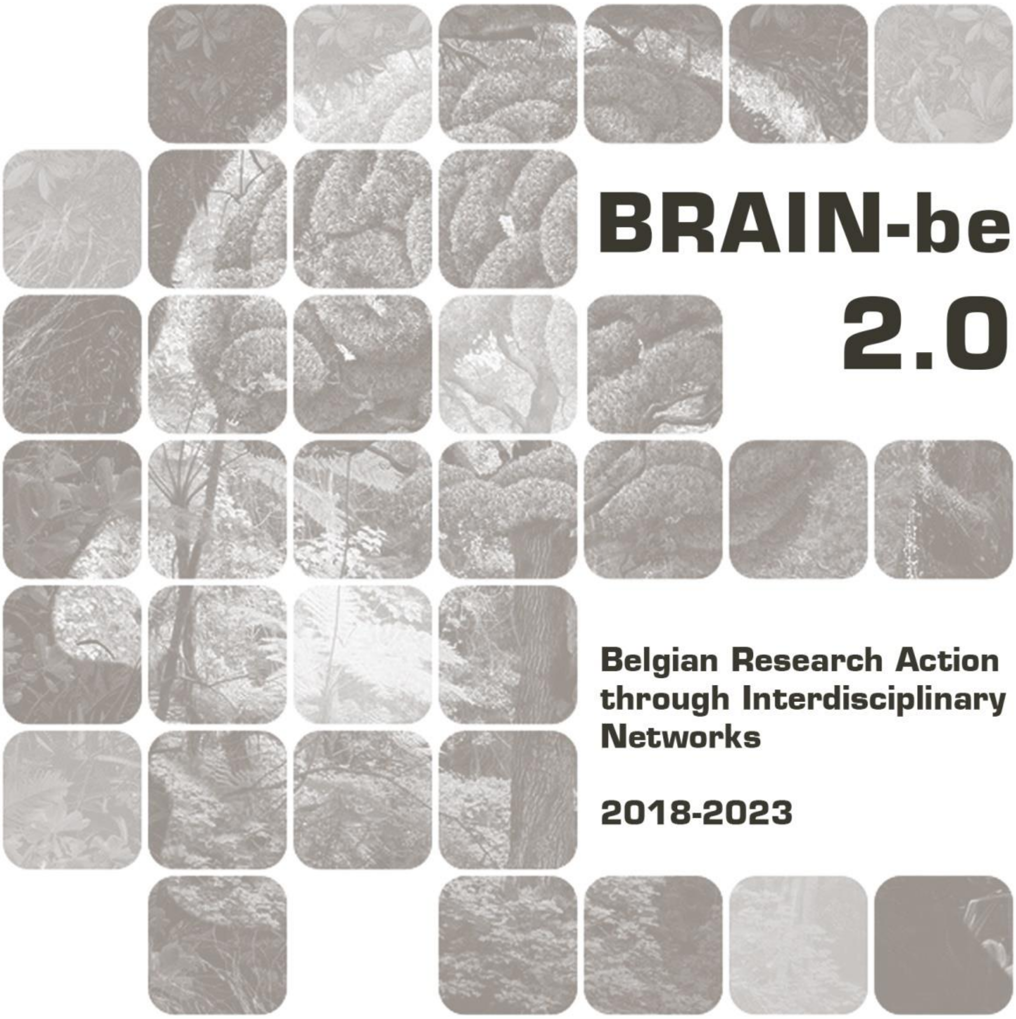

BRAIN-be
2.0

Belgian Research Action
through Interdisciplinary
Networks

2018-2023

CT-CEPH

A fresh look at Devonian, early Carboniferous and latest Cretaceous to Paleogene nautilid cephalopods from Belgium.

Stijn Goolaerts (OD Earth & History of Life (EHL) and Scientific Service of Heritage (SSH), Royal Belgian Institute of Natural Sciences) – Bernard Mottequin (OD Earth & History of Life (EHL), Royal Belgian Institute of Natural Sciences)

Pillar 2: Heritage science

NETWORK PROJECT

CT-CEPH

A fresh look at Devonian, early Carboniferous and latest Cretaceous to Paleogene nautilid cephalopods from Belgium

Contract - B2/192/P2/CT-CEPH

FINAL REPORT

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Published in 202X by the Belgian Science Policy Office
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Goolaerts, S. & Mottequin, B. CT-CEPH - A fresh look at Devonian, early Carboniferous and latest Cretaceous to Paleogene nautilid cephalopods from Belgium. Final Report. Brussels: Belgian Science Policy Office 2025 – 53 p. (BRAIN-be 2.0 - (Belgian Research Action through Interdisciplinary Networks))

TABLE OF CONTENTS

ABSTRACT

CT-CEPH aimed at gaining better insights in the complex evolutionary history of the Order Nautilida (Phylum Mollusca, Class Cephalopoda, Subclass Nautilia), the lineage leading up to the single surviving stock of externally shelled cephalopods alive today, the extant nautilus. It focused on Devonian, early Carboniferous and latest Cretaceous to Paleogene time slices of nautilid history, intervals during which major steps in their evolution occurred that remain incompletely understood, and for which the Royal Belgian Institute of Natural Sciences (RBINS) and Royal Museum for Central Africa (RMCA) collections hold a large number of important specimens. The project exploited the ongoing mass-accumulation of micro-CT scanning data of RBINS and RMCA type specimens (DIGIT & DiSSCo-Fed projects), combined with the knowledge and expertise of RBINS. It also aimed to make a major contribution to the scientific valorization of the collections of the federal scientific institutions by executing innovative research.

CT-CEPH revealed that the Belgian nautilid fauna is exceptionally diverse and well-preserved, both externally and internally, as demonstrated by micro-CT imaging. The project established that the fossil record of the Belgian latest Cretaceous and Paleogene is far more diverse than previously assumed, with a high proportion of formally undescribed or unrecorded diversity. Among the outcomes, the project formally documented for the first time the occurrence of *Angulithes westphalicus*, a nautilid with a remarkable angular whorl section at adulthood, in the Santonian of Belgium. It also led to the identification of the most diverse late Maastrichtian pre-Cretaceous/Paleogene (K/Pg) boundary nautilid fauna known worldwide, comprising four genera and six species, with marked disparity in shell shape, suture and septal morphology, embryo size, and siphuncle position. Furthermore, the work revealed that preservation of soft-tissue structures of the siphuncle is far more common than generally assumed. The project reported on two nautilids with notable historical context and demonstrated that the CT-CEPH methodology can be successfully applied to other cephalopod groups such as sepiids.

The early Carboniferous record in Belgium clearly illustrates the explosion in nautilid taxonomic and morphological diversity, and that even more taxa are to be described, like a new species of the genus *Temnocheilus*, represented by the largest specimen of the genus known to date. The project also reported on putative cephalopod eggs from the Belgian Carboniferous. Devonian Nautilida were found to be absent; all previously cited records were refuted.

The project underscores the significant potential of integrating novel analytical techniques with traditional paleontological approaches. Throughout, the application of micro-CT imaging proved pivotal in the 2D and 3D non-invasive examination of fossil material, and the outcomes have set a standard, micro-CT will henceforth be an indispensable component of cephalopod research.

1. INTRODUCTION

X-ray computed tomography (CT-) scanning is completely revolutionizing the study of extinct organisms. Its non-invasive and non-destructive nature makes it by far the most powerful method currently available for investigating fossils in three dimensions and in unprecedented detail. Crucially, CT-scanning looks through and inside objects, revealing internal (hidden) structures and characters. Recent innovations in the field of CT-scanning allow obtaining unprecedented detail, up to a few micrometers in (voxel) resolution, and higher quality images for relatively dense materials such as fossils, even when entirely encased in a hard sediment.

In 2016, the Royal Belgian Institute of Natural Sciences (RBINS, IRSNB in specimen numbers) acquired two high-end X-ray CT-scanners: the micro-CT RX EasyTom (http://www.rxsolutions.fr) and the nano-CT XRE UniTom (https://xre.be/) (funded via the ‘One Shot’ call by State Secretary E. Sleurs) (Fig. 1). Both instruments are nearly full time in use to help to accomplish the gigantic task of the full digitization of the RBINS and Royal Museum for Central Africa (RMCA) type collections*, the aim of two multi-year Belspo funded projects, DiSSCo-Fed (2018-2023) and DIGIT-4 (2019-2024). With about 300.000 types and 48.000.000 general specimens, 45.000 and 3.000.000 respectively in their paleontology collections, the results of nearly two centuries of intensive collecting and research, the two Belgian Federal Scientific Institutions (FSI’s) are one of the major players in the European framework of scientific research infrastructures for natural history.

One of the groups of fossils that is very well-represented within the RBINS paleontology collections are the Cephalopoda (Phylum Mollusca). Cephalopods are among the most diverse, intelligent and rapidly evolving marine invertebrates that have explored a multitude of evolutionary pathways since their entry point more than 500 myr ago. Their invention of a chambered shell, enabling energy-efficient vertical movement in the water column, distinguishes them from all other mollusks. It is especially the internal organization of this complex three-dimensional buoyancy mechanism that allows to document major steps in their evolution. The latter makes from CT-scanning an extremely powerful method in the study of the evolutionary history of the Cephalopoda. It allows for the first time correct and detailed measurements of typical conch (shell) parameters, as well as the introduction and exploitation of new and/or previously underexplored and (partly) hidden parameters that will induce new insights in their evolutionary processes.

This project focused on the complex evolutionary history of the Nautilida, the lineage leading up to the only extant externally shelled cephalopods: the chambered *nautilus*. It explored the significance of Belgian (and select African) paleontological heritage for understanding key episodes in nautilid evolution during the Devonian, early Carboniferous, and Late Cretaceous-Paleogene. The project capitalized on the ongoing mass-accumulation of micro-CT and nano-CT imaging data of the RBINS and RMCA type collections.

The research made a significant contribution to the scientific valorization of the collections through innovative approaches, in full alignment with the goals of the BRAIN-be 2.0 Pillar 2 program for Heritage Science.

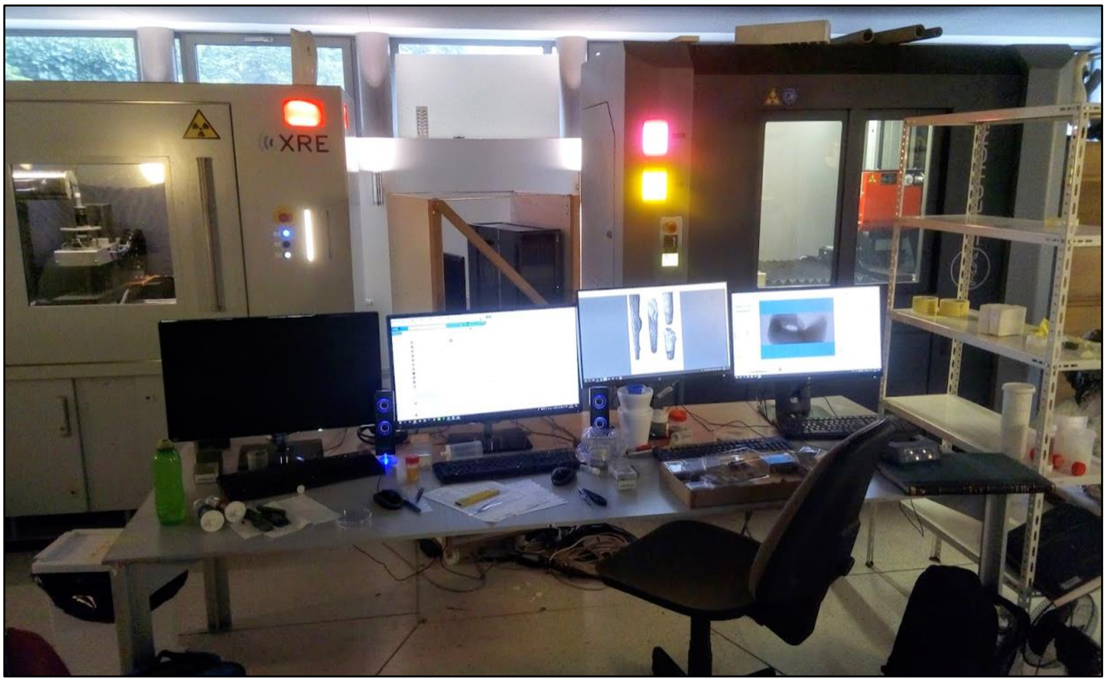


Figure 1. The RBINS X-ray imaging set-up, with two high-end X-ray CT-scanners: the RBINS micro-CT RX EasyTom (http://www.rxsolutions.fr) and the RBINS nano-CT RBINS XRE UniTom (https://xre.be/). Both were funded via the 'One Shot' call by State Secretary E. Sleurs, and operated via two multi-year Belspo funded projects, DiSSCo-Fed (2018-2023) and DIGIT-4 (2019-2024).

[*type specimens are defined as follows: taxonomic types (holotype, paratype, etc.) plus figured and referred specimens, this is, those specimens which have a relationship to earlier published studies and are listed as such in the type specimen catalogs of the FSI's.]

2. STATE-OF-THE-ART AND OBJECTIVES

The core of this project was the study of the evolutionary history of the Nautilida, an order which was traditionally classified within the Subclass Nautiloidea (Dzik, 1984), but major discussion remains on cephalopod phylogeny, in particular on the arrangement of stem and crown groups deep in the Paleozoic (Kröger et al., 2011; Mutvei, 2015; King & Evans, 2019; Klug et al., 2019). The most recent attempt to classify nautiloid cephalopods, proposed as a guide in the revision of the Treatise on Invertebrate Paleontology Part K (Moore, 1964), uses muscle attachment scars, imprints on the inner side of the shell made by the muscles attaching the animal to its shell, as the main criterion for higher level classification. In this scheme, the Nautilida are now the single order of the Subclass Nautilia (King & Evans, 2019).

The subordinal and superfamilial classification within the mainly pleuromyarian Nautilida has a complex history and also still requires further analysis (Dzik & Korn, 1992; Manda & Turek, 2009, 2011, 2019; King & Evans, 2019). Significantly different systematic schemes and approaches were adopted in the past (compare e.g. Ruzhentsev et al., 1962; Teichert et al., 1964; Moore, 1964; Shimansky, 1967, 1975; Teichert, 1988; Shevyrev, 2006; Manda & Turek, 2009, 2011, 2019), and a satisfying consensus is lacking. Muscle attachment scars remain also insufficiently documented within the Nautilida (Miller, 1951; Dzik & Korn, 1992; Klug & Lehmkuhl, 2004; King & Evans, 2019). Major recent modifications to the classification of the Nautilida are the exclusion of the Rutoceratoidea and the establishment of the new Suborder Lechritrochoceratina as basal nautilids [Manda & Turek, 2011, 2019). Within the Meso-Cenozoic Nautilida, many unresolved taxonomical issues at genus and species level add to the classification discussions (Chirat & Bucher, 2006; Ward et al., 2016).

The proper interpretation of the value of external morphology of the shell (mode of coiling, growth trajectory, whorl expansion, ornament, etc.), the early ontology (size and shape of first chamber and embryonic conch, number of chambers, degree of coiling, ornament, etc.), the adaptive values of the buoyancy mechanism (septal spacing, shape and thickness, properties of the siphuncle, etc.) as well as the muscle attachment scars are of crucial importance for the understanding of the taxonomy, diversity, ecology, phylogeny, dispersal and evolutionary history of the Nautilida (Ward, 1980; Dzik & Korn, 1992; Tintant, 1993; Barskov et al., 2008; Manda & Turek, 2019). Many of these characters are fully three-dimensional and not completely exposed, the reason why micro-CT and nano-CT imaging is a powerful method for studying fossil cephalopods (Kruta et al., 2011; Hoffmann et al., 2014, 2018; Lemanis et al., 2015, 2016; Tajika et al., 2015; Inoue & Kondo, 2016; Landman et al., 2017), allowing for a much better measurement, visualization and analysis of these characters, especially for type specimens, where destructive analysis (Naglik et al., 2015, 2016) is not at all an option.

The RBINS-RMCA type collections are of particular importance for the study of nautilid history during Devonian to early Carboniferous and latest Cretaceous to Paleogene times. This is related to the 19th up to midst 20th century works of de Koninck, de Ryckholt, Bosquet, Vincent, Maillieux, Demanet and Miller [e.g. de Koninck, 1838, 1843-1844, 1868, 1878, 1880; de Ryckholt, 1852; Vincent et al., 1913; Maillieux, 1925, 1933, 1940; Demanet, 1941; Miller, 1951), describing many of well-preserved fossils from the exceptionally expanded Belgian stratigraphic record of these intervals, and a smaller but not less important number of Paleogene nautilids from Africa. During these times, major steps in nautilid evolution took place, like their initial (moderate) diversification pulse followed by a near extinction (Devonian), the biggest radiation of their history, reaching an all-time generic diversity high (early Carboniferous) and their survival of the K/Pg boundary mass-extinction followed by dispersal and innovations in their buoyancy apparatus (latest Cretaceous-Paleogene) (Dzik, 1984; Teichert, 1988). None of these steps are fully explored and understood, nor from a taxonomical, diversity, paleoecological or phylogenetical point of view, nor for the factors and forces driving these evolutions [e.g., Miller, 1949; Ward, 1980; Barskov et al., 2008; Landman et al., 2014, 2015). The restudy of the RBINS-RMCA specimens, with the new data obtained from CT-scanning has a high potential to allow furthering our understanding of each of these three major steps in their evolutionary history, in particular due to the combination of large number of well-preserved specimens for the successive time intervals (Goolaerts et al., 2014), the historical importance for the description of nautilid diversity (e.g. many Carboniferous genera are based on species first described by de Koninck) (Histon, 1999) and a higher diversity than in most other parts of the world (latest Cretaceous-Paleogene), making it easier to identify patterns and changes (Goolaerts, 2018).

By combining data obtained from large scale FSI digitization efforts, important Belgian and (some) African paleontological heritage curated by FSI's and interdisciplinary expertise present at the RBINS RU Paleobiosphere Evolution, this project focused on obtaining better insights in:

1) how nautilids survived the K/Pg boundary mass-extinction and radiated afterwards during the Paleogene (this is, during their last surge);

2) how nautilids diversified during the biggest radiation event in their history by taking a 'fresh look' at 'old' Belgian early Carboniferous nautilids;

3) whether nautilids are present in the Belgian Devonian fossil record (this is, the record leading up to the early Carboniferous radiation).

3. METHODOLOGY

The main novel methodology used in CT-CEPH to study nautilid fossils was micro-CT imaging. Imaging data were primarily obtained through the ongoing mass-digitisation of the RBINS collection, carried out as part of two multi-year BELSPO-funded projects: DiSSCo-Fed (2018–2023) and DIGIT-04 (2019–2024). Most scans used in the project were produced using the RBINS RX EasyTom (RX Solutions, Chavanod, France; http://www.rxsolutions.fr), typically with a copper filter and beam voltages between 120 and 150 kV. Reconstructions were performed using X-Act (RX) software. The RX system offers higher maximum beam voltage than the RBINS XRE UniTom (XRE, Ghent, Belgium; now Tescan, https://info.tescan.com/micro-ct), and is better suited for scanning fossils over 1 cm in diameter, particularly those still embedded in (dense) sediment matrix.

Micro-CT imaging data were delivered as bundles of 16-bit TIFF files, accompanied by metadata including voxel size. The first step in the CT-CEPH workflow involved loading these TIFF stacks into 3D visualization software. Dragonfly ORS, a powerful tool available free of charge for researchers, was used on dedicated RBINS workstations.

Once imported, the data were manipulated for 2D and 3D rendering, allowing observation of internal structures such as siphuncles, septa, and to collect measurements of various parameters. Regions of interest (ROI) were segmented, manually or semi-automatically, and visualized in 3D, or in Dragonfly ORS itself, or as meshes in .ply or .stl format in GOM Inspect.

Figures of 2D and 3D renders were produced with the Dragonfly ORS ‘export screenshot’ function, after optimizing the rendering by adjusting the histogram, contrast, shading (3D), light source position (3D), transparency (3D), hard gradient (3D) and turning off all annotations, except for scale bars. In several cases, video or .gif formats were also exported, of the 2D TIFF stack, allowing to virtually run through the specimen without specialized software, or, of the 3D rendering, with the specimen turning 360° along two axes at 90° allowing the specimen to be inspected from every angle.

For publications, screenshots exported from Dragonfly ORS, and screenshots from meshes in GOM Inspect, were imported into image processing software like Affinity Photo for scaling to 600 dpi, and assembling them into plates in Affinity Photo, or combined with drawings, in CorelDRAW.

Next to micro-CT imaging, the project explored surface scanning with Artec Spider and Keyence VR-5000. However, for the majority of the specimens studied, micro-CT imaging proved the most effective method.

All these were combined with traditional paleontological approaches, like collection searches, hands-on comparisons, measurements of conventional parameters with vernier calliper, drawings of suture lines with masking tape, digital photography and other. In addition, the stratigraphical position of the studied specimens was reevaluated. For selected specimens, sampling for calcareous nannofossils was also attempted, by removing a few grams of sediment of the matrix, but without useful results due to poorly preserved nannofossils (E. Steurbaut, pers. comm.).

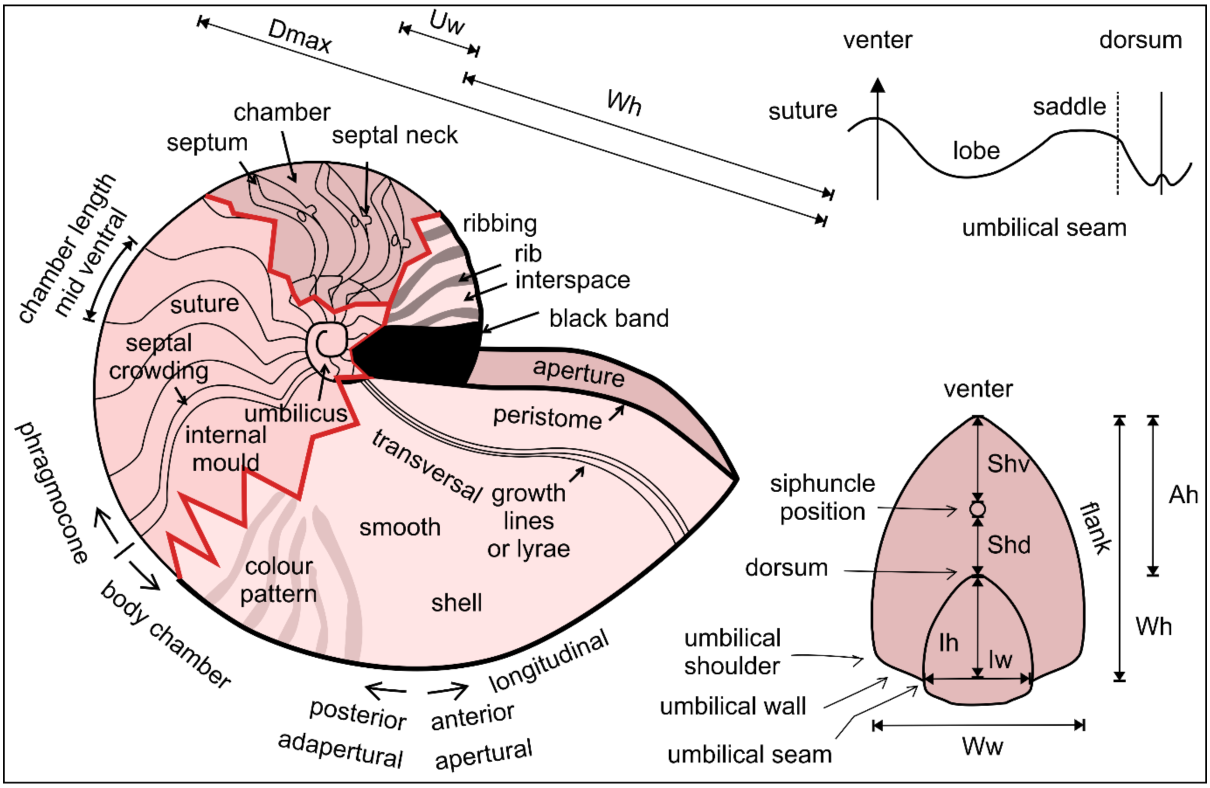


Figure 2. Terminology of nautilid shells. Abbreviations: A, aperture; D, diameter; d, dorsal; h, height; I, imprint zone; max, maximal; S, siphuncle; U, umbilicus; v, ventral; W, whorl; w, width. From Goolaerts & Mottequin (2023a, fig. 2).

The project also benefited from observations made earlier to the start of the project in collections worldwide. While it was originally intended to also study the specimens from African localities housed at the RMCA, the covid crisis threw us some unforeseen hurdles. We were not able to fully incorporate them into our research in a timely manner, the reason why these plans were aborted. However, we studied their literature and had an ‘old school’ look at them. As these remain interesting for further research, they could be incorporated in a future project proposal.

The descriptive terminology of nautilid shells used in this project is summarized in Fig. 2.

4. SCIENTIFIC RESULTS AND RECOMMENDATIONS

4.1. Diversity dynamics in latest Cretaceous to Paleogene nautilids

4.1.1. General account

To document the diversity dynamics of Nautilida in the Upper Cretaceous and Paleogene of Belgium, we undertook an integrated approach combining an exhaustive literature review, extensive searches in the RBINS Meso-Cenozoic invertebrate collections, including the Type and Figured collections, and detailed study of micro-CT datasets. Numerous specimens were loaned for study, enabling the acquisition of a large set of new observations, precise measurements, and high-resolution 2D/3D visualisations and animations.

Our research demonstrates that the Belgian Late Cretaceous to Paleogene nautilid record is globally significant: exceptionally rich, highly diverse, generally well-preserved, and largely unpublished in formal taxonomic context. Specimens originate from a large number of stratigraphic units spanning the interval, and many horizons are represented by numerous specimens in the federal collection. Preservation ranges from poor to exceptional, with the latter being dominant. Material includes shells retaining original aragonite, shells replaced by calcite or silica, and internal moulds. For the latter, the degree of compactional deformation and bioturbation varies according to sediment type and depositional conditions. Micro-CT imaging provided invaluable for assessing deformation, visualizing internal structures and detecting evidence of bioturbation.

In several late Maastrichtian specimens, dense concentrations of crustacean faecal pellets were identified, evidencing the palaeoecological role of dead shells on the seafloor. Micro-CT also revealed soft-tissue preservation in the form of connecting rings of the siphuncle (see e.g., Fig. 5 in section 3.1.3), a notable finding, as it indicates that such preservation is more widespread than previously recognized, typically occurring as ghost structures within early lithified sediment casts. This also allows to extract them as a 3D mesh. No other soft-tissue remains were observed. In none of the specimens did we find buccal elements such as rhyncholites (calcified parts of the upper jaw) or conchorynchs (calcified parts of the lower jaw) preserved in situ in the body chamber, which is unsurprising given that such preservation is globally rare and generally restricted to a handful of specimens from Cretaceous Lagerstätten in Lebanon. Another unexpected result was the detection, via micro-CT, of abundant mollusc shells within nautilid shells of the Eocene Brussels Formation.

In summary, the Belgian Late Cretaceous to Paleogene nautilid record stands out internationally due to the combination of numerous fossiliferous horizons, large specimen counts, high taxonomic diversity, and varied but often excellent preservation. However, most material remains unstudied in detail and unpublished in the modern sense. The bulk of published references are from 19th- to 20th-century stratigraphic works that cite occurrences and apply species names without formal descriptions or illustrations, rendering their taxonomy outdated and unreliable. Additionally, several nominal species introduced in these works are best considered nomina nuda, and even those described to minimal standard are in urgent need of revision.

Examples of formally introduced species are *Nautilus depressus* Binkhorst van den Binkhorst, 1862, *Nautilus heberti* Binkhorst van den Binkhorst, 1862, and *Aturia linicentensis* Vincent, 1901. However, our research on the first two species, largely aided by micro-CT, invalidates Binkhorst's description, and a full revision of the two species are prepared, including the description of new species (see section 3.1.3). The holotype of the latter is too fragmentary nature for a robust revision, though it is better referred to the genus *Aturoidea*.

Good examples of nomina nuda are Delvaux's (1885) *Nautilus disciformis*, *Nautilus Darwini*, *Nautilus Crepini*, and *Nautilus Falyi* (op. cit.), all named in his account of the fauna from the 'Paniselien' (Eocene) of Beaufaux. Delvaux (1885) described the locality as particularly rich for nautilids, including pathologic specimens and individuals reportedly exceeding 1 m in diameter. If accurate, the latter represent the largest Eocene nautilids known. Only a few Delvaux specimens from Beaufaux survive in the RBINS collections; no others are known elsewhere. The surviving material is insufficient to confirm his diversity claims or to resurrect the new species, which remain nomina nuda due to absence of adequate descriptions or figures. Beaufaux has, to our knowledge, not been resampled for nautilids since.

Another case is *Ammonites wapperi* Van Mons, 1833, referring to the geologically youngest nautilid records from Belgium, found in the Oligocene (Rupelian) Boom Formation and referable to the genus *Aturia*. These are exceptionally preserved, retaining original aragonitic shells. Micro-CT scans of several uncrushed, sediment-free subadult specimens enabled high-quality virtual sectioning (e.g., used in the CT-CEPH logo, Fig. 27) and transparent 3D rendering (see Fig. 29). Their precise stratigraphic position within the Boom Formation remains unresolved; most material comes from historical collections. Calcareous nannofossil analysis of adhering sediment failed to clarify a more detailed stratigraphic provenance.

At genus level, the Belgian record contains representatives of *Angulithes*, *Aturia*, *Aturoidea*, *Cimomia*, *Cymatoceras*, *Epicymatoceras*, *Euciphoceras*, *Eutrephoceras*, *Hercoglossa*, *Simplicioceras*, and possibly a new genus related to the *Nautilus-Allonautilus* lineage. Interestingly, a high turnover rate of nautilid faunas is identified, every few millions of years, the faunal composition becomes different, not only in taxonomy but also in outer and inner shell morphology, with the largest break identified just after the K/Pg boundary, in addition to significant loss of typical *Cymatoceras* ribbed forms between the latest Campanian and earliest Maastrichtian, the disappearance of *Epicymatoceras* after the early Maastrichtian, and the influx of new lineages in the Paleocene, Eocene and Oligocene.

The following sections summarise selected Late Cretaceous to Paleogene nautilid case studies prioritised for publication within the CT-CEPH timeframe: 1) discovery of the keeled nautilid *Angulithes westphalicus* in the Santonian of Belgium, with implications for the lithostratigraphy of the Campine Basin; 2) identification of an exceptionally diverse pre-K/Pg boundary nautilid fauna; 3) documentation of two Eocene nautilids with notable historical context; 4) application of our imaging and analytical methodology to new finds of stem-group sepiid cephalopods from the Eocene of Belgium, combined with a review of historical records and specimens in the RBINS collections.

4.1.2. *Angulithes westphalicus* from the Santonian of the Belgian Campine

One of the outcomes of our detailed searches in the RBINS collections was the discovery of *Angulithes westphalicus* (Schlüter, 1872), a Late Cretaceous nautilid with a globular involute smooth shell and a distinctly keeled venter, in the Santonian of the Campine basin (Fig. 3-4). This species was previously never formally recorded from Belgian Cretaceous strata.

The fossils studied were collected in the 1930s by RBINS staff from the Voort Shafts I and II of the Zolder colliery (northeastern Belgium), from a depth between 579.5 and 584.3 m. They originate from a glauconitic calcareous sandstone traditionally referred to as ‘Smectite de Herve’, lithostratigraphically corresponding to the Vaals Formation, either the upper part of the Asdonk Member or the lower part of the Sonnisheide Member. Biostratigraphic indicators, including the belemnite cephalopod *Gonioteuthis westfalicagranulata*, ammonite cephalopods, inoceramid bivalves and calcareous nannofossil, confirm a late middle Santonian age, more precisely the *Gonioteuthis westfalicagranulata* Belemnite Zone.

Micro-CT imaging was essential in this study. Despite suboptimal preservation, internal structures, including the siphuncle, were visualized for the first time in this species (Fig. 3). Its position, closer to the venter than the dorsum, confirms a close evolutionary relationship with *Angulithes galea*, considered its presumed ancestor, known from Turonian–Coniacian levels.

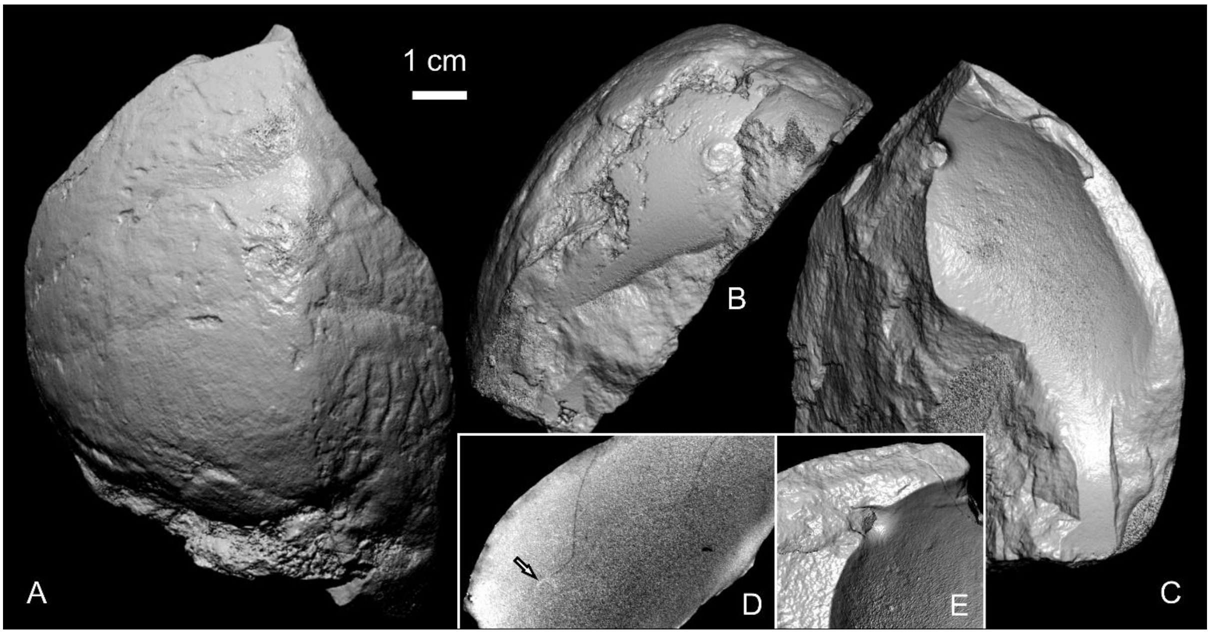


Figure 3. *Angulithes westphalicus* (Schlüter, 1872) from the Voort Shaft II, Zolder colliery, from a depth of 582.50 m, specimen IRSNB 11508. Screenshots from 3D rendering of micro-CT imaging data (**A–C, E**), and a virtual cross-section (**D**), showing the shape of the septal neck, next to some preserved remains (arrow) of the siphuncular tube (probably phosphatised originally organic material of the connecting rings). From Goolaerts & Mottequin (2023a, fig. 4).

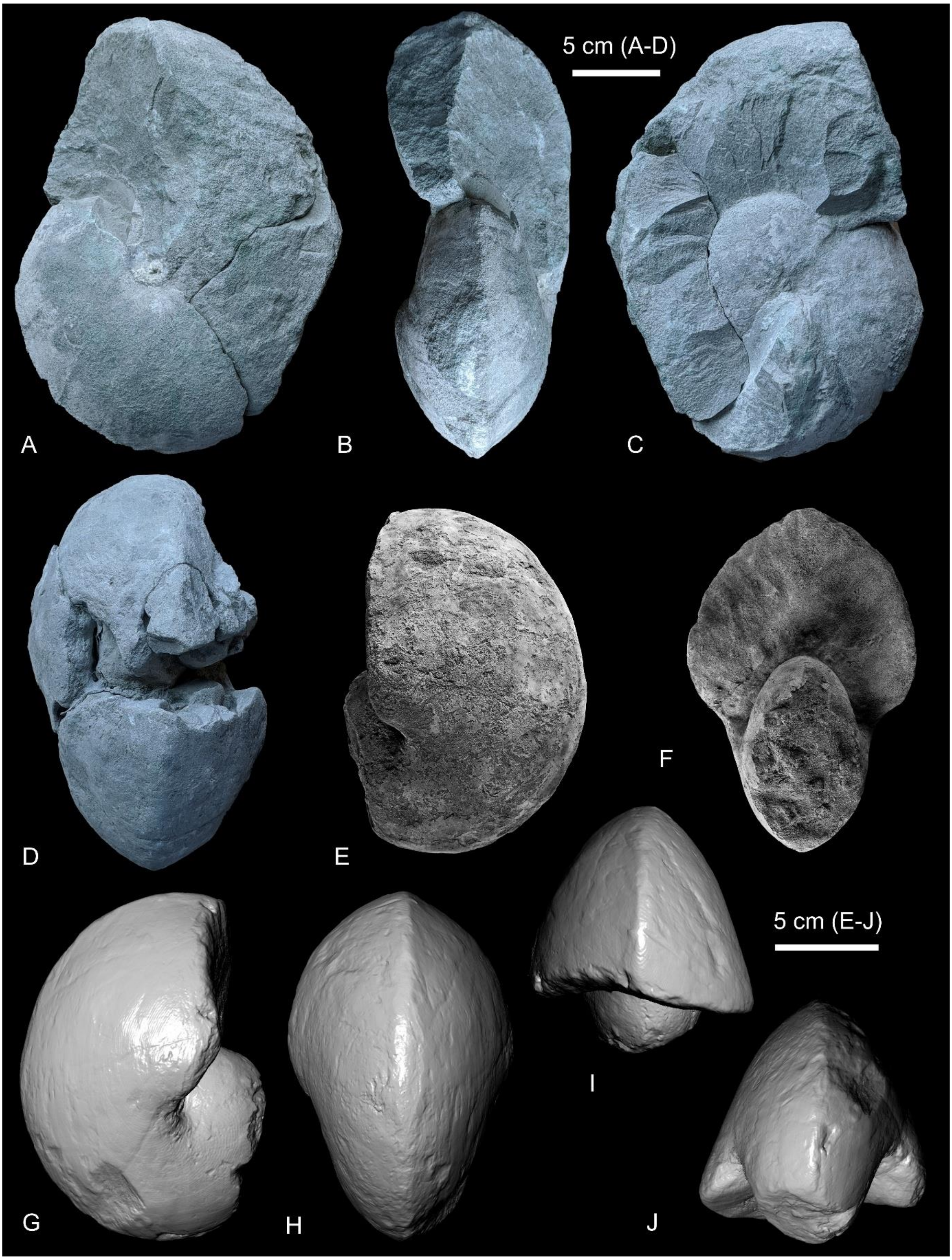


Figure 4. *Angulithes westphalicus* (Schlüter, 1872) from the Voort Shafts I and II, Zolder colliery. **A–C.** Specimen IRSNB 11504, photographed under natural light, from Shaft I, at a depth between 582–584.30 m. **D.** Keeled venter of Specimen IRSNB 11507, photographed under natural light, from Shaft II at a depth of 582.50 m. **E–J.** Specimen IRSNB 11506, from Shaft I at a depth of 579.50–582 m, photographed under white light after coating with NH4Cl (E, F) and screenshots of a 3D mesh obtained from segmenting a micro-CT imaging data set. From Goolaerts & Mottequin (2023a, fig. 3).

Beyond taxonomic and evolutionary implications, our work also highlighted inconsistencies in the age interpretation of the Asdonk and Sonnisheide members. Contrary to traditional lower Campanian assignments, our review of the available data shows that the full fossiliferous sandy sequence below 571 m depth at Zolder and Houthalen is entirely Santonian in age. This necessitates revision of the regional stratigraphy and supports a Santonian marine transgression over the Brabant Massif, consistent with earlier interpretations (e.g., Jagt et al., 1995) and conflicting with prior dinoflagellate-based interpretations lacking direct sampling from these intervals.

The results were published in the peer-reviewed journal *Geologica Belgica* (Goolaerts & Mottequin, 2023a). Crustaceans from the same beds, such as *Mesostylus faujasi*, were also figured. The stratigraphic and paleoenvironmental findings from our study were also integrated into a separate paper describing a new crustacean species, *Binkhorstia desaegheri* Van Bakel et al., 2024, named in honour of Patrick De Saegher, RBINS volunteer, who helped inventory all fossils from the 'Smectite de Herve' of the Campine collieries in the RBINS collections.

4.1.3. An exceptionally diverse pre-K/Pg boundary nautilid fauna

One of the persistent gaps in understanding nautilid evolution concerns their survival across the end-Cretaceous mass extinction. This uncertainty stems largely from the rarity of well-preserved and well-documented nautilid faunas from the latest Maastrichtian and earliest Paleocene. To address this, we caried out a comprehensive revision of the nautilid assemblages from the type-Maastrichtian (Belgium, the Netherlands), examining large specimens sets from the Maastricht and Kunrade formations housed at the RBINS (including historical collections of Bosquet and Ubaghs), as well as material from Natuurhistorisch Miuseum Maastricht (Maastricht, the Netherlands; NHMM; data collected during CT-CEPH), Museum für Naturkunde (Berlin, Germany; MfN), Muséum national d'Histoire naturelle – Université Sorbonne (Paris, France; MNHN), Natural History Museum (London, UK; NHM) and American Museum of Natural History (New York, USA; AMNH) (data collected before the start of the project).

Combining traditional morphological analysis with micro-CT imaging and a new analytical approach to septal spacing analysis, we identified six species across four genera (*Eutrephoceras*, *Euciphoceras*, *Angulithes*, *Cimomia*). Three species are newly recognized, for three other, we fully revised existing names. Considerable time was invested to collect all data on the different species, from embryo up to adult. Micro-CT imaging was absolutely essential in this study, to access internal structures like the siphuncle position and embryonic development. Without this technique, a full understanding would not have been possible (Fig. 5). In addition, it allowed to detail bioturbation in the sediment infills, including also crustacean faecal pellets.

Our research reveals that the Maastrichtian type area represents a diversity hot spot for late Maastrichtian nautilids, it is the most diverse late Maastrichtian nautilid fauna known to date. The assemblage is also marked by high disparity in shell morphology: cross-sectional profiles range from rounded to angular, and from compressed to depressed; umbilici range from fully closed to partially open; sutures vary from straight to sinusoidal; and siphuncle positions differ among species. Embryo and adult sizes also span a wide spectrum, from small to very large. In contrast, ornamental features are comparatively uniform. Ribbing is absent, except for reticulate ornamentation on embryonic shells, subtle, rib-like folding on the end of the body chamber in one species and subtle but broad ribbing in one of the species. The limited variation in ornamentation may reflect ecological constraints or evolutionary conservatism in external features during this interval, but generally is the result of the extinction of the heavily ribbed morphologies (sensu *Cymatoceras*) earlier in the latest Cretaceous (late Campanian–early Maastrichtian).

Some of the species show a restricted stratigraphic distribution, having only been identified from the Kunrade or equivalent, and may not extend into the latest Maastrichtian, or on the contrary, entered the type Maastrichtian area only by the final ~100 kyr before the K/Pg boundary. These distribution patterns are thought to reflect palaeoenvironmental shifts, similar to those observed in contemporaneous ammonite faunas just below the extinction interval.

A single, fragmentary nautilid shell from the basal Paleocene (top of the Maastricht Formation, subunit IVf-7) may tentatively be referred to one of the six Maastrichtian species. Apart from this specimen, only some remains of the buccal mass are known, which cannot be identified to species level. It is only by the mid Danian, more than 2.5 myr later, nautilids reappear in larger numbers, both in the type Maastrichtian area and in the Mons Basin at larger numbers, with faunas that are fully different from the latest Maastrichtian ones (Fig. 6).

Preliminary results were presented at scientific conferences, and to citizen-scientists and the public. A large scientific paper detailing these findings is in an advanced state of preparation.

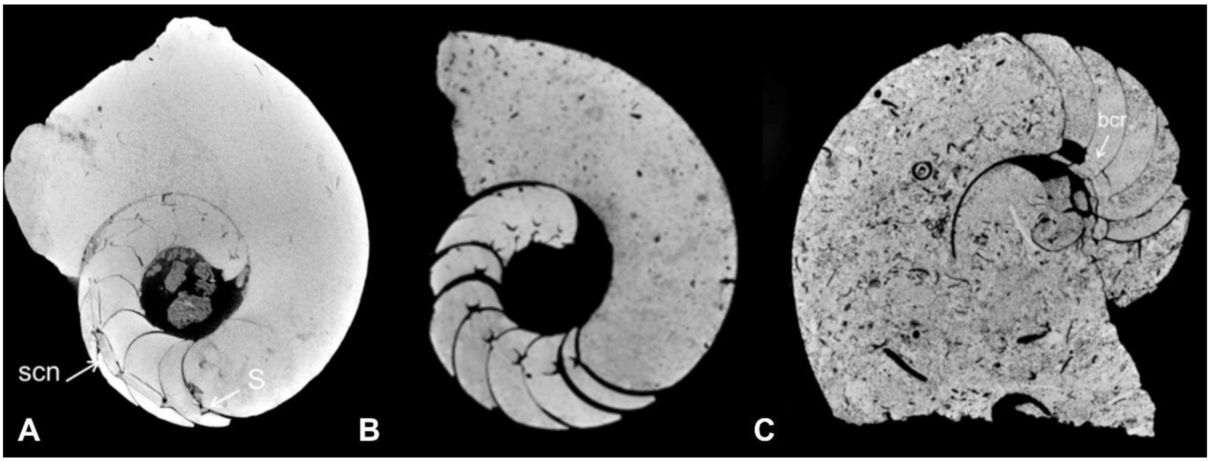


Figure 5. Micro-CT imaging as essential methodology to understand the diversity of late Maastrichtian Nautilida from the Maastrichtian type area (Belgium, the Netherlands) (not to scale). In this case, it was crucial to help to differentiate a group of smooth-shelled nautilids, revealing three species with different siphuncle position (high, low, very low). Abbreviations: bcr, broken connecting ring; S, siphuncle; scn, connecting ring. From Goolaerts et al. (in prep.).

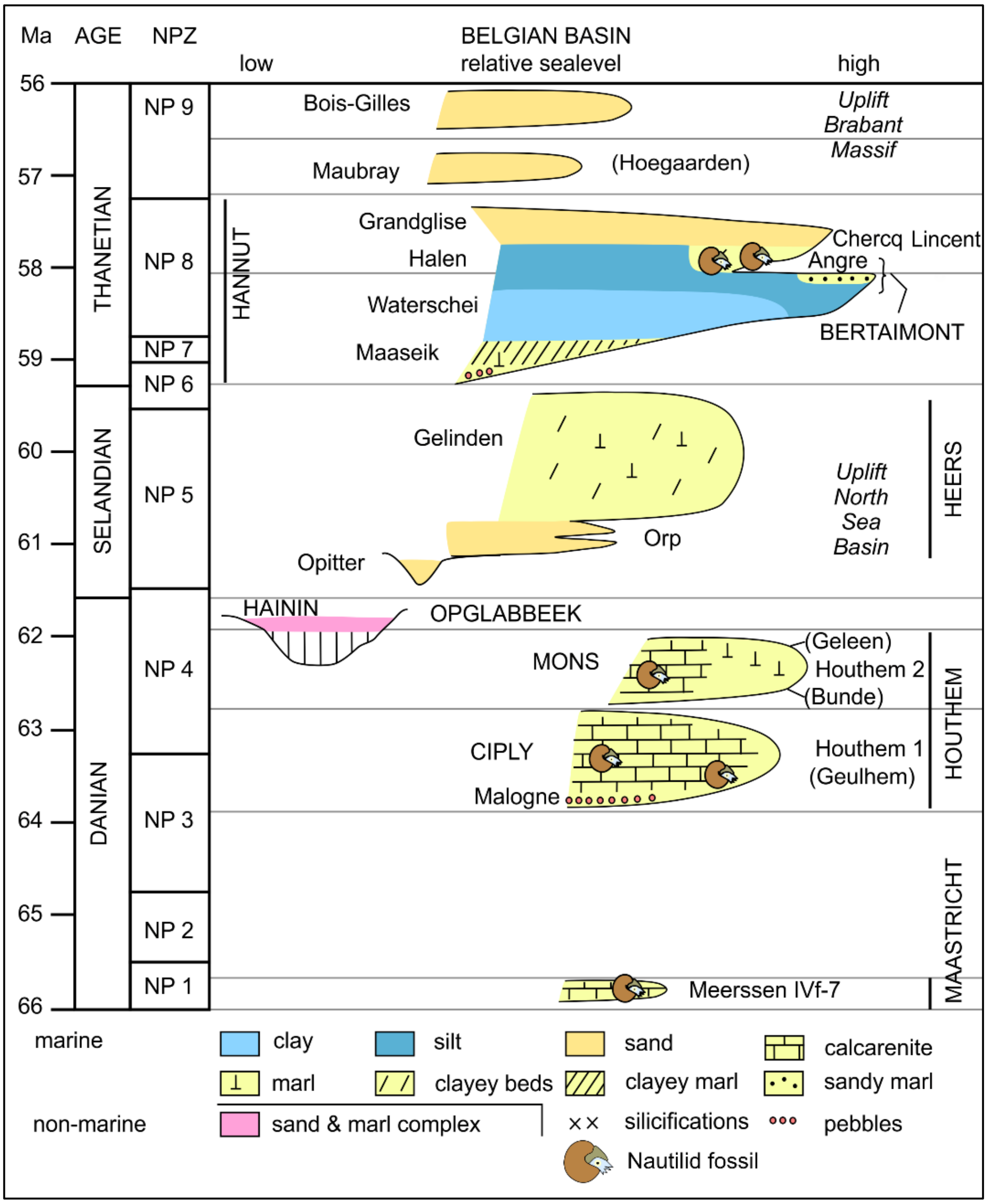
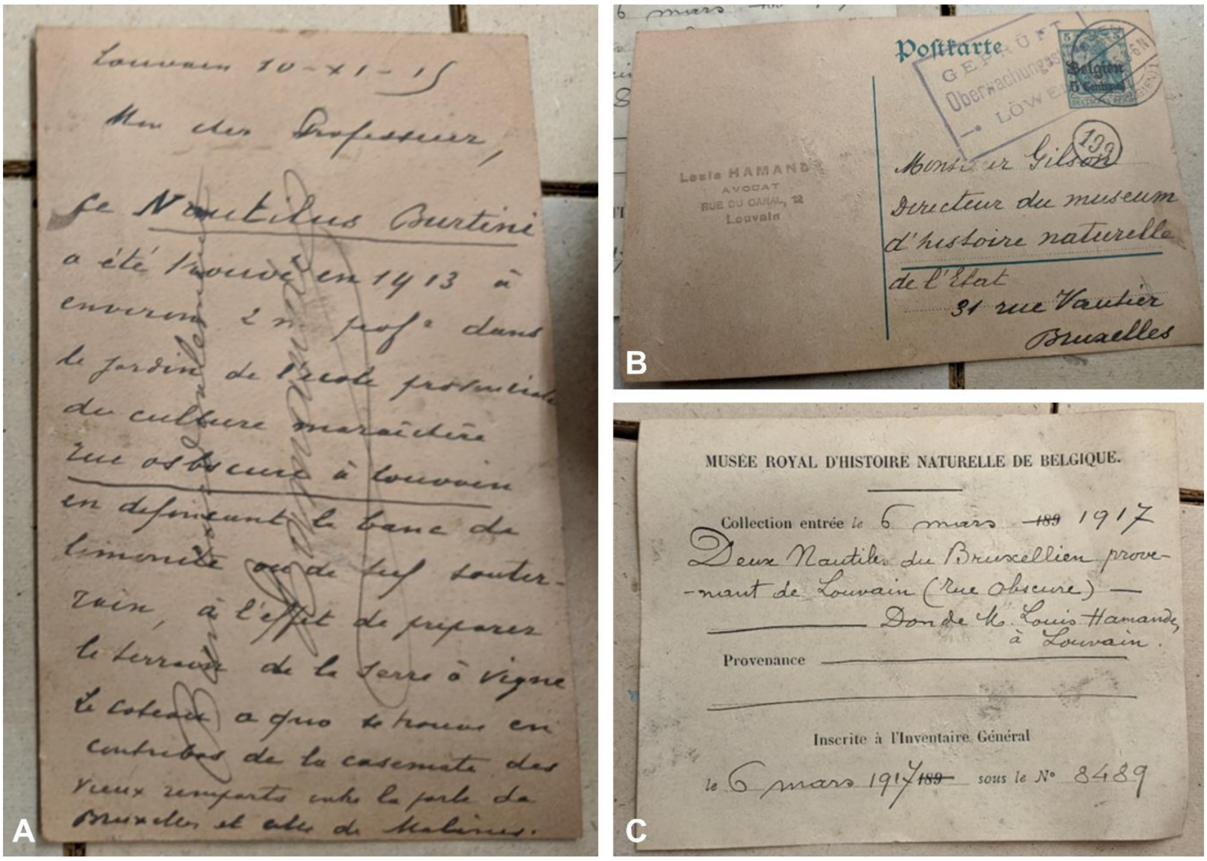


Figure 6. Nautilid occurrences from Belgium and the Netherlands postdating the Cretaceous-Paleogene boundary plotted next to the stratigraphy (Paleocene). From Goolaerts et al. (in prep.).

4.1.4. Two nautilid fossils found in the garden of the Provincial School of Horticulture at Leuven

Our collection searches also led us to fossils with remarkable histories. One such case involves two well-preserved Eocene nautilid fossils found during World War I in the garden of the Provincial School of Horticulture at Leuven and send to the RBINS director Gustave Gilson by Leuven-based lawyer Louis Hammande (Figs 7-8). A popular science article was written on these two specimens (Goolaerts, 2020a), next to posts on social media, bringing attention to the CT-CEPH project.



Louvain 10-XI-15

Mon cher Professeur,

Ce Nautilus Burtini
a été trouvé en 1913 à
environ 2 m prof. dans
le jardin de l'école provincial
de culture maraîchère
rue obscure à Louvain
en défonçant le banc de
limonite ou de tuf souter-
rain, à l'effet de preparer
le terrain de la serre à vigne
le coteau a quo se trouve en
contrebas de la casemate des
vieux remparts entre la porte de
Bruxelles et celle de Malines.

Postkarte

GEPRÜFT
Überwachungsst
LÖWEN

Belgien
5 Centimes

Louis HAMANDE
AVOCAT
RUE DU CANAL, 12
Louvain

199

Monsieur Gilson
Directeur du museum
d'histoire naturelle
de l'Etat
31 rue Vautier
Bruxelles

MUSÉE ROYAL D'HISTOIRE NATURELLE DE BELGIQUE.

Collection entrée le 6 mars ~~189~~ 1917
Deux Nautiles du Bruxellien prove-
-nant de Louvain (Rue obscure) —
Don de M. Louis Hamande,
à Louvain.

Provenance

Inscrite à l'Inventaire Général

le 6 mars 1917 ~~189~~ sous le N° 8489

Figure 7. A-B. Postcard from lawyer Louis Hammande (Louvain, Leuven) to RBINS director Gilson on two nautilid fossils found in the garden of garden of the Provincial School of Horticulture at Donkerstraat Leuven. Text (A) says (original / translation): Louvain 10-XI-15 (Leuven November 10th 1915) – Mon cher Professeur, (My dear Professor,) – Ce *Nautilus burtini* a été trouvé en 1913 à environ 2 m profondeur dans le jardin de l'école provinciale de culture maraîchère rue obscure à Louvain en défonçant le banc de limonite ou de tuf souterrain, à l'effet de préparer le terrain de la serre à vigne. Le coteau a quo se trouve en contrebas de la casemate des vieux remparts entre la porte de Bruxelles et celle de Malines. (This *Nautilus burtini* was found in 1913 at a depth of about 2 meters in the garden of the Provincial School of Horticulture on Donkerstraat in Leuven, during the breaking up of a bank of ironstone or underground tuff to prepare the ground for the vineyard greenhouse. The hill in question lies below the casemates of the old ramparts between the 'Brusselse Poort' and the 'Mechelse Poort'. The postcard is written in French, the common language in official, academic, and administrative contexts at the time, both in Leuven and at the RBINS, although the everyday spoken language of the local population in Leuven was Dutch. It was sent under German occupation during World War I (B), as indicated by the terms "Postkarte," "Belgien," and the postmark "Löwen (B). **C.** Record created upon the official registration of the two fossils in the collections of the RBINS. The two fossils were assigned the General Inventory (IG) number 8489. Modified from Goolaerts (2020a).

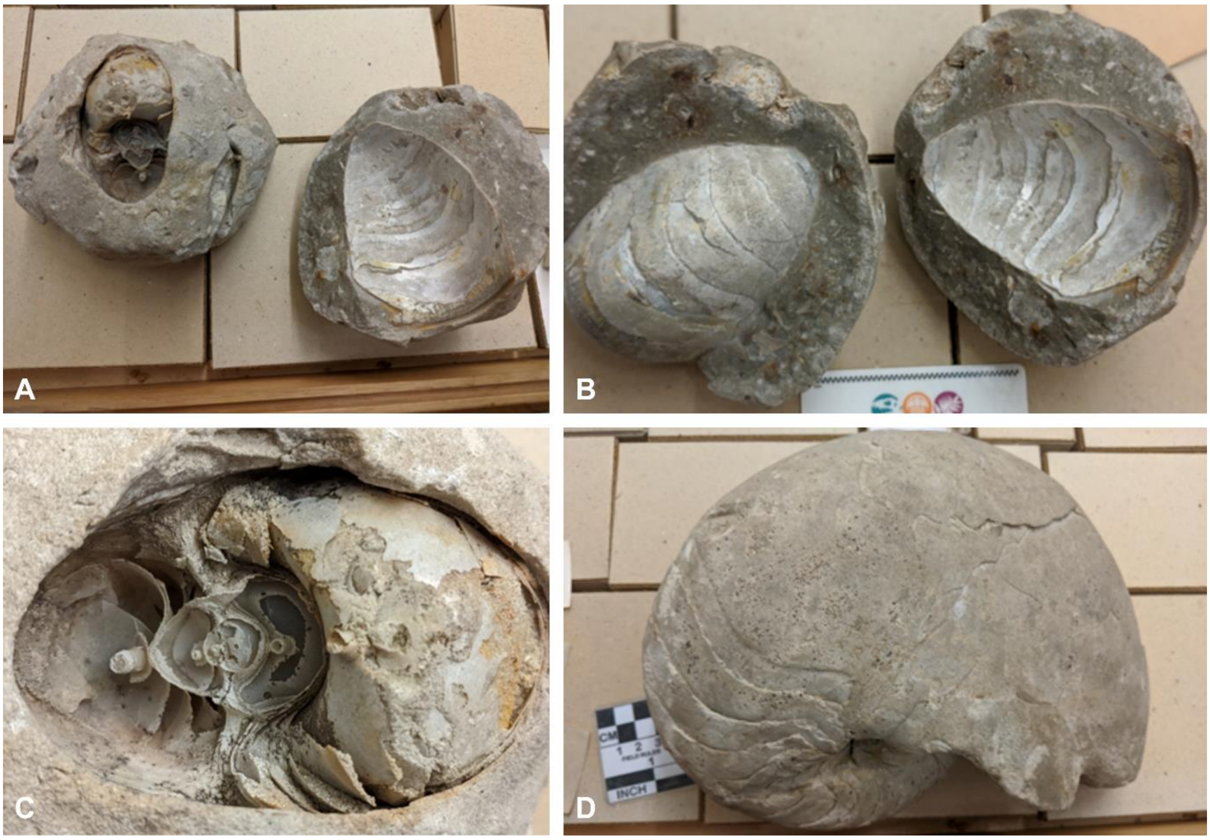


Figure 8. The two nautilid fossils found in the garden of the Provincial School of Horticulture at Donkerstraat Leuven in 1913 and sent to the RBINS by lawyer Louis Hammande. **A-C.** Specimen IRSNB Invert-8489-0001, partly silicified, inside a sandstone concretion, revealing partial preservation of the shell on one side (A-B), and a nice dissection on the other side (C). **D.** Specimen IRSNB Invert-8489-0002, the larger specimen, with well discernible suture lines. Modified from Goolaerts (2020a).

4.1.5. Application of micro-CT imaging in the study of Belosaepiids from the Eocene of Belgium

Although CT-CEPH primarily targeted Nautilida, its core methodology — non-destructive micro-computed tomography — was also applied to a different but important group of Eocene cephalopods: the Belosaepiidae Dixon, 1850 (Subclass Coleoidea Bather, 1888). This expansion was prompted by citizen scientists who brought newly collected *Belosaepia* fossils to our attention from the two key middle Ypresian sites: the Ampe quarry at Egem and the Koekelberg quarry at Marke. These specimens, very rare in the Belgian early Eocene, together with a revision of the sparse historical material housed in the RBINS collections, provided an excellent opportunity to refine and test the imaging pipeline developed under CT-CEPH (Figs 9-19).

Belosaepiidae are stem-group sepiids (Order Sepiida Gray, 1849) known exclusively from calcified skeletal remains of their internalized buoyancy device, a complex 3D shaped structure composed of multiple layers of $CaCO_3$. This includes a posterior guard, an anterior dorsal shield with rugose ornamentation, and a phragmocone with conotheca, septa and a siphuncle (Fig. 9, 11). In most fossils, only the heavily calcified guard is preserved, and as a result, taxonomy is almost exclusively based on its external shape. While there are notable resemblances to the cuttlebone of extant sepiids (Fig. 10),

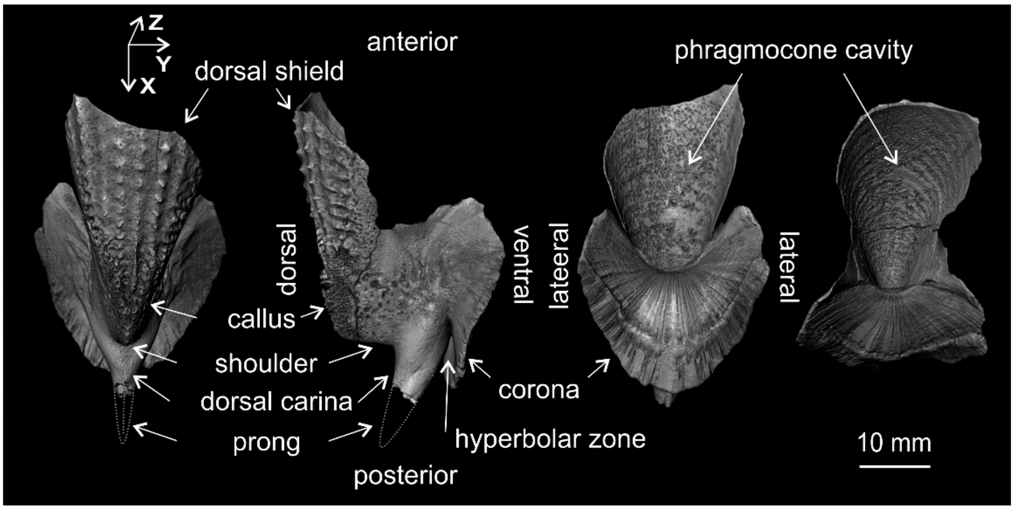


Figure 9. Terminology of the *Belosaepia* skeleton. Images are screenshots from a 3D rendering based on a micro-CT scan with a very high signal-to noise ratio of specimen IRSNB 00385. a syntype of *Belosaepia proxima* Vincent, 1901 (originally described as *Belosepia proxima*, p. 16, pl. 2, figs 8-10), from the Wemmel Sand Member, Maldegem Formation, Lutetian, Belgium. From Goolaerts et al. (2022a, fig. 4).

it remains unknown whether lamellae and pillar structures were present in the *Belosaepia* phragmocone.

Micro-CT imaging enabled detailed visualisation of the internal morphology of the guard, previously studied only through destructive methods or limited external observation. The scans revealed growth interruptions and resorption surfaces within the prong, potentially reflecting annual cycles. In addition, some specimens displayed up to 95 discernible growth bands, suggesting a short life span consistent with modern coleoid reproductive strategies and contrasting sharply with the longevity of extant nautilids.

In addition to internal morphological data, our micro-CT imaging revealed microfossils, especially *Nummulites*, in the surrounding matrix, allowing for improved age control (Fig. 16). Segmentation also enhanced the visibility and identification of specific features, including bioerosion traces preserved in the guard (Fig. 18).

These combined observations supported their assignment to *Belosaepia tricarinata* (Watelet, 1851), a species originally described from the Paris Basin and also recognized in the Hampshire and London basins. This identification reinforces the concept of faunal connectivity across the southern North Sea Basin during the early Eocene (Fig. 12-13).

Beyond providing key data and stunning visualisations for scientific research, this case also underscored the educational potential of micro-CT imaging. A particularly informative comparison was made between the phragmocone cavities of stem-group sepiids and those of stem-group spirulid *Beloptera belemnitoidea* de Blainville, 1825 (Order Spirulida Haeckel, 1866) (see Figs 17, 19).

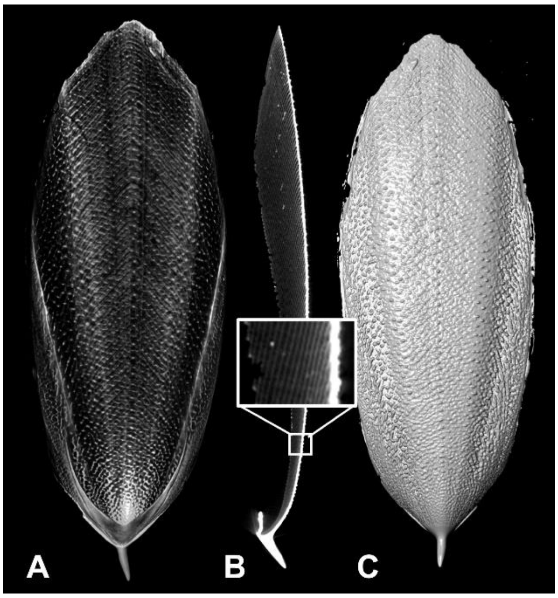


Figure 10. Cuttlebone of extant *Sepia winckworthi* Adam, 1939 (RBINS collection). **A, C.** 3D renders, ventral (A) and dorsal (B) views with phragmocone made transparent in A. **B.** Virtual cut, revealing the large differences in thickness between the dorsal shield and the septa and pillars of the phragmocone. From Goolaerts et al. (in prep.).

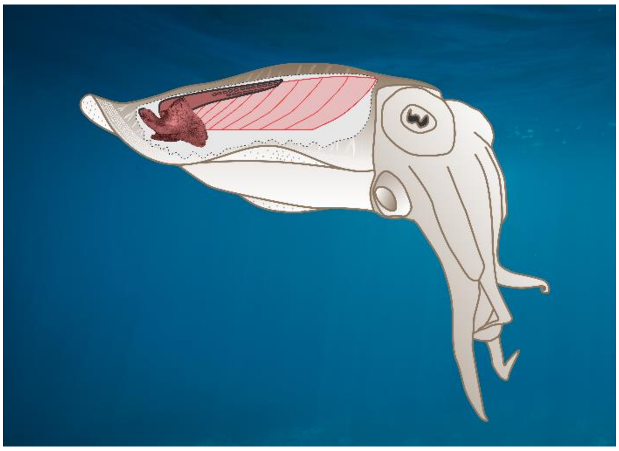


Figure 11. Hypothetical reconstruction of the *Belosaepia tricarinata* animal. From Goolaerts et al. (2022a, fig. 5).

This case study illustrated the versatility and value of micro-CT imaging in cephalopod paleontology well beyond the Nautilida. The results were published in the peer-reviewed journal *Rivista Italiana di Paleontologia e Stratigrafia* (Goolaerts et al., 2022), and visualizations of the *Belosaepia* and *Beloptera* phragmocone cavities were also featured in a popular science article in the journal *Hona* (Goolaerts et al., 2020a). Our case study also made it to the RBINS annual report (Goolaerts & Mottequin, 2023b,c,d).

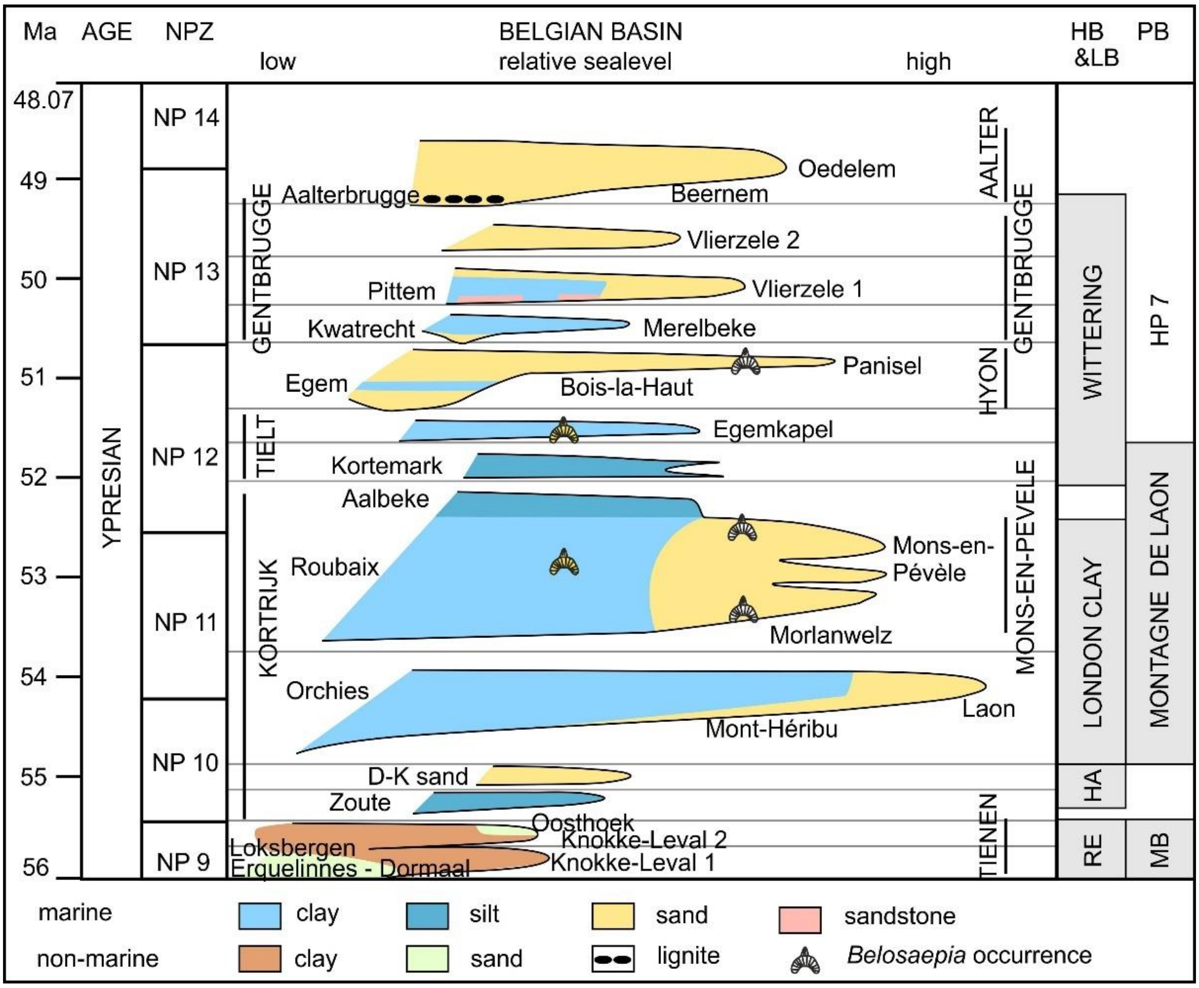


Figure 12. Stratigraphy of the Belgian Ypresian and the stratigraphic positioning of the new finds and the probable stratigraphic position of the 19th and 20th century finds of *Belosaepia tricarinata* (Watelet, 1851) in Belgium. Abbreviations: HB & LB, Hampshire and London basins; PB, Paris Basin. From Goolaerts et al. (2022a, fig. 3).

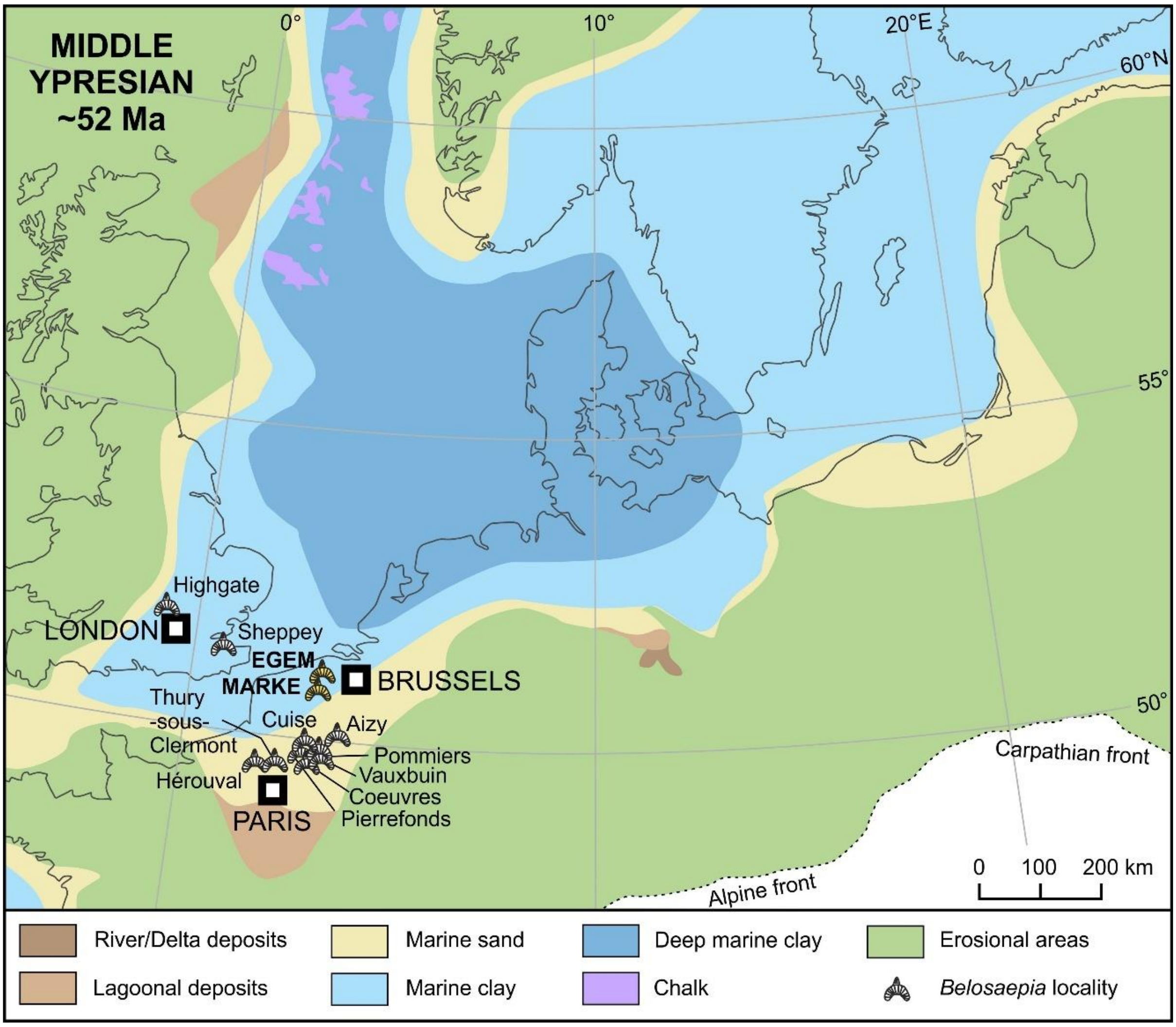


Figure 13. Middle Ypresian paleogeographic map, modified from Knox et al. (2010), showing the locations of the Belgian localities Egem and Marke (yellow pictograms), as well as French and English localities where *Belosaepia tricarinata* (Watelet, 1851) is known from (white pictograms). From Goolaerts et al. (2022a, fig. 2).

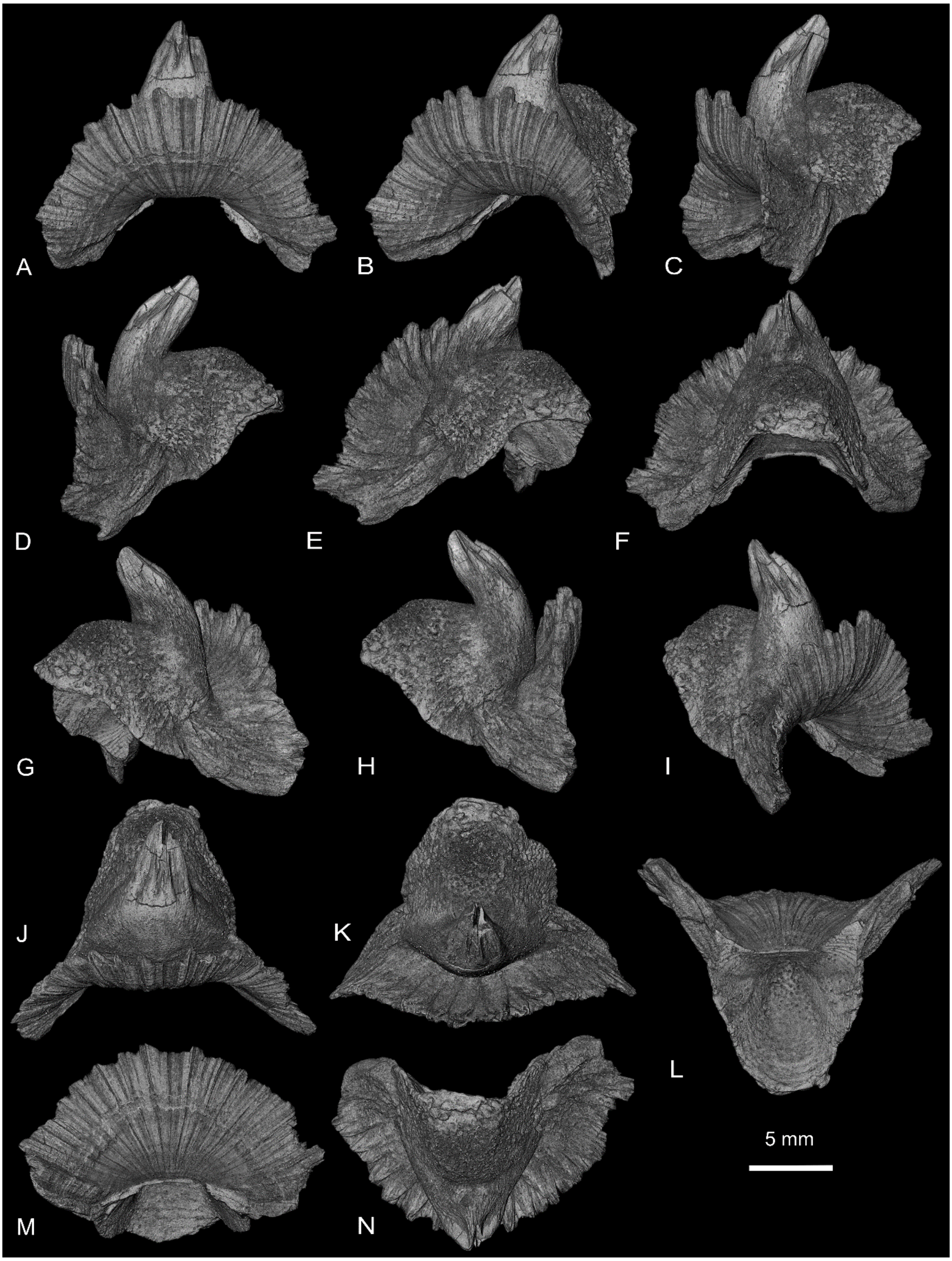


Figure 14. *Belosaepia tricarinata* (Watelet, 1851) from the base of the Egemkapel Clay Member at Ampe quarry at Egem, specimen IRSNB 07689. **A-N.** Surface renderings. From Goolaerts et al. (2022a, fig. 8).

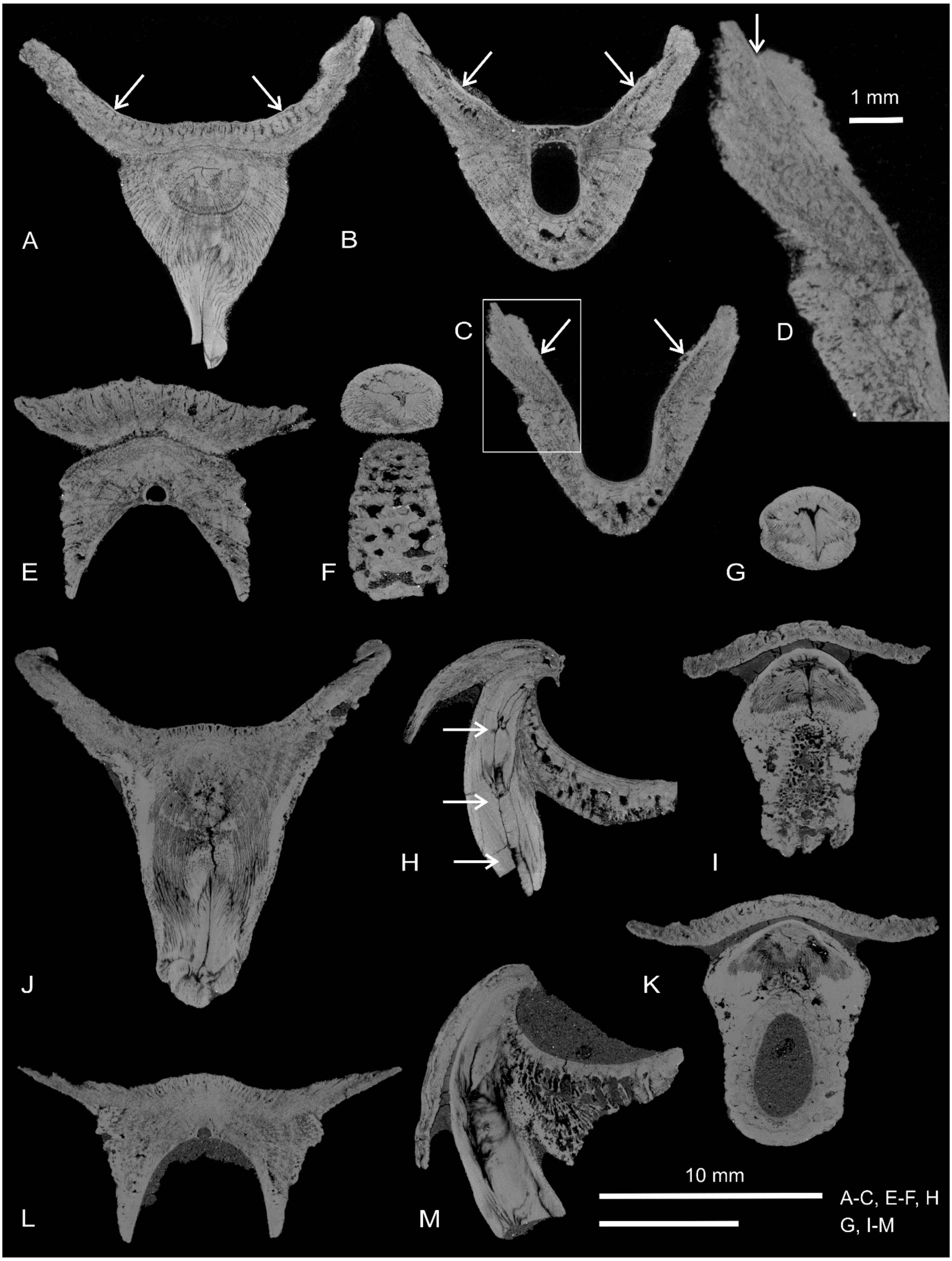


Figure 15. *Belosaepia tricarinata* (Watelet, 1851) from the base of the Egemkapel Clay Member at Ampe quarry at Egem, specimens IRSNB 07689 (A-F, H) and IRSNB 07691 (G, I-M). **A-M.** Virtual sections along X-Y (A-D, J), Y-Z (E-I, K-L) and X-Z (H, M) planes. D: enlargement of rectangle of C. From Goolaerts et al. (2022a, fig. 9).

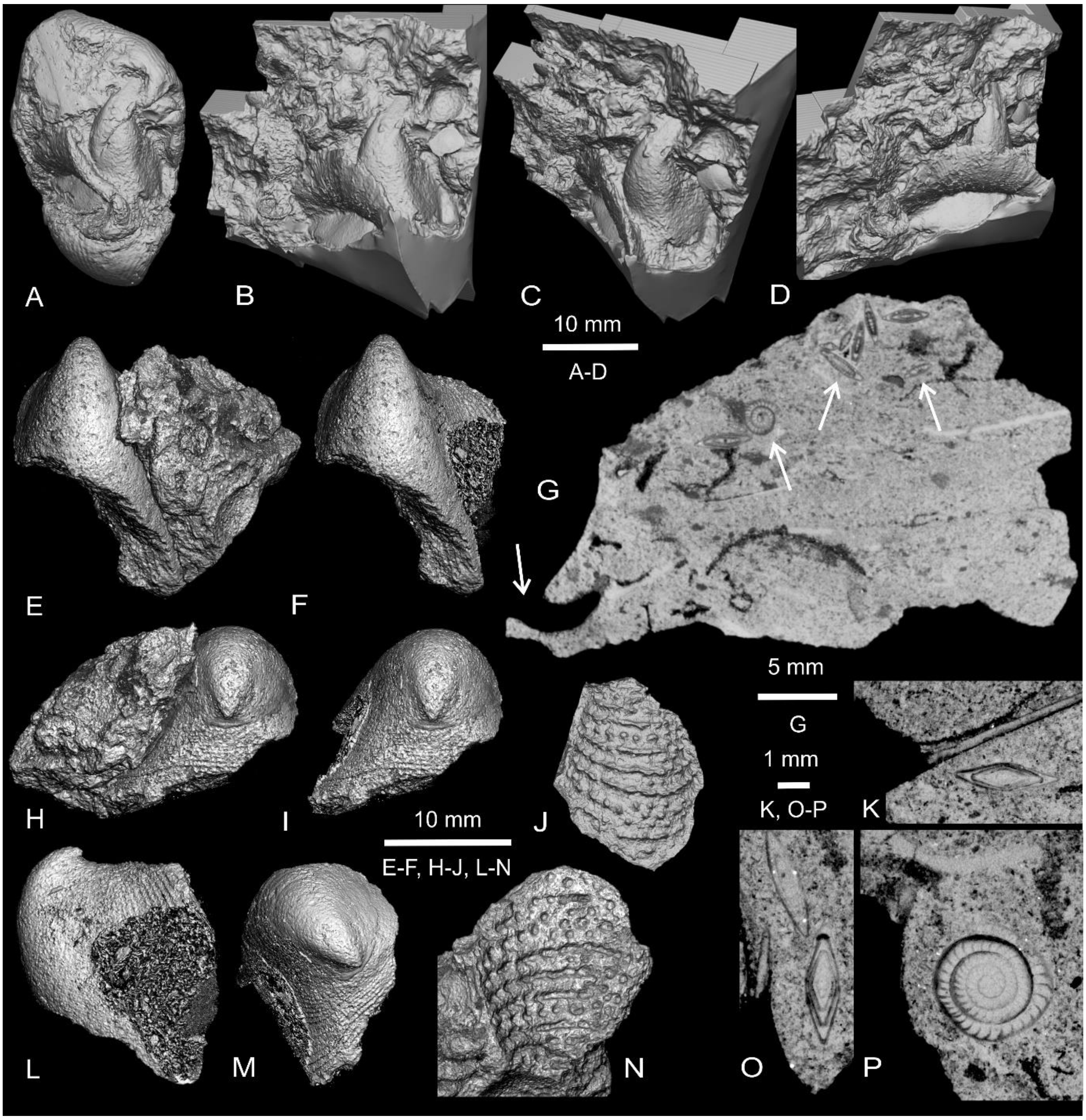


Figure 16. One of the historical specimens (IRSNB 07688) described by Vincent (1901, pl. 1, figs 14-15). **A-D, G.** Guard. A: Screenshot of a 3-model of the cast of Vincent (1901). B-D: Screenshot of a new 3-model digitally reconstructed from the external cast. G. Virtual section through the external cast (downward arrow) with several *Nummulites involutus* fossils visible (upward arrows). **E-F, H-I, K-M, O-P**. Phragmocone. E-F, H-I, K-M: Surface renderings of the sediment cast of the phragmocone before (E-H) and after virtual preparation (F, I, L-M). K, O-P: Virtual sections through a single well-preserved *Nummulites involutus* fossil embedded in the sediment cast. **J, N.** Dorsal shield. J: Screenshot of a 3D-model of the external cast. N: Surface rendering of the external cast preserved in sandstone.

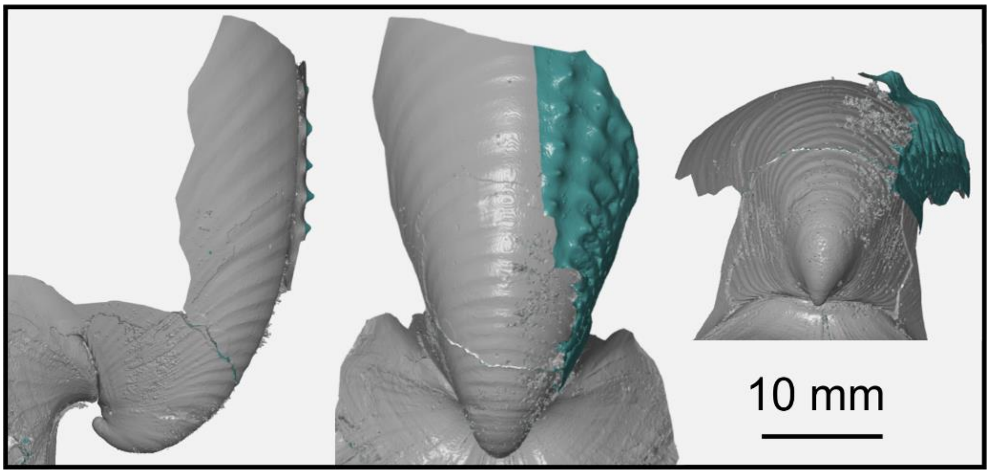


Figure 17. Screenshots of a 3D model of the phragmocone cavity, providing enhanced visualization and identification of the ontogenetic changes in phragmocone chamber size and shape, beginning from the protoconch. The model was created from the same specimen shown in Fig. 9, namely specimen IRSNB 00385, syntype of *Belosaepia proxima* Vincent, 1901. From Goolaerts et al. (2022a, fig. 15).

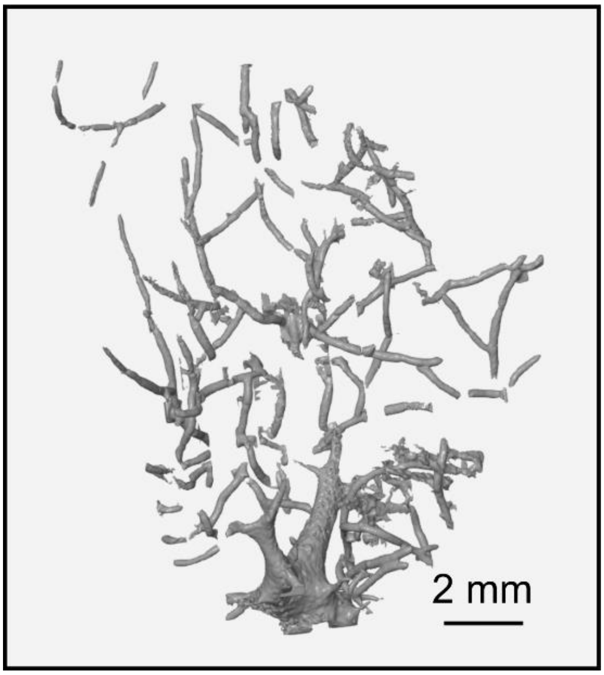


Figure 18. Screenshot of a 3D model generated from the borings in the guard of specimen IRSNB 07692 from the Koekelberg quarry at Marke, Belgium. Two distinct types of borings are visible. The first consists of branching tubes with small diameters (170–190 µm), mostly straight with some curved examples, and is identifiable as *Talpina ramosa* von Hagenow, 1840 — a bioerosion trace commonly found in cephalopod hard parts such as belemnite rostra. The second type consists of irregular tubes (approximately 0.5 mm in diameter) radiating from a central chamber, and are attributed to the bioerosion trace *Entobia* isp. From Goolaerts et al. (2022a, fig. 16).

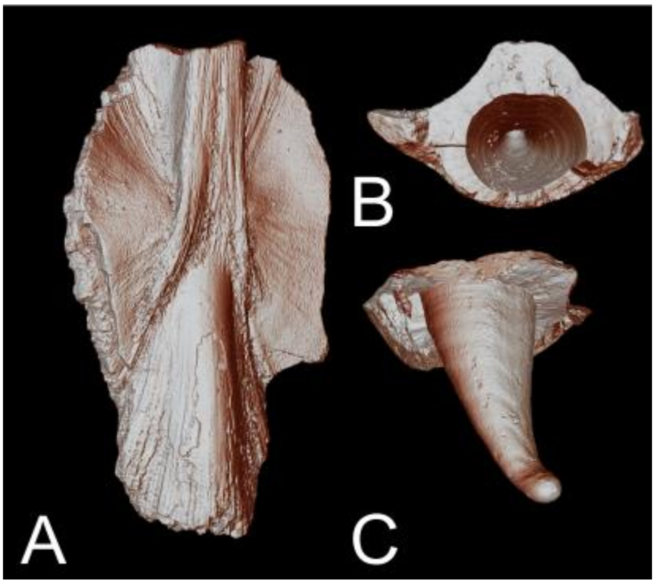


Figure 19. Calcified remains of the spirulid *Beloptera belemnitoidea* de Blainville, 1825 from the middle Eocene of Belgium, specimen IRSNB 00383, previously figured by Vincent (1901, pl. 1, fig. 4). **A-C.** Screenshots of a 3D model of the specimen (A), and the phragmocone cavity (B-C), providing enhanced visualization and comparison with *Belosaepia*. From Goolaerts et al. (2020a, fig. 7A-C).

4.2. A 21st century look at early Carboniferous nautilids from Belgium

4.2.1. Large diversity in species, genera and shell shapes

Following the Devonian/Carboniferous boundary, Nautilida underwent a major radiation in taxonomy, shell morphology, and geographic range. Many new or previously uncommon shell morphologies emerged. Belgium played a historically central role in documenting this diversification, with material from both the Tournaisian and Visean described by de Ryckholt (1851, 1852, 1854), de Koninck (1844, 1851, 1878-1880), Hyatt (1883-1884, 1893), Miller & Kemp (1947) and Kummel (1963, 1964). Most specimens described by de Ryckholt and de Koninck are preserved in the RBINS collection, while Hyatt's material is housed at the Harvard Museum of Comparative Zoology (Boston, USA). Many of de Koninck's species are now genotypes, yet the sole published illustrations are his stylized pencil drawings, often artistically enhanced. In addition, our research clearly reveals that these enhancements are sometimes inconsistent with the actual specimens (see section 4.2.2 and Fig. 21).

At the start of CT-CEPH, we assumed a full taxonomic revision of Belgium's early Carboniferous nautilids would be manageable. However, we soon recognized the depth of unresolved issues, making such task unfeasible within the project's timeframe. Moreover, during collection searches for the COLOURINPALAEO project, additional early Carboniferous material was found in the ULiège collections and at the Centre Grégoire Fournier (CGF) of the Maredsous Abbey. Travel restrictions during the COVID pandemic further delayed essential work in the Boston collections. Together, these developments call for a dedicated follow-up project.

Figure 20. Early Carboniferous Nautilida explored a wide variety of shell shapes, exemplified here by a collection of screenshots of 3D meshes obtained from micro-CT imaging of RBINS specimens published by de Koninck (1878-1880). These meshes can be easily manipulated, allowing to document for the first time the significant volumetric increase of the shell at the end of the embryonic stage (image top left). Modified from Goolaerts et al. (2021); not to scale.

Despite this, we did gather a substantial number of new observations, both from physical specimens and micro-CT datasets. The latter revealed previously hidden features, notably regarding the siphuncle and embryonic development. Our 3D meshes enabled, for the first time, full documentation of the sudden volumetric expansion of the shell at the end of the embryonic stage (see Fig. 20, image top left). Preliminary results were presented at conferences (e.g., Fig. 20), we initiated a revision of the genus *Temnocheilus* (see section 4.2.2), and contributed on putative cephalopod egg cases with VERTIGO Brain-be project researchers (see section 4.2.3).

4.2.2. *Temnocheilus*

A remarkable genus emerging during the early Carboniferous radiation is *Temnocheilus* M'Coy, 1844. It is characterized by evolute coiling with a perforate umbilicus, a trapezoidal whorl-section, and a single row of prominent nodes or tubercles along the umbilical shoulder, which persist into the adult stage. While the genus spans the entire Carboniferous and Permian, the best-described records mostly date from the late Carboniferous to the Permian (Kummel, 1964; Shimansky, 1967). Early Carboniferous occurrences are rare and often represented by very few specimens (Korn & Klug, 2023), with incomplete stratigraphic control obscuring the timing of its origination.

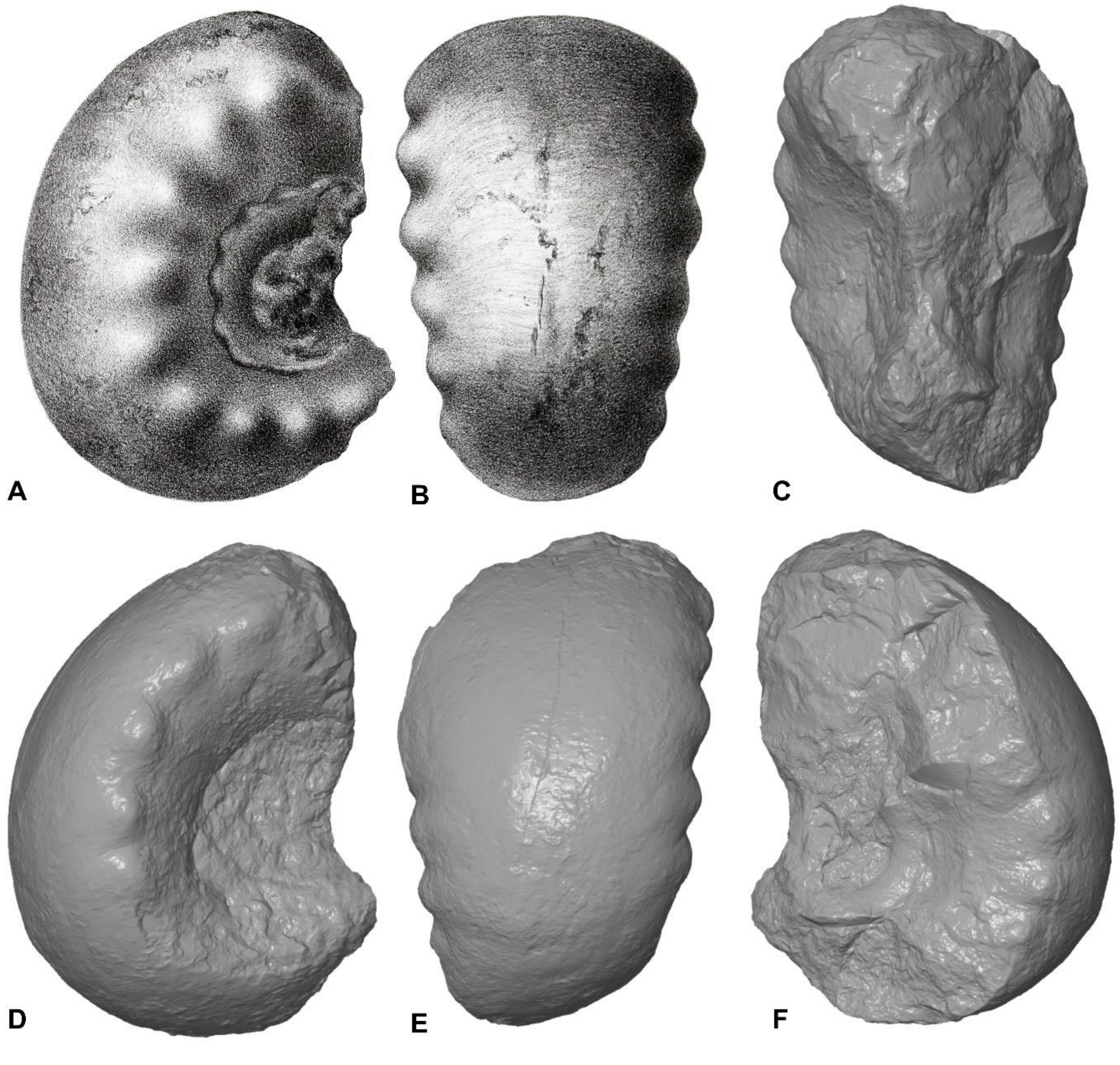


Figure 21. An example of moderate artistic enhancement of a specimen by de Koninck when describing the Carboniferous Nautilida from Belgium: *Temnocheilus coronatus* M'Coy, 1844, specimen IRSNB a03314. **A-B.** De Koninck's (1878, pl. 24, fig. 2a-b) original figuration. **C-F.** Screenshots from a 3D model, based on micro-CT imaging of the actual specimen. From Goolaerts & Mottequin (in prep.).

Figure 22. A remarkable discovery: the largest yet known specimen of the genus to date, representing also a new species of *Temnocheilus* from the Carboniferous of Belgium; unregistered CGF specimen. From Goolaerts & Mottequin (in prep.).

In Belgium, *Temnocheilus* is also rare within the otherwise rich early Carboniferous nautilid assemblages. Only two records of so-called 'tuberculati', namely *Nautilus coronatus* M'Coy, 1844 and *Nautilus latus* Meek and Worthen, 1870 were previously recorded by de Koninck (1878) from the Tournaisian and Visean. Work conducted within CT-CEPH has now doubled the number of Belgian specimens attributable to this genus. Furthermore, comparisons between the original figures by de Koninck and the physical specimens revealed notable discrepancies (see Fig. 21). Remarkably, a newly identified and exceptionally large specimen likely represents the largest known individual of the genus and may constitute a new species. A dedicated publication on these findings is in preparation.

4.2.3. Cephalopod egg cases

We were asked by researchers from the VERTIGO Brain-be project (B2/202/P1/VERTIGO) to provide our opinion on a group of enigmatic organic fossils from the late Carboniferous (Pennsylvanian) of Belgium, which had previously been suggested to represent possible cephalopod egg cases. These fossils are slightly fusiform in shape, with a surface texture composed of numerous narrow, longitudinal and often twisted filaments, resembling a tangled mass of threads (Fig. 23). They were described as *Scapellites* Pruvost, 1922, to which only two species have been assigned: the type species *Scapellites cottoni* Pruvost, 1922, and *Scapellites minor* Pruvost, 1930. Unfortunately, due to the flattened preservation of the specimens, micro-CT imaging would not yield useful internal data.

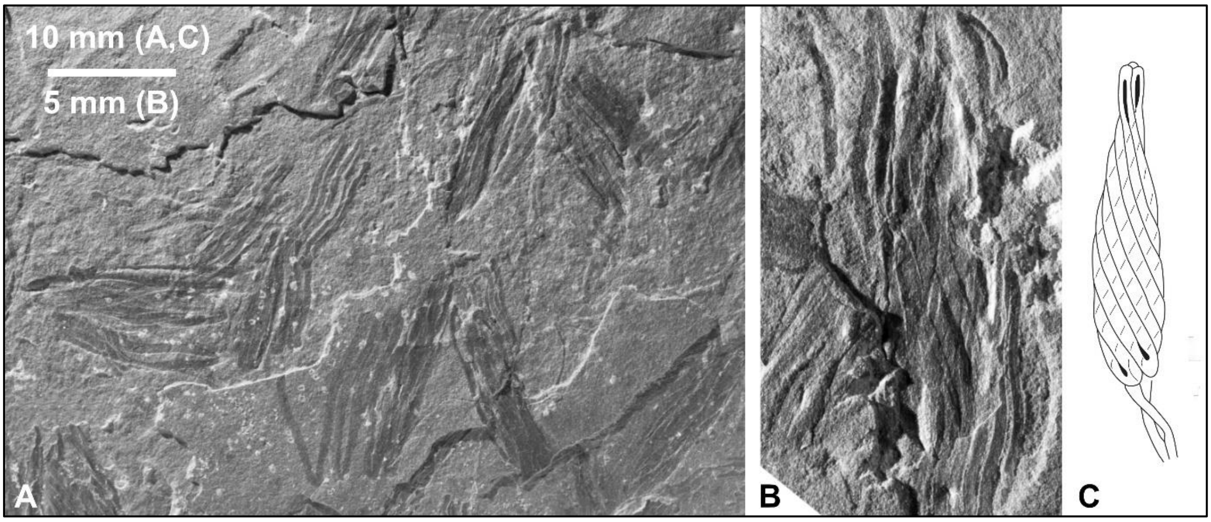


Figure 23. Enigmatic organic fossils *Scapellites cottoni* Pruvost, 1922 from the Pennsylvanian of Belgium. **A-B.** Lectotype, specimen IRSNB a7719. **C.** Facsimile of the reconstitution of *Scapellites cottoni* Pruvost, 1922 by Pruvost (1930, text-fig. 3). Modified from Mottequin et al. (2022, modified).

When Pruvost (1922) introduced *Scapellites*, he interpreted his new genus as representing egg capsules of chondrichthyan fishes, possibly *Cestracion* (= *Heterodontus*) or *Helodus*, from the coal measures, by comparison with egg capsule morphotypes of *Palaeoxyris*, *Fayolia*, and *Vetacapsula*. This interpretation was challenged by Lebrun (in Pruvost, 1922), who proposed a molluscan or cephalopod origin—an idea later supported by Renier (1942), based on the presence of the fossils in marine-influenced horizons (notably the *Gastrioceras subcrenatum* Horizon at the base of the Ransart Member, Châtelet Formation, Westphalian A) in the Liège district. However, neither Pruvost, Lebrun, nor Renier provided substantiating evidence for these interpretations.

Although exceptionally preserved early coleoids are known from Carboniferous Lagerstätten in the USA (e.g. Mazon Creek and Bear Gulch; Doguzhaeva et al., 2010; Wittry, 2012; Klug et al., 2019; Whalen and Landman, 2022), and while the fossils show some resemblance to egg clusters of modern coleoids (e.g. festoons of octopods; von Boletzky, 1998), the cephalopods recorded from the Belgian Coal Measures Group—namely ammonoids (abundant) and nautiloids (very rare)—are unlikely producers. The absence of embryonic shell remains in the structures, and the lack of equivalent fossils interpreted as cephalopod egg cases elsewhere, argue against such an origin. Moreover, extant nautiloids, and likely many fossil forms, exhibit a K-strategy involving few, large eggs (Arnold, 2010), contrasting with the structure of *Scapellites*. Still, these arguments are not definitive.

This reasoning was published in the peer-reviewed journal *The Science of Nature* (Mottequin et al., 2022). In this paper, we concluded that the producer of *Scapellites* currently remains unidentified, and that, awaiting further study, a chondrichthyan origin is the current most proper interpretation.

4.3. In search for Devonian Nautilida from Belgium

4.3.1. Belgium's oldest nautilid fossil?

The stratigraphically oldest possible nautilid fossil was, for considerable time, thought to be specimen specimen IRSNB a13851, found at Trou Bodet at Couvin by Eugène Maillieux (Figs. 24-25). It was first identified by Maillieux as *Cryptoceras*, an assignment he later changed into *Nautilus* Breyn (Maillieux, 1908, p. 175) and, in 1928, into '*Nautilus*' sp. indeterminate to genus and species level. It was also listed as *Nautilus* sp. in his unpublished inventory of the RBINS paleontology collection, in his unpublished species list for the Trou Bodet locality (recorded in the minutes of the inventory of fossiliferous localities), in the Belgian Geological Survey minutes of locality 191E0303, and on his published list of fossils occurring in the 'Cobn2' in the explanatory notes of the geological map of Couvin (Maillieux, 1912, p. 53).

Cryptoceras is an outdated and invalid name, both in the version introduced by Barrande (1846) and that by d'Orbigny (1850). Barrande's *Cryptoceras* was quickly replaced by *Ascoceras* Barrande by von Hauer, 1847; this genus remains valid and groups Silurian nautiloid cephalopods with a very distinctive conch. It is clearly *Cryptoceras* d'Orbigny 1850 that Maillieux intended. That name was later replaced by *Solenochilus* Meek & Worthen, 1870 (sometimes misspelled as *Solenocheilus*), a true member of the Order Nautilida (Family Solenochilidae Hyatt, 1893; see Meek & Worthen, 1870; Teichert et al., 1964, p. K441 and Mikesh & Glenister, 1966). The genus *Solenochilus* ranges from the Carboniferous to the Permian and is characterized by touching whorls, a depressed whorl section, a ventrally positioned siphuncle, and, large dorsolateral spines in adulthood (Teichert et al., 1964).

On internal molds of specimens that have lost all carbonate material from the shell and siphuncle, one may falsely perceive a narrow and deep external suture lobe. This phenomenon is well illustrated in Teichert et al.'s (1964, fig. 318.2a), in Demanet & Van Straelen's (1938, p. 170, pl. 129, fig. 11) specimen of *Solenochilus latiseptatus* (de Koninck, 1878) from the late Carboniferous of Bray, Belgium (refigured in Goolaerts, 2023 and here, Fig. 24), and in one of de Koninck's (1878, pl. XXII, fig. 2b) drawings of *Nautilus latiseptatus* from the early Carboniferous (Tournaisian) of Belgium. It is likely this same effect that led Maillieux to assign specimen IRSNB a13851 to *Cryptoceras*. His old label (Fig. 25) notes 'siphon sur le bord convexe' (siphuncle along the convex side).

Importantly, if the assignment to *Solenochilus* had been correct – or if the specimen had indeed belonged to the Order Nautilida – it would have been the oldest 'nautilus' fossil of Belgium and would have provided valuable data on the early evolution of the order. Basal Nautilida fossils are rare, contributing to the complexity and uncertainty surrounding the origin and higher-level classification of the group (e.g., Dzik & Korn, 1992; Manda & Turek, 2009, 2011, 2019; King & Evans, 2019). Significantly different systematic schemes and approaches were adopted in the past, and no full consensus has yet been reached. Major recent modifications to the classification of the Nautilida are the exclusion of the Rutoceratidea and the establishment of the new Suborder Lechritrochoceratina as basal nautilids (Manda & Turek, 2011, 2019).

The specimen was therefore examined using micro-CT imaging (Fig. 24F–I), which significantly enhanced its documentation. First, it revealed that the specimen is more complete than visible externally. Second, it enabled measurement of conch parameters through virtual cross-sections, showing very strongly embracing whorls (IZR = 0.39–0.57), a moderate to low expansion rate (WER = 1.64–1.77), and a narrow umbilicus (subinvolute conch) (uw/dm evolving from 0.34 at dm 17.73 mm to 0.17 at dm 38.18 mm), using the criteria defined by Korn, 2010 and Klug et al., 2015). Third, it confirmed the absence of a large, nautilid-type siphuncle and instead revealed an ammonoid-type siphuncle located near the venter (e.g., last two septa in Fig. 24G).

Together, the external and internal evidence clearly refute any nautilid affinity and support assignment of the specimen to Subclass Ammonoidea, Order Agoniatitida, Suborder Anarcestina, Superfamily Anarcestoidea, Family Anarcestidae, and more specifically to the species *Subanarcestes macrocephalus* Schindewolf, 1933. Notably, this species had not previously been recorded from Belgium and contributes significantly to the sparse ammonoid record from the Belgian Eifelian. The detailed results of this investigation were published in *Geologica Belgica* (Goolaerts, 2023).

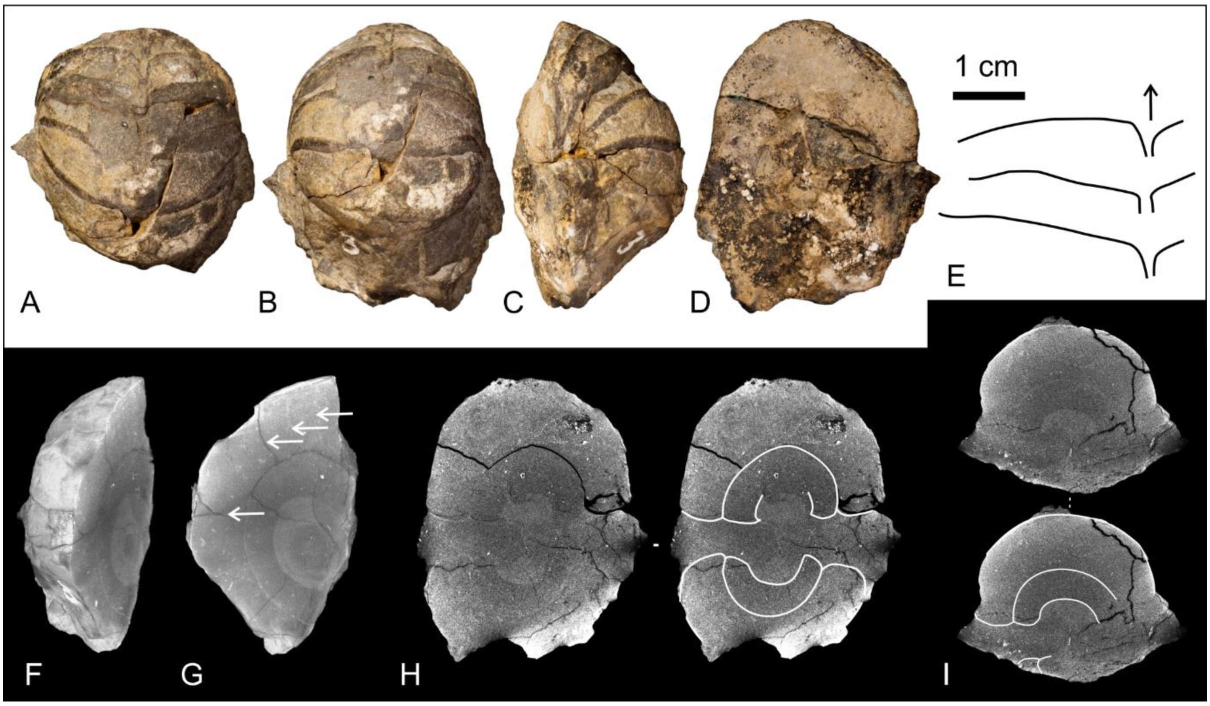
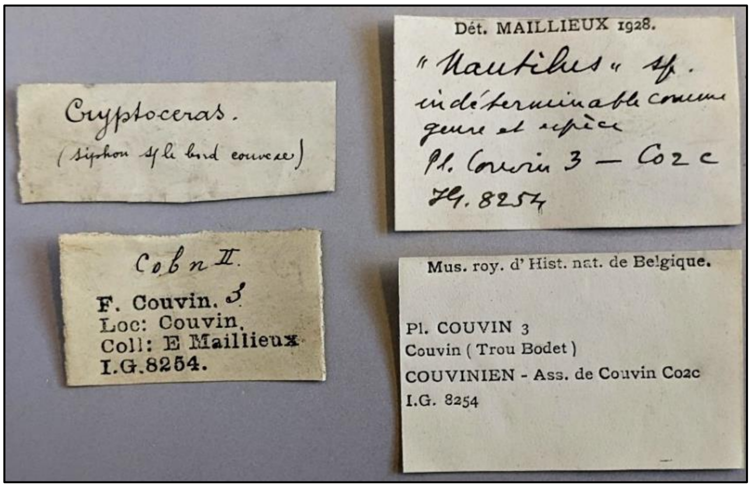


Figure 24. The specimen formerly considered as the oldest nautilid fossil from Belgium, collected from the from the ‘Couvinien’ (now Chavées Member, Jemelle Formation, Eifelian, Middle Devonian) at Trou Boudet, Couvin. Specimen IRSNB a13851 was shown through our research – particularly via micro-CT imaging, not to be a nautilid, but the ammonoid *Subanarcestes macrocephalus* Schindewolf, 1933, a species not previously recorded in Belgium. **A–D.** Ventral (A, B, D) and lateral (C) views. **E.** Drawing of sutures. **F–G.** 3D-rendering of the specimen, with virtual sectioning; note the narrower spaced septa (arrows) near the apertural end. **H–I.** Virtual cross-sections. From Goolaerts (2023, fig. 3).



Cryptoceras.
(siphon s/le bord convexe)

Dét. MAILLIEUX 1928.
"Nautilus" sp.
indéterminable comme
genre et espèce
Pl. Couvin 3 — Co2c
IG. 8254

Cob n II.
F. Couvin. 3
Loc: Couvin.
Coll: E Maillieux
I.G.8254.

Mus. roy. d' Hist. nat. de Belgique.
Pl. COUVIN 3
Couvin (Trou Bodet)
COUVINIEN - Ass. de Couvin Co2c
I.G. 8254

Figure 25. Labels associated with specimen IRSNB a13851, documenting its identification history as the presumed stratigraphically oldest nautilid fossil from Belgium. The earliest label (top left), handwritten by Eugène Maillieux, reads: '*Cryptoceras* sp. – siphon sur le bord convexe' ('*Cryptoceras* sp. – siphuncle along the convex side'). In 1928, Maillieux's revised the identification to '"*Nautilus*" sp., indéterminable comme genre et espèce' ('*Nautilus*' sp., indeterminable to genus and species). From Goolaerts (2023, fig. 5).

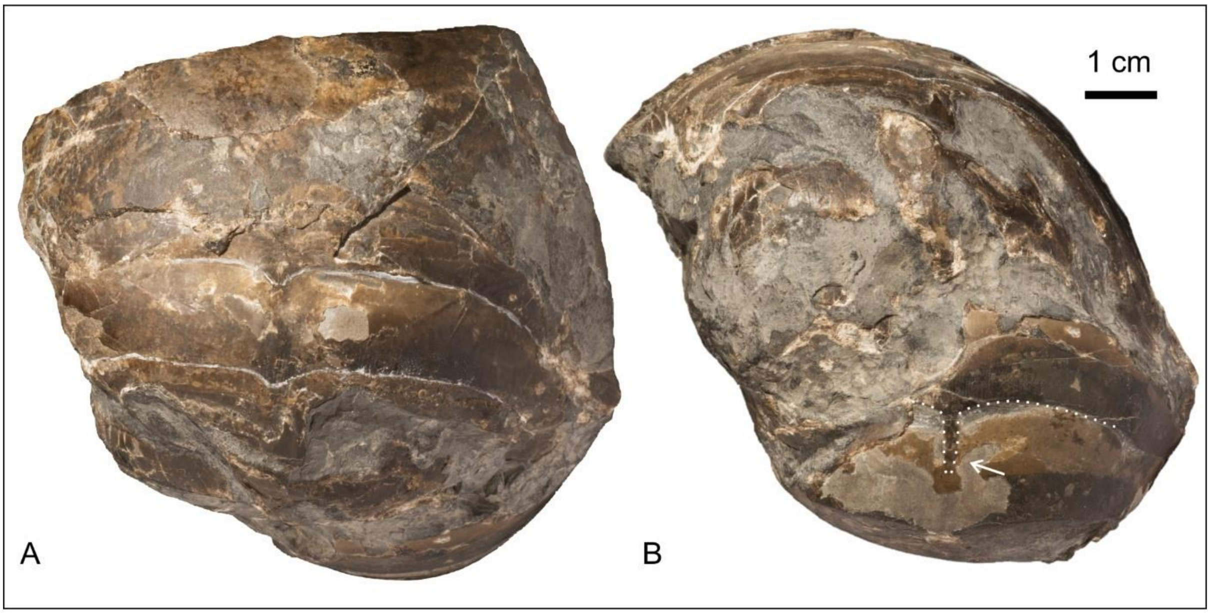


Figure 26. A–B. Example of a false narrow and deep ventral lobe in the suture of Nautilida, a visual effect caused by the siphuncle being positioned just below the venter. Shown are ventral views of specimen IRSNB a06741, identified as *Solenochilus latiseptatus* (de Koninck, 1878) by Demanet & Van Straelen's (1938, p. 170, pl. 129, fig.11) and later refigured by Demanet (1943, p. 125, pl. 5, fig. 21). The specimen originates from the 'Charbonnages de Bray' (Bray colliery), ~12 km E of Mons, from the roof of the Petit-Buisson marine horizon with ammonoid cephalopod *Anthracoceras aegiranum*, Meeuwen Member, Flénu Formation, Belgian Coal Measures Group, lower Moscovian (base of Westphalian C according to the traditional subdivision), upper Carboniferous. Lithostratigraphic nomenclature follows Delmer et al. (2002). From Goolaerts (2023, fig. 5).

4.3.2. Dupont's (1872) *Nautilus aborigenum*

One more '*Nautilus*' fossil has historically been attributed to the Belgian Devonian, namely *Nautilus aborigenum*, introduced by Dupont (1872, p. 159). The specimen was discovered during excavations at the Trou de Chaleux cave (Hulsonniaux, Houyet, Namur Province) and was associated with Magdalenian human occupation. The species name clearly refers to the ancient people who collected the specimen. The fossil consisted of a sediment cast of single chamber of a large, chambered shell said to originate from the *Psammites du Condroz* (Famennian) (Mourlon, 1881, p. 21), the Upper Devonian strata that underlie the Carboniferous limestones in which the caves system developed.

The specimen was not among type and figured specimens of the RBINS paleontology collections, nor was it catalogued in the RBINS palaeoanthropology collections. However, through collaboration with curators Patrick Semal and Ivan Jadin, the original specimen was successfully located, along with a second, fragmentary example, also consisting of a single cephalopod chamber, recovered from the same archaeological site, but out of context within the RBINS palaeoanthropology collections.

Of particular interest is that the type specimen bears figurative carving, previously described as difficult to interpret. Our preliminary reassessment (Ivan Jadin, pers. comm.) suggests a dual carving, and the second specimen shows signs of geometric engraving.

Initial macroscopic inspection of both specimens confirmed that they represent isolated phragmocone chambers of a fossil nautilid. Micro-CT imaging was initiated to further investigate the fossil and its composition to gather more data that may help to narrow down the geological age and potential source area of the material. Altogether, this allowed to firmly rule out a Devonian or even Paleozoic origin of both specimens. The preservation and overall morphology strongly suggest a post-Paleozoic provenance, possibly from outside Belgium.

Since addressing the specimen's combined paleontological and archaeological significance would involve a broader reassessment of related Magdalenian finds across Belgian and French cave sites, beyond CT-CEPH's objectives, it was excluded from further analysis within the project.

4.4. Prospects for future research

One of the clearest outcomes of the CT-CEPH project is the confirmation that micro-CT imaging has become an indispensable tool in cephalopod research. Unlike traditional methods, it offers high-resolution imaging (often well below 100 µm), using X-rays to non-destructively visualize both external and internal structures of fossils in 2D and 3D, making it particularly valuable for type and other scientifically significant specimens.

Micro-CT enables detailed 3D reconstructions and allows for virtual 2D cuts in any direction, revealing hidden characters and permitting targeted segmentation of regions of interest. It facilitates not only standard morphometric measurements but also to explore novel 3D parameters, such as chamber volumes, many of which were previously inaccessible or unreliable. These capabilities provide a more complete and objective basis for taxonomic revision and evolutionary studies.

In addition to its analytical power, micro-CT enhances scientific collaboration. Scanned fossils can be virtually ‘shared’ with colleagues across the globe, either directly or via platforms like the RBINS Virtual Collections, supporting open, reproducible research and reducing the need for physical specimen loans. In essence, a single scanned fossil becomes a digital dataset—measurable, revisitable, and re-analyzable.

Despite these advantages, micro-CT remains underutilized in nautilid cephalopod research. CT-CEPH has demonstrated that this versatile imaging method can be a game-changer, especially for the (re)description of historical types, where preservation is excellent but access has been limited. Moving forward, the use of micro-CT imaging will be standard practice in our cephalopod research—offering not only better data, but broader and more inclusive science. From a single fossil to a treasure trove of information: micro-CT is the future!

CT-CEPH revealed that the Belgian Late Cretaceous to Paleogene nautilid record stands out internationally, and that there remains an enormous amount of work to fully document the fauna in all of its details. In addition, as we also explored, our methodology can safely be adapted to other cephalopod groups, like sepiids and spirulids, for which Belgian has also a very important fossil record which needs further study.

CT-CEPH revealed the necessity to fully revise the Nautilida, and by extension all Cephalopoda, from the Belgian Carboniferous. Far more material is on hand, both in the RBINS, GCF, and ULiège collections, that was never studied in detail. For most if not all of the species introduced by L.-G. de Koninck, his in cases artistically enhanced drawings are the sole figurations available in scientific literature. This could be the topic of a follow-up project.

With the exclusion of Maillieux’s Eifelian specimen, Dupont’s *Nautilus aborigenum*, and the Rutoceratoidea, Nautilida appear to be absent in the Belgian Devonian. However, a number of putative Rutoceratoidea, as well as the entire cephalopod fauna of the Belgian Devonian are in urgent need of study. In recent years, numerous cephalopod specimens have been collected, by the authors and RBINS colleagues (e.g., at Lompret Quarry and with Brain-be project B2/202/P1/VERTIGO) as well as by private collectors, from both the Lower, Middle and Upper Devonian of Belgium, suggesting a fauna far richer than historically assumed. A few ‘Nautiloidea’ have been figured in recent literature, though without detailed taxonomic assessment (e.g., Goolaerts, 2022 - Frasnian; Mottequin et al., 2024, fig. 4X - Famennian; Olive et al., 2023 - Pragian; Lefebvre et al., 2025 - Pragian). In short, also for this time slice, Belgium’s fossil cephalopod record is of high importance and in urgent need for study.

Our CT-CEPH efforts made us invited in several studies on non-Belgian material, like e.g., on the Cenozoic cephalopods of Malta (Cilia et al., 2024), a study of Nautilida from Jordan (Goolaerts et al., in prep.), and a pathological belemnite from the Maastrichtian of Denmark (Milan et al., in prep.).

5. DISSEMINATION, VALORISATION AND EXPLOITATION

5.1. Project logo

In order to give more outreach to both the scientific community and broader public, a project logo was designed in the first weeks of the CT-CEPH project.

Figure 27. Project logo of the CT-CEPH project, designed by S. Goolaerts, used on all oral and poster presentations, on the RBINS website and the Twitter page.

5.2. Dissemination to scientific community

Results of the CT-CEPH project have been widely released to the scientific community through 5 talks and 4 posters at 6 (inter)national meetings (see also chapter 6.3):

- 1 talk with abstract (Goolaerts, 2020c) at GSA 2020 Connects Online, Topical Session T70 Cephalopods Present and Past: Insights into Evolution, Paleobiology and Links to Paleoenvironmental Change, October 26-30, 2020;
- 1 talk and 1 poster with abstracts (Goolaerts et al., 2021; Goolaerts & Mottequin, 2021) at 7th International Geologica Belgica Meeting - Geosciences Made in Belgium, at RMCA, Belgium, September 15-17th 2021;
- 1 talk and 2 posters with abstracts (Goolaerts et al., 2022b, c, d) at the 11th International Symposium Cephalopods Present and Past (ISCPP11), at Natural History Museum, London, UK, September 12-16th 2022;
- 1 talk with abstract (Goolaerts & Mottequin, 2022) at the 11th International Symposium on the Cretaceous System, at Warsaw, Poland, August 22-26th 2022 (unable to attend);
- 1 poster without abstract at Taxonomy Recognition Day at RBINS, Brussels, Belgium, May 23rd, 2024: Goolaerts, S., Mottequin, B., 2024. The power of micro-CT imaging in taxonomy. Examples from fossil Nautilida (Class Cephalopoda, Phylum Mollusca);
- 1 talk with abstract (Goolaerts et al., 2024) at The 175th Anniversary of the Maastrichtian – a Celebratory Meeting, Maastricht, the Netherlands, September 8-11, 2024.

Results of the CT-CEPH project were published through 5 research papers in peer-reviewed journals (see section 6) and others are in preparation or almost ready to submit.

An exceptionally diverse pre-K/Pg boundary nautilid fauna from the type-Maastrichtian area (the Netherlands and Belgium)

Stijn GOOLAERTS, Bernard MOTTEQUIN & John W.M. JAGT

Maastrichtian 175 years

Figure 28. First slide of talk with abstract (Goolaerts et al., 2024) for scientific audience at the 'The 175th Anniversary of the Maastrichtian – a Celebratory Meeting' at Maastricht, the Netherlands (September 8-11, 2024).

5.3. Dissemination to general public

At the beginning of the project, a Twitter page was created (https://x.com/CtCeph), and a description of the CT-CEPH project has been published on the website of the RBINS (Fig. 29): https://www.naturalsciences.be/en/science/research/ecosystems-over-time/projects/ct-ceph

as well as that of Belspo Brain:
https://www.belspo.be/belspo/Fedra/proj.asp?l=en&COD=B2%2F191%2FP2%2FCT%2DCEPH.

Three popular science texts were published, focussing on the two nautilids found in the garden of the Provincial School of Horticulture at Leuven during WWI (Goolaerts, 2020a) (see section 4), showcasing the differences between the phragmocone of stem-group sepiids and stem-group spirulids in a report on the astonishing observation of a living spirulid (Goolaerts, 2020b), and an account on Devonian Nautiloidea in an exhibition guide (Goolaerts, 2022) (see section 6.2). In addition, a synopsis of our paper on *Belosaepia* was included in the RBINS annual report 2022 (Goolaerts & Mottequin, 2023a,b,c).

Results of the CT-CEPH project have been widely released to the broader public through 3 talks and 2 posters at 5 events:

- 1 talk without abstract at PaleoTime, Sunday Nov 12th 2023, at Herselt, Belgium, 70 people (Goolaerts, S., 'Ammoniet & Nautilusfossielen in de CT-scanner', in Dutch, see also Fig. 30);
- 1 talk without abstract at 'Celebration 175th anniversary Maastrichtian' at Oertijdmuseum, Boxtel, the Netherlands, Saturday April 20th 2024, 120 people. Goolaerts., S., 'Over unieke nautilus en ammonietenfauna's en hun date met de CT-scanner', in Dutch, organized by the 'Landelijke Vereniging Geologische Activiteiten or LVGA');

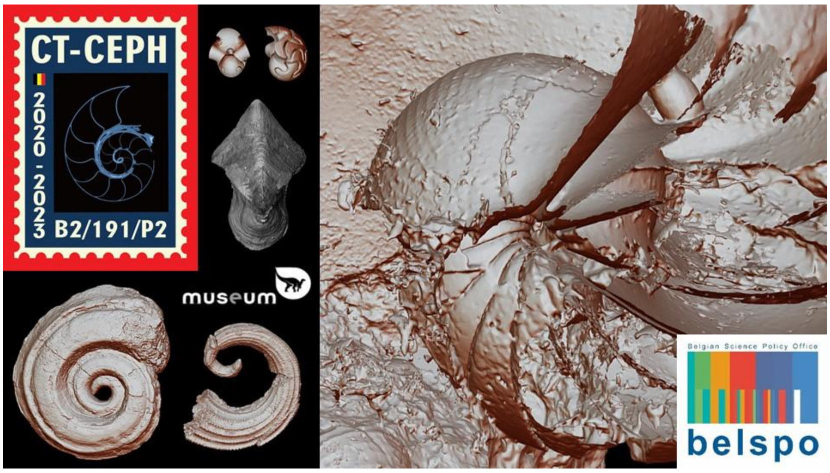


Figure 29. Figure produced for the RBINS website, with the logos of Belspo, the project and the RBINS, with both Paleozoic, Mesozoic and Cenozoic Nautilida, made by S. Goolaerts.

Figure 30. Flyer distributed on social media (Facebook, Twitter) advertising the talk for broad audience at PaleoTime-Be, figuring three nautilid fossils, two that were imaged by micro-CT (transparent 3D render on the left, virtual 2D cut on the right).

- 1 workshop without abstract at Genk, Belgium for the the 'Werkgroep Krijt & Vuursteen' (15 people), Sunday March 10th 2024. Goolaerts, S., 2024. 'Hoe divers zijn Nautiliden uit ons Maastrichtiaan', in Dutch;
- 1 poster without abstract at BePaleo 2024, at RBINS, Belgium, April 27th 2024 (recycling of Goolaerts et al., 2022d presented at 11th ISCPP);
- 1 poster without abstract at BePaleo, RBINS, Brussels, Belgium, March 29, 2025 (recycling of poster Goolaerts, S., Mottequin, B., 2024. The power of micro-CT imaging in taxonomy. Examples from fossil Nautilida (Class Cephalopoda, Phylum Mollusca - presented at Taxonomy Recognition Day 2024).

6. PUBLICATIONS

6.1. Peer-reviewed research papers

Goolaerts, S., Christiaens, Y., Mollen, F., **Mottequin, B.** & Steurbaut, E., 2022a. 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. *Rivista Italiana di Paleontologia e Stratigrafia* 128(3): 585-606. [Open access] https://doi.org/10.54103/2039-4942/16617

Mottequin, B., Fischer, J., **Goolaerts, S.** & Olive, S., 2022. Revisiting the chondrichthyan egg capsules inventory from the Pennsylvanian (Carboniferous) of Belgium: new data and perspectives. *The Science of Nature* 109:39. https://doi.org/10.1007/s00114-022-01809-6

Goolaerts, S., 2023. On the first Belgian record of the Eifelian (Middle Devonian) ammonoid cephalopod *Subanarcestes* (Suborder Anarcestina). *Geologica Belgica*, 26(1-2), 93-100. https://doi.org/10.20341/gb.2023.004 [Open Access]

Goolaerts, S. & **Mottequin, B.**, 2023. A Santonian record of the nautilid cephalopod *Angulithes westphalicus* (Schlüter, 1872) from the subsurface of the Campine, north-east Belgium, with comments on regional lithostratigraphic problems. *Geologica Belgica* 26(1-2), 101-113. https://doi.org/10.20341/gb.2023.007 [Open Access]

6.2. Popular scientific papers

Goolaerts, S., 2020a. Twee nautilusfossielen gevonden in de Donkerstraat in Leuven! *HONA* 55(1): 37-42. [in Dutch]

Goolaerts, S., 2020b. Spiraaltjes op het strand en onderste boven in de oceaan: de Posthoorninktvis *Spirula spirula* weet iedereen te verbazen. *HONA* 55(4): 56-58. [in Dutch]

Goolaerts, S., 2022. Les céphalopodes nautiloïdes et ammonoïdes. *Lompret-sur-Mer, Merveilles géologiques de la Fagne, Catalogue d'exposition, Musée du Marbre Rance*, 24-27. [in French]

6.3. Conference proceedings

Goolaerts, S., 2020c. Applying micro-CT imaging in the study of fossil sepiids and nautilids (Cephalopoda): examples from the Eocene of Belgium. GSA 2020 Connects Online. *Geological Society of America Abstracts with Programs* 52/6, 135-3. https://doi.org/10.1130/abs/2020AM-357179

Goolaerts, S. & **Mottequin, B.**, 2021. CT-CEPH: Applying micro-CT imaging in the study of Belgian fossil Nautilid Cephalopods. *In* Delvaux, D., Dewitte, O., Fernandez-Alonso, M., Hubert-Ferrari, A. & Elsen, J. (eds), 7th International Geologica Belgica Meeting 15-17 September 2021 - AfricaMuseum Tervuren (Belgium), Geosciences Made in Belgium, Conference Program and abstract book. *Geologica Belgica Conference Proceedings* 4 (2021), 195-196. https://doi.org/10.20341/gbcp.vol4

Goolaerts, S., Locatelli, C., Brecko, J., d'Udekem D'Acoz, C., Folie, A., Henrard, A., Mathys, A. & Van De Gehuchte, E., 2021. X-ploring new tools for paleontologists: the RBINS-RMCA micro-CT lab at your service! *In* Delvaux, D., Dewitte, O., Fernandez-Alonso, M., Hubert-Ferrari, A. & Elsen, J. (eds), 7th International Geologica Belgica Meeting 15-17 September 2021 - AfricaMuseum Tervuren (Belgium), Geosciences Made in Belgium, Conference Program and abstract book, *Geologica Belgica Conference Proceedings* 4 (2021), 197-198. https://doi.org/10.20341/gbcp.vol4.

Goolaerts, S., d'Udekem d'Acoz, C., Folie, A., Locatelli, C., Mathys, A., **Mottequin, B.**, Samyn, Y. & **Semal, P.**, 2022b. Into the digital cephalopod world: tales from digitizing the Cephalopoda from the RBINS type-and-figured collections. 11th International Symposium Cephalopods Present and Past (ISCPP11), NHM London, UK, Sep 12-16th 2022. Abstract book, p. 5-6.

Goolaerts, S., **Kruta, I.**, Tajika, A., Hughes, Z. & Landman, N., 2022c. An 85-million-year-old diet: buccal mass and digestive system in fossil and extant Nautilida. 11th International Symposium Cephalopods Present and Past (ISCPP11), NHM London, UK, Sep 12-16th 2022. Abstract book, p. 32-33.

Goolaerts, S., Houben, H., Tolisz, N., Coron, J., Devleeschouwer, X. & Gouwy, S., 2022d. From minions to giants: exceptional upper Devonian cephalopods from the Lompret quarry, Belgium. 11th International Symposium Cephalopods Present and Past (ISCPP11), NHM London, UK, Sep 12-16th 2022. Abstract book, p. 33-34.

Goolaerts, S. & **Mottequin, B.**, 2022. A DIGITAL CEPHALOPOD WORLD: micro-CT imaging in the study of Cretaceous Cephalopod. In Jagt, J.W.M., Jagt-Yazykova, E., Walaszcyk, I. & Zylinska, A. (eds), 11th International Cretaceous Symposium, Warsaw, Poland, August 22-26th 2022, Abstract Volume, 169-170.

Goolaerts, S., **Mottequin, B.** & **Jagt, J.W.M.**, 2024. An exceptionally diverse pre-K/Pg boundary nautilid fauna from the Maastrichtian type area (the Netherlands and Belgium). In Jagt, J.W.M., Jagt-Yazykova, E.A., del Prado-Rebordinos, A., Teschner, E.M. (eds), The 175th Anniversary of the Maastrichtian – a Celebratory Meeting Maastricht, September 8-11, 2024, Abstract Volume and Programme, 54-55. ISBN 9789464916560.

7. ACKNOWLEDGEMENTS

Many people have participated to some extent in the success of our project and deserve a warm thank you. From the RBINS, we would like to thank the following colleagues who helped with analyses or access to bibliographical resources, physical and/or digital specimens and collections: dr. Marie Coen-Aubert, Cécilia Cousin, Marleen De Ceukelaire, Alain Dreze, dr. Cédric d'Udekem d'Acoz, Julien Lalanne, dr. Annelise Folie, Thierry Hubin, dr. Ivan Jadin, Camille Locatelli, Aurore Mathys, dr. Etienne Steurbaut, Nathan Vallée-Gillette, Reinout Verbeke. From the RMCA, we especially thank curator dr. Florias Mees. Further on, we got help from a large number of citizen-scientists and fossil collectors, in particular from Yoeri Christiaens (RBINS), Bert Gijsen (ERB), Frederik Mollen (ERB), Ludo Indeherberghe (WKV), Viktor Strybos (WKV),

palaeontologists who collaborated on the CT-CEPH project and/or helped us identify fossil specimens and/or their age, or brought material to our attention: dr. John W.M. Jagt (Natuurhistorisch Museum Maastricht), prof. dr. Eddy Poty (ULiège), prof. dr. Valentin Fischer (ULiège), dr. James Witts (AMNH), prof. dr. Neil Landman (AMNH),

CT-CEPH also benefited from research trips to collections in Europe and the USA executed prior to the start of the project, but which proved essential for its execution, for which we would like to thank in particular Zoë Hughes (NHM), dr. Dieter Korn (MfN), dr. Didier Merle (MNHN), Jean-Michel Pacaud (MNHN), dr. Jonas Hagström (NRM), Bushra Husseini and dr. Neil H. Landman (AMNH), and the Synthesys and AMNH Collection study grant programs.

We warmly thank the members of the CT-CEPH follow-up committee: prof. dr. I. Kruta (Sorbonne University), dr. J.W.M. Jagt (Natuurhistorisch Museum Maastricht), dr. B. Kröger (Finnish Museum of Natural History), dr. Andy King (Geckoella Ltd), and dr. P. Semal (RBINS).

Finally, we warmly thank Belspo for the funding, both for CT-CEPH project, as well as for the DiSSCo-Fed (2018-2023) and DIGIT-04 (2019-2024) projects supplying access to micro-CT imaging, and the help throughout the duration of the project.

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