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A Revision of the Tonnoidea (Caenogastropoda, Gastropoda) from the Miocene Paratethys and their Palaeobiogeographic Implications

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2 Text-Figures, 10 Plates

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Biogeographie
Taxonomie

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Revision der Tonnoidea (Caenogastropoda, Gastropoda) aus dem Miozän der Paratethys und paläobiogeographische Folgerungen

Zusammenfassung

Die im Miozän der Paratethys vertretenen Gastropoden der Überfamilie Tonnoidea werden beschrieben und diskutiert. Insgesamt können 24 Arten nachgewiesen werden. Tonnoidea weisen generell eine ungewöhnliche weite geographische und stratigraphische Verbreitung auf, wie sie bei anderen Gastropoden unbekannt ist. Dementsprechend sind die paratethyalen Arten meist auch in der mediterranen und der atlantischen Bioprovinz vertreten. Einige Arten treten zuerst im mittleren Miozän der Paratethys auf. Insgesamt dokumentiert die Verteilung der tonnoiden Gastropoden in der Paratethys einen starken klimatischen Einfluss. Höchste Diversitäten korrelieren mit dem mittelmiozänen Klima-Optimum, während die anschließende Abkühlung mit einer schrittweisen Abnahme der Diversitäten einhergeht. Phasen geodynamisch bedingter Isolation der Paratethys wie im Ottnangium werden durch erhöhten Endemismus angezeigt.

Cassidaria (Galeodea) cingulifera HOERNES & AUINGER, 1884 und *Galeodea stephaniophora* FONTANNES, 1880 sind beide jüngere, subjektive Synonyme von *Eudolium subintermedium* (D'ORBIGNY, 1852). *Echinophora hoernesi* SACCO, 1890 ist ein jüngeres, subjektives Synonym von *E. haueri* (HOERNES & AUINGER, 1884). Ebenso ist *Triton tarbellianum* GRATELOUP, 1847 ein jüngeres, subjektives Synonym von *Sassia (Sassia) turrita* EICHWALD, 1830, *Triton parvulum* MICHELOTTI, 1853 von *Cymatiella tritonea* (GRATELOUP, 1847), *Ranella (Lampas) austriaca* HOERNES & AUINGER, 1884 von der rezenten *Bursa ranelloides* (REEVE, 1844) sowie *Ranella papillosa* PUSCH, 1837, *Ranella lessonae* BELLARDI, 1873 und *Apollon lessonae race occidentalis* COSSMANN & PEYROT, 1924 von der rezenten *Bursa corrugata* (PERRY, 1811).

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Abstract

The 24 species of Tonnoidea present in the Miocene Paratethyan assemblages are described and discussed. Species of tonnoideans have wide geographical and time ranges, unparalleled in any other gastropod group. Consequently, most Paratethyan species are widespread in the Mediterranean and Atlantic bioprovinces. Several species display their first appearance in the Middle Miocene of the Paratethys Sea. Moreover, the distribution of tonnoidean gastropods within the Paratethys documents a strong climate forcing due to the Mid-Miocene Climate Optimum, indicated by diversity peaks, and the subsequent Miocene cooling indicated by a step-wise decline of diversities. Phases of geodynamically induced isolation, such as the Ottnangian, coincide with distinctly increasing endemicity.

Cassidaria (Galeodea) cingulifera Hoernes & Auinger, 1884 and *Galeodea stephaniophora* Fontannes, 1880 are both considered junior subjective synonyms of *Eudolium subintermedium* (d'Orbigny, 1852). *Echinophora hoernesi* Sacco, 1890 is considered a junior subjective synonym of *E. haueri* (Hoernes & Auinger, 1884). *Triton tarbellianum* Grateloup, 1847 is considered a junior subjective synonym of *Sassia (Sassia) turrita* Eichwald, 1830, *Triton parvulum* Michelotti, 1853 is considered a junior subjective synonym of *Cymatiella tritonea* (Grateloup, 1847), *Ranella (Lampas) austriaca* Hoernes & Auinger, 1884 is considered a junior subjective synonym of *Bursa ranelloides* (Reeve, 1844), which has a Recent type specimen. *Ranella papillosa* Pusch, 1837, *Ranella lessonae* Bellardi, 1873 and *Apollon lessonae race occidentalis* Cossmann & Peyrot, 1924 are all considered junior subjective synonyms of *Bursa corrugata* (Perry, 1811), which also has a Recent type.

1. Introduction

The revision of the tonnoidean gastropods from the Early Pliocene of Estepona (Landau et al., 2004) highlighted the need for a modern taxonomic revision of the assemblages from other Neogene Basins, even within a group as extensively studied as the Tonnoidea, taking into account changes in the understanding of the Recent species and their distribution.

As discussed by Landau et al. (2004) and Beu (in press), the tonnoideans are almost unique amongst the Gastropoda in the large number of species with an amphiatlantic and circumglobal distribution (some Architectonicidae have similar ranges [Bieler, 1993]). Some taxa have long evolutionary lineages in the European area, such as *Cypraecassis cypraeformis* (Borson), of which *C. pseudocrumena* (d'Orbigny), the Pliocene form, is considered a synonym (Landau et al., 2004), *Semicassis laevigata* (Defrance) – *S. saburon* (Bruguière), *Monoplex subcorrugatus* (d'Orbigny) – *M. corrugatus* (Lamarck) and *Aspa subgranulata* (d'Orbigny) – *A. marginata* (Gmelin). Other species have remained unchanged throughout Neogene time in Europe (*Ranella olearium* Linnaeus, *Charonia lampas* Linnaeus) but extended their ranges to the Southern Hemisphere (*C. lampas* during Middle Miocene time, *R. olearium* during Pleistocene or Holocene time).

The aim of this paper is firstly to revise the taxonomy of the Paratethyan tonnoideans based on the extensive collections present in the Naturhistorisches Museum Wien, Vienna, the Geological Survey in Vienna, and the Paratethyan literature and, based on this revised taxonomy, to revise their palaeobiogeography.

The most important works dealing with Paratethyan tonnoidean taxonomy are the classic 19th century works by Moriz Hörnes (1851–1870) and Rudolf Hoernes & Mathias Auinger (1879–1891). More recent works have dealt systematically with complete assemblages (i. e. Strausz, 1966; Bałuk, 1995), but no specialized revision of the Paratethyan tonnoidean gastropods has been undertaken until now.

This revision follows the format of Landau et al. (2004), and for the sake of brevity, for taxa common to both areas, the reader should refer to Landau et al. (2004) for description, discussion and distribution. For the species dealt with systematically in both papers, a more complete chresonymy pertinent to the Paratethys is given, plus any additions since 2004. For references outside the Paratethys the reader should refer to Landau et al. (2004).

2. Geography and Stratigraphy

The Paratethyan material discussed here covers an interval from the middle Early Miocene to the middle Middle Miocene, spanning the Burdigalian, Langhian and early Serravallian stages. In terms of regional stratigraphy this succession represents the regional stages Eggenburgian (~Lower Burdigalian), Ottnangian ("middle" Burdigalian), and Karpatian (~Upper Burdigalian) to the Middle Miocene regional stage Badenian (Langhian to Lower Serravallian). The oldest records from the Eggenburgian, with an age of c. 20 Ma, derive from Loibersdorf in Lower Austria (Schaffer, 1912) and from the Kaltenbachgraben section in Bavaria (Hölzl, 1958). The rare Ottnangian records are c. 18 Ma old and are represented by Ottnang in Upper Austria and the Kaltenbachgraben section in Bavaria (Steininger, 1973). Tonnoidean-bearing Karpatian localities are rare as well, and are confined to Laa, Kleinebersdorf, Karnabrunn, and Niederkreuzstetten in Lower Austria and Slup in the Czech Republic (Harzhauser, 2002; 2004). Their age ranges around 16.5 Ma.

Thereafter, with the onset of the Middle Miocene, the documentation booms and tonnoidean-bearing Badenian assemblages are known from the entire Paratethys area. The northernmost localities are those in Poland with Korytnica as the most important one. It formed during the early Badenian along the northern coast of a branch of the Paratethys Sea that covered the Carpathian foredeep. Contemporaneous localities of early Badenian age (c. 16–15 Ma.) are Grund, Immendorf and Weitendorf (Austria), Várpalota (Hungary) and Lăpugiu de Sus (= Lapugy) and Coşteiu de Sus (= Kostej) in Romania. The classical Austrian assemblages from Vöslau, Baden, Sooß, Gainfarn, Enzesfeld, Traiskirchen, Möllersdorf, Walbersdorf and Pfaffstätten are late early to middle Badenian (c. 14.5–13.6 Ma). Slightly younger localities of Late Badenian age (c. 13.6–12.8 Ma) are Forchtenau, Pötzleinsdorf and Grinzing in Austria and Devínska Nová Ves (Slovak Republic). For many other Badenian localities, mentioned in the distribution chapters in the systematic part, a precise dating within the Badenian is not known.

The tonnoidean record in the Paratethys Sea ends abruptly at c. 12.8 Ma, at the Badenian/Sarmatian boundary. At that time, a major local extinction wiped out 97 % of the gastropods along with corals, echinoderms and many foraminifera (see Harzhauser & Piller, 2007). This Badenian–Sarmatian extinction event (BSEE) was most probably triggered by severe changes in water chemistry, bottom hypoxia and eutrophication at the water surface. Although normal marine conditions became re-established soon after, the molluscan fauna remained fully endemic and re-immigration of Mediterranean species was insignificant (Harzhauser & Kowalke, 2002). So-called Tortonian localities as variously referred to in the older literature (e. g. Strausz, 1966; Zelinskaya et al., 1968) are based on historical miscorrelations of the Middle Miocene Badenian stage with the Upper Miocene Tortonian of the Mediterranean area dating back to the 19th century (see Harzhauser et al. [2003] for further discussion).

3. Material

The described Paratethyan shells are stored in the collections of the Natural History Museum Vienna and the Geological Survey of Austria. Additional material for comparison was utilised from the Bernard Landau private collection and from the collections of the Netherlands Nationaal Museum van Natuurlijke Historie, in Leiden.

Abbreviations of Institutions

NHMW: Naturhistorisches Museum Wien, Vienna
GBA: Geological Survey of Austria
RGM: Fossil collections of Netherlands Nationaal Museum van Natuurlijke Historie, Leiden (formerly Rijksmuseum van Geologie en Mineralogie)
BL: collection Bernard Landau

4. Systematics

The classification adopted here is according to Beu (1988, 1998) and Bouchet & Rocroi (2005). The superfamily name Tonnoidea Suter, 1913 (1825) is conserved in preference to the name Cassoidea Latreille, 1825 suggested by Bandel & Riedel (1994) and Riedel (1994, 1995) (see Beu, 1988, p. 21).

Riedel (1994) considered the Ficidae to constitute a separate superfamily, Ficoidea, on the basis of protoconch, teleoconch and soft part morphology. Until then, the Ficidae had been included in the Tonnoidea (Thiele, 1929; Fretter & Graham, 1981; Vaught, 1989). Ficidae have, therefore, been excluded from this monograph.

4.1. Family Tonnidae Suter 1913 (1825)

Class: Gastropoda Cuvier 1797
Subclass: Prosobranchia Milne-Edwards, 1848
Superorder: Caenogastropoda Cox, 1960
Order: Neotaenioglossa Haller, 1882
Superfamily: Tonnoidea Suter, 1913 (1825)
Family: Tonnidae Suter, 1913 (1825)
Genus: *Eudolium* Dall, 1889

Eudolium subintermedium (d'Orbigny, 1852)

(Pl. 1, Figs. 1–6)

1833 *Cassis intermedia* Grateloup, p. 200 (non Brocchi, 1814).
1840 *Cassis intermedia* Grateloup, Pl. 46, Fig. 7 (non Brocchi, 1814).
1852 *Cassis subintermedia* d'Orbigny, no. 1671.
1867 *Casidaria echinophora* Lam. – Pereira Da Costa, p. 133, Pl. 17, Fig. 2.
1880 *Galeodea stephaniophora* Fontannes, p. 101, Pl. 7, Fig. 2.
1884 *Cassidaria (Galeodea) cingulifera* Hoernes & Auinger, p. 161, Pl. 17, Figs. 17, 19, 20.
1890b *Eudolium stephaniophorum* (Font.) – Sacco, p. 10, Pl. 1, Fig. 10.
1890b *Eudolium stephaniophorum* var. *miotransiens* Sacco, p. 10, Pl. 1, Fig. 11.
1890b *Eudolium stephaniophorum* var. *gigantula* Sacco, p. 11, Pl. 1, Fig. 12.
1890b *Eudolium stephaniophorum* var. *recurvicauda* Sacco, p. 11, Pl. 1, Fig. 13.
1890b *Eudolium stephaniophorum* var. *pliotransiens* Sacco, p. 11, Pl. 1, Fig. 14.
1890b *Eudolium stephaniophorum* var. *elongata* Sacco, p. 12, Pl. 1, Fig. 15.
1890b *Eudolium stephaniophorum* var. *tricingulata* Sacco, p. 12, Pl. 1, Fig. 16.
1890b *Eudolium stephaniophorum* var. *quatuorcingulata* Sacco, p. 12.
1890b *Eudolium stephaniophorum* var. *alternituberculata* Sacco, p. 12, Pl. 1, Fig. 17.
1890b *Eudolium stephaniophorum* var. pluricingulata Sacco, p. 12.
1890b *Eudolium stephaniophorum* var. *acutituberculata* Sacco, p. 13, Pl. 1, Fig. 18.
1904 *Eudolium (Tuberculodolium) stephaniophorum* var. *quatuorcingulata* Sacco, p. 100, Pl. 22, Fig. 4.
1924 *Semicassis subintermedia* d'Orbigny – Cossmann & Peyrot, p. 422, no. 717, Pl. 11, Figs. 40–41.
1954 *Cassidaria cingulifera* Hoernes et Auinger – Csepreghy-Meznerics, p. 33, Pl. 4, Fig. 7.
1960 *Cassidaria (Cassidaria) cingulifera* Hoernes & Auinger 1882 [sic] – Kojumdgieva & Strachimirov, p. 135, Pl. 37, Fig. 5.
1966 *Cassidaria cingulifera* Hoernes & Auinger, 1876 [sic] – Strausz, p. 241, Fig. 116.
1966 *Dolium (Eudolium) subfasciatum* Sacco, 1891 [sic] – Strausz, p. 253, Pl. 64, Fig. 6.
1979 *Eudolium stephaniophorum* (Fontannes, 1879 [sic]) – Martinell, p. 146, Pl. 5, Figs. 7–8.
1988 *Eudolium stephaniophorum* (Fontannes, 1879 [sic]) – González Delgado, p. 140, Pl. 5, Figs. 12–13.
1992 *Eudolium stephaniophorum* (Fontannes, 1880) – Cavallo & Repetto, p. 70, Fig. 131.
1995 *Cassidaria cingulifera* Hoernes & Auinger, 1884 – Baluk, p. 201, Pl. 16, Figs. 9–10.
2003 *Cassidaria cingulifera* Hoernes and Auinger, 1884 – Ceranka & Zlotnik, p. 494, Text-Figs. 2 C–D.

Material: Maximum height 46 mm (incomplete). Grund (5, 1 complete), Vöslau (1).

Description: Shell medium-sized, fragile, globose, with relatively depressed spire. Protoconch missing. Three teleoconch whorls preserved, convex, periphery at abapical suture on spire whorls. Suture linear, impressed. First whorl evenly convex, sculptured with four narrow, elevated spiral cords, with a fifth appearing at abapical suture and secondary cords appearing in interspaces at about one quarter to half whorl. Second whorl weakly shouldered, bearing two spiral cords, upper delimiting sutural ramp forming shoulder, lower between shoulder and abapical suture, gaining in strength abapically and slightly nodulose. Axial sculpture of strongly prosocline, close-set riblets, overriding spiral elements. Last whorl 90 % of total height, globose, strongly constricted at base; sculpture of about seven narrow primary cords, with 1 secondary cord and 1–2 spiral threads in each interspace. Between one and six primary cords develop many small spinose tubercles. Axial sculpture of close-set, prosocline growth lines. Aperture ovate, very wide, approximately 80 % of total height, outer lip weakly thickened by narrow labral varix. Outer lip denticulate on inner edge, with 24 small denticles, arranged in pairs. Anal canal not developed. Siphonal canal damaged in all specimens. Parietal callus considerably expanded, thin and adherent, with spiral sculpture of last whorl showing through. Columella excavated medially, straight below, with some irregular denticles and ridges present in abapical portion. Siphonal fasciole damaged in all specimens, bearing narrow spiral cords.

Variability: Only two of the five specimens available in the NHMW collections have an intact aperture, making it difficult to appreciate the variability in the thickness of the labral varix, but it seems to vary from very thin to thin. The number of spiral cords on the last whorl that produce tubercles is highly variable. This character does not seem to vary with ontogeny, as specimens of the same size have a variable number of tuberculose cords.

Discussion: The Recent species of *Eudolium* were revised by Marshall (1992). He distinguished *Eudolium* from *Tonna* by the markedly narrower spiral cords of *Eudolium* than of *Tonna*, and by the presence of obvious, fine, close, well raised axial ridgelets on *Eudolium* species that have not been reported from species referred to *Tonna*. All other characters appear to be shared by the two genera: the shape, size and sculpture of the protoconch, radular characters, the presence of an operculum in the larval stage but not in the adult, thickening or not of the outer lip, and the unique mode of feeding by ingesting whole holothurians. More recently Vos & Terryn (2007) revised Marshall's (1992) Recent species of *Eudolium* and recognized only two living species, both with a world-wide distribution. Beu (in press) pointed out that the fine axial sculpture reported by Marshall (1992) in *Eudolium* is also present on early spire whorls of *Tonna galea* (Linnaeus, 1758), the type species of *Tonna*, further blurring the distinction between these genera.

The shells from Grund have closely spaced, narrow, tuberculose spiral cords and fine axial riblets, distinctive of the genus *Eudolium*. Small tubercles develop at the shoulder of the penultimate whorl and on a variable number of rows on the last whorl. One damaged specimen has six spiral rows of tubercles (Pl. 1, Fig. 4), whereas in the only complete specimen (Pl. 1, Fig. 1) the tubercles are hardly developed at all.

This species has usually been referred to as *Eudolium stephaniophorum* (Fontannes, 1890), which was described from the Pliocene of France. However, the subadult shell illustrated by Cossmann & Peyrot (1924, Pl. 11, Figs. 40–41) as *Semicassis subintermedia* (d'Orbigny, 1852) from the Middle Miocene, Serravallian of Saubrigues, France has the very broad aperture, shallow anal canal and narrow labral varix characteristic of *E. stephaniophorum*, and represents the same species. *E. stephaniophorum* (Fontannes, 1890) must therefore be considered a junior subjective synonym of *Eudolium subintermedium* (d'Orbigny, 1852). *Cassidaria (Galeodea) cingulifera* Hoernes & Auinger, 1884 is also a junior subjective synonym.

Eudolium subfasciatum, 1890 was described from the Lower Miocene, Burdigalian of the Turin Hills. The numerous illustrations given by Sacco (1890b, Pl. 1, Figs. 4–8) and the sheer number of varieties described reveal a similar degree of variability to that of *E. subintermedium*, especially in the strength and number of beaded cords. However, judging from Sacco's Figs. (as *E. stephaniophorum*), the aperture of *E. subfasciatum* seems to be consistently different from that of *E. subintermedium*, as it is narrower, with a more strongly developed denticulate labral varix and a much deeper, more strongly developed anal canal.

Interestingly, *E. subfasciatum* occurs in the Caribbean Burdigalian deposits of the Chipola Formation of Florida (Vokes, 1986) and the Cantaure Formation of Venezuela (Gibson-Smith & Gibson-Smith, 1988; Beu, in press). We (BL coll.) have eight complete specimens from the Cantaure Formation of Venezuela and confirm the differences discussed above. The two species differ most markedly in the characters of their apertures. In our shells from Venezuela the shape of the outer lip is different, sinuous in profile in the mid-portion; weakly rounded in *E. subintermedium*. The anal canal is very deep and narrow, with its outer border delimited by two labral denticles that are more prominent than their neighbours. These denticles are not clearly seen in Sacco's figures, but they are all subadult shells (max length 31 mm [Sacco, 1890b, p. 6]). Our largest shell from Venezuela is 60 mm in length. The outer lip is very strongly sinuous, the labral varix broad and flattened ventrally and very strongly denticulate, the denticles extending across the whole width of the varix. The columellar callus is more strongly developed than in any specimen of *E. stephaniophorum* and raised into a free shelf over the faciole and finally, the siphonal canal is longer and more closed than in *E. stephaniophorum*.

Distribution:

- Miocene Paratethys (Badenian): Poland: Korytnica (Baluk, 1995); Austria: Grund (Hoernes & Auinger, 1884); Romania: Coşteiu de Sus (= Kostej); Bulgaria (Kojumdgieva & Strachimirov, 1960).
- Middle Miocene Atlantic (Langhian): France: Saubrigues, Aquitaine Basin (Cossmann & Peyrot, 1924).
- Late Miocene Mediterranean (Tortonian): Italy: Tetti Borelli (Sacco, 1890b).
- Early Pliocene Atlantic: Guadalquivir Basin, Spain (González Delgado, 1988); northeastern Spain (Martinell, 1979).
- Pliocene (indeterminate) Mediterranean: Italy (Sacco, 1890b, 1904; Cavallo & Repetto, 1992).

Genus: *Malea* Valenciennes, 1832

Malea orbiculata **(Brocchi, 1814)**

(Pl. 1, Figs. 7–10)

1814 *Buccinum orbiculatum* Brocchi, p. 647, Pl. 15, Fig. 22.
1852 *Dolium denticulatum* Desh. – Hörnes, p. 164, Pl. 15, Fig. 1.
1884 *Dolium (Cadium) denticulatum* Desh. – Hoernes & Auinger, p. 149, Pl. 16, Figs. 1–4.
1954 *Dolium (Cadium) orbiculatum* – Csepreghy-Meznerics, p. 35, Pl. 4, Fig. 5.
1966 *Dolium orbiculatum* Brocchi, 1814 – Strausz, p. 253, Fig. 120, Pl. 64, Fig. 7.
1995 *Malea denticulata* (Deshayes, 1836) – Baluk, p. 200, Pl. 16, Fig. 11.
2004 *Malea orbiculata* (Brocchi, 1814) – Landau et al., p. 39, Pl. 1, Fig. 2 (cum syn.).
2008 *Malea orbiculata* (Brocchi, 1814) – Chirli, p. 74, Pl. 28, Figs. 7–12.

Material: Largest 67.7 mm. Grund (18), Guntersdorf (1).

Description: See Landau et al. (2004, p. 40).

Discussion: The Paratethyan shells do not differ from specimens found in numerous Atlantic and Mediterranean Pliocene localities and discussed by Landau et al. (2004, p. 40).

Distribution: (Paratethys; for complete distribution see Landau et al. [2004, p. 40]):

- Early Miocene Paratethys (Karpatian): Hungary: Várpalota (Kókay, 1967).
- Middle Miocene Paratethys (Badenian): Poland: Korytnica (Baluk, 1995); Austria: Grund, Weitendorf (Hörnes, 1852; Hoernes & Auinger, 1884; Harzhauser, 2004). Hungary: Várpalota (Strausz, 1966).

Middle Miocene Mediterranean (Langhian or Serravallian): Turkey: Karaman Basin (Van de Voort coll., BL personal observation).

4.2. Family Cassidae Latreille 1825

Subfamily: Cassinae Latreille, 1825
Genus: *Cassis* Scopoli, 1777

Cassis postmamillaris **Sacco, 1890**

(Pl. 2, Figs. 1–4)

1852 *Cassis mammillaris* [sic] Grat. – Hörnes, p. 174, Pl. 14, Figs. 3–5.
1884 *Cassis (Cassidea) mamillaris* Grat. – Hoernes & Auinger, p. 158, Pl. 17, Fig. 15.
1890a *Cassis postmamillaris* Sacco, p. 16, Pl. 1, Fig. 11.
1958 *Cassis (Cassis) postmamillaris* Sacco – Erünal-Erentöz, p. 48, Pl. 7, Fig. 3.
1960 *Cassis (Cassis) postmamillaris* Sacco – Kojumdgieva & Strachimirov, p. 133, Pl. 36, Fig. 6.
1984 *Cassis postmamillaris* Sacco, 1890 – Ferrero Mortara et al., p. 12, Pl. 1, Fig. 4.
1998 *Cassis (Cassis) postmamillaris* Sacco *postmammillaris* [sic] Sacco – Schultz, p. 62, Pl. 24, Fig. 1.

Material: 15+ adult specimens. Largest 110 mm height, 74.3 mm width. Gainfarn (9), Pötzleinsdorf (3), Vöslau

(5), Lăpugiu de Sus (10), Coşteiu de Sus (1), Kienberg at Mikulov (2), Bulhary (= Pulgram) (1).

Description: Shell large, solid, helmet-shaped with short spire. Protoconch poorly preserved in one juvenile; small, of about three smooth whorls. First teleoconch whorl sculptured with fine, close-set spiral cords. Weakly prosocline axial ribs appear on second whorl. Third whorl shouldered, with axial ribs obsolete on sutural ramp, wider and stronger towards abapical suture. Spiral sculpture obsolete on fourth and fifth whorls. Axial ribs obsolete, but forming tubercles immediately above and below sutures. Suture impressed, weakly undulating. Last whorl 90–93 % of total height, with three rows each of six to eight rounded tubercles, adapical row at shoulder largest, weakly pointed, dorsal tubercle largest. Tubercles weakening abapically, third row becoming subobsolete towards outer lip. Several elevated axial rugae develop on the last part of the last whorl, most prominent towards outer lip. Aperture c. 75 % of total height, elongate, wider ad- and abapically, narrowed in the central portion through enlargement of denticles on outer lip. Anal canal rounded, weakly developed. Outer lip strongly thickened, wider centrally than above or below, flattened ventrally, bearing eight–nine prominent denticles on inner edge. Middle three or four denticles larger than others, bifid. Columella broadly excavated in abapical half, bearing numerous irregular horizontal folds and denticles on inner edge, central denticles weakly bifid. Columella and parietal calluses broad, flattened, greatly thickened, forming triangular apertural shield, flared and wing-like adapically. Siphonal canal deep, narrow, strongly recurved posteriorly and adapically.

Variability: Most specimens are relatively constant in shape, characterised by the very triangular shape and the strongly flared parietal portion of the shield. The largest specimen from Lăpugiu de Sus (Pl. 2, Fig. 2) is somewhat unusual in having a more elevated spire, the whole of the outer lip is strongly thickened rather than just the mid-portion and the shield is more regular, less expanded in the parietal region. The strength of the tubercles is somewhat variable.

Discussion: It is difficult to be certain of the number of *Cassis* species present in the European fossil assemblages, as specimens are rarely adult and almost always rare. At least three distinct species of *Cassis* occur in the Mediterranean and Paratethyan Miocene. *Cassis bellardii* Michelotti, 1847 has a large oval shell, with three rows of evenly sized nodules, a mucronate surface sculpture between these rows, and a rather thin parietal shield. This has been found only in the Burdigalian of the Turin Hills, Italy. The second, *Cassis pedemontana* Sacco, 1890, from the Burdigalian (early Miocene) of the Turin Hills, is also ovate, has two relatively prominent rows of spiral tubercles adapically and two weaker rows abapically, but no sculpture between the rows on the last whorl, the parietal shield and outer lip are moderately thickened and the outer lip bears 14 moderate-sized denticles within. Sacco (1890a, Pl. 1, Fig. 6) illustrated one good adult specimen. His Figs. 7–10 all represent juvenile shells and are difficult to interpret. The third species, *Cassis postmamillaris*, Sacco, 1890 has three rows of relatively widely spaced nodules, the shoulder row more strongly developed with the dorsal tubercle the most prominent. The parietal shield is massive and triangular in shape and the denticles within the outer lip are strongly developed (8–9 in number). This species occurs in the Mediterranean and Paratethyan Miocene.

Abbott (1968) treated all the European Oligocene and Miocene species as subspecies of the French Oligocene *Cassis mamillaris* Grateloup, 1827. However, this is unjustified as there seem to be at least two distinct lineages within the European Miocene cassids; *C. bellardii* seems most closely allied to the thin-shelled West African *Cassis tessellata* (Gmelin, 1791), whereas *C. postmamillaris* seems more closely related to the thick-shelled Caribbean *C. tuberosa* group.

Several taxa have been proposed for Oligocene forms; from the Italian Oligocene *Cassis apenninica* Sacco, 1890 is quite similar to *C. postmamillaris*, with a similar number of tubercles at the shoulder, but these are subequal and not more strongly developed on the dorsum, the parietal shield is also triangular, but less flared adapically. Although cited as common, the original Fig. of *Cassis nummulitiphila* Sacco, 1890 (1890a, Pl. 1, Fig. 4) is the only illustration we have found of this species. It seems to represent quite a distinct small-medium sized fusiform cassid, with a relatively tall spire for the genus, and a narrow last whorl with only two rows of tubercles on the last whorl. Only the dorsum is illustrated and the shell outline is not unlike that of *Cypraecassis* Stutchbury, 1837.

In the French Miocene there are at least six to eight species of *Cassis*. Unfortunately, Grateloup's collection in Bordeaux (examined by one of us, AGB) is muddled and many of the type specimens are broken beyond recognition, including the type of *C. major* Grateloup, 1827. Further species occur in the French Oligocene; *Cassis mamillaris* Grateloup, 1827 is restricted to the Upper Oligocene (Lozouet, 1986). Both the original Fig. (Grateloup, 1840, Pl. 34, Fig. 4) and the specimen illustrated by Lozouet (1986, Pl. 29, Figs. 1–2) show a medium-sized, very solid *Cassis*, with prominent sculpture of broad, elevated, axial rugae on the last whorl. The parietal shield is also well-developed, but more ovate than that seen in *C. postmamillaris*. Sacco (1890a, p. 16) distinguished the Miocene *C. postmamillaris* from the Oligocene form by having fewer tubercles at the shoulder and fewer denticles inside the outer lip. This does not seem correct, however, as the numbers of tubercles at the shoulder of the last whorl are similar in the two species, and the number of denticles inside the outer lip 8–9, within the range seen in the Paratethyan populations of *C. postmamillaris*. Nevertheless, the characters of the prominent axial rugae and the rounded parietal shield are not present in the Miocene shells and clearly distinguish the two species.

A further species occurs in the Lower Oligocene, Rupelian (= Stampian) of France: *Cassis elegans* Grateloup 1827. We have examined several specimens from the locality of Gaas in France (largest, height 61.2 mm; BL coll.). This has quite a different sculpture on the last whorl, consisting of four rows of tubercles, weakening abapically, with non-tuberculate secondary and tertiary spiral cords in the interspaces. The number of tubercles at the shoulder of the last whorl must be interpreted with care as, at least in *C. elegans*, this number decreases significantly with ontogeny. One juvenile specimen (height 36.5 mm) has 22 axial ribs on the last whorl, whereas a slightly more adult specimen (height 43.1 mm) has 16 ribs on the last whorl.

The European Oligocene to Miocene species of *Cassis* require revision, however, the Paratethyan *C. postmamillaris* seems distinct from all the French taxa.

Cassis seems to have been present and fairly widely distributed in the Oligocene Proto-Mediterranean and Paratethys, represented in both the Oligocene and Miocene by at least three species in each. However, *Cassis* did not return to the Mediterranean following the Messinian salinity crisis, despite the tropical conditions that prevailed during the Early Pliocene. There is no fossil record of *Cassis* for the Atlantic Miocene south of France, but it is possible that *C. bellardii* gave rise to the extant West African species *C. tesellata*.

Distribution:

• Middle Miocene Paratethys (Badenian): Austria: Forchtenau, Grund, Gainfarn, Enzesfeld, Vöslau, Nussdorf, Pötzleinsdorf (Hörnes, 1852; Schultz, 1998); Slovak Republic: Devínska Nová Ves (= Neudorf an der March) (Hörnes, 1852); Czech Republic: Kienberg at Mikulov, Bulhary (= Pulgram) (Hörnes, 1852); Romania: Lăpugiu de Sus (= Lapugy), Coşteiu de Sus (= Kostej); Bulgaria (Kojumdgieva & Strachimirov, 1960).

• Late Miocene Mediterranean (Tortonian): Italy: Stazzano (Sacco, 1890a); Turkey: Adana Basin, Bicilganh (Erünal-Erentöz, 1958).

Genus: *Cypraecassis* Stutchbury, 1837

Cypraecassis cypraeformis (Borson, 1820)

(Pl. 3, Figs. 3–5)

1820 *Cassis cypraeiformis* Borson, p. 229, Pl. 1, Fig. 20.
1852 *Cassis crumena* – Hörnes, p. 180, Pl. 16, Figs. 1–3.
1884 *Cassis* (c. Cassidea) *cypraeformis* Bors. – Hoernes & Auinger, p. 159, Pl. 17, Figs. 8–10.
1912 *Cassis cypraeiformis* Bors. – Friedberg, p. 115, Pl. 6, Fig. 4.
1956 *Cassis cypraeiformis* Bors. – Csepreghy-Meznerics, p. 456, Pl. 4, Figs. 17–18.
1959 *Cassis cypraeiformis* Bors. – Eremija, Pl. 2, Fig. 11.
1966 *Cypraecassis crumena cypraeformis* Borson, 1820 – Strausz, p. 246, Pl. 64, Figs. 10–11.
1985 *Cypraecassis (Cypraecassis) cypraeformis* (Borson, 1820) – Atanackovíc, 136, Pl. 30, Figs. 17–18.
1995 *Cassis cypraeiformis* (Borson, 1820) – Baluk, p. 202, Pl. 16, Figs. 5–6.
2003 *Cassis cypraeiformis* (Borson, 1820) – Ceranka & Zlotnik, p. 494, Text.-Fig. 2 E.
2004 *Cassis cypraeiformis* (Borson, 1820) – Landau et al., p. 40, Pl. 1, Figs. 3–6, Pl. 2, Fig. 1 (cum syn.).
2008 *Cypraecassis pseudocrumena* d'Orbigny, 1851 [sic] – Chirli, p. 79, Pl. 29, Figs. 13–16, Pl. 30, Figs. 1–8.

Material: Largest height 62.9 mm. Grund (2), Immendorf (1), Vöslau (20+), Lăpugiu de Sus (= Lapugy), (6), Mikulov (5).

Description: See Landau et al. (2004, p. 41).

Discussion: As discussed by Landau et al. (2004), we recognise a single Miocene–Pliocene species *Cypraecassis cypraeformis* (Borson, 1820). Typical specimens of *C. cypraeformis* from the Middle Miocene, Atlantic, Tethys and Paratethys have a relatively broad shell, strong axial sculpture with well-developed tubercles at the shoulder and a greatly thickened labial varix and basal callus, which extends onto the lateral wall to form a thick marginal callus. Shells in the Late Miocene and Pliocene populations from the Mediterranean and adjacent Atlantic are typically more elongate than those of chronologically older assemblages and have weak nodules at the shoulder and a thinner labial varix and basal callus, which is clearly delimited but does not extend beyond the base. However, shells with ancestral morphological characters can be found in Pliocene assemblages and vice versa. It seems, therefore, that there is no constant teleoconch character that separates the various nominal Neogene *Cypraecassis* taxa reliably. The differences in the prominence and thickness of the apertural armature are analogous to those seen between the Miocene and Pliocene forms of *Semicassis laevigata* (Defrance, 1817), the Miocene forms usually having a thicker outer lip and more developed parietal callus (see under *S. laevigata*).

Distribution (Paratethys; for complete distribution see Landau et al. [2004, p. 43]):

• Middle Miocene Paratethys (Badenian): Poland: Korytnica (Friedberg, 1912; Bałuk, 1995); Austria: Gainfarn, Forchtenau, Sooß (Hörnes, 1856; Hoernes & Auinger, 1884; Glibert, 1963), Czech Republic: Mikulov (= Nikolsburg) (Hörnes, 1852); Hungary: Szob, Letkés (Strausz, 1966; Csepreghy-Meznerics, 1969); Romania: Lăpugiu de Sus (= Lapugy) (Hoernes & Auinger, 1884); Bosnia: Hrvacani (Atanackovíc, 1985).

Genus: *Galeodea* Link, 1807

Galeodea echinophora (Linnaeus, 1758)

(Pl. 3, Figs. 1–2)

1758 *Buccinum echinophorum* Linnaeus, p. 735.
1837 *Cassidaria echinophora* Lamarck – Pusch, p. 126, Pl. 11, Fig. 10.
1852 *Cassidaria echinophora* Lam. – Hörnes, p. 183, Pl. 16, Figs. 4–6.
1884 *Cassidaria (Galeodea) echinophora* Linné. – Hoernes & Auinger, p. 161.
1896 *Morio echinophorus* L. var. – Boettger, p. 58.
1902 *Morio echinophorus* (L.) – Boettger, p. 24.
1958 *Cassidaria taurinensis* (Sacco) – Hölzl, p. 217, Pl. 19, Fig. 9.
2004 *Galeodea echinophora* (Linnaeus, 1758) – Landau et al., p. 43, Pl. 2, Fig. 2 (cum syn.).
2008 *Galeodea echinophora* (Linné, 1758) – Chirli & Richard, p. 31, Pl. 5, Fig. 3.
2008 *Galeodea echinophora* (Linné, 1758) – Chirli, p. 80, Pl. 30, Figs. 9–16, Pl. 31, Figs. 1–2.
2008 *Galeodea echinophora* (Linné, 1758) – Beu, p. 300, Figs. 1G, H; 6C, D; 11A, C, E; 14G–J; 21B (cum syn.).

Material: Largest complete 70.0 mm (incomplete). Vöslau (3), Grund (3), Forchtenau (2), Möllersdorf (6 incomplete), Sollenau (1), Baden (8), Sooß (4), Traiskirchen (12), Pfaffstätten (14), Mattersburg (1), Walbersdorf (7), Lăpugiu de Sus (1).

Description: See Landau et al. (2004, p. 44).

Discussion: *Galeodea echinophora* (Linnaeus, 1758) is a highly variable species, as illustrated in the living fauna by Settepassi (1970), who recognised about 70 varieties. Similarly, in the Miocene and Pliocene Italian populations, Sacco (1890a) described *G. echinophora* under 28 subspecific names. Beu (2008, Figs. 14G–J) illustrated the Recent Mediterranean lectotype and paralectotype, in the Linnean Society of London collection.

Complete specimens from the Paratethys examined in the NHMW collections do not attain the large size of some of the Pliocene shells, although some fragments are present in the NHMW collections suggesting a fully adult size comparable to that of the Pliocene to Recent shells. They tend to have relatively high spires in relation to total height, but like the Pliocene populations, the shells are highly variable in shape and sculpture.

Sacco (1890a) distinguished a second species, *Galeodea taurinensis* Sacco, 1890, coexisting with *G. echinophora* in the Early Miocene of the Turin Hills, Italy. In his discussion of the new species (Sacco, 1890a, p. 62) he says this taxon previously had been confused with *Galeodea echinophora* (Linnaeus, 1758) and differs in its smaller shell, its spiral cords being more numerous and closer-set, and its rounded tubercles. Sacco (1890, p. 62) placed Hörnes' (1852) Paratethyan record of *Cassidaria echinophora* within the chresonymy of *G. taurinensis*.

We (AGB) have examined a large number of specimens in the Museum of Evolution, University of Bologna collections from the Turin Hills and consider *Galeodea taurinensis* to be a distinct species. Apart from the differences highlighted by Sacco, *G. taurinensis* has a taller spire than *G. echinophora* and the rounded tubercles are more close-set than in *G. echinophora*. *G. taurinensis* is more closely related to the Recent Indo-Pacific species *G. bituminata* (Martin, 1933) (also known as *G. echinophorella* Habe, 1961; see Beu [2005, 2008)] than to *G. echinophora*.

For comparison with *Galeodea rugosa* (LINNAEUS, 1771) and *Galeodea bicatenata* (J. SOWERBY [1816], see LANDAU et al. [2004, p. 45]).

Distribution (Paratethys; for complete distribution see LANDAU et al. [2004, p. 45]):

- Early Miocene Paratethys (Eggenburgian): Germany: Bavaria, Kaltenbachgraben (HÖLZL, 1958).
- Middle Miocene Paratethys (Badenian): Austria: Grund, Baden, Sooß, Traiskirchen, Möllersdorf, Vöslau, Grinzing, Pfaffstätten, Mattersburg, Walbersdorf, Forchtenau (HÖRNES, 1852; HOERNES & AUINGER, 1884; GLIBERT, 1963); Romania: Lăpugiu de Sus (= Lapugy), Coşteiu de Sus (= Kostej) (HOERNES & AUINGER, 1884; BOETTGER, 1902); Bulgaria (KOJUMDGIEVA & STRACHIMIROV, 1960).

Subfamily: Phaliinae BEU, 1981
Genus: *Echinophoria* SACCO, 1890

Echinophoria haueri (HOERNES & AUINGER, 1884)

(Pl. 3, Figs. 6–8; Pl. 9, Fig. 8)

1852 *Cassis variabilis* BELL. et MICHT. – HÖRNES, p. 176, Pl. 15, Fig. 9.
1884 *Cassis (b. Cassidea) Haueri* HOERNES & AUINGER, p. 158, Pl. 17, Fig. 13.
1890a *Echinophoria Hoernesi* SACCO, p. 50, Pl. 1, Fig. 51.
1896 *Cassis (Cassidea) haueri* M. HÖ. – BOETTGER, p. 58.
1902 *Cassis (Cassidea) haueri* M. HÖ. – BOETTGER, p. 24.
1993 *Cassidaria haueri* (M. HOERNES, 1856) – NIKOLOV, p. 70, Pl. 4, Figs. 1–2.
1998 *Phalium (Echinophoria) haueri* (HOERNES & AUINGER) – SCHULTZ, p. 62, Pl. 24, Fig. 3.

Holotype: NHMW 1865/I/180.

Locus typicus: Lăpugiu de Sus, Romania.

Stratum typicum: Lower Badenian clay and silt.

Material: Largest height 44.9 mm. Sooß (6), Lăpugiu de Sus (= Lapugy) (2).

Description: Shell of medium size and thickness, globose-fusiform, with short, conical spire. Protoconch of 3.75 smooth whorls with small nucleus. Junction with teleoconch clearly delimited. Teleoconch of 4–4.5 convex, weakly shouldered whorls, with periphery at abapical suture on spire whorls. Suture impressed, linear. Spire whorls with two cords more prominent than others, adapical cord just below suture, abapical cord delimiting sutural ramp; further cords of irregular strength covering entire surface. Axial sculpture of numerous, weak, strongly prosocline riblets, spiral cords overriding axial elements. Last whorl greatly expanded, 90 % of total height, globose, base rounded, constricted abapically by narrow peribasal band. Spiral sculpture of numerous narrow spiral cords, alternating in strength on most specimens, each cord slightly wider than their interspaces. As on spire, two cords more prominent than others, upper delimiting sutural ramp, lower at shoulder angle, becoming somewhat nodulose at intersections with axial riblets. Two axial ridges are present abapically, one at shoulder, other towards base, which are not continuous but offset from each other. Aperture elongate-ovate, approximately 75 % total height. Outer lip weakly thickened by narrow labral varix, broadly convex, weakly prosocline in profile. Outer lip irregularly denticulate within, denticles only developed on abapical portion of some specimens. Anal canal weakly developed. Siphonal canal short, deep, of variable width, strongly abapically recurved. Parietal callus adherent, thin to well delimited, expanded, bearing irregular folds on some specimens. Columellar callus thickened, detached. Columella weakly excavated, abapical portion bearing strong folds or tubercles.

Variability: The description is based on a previously unfigured specimen in the NHMW collections from Sooß. Considering the scant material available, *Echinophoria haueri* (HOERNES & AUINGER, 1884) is remarkably variable in the axial sculpture of the last whorl, the thickness of the labral varix, the dentition on both the inner and outer lips and the thickness of the columellar callus. The axial sculpture is particularly variable, not only between adult shells, but also with age. Subadult shells tend not to have tubercles developed at the shoulder and to have a somewhat higher spire in relation to total height than in adults.

Discussion: The Paratethyan populations were originally considered to be conspecific with the Italian Middle Miocene *E. variabilis* (BELLARDI & MICHELOTTI, 1840) (HÖRNES, 1952, p. 176, Pl. 15, Fig. 9). The difficulties with the taxonomy of the Mediterranean to Pliocene members of the genus *Echinophoria* were discussed by LANDAU et al. (2004, p. 46), who recognized only two species in the Mediterranean Neogene; the Middle Miocene *E. variabilis* and Late Miocene and Pleistocene *E. intermedia*. *Echinophoria variabilis* has five rows of smaller tubercles, whereas *E. intermedia* has three to four rows of more prominent tubercles. Both these Mediterranean species differ from the Middle Miocene Paratethyan *Echinophoria haueri* in having distinct rows of tubercles on the last whorl, whereas in *E. haueri* these are indistinct, interrupted vertical ridges rather than well defined horizontal rows of tubercles. The tubercles can become vertically elongated in *E. intermedia*, but are still arranged in rows, and are never as irregular as in *E. haueri*. Apart from the differences in the sculpture, *E. intermedia* is a much larger species than *E. haueri*, with a more globose last whorl.

SACCO (1890a, p. 50, Pl. 1, Fig. 51) described a small cassid from the Burdigalian of the Turin Hills as *Echinophora hoernesi*, which is remarkably similar to *E. haueri*. SACCO himself noted the similarity, and said his new taxon differed from the Paratethyan species in being smaller, more oval, with more rounded whorls and a different pattern of vertical tubercular folds, although this last character could be variable. Unfortunately this taxon has not been refigured, it does not seem to be in the BELLARDI and SACCO collections in Turin, as it is not listed in FERRERO MORTARA et al. (1984). The size range given by SACCO (height 26–38 mm) is somewhat smaller than that of *E. haueri* in the NHMW collections. The smaller subadult shells of *E. haueri* do tend to have a higher spire in relation to the total height than the fully adult shells, with the spire whorls more rounded. We see no difference between the axial sculpture in the specimen figured by SACCO and that seen in subadult specimens of *E. haueri* in which the tubercles at the shoulder are not yet developed. We therefore consider *Echinophora Hoernesi* SACCO, 1890 to be a junior subjective synonym of *E. haueri*.

Distribution:

- Early Miocene proto-Mediterranean: Italy: Baldissero, Turin Hills (SACCO, 1890a).
- Middle Miocene Paratethys: Austria: Baden, Sooß, Walbersdorf (HÖRNES, 1852; SCHULTZ, 1998); Romania: Lăpugiu de Sus (= Lapugy), Coşteiu de Sus (= Kostej) (HOERNES & AUINGER, 1884; BOETTGER, 1902); Bulgaria: Jasen, Opanec Formation (NIKOLOV, 1993).

Genus: *Semicassis* MÖRCH, 1853

Semicassis laevigata (DEFRANCE, 1817)

(Pl. 4, Figs. 1–2)

1817 *Cassis laevigata* DEFRANCE, vol. 7, p. 210.
1837 *Cassis Saburon* ADAMS. var. – PUSCH, p. 124, Pl. 11, Fig. 3.

1852 *Cassis saburon* Lam. – Eichwald, p. 2, Pl. 7, Fig. 24.
1852 *Cassis saburon* Lam. – Hörnes, p. 177, Pl. 15, Figs. 2–7.
1853 *Cassis saburon* Lam. – Eichwald, p. 173.
1896 *Cassis (Cassidea) saburon* Adans. var. *laevigata* Defr. – Boettger, p. 58.
1902 *Cassis (Semicassis) saburon* Adans. – Boettger, p. 24.
1911 *Cassis saburon* Lam. – Friedberg, p. 112, Pl. 6, Fig. 3.
1936 *Cassis (Semicassis) miolaevigata* Sacco – Bogsch, p. 75, Pl. 3, Fig. 13.
1956 *Semicassis miolaevigata* Sacco – Csepreghy-Meznerics, p. 456, Pl. 4, Figs. 9–10.
1960 *Phalium (Semicassis) miolaevigata* (Sacco 1890) – Kojumdgieva & Strachimirov, p. 134, Pl. 37, Figs. 2–3.
1963 *Phalium (Semicassis) miolaevigata* Sacco – Atanackovíc, p. 71, Pl. 12, Fig. 7.
1966 *Phalium (Semicassis) saburon miolaevigatum* Sacco, 1890 – Strausz, p. 244, Pl. 64, Fig. 4, Pl. 72, Figs. 15–17, Pl. 73, Figs. 1–5.
1968 *Phalium saburon* (Lamarck, 1822) – Zelinskaja, p. 182, Pl. 43, Figs. 5–6.
1968 *Phalium (Semicassis) miolaevigatum* – Hinculov, p. 138, Pl. 34, Fig. 3.
1969 *Phalium (Semicassis) miolaevigatum* Sacco – Csepreghy-Meznerics, p. 24, Pl. 7, Figs. 1–3.
1971 *Cassis (Semicassis) saburon* (Lam.) – Eremija, p. 38, Pl. 9, Figs. 4–5.
1985 *Semicassis (Semicassis) miolaevigata* Sacco – Atanackovíc, p. 136, Pl. 30, Figs. 15–16.
1994 *Phalium saburon miolaevigatum* Sacco – Ionesi & Nicorisi, p. 59, Pl. 2, Figs. 13–14.
1995 *Semicassis (Semicassis) miolaevigata* Sacco, 1890 – Baluk, p. 203, Pl. 16, Figs. 1–4.
1996 *Semicassis (Semicassis) miolaevigata* Sacco – Baluk & Radwański, Pl. 2, Fig. 10, Pl. 3, Figs. 6–8.
1998 *Phalium (Semicassis) miolaevigata* Sacco – Schultz, p. 62, Pl. 24, Fig. 2.
2002 *Phalium (Semicassis) miolaevigata* (Sacco, 1890) – Harzhauser, p. 91, Pl. 5, Figs. 18–19.
2003 *Semicassis miolaevigata* Sacco, 1890 – Ceranka & Zlotnik, p. 494, Text.-Figs. 2 A–B.
2004 *Semicassis laevigata* (Defrance, 1817) – Landau et al., Pl. 3, Figs. 1–2 (cum syn.).
2004 *Semicassis (Semicassis) miolaevigata* (Sacco, 1890) – Schnetler, p. 94, Pl. 5, Fig. 7.
2008 *Phalium saburon* (Bruguière, 1972) – Chirli, p. 85, Pl. 31, Figs. 10–16, Pl. 32, Figs. 1–2.

Material: 200+ specimens. Largest height 72.1 mm, width 63.0 mm. All localities given below by Hörnes (1856, p. 692) plus Sooß (20+), Traiskirchen (20+), Mattersburg (2), Walbersdorf (5), Pötzleinsdorf (5), Guntersdorf (5), Mikulov (3), Bulhary (= Pulgram) (3), Lăpugiu de Sus (= Lapugy) (20+).

Description: See Landau et al. (2004, p. 48).

Discussion: As discussed by Landau et al. (2004), these Paratethyan Miocene shells have usually been identified as *Semicassis miocenica* Sacco, 1890. Whilst the shells in the NHMW collection tend to be broader and thicker than typical Pliocene Mediterranean shells of *Semicassis laevigata* (Defrance, 1817), with a more thickened labral varix, a whole range of variability can be observed within the Paratethyan specimens, and they intergrade with typical Pliocene *S. laevigata*.

Distribution (Paratethys; for complete distribution see Landau et al. [2004, p. 49]):

• Early Miocene Paratethys (Karpatian): Austria: Kleinebersdorf, Karnabrunn, Laa an der Thaya; Czech Republic: Slup (Harzhauser, 2004).

• Middle Miocene Paratethys (Badenian): Poland: Žukowce, Korytnica, Lipa, Holubica, Jasionów, Podhorce, Olesko, Zborów, Zukowce, Zabiak, Zalise, Rydoml, Wolynui, Podolski (Friedberg, 1911; Baluk, 1995; Baluk & Radwański, 1996); Austria: Grund, Baden, Vöslau, Möllersdorf, Grinzing, Forchtenau, Gainfarn, Enzesfeld, Steinabrunn (Hörnes, 1852; Schultz, 1998; Harzhauser, 2002; 2004); Czech Republic: Mikulov (= Nikolsberg, Kienberg), Bulhary (= Pulgram) (Hörnes, 1852; Harzhauser, 2004); Hungary: Nógrádszakál (Bogsch, 1936), Szob, Letkés (Csepreghy-Meznerics, 1956); Bosnia: Jazovac (Atanackovíc, 1963, 1985); Romania: Coşteiu de Sus (= Kostej), Criviineni, Valea Satului (Boettger, 1902; Ionesi & Nicorici, 1994; Hinculov, 1968); Bulgaria (Kojumdgieva & Strachimirov, 1960).

Semicassis neumayri (Hoernes, 1875)

(Pl. 4, Figs. 3–5; Pl. 10, Fig. 1)

1875 *Cassis Neumayri* Hoernes, p. 350, Pl. 11, Figs. 11–12.
1884 *Cassis (b. Semicassis) Neumayri* R. Hoern. – Hoernes & Auinger, p. 156, Pl. 17, Figs. 11–12.
1973 *Semicassis neumayeri* (R. Hoernes, 1875) – Steininger, p. 414, Pl. 5, Figs. 4–6.

Syntype A: GBA No.: 1875/001/0011 (Hoernes, p. 350, Pl. 11, Figs. 11)

Syntype B: GBA No.: 1875/001/0011 (Hoernes, p. 350, Pl. 11, Figs. 12)

Locus typicus: Ottnang, Austria.

Stratum typicum: Lower Miocene clay, silt and fine sand of the Ottnang Formation, Ottnangian stage.

Material: 12 specimens. Maximum height 39.0 mm (incomplete) all from Ottnang.

Description: Shell small for genus, of medium thickness, globose, with short spire. Protoconch dome-shaped, of just under four whorls, with small nucleus. Junction with teleoconch sharply delimited, prosocline. Teleoconch of about three whorls, with periphery at abapical suture on spire whorls. Suture impressed, very narrowly canaliculate. Spiral sculpture of two primary cords on first teleoconch whorl, three on second, with secondary cords in interspaces. Shallow, weakly concave sutural ramp developing on second teleoconch whorl between adapical primary spiral cord, adjacent to upper suture, and second primary cord, which forms shoulder angle. Axial sculpture of close-set, prosocline growth lines, developed into low ridges on adapical cord. Last whorl 88 % of total height, globose, weakly shouldered, with relatively narrow sutural ramp, regularly convex below, constricted at base. Spiral sculpture of about 25 flattened, subequal, poorly defined spiral cords, with one secondary thread in each interspace. Prominent varix present on largest specimen 240° before labral varix. Aperture wide, pyriform, approximately 70 % of total height. Outer lip moderately thickened by labral varix, regularly rounded, slightly prosocline in profile, bearing several weakly developed denticles inside. Anal canal poorly developed. Siphonal canal very short, deep, narrow, strongly recurved posteriorly. Parietal callus thickened, expanded, adherent, sharply delimited. Columella weakly excavated, bearing a few irregular folds and tubercles on abapical portion of columellar callus. Columellar callus greatly thickened. Siphonal fasciole very short, rounded, abaxially recurved.

Variability: Material of this species is scant in the NHMW collections and only three of the six available specimens are adult. They are all somewhat antero-dorsally compressed. All are fairly consistent in shape and in the character of their sculpture. A single varix in addition to the labral varix is present on two of the three adult specimens.

Discussion: *Semicassis neumayri* (Hoernes, 1875) is a very small species of *Semicassis* found only at the Ottnang locality in Austria. The small size causes taxonomic problems, as members of the genus *Semicassis* change significantly during ontogeny. All juvenile specimens of *Semicassis* species have much more prominent sculpture than adult specimens of the same species, e. g., spirals over the whole shell when none are present on the adult last whorl, and lots of fine axials that are not present on adults. It is, therefore, possible that *S. neumayri* simply represents juvenile specimens of another taxon.

However, we have examined a growth series of *Semicassis laevigata* (DEFRANCE, 1817) and none have the axial riblets on the early teleoconch whorls as developed as in *S. neumayri*, nor do they form low ridges on the adapical cord.

Another possible candidate is *Semicassis grateloupi* (DESHAYES, 1853), which is characterised by its axial sculpture on the spire whorls often persisting on the adult shells. We have compared the Ottnang shells with a growth series of *S. grateloupi* from the Lower Miocene, Burdigalian of France, and for similar-sized shells *S. grateloupi* is higher-spired, the axial sculpture is far more prominent and the shape of the last whorl is different, less inflated than in *S. neumayri*. Moreover, there is no verified occurrence of *S. grateloupi* in the Paratethyan Miocene.

S. neumayri differs from the slightly older *Semicassis subsulcosa* (HOERNES & AUINGER, 1884) in having a smaller shell, a more globose last whorl with a narrow sutural ramp and more numerous, flattened, rather poorly differentiated spiral cords rather than the prominent rounded cords seen in *S. subsulcosa*. Unfortunately we do not have a growth series of *S. subsulcosa*, but there is no trace of axial ribbing on any of the specimens examined.

Although it is possible that *S. neumayri* is based on juvenile shells of another species, the available specimens do not match juvenile shells of any known *Semicassis* species. We therefore consider it a distinct species endemic to the Paratethyan Ottnangian, which is not suprising considering the high endemicity of the marine Ottnangian mollusc fauna (HARZHAUSER & PILLER, 2007).

Distribution:

- Early Miocene Paratethys (Ottnangian): Austria: Ottnang (HOERNES, 1875; HOERNES & AUINGER, 1884; STEININGER, 1973).

Semicassis subsulcosa (HOERNES & AUINGER, 1884)

(Pl. 4, Figs. 6–8)

1852 *Cassis sulcosa* LAM. – HÖRNES, p. 179, Pl. 15, Fig. 8.
1884 *Cassis subsulcosa* HOERNES & AUINGER, p. 156.
1912 *Cassis (Semicassis) subsulcosa* HÖRN. et AUING. – SCHAFFER, p. 147, Pl. 51, Figs. 8–11.
1958 *Semicassis (Semicassis) subsulcosa* (R. HÖRN. et AUING.) – HÖLZL, p. 217, Pl. 20, Fig. 3.
1966 *Phalium (Semicassis) subsulcosum* HOERNES & AUINGER, 1884 – STRAUSZ, p. 244, Fig. 118.
1971 *Semicassis subsulcosa* (R. HOERNES et AUINGER 1884) – STEININGER, p. 396, Pl. 9, Fig. 8.
1972 *Phalium (Semicassis) subsulcosum* (HOERNES-AUINGER, 1879) – ONDREJIČKOVÁ, p. 115.
1973 *Semicassis subsulcosa* (R. HOERNES et AUINGER 1884) – STEININGER, p. 413, Pl. 5, Fig. 3.

Holotype A: NHMW 1851/VI/100a.

Locus typicus: Loibersdorf, Austria.

Stratum typicum: Lower Miocene, Loibersdorf Formation (Eggenburgian stage).

Material: 6 specimens, only one complete. Maximum height 53.3 mm (spire missing) all from Loibersdorf (Austria).

Description: Shell of medium size and thickness, globose, with short spire. Protoconch eroded in all specimens. Teleoconch of about four whorls, with periphery at abapical suture on spire whorls. Suture linear, superficial. Surface of spire whorls decorticated in all specimens. Sculpture on penultimate whorl of two or three broad, rounded spiral cords. Last whorl 90 % of total height, globose, regularly convex in profile, strongly constricted at base. Spiral sculpture of 15–17 rounded spiral cords, slightly wider at periphery than elsewhere, narrowing abapically, separated by narrow interspaces. Aperture wide, pyriform, approximately 70 % of total height. Outer lip moderately to strongly thickened by labral varix, regularly rounded and slightly prosocline in profile, somewhat flared abapically, extending beyond siphonal canal, bearing 15–16 elongate denticles inside, denticles continuing into aperture. Denticles weakest adapically and more strongly developed on abapical, flared portion of outer lip. Anal canal poorly developed. Siphonal canal very short, deep, narrow, strongly recurved posteriorly. Parietal callus greatly thickened, expanded, adherent, sharply delimited. Columella broadly excavated, bearing a few irregular folds and tubercles on abapical portion of columellar callus. Columellar callus greatly thickened. Siphonal fasciole very short, rounded, abaxially recurved.

Variability: All except one of the specimens in the NHMW collections is laterally distorted to some degree, and material from Loibersdorf is heavily decalcified. The shell shape is fairly constant. However, there is some variability in the character of the cords on the last whorl. The largest specimen has cords of alternating strength around the centre of the last whorl. No varices are present on any of the specimens.

Discussion: In their original description, HOERNES & AUINGER (1884, p. 156) referred to the shell illustrated by HÖRNES, 1852 (Pl. 15, Fig. 8), which is therefore the holotype, and is illustrated again here (Pl. 4, Fig. 7).

Semicassis subsulcosa (HOERNES & AUINGER, 1884) is found only at a few localities, and seems to be endemic to the Paratethyan Eggenburgian. It is immediately distinguishable from *Semicassis laevigata* (DEFRANCE, 1817) by the character of the spiral sculpture on the last whorl, with strong rounded ribs present over the entire surface rather than a few cords restricted to the areas adjacent to the suture and base as seen in *S. laevigata*. The shell is also more inflated in *S. laevigata*, with a somewhat depressed sutural area not seen in *S. subsulcosa*. The character of the spiral sculpture is more like that of the Atlantic Early and Middle Miocene *Semicassis grateloupi* (DESHAYES, 1853) but *S. grateloupi* has a more elevated spire with axial sculpture on the spire whorls. There is no axial sculpture on any specimens we have seen of *S. subsulcosa*. The folds on the columella are also coarser and less numerous in *S. subsulcosa* than in *S. grateloupi*.

SACCO (1890a, p. 38, Pl. 1, Fig. 37) described a subspecies of the Paratethyan species from the Middle Miocene Po Valley of Italy as *S. subsulcosa* var. *pedemontana*. His figure, as well as the photograph of the holotype (FERRERO MORTARA et al., 1984, Pl. 1, Fig. 5), show this shell to have a relatively elevated spire with axial sculpture, and it is more likely to be a specimen of *S. grateloupi*.

According to SCHAFFER (1912), *Semicassis subsulcosa* differs from *S. sulcosa* (= *S. undata* (GMELIN, 1791)) in being smaller, having a much weaker outer lip and narrower spiral cords. One of the specimens figured by SCHAFFER (1912, Pl. 51, Fig. 10) from Loibersdorf actually has a strongly thickened outer lip, not seen in the photo (NHMW coll.).

HÖLZL (1958, Pl. 20, Figs. 1–2) illustrated two shells from Nonnenwald-Schacht (Penzberg) as *Phalium (Semicassis) grateloupi*, which do show axial sculpture on the spire. We have found no specimens in the Vienna collections attributable to this species.

Distribution:
- Early Miocene Paratethys (Eggenburgian): Germany: Bavaria, Kaltenbachgraben (HÖLZL, 1958; STEININGER, 1973); Austria: Loibersdorf (HÖRNES, 1852; HOERNES & AUINGER, 1884; SCHAFFER, 1912; STEININGER, 1971); Slovak Republic: Lipovany (ONDREJIČKOVÁ, 1972); Hungary: Borsod (STRAUSZ, 1966).

Genus: *Sconsia* GRAY, 1847

Sconsia ottnangiensis (SACCO, 1890)

(Pl. 5, Figs. 1–2; Pl. 10, Fig. 2)

1875 *Cassidaria striatula* BON. – HOERNES, p. 351, Pl. 11, Fig. 13.
1884 *Cassidaria (c. Galeodea) striatula* BON. – HOERNES & AUINGER, p. 162, Pl. 17, Fig. 14.
1890a *Galeodosconsia ottnangiensis* SACCO, p. 70.
1973 *Sconsia (S.) striatula ottnangensis* [sic] (SACCO) – STEININGER, p. 414, Pl. 5, Fig. 2.

Holotype: Collection of Geological Survey GBA 1875/01/12.

Locus typicus: Ottnang, Austria.

Stratum typicum: Lower Miocene clay, silt and fine sand of the Ottnang Formation, Ottnangian stage.

Material: 4 specimens. Maximum height 28.3 mm, all from Ottnang.

Description: Shell small for genus, of medium thickness, globose, with short spire and relatively long siphonal canal. Protoconch slightly heterostrophic, paucispiral, consisting of just under two whorls, with small nucleus. Junction with teleoconch sharply delimited, prosocline. Teleoconch of four whorls, with periphery at abapical suture on spire whorls. Suture impressed, very narrowly canaliculate. Spiral sculpture of four rounded primary cords on first teleoconch whorl, seven on second, roughly equal in width to their interspaces. On third teleoconch whorl secondary cords develop in interspaces. Last whorl 80 % of total height, globose, very weakly shouldered, with relatively wide, poorly delimited sutural ramp, regularly convex below, strongly constricted at base. Spiral sculpture of about 40 narrow, rounded spiral cords, with a single secondary cord in each interspace on most specimens. Aperture wide, pyriform, approximately 75 % of total height. Outer lip moderately thickened by labral varix, slightly flared adapically, sinuous in profile, bearing about eight stout denticles within. Two largest denticles delimit lateral borders of anal and siphonal canals, with larger gap between these and central group of denticles, which are equally spaced and subequal in strength. Anal canal clearly developed, deep. Parietal callus thickened, expanded, adherent, sharply delimited, bearing prominent parietal tooth adapically. Columella excavated in centre, bearing irregular folds along its entire length. Columellar callus moderately thickened. Siphonal canal relatively long for genus, narrow, almost straight, very slightly recurved posteriorly.

Variability: Three of the four specimens present in the GBA and NHMW collections are complete. All are somewhat compressed. They differ slightly in their surface ornament, the cords in one specimen are fine and of subequal strength rather than alternate. The aperture is only visible in two shells. In one the denticles are strongly developed, in the other less so, although the disposition of the denticles is similar.

Discussion: Specimens from the Paratethyan assemblages were originally considered conspecific with those from the Italian Burdigalian identified as *Galeodosconsia striatula* SACCO, 1890 (note that *Cassidaria striatula* BONELLI is a manuscript name). SACCO (1890, p. 70) suggested the name *Galeodosconsia ottnangiensis* for the shells from Ottnang, whilst on the same page including the references by HOERNES (1875) and HOERNES & AUINGER (1884) within the chresonomy of *G. striatula*.

With the scant material available it is difficult to get a true idea of the variability of this species. However, we agree with SACCO that the Paratethyan form seems to have a more globose last whorl, especially in the adapical portion, than specimens illustrated from the Italian Miocene (SACCO, 1890a, Pl. 2, Fig. 27; SACCO, 1904, Pl. 21, Figs. 20–21; FERRERO MORTARA et al., 1984, Pl. 3, Fig. 3). Moreover, in the few illustrations of *G. striatula* in which the denticles on the inside of outer lip are visible, they seem to be evenly distributed along the inside edge of the outer lip and not as described above. Further material may prove the two to be synonymous, but we provisionally separate the Paratethyan shells as a distinct taxon.

Distribution:
- Early Miocene Paratethys (Ottnangian): Austria: Ottnang (HOERNES, 1875; HOERNES & AUINGER, 1884; STEININGER, 1973).

4.3. Family Ranellidae J.E. GRAY, 1854

Subfamily: Ranellinae J.E. GRAY, 1854
Genus: *Ranella* LAMARCK, 1816

Ranella olearium (LINNAEUS, 1758)

(Pl. 5, Figs. 3–4)

1758 *Murex olearium* LINNAEUS, p. 748.
1853 *Ranella reticularis* DESH. – HÖRNES, p. 211, Pl. 21, Figs. 1–2.
1884 *Ranella (Apollon) gigantea* LAMK. – HOERNES & AUINGER, p. 188, Pl. 23, Figs. 1–5.
1906 *Ranella (Apollon) gigantea* LAM. – BOETTGER, p. 40.
1969 *Bursa (Ranella) gigantea* LAM. – CSEPREGHY-MEZNERICS, p. 80, Pl. 3, Figs. 13, 16–17.
1995 *Argobuccinum (Ranella) giganteum* (LAMARCK, 1822) – BALUK, p. 205, Pl. 18, Figs. 9–11.
2004 *Ranella olearium* (LINNAEUS, 1758) – LANDAU et al., p. 51, Pl. 3, Figs. 5–6 (cum syn.).
2008 *Ranella olearia* (LINNÉ, 1758) – CHIRLI & RICHARD, p. 31, Pl. 5, Fig. 4.
2008 *Ranella olearia* (LINNÉ, 1758) – CHIRLI, p. 88, Pl. 32, Figs. 3–10.

Material: Largest (70 mm incomplete). Steinabrunn (1), Sooß (3), Forchtenau (4), Vöslau (1), Walbersdorf (1), Grund (2), Rudice (= Ruditz) (4), Jaromierčic (= Jaroměřice) (3), Lăpugiu de Sus (= Lapugy) (12).

Description and Discussion: See LANDAU et al. (2004, p. 51).

Distribution (Paratethys; for complete distribution see LANDAU et al. [2004, p. 52]):
- Middle Miocene Paratethys (Badenian): Austria: Gainfarn, Grund, Steinabrunn, Sooß, Forchtenau, Vöslau, Walbersdorf (HÖRNES, 1853); Czech Republic: Rudice (= Ruditz), Jaromierčic (= Jaroměřice) (HOERNES & AUINGER, 1884); Romania: Lăpugiu de Sus (= Lapugy), Coşteiu de Sus (= Kostej) (HOERNES & AUINGER, 1884; BOETTGER, 1906).

Subfamily: Cymatiinae IREDALE, 1913

We follow BEU (in press) in ranking as genera the groups formerly ranked subgenera of *Cymatium* (for discussion see BEU, in press).

Genus: *Charonia* GISTEL, 1848

Charonia lampas **(LINNAEUS, 1758)**

(Pl. 5, Figs. 5–7)

1758 *Murex lampas* LINNAEUS, p. 748.
1853 *Triton nodiferum* LAM. – HÖRNES, p. 201, Pl. 19, Figs. 1–2.
1884 *Triton nodiferum* LAMK. – HOERNES & AUINGER, p. 173, Pl. 21, Fig. 1.
1912 *Triton nodiferum* LAM. – FRIEDBERG, p. 127, Pl. 7, Fig. 3.
1995 *Charonia (Charonia) nodifera* (LAMARCK, 1822) – BALUK, p. 205, Pl. 19, Figs. 1–3.
2004 *Charonia lampas* (LINNAEUS, 1758) – LANDAU et al., p. 53, Pl. 4, Fig.1 (cum syn.).
2008 *Charonia lampas* (LINNÉ, 1758) – CHIRLI, p. 97, Pl. 35, Figs. 9–16.

Material: Height 123.9 mm Grund (1) (specimen Pl. 19, Fig. 1 of HÖRNES [1856]), height 63.7 mm Baden (2) (specimen Pl. 19, Fig. 2 of HÖRNES [1853]) large damaged shell height 203 mm Grund (1, 2 fragments of very large specimens), Vöslau (1), Guntersdorf (2).

Description and Discussion: See LANDAU et al. (2004, p. 54).

Distribution (Paratethys; for complete distribution see LANDAU et al. [2004, p. 54]):
- Middle Miocene Paratethys (Badenian): Poland: Korytnica (FRIEDBERG, 1912; BALUK, 1995); Austria: Grund, Guntersdorf, Baden, Forchtenau (HÖRNES, 1853); Romania: Lăpugiu de Sus (= Lapugy) (HOERNES & AUINGER, 1884).

Genus: *Monoplex* PERRY, 1810

Monoplex corrugatus **(LAMARCK, 1816)**

(Pl. 6, Figs. 1–2)

1822 *Triton corrugatum* LAMARCK, p. 181.
1837 *Triton leucostoma* var. *polonica* PUSCH, p. 139, Pl. 11, Fig. 25.
1853 *Triton corrugatum* LAM. – HÖRNES, p. 205, Pl. 20, Figs. 1–4.
1884 *Triton (b. Simpulum) affine* DESH. – HOERNES & AUINGER, p. 175, Pl. 21, Figs. 12–15.
1902 *Triton (Simpulum) affinis* DESH. – BOETTGER, p. 25.
1912 *Triton affine* DESH. – FRIEDBERG, p. 130, Pl. 7, Fig. 6.
1950 *Cymatium (Lampusia) affine friedbergi* COSSMANN-PEYROT – CSEPREGHY-MEZNERICS, p. 398, Pl. 1, Figs. 11–12.
1960 *Cymatium (Lampusia) affinis* var. *riedbergi* COSSMANN-PEYROT 1923 – KOJUMDGIEVA & STRACHIMIROV, p. 136, Pl. 38, Fig. 2.
1966 *Cymatium (Lampusia) affine* DESHAYES, 1832 – STRAUSZ, p. 247, Pl. 29, Figs. 8–11, Pl. 30, Figs. 1–5.
1968 *Cymatium affine* (DESHAYES, 1832) – ZELINSKAJA, p. 183, Pl. 43, Figs. 9–10.
1969 *Cymatium (Lampusia) affine friedbergi* COSSMANN-PEYROT – CSEPREGHY-MEZNERICS, p. 24, Pl. 7, Figs. 16, 20.
1995 *Cymatium (Lampusia) affine* (DESHAYES, 1832) – BALUK, p. 207, Pl. 20, Figs. 5–11.
1996 *Cymatium (Lampusia) affine* (DESHAYES) – BALUK & RADWAŃSKI, Pl. 1, Fig. 4, Pl. 4, Fig. 4, Pl. 6, Figs. 8–9, Pl. 7, Fig. 1.
1998 *Cymatium (Lampusia) affine friedbergi* COSSMANN-PEYROT – SCHULTZ, p. 62, Pl. 24, Fig. 4.
2002 *Cymatium corrugatum* (LAMARCK, 1816) – GOFAS & BEU, p. 102, Fig. 8A–J.
2004 *Cymatium (Monoplex) corrugatum* (LAMARCK, 1822) – LANDAU et al., p. 55, Pl. 4, Fig. 2 (cum syn.).
2008 *Cymatium corrugatum* (LAMARCK, 1816) – CHIRLI & RICHARD, p. 32, Pl. 5, Fig. 5.
2008 *Cymatium corrugatum* (LAMARCK, 1816) – CHIRLI, p. 90, Pl. 32, Figs. 11–16, Pl. 33, Figs. 1–5.

Material: Largest height 90.5 mm. Grund (30+), Braunsdorf (1), Guntersdorf (5), Sooß (3), Pfaffstätten (1), Gainfarn (8), Steinabrunn (10), Vöslau (20+), Forchtenau (6), Szob (4), Lăpugiu de Sus (= Lapugy) (26), Hrušovany (= Grußbach) (3), Lysice (= Lissitz) (2), Korytnica (10).

Description: See Landau et al. (2004, p. 55).

Discussion: COSSMANN & PEYROT (1924) considered the Central European shells to be different from *M. affinis* (DESHAYES, 1833) (i. e., *M. corrugatus*) in having squatter shells, with a shorter siphonal canal and more strongly nodulose axial ribs. They proposed the name *Eutritonium (Lampusia) friedbergi* for the Paratethyan population. *Monoplex corrugatus* (LAMARCK, 1816) is highly variable and more elongated specimens with longer siphonal canals indistinguishable from Italian Pliocene shells are also present in the NHMW collections (see LANDAU et al., 2004).

Monoplex subcorrugatus (D'ORBIGNY, 1852), from the Early Miocene Aquitanian and Burdigalian of the Aquitaine Basin, France (LOZOUET et al., 2001, p. 46, Pl. 19, Fig. 1a, b) seems likely to have been ancestral to *M. corrugatus*. It is similar to *M. corrugatus* in most characters, but differs in its smaller maximum size, wider shape, more prominent spiral cords, and much heavier, thicker varices. LOZOUET et al. (2001, p. 46) pointed out that nearly all the species proposed in *Eutritonium* and *Ranularia* by COSSMANN & PEYROT (1924) are synonyms of *M. subcorrugatus* (*E. aquitanicum, E. dolarioides, R. multicostata, R. duvergieri*).

The Paratethyan populations seem intermediate between the two, but closer to *M. corrugatus*. It is likely that *M. corrugatus* evolved gradually from *M. subcorrugatus* in the Paratethys, or perhaps during the time interval represented by the Middle Miocene of the Paratethys.

Distribution (Paratethys; for complete distribution see LANDAU et al. [2004, p. 56]):
- Middle Miocene Paratethys (Badenian): Poland: Korytnica, Dryszczów (FRIEDBERG, 1912; BALUK & RADWAŃSKI, 1996; BALUK, 1995); Ukraine (ZELINSKAJA, 1968); Austria: Grund, Gainfarn, Braunsdorf, Guntersdorf, Enzesfeld, Steinabrunn, Baden, Sooß, Vöslau, Pfaffstätten, Forchtenau (HÖRNES, 1853; HOERNES & AUINGER, 1884); Czech Republic: Hrušovany (= Grußbach), Lysice (= Lissitz), Třebovice (= Triebitz) (HÖRNES, 1853); Hungary: Szob, Sámsonháza, Méretek (HÖRNES, 1853; CSEPREGHY-MEZNERICS, 1950); Romania: Coşteiu de Sus (= Kostej) (BOETTGER, 1902); Bulgaria (KOJUMDGIEVA & STRACHIMIROV, 1960).

Monoplex heptagonus **(BROCCHI, 1814)**

(Pl. 6, Figs. 3–4)

1814 *Murex heptagonus* BROCCHI, p. 404, Pl. 9, Fig. 2.
1853 *Triton heptagonum* BROCC. – HÖRNES, p. 206, Pl. 20, Figs. 5–6.
1884 *Triton (b. Simpulum) Wimmeri* HOERNES & AUINGER, p. 177, Pl. 21, Figs. 17–18.
1912 *Triton heptagonum* BROCC. – FRIEDBERG, p. 132, Pl. 7, Fig. 7.
1950 *Cymatium (Ranularia) heptagona vindobonica* COSSMANN-PEYROT – CSEPREGHY-MEZNERICS, p. 398, Pl. 1, Figs. 5–6.
1960 *Cymatium (Ranularia) heptagona* var. *vindobonica* (COSSMANN & PEYROT 1923 [sic]) – KOJUMDGIEVA & STRACHIMIROV, p. 138, Pl. 37, Figs. 6–8.
1966 *Cymatium (Ranularia) heptagonum vindobonicum* COSSMANN & PEYROT, 1923 [sic] – STRAUSZ, p. 248, Pl. 29, Fig. 7.
1969 *Cymatium (Ranularia) heptagona vindobonica* COSSM. et PEYROT – CSEPREGHY-MEZNERICS, p. 24, Pl. 7, Figs. 11, 13.
2004 *Cymatium (Monoplex) heptagonum* (BROCCHI, 1814) – LANDAU et al., p. 58, Pl. 4, Fig. 5, Pl. 9, Fig. 2 (cum syn.).
2008 *Cymatium heptagonum* (BROCCHI, 1814) – CHIRLI, p. 94, Pl. 34, Figs. 9–16, Pl. 35, Figs. 1–2.

Material: Grund (4), Gainfarn (2), Sooß (4), Vöslau (15). Forchtenau (7), Lăpugiu de Sus (= Lapugy) (30+), Korytnica (6).

Description: See LANDAU et al. (2004, p. 59).

Discussion: There has been much discussion in the Paratethyan literature on the identity of the specimens ascribed by several authors to *Monoplex heptagonus* (BROC-

CHI, 1814). Most authors have agreed that the Paratethyan form is not identical to Italian Pliocene specimens. BALUK (1995, p. 208) studied a large series of specimens from the Middle Miocene of Poland and concluded that there was no constant difference between *M. affine* (here considered a junior synonym of *M. corrugatus*) and the Paratethyan shells described as *M. heptagonus*, and that the latter were not conspecific with BROCCHI's species. However, we have examined HOERNES & AUINGER's (1884, p. 176) material and much other Paratethyan material in NHMW and comparable material in the Senckenberg Museum, Frankfurt, and found it inseparable from Italian Pliocene material of *M. heptagonus*. Some of the largest specimens, from Lăpugiu de Sus and Coşteiu de Sus (Middle Miocene, early Badenian) in Romania, have more obvious median grooves on the spiral cords than in smaller specimens, and some of these have a taller spire and a more heavily ridged aperture than smaller specimens. However, these characters all develop as the shell grows, just as in the closely related Recent species *M. exaratus* (REEVE, 1844). *Triton wimmeri* HOERNES & AUINGER (1884, p. 177), from Lăpugiu de Sus, Romania, is also a synonym of *M. heptagonus* (LANDAU et al., 2004, p. 59). In our opinion there is no doubt that *M. heptagonus* is widespread in European Miocene and Pliocene rocks, including throughout the Paratethyan region, and specimens are easily separable from *M. corrugatus*. For further discussion see LANDAU et al. (2004).

Distribution (for complete distribution see LANDAU et al. [2004, p. 60]):

Middle Miocene Paratethys (Badenian): Poland: Korytnica (FRIEDBERG, 1912; BALUK, 1995); Austria: Grund, Gainfarn, Sooß, Vöslau, Forchtenau (HÖRNES, 1853; HOERNES & AUINGER, 1884); Hungary: Sámsonháza, Méretek (CSEPREGHY-MEZNERICS, 1950); Romania: Lăpugiu de Sus (= Lapugy) (HOERNES & AUINGER, 1884, as *Triton wimmeri*).

Genus: *Turritriton* DALL, 1904

Turritriton grundensis **(HOERNES & AUINGER, 1884)**

(Pl. 6, Fig. 5)

1884 *Triton (d. Simpulum) Grundense* HOERNES & AUINGER, p. 177, Pl. 21, Fig. 16.

1995 *Cymatium (Lampusia) grundense* (HOERNES & AUINGER, 1884) – BALUK, p. 209, Pl. 20, Figs. 3–4.

Holotype: NHMW Inv. 1851/2/31.

Locus typicus: Grund, Austria.

Stratum typicum: Silt and fine sand of the Grund Formation (lower Middle Miocene, Badenian).

Material: Grund (1) (Holotype height 20.8 mm).

Description: Shell small, solid, squat, with medium-height scalate spire and finely reticulate sculpture. Protoconch missing. Four convex teleoconch whorls preserved, with periphery mid-whorl on spire. Each spire whorl with relatively broad, sloping, sutural ramp; periphery formed by two primary cords of equal strength, whorl profile concave between sutures and cords, and between cords. Suture impressed, canaliculate. Two elevated primary spiral cords on spire whorls, much narrower than their interspaces, with several spiral threads in each interspace. Axial sculpture of 12 rounded, weakly prosocline primary ribs, much narrower than their interspaces, with three secondary riblets in each interspace. Spiral sculpture overriding axial elements, rendering entire shell surface finely reticulate. Last whorl 75 % of total height; strongly shouldered by two primary cords, weakly convex below, somewhat constricted at base. Spiral sculpture on last whorl of secondary cords on sutural ramp, and five sets of cords arranged in groups of three below shoulder, with central primary cord and one secondary cord on either side. Last whorl bearing one varix about 240° before labral varix. Aperture ovate, 54 % of total height. Outer lip convex, slightly flared in region of anal canal, thickened by prominent labral varix, bearing six prominent denticles within. Anal canal rounded, delimited medially by prominent parietal tooth. Siphonal canal relatively long, narrow, straight. Columella concave, with two denticles deep inside inner border in the centre and one prominent ridge delimiting lateral border of siphonal canal. Parietal callus thickened, sharply delimited, but weakly expanded, continuous with thickened, adherent columellar callus. Siphonal fasciole elongate, bearing eight spiral cords.

Discussion: This species is represented in the Vienna collections by the holotype alone. It is characterised by its finely reticulate surface sculpture and the spiral cords on the last whorl, which are arranged in groups of three, with a raised central cord and a lower one on either side. This sculpture indicates a position in the genus *Turritriton* DALL, 1904 (LANDAU et al., 2004, p. 60; BEU, 2005, p. 100).

The drawing published by HÖRNES & AUINGER (1879) is not accurate, as it does not convey either the fasciculate nature of the spiral cords or the obvious, fine, regular axial costellae, and the peripheral keel is considerably narrower than the drawing indicates. The two main fasciculate cords around the periphery are closely spaced, as in most material of all the other species assigned by BEU (in press) to *Turritriton*, and the other main spiral cords are more widely separated and have a single narrow thread in the centre of each spiral interspace, as in all other *Turritriton* species. *Turritriton grundensis* has since been recorded correctly from the Korytnica clays (Middle Miocene, Badenian) in the Holy Cross Mountains, Poland, by BALUK (1995: 209, Pl. 20, Figs. 3–4); the specimen in BALUK's Fig. (1995: Pl. 20, Fig. 3) closely resembles the holotype.

Turritriton grundensis superficially resembles *Monoplex heptagonus* (BROCCHI, 1814), also present in the Paratethyan assemblages, but is immediately distinguished by the character of the surface sculpture, the almost horizontal sutural ramp and canaliculate suture in *M. heptagonus*, and by the bifid labral denticles and longer siphonal canal in *M. heptagonum*.

The presence of the genus *Turritriton* in the Paratethys is unexpected, as there is no record of the genus in Europe before or after *T. grundensis*. BEU (in press) recognised three distinct species groups within the genus. The more prominently spirally sculptured group of smaller species (*T. domingensis* (GABB, 1873) and *T. labiosus* (WOOD, 1828)) apparently diverged before late Early Miocene time from the group of less strongly sculptured, very similar, slightly larger species (*T. grundensis, T. gibbosus* (BRODERIP, 1833) and *T. kobelti* (von MALTZAN, 1884)), whereas the taller and narrower *T. tenuiliratus* group (*T. tenuiliratus* (LISCHKE, 1873) and the doubtfully distinct form *T. fittkaui* PARTH, 1991) seems to have been limited to the Indo-West Pacific province since Miocene time, before joining the Pleistocene–Holocene migrants into the Atlantic. The *T. domingensis-labiosus* group has a Caribbean and Tethyan distribution, whereas the *T. grundensis-gibbosus-kobelti* group is limited to the Middle Miocene Paratethys in Europe, and today is limited to the eastern Pacific, western Atlantic and West Africa, with a single record from the Pliocene (?) of Atlantic Colombia (BEU, in press).

It is most unusual amongst the Cymatiinae in the European Neogene assemblages for a species to be represented by so few individuals (a single specimen from Austria, the holotype, and possibly five specimens from Poland; Baluk, 1995, p. 209).

Distribution:

- Middle Miocene Paratethys (early Badenian): Poland: Korytnica (Baluk, 1995); Austria: Grund (Hoernes & Auinger, 1884).

Genus: *Sassia* Bellardi, 1873

Sassia apenninica **(Sassi, 1827)**

(Pl. 6, Figs. 6–7)

1827 *Triton apeninnicum* Sassi, p. 480 (nomen protectum).
1853 *Triton Apenninicum* Sassi. – Hörnes, p. 202, Pl. 19, Figs. 3–4.
1884 *Triton (a. Sassia) Apenninicum* Sassi. – Hoernes & Auinger, p. 178, Pl. 21, Figs. 2–7.
1906 *Eutritonium (Sassia) apenninicum* (Sassi) – Boettger, p. 39.
1956 *Charonia (Sassia) apenninica* Sassi – Csepreghy-Meznerics, p. 456, Pl. 4, Figs. 13–14.
1960 *Cymatium (Sassia) apenninicum* Sassi 1827 – Kojumdgieva & Strachimirov, p. 137, Pl. 37, Figs. 9–10.
1966 *Charonia (Sassia) apenninica* Sassi, 1827 – Strausz, p. 250, Pl. 30, Figs. 6, 10, 11, Pl. 31, Fig. 1.
1969 *Charonia (Sassia) apenninica* Sassi – Csepreghy-Meznerics, p. 24, Pl. 7, Figs. 12, 18.
1995 *Charonia (Sassia) apeninnica* (Sassi, 1827) – Baluk, p. 206, Pl. 18, Fig. 8.
2004 *Sassia apenninica* (Sassi, 1827) – Landau et al., p. 62, Pl. 5, Fig. 1, Pl. 10, Fig. 3, Text-Fig. 3.1 (cum syn.).
2008 *Sassia apenninica (Sasso* [sic], 1827) – Chirli & Richard, p. 33, Pl. 5, Fig. 7.
2008 *Sassia apenninica (Sasso* [sic], 1827) – Chirli, p. 99, Pl. 36, Figs. 1–11.

Material: Largest 41.7 mm. Vöslau (20), Möllersdorf (20), Sooß (21), Enzesfeld (4), Gainfarn (1), Steinabrunn (15), Traiskirchen (1), Walbersdorf (15), Lysice (= Lissitz) (5), Jaromierčic (= Jaroměřice) (10).

Description and Discussion: See Landau et al. (2004, p. 63).

Distribution (Paratethys; for complete distribution see Landau et al. [2004, p. 64]):
Middle Miocene Paratethys (Badenian): Poland: Korytnica (Baluk, 1995); Austria: Baden, Sooß, Vöslau, Möllersdorf, Steinabrunn, Enzesfeld, Gainfarn, Traiskirchen, Walbersdorf (Hörnes, 1853; Hoernes & Auinger, 1884); Czech Republic: Jaromierčic (= Jaroměřice), Porstendorf (= Borsov), Lissitz (= Lysice) (NHMW coll.); Hungary: Szob, Letkés (Csepreghy-Meznerics, 1956); Romania: Coşteiu de Sus (= Kostej) (Boettger, 1906), Bulgaria (Kojumdgieva & Strachimirov, 1960).

Sassia turrita **(Eichwald, 1830)**

(Pl. 6, Figs. 8–9; Pl. 7, Figs. 1–3)

1830 *Tritonium turritum* Eichwald, p. 225.
1840 *Triton Tarbellianum* Grateloup, Pl. 29, Figs. 11, 14.
1852 *Triton turritum* Eichwald, Pl. 8, Fig. 13.
1853 *Trit. turritum* Eichwald, p. 194.
1853 *Triton Tarbellianum* Grat. – Hörnes, p. 203, Pl. 20, Figs. 7–11.
1854 *Triton Tarbellianum* Grat. – Beyrich, p. 736.
1884 *Triton (b. Simpulum) Tarbellianum*. – Hoernes & Auinger, p. 173, Pl. 21, Figs. 8–11.
1902 *Triton (Simoulum) tarbellianus* Grat. – Boettger, p. 25.
1912 *Triton tarbellianum* Grat. – Friedberg, p. 129, Pl. 7, Figs. 4–5.
1914 *Tritonium (Lampusia) Tarbellianum* Grat. – Telegdi-Roth, p. 14, Pl. 1, Figs. 5–6.
1924 *Eutritoneum (Sassia) Tarbellianum* (Grateloup) – Cossmann & Peyrot, no. 821, Pl. 15, Figs. 40–41, Pl. 16, Figs. 26–27.
1925 *Tritonium (Sassia) Tarbellianum* Grat. – Kautsky, p. 90, Pl. 7, Fig. 15.
1944 *Charonia (Sassia) tarbelliana* (Grateloup) – Voorthuysen, p. 53, Pl. 6, Figs. 19–23, 32.
1952 *Cymatium (Sassia) tarbellianum* Grateloup, sp. 1840 – Glibert, p. 87, Pl. 7, Fig. 3.
1956 *Charonia (Sassia) tarbelliana* (Grat.) – Csepreghy-Meznerics, p. 456, Pl. 4, Figs. 11–12.
1957 *Charonia (Sassia) tarbelliana* (Grat.) – Sieber, p. 143.
1958 *Charonia (Sassia) tarbellianum* (Grateloup) – Erünal-Erentöz, p. 50, Pl. 7, Figs. 5–6.
1960 *Cymatium (Sassia) tarbellianum* (Grateloup 1840) – Kojumdgieva & Strachimirov, p. 138, Pl. 38, Fig. 1.
1963 *Charonia (Sassia) tarbelliana* Grateloup, sp. 1847 – Glibert, p. 123.
1964 *Charonia (Sassia) tarbelliana* (Grateloup, 1833 [sic]) – Anderson, p. 232, Pl. 21, Fig. 166.
1966 *Charonia (Sassia) tarbelliana* Grateloup, 1840 – Strausz, p. 249, Pl. 30, Figs. 7–8.
1968 *Cymatium tarbellianum* (Grateloup, 1840) – Zelinskaja, p. 184, Pl. 43, Figs. 13–14.
1969 *Charonia (Sassia) tarbelliana* (Grateloup 1833 [sic]) – Janssen, A., p. 175, Pl. 8, Figs. 9–10.
1973 *Charonia tarbelliana transiens* n. subsp. Baldi, p. 282, Pl. 35, Figs. 6–7.
1978 *Charonia (Sassia) tarbelliana* (Grateloup 1833 [sic]) – Janssen, R., p. 200, Pl. 14, Fig. 89.
1984 *Charonia (Sassia) tarbelliana* (Grateloup, 1840) – Janssen, A., p. 208, Pl. 58, Fig. 6.
1995 *Charonia (Sassia) tarbelliana* (Grateloup, 1847) – Baluk, p. 207, Pl. 20, Figs. 1–2.
1998 *Charonia (Sassia) tarbelliana* (Grateloup) – Schultz, p. 62, Pl. 24, Fig. 5.
2001 *Charonia (Sassia) tarbelliana* (Grateloup, 1833 [sic]) – Wienrich, p. 438, Pl. 70, Fig. 10, Pl. 90, Fig. 5.
2001 *Charonia (Sassia) tarbellianum* Grateloup – Tiţă, p. 548, Fig. 5d.

Material: Largest height 51.8 mm. Gainfarn (20+), Baden (2), Vöslau (4), Steinabrunn (22), Sooß (2), Traiskirchen (2), Lăpugiu de Sus (= Lapugy) (5).

Description: Shell medium-sized for genus, fusiform, very solid, with elevated spire. Protoconch dome-shaped, of 2.75 smooth, convex whorls, with small nucleus. Junction with teleoconch prosocline, sharply delimited. Teleoconch of seven or eight convex whorls. Suture impressed, undulating. First teleoconch whorl with sculpture of four very narrow spiral cords and 10 raised, rounded axial ribs, each wider than one interspace; axial sculpture overriding spiral cords. From second teleoconch whorl one prominent varix developed per whorl. Spire whorls weakly shouldered from third whorl, with wide, steep sutural ramp. Axial ribs crossing sutural ramp, forming small tubercle at shoulder angle and continuing widened to abapical suture. Abapically, whorls become regularly convex again, both primary spiral and axial sculpture become obsolete, or almost so on penultimate and last whorls; spiral cords only visible just anterior to varices. Surface covered by very fine, indistinct spiral threads and axial growth lines. Last whorl 58–69 % of total height, regularly rounded and constricted at base. Aperture ovate, 41–44 % of total height. Outer lip thickened by labral varix, convex, very slightly flared abapically, bearing seven pointed denticles within, most adapical two larger than those below. Columella concave, bearing irregular folds and tubercles along entire length and one modest parietal tooth. Parietal callus thin, sharply delimited, weakly expanded. Columellar callus slightly thickened, adherent. Siphonal canal long, narrow, abaxially recurved. Siphonal fasciole long, bearing numerous narrow spiral cords.

Variability: *Sassia turrita* (Eichwald, 1830) is easily recognised and is distinguished from its congeners by its tendency for the sculpture to become obsolete on the late teleoconch whorls. This is variable, with some specimens retaining vestiges of the spiral and axial sculpture on the last whorl, as well as a suggestion of two rows of tubercles at the periphery. Juvenile specimens are more strongly sculptured (Pl. 7, Fig. 3), which probably led BALUK (1995, p. 207) to comment that the subadult shells illustrated by A. JANSSEN (1984, Pl. 58, Fig. 6) from the Miocene North Sea Basin were not this species.

Discussion: The earliest name for this taxon, *Tritonium turritum* EICHWALD, 1830 seems to have been overlooked by subsequent authors. Although the shell was not figured by EICHWALD until 1852, there is a valid description of the shell in his earlier publication (EICHWALD, 1830, p. 225). It is unfortunate that the more established name *Triton tarbellianum* GRATELOUP, 1840 must be replaced, but there are insufficient grounds to argue for GRATELOUP's taxon to become a nomen protectum under ICZN Article 23.9.

Although variable, *Sassia turrita* is very distinctive and impossible to confuse with any of its congeners. It is also extremely widespread in the European Neogene, and is present in the North Sea Basin, Atlantic and Paratethys, but inexplicably absent from the Mediterranean assemblages. Several taxa have been described from the Lower Miocene of Italy and France for small *Sassia* species similar to *S. turrita*, but usually smaller and with even smoother sculpture; *Sassia laevigata* (DE SERRES, 1829) (COSSMANN & PEYROT, 1924, p. 282, Pl. 16, Figs. 32–33; they include *Triton obliquatum* BELLARDI & MICHELOTTI, 1840 in the synonymy) is a very distinctive, small, wide, almost smooth species, with weakly gemmate surface sculpture and a small smooth protoconch. *Sassia hissingeri* (GRATELOUP, 1840) is a very smooth *Sassia* species from the Lower Oligocene, Rupelian, of Gaas (France) very similar to *S. turrita*. We have not seen a specimen of this taxon to compare directly.

Distribution:

- Late Oligocene North Sea Basin (Chattian): Germany: Glimmerode, Rumeln, etc. (R. JANSSEN, 1978).
- Late Oligocene Paratethys (Egerian): Eger (TELEGDI-ROTH, 1914).
- Middle Miocene North Sea Basin: Netherlands (VOORTHUYSEN, 1944; GLIBERT, 1963; A. JANSSEN, 1984); Belgium (GLIBERT, 1952); Germany (KAUTSKY, 1925; ANDERSON, 1964; A. JANSSEN, 1969; WIENRICH, 2001).
- Middle Miocene Atlantic (Langhian): France: Saubrigues (COSSMANN & PEYROT, 1924).
- Middle Miocene Paratethys (Badenian): Poland: Dryszczów, Hołdy, Hołubica, Zborów, Žukowce, Stary Poczajów, Szuszkowce, Zapadnia, Korytnica (FRIEDBERG, 1912; BALUK, 1995); Austria: Gainfarn, Baden, Sooß, Vöslau, Möllersdorf, Gumpoldskirchen, Steinabrunn, Nikolsberg, Forchtenau, Traiskirchen (HÖRNES, 1853; HOERNES & AUINGER, 1884); Czech Republic: Mikulov (= Kienberg) (HOERNES & AUINGER, 1884); Hungary: Szob, Letkés (CSEPREGHY-MEZNERICS, 1956); Romania: Coşteiu de Sus (= Kostej) (BOETTGER, 1906), Bahna, southern Carpathians (TIŢĂ, 2001); Bulgaria (KOJUMDGIEVA & STRACHIMIROV, 1960).
- Middle Miocene Mediterranean (Langhian or Serravallian): Turkey: Lale Köy, Karaman Basin (ERÜNAL-ERENTÖZ, 1958).

Genus: *Cymatiella* IREDALE, 1924

The genus *Cymatiella* contains the smallest ranellids, few exceeding 20 mm in height, with a relatively tall, straight-sided spire and a short, rounded last whorl and short, open siphonal canal, simple sculpture of spiral and axial ridges, and a correspondingly small, smooth, turbiniform protoconch. This genus seems a suitable position for many of the small, generalised, relatively tall-spired species (BEU, in press).

Cymatiella tritonea (GRATELOUP, 1847)

(Pl. 7, Figs. 4–9; Pl. 10, Fig. 3)

1847 *Murex tritoneum* GRATELOUP, Pl. 29, Fig. 23.
1847 *Triton parvulum* MICHELOTTI, p. 249, Pl. 18, Fig. 10.
1853 *Triton parvulum* MICHELOTTI – HÖRNES, p. 208, Pl. 20, Fig. 12.
1884 *Triton (a. Sassia) parvulum* MICHTI. – HOERNES & AUINGER, p. 179, Pl. 21, Figs. 19–22.
1902 *Triton (Sassia) parvulus* MICHTI. – BOETTGER, p. 25.
1904 *Triton (Sassia) parvulum* MICHT. – SACCO, p. 38, Pl. 10, Figs. 21–22.
1912 *Triton parvulum* MICHT. – FRIEDBERG, p. 132, Pl. 7, Fig. 8.
1924 *Eutritoneum (Sassia) tritoneum* (GRATELOUP) – COSSMANN & PEYROT, no. 826, Pl. 15, Figs. 50–51, Pl. 16, Figs. 21–22.
1954 *Charonia (Sassia) parvula* (MICHT.) – CSEPREGHY-MEZNERICS, p. 34, Pl. 4, Fig. 15.
1960 *Cymatium (Sassia) parvulum* (MICHELOTTI 1847) – KOJUMDGIEVA & STRACHIMIROV, p. 137, Pl. 37, Fig. 11.
1966 *Charonia (Sassia) parvula* (MICHT.) – KÓKAY, p. 130, Pl. 7, Fig. 15.
1966 *Charonia (Sassia) parvula* MICHELOTTI, 1847 – STRAUSZ, p. 250, Pl. 30, Fig. 9.
1968 *Cymatium parvulum* (MICHELOTTI, 1847) – ZELINSKAJA, p. 183, Pl. 43, Figs. 11–12.
1986 *Sassia tritonea* (GRATELOUP, 1847) – LOZOUET, p. 367, Pl. 30, Fig. 7.
2001 *Cymatiella tritonea* (GRATELOUP, 1847) – LOZOUET et al., p. 46, Pl. 19, Fig. 2.
2002 *Sassia parvula* (MICHELOTTI, 1847) – HARZHAUSER, p. 92, Pl. 5, Fig. 17.

Material: Largest 14.1 mm. Lăpugiu de Sus (= Lapugy) (30+), Forchtenau (7).

Description: Shell very small for genus, fusiform, solid, with elevated spire. Protoconch dome-shaped, of 3.0–3.25 smooth, convex whorls, with small nucleus. Junction with teleoconch prosocline, sharply delimited. Teleoconch of five convex whorls. Suture impressed, undulating. First teleoconch whorl with sculpture of three narrow spiral cords and 10–11 raised, rounded axial ribs, each equal in width to one interspace. Axial sculpture overrides spiral cords, forming slightly thickened, horizontally elongate tubercles at intersections. From second teleoconch whorl one or two prominent varices are present per whorl. On third whorl, adapical primary cord becomes slightly further placed from lower two, and secondary spiral sculpture appears in interspaces. Last whorl 60–65 % of total height, with short, slightly concave sutural ramp, strongly rounded at periphery and weakly constricted at base. Surface sculpture reticulate, with seven or eight spiral cords and 13–15 axial ribs, ribs slightly more prominent than cords. Three to four secondary cords present in each spiral interspace between primary cords, interrupted in places by prominent axial growth lines. Aperture small, ovate, 40–42 % of total height. Outer lip thickened by labral varix, convex, bearing seven pointed denticles within, most adapical two larger than those below, second of which is most strongly developed. Columella concave, bearing one prominent parietal ridge and three or four well-developed folds in abapical portion. Parietal callus thin, poorly delimited, not expanded. Columellar callus slightly thickened, adherent. Siphonal canal short, narrow, slightly abaxially recurved. Siphonal fasciole short, poorly defined, bearing four or five spiral cords.

Variability: *Cymatiella tritonea* (GRATELOUP, 1847) has a highly variable little shell, not only in shape, which can be relatively tall and high-spired to squat with an inflated last whorl, but also in the character of the sculpture, especially the number and strength of the axial ribs. There are also differences between populations (see below).

Discussion: All authors have separated the Middle Miocene Mediterranean and Paratethyan populations under the name *Sassia parvula* (MICHELOTTI, 1847) from the Late Oligocene to Early Miocene French Atlantic populations known as *Sassia tritonea* (GRATELOUP, 1847). LANDAU et al. (2004, p. 65) suggested that the two may in fact represent a single taxon. We have now compared shells from the Early Miocene, Aquitanian of St-Martin-d'Oney, Landes, France (BL coll.) with shells from the Paratethys and see no reason to separate the two. Specimens from the Early Miocene, Lower Burdigalian of Peloua, Saucats, France (BL coll.) are a little different in having somewhat squatter shells, with a lower spire and a more inflated last whorl. They also have fewer axial ribs, which are stronger and the dorsum is somewhat gibbose. These are the differences which led COSSMANN & PEYROT (1924) to separate the two taxa, probably whilst examining shells from the classic locality of La Peloua. However, some Paratethyan shells also have fewer but stronger axial ribs (see HARZHAUSER, 2002, Pl. 5, Fig. 17) and the same applies to the Mediterranean populations (see SACCO, 1904, Pl. 10, Figs. 21–22).

It is not clear exactly when MICHELOTTI's work was published. However, the copy of GRATELOUP in the Institute of GNS Science, New Zealand has the foreword by GRATELOUP dated 31st December 1846, which would suggest the work was published early in 1847. Note also that SHERBORN (1930) accepted 1847 as the date of publication of the entire work. As a precise date is not known for MICHELOTTI's (1847) work, under ICZN Article 21.3.2 we take the date to be 31st December 1847. Therefore, *Triton parvulum* MICHELOTTI, 1847 is considered here a junior subjective synonym of *Murex tritoneum* GRATELOUP, 1847.

Distribution:
- Late Oligocene Atlantic (Chattian): France (LOZOUET, 1986).
- Early Miocene Atlantic (Aquitanian, Burdigalian): France (LOZOUET et al., 2001).
- Early Miocene proto-Mediterranean (Burdigalian): Italy: Turin Hills (SACCO, 1904).
- Early Miocene Paratethys (Karpatian): Austria: Niederkreuzstätten (HÖRNES, 1853; HOERNES & AUINGER, 1884; HARZHAUSER, 2002).
- Middle Miocene Paratethys (Badenian): Poland: Wołyn, Žukowce (FRIEDBERG, 1912); Austria: Forchtenau (NHMW coll.); Romania: Lăpugiu de Sus (= Lapugy), Coşteiu de Sus (= Kostej) (HOERNES & AUINGER, 1884; BOETTGER, 1902); Bulgaria (KOJUMDGIEVA & STRACHIMIROV, 1960).
- Late Miocene Mediterranean (Tortonian): Sant' Agata (BELLARDI, 1873).

4.4. Family Bursidae THIELE, 1925

Genus: *Bursa* RÖDING, 1798

Bursa scrobilator (LINNAEUS, 1758)

(Pl. 7, Figs. 10–11)

1758 *Murex scrobilator* LINNAEUS, p. 749.
1853 *Ranella scrobiculata* KIENER. – HÖRNES, p. 212, Pl. 21, Figs. 3–5.
1995 *Bursa (Bufonariella) nodosa* (BORSON, 1825) – BALUK, p. 210, Pl. 18, Figs. 4–5.
2004 *Bursa scrobilator* (LINNAEUS, 1758) – LANDAU et al., p. 66, Pl. 5, Figs. 3–5, Pl. 10, Fig. 1 (cum syn.).
2008 *Bursa scrobilator* (LINNÉ, 1758) – CHIRLI, p. 103, Pl. 37, Figs. 11–16, Pl. 38, Figs. 1–4.

Material: Largest 54.5 mm. Grund (4), Vöslau (1),

Description and Discussion: The Paratethyan shells are of the "nodosa form"; see LANDAU et al. (2004, p. 66).

Distribution (Paratethys; for complete distribution see LANDAU et al. [2004, p. 68]):
- Middle Miocene Paratethys (Badenian): Poland: Korytnica (BALUK, 1995); Austria: Grund, Baden, Forchtenau (HÖRNES, 1853).

Bursa ranelloides (REEVE, 1844)

(Pl. 8, Figs. 1–6; Pl. 10, Fig. 4)

1844a *Triton ranelloides* REEVE, Pl. 3, Fig. 10.
1844c *Triton ranelloides* REEVE, p. 111.
1870 *Simpulum papillosum* A. ADAMS, p. 49.
1884 *Ranella (Lampas) austriaca* HOERNES & AUINGER, p. 186, Pl. 23, Figs. 10–12.
1902 *Ranella (Lampas) papillosa* PUSCH – BOETTGER, p. 25.
1902 *Lotorium ranelloides* REEVE – G.B. SOWERBY III, p. 95.
1906 *Bursa (Lampas) ranelloides* var. *tenuisculpta* DAUTZENBERG & FISCHER, p. 36, Pl. 2, Figs. 15–18.
1960 *Bufonariella ranelloides* (REEVE) – OYAMA & TAKEMURA, Pl. *Colubrellina-Bufonariella*, Figs. 8–11.
1962 *Bufonariella ranelloides* (REEVE) – HABE, p. 47, Pl. 24, Fig. 3.
1962 *Bursa finlayi* MCGINTY, p. 39, Pl. 3, Fig. 2 (partim; holotype only).
1964 *Bufonariella ranelloides* (REEVE) – HABE, p. 76, Pl. 24, Fig. 3.
1971 *Bufonariella ranelloides* (REEVE) – KURODA et al., p. 203, Pl. 33, Figs. 5–6.
1971 *Bufonariella ranelloides* (REEVE, 1844) – BEU, p. 110, Pl. 8, Fig. 8.
1974 *Bursa (Colubrellina) tenuisculpta* (DAUTZENBERG and FISCHER, 1906) – ABBOTT, p. 166, Fig. 1778.
1975 *Bursa (Colubrinella)* (sic) *canarica* NORDSIECK, p. 4, Fig. 16.
1978 *Bursa (Colubrellina) benvegnuae* PENNA-NEME & LEME, p. 285, Figs. 25–26.
1978 *Bursa (Colubrellina) tenuisculpta* DAUTZENBERG & FISCHER – PENNA-NEME & LEME, p. 284, Figs. 1–10, 24, 27.
1979 *Bursa pygmaea* KOSUGE, p. 31, Pl. 5, Fig. 5; Pl. 6, Fig. 23.
1981 *Bursa (Bufonariella) ranelloides ranelloides* (REEVE, 1844) – BEU, p. 290, Figs. 18 d, f–i.
1981 *Bursa (Bufonariella) ranelloides tenuisculpta* DAUTZENBERG & FISCHER, 1906 – BEU, p. 292, Figs. 19 a–k.
1985 *Bursa (Colubrellina) ranelloides ranelloides* (REEVE, 1844) – BEU, p. 64.
1985 *Bursa (Colubrellina) ranelloides tenuisculpta* DAUTZENBERG & FISCHER, 1906 – BEU, p. 64.
1985 *Bursa (Colubrellina) ranelloides benvegnuae* PENNA-NEME & LEME, 1978 – RIOS, p. 79, Pl. 28, Fig. 348.
1985 *Bursa (Colubrellina) ranelloides tenuisculpta* DAUTZENBERG & FISCHER, 1906) – RIOS, p. 79, Pl. 28, Fig. 349.
1994 *Bursa (Colubrellina) ranelloides tenuisculpta* DAUTZENBERG & FISCHER, 1906) – RIOS, p. 92, Pl. 31, Fig. 366.
1994 *Bursa ranelloides tenuisculpta* (DAUTZENBERG & FISCHER) – PAULMIER, p. 9, Fig. 24.
1994 *Bursa (Colubrellina) ranelloides* (REEVE, 1844) and forms *tenuisculpta, benvegnuae* – COSSIGNANI, p. 86–87.
1995 *Bursa ranelloides benvegnuae* P. NEME & LEME, 1978 – COLTRO, p. 52, Fig. 4.
1998 *Bursa ranelloides* (REEVE, 1844) – BEU, Pl. 49, Figs. f–g.
2000 *Bursa (Tritonoranella) ranelloides* (REEVE, 1844) – OKUTANI, 2000: 269, Pl. 133, Fig. 3.
2001 *Bursa (Tritonoranella) ranelloides* (REEVE, 1844) – HIGO et al., Pl. 49, Fig. G1622.
2002 *Bursa ranelloides* (REEVE, 1844) – GOFAS & BEU, p. 102, Figs. 8A–J.
2004 *Bursa ranelloides* (REEVE, 1844) – ZHANG & MA, p. 180, Text-Fig. 112, Pl. 4, Fig. 8.
2004 *Bursa (Colubrellina) ranelloides tenuisculpta* DAUTZENBERG & FISCHER, 1906 – ARDOVINI & COSSIGNANI, p. 132, central right and lower left Figs.

Material: Largest 47.3 mm. Sooß (5).

Description: Shell thick, solid, fusiform, slightly anterodorsally compressed, of moderate size for genus, with elevated spire. Protoconch dome-shaped, of about three smooth, convex whorls, with small nucleus. Junction with teleoconch sharply delimited, prosocline. Teleoconch of five whorls, with periphery just above abapical suture on spire whorls. Suture superficial, undulating. Sculpture on first teleoconch whorl of two spiral cords with small sharp tubercles. Half a whorl later, two secondary cords with smaller tubercles appear in each interspace. From second whorl, adapical primary cord situated just below upper suture and abapical cord situated a short distance above lower suture; lower cord developing more prominent, pointed tubercles, which form periphery of spire whorls. Surface with secondary reticulate sculpture, formed by extremely fine, elevated riblets and spiral threads of equal strength. On first three to four teleoconch whorls, the varices are aligned directly above each other and continuous, and are positioned at the peripheries. Adapically varix on subsequent whorls becomes staggered and slightly in front of that on preceding whorl. Last whorl 70–72 % of total height, angularly convex in profile, strongly constricted at base. Sculpture of two rows of 10–12 sharp pointed tubercles, situated above and below mid-whorl, with one row of secondary tubercles above shoulder, one row of tertiary tubercles between two primary rows, and alternating rows of secondary and tertiary tubercles below. Aperture ovate, 46–48 % of total height. Outer lip convex, thickened by prominent labral varix, slightly flared in abapical portion, with nine denticles within. Denticles simple, more strongly developed on flared abapical portion. Anal canal deep, narrow, extending adapically to outer edge of labral varix. Siphonal canal relatively short, narrow, slightly adaxially recurved. Columella weakly excavated, with numerous irregular ridges and tubercles along its entire length. Parietal callus weakly thickened, sharply delimited. Columellar callus more strongly thickened, adherent. Siphonal fasciole short, bearing about five beaded cords.

Variability: Paratethyan shells of *Bursa ranelloides* (REEVE, 1844) are characterised by sharp pointed tubercles and very fine secondary reticulate sculpture, which covers the entire shell surface. The type lot of *Ranella austriaca* consists of five shells from Sooß. Three of them are almost identical, conforming to the description given above. The fourth (illustrated by HOERNES & AUINGER, 1884, Pl. 23, Fig. 12) (Pl. 8, Fig. 3) is somewhat more elongate, with more rounded, close-set tubercles. However, the sculpture of the early whorls is the same, and the surface is covered in the characteristic secondary sculpture described above.

Discussion: HOERNES & AUINGER (1884, p. 186) placed part of HÖRNES's *Ranella scrobiculata* (1853, Pl. 21, Figs. 3–5) in their chresonomy of *R. austriaca*. However, the specimens illustrated by HÖRNES are indeed *Bursa scrobilator* (LINNAEUS, 1758).

Several bursid taxa described from the European Neogene need to be discussed and compared. *Ranella tuberosa* BONELLI from the Burdigalian of the Turin Hills in Italy was illustrated by BELLARDI (1873) and SACCO (1904). Unfortuntely, BONELLI's name is a manuscript name (see FERRERO MORTARA, 1981; LOZOUET et al., 2001). LOZOUET et al. (2001, p. 46) therefore reintroduced the name *Ranella tuberosa* GRATELOUP, 1833 for the French Atlantic Late Oligocene and Early–Middle Miocene taxon named *R. subtuberosa* by D'ORBIGNY, 1852 and *Apollon pelouatensis* by COSSMANN & PEYROT, 1924, both of these chresons thus becoming junior synonyms. Unfortunately, we have not seen any of the Turin material, and most of the specimens are poorly preserved. One shell illustrated by SACCO (1904, Pl. 11, Fig. 8) as variety *spinulosa* MICHELOTTI, 1847 is very similar to the Paratethyan shells known under the name *B. austriaca* in having two rows of sharply pointed tubercles on the last whorl, although there seem to be fewer tubercles in each row. This shell is quite unlike the shell illustrated as *R. tuberosa* by BELLARDI (1873, Pl. 15, Fig. 7), which is probably conspecific with *Ranella tuberosa* GRATELOUP, 1833 (see below). We have insufficient material clearly to define what is meant by *R. tuberosa* BONELLI, or to conclude how many taxa are present in the Early Miocene Turin material, however, it is likely that some of the forms are conspecific with *B. austriaca*.

Ranella tuberosa GRATELOUP, 1833 [= *R. subtuberosa* d'ORBIGNY, 1852; = *Apollon pelouatensis* COSSMANN & PEYROT, 1924 (see LOZOUET et al., 2001)] from the Atlantic Late Oligocene to Early–Middle Miocene of France is of similar size to *B. austriaca*, but is immediately distinguished by its broad rounded tubercles and strongly papillate fine surface sculpture. It is much closer to the Paratethyan shells known as *Ranella papillosa* PUSCH, 1837 (see below).

None of the researchers working with the fossil assemblages seem to have compared the fossil *B. austriaca* with extant taxa. The Austrian shells cannot be distinguished from the Recent species *Bursa ranelloides* (REEVE, 1844). The shell of *B. ranelloides* can be somewhat variable, with more or less nodulose specimens and populations present (see COSSIGNANI, 1994, p. 86–87; BEU, in press). The Austrian material has a higher proportion of coarsely nodulose specimens than in most modern population, other than the shallow-water population in southern Japan, which might reflect their living in quite shallow waters. Unfortunately, no data on the Austrian paleoenvironment are available. At the Baden-Sooß section nearshore taxa have been transported into deeper basinal settings and it is impossible to separate the specimens in the historical collections according to their paleoenvironment. Most modern specimens of *B. ranelloides* are collected from relatively deep waters (100–400 m, and more). As a general rule, with all bursids and ranellids the spire increases in height, the colour fades away, and the sculpture becomes weaker/finer, progressively as the species goes out into increasingly deep water. With no consistent morphological features to separate the fossil and Recent shells, we consider *Ranella (Lampas) austriaca* HOERNES & AUINGER, 1884 a junior subjective synonym of *Bursa ranelloides* (REEVE, 1844), which originally was based on Recent specimens.

Bursa inaequicrenata (COSSMANN & PEYROT, 1924) from the Atlantic Burdigalian of France is a species with a larger, higher-spired shell, in which the whorls are more angular due to the much greater development of the adapical row of tubercles. The sutural ramp in the French species is narrower and distinctly concave as opposed to broad, steeply sloping and weakly convex in *B. ranelloides*. The sculpture on the first teleoconch whorl is also quite different, consisting of five beaded cords, of which the second most abapical cord is already more strongly developed on the first whorl and forms the periphery. The fine surface sculpture in *B. inaequicrenata* is papillate rather than cancellate as seen in *B. ranelloides*.

This synonymy has interesting palaeobiogeographical implications for the species. Along with the Burdigalian records from Italy, these Langhian Paratethyan records are now the earliest for the species, together with a single record for the Middle Miocene of Trinidad in the Caribbean (BEU, in press). There are a few western Atlantic Pliocene records and it is known from the Pliocene and Pleistocene of Japan (OGASAWARA, 2002). Today the species is widespread (see below under distribution), although no fossil or Recent material is recorded from the eastern Pacific. This suggests a possible Tethyan or Paratethyan origin for the species.

Distribution:

- Early Miocene (Burdigalian): Italy: Turin Hills (Sacco, 1904).
- Middle Miocene Paratethys (Badenian): Austria: Sooß (Hoernes & Auinger, 1884); Romania: Coşteiu de Sus (= Kostej) (Boettger, 1902).
- Middle Miocene western Atlantic: Trinity Hill Sandstone member of Moruga Formation, Trinidad (Beu, in press).
- Pliocene western Atlantic: Panama: Cayo Agua Formation, Bocas del Toro Basin (Beu, in press); Pliocene Pacific: Japan: Shinzato Formation of Okinawa (Ogasawara, 2002).
- Pleistocene, Italy: Details to add from Beu (in press); material in collection of Paolo Crovato, Naples.
- Middle Pleistocene Pacific: Japan: Ryukyu Limestone of Kikaijima, Ryukyu Islands (Ogasawara, 2002).
- Recent: western Atlantic: Bermuda and southern Florida south to "northeast Brazil" (Rios, 1994), West Indies (Paulmier, 1994); mid and eastern Atlantic: Azores (Gofas & Beu, 2002); Madeira and the Cape Verde Islands (Beu, in press); South Africa: Natal (G.B. Sowerby III, 1902), northeastwards into the western Indian Ocean (Beu, in press); Indian Ocean: Réunion Island (Beu, 1998); Japan: Boso Peninsula southwards (Kuroda et al., 1971; Okutani, 2000); for more detailed Recent distribution see Beu (in press).

Bursa corrugata (Perry, 1811)

(Pl. 8, Figs. 7–10; Pl. 10, Fig. 5)

1811 *Biplex corrugata* Perry, Pl. 5, Fig. 1.
1822 *Ranella semigranosa* Lamarck, p. 153.
1833 *Ranella caelata* Broderip, p. 179.
1835 *Ranella caelata* Brod. – G.B. Sowerby II, Pl. 85, Fig. 8.
1837 *Ranella papillosa* Pusch, p. 139, Pl. 12, Fig. 7.
1841 *Ranella semigranosa* Lam. – Kiener, p. 19, Pl. 11, Fig. 2.
1844b *Ranella ponderosa* Reeve, Pl. 3, Fig. 10.
1844b *Ranella pustulosa* Reeve, Pl. 3, Fig. 11.
1844b *Ranella caelata* – Reeve, Pl. 3, Fig. 10.
1860 *Ranella (Apollon) caelata* – Mörch, p. 81.
1873 *Ranella Lessonae* Bellardi, p. 240, Pl. 15, Fig. 10.
1884 *Ranella (Lampas) papillosa* Pusch – Hoernes & Auinger, p. 188, Pl. 23, Figs. 6–9.
1912 *Ranella papillosa* Pusch – Friedberg, p. 126, Pl. 7, Fig. 2.
1924 *Apollon Lessonae* [Bellardi] race *occidentalis* Cossmann & Peyrot, no. 844, Pl. 16, Figs. 16–17.
1942 *Bursa pustulosa* var. *jabik* Fischer-Piette, p. 216.
1948 *Bursa caelata louisa* M. Smith, p. 28, Pl. 9, Fig. 4.
1954 *Bursa (Colubrellina) corrugata* Perry – Abbott, p. 198, Pl. 9k.
1958 *Bursa (Colubrellina) corrugata* Perry 1811 – Abbott, p. 60, Pl. 1i, Text-Fig. 2.
1960 *Bursa (Lampasopsis) papillosa* (Pusch 1837) – Kojumdgieva & Strachimirov, p. 141, Pl. 38, Fig. 10.
1962 *Bursa (Colubrellina) corrugata* Perry, 1811 – Warmke & Abbott, 103, Pl. 18m.
1963 *Bursa mexicana* Perrilliat, p. 19, Pl. 4, Figs. 18–19.
1968 *Bursa papillosa* (Pusch, 1837) – Zelinskaja, p. 184, Pl. 43, Figs. 15–16.
1970 *Bursa corrugata* Perry, 1811 – Kaufmann & Götting, p. 372, Fig. 88.
1971 *Bursa (Colubrellina) corrugata* (Perry, 1811) – Coelho & Matthews, p. 51, Figs. 9–10.
1971 *Bursa caelata* (Broderip, 1833) – Keen , p. 508, Fig. 964.
1974 *Bursa corrugata* (Perry, 1811) – Abbott, p. 167, Pl. 7, Fig. 1780 (as *B. caelata* in Pl. caption).
1975 *Bursa (Colubrellina) corrugata* (Perry, 1811) – Rosewater, p. 18, Fig. 8.
1975 *Bursa corrugata* (Perry, 1811) – Rios, p. 81, Pl. 22, Fig. 330.
1977 *Bursa pustulosa* Reeve, 1844 – Burnay & Monteiro, p. 34, Fig. 27.
1983 *Bursa (Colubrellina) corrugata* (Perry, 1811) – H. & E. Vokes, p. 23, Pl. 11, Fig. 13.
1984 *Bursa corrugata* (Perry, 1811) – Bernard, p. 64, Fig. 102.
1985 *Bursa (Colubrellina) corrugata* (Perry, 1811) – Rios, p. 79, Pl. 28, Fig. 345.
1985 *Bursa (Colubrellina) corrugata corrugata* (Perry, 1811) – Beu, p. 64.
1985 *Bursa (Colubrellina) corrugata ponderosa* (Reeve, 1844) – Beu, p. 64.
1985 *Bursa (Colubrellina) corrugata pustulosa* (Reeve, 1844) – Beu, p. 64.
1994 *Bursa (Colubrellina) corrugata corrugata* (Perry, 1811) – Cossignani, p. 69.
1994 *Bursa (Colubrellina) corrugata ponderosa* (Reeve, 1844) – Cossignani, p. 70.
1994 *Bursa (Colubrellina) corrugata pustulosa* (Reeve, 1844) – Cossignani, p. 71–72.
1994 *Bursa (Colubrellina) corrugata ponderosa* (Reeve, 1844) – Rios, p. 92, Pl. 31, Fig. 363.
1994 *Bursa corrugata* (Perry) – Paulmier, p. 9, Fig. 22.
1994 *Bursa corrugata* (Perry, 1811) – Diaz & Puyana, p. 174, Fig. 649.
1995 *Bursa (Bursa) papillosa* (Pusch, 1837) – Baluk, p. 209, Pl. 18, Figs. 1–3.
1999 *Bursa corrugata corrugata* (Perry, 1811) – Hickman & Finet, p. 73, Fig. 66.
2000 *Bursa (Bursa) corrugata pustulosa* Reeve, 1844 – Guerreiro & Reiner, p. 118–119.
2001 *Bursa (Colubrellina) corrugata ponderosa* (Reeve, 1844) – Redfern, p. 57, Pl. 29, Fig. 246A–B.
2001 ?*Bursa (Colubrellina)* cf. *B. (C.) corrugata* (Perry, 1811) – Macsotay & Campos Villarroel, p. 70.
2001 *Bursa (Colubrellina) granularis cubaniana* (d'Orbigny, 1842) – Macsotay & Campos Villarroel, p. 70, Pl. 13, Fig. 5 (non *Bursa granularis* Röding, 1798).
2004 *Bursa corrugata pustulosa* (Reeve, 1844) – Ardovini & Cossignani, p. 132, upper right Fig. and central left 2 Figs.
2007 *Bursa (Colubrellina) corrugata corrugata* (Perry, 1811) – Kaiser, p. 39, Pl. 26, Fig. 6a–b.
non 1960 *Colubrellina corrugata* (Perry) – Oyama & Takemura, Pl. *Colubrellina-Bufonariella*, Figs. 1–2 [*Bursa granularis* (Röding, 1798)].

Material: Largest 45.4 mm. Lăpugiu de Sus (= Lapugy) (28), Vöslau (1).

Description: Shell thick, solid, fusiform, slightly anterodorsally compressed, of moderate size for genus, with elevated spire. Protoconch dome-shaped, of 3.5 smooth, convex whorls, with small nucleus. Junction with teleoconch sharply delimited, prosocline. Teleoconch of 4–5 whorls, with periphery just above abapical suture on spire whorls. Suture superficial, undulating. Sculpture on early teleoconch whorls highly irregular, with narrow inconspicuous spiral cords and broad undulating axial ribs; two ribs descend from suture and fuse at periphery into one tubercle, then continue to lower suture as one broader rib on many specimens. On third teleoconch whorl 10 stout rounded tubercles present at periphery, with slightly more numerous smaller tubercles below adapical suture. Entire surface covered with small rounded papillae. On first three to four teleoconch whorls, the varices are aligned directly above each other and continuous, and are positioned at the peripheries. Adapically varix on subsequent whorls becomes staggered and is situated slightly in front of that on preceding whorl. Last whorl approximately 73 % of total height, angularly convex in profile, strongly constricted at base. Sculpture of one row of small tubercles immediately below adapical suture, one row of fewer, stronger tubercles at periphery, third row of smaller tubercles at height of anal canal, and two further rows of alternating strength below. Aperture ovate, approximately 46 % of total height, outer lip convex, thickened by prominent labral varix, denticulate within. In fully thickened specimens denticles arranged in two rows, parallel to outer margin of lip, i. e., one exterior to the other, with narrow, smooth area between rows. Denticles simple, subequal in strength, except for one more prominent, adapical denticle delimiting lateral border of anal canal. Anal canal relatively deep, narrow, extending adapically almost to outer edge of labral varix. Siphonal canal relatively short, narrow, slightly adaxially recurved. Columella almost straight, with numerous irregular ridges and tubercles along its entire length. Parietal callus weakly thickened, sharply delimited in most specimens. Columellar callus more strongly thickened, adherent. Siphonal fasciole short, bearing about nine beaded cords.

Variability: The Paratethyan specimens, originally described as *Bursa papillosa* (PUSCH, 1837), are characterised by their rounded tubercles, three primary rows of tubercles on the last whorl, with a single row of secondary tubercles intercalated, and very fine secondary papillate sculpture, which covers the entire shell surface. The shoulder row of tubercles is more strongly developed, but less distinctly so than in other European Neogene congeners. BALUK (1995) noted that his specimens from Korytnica were not particularly variable and we agree with this observation based on the series from Lăpugiu de Sus.

Discussion: *Bursa papillosa* (PUSCH, 1837) [= *Bursa corrugata* (PERRY, 1811)] is easily distinguished from *Bursa austriaca* (HOERNES & AUINGER, 1884) [= *Bursa ranelloides* (REEVE, 1844)] in the character of the tubercles on the last whorl; rounded in *B. papillosa,* pointed in *B. austriaca. Bursa papillosa*, as the name suggests, has its entire surface covered in papules, or pustules, whereas the secondary sculpture in *B. austriaca* is finely reticulate.

Once again, none of these fossil taxa have been compared to Recent bursids. There is no discernable difference between the fossil shells described as *Ranella papillosa* and the Recent taxon *Bursa corrugata* (PERRY, 1811). We therefore consider *Ranella papillosa* to be a junior subjective synonym of *Bursa corrugata* (PERRY, 1811).

We have not been able to see any of the material from the Burdigalian of Turin described by BELLARDI (1873) as *Ranella lessonae*, where this species is apparently extremely rare (BELLARDI, 1873, p. 240), but we have directly compared the Paratethyan shells with specimens from Le Peloua, France, type locality for *Apollon lessonae* race *occidentalis* COSSMANN & PEYROT, 1924, and we can see no consistent difference between the two populations. We therefore consider *Ranella lessonae* BELLARDI, 1873 and *Apollon lessonae* race *occidentalis* COSSMANN & PEYROT, 1924 both to be further junior subjective synonyms of *Bursa corrugata* (PERRY, 1811).

Ranella tuberosa GRATELOUP, 1833 [= *R. subtuberosa* D'ORBIGNY, 1852; = *Apollon pelouatensis* by COSSMANN & PEYROT, 1924; see LOZOUET et al., 2001] from the Atlantic Late Oligocene to Early-Middle Miocene of France is of similar size to *B. corrugata*, but differs in having tubercles clearly developed only at the shoulder on the last whorl, the tubercles being stronger and less numerous than in *B. corrugata* (6–7 in *B. tuberosa* vs. 9–11 in *B. corrugata*). In fully mature specimens of *B. tuberosa* the dorsal tubercles on the last whorl are even further developed giving the dorsum a somewhat humped appearance. The last whorl in *B. tuberosa* is broader than in *B. corrugata*, the aperture is slightly smaller and the siphonal canal shorter, but bordered laterally by a more developed, broader and more rounded siphonal fasciole. The specimen illustrated by BELLARDI (1873, Pl. 15, Fig. 7) as *Ranella tuberosa* BONELLI also shows only the shoulder tubercles clearly developed and is probably conspecific. The specimens figured by JANSSEN (1969, Pl. 8, Fig. 11) as *Bursa (Lampasopsis) austriaca* (HOERNES & AUINGER 1884) and JANSSEN (1982, Pl. 58, Fig. 11) as *Bursa (Bufonariella) pelouatensis* (COSSMANN & PEYROT, 1923 [sic]) from the Middle Miocene North Sea Basin also seem to be *B. tuberosa*.

Bursa inaequicrenata (COSSMANN & PEYROT, 1924) from the Atlantic Early–Middle Miocene of France is a larger species, with the shoulder tubercles more strongly developed and pointed rather than rounded, and does not have sculpture of alternating primary and secondary rows of tubercles on the last whorl as seen in *B. corrugata*. It is not, therefore, a synonym of *B. corrugata* as suggested by BALUK (1995, p. 209).

As with the previous species, this revision has profound implications for the palaeobiogeography of the species. These Tethyan and Paratethyan Early–Middle Miocene records are now the earliest for the species. Specimens recorded from Miocene and Pliocene localities in the western Pacific as *Bursa corrugata* (e. g., VAN REGTEREN ALTENA, 1942, p. 107: Kendeng beds of Java, Pliocene) have been examined in the RGM, and are all based on *B. granularis*. There are no authentic fossil or Recent records of *B. corrugata* from the Indo-West Pacific region. Records exist for the Middle Pliocene western Atlantic from Mexico (PERRILLIAT, 1963; BEU, in press) and Pliocene and Pleistocene records for the eastern Pacific of Ecuador and Galápagos Islands (BEU, in press). Today the species has a widespread distribution including the tropical eastern Atlantic (NORDSIECK & GARCIA-TALAVERA, 1979), mid and western Atlantic (ROSEWATER, 1975; ABBOTT, 1974) and eastern Pacific (KEEN, 1971).

These occurrences suggest that both *Bursa corrugata* and *B. ranelloides* had their origins in the Tethys and Paratethys seaways along with some *Monoplex* species such as *M. corrugatus* as already demonstrated for other invertebrates by HARZHAUSER et al. (2007b) (see also maps in RÖGL [1998]).

Distribution:

- Early Miocene Atlantic (Burdigalian): France: Aquitaine Basin (COSSMANN & PEYROT, 1924).
- Early Miocene proto-Mediterranean (Burdigalian): Italy: Termo-fourà, Turin Hills (BELLARDI, 1873).
- Middle Miocene Paratethys (Badenian): Poland: Korytnica (FRIEDBERG, 1912; BALUK, 1995); Austria: Vöslau (NHMW coll.); Romania: Lăpugiu de Sus (= Lapugy) (HOERNES & AUINGER, 1884); Bulgaria (KOJUMDGIEVA & STRACHIMIROV, 1960).
- Middle Pliocene western Atlantic: Mexico: Agueguexquite Formation (PERRILLIAT, 1963; BEU, in press).
- Pliocene–Pleistocene Pacific: Galápagos Islands (BEU, in press).
- Pleistocene eastern Pacific: Ecuador (BEU, in press).
- Pleistocene Mediterranean: southern Italy: Tyrrhenian conglomerate, Reggio Calabria (BEU, in press).
- Holocene western Atlantic: Cubagua Island: Tortuga Formation, Las Calderas Canyon (BL coll.).
- Recent: tropical eastern Atlantic: Canary Islands (NORDSIECK & GARCIA-TALAVERA, 1979) and Mauretania to at least as far south as Gabon (BERNARD, 1984) and Angola (GOFAS et al., 1984, as *B. pustulosa*); mid Atlantic: St. Helena and Ascension Island (ROSEWATER, 1975); western Atlantic: Florida and the Bahamas to northern Brazil (ABBOTT, 1974); eastern Pacific: Panamic western America, from Sonora to northern Peru (KEEN, 1971), Galápagos Islands (HICKMAN & FINET, 1999); for more detailed Recent distribution see BEU, in press.

Genus: *Aspa* H. & A. ADAMS, 1853

***Aspa marginata* (GMELIN, 1791)**

(Pl. 9, Figs. 1–2)

1791 *Buccinum marginatum* GMELIN, 1791, p. 3486.

1853 *Ranella marginata* BRONG. – HÖRNES, p. 214, Pl. 21, Figs. 7–11.

1884 *Ranella (Aspa) marginata* MARTINI sp. – HOERNES & AUINGER, p. 190, Pl. 24, Figs. 1–2.

1896 *Ranella (Aspa) marginata* MART. – BOETTGER, p. 58.

1912 *Ranella marginata* MART. – FRIEDBERG, p. 125, Pl. 7, Fig. 1.

1954 *Bursa (Aspa) depressa* (GRATELOUP) – CSEPREGHY-MEZNERICS, p. 34, Pl. 4, Figs. 4, 8.

1960 *Aspa (Aspa) marginata* (MARTINI 1777) – KOJUMDGIEVA & STRACHIMIROV, p. 142, Pl. 38, Figs. 8–9.

1966 *Bursa (Aspa) marginata depressa* GRATELOUP, 1840 – STRAUSZ, p. 250, Pl. 29, Figs. 5–6, Pl. 63, Figs. 14–18.

1968 *Aspa marginata* (MARTINI, 1777) – ZELINSKAJA, p. 184, Pl. 43, Figs. 17–18.

1973 *Gyrineum (Aspa) marginatum* (BRONGNIART 1823) – STEININGER, p. 416, Pl. 6, Fig. 1.

1985 *Gyrineum (Aspa) marginatum* (MARTINI, 1777) – ATANACKOVÍC, 137, Pl. 30, Figs. 19–20.

1995 *Gyrineum (Aspa) marginatum* (MARTINI, 1777) – BALUK, p. 210, Pl. 18, Figs. 6–7.

1996 *Gyrineum (Aspa) marginatum* (MARTINI) – BALUK & RADWAŃSKI, Pl. 2, Figs. 7–8, Pl. 5, Figs. 1, 4, Pl. 7, Fig. 2.

1998 *Gyrineum (Aspa) marginatum* (BRONGNIART) – SCHULTZ, p. 62, Pl. 24, Fig. 6.

2004 *Bufonaria (Aspa) marginata* (GMELIN, 1791) – LANDAU et al., p. 69, Pl. 5, Figs. 6–7, Pl. 10, Fig. 2 (cum syn.).

2008 *Bufonaria marginata* (GMELIN in L., 1791) – CHIRLI & RICHARD, p. 33, Pl. 5, Fig. 8.

2008 *Bufonaria marginata* (GMELIN in LINNÉ, 1791) – CHIRLI, p. 105, Pl. 38, Figs. 5–16.

Material: Largest height 54.3 mm. Grund (5), Baden (20+), Vöslau (20+), Forchtenau (16), Sooß (11), Gainfarn (20+), Niederleis (14), Braunsdorf (15), Guntersdorf (10), Immensdorf (5), Steinabrunn (5), Lăpugiu de Sus (= Lapugy) (21), Coşteiu de Sus (= Kostej) (5).

Description: See LANDAU et al. (2004, p. 70).

Discussion: We follow BEU (in press) in ranking *Aspa* H. & A. ADAMS, 1853 at genus level (for discussion see BEU, in press).

As discussed in LANDAU et al. (2004, p. 70), we consider the Middle Miocene to Recent populations to represent a single species, *Aspa marginata* (GMELIN, 1791), forming part of an evolutionary lineage with *Aspa subgranulata* (D'ORBIGNY, 1852) ancestral to it. However, unlike the *M. subcorrugatus-corrugatus* lineage, in which intermediate forms exist in the Paratethys suggesting that the transition between the two forms may have occurred within the Paratethys, the Paratethyan specimens of *Aspa marginata* are clearly of the Pliocene–Recent form. This is the commonest tonnoidean found in the Paratethyan assemblages, where it can be present in considerable numbers and attains a great size.

Distribution (Paratethys; for complete distribution see LANDAU et al. [2004, p. 71]):

- Early Miocene Paratethys (Ottnangian): Germany: Kaltenbachgraben in Bavaria (STEININGER, 1973).
- Early Miocene Paratethys (Karpatian): Austria: Laa an der Thaya (HARZHAUSER [2004] as *Gyrineum depressum* GRATELOUP).
- Middle Miocene Paratethys (Badenian): Poland: Korytnica, Biaɫogon (Friedberg, 1912; BALUK, 1995; BALUK & RADWAŃSKI, 1996); Austria: Grund, Baden, Vöslau, Steinabrunn, Forchtenau, Sooß (HÖRNES, 1853); Bosnia: HRVAĆANI (ATANACKOVÍC, 1985); Romania: Lăpugiu de Sus (= Lapugy), Coşteiu de Sus (= Kostej) (HOERNES & AUINGER, 1884); Bulgaria (KOJUMDGIEVA & STRACHIMIROV, 1960).

4.5. Family Personidae J.E. GRAY, 1854

Genus: *Distorsio* RÖDING, 1798

***Distorsio cancellina* (LAMARCK, 1803)**

(Pl. 9, Figs. 3–4)

1803 *Murex cancellinus* LAMARCK, p. 225.

1884 *Triton (a. Distorsio = Persona) tortuosum* BORS. – HOERNES & AUINGER, p. 183, Pl. 22, Figs. 11–13.

1906 *Eutritonium (Distorsio) tortuosum* (BROCC.) – BOETTGER, p. 39.

2004 *Distorsio cancellina* (LAMARCK, 1803) – LANDAU et al., p. 71, Pl. 6, Figs. 1–3 (cum syn.).

2008 *Distorsio tortuosa* (BORSON, 1821) – CHIRLI, p. 102, Pl. 37, Figs. 4–10.

Material: Largest height 65.2 mm. Lăpugiu de Sus (= Lapugy) (5), Coşteiu de Sus (= Kostej) (1), Niederleis (1), Forchtenau (4).

Description and Discussion: See LANDAU et al. (2004, p. 72).

Distribution (Paratethys; for complete distribution see LANDAU et al. [2004, p. 74]):

- Middle Miocene Paratethys (Badenian): Austria: Forchtenau (HOERNES & AUINGER, 1884); Romania: Lăpugiu de Sus (= Lapugy) (21), Coşteiu de Sus (= Kostej) (BOETTGER, 1906).

Genus: *Personopsis* BEU, 1988

***Personopsis grasi* (D'ANCONA, 1872)**

(Pl. 9, Figs. 5–7)

1884 *Triton (b. Distorsio = Persona) Grasi* BELL. – HOERNES & AUINGER, p. 184, Pl. 22, Figs. 14–16.

2004 *Personopsis grasi* (BELLARDI in D'ANCONA, 1873) – LANDAU et al., p. 74, Pl. 6, Figs. 5–6 (cum syn.).

Material: Largest height 23.5 mm. Lăpugiu de Sus (= Lapugy) (6), Forchtenau (2).

Description: See LANDAU et al. (2004, p. 74).

Discussion: Although we have identified the fossil Paratethyan and Recent shells as the Italian Pliocene fossil *Personopsis grasi* (D'ANCONA, 1872), there are some differences between the three groups; the Recent specimens tend to be shorter and wider than the Pliocene shells and have less prominent spiral sculpture (see BEU, 1998, Figs. 67i–k). The Paratethyan shells appear smaller and narrower than either the Recent or Italian Pliocene shells and slightly more finely sculptured. Unfortunately, only a few specimens of each group are available to us, but morphometric measurements of height/width and height last whorl/width overlapped in all three groups.

These slight differences, which seem confined to the overall shape of the shell, are possibly habitat-dependent; the Recent specimens have all been found in relatively deep waters (275–480 m [GOFAS & BEU, 2002]). SPADINI (1994, p. 285) suggested that *D. tortuosa* [= *D. cancellina* (LAMARCK, 1803)] and *P. grasi* lived in different habitats, the former present in the upper levels of infralittoral and circalittoral environments, whereas the latter was a bathyal species. In Estepona, however, *P. grasi* has not been found in the deeper-water deposits and both species are found together in the Velerín conglomerates and El Lobillo deposits, which we consider represent infralittoral and circalittoral habitats (LANDAU et al., 2004). These bathymetric differences, at least in some groups such as the Bursidae, result in important changes in shell morphology (see under *Bursa ranelloides* (REEVE, 1844)). In the Paratethys, both species seem to co-occur and derive from basinal clays for which a water depth of 50–200 m may be expected (RÖGL et al., 2008). However, as already discussed for *Bursa ranelloides*, it is impossible to affiliate the shells from the historical collections with any particular paleoenvironment.

For further discussion on *P. grasi* see LANDAU et al. (2004, p. 74); illustrations of extant specimens will be presented in BEU (in press).

Distribution (Paratethys; for complete distribution see LANDAU et al. [2004, p. 75]):

- Middle Miocene Paratethys (Badenian): Austria: Forchtenau (HOERNES & AUINGER, 1884); Romania: Lăpugiu de Sus (= Lapugy).

5. Distribution of Species in Paratethyan Assemblages

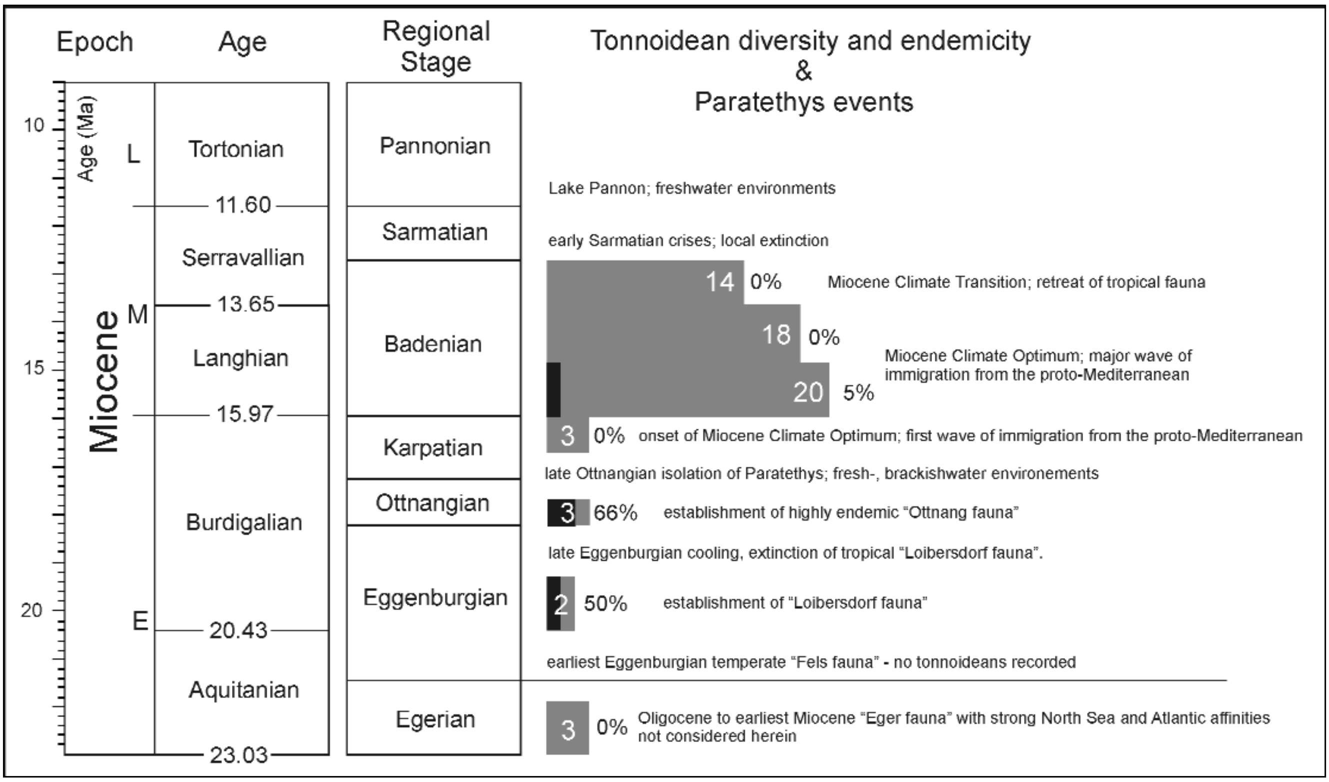
5.1. Diversity versus Stratigraphy

The described tonnoidean gastropods display a distinct pattern of distribution in terms of stratigraphy as well as from the viewpoint of paleogeography (Fig. 1). The Early Miocene gastropod assemblages contain only a few tonnoideans. The Eggenburgian Loibersdorf fauna yields two species of which *Semicassis subsulcosa* (HOERNES & AUINGER, 1884) seems to be endemic to the Paratethys. The origin of this species remains enigmatic. Thereafter, the tonnoideans seemingly retreat from the Paratethys during the late Eggenburgian. This might be related to a slight cooling which led to a faunal turnover (MANDIC & STEININGER, 2003). The still temperate early Ottnangian is characterised by low diversity and a largely endemic tonnoidean fauna, with three species. The endemics *Semicassis neumayri* (HOERNES, 1875) and *Sconsia ottnangiensis* (SACCO, 1890) are only known from the so-called Schlier facies, which represents a conspicuous alternation of bioturbated clay, silt and fine sand that developed in a shallow marine, probably current-influenced depositional environment off the coast (RUPP & VAN HUSEN, 2007). The late Ottnangian fauna was influenced by a major drop in sea level, which led to the breakdown of marine conditions in parts of the Paratethys (RÖGL, 1998). The associated local extinction was termed the Ottnangian extinction event (LOEE) by HARZHAUSER & PILLER (2007) and consequently, tonnoideans are locally missing during that time (Text-Fig. 1).

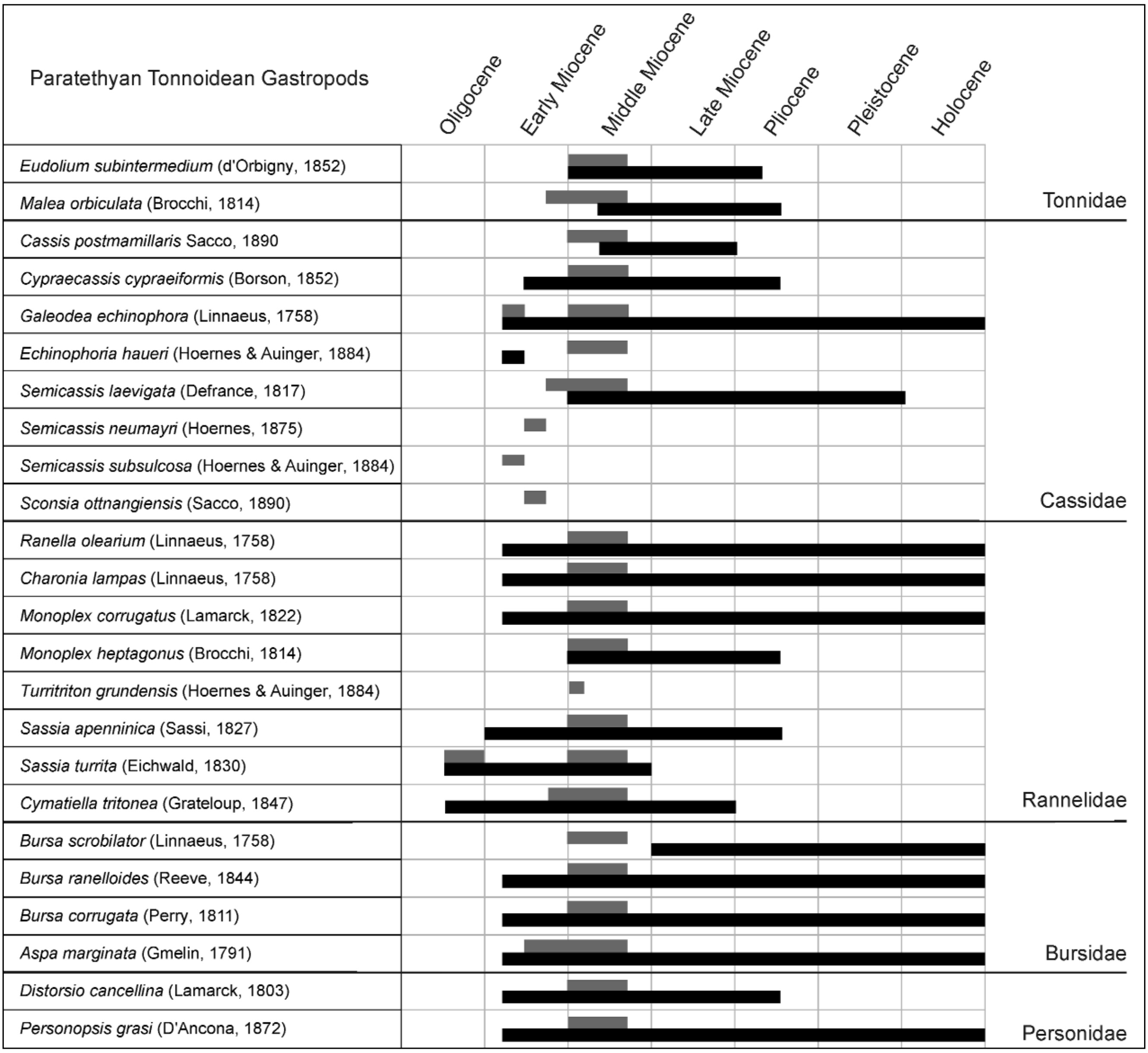
This crisis was overcome during the late Karpatian when the onset of the Mid-Miocene Climate Optimum (MMCO) allowed the first wave of immigrations from the proto-Mediterranean and Atlantic into the Paratethys (HARZHAUSER et al., 2003). Three species are recorded from that latest Early Miocene time: *Semicassis laevigata* (DEFRANCE, 1817), *Malea orbiculata* (BROCCHI, 1814), *Cymatiella tritonea* (GRATELOUP, 1847). None of these is endemic to the Paratethys and 2 have roots in the Burdigalian of the proto-Mediterranean.

The most outstanding event in Paratethyan tonnoidean diversity is observed in the early Badenian, which corresponds to the beginning of the early Middle Miocene. This phase is the heyday of the MMCO and the northward shift of the climate zones is followed by a northward migration of thermophilic molluscs into the Paratethys (HARZHAUSER et al., 2003). This early Badenian build-up event (EBBE) is indicated by the arrival of c. 500 gastropod species in the Paratethys (HARZHAUSER & PILLER, 2007). Among these, 20 tonnoidean species are recorded. Only *Turritriton grundensis* (HOERNES & AUINGER, 1884) is endemic to the Paratethys at that time. Most others are already known from Burdigalian deposits of Italy or France (Text-Fig. 2). Clearly, the Mediterranean was the source for this immigration, as the Eastern Paratethys did not contain any tonnoideans (see ILJINA, 1993).

After that immigration event, the diversity declined successively. Already the middle Badenian seems to lack *Malea orbiculata* (BROCCHI, 1814) and *Turritriton grundensis* (HOERNES & AUINGER, 1884). The onset of the Miocene Climatic Transition (MCT) is possibly heralded by this minor decline. The late Badenian is already fully affected by the



Text-Fig. 1.
Tonnoidean diversity in the Paratethys during the Miocene.
A clear forcing by geodynamic and climatic events is evident from the uneven distribution.



Text-Fig. 2.
Stratigraphic ranges of Miocene Paratethyan tonnoidean gastropods.
Black bars represent total distribution in the Western Atlantic and the Mediterranean. Grey bars represent Paratethyan occurrences. The ranges are taken from this paper and LANDAU et al. (2004) [note that some ages of Italian localities given as Middle Miocene in LANDAU et al. (2004) have been corrected according to FERRERO MORTARA et al. (1981) and are now treated as Burdigalian].

MCT and the fauna had to cope with changing oceanographic regimes (BALDI, 2006). These factors possibly caused the observed decline of tonnoidean diversity, which dropped to 14 species.

5.2. The North–South Gradient

A slight north–south gradient is possibly also reflected in the tonnoidean records. The early Badenian was the most tropical phase in the Paratethys. During that time, Korytnica in Poland represents the northern margin of the Paratethys whereas Lăpugiu de Sus in Romania is quite a southern locality. Austrian localities such as Grund and Hungarian Varpalota represent an intermediate position. Interestingly, at least 5 species [*Galeodea echinophora* (LINNAEUS, 1758), *Echinophoria haueri* (HOERNES & AUINGER, 1884), *Cassis postmamillaris* SACCO, 1890, *Distorsio cancellina* (LAMARCK, 1803), *Personopsis grasi* (D'ANCONA, 1872), *Ranella olearium* (LINNAEUS, 1758)] seem to be unknown from the northernmost localities in the Polish foredeep. Similar patterns have been observed within the stromboidean and xenophorid gastropods (HARZHAUSER et al., 2003) and were explained by a sea surface temperature gradient. Based on stable isotope data and the temperature requirements of extant relatives LATAL et al. (2005) and HARZHAUSER et al. (2003; 2007a) calculated minimum SSTs of 16–18°C for the southern and mid-latitude basins of the early Badenian Paratethys, whereas minimum SSTs of c. 14–15°C were estimated for the Polish foredeep.

5.3. Comparison with the Pliocene Tonnoidean Fauna

As discussed above, tonnoideans are well-known for their long-lived, widely distributed species. It is therefore not surprising that at the generic level the composition of the Middle Miocene Paratethyan fauna is not unlike that seen in the Mediterranean in the Early Pliocene, where tropical conditions also prevailed (SILVA & LANDAU, 2007).

However four genera present in the Middle Miocene Paratethys do not occur in the Mediterranean Pliocene.

- ***Cassis:*** Although well-represented by several taxa in the European Oligocene and Miocene, widespread, and present in the Atlantic, Mediterranean and Paratethys, the thermophilic genus *Cassis* never re-entered the Mediterranean following the Messinian Salinity Crisis despite the Early Pliocene Mediterranean waters being tropical in nature.
- ***Cymatiella:*** The thermophilic genus *Cymatiella* has a long history in the European Caenozoic deposits, with several species from the Paris Basin Eocene attributable to the genus. In the Neogene it seems to be widespread, with Miocene species recorded from Europe, Australia, Indonesia and the Caribbean (Beu, in press). However, it also seems not to have re-entered the Mediterranean following the Messinian Salinity Crisis.
- ***Sconsia:*** The thermophilic genus *Sconsia* is one of the major cassid genera in the Cenozoic rocks of tropical America, but today occurs only in the Caribbean in relatively deep waters (30–200 m) (Beu, in press). In the Neogene it was more widespread, with two species recorded from Indonesia (*S. pulchra* Pannekoek, 1936 and *S. martini* van Regteren Altena, 1942 [Beu, 2005]), and several species occurred in Europe during Paleogene and Miocene time. There are no European Pliocene records.
- ***Turritriton:*** The presence of the thermophilic genus *Turritriton* in the Paratethyan assemblages is problematic, as it is represented by at most half a dozen specimens, it is not recorded anywhere else in the European Neogene, and there is no chronological European record before or after the Middle Miocene. The origin of these specimens is at present unknown.
- ***Pisanianura:*** There are no representatives of the tonnoidean family Laubierinidae Warén & Bouchet, 1990 in the Paratethyan Middle Miocene, despite the genus *Pisanianura* Rovereto, 1899 being present in the Atlantic and Mediterranean from the Late Oligocene to Early Pliocene (Landau et al., 2004, p. 51). Today the family occurs in deep waters (Beu, in press), whereas the European fossil specimens are not found in deep water assemblages. However, they are always rare.

6. Conclusions

The tonnoidean gastropod fauna found in the Early and Middle Miocene Paratethys is rich and varied (Text-Fig. 2); 24 species are recorded, of which 9 (37.5 %) are still living at present. Within the Bursidae and Personidae this percentage is even higher at 83 %, whereas the Cassidae and Tonnidae display the lowest number of extant species (10 %; Text-Fig. 2). This is a much higher figure than in the extant gastropod species found in the Paratethyan Miocene as a whole, but this is hardly surprising, as the tonnoideans are well-known to be widely distributed geographically and spatially. Tonnoidean species usually have large multispiral protoconchs (Beu, 1988, p. 75), suggesting a planktotrophic distribution (Jablonski & Lutz, 1980) and the veligers of modern species have been shown to live for up to a year in the plankton, and are known as teleplanic larvae (Scheltema, 1966, 1971; Jablonski & Lutz, 1980; Scheltema & Williams, 1983; Pechenik et al., 1984), allowing them time to be carried vast distances passively in ocean currents (Beu, 1988, p. 73). This type of larval development and distribution leads to species with wide geographical and geological ranges, unparalleled in any other gastropod group, other than the Architectonicidae and a few other taxa such as the cerithioidean genus *Litiopa*.

Of the 24 species recorded only four (17 %) (*Semicassis neumayri* (Hoernes, 1875), *Semicassis subsulcosa* (Hoernes & Auinger, 1884), *Sconsia ottnangiensis* (Sacco, 1890) and *Turritriton grundensis* (Hoernes & Auinger, 1884)) are endemic to the Paratethys. Interestingly, the endemicity is highest during the Early Miocene, especially during the short interval of the early Ottnangian (Figs. 1, 2). This fits the observation by Harzhauser & Piller (2007) that endemicity is generally highest in the Paratethys during geodynamically active phases, which cause disconnections of sea ways. Three out of four of the endemic taxa are within the subfamily Phaliinae. Four species previously thought to be endemic to the Paratethys are shown to be junior subjective synonyms of more widespread taxa: *Cassidaria (Galeodea) cingulifera* Hoernes & Auinger, 1884 is a synonym of *Eudolium subintermedium* (d'Orbigny, 1852), *Ranella (Lampas) austriaca* Hoernes & Auinger, 1884 is a synonym of *Bursa ranelloides* (Reeve, 1844), originally described in the Recent fauna, *Ranella papillosa* Pusch, 1837 is a synonym of *Bursa corrugata* (Perry, 1811), also originally described in the Recent fauna, and *Echinophora hoernesi* Sacco, 1890, described from the Italian Miocene deposits, is a synonym of *Echinophoria haueri* (Hoernes & Auinger, 1884).

Several evolutionary lineages are now recognised within the European Neogene tonnoideans involving species that seem clearly phylogenetically linked; i. e. *Semicassis laevigata – S. saburon, Monoplex subcorrugatus – M. corrugatus, Aspa subgranulata – A. marginata*. Unfortunately, there will always be some degree of subjectivity as to how to define a particular species in the fossil faunas, as the soft parts cannot be examined, and not all authors will agree with our conclusions. However, the detailed study of the protoconchs has in some circumstances helped to distinguish between species (i. e. *Cypraecassis, Aspa subgranulata – A. marginata*; Landau et al. [2004]) and we have retained a distinction at the species level when there is a significant and constant difference between populations that are isolated chronologically or geographically.

The Paratethys seaways seem to have been the source for some of the species discussed. Within the *Monoplex subcorrugatus – M. corrugatus* lineage, specimens found in the Paratethyan assemblages seem to show intermediate characteristics, but leaning closer to *M. corrugatus*, and it is probable that the transition between the two species occurred in the Paratethys at the beginning of or during the Middle Miocene. Following the review of the Bursidae occurring in these deposits, the Paratethyan records are now the earliest for the Recent species *Bursa ranelloides* (Reeve, 1844), which is now widespread in the Atlantic and Indian Oceans (occurring also in Japan and Hawaii, apparently a relic of a formerly wide distribution) and *Bursa corrugata* (Perry, 1811), which is now widespread in the tropical Atlantic and eastern Pacific. These occurrences suggest that both *B. corrugata* and *B. ranelloides* had their origins in the Tethys and Paratethys seaways. Nevertheless, the position of the Paratethys as an evolutionary catalyser during the early Middle Miocene should not be overemphasised. Coeval mollusc-bearing Langhian deposits are very rare in the proto-Mediterranean area. Therefore, most of our knowledge of Langhian (= early Badenian) faunas is based on Paratethyan localities.

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Plate 1

Eudolium subintermedium (d'Orbigny, 1852)

Fig. 1: NHMW 1864/I/471.
Height 35 mm.
Middle Miocene, Badenian, Grund, Austria (shell illustrated by Hoernes & Auinger, 1884, Pl. 17, Fig. 17 as *Cassidaria (C.) cingulifera*).

Fig. 2: NHMW 1864/I/471.
Height 43 mm.
Middle Miocene, Badenian, Grund, Austria (shell illustrated by Hoernes & Auinger, 1884, Pl. 17, Fig. 19 as *Cassidaria (C.) cingulifera*).

Fig. 3: NHMW 1864/I/471.
Height 34 mm.
Middle Miocene, Badenian, Grund, Austria (shell illustrated by Hoernes & Auinger, 1884, Pl. 17, Fig. 20 as *Cassidaria (C.) cingulifera*).

Fig. 4: NHMW (no number).
Height 29.5 mm.
Middle Miocene, Badenian, Vöslau, Austria.

Fig. 5: BL coll.
Height 36.8 mm.
Early Pliocene, Zanclean, Lucena del Puerto, Huelva, Guadalquivir Basin, Spain.

Fig. 6: BL coll.
Height 35.5 mm.
Early Pliocene, Zanclean, Lucena del Puerto, Huelva, Guadalquivir Basin, Spain.

Fig. 7: BL coll.
Height 35.1 mm.
Early Pliocene, Zanclean, Banyuls dels Aspres, River Têt, Roussillon, France.

Malea orbiculata (Brocchi, 1814)

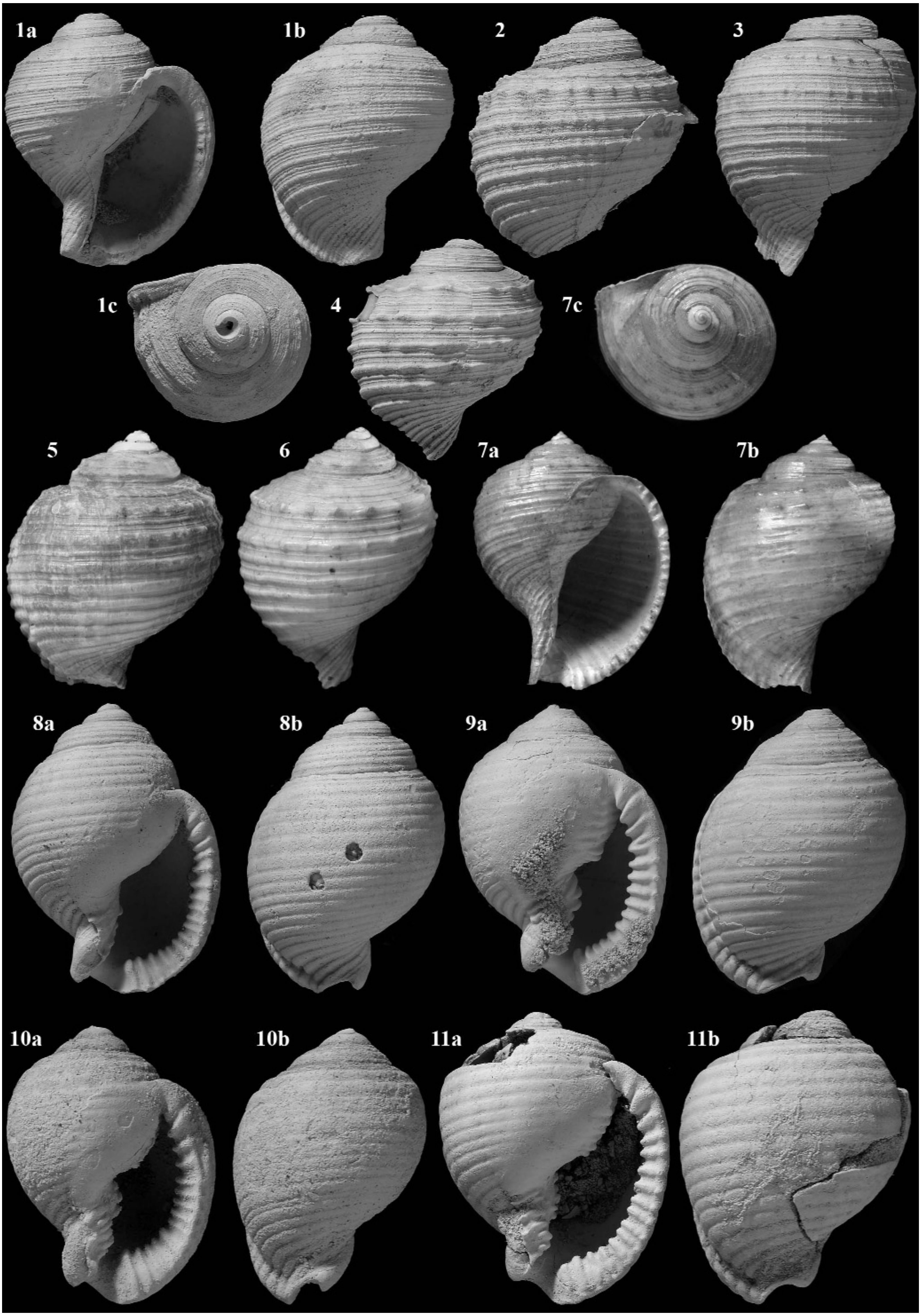
Fig. 8: NHMW 1851/XIII/108.
Height 46 mm.
Middle Miocene, Badenian, Grund, Austria (shell illustrated by Hoernes & Auinger, 1884, Pl. 16, Fig. 1 as *Dolium (Cadium) denticulatum*).

Fig. 9: NHMW 1851/XIII/108.
Height 45 mm.
Middle Miocene, Badenian, Grund, Austria (shell illustrated by Hoernes & Auinger, 1884, Pl. 16, Fig. 2 as *Dolium (Cadium) denticulatum*).

Fig. 10: NHMW 1851/XIII/108.
Height 29 mm.
Middle Miocene, Badenian, Grund, Austria (shell illustrated by Hoernes & Auinger, 1884, Pl. 16, Fig. 3 as *Dolium (Cadium) denticulatum*).

Fig. 11: NHMW 1851/XIII/108.
Height 38 mm.
Middle Miocene, Badenian, Grund, Austria (shell illustrated by Hoernes & Auinger, 1884, Pl. 16, Fig. 4 as *Dolium (Cadium) denticulatum*).

All photos NHMW coll. by Alice Schumacher. All photos BL coll. by Bernard Landau.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11b

Plate 2

Cassis postmamillaris SACCO, 1890

Fig. 1: Collection of Geological Survey (Coll. No. 1852/14/04).
Height 67.5 mm.
Middle Miocene, Badenian, Gainfarn, Austria (shell illustrated by HÖRNES, 1852, Pl. 14, Fig. 4 as *Cassis mamillaris*).

Fig. 2: NHMW 1854/XXXV/143.
Height 111.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania (shell illustrated by HÖRNES, 1852, Pl. 14, Fig. 3 as *Cassis mamillaris*).

Fig. 3: NHMW (no number).
Height 78.0 mm.
Middle Miocene, Badenian, Pötzleinsdorf, Austria (shell illustrated by SCHULTZ, 1998, Pl. 24, Fig. 1 as *Cassis (C.) mamillaris postmamillaris*).

Fig. 4: NHMW 1855/XLIII/13.
Height 113.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania.

All photos NHMW coll. by Alice SCHUMACHER.

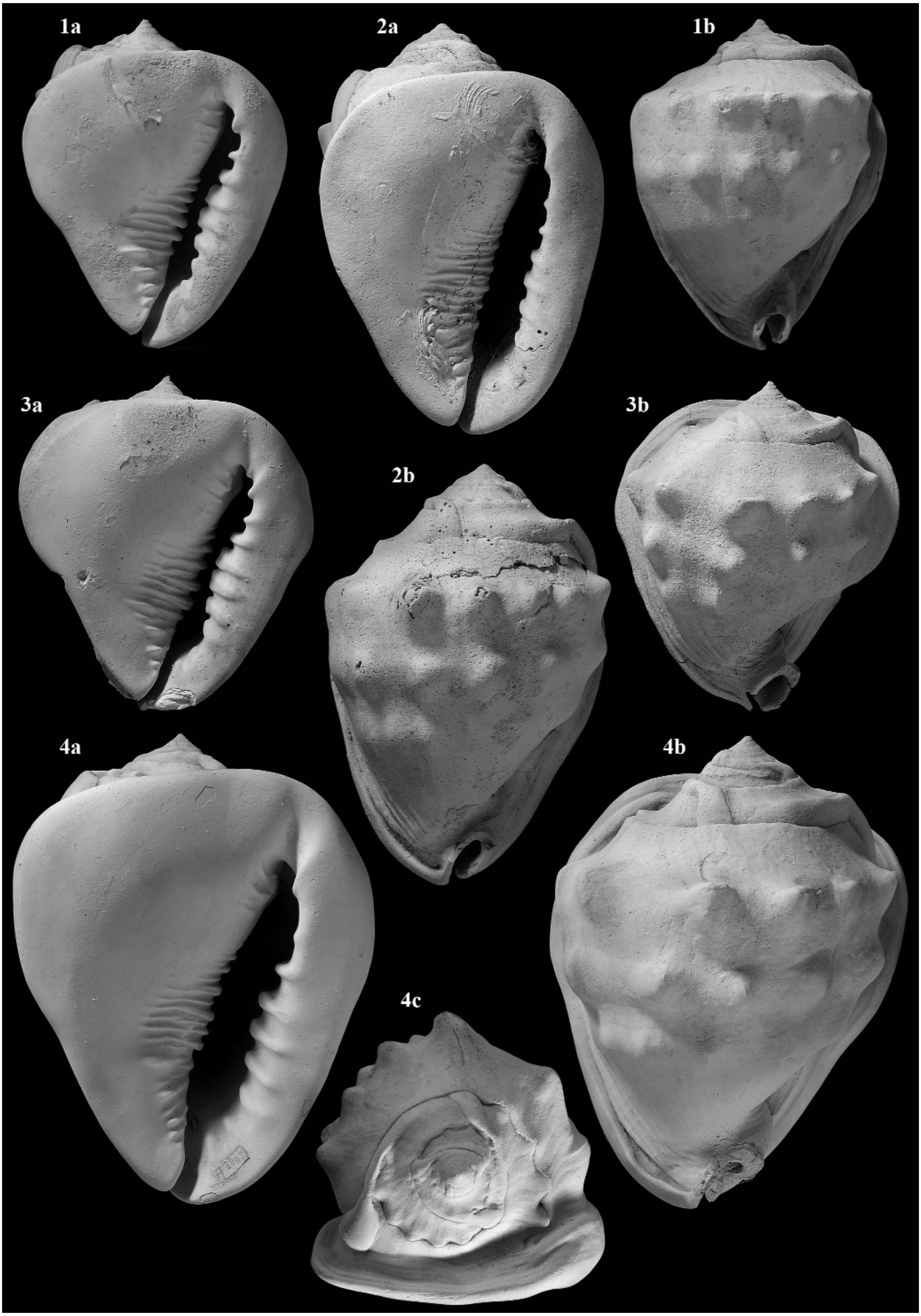
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Plate 3

***Galeodea echinophoria* (LINNAEUS, 1758)**

Fig. 1: NHMW 1846/37/179.
Height 42.0 mm.
Middle Miocene, Badenian, Baden, Austria (shell illustrated by HÖRNES, 1852, Pl. 16, Fig. 5).

Fig. 2: NHMW 1970/1396/1473.
Height 45.0 mm.
Middle Miocene, Badenian, Marz, Austria.

***Cypraecassis cypraeformis* (BORSON, 1820)**

Fig. 3: NHMW 1847/37/57.
Height 48.0 mm.
Middle Miocene, Badenian, Grund, Austria (shell illustrated by HÖRNES, 1852, Pl. 16, Fig. 1 as *Cassis crumena*).

Fig. 4: NHMW 1857/XIX/83.
Height 31.0 mm.
Middle Miocene, Badenian, Mikulov (= Nikolsburg), Czech Republic (shell illustrated by HÖRNES, 1852, Pl. 16, Fig. 2 as *Cassis crumena*).

Fig. 5: NHMW 1860/I/172.
Height 39.0 mm.
Middle Miocene, Badenian, Mikulov (= Nikolsburg), Czech Republic (shell illustrated by HÖRNES, 1852, Pl. 16, Fig. 3 as *Cassis crumena*).

***Echinophoria haueri* (HOERNES & AUINGER, 1884)**

Fig. 6: Holotype.
NHMW 1865/I/180.
Height 45.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania.

Fig. 7: NHMW 2001.
Height 35.0 mm.
Middle Miocene, Badenian, Baden, Austria.

Fig. 8: NHMW 1856/L/445.
Height 35.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania.

All photos NHMW coll. by Alice SCHUMACHER.

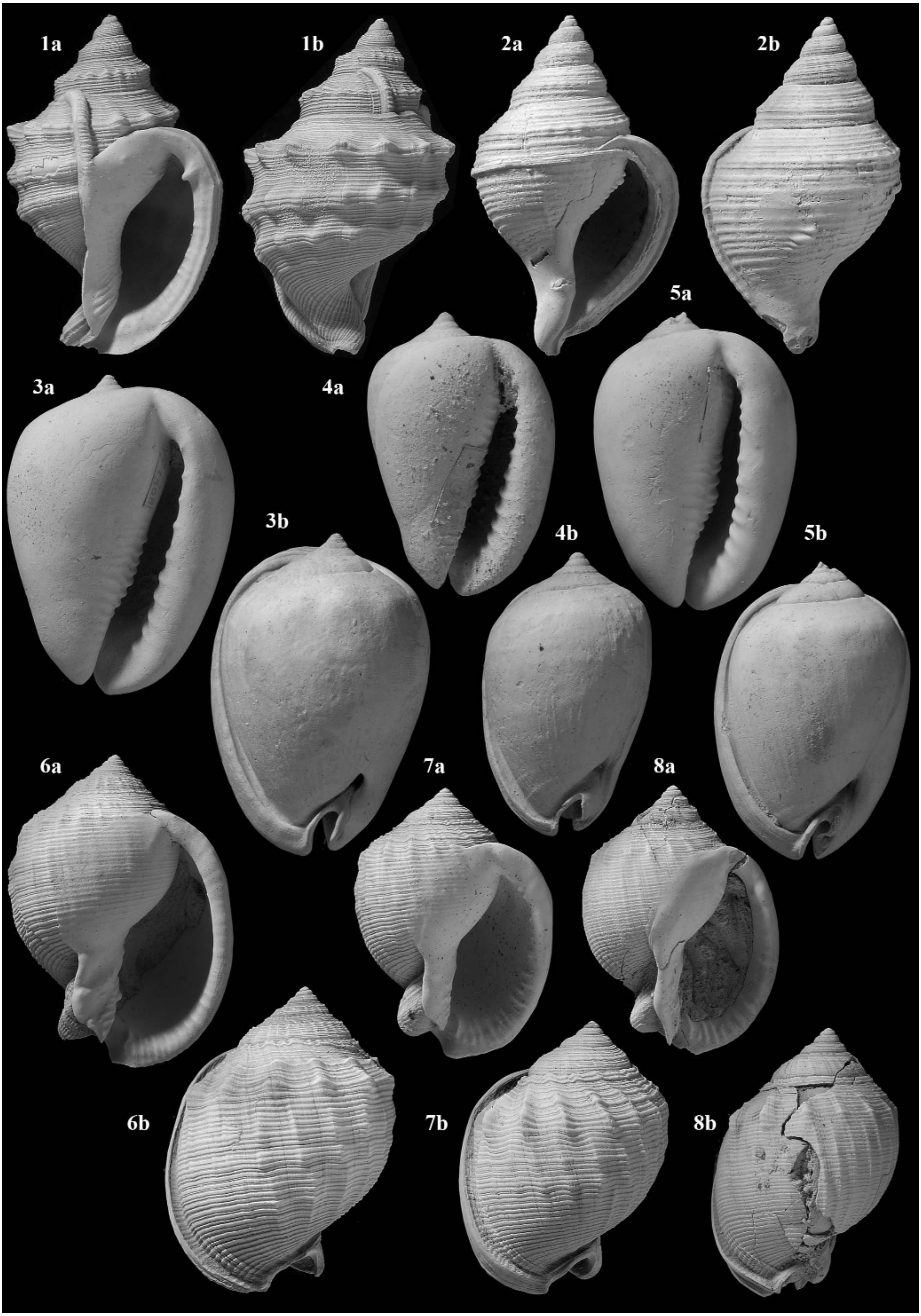
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Plate 4

Semicassis laevigata (DEFRANCE, 1817)

Fig. 1: NHMW 1856/VII/23.
Height 68.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania.

Fig. 2: NHMW 1857/XIX/82.
Height 75.0 mm.
Middle Miocene, Badenian, Grund, Austria.

Semicassis neumayri **(HOERNES, 1875)**

Fig. 3: Collection of Geological Survey (Coll. No. 1875/01/11).
Height 14.5 mm.
Early Miocene, Ottnangian, Ottnang, Austria (shell illustrated by HOERNES, 1875, Pl. 11, Fig. 11 and HOERNES & AUINGER, 1884, Pl. 17, Fig. 12).

Fig. 4: Collection of Geological Survey (Coll. No. 1875/01/11).
Height 16.0 mm.
Early Miocene, Ottnangian, Ottnang, Austria.

Fig. 5: NHMW A 719.
Height 25.0 mm.
Early Miocene, Ottnangian, Ottnang, Austria.

Semicassis subsulcosa **(HOERNES & AUINGER, 1884)**

Fig. 6: NHMW 1850/IX/34.
Height 56.0 mm.
Early Miocene, Eggenburgian, Loibersdorf, Austria (shell illustrated by SCHAFFER, 1912, Pl. 41, Fig. 8 as *Cassis sulcosa*).

Fig. 7: Holotype.
NHMW 1851/VI/100a.
Height 35.0 mm.
Early Miocene, Eggenburgian, Loibersdorf, Austria (shell illustrated by SCHAFFER, 1912, Pl. 41, Fig. 10).

Fig. 8: NHMW 1851/VI/100b.
Height 35.0 mm.
Early Miocene, Eggenburgian, Loibersdorf, Austria (shell illustrated by SCHAFFER, 1912, Pl. 41, Fig. 11).

All photos NHMW coll. by Alice SCHUMACHER. All photos BL coll. by Bernard LANDAU.

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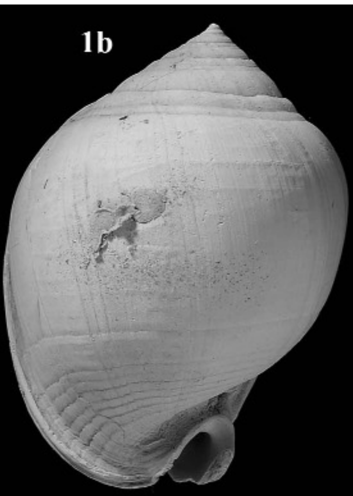

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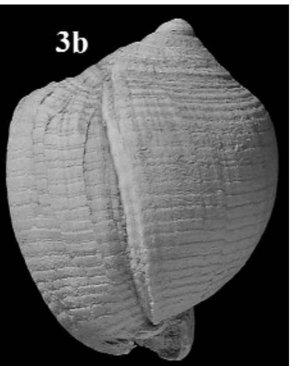

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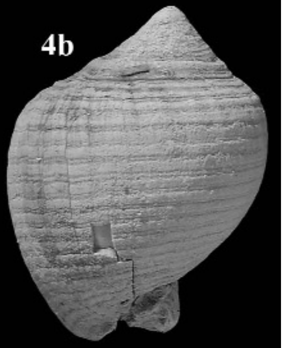

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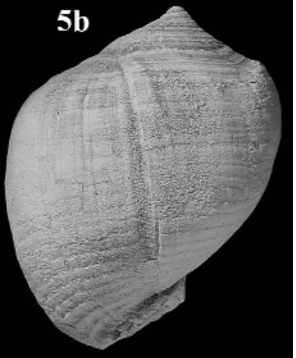

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Plate 5

***Sconsia ottnangensis* (SACCO, 1890)**

Fig. 1: Holotype.
Collection of Geological Survey GBA 1875/01/12.
Height 27.0 mm.
Early Miocene, Ottnangian, Ottnang, Austria (shell illustrated by HOERNES, 1875, Pl. 11, Fig. 13 as *Cassis striatula*).

Fig. 2: NHMW 1850/IX/34.
Height 44.0 mm.
Early Miocene, Ottnangian, Ottnang, Austria.

***Ranella olearium* (LINNAEUS, 1758)**

Fig. 3: NHMW 1863/XV/172.
Height 76.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania (shell illustrated by HOERNES & AUINGER, 1884, Pl. 23, Fig. 3 as *Ranella (Apollon) giganteum*).

Fig. 4: NHMW 1862/XXIX/25.
Height 51.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania (shell illustrated by HOERNES & AUINGER, 1884, Pl. 23, Fig. 5 as *Ranella (Apollon) giganteum*).

***Charonia lampas* (LINNAEUS, 1758)**

Fig. 5: Collection of Geological Survey (no number).
Height 127.0 mm.
Middle Miocene, Badenian, Grund, Austria (shell illustrated by HÖRNES, 1853, Pl. 19, Fig. 1 as *Triton nodiferum*).

Fig. 6: NHMW 1866/I/640.
Height 58.0 mm.
Middle Miocene, Badenian, Sooß, Austria (shell illustrated by HÖRNES, 1853, Pl. 19, Fig. 2 as *Triton nodiferum*).

Fig. 7: NHMW 1858/XXVII/135.
Height 36.0 mm.
Middle Miocene, Badenian, Grund, Austria (shell illustrated by HOERNES & AUINGER, 1884, Pl. 21, Fig. 1 as *Triton nodiferum*).

All photos NHMW coll. by Alice SCHUMACHER. All photos BL coll. by Bernard LANDAU.

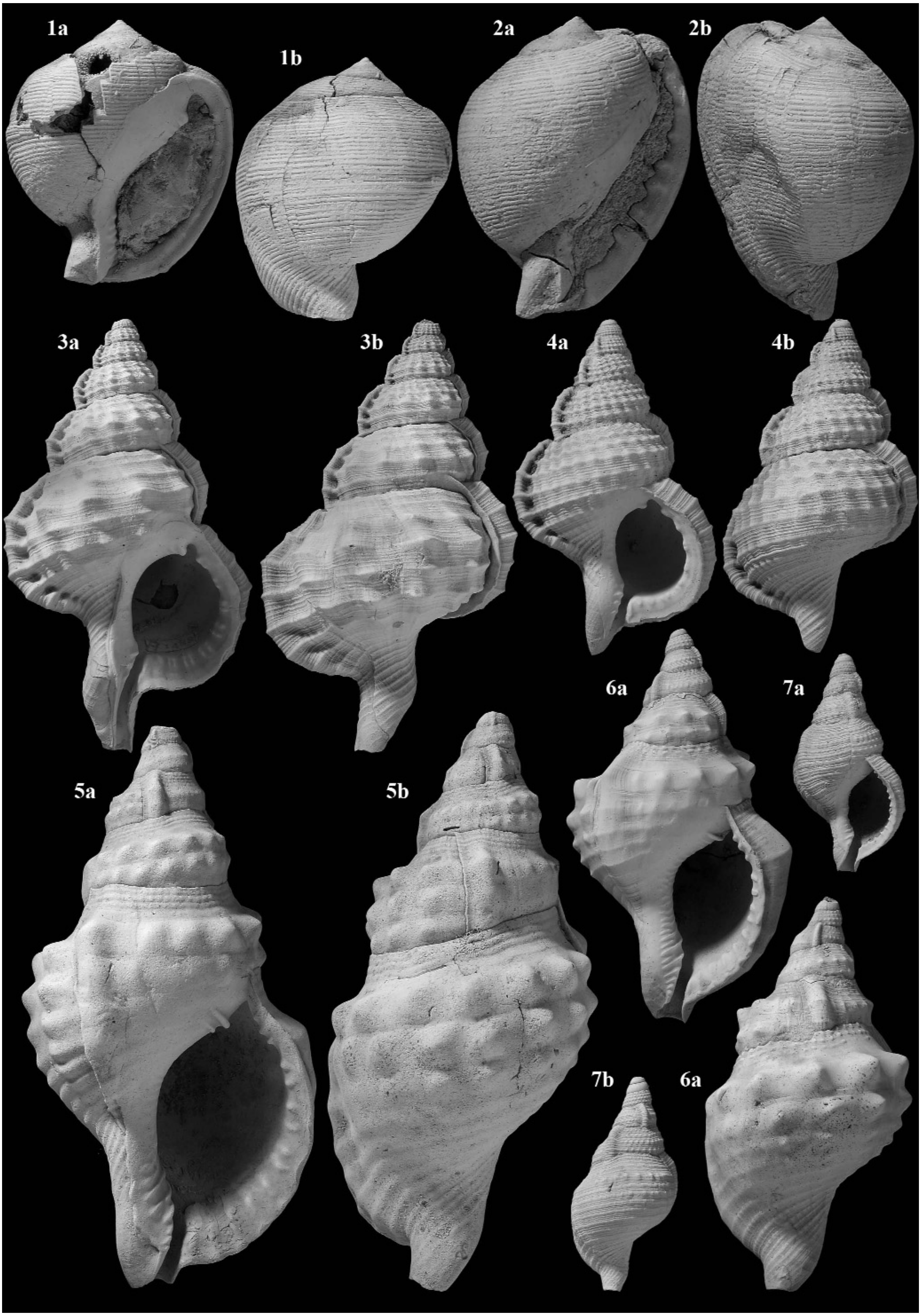
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Plate 6

Monoplex corrugatus **(LAMARCK, 1816)**

Fig. 1: NHMW 1852/XII/15.
Height 75.0 mm.
Middle Miocene, Badenian, Grund, Austria (shell illustrated by HÖRNES, 1853, Pl. 20, Fig. 1).

Fig. 2: NHMW 1855/XLV/74.
Height 75.5 mm.
Middle Miocene, Badenian, Steinebrunn, Austria (shell illustrated by HOERNES & AUINGER, 1884, Pl. 21, Fig. 12 as *Triton (Simpulum) affine*).

Fig. 3: NHMW 1854/XXXV/160.
Height 26.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania (shell illustrated by HOERNES & AUINGER, 1884, Pl. 21, Fig. 17 as *Triton (Simpulum) wimmeri*).

Fig. 4: NHMW 1854/XXXV/160.
Height 33.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania (shell illustrated by HOERNES & AUINGER, 1884, Pl. 21, Fig. 18 as *Triton (Simpulum) wimmeri*).

Turritriton grundensis **(HOERNES & AUINGER, 1884)**

Fig. 5: Holotype NHMW 1851/2/31.
Height 28.5 mm.
Middle Miocene, Badenian, Grund, Austria (shell illustrated by HOERNES & AUINGER, 1884, Pl. 21, Fig. 16).

Sassia apenninica **(SASSI, 1827)**

Fig. 6: NHMW 1846/37/197.
Height 40.0 mm.
Middle Miocene, Badenian, Möllersdorf, Austria (shell illustrated by HÖRNES, 1853, Pl. 19, Fig. 3).

Fig. 7: NHMW 1858/XXVII/135.
Height 36.0 mm.
Middle Miocene, Badenian, Möllersdorf, Austria (shell illustrated by HOERNES & AUINGER, 1884, Pl. 21, Fig. 7).

Sassia turrita **(EICHWALD, 1830)**

Fig. 8: NHMW 1851/XIII/5.
Height 48.0 mm.
Middle Miocene, Badenian, Baden, Austria (shell illustrated by HOERNES & AUINGER, 1884, Pl. 21, Fig. 8).

Fig. 9: NHMW 1869/I/75.
Height 39.0 mm.
Middle Miocene, Badenian, Sooß, Austria (shell illustrated by HOERNES & AUINGER, 1884, Pl. 21, Fig. 9).

All photos NHMW coll. by Alice SCHUMACHER.

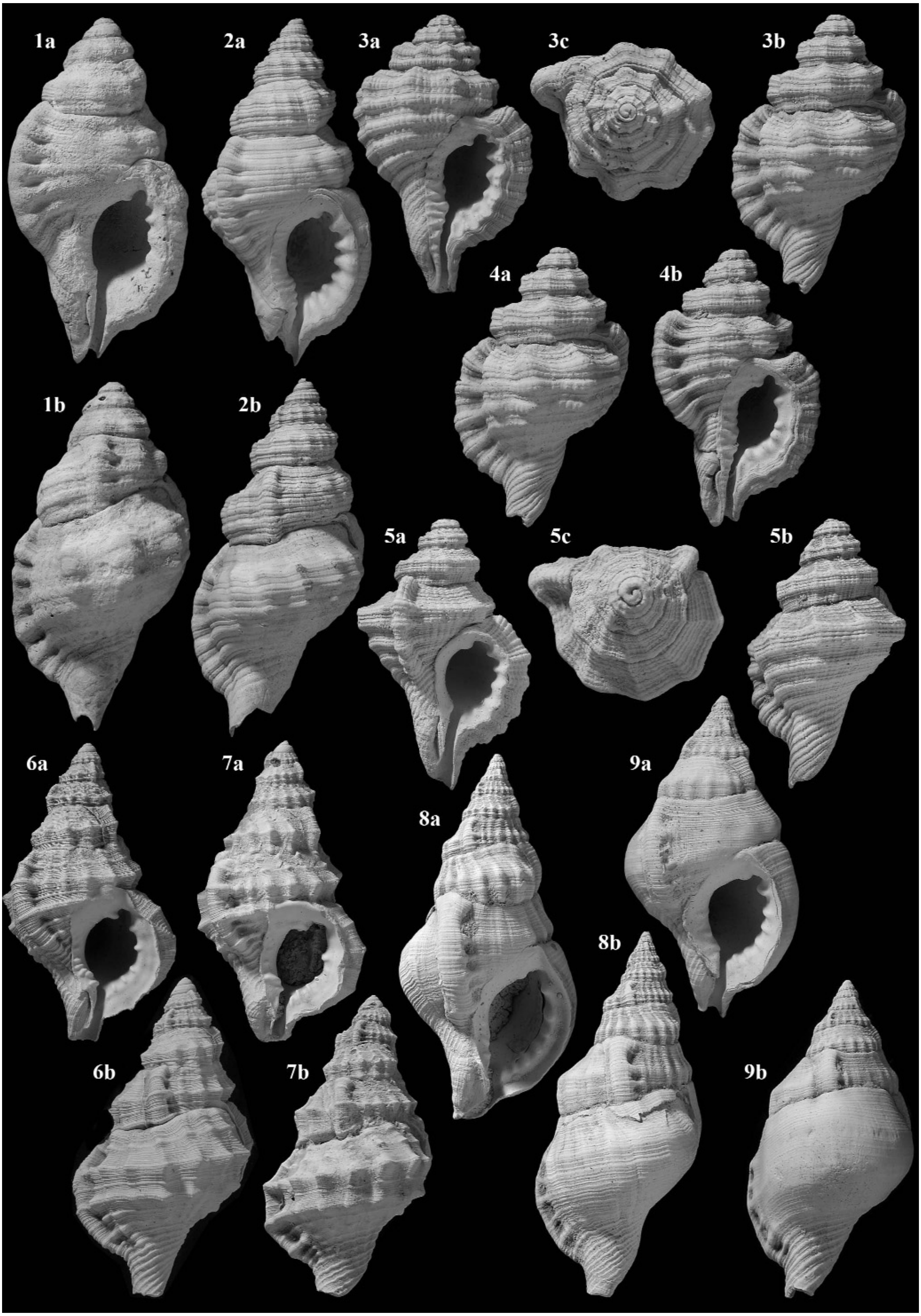
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Plate 7

Sassia turrita (EICHWALD, 1830)

Fig. 1: NHMW A134.
Height 49.0 mm.
Middle Miocene, Badenian, Steinebrunn, Austria.

Fig. 2: NHMW A134.
Height 48.0 mm.
Middle Miocene, Badenian, Steinebrunn, Austria.

Fig. 3: NHMW 1859/XL/16.
Height 23.5 mm (subadult).
Middle Miocene, Badenian, Zalisce, Volhynia, Ukraine.

Cymatiella tritonea (GRATELOUP, 1847)

Fig. 4: NHMW 1858/XLIII/32.
Height 15.5 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania (shell illustrated by HOERNES & AUINGER, 1884, Pl. 21, Fig. 19 as *Triton (Sassia) parvulum*).

Fig. 5: NHMW 1858/XLIII/32.
Height 16.2 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania (shell illustrated by HOERNES & AUINGER, 1884, Pl. 21, Fig. 20 as *Triton (Sassia) parvulum*).

Fig. 6: NHMW 1854/XXXV/157.
Height 13.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania (shell illustrated by HOERNES & AUINGER, 1884, Pl. 21, Fig. 21 as *Triton (Sassia) parvulum*).

Fig. 7: BL coll.
Height 15.9 mm.
Lower Miocene, Aquitanian, St-Martin-d'Oney, Landes, France.

Fig. 8: BL coll.
Height 13.6 mm.
Middle Miocene, Lower Burdigalian, Le Peloua, Saucats, France.

Fig. 9: BL coll.
Height 12.0 mm.
Middle Miocene, Lower Burdigalian, Le Peloua, Saucats, France.

Bursa scrobilator (LINNEAUS, 1758)

Fig. 10: NHMW 1863/XV/1268.
Height 54.5 mm.
Middle Miocene, Badenian, Grund, Austria (shell illustrated by HÖRNES, 1853, Pl. 201, Fig. 3).

Fig. 11: NHMW 1851/II/40.
Height 34.0 mm.
Middle Miocene, Badenian, Grund, Austria (shell illustrated by Hörnes, 1853, Pl. 201, Fig. 4).

All photos NHMW coll. by Alice SCHUMACHER. All photos BL coll. by Bernard LANDAU.

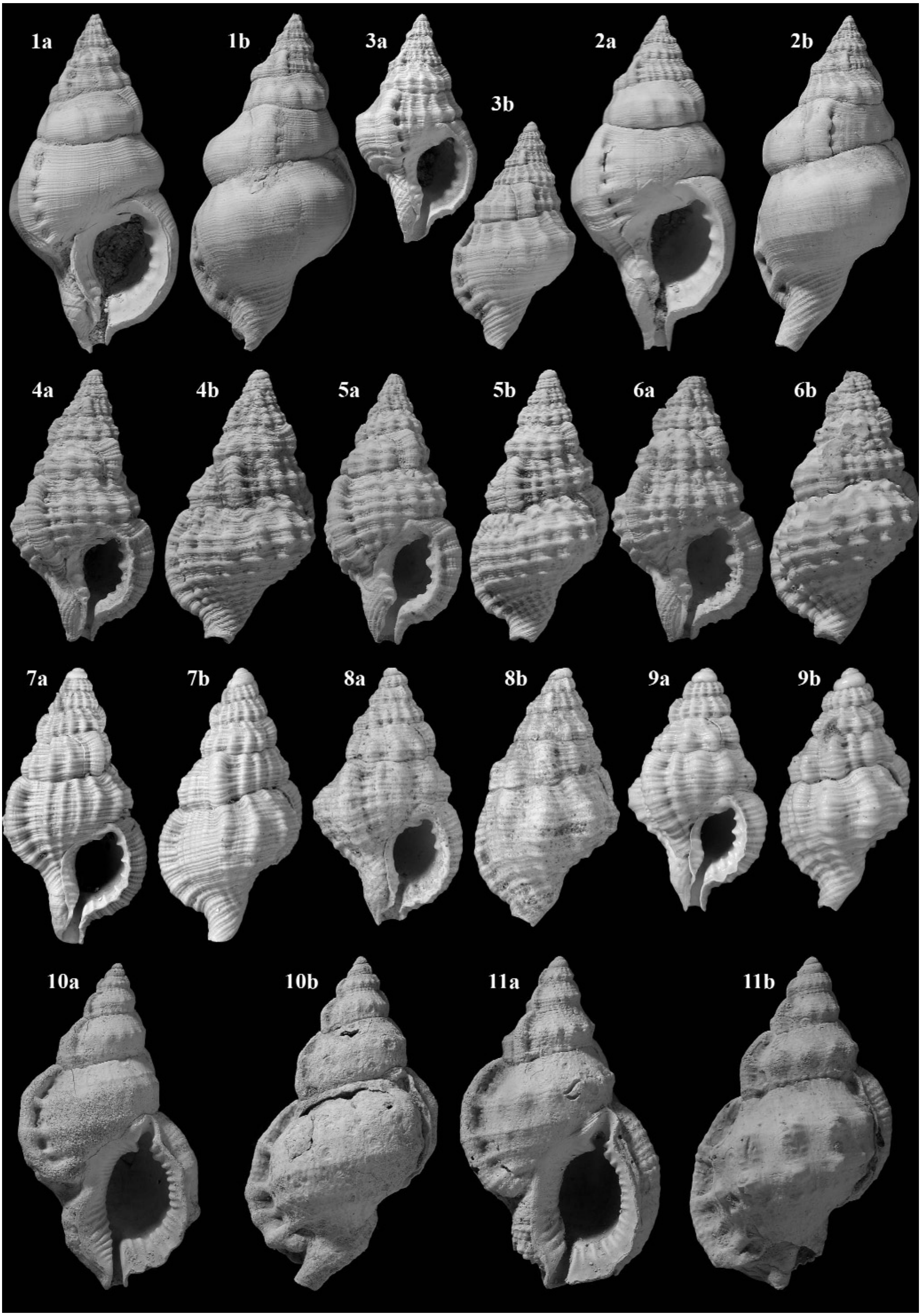
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Plate 8

Bursa ranelloides (REEVE, 1844)

Fig. 1: Lectotype of *Bursa austriaca* (HOERNES & AUINGER, 1884).
NHMW 1866/XL/190.
Height 41.0 mm.
Middle Miocene, Badenian, Sooß, Austria (shell illustrated by HOERNES & AUINGER, 1884, Pl. 23, Fig. 10).

Fig. 2: NHMW 1872/XXX/36.
Height 47.0 mm.
Middle Miocene, Badenian, Sooß, Austria (shell illustrated by HOERNES & AUINGER, 1884, Pl. 23, Fig. 11).

Fig. 3: NHMW 1872/XXX/36.
Height 41.0 mm.
Middle Miocene, Badenian, Sooß, Austria (shell illustrated by HOERNES & AUINGER, 1884, Pl. 23, Fig. 12).

Fig. 4: NHMW 1872/XXX/36.
Height 43.0 mm.
Middle Miocene, Badenian, Sooß, Austria.

Fig. 5: NHMW 1847/XXIV/37.
Height 41.0 mm.
Middle Miocene, Badenian, Vöslau, Austria.

Fig. 6: NHMW 1872/XXX/36.
Height 41.0 mm.
Middle Miocene, Badenian, Vöslau, Austria.
Detail of surface reticulate secondary sculpture.

Bursa corrugata (PERRY, 1811)

Fig. 7: NHMW 1890/I/154.
Height 34.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania.

Fig. 8: NHMW 1890/I/154.
Height 44.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania.

Fig. 9: NHMW 1866/XL/277.
Height 45.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania.

Fig. 10: NHMW 1890/I/154.
Height 34.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania.
Detail of surface reticulate secondary sculpture.

All photos NHMW coll. by Alice SCHUMACHER.

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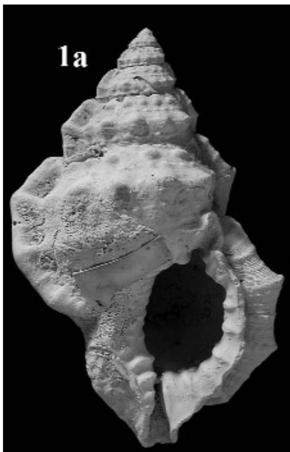

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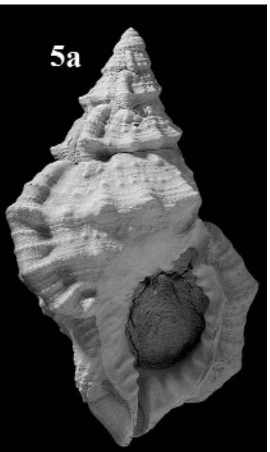

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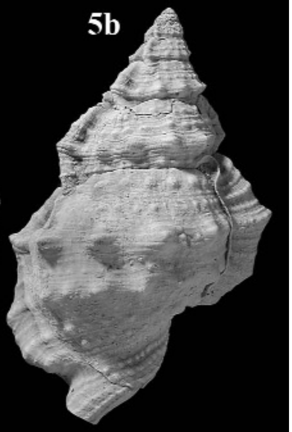

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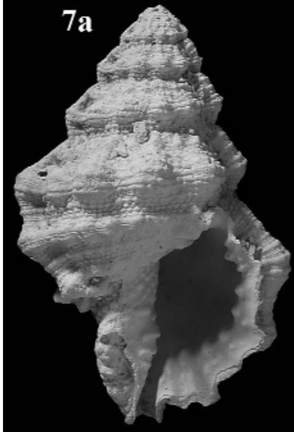

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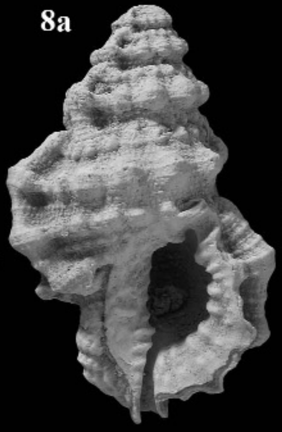

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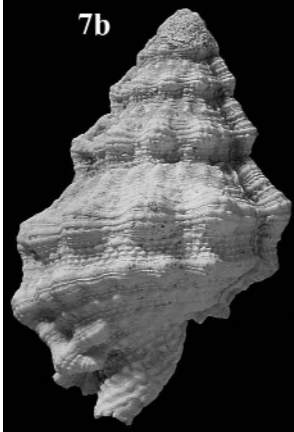

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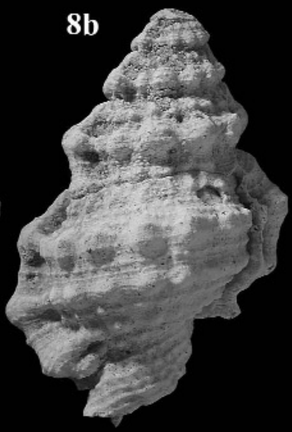

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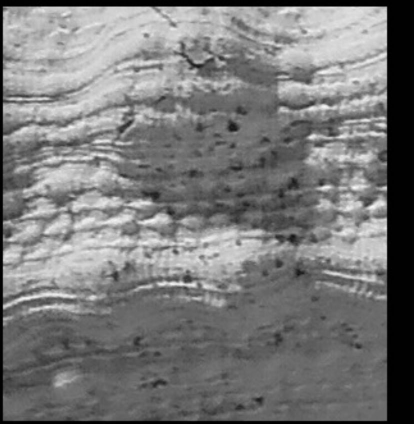

Plate 9

***Aspa marginata* (GMELIN, 1791)**

Fig. 1: NHMW 1853/XXVI/29.
Height 59.5 mm.
Middle Miocene, Badenian, Grund, Austria (shell illustrated by HÖRNES, 1853, Pl. 21, Fig. 7).

Fig. 2: NHMW 1848/XX/14.
Height 26.0 mm (subadult).
Middle Miocene, Badenian, Baden, Austria (shell illustrated by HÖRNES, 1853, Pl. 21, Fig. 10).

***Distorsio cancellina* (LAMARCK, 1803)**

Fig. 3: NHMW 1858/XXXVII/16.
Height 66.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania.

Fig. 4: NHMW 1855/XLIII/23.
Height 59.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania (shell illustrated by HOERNES & AUINGER, 1884, Pl. 21, Fig. 11 as *Triton (Distorsio = Persona) tortuosa)*.

***Personopsis grasi* (D'ANCONA, 1872)**

Fig. 5: NHMW 1847/XXV/20.
Height 21.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania (shell illustrated by HOERNES & AUINGER, 1884, Pl. 22, Fig. 14).

Fig. 6: NHMW 18479/I/475.
Height 23.5 mm.
Middle Miocene, Badenian, Forchtenau, Austria (shell illustrated by HOERNES & AUINGER, 1884, Pl. 22, Fig. 15).

Fig. 7: NHMW 1847/XXV/20.
Height 22.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania.

***Echinophoria haueri* (HOERNES & AUINGER, 1884)**

Fig. 8: NHMW (no number).
Height 45.0 mm.
Middle Miocene, Badenian, Sooß, Austria (= Pl. 3, Fig. 6).
Detail of protoconch.

All photos NHMW coll. by Alice SCHUMACHER.

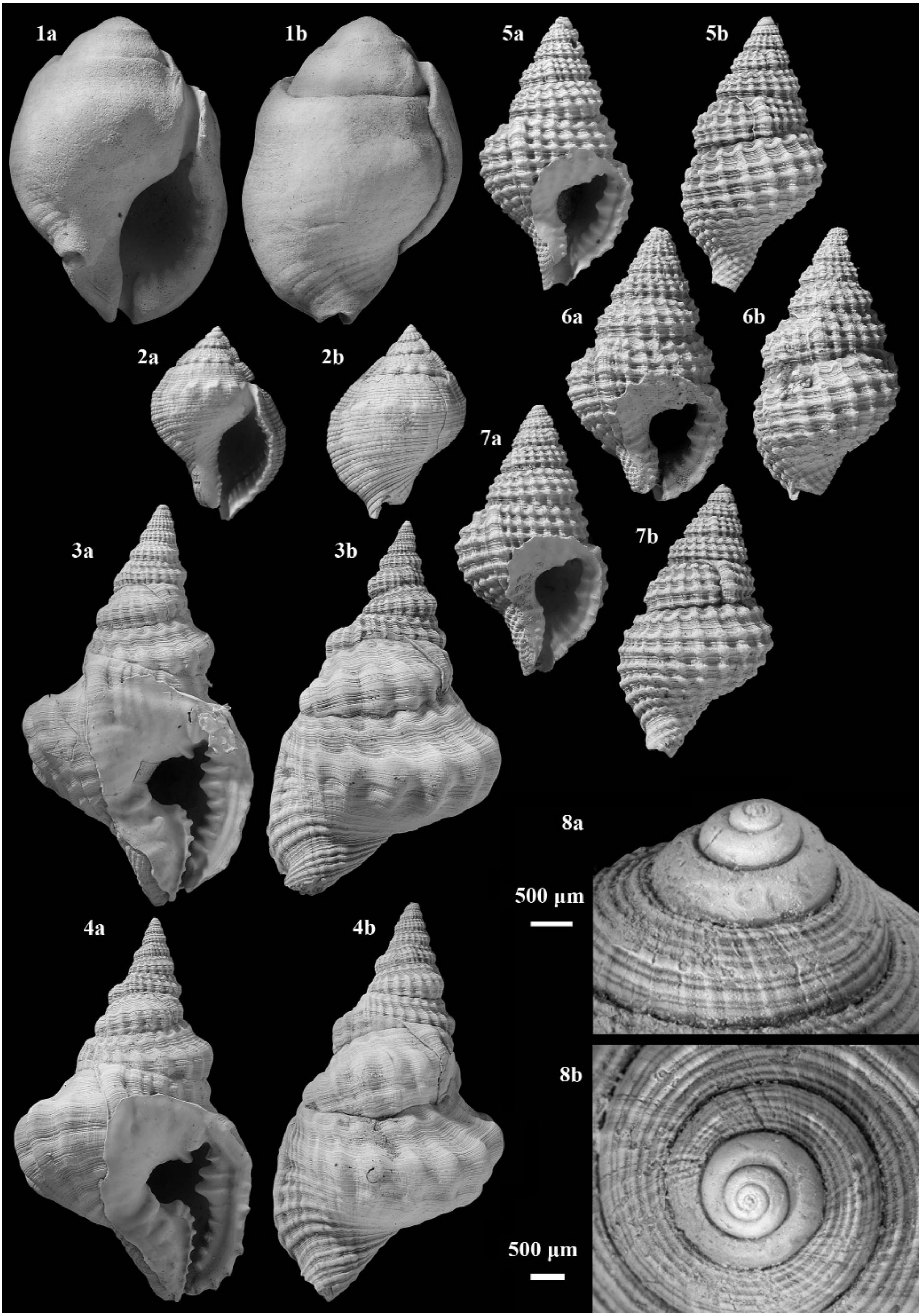
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Plate 10

***Semicassis neumayri* (HOERNES, 1875)**

Fig. 1: NHMW A 719.
Height 25.0 mm.
Middle Miocene, Ottnangian, Ottnang, Austria (= Pl. 4, Fig. 5).
Detail of protoconch.

***Sconsia ottnangensis* (SACCO, 1890)**

Fig. 2: NHMW 1854/XXIII/11.
Height 32.0 mm.
Early Miocene, Ottnangian, Ottnang, Austria.
Detail of protoconch.

***Cymatiella tritonea* (GRATELOUP, 1847)**

Fig. 3: NHMW 1858/XLIII/32.
Height 16.2 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania (shell illustrated by HOERNES & AUINGER, 1884, Pl. 21, Fig. 20 as *Triton (Sassia) parvulum*) (= Pl. 7, Fig. 5).
Detail of protoconch.

***Bursa ranelloides* (REEVE, 1844)**

Fig. 4: NHMW 1872/XXX/36.
Height 41.0 mm.
Middle Miocene, Badenian, Sooß, Austria (shell illustrated by HOERNES & AUINGER, 1884, Pl. 23, Fig. 12) (= Pl. 8, Fig. 3).
Detail of protoconch.

***Bursa corrugata* (PERRY, 1811)**

Fig. 5: NHMW 1890/I/154.
Height 17.0 mm.
Middle Miocene, Badenian, Lăpugiu de Sus, Romania.
Detail of protoconch.

All photos NHMW coll. by Alice SCHUMACHER.

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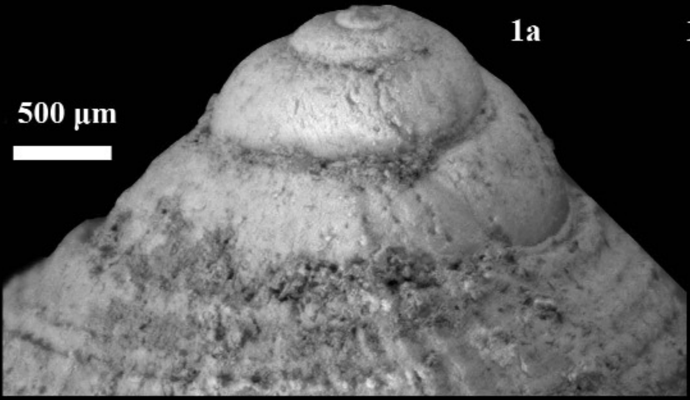

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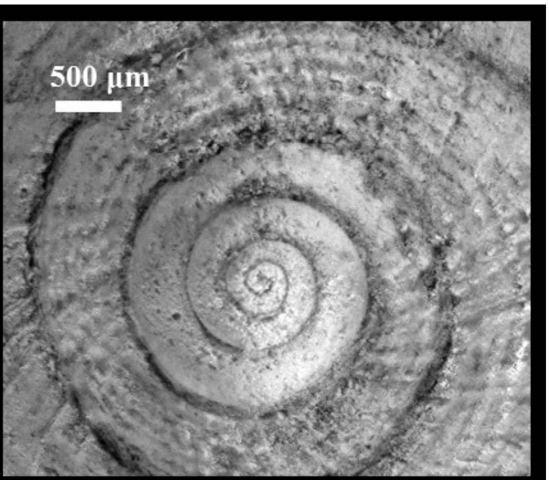

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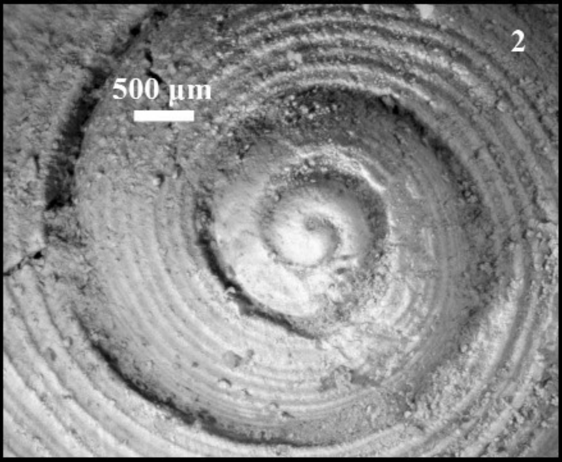

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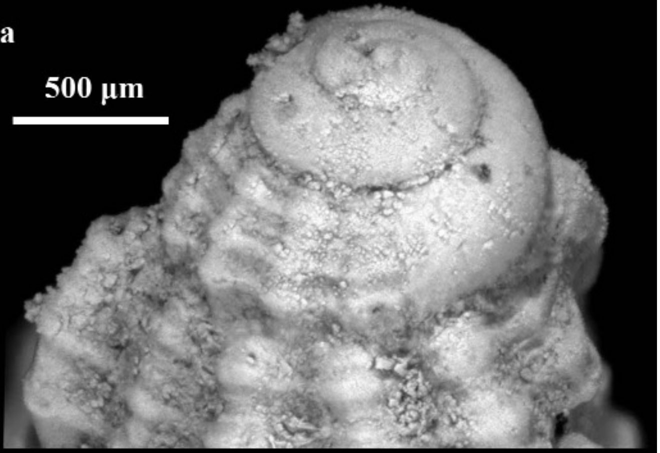

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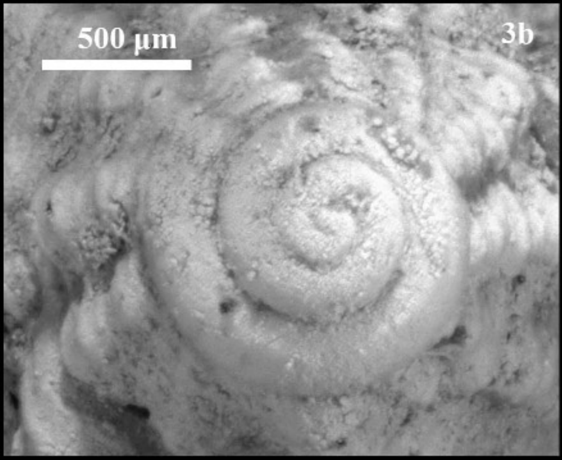

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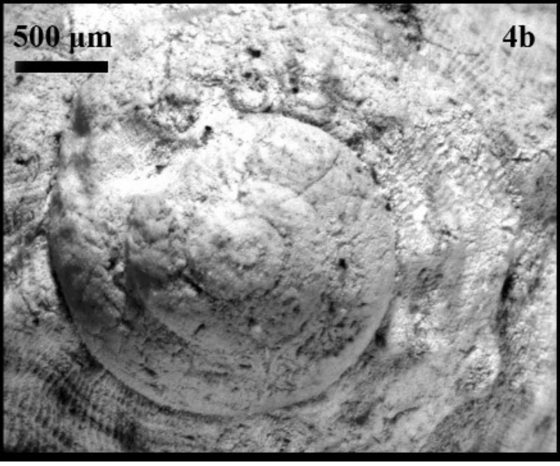

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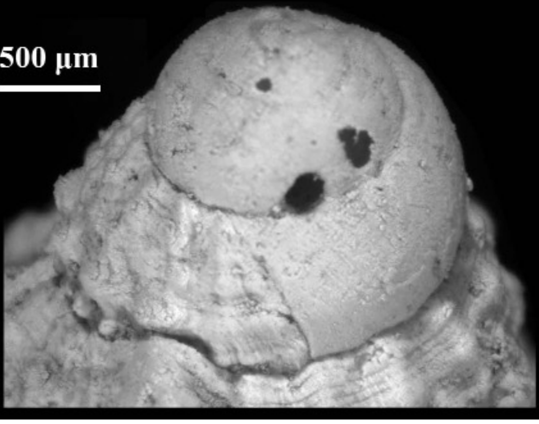

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