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Source: Acta Palaeontologica Polonica, 58(4) : 785-802

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2011.0130

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The Neogene strombid gastropod *Persististrombus* in the Paratethys Sea

MATHIAS HARZHAUSER and GIJS C. KRONENBERG

Harzhauser, M. and Kronenberg, G.C. 2013. The Neogene strombid gastropod *Persististrombus* in the Paratethys Sea. *Acta Palaeontologica Polonica* 58 (4): 785–802.

Strombids are frequent fossils in Neogene nearshore deposits but are rarely used for biostratigraphy due to their poorly defined stratigraphic ranges. Herein, we document the biostratigraphic value of the group based on a succession of short-lived distinct species in Neogene deposits in the circum-Mediterranean area. These have been intermingled so far into two "super-species", viz. *Persististrombus bonelli* and *P. coronatus*, seemingly ranging from the Oligocene to the Pliocene. Based on morphometric measurements on 219 specimens we refine the taxonomic concept for this group and document at least 5 distinct species of high biostratigraphic and biogeographic significance. European *Persististrombus* species display a tendency to produce strongly sculptured populations with marked spines or to form populations with elongate shells and reduced sculpture. The development of sculptured morphs is an iterative process as exceptionally sculptured taxa occur in stratigraphically and geographically discrete phases and areas. Yet, within these species the morphology is very variable. Although some of these taxa are distinct species, there is no continuous evolutionary lineage leading to the Pliocene *P. coronatus* with which some of these taxa were confused in the literature so far. Successfully reproducing populations of extant species of *Persististrombus* in the Panamic Province and the African-Eastern Atlantic Province are limited in their distribution by the 20°C isotherm. This value may thus be a realistic estimate for the cool-season sea surface temperatures for *Persististrombus*-bearing formations. *Persististrombus pannonicus* sp. nov. is established for a late Badenian species.

Key words: Gastropoda, Strombidae, *Persististrombus*, paleobiogeography, Miocene, Paratethys Sea, Mediterranean Sea.

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Received 1 September 2011, accepted 21 February 2012, available online 27 February 2012.

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Introduction

The Family Strombidae arose during the Eocene and diversified during the Late Oligocene and Early Miocene (Williams and Duda 2008 and references therein) and is currently represented by about 100 species, restricted to the tropics (Abbott 1960). Most strombids live in shallow water environments. They are among the most eye-catching gastropods, and attract a broad community of scientists and collectors. From the Eocene about five species have been described within the genus *Strombus* sensu Abbott (1960), and during Late Oligocene and Miocene times strombids experienced their first main radiation with about 40 species described from the Miocene (Wieneke et al. 2011). The phylogeny and the generic affiliations of the various fossil and extant taxa, however, have only been slowly resolved. After early attempts of Abbott (1960), no major breakthrough was achieved before the 21st century when a set of papers tried to clarify the validity of genus-rank taxa and to allocate species groups to these genera (Kronenberg and Vermeij 2002; Kronenberg and Lee 2005, 2007; Bandel 2007). Molecular data generally support their conclusions (Latiolais et al. 2006) and suggest very complex phylogeographic patterns. This newly established system has also been gradually applied to fossil taxa (Harzhauser and Kronenberg 2008; Wieneke et al. 2011). The correct allocation of all these taxa is crucial for supporting molecular data with the fossil record.

The deposits of the various European basins, which were covered by the Miocene Paratethys Sea, present an outstanding archive of fossil strombids. Since the 19th century, the Middle Miocene strombids of the Paratethys and the proto-Mediterranean Sea have been usually treated as *Strombus coronatus* Defrance, 1827—a largely Pliocene species—or *Strombus bonelli* Brongniart, 1823, which is an Early Mio-

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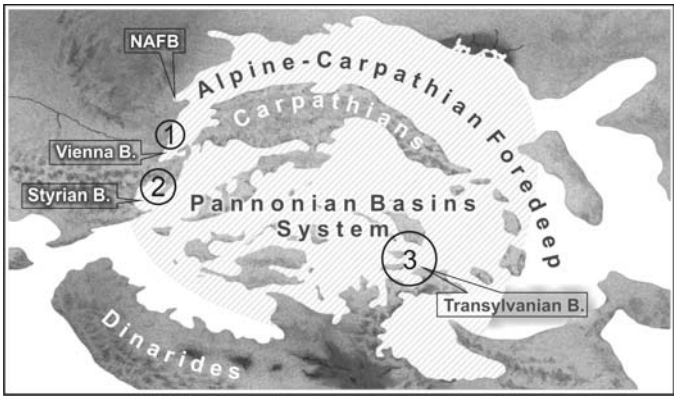

Fig. 1. Distribution of the *Persististrombus* species plotted on a map of the Middle Miocene Paratethys Sea (modified from Harzhauser et al. 2007). Stippled area represents the distribution of *Persististrombus inflexus* (Eichwald, 1830). 1, *Persististrombus exbonellii* (Sacco, 1893); 2, *Persististrombus pannonicus* Harzhauser and Kronenberg nov. sp.; 3, *Persististrombus lapugyensis* (Sacco, 1893); NAFB, North Alpine Foreland Basin. Note that this map shows an Early Langhian situation, whereas the distribution data unite Langhian and Serravallian occurrences.

cene species. Generally, robust shells with strongly developed spines were treated as *S. coronatus* whilst more slender specimens with reduced sculpture were tentatively treated as *S. bonelli*. Many authors, such as Hörnes (1853), Hoernes and Auinger (1884), Strausz (1966), and Bałuk (1995), emphasized the problems in assigning the specimens to one of the taxa due to the presence of intermediate morphologies. This vague taxonomic concept resulted in an apparent stratigraphic range of c. 20 Ma., from the Late Oligocene to the Pliocene, for *Strombus coronatus*. Especially during the early 19th century, during what might be called the "pioneer phase of conchology", authors were unaware of the exact stratigraphic age of the various localities and this led to unrealistically long stratigraphic ranges for species. Similarly, biogeographic patterns have been obscured, as even eastern African fossils were treated as *Strombus bonelli* (Collignon and Cottreau 1927). Herein, we try to evaluate the taxonomic concepts applied to the various Paratethyan and some proto-Mediterranean representatives of *Persististrombus* to clarify their biostratigraphic and biogeographic value.

Institutional abbreviations.—GBA, Geological Survey Vienna; NHMW, Natural History Museum Vienna. All measured shells are stored in the collections of the Natural History Museum Vienna (Austria), the Krahuletz Museum, Eggenburg (Austria), and the Naturalis Biodiversity Center, Leiden (The Netherlands) as indicated in the supplementary data table (SOM, Supplementary Online Material at http://app.pan.pl/SOM/app58-Harzhauser_Kronenberg_SOM.pdf).

Geological setting

The discussed strombids derive from three palaeogeographic areas: the Paratethys Sea, the proto-Mediterranean Sea, and the Eastern Atlantic. In terms of biogeography, all three belonged to the Proto-Mediterranean-Atlantic Region during the Early to Middle Miocene (Harzhauser et al. 2002). Its geographic extent roughly corresponds to the limits of the modern Mediterranean-Atlantic Region (sensu Briggs 1995). The mentioned strombids from Turkey, Greece, Northern Italy, and France belong to this biogeographic unit, which was part of the Proto-Mediterranean-Atlantic Region during the Burdigalian (Harzhauser et al. 2002). Most of the discussed taxa are found in deposits of the Paratethys Sea, which appeared as a distinct palaeogeographic and paleobiogeographic unit around the Eocene–Oligocene boundary and lasted until the Pliocene (Rögl 1998). During its maximum extent, the Paratethys Sea spread from the Rhône Basin in France towards Inner Asia.

This sea underwent an extraordinary history of total or partial isolation, reflected in a phase of high endemism, alternating with various connections to the adjacent seas (Harzhauser and Piller 2007). Strombids from Bosnia, Austria, Romania, Hungary, Poland, and NW Bulgaria, mentioned in this paper, belong to the fauna of the Paratethys Sea (Fig. 1). The peculiar development that was forced mainly by geodynamic processes renders a system of regional stages necessary, as the regional stage boundaries do not always correlate with those of the Mediterranean standard scale (Fig. 2). A synopsis of the paleogeography of the area in several time slices was presented by Rögl (1998) and Popov et al. (2004). Harzhauser et al. (2002) and Harzhauser and Piller (2007) present a detailed introduction into the Oligocene to Miocene

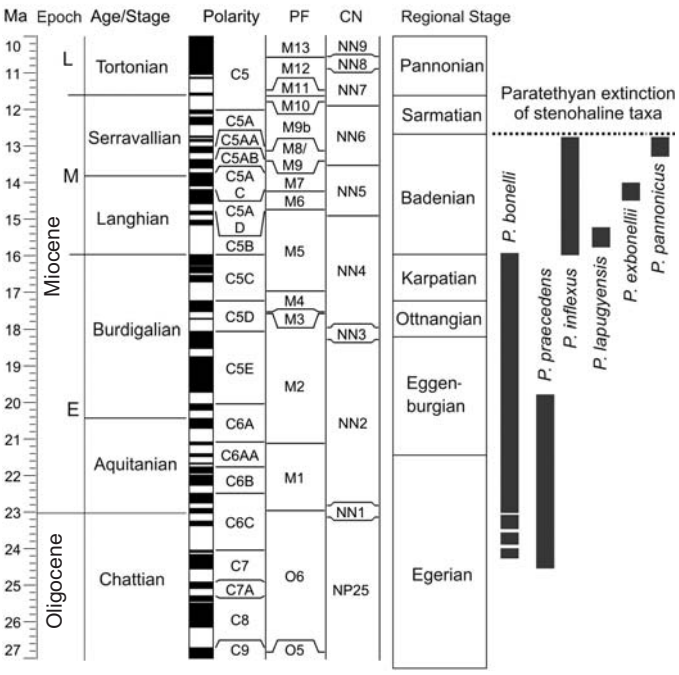

Fig. 2. Oligocene–Miocene chronostratigraphy, magnetostratigraphy, and biostratigraphy after Hilgen et al. (2009) with regional Paratethys stages after Piller et al. (2007). The figure is modified from a chart produced with the Time Scale Creator program, provided by the International Commission on Stratigraphy (available at https://engineering.purdue.edu/Stratigraphy/tscreator/index/index.php). The ranges of the treated strombid taxa are indicated as grey bars. Abbreviations: CN, calcareous nannoplankton; PF, planktonic Foraminifera.

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paleobiogeography in the circum-Mediterranean area with emphasis on the Paratethys Sea. An update of the chronostratigraphy and the use of the regional stages are presented in Piller et al. (2007). For the ages and biostratigraphic correlations of the most important localities mentioned in text see Studencka et al. (1998), Harzhauser et al. (2003), Rögl et al. (2008), Harzhauser and Piller (2007), and Zuschin et al. (2007, 2011); geographic maps showing all the localities in great detail are presented by Kroh (2005).

Material and methods

We compiled morphometric data on a total of 219 Miocene to Pliocene European strombid shells. The Miocene shells derive from the Egerian (= Chattian–lower Aquitanian), Eggenburgian (= lower Burdigalian) and Badenian (= Langhian–lower Serravallian) stages. The material comprises juvenile to adult specimens of *Persististrombus nodosus* (n = 8), *P. praecedens* (n = 4), *P. inflexus* (n = 36), *P. exbonellii* (n = 70), *P. lapugyensis* (n = 48), *P. pannonicus* (n = 6), and *P. coronatus* (n = 47). The measurements focused on the total height, the maximum width, the maximum width without spines, the width in dorsal-ventral direction with and without spines, of the last whorl and of the last spire whorl, and the angles of the apex and of the last whorl (Fig. 3, SOM). To evaluate the robustness of our taxonomic concept we performed principal component analysis with the software package PAST (Hammer et al. 2001).

Each taxon is described and we try to present a chresonymy (sensu Smith and Smith 1972) for each species, focusing only on relevant references with illustrations of Paratethyan occurrences (aside from *P. nodosus*). This strict use of "synonymy lists" avoids biasing the stratigraphic and geographic pattern by including poorly documented literature data. Moreover, we avoid a subjective interpretation of the original reference. In several 19th century papers, new taxa are introduced as variation names within chapters on other species. These names are often not accompanied by a clear assignment to a certain genus (e.g., Sacco 1893).

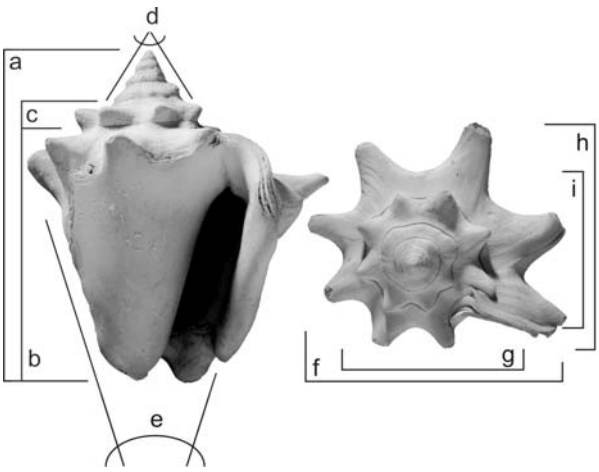

Fig. 3. Measurements used for the statistical analysis. Abbreviations: a, maximum height; b, height of last whorl; c, height of last spire whorl; d, apical angle; e, basal angle; f, dorsal width; g, dorsal width without spines; h, ventral width; i, ventral width without spines.

Systematic paleontology

This paper was triggered by studies of species previously allocated to *Strombus* (*Lentigo*) by Lozouet and Maestrati (1986). These were followed by other studies by Jung and Heitz (2001) and Kronenberg and Lee (2007). In all of these papers, the influential monograph by Abbott (1960) has been the starting point of the assignment of the lineage to *Lentigo* Jousseaume, 1886 (type species by monotypy: *Strombus lentiginosus* Linnaeus, 1758). Lozouet and Maestrati (1986) focused on the affinities of the extant *Strombus granulatus* Swainson, 1822 with the Paleogene European representative of the genus. Thereafter, Jung and Heitz (2001) tried to shed light on the little-known history in the Americas. Kronenberg and Lee (2007) pointed out that the allocation to *Lentigo* was incorrect, and described a new genus, *Persististrombus*, to incorporate a number of these species, based on both shell morphology and DNA research (Latiolais et al. 2006). The genus was established for the extant *Strombus granulatus* Swainson, 1822 in the Panamic Province. Kronenberg and Lee (2007) list several extinct American *Persististrombus* species, to which *Strombus goeldii* Ferreira and Cunha, 1957, described from the Paribas Formation (Lower Miocene) of Brazil, should be added. Later, this concept was also applied to *Strombus latus* Gmelin, 1791 from the African-Eastern Atlantic Province and the Pliocene *Strombus coronatus* Defrance, 1827 in the Mediterranean Sea (Harzhauser and Kronenberg 2008).

Taxonomic concept.—"The species problem" has been already discussed in numerous contributions (see Hausdorf 2011 for a recent overview). Unfortunately it is impossible to extract DNA or examine soft parts of fossil strombids. Thus, we can rely only on shell morphology. As far as our species concept is concerned, we take a pragmatic approach. When morphometric data combined with a passing in geological time (eventually coinciding with a change in paleoenvironmental conditions) show that samples differ from one another, we consider them to be distinct morphospecies. Although this morphospecies concept is inadequate for modern biology, the interpretation of the paleontological record is obviously limited to it. In the case of strombids, however, the molecular analysis of numerous extant strombid taxa, performed by Latiolais (2003) and Latiolais et al. (2006), was not in conflict with the traditional morphospecies assignments. This points to a useful level of reliability of recognizing strombid species based on shell morphology.

Simpson (1961) defined a lineage as "an ancestral-descendant sequence of populations" forming an evolutionary species. Herein, we consider the long-lived and widespread *Persististrombus inflexus* to represent such a lineage. The geo-

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graphically rather isolated and stratigraphically restricted taxa are treated herein as offshoots of this main-lineage. Offshoot is a widely used but not strictly defined term. It may refer to species or to higher taxa (e.g., Strong and Köhler 2009). The term offshoot is used herein sensu Grant (1963), who stated that ancestral species may form offshoot populations which develop into daughter species. In this sense, the term was frequently used to describe a speciation event from the predominant lineage with phenotypic differentiation in both vertebrates and invertebrates (Eldredge and Gould 1972; Johnson 1980; see also Miller 2001). The trigger, which allowed offshoots to develop into distinct morphospecies, might largely have been geographic separation, in the case of Paratethyan strombids. A comparable but much more pronounced speciation event due to geographic isolation has been documented for the Sarmatian Paratethys, when more than 100 new mollusc species evolved endemically in that completely isolated sea (Papp 1954; Harzhauser and Kowalke 2002).

Class Gastropoda Cuvier, 1797

Subclass Caenogastropoda Cox, 1960

Order Littorinimorpha Golikov and Starobogatov, 1975

Family Strombidae Rafinesque, 1815

Genus *Persististrombus* Kronenberg and Lee, 2007

Type species: *Strombus granulatus* Swainson, 1822; Recent, Panamic Faunal Province.

Persististrombus nodosus (Borson, 1820) comb. nov.

Fig. 4A–C.

1820 *Mitra Nodosa* nobis; Borson 1820: 208, pl. 1: 9.
1823 *Str. Bonelli* A. B.; Brongniart 1823: 74, pl. 6: 6a, 6b.
1825 *S. Bonelli*; Basterot 1825: 69.
1847 *Str. Bonelli* Al. Br.; Grateloup 1847: pl. 32: 12.
1847 *Str. lentiginosus* Lin.; Grateloup 1847: pl. 32: 16 (non *Strombus lentiginosus* Linnaeus, 1758).
1893 *Strombus nodosus* (Bors); Sacco 1893: 4.
1923 *Strombus* (*Canarium*) *Bonellii* Brongniart; Cossmann and Peyrot 1923: 326, pl. 8: 1–4, 10.
1984 *Strombus nodosus* var. *mediocanaliculata* Sacco; Fererro-Mortara et al. 1984: 138, pl. 22: 1a, 1b.
1986 *Strombus bonellii* Brongniart, 1825 (sic!); Lozouet and Maestrati 1986: 12, figs. J–K.
2001 *Strombus bonellii* Brongniart, 1823; Lozouet et al. 2001a: 37, pl. 15: 1°, b (cum syn.).

Material.—Eight specimens from the Early Miocene of France (Corbicu Moulin-de-Cerreau, St. Paul-de-Dax Cabanes, Saucats, Pelona; collections: NHMW, Naturalis.

Description.—*Persististrombus nodosus* is a quite polymorphic species. Generally, it is slender with high spire with an apical angle of c. 50° and spire whorls with strong nodes or spines. The last whorl and especially the sutural ramp bear spiral ribs, which vary considerably in number and strength. A very characteristic feature is the somewhat crumpled surface of the last whorl. Another typical feature is a slightly concave area on the last whorl below the shoulder nodes. This concavity passes into the wing, which is rather straight sided or may even be slightly concave in the middle part.

Remarks.—The high spire with the rather narrow apical angle, the spire whorls, which are undercut by the sutures and the crumpled appearance of the last whorl are highly reminiscent of the extant *P. granulatus* (Swainson, 1822). Both features are untypical for Middle Miocene shells of *P. inflexus* (Eichwald, 1830). In ventral view, the rather narrow wing of *P. nodosus* has a nearly straight margin whilst *P. inflexus* develops a convex margin and thickened outer lip.

Borson's (1820: pl. 1: 9) original illustration shows obviously a juvenile strombid, erroneously allocated to *Mitra*. Prior to Borson's *Strombus nodosus*, the name had been used by Röding (1798: 100, species 1287). Röding's (1798) name appeared without a reference and is to be considered as a nomen nudum and thus unavailable. Also, to our knowledge, Röding's name has not been used since its introduction, and is therefore, a nomen oblitum. Pavia (1976) did not locate the specimen during his revision of the Borson collection and therefore he considered *Mitra nodosa* a nomen oblitum. The absence of type specimens, however, is not a justification for Pavia's (1976) action. Moreover, *Strombus nodosus* (Borson, 1820) had been used as a valid name of a strombid, e.g., by Collignon and Cottreau (1927) and Noszky (1940). Therefore, *Strombus nodosus* (Borson, 1820), cannot be considered a nomen oblitum. Much more recently, Nikolov (1993) used the name *Strombus nodosus* in the combination *Strombus* (*Strombus*) *nodosus subcancellata* (Grateloup, 1843?) [sic!].

The name *Strombus bonelli* [sic!], introduced by Brongniart (1823), has been used to denote this species. Sacco (1893) emended the ending to *S. bonellii* in his synonymy list of *Strombus nodosus*. Although the synonymy of *S. nodosus* (Borson, 1820) with *S. bonelli* is widely accepted, as we do also, we cannot rule out the possibility that future research may reveal that *S. bonelli* is distinct from *S. nodosus*. Therefore, it is important to note that Sacco's (1893) emendation, although subsequently widely used, is an incorrect subsequent spelling according to ICZN (1999: article 33.4)

Numerous subspecies and variations have been affiliated with *Persististrombus nodosus* by Sacco (1893) and Cossmann and Peyrot (1923). These Aquitanian and mainly Burdigalian taxa from the Aquitaine and the Colli Torinesi are largely conspecific with *P. nodosus*. Exceptions are "*Strombus" intermedius* Grateloup, 1834—a relatively small sized species with strongly sculptured last whorl and distinct inner lip, that is probably a *Persististrombus* and "*Strombus*" *mitroparvus* Sacco, 1893, (see Lozouet et al. 2001b for illustrations) that may be ancestral to the Western Pacific "*Strombus*" *micklei* Ladd, 1972 and "*Strombus*" *blanci* Tröndle and Salvat, 2010.

Stratigraphical and geographical range.—Unequivocal representatives of *Persististrombus nodosus* are known from the Early Miocene of France and Italy. Additional occurrences of poorly preserved specimens are reported from the Burdigalian of Turkey, Greece and the Iranian Qom Basin (Harzhauser et

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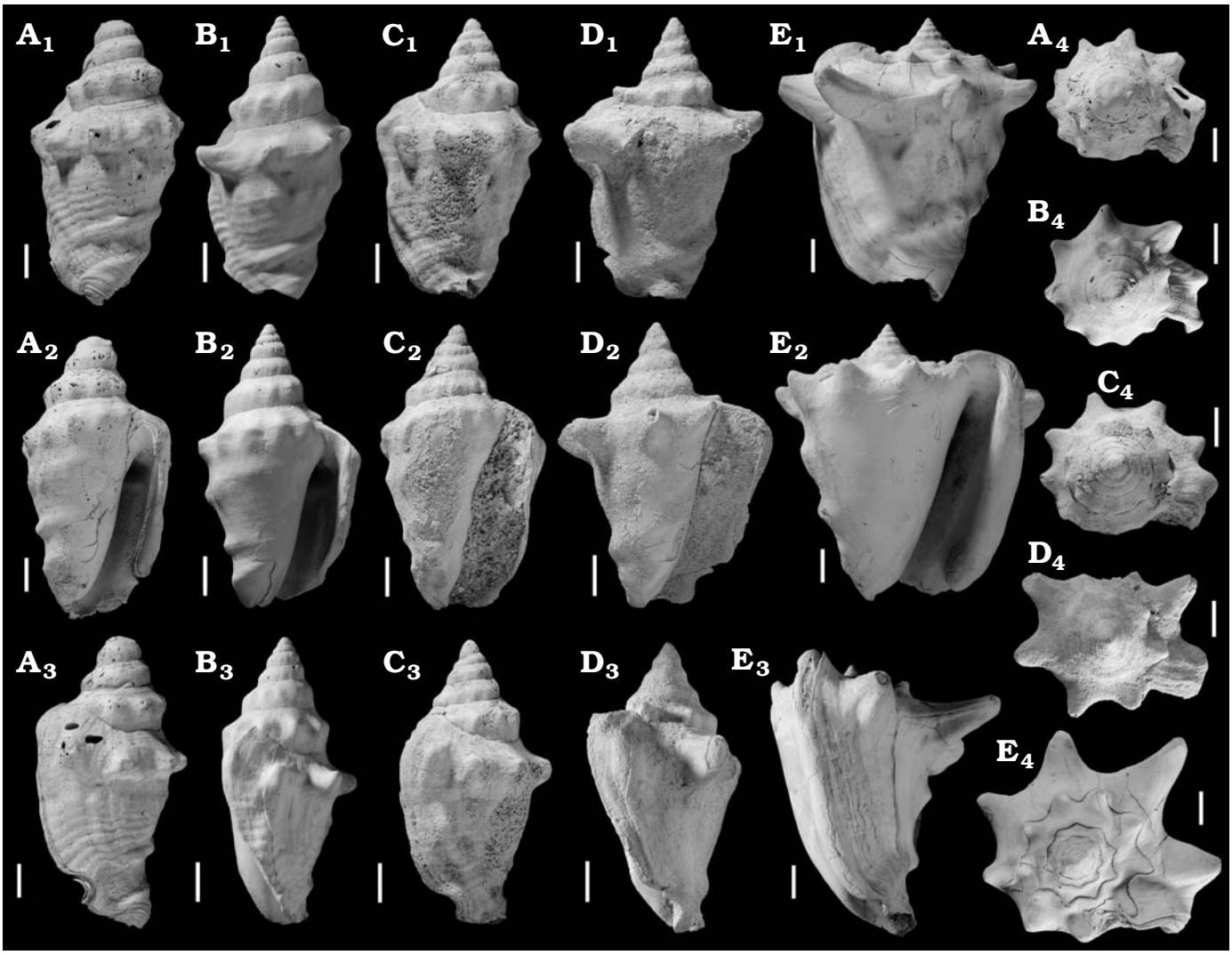

Fig. 4. Miocene–Pliocene strombid gastropods from Europe. **A**–**C**. *Persististrombus nodosus* (Borson, 1820) from the Burdigalian (Early Miocene). **A**. NHMW1911/0006/0290, Pelona, France. **B**. NHMW 2013/0299/001, Saucats, France. **C**. NHMW1851/0017/0116; Colli Torinesi, Italy. **D**. *Persististrombus praecedens* (Schaffer, 1912) from the Burdigalian of Loibersdorf in Lower Austria, NHMW1866/0011/0004. **E**. *Persististrombus coronatus* (Defrance, 1827) from the Pliocene of Tresanti in Italy, NHMW A2588. Dorsal (A_1–E_1), ventral (A_2–E_2), lateral (A_3–E_3), and apical (A_4–E_4) views. Scale bars 10 mm.

al. 2002). Reports of *Strombus nodosus* from the Miocene of Madagascar in Collignon and Cottreau (1927) are dubious. These specimens might rather be related to *Persististrombus deperditus* (Sowerby, 1840) or *Persististrombus kronenbergi* Harzhauser, 2009.

Persististrombus praecedens (Schaffer, 1912) comb. nov.

Fig. 4D.

1912 *Strombus coronatus* Defr. var. *praecedens* Schff.; Schaffer 1912: 149, pl. 51: 21–22.

1971 *Strombus* (*Canarium*) *bonelli praecedens* Schaffer, 1912; Steininger et al. 1971: 391, pl. 9: 1.

1973 *Strombus coronatus* Defrance, 1827; Báldi 1973: 270, pl. 34: 7–8.

1975 *Strombus coronatus* Defrance, 1827; Báldi and Steininger 1975: 345, pl. 3: 6.

Lectotype: Schaffer (1912) illustrates two specimens without designating a type specimen; both specimens are stored in the GBA collection (Schaffer 1912: fig. 21, GBA 1912/004/0011/1; fig. 22, GBA 1912/004/0011/2). Herein, we designate the specimen illustrated as fig. 21 in Schaffer (1912) as lectotype.

Type locality: Loibersdorf, Austria.

Type horizon: North Alpine Foreland Basin, Loibersdorf Formation, Eggenburgian stage (= lower Burdigalian, Lower Miocene), ~20 Ma.

Material.—Four specimens in the NHMW collection and two specimens in the GBA collection from Loibersdorf, Austria.

Description.—A small *Persististrombus*, which does not exceed 75 mm in height. It is characterised by a high spire with an apical angle of 50–62° and a narrow last whorl with an angle of 31–36°. The last whorl accounts for 75–80% of the total height. The spire is stepped; the whorls display a convexity in their middle, which grades into blunt nodes on the last spire whorl. The last whorl develops 6–7 long spiny nodes. These are oriented in adapical direction in Chattian specimens but more horizontal in early Burdigalian ones. The sur-

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face of the last whorl is nearly smooth except for faint traces of spiral threads. Additional spiral threads may occur on spire whorls and on the sutural ramp. A pronounced spiral swelling may appear in the lower third terminating in the stromboid notch. A shallow concavity arises below the spines on the outer surface of the wing. The wing is moderately wide, straight sided and terminates in a weakly thickened outer lip. The outline of the adapical part of the wing follows the slight sutural ramp of the last whorl. It is attached to the spines and does not reach up to the spire whorls.

Remarks.—This species seems to be a Paratethyan offshoot of *P. nodosus* from which it differs in its distinctly smaller size, the lower height of the spire whorls, and the fewer but much more prominent nodes. It might be closely related to the younger *P. inflexus* (Eichwald, 1830) and is somewhat reminiscent of *P. lapugyensis* (Sacco, 1893). A specific separation is based on the smaller size, the lower number of spines, and the lower angle of the last whorl. Moreover, the spiral swelling in the last third of the last whorl is absent in *P. inflexus*. A separation from *P. lapugyensis* is further indicated by the strongly different angle of the aperture-plane relative to the axis, which ranges around 20° in *P. praecedens* but measures 25–30° in *P. lapugyensis*. Finally, the outer lip is strongly thickened in *P. lapugyensis*.

Stratigraphical and geographical range.—The species originates during the Late Oligocene (Chattian) when it is found as rare element in the Hungarian Basin (Báldi 1973). By the Early Miocene (early Burdigalian) it is a typical species in the Loibersdorf Fauna of Lower Austria (Steininger et al. 1971). There, it occurs in sandy coastal deposits associated with a shallow marine mollusc fauna dominated by turritellids, glycymerids and large cardiids (cf. Mandic et al. 2004). Reported occurrences of "*Strombus bonelli*", also spelled as "*S. bonellii*", in the middle and upper Burdigalian deposits of Bavaria and Austria (Hölzl 1973; Harzhauser 2002) may also represent *P. praecedens*. The preservation of that material, however, does not allow a clear identification.

Persististrombus inflexus (Eichwald, 1830) comb. nov.

Fig. 5A–E.

1830 *Strombus inflexus* mihi; Eichwald 1830: 222.

1837 *Strombus tuberculiferus* M. de Serres; Pusch 1837: 127, pl. 11: 12a, b.

1853 *Strombus inflexus* mihi; Eichwald 1853: 210, pl. 8: 18.

1853 *Strombus coronatus* Defr.; Hörnes 1853: 187, pl. 17: 1.

1884 *Strombus coronatus* Defr.; Hoernes and Auinger 1884: 163, pl. 18: 4–5, pl. 19: 1.

1893 var. *voeslauensis*; Sacco 1893: 6 (referring to Hoernes and Auinger 1884, pl. 18: 4).

1893 var. *propenodosa*; Sacco 1893: 6 (referring to Hörnes 1853, pl. 17: 1).

1893 var. *enzesfeldensis*; Sacco 1893: 11 (referring to Hoernes and Auinger 1884, pl. 19: 1).

1912 *Strombus Bonelli* Brongn.; Friedberg 1912: 136, text-fig. 38, pl. 7: 10.

1960 *Strombus* (*Canarium*) *bonelli* Brongniart, 1823; Kojumdgieva and Strachimirov 1960: 130, pl. 35: 3–4.

1966 *Strombus bonellii* Brongniart, 1823; Strausz 1966: 221, pl. 25: 1, pl. 66: 6.

1995 *Strombus* (*Strombus*) *bonellii* Brongniart, 1823; Bałuk 1995: 180, pl. 6: 4–10.

1998 *Strombus* (*Strombus*) *coronatus* Defrance; Schultz 1998: 60, pl. 23: 6.

Material.—36 specimens in the NHMW collection from the Vienna Basin (Grund, Niederleis, Enzesfeld, Vöslau, Baden, Steinebrunn, Grinzing).

Description.—Moderately large robust shells of 70–90 mm height, with exceptionally large specimens of up to 108 mm. Mean apical angle ranges around 58°; the bulky body whorl has an mean angle of 37° and accounts for 70–80% of the total height. A characteristic feature is that the knobby nodes on the spire whorls are often partly covered along their base by a concave sutural band of the following whorl. This feature causes a gradate or regularly conical spire outline. Spire whorls display fine spiral threads in the upper half; these are often crossed by growth lines resulting in a cancellate pattern. Strong spines are frequently developed along the shoulder of the last whorl, usually pointing slightly in adapical direction. Their strength and number is highly variable and their morphology ranges from knobs to spiny nodes. The collection of the NHMW includes specimens with 4–9 spines, but also shells with strongly reduced spines.

While the last whorl of many species allocated to *Persististrombus* have an irregular shell surface with folds, knobs and/or axial swellings, the shell surface of the last whorl of *Persististrombus inflexus* is rather smooth. Nevertheless, several specimens display weak spiral ribs or faint spiral threads on the last whorl. A row of axially elongate nodes may occur close below the row of spines. If these knobs are reduced, at least an indistinct angulation is developed. The wing is wide and terminates in a convex margin with a considerably thickened outer lip. The tip of the wing is slightly expanding up to the height of the last spire whorl but its attachment does not reach above the shoulder or the suture. A thin glossy layer covers the base partly but never develops into a callous pad.

Remarks.—This species is larger and broader than *Persististrombus exbonellii* (Sacco, 1893). The sutural ramp is wider than in *P. lapugyensis* (Sacco, 1893) but distinctly shorter than in *P. exbonellii*. The reduced surface sculpture, the lack of a spiral swelling in the lower third of the last whorl, the wider wing with the expanding tip, and the convex margin of the thickened outer lip allow a separation from the older *P. nodosus*. In addition, the spire whorls of *P. nodosus* are often undercut by the sutures but gradate in *P. inflexus*.

This species was originally described from the Polish-Carpathian Foredeep (Eichwald 1830). The description of Eichwald (1830) appears in a footnote in Latin. Therefore, the name *Strombus inflexus* is available from Eichwald (1830) and is clearly valid. The illustration of the specimen appeared much later, in Eichwald (1853). Thereafter, this taxon was ignored as most palaeontologists considered the Paratethyan specimens as conspecific with *Strombus coronatus* Defrance,

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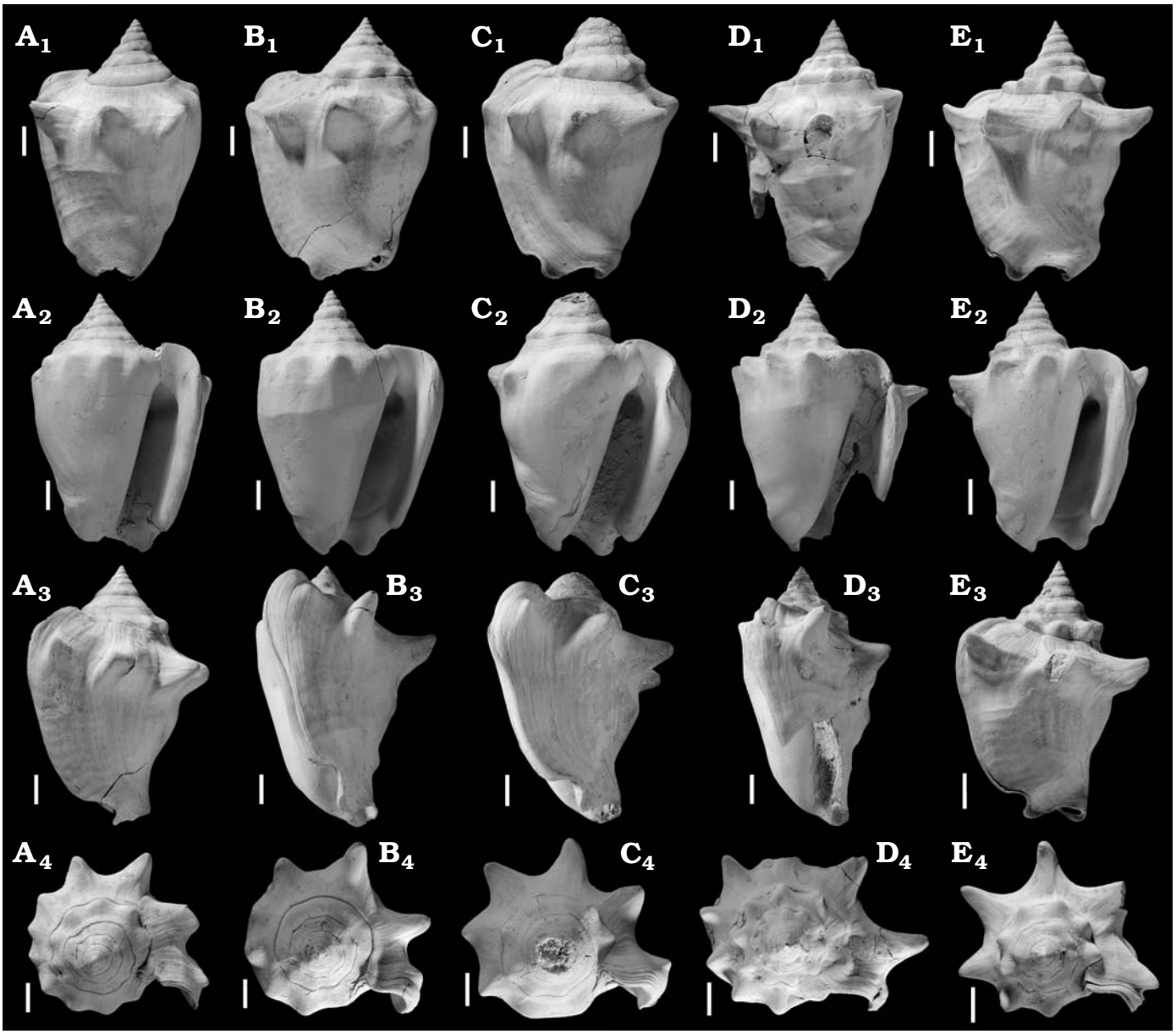

Fig. 5. Strombid gastropod *Persististrombus inflexus* (Eichwald, 1830) from the Middle Miocene of the Vienna Basin. **A**. NHMW2012/0080/0001, Vöslau. **B**. NHMW2012/0081/0001, Enzesfeld. **C**. NHMW1855/0002/0052, Enzesfeld, illustrated in Hoernes and Auinger (1884: pl. 19: 1). **D**. NHMW1874/00024/0041, Vöslau, illustrated in Hoernes and Auinger (1884: pl. 18: 4). **E.** NHMW 2012/0081/0002, Enzesfeld. In dorsal (A_1–E_1), ventral (A_2–E_2), lateral (A_3–E_3), and apical (A_4–E_4) views. Scale bars 10 mm.

1827 or *S. bonelli* Brongniart, 1823 (= *P. nodosus* (Borson, 1820)), which then would have gained priority. Sacco (1893) doubted this synonymy and created a set of new variation names based on Hörnes (1853) and Hoernes and Auinger (1884) without considering *S. inflexus* Eichwald, 1830 and without studying the concerned specimens personally.

The type specimen in Eichwald (1853) is a robust specimen with reduced sculpture, knobby spines and poorly defined nodes on the spire whorls. This morphology is prevalent in the Northern Carpathian Foredeep (e.g., Bałuk 1995) and also typical in the Pannonian Basin (Strausz 1966) and in Bulgaria (Kojumdgieva and Strachimirov 1960). Although this morphotype is predominant, Hörnes (1853: pl. 17: 1) and Hoernes and Auinger (1884: pl. 18: 4) illustrated a rare spiny morphotype with pronounced sculpture. Sacco (1893) proposed the variety names *Strombus nodosus* var. *propenodosa* and *Strombus nodosus* var. *voeslauensis*, respectively, for these shells although both derive from the same clay pit at Vöslau close to Vienna. Thus, this certain morphotype seems to be mainly found in pelitic deposits and might have preferred slightly deeper soft bottom habitats.

Persististrombus inflexus was probably not restricted to the Paratethys. Shells from the Middle Miocene of the Touraine in France, mentioned and illustrated by Gignoux (1913), Peyrot (1938), Glibert (1949; 1952), and those from the Turkish Karaman Basin (Erünal-Erentöz 1958; and in the collections

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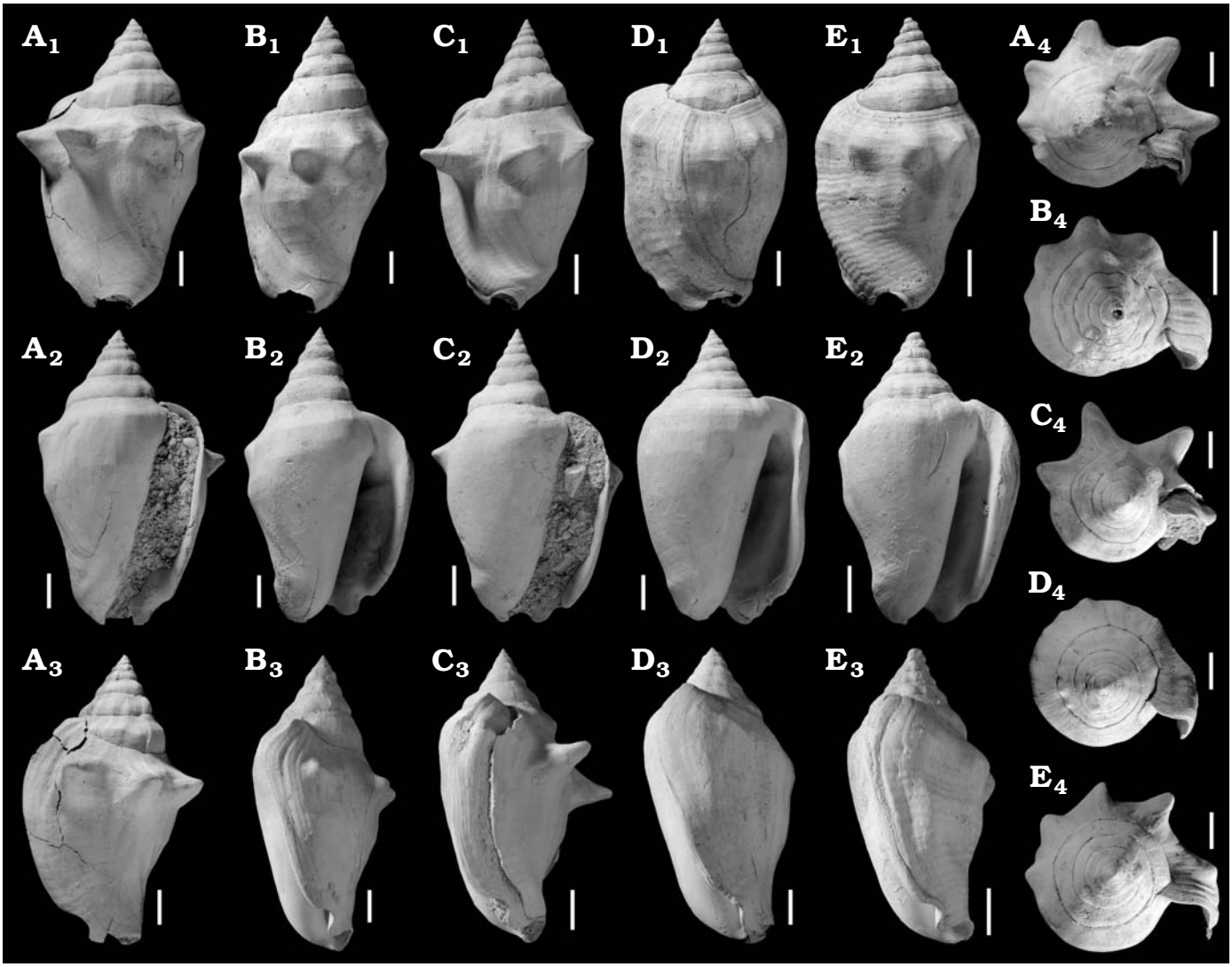

Fig. 6. Strombid gastropod *Persististrombus exbonellii* (Sacco, 1893). **A**–**D**. Middle Miocene of Gainfarn in Lower Austria. **A**. NHMW1855/0045/0420. **B**. NHMW1855/0045/0419. **C**. NHMW1846/0037/0185. **D**. NHMW1847/0037/0058. **E**. NHMW62275, Middle Miocene of Vöslau in Lower Austria. In dorsal (A_1–E_1), ventral (A_2–E_2), lateral (A_3–E_3), and apical (A_4–E_4) views. Scale bars 10 mm.

of the Naturalis Biodiversity Center) are considered herein to belong to the same lineage.

Stratigraphical and geographical range.—Widespread during the Langhian and Early Serravallian in the entire Central Paratethys. Langhian occurrences from the proto-Mediterranean are unknown probably because of the low amount of shallow marine fossiliferous Middle Miocene deposits in that area. The species (or a closely related species) reached the Loire Basin along the Atlantic coast and the Karaman Basin in Turkey during the Serravallian.

Persististrombus exbonellii (Sacco, 1893) comb. nov.

Figs. 6A–E, 7A.

1853 *Strombus bonellii* Brong.; Hörnes 1853: 189, pl. 17: 2–6.

1884 *Strombus bonellii* Brongn.; Hoernes and Auinger 1884: 164, pl. 19: 2a, 2b.

1893 var. *exbonellii*; Sacco 1893: 11 (referring to Hoernes and Auinger 1884, pl. 19: fig. 2).

Holotype: NHMW1855/0045/0419, complete shell (Fig. 6B).

Type locality: Gainfarn, Austria.

Type horizon: Vienna Basin, Badenian (= Langhian, Middle Miocene), upper Lagenidae Zone; ~14.5–14.0 Ma; illustrated in Hoernes and Auinger (1884: pl. 19: 2a, 2b).

Material.—70 specimens from the NHMW collection from Gainfarn and Vöslau (Vienna Basin, Austria).

Description.—Elongate and rather delicate shells of 60–90 cm adult height. Protoconch with 3.25–3.75 smooth rapidly enlarging whorls of increasing convexity. Nepionic whorl slightly sunken. Close to the abapical suture one specimen exhibits faint traces of a spiral ornamentation on the last protoconch whorl. Spiral ribs of the teleoconch start abruptly after the slightly opisthocyrt termination of the protoconch. The high spire has an apical angle of 51–65° with a mean of 57°. The body whorl angle of adult specimens ranges from 30° to 40° with a mean of 35°; its height accounts for 76% of

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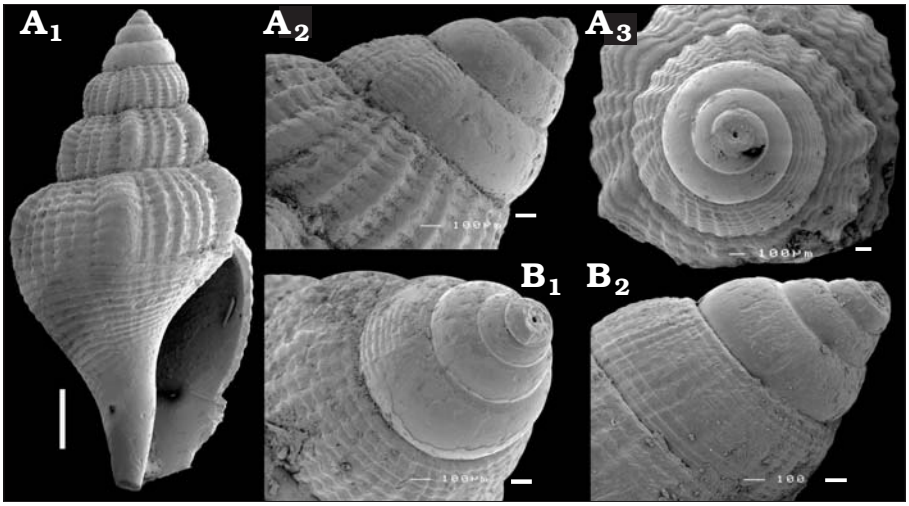

Fig. 7. Strombid gastropods from Austria and Turkey. **A**. Juvenile specimen with protoconch of *Persististrombus exbonellii* (Sacco, 1893), NHMW 2013/0299/0002, from the Middle Miocene of Gainfarn in Lower Austria, in ventral (A_1, A_2), and apical (A_3) views. **B**. Protoconch of *Persististrombus inflexus*, NHMW 2013/0299/0003, from the Serravallian of Karaman in Turkey, in ventro-apical (B_1) and ventral (B_2) views. Scale bars 1 mm.

the total height on average. The spire whorls are high and develop indistinct knobs or only a weak angulation. The last whorl develops a shoulder with nodes or spines, which is separated from the thread-like sutures by a wide and steep sutural ramp. The specimens are characterised by reduced sculpture; spines are restricted to the dorsal part of the last whorl and are only developed on adult specimens. Their number ranges around 4–5; higher numbers are very rare whilst many species lack spines even as adults. No additional spiral ribs with nodes are usually developed on the last whorl, although a distinct angulation may occur. The ventral part of the last whorl is smooth, covered by a thin slightly glossy layer. Its shoulder is only slightly angulated and lacks any nodes or spines. Shell surface is usually smooth; spiral sculpture is strongly reduced but may be present in the upper part of the spire whorls and sometimes may appear close to the edge of the outer lip. The wing is thin shelled and terminates in an insignificantly thickened lip, with slightly convex margin in most specimens. Typically, the wing expands slightly adapically and is attached to the shoulder or may even reach up to the suture. Its posterior part of the wing is always sloping without forming a tip or lobe.

Remarks.—The high, regularly conical spire and the sloping sutural ramp with the low position of the shoulder on the last whorl are unique in *Persististrombus*. The angle formed by the aperture-plane relative to the shell axis ranges from 16° to subparallel, whilst all other species display a larger angle.

We consider this taxon to be an offshoot from the widespread *Persististrombus inflexus*-lineage. However, it should be noted that *P. exbonellii* has only a limited, i.e., local, distribution. It is also restricted to a very short time slice within the Middle Miocene, and may therefore be an ecomorph. On the other hand, in its high abundance (it is represented by hundreds of shells in many museum and private collections) it is very homogenous in its morphology. The commonness of this species was the main reason for the long discussions by Hörnes (1853) and Hoernes and Auinger (1884) about the presence of *Strombus bonelli* within the Middle Miocene of the Vienna Basin.

Stratigraphical and geographical range.—This species is known so far only from the area of Gainfarn and Vöslau in Lower Austria. There, it developed a huge populations in seagrass meadows within a protected embayment (Zuschin et al. 2007).

Persististrombus lapugyensis (Sacco, 1893) comb. nov.

Fig. 8A–C.

1884 *Strombus coronatus* Defr.; Hoernes and Auinger 1884: 163, pl. 18: 1–3.

1884 *Strombus bonelli* Brongn.; Hoernes and Auinger 1884: 164, pl. 19: 3–4.

1893 *S. coronatus* la var. *lapugyensis*; Sacco 1893: 11 (referring to Hoernes and Auinger 1884, pl. 18: 1).

Holotype: NHMW1866/0040/0270, adult specimen (Fig. 8C).

Type locality: Lãpugiu de Sus (= Lapugy), Romania.

Type horizon: Transylvanian Basin, Badenian (= Langhian, Middle Miocene), lower Lagenidae Zone; ~16–15 Ma; illustrated in Hoernes and Auinger (1884: pl. 18: 1).

Material.—29 specimens in the NHMW collection from the Transylvanian Basin (localities Lãpugiu de Sus, Bujtur, Coşteiu de Sus), Romania.

Description.—Robust shells; moderately high spire with a mean apical angle of 62°. The height of adult shells ranges from 50 to 110 mm with a mean of 87 mm; the body whorl height attains up to 90% of the total height with a mean of 79%. The last spire whorl, and sometimes already the penultimate one, develop pronounced spines; the suture of the following whorl runs distinctly below these spines. The last whorl is characterised by 7–9 very large and long spines; most shells bear 8 spines; rarely up to 12 may be developed. The low sutural shelf is smooth or may bear faint spiral threads. Below the shoulder, the smooth last whorl is rapidly

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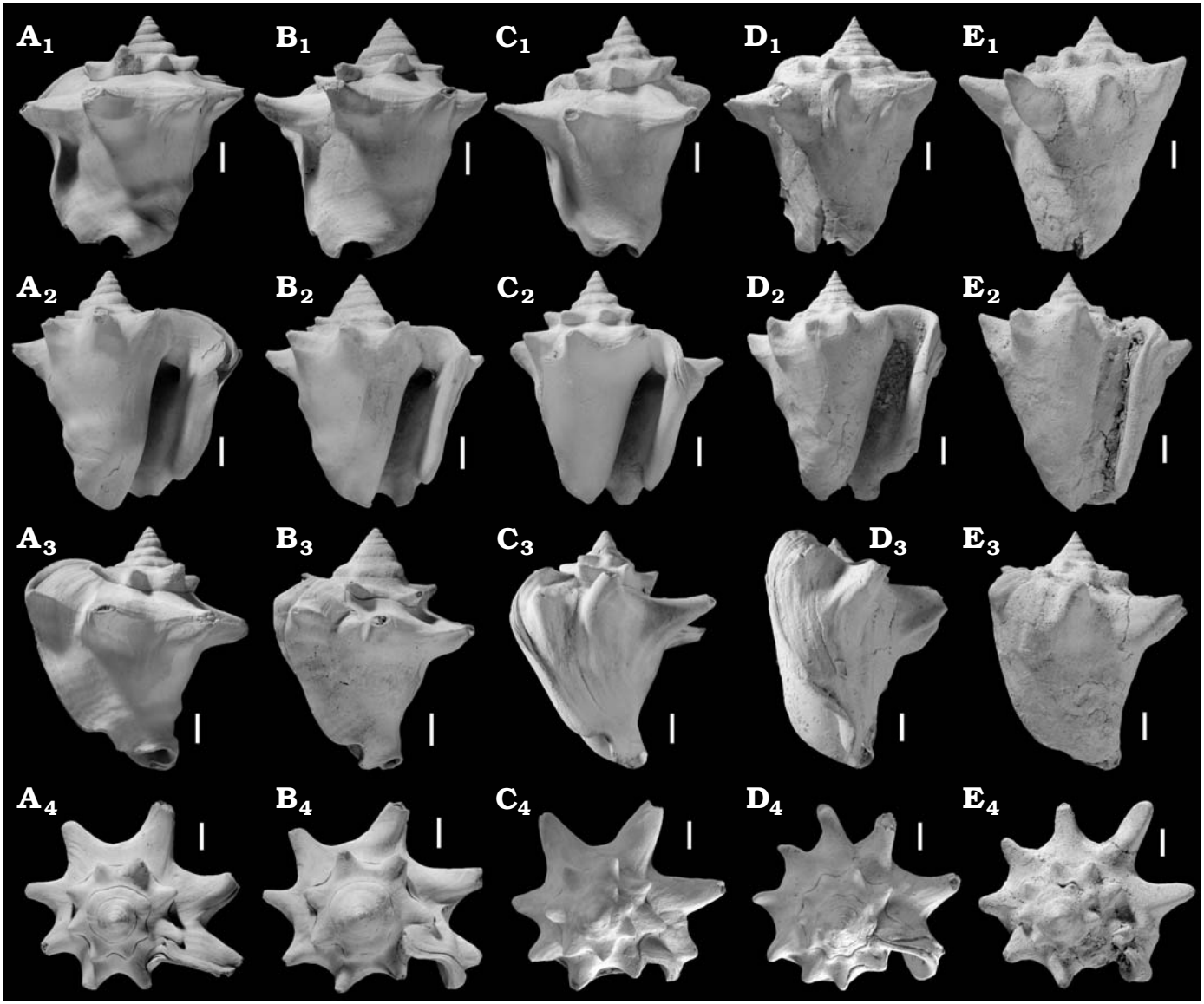

Fig. 8. Strombid gastropods from Europe. **A**–**C**. *Persististrombus lapugyensis* (Sacco, 1893) from the Langhian (Middle Miocene) of Lãpugiu de Sus in Romania. **A**. NHMW1854/0035/0150. **B**. NHMW1855/0043/0017. **C**. NHMW1866/0040/0270, illustrated in Hoernes and Auinger (1884: pl. 18: 1). **D**, **E**. *Persististrombus pannonicus* sp. nov. from the Serravallian of the Oberpullendorf Basin. **D**. Holotype, NHMW1930/0006/0058, Ritzing, Austria. **E**. Paratype, NHMW1970/1396/0609, Brennberg, Austria. Note the different angles between the aperture and the axis in both species (A_3–E_3) and the different spine morphology (A_4–E_4). In dorsal (A_1–E_1), ventral (A_2–E_2), lateral (A_3–E_3), and apical (A_4–E_4) views. Scale bars 10 mm.

contracting with a mean angle of 35°. Rarely, a spiral row of low nodes is developed which terminates in the wide stromboid notch. The wing is expanding and grades into a strongly thickened outer lip. A glossy sheet of several layers covers the base but never forms a callous pad.

Remarks.—These shells were the main reason for the frequent confusion by many authors with the Pliocene *Persististrombus coronatus* (Defrance, 1827). Sacco (1893) recognized that the specimens from the Paratethys are not fully conspecific with the younger Italian ones representing true *P. coronatus* (Fig. 4E). He tried to overcome this problem by proposing the variation name *Strombus coronatus lapugyensis* for the stratigraphically older specimens. The similarities with *P. coronatus*, however, are only superficial. A main difference is the morphology of the spire: the fourth and fifth teleoconch whorls of *P. coronatus* are very low. Therefore, the suture runs along the backs and tips of the spines of the preceding whorls. In contrast, the sutures of the corresponding whorls of *P. lapugyensis* are usually distinctly below the knobs. Juvenile shells of *P. coronatus* develop a distinct shoulder of the last whorl, whereas juveniles of *P. lapugyensis* display a convex outline without prominent shoulder. The stromboid notch of *P. lapugyensis* (and all other species) is shallower and relatively wider than that of *P. coronatus.* The Pliocene strombid tends to develop two spiral ridges or two rows of knobs on the dorsal side of the last whorl aside from the shoulder spines. *P. lapugyensis* lacks the middle row and even the lower row occurs only in few specimens.

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We consider this taxon to be a geographically distinct offshoot of *Persististrombus inflexus*. It seems to be restricted to the early Langhian in the Transylvanian Basin, where it occurs in large numbers. Its occurrence coincides with the Middle Miocene Climatic Optimum (Harzhauser and Piller 2007) and thus, this species might be indicative of near-tropical conditions in the southern Paratethys Sea during the early Langhian. This is supported by the co-occurrence of the strombid *Europrotomus schroeckingeri* (Hörnes in Hoernes and Auinger 1884), which is restricted to this short time span and was shown to be a thermophilic species by Kronenberg and Harzhauser (2012).

Stratigraphical and geographical range.—*Persististrombus lapugyensis* is restricted to the early Badenian (early Langhian) of the Transylvanian Basin where it is recorded from Lãpugiu de Sus, Bujtur and Coşteiu de Sus in Romania.

Persististrombus pannonicus sp. nov.

Fig. 8D, E.

1932 *Strombus coronatus* Defr.; Janoschek 1932: 75, 83, 85.
1932 *Strombus* (*Canarium*) *bonelli* Brongn.; Janoschek 1932: 75.

Etymology: Referring to the Roman province of Pannonia.

Type material: Holotype: NHMW 1930/0006/0058, height: 88.8 mm, diameter: 78.4 mm, Ritzing, Fig. 8D; Paratype: NHMW 1970/1396/0609, height: 102.7 mm, diameter: 86.9 mm, Brennberg, Fig. 8E.

Type locality: Ritzing, Kuchelbach section, Oberpullendorf Basin, Austria.

Type horizon: Coastal sand of the Ritzing Formation, Badenian, Serravallian, Middle Miocene; c. 13 Ma.

Material.—Six shells from Ritzing and Brennberg (Austria) in the NHMW collection.

Description.—Bulky robust shells with pronounced sculpture. The height ranges around 80–100 mm; the spire is broad with an angle of c. 60–70°. Nodes appear already on the penultimate spire whorl and grade into prominent spines on the last spire whorl. Early spire whorls are covered up to their middle by the following whorl, often forming a wavy sutural band, which covers the spines up to just below their tips. On later spire whorls, the suture is gradually shifting slightly below the tips of the spines but the following whorl covers always the base of the spines. The spines of the last whorl are very irregular in shape; they are axially elongate at their base, much higher than wide in cross section, and often display concave areas along their flanks. They are deflected leftwards in apical view and point in adapical orientation. Aperture moderately wide with broad sinuous adapical tip which is attached to the suture; outer lip thickened with straight sided or sigmoidal margin. Shell surface of adult shells smooth; only subadults display weak spiral threads.

Remarks.—The sculpture of this species is highly reminiscent that of *P. coronatus*. The two forms differ, however, in the wider and shallower stromboid notch and the higher spire of *P. pannonicus*. The angle of the last whorl is smaller compared to the squat *P. coronatus* and the surface of the last whorl lacks the spiral sculpture of nodes as typical for *P. coronatus*. Its adult shells do not attain the large size of *P. coronatus*. Despite the similarities, we consider this taxon to be a distinct species, which derived from the *P. inflexus*-lineage, occupying the morphospace that is realized later by *P. coronatus* during the Pliocene. Coeval shells from the more northern Vienna Basin (e.g., Grinzing section) represent typical *P. inflexus*.

The laterally compressed morphology of the spines is unique within Paratethyan representatives of *Persististrombus inflexus* and allows a clear separation from the older *P. lapugyensis*. Moreover, the spines of the last spire whorl are free in *P. lapugyensis* but partly covered in *P. pannonicus*.

The type of spine morphology might be characteristic for late Middle Miocene shells of a species related to the *Persististrombus inflexus*-lineage. Shells in the collection of the Naturalis Biodiversity Center from the Serravallian of the Turkish Karaman Basin (Fig. 7B) display similar tendencies. Their spire angle is smaller than in *P. pannonicus*, the shells are more elongate on average, and the largest shells attain up to 107 mm in height.

Stratigraphical and geographical range.—This species is known so far only from the late Badenian of the Oberpullendorf Basin within the Pannonian basins complex, where it was found at several localities (Janoschek 1932).

Discussion

Morphometrics.—The comparable outline of the specimens and the broad range of intraspecific variability prevent a clear separation of the proposed taxa based only on height-width data (SOM). Moreover, juvenile specimens hardly differ morphometrically. Therefore, the data set was reduced to adult shells in Fig. 9. The best separation of the taxa in scatter plots is achieved when the relation of the height of the last spire whorl with the total height is compared to the apical angle. Especially the height of the last spire whorl is a significant character, which allows distinguishing *P. coronatus*-like species from the Pliocene *P. coronatus*. Fig. 9 illustrates a clear transition from the *P. nodosus*-field, via *P. praecedens*, and a cluster of *P. exbonellii* to *P. lapugyensis*. Although overlapping with *P. pannonicus* and *P. lapugyensis*, the bulk of *P. coronatus* forms a clearly separate cluster.

A principal component analysis on the full data set including all specimens reveals a similar pattern (Fig. 10). A separation of a cluster with subadult specimens is mainly caused by size effects. This indicates that all juvenile shells of the *Persististrombus inflexus*-lineage are very similar and that species-specific features arise only later during ontogeny. Adult shells cluster in separate fields: *P. nodosus* and *P. praecedens* show no overlap. Similarly, adult shells of *P. coronatus, P. lapugyensis*, and *P. exbonellii* settle in separate areas in the plot, being separated mainly by the characters "spire angle", "height of the last spire whorl" and the "number of spines on the last whorl". As the characters "height of the last spire whorl" and "apical angle" turned out to be sig-

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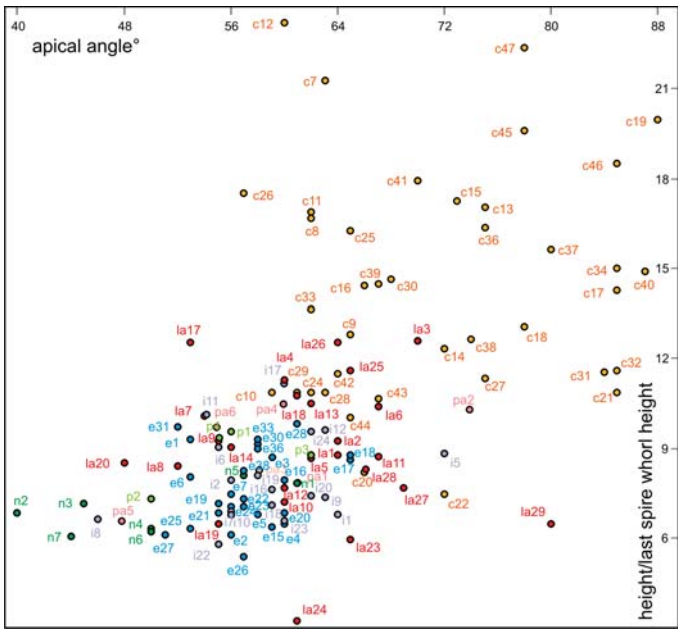

Fig. 9. Scatter plot of adult specimens of various *Persististrombus* species based on the apical angle and the relation between total height and the height of the last spire whorl. Abbreviations refer to the specimens indicated in SOM: c, *P. coronatus*; e, *P. exbonellii*; i, *P. inflexus*; la, *P. lapugyensis*; n, *P. nodosus*; p, *P. praecedens*; pa, *P. pannonicus*.

nificant, a further PCA was performed on a reduced data set including the relation "height/width (max)" (Fig. 11). Again, *P. coronatus* separates from the *P. inflexus* and its offshoots. The latter being split into a *P. lapugyensis* and a *P. exbonellii* cluster with specimens of *P. inflexus* as intermediates. The analyses document the difficulties to separate juvenile shells of *Persististrombus* based on the implemented measurements but perform successful for adult shells. In all analyses, a separation of the Late Miocene to Pliocene *Persististrombus coronatus* from Early to Middle Miocene members of the *Persististrombus inflexus*-lineage and its offshoots is obvious.

Extrinsic factors triggering speciation.—As a whole, all specimens of the *P. inflexus*-lineage display a degree of variability similar to that of Recent species of *Persististrombus*, viz. *P. granulatus* (Kronenberg and Lee 2005) and, to a slightly lesser extent, *P. latus* (DeTurck et al. 1999). Our data show that there is a tendency for an iterative but independent development of spiny morphs. This phenomenon is not restricted to the *P. inflexus*-lineage and its offshoots but was also documented for other strombids (Landau et al. 2011). Absence or presence of predators has bearing on shell morphology. In laboratory conditions, the presence of the lobster *Panulirus argus* induced changes in both behavior and shell growth, i.e., shells exposed to the lobsters grew slower, yet the shell weight remained the same (Delgado et al. 2002). Also Herbert et al. (2004) noted the development of anti-predatory traits in members of the *Strombus alatus* complex in presence of a predator. This pressure was concluded based on an increase in repair-marks by over 90%. Anti-predatory trait evolution in these *Strombus* was inferred from increases in adult mean size and lip thickness, the percentage of individuals with knobs on the last whorl, the maximum number

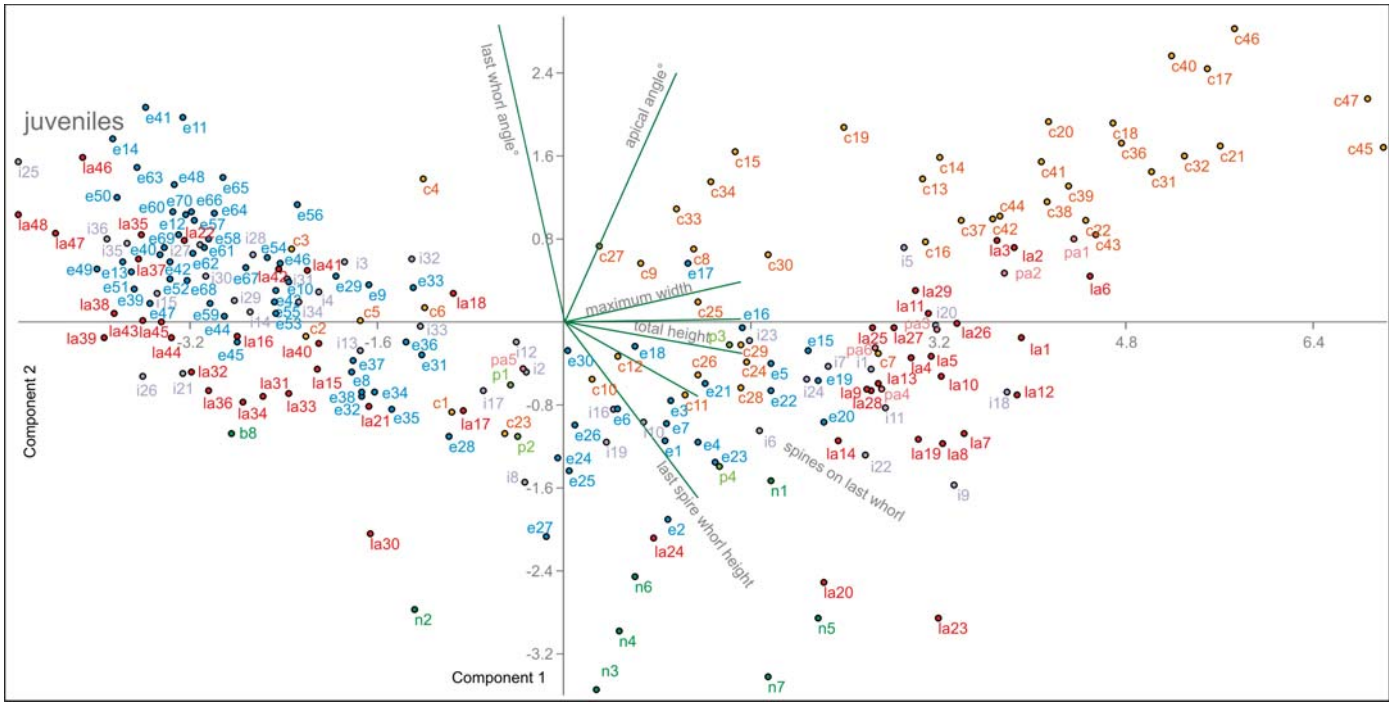

Fig. 10. Principal component analysis based on all specimens (see text for details) performed with the software package PAST (Hammer et al. 2001). Abbreviations refer to the specimens indicated in SOM: c, *P. coronatus*; e, *P. exbonellii*; i, *P. inflexus*; la, *P. lapugyensis*; n, *P. nodosus*; p, *P. praecedens*; pa, *P. pannonicus*.

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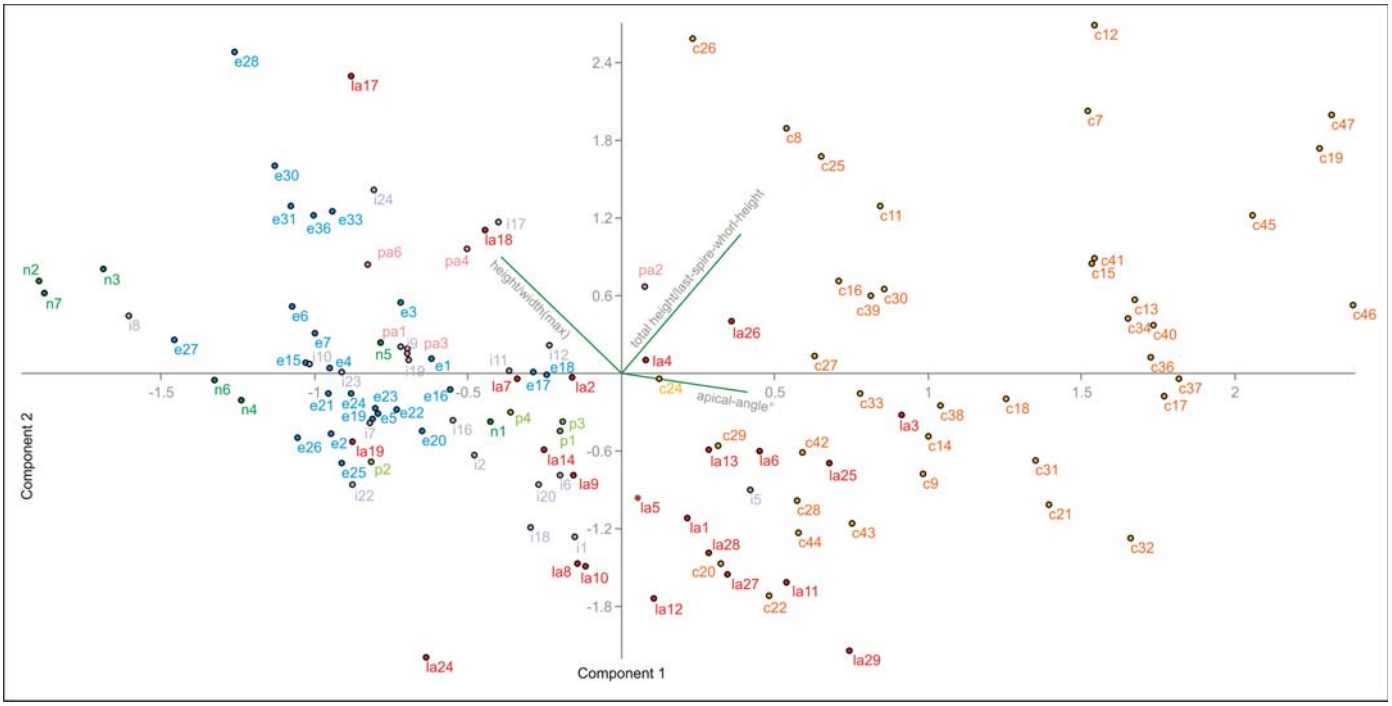

Fig. 11. Principal component analysis based on adult specimens (see text for details) performed with the software package PAST (Hammer et al. 2001). Abbreviations refer to the specimens indicated in SOM: c, *P. coronatus*; e, *P. exbonellii*; i, *P. inflexus*; la, *P. lapugyensis*; n, *P. nodosus*; p, *P. praecedens*; pa, *P. pannonicus*.

of knobs on the last whorl and the growth rates, deduced from oxygen stable isotope sclerochronology. A similar scenario might have played a role in the development of the strongly spined species in the Paratethys. A statistical analysis of repair-marks is beyond the scope of this study. Nevertheless, our unpublished observations indicate that the frequency of repair-marks on shells of the spiny *P. lapugyensis* does not differ very much from that of the rather smooth *P. exbonellii* and is low in both cases.

Another factor influencing the radiation of the *P. inflexus*-lineage in the Paratethys might be related to paleogeography. Three of the described species are chronologically and geographically well separated from each other (Fig. 1). This pattern might be caused by the archipelago character of the Central Paratethys during the Middle Miocene (Rögl 1998). The Paratethys was connected to the Proto-Mediterranean Sea only through relatively narrow channels (Fig. 1), whilst the Central Paratethys itself was a dead end sea, i.e., with no connections to other ocean basins. These channels in all probability have hampered faunal exchanges, as now is the case between the Mediterranean Sea and the Black Sea, the Atlantic and the Mediterranean Sea, and the Red Sea and Persian Gulf with the Indian Ocean. The rapid changes in relative sea-level combined with the tectonic activity in an active back-arc/fore-arc basins system may have led to a series of separations and reconnections of shallow marine faunas. Large scale separations of the north-eastern branch of the Paratethys (e.g., Polish-Carpathian Foredeep) and the southern parts (Pannonian basins complex) also had significant impact on the stable isotope composition of the sea-water (Latal et al. 2006). Thus, the geographic isolation of populations might have had a strong impact on speciation as already documented for some nassariid gastropods (Harzhauser and Kowalke 2004).

Oligocene to Holocene biogeography of *Persististrombus*.—The roots of the genus reach back to the Tethyan Oligocene. The oldest species that can be attributed to *Persististrombus* is *Strombus radix* Brongniart, 1823, from the Piedmont Basin and the Vicentin in Italy (Rovereto 1900; Fuchs 1870), the Mesohellenic Basin in Greece (MH own observation), and Bulgaria (Karagiuleva 1964). In the west, it reached even the Adour Basin in France (Lozouet and Maestrati 1986). Its easternmost occurrences are recorded from the Rupelian of the Central Iranian Esfahan-Sirjan Basin and the Kutch Basin in India (Harzhauser 2004; Harzhauser et al. 2009). This Oligocene species is unknown so far from the Paratethys. Already during the Oligocene, an eastern lineage established in the Rupelian *Acropora* reefs of the Arabian Peninsula, represented by the small and spiny *Persististrombus bernielandaui* (Harzhauser, 2007). This lineage continued into the Early Miocene and is represented by *P. gijskronenbergi* (Harzhauser, 2007) in Oman and *P. kronenbergi* Harzhauser, 2009 in Tanzania during Aquitanian times. Burdigalian species in this lineage are *P. deperditus* (Sowerby, 1840) in Kutch in northern India and *P. quilonensis* (Dey, 1961) from Kerala in southern India. The last known species in the Indo-West-Pacific Region (IWP) is *P. preoccupatus* (Finlay, 1927) from the Late Miocene of Borneo (Beets 1941). Thus, the genus seems to have become extinct in the IWP around the Miocene/Pliocene boundary. However, a genus still pending de-

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scription that probably arose from a *Persististrombus* ancestor, was present in Indonesia during the Miocene, and persisted until the latest Pliocene (GCK, unpublished data).

Transatlantic migration of the genus into the Americas took place during the Early Miocene when *Persististrombus* appears as *P. goeldii* (Ferreiro and Cunha, 1957) in the Paribas Formation of Brazil, and as *P. aldrichi* (Dall, 1890), *P. chipolanus* (Dall, 1890), and *P. mardieae* (Petuch, 2004) in the Chipola Formation of Florida (Petuch 2004). After a major stratigraphic gap, the genus re-appears in the Americas and enters the eastern Pacific. At present it is not clear whether *Persististrombus* got extinct and re-invaded the Americas or that specimens are not preserved or not yet discovered. Based on the morphology of *P. granulatus*, which is rather close to *P. radix* and *P. nodosus* we are inclined to believe the latter to be the most likely scenario. Afterwards, *P. toroensis* (Jung and Heitz, 2001) and *P. insulanus* (Jung and Heitz, 2001), possibly synonyms of *P. granulatus* (Swainson, 1822), are reported from the Pliocene of Panama. *P. barrigonensis* (Jung and Heitz, 2001), subsequently synonymized with *P. granulatus* by Landau and Silva (2010), occurs in the Late Miocene or Pliocene of Venezuela, and *P. obliteratus* (Hanna, 1926) in the Pliocene of California (all data from Wieneke et al. 2010, see also Kronenberg and Lee 2007). *Persististrombus granulatus* has been reported from the Lower Pliocene member of the Imperial Formation in California (Powell, 1988), and survives to the Recent in the Panamic province (Emerson and Old 1963).

In the Western Tethys, the Oligocene *P. radix* was followed during the Aquitanian and Burdigalian by *P. nodosus* (Borson, 1820). Its geographic range was comparable to that of its Oligocene precursor spanning from the Bay of Biscay in the west via the Mediterranean area probably to the Qom Basin in the east (Harzhauser et al. 2002). Unequivocal Early Miocene Paratethyan occurrences are unknown so far. The small *P. praecedens* (Schaffer, 1912), however, dwelled as Paratethyan endemic from Chattian to early Burdigalian times. The development of *Persististrombus* in the Paratethys during the late Burdigalian (Ottnangian and Karpatian regional stages) is unclear as the few specimens are too fragmentary or poorly preserved for identification at the species level.

With the onset of the Middle Miocene Climatic Optimum, the genus become very successful in the Paratethys and as *P. inflexus* (Eichwald, 1830) is present in even the northernmost basins in the Polish-Carpathian Foredeep. Nevertheless, it did not enter the Eastern Paratethys where no strombids are known so far (Iljina 1993).

P. lapugyensis developed geographically discrete populations around 16–15 Ma. in the southern part of the Paratethys during the Middle Miocene Climatic Optimum. At the same time, *P. inflexus* is recorded in all northern basins such as the North Alpine Foreland Basin, the Vienna Basin and the Polish-Carpathian Foredeep (see systematic chapter). A second offshoot, the delicate and elongate *P. exbonellii* (Sacco, 1893), developed around 14.5–14.0 Ma. in the seagrass meadows along the western margin of the Vienna Basin and disappeared soon thereafter. The evolution of this species coincides with the cooling during Miocene Climate Transition when a drastic reduction of gastropod species occurred in the Paratethys Sea (Harzhauser and Piller 2007). The last, regionally defined offshoot developed during the Serravallian in an embayment of the Pannonian basins complex around 13.0 Ma ago, resulting in the *P. coronatus*-like *P. pannonicus*. Still, *P. inflexus* was represented at least as far north as the Vienna Basin. At that time, *P. inflexus* also occurred in the Mediterranean Sea, where it formed huge populations in the Turkish Karaman Basin (MH unpublished data) and appeared even in the Loire Basin (Glibert 1949). The poor documentation of the genus in the Middle Miocene of the Mediterranean area is probably linked to the low amount of shallow marine siliciclastic in Middle Miocene deposits. The wealth of Langhian and Serravallian deposits in the Paratethys Sea is contrasted by relatively few coeval outcrops in the Mediterranean area. Therefore, the impression that the *Persististrombus inflexus*-lineage experienced an extraordinary bloom only in the Paratethys Sea has to be considered with caution.

Due to the changing water chemistry of the Paratethys, the entire *Persististrombus inflexus*-lineage became extinct during at the end of the Serravallian together with most stenohaline marine taxa (Rögl 1998; Harzhauser and Piller 2007). It seems to have vanished also in the Mediterranean area around the Middle/Late Miocene boundary and became replaced by *Persististrombus coronatus*. This species appears during the Tortonian in the Mediterranean Sea (Sacco 1893) and persisted to the Messinian of Libya from where Bandel (2007) reported on aberrant specimens. Later it becomes a very common species during the Zanclean and the Early Piacenzian (Sacco 1893; Stchépinsky 1939, 1946; Harzhauser and Kronenberg 2008). It might have originated along the West African Coast as suggested by a report of the species by Brébion (1983) from the Middle or Late Miocene of Angola. An Atlantic distribution of *P. coronatus* is documented by Meco (1977) from the Pliocene of the Canary Islands.

Persististrombus coronatus disappears from the Mediterranean Sea completely with the onset of the Late Pliocene cooling (Landau et al. 2004) and seems to be extinct thereafter. During the Pleistocene *Persististrombus latus* (Gmelin, 1791) represents the European *Persististrombus*-lineage. This extant species is restricted to the African-Eastern Atlantic Province but invaded the Mediterranean Sea during the Pleistocene. There it appears during the warm phases of the Marine Isotope Stages 7 and 5 (De Torres et al. 2009) and probably also during MIS 3 (Zazo et al. 1984; Rögl et al. 1997).

Implications for paleoclimate reconstructions.—The genus is represented by two extant species: *P. granulatus* (Swainson, 1822) in the Panamic Province and *Persististrombus latus* (Gmelin, 1791) in the African-Eastern Atlantic Province. The distribution data of both taxa are shown in Fig. 12 and compared with long-term summer and winter sea surface temperatures, based on LEVITUS (1994).

Persististrombus latus occurs in an area from the Rio d'Oro in Morocco/Mauritania in the north to Angola in the

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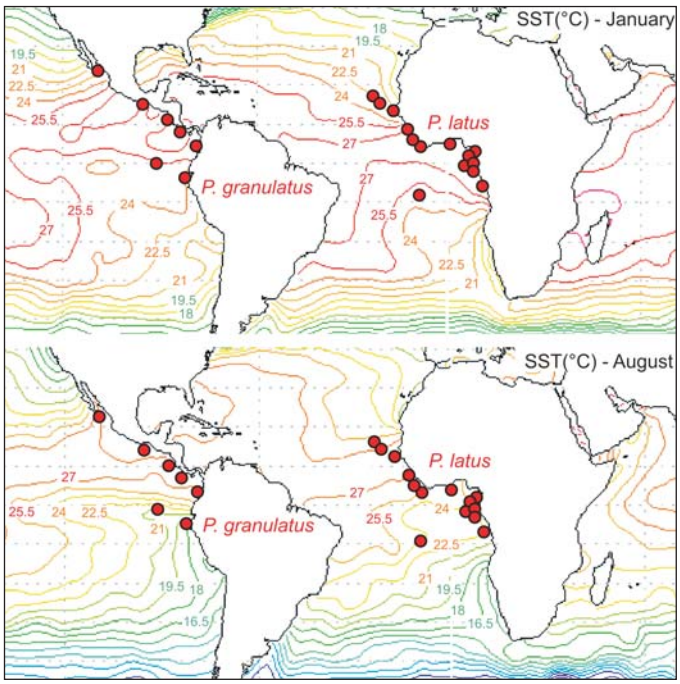

Fig. 12. Distribution of the two extant species of *Persististrombus* in the Panamic Province and the African-Eastern Atlantic Province (after Meco 1977 and Kreipl and Poppe 1999). The data are plotted on sea surface temperature maps generated with the World-Ocean-Atlas-Data visualization program of the NOAA based on the LEVITUS 1994 data sets (http://www.esrl.noaa.gov/psd/).

south (Rolán and Ryall [1999]), being limited in the north by the Canary Current and in the south by the Benguela Current (Meco et al. 1997). In both areas, the 20–21°C SST isotherms seem to be a limiting factor for its frequent distribution. Its northern-most limit is the Cape Verde Islands (Kreipl and Poppe in De Turck et al. 1999) where water temperatures are usually warmer than 16°C (Meco 1977), which seems to be the very limit for dispersal of this species.

Persististrombus granulatus occurs from the Baja California in the north via Panama and Costa Rica to Ecuador in the South to the Galapagos Islands in the west (Kreipl and Poppe in De Turck et al. 1999). Its northern boundary coincides with the cool California Current in the north and the Peru Current in the south. Sea surface temperature maps indicate that the 20–21°C isotherm is an important barrier for this species as well. The temperature requirements of both extant species, which are genetically separated for several million years, are thus very similar. Therefore, the limiting sea surface temperature for extinct species of *Persististrombus* may have ranged around the same level with 16°C as absolute minimum and ~20°C as realistic scenario.

Conclusions

Strombids are frequent fossils in shallow water deposits worldwide. Inadequate taxonomic concepts completely camouflaged their biostratigraphic significance in the European Miocene. Mediterranean and Paratethyan carbonate platforms often lack adequate microfossils for biostratigraphic datings and are far from being stratigraphically well resolved. The application of the herein presented taxonomic concept will allow at least a quick separation of Lower, Middle and Upper Miocene deposits.

The frequent confusion of Miocene Paratethyan strombids with the Pliocene *P. coronatus* in the literature was based on the spiny morphologies. Such spiny morphs formed independently several times also in other strombids (see e.g., Landau et al. 2011). The first developed already during the Chattian (*P. praecedens*), the second during the early Langhian (*P. lapugyensis*) and the third one during the Serrvallian (*P. pannonicus*). A fourth yet undescribed group arose during the Serravallian in the Turkish Karaman Basin. These taxa are stratigraphically and geographically disjunct and have a distinct set of morphological characters, documenting an iterative development. This iterative evolution of highly reminiscent morphologies is also evident for the geographically and stratigraphically strongly separated specimens of the extant *P. granulatus* from Panama and its look-alikes from the Burdigalian of France (cf. Lozouet and Maestrati 1986). The distribution of the taxa is a good example for the outcrop-area effect on biodiversity and biogeography estimates. An extraordinary wealth of Langhian and Serravallian fossils in the area of the former Paratethys Sea is contrasted by relatively few coeval faunas in the Mediterranean area. This imbalance accounts for the impression that the *Persististrombus inflexus*-lineage bloomed only in the Paratethys Sea, although rare occurrences in the Middle Miocene of Turkey and the Loire Basin point to a much wider distribution.

The updated taxonomic concept allows utilizing ecological and climatic data of extant congeners which indicate that the 20°C was the limiting temperature for the successful distribution of all *Persististrombus* species. Minimum sea surface temperatures of 16°C were probably the final barrier for reproduction.

Acknowledgements

Warren D. Allmon (Paleontological Research Institution, Cornell University, Ithaca, USA) and Jeffrey D. Stilwell (School of Geosciences, Monash University, Melbourne, Australia) greatly improved the quality of this paper by their valuable comments and suggestions. We are grateful to Frank Wesselingh (Naturalis, Leiden, Netherlands) and Irene Zorn (GBA, Vienna, Austria) for providing access to their collections. Photos were made by Alice Schumacher (NHM, Vienna, Austria). This paper contributes to the FWF-Project P-23492: Mediterranean Oligo-Miocene stratigraphy and palaeoecology.

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