The late middle Miocene non-marine mollusk fauna of Vračević (Serbia): filling a gap in Miocene land snail biogeography

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In this paper, we describe a non-marine mollusk fauna deriving from late middle Miocene (late Serravallian; Sarmatian) deposits of western Serbia. The assemblage encompasses a diverse land snail fauna with twenty-four species, along with four species of freshwater pulmonate gastropods and one bivalve species. While the aquatic snails are ubiquitous elements in Europe during the middle Miocene, the terrestrial gastropod fauna, consisting of both common and rare species, offers the first comprehensive insight into land snail diversity on the Balkan Peninsula during that time and permits conclusions on regional biogeography. The fauna shows high affinities to the middle Miocene faunas of central Europe and shares only few elements with western and eastern European and Anatolian assemblages. Ecologically, the freshwater mollusks point to a standing or slowing moving, probably highly vegetated, lacustrine environment. The land snails indicate the presence of humid forests around Lake Vračević, which is in line with current climatic reconstruction for the Sarmatian of southeastern Europe. ?*Vertigo vracevicensis* Neubauer & Harzhauser sp. nov. and *Pisidium mionicense* Neubauer, Harzhauser & Mandic sp. nov. are introduced as new species. *Discus costatus* (Gottschick, 1911) is shown to be a junior objective synonym of *Discus solarioides* (Sandberger, 1872). • Key words: terrestrial gastropods, freshwater gastropods, bivalve, taxonomy, systematics, Sarmatian, Serravallian.

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The European land snail fossil record is patchy at best. The middle Miocene is a comparably well-studied time interval, but the majority of species still derives from few localities in central Europe, such as Steinheim am Albuch (*e.g.*, Miller 1900, Gottschick 1911, Jooss 1912, Finger 1998), Undorf (Clessin 1877, 1885, 1894, 1912) and the Upper Freshwater Molasse (*e.g.*, Schlickum 1976; Salvador 2014; Salvador & Rasser 2014, 2016a, b; Salvador *et al.* 2015a, 2016a–c) in southern Germany, the Rein Basin in Austria (Harzhauser *et al.* 2014a), the Bakony Mts. in Hungary (Kókay 2006), and Nowa Wieś Królewska near Opole [= Königlich Neudorf bei Oppeln] in southern Poland (Andreae 1902a, b; 1904). In contrast, faunas for western and eastern Europe, as well as Anatolia, are based on single assemblages (*e.g.*, Steklov 1966, Schütt 1994, Fischer 2000; see also Esu 1999 for a summary) and there are still many blank spots on the map.

The diverse non-marine mollusk assemblage recovered from Sarmatian deposits at Vračević in western Serbia (Fig. 1) has the potential to increase our knowledge on middle Miocene terrestrial faunas. The fauna was initially detected by Stevanović (1953), who mentioned a few terrestrial and freshwater gastropod genera. Half a century later, Prysjazhnjuk *et al.* (2000) re-investigated the area west of Vračević and recovered a diverse non-marine gastropod fauna in the valley of the Grabovac brook. Two subsequent papers commented on several species of the freshwater snails from that assemblage (Kovalenko 2004, Prisyazhnyuk & Rudyuk 2005), but the terrestrial fauna

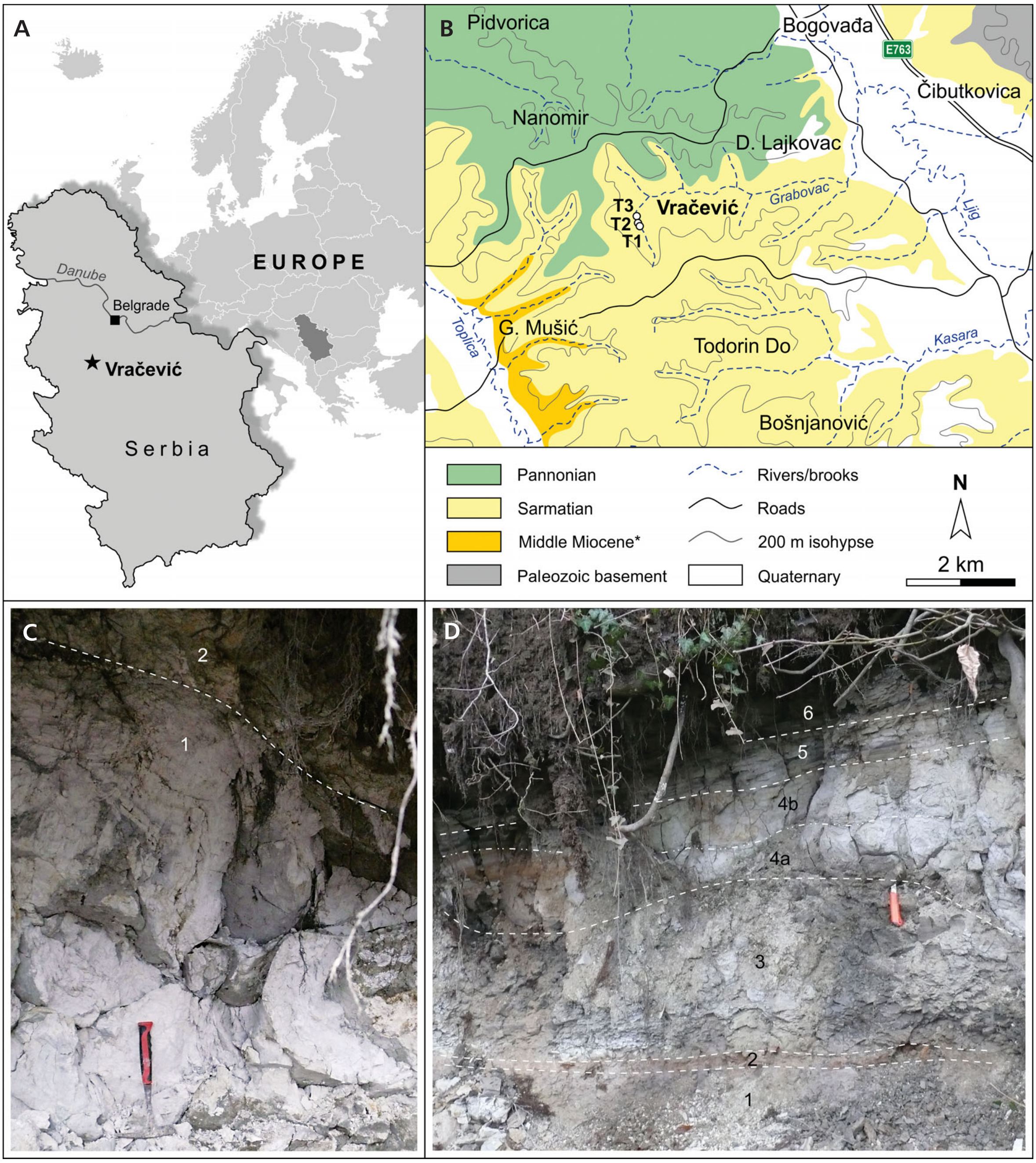


Figure 1. Geographical (A) and geological (B) overview of the study area, and photos of sections T2 (C) and T3 (D) with indication of the sampled beds (see text for details). The geological overview is based on the geological map 1:100 000 by Filipović *et al.* (1976). * – Apart from Sarmatian deposits, there are undifferentiated Middle Miocene sediments in the area of Gornji Mušić.

remained undescribed. A sampling campaign was recently conducted in the outcrop area of Vračević to collect new material for filling this gap. Besides, the material from the original campaign collected for micromammal stratigraphy and housed at Natural History Museum Belgrade was included in the present study as well.

Being the first diverse terrestrial gastropod fauna from the Balkan Peninsula for the middle Miocene, it fills a gap between the well-documented faunas of central Europe and the patchy records for Eastern Europe and Anatolia. Thereby, it might shed light on regional diversity and biogeography. The focus of the present paper is to provide details about the taxonomy and systematics of the mollusks occurring at Vračević and to conclude with discussion about possible paleobiogeographic inferences and paleoecological interpretations.

Geological setting

The locality Vračević is situated in the Mionica Basin at the southern margin of the Pannonian Basin in western Serbia. The intramontane basin was largely formed on the Jadar block in the NE Dinarides, which is part of the Jadar-Kopaonik thrust sheet, derived from the most distal Adriatic passive margin (Schmid *et al.* 2008). The Jadar block is composed of non-metamorphic Paleozoic basement overlain by Permian and Triassic shallow-marine carbonates, obducted in the Jurassic by ophiolites of the Western Vardar Ocean. The Mionica Basin, an elongated, about 75 km long and 15 km wide, E-W striking basin, formed in the Middle Miocene during the maximum extension phase of the southeastern Pannonian Basin (Matenco & Radivojević 2012). During the middle–late Miocene it represented an isolated lacustrine basin that was occasionally flooded from the north by Paratethys and Lake Pannon waters (Stevanović 1953). Basinal infill comprises transgressive, restricted marine and freshwater Sarmatian deposits, followed by Pannonian brackish and freshwater lacustrine series (Filipović *et al.* 1978). The rich terrestrial mammal fauna, comprising several hundred specimens collected from the Sarmatian freshwater sediments of Vračević, allowed correlation of the deposits with the MN 7+8 zone, which is in accordance with previous stratigraphic classifications (Marković 2003). Reptile remains were quoted from the locality by Jovanović *et al.* (2002).

Material and methods

Three nearby sections exposing Sarmatian deposits in the valley of the Grabovac brook in the west of Vračević were sampled for the present study (Fig. 1). Section T1 (44° 17´ 34.4˝ N, 20° 09´ 54.5˝ E) was sampled by Z. Marković and D. Đurić in 1999, sections T2 (44° 17´ 36.84˝ N, 20° 09´ 52.8˝ E) and T3 (44° 17´ 42.1˝ N, 20° 09´ 51.4˝ E) by one of the present authors (GJ) in 2015. At that time, T1 was found collapsed and inaccessible anymore. Section T2 comprises two layers adding up to a total thickness of 2 m. Bed 1 (*c.* 140 cm) consists of clay and exposes examples of sediment slump structures (contorted strata in a slide-slump unit). Bed 2 (60 cm, sample T2) is composed of clay and contains mollusk remains. Section T3 comprises six distinct layers, which likewise add up to a thickness of 2 m. Bed 1 (60 cm, sample T3-1) consists of gray clay with coaly intercalations. The few-centimeter-thick bed 2 is composed of limonitic sandstone (sample T3-2). Bed 3 (40–60 cm, sample T3-3) is composed of clay with accumulations of mollusk shells and represents the main fossiliferous layer. Upsection follows silty clay (20–40 cm, sample T3-4a), coarse sand (10–30 cm, sample T3-4b) and bedded brownish clay (20 cm, sample T3-5). Bed 6 (20 cm, sample T3-6), finally, is composed of clay and lacks mollusk remains.

Samples were washed over a 0.2 mm-sieve and picked under the stereomicroscope. A total of 475 specimens have been identified. The material is stored at the Natural History Museum Belgrade under the inventory numbers K 6878 to K 6940. SEM images were made with a JEOL JSM-6610LV at the Natural History Museum Vienna, using an output voltage of 10 kV. The macro-photographs were made with a ZEISS Discovery.V20 stereomicroscope with attached AxioCam MRc5 using the stacking module of the software ZEISS AxioVision SE 64 4.9 to obtain throughout focused images.

Systematic palaeontology

The systematic arrangement is according to Bouchet & Rocroi (2005), Wade *et al.* (2006) and MolluscaBase (2016). Measurements are given as height × width for Gastropoda and height × width × convexity for Bivalvia, respectively. Terminology of apertural dentition in Strobilopsidae follows Moore (1960), those in Vertiginidae follows Nekola & Coles (2010). Stratigraphic ages of localities mentioned in this chapter are based on latest publications and were summarized in Neubauer *et al.* (2015b). A stratigraphic correlation chart combining the chronostratigraphic, regional stratigraphic and biostratigraphic terms used herein is provided in the discussion.

The synonymy lists cover papers providing first descriptions or illustrations, records synonymized here for the first time or those referred to in the discussion; other records can be found in more thorough lists such as those provided by Wenz (1923).

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Order Littorinimorpha Golikov & Starobogatov, 1975
Superfamily Littorinoidea Children, 1834
Family Pomatiidae Newton, 1891
Subfamily Pomatiinae Newton, 1891

Genus *Pomatias* Studer, 1789

Type species. – *Nerita elegans* Müller, 1774; by monotypy. Recent, Europe.

***Pomatias* sp.**
Figure 2A, B, E

Material. – 6 spire fragments and two opercula from T1 (K 6884, K 6933); 1 operculum from T2 (K 6885); 1 operculum from T3-3 (K 6937).

Dimensions. – Largest spire fragment: 3.50 × 3.91 mm (Fig. 2A, E); Operculum: 3.31 × 2.93 mm (Fig. 2B).

Description. – Protoconch smooth, comprises 1.7 whorls, measures 2.5 mm in maximum diameter; transition to teleoconch clearly marked by sharp onset of numerous distinct spiral ridges and distinct orthocline growth lines. Preserved teleoconch whorls highly and regularly convex. Aperture ovoid, almost circular. Umbilicus wide and deep.

Remarks. – Only opercula and thick-shelled apices are available, precluding more detailed description and identification at the species level. *Pomatias* is a common element in the European Neogene – Wenz (1923) listed eleven species for middle Miocene deposits.

Order unassigned
Superfamily Cyclophoroidea Gray, 1847
Family Cochlostomatidae Kobelt, 1902

Genus *Cochlostoma* Jan, 1830

Type species. – *Cyclostoma maculatum* Draparnaud, 1805 [currently considered as a junior synonym of *Cochlostoma septemspiralis* (Razoumowsky, 1789)]; subsequent designation by Wenz (1923). Recent, France.

***Cochlostoma* sp.**
Figure 2C, D, F, G

? 1967 *Cochlostoma (Obscurella) excellens* (Jooss). – Schütt, p. 200.
? 2006 *Cochlostoma septemspirale* (Razum., 1789). – Kókay, p. 31, pl. 3, figs 2–3 (non *Helix septemspiralis* Razoumowsky, 1789).

Material. – 6 spire fragments from T2 (K 6934); 17 spire fragments, 3 fragments of adult specimens and 1 subadult specimen from T3-3 (K 6886–6887, K 6937).

Dimensions. – 2.41 × 1.66 mm (Fig. 2G; specimen broken after imaging); 1.42 × 1.22 mm (Fig. 2C, D, F).

Description. – Slender conical shell with a maximum of five whorls preserved. Protoconch narrow, broad, consists of *c.* 1.4 whorls that measure *c.* 610 μm in diameter; starts with small nucleus but increases rapidly in diameter, producing slightly inflated early protoconch; nucleus surface weakly granulose; remaining protoconch surface appears smooth in center of whorls but wrinkled at upper sutures (towards nucleus). Transition to teleoconch marked by onset of weak axial ribs that increase quickly in strength. Spacing of ribs on first teleoconch whorls rather narrow (*c.* 30–40 μm), surface of interspaces highly granulose to pitted. Sculpture changes instantaneously after three quarters of a whorl, with marked increase of rib interspaces, disappearance of granulose/pitted surface pattern and change from blunt, broad ribs to sharp triangular crests. From that point onwards, ribs become constantly stronger while interspaces increase only weakly for next few whorls and then stay about the same. While early ribs form rather narrow, low-profile crests; ribs on second and third teleoconch whorls are pronounced, blade-like, protruding over 50 μm from whorl surface. In front view, ribs are steep prosocline, accompanied by numerous, faint, and parallel growth lines. Fragments of later whorls show more densely spaced and slightly weaker ribs. Whorls highly convex. Base straight, inclined with *c.* 30°; ribs persist on base as weak, blunt riblets. Aperture (of juvenile shell) broadly elliptical; columella weakly granulose. Umbilicus not developed in juvenile shells.

Remarks. – Only three cochlostomatid species are known from middle Miocene deposits of Europe, *i.e.*, *Cochlostoma ebfraasii* (Jooss, 1902) and *C. excellens* (Jooss, 1912) from Steinheim am Albuch, Germany, and *C. polonicum* (Łomnicki, 1902) from Krakow region, Poland. *Cochlostoma ebfraasii* differs from the present species in the less convex, centrally flattened whorls and the weaker ribs (Jooss 1902, 1912; Salvador *et al.* 2016c). The syntopical *C. excellens* is poorly known because the single specimen Jooss (1912) had at hand when describing the species consists of the last three whorls only (Salvador *et al.* 2016c), which complicates comparison with our apical fragments. The Steinheim species has highly convex whorls, numerous, delicate, narrowly placed ribs and an open umbilicus. Since the type of ribbing changes considerably in *Cochlostoma* during ontogeny (see also Manganelli & Giusti 1997), the difference in sculpture must not be taken as criterion for differentiation, though. Apical fragments from the Sarmatian of the Bakony Mts. illustrated and identified as Recent *C. septemspirale* (Razoumowsky, 1789) by Kókay (2006) agree well with the present specimens. Similarly, Schütt (1967) attributed apical fragments found in Sarmatian deposits at Hollabrunn to *C. excellens*. Unfortunately, he did not provide illustrations, but the description perfectly matches the Vračević material.

Cochlostoma polonicum has a more pointed spire and more, densely spaced and stronger inclined ribs (Łomnicki 1902). A very similar species in terms of shape and sculpture is *C. esuanum* Manganelli & Giusti, 1997 from the latest Miocene to early Pliocene of Italy; it differs from the present species in the wider placement and lower inclination of the ribs and the presence of an umbilicus (Manganelli & Giusti 1997; Harzhauser *et al.* 2015).

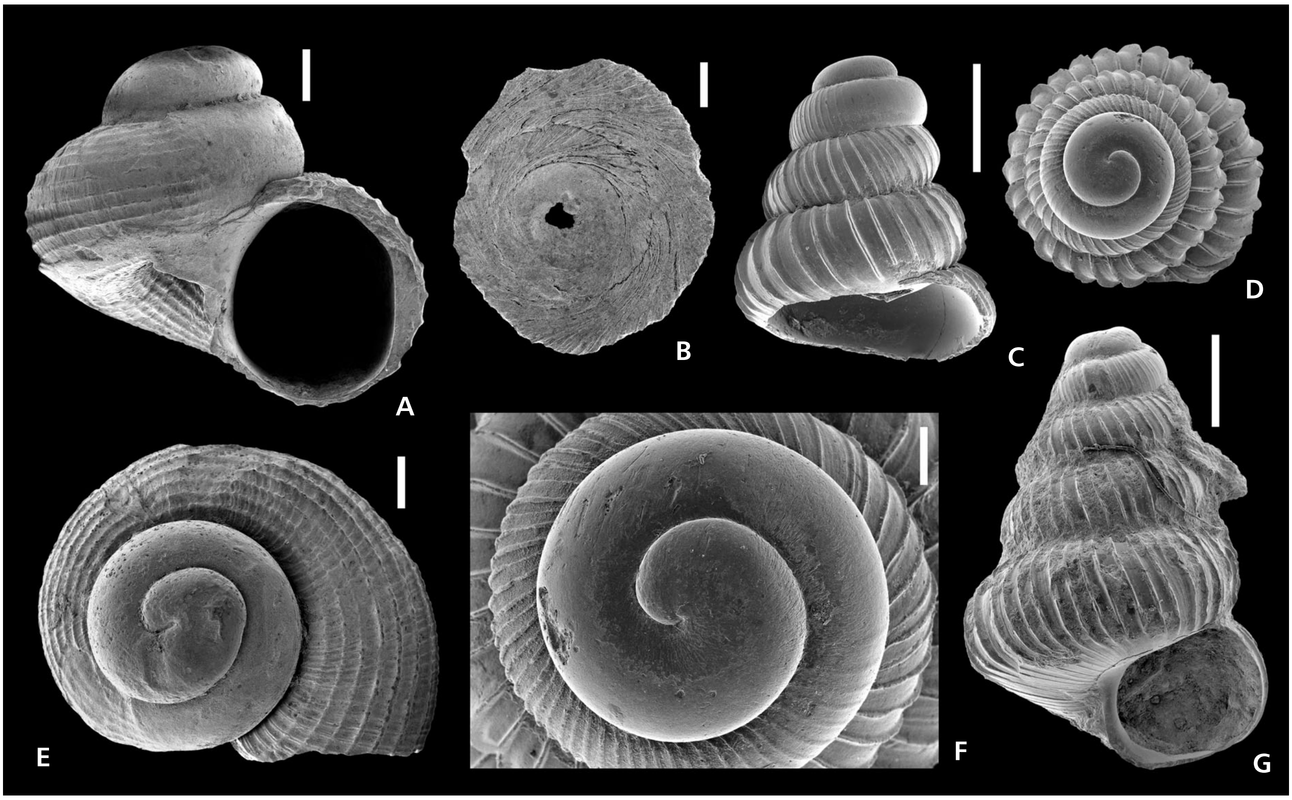


Figure 2. Pomatiidae and Cochlostomatidae. • A, E – *Pomatias* sp. Apex fragment, K 6884, from T1. • B – *Pomatias* sp. Operculum, K 6885, from T2. • C, D, F – *Cochlostoma* sp. Apex fragment, K 6886, from T3-3. • G – *Cochlostoma* sp. subadult shell, K 6887, from T3-3. Scale bars correspond to 500 µm (A–E, G) and 100 µm (F).

Clade Panpulmonata Jörger *et al.*, 2010
Order Hygrophila Férussac, 1822
Suborder Branchiopulmonata Morton, 1955
Infraorder Lymnaeoinei Minichev & Starobogatov, 1975
Superfamily Lymnaeoidea Rafinesque, 1815
Family Lymnaeidae Rafinesque, 1815

Genus *Stagnicola* Jeffreys, 1830

Type species. – *Limneus communis* Jeffreys, 1830; by monotypy. Recent, British Isles.

***Stagnicola* cf. *palustriformis* (Gottschick, 1911)**
Figure 3A–E

cf. *1911 *Limnaea* (*Limnophysa*) *palustriformis* Gottschick; Gottschick, p. 512, pl. 7, figs 7–9.
cf. 1920b *Limnaea* (*Limnophysa*) *armaniacensis palustriformis* Gottschick. – Gottschick, p. 113, pl. 2, fig. 8c.
cf. 1923 *Galba* (*Galba*) *armaniacensis palustriformis* (Gottschick). – Wenz, p. 1352.
2004 *Lymnaea* (*Omphiscola*) *armaniacensis palustriformis* Gottschick. – Kovalenko, p. 329, pl. 1, fig. 5a.
2004 *Lymnaea* (*Galba*) *turrita* Klein. – Kovalenko, p. 331, pl. 2, fig. 9 (non *Lymnaea turrita* Klein, 1853).
2006 *Stagnicola armaniacensis palustriformis* (Gottschick, 1911). – Kókay, p. 51, pl. 17, figs 2–3.

Material. – Only juvenile and fragmented shells are available: 65 specimens from T1 (K 6888–6889, K 6933); 8 specimens from T2 (K 6934); 1 specimen from T3-1 (K 6935); 1 specimen from T3-2 (K 6936); 43 specimens from T3-3 (K 6890, K 6937); 10 specimens from T3-4a (K 6938); 1 specimen from T3-5 (K 6940).

Dimensions. – 10.68 × 4.3 mm (almost complete shell; Fig. 3A, B), 7.66 × 4.14 mm (spire fragment; Fig. 3C), 2.47 × 1.32 mm (juvenile; Fig. 3D, E).

Description. – Slender elongate shell, with at least six highly convex whorls. Spire angle varies slightly; occasionally also slightly broader specimens occur. Whorl convexity decreases over time, is highest in whorl center. Whorls are tightly coiled, with narrow, not incised sutures. Last (preserved) whorl attains over 70% of shell height. Aperture slender ovate. Umbilicus narrow, slit-like. Growth lines orthocline.

Remarks. – Kovalenko (2004) listed as many as ten lymnaeid species for the middle Miocene of Serbia, five of which he claimed to occur in Vračević, *i.e.*, *L.* (*Omphiscola*) *serbica* Kovalenko, 2004; *L.* (*Omphiscola*) *ukrainica* Kovalenko, 2004; *L.* (*Omphiscola*) *palustriformis* Gottschick, 1911; *L.* (*Galba*) *truncatula* (Müller, 1774) and *L.* (*Galba*) *turrita* Klein, 1853. However, most of his identifications, as well as new species, seem to be based on fragments and juvenile specimens that hardly allow such detailed assessment. Unfortunately, his criteria to separate species are not comprehensible and he apparently disregarded morphological variability entirely, which is an important feature in Lymnaeidae (*e.g.*, Glöer 2002, Welter-Schultes 2012). For the Vračević material, he presented only poor drawings of two juvenile specimens that preclude any identification, on neither the species nor the genus level. Our material too comprises mostly fragments and juveniles but we consider them to belong to a single species. Kovalenko's (2004) drawings of the two species (*L. palustriformis*, *L. turrita*) correspond well to our material. Judging from the drawings of the other three species he listed for Vračević, they might as well belong to *S. palustriformis*, but examination of his material is necessary to clarify their status.

The species is reminiscent of *S. palustriformis*, which was originally described from Steinheim. That species has a slender shell and shows considerable variability concerning whorl convexity. Morphologies with prominent convexity (*e.g.*, Gottschick 1911, pl. 7, fig. 7) resemble the present species very closely and might be conspecific. The identification remains tentative because we lack complete shells and the details of the aperture are unknown.

Stagnicola glabraeformis Gottschick, 1911, likewise from Steinheim, resembles the present species in terms of whorl convexity but differs in its much more elongate shell and comparably small last whorl. *Lymnaea turrita* Klein, 1853, with which a part of the material from Vračević was determined by Kovalenko (2004), is a *nomen dubium* described from the vicinity of Zwiefalten (Upper Freshwater Molasse, southern Germany). Klein (1853) based this species on a few very slender but still juvenile shells, while later authors illustrated rather broad individuals (Sandberger 1872, pl. 28, fig. 26; Schlickum 1976, pl. 1, fig. 15). Neither of both morphologies resembles the present species.

A very similar species is a recently described *Lymnaea* from early late Miocene (Khersonian–Maeotian) deposits of Maikop, southern Russia (Vinarski & Frolov 2016; note that we omit the name of the new species on purpose because the respective paper has not been published in print and does not meet the criteria for an available publication in the sense of the ICZN). That morphologically quite variable species differs from the present shells in its peculiar and unique suture structure, being a narrow groove that penetrates deep into the shell matter (Vinarski & Frolov 2016). The widespread middle Miocene species *Stagnicola armaniacensis* (Noulet, 1857) from Sansan, France, is much broader (Sandberger 1870–1875, Bourguignat 1881, Schlickum 1976, Harzhauser *et al.* 2014a). The early middle Miocene *Lymnaea klaici* Brusina, 1884 from the Sinj and Drniš basins in Croatia can be distinguished by the presence of a laterally flattened last whorl (Neubauer *et al.* 2016). Late early Miocene *Stagnicola praebouilleti* Schlickum, 1970 from southern Germany has similarly slender shell but poorly convex whorls that increase slowly in height and diameter. The widespread early Miocene *Stagnicola subpalustris* (Thomä, 1845) has a distinctly coeloconoid outline and less convex whorls (*e.g.*, Harzhauser *et al.* 2014b). ?*Galba suevica* (Wenz, 1916) from the early Miocene Öpfingen Beds of Donaurieden (Germany) in the North Alpine Foreland Basin can be distinguished in the gradate spire (*cf.* Wenz 1916).

The systematic classification of *Stagnicola* is based on the slender elongate shape, which is found only among recent representatives of that genus (Glöer 2002, Welter-Schultes 2012). *Lymnaea* s.s. has a much more pointy and strongly coeloconoid spire; *Omphiscola*, in turn, is slender drop-shaped, with low-convex whorls that increase rapidly in height (Glöer 2002, Welter-Schultes 2012).

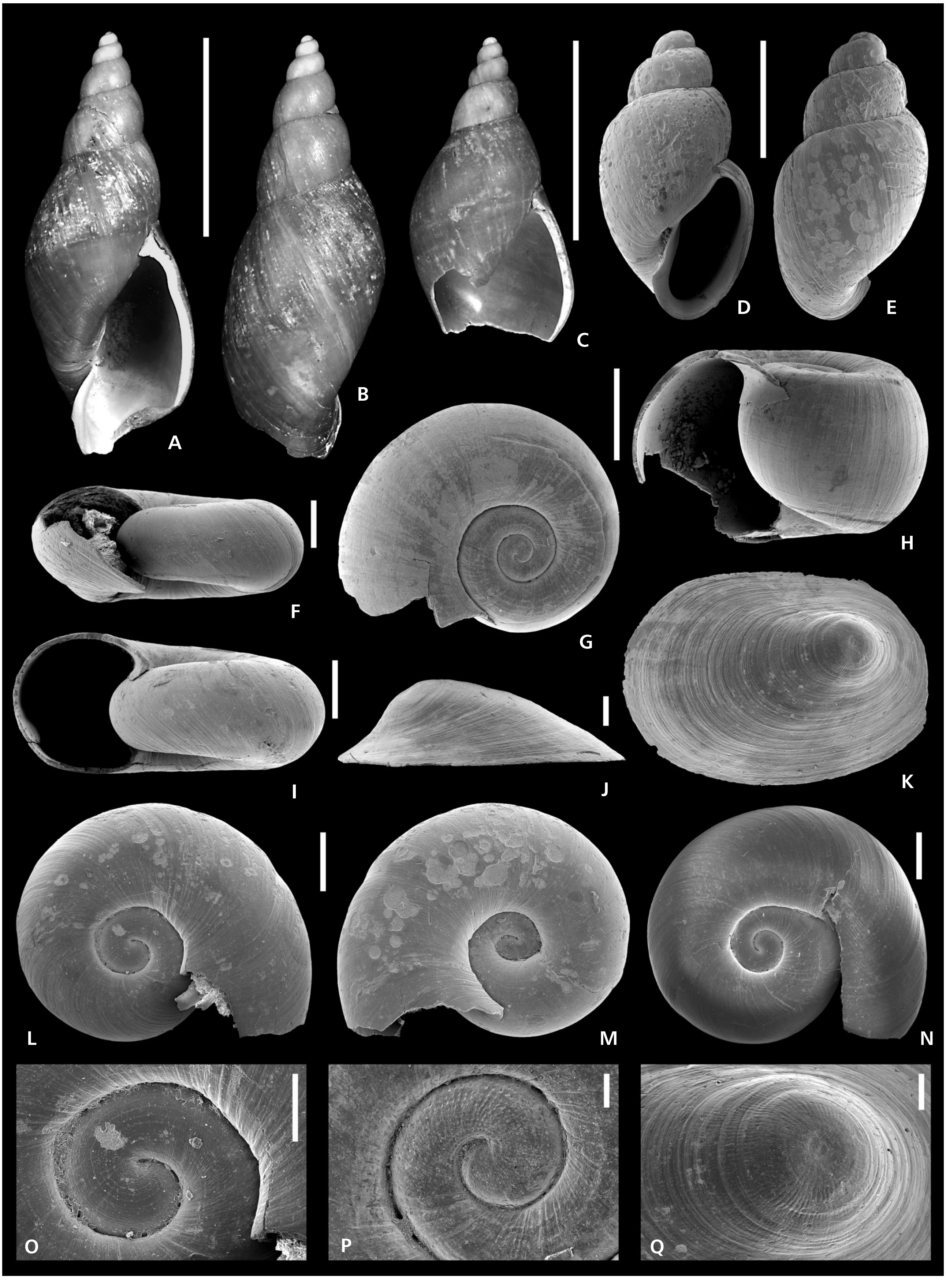
Occurrence. – Apart from the type locality Steinheim (MN 7), the species was reported from late Badenian and Sarmatian layers of the Bakony Mts. by Kókay (2006). Another tentative identification was listed by Bernor *et al.* (2004) for material from the early Pannonian (MN 9) of Rudabánya, Hungary.

Superfamily Planorboidea Rafinesque, 1815
Family Planorbidae Rafinesque, 1815
Subfamily Ancylinae Rafinesque, 1815

Genus *Ferrissia* Walker, 1903

Type species. – *Ancylus rivularis* Say, 1817; by original designation. Recent, North America.

Figure 3. Lymnaeidae and Planorbidae. • A, B – *Stagnicola* cf. *palustriformis* (Gottschick, 1911). Subadult shell, K 6888, from T1. • C – *Stagnicola* cf. *palustriformis* (Gottschick, 1911). Apex fragment, K 6889, from T1. • D, E – *Stagnicola* cf. *palustriformis* (Gottschick, 1911). Juvenile specimen, K 6890, from T3-3. • F, N – *Gyraulus kleini* Gottschick & Wenz, 1916. Juvenile specimen, K 6891, from T3-3. • G, H, P – *Planorbarius mantelli* (Dunker, 1848). Juvenile specimen, K 6893, from T1. • I, L, M, O – *Gyraulus kleini* Gottschick & Wenz, 1916. Juvenile specimen, K 6892, from T3-3. • J, K, Q – *Ferrissia deperdita* (Desmarest, 1814). K 6894, from T2. Scale bars correspond to 5 mm (A–C), 1 mm (D, E, G, H), 200 μm (F, I–N) and 100 μm (O–Q).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***Ferrissia deperdita* (Desmarest, 1814)**
Figure 3J, K, Q

*1814 *anc. Deperditus*; Desmarest, p. 19, pl. 1, fig. 14.
1923 *Pseudancylus deperditus deperditus* (Desmarest). – Wenz, p. 1692 (cum syn.).
1976 *Ferrissia deperdita* (Desmarest). – Schlickum, p. 7, pl. 1, fig. 20.
2005 *Ancylus wittmani* [*sic!*] Schlickum, 1964 – Prisyazhnyuk & Rudyuk, p. 226, pl. 1, figs 5–9 (non *Ancylus wittmanni* Schlickum, 1964).
2014a *Ferrissia deperdita* (Desmarest, 1814). – Harzhauser *et al.*, p. 17, pl. 5, figs 1–2, 5, 12 (cum syn.).
2015b *Ferrissia deperdita* (Desmarest, 1814). – Salvador *et al.*, p. 256, fig. 3c.
2016b *Ferrissia deperdita* (Desmarest, 1814). – Salvador & Rasser, p. 114, fig. 7.

Material. – 1 complete shell from T2 (K 6894); 1 fragmented specimen from T3-1 (K 6935); 4 fragmented specimens from T3-3 (K 6937).

Dimensions. – 2.06 × 1.44 × 0.60 mm (complete specimen; Fig. 3J, K, Q).

Remarks. – That widespread and well-known species was described in detail by Harzhauser *et al.* (2014a). For detailed synonymy lists and discussion see there.

Specimens from Vračević were confused previously with *Ancylus wittmanni* Schlickum, 1964 by Prisyazhnyuk & Rudyuk (2005). That late early Miocene species can be distinguished based on its cup-shaped apex, the flatter shell, the narrow elliptical outline and the distinct radial striae on the distal anterior shell portion (*cf.* Harzhauser *et al.* 2014a).

Occurrence. – Known from numerous middle Miocene localities in Austria, southern Germany, Hungary, Switzerland and the Rhône Basin in southern France (Wenz 1923, Kókay 2006, Harzhauser *et al.* 2014a, Salvador *et al.* 2015b).

Subfamily Planorbinae Rafinesque, 1815

Genus *Gyraulus* Charpentier, 1837

Type species. – *Planorbis albus* Müller, 1774; subsequent designation by Dall (1870). Recent, Europe.

***Gyraulus kleini* Gottschick & Wenz, 1916**
Figure 3F, I, L–O

*1916 [*Gyraulus multiformis*] *kleini* n. (= *laevis* Klein.); Gottschick & Wenz, p. 101.
1923 *Gyraulus* (*Gyraulus*) *trochiformis kleini* (Gottschick et Wenz). – Wenz, p. 1595 (cum syn.).
1978 *Anisus* (*Gyraulus*) *applanatus kleini* Gottschick et Wenz. – Gozhik & Prysjazhnjuk, p. 77, pl. 7, figs 1–9.
1997 *Gyraulus kleini* (Gottschick i Wenz, 1916). – Piechocki, p. 113, fig. 10.
1998 *Gyraulus kleini*. – Finger, p. 9, pl. 1, figs a–f, pl. 2, figs a–f, pl. 3, figs a–f, pl. 4, figs a–f.
2005 *Anisus* (*Gyraulus*) *kleini* Gottschick et Wenz, 1916. – Prisyazhnyuk & Rudyuk, p. 227, pl. 2, figs 1–7.
? 2005 *Anisus* (*Gyraulus*?) sp. – Prisyazhnyuk & Rudyuk, p. 227, pl. 2, fig. 8.
2006 *Gyraulus trochiformis kleini* Gottschick et Wenz, 1921. – Kókay, p. 57, pl. 19, figs 16–17.
2013 *Gyraulus kleini*. – Rasser, p. 15, figs 5a, 6a.
2014a *Gyraulus kleini* (Gottschick & Wenz, 1916). – Harzhauser *et al.*, p. 12, pl. 3, figs 1–4, 6, 14 (cum syn.).
2015b *Gyraulus kleini* (Gottschick & Wenz, 1916). – Salvador *et al.*, p. 256, figs 3d–f.
2016c *kleini* Gottschick & Wenz, 1916, *Gyraulus multiformis*. – Salvador *et al.*, p. 29.
2016c *Gyraulus kleini* Gottschick & Wenz, 1916. – Salvador *et al.*, pl. 5, figs 16a–c.

Material. – Only juvenile shells and fragments have been found: 18 specimens from T2 (K 6934); 5 specimens from T3-1 (K 6935); 44 specimens from T3-3 (K 6891–6892, K 6937); 1 specimen from T3-4b (K 6939).

Dimensions. – 0.49 × 1.07 mm (Fig. 3F, N); 0.54 × 1.17 mm (Fig. 3I, L, M, O).

Remarks. – Although no entire adult specimen is available, the morphology is highly reminiscent of the widespread *G. kleini* and corresponds well to that of the juvenile specimens illustrated by Finger (1998) and Rasser (2013) from the type locality Steinheim. The species has been described in detail by Harzhauser *et al.* (2014a) and Salvador *et al.* (2015b). The species was already identified in the Vračević deposits by Prisyazhnyuk & Rudyuk (2005). The specimens they determined as "*Anisus* (*Gyraulus*?) sp." also agree well with the species and are considered synonymous.

Occurrence. – This species is a common element in many middle Miocene localities in Austria, Czech Republic, southern Germany, Hungary, Poland, Switzerland and Ukraine (Wenz 1923, Gozhik & Prysjazhnjuk 1978, Piechocki 1997, Gál *et al.* 2000, Kókay 2006, Harzhauser *et al.* 2014a, Salvador *et al.* 2015b).

Genus *Planorbarius* Duméril, 1805

Type species. – *Helix cornea* Linnaeus, 1758; by subsequent monotypy (Froriep 1806). Recent, Europe.

***Planorbarius mantelli* (Dunker, 1848)**
Figure 3G, H, P

*1848 *Planorbis Mantelli*, Dkr.; Dunker, p. 159, pl. 21, figs 27–29.
1923 *Coretus cornu mantelli* (Dunker). – Wenz, p. 1452 (cum syn.).
2005 *Planorbarius cornu mantelli* Dunker, 1848. – Prisyazhnyuk & Rudyuk, p. 225, pl. 1, figs 1–4.
2014a *Planorbarius mantelli* (Dunker, 1848). – Harzhauser *et al.*, p. 15, pl. 3, figs 5, 7–13, 15–16 (cum syn.).
2014 *Planorbarius cornu* (Brongniart, 1810). – Salvador & Rasser, p. 193, figs 26–28 (non *Planorbis cornu* Brongniart, 1810).
2015a *Planorbarius cornu* (Brongniart, 1810). – Salvador *et al.*, p. 205, fig. 2j (*non* Brongniart, 1810).
2015b *Planorbarius cornu* (Brongniart, 1810). – Salvador *et al.*, p. 256, fig. 3g–h (*non* Brongniart, 1810).
2016a *Planorbarius mantelli* (Dunker, 1848). – Salvador & Rasser, p. 44, fig. 2i–j.
2016b *Planorbarius mantelli* (Dunker, 1848). – Salvador & Rasser, p. 115, figs 9–11.
2016a *Planorbarius cornu* (Brongniart, 1810) – Salvador *et al.*, p. 135, fig. 2p–q (*non* Brongniart, 1810).
2016b *Planorbarius mantelli* (Dunker, 1848). – Salvador *et al.*, p. 482, fig. 5j.

Material. – A single juvenile specimen from T1 (K 6893).

Dimensions. – 2.30 × 3.07 mm; adult specimens may attain a diameter of up to 38 mm (Harzhauser *et al.* 2014a).

Remarks. – *Planorbarius mantelli* is one of the most common species in the late early to late Miocene of Europe. Most of the middle Miocene records have been formerly and are still often identified as its supposed phylogenetic predecessor, the Oligocene–early Miocene *P. cornu* (Brongniart, 1810). For discussion on the matter as well as a detailed description, see Harzhauser *et al.* (2014a).

Occurrence. – Appears in the late early Miocene in the North Alpine Foreland Basin and the Korneuburg Basin (*e.g.*, Wenz 1923, Binder 2002, Jost *et al.* 2007), becomes ubiquitous during the middle Miocene (*e.g.*, Schlickum 1976; Gál *et al.* 2000; Kókay 2006; Hír & Kókay 2010; Harzhauser *et al.* 2014a; Salvador *et al.* 2015a, b, 2016b; Salvador & Rasser 2016a; partly as *P. cornu*) and disappears during the late Miocene (Harzhauser & Binder 2004).

Superorder Eupulmonata Haszprunar & Huber, 1990
Infraorder Acteophila Dall, 1885
Superfamily Ellobioidea H. Adams & A. Adams, 1855
Family Carychiidae Jeffreys, 1830

Genus *Carychium* Müller, 1773

Type species. – *Carychium minimum* Müller, 1774; by subsequent monotypy. Recent, Europe.

***Carychium gibbum* Sandberger, 1875**
Figure 4F–I, K, L, P

*1875 *Carychium gibbum*; Sandberger, p. 583.
1885 *Carychium gibbum* Sdbgr. – Clessin, p. 87, pl. 7, fig. 9a–b.
1923 *Carychium nouleti gibbum* Sandberger. – Wenz, p. 1197 (cum syn.).
1967 *Carychium nouleti suevicum* O. Boettger. – Schütt, p. 203, fig. 4 (non *Carychium suevicum* O. Boettger, 1877).
1972 *Carychium nouleti gibbum* Sandberger. – Gall, p. 14.
1976 *Carychium nouleti gibbum* Sandberger. – Schlickum, p. 4, pl. 1, figs 10–11.
1977 *Carychium* (*Saraphia*) *nouleti* Bourguignat, 1857 s. l. – Strauch, p. 162, pl. 15, fig. 25 (*partim*, non *Carychium nouleti* Bourguignat, 1857).
1999a *Carychium rhenanum* Strauch, 1977. – Stworzewicz, p. 265, figs 7–8 (non *Carychium rhenanum* Strauch, 1977).
2004 *Carychium nouleti gibbum* Sandberger. – Hír & Kókay, p. 85, fig. 6:7.
2006 *Carychium nouleti gibbum* Sandberger, 1874. – Kókay, p. 47, pl. 15, figs 10–11.
2014a *Carychium gibbum* Sandberger, 1875. – Harzhauser *et al.*, p. 20, pl. 6, figs 1–4, 9, 12 (cum syn.).
2015 *Carychium* (*Carychium*) *galli* n. sp. – Salvador, p. 39, figs 2–4.
2016 *Carychium gibbum* (Sandberger, 1875). – Jochum *et al.*, p. 90, figs 4a–f, 5c–d.
2016a *Carychium* (*Carychium*) *galli* Salvador, 2015. – Salvador *et al.*, p. 136, fig. 2s–t.

Material. – 4 specimens from T2 (K 6934); 11 specimens from T3-3 (K 6898–6899, K 6937).

Dimensions. – 1.57 × 0.81 mm (Fig. 4F, G, K, L); 1.47 × 0.73 mm (Fig. 4H, I, P).

Remarks. – The present material corresponds well with specimens from the type locality Undorf and the early middle Miocene ones of the Rein Basin (Harzhauser *et al.* 2014a; for a description see there). The only difference seems to be the pitted surface of the teleoconch in the Vračević shells, which has not been observed in other populations of the species. Jochum *et al.* (2016) recently suggested that the retention of protoconch sculpture on the teleoconch of carychiids indicates a paedomorphic life strategy, likely being an adaptation to the prevailing ecological conditions. So far, such a pattern has only been observed in Miocene representatives of *Carychiella* (Harzhauser *et al.* 2014a, b, 2015; Jochum *et al.* 2016) but not in *Carychium*.

The first illustrations of *C. gibbum* from the type locality Undorf provided by Clessin (1885) are quite misleading because they show an over-sized last and penultimate whorl. Also the angle of the aperture and the expression of the denticles are poorly drawn.

Wenz (1923) ranked the species as a subspecies of *C. nouleti* Bourguignat, 1857, a species described from the middle Miocene of Sansan. Strauch (1977) considered the differences between both species not enough to justify taxonomic separation and synonymized them. In our opinion, however, the two taxa can be well distinguished, especially based on the columellar apparatus (*Carychium*-type in *C. gibbum* vs. *Saraphia*-type in *C. nouleti*), and should be treated as separate species.

A similar species is *Carychium suevicum* O. Boettger, 1877, which had been ranked as subspecies of *C. nouleti* by Wenz (1923) but considered a distinct species by Strauch (1977) based on differences of the columellar apparatus. The specimen from Steinheim he illustrated (pl. 13, fig. 8) shows a slender habitus and a not inflated penultimate whorl. After Gottschick (1920b) the species is very variable and occasionally bulgy specimens occur (*e.g.*, Finger 1998: pl. 10, fig. b), but their penultimate whorls are not inflated either. The two specimens from Hollabrunn identified as *C. suevicum* by Schütt (1967), however, do show the typical inflation and therefore are considered to represent *C. gibbum*.

Stworzewicz (1999a) identified specimens from the early to middle Miocene of Bełchatów, southern Poland, with the late Pliocene species *C. rhenanum* Strauch, 1977. That species is much more slender, lacks the inflation of the penultimate whorl and has a very prominent parietal lamella. The broad, finely striate shell with the slightly inflated penultimate whorl and a simple lamella rather argues for an attribution to *C. gibbum*.

The species was also mentioned from the Upper Freshwater Molasse deposits at Sandelzhausen in southern Germany by Gall (1972). That record was recently revised by Salvador (2015), who introduced the new species *C. galli* for that material. Salvador (2015) did not discuss similarities between both species, although the shells he illustrated are strikingly similar to *C. gibbum*; they are slightly more slender but otherwise fully correspond, including also the simple lamella. The specimens from nearby Riedensheim and Adelschlag Salvador *et al.* (2016a) identified as *C. galli* match *C. gibbum* even closer, showing broad shells and the typically inflated penultimate whorls. Therefore, we consider *C. galli* as a junior synonym of *C. gibbum*. The single shell from the early Miocene (Ottnangian) Upper Brackish Water Molasse at Buttenwiesen determined as *C.* cf. *galli* by Salvador *et al.* (2016b) does not have the inflated penultimate whorl and a strongly reduced palatal denticle and probably represents a different species.

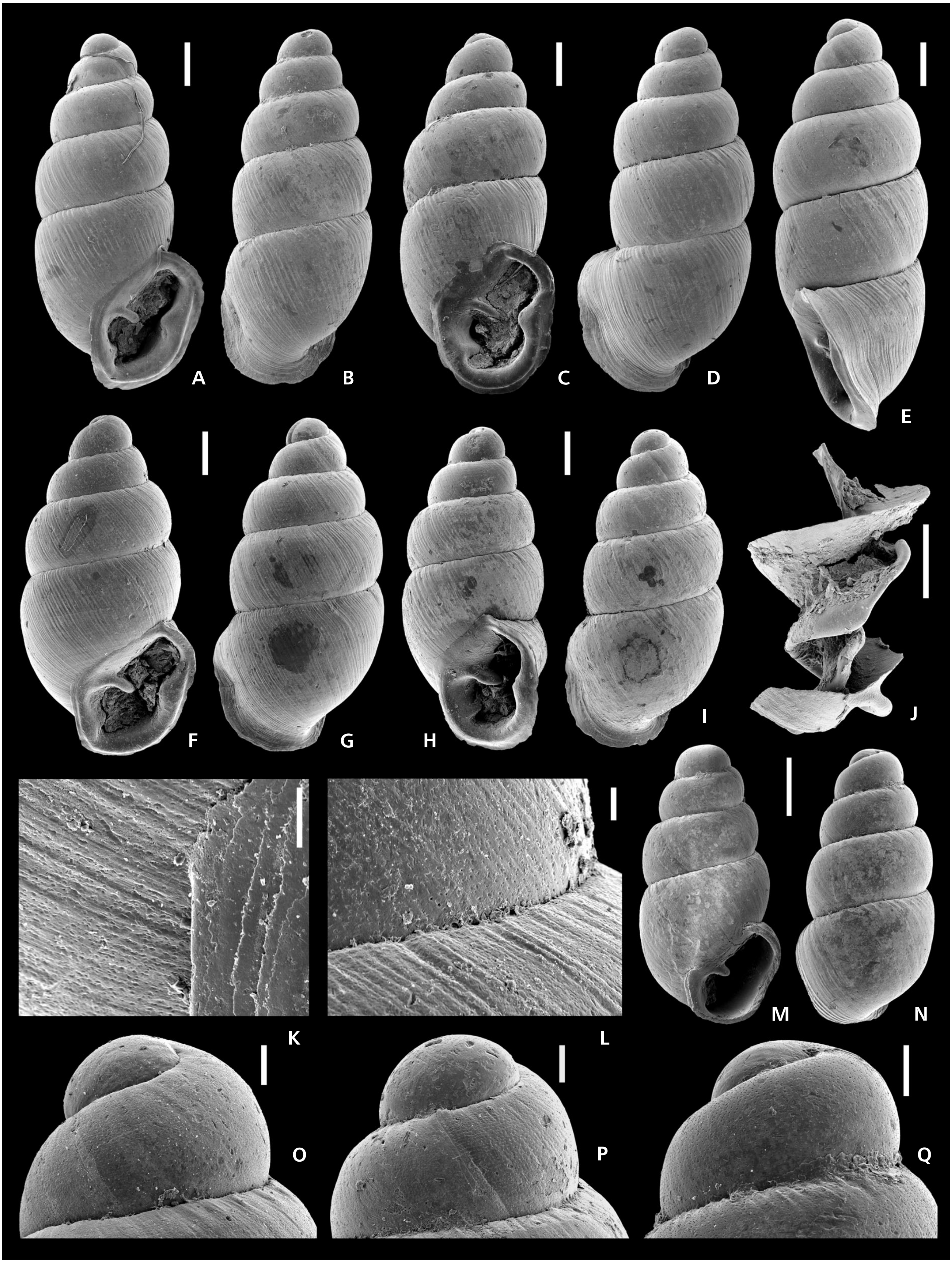
Occurrence. – Undorf, southern Germany (late early to early middle Miocene, MN 5; Sandberger 1870–1875); Upper Freshwater Molasse at Adelschlag, Hohenmemmingen, Mörsingen, Riedensheim, Sandelzhausen and Zwiefaltendorf in southern Germany and Handreute and Flühlen in western Austria (MN 5; partly as *C. galli*; Wenz 1923, 1935; Schlickum 1976; Salvador 2015; Salvador *et al.* 2016a); Enzenbach (Rein Basin) and Strassgang (Graz Basin), Austria (early middle Miocene, late MN 5; Harzhauser *et al.* 2014a); Mátraszőlős and the Bakony Mts., Hungary (late Badenian; Gál *et al.* 2000, Hír & Kókay 2004, Kókay 2006); Wiesen and Hollabrunn, Austria (Sarmatian; partly as *C. suevicum*; Papp 1939, Schütt 1967); Bełchatów, Poland (misidentified as *C. rhenanum*; Stworzewicz 1999a), layers Beł-C (late early Miocene, MN 4), Beł-B (late early Miocene, early MN 5) and Beł-A (early late Miocene, MN 9).

Carychium nouleti Bourguignat, 1857 s.l.

Figure 4 A–E, J, O

*1857 *Carychium Nouleti*; Bourguignat, p. 226.
1860 *Carychium Nouleti*. – Bourguignat, p. 56, pl. 11, figs 9–10.
1902 *Carychium minimum* (M.) v. *elongata* [*sic!*] Villa. – Andreae, p.22 (non *Carychium elongatum* A. & J.B. Villa, 1841).
1923 *Carychium nouleti nouleti* Bourguignat. – Wenz, p. 1195 (cum syn.).
1923 *Carychium sandbergeri* Handmann. – Wenz,

Figure 4. Carychiidae. • A, B – *Carychium nouleti* Bourguignat, 1857 s.l. K 6895, from T3-3. • C, D – *Carychium nouleti* Bourguignat, 1857 s.l. K 6896, from T3-3. • E, O – *Carychium nouleti* Bourguignat, 1857 s.l. K 6897, from T3-3. • F, G, K, L – *Carychium gibbum* Sandberger, 1875. K 6898, from T3-3. Detail images show the pitted shell surface on the base of the last whorl (K) and on first and second teleoconch whorl (L). • H, I, P – *Carychium gibbum* Sandberger, 1875. K 6899, from T3-3. • J – *Carychium nouleti* Bourguignat, 1857 s.l. Columellar apparatus, K 6900, from T3-3. • M, N, Q – *Carychiella eumicrum* (Bourguignat, 1857). K 6901, from T3-3. Scale bars correspond to 200 µm (A–J, M, N), 50 µm (O–Q) and 20 µm (K, L).


A
B
C
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p. 1199 (*partim*; only regarding records by Andreae from Nowa Wieś Królewska).

1967 *Carychium sandbergeri* Handmann – Schütt, p. 204, fig. 5 (non *Carychium sandbergeri* Handmann, 1887).

1977 *Carychium* (*Saraphia*) *nouleti* Bourguignat, 1857 s.l. – Strauch, p. 162, pl. 15, figs 24, 26–27, pl. 18, fig. 61, pl. 20, fig. 83. (*partim*; non pl. 15, fig. 25 = *C. gibbum*).

1994 *Carychium* (*Saraphia*) *nouleti* Bourguignat, 1857. – Schütt, p. 168, pl. 1, fig. 4.

? 2000 *Carychium sandbergeri* Handmann, 1887. – Reischütz, p. 25.

2006 *Carychium sandbergeri* Handmann, 1887. – Kókay, p. 47, pl. 15, fig. 12 (*partim*; non *Carychium sandbergeri* Handmann, 1887).

non 2006 *Carychium nouleti nouleti* Bourguignat, 1877. – Kókay, p. 47, pl. 15, fig. 9.

2013 *Carychium starobogatovi* Steklov, 1966. – Stworzewicz *et al.*, p.183, fig. 3b (non *Carychium starobogatovi* Steklov, 1966).

Material. – 2 specimens from T1 (K 6933); 2 specimens from T3-1 (K 6935); 21 specimens from T3-3 (K 6895–6897, K 6900, K 6937); 1 specimen from T3-5 (K 6940).

Dimensions. – 1.64 × 0.78 mm (Fig. 4A, B); 1.90 × 0.72 mm (Fig. 4C, D); 1.68 × 0.82 mm (Fig. 4E, O).

Description. – Slender elongate shell, with up to 4.75 whorls. Protoconch makes up little less than one whorl that forms small, weakly bulbous cap with initial part immersed; surface densely covered by tiny, more or less spirally arranged pits, which are absent close to upper suture and on initial part; transition to teleoconch marked by inconspicuous growth stop. Following teleoconch whorl surface granulose to irregularly pitted. Penultimate whorl slightly, occasionally very distinctly, inflated. Last whorl attains 53–58% of total shell height. Aperture widely elliptical, with thickened and expanded peristome; parietal lamella strong, columellar lamella distinct but weaker, palatal knob marked. Interior apparatus of *Saraphia*-type: parietal lamella typically sinuate, marginally weakly thickened, adapical and abapical lobes only weakly turned; columellar lamella broad, weakly sinuate (Fig. 4J).

Remarks. – Strauch (1977) joined a great variety of morphotypes under the name *C. nouleti* "sensu lato", ranging from the small, slender and short morphology of specimens from the type locality Sansan (pl. 15, fig. 24) to broad specimens previously attributed to *C. gibbum* (pl. 15, fig. 25; see discussion of that species above) and the very elongate forms from Nowa Wieś Królewska near Opole (pl. 15, fig. 27; "*elongata*" Andreae, *non* Villa & Villa). Nevertheless, he conceded that the species needs revision. Our specimens, and particularly the columellar apparatus, fit perfectly the description and some of the illustrations in Strauch (1977). Especially the Opole specimens are very similar to the present shells in terms of habitus and columellar apparatus. However, there is considerable uncertainty whether those specimens actually match material from the type locality Sansan. Specimens of *C. nouleti* from Sansan illustrated in Bourguignat (1862: pl. 4, figs 22–23), Sandberger (1872: pl. 28, fig. 29) and even Strauch (1977: pl. 15, fig. 24) clearly lack inflation of the penultimate whorl. Moreover, that lack was one of the reasons for Sandberger (1875) to distinguish his *C. gibbum* from *C. nouleti*. Since we lack specimens for original *C. nouleti* from Sansan and information on their columellar apparatus, we preliminarily accept the treatment by Strauch (1977) and attribute the specimens to *C. nouleti* sensu lato.

Schütt (1967) identified specimens from the Sarmatian of Hollabrunn, Austria, with *Carychium sandbergeri* Handmann, 1887, albeit admitting that the Sarmatian forms are shorter than the original Pannonian ones described from Leobersdorf. *Carychium sandbergeri* is, in fact, much larger [up to 2.3 mm after Strauch (1977)] and more elongate and has slightly more and less convex whorls. The shells from Hollabrunn correspond well to the present material instead. Very likely, also the record from the Sarmatian of Hautzendorf by Reischütz (2000) belongs to *C. nouleti*.

Similarly, a shell from the Sarmatian of the Bakony Mts. identified as *C. sandbergeri* by Kókay (2006) corresponds to the present shells in terms of size, shape and columellar apparatus. A specimen from the early Badenian of that area Kókay (2006) misidentified as *C. nouleti* can be distinguished from the species by its stout shape, the smaller size and the markedly stepped whorls.

The Vračević material also resembles *Carychium suevicum* O. Boettger, 1877 from Steinheim in overall shape and size. That species differs in its columellar apparatus, showing a weaker, less undulated parietal lamella and a not thickened columellar lamella.

Stworzewicz *et al.* (2013) determined shells from the Sarmatian of Zwierzyniec as *Carychium starobogatovi* Steklov, 1966. That species is, however, more slender and lacks the inflated penultimate, which is also present in the Polish specimen illustrated by Stworzewicz *et al.* (2013). The columellar apparatus of *C. starobogatovi* (which is unknown for the Polish shells) is characterized by a weak, slightly undulated parietal lamella. Because of the high degree of similarity with the present material, we attribute the specimens that were identified as *C. starobogatovi* by Stworzewicz *et al.* (2013) to *C. nouleti* s.l.

Occurrence. – Apart from the type locality Sansan in France (late Langhian, MN 6), Wenz (1923) listed the species from the early Miocene of the Aquitaine Basin, the middle Miocene of Ukraine, the Pliocene of Romania and Algeria, but many of those records require re-examination. Other records all come from Sarmatian deposits: Hollabrunn and (tentatively) Hautzendorf in Austria (Schütt 1967, Reischütz 2000), Nowa Wieś Królewska near Opole (Andreae 1902b, Strauch 1977), Bakony Mts. (Kókay 2006), Zwierzyniec (Stworzewicz *et al.* 2013) and Çifteçesme near Ayvalı in Turkey (Schütt 1994).

Genus *Carychiella* Strauch, 1977

Type species. – *Carychium eumicrum* Bourguignat, 1857; by original designation (albeit misspelt as "*eumicron*"). Miocene, Europe.

***Carychiella eumicrum* (Bourguignat, 1857)**
Figure 4M, N, Q

- *1857 *Carychium eumicrum*; Bourguignat, p. 223.
- 1923 *Carychium eumicron eumicron* [*sic!*] Bourguignat. – Wenz, p. 1187 (cum syn.).
- 1977 *Carychium* (*Carychiella*) *eumicron* [*sic*!] Bourguignat, 1857. – Strauch, p. 159, pl. 14, figs 13–15, pl. 17, fig. 53, pl. 19, fig. 76.
- 1999a *Carychium eumicrum* Bourguignat, 1857. – Stworzewicz, p. 264, figs 5–6.
- 2006 *Carychium* (*Carychiella*) *eumicron eumicron* [*sic!*] Bourguignat, 1857. – Kókay, p. 48, pl. 16, fig. 5.
- 2014a *Carychium eumicrum* Bourguignat, 1857. – Harzhauser *et al.*, p. 19, pl. 6, figs 6–7, 10.
- 2014b *Carychiella eumicrum* (Bourguignat, 1857). – Harzhauser *et al.*, p. 837, fig. 5h–j (cum syn.).
- 2015 *Carychium* (*Carychiella*) *eumicron* [*sic!*] Bourguignat, 1857. – Salvador, p. 38, fig. 1.
- 2016a *Carychium eumicrum* Bourguignat, 1857. – Salvador *et al.*, p. 135, fig. 2r.

Material. – A single shell from T3-3 (K 6901).

Dimensions. – 0.96 × 0.49 mm.

Remarks. – The shell corresponds well to the specimens from Opole illustrated by Strauch (1977). The ones from the early middle Miocene of the Rein Basin studied by Harzhauser *et al.* (2014a) have a more inflated protoconch but otherwise agree in shape, the arrangement of the teeth, the pitted surface and the growth lines occasionally forming riblets. *Carychiella crossei* (Denainvilliers, 1875), first described for early Miocene material from Dadonville, France, but also recorded from the early Miocene of the Mainz Basin (Germany) and the middle Miocene of Opole (Poland), is larger and much more slender than the present species (*cf.* Strauch 1977). The late Miocene (late Sarmatian–Maeotian) *Carychiella marinae* (Steklov, 1966) from Maikop in southern Russia is likewise more slender and has poorly convex whorls. *Carychiella puisseguri* (Truc, 1972), originally described from the Pliocene of Celleneuve, France, and recorded from the Messinian of Moncucco Torinese, Italy (Harzhauser *et al.* 2015), has a stronger parietal lamella and more convex whorls. *Carychiella eumicrum unidentata* (Kókay, 2006) from the early Miocene of Somlóvásárhely, Hungary, has a conical shape, a larger last whorl and a single, very weak denticle at the transition between columellar and parietal margin.

Occurrence. – Hochheim am Main, Germany (late Oligocene–early Miocene; Bourguignat 1857); Bełchatów, Poland, layers Beł-B (early MN 5; Stworzewicz 1999a); Tuchořice, Lipno and Kralupy, Czech Republic (early Miocene, MN 3b; Harzhauser *et al.* 2014b); Undorf and Sandelzhausen, southern Germany (MN 5; Stworzewicz 1999a, Salvador 2015, Salvador *et al.* 2016a); Rein Basin, Austria (late MN 5; Harzhauser *et al.* 2014a); Nowa Wieś Królewska near Opole, Poland (MN 6–7; Strauch 1977, Stworzewicz 1999a); Várpalota, Hungary (Sarmatian; Kókay 2006).

Infraorder Stylommatophora Schmidt, 1855
Non-achatinoid clade *sensu* Wade *et al.* (2006)
Unassigned "subclade" Orthuretha Pilsbry, 1900
Superfamily Cochlicopoidea Pilsbry, 1900 (1879)
Family Cochlicopidae Pilsbry, 1900

Genus *Cochlicopa* Férussac, 1821

Type species. – *Helix lubrica* Müller, 1774; subsequent designation by Bourguignat (1856). Recent, Europe.

***Cochlicopa* sp.**
Figure 5A–D

Material. – A single fragmented juvenile fragment from T3-3 (K 6902).

Dimensions. – 1.59 × 0.89 mm.

Description. – Slender conical shell with three convex whorls. Protoconch smooth, low domical; transition to teleoconch unclear. Teleoconch whorl surface smooth except faint irregular threads near upper suture and occasional weak orthocline growth lines. Sutures narrow, not incised. Aperture (of juvenile) slender drop-shaped with simple outer lip and sheet-like inner lip.

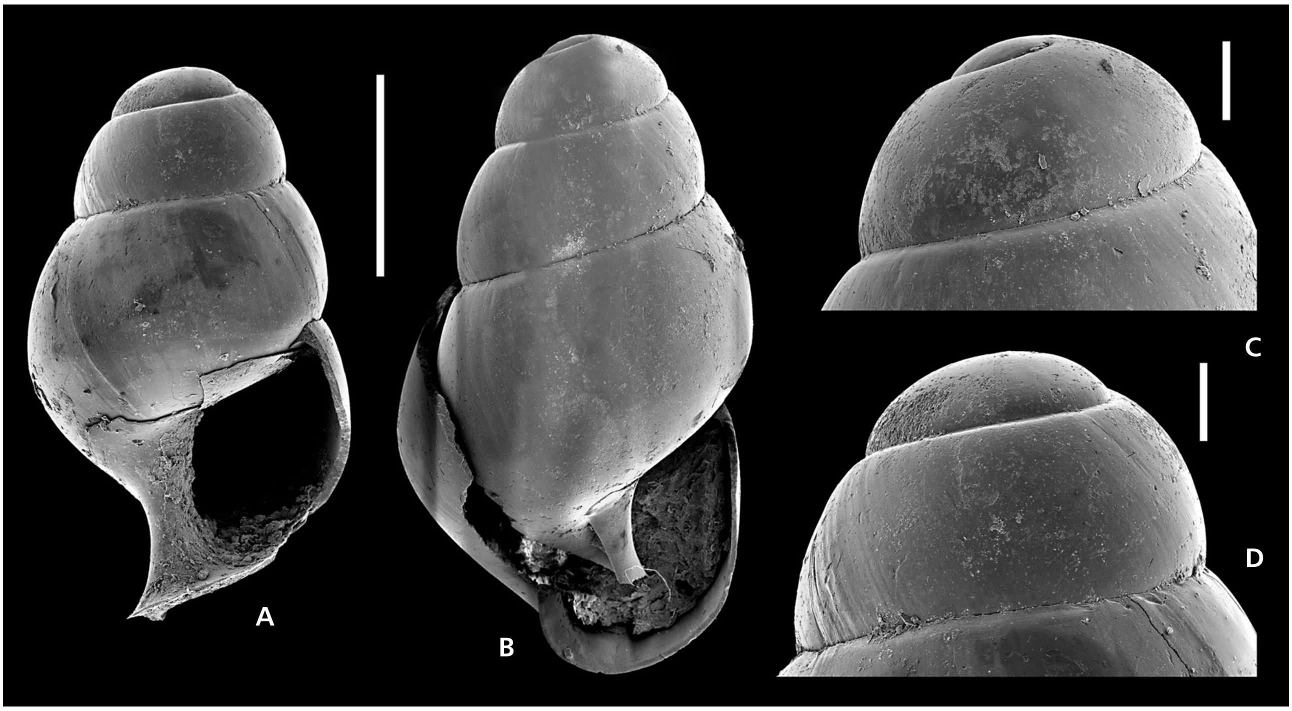


Figure 5. A–D – *Cochlicopa* sp. (Cochlicopidae). Juvenile specimen, K 6902, from T3-3. Scale bars correspond to 500 μm (A, B) and 100 μm (C, D).

Remarks. – Shape and size of the early whorls agree with features found in recent species of *Cochlicopa*. An affiliation with the cochlicopoid genus *Azeca* is ruled out because of its more obtuse and broadly ovoid apex consisting of much lower and poorly convex whorls.

Wenz (1923) listed several Cochlicopidae for the European Miocene, all of which he classified as subspecies of "*Cochlicopa*" *subrimata* (Reuss in Reuss & Meyer, 1849). That species, described from the early Miocene of Tuchořice, differs from recent *Cochlicopa* species in the broadly obtuse apex and the low convex whorls. Because of these characteristics, Harzhauser *et al.* (2014b) classified that species within the genus *Hypnophila* Bourguignat, 1858 (Acezidae). Following this approach, Salvador & Rasser (2016b) recently transferred "*Cochlicopa*" *loxostoma* (Klein, 1853) to *Hypnophila* too. Consequently, many of the other alleged *Cochlicopa* records from the European fossil record must be reviewed carefully. The only confirmed fossil *Cochlicopa* species seems to be *C. dormitzeri* (Reuss in Reuss & Meyer, 1849) from Tuchořice; it differs from the present shell in the more inflated protoconch and the slightly less convex whorls.

Superfamily Pupilloidea Turton, 1831
Family Strobilopsidae Wenz, 1915

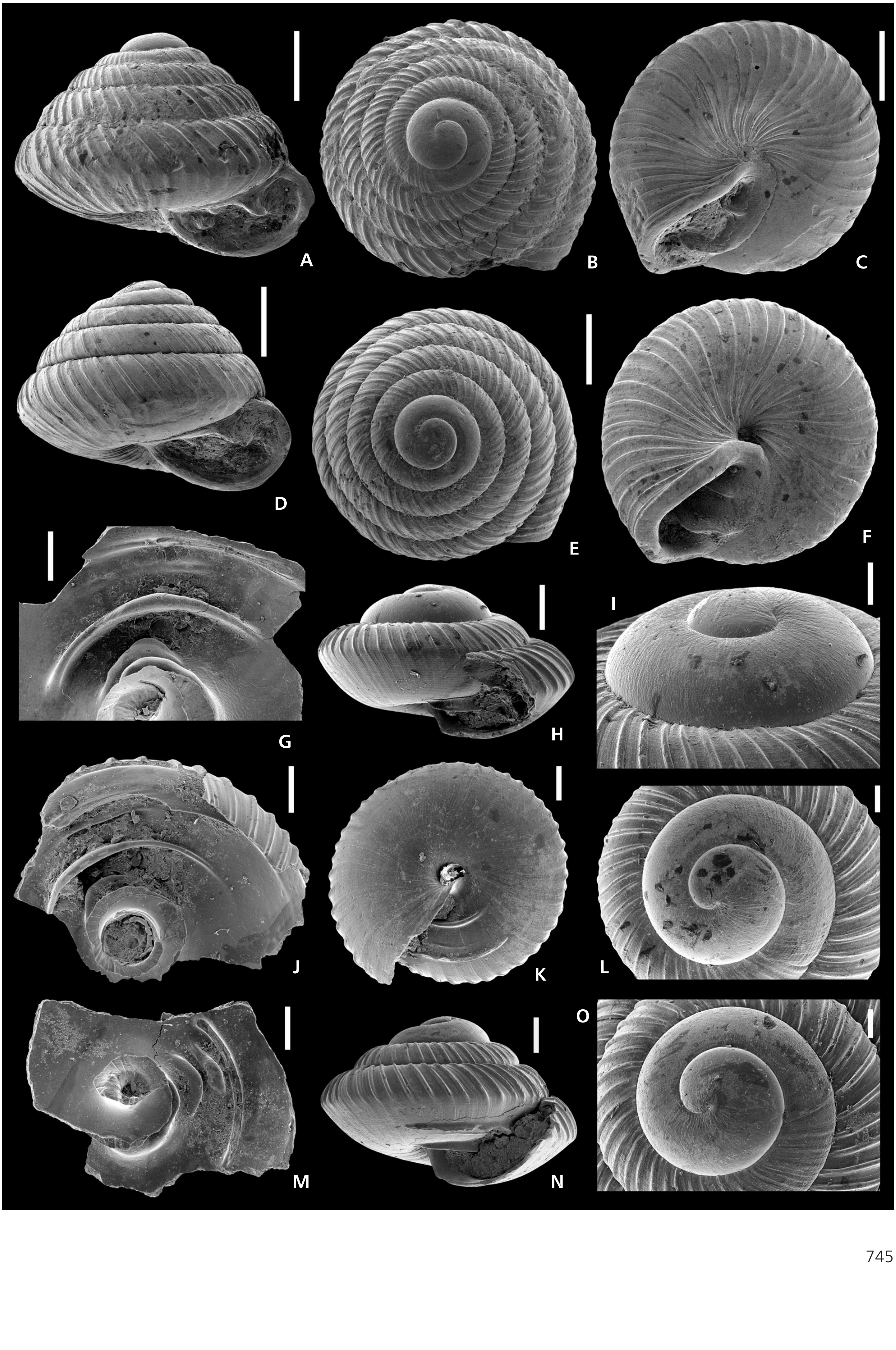
Genus *Strobilops* Pilsbry, 1893

Type species. – *Helix labyrinthica* Say, 1817; by typification of replaced junior homonym *Strobila* Morse, 1864, *non* Sars, 1829. Recent, North America.

***Strobilops costatus* (Clessin, 1877)**
Figure 6A–O

*1877 *Strobilus costatus* Sdbgr. in litt.; Clessin, p. 37.
1885 *Strob. costatus* Sdbgr. in Clessin. – Clessin, p. 79, pl. 7, fig. 10.
1885 *Str. bilamellatus* n. sp.; Clessin, p. 79, pl. pl. 7, fig. 9.
1902 *Strobilus costatus* Sandberger. – Andreae, p. 11, fig. 6.
1915 *Strobilops* (*Str.*) *costata* (Sdbg. emend. Clessin). – Wenz, p. 79, pl. 4, figs 15–16.
1923 *Strobilops* (*Strobilops*) *costata* (Clessin). – Wenz, p. 1041 (cum syn.).

Figure 6. *Strobilops costatus* (Clessin, 1877) (Strobilopsidae). • A, B – K 6903 from T3-3. • C, D – K 6904, from T1. Note that the umbilicus is covered with sediment. • E, F – K 6905, from T1. • G – basal folds, K 6906, from T3-3. • H, I, L – juvenile specimen, K 6907, from T3-3. • J – basal folds, K 6908, from T3-3. • K, N, O – juvenile specimen, K 6909, from T3-3. • M – basal folds, K 6910, from T3-3. Scale bars correspond to 500 μm (A–F), 200 μm (G, H, J, K, M, N) and 100 μm (I, L, O).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non 1966 *Strobilops* (*Strobilops*) *costata* Clessin. – Steklov, p. 171, pl. 5, figs 99–100.
1967 *Strobilops* (*Strobilops*) *costata* (Clessin). – Schütt, p. 213, fig. 15.
1999b *Strobilops costata* (Clessin, 1877). – Stworzewicz, p. 152, figs 34–37.
2002 *Strobilops costata* (Clessin, 1877). – Harzhauser & Kowalke, p. 76, pl. 10, fig. 3.
non 2006 *Strobilops costata* (Clessin), 1885. – Kókay, p. 72, pl. 26, figs 11–13.
non 2006 *Strobilops costata bilamellata* (Clessin), 1885. – Kókay, p. 72, pl. 26, figs 14–15.
2016a *Strobilops costata* (Clessin, 1877). – Salvador *et al.*, p. 141, fig. 3s.
2016c *bilamellatus* Clessin, 1885, *Strobilus*. – Salvador *et al.*, p. 20.
2016c *costatus* Clessin, 1877, *Strobilus*. – Salvador *et al.*, p. 22.
2016c *Strobilops costata* (Clessin, 1877). – Salvador *et al.*, pl. 2, fig. 1, pl. 3, fig. 3.

Material. – 5 shells from T1 (K 6904–6905, K 6933); 1 adult shell, 2 subadult shells and 3 fragments from T2 (K 6934); 1 fragment from T3-1 (K 6935); 1 adult shell, 2 juvenile shells and 22 fragments from T3-3 (K 6903, K 6906–6910, K 6937).

Dimensions. – 1.62 × 2.16 mm (Fig. 6A, B); 1.75 × 1.88 mm (Fig. 6C, D); 1.51 × 1.97 mm (Fig. 6E, F).

Description. – Broad, trochiform shell, with very weakly ovoid spire and up to 5.4 whorls. Protoconch bulbous, with inflated initial part, consists of 1.5 whorls that measure c. 670–680 μm (one with 750 μm) in diameter; surface weakly granulose, near transition to teleoconch spiral threads appear; transition marked by growth rim and onset of ribs. Granulose surface pattern, with occasional spiral thread, persists on teleoconch. In addition, entire teleoconch covered by strong, oblate, widely spaced, steeply prosocline ribs; strength and spacing of ribs increase slightly but constantly during ontogeny (on last whorl ribs are *c.* 25 μm wide, interspaces measure *c.* 100 μm); ribs persist on base but are weaker (occasionally almost entirely reduced, *e.g.*, in juveniles) and broadly sigmoidal. Teleoconch whorls moderately convex. Last whorl attains 55–65% of total shell height, passes over marked angulation into weakly convex to finally straight base. Aperture broadly semilunar, with broadly thickened peristome. Three parietal lamellae are present: parietal lamella strong, broad, weakly curved towards outer lip, reaches up to margin of inner lip; infraparietal lamella small, knob-like in front view, does not reach up to margin of inner lip; interparietal lamella very weak, internally situated, not visible from outside (Fig. 6K). Columellar lamella internal, short but thick. Internal basal folds highly variable in shape in number; up to four folds were counted, with first being short but thick, second being elongate and highest of all, third being weak, low, elongate but shorter than second, fourth being very long, elongate, narrow (Fig. 6G, J, M). Umbilicus narrow, not deep.

Remarks. – The present shells correspond almost perfectly to original *S. costatus* from Undorf, compared to the illustrations of Wenz (1915) and Salvador *et al.* (2016a, c) and a specimen stored in the collection of the Natural History Museum Vienna. They all agree in shape, ribbing and the strength and position of the parietal lamellae. The rather poor drawings in Clessin (1885) are misleading, showing an exceptionally broad shell with vertical ribbing (compare image of the supposed syntype in Salvador *et al.* 2016c). The only difference between the Undorf and our specimens is the arrangement of the basal folds. Wenz (1915) indicated three folds, which increase in length towards the outer margin and of which the second is the most prominent. In shells from Vračević, folds are much longer and more massive than indicated for typical *S. costatus* and often there is an additional, weak fold (Fig. 6G, J). The arrangement of the basal folds seems to be a variable feature though, specimens from Bełchatów identified as *S. costatus* by Stworzewicz (1999b) show a variable set of basal folds, ranging from one to four. The illustrated shell shows three distinct but short folds, of which the second is the weakest. In addition, there is a fourth, very faint fold on the periphery of the basal region. Since all other characteristics of the Serbian and Polish shells correspond to the original ones, a taxonomic separation is hardly useful; the variation of the basal folds rather ranges within intraspecific variability.

Strobilops costatus can be differentiated from coeval *S. joossii* (Gottschick, 1911) from the Steinheim Basin in the stouter shell and the less distinct infraparietal lamella of the latter species. *Strobilops boettgeri* (Andreae, 1902) from Nowa Wieś Królewska, which co-occurs there with *S. costatus*, has a non-ribbed shell and two strong, slightly outwards curved parietal lamellae, both of which extend as far as the margin of the parietal callus; in some specimens, they protrude stronger and form a convex parietal margin (pers. obs. on material from the type locality).

A very similar species is *S. sandbergeri* (Łomnicki, 1886) from the middle Miocene of Polskie Folwarki and Goncharivka (former Wyczólki), Ukraine. The original description and the drawings are quite reminiscent of *S. costatus*, leading Wenz (1915, 1923) to assume that both species might be conspecific. However, without knowing details about the lamellae and folds it is impossible to clarify its taxonomic status.

Finally, we agree with Wenz (1923) and Salvador *et al.* (2016c) to synonymize *S. bilamellatus* (Clessin, 1885) from Undorf with co-occurring *S. costatus*.

The specimen from the late Miocene of Caucasus region illustrated by Steklov (1966) has a more depressed spire, weaker ribs and a wider umbilicus and represents a different species. The Sarmatian *Strobilops ukrainica* Steklov, 1966 from Ukraine and Caucasus region, in turn, resembles *S. costatus* more closely in terms of general shape, whorl outline, ribbing, size of the umbilicus and the presence of three basal lamellae that increase in length towards the outer margin (matching the pattern observed on Undorf specimens by Wenz 1915). *Strobilops ukrainica* differs only from the present species in the slightly higher spire and the massive parietal lamella. These differences likely range within the general morphological variability, but inspection of Steklov's material is required to evaluate whether the species should be considered as a junior synonym of *S. costatus*.

Specimens from the Sarmatian of the Bakony Mts. identified as *S. costata* and *S. costata bilamellata* by Kókay (2006) very likely do not belong to the present species. The illustrated specimens have much narrower shells, stronger parietal lamellae and a reduced surface sculpture.

Strobilops costata govorkaensis Prysjazhnjuk in Gozhik & Prysjazhnjuk, 1978 from the Sarmatian (Volhynian) of Zamekhov has a more depressed shell and a markedly thickened parietal lamella; the basal folds resemble some of the present specimens (Fig. 6M).

Nomenclatural notes. – *Strobilops* is commonly treated as feminine in the literature, but after Art. 30.1.4.3 of the ICZN (1999) the gender of names ending in *-ops* is deemed to be masculine, irrespective of its etymology or treatment by its author. Obviously based on a letter, Clessin (1877) attributed the authority of the species to F. Sandberger ("Sdbgr. in litt."). It is, however, unclear whether the species description derived from Sandberger or Clessin. In such a case of doubt, the author is deemed to be the person who publishes the work, *i.e.*, Clessin (ICZN Art. 50.1.1).

Occurrence. – Undorf, Germany (MN 5; Clessin 1877); Upper Freshwater Molasse at Riedensheim in southern Germany and Handreute and Flühlen in western Austria (MN 5; Wenz 1935, Salvador *et al.* 2016a); Nowa Wieś Królewska near Opole, Poland (MN 6–7; Andreae 1902b); Bełchatów, Poland, layers Beł-C (MN 4) and Beł-B (early MN 5; Stworzewicz 1999b); Hollabrunn, Hautzendorf and St. Veit an der Triesting, Austria (Sarmatian; Troll-Obergfell 1944, Schütt 1967, Reischütz 2000). The record from the Sarmatian of Moldova by Prysyazhniuk (2015) needs to be confirmed.

Family Valloniidae Morse, 1864

Remarks. – The genera *Acanthinula* and *Spermodea* have been commonly classified within the Valloniidae: Acanthinulinae (*e.g.*, Zilch 1959, Falkner 1974, Nordsieck 2014). *Pupisoma* has been variably attributed to Acanthinulinae (Zilch 1959, Falkner 1974, Gittenberger & van Bruggen 2013), Vertigindae (Pilsbry 1920, Nordsieck 2014) or in a separate family (Iredale 1940; see also Hausdorf 2007). Recent molecular analyses suggested that both *Acanthinula* and *Pupisoma* represent own branches distinct from *Vallonia* and unrelated with Vertiginidae, respectively (Nekola & Coles 2016). Until a systematic revision of the Pupilloidea is available, we list the three genera *Acanthinula*, *Pupisoma* and *Spermodea* in the Valloniidae.

Subfamily Acanthinulinae Steenberg, 1917

Genus *Acanthinula* Beck, 1847

Type species. – *Helix aculeata* Müller, 1774; by subsequent designation by Martens in Albers (1860). Recent, Europe.

***Acanthinula trochulus* (Sandberger, 1872)**
Figure 7A–D

*1872 [*Pupa*] *trochulus* [Sandb.]; Sandberger, pl. 29, fig. 25–25b.
1875 *Pupa* (*Modicella*) *trochulus* Sandberger. – Sandberger, p. 601.
? 1911 *Theba* (*Acanthinula*) *tuchoricensis* Klika sp. – Gaál, p. 66, pl. 2, fig. 5 [non *Helix* (*Acanthinula*) *tuchoricensis* Klika, 1891].
1923 *Acanthinula trochulus* (Sandberger). – Wenz, p. 977 (cum syn.).
1976 *Acanthinula trochulus* (Sandberger). – Schlickum, p. 11, pl. 2, fig. 30.
? 1981 *Acanthinula trochulus* (Sandberger). – Lueger, p. 34, pl. 3, fig. 14.
1999b *Acanthinula trochulus* (Sandberger, 1874). – Stworzewicz, p. 149, figs 27–29.
? 2004 *Acanthinula trochulus* (Sandberger, 1874). – Harzhauser & Binder, p. 16, pl. 7, figs 1–3.
? 2004 *Acanthinula trochulus* (Sandberger). – Harzhauser & Tempfer, p. 64, fig. 7 (9).
? 2006 *Acanthinula trochulus* (Sandberger), 1874. – Kókay, p. 70, pl. 26, fig. 1.

Material. – 1 shell from T1 (K 6911); 1 apical fragment from T3-3 (K 6937).

Dimensions. – 2.45 × 1.85 mm (Fig. 7A–D).

Description. – Shell broadly conical, comprising four whorls. Protoconch bulbous, dome-shaped, consists of slightly more than one whorl; covered by numerous spiral furrows, which are about as broad as interspaces and do not reach to lower suture; whorl portion below lowermost furrow

40–50 µm high, surface granulose. Transition to teleoconch marked by clear stop of broad furrows but onset of faint, narrow, much more densely spaced grooves; prosocline growth lines start already before transition. In addition to spiral sculpture and growth lines, widely spaced, distinct, sharp prosocline ribs cover entire teleoconch; strength of ribs and width of interspaces (*c.* 100 µm) hardly vary between first and last whorl. Whorls highly convex to weakly stepped, with maximum convexity slightly above whorl mid-height. Sutures narrow. Last whorl attains *c.* 65% of total shell height. Base rather flat, straight. Aperture widely ovate, with slightly expanded, sharply edged peristome. Umbilicus wide and deep.

Remarks. – The early Miocene *Acanthinula tuchoricensis* (Klika, 1891) is stouter and has weaker ribs (Harzhauser *et al.* 2014b). Similarly, *A. hesslerana* Jooss, 1911 from the early Miocene of the Mosbach-Biebrich (Mainz Basin, Germany) differs from the present species in its broadly ovoid shape (*e.g.*, Salvador *et al.* 2016c). The specimens from late Miocene (Pannonian) strata of Austria identified and illustrated as *A. trochulus* by Lueger (1981), Harzhauser & Binder (2004) and Harzhauser & Tempfer (2004) are broader and expose a characteristic angulation around the center of the whorl flank. These specimens might represent a younger, yet undescribed species. Wenz (1923) synonymized the record of *A. tuchoricensis* by Gaál (1910, 1911) from the Sarmatian of Răcăștia [= Rákosd], Romania, with *A. trochulus*. Although this action seems reasonable with respect to the middle Miocene age, compared to the early Miocene age of Tuchořice, the type locality of *A. tuchoricensis*, the identity of the species is impossible to clarify from the poor description and illustration alone. Examination of Gaál's material is necessary to clarify its taxonomic attribution. Similarly, the incomplete specimen from the Sarmatian of Várpalota, Hungary, illustrated by Kókay (2006) appears stouter and weakly angulated.

Nomenclatural notes. – Sandberger's description of the species on p. 601 of his monograph was issued in 1875, while the illustration on plate 29 appeared already in 1872 (see Woodward 1906). After ICZN Art. 31.2.2 the species epithet is to be treated as a noun in apposition and does not need to agree in gender with the genus name.

Occurrence. – Mörsingen, Hohenmemmingen, Zwiefaltendorf and Undorf, S Germany (MN 5; Sandberger 1870–1875, Clessin 1885, Wenz 1923, Schlickum 1976); Nowa Wieś Królewska near Opole, Poland (MN 6–7; Andreae 1902, Stworzewicz 1999b); Bełchatów, Poland, layers Beł-C (MN 4) and Beł-B (early MN 5; Stworzewicz 1999b).

Genus *Pupisoma* Stoliczka, 1873

Type species. – *Pupa lignicola* Stoliczka, 1871; by original designation. Recent, Burma.

***Pupisoma* cf. *distans* Falkner, 1974**
Figure 7G, J, L

cf. *1974 *Pupisoma* (*Ptychopatula*) *distans* n. sp.; Falkner, p. 234, pl. 10, fig. 3, pl. 11, figs 7–8.

Material. – A single apical fragment from T3-3 (K 6914).

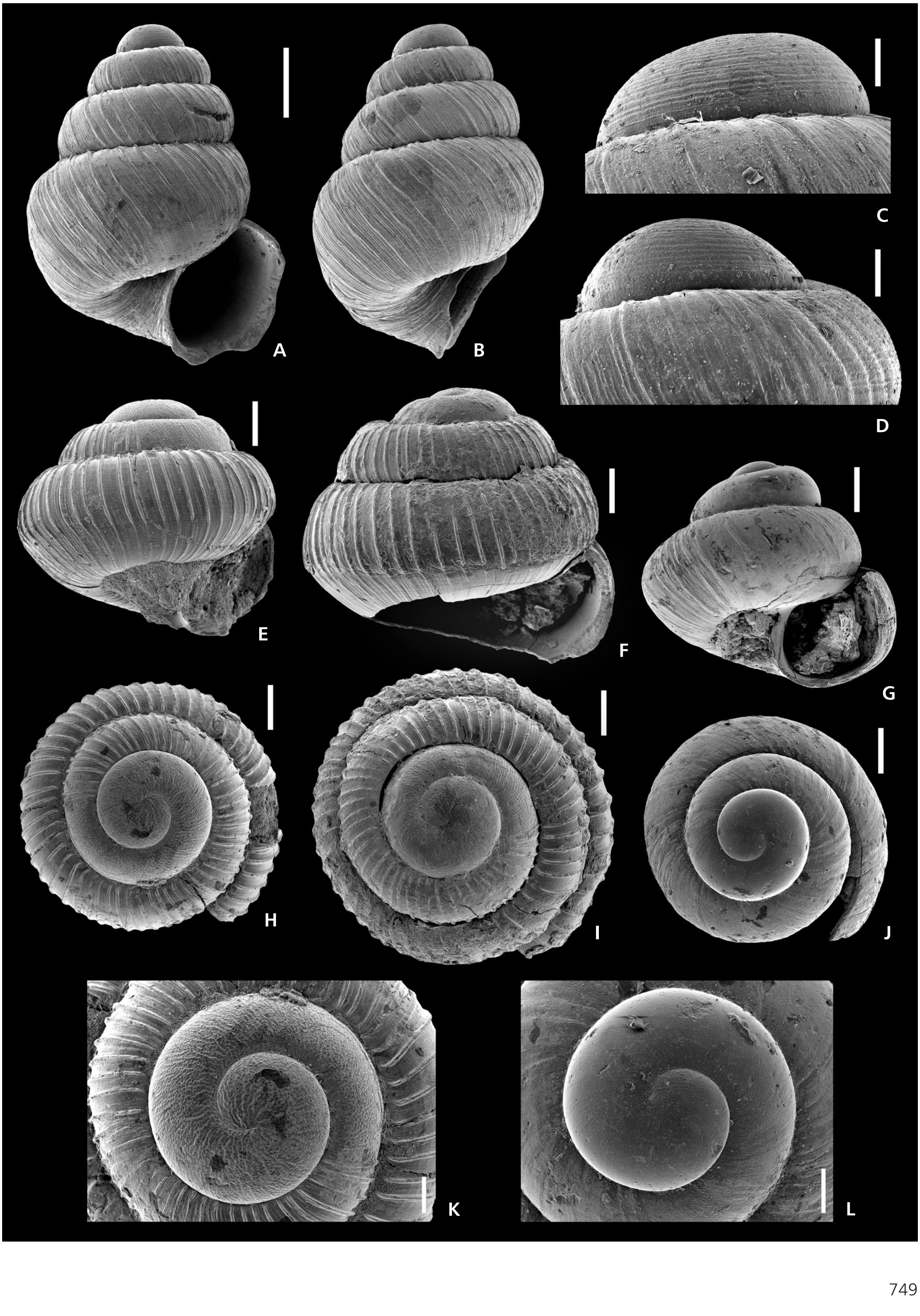
Dimensions. – 1.01 × 1.14 mm.

Description. – Broad, trochiform shell with *c.* 2.7 whorls preserved. Protoconch highly granulose, coarse near upper suture and progressively finer towards lower suture; microsculpture becomes rather pitted after about one whorl. Extent of protoconch unknown because transition to teleoconch is smooth and microsculpture persists; first protoconch whorl measures *c.* 530 µm. Teleoconch whorls highly convex, with highest convexity at transition to base. Umbilicus present but covered. Last whorl and aperture not preserved. Steep orthocline growth lines of variably strength cover shell.

Remarks. – Our specimen differs slightly from the single specimen Falkner (1974) had at hand from Zwiefaltendorf. The Serbian shell is slightly broader and the convexity at the transition between whorl flank and base is more pronounced. On the other hand, the two shells agree well in terms of dimensions and microsculpture. Probably, the variation in shape and convexity range within intraspecific variability, but more material is required to confirm this hypothesis.

Pupisoma distans is the only representative of the genus in Europe and the European fossil record in particular. Shape and sculpture agree perfectly with recent species from North America and Africa (Hausdorf 2007, Gittenberger & van Bruggen 2013). Falkner (1974) attributed the *P. distans* to the subgenus *Ptychopatula* Pilsbry, 1889. That taxon is, however, readily differentiated from *Pupisoma* sensu stricto in the presence of distinct spiral lines (Hausdorf 2007, Gittenberger & van Bruggen 2013).

Figure 7. Valloniidae. • A–D – *Acanthinula trochulus* (Sandberger, 1872). K 6911, from T1. • E, H, K – *Spermodea candida* Falkner, 1974. Apical fragment, I K 6912, from T3-3. • F, I – *Spermodea candida* Falkner, 1974. Apical fragment, K 6913, from T3-3. • G, J, L – *Pupisoma* cf. *distans* Falkner, 1974. Apical fragment, K 6914, from T3-3. Scale bars correspond to 500 µm (A, B), 200 µm (E–J) and 100 µm (C, D, K, L).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Occurrence. – So far only known from the type locality Zwiefaltendorf in southern Germany (MN 5; Falkner 1974).

Genus *Spermodea* Westerlund, 1902

Type species. – *Helix lamellata* Jeffreys, 1830; by subsequent designation by Pilsbry (1926). Recent, British Isles.

***Spermodea candida* Falkner, 1974**
Figure 7E, F, H, I, K

*1974 *Spermodea candida* n. sp.; Falkner, p. 231, pl. 10, figs 1–2, pl. 11, figs 5–6.
1999b *Spermodea* cf. *candida* Falkner, 1974. – Stworzewicz, p. 149, figs 30–31.
2006 *Spermodea candida* Falkner, 1974 var. – Kókay, p. 70, pl. 26, fig. 2.

Material. – 2 apical fragments from T3-3 (K 6912–6913).

Dimensions. – 1.22 × 1.39 mm (Fig. 7F, I); 1.06 × 1.16 mm (Fig. 7E, H, K).

Description. – Available fragments comprise protoconch and up to two teleoconch whorls, suggesting broad ovoid shell with moderately, slightly stepped whorls. Protoconch low domical, comprises *c.* 1.3 whorls that measure *c.* 660 μm in diameter; surface massively rugose, being coarsest near upper suture and finer near lower suture; transition to teleoconch marked by clear stop of rugose pattern and start of axial ribs. Ribs are pronounced but rather blunt, orthocline, weakly oblique crests that only weakly increase in strength and spacing throughout ontogeny; ribs are about equally strong across whorl flank but become weaker at transition to base. Between ribs, intricate interplay of faint, narrow spiral grooves, which are most distinct and cross ribs at base, and very thin, slightly raised, irregularly axially arranged and interweaved lines. Last whorl and aperture not preserved. Umbilicus covered with sediment in one specimen but apparently present.

Remarks. – The genus *Spermodea* is represented by only five species in the fossil record, which dates back to the late Oligocene. The late Oligocene to middle Miocene *S. plicatella* (Reuss in Reuss & Meyer, 1849), originally described from the early Miocene of Tuchořice, differs in having a broad depressed shell (see also Harzhauser *et al.* 2014b). The late Miocene *Spermodea augusti* Schlickum, 1978 from Öcs, as well as the early Pliocene *Spermodea demarcqui* Schlickum & Truc, 1972 from Celleneuve, France (MN 14; Esu 1999), are typically ton-shaped. *Spermodea puisseguri* Schlickum & Truc, 1972 from the late Pliocene to early Pleistocene (MN 16; Esu 1999) of Cessey-sur-Tille, France, resembles the present species regarding the stout ovoid spire but differs in the higher number of whorls and the weak ribs.

Occurrence. – Apart from the type locality Undorf in southern Germany (MN 5), the species has been reported from deposits of the Upper Freshwater Molasse at Zwiefaltendorf and Mörsingen (MN 5; Falkner 1974, Schlickum 1976), Bełchatów, layer Beł-B (early MN 5; Stworzewicz 1999b), and the Sarmatian of Várpalota, Bakony Mts. (Kókay 2006).

Family Vertiginidae Fitzinger, 1833
?Subfamily Vertigininae Fitzinger, 1833

Genus *Vertigo* Müller, 1773 sensu lato

Type species. – *Vertigo pusilla* Müller, 1774; by subsequent monotypy. Recent, Denmark.

?*Vertigo vracevicensis* Neubauer & Harzhauser sp. nov.
Figure 8A–C, E, F, I

Holotype. – K 6878; 1.81 × 1.27 mm (Fig. 8A, B, E, I). Additional measurement: 1.71 × 1.15 mm (Fig. 8C, F).

Derivation of name. – Named after the type locality.

Type locality. – Vračević, Lajkovac municipality, Kolubara district, Serbia; sampling location T1.

Type horizon. – Late middle Miocene, late Serravallian, Sarmatian.

Material. – 1 complete specimen from T1 (K 6878); 2 broken specimens from T3-3 (K 6879, K 6937; one broke after image processing; Fig. 8C, F).

Diagnosis. – Ovate-conical shell with open umbilicus; dentition consisting of a broad, weakly curved parietal lamella, a weak, broad, deeply situated lower palatal lamella and a small upper palatal lamella; shell surface weakly granulose to pitted.

Description. – Protoconch slightly bulbous, dome-shaped, surface weakly granulose; transition to teleoconch marked by onset of strongly inclined prosocline growth lines. Strength of growth lines varies locally, resulting in uneven surface sculpture. Whorls highly convex; last whorl attains 60% of total shell height, passes into straight base; in lateral view, constriction occurs such that width of penultimate whorl exceeds that of final half of last whorl (Fig. 8C). Umbilicus open, rather wide in most available specimens such as the holotype (Fig. 8A, B, E, I). Aperture rounded-triangular, slightly expanded; inner surface locally smooth, in other places (like at transition from columellar to parietal region and in front of palatal lamellae) irregularly knobbly. Dentition comprises three lamellae: parietal lamellae prominent, passing from narrow, elongate crest near peristome over curvature, which is directed towards columella, to broad knob that is centrally placed on parietal margin and densely covered by fine nodules; lower and upper palatal lamellae both deeply situated, narrow and elongate, with lower one being broader. Entire shell surface covered by small-sized granulose pattern; locally, pattern may vary and show densely arranged pits (*e.g.*, shell portion behind the aperture).

Remarks. – The generic and subfamily classification of this new species is unresolved at present. The characteristic shape and microsculpture distinguish the species clearly from other known fossil European Vertiginidae. The ovate-conical shape with rather wide umbilicus, the reduced dentition, and the weakly granulose to pitted microsculpture remind of the Neotropical nesopupine genus *Bothriopupa* Pilsbry, 1898. However, representatives of that genus always have a columellar lamella and microsculpture appears to be coarser (*e.g.*, Pilsbry 1916–1918, van der Schalie 1948). Compared to the little resemblance with *Vertigo* s.s., the high similarities with *Bothriopupa* might nevertheless argue for a placement in the Nesopupinae. That subfamily has already been reported for the European fossil record, as documented by Manganelli *et al.* (2008) and Nordsieck (2014). Manganelli *et al.* (2008) listed three species in total, two from the late Oligocene and the middle (not early late!) Miocene considered belonging in the genus *Nesopupa* Pilsbry, 1900, and one Pliocene species classified in *Staurodon* Lowe, 1852. The earlier classification of a *Vertigo* species from Bełchatów in *Nesopupa* by Stworzewicz (1999b) was not accepted (see also discussion in Harzhauser *et al.* 2014b). Nordsieck (2014) revised much of the earlier classifications, introduced three new genera for fossil European Nesopupinae and attributed several more species to that subfamily. None of those, however, matches the Vračević shells.

Family Gastrocoptidae Pilsbry, 1918

Genus *Gastrocopta* Wollaston, 1878

Type species. – *Pupa acarus* Benson, 1856; by subsequent designation by Pilsbry (1916). Recent, Azores.

***Gastrocopta nouletiana* (Dupuy, 1850)**
Figure 8D, J

*1850 *Pupa Nouletiana*; Dupuy, p. 309, pl. 15, fig. 6.
1875 *P.*[*upa*] *gracilidens* Sandb. – Sandberger, p. 600.
1923 *Gastrocopta* (*Sinalbinula*) *nouletiana nouletiana* (Dupuy). – Wenz, p. 930 (cum syn.).
1923 *Gastrocopta* (*Sinalbinula*) *nouletiana gracilidens* (Sandberger). – Wenz, p. 934 (cum syn.).
1966 *Gastrocopta* (*Sinalbinula*) *nouletiana* Dupuy. – Steklov, p. 140, fig. 48, pl. 2, figs 40–42.
1966 *Gastrocopta* (*Sinalbinula*) *gracilidens* Sandberger. – Steklov, p. 141, pl. 2, fig. 43.
1967 *Gastrocopta* (*Sinalbinula*) *nouletiana* (Dupuy). – Schütt, p. 208, fig. 12.
1976 *Gastrocopta* (*Sinalbinula*) *nouletiana* (Dupuy). – Schlickum, p. 10, pl. 2, fig. 27.
1978 *Gastrocopta* (*Sinalbinula*) *nouletiana* Dupuy. – Gozhik & Prysjazhnjuk, p. 94, pl. 12, figs 7–11.
1979 *Gastrocopta* (*Sinalbinula*) *hartmutnordsiecki* n. sp.; Schlickum, p. 409, pl. 23, fig. 7.
1981 *Gastrocopta* (*Sinalbinula*) *nouletiana* (Dupuy). – Lueger, p. 25, pl. 2, figs 16–19, 22 (cum syn.).
1994 *Gastrocopta* (*Sinalbinula*) *nouletiana* (Dupuy, 1850). – Schütt, p. 169, pl. 1, fig. 11.
1994 *Gastrocopta* (*Sinalbinula*) *nouletiana gracilidens* (Sandberger, 1874). – Schütt, p. 175, pl. 2, fig. 12.
1998 *Gastrocopta nouletiana*. – Finger, p. 19, pl. 8, figs a–c.
1999b *Gastrocopta nouletiana* (Dupuy, 1850). – Stworzewicz, p. 163, figs 59–61.
2004 *Gastrocopta* (*Sinalbinula*) *nouletiana* (Dupuy, 1850). – Harzhauser & Binder, p. 19, pl. 8, figs 9–11.
2006 *Gastrocopta* (*Sinalbinula*) *nouletiana nouletiana* (Dupuy, 1850). – Kókay, p. 66, pl. 24, figs 9–10, pl. 25, fig. 1.
2006 *Gastrocopta* (*Sinalbinula*) *nouletiana gracilidens* (Sandberger, 1874). – Kókay, p. 66, pl. 25, figs 3–4.
2006 *Gastrocopta* (*Sinalbinula*) *nouletiana tapeina* (Bourguignat, 1881). – Kókay, p. 66, pl. 25, fig. 2.
2006 *Gastrocopta nouletiana* (Dupuy, 1850). – Stworzewicz & Prisyazhnyuk, p. 167, fig. 2f.
2008 *Gastrocopta* (*Sinalbinula*) *nouletiana gracilidens* (Sandberger, 1874). – Prysjazhnjuk, p. 90, pl. 3, figs 18–19, pl. 4, figs 29–33.
2013 *Gastrocopta nouletiana* (Dupuy, 1850) sensu lato. – Stworzewicz *et al.*, p. 187, fig. 4b.
2015 *Gastrocopta nouletiana* (Dupuy, 1850). – Salvador, p. 43, figs 8–11.
2016a *Gastrocopta nouletiana* (Dupuy, 1850). – Salvador *et al.*, p. 140, fig. 3q–r.
2016a *Gastrocopta nouletiana* (Dupuy, 1850). – Salvador & Rasser, p. 47, fig. 2x.

Material. – 2 shells from T1 (K 6915, K 6933); 1 apertural fragment from T3-1 (K 6935); 1 apertural fragment from T3-3 (K 6937).

Dimensions. – 1.93 × 1.27 mm (Fig. 8D, J).

Description. – Ton-shaped shell with 4 whorls. Protoconch broad domical; surface and size unknown due to corrosion. Teleoconch whorls highly convex. Penultimate and last whorls have approximately same width; last whorl attains 57% of total shell height in illustrated specimen. Aperture broadly elliptical, with seven lamellae visible: prominent, deeply reaching angulo-parietal lamella with broad base and angular part entirely fused, forming small, elongate, not protruding cusp on the right side; infraparietal lamella small, round; columellar and basal lamella about equally strong and narrow; lower palatal lamella prominent, narrow; upper palatal slightly less prominent, but similarly narrow; suprapalatal lamella could not be seen. Inner aperture surface densely covered with coarse pustules. Umbilicus small.

Remarks. – *Gastrocopta gracilidens* (Sandberger, 1875) was introduced for individuals having a longer parietal lamella with unequally formed cusps and an additional palatal lamella (Sandberger 1875, O. Boettger 1884). As noted previously by several authors, both types, as well as transitional morphologies, co-occur in many localities, suggesting that both are just extremes of a single polymorphic species (*e.g.*, Lueger 1981, Stworzewicz 1999b). Similarly, Wenz (1923) synonymized *G. tapeina* (Bourguignat, 1881) from Sansan, which has a slightly reduced dentition but otherwise corresponds in shape and characteristics of the parietal lamella, with the present species. This approach is followed herein.

Gastrocopta suevica (Miller, 1900) from Steinheim is much more slender and the bifurcation of the parietoangular lamella is more laterally oriented than in *G. nouletiana* (Miller 1900, Finger 1998). Note that the authority of *G. suevica* is usually attributed to Sandberger (1875: p. 654), who first mentioned the name but never described or illustrated the species or provided any criteria to separate it from others. After inspection of all mentions of the species in the literature listed by Wenz (1923), the first who validly introduced it was Miller [1900; as *Pupa* (*Leucochilus*) *suevica*].

Schlickum (1979) introduced the new species *G. hartmutnordsiecki* for specimens from the late Miocene of Öcs, Hungary, that were earlier identified as *G. nouletiana*. His comparison with that species, however, seems to be based on a wrong concept of *G. nouletiana*. He indicated his new species, measuring 2.4 × 1.3 mm, to be about the double size of *G. nouletiana*, for which Dupuy (1850) gave a height of up to 2.5 mm and a width of up to 1.25 mm. Moreover, Schlickum (1979) claimed his species to differ from *G. nouletiana* in its strongly deviating, slender barrel-shaped morphology, although the illustration provided by Dupuy (1850) shows exactly such a specimen. Thus, we agree with Lueger (1981) and synonymize *G. hartmutnordsiecki* with *G. nouletiana*.

Occurrence. – Widespread species in the late early to late Miocene of Europe (for the numerous localities see Wenz 1923 and records given in the synonymy list, as well as Table 1). Additional records not accompanied by descriptions or illustrations (*e.g.*, shells from Sarmatian deposits of Ukraine and Moldova mentioned by Prysiazhniuk 2014 and Prysyazhniuk 2015) need re-examination.

Unassigned "subclade"
Superfamily Clausilioidea Gray, 1855
Family Clausiliidae Gray, 1855
Subfamily Phaedusinae Wagner, 1922 s.l.

Genus *Serrulina* Mousson, 1873

Type species. – *Clausilia sieversi* L. Pfeiffer, 1871; by subsequent designation by Lindholm (1924). Recent, Iran.

Remarks. – The attribution of the genus to Phaedusinae follows a personal comment by H. Nordsieck (06/2016).

?*Serrulina* sp.
Figure 8G, H

Material. – 1 apical fragment from T2 (K 6934); 6 apical fragments from T3-3 (K 6916, K 6937).

Description. – Among the few apical fragments the largest specimen comprises four initial whorls showing a smooth, not inflated protoconch passing without clear transition into densely but faintly ribbed teleoconch whorls that increase steadily but slowly in height and diameter. The riblets are strongest adapically, occasionally forming a serrated margin at the upper suture, and fade out towards the base.

The last portion of the fourth whorl preserved indicates a coeloconoid outline for the early shell.

Remarks. – The limited material and poor preservation precludes a precise determination, but the weakly ribbed early shell indicates a classification in *Serrulina*.

Unassigned "subclade"
Superfamily Punctoidea Morse, 1864
Family Discidae Thiele, 1931

Genus *Discus* Fitzinger, 1833

Type species. – *Helix ruderata* Hartmann, 1821; by subsequent designation by Gray (1847). Recent, Europe.

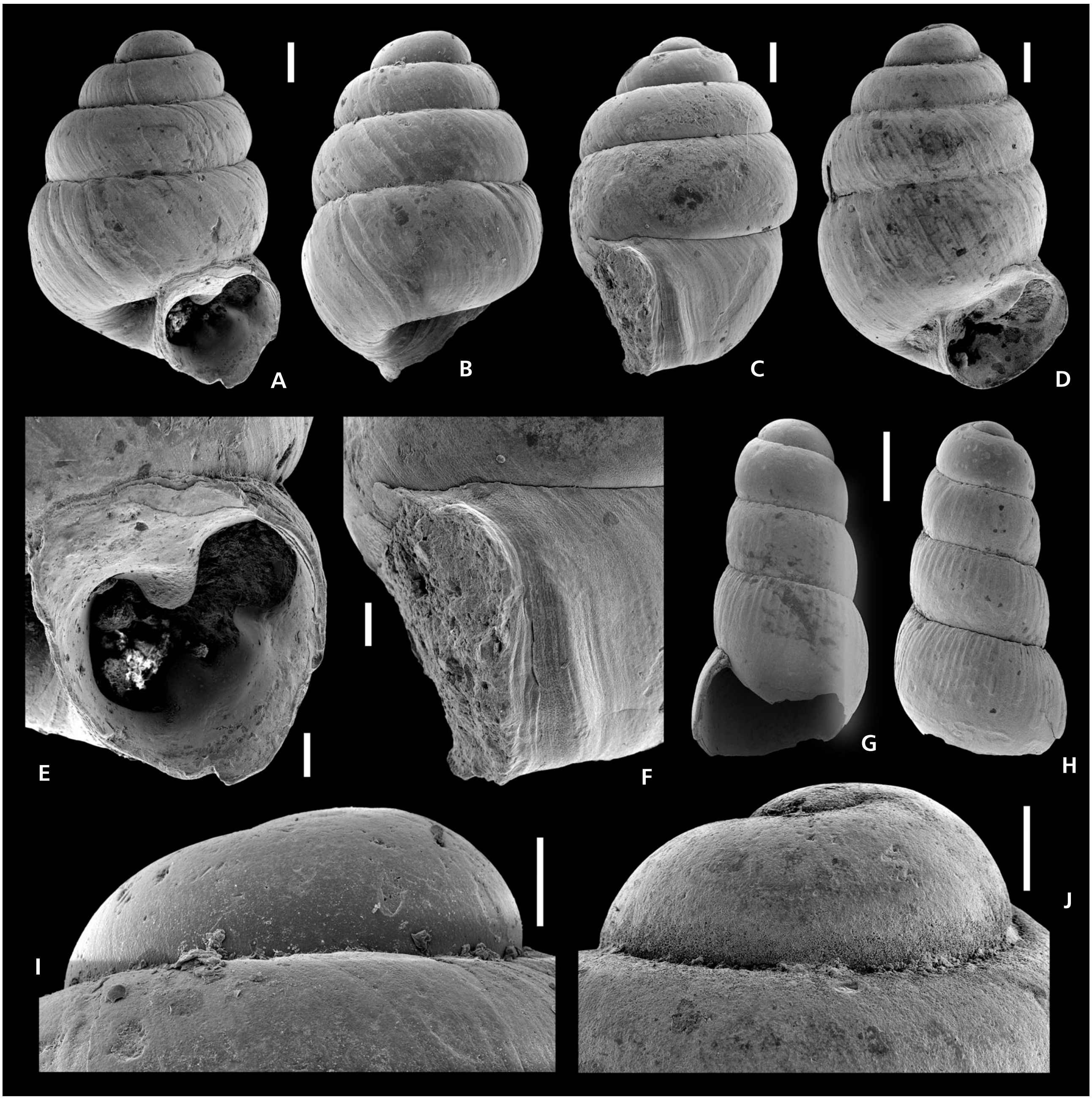

Figure 8. Vertiginidae, Gastrocoptidae and Clausiliidae. • A, B, E, I – ?*Vertigo vracevicensis* Neubauer & Harzhauser sp. nov. Holotype, K 6878 , from T1. • C, F – ?*Vertigo vracevicensis* Neubauer & Harzhauser sp. nov. K 6879, from T3-3 (specimen broken after imaging). • D, J – *Gastrocopta nouletiana* (Dupuy, 1850). K 6915, from T1. • G, H – ?*Serrulina* sp. Apical fragment, K 6916, from T3-3. Scale bars correspond to 500 µm (G, H), 200 µm (A–D) and 100 µm (E, F, I, J).

***Discus solarioides* (Sandberger, 1872)**
Figure 9A, B, D, E, G

*1872 *Patula solarioides* A. Braun; Sandberger, pl. 28, fig. 7–7c.

1875 *P. solarioides* A. Braun MS. – Sandberger, p. 583, 648 (in synonymy of *P. euglyphoides*).

1900 *Patula euglyphoides* Sandb. – Miller, p. 395, pl. 7, fig. 7 (non *Patula euglyphoides* Sandberger, 1872).

1911 *Patula* (*Charopa*) *costata* Gottschick; Gottschick, p. 501, pl. 7, fig. 15–15c.

1923 *Gonyodiscus* (*Gonyodiscus*) *costatus* (Gottschick). – Wenz, p. 326 (cum syn.).

1998 *Discus costatus* (Gottschick, 1911). – Finger, pl. 10, fig. d–f.
2008 *Discus euglyphoides* (Sandberger, 1874). – Harzhauser *et al.*, p. 52, fig. 6.4 (non *Patula euglyphoides* Sandberger, 1872).
2013 *Discus costatus* (Gottschick, 1911). – Stworzewicz *et al.*, p. 193, figs 5d–f.

Material. – 4 apical fragments from T3-3 (K 6917–6918, K 6937).

Dimensions. – 0.89 × 1.74 mm (juvenile, most complete shell; Fig. 9A, B, D, G).

Description. – Shell broad, low-trochiform; number of whorls unknown since no complete adult shell is available. Protoconch only weakly raised, measures 800 µm and comprises 1.25 whorls; near sutures, protoconch surface is covered by numerous delicate spiral grooves that become weaker and sometimes fade out towards whorl center; in addition, weak, very short axial riblets occur at upper suture; nucleus small, shows no difference from rest of protoconch; transition to teleoconch marked by onset of distinct axial ribs that cover whorls entirely. Ribs are broad (*c.* 14–17 µm), obtuse, opisthocyrt in whorl center to weakly sigmoidal towards thin sutures; interspaces between ribs are about three times the width of a rib; ribs are slightly weaker on umbilical side. Maximum whorl convexity shifted towards upper suture, producing blunt adapical angulation. Umbilicus wide and deep. Aperture unknown but available specimens indicate kidney-shaped opening with relatively thick inner lip.

Remarks. – No complete adult specimen is available to us, but the adapically angulated whorls and the teleoconch being ribbed all around is indicative of the species. The shape of the early shell is reminiscent of the middle Miocene *Discus pleuradrus* (Bourguignat, 1881), described from Sansan, France, and mentioned and illustrated from Hollabrunn by Schütt (1967), the Upper Freshwater Molasse by Schlickum (1976) and the Rein Basin by Harzhauser *et al.* (2014a). However, we do not agree with Lueger (1981) to synonymize both species. *Discus pleuradrus* differs from *D. solarioides* in the regularly rounded whorls and the lack of ribs on the umbilical side, which are present in both juvenile and adult specimens of *D. solarioides* (*e.g.*, Gottschick 1911, Finger 1998; as *D. costatus*).

Discus euglyphoides (Sandberger, 1872) from the late early to middle Miocene of the Upper Freshwater Molasse in southern Germany has a more depressed spire and develops a distinct keel (Gottschick 1911, Schlickum 1976). The specimens from Sarmatian deposits of the Styrian Basin determined as *D. euglyphoides* by Harzhauser *et al.* (2008) lack that keel but correspond fully to the present shells and are considered conspecific therefore.

The early Miocene *Discus rasseri* Harzhauser, Neubauer & Georgopoulou in Harzhauser *et al.*, 2014b and *Discus zagorseki* Harzhauser, Neubauer & Georgopoulou in Harzhauser *et al.*, 2014b from Tuchořice, Czech Republic, differ in the presence of a marked angulation near the upper suture, along with adapically enhanced and more sigmoidal ribs; additionally, *D. rasseri* has a higher spire. The similarly low-trochiform *Discus euglyphus* (Reuss in Reuss & Meyer, 1849), also from Tuchořice, has a more centrally placed angulation and stronger inclined ribs.

Nomenclatural notes. – The name *Patula solarioides* was introduced for a specimen from Steinheim on plate 29 of Sandberger's monograph, which was issued in 1872. The corresponding text passages was published in 1875, when Sandberger revised his earlier opinion and considered *P. solarioides* as a juvenile form and junior synonym of *P. euglyphoides* Sandberger, 1872. Gottschick (1911) reinstated the separation between both taxa, referred to the text passages in Sandberger (1875) and even stated that Sandberger had originally introduced *solarioides* for the Steinheim species but had the name retracted later. Nonetheless, Gottschick (1911) introduced another name, *Patula* (*Charopa*) *costata*, for the Steinheim material. Regardless of Sandberger's opinion in 1875, the name *solarioides* is available from its original publication, which makes *costata* a junior objective synonym of *solarioides*. This issue has been overlooked by later workers; the name *solarioides* does not appear in Wenz' Fossilium Catalogus (1923).

Occurrence (mostly for "D. costatus"). – Steinheim a. A., Germany (MN 7; Sandberger 1870–1875, Gottschick 1911); Zwierzyniec, Poland (Sarmatian; Stworzewicz *et al.* 2013). The record from the Pannonian of Leobersdorf, Austria, mentioned by Wenz (1923) needs verification.

Family Helicodiscidae F.C. Baker, 1927

Genus *Lucilla* Lowe, 1852

Type species. – *Helix scintilla* Lowe, 1852; by monotypy. Recent, Madeira.

***Lucilla subteres* (Clessin, 1877)**
Figure 9C, F, H, I

*1887 *Hel.* (*Patula*) *subteres*, n. sp.; Clessin, p. 35.
1885 *Patula subteres* Sdbgr. – Clessin, p. 76, pl. 6, fig. 6 (captions reads erroneously as "*Helix teres* Sandbgr.").

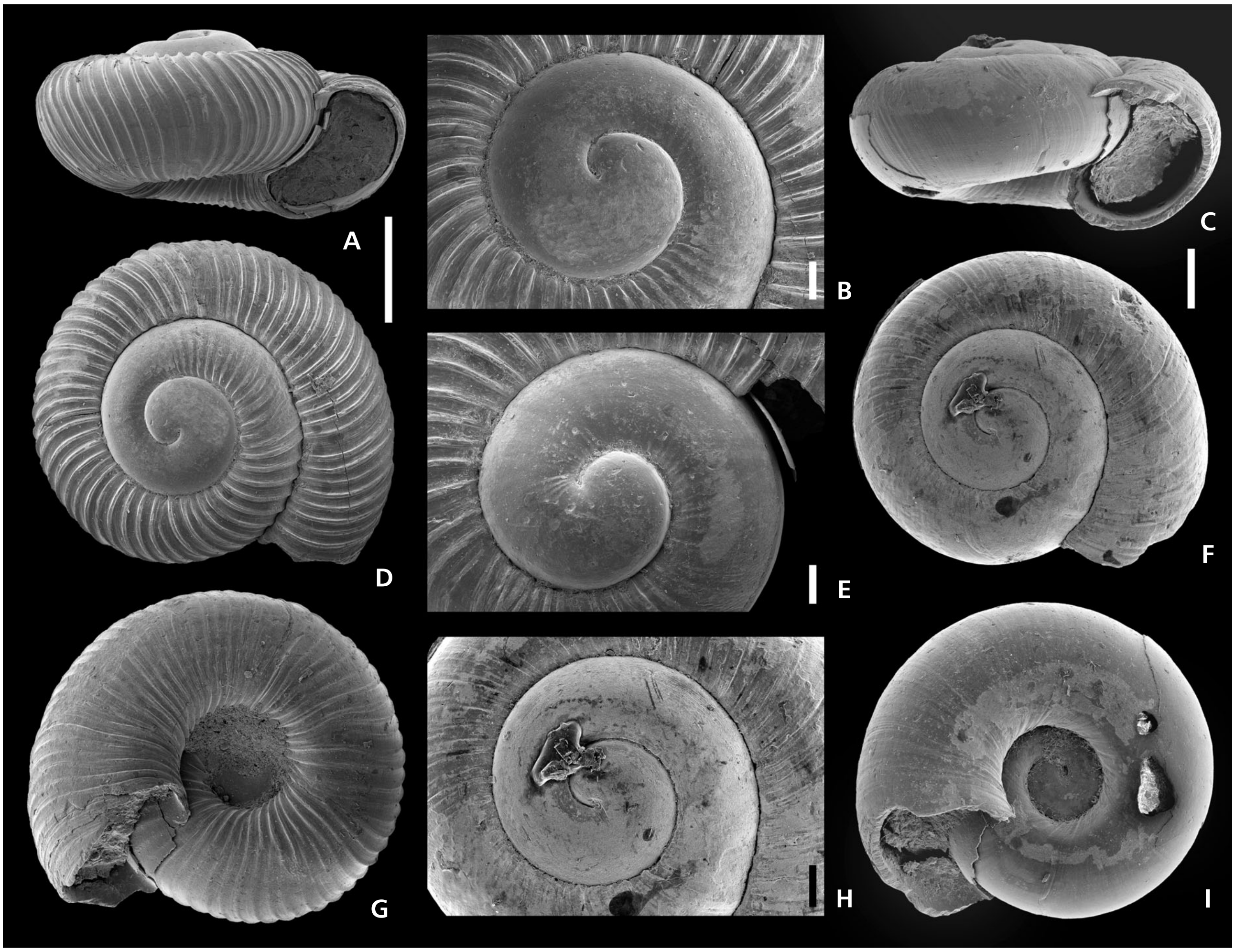

Figure 9. Discidae and Helicodiscidae. • A, B, D, G – *Discus solarioides* (Sandberger, 1872). Juvenile specimen, K 6917, from T3-3. • E – *Discus solarioides* (Sandberger, 1872). Protoconch of apical fragment, K 6918, from T3-3. • C, F, H, I – *Lucilla subteres* (Clessin, 1877). Juvenile specimen, K 6919, from T3-3. Scale bars correspond to 500 µm (A, D, G), 200 µm (C, F, I) and 100 µm (B, E, H).

1923 *Pyramidula subteres* (Clessin). – Wenz, p. 1062 (cum syn.).
1976 *Helicodiscus* (*Hebetodiscus*) *subteres* (Clessin). – Schlickum, p. 11, pl. 2, fig. 35.
1979 *Helicodiscus* (*Hebetodiscus*) *subteres* (Clessin). – Schlickum, p. 68, fig. 2.
2006 *Helicodiscus* (*Hebetodiscus*) *subteres* (Clessin), 1885. – Kókay, p. 74, pl. 27, figs 14–16.
2014 *Lucilla subteres* (Clessin, 1877). – Salvador, p. 280, fig. 24 (cum syn.).
2014 *Lucilla subteres* (Clessin 1877). – Salvador & Rasser, p. 195, figs 34–35.
2016c *subteres* Clessin, 1877, *Helix* (*Patula*). – Salvador *et al.*, p. 37.
2016c *Lucilla subteres* (Clessin, 1877). – Salvador *et al.*, pl. 9, fig. 1.

Material. – 2 apical fragments from T3-3 (K 6919, K 6937).

Dimensions. – 0.66 × 1.24 mm (Fig. 9C, F, H, I).

Description. – Broad, depressed shell, with c. 2.3 whorls preserved. Protoconch convex, almost fully immersed, consist of *c.* 1.3 whorls, which measure 700 µm in diameter; transition to teleoconch clearly marked by onset of growth lines; surface largely eroded, in some areas remains of thin, irregularly spaced, raised, slightly wavy, spiral threads are visible. Preserved teleoconch whorls regularly convex, semicircular in profile. Aperture broad kidney-shaped, with sheet-like inner lip covering base of penultimate whorl. Last whorl and peristome not preserved. Umbilicus wide, shallow. Entire teleoconch covered by spiral grooves. Growth lines weakly sigmoidal (adapically weakly prosocyrt, abapically broadly and weakly opisthocyrt).

Remarks. – The present shell matches perfectly the descriptions and illustrations of specimens from the Upper Freshwater Molasse at Gündlkofen and Sandelzhausen by Gall

(1980), Salvador (2014) and Salvador & Rasser (2014) in terms of size, shape and microsculpture. These specimens differ slightly from the type material from Undorf illustrated by Salvador *et al.* (2016c), showing a comparably high-spired specimen, while those from Gündlkofen and Sandelzhausen (as well as the present ones) are broader and flatter. Much of the morphological differences among available specimens result, however, from individual age differences. While the early shell is relatively depressed, adult individuals tend to have a higher spire. Nevertheless, a certain degree of variability in spire height is evident (compare also Schlickum 1976, 1979 and Kókay 2006).

We follow the systematic placement as proposed by Salvador (2014) and Salvador & Rasser (2014). The low-trochiform shell with wide umbilicus, round aperture and spiral microsculpture corresponds well to those of recent species of *Lucilla* (see, *e.g.*, Horsák *et al.* 2009, Welter-Schultes 2012).

Lucilla miocaenica Harzhauser *et al.*, 2015 from the Messinian of the Moncucco Torinese site in Italy has a similarly flattened but broader shell at about the same size. [Note that (Harzhauser *et al.* 2015) erroneously stated that threads are absent in *Lucilla*.]

Nomenclatural notes. – Clessin (1877) attributed the authority of the species to F. Sandberger ("Sandbg. in litt."), but there is no evidence that the description really derived from that author. As for the case of *Strobilops costatus* discussed above, the authority is, thus, deemed to be Clessin (ICZN Art. 50.1.1).

Occurrence. – Apart from the type locality Undorf (MN 5), the species is known from deposits of the Upper Freshwater Molasse at Bieswang, Dischingen (Michaelsberg), Gündlkofen, Landshut (Schlossberg), Mörsingen, Oberbirnbach, Sandelzhausen and Zwiefaltendorf in southern Germany (MN 5–6; Wenz 1923, Schlickum 1979, Salvador 2014, Salvador & Rasser 2014). Based on identifications by G. Falkner of material stored in the Bavarian State Collection for Palaeontology and Geology, Munich, Schlickum (1979) also listed the species from Nowa Wieś Królewska near Opole in Poland (MN 6–7; Nordsieck 1982) and Enzenbach in the Rein Basin (early middle Miocene) and Leobersdorf (Pannonian) in Austria. These three records require re-examination of the material since the species has not been mentioned from those localities by Andreae (1902a, b; 1904), Lueger (1981) and Harzhauser *et al.* (2014a).

Unassigned "subclade" Limacoidea Lamarck, 1801

Remarks. – The identification of slugs based on the internal shell alone is difficult if not impossible at all, even on the generic and family level (Wiktor & Likharev 1979, Reuse 1983). In addition, there is considerable morphological variability among shells of the same species (*e.g.*, Welter-Schultes 2012). Therefore, we refrain from an attribution to described slug species, many of which can be hardly separated and might be junior synonyms. The attribution of the vestigal shells to Limacidae and Milacidae, respectively, is based on their asymmetric vs. symmetric shape (South 1992).

Family Limacidae Batsch, 1789

***Limacidae* gen. et sp. indet.**
Figure 10F, G

Material. – 2 vestigial shells from T3-3 (K 6922, K 6937).

Dimensions. 1.71 × 1.25 mm (Fig. 10F, G).

Description. – Shell inequilateral, broadly elliptical. Nucleus small, accompanied by small indentation on left-hand side and steep, straight margin on right-hand side (in dorsal view). Dorsal surface marked by distinct concentric growth lines. Ventral side concave, with raised margins; surface consist of small calcite crystals.

Remarks. – Among the limacid species described for middle Miocene European deposits, "*Limax*" *excavatus* Andreae, 1904 from Nowa Wieś Królewska resembles our specimens most closely. The shell illustrated by Andreae (1904) exhibits a similar asymmetric, broadly elliptical shape with a weak indentation next to the nucleus. Species from the Undorf and the Upper Freshwater Molasse, *i.e.*, *Milax gracilior* (Sandberger, 1875), *M. crassus* (Clessin, 1894) and *M. diezi* (Clessin, 1894), have more subrectangular shapes (genus classifications after Wenz 1923). Similarly, *Limacus crassitesta* (Reuss, 1868), originally described from the early Miocene of Tuchořice and reported from the middle Miocene of Nowa Wieś Królewska by Andreae (1902), differs in the subrectangular shell (Harzhauser *et al.* 2014b).

Family Milacidae Ellis, 1926

***Milacidae* gen. et sp. indet.**
Figure 10A–E

Material. – 6 vestigial shells from T1 (K 6933); 4 partly fragmented vestigial shells from T2 (K 6934); 6 partly fragmented vestigial shells from T3-3 (K 6920–6921, K 6937).

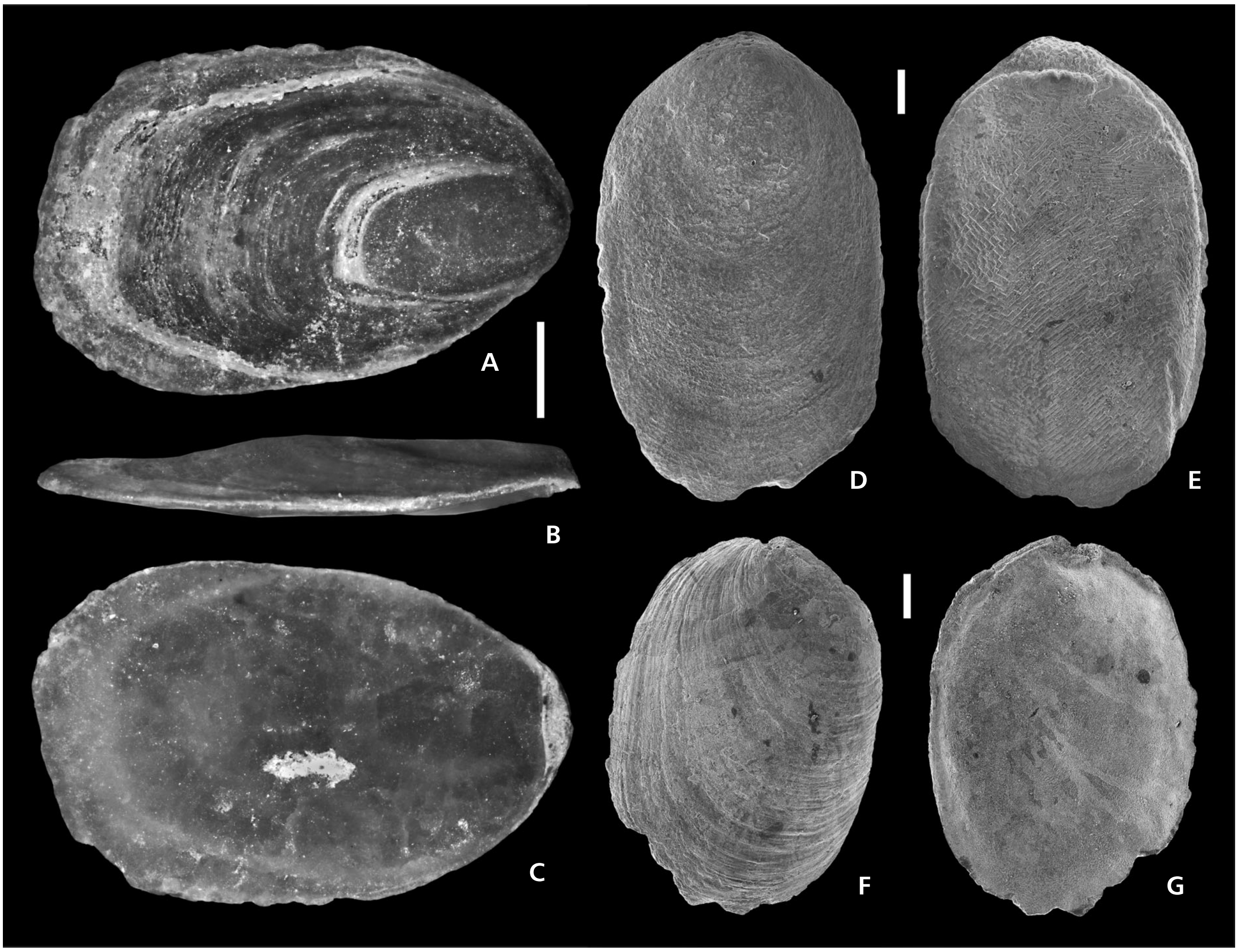

Figure 10. Limacidae and Milacidae. • A–C – Milacidae gen. et sp. indet. K 6920 from T3-3. • D, E – Milacidae gen. et sp. indet. Juvenile specimen, K 6921, from T3-3. • F, G – Limacidae gen. et sp. indet. K 6922, from T3-3. Scale bars correspond to 1 mm (A–C) and 200 µm (D–G).

Dimensions. – 5.80 × 3.86 × 0.87 mm (largest shell; Fig. 10A–C); 2.13 × 1.31 mm (Fig. 10D–E).

Description. – Shell slender elliptical to subrectangular; symmetric in early ontogeny (Fig. 10D–E), becomes slightly asymmetric in later growth stages (Fig. 10A–C). Dorsal surface marked by distinct concentric growth lines. Ventral side smooth, slightly depressed, made up from large individual calcitic crystals. Nucleus broad, narrow, with coarsely rugose surface; bulge occurs below, being prominent in early ontogeny. Low profile in lateral view, weakly and irregularly increasing from anterior margin to nucleus.

Remarks. – The species might be conspecific with *Milax sandbergeri* (Clessin, 1885) from Undorf, which agrees with the present shells in the slender elongate, low-profile shape and the angled nuclear region. The Undorf species is, however, more oval rather than elliptical to subrectangular, but this difference might range within intraspecific variability. *Amalia lorentheyi* Gaál, 1910 from the Sarmatian of Răcăștia [= Rákosd], Romania, which was classified as *Milax* by Wenz (1923), differs in the well-rounded, broader shell with a more elevated nucleus. Coeval ?*Limax crassissimus* Jooss, 1902 from Steinheim can be distinguished by the two wing-like protuberances on each side of the nucleus. The middle Miocene *M. oppoliensis* (Andreae, 1904) from Nowa Wieś Królewska and *Sansania lartetii* (Dupuy, 1850) from Sansan differ in their elevated nuclei.

Superfamily Gastrodontoidea Tryon, 1866
Family Gastrodontidae Tryon, 1866

Genus *Zonitoides* Lehmann, 1862

Type species. – *Helix nitida* Müller, 1774; by monotypy. Recent, Europe.

***Zonitoides* cf. *suevicus* (Jooss, 1918)**
Figure 11A, D, G, J

cf. *1918 *Polita suevica* n. sp.; Jooss, p. 289.
cf. 1923 *Zonitoides* (*Zonitoides*) *suevicus* (Jooss). – Wenz, p. 298.
cf. 1976 *Zonitoides* (*Zonitoides*) *suevicus* (Jooss). – Schlickum, p. 18, pl. 5, fig. 67.
2006 *Zonitoides suevicus* (Jooss), 1918 var. – Kókay, p. 78, pl. 30, figs 7–11.
cf. 1916c *suevica* Jooss, 1918b, *Hyalinia* (*Polita*). – Salvador *et al.*, p. 37.
cf. 1916c *Zonitoides suevicus* (Jooss, 1918). – Salvador *et al.*, pl. 9, fig. 7a–c.

Material. – A single juvenile shell from T3-3 (K 6923).

Dimensions. – 1.00 × 1.70 mm.

Description. – Low-trochiform shell with 2.3 whorls preserved. Protoconch consists of 1.3 whorls that measure *c.* 875 μm in maximum diameter; nucleus covered by irregular spiral grooves that become regular on early protoconch and are soon after accompanied by radial furrows, producing a net-like surface. Protoconch terminated by growth rim. Spiral grooves are maintained on teleoconch, in addition to weakly sigmoidal (centrally opisthocyrt) growth lines. Preserved teleoconch whorl regularly semicircular in profile, passing into straight base; available whorls suggest a weakly ovoid spire. Sutures narrow, not incised. Aperture round with almost perfectly circular, sharp outer lip. Umbilicus rather wide; covered with sediment.

Remarks. – The tentative attribution of the single fragment to *Zonitoides suevicus* rests upon similarities regarding the weakly ovoid spire, starting from an almost immersed protoconch, the size of the first whorl, the wide and regularly rounded aperture and the rather wide umbilicus (based on comparison with the illustration of the holotype (?) by Salvador *et al.* 2016c). The generic classification of the species is based on the shape of the entire shell (as documented by Salvador *et al.* 2016c), the shape and size of the aperture, the presence of a small and deep umbilicus and the spiral striation, all of which agree well with extant species of *Zonitoides* (*e.g.*, Burch & Jung 1988, Welter-Schultes 2012).

The middle Miocene oxychilid species *Aegopinella subnitens* (Klein, 1853) and *A. procellaria* (Jooss, 1918) both resemble the present species in terms of the broad shape and the rounded aperture but differ in their distinctly larger protoconchs.

The likewise middle Miocene *Nesovitrea boettgeriana* (Clessin, 1877) from Undorf and *N. subhammonis* (Gottschick, 1928) (Oxychilidae) from Altheim near Ehingen differ in the low, obtuse spire and the inclined aperture. Judging from the illustrations of type material in Salvador *et al.* (2016c) the two species might be conspecific. There, the species were classified in the genus *Perpolita* H.B. Baker, 1928, which is today mostly regarded as a junior synonym of *Nesovitrea* Cooke, 1921 (*e.g.*, Welter-Schultes 2012). After Harzhauser *et al.* (2008), *N. boettgeriana* also differs in the microsculpture: the protoconch is smooth except for delicate spiral threads close to the suture and the teleoconch only bears growth lines. The Pannonian species *Nesovitrea disciformis* (Lueger, 1981) from the Vienna Basin also has a lower spire and a much larger protoconch (*cf.* Harzhauser & Binder 2004). *Zonitoides schaireri* Schlickum, 1978 from the Pannonian of Öcs, Hungary, has a higher spire and a vertically slightly depressed aperture.

Occurrence. – Originally described from the Upper Freshwater Molasse at Dischingen, southern Germany (MN 5). Our specimens match perfectly the shells from the late Badenian of Herend and the Sarmatian of Várpalota, Hungary, illustrated by Kókay (2006).

Family Pristilomatidae Cockerell, 1891

Genus *Vitrea* Fitzinger, 1833

Type species. – *Glischrus diaphana* Studer, 1820; by monotypy. Recent, Europe.

***Vitrea procrystallina* (Andreae, 1902)**
Figure 11C, F, L

*1902b *Hyalinia* (*Vitrea*) *procrystallina* n. sp.; Andreae, p. 10, fig. 4.
? 1911 *Hyalinia* (*Vitrea*) *procrystallina* Andreae. – Gaál, p. 54, pl. 2, fig. 11 (erroneously indicated as "fig. 13"on p. 54).
1923 *Vitrea procrystallina procrystallina* (Andreae). – Wenz, p. 293.
? 1976 *Vitrea procrystallina* (Andreae). – Schlickum, p. 12, pl. 2, fig. 38.
? 1978 *Vitrea procrystallina* Andreae. – Gozhik & Prysjazhnjuk, p. 114, pl. 19, figs 1–3.
1981 *Vitrea* (*Vitrea*) *procrystallina steinheimensis* Gottschick. – Lueger, p. 42, pl. 5, figs 4a–b, 7a–c [non *Vitrea* (*Vitrea*) *procrystallina steinheimensis* Gottschick, 1920].
2004 *Vitrea procrystallina steinheimensis* Gottschick 1920. – Harzhauser & Binder, p. 25, pl. 11,

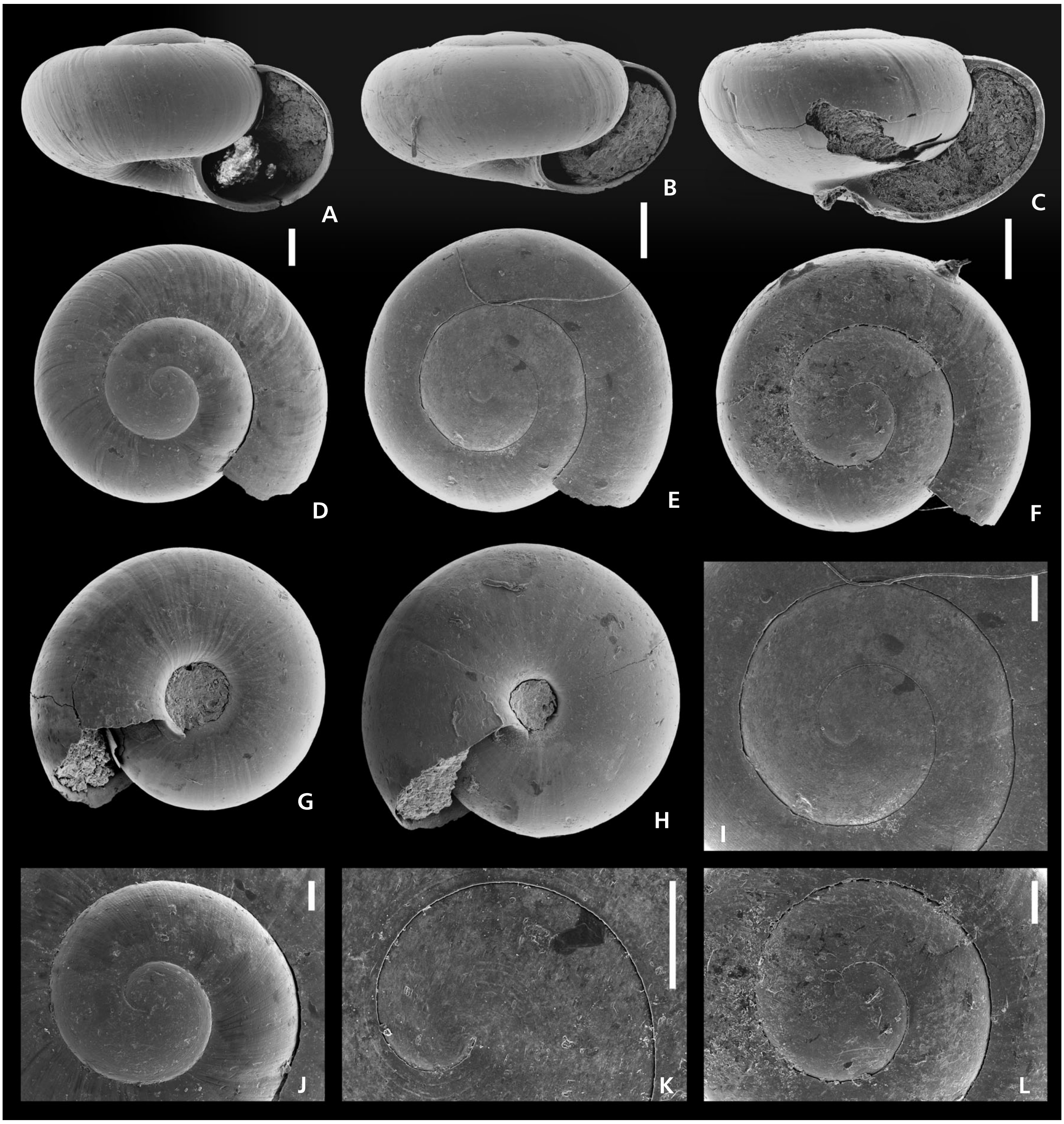

Figure 11. Gastrodontidae and Pristilomatidae. • A, D, G, J – *Zonitoides* cf. *suevicus* (Jooss, 1918). Juvenile specimen, K 6923, from T3-3. • B, E, H, I, K – *Vitrea steinheimensis* Gottschick, 1920. Juvenile specimen, K 6924, from T3-3. • C, F, L – *Vitrea procrystallina* (Andreae, 1902). Apical fragment, K 6925, from T3-3. Scale bars correspond to 200 µm (A–H) and 100 µm (I–L).

figs 11–13 [non *Vitrea* (*Vitrea*) *procrystallina steinheimensis* Gottschick, 1920].

non 2006 *Vitrea procrystallina* (Andreae), 1902. – Kókay, p. 75, pl. 28, figs 8–9.

2013 *Vitrea procrystallina* Andreae, 1902 – Stworzewicz *et al.*, p. 194, fig. 5i.

? 2014b *Vitrea* cf. *procrystallina* (Andreae, 1902) – Harzhauser *et al.*, p. 877, fig. 14s–u.

Material. – 1 apical fragment from T2 (K 6934); 4 apical fragments from T3-3 (K 6925, K 6937).

Dimensions. – 0.65 × 1.15 mm (Fig. 11C, F, L).

Description. – Shell depressed, with slightly more than two whorls preserved. Protoconch little elevated, hardly convex, attains *c.* 1.3 whorls that measure *c.* 685 µm; surface poorly preserved. Teleoconch whorls adapically flattened, grading over pronounced but blunt angulation into convex whorl flank and finally poorly convex base. Umbilicus small, deep. Aperture rather narrow, kidney-shaped; inner lip sheet-like, with granulose surface. Traces of numerous, faint spiral grooves are visible on some portions of teleoconch.

Remarks. – The shells from Vračević compare well to the description of Andreae (1902b) and specimens from the type locality Nowa Wieś Królewska stored in the collection of the Natural History Museum Vienna. A superficially very similar, coeval occurring species is *V. steinheimensis* Gottschick, 1920 from Steinheim. Based on comparison of *Vitrea* specimens from the type localities Nowa Wieś Królewska and Steinheim, following diagnostic differentiation criteria can be summarized: *V. steinheimensis* is slightly smaller, has a smaller protoconch with comparatively small nucleus and an elevated instead of a flattened apex. Both species share the blunt adapical angulation, which appears more pronounced in *V. procrystallina* due to the flattened apex. While spire height and whorl angulation vary slightly in both species, the size of the shell and the size and shape of the protoconch seem to be the best criteria for differentiation. Since *V. procrystallina* and *V. steinheimensis* can be well distinguished, a separation on species level is suggested.

Specimens from the late Miocene (early Pannonian) of Leobersdorf and Richardhof in the Vienna Basin, Austria, identified as *V. procrystallina steinheimensis* by Lueger (1981) and Harzhauser & Binder (2004) fully match *V. procrystallina* in terms of protoconch shape and size. The partly slightly more elevated spire might have led those authors to attribute the late Miocene specimens to *V. steinheimensis*.

Shells from the early Miocene of Tuchořice identified as *Vitrea* cf. *procrystallina* by Harzhauser *et al.* (2014b) differ from the present specimens in the slightly elevated apex and the much larger protoconch (*c.* 990 µm in diameter) and represent certainly a different species. Kókay (2006) misidentified individuals from the Badenian of Tapolca and Várpalota in Hungary as *V. procrystallina*; the illustrated shell has a distinctly elevated spire and a marked adapical angulation. The limited description and illustrations of a single incomplete specimen found in Sarmatian deposits at Răcăştia [= Rákosd] in Romania by Gaál (1910, 1911) do not allow a reliable identification; the record remains doubtful.

Only two further Miocene species were attributed to *Vitrea* by Wenz (1923) and Salvador *et al.* (2016c), *i.e.*, *Hyalina ammoni* Clessin, 1894 and *H. subdiaphana* Clessin, 1885 from Undorf in southern Germany. However, neither of the two species belongs to *Vitrea*. *Hyalina ammoni* has a distinctly wider aperture and *H. subdiaphana* shows a broadly ovoid spire; both characteristics are untypical for *Vitrea* and suggest placement within Oxychilidae or Gastrodontidae. Closer inspection of protoconch features is required here.

Occurrence. – Andelfinger Berg near Riedlingen and Zwiefaltendorf in southern Germany and Ruggburg in western Austria (MN 5; Gottschick 1920a, Wenz 1935, Schlickum 1976); Nowa Wieś Królewska near Opole (MN 6–7; Andreae 1902); Zwierzyniec (Sarmatian; Stworzewicz *et al.* 2013); several middle to late Miocene localities of Ukraine and Moldova (Gozhik & Prysjazhnjuk 1978, Prysiazhniuk 2014, Prysyazhniuk 2015); late Miocene of the Vienna Basin (as *V. steinheimensis*; Lueger 1981, Harzhauser & Binder 2004). Many of those records need re-examination of the protoconch in order to assure their taxonomic classification.

***Vitrea steinheimensis* Gottschick, 1920**
Figure 11B, E, H, I, K

*1920a *Vitrea* (*Vitrea*) *procrystallina steinheimensis* n. v.; Gottschick, p. 37.
1923 *Vitrea procrystallina steinheimensis* Gottschick. – Wenz, p. 294.
non 1981 *Vitrea* (*Vitrea*) *procrystallina steinheimensis* Gottschick. – Lueger, p. 42, pl. 5, figs 4a–b, 7a–c [= *Vitrea procrystallina* (Andreae, 1902)].
non 2004 *Vitrea procrystallina steinheimensis* Gottschick 1920. – Harzhauser & Binder, p. 25, pl. 11, figs 11–13 [= *Vitrea procrystallina* (Andreae, 1902)].
? 2006 *Vitrea procrystallina steinheimensis* Gottschick, 1920. – Kókay, p. 76, pl. 28, figs 10–12.

Material. – A single juvenile shell from T3-3 (K 6924).

Dimensions. – 0.59 × 1.13 mm.

Description. – Shell depressed, with 2.6 whorls preserved. Protoconch weakly raised, hardly convex, comprising 1.5 whorls, measuring 590 µm; initial part flattened, entirely immersed; nucleus weakly granulose; rest of protoconch covered by numerous spiral grooves, which appear irregular under high magnification, showing unequal depths; measured distances between grooves range from 3.6 µm to 6.6 µm. Transition to teleoconch marked by weak growth rim and by change of microsculpture: spiral grooves become more densely spaced and lose their previously pitted character; grooves cover entire shell. Teleoconch whorls regularly and broadly convex, grading into straight, slightly flattened base. Umbilicus small, deep. Aperture narrow, obliquely kidney-shaped; inner lip very thin, sheet-like.

Remarks. – Shell shape and size of the protoconch compare well with material from the type locality Steinheim. For detailed comparison with co-occurring *V. procrystallina*, as well as discussion of records considered synonymous or misidentified, see there.

Occurrence. – Steinheim (MN 7; Gottschick 1920a). The record from the Sarmatian of Várpalota in the Bakony Mts., Hungary, by Kókay (2006) needs re-examination of the protoconch, which is neither mentioned in text nor illustrated in apical view.

Achatinoid clade *sensu* Wade *et al.* (2006)
Family Ferussaciidae Bourguignat, 1883

Genus *Cecilioides* Férussac, 1814

Type species. – *Buccinum acicula* Müller, 1774; by monotypy. Recent, Germany.

***Cecilioides aciculella* (Sandberger, 1872)**
Figure 12A–D

*1872 *Caecilionella* [*sic!*] *aciculella* Sandb.; Sandberger, pl. 29, fig. 15–15a.
1875 *Caecilianella aciculella* Sandberger. – Sandberger, p. 595.
1900 *Caecilianella aciculella* Sandberger. – Miller, p. 399, pl. 7, fig. 18.
1923 *Cecilioides* (*Cecilioides*) *aciculella* (Sandberger). – Wenz, p. 1088 (cum syn.).
1967 *Cecilioides* (*Cecilioides*) *aciculella* (Sandberger). – Schütt, p. 214.
1976 *Cecilioides* (*Cecilioides*) *aciculella* (Sandberger). – Schlickum, p. 19, pl. 5, fig. 68.
1981 *Cecilioides* (*Cecilioides*) *aciculella* (Sandberger). – Lueger, p. 49, pl. 7, fig. 1.
1998 *Cecilioides aciculella* (v. Klein 1853 [*sic!*]). – Finger, p. 18, pl. 12, fig. I.
2004 *Cecilioides* (*Cecilioides*) *aciculella* (Sandberger, 1874). – Harzhauser & Binder, p. 21, pl. 9, figs 8–11.
2004 *Cecilioides aciculella* (Clessin [*sic!*]). – Hír & Kókay, p. 89, fig. 9:3.
2014a *Cecilioides aciculella* (Sandberger, 1875). – Harzhauser *et al.*, p. 28, pl. 9, figs 14–15.

Material. – 1 fragment from T2 (K 6934); 8 mostly fragmented shells from T3-3 (K 6926–6928, K 6937).

Dimensions. – 2.51 × 0.97 mm (Fig. 12A, B).

Description. – Fragile, slender elongate shell, with 3.5 low convex whorls preserved. Protoconch regularly hemispheric, with sutures almost invisible; surface entirely smooth; transition to teleoconch unclear; initial whorl measures *c.* 430 μm in diameter. Last whorl attains 75% of total shell height (in most complete but perhaps still subadult specimen). Aperture slender drop-shaped, lanceolate; peristome margin not preserved. Numerous, narrow, faint spiral grooves are visible on some shell portions.

Remarks. – Because of its subterranean lifestyle and very thin shell *Cecilioides* is a comparatively rare element in fossil terrestrial gastropod assemblages. *Cecilioides aciculella* is the only currently accepted species described for middle Miocene deposits of Europe (Wenz 1923). The specimens from Vračević differ slightly from those reported by Finger (1998) from the Steinheim Basin and Harzhauser *et al.* 2014a) from the Rein Basin, both of which have a slightly inflated protoconch.

Nomenclatural notes. – The species description in Sandberger's monograph on p. 595 was issued in 1875, but the illustration on plate 29 already was published in 1872 (see Woodward 1906).

Occurrence. – Upper Freshwater Molasse deposits at Mörsingen, southern Germany (MN 5; Sandberger 1870–1875); Steinheim am Albuch, Germany (MN 7; Finger 1998), Polskie Folwarki and Goncharivka (former Wyczólki), Ukraine (middle Miocene; Łomnicki 1886); Mátraszőlős and Felsőtárkány, Hungary (MN 7+8; Hír *et al.* 2001, Hír & Kókay 2004); Richardhof, Austria (Pannonian, MN 9; Harzhauser & Binder 2004).

Superfamily Helicoidea Rafinesque, 1815
Family Helicodontidae Kobelt, 1904
Subfamily Helicodontinae Kobelt, 1904

***Helicodontinae* gen. et sp. indet.**
Figure 12E, F, H, K

Material. – Single fragment including the protoconch and the apical portion of the first three teleoconch whorls from T2 (K 6929).

Description. – Apical region weakly immersed. Protoconch almost smooth apart from weak traces of few spiral ridges; comprises *c.* 0.7 whorls, measure *c.* 720 μm; termination marked by onset of growth lines and weak axial riblets. Teleoconch whorls moderately convex; sutures deeply incised. Whorl surface shows characteristic pattern of regularly spaced papillae that form bases of periostracal hairs. Papillae are elongate structures with pitted surface and measure *c.* 25 × 12 μm; they are situated in small depressions. Shell surface between papillae covered by about regularly spaced pinprick-like depressions.

Remarks. – The fragmentary preservation does not allow identification at the species or even genus level. The observed features, particularly the shape of the apical region and the arrangement of hair pits, suggest a placement among Helicodontinae. Very likely, the specimens belong to a species of *Helicodonta* Férussac, 1821 or *Protodrepanostoma* Germain, 1929. These genera are represented by several species in the Neogene of Europe (Wenz 1923), but can only be distinguished based on characteristics of the aperture (Harzhauser *et al.* 2014b, Nordsieck 2014).

Family Elonidae Gittenberger, 1979
Subfamily Eloninae Gittenberger, 1979

?*Eloninae* gen. et sp. indet.
Figure 12G, J

Material. – 2 protoconch fragments from T3-3 (K 6930–6931).

Description. – Available protoconchs start with smooth to weakly rugose nucleus. Original extent of protoconch unclear; largest fragment measures 2.3 mm in maximum diameter and comprises *c.* 1.3 whorls (Fig. 12J). At about 0.25 whorls irregularly elongate papillae occur that partly grade into each other, resembling axial riblets. Over next 0.25 whorls density of arrangement of papillae increases rapidly, while they become smaller and rounder. That pattern is maintained until preserved rest of protoconch.

Remarks. – The peculiar protoconch surface resembles those reported for species of the elonid genera *Apula* C. Boettger, 1909, *Elona* H. Adams & A. Adams, 1855, *Klikia* Pilsbry, 1895 and *Norelona* Nordsieck, 1986 (*e.g.*, Gittenberger 1979; Binder 2002, 2004, 2008; Harzhauser *et al.* 2014a, b; Nordsieck 2014). The rather large size of the protoconch makes an affiliation with the comparably small Klikiinae genera *Apula* and *Klikia* unlikely but rather suggest placement in Eloninae (compare Harzhauser *et al.* 2014a, b; Nordsieck 2014). The dense organization of elongate papillae resembles the pattern reported for the type species of *Elona*, Recent *Elona quimperiana* (Blainville in Cuvier, 1821); moreover, the size of its protoconch is comparable (2.75 mm after Binder 2008). The fragmentary preservation impedes a clear attribution, though.

The protoconch sculpture found in the larger elonid taxa *Tropidomphalus* Pilsbry, 1895 and *Pseudochloritis* C. Boettger, 1909 consists of rounder, spiky or knobbly, and more widely spaced papillae (Truc 1971; Binder 2002, 2004, 2008). Species previously attributed to the genus *Galactochilus* Sandberger, 1875 have similarly dense and irregular papillae but much larger protoconchs (Kadolsky *et al.* 2016).

***Helicoidea* gen. et sp. indet.**
Figure 12I

Material. – Only apical/protoconch fragments are available: 3 from T1 (K 6932–6933), 6 from T3-3 (K 6937).

Description. – Protoconch flattened, large-sized (*c.* 2.9 mm), consisting of 1.3 whorls that bear traces of weak axial riblets; nucleus large granulose. Protoconch is well demarcated from teleoconch by weak growth rim and onset of prosocline (in top view) growth lines.

Remarks. – Apart from ?Eloninae gen. et sp. indet. mentioned above at least one other helicoid species is found in the samples, represented by protoconch fragments only. The large size of the protoconch suggests that the adult shell was probably not smaller than 15 mm in diameter.

Class Bivalvia Linnaeus, 1758
Superorder Heterodonta Neumayr, 1883
Order Venerida Gray, 1854
Family Sphaeriidae Deshayes, 1855
Subfamily Sphaeriinae F.C. Baker, 1927

Genus *Pisidium* C. Pfeiffer, 1821

Type species. – *Tellina amnica* Müller, 1774; by subsequent designation by Gray (1847). Recent, Europe.

***Pisidium mionicense* Neubauer, Harzhauser & Mandic sp. nov.**
Figure 13A–K

Holotype. – Left valve, K 6880; 2.50 × 3.01 × 0.90 mm (Fig. 13A–C, K).

Paratypes. – Left valve, K 6881; 1.93 × 2.25 × 0.59 mm (Fig. 13D, E, J); right valve, K 6882; 1.81 × 2.23 × 0.60 mm (Fig. 13F, I); juvenile right valve, K 6883; 0.95 × 1.13 × 0.30 mm (Fig. 13G, H).

Derivation of name. – After the Mionica Basin, to which the deposits at Vračević belong.

Type locality. – Vračević, Lajkovac municipality, Kolubara district, Serbia; section T2.

Figure 12. Ferussaciidae and Helicoidea. • A, B – *Cecilioides aciculella* (Sandberger, 1872). Subadult specimen, K 6926, from T3-3. • C – *Cecilioides aciculella* (Sandberger, 1872). Juvenile specimen, K 6927, from T3-3. • D – *Cecilioides aciculella* (Sandberger, 1872). Protoconch, K 6928, from T3-3. • E, F, H, K – Helicodontinae gen. et sp. indet. Apical fragment, K 6929, from T2. Detail images show the protoconch (E), the arrangement of papillae on the last preserved teleoconch whorl (H) and a papilla from the same image section (K). • G – ?Eloninae gen. et sp. indet. Protoconch, K 6930, from T3-3. • I – Helicoidea gen. et sp. indet. Apical fragment, K 6932, from T1. • J – ?Eloninae gen. et sp. indet. Protoconch, K 6931, from T3-3. Scale bars correspond to 500 μm (A–C, F, G, I, J), 100 μm (D, E, H) and 5 μm (K).

Type horizon. – Bed 3; late middle Miocene, late Serravallian, Sarmatian.

Material. – 3 LV and 4 RV from T1 (K 6933); 2 LV, 2 RV and 14 fragments from T2 (K 6934); 1 LV and 2 RV from T3-1 (K 6935); 9 LV, 11 RV and 35 fragments from T3-3 (K 6880–6883, K 6937).

Diagnosis. – Obtuse triangular, domed shell with rather thin hinge plate; C3 weakly curved, posteriorly thickened;

C2 massive, triangular; C4 curved, posteriorly thickened; anterior teeth stronger pronounced than posterior ones; inner shell surface slightly irregular, densely perforate.

Description. – Shell obtuse triangular, with weakly convex dorsal margins and well-rounded ventral margins. Shell domed in profile, forming wide weak dorsal–ventral convexity and weak concavities on anterior and posterior side of umbo. Umbo well-rounded, not distinct, with smooth elliptical prodissoconch. Juvenile shell almost perfectly elliptical (Fig. 13G, H). Irregular, densely perforate inner shell surface only visible in some specimens. Both muscle scars rather distinct. Hinge plate narrow in both valves. Hinge characters of left valve: A2 pronounced, massive, tall, elongate, dorsally accompanied by deep groove; P2 small, narrow, producing only weak bulge of hinge plate; C2 small but massive, tall, elongate triangular; C4 elongate drop-shaped, passing from knobbly thickened posterior end into narrow, lamellate anterior end. Right valve: A1 broad, elongate, strongly protruding; A3 rather weak and short; both anterior teeth have knobbly surface at contact to A2; C3 elongate, usually weakly, rarely stronger, curved (but never angled), passing from a thickened posterior part to a narrow, weakly thickened anterior end; accompanied by ventral and dorsal depressions; posterior teeth similar to anterior ones but weaker, more delicate, less protruding; also bearing knobbly sculpture at contact to P2. Ligament groove in both valves long, lanceolate, extending from below umbo (coinciding with posterior end of C2 and center of C3) almost to P2.

Remarks. – The new species can be distinguished from the about coevally living *Pisidium steinheimense* Gottschick, 1921 from the Steinheim Basin, which has an elongate-ovoid shell and has a more massive hinge. Specimens from the Upper Freshwater Molasse of southern Germany identified as recent *Pisidium amnicum* (Müller, 1774) by Schneider & Prieto (2011) are similarly obtuse-triangular like the present species, but, like extant *P. amnicum*, have a distinctly arched C3 and a narrow triangular C2 and stronger inclined C4 (Zeissler, 1971). The early middle Miocene *P. bellardii* Brusina, 1884 from Miočić, Croatia, also has an elongate ovoid shell but a much more delicate hinge than the present species and subtle, regularly spaced growth lines (Neubauer *et al.* 2016). *Pisidum vukovici* Neubauer *et al.*, 2013 from the early middle Miocene of the Gacko Basin in Bosnia and Herzegovina is narrow triangular and has a massive hinge plate (Neubauer *et al.* 2013). Specimens from the Aflenz Basin determined as *Pisidium* cf. *casertanum* Poli, 1791 by Harzhauser *et al.* (2012) have a similarly obtuse-triangular shape but a shorter and narrower ligament and the C3 is less curved and not thickened posteriorly. The species furthermore differs from *P. personatum* Malm *sensu* Kuiper, 1972 and Harzhauser & Binder, 2004 from the Pannonian of the Vienna Basin, which has a well-rounded, elongate shell and a weaker hinge. *Pisidium annandalei* sensu Piechocki (1997) from Bełchatów has a very similar hinge but a more triangular shape and a much stronger hinge plate. The recent *Pisidium annandalei* Prashad, 1925 from India, with which Piechocki confused his specimens, is strikingly similar regarding hinge characteristics but has a more rounded shell and a far more posteriorly placed ligament. The specimens Piechocki (1997) identified as *Pisidium casertanum* f. *ponderosum* (Stelfox, 1918) have a conspicuous similarity with *P. amnicum* sensu Schneider & Prieto, 2011 and Zeissler, 1971.

Discussion

Faunal composition and palaeobiogeography

The here presented fauna consists of 29 species, including four species of freshwater gastropods (Lymnaeidae, Planorbidae), 24 species of terrestrial gastropods (Pomatiidae, Cochlostomatidae, Carychiidae, Cochlicopidae, Strobilopsidae, Valloniidae s.l., Vertiginidae, Gastrocoptidae, Clausiliidae, Discidae, Helicodiscidae, Limacidae, Milacidae, Gastrodontidae, Pristilomatidae, Ferussaciidae, Helicodontidae, Elonidae) and one bivalve species (Sphaeriidae). Prisyazhnyuk & Rudyuk (2005) recorded four additional planorbid species that have not been found in our material, *i.e.*, *Planorbis* sp., *Anisus* sp., *Armiger gracilis* Gozhik & Prysjazhnjuk, 1978 and *Segmentina lartetii* (Noulet, 1854). Since many taxa are represented by single or few specimens each, the faunal inventory is very likely to grow with further sampling. Especially large-sized species are rare and represented by fragments only.

Biogeographically, the freshwater gastropod fauna of Lake Vračević was attributed to the Balkan Region by Neubauer *et al.* (2015a), largely because of geographic coherence. However, that biogeographic scheme is mostly based on the diverse faunas of long-lived lakes, while the short-lived faunas (such as the present one) usually take outlier positions. The Vračević fauna has, in fact, much more in common with those of the Central-West European (including Lake Steinheim, the Upper Freshwater Molasse and Lake Rein), Peri-Paratethyan (including Bakony) and North European regions (including Zwierzyniec and the Fore-Carpathian Basin) (Table 1). Compared to the highly endemic and provincial long-lived lake faunas, short-lived (pulmonate-dominated) faunas mostly consist of widespread species (Neubauer *et al.* 2015a, d; Georgopoulou *et al.* 2016a, b), such as the here found *Planorbarius mantelli*, *Gyraulus kleini* and *Ferrissia deperdita*, which have been documented from numerous middle Miocene freshwater systems in Europe (*e.g.*, Harzhauser *et al.* 2014a; Salvador

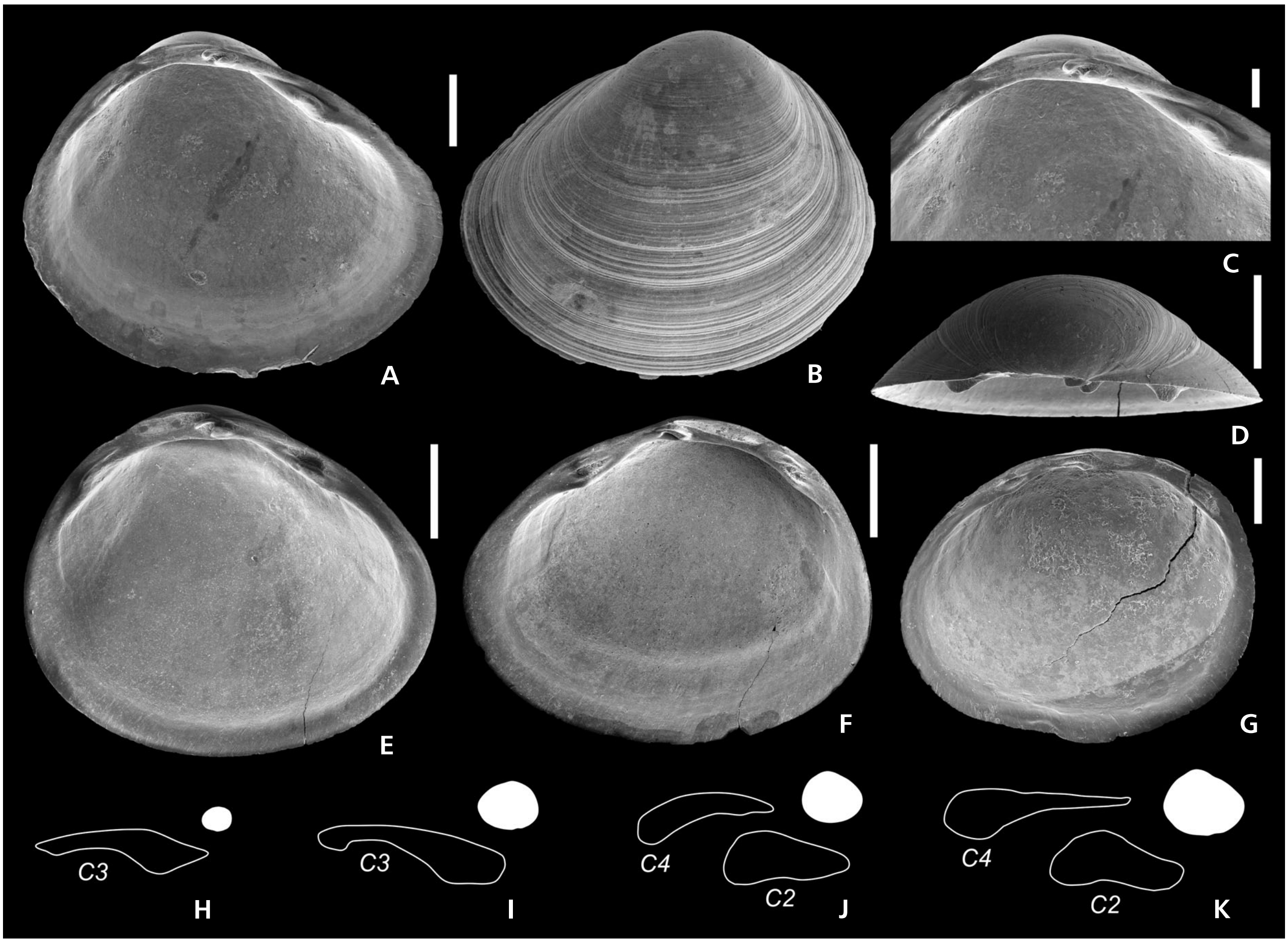

Figure 13. *Pisidium mionicense* Neubauer, Harzhauser & Mandic sp. nov. (Sphaeriidae). The bottom row shows line drawings of the cardinal teeth of the four depicted specimens, in the order of their ontogenetic age. The relative sizes of the entire shells are represented by equally scaled white outlines. • A–C, K – holotype, left valve, K 6880, from T3-3. • D, E, J – paratype, left valve, 6881, from T3-3. • F, I – paratype, right valve, K 6882, from T3-3. • G, H – juvenile right valve, K 6883, from T3-3. Scale bars correspond to 500 μm (A, B, D–F) and 200 μm (C, G).

& Rasser 2016a, b; Salvador *et al.* 2016a, b; Table 1). Given the geographic ranges of these pulmonate gastropods across hydrologically unconnected regions, the most probable long-distance dispersal vector seems to be waterfowl. Several examples of bird-mediated dispersal have been adduced for both recent (*e.g.*, Green & Figuerola 2005; Kappes & Haase 2012; van Leeuwen & van der Velde 2012; van Leeuwen *et al.* 2012a, b, 2013) and fossil freshwater snails (Wesselingh *et al.* 1999, Neubauer *et al.* 2015c, Harzhauser *et al.* 2016). In fact, dispersal via waterfowl may have been a much more common mode for gastropod to expand their ranges than assumed so far.

The terrestrial fauna of Vračević consists of elements typical of the middle Miocene – except for the new Vertiginidae species, all 14 species identified at the species level have been previously documented from middle Miocene deposits. Comparing single assemblages, the Vračević fauna is most similar to the early middle Miocene faunas of the Upper Freshwater Molasse (MN 5–6; 11 shared species) and Undorf (MN 5; 7 shared species) (Table 1, Fig. 14). The younger faunas from Sansan (MN 6; 2 shared species), Steinheim (MN 7; 4 shared species), Nowa Wieś Królewska near Opole (MN 6–7; 6 shared species), Hollabrunn (MN 7+8; 5 shared species), Bakony (MN 7+8; 5 shared species) and Zwierzyniec (MN 7+8; 4 shared species) have less in common (compare also Höltke *et al.* 2016). The overall number of species represented in MN 7+8 localities (13 shared species) is, however, higher than for MN 5–6 localities (11 shared species), supporting the proposed Sarmatian age of the deposits at Vračević.

While there is much overlap with Badenian faunas, few of the occurring species have been reported from early or late Miocene deposits. Much of the previously mentioned faunal overlap between Sarmatian and Pannonian faunas (*e.g.*, Lueger 1981) must be reconsidered in the light of revised species determinations, such as those proposed herein. For instance, only four species are shared with the

Table 1. Taxa occurring in Vračević and selected Miocene localities/regions. For literature sources see text and caption of Figure 14. The records for Richardhof are based on material from the lower strata (MN 9) detailed in Harzhauser & Binder (2004). Abbreviations same as in Figure 14.

Locality/region	Tuchořice	Bełchatów-C	Bełchatów-B	Undorf	Rein	OSM	Sansan	Steinheim	Opole	Bakony Mts.	FCB	Bakony Mts.	FCB	Hollabrunn	Zwierzyniec	Răcăştia	Ctr. Anatolia	Leobersdorf SG	Leobersdorf Br.	Bełchatów-A	Richardhof
Biostratigraphy / Taxon	MN 3b	MN 4	early MN 5	MN 5	late MN 5	MN 5-6	MN 6	MN 7	MN 6–7	~MN 5-MN 7	~MN 5-MN 7	MN 8	MN 8	late MN 8	late MN 8	late MN 8	late MN 8	boundary MN 8/9	MN 9	MN 9	late MN 9
Pomatias sp.																					
Cochlostoma sp.																					
Stagnicola cf. *palustriformis* (Gottschick, 1911)								x		x		x	x								
Ferrissia deperdita (Desmarest, 1814)				x	x	x		x		x		x									
Gyraulus kleini Gottschick & Wenz, 1916		x		x	x	x		x		x	x	x	x								
Planorbarius mantelli (Dunker, 1848)		x	x	x	x	x	x	x		x	x	x	x				x				x
Carychium gibbum Sandberger, 1875		x	x	x	x	x				x				x						x	
Carychium nouleti Bourguignat, 1857 s.l.							x		x	x				x	x		x				
Carychiella eumicrum (Bourguignat, 1857)	x		x	x	x	x			x	x		x									
Cochlicopa sp.																					
Strobilops costatus (Clessin, 1877)		x	x	x		x			x					x							
Acanthinula trochulus (Sandberger, 1872)		x	x	x		x			x							?			x		x
Pupisoma cf. *distans* Falkner, 1974						x															
Spermodea candida Falkner, 1974			x	x		x						x									
?*Vertigo vracevicensis* sp. nov.																					
Gastrocopta nouletiana (Dupuy, 1850)			x	x		x	x	x		x	x	x	x	x	x		x	x	x	x	x
?*Serrulina* sp.																					
Discus solarioides (Sandberger, 1872)								x							x			?	?		
Lucilla subteres (Clessin, 1877)				x	?	x			?												
Limacidae gen. et sp. indet.																					
Milacidae gen. et sp. indet.																					
Zonitoides cf. *suevicus* (Jooss, 1918)						x				x		x									
Vitrea procrystallina (Andreae, 1902)	?					x			x		x		x		x	?		x	x		x
Vitrea steinheimensis (Gottschick, 1920)								x				x									
Cecilioides aciculella (Sandberger, 1872)						x		x						x							x
Helicodontinae gen. et sp. indet.																					
?Eloninae gen. et sp. indet.																					
Helicoidea gen. et sp. indet.																					
Pisidium mionicense sp. nov.																					
Total	2	5	7	10	6	14	3	8	6	9	4	9	5	5	4	2	3	3	4	2	5

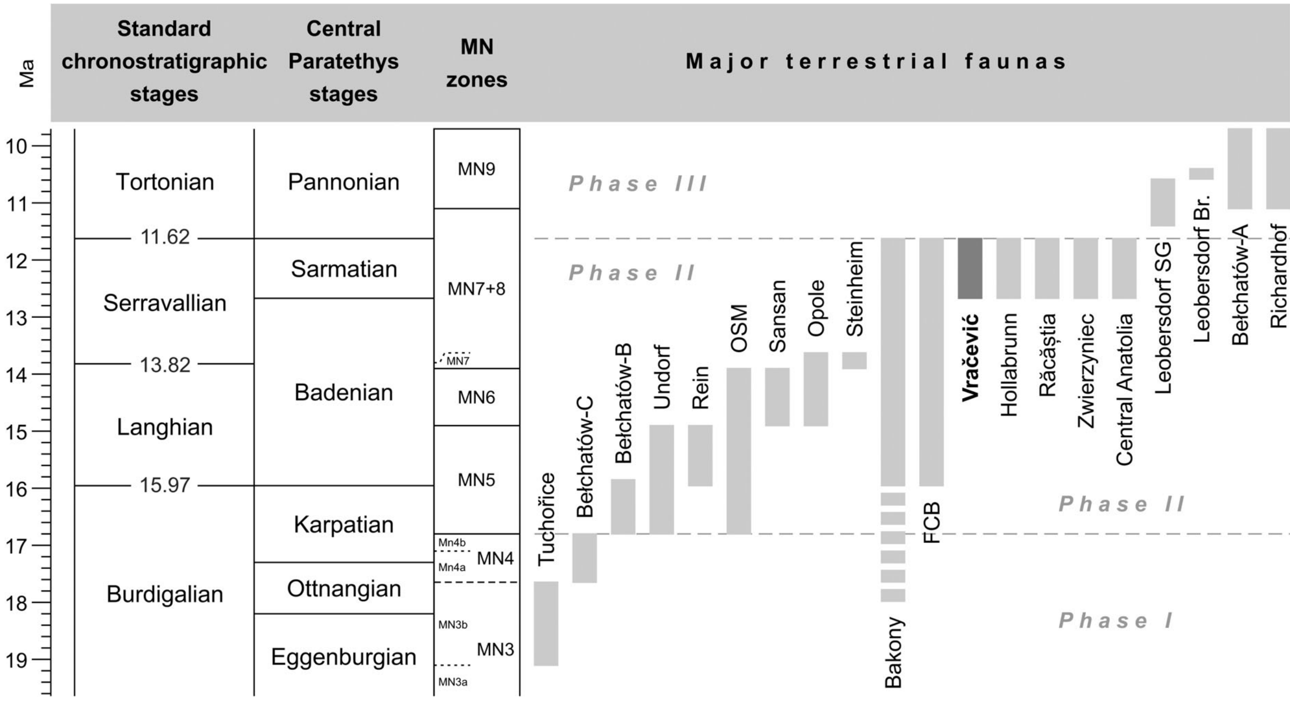

Figure 14. Stratigraphic correlation chart showing the stratigraphic ages of major terrestrial faunas mentioned in the text and according phases of faunal evolution of European land snails.. International chronostratigraphic stages are based on Gradstein *et al.* (2012), Central Paratethys stages follow Piller *et al.* (2007) and Central European Neogene mammal (MN) stages are adopted from Kälin & Kempf (2009; and references therein). Information on the stratigraphic ages of the faunas derives from Gaál (1910, 1911), Schütt (1967), Gozhik & Prysjazhnjuk (1978), Lueger (1981), Esu (1999), Kadolsky & Piechocki (2000), Harzhauser & Binder (2004), Kókay (2006), Stworzewicz *et al.* (2013), Harzhauser *et al.* (2014a, b) and Salvador *et al.* (2015a). The assemblages of the Bakony Mts. studied by Kókay (2006) also include early Miocene faunas, which are not discussed here because they have no species in common with Vračević. The gray dashed lines indicate major turnovers in European terrestrial gastropod faunas. Abbreviations: FCB – Fore-Carpathian Basin; Leobersdorf Br. – Leobersdorf brickyard; Leobersdorf SG – sand pit and gravel pit; OSM – Upper Freshwater Molasse.

lower strata of Richardhof (MN 9; Harzhauser & Binder 2004), three with Leobersdorf Sandgrube/Schottergrube (Pannonian biozone B/C, correlated to latest MN 8 to early MN 9 after Kälin & Kempf 2009) and two with Bełchatów-A (early Pannonian; MN 9; Stworzewicz 1999a, b). The marked turnover in terrestrial gastropod diversity at the middle–late Miocene boundary has been documented earlier (*e.g.*, Harzhauser *et al.* 2008) and goes along with climate cooling and drying in Europe (Zachos *et al.* 2008, Ivanov *et al.* 2011). Very likely, many of the thermophilous and humidity-adapted taxa successively moved towards the Mediterranean realm.

Most species found in Vračević have been originally described from central Europe, and few have been reported from western and eastern European and Anatolian localities. The middle Miocene non-marine deposits of the Fore-Carpathian Basin in Ukraine (Fig. 15) studied by Gozhik & Prysjazhnjuk (1978) share only wide-spread *Gastrocopta nouletiana* and *Vitrea procrystallina*. Similarly, late Serravallian terrestrial faunas of Turkey (localities Koçgazi and Çifteçesme near Ayvalı in central Anatolia; Schütt 1994), as well as the MN 6 locality Sansan in France only have *G. nouletiana* and *Carychium nouleti* in common with Vračević [Note that Schütt (1994) and Neubauer et al. (2015b) erroneously attributed the deposits of that locality to the late Miocene]. Ubiquitous *G. nouletiana* is the only element found also in middle Miocene deposits of southern Russia (Steklov 1966). Disregarding potential taxonomic and preservational biases, the little biogeographic overlap with those regions likely roots in differences of regional climate (compare, *e.g.*, Ivanov *et al.* 2011) and, along with that, local environment (*e.g.*, forested vs. open habitats). Moreover, direct terrestrial pathways to Anatolia and the Caucasus region were limited or unavailable during Sarmatian times (Popov *et al.* 2004; fig. 15).

Paleoecology

Information on the autecology of recent representatives of the recorded genera presently occurring in Europe derives from Welter-Schultes (2012); data sources for genera not living in Europe at present are indicated below.

The freshwater fauna of Lake Vračević consists of pulmonate gastropods and a sphaeriid bivalve, which are

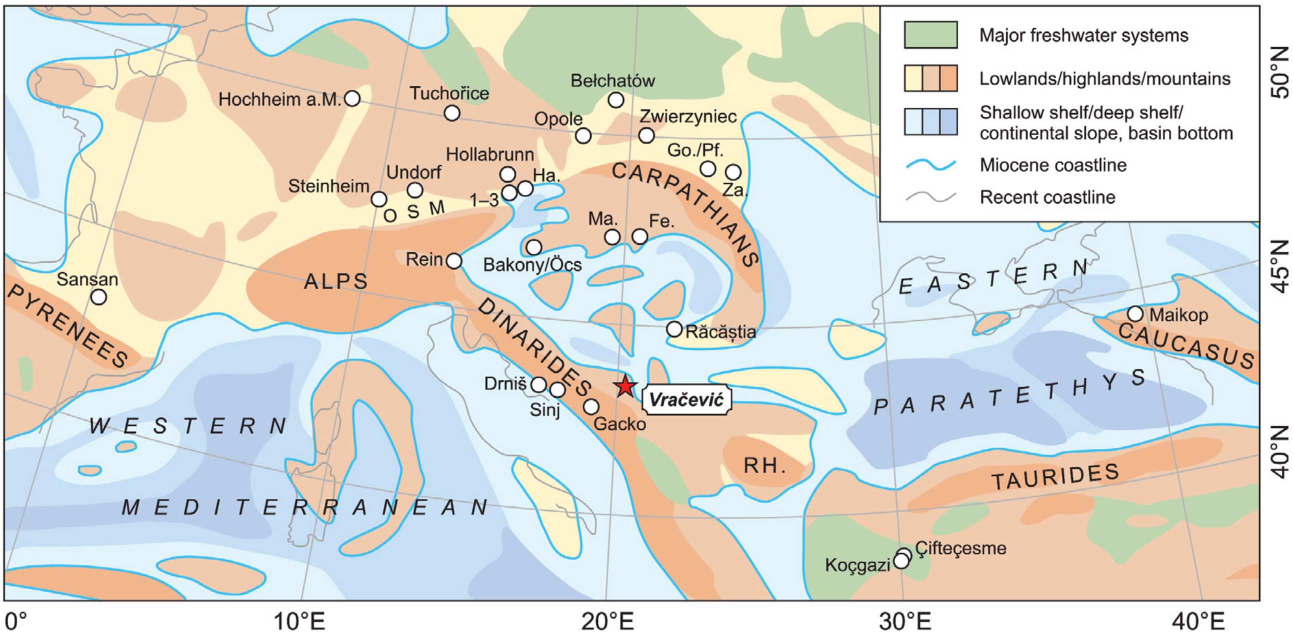

Figure 15. Paleogeographic sketch showing the land-sea configuration during the Sarmatian (late Serravallian) and major localities with non-marine faunas mentioned in the text (modified from Popov *et al.* 2004). Note that all localities were placed in this paleogeographic context regardless of the actual stratigraphic age of their deposits; see Figure 14 and Table 1 for their stratigraphic classifications. Abbreviations: 1–3 – Leobersdorf, Richardhof and St. Veit an der Triesting; Fe. – Felsőtárkány; Go./Pf. – Goncharivka (former Wyczólki) and Polskie Folwarki; Ha. – Hautzendorf; Ma. – Mátraszőlős; OSM – Upper Freshwater Molasse; Za. – Zamekhov.

indicative of silent to slowing running, often highly vegetated water. The generic composition, particularly the lack of caenogastropod species, resembles many present-day European lake faunas and is indicative of geologically short-lived environments (Neubauer *et al.* 2015d; Georgopoulou *et al.* 2016a, b).

The terrestrial fauna is much more diverse and needs closer inspection. *Pomatias* is found on calcareous or loamy soils in open woods, forests, shrub lands, rock rubbles and maritime grasslands. *Cochlostoma* lives today in open or forested, humid to dry, rocky (usually limestone) habitats, feeding on dead plant matter and microflora. Species of *Carychium* require permanently humid conditions and live under leaf litter or between stones in meadows, swamps and forests, often near water bodies. The *Cochlicopa* species found today in Europe all have wide geographic distributions and partly wide ecological amplitudes. They occur in moderately humid to moist habitats, including meadows and forests, periodically flooded swamps and irrigation canals, as well as in plains and highlands. Recent species are often associated with limestone and dwell under stones and wood. *Strobilops* sensu stricto is found living only in the Americas, ranging from the southeastern Canada over Central America and the West Indies to northern South America. Records from eastern to southeastern Asia actually belong to species of the genera *Discostrobilops*, *Enteroplax* and *Eostrobilops*, which were formerly ranked as subgenera of *Strobilops* (Miller & Christensen 1980, Manganelli *et al.* 1989). According to Pilsbry (1927–1935), extant species of *Strobilops* live in decaying logs and dead leaves in moderately humid forests. *Acanthinula* lives in leaf litter and under fallen timber in shady places in deciduous forests and under shrubs, often on calcareous substrate such as overgrown limestones rocks in forests. Similarly, related *Spermodea* is found in humid leaf litter of deciduous forests and under rotting trees and branches. The circumtropical genus *Pupisoma* dwells on bark and leaves of trees and other plants (Pilsbry 1948, van Bruggen & Appleton 1977, Hausdorf 2007). *Gastrocopta* is a wide-spread and species-rich genus today, occurring in the Americas, Africa, central to eastern and southern Asia, Australia, as well as Oceania (*e.g.*, Pilsbry 1927–1935, van Bruggen & Appleton 1977, Egorov 2008, Brook 2010, Nekola & Coles 2010, Schileyko 2011, Budha *et al.* 2015). Species dwell in a great variety of habitats, ranging from xeric to wet settings, forested areas to shrublands and open grasslands and floodplains, in leaf litter, under logs or stones and on bedrock outcrops (Nekola & Coles 2010). Recent European *Serrulina* live in wet deciduous forests under rotting bark and inside humid disintegrating wood of large logs, occasionally also on tree trunks (Loosjes 1953). *Discus* is typical of shady, humid, often mountainous, environments. It lives in leaf or soil litter, on humus or dead wood logs or under rotting wood and stones in forests, occasionally also in humid, shady places of open habitats. Both species of

Lucilla occurring in Europe nowadays are blind, subterranean snails, living in rootlet holes and shrinkage cracks down to depths of a meter (Kerney 1999); they are often found in river deposits. Most Limacidae dwell in forests or in mountains above the timberline. Milacidae occur in a very broad spectrum of habitats, both open and well-shaded, moist and dry, low and high altitude; several species live in stony, often calcareous, habitats. *Zonitoides* lives in woodlands and humid habitats, such as meadows, river woods and swamps. The genus *Vitrea* is nowadays represented by numerous species in Europe, living in a broad variety of habitats and temperature and humidity ranges. Several species live in warm and dry habitats and are associated with calcareous substrate, while the most common species, *V. crystallina* (Müller, 1774), dwells under leaf litter or in mosses of humid forests, meadows and swamps. *Cecilioides* lives in subterranean soil habitats. Helicodontinae live in leaf and ground litter, on old wood or bark, or on rock rubble in humid, shady places in mountain forests of lower altitudes. Recent Eloninae dwell in humid habitats in woods, shrub lands and gardens, on rocks, as well as in caves or near the entrances of such.

In summary, the majority of terrestrial gastropod species of Vračević are indicative of humid, forested environments, which is corroborated by its mammal fauna (Marković 2003). Not a single of the occurring genera is fully restricted to open and dry habitats today, suggesting that the lakesides of Lake Vračević were fringed by humid forests. This paleoenvironmental interpretation fits climate reconstructions based on fossil Sarmatian floras from Serbia by Ivanov *et al.* (2011). These authors indicated the presence of mixed mesophytic forests with deciduous elements and possible seasonality of precipitation, as well as riparian and swamp forests in river valleys and floodplains and around lakes, and mixed conifer-laurel forests in higher altitudes in an overall subtropical/warm-temperate and humid climate.

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