

Europrotomus (Mollusca: Caenogastropoda: Strombidae): a new Middle Miocene European strombid genus (Revision of *Euprotomus* Gill, 1870. Part 4)

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Abstract The medium-sized, strongly ornamented nominal species *Strombus schroeckingeri* Hörnes in Hoernes & Auinger, 1884 is well known from Langhian deposits of the Paratethys Sea. Its traditional generic affiliation in the literature with *Euprotomus* Gill, 1870, implicated a biogeographic relation of the Paratethys and the proto-Mediterranean with the Neogene Indo-West-Pacific region. This relation, however, is problematic because the Tethys Seaway was already closed or a very shallow, strongly evaporitic passage at that time. Despite its superficial similarity with extant genera of the IWP region, the genus is unrelated to all known strombid genera and represents a new genus, which is introduced herein as *Europrotomus* nov. gen. The genus comprises only one or maybe two species, which occur in the European Middle Miocene geological record. No ancestors are known so far. This sudden occurrence is discussed as immigration from an adjacent bioprovince rather than as a result of autochthonous evolution. Hypothetically, such a biogeographic source area might have been established along the coasts of tropical West Africa—a scenario that is already documented for Pleistocene times.

Keywords Gastropoda · Strombidae · *Euprotomus* · New genus · Miocene · Biogeography · Paratethys

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Kurzfassung Die nominale Art *Strombus schroeckingeri* Hörnes in Hoernes & Auinger, 1884 ist ein stark ornamentierter Strombidae von mittlerer Größe, der aus dem Langhium der Paratethys gut dokumentiert ist. Die traditionelle generische Zuordnung zu *Euprotomus* Gill, 1870 implizierte eine biogeographische Beziehung zwischen der Paratethys und dem Proto-Mediterran sowie der neogenen Indo-West-Pazifischen Region. Diese Verbindung ist jedoch problematisch, da der Tethys-Seeweg zu dieser Zeit bereits geschlossen war oder nur eine sehr seichte, stark evaporitische Passage repräsentierte. Die Gattung zeigt keine nähere Verwandtschaft mit den bekannten Strombiden-Gattungen, trotz der oberflächlichen Ähnlichkeiten mit einigen modernen Vertretern in der IWP-Region. Daher wird hier für dieses Taxon *Europrotomus* nov. gen. als neue Gattung eingeführt. Diese Gattung beinhaltet nur ein oder zwei Arten, die ausschließlich aus dem europäischen Mittel-Miozän bekannt sind. Bisher konnten keine Vorgänger nachgewiesen werden, weshalb autochthone Evolution als eher unwahrscheinlich betrachtet wird. Stattdessen könnte dieses plötzliche Auftreten durch Immigration von einer benachbarten biogeographischen Provinz erklärt werden. Ein derartiges biogeographisches Herkunftsgebiet könnte hypothetisch entlang der tropischen Küsten West-Afrikas etabliert gewesen sein—ein Szenario, das auch aus dem Pleistozän dokumentiert ist.

Schlüsselwörter Gastropoda · Strombidae · *Euprotomus* · neue Gattung · Miozän · Biogeographie · Paratethys

Introduction

The wealth of taxa of the family Strombidae in the modern Indo-West Pacific Region (IWP) has its roots in the

Miocene. At that time a major radiation of genera and species occurred there, which continued into Pliocene times (Vredenburg 1925; Abbott 1960; Harzhauser 2007). An important event in the evolutionary history of the Tethyan lineages was the final closure of the Tethys Seaway around the Early/Middle Miocene boundary. At that time the IWP lineages became cut off from the western Tethyan area, which transformed into the proto-Mediterranean Sea and the Paratethys (Harzhauser et al. 2002; Harzhauser and Piller 2007). Several authors discuss a short reconnection via Mesopotamia during the earliest Middle Miocene (Rögl 1998; Popov et al. 2004; Fig. 1). Widespread Middle Miocene evaporites in the crucial area, however, indicate a shallow and hypersaline seaway that was probably not suitable for major faunal exchange.

Taxa with affinities with Indo-Pacific genera appearing in the proto-Mediterranean during the phase of ceasing connectivity are therefore highly interesting for discussions on biogeographic and palaeogeographic reconstructions during the Middle Miocene (Grecchi 1978; Rögl 1998). One of these striking taxa is the nominal strombid species *Strombus schroeckingeri* Hörnes in Hoernes & Auinger, 1884, which is in some morphological characters reminiscent of representatives of the genus *Euprotomus*. A Middle Miocene occurrence of this purely IWP genus in

the Mediterranean area would clearly imply a marine passage between the Indo-Pacific and the Mediterranean seas at that time. Moreover, it would even point to a western origin of the genus, which is known so far in the IWP only from Pliocene strata (Abbott 1960).

Thus, in the course of our research on the Paratethyan *Persististrombus* lineages (for some preliminary notes, see Harzhauser and Kronenberg 2008) and a continuation of the revision of *Euprotomus* Gill, 1870 (Kronenberg 1998, 1999, 2002a, b), we examined a number of specimens of the nominal taxon *Strombus schroeckingeri* Hörnes in Hoernes & Auinger, 1884.

Strombus schroeckingeri has usually been allocated to *Monodactylus* Mörch, 1852 (TS by SD (subsequent designation): *Strombus adustus* Chemnitz [not available] = *Lambis aratrum* Röding, 1798) by Hörnes in Hoernes & Auinger (1884: 165) and Cossmann (1904: 8), or *Euprotomus* Gill, 1870 (TS by monotypy *Strombus aurisdianae* Linnaeus, 1758) by e.g.; Csepregy-Meznerics (1954: 398), Kojumdigieva and Strachimirov, (1960: 130), Strausz (1966: 223) and Atanackovic (1985: 128). Bandel (2007: 148) more or less explicitly advocated inclusion of *S. schroeckingeri* in *Lentigo* Jousseume, 1886 (TS by monotypy *Strombus lentiginosus* Linnaeus, 1758). As *Strombus schroeckingeri* lived about the same time as the representatives of *Persististrombus* Kronenberg & Lee, 2007 [TS by OD (original designation)] *Strombus granulatus* Swainson, 1822, in the southern basins of the Central Paratethys one might also expect a close relationship between *S. schroeckingeri* and one or more species allocated to *Persististrombus*. Therefore, we will take the opportunity to briefly discuss the taxonomic odyssey of the taxa involved.

Analysis of the concepts of *Monodactylus*, *Euprotomus* and *Lentigo*

Most authors allocated *schroeckingeri* Hörnes in Hoernes & Auinger, 1884, to *Monodactylus* Mörch, 1852, or to *Euprotomus* Gill, 1870. Based on shell characters, this allocation appears to be far-fetched, yet in light of the complex history of the genus-level taxon, this allocation is not as strange as one might think.

Klein (1753: 98) introduced the name *Monodactylus* as a genus of his “classis” *Alata* and referred to illustrations in Buonanni (1681), Petiver (1708 [not seen]), Lister (1685–1692), and Rumphius (1705) (Table 1). The figures in these works represent specimens with one digit at the tip of the outer wing, now considered to be in *Euprotomus*; *Lobatus* Iredale, 1921 [TS by monotypy *Strombus bituberculatus* Lamarck, 1822 (= *Strombus raninus* Gmelin, 1791)]; or *Tricornis* Jousseume, 1886 [TS by monotypy *Strombus tricornis* Lamarck, 1816 (= *Strombus tricornis* Lightfoot,

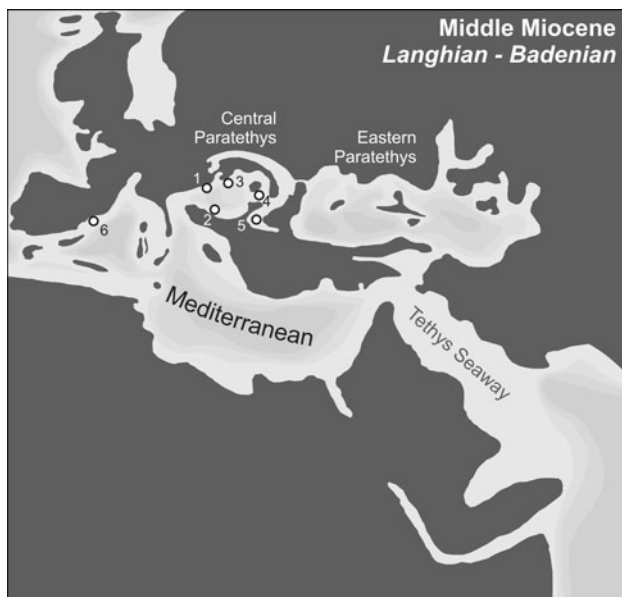


Fig. 1 Occurrences of *Euprotomus* plotted on the palaeogeography of the circum-proto-Mediterranean area during the early Middle Miocene (after Harzhauser and Piller 2007). The Tethys Seaway connecting the proto-Mediterranean Sea with the early Indo-Pacific Ocean was either closed or extremely shallow and evaporitic (Rögl 1998; Popov et al. 2004). Localities: 1 Weitendorf, Wetzelsdorf (Austria), 2 Hrvacani (Bosnia and Herzegovina), 3 Sámsónháza, Márkháza (Hungary), 4 Coșteiu de Sus, Lăpugiu de Sus, (Romania), 5 Tarnene, Pleven (Bulgaria), 6: Montjuic at Barcelona (Spain)

Table 1 References to figures and descriptions referred to by Klein (1753) to his concept of *Monodactylus*

1. Lister 873/29 = *Tricornis tricornis*
2. Lister 871/25 = cf. *Lobatus raninus*
Petiver p. 189 no. 3
3. Lister 874/30 = *Lobatus gallus*
4. Buonanni 309; 310 = *Lobatus gallus*
5. a. Rumphius caption to pl. 37
Buonanni 301 = *Euprotomus aurisdianae*
Lister 872 = *Euprotomus aratrum* and *E. bulla*
- b. Rumphius 111 # XI; text refers to *E. aurisdianae* and *E. bulla*
- c. Buonanni 302 = *Euprotomus bulla*
Figure in Klein (1753) pl. 6/106 = cf. *Tricornis tricornis*
- d. Lister 871/26 = *Euprotomus* cf. *aurisdianae*
- e. Buonanni 306 = ?? „*Tricornis*“s.l.

The Petiver reference has not been checked

1786)] except for fig. 306 [mirror imaged] in Buonanni (1681), which is definitely a strombid, but without a digit at the tip of the wing. This specimen cannot be identified with certainty, but the shape of the elongated anterior canal suggests a specimen of *Lobatus* that has been tampered with. As Klein (1753) is a pre-Linnaean work, his names are not available anyway (International Commission on Zoological Nomenclature (1999) Art. 3.1).

Mörch (1852) was the first author to make the name *Monodactylus*, attributed to Klein (1753), meet the requirements of the International Commission on Zoological Nomenclature (1999). Unfortunately, the name was preoccupied by de Lacépède (1801) who had established it for a perciform fish. In his list of species allocated to *Monodactylus*, Mörch (1852: 62) mentioned four species that are now allocated to *Euprotomus*, but also the nominal taxa *Strombus lentiginosus* Linnaeus, 1758 (the type species of *Lentigo* Jousseume, 1886) and *S. fasciatus* Born, 1778 (now allocated to *Conomurex* Bayle in P. Fischer, 1884). Both these species do not have a “monodactylus.” Adams and Adams (1853) returned to Klein’s original concept, i.e., included all “monodactyl” species in *Monodactylus*, and excluded both *S. lentiginosus* and *S. fasciatus* from that taxon. Although there is an overlap with *Euprotomus*, it should be noted that the concept of *Monodactylus* Mörch (non Lacépède) is not the same as the concept of *Euprotomus*.

Tryon (1885) was probably one of the first authors who used both *Monodactylus* and *Euprotomus* as valid genus level taxa. Like Mörch (1852) and Adams and Adams (1853), Tryon was not aware that the name *Monodactylus* was preoccupied as he selected *S. pacificus* Swainson, 1821 (= *Lambis vomer* Röding, 1798) as type species. Cossmann (1904: 7) did not follow this designation, but selected yet another species, viz. *S. gallus* Linnaeus, 1758, a species not

listed by Mörch (1852), and therefore not eligible as type species of *Monodactylus*. Cossmann (1904) further listed two fossil species, viz. *S. trigonus* Grateloup and *S. schroeckingeri*, in *Monodactylus*. For a summary of type designations for *Monodactylus*, see Abbott (1960: 125).

Tryon (1885) designated *Strombus laciniatus* “Chemnitz” Dillwyn, 1817 (= *Strombus sinuatus* [Lightfoot], 1786) as type species of *Euprotomus*. This is an invalid designation as *Strombus aurisdianae* was the only species mentioned by Gill (1870). By his action, Tryon in fact changed the whole concept of *Euprotomus*. Apart from the type species, Tryon allocated five more species within *Euprotomus*. Of these, two are now allocated to *Lentigo*; the other four are now allocated to *Sinustrombus* Bandel, 2007, and *Thersistrombus* Bandel 2007. For a preliminary discussion on these taxa, see Kronenberg (2009). None of these species is currently allocated to *Euprotomus*.

In his influential work Abbott (1960) brought an end to the confusion about *Monodactylus* and *Euprotomus*. Abbott pointed out that *Monodactylus* Mörch was preoccupied and restricted the concept of *Euprotomus*. Indeed, *Euprotomus* sensu Abbott is a morphologically coherent group that is probably monophyletic. This has been confirmed by molecular data by Latiolais (2003, 2006). In the consensus tree as presented by Latiolais et al. (2006), the nominal taxa *Lambis vomer* (Röding, 1798), *L. bulla* (Röding, 1798) and *Strombus aurisdianae* Linnaeus, 1758—all allocated to *Euprotomus* by Abbott (1960)—plot out as a clade that is sister to the clade of Panamic, western and eastern Atlantic strombids.

Apart from the retroactive allocation to *Lentigo* of its possible synonym *S. almerai* (see Almera and Bofill y Poch 1885), only Bandel (2007) allocated this species to *Lentigo* Jousseume, 1886. Originally, this genus was introduced with only one species allocated to it, viz. *Strombus lentiginosus*. Apart from the type species, Abbott (1960) allocated four more recent species to *Lentigo*: the nominal taxa *L. pipus*, *S. fasciatus*, *S. latus* and *S. granulatus*. Moolenbeek and Dekker (1993) pointed out that, based on shell morphology and characters of the radula, the position of *S. fasciatus* in *Lentigo* is no longer tenable, and they allocated this species to *Conomurex*. Subsequently, Kronenberg and Lee (2007) allocated *S. granulatus* and *S. latus* to their new genus *Persististrombus*, retaining only *S. lentiginosus* and *L. pipus* in *Lentigo*. In their discussion, Kronenberg and Lee (2007) implicitly redescribed *Lentigo* on shell characters. They discriminated *Lentigo* from *Persististrombus* by the two notches on the adapical part of the outer lip, resulting in two lobes, of which the adaxial one is attached to the spire; a more distinct posterior canal; presence of a number of small triangular projections at the abapical side of the outer lip on the flange between the strombid notch and the anterior canal, and the columellar callus that does not reach the base of the columella, yet

Table 2 Concepts of the genus level taxa *Monodactylus*, *Euprotomus* and *Lentigo*, by alphabetical arrangement of the species allocated to these taxa by different authors

Genus	Mörch, 1852	Adams & Adams, 1853	Tryon, 1884	Cossmann, 1904	Abbott, 1960	Kronenberg et al., 2010/2011
<i>Monodactylus</i>	<u><i>Adustus</i></u> (= <i>aratum</i>) [<i>Euprotomus</i>] <i>aratum</i> (= <i>vomer</i>) [<i>Euprotomus</i>] <i>aurisdianae</i> (= <i>bulla</i>) [<i>Euprotomus</i>] <i>fasciatus</i> [<i>Conomurex</i>] <i>lentiginosus</i> [<i>Lentigo</i>] <i>striatogranulatus</i> (= <i>aurisdianae</i>) [<i>Euprotomus</i>]	<u><i>Adustus</i></u> (= <i>aratum</i>) [<i>Euprotomus</i>] <i>aratum</i> (= <i>vomer</i>) [<i>Euprotomus</i>] <i>aurisdianae</i> [<i>Euprotomus</i>] <i>australis</i> (= <i>iredalei</i>) [<i>Euprotomus</i>] <i>costo-muricatus</i> (= <i>raninus</i>) [<i>Lobatus</i>] <i>gallus</i> [<i>Lobatus</i>] <i>guttatus</i> (= <i>bulla</i>) [<i>Euprotomus</i>] <i>peruvianus</i> [<i>Lobatus</i>] <i>striatogranulatus</i> (= <i>aurisdianae</i>) [<i>Euprotomus</i>] <i>tricornis</i> [<i>Tricornis</i>]	<i>Aurisdianae</i> (= <i>aurisdianae</i> + <i>bulla</i>) <i>aurisdianae</i> var. <i>melanostomus</i> (= <i>aratum</i>) <i>bituberculatus</i> (= <i>raninus</i>) [<i>Lobatus</i>] <i>gallus</i> [<i>Lobatus</i>] <i>pacificus</i> (= <i>vomer</i>) <i>pacificus</i> var. <i>australis</i> (= <i>iredalei</i>) <i>peruvianus</i> [<i>Lobatus</i>] <i>tricornis</i> [<i>Tricornis</i>]	<u><i>Gallus</i></u> [<i>Lobatus</i>] <i>schroeckingeri</i> † <i>trigonus</i> † [allocated to <i>Tricornis</i> by Abbott 1960]		
<i>Euprotomus</i>			<u><i>Laciniatus</i></u> (= <i>sinuatus</i>) [<i>Sinuistrostomus</i>] <i>latissimus</i> [<i>Sinuistrostomus</i>] <i>lentiginosus</i> [<i>Lentigo</i>] <i>papilio</i> (= <i>pipus</i>) [<i>Lentigo</i>] <i>ponderosus</i> (= <i>thersites</i>) [<i>Thersistrostomus</i>] <i>taurus</i> [<i>Sinuistrostomus</i>]	<i>Laciniatus</i> (= <i>sinuatus</i>) [<i>Sinuistrostomus</i>]	<i>Aurisdianae</i> <i>aratum</i> <u><i>aurisdianae</i></u> <u><i>aurisdianae</i></u> <i>bulla</i> <i>vomer vomer</i> <i>vomer hawaiiensis</i> <i>vomer iredalei</i>	<i>Aratum</i> <u><i>aurisdianae</i></u> <i>aurora</i> <i>bulla</i> <i>chrysostomus</i> <i>hawaiiensis</i> <i>iredalei</i> <i>vomer</i>
<i>Lentigo</i>					<i>Fasciatus</i> [<i>Conomurex</i>] <i>granulatus</i> [<i>Persististrostomus</i>] <i>latus</i> [<i>Persististrostomus</i>] <u><i>lentiginosus</i></u> <i>pipus</i>	<u><i>Lentiginosus</i></u> <i>pipus</i>

Extinct taxa accompanied by a dagger (†). Current species names between brackets (), current generic allocation between square brackets []. Type species, when designated, underlined. See also text

thickened at the abapical part but not forming a distinct pad. This opinion was echoed by Landau and da Silva (2010). For an overview of species' allocations to the genera mentioned above, see Table 2.

Abbreviations

GCKE Private collection Gijs C. Kronenberg, Eindhoven, the Netherlands; to be deposited in NCBNaturalis
NHMW Naturhistorisches Museum Wien, Austria

Systematic palaeontology

Family Strombidae Rafinesque, 1815

Genus *Europrotomus* Kronenberg & Harzhauser gen. nov.

Type species designated herein: *Strombus* (*Monodactylus*) *schroeckingeri* Hörnes in Hörnes & Auinger, 1884.

Diagnosis: Strombid genus encompassing shells of medium size, with medium-sized spire, flaring outer lip with sharp rim, short anterior canal, distinct row of shoulder knobs on the last three whorls, becoming trifid, and diverging cords on abapertural side of the last whorl.

Description: See description of *Europrotomus schroeckingeri* below.

Derivation of name: Compound noun of “Euro,” referring to the European distribution of this genus as known so far, and “protomus” as allusion to the genus *Euprotomus* Gill, 1870, to which the type species has been allocated.

Distribution: This fossil strombid genus is known so far only from the European Middle Miocene and was restricted to the Mediterranean Sea and the adjacent Paratethys Sea.

Remarks: Other species assigned to *Europrotomus* gen. nov.: *Strombus almerai* Crosse, 1885; but see below.

***Europrotomus schroeckingeri* (Hörnes in Hoernes & Auinger, 1884) comb. nov.**

Figs. 2a–f, 3a–g

- *1884 *Strombus (Monodactylus) schroeckingeri* Hörnes in Hoernes & Auinger: 165, pl. 19, figs. 6–7
- 1904 *Strombus (Monodactylus) schroeckingeri* Hörnes.—Cossman: 8
- 1954 *Strombus (Euprotomus) schroeckingeri* Hörnes.—Csepregy-Meznerics: 398, pl. 2, figs. 1–2
- 1960 *Strombus (Euprotomus) schroeckingeri* Hörnes.—Kojumdgieva & Strachimirov: 130, pl. 35, figs. 5a–5b
- 1966 *Strombus (Euprotomus) schroeckingeri* Hörnes.—Strausz: 223, fig. 104
- 1985 *Canarium (Euprotomus) schroeckingeri* (Hoernes).—Atanackovic: 128, Pl. 24, figs. 10–11
- 1993 *Strombus (Strombus) coronatus* Defrance.—Nikolov (1993): 69, pl. 3, figs. 7–8
- 1993 *Strombus (Strombus) nodosus subcancellata* (Grateloup).—Nikolov: 70, pl. 3, figs. 9–10
- 2003 *Strombus (Euprotomus) schroeckingeri* (Hörnes).—Harzhauser et al.: 333, fig. 8
- 2007 *Strombus (Lentigo) schroeckingeri* Hörnes, 1880 [sic!].—Bandel: 148
- 2006 *Strombus schroeckingeri* [sic!].—Hiden (2006): 6
- ? 1885 *Strombus lentiginosus* Linné Var.—Almera & Bofill y Poch: 32, pl. 1 figs 1, 2 [non *Strombus lentiginosus* Linnaeus, 1758]
- ? 1885 *Strombus almerai* Crosse: 242. nom nov. pro *Strombus lentiginosus* Almera & Bofill y Poch, non Linnaeus
- ? 1886 *Strombus almerae* Crosse.—Almera & Bofill y Poch: 402, pl. 10, figs. 1–2 [unjustified emendation of *S. almerai* Crosse]

Lectotype: designated herein: NHMW 1867/XIX/72; Fig. 2a; illustrated in Hoernes and Auinger (1884; pl. 19, fig. 7).

Locus typicus: Coșteiu de Sus, Romania; Transylvanian Basin.

Stratum typicum: marly sandstone of the lower Badenian (= lower Langhian).

Measurement: height: 43.4 mm.

Paralectotype 1: Coșteiu de Sus, Romania; Transylvanian Basin; height: 47.2 mm (Fig. 2b), NHMW 1855/XLIII/19b.

Paralectotype 2: Coșteiu de Sus, Romania; Transylvanian Basin; height: 53.8 mm (Fig. 2c), NHMW 1867/XIX/72; previously illustrated by Hoernes and Auinger (1884; pl. 19, fig. 6).

Paralectotype 3: Lăpugiu de Sus, Romania; Transylvanian Basin; height: 52 mm (Fig. 3a); NHMW 1855/XLIII/19a

Paralectotype 4: Lăpugiu de Sus, Romania; Transylvanian Basin; height: 52 mm (Fig. 3b); NHMW 1872/V/25;

Additional specimens from the type locality Coșteiu de Sus (leg. et don. Anton and Thomas Breitenberger):

NHMW 2007z0114/0005; Fig. 2d; height: 42 mm.

NHMW 2007z0114/0008; Fig. 2e; height: 52 mm.

NHMW 2007z0114/0007; Fig. 2f; height: 51.5 mm.

NHMW 2007z0114/0001; Fig. 3c; height: 23 mm (juvenile).

NHMW 2007z0114/0002; Fig. 3d; height: 23 mm (juvenile).

NHMW 2007z0114/0004; Fig. 3e; height: 30.5 mm (dwarf specimen).

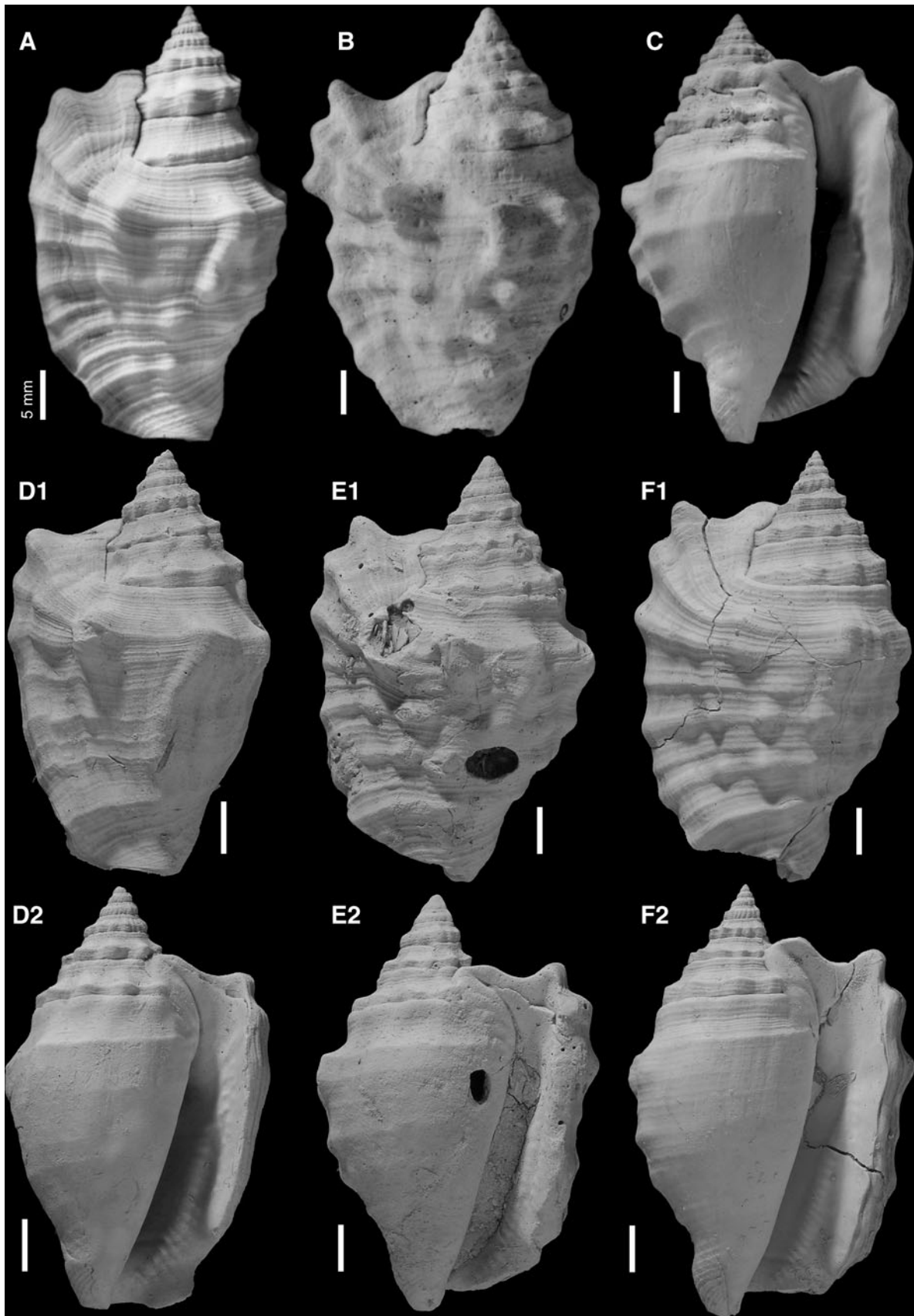
NHMW 2007z0114/0006; Fig. 3f; height: 41 mm.

NHMW 2007z0114/0009; Fig. 3g; height: 49.5 mm.

Additional specimens from Lăpugiu de Sus (leg. et don. Anton and Thomas Breitenberger):

GCKE 6306.

Description: Medium-sized shells of eight teleoconch whorls. Protoconch strongly abraded in all available specimens and seems to consist of about 2.5 rather high, moderately convex whorls. Up to three varix-like swellings appear on earliest teleoconch whorls aside from numerous oblique axial ribs, soon passing into pointed knobs or nodes. Spire whorls bear a prominent keel, situated variably in the area from the middle of the whorl to the anterior suture. Concave sutural ramp bearing distinct growth lines that are crossed by stronger spiral threads. Spiral threads accompanied by 8–10 blunt spiral ridges on the body whorl, which bears irregular nodes of variable strength; most prominent and pointed ones appear along the shoulder of the body whorl.



◀ **Fig. 2** *Europrotomus schroeckingeri* (Hörnes in Hoernes & Auinger, 1884) comb. nov. from Coșteiu de Sus in Romania (Langhian). **a** Lectotype, NHMW 1867/XIX/72, **b** Paralectotype 1, NHMW 1855/XLIII/19b, **c** Paralectotype 2 NHMW 1867/XIX/72, **d** NHMW 2007z0114/0005, **e** NHMW 2007z0114/0008, **f** NHMW 2007z0114/0007

Outer lip expanding, attaches up to the 4th and 5th spire whorl; thickened posterior to the strombid notch but thin anterior to it. In the anterior 2/3 of the outer lip a swelling with strong lirae is developed about 5–7 mm deep in the aperture. Three (Hoernes and Auinger 1884: pl. 19 fig. 7a, b here refigured Fig. 2a) to seven (Hoernes and Auinger 1884: pl. 19 fig. 6a, b, here refigured Fig. 2c) broad, low axial lobes occur especially in its posterior part, but also extending to the lateral part as well, bordered by a narrow, moderately deep canal where the wing attaches to the spire. These lobes are a continuation of well-developed spiral cords on the dorsal side of the shell. The two to three most adapical of these cords develop only at the point where the outer lip starts to expand, but the others, when present, are a continuation of strong, knob-bearing, spiral cords already present on the dorsal side of the shell. Columellar callus extending on the base without covering it completely. Further lirae occur in the very anterior part and the posterior termination of the columella.

Comparison of shell characters: the shells show a broad, glossy columellar callus partially covering the base. In this feature it is quite close to the modern representatives of *Euprotomus*. However, *Europrotomus* is readily distinguished from *Euprotomus* by the difference in the much shorter and the less bent anterior canal, and the absence of the finger-like digit on the outer lip. The sculpture of the outer lip has some counterpart in the shells of the modern *Euprotomus vomer-hawaiensis-iredalei* complex. Even the lirated axial ridge in the inner side of the outer lip is, although much weaker, still presented in the modern species group. Another similarity is the narrow posterior canal, the presence of varices on the early teleoconch whorls. The paucispiral protoconch of the extant *Euprotomus iredalei* (Abbott 1960) resembles that of *Europrotomus schroeckingeri* in its rather low, bulbous shape (about 2–2.5 whorls).

As far as *Lentigo* is concerned, the general appearance of *Europrotomus* is quite similar, and this is also true for the dorsal sculpture. In *Lentigo* there are however only two lobes on the posterior part of the outer lip, contrary to the three to seven in *Europrotomus*. Moreover, in *Europrotomus* these lobes are clearly a continuation of the well-developed spiral cords, which is not the case in *Lentigo*. Also, the triangular projections on the strombid notch and flange between the strombid notch and anterior canal present in *Lentigo* are missing in *Europrotomus*.

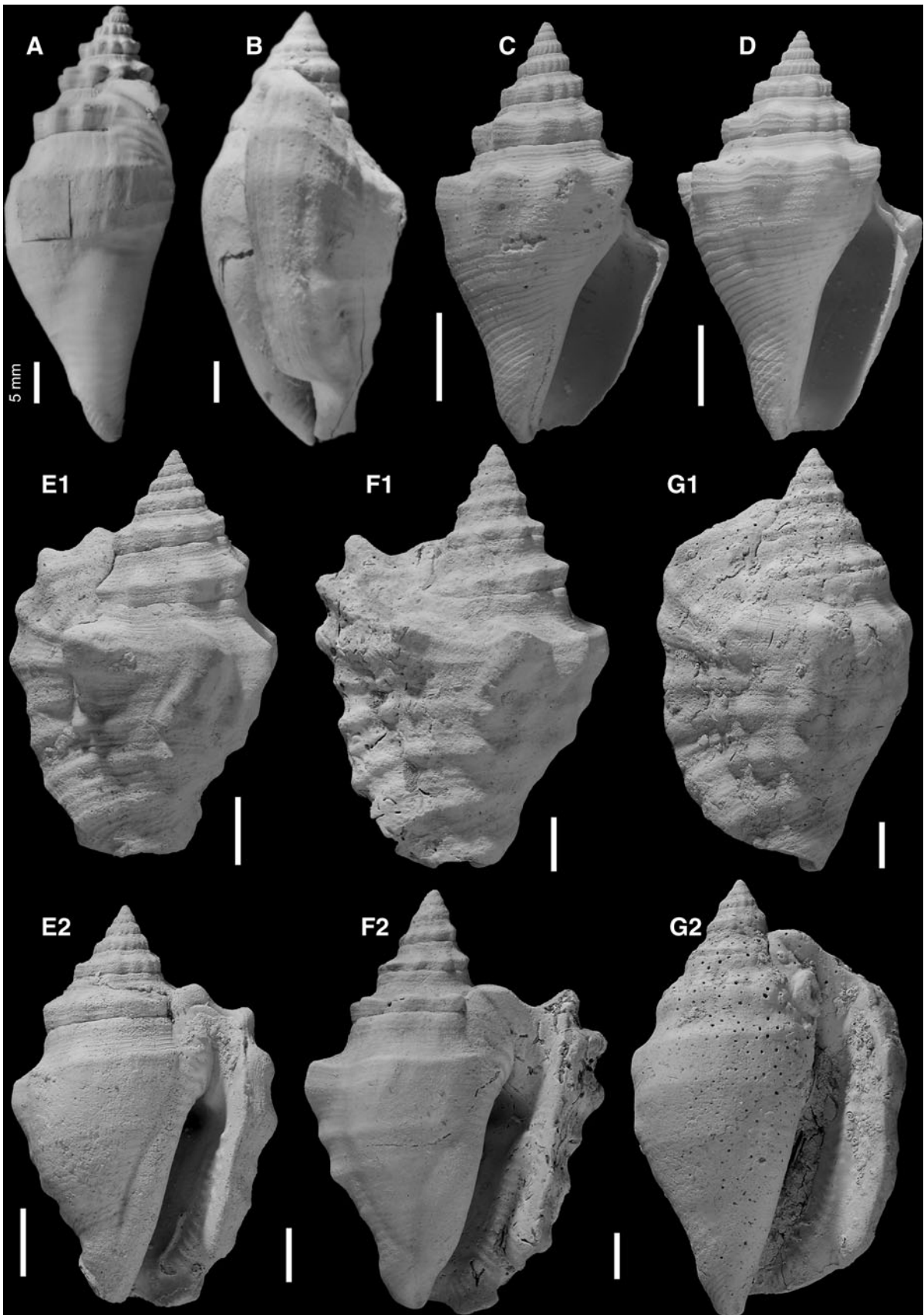
In *Persististrombus* Kronenberg & Lee, 2007, the edge of the outer lip has no lobes at all, and the outer lip is attached to the shell much more abapically.

The presence of the lobes on the rim of the outer lip is slightly reminiscent of the lobes as seen in *Sinuistrombus sinuatus* ([Lightfoot], 1786), but in the latter species the lobes are much better developed, the outer lip is attached much closer to the apex, and the flange between the strombid notch and the anterior canal. Also, in *S. sinuatus* the rim of the outer lip is bent sharply towards the columella when reaching adulthood, a character not observed in *Europrotomus*.

The continuation of the spiral cords into the lobes at the rim of the outer lip is somewhat reminiscent of the way the digits are formed in *Lambis* and *Harpago*. In *Lambis* and *Harpago*, however, these digits are much longer and are formed by distinct lobes at the mantle edge, where the lateral sides of the mantle edge are bent to reach other, thus forming a hollow cone that is subsequently filled with shell material. The place where the rims of the lobes touched each other remains visible as a very narrow furrow. Moreover, the anterior canal in *Lambis* is very much elongated.

Based on shell morphology, we conclude that *S. schroeckingeri* cannot be allocated to *Persististrombus*, nor can it be allocated to either *Euprotomus* or *Lentigo*. The previous taxonomic confusion is largely based on the strongly changing concepts of *Monodactylus* Mörch (non Lacépède) and *Euprotomus*. As no other genus level taxon within the family Strombidae appears to fit to accommodate this species, *Europrotomus* is introduced as a new genus.

Remarks: A poorly preserved strombid from the Langhian and lower Serravallian of Spain, erroneously identified as *Strombus lentiginosus* (Almera & Bofill y Poch, 1885), was subsequently renamed by Crosse (1885) as *S. almerai* and accepted by Almera and Bofill y Poch (1886) as *S. almerae*. The change in spelling of the specific epithet is however an unjustified emendation of *S. almerai* (International Commission on Zoological Nomenclature (1999) Art. 33.2.3). This species closely resembles *S. schroeckingeri* in size and ornamentation. Unfortunately, the sculpture of the aperture is poorly described, except for some comments on granulations of the columella. Additionally, its wing is described as expanding and undulated in its posterior part, and a faint posterior canal is also mentioned by Almera and Bofill y Poch (1885, 1886). Differences, however, are the stout spire and the shoulder of the last whorl, which seems to be closer to the suture than in *Europrotomus* gen. nov. *schroeckingeri*. Hence, this specimen might be conspecific with the Paratethyan *Europrotomus schroeckingeri*, but a clear decision depends on the availability of more material.



◀ **Fig. 3 a–b** *Europrotomus schroeckingeri* (Hörnes in Hoernes & Auinger, 1884) comb. nov. from Lăpuşiu de Sus in Romania (Langhian). **a** Paralectotype 3, NHMW 1855/XLIII/19a, **b** Paralectotype 4, NHMW 1872/V/25, **c–g** *Europrotomus schroeckingeri* (Hörnes in Hoernes & Auinger, 1884) comb. nov. from Coşteiu de Sus in Romania. **c** Juvenile specimen NHMW 2007z0114/0001, **d** juvenile specimen, NHMW 2007z0114/0002, **e** dwarf specimen NHMW 2007z0114/0004, **f** strongly sculptured specimen, NHMW 2007z0114/0006, **g** specimen with reduced sculpture, NHMW 2007z0114/0009

Palaeoecology: All specimens are found in marly silty sandstone in association with a diverse subtropical mollusc fauna pointing to shallow marine soft bottom environments with normal salinity. It is unknown from the Middle Miocene reefs and coral carpets of the Paratethys (own observation). It is only very rarely found associated with other Stromboidea except for *Tibia dentata* (Grateloup 1827).

Distribution: Weitendorf, Wetzelsdorf (Styrian Basin, Austria); Sámsonháza, Márkháza (Cserhát Mountains, Hungary); Coşteiu de Sus, Lăpuşiu de Sus (Transylvanian Basin, Romania); Hrváčani (southern Pannonian Basin, Bosnia and Herzegovina), Tarnene and Pleven (Carpathian Basin, Bulgaria) (see Harzhauser et al. 2003 for map).

Discussion

A guest from the east or a home-made western Tethyan element?

Europrotomus schroeckingeri displays a remarkable distribution. From literature references, it is seemingly confined to the Central Paratethys, which is possibly rather a matter of a lack of investigations in adjacent regions. Within the Paratethys it is restricted to the southern basins (Harzhauser et al. 2003). The rare shell is found in Romania, Bulgaria, Hungary, Bosnia and Herzegovina and in the Styrian Basin in Austria. It is unknown from the North Alpine Foreland Basin, the Vienna Basin and the more northern Carpathian Foredeep. During the early Middle Miocene, the southern Paratethys basins, e.g., the Styrian and Pannonian basins, had a direct connection to the proto-Mediterranean Sea, while the northern basins, e.g., the Vienna and Carpathian basins, were fed by a more eastern connection. Both water masses were probably separated by emerged areas that now form the Danube Basin. This assumption is supported by geochemical data on stable isotope composition of mollusc shell aragonite, which clearly indicates strongly deviating water chemistry between these two branches of the Paratethys Sea (Latal et al. 2005). Therefore, the strombid was hindered on its way to the north. In respect to the generally low endemism

of the southern Paratethyan mollusc faunas at that time (Harzhauser and Piller 2007), it may be expected that *Europrotomus schroeckingeri* was also distributed in the proto-Mediterranean area. Its absence from the fossil record may be explained by the fact that coeval Langhian deposits in the Mediterranean area are rare and mainly represented by deep water deposits (e.g., Mourik et al. 2011). None of the rare Langhian shallow water faunas from the Monte dei Cappuccini in the Turin Mountains (Sacco 1893) and from the Mut Basin in Turkey (Mandic et al. 2004) yielded *Europrotomus schroeckingeri*.

Only the occurrence of *Europrotomus almerai* (Crosse 1885) in the Middle Miocene of Spain suggests a wider distribution of the genus. Nevertheless, its sudden appearance and the lack of obvious ancestors might point to immigration from a nearby bioprovince.

Immigration from western Africa would be a realistic scenario. This hypothesis, however, is a hard test as there are no fossil-bearing Lower and Middle Miocene deposits known along the West African coast. The Paleocene molluscan fauna from Nigeria has been discussed by Newton (1905, 1922), Eames (1957) and Adegoke (1977), and from the Gold Coast (= Ghana) by Cox (1952), but although there are stromboideans discussed (Rimellidae, Rostellariidae and Seraphsidae) in those papers, no strombids are mentioned. It is quite unlikely that *Europrotomus schroeckingeri* arose from one of these stromboidean families. Therefore, no potential West African ancestor can be shown.

Immigration from the East is unlikely as there is also no evidence of *E. schroeckingeri* in the contemporaneous but always lowly diversified faunas of the Eastern Paratethys (Ilyina 1993). Hence, it would be tempting to explain this erratic appearance by immigration from either the Americas in the west or the proto-Indo-West-Pacific Region in the east. An arrival of *Europrotomus* from the western biogeographic units of the Central Americas, however, is extremely unlikely in respect to the fossil record (e.g., Jung and Heitz 2001). A connection of the Mediterranean or the Paratethys with the early Indo-Pacific existed during the Early Miocene (Rögl 1998; Harzhauser et al. 2007). Hypothetically, this marine connection would have allowed the immigration of *Europrotomus*. Nonetheless, it has to be kept in mind that all Oligocene-Miocene mollusc faunas of Arabia, Eastern Africa, Pakistan, India, Java and Borneo lack any clear evidence for a *Europrotomus*-*Euprotomus*-related strombid (see Vredenburg 1925; Beets 1941; Abbott 1960; Hoek Ostende et al. 2002; Harzhauser 2007, 2009; Harzhauser et al. 2009). Thus, there is little reason to hypothesize a westward immigration into the Mediterranean area. Moreover, during the Middle Miocene when *Europrotomus* appears, the eastern route via the Tethys Seaway was already closed or hard to cross (Rögl 1998, Harzhauser et al. 2007).

All the occurrences are concentrated in the southern basins of the Paratethys Sea, which was a northern gulf of the proto-Mediterranean Sea (Rögl 1998; Popov et al. 2004; Harzhauser and Piller 2007). Soon after, the genus vanishes completely from the Paratethys Sea and is unknown from deposits younger than 14–13 Ma. This range coincides conspicuously with the mid-Miocene Climatic Optimum (Zachos et al. 2001), while its sudden decline coincides with the Mid-Miocene climate transition (Shevenell et al. 2004). This climate-related stratigraphic and biogeographic pattern was documented for a wide range of Paratethyan taxa of gastropods and foraminifers (Harzhauser and Piller 2007) as well as bivalves (Harzhauser et al. 2003).

Hypothetical relations and roots

Although *Europrotomus* can easily be distinguished from other genus level taxa, morphological elements of the last whorl suggest some affinities with the genera to which it is compared above, e.g., *Euprotomus*, *Lentigo*, *Persististrombus*, *Sinustrombus*, *Harpago* and *Lambis*. In his thesis, Latiolais (2003: fig. 1) illustrates a maximum likelihood tree constructed from 325 bp of nuclear histone H3 for numerous species of Strombidae. Unfortunately, in the tree constructed from 640 bp of mitochondrial COI (Latiolais 2003: fig. 2), some of the species are not represented, so these species are also missing in the consensus tree (Latiolais 2003: fig. 3; Latiolais et al. 2006). Based upon the nuclear histone H3 results, *Europrotomus* gen. nov. may be derived from a *Canarium*-like ancestor and at the root of the clade that leads to all recent American and West African genera (*Lobatus*; *Persististrombus*; *Strombus*) and also the Indo-Pacific genera *Conomurex*, *Euprotomus*, *Gibberulus*, *Harpago*, *Lambis*, *Lentigo*, *Sinustrombus*, *Thersistrombus* and *Tricornis* (names following Kronenberg et al. 2010/2011). This may be an indication of a Miocene “explosion” of genus level taxa (Williams and Duda 2008).

The proposed relation with a *Canarium*-like ancestor, however, is highly speculative, as *Europrotomus* appears abruptly in the fossil record and is restricted to a rather narrow time span during the Middle Miocene. Only few strombid genera are present in the Early Miocene of the Western Tethys. Of these, only *Persististrombus* is recorded from numerous localities, documenting a continuous occurrence of the lineage from the Oligocene up to the Pliocene (Lozouet and Maestrati 1986; Harzhauser and Kronenberg 2008). A close relation of *Persististrombus* with *Europrotomus*, as discussed above, is very unlikely. Similarly, a phylogenetic relation with *Dilatilabrum* Cossmann, 1904, which occurs as a Palaeogene relic in the Lower Miocene of the Aquitaine Basin in France, can be ruled out. Representatives of *Dilatilabrum* are

characterized by extremely solid shells with wing-like outer lips with straight edges. Finally, a third—still unnamed—strombid genus is known from the Lower Miocene of the Aquitaine Basin in France and the Turin Mountains in Italy. It is represented only by the species “*Strombus*” *mitroparvus* Sacco, 1893. This small elongate strombid with strong nodes and a narrow wing might be the earliest species of a lineage that is represented in the Miocene to Pleistocene of the IWP by “*Strombus*” *micklei* Ladd, 1972, and “*Strombus*” *blanci* Tröndlé & Salvat, 2010 (Ladd 1972; Tröndlé and Salvat 2010). “*Strombus*” *mitroparvus*, with its very narrow aperture and an insignificant wing that does not reach the spire, differs fundamentally from *Europrotomus* and is a very unlikely ancestor candidate.

Conclusions

The Neogene strombid fauna of the proto-Mediterranean and Paratethys seas was dominated by representatives of the *Persististrombus* lineage. Apart from *Dilatilabrum* and “*Strombus*” *mitroparvus* from the Early Miocene, the only other genus present was *Europrotomus* known solely from the Middle Miocene. It remained rather rare and did not radiate as it is known so far only from a single species, although a second one, viz. *Strombus almerai*, might have existed in the western Mediterranean.

This taxon has no obvious roots in the fossil record and is unrelated to the known Early Miocene strombids of the entire Tethys Realm. Moreover, it has no direct relation with the modern genera to which it has been assigned in the literature so far. The lack of potential ancestor species in the Lower Miocene deposits of Eurasia might indicate that *Europrotomus schroeckingeri* is an immigrant, which expanded its tropical distribution area toward the north during the warm Langhian. As the connection into the early Indo-Pacific was already ceasing during the Middle Miocene, this passage is an unlikely immigration route. Hence, an arrival from the west would be more realistic. Especially the tropical coasts of West Africa might have acted as source area. This ad-hoc hypothesis, however, is hard to test because of the lack of Miocene faunas in West Africa. Some support for this hypothesis is a Pleistocene pendent scenario within the *Persististrombus* lineage. With the Pliocene cooling, this thermophilic strombid retreated from the Mediterranean Sea and survived as *Persististrombus latus* (Gmelin 1791) along the coasts of West Africa. From there, it re-entered the Mediterranean during the Marine Isotope Stages 7 and 5 (De Torres et al. 2009) and probably also during MIS 3 (Rögl et al. 1997; Zazo et al. 1984).

The case of *Europrotomus*, with its superficial similarities with extant IWP-genera, clearly documents the

negative impact of outdated genus-concepts on biogeography and palaeogeography conclusions.

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