

APPLYING MICRO-CT IMAGING IN THE STUDY OF HISTORICALLY AND NEWLY COLLECTED SPECIMENS OF *BELOSAEPIA* (SEPIIDA, COLEOIDEA, CEPHALOPODA) FROM THE EARLY EOCENE (YPRESIAN) OF BELGIUM

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Abstract. The application of high-resolution X-ray computed tomography permits an appraisal of historically and newly collected specimens of *Belosaepia* (Belosaepiidae, Coleoidea, Cephalopoda) from the Ypresian (Early Eocene) of Belgium and provides resolution into the taxonomy of stem-group sepiids. The new finds are from the basal beds of the Egemkapel Clay Member (Tielt Formation) in the Ampe claypit at Egem and in the middle of the Roubaix Clay Member (Kortrijk Formation) in the Koekelberg claypit at Marke (province of West-Flanders, Belgium). Combining the historically and newly collected material allows us to conclude that only a single species can be positively identified, namely *Belosaepia tricarinata* (Watelet, 1851), and that all currently documented occurrences are restricted to the middle Ypresian (NP11-NP12). This seems to correspond well with the occurrence of *Belosaepia tricarinata* in the Paris, London, and Hampshire basins. Micro-CT imaging is an excellent, non-destructive tool in the study of the calcified remains. In the *Belosaepia* skeleton, this method allowed us to identify growth lines, ontogenetic changes, and resorption. Utilised in conjunction with a biostratigraphic assessment, this technology has the potential to be a major aid in taxonomic assignments and revisions. In the current study, it also highlighted stratigraphically important fossils (e.g. *Nummulites*) retained in the residual sediment attached to the specimens. This provides additional stratigraphic information that may otherwise be lost, or not recorded in older samples.

INTRODUCTION

Calcified skeletal remains of stem-group sepiid coleoid cephalopods (Belosaepiidae Dixon, 1850), such as *Belosaepia* Voltz, 1830, were reported from

the Belgian Eocene as early as 1784, when ‘Oryctographie de Bruxelles’, one of the oldest paleontological contributions in the world, was published by François-Xavier Burtin (p. 90, pl. 2, fig. A). Although there was no consensus on the taxonomic position of these remains at that time, Burtin (1784) thought they might correspond to an interior bone of a fish skull. Except for some other early contributions by

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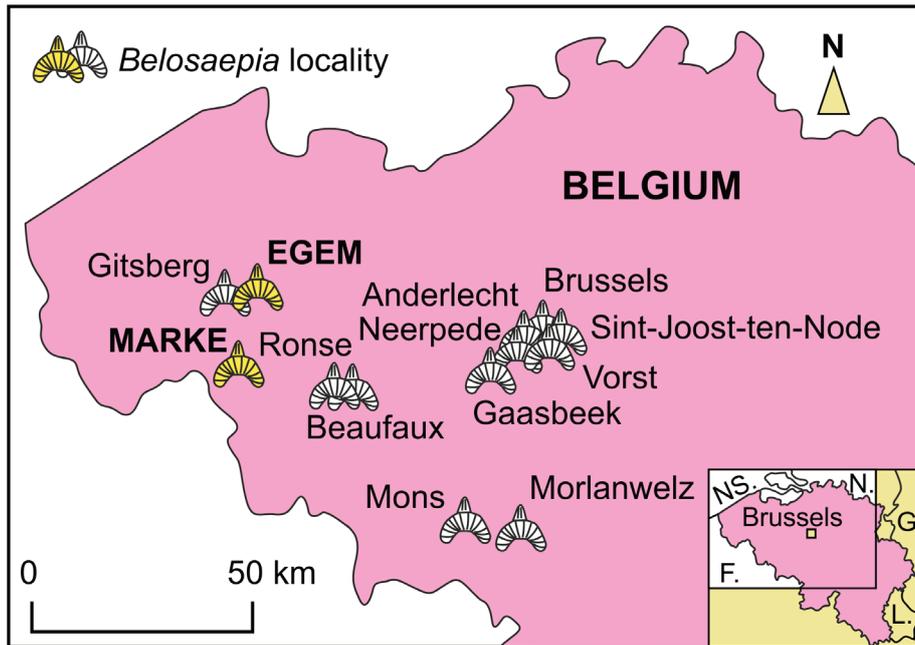


Fig. 1 - Map of Belgium with localization of Egем and Marke (i.e. yellow pictograms) and the other Belgian localities (i.e. white pictograms) discussed in the text. Abbreviations: F.: France, G.: Germany, N.: The Netherlands, L., Luxemburg, NS.: North Sea.

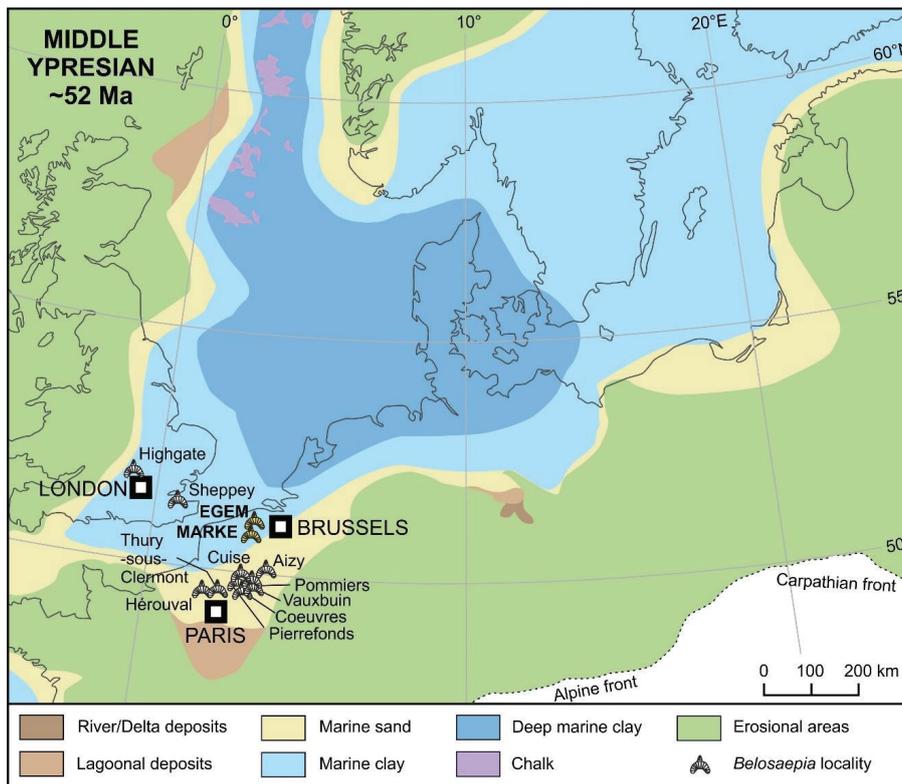
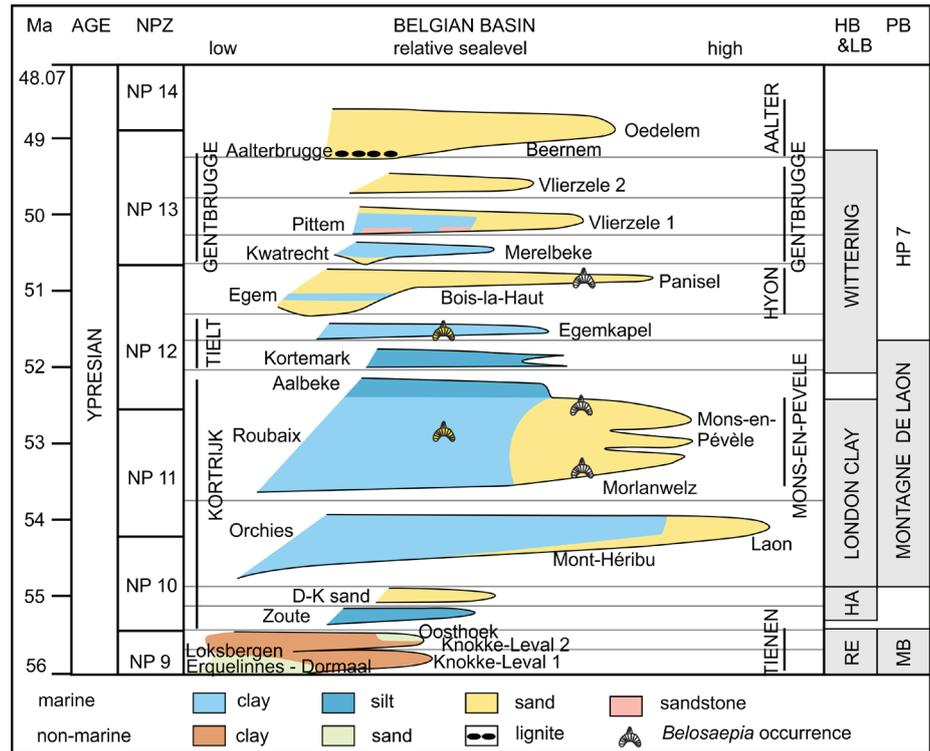


Fig. 2 - Middle Ypresian paleogeography, modified from Knox et al. (2010), with localization of Egем and Marke (i.e. yellow pictograms) and the French and English localities (i.e. white pictograms) mentioned in the text.

Galeotti (1837) and Nyst (1843), most of the Belgian Cenozoic coleoid records date from the last and first quarters of the 19th and 20th centuries respectively (e.g., Nyst in Dewalque 1868, 1880; Vincent 1872, 1876; Cornet & Briart 1874; Mourlon 1881; Delvaux 1885a,b; Vincent 1901; Maillieux 1922, 1933; Janssen & Müller 1984). These finds allow us to document the

presence of the sepiids *Belocurta* Avnimelech, 1958 (Danian), *Belosaepia* Voltz, 1830 (Ypresian-Lutetian) and *Stenosepia* Vincent, 1901 (Lutetian), as well as the spirulids *Belopterina* Munier-Chalmas, 1872 (Thanetian), *Beloptera* de Blainville, 1825 (Lutetian) and *Spirulirostra* d'Orbigny, 1842 (Miocene; is *Spirulirostrina* Canavari, 1892 *vide* Fuchs & Lukenender 2014).

Fig. 3 - Stratigraphy of the Belgian Ypresian and the stratigraphic positioning of the new finds and the probable stratigraphic position of the 19th and 20th century finds. Lithostratigraphic units: Members and FORMATIONS, except for the Montagne de Laon Group. Abbreviations: HA: Harwich Formation, HB: Hampshire Basin; HP7: hiatus HP7 of Pomerol (1989) (see also King, 2016), PB: Paris Basin; LB: London Basin; MB: Mont Bernon Formation; RE: Reading Formation. The Mons-en-Pèvele unit is both regarded as a Member and a Formation. After Steurbaut (2015) and King (2016), both modified, with age estimates for the lower and upper boundaries of the Ypresian following Speijer et al. (2020).



While sepiid fossils are relatively common in the Belgian Lutetian, the literature cites very few specimens from the Ypresian sediments in Belgium suggesting they were rare during this period. Intensive collecting efforts of the second and third author in the Ypresian of Belgium allow us to add two new occurrences, one at the base of the Egemkapel Clay Member (Tielt Formation, upper middle part of Zone NP12, Subzone VI of Steurbaut 1998) in the Ampe claypit at Egem, and another in the middle of the Roubaix Clay Member (Kortrijk Formation, lower middle part of Zone NP12, Subzone IIIb2 of Steurbaut 1998) in the Koekelberg claypit at Marke (Figs 1-3). These new finds are exceptional as no *Belosaepia* remains were previously reported in the literature, either from both quarries, or from these stratigraphic levels elsewhere in Belgium (e.g., compare lists of van Nieulande 2002, van Nieulande & Mermuys 2001, Van Simaey 1994 and Iserbyt & Christiaens 2004). Moreover, the Egem material now constitutes both the largest collection and the best preserved *Belosaepia* specimens from the Ypresian of Belgium. This paper explores the application of micro-CT imaging in the study of *Belosaepia* fossils, combining the reappraisal of the historic records with the description of the newly collected specimens from Egem and Marke.

MATERIALS AND METHODS

An overview of the so-called historically collected material was generated by combining a thorough literature search with an extensive search in the paleontology collections of the Royal Belgian Institute of Natural Sciences (RBINS) for Ypresian specimens regardless of their publication status (previously figured, referred or un-referred). This led for example to the rediscovery of some (but not all) of the figured and referred specimens of Vincent (1901), the only author that figured *belosaepiids* from the Ypresian of Belgium. Specimens from the RBINS collection mentioned in the text have the numbers in the following format: IRSNB for figured specimens and Invert for yet unfigured specimens. In the latter, the first five digits refer to the IG or General Inventory number, and more than one specimen may reside under the same (lot) number.

The newly collected material of Egem consists of 15 specimens found (by Y. Christiaens; IG 34334) at the base of the Egemkapel Clay Member (= layer IV in the detailed log of Steurbaut 2006, fig. 8) in the Ampe quarry. The new material of Marke consists of three specimens collected [one by Bert Gijzen (Elasmobranch Research Belgium) and two by F.H. Mollen; IG 34333] from a 5-cm thick oyster and *Turritella* bed in the middle of layer 7 of Steurbaut (1998), subsequently referred to as layer C by Iserbyt & Christiaens (2004) and bed 7b by Steurbaut & King (2017) in the Koekelberg quarry (for an annotated photograph and a detailed log of the section see Steurbaut 2015 and Steurbaut & King 2017 respectively). These new specimens were found during the search for (micro)vertebrate fossils, during the extraction of the sediment (Egem) or during the sieving process that followed (Egem and Marke). Freshly exposed specimens were highly fragile at both localities, and only those that were found prior to the sieving process, and that were carefully put aside, wrapped, dried, and impregnated with Paraloid B72 remained intact and did not partially or even fully crumble away (Egem).

Excluded from this study are *belosaepiid* records from the Brussel Sand Formation [mainly *Belosaepia sepioidea* de Blainville, 1825

Specimen N°	Acquisition mode	Beam kV	Beam μ A	Voxel size (μ m)	Additional specimen number
IRSNB 7689	small spot	150	67	12,9393	Egem-YC-1
IRSNB 7690	small spot	150	67	12,9394	Egem-YC-2
IRSNB 7691	small spot	150	67	19,7048	Egem-YC-3
IRSNB 7692	small spot	150	67	14,7700	Marke-FHM-1
IRSNB 7693	small spot	150	67	14,7700	Marke-FHM-2
IRSNB 7694	small spot	150	67	11,0301	Marke-BG-1
IRSNB 7687	small spot	150	67	12,0090	Invert-9219-0058
IRSNB 7688d	small spot	150	67	15,4981	Invert-9219-0059 - Block of sediment with imprint of dorsal shield
IRSNB 7688e	small spot	150	67	16,8621	Invert-9219-0059 - Block of sediment with phragmocone
IRSNB 7688a	small spot	150	67	20,5463	Invert-9219-0059 - Vincent's original cast of the guard
IRSNB 7688b	middle spot	150	161	32,7879	Invert-9219-0059 - Block of sediment with cast of guard

Tab. 1 - Details of the micro-CT imaging (acquisition mode, power of X-ray source (beam kV and μ A) and obtained voxel sizes (in μ m) of the scanning results for each specimen that was scanned with the RBINS RX EasyTom 150 studied in this paper.

and *Stenosepia compressa* (de Blainville, 1827) *vide* Vincent 1901]. Since the designation of the GSSP for the base of the Lutetian at Gorrondatxe (Spain) (Molina et al. 2011), it has remained unclear whether this lithostratigraphic unit, and thus also its fossil content, are of latest Ypresian or earliest Lutetian age. Historically, the 'Bruxelien' was never intended to become part of Dumont's (1850, 1852) 'système Ypresien'. Recently, Steurbaut (in Steurbaut & Nolf 2021) further documented the correlative nature of the Brussel Sand Formation and the 'Glaucanie Grossière' of the Paris Basin, the latter being formally included in the Lutetian (Molina et al. 2011). According to Steurbaut's findings the Brussel Sand Formation and its fossil content are thus best regarded as lowermost Lutetian.

Six specimens of the newly collected material, and all figured specimens from the historical records that we were able to find in the collections of the RBINS, were analyzed (by SG) using the RBINS micro-CT scan RX EasyTom 150 with settings and voxel sizes depending on the nature of the specimens scanned (Table 1). After scanning, extraction into 16-bit TIFFs was performed with X-Act software, and then 3D-rendering and segmentation was completed using Dragonfly ORS. Figures were produced with the 'export screenshot' function, after optimizing the 3D rendering (adjusting the histogram, contrast, shading, light source position, hard gradient and removing all annotations except the scale bar). In a final step, an image processing software was used to scale the image to 600 dpi. This workflow results in much higher quality images that retain much more textural information than when taking screenshots of exported 3D meshes. In addition to this, 3D-models were added to the RBINS Virtual Collections Platform (<http://virtualcollections.naturalsciences.be/>) and can be consulted there. The primary scanning data and the set of Y slices are stored on Belspo's LTP platform and can be consulted upon request to the RBINS paleontology collection manager.

The reviewed terminology of the belosaepiid skeleton of Yancey et al. (2010) was applied in the present paper (Figs 4, 5).

RESULTS

The historical records - a review of their stratigraphy

Belosaepia was previously mentioned, described and/or figured (spelt wrongly as *Belosepia*) from three different stratigraphic levels within the Belgian Ypresian:

- '*Couches argilo-sableuses à Nummulites planulatus de Carnières et Morlanwelz*'. Cornet & Briart (1874: 540-541) were the first to report on the presence of *Belosaepia* in the '*Couches argilo-sableuses à Nummulites planulatus de Carnières et Morlanwelz*', which were subsequently attributed to the '*Argilite ypresienne de Morlanwelz*' by Vincent (1876). Initially, the specimens were identified by Cornet & Briart (1874) as *B. sepioidea* de Blainville, 1825 (see also Vincent 1876: 128-129). Later, Vincent (1901: 15) stated that these specimens were likely to be *B. tricarinata* (Watelet, 1851) but the fact that Morlanwelz, the locality from which *B. tricarinata* was known, was not included in his synthesis of Belgian coleoid occurrences (op cit., p. 10), suggests Vincent was unsure of this taxonomic assessment. Unfortunately, no specimens were figured, and their whereabouts today are unknown. Possibly they are stored in the collections of the Université de Mons (Belgium). No specimens from this stratigraphic deposit or locality were found within the collections of the RBINS. According to the information in Cornet & Briart (1874), the specimens must have come from the basal part of the Mons-en-Pévèle Sand Formation sensu Steurbaut et al. (2016), which is attributable to the lower middle part of nannofossil zone NP11 (probably top of subzone II of Steurbaut 1998, 2011) and of mid-Ypresian age (Steurbaud 2006) (Fig. 3).

- '*Assise supérieure de l'Ypresien*'. Vincent (1876: 129), Vincent & Rutot (1879: 89) and Murlon (1881: 153) reported the presence of *B. tricarinata* in the '*Ypresien supérieur des environs de Bruxelles*', with an additional record of a possible second species (*B. sp.?*) by Vincent (1876), but there are no descriptions or figures of them. *Belosaepia* was also

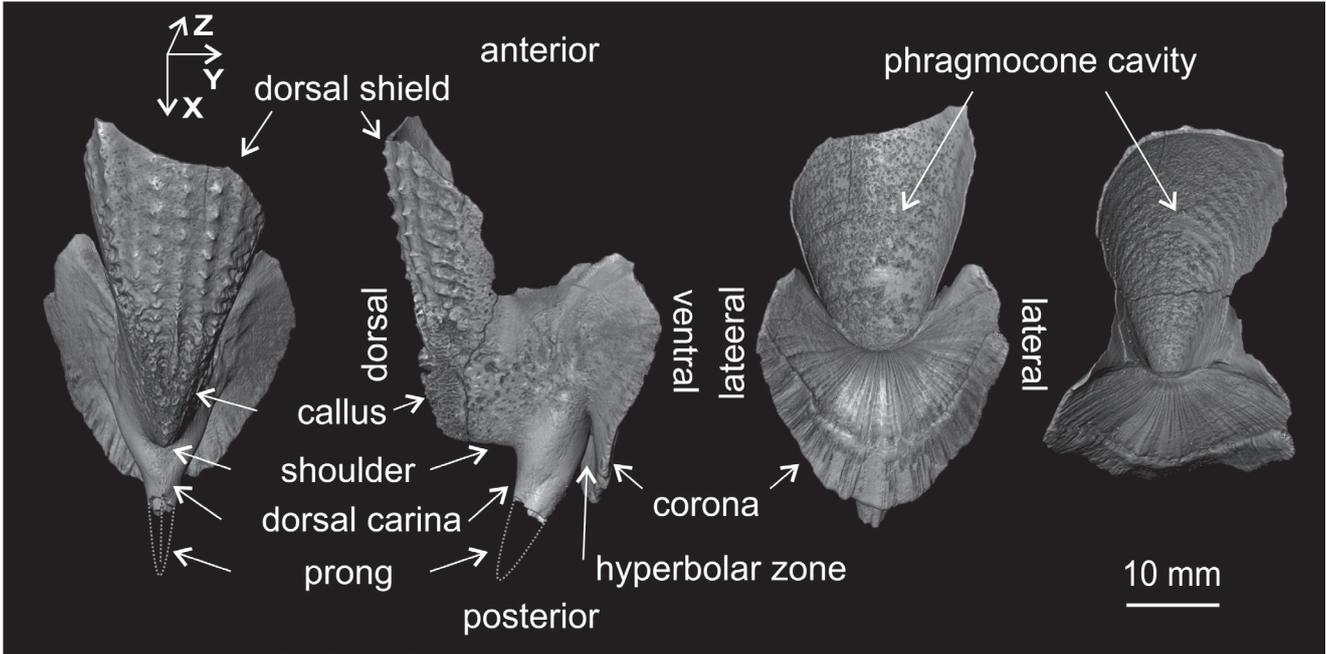
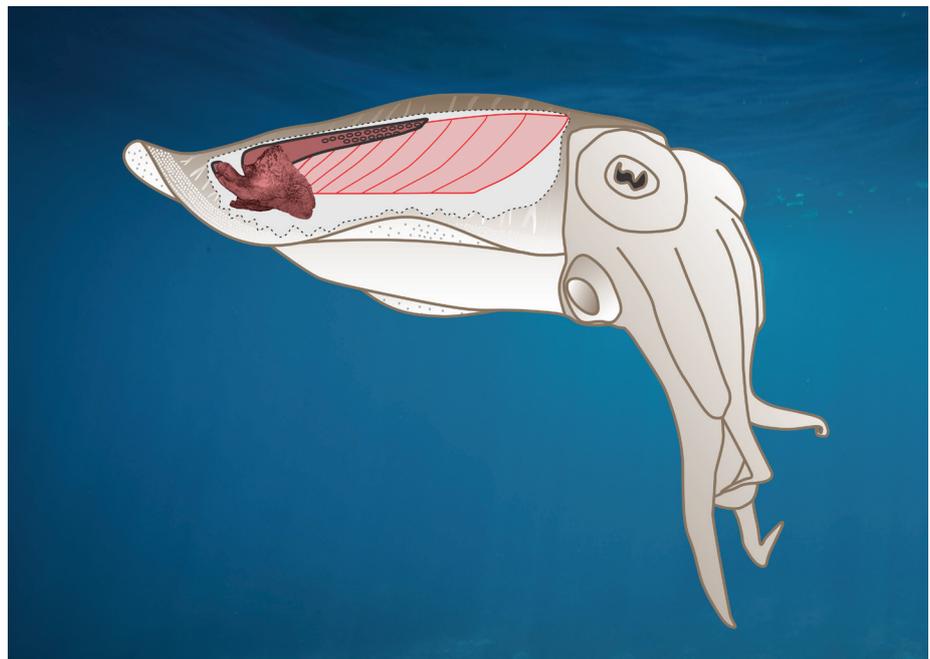


Fig. 4 - Terminology of the *Belosaepia* skeleton. (Images are screenshots of a 3D-rendering from a micro-CT scan with a very high signal-to-noise ratio of specimen IRSNB 0385. This is a syntype of *Belosaepia proxima* Vincent, 1901 (as *Belosepia proxima*, p. 16, pl. 2, figs 8-10), from the Wemmel Sand Member, Maldegem Formation, Lutetian, Belgium).

recorded from two sites at Ronse (Renaix), in deposits with *Nummulites planulatus* (now *N. involutus*; see Baccaert 2017). Delvaux (1885a,b: 70 and 52 respectively) lists *B. tricarinata* in the Waayenberghe section, and Delvaux (1885c,d: 86 and 76 respectively) *B. sp.?* in a section close to the Muziekberg.

In addition to Delvaux's (1885a,b) record, Vincent (1901: 10) also mentioned *B. tricarinata* from the 'Ypresien' of Gaasbeek, Neerpede and Sint-Joosten-Noode (Saint-Josse-ten-Noode). He also gave detailed descriptions of a series of specimens in his personal collection; three from Belgium, one from

Fig. 5 - Hypothetical reconstruction of the *Belosaepia tricarinata* animal.



France (Cuise-la-Motte) and another from England (Sheppey). Two of the Belgian specimens and the one from Sheppey were figured (pl. 1, figs 12-13, pl. 1, figs 14-15 and unnumbered text-fig. on p. 12, respectively). All three Belgian specimens are in the collections of the RBINS (Invert-9219-0057 from Gaasbeek, and IRSNB 7687 and IRSNB 7688 from Sint-Joost-ten-Noode), along with two specimens from Cuise-la-Motte (in lot Invert-9219-0117). One of the latter two is probably the one mentioned in the text (op. cit, p. 11). We were unable to find the specimen from Sheppey in the RBINS collection.

Two additional *Belosaepia* specimens (Invert-23093-0001) were collected by RBINS staff from beds with *Nummulites planulatus* (now *N. involutus* Schaub, 1951; see Baccaert 2017) during an exploration mission in the 'Avenue du Globe' at Vorst (Forest) in 1964. These beds can with certitude be assigned to the middle part of the Mons-en-Pévèle Sand Formation (base NP12). Most probably, the specimens from Sint-Joost-ten-Noode and Ronse are from the same stratigraphic unit, as it is, with less certainty the recorded occurrence at Neerpede. For the specimens from Sint-Joost-ten-Noode, which are refigured here in Fig. 6A-L and Fig. 7A-P, additional confirmation for their middle Ypresian age comes from the micro-CT imaging. This allowed us to determine the presence of some well-preserved *Nummulites involutus* in the small amount of sediment still attached to specimen IRSNB 7687 (Fig. 6J). Many more are present both individually and in clusters in the friable sandstone of specimen IRSNB 7688 (Fig. 7G, K, O-P). In the Belgian Ypresian, the occurrence of these larger foraminifera is restricted to certain stratigraphic intervals, related to two successive immigrations. The first, from the south, occurred during the upper part of NP11 and lasted until the middle of NP12 (dominated by *N. involutus*), and corresponds with the Mons-en-Pévèle Sand Formation. The second immigration occurred during the upper part of NP12 (predominantly *N. aquitanicus* Benoist, 1889) and corresponds with the Egem and Panisel members of the Hyon Formation (King 2016; Baccaert 2017).

- 'Panisélien'. *B. sepioidea* was reported by Houzeau de Lehaie (1874: 557) from the 'Panisélien' of the Mont-Panisel at Mons, co-occurring with *Nummulites planulata* in clayey sand, now classified as the Mont-Panisel Sand Member. They were also noted by Vincent (1876) from the 'Panisélien'

of Anderlecht. Additional records of *Belosaepia* come from the section of Beaufaux, and are listed as *Belosepia* sp.? (Delvaux 1885a,b: 74 and 59 respectively). Specimens listed as *Belosepia* sp.? (Mourlon 1881: 159) are noted from the 'Panisélien inférieur' along the left bank of the Senne river in Brussels. Again, none of these specimens were figured or found, even though many other cephalopods of Beaufaux from Delvaux's collection are in the paleontological collections of the RBINS (SG pers. obs.). Vincent (1901) stated that he only had two specimens from the 'Panisélien', one from Anderlecht and one from Gitsberg, which he identified as *B. tricarinata* and of which only one was figured (op. cit. pl. 1, fig 16). Unfortunately, the legend of plate 1 does not give the locality details. Even more unfortunate, this specimen was not in the cohort of the type and figured specimens of the paleontology collections of the RBINS, and no specimens from the 'Panisélien' of Anderlecht, Gitsberg and the Mons or Brussels area were found in the general collections in a whole, or within the collection of E. and G. Vincent (IG 9219). The personal collection only entered the RBINS on July 29th, 1929, thus long after Vincent's monograph of 1901. Vincent (1901) clearly referred all Belgian 'Panisélien' records to *B. tricarinata*. According to the original data, with exception of the record from Gitsberg, all these came from the Mont-Panisel Sand Member. The latter represents the uppermost part of the Hyon Sand Formation and the top of nannofossil zone NP12 (subzone VIIIb of Steurbaut 1998), dated as upper middle Ypresian (Steurbaud 2011) (Fig. 3). At Gitsberg, the Mont-Panisel Sand Member is not present, and the beds occurring below the Quaternary cover are assigned to the Pittem Clay Member (Gentbrugge Formation, NP 13, upper Ypresian) (Fig. 3). This member has a glauconiferous base rich in reworked fossils, called the Hooglede Sandstone bed (Steurbaud et al. 2016: 53), so that it remains unknown from which level within the Ypresian Vincent (1901)'s specimen may have originated.

To conclude, nearly all previously published *Belosaepia* occurrences from the Belgian Ypresian were referred to as *Belosaepia tricarinata*. This species was introduced by Watelet in 1851 (p. 15, pl. 2, figs 27-29) though named *Sepiostera tricarinata*, based on fossils from the unit in which it was found, the 'sables inférieurs - groupe n°2', that crops out

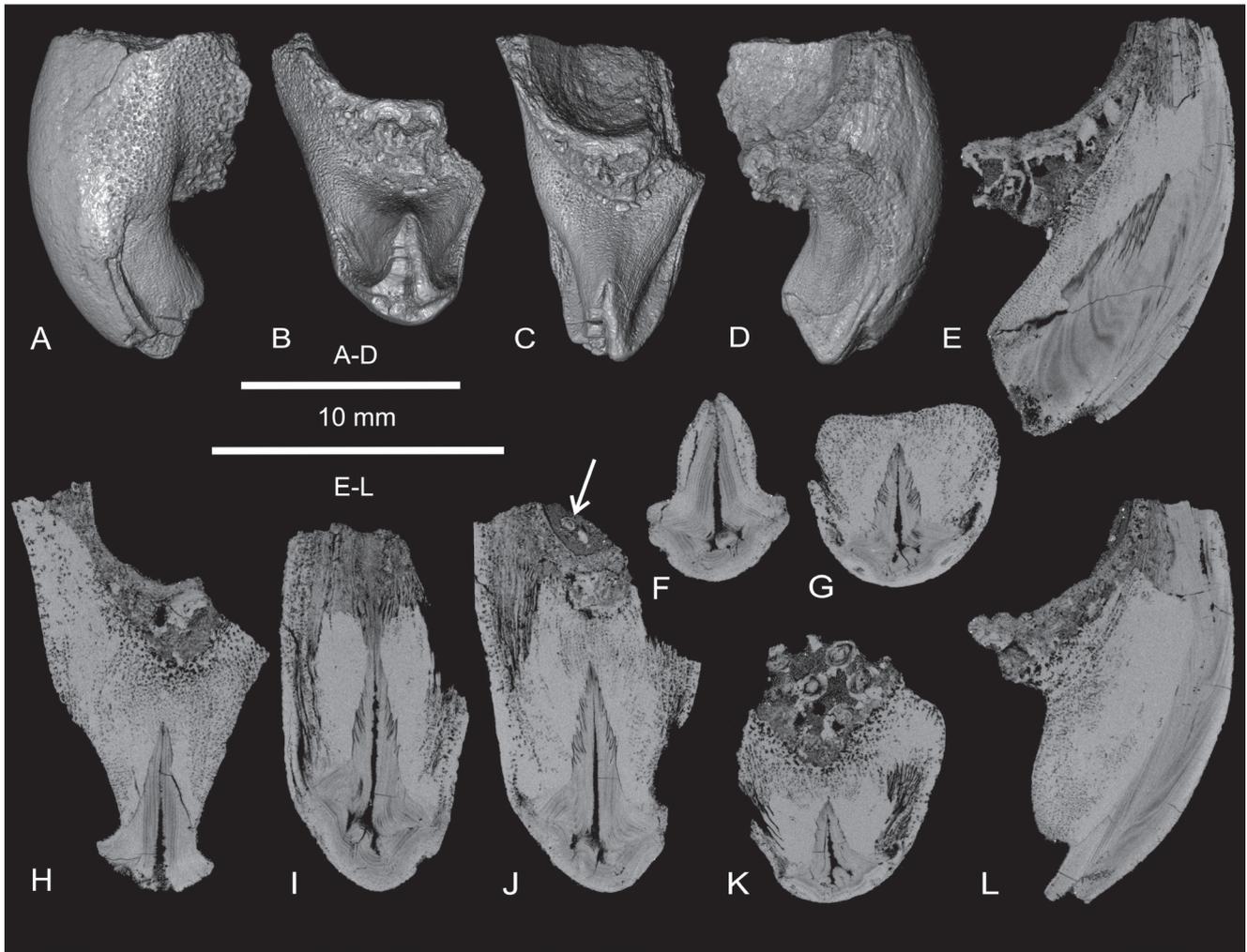


Fig. 6 - Different views of specimen IRSNB 7687, the specimen figured by Vincent (1901) on pl. 1 figs 12-13. A-D) Surface renderings. E-L) Virtual sections along X-Y (H-J), Y-Z (F-G, K) and X-Z (E, L) planes.

at Pommiers and Vauxbuin in the Soissons area (France). Additional description and figurings of this species were given by Deshayes (1865: 616, pl. 106, figs 13-16). By the time of Vincent (1901), the species was already additionally known from the 'sables inférieurs' of Aizy, Coevres, Hérouval, Cuise, Thury-sous-Clermont and Pierrefonds in France (regrouped into the Cuise Formation by Aubry et al. 2005), and from the 'argile de Londres' of Sheppey and Highgate. All these units are mid-Ypresian in age. Although the species is easily recognizable (*dixit* Deshayes 1865), some early authors have clearly confused it with *B. sepioidea* or *B. sepioidea* var. *blainvilliei* Edwards, 1849 (see also Vincent 1901 for discussion). Evidently, the figures of Watelet (1851) were far from ideal and left room for confusion. However, the species name is a giveaway and refers to the proximal end of the prong having two shortly ex-

tending ventrolateral carinas next to the main dorsal carina. These three carinas make it easy to separate younger representatives of *Belosaepia* such as *B. sepioidea* from *B. tricarinata*.

The historical records - a review of their taxonomy

The majority of previously published specimens from the Ypresian of Belgium cannot be reassessed at a species level due to the absence of detailed descriptions and/or figures, or from the absence of the fossil remains themselves. Therefore, these records can only be cited as possible occurrences of *B. tricarinata*. The same holds true for Vincent's (1901) record of *B. tricarinata* of the 'Panisellen' of Anderlecht and Gitsberg. The only figured specimen of these two localities (Vincent (1901), pl. 1, fig 16) is a cast from an external cast, which

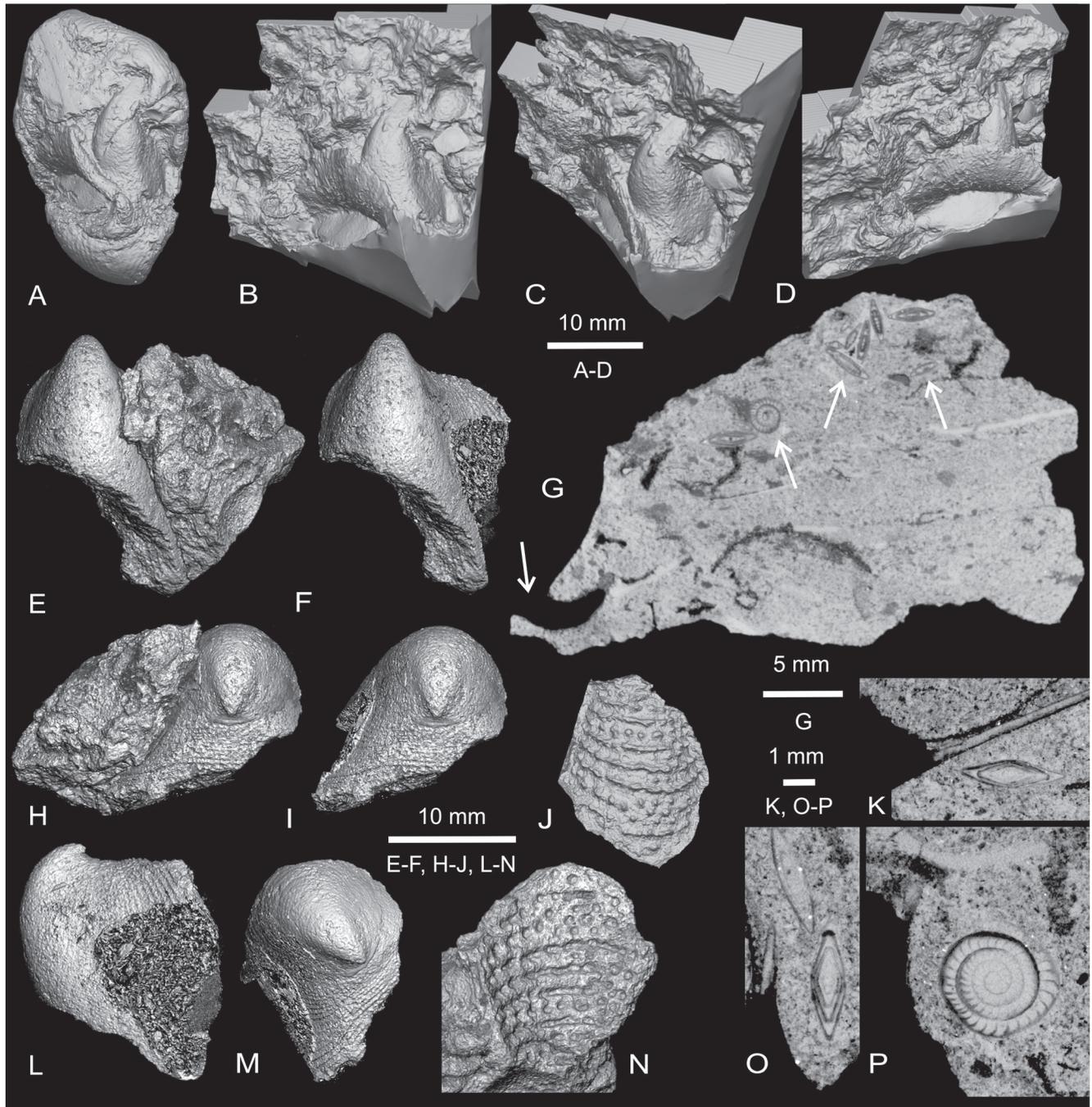


Fig. 7 - Different views of specimen IRSNB 7688, the specimen figured by Vincent (1901) on pl. 1 figs 14-15. A-D, G) Guard. A: Screenshot of a 3D-model of the cast of Vincent (1901). B-D: Screenshot of a new 3D-model made digitally from the external cast. G: Virtual section through the external cast (downward facing arrow) and several *Nummulites involutus* fossils (upward facing arrows). E-F, H-I, K-M, O-P) Phragmocone. E-F, H-I, L-M: Surface renderings of the sediment cast of the phragmocone, before (E-H) and after virtual preparation (F, I, L-M). J, N) Dorsal shield. J: Screenshot of 3D-model of the external cast. N: Surface rendering of the external cast in sandstone. K, O-P: Virtual sections through a single well-preserved specimen of *Nummulites involutus* fossil hidden in the sediment cast of the phragmocone. Scale bars: 10 mm (A-D, E-F, H-I, L-M), 5 mm (G), 1 mm (K, O-P).

only preserves parts of the conotheca and the guard. From the published figure alone, it is impossible to confidently affirm or reject Vincent's (1901) assignment to *B. tricarinata*.

The specimen from the 'Assise supérieure de l'Ypresien' of Sint-Joost-ten-Noode figured by Vin-

cent (1901: pl 1, figs 12-13) (IRSNB 7687, refigured here on Fig. 6A-L) is a fragmentary part of the calcified prong. It is tricarinate so it can be positively assigned to *B. tricarinata*. The other specimen from Sint-Joost-ten-Noode figured by Vincent (1901: pl. 1, figs 14-15) (IRSNB 7688, refigured here on Fig.

7A-P) actually consists out of two casts, taken from external casts in two blocks of friable carbonate-cemented sandstone. An additional element, a sediment cast of a phragmocone, was found stored with these two blocks in the same box. However, it remains uncertain if these three parts belong to the same specimen, as attempts to confidently reassemble the parts failed, possibly due to the deterioration of the joints over time. Despite this ambiguity, the casts illustrated by Vincent (1901: pl. 1, figs 14-15) clearly figure the side of the prong and the corona, and a part of the dorsal shield, respectively. The imprint of the side of the prong suggests it belongs to the species *B. tricarinata* but there is no certainty. A more complete digital cast of the guard was made from the image stack obtained from the micro-CT imaging of the original sediment block (compare Fig. 7B-D with 7A). However, this did not provide additional data on the shape of the prong. A virtual 3D-model was also made of the dorsal shield (Fig. 7J), next to renderings of the sediment casts of the dorsal shield (Fig. 7N) and the phragmocone (Fig. 7H-I, L-M). The unfigured specimen from Gaasbeek (Invert-9219-0057) is a minute part of a partly eroded posterior end of a prong evidencing two ventrolateral carinas and a possible assignment to *B. tricarinata*.

The two specimens from Vorst (Invert-23093-0001) are fairly poorly preserved fragments of the prong and are not recognizable to a species.

The newly collected specimens - Egem

The specimens from Egem (Figs 8-11) only preserve the heavily calcified posterior portion of the skeleton, called guard. It has a solid prong, a thin fan-like corona attached to the ventral base of the prong, and a rough dorsal callus located above the protoconch and juvenile portion of the phragmocone. No remnants of the rugose anterior dorsal shield, the phragmocone septa or siphuncle are preserved, even in those specimens where the phragmocone cavity was filled in with sediment (e.g. IRSNB 7691). However, two specimens (IRSNB 7689 and IRSNB 7690) do preserve some remains of the phragmocone conotheca, close to the protoconch, along the ventral walls of the phragmocone (Figs 8L, 9A-D, 10K, N, P-Q). Interestingly, these conotheca remnants have a different reflectance under long UV light than the walls of the phragmocone cavity.

The prongs of the Egem specimens have large, thick bases that are semi-ovoid shaped along the ventral side and flattened on the dorsal side. The prongs are also long and strongly curved along their length on the ventral side. On the dorsal side, the posterior part projects at a greater angle than the anterior section. In cross-section, the posterior part is first somewhat triangular, then the dorsal carina develops, and two additional carinas develop near the posterior end of the prong. The latter are positioned in a more ventral than central or dorsal position, hence these are ventrolateral carinas. Some folds and grooves developed on the ventral surface of the proximal end of the prong in specimen IRSNB 7689. In the largest specimen (IRSNB 7691), the proximal end of the prong is incomplete. None of the specimens of the lot have a well-developed fissure plane along the outside of the specimen.

The corona has a rounded posterior outline, which evolves from a semi-circular to a more rounded V-shape during growth. IRSNB 7689 has the best-preserved corona. All these characters confirm the assignment of the Egem specimens to *B. tricarinata*.

The newly collected specimens - Marke

The specimens from Marke (Figs 12-14) are much less complete than those from Egem. IRSNB 7694, the smallest of them, has a prominent tricarinate shape of the prong. IRSNB 7692 has a very thick prong base that is flanked by the remnants of two shoulders. The same is true for IRSNB 7693. The Marke specimens can therefore also be assigned to *B. tricarinata*.

Parts of the phragmocone conotheca are preserved in IRSNB 7693 and IRSNB 7694, and are located along the walls of the phragmocone (e.g. Fig. 13E-F) and the anterior portion of the corona (e.g. Fig. 13J). The preservation of these delicate features indicates the specimens were not transported over considerable distances or reworked from older deposits. Additionally, evidence of bioerosion in all three specimens (Figs 12-14) supports this and suggests that the specimens must have resided for some time on the seafloor prior to burial. Given the fragile nature of the specimens, it is likely that the incompleteness observed is a result of the collection method (i.e., sieving) rather than taphonomic processes.

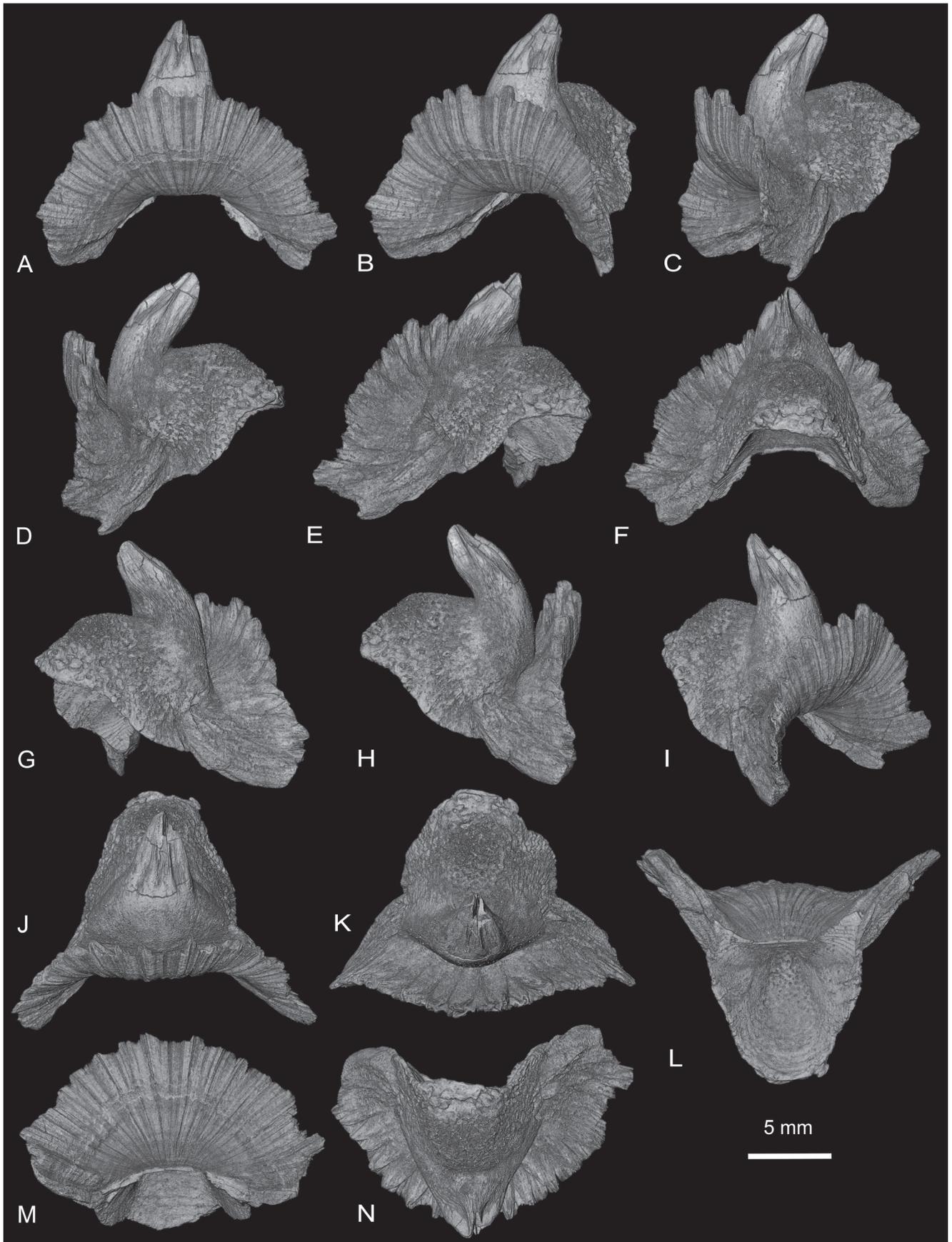


Fig. 8 - *Belosæpia tricarinata* from the base of the Egemkapel Clay Member at Ampe quarry at Egem, specimen IRSNB 7689. A-N) Surface renderings.

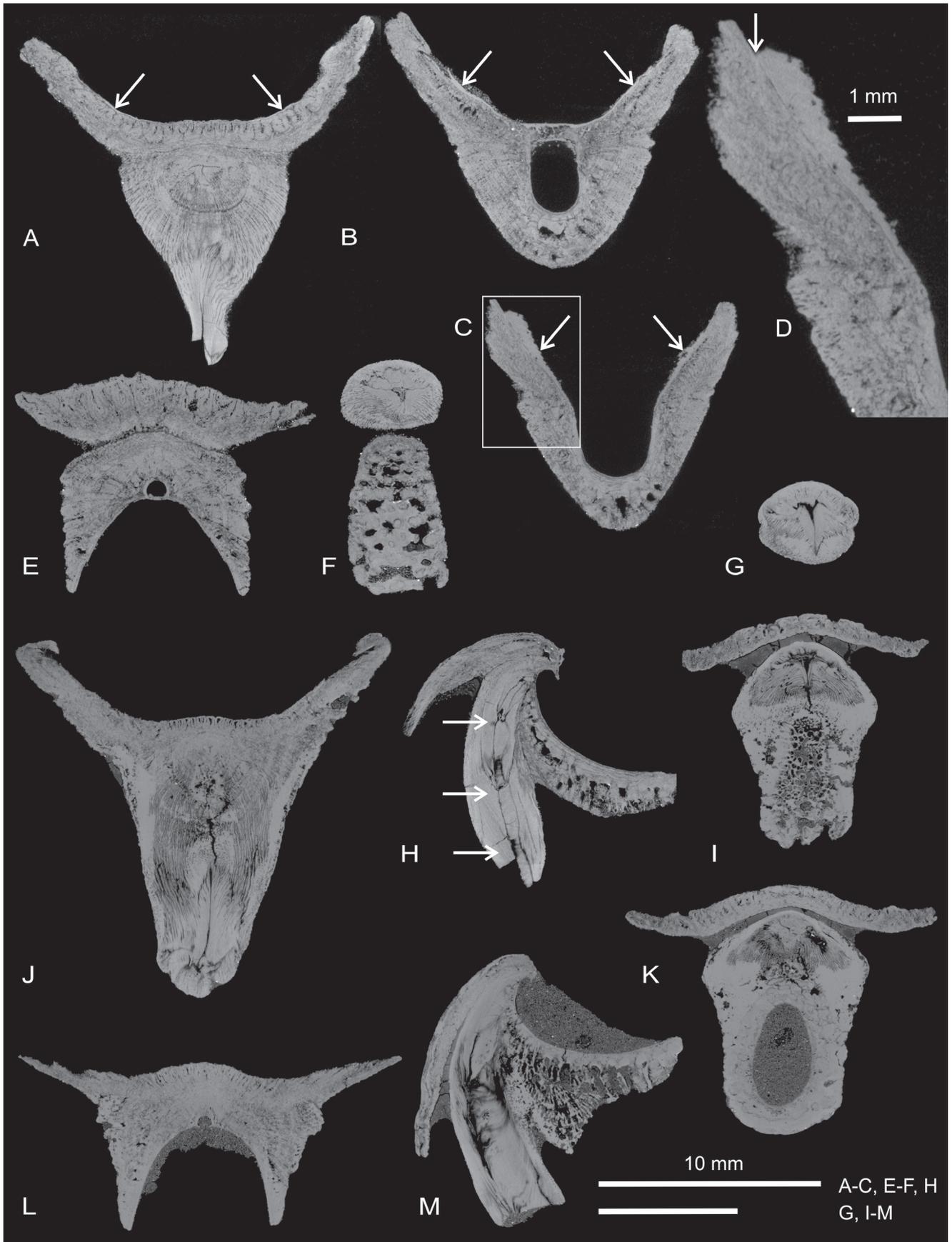


Fig. 9 - *Belosaepia tricarinata* from the base of the Egemkapel Clay Member at Ampe quarry at Egem, specimens IRSNB 7689 (A-F, H) and IRSNB 7691 (G, I-M). A-M: Virtual sections along X-Y (A-D, J), Y-Z (E-I, K-L) and X-Z (H, M) planes. D: Enlargement of rectangle of C.

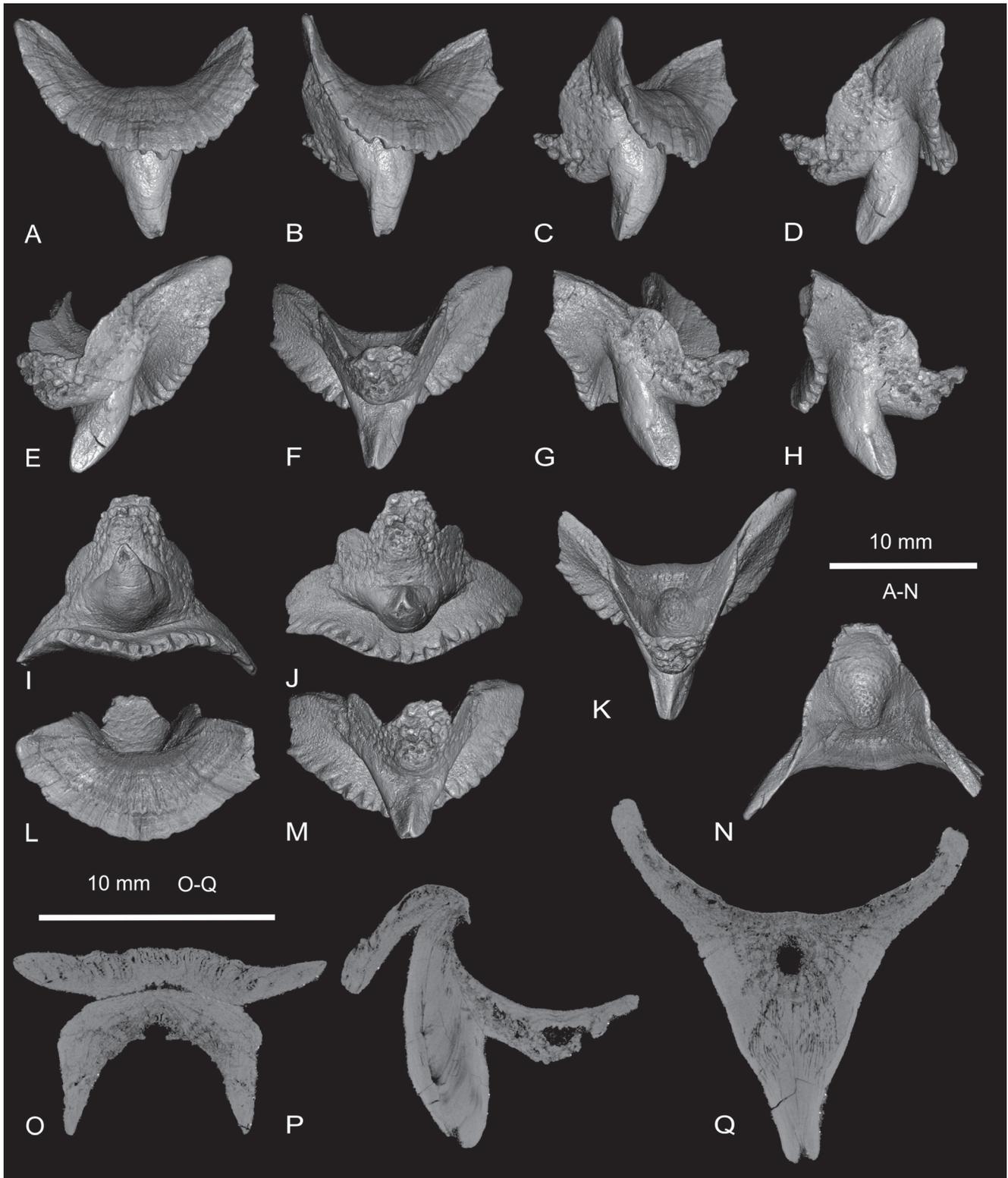


Fig. 10 - *Belosaepia tricarinata* from the base of the Egemkapel Clay Member at Ampe quarry at Egem, specimen IRSNB 7690. A-N) Surface renderings. O-Q) Virtual sections along X-Y (Q), Y-Z (O) and X-Z (P) planes.

Discussion – Micro-CT imaging, a remarkable tool for analyzing *Belosaepia* fossils

The non-invasive and non-destructive character of high-resolution X-ray computed tomography

(micro-CT) offers significant new opportunities in paleontological research (Cunningham et al. 2014). A decade ago, micro-CT imaging was very expensive and only executable on a very limited number of

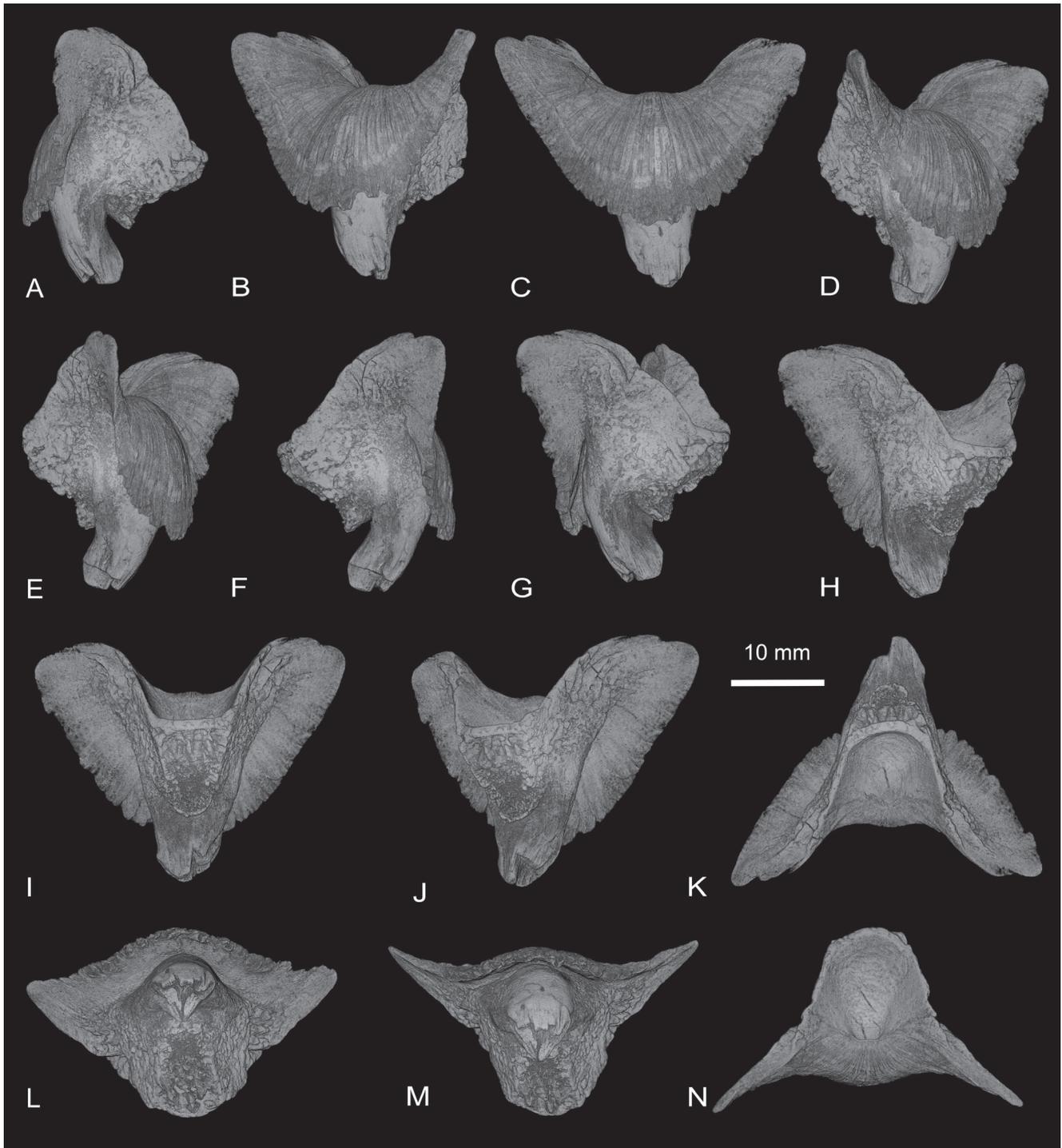


Fig. 11 - *Belosaepia tricarinata* from the base of the Egemkapel Clay Member at Ampe quarry at Egem, specimen IRSNB 7691. A-N) Surface renderings.

specimens. Today, with ongoing large scale digitization efforts including micro-CT imaging by an ever-growing number of taxonomic facilities across the world (e.g. RBINS, part of the European DiSSCo consortium), micro-CT imaging data are becoming accessible on a much larger number of specimens and taxonomic groups and increasingly accessible

to a wider group of researchers than ever before.

Within invertebrates, micro-CT imaging offers fantastic opportunities especially in the study of fossil cephalopods (see e.g., Hoffmann et al. 2018; Inoue & Kondo 2016; Kruta et al. 2011; Lemanis et al. 2015, 2016; Tajika et al. 2015, 2020; Tajika & Klug 2020). Given the near absence of soft-tissue

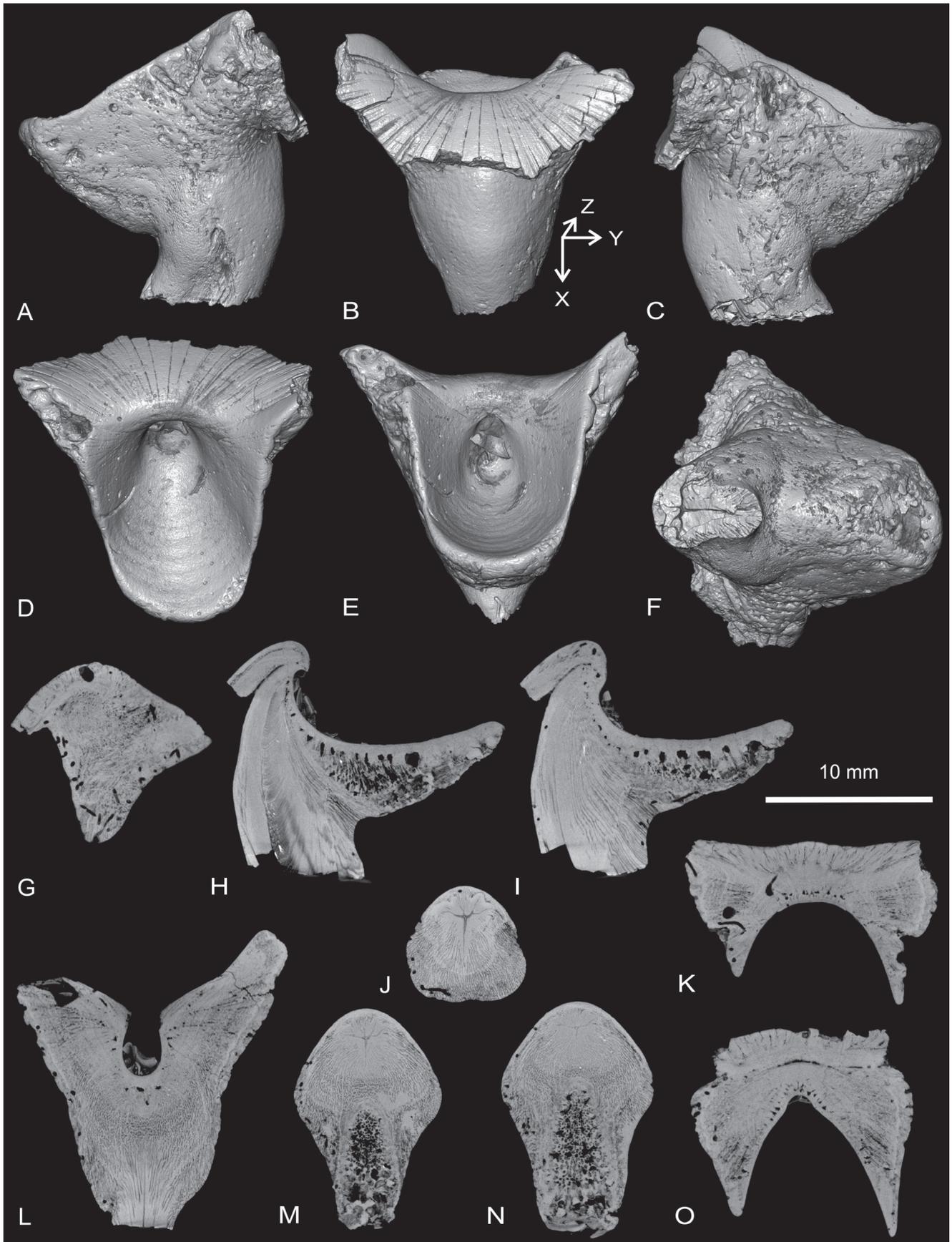


Fig. 12 - *Belosaepia tricarinata* from the Roubaix Clay Member at the Koekelberg quarry at Marke, specimen IRSNB 7692. A-F) Surface renderings. G-O) Virtual sections along X-Y (J, K, M-O), Y-Z (L) and X-Z (G-I) planes.

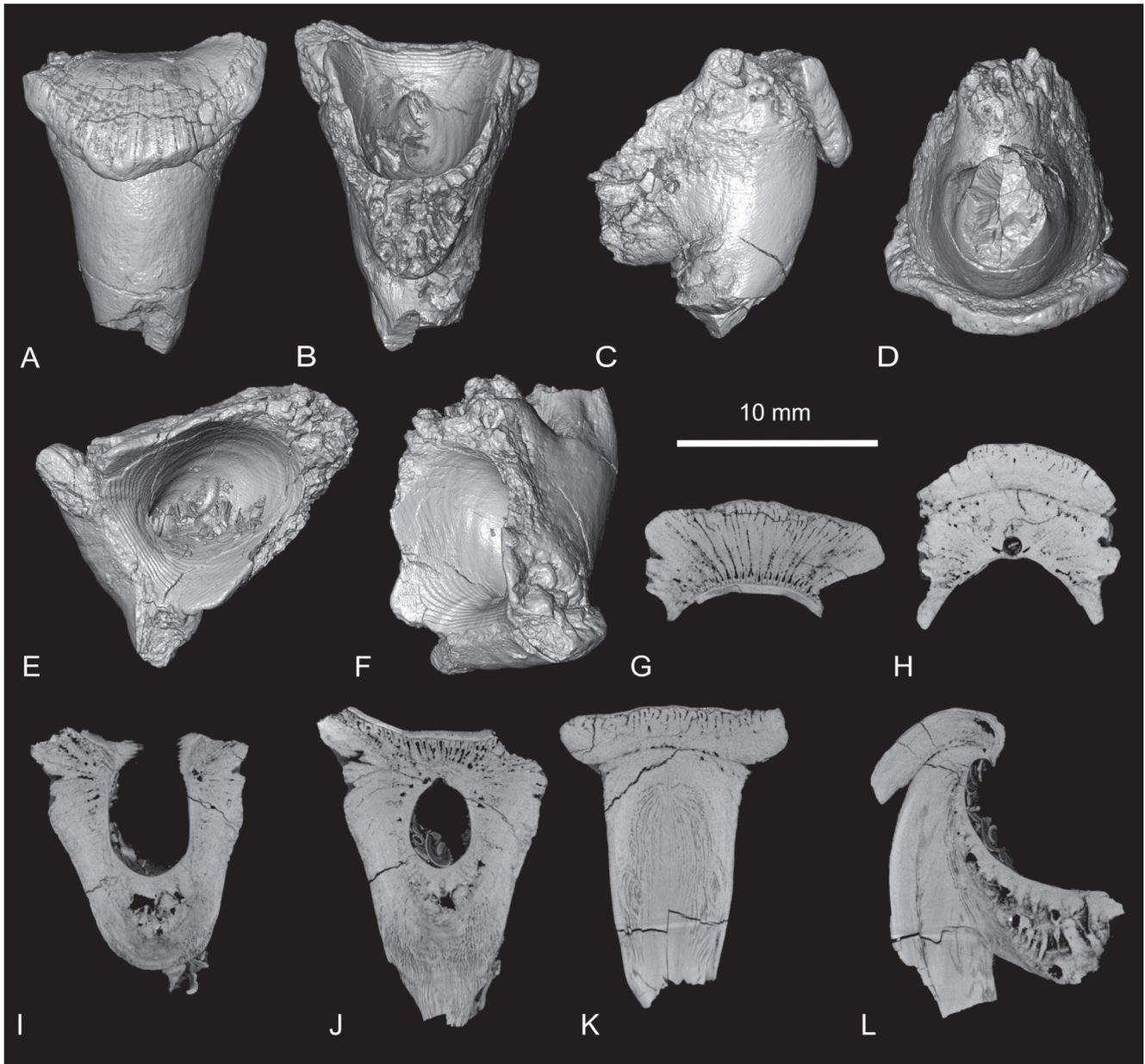


Fig. 13 - *Belosaepia tricarinata* from the Roubaix Clay Member at the Koekelberg quarry at Marke, specimen IRSNB 7693. A-F) Surface renderings. G-L) Virtual sections along X-Y (I-K), Y-Z (G-H) and X-Z (L) planes.

preservation, nearly all that remains from the cephalopod animal are remnants of the calcified buoyancy device, which is a complex 3D shaped structure. For fossil sepiids, and *Belosaepia* in particular, it is composed of multiple layers of CaCO_3 spread across a calcified posterior guard, a rugose anterior dorsal shield and a phragmocone with conotheca, septa and siphuncle. In the majority of the *Belosaepia* fossils found, only parts of the heavily calcified guard are preserved, and therefore, the established taxonomy is almost exclusively based on the readily visible peculiarities of the outer shape and surface

of this guard. The large majority of *Belosaepia* taxonomy is rooted in 19th and early 20th century work. Many species may not be valid as they were assigned based on possibly invalid characters, leading many recent authors to suggest a much-needed revision of nearly all the previously described species (e.g., Riegraf et al. 1998; Yancey et al. 2010; Košťák & Hoşgör 2012). It is in the context of this revision that micro-CT imaging may become a highly useful problem-solving tool.

One of the major pitfalls for *Belosaepia* taxonomy are the possible major changes throughout on-



Fig. 14 - *Belosaepia tricarinata* from the Roubaix Clay Member at the Koekelberg quarry at Marke, specimen IRSNB 7694. A-F, H-I) Surface renderings. G, J-P) Virtual sections along X-Y (J, L, O), Y-Z (M-N) and X-Z (G, K, P) planes.

togeny of the outer surface of the guard, not least in the adult stage when resorption may become more important than skeletal secretion. Yancey et al. (2010) documented the nearly complete resorption of the corona in the latest growth stage of *Belosaepia unguia*, a species from the Bartonian of Texas (USA). They listed several characters that may help identifying the presence of resorption in a specimen, such as truncation of growth lines on the outer surface of the skeleton. However, resorption is a 3D phenomenon and its presence or absence, as well as its intensity, cannot be fully assessed looking at the outer surface alone.

Micro-CT imaging allows us to make an infinite number of (virtual) cross-sections in any pos-

sible direction through the specimen. It therefore has the potential to become an important tool that enables to inspect, visualize, and quantify ontogenetic changes in taxonomically important parts of the skeleton, as well as enabling a much better inspection and quantification of the amount of resorption present throughout the guard. In addition, its non-destructive character is of particular importance for the re-examination of type specimens and other delicate specimens.

Figure 9H reveals one of these virtual cross-sections, through the prong of specimen IRSNB 7689. It allows us to identify at least three interruptions in the growth bands (approximately after 2.3, 2.9 and 3.2 mm, respectively (measured along the

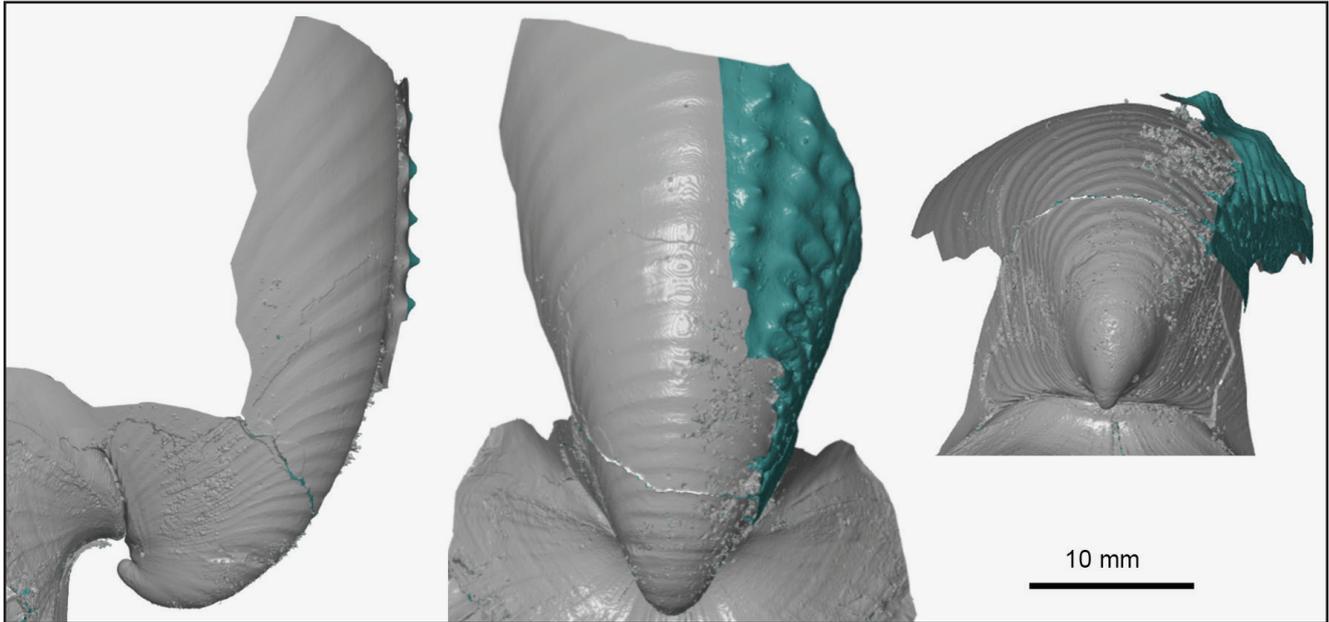


Fig. 15 - Screenshots of a 3D model of the phragmocone cavity allowing a better visualization and identification of the ontogenetic changes in size of shape of the phragmocone chambers, starting from the protoconch. 3D model made from the same specimen as figured in Fig. 4.

median line of the prong), possibly resulting from three cycles of growth plus a fourth ongoing one with additional resorption. This may represent yearly growth halts, which would corroborate the three-to-four-year life span of *Belosaepia* animals previously suggested in literature (e.g. Yancey et al. 2010), a life span that is similar to that of many extant sepiids (von Boletzky 1983). However, IRSNB 7689 is the smallest specimen of the three figured Egem specimens, implying a much longer presumed lifespan. In addition, similar growth halts with clear evidence of resorption were not recognized in the other specimens studied. While counting growth bands was easy in some parts of the prong, it was especially difficult to execute in its earliest ontogenetic part. Growth bands were more readily recognizable in the specimens from Marke than in those from Egem. In IRSNB 7689, 12 (or 13) growth bands were recognizable between the 1st and 2nd identified growth halts, and 16 bands were identifiable following the 2nd halt. In IRSNB 7692, IRSNB 7693 and IRSNB 7694, at least 95, 90 and 60 growth bands were counted, along a trajectory across the median line of the prong of 12.1, 13.2 and 8.2 mm respectively. It is currently unknown how much time a growth band represents. In extant sepiids like *Sepia officinalis*, the time necessary to add another layer of carbonate seems to not only depend on biological and environ-

mental factors, but also on which carbonate structure is concerned (Chung et al. 2020). For example, statoliths are thought to grow daily (Bettencourt & Guerra 2001), while cuttlebone lamellae take longer, with faster growth in summer than winter and differing growth rates throughout ontogeny and during periods of migration or reproduction (Bettencourt & Guerra 2001; Chung et al. 2020). For *Sepia officinalis*, a mean of 1.75 days for adding one additional lamella was calculated, but for other species, this mean seems to differ (Chung & Wang 2013; Chung et al. 2020). With at least 95 bands observed in IRSNB 7692, the life span of the *Belosaepia* fossils studied was at least 3.5 months in the ‘one-band-a-day’ scenario, more than 6 months in a scenario mimicking the lamellae of *Sepia officinalis* or more than one year if the number of growth bands correspond with the number of interstreaks on the cuttlebone’s surface (see Le Goff et al. 1998). Contrary to extant *Nautilus* which has a longevity of 20+ years, almost all extant, and thus presumably also fossil, Coleoidea share the same ‘grow fast die young’ strategy (Landman & Cochran 2010; Dunstan et al. 2011; Hoffmann & Stevens 2020). However, without isotope studies identifying seasonality, it is currently impossible to make funded statements on the life span of belosaepiids.

The virtual cross-sections also allow us to identify otherwise undetectable microfossils that

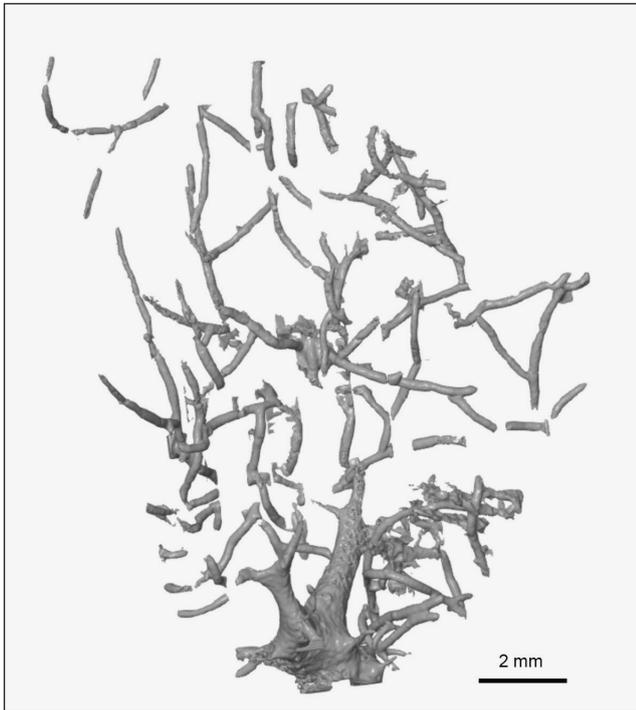


Fig. 16 - Screenshots of a 3D model made from the borings in the guard of specimen IRSNB 7692 from the Koekelberg Quarry at Marke, Belgium. Two different sets of borings can be identified. One boring is characterized by branching tubes with small diameters (170-190 μm). These are mostly more or less straight, though more curved ones are also present. These can be identified as *Talpina ramosa* von Hagenow, 1840, a bioerosion trace well-known in other cephalopod hard parts like belemnite rostra (Wisshak et al. 2017). The second is comprised of irregular tubes (diameter in the range of 0.5 mm) radiating from a single chamber and can be identified as the bioerosion trace *Entobia* isp.

are hidden in associated sediment. This aids in the reevaluation of the stratigraphic intervals of specimens originally described in the 19th and 20th centuries (e.g. those of Vincent 1901) for whom these data have been lost.

An additional bonus is that, at least when a high signal-to-noise ratio was obtained, very high-quality surface photographs of the specimens can be produced directly from the 3D renderings of the 2D image stack (e.g., Figs 4, 7E-F, H-I, L-N, 8A-N, 10A-N, 11A-N, 12A-F, 13A-F, 14A-F, H-I). A big advantage of this method is that the specimen can also be virtually cleaned of residual sediment (e.g. in the phragmocone cavity) preventing the destruction of highly delicate remains of phragmocone chambers and/or siphuncle.

Through segmentation, 3D-models can be made, not only of the specimens themselves, but virtual casts can also be extracted, which tend to

be more complete than their physical counterparts (compare Vincent's 1901 cast of the guard in Fig. 7A, the basis for his drawing on his pl.1 fig. 14, with the new virtual cast in Fig. 7B-D). This method can be used to make informative virtual models of the juvenile parts of the belosaepiid phragmocone (Fig. 15). Also, while traces of bioerosion are visible on the external surface of specimen IRSNB 7692 (Fig. 12C-D, F) and observable in the virtual cross-sections (Fig. 12G, I-K, L), their true extent becomes much more visible in a 3D model (Fig 16), and allows us to discriminate two different sets of borings.

Micro-CT imaging also has a set of limitations. First, scan results must have a high signal-to-noise ratio, as well as a sufficiently high contrast in density between the objects to be studied. Both of these requirements were fulfilled in the scans of the specimens from Egem and Marke and those of Vincent (1901), as well as for an additional number of scans of other *Belosaepia* species from other Belgian localities of Lutetian age. Second, there are limitations to the obtained resolutions. For the specimens studied here, voxel sizes of 11-20 μm gave good results and allowed us to observe many growth bands. However, for some detailed studies on the microstructure, resolution needs to be much higher. Therefore, micro-CT imaging cannot fully replace conventional (and thus destructive) thin sectioning, nor SEM or TEM imaging.

Unlike thin sections or serial grinding (e.g. Naglik et al. 2015), micro-CT only exports in intensities of grey. As such, it does not preserve the color information like the more destructive methods. One of the largest benefits of executing micro-CT imaging prior to any destructive sampling, is that the results of these analyses can be placed in a full 3D context.

CONCLUSIONS

The major conclusions that can be drawn from this study are:

1. Micro-CT imaging proves to be an excellent tool for investigating the calcified remains of the *Belosaepia* skeleton and allows an infinite number of virtual cross-sections in any possible direction through the specimen without damaging it. Growth lines can be easily identified and traced in

three dimensions, enabling us to inspect, visualize and quantify ontogenetic changes, which allow for precise taxonomic assignments and discussions on the estimation of the age and longevity of individual specimens. The high signal to noise ratio of the obtained scanning results also allows us to produce high-quality surface images of the guards. In addition, micro-CT imaging permits recognition of stratigraphically important fossils (e.g. *Nummulites*) in the residual sediment attached to the specimens. This gives further information of the stratigraphical origin in particular for those that were collected a very long time ago.

2. Although this in part reflects collection bias related to limited outcrop conditions, fossilized remains of *Belosaepia* are fairly rare in the Belgian Ypresian. They are currently only known from the basal and middle part of the Mons-en-Pévèle Sand Formation, from the base of the Egemkapel Member of the Tielt Formation and from the Mont Panisel Member of the Hyon Sand Formation. All these records are early middle to late middle Ypresian in age (NP11-NP12). Fossilized remains of species of *Belosaepia* remain undocumented from the Belgian lower and upper Ypresian.

3. Only a single species, *Belosaepia tricarinata* (Watelet, 1851) was positively identified within these Belgian middle Ypresian deposits. This seems to correspond with the occurrence of the same species in the London, Hampshire and Paris basins, with whom the Belgian basin formed part of the same paleogeographical and paleoecological continuum known as the southern shallow marine extent of the North Sea Basin (Figs 2-3).

4. The newly collected specimens from the Ampe quarry in Egem are by far the best preserved *Belosaepia* specimens as well as the largest single suite of specimens currently known from the Ypresian of Belgium.

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