 2.46 mm; $CaL_{holotype}$ (CaL_{max}): 2.52 mm; $CaH_{holotype}$ (CaH_{max}): 0.3 mm.

Discussion—The species described herein is very similar in shape to the other species of *Protoelops*, especially to *Protoelops cuneiformis* (Frost, 1924) from Tithonian (Upper Jurassic) of England and to the *Protoelops scalpellum* (Nolf, 2004) from Aptian (Lower Cretaceous) of Spain. *Protoelops gracilis* sp. nov. are characterized by slender margins of posterior and anterior part of the otolith as in *P. scalpellum*. *Protoelops gracilis* sp. nov. differs from *P. scalpellum* by its curved posterior tip of cauda, and the larger anterior angle. *Protoelops gracilis* sp. nov. has an ostial colliculum and antirostrum which is lacking in *P. scalpellum*.

Since specimens of *P. gracilis* sp. nov. have no rostrum preserved, we could not compare this feature with that of *P. scalpellum*.

Stratigraphic and Geographic Range—Valanginian of Wawął, central Poland.

Order ARGENTINIFORMES Bertelsen, 1958

Family ARGENTINIDAE Bonaparte, 1846

Genus *PALAEOARGENTINA*, gen. nov.

Etymology—A combination of *palaios* (Greek = old) and the genus name *Argentina* indicating that current genus is older than other argentinids in the fossil record.

Type Species—*Palaeoargentina plicata* sp. nov. from Valanginian, Wawął, central Poland.

Species Included—*Argentinida bergantina* Nolf, 2004, from the lower Aptian (lower Cretaceous) of Maestrazgo, Spain, and *Argentina*? *texana* Schwarzhans, Stringer, and Welton, 2022, from upper Albian (lower Cretaceous) of Texas, U.S.A.

Diagnosis—Argentinid otolith with ventrally expanded ostium. Ostial collicullum present, cauda straight. Rostrum triangular, dorsally limited by ostium. Ventral rim rounded, mostly smooth or with small crenulation. The posterodorsal angle of the otolith well-developed. Dorsal rim of the otolith with 2–4 large crenulations. The dorsal rim abutting cauda with crista superior. The crista inferior present and well developed.

Comparison—The otolith species of *Palaeoargentina* are similar to those of *Argentina* in having elongated ostium, straight cauda, and lobed dorsal rim but differ by well-developed posterior rim, and ventral rim less-developed than in other argentinid otoliths (compare Nolf, 2013). The oldestknown otolith of *Argentina* is *Argentina voigti* Schwarzhans, 2010, and comes from the Maastrichtian (Upper Cretaceous) of Bavaria, thus being ca. 30 Myr younger than the youngest species of *Palaeoargentina*, *P. texana* coming from upper Albian of Texas. *Argentina voigti* is similar to otoliths of *Palaeoargentina* but it lacks the curved posterior rim and lobe-like ornamentation on the ventral rim. These two morphological features are distinctive and consistent among the specimens included into *Palaeoargentina plicata* sp. nov. in our collection and in *P. bergantina* figured by Nolf (2013), warranting the erection of a new otolith-based genus, even though the features diagnostic for otoliths of *Argentina* remained poorly defined (Nolf, 2013). *Palaeoargentina* reveals many features that relate argentiniforms to leptolepid-like ancestors and suggesting that it represents otoliths of basal argentinids. Most likely, the well-developed posterior rim, anterodorsal angle, and oval ventral rim with ornamentation are plesiomorphic characters of argentinid otoliths that were subsequently lost during evolution since younger and extant argentinid otoliths have a much shorter dorsal rim, anterodorsal angles, and posterior rims weakly developed. Numerous small specimens of "*Argentina lobata* (Stinton, 1973)" seem to share many features with species of *Palaeoargentina*, though its large specimens are usually more rectangular with more developed dorsal part. Since type material of Stinton's (1973) species is poorly preserved, we feel that the taxonomic position of "*Argentina lobata*" requires more study and additional collection effort.

PALAEOARGENTINA PLICATA, sp. nov.

(Fig. 5D, E)

Etymology—From Latin plica (fold) after lobed dorsal and ventral parts of the otolith.

Holotype—ZPAL P. 11/16 (Fig. 5D), from sample S1.

Type Locality—Wawął, central Poland.

Type Horizon—Valanginian, Lower Cretaceous (*Platylenticeras involutum* zone).

Material—144 specimens, including 114 well preserved, and 30 with broken posterior or anterior parts: S1 (6 specimens), R1 (8 specimens), Q1 (20 specimens), P1 (11 specimens), O1 (7 specimens), N1 (17 specimens), M1 (6 specimens), L1 (3 specimens), K1 (2 specimens), J1 (8 specimens), I1 (14 specimens), H1 (4 specimens), G1 (12 specimens), F1 (1 specimen), D1 (2 specimens), C1 (1 specimen), B1 (2 specimens), F2 (1 specimen), E2 (13 specimens), D2 (1 specimen), C2 (1 specimen), B2 (1 specimen), B5 (1 specimen), A5 (2 specimens).

Diagnosis—Narrow rostrum, with triangular ostium colliculum. Straight cauda, terminating close to well-developed posterior rim. Lobate (small lobes), oval-shaped ventral rim and rostrum, both ornamented. Dorsal rim with larger lobes but shorter than at ventral rim.

Description—Pentagonal, leptolepid-like, ostial otolith. Narrow rostrum. Ostium anteriorly depressed with large, triangular ostial colliculum. Small excisura. Straight, long cauda inclined almost to the posterior margin. In the larger specimens the cauda abuts the crista superior and the crista inferior. Crista superior shorter than the crista inferior. Small depression between dorsal margin and crista superior. Dorsal rim with 3–4 crenulations. Convex, rectangular posterior rim with tip closely approaching cauda. On large specimens the ornamentation is more pronounced than on the smaller specimens. Larger specimens are also thicker than the smaller ones. Dimensions of the otolith: $OL_{holotype}$: 2.12 mm; $OH_{holotype}$: 1.45 mm; $CaL_{holotype}$: 1.35 mm; $CaH_{holotype}$: 0.25 mm; $OsL_{holotype}$: 0.86 mm; $OsH_{holotype}$: 0.45 mm.

Discussion—The ostium is ventrally expanded, and the cauda is straight, similar to "*Argentina lobata* (Stinton, 1973)" and *Palaeoargentina bergantina*. The ornamentation of ventral margin and ventral part of rostrum is similar to *Palaeoargentina bergantina*. However, similar bur finer ornamentation is present in *Argentina sphyraena* (Linnaeus, 1758), *A. celata* (Schwarzhans, 1994), and *A. extenuata* (Stinton & Casier, 1966). On the other hand, *Palaeoargentina plicata* sp. nov. is more gracile and less robust than *Protoargentina bergantina* or "*Argentina lobata*." Its morphology, especially in small specimens, more resembles *Argentina voigti* from the Maastrichtian of Bavaria. Smaller specimens of *Palaeoargentina plicata* sp. nov. have smooth posterior and ventral parts of the otolith, smaller ostial opening with longer ostium than in A. *voigti*. Overall morphology of small specimens of *Palaeoargentina plicata* sp. nov. resembles that of *Argentina voigti* (Schwarzhans, 2010) but larger specimens of *P. plicata* sp. nov. are more clearly pentagonal and cusped. *Palaeoargentina plicata* sp. nov. occurs throughout the section at Wawął. *Palaeoargentina plicata* sp. nov. decreases in abundance in the upper part of the Wawął section. No species of *Argentina* is known from the Early Cretaceous (cf. Nolf, 2004; Schwarzhans, 2018).

Stratigraphic and Geographic Range—Valanginian, of Wawął, central Poland.

Order and family uncertain

Genus *ARCHAEOTOLITHUS* Stolley, 1912

Type Species—*Archaeotolithus trigonalis* Stolley, 1912; Jurassic of Germany, subsequently designated by Schwarzhans and Keupp (2022).

ARCHAEOTOLITHUS APTYCHOIDES, sp. nov.

(Fig. 5F)

Etymology—Named by the similarity to ammonite aptychus.

Holotype—ZPAL P. 11/18 (Fig. 5F), from sample J1.

Type Locality—Wawął, central Poland.

Type Horizon—Valanginian, *Platylenticeras involutum* zone.

Material—Unique holotype.

Diagnosis—Triangular otolith without discernible sulcus on inner face. Outer face slightly concave with weak radial furrows from the tip, crossed by one medial ring and several less visible rings on the margin. Inner face strongly convex with weak radial furrows from the tip and visible ridge from tip to margin on the right side of the otolith.

Description—Triangular, medium-sized otolith without discernible sulcus. $OL_{holotype}$: 3.60 mm; $OH_{holotype}$: 2.99 mm; $OL_{holotype}$: $OH_{holotype}$: 1.2 mm. Tip of inner face of the otolith is slightly curved to the right. Left side of the ridge of the otolith is larger than the right. No other morphological features visible.

Discussion—*Archaeotolithus aptychoides* sp. nov. morphologically resembles *Archaeotolithus bornholmiensis* (Malling & Grønwall, 1909), but differs in having much weaker radial furrows. The inner (convex) face of *A. aptychoides* sp. nov. is much more robust than the other species of *Archaeotolithus* (i.e., *A. bornholmiensis*, *A. doppelsteini* Schwarzhans and Keupp, 2022, and *A. trigonalis* Stolley, 1912). The outer face of *A. aptychoides* sp. nov. is smooth. The dorsal part is also smooth and similar to that of *A. doppelsteini*. A shallow furrow visible on the right of the ridge could be interpreted as a weak sulcus (Stolley, 1912). The large size of the otolith excludes it to be a lapillus of siluriform teleost (Schwarzhans, 2018). It is similar to paleonisciform sacculus (Schwarzhans, 2018), but the youngest representatives of this group currently known were identified from the Middle Jurassic deposits of freshwater environments (Skrzycka, 2014). *Archaeotolithus* was considered as belonging to Paleonisciformes (Schwarzhans, 2018), but it also resembles presumed sagittae of basal teleosteomorphs such as Ginglymodi or pholidophoriforms (Schwarzhans et al., 2019; Schwarzhans & Keupp, 2022). It shows some affinity to Thoracopteridae of Peltopleuriformes (Tintori & Sassi, 1992), and Neopterygii (Xu et al., 2014) due to triangular shape and radial ornamentation present in both *A. aptychoides* sp. nov. and *Thoracopterus magnificus* Tintori and Sassi, 1987. The otolith of *A. aptychoides* sp. nov. is superficially resembling aptychus (ammonoid body part, possibly a jaw fragment and an operculum), because of the triangular, convex shape with ridged ornamentation, however, it is much more complicated morphologically and lacks symmetry between left and right side of the ridge.

Archaeotolithus aptychoides sp. nov. represents the youngest species of the *Archaeotolithus* in the fossil record.

Stratigraphic and Geographic Range—Lower Valanginian, Wawął, central Poland

DISCUSSION

Structure of the Assemblage

The collection studied here consists of 568 otoliths (Table 1) and one statolith (described separately by Pindakiewicz et al., 2022). The otolith assemblage from Wąwał is dominated by Albuliformes, which contribute as much as 58% of the entire collection (Fig. 6A). The most abundant in the number of individuals are species of an argentiniform *Palaeoargentina plicata* sp. nov. (25.4%), and albuliform *Palealbula depressidorsalis* (21.5%). Albuliformes are also the most diverse group of teleosts in Wąwał (Fig. 6B). The lower Valanginian and upper Valanginian display the highest species diversity (8 species) while the lower part of upper Valanginian is less diverse with only 4 species (Fig. 1B). The latter is most likely related to the eustatic sea level rise in the early late Valanginian (Kaim, 2001; Kutek & Marcinowski, 1996), which could have restricted the abundance of teleost fishes in Wąwał, as indicated by the low number of otoliths recovered from samples of this age (36 specimens), for example by reducing the number of ecological niches available for fish to occupy. Early late Valanginian teleost diversity reduction confirms the pattern known also from benthic invertebrates (Kaim, 2001). *Pteralbula polonica* sp. nov. is abundant in the lower Valanginian (shallower part of the section and in the deep-water middle part), while it is absent in the upper Valanginian, where it is replaced by *Pteralbula galtina*. Simultaneously, *Palealbula neocomiensis* gradually replaces *Palaeoargentina plicata* sp. nov. and *Protalbula pentangularis* sp. nov. As a result, the late Valanginian otolith assemblage of the upper part of the Wąwał section strikingly resembles the Albian otolith assemblage of the Gault Clay (Young et al., 2010). This suggests that this type of teleost fish assemblage known previously from the mid-Cretaceous deposits has a much earlier origin.

Some species described from Wąwał (*Kokenichthys kuteki* sp. nov*.*, *Palaeoargentina plicata* sp. nov.) belong to groups with first occurrences previously known from the Santonian (Upper Cretaceous; Nolf, 1985) and Albian (uppermost Lower Cretaceous; Schwarzhans et al., 2022). Conversely, *Archaeotolithus aptychoides* sp. nov. and *Protoelops gracilis* sp. nov. belong to groups which previously have been known from deposits as old as the Jurassic (three species of *Archaeotolithus* from Lower Jurassic, and *Protoelops tenuirostris* and *P. cuneiformis* from Middle and Late Jurassic, respectively; Schwarzhans, 2018; Schwarzhans & Keupp, 2022). The Valanginian (Early Cretaceous) otolith assemblage from Wąwał is thus a mixture of geologically older (Jurassic) and younger (late Early and Late Cretaceous) groups. This implies that the teleost radiation (cf. Arratia, 2004; Cavin, 2008; Giersch et al., 2008) was a gradual process which started at least during the early Early Cretaceous (and perhaps even during the latest Jurassic), and lasted until the Paleocene (Arratia 2004). Accordingly, radiations of each teleost group took place at different times, possibly caused by changes in seawater temperature, paleogeography, or other paleoenvironmental factors (Cavin et al., 2007). The Wąwał assemblage studied herein seems to support this hypothesis, at least in the case of albuliforms. The radiation of this particular group started earlier than previously reported, when the temperature of seawater was lowest in the Cretaceous and roughly at the same time when the radiation of some freshwater fish took place (Cavin & Suteethorn, 2006). For example, the oldest Palealbula otoliths (*P. korchinskyi* and *P. moscoviensis*) came from Volgian (latest Jurassic–earliest Cretaceous) deposits from the Moscow area in Russia (Schwarzhans & Mironenko, 2020) and were found well within temperate waters of the Boreal Realm. Furthermore, during the Early Cretaceous, the albuliforms, in addition to marine waters, also inhabited inshore and estuarine settings, as exemplified by the early Albian *Bullichthys santanensis* from the Romualdo Member of Santana Formation, Brazil (Fara et al., 2005). Thus it is quite likely that the first albuliforms—unlike extant albuliforms, which prefer warm tropical waters (Adams et al., 2008, Nelson et al., 2016, Wallace 2014)—could have tolerated broader bathymetric, salinity, and temperature ranges than their extant descendants.

Abundance Ratio of Teleost Otoliths vs. Cephalopod Statoliths

The abundance ratio of teleost otoliths vs. cephalopod statoliths in the Lower Cretaceous (Valanginian) of Wąwał is very different from any of the Jurassic sites reported so far. The fossil assemblage at Wąwał investigated herein consists of almost 600 teleost otoliths but only a single cephalopod statolith (Pindakiewicz et al., 2022). In the Middle Jurassic localities, teleost otoliths are rare while cephalopod statoliths are common. This is well evidenced by statolith/otolith assemblages in three investigated localities in Europe: Gnaszyn (Bathonian) and Gołaszyn (Callovian) from Poland (Pindakiewicz et al., 2022), and Christian Malford (Callovian) from England (Hart et al., 2015). Our preliminary results from Gnaszyn and Gołaszyn showed that otoliths are slightly more common there than in Christian Malford (otoliths : statoliths ratio of 19% : 81% for Gnaszyn, 22% : 78% for Gołaszyn, and 7.5% : 92.5% in Christian Malford according to Hart et al., 2016). These samples indicate that the abundance ratio of teleost otoliths vs cephalopod statoliths reversed between the Middle Jurassic and Early Cretaceous (Fig. 7), possibly due to the increased abundance of teleost fishes, while statolith-bearing cephalopods started to decline somewhere between the Middle Jurassic and Early Cretaceous. The trend culminates in even younger Cretaceous deposits, as the data from Speeton Clay, U.K. (Aptian) indicate that fish otoliths comprise 75% of ear stone assemblages (Pindakiewicz et al., 2022), and in the upper Campanian samples from the type locality of Coon Creek Formation we found exclusively teleost otoliths (see also Larson, 2012; Stringer, 2016). This phenomenon could be interpreted as an impact of teleost fish radiation on abundance of cephalopods in light of the Great Teleost Radiation (Giersh et al., 2008). Possible reasons may involve the competition for prey or predation pressure on cephalopods (Smale, 1996), in particular larval and juvenile. There is evidence of fish predation on cephalopods as old as Jurassic (Prikryl et al.,2012), and it is possible that predation by ancient teleosts could have contributed to the statolithbearing cephalopod decline. In modern oceans, cephalopods are mostly preyed upon by chondrichthyans (Stevens, 1984; Smale 1996) and only a few teleosts (Maksimov, 1971; Sedberry 1983; Sedberry & Cuellor 1993). However, some extant teleosts (e.g., yellowfish tuna *Thunnus albacores* and common dolphinfish *Coryphaena hippurus*) prey on adult and subadult squids and octopods (Staudinger et al., 2013). The magnitude of teleost predation on cephalopods in extant oceans is limited by factors such as seasons, temperature and depth of water and the diversity of fish assemblages in each region (Salini et al., 1994; Smale, 1996). Modern teleost predation on cephalopod larvae and paralarvae has not been reported as significant, with the exception of the El Niño episode in 1987, when squid paralarvae and larvae bloomed and were subsequently found in stomach contents of nocturnal teleost planktivores (Vecchione, 1987). Nevertheless, the causes of negative correlation between otolith and statolith abundance could be more complex and more work on cephalopod statoliths is certainly required, in particular from the transition period between Oxfordian (Late Jurassic) and Berriasian (Early Cretaceous). Further research on localities from that period are needed to find and better understand the causes of the huge abundance shift between teleosts and cephalopods.

CONCLUSIONS

The collection of otoliths from Wawął, Poland, records a fairly diverse marine ichthyofauna in the Valanginian (Early Cretaceous) epicontinental sea. The taxa identified herein indicate that the Cretaceous teleost radiation started earlier, and also was a more gradual and long-lasting process, than previously perceived. The Early Cretaceous otolith assemblage from Wawął shows a unique mixture of Jurassic (e.g., *Archaeotolithus*, *Protoelops*) and mid- to Late Cretaceous (e.g., *Paleoargentina*, *Kokenichthys*) taxa. The material from Wawął, in addition to data from Jurassic sites, evidences a significant turnover in abundance between fish and statolith-bearing cephalopods between the Middle Jurassic and the Early Cretaceous. The reasons for this shift in abundance ratios are currently unknown, and require further investigation.

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AUTHOR CONTRIBUTIONS

MKP designed the project, analysed data, and drafted the manuscript. KH supervised the project. AK performed fieldwork and collected materials, conceived and supervised the project. All authors edited the manuscript.

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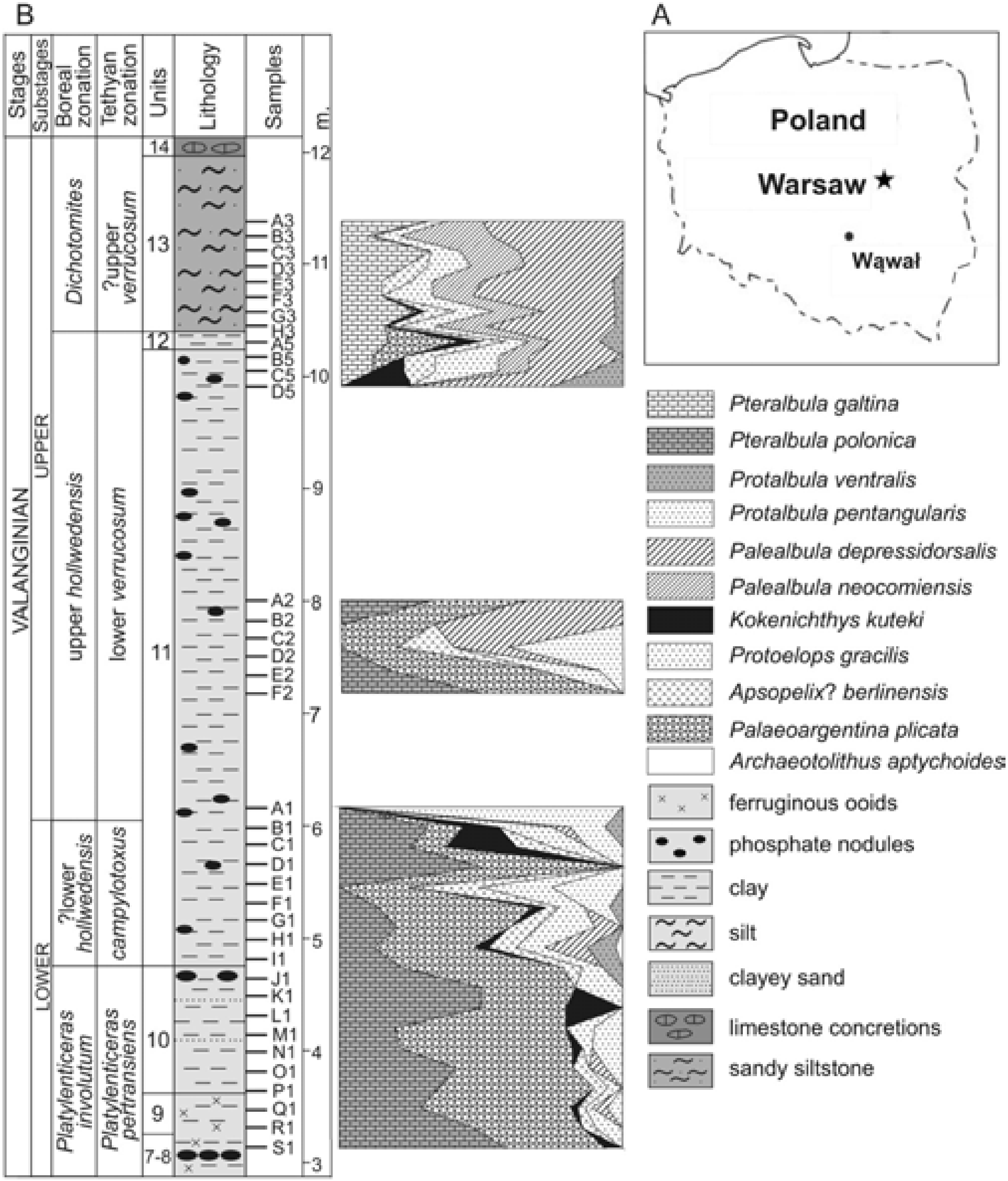

FIGURE 1. FIGURE 1. Wawął locality. A, map presenting the location of Wawął. B, vertical otolith species succession in the Valanginian at Wawął.

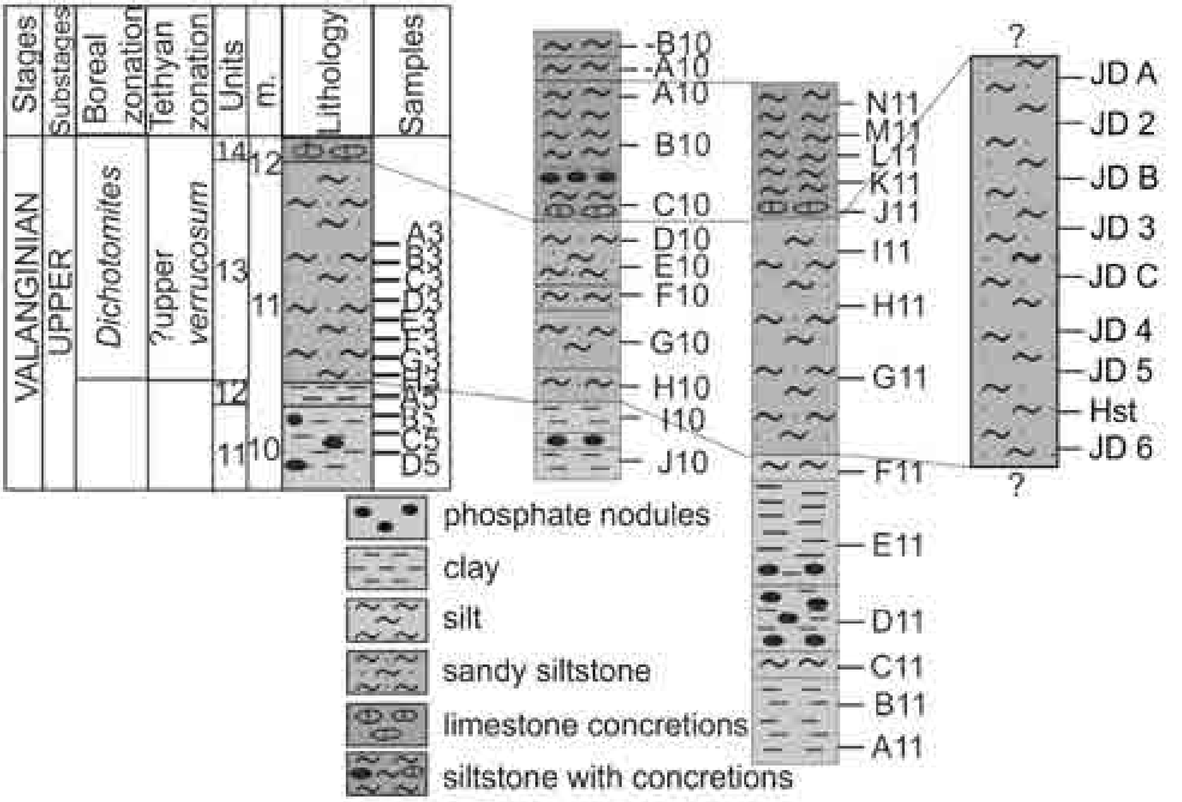

FIGURE 2. Profiles correlation in the the upper part of Wąwał section.

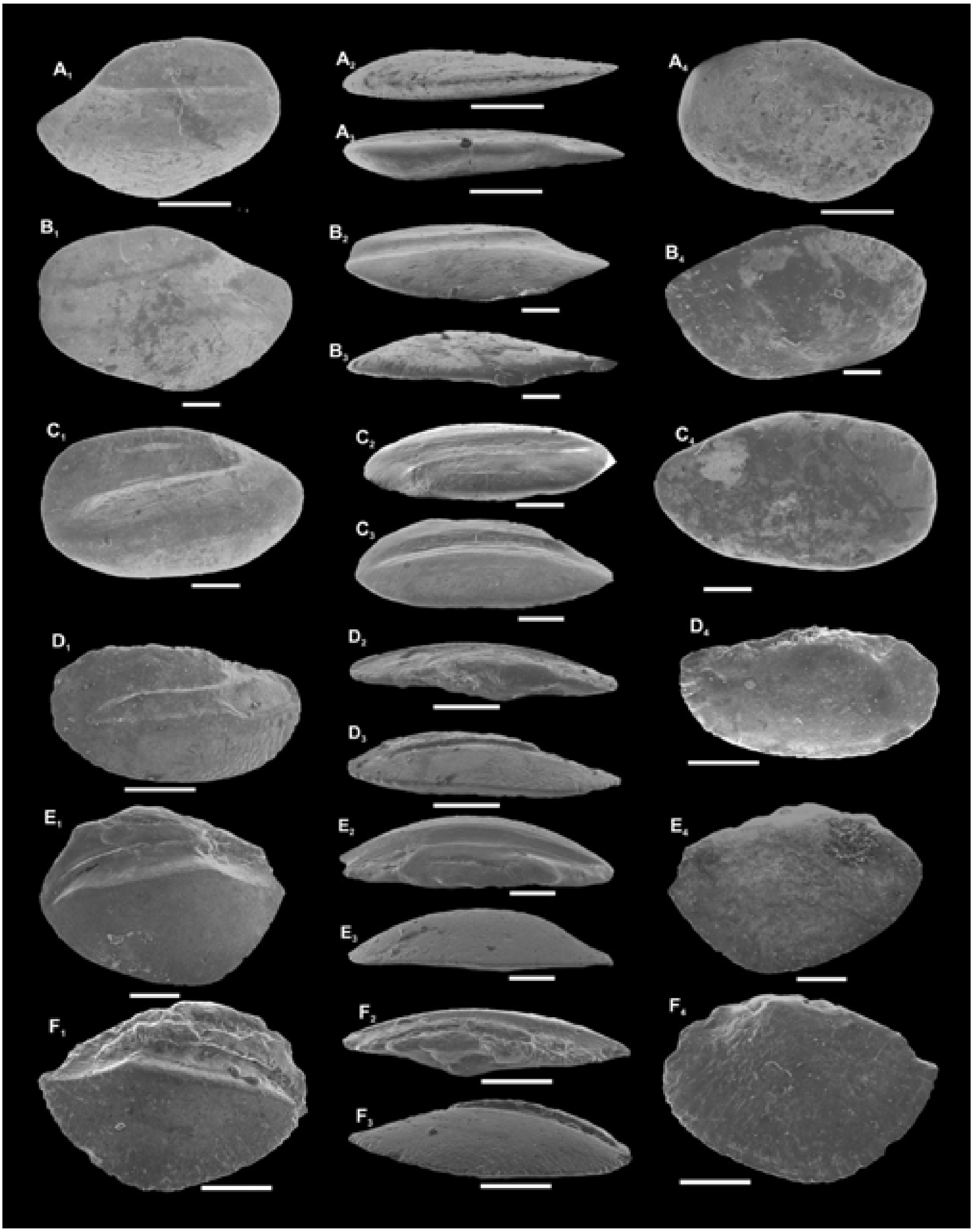

FIGURE 3. Valanginian, Early Cretaceous, teleost otoliths from Wawął, central Poland. A–C, *Pteralbula polonica* sp. nov. (ZPAL P. 11/1–3; Holotype: ZPAL P. 11/1, Fig. 3A); D, *Pteralbula galtina* KOKEN, 1891 (ZPAL P. 11/4); E, F, *Protalbula ventralis* (Weiler, 1971) (ZPAL P. 11/5–6). Abbreviations: 1, inner face, 2, ventral side, 3, dorsal side, 4, outer face. Scale: A1–A4, B1–B4 0.2 mm, C1–C4 0.5 mm, D1–D4 1 mm, E1–E4 1 mm, F1–F4 1 mm.

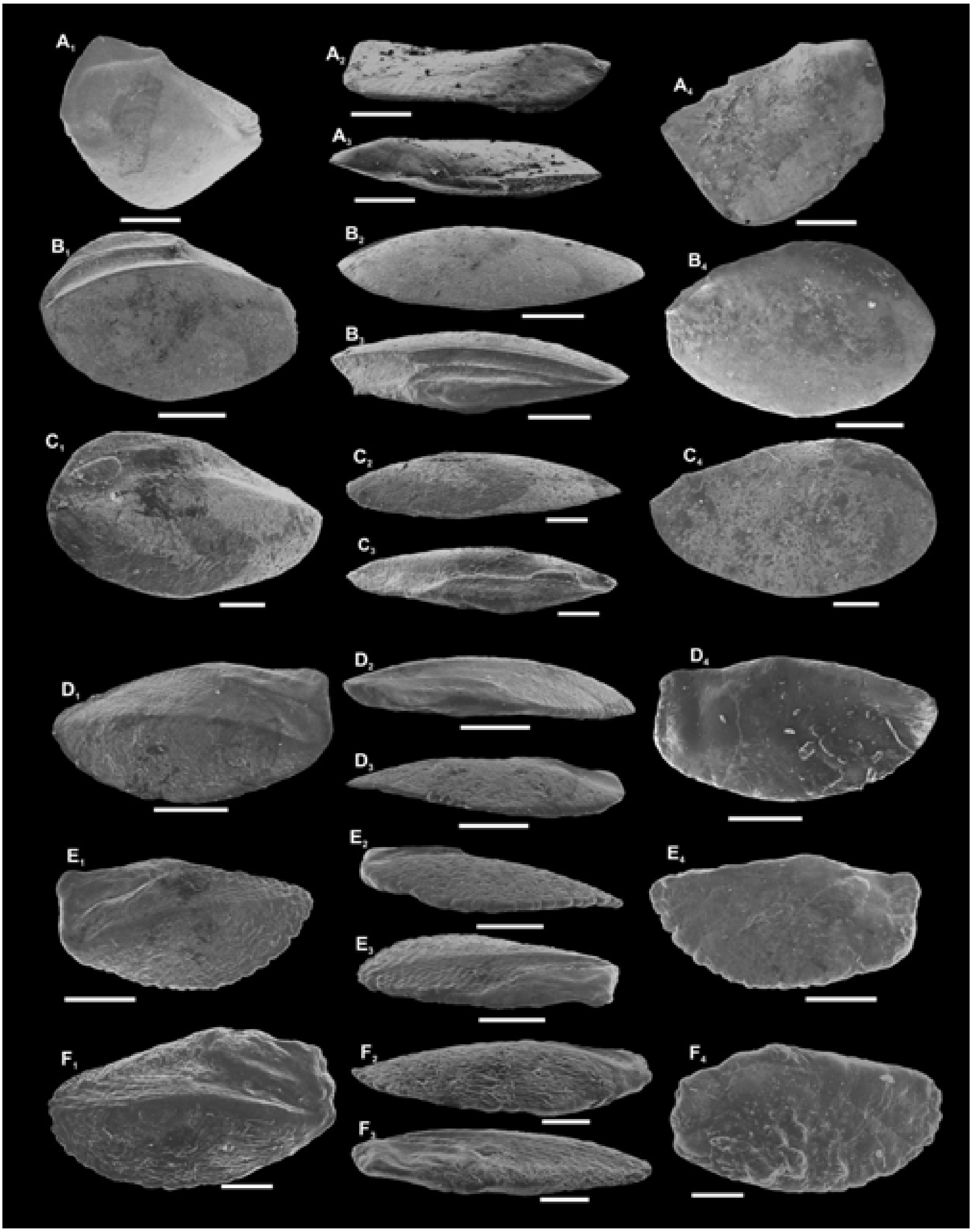

FIGURE 4. Valanginian, Early Cretaceous, teleost otoliths from Wawął, central Poland. A, *Protalbula pentangularis* sp. nov. (Holotype: ZPAL P. 11/7, Fig. 4A); B, *Palealbula neocomiensis* Priem, 1908 (ZPAL P. 11/8); C, *Palealbula depressidorsalis* Schwarzhans, 2018 (ZPAL P. 11/9); D–F, *Kokenichthys kuteki* sp. nov. (ZPAL P. 11/10–12; Holotype: ZPAL P.11/10, Fig. 4E). Abbreviations: 1, inner face, 2, ventral side, 3, dorsal side, 4, outer face. Scale: A_1–A_4 1 mm, B_1–B_4 1 mm, C_1–C_4 0.5 mm, D_1–D_4 0.5 mm, E_1–E_4 0.5 mm, F_1–F_4 0.2 mm.

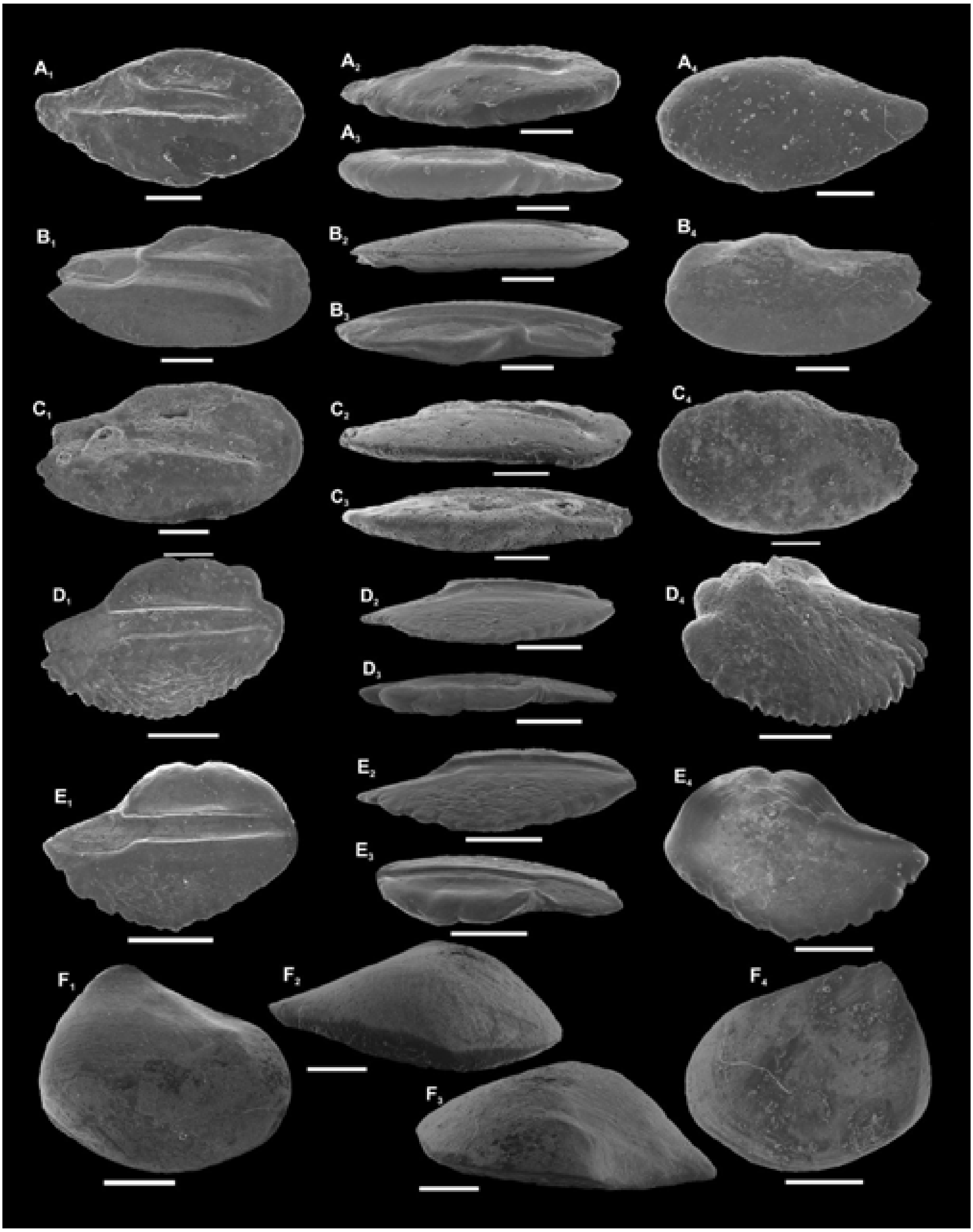

FIGURE 5. Valanginian, Early Cretaceous, teleost otoliths from Wawął, central Poland. A, *Apsopelix*? *berlinensis* Schwarzhans, 2018 (ZPAL P. 11/15);; B, C, *Protoelops gracilis* sp. nov. (ZPAL P. 11/13–14; Holotype: ZPAL P.11/13, Fig. 5B), D, E, *Palaeoargentina plicata* gen. sp. nov. (ZPAL P. 11/16–17; Holotype: ZPAL P. 11/16, Fig. 5D; Fig. D_4 in oblique view); F, *Archaeotolithus aptychoides* sp. nov. (Holotype: ZPAL P. 11/18). Abbreviations: 1, inner face, 2, ventral side, 3, dorsal side, 4, outer face. Scale: A_1–A_4 1 mm, B_1–B_4 0.5 mm, C_1–C_4 0.2 mm, D_1–D_4 0.5 mm, E_1–E_4 0.5 mm, F_1–F_4 1 mm.

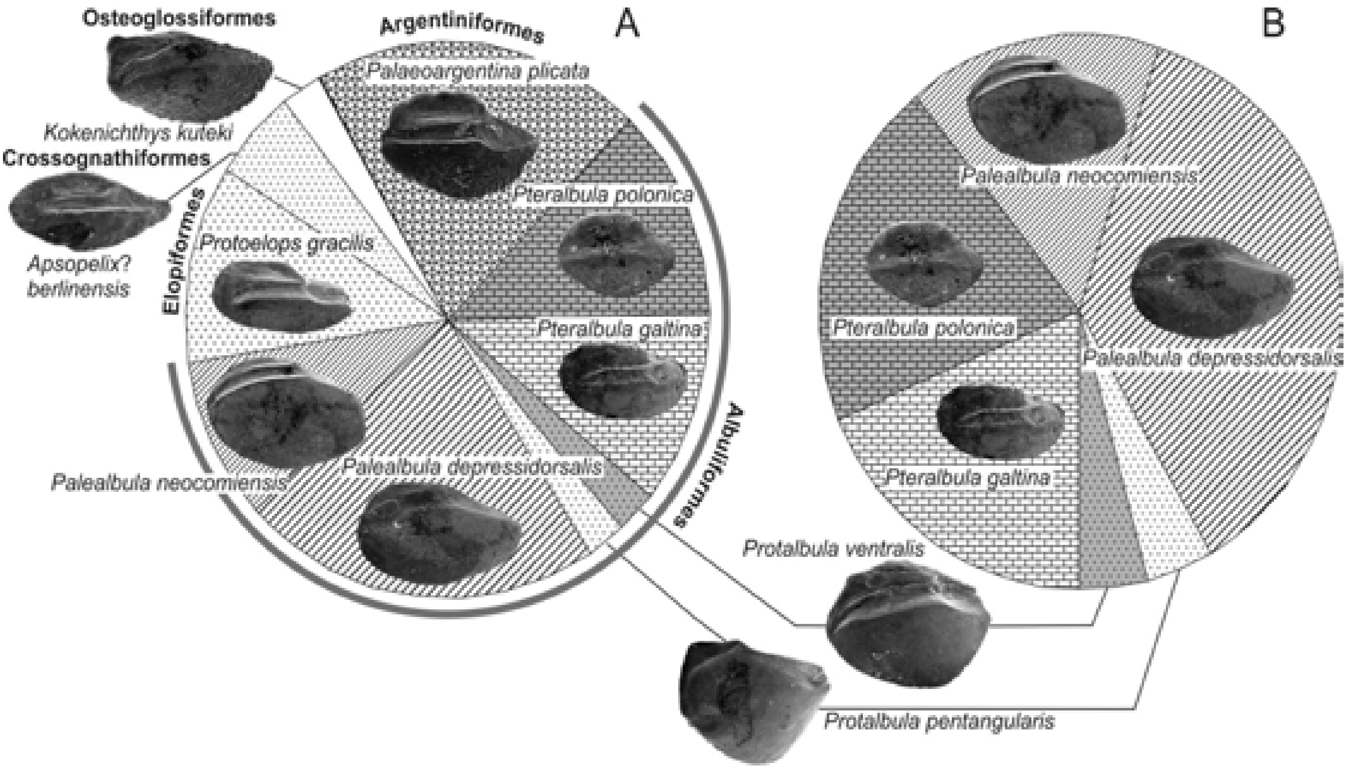

FIGURE 6. . Species abundance diagrams in Wawął section. A, overall; B, for albuliforms.

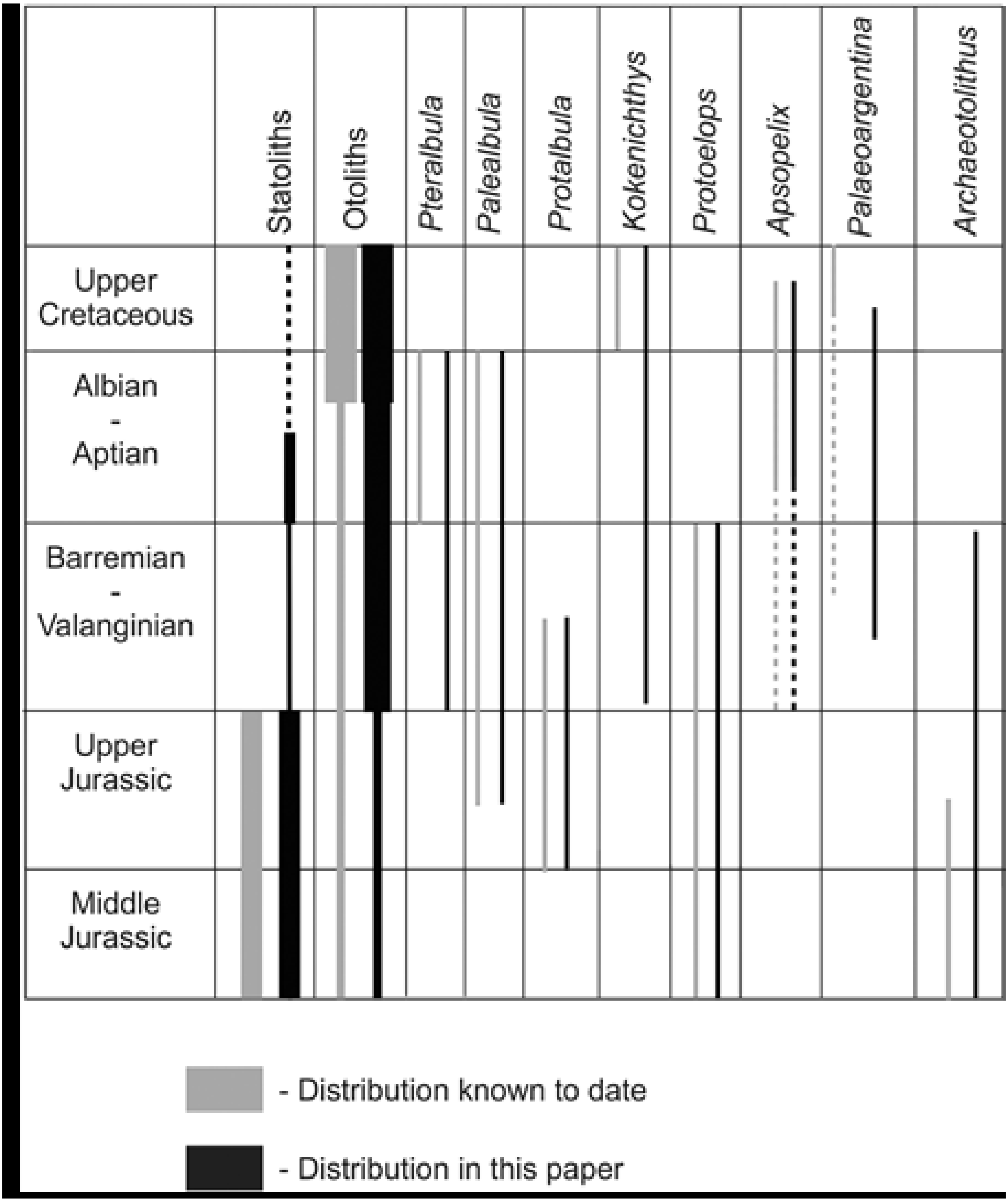

FIGURE 7. Stratigraphical distribution of cephalopod statoliths, teleost otoliths, and otolith-based genera known from Wąwał.

Species	Order	Number of Specimens	% of Assemblage
Pteralbula galtina	Albuliformes	81	11.6
Pteralbula polonica	Albuliformes	89	12.7
Protalbula pentangularis	Albuliformes	18	2.6
Protalbula ventralis	Albuliformes	19	2.6
Palealbula depressidorsalis	Albuliformes	160	22.9
Palealbula neocomiensis	Albuliformes	68	9.7
Palaeoargentina plicata	Argentiniformes	147	21.0
Kokenichthys kuteki	Osteoglossiformes	18	2.6
Protoelops gracilis	Elopiformes	83	11.9
Apsopelix? berlinensis	Crossognathiformes	38	5.4
Archaeotolithus aptychoides	Unknown	1	0.1

TABLE 1. Absolute and relative abundances of Valanginian, Early Cretaceous, teleost otolith species from Wawął, central Poland.

Chapter III

A microfossil evidence for the composition of fish communities in the Late Triassic of Tethys: examples from Cassian Formation, Italy

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ABSTRACT— During the Triassic, fish were the most abundant group of marine vertebrates – in terms of both species richness and number of niches they occupied – as indicated by their rich skeletal record. However, the Triassic ichthyolith record is relatively poor, unlike that from younger time periods, what skews the published palaeontological data heavily towards skeletal materials. Our bulk collecting targeting fish microfossils from soft siliciclastics in the Cassian Fm. resulted in a collection of several ichthyoliths (i.e. bone fragments, teeth and scales) and otoliths in Picolbach, Settsass Scharte, Stuores and Misurina Skilift localities in Dolomites, Southern Calcareous Alps, Italy. We compare this microichthyofauna with other such faunas and in particular with the Jurassic–Cretaceous otolith-based faunas and their Cenozoic and Recent counterparts. We argue that most of the otoliths from Picolbach belong to a variety of actinopterygians, from stem- neopterygians (most likely peltopleuriforms), to holosteans. Otoliths from Settsass Scharte are reminiscent of teleost otoliths rather than 'palaeoniscid' otoliths as it was suggested previously, and may therefore constitute the earliest-known occurrence of such otoliths to date. From the microfossil point of view, the Cassian Fm. fish associations were comparable to the roughly coeval skeletal associations of the late Ladinian–Carnian, and Norian age from Austria and northern Italy (e.g. Raibl, Polzberg and Bergamo Lagerstätten). We argue that Carnian (Late Triassic) Tethyan marine fish fauna was quantitatively dominated by neopterygians other than teleosts, and may represent a very early stage of teleost diversification. It seems also that Triassic Tethyan chondrichthyan fauna was limited to durophagous forms only.

SUPPLEMENTARY FILE(S)—Supplementary file(s) are available for this article for free at:
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INTRODUCTION

The Permian–Triassic and Early Triassic extinction events – as well as the post-extinction recovery of metazoans during the Triassic – resulted in pronounced changes in the composition of marine fish communities (Stanley 2009; Benton *et al*. 2013; Romano 2021; Benton & Wu 2022). Among elasmobranchs, for example, neoselachians comprising modern sharks, diversified slowly from the Early Triassic onwards (Cuny & Benton 1999), but it was more ancient hybodontiforms that remained the dominant sharks during the Triassic. Some other groups, like the modern ray-finned fishes (i.e. neopterygians) diversified strongly during the Triassic, as indicated by the skeletal fossil record (Tintori *et al.* 2014), and teleosts, a clade of neopterygians comprising 96% of extant bony fish species, probably emerged somewhere around late Ladinian and early Carnian (Arratia 2013, 2017; Tintori *et al.* 2015). It suffice to say that the foundations of modern marine fish fauna were laid during the Middle–Late Triassic. While it was in fact a drawn-out process which cannot be tied to any single cause or moment in time, but should be seen as a part of broader increase of predatory behaviours termed Mesozoic Marine Revolution, which started sometime during the Triassic and accelerated around the Late Triassic (Tintori *et al.* 2014; Benton & Wu 2022).

The fossil record of bony fishes is based on both macro-, and microichthyofossils, the former comprising variously preserved skeletons, and the latter of ichthyoliths, i.e. isolated teeth, scales and bone fragments as well as otoliths. Otoliths are paired, calcareous (mostly aragonite, rarely vaterite) and protein structures inside of fish inner ears, responsible chiefly for the sense of balance. Otoliths grow continuously during the fish lifetime, and their morphology is genus, or even species-specific (Nolf 2013). Jurassic and Cretaceous fish otoliths are becoming increasingly well-known and provided important information on later Mesozoic fish evolution in addition to rich skeletal materials (Stinton 1973; Stringer 2016; Stringer *et al.* 2016, 2020; Schwarzhans 2018; Schwarzhans & Mironenko 2020; Schwarzhans & Keupp 2022; Schwarzhans *et al.* 2022; Pindakiewicz *et al*. 2023). On the contrary, very little is known about Triassic fish microichthyofossils and otoliths (cf. Tintori & Sassi 1992; Tackett *et al.* 2023). This potentially could have broad implications for the knowledge of Triassic fish history, especially in the sequences where the skeletal fossils are rare or absent.

In this study we present new findings of microichthyofossils (ichthyoliths and otoliths) from the Carnian (Upper Triassic) Cassian Formation in the Northern Italy, during the Middle–Late Triassic diversification of bony fishes. The Cassian Formation is world-renowned for its exquisitely preserved and highly diverse invertebrate fossils, mostly bivalves and gastropods (e.g. Bandel 1996; Nützel 1998; Nützel & Kaim 2014). Vertebrate fossils are much less common in the formation and comprise, among others large marine reptiles (Bizzarrini *et al.* 2001), and only a few chondrichthyan and actinopterygian teeth and scales (Bernardi *et al*. 2011). Otolith findings in the Cassian Formation are excessively rare, as only two specimens were previously reported from Settsass Scharte locality by Nützel & Kaim (2014). In this paper we describe a new collection of otoliths from the Cassian Formation. Given the different preservation potential of otoliths versus fish macrofossils, we discuss various ramifications of our discovery, in particular for the Cassian Fm. fish ecology and general Late Triassic history of marine fish communities.

GEOLOGICAL SETTINGS

The Cassian Formation is world-renowned for yielding exceptionally well-preserved fossil invertebrates and crops out at several localities in Northern Italy (Southern Calcareous Alps). The base of the Cassian Formation is dated as Ladinian in age (Middle Triassic), while the remaining strata are Carnian in age (Late Triassic; Fürsich & Wendt 1977; Mietto *et al*. 2012). The section of the Cassian Formation at Stuores Wiesen exposes also Global Boundary Stratotype Section and Point (GSSP) of the Carnian Stage (Mietto *et al*. 2012). The Cassian Formation was deposited in an open marine, tropical setting during breakup of Pangea at the western end of Palaeotethys/Neotethys system (Bernardi *et al.* 2018) (Fig. 1). It consists of sediments of slope and central basin floor, including those redeposited from shallow water carbonate platform settings (e.g. back-reef). These redeposited shallow water deposits, including iconic carbonate 'Cipit Boulders' (platform-derived olistoliths and clasts fed to the basin and not affected by the extensive dolomitization as happened to the platforms themselves), provided up to date over 1400 species of invertebrates, mostly molluscs and echinoderms (e.g. Roden *et al.* 2020a, b).

Skeletal fish fossils from the Cassian Formation, collected from as early as the first half of twentieth century, contain mostly scales, teeth and other isolated skeletal remains (Boni 1941). Only a few hybodont sharks and colobodontid fishes were described from the Cassian Fm., based on fragmentary spines, scales and teeth (Bernardi *et al.* 2011). The fish material described herein was found at four localities: Misurina Skilift (near Cortina d'Ampezzo – 46°35'26.6'N 12°15'36.8'E) Picolbach (within Stuores Wiesen – 46°32'03.4'N 11°55'21.1'E), Settsass Scharte (46°31'02.0'N 11°57'30.2'E), and Stuores-02 (46°31'43.6'N 11°56'12.5'E) (Fig. 2). Deposits cropping out at these localities each represent slightly different environments. Deposits cropping out at Misurina Skilift are brown and greyish marlstones with fragments of larger grains, and fauna is mostly allochthonous (Nützel *et al.* 2010). At Picolbach and Stuores-02 localities, the deposits comprise greyish marlstones mixed with calcareous marls or limestone grains, mostly autochthonous or parautochthonous (Urlichs 1974). The sediments cropping out at Settsass Scharte are composed mostly of brownish, grey, poorly lithified claystones to marlstones, with some thin interbeds of marly, grey to orange limestones (Nützel & Kaim 2014). All four localities represent an open marine environment (Fig. 3), with Misurina Skilift representing the shallow part and most proximal to the carbonate platform, while Picolbach the deeper part, distalmost to the platform (Roden *et al*. 2020b). Based on the invertebrate fauna found in these localities, the age of the sediments was determined as early Carnian (Urlichs 1994). The invertebrate fossil faunas from Settsass Scharte and Picolbach have more autochthonic appearance in contrast to their counterparts from the Alpe di Specie, Misurina Skilift, and Rumerlo (Roden *et al.* 2020a) which are characterized by more considerable admixture of shells redeposited from shallower settings (mostly carbonate platforms).

MATERIAL AND METHODS

We sampled several localities in Cassian Formation known to yield invertebrate fossils, but only four of them yield ichthyoliths and/or otoliths. Out of these four localities (Misurina Skilift, Picolbach, Settsass Scharte and Stuores-02), scales, fish bones and fragments of jaws were found only at Picolbach. The same locality yielded also the majority (nine) of the otoliths in our collection. Three additional otoliths were found at Settsass Scharte, and two in the Misurina Skilift section. No cephalopod statoliths have been identified in the investigated samples. All the otoliths are complete with visible morphological features, without traces of envelopment or digestion. Two shark teeth were found at Settsass Scharte. We also identified chondrichthyan scales and cephalic spine in Stuores-02 locality. All these fossils (with the exception of the cephalic spine and jaw) are mostly well preserved with recognizable morphological features, without traces of digestion or envelopment.

This research is based on surface collection and bulk samples from localities of Cassian Fm. known to yield rich fossil assemblages. Surface samples were collected first, after searching for the richest places in each locality, within a 1–1.5 hour time span, and later the material-rich spots were bulk sampled. Collected material was processed at the Institute of Paleobiology of Polish Academy of Sciences, Warsaw, Poland.

The bulk samples were first dried, and next wet sieved in water with detergent (without using hydrogen peroxide), with mesh diameter of 0.375 mm. After drying, the fossils were picked manually from residue under a binocular. The fish specimens were identified, and documented under SEM. One of the otoliths (PZO 16408) has been scanned in a micro-CT scanner at the Laboratory of Microtomography, Institute of Paleobiology PAS, to better depict its 3D morphology. The material described in this paper is deposited in Naturmuseum Südtirol, Bozen, Italy (prefix PZO).

In case of otoliths, we decided against employing formal taxonomy in this paper due to difficulties in establishing diagnostic characters, which would be satisfactory to differentiate biological taxa of low rank (genera and species). The two crucial points that led us to such a decision are: 1) most otoliths in our materials likely belong to young juveniles, when taxonomically important features of the otoliths have not fully developed yet; and 2) very little data is available on Triassic otoliths to date, especially in comparison to their Jurassic, Cretaceous and Cenozoic counterparts. Therefore, we decided to provide only the preliminary high rank taxa interpretations. For higher rank taxonomy, we followed phylogenetic works on Triassic actinopterygians from China and their phylogeny by Xu (2020, 2021). The following anatomical abbreviations were used: H, height, L, length,

RESULTS

Teeth from Settsass Scharte

The teeth found at Settsass Scharte (PZO 16405, PZO 16406; Fig. 4A, B) have edged series of cusps with anastomosing ridges on the crowns. Shape of the crown is coarse, with complex ornamentation (PZO 16405; Fig. 4A). The crown grows on elongated, bulbous base. One of the teeth comprise two crowns fused with their bases (PZO 16406; Fig. 4B).

Scale from Stuores-02

The dermal denticle found in Stuores-02 is robust, with several odontoids (PZO 16403; Fig. 4C). The odontoids are flattened, and oriented in one direction. The basal part of the scale connects all odontoids. The scale is eroded and broken on the margins.

Cephalic spine from Stuores-02

The cephalic spine (PZO 16404; Fig. 4D) is incomplete, with triradiate base and small fragment of spine preserved. Most of fish microfossils from Misurina Skilift, Settsass Scharte, and Picolbach, are otoliths (Figs 5–7).

Otolith morphotype A and B

The slender otoliths from Misurina Skilift, Settsass Scharte and Picolbach (PZO 16394, PZO 16395; Fig. 5A, B, PZO 16407; Fig. 5C, and PZO 16396; Fig. 5D) are rectangular and in gross morphology reminiscent of rhomboidal chondrostean fish scales. These otoliths are robust, with undulated inner face. The smaller otolith is thicker, with basal rounded base, and the thinner, more oval, and flattened part, that grows from the otolith base (PZO 16394; Fig. 5A). The larger otolith is more robust, undulated and massive, than the smaller specimen (PZO 16395; Fig. 5B).

Otoliths from Settsass Scharte

The two left otoliths found in Settsass Scharte (PZO 16408, PZO 16409; Fig. 6A–C, Supplementary File 1) are large, have well-developed dorsal and ventral rims. The inner face of the otolith has a medial, shallow sulcus, a long antirostrum and shallow excisura. The sulcus opens anteriorly with a short and only slightly widened ostium; the cauda is posteriorly distinctly widened and approaches close to the posterior rim of the otolith. The dorsal depression is elongated, terminated at the antirostrum. The dorsal rim has large anterodorsal angle, and small posterodorsal angle, close to the posterior rim. The ventral part of the otolith is wide, with a medial angle. The ventral rim is thinner than the dorsal rim.

Otoliths from Picolbach

The otoliths found in Picolbach display more complicated morphologies (Fig. 7A–E) and are characterized by a presence of right and left counterparts. The morphology of the first pair (Triassic Otolith Morphotype C) differs from all the other otoliths in triangular, robust basal part, and a thin, long oval margin growing from the base of the otolith (PZO 16397; Fig. 7A). The second and third pair (Triassic Otolith Morphotype D) consist of small, robust, and ovalshaped otoliths, with a depression on the inner face (PZO 16398, PZO 16399; Fig. 7B, C). The otoliths of the fourth pair (Triassic Otolith Morphotype E, PZO 16400; Fig. 7D) are elongated and deltoid-shaped, with a massive posterior part and much thinner anterior. The anterior part of the otolith ends up with a triangular and thin tip. The inner face of the otoliths is undulated. Another otolith from Picolbach (Triassic Otolith Morhotype F, PZO 16401; Fig. 7E) is massive, bivalve-shaped with thinner margins.

Jaw fragment from Picolbach

The jaw fragments found in Picolbach (PZO 16402; Fig. 8A) possess two sets of small, conical teeth. Some of them resemble teeth attributed to *Colobodus* sp. (Fig. 8A$_5$) by Stolley (1920).

DISCUSSION

We attribute the shark teeth found at Settsass Scharte (PZO 16405–6) to *Acrodus*, a genus of large hybodontid sharks in marine environments ranging from Permian to Paleocene (Mutter, 1998, Niedźwiedzki *et al*. 2021). One of the two identified teeth (PZO 16406) has two crowns, which emerge from a single massive base (Fig. 4B) and most likely represents a pathological feature, i.e. the old tooth was too firmly attached to a new one and both remained in the jaw after teeth replacement. Such pathology may result from a fusion or germination. Similar teeth pathological replacement is more common in carnivorous sharks (Miller *et al.* 2022), with fossil records as old as the Devonian (Botella *et al.* 2009). Very similar pathologies were also found in *Lissodus* teeth from the terminal Permian of Russia (Pindakiewicz *et al.* 2020). Both *Acrodus* and *Lissodus* are interpreted as durophagous sharks (Hagdorn 2002; Hagdorn *et al.* 2011). Two caveats here are that: 1) teeth pathologies are uncommon among durophagous sharks (Becker *et al.* 2000); and 2) a spectrum of pathologies is known in teeth of older, carnivorous sharks (Botella *et al.* 2009). Hence, the pathological tooth from Cassian Formation could indicate a carnivorous ancestry of *Acrodus*, or the species of this genus had a more opportunistic diet (Bernardi *et al.* 2011). The scale found in Settsass Scharte resembles the scales of more basal groups of sharks. Hybodonts display a number of scale types that are unique for the group co-occurring within single shark specimen (Ginter 2014). Cephalic spine (Fig. 4D) found in Settsass Scharte is not very informative but its morphology is typical of hybodonts (Romano & Brinkmann 2010).

The main group of fish microfossils in the Cassian Fm. are otoliths (Figs 5–7). Three pairs of neopterygian otoliths (interpreted herein as stem-neopterygian, most likely peltopleuriform otoliths), and those of basal teleosts occur in the assemblage. Stemneopterygian otoliths from Misurina Skilift called Triassic Otolith Morphotype A and B (Fig. 5A, B) resemble the utricular otoliths (lapilli) of *Thoracopterus magnificus* (Tintori & Sassi 1992; see also Xu *et al*. 2013 for general position of Thoracopteridae within Actinopterygi). In case of Triassic Morphotype B the resemblance is strong enough to consider assigning it to Thoracopteridae indet. More stem-neopterygian otoliths were found at the Misurina Skilift, Settsass Scharte and Picolbach (Table 1), suggesting that they were broadly distributed throughout the basin. The relative similarity between Triassic otolith Morphotypes A and B in terms of shape and size indicate that they may belong to closely related, or even a single species. The only stem-neopterygian found in Cassian Fm. is *Colobodus* (Bizzarinni *et al.* 2001, Bernardi *et al.* 2011). In Picolbach we found a fragmental jaw of ?*Colobodus* sp. with teeth we interpret as larval because of: 1) monotrichous arrangement of simple, conical teeth; and 2) the absence of fully developed acrodin cup located next to the fully developed, barrel-like teeth typical for adult fish (PZO 16402), as observed in teeth of *Polypterus* and *Lepisosteus* (Wacker *et al.* 2001; Sasagawa *et al.* 2013) The fragments of juvenile ?*Colobodus* sp. could be transported to the deepest part of the Cassian basin either from shallow water settings, or from the water column (epipelagial).

The two otolith specimens from Settsass Scharte figured previously by Nützel & Kaim (2014) were then interpreted as a palaeoniscoid type (following Nolf 1985). Indeed, features like: 1) well-developed dorsal rim; 2) well-developed posterior rim; 3) narrow, straight, concave structure from posterior rim towards the ventral rim; 4) medial sulcus; 5) deep ventral rim; and 6) irregular, convex outer face, are similar to those of palaeoniscid-attributed otoliths described from the Palaeozoic (Nolf 1985, 2013). However, the identity of palaeoniscids is currently debated, and the consensus is that the group is polyphyletic and represents a bucket taxon for various lower actinopterygians (Gardiner & Schaeffer 1989; Coates 1998; Stack & Gottfried 2022). In any case, we consider the otoliths figured by Nützel & Kaim (2014) to represent the same taxon as our basal teleostean morphotype in Figure 6 and Supplementary File 1 found at the same location.

The medial, shallow concave structure of the otoliths in question is reminiscent of *sulcus acousticus* of teleost sagitta and *fossa acoustica* of teleost asteriscus but not with convex *gibbus maculae* of lapillus (Assis 2003, 2005). After rendering a 3D model, and removal of adhering sediment and recrystallization remains (Supplementary File 1a, b) we recovered features, which allow to interpret this otolith as a sagittal otolith of potentially basal teleost affinities: 1) the dorsal depression elongated and terminated at the antirostrum; 2) two dorsal angles; large anterodorsal, and small posterodorsal, close to the posterior; 3) the thin ventral rim, with medial angle; 4) long antirostrum; 5) shallow excisura; and most importantly, 6) presence of a sulcus with indication of ostium and cauda.

Teleost fossils like ichthyokentemids and pholidophorids have been found in the area (Dalla Vecchia 2020; Griffith 1977; Tintori & Lombardo 2018; Tintori & Castelnuovo 2023). As the paleoenvironment at Picolbach and Settsass Scharte was characterized by relatively slow sediment accumulation rates and restricted transport of the material, our finding could indicate, that basal teleosts could have lived in relatively open marine environments. During Carnian, teleosts and their closest relatives were common in some environments (Griffith 1977), although they were mostly of small size (between 32–64 mm long) and relatively species-poor, but their diversity gradually increased over time (Romano *et al.* 2016).

The majority of otoliths at our disposal were found at Picolbach, i.e. at a locality with sediments representing the deepest part of the basin (according to Roden *et al.* 2020b). Among nine otoliths found at Picolbach, there seems to be four pairs, one pair of Triassic otolith Morphotype C interpreted here asputative lapilli (Fig. 7A), two pairs of Triassic Otolith Morphotype D also interpreted here as putative lapilli (Fig. 7B, C), one pair of unusually elongate Triassic Otolith Morphotype E (Fig. 7D), and one additional specimen of Triassic Otolith Morphotype F (Fig. 7E). Morphologically they resemble larval otoliths of alligator gars (Long & Snow 2016) belonging to Ginglymodi, a holostean clade uniting extant gars and their extinct relatives (López-Arbarello 2012). The identification of the ginglymodian, or more generally the holostean otoliths is much more difficult than their teleost counterparts (Nolf 2013), hence the identification of our materials is rather generic. The morphology of ginglymodian larval otoliths is changing during ontogeny, adapting to the growing inner ear of the fish (Long & Snow 2016). We are not aware of any studies of ontogenetic changes in otolith shape in other extant or extinct holostean fish otoliths other than alligator gars, but based on this example, we speculate it might occur also in other extant and extinct holostean taxa. We also argue that paired otoliths from Picolbach cannot be safely placed in any major Triassic fish clade other than perhaps Holostei. Based on their relative morphological similarity, we could not state with sufficient confidentiality that they belong to one or more species, or even to family. It is worth noting however, that these putative Triassic holostean otoliths from Picolbach are very similar to their recent counterparts, what may suggest little evolutionary change of this structure since the Triassic times.

Although morphologically the Triassic Otolith Morphotypes C and D studied here have features indicating that they came from a juvenile animal, and are of similar shape, they are six-seven times larger than equivalent structures in alligator gar larvae, the only extant counterpart of holostean larval otoliths (L/H in Triassic Otolith Morphotype D: 1.2–1.5 vs L/H in alligator gar larvae lapilli: 1.2; L in Triassic Otolith Morphotype D: 0.51–0.75 mm vs L in alligator gar larvae lapilli: 0.26 mm; L/H in Triassic Otolith Morphology C: 1.5–1.6 vs. L/H of alligator gar larvae: 1.4; L in Triassic Otolith Morphotype C: 0.73 mm vs L of alligator gar larvae asterisci: 0.15 mm; data on modern gars from Long and Snow 2016). The size difference could suggest that they do not belong to the larvae of ginglymodian relatives, but to some other holosteans. At this point it is difficult ascertain whether it is derived morphology of ginglymodians or the ancestral form of lower holosteans.

The Cassian Formation is well-known for its rich invertebrate (especially molluscan) faunas of autochthonous, parautochthonous, and allochthonous origin. The lower diversity of some invertebrate Cassian Fm. faunas (e.g. Picolbach) with relative abundance of fragile fish microfossils, suggest more autochthonous and parautochthonous (basinal) origins of such faunas (Hausmann *et al.* 2021). Somewhat similar environments could be also present in the Misurina Skilift locality (Roden *et al.* 2020a). Settsass Scharte displays sediments of a deeper part of the marine basin in comparison to the Misurina Skilift locality, although the fauna from Settsass Scharte is still rich in invertebrates and especially in infaunal taxa (Nützel & Kaim 2014). Picolbach represents the deepest part of the basin, with most autochthonic infaunal benthic invertebrates, and very slow or almost absent currents (Roden *et al.* 2020b). Based on the depositional environment and richness of invertebrates, and relative abundance of otoliths and shark teeth within these localities we can conclude that: 1) the Carnian ichthyofauna from the deeper parts of the

Cassian palaeobasin was composed of neopterygians, especially holosteans; and 2) putative basal teleosts were less abundant than neopterygians and stem-neopterygians.

To date, the only fragments of stem-neopterygians (?*Colobodus* sp.) and ichthyoliths of hybodonts (Bernardi *et al*. 2014) were found in the Cassian Formation. The variety of otoliths reported in this contribution displays a more diverse ichthyofauna, than suggested from fragmented, skeletal fossils remains. This 'overlap' is in agreement with skeletal data from slightly older (late Ladinian–early Carnian) localities of Raibl Formation, Northern Calcareous Alps, Northern Italy (Tintori & Castelnuovo 2023), and from Polzberg Lagerstätte in Northern Calcareous Alps, Austria (Griffith 1977; Lukeneder & Lukeneder 2021), roughly coeval to Cassian Fm., and from younger (Norian) localities of Zorzino Limestone Formation, near Bergamo, Southern Calcareous Alps, Italy (Tintori & Lombardo 2018). The Raibl localities represent shallow marine environment with limited terrestrial influence from islands (Dalla Vecchia 2020). Polzberg represents a shallow part of the basin, with fluvial influence (Lukeneder & Lukeneder 2021). The Zorzino Limestone of Bergamo represents a fully marine environment (Tintori 1998; Tintori & Lombardo 2018).

Ichthyofaunas found in these three abovementioned localities include lower actinopterygians (saurichthyiforms, birgeriiforms), stem-neopterygians (colobodontids, peltopleuriforms), holosteans, and basal teleosts (pholidophorms and ichthyokentiforms). The main predators were likely large actinopterygians like *Saurichthys* and *Thoracopterus*, while neopterygians like holosteans and basal teleosts filled lower trophic niches (Griffith 1977; Tintori & Castelnuovo 2023). The niche of large durophagous fishes was largely filled by some hybodontid sharks, while their more carnivorous relatives have not been recorded (Bernardi *et al*. 2011; Krainer *et al*. 2011; Lukeneder & Lukeneder 2021). Smaller fishes with durophagous behaviour were mostly represented by stem-neopterygians, most likely peltopleuriforms (Tintori & Castelnuovo 2023). The composition of the otolith assemblage studied here suggest that the fauna comprised a higher abundance of holosteans than stem-neopterygians and rare putative teleosts. The otolith assemblage resembles mostly open marine ecosystem, described from Norian localities near Bergamo, where also the most abundant fishes were holosteans (Tintori & Lombardo 2018).

The ichthyolith assemblage from Cassian Fm. shares hybodontid shark (*Acrodus* sp. represented by tooth, scale and cephalic spine) with both Raibl and Polzberg faunas. Only one fragment of a jaw of a juvenile stem neopterygian (?*Colobodus* sp.) was found, but no fragments from adults. Likewise, no teeth of *Saurichthys* were found in our materials; only a single tooth of this large predator was found in Cassian Fm. to date (Bizzarinni *et al*. 2001), which indicates this fish could have been quite rare in this basin. The summary of the above otolith and ichthyolith evidence from our study and those published elsewhere indicates an open marine character of Cassian Fm. fish assemblage, with some contribution of more cosmopolitan, and even coastal elements.

The possible occurrence of basal teleost otoliths in the Carnian is plausible since in the Ladinian (Middle Triassic) this group has just started to slowly diversify (Tintori 1990, Tintori *et al.* 2015, Arratia 2017). It was hypothesized that this diversification of teleosts have accelerated around the Carnian Pluvial Episode, between *Trachyceras aonoides* and *T. austriacum* Biochrone transition, and *Tropites subbulatus*

Biochrone in the Carnian, i.e. shortly after the Cassian Formation was deposited (Arratia 2017; Bernardi *et al*. 2018). Thus, the rarity of possible teleosts in the Cassian Formation could be partially explained on stratigraphic and evolutionary grounds. It could also be taphonomic, because thin bones and scales, and small teeth have lower preservation potential than thicker scales and larger teeth of other actinopterygians. Elsewhere, teleosts are represented in the Carnian by some pholidophoriforms (Arratia 2017) in Raibl, and ichtyokenentemids (Griffith 1977) in Polzberg.

CONCLUSIONS

The upper part of the Cassian Formation (Carnian, Italy) does not yield well-preserved skeletal fish fossils but their microfossils could be useful in determining the composition of the ichthyofauna in the Cassian Fm. The ichtyolith data presented herein document a tropical marine fish fauna from the Cassian palaeobasins prior to establishment of marine fish faunas dominated by teleost fishes. The otolith, teeth and scale assemblage shows that open marine waters were populated by stem-neopterygians and holosteans, while putative basal teleosts were less common, and sharks were represented by large durophages. The basinal fish microfossil assemblage from the Cassian Formation is reminiscent roughly of the Carnian Raibl skeletal fish assemblage from the Northern Calcareous Alps, and the Norian Bergamo (Zorzino Limestone) skeletal fish assemblage from the Southern Calcareous Alps. Our findings indicate that holosteans and basal teleosts were relatively common in the Late Triassic Cassian palaeobasins, a conclusion partially overlapping with that drawn based on general skeletal data for other Late Triassic settings (Romano *et al.* 2016). The morphology of otoliths from Picolbach resembles to some extent that of the otoliths of alligator gar larvae, suggesting that this structure (and perhaps the whole inner ear) could be a conservative structure within some holosteans. In agreement with other studies, our results indicate that putative teleosts were less common in Carnian marine ecosystem than other groups of neopterygians. This study illustrates the applicability of ichtyoliths, especially otoliths, as a tool for gathering information on fish communities during the Late Triassic in the absence or scarcity of interpretable articulated skeletons.

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AUTHOR CONTRIBUTIONS

MKP designed the project, analysed data, and drafted the manuscript. KH supervised the project. KJ prepared supplement data. AK performed fieldwork and collected materials, conceived and supervised the project. All authors edited the manuscript.

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FIGURE CAPTIONS

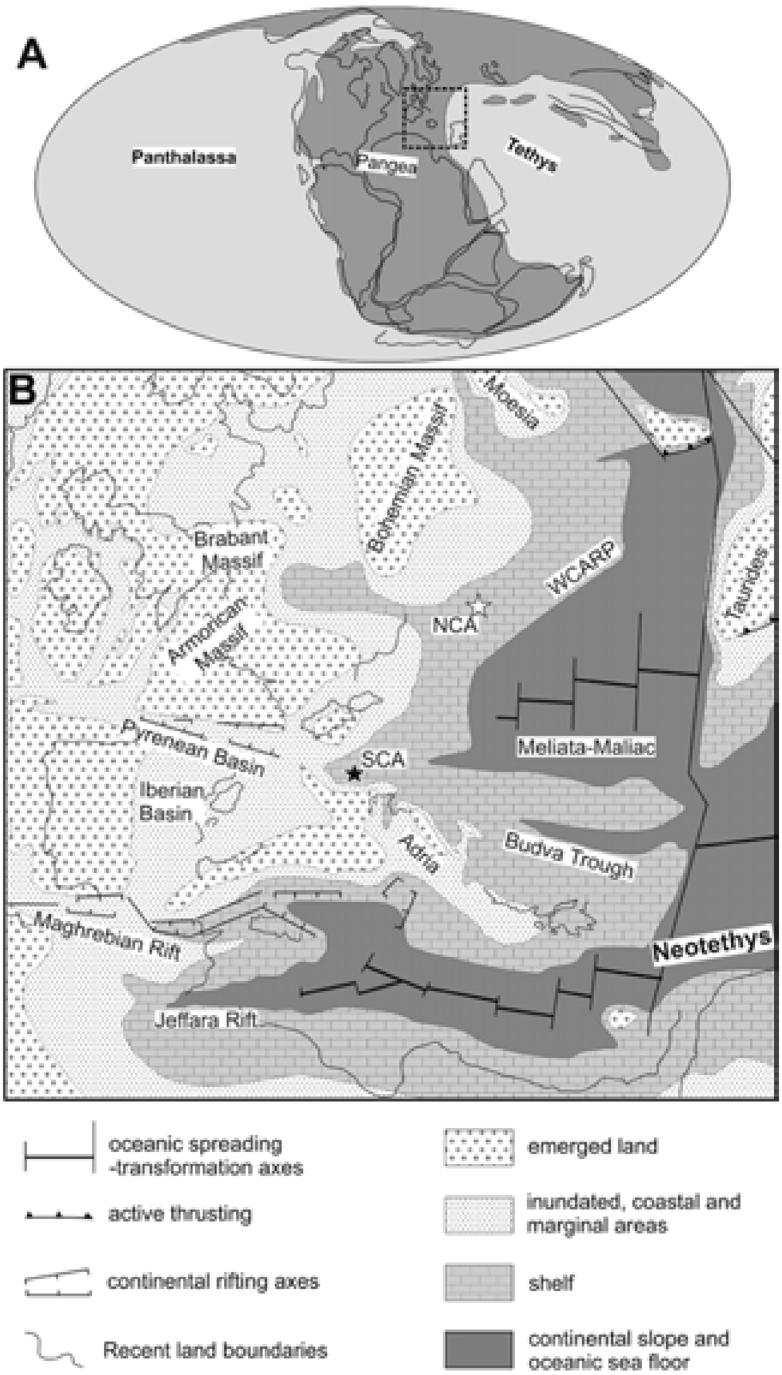

FIGURE 1. Palaeogeographical location of the material studied. A, location (square) of the Western Tethys within the general Late Triassic palaegeography. B, location of Southern Calcareous Alps (SCA) with Cassian Fm, Bergamo and Raibl and Northern Calcareous Alps (NCA) with Polzberg, within the Western Tethys; based on Bernardi *et al*. (2018) WCARP, Western Carpathians.

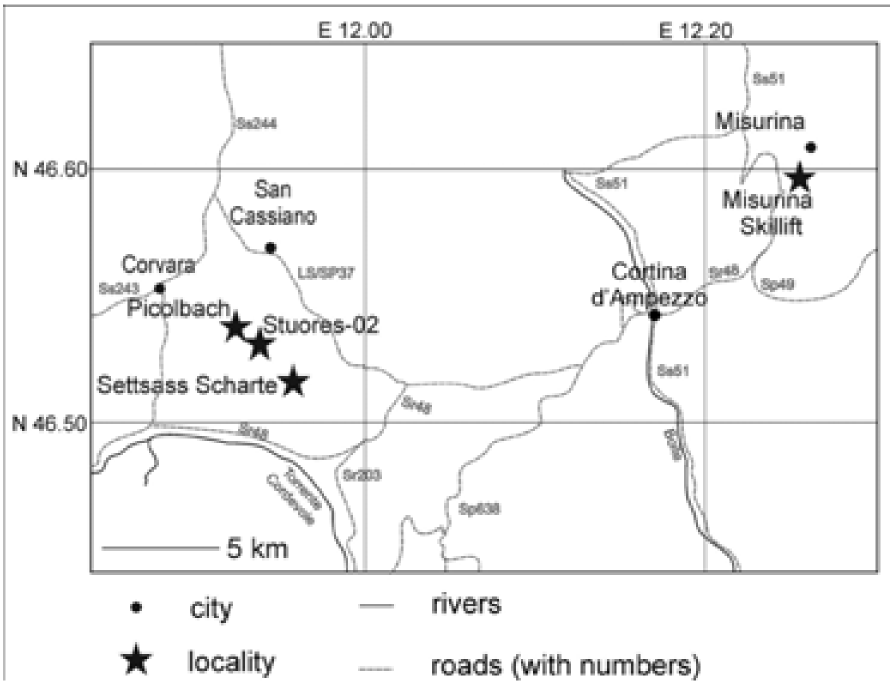

FIGURE 2. Map of described localities.

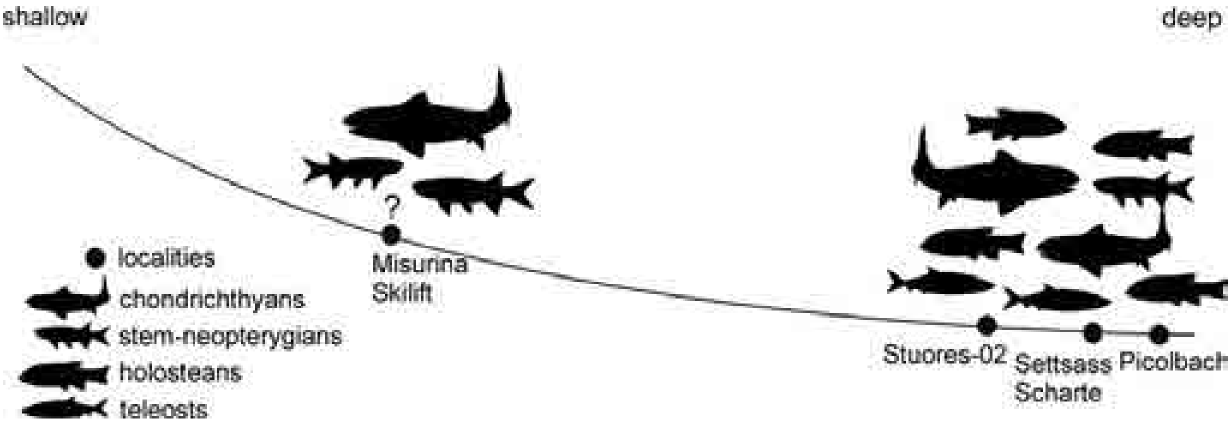

FIGURE 3. Palaeobathymetric interpretation of Cassian Fm. ichtyolithic assemblages from the investigated localities. Palaeobathymetric interpretation after Roden *et al.* 2020b, palaeobathymetry of Misurina Skilift interpolated from nearby locality Misurina Landslide.

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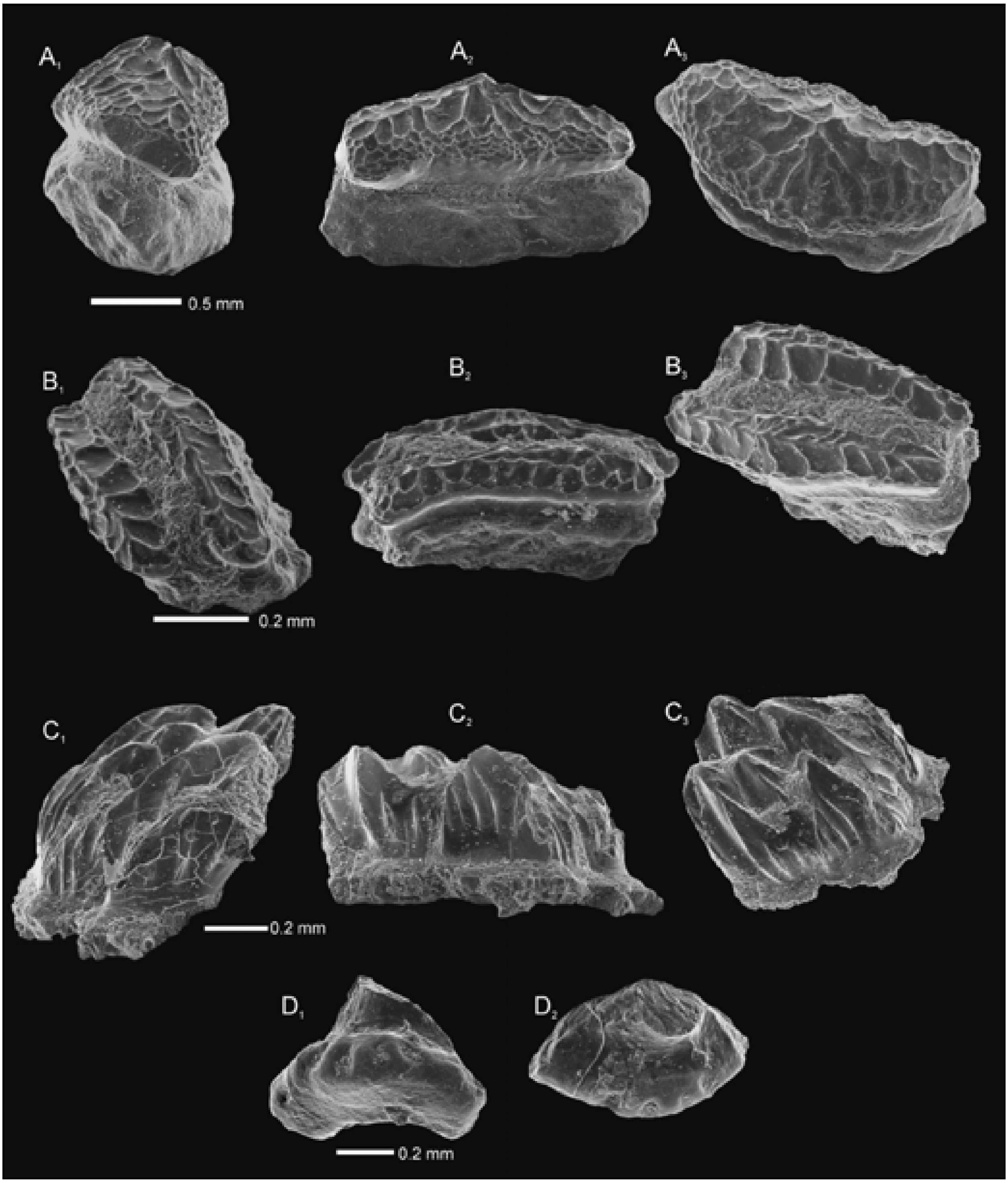

FIGURE 4. Ichthyoliths from Carnian, Upper Triassic of Cassian Formation at Settsass Scharte and Stuores, Dolomites, Northern Italy. A, tooth of *Acrodus* sp. from Settsass Scharte (PZO 16405); B, pathological teeth of *Acrodus* sp. from Settsass Scharte (PZO 16406); C, hybodont scale from Stuores (PZO 16403); D, fragment of the cephalic spine from Stuores-02 (PZO 16404). Abbreviations: 1, lateral view, 2, anterior view, 3, upper view. All SEM images.

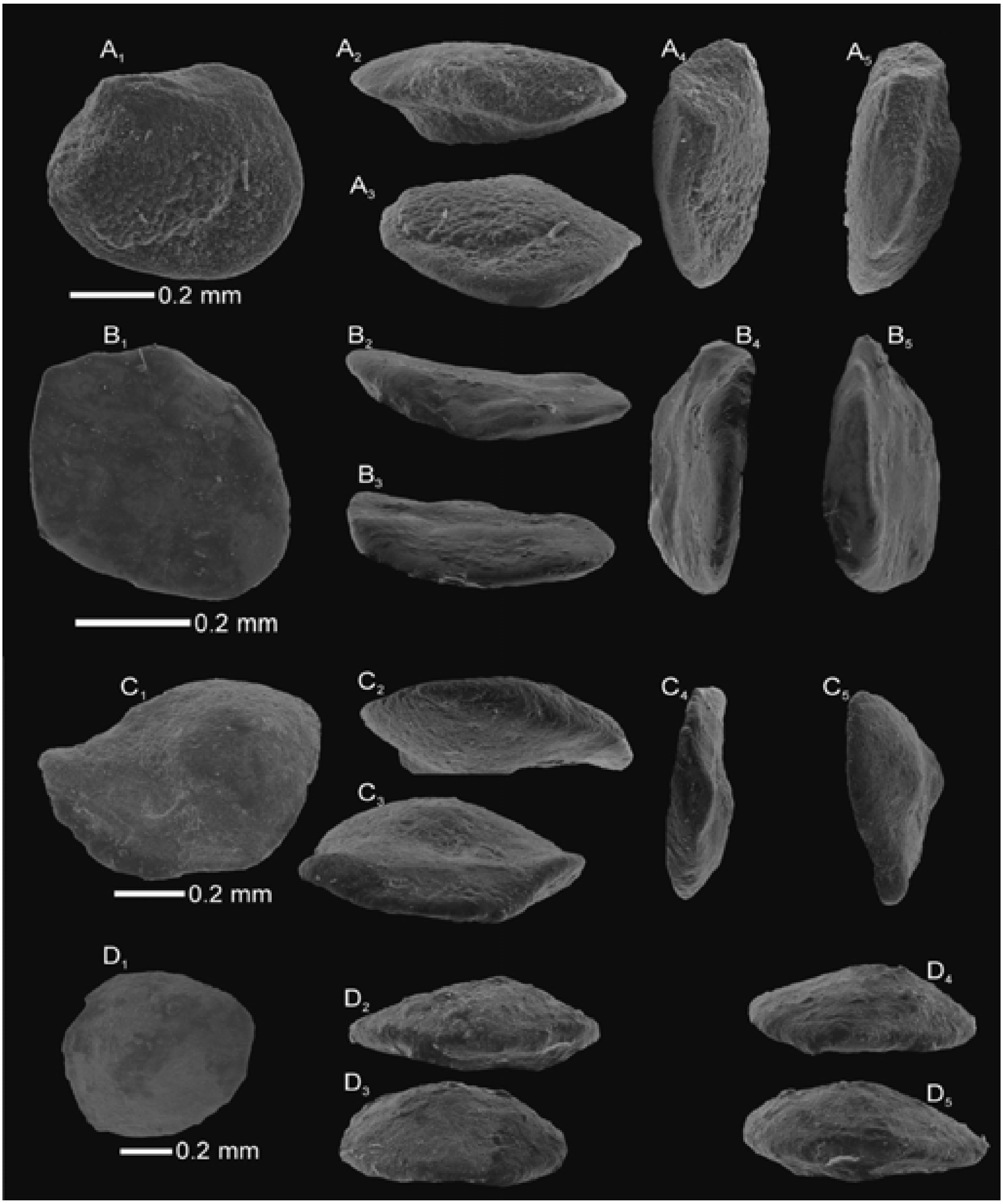

FIGURE 5. Stem-neopterygian utricular otoliths (lapilli) from Carnian, Upper Triassic of Cassian Formation, Dolomites, Northern Italy. A, Triassic Otolith Morphotype A, Misurina Skilift, (PZO 16394). B, Triassic Otolith Morphotype B–Thoracopteridae indet., Misurina Skilift,
(PZO 16395). C, Triassic otolith Morphotype B–Thoracopteridae indet., Settsass Scharte (PZO 16407). D, Triassic Morphotype A, Picolbach (PZO 16396); Abbreviations: 1, inner face, 2, ventral side, 3, dorsal side, 4, anterior side, 5, posterior side. All SEM images.

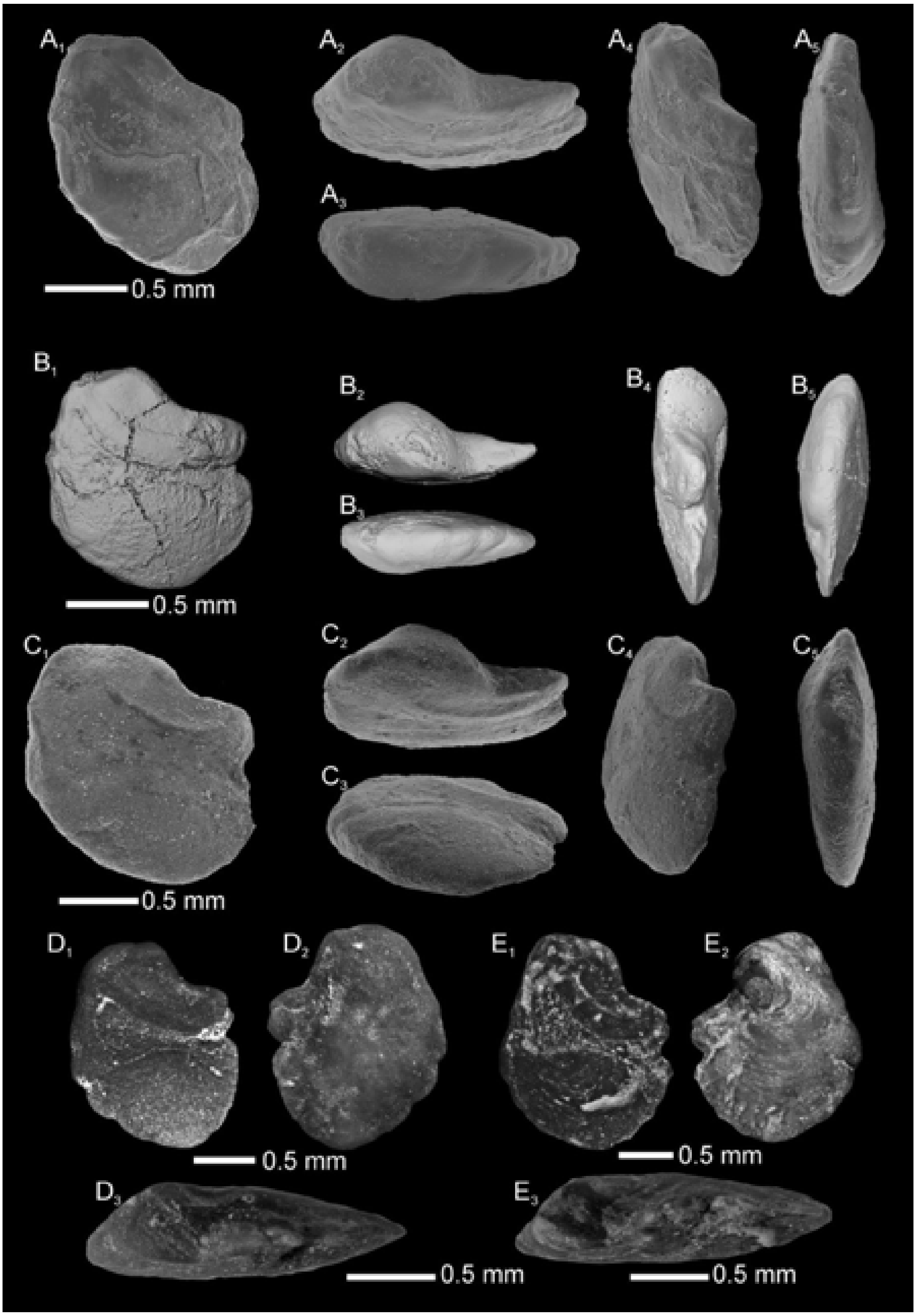

FIGURE 6. Basal teleost otolith from Carnian, Upper Triassic of Cassian Formation at Settsass Scharte, Dolomites, Northern Italy. Left otoliths. A, B, basal teleost otolith (PZO 16408), A series from SEM, B series from CT Scans. C, basal teleost otolith (PZO 16409), SEM images. D, E, otoliths of 'palaeoniscoid type' from Nützel & Kaim 2014 (NMS BOZ 5063 and 5064 respectively) interpreted here as basal teleost otoliths of the same taxon as PZO 16408 and 16409, digital photos, specimens not sputtered. Abbreviations (for A–C): 1. inner face, 2. dorsal side, 3. ventral side, 4. anterior side, 5. posterior side, (for D and E): 1. inner face, 2. outer face, 3. dorsal side.

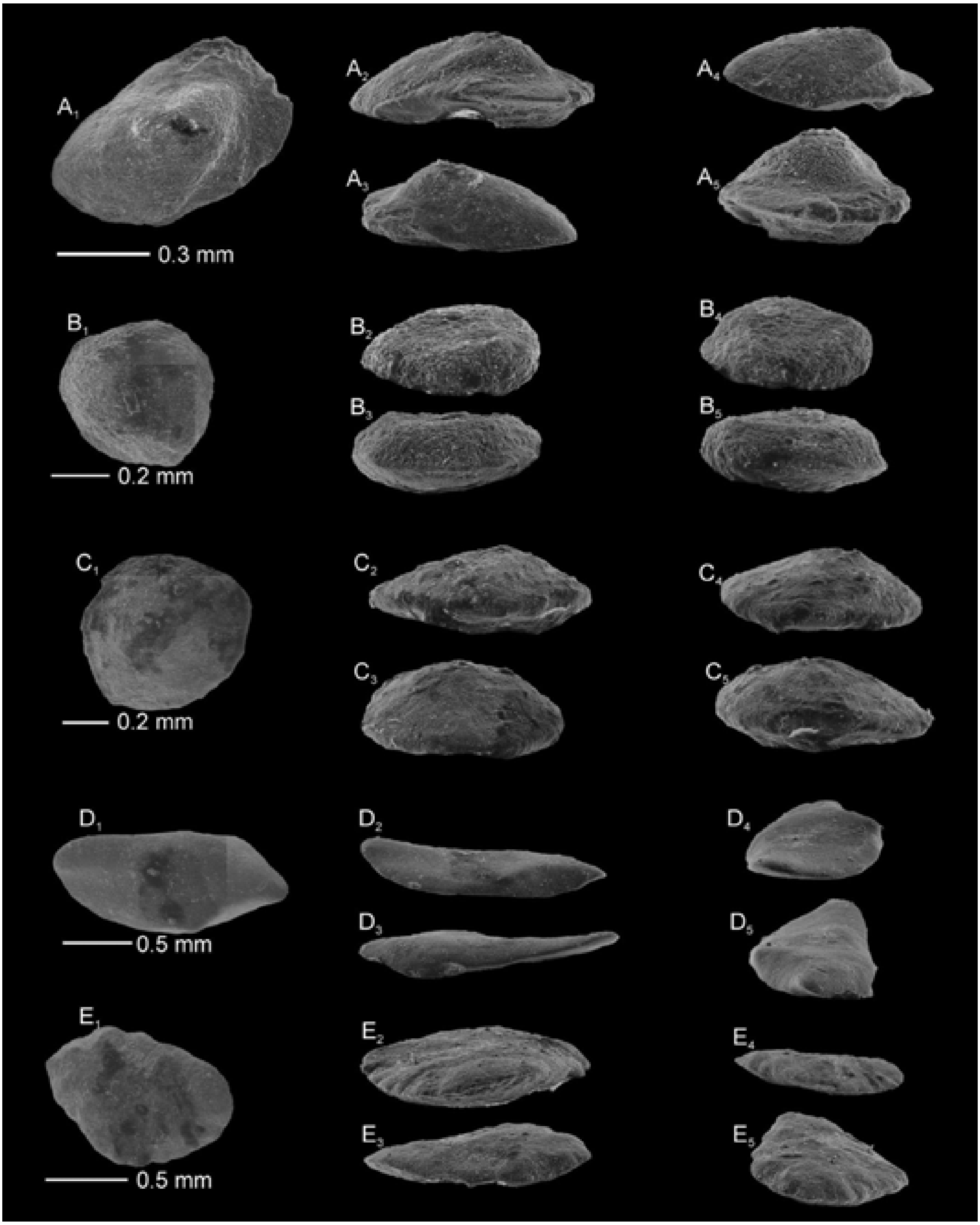

FIGURE 7. Otoliths from the Carnian, Upper Triassic of Cassian Formation at Picolbach, Dolomites, Northern Italy. A, Otolith Morphotype C, a putative lapillus (PZO 16397). B, Otolith Morphotype D, a putative lapillus (PZO 16398). C, Otolith Morphotype D, a putative lapillus (PZO 16399). D, Otolith Morphotype E (PZO 16400). E, Otolith Morphotype F (PZO 16401). Abbreviations: 1, inner face, 2. dorsal side, 3. ventral side, 3. anterior side, 5. posterior side. All SEM images.

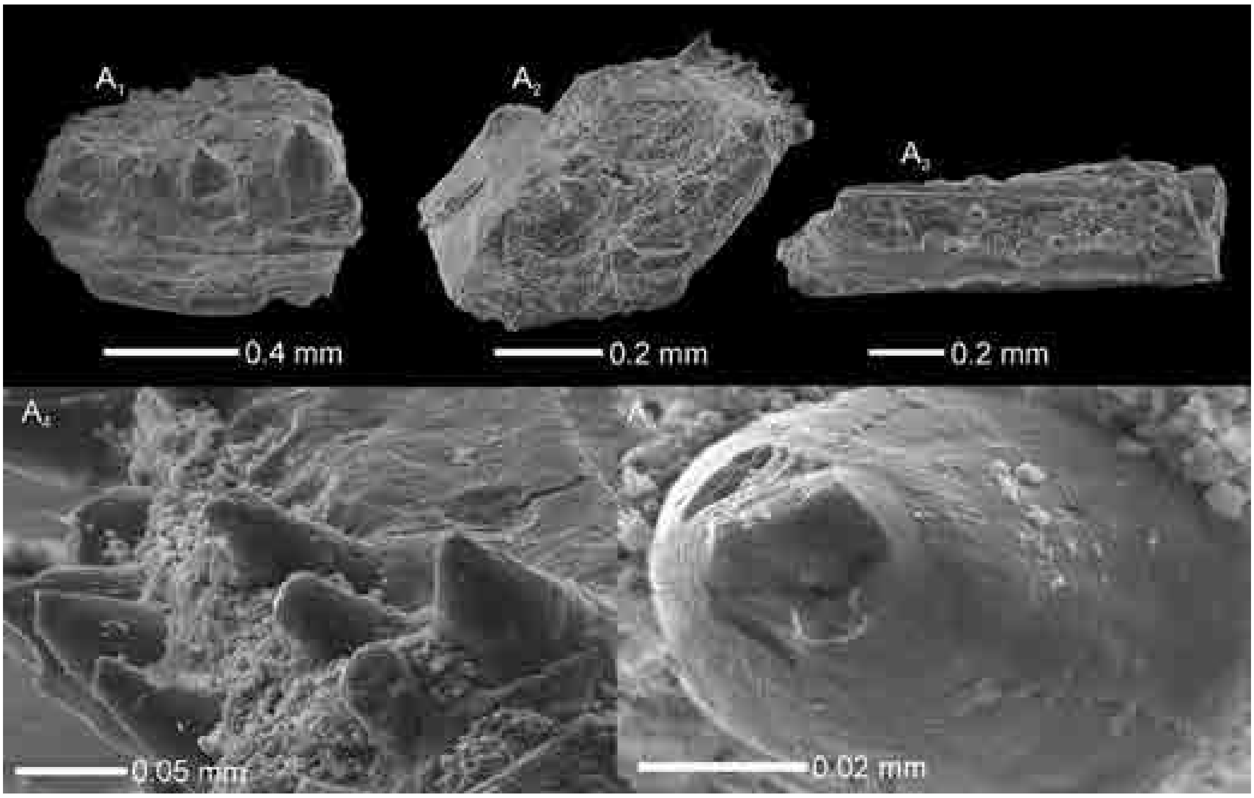

FIGURE 8. Fragment of stem-neopterygian ?*Colobodus* sp. jaw with larval teeth (PZO 16402) from Carnian, Upper Triassic of Cassian Formation at Picolbach, Dolomites, Northern Italy. Abbreviations: 1, upper view, magnified, 2, lateral view, 3, lower view, whole specimen, 4, enlargement of the jaw part, 5, enlargement on the tooth. All SEM images.

TABLES

	Stem-neopterygians	Holosteans	Basal teleosts	Hybodontiforms (teeth & other)
Stuores-02	0	0	0	2
Misurina Skilift	2	0	0	0
Settsass Scharte	1	0	4	2
Picolbach	2	7	0	0

TABLE 1. Comparison of the number of each fish group otoliths, within localities from this article.

SUPPLEMENTARY FILES

SUPPLEMENTARY FILE 1A: MicroCT rendering of the otolith of a basal teleost (PZO 16408) from Carnian, Late Triassic Cassian Formation at Settsass Scharte, Dolomites, Northern Italy. 1A: 3D pdf model.

SUPPLEMENTARY FILE 1B: movie with rotating specimen.

CHAPTER IV

Jurassic teleosts diversity and abundance changes, recorded by otolith and cephalopod statolith assemblages

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ABSTRACT—We describe otolith and cephalopod statolith assemblages from the Jurassic of Lithuania, Poland, and the United Kingdom. We report two new teleost fish genera (*Juraelops* gen. nov., and *Vodyanoi* gen. nov.), and eight new fish species (*Pteralbula jurassica* sp. nov., *Protalbula dorsetensis* sp. nov., *Palealbula ventai* sp. nov., *Palealbula crenulata* sp. nov., *Juraelops prodigiosum* sp. nov., *Vodyanoi schwarzhansi* sp. nov., *Vodyanoi stringeri* sp. nov., and *Archaeotolithus solidus* sp. nov.). We find significant dominance of basal decabrachians over bony fish in nearly all investigated assemblages and that teleosts are numerically dominated by leptolepiforms. Based on our findings, we propose that crown-teleosts diversified during the Middle Jurassic and that their radiation started in the Late Jurassic. The shift between statolith-to-otolith abundance ratios in the investigated assemblages documents a change from a cephalopod-dominated nekton during the Jurassic to a mostly teleost-dominated nekton during the Cretaceous. We propose that this change started as early as during the latest Jurassic.

SUPPLEMENTARY FILE(S)—Supplementary file(s) are available for this article for free at
https://www.morphosource.org/concern/media/000740842?locale=en
https://www.morphosource.org/concern/media/000740846?locale=en

INTRODUCTION

Ear stones are mostly aragonitic, paired structures growing in an animal’s inner ear. They are especially well-developed in nektonic animals and known as statoliths in cephalopods and otoliths in bony fishes, where they assist with balance and hearing. Both cephalopod statoliths and bony fish otoliths are formed through continuous addition of aragonite during growth and possess growth lines, which make them a useful tool for age determination. Many cephalopod statoliths and teleost otoliths have species-specific morphologies and are therefore taxonomically informative. Fossilized cephalopod statoliths and bony fish otoliths are found mostly in clays, marls, and sands whenever aragonite is preserved. In-situ otoliths are restricted to articulated fish skeletons (e.g., Schwarzhans et al., 2018), whereas statoliths may be found in situ only in exceptionally well-preserved cephalopods (see e.g., Klug et al., 2016). In the paleontological record, in-situ otoliths are more common in younger (Cenozoic) assemblages as evidenced by rich middle Miocene materials of the Paratethys (Reichenbacher & Bannikov, 2022, 2023; Schwarzhans et al., 2017a, 2017b, 2017c, 2017d, 2017e).

Cenozoic otoliths are relatively abundant (Nolf, 2013), whereas until recently otoliths from the Mesozoic were much less frequent (e.g., Nolf & Stringer, 1996; Pindakiewicz et al., 2022, 2023, 2024; Schwarzhans, 2010, 2018; Schwarzhans & Keupp, 2022; Schwarzhans & Wakefield, 2024; Schwarzhans et al., 2022). Some examples of ancient cephalopod statoliths from the Jurassic and early Paleogene have been known for decades (Clarke, 1978, 2003; Clarke et al., 1980; Hart, 2019; Neige et al., 2016), whereas Cretaceous examples have been reported only recently (Pindakiewicz et al., 2022). Using the ratio of ear stones, Pindakiewicz et al. (2022) observed a change in Jurassic and Cretaceous assemblages from seas populated mostly by cephalopods and a lower abundance of fish, to seas dominated by crown teleosts. Cause and exact timing of this shift in the composition of the nekton remain elusive. Teleost diversification began in the Cenomanian with a peak in diversity in the Maastrichtian. After the Cretaceous/Paleogene extinction event teleosts diversified again, even exceeding the levels known from Mesozoic times, a trend that continues until today (Friedman, 2010; Schwarzhans, 2004; Schwarzhans & Stringer, 2020; Schwarzhans et al., 2024; Stringer et al., 2020).

We report a collection of Jurassic otoliths from the Bathonian and Callovian (Middle Jurassic) of Poland; the Callovian and Oxfordian (Middle–Upper Jurassic) of Lithuania; and the Pliensbachian (Lower Jurassic), Oxfordian, and Kimmeridgian (Upper Jurassic) of the United Kingdom. We compare those otoliths to several known assemblages from the Lower and Middle Jurassic of Germany, the Upper Jurassic of the Kostroma Oblast in Russia, and previously described Jurassic materials from the United Kingdom. We characterize the turnover observed in Jurassic cephalopod statolith and fish otolith assemblages and discuss possible causes.

GEOLOGICAL SETTINGS

The material studied herein was collected during several field seasons in Lithuania, Poland, and the United Kingdom (Fig. 1). The majority of studied localities are well known and we provide only a brief summary herein and refer the reader to more detailed descriptions elsewhere. The localities are listed below in chronostratigraphic sequence.

Eype, Dorset, United Kingdom

The oldest material comes from the Eype Clay member of the Dyrnham Formation (upper Pliensbachian, Lower Jurassic) in Dorset, United Kingdom (Buckman, 1922; Hesselbo & Jenkyns, 1995; Simms, 2004). The material was collected from under the cliffs between Seatown and Eype beach in situ in 2021 and 2023 (50°43'04.4"N, 2°47'28.1"W). The sediment is a light, bluish-gray sandy clay deposited in a fully marine offshore basin (Hesselbo & Jenkyns, 1995). Based on ammonite biostratigraphy, the Eype Clay member belongs to the upper Pliensbachian (*Stokesi* subzone, *Margaritatus* Zone) (Hesselbo & Jenkyns, 1995). Macrofossils are rare and consist primarily of ammonites and belemnites.

Otoliths and statoliths are uncommon compared to other Jurassic localities in the present study (e.g., Gnaszyn, Gołaszyn, Osmington Mills), and they are usually coated in a light-gray crust of micaceous sediment making observations difficult.

Złote Góry, Wieluń Region, central Poland

A clay pit located southwest of Wieluń (51°09'40.5"N, 18°26'19.3"E). During collection in 1999 only about one meter of black clay was exposed in the section. This deposit of upper Bajocian age (Kaim, 2004), most likely from the *Parkinsoni* Zone (Zatoń et al., 2006).

Gnaszyn, Anna, and Sowa, western suburbs of Częstochowa, central Poland

These localities collectively expose the upper part of the Middle Jurassic (upper Bajocian–upper Bathonian) "Ore-Bearing Częstochowa Clay Formation". The locality in Gnaszyn is an active clay pit owned and operated by Wienerberger IG (50°48'12.4"N, 19°02'25.2"E) and preserves a silicilastic section of dark gray, organic-rich mudstones mixed with sandy horizons and clayey siderite concretions from the upper lower Bathonian (*Tenuiplicatus* to *Retrocostatum* ammonite zones) (see Gedl et al., 2003; Matyja et al., 2006; Dayczak-Calikowska & Kopik, 1973; Gedl & Kaim, 2012; and unpublished recent observations by AK and PS). The mudstones and claystones exposed in Gnaszyn represent a delta-influenced shallow-marine environment with terrigenous material supplied mainly from the Bohemian Massif to the south (Gedl et al., 2012). The Formation was deposited on the continental shelf. The siderite concretions intercalated with dark clays indicate cycles of intensive episodic and slow background sedimentation (Gedl et al., 2003). A similar scenario is assumed for the nearby Anna clay pit 1.5 km to the east of Gnaszyn (50°48'26.0"N 19°04'08.1"E), where the lower upper Bathonian (*Retrocostatum* Zone; Matyja &

Wierzbowski, 2003; Kaim, 2011) is exposed. The Sowa clay pit, 1.5 km to the south of Gnaszyn (50°47'08.7"N 19°02'38.3"E), displays siltier and slightly older (late Bajocian–early Bathonian) sediments (Gedl et al., 2012; Zatoń, 2010a, b). The locality of Gnaszyn has seen numerous research activities, including studies of foraminiferans (Smoleń, 2012), dinoflagellates (Gedl, 2012), gastropods (Kaim, 2012), bivalves (Kaim & Sztajner, 2012), cephalopods (Zatoń, 2010a, b), echinoderms (Boczarowski, 2012), shark teeth (Rees, 2012), serpulids (Słowiński et al., 2022), and cephalopod statoliths (Pindakiewicz et al., 2022). The succession in Gnaszyn is also known to contain distinct aggregates of sharp-edged molluscan shell fragments interpreted as regurgitates (Zatoń et al., 2007), as well as sunken wood associations (Kaim, 2011).

Wrzosowa (= Dylikowski's claypit), south of Częstochowa, central Poland

An abandoned clay pit, located west of the village of Wrzosowa and south of Częstochowa (50°45'07.1"N 19°07'16.1"E). Exposed sediments are dark clays of the "Ore-Bearing Częstochowa Clay Formation" that correlate to the *Subcontractus*-*Morrisi* ammonite biozones of the middle Bathonian (Zatoń, 2010a, b).

Blanowice, Zawiercie Region, central Poland

The southernmost of two clay pits in Blanowice, the eastern district of Zawiercie (50°30'19.6"N 19°27'10.1"E), exploiting the "Ore-Bearing Częstochowa Clay Formation". The clay pit is located on the slope of the cuesta of the Polish Jura and exposes Bajocian to Oxfordian sediments (Różycki, 1953). The profile exposed in the clay pit represents the *Morrisi* ammonite biozone of the middle Bathonian (Zatoń, 2010a, b).

Ogrodzieniec, Zawiercie Region, central Poland

The locality was referred to as Ogrodzieniec-Wiek by Różycki (1953). The locality consists of two clay pits close to one another and situated between Fugasówka and Ogrodzieniec (50°27'30.8"N, 19°30'14.2"E). In 1953, the exposed sections consisted of black clay which, according to Różycki (1953), ranged from the lower Bajocian to the upper Bathonian. Most probably only the upper part of the section was exposed during the collection of our samples (1995–2005) and can be correlated to the upper Bathonian *Retrocostatum* Zone (Zatoń et al., 2006).

Gołaszyn, suburbs of Łuków, eastern Poland

Material from Gołaszyn was collected from a test pit (51°57'21.1"N, 22°21'13.0"E) that was prepared for the fieldtrip of the 86th meeting of the Polish Geological Society 2018, held in Łuków. The deposits exposed in the test pit consists of gray clay belonging to a structure similar to the Łuków Łapiguz glacial drift which is known for exceptionally preserved ammonites (Makowski, 1952) and gastropods (Kaim, 2004, 2008). Similar to the Łuków Łapiguz glacial drift, the clays at Gołaszyn represent the upper Callovian *Athleta–Lamberti* zones (Mizerski & Szamałek, 1985; Wierzbowski, 2018). The entire glacial drift was glacially transported from the Baltic Sea during the Pleistocene (Jahn, 1949). Ostracods from Gołaszyn indicate a cooler, more boreal part of the marine basin than its northwestern counterpart in western Pomerania (Olempska & Błaszyk, 2001). Some cephalopod statoliths from the Gołaszyn test pit were depicted by Pindakiewicz et al., (2022).

Papartynė, Žemaitija Region, Lithuania

The material was collected in 2023 from a surface outcrop on the right bank of the Venta River (56°07'28.4"N, 22°51'31.0"E). There, rusty sandstones and loose gray sands with yellowish marls belong to the Papartynė Formation (Paškevicius, 1997). This formation is rich in bivalve, gastropod, and brachiopod shells and fragments of crinoids and foraminifera (Paškevicius, 1997). The lower part of the Papartynė Formation that crops out at the locality comprises clayey gray sands and sandstones (Marynowski & Zatoń, 2010) that were deposited in a shallow marine environment. These deposits correlate to the middle Callovian *Jasoni* to *Coronatum* zones (Rotkytė, 1987; Grigelis, 1994).

Jurakalnis Gully, Žemaitija Region, Lithuania

The material was collected in 2023 from a small forested gully in the Venta Geological Park, approximately 100 m from the left bank of the Venta river near the town of Papilė (56°08'40.5"N, 22°46'56.2"E). The outcrop comprises black calcareous clays and silty clays with scarce fossils. Apart from the ear stones, the clay samples yielded infrequent small gastropods, ammonites, and bivalves. The black clays in this area correlate to the *Cordatum* to *Mariae* zones of the lower Oxfordian (Rotkytė, 1987; Paškevicius, 1997) and are interpreted as a fully marine, offshore setting.

Redcliff Point, Weymouth Bay, Dorset Coast, United Kingdom

The material was collected in 2021 at a cliff near Redcliff Point (50°38'03.8"N, 2°24'37.9"W), close to the potential GSSP of the Callovian/Oxfordian boundary (Page et al., 2009). The dark clay beds with abundant molluscan shells lay nearly horizontal in this locality. The most common fossils are oysters (*Gryphea*), pyritized ammonites (*Cardioceras*), and belemnites (*Hibolites*) (Martill & Hudson, 1991). Clays of Redcliff Point belong to the Weymouth member of the upper Oxford Clay Formation from the early Oxfordian (Page et al., 2009). Sediments were deposited in a marine setting on the offshore shelf (House, 1993).

Eweleaze Beach, Weymouth Bay, Dorset Coast, United Kingdom

The material was collected to the east of Redcliff Point (50°38'06.6"N 2°24'17.9"W) in 2021. The sediments are very similar to the clay beds of Redcliff Point. Calcareous fossils are poorly preserved and mostly fragmented in contrast to apatitic fossils, which are in much better condition. The age of these clays is presumably the same as at Redcliff Point (House, 1993), or slightly younger (Bowleaze Clay member or the upper part of Weymouth member) as suggested by Wright and Cox (2001). The fact that the preservation of apatite fossils is better than that of calcareous fossils suggests that the deposition took place under anoxic or dysoxic conditions that have been suggested for the lower Oxford Clay (Duff, 1975, 1978; Hart et al., 2019).

Popovo, Kostroma Oblast, Russia

This Oxfordian, Late Jurassic, material originates from a pilot sample from Popovo, Russia, provided in 2000 to AK by V. Mitta (Moscow, Russia). A single otolith was found within a light gray siltstone with yellowish clasts, which also yielded abundant maturifusid gastropod shells.

Blackhead, Dorset Coast, United Kingdom

We collected samples in 2023 from the freshly exposed dark clays in the cliffs close to Blackhead (50°38'11.5"N, 2°23'16.7"W). The deposit cropping out in this locality consists chiefly of dark gray clays with abundant mollusc shells with aragonite preservation. The section at Blackhead is part of upper Kimmeridgian lower Kimmeridge Clay based on ammonite biostratigraphy (*Autissiodorensis* and *Elegans–Pectinatus* zones; Cox & Gallois, 1981; Wignall, 1990). The Kimmeridge Clay is brighter than the Oxford Clay, contains many well-preserved otoliths and statoliths, and was deposited in a fully marine environment on a soft seafloor up to 100 m deep (Martill et al., 2020). Recent landslides exposed fresh clay outcrops which seem to be in better condition than those previously reported by Clausen and Wignall (1988). The clays are known to yield perisphinctid ammonites, compound corals, echinoderms, and fragments of decapods, fishes, and marine reptiles. The most common fossils at Blackhead are the bivalve *Deltoideum delta* and the brachiopod *Torquirhynchia inconstans* (Martill et al., 2020; Wignall, 1990).

Osmington Mills, Dorset Coast, United Kingdom

We collected the material in 2021 and 2023 from freshly exposed clays in the cliff under the car park of the Smugglers Inn in Osmington Mills (50°38'04.1"N, 2°22'34.5"W). Sedimentology and depositional environment are very similar to the coeval clays at Blackhead and are dated to the late Kimmeridgian, representing the lower Kimmeridge Clay of the *Autissiodorensis* and *Elegans–Pectinatus* zones (Wright & Cox, 2001; Ziegler, 1962). The clays of the Osmington Mills outcrop differ from those at Blackhead by having a much higher abundance and variety of calcareous fossils (Martill et al., 2020). Abundant fossils are molluscs (gastropods, belemnites, bivalves, ammonite fragments, and small shells), echinoderms, fish remains (scales and teeth), and bone fragments of marine reptiles. Some otoliths, e.g. *Sphaeronchus rundlei*, were previously reported from this locality by Schwarzhans (2018).

MATERIAL AND METHODS

This study is based on 751 otoliths and 1942 statoliths. Unless otherwise stated, all otoliths described herein are saccular otoliths (sagittae). The materials in the ZPAL collections were obtained over several years (1995–2024) through bulk sampling of Polish outcrops and more recent fieldwork in England (2021–2023) and Lithuania (2023) by AK.

The spots for collecting bulk samples were chosen based on high abundance of well-preserved aragonite fossils in easily water degradable siliciclastic sediments (clays, silts and sands). The amount of collected material varied depending on outcrop size, source-rock availability, and abundance of fossils in the sediment. Samples of 5–10kg of dry sediment (weight varied depending on water content in the rock) were collected in bags with a maximum volume of 80 litres. The number of samples per outcrop (1–50) varied due to the size of the outcrop, number of visits, and technical feasibility to transport the samples to the lab (Table 1). In the laboratory, sediment was dried and then soaked in water to which laundry detergent powder that is safe to use with aragonitic fossils was added. The resulting mud was wet screened on sieves of 0.375 mm diameter mesh size. Otoliths and statoliths were extracted from the residue under a binocular microscope, fixed with tragacanth resin to stubs, and photographed under SEM. The majority of specimens were fixated to stubs with their outer faces not turned after fixation to avoid potential damage so that only the inner faces of these otoliths could be photographed. Two lapilli (*Lapillus* sp. 1 and *Lapillus* sp. 2) have been µ-CT scanned at the Laboratory of Microtomography, Institute of Paleobiology PAS, to better depict their three-dimensional morphology. Large-sized specimens from the MGUS collections (*Vodyanoi* gen. nov. lapilli and twenty-six *Archaeotolithus* otoliths from "Ore-Bearing Częstochowa Clay Formation" localities) were surface-collected by PS. They were covered in ammonium chloride and photographed under a microscope with a camera mount at MGUS. The terminology used for the description of *Vodyanoi* gen. nov. lapilli is based on Assis (2005) and Sánchez and Martinez (2017).

Institutional Abbreviations—**MGUS**, Institute of Marine and Environmental Sciences, University of Szczecin, Poland; **ZPAL**, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Anatomical Abbreviations—**CaL**, cauda length; **OH**, otolith height; **OHHol**, otolith height of the holotype; **OL**, otolith length; **OLHol**, otolith length of the holotype; **OsH**, ostium height; **OsL**, ostium length; **OT**, otolith thickness; **OTHol**, otolith thickness of the holotype; **SuL**, sulcus length.

SYSTEMATIC PALAEONTOLOGY

Class ACTINOPTERYGII sensu Goodrich, 1930
Subclass NEOPTERYGII Regan, 1923
Infraclass TELEOSTEI Müller, 1845
Order LEPTOLEPIFORMES Nicholson & Lydekker, 1889
Family LEPTOLEPIDAE Nicholson & Lydekker, 1889
Genus *LEPTOLEPIS* Agassiz, 1832

Type species—*Cyprinus coryphaenoides* Bronn, 1830, Toarcian, Lower Jurassic, Western Germany.

LEPTOLEPIS PRAEELOPS (Stinton in Stinton & Torrens, 1968)

(Fig. 2A–J)

1954 Otol. (*Lycopteridarum*?) *ornatus* Weiler, 1953—Martin and Weiler, pl. 1, fig. 1.

1968 *Pholidophorus prae-elops*.–Stinton and Torrens:figs. 6, 7.

2018 *Leptolepis praeelops* (Stinton & Torrens 1968).—Schwarzhans, Fig. 2F–G.

Material—198 otoliths (25 well-preserved and 148 broken specimens from the Callovian of Gołaszyn; 7 well-preserved and 5 broken specimens from the Callovian of Papartynė; 5 well-preserved and 8 broken specimens from the Oxfordian of Jurakalnis Gully).

Description—OL: 1.2–2.4 mm, OH: 0.7–1.3 mm, OL:OH 1.72–1.8 (n = 4). Deltoidal, thick otolith. Long, narrow ostium. Convex dorsal rim. Long, narrow cauda. Cauda termination close to the posterior angle. Well-developed crista. Well-developed posterior angle. Short, narrow dorsal rim. Two or three prominent, small dorsal angles. Long, convex, folded or serrated ventral rim.

Discussion—The *Leptolepis praeelops* specimens described herein are slightly more elongated than the holotype and the paratypes (OL:OH of *Leptolepis praeelops* from our collection 1.72–1.8 vs OL:OH of *L. praeelops:* 1.55–1.65). The dorsal rim of *L. praeelops* with two-to-three small angles, as in the Early Jurassic *Leptolepis sculptus* (Weiler, 1965), *L. normandica* Nybelin, 1962, and *L. ornatus* (Weiler in Neth & Weiler, 1953). The ventral rim of *L. praeelops* resembles that of *L. normandica*, and *L. ornatus*. Our specimens of *L. praeelops* are from the Callovian and Oxfordian of Poland and Lithuania. It is the only otolith-based species from the Jurakalnis Gully in Lithuania. Because this locality is dated to the Oxfordian this material extends the stratigraphic and geographic range of the species.

Stratigraphic and Geographic Range—Bathonian–Oxfordian (Middle–Upper Jurassic) of northern Germany, the United Kingdom, Poland, and Lithuania.

LEPTOLEPIS CIRCULARIS (Stinton in Stinton & Torrens, 1968)

(Fig. 2K)

1968 *Sphaeronchus circularis*–Stinton & Torrens:figs. 3, 4 (original description).

2018 *Leptolepis circularis* (Stinton 1968)—Schwarzhans: figs. 2A, B.

Material—7 specimens (1 well-preserved, 6 broken), all from the Bathonian of Gnaszyn, central Poland.

Description—OL 3.3 mm, OH: 2.7 mm, OL:OH 1.2 (n = 1). Round, short otolith with triangular ostium. Sulcus supramedial, terminates at the posterior rim of the otolith. Dorsal rim smooth and short with small depression above crista superior. Ventral rim well-developed, smooth, and evenly rounded.

Discussion—The well-preserved specimens have a slightly longer ostium and shorter dorsal rim than the holotype. However, the sulcus narrows at the end like it does in the holotype of *L. circularis*. *Leptolepis circularis* is found at the same locality as *Sphaeronchus dorsetensis*. Previously, the otoliths of *L. circularis* were known only from the Bathonian (Middle Jurassic) Rodden Hive Point, Dorset (Schwarzhans, 2018; Stinton & Torrens, 1968). The new material suggests a wider paleogeographical range of *Leptolepis circularis*.

Stratigraphic and Geographic Range—Bathonian (Middle Jurassic) of Dorset, United Kingdom, and central Poland.

LEPTOLEPIS DENSUS Stinton in Stinton & Torrens, 1968

(Fig. 2L–X)

1968 *Leptolepis densus*—Stinton & Torrens:fig. 10 (original description).

2018 *Leptolepis densus*—Schwarzhans:fig. 2C–D.

2024 *Leptolepis densus*—Schwarzhans & Wakefield:fig. 7A–Z

Material—459 otoliths (128 well-preserved and 291 broken specimens from the Bathonian of Gnaszyn; 18 well-preserved and 22 broken specimens from the Callovian of Gołaszyn).

Description—OL: 1.1–2.6 mm, OH: 0.6–1.8 mm, OL:OH 1.4–1.8 (n = 11). Oval otolith. Supramedial sulcus of the otolith with wide ostium. Cauda inclined ventrally. Cauda termination close to the posterior rim. Poorly developed angles on the dorsal rim. Dorsal rim shorter than ventral rim. Ventral rim smooth, uniformly and deeply curved. Inner face more convex than the outer face.

Remarks—The larger otoliths of *Leptolepis densus* from Gnaszyn (Bathonian) and Gołaszyn (Callovian) are similar to the holotype in general outline, straight cauda, and wide ostium. The dorsal rim of the otoliths from both localities is high, but more angular and less rounded than in the holotype. The morphology of the dorsal rim resembles that of *Leptolepis buttenheimiensis* from Franconia, Germany (Schwarzhans & Keupp, 2022). Most *Leptolepis densus* otoliths are relatively small (less than 1.5 mm length) and quite rounded. The *Leptolepis densus* otoliths from the Bathonian "Ore-Bearing Częstochowa Clay Formation" in Gnaszyn and from the Callovian glacial drift in Gołaszyn, Poland, resemble those from the roughly coeval (Bathonian) Lealt Shale Formation of the Inner Hebrides, Scotland (Schwarzhans & Wakefield, 2024), but with relatively more large specimens from Poland (more than 60% of specimen are larger than 1.5 mm length). We assume that this is because of the open-marine character of the deposits at Gnaszyn and Gołaszyn (e.g., Gedl et al., 2012; Olempska & Błaszyk, 2001) which preserve populations of adult *L. densus*. The mostly estuarine character of the Lealt Shale Formation, on the other hand, could have served as a nursery for leptolepiforms, including *L. densus* (Schwarzhans & Wakefield 2024).

Stratigraphic and Geographic Range—Bathonian–Callovian (Middle Jurassic) of the Hebrides and Dorset, United Kingdom, and northern Germany and central Poland.

LEPTOLEPIS ROTUNDATUS (Weiler in Martin & Weiler, 1954)

(Fig. 3A)

1954 Otol. (inc. sed.) *rotundatus*—Martin and Weiler: pl. 3, fig. 74 (original description).

2018 *Leptolepis rotundatus* (Weiler, 1954)—Schwarzhans: figs. 1L–N.

Material—8 specimens (2 well-preserved and 6 broken) from the Callovian of Gołaszyn.

Description—OL 1.7 mm, OH: 1.3 mm, OL:OH 1.3 (n = 1). Round otolith with triangular ostium. Straight supramedial sulcus terminating at the edge of posterior rim. Well-developed crista. Dorsal rim with large mediodorsal angle. Rounded ventral rim with crenulations.

Remarks—Our specimens differ from the holotype in the smaller and smoother anterior angle of the dorsal rim. On the other hand, the supramedial ostium is short, and the straight cauda terminates very close to the posterior rim. The outline of otoliths is round as in the type material of *Leptolepis rotundatus*. The ventral rim seems subtly folded although it could be due to erosion as seen on the tip of the rostrum. These specimens represent the youngest record of *L. rotundatus*.

Stratigraphic and Geographic Range—Bathonian of northern Germany and Callovian of eastern Poland (both Middle Jurassic).

LEPTOLEPIS aff. *INAEQUALIS* (Weiler in Martin & Weiler, 1954)

(Fig. 3B)

1954 *Otolithopsis* (incertae sedis) *inaequalis*–Weiler in Martin & Weiler:pl. 4, fig. 170 (original description).

2018 *Leptolepis inaequalis* (Weiler, 1954)–Schwarzhans:fig. 2E.

Material—9 specimens (6 specimens from the Oxfordian of Redcliff Point, including 2 broken specimens and 4 specimens with broken tips of rostrum or fragment of rim, and 3 broken specimens from the Kimmeridgian of Osmington Mills).

Description—OL 2.2 mm, OH: 1.4 mm, OL:OH 1.6 (n = 1). Oval otolith. Wide ostium, merged with dorsal tip. Discernible ostial colliculum. Straight sulcus with well-developed crista. Straight posterior rim. Termination of the sulcus at level of straight posterior rim. Straight dorsal rim with predorsal angle. Ventral rim evenly rounded and smooth.

Discussion—The specimens herein identified as *Leptolepis inaequalis* are better preserved than the holotype of Weiler in Martin & Weiler (1954), and slightly more elongated (OL: $\mathrm{OH}_{\mathrm{Hol}}$ 1.50, OL: $\mathrm{OH}_{\mathrm{ZPAL\ P.22/Om/2}}$ 1.54). The cauda is straight and terminates at some distance from the posterior angle of the otolith and resembles the holotype. The right postdorsal angle and smooth, evenly-rounded ventral rim match the holotype. Specimens differ from the holotype of *L. inaequalis* in the well-developed anterodorsal angle that is absent in holotype and paratypes from southern Germany. Most otoliths of *L. inaequalis* are known from Callovian (Middle Jurassic) localities and only holotype was found in the Oxfordian (Late Jurassic) (see Schwarzhans, 2018, for discussion on alternative age). Due to the slight difference in morphology between the British specimens reported in the present study and those from Germany, and because of the uncertain stratigraphic range of *L. inaequalis* (Weiler in Martin & Weiler, 1954) in Germany, we refer our specimens only tentatively to this species.

LEPTOLEPIS cf. *PLICATILIS* (Frost, 1924)

(Fig. 3C)

1924 *Otolithus (Leptolepidarum) picatilis*—Frost:pl.5, fig. 2

1924 *Otolithus (Leptolepidarum) simplex*—Frost:pl.5, fig. 1

1924 *Otolithus (Leptolepidarum) cristatus*—Frost:pl.5, fig. 3

2018 *Leptolepis plicatilis* (Frost, 1924)—Schwarzhans:fig. 3A–C

Material—70 specimens (29 well-preserved and 38 broken from the Kimmeridgian of Osmington Mills; 4 broken specimens from the Kimmeridgian of Blackhead; 1 encrusted with sediment and 2 broken specimens from the Oxfordian of Redcliff Point).

Description—OL 1.72–1.91 mm, OH 1.05–1.33 mm OL:OH 1.44–1.64 (n = 2). Small otolith with narrow, triangular ostium. Rostrum moderately long (42% of OL), pointed; minute excisura and antirostrum. Cauda relatively long (OsL:CaL 0.72). Termination of cauda narrow and shallow. Crista superior and inferior visible on the anterior part of the otolith. Dorsal rim with two well-developed rounded angles. Posterodorsal angle smooth. Ventral rim with irregular serrations.

Discussion—Smaller specimens of *Leptolepis plicatilis* show the following plesiomorphic leptolepid otolith features: (i) discernible collicullum; (ii) short, horizontal sulcus; (iii) flat outer and inner face; and (iv) strong rostrum without excisura or antirostrum. However, our specimens possess a visible excisura between ostium and dorsal rim, matching the paratype of *L. plicatilis* (Schwarzhans, 2018:fig. 3A, B). Small specimens in our collection most likely belong to young individuals of *L. plicatilis*. The discovery of *Leptolepis plicatilis* in the Oxfordian of Redcliff Point, Dorset, United Kingdom, indicates that the species appeared earlier (Oxfordian) than previously reported (Tithonian).

LEPTOLEPIS sp.

(Fig. 3D)

Material—One well-preserved specimen from the Oxfordian of Popovo, Kostroma Oblast, Russia.

Description—OL 2.93 mm, OH 1.26 mm, OL:OH 1.82 (n = 1). Thin, slender otolith. Triangular, pointed rostrum. Short, narrow cauda. Rounded posterior rim. Smooth, elongated dorsal rim. Smooth, oval ventral rim. No ornamentation.

Discussion—This is the only *Leptolepis* specimen from Russia in the present study. The otolith has a slender outline and pointed rostrum. *Leptolepis* sp. has a more dorsally-curved ostium than in *L. plicatilis* and *L. inaequalis*. The ostium of *Leptolepis* sp. seems to be well-developed and has a small recess at the beginning of the dorsal rim. The posterior part of the sulcus is covered with some sediment. The posterior rim of the otolith has a small triangular angle. Neither the dorsal or ventral rim is ornamented; whether this is a primary or erosional feature is unknown. The otolith is placed in *Leptolepis* because of: (i) medial, slightly-curved sulcus, (ii) massive, wide triangle-shaped ostium, (iii) curved dorsal rim, and (iv) visible dorsal depression. Those features are not diagnostic for any species and more material is needed.

Family indet.

Genus *SPHAERONCHUS* Stinton in Stinton & Torrens, 1968

Type species—*Sphaeronchus dorsetensis* Stinton & Torrens, 1968; Bathonian, Middle Jurassic, Dorset, United Kingdom.

SPHAERONCHUS DORSETENSIS Stinton in Stinton & Torrens, 1968

(Fig. 3E)

1968 *Sphaeronchus dorsetensis*—Stinton and Torrens:fig. 2.

2018 *Sphaeronchus dorsetensis* Stinton and Torrens, 1968—Schwarzhans:fig. 4E.

Material—12 specimens (3 well-preserved and 9 broken) from the Bathonian of Gnaszyn.

Description—OL 3.2 mm, OH 2.8 mm, OL:OH 1.14 (n = 1). Rounded otolith. Medial sulcus with wide cauda. Short dorsal rim with well-developed posterodorsal angle. Deep, rounded, and smooth ventral rim.

Remarks—*Sphaeronchus* otoliths are quite rare compared to those of *Leptolepis*. Our findings indicate that *Sphaeronchus dorsetensis* had a broader paleogeographic range than previously known.

Stratigraphic and Geographic Range—Bathonian (Middle Jurassic) of Dorset, United Kingdom, and central Poland.

SPHAERONCHUS RUNDLEI Schwarzhans, 2018

(Fig. 3F)

2018 *Sphaeronchus rundlei—*Schwarzhans:fig. 4F.

Material—17 specimens **(**2 well-preserved and 2 broken) from the Kimmeridgian of Osmington Mills, and 13 specimens (6 well-preserved and 7 broken) from the Kimmeridgian of Blackhead.

Description—OL 0.7 mm, OH 0.6 mm, OL:OH 1.17 (n = 1). Rounded otolith. Rostrum broadly rounded. Cauda wide, superior and inferior cristae well developed. Short dorsal rim, regularly raising from ostium to posterodorsal angle. Deep, semicircular ventral rim with smooth margin.

Remarks—Most complete and overall better-preserved specimens are small (OL ~ 0.73 mm, Fig. 3F). Larger specimens are poorly preserved and very similar to *Sphaeronchus dorsetensis* with a rounded posterior part of the otolith with massive postdorsal angle; wide cauda; and deep, semicircular ventral rim. They also lack a preserved anterior part including ostium and rostrum.They resemble the holotype of *Sphaeronchus rundlei* in the shape of their rostra and short dorsal rim, regularly descending from posterodorsal angle to ostium. The only difference between our material and the holotype (Schwarzhans, 2018; Fig. 4F) is the shape of posterior rim: straight in our material and rounded in the holotype. However, the posterior rims of five smaller specimens from our material are more rounded, than in the remainder of the specimens in our material and in the holotype. The difference between the holotype and the smaller specimens could be related to ontogenetic changes or intraspecific variation.

Stratigraphic and Geographic Range—Oxfordian–Kimmeridgian (Upper Jurassic), Dorset, United Kingdom.

Order ALBULIFORMES Jordan, 1923

Family PTEROTHRISSIDAE Gill, 1893

Genus *PTERALBULA* Stinton, 1973

Type Species—*Otolithus* (*Atherina*) *cantiana* (Shepherd, 1916); Gault Clay, Albian, Lower Cretaceous, Folkestone, Kent, United Kingdom.

PTERALBULA JURASSICA, sp. nov.

(Fig. 4A–K)

Etymology—Named after the system from which the holotype was obtained.

Holotype—ZPAL P. 22/Bh/1 (Fig. 4A), from sample BH-2023-A3.

Type Locality—Blackhead, Dorset, United Kingdom.

Type Horizon—*Autissiodorensis* Zone of the upper Kimmeridgian (Upper Jurassic).

Paratypes—10 specimens, including ZPAL P. 22/Gn/11 from the Bathonian, Middle Jurassic of Gnaszyn, Poland; ZPAL P. 22/Gl/3 and ZPAL P. 22/Gl/10–14 from the Callovian, Middle Jurassic of Gołaszyn, Poland; and ZPAL P. 22/Bh/2–4 from the Kimmeridgian, Upper Jurassic of Blackhead, UK (Fig. 4B–K).

Other Material—252 specimens, (14 complete and 52 broken specimens from the Callovian of Gołaszyn, Poland; 4 well-preserved and 47 broken specimens from the Bathonian of Gnaszyn, Poland; 1 well-preserved and 13 broken specimens from the Kimmeridgian of Blackhead, United Kingdom; and 33 well-preserved and 90 broken specimens from the Kimmeridgian of Osmington Mills, United Kingdom).

Diagnosis—Oval, elongated otolith with triangular ostium. Long, straight cauda terminating close to posterior rim of otolith. Crista superior of cauda curved at the end of sulcus. Dorsal field of otolith with a shallow depression and elongated predorsal and postdorsal angles on the dorsal rim. Predorsal angle slightly larger than postdorsal angle. Ventral field of otolith oval and larger than dorsal field. Ventral rim of otolith is sharp and continuous with large rostrum. Outer face of otolith flat. Inner face of otolith undulated.

Description—$\mathrm{OL}_{\mathrm{Hol}}$ 3.8 mm, $\mathrm{OH}_{\mathrm{Hol}}$ 2.4 mm, $\mathrm{OL}_{\mathrm{Hol}}:\mathrm{OH}_{\mathrm{Hol}}$ 1.58, OL 2.8–3.8 mm, OH 1.8–2.4 mm, OL:OH 1.40–1.82 (n = 14). Oval otolith. Open, triangular ostium. Straight, long cauda with curved ending. Dorsal depression and crista superior well-developed. Two angles on the dorsal rim. Smooth, convex ventral rim. Flat inner face.

Discussion—*Pteralbula jurassica* sp. nov. is the oldest-known species of *Pteralbula*, and oldest discovered albuliform. It shares many morphological features with *Pteralbula galtina* (Koken, 1891), i.e. oval, elongated shape with deep, broad, and evenly convex ventral rim; slightly curved dorsal end of the cauda; well-developed crista superior of the cauda; and smooth, long ventral rim terminating on ostium. The ostium and anterior part of *Pteralbula jurassica* sp. nov. resemble that of *Pteralbula polonica* (Pindakiewicz et al., 2023), while dorsal and posterior rims are similar to *P. galtina*. The posterior dorsal angle is greater than the anterior of *P. galtina* and *P. cantiana* (Shepherd, 1916), although not as strong.

Specimens of *P. jurassica* sp. nov. from older localities are shorter and broader than those from younger localities (*Pteralbula jurassica* sp. nov. from the Bathonian and Callovian, Middle Jurassic, of Poland: OL 2.8–3.1 mm, OH 1.8–2.1 mm, OL:OH 1.4–1.6 vs *Pteralbula jurassica* sp. nov. from the Kimmeridgian, Upper Jurassic, of the United Kingdom: OL 3.3–3.8 mm, OH 1.8–2.4 mm, OL:OH 1.58–1.82). These older specimens are more variable in number and shape of angles on the dorsal rim and in presence of an additional mediodorsal angle (see Fig. 4E–G). Similar morphological variability occurs among some albuliform otoliths from the Valanginian, Lower Cretaceous, of Wąwał, Poland, and their younger conspecifics from the Aptian–Albian (Lower Cretaceous) of Speeton and Folkestone, United Kingdom, respectively (Pindakiewicz et al., 2023).

Stratigraphic and Geographic Range—Bathonian and Callovian (Middle Jurassic) of Poland, and Kimmeridgian (Upper Jurassic) of Dorset, United Kingdom

Family indet.

Genus *PALEALBULA* Frizzell 1965a

Type Species—*Otolithus* (*Clupeidarum*) *neocomiensis* (Priem, 1908); Hauterivian, Lower Cretaceous, Paris Basin, France.

PALEALBULA VENTAI, sp. nov.

(Fig. 4L)

Etymology—Named after the Venta River, near the Papartynė locality.

Holotype—ZPAL P. 22/Pap/6 (Fig. 4E), from sample PAP-2023-2S.

Type Locality—Papartynė, northern Lithuania.

Type Horizon—*Jasoni–Coronatum* zones of the middle Callovian (Middle Jurassic).

Other Material—6 specimens (2 complete and 4 broken) from the Callovian, Middle Jurassic of Papartynė, Lithuania.

Diagnosis—Long, ellipsoidal otolith. Ostium long, narrow, and connected to the dorsal rim by a long recess. Sulcus long and ventrally curved. Cauda terminated at posterior rim. Well-developed crista superior and crista inferior. Dorsal field narrow, dorsal rim with two flattened angles. Posterior angle poorly developed and smooth. Ventral rim deep, uniformly convex, and smooth.

Description—$\mathrm{OL}_{\mathrm{Hol}}$ 2.74 mm, $\mathrm{OH}_{\mathrm{Hol}}$ 1.68 mm, $\mathrm{CaL}_{\mathrm{Hol}}$ 1.64 mm, $\mathrm{Os}_{\mathrm{Hol}}$ 0.83 mm, $\mathrm{OL}_{\mathrm{Hol}}$:$\mathrm{OH}_{\mathrm{Hol}}$ 1.63, $\mathrm{OL}_{\mathrm{Hol}}$: $\mathrm{CaL}_{\mathrm{Hol}}$ 1.67, OL 2.74–2.92 mm, OH 1.68–1.95 mm, OL:OH 1.5–1.63 (n = 2). Long and narrow ostium. Long excisura. Long, curved sulcus. Cauda terminates at poorly-developed posterior angle. Narrow dorsal rim. Flattened dorsal angles. Poorly developed dorsal depression. Deep, regularly curved, smooth ventral rim.

Discussion—The otoliths of *Palealbula ventai* sp. nov. are older than those of *Palealbula crenulata* sp. nov. (Kimmeridgian), *Palealbula moscoviensis* Schwarzhans &

Mironenko, 2020 (Tithonian), *Palealbula korchinskyi* Schwarzhans & Mironenko, 2020 (Tithonian), *Palealbula neocomiensis* (Priem, 1908) (Valanginian–Hauterivian), and *Palealbula depressidorsalis* Schwarzhans, 2018 (Valanginian–Albian). The dorsal rim of *Palealbula ventai* sp. nov. somewhat resembles that of *Palealbula crenulata* sp. nov. and *P. neocomiensis* and is wider than in *P. moscoviensis* and *P. korchinskyi*. *Palealbula ventai* sp. nov. differs from *Palealbula crenulata* sp. nov. by the lack of crenulation on the ventral rim of the otolith, the cauda termination on the posterior angle, small postdorsal angle, and visible dorsal depression. *Palealbula ventai* sp. nov. is more elongated than *Palealbula crenulata* sp. nov. $\mathrm{OL}_{P.\ ventai}$ 2.74–2.92 mm vs $\mathrm{OL}_{P.crenulata}$ 3.73 mm). Unlike *P. crenulata* sp. nov., the ventral rim of *P. ventai* sp. nov. is not crenulated. Ventral rims of specimens of *Palealbula ventai* sp. nov. are well-preserved and not affected by erosion, therefore it is unlikely that the lack of crenulations is a taphonomic feature. Furthermore, the specimens we attribute to *P. ventai* sp. nov. are similar in size to those of *P. crenulata* sp. nov., which indicates the differences in ventral rim morphology in two species (smooth in in *P. ventai* sp. nov. vs. crenulated in *P. crenulata* sp. nov.) is likely not ontogenetic. The dorsal field in *Palealbula ventai* sp. nov. is set off at an angle from the remainder of the inner face similar to *P. korchinskyi* and *Palealbula depressidorsalis* Schwarzhans, 2018. However, the dorsal field of *Palealbula ventai* sp. nov. is larger than that of *P. depressidorsalis* and possesses a shallow depression. *Palealbula ventai* sp. nov. is the oldest *Palealbula* species known from the fossil record and indicates that albuliformes appeared as early as the Middle Jurassic.

Stratigraphic and Geographic Range—Callovian (Middle Jurassic) of Papartynė, northern Lithuania.

PALEALBULA CRENULATA, sp. nov.

(Fig. 4M)

Etymology—Named after the small crenulation on the margin of the ventral rim.

Holotype—ZPAL P. 22/Om/7 (Fig. 4F), a specimen with partially eroded dorsal rim from sample OM-2023-01.

Type Locality—Osmington Mills, Dorset, United Kingdom.

Type Horizon—*Autissiodorensis* Zone of upper Kimmeridgian (Upper Jurassic).

Material—9 specimens (3 complete and 4 broken specimens from the Kimmeridgian of Osmington Mills, and 2 broken specimens from the Kimmeridgian of Blackhead).

Diagnosis—Long, ellipsoidal otolith. Ostium long and narrow and continuous with dorsal rim. Sulcus long and narrow. Cauda terminates a short distance from posterior rim. Well-developed crista superior, ventrally-curved at the caudal termination. Dorsal rim flattened with small predorsal angle. Oval posterior rim. Ventral rim with small crenulation along margin.

Description—OL_{Hol} 3.73 mm, OH_{Hol} 2.66 mm, CaL_{Hol} 1.92 mm, Os_{Hol} 1.69 mm, OL_{Hol}:OH_{Hol} 1.4, OL_{Hol}:CaL_{Hol} 1.94. Narrow ostium. Ostium and dorsal rim continuous. Long and narrow sulcus. Cauda ventrally-curved close to the posterior rim. Narrow dorsal field. Small predorsal angle. Oval-shaped posterior rim. Deep, regularly-curved ventral rim with folded ornamentation and fine crenulations.

Discussion—*Palealbula crenulata* sp. nov. differs from *Palealbula ventai* sp. nov., *P. moscoviensis*, and *P. korchinskyi* in having an ornamented ventral rim with crenulation along the margin. The other Early Cretaceous species of *Palealbula* (e.g., *P. depressidorsalis* and *P. neocomiensis*) have a smooth ventral rim (Pindakiewicz et al., 2023; Schwarzhans, 2018). *Palealbula crenulata* sp. nov. is more compressed than *Palealbula ventai* sp. nov., *P. moscoviensis,* and *P. korchinskyi* (OL:OH of *Palealbula crenulata* sp. nov. 1.4 vs OL:OH of *Palealbula ventai* sp. nov. 1.5–1.63 vs OL:OH of *P. moscoviensis* 1.8–1.9 vs OL:OH of *P.*

korchinskyi 1.9–2.0). Both cauda and ostium of *P. crenulata* sp. nov. are narrower than those of *P. moscoviensis*, and *P. korchinskyi* and similar to *Palealbula ventai* sp. nov. The shape of the dorsal rim of *P. crenulata* sp. nov. resembles *P. korchinskyi* and *P. neocomiensis*.

Stratigraphic and Geographic Range—Kimmeridgian (Upper Jurassic), Osmington Mills, Dorset, United Kingdom.

PALEALBULA cf. *DECLIVIS* Schwarzhans, 2018

(Fig. 5A)

?2018 *Palealbula declivis* sp. nov.—Schwarzhans: fig. 6B.

Material—86 specimens (including 18 complete and 62 broken specimens from Kimmeridgian of Osmington Mills, and 6 broken from Kimmeridgian of Blackhead).

Description—OL 1.2–1.65 mm, OH 0.66–0.82 mm, OL:OH 1.8–2.0 (n = 3). Elongate, thick otolith with long, massive and pointed rostrum. Long, narrow ostium with horizontal margin, dorsally opened. Long and straight cauda. Uneven thick crista superior, even and thick crista inferior. Dorsal rim thick, dorsal field narrow with dorsal depression present. Singular, obtuse mediodorsal angle on the dorsal rim. Ventral rim moderately deep with coarse radial crenulations. Inner face convex with radial ornamentation.

Remarks—Current otoliths from Kimmeridgian of Osmington Mills and Blackhead strongly resemble the holotype (and sole specimen) of *Palealbula declivis* Schwarzhans, 2018, from middle Valanginian of Germany. They share similar index (OL:OH 1.8–2.0 in the specimens studied herein vs 2.0 in the holotype of *P. declivis*), short dorsal rim, obtuse mediodorsal angle, supramedian cauda with well-developed superior and inferior cristae, pointed tip of the rostrum, and moderately-deep curved ventral rim. Current otoliths differ from the holotype *P. declivis*, however, in a somewhat lower dorsal field, unevenly thick crista superior, and lack of a postdorsal angle, absence of crenulation on ventral rim, and radial ornamentation on the inner face. Because the current specimens are small compared to the holotype of *P. declivis* (OL 1.2–1.65 mm vs OL 4.3 mm), we consider it plausible that they represent juveniles of that species, and the differences in shape are ontogenetic. On the other hand, the otoliths from the Kimmeridgian of Osmington Mills and Blackhead have relatively deep caudae, and well-developed cristae, which should not be the case in juvenile otoliths. Furthermore, *P. declivis* is known only from a single specimen and until more specimens are available for study we decided to tentatively assign our specimens to that species.

Genus *PROTALBULA* Frizzell, 1965a

Type Species—*Protalbula sohli* Frizzell, 1965a; Campanian, Upper Cretaceous, Georgia, U.S.A.

PROTALBULA DORSETENSIS, sp. nov.

(Fig. 5B)

Etymology—Named after the type area.

Holotype—ZPAL P. 22/Om/3 (Fig. 4G), from sample OM-2021-02.

Type Locality—Osmington Mills, Dorset, United Kingdom.

Type Horizon—*Autissiodorensis* Zone of the upper Kimmeridgian (Upper Jurassic).

Material—39 specimens (23 complete and12 broken specimens from the Kimmeridgian of Osmington Mills, and 4 complete specimens from the Kimmeridgian of Blackhead).

Diagnosis—Broad, triangular rostrum with short and wide ostium. Broad, supermedially-positioned cauda with straight termination. Dorsal rim with well-developed pointed predorsal angle and well-developed rounded postdorsal angle. Ventral rim deep and strongly convex with thin margin. Flat inner face.

Description—OL_{Hol} 1.75mm, OH_{Hol} 1.6 mm, OL_{Hol}:OH:$_{Hol}$ 1.1 (only holotype was measured). Pentagonal, thin otolith. Long, narrow ostium with steeply-inclined ventral margin. Straight cauda in supramedian position, terminating close to the posterior rim of otolith. Visible predorsal and postdorsal angles on nearly flat dorsal rim. Deeply-lobate ventral rim. Dorsal rim shorter than ventral rim.

Discussion—*Protalbula dorsetensis* sp. nov. is most similar to *Protalbula pentangularis* Pindakiewicz, Hryniewicz, & Kaim, 2023, especially in its pentagonal shape, shallow cauda, longer ostium, and curved, deep ventral rim. *Protalbula dorsetensis* sp. nov. differs from *P. pentangularis* in the broader cauda, which is straighter than in *Protalbula pentangularis*. The OL:OH ratio of *P. dorsetensis* sp. nov. is lower than that of *P. pentangularis* or *Protalbula ventralis* (Weiler, 1971) with 1.1 in *Protalbula dorsetensis* sp. nov. vs. 1.2–1.3 in *P. pentangularis* and vs. 1.3–1.4 in *P. ventralis*. The postdorsal angle is more pronounced than in other *Protalbula* species. Gross morphology could suggest a closer relation between *P. dorsetensis* sp. nov. and *P. pentangularis*. However, the shorter ostium and broader cauda with a straight termination, the width of the otolith, and the well-developed postdorsal angle strongly supports a species-level distinction.

Stratigraphic and Geographic Range—Kimmeridgian (Upper Jurassic), Osmington Mills, Dorset.

Order ELOPIFORMES Linnaeus, 1766

Family indet.

Genus *JURAELOPS*, gen. nov.

Etymology—Combination of "*Jura-*" from "Jurassic", and "*-elops"* based on similar morphology to *Elops* otoliths.

Type Species—*Juraelops prodigiosum* sp. nov.; Kimmeridgian, Upper Jurassic, Osmington Mills and Blackhead, Dorset, United Kingdom.

Species included—Type species only.

Diagnosis—As for the type species.

Comparison—The morphology of *Juraelops* gen. nov. strongly differs from other Jurassic otoliths. The rostrum is massive and straight, with its axis inclined downwards, which gives the otolith a distinctive shape among Jurassic sagittal otoliths. The ventral rim of the otolith is weakly lobate and thin. The sulcus of *Juraelops prodigiosum* gen. nov. et sp. nov. is relatively short (OL:SuL ca. 0.79) in comparison to other Jurassic otoliths we studied.

JURAELOPS PRODIGIOSUM, gen. et sp. nov.

(Fig. 5C–D)

Etymology—From Latin *prodigiosum*, meaning "bizarre", referring to an unusual morphology of the otolith.

Holotype—ZPAL P. 22/Om/5 (Fig. 5C), from sample OM-2021-02.

Type Locality—Osmington Mills, Dorset, United Kingdom.

Type Horizon—*Autissiodorensis* Zone of the upper Kimmeridgian (Upper Jurassic).

Paratype—A single well-preserved specimen ZPAL P.22/Bh/6 (from the Kimmeridgian, Upper Jurassic, Blackhead, United Kingdom) (Fig. 5D).

Other material—19 broken specimens from the Kimmeridgian of Osmington Mills, a single complete and 2 broken specimens from the Kimmeridgian of Blackhead.

Diagnosis—Fusiform, elongated otolith, leptolepid-like sulcus without antirostrum and excisura. Long, straight cauda that terminates distant from posterior tip of otolith. Tip of the rostrum weakly-developed inferior, axis of the rostrum weakly inclined downwards. The ventral rim is irregularly lobate and thin. Narrow depression between crista inferior and ventral rim. A very shallow mediodorsal angle. A dorsal depression located between cauda and dorsal rim.

Description—$\mathrm{OL}_{\mathrm{Hol}}$ 1.56 mm, $\mathrm{OH}_{\mathrm{Hol}}$ 0.64 mm, $\mathrm{CaL}_{\mathrm{Hol}}$ 0.74 mm, $\mathrm{OsL}_{\mathrm{Hol}}$ 0.54 mm, $\mathrm{OL}_{\mathrm{Hol}}$:$\mathrm{OH}_{\mathrm{Hol}}$ 2.44, OL 1.1–1.56 mm, OH 0.57–0.64 mm, OL:OH 1.93–2.44 (n = 2). Fusiform otolith. Straight cauda. Ostium without collicullum. Shallow ventral rim with crenulation. Broadly-rounded, smooth mediodorsal angle. Dorsal field with depression. Undulated inner face of the otolith.

Discussion—*Juraelops prodigiosum* sp. nov. is unique among Mesozoic teleost otoliths due to its: i) broad, inferior rostrum, ii) short ostium, iii) cauda terminating distant from posterior tip of otolith, and iv) ventral field with narrow depression below sulcus. Leptolepid-like rostrum and cauda are plesiomorphic in those Mesozoic groups that emerged during the Jurassic and Early Cretaceous (Schwarzhans, 2018). The lack of a collicullum in *Juraelops prodigiosum* gen. et sp. nov. somewhat resembles otoliths included in the genera *Protoelops* and *Leptoelops*. However, the shape of rostrum and ventral rim of *Juraelops prodigiosum* sp. nov. is unique among Jurassic otoliths (combination of inferior rostrum, short cauda terminating distant from posterior tip, and depression below sulcus on ventral rim).

Stratigraphic and Geographic Range—Kimmeridgian (Upper Jurassic) of Dorset, United Kingdom.

Order Osteoglossiformes, Regan, 1909

Family uncertain

Genus *KOKENICHTHYS* Schwarzhans, 2010

Type species—“?*Albulida*” *ensis* Nolf & Dockery, 1990, Campanian, Upper Cretaceous, Alabama, U.S.A.

KOKENICHTHYS sp.

(Fig. 5E)

Material—3 specimens: 1 specimen with slightly eroded dorsal margin of the otolith and broken rostral tip and 2 broken specimens with only posterior parts preserved. All from the Kimmeridgian of Osmington Mills.

Description—OH 0.51 mm, OL ca. 0.96 mm, OL:OH 1.88. Deltoidal otolith without ornamentation. Deep, dorsally-shifted and dorsally-opened sulcus without collicullum. Dorsal field short. Well-developed postdorsal angle. Ventral rim well developed. The inner face is smooth.

Discussion—In the most complete specimen from Osmington Mills the part of the sulcus is eroded, therefore it is unknown if it was ornamented like *Kokenichthys kuteki* Pindakiewicz, Hryniewicz & Kaim, 2023, or smooth like *Kokenichthys atavus* (Nolf, 2004). In otolith shape this species resembles *K. ensis* (Nolf & Dockery, 1990), but the well-developed postdorsal angle mirrors that of *Kokenichthys kuteki*. The specimens described herein differ from *K. kuteki* in the ornamentation along the ventral rim, which is irregularly folded. The available specimens are not preserved completely enough for a species identification.

Infraclass HOLOSTEI Müller, 1846

Order indet.

Family indet.

Genus *ARCHAEOTOLITHUS* Stolley, 1912

Type species—*Archaeotolithus trigonalis* Stolley, 1912; Jurassic of Germany.

ARCHAEOTOLITHUS SOLIDUS, sp. nov.

(Fig. 6A, B)

Etymology—From Latin term “solidus” meaning “massive, solid”.

Holotype—MGUS/Sz 4703 (FIG. 6A).

Type Locality—Gnaszyn, central Poland.

Type Horizon—*Subcontractus–Bremeri* zones of the upper Bathonian (Middle Jurassic).

Paratype—A single well-preserved specimen MGUS/Sz 4725 (upper Bajocian, Middle Jurassic, Złote Góry, Poland) (Fig. 6B).

Other material—5 specimens (4 eroded but otherwise complete specimens from the Bathonian of Gnaszyn, and 1 damaged specimen from the Bajocian–Bathonian of Sowa).

Diagnosis—Triangular, massive otolith with strongly-convex inner face without discernible sulcus on smaller specimen. Sulcus faintly developed in larger specimens covering entire posterior part of otolith. Dorsal part of otolith with narrow tip and nucleus. Ventral part much wider than dorsal part and poorly ornamented. Ventral field with medial growth ring and radials. Outer face of otolith flat without ornamentation or with delicate radials. Outer face of otolith undulated with concave central part.

Description—OL_{Hol} 7.77 mm, OH_{Hol} 7.81 mm, OT_{Hol} 3.2 mm, $OL_{Hol}:OH_{Hol}$ 0.99. OL 6.78–7.77 mm, OH 6.85–7.81 mm, OT 3.2–4.5 mmm, OL:OH 0.99 (n = 2). Triangular, massive otolith. Strongly-convex inner face. Sulcus poorly marked or absent. Ornamentation on ventral rim with medial growth ring on ventral field. Undulated outer face with concave central part.

Discussion—The smaller specimens of *Archaeotolithus solidus* sp. nov. differ from those of most Jurassic *Archaeotolithus* species in its smooth inner face and the lack of a discernible sulcus. The outline of the inner face and the indistinct sulcus resemble that of *A. bornholmiensis* (Malling & Grønwall, 1909) from the Pliensbachian, Lower Jurassic of southern Germany and of *A. aptychoides* Pindakiewicz, Hryniewicz & Kaim, 2023, from the Valanginian of central Poland. The asymmetry of the inner face is similar to that of *A. trigonalis* Stolley, 1912, and *A. aptychoides* (with larger anterior than posterior part of the otolith). The very faint, radial ornamentation of the inner face and the undulated outer face differentiate *Archaeotolithus solidus* sp. nov. from the smooth inner face and straight outer face of *A. bornholmiensis*. The paratype of *A. solidus* sp. nov. (Fig. 6B) has a poorly-developed sulcus and is thinner than the holotype (Fig. 6A). The differences in shape between specimens of *Archaeotolithus solidus* sp. nov. could be ontogenetic, as is the case in *Archaeotolithus eiggensis* (Schwarzhans & Wakefield, 2024). *Archaeotolithus solidus* sp. nov., *A. bornholmiensis*, and *A. aptychoides* are morphologically similar and they most likely belong to morphotype 2 of *Archaeotolithus* species, which is characterized by a massive inner face with poorly developed sulcus (Schwarzhans & Wakefield, 2024).

Stratigraphic and Geographic Range—Bajocian–Bathonian (Middle Jurassic), central Poland.

ARCHAEOTOLITHUS EIGGENSIS Schwarzhans & Wakefield, 2024

(Fig. 6C)

2024 *Archaeotolithus eiggensis* n. sp.—Schwarzhans and Wakefield:fig. 5a–p.

Material—2 specimens (1 well-preserved specimen from the Bajocian–Bathonian of Sowa, and 1 broken specimen from the Bathonian of Gnaszyn).

Description—OL_{Hol} 11.32 mm, OH_{Hol} 9.53 mm, $OL_{Hol}:OH_{Hol}$ 1.18. Thin trapezoid otolith. Short sulcus. Rounded dorsal tip. Folded ventral rim.

Discussion—The sulcus of *Archaeotolithus eiggensis* resembles that of *A. doppelsteini* and *A. trigonalis,* although it is narrower than in *A. trigonalis*. The ventral rim of *Archaeotolithus eiggensis* is ornamented similar to *A. trigonalis* with short radials on the outer face. The inner face of *Archaeotolithus eiggensis* is covered with elongated dendroidal structures, which we interpret as fossilized bryozoans. The preservation of their surface suggests that this specimen of *Archaeotolithus eiggensis* was exposed on the seabed for some time before being covered with sediment. Our specimens are slightly older stratigraphically than the holotype and paratypes from Scotland (Schwarzhans & Wakefield, 2024).

Stratigraphic and Geographic Range—Upper Bajocian–middle Bathonian (Middle Jurassic), central Poland and Scotland, United Kingdom.

ARCHAEOTOLITHUS TRIGONALIS Stolley, 1912

(Fig. 6D–F)

1912 *Archaeotolithus trigonalis*—Stolley:pl. 7, figs 1–3.

2014 *Archaeotolithus* group 2—Hesse:fig. 29A–E.

2018 *Archaeotolithus trigonalis* Stolley, 1912—Schwarzhans:fig. 8K.

2022 *Archaeotolithus trigonalis* Stolley, 1912—Schwarzhans & Keupp:pl. 4, fig. 5–7.

Material—33 specimens (19 complete specimens and 14 specimens with slightly-eroded tip; 20 from Gnaszyn, 4 from the Bathonian of Blanowice, 2 from the Bathonian of Wrzosowa and 2 from the Bajocian of Złote Góry, all central Poland, and 5 from the Callovian of Papartynė, northern Lithuania).

Description—Trigonal, massive otolith. Convex inner face with broad, visible sulcus. Outer face smooth and flat with radials. The inner face of the otolith is divided by a ridge. The posterior part is flat and narrows towards the ventral rim. The anterior part has a ventrally-curved sulcus that terminates close to the anterior rim.

Remarks—Large, trigonal otoliths with folded ventral and lateral rims. Most of the specimens of *A. trigonalis* in our sample have a more faintly-developed sulcus than the holotype, resembling the state in *A. bornholmiensis* and *A. aptychoides* (Pindakiewicz et al., 2023).

Stratigraphic and Geographic Range—Pliensbachian–Callovian (Lower–Middle Jurassic), Germany, Lithuania, and central Poland.

ARCHAEOTOLITHUS sp.

(Fig. 6G)

Material—One specimen (ZPAL P. 22/Pap/2) with broken dorsal part including the nucleus from the Callovian of Papartynė, northern Lithuania.

Description—Pentagonal massive otolith. Inner face convex, thins towards the anterior rim. Smooth rims. Outer face flat and smooth. OL 3.42 mm.

Discussion—The outline of this specimen resembles *Archaeotolithus doppelsteini* Schwarzhans & Keupp, 2022, more than any other species. *Archaeotolithus* sp. has a thin anterior rim, its anterior side of the inner face is short and mostly covered by curved sulcus. The entire surface of the inner face of *Archaeotolithus* sp. is smooth like that of *A. bornholmiensis*. Despite the incomplete dorsal part, the morphology of the sulcus resembles *A. doppelsteini* and *A. invernizziae* Schwarzhans and Wakefield 2024. The Callovian (Middle Jurassic) *Archaeotolithus* sp. and the new records of *Archaeotolithus trigonalis* in Poland and Lithuania fill the gap of this genus in the fossil record between the Bathonian and Valanginian (Schwarzhans, 2018; Schwarzhans et al., 2018b; Schwarzhans & Keupp, 2022; Pindakiewicz et al., 2023).

LAPILLI

Order and family indet.

Genus *VODYANOI*, gen. nov.

Etymology—Inspired by the name of fish people from “The Witcher” books by Andrzej Sapkowski; gender masculine.

Type Species—*Vodyanoi schwarzhansi* sp. nov. from the Bathonian, Middle Jurassic, Anna clay pit, Gnaszyn, central Poland.

Species Included—*Vodyanoi schwarzhansi* sp. nov. and *Vodyanoi stringeri* sp. nov. from the Bathonian, Middle Jurassic, central Poland.

Diagnosis—A large circular lapillus with centrally-positioned rounded and flattened *gibbus maculae* surrounded by horseshoe-shaped confluentia gibbi maculae and filled with colliculum. Surface of *gibbus maculae* uneven.

Discussion—*Vodyanoi* gen. nov. otoliths are flattened and round which we interpret as lapilli. One face is thickened, which we interpret as gibbus maculae (Assis, 2005) and which is surrounded by a horseshoe-shaped depression on the surface. This depression is filled with a colliculum-like structure that we interpret as equivalent to a confluentia gibbi maculae in typical lapilli. The overall morphology and large size of these lapilli resemble those of modern Ostariophysi (Sánchez & Martinez, 2017). If they are Ostariophysi, the structure that we interpret as confluentia gibbi maculae corresponds to a combined sulcus and sulcus minor of Sánchez and Martinez (2017:fig. 2a). The homologous structure in *Vodyanoi* gen. nov. is much broader and deeper than in modern lapilli and filled with a collliculum-like structure, which we have not seen in modern lapilli. The oldest putative Ostariophysi are Berriassian–Valanginian (Early Cretaceous) in age (Fara et al., 2010; Grande & Poyato-Arriza, 1999), ca. 35 Ma younger than the lapilli reported herein. The symmetry of *gibbus maculae* and *confluentia gibbi maculae* in *Vodyanoi* gen. nov. is similar to that of gadiform lapilli (Nolf, 2013). However, their oldest-known representatives are from the Late Cretaceous and nearly 100 Ma younger (Schwarzhans et al., 2024).

The species assigned to *Vodyanoi* possess large lapilli and are rare with only 4 specimens. They have been found only during surface collecting and do not occur in washed samples where other, smaller otoliths are common. The rarity of *Vodyanoi* is unlikely a result of taphonomy as it is large and robust and is more likely to be preserved than smaller otoliths which are nonetheless common in the studied material. We thus hypothesize that *Vodyanoi* lapilli represent a rare component of Middle Jurassic marine environments in central Poland and that those fish were large. *Vodyanoi* could have been an occasional visitor to the marine environment, similar to what has been proposed for the latest Cretaceous siluriform? *Vorhisia vulpes* Frizzell, 1965b, which spawned in estuarine and matured in marine environments (Carpenter et al., 2003). *Vorhisia vulpes* otoliths are occasionally very abundant in shallow-marine environments with strong riverine influence (Stringer & Schwarzhans, 2021), but otherwise are uncommon in open marine strata. The pattern of occurrence and gross morphological similarity to lapilli of Ostariophysi indicates that species of *Vodyanoi* may display a similar environmental trend and that this trend can partially explain its rarity in the relatively open marine Middle Jurassic strata of Poland. Irrespective of their uncertain systematic affinity we feel that these otoliths are distinct enough to warrant the description of a new genus with two species.

VODYANOI SCHWARZHANSI, sp. nov.

(Fig. 7A)

Etymology—Named in honour of Werner Schwarzhans for his foundational work on ancient otolith taxonomy.

Holotype—MGUS/Sz 2532 (Fig. 7A), lapillus from Anna clay pit.

Type locality—Anna clay pit in Gnaszyn, central Poland.

Type Horizon—*Retrocostatum* Zone of the upper Bathonian.

Other Material—2 broken specimens from the Bathonian of Gnaszyn clay pit.

Diagnosis—A large flattened lapillus of roughly circular shape with concave median margin and broadly arcuate lateral margin. Gibbus maculae centrally located, rounded and flattened, surrounded with horseshoe-shaped confluentia gibbi maculae filled with collicullum-like structure separated from otolith margin. Surface of gibbus maculae uneven.

Description—Flattened thin otolith, slightly longer than wide, somewhat elliptical in plain view with longest dimension oblique to anteroposterior axis. Lateral margin broadly rounded, median margin concave with small deep sinus near its terminus. Dorsal face nearly flat with weak depression parallel to median side, ventral face weakly convex. Gibbus maculae occupying ca. half of ventral face, rounded, with uneven surface. Confluentia gibbi maculae horseshoe-shaped, surrounding nearly whole gibbus maculae apart from its median margin, broad, with single collicullum-like structure occupying most of confluentia gibbi maculae apart from its posterior part. Incisura linea basalis absent.

Discussion—The dorsal surface of the otolith is covered with encrusting epibionts which we interpret as serpulids or sabellids (compare Słowiński et al., 2022). Their presence indicates that the otolith was exposed on the sediment surface for some time before final burial. Similar colonization by epibionts occurs on the surface of some other otoliths (e.g., *Archaeotolithus eiggensis* in Fig. 6C; *Protalbula ventralis* in Pindakiewicz et al. 2023:fig. 3F), indicating that some otoliths may survive such an exposure.

Stratigraphic and Geographic Range—Bathonian, Middle Jurassic, Anna and Gnaszyn clay pits, central Poland.

VODYANOI STRINGERI, sp. nov.

(Fig. 7B)

Etymology—Named in honour of Gary Stringer for his foundational work on ancient otolith taxonomy.

Holotype—MGUS/Sz 2531 (Fig. 6B), lapillus from Ogrodzieniec clay pit.

Type Locality—Ogrodzieniec, central Poland.

Type Horizon—*Retrocostatum* Zone of the upper Bathonian.

Diagnosis—A large tear-drop shaped lapillus with pointed median margin and broadly arcuate lateral margin. *Gibbus maculae* centrally located, rounded and flattened, surrounded by horseshoe-shaped confluentia gibbi maculae filled with collicullum-like structure which adheres to the lateral margin of otolith. Surface of gibbus maculae uneven.

Description—Otolith roughly tear-drop shaped with broadly rounded lateral margin and bluntly-pointed median margin. Domed lapillus, dorsal face convex, ventral face only slightly convex. Gibbus maculae occupies more than half of the ventral face, rounded with bluntly-pointed median margin and with uneven surface. Confluentia gibbi maculae horseshoe-shaped, surrounding nearly whole gibbus maculae apart from its median margin, with single collicullum occupying most of length of confluentia gibbi maculae apart from its posteriormost margin. Incisura linea basalis absent

Discussion—The general morphology of this species, with centrally positioned gibbus maculae and broad confluentia gibbi maculae filled with single, thick collicullum is similar to *V. schwarzhansi* sp. nov. described above from other Middle Jurassic localities in Poland. Some clear differences between the species are the (concave median margin in *V. schwarzhansi* vs. bluntly-pointed median margin in *V. stringeri*); the thin and flat dorsal face in *V. schwarzhansi* vs. domed, convex dorsal face in *V. stringeri*); and the size of the *gibbus maculae* relative to the surface of the ventral face (<50% of surface in *V. schwarzhansi* vs more than 50% in *V. stringeri*).

Stratigraphic and Geographic Range—Bathonian (Middle Jurassic), Ogrodzieniec, central Poland.

Unidentified Lapilli morphotypes

Remarks—The majority of Cretaceous and Jurassic lapilli have been loosely assigned to broad teleost groups or remain unassigned (e.g., Schwarzhans 2018; Schwarzhans et al., 2018a, 2022; Stringer et al., 2020), an approach we follow for the Jurassic lapilli morphotypes described below. Only the lapilli of ancient Ostariophysi are taxonomically determinable, but they are restricted to strata of latest Cretaceous and Cenozoic ages (Aguilera et al., 2013; Kocsis et al., 2024; Nolf, 2013; Sánchez & Martinez, 2017; Schwarzhans & Stringer, 2020, 2021).

LAPILLUS sp. 1.

(Fig. 7C, Appendix 1)

Material—One lapillus with eroded ventral side from the Kimmeridgian of Osmington Mills.

Description—Flattened otolith, longer than wide. Lateral margin convex, median margin broken with exact shape difficult to ascertain. Dorsal face flat and unornamented, ventral face flat with short crenulations in the median area perpendicular to the breakage plane. Gibbus maculae located ca. mid-length, large, rounded, and strongly projecting laterally; prominentia marginalis coincident with curvature of gibbus maculae. Confluentia gibbi maculae not detected. Linea basalis not detected.

Discussion—This lapillus is more flattened than the majority of teleost lapilli but has a developed gibbus maculae similar to teleost lapilli (Assis, 2005). Alleged Triassic non-teleost lapilli (Pindakiewicz et al., 2024) have different morphology, which may suggest that this lapillus might belong to a teleost. Lapilli of this type were previously unknown from the Jurassic (see Nolf, 2013, Schwarzhans, 2018). Breakage and flat, featureless faces indicate the lapillus might be abraded and therefore a formal description is not meaningful.

Lapillus sp. 2

(Fig. 7D, Appendix 2)

1926 cf. *Otolithus* (incertae sedis) *hartwellensis*—Frost:83, pl. IV, fig. 7.

2018 *Lapillus* sp. 2—Schwarzhans:fig. 8E.

Materials—9 complete specimens from the Kimmeridgian of Osmington Mills.

Remarks—Shape ranges from rhomboidal to trilobate. Short gibbus maculae with lobate tip on regio apicale gibbi maculae. The basal line of gibbus maculae is visible only from posterior and anterior side. Undulated ventral face of the otolith with straight extremum posterior and elongated, triangular extremum anterior. Deep and narrow confluentia gibbi maculae between gibbus maculae and prominenta marginalis. Smooth and flat dorsal face.

Discussion—The morphology of this trilobate lapillus with a deep and narrow confluentia gibbi maculae is similar to *Otolithus* (incertae sedis) *hartwellensis* described previously from the Tithonian (uppermost Jurassic) of Hartwell, Dorset (Frost 1926; Schwarzhans 2018). We decided to not assign these lapilli to any particular group because of the simple morphology and the generally poor understanding of fossil lapilli that are older than latest Cretaceous.

Stratigraphic and Geographic Range—Kimmeridgian–Tithonian (Upper Jurassic), Osmington Mills and Hartwell, Dorset.

DISCUSSION

Diversity of Cephalopod Statoliths and Fish Otoliths during the Jurassic period

The majority of ear stones found in Jurassic siliciclastic sediments at the investigated localities are cephalopod statoliths. Nearly all of those belong to the Morphotype A (Fig. 8) described by Clarke (2003), which is the most common morphotype in Jurassic sediments (Hart, 2019; Hart et al., 2015, 2016). Morphotype A most likely belongs to belemnoids or basal decabrachians (Pindakiewicz et al., 2022). Other morphotypes of Hart et al. (2015) are known exclusively from British localities.

Fish otoliths are less abundant than statoliths in the investigated Jurassic sections (Fig. 9). However, the diversity and number of fish otoliths changes during the Jurassic, so that Upper Jurassic assemblages start to resemble those from Lower Cretaceous sediments (Pindakiewicz et al., 2023). Lower and Middle Jurassic otolith assemblages are dominated by leptolepiforms (*Leptolepis* and *Sphaeronchus*) and also *Archaeotolithus*. The Bathonian (Middle Jurassic) to Oxfordian (Upper Jurassic) sections contain almost exclusively leptolepiforms and singular species of albuliform, elopiform, and large lapilli of *Vodyanoi* were recovered. Starting with the Kimmeridgian (Upper Jurassic), the otoliths are more diverse with albuliforms and elopiforms similar to the assemblage from the Valanginian (Lower Cretaceous) of Wąwał, central Poland (Pindakiewicz et al., 2023).

The oldest otoliths from our collection are from the Pliensbachian (Lower Jurassic) Eype Clay of Dorset, England. These comprise 5 specimens coated with sediment which makes their genus and species identification difficult.

The Middle Jurassic otolith assemblages from Poland and Lithuania are similar to one another with respect to the diversity of possible non-teleostean *Archaeotolithus* (three species from central Poland, and two from Papartynė) and leptolepiform *Leptolepis* (six species from Poland; three species from Gnaszyn, three from Gołaszyn, and one from Papartynė) with incidental otoliths of other genera (*Leptoalbula, Vodyanoi, Sphaeronchus*). In localities from central Poland, we identified three leptolepiform otolith species (*Leptolepis densus*, *L.*

circularis and *Sphaeronchus dorsetensis*), three species of *Archaeotolithus* (*A. solidus* sp. nov., *A. eiggensis* and *A. trigonalis*), and large lapilli of *Vodyanoi schwarzhansi* sp. nov. and *V. stringeri* sp. nov. which are all of unresolved systematic affinity. Regardless of their affinity, dimensions of some of those otoliths (species of *Archaeotolithus* and *Vodyanoi* gen. nov.) indicate they might have come from relatively large fish. Aggregations of fossils with sharp-edged molluscan shell fragments were discovered in Gnaszyn and other roughly coeval localities in Polish ore-bearing clays and interpreted as regurgigates of chondrichthyan or pycnodontiform durophagous fishes (Zatoń et al., 2007). The teeth of neoselachians from ore-bearing clays are too fragile to crush thick shells of bivalves or ammonites (Rees, 2012). Thus, we hypothesize that some non-teleost neopterygians (e.g., Pycnodontiformes and Dapediiformes) could have contributed to the shell-crushing predation in the Middle Jurassic environment of central Poland. Another fish that could have preyed on molluscs was the albuliform *Pteralbula jurassica* sp. nov, similar to the modern albulid *Albula vulpes* (Crabtree et al., 1998). *Pteralbula jurassica* sp. nov. is the currently oldest-known albuliform and predates known albuliform otoliths from the Upper Jurassic (Kimmeridgian) and the albuliform skeletal record that begins in the Lower Cretaceous (Valanginian; Filleul, 2001). Morphologically, *Pteralbula jurassica* sp. nov. displays a transition between leptolepiform and albuliform otolith morphology (triangular ostium, long rostrum faint angles on dorsal rim, and supramedial sulcus).

The Callovian otolith assemblages from Gołaszyn and Papartynė, although coeval, differ markedly. The assemblage from Gołaszyn consists mostly of leptolepiform (*Leptolepis densus*, *L. praeelops*, and *L. rotundatus*) and basal albuliform otoliths (*Pteralbula jurassica* sp. nov.). The assemblage of Papartynė contains only one species of leptolepiform otolith (*Leptolepis praeelops*) and two species of *Archaeotolithus* (*A. trigonalis* and *Archaeotolithus* sp.). Both localities represent different parts within the same marine basin. Gołaszyn is located in a distal, more open marine part, whereas Papartynė represents a more proximal, coastal part. We thus infer that the observed differences reflect different environment preferences of Jurassic fish species. Leptolepiform fish had a broad distribution and were apparently not restricted to any particular zone within the basin. *Archaeotolithus* likely belonged to fish preferring shallow and coastal waters, whereas albulids preferred more open marine environments. The identity of *Archaeotolithus* otoliths is still a matter of debate. Previously, they were hypothesized to belong to a late form of palaeoniscid (Schwarzhans, 2018). The Paleonisciformes are a polyphyletic group uniting some basal actinopterygians, which, from the Jurassic onward, were strictly freshwater (Skrzycka, 2014; Wang et al., 2018). *Archaeotolithus* otoliths could belong to holosteans (Schwarzhans, 2018; Schwarzhans & Keupp, 2022; Schwarzhans & Wakefield, 2024). Chondrostean acipenseriforms leading to extant polyodontids (paddlefishes) and acipenserids (sturgeons) appeared during the Jurassic, however, they were also strictly freshwater (Bemis et al., 1997), whereas otoliths very similar to *Archaeotolithus* are known also from Gondwana (Schwarzhans et al., 2018b). Pholidopleuriform skeletal remains are known only from the Triassic, whereas the oldest *Archaeotolithus* is recorded from the Pliensbachian (Early Jurassic), which suggests *Archaeotolithus* is unlikely to belong to that group. The newly discovered Triassic otoliths are much different from *Archaeotolithus* (Pindakiewicz et al., 2024).

The triangular, bell-shaped outline and straight, broad sulcus without ostium are features that appear both in *Archaeotolithus* and *Lepisosteus* otoliths (Nolf, 2013). Lepisosteiformes is an order of freshwater ginglymodian fishes that belong to holosteans (a major clade of neopterygians separate from teleosts), and lepisosteiform otoliths are quite similar to *Archaeotolithus* morphotype 1 (see Schwarzhans & Wakefield, 2024). The fossil record of marine lepisosteiforms extends to the Late Jurassic (Brito et al., 2017) and their scales are as old as Middle Jurassic (Kovalchuk & Afimova, 2020), which makes an assignment of *Archaeotolithus* to this group plausible. Triangular, almost bell-shaped otoliths are also typical for amiids (Nolf, 2013), belonging to halecomorphs, another group of holostean neopterygian fish. Marine halecomorphs existed from the Middle Triassic to the Early Cretaceous (Xu et al., 2014). In addition, there were other holostean fishes during the Jurassic (i.e., Macrosemiiformes, Aspidorhynchiformes, Pachycormiformes, Semionotoformes, Pycnodontiformes), but their otoliths are unknown and many of them went extinct before the Early Cretaceous. The gar-like aspidorhynchids` stratigraphic range is roughly coeval to *Archaeotolithus*. Therefore, we hypothesize that *Archaeotolithus* belongs to some unknown holostean fish, possibly a ginglymodian, in line with interpretations of Schwarzhans and Wakefield (2024). This hypothesis requires further investigation.

Pteralbula jurassica sp. nov., representing the oldest albuliform otolith and the oldest albuliform fossil, was found in the sediments of a deep part of the basin. The preference of the Middle Jurassic albuliforms for open marine instead of shallow marine settings agrees with previous observations of high abundance and diversity of albuliform otoliths in the Valanginian (Lower Cretaceous) open marine deposits of Wąwał, central Poland (Pindakiewicz et al., 2023), where otoliths of this group were the most abundant and diverse.

Leptolepiform otoliths of the Late Jurassic and Early Cretaceous are less diverse and less abundant in comparison to their Middle Jurassic counterparts (Schwarzhans, 2018; Schwarzhans & Keupp, 2022). *Leptolepis praeelops* and *L.* cf. *inaequalis* are examples of leptolepiform fish that survived to the Late Jurassic (Schwarzhans, 2018; Schwarzhans & Keupp, 2022) and Early Cretaceous (Sutherland et al., 2017). *Leptolepis praeelops* was found in the Oxfordian of Jurakalnis Gully together with small, unidentified teeth. Two species of *Leptolepis* were also found in the Upper Jurassic of Dorset, United Kingdom (*Leptolepis* aff. *plicatilis* at Redcliff and Osmington Mills, and *L.* cf. *inaequalis* at Osmington Mills). In the upper Oxfordian and Kimmeridgian, we found albuliform (*Protalbula* and *Palealbula*) and elopiform (*Leptoelops* and *Protoelops*) otoliths as well as otoliths which are more common in the Cretaceous, i.e., *Kokenichthys* sp., and *Pteralbula jurassica* sp. nov. (Dorset). The increased otolith diversity in the Kimmeridgian of Osmington Mills (9 species in 4 orders: leptolepiforms: *Leptolepis* aff. *plicatilis*., *L.* cf. *inaequalis*, albuliforms: *Protalbula dorsetensis* sp. nov., *Pteralbula jurassica* sp. nov. *Palealbula crenulata* sp. nov., *Palealbula* cf. *declivis*, elopiforms: *Juraelops prodigiosum* gen. nov. sp. nov., and osteoglossiforms: *Kokenichthys* sp.) may suggest that the first extensive teleost radiation occurred during the Jurassic (Pindakiewicz et al., 2023; Schwarzhans, 2018). Indeed, the teleost otolith diversity resembles that known from the Valanginian (Early Cretaceous) assemblage from Wąwał, (Pindakiewicz et al., 2023), with the caveat that we present a composite diversity from several localities of different ages rather than from a single locality. Nonetheless, otolith diversity from Jurassic sites discussed herein indicates that the general pattern of teleost otoliths was established already during the Early Jurassic (Clarke & Friedman, 2018) and continued to develop throughout the Jurassic (Schwarzhans, 2018; Pindakiewicz et al., 2023).

Abundance of Teleost Otoliths vs. Cephalopod Statoliths during the Jurassic period

Our collection of Jurassic ear stones shows an abundance of stem-group decabrachian statoliths throughout that period (Fig. 9). The large number of cephalopod statoliths in comparison to fish otoliths indicates that stem-group decabrachian cephalopods were the primary nektonic animals in marine ecosystems during the Jurassic (2589 decabrachian statoliths vs. 1294 fish otoliths in our collections). This proportion remained stable until the Early Cretaceous (Pindakiewicz et al., 2022, 2023), even though the abundance of fish otoliths started to increase slowly. In addition to the increasing number of teleost otoliths among ear stones throughout the Jurassic, the composition of teleost assemblages was gradually changing. Lower to Middle Jurassic sediments record an increase in teleost abundance relative to possible holostean otoliths (represented by *Archaeotolithus* otoliths) (Fig. 9). Interestingly, non-teleost neopterygian otoliths occur also in the Late Triassic otolith assemblage of the Cassian Fm. in Italy (Pindakiewicz et al., 2024), although the rarity of Triassic otoliths in general complicates comparisons with Jurassic counterparts. The otoliths of *Archaeotolithus* are relatively common until the Callovian (reported herein); they are yet unknown from the Late Jurassic and the youngest record is from the Valanginian (Pindakiewicz et al., 2023).

The most abundant Jurassic teleost otoliths belong to leptolepiforms (ca. 67% of all otoliths; 858 of 1281 teleost otoliths of all Jurassic otoliths in our collection). The abundance of other teleost otoliths is generally low, and leptolepiform otoliths become rarer and other teleost otoliths more abundant (ca. 26%; 96 from teleost 265 teleost otoliths) only in sediments as young as the Kimmeridgian, Late Jurassic (Fig. 9–10). However, although otoliths slowly increase in abundance throughout the Jurassic, even in the Kimmeridgian otolith abundance seems to be insignificant in comparison to the number of cephalopod statoliths.

The exception to that rule are our samples from the Oxfordian (Upper Jurassic) of Dorset where cephalopod statoliths are rare, e.g., in the sample from Eweleaze Beach we recovered 73 poorly-preserved leptolepid-like otoliths and only 4 statoliths. We hypothesize that this is because the Oxfordian sequence in Dorset was deposited under anoxic or deoxygenated conditions to much greater degree than those from other successions (Duff, 1975). Among several cephalopod groups hypothesized to be the source of Jurassic statoliths the most likely are belemnoids (Clarke, 2003; Hart, 2019; but see Pindakiewicz et al., 2022 for other possible explanations), which were likely spending a significant part of their life in deeper waters (e.g., Alberti et al., 2012). Coincidentally, basinal waters were strongly affected by anoxic bottom waters during Jurassic anoxic events (e.g. Ullman et al., 2014). Based on available evidence, we therefore hypothesize that the paucity of cephalopod statoliths in the Oxfordian localities of Dorset is caused by environmental conditions rather than for evolutionary reasons.

When comparing the Kimmeridgian localities of Dorset with the Lower Cretaceous locality of Wąwał (Pindakiewicz et al., 2023), we observe a profound shift in abundance between cephalopod statoliths and teleost otoliths. An increase in abundance of bony fish otoliths and the decrease in abundance of cephalopod statoliths is already visible in the Late Jurassic but it culminates in Early Cretaceous and younger localities where statoliths become exceedingly rare (Pindakiewicz et al., 2022). The disappearance of stem-group decabrachian statoliths after the Late Jurassic is a mystery because belemnites and ammonites are still common in the Early Cretaceous (see Pindakiewicz et al., 2022). More material from the Tithonian–lower Valanginian interval is necessary to properly investigate this phenomenon.

One possible explanation for this shift is an extinction event during the transition from the Jurassic and Cretaceous (Sepkoski & Raup, 1986) which influenced the nektonic cephalopod-to-fish ratio in the oceans. During this time the central Atlantic opened, separating North America from the Iberian Peninsula and North Africa and connecting the Tethys with the Pacific and Boreal oceans (Tremolada et al., 2006). Based on calcareous nannoplankton, this change triggered a shift in ocean circulation and climate, transitioning from wet and warm to drier and cooler conditions and restricting nutrient availability in shallow-marine environments during the Tithonian (Tremolada et al., 2006). Additionally, spreading of the Atlantic also caused a eustatic sea level rise and created new and deepened the existing marine basins, all of which could have contributed to an accelerated teleost and vampyropod radiation (Kruta et al., 2018). Other nektonic groups, such as basal neopterygians or stem-group cephalopods, could have been pushed to the deep sea or into freshwater refugia (Schwarzhans et al., 2018b). Newly evolved teleost species could also predate on larvae of statolith-bearing cephalopods (Pindakiewicz et al., 2022), which could have contributed to a subsequent decline of the latter. The combination of growing predation pressure with the decrease in nutrient levels, decline of spawning areas, and growing competition from teleosts could have caused the observed shift in abundance of cephalopods and teleosts.

Similar factors could be essential also for leptolepiforms, the source of the most abundant otoliths in the Early and Middle Jurassic material (Fig. 10). The shift observed in the abundance of leptolepiform and other teleost otoliths was sudden and started during the Callovian and Oxfordian (Middle/Late Jurassic) transition. It is noteworthy that the acme of *Leptolepis* coincides with the high abundance of cephalopod statoliths and the latter started to decline when leptolepids were replaced by other teleosts.

CONCLUSIONS

Jurassic cephalopod statoliths and fish otoliths from Poland, Lithuania, and the United Kingdom fill the gap in their record during the Mesozoic. This study indicates that Jurassic leptolepiform teleosts were the most speciose Jurassic teleosts. We also argue that taxonomic radiation and emergence of albuliform and elopiform teleosts happened prior to their major diversification in the Early Cretaceous. For example, the Bathonian (Middle Jurassic) albuliform otolith *Pteralbula jurassica* sp. nov. indicates a Jurassic origin of this clade. Assemblages from localities described herein, together with previous studies on Mesozoic cephalopod statoliths and fish otoliths (Hart et al., 2015, 2016; Schwarzhans, 2018; Pindakiewicz et al., 2022, 2023; Schwarzhans & Keupp, 2022), suggest dominance of stem-group decabrachians and abundance of leptolepiforms throughout the Jurassic.

The Late Jurassic witnessed the increasing replacement of Leptolepiformes by other teleosts (i.e., Albuliformes, Elopiformes, Osteoglossiformes). Otolith diversity from

Osmington Mills (lower Kimmeridgian, Upper Jurassic) resembles that of Wąwał, Poland (Valanginian, Lower Cretaceous), much closer than the assemblages from the older Jurassic localities herein reported. That similarity shows that the teleost radiation took place earlier than the Late Jurassic/Early Cretaceous boundary and that it likely started as early as in the Bathonian. In that time the most diversified teleosts were albuliforms and elopiforms. The events that took place during the transition may have drastically shifted the ratio of cephalopod statoliths and teleost otoliths.

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AUTHOR CONTRIBUTIONS

MKP designed the project, performed fieldwork, gather and analysed data, and drafted the manuscript. KH supervised the project and performed fieldwork. SR performed fieldwork and collected data. PS performed fieldwork and gather data. KJ prepared supplement data. AK performed fieldwork, collected material, and supervised the project. All authors edited the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in MorphoSource at https://www.morphosource.org/concern/media/000740842?locale=en, reference number Media 000740842 (Appendix 1), and https://www.morphosource.org/concern/media/000740846?locale=en, reference number Media 000740846 (Appendix 1).

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APPENDICES

Appendix 1. A three-dimensional model of *Lapillus* sp. 1 (ZPAL P. 22/Om/8) from Osmington Mills, Dorset, United Kingdom, Kimmeridgian, Upper Jurassic, based on computed microtomography (μ-CT).

Appendix.2 A three-dimensional model of *Lapillus* sp. 2 (ZPAL P. 22/Om/9) from Osmington Mills, Dorset, United Kingdom, Kimmeridgian, Upper Jurassic, based on computed microtomography (μ-CT).

FIGURE CAPTIONS

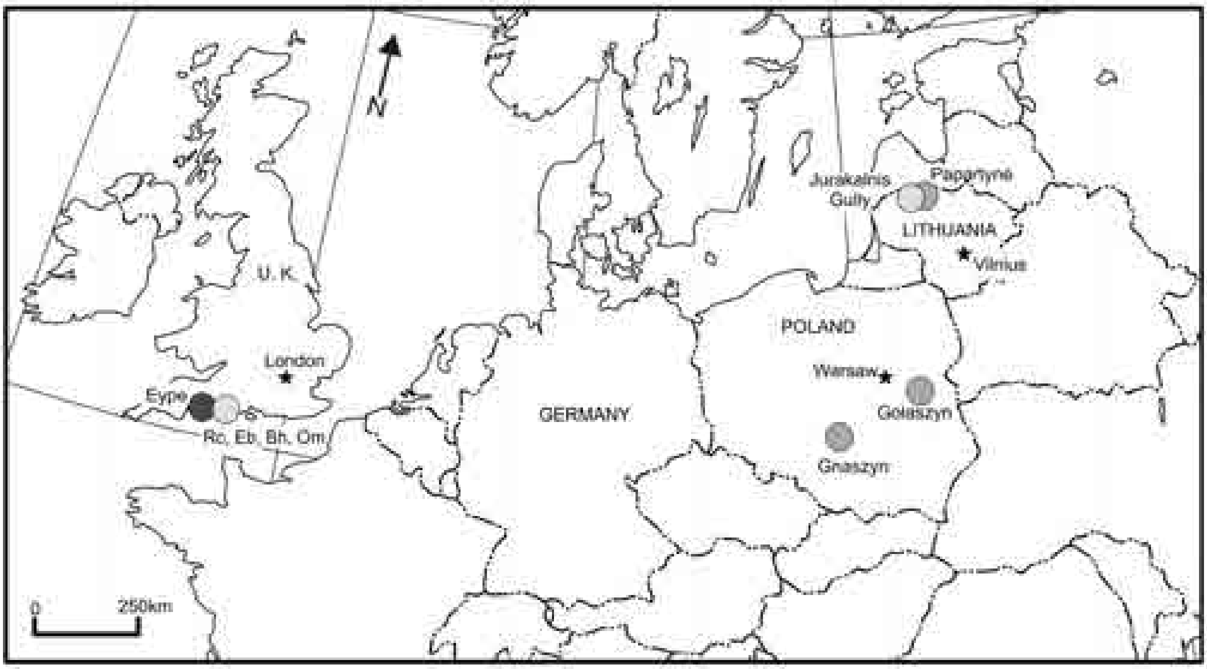


FIGURE 1. Map showing the investigated localities (**Rc**, Redcliff, **Eb**, Eweleaze Beach, **Bh**, Blackhead, **Om**, Osmington Mills). Złote Góry, Wrzosowa, Blanowice, Ogrodzieniec in the same general area as Gnaszyn. Scale 1: 33 870 215.

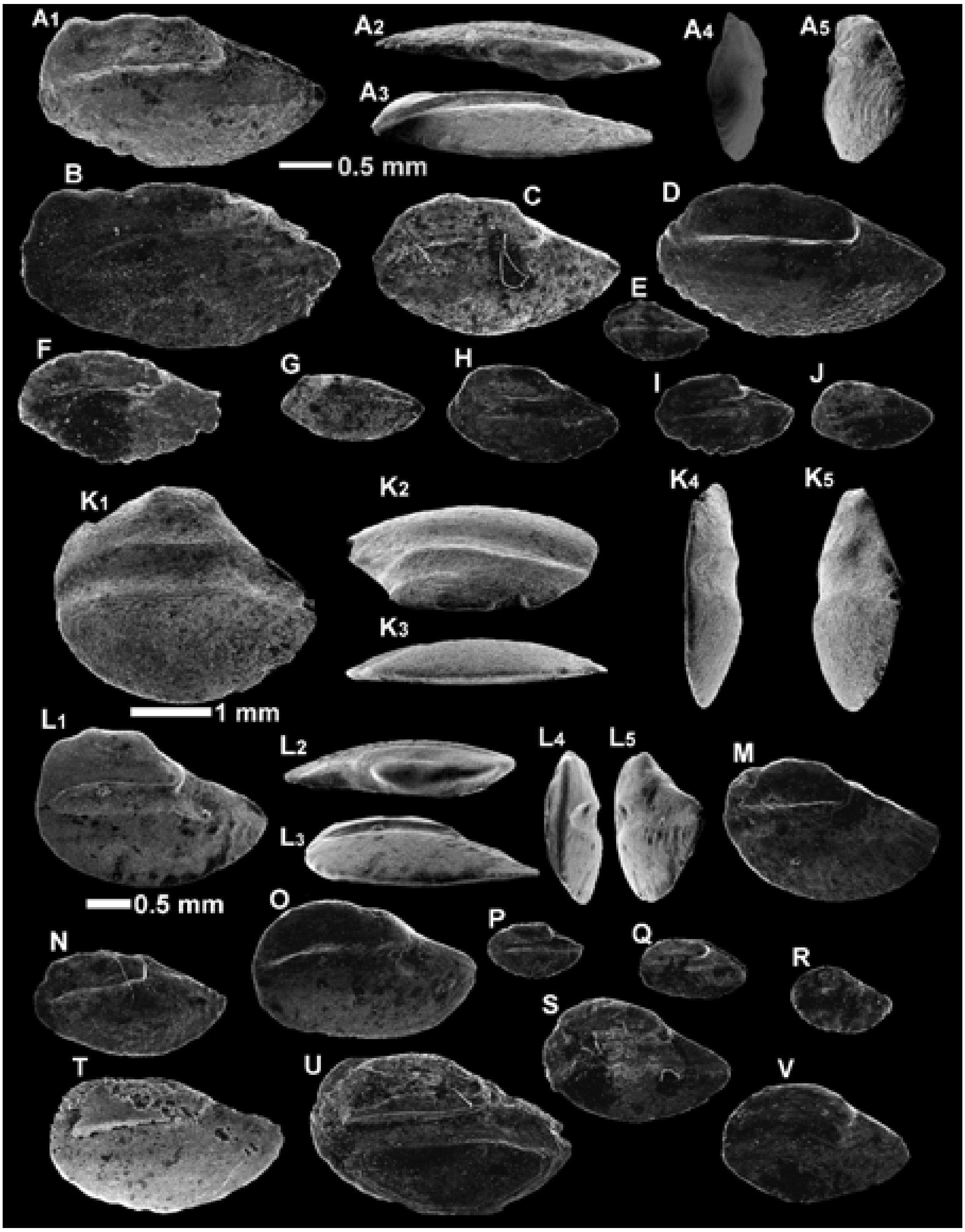


FIGURE 2. Leptolepiform otoliths. **A–J**, *Leptolepis praeelops* (ZPAL P. 22/Gl/1, 2A), from the Callovian, Middle Jurassic, Gołaszyn, Poland. **B**, ZPAL P. 22/Gl/2, from the Callovian, Middle Jurassic, Gołaszyn, Poland. **C**, ZPAL P. 22/Pap/3, from the Callovian, Middle Jurassic, Papartynė, Lithuania. **D**, ZPAL P.22/Gl/4 from the Callovian, Middle Jurassic, Gołaszyn, Poland. **E–F**, ZPAL P. 22/Pap/4-5, from the Callovian, Middle Jurassic, Papartynė, Lithuania. **G**, ZPAL P. 22/Gl/5, from the Callovian, Middle Jurassic, Gołaszyn, Poland. **H–J**, ZPAL P.22/JG/1-3, from the Oxfordian, Late Jurassic, Jurakalnis Gully, Lithuania, **K**, *Leptolepis circularis* (Stinton & Torrens, 1968) (ZPAL P. 22/Gn/1) from the Bathonian, Middle Jurassic, Gnaszyn, Poland. **L–X**, *Leptolepis densus* Stinton and Torrens, 1968, **L–Q**, ZPAL P. 22/Gn/2-7 from the Bathonian, Middle Jurassic, Gnaszyn, Poland. R. ZPAL P.22/Gl/6, from the Callovian, Middle Jurassic, Gołaszyn, Poland. S. ZPAL/Gn/8, from the Bathonian, Middle Jurassic, Gnaszyn, Poland. **T–U**, ZPAL P.22/Gl/7-8, from the Callovian, Middle Jurassic, Gołaszyn, Poland. V. ZPAL P.22/Gn/9, from the Bathonian, Middle Jurassic, Gnaszyn, Poland. **Abbreviations**: **1**, inner face, **2**, ventral side, **3**, dorsal side, **4**, posterior side, **5**, anterior side

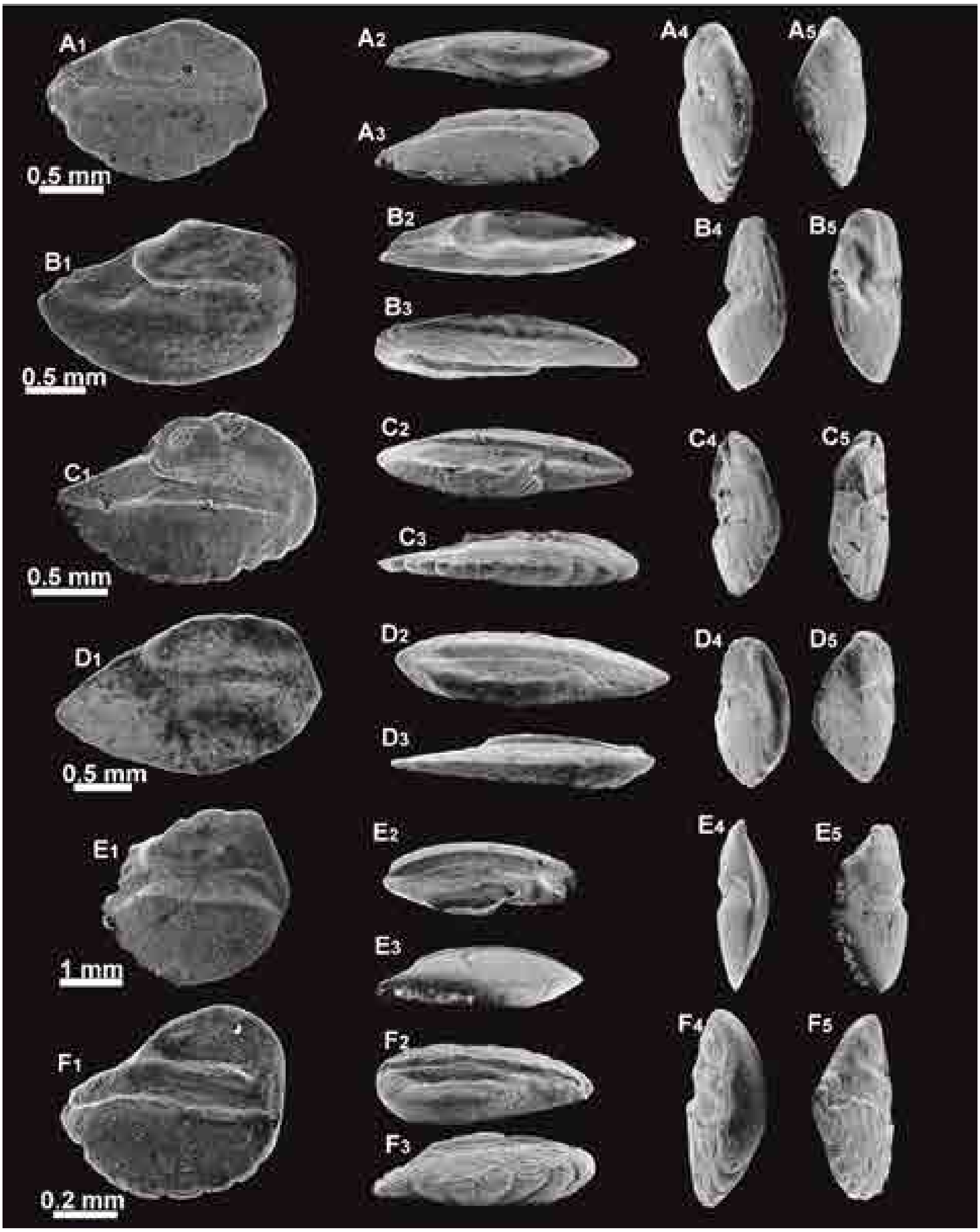


FIGURE 3. Leptolepiform otoliths. **A**, *Leptolepis rotundatus* (Weiler in Martin & Weiler, 1954), (ZPAL P. 22/Gl/9) from the Callovian, Middle Jurassic, Gołaszyn, Poland. **B**, *Leptolepis* cf. *inaequalis* (Weiler in Martin & Weiler 1954), (ZPAL P. 22/Om/2), from the Kimmeridgian, Late Jurassic, Osmington Mills, United Kingdom. **C**, *Leptolepis* aff. *plicatilis* (ZPAL P. 22/Om/1), from the Kimmeridgian, Late Jurassic, United Kingdom. **D**, *Leptolepis* sp. (ZPAL P. 22/Pop/1) from Oxfordian, Late Jurassic, Popovo, Russia. E. *Sphaeronchus dorsetensis* Stinton and Torrens, 1968 (ZPAL P. 22/Gn/10), from the Bathonian, Middle Jurassic, Gnaszyn, Poland. **F**, *Sphaeronchus rundlei* Schwarzhans, 2018 (ZPAL P. 22/Bh/5) from the Kimmeridgian, Late Jurassic, Blackhead, United Kingdom. **Abbreviations**: **1**, inner face, **2**, ventral side, **3**, dorsal side, **4**, posterior side, **5**, anterior side.

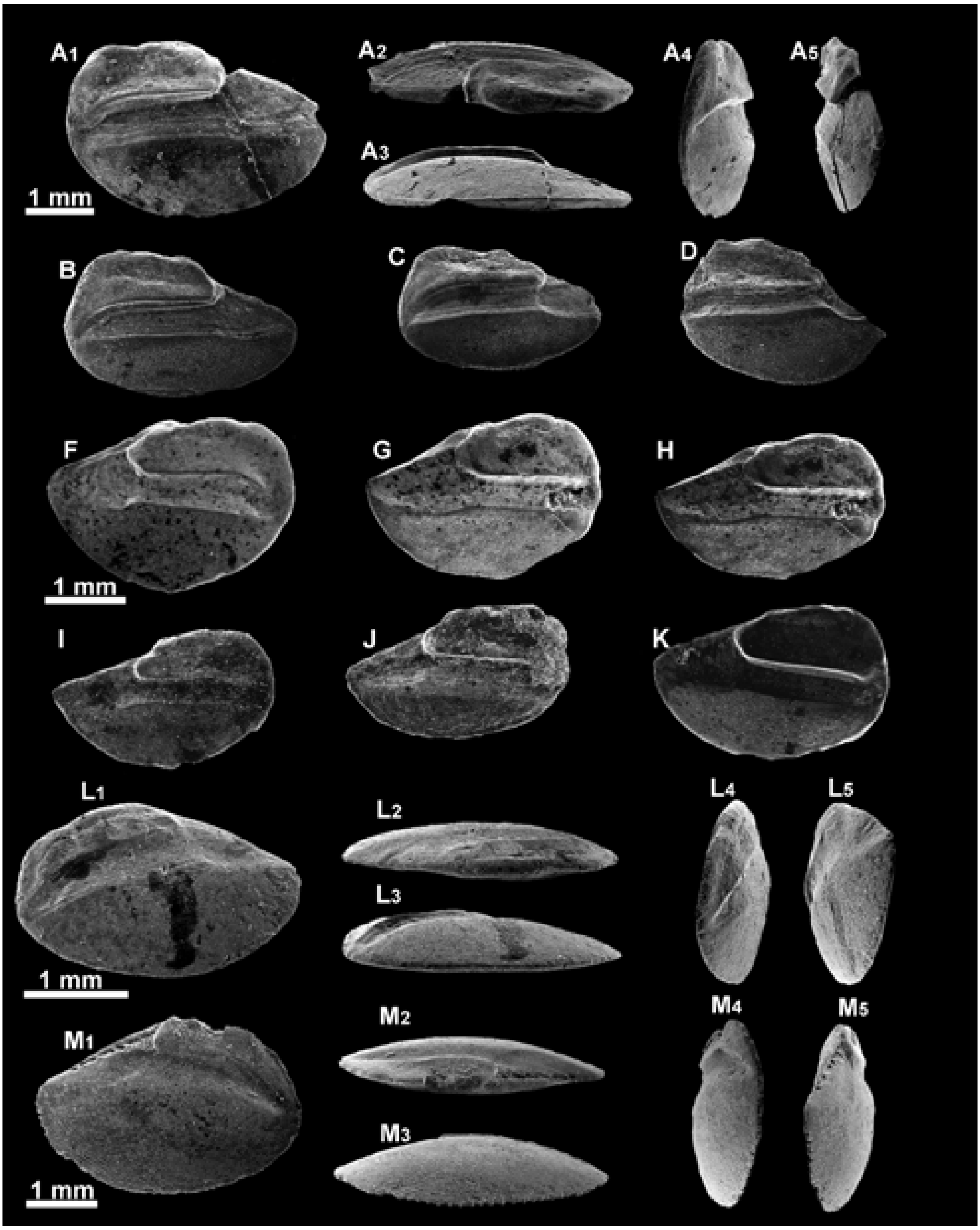


FIGURE 4. Albuliform otoliths: **A–K**. *Pteralbula jurassica* sp. nov. (ZPAL P. 22/Bh/1–4, Holotype ZPAL P.22/Bh/1; 4A, Paratypes ZPAL P.22/Bh/2–4), from the Kimmeridgian, Late Jurassic, Blackhead, United Kingdom. E. ZPAL P. 22/Gl/3), paratype, from the Callovian, Middle Jurassic, Gołaszyn, Poland. F–I. ZPAL P.22/Gl/10–13, paratypes, from the Callovian, Middle Jurassic, Gołaszyn, Poland. J. ZPAL P. 22/Gn/11, paratype, from the Bathonian, Middle Jurassic, Gnaszyn, Poland. K. ZPAL P.22/Gl/14, paratype, from the Callovian, Middle Jurassic, Gołaszyn, Poland. L. *Palealbula ventai* sp. nov. (Holotype: ZPAL P. 22/Pap/6), from the Callovian, Middle Jurassic, Papartynė, Lithuania. M. *Palealbula crenulata* sp. nov. (Holotype: ZPAL P. 22/Om/7) from the Kimmeridgian, Late Jurassic, Osmington Mills, United Kingdom. **Abbreviations**:**1**, inner face, **2**, ventral side, **3**, dorsal side, **4**, posterior side, **5**, anterior side.

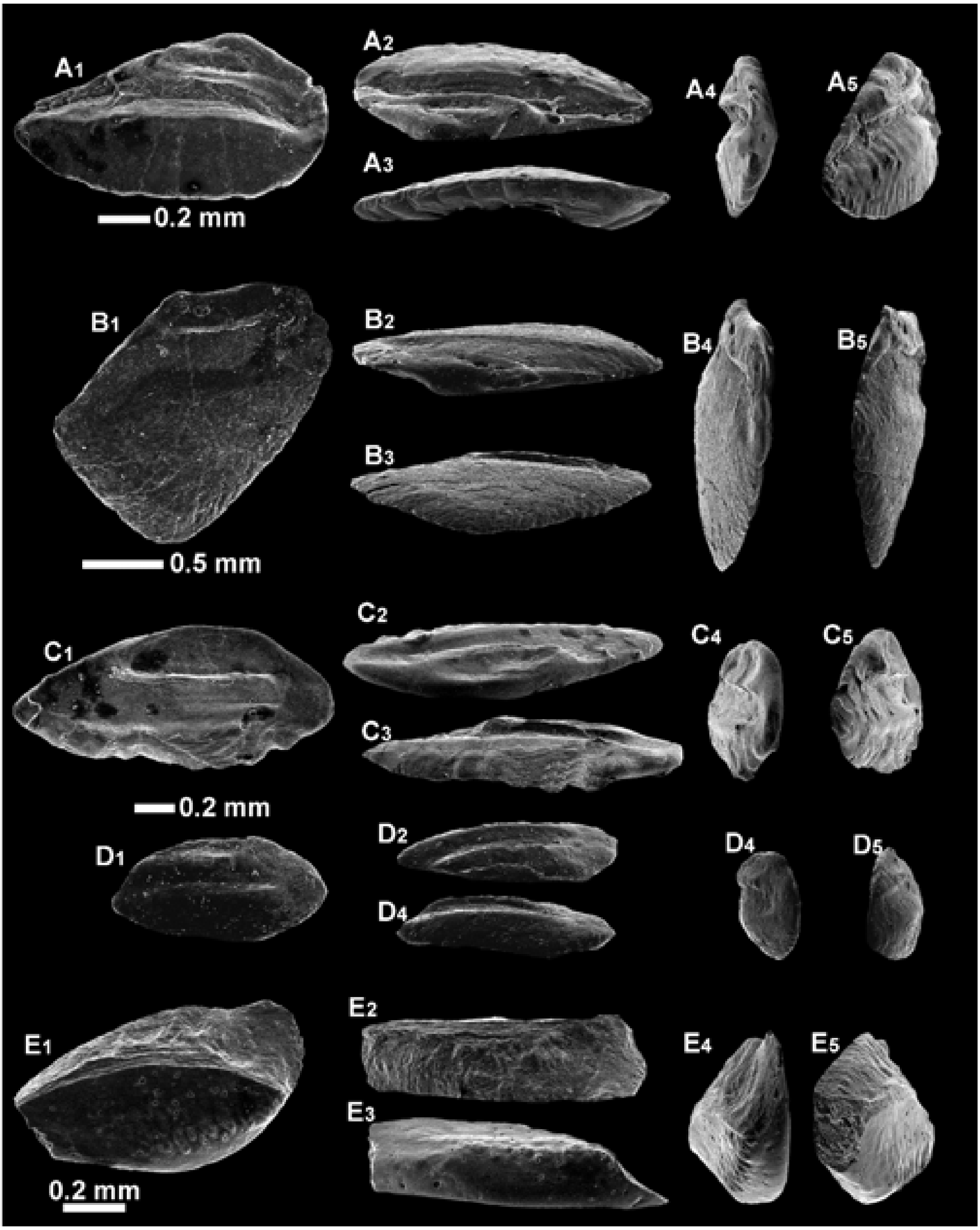


FIGURE 5. Albuliform, elopiform, and osteoglossiform otoliths: **A**, *Palealbula* cf. *declivis* Schwarzhans, 2018 (ZPAL P. 22/Om/4) from the Kimmeridgian, Upper Jurassic, Osmington Mills, United Kingdom. **B**, *Protalbula dorsetensis* sp. nov. (Holotype: ZPAL P.22/Om/3) from the Kimmeridgian, Upper Jurassic, Osmington Mills, United Kingdom. **C–D**, *Juraelops prodigiosum* sp. nov. (Holotype: ZPAL P. 22/Om/5; 5I) from the Kimmeridgian, Upper Jurassic, Osmington Mills, United Kingdom. J. ZPAL P.22/Bh/6) from the Kimmeridgian, Upper Jurassic, Blackhead, United Kingdom. E. *Kokenichthys* sp. (ZPAL P. 22/Om/6) from the Kimmeridgian, Upper Jurassic, Osmington Mills, United Kingdom. **Abbreviations**: **1**, inner face, **2**, ventral side, **3**, dorsal side, **4**, posterior side, **5**, anterior side.

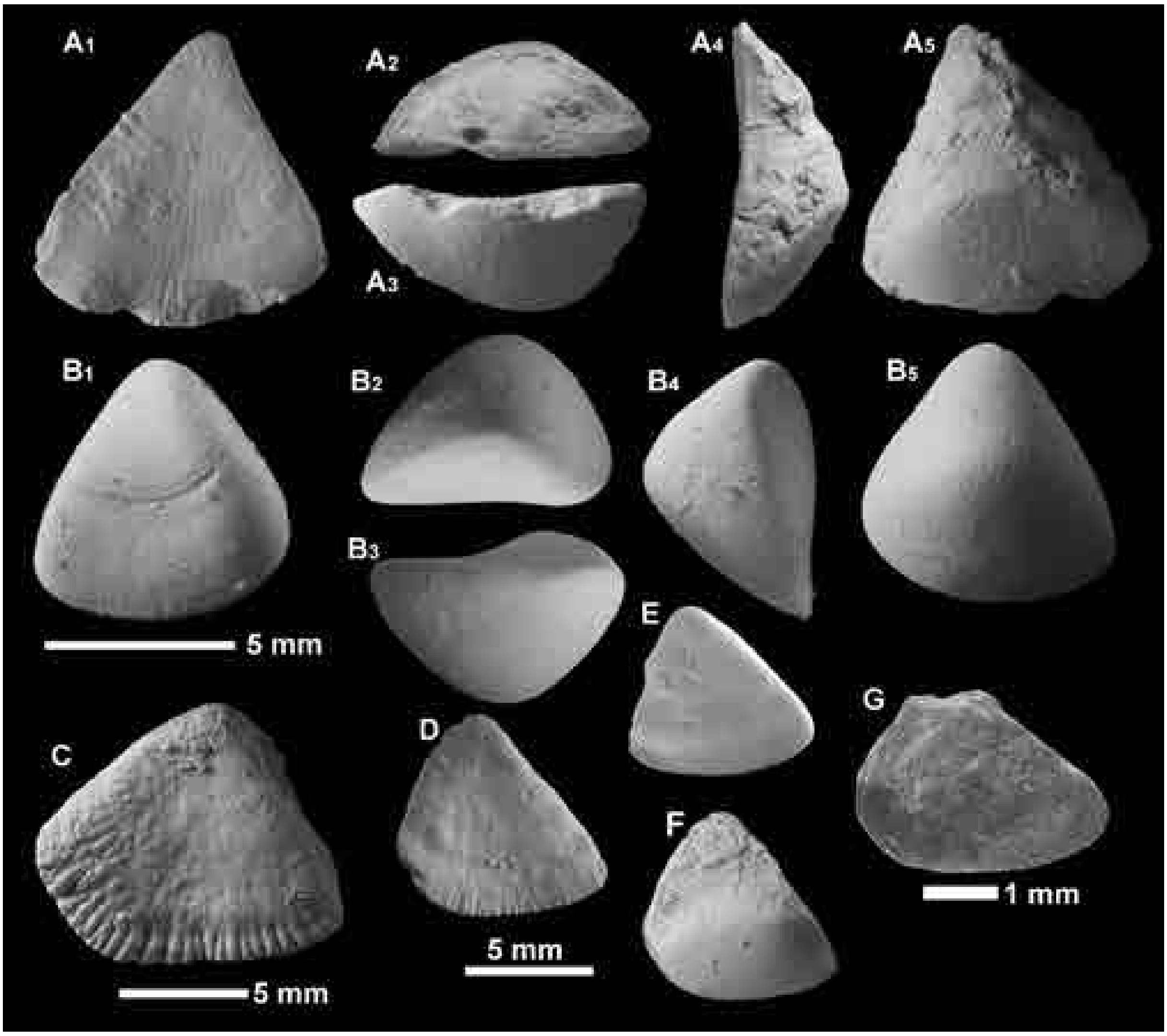


FIGURE 6. Possible ginglymodian otolith *Archaeotolithus*. **A–B**, *Archaeotolithus solidus* sp. nov. **A**, (Holotype: MGUS/Sz 4703) from the Bathonian, Middle Jurassic, Gnaszyn, Poland. **B**, (Paratype, MGUS/Sz 4725) from upper Bajocian, Middle Jurassic, Złote Gory, Poland. **C**, *Archaeotolithus eiggensis* Schwarzhans & Wakefield, 2024 (MGUS/Sz 4706) from upper Bajocian/lower Bathonian, Middle Jurassic, Gnaszyn, Poland. **D–F**, *Archaeotolithus trigonalis* Stolley, 1912 (MGUS/Sz 4708–10) from the Bathonian, Middle Jurassic, Zawiercie, central Poland. **G**, *Archaeotolithus* sp. (ZPAL P. 22/Pap/2) from the Callovian, Middle Jurassic, Papartyne, Lithuania. **Abbreviations**: **1**, inner face, **2**, ventral side, **3**, dorsal side, **4**, posterior side, **5**, outer face (in F is inner face)

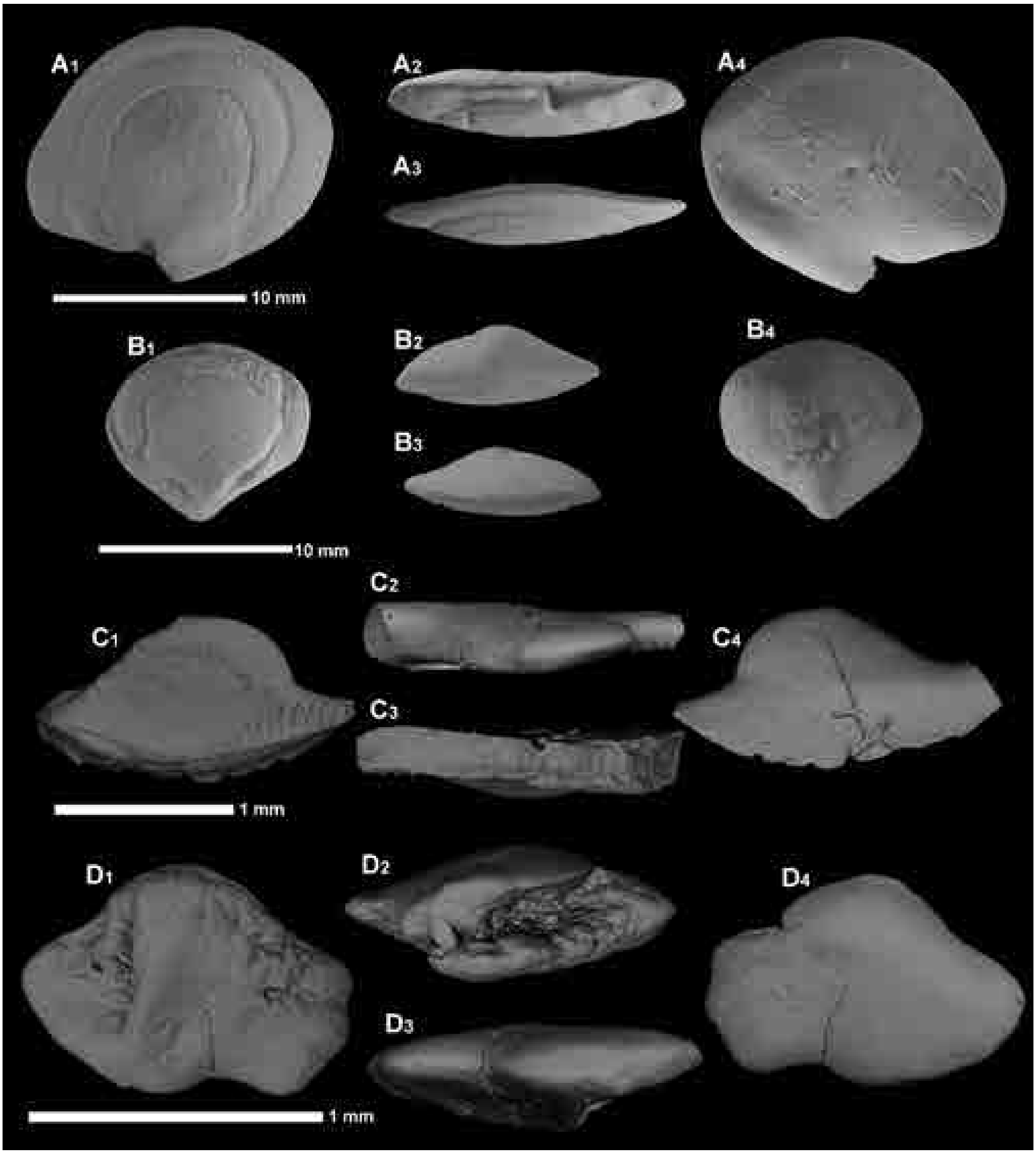


FIGURE 7. Jurassic lapilli **A**, *Vodyanoi schwarzhansi* gen. et sp. nov., holotype, MGUS/Sz 2532, Bathonian, Middle Jurassic, Anna clay pit, Gnaszyn, Poland. **B**, *Vodyanoi stringeri* gen. et sp. nov., holotype, MGUS/Sz 2531, Bathonian, Middle Jurassic, Ogrodzieniec, Poland. **C**, *Lapillus* sp. 1, ZPAL P. 22/Om/8, Kimmeridgian, Upper Jurassic, Osmington Mills, United Kingdom. **D**, *Lapillus* sp. 2, ZPAL P. 22/Om/9, Kimmeridgian, Upper Jurassic, Osmington Mills, United Kingdom. **Abbreviations**: **1**, ventral view, **2**, lateral view, **3**, median view, **4**, dorsal view.

FIGURE 8. Jurassic statoliths. Jurassic Morphotype A cephalopod statoliths. **A**, ZPAL P. 22/E/1 from the Pliensbachian, Lower Jurassic, Eype, United Kingdom. **B**, ZPAL P. 22/Gn/13 from the Bathonian, Middle Jurassic, Gnaszyn, Poland. **C**, ZPAL P. 22/Om/10 from the Kimmeridgian, Upper Jurassic, Osmington Mills, United Kingdom. **D–E**, ZPAL P. 22/Gn/14–15 from the Bathonian, Middle Jurassic, Gnaszyn, Poland, **F–G**, ZPAL P. 22/Gl/16–17 from the Callovian, Middle Jurassic, Gołaszyn, Poland.

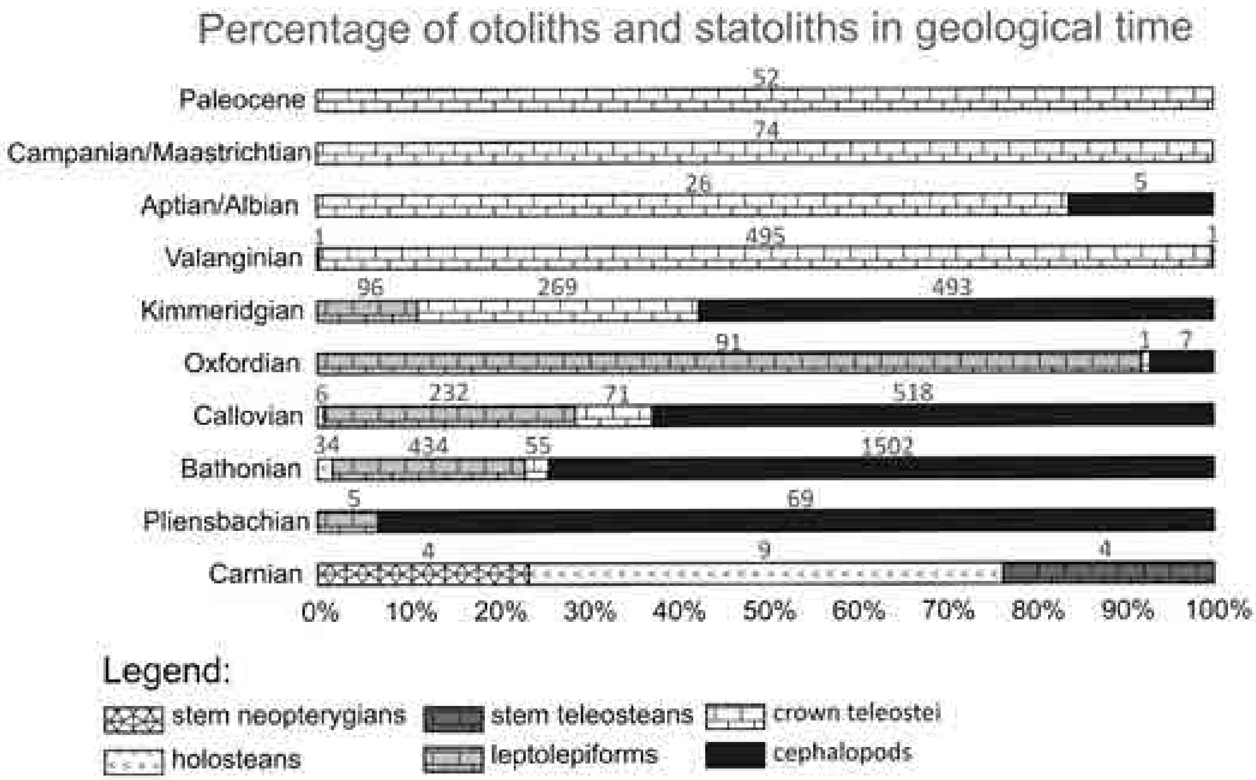


FIGURE 9. Abundance of cephalopod statoliths and fish otoliths in the investigated localities. Data compilated from the following localities: Carnian (Cassian Fm., Italy), Pliensbachian (Eype Clay), Bathonian (Gnaszyn), Callovian (Papartynė and Gołaszyn), Oxfordian (Jurakalnis, Redcliff and Eweleaze Beach), Kimmeridgian (Blackhead and Osmington Mills), Valanginian (Wąwał, Poland), Aptian/Albian (Speeton and Folkestone), Campanian/Maastrichtian (Coon Creek, McGee Creek, and Owl Creek, all U.S.A.), Paleocene (Babica Clays, Poland), data from our collections. Data for Speeton/Folkestone, Babica and U.S.A. localities are from our materials only, Cassian Fm. From Pindakiewicz et al. (2024), and from Wąwał from Pindakiewicz et al. (2022).

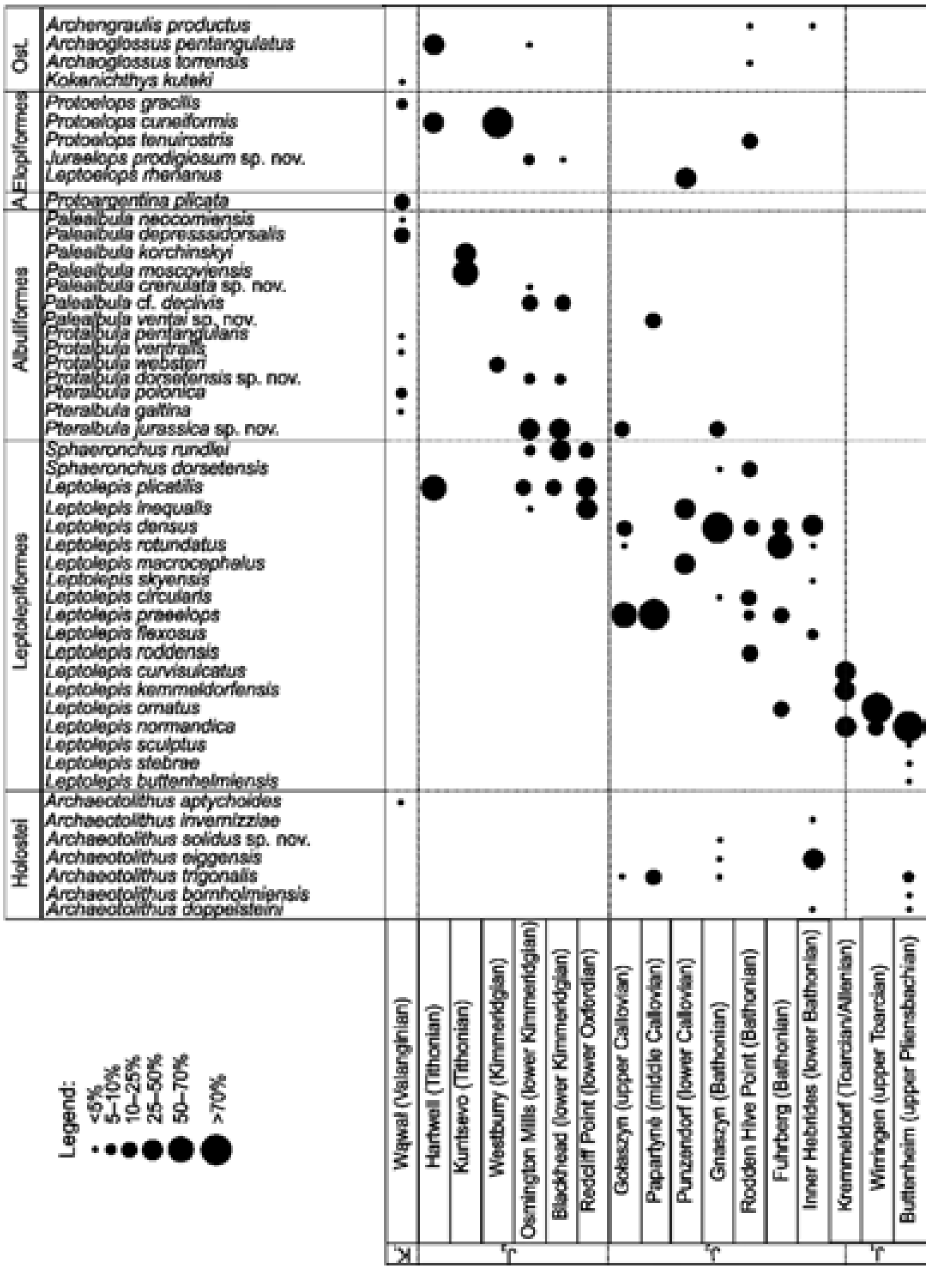
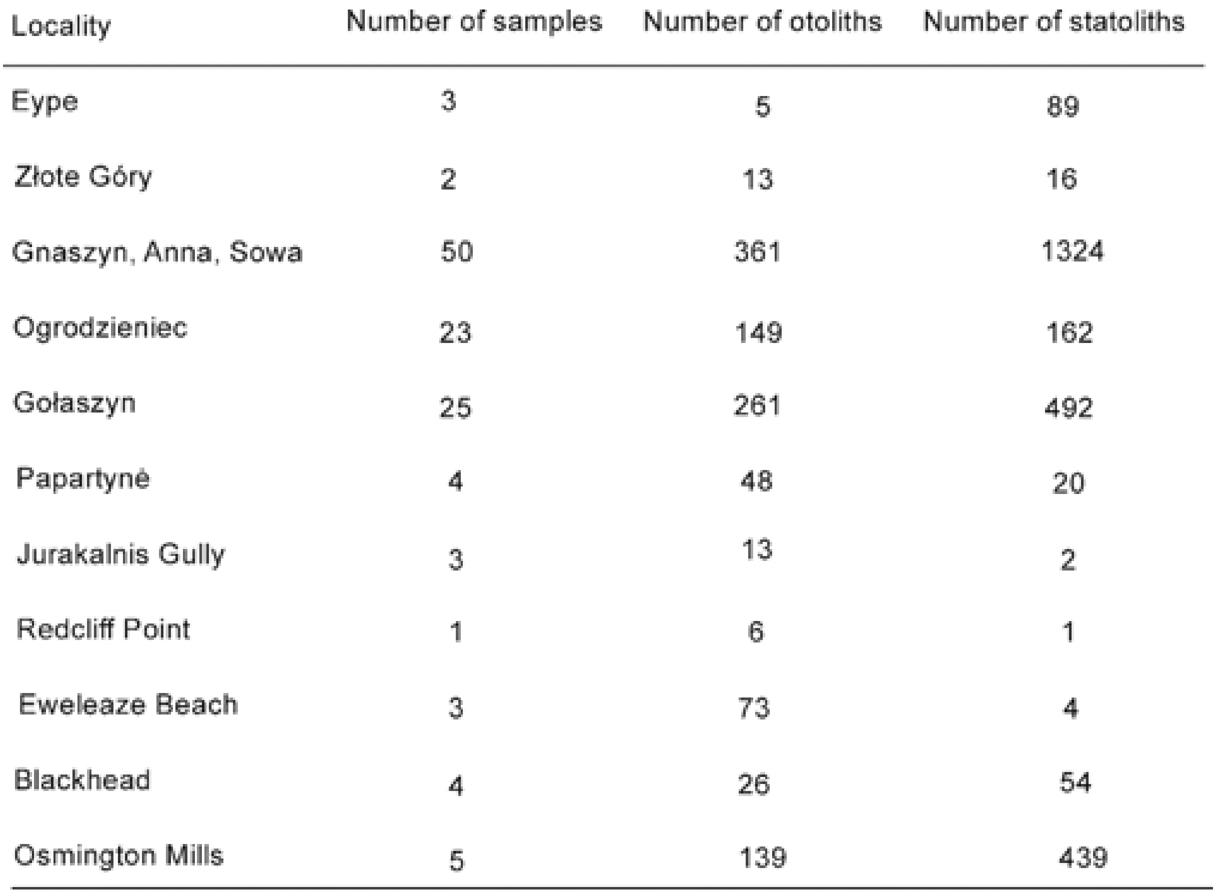


FIGURE 10. Abundance of fish otoliths in Jurassic and Lower Cretaceous (Valanginian) localities studied herein and compiled from literature (Schwarzhans, 2018; Schwarzhans & Keupp, 2022; Schwarzhans & Mironenko, 2020; Schwarzhans & Wakefield, 2024). Only localities with more than one described otolith-based species were included. **Abbreviations**: **A**, Argentiniformes, **Ost**, Osteoglossiformes, **J$_1$**, Lower Jurassic, **J$_2$**, Middle Jurassic, **J$_3$**, Upper Jurassic, **K$_1$**, Lower Cretaceous.

TABLE CAPTIONS



Locality	Number of samples	Number of otoliths	Number of statoliths
Eype	3	5	89
Złote Góry	2	13	16
Gnaszyn, Anna, Sowa	50	361	1324
Ogrodzieniec	23	149	162
Gołaszyn	25	261	492
Papartynė	4	48	20
Jurakalnis Gully	3	13	2
Redcliff Point	1	6	1
Eweleaze Beach	3	73	4
Blackhead	4	26	54
Osmington Mills	5	139	439

TABLE 1. Number of teleost otoliths and cephalopod statoliths from each locality.

Conclusions

Otoliths and statoliths (so-called ear stones) are mostly aragonite, paired structures, that grow inside of animal's inner ear. The ear stones are particularly well-developed in nektonic organisms (e.g. fishes and cephalopods), because they are responsible for sense of orientation and direction while swimming. To sustain that role, the ear stones grow within animal's inner ear during its lifetime. Traditionally the ear stones that grow in invertebrates are called "statoliths" and their vertebrate counterparts are known as "otoliths". Statoliths and otoliths are considered to be analogous rather than homologous structures (Clarke 2003, Schulz-Mirbach et al. 2019, Schwarzhans 2018, Sleight 2023). Both statoliths and otoliths are commonly used for the age identification of the animal by counting their growth lines (Gauldie and Nelson 1990, Jackson 1989a, Miller and Storck 1992, Richardson et al. 2005) and for deciphering environment conditions by observation of ear stone morphology anomalies or changes in mineralogy (Gauldie 1986, Neves et al. 2017, Austad et al. 2021). Otoliths are known in the fossil record from the Middle Devonian (Nolf 1985, Talimaa 1985), and statoliths from the Lower Jurassic (Clarke 2003, Schwarzhans 2018). For many years otoliths and especially statoliths were ignored or misinterpreted and the first worthwhile contribution on fossil otoliths is known from the 2nd half of the nineteenth century (Koken 1884). More systematic works started in the 20th century (Stolley 1912, Frost 1924, 1926, Martin and Weiler 1953, 1954, 1965, Rundle 1967, Stinton and Torrens 1968). Since that time the Cenozoic otoliths have been relatively well researched (Radwańska 1984, 1992, Schwarzhans 1986, 1994, 2004, Reichenbacher 1998, Nolf 1991, 2013, Nolf et al. 2006, Brzobohatý et al. 2007, 2016, 2022, Aguilera et al. 2014, Lin et al. 2015, Brzobohatý and Bubik 2019, Stringer and Hulbert Jr 2020, Agiadi et al. 2022, Schwarzhans and Radwańska 2022, Cicimurri et al. 2025), while the Mesozoic and older otoliths were investigated to much lesser extent (Talimaa 1985, Nolf 1985, 2003, 2004, 2013; Schwarzhans 2010, 2018). The Mesozoic cephalopod statoliths were virtually unknown until papers by Malcolm R. Clarke (Clarke 1978, 2003, Clarke et al. 1980) and Malcolm B. Hart (Hart 2019, Hart et al. 2015, 2016).

In the following chapter I present the a summary of knowledge on Mesozoic ear stones with the highlights on the new data provided in this dissertation.

1. Cephalopods

The cephalopods evolved most likely in the late Cambrian (Landing et al. 2023), quickly diversified and rapidly colonized marine ecosystems of the Palaeozoic and Mesozoic. Majority of the fossil record belongs to the cephalopods with internal skeleton i.e., nautiloids, ammonites and belemnoids. The latter two, however, went extinct during and shortly after K/Pg extinction event (Doyle 1992, Landman et al. 2014, Machalski 2005, Machalski et al. 2022). The nautiloids survived, however their diversity was strongly reduced and only one lineage with two genera endured to the Recent times (e.g. Bonacum et al. 2011). No representatives of these three groups are known to preserve statoliths associated with the internal skeleton save the exception of a single record of belemnoid with its statoliths still *in situ*, albeit to poorly preserved to display any morphological characters (Klug et al. 2016). The statoliths in nautilids are small grains of calcium carbonate located in a sack-like structures known as statoconia. Most likely ammonites had very similar inner ear structure (Neumeister and Budelmann 1997) and for this reason potential of ammonite ear stones in the fossil record is rather low.

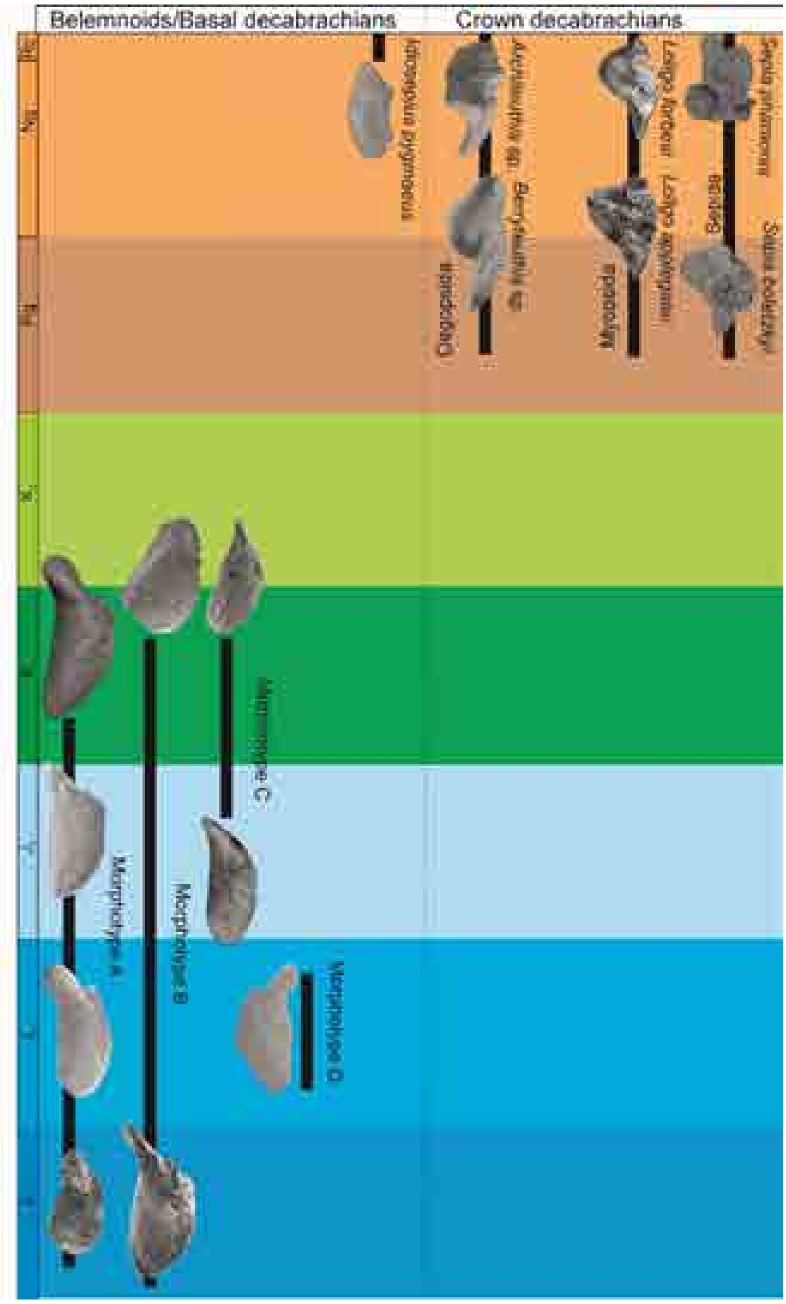


Fig. 1. Stratigraphical ranges of cephalopod statoliths known to date. Photographs are from: Clarke 2003; Clarke and Fitch 1979; Hart 2019; Lipiński 1997; Neige et al. 2016; Pindakiewicz et al. 2022.

The extant soft-bodied cephalopods, i.e. neocoleoids are diverse and abundant in the marine ecosystems. The neocoleoids are divided into decabrachians (squids and cuttlefishes) and vampyromorphs (octopuses and vampire squids). The fossil record of neocoleoids in the Mesozoic is rather modest and restricted to a few Lagerstätten like Callovian (Middle Jurassic) La Voulte-sur-Rhône in France (Charbonnier et al. 2014), Tithonian (Upper Jurassic) Solnhofen in Germany (Fuchs et al. 2007) and Cenomanian (Upper Cretaceous) Plattenkalks in Lebanon (Fuchs and Larson 2011). Most of well-preserved fossils of soft-bodied cephalopods belong to vampyromorphs, while decabrachian fossils are unknown, possibly because that group evolved buoyancy mechanism different than in vampyromorphs (Clements et al. 2017). There is only very limited number of fossils, that belong to decabrachians, a good example being the remains of sepiids from the Upper Cretaceous of Netherlands (Hewitt and Jagt 1999). Overall the fossil record of neocoleoids, especially decabrachians is fragmentary (Hewitt and Jagt 1999; Jattiot et al. 2015) and in some cases debatable (Doguzhaeva et al. 2004). This rarity of Mesozoic decabrachian fossils makes it difficult to investigate their evolution and calibrate molecular clock estimates (Klug et al. 2016, Tanner et al. 2017). Some of these shortcomings, however, might be filled in with data from Mesozoic cephalopod statoliths.

Prior to this dissertation, the oldest record of statoliths of undisputed crown decabrachians was documented from the Eocene of France (Neige et al. 2016), and recrystallized statoliths of vampyromorph were identified *in situ* of the body fossil of an octopod from the Eocene of Bolca, Italy (Mironenko et al. 2024). Several older *ex situ* cephalopod statoliths were described by Clarke (2003), Hart et al. (2015, 2016) and Hart (2019) from the Jurassic of the United Kingdom. None of them was ascribed to any biological species but divided into four morphotypes instead. The most common of all is the Morphotype A of Clarke (2003), which was reported subsequently from other Jurassic localities (Hart 2019; Hart et al. 2013, 2015, 2016. Other morphotypes are uncommon and found only in some localities (Hart et al. 2013, 2015). Clarke and Maddock (2013) suggested that these Jurassic cephalopod statoliths belong to belemnoids.

In the course of my studies I investigated Jurassic marine siliciclastic sediments at several localities and confirmed that these four morphotypes are very abundant in many of them (Pindakiewicz et al. 2022, in press). I also concluded that, in agreement to previous suggestions of Clarke and Maddock (2013), the Morphotype A most likely belongs to belemnoids or basal decabrachians (Pindakiewicz et al. 2022). This morphotype had been proposed to have complex ontogeny (Clarke 2003), however, the observed size of statoliths from each stage of the supposed ontogeny seems to be at odds with that hypothesis (Pindakiewicz et al. in press). It seems to be more likely that the statoliths of Morphotype A could derive from several coleoid species with low intraspecific morphological variability of ear stones.

I found statoliths similar to the Morphotype A, B and C also in Early Cretaceous deposits of Valanginian age at Wąwał (Poland) and of Aptian/Albian aged Speeton Clay at Speeton (United Kingdom) (Pindakiewicz et al. 2022). These statoliths were rather uncommon in Speeton Clay and extremely rare in Wąwał, suggesting that their host animals were rare in the Early Cretaceous epicontinental seas. As suggested by Clarke and Maddock (2013), the Jurassic cephalopod statoliths may belong to the belemnoids and there is indeed a positive correlation between abundance of cephalopod statoliths and belemnoid rostra in the Jurassic localities (Hart et al. 2016, Pindakiewicz et al. in press). In Wąwał there was only one statolith found in all of the investigated samples, while belemnoid rostra were totally absent. In Speeton Clay, belemnoid rostra were moderately common and statoliths rather uncommon but present. I also investigated Late Cretaceous deposits at Coon Creek (Tennessee, USA) and failed to find any cephalopods statoliths and belemnoid rostra in spite of extensive sampling effort. Therefore the rarity of cephalopod statoliths in Cretaceous localities the investigated so far corresponds with the rarity of belemnoids in these sections (Pindakiewicz et al. 2022) and supports the suggestion of Clarke and Maddock (2013) that morphotypes A–C of cephalopod statoliths belong to belemnoids. There are no cephalopod statoliths found in Late Triassic deposits so far (Pindakiewicz et al. 2024) though potentially they could be present in some belemnoid-rich localities, e.g. in Polzberg (Lukeneder and Lukeneder 2022). Therefore the correlation of cephalopod statoliths and belemnoid rostra occurrences requires further collection effort to confirm the belemnoid affinity of statolith morphotypes A–C (Pindakiewicz et al. 2022).

The comparison of the Mesozoic cephalopod statoliths and those of modern neocoeloids has shown that morphology in both groups is significantly different. Mesozoic cephalopod statoliths have convex spur and lack the wing (Clarke 2003). The statoliths of modern neocoeloids have concave spur and semi-organic wing attached to a well-developed detachment area (Clarke and Maddock 2013). Characters similar to those of Mesozoic cephalopod statoliths are known so far only in the modern statoliths of *Idiosepius pygmaeus* Steenstrup, 1881 (Jackson 1989b). A detailed comparison of Mesozoic cephalopod statoliths and Recent statoliths of *I. pygmaeus* performed using CT-scans (Pindakiewicz, et al. 2022) has shown significant similarities: (i) presence of convex spur, (ii) absence of the wing and detachment area, and iii) well-developed rostrum. The only difference between the statoliths of Mesozoic cephalopod and *Idiosepius pygmaeus* is a well-developed, curved lateral dome other neocoleoids (Pindakiewicz et al. 2022). Most likely, a convex spur in Mesozoic cephalopod and *I. pygmaeus* statoliths served the same purpose as the wing in neocoleoid counterparts. The similarity of Mesozoic cephalopod statoliths and those of idiosepiids suggests some Mesozoic cephalopod statoliths could actually belong to basal neocoeloids (Pindakiewicz et al. 2022). These basal neocoleoids may have been closely related to the idiosepiids or other decabrachians, and may explain the undetermined position of Idiosepiidae within phylogenetic tree of cephalopods (Bonnaud et al. 2002, Kröger et al. 2011).

2. Subholosteans and Holosteans

Subholosteans (or stem-neopterygians, depending on classification) are an extinct group of mostly marine bony fishes, which were abundant in the Triassic (Romano et al. 2016). Their affinity to neopterygians (Holostei + Teleostei) is still debated (Tintori et al. 2014; Arratia 2017; Xu 2021). The only known Mesozoic subholostean otoliths reported so far belong to Thoracopteridae—the Triassic “flying fishes”. Tintori and Sassi (1992) reported Norian thoracopterid otoliths associated *in situ* with *Thoracopterus magnificus* skeleton. I found similar otoliths *ex situ* in the Carnian Cassian Formation (Pindakiewicz et al. 2024).

The extant holostean fishes are limited only to freshwater halecomorphs that include bowfins (Amiidae) and ginglymodians like gars (Lepisosteidae). However, in the Triassic and Jurassic they were much more diverse than teleosts, also in marine ecosystems (Romano et al. 2016, Clarke and Friedman 2018). Holosteans displayed wide ecological diversity including cyprinid-like herbivorous semionotiforms, pan-shaped durophagous pycnodontiforms, and gar-like aspidorynchiforms, and large marline-like pachycormiforms like Late Jurassic planktivorous *Leedsichthys* (Ginter 2014). However from the Early Cretaceous onwards only pycnodontiforms remained marine, while other groups of holosteans were mostly freshwater (Vullo et al. 2017, Clarke and Friedman 2018, Schwarzhans et al. 2018c).

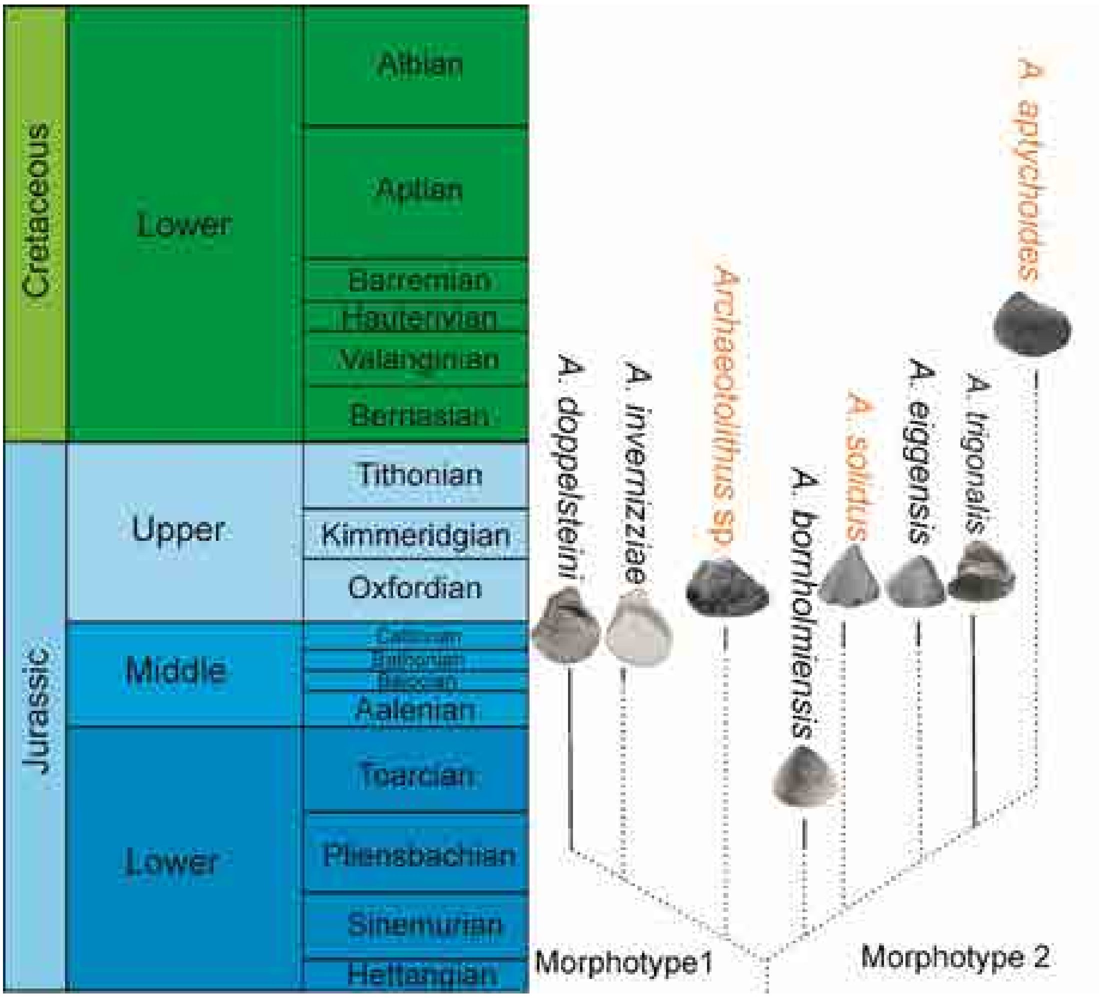


Fig.2. Diversity and stratigraphic ranges of otolith species of *Archaoetolithus* showing a division into two distinct morphotypes. Based on Schwarzhans 2018, Schwarzhans and Keupp 2022, and Pindakiewicz et al. 2023, in press.

I found the oldest putative holostean otoliths to date in the Cassian Formation (Carnian, Upper Triassic). The latter material is constituted mostly from lapilli that are similar to alligator gar larvae otoliths (compare Long and Snow 2016). The other, more widely reported Mesozoic holostean ear stones belong to otolith genus *Archaeotolithus* (Stolley 1912), which has not been associated with any parent fish yet. The oldest *Archaeotolithus* are from the Lower Jurassic of Germany (Schwarzhans and Keupp 2022), while the youngest were discovered during the course of this thesis and come from the Lower Cretaceous of Poland (Pindakiewicz et al. 2023). *Archaeotolithus* comprises eight species divided in two morphotypes. The Morphotype 1 represents pentagonal, bell-shaped otolith with curved sulcus running approximately horizontally through mid-line of otolith like in lepisosteid otoliths. The Morphotype 2 represents. triangular *Archaeotolithus* ornamented and with straight sulcus, terminating close to the posterior rim of the otolith like in teleosts (Schwarzhans and Wakefield 2024). The species of *Archaeotolithus* of Morphotype 1 and 2 were relatively abundant in the Early and Middle Jurassic (Schwarzhans and Keupp 2022, Schwarzhans and Wakefield 2024). I observed, that the only species that persisted to the Early Cretaceous (*Archaeotolithus aptychoides* Pindakiewicz, Hryniewicz and Kaim, 2023) belong to Morphotype 2 (Pindakiewicz et al. in press) (Fig.2).

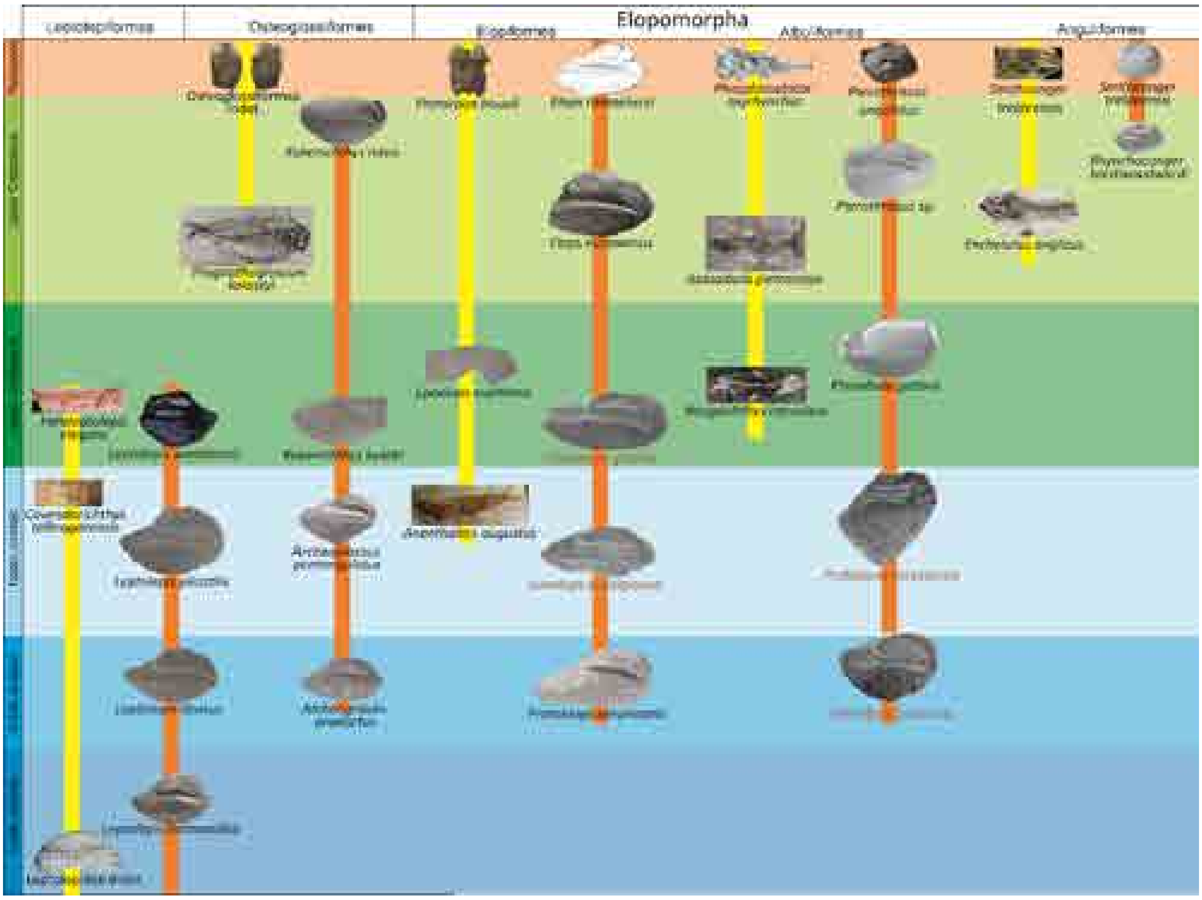


Fig. 3. Comparison of skeletal and otolith fossil record of Leptilepiformes, Osteoglossiforms and Elopomorpha. The skeletal fossils and reconstructions are from: Arratia and Hikuroa 2010; Bean 2017; Capobianco et al. 2021; Carnevale et al. 2022; Filleul 2001; Khalloufi et al. 2019; Smith 2016; Taverne and Capasso 2012,2018; Yabumoto et al. 2006, and otoliths are from: Schwarzhans 2018b and Pindakiewicz et al. 2023, in press.

3. Basal Teleostei and leptolepiforms (Fig. 3)

The origin of teleosts is debated (Arratia 2017, Schwarzhans et al. 2018c). There is consensus, however, that leptolepiforms are the basal teleosts. Leptolepiforms were externally sardine-like bony fishes with cycloidal scales. They appeared in the Early Jurassic and soon achieved worldwide distribution (Konwert and Stumpf 2017, Arratia and Hikuroa 2010). The last leptolepiforms are known from Early Cretaceous freshwater environments (Sutherland et al. 2017, Yabumoto et al. 2006).

I identified the oldest teleost otoliths in the lower Carnian Cassian Formation of the Dolomites, Italy (Pindakiewicz et al. 2024). Initially such otoliths were reported by Nützel and Kaim (2014) but interpreted as belonging to palaeoniscids. A new collecting effort resulted in additional specimens, which allowed to identify the otoliths in question as belonging to basal teleost (Pindakiewicz et al. 2024). However, unlike in the case of Jurassic leptolepiforms (Schwarzhans 2018, Schwarzhans et al. 2018c) there are no Triassic teleost skeletal remains with otoliths *in situ* and for that reason we decided to leave these forms formally unnamed (Pindakiewicz et al. 2024).

Leptolepiform otoliths are divided into five genera: (i) elongated, oval *Leptolepis* with straight cauda, and thick dorsal and ventral rims, (ii) wider, rounded *Spheronchus*, (iii) *Xenoleptolepis*, whose otoliths somewhat resemble actinopterygian-like *Lepisosteus* and *Archaeotolithus* (Schwarzhans and Wakefield 2024), (iv) Gondwanan freshwater teleost *Luisella* (Sferco et al. 2015), to which recrystallized otoliths from localities bearing skeletal materials of *Luisella* were assigned by Schwarzhans et al. (2018c), and (v) elongated pentagonal otoliths of *Doggerichthys,* from the Middle Jurassic of England (Schwarzhans 2018). After compiling all available published accounts and new data collected in the course of my this study I found out that the highest diversity of leptolepiform otoliths was in the Bathonian, Middle Jurassic (Pindakiewicz et al. in press: fig. 10). These otoliths belong to the genus *Leptolepis* with 8 species (Pindakiewicz et al. in press: fig. 10). However the leptolepiform otolith species identification is difficult, mostly due to their high intraspecific variability and low morphological infraspecific disparity (Schwarzhans and Wakefield, 2024).

Leptolepiform diversity decreased during the Late Jurassic, and similarly to cephalopod statoliths they became rare in the Early Cretaceous and known only from brackish sediments of Wealden in United Kingdom (Sutherland et al. 2017) and in the freshwater ecosystems of Gondwana (Schwarzhans et al. 2018c) where they survived until the end of the Early Cretaceous (Wang et al. 2018).

4. Osteoglossomorphs (Fig. 3)

The extant osteoglossomorphs are freshwater fishes of both North and South America, and Africa, and are represented by mooneyes (hiodontids), arapaima (arapaimaids), butterflyfishes (pantodontids), and elephantfishes (mormyrids). They were more diverse in the Cretaceous, when they lived in marine waters. The oldest alleged osteoglossomorphs were ichthyodectiforms from the Middle Jurassic, however, the status of the latter group is debated as several authors (e.g. Patterson and Rosen 1977, Arratia 1997, 2001, Taverne 1998, Hilton 2003) consider them stem-group teleosts rather than osteoglossmorphs. The other, freshwater osteoglossomorphs are known from the Cretaceous (Guo-Qing and Wilson 1991, de Castro Leal and Brito 2004, Lan et al. 2024). Marine pantodontids are also known from the Mesozoic fossil record but they are so far represented only by a single species of *Prognathoglossum kalassyi* (Taverno and Capesso 2012) from the Cenomanian (Upper Cretaceous) of Lebanon.

The oldest otoliths of osteoglossiforms are from the Bathonian of England and belong to *Archengraulis productus* Schwarzhans and Wakefield 2024, and *Archeoglossus torrensi* Schwarzhans, 2018. Both are characterized by pentagonal outline and small straight cauda with wide ostium. The youngest known *Archengraulis* is from the Tithonian (Upper Jurassic) of England (Schwarzhans 2018). Another osteoglossiform known only from otoliths is *Kokenichthys* Schwarzhans 2010. During this study I identified the oldest occurrence of that genus in the Kimmeridgian (Upper

Jurassic) of United Kingdom, but I left it in open nomenclature due to its imperfect preservation (Pindakiewicz et al. in press). The oldest formally named species is *Kokenichthys kuteki* Pindakiewicz, Hryniewicz, and Kaim 2023, comes from the Valanginian of central Poland (Pindakiewicz et al. 2023). Other species of this genus are known from the Aptian, Lower Cretaceaous, and Upper Cretaceous (Schwarzhans, 2018). Since all osteoglossomorph otoliths mentioned above were found in marine deposits, there is a suspicion that they may have belonged to marine only ichthyodectiforms, whose attribution to osteoglossomorphs is debatable. This, however requires further studies since no otoliths have been found *in situ* in the skeletons so far.

5. Elopomorphs (Fig. 3)

Elopomorpha unites ladyfishes (elopiforms), bonefishes (albuliforms) as well as elongated eels (anguiliforms) and gulper eels (saccopharyngiforms). Elopomorphs are marine bony fishes characterised by leptocephalic larvae as a distinct ontogenetic stage in their life cycles. Most well-known are catadromous migrating fishes, like European eels (*Anguila anguila*), which migrate to Sargasso Sea to breed but some species have entirely freshwater life cycle. Remaining elopomorphs thrive in a variety of marine settings and display a wide range of ecological adaptations from shallow water durophagous bonefish (*Albula albula*), open water planktivorous ladyfish (*Elops elops*), deep-water gissu (*Pterothrissus gissu*) to abyssal slow-swimming carnivores like gulper eel (*Eurypharynx pelecanoides*). The oldest skeletal fossils of elopomorphs are elopiforms from the Tithonian, Upper Jurassic, of Germany (Poyato-Ariza 1999). The oldest skeletal record of albuliforms is from the Valanginian, Lower Cretaceous, of England (Sweetman 2013) and well-preserved specimens of *Baugeichthys caeruleus* from the Hauterivian of France (Filleul 2001). The oldest eels are known from the Cretaceous of the Lagerstätte Hjoula in Lebanon (Taverne 2004). Crossognathiforms, which were mostly marine predators with elongated, herring-shaped body and commonly display a characteristic dorsal fin spine like in *Apsopelix* (Miyata et al. 2022). The oldest skeletal record is reported by Arratia and Tischlinger (2010) from the Late Jurassic who also suggest that crossognathiforms may belong to elopomorphs. This attribution is, however, under debate since most authors considers them closer to clupeomorphs (Taverne 1989, Sferco et al. 2015, Medina-Castañeda et al. 2025; see also below).

The otolith-based fossil record shows that elopomorphs appeared much earlier and were more diverse than it is suggested by the skeletal record. The oldest-known elopomorph otoliths are from the Bathonian (Middle Jurassic) and are described as elopiform *Protoelops tenuirostris* (Stinton 1968). Of the same first occurrence age is the basal albuliform *Pteralbula jurassica* described from the Bathonian–Callovian (Middle Jurassic) of Poland and Kimmeridgian (Upper Jurassic) of England in the course of this dissertation (Pindakiewicz et al. in press). A review prepared as part of this thesis (Pindakiewicz et al. in press) shows that elopomorph otoliths are common in marine fine-grained siliciclastic deposits from the Bathonian (Middle Jurssic) to Albian (Early Cretaceous) age (Stinton and Casier 1966, Schwarzhans 2018, Schwarzhans et al. 2022, Pindakiewicz et al. 2023, Miyata et al. 2024), with highest diversity peak in the Kimmeridgian (six otolith-based genera in total). In the course of this study I described one new elopiform genus *Juraelops,* several new species from elopiforms *Protoelops, Juraelops,* and albuliforms *Palealbula, Protalbula,* and *Pteralbula* (Pindakiewicz et al. 2023, in press). It remains, uncertain which family they belong to. Most of the Late Cretaceous elopomorph otoliths were suggested to belong to pterothrissid albuliforms and congerid anguiliforms (Schwarzhans and Stringer 2020, Schwarzhans et al. 2024). The significance of elopomorphs among marine teleosts decreased during the Late Cretaceous, when other groups of teleosts radiated (Cavin 2008, Schwarzhans and Jagt 2022, Schwarzhans and Stringer 2024, Schwarzhans et al. 2024).

6. Clupeomorpha (Fig. 4)

Modern clupeomorpha are exclusively marine. Apart from the already mentioned crossognathiforms which are included either into clupeomorphs (Sferco et al. 2015, Medina-Castañeda et al. 2025) or elopomorphs (Arratia and Tischlinger 2010; Arratia 2018), Mesozoic clupeomorphs comprise stem-clupeids and basal clupeids. Most likely crossognathiforms are not monophyletic, and for example Varasichthyidae are more closely related to leptolepiforms or elopomorphs (Arratia and Tischlinger 2010, Sferco et al. 2015), while the remainder (like crossognathids and pachyrhizodontids) may belong to clupeomorphs as suggested by Taverne (1989) and Sferco (2015). If this interpretation, if correct, then the fossil record of clupeomorphs would be extended to the Late Jurassic (Arratia and Tischlinger 2010).

The oldest stem-clupeid fossils were from brackish sediments of Early Cretaceous of Brazil (*Ellimmichthys longicostatus* (Cope 1886) de Figueiredo and Gallo 2021) and Spain (*Ezkutuberezi carmeni* Poyato-Ariza, López-Horgue, and García-Garmilla 2000). The oldest skeletal record of basal clupeid are known from the Late Cretaceous including small predator *Italoclupea nolfi* Taverne 2007, and large carnivore *Nardoclupea grandei* (Taverne, 2002) from the Campanian and Maastrichtian of Salento, Italy.

The oldest Mesozoic otoliths of undisputed clupeomorph otoliths are known from freshwater Maastrichtian sediments in India (Rana and Sahni 1989, Nolf et al. 2008). If some crossognathiforms are indeed clupeomorphs as suggested by Taverne (1989), Sferco (2015), and Medina-Castañeda (2025) then the fossil record of clupeomorph otoliths moves back to the Lower Cretaceous as with *Apsopelix*? *berlinensis*, (an otolith of alleged crossognathid crossognathiform) known to occur in Germany, Poland and Spain (Schwarzhans 2018, Pindakiewicz et al. 2023).

7. Ostariophysians (Fig. 4)

Ostariophysians are characterized by different inner ear structure than other teleosts. The oldest skeletal fossil of that group is a basal ostariophysian *Tischlingerichthys viohli*, from the Tithonian (Upper Jurassic) of Solnhofen, Germany (Arratia 2018). Skeletal fossils of small-sized characiforms and gonorynchiforms are known from the Lower Cretaceous of Brazil (Davis and Martill 1999, Grande and

Poyato-Arriza 1999, Filleul and Maisey 2004, Fara et al. 2010). Based on the skeletal fossil record, the ostariophysians appeared in the Late Jurassic and had two major diversifications, first around the Jurassic/Cretaceous transition, and the second during the Miocene (Chen et al. 2013). The only confirmed Mesozoic marine ostariophysian ear stones are Late Cretaceous siluriform lapilli identified as belonging to *Arius* (Santonian–Maastrichtian) and to alleged siluriform *Vorhisia* (Maastrichtian) (Schwarzhans et al. 2018b, 2024, Stringer and Sloan 2023, Stringer et al. 2020). *Arius* is known to survive K/Pg extinction event and then to diversify as shown by the increased diversity of its otoliths (Schwarzhans et al. 2024). In the Bathonian of central Poland I found large lapilli, which I and co-authors described as a new genus *Vodyanoi*. However their possible relationship to ostariophysians requires further studies (Pindakiewicz et al. in press).

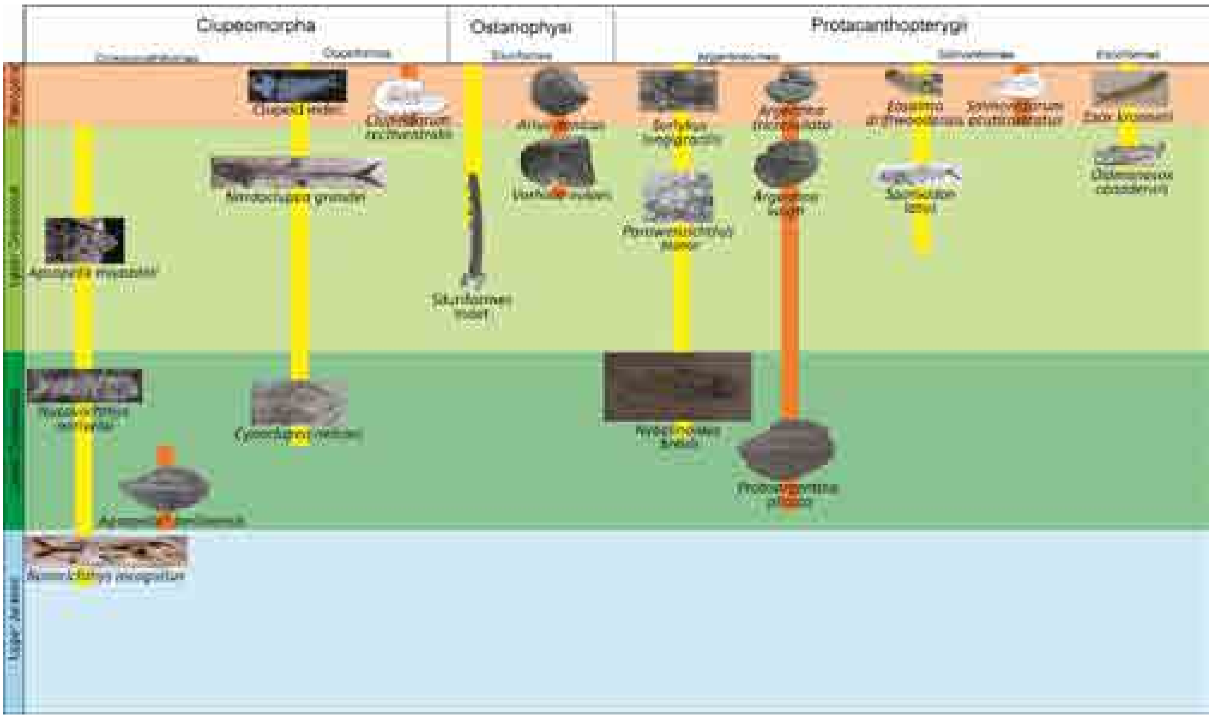


Fig. 4. Comparison of skeletal and otolith fossil record of Clupeomorpha, Ostariophysi, Protacanthopterygii. The skeletons are from: Alvarado-Ortega and Alves 2022; Alvarado-Ortega et al. 2015; Alves et al. 2019; Ane and Carnevale 2023; Arratia and Tischlinger 2010; Brinkman et al. 2025; De Figueiredo et al. 2012; Grande 1999; Malabarba and Di Dario 2017; Poyato-Ariza 1999; Schwarzhans 2018a,b; Schwarzhans et al. 2024; Taverne 2002; Taverne and Filleul 2003; Wilson and Williams 1991; Yabumoto et al. 2012, and otoliths are from: Pindakiewicz et al. in press; Schwarzhans 2004, 2018b; Schwarzhans et al. 2024.

8. Protacanthopterygians (Fig. 4)

According to Nelson (2006) this group unites marine argentines (Argentiniformes), anadromous salmons (Salmoniformes), and freshwater pikes (Esociformes). The oldest argentinoid and salmoniform skeletal records are known from the marine sediments of middle Albian (Early Cretaceous) of Canada, Turonian (Late Cretaceous) of France (De Figueiredo et al. 2012), and Barremian/Aptian of Belgium (Taverne 1982). Cretaceous esociforms were freshwater carnivores, like Common Pike (*Esox lucius*) today (Wilson et al. 1992, Brinkman et al. 2025).

The otoliths of pikes and salmons are not known from the Mesozoic. Most of Mesozoic protacanthopterygian otoliths belong to Late Cretaceous species of *Argentina* (Nolf 2013), and Valanginian–Albian (Early Cretaceous) *Palaeoargentina* (Pindakiewicz et al. 2023). Otoliths of *Palaeoargentina* differ from those of *Argentina* by well-developed posterior angle and more rounded ventral rim. The otoliths of Esociformes are not known from fossil record (Nolf 2013).

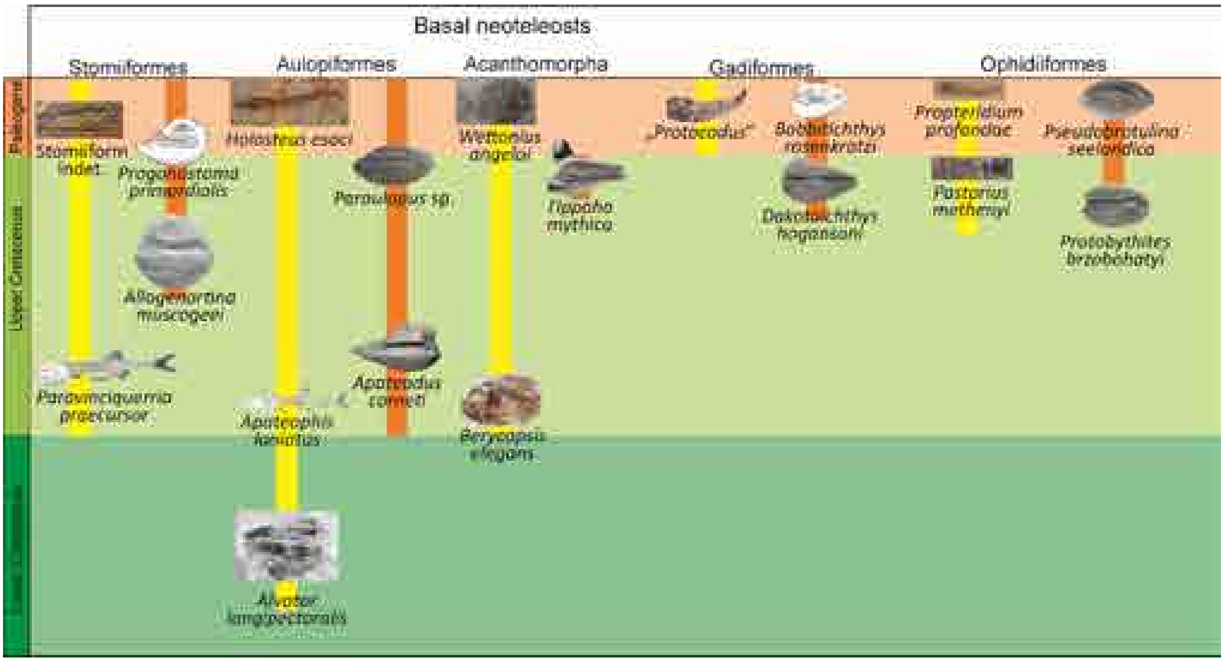


Fig. 5. Comparison of skeletal and otolith fossil record of basal neoteleosts. The skeletons are from: Carnevale and Bannikov 2018; Carnevale and Johnson 2015; Carnevale and Rindone 2011; González-Rodríguez et al., 2013; Přikryl and Carnevale 2018; Schwarzhans 2018a,b; Schwarzhans et al., 2024, and otoliths are from: Schwarzhans 2004, 2018b; Schwarzhans et al. 2024.

9. Basal neoteleosts (Fig. 5)

This broad group of bony-fishes comprise stomiiforms, aulopiforms, myctophiforms, polymixiiforms, percopsiforms, gadiforms, ophidiiforms and other acantomorphs. They are interpreted as mostly marine carnivores, that evolved during the Late Cretaceous, affected by the K/Pg extinction event, with some groups recovered and diversified afterwards, while others more or less significantly reduced in diversity. Stomiiforms probably appeared in the Late Cretaceous, and occupied deep waters (Carnevale and Rindone 2011) where they persisted until today. Aulopiformes in the Cretaceous were highly diversified pelagic predators (Davis 2010, Schwarzhans et al. 2024) and only one family of small species (Paraulopidae) survived and re-diversified during the Cenozoic. The oldest skeletal remains of myctophiforms (lanternfishes) are known from the Upper Cretaceous of Lebanon and Europe, however, their affinity to this order is debated (Schwarzhans and Carnevale 2021). There are several fossils from Cenomianian to Santonian that are reminiscent of pomylixiiforms, however their affinity is uncertain (Schwarzhans et al. 2024). Ophidiiforms, have the oldest skeletal record already in the Campanian (Upper Cretaceous), represented by basal Bythidae (Schwarzhans et al. 2024), and become more diverse in the Paleogene.

The oldest stomiiform otoliths could be those of *Allogenartina muscogeei* from the Santonian (Upper Cretaceous) of USA (Schwarzhans et al. 2017), however its identity as a stomiiform is questioned (Schwarzhans and Stringer 2020, Schwarzhans et al. 2022; Stringer and Sloan 2023). If this questionable record is disregarded, than the oldest stomiiform otoliths are *Auriculithus pattersoni* and *Palaeostomias praematurus* from the Maastrichtian of Germany (Schwarzhans 2010). The otoliths of Mesozoic aulopiforms are represented mostly by *Apateodus corneti* with abhorrent ventral rim and *Thrax acutus* with well-developed dorsal rim and posterodorsal angle (Schwarzhans et al. 2018b, Stringer et al. 2020). Oldest aulopiform otoliths are known from the Albian (Lower Cretaceous) (Schwarzhans et al. 2022), with more common records starting in the Santonian–Maastrichtian (Upper Cretaceous) (Schwarzhans et al. 2017, Schwarzhans and Stringer 2020, Schwarzhans and Jagt 2021, 2022; Stringer and Sloan 2023, Schwarzhans et al. 2024). There is no documented lanternfish otoliths from the Mesozoic (Schwarzhans and Carnevale 2021). Many basal acanthomorph otoliths from the Maastrichtian (Late Cretaceous age) were ascribed earlier to perciform, beryciform or holocentriform fishes (Nolf 2013), however their affinity is unclear. For example, highly unusual sagittae of *Tippaha* resemble gadiform otoliths in some respects (like shallow sulcus and well-developed anteriodorsal angle), than the otoliths of other basal acanthomorphs (Schwarzhans et al. 2024). The otolith record indicates that gadiforms originated sometime during the Late Cretaceous (Campanian; Schwarzhans and Stringer 2024; Schwarzhans et al. 2024) and attained a considerable diversity by the end of the Late Cretaceous (Stringer and Sloan 2023, Schwarzhans et al. 2024). Very similar diversity pattern occurs among ophidiiforms which occur in Maastrichtian (Schwarzhans and Stringer 2020, Stringer et al. 2020; Schwarzhans and Jagt 2021).

10. Acanthopterygians (Fig. 6)

Well-preserved skeletal fossils of basal beryciforms, trachichthyforms, holocentriforms, and zeiforms come from the Maastrichtian (Upper Cretaceous). The oldest representatives are *Hoplopteryx* and other trachichthyiforms, which are known already from the Cenomianian (Schwarzhans et al. 2018a, 2024), and stem-beryciform *Handuichthys interopercularis* is known from the Albian (Lower Cretaceous) (González-Rodríguez et al. 2013). Majority of acanthopterygians were small- and medium-sized predators. They were quite abundant in marine ecosystems from the late part of Early Cretaceous to the end of Palaeocene. Zeiforms were quite rare in the Late Cretaceous and only one species *Cretazeus rinaldii* was described so far (Tyler et al. 2000, Tyler and Santini 2005). It was found in the marine sediments of Late Campanian/Early Maastrichtian age from Italy (Tyler et al. 2000). Zeiforms diversified after the K/Pg extinction event (Schwarzhans et al. 2024).

The oldest otoliths of beryciforms are recorded from the Santonian (Schwarzhans et al. 2018b). The otolith fossil record of zeiforms show similar pattern to skeletal remains, with the oldest record of putative zeiform otolith coming from Santonian (Upper Cretaceous) (Schwarzhans et al. 2018b), and three species of otolith-based genus *Isozen* known from the Maastrichtian (Schwarzhans et al. 2024). The oldest otoliths of holocentriforms and trachythiforms are also known from the Maastrichtian (Stringer et al. 2020). In the Maastrichtian the diversity of beryciform acanthopterygians

(Berycida) was significantly higher than in the Paleogene. Pelagic predatory acathopterygians, like aulopiforms, were strongly affected by K/Pg extinction event and did not re-acquire their Cretaceous diversity during the Paleogene (Schwarzhans et al. 2024).

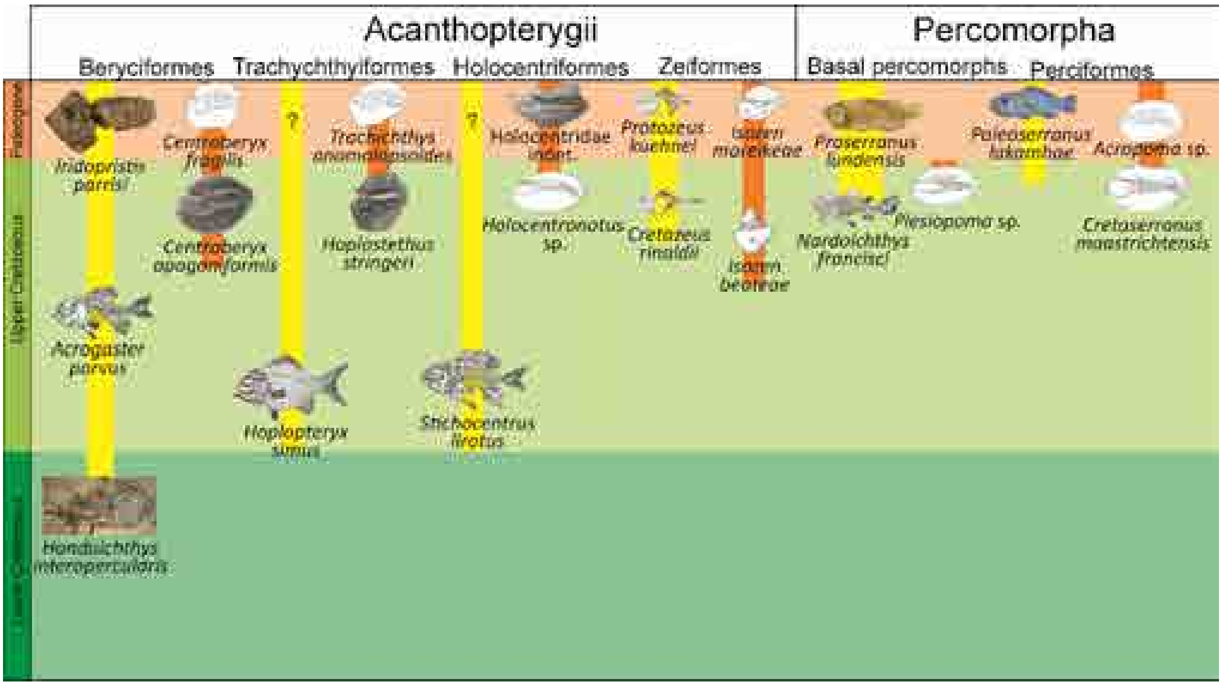


Fig. 6. Comparison of skeletal and otolith fossil record of Acanthopterigii and Percomorpha. The skeletons are from: Alvarado-Ortega et al. 2015; Andrews et al. 2023; González-Rodríguez et al. 2013; Schwarzhans 2018a,b; Schwarzhans et al. 2024, and otoliths are from: Schwarzhans 2004, 2018b; Schwarzhans et al. 2024.

11. Percomorpha (Fig. 6)

Percomorphs are the most diverse and abundant group of bony fishes today. They colonized both marine and freshwater ecosystems, occupying a variety of niches from small demersal durophages to large pelagic predators. Many percomorphs are important for fishery (next to clupeomorphs and gadiforms). Percomorph origin is debated (Patterson 1993, Arratia et al. 2004, Nelson 2006) but most likely they appeared in the Late Cretaceous. Percomorphs diversification accelerated after the K/Pg extinction event (Friedman et al. 2023). The oldest known skeletal fossil record of percomorphs is the Campanian *Nardoichthys* (Arratia et al. 2004). The other Mesozoic fossils and most of otoliths described as belonging to percomorpha were likely misinterpreted as holocentriform and ophiidiform otoliths (Schwarzhans and Stringer 2020, Schwarzhans and Jagt 2021, Schwarzhans et al. 2024).

The only convincingly identified Mesozoic percomorph otoliths are from the Maastrichtian putative percomorph *Plesiopoma* and two species from otolith-based perciform genera, i.e. *Cretaserranus maastrichtensis* (Schwarzhans and Jagt 2021) and *“Serranus” caribbaeus* (Nolf and Dockery 1993).

Palaeoecology and diversification pattern

The Mesozoic fossil record of otoliths is congruent with that of skeletal remains and also fills the gaps in knowledge (Schwarzhans et al. 2024). Mesozoic bony fish otoliths and cephalopod statoliths commonly extend the stratigraphic range of particular groups and help to reconstruct their evolutionary history (Fig. 3–6). According to Lin and Schwarzhans (2019), fossilized otoliths belong rather to demersal than to neritic fishes ones because the anoxic (or dysoxic) conditions are needed to preserve otoliths detached from the skeleton (Nolf 1985, Schwarzhans 2019). This thesis partially supports the above claim. However, otoliths from Picolbach in the Carnian of the Dolomites studied as part of this thesis (Pindakiewicz et al. 2024), or from the middle part of the section in Wąwał (Pindakiewicz et al. 2023) belonged to fishes that lived in the higher parts of the water column. Most of the otoliths and statoliths studied for this thesis were small-sized, and could have come from individuals consumed by carnivores. I suspects, because I observed large number of cephalopod statoliths with broken edges. Similar observation on statoliths is stated by Clarke (2003) who suggested the damage happened during the scree-washing or other mechanic method of cleaning material from sediments. However, among the materials studied for this thesis I found such specimens with adhering matrix, therefore these specimens had to be broken before the final burial. However, I could not find straightforward traces of digestion or morphological anomalies caused by digestion either (like flattened sulcus, lack of lobation on margins, thinned rostrum, diffuse shape, and indistinctive sulcus and rostrum; Tollit et al. 1997), therefore there is no clear indication that the specimens went through a digestive system of any carnivore, and could have easily come, from example, from regurgigates. It is also likely that many of the ear stones had erosion traces caused during the exposure on the sea floor which took place after final deposition but prior to fossilization.

After studying ear stones from several Mesozoic sections while preparing this thesis (Pindakiewicz et al. 2022, 2023, 2024, in press) I observed that the cephalopod statoliths were very common throughout the Jurassic with the peak of morphological diversity in the Kimmeridgian (Upper Jurassic), and significant decrease in abundance towards near-absence in the Lower Cretaceous. The only exception to this pattern are a few localities from Oxfordian (Upper Jurassic) in which only small number of leptolepiform otoliths was found, what I interpret as an anomaly evoked by anoxic bottom conditions (Pindakiewicz et al. in press). The youngest Mesozoic statoliths of “Jurassic type” which I studied come from Aptian (Fig. 1). Mesozoic cephalopod statoliths are not as diverse as shells of ammonoids and nautiloids, or belemnoid rostra. However, ear stones are far better tool to estimate the abundance of both cephalopods and teleosts in the same localities than their skeletal remains due to the similar mineralogy and preservation potential. I compared abundance of both cephalopod statoliths and teleost otoliths in the studied localities and observed that cephalopod statoliths were much more abundant than teleost otoliths throughout the Jurassic. I interpret this as Jurassic nektonic community with cephalopods more abundant than teleosts. However, the reverse pattern of rare cephalopod statoliths was observed in the Lower Cretaceous, with no statoliths in the Upper Cretaceous. I interpret that as an evidence for Cretaceous nektonic communities vastly dominated by teleosts (Pindakiewicz et al. 2022, in press).

The occurrences of otoliths of teleosts taxa commonly predate their first skeletal occurrences. The good example of that are Elopomorpha. The sections I investigated for this thesis display a gradually growing diversity of elopomorphs from the Middle Jurassic onwards, and literature data (Cavin 2008) suggest and expansion of their morphological disparity around the early Late Cretaceous (Fig.3). However, it is noteworthy that in the interval I studied

(Jurassic–Early Cretaceous), the otoliths of leptolepiforms, elopomorphs, and argentiforms share very similar morphologies—slender outline, with singular ostium and mostly straight cauda. The different morphology in otoliths appeared only in ostariophysian teleosts, caused by different inner ear structure. Literature data (Schwarzhans 2018) indicate that different, more diverse otolith morphologies developed later, during the Late Cretaceous, among acanthopterygians, like beryciforms and holocentriforms, and in the crown percomorphs in the Paleogene (Schwarzhans et al. 2017).

After comparison of diversity of teleost otoliths in the localities investigated in the course of this dissertation and data from the literature I observed a succession of three distinct assemblages (Fig.7). The oldest Jurassic assemblages (upper Pliensbachian–lower Bathonian) contain mostly otoliths of leptolepiforms accompanied by *Archaeotolithus* otoliths of alleged holostean origin (Pindakiewicz et al. in press). The youngest Jurassic record displays only one species of leptolepiform (Schwarzhans 2018). Localities with leptolepiform assemblage are known so far only from Europe: Germany, Poland, Lithuania, and the United Kingdom (Fig.8).

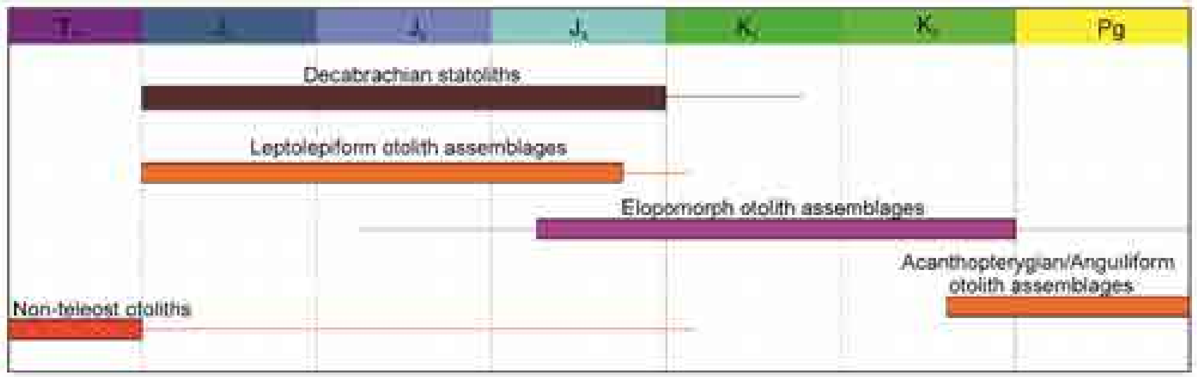


Fig. 7. Stratigraphical ranges of the proposed Mesozoic ear stones assemblages.

The second assemblage (ranging Upper Jurassic to Upper Cretaceous) is dominated by elopomorph otoliths (Albuliformes+Elopiformes). The oldest example of this assemblage comes from the Bathonian (Middle Jurassic) of Poland (Pindakiewicz et al. in press). The elopomorph assemblage acquired its full development around the Kimmeridgian (Fig.7). The diverse community of elopomorph otoliths is accompanied by otoliths of leptolepiforms (in the Jurassic), argentiniforms (in the Cretaceous), and less abundant osteoglossiform and crossognathiform ear stones. Otoliths mentioned above share very similar general outline, i.e., (i) slender, elongated outline, (ii) straight cauda, (iii) ostial opening sulcus, (iv) triangular ostium, merged with elongated rostrum. The level of disparity between otolith-based genera in this assemblage is quite low. The elopomorph otolith assemblage come from teleosts dominating marine fish communities from the Late Jurassic to the Late Cretaceous. Localities with that kind of assemblage were found throughout Northern Hemishpere, especially in the United Kingdom (Stinton and Casier 1966), North America (Schwarzhans et al. 2022), Poland (Pindakiewicz et al. 2023), and Japan (Miyata et al. 2024) (Fig.9).

Fig. 8. Localities with leptolepiform otoliths assemblages reported. Abbreviations (from left to right): Hb, Hebrides (Bathonian, Middle Jurassic), RHP, Roden Hill Point (Bathonian, Middle Jurassic), E, Eype (Pliensbachian, Lower Jurassic), RP, Redcliff Point (Oxfordian, Upper Jurassic), Hr, Horsham (Hauterivian, Lower Cretaceous), F, Fuhrberg (Bathonian, Middle Jurassic), W, Wirringen (Toarcian, Lower Jurassic)), B, Buttenheim (Pliensbachian, Lower Jurassic)), P, Punzendorf (Callovian, Middle Jurassic), K, Kremmeldorf (Toarcian/Allenian, Lower/Middle Jurassic), Gn, Gnaszyn (Bathonian, Middle Jurassic), GL, Gołaszyn (Callovian, Middle Jurassic), JG, Jurakalnis Gully (Oxfordian, Upper Jurassic), Pp, Papartyné (Callovian, Middle Jurassic).

Third and the last teleost otolith-based Mesozoic assemblage was not studied during this thesis but is extensively discussed in the literature. It comprise otoliths of acanthopterygian fishes (beryciformes and holocentriforms), and eels (anguiliforms). The oldest examples of this assemblage are of Santonian (Late Cretaceous) age and come from North America (Schwarzhans et al. 2018b). This beryciform/anguiliform otolith assemblage comprise also rare pterothrissid, osteoglossiform, siluriform, and rare gadiform otoliths. The morphological disparity within this assemblage is high between the otolith-based genera. For example, first acanthopterygian ear stones with heterosulcoid, medial sulcus and no ostium connected to the rostrum appear in this assemblage. This assemblage become the most abundant in the northern hemisphere after K/Pg extinction event (Brzobohatý and Bubík 2019, Schwarzhans et al. 2024, Schwarzhans 2004). The lack of information on otolith assemblages from epicontinental seas in Southern Hemisphere is most likely biased by insufficient collection efforts, especially in marine deposits. All otolith-based assemblages from Mesozoic of southern hemisphere are known from lacustrine sediments (Rana and Sahni 1989, Nolf et al. 2008, Schwarzhans et al. 2018c), what might be partially caused by paleogeographic configuration of the continents at that time, with the dominance of Gondwana supercontinent in the south.

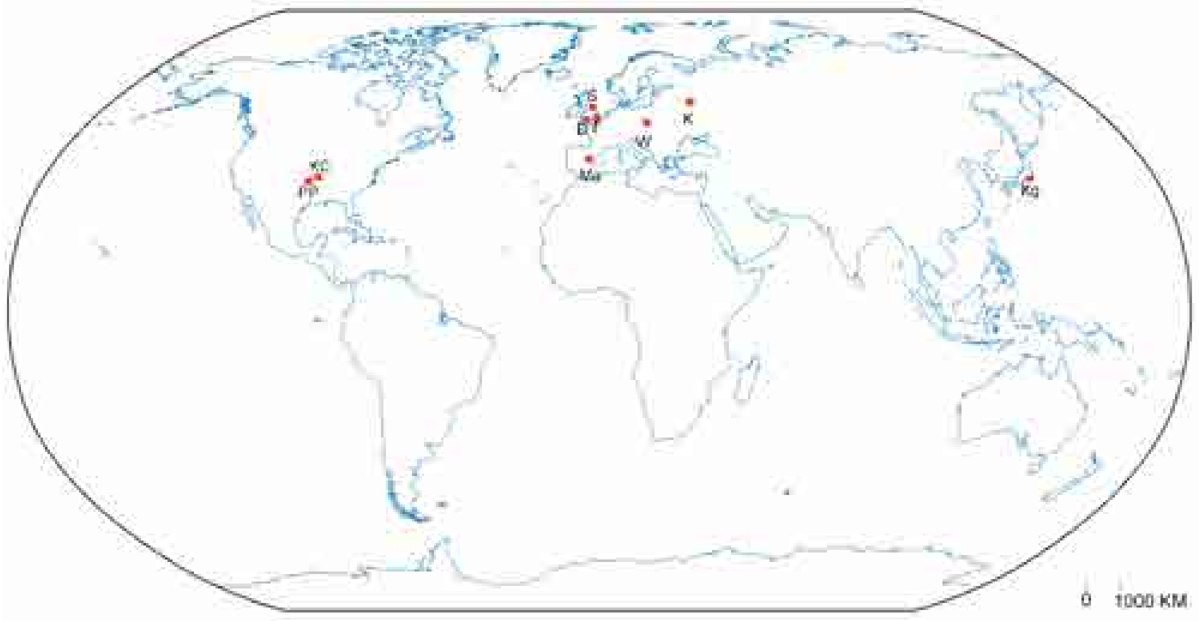


Fig. 9. Localities of elopomorph otoliths assemblages reported. Abbreviations (from left to right): PP, PawPaw Formation (Albian, Lower Cretaceous), KC, Kemp Clay (Maastrichtian, Upper Cretaceous), D, Dorset (Osmington Mills+ Blackhead) (Kimmeridgian, Upper Jurassic), F, Folkestone (Albian, Lower Cretaceous), S, Speeton Clay (Aptian, Lower Cretaceous), Ma, Maestrazgo (Aptian, Lower Cretaceous), W, Wąwał (Valanginian, Lower Cretaceous), K, Kuntsevo (Tithonian, Upper Jurassic), Kg, Kagome Bay (Barremian, Lower Cretaceous).

Summary

This thesis has shown that Mesozoic cephalopod statoliths and teleost otoliths can not only be useful for taxonomy and palaeoecology (like their Cenozoic counterparts), but also to fill the gaps in evolutionary history of both cephalopods and teleosts. The thesis contributes in establishing faunal dynamics of two major groups of nekto-benthic and nektonic animals (i.e., cephalopods and fishes) in the Mesozoic times. The results can be summarized as follows:

- Discovery of the oldest Mesozoic otolith-based assemblage of the Late Triassic age, and identification of stem-neopterygians, holosteans and basal teleosts based on otoliths.
- Identification of the oldest albuliform otoliths (Bathonian, Middle Jurassic).
- Outlining and expanding the diversity of Mesozoic teleosts by identifying new genera (three) and species (fourteen), and expanding the stratigraphical and geographical range of previously known otolith-based taxa (thirteen).
- Description of thirteen new otolith-based assemblages from Jurassic and Early Cretaceous, and comparison of them to those previously known from literature.

- Outlining the teleost evolution between Middle Jurassic and Early Cretaceous based on otoliths.
- Identification of first cephalopod statoliths from the Cretaceous,.
- Documenting statoliths of recent idiosepiid *Idiosepius pygmaeus*.
- Outlining the possible relations of Mesozoic cephalopod statoliths with neocoleoids.
- Comparison of cephalopod statolith and teleost otolith abundance from Jurassic and Cretaceous sediments and showing the turnover in both groups.

Both cephalopod statoliths and bony fish otoliths have species-specific morphology that allows to estimate the diversity of Mesozoic fishes and cephalopods and to fill the gap in their skeletal fossil record. Mesozoic cephalopod statoliths appear to belong to the basal decabrachians or belemnoids, that are more closely related to crown decabrachians than to vampyromorphs. The oldest otolith assemblage show marine community dominated by non-teleost neopterygians and stem-neopterygians. In this assemblage I also reported the oldest-known teleost otoliths. Based on statolith/otolith ratio in the investigated samples, it seems that in the Jurassic the most common and abundant nektonic and nekto-benthic animals were cephalopods. However, based on similar premise I assume that from the Early Cretaceous onward the marine nekton has been dominated by teleost fishes. The cause of this major turnover of cephalopod and teleost fish abundance between Late Jurassic and Early Cretaceous remains unclear. By identifying and comparing otolith-based genera and species from Mesozoic epicontinental seas, I concluded that teleosts started to diversify in the Middle Jurassic, and continued to do so throughout the Late Jurassic and Early Cretaceous, with literature data suggesting this process carried on in the Late Cretaceous and the Paleogene. I observed a sequence of two types of partially overlapping otolith assemblages (and a third one I deduced from the literature data), highlighting how marine communities of teleosts have evolved during the Mesozoic times.

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OŚWIADCZENIE/DECLARATION

Rozprawa pod tytułem „Otolity ryb i statolity głowonogów mezozoicznych: ich znaczenie filogenetyczne i środowiskowe” składa się z czterech rozdziałów. Wszystkie rozdziały są dziełami współautorskimi. Następne strony niniejszego oświadczenia zawierają szczegóły dotyczące mojego udziału w poszczególnych rozdziałach.

The dissertation entitled "Fish otoliths and statoliths of Mesozoic cephalopods: their phylogenetic and environmental significance " consists of four chapters. All chapters are co-authored works. The following pages of this statement contain details of my contribution to particular chapters.

Maciej K. Pindakiewicz

Rozdział I / Chapter I

First Cretaceous cephalopod statoliths fill the gap between Jurassic and Cenozoic forms

Rozdział I powstał we współpracy z Andrzejem Kaimem, Krzysztofem Hryniewiczem, oraz Katarzyną Janiszewską (wszyscy Instytut Paleobiologii Polskiej Akademii Nauk, Warszawa, Polska).

Andrzej Kaim udostępnił materiał do badań ze swojej kolekcji, zorganizował okazy mątewki pigmejki (*Idiosepius pygmaeus*) do zeskanowania, oraz redagował tekst i figury manuskryptu razem z autorem. Krzysztof Hryniewicz redagował tekst i figury manuskryptu razem z autorem, Katarzyna Janiszewska wykonała skany statolitów w mikrotomografie komputerowym i przygotowała modele 3D. Mój udział polegał na postawieniu hipotezy badawczej, wyselekcjonowaniu materiału, identyfikacji statolitów, wykonaniu i obróbce zdjęć z mikroskopu SEM, interpretacji wyników i weryfikacji hipotezy badawczej, przygotowaniu i rewizji manuskryptu i oraz grafik.

Chapter I was co-authored with Andrzej Kaim, Krzysztof Hryniewicz and Katarzyna Janiszewska (all Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland).

Andrzej Kaim made the material from his collection available for research, managed to obtain specimens of the pygmy squid (*Idiosepius pygmaeus*) to scan, and participated in preparation revision of the text and figures of the manuscript. Krzysztof Hryniewicz revised the text and figures of the manuscript, Katarzyna Janiszewska made scans of statoliths in mCT scanner and prepared 3D models for the manuscript. My contribution consisted in presenting a research hypothesis, selecting material, identifying statoliths, taking and processing images from SEM microscope, verification of the research hypothesis and interpretation of the results, preparation and revision of the text and figures of the manuscript.

Oświadczam, że mój wkład w przygotowaniu rozdziału wynosi około 75 %.

I declare that my contribution to the chapter is approximately 75 %.

Podpis współautorów / signature of the co-authors:

Andrzej Kaim

Krzysztof Hryniewicz

Katarzyna Janiszewska
Janiszewska

Rozdział II / Chapter II

Early Cretaceous radiation of teleosts recorded by the otolith-based ichthyofauna from the Valanginian of Wąwał, central Poland.

Rozdział II powstał we współpracy z Andrzejem Kaimem i Krzysztofem Hryniewiczem (obaj Instytut Paleobiologii Polskiej Akademii Nauk, Warszawa, Polska)

Andrzej Kaim udostępnił materiał do badań ze swojej kolekcji, uczestniczył w przygotowaniu i rewizji tekstu i figur manuskryptu. Krzysztof Hryniewicz pomagał przygotowaniu i rewizji tekstu i figur manuskryptu. Mój udział polegał na prowadzeniu badań, wyselekcjonowaniu materiału, identyfikacji otolitów, wykonaniu i obróbce zdjęć z mikroskopu SEM, interpretacji wyników, przygotowaniu i rewizji tekstu oraz figur w manuskrypcie.

Chapter II was co-authored with Andrzej Kaim and Krzysztof Hryniewicz (both Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland)

Andrzej Kaim made the material from his collection available for research, and participated in preparation revision of the text and figures of the manuscript . Krzysztof Hryniewicz participated in preparation revision of the text and figures of the manuscript. My contribution consisted of conducting research, formulating research hypothesis, selecting the material, identifying otoliths, taking and processing SEM microscope images, interpretation of the results and verification of the research hypothesis preparation and revision of the text and figures of the manuscript .

Oświadczam, że mój wkład w przygotowaniu rozdziału wynosi około 80 %.

I declare that my contribution to the chapter is approximately 80 %.

Podpis współautorów / signature of the co-authors:

Andrzej Kaim

Krzysztof Hryniewicz

Rozdział III / Chapter III

A microfossil evidence for the composition of fish communities in the Late Triassic of Tethys: examples from Cassian Formation, Italy.

Rozdział III powstał we współpracy z Andrzejem, Krzysztofem Hryniewiczem oraz Katarzyną Janiszewską (wszyscy Instytut Paleobiologii Polskiej Akademii Nauk, Warszawa, Polska).

Andrzej Kaim organizował prace terenowe i w nich uczestniczył, uczestniczył w przygotowaniu i rewizji tekstu i figur w manuskrypcie . Krzysztof Hryniewicz brał udział w pracach terenowych, uczestniczył w przygotowaniu i rewizji tekstu oraz figur manuskryptu, Katarzyna Janiszewska wykonała skany statolitów w mikrotomografie komputerowym i przygotowała modele 3D na potrzeby manuskryptu. Mój udział polegał na udziale w pracach terenowych, postawieniu hipotezy badawczej, wyselekcjonowaniu okazów, identyfikacji mikroskamieniałości, wykonaniu i obróbce zdjęć z mikroskopu SEM, interpretacji wyników, weryfikacji hipotezy badawczej oraz przygotowaniu i rewizji tekstu i figur w manuskrypcie.

Chapter III was co-authored with Andrzej Kaim, Krzysztof Hryniewicz and Katarzyna Janiszewska (all Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland).

Andrzej Kaim organized fieldwork, took part in the fieldwork participated in preparation and revision of the text and figures of the manuscript. Krzysztof Hryniewicz took part in fieldwork, participated in preparation and revision of the text and figures of the manuscript, Katarzyna Janiszewska made scans of statolites in a microCT scanner and prepared 3D models for the manuscript. My contribution consisted in participation in fieldwork, formulating a research hypothesis, selection of specimens, identification of microfossils, taking and processing SEM microscope images, interpretation of results, participated in preparation and revision of the text and figures of the manuscript.

Oświadczam, że mój wkład w przygotowaniu rozdziału wynosi około 75 %.

I declare that my contribution to the chapter is approximately 75 %.

Podpis współautorów / signature of the co-authors:

Andrzej Kaim	Krzysztof Hryniewicz	Katarzyna Janiszewska
	Hryniewicz	Janiszewska

Rozdział IV / Chapter IV

Jurassic teleosts diversity and abundance changes, recorded by otolith and cephalopod statolith assemblages.

Rozdział IV powstał we współpracy z Krzysztofem Hryniewiczem (Instytut Paleobiologii Polskiej Akademii Nauk, Warszawa, Polska), Simoną Rinkevičiūtė (Wydział Geologii i Mineralogii Uniwersytetu Wileńskiego, Wilno, Litwa), Przemysławem Sztajnerem (Instytut Morski i Nauk Przyrodniczych Uniwersytetu Szczecińskiego, Szczecin, Polska), Katarzyną Janiszewską, oraz z Andrzejem Kaimem (oboje Instytut Paleobiologii Polskiej Akademii Nauk, Warszawa, Polska).

Krzysztof Hryniewicz brał udział w pracach terenowych uczestniczył w przygotowaniu oraz rewizji tekstu oraz figur manuskryptu. Simona Rinkevičiūtė uczestniczyła w organizacji i brała udział w pracach terenowych w Litwie i uczestniczyła w przygotowaniu oraz rewizji tekstu oraz figur manuskryptu. Przemysław Sztajner udostępnił materiał do badań ze swojej kolekcji, oraz wykonał zdjęcia okazów ze swojej kolekcji i uczestniczył w przygotowaniu oraz rewizji tekstu a także figur manuskryptu. Katarzyna Janiszewska wykonała skany wybranych okazów w mikrotomografie komputerowym i wykonała model 3D na potrzeby manuskryptu, i uczestniczyła w przygotowaniu oraz rewizji tekstu oraz figur manuskryptu. Andrzej Kaim udostępnił materiał do badań ze swojej kolekcji, organizował prace terenowe, uczestniczył w pracach terenowych oraz w przygotowaniu oraz rewizji tekstu oraz figur manuskryptu. Mój udział polegał na zebraniu materiału do badań, udziału w pracach terenowych, sformułowaniu hipotezy badawczej, sfotografowaniu materiałów, identyfikacji otolitów i statolitów, interpretacji wyników, weryfikacji hipotezy badawczej, przygotowaniu i rewizji tekstu oraz figur manuskryptu.

Chapter IV was written in cooperation with Krzysztof Hryniewicz (Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland), Simona Rinkevičiūtė (Department of Geology and Mineralogy, Vilnius University, Lithuania), Przemysław Sztajner (Institute of Marine and Environmental Sciences, University of Szczecin, Poland), Katarzyna Janiszewska, and Andrzej Kaim (Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland).

Krzysztof Hryniewicz participated in field work and in preparation and revision of text and figures of the manuscript. Simona Rinkevičiūtė helped to organize and took part in the fieldwork in Lithuania, and participated in field work and in preparation and revision of text and figures of the manuscript. Przemysław Sztajner made available material for research from his collection, photographed specimens from his collection, and participated in field work and in preparation and revision of text and figures of the manuscript. Katarzyna Janiszewska made scans of selected specimens in a microCT scanner and made a 3D model for the manuscript. Andrzej Kaim made material from his collection available for research, organized and participated in fieldwork, and participated in preparation and revision of text and figures of the manuscript s. My participation consisted in participation in fieldwork, formulating a research hypothesis, assembling the collected material, photographing the specimens, identifying otoliths and statoliths, interpreting the results, verification of the research hypothesis and preparation and revision of the text and figures of the manuscript..

Oświadczam, że mój wkład w przygotowaniu rozdziału wynosi około 70 %.

I declare that my contribution to the chapter is approximately 70 %.

Podpis współautorów / signature of the co-authors:

Krzysztof Hryniewicz   Simona Rinkevičiūtė   Przemysław Sztajner   Katarzyna Janiszewska   Andrzej Kaim

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