The Early–Middle Miocene freshwater mollusk fauna of the Mecsek Mts. (S Hungary): a biogeographic stepping stone

Thomas A. Neubauer, Oleg Mandic & Krisztina Sebe

The Mecsek Mts. in southern Hungary were fringed by a freshwater paleolake during the late Early–early Middle Miocene. Its position just north of the Dinarides places the lake at the biogeographic crossroads between the highly endemic faunas of the Dinaride Lake System and the more widely distributed freshwater systems scattered around the Central Paratethys. However, only few species have been identified from the deposits so far, complicating an in-depth assessment of biogeographic affinities. Here, we provide a thorough taxonomic assessment of the fauna based on new material from freshwater deposits exposed at six localities, primarily at the southeastern margin of the Mecsek Mts. We expand the species inventory to a total of 17 species, comprising 12 genera and 8 families. Six species and one genus are newly described: *Pyrgula sopianae* sp. nov. (Hydrobiidae: Pyrgulinae), *Asymmetrorbis pseudovitrina* gen. et sp. nov., *Gyraulus ianus* sp. nov., *Gyraulus magyari* sp. nov., *Gyraulus pseudodalmaticus* sp. nov. (Planorbidae), and *Potomida schneideri* sp. nov. (Unionidae), all of which are endemic to Lake Mecsek. Based on a biogeographical analysis of selected Central to Southeastern European Early–Middle Miocene freshwater mollusk faunas, we find strong affinities between the Mecsek fauna and coeval assemblages of the Southern Pannonian Basin. These faunas show about equal similarity to those of the Dinaride Lake System in the south as well as to Central European ones in the north, rendering the Southern Pannonian Basin and Lake Mecsek in particular as an important stepping stone connecting these biogeographic regions. • Key words: Gastropoda, Bivalvia, taxonomy, biogeography, paleoecology.

Neubauer, T.A., Mandic, O. & Sebe, K. 2025. The Early–Middle Miocene freshwater mollusk fauna of the Mecsek Mts. (S Hungary): a biogeographic stepping stone. *Bulletin of Geosciences 100(3)*, 319–357 (14 figures, 2 tables). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received August 20, 2025; accepted in revised form November 13, 2025; published online December 21, 2025; issued December 21, 2025.

Thomas A. Neubauer (corresponding author), SNSB – Bavarian State Collection for Palaeontology and Geology, Richard-Wagner-Straße 10, 80333 Munich, Germany & Department of Earth and Environmental Sciences, Palaeontology and Geobiology, Ludwig-Maximilians-Universität München, Richard-Wagner-Str. 10, 80333 Munich, Germany & Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, The Netherlands; neubauer@snsb.de • Oleg Mandic, Geological-Paleontological Department, Natural History Museum Vienna, Burgring 7, 1010 Vienna, Austria & Department of Geology, Faculty of Earth Sciences, Geography and Astronomy, University of Vienna, Josef-Holaubek-Platz 2 (UZA II), 1090 Vienna, Austria • Krisztina Sebe, HUN-REN–MTM–ELTE Research Group for Paleontology, 1083 Budapest, Ludovika tér 2., Hungary

The Mecsek Mts., today a small mountain range in southern Hungary (Fig. 1), underwent considerable paleogeographic reconfiguration during the Cenozoic. Throughout the Oligocene to the end of the Early Miocene (late Burdigalian, Karpatian), the Mecsek Mts. formed a local high along the southern margin of the Central Paratethys (Mandic *et al.* 2012, Kováč *et al.* 2017). With the mid-Langhian flooding and the expansion of the Central Paratethys into the southern Pannonian Basin, the area around the Mecsek Mts. became separated from the Dinarides (Popov *et al.* 2004, Kováč *et al.* 2017, Harzhauser *et al.* 2024). Despite major environmental alterations, the demise of the Central Paratethys and rise of Lake Pannon in its stead, the Mecsek island continued to exist as such (in various extent) until the filling of the Pannonian Basin by the paleo-Danube during the Late Miocene (late Pannonian) around 7 Ma (Magyar *et al.* 1999, 2013; Neubauer *et al.* 2016a).

During the late Early to early Middle Miocene (late Burdigalian–early Langhian, Karpatian–early Badenian), a lake existed around the Mecsek Mts. – Lake Mecsek (Neubauer *et al.* 2015a, Sebe *et al.* 2019). Until recently, only three species had been identified from the deposits: the bithyniid gastropod *Ferebithynia vadaszi* (Wenz, 1931) and the dreissenid bivalve *Trigonipraxis boeckhi* (Wenz, 1931), both common and widespread species (Wenz 1931, Sebe *et al.* 2019), along with the record of *Stenothyra schwartzi* (Hörnes, 1856) deriving from an unspecified locality and stratum (Strausz 1966).

DOI 10.3140/bull.geosci.1948

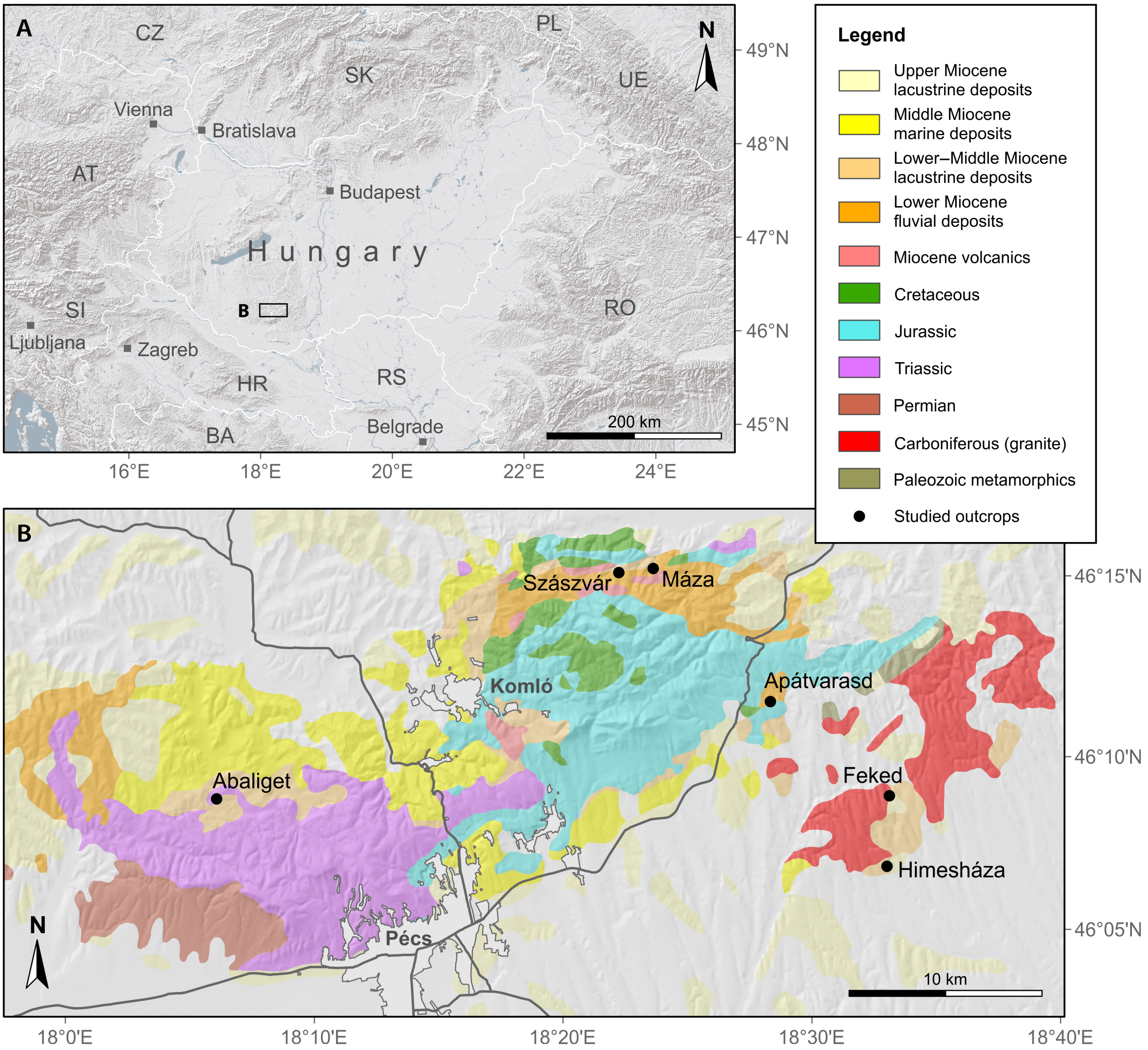


Figure 1. Geographical and geological overview of the study area in the Mecsek Mts. • A – geographic position of the study area in southern Hungary. Country abbreviations refer to ISO 3166-1 alpha-2 standard codes. Map was created in ESRI ArcGIS Pro v. 3.5 using the World Shaded Relief basemap of ESRI (2009). • B – geological map of the Mecsek Mts. with indication of the sampled outcrops. Base map modified from Gyalog (2013).

This seemingly depauperate fauna was considered to belong to the Illyrian Biogeographic Region during the late Early Miocene, including also the highly endemic long-lived lake faunas of the Dinaride Lake System (DLS; Mandic *et al.* 2012; Neubauer *et al.* 2015a, b). In part, this attribution was due to the geographic position of Lake Mecsek at the northern edge of the Dinaric Peninsula at that time, since the low number of species complicated a statistical approach (Neubauer *et al.* 2015a). On the other hand, during the Karpatian, extensive dreissenid-rich accumulations of DLS-type also occurred further north, in the Bakony Mts. in central Hungary (Kókay 2006), as well as the Fohnsdorf Basin (Hölzel & Wagreich 2004) and the Vienna Basin in eastern Austria (Schultz 2005, Mandic *et al.* 2012). Moreover, the common Mecsek species *Ferebithynia vadaszi* and *Trigonipraxis boeckhi* have also been reported from the Bakony Mts. (Kókay 2006). Mandic *et al.* (2012) even considered all these occurrences to belong to the Illyrian Region. However, despite similarities, this grouping was not supported by a biogeographic analysis based on gastropods (Neubauer *et al.* 2015a). Hence, the biogeographic affinities of the Mecsek fauna are largely unresolved at present.

In recent years, new data have become available through extensive field campaigns on the lacustrine mollusk fauna of Lake Mecsek, containing a number of new species as well as taxa previously unreported from the area. Here, we present an updated taxonomic account of the freshwater gastropod and bivalve species occurring at Lake Mecsek during the late Early to early Middle Miocene. We discuss the paleoecological and paleobiogeographic implications of our findings, which elucidate the role of the Mecsek fauna at the biogeographic crossroads between the Dinaride Lake System and Peri-Paratethyan faunas.

Geological setting

In the Mecsek Mts., sedimentation in the Early to Middle Miocene is linked to the rifting of the Pannonian Basin, and is represented initially by fluvial and lacustrine, later by marine deposits (Hámor 1970, Chikán 1991, Sebe *et al.* 2019; Fig. 1). The sampled deposits belong to the first two units.

The fluvial succession is referred to as Szászvár Formation. Its age is Eggenburgian to early Badenian (early Burdigalian to early Langhian), with the upper boundary being diachronous (Sebe 2024). With a general fining-upward trend, the upper part of the formation shows transitional features towards the lacustrine environment, with interfingering paludal and delta sediments.

The outcrop at Apátvarasd (Fig. 1) represents the lower part of the transitional interval (Hámor 1970), with fluvial sands interbedded with lignite layers. Only unidentifiable, thin-shelled mollusks have been reported from here previously (Hámor 1970). Palynological investigations indicate the presence of willow (*Salix*) forests in the area at the time of deposition, which later were replaced by fern-dominated vegetation (Hámor 1970). In a nearby borehole, a rhyolite tuff at the boundary between the fluvial and the lacustrine units was dated to 15.8 ± 0.7 Ma (Hámor *et al.* 1979).

Szászvár and Máza samples were taken roughly from the same horizon in two neighboring valleys (Fig. 1). They are located in the uppermost section of the Szászvár Fm., consisting of lacustrine delta layers (Sebe *et al.* 2024). Hámor (1970) interpreted this transitional interval as paludal-fluvial and paludal-lacustrine deposits. Among the fauna, he listed *Theodoxus*, *Brotia escheri*, *Melania*, *Unio*, planorbids, and gastropod opercula. Rhyolite tuff

Table 1. Overview of the studied localities, with details on geographic position, sedimentological, lithostratigraphic, and paleoenvironmental information, as well as geological age.

Locality	Locality details	Latitude (N)	Longitude (E)	Lithology	Depositional environment	Lithostratigraphic unit	Stratigraphic age
Abaliget	Kis-kő-hegy	46.143755	18.097198	clay marl, silt	lacustrine sublittoral	Kiskunhalas Fm. Komló Clay marl Mb.	Karpatian; tuff interbed 16.82 ± 0.65 Ma
Feked 1	Kis-völgy	46.1478082	18.549804	lignite, mollusk coquina	lacustrine littoral	Kiskunhalas Fm. Komló Clay marl Mb.	Karpatian/early Badenian
Feked 2	Kis-völgy	46.1478082	18.549804	sandy silt	lacustrine sublittoral	Kiskunhalas Fm. Komló Clay marl Mb.	Karpatian/early Badenian
Himesháza	Engesgraben	46.1150646	18.548113	mollusk coquina	lacustrine littoral	Kiskunhalas Fm. Pécsvárad Mb.	Karpatian/early Badenian
Máza	Dóra-irtás	46.25261	18.3886	clay, silt, sand	lacustrine delta	top of Szászvár Fm.	Karpatian/early Badenian; underlying tuff dated 17.055 ± 0.024 Ma
Szászvár 1	Fő-völgy	46.2503601	18.367263	sandy, clayey silt	lacustrine delta	top of Szászvár Fm.	Karpatian/early Badenian; underlying tuff dated 17.055 ± 0.024 Ma
Szászvár 2	Fő-völgy	46.25101	18.36667	clayey silt	lacustrine delta	top of Szászvár Fm.	Karpatian/early Badenian; underlying tuff dated 17.055 ± 0.024 Ma
Apátvarasd	Szénárok	46.19158	18.47111	lignite, clay	fluvial	Szászvár Fm.	Karpatian/early Badenian; overlying tuff dated 15.8 ± 0.7 Ma

in the lower part of the fluvial succession in Szászvár was dated to 17.7 ± 1.9 Ma (plagioclase) and 22.2 ± 1.9 Ma (biotite) (Hámor *et al.* 1979). Newer data, however, recently derived from U-Pb zircon dating of strata at Máza suggest a younger age of 17.055 ± 0.024 Ma (Harangi & Lukács 2019).

The sampled deposits at Himesháza, Feked, and Abaliget (Fig. 1) belong to the lacustrine Kiskunhalas Formation, which is Karpatian to lower Badenian (upper Burdigalian to lower Langhian) in age (Lemberkovics *et al.* 2024). Littoral sediments are represented by lignite and mollusk coquinas, while sublittoral ones by sandy silts or clay marls. A radiometric age constraint is available for Abaliget, where a dacite tuff layer just a few meters above the sample yielded an age of 16.8 ± 0.65 Ma (Sebe *et al.* 2019).

Material and methods

Material was acquired during field campaigns in 2017, 2018, 2021, 2022, 2023, and 2024 at six localities (Tab. 1). At each site, 10–15 kg of sediment samples were collected and wet-sieved through a 0.5 mm or 1 mm sieve. Larger mollusks were hand-picked in the field. In case it was necessary, impregnation with cyanoacrylate was applied. Samples were also checked for micromammals (János Hír), but none were detected.

The material is primarily stored at the Bavarian State Collections of Natural History, Bavarian State Collection for Palaeontology and Geology, Munich (SNSB-BSPG, coll. no. 2025 IX 1–80) and the Geological-Paleontological Department of the Natural History Museum Vienna (NHMW-GPA, coll. no. NHMW 2025/0246/0001–0043); paratypes of the new species are deposited in the Hungarian Natural History Museum, Budapest (HNHM, coll. no. PAL 2025.29.1.–PAL 2025.46.1.). We also studied comparative material at the Natural History Museum in Zagreb (NHMZ).

Photographs of the shells stored at the SNSB-BSPG were taken with a Keyence VHX-7100, using the stacking function, and a Phenom XL raster electron microscope (Thermo Fisher Scientific Inc.). For the electron microscopy, specimens were coated with gold using a Quorum Q150R S coater. Specimens stored at the NHMW-GPA were photographed with a Nikon D7000 16.2-megapixel digital single-lens reflex camera and an Axio Cam MRc5 mounted on a Zeiss Stereo Discovery V20 Modular Stereo Microscope.

The systematic arrangement follows Bouchet *et al.* (2017) for Gastropoda and Bouchet & Rocroi (2010) for Bivalvia, with recent updates as available via MolluscaBase eds (2025). Measurements are given as height × width for Gastropoda and length × height × width for Bivalvia, respectively. The chresonymy/synonymy lists include first descriptions, relevant taxonomic studies, works including illustrations, and those that specifically deal with material from Mecsek. For *Tinnyea lauraea*, extensive synonymies are avoided given that the species complex needs considerable revision. This work is registered in ZooBank under *https://zoobank.org/C7E20735-8E28-47CA-8950-236DE1E1D460.*

For the assessment of the biogeographic relationships of the Mecsek fauna, we compiled a dataset on selected Early–Middle Miocene mollusk faunas for comparison. The dataset includes well-known faunas of the Dinaride Lake System (Illyrian Region sensu Neubauer *et al.* 2015a), Serbian Lake System (SLS; Balkan Region), Peri-Paratethyan Region, and Central-West European Region. Comprehensive data on freshwater gastropod occurrences are available from previous publications (Neubauer *et al.* 2021, Neubauer & Georgopoulou 2021), which were updated following latest revisions (including the taxonomic decision made herein). Species occurrences of bivalves were assembled from the literature (Neumayr 1880; Živković 1893; Andrusov 1897; Brusina 1897, 1902; Gottschick 1921; Pavlović 1931, 1933; Kochansky-Devidé & Slišković 1978, 1981; Žagar-Sakač 1987, 1990; Dumurdzanov & Krstić 1999; Kókay 2006; Neubauer *et al.* 2011, 2013a, b, 2016c, 2020; Harzhauser *et al.* 2014a; Mandic *et al.* 2019b, 2020). Faunas extending over longer time periods were constrained stratigraphically: the fauna of the Bakony Mts. was limited to the middle Burdigalian–early Serravallian (Ottnangian–Badenian) portion; for lakes Metohia and Skopje, only the Middle Miocene parts were considered (compare Neubauer *et al.* 2015a). Taxa were finally checked against MolluscaBase (MolluscaBase 2025) to account for taxonomic and systematic revisions. *Nomina nuda*, *nomina dubia*, and *taxa inquirenda* were excluded from the analyses, as were uncertain identifications (cf., aff.). All analyses were carried out on the species level.

For the statistical evaluation, we used the statistical environment R v. 4.3.2 (R Core Team 2023) with the packages 'vegan' v. 2.6-4 (Oksanen *et al.* 2022) and 'betapart' v. 1.6 (Baselga & Orme 2012, Baselga *et al.* 2023). To compare the faunal inventories, we calculated beta diversity using the Jaccard distance. We focus here primarily on the turnover component of the distance metric, which is related to differences in species composition while disregarding differences in species numbers among faunas (Baselga 2010). Distances were then subjected to a hierarchical cluster analysis using UPGMA (unweighted pair group method with arithmetic mean) as agglomeration method.

The maps in Figures 1 and 14 were generated in ESRI ArcGIS Pro v. 3.5 using the World Shaded Relief basemap of ESRI (2009).

Systematic paleontology

Class Gastropoda Cuvier, 1795
Subclass Neritimorpha Golikov & Starobogatov, 1975
Order Cycloneritida Frýda, 1998
Superfamily Neritoidea Rafinesque, 1815
Family Neritidae Rafinesque, 1815
Subfamily Neritininae Poey, 1852

Genus *Theodoxus* Montfort, 1810

Type species. – *Theodoxus lutetianus* Montfort, 1810 [= *Theodoxus fluviatilis* (Linnaeus, 1758)]; by original designation. Recent, Europe.

Theodoxus sp.

Figure 2A–F

? 2012 *Theodoxus*. – Nagymarosy & Hámor, p. 166.

Material. – Four specimens from Máza (NHMW 2025/0246/0023–0024, NHMW 2025/0246/0040, SNSB-BSPG 2025 IX 1), 14 from Szászvár 1 (NHMW 2025/0246/0004, NHMW 2025/0246/0006, NHMW 2025/0246/0013).

Dimensions. – 5.49 × 4.43 mm (SNSB-BSPG 2025 IX 1; Fig. 2A–C); 8.54 × 8.01 mm (NHMW 2025/0246/0040; Fig. 2D).

Remarks. – Our material contains only few, poorly preserved specimens of once probably globular shells with depressed apex, weak subsutural bulge (although this might be the result of compression), and broad but apparently non-denticulate callus. Some specimens indicate a weak, blunt angulation near the upper suture (Fig. 2A–D), but this may be the result of preservation. The shells have a brownish coloration, sometimes as solid color, sometimes as thin, wavy, vertical lines, interspersed with white spots of variable size and density.

The poor preservation of the material complicates taxonomic identification of this species. The color pattern with white spots on dark ground (Fig. 2D) also occurs in one syntype of *Theodoxus barakovici* (Brusina, 1902), described from the earliest Middle Miocene of Dugo Selo Lasinjsko (Brusina 1902, pl. 14, fig. 69). However, this species is characterized by an elliptical shell with low to depressed spire and broad, but weakly serrated callus (observed on other syntype material stored at NHMZ). Most shells seem to have spirally arranged color bands though (Brusina 1902).

Specimens from the Lower Badenian of the Bakony Mts. identified by Kókay (2006, pl. 2, figs 1–6) as *Theodoxus barakovici* (Brusina, 1902) closely resemble our specimens in terms of the globular shell, the smooth callus, and (in part) the color pattern. In one specimen, the apex is slightly higher (pl. 2, fig. 2), and generally the coloration patterns seem more variable, including also solid-colored and vertically striped ones. Also some Badenian specimens of *Theodoxus grateloupianus* (Férussac, 1823) *sensu* Kókay (2006, pl. 1, figs 1, 2) are similar, but the Bakony shells are more elongate.

A similar color pattern as in the Mecsek material is also found in some specimens of the Early–Middle Miocene Molasse Basin species *Theodoxus cyrtocelis* (Krauss, 1852), showing white spots on a background of densely arranged brown axial lines (Salvador *et al.* 2016b). The species also has a depressed spire and an obtuse angulation, but the aperture is very broad, leading to a generally broader shape, and the callus is serrated. *Theodoxus obtusangula* (Krauss, 1852) from the same region has a similarly globular shape but an elevated spire. The widely distributed Miocene species *Theodoxus crenulatus* (Klein, 1853) also has a denticulate callus, a more elliptical shell, and a smaller spire.

More and better-preserved material is required to uncover the identity of the species.

Subclass Caenogastropoda Cox, 1960
Caenogastropoda *incertae sedis*
Superfamily Cerithioidea Fleming, 1822
Family Melanopsidae Adams & Adams, 1854

Genus *Melanopsis* Férussac, 1807 *in* Férussac & Férussac (1807)

Type species. – *Melania costata* Olivier, 1804; by subsequent designation by Gray (1847, p. 153). Recent, Syria.

Remarks. – We identified two species of melanopsids, which are differentiated based on sculptural elements in later ontogeny. A large part of the material consists of fragmented apices, which cannot be unequivocally assigned to either species. These are listed in the material list in the Results and Discussion chapter but not for any of the species below.

Melanopsis sp. 1

Figure 2I–L, N–R

Material. – Twelve specimens from Máza (NHMW 2025/0246/0019–0022, NHMW 2025/0246/0041, SNSB-BSPG 2025 IX 2–3).

Dimensions. – 11.53 × 5.91 mm (NHMW 2025/0246/0019; Fig. 2I, J); 10.98 × 4.81 mm (NHMW 2025/0246/0021; Fig. 2N, O); 8.61 × 4.76 mm (SNSB-BSPG 2025 IX 2; width probably biased by compression; Fig. 2P–R).

Remarks. – The preservation of the available material does not allow a straightforward identification. The few complete or nearly complete specimens indicate a comparatively slender shell with conical to weakly coeloconoid spire and two rows of knobs below the suture on the last or last two whorls. Typically, the lower row of knobs is stronger. The expression of the knobs varies from delicate and subtle (Fig. 2K, L, N, O) to broad and bulky (Fig. 2I, J, P–R). Sometimes knobs may be vertically aligned, creating the impression of axial sculpture (Fig. 2P, R).

Shape-wise the species resembles *Melanopsis lanzaeana* Brusina, 1874 from the Middle Miocene of the Sinj Basin. *Melanopsis lanzaeana* morphotype B *sensu* Neubauer *et al.* (2011) also bears weak ornamentation in the form of broad, axially slightly elongated knobs. The two rows of circular, small nodules of *Melanopsis* sp. 1 rather remind of *Melanopsis astrapaea* Brusina, 1876, co-occurring with *M. lanzaeana* in the Sinj Basin. That species, however, has additional distinct, axial ribs. A third form from Sinj, *Melanopsis bicoronata* Brusina, 1884, has a similar shape and two rows of nodules too, but the rows appear more crest-like (hence the name). *Melanopsis camptogramma* Brusina, 1876, yet another species described from the Sinj Basin, shares the general morphology but lacks sculpture. Moreover, it shows a weak bulge at the inner lip, which is not detected in the material from Mecsek.

The slender shape further reminds of *Melanopsis praemorsa* sensu Brusina, 1897 (= *M. spiridioni* Pallary, 1916) and *M. sostarici* Brusina, 1902 from Dugo Selo Lasinjsko, but both species are much larger and lack any sculpture.

***Melanopsis* sp. 2**
Figure 2G, H, M

Material. – Six specimens from Máza (NHMW 2025/0246/0016–0018, NHMW 2025/0246/0032).

Dimensions. – 9.71 × 6.05 mm (NHMW 2025/0246/0016; Fig. 2G); 11.76 × 5.70 mm (NHMW 2025/0246/0032; Fig. 2H); 8.10 × 3.91 mm (NHMW 2025/0246/0017; Fig. 2M).

Remarks. – The second species differs from *Melanopsis* sp. 1 in being distinctly broader, with a large, bulbous last whorl, but devoid of sculpture. It also shows a comparatively thick callus on the inner lip near the adapical tip, a feature common for many melanopsid species.

The morphologically closest species seems to be the Molasse Basin species *Melanopsis kleinii* Kurr, 1856. Its shell is also smooth, has a weakly coeloconoid spire, and a distinct callus on inner lip. However, it typically has a slightly more slender shell with slightly higher spire (Locard 1893, Höltke *et al.* 2018). Also close is *Melanopsis camptogramma* Brusina, 1876 from the Sinj Basin, which has a more deltoid shell with more convex whorls. It also has a weak bulge on the central part of the inner lip, which is not visible (due to preservation) on our material. The DLS species *Melanopsis lanzaeana* Brusina, 1874 has a higher last whorl and a generally more elongate shell. *Melanopsis impressa* Krauss, 1852, a common species in the late Early to early Late Miocene in the Central Paratethys and Pannonian Basin System is more slender, with an even higher last whorl, shorter spire, and a flattened whorl flank (Salvador *et al.* 2016a).

More well-preserved material is required to study this species in detail.

Family Pachychilidae Fischer & Crosse, 1892

Genus *Tinnyea* Hantken, 1887

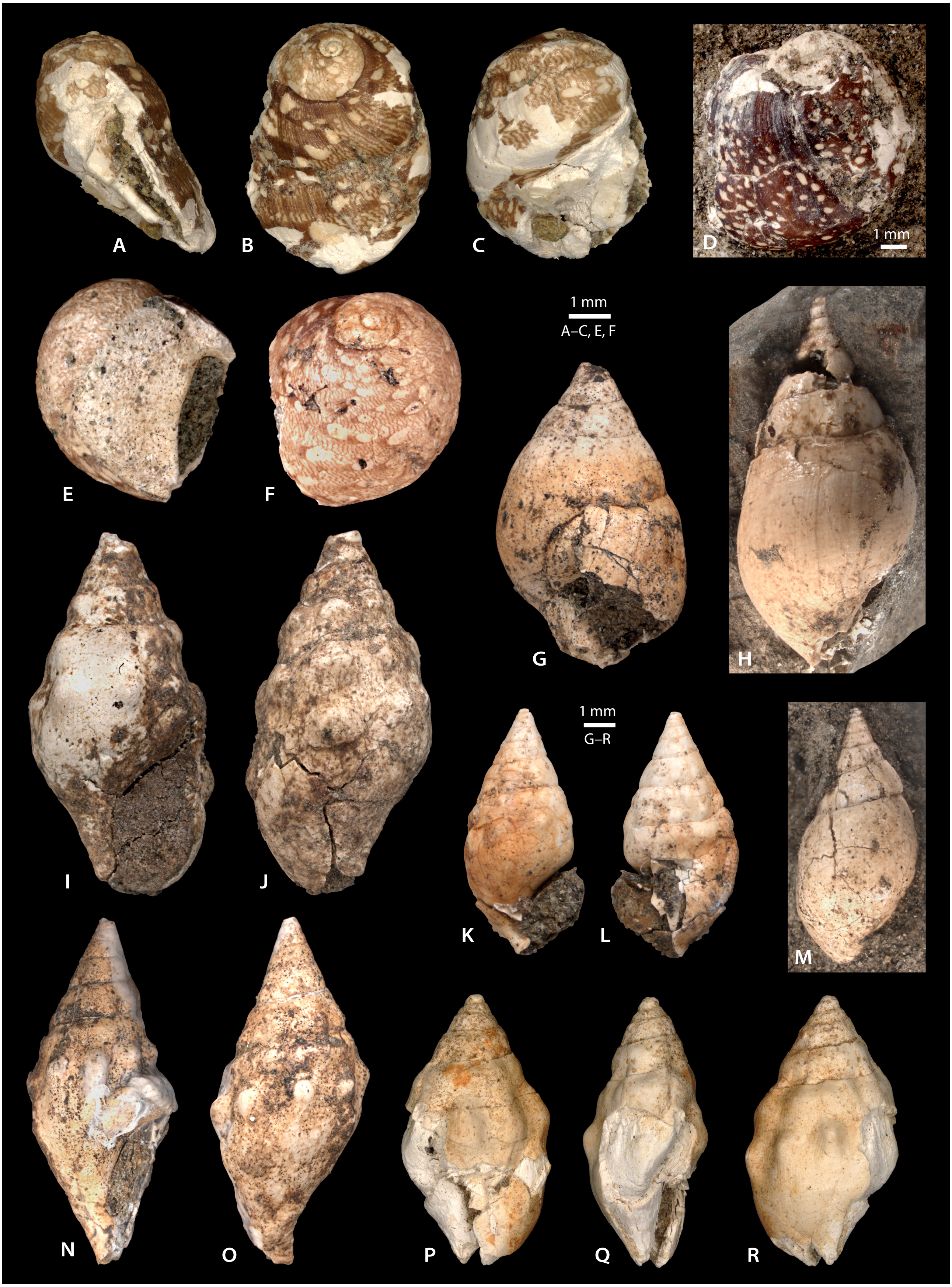
Type species. – *Tinnyea vasarhelyii* Hantken, 1887; by monotypy. Late Miocene, Hungary.

***Tinnyea lauraea* (Matheron, 1843)**
Figure 3A–H

*1843 *Melania lauraea*, Math.; Matheron, p. 291, pl. 36, figs 23, 24.
1880 *Melania Pilari* n. f.; Neumayr, p. 481.
1883 *Melania Verbasensis* nov. form.; Neumayr, p. 41, pl. 1, fig. 10.
1902 *Melania Pilari* Neum. – Brusina, p. 7, pl. 5, fig. 5.
1902 *Melania verbasensis* Neum. – Brusina, p. 7, pl. 5, figs 1–4.
1929 *Brotia escheri pilari* (Neumayr). – Wenz, p. 2596.
1929 *Brotia escheri verbasensis* (Neumayr). – Wenz, p. 2601.
? 2012 *Brotia*. – Nagymarosy & Hámor, p. 166.
2016a *Tinnyea* sp. – Neubauer *et al.*, p. 281.
2019b *Tinnyea pilari* (Neumayr, 1880). – Mandic *et al.*, p. 207.

Material. – Seventy-three specimens: 71 incomplete specimens or fragments (NHMW 2025/0246/0026, NHMW 2025/0246/0031, NHMW 2025/0246/0033–

Figure 2. Neritidae and Melanopsidae from the Mecsek Mts. • A–F – *Theodoxus* sp., from Máza; A–C – SNSB-BSPG 2025 IX 1; D – NHMW 2025/0246/0040; E, F – NHMW 2025/0246/0023. • G, H, M – *Melanopsis* sp. 2, from Máza; G – NHMW 2025/0246/0016; H – NHMW 2025/0246/0032; M – NHMW 2025/0246/0017. • I–L, N–Q – *Melanopsis* sp. 1, from Máza; I, J – NHMW 2025/0246/0019; K, L – NHMW 2025/0246/0020; N, O – NHMW 2025/0246/0021; P, Q – SNSB-BSPG 2025 IX 2.


A
B
C
D
1 mm
1 mm
A–C, E, F
E
F
G
H
I
J
1 mm
G–R
K
L
M
N
O
P
Q
R

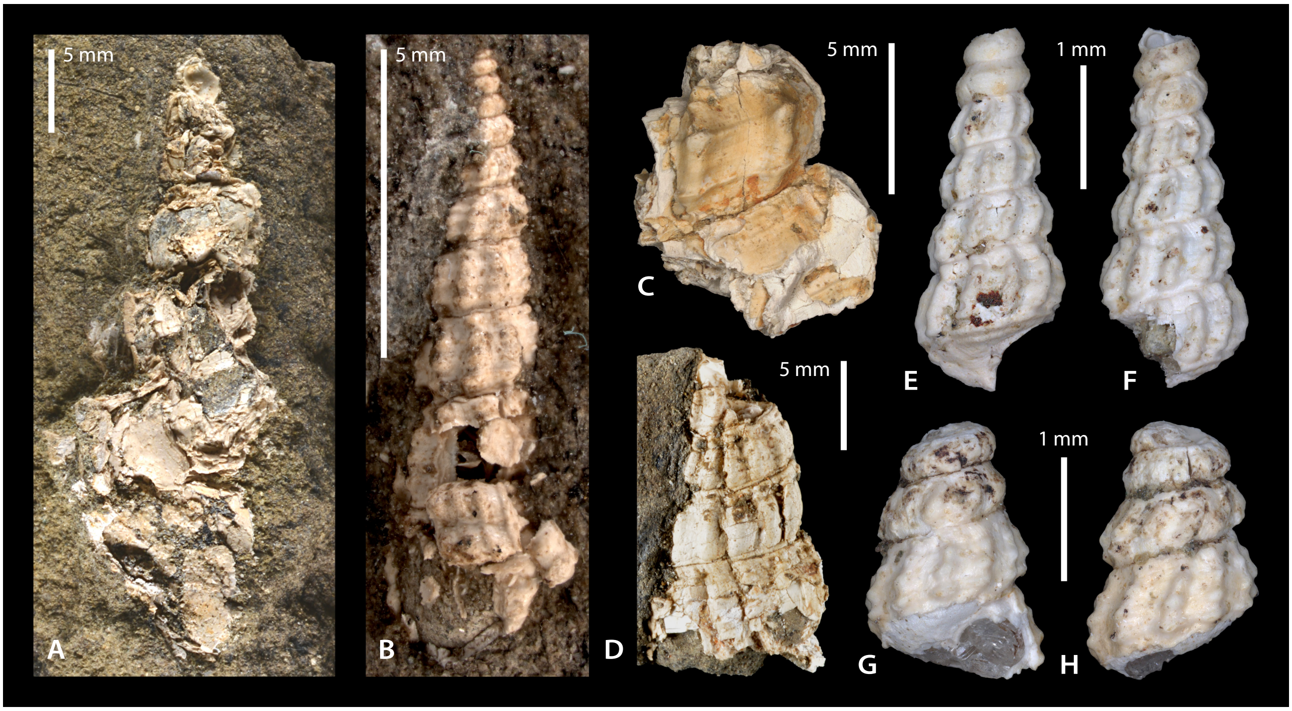


Figure 3. *Tinnyea lauraea* (Matheron, 1843) (Pachychilidae) from the Mecsek Mts. A – NHMW 2025/0246/0014, from Szászvár 1. B – NHMW 2025/0246/0033, from Máza. C – fragment of whorl showing spiky sculpture of the *pilari*-type, SNSB-BSPG 2025 IX 5, from Máza. D – apical fragment, NHMW 2025/0246/0015, from Szászvár 1. E, F – apical fragment, SNSB-BSPG 2025 IX 6, from Máza. G, H – apical fragment, SNSB-BSPG 2025 IX 7, from Máza.

0034, NHMW 2025/0246/0039, NHMW 2025/0246/0042, SNSB-BSPG 2025 IX 5–9) from Máza, 2 specimens from Szászvár 1 (NHMW 2025/0246/0014–0015).

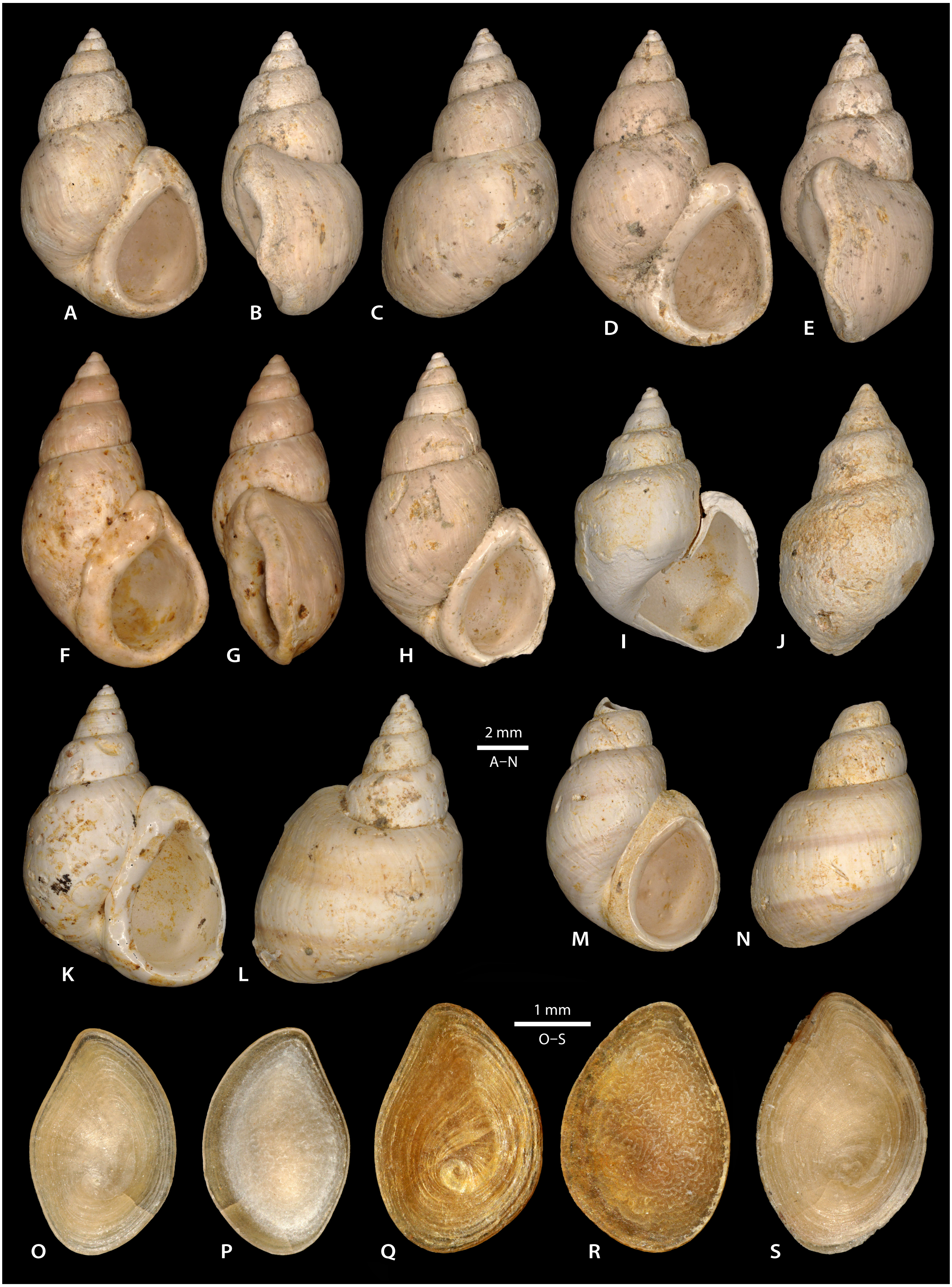
Dimensions. – The mostly poor preservation of the material complicates taking measurements. The largest specimen measures approximately 37 × 14 mm (NHMW 2025/0246/0014; Fig. 3A).

Remarks. – *Tinnyea lauraea* (Matheron, 1843) is an extremely variable species for which many names have been introduced in the literature. Most have been differentiated based on the type of ornamentation, sometimes featuring spiral crests of spikes or nodes, sometimes axial ribs, sometimes a combination thereof in various strength and expression; even nearly smooth forms only bearing spiral grooves have been found (“*Brotia*” *escheri inornata* Wenz, 1932 from the early Serravallian/late Badenian of Hidas in the Mecsek Mts.).

From DLS deposits, Neumayr (1880, 1883) and Brusina (1902) distinguished two species, both described from lower Middle Miocene strata – “*Melania*” *pilari* Neumayr, 1880 from Dugo Selo Lasinjsko (Croatia) and “*Melania*” *verbasensis* Neumayr, 1883 from Banja Luka (Bosnia-Herzegovina) (see also Neubauer *et al.* 2016b). “*Melania*” *verbasensis* is characterized by a dense spiral sculpture crossed by axial ribs (Neumayr 1883). Brusina (1902) also considered shells where the axial ribs form small spikes near the upper suture to belong to that species, which Neumayr (1883) treated as transitional form between both species. “*Melania*” *pilari* has fewer ribs bearing strong spikes, whereas the spikes are occasionally weakly connected spirally. The early ontogenetic whorls of both species are indistinguishable, showing the weakly inclined axial ribs crossed by spiral threads we also find in our material.

Several studies have shown that differences in sculpture are, however, not diagnostic for they are too variable even within populations (*e.g.*, Harzhauser *et al.* 2002,

Figure 4. *Ferebithynia vadaszi* (Wenz, 1931) (Bithyniidae) from the Mecsek Mts. A–C – SNSB-BSPG 2025 IX 10, from Feked 1. D, E – SNSB-BSPG 2025 IX 11, from Feked 1. F, G – SNSB-BSPG 2025 IX 12, from Feked 1. H – SNSB-BSPG 2025 IX 13, from Feked 1. I – specimen with stepped architecture and weak mid-whorl concavity (*tylopomoides*-type), SNSB-BSPG 2025 IX 14, from Himesháza. J – SNSB-BSPG 2025 IX 15, from Himesháza. K, L – specimen with laterally flattened body whorl and color pattern, SNSB-BSPG 2025 IX 16, from Himesháza. M, N – specimen with color pattern, SNSB-BSPG 2025 IX 17, from Himesháza. O, P – operculum, SNSB-BSPG 2025 IX 18, from Máza. Q, R – operculum, SNSB-BSPG 2025 IX 19, from Máza. S – operculum, SNSB-BSPG 2025 IX 20, from Máza.


A
B
C
D
E
F
G
H
I
J
K
L
2 mm
A–N
M
N
1 mm
O–S
O
P
Q
R
S

Kowalke 2004). We follow Harzhauser *et al.* (2002) and treat the Middle Miocene DLS "species" as phenotypes of a single polymorphic species. Already Mandic *et al.* (2019b) had suggested to treat *verbasensis* as a phenotype of *pilari*.

Note that the species lineage is usually referred to as "*escheri*"-lineage in the older literature, but as pointed out by Kowalke (2004) that name is based on a *nomen nudum* in Cuvier & Brongniart (1822) and the earliest available name for the species group is *Melania lauraea* Matheron, 1843. The species was originally described from the Oligocene of southern France.

Our material contains both the *verbasensis*-phenotype with axially dominated sculpture (Fig. 3B, D) and the *pilari*-phenotype with widely spaced spikes (Fig. 3C). We do not aim at a full revision of the species group; therefore, we include in the synonymy list, aside from the original description of *T. lauraea*, only records that refer to the two phenotypes.

Melanoides procurvicosta Kókay, 2006 from the Badenian of the Bakony Mts. shows a similar type of primarily axial sculpture crossed by spiral lines but no distinct subsutural spiral crest; the species is probably a synonym as well. Note that Kókay (2006) used two spellings, *procurvicosta* in the plate captions and *procurvirostra* in the species description. He referred it as the precursor to "*Melanoides curvirostra* (Deshayes)", which is however a misspelling of *M. curvicosta* (Deshayes, 1835). Accordingly, the correct spelling must be *procurvicosta*.

The Pannonian *Tinnyea lauraea* phenotype *vasarhelyii* Hantken, 1887 *sensu* Harzhauser *et al.* (2002) shows a very similar architecture in early ontogeny but typically much stronger spikes in adulthood, although a slender type with small or even absent spines exists in lower Pannonian strata as well (Harzhauser *et al.* 2002).

Occurrence. – The species lineage originated during the Oligocene, potentially even the latest Eocene, in central Europe (Hungary, Bavaria, Slovenia) and persisted into at least the Late Miocene, when it was widely distributed in the Pannonian Basin System (Austria, Croatia, Czech Republic, Hungary, Romania, Serbia) and also occurred in Italy, Greece, and Turkey (Wenz 1923, Chaput & Gillet 1939, Wenz 1942b, Kühn 1963, Strausz 1966, Gillet *et al.* 1978, Harzhauser *et al.* 2002). The Middle Miocene DLS phenotypes were reported from the Banja Luka, Tešanj, Glina, and Požega (*e.g.*, Gradište) basins, as well as from Bidrovec on Mt. Medvednica near Zagreb. Wenz (1929) additionally listed *pilari* from Upper Miocene strata of the Sarajevo Basin and Lake Pannon. Considering the lack of a proper revision of the group, the list of occurrences may need revision. The Mecsek specimens studied by us were retrieved at Máza.

Order Littorinimorpha Golikov & Starobogatov, 1975
Superfamily Truncatelloidea Gray, 1840
Family Bithyniidae Gray, 1857 *in* Turton (1857)

Genus *Ferebithynia* Kókay, 2006

Type species. – *Bulimus vadaszi* Wenz, 1931; by original designation. Miocene, Hungary.

Ferebithynia vadaszi (Wenz, 1931)

Figures 4A–S, 5A–F

*1931	*Bulimus vadászi vadászi*; Wenz, p. 118, pl. 10, fig. 2a–c.
*1931	*Bulimus vadászi tylopomoides*; Wenz, p. 120. [*nov. syn.*]
1966	*Bithynia vadászi* Wenz. – Strausz, p. 66, pl. 47, figs 17, 18.
1967	*Bulimus vadászi* Wenz. – Kókay, p. 85, pl. 9, figs 1–6.
2006	*Ferebithynia vadaszi* (Wenz), 1931. – Kókay, p. 40, pl. 10, figs 1–7.
2013	*Ferebithinia* [sic] *vadaszi* (Wenz). – Kókay, p. 151.
2019	*Ferebithynia* (*Bulimus*) *vadászi*. – Sebe *et al.*, p. 89, fig. 4c.
? 2019	*Stagnicola*? sp. – Sebe *et al.*, p. 89.

Material. – 426 shells and > 2200 opercula: 45 opercula from Abaliget (SNSB-BSPG 2025 IX 25), 214 shells (mostly apices and juvenile shells) and 311 opercula (SNSB-BSPG 2025 IX 21, SNSB-BSPG 2025 IX 26–28) from Feked 1, 18 shells and 83 opercula from Feked 2 (SNSB-BSPG 2025 IX 29), 153 shells (22 large to medium ones, otherwise juvenile shells and apices) and 265 opercula from Himesháza (SNSB-BSPG 2025 IX 14–17, SNSB-BSPG 2025 IX 22–24, SNSB-BSPG 2025 IX 30–31), 41 shells (mostly apices of probable attribution and fragments) and > 1000 opercula from Máza (NHMW 2025/0246/0036, SNSB-BSPG 2025 IX 18–20, SNSB-BSPG 2025 IX 32–35), > 500 opercula from Szászvár 1 (NHMW 2025/0246/0002, NHMW 2025/0246/0005, NHMW 2025/0246/0012, SNSB-BSPG 2025 IX 36), 47 opercula from Szászvár 2 (SNSB-BSPG 2025 IX 37), 2 opercula from Apátvarasd (SNSB-BSPG 2025 IX 38).

Description. – Sturdy, slender, weakly cyrtoconoid shell of more than 12 mm in height and up to 6 whorls. Protoconch includes slightly more than 1 whorl, but transition to teleoconch is barely visible in most shells. Diameter first whorl variable, measuring between 590 μm (Fig. 5D) and 720 μm (Fig. 5E). Teleoconch whorls convex, slightly flattened centrally; high convexity near sutures creates slightly stepped appearance. Rarely, stouter shells occur with strongly stepped architecture and more pronounced convexity, accompanied by a faint mid-whorl concavity (Fig. 4I; intermediate form: 4K, L). Early teleoconch

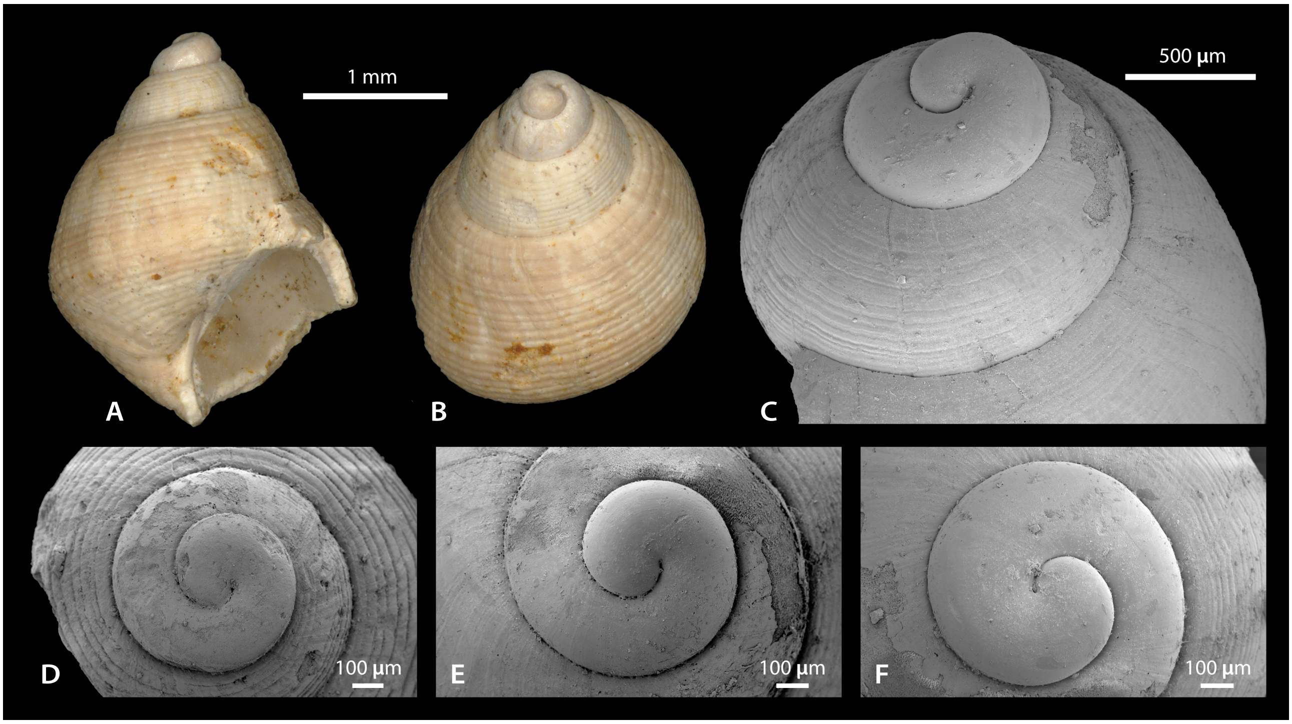


Figure 5. *Ferebithynia vadaszi* (Wenz, 1931) (Bithyniidae) from the Mecsek Mts. A, B – juvenile specimen, showing dense striation, SNSB-BSPG 2025 IX 21, from Feked 1. C, F – juvenile specimen, with smooth protoconch but densely striated teleoconch, SNSB-BSPG 2025 IX 22, from Himesháza. D – protoconch, SNSB-BSPG 2025 IX 23, from Himesháza. E – protoconch, SNSB-BSPG 2025 IX 24, from Himesháza.

whorls bear ornamentation of numerous, densely spaced spiral furrows, which fade out around 3rd to 4th teleoconch whorl. Last whorl attains 66–68% of total shell height. Base weakly convex; *c.* 45° in slender phenotype, distinctly shallower in stepped phenotype. Aperture broadly drop-shaped; peristome massively thickened, especially at apical tip and inner lip; thickening extends on base of penultimate whorl and mostly covers umbilicus, which remains visible in some shells as narrow slit. Some shells show thin apical canal (Fig. 4F, G). Peristome expanded laterally and apically, which is particularly visible in lateral view (Fig. 4B, E, G); outer lip sinuate, double-S shaped in lateral view. Few shells have color pattern preserved, consisting of brown spiral bands of various width (Fig. 4K–N). Operculum classically bithynoid in shape, with external side bearing concentric lamellae originating from subcentral, spiral nucleus (Fig. 4O, Q, S); internal side nearly smooth or with labyrinth-like pattern (Fig. 4P, R).

Dimensions. – Shells: 11.36 × 7.30 mm (SNSB-BSPG 2025 IX 10; Fig. 4A–C); 12.38 × 7.91 mm (SNSB-BSPG 2025 IX 11; Fig. 4D, E); 12.36 × 7.36 mm (SNSB-BSPG 2025 IX 12; Fig. 4F, G); 2.33 × 7.44 mm (SNSB-BSPG 2025 IX 13; Fig. 4H); 10.64 × 6.07 mm (SNSB-BSPG 2025 IX 15; Fig. 4J); 11.81 × 7.94 mm (SNSB-BSPG 2025 IX 16; Fig. 4K, L).

Opercula: 3.30 × 2.23 mm (SNSB-BSPG 2025 IX 19; Fig. 4Q, R); 3.45 × 2.26 mm (SNSB-BSPG 2025 IX 20; Fig. 4S); 2.99 × 1.94 mm (SNSB-BSPG 2025 IX 18; Fig. 4O, P).

Remarks. – *Ferebithynia vadaszi* is the only species in the genus *Ferebithynia*, which was introduced by Kókay (2006) to distinguish it from *Bithynia* because of the spiral sculpture, the thickened peristome, and the operculum having an eccentrically placed nucleus and spiral growth lines. We cannot confirm the spiral growth lines on the opercula but, like Wenz (1931), find them to be concentric. However, the thickened and expanded peristome and the spiral sculpture are indeed atypical for *Bithynia* and justify in our opinion the placement in a distinct genus.

Wenz (1931) originally distinguished forms with a stronger spiral striation that extends on all whorls (albeit being still finer on the last whorl) and with whorls showing a central concavity bounded by two spiral bulges as a distinct subspecies, *Bulimus vadaszi tylopomoides*. We found one specimen showing the central concavity, but the shell is incomplete and its surface too poorly preserved to detect any spiral striation on later whorls (Fig. 4I). Also, transitional forms with flattened but not convex whorls exist (Fig. 4K, L). Given the rather high morphological plasticity of the species in general we consider this as intraspecific variation and *tylopomoides* as a subjective synonym of *F. vadaszi*.

Specimens identified as *Stagnicola*? sp. by Sebe *et al.* (2019) probably represent *Ferebithynia vadaszi* as well.

Occurrence. – Reported from Karpatian–lower Badenian strata at several localities in the Mecsek Mts. (Geresd, *i.e.*, the type locality, Kisbeszterce, Feked, Komló) and the Badenian of the Bakony Mts. (Várpalota, Berhida) by Wenz (1931) and Kókay (2006, 2013). Here, the Mecsek localities Abaliget, Himesháza, Máza, Szászvár, and Apátvarasd are added to the list.

Family Hydrobiidae Stimpson, 1865

Genus *Pyrgula* De Cristofori & Jan, 1832

Type species. – *Turbo annulatus* Linnaeus, 1758; by monotypy. Recent, Italy.

Pyrgula sopianae Neubauer sp. nov.

Figure 6A–J

LSID. – urn:lsid:zoobank.org:act:E860BBA8-0657-42F4-BEF8-68EC224F9B6B

Type material. – Holotype: SNSB-BSPG 2025 IX 39 (Fig. 6C–E). Paratypes: HNHM PAL 2025.29.1. (Fig. 6A), SNSB-BSPG 2025 IX 40 (Fig. 6B), HNHM PAL 2025.30.1. (Fig. 6F), SNSB-BSPG 2025 IX 41 (Fig. 6G–I), SNSB-BSPG 2025 IX 43 (Fig. 6K), HNHM PAL 2025.31.1., HNHM PAL 2025.32.1., HNHM PAL 2025.33.1.

Type horizon and locality. – Lacustrine delta deposits at top of Szászvár Formation; upper Burdigalian/Karpatian or lower Badenian/Langhian (underlying tuff was dated 17.055 ± 0.024 Ma; Harangi & Lukács 2019). Máza, Dóra-irtás, Mecsek Mts., Baranya county, southern Hungary (46.25261° N, 18.3886° E, WGS84).

Additional material. – Forty-four specimens from Máza, including 2 shells embedded in sediment and a few fragments (SNSB-BSPG 2025 IX 42, SNSB-BSPG 2025 IX 44–45, SNSB-BSPG 2025 IX 47), 1 from Szászvár 2 (SNSB-BSPG 2025 IX 46).

Etymology. – After Sopianae, the Roman name for the nearby city of Pécs. The name is a noun in apposition.

Diagnosis. – Small shell of up to ~ 2.9 mm in height, with conical to weakly cyrtoconoid spire and up to 4.5 whorls. Distinct keel appears on 2nd to 3rd teleoconch whorl near lower suture. Aperture narrowly ovoid, leaving slit-like umbilicus.

Description. – Small conical to weakly cyrtoconoid shell, consisting of up to 4.5 whorls. Protoconch low domical; extent unknown, boundary to teleoconch not visible; first whorl measures ~ 330 µm. On 2nd to 3rd teleoconch whorl distinct keel appears near lower suture. Keel sometimes broadly blunt, sometimes thinner or almost sharp and triangular. Whorl portion above weakly convex or straight. Last whorl ~ 62–66% of total height. Final shell portion slightly tapered, growing a bit more in abapical direction (Fig. 6E, H, K). Base of last whorl convex above, straight to faintly concave towards base of aperture. Aperture narrow ovoid, distinctly oblique, with line describing maximum diameter being inclined ~ 30° to columella. Umbilicus closed (clearly visible only in one small specimen, peristome not fully preserved in most specimens).

Dimensions. – 2.11 × 1.32 mm (holotype, SNSB-BSPG 2025 IX 39; Fig. 6C–E); 2.86 × 1.74 mm (paratype, HNHM PAL 2025.29.1.; Fig. 6A); 1.80 × 1.28 mm (paratype, HNHM PAL 2025.30.1.; base of aperture slightly damaged; Fig. 6F); 1.92 × 1.20 mm (paratype, SNSB-BSPG 2025 IX 41; base of aperture slightly damaged; Fig. 6G–I); 1.78 × 0.98 mm (paratype, SNSB-BSPG 2025 IX 43; Fig. 6K).

Remarks. – Despite the rather common morphology, only two species of similar age are known to us. The first concerns one of the syntypes of *Bythinella dokici* Brusina, 1902 (pl. 9, fig. 35) from Dugo Selo Lasinjsko in the Glina Basin (Croatia) (syntypes stored at NHMZ, coll. no. 2598-244/1-4). It is similarly small but has a broader, more ovoid shape, the last whorl is larger, and the keel is weaker and blunt. The species was tentatively placed in the genus *Bania* by Neubauer *et al.* (2013a). The second is *Pyrgula* cf. *dalmatina* Brusina, 1882 *sensu* Jurišić-Polšak *et al.* (1993) from the upper Burdigalian or lower Langhian of the Udbina Basin in Croatia, which differs in the more elongated shell with a median keel. The shells were probably misidentified considering that the species as described by Brusina (1882), from the lower Middle Miocene of the Drniš Basin, shows a much slenderer shell with spirally arranged nodules (Neubauer *et al.* 2016c).

We found no other species with a similar shell from Lower or lower Middle Miocene strata of Europe, but a number of forms from younger deposits. The early Sarmatian *Pyrgula soceni* Jekelius, 1944 from Soceni (Romania) has a larger and more elongate shell, already in early ontogeny. The species was considered a junior synonym of *Pyrgula eugeniae* (Neumayr, 1875) *in* Herbich & Neumayr (1875) by Roshka (1973), which seems unlikely considering that *P. eugeniae* was described from Pliocene strata. *Pyrgula eugeniae* does have a similar shape, but it is much larger, has more whorls, and the last whorl is tapered (Wenz 1942a). The Late Miocene (Maeotian) *Pontohydrobia kelterborni* (Wenz, 1927) *in* Krejci & Wenz (1927) has a similarly shaped top part but

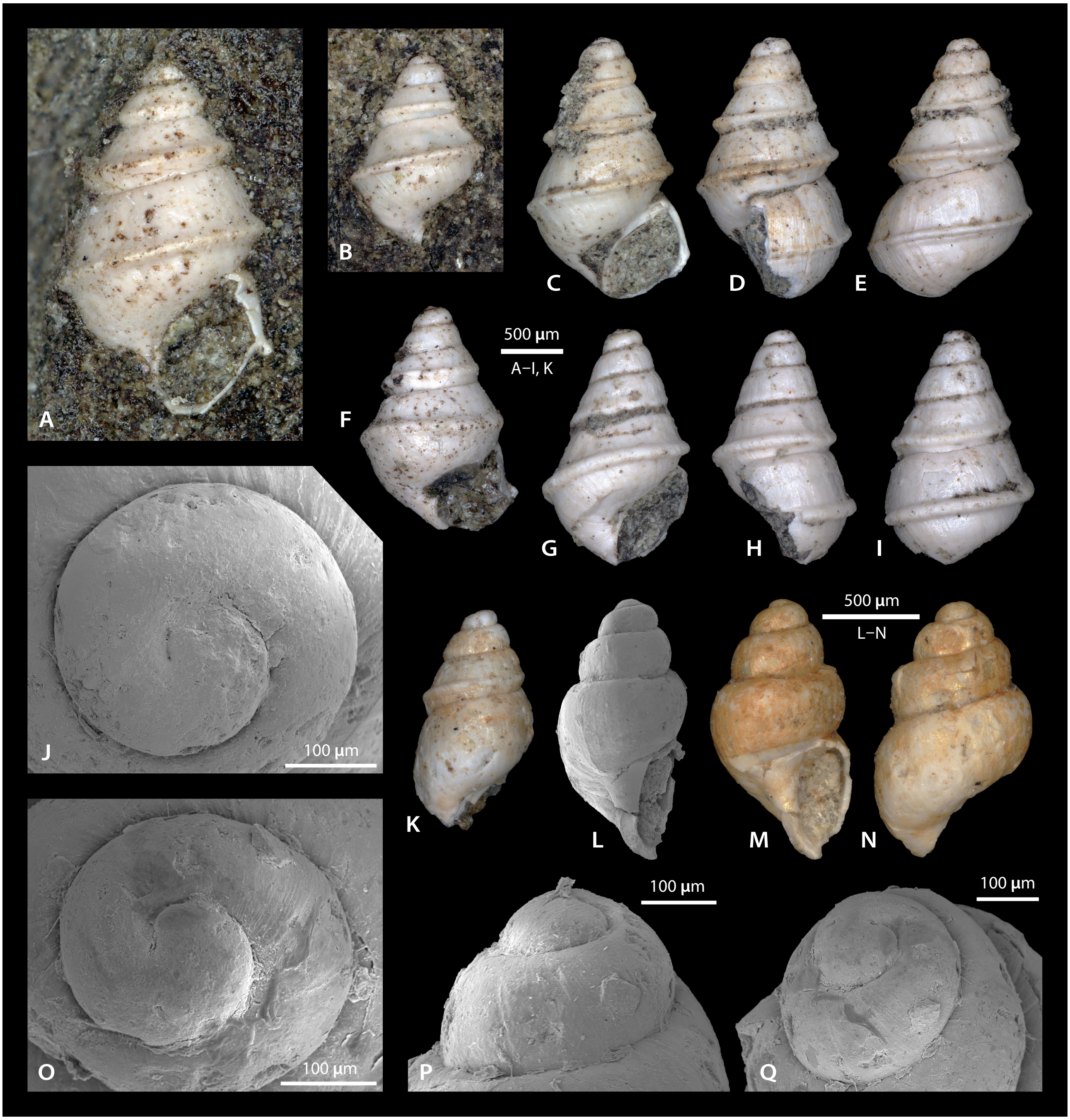


Figure 6. Hydrobiidae from the Mecsek Mts. • A–K – *Pyrgula sopianae* sp. nov., from Máza; A – paratype, HNHM PAL 2025.29.1.; B – paratype, SNSB-BSPG 2025 IX 40; C–E – holotype, SNSB-BSPG 2025 IX 39; F – paratype, HNHM PAL 2025.30.1.; G–I – paratype, SNSB-BSPG 2025 IX 41; J – SNSB-BSPG 2025 IX 42; K – paratype, SNSB-BSPG 2025 IX 43. • L–Q – *Bania*? sp. SNSB-BSPG 2025 IX 48, from Máza.

more whorls, and the shell is generally larger (see also Wenz 1942a).

Pyrgula laminatocarinata (Andrusov, 1890) from the Maeotian of the Crimean Peninsula shows a similarly, conical shell with nearly basal keel, but the keel starts earlier and is sharper, and the shell is broader. Note that Iljina *et al.* (1976, p. 104) synonymized that species with *Turricaspia carinata* (Andrusov, 1890) described from the same region and time interval. Typical *T. carinata* are more elongate and slender and often have additional spiral lirae below the keel. *Pontohydrobia striatocarinata* (Andrusov, 1890), again from the same deposits and region, also has a similar, conical shape and a basal keel, but also in that species the keel is sharper. In addition, the whorl portion above the keel is straight and the aperture is rounder (see also Iljina *et al.* 1976, Badzoshvili 1979).

Finally, the co-occurring *Pontohydrobia panticapaea* (Andrusov, 1890) exposes a similarly broad keel, but it is placed higher, around mid-whorl, and the whole shell is more slender (Iljina *et al.* 1976, Badzoshvili 1979).

Pyrgula unicarinata Brusina, 1902 from the Late Miocene to Pliocene of Slavonia (Croatia) has a more elongate shell, and the keel is higher positioned. The Late Pliocene *Pyrgula nodotiana* Tournouër, 1866 from France has a similar, conical shape with basal keel, but the keel is sharper, the whorl portions above and below are straight, and the aperture is more rounded (Schlickum & Puisségur 1977). Other similar species have been described from Quaternary or extant shells of Turkey under the names *Falsipyrgula osmana* (Bukowski, 1930) and *Kirelia carinata* Radoman, 1973, but these are larger at approximately the same number of whorls (see also Neubauer & Wesselingh 2023).

Finally, *Pyrgula sopianae* sp. nov. also shows similarities to *Aenigmapyrgus martinsoni*, *A. steklovi*, and *A. subcarinatus*, all described by Popova & Starobogatov in Popova *et al.* (1970) from the Pliocene of the Chuya depression (Altay Mts., Russia). The shells show a similarly conical, albeit even more elongate shell, with a subcentrally to basally positioned keel of various strengths. In addition to the more elongate shape, these species are about twice as large as *Pyrgula sopianae* sp. nov. As a side remark, the taxonomic distinctness of the three *Aenigmapyrgus* species seems doubtful. They are part of a morphological series of eight co-occurring species ranging from smooth via weakly carinated to heavily keeled shells. In addition to the presence or absence of a keel, some of the species also differ in their general shell morphology; others seem fairly similar when comparing the drawings of Popova & Starobogatov. A thorough revision of the species flock is required to ascertain the taxonomic identities of the species involved.

Genus classification in fossil pyrguline hydrobiids is in a great need of a revision, there are numerous names for very similar morphologies. The type of small, conical shell with a keel shown by *Pyrgula sopianae* sp. nov. is common among several genera in Pyrgulinae. Most species with such a morphology have been classified in the dustbin genus *Pyrgula*, which is actually based on a recent type species (*P. annulata*) with slender ovoid shell and two sharp keels. Other genus names that have been proposed for similar types of morphologies include *Pontohydrobia* (Late Miocene–Early Pliocene; Badzoshvili 1979), *Turricaspia* (Late Miocene–recent) or any of its subgenera (*e.g.*, Roshka 1973, Iljina *et al.* 1976), *Falsipyrgula* (Pleistocene–Recent), and *Kirelia* (Recent). More elongate forms were occasionally placed in *Micromelania* (*e.g.*, Willmann 1981), a similarly problematic and ill-defined genus.

Given the uncertainty of the concepts of many previously introduced genera, the lack of sufficient criteria for differentiation, and the insufficient knowledge on the protoconch characteristics of the new species, we presently describe it within *Pyrgula* s.l.

Occurrence. – Only known from the Early Miocene of the Mecsek Mts. (Máza, Szászvár).

Genus *Bania* Brusina, 1896

Type species. – *Stalioa prototypica* Brusina, 1872; by monotypy. Middle Miocene, Croatia.

Bania? sp.

Figure 5L–Q

Material. – One specimen from sample Máza (SNSB-BSPG 2025 IX 48).

Dimensions. – 1.32 × 0.82 mm.

Remarks. – A single, poorly preserved shell of a hydrobiid species was detected. The slender, slightly ovoid shell comprises approximately 3.5 convex and slightly stepped whorls. The last whorl makes up about 70% of the total shell height. The aperture is broken but the available parts suggest a rather narrow elliptical form. No umbilicus is visible.

Concerning size and overall shape the shell reminds of several species of the genus *Bania* Brusina, 1896. *Bania goehlichae* Mandic, Harzhauser & Neubauer, 2020 from the Langhian of the Bugojno Basin (Bosnia and Herzegovina), *B. pauluccii* (Brusina, 1907) from the Sinj Basin (Croatia), and *B. valvatoides* (Brusina, 1874) from the Langhian of the Gacko (Bosnia and Herzegovina) and Drniš (Croatia) basins have similar sizes but much more globular shells, with larger last whorls and distinct umbilici (Neubauer *et al.* 2013b, 2016c; Mandic *et al.* 2020). *Bania pachychila* (Brusina, 1902) from the Langhian of Džepi in the Prozor Basin (Bosnia and Herzegovina), *B. stosiciana* (Brusina, 1874) and *B. torbariana* (Brusina, 1874) from the Drniš Basin, and *B. gobanzi* (Frauenfeld, 1864) from the Rein Basin all have broader and more conical shells (Harzhauser *et al.* 2014a; Neubauer *et al.* 2016b, c). *Bania globulina* (Kókay, 2006) from the Late Badenian (Serravallian) and *B. praeglobulina* (Kókay, 2006) from the Lower Miocene of the Bakony Mts. are both globular. The Oligocene–Early Miocene *B. helicella* (Braun, 1851) from the Mainz Basin (Germany), the Middle–Late Miocene *B. immutata* (Hörnes, 1856) from the Vienna Basin (Austria), and the Pannonian *B. hoeckae* (Harzhauser & Binder, 2004) from the same region have more slender shells than most of the other *Bania* species,

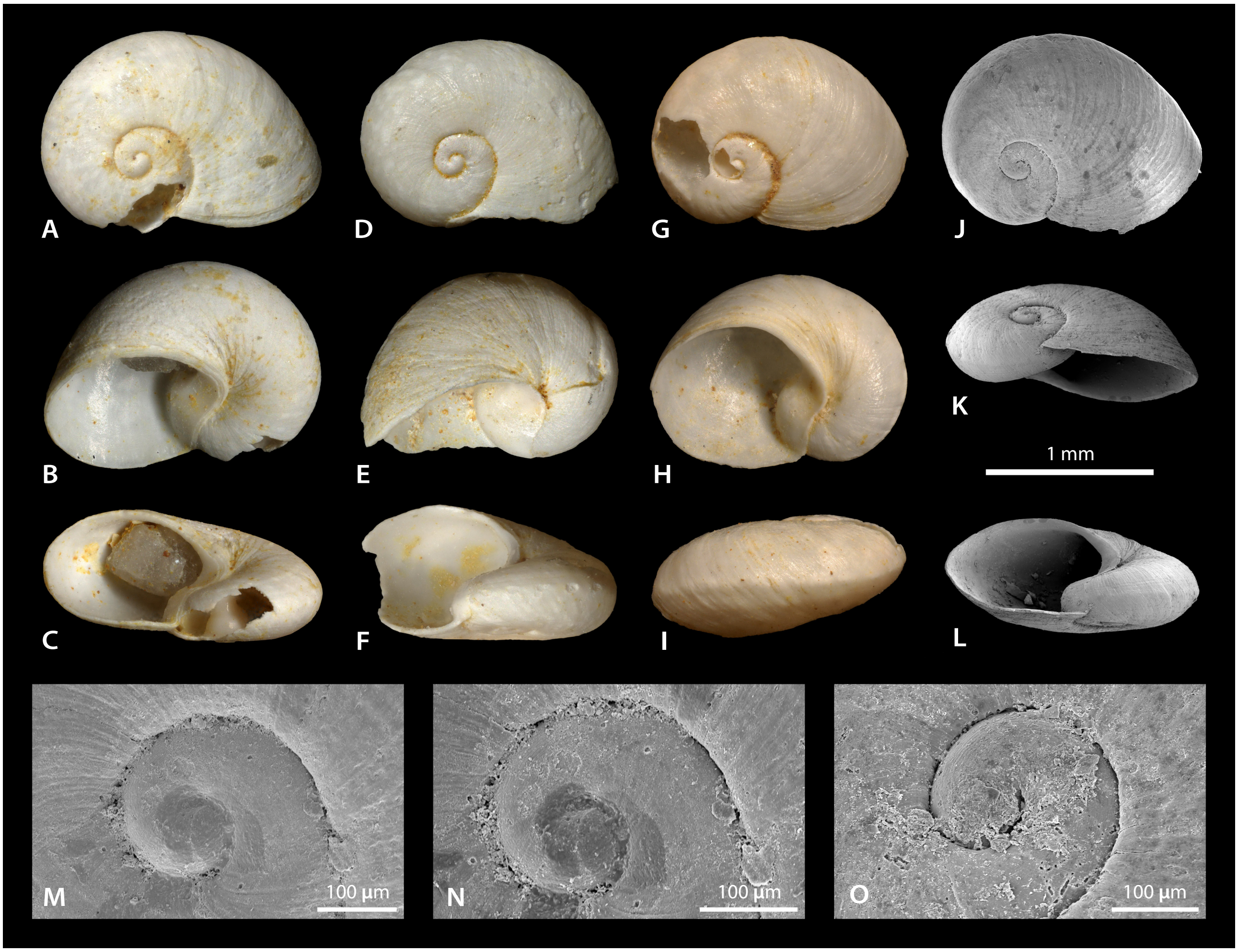


Figure 7. *Asymmetrorbis pseudovitrina* gen. et sp. nov. (Planorbidae) from the Mecsek Mts. A–C – holotype, SNSB-BSPG 2025 IX 49. D–F, M, N – paratype, SNSB-BSPG 2025 IX 50. G–I – paratype, HNHM PAL 2025.34.1. J–L, O – paratype, SNSB-BSPG 2025 IX 51. All specimens from Himesháza.

but they are still broader than our specimen from Mecsek; also, they are larger (Harzhauser & Binder 2004).

Generally, all *Bania* species seem to have an umbilicus, which is not observed in the Mecsek specimen, therefore we place the specimen in the genus only with uncertainty.

Clade Panpulmonata Jörger *et al.*, 2010
Order Hygrophila Férussac, 1822
Superfamily Lymnaeoidea Rafinesque, 1815
Family Planorbidae Rafinesque, 1815
Subfamily Planorbinae Rafinesque, 1815

Genus *Asymmetrorbis* Neubauer gen. nov.

LSID. – urn:lsid:zoobank.org:act:C805B05C-B088-4425-B782-03197AA23456

Type species. – *Asymmetrorbis pseudovitrina* Neubauer gen. et sp. nov. Only included species.

Etymology. – Name derived from the unusually asymmetric type of coiling and "orbis", meaning circle or disc in Ancient Greek, a common ending for many planorbid genera.

Diagnosis. – As for type species.

***Asymmetrorbis pseudovitrina* Neubauer sp. nov.**
Figure 7A–L

LSID. – urn:lsid:zoobank.org:act:68CC08CB-C3A4-44E1-ACCB-2134A7F22794

Type material. – Holotype: SNSB-BSPG 2025 IX 49 (Fig. 7A–C). Paratypes: SNSB-BSPG 2025 IX 50 (Fig. 7D–F, M, N), HNHM PAL 2025.34.1. (Fig. 7G–I), SNSB-BSPG 2025 IX 51 (Fig. 7J–L, O), HNHM PAL 2025.35.1., HNHM PAL 2025.36.1., HNHM PAL 2025.37.1., HNHM PAL 2025.38.1., SNSB-BSPG 2025 IX 52–54.

Type horizon and locality. – Mollusk coquina in littoral lacustrine deposits of the Pécsvárad Member (Kiskunhalas Formation); upper Burdigalian/lower Langhian (Karpatian/lower Badenian). Himesháza, Engesgraben, Mecsek Mts., Baranya county, southern Hungary (46.11506° N, 18.54811° E, WGS84).

Etymology. – Named for its superficial resemblance with terrestrial semi-slugs of the family Vitrinidae. The word is a noun in apposition.

Additional material. – One broken specimen (SNSB-BSPG 2025 IX 55).

Diagnosis. – Small, asymmetrically shaped, valvatiform shell with flattened umbilical side, weak keel at periphery, broadly expanded aperture that covers apex entirely, and striate ornament on both protoconch and teleoconch.

Description. – Shell small, less than 2 mm in maximum diameter, with up to ~ 2.25 whorls. Shell distinctly asymmetrical, creating pseudodextral, valvatiform shape. Umbilical side flattened to slightly convex, with immersed protoconch. Protoconch measures *c*. 0.8 whorls and 270–280 µm in maximum diameter; surface ornamented with numerous, narrowly arranged spiral threads; transition to teleoconch marked by weak growth rim. Teleoconch whorls rapidly expand in diameter as well as towards apex, producing a large, expanded aperture that fully covers apex. Last whorl well rounded or sometimes with traces of faint mid-whorl angulation. Teleoconch bears all around weak, shallow, spiral furrows of slightly irregular strength and arrangement.

Dimensions. – 0.83 × 1.68 mm (holotype, SNSB-BSPG 2025 IX 49; Fig. 7A–C); 0.86 × 1.61 mm (paratype, SNSB-BSPG 2025 IX 50; Fig. 7D–F, M, N); 0.74 × 1.54 mm (paratype, HNHM PAL 2025.34.1.; Fig. 7G–I); 0.75 × 1.56 mm (paratype, SNSB-BSPG 2025 IX 51; Fig. 7J–L, O).

Remarks. – The valvatiform shape of the new genus and the absence of an apex ("umbilicus") are rather untypical of the family Planorbidae. Its placement therein is based on the following characteristics: (i) the protoconch with a similar number of whorls and diameter and striate ornamentation known also for other planorbids (*e.g*., the co-occurring species of *Gyraulus*), although the striation seems more dense in the new genus than for species of *Gyraulus*; (ii) the planorbid-type shape of the umbilical ("top") side, with the characteristically curved apertural margin; (iii) the inclined, non-reflected aperture with an inner lip covering the penultimate whorl sheet-like.

A valvatiform shape is also known in other planorbid genera, *e.g*., in species of the genus *Choanomphalus* (*e.g*., Sitnikova 2019). However, we are unaware of any species or genus in the family where the aperture overgrows the apex as in the Mecsek species. Considering the unique combination of features, we feel the introduction of a new genus justified. Moreover, fossil representatives of *Choanomphalus* have so far been only reported from the Upper Cretaceous of the southern Nemegt Uul Basin in SE Mongolia (Martinson 1961), the Paleogene of Xinjiang, China (Guo & Wei 1984), and the Miocene of the Tankhoy region, eastern Baikal, Russia (Martinson 1951).

The new genus superficially resembles terrestrial semi-slugs of the families Vitrinidae and Oxychilidae (subfamily Daudebardiinae). However, the connected and slightly thickened inner lip is untypical for semi-slugs, as is the distinct spiral furrows present in *Asymmetrorbis pseudovitrina* gen. et sp. nov. (see also Schlickum & Strauch 1979; Welter-Schultes 2012; Salvador *et al.* 2016a, c). Semi-slugs usually also have thinner shells and much larger protoconchs (Welter-Schultes 2012). In addition, vitrinids lack the striae typical of planorbids on the protoconch but bear pits instead (*e.g*., Finger 1998, Harzhauser *et al.* 2014b).

Occurrence. – Only known from the Early/Middle Miocene of the Mecsek Mts. (Himesháza).

Genus *Gyraulus* Charpentier, 1837

Type species. – *Planorbis albus* Müller, 1774; by subsequent designation by Dall (1870, p. 351). Recent, Europe.

Gyraulus ianus Neubauer sp. nov.

Figure 8A–Z

1931	*Gyraulus* sp. – Wenz, p. 121.
? 2009	*Gyraulus* sp. B., ?n. sp. – Bulić & Jurišić-Polšak, p. 141, pl. 1, figs 7–9.

LSID. – urn:lsid:zoobank.org:act:F35936DE-F0A9-4CF4-84E2-CE549B4BFAB2

Type material. – Holotype: SNSB-BSPG 2025 IX 56 (Fig. 8D–F). Paratypes: SNSB-BSPG 2025 IX 57 (Fig. 8A–C), HNHM PAL 2025.39.1. (Fig. 8G–I), HNHM PAL 2025.40.1. (Fig. 8J–L), SNSB-BSPG 2025 IX 58 (Fig. 8M–O), SNSB-BSPG 2025 IX 59 (Fig. 8P, Q), SNSB-BSPG 2025 IX 60 (Fig. 8R–T), HNHM PAL 2025.41.1. (Fig. 8U–W), HNHM PAL 2024.42.1. (Fig. 8X–Z).

Type horizon and locality. – Mollusk coquina in littoral lacustrine deposits of the Pécsvárad Member (Kiskunhalas

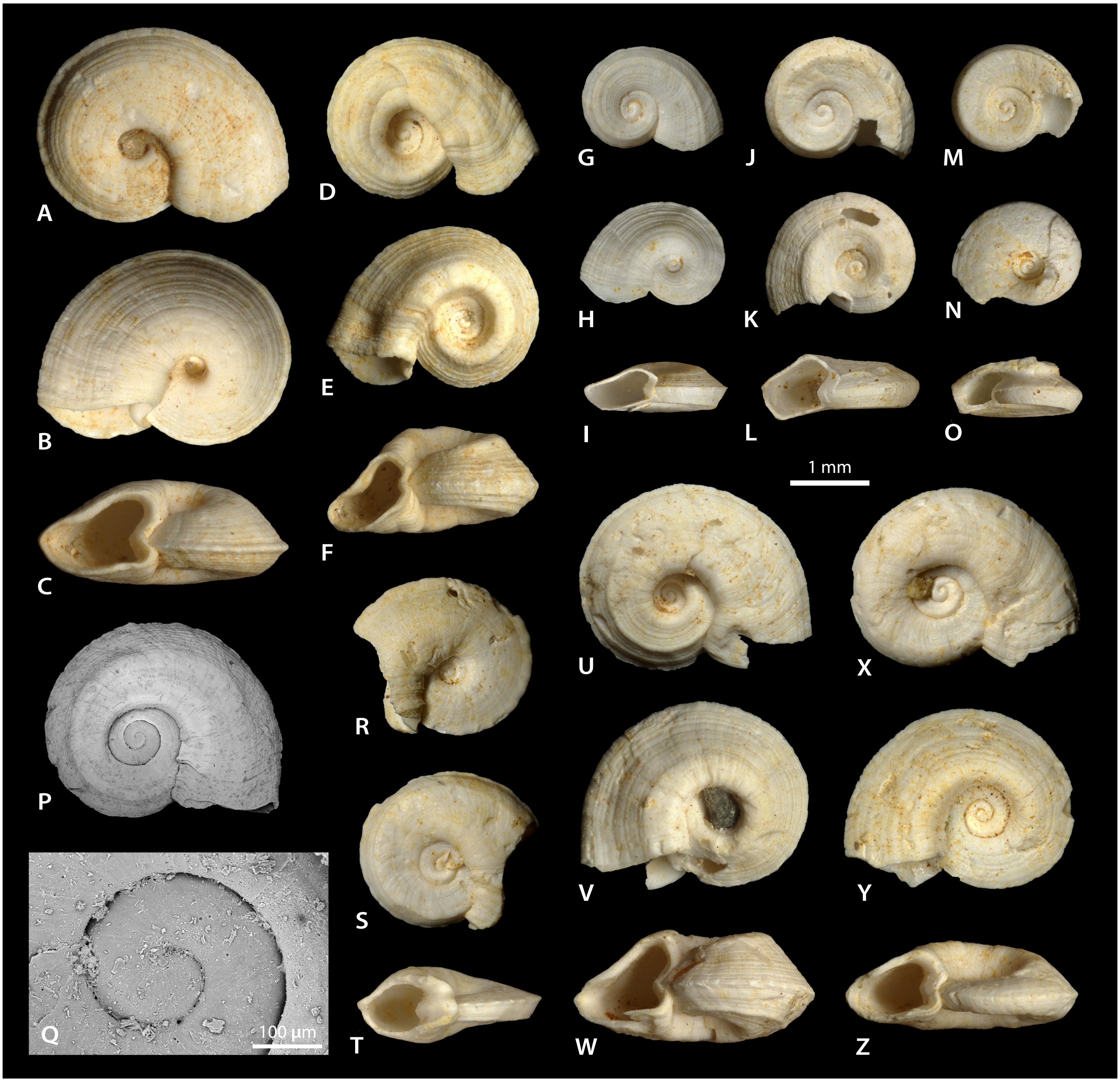


Figure 8. *Gyraulus ianus* sp. nov. (Planorbidae) from the Mecsek Mts. A–C – paratype, phenotype 1, SNSB-BSPG 2025 IX 57. D–F – holotype, phenotype 1, SNSB-BSPG 2025 IX 56. G–I – paratype, intermediate phenotype, HNHM PAL 2025.39.1. J–L – paratype, phenotype 2, HNHM PAL 2025.40.1. M–O – paratype, phenotype 2, SNSB-BSPG 2025 IX 58. P, Q – paratype, phenotype 1, SNSB-BSPG 2025 IX 59. R–T – paratype, intermediate phenotype, SNSB-BSPG 2025 IX 60. U–W – paratype, phenotype 1, HNHM PAL 2025.41.1. X–Z – paratype, intermediate phenotype, HNHM PAL 2024.42.1. All specimens from Himesháza.

Formation); upper Burdigalian/lower Langhian (Karpatian/lower Badenian). Himesháza, Engesgraben, Mecsek Mts., Baranya county, southern Hungary (46.11506° N, 18.54811° E, WGS84).

Additional material. – 202 specimens: 122 from Feked 1 (SNSB-BSPG 2025 IX 61), 16 from Feked 2 (SNSB-BSPG 2025 IX 62), 2 incomplete shells from Feked 1 (SNSB-BSPG 2025 IX 64), which are only tentatively affiliated with the species, 62 from Himesháza (SNSB-BSPG 2025 IX 63).

Etymology. – Named after the Roman God Ianus, the god of duality, transitions, beginnings and endings, referring to the dual nature of the species' shell morphology.

Diagnosis. – Extremely variable, spirally ornamented shell with inequilateral growth. In apertural view, shell shape ranges from comparatively flat, with angulate aperture and almost evolute shell on lower side and moderately involute growth on upper side, to high and bulky, with oblique heart-shaped aperture and almost completely involute growth on both sides. Shells bear central to sub-central keel on periphery, in most specimens also additional keel or bulge on lower side, and dense spiral striation of various intensity.

Description. – Small planorbid shell with up to 3.25 whorls. Shell morphology shows peculiar dimorphism: phenotype A characterized by nearly symmetrical shell with both apical and umbilical sides being strongly involute. On both sides bulgy rim may occur at transition between whorl top and apical/umbilical funnel. Shell periphery bears central to subcentral, sometimes distinctly offset keel. Phenotype B has nearly identical apical side (involute, occasionally with bulge), but umbilical side is almost entirely flat. Keel is sharp but rarely offset. In general, shell is flatter and thinner than that of phenotype A. In both phenotypes, lower side usually bears additional, centrally to more peripherally placed keel or bulge. Keel may be distinct and narrow, often coinciding with angulation towards whorl flank (especially in thin phenotype B, where keel is placed near periphery), or more subtle (rather appearing like particularly strong spiral stria), or (rarely) missing altogether. Keel may even appear or disappear during ontogeny. Intermediate forms between phenotypes exist, showing transition between comparatively flat phenotype B in early ontogeny into more bulgy phenotype A in later ontogeny (Fig. 8R–T, X–Z). During transition whorl portions quickly expand in height and width, resulting in overlapping of preceding shell parts. Dimorphism seems independent of ontogeny, both phenotypes and transitional stages occur at various sizes and growth stages. Aperture heart-shaped in phenotype A, but variably inclined in lateral view, partly depending on position of keel and occurrence of bulges. Phenotype A with strong bulges on both sides often has distinctly oblique aperture (Fig. 8F), while specimens without bulges and more regular growth are almost symmetrical (Fig. 8C). In phenotype B, aperture is more angulate because of sharper keels instead of bulges. Shell is covered with spiral grooves and ridges of various intensity; rarely specimens occur without or locally reduced striation (*e.g.*, only on upper or lower side).

Dimensions. – Phenotype A: 1.36 × 2.74 mm (holotype, SNSB-BSPG 2025 IX 56; Fig. 8D–F); 1.34 × 3.28 mm (paratype, SNSB-BSPG 2025 IX 57; Fig. 8A–C); 1.44 × 3.06 mm (paratype, HNHM PAL 2025.41.1.; Fig. 8U–W). Intermediate forms: 1.14 × 2.99 mm (paratype, HNHM PAL 2024.42.1.; Fig. 8X–Z); 0.65 × 1.86 mm (paratype, HNHM PAL 2025.39.1.; Fig. 8G–I). Phenotype B: 0.84 × 2.01 mm (paratype, HNHM PAL 2025.40.1.; Fig. 8J–L).

Remarks. – This species exposes a peculiar dimorphism rarely observed in planorbids so far. Found separately, one may be inclined to consider the two phenotypes as distinct species. However, there are intermediate forms showing the transition between the comparatively flat second phenotype in early ontogeny into a more bulgy form in later ontogeny (Fig. 8R–T, X–Z), which is why we are confident that the specimens belong to a single, polymorph species.

The species is most certainly the one called *Gyraulus* sp. by Wenz (1931), who referred to small, keeled shells of about two whorls (apparently, he had only juvenile specimens at hand) with additional bulges near the sutures on both upper and lower side and fine spiral striation. He also mentioned the variability of the bulges. Wenz compared the species with the Pannonian *Gyraulus jukici* (Brusina, 1902) from Markuševec (today part of Zagreb, Croatia), which indeed shows similarities, especially with the flat, more strongly keeled phenotype. However, *G. jukici* is flatter, more regularly coiled, and has a more centrally placed keel on the lower side.

Shells from upper Burdigalian deposits of Pag Island (Croatia) left in open nomenclature by Bulić & Jurišić-Polšak (2009) closely resemble our shells in terms of the involute shell with median keel and bulges towards the umbilicus and apical sides as well as numerous spiral striae. Without examining the material, we only tentatively refer their specimens to our *Gyraulus ianus* sp. nov.

Gyraulus ianus sp. nov. also has similarities with juvenile *Gyraulus nisseanus* (Pavlović, 1931) from the mid-Miocene of the Serbian Lake System, sharing the median blunt keel and the two bulges, however the shells are typically symmetrical in early ontogeny and develop a distinct asymmetry and strong keels instead of bulges when fully grown (Pavlović 1931, Neubauer *et al.* 2020). In addition, the median keel is shifted upwards and the whorl flank between the upper and median keel is concave. The bottom side is flattened, similar to the second phenotype of *Gyraulus ianus* sp. nov., but the flattened area is much narrower since the lower keel is placed closer to the center of the shell.

Gyraulus verticilloides (Pavlović, 1931), from the same deposits as *G. nisseanus*, has a similarly involute and high, albeit a more symmetric shell. It has a median angulation, but keels or bulges are absent. Also, it lacks the spiral striation but has distinct growth lines instead.

Gyraulus ianus sp. nov. also superficially reminds of species of *Anisus* (*Pseudocarinogyraulus*) described by Popova & Starobogatov *in* Popova *et al.* (1970) from Pliocene deposits of the Chuya Depression (Altay Mts., Russia), *e.g.*, *A.* (*P.*) *lungershauseni* and *A.* (*P.*) *altaicus*.

They share the keeled and comparatively high shell but differ in the more regular, distinct, centrally placed keel on the upper and lower sides while lacking the spiral striation. The status of the eight *Anisus* (*Pseudocarinogyraulus*) species described by Popova & Starobogatov is highly doubtful, since they seem to be distinguished mostly based on only subtle morphological differences while deriving all from the same deposits. A thorough revision is required to assess whether all could belong to a single polymorphic species, similar to the extraordinary morphological variety observed for *Gyraulus ianus* sp. nov. Finally, the revision may also address the placement of *Pseudocarinogyraulus* as subgenus of *Anisus*, which seems unlikely considering that today the genus comprises primarily species with flat, evolute shells with slow-growing whorls (*e.g.*, Welter-Schultes 2012, Glöer 2019). Note however that (Popova *et al.* 1970) generally followed a different systematic approach, placing also *Gyraulus* as a subgenus of *Anisus*.

"*Gyraulus verticillus* (Brusina) var." of Kókay (2006) from the Lower Badenian of Nagygörbö is similarly involute but has a blunt mid-whorl angulation instead of a keel, and it lacks the bulges. In fact, it more closely resembles *G. oncostomus* (Brusina, 1902) from Dugo Selo Lasinjsko, Croatia (see below).

Occurrence. – Only known from the Early/Middle Miocene of the Mecsek Mts. (Feked, Himesháza) and potentially from the Lower Miocene of Pag Island (Bulić & Jurišić-Polšak 2009).

Gyraulus magyari **Neubauer sp. nov.**
Figure 9A–L

LSID. – urn:lsid:zoobank.org:act:F788917B-5295-47A4-874A-6CC886F9B828

Type material. – Holotype: SNSB-BSPG 2025 IX 65 (Fig. 9A–C). Paratypes: SNSB-BSPG 2025 IX 66 (Fig. 9G, H, K, L), HNHM PAL 2025.44.1. (Fig. 9I, J), HNHM PAL 2025.43.1. (Fig. 9D–F) from Feked 1.

Type horizon and locality. – Mollusk coquina in littoral lacustrine deposits of the Pécsvárad Member (Kiskunhalas Formation); upper Burdigalian/lower Langhian (Karpatian/lower Badenian). Himesháza, Engesgraben, Mecsek Mts., Baranya county, southern Hungary (46.11506° N, 18.54811° E, WGS84).

Additional material. – None.

Etymology. – Named after Imre Magyar (MTA-MTM-ELTE Research Group for Paleontology and MOL Hungarian Oil and Gas Company Plc.) for his contributions to Neogene mollusk paleontology.

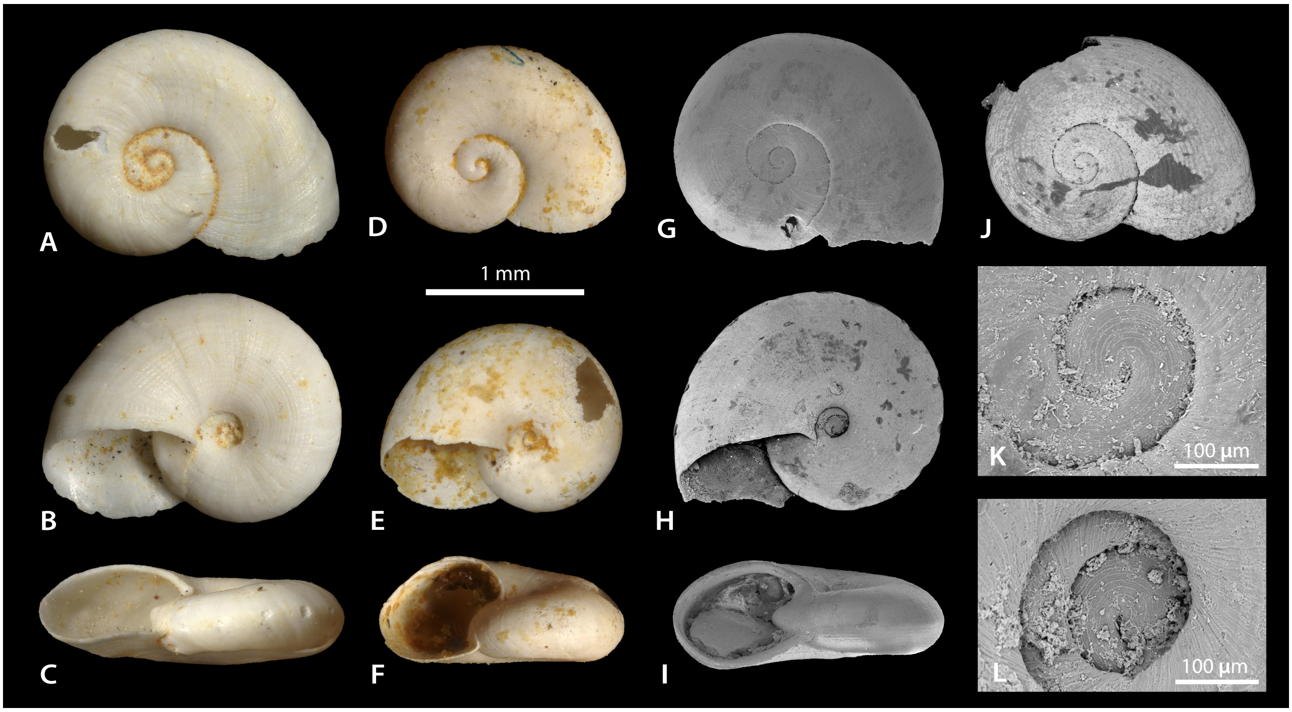


Figure 9. *Gyraulus magyari* sp. nov. (Planorbidae) from the Mecsek Mts. A–C – holotype, SNSB-BSPG 2025 IX 65, from Himesháza. D–F – paratype, HNHM PAL 2025.43.1., from Feked 1. G, H, K, L – paratype, SNSB-BSPG 2025 IX 66, from Himesháza. I, J – paratype, HNHM PAL 2025.44.1., from Himesháza.

Diagnosis. – Flat, slightly asymmetrical planorbid shell with well rounded whorl periphery and fast whorl growth. Upper shell side moderately involute, with moderately deep pseudoumbilicus; lower side flattened, entirely or almost entirely evolute. Shell bears fine striation all around.

Description. – Rather small planorbid shell, less than 2 mm in maximum diameter, with up to ~ 2.7 whorls. Protoconch ~ 0.75 whorls, bearing 12 striae that fade out towards teleoconch (Fig. 9K). Whorls gain rapidly in diameter and grow asymmetrically: lower side shallow concave, almost flat, with entirely evolute (Fig. 9A, D, J) or nearly evolute (Fig. 9G) whorls; upper side moderately involute, with current whorl overgrowing approximately two thirds to three quarters of preceding one, forming narrow pseudoumbilicus (Fig. 9B, E, H); whorl periphery regularly convex. Aperture broadly kidney-shaped (Fig. 9F) to more elongate, nearly elliptical (Fig. 9C, I). Shell covered all around with fine, irregularly placed spiral grooves.

Dimensions. – 0.64 × 1.93 mm (holotype, SNSB-BSPG 2025 IX 65; Fig. 9A–C; 0.69 × 1.56 mm (paratype, HNHM PAL 2025.43.1.; Fig. 9D–F); 0.80 × 1.80 mm (paratype, SNSB-BSPG 2025 IX 66; Fig. 9G, H, K, L); 0.69 × 1.78 mm (paratype, HNHM PAL 2025.44.1.; Fig. 9I, J).

Remarks. – This species is characterized by its fast, asymmetrical growth, which is rarely found in planorbids. A similar species is the Middle Miocene *Gyraulus pavlovici* (Brusina, 1893) from the Serbian Lake System (Neubauer *et al.* 2020), which has a similar size and whorl expansion rate. It differs in the more regular coiling and more typical, symmetric shape with well-rounded periphery, while *Gyraulus magyari* sp. nov. is characterized by a flat and nearly evolute umbilical side but a strongly convex, involute apical side. *Gyraulus pavlovici* also lacks the spiral striation on the teleoconch.

The co-occurring *Gyraulus pseudodalmaticus* sp. nov. has a very similar apical side, showing a comparably involute shell with spiral grooves. However, *G. pseudodalmaticus* sp. nov. is flatter and consistently bears a keel. Also, the aperture is relatively smaller compared to *Gyraulus magyari* sp. nov.

The type of slightly asymmetrical morphology with comparatively rapid whorl growth and small apex and umbilicus is also found in *Gyraulus macroconcha* (Popova & Starobogatov, 1970) *in* Popova *et al.* (1970) from the Pliocene of the Chuya depression in the Altay Mts., Russia (Popova *et al.* 1970). It also shares the well-rounded periphery and the spiral teleoconch striation; it is, however, with a shell width of up to 13 mm at a similar number of whorls much larger than *Gyraulus magyari* sp. nov.

Occurrence. – Only known from the Early/Middle Miocene of the Mecsek Mts. (Feked, Himesháza).

***Gyraulus nedici* (Brusina, 1902)**
Figure 10A–I, K–M, X

*1902 *Planorbis Nedići* Brus.; Brusina, p. 8, pl. 3, figs 25–27.

? *1902 *Planorbis oncostomus* Brus.; Brusina, p. 8, pl. 3, figs 25–27.

1923 *Gyraulus* (*Gyraulus*) *nedići* (Brusina). – Wenz, p. 1564.

? 1923 *Gyraulus* (*Gyraulus*) *oncostomus* (Brusina). – Wenz, p. 1566.

? 1959 *Gyraulus solenoeides* (Lörenthey). – Boda, pp. 638, 737, pl. 35, fig. 10.

1974 *Gyraulus* (*Gyraulus*) *nedici* (Brusina). – Milan *et al.*, p. 122.

? 1974 *Gyraulus* (*Gyraulus*) *oncostomus* (Brusina). – Milan *et al.*, p. 123.

1999 *Gyraulus nedici* (Brusina). – Gál *et al.*, p. 41, figs 11a, b, 12a, b.

2000 *Gyraulus nedici* (Brusina). – Gál *et al.*, p. 41, 42.

? 2001 *Gyraulus nedici* (Brus.). – Hír *et al.*, p. 44.

2004 *Gyraulus nedici* (Brusina). – Hír & Kókay, p. 86, fig. 6(2–5).

2006 *Gyraulus nedici* (Brusina), 1902. – Kókay, p. 55, pl. 19, figs 1–3.

? 2006 *Gyraulus microstatus* (Bourguignat), 1881. – Kókay, p. 55, pl. 19, figs 4, 5 [non *Planorbis microstatus* Bourguignat, 1881].

2011 *Gyraulus nedici* (Brusina, 1902). – Hír & Kókay, p. 69.

Material. – Eight specimens: 1 from Himesháza (SNSB-BSPG 2025 IX 70), 5 from Máza (SNSB-BSPG 2025 IX 67–68, SNSB-BSPG 2025 IX 71), 2 from Szászvár 1 (SNSB-BSPG 2025 IX 69, SNSB-BSPG 2025 IX 72).

Type material. – Originally described from lowermost Middle Miocene strata (~ 15.9 Ma; Mandic *et al.* 2012) at Dugo Selo Lasinjsko (Dugoselo), municipality of Gvozd, Sisak-Moslavina county, Croatia. Milan *et al.* (1974) listed three syntypes; here, we select the specimen illustrated on Fig. 10G–I (NHMZ 2441-87/1; Brusina 1902, pl. 3, fig. 25) as the lectotype.

Description. – Shell of up to 3.5 whorls. Protoconch consists of approximately 0.5 whorls (boundary to teleoconch not visible but indicated faintly by onset of growth lines), bearing faint traces of widely spaced spiral striae typical

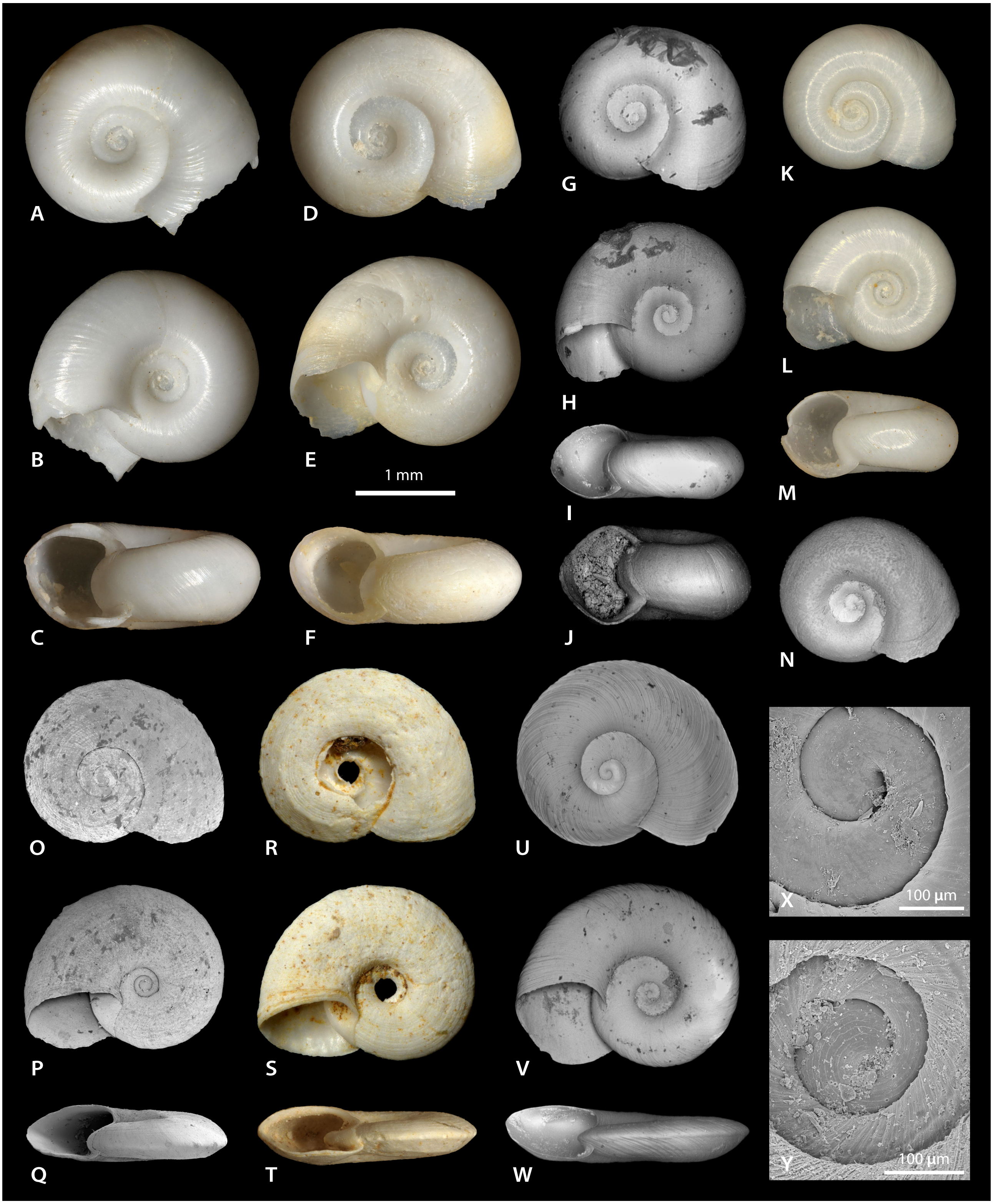


Figure 10. Planorbidae from the Mecsek Mts. and comparative material. • A–I, K–M, X – *Gyraulus nedici* (Brusina, 1902); A–C – SNSB-BSPG 2025 IX 67, from Máza; D–F – SNSB-BSPG 2025 IX 68, from Máza; G–I – lectotype, designated herein (NHMZ 2441-87/1), from Dugo Selo Lasinjsko, Croatia; K–M, X – SNSB-BSPG 2025 IX 69, from Szászvár 2. • J, N – *Gyraulus oncostomus* (Brusina, 1902), lectotype, designated herein (NHMZ 2435-81/3), from Dugo Selo Lasinjsko. • O–Q, R–T, Y – *Gyraulus pseudodalmaticus* sp. nov., from Himesháza; O–Q, Y – holotype, SNSB-BSPG 2025 IX 73; R–T – paratype, HNHM PAL 2025.45.1. • U–W – *Gyraulus dalmaticus* (Brusina, 1884), potential syntype, from Trnovača, Sinj Basin, Croatia.

of the genus (Fig. 9X). Whorls highly, regularly convex, expanding slowly but regularly in diameter and rather quickly in height, compared to other species of the genus. Shell slightly asymmetric in apertural view, especially evident in later ontogeny, with terminal shell portion growing more upwards. Accordingly, overlap of preceding whorl is slightly higher on shell top (~ half) than on bottom side (~ a third). Aperture kidney-shaped; almost symmetric in early stages (Fig. 10M), more asymmetric in later ontogeny (Fig. 10C, F). Surface glossy, without ornamentation except for fine growth lines.

Dimensions. – 1.09 × 2.39 mm (SNSB-BSPG 2025 IX 67; Fig. 10A–C); 0.99 × 2.37 mm (SNSB-BSPG 2025 IX 68; Fig. 10D–F); 0.89 × 1.79 mm (SNSB-BSPG 2025 IX 69; Fig. 10L–M, X).

Remarks. – Originally figured by Brusina (1902), the species has never been properly described but was only listed in catalogues and briefly reported in a few works. Here, we provide a full description, which is primarily based on the material from Mecsek but matching well the lectotype stored at NHMZ.

The present shells closely resemble the lectotype from Dugo Selo Lasinjsko concerning the shell size, the number and convexity of the whorls, the slightly asymmetric shape, and the degree of whorl expansion and overlap – leaving no doubt about them being conspecific. At the same number of whorls (slightly less than three), the lectotype has the same size as the specimen from Máza illustrated in Fig. 10K–M, X.

Gyraulus oncostomus (Brusina, 1902) described from the same locality and strata as *G. nedici* shows a fairly similar shell, being slightly more involute and higher, and the aperture is slightly angular, resulting in a symmetrically triangular shape. Also, the whorl profile is slightly asymmetric, with the maximum convexity below the whorl center. One of our shells has a relatively higher shell and aperture (Fig. 10M), reminding of *Gyraulus oncostomus*, but not the angulated periphery. Possibly, considering the high shell plasticity known among DLS planorbids, *nedici* and *oncostomus* could belong to one polymorph species, but without further material documenting the morphological range we refrain from any taxonomic conclusions. Nonetheless, to fix the name-bearing type of *oncostomus* we designate herewith the specimen illustrated on Fig. 10J, N (NHMZ 2435-81/3; Brusina 1902, pl. 3, fig. 9) as the lectotype.

Hír & Kókay (2004) and Kókay (2006) listed among the synonymy of *G. nedici* the record of *Gyraulus solenoeides* (Lörenthey, 1902) *sensu* Boda (1959). However, the specimen illustrated by Boda (1959) is more evolute than classical *G. nedici*, which is why we are uncertain whether it truly is the same species. Note also that Boda (1959) did not indicate any locality or stratum (other than Sarmatian of Hungary).

Specimens from the Upper Badenian of the Bakony Mts. attributed to *Gyraulus microstatus* (Bourguignat, 1881) by Kókay (2006) closely resemble the lectotype of *G. nedici* and the material from the Mecsek Mts. and may be conspecific. Bourguignat's species was described from the Middle Miocene (mammal zone MN 6) of Sansan. It was questionably attributed to *Bathyomphalus* by Fischer (2000), but poorly illustrated. The shell appears to have a larger aperture than the specimens illustrated by Kókay (2006).

The Mecsek specimens also resemble *G. dealbatus* (Braun, 1851), originally described from the Lower Miocene of the Mainz Basin in Germany and recently reported from Serravallian deposits of the locality Hidas in the Mecsek Mts (Neubauer *et al.* 2025). Shells of that species are similarly bulbous with a well-rounded periphery, but they are consistently flatter at the same size. *Gyraulus nedici* has a broad, nearly symmetrical, kidney-shaped aperture already in early ontogeny and comparatively deep umbilical and apical sides.

Gyraulus albertanus (Clessin, 1877) has a similarly broad and symmetric shell, but its whorls expand fast in diameter, and it is much larger at the same number of whorls [diameter of 2.9 mm of a specimen from Sandelzhausen (Salvador & Rasser 2014) compared to our ~ 1.8 mm, both with ~ 2.75 whorls; see also Salvador *et al.* 2016b, c].

Gyraulus alienus (Rolle, 1862) from the upper Badenian (Serravallian) of the nearby locality Hidas is similarly small and involute, but the shell is more irregularly coiled, and the aperture is reflected (Neubauer *et al.* 2025).

Gyraulus austroalpinus (Harzhauser & Neubauer, 2012) *in* Harzhauser *et al.* (2012) from the Middle Miocene of the Aflenz Basin (Austria) has a similarly involute shell, but it is even smaller and more bulbous than *Gyraulus nedici*, and it occasionally bears a weak mid-whorl angulation.

Occurrence. – Dugo Selo Lasinjsko in Croatia (earliest Middle Miocene) (Brusina, 1902) and Mátraszőlős (latest Langhian, MN 7) (Gál *et al.* 1999, 2000; Hír & Kókay 2004, 2011), Nyirád and Várpalota (Sarmatian) (Kókay 2006) in Hungary. Hír *et al.* (2001) further listed the species from the Sarmatian of Felsőtárkány without description or illustration; the record needs confirmation. Hír & Kókay (2004) listed a record from the Badenian of Sámsonháza, referring to the publication on that fauna by Hír *et al.* (1998). However, *G. nedici* is not listed in that publication. In the Mecsek Mts., the species occurs in Karpatian–lower Badenian deposits at Himesháza, Máza, and Szászvár.

Gyraulus pseudodalmaticus **Neubauer sp. nov.**
Figure 10O–T, Y

LSID. – urn:lsid:zoobank.org:act:B0D78583-9A69-402F-BC06-BAE92FDB2335

Type material. – Holotype: SNSB-BSPG 2025 IX 73 (Fig. 10O–Q, Y). Paratype: HNHM PAL 2025.45.1. (Fig. 10R–T).

Type horizon and locality. – Mollusk coquina in littoral lacustrine deposits of the Pécsvárad Member (Kiskunhalas Formation); upper Burdigalian/lower Langhian (Karpatian/lower Badenian). Himesháza, Engesgraben, Mecsek Mts., Baranya county, southern Hungary (46.11506° N, 18.54811° E, WGS84).

Additional material. – None.

Etymology. – Named for the species' resemblance to the DLS species *Gyraulus dalmaticus* (Brusina, 1884).

Diagnosis. – Flat, asymmetric shell with fast whorl expansion, central to subcentral keel, weak angulation near whorl center on bottom side, and numerous distinct spiral grooves.

Description. – Shell flat, with up to 3 whorls. Protoconch ~ 1 whorl, with clearly marked protoconch/teleoconch boundary; bears characteristic spiral striae that fade out towards boundary; 11 are counted on the holotype (Fig. 10Y). Whorls gain rapidly in diameter and grow asymmetrically: whorls almost evolute on lower side (Fig. 10O, R), moderately involute on upper side, with current whorl overgrowing approximately half to two thirds of preceding one, forming moderately narrow pseudoumbilicus (Fig. 10P, S). In lateral view, distinct keel is formed at or slightly below whorl center (Fig. 10Q, T). Additionally, angulation occurs on lower side demarcating narrow, straight whorl portion towards keel, measuring approximately one third of whorl width; inner two thirds flattened, with slightly immersed umbilical region. Aperture slightly asymmetrically heart-shaped, distinctly oblique in lateral view; inner lip extends far on penultimate whorl (Fig. 10P, S). Bottom and top sides covered by dense pattern of spiral grooves.

Dimensions. – 0.59 × 2.11 mm (holotype, SNSB-BSPG 2025 IX 73; Fig. 10O–Q, Y); 0.63 × 2.27 mm (paratype, HNHM PAL 2025.45.1.; Fig. 10R–T).

Remarks. – The species is named for its similarity to the DLS species *Gyraulus dalmaticus* (Brusina, 1884) from the Sinj and Drniš basins (Fig. 10U–W). Both species share the flattened, keeled shell, but *G. dalmaticus* is less involute (although Brusina's original drawings indicate otherwise), has distinct growth lines, and lacks the spiral striation as well as the faint angulation on the umbilical side. Also, the keel is positioned closer to the top side in *G. dalmaticus*. We show for comparison the specimen illustrated previously by Brusina (1897, pl. 2, figs 17–19) from the type locality Trnovača in the Sinj Basin (NHMZ 2949-595; Fig. 10U–W). Note that this specimen was labeled as the "holotype" by Milan *et al.* (1974, p. 118), but it is uncertain whether it was part of the original material of Brusina (1884) or derived from newly collected material. It does not constitute a valid lectotype designation according to ICZN Art. 74.5.

Gyraulus sachsenhoferi Harzhauser & Neubauer, 2012 *in* Harzhauser *et al.* (2012) from the Middle Miocene of the Aflenz Basin (Austria) shows a similarly flat and keeled shell, but the keel is much more pronounced, the shell is larger, and its surface bears distinct growth lines. *Gyraulus soceni* Jekelius, 1944 from the Sarmatian of Soceni (Romania) has a smaller (1.5 mm diameter) but relatively higher shell, an angulation rather than a distinct keel, and a weak concavity on the central whorl portion on the lower side, rarely also on the upper side (Jekelius 1944).

Gyraulus turislavicus Jekelius, 1944 from Pannonian deposits of the same locality has a more distinct keel bordered by a weak concavity, a more flattened top side, typically a more oblique aperture, and the shell lacks the spiral striation (Sauerzopf 1953, Harzhauser *et al.* 2002). *Gyraulus protectus* Jekelius, 1944 from the same deposits has the same type of keel and flattened shell top as *G. turislavicus*, but it bears a second keel on the lower side, approximately where *Gyraulus pseudodalmaticus* sp. nov. shows the angulation. *Gyraulus protectus* is, however, more involute on the top side and lacks the spiral grooves. The Pannonian *Gyraulus marinkovici* (Brusina, 1892) from Croatia has a similar size and morphology, but the shell is more involute on the upper side and lacks the angulation typical of *Gyraulus pseudodalmaticus* sp. nov. on the lower side (Sauerzopf 1953, Harzhauser *et al.* 2002). *Gyraulus pseudhomalosomus* (Sauerzopf, 1953) from the Pannonian of Austria is similar to *G. turislavicus* but has a less pronounced keel and less oblique aperture, which in turn resembles *G. pseudodalmaticus*. However, its top side is more evolute and, again, the shell is devoid of spiral sculpture.

Gyraulus pseudodalmaticus sp. nov. has similarities to members of the genus *Hippeutis*, but the keel is not as distinct and the shell top and bottom are not as flattened as in, *e.g.*, *Hippeutis complanatus* (Linnaeus, 1758).

Occurrence. – Only known from the Early/Middle Miocene of the Mecsek Mts. (Himesháza).

Class Bivalvia Linnaeus, 1758
Subclass Autobranchia Grobben, 1894
Infraclass Heteroconchia Gray, 1854
Subterclass Euheterodonta Giribet & Distel, 2003
Superorder Imparidentia Bieler, Mikkelsen & Giribet, 2014 *in* Bieler *et al.* (2014)
Order Myida Stoliczka, 1870
Superfamily Dreissenoidea Gray, 1840
Family Dreissenidae Gray, 1840
Subfamily Congeriinae Mandic & Harzhauser, 2016 *in* Neubauer *et al.* (2016c)

Genus *Trigonipraxis* Starobogatov, 1970

Type species. – *Congeria triangularis* Partsch, 1835; by original designation. Late Miocene, Central Europe.

Trigonipraxis boeckhi (Wenz, 1931) comb. nov.

Figure 11A–N, P–Q

*1931 *Congeria böckhi*; Wenz, p. 117, pl. 10, fig. 1a–c.
1967 *Congeria böckhi* Wenz. – Kókay, pp. 77, 78.
non 1978 *Congeria boeckhi* Wenz 1931. – Kochansky-Devidé & Slišković, p. 47, 90, pl. 5, figs 1–14 (*cf*. pl. 5, fig. 15).
2006 *Congeria boeckhi* Wenz, 1931. – Kókay, p. 94, pl. 36, fig. 5.
2010 *M.*[*ytilopsis*] *boeckhi* (Wenz, 1931). – Harzhauser & Mandic, p. 13.
2013 *Congeria boeckhi* Wenz. – Kókay, p. 151.
2019 *Congeria boeckhi*. – Sebe *et al.*, p. 89, fig. 4d.

Material. – Sixty-one valves: 7 adult from Feked 1 (HNHM PAL 2025.48.1.–PAL 2025.54.1.), 26 juvenile from Feked 1 (SNSB-BSPG 2025 IX 78), 28 juvenile from Himesháza (SNSB-BSPG 2025 IX 74–77, SNSB-BSPG 2025 IX 79).

Dimensions. – 56 (incomplete) × 40 × 26 mm Fig. 11A, B); 45.0 × 33.0 × 18.5 mm (HNHM PAL 2025.48.1, Fig. 11C–F).

Remarks. – Available for the present study are mainly juvenile specimens up to ~ 4 mm in length (Fig. 11K–N); about half of them come from the type locality Feked. From there, Wenz (1931) provided drawings of a right valve with a shell length of 39 mm. From the same locality, Sebe *et al.* (2019) provided the only photographs of a topotype, a left valve documenting for the first time the extraordinary size of the species (Fig. 11A, B). Our specimens from the same locality are represented only by one complete specimen – a right valve of 45 mm length (Fig. 11C–F). Other specimens are up to 41 mm long, more or less posteriorly fragmented valves (two left valves, four right valves), with a conspicously broadened septum and a ligament area adjoined by partly massive interior surface calcifications. In agreement with the original placement of *Congeria boeckhi* Wenz, 1931 into the *triangularis*-group of Andrusov (1897), we combine here this species for the first time with *Trigonipraxis* Starobogatov, 1970.

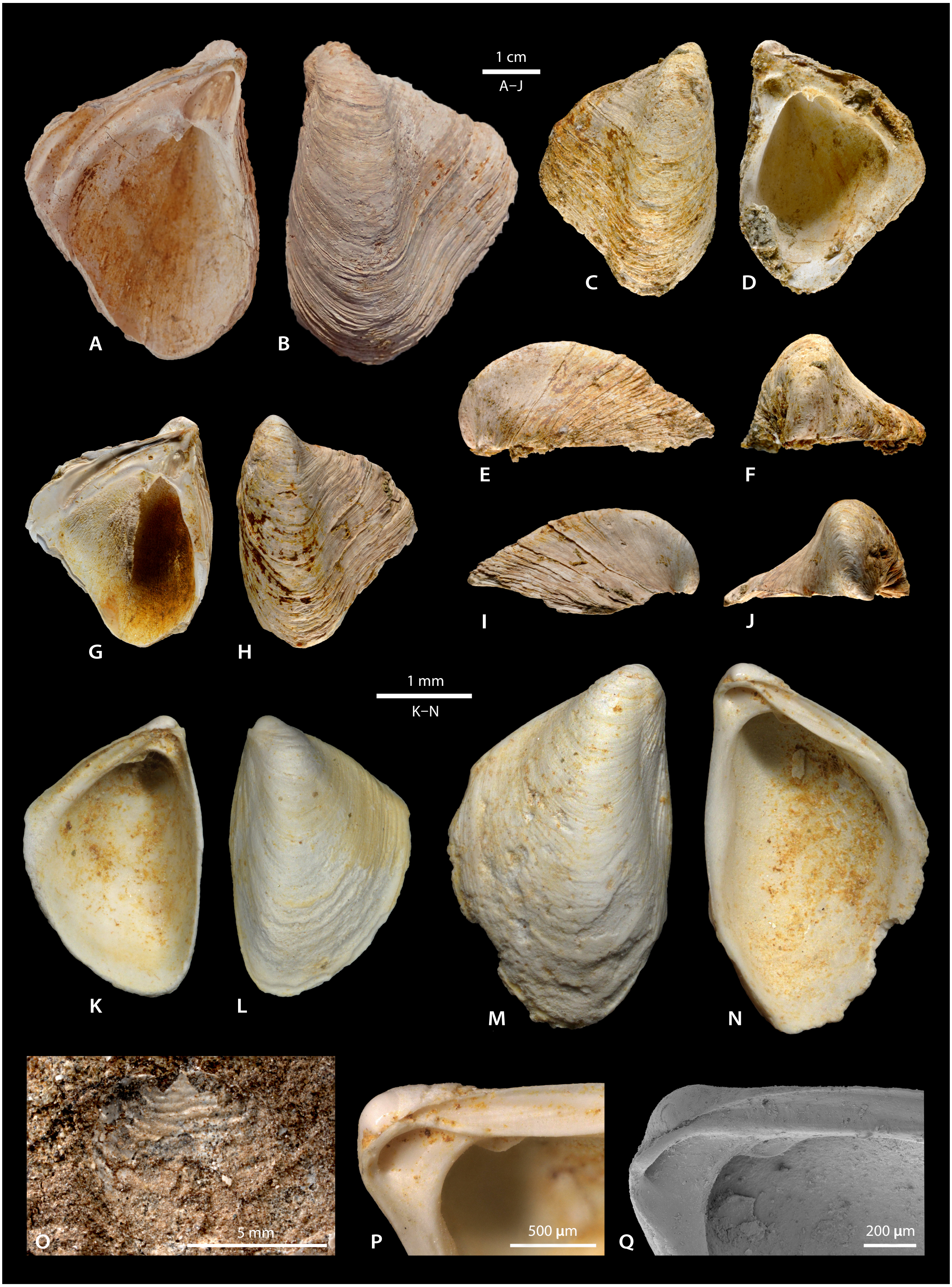
A similar and probably closely related species is *Trigonipraxis zoici* (Andrusov, 1897) from the Glina Basin in Croatia. That species is known only from fragmented or deformed specimens. Its maximal length was originally reconstructed to 40 mm (Andrusov 1897) but subsequently reduced to only 27 mm based on a re-evaluation of the syntype series along with numerous additional specimens (Kochansky-Devidé & Slišković 1978). *Trigonipraxis zoici* is therefore considerably smaller than *T. boeckhi*. It also has a smooth exterior surface missing the coarse, projecting, and wavy growth lines, its beak is pointed, triangular, and not rounded, the hinge plate is broader and deeper, the ligament ledge thinner, its keel area is much more broadly convex, the anterior flanks are not laterally impressed but planoconvex, and its posteroventral margin is straightened and not broadly rounded.

Kochansky-Devidé & Slišković (1978) misidentified specimens from the lower–middle Miocene lacustrine deposits of Mt. Medvednica (Gornja Planina, Vukov dol near Gornja Planina, Vidovec, and Blaguša), the Sava Basin (borehole at Novo Brdo), and the Derventa Basin in northern Bosnia and Herzegovina as *Congeria boeckhi*. Based on their outline, size, and the shape and position of the keel, the illustrated specimens from Mt. Medvednica sites represent most likely more or less deformed individuals of *Trigonipraxis pilari* (Kochansky-Devidé, 1978).

Occurrence. – Originally described from "Helvetian" deposits of Feked and Geresd in the Mecsek Mts. and Várpalota in the Bakony Mts (Wenz 1931). Our specimens come from the localities Feked and Himesháza.

Subterclass Palaeoheterodonta Newell, 1965
Order Unionida Gray, 1854

Figure 11. Dreissenidae and Unionidae from the Mecsek Mts. • A–N, P, Q – *Trigonipraxis boeckhi* (Wenz, 1931); A, B – left valve, from Feked, depicted *in* Sebe *et al.* (2019, fig. 4d); C–F – right valve, HNHM PAL 2025.48.1, from Feked; G–J – left valve, HNHM PAL 2025.49.1. from Feked; K, L – left valve, SNSB-BSPG 2025 IX 76, from Himesháza; M, N, P – right valve, SNSB-BSPG 2025 IX 75, from Himesháza; Q – hinge of the left valve, SNSB-BSPG 2025 IX 74, from Himesháza. • O – Unionidae gen. et sp. indet., beak imprint, NHMW 2025/0246/0009, from Szászvár 1.


1 cm
A–J
A
B
C
D
E
F
G
H
I
J
1 mm
K–N
K
L
M
N
O
5 mm
P
500 µm
Q
200 µm

Suborder Unionidina Gray, 1854
Superfamily Unionoidea Rafinesque, 1820
Family Unionidae Rafinesque, 1820
Subfamily Gonideinae Ortmann, 1916

Genus *Potomida* Swainson, 1840

Type species. – *Mysca* (*Potomida*) *corrugata* Swainson, 1840 [= *Potomida littoralis* (Cuvier, 1797)]; by original designation. Recent, Europe.

Potomida schneideri Mandic sp. nov.

Figure 12A–G

LSID. – urn:lsid:zoobank.org:act:BA78F1CE-C05F-42D7-9F9B-7E5ED150251A

Type material. – Holotype: articulated valve, NHMW 2025/0246/0043 (Fig. 12F, G). Paratype: single right valve, HNHM PAL 2025.46.1. (Fig. 12A–C).

Type horizon and locality. – Lacustrine delta deposits at top of Szászvár Formation; upper Burdigalian/Karpatian or lower Badenian/Langhian (underlying tuff was dated 17.055 ± 0.024 Ma; Harangi & Lukács 2019). Máza, Dóra-irtás, Mecsek Mts., Baranya county, southern Hungary (46.25261° N, 18.3886° E, WGS84).

Additional material. – Seven specimens from the type locality: 1 small articulated shell (NHMW 2025/0246/0027, Fig. 12D, E), 1 anterior part of an articulated valve and 1 fragmented left valve (NHMW 2025/0246/0027), 3 poorly preserved small articulated shells and 2 poorly preserved small single valves (NHMW 2025/0246/0037–0038).

Etymology. – Named after Simon Schneider (CASP, Cambridge, UK) for his contributions to unionid taxonomy.

Diagnosis. – Large, thick-shelled, subquadrate, inequilateral, postero-ventrally elongated *Potomida* with broadly inflated beak, blunt postero-dorsal keel, and right hinge showing massive anterior and faint posterior pseudocardinal cusp, adjoined by ledge-like posterior lateral tooth.

Description. – Large-sized, massive, thick-walled shell, strongly inequilateral, elongated posteroventrally with oval to subtrigonal outline showing straightened dorsal margins meeting at suborthogonal angle. Dorsal and anterior margins narrowly convex, ventral margin broadly convex, posterior one straightened, dipping backwards. Umbonal area broadly arched, joined posteriorly by broad keel, gradually fading distally. Umbo projecting over curved hinge plate. Exterior surface smooth in first third of ontogeny, followed distally by coarse growth rugae and constrictions toward margin. Umbonal cavity shallow. Hinge bears one elongated, massive pseudocardinal cusp and one faint, shortly elongated posterior cusp followed posterodorsally by prominent, ledge-like posterior lateral tooth.

Dimensions. – 87 × 68 × 22 mm (holotype, articulated valve, NHMW 2025/0246/0043; Fig. 12F, G); 97 × 75 × 20 mm (paratype, single right valve, HNHM PAL 2025.46.1.; Fig. 12A–C); 27 × (>18) × 6 mm (deformed articulated specimen, Fig. 12D, E).

Remarks. – The classification with *Potomida* is based on the hinge type, shell size, thickness and outline, and a strongly inflated beak projecting over the hinge line. Considering its late Burdigalian or early Langhian age, it represents the oldest known member of the genus, whose successors are still living in the peri-Mediterranean region. This finding shifts back not only the origin of the genus but also the time frame for the presumed immigration of Lamprotulini from Asia considerably (compare Schneider & Linse 2023).

Following a thorough review of Miocene *Potomida* in Europe, we additionally detected a slightly younger and widely overlooked Middle Miocene species that also belongs in the genus, *i.e.*, *Unio lorioli* Locard, 1893. This species originated from the Middle Miocene Upper Freshwater Molasse (13.5–14.0 Myr; Kälin *et al.* 2001) of Le Locle in the Swiss Jura. It is known only by a single small-sized (40 × 25 × 7 mm) articulated specimen, according to its author closely resembling the living *Potomida littoralis*. The only additional record of this species was reported by Kókay (2006, p. 96, pl. 38, figs 4, 5) from a borehole located near Bántapuszta in Veszprém county of Western Transdanubia, Hungary, providing two incomplete valves. He illustrated a small-sized (30 × 19 mm) anterodorsally fragmented left valve marked by a prominent umbonal ornament. The shells originate from the regressive brackish-water interval on top of the initial Middle Miocene (Badenian) marine cycle, probably related to the Langhian–Serravallian boundary (13.8 Ma; Mandic *et al.* 2019a). Compared to *Potomida lorioli* nov. comb. the new species from Máza is not only three times larger but shows a subquadrate and distinctly less elongated outline, with a more strongly bent hinge plate and a much more broadly inflated beak. Also, the umbonal ornament is not present in our specimens, which might be however an expression of intraspecific variability.

Occurrence. – Only known from the Miocene of Máza in the Mecsek Mts.

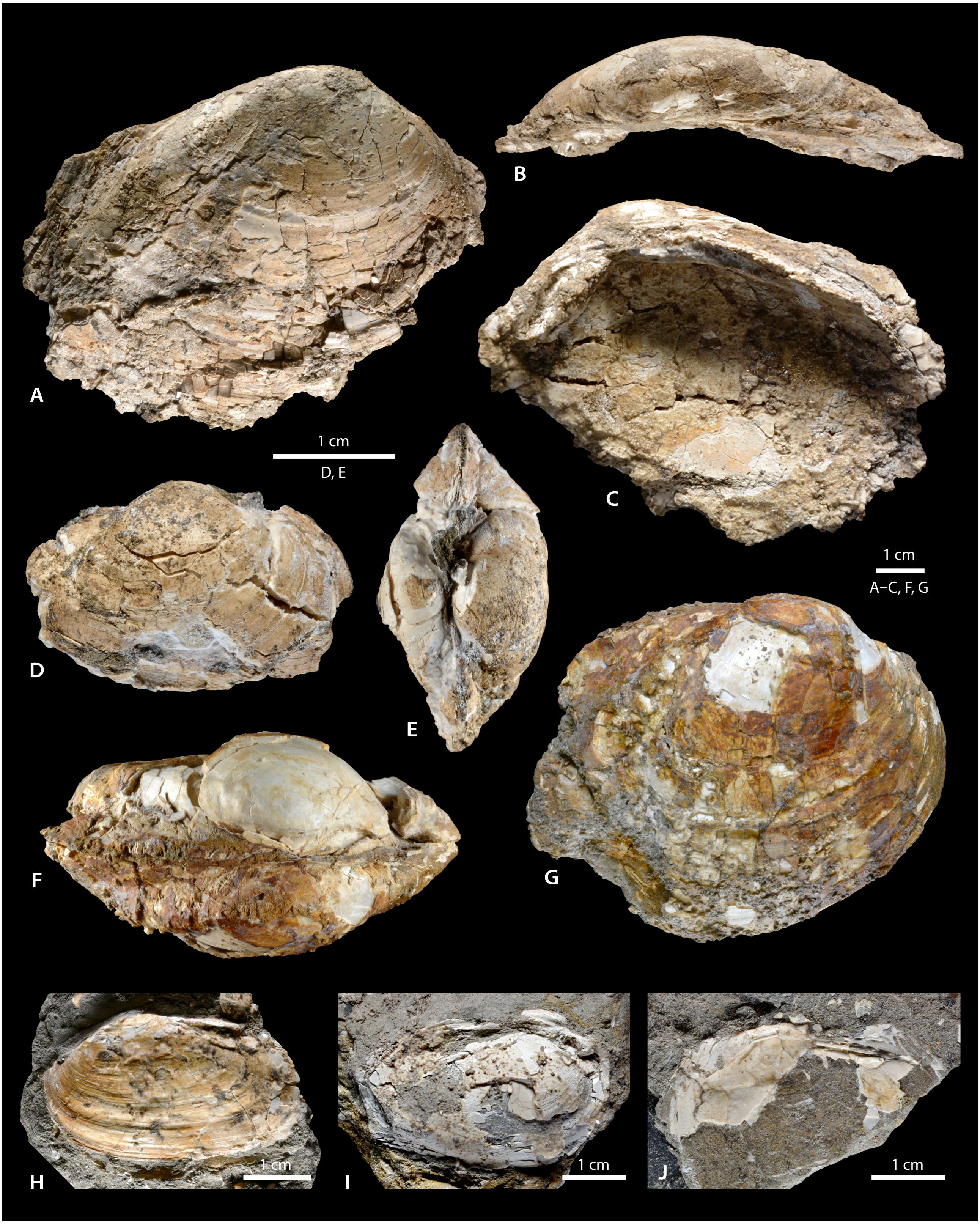


Figure 12. Unionidae from the Mecsek Mts. • A–G – *Potomida schneideri* sp. nov., from Máza; A–C – paratype, right valve, HNHM PAL 2025.46.1; D, E – articulated shell, NHMW 2025/0246/0027; F, G – holotype, articulated shell, NHMW 2025/0246/0043. • H – *Elliptio*? cf. *larteti* (Noulet, 1846), left valve, NHMW 2025/0246/0025, from Máza • I – *Unio* sp., NHMW 2025/0246/0008, from Szászvár 1 • J – Unionidae gen. et sp. indet., fragments, NHMW 2025/0246/0010, from Szászvár 1.

Subfamily Ambleminae Rafinesque, 1820

Genus *Elliptio* Rafinesque, 1819

Type species. – *Unio* (*Elliptio*) *nigra* Rafinesque, 1820 [= *Elliptio crassidens* (Lamarck, 1819)]; by original designation. Recent, United States.

Elliptio? cf. *larteti* Noulet, 1846

Figure 12H

cf. *1846 *Unio Larteti* Noul.; Noulet, p. 238, pl. 5, fig. 3.
cf. 1881 *Unio Larteti*. – Bourguignat, p. 154, fig. 302.
cf. 1943 *Elliptio larteti* Noulet. – Modell, p. 110, pl. 1, figs 1a–c, 2a, b.
cf. 1950 *Elliptio larteti* Noulet. – Modell, p. 40, pl. 8, fig. 12.
2006 *Unio larteti* Noulet. – Kókay, p. 96, pl. 37, figs 4, 5.

Material. – One single articulated specimen with exposed left valve from Máza (NHMW 2025/0246/0025).

Dimensions. – 39.5 × 22.6 × 4.0 mm (Fig. 12H).

Remarks. – *Unio larteti* from the Lower–Middle Miocene Armagnac lacustrine limestone of Seissan (France) is currently only known from its original drawing, which is based on the exterior side of a right valve. The specimen was not found in the Noulet collection stored at the Muséum national d'Histoire naturelle in Paris (Wackenheim, pers. comm. 2025).

The classification of this species in the American genus *Elliptio* was proposed by Modell (1943, 1950), based on specimens from the Egerian (Chattian to Aquitanian) of Hausham in southern Germany, which he compared with the living *E. complanatus* regarding the identical umbonal ornament. Yet, in a subsequent review, Haas *in* Cox *et al.* (1969) again restricted *Elliptio* to North America, prompting Kókay (2006) to place the species again in *Unio*. Until further information on the interior of the type specimen is known, we preliminarily follow Modell's classification.

Kókay (2006) documented this species from the lower Badenian (Langhian) of Nagygörbő in western Hungary. Our specimen coincides in size, outline, and umbonal ornament roughly with the French, German, and Hungarian specimens. Also, it shares with the type specimen the same high/length ratio of 57%. However, since interior shell features remain unknown, we only tentatively affiliate the specimen from Máza with *E. larteti*.

Sandberger (1875, p. 618) pointed out that *E. larteti* has a shell shape identical to *Unio mandelslohi* Dunker, 1848 from the Upper Brackish Water Molasse of Günzburg in southern Germany (middle Burdigalian, Kirchberg Formation), and only the unknown interior shell features prevented him from their reunion. Modell (1941) restudied the type series of *U. mandelslohi* and excluded the specimen illustrated by Dunker (1848, pl. 3, fig. 24) as *Unio jaccardi* Locard, 1893. Modell thereby confirmed its classification as *Unio,* placing it however in the *Unio pictorum* lineage (see also Modell 1958).

Occurrence. – The species was originally described from the upper Lower–lower Middle Miocene of Seissan (Dép. Gers) in southern France (Noulet 1846, Bourguignat 1881) and has been reported from Upper Oligocene–Lower Miocene strata of southern Germany (Modell 1943, 1950; Hölzl 1957) and lower Middle Miocene deposits of western Hungary (Kókay 2006).

Subfamily Unioninae Rafinesque, 1820

Genus *Unio* Philipsson, 1788 *in* Retzius (1788)

Type species. – *Mya pictorum* Linnaeus, 1758; by subsequent designation by ICZN (1957). Recent, Europe.

Unio sp.

Figure 12I

? 2012 *Unio*. – Nagymarosy & Hámor, p. 166.

Material. – Five specimens: 1 peeled articulated shell (NHMW 2025/0246/0008, Fig. 12I) and 1 deformed and peeled articulated shell from Szászvár 1 (NHMW 2025/0246/0001), 2 partly deformed articulated shells (NHMW 2025/0246/0029–0030) and 1 fragmented and deformed articulated shell in butterfly position from Máza (NHMW 2025/0246/0035).

Dimensions. – 41 × 21 × ~ 6 mm (NHMW 2025/0246/0008; Fig. 12J)

Remarks. – The shell is small-sized, elongated, moderately but regularly convex, and inequilateral. Its anterior side makes up 18% of the shell length, the outline is anteriorly rounded and posteriorly pointed, and the umbo is prosogyrate and projects over the hinge line. The hinge of the left valve is slightly curved with prominent pseudocardinal cusps, which are anteriorly high, elongated and narrow, and posteriorly trigonal; the anterior teeth are made of two blade-like ledges. This type of morphology allows classification in the genus *Unio*, but the deformation, fragmentation, and surface erosion hinder a species-level determination. The general shell shape and hinge features remind somewhat the Early Miocene *Unio eseri* Krauss, 1852 and the Late Miocene *Unio atavus* Hörnes, 1864, both of which are however distinctly larger.

Unionidae gen. et sp. indet.
Figure 11O, 12J

Material. – One cluster of shell fragments (NHMW 2025/0246/0010; Fig. 12J), 1 beak imprint (NHMW 2025/0246/0009; Fig. 11O), and 1 fragment (SNSB-BSPG 2025 IX 80) from Szászvár 1.

Remarks. – The residual unionid material comprises fragments and imprints of shells not allowing precise classification. A closer inspection of the specimen illustrated in Fig. 12J reveals that it is most probably composed of fragments of several shells. Its beak showing commarginal–wavy umbonal sculpture along with other adjoined shell fragments are, however, conspicuously flat thus likely differing from the species described above. An additional beak imprint (Fig. 11O) from the same sample shows a similar type of concentric umbonal sculpture.

Results and Discussion

Faunal composition

The here described fauna comprises 17 species, including 12 species of gastropods (1 Neritidae, 2 Melanopsidae, 1 Pachychilidae, 1 Bithyniidae, 2 Hydrobiidae, 5 Planorbidae) and five species of bivalves (1 Dreissenidae, at least 4 Unionidae) (Tab. 2). Eleven could be identified to the species level (one of which tentatively), six were left in open nomenclature due to poor preservation. Six species and one genus were found new to science: *Pyrgula sopianae* sp. nov. in the family Hydrobiidae (subfamily Pyrgulinae), *Asymmetrorbis pseudovitrina* gen. et sp. nov., *Gyraulus ianus* sp. nov., *Gyraulus magyari* sp. nov., and *Gyraulus pseudodalmaticus* sp. nov. in the family Planorbidae, and the bivalve *Potomida schneideri* sp. nov. (family Unionidae).

Table 2. Material list of the Early–Middle Miocene mollusk taxa identified from the Mecsek Mts. herein. See Table 1 for locality details.

Species	Family	Abaliget	Feked 1	Feked 2	Himesháza	Máza	Szászvár 1	Szászvár 2	Apátvarasd
Theodoxus sp.	Neritidae					4	14		
Melanopsis sp. 1	Melanopsidae					12			
Melanopsis sp. 2	Melanopsidae					6			
Melanopsis sp.	Melanopsidae					71	1?		
Tinnyea lauraea (Matheron, 1843)	Pachychilidae					22	2		
Ferebithynia vadaszi (Wenz, 1931)	Bithyniidae	45	525	101	418	> 1000	>500	47	2
Pyrgula sopianae Neubauer sp. nov.	Hydrobiidae					44		1	
Bania? sp.	Hydrobiidae					1			
Asymmetrorbis pseudovitrina Neubauer sp. nov.	Planorbidae				12				
Gyraulus ianus Neubauer sp. nov.	Planorbidae		124	16	71				
Gyraulus magyari Neubauer sp. nov.	Planorbidae		1		3				
Gyraulus nedici (Brusina, 1902)	Planorbidae				1	5	2		
Gyraulus pseudodalmaticus Neubauer sp. nov.	Planorbidae				2				
Trigonipraxis boeckhi (Wenz, 1931)	Dreissenidae		33		28				
Potomida schneideri Mandic sp. nov.	Unionidae					9			
Elliptio? cf. *larteti*	Unionidae					1			
Unio sp.	Unionidae					3	2		
Unionidae gen. et sp. indet.	Unionidae						3		

From the taxa we identified to the species level, only *Ferebithynia vadaszi* and *Trigonipraxis boeckhi* have been previously reported from the upper Lower Miocene to lower Middle Miocene freshwater deposits of the Mecsek Mts. (Wenz 1931, Sebe *et al.* 2019). Wenz (1931) referred to a keeled *Gyraulus* sp., most likely representing our *Gyraulus ianus* sp. nov. Nagymarosy & Hámor (2012) additionally mentioned the presence of the genera *Theodoxus*, "*Brotia*" (? = *Tinnyea lauraea*), and *Unio* in the Szászvár Formation but without providing further details. Specimens identified as *Stagnicola*? sp. by Sebe *et al.* (2019) are probably conspecific with *Ferebithynia vadaszi*. New occurrences of previously described species concern the widely distributed pachychilid species *Tinnyea lauraea* and the DLS planorbid species *Gyraulus nedici*.

Strausz (1966, p. 66, pl. 13, figs 24–27, text-fig. 38) indicated an additional species, *Stenothyra schwartzi* (Hörnes, 1856), from an unspecified locality in the Mecsek Mts. This species was not encountered during our expeditions.

Summarizing the available information, old and new, the species inventory of the Mecsek Mts. during the late Early to early Middle Miocene increased to at least 18 species. In terms of relative abundance, *Ferebithynia vadaszi* is the most common species in our samples. With numerous shells and even more (> 2200) opercula it represents approximately 70% of the pooled assemblages (counting only opercula). However, our sampling was not quantitative and especially *Trigonipraxis boeckhi*, otherwise a ubiquitous fossil, is not well represented in our material due to the difficulties of extracting intact valves from the sediment. Both species occur in rock-forming quantities (Sebe *et al.* 2019).

Paleoecology

The here described fauna contains a mix of different assemblages from different environments and, potentially, slightly different ages (Tab. 2). The samples from the Szászvár Formation correspond to deposits of a lacustrine delta (Máza and Szászvár) or a river (Apátvarasd). In turn, the assemblages deriving from the Komló Claymarl and the Pécsvárad Members (Kiskunhalas Formation) were interpreted to have formed under littoral (Feked 1 and Himesháza) to sublittoral (Abaliget and Feked 2) lacustrine settings (Sebe *et al.* 2019). While the Komló Claymarl and Pécsvárad Members are considered coeval and Karpatian to early Badenian in age, the Szászvár Formation is probably slightly older. A K-Ar radiometric age of 16.82 ± 0.65 Ma (Karpatian/late Burdigalian) has been recently derived for a tuff interlayer in the Komló Claymarl at Abaliget (Sebe *et al.* 2019). Tuffs underlying the sampled beds of the Szászvár Formation at Máza and Szászvár, previously yielding K-Ar ages of 22.2 ± 1.9 Ma (biotite) and 17.7 ± 1.9 Ma (plagioclase) (Hámor *et al.* 1979), were recently U-Pb dated to a younger age of 17.055 ± 0.024 Ma (Harangi & Lukács 2019). The mollusk-bearing deposits are thus likely Karpatian/late Burdigalian, or potentially early Badenian/Langhian in age.

The different stratigraphic ages and paleoecological interpretations are reflected in the here identified mollusk faunas. The deltaic, river-influenced samples contain abundant *Ferebithynia*, common *Melanopsis* and *Pyrgula*, along with occurrences of *Theodoxus*, *Tinnyea*, *Bania*, *Gyraulus*, and *Unio*. Especially *Theodoxus, Melanopsis*, and unionids are today typical inhabitants of fluvial environments (Welter-Schultes 2012, Glöer 2019). Also the fossil pachychilid genus *Tinnyea* was interpreted as a primarily riverine dweller (Kowalke 2004). Many of the genera would occur in other settings as well – for example, *Theodoxus* and *Melanopsis* are common constituents of many Miocene lakes (*e.g.*, Harzhauser *et al.* 2002; Neubauer *et al.* 2011, 2013b, 2016b) – but the overall composition, and particularly the low frequency of classical lacustrine elements such as pulmonate gastropods, suggests lotic conditions. While many melanopsids, bithyniids, and even some species of *Theodoxus* nowadays tolerate oligohaline conditions, the general composition as well as the presence of unionids indicate pure freshwater environments (compare Verbrugge *et al.* 2012).

The lacustrine assemblages are also dominated by *Ferebithynia*, which seems to be an ecological generalist, occurring across a variety of environments, much like modern *Bithynia tentaculata* (Linnaeus, 1758) (Welter-Schultes 2012). Additionally occurring taxa are the five species of planorbids and *Trigonipraxis boeckhi*. The abundance of planorbids and the lack of common fluvial taxa like *Theodoxus*, *Melanopsis*, *Tinnyea*, and *Unio* are indicative of low-energy conditions (Welter-Schultes 2012, Glöer 2019). Also, the fossil dreissenid genus *Trigonipraxis* is commonly found in lake sediments (Neubauer *et al.* 2020).

Paleobiogeography

The new species records presented here shed new light on the biogeographic affiliation of the Mecsek fauna. In earlier biogeographic analyses, Harzhauser & Mandic (2008) and Krstić *et al.* (2012) indicated the southern Hungarian faunas to be part of the Dinaride Lake System, although neither of them specifically referred to the Mecsek fauna. Mandic *et al.* (2012) coined the term Illyrian Bioprovince for the faunas of the region, including

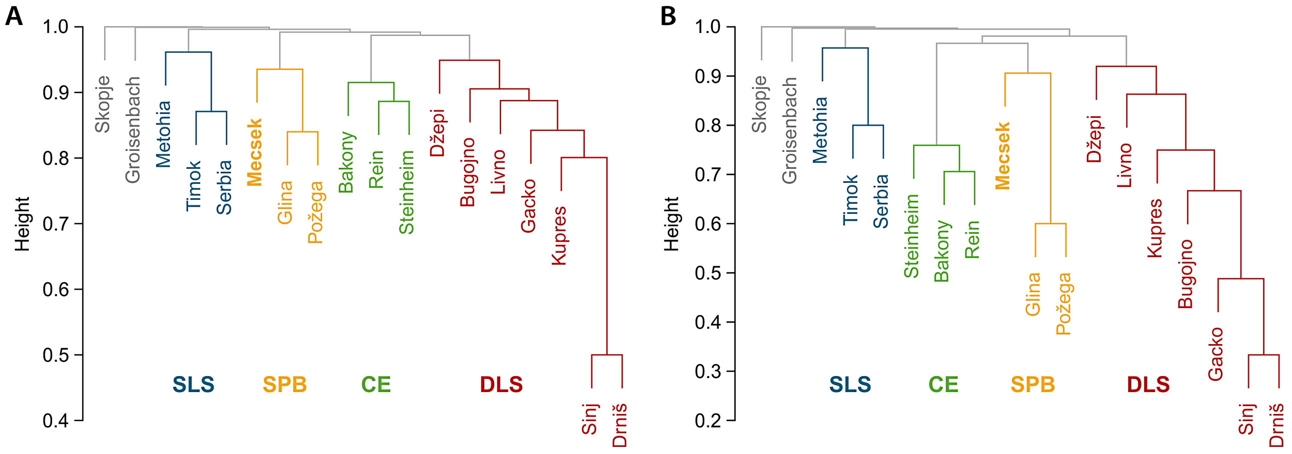


Figure 13. Dendrograms of the cluster analyses showing the similarities of selected late Early to early Middle Miocene Central to Southeastern European faunas. • A – overall Jaccard distance. • B – turnover component of the Jaccard distance, indicating differences in species composition while disregarding differences in species numbers. In both analyses, the four main clusters coinciding with geographic units are highlighted (see also Fig. 14).

those from both the DLS and the Mecsek Mts. They also considered the assemblages from the Bakony Mts. in central Hungary (Kókay 2006), as well as the Fohnsdorf Basin (Hölzel & Wagreich 2004) and the Vienna Basin in eastern Austria (Schultz 2005, Mandic *et al.* 2012), to belong to that unit because of widespread occurrences of dreissenid bivalves. Based on a statistical reevaluation of biogeographic relationships of European Neogene gastropod faunas, Neubauer *et al.* (2015a) considered the Mecsek Mts. fauna also to belong in the Illyrian Region (see also Sebe *et al.* 2019). However, the abovementioned Austrian and mid-Hungarian faunas were considered to belong in other regions. Moreover, the attribution of the Mecsek fauna was purely based on its geographic vicinity to the DLS rather than because of its – back then inadequately known – fauna.

Here, for the first time, we used a statistical approach combining both bivalve and gastropod species occurrences

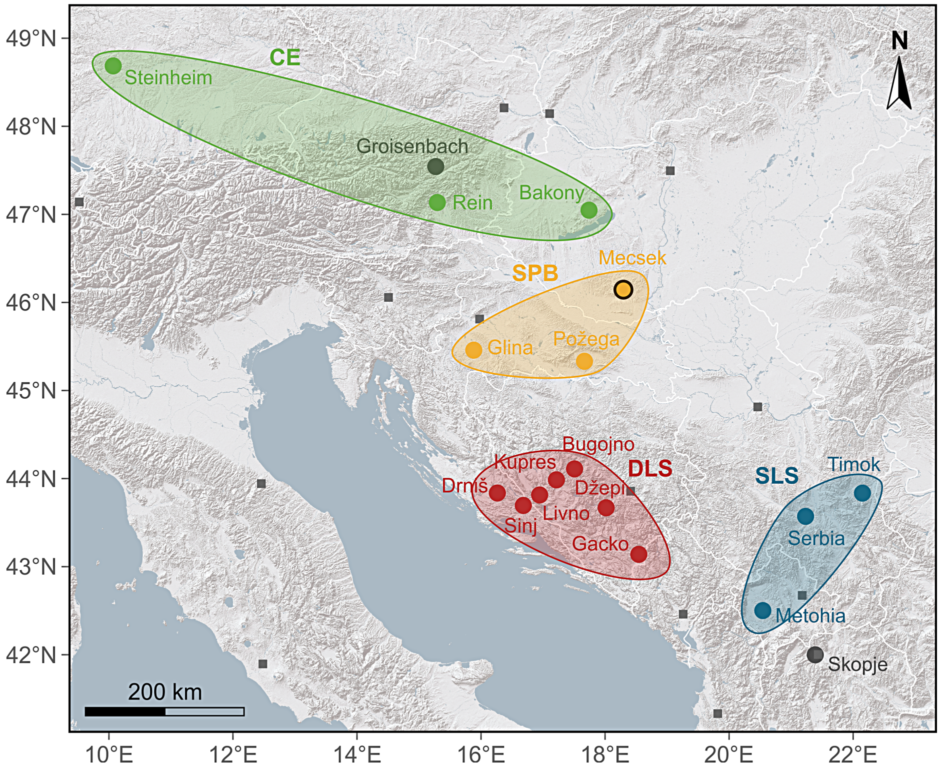


Figure 14. Map of the late Early to early Middle Miocene Central to Southeastern European faunas selected for the cluster analyses. Colors match Fig. 13 and indicate the main clusters; outliers are given in gray. Note that the convex hulls here group only the included localities but do not cover the entire geographic range of the respective systems. Abbreviations: CE – Central European; DLS – Dinaride Lake System; SLS – Serbian Lake System; SPB – Southern Pannonian Basin. Map was created in ESRI ArcGIS Pro v. 3.5 using the World Shaded Relief basemap of ESRI (2009).

to infer biogeographic relationships. The analyses show similar results for the overall beta diversity and the turnover component, related to differences in species composition (Fig. 13). In both analyses, four consistent clusters are recognized showing a clear geographic pattern (Fig. 14): (i) the DLS faunas (lakes Sinj, Drniš, Gacko, Kupres, Livno, Džepi, and Bugojno); (ii) the SLS faunas (Serbia, Timok), including here also the Lake Metohia in Kosovo); (iii) faunas of central Europe (CE) (Bakony, Steinheim am Albuch, Rein); and (iv) Southern Pannonian Basin (SPB) faunas, including Mecsek, Glina, and Požega. Lakes Groisenbach (Austria) and Skopje (North Macedonia) form outliers. The relationships of the four main clusters varies slightly between the two analyses, especially concerning the similarity of the cluster including the Mecsek fauna. The dendrogram of overall beta diversity suggests a marginally higher similarity between DLS and central European faunas than with SPB faunas (Fig. 13A), while the distances based on turnover component show a stronger association between central European and SPB faunas (Fig. 13B).

Both analyses evidence the biogeographic intermediate position of Mecsek, and SPB faunas in general, between the DLS and central European faunas. The revised biogeographic scheme we show here differs in part from previous assessments (Mandic *et al.* 2012, Neubauer *et al.* 2015a), potentially for several reasons. Except for the revised and expanded species inventory of the Mecsek fauna, the inclusion of bivalves in the analyses as well as the selection of the faunas for comparison and different stratigraphic constraints (here summarizing late Early to Middle Miocene faunas compared to a separate Early vs. Middle Miocene approach in Neubauer *et al.* 2015a) certainly contribute to the different results.

More specifically, the new occurrences of *Tinnyea lauraea* and *Gyraulus nedici* for Mecsek link the fauna with that of the Glina Basin. The fauna of the Požega Basin in northeastern Croatia (Mandic *et al.* 2019b), which was not considered in previous analyses, shares with Mecsek *Tinnyea lauraea*. The record of *Trigonipraxis boeckhi* from that basin is probably a misidentification of *T. pilari* (see chapter Systematic paleontology). *Tinnyea lauraea*, *Gyraulus nedici*, and *Trigonipraxis boeckhi*, as well as *Ferebithynia vadaszi*, are also present in the Bakony Mts. (Kókay 2006). In turn, the Glina fauna includes *Orygoceras dentaliforme* Brusina, 1882, a signature species for the DLS and SLS. Additionally corroborating the affinity of Mecsek with DLS faunas – but not statistically evaluable – are the potential occurrence of *Gyraulus ianus* sp. nov. in DLS deposits of Pag Island (Croatia), as well as the potential sister species relationship of *Gyraulus dalmaticus* (Brusina, 1884) and *Gyraulus pseudodalmaticus* sp. nov. The SPB Lake Požega contains a dreissenid species of the genera *Trigonipraxis* and *Illyricocongeria*, which are typical elements of the DLS and SLS (Neubauer *et al.* 2016c, 2020) but not found in northern assemblages such as the Bakony Mts. or the Vienna Basin.

Since our analyses included only selected faunas from the Peri-Paratethyan and Central-West European regions *sensu* Neubauer *et al.* (2015a), the relationships of SPB faunas with these regions still need to be assessed in future studies. Moreover, many a fauna included here is in urgent need of taxonomic revision, which may yet again change the picture.

Acknowledgments

We are grateful to János Hír for providing the sieved materials for some of the outcrops; to Máté Gregorits for collecting and preparing much of the Máza and Szászvár mollusks; to Mathias Harzhauser and Maxim Vinarski for fruitful discussions on the taxonomy and systematic placement of the new genus; to Zlata Jurišić-Polšak for making specimens at NHMZ made available for study; to Hrvoje Posilović and Nives Borčić for providing photographs of type material stored at NHMZ; to Alfréd Dulai for providing HNHM collection numbers; to Quentin Wackenheim for searching after the Noulet types at the Muséum national d'Histoire naturelle in Paris; to Katharina Peter for assisting with material sorting; and finally to Olaf Höltke and Vitaliy V. Anistratenko for constructive comments on an earlier draft. Field work was carried out in the frame of the project NKFIH FK148576. This research was funded in part by the Austrian Science Fund (FWF) grants DOI 10.55776/I6504 and DOI 10.55776/P18519. For open access purposes, the author has applied a CC BY public copyright license to any author accepted manuscript version arising from this submission. The former grant contributes to a bilateral research project through the Weave initiative with the Deutsche Forschungsgemeinschaft (DFG), grant no. TO 1364/3-1 (DRASTIC). This is HUN-REM–MTM–ELTE Paleo contribution No. 431.

References

Adams, H. & Adams, A. 1853–1858. *The Genera of Recent Mollusca Arranged According to Their Organizations*. 2 vol. of text, 661 pp., 1 vol. of plates. Van Voorst, London. DOI 10.5962/bhl.title.4772

Andrusov, N. 1890. Kerchenskiy izvestnyak i yego fauna. *Zapiski Imperatorskago S.-Petersburgskago Mineralogicheskago Obshchestva, seriya 2 26*, 193–344.

Andrusov, N. 1897. *Iskopayemyya i zhivushchiya Dreissensidae Yevrazii [Fossile und lebende Dreissenidae Eurasiens]*. Text, 683 pp.; atlas, 20 pls. Tipografiya M. Merkusheva, St. Petersburg.

Badzoshvili, T.I. 1979. *Mollyuski meotisa zapadnoy Gruzii*. 144 pp. Metsniereba, Tbilisi.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography 19*, 134–143. DOI 10.1111/j.1466-8238.2009.00490.x

Baselga, A. & Orme, C.D.L. 2012. Betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution 3(5)*, 808–812. DOI 10.1111/j.2041-210X.2012.00224.x

Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieur, F., Martinez-Santalla, S., Martin-Devasa, R., Gomez-Rodriguez, C. & Crujeiras, R.M. 2023. Betapart: Partitioning beta diversity into turnover and nestedness components. R package version 1.6. *http://CRAN.R-project.org/package=betapart*

Bieler, R., Mikkelsen, P.M., Collins, T.M., Glover, E.A., González, V.L., Graf, D.L., Harper, E.M., Healy, J., Kawauchi, G.Y., Sharma, P.P., Staubach, S., Strong, E.E., Taylor, J.D., Tëmkin, I., Zardus, J.D., Clark, S., Guzmán, A., McIntyre, E., Sharp, P. & Giribet, G. 2014. Investigating the Bivalve Tree of Life – an exemplar-based approach combining molecular and novel morphological characters. *Invertebrate Systematics 28(1)*, 32–115. DOI 10.1071/IS13010

Boda, J. 1959. A magyarországi szarmata emelet és gerinctelen faunája. *A Magyar Állami Földtani Intézet Évkönyve 47(3)*, 569–862.

Bouchet, P. & Rocroi, J.-P. 2010. Nomenclator of Bivalve Families; with a classification of bivalve families by R. Bieler, J.G. Carter, and E.V. Coan. *Malacologia 52(2)*, 1–184. DOI 10.4002/040.052.0201

Bouchet, P., Rocroi, J.-P., Hausdorf, B., Kaim, A., Kano, Y., Nützel, A., Parkhaev, P., Schrödl, M. & Strong, E.E. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia 61(1–2)*, 1–526. DOI 10.4002/040.061.0201

Bourguignat, J.R. 1881. Histoire malacologique de la Colline de Sansan, précédée d'une notice géologique et suivie d'un apercu climatologique et topographique de Sansan, a l'époque des dépôts de cette colline. *Annales des sciences géologiques 11(5)*, 1–175.

Braun, A. 1851. Darstellung der geognostischen Verhältnisse des Mainzer Beckens und seiner fossilen Fauna und Flora, 1121–1169. *In* Walchner, F.A. (ed.) *Handbuch der Geognosie zum Gebrauche bei seinen Vorlesungen und zum Selbststudium mit besonderer Berücksichtigung der geognostischen Verhältnisse des Grossherzogthums Baden*. Christian Theodor Gross, Karlsruhe.

Brusina, S. 1872. Naravoslovne crtice sa sjevero-istočne obale Jadranskoga mora. Dio prvi. Putopis. *Rad Jugoslavenske akademije znanosti i umjetnosti 19*, 105–177.

Brusina, S. 1874. *Fossile Binnen-Mollusken aus Dalmatien, Kroatien und Slavonien nebst einem Anhange*. 138 pp. Actienbuchdruckerei, Agram. DOI 10.5962/bhl.title.159142

Brusina, S. 1876. Decription d'espèces nouvelles, provenant des terrains tertiaires de Dalmatie. *Journal de Conchyliologie 24*, 109–116.

Brusina, S. 1882. Le Pyrgulinae dell'Europa orientale. *Bollettino della Società Malacologica Italiana 7(13–19)*, 229–292.

Brusina, S. 1884. Die *Neritodonta* Dalmatiens und Slavoniens nebst allerlei malakologischen Bemerkungen. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft 11*, 17–120.

Brusina, S. 1892. Fauna fossile terziaria di Markuševec in Croazia. Con un elenco delle Dreissensidae della Dalmazia, Croazia e Slavonia. *Glasnik Hrvatskoga naravoslovnoga društva 7*, 113–210.

Brusina, S. 1893. Frammenti di Malacologia terziaria Serba. *Annales Géologiques de la Péninsule Balkanique 4(2)*, 25–74.

Brusina, S. 1896. Neogenska zbirka iz Ugarske, Hrvatske, Slavonije i Dalmacije na budimpeštanskoj izložbi. *Glasnik Hrvatskoga naravoslovnoga društva 9*, 98–150.

Brusina, S. 1897. Gragja za neogensku malakološku faunu Dalmacije, Hrvatske i Slavonije uz neke vrste iz Bosne i Hercegovine i Srbije. *Djela Jugoslavenske akademije znanosti i umjetnosti 18*, 1–43.

Brusina, S. 1902. *Iconographia Molluscorum Fossilium in tellure tertiaria Hungariae, Croatiae, Slavoniae, Dalmatiae, Bosniae, Herzegovinae, Serbiae and Bulgariae inventorum*. 10 pp., 30 pls. Officina Soc. Typographicae, Agram.

Brusina, S. 1907. Naravoslovne crtice sa sjevero-istočne obale Jadranskoga mora. Dio cetvrti i posljednji. Specijalni. *Rad Jugoslavenske akademije znanosti i umjetnosti 169*, 195–251.

Bukowski, G. 1930. Bemerkungen über die Binnenablagerungen in der Umgebung des Buldur Giöl in Kleinasien. *Annales Societatis Geologorum Poloniae 6*, 73–90.

Bulić, J. & Jurišić-Polšak, Z. 2009. Macropalaeontology and Stratigraphy of Lacustrine Miocene Deposits at Crnika Beach on the Island of Pag (Croatia). *Geologia Croatica 62(3)*, 135–156. DOI 10.4154/GC.2009.16

Chaput, E. & Gillet, S. 1939. Les faunes de Mollusques des terrains á *Hipparion gracile* de Küçük Çekmece près Istanbul (Turquie). *Bulletin de la Société Géologique de France, cinquième série 8(5–6)*, 363–388.

Charpentier, J. de 1837. Catalogue des mollusques terrestres et fluviatiles de la Suisse. Formant la seconde partie de la faune Helvétique. *Neue Denkschriften der Allg. Schweizerischen Gesellschaft für die Gesammten Naturwissenschaften / Nouveau mémoires de la Société helvétique des sciences naturelles 1*, 1–28. DOI 10.5962/bhl.title.10700

Chikán, G. 1991. A Nyugati-Mecsek kainozóos képződményei. *Magyar Állami Földtani Intézet évkönyve 72(1)*, 5–281.

Clessin, S. 1877. Die tertiären Binnenconchylien von Undorf. *Correspondenz-Blatt des zoologisch-mineralogischen Vereines in Regensburg 31(3)*, 34–41.

Cox, L.R. 1960. Thoughts on the classification of the Gastropoda. *Proceedings of the Malacological Society of London 33*, 239–261.

Cox, L.R., Newell, N.D., Boyd, D.W., Branson, C.C., Casey, R., Chavan, A., Coogan, A.H., Dechaseaux, C., Fleming, C.A., Haas, F., Hertlein, L.G., Kauffman, E.G., Keen, A.M., LaRocque, A., McAlester, A.L., Moore, R.C., Nuttall, C.P., Perkins, B.F., Puri, H.S., Smith, L.A., Soot-Ryen, T., Stenzel, H.B., Trueman, E.R., Turner, R.D. & Weir, J. 1969. Part N. Mollusca 6, Bivalvia, 1–951. *In* Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology*. Geological Society of America and University of Kansas Press, Lawrence, Kansas.

Cuvier, G. 1795. Second Mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société d'Histoire Naturelle de Paris, le 11 prairial an troisième. *Magasin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts 2*, 433–449.

Cuvier, G. 1797. *Tableau élémentaire de l'histoire naturelle des animaux*. 710 pp. Beaudouin, Paris. DOI 10.5962/bhl.title.11203

Cuvier, G. & Brongniart, A. 1822. Description géologique des couches des environs de Paris, parmi lesquelles se trouvent les gypses à ossemens. *In* Cuvier, G. (ed.) *Recherches sur les ossemens 2(2)*. 428 pp. G. Dufour & E. d'Ocagne, Paris. DOI 10.5962/bhl.title.149831

Dall, W.H. 1870. On the genus *Pompholyx* and its allies, with a revision of the Limnaeidae of authors. *Annals of the Lyceum of Natural History of New York 9*, 333–361. DOI 10.1111/j.1749-6632.1870.tb00201.x

De Cristofori, G. & Jan, G. 1832. *Catalogus in IV. sectiones divisus rerum naturalium in museo exstantium Josephi De Cristofori et Georgii Jan plurium Acad. Scient. et Societ. Nat. Cur. Sodalium complectens adumbrationem oryctognosiae et geognosiae atque prodromum faunae et floriae Italiae Superioris. Sectio II. Conchyliologia. Pars I. Conspectus methodicus molluscorum. Fasc. 1. Testacea terrestria et fluviatilia*. pp. 1–2 [unnumbered] [Dispositio methodica generum], pp. 1–8 [Conchylia terrestria et fluviatilia], 1–4 [Mantissa in secundam partem catalogi testaceorum exstantium in collectione quam possident], 1–4 [Excerptum e primo nostre programmate], 1–16 [Conchylia fossilia]. Carmignani, Parma. DOI 10.5962/bhl.title.59812

Deshayes, G.P. 1835. Mollusques, 81–203. *In* Bory de Saint-Vincent, J.-B. (ed.) *Expédition scientifique de Morée. Section des sciences physiques. Tome III. – 1.re Partie. Zoologie. Première Section*. F.G. Levrault, Paris.

Dumurdzanov, N. & Krstić, N. 1999. The Skopje Neogene basin in the Republic of Macedonia. *Geologica Macedonica 13*, 47–56.

Dunker, W. 1848. Über die in der Molasse bei Günzberg unfern Ulm vorkommenden Conchylien und Pflanzenreste. *Palaeontographica 1(4)*, 155–168.

ESRI 2009. World Shaded Relief [basemap]. Created on December 12, 2009, updated on April 11, 2025. *https://www.arcgis.com/home/item.html?id=9c5370d0b54f4de1b48a3792d7377ff2*

Férussac, A.E.J.P.J.F. d'Audebard de. 1822–1823. *Histoire naturelle générale et particulière des mollusques terrestres et fluviatiles tant des espèces que l'on trouve aujourd'hui vivantes, que des dépouilles fossiles de celles qui n'existent plus; classés d'après les caractères essentiels que présentent ces animaux et leurs coquilles. Mélanopsides fossiles*. Livr. 15: pl. 1 (1822); livr. 21: pl. 2 (1823). J.-B. Bailliere, Paris.

Férussac, A.E.J.P.J.F. d'Audebard de 1823. *Histoire naturelle générale et particulière des mollusques terrestres et fluviatiles tant des espèces que l'on trouve aujourd'hui vivantes, que des dépouilles fossiles de celles qui n'existent plus; classés d'après les caractères essentiels que présentent ces animaux et leurs coquilles. Nérites fossiles.* 2 pls, J.-B. Bailliere, Paris.

Férussac, J.B.L. d'Audebard de & Férussac, A.E.J.P.J.F. d'Audebard de. 1807. *Essai d'une méthode conchyliologique appliquée aux mollusques fluviatiles et terrestres d'après la considération de l'animal et de son test. Nouvelle édition augmentée d'une synonymie des espèces les plus remarquables, d'une table de concordance systématique de celles qui ont été décrites par Géoffroy, Poiret et Draparnaud, avec Müller et Linné, et terminée par un catalogue d'espèces observées en divers lieux de la France*. 142 pp. Delance, Paris.

Finger, I. 1998. Gastropoden der *kleini*-Schichten des Steinheimer Beckens (Miozän, Süddeutschland). *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) 259*, 1–51.

Fischer, J.-C. 2000. La malacofauna de Sansan, 129–154. *In* Ginsburg, L. (ed.) *La faune miocéne de Sansan et son environment. Mémoires du Muséum national d'histoire naturelle 183*.

Fischer, P. & Crosse, H. 1880–1902. Études sur les mollusques terrestres et fluviatales du Mexique et du Guatemala, 1–731. *In* Milne Edwards, H. (ed.) *Recherches Zoologiques pour servir à l'histoire de la faune de l'Amérique Centrale et du Mexique. Septième partie. Tome second.*

Fleming, J. 1822. *The Philosophy of Zoology, a General View of the Structure, Functions and Classification of Animals 2*. 618 pp. Constable & Co., Edinburgh. DOI 10.5962/bhl.title.24597

Frauenfeld, G. von 1864. Verzeichniss der Namen der fossilen und lebenden Arten der Gattung *Paludina* Lam. nebst jenen der nächststehenden und Einreichung derselben in die verschiedenen neueren Gattungen. *Verhandlungen der zoologisch-botanischen Gesellschaft in Wien 14*, 561–672.

Frýda, J. 1998. Higher classification of the Paleozoic gastropods inferred from their early shell ontogeny, 108. *In* Bieler, R. & Mikkelsen, P.M. (eds) *13th International Malacological Congress, Abstracts*. Unitas Malacologica, Washington, D.C.

Gál, E., Hír, J., Kessler, E., Kókay, J., Mészáros, L. & Vencel, M. 1999. Középső-miocén ősmaradványok, a Mátraszőlős, Rákóczi-kápolna alatti útbevágásból I. A Mátraszőlős 1. lelőhely. *Folia Historico Naturalia Musei Matraensis 23*, 33–78.

Gál, E., Hír, J., Kessler, E., Kókay, J. & Venczel, M. 2000. Középső-miocén ősmaradványok, a Mátraszőlős, Rákóczi-kápolna alatti útbevágásból I. A Mátraszőlős 2. lelőhely. *Folia Historico Naturalia Musei Matraensis 24*, 39–75.

Gillet, S., Gramann, F. & Steffens, P. 1978. Neue biostratigraphische Ergebnisse aus dem brackischen Neogen an Dardanellen und Marmara-Meer (Türkei). *Newsletters on Stratigraphy 7(1)*, 53–64. DOI 10.1127/nos/7/1978/53

Giribet, G. & Distel, D.L. 2003. Bivalve phylogeny and molecular data, 45–90. *In* Lydeard, C. & Lindberg, D.R. (eds) *Molecular Systematics and Phylogeography of Mollusks*. Smithsonian Institution, Washington, D.C.

Glöer, P. 2019. *The Freshwater Gastropods of the West-*

Palaearctis. Volume I. Fresh- and Brackish Waters except Spring and Subterranean Snails. Identification Key, Anatomy, Ecology, Distribution. 399 pp. Privately published.

Golikov, A.N. & Starobogatov, Ya.I. 1975. Systematics of prosobranch gastropods. *Malacologia 15(1)*, 185–232.

Gottschick, F. 1921. Die Land- und Süßwassermollusken des Tertiärbeckens von Steinheim am Aalbuch. 7. Fortsetzung. *Archiv für Molluskenkunde 53(3)*, 163–181.

Gray, J.E. 1840. Shells of molluscous animals, 105–152. *In Synopsis of the Contents of the British Museum, 42th Ed.* G. Woodfall, London.

Gray, J.E. 1847. A list of the genera of recent Mollusca, their synonyma and types. *Proceedings of the Zoological Society of London 15*, 129–242.

Gray, J.E. 1854. A revision of the arrangement of the families of bivalve shells (Conchifera). *Annals and Magazine of Natural History (2) 13(77)*, 408–418. DOI 10.1080/03745485709496364

Grobben, K. 1894. Zur Kenntnis der Morphologie, der Verwandtschaftsverhältnisse und des Systems der Mollusken. *Sitzungsberichte der kaiserlichen Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Classe 103*, 61–86.

Guo, F. & Wei, J. 1984. Gastropoda, 83–93. *In* Geological Survey Department of Bureau of Petroleum of Xinjiang Autonomous Region, and Regional Geological Survey Team, Bureau of Geology & Mineral Resources of Xinjiang Autonomous Region (ed.) *Paleontological Atlas of northwestern China, Volume Xinjiang, vol. 3*. Geological Publishing House, Beijing.

Gyalog, L. (ed.) 2013. *Geological Map of Hungary 1:500 000*. Geological and Geophysical Institute of Hungary, Budapest.

Hámor, G. 1970. A Kelet-mecseki miocén. *Magyar Állami Földtani Intézet évkönyve 53(1)*, 7–483.

Hámor, G., Ravasz-Baranyai, L., Balogh, K. & Árva-Sós, E. 1979. K/Ar dating of Miocene pyroclastic rocks in Hungary. *Annales Géologiques des Pays Helléniques, tome hors série 2*, 491–500.

Hantken, M. von. 1887. *Tinnyea Vásárhelyii* nov. gen. et nov. spec. *Földtani Közlöny 17(4)*, 345–348.

Harangi, S. & Lukács, R. 2019. A Kárpát-Pannon térség neogén-kvarter vulkanizmusa és geodinamikai kapcsolata. *Földtani Közlöny 149(3)*, 197. DOI 10.23928/foldt.kozl.2019.149.3.197

Harzhauser, M. & Binder, H. 2004. Synopsis of the Late Miocene mollusc fauna of the classical sections Richardhof and Eichkogel in the Vienna Basin (Austria, Pannonian, MN 9-MN11). *Archiv für Molluskenkunde 133(1–2)*, 1–57. DOI 10.1127/arch.moll/133/2004/109

Harzhauser, M. & Mandic, O. 2008. Neogene lake systems of Central and South-Eastern Europe: Faunal diversity, gradients and interrelations. *Palaeogeography, Palaeoclimatology, Palaeoecology 260(3–4)*, 417–434. DOI 10.1016/j.palaeo.2007.12.013

Harzhauser, M. & Mandic, O. 2010. Neogene dreissenids in Central Europe: evolutionary shifts and diversity changes, 11–28. *In* van der Velde, G., Rajagopal, S. & bij de Vaate, A. (eds) *The Zebra Mussel in Europe*. Backhuys Publishers, Leiden/Margraf Publishers, Weikersheim.

Harzhauser, M., Kowalke, T. & Mandic, O. 2002. Late Miocene (Pannonian) Gastropods of Lake Pannon with Special Emphasis on Early Ontogenetic Development. *Annalen des Naturhistorischen Museums in Wien, Serie A 103*, 75–141.

Harzhauser, M., Neubauer, T.A., Mandic, O., Zuschin, M. & Ćorić, S. 2012. A Middle Miocene endemic freshwater mollusc assemblage from an intramontane Alpine lake (Aflenz Basin, Eastern Alps, Austria). *Paläontologische Zeitschrift 86(1)*, 23–41. DOI 10.1007/s12542-011-0117-x

Harzhauser, M., Neubauer, T.A., Gross, M. & Binder, H. 2014a. The early Middle Miocene mollusc fauna of Lake Rein (Eastern Alps, Austria). *Palaeontographica Abt. A 302(1–6)*, 1–71. DOI 10.1127/pala/302/2013/1

Harzhauser, M., Neubauer, T.A., Georgopoulou, E. & Harl, J. 2014b. The Early Miocene (Burdigalian) mollusc fauna of the North Bohemian Lake (Most Basin). *Bulletin of Geosciences 89(4)*, 819–908. DOI 10.3140/bull.geosci.1503

Harzhauser, M., Landau, B., Mandic, O. & Neubauer, T.A. 2024. The Central Paratethys Sea—rise and demise of a Miocene European marine biodiversity hotspot. *Scientific Reports 14(1)*, 16288. DOI 10.1038/s41598-024-67370-6

Herbich, F. & Neumayr, M. 1875. Beiträge zur Kenntniss fossiler Binnenfaunen. VII. Die Süsswasserablagerungen im südöstlichen Siebenbürgen. *Jahrbuch der k.k. geologischen Reichsanstalt 25(4)*, 401–431.

Hír, J. & Kókay, J. 2004. Middle Miocene molluscs and rodents from Mátraszőlős (Mátra Mountains, Hungary). *Fragmenta Palaeontologica Hungarica 22*, 83–97.

Hír, J. & Kókay, J. 2011. Late Badenian (MN 7/8) molluscs and rodents from Mátraszőlős (Northern Hungary). *Fragmenta Palaeontologica Hungarica 29*, 69–78.

Hír, J., Kókay, J., Lukács, M. & Márton, V. 1998. Középső miocén puhatestű és gerinces maradványok a sámsonházi Oszkoruzsa-árokból. *A Nógrád megyei múzeumok évkönyve 22*, 171–196.

Hír, J., Kókay, J., Venczel, M., Gál, E. & Kessler, E. 2001. Előzetes beszámoló a felsőtárkányi 'Güdörkert' n. őslénytani lelőhelykomplex újravizsgálatáról. *Folia Historico-Naturalia Musei Matraensis 25*, 41–64.

Höltke, O., Salvador, R.B. & Rasser, M.W. 2018. Miocene continental gastropods from the southern margin of the Swabian Alb (Baden-Württemberg, SW Germany). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 287(1)*, 17–44. DOI 10.1127/njgpa/2018/0704

Hölzel, M. & Wagreich, M. 2004. Sedimentology of a Miocene delta complex: the type section of the Ingering Formation (Fohnsdorf Basin, Austria). *Austrian Journal of Earth Sciences 95–96*, 80–86.

Hölzl, O. 1957. Die Corbiculidae der oligozänen und miozänen Molasse Oberbayerns, sowie Bemerkungen zu den oberbayerischen Cyrenenschichten nebst Beschreibung neuer Arten. *Geologica Bavarica 29*, 1–85.

Hörnes, M. 1851–1856. Die fossilen Mollusken des Tertiär-Beckens von Wien. I. Univalven. *Abhandlungen der Geologischen Reichsanstalt 3*, 1–736, pls 1–52 [pp. 1–42, 1–5

(1851); pp. 43–184, pls 6–15 (1852); pp. 185–296, pls 16–32 (1853); pp. 297–384, pls 33–40 (1854); pp. 385–460, pls 41–45 (1855); pp. 461–736, pls 46–52 (1856)].

Hörnes, M. 1859–1870. Die fossilen Mollusken des Tertiär-Beckens von Wien. II. Band: Bivalven. *Abhandlungen der Geologischen Reichsanstalt 4*, 1–479, pls 1–85 [pp. 1–116, 1–11 (1859); pp. 117–214, pls 12–31 (1861); pp. 215–342, pls 32–44 (1864); pp. 343–430, pls 45–67 (1867); pp. 431–479, pls 68–85 (1870)].

ICZN 1957. Opinion 495. Designation under the Plenary Powers of a type species in harmony with accustomed usage for the nominal genus *Unio* Philipsson, 1788 (class Pelecypoda) and validation under the same Powers of the family-group name Margaritiferidae Haas, 1940. *Opinions and Declarations rendered by the International Commission on Zoological Nomenclature 17(17)*, 287–322. DOI 10.5962/p.149634

Iljina, L.B., Nevesskaya, L.A. & Paramonova, N.P. 1976. *Zakonomernosti razvitiya mollyuskov v opresnennykh basseinakh neogena Evrazii (pozdnii Miocen-rannii Pliocen)*. 288 pp. Izdatel'stvo Nauka, Moskva.

Jekelius, E. 1944. Sarmat und Pont von Soceni (Banat). *Memoriile Institutului geologic al României 5*, 1–167.

Jörger, K.M., Stöger, I., Kano, Y., Fukuda, H., Knebelsberger, T. & Schrödl, M. 2010. On the origin of Acochlidia and other enigmatic euthyneuran gastropods, with implications for the systematics of Heterobranchia. *BMC Evolutionary Biology 10*, 323. DOI 10.1186/1471-2148-10-323

Jurišić-Polšak, Z., Krizmanić, K. & Hajek-Tadesse, V. 1993. Freshwater Miocene of Krbavsko Polje in Lika (Croatia). *Geologia Croatica 46(2)*, 213–228.

Kälin, D., Weidmann, M., Engesser, B. & Berger, J.-P. 2001. Paléontologie et âge de la Molasse d'eau douce supérieure (OSM) du Jura neuchâtelois. *Schweizerische Paläontologische Abhandlungen 121*, 64–99.

Klein, A. 1853. Conchylien der Süsswasserkalkformation Württembergs. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg 9*, 203–223.

Kochansky-Devidé, V. & Slišković, T. 1978. Miocenske kongerije Hrvatske, Bosne i Hercegovine. *Palaeontologia jugoslavica 19*, 1–98.

Kochansky-Devidé, V. & Slišković, T. 1981. Mlade miocenske kongerije Livanjskog, Duvanjskog i Kupreškog polja u jugozapadnoj Bosni i Hodova u Hercegovini. *Palaeontologia jugoslavica 25*, 1–25.

Kókay, J. 1967. A Bakony-hegység felsőtortonai képződményei. *Földtani Közlöny 97*, 74–90.

Kókay, J. 2006. Nonmarine mollusc fauna from the Lower and Middle Miocene, Bakony Mts., W Hungary. *Geologica Hungarica, Series Palaeontologica 56*, 1–196.

Kókay, J. 2013. Study of the Middle Miocene (Badenian and Sarmatian) formations in the Várpalota Neogene Basin. *Földtani Közlöny 143(2)*, 145–156.

Kováč, M., Hudáčkova, N., Halásová, E., Kováčova, M., Holcová, K., Oszczypko-Clowes, M., Báldi, K., Less, G., Nagymarosy, A., Ruman, A., Klučiar, T. & Jamrich, M. 2017. The Central Paratethys palaeoceanography: a water circulation model based on microfossil proxies, climate, and changes of depositional environment. *Acta Geologica Slovaca 9(2)*, 75–114.

Kowalke, T. 2004. Evolution of the Pachychilidae Troschel, 1857 (Caenogastropoda, Cerithioidea) – from the Tethys to modern tropical rivers. *Zitteliana A 44*, 41–50.

Krauss, F. 1852. Die Mollusken der Tertiärformation von Kirchberg an der Iller. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg 8*, 136–157.

Krejci, K. & Wenz, W. 1927. Beobachtungen im Schacht I auf Grube Bucea, Câmpina. *Centralblatt für Mineralogie, Geologie und Paläontologie 1927B*, 416–423.

Krstić, N., Savić, L. & Jovanović, G. 2012. The Neogene Lakes of the Balkan Land. *Annales Géologiques de la Péninsule Balkanique 73*, 37–60. DOI 10.2298/GABP1273037K

Kühn, O. 1963. Das Süsswassermiozän von Attika. *Praktika tis Akademias Athinon 38*, 370–400.

Kurr, J.G. von 1856. Land- und Süsswasserconchylien der Tertiärformation Oberschwabens. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg 12*, 38–43.

Lamarck, J.-B.P.A. de M. de. 1819. *Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels, enfin, l'exposition des principes fondomentaux de la zoologie. Tome sixième, première partie*. 343 pp. Privately published, Paris.

Lemberkovics, V., Sebe, K., Selmeczi, I. & Vető, I. 2024. Kiskunhalas Formation, 73–74. *In* Babinszki, E., Piros, O., Csillag, G., Fodor, L., Gyalog, L., Kercsmár, Zs., Less, G., Lukács, R., Sebe, K., Selmeczi, I., Szepesi, J. & Sztanó, O. (eds) *Lithostratigraphic Units of Hungary II. Cenozoic Formations*. Supervising Authority of Regulated Activities, Budapest.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata*. 824 pp. Laurentius Salvius, Holmiae. DOI 10.5962/bhl.title.542

Locard, A. 1893. Monographie des mollusques tertiaires terrestres et fluviatiles de la Suisse. Deuxième partie. *Mémoires de la Société Paléontologique Suisse 19*, 131–275.

Lörenthey, E. 1902. Die Pannonische Fauna von Budapest. *Palaeontographica 48(4–6)*, 137–256, 257–296.

Magyar, I., Geary, D.H. & Müller, P. 1999. Paleogeographic evolution of the Late Miocene Lake Pannon in Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology 147*, 151–167. DOI 10.1016/S0031-0182(98)00155-2

Magyar, I., Radivojević, D., Sztanó, O., Synak, R., Ujszászi, K. & Pócsik, M. 2013. Progradation of the paleo-Danube shelf margin across the Pannonian Basin during the Late Miocene and Early Pliocene. *Global and Planetary Change 103*, 168–173. DOI 10.1016/j.gloplacha.2012.06.007

Mandic, O., De Leeuw, A., Bulić, J., Kuiper, K.F., Krijgsman, W. & Jurišić-Polšak, Z. 2012. Paleogeographic evolution of the Southern Pannonian Basin: 40Ar/39Ar age constraints on the

Miocene continental series of northern Croatia. *International Journal of Earth Sciences 101(4)*, 1033–1046. DOI 10.1007/s00531-011-0695-6

Mandic, O., Sant, K., Kallanxhi, M.-E., Ćorić, S., Theobalt, D., Grunert, P., De Leeuw, A. & Krijgsman, W. 2019a. Integrated bio-magnetostratigraphy of the Badenian reference section Ugljevik in southern Pannonian Basin – implications for the Paratethys history (middle Miocene, Central Europe). *Global and Planetary Change 172*, 374–395. DOI 10.1016/j.gloplacha.2018.10.010

Mandic, O., Hajek-Tadesse, V., Bakrac, K., Reichenbacher, B., Grizelj, A. & Miknic, M. 2019b. Multiproxy reconstruction of the middle Miocene Požega palaeolake in the Southern Pannonian Basin (NE Croatia) prior to the Badenian transgression of the Central Paratethys Sea. *Palaeogeography, Palaeoclimatology, Palaeoecology 516*, 203–219. DOI 10.1016/j.palaeo.2018.12.003

Mandic, O., Harzhauser, M. & Neubauer, T.A. 2020. Taxonomy, palaeoecology and stratigraphy of the middle Miocene mollusk fauna from the Gračanica coal pit near Bugojno in Bosnia and Herzegovina. *Palaeobiodiversity and Palaeoenvironments 100(2)*, 519–549. DOI 10.1007/s12549-020-00423-6

Martinson, G.G. 1951. Tretichnaya fauna mollyuskov Vostochnogo Pribaykal'ya. *Trudy Baikal'skoy Limnologicheskoy Stantzii Akademii Nauk SSSR 13*, 5–92.

Martinson, G.G. 1961. Mezozoiskie i Kainozoiskie Molliuski kontinentalnykh otlozhenii Sibirskoi Platformy Zabaikalia i Mongolii. *Trudy Baikal'skoy Limnologicheskoy Stantzii Akademii Nauk SSSR 19*, 1–332.

Matheron, P. 1843. Catalogue méthodique et descriptif des corps organisés fossiles du départment des Bouches-du-Rhône et lieux circonvoisins. *Répertoire des travaux de la Société de statistique de Marseille 6*, 81–341.

Milan, A., Sakač, K. & Žagar-Sakač, A. 1974. *Katalog originala tipova vrsta pohranjenih u Geološko-paleontološkom muzeju u Zagrebu*. 186 pp. Geološko-paleontološki muzej u Zagrebu, Zagreb.

Modell, H. 1941. Tertiäre Najaden II. *Archiv für Molluskenkunde 73*, 129–139.

Modell, H. 1943. Tertiäre Najaden III. *Archiv für Molluskenkunde 75*, 107–117.

Modell, H. 1950. Tertiäre Najaden V. *Archiv für Molluskenkunde 79(1–3)*, 37–44.

Modell, H. 1958. Die tertiären Najaden des ungarischen Beckens. *Geologisches Jahrbuch 75*, 197–249.

MolluscaBase eds. 2025. *MolluscaBase*. DOI 10.14284/448

Montfort, P.D. de. 1810. *Conchyliologie systématique et classification méthodique de coquilles; offrant leurs figures, leur arrangement générique, leurs descriptions caractéristiques, leurs noms; ainsi que leur synonymie en plusieurs langues. Ouvrage destiné à faciliter l'étude des coquilles, ainsi que leur disposition dans les cabinets d'histoire naturelle. Coquilles univalves, non cloisonnées. Tome second*. 676 pp. Schoell, Paris.

Müller, O.F. 1773–1774. *Vermium terrestrium et fluviatilium historia, seu animalium Infusoriorum, Helminthicorum et Testaceorum non marinorum succincta historia*. 135 + 214 pp. Heineck & Faber, Havniae et Lipsiae. DOI 10.5962/bhl.title.46299

Nagymarosy, A. & Hámor, G. 2012. Genesis and Evolution of the Pannonian Basin, 149–200. *In* Haas, J. (ed.) *Geology of Hungary*. *Regional Geology Reviews*. Springer, Berlin, Heidelberg. DOI 10.1007/978-3-642-21910-8_3

Neubauer, T.A. & Georgopoulou, E. 2021. Extinction risk is linked to lifestyle in freshwater gastropods. *Diversity and Distributions 27(12)*, 2357–2368. DOI 10.1111/ddi.13404

Neubauer, T.A. & Wesselingh, F.P. 2023. The Early Pleistocene freshwater mollusks of the Denizli Basin (Turkey): a new long-lived lake fauna at the crossroads of Pontocaspian and Aegean-Anatolian realms. *Zitteliana 97*, 53–88. DOI 10.3897/zitteliana.97.115682

Neubauer, T.A., Mandic, O. & Harzhauser, M. 2011. Middle Miocene Freshwater Mollusks from Lake Sinj (Dinaride Lake System, SE Croatia; Langhian). *Archiv für Molluskenkunde 140(2)*, 201–237. DOI 10.1127/arch.moll/1869-0963/140/201-237

Neubauer, T.A., Mandic, O., Harzhauser, M. & Hrvatović, H. 2013a. A new Miocene lacustrine mollusc fauna of the Dinaride Lake System and its palaeobiogeographic, palaeoecologic, and taxonomic implications. *Palaeontology 56(1)*, 129–156. DOI 10.1111/j.1475-4983.2012.01171.x

Neubauer, T.A., Mandic, O. & Harzhauser, M. 2013b. The Middle Miocene freshwater mollusk fauna of Lake Gacko (SE Bosnia and Herzegovina): taxonomic revision and paleoenvironmental analysis. *Fossil Record 16(1)*, 77–96. DOI 10.1002/mmng.201300003

Neubauer, T.A., Harzhauser, M., Kroh, A., Georgopoulou, E. & Mandic, O. 2015a. A gastropod-based biogeographic scheme for the European Neogene freshwater systems. *Earth-Science Reviews 143*, 98–116. DOI /10.1016/j.earscirev.2015.01.010

Neubauer, T.A., Harzhauser, M., Georgopoulou, E., Kroh, A. & Mandic, O. 2015b. Tectonics, climate, and the rise and demise of continental aquatic species richness hotspots. *Proceedings of the National Academy of Sciences of the United States of America 112(37)*, 11478–11483. DOI 10.1073/pnas.1503992112

Neubauer, T.A., Harzhauser, M., Mandic, O., Kroh, A. & Georgopoulou, E. 2016a. Evolution, turnovers and spatial variation of the gastropod fauna of the late Miocene biodiversity hotspot Lake Pannon. *Palaeogeography, Palaeoclimatology, Palaeoecology 442*, 84–95. DOI 10.1016/j.palaeo.2015.11.016

Neubauer, T.A., Mandic, O. & Harzhauser, M. 2016b. The early Middle Miocene lacustrine gastropod fauna of Džepi, Bosnia and Herzegovina (Dinaride Lake System): high endemism in a small space. *Bulletin of Geosciences 91(2)*, 271–296. DOI 10.3140/bull.geosci.1584

Neubauer, T.A., Mandic, O. & Harzhauser, M. 2016c. The freshwater mollusk fauna of the Middle Miocene Lake Drniš (Dinaride Lake System, Croatia): a taxonomic and systematic revision. *Austrian Journal of Earth Sciences 108(2)*, 15–67. DOI 10.17738/ajes.2015.0013

Neubauer, T.A., Mandic, O., Jovanović, G. & Harzhauser, M. 2020. The Serbian Lake System: a stepping stone for freshwater molluscs in the middle Miocene. *Papers in Palaeontology 6(4)*, 533–569. DOI 10.1002/spp2.1308

Neubauer, T.A., Hauffe, T., Silvestro, D., Schauer, J., Kadolsky, D., Wesselingh, F.P., Harzhauser, M. & Wilke, T. 2021. Current extinction rate in European freshwater gastropods greatly exceeds that of the late Cretaceous mass extinction. *Communications Earth & Environment 2*, 97. DOI 10.1038/s43247-021-00167-x

Neubauer, T.A., Harzhauser, M. & Sebe, K. 2025. A mixed marine/non-marine mollusk assemblage from the Middle Miocene of Hidas (Hungary). *Bulletin of Geosciences 100(1)*, 57–86. DOI 10.3140/bull.geosci.1917

Neumayr, M. 1880. Tertiäre Binnenmollusken aus Bosnien und der Hercegovina. *Jahrbuch der k. k. geologischen Reichsanstalt 30(2)*, 463–486.

Neumayr, M. 1883. Ueber einige tertiäre Süsswasserschnecken aus dem Orient. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie 1883(2)*, 37–44.

Newell, N.D. 1965. Classification of the Bivalvia. *American Museum Novitates 2206*, 1–25.

Noulet, J.-B. 1846. Mémoire sur quelques coquilles fossiles nouvelles découvertes dans la région Aquitanique du Bassin sous-Pyrénéen. *Mémoires de l'Académie royale des Sciences, Inscriptions et Belle-Lettres de Toulouse, troisème série 2*, 225–240. DOI 10.5962/bhl.title.164202

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner, H. 2022. *Vegan: Community Ecology Package. R package version 2.6-4. http://CRAN.R-project.org/package=vegan*

Olivier, G.A. 1804. *Voyage dans l'Empire Othoman, l'Égypte et la Perse, fait par ordre du gouvernement, pendant les six premières années de la République. Tome second*. 466 pp. Agasse, Paris.

Ortmann, A.E. 1916. The anatomical structure of *Gonidea angulata* (Lea). *The Nautilus 30(5)*, 50–53.

Pallary, P. 1916. Observations relatives à la nomenclature des *Melanopsis* fossiles. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord 7(3)*, 70–87.

Partsch, P. 1835. Über die sogenannten versteinerten Ziegenklauen aus dem Plattensee in Ungarn, und ein neues, urweltliches Geschlecht zweischaliger Conchylien. *Annalen des Wiener Museums der Naturgeschichte 1*, 93–102.

Pavlović, P.S. 1931. O fosilnoj fauni mekušaca iz Skopske Kotline. *Glasnik Skopskog naucnog društva, Odeljenje prirodnih Nauka 9(3)*, 1–28.

Pavlović, P.S. 1933. O fosilnoj fauni mekušaca iz okoline Peći. *Glas Srpske Kraljevske Akademije 158(78)*, 75–91.

Poey, F. 1852. Introduccion a los Ciclostomas con generalidades sobre los moluscos gastropodos y particularmente sobre los terrestres operculados. *Memorias sobre la historia natural de la isla de Cuba 1(8)*, 77–96.

Popov, S.V., Rögl, F., Rozanov, A.Y., Steininger, F.F., Shcherba, I.G. & Kováč, M. 2004. Lithological-Paleogeographic maps of Paratethys. 10 Maps. Late Eocene to Pliocene. *Courier Forschungsinstitut Senckenberg 250*, 1–46.

Popova, S.M., Devyatkin, Y.V. & Starobogatov, Ya.I. 1970. *Mollyuski kyzylgirskoy svity Gornogo Altaya*. 95 pp. Nauka, Moskva.

R Core Team. 2023. *R: A language and environment for statistical computing. Version 4.3.2*. R Foundation for Statistical Computing, Vienna. *https://www.r-project.org/*

Radoman, P. 1973. New classification of fresh and brakish water Prosobranchia from the Balkans and Asia Minor. *Prirodnjacki Muzej u Beogradu, Posebna Izdanja 32*, 3–30.

Rafinesque, C.S. 1815. *Analyse de la nature ou tableau de l'univers et des corps organisés*. 223 pp. Privately published by author, Palermo. DOI 10.5962/bhl.title.106607

Rafinesque, C.S. 1819. Prodrome de 70 nouveaux genres d'animaux découverts dans l'intérieur des Etas-Unis d'Amérique, durant l'année 1818. *Journal de Physique, de Chimie et d'Histoire Naturelle 88*, 417–429.

Rafinesque, C.S. 1820. Monographie des coquilles bivalves fluviatiles de la Rivière Ohio, contenant douze génères et soixante-huit espèces. *Annales générales des sciences Physiques 5*, 287–322.

Retzius, A.J. 1788. *Dissertatio historico-naturalis sistens nova testaceorum genera. Quam præside D. M. Andr. J. Retzio (...) ad publicum examen defert Laurentius Münter Philipsson* 23 pp. University of Lund, Sweden, Lund.

Rolle, F. 1862. Über einige neue oder wenig gekannte Mollusken-Arten aus Tertiär-Ablagerungen. *Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften 44(1)*, 205–223.

Roshka, V.K. 1973. *Mollyuski meotisa severo-zapadnogo prichernomor'ya*. 284 pp. Shtiintsa, Kishinev.

Salvador, R.B. & Rasser, M.W. 2014. The fossil pulmonate snails of Sandelzhausen (Early/Middle Miocene, Germany) (Hygrophila, Punctoidea and limacoids). *Archiv für Molluskenkunde 143(2)*, 187–202. DOI 10.1127/arch.moll/1869-0963/143/187-202

Salvador, R.B., Höltke, O., Rasser, M.W. & Kadolsky, D. 2016a. Annotated type catalogue of the continental fossil gastropods in the Staatliches Museum für Naturkunde Stuttgart, Germany. *Palaeodiversity 9*, 15–70. DOI 10.18476/pale.v9.a3

Salvador, R.B., Pippèrr, M., Reichenbacher, B. & Rasser, M.W. 2016b. Early Miocene continental gastropods from new localities of the Molasse Basin in southern Germany. *Paläontologische Zeitschrift 90(3)*, 469–491. DOI 10.1007/s12542-016-0291-y

Salvador, R.B., Prieto, J., Mayr, C. & Rasser, M.W. 2016c. New gastropod assemblages from the Early/Middle Miocene of Riedensheim and Adelschlag-Fasanerie, southern Germany. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 279(2)*, 127–154. DOI 10.1127/njgpa/2016/0546

Sandberger, C.L.F. 1870–1875. *Die Land- und Süßwasser-Conchylien der Vorwelt*. livr. 1–3: pp. 1–96, pl. 1–12 (1870); livr. 4–5: pp. 97–160, pl. 13–20 (1871); livr. 6–8: pp. 161–256, pl. 21–32 (1872); livr. 9–10: pp. 257–352, pl. 33–36 (1873);

livr. 11: pp. i–viii + 353–1000 (1875). C.W. Kreidel, Wiesbaden. DOI 10.1016/S0140-6736(02)77759-3, DOI 10.1038/006256a0

Sauerzopf, F. 1953. Die Planorbidae aus dem Pannon des Alpenostrandes. *Burgenländische Heimatblätter 15(2)*, 49–66.

Schlickum, W.R. & Puisségur, J.-J. 1977. Die Molluskenfauna des Altpleistozäns von St. Bernard (Département Côte-d'Or). *Archiv für Molluskenkunde 107(4–6)*, 273–283.

Schlickum, W.R. & Strauch, F. 1979. Die Land- und Süßwassermollusken der pliozänen Deckschichten der rheinischen Braunkohle. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 536*, 1–144.

Schneider, S. & Linse, U. 2023. Pliocene–Pleistocene Unionida from Rhodes (Dodecanese, Greece): insights into the evolution of Eastern Mediterranean freshwater mussels. *Archiv für Molluskenkunde International Journal of Malacology 152(1)*, 43–69. DOI 10.1127/arch.moll/152/043-069

Schultz, O. 2005. Band 1, Teil 3. Bivalvia neogenica (Solenoidea-Clavagelloidea), 691–1211. *In* Piller, W.E. (ed.) *Catalogus Fossilium Austriae*. Österreichische Akademie der Wissenschaften, Wien. DOI 10.1553/0x000d1cf8

Sebe, K. 2024. Szászvár Formation, 71. *In* Babinszki, E., Piros, O., Csillag, G., Fodor, L., Gyalog, L., Kercsmár, Zs., Less, G., Lukács, R., Sebe, K., Selmeczi, I., Szepesi, J. & Sztanó, O. (eds) *Lithostratigraphic Units of Hungary II. Cenozoic Formations*. Supervising Authority of Regulated Activities, Budapest.

Sebe, K., Selmeczi, I., Szuromi-Korecz, A., Hably, L., Kovács, Á. & Benkó, Z. 2019. Miocene syn-rift lacustrine sediments in the Mecsek Mts. (SW Hungary). *Swiss Journal of Geosciences 112(1)*, 83–100. DOI 10.1007/s00015-018-0336-1

Sebe, K., Szabó, M., Szentesi, Z., Pandolfi, L., Budai, S. & Gregorits, M. 2024. Macrofauna of the Lower–Middle Miocene lacustrine sediments of the Mecsek mountains, SW Hungary: preliminary results, 73. *In* Bartol, M., Ivančič, K. & Horvat, A. (eds) *10th Neogene of Central and South-Eastern Europe. Abstract Volume*. Geološki zavod Slovenije, Ljubljana.

Sitnikova, T.Ya. 2019. Baikal gastropods described by W.A. Lindholm. *Proceedings of the Zoological Institute RAS 323(3)*, 214–252. DOI 10.31610/trudyzin/2019.323.3.214

Starobogatov, Ya.I. 1970. *Fauna mollyuskov i zoogeographicheskoye rayonirovaniye kontinental'nykh vo do emov zemnogo shara*. 372 pp. Nauka, Leningrad.

Stimpson, W. 1865. Diagnoses of newly discovered genera of gasteropods, belonging to the sub-fam. Hydrobiinae of the family Rissoidae. *American Journal of Conchology 1(1)*, 51–54.

Stoliczka, F. 1870. The Pelycopoda, with a review of all known Genera of this class, fossil and recent, 1–538. *In* Oldham, T. (ed.). *Paleontologia Indica, being figures and descriptions of the organic remains procured during the progress of the Geological Survey of India. Cretaceous Fauna of Southern India 3*.

Strausz, L. 1966. *Die miozän-mediterranen Gastropoden Ungarns*. 693 pp. Akadémiai Kiadó, Budapest.

Swainson, W. 1840. *A Treatise on Malacology; or, the Natural Classification of Shells and Shell Fish*. 419 pp. Longman, Orme, Brown, Green & Longmans; John Taylor, London. DOI 10.5962/bhl.title.8027

Tournouër, R. 1866. Sur les terrains tertiaires de la vallée supérieure de la Saône. *Bulletin de la Société Géologique de France, deuxième série 23*, 769–804.

Turton, W. 1857. *A Manual of the Land and Freshwater Shells of the British Islands, with Figures of Each of the Kinds. A New Edition, Thoroughly Revised and Much Enlarged, by John Edward Gray*. 335 pp. Longman, Brown, Green, Longmans, and Roberts, London. DOI 10.5962/bhl.title.124019

Verbrugge, L.N.H., Schipper, A.M., Huijbregts, M.A.J., Van der Velde, G. & Leuven, R.S.E.W. 2012. Sensitivity of native and non-native mollusc species to changing river water temperature and salinity. *Biological Invasions 14(6)*, 1187–1199. DOI 10.1007/s10530-011-0148-y

Welter-Schultes, F.W. 2012. *European Non-Marine Molluscs, a Guide for Species Identification*. 679 pp. Planet Poster Editions, Göttingen.

Wenz, W. 1923–1930. *Fossilium Catalogus I: Animalia. Gastropoda extramarina tertiaria.* Diener, C. (I–VII) & Pompeckj, J.F. (VIII–XI) (eds). pp. 1–352 (1923), II: pp. 353–736 (1923), III: pp. 737–1068 (1923), IV: pp. 1069–1420 (1923), V: pp. 1421–1734 (1923), VI: pp. 1735–1862 (1923), VII: pp. 1863–2230 (1926), VIII: pp. 2231–2502 (1928), IX: pp. 2503–2886 (1929), X: pp. 2887–3014 (1929), XI: pp. 3015–3387 (1930). W. Junk, Berlin.

Wenz, W. 1931. Süßwassermollusken aus den Mediterranablagerungen des Mecsekgebirges. *Archiv für Molluskenkunde 63(3)*, 116–122.

Wenz, W. 1932. *Brotia escheri inornata* n. subsp. aus Süßwasserablagerungen des Tortons von Hidasd (Korn. Tolna, Ungarn). *Archiv für Molluskenkunde 64*, 15–17.

Wenz, W. 1942a. Die Mollusken des Pliozäns der rumänischen Erdöl-Gebiete als Leitversteinerungen für die Aufschluß-Arbeiten. *Senckenbergiana 24*, 1–293.

Wenz, W. 1942b. Zur Kenntnis der fossilen Land- und Süßwassermollusken Venetiens. *Memorie dell'Istituto Geologico della R. Università di Padova 14*, 1–51.

Willmann, R. 1981. Evolution, Systematik und stratigraphische Bedeutung der neogenen Süßwassergastropoden von Rhodos und Kos/Ägäis. *Palaeontographica Abteilung A 174*, 10–235.

Žagar-Sakač, A. 1987. O unionacejskoj fauni miocenskih slatkovodnih naslaga srednje Dalmacije. *Rad Jugoslavenske Akademije znanosti i umjetnosti 431*, 69–91.

Žagar-Sakač, A. 1990. O vrsti *Unio čubranovići* Brusina iz miocenskih slatkovodnih naslaga Lovče u Baniji, Središnja hrvatska. *Rad Jugoslavenske Akademije znanosti i umjetnosti 449*, 251–260.

Živković, M. 1893. Über das Tertiär des mittleren Timok-Beckens. *Annales Géologiques de la Péninsule Balkanique 4(1–2)*, 37–118, 147–168.