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An exceptional concentration of marine fossils associated with wood-fall in the Terhagen Member (Boom Formation; Schelle, Belgium), Rupelian of the southern North Sea Basin

This paper is dedicated to the memory of Dr Jacques Herman (1948–2022), for his longstanding contributions to the knowledge of extinct and extant elasmobranch fishes.

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ABSTRACT

A large fragment of driftwood was discovered in the marine Terhagen Member (Boom Formation, NP23) at Schelle (Belgium), representing the first well-documented case of wood-fall in the Rupelian of the North Sea Basin. This trunk with a side-branch, identified as *Cupressinoxylon* sp. (Cupressaceae), caused a large irregularity on the sea bottom, creating a unique microenvironment which allowed colonization by some taxa virtually absent elsewhere in the Boom Formation. The fossils were further concentrated in a silty lens against the trunk by the effects of prolonged wave-driven turbulence. This lens comprised a large set of compartmental plates of the turtle barnacle *Protochelonibia hermani* Gale sp. nov., possibly part of a single colony originally attached to a turtle. The material includes the best preserved plates of *Protochelonibia* known to date, yielding new information on the construction of its shell. Additionally, a disarticulated tooth set of 154 teeth of *Carcharias contortidens* (Agassiz, 1843) was found, the first such discovery in more than 100 years. An articulated dentition of this taxon, initially studied by Leriche (1910), is refigured herein. Some very rare valves of the bivalve *Palliolum permistum* (Beyrich, 1848) are identified and the gastropod *Amblyacrum* cf. *roemeri* (von Koenen, 1867) is reported here for the first time from the Belgian Rupelian. The teleost otolith assemblage comprises ca 30,000 specimens belonging to 11 species only, of which *Trachurus reineckei* Hoedemakers sp. nov. is new to science and *Myoxocephalus primas* (Koken, 1891) and *Capros siccus* Schwarzhans, 2008 are new for the Belgian Rupelian. The new species represents the earliest record of the thermophilic genus *Trachurus* in the Oligocene of the North Sea Basin. *Liparis minusculus* Nolf, 1977 is synonymized with *Myoxocephalus primas*, whereas *Erythrocles ohei* Schwarzhans, 1994 is transferred to the genus *Trachurus*.

KEYWORDS

Oligocene,
wood-fall,
Elasmobranchii,
mollusca,
teleostean otoliths,
turtle barnacles,
Cupressaceae,
palaeoenvironment

1. Introduction

The essentially clayey Boom Formation was deposited in an open marine environment at the southern border of the North Sea Basin during the Rupelian (early Oligocene). It is one of the thickest and most intensively studied stratigraphic units of Flanders (northern Belgium) and is of considerable scientific and industrial interest. The Boom Clay is studied in the subsurface as a potential host rock for nuclear waste. For more than two hundred years, the clay has been excavated for the brick and roof tile industry in both the Rupel (province of Antwerp) and Waasland regions (province of Oost-Vlaanderen); numerous abandoned clay pits shape the landscape today. The thick clay deposits around the Rupel River are the historical stratotype for the international Rupelian stage (Van Simaeys & Vandenberghe, 2006; Speijer et al., 2020). However, the Rupelian Global Boundary Stratotype Section (GSSP) in the Italian Massignano section is about 1.5 to 2 million years older than the base of the historical stratotype (Speijer et al., 2020). The Boom Formation is known for its diverse macrofauna, including elasmobranchs (e.g. Van Beneden, 1860; Leriche, 1910; Steurbaut & Herman, 1978; Hovestadt & Hovestadt-Euler, 1995), teleost fishes (e.g. Nolf, 1977, Steurbaut & Herman, 1978, Taverne et al., 2006) and molluscs (e.g. Nyst, 1835, 1845; De Koninck, 1838; Vincent, 1930; Glibert, 1955, 1957; Marquet, 2010, 2016). In the 19th and early 20th centuries, the clay was generally extracted manually, resulting in the discovery of numerous spectacular fossils, including associated elasmobranch and teleostean remains. From the Boom Formation, Leriche (1910) mentioned an articulated dentition of *Carcharias contortidens* (Agassiz, 1843), commonly listed in the palaeontological literature with the specific name of *Carcharias acutissima* (Agassiz, 1843) and refigured herein. Although macrofossils in the Boom Formation are generally sparsely distributed, some levels proved to contain slightly higher concentrations of isolated fossils (Steurbaut & Herman, 1978).

In 2008, an exceptional discovery was made in the Ceulemans clay pit, located in the municipality of Schelle (Fig. 1). A large fragment of driftwood, about three meters long, was found on top of the pink 'R horizon' in the Terhagen Member (Boom Formation). It was surrounded by a small silty lens, containing a rich assemblage of elasmobranch and teleost remains, molluscs and barnacles. Many of these finds are very rare; the irregularity caused by the driftwood on the seabed provided a unique opportunity to preserve a palaeontological biocoenosis of species that lived together in the vicinity of the sunken trunk during a constrained period of time. Some species are new to science. In the present paper, a general overview of the recorded fossil assemblage is presented and ecological considerations are made based on the recorded invertebrates and teleost otoliths.

2. Geological background

A strong global cooling occurred around the NP21/NP22 biochron boundary (Prothero et al., 2003), about 200,000 years after the start of the Oligocene (Bohaty et al., 2012; Hutchinson et al., 2021). As the Antarctic icecap was rapidly expanding, the global sea level dropped several tens of meters (Miller et al., 1991, 2005). In the Antwerp–Rupel area (northern Belgium), this global sea-level drop is reflected in a regression marked by an erosive surface (Vandenberghe et al., 2003; Vandenberghe, 2017). Afterwards clayey to silty lagoonal sand (Wintham Silt?) was deposited in the study area, covered by the shallow marine sand of the Ruisbroek Member (lowstand systems tract) during biochron NP22 (Steurbaut, 1992; Vandenberghe et al., 2003). At the time of the NP22/NP23 biochron boundary, sedimentation ceased and the sea bottom became cemented, probably due to the upwelling of phosphate. When transgression resumed, this apatite-hardground was broken up, slightly reworked and covered by the silty clays of the Boom Formation (Vandenberghe et al., 2002; Herman & Marquet, 2012; Herman

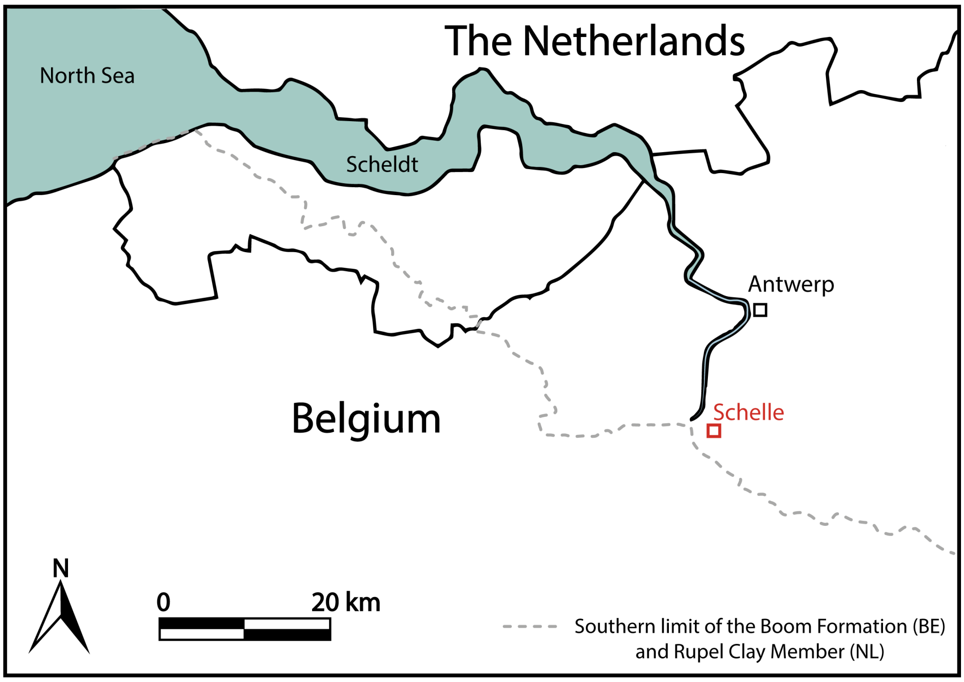

Figure 1. Location of the Ceulemans clay pit at Schelle (51°07'01.22" N, 4°21'21.30" E). The southern limit of the Boom Formation is based on Vis et al. (2016) and Vandenberghe (2017). The former also mapped the southern limit of the Rupel Clay Member, the Dutch equivalent of the Boom Formation.

et al., 2013).

The Boom Formation is the historical unit stratotype of the Rupelian. It consists of laterally continuous, banded layers with rhythmic variations in silt/clay content, carbonate and organic material (Vandenberghe, 1978), representing glacio-eustatic sea-level oscillations (Vandenberghe et al., 1997; 1998). Abels et al. (2007) showed that these glacio-eustatic sea-level oscillations were largely driven by the 41 ka obliquity cycle, with a secondary influence of the 100 and 405 ka eccentricity. Lower frequency grain-size cycles could also be influenced by vertical tectonics in and around the basin (Vandenberghe & Mertens, 2013). Lithostratigraphically, the Boom Formation is subdivided into the very silty Belsele-Waas, the grey Terhagen, the black Putte and the silty Boeretang members, with the latter being only present in the Campine subsurface, where the Boom Formation can reach a thickness of up to 140 m (Vandenberghe et al., 2001, 2014). The Terhagen Member, of further interest in the present paper, was deposited within calcareous nannoplankton zone NP23 (Steurbaut, 1992, fig. 8).

In the past decades, the sequence stratigraphy of the Boom Formation has been widely established, and multiple third-order eustatic sequences have been recognized within its grain-size distributions (Vandenberghe et al., 1998, 2004). Starting from the base of the Boom Formation (the phosphate bed), a grain-size fining upward trend is observed throughout the Belsele-Waas and lower Terhagen members. Maximum fining is reached within the pink R-horizon (Terhagen Member) (Fig. 2), which is consequently interpreted as the first maximum flooding surface, with the deepest bathymetry of the Terhagen Member (Vandenberghe et al., 1998, 2014). Above, the sediment coarsens slightly upwards until the very silty, fine sandy Double Band (DB), which is a key level in the Putte Member. Studying benthic foraminifera in these successions, De Man & Van Simaeys (2004) estimated water depths of around 100 m and noted that deposition occurred in a normal marine shelf environment with open marine connections to the oceanic realm. Moreover, they mainly recovered cold- to cold-temperate taxa, estimating that the bottom water palaeotemperature always remained between 5 and 10 °C (De Man & Van Simaeys, 2004, fig. 4). Vandenberghe et al. (2014) suggested that water depths varied between 50 m in the silty clay layers and 150 m in the pure clay layers. The sea bottom was periodically within and beyond the wave turbulence base and silty beds formed when the wave turbulence reached the sea bottom.

3. Location and stratigraphy of the clay pit

The Ceulemans clay pit at Schelle (51°07'01.22" N, 4°21'21.30" E), formerly known as the Steenbakkerij Damman, is located in the province of Antwerp, northwestern Belgium (Fig. 1). In this quarry, both the Terhagen Member and the lower part of the Putte Member are exposed. The fossil assemblage was encountered on top of the pink R-horizon (base of bed 22 sensu Vandenberghe et al., 2014, fig. 12) in the Terhagen Member (Fig. 2), which can be attributed to the early Rupelian NSO3 dinoflagellate biozone (between 31.6–30.9 Ma) of Van Simaeys et al. (2005) and the NP23 calcareous nannoplankton zone (Steurbaut, 1992; Vandenberghe et al., 2014), and is dated at approximately 31.5 Ma (based on Lagrou et al., 2004 and Speijer, et al., 2020).

4. Material and methods

In June 2008, a large fragment of driftwood was observed on the surface of the clay pit; unfortunately it had already been partially shattered by the dredger. The large trunk, measuring around 3 m in length and oriented in a north-south direction, was carefully excavated (Plate 1). A side-branch of ca 80 cm in length was oriented in a south-east direction. Enclosed between the main trunk and the side-branch, a locally restricted fossiliferous lens of more coarse, silty sediment was encountered. The entire lens, almost 300 kg in mass, was sampled in plastic bags. The silty sediment was then broken into smaller pieces, dried and subsequently wet-sieved through mesh sizes of 2, 1 and 0.3 mm. This whole process took around three months. The residues were then handpicked for fossils (Fig. 3). A sediment sample is stored at the Geological Survey of Belgium to allow micropalaeontological analyses in the future.

The fossil material figured in this paper is housed in the collections of the Royal Belgian Institute of Natural Sciences (RBINS; Brussels) under registration numbers IRSNB P 10299 to P 10349, 7705 to 7736 and b9669–9670 (see Table 1). In

Figure 2. Stratigraphy of the Ceulemans clay pit (Schelle) in June 2008. The Putte and Terhagen members are indicated, together with some stratigraphic reference levels (S = Septaria levels; DB = Double band; R = pink R-level; after Vandenberghe et al., 2014). The sunken trunk lay on top of the R-horizon in the Terhagen Member (indicated by the arrow).

addition, some representative specimens of *Cocculina reineckei* and *Palliolum permistum* have been donated to the palaeontological collection of Senckenberg Forschungsinstitut (Frankfurt, Germany).

5. Palaeontology

5.1. Plantae (JS & VK)

Systematics follows Christenhusz et al. (2011).

Subclass Pinidae Cronquist, Takhtajan & Zimmermann, 1966 (= conifers)
Order Cupressales Link, 1829
Family Cupressaceae Gray, 1822
Genus *Cupressinoxylon* Göppert, 1850

***Cupressinoxylon* sp.**
Plate 2.A–F (Sample: IRSNB b9669) and Fig. 4 (IRSNB b9670)

By the absence of (1) normal resin canals and spirals on tracheid walls, and the presence of (2) rather abundant axial parenchyma, (3) uniseriate abietoid pitting on radial tracheid walls, and (4) cupressoid cross-field pitting (Plate 2), we can confidently assign the wood to the family Cupressaceae (see Teodoridis & Sakala, 2008, p. 300), more precisely to the Cupressaceae *sensu stricto* (see Sakala, 2003). According to the key presented by Vaudois & Privé (1971), (1) the absence of both juniperoid and callitroid thickenings, (2) the regular presence of axial parenchyma with smooth transverse end walls, (3) cupressoid cross-field pits, (4) smooth horizontal ray walls, and (5) the roundish shape of the tracheids in cross-section strongly point in the direction of the *Cupressinoxylon* A/ *Tetraclinoxylon* complex. Hence, regarding its preservation, where some key features are missing or only hardly visible, we propose to leave our wood in open nomenclature and designate it as *Cupressinoxylon* sp. This fossil genus is regularly recorded in the Tertiary floras of Europe (e.g. Dolezych & Schneider, 2006; Kłusek, 2014).

We used the following combination of features sensu Esteban et al. (2004): P5 (axial parenchyma with resin) and R34 (ray parenchyma with resin), which are both very conspicuous in our fossil (Plate 2A–E). Compared to similar types of modern wood, such a combination is present in *Hesperocyparis* (= *Cupressus*) *bakeri* Jeps., *Cupressus goveniana* Gordon var. *goveniana*, *C. guadalupensis* S. Watson, *C. lusitanica* Mill var. *benthamii* (Endl.) Carrière, and *C. sempervirens* L. (Esteban et al., 2004). Since this fragment of Rupelian driftwood does not allow to define a more specific relationship with present-day species, we refrain from a detailed comparison or illustration. Interestingly, all aforementioned species, except for *C. sempervirens*, are typical of today's North American region (Román-Jordán et al., 2016).

5.2. Cirripedia (AG)

Class Thecostraca Gruvel, 1905
Infraclass Thoracica Darwin, 1854
Superorder Thoracicalcarea Gale, 2015
Order Balanomorpha Pilsbry, 1916
Superfamily Coronuloidea Leach, 1817
Family Chelonibiidae Pilsbry, 1916

Figure 3. Fossil accumulation after sieving, yielding wood fragments, shark teeth, mollusc debris and otoliths, ready to be handpicked.

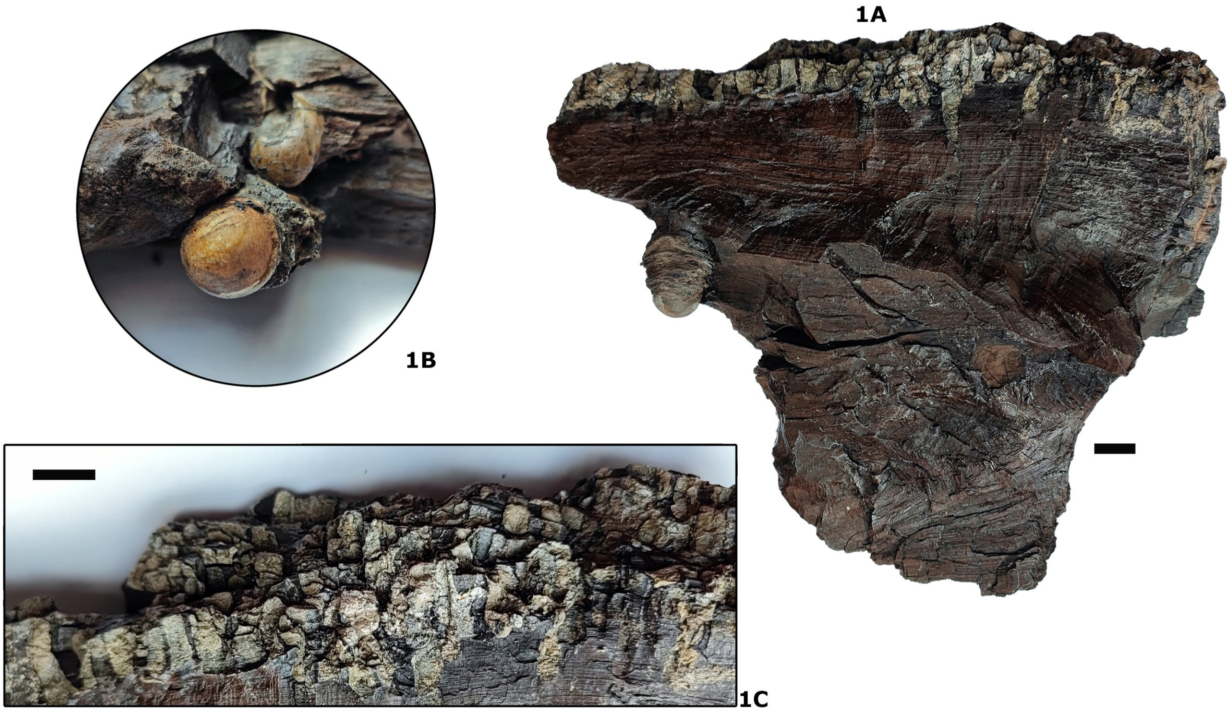

Figure 4. *Cupressinoxylon* sp. wood fragment (IRSNB b9670). **1A.** General view. **1B.** Detail of globular casts of teredinid shells (maximum diameter 12 mm). **1C.** Detail of dense network of teredinid borings in the bark. Some borings penetrate the wood to depths of 6 cm. Scale bars = 10 mm.

Remarks. Harzhauser et al. (2011) created the subfamily Protochelonibiinae to accommodate their genus *Protochelonibia.* However, as discussed below, the genus is remarkably close morphologically to *Chelonibia* itself. Furthermore, molecular studies (Pérez-Losada et al., 2014) place only two extant genera in the Chelonibiidae, *Chelonibia* itself and *Stephanolepas* Fischer, 1886, a small barrel-shaped taxon which embeds in turtles and was previously referred to the Platylepadidae (e.g. Hayashi, 2013). This genus is morphologically very different from both *Chelonibia* and *Protochelonibia*, and Zonneveld et al. (2022) do not consider it to be a chelonibiid. Therefore, I provisionally leave all three taxa as Chelonibiidae without any subfamilial designation.

Genus *Protochelonibia* Harzhauser & Newman, 2011

Diagnosis. Shell wall made up of 8 plates, unfused rostrum and rostromarginals; profile low, sides straight to weakly concave; articular sutures between compartments simple; septa thin, do not reach basal margin. Inner lamina absent.

Type species. *P. submersa* Harzhauser & Newman, in Harzhauser et al., 2011.

Included species. In addition to the type species, *Chelonibia melleni* Zullo, 1982, *P. starnesi* Perreault et al., 2022; *P. hermani* sp. nov. and possibly *Chelonibia capellinii* De Alessandri, 1895.

Discussion. There is some uncertainty as to the number of species of *Protochelonibia* and precisely how these are diagnosed. Harzhauser et al. (2011) used the "depressed profile" as a diagnostic character of *P. submersa* as distinguishing it from the higher profile of *P. capellinii* (De Alessandri, 1895); however, as the type material of *P. submersa* is flattened by compaction (see Harzhauser et al., 2011, fig. 2)—the valves are broken and some separated—this is not really a valid argument. Harzhauser et al. (2011) also stated that the internal ribbing in *P. submersa* showed irregular development, as compared to the regular primary, secondary and tertiary ribbing in *P. capellinii*; however, a further specimen of *P. capellinii* figured by De Alessandri (1906, pl. 18, fig. 4) also has irregular ribbing. Both species are of early Miocene age, and were found approximately 600 km apart, no great distance for cirripedes attached to swimming sea turtles. For these reasons, *P. submersa* is probably a subjective junior synonym of *Chelonibia capellinii* De Alessandri, 1895. A decision must await redescription and better illustration of *C. capellinii*.

Zullo (1982) described *Chelonibia melleni* from the Lower Oligocene of Mississippi, USA, on the basis of five isolated compartments, including a carina, a rostrum, two rostromarginals and a marginal or carinomarginal plate. This species was subsequently referred to *Protochelonibia* (Collareta & Newman, 2020), and *P. melleni* was later identified from the Oligocene (Rupelian) of Germany, on the basis of a crushed colony (Collareta et al., 2021) and specimens attached to a turtle (Collareta et al., 2022b) from the Rauenberg lagerstätte in southern Germany. Collareta & Newman (2020) argued that *Protochelonibia* differed from *Chelonibia* in the unfused rostrum-rostromarginals, and in the acutely triangular apices of these compartments. They also considered that *P. melleni* and *P. submersa* differed primarily in the presence of a corrugated basal compartmental margin on a single plate (Zullo, 1982, figs 1–2). Recently, Perreault et al. (2022) described a new species of *Protochelonibia*, *P. starnesi*, from the Early Oligocene of Mississippi, USA, from which they also recorded and figured a well-preserved carinomarginal of *P. melleni* (Perreault et al., 2022, fig. 3). This specimen provides details of the interior structure of the plate, refigured here (Fig. 5) for comparison with *P. hermani* sp. nov. (Plate 3.1–3, 5–7; Plate 4.1–7; Plate 5.1, 3, 5–7; see below).

New investigations of extant *Chelonibia* show that the rostrum and rostrolaterals are in fact unfused in *C. testudinaria* forma *patula* (Plate 3.4, 8), although the sutures are not visible on the external surface (Plate 3.4B). Also, the apices of the rostral and rostromarginal parietes are equally acutely triangular in both *C. patula* and *Protochelonibia* (compare Plate 3.2, 5–7 with Plate 3.4, 8). *Chelonibia* and *Protochelonibia* differ most significantly in the following characters:

- In lateral profile, *Protochelonibia* has a low, domed form with slightly concave sides ventrally (Plate 3.3; Plate 5.6) and straight sides dorsally (Plate 5.1C, 3C). *Chelonibia*, in contrast, has the form of a rounded dome with convex sides (Plate 5.2, 4), less convex ventrally.
- The sutures between compartments are different in the two genera. In *Protochelonibia* the contact between the rostrum and rostromarginals (Plate 5.6) is smooth, showing only growth lines, whereas in *C. testudinaria* forma *patula* the plates articulate by fine ridges and intervening grooves (Plate 5.4). Articulations between the rostromarginals, marginals and carinomarginals are complex in *C. testudinaria* forma *testudinaria* (e.g. Plate 5.2C) which has an oval, elongated facet on the ala bearing divergent grooves and ridges for articulation with the ridged radial margin of the adjacent plate (a in Plate 5.2C). The homologous surface is poorly developed in *Protochelonibia* (Plate 5.5). A further surface is present in *C. testudinaria* forma *testudinaria* (Plate 5.2C) which comprises interlocking denticles, entirely absent in *Protochelonibia* (Plate 5.5).
- The external surface of the parietes of *Protochelonibia* species (e.g. Plate 3.2B, 5B; Plate 4.1B, 3A; see also Zullo, 1982, figs 14, 5, 8, 11; Harzhauser et al., 2011, fig. 2a; Collareta et al., 2021, fig. 2) bears an apicobasal sculpture comprising either very fine ribs when worn (e.g. Plate 3.1–2) or more widely separated narrow grooves between low, weakly convex ribs (e.g. Plate 5.1B). In contrast, the external surfaces of *Chelonibia testudinaria* are either smooth with weak commarginal growth lines (Plate 3.4B, 8B, 9B) or weakly reticulate (Plate 5.2B).
- The septa have very different structures in the two genera (Perreault et al., 2022). In *Protochelonibia*, these are thin (notably crushed in some specimens—e. g. Plate 3.5A), smooth, and do not all descend to the basal surface. In *Chelonibia*, the septa are robust, striated vertically, and flush with the basal margin (Plate 5.2A). The ribbing is expressed internally as interpenetrant V-shaped bundles of calcite crystals (Collareta et al., 2022a, fig. 5c).
- In *Chelonibia* an inner lamina descends from the sheath to the basal margin—*C. testudinaria* forma *testudinaria* (Plate 5.2A), or as a series of flat prongs separated by U-shaped spaces in *C. t.* forma *patula* (Plate 3.4A, 9B). In *Protochelonibia*, the rostrum and rostromarginals lack an inner lamina, but in *P. hermani* sp. nov. a short, vertically striated flange descends from the base of the sheath in the marginals and carinomarginals (Plate 4.1A; Plate 5.1A). In the carinae, a series of short, striated flanges descend from the sheath (Plate 4.7), but are broken away in some specimens (e.g. Plate 5.3B).

In conclusion, *Chelonibia* and *Protochelonibia* are closely related, and the former evolved from the latter (Harzhauser et al., 2011; Collareta et al., 2021) by developing complex articulation structures between compartments, an inner lamina and strengthened septa which all descend to the basal margin

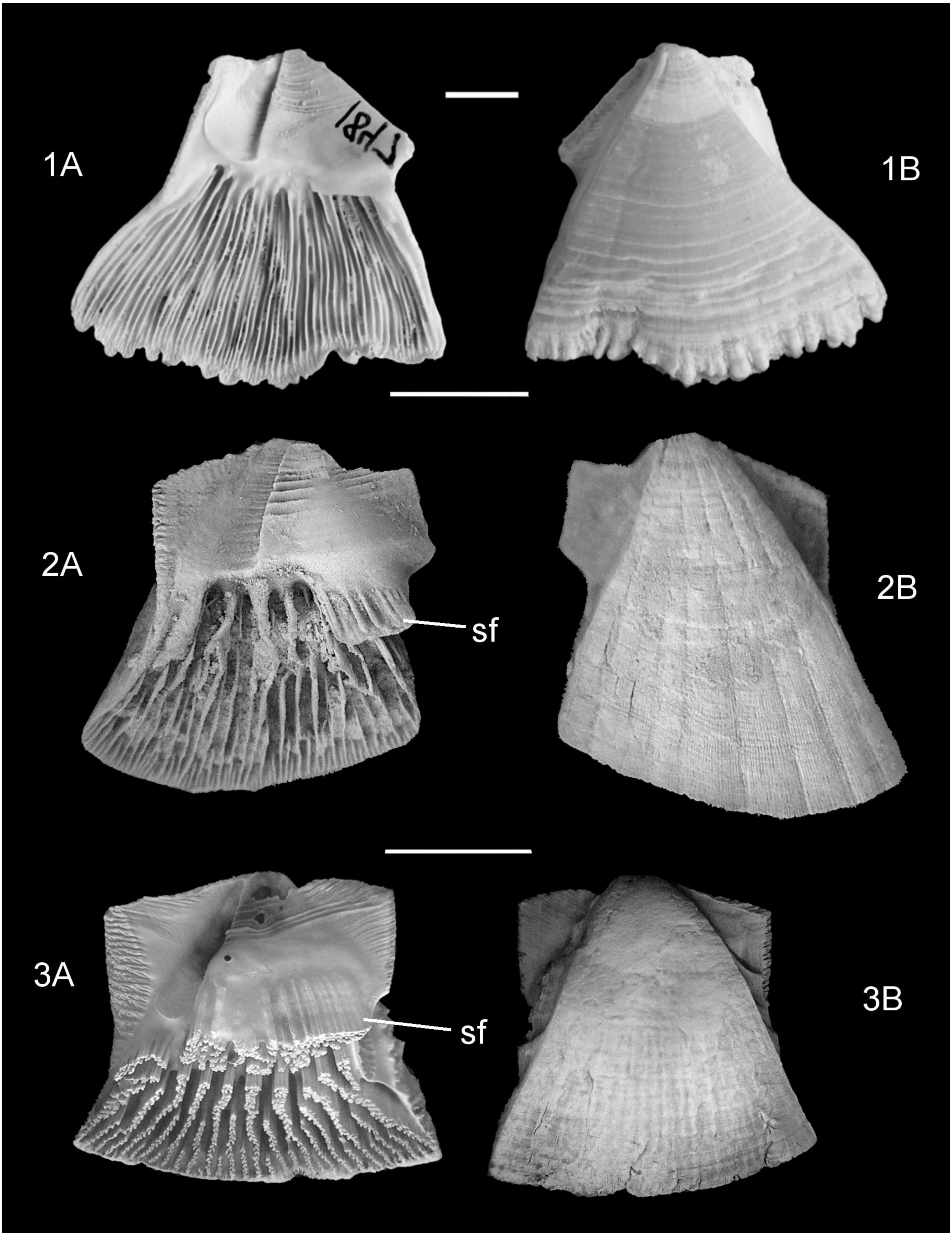

Figure 5. Comparison of the parietal structure of *Protochelonibia melleni* (Zullo, 1982), *P. hermani* sp. nov. and *Chelonibia testudinaria* forma *testudinaria* (Linnaeus, 1758). **1A.** Internal, **1B**, external views of carinomarginal of *P. melleni,* figured after Perreault et al., 2022, fig. 3. Marianna Formation, Rupelian, Smith County, Mississippi, USA (MMNS-IP 1847). **2A.** Internal, **2B**, external views of holotype marginal of *P. hermani* sp. nov. (IRSNB 7718). **3A.** Internal, **3B**, external views of marginal of *Chelonibia testudinaria* forma *testudinaria*. Present day, North Carolina, USA. Scale bars = 5 mm.

Note presence of a striated flange (sf) descending from the base of the sheath in *P. hermani* sp. nov. (2A), incorporated into the sheath in *C. testudinaria* (3A). Also note crenulated basal margin in *P. melleni* (1A, 1B), smooth in *P. hermani* sp. nov. (2A, 2B) and the denser internal ribbing in *P. melleni* (1A).

and are supported by vertical ribs. New material probably representing *C. submersa* from the Miocene of the Netherlands is morphologically intermediate between Oligocene *Protochelonibia* and Miocene to present day *Chelonibia*.

Protochelonibia hermani Gale sp. nov.
https://zoobank.org/urn:lsid:zoobank.org:act:E43C6AFC-5011-4A9C-9F12-C1BAF6F8A59F
Plate 3.1–3, 5–7; Plate 4.1–7; Plate 5.1, 3, 5–7; Fig. 5.2

Diagnosis. *Protochelonibia* in which the marginals, carinomarginals and carinae bear one or several striated processes descending from the base of the sheath.

Types. The marginal plate figured here (Plate 5.1) is the holotype (IRSNB 7718), all other figured specimens are paratypes (IRSNB 7705–7717, 7719–7722).

Material. 68 isolated compartmental plates and partially articulated individuals.

Locus typicus. Ceulemans clay pit at Schelle, 51°07'01.22" N, 4°21'21.30" E.

Stratum typicum. Silty lens associated with a tree trunk on top of pink R-horizon, Terhagen Member, Boom Formation, Rupelian (NP23), Oligocene.

Derivatio nominis. In honour of Dr Jacques Herman (1948–2022), for his friendship and longstanding contributions to the knowledge of extinct and extant elasmobranchs.

Description. Shell with low profile, sides flat to weakly concave (Plate 3.3), rostrum and rostromarginals unfused, united by flat articulation surface (Plate 5.6). External surfaces of compartments bear shallow, broad apicobasal ribs, separated by narrow grooves (Plate 3.2B, 5B; Plate 4.1B, 3A; Plate 5.1B, 3A, 7A); slightly eroded surfaces display fine ribbing (Plate 3.1A, 2B). Internal septa numerous, thin, smooth, not organised into well-defined sets, do not extend to basal surface (Plate 3.5A, 7; Plate 5.3B, 7). Sheaths proportionately tall (40–70% total compartment height), variable in height (compare Plate 3.6; Plate 4.4–7). Short, striated flange extends from base of sheath on marginals and carinomarginals (Plate 4.1A; Plate 5.1B); variably developed as series of short flanges on carinae (Plate 4.7). Superior margins of radii variably angled to lateral margins (Plate 4.4–7). Sutural margins of radii strongly denticulate, articulate with notched groove on alar surfaces (Plate 5.5). Height of rostra 1.5–2× greater than breadth; rostromarginals bear broad alae (Plate 3.5; Plate 4.4–6). Marginals (Plate 5.1A–C) and carinomarginals (Plate 4.1A–C) similar, distinguished by angle between upper and lateral alar margins (100° in marginals, 160° in carinomarginals). Both asymmetrically triangular and have convex basal margins. Marginals in specimens which were crowded by adjacent individuals strongly asymmetrical (Plate 4.2A, B) with triangular extension and very high sheath. Carinae (Plate 4.7; Plate 5.3A–C) with flat external surface, short alae, sheath angled to external surface.

Discussion. *P. hermani* sp. nov. differs from *P. submersa* in the presence of broad apicobasal ribbing on the parietes and details of compartmental articulation. *P. hermani* sp. nov. differs from *P. melleni* most importantly in the development of striated flanges descending from the base of the sheath in the carinae, carinomarginals and marginals (compare Fig. 5.1A, 2A). These are absent on the rostromarginals and rostrum in both species. Additionally, the basal margin of *P. melleni* is crenulate (see also Collareta & Newman, 2020), but smooth in *P. hermani* sp. nov. (compare Fig. 5.1B, 2B). The density of the internal ribbing on the marginals and carinomarginals is much greater in *P. melleni* (50+ per plate) than in *P. hermani* sp. nov. (25+ per plate). In the extant species *Chelonibia testudinaria*, the striated flange is incorporated into the lower part of the sheath (Fig. 5.3A). *P. hermani* sp. nov. is thus displays internal characters which are intermediate in morphology between *Protochelonibia* and *Chelonibia*.

P. melleni was recorded from the Oligocene (Rupelian) of Germany (Collareta et al., 2021) on the basis of crushed colony of specimens. In my view, these are too poorly preserved for specific identification.

Palaeoecology. *Chelonibia* lives epizoically on turtles and also occurs on manatees; *Chelonibia testudinaria* forma *patula* attaches to crustaceans and the chelicerate arthropod *Limulus* (Ross & Frick, 2007). It has also been found attached to mammalian bones (Collareta & Bianucci, 2021). Molecular study has shown that many of the “species” of *Chelonibia* are actually ecomorphs of a single species, *C. testudinaria* (Zardus et al., 2014). *Protochelonibia* attached to turtles, as demonstrated by specimens attached to an indeterminate cheloniid from the Oligocene of Germany (Collareta et al., 2022b). Diverse turtles are known from the Boom Clay (Smets, 1886a, 1886b, 1887a, 1887b, 1888) and would offer suitable substrates for *Protochelonibia.* The material described here may form part of a single association of individuals (“colony”) originally attached to one turtle.

5.3. Mollusca (SE)

The molluscan assemblage contains several species that are poorly known from the Boom Formation, one has never been cited from the Belgian Rupelian. Many shells are broken or fragmented, which is especially the case for thin fragile pectinids. The gastropods are represented by some very small species and juvenile specimens of larger species. It can be noted that no Pteropoda were encountered, despite the fact that *Clio blinkae* Janssen, 1989 can be abundant in the underlying pink R-horizon (Gürs & Janssen, 2004).

Class Bivalvia Linnaeus, 1758
Subclass Protobranchia Pelseneer, 1889
Order Nuculida Dall, 1889
Family Nuculidae Gray, 1824
Genus *Nucula* Lamarck, 1799

Type species. Arca nucleus Linnaeus, 1758

Nucula duchasteli Nyst, 1835
Plate 6.7 (IRSNB 7730)

1835 *Nucula Duchastelii* Nyst, p. 16, pl. 3, fig. 64.
1845 *Nucula Chastelii* Nyst, p. 235, pl. 9, fig. 1.
1957 *Nucula duchasteli* Nyst, 1835; Glibert, p. 11, pl. 1, fig. 4.
2010 *Nucula (Nucula) duchasteli* Nyst, 1835; Marquet, p. 256, pl. 3, fig. 2.

Material. 4 disarticulated valves, 4 bivalved specimens, 12 fragments.

Description. Typical asymmetric nuculid with opistogyrate umbo and a taxodont hinge, with fine hinge teeth. The dimensions of the largest shell are 10 mm in height (H) × 15 mm in length (L). The umbo lies at ca 1/3 of the dorsal margin.

The valves have a triangular shape, as the ventral margin makes a gentle angle with the anterior and posterior margins. A fine crenulation is present on the ventral margin. *Nucula duchasteli* is characterized by its particular ornamentation, consisting of strong, irregular concentric ribs, making it easily distinguishable from the other *Nucula* species in the Belgian Oligocene (Glibert, 1957; Marquet et al., 2012).

Remarks. Besides *Nucula duchasteli*, also *Nucula orbignyi* Glibert, 1955 is present in the Boom Formation. The former is more common than the latter (Marquet, 2010). The extant European *Nucula* species have a broad bathymetric distribution, occurring from a few meters to as much as 400 meters water depth (Poppe & Goto, 1993). The presence of articulated specimens points to a calm environment in which the shells could be buried in (quasi) life position.

Subclass Autobranchia Grobben, 1894
Order Myida Stoliczka, 1870
Family Teredinidae Rafinesque, 1815

Teredinidae indet.
Plate 6.6 (IRSNB 7729); Plate 7.3 (IRSNB 7725)

2010 Teredinidae indet.; Marquet, p. 269.

Material. 2 valve fragments and more than 30 tube fragments from the sediment surrounding the tree trunk and numerous burrows in pieces of wood.

Description. Calcareous, hollow tubular fragments with diameters ranging between 1 and 5 mm. Locally, the wood surface is very densely covered with burrows (up to 6 cm deep). In a broken wood fragment, globular casts of the reduced shells are observed, with a maximum diameter of 12 mm (Fig. 4). The small, reduced inequilateral shells have a characteristic shape, with a distinct small apophysis. Probably due to damage, no distinct auricle (= posterior lobe) is observed. The anterior lobe is covered by fine ridges, running parallel to the hinge. These ridges make an angle of about 90° with the longitudinal ridges on the anterior disc. This type of ornamentation is absent on the median disc. Unfortunately, the valve is too fragmented to allow further identification.

Remarks. Teredinidae, often called 'shipworms', are a group of highly specialized, obligate xylophagous bivalves colonizing driftwood, existing since the Cretaceous at least (Robin et al., 2018). They are common in (sub)tropical regions in a wide range of environments, from the intertidal zone up to fully marine conditions (Robin et al., 2018). Teredinidae were already mentioned from driftwood in the S30 level of the Terhagen Member at Niel/Schelle (Marquet, 2010), only a few meters below the horizon of this study. Marquet (2010) and Marquet & Herman (2012) also reported Teredinidae from "transitional layers" above the Putte Member in the Mol borehole, nowadays attributed to the Boeretang Member.

Family Corbulidae Lamarck, 1818
Genus *Varicorbula* Grant & Gale, 1931

Type species. *Tellina gibba* Olivi, 1792

Varicorbula gibba (Olivi, 1792)
Plate 7.1 (IRSNB 7723)

1792 *Tellina gibba* Olivi, p. 101.
1845 *Corbula gibba* Oliv.; Nyst, p. 65.
1957 *Corbula (Varicorbula) gibba* Olivi, sp. 1792; Glibert, p. 46.
2010 *Corbula (Varicorbula) gibba gibba* (Olivi, 1792); Marquet, p. 269.
2010 *Varicorbula gibba* (Olivi, 1792); Moerdijk et al., p. 243, fig. 462.
2012 *Corbula (Varicorbula) gibba gibba* (Olivi, 1792); Marquet et al., p. 85, pl. 32, fig. 3.

Material. 55 disarticulated valves, 55 bivalved specimens.

Description. Juvenile, small (figured specimen H = 3.4 mm, L = 3.8 mm), tumid asymmetric shells with an oval to subtriangular shape. The left valve is smaller than the right valve. Some concentric ribs are observed on the right valves. The articulated specimens are pyritized. See also the description by Marquet (2005, p. 89).

Remarks. *Varicorbula gibba* is a true living fossil, already occurring during the Paleogene in a multitude of palaeoenvironments (e.g. Moerdijk et al., 2010; Marquet, 2010). The species has a broad bathymetry, occurring from the intertidal zone to depths of 200 m (e.g. Marquet, 2005; Hrs-Brenko, 2006). It is characteristic of stressed environments with a low biodiversity, due to its good tolerance for eutrophic conditions (nowadays a pollution indicator), low oxygen levels and turbidity. After catastrophic anoxic events, *Varicorbula* can 'boom' and dominate during recovery periods of the benthic community, due to its capacity of producing large amounts of eggs (Hrs-Brenko, 2006). This might be a partial explanation for the local occurrence of dense, almost monospecific, small clusters of *Varicorbula gibba* in the Boom Formation between S30 and S40 (Marquet, 2010). Indeed, periods with low oxygen levels did occur during the deposition of the Boom Formation, which is reflected in the mollusc fauna of the Putte Member (Marquet & Herman, 2012). However, it should be noted that the bottom waters of the Rupelian sea were not anoxic but suboxic (Vandenberghe et al., 2014).

Order Pectinida Gray, 1854
Family Pectinidae Rafinesque, 1815
Genus *Palliolum* Monterosato, 1884

Type species. *Pecten incomparabilis* Risso, 1826

Palliolum permistum (Beyrich, 1848)
Plate 6.8–10 (IRSNB 7731–7733)

1848 *Pecten permistus* Beyrich, p. 60.
1868 *Pecten permistus* Beyr.; von Koenen, 231, pl. 7, fig. 20a–c.
1930 *Chlamys (Aequipecten) permista* Beyrich; Vincent, p. 4, fig. 4a–b.
1943 *Pecten* cf. *permistus* Beyrich; Albrecht & Valk, p. 120, pl. 11, fig. 363–366.
1957 *Chlamys permista* Beyrich, sp. 1848; Glibert, p. 20.
1973 *Chlamys (Chlamys) permista* (Beyrich, 1848); Neuffer, p. 40, pl. 5, figs 16–17.
2000 *Palliolum* (s.lat.) *permistum* (Beyrich, 1848); Moths, p. 46, pl. 16, fig. 6.
2011 *Chlamys permista* (Beyrich, 1848); Müller, p. 31, pl. 16, figs 8–9.
2010 *Palliolum permistum* (Beyrich, 1848); Marquet, p. 263.

Material. 7 valves, 19 fragments.

Description. Fragile and thin, nearly equilateral shells. The auricles are mostly damaged or missing. The largest valve measures 21 mm (H) × 20 mm (L), the smallest 6 × 6 mm. The disc is almost circular and rather flat. The shells show a distinct ornamentation, with many fine and closely interspaced radial ribs, often covered by abundant fine scales. The presence and abundance of these scales are highly variable. Also, the number of ribs can strongly vary: ca 35 ribs were counted on the smallest specimen, ca 70 on the largest specimen.

Remarks. Vincent (1930) mentioned ten specimens of *Chlamys permista* from the Boom Formation, exhibiting a maximum height of 24 mm; one is refigured here (IRSNB IST 1804 or 1805, Fig. 6.3). Our specimens closely resemble those figured by Vincent (1930, fig. 3). Since Vincent (1930), no additional occurrences have been reported for the Boom Formation (see Marquet, 2010). Our specimens match well with the original description of Beyrich (1848), with the exception of the generally higher number of radial ribs. However, Beyrich studied only two shells, including a bivalved specimen with 25 radial ribs on the left valve, and more than 40 on the right valve. In contrast, von Koenen (1868) mentioned a right valve with more than 70 ribs. Also, Neuffer (1973) figured valves with similar high rib numbers, while the specimen figured by Moths (2000) has only ca 40 ribs. Albrecht & Valk (1943) mention the presence of ca 25 ribs on the left valve and ca 50 on the right valve. Vincent (1930) also noted a strong variability in the presence or absence of scales on the ribs, which is also the case in the specimens figured by Müller (2011). Given all these similarities and the inferred intraspecific variability, an identification of our material as *Palliolum permistum* seems appropriate. However, it should be taken into account that the current status of Beyrich's type material remains unknown, as it is probably lost (see also the remark of Neuffer, 1973). Given the large number of specimens we recovered of this otherwise very rare species, it can be supposed that a small community was present in the vicinity of the sunken trunk.

Palliolum delheidi (Vincent, 1930)
Plate 6.11 (IRSNB 7734)

1930 *Chlamys (Hilberia) Delheidi* Vincent, p. 6, fig. 5.
1957 *Chlamys delheidi* Vincent, E., 1930; Glibert, p. 19.
2010 *Palliolum delheidi* Vincent, 1930; Marquet, p. 263.

Material. 1 fragment.

Description. Thin, flat fragment (25 mm) of a much larger shell. Faint, wide radial ribs are present, together with concentric growth lines (see also Vincent, 1930).

Remarks. In the caption of his text-figure 5, Vincent (1930) stated that both syntypes (IRSNB IST 1806–1807, former Delheid collection) originate from the Steendorp clay pit. However, the original labels in the RBINS collection mention the Niel pit, which was also adopted by Glibert (1957) and Marquet (2010). The latter refigured one of both syntypes, the other is shown here (Fig. 6.4). In total, 6 specimens are known from Niel, Noeveren and Steendorp (Vincent, 1930; Glibert, 1957). Marquet (2010) did not encounter this species in his recent surveys. Therefore, our fragment is the first published record from the Boom Formation in a century.

***Palliolum* indet.**

Material. 1 nearly complete specimen, 10 fragments.

Description. Fragments with variable ornamentation, all without scales on the ribs. One more complete valve (L = 22 mm) with broken ventral margin, displaying very fine, faint radial ribs, disappearing towards the centre and outer edges of the disc.

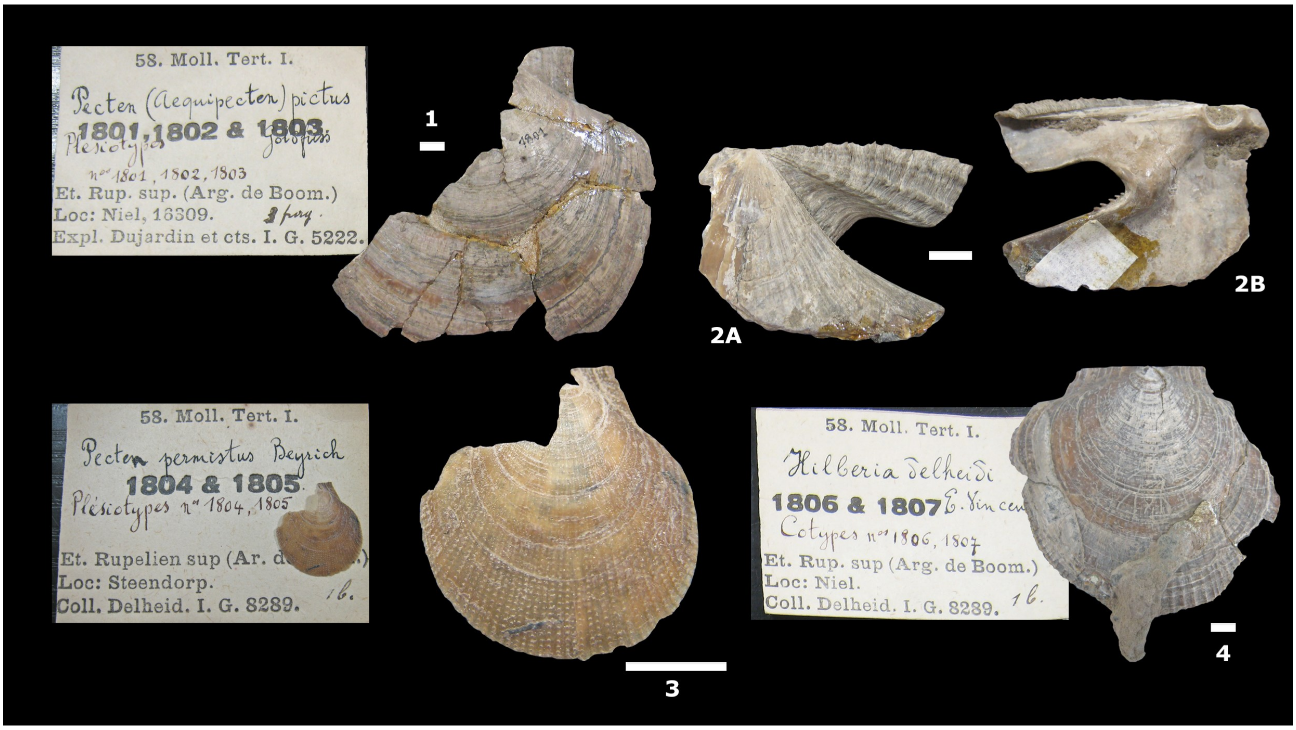

Figure 6. Some important Pectinidae from the Boom Formation in the RBINS collection, refigured after Vincent (1930). **1.** *Palliolum deshayesi* (Nyst, 1836), fragment with posterior auricle, IRSNB IST 1801 (as "*Chlamys picta* Goldfuss" in Vincent, 1930, fig. 1). **2A–B.** Idem, fragment with anterior auricle, IRSNB IST 1802 (Vincent, 1930, fig. 2). **3.** *Palliolum permistum* (Beyrich, 1848), IRSNB IST 1804-1805 (other specimen unrecognisable due to pyrite decay; as "*Chlamys permista* Beyrich" in Vincent, 1930, fig. 4A). **4.** *Palliolum delheidi* (Vincent, 1930), IRSNB IST 1806-1807 (other syntype refigured by Marquet, 2010, pl. 3, fig. 6; as "*Chlamys delheidi*" in Vincent, 1930, fig. 5B). Scale bars = 5 mm.

Remarks. These specimens cannot be identified to the species level, as we do not have enough material to properly assess the range in intraspecific ornamental variability of *Palliolum permistum*. It is likely that many fragments actually belong to this species. However, *Palliolum deshayesi* (Nyst, 1836) cannot be excluded either, as it is more common in the Belgian Oligocene. The latter species was mentioned by Vincent (1930) and Glibert (1957) as *Chlamys picta* (Goldfuss, 1834) (forma *diomedes* d'Orbigny, 1852), but synonymized with *P. deshayesi* by Marquet (2010). The large valves (maximum H = 65 mm, L = 70 mm) described from the Boom Formation by Vincent (1930) show little ornamentation, with the exception of concentric growth lines (Fig. 6.1–2) and some (very) faint radial ribs on the oldest parts of the shells. In contrast, Neuffer (1973, pl. 6) showed extreme variation within the sculpture of this species, which is also the case for the Recent *Palliolum tigerinum* (Müller, 1776) (Janssen & Dijkstra, 1996). Given the wide variation and existing ambiguities, our fragments are kept in open nomenclature.

Class Gastropoda Cuvier, 1797
Subclass Heterobranchia Burmeister, 1837
Familia Pyramidellidae Gray, 1840
Genus Odostomia Fleming, 1813

Type species. *Turbo plicatus* Montagu, 1803.

Odostomia* cf. *acutiuscula (Braun *in* Walchner, 1851)
Plate 7.7 (IRSNB 7728)

1851 *Actaeon acutiusculum* Braun *in* Walchner, p. 1123.
1863 *Odontostoma acutiusculum* A. Braun sp.; Sandberger, p. 170, pl. 15, fig. 1.
1954 *Odostomia (Megastomia) acutiusculum* Sandberger, sp., 1863; Glibert & De Heinzelin, p. 360.
2000 *Odostomia (Megastomia) acutiuscula* (Braun, 1850); Moths, p. 36, pl. 12, fig. 6.
2012 Odostomia acutiuscula (Braun, 1850); Lozouet & Maestrati, p. 294, fig. 191.
2012 *Odostomia acutiuscula* (Braun, 1850); Marquet & Herman, 2012, p. 111.
2016 ? *Odostomia* cf. *acutiuscula* (Braun *in* Walchner, 1851); Marquet et al., p. 77, pl. 21, fig. 4.

Material. 4 specimens.

Description. Small (figured specimen H = 2.0 mm, width (W) = 0.9 mm), elongated shells with 4 to 5, rather flat, only slightly convex whorls. The last whorl displays a carina and is a little less than half the height of the shell. A small columellar tooth is present. No visible sculpture/ornamentation. Small heterostrophe protoconch.

Remarks. Marquet & Herman (2012) mentioned *Odiostoma acutiuscula* from the Boom Formation, but only from the septaria level S50 in the Putte Member. Unfortunately, no images were provided. This genus had not been previously described from the Boom Formation, probably because collecting was mainly done visually during the 19th and early 20th centuries. As a result, very small shells were often overlooked in the field. Lozouet & Maestrati (2012) figured a specimen of *Odiostoma acutiuscula* from the sandy French Rupelian ("Stampien"), which is very similar to our specimens. However, several other *Odostomia* species occur in the lowermost Oligocene of Belgium (Glibert & de Heinzelin, 1954; Marquet et al., 2016). Due to the large diversity within this genus and the many species described in older works, an identification of *Odostomia* species is often difficult. For now, we cautiously maintain the name *Odostomia* cf. *acutiuscula* for the specimens of the Boom Formation, following Marquet & Herman (2012) and Marquet et al. (2016). However, it cannot be excluded that a future revision may reveal that this material actually belongs to other species. For example, the whorls of the specimens figured by Sandberger (1863, plate XV, fig. 1) and Moths (2000) are more convex than observed in our material. The original description by Braun *in* Walchner (1851) brings no clarity. Extant *Odostomia* spp. live in a broad range of habitats (from 0 to 700 m water depth, van Aartsen et al., 1998) and are known as ectoparasites on both molluscs and polychaetes (Cole & Hancock, 1955)

Subclass Caenogastropoda Cox, 1960
Order Littorinimorpha Golikov & Starobogatov, 1975
Family Naticidae Guilding, 1834
Genus *Euspira* Agassiz, 1837

Type species. *Natica glaucinoides* Sowerby, 1812

Euspira* cf. *achatensis (De Koninck, 1838)
Plate 7.6 (IRSNB 7727)

1838 *Natica achatensis* De Koninck, p. 9.
1943 *Polynices (Lunatia) achatensis* (Récluz); Albrecht & Valk, p. 53, pl. 4, figs 91–96.
1957 *Natica (Lunatia) achatensis* (Recluz) De Koninck, sp., 1837; Glibert, p. 57, pl. 6, fig. 12.
2000 *Polinices (Lunatia) achatensis* (Koninck, 1838); Moths, p. 20, pl. 3, fig. 2.
2012 *Euspira achatensis* (de Koninck, 1837); Lozouet & Maestrati, p. 286, pl. 185, figs 7–9.
2016 *Euspira helicina achatensis* (De Koninck, 1837); Marquet, p. 17.
2016 *Euspira achatensis* (De Koninck, 1837); Marquet et al., p. 17, pl. 3, fig. 4.

Material. 5 specimens.

Description. Juvenile, very small (figured specimen H = 2.1 mm, W = 2.1 mm) globular shells. Apex barely protruding. Distinct suture. Tumid, rather contiguous whorls, giving the transition between the whorls a rather smooth appearance. No visible sculpture/ornamentation is present on the whorls. The specimens display little callus and have a small umbilicus with some very fine lines/folds in the curvature.

Remarks. *Euspira achatensis* was described by De Koninck (1838) from the Boom Formation. It is the most common Naticidae in this formation, and was encountered in almost all levels (Glibert, 1957; Marquet, 2016). Albrecht & Valk (1943) described this species from the Oligocene of the Netherlands (southern Limburg). In Germany, the species is very common in the Rupelian clay of Malliß (Mecklenburg-Vorpommern) (Moths, 2000). In addition, Lozouet & Maestrati (2012) figured it from the sandy "Stampien" of the Paris Basin. Given the (very) juvenile life stage of the shells, we maintain them as *Euspira* cf. *achatensis*.

Order Neogastropoda Wenz, 1938
Family Mangeliidae Fischer, 1883
Genus *Amblyacrum* Cossmann, 1889

Type species. *Pleurotoma rugosa* Deshayes, 1834

Amblyacrum* cf. *roemeri (von Koenen, 1867)
Plate 6.12 (IRSNB 7736)

1867 *Mangelia roemeri* von Koenen, p. 95, pl. 6, fig. 9a–d.
1979 *Amblyacrum roemeri* (Koenen, 1867); Janssen, p. 325, pl. 18, fig. 71–72.
1987 *Amblyacrum roemeri* (von Koenen, 1867); Schnetler & Beyer; p. 205.
1998 *Sorgenfreispira roemeri* (Koenen, 1867); Welle, p. 96; pl. 18, fig. 4.
2000 *Sorgenfreispira roemeri* (Koenen, 1867); Moths, p. 32, pl. 10, fig. 2.

Material. 5 specimens.

Description. Juvenile, very small fusiform shells (figured specimen H = 2.3 mm, W = 1.2 mm). The shells are narrow and elongated, with a rather short siphonal canal and a relatively deep suture. The protoconch is dome-shaped, with ca 3 smooth convex whorls. The nucleus is very small. Although its surface is not well preserved, no obvious sculpture/ornamentation is present. The transition to the teleoconch is vaguely demarcated, some very short, vague lines (possible spirae?) were observed on the last whorl of the protoconch. On the teleoconch, ca 10 widely interspaced, pronounced ophistocline axial ribs are present per whorl, covered by 5–6 coarse spiral ribs on the first teleoconch whorl. The sinus of the growth lines is slightly curved (elongated, inverted S-shape).

Remarks. Von Koenen (1867) mentioned this species from the German Rupelian (Freienwalde) and Chattian (Sternberger Gestein, Krefeld, Hohenkirchen, etc.). The protoconch consists of 2½ to 3 smooth whorls. The Rupelian specimens differ from the Chattian shells by their more compact shape, and by the absence of finer spiral lines between the broader spiral ribs on the last whorls (von Koenen, 1867). Janssen (1979) described and figured *Amblyacrum roemeri* from the German Chattian: the protoconch of his material consisted of 3 smooth whorls, followed by 7 spiral ribs (more than on our specimens). Moths (2000) identified this species in the Rupelian of Malliß, but mentioned that his material resembled the Chattian form with a fine sculpture on the protoconch. The latter characteristic was not observed in our material. *Amblyacrum roemeri* also occurs in the Chattian Brejning Member (Vejle Fjord Formation) of Denmark (Schnetler & Beyer, 1987), but no images were provided. Welle (1998) described 15 specimens (as *Sorgenfreispira roemeri*) from the Chattian of Schacht 8 (Sophia Jacoba mine) near Erkelenz (Germany). His figured shell is similar, but not identical to our material: more abundant, fine spiral ribs are present. This genus and species are new for the Belgian Oligocene; neither was ever mentioned by Glibert & de Heinzelin (1954), Glibert (1957) and Marquet & Herman (2012). Given the juvenile nature of our material and the subtle differences between the forms mentioned in the literature, we attribute our specimens to *Amblyacrum* cf. *roemeri*.

Subclass Neomphaliones (see also Bouchet et al., 2017)
Order Cocculinida Haszprunar, 1987
Family Cocculinidae Dall, 1882
Genus *Cocculina* Dall, 1882

Type species. *Cocculina rathbuni* Dall, 1882.

Cocculina reineckei Marquet, 2016
Plate 7.4 (IRSNB 7726) and Plate 7.5 (specimen lost during scanning)

2016 *Cocculina (Cocculina) reineckei* Marquet, p. 15, pl. 1, figs 3–4.

Material. 35 specimens.

Description. Very small limpet shells with the umbo close to the posterior margin. The figured specimen has a total shell length of 3.0 mm. For a more detailed description, see Marquet (2016). In our material, some specimens with damaged protoconchs are present (Plate 7.5). Unfortunately, the outer shell layers are damaged and partly missing, displaying no ornamentation/sculpture on the protoconch.

Remarks. The discovered assemblage represents the largest known association of this species. Marquet (2016) described 15 shells associated with driftwood in the S30 level of the Terhagen Member. Our material was found in a similar setting, only a little higher in the same succession (Fig. 2). Extant Cocculinidae and Pseudococculinidae are opportunistic deep-water limpets typical of bathyal and abyssal depths, colonizing decaying driftwood sinking from shallow water into the aphotic zone (e.g. Marshall, 1985; McLean & Harasewych, 1995; Ardila & Harasewych, 2005). These limpets exploit decomposing wood as a substrate, and most probably feed on the microbes involved in the decaying process (Marshall, 1985). At a presumed water depth of ca 100 m, the cocculinid population of the Boom Formation lived in a relatively shallow environment compared to many of its extant relatives. Similar limpets are well known from the Oligocene of the North Sea Basin; Marquet (2016) mentioned *Acmaea schreiberi* Welle, 2009 and *Cocculina papyracea* (Sandberger, 1861) from the German Rupelian, and *Lepetella helgae* Schnetler & Beyer, 1990, *Lepetella jyttae* Schnetler & Beyer, 1990 and *Cocculina megapolitana* (Wiechmann, 1868) from the Danish and German Chattian. Also in the Neogene, multiple (pseudo)cocculinids occur, e.g. very rare *Cocculina dittmeri* (Anderson, 1964) and *Cocculina miocaenica* Boettger, 1901 from the Langhian of Miste (the Netherlands) (Janssen, 1984). However, recent literature assigns these Langhian species to the genera *Pseudococculina* and *Notocrater* respectively, both Lepetelloidea (Stein et al., 2016). Although historically classified together with the Cocculinoidea (including the Cocculinidae and Bathysciadiidae) in the Cocculiniformia, molecular phylogeny showed that the latter group was paraphyletic (McArthur & Harasewych, 2003) and that the Lepetelloidea and Collucinoidea belong to the subclasses of the Vetigastropoda and the Neomphaliones respectively (Bouchet et al., 2017). Nevertheless, the shells of Cocculinidae and Pseudococculinidae are similar; the morphology of the protoconch and radula is therefore often used to separate these families (McLean & Harasewych, 1995). Unfortunately, the protoconch is often damaged or even missing (e.g. the holotype of *C. reineckei*) and the radula does not fossilize. The protoconch of Cocculinidae (e.g. *Cocculina*, *Coccopigya*) generally has a rather short and broad apical fold with a free protoconch tip, while the Pseudococculinidae (e.g. *Pseudococculina, Notocrater*) display a long and narrow protoconch apical fold, and a fused protoconch tip (Marshall, 1985). The general shape of the protoconch of our specimen resembles that of the Cocculinidae. Unfortunately, the surface layers of the protoconch are missing, making it unknown whether the typical reticulate sculpture of the Cocculinidae was present.

Class Scaphopoda Bronn, 1862
Order Dentaliida Starobogatov, 1974
Family Rhabdidae Chistikov, 1975

Genus *Rhabdus* Pilsbry & Sharp, 1897

Type species. *Dentalium rectius* Carpenter, 1864

Rhabdus parallelus (Zinndorf, 1928)
Plate 7.2 (IRSNB 7724)

1928 *Dentalium parallelum* Zinndorf, p. 38, pl. 1, fig. 8.
1978 *Rhabdus* aff. *parallelum* Zinndorf, 1928; Janssen, p. 140.
1996 *Rhabdus* aff. *parallelum* Zinndorf, 1928; Moths et al., p. 14, pl. 1, fig. 4.

Material. 1 specimen.

Description. Thin calcareous tube with a length of 2.85 mm and a diameter of 0.69 mm. No ornamentation. The core of the tube is filled with pyrite.

Remarks. These very small Scaphopoda are often overlooked and confused with worm tubes. Zinndorf (1928) described this species based on four specimens found in the "Rupelton" at Offenbach am Main. His longest specimen attained a length of 11 mm and a diameter of 0.5 mm. *Rhabdus* aff. *parallelus* is also known from the Chattian of Germany (Janssen, 1978; Moths et al., 1996).

5.4. Elasmobranchii (PDS)

Systematics follows Nelson et al. (2016), whereas anatomical tooth terminology follows Cappetta (2012). Despite the high number of recovered elasmobranch teeth, only five species are represented (Table 1). For additional illustrations of these taxa, the reader is referred to Hovestadt & Steurbaut (2023).

Class Chondrichthyes Huxley, 1880
Order Lamniformes Berg, 1958
Family Carchariidae Müller & Henle, 1838
Genus *Carcharias* Rafinesque, 1810

Type species. *Carcharias taurus* Rafinesque, 1810, by original monotypy.

Carcharias contortidens (Agassiz, 1843)
Plate 8.1–12 (IRSNB P 10299–10310)

1843 *Lamna (Odontaspis) contortidens* Agassiz, p. 294, vol. 3, tab. 37a, figs 17–23.
1910 *Odontaspis acutissima* L. Agassiz, 1844; Leriche, p. 245, 261, figs 73–76, pl. 14, figs 1–27.
1988 *Synodontaspis acutissima* (Agassiz, 1844); Nolf, p. 140, pl. 44, figs 1–9.
1999 *Synodontaspis acutissima* (Agassiz, 1844); Baut & Génault, p. 16, pl. 3, figs 1–2.
2001 *Carcharias acutissimus* (Agassiz, 1844); Reinecke et al., p. 11, pls 10–15.
2010 *Carcharias acutissima* (Agassiz, 1843); Hovestadt et al., figs 3–4.
2020 *Carcharias contortidens* (Agassiz, 1843); Höltke et al., p. 11, pl. 2, figs 8–10, pl. 3, figs 1–3.

Material. 154 teeth representing all tooth positions.

Description. The tooth set comprises 154 disarticulated teeth, which range in size from 2 mm (posterior) to 25 mm (lower anterior). A representative sample of all tooth positions is shown in Plate 8. As observed in *Carcharias taurus*, the dentition of *C. contortidens* consists of three upper (UA1-UA3) and four lower anterior teeth (LA1-LA4) (see also Reinecke et al., 2011, fig. 10). Multiple intermediate files may have been present, but this feature is very variable within the genus *Carcharias*, as is the number of lateral and posterior files (e.g. Applegate, 1965; Sadowsky, 1970).

Comparisons with dental characters of the extant sand tiger shark *C. taurus* (see Cunningham, 2000) revealed that all tooth positions are represented in our fossil sample. The marked degrees of dignathic and monognathic heterodonty simplified the determination of each tooth position. Elongated, more slender teeth were separated from those with a shorter crown and were assigned to anterior positions. The upper and lower teeth were grouped based on the amount of lingual curvature of the crown, recurvature of the crown-tip, and angle between the root-lobes. Teeth with a strong lingual curvature of the crown and strong lingual protuberance of the root were assigned to lower positions. The remaining teeth, having strongly recurved crown tips, were assigned to the upper jaw. Their position was then determined by considering the increasing angle of root-lobe divergence in distal direction. Some teeth are preserved only as thin enamel "shells" lacking the root. These incomplete teeth represent replacement teeth.

The UA1 (IRSNB P 10299 - Plate 8.1A–C) is smaller in size than the remaining upper anterior teeth. In distal view (Plate 8.1A), the strongly labially recurved crown tip, characteristic of upper tooth positions, is clearly noticeable. The UA2 (IRSNB P 10300 - Plate 8.2A–C) has relatively short root lobes compared to the remaining anterior ones. The UA3 (IRSNB P 10301 - Plate 8.3A–C) has a distinctive morphology with a long and elongated mesial root lobe and a compressed distal one. The crown is distally directed but exhibits a slight mesial slant. The concave mesial edge of the crown is to conform to the distal margin of the anterior hollow in the palatoquadrate (see Siverson, 1999, fig. 3a). Three intermediate teeth are present, two of which are well preserved (IRSNB P 10303 - Plate 8.5A–B & IRSNB P 10304 - Plate 8.6A–C). Interestingly, both specimens display a secondary distal cusplet. Upper lateral teeth (IRSNB P 10302 - Plate 8.4A–C) have a distally directed crown.

The LA1 (IRSNB P 10305 - Plate 8.7A–C) is the smallest anterior tooth position. It is strongly mesiodistally compressed with a much longer distal root lobe. The LA2 (IRSNB P 10306 - Plate 8.8A–C) and LA3 (IRSNB P 10307 - Plate 8.9A–C) are the largest teeth in the jaw and very similar to each other in morphology, the former being more symmetrical than the latter, which is slightly distally directed. The LA4 (IRSNB P 10308 - Plate 8.10A–C) is strongly distally directed. Lower lateral teeth (IRSNB P 10309 - Plate 8.11A–C) have a short, straight crown. Posterior teeth are significantly smaller in size compared to the lateral teeth and possess very short and low crowns (IRSNB P 10310 - Plate 8.12A–B). Some teeth bear marginal folds at the labial crown base (Plate 8.12B).

Remarks. The family Odontaspididae Müller & Henle, 1839 traditionally consists of two extant (*Carcharias* and *Odontaspis* Agassiz, 1838) and numerous extinct genera (see Cappetta & Nolf, 2005). However, based on both molecular (e.g. Naylor et al, 1997; Vélez-Zuazo & Agnarsson, 2011) and morphological data (e.g. Stone & Shimada, 2019), the family Carchariidae Müller & Henle, 1838 was resurrected to separate the genus *Carcharias* from the family Odontaspididae *sensu stricto* for *Odontaspis* (e.g. Adolfssen & Ward, 2015).

There is still disagreement about the use of the genus name *Carcharias* for the many fossil species currently attributed to it (e.g. Adolfssen & Ward, 2015). A reclassification of the fossil 'odontaspidids' is needed, but beyond the scope of this study. However, *C. contortidens* probably belongs to the same lineage

Table 1. List of taxa found in the silty lens associated with a tree trunk on top of pink R-horizon, Terhagen Member, Boom Formation, Rupelian (NP23), Oligocene.

Class - Family	Species	Number of specimens	Iconography	RBINS number
EQUISETOPSIDA				
Cupressaceae Gray, 1822	*Cupressinoxylon* sp.	1	Text-Fig. 4; Pl. 2, Figs A-F	b9669-9670
BIVALVIA				
Nuculidae Gray, 1824	*Nucula duchasteli* Nyst, 1835	8 + fragments	Pl. 6, Fig. 7	7730
Teredinidae Rafinesque, 1815	Teredinidae indet.	2 + >30 tube fragments	Pl. 6, Fig. 6; Pl. 7, Fig. 3	7729, 7725
Corbulidae Lamarck, 1818	*Varicorbula gibba* (Olivi, 1792) *s.l.*	110	Pl. 7, Fig. 1	7723
Pectinidae Rafinesque, 1815	*Palliolum permistum* (Beyrich, 1848)	7 + fragments	Pl. 6, Figs 8-10	7731-7733
	Palliolum delheidi (Vincent, 1930)	1 fragment	Pl. 6, Fig. 11	7734
	Palliolum indet.	fragments	-	-
GASTROPODA				
Pyramidellidae Gray, 1840	*Odostomia* cf. *acutiuscula* (Braun in Walchner, 1851)	4	Pl. 7, Fig. 7	7728
Naticidae Guilding, 1834	*Euspira* cf. *achatensis* (Récluz in De Koninck, 1837)	5	Pl. 7, Fig. 6	7727
Mangeliidae Fischer, 1883	*Amblyacrum* cf. *roemeri* (von Koenen, 1867)	5	Pl. 6, Fig. 12	7736
Cocculinidae Dall, 1882	*Cocculina reineckei* Marquet, 2016	35	Pl. 7, Figs 4-5	7726
SCAPHOPODA				
Rhabdidae Chistikov, 1975	*Rhabdus parallelum* (Zinndorf, 1928)	1	Pl. 7, Fig. 2	7724
THECOSTRACA				
Chelonibiidae Pilsbry, 1916	*Protochelonibia hermani* Gale sp. nov.	68	Text-Fig. 5.2; Pl. 3, Figs 1-3, 5-7; Pl. 4, Figs 1-7; Pl. 5, Figs 1, 3, 5-7	7705-7722
MALACOSTRACA				
Mathildellidae Karasawa & Kato, 2003	*Coeloma rupeliense* Stainier, 1887	1	Pl. 6, Fig. 5	7735
CHONDRICHTHYES				
Carchariidae Müller & Henle, 1838	*Carcharias contortidens* (Agassiz, 1843)	154	Pl. 8, Figs 1-12	P 10299-10310
Lamnidae Bonaparte, 1835	*Isurolamna gracilis* (Le Hon, 1871)	1	Pl. 6, Fig. 1	P 10311
Lamnidae Bonaparte, 1835	*Keasius parvus* (Leriche, 1908)	Gill rakers	Pl. 6, Fig. 2	P 10312
Squalidae, 1838	*Squalus alsaticus* (Andreae, 1890)	113	Pl. 6, Figs 3-4	P 10313-10314
Arhynchobatidae Fowler, 1934	*Atlantoraja cecilae* (Steurbaut & Herman, 1978)	4	-	-
OSTEICHTHYES				
Anguillidae Rafinesque, 1810	*Anguilla rouxi* Nolf, 1977	16	Pl. 9, Figs 1-2	P 10315-10316
Argentinidae Bonaparte, 1846	*Argentina parvula* (Koken, 1891)	409	Pl. 9, Figs 3-6	P 10317-10320
Merluccidae Rafinesque, 1815	*Palaeogadus emarginatus* (Koken, 1884)	1	-	-
Ranicipitidae Bonaparte, 1835	*Raniceps tuberculosus* (Koken, 1884)	161	Pl. 9, Figs 7-8	P 10321-10322
Gadidae Rafinesque, 1810	*Trisopterus elegans* (Koken, 1884)	ca. 29000	Pl. 9, Figs 9-11	P 10323-10325
Bythitidae Gill, 1861	*Otarionichthys occultus* (Koken, 1891)	155	Pl. 11, Figs 1-3	P 10326-10328
Carangidae Rafinesque, 1815	*Trachurus reineckei* Hoedemakers sp. nov.	149	Pl. 10, Figs 1-8	P 10329-10336
Malacanthidae Günther, 1861	*Malacanthus ellipticus* (Koken, 1884)	74	Pl. 11, Figs 4-6	P 10337-10339
Cottidae Bonaparte, 1831	*Myoxocephalus primas* (Koken, 1891)	235	Pl. 12, Figs 1-9	P 10340-10347
Caproidae Bonaparte, 1835	*Capros siccus* Schwarzhans, 2008	6	Pl. 11, Fig. 7	P 10348
Lophiidae Rafinesque, 1810	*Lophius gibbosus* Nolf, 1977	1	Pl. 11, Fig. 8	P 10349

as the present-day *C. taurus*, which is fairly common since the early–middle Miocene (e.g. Bor et al., 2012; Everaert et al., 2019), as teeth of both species are morphologically very similar (e.g. Cappetta & Nolf, 1991; Ward & Bonavia, 2001).

For a long time, these teeth were attributed to *Carcharias acutissima* (Agassiz, 1843) (e.g. Cappetta, 2012) or, following the International Code of Zoological Nomenclature (ICZN), *C. acutissimus* (e.g. Reinecke et al., 2001). However, both syntypes of *C. acutissimus* are morphologically very close to *Carcharoides catticus* (Philippi, 1846), with the exception of the folds on the lingual crown surface, which are well visible on Agassiz's illustrations (1843, pl. 37a, figs 33–34) (see Höltke et al., 2020). Since Agassiz's work, teeth of this type have not been reported in literature (Höltke et al., 2020). In the same volume, Agassiz (1843, p. 294–295, pl. 37a, figs 17–23) also described and figured a series of teeth that he assigned to *Carcharias contortidens*. The latter is much more commonly found and morphologically very similar to the mass occurrences of teeth labelled as *C. acutissimus* in the available literature. The type material of both species is probably lost, but based on the different morphology of the teeth, *C. acutissimus* and *C. contortidens* are regarded as separate species (Höltke et al., 2020). Consequently, also the *C. acutissimus* teeth from Oligocene deposits of Belgium (e.g. Leriche, 1910) should be reassigned to *C. contortidens*.

The largest part of our material probably belongs to a single individual based on the same size range, morphology and preservation state. All teeth occurred on the same bedding plane between the trunk and side-branch, within a limited area of less than 1 m^2. In contrast to this concentration, larger shark teeth are generally very rarely found nowadays and scattered in the Boom Clay. Unfortunately, no vertebrae or jaw remains were discovered. Nevertheless, a number of teeth seem to belong to smaller individuals which can be expected in such an accidental association. In addition, the Boom Formation has yielded several associated tooth sets in the past (see Leriche, 1910).

Leriche (1910, p. 264, text-figs 73–76, plate XIV) described and figured an important articulated tooth set of *C. contortidens* (IRSNB P 678, as *Odontaspis acutissima*), found in Niel, situated only 2 km south of the clay pit at Schelle. That specimen, featuring fragments of the palatoquadrate (upper jaw) and Meckel's cartilage (lower jaw), is refigured in Figure 7. While the lateral teeth detached during excavation (Leriche, 1910, p. 264), the anterior tooth files display their original arrangement. Figure 7A–B (IRSNB P 678f, Leriche 1910, pl. XIV, figs 6, 6a, 6b) represent the lower symphysis, consisting of the left jaw half, including four anterior tooth files (LA1 to LA4) and the right jaw half showing the first three anterior tooth files (LA1 to LA3) (LA1 = 'symphyseal' and LA4 = 'first lateral' in Leriche, 1910). Figure 7B represents IRSNB P 678f rotated by 90° buccally. Interestingly, there is an upper intermediate tooth on this lower jaw fragment, oriented in the opposite direction as the lower anterior teeth, which is in contradiction with Leriche (1910, p. 265), who explicitly indicated no intermediate teeth were found. Figure 7C (IRSNB P 678g, Leriche 1910, pl. XIV, fig. 7) represents a partial right lower jaw, detached from IRSNB P 678f (Fig. 7A–B) (Leriche, 1910, p. 266), showing teeth belonging to the second to fourth lower tooth files (LA2 to LA4). Finally, Figure 7D (IRSNB P 678a, Leriche 1910, pl. XIV, figs 1, 1a) represents the upper symphysis, consisting of the left jaw half including three anterior tooth files (UA1 to UA3) and the right jaw half showing the first two anterior tooth files (UA1-UA2) (UA1 = 'symphyseal' in Leriche, 1910). Leriche (1910, p. 267) also observed that, while the majority of the teeth possess folds on the lingual crown face, some teeth have a smooth lingual crown surface, strongly limiting the taxonomic value of this character.

Family Lamnidae Bonaparte, 1835
Genus *Isurolamna* Cappetta, 1976

Type species. Isurolamna affinis (Casier, 1946)

Isurolamna gracilis (Le Hon, 1871)
Plate 6.1 (IRSNB P 10311)

1871 *Oxyrhina gracilis* Le Hon, p. 11, text-fig.
1871 *Otodus rupeliensis* Le Hon, p. 11, text-fig.
1910 *Lamna rupeliensis*, Le Hon, 1871; Leriche, p. 271, pl. 15, figs 22–47.
1910 *Oxyrhina Desori* (L. Agassiz) Sismonda, 1849; Leriche, p. 275, pl. 16, figs 16–31.
1999 *Isurus desori* (Sismonda, 1849); Baut & Génault, p. 17, pl. 3, figs 7–8, ?9.
1999 *Rhizoquadrangulus rupeliensis* (Le Hon, 1871); Baut & Génault, p. 21, text-fig. 10, pl. 4, figs 1–3.
2001 *Isurolamna gracilis* (Le Hon, 1871); Reinecke et al., p. 21, pl. 31, figs a–g; pl. 32, fig. b; pl. 33, figs a–f; pl. 34, figs a–g.
2012 *Isurus desori* (Sismonda, 1849); Génault, pl. 193, figs 2–3, ?4.
2012 *Isurolamna rupeliensis* (Le Hon, 1871); Génault, pl. 193, figs 7–8.

Material. A single (?upper) anterior tooth.

Description. This anterior tooth measures 29 mm in height, but the root is strongly abraded. The large crown is distally directed and slightly sigmoidal in profile. The cutting edges are smooth and stop just before the crown base. There are no visible lateral cusplets.

Remarks. *Isurolamna gracilis* is one of the most common species of large-sized sharks in the Oligocene of the North Sea Basin (e.g. Baut & Génault, 1999; Reinecke et al., 2001; Génault, 2012). For a good iconography, see Leriche 1910, plates 15 (lateral teeth) and 16 (anterior teeth reported as *Oxyrhina desori* Sismonda, 1849).

Family Cetorhinidae Gill, 1862
Genus *Keasius* Welton, 2013

Type species. Keasius taylori Welton, 2013

Keasius parvus (Leriche, 1908)
Plate 6.2 (IRSNB P 10312)

1908 *Cetorhinus parvus* Leriche, p. 877 (gill rakers).
1910 *Cetorhinus parvus*, Leriche, 1908; Leriche, p. 294, text-figs 91–94 (gill rakers).
1978 *Cetorhinus parvus* Leriche, M., 1908; Steurbaut & Herman, p. 303 (table only).
1979 *Cetorhinus parvus* Leriche, 1908; Herman, p. 366, text-fig. 5; pl. 3, figs 1–2.
2001 *Cetorhinus parvus* Leriche, 1908; Reinecke et al., p. 24, pl. 36; pl. 37, figs a–c; pl. 38, figs a–d.
2012 *Cetorhinus parvus* Leriche, 1910; Hovestadt & Hovestadt-Euler, p. 72, fig. 3.
2013 *Keasius parvus* (Leriche, 1908); Welton, p. 39.
2015 *Keasius parvus* (Leriche, 1908); Reinecke et al., p. 54, figs 12–16, 22A, 22B, 24.

Material. Several fragmentary gill rakers. No teeth were found.

Description. See Welton (2013) and Reinecke et al. (2015)

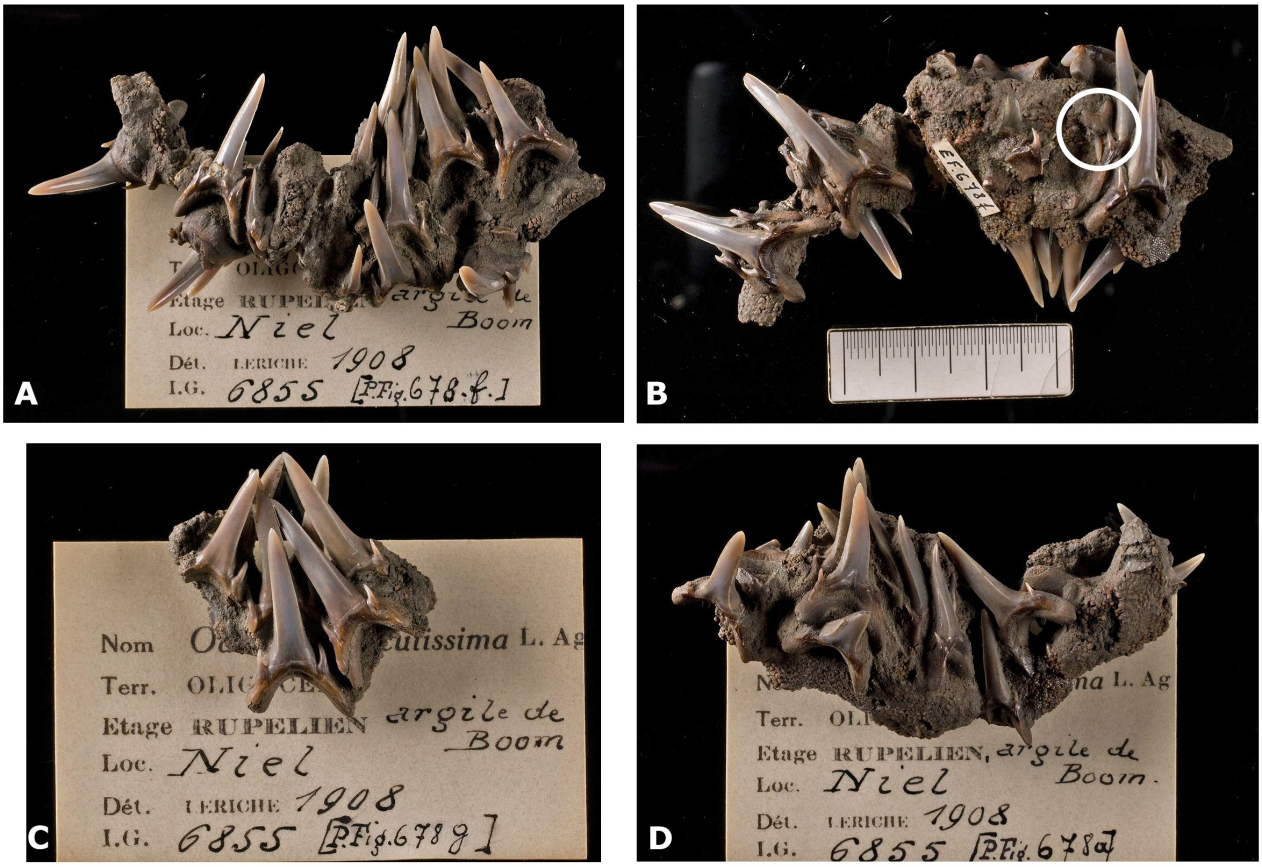

Figure 7. *Carcharias contortidens* (Agassiz, 1843) articulated tooth set. **A.** IRSNB P 678f – lower symphysis (Meckel's cartilage). **B.** IRSNB P 678f, rotated by 90° buccally. The upper intermediate tooth is encircled in white. **C.** IRSNB P 678g - partial right lower jaw half, detached from IRSNB P 678f. **D.** IRSNB P 678a - upper symphysis (palatoquadrate cartilage).

for gill raker terminology.

The genus *Keasius* is represented by some fragments of gill rakers only. They are strongly abraded and often lack diagnostic characters. However, one specimen (IRSNB P 10312 - Plate 6.2) is suitable for comparison, with the raker base and lower part of the filament preserved. The filament is narrow and moderately curved. The axe-shaped raker base is moderately long, with a large basal height. The attachment surface exhibits numerous small foramina. There is a slight distal protuberance. The mesial edge is rounded and convex. The basal edge is rounded to subangular. The medial process is relatively long and narrow. The bight shape is subangular.

Remarks. This specimen fits well within the diagnosis of *Keasius parvus* (Leriche, 1908) (see Welton, 2013; Reinecke et al., 2015), the only cetorhinid species to have been reported from the Belgian Oligocene (e.g. Leriche, 1910; Herman, 1979; Hovestadt & Hovestadt-Euler, 2012, as *Cetorhinus parvus*; Reinecke et al., 2015). For a long time, it was included within the genus *Cetorhinus*, along with the extant basking shark *C. maximus* (Gunnerus, 1765); however, based on teeth, gill rakers and vertebrae, Welton (2013) created the genus *Keasius* for his newly erected species *K. taylori* and included the species *parvus*.

Order Squaliformes Goodrich, 1909
Family Squalidae Bonaparte, 1838
Genus *Squalus* Linnaeus, 1758

Type species. Squalus acanthias Linnaeus, 1758

Squalus alsaticus (Andreae, 1890)
Plate 6.3-4 (IRSNB P 10313–10314)

1890 *Acanthias alsaticus* Andreae, p. 108, text-fig. 2.
? 1910 *Acanthias,* sp.; Leriche, p. 250, text-fig. 65. (spine)
1978 *Squalus alsaticus* (Andreae, 1892); Steurbaut & Herman, p. 304, pl. 1, figs 1–2.
2001 *Squalus alsaticus* (Andreae, 1892); Reinecke et al., p. 8, pl. 6, figs a–d; pl. 7, figs a–g.

Material. 113 teeth.

Description. A description of the teeth of *S. alsaticus* and a comparison with those of the extant *S. acanthias* were provided by Steurbaut & Herman (1978). Some teeth in our sample are strongly mesio-distally elongated (Plate 6.4), representing (?lower) posterior teeth (Herman et al., 1989).

Remarks. The presence of *Squalus alsaticus* (Andreae, 1890) can be expected as it is the most common elasmobranch species across the Boom Formation (e.g. Steurbaut & Herman, 1978; Hovestadt & Hovestadt-Euler, 1995). Extant species of the genus *Squalus* are known to form large schools (e.g. Compagno, 1984; Ebert et al., 2021) which could explain this large concentration of teeth. *Squalus* is an opportunistic scavenger, known to feed on carcasses (e.g. Auster et al., 2020).

Order Rajiformes Berg, 1937
Family Arhynchobatidae Fowler, 1934
Genus *Atlantoraja* Menni, 1972

Type species. Atlantoraja cyclophora (Regan, 1903)

Atlantoraja cecilae (Steurbaut & Herman, 1978)

1978 *Raja cecilae* Steurbaut & Herman, p. 306, pl. 2, fig. 4.
1978 *Raja heinzelini* Steurbaut & Herman, p. 306, pl. 2, fig. 2.
1978 *Raja terhagenensis* Steurbaut & Herman, p. 307, pl. 2, fig. 3.
1995 *Raja cecilae* Steurbaut & Herman, 1978; Hovestadt & Hovestadt-Euler, p. 265, pl. 3, figs la–1d; pl. 4, figs la–1d; pl. 5, figs la–1d; pl. 6, figs 1a–lc; pl. 7, figs 1a–lc; pl. 8, figs 1a–lc.
2015 *Atlantoraja cecilae* (Steurbaut & Herman, 1978); Reinecke, p. 3., figs 3a & 6b.

Material. 4 abraded teeth

Description. See Hovestadt & Hovestadt-Euler (1995) for a review and description of these teeth.

Remarks. Steurbaut & Herman (1978) described three rajoid species from the Boom Formation, *Raja terhagenensis*, *Raja heinzelini* and *Raja cecilae*, which were later considered to be different morphs of a single valid species, *R. cecilae* (Hovestadt & Hovestadt-Euler, 1995). Reinecke (2015) confirmed these observations and reassigned *R. cecilae* to the extant genus *Atlantoraja* Menni, 1972.

5.5. Teleostean otoliths (KH)

The otoliths generally are of good preservation. Ten different species have been identified, figured on Plates 9 to 12 and listed in Table 1. Since most species discovered in the present study are well known, comments will only be provided for the new species as well as for *Myoxocephalus primas* (Koken, 1891) and *Lophius gibbosus* Nolf, 1977. *Capros siccus* Schwarzhans, 2008 (Plate 11.7) is new for the Belgian Rupelian. Systematics follows Nelson et al. (2016).

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii Klein, 1885
Division Teleostei Müller, 1846
Order Carangiformes Jordan, 1923
Family Carangidae Rafinesque, 1815
Genus *Trachurus* Gronow in Gray, 1854

Trachurus reineckei Hoedemakers sp. nov.
https://zoobank.org/urn:lsid:zoobank.org:act:C6F25691-62E2-4A82-B204-5B6AC92764A6
Plate 10.1–8

2000 *Erythrocles* cf. *ohei* Schwarzhans; Müller & Rozenberg, p. 109–110, pl. 6, figs 7, ?9.

Diagnosis. Elongated otoliths characterized by a postdorsal angle of ca 90°, a coarse lobation on the posterior rim, posterior dorsal rim and posterior ventral rim, a large, rounded posterior extension at the height of the posterior part of the cauda and a lobation in the centre of the outer face only.

Types. Holotype: left otolith (IRSNB P 10334), 7 paratypes (IRSNB P 10329–10333, 10335–10336).

Material. 149, of which 8 are type specimens.

Locus typicus. Ceulemans clay pit at Schelle, 51°07'01.22" N, 4°21'21.30" E.

Stratum typicum. Silty lens associated with a tree trunk on top of pink R-horizon, Terhagen Member, Boom Formation, Rupelian (NP23), Oligocene.

Derivatio nominis. Named after Dr Thomas Reinecke (Bochum, Germany), in recognition of his contributions to palaeoichthyology, his much-appreciated help with photography and his friendship.

Description. Dimensions of holotype: L = 5.4 mm, H = 2.9 mm, thickness (T) = 0.9 mm, L/H = 1.9; L/T = 6.0. All other specimens are damaged at the rostrum and cannot be reliably measured. Outer face slightly convex and lobated at centre; lobes mostly not reaching rims but sometimes reaching to the dorsal rim in specimens about 4 mm or larger; smaller specimens strongly lobated at rims but not in centre. Inner face smooth, convex in antero-posterior direction; shallow ventral furrow present along ventral rim; distinct dorsal depression extending along entire crista superior. Dorsal and posterior rims as well as posterior part of ventral rim lobated, sometimes remnants (due to erosion) of fine crenulation present on anterior part of ventral rim; posterior lobation decreasing in largest specimen (Plate 10.1); ventral rim regularly convex, with distinct postventral angle; rostrum pointed and elongated; excisura mostly rounded and connecting to small antirostrum, dorsal rim with a few large lobes and gently sloping to postdorsal angle which generally is the highest point of the otolith and connecting to posterior rim at an angle of ca 90°; posterior rim straight in upper part, then oblique, mostly lobated (sometimes coarsely), with a rounded extension at the height of the posterior part of the cauda. Sulcus median, elongated, deep, with distinct cristae, divided in ostium (ca 40% of sulcus length) and cauda; posterior part of cauda turning toward ventral rim at angle of ca 45°, but not connecting to it. Specimens under 4 mm in length (Plate 10.8) have more crenulated rims and a less sloping dorsal rim with sometimes a less distinct postdorsal angle in very small specimens but with an elongated sulcus readily fitting them in an ontogenetic series of *T. reineckei*.

Discussion. Otoliths of species of *Trachurus* can be encountered in many associations of the Oligocene and Neogene, but mostly damaged and in small numbers, so that are usually left in open nomenclature. One otolith of Carangidae indet. is known from the Boom Formation (Steurbaut & Herman, 1978). We inspected it and found it to be a small and very eroded specimen that might nevertheless belong to the new species. Its state of preservation, however, does not allow any definite conclusion on the identity. One species based on a skull, *Belgocaranx luypaertsi* Taverne et al., 2006, could not be assigned to any of the extant genera of Carangidae. Leriche (1910, p. 305) mentioned findings of carangid vertebrae, but without further identification. Carangid otoliths discovered in Neogene associations often represent extant species (see Nolf, 2013, p. 99, pls 241–242). An exception is the Miocene *Trachurus miosensis* Lafond-Grellety in Nolf & Steurbaut, 1979, which can be found in large numbers in Serravallian deposits in SW France (Nolf & Steurbaut, 1979; Steurbaut, 1984). These otoliths differ from those of *Trachurus reineckei* in the smaller and less rounded to pointed posterior extension, the entirely crenulated ventral rim, the less distinct dorsal depression, a different postdorsal angle and the absence of a ventral furrow and lobation on the outer face. Another early Miocene species well represented in the North Sea Basin is *Trachurus elegans* Jonet, 1973 (Schwarzhans, 2010, p. 198, 200, pl. 77.1–7), whose otoliths differ from those of *T. reineckei* in the less sloping dorsal rim, a different postdorsal angle, more and finer crenulation on all rims, and the absence of a marked posterior extension.

Otoliths of the extant *Trachurus picturatus*, *T. trachurus* and *T. mediterraneaus* were studied in the collection of Recent otoliths as well as from illustrations on the AFORO website (Lombarte et al., 2006) and in Nolf et al. (2009) for *T. trachurus*. Otoliths of all three species differ from those of *T. reineckei* in the crenulation of the rims, the absence of an extended posterior rim and in many individuals by the distinct postdorsal angle as well.

One specimen of *Erythrocles* cf. *ohei* in Müller & Rozenberg (2000, pl. 6, fig. 7) shows the characteristics of *Trachurus reineckei* sp. nov. (including the lobation on the outer face, reaching the dorsal rim) and is herein synonymized with it. The other specimen figured by Müller & Rozenberg (2000, pl. 6, fig. 9) is larger and less high than the previous one, but still within the range of otoliths of *T. reineckei*, and is tentatively synonymized with it; the uncertainty is due to the almost unlobated dorsal rim (vs strongly lobated in *T. reineckei*) and the lobation on the outer face is invisible due to attached sediment.

Schwarzhans (1994) described and figured otoliths of *Erythrocles ohei* from the Chattian of Germany. We inspected the three type specimens kept at the Gutenberg University (Mainz, Germany) and compared them directly with our material; they are in many aspects similar with our specimens: elongated cauda, all cristae, distance cauda to ventral rim, ventral rim regularly convex, notched posterior rim and lobated outer face (still visible despite erosion). They differ, however, from the new species in the more convex dorsal rim which expands the dorsal portion (vs dorsal rim gently sloping posteriorly in *T. reineckei* giving the otoliths a smaller dorsal portion), the more oblique posterior rim caused by of the more massive posterior extension, the less lobated rims, a different postdorsal angle and a rounded rostrum (vs pointed rostrum in *T. reineckei*). An important difference is observed in ventral view: the ventral rim is concave on the outer face in the Chattian otoliths versus convex in those of *T. reineckei*. Otoliths of *T. reineckei* also differ from the Chattian *Trachurus opprimatus* Schwarzhans, 1994, which has a more crenulated ventral rim, a more pointed posterior rim, a more rounded dorsal rim, a posterior widening of the cauda and a different postdorsal rim.

Otoliths of *Erythrocles* Jordan, 1919 lack the posterior extension, generally have less convex rims and a more crenulated ventral rim, as opposed to otoliths of the genus *Trachurus* Rafinesque, 1810 (compare iconography in Lombarte et al., 2006; Nolf et al., 2009; Lin & Chang, 2012). For these reasons, we transfer the Chattian specimens to the genus *Trachurus* as *Trachurus ohei* (Schwarzhans, 1994).

Order Scorpaeniformes Garman, 1899
Family Cottidae Bonaparte, 1831
Genus *Myoxocephalus* Tilesius, 1811

Myoxocephalus primas (Koken, 1891)
Plate 12.1–9

1891 Otolithus (?*Agonus*) *primas* Koken, p. 131–132 (not figured).
1977 *Liparis minusculus* Nolf, p. 45–46, pl. xiii; figs 14–16.
1978 Congridarum *trapezioides* n. sp.; Gaemers & van Hinsbergh, p. 8–9, pl. 2, fig. 3 (based on an eroded specimen).
2013 "*Agonida*" *minuscula* Nolf; Nolf, p. 86, pl. 189.
2016 "*Agonida*" *minuscula* Nolf; Hoedemakers & Schneider, p. 128 (table), pl. 8, fig. 1.

See Schwarzhans (2008) for a more detailed synonymy list regarding *M. primas*.

Our specimens compare well with the type and other specimen described and figured by Weiler (1942, p. 66–67, pl. 4, figs 22–23) and refigured by Schwarzhans (1994, 135, figs 329–330) based on the summary description by Koken (1891, not figured). They show a cauda which is ca ¾ times as long as the ostium, with a large posterior portion behind the cauda and a high dorsal area. In these aspects, they differ from those figured by Schwarzhans (2008, p. 23, fig. 5d–e) which appear more elongate, less high and somewhat more thickset. We figure a growth series of otoliths (Plate 12.1–8) as well as the holotype of *Liparis minusculus* (Plate 12.9). The sulcus of all specimens shows a long ostium, widely opening on the anterior rim, and a shorter cauda. The outline is very similar in all specimens, with a notched ventral rim in the smaller specimens, the ventral rim gently sloping towards the anterior rim which has a large rostrum but no anti-rostrum. The anterior rim gently connects to the convex dorsal rim which has a straight posterior part with a rounded postdorsal angle connecting with a convex posterior rim. The posterior rim passes into the ventral rim without postventral angle (compare Plate 12.5–6 with Plate 12.9). The small specimens are more thickset in ventral view than the larger ones. The holotype of *L. minusculus* perfectly fits in the growth series of *M. primas* and is therefore synonymized with the latter.

Order Lophiiformes Garman, 1899
Family Lophiidae Rafinesque, 1810
Genus *Lophius* Linnaeus, 1758

***Lophius gibbosus* Nolf, 1977**
Plate 11.8

1977 "genus Lophiidarum" *gibbosus* Nolf, p. 20–21, pl. xi, fig. 29.
2013 "*Lophiida*" *gibbosa* Nolf; Nolf, p. 71, pl. 145.

One left otolith, L = 6.4 mm, H = 4.9 mm, T = 1.4 mm (IRSNB P 10380). Our specimen is slightly more than twice as large as the holotype of *Lophius gibbosus* Nolf, 1977 from the Rupelian of Kruibeke. It is much thinner in ventral view and the posterior rim is rounded versus pointed. Its dorsal rim is more lobated than that of the holotype. Specimens of similar size of the extant species *Lophius piscatorius* indicate that the fossil specimen from Schelle may have derived from a fish of ca 40 cm total length (TL).

A comparison with otoliths of the *L. piscatorius* Linnaeus, 1758 from the Gulf of Biscay was made to understand the growth trend. These modern otoliths show an ontogenetical evolution: small otoliths (L=3–4 mm) derived from fish of 18–20 cm TL are quite thickset overall in ventral view, whereas larger otoliths are thickset only in the central part in ventral view. The posterior rim is acuminated in many otoliths, but sometimes it is rounded, so this character cannot be used with confidence to characterize otolith-based species, even more so as it is independent of ontogeny. Generally, adult otoliths of *L. piscatorius* become larger anteroposteriorly, but not ventrodorsally. Large otoliths of *L. piscatorius* become strongly lobated on the dorsal rim. The ventral rim can be slightly convex to almost straight in otoliths of any length. Summarizing, otoliths of *L. piscatorius* tend to become thinner, more lobated dorsally and larger anteroposteriorly with ontogeny.

The holotype of *L. gibbosus* appears quite high and has an L/H ratio of 1.4, whereas this ratio in our specimen is 1.3. Because very few otoliths of *L. gibbosus* are known, the ontogeny cannot be reconstructed with certainty. The holotype of *L. gibbosus* and our specimen have a comparable L/H ratio.

The holotype is thickset with an unlobated dorsal rim, whereas the specimen in our sample is thinner and has a lobated dorsal rim. After comparison with a growth series of otoliths of *L. piscatorius*, we conclude that the specimen from the wood-fall assemblage putatively fits in a growth series of *L. gibbosus*, whereby the holotype is interpreted as having derived from a juvenile fish.

5.6. Miscellanea

A number of additional fossils were found, including several large benthic foraminifera. Furthermore, a fragment of a portunoid dactylus was encountered (Plate 6.5 - IRSNB 7735), most probably belonging to *Coeloma rupeliense* Stainier, 1887 (Van Bakel, pers. comm., 2021). This species dominates the crab fauna of the Boom Formation, but is mostly preserved in nodules (Verheyden, 2002).

6. Palaeoecology

Driftwood as wood-fall in Rupelian clay deposits in the North Sea Basin

All fossils described herein were discovered in connection with a fragment of sunken driftwood in a 5 to 10 cm thick layer of silty sediment trapped between the trunk and a side branch. The presence of driftwood in the Boom Formation was reported before by Van den Broeck (1887) and in bed 28 of the Terhagen Member by Vandenberghe (1978, 2017, fig. 9). Terrestrial phytoclasts in the clay are well known on a microscopic scale: black stained layers in the Boom Formation are dark coloured due to the influx of detrital terrestrial organic matter (total organic carbon content of 1–5 wt.%) (Vandenberghe, 1976; Vandenberghe et al., 2014). This model invokes the periodic destruction of coastal vegetation due to eustatic sea-level rise. The vegetation cover of that submerged land is destroyed and the plants are transported into the basin where they are mostly deposited as silt-sized phytoclast particles, and this periodically from the top of an individual silt horizon till the middle of the overlying clay horizon (Vandenberghe, 1976; Vandenberghe et al., 2014). The driftwood has a similar origin as the phytoclasts and only differs from the latter by its size and therefore by its settling history.

Driftwood in the Boom Formation is occasionally associated with a specific fossil assemblage, with taxa usually different from those occurring in the surrounding soft-bottom environments, as was discovered near a tree trunk in the S30 level at Niel (Marquet & Herman, 2012; Marquet, 2016). According to the explanation of Marquet & Herman (2012), these floating and subsequently submerged wood fragments form a small local slack water environment, assembling a much richer fossil assemblage than usual at any level. A similar phenomenon has been described by Hoedemakers & Schneider (2016) from Bad Freienwalde (Germany), where an unusually high number of otoliths, representing 26 taxa, was concentrated against a piece of driftwood in a similar 'Rupel Clay/ Septarienton' deposit. This association is dominated by otoliths of *Trisopterus elegans* (as *Palimphemus parvus*), *Argentina parvula*, *Palaeogadus compactus* and *Hoplobrotula acutangula*, which together constitute more than 95.5% of all otoliths discovered. The association of fossils and driftwood at Schelle is therefore another rare occasion to further investigate this remarkable phenomenon. The large quantity of macrofossils associated with the studied trunk in Schelle warrants an explanation as macrofossils in the Rupelian clay usually are very dispersed. After sinking to the bottom, the trunk formed a large bottom irregularity, which probably increased local wave-induced turbulence on the seafloor, contributing to the local concentration of relatively coarser sediments and macrofossils near the trunk. Given the low sedimentation rates (the Boom Formation banding pattern is primarily driven by the 41 ka obliquity cycle; Abels et al., 2007), concentrating effects due to turbulence can be substantial after a long time. This process may have taken several hundreds to perhaps a couple of thousand years, until the driftwood was entirely covered by sedimentation. However, such a simple concentration by turbulence cannot be the only explanation for the large size of the encountered fossil assemblage, as the volume of clay that would have to be concentrated would be excessively large in view of the low number of macrofossils usually present in the Boom Clay. The presence of a large number of species unique or very rare to the Boom Formation indicates that the driftwood may have been a particular substrate that allowed colonization by multiple organisms, i.e., a case of wood-fall. In order to assess this special habitat, we compared with cases of wood-fall in past and present as well as with present-day man-made obstacles on the seafloor.

Past and present-day wood-falls and man-made obstacles on the seafloor

Data from Late Eocene to Miocene wood- and whale-falls from bathyal depths in the NE Pacific are available (Kiel & Goedert, 2006). This wood was heavily bored by teredinid or xylophagain bivalves. All other associated molluscs (among others an unidentified cocculinid gastropod, three species of *Nuculana* and a pectinid), including predators (e.g., naticids, turrids, *Dentalium laneensis*), were found in close proximity. No data on elasmobranch or teleost fishes were given.

The diversity of organisms associated with present-day wood-fall depends on the type of wood and depth of deposition (Bienhold et al., 2013; Saulsbury, 2014; Judge & Barry, 2016). Most present-day experiments (i.e. wood dropped on the sea bottom) are executed at greater depths and involve tree species different from the one at Schelle, but generally develop largely endemic and highly diverse communities with predators upon them within a few years (Voight, 2007; McClain & Barry, 2014; McClain et al., 2016; Webb et al., 2016). These communities are distinct from those in the surrounding sediment (McClain et al., 2016). Early colonizers are wood-boring bivalves (Voight, 2007; Bienhold et al., 2013; McClain & Barry, 2014), but a large diversity of invertebrates was also observed (Judge & Barry, 2016; McClain et al., 2016). No data on fishes are available from these studies.

Man-made obstacles of all sorts on the seafloor of shallow seas (e.g., oil rigs, platforms for windmills, shipwrecks) constitute artificial reefs and provide hard substrates on soft bottoms, attracting substrate-associated species as well as demersal fish species that live on or near them. Studies show that the density and diversity of this fauna and flora increase over the years (see e.g. Santos et al., 2012; Coolen et al., 2020; De Backer et al., 2021), with higher levels of species richness and abundance than on the soft bottoms at a short distance from them (Zintzen, 2007; Consoli et al., 2015).

An experimental artificial reef composed of blocks of stabilized coal-fired power station waste, consisting of eight conical units (each ca 1 m high and ca 8 m across), was established in Poole Bay (English Channel, UK) at a depth of ca 10 m to observe the colonization by living organisms (Jensen et al., 1994). The first settlers were tube worms, followed by species of Tunicata, algae, bryozoans and hydroids. Decapoda came and went as mobile species living on site on the artificial reef but also moving away at other times. Worms and sponges moved in as space became available, seasonal colonizers were barnacles. All these species were observed preying on each other. After one year, colonization was complete, meaning that the faunal composition on the artificial reef was comparable with that on natural reefs in the area. The most important fish species associated with different parts of the reef was *Trisopterus luscus* which preyed extensively on the invertebrates.

Present-day shipwrecks at shallow depths (<60 m) in the southern North Sea provide protection from predators, currents and sand scouring, and change the hydrodynamic regime in the surrounding sediment (Zintzen, 2007; Lengkeek et al., 2013). Zintzen (2007) observed a shift from a habitat dominated by bivalves and polychaetes on soft sediments to shipwrecks dominated by crustaceans, polychaetes and cnidarians. On shipwrecks, crustaceans are often very abundant (Jensen et al., 1994; Lengkeek et al., 2013); in one case, amphipods and nematodes were the most abundant groups (Mallefet et al., 2008).

It can be concluded that hard-substrate obstacles on the seafloor are quickly colonized by various groups of invertebrates, which prey and are preyed upon among themselves.

7. Discussion and conclusion

Based on the sedimentological, taphonomic and faunistic data, combined with the abovementioned studies, a reconstruction can be made of the development of the fossil concentration associated with the driftwood at Schelle. First, the trunk of *Cupressinoxylon* sp. was transported from the hinterland into the basin by rivers or directly during inundation and destruction of coastal forests by the rising sea. During its transport on the water surface, the driftwood became colonized by xylophagous Teredinidae (see Romano et al., 2020), which was already noted by Van den Broeck (1887). This may even have started in a brackish water area with continuing colonization in the open marine environment, probably also after sinking. The deepest burrow in the wood measured 6 cm. Based on growth rates reported for *Teredo navalis* (1.8 mm d^{-1}), *Teredo gregoryi* (0.54 mm d^{-1}) and *Lyrodus pedicellatus* (0.59 mm d^{-1}) (Edmondson, 1962; Gallager et al., 1981; Paalvast & van der Velde, 2011), colonization by teredinids was probably complete within a few months (at least 30 days, possibly exceeding 100 days). Finally, when the wood became waterlogged, the trunk started to sink to the bottom. After having sunk, the water-logged trunk was also colonized by *Cocculina reineckei*, using the wood as a substrate to consume its associated wood-degrading bacteria. The trunk provided a natural irregularity on the sea bottom, until it became covered by sediment. The large number of macrofossils associated with the trunk and the fact that it survived at all may indicate that it was at some time accessible for colonization by demersal species, but the exact duration remains unknown. Remains of preserved invertebrates are quite rare, but most of these species were not fossilized and their presence can only be inferred from the presence of predators based on comparison with modern artificial reefs. For example, pyramidellid snails like *Odostomia* are ectoparasites on polychaetes and molluscs (Cole & Hancock, 1955; Høisæter, 2014). While they are very rare elsewhere in the Boom Formation, the presence of these snails may indicate the presence of polychaetes near the sunken trunk. Our sample also contained abundant otoliths of *Trisopterus elegans*, a small gadoid species, which probably preyed on the invertebrates on and near the trunk as the present-day *Trisopterus luscus* does. It is accepted that otoliths commonly enter the sediment through excrements of predators (Nolf, 2013), implying that 'larger' predators were also present. Remains of large elasmobranchs are rare, except for *Carcharias contortidens* and *Squalus alsaticus*, the latter living benthically. The teeth of *Carcharias contortidens* were largely derived from a single dead specimen, which may have floated against the tree trunk prior to or during rotting, whereupon its teeth were concentrated, as was the case with the teleost otoliths, probably due to long-term effects of turbulence. Interestingly, no shark vertebrae have been preserved. Some mollusc species are probably present simply because they were common in the palaeoenvironment of the Boom Formation (e.g. *Nucula duchasteli*, *Euspira achatensis*). For some other rare species (e.g. *Palliolum permistum*, *Amlyacrum* cf. *roemeri*), it is less clear whether their presence can be linked to the unique environment of the sunken trunk or merely due to the coincidental proximity of their populations.

The studied fossil association has a unique composition. For the first time since Vincent (1930), complete specimens and fragments of *Palliolum permistum* have been found, while the gastropod *Amblyacrum* cf. *roemeri* is even completely new to the Belgian Rupelian. The same applies to a unique set of well-preserved turtle barnacle compartmental plates (*Protochelonibia*), never reported before from the Boom Formation, representing the largest known concentration from any location of Rupelian age (see e.g. Collareta et al., 2021; Perreault et al., 2022). These can indirectly attest to the presence of sea turtles, reported before from the Rupelian (e.g. Smets, 1886a, 1886b, 1887a, 1887b, 1888). The mollusc fauna studied here differs considerably from another mollusc assemblage associated with driftwood, found in the septaria level S30 of the Terhagen Member in Niel (Marquet, 2010). For example, the latter fauna contained the bivalve genus *Thyasira* Leach, 1818. *Thyasira* is also reported from the Mediterranean in present-day wood-falls (Bienhold et al., 2013), a Miocene whale-fall (Danise et al., 2016) as well as from Cenozoic wood- and whale-falls in the NE Pacific (Kiel & Goedert, 2006). In contrast to our assemblage, large genera like *Arctica* and *Glycymeris* were also found associated with the S30 driftwood (Marquet, 2010). Normally, both genera are very rare in the clays of the Boom Formation and are more common in shallow, sandy deposits of the Kerniel and Berg members (Bilzen Formation) and the Grimmertingen Member (Sint-Huibrechts-Hern Formation) in Limburg (Vervoenen, 1995; Marquet et al., 2012). Marquet (2010) mentions two juvenile specimens of *Glycymeris lunulata lunulata* auct. non. Nyst, 1836 from Niel. Like Glibert's (1957) specimens, these are eroded. Marquet (2010) therefore suggested that they may have been transported over a long distance, which is quite unusual for the Boom Formation. Besides, also several dozens of *Callucina (Callucina) thierensi* (Hébert, 1849) were encountered near the S30 driftwood, a species previously not reported from the Boom Formation and absent in our fauna.

Interestingly, there are also some similarities in molluscs between the Cenozoic wood-falls in the NE Pacific (Kiel & Goedert, 2006) and our association: both contain teredinids, cocculinids, pectinids, naticids and a scaphopod. Another similarity is with present-day shallow-water anomalies (shipwrecks and experimental artificial reefs) where the teleost associations are dominated by a species of *Trisopterus*. The teleosts show more similarities with a contemporaneous piece of driftwood from Bad Freienwalde (Hoedemakers & Schneider, 2016), with nine species in common, including the same two dominating species (*Tristoperus elegans*, then described as *Palimphemus parvus*, and *Argentina parvula*). Most species indicate open-marine shelf conditions (<100 m). The concentration of otoliths was hypothesized to have occurred through accumulation near an obstruction on the seafloor or by burrowing sedentary predators (Hoedemakers & Schneider, 2016). It seems more likely, however, that the driftwood at Bad Freienwalde provided the same type of artificial reef with associated fauna as the tree trunk at Schelle, combined with long-term concentration due to wave-driven turbulences.

In conclusion, the presence of a large tree trunk on top of the R-horizon (base bed 22) of the Terhagen Member represents a wood-fall, providing a snapshot of the surrounding biological communities in Schelle during the Rupelian. A mix of common and fairly unique species was preserved in an exceptionally large concentration for the Boom Formation. Since wood-fall is a relatively rare phenomenon in the Boom Formation, future finds could also include the study of microfossils to investigate whether they are concentrated in the same way as macrofossils and which of these, if any, are dominant. Moreover, each trunk seems to have its own unique assemblage of macrofossils, so new finds of driftwood could possibly lead to the discovery of unknown taxa of various groups in the European Rupelian.

Author contributions

Geert De Borger and Walter Van Remoortel discovered and excavated the driftwood and collected and picked-out the fossils. Pieter De Schutter conceptualised this paper and described the elasmobranch remains. Stijn Everaert wrote the "Geological background” chapter and studied the molluscs. Andy Gale described the turtle barnacles. Kristiaan Hoedemakers studied the otoliths and co-edited the paper. Jakub Sakala and Vít Koutecký identified the woody remains. Stijn Everaert, Kristiaan Hoedemakers and Pieter De Schutter contributed to the “Palaeoecology” and “Discussion and conclusion” chapters.

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Data availability

All studied specimens are housed in official repositories guaranteeing their long-term safekeeping and availability to other researchers for future studies.

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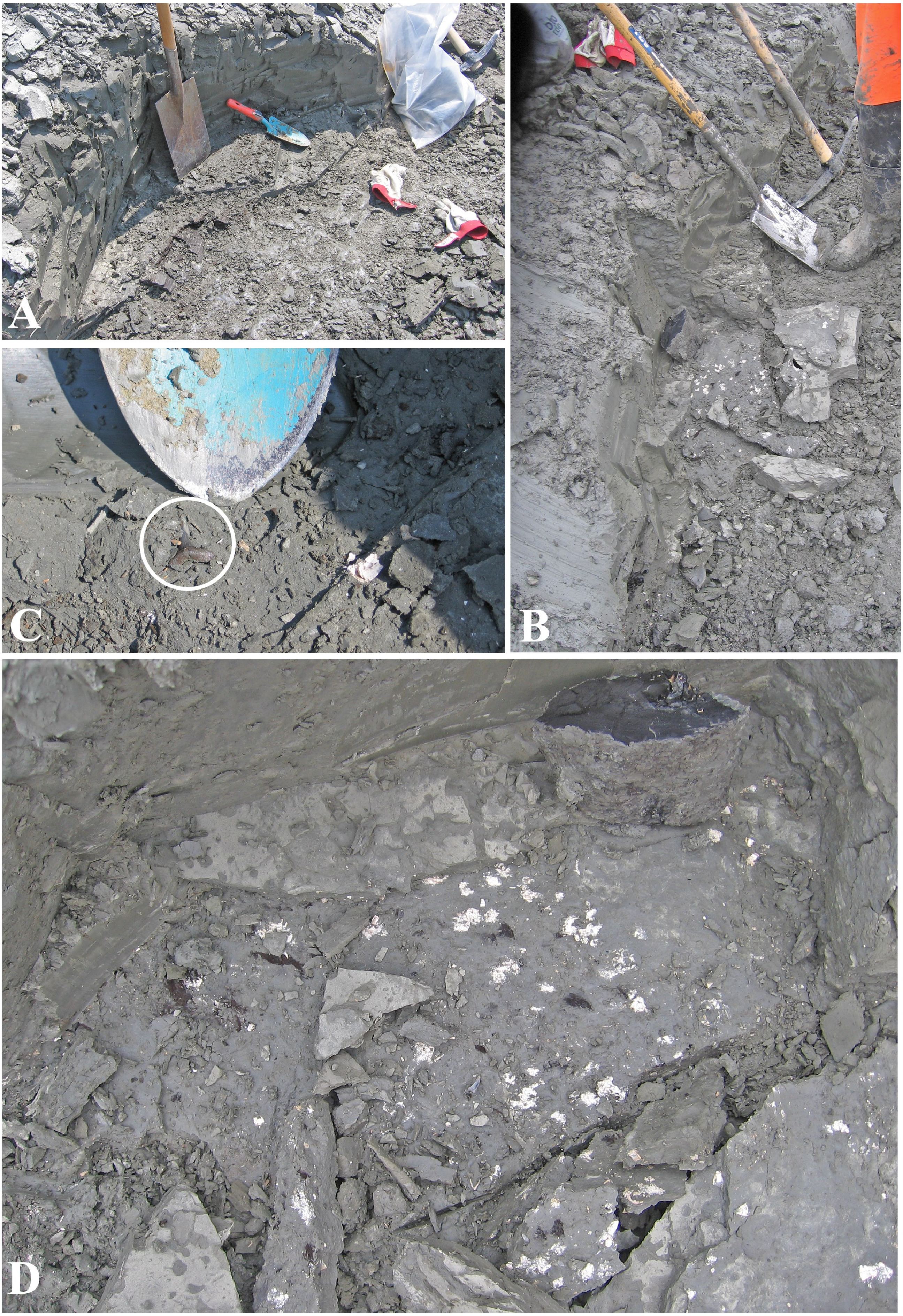

Plate 1. View of the excavation. **A–B.** General view. **C.** Lower lateral tooth of *C. contortidens in situ*. **D.** Detail of the lens. The black spots are wood fragments, while the white spots represent the remains of calcareous fossils.

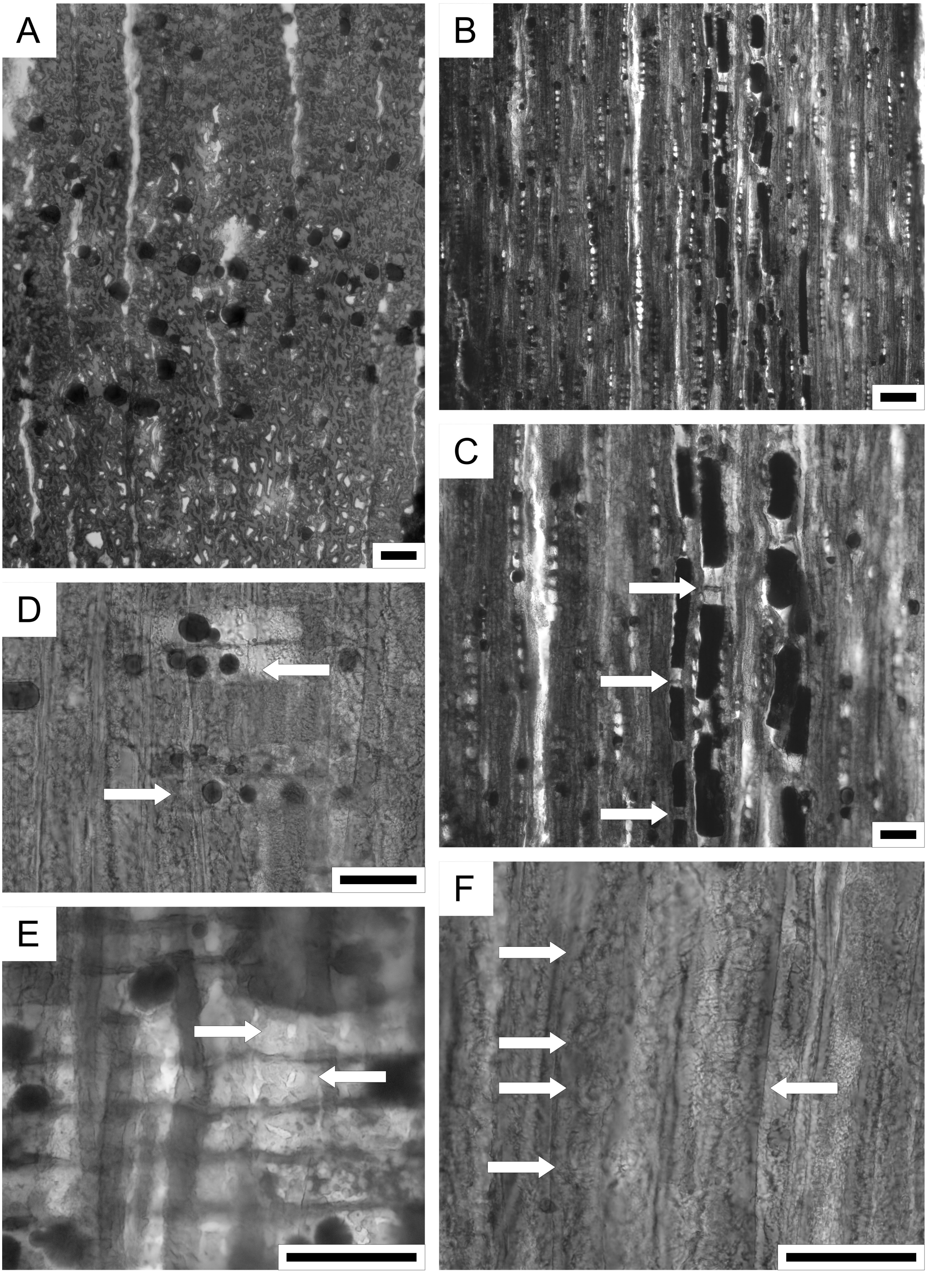

Plate 2. *Cupressinoxylon* sp., sample: IRSNB b9669. **A.** Early- and latewood tracheids destructed by compression, axial parenchyma diffuse and abundant, transverse section. **B.** Uniseriate rays medium in average high, axial parenchyma with thin and smooth to beaded transverse end walls, tangential longitudinal section. **C.** Axial parenchyma with thin and smooth to beaded transverse end walls (arrows), tangential longitudinal section. **D.** Ray parenchyma cells with thin and smooth horizontal walls and resiniferous infill (arrows), radial longitudinal section. **E.** One cupressoid pit per cross-field (arrows), radial longitudinal section. **F.** Rounded bordered pits in radial tracheid wall (arrows) arranged in one vertical row, radial longitudinal section. Scale bars: A, C, D, E, F = 50 µm, B = 100 µm.

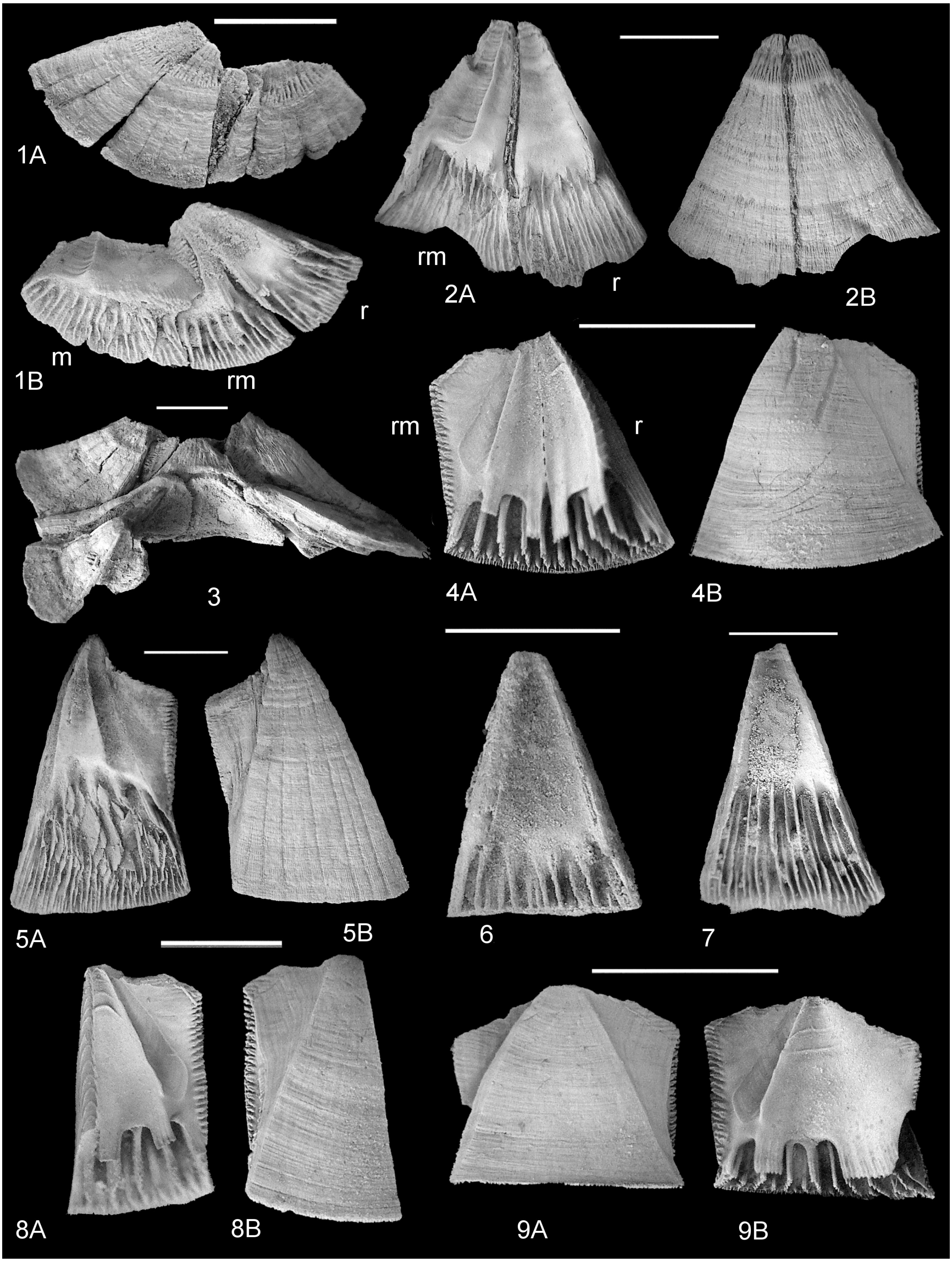

Plate 3. Cirripedia. **1–3**, **5–7.** *Protochelonibia hermani* sp. nov. 1A (external), 1B (internal) views of articulated rostrum, rostromarginal and marginal of small specimen (IRSNB 7705). 2A (internal), 2B (external) views of articulated rostrum and rostromarginal (IRSNB 7706). 3, partially articulated group of specimens (IRSNB 7707). 5A (internal) and 5B (external) views of large rostromarginal (IRSNB 7708). 6, 7, internal views of rostra (IRSNB 7709, 7710). **4, 8, 9.** *Chelonibia testudinaria* (Linnaeus, 1858), forma *patula* (Ranzani, 1817), present day, Florida, USA. 4A (internal), 4B (external) views of articulated rostrum and rostromarginal. 8A (internal), 8B (external) views of rostromarginal. 9A (external), 9B (internal) views of marginal. Scale bars = 5 mm.

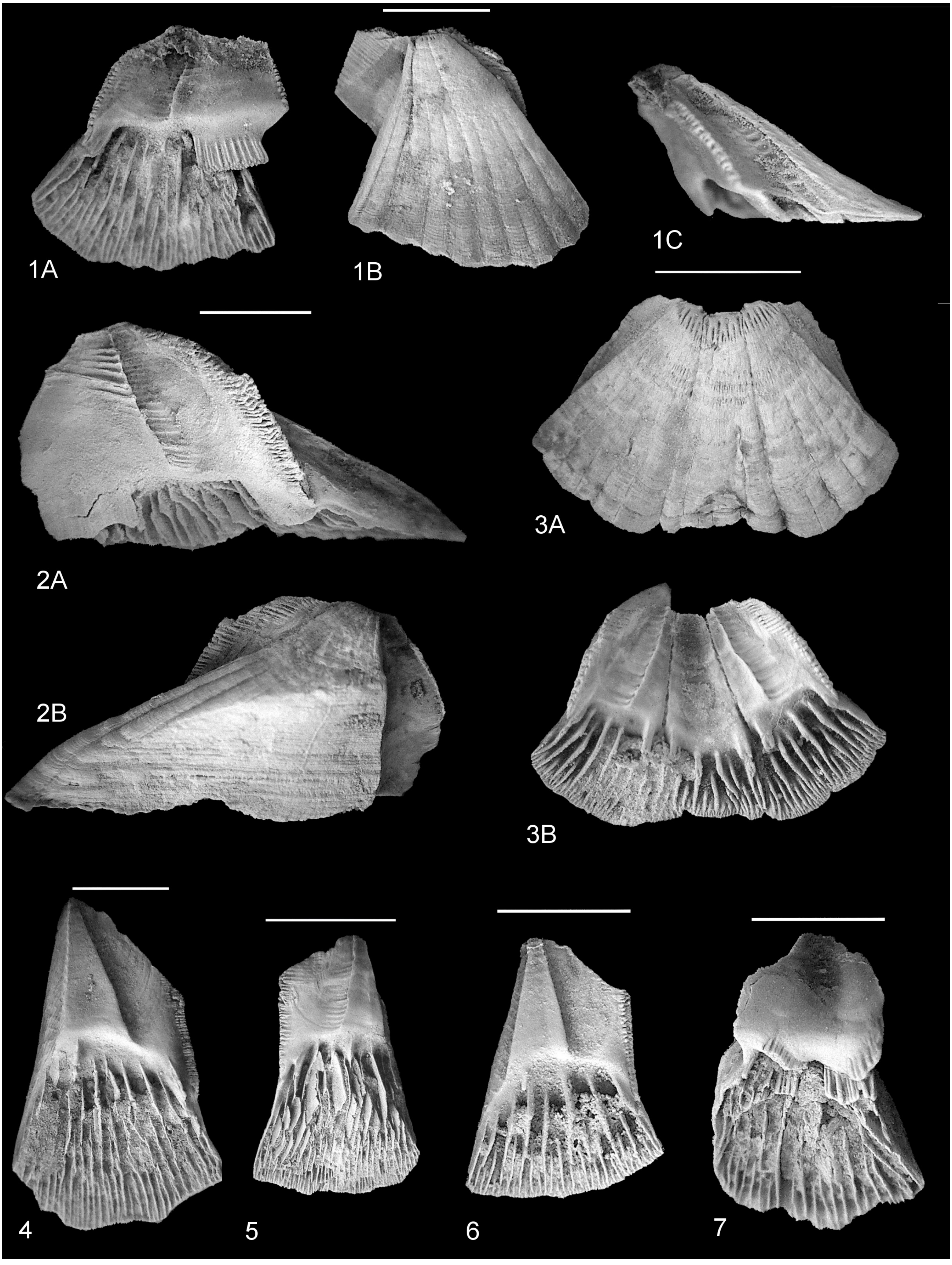

Plate 4. Cirripedia. **1–7.** *Protochelonibia hermani* sp. nov. 1A (internal), 1B (external) and 1C (lateral) views of carinomarginal (IRSNB 7711). 2A (internal) and 2B (external) views of elongated marginal (IRSNB 7712). 3A (external) and 3B (internal) views of articulated rostrum and rostromarginals (IRSNB 7713). 4–6, internal views of rostromarginals, showing variation in angle of superior radial margin, from strongly (4) to less (5, 6) inclined (IRSNB 7714-7716). 7, internal view of carina with weakly dependant sheath overlying ridged processes (IRSNB 7717). Scale bars = 5 mm.

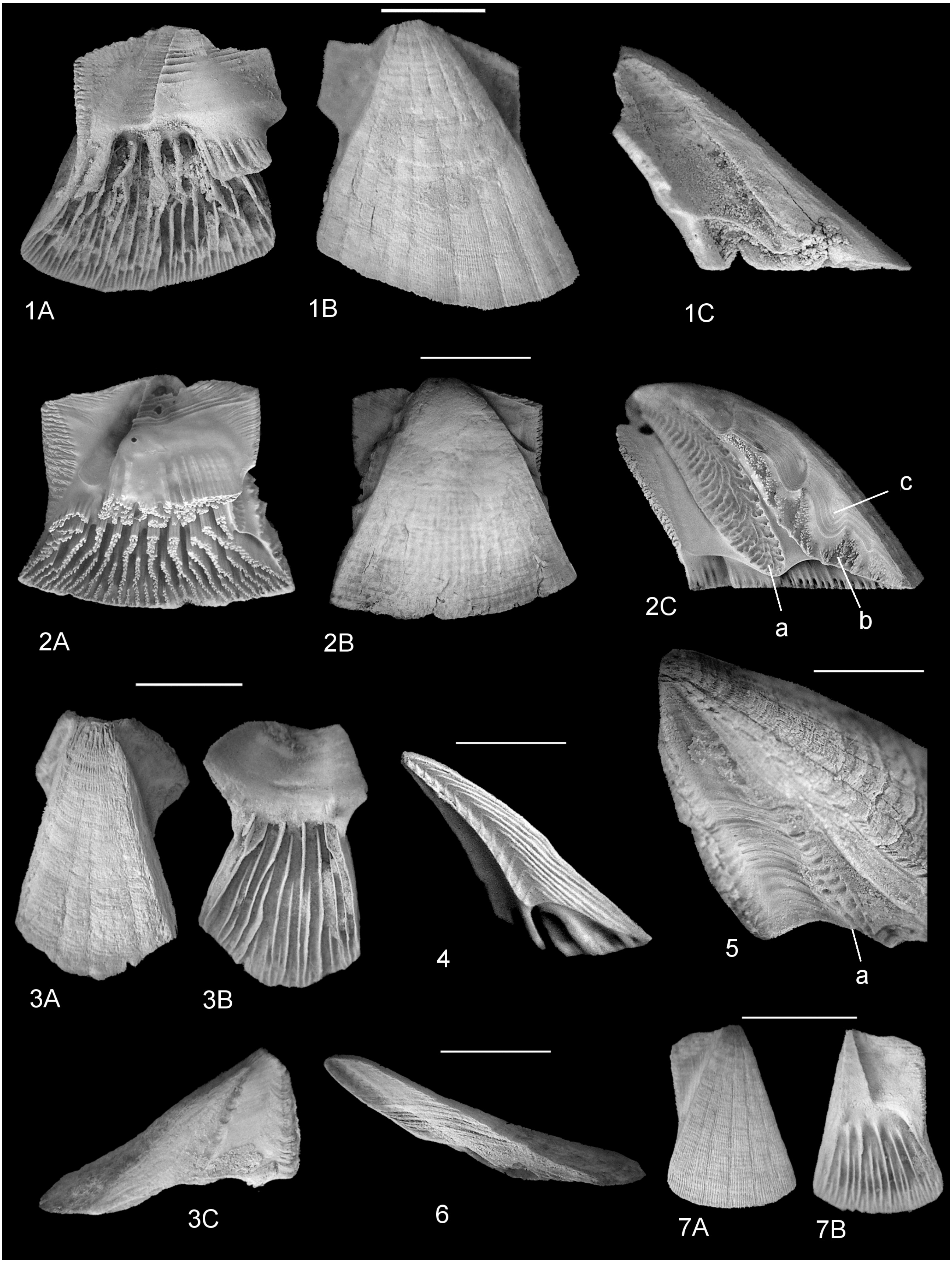

Plate 5. Cirripedia. **1, 3, 5–7.** *Protochelonibia hermani* sp. nov. 1A (internal), 1B (external) and 1C (lateral) views of holotype marginal (IRSNB 7718). 3A (external), 3B (internal), 3C (lateral) views of carina (IRSNB 7719). 5, enlarged image of ala of marginal plate (IRSNB 7721) to show narrow, pitted surface for articulation with radius of adjacent plate (a); note absence of denticulate surface (b) present in *C. testudinaria* (2C). 6, lateral view of articular surface of rostrum (IRSNB 7720) for comparison with *C. testudinaria* (4); note concave profile and lack of articular ridges. 7A (external), 7B (internal) views of small rostromarginal (IRSNB 7722). **2, 4.** *Chelonibia testudinaria* (Linnaeus, 1858), present day, North Carolina, USA. 2A (internal), 2B (external), 2C (lateral) views of marginal of *Chelonibia testudinaria* forma *testudinaria* (Linnaeus, 1758). Note strongly developed articulation surfaces. 4, *Chelonibia testudinaria* forma *patula*, articulation surface of rostrum. Note narrow ridges and grooves.

Abbreviations: a, specialised pitted articular surface on ala for denticulate ridge on radius of adjacent plate; b, articulation surface between adjacent parietes comprising columns of small denticles; c, depressions between parietes. Scale bars = 5 mm.

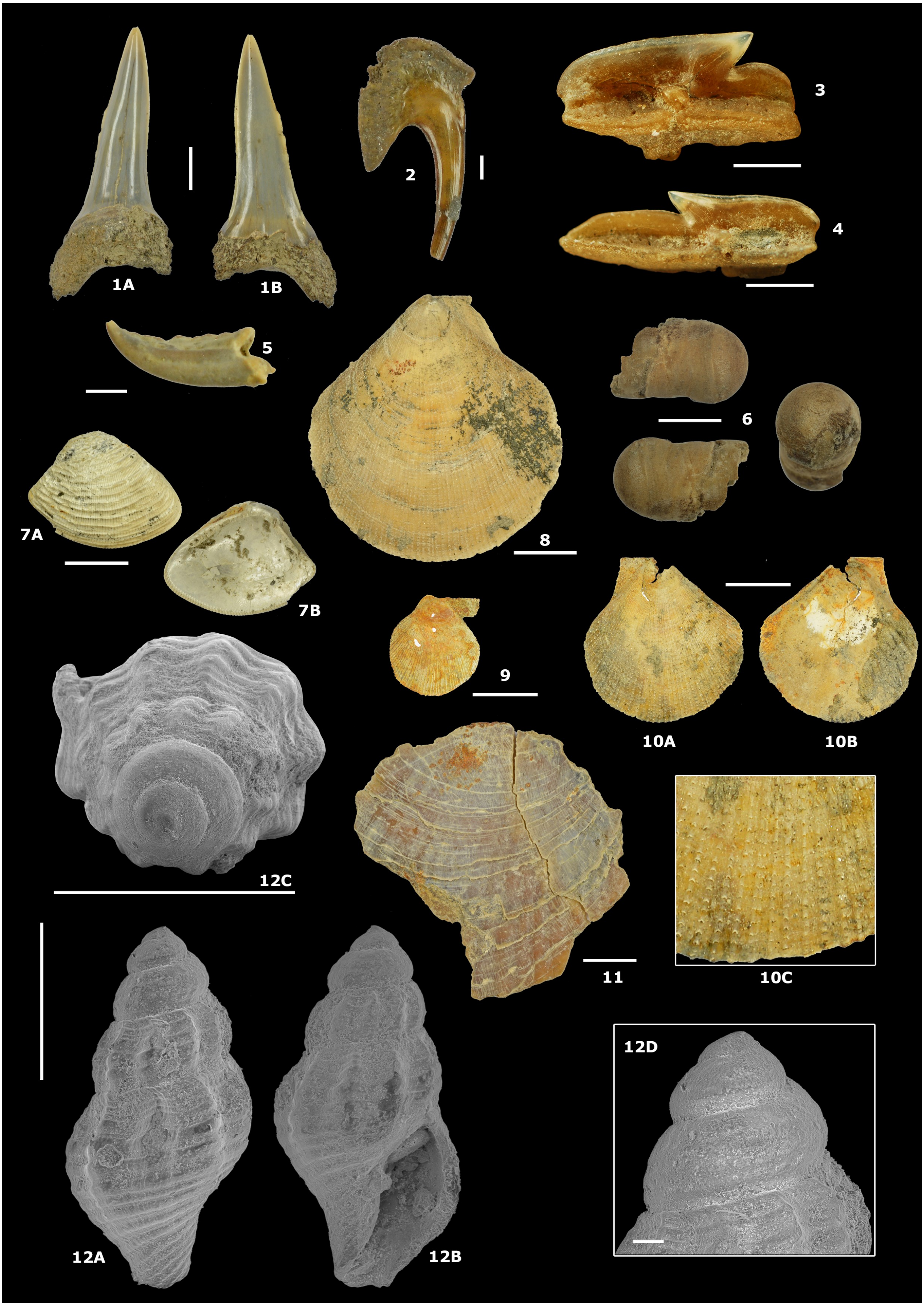

Plate 6. Shark teeth, decapod dactylus and molluscs. Scale bars = 5 mm, unless specified otherwise. **1A–B.** *Isurolamna gracilis* (Le Hon, 1871) - IRSNB P 10311 - anterior tooth; lingual (A) and labial (B) views. **2.** *Keasius parvus* (Leriche, 1908) - IRSNB P 10312 - gill raker. Scale bar = 1 mm. **3.** *Squalus alsaticus* (Andreae, 1890) - IRSNB P 10313. Scale bar = 1 mm. **4.** *Squalus alsaticus* (Andreae, 1890) - IRSNB P 10314. Scale bar = 1 mm. **5.** *Coeloma rupeliense* Stainier, 1887, dactylus - IRSNB 7735. Scale bar = 1 mm. **6.** Teredinidae indet. – calcareous tube - IRSNB 7729. **7A–B.** *Nucula duchasteli* Nyst, 1835 - IRSNB 7730. **8.** *Palliolum permistum* (Beyrich, 1848) - IRSNB 7731. **9.** *Palliolum permistum* (Beyrich, 1848) - IRSNB 7732. **10A–C.** *Palliolum permistum* (Beyrich, 1848) - IRSNB 7733. Detail of ornamentation (C). **11.** *Palliolum delheidi* (Vincent, 1930) - IRSNB 7734. **12A–D.** *Amblyacrum* cf. *roemeri* (von Koenen, 1867) - IRSNB 7736. Abapertural (A), apertural (B) & apical (C) views & detail of the protoconch (D). Scale bars = 1 mm (A–C) and 100 µm (D).

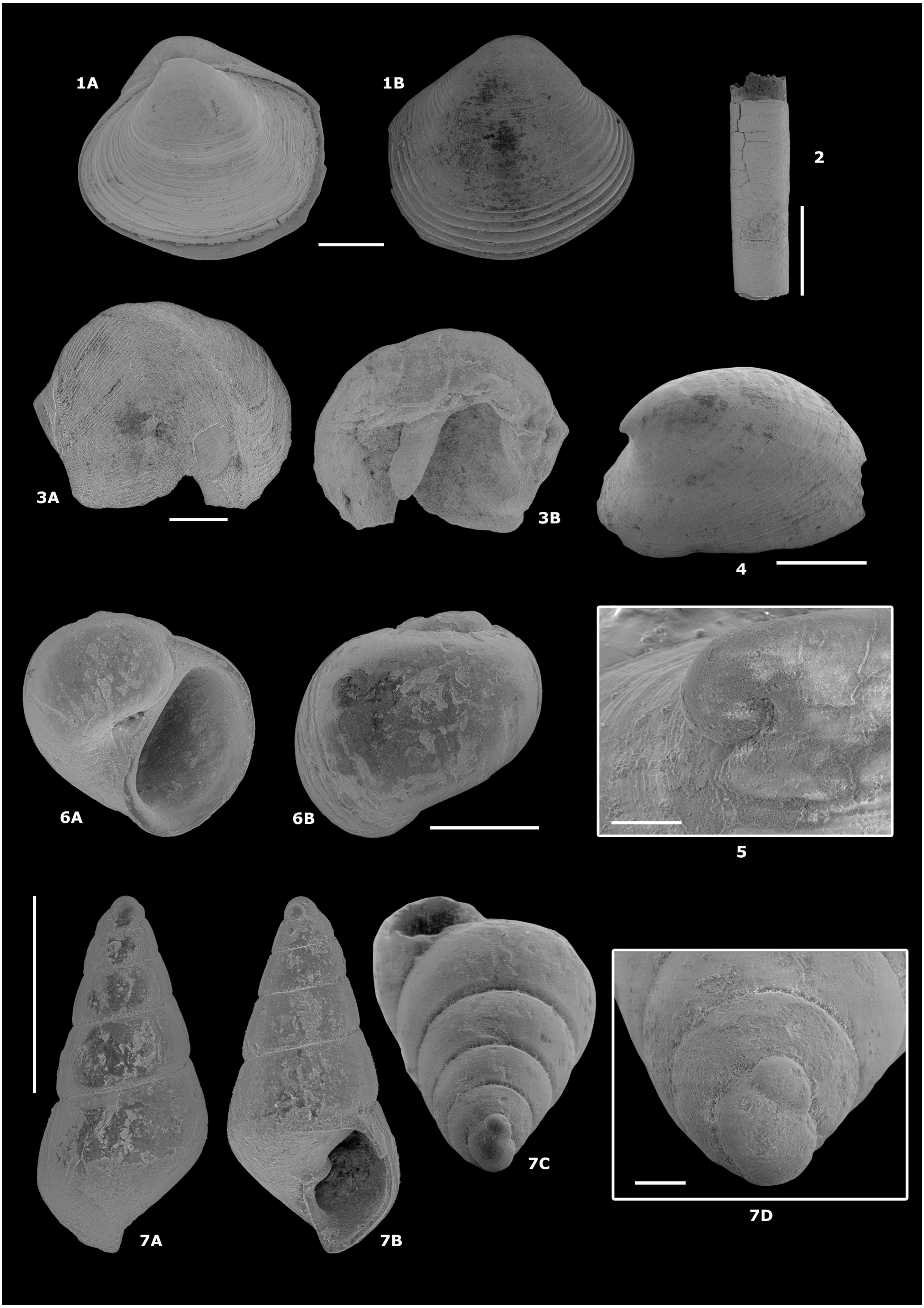

Plate 7. Molluscs. Scale bars = 1 mm, unless specified otherwise. **1A–B.** *Varicorbula gibba* (Olivi, 1792) *s.l.* - IRSNB 7723. Left valve (A), right valve (B). **2.** *Rhabdus parallelus* (Zinndorf, 1928) - IRSNB 7724. **3A–B.** Teredinidae indet. - IRSNB 7725. Left valve, exterior (A) and interior (B) views. **4.** *Cocculina reineckei* Marquet, 2016 - IRSNB 7726. **5.** *Cocculina reineckei* Marquet, 2016 - specimen lost during scanning. Scale bar = 100 µm. **6A–B.** *Euspira* cf. *achatensis* (De Koninck, 1838) - IRSNB 7727. Apertural (A) & abapertural (B) views. **7A–D.** *Odostomia* cf. *acutiuscula* (Braun in Walchner, 1851) - IRSNB 7728. Abapertural (A), apertural (B) & apical (C) views & detail of the protoconch (D). Scale bars = 1 mm (A–C) and 100 µm (D).

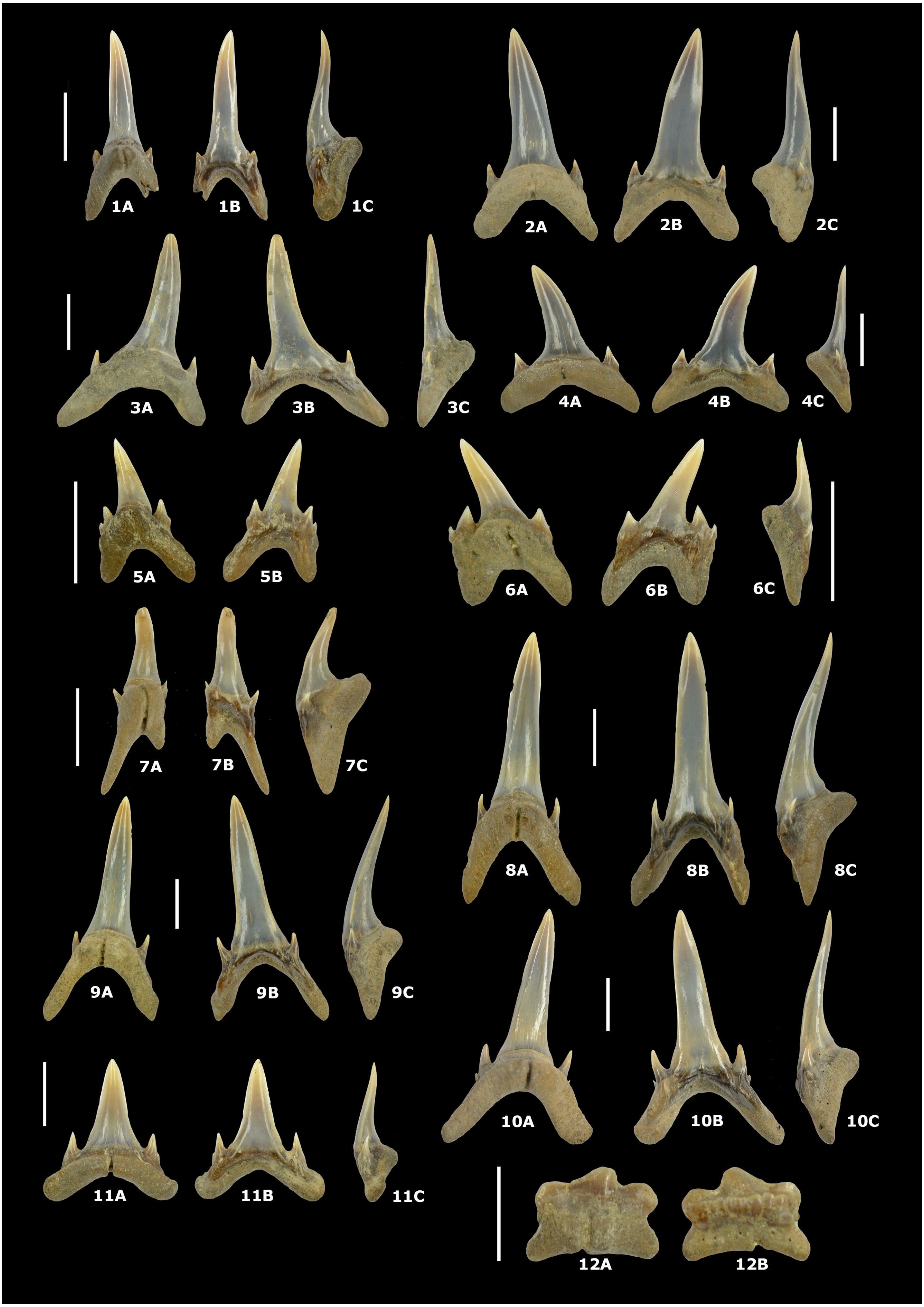

Plate 8. *Carcharias contortidens* (Agassiz, 1843); lingual (A), labial (B) and mesial/distal (C) views. Scale bars = 5 mm, unless specified otherwise. **1A–C.** IRSNB P 10299 - First upper anterior tooth (UA1). **2A–C.** IRSNB P 10300 - Second upper anterior tooth (UA2). **3A–C.** IRSNB P 10301 - Third upper anterior tooth (UA3). **4A–C.** IRSNB P 10302 - Upper lateral tooth (UL). **5A–B.** IRSNB P 10303 - Intermediate tooth. **6A–C.** IRSNB P 10304 - Intermediate tooth. **7A–C.** IRSNB P 10305 - First lower anterior tooth (LA1). **8A–C.** IRSNB P 10306 - Second lower anterior tooth (LA2). **9A–C.** IRSNB P 10307 - Third lower anterior tooth (LA3). **10A–C.** IRSNB P 10308 - Fourth lower anterior tooth (LA4). **11A–C.** IRSNB P 10309 - Lower lateral tooth (LL). **12A–B.** IRSNB P 10310 - Lower posterior tooth. Scale bar = 2 mm.

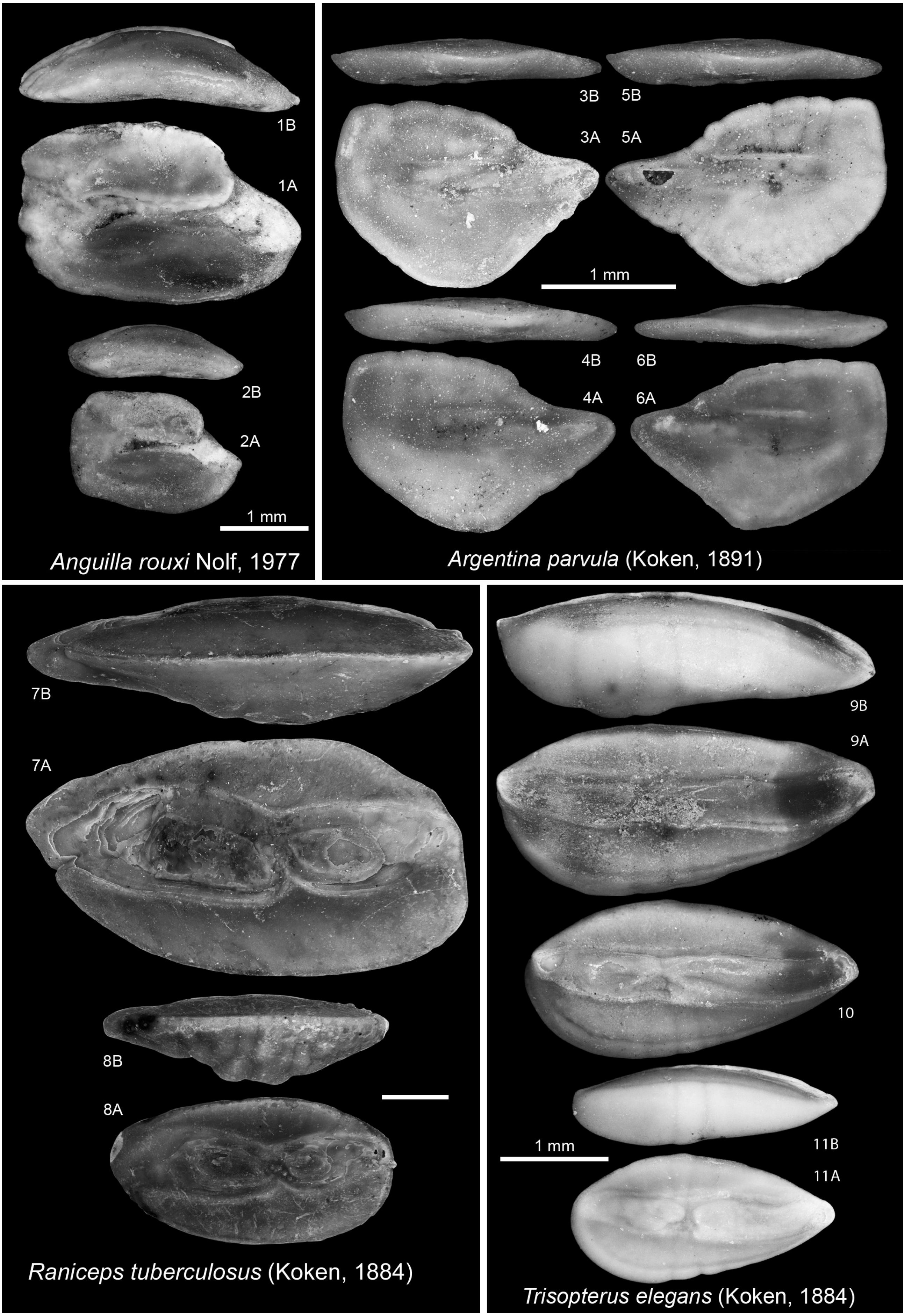

Plate 9. 1–2. *Anguilla rouxi* Nolf, 1977. 1. IRSNB P 10315. 2. IRSNB P 10316. **3–6.** *Argentina parvula* (Koken, 1891). 3. IRSNB P 10317. 4. IRSNB P 10318. 5. IRSNB P 10319. 6. IRSNB P 10320. **7–8.** *Raniceps tuberculosus* (Koken, 1884). 7. IRSNB P 10321. 8. IRSNB P 10322. **9–11.** *Trisopterus elegans* (Koken, 1884). 9. IRSNB P 10323. 10. IRSNB P 10324. 11. IRSNB P 10325. A = inner view; B = ventral view.

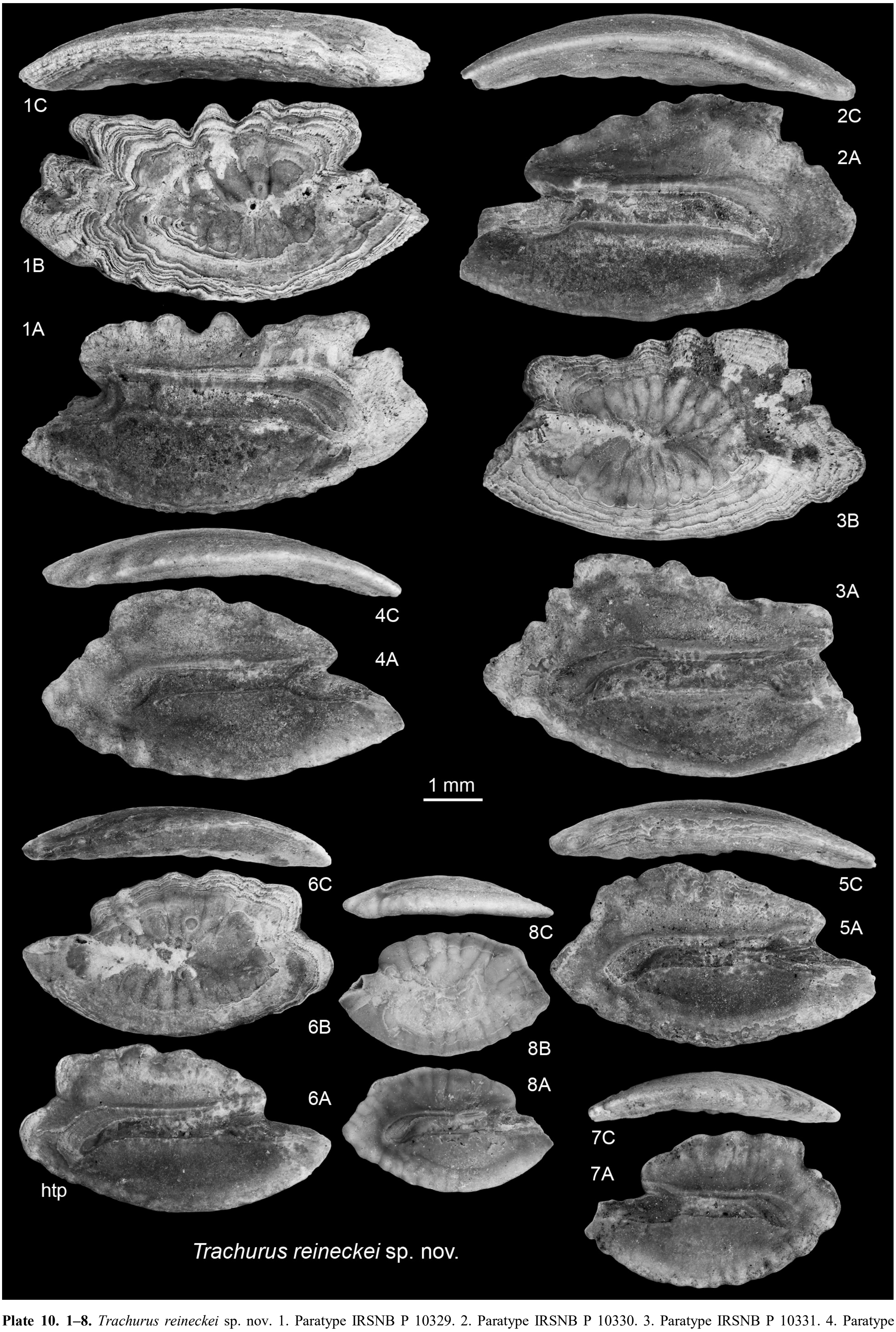

Plate 10. 1–8. *Trachurus reineckei* sp. nov. 1. Paratype IRSNB P 10329. 2. Paratype IRSNB P 10330. 3. Paratype IRSNB P 10331. 4. Paratype IRSNB P 10332. 5. Paratype IRSNB P 10333. 6. Holotype IRSNB P 10334. 7. Paratype IRSNB P 10335. 8. Paratype IRSNB P 10336. A = inner view; B = outer view; C = ventral view. Abbreviation: htp = holotype.

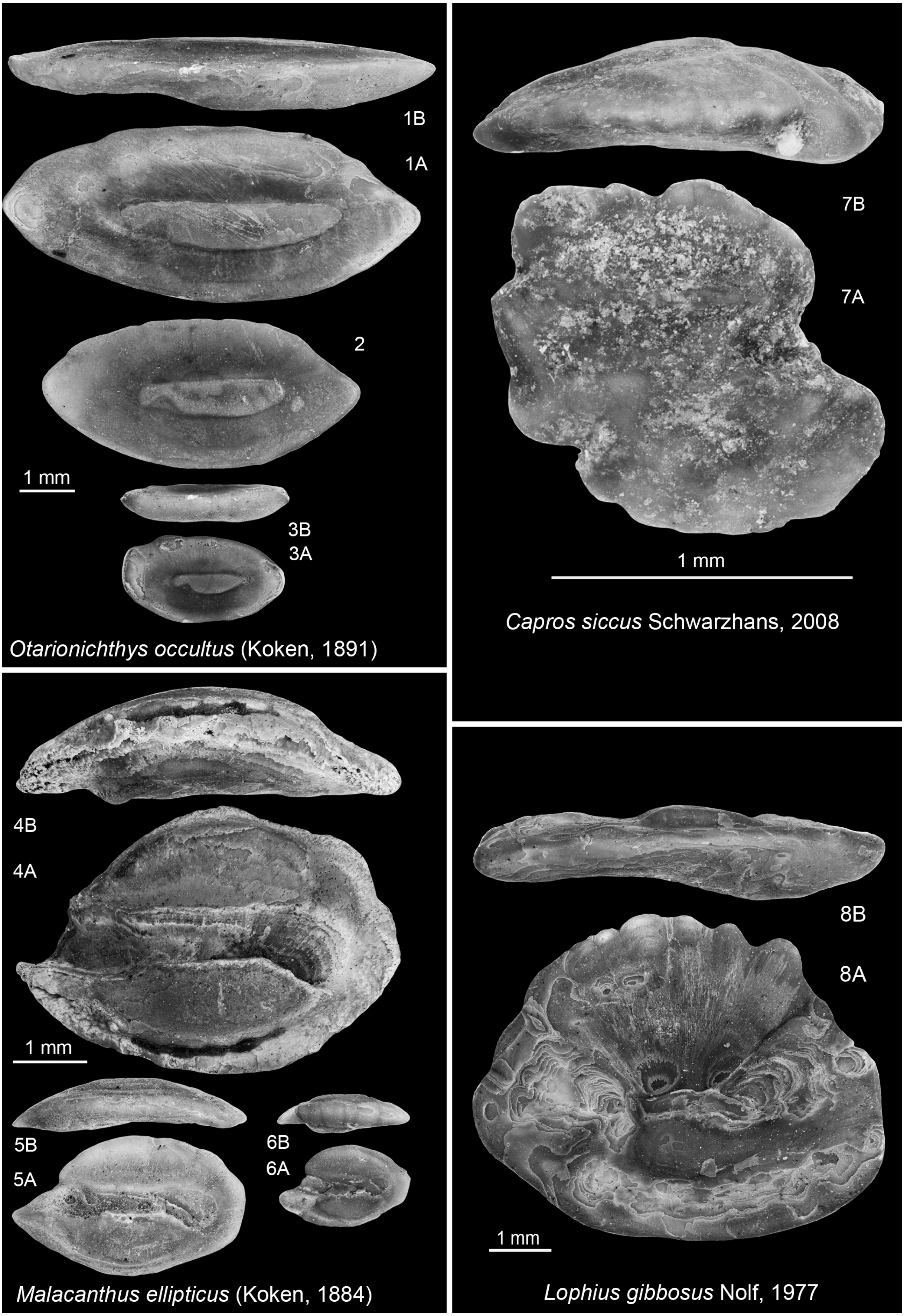

Plate 11. 1–3. *Otarionichthys occultus* (Koken, 1891). 1. IRSNB P 10326. 2. IRSNB P 10327. 3. IRSNB P 10328. **4–6.** *Malacanthus ellipticus* (Koken, 1884). 4. IRSNB P 10337. 5. IRSNB P 10338. 6. IRSNB P 10339. **7.** *Capros siccus* Schwarzhans, 2008, IRSNB P 10348. **8.** *Lophius gibbosus* Nolf, 1977, IRSNB P 10349. A = inner view; B = ventral view.

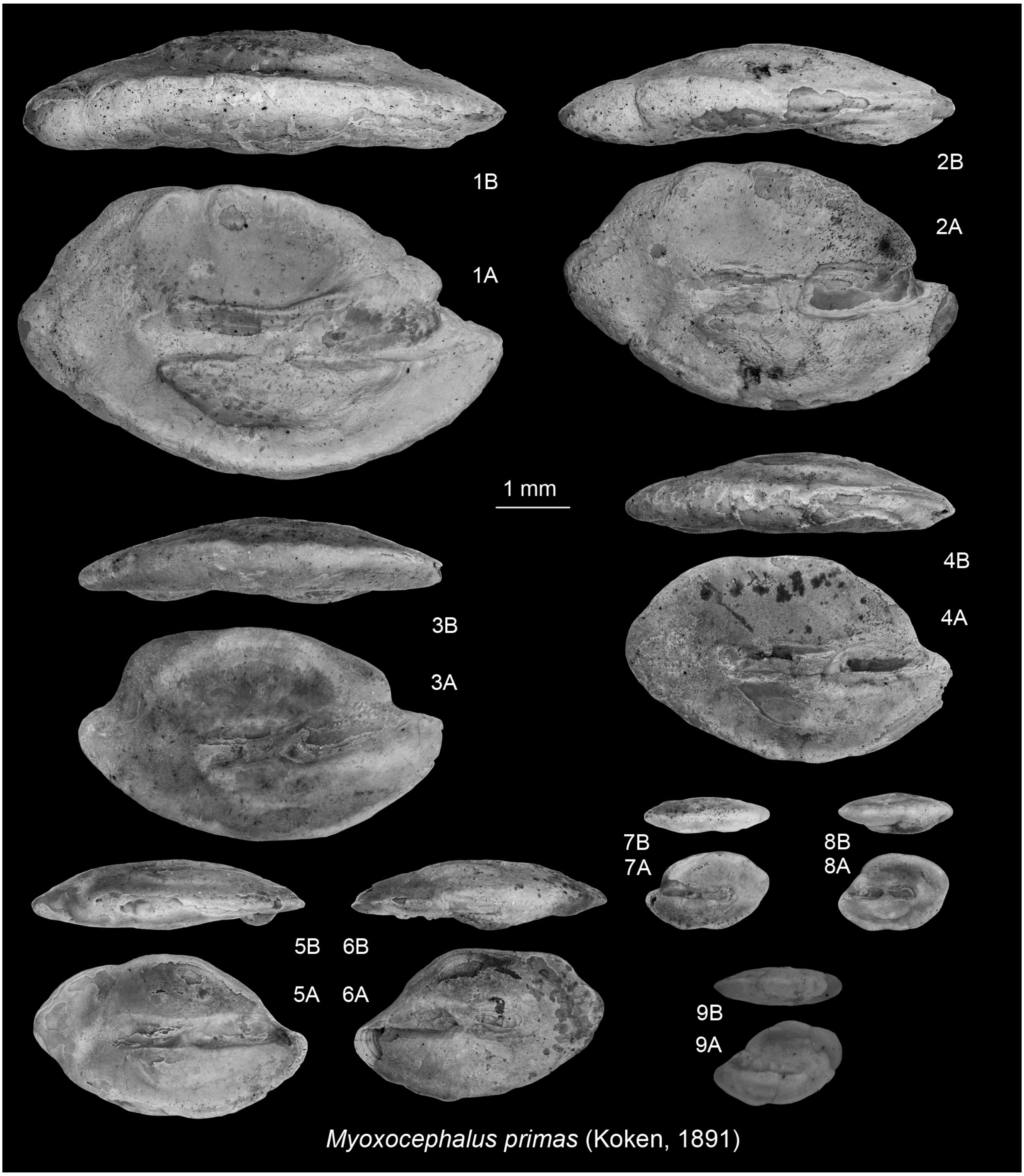

Plate 12. 1–9. *Myoxocephalus primas* (Koken, 1891). 1. IRSNB P 10340. 2. IRSNB P 10341. 3. IRSNB P 10342. 4. IRSNB P 10343. 5. IRSNB P 10344. 6. IRSNB P 10345. 7. IRSNB P 10346. 8. IRSNB P 10347. 9. Holotype of *Liparis minusculus* Nolf, 1977, Rupelian of Kruibeke, IRSNB P 02569. A = inner view; B = ventral view.