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ISSN (imprimé / print) : 1631-0683/ ISSN (électronique / electronic) : 1777-571X

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Submitted on 20 January 2021 | Accepted on 15 June 2021 | Published on 17 October 2022

urn:lsid:zoobank.org:pub:BE90FC7C-409E-4B76-BF0C-4D9247767AF7

Pindakiewicz M. K., Hryniewicz K., Janiszewska K. & Kaim A. 2022. — First Cretaceous cephalopod statoliths fill the gap between Jurassic and Cenozoic forms. *Comptes Rendus Palevol* 21 (36): 801–813. <https://doi.org/10.5852/cr-palevol2022v21a36>

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 belemnite identity of these forms can be neither confirmed nor rejected though some positive correlation in the investigated materials between findings of belemnite rostra and statoliths do occur. These finds support also some previous suggestions that decabrachians and vampyropods 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.

KEY WORDS

Statolith,
Cretaceous,
Valanginian,
Aptian,
Yorkshire,
Speeton,
Wawel,
Poland.

RÉSUMÉ

Première découverte de statolithes de céphalopodes crétacés comblant la lacune entre les formes du Jurassique et du Cénozoïque.

L'article est consacré à la découverte de premiers statolithes crétacés. Ces microfossiles uniques en leur genre sont similaires à des statolithes jurassiques et permettent de combler la lacune entre ceux-ci et les formes cénozoïques. La comparaison des statolithes du Secondaire avec ceux appartenant aux céphalopodes décabrachiaux du Cénozoïque et actuels conduit à reconnaître la plus grande ressemblance avec les *Idiosepiidae* actuels. Nous proposons donc que les statolithes du Secondaire ont pu appartenir à des représentants d'un groupe basal des céphalopodes décabrachiaux. On ne peut ni confirmer ni rejeter l'appartenance de ces formes aux bélemnites, même si, dans le matériel étudié, il y a quelques corrélations positives entre les trouvailles de statolithes et de rostrés des bélemnites. Un changement net dans les proportions des statolithes et des otolithes de poissons a lieu, avec la domination des statolithes au Jurassique et la diminution de leur diversité au Crétacé. Ces conclusions sont en lien avec l'hypothèse de la divergence des céphalopodes décabrachiaux et des vampyropodes avant le Jurassique inférieur.

MOTS CLÉS

Statolithe,
Crétacé,
Valanginien,
Aptien,
Yorkshire,
Speeton,
Wawel,
Pologne.

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 belemnites. There are examples of poorly preserved statoliths *in situ* within belemnite (Klug *et al.* 2016) and belemnite body fossils (Wilby *et al.* 2004), but their morphology is too diagenetically altered to allow meaningful comparisons with other known Jurassic statoliths.

GEOLOGICAL SETTING

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 Aptian-Albian 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.

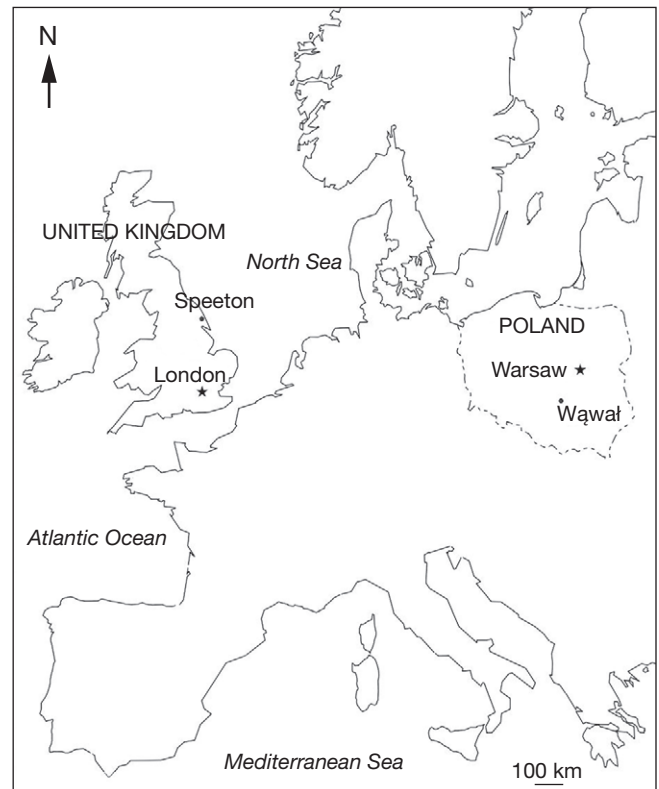


Fig. 1. — Map showing Cretaceous statolith-bearing localities discussed in this paper.

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



FIG. 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.

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

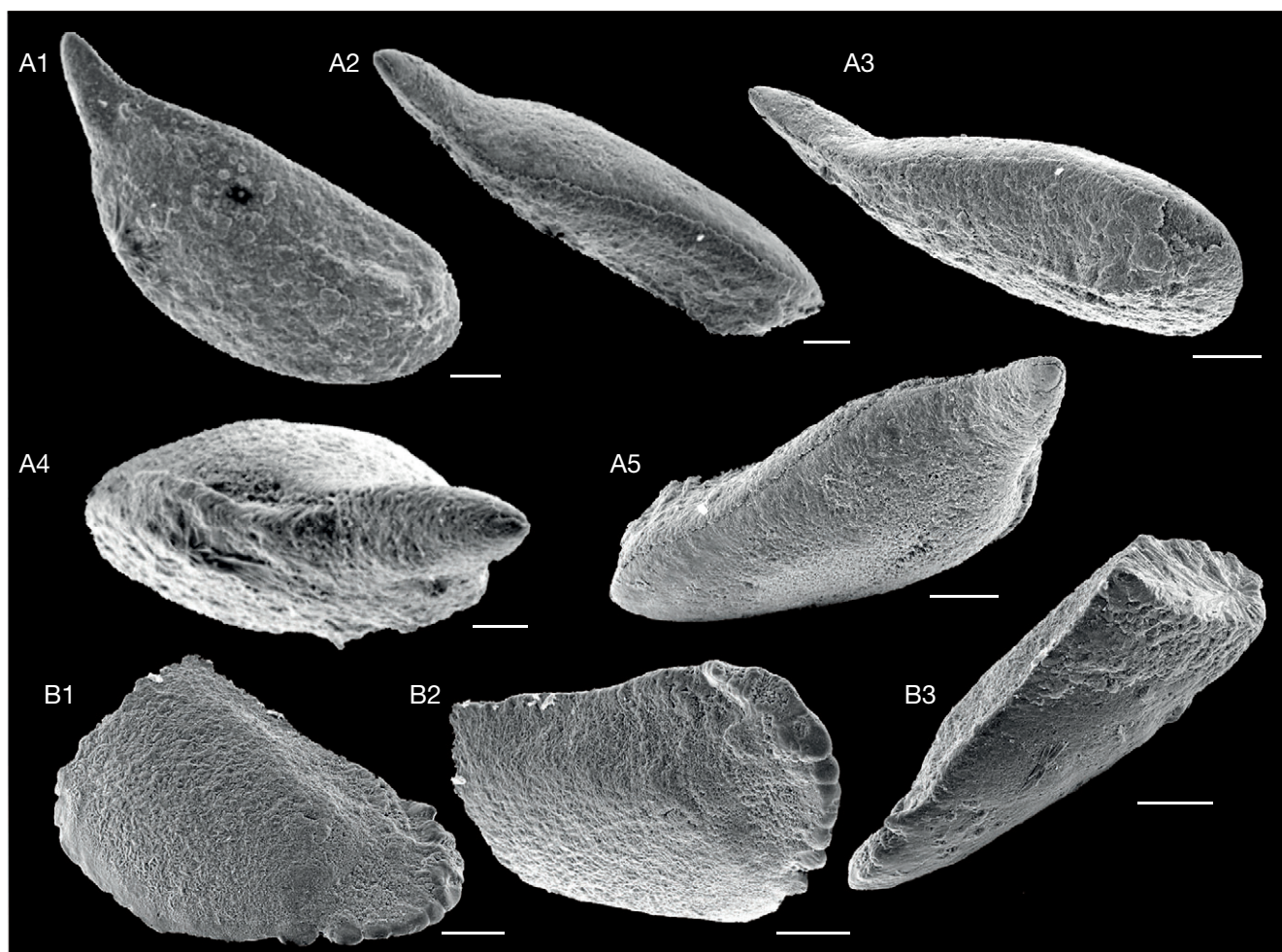


FIG. 3. — Early Cretaceous (Aptian) statoliths from Speeton, Yorkshire, United Kingdom. **A**, Speeton Statolith 1 (SS1), right statolith ZPAL B.II/2-3, Aptian, views: **A1**, outer; **A2**, dorsal; **A3**, anterior; **A4**, postero-dorsal; **A5**, antero-dorsal; **B**, Speeton Statolith 2 (SS2), left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

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

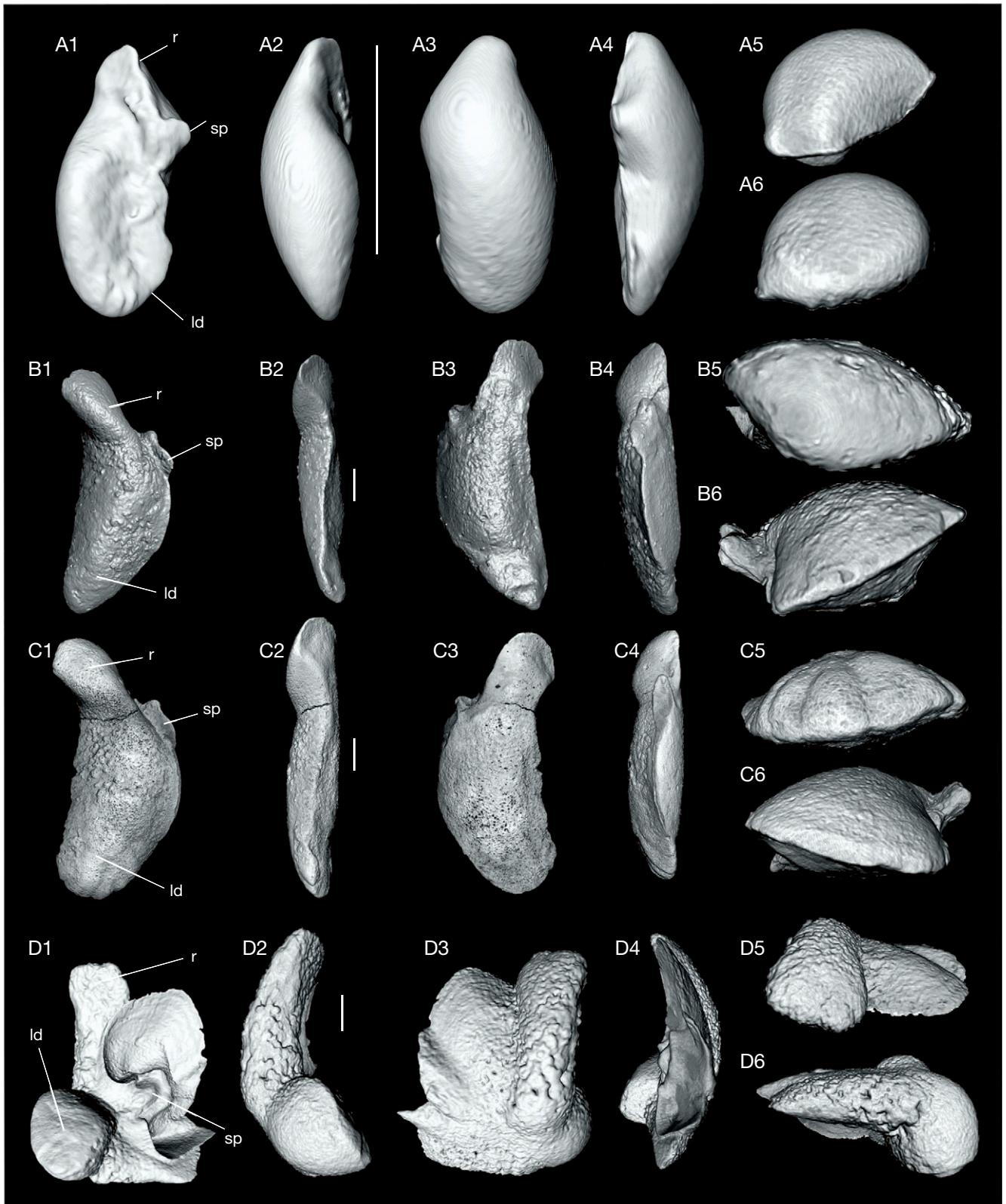


FIG. 4. — Comparison between left statoliths of *Idiosepius pygmaeus* Steenstrup, 1881, ZPAL B.II/6. **A:** Recent, Sea of Japan; **B:** Early Cretaceous (Valanginian) statolith (ZPAL B.II/1) from Wawal, Poland; **C:** Middle Jurassic (Callovian) statolith (ZPAL B.II/7) from Golaszyn, Poland; **D:** 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 μ m.

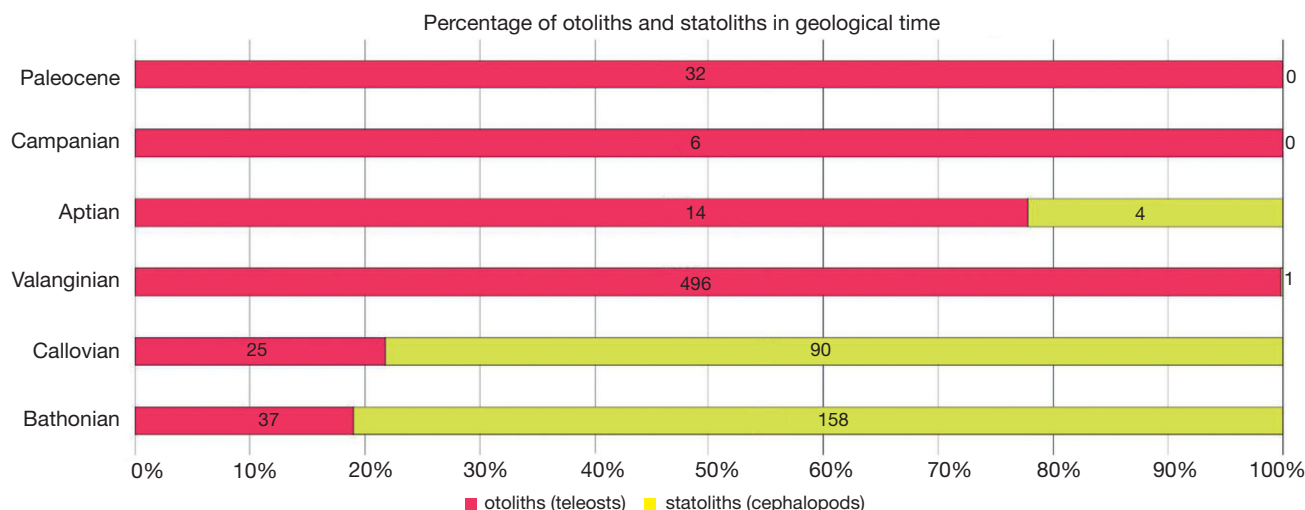


FIG. 5. — Abundance of cephalopod statoliths and fish otoliths in investigated localities (data for Coon Creek are from pilot samples only). Data compiled from the following localities: Gnaszyn (Bathonian), Golaszyn (Callovian), Wąwał (Valanginian), Speeton Clays (Aptian), Coon Creek (Campanian), Babica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

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 Wąwał 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 & Fitch 1979). 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 belemnites 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 belemnite macrofossils in Jurassic strata (Table 1). In the Callovian (Middle Jurassic) locality of Łuków-Golaszyn we found statoliths in layers where belemnites and aragonitic rostra of *Belemnoteuthis polonica* were reported by Makowski (1952). Similarly, in the Bathonian (Middle Jurassic) locality of Gnaszyn, the belemnites are relatively common (Wierzbowski 2013) in statolith-bearing strata. Statoliths from Łuków-Golaszyn 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 belemnites and belemnites 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 belemnite (Klug *et al.* 2016) and belemnite (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 belemnites in the Callovian, Middle Jurassic of England (Wilby *et al.* 2004; Hart *et al.* 2016). Therefore, neither belemnites nor belemnites can be

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

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

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 & Fitch 1979). 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 cling-

ing 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 belemnites. 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.

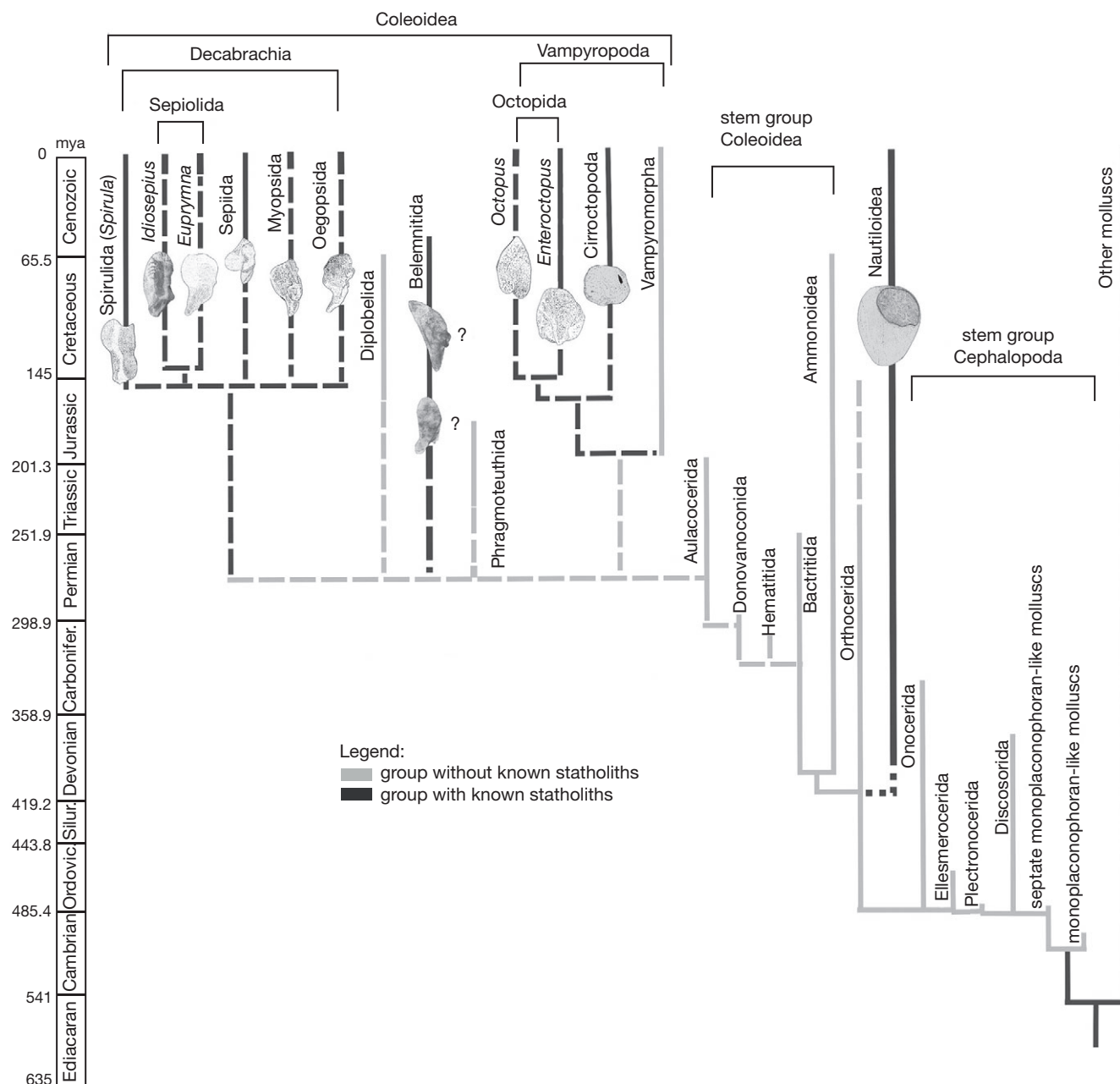


Fig. 6. — Evolutionary tree of cephalopods based on Kröger *et al.* (2011), with illustrations of typical morphology of statholiths in each group (if known).

Acknowledgements

We thank Shouzo Ogiso from the Noto Marine Laboratory of the Kanazawa University for catching specimens of *Idiosepius pygmaeus* in Tsukumo Bay and Robert G. Jenkins from the Kanazawa University for arranging it for us. We also thank two anonymous referees, and the associate editor, Annalisa Ferretti, for helpful comments. The study was supported by a grant from the National Science Centre of Poland (No.2019/35/N/ST10/04160) titled “Paleoecology, paleogeography, bathymetric distribution, and diversification pattern of fishes and cephalopods in Mesozoic epicontinental seas based on otoliths and statholiths”. Micro-CT scans for this article were done in

the Laboratory of Microtomography, Institute of Paleobiology PAS, Warsaw, Poland. SEM photos for this work were done in the Laboratory of SEM Microphotography, Institute of Paleobiology PAS, Warsaw, Poland.

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*Submitted on 20 January 2021;
accepted on 15 June 2021;
published on 17 October 2022.*

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. https://doi.org/10.5852/cr-palevol2022v21a36_S1

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. https://doi.org/10.5852/cr-palevol2022v21a36_S2

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. https://doi.org/10.5852/cr-palevol2022v21a36_S3

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. https://doi.org/10.5852/cr-palevol2022v21a36_S4