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We describe a mixed assemblage of polyhaline, freshwater, and terrestrial mollusks from late Middle Miocene (early Serravallian, late Badenian) strata near the town of Hidas, southern Hungary. It comprises 19 species in 16 families – seven polyhaline to normal-marine gastropod species (Neritidae, Hydrobiidae, Nassariidae, Potamididae, Batillariidae, Litiopidae), four gastropod and one bivalve species from freshwater settings (Lymnaeidae, Planorbidae, Sphaeriidae), and seven species of terrestrial gastropods (Ellobiidae, Strobilopsidae, Vertiginidae, Gastrocoptidae, Discidae, Gastrodontidae, Elonidae). The polyhaline/marine taxa identified to the species level are widely distributed species, all of which have been previously reported from Hidas. The freshwater and terrestrial species, in turn, all represent new occurrences. Most of them are common components of Middle Miocene peri-Paratethyan non-marine faunas. Biostratigraphically, the fauna agrees with the early Serravallian (late Badenian) age suggested by a previous study on microvertebrates. We provide a systematic account of all species, along with a critical discussion of the non-marine species previously recorded from Hidas. The assemblage was likely deposited in a low-energy freshwater setting, perhaps a pond, oxbow lake or backwater swamp. We assume that the brackish elements were transported from a nearby mudflat or mangrove environment, perhaps during an overspill or flooding event. • Key words: Gastropoda, Bivalvia, taxonomy, paleoecology, Badenian, Serravallian.

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 (5 figures, 2 tables). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received December 13, 2024; accepted in revised form February 24, 2025; published online April 13, 2025; issued April 13, 2025.

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The Central Paratethys was a huge epicontinental sea that existed from the latest Eocene to the end of the Middle Miocene (Popov *et al.* 2004, Palcu *et al.* 2023). Particularly during the Middle Miocene, tropical to subtropical climatic conditions favored the development of a hyper-diverse, partly endemic marine mollusk fauna (*e.g.*, Studencka *et al.* 1998; Harzhauser *et al.* 2003, 2024a, b). Along its margins, diverse freshwater and terrestrial mollusk communities flourished, documented by an impressive literature record (*e.g.*, Neubauer *et al.* 2015a, b; Höltke *et al.* 2016; Harzhauser & Neubauer 2021).

Especially in the non-marine fossil record there are still considerable knowledge gaps for Middle Miocene mollusk faunas, particularly among terrestrial assemblages. Here we document a mixed assemblage of brackish-water, freshwater, and terrestrial mollusks from late Middle Miocene (early Serravallian, late Badenian) strata near the town of Hidas in the Mecsek Mountains in southern Hungary (Fig. 1).

Paleontological work on fossil mollusk material from this locality started in the second half of the 19th century, with the description of a single species of freshwater gastropod (Rolle 1862). First marine gastropod species were described by Hoernes & Auinger (1879–1891). Further works in the 20th century added a few species to the freshwater mollusk fauna of Hidas (Wenz 1932; Kókay 1967, 2006). The marine fauna of this locality was first assessed by Csepreghy-Meznerics (1950), who documented 111 species of gastropods and 70 species of bivalves. In addition, she listed oligohaline to freshwater taxa, including several species of Hydrobiidae, two species of Dreissenidae, and each one species of Pachychilidae, Lymnaeidae, Planorbidae, and Unionidae. Földi (1966) discussed the geological setting and biotic succession at

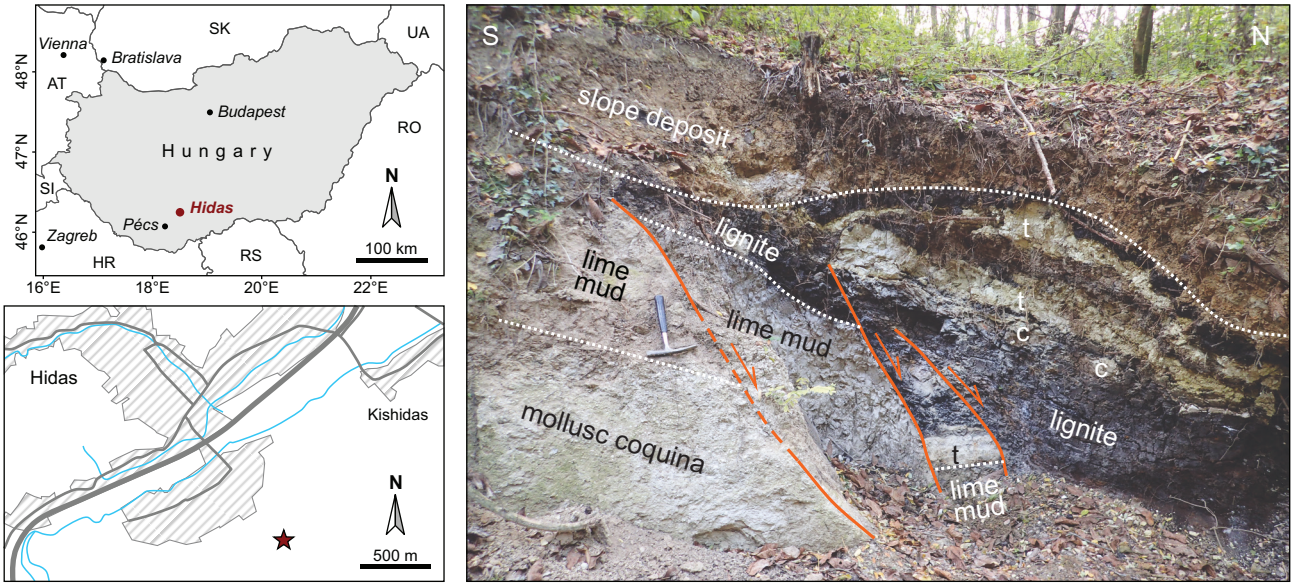

Figure 1. Geographic overview and position of the studied outcrop (right) southeast of the town of Hidas in southern Hungary (left). Abbreviations in the upper left figure refer to country codes (ISO 3166-1 alpha-2 standard). Shaded areas in the lower left figure indicate urban areas. The red star marks the location of the outcrop. Modified after Hír *et al.* (2024). Abbreviations in the right figure: t – tuff; c – clay lens.

Hidas. Strausz (1966) and Bohn-Havas (1973) further expanded the faunal list especially from a marine perspective, but also added records of a freshwater and a land snail species. Selmeczi (1987) discussed the paleobiogeographical relationship of the mollusk fauna of Hidas with the Eastern Paratethys. In recent decades, a number of works added to the inventory or provided revisions of taxa occurring from Hidas (*e.g.*, Harzhauser & Landau 2012, 2016, 2019, 2021a, b, 2023, 2024; Kovács & Vicián 2014, 2021; Kovács 2020; Harzhauser *et al.* 2023a, 2024c, 2025).

We give a systematic account of 19 brackish-water, freshwater, and terrestrial species from a recently sampled mixed assemblage, discuss the age of the deposits, and reconstruct the paleoenvironmental setting. Furthermore, we critically discuss previously recorded non-marine species to provide a revised list of taxa occurring at Hidas.

Material and methods

The studied material comes from a small outcrop exposing the Hidas Formation south of the town of Hidas in southern Hungary, along the southeastern margin of the Mecsek Mountains (Fig. 1). The Hidas Formation comprises an alternation of lignites, clays, marls, lime muds, and mollusk coquinas, formed under brackish-water and freshwater conditions in a subtropical climate (Csepreghy-Meznerics 1950, Bohn-Havas 1973, Hír *et al.* 2024). Based on recent microvertebrate finds, the formation was considered to have an upper Middle Miocene (lower Serravallian, upper Badenian, MN 7+8 Zone, approximately 13.5–13.3 Ma) age (Hír *et al.* 2024).

The outcrop (46° 14′ 55.4″ N, 18° 30′ 14.2″ E; Fig. 1) is about 2 m in height and exposes a succession of three beds lying conformably atop each other, apart from local displacement due to landslides (Hír *et al.* 2024). The bottom layer is a mollusk coquina of approximately 1 m (lower boundary unknown) primarily consisting of brackish-water mollusks, dominated by mudwhelks (Potamididae, Batillariidae), nassariids, and small ostreids. It is well sorted, grain-supported, with calcarenite matrix. Shells can be intact or fragmentary and are oriented subparallel to the bedding plane. These features point to a high-energy littoral sedimentary environment. On top follows a whitish gray lime mud of 0.8–1.0 m in thickness, including freshwater gastropod shells and bone fragments. Based on the fossil content, it was interpreted as a shallow freshwater environment, potentially a pool or a swamp (Hír *et al.* 2024). Above lies a dark brown lignite of up to 1 m in thickness, with lenses of light gray clay and a few centimeter thick beds of yellowish white, porous dacite tuff.

In the course of a sampling campaign for microvertebrates, two tons of sediment were sampled in 2022 from the lime mud layers (Hír *et al.* 2024). Sediments were processed with H_2O_2 and washed over a 0.5 mm sieve. For this study, the residue was additionally washed over a 1 mm sieve. Shells were primarily picked from the > 1 mm fraction using a Zeiss Stemi 508 stereomicroscope, but also the 0.5–1 mm fraction was checked for small-sized species and fragments. *Carychium* was only detected in the smaller grained residue, along with numerous juvenile

specimens of planorbids and fragments of other species. Given the huge amount of material of approximately 43 kg, we picked only a representative number of specimens (765) to infer semi-quantitative frequencies of the individual species.

Photographs were taken with a Keyence VHX-7100, using the stacking function, and a Phenom XL raster electron microscope (Thermo Fisher Scientific Inc.) at the Bavarian State Collections of Natural History, Bavarian State Collection for Palaeontology and Geology, Munich (SNSB-BSPG). For the electron microscopy, specimens were coated with gold using a Quorum Q150R S coater. The lectotype of *Gyraulus alienus* (Rolle, 1862) was imaged using a ZEISS Discovery V20 at the Natural History Museum Vienna, Austria (NHMW). All material is stored at SNSB-BSPG under inventory numbers 2024 X 1–48.

The systematic arrangement follows Bouchet *et al.* (2017) for Gastropoda and Bouchet *et al.* (2010) for Bivalvia, with recent updates as available via MolluscaBase eds (2024). Measurements are given as height × width for Gastropoda and length × height × width for Bivalvia, respectively. Terminology of apertural dentition in Strobilopsidae follows Moore (1960), those in Vertiginidae follows Nekola & Coles (2010). The chresonymy/synonymy lists include first descriptions, major revisions, and works referred to in the Remarks sections and those that specifically deal with material from Hidas. Extensive synonymies are avoided for taxa that have been recently revised.

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 *Vitta* Mörch, 1852

Type species. – *Nerita virginea* Linnaeus, 1758; by subsequent designation by H.B. Baker (1923, p. 137). Recent, Caribbean.

***Vitta tuberculata* (Schréter *in* Horusitzky, 1915)**
Figure 2A–C

*1915 *Neritina tuberculata* Schréter; Horusitzky, p. 22.
1950 *Neritina picta hörnesi* n. sp.; Csepreghy-Meznerics, pp. 17, 18.
1952 *Clithon* (*Vittoclithon*) *pictus tuberculatus* (Schreter). – Papp, pp. 109, 110, pl. 1, figs 21–24.
1955 *Clithon* (*Vittoclithon*) *tuberculatus* (Schréter). – Seneš, p. 88, pl. 6, figs 7–13.
1960 *Clithon* (*Vittoclithon*) *tuberculatus* (Schréter). – Švagrovský, pp. 57, 58, pl. 4, figs 8–11.
1964 *Clithon pictus tuberculatus* (Schréter). – Švagrovský, pl. 16, fig. 2.
1966 *Neritina picta pachii* Hörnes (in Czjzek & Handmann) 1848 (sen 1883). – Strausz, pp. 58, 59, textfig. 34 [only concerning synonymy of *Neritina picta hörnesi* Csepreghy-Meznerics, 1950; non *Nerita* (*Neritina*) *pachii* Handmann, 1889].
1972 *Neritina* (*Theodoxus*) cf. *picta* Ferussac. – Nicorici, pl. 15, figs 13, 14 [non *Neritina picta* Férussac, 1823].
1973 *Neritina picta hörnesi* Mezn. – Bohn-Havas, p. 964 [20].
1982 *Neritina tuberculata* Schréter in Horusitzky, 1915. – Švagrovský, p. 10, pl. 2, fig. 5.
2013 *Clithon pictus tuberculatus* (Schréter). – Hladilová & Fordinál, fig. 5f, g.
v 2018 *Vitta tuberculata* (Schréter in Horusitzky, 1915). – Harzhauser *et al.*, pp. 155, 159, 162, 163, 165, fig. 10a–d.

Material. – 5 specimens (SNSB-BSPG 2024 X 1–2).

Dimensions. – 3.55 × 3.63 mm (Fig. 2A–C).

Remarks. – Our material matches well the description of Schréter in Horusitzky (1915) concerning the more or less rectangular shell, created by two angulations towards base and apex, of which the latter bears the characteristic knobs. The shells from Hidas lack only the distinct concavity between the angulations that is typical of the species. However, they are somewhat smaller than those illustrated in other studies (*e.g.*, Hladilová & Fordinál 2013, Harzhauser *et al.* 2018) and probably represent subadult specimens. Similarly to the shells shown by Papp (1952) and Harzhauser *et al.* (2018) the color pattern is coarser-meshed and less dense around at the angulations. On the whorl flank it consists of irregular, brown zigzag lines, on the whorl top the lines are slightly more narrowly placed and less wriggly. The aperture is bordered by a broad callus pad, again matching the shells shown in previous studies.

There is some uncertainty as to whether this species is distinct or potentially a junior synonym of *Nerita anomala* Eichwald, 1830 (as, *e.g.*, indicated by Landau *et al.* 2013). That species is comparatively poorly known, but early drawings by Eichwald (1851) indicate a similar, stout shell that is also adorned with knobs on the whorl top. Photos of the syntypes of Eichwald's material stored at the Paleontological Museum of Saint-Petersburg State University (coll. no. 3/452) and the Zoological Institute of the Russian Academy of Sciences (coll. no. 62420) show, however, a rather elongate shell with pointed apex

and a rugose shell surface rather than distinct knobs. Despite those differences, synonymy cannot be ruled out considering that *Vitta tuberculata* shows considerable variability. An alternative view was presented by Il'ina (1993) who treated *Nerita anomala* as a junior synonym of *Vitta picta* (Férussac, 1823). A more thorough study of type materials and large quantities of specimens is needed to assess the morphological variability of the species involved.

In addition, Csepreghy-Meznerics (1950) described the new variety *Neritina picta hoernesi*, yet only with a short description but no illustration. The single sentence says "the rim-like edge is so developed that it almost forms a cam-like protrusion" (translated from the original Hungarian). This description fits to our specimens as well as to the original description of *Vitta tuberculata*, which is why we consider it a synonym herein. The subspecies was considered a synonym of "*Neritina picta pachii* Hörnes" [= *Vitta pachii* (Handmann, 1889)] by Strausz (1966). That taxon differs from *V. tuberculata* in the strong central concavity, sometimes bordered by keels, and the lack of the characteristic knobs (Handmann 1889, Harzhauser 2003).

Occurrence. – Widely distributed in the Central Paratethys, reported from localities in Austria (Papp 1952, Harzhauser *et al.* 2018), Hungary (Horusitzky 1915), Romania (Nicorici 1972), and Slovakia (Švagrovský 1960, 1964, 1982; Hladilová & Fordinál 2013).

Subclass Caenogastropoda Cox, 1960
Order Littorinimorpha Golikov & Starobogatov, 1975
Superfamily Truncatelloidea Gray, 1840
Family Hydrobiidae Stimpson, 1865

Hydrobiidae gen. et sp. indet.
Figure 2T–W

Material. – 7 specimens (SNSB-BSPG 2024 X 3–5).

Dimensions. – 2.39 × 1.21 mm (Fig. 2T–V).

Remarks. – We encountered a few specimens of a smooth-shelled, slender conical Hydrobiidae with approximately five regularly and highly convex whorls, which slowly increase in height and width, a protoconch with wrinkled initial part and without clear transition to the teleoconch, an ovoid aperture, and narrow umbilicus. The rather small size of up to about 2.4 mm in height suggests the shells might be juveniles. Potential candidate Middle Miocene species are *Hydrobia alpha* Jekelius, 1944 (= *Hydrobia subprotracta* Jekelius, 1944, *non* Zhizhchenko, 1936), from the Sarmatian of Romania, *Sarmata frauenfeldi* (Hörnes, 1856), a common species in the Sarmatian of the Central Paratethys, and *Sarmata protracta* (Eichwald, 1850), described from Sarmatian deposits of Ukraine (Friedberg 1923, Il'ina 1993, Harzhauser & Kowalke 2002, Tămaș *et al.* 2013, Neubauer *et al.* 2014a, Kadolsky 2021). All share with our specimens the conical shape, the smooth, convex whorls, and the narrow umbilicus. Another superficially similar species is *Hydrobia neofrauenfeldi* Guzhov, 2022 from the Sarmatian of southwestern Russia (Republic of Adygea). In addition to a wrinkled surface, it bears spiral threads on the protoconch, which rather remind of Pontocaspian Turricaspiinae (Neubauer *et al.* 2018) than Hydrobiinae. Also, shells often have a weak mid-whorl angulation (Guzhov 2022); a closer affiliation with that species is unlikely for our material. The small *Hydrobia soceni* Jekelius, 1944 from the Sarmatian of Romania has more convex whorls and a larger last whorl.

In the end, attribution to any Middle Miocene Hydrobiidae species is very difficult due to the low number of diagnostic characters, the poor knowledge of protoconchs of most species, and generally the poor documentation of many species and their shell variability. Even on the genus level, there is considerable confusion about the identity of most hydrobiids. Classically most have been placed in the dustbin taxon *Hydrobia*, but many a classification has been revised over recent years upon closer inspection (*e.g.*, Kadolsky 2021; Guzhov 2022, 2023).

Order Neogastropoda Wenz, 1938
Superfamily Buccinoidea Rafinesque, 1815
Family Nassariidae Iredale, 1916 (1835)
Genus *Tritia* Risso, 1826

Type species. – *Buccinum reticulatum* Linnaeus, 1758; by subsequent designation Gray (1847, p. 139). Recent, Europe.

***Tritia*? *schoenni* (Hoernes & Auinger, 1882)**
Figure 2D, E

*1882 *Buccinum* (c. *Niotha*) *Schönni* nov. form.; Hoernes & Auinger, p. 125, pl. 15, figs 18–20.
1950 *Nassa* (*Arcularia*) *schönni* Hörnes-Auinger. – Csepreghy-Meznerics, p. 53, pl. 3, fig. 5.
1973 *Nassa* (*Arcularia*) *schönni* (Hoernes et Auinger) 1879. – Bohn-Havas, p. 1054 [110], pl. 5, figs 7, 8.
1997 *Sphaeronassa schoenni* (Hoernes & Auinger, 1882). – Bałuk, pp. 7, 8, pl. 1, figs 1–3.
v 2004 *Nassarius schoenni* (Hoernes & Auinger 1882). – Harzhauser & Kowalke, p. 25, pl. 3, figs 11, 12.
v 2013 *Nassarius schoenni* (Hoernes & Auinger, 1882). – Landau *et al.*, pp. 178–180, pl. 26, fig. 15, pl. 27, fig. 1 [cum syn.].
v 2018 *Tritia schoenni* (Hoernes & Auinger, 1882). – Harzhauser *et al.*, pp. 155, 161, fig. 10m.

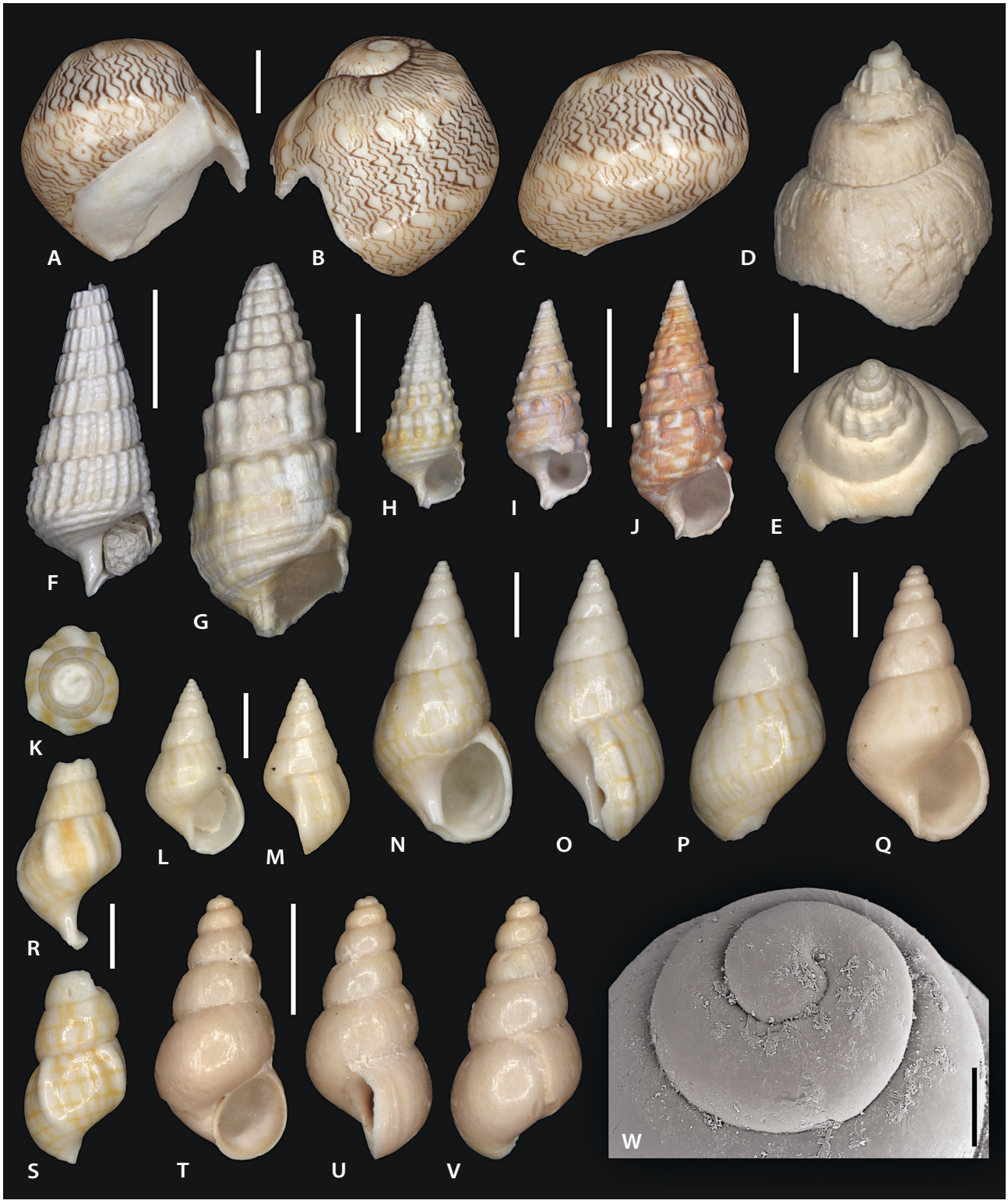

Figure 2. Brackish-water gastropod species at Hidas. • A–C – *Vitta tuberculata* (Schréter *in* Horusitzky, 1915) (SNSB-BSPG 2024 X 1). • D, E – *Tritia*? *schoenni* (Hoernes & Auinger, 1882); D – (SNSB-BSPG 2024 X 6); E – (SNSB-BSPG 2024 X 7). • F – *Terebralia duboisi* (Hörnes, 1855) (SNSB-BSPG 2024 X 14). • G, H – *Pustulosia submitralis* (Eichwald, 1851); G – (SNSB-BSPG 2024 X 8); H – (SNSB-BSPG 2024 X 9). • I, J – *Tiaracerithium pictum* (Basterot, 1825); I – (SNSB-BSPG 2024 X 11); J – (SNSB-BSPG 2024 X 12). • K, R – *Gibborissoia* cf. *varicosa* (Basterot, 1825) (SNSB-BSPG 2024 X 15). • L, M, N–Q, S – *Gibborissoia* cf. *varicosa* (Basterot, 1825); L, M – (SNSB-BSPG 2024 X 16); N–P – (SNSB-BSPG 2024 X 17); Q – (SNSB-BSPG 2024 X 18); S – (SNSB-BSPG 2024 X 19). • T–V – Hydrobiidae gen. et sp. indet. (SNSB-BSPG 2024 X 3). • W – Hydrobiidae gen. et sp. indet., protoconch (SNSB-BSPG 2024 X 4). Scale bars: 5 mm (F–J), 1 mm (A–E, K–V), 100 µm (W).

Material. – 2 fragments (SNSB-BSPG 2024 X 6–7).

Remarks. – The species was thoroughly described and illustrated by Harzhauser & Kowalke (2004) and extensively discussed by Landau *et al.* (2013). The two specimens from Hidas, both representing fragments of the upper part of the shell, fit well to that species in terms of the comparatively broad, stepped shell and the conspicuous ornamentation, with only the second and third teleoconch whorl bearing blunt, swollen axial ribs crossed by weaker, narrow-spaced spiral ribs. The lower part of the shell, consisting of a bulky last whorl with inflated, canaliculate peristome, dentate outer lip, and – occasionally – numerous spiral grooves on the base (*e.g.*, Harzhauser & Kowalke 2004, Landau *et al.* 2013), is missing in our material. There is considerable variability in shell shape and the degree of inflation of the peristome (Bałuk 1997, Harzhauser & Kowalke 2004), but the characteristic sculpture on the early teleoconch compared to smooth whorls in later ontogeny avert confusion with other species.

The genus allocation of this species is under debate. According to phylogenetic data, all extant eastern Atlantic and Mediterranean species formerly placed in *Nassarius* are currently placed in the genus *Tritia* (Galindo *et al.* 2016, Yang *et al.* 2024). These authors claim that traditionally used morphological characters are insufficient to delimit genera among nassariids because of overlapping character states. Yang *et al.* (2024) further provided age estimates of major divergence events within Nassariinae, indicating an origin of the genus in the earliest Miocene and diversification in the Miocene. Accordingly, we tentatively place the species in the genus *Tritia* pending a thorough systematic revision.

Distribution. – The species is widely distributed in the Early–Middle Miocene of the Paratethys and Proto-Mediterranean Sea, recorded from numerous localities in Austria, Bosnia and Herzegovina, Hungary, Poland, Romania, Serbia, Slovenia, Spain, and Turkey (for more details see Landau *et al.* 2013).

Caenogastropoda *incertae sedis*
Superfamily Cerithioidea J. Fleming, 1822
Family Batillariidae Thiele, 1929
Genus *Pustulosia* Harzhauser, Guzhov & Landau, 2023

Type species. – *Cerithium submitrale* Eichwald, 1851; by original designation. Miocene, Ukraine.

***Pustulosia submitralis* (Eichwald, 1851)**
Figure 2G, H

*1851 *Cerith*[*ium*]. *submitrale* m.; Eichwald, p. 88, pl. 7, fig. 16.
1950 *Potamides bicostatus* Eichwald. – Csepreghy-Meznerics, p. 27, pl. 1, fig. 15.
1950 *Potamides petersi* Auinger (in coll.). – Csepreghy-Meznerics, p. 27, pl. 1, fig. 14.
1973 *Pirenella nodosoplicata* (Hörnes) 1856. – Bohn-Havas, p. 1045 [101], pl. 4, fig. 7.
1966 *Potamides* (*Pirenella*) *nodosoplicatus* Hörnes, 1856. – Strausz, pp. 151, 152, pl. 7, fig. 20.
1966 *Potamides* (*Pirenella*) *nodosoplicatus petersi* Auinger (in Friedberg), 1928. – Strausz, p. 152, pl. 7, fig. 19.
v 2023a *Pustulosia submitralis* (Eichwald, 1851). – Harzhauser *et al.*, pp. 158–162, figs 32a–f, 33a–h [cum syn.].

Material. – 12 specimens (SNSB-BSPG 2024 X 8–10).

Dimensions. – 15.85 × 6.94 mm (Fig. 2G); 3.54 × 8.75 mm (Fig. 2H).

Remarks. – In their recent comprehensive revision of the Potamididae and Batillariidae of the Paratethys Sea (Harzhauser *et al.* 2023a) thoroughly described, discussed, and illustrated *Pustulosia submitralis*, along with an extensive synonymy list. The shell of this species is highly variable, which has led to considerable confusion and the introduction of many names in the past. It always bears ornamentation in the form of spirally arranged knobs in the upper half of the whorls and weak spiral cords on the lower half (Harzhauser *et al.* 2023a). Earliest teleoconch whorls only show spiral cords without any knobs. The stepped whorl arrangement visible in some of our shells (Fig. 2G; *melanopsiformis*-morphotype) is less common but falls within the range of intraspecific variability according to Harzhauser *et al.* (2023a).

A similar species is *Pustulosia hornensis* (Schaffer, 1912), described from the Early Miocene of the Vienna Basin (Austria). It resembles *Pustulosia submitralis* with respect to shell shape and the presence of spirally arranged knobs, but it has more rows of knobs and spiral striae in between (Harzhauser *et al.* 2023a). *Potamides bicostatus* (Eichwald, 1852) and *Potamides petersi* (Friedberg, 1914), as which specimens from Hidas were identified by Csepreghy-Meznerics (1950), are synonyms of *Pustulosia submitralis* according to Harzhauser *et al.* (2023a).

Occurrence. – The species existed from the Early to the Middle Miocene (Burdigalian to Serravallian) across the Central and Eastern Paratethys and the Proto-Mediterranean Sea, including numerous records from Austria, Azerbaijan, Bulgaria, Croatia, Czech Republic, Hungary, Kazakhstan, Poland, Romania, Russia, Slovakia, Slovenia, Spain, Turkey, Turkmenistan, and Ukraine (for more details see Harzhauser *et al.* 2023a, b).

Genus *Tiaracerithium* Sacco, 1895a

Type species. – *Cerithium pseudotiarella* d'Orbigny, 1852; by original designation. Miocene, France.

***Tiaracerithium pictum* (Basterot, 1825)**
Figure 2I, J

*1825 *C*[*erithium*]. *pictum* Nob.; Basterot, p. 57, pl. 3, fig. 6.
1950 *Potamides mitralis* Eichwald. – Csepreghy-Meznerics, p. 26, pl. 1, fig. 10.
1950 *Potamides mitralis florianus* Hilber. – Csepreghy-Meznerics, p. 27, pl. 1, fig. 11.
1966 *Potamides* (*Pirenella*) *pictus melanopsiformis* Auinger (in Friedberg), 1928. – Strausz, pp. 146, 147, pl. 8, fig. 20.
1973 *Pirenella picta mitralis* (Eichwald) 1853. – Bohn-Havas, p. 1045 [101], pl. 3, figs 20, 21.
v 2023a *Tiaracerithium pictum* (de Basterot, 1825). – Harzhauser *et al.*, pp. 144–153, figs 29d–f, 30a–n, $32f_1$–f_2 [cum syn.].

Material. – 10 specimens (SNSB-BSPG 2024 X 11–13).

Dimensions. – 10.99 × 4.45 mm (Fig. 2J); 8.92 × 3.64 mm (Fig. 2I).

Remarks. – As for the previous species, *Tiaracerithium pictum* was revised comprehensively by Harzhauser *et al.* (2023a). This species is similarly common and similarly variable as *Pustulosia submitralis* above, combining a great range of morphologies. All share a pattern of spiral sculpture that consists of an upper row of knobs followed below by several cords, of which the uppermost is occasionally irregular and slightly knobbed. The cords may be accompanied by additional, thin spiral striae. Our specimens match perfectly the typical morphology. Some specimens show a color pattern of densely arranged, orange zigzag lines (Fig. 2J).

The otherwise similar *Tiaracerithium thiarella* (Grateloup, 1832) from the Early Miocene of France differs in the spikier knobs in the upper row and the bead-like spiral cords. *Potamides mitralis* (Eichwald, 1830) and *Potamides mitralis florianus* (Hilber, 1879), as which this species was identified by Csepreghy-Meznerics (1950), are synonyms of *T. pictum* (Harzhauser *et al.* 2023a).

Occurrence. – *Tiaracerithium pictum* existed from the late Early Miocene to the early Late Miocene (Burdigalian to Tortonian) and was widely distributed across the Central and Eastern Paratethys as well as the Proto-Mediterranean Sea and northeastern Atlantic. Harzhauser *et al.* (2023a, b) listed localities in Austria, Azerbaijan, Bulgaria, Croatia, Czech Republic, France, Germany, Hungary, Italy, Kazakhstan, Moldova, Poland, Portugal, Romania, Russia, Slovakia, Spain, Turkey, and Ukraine.

Family Potamididae H. Adams & A. Adams, 1854

Genus *Terebralia* Swainson, 1840

Type species. – *Strombus palustris* Linnaeus, 1767; by subsequent designation by Cossmann (1889, p. 72). Recent, Indo-Pacific.

***Terebralia duboisi* (Hörnes, 1855)**
Figure 2F

*1855 *Cerithium Duboisi* Hörn.; Hörnes, p. 399, pl. 42, figs 4, 5.
1950 *Terebralia lignitarum* (Eichwald). – Csepreghy-Meznerics, p. 28, pl. 1, fig. 18 [*non* Eichwald, 1830].
1973 *Terebralia lignitarum* (Eichwald) 1853. – Bohn-Havas, p. 1044 [100], pl. 4, fig. 5 [*non* Eichwald, 1830].
v 2023a *Terebralia duboisi* (Hörnes, 1855). – Harzhauser *et al.*, pp. 94–97, figs 15d–f, 16c, 16j, 17a [cum syn.].
v 2023 *Terebralia duboisi* (Hörnes, 1855). – Thivaiou *et al.*, pp. 248, 249, fig. 1a.

Material. – 1 specimen (SNSB-BSPG 2024 X 14).

Dimensions. – 13.31 × 5.77 mm (Fig. 2F).

Remarks. – A single specimen of about seven whorls, lacking the apex and the aperture, was found. The shell outline is almost perfectly conical. It bears a dense, reticulate sculpture of four densely beaded spiral cords, where the beads are merged into axial riblets. On the base, additional spiral cords are present. The densely beaded ornamentation is found in several species of *Terebralia*, i.e., *Terebralia duboisi* (Hörnes, 1855), from the Badenian (Langhian) of the Vienna Basin, *Terebralia menestrieri* (d'Orbigny, 1845), from the Sarmatian (late Serravallian) of Moldova, and *Terebralia lignitarum* (Eichwald, 1830), from the Badenian of Ukraine. All three are fairly common species in the Paratethys Sea and regularly co-occur, especially *T. duboisi* and *T. lignitarum*, which also inhabited the Proto-Mediterranean Sea and northeastern Atlantic (Harzhauser *et al.* 2023a). The three species primarily differ in the shell outline, which is more distinctly cyrtoconoid in *T. lignitarum* and *T. menestrieri* but conical to weakly cyrtoconoid in *T. duboisi*. The latter species also exposes the axial riblets we observed on the specimen from Hidas.

Occurrence. – The species is common throughout the Central and Eastern Paratethys and was found also in deposits of the Proto-Mediterranean Sea and northeastern

Atlantic. Records come from Austria, Bulgaria, Czech Republic, France, Hungary, Italy, Moldova, Poland, Romania, Slovakia, Slovenia, Turkey, and Ukraine (see Harzhauser *et al.* 2023a, b for details).

Family Litiopidae Gray, 1847

Genus *Gibborissoia* Sacco, 1895b

Type species. – *Bulimus costellatus* Grateloup, 1828; by original designation. Miocene, France.

***Gibborissoia* cf. *varicosa* (Basterot, 1825)**
Figure 2K–S

*1825 *Rissoa varicosa* Nob.; Basterot, p. 37, pl. 1, fig. 2.
1966 *Alaba costellata anomala* Eichwald, 1853. – Strausz, p. 128, pl. 13, fig. 3, pl. 45, fig. 19.
2001 *Gibborissoa varicosa* (Basterot, 1825). – Lozouet *et al.*, pp. 25, 26, pl. 6, figs 8, 9 [*partim*; non *Phasianella prevostina* Basterot, 1825].
v 2013 *Gibborissoia varicosa* (de Basterot, 1825). – Landau *et al.*, pp. 49, 50, pl. 4, fig. 9 [cum syn.].
v 2018 *Gibborissoia varicosa* (de Basterot, 1825). – Harzhauser *et al.*, p. 155, fig. 10n.
2019 *Gibborissoia varicosa* (de Basterot, 1825). – Pacaud, p. 111 [*partim*; non *Phasianella prevostina* Basterot, 1825].
v 2019 *Gibborissoia varicosa* (Basterot, 1825) – Thivaiou *et al.*, p. 332, fig. 4c1–c3).

Material. – 30 specimens (SNSB-BSPG 2024 X 15–20).

Dimensions. – 4.36 × 2.17 mm (Fig. 2N–P); 4.25 × 2.20 mm (Fig. 2Q); 2.71 × 1.54 mm (Fig. 2L, M).

Remarks. – Typical for the species are the eponymous varices that occur variably on later teleoconch whorls. Shell shape is highly variable (compare Lozouet *et al.* 2001, Landau *et al.* 2013), sometimes reflecting slightly irregular growth. In addition to the varices, faint spiral striae cover the shell. Our material shows the typical varices, but not the striae; also, shells are smaller, the coiling is rather regular, and whorls are more weakly convex compared to shells illustrated by Lozouet *et al.* (2001) and Landau *et al.* (2013). In fact, because of that the shells remind of and may be confused with brackish-water hydrobiids, especially since the aperture is missing in most shells. Still the overall similarities suggest a tentative placement in *Gibborissoia varicosa*. We assume that the observed differences may relate to our shells mostly representing juvenile to subadult specimens.

Gibborissoia morgani (Cossmann & Peyrot, 1918) has a similar shell shape but a distinct basal angulation, and it lacks the varices (Van Dingenen *et al.* 2016). It is so far only known from the Middle Miocene and Early Pliocene of France (Van Dingenen *et al.* 2016).

Phasianella prevostina Basterot, 1825 was synonymized with *Gibborissoia* cf. *varicosa* (Basterot, 1825) by Lozouet *et al.* (2001) and Pacaud (2019). However, as Landau *et al.* (2018) pointed out, that species is not a *Gibborissoia* but belongs in Littorinidae and the genus *Littorinopsis*. The placement of *Gibborissoia* in Litiopidae follows Thivaiou *et al.* (2019) and is based on the similarity with the extant litiopid genus *Alaba*.

Some of the specimens from Hidas show a fine yellow reticulate color pattern (Fig. 2L–P, S), sometimes accompanied by broader yellow axial bands (Fig. 2K, R). To our knowledge, this is the first time the coloration is preserved in that species. It differs from that of *Gibborissoia angulosa* Landau, Harzhauser, İslamoğlu & Silva, 2013, which shows reddish, wavy axial bands (Landau *et al.* 2013).

Occurrence. – *Gibborissoia varicosa* was originally described from the Early Miocene of France. It also occurred in the Proto-Mediterranean Sea during the Early–Middle Miocene (Italy, Turkey) and in the Central Paratethys Sea during the Middle Miocene (Austria, Bosnia and Herzegovina, Czech Republic, Hungary, Poland, Romania) according to Landau *et al.* (2013).

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

Genus *Stagnicola* Jeffreys, 1830

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

***Stagnicola armaniacensis* (Noulet, 1857)**
Figure 3A–D

*1857 *Limnea armaniacensis* nov. sp.; Noulet, p. 22.
2005 *S. armaniacensis* (Noulet 1857). – Kowalke & Reichenbacher, p. 631, fig. 9(6–7).
v 2014a *Stagnicola armaniacensis* (Noulet 1857). – Harzhauser *et al.*, pp. 11, 12, pl. 2, figs 4–11 [cum syn.].
2016b *Stagnicola armaniacensis* (Noulet, 1857). – Salvador *et al.*, pp. 480, 481, fig. 5b.

Material. – 70 specimens (SNSB-BSPG 2024 X 21–23).

Dimensions. – 4.30 × 2.29 mm (Fig. 3A, B); 3.51 × 2.04 mm (Fig. 3C, D).

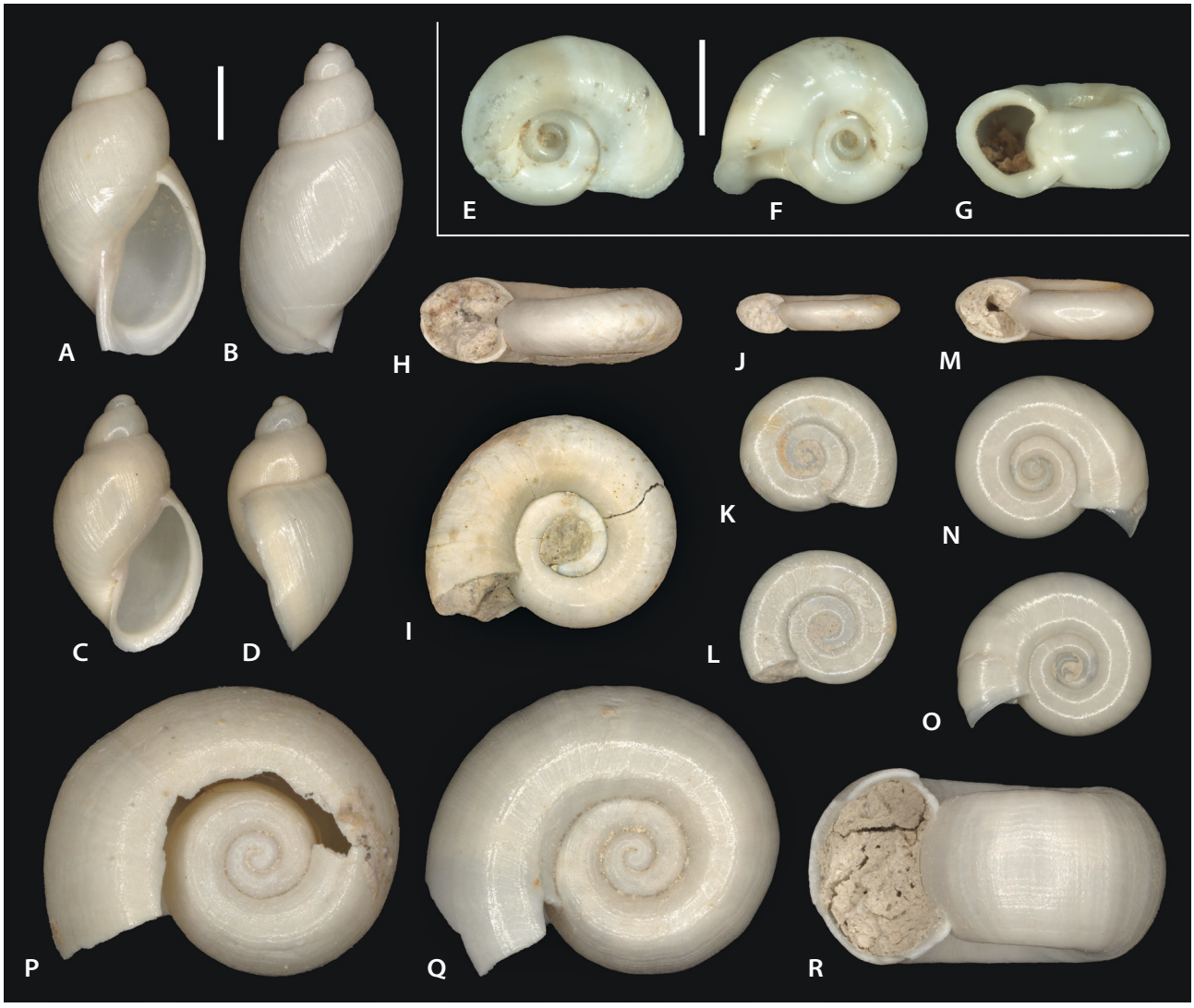

Figure 3. Freshwater gastropod species at Hidas. • A–D – *Stagnicola armaniacensis* (Noulet, 1857); A, B – (SNSB-BSPG 2024 X 21); C, D – (SNSB-BSPG 2024 X 22). • E–G – *Gyraulus alienus* (Rolle, 1862); lectotype, designated herein (NHMW 1859/0042/0059); from a stratum with only freshwater taxa at Hidas (Rolle 1862, p. 211), but the exact locality remains unknown. • H, I, M–O – *Gyraulus dealbatus* (Braun *in* Walchner, 1851); H, I – (SNSB-BSPG 2024 X 24); M–O – (SNSB-BSPG 2024 X 25). • J–L – *Gyraulus* sp. (SNSB-BSPG 2024 X 27). • P–R – *Planorbarius* cf. *mantelli* (Dunker, 1848); P – (SNSB-BSPG 2024 X 29); Q, R – (SNSB-BSPG 2024 X 30). Scale bars: 1 mm.

Remarks. – Numerous specimens of a small lymnaeid were found at Hidas, putatively all representing juvenile stages or fragments. The shells closely resemble juvenile specimens of *Stagnicola armaniacensis* (Noulet, 1857) illustrated by Kowalke & Reichenbacher (2005), from the Early Miocene of the Molasse Basin in southern Germany, and Harzhauser *et al.* (2014a), from the early Middle Miocene of the Rein Basin in Austria. All share the slender profile with regularly convex whorls and blunt apex; the shells from the Rein Basin also show a similarly elongate aperture with reflected peristome and a weak fold on the inner lip.

Stagnicola subovatus (Zieten, 1832), another common species in the Oligocene to Middle Miocene, has a broader shell and a comparatively smaller apex (Kadolsky 2020). Shells of *Stagnicola* cf. *palustriformis* (Gottschick, 1911) recorded at Vračević have an even blunter apex and more stepped whorls (Neubauer *et al.* 2017). The late Early to Middle Miocene species *Stagnicola jaccardi* (Maillard, 1892), originally described from Switzerland, has a more slender shell and a more pointy apex. *Galba dupuyiana* (Noulet, 1854), described from the Middle Miocene of France, has a very similar morphology and size, but the shell is a bit more slender, the aperture is narrower, and the whorls are slightly stepped.

Original drawings of *Galba sandbergeri* (Łomnicki, 1886) from the Middle Miocene of Ukraine suggest a slenderer morphology with very narrow aperture,

but drawings by Prysjazhnjuk *et al.* (2006) of juvenile material indicate a rather broad shell similar to (albeit slightly stouter than) the material from Hidas. Similarly, juvenile forms of *Stagnicola kreutzii* (Łomnicki, 1886) (*subfusca*-morphotype) from the same deposits as *Galba sandbergeri* have a similarly slender shell as juveniles of *S. armaniacensis*. Only, the drawings by Łomnicki (1886) indicate a weakly concave base.

Given the huge shell variability of lymnaeids known from several extant species (*e.g.*, Vinarski 2014), a careful revision of some of the Miocene species is necessary, both on the genus and species level. This particularly concerns a number of species from eastern Europe that have not been properly illustrated or revised and remain poorly known to date.

Occurrence. – Known from late Early to Middle Miocene deposits of Austria, France southern Germany, Switzerland (Harzhauser *et al.* 2014a), and Hungary (this study).

Family Planorbidae Rafinesque, 1815
Subfamily Planorbinae Rafinesque, 1815

Genus *Gyraulus* Charpentier, 1837

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

***Gyraulus dealbatus* (Braun *in* Walchner, 1851)**
Figure 3H, I, M–O

*1851 *Planorbis dealbatus* A. Braun; Walchner, p. 1134.
2005 *Gyraulus applanatus* (Thomae, 1845). – Kowalke & Reichenbacher, p. 631, fig. 9(1–3) [non *Planorbis applanatus* Thomä, 1845].
non 2014b *Gyraulus dealbatus* (Braun in Walchner, 1851). – Harzhauser *et al.*, pp. 831–834, fig. 3i–n [= *Gyraulus applanatus* (Thomä, 1845)].
2014 *Gyraulus dealbatus* (Braun 1851). – Salvador & Rasser, pp. 192, 193, figs 16, 17, 20–23 [?figs 18, 19].
2015 *Gyraulus applanatus* (Thomae, 1845). – Salvador *et al.*, p. 205, fig. 2h, i [*partim*, *non* Thomä, 1845; concerning figured specimen and records referring to *dealbatus*-type morphology].
2016 *Gyraulus applanatus* (Thomä, 1845). – Salvador & Rasser, p. 44, fig. 2g, h [*partim*, *non* Thomä, 1845; concerning figure and records referring to *dealbatus*-type morphology].
2016c *Gyraulus applanatus* (Thomä, 1845). – Salvador *et al.*, pp. 134, 135, fig. 2k–m [*partim*, *non* Thomä, 1845; concerning figure and records referring to *dealbatus*-type morphology].
2023 *Gyraulus dealbatus* (A. Braun 1851). – Kadolsky, pp. 97–99, pl. 5, figs 14, 15 (*cf.*), textfig. 3 [cum syn.].

Material. – 467 specimens (SNSB-BSPG 2024 X 24–26).

Dimensions. – 1.22 × 3.55 mm (Fig. 3H, I); 0.91 × 2.76 mm (Fig. 3M–O).

Remarks. – This species is the most common of the assemblage described here. It is characterized by a glossy, planispiral shell with nearly symmetrical cross-section. In some specimens, there is a very weak angulation slightly more closely towards the apical side. Whorls expand moderately fast; the terminal part of the last whorl attains slightly more than one third of the total diameter. Whorls overlap about one third of the preceding whorl. These characteristics place the specimens in the species group formed by *Gyraulus applanatus* (Thomä, 1845), *G. dealbatus* (Braun *in* Walchner, 1851), and *G. kleini* Gottschick & Wenz, 1916. The identities of these three species have been debated repeatedly over the past years. Recently, Kadolsky (2023) reviewed the type series of *Gyraulus applanatus* and *G. dealbatus*, both described from the Early Miocene of the Mainz Basin, along with ample material from that region. He concluded that the two species can be well delimited only in later ontogeny – shells of *G. applanatus* are flatter and whorls increase more slowly in diameter, and the blunt angulation is placed closer towards the apical side.

Previous concepts, for example by Gottschick & Wenz (1916), Kowalke & Reichenbacher (2005), Harzhauser *et al.* (2014a, b), Salvador *et al.* (2015, 2016c), Salvador & Rasser (2016), and Rasser & Salvador (2019) differ markedly in that regard. Gottschick & Wenz (1916) originally considered *G. kleini* to have an even weaker angulation than *G. dealbatus* and an almost symmetric whorl cross-section, but the syntypes illustrated by Salvador *et al.* (2016a) show a clear asymmetry. Kadolsky (2023) also emphasized that Gottschick & Wenz (1916) overestimated the diagnostic relevance of the angulation. *Gyraulus dealbatus* from the Early Miocene of the Most Basin (Czech Republic) as understood by Harzhauser *et al.* (2014b) rather corresponds to *G. applanatus* sensu Kadolsky (2023).

Gyraulus kleini was synonymized with *G. applanatus* by Rasser & Salvador (2019), and rightly so in our opinion, since the syntype shows indeed a similar whorl expansion rate and lateral profile as *G. applanatus* as illustrated by Kadolsky (2023). However, their concept of *G. applanatus* (which is primarily based on Middle Miocene occurrences) includes a much greater morphological variation, including shells that Kadolsky's (2023) concept would place in *G. dealbatus*. Accordingly, parts of previous authors' materials (see synonymy list) need to be

re-investigated to clarify the identities of the mentioned species.

Other similar Middle Miocene species include *Gyraulus pulici* (Brusina, 1897) from the Gacko Basin (Bosnia and Herzegovina) and *Gyraulus geminus* (Brusina, 1897) from the Sinj Basin (Croatia). Both differ in their higher whorl expansion rate, *G. pulici* also in the shell being higher (Neubauer *et al.* 2011, 2013).

One additional species was originally described from Hidas – *Gyraulus alienus* (Rolle, 1862) – but could not be detected in our study. The type material of that species stored at the Natural History Museum of Vienna shows a small, comparatively high shell with deep umbilicus and apex, large last whorl, expanded aperture, and weak growth irregularities. As such, it differs markedly from all other Miocene *Gyraulus* species known to us. To fix a name-bearing type for that species, we hereby designate the specimen illustrated in Fig. 3E–G (NHMW 1859/0042/0059) as the lectotype; in addition, Rolle's material includes 36 paralectotypes.

Occurrence. – Originally described from the Early Miocene of the Mainz Basin and widely distributed in the Early–Middle Miocene of the Molasse Basin (*e.g.*, Salvador *et al.* 2015, 2016b, c; Kadolsky 2023). Reported also from Early–Middle Miocene deposits of the Hanau Basin and the Rhön Mountains (Germany), the Aquitaine Basin (France), as well as Austria, Czech Republic, Hungary, Poland, Serbia, and Ukraine (Wenz 1923, Moayedpour 1977, Gozhik & Prysjazhnjuk 1978, Piechocki 1997, Binder 2004, Kókay 2006, Prysjazhnjuk 2008). Given the revised concept of the species, many of these records need confirmation.

***Gyraulus* sp.**
Figure 3J–L

Material. – 2 specimens (SNSB-BSPG 2024 X 27–28).

Dimensions. – 0.56 × 2.25 mm (Fig. 3J–L).

Remarks. – Most of our *Gyraulus* material fits well to *Gyraulus dealbatus* as revised by Kadolsky (2023), showing the typical convex, low-angulate shells. Two specimens, however, form an exception, displaying slightly smaller and comparatively narrow shells with more distinct adapical angulation. These shells superficially resemble *Gyraulus applanatus* (Thomä, 1845), but they are much flatter in relation to their small size; in *G. applanatus*, similarly flat shells are usually distinctly larger (see, *e.g.*, Salvador & Rasser 2014, 2017). Also, *G. applanatus* is more inequilateral, with a deeper apical side, and has more convex whorls on the umbilical side. Another similar species is *Gyraulus krohi* Neubauer & Harzhauser *in* Harzhauser *et al*., 2014a from the Langhian of the Rein Basin (Austria), with a similarly flat and weakly inequilateral shell but a higher number of whorls.

Because of the low number of individuals and uncertainty as to its classification, we keep this species in open nomenclature, pending a more thorough investigation of more comprehensive material.

Genus *Planorbarius* Duméril, 1805

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

***Planorbarius* cf. *mantelli* (Dunker, 1848)**
Figure 3P–R

cf. *1848 *Planorbis Mantelli*, Dkr.; Dunker, p. 159, pl. 21, figs 27–29.
cf. 2014a *Planorbarius mantelli* (Dunker 1848). – Harzhauser *et al.*, pp. 15, 16, pl. 3, figs 5, 7–13, 15, 16 [cum syn.].
cf. 2017 *Planorbarius mantelli* (Dunker, 1848). – Neubauer *et al.*, p. 739, fig. 3g, h, p [cum syn.].
cf. 2020 *Planorbarius mantelli* (Dunker, 1848). – Mandic *et al.*, pp. 530, 531, fig. 8g, h.

Material. – 116 specimens (SNSB-BSPG 2024 X 29–31).

Dimensions. – The largest complete specimen found is a juvenile shell measuring 2.69 × 5.04 mm (Fig. 3Q, R).

Remarks. – No complete adult specimen could be retrieved. The available shells exhibit a sub-rectangular profile with immersed apex and umbilicus, highly convex whorls, symmetrical, kidney-shaped aperture, and striate microsculpture. These features are typical for *Planorbarius mantelli* (Dunker, 1848), the most widely distributed species of the genus in the Middle Miocene of Europe.

A number of other species have been recorded from Middle Miocene strata of Europe, *e.g.*, *Planorbarius cornu* (Brongniart, 1810) (Late Eocene to Middle Miocene), *P. cornucopia* (Baily, 1858) (Middle Miocene), *P. incrassatus* (Rambur, 1862) (Early–Middle Miocene), *P. sansaniensis* (Noulet, 1854) (Middle Miocene), and *P. thiollieri* (Michaud, 1855) (Early Miocene to Pleistocene). Some of these species seem incredibly long-lived, yet their identities are questionable in part. A thorough investigation is necessary to establish clear species boundaries.

Since only subadult shells are available we only tentatively place our specimens in *P. mantelli*. Adult shells of *P. mantelli* differ from those of *Planorbarius cornu*, a species common in the Oligocene and Early Miocene, in being flatter with less bulbous whorls (Harzhauser *et al.* 2014b).

Occurrence. – *Planorbarius mantelli* is a common species during the late Early Miocene to Late Miocene found in numerous localities across Austria, Bosnia and Herzegovina, Croatia, Czech Republic, France, Germany, Greece, Hungary, Italy, Kazakhstan, Moldova, Poland, Portugal, Romania, Serbia, Slovakia, Spain, Switzerland, Turkey, and Ukraine (Wenz 1923, Schütt & Besenecker 1973, Gozhik & Prysjazhnjuk 1978, Kókay 2006, Harzhauser *et al.* 2014a, Neubauer *et al.* 2017, Salvador & Rasser 2017, Mandic *et al.* 2020).

Superorder Eupulmonata Haszprunar & Huber, 1990
Order Ellobiida Van Mol, 1967
Superfamily Ellobioidea H. Adams & A. Adams, 1855
Family Ellobiidae L. Pfeiffer, 1854 (1822)
Subfamily Carychiinae Jeffreys, 1830
Genus *Carychium* Müller, 1773

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

***Carychium gibbum* Sandberger, 1875**
Figure 4A–E

*1875 *Carychium gibbum* Sandberger; Sandberger, p. 583.
v 2014a *Carychium gibbum* Sandberger, 1875. – Harzhauser *et al.*, p. 20, pl. 6, figs 1–4, 9, 12 [cum syn.].
v 2017 *Carychium gibbum* Sandberger, 1875. – Neubauer *et al.*, pp. 739, 740, fig. 4f–i, k, l, p [cum syn.].

Material. – 21 specimens (SNSB-BSPG 2024 X 32–34).

Dimensions. – 1.80 × 0.96 mm (Fig. 4A, D, E); 1.58 × 0.91 mm (Fig. 4B, C).

Remarks. – The available material exhibits rather broad shells with slightly stepped whorls, slightly inflated penultimate whorl, distinct growth lines, pitted protoconch, and three apertural teeth – a strong, narrow parietal denticle, a weak, basal columellar lamella, and a broad, knob-like palatal denticle. All these features place the specimens in *Carychium gibbum* as described and discussed thoroughly in Harzhauser *et al.* (2014a) and Neubauer *et al.* (2017). The sometimes co-occurring *Carychium nouleti* Bourguignat, 1857, originally described from the Middle Miocene of Sansa (France), has a narrower shell and one additional whorl. The Middle Miocene *Carychium suevicum* Boettger, 1877 from Steinheim (Germany), which also occasionally shows similarly bulky shells, usually lacks the inflated penultimate whorl (Finger 1998, Neubauer *et al.* 2017).

Occurrence. – Fairly common species in the European Middle Miocene, known from localities in Austria, Germany, Hungary, Poland, and Serbia (see Neubauer *et al.* 2017 for details).

Order Stylommatophora Schmidt, 1855
Infraorder Pupilloidei
Superfamily Pupilloidea Turton, 1831
Family Strobilopsidae Wenz, 1915 *in* Fischer & Wenz (1915)
Genus *Strobilops* Pilsbry, 1893

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

***Strobilops costatus* (Clessin, 1877)**
Figure 4F–J, P, Q

*1877 *Strobilus costatus* Sdbgr. in litt.; Clessin, p. 37.
v 2017 *Strobilops costatus* (Clessin, 1877). – Neubauer *et al.*, pp. 744–747, fig. 6a–o [cum syn.].
v 2018 *Strobilops costatus* (Clessin, 1877). – Harzhauser & Neubauer, p. 96, fig. 6j–m [cum syn.].

Material. – 2 specimens (SNSB-BSPG 2024 X 35–36).

Dimensions. – 1.63 × 2.06 mm (Fig. 4F, G, Q); 1.14 × 1.54 mm (Fig. 4H–J, P).

Remarks. – *Strobilops costatus* was described and discussed in detail by Neubauer *et al.* (2017) and Harzhauser & Neubauer (2018). Our specimens show the same type of low-trochiform shell with basal angulation, narrow umbilicus, strong oblique-axial ribs, strong parietal lamellae and small infraparietal lamella. Only the weak interparietal lamella shown by Neubauer *et al.* (2017) is not visible in our material, but this may be a result of preservation or intraspecific variation.

Occurrence. – The species is found in late Early to Middle Miocene strata of Austria, Germany, Poland, Serbia, potentially Moldova (Neubauer *et al.* 2017; for details see there), and Hungary (this study).

Family Vertiginidae Fitzinger, 1833

Genus *Vertigo* Müller, 1773

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

***Vertigo diversidens* (Sandberger, 1872)**
Figure 4K, L, O

*1872 [*Pupa*] *diversidens* Sandb.; Sandberger, pl. 29, fig. 23–23b.

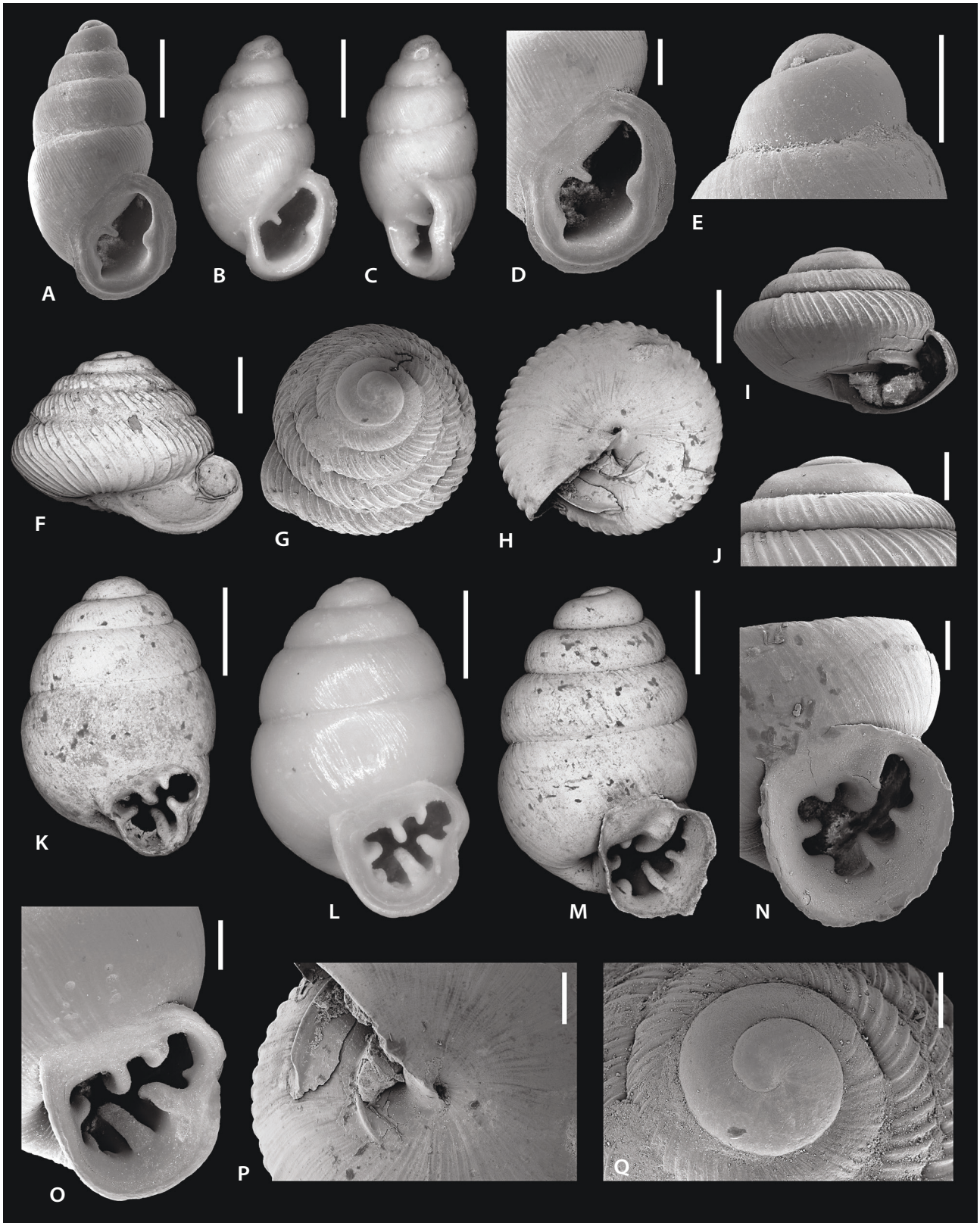

Figure 4. Terrestrial gastropod species at Hidas. • A–E – *Carychium gibbum* Sandberger, 1875, A, D, E – (SNSB-BSPG 2024 X 32); B, C – (SNSB-BSPG 2024 X 33). • F–J, P, Q – *Strobilops costatus* (Clessin, 1877); F, G, Q – (SNSB-BSPG 2024 X 35); H–J, P – (SNSB-BSPG 2024 X 36). • K, L, O – *Vertigo diversidens* (Sandberger, 1872); K – (SNSB-BSPG 2024 X 37); L, O – (SNSB-BSPG 2024 X 38). • M, N – *Gastrocopta nouletiana* (Dupuy, 1850); M – (SNSB-BSPG 2024 X 40); N – (SNSB-BSPG 2024 X 41). Scale bars: 500 µm (A–C, F–I, K–M), 200 µm (D, E, J, N–Q).

1875 *Pupa* (*Vertigo*) *diversidens* Sandberger. – Sandberger, pp. 549, 550.
1999 *Vertigo diversidens* (Sandberger, 1874). – Stworzewicz, p. 138, fig. 8 [cum syn.].
2006 *Vertigo callosa diversidens* (Sandberger) 1874. – Kókay, p. 63, pl. 23, figs 2, 3, 9.
2014b *Vertigo callosa* (Reuss in Reuss & Meyer, 1849). – Harzhauser *et al.*, p. 853, fig. 8g [*partim*, second morphotype only; non *Vertigo callosa* Reuss, 1849].
2020 *Vertigo diversidens* (Sandberger, 1872). – Mandic *et al.*, pp. 534, 535, fig. 9m, n [cum syn.].

Material. – 7 specimens (SNSB-BSPG 2024 X 37–39).

Dimensions. – 1.60 × 1.11 mm (Fig. 4K), 1.94 × 1.24 (Fig. 4L, O).

Remarks. – We retrieved seven specimens of *Vertigo* with minute, sturdy shells with low whorl convexity, distinct growth lines, and strong apertural dentition. Shell shape varies from nearly globular to slightly higher forms. In only two well-preserved specimens, the dentition was fully visible, showing a strong parietal and smaller angular lamella, a strong columellar lamella, two weak basal lamellae, a very prominent lower palatal and slightly less strong upper palatal lamella, as well as a tiny suprapalatal lamella. In one of the specimens, an additional tiny infraparietal lamella occurs.

The variability in shape and dentition makes the identification and delimitation of this species difficult. The closest match for our specimens is *Vertigo diversidens* (Sandberger, 1872), originally described from Langhian deposits at Sansan (France). The species was further discussed and illustrated by Stworzewicz (1999) and Mandic *et al.* (2020). The type material of *V. diversidens*, supposedly stored in Sandberger's collection at the Museum Wiesbaden, could not be found (F. Geller-Grimm, pers. comm. 2024/11). Topotypic material of *V. diversidens* from Sansan stored in the collection of the Senckenberg Research Institute and Natural History Museum in Frankfurt (SMF273994) shows variation in the dentition of this species: the infraparietal, supraparietal, and suprapalatal lamellae are only present in some specimens (partly in different combinations). In addition, shell shape, whorl convexity, and aperture shape vary considerably – from rather elongate shells with low convex whorls and narrow aperture to bulkier ones with highly convex whorls with broad aperture. Four of the five shells from Sansan available to us have more elongate shells with low whorl convexity.

A second species that shows close similarities to *V. diversidens* is *Vertigo callosa* Reuss, 1849, described from the Early Miocene of Tuchořice (Czech Republic) and documented from numerous Early–Middle Miocene localities across Central Europe (Stworzewicz 1999; Harzhauser *et al.* 2014a, b; Mandic *et al.* 2020). Both species have occasionally been recorded from the same localities (Stworzewicz 1999, Mandic *et al.* 2020). *Vertigo callosa* exposes a similar degree of variability when it comes to shell shape and dentition. In fact, the variability documented in the literature casts serious doubts about the distinctness of the two species. Stworzewicz (1999) noted for *V. callosa* from Bełchatów (Poland) that about a quarter of her specimens had a suprapalatal tooth. Harzhauser *et al.* (2014b) noted the presence of two morphotypes – one with a single, broad basal lamella and, rarely, a small infraparietal lamella, the second one (being less abundant) with an additional weak suprapalatal lamella and a very low, usually two-fold basal lamella. The latter type perfectly matches some *V. diversidens* specimens from Sansan and Hidas studied by us.

Unfortunately, the type material of *Vertigo callosa* required to properly solve this issue is missing as well. Despite contacting several institutes that may potentially host Reuss' material (Institute of Geology and Paleontology, Charles University, Prague; Natural History Museum, Prague; Hungarian Natural History Museum, Budapest; Natural History Museum, Vienna; Geological Survey of Austria, Vienna) and checking type catalogues (Pálfy *et al.* 2008), we could not find any hints on its whereabouts so far. Until more information about the type materials of the two species can be obtained and/or more specimens can be studied for a thorough investigation of morphological variability, we maintain the two species as separate entities.

Vertigo diversidens (and *V. callosa*) can be well distinguished from other Miocene species. The Middle–Late Miocene *Vertigo trolli* Wenz, 1915 *in* Fischer & Wenz (1915) has stronger upper palatal and upper parietal lamellae (Harzhauser & Neubauer 2018). *Vertigo minor* Boettger, 1870, from the Early Miocene of the Most Basin (Czech Republic), has a similar dentition (albeit less dense) but more convex shell and a narrower last whorl (Harzhauser *et al.* 2014b). The Early–Middle Miocene *Vertigo angulifera* Boettger, 1884 differs in the narrower shell and reduced dentition, showing a massive columellar and comparatively small upper palatal, parietal, and angular lamellae (Stworzewicz 1999). The long-lived, Late Oligocene to Late Miocene *Vertigo protracta* (Sandberger, 1875) has a slightly more slender shell with a narrower last whorl and a finer dentition (Harzhauser & Neubauer 2018). *Vertigo moldavica* Prisyazhnyuk, 1973 from the Sarmatian of Moldova (Prisyazhnyuk 1973) has a more ovoid shell and a thicker dentition. *Vertigo likharevi* Prysjazhnjuk *in* Gozhik & Prysjazhnjuk, 1978 from the early Sarmatian of Ukraine is distinguished by a very prominent columellar lamella and apparently two strong lower palatal lamellae.

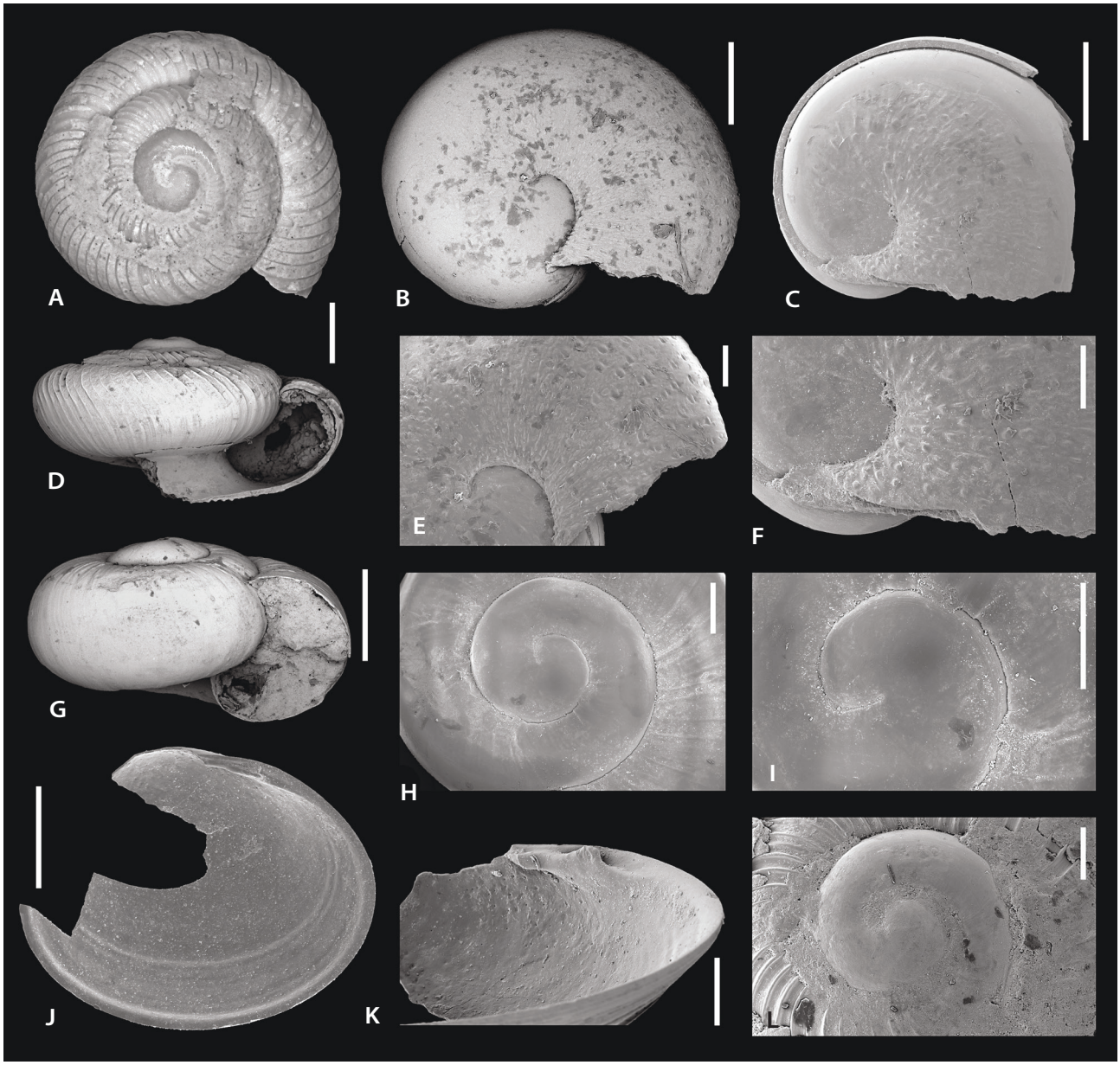

Figure 5. Terrestrial gastropod and freshwater bivalve species at Hidas. • A, D, L – *Discus solarioides* (Sandberger, 1872) (SNSB-BSPG 2024 X 43). • B, C, E, F – Eloninae? gen. et sp. indet.; B, E – (SNSB-BSPG 2024 X 45); C, F – (SNSB-BSPG 2024 X 46). • G–I – *Zonitoides* cf. *suevicus* (Jooss, 1918) (SNSB-BSPG 2024 X 44). • J, K – *Pisidium* s.l. sp. (SNSB-BSPG 2024 X 47). Scale bars: 500 µm (A–D, J), 200 µm (E, F, H, I, K, L).

Occurrence. – The species is known from the Early Miocene of Poland (Stworzewicz 1999) and the Middle Miocene of France (Sandberger 1870), Germany (Finger 1998), Bosnia and Herzegovina (Mandic *et al.* 2020), and Hungary (Kókay 2006; this study).

Family Gastrocoptidae Pilsbry, 1918
Genus *Gastrocopta* Wollaston, 1878

Type species. – *Pupa acarus* Benson, 1856; by subsequent designation by Pilsbry (1916, p. 7). Recent, Azores.

***Gastrocopta nouletiana* (Dupuy, 1850)**
Figure 4M, N

*1850 *Pupa Nouletiana*; Dupuy, pp. 309, 310, pl. 15, fig. 6.
2016c *Gastrocopta nouletiana* (Dupuy, 1850). – Salvador *et al.*, pp. 140, 141, figs 3q, r.
v 2017 *Gastrocopta nouletiana* (Dupuy, 1850). – Neubauer *et al.*, pp. 751, 752, fig. 8d, j [cum syn.].

Material. – 7 specimens (SNSB-BSPG 2024 X 40–42).

Dimensions. – 1.98 × 1.31 mm (Fig. 4M).

Remarks. – Our shells fit well the description of *Gastrocopta nouletiana* by Neubauer *et al.* (2017) based on late Middle Miocene material from Vračević (Serbia). The shells from Hidas show similarly bulky shells with highly convex whorls, distinct growth lines, and narrow umbilicus. They also share the characteristic dentition consisting of a prominent, deeply reaching angulo-parietal lamella with the angular part being entirely fused, a small infraparietal, about equally strong columellar and basal lamellae, a strong, narrow lower palatal, and a less prominent upper palatal lamella. Unlike the shells from Vračević, the Hidas specimens also show a suprapalatal lamella, forming a faint knob. In turn, like in the Vračević specimens, there is no interpalatal tooth, which is present in material illustrated by Salvador *et al.* (2016c).

Occurrence. – The species is widespread in the late Early to Late Miocene of Europe and has been recorded from numerous locations in Austria, France, Germany, Hungary, Poland, Serbia, Switzerland, Ukraine, and potentially Moldova (Wenz 1923, Neubauer *et al.* 2017).

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

Genus *Discus* Fitzinger, 1833

Type species. – *Helix ruderata* Hartmann, 1821; by subsequent designation by Gray (1847, p. 174). Recent, Europe.

***Discus solarioides* (Sandberger, 1872)**
Figure 5A, D, L

*1872 *Patula solarioides* A. Braun; Sandberger, pl. 28, fig. 7–7c.
1911 *Patula* (*Charopa*) *costata* Gottschick; Gottschick, p. 501, pl. 7, fig. 15–15c.
v 2017 *Discus solarioides* (Sandberger, 1872). – Neubauer *et al.*, pp. 753, 754, fig. 9a, b, d, e, g [cum syn.].
v 2018 *Discus solarioides* (Sandberger, 1872). – Harzhauser & Neubauer, p. 112, fig. 9s, t [cum syn.].

Material. – 1 specimen (SNSB-BSPG 2024 X 43).

Dimensions. – 1.38 × 2.64 mm (Fig. 5A, D, L).

Remarks. – Characteristic for this species is the low-trochiform shell with strong, blunt, densely placed and equally spaced ribs that are opisthocyrt in the whorl center to weakly sigmoidal towards the sutures. Ribs also extend to the umbilical side. Maximum convexity is above whorl mid-height, the aperture is kidney-shaped, and the umbilicus is relatively wide. The protoconch consists of approximately one whorl, bearing delicate spiral grooves; the transition to the teleoconch is marked by the onset of ribs. In the Hidas specimen these grooves are faint, and the transition to the teleoconch is covered by sediment, but all other characteristics match perfectly to the species as revised by Neubauer *et al.* (2017) and Harzhauser & Neubauer (2018).

Occurrence. – Known from the late Langhian of southern Germany (Sandberger 1870–1875, Gottschick 1911), the late Langhian and late Serravallian of Poland (Stworzewicz *et al.* 2013, Harzhauser & Neubauer 2018), the early Serravallian of Hungary (this study), and the late Serravallian of Serbia (Neubauer *et al.* 2017). A further potential record from the early Tortonian (Pannonian) of Austria listed by Wenz (1923) needs verification.

Superfamily Gastrodontoidea Tryon, 1866
Family Gastrodontidae Tryon, 1866

Genus *Zonitoides* Lehmann, 1862

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

***Zonitoides* cf. *suevicus* (Jooss, 1918)**
Figure 5G–I

cf. *1918 *Polita suevica* n. sp.; Jooss, p. 289.
v 2017 *Zonitoides* cf. *suevicus* (Jooss, 1918). – Neubauer *et al.*, p. 758, fig. 11a, d, g, j [cum syn.].

Material. – 1 specimen (SNSB-BSPG 2024 X 44).

Dimensions. – 1.02 × 1.77 mm (Fig. 5G–I).

Remarks. – The sole available specimen matches well *Zonitoides* cf. *suevicus* (Jooss, 1918) of Neubauer *et al.* (2017) from late Serravallian strata of Vračević (Serbia) concerning size (1.00 × 1.70 mm), the low-trochiform shell with high, strongly convex whorls, and the low protoconch with faint spiral grooves. In the specimen from Hidas, however, the ornamentation is visible on faintly near the margin compared to the well-preserved surface of the Vračević specimen.

Occurrence. – *Zonitoides suevicus* was described and has been recorded from a few localities in the Upper Freshwater Molasse (Wenz 1923, Schlickum 1976, Salvador *et al.* 2016a). The species was also documented from late

Badenian and Sarmatian strata of Hungary (Kókay 2006) and late Serravallian deposits of Serbia (Neubauer *et al.* 2017).

Superfamily Helicoidea Rafinesque, 1815
Family Elonidae Gittenberger, 1979
Subfamily Eloninae Gittenberger, 1979

Eloninae? gen. et sp. indet.
Figure 5B, C, E, F

? 2017 ?Eloninae gen. et sp. indet. – Neubauer *et al.*, p. 762, fig. 12g, j.

Material. – 2 protoconch fragments (SNSB-BSPG 2024 X 45–46).

Dimensions. – Maximum diameters are 2.20 mm (Fig. 5B, E) and 1.70 mm (Fig. 5C, F).

Remarks. – Similarly as in the study of Neubauer *et al.* (2017), we encountered two protoconch fragments of land snails bearing an irregular sculpture of hair pits and pustules together with irregular, weak, spiral rugae. In terms of sculpture and size, these features strongly remind of the genera *Pseudochloritis* and *Joossia* (Elonidae: Eloninae; *e.g.*, Binder 2002, 2004, 2008). The Klikiinae genera *Apula* and *Klikia* share a similar protoconch sculpture but have smaller shells and protoconchs (*e.g.*, Nordsieck 2014, Harzhauser & Neubauer 2018).

Class Bivalvia Linnaeus, 1758
Superorder Heterodonta Neumayr, 1883
Order Venerida Gray, 1854
Family Sphaeriidae Deshayes, 1855
Subfamily Sphaeriinae F.C. Baker, 1927
Genus *Pisidium* C. Pfeiffer, 1821 s.l.

Type species. – *Tellina amnica* Müller, 1774; by subsequent designation by Gray (1847, p. 185). Recent, Europe.

***Pisidium* s.l. sp.**
Figure 5J, K

Material. – 2 fragmented left valves (SNSB-BSPG 2024 X 47–48).

Dimensions. – 1.40 × 1.75 mm (Fig. 5J, K).

Remarks. – Only two incomplete left valves of this species are available. The more complete one lacks the posterior part of the hinge and parts of the umbo (Fig. 5J, K). The specimen has a thin, nearly perfectly elliptical shell, with clear but fine growth lines on the external shell surface and a porate inner surface. The hinge plate is narrow, the anterior tooth (A2) forms a distinct, narrow, blunt cusp.

In terms of shape, size, and the available shell characteristics, the specimen shows similarities to and might be conspecific with *Pisidium* sp. of Harzhauser & Neubauer (2018, fig. 14l–n, o–q, r) from the Langhian of Opole (Poland). More material is required to ascertain the identity of this species. Given the recently revised supraspecific classification of sphaeriids (Bespalaya *et al.* 2024), we place this species tentatively and traditionally in *Pisidium* s.l.

Results and Discussion

Faunal composition

The assemblage documented here comprises in total 19 species – 11 species of aquatic gastropods, 7 species of terrestrial gastropods, 1 species of bivalve – in 16 families (Tab. 1). All of the polyhaline to normal-marine species (Neritidae, Nassariidae, Potamididae, Batillariidae, Litiopidae, and potentially Hydrobiidae) have already been reported from Hidas by previous studies (Csepreghy-Meznerics 1950, Strausz 1966, Bohn-Havas 1973), albeit many under different names. Concerning the freshwater fauna (Lymnaeidae, Planorbidae, Sphaeriidae), four species are new for Hidas, i.e., *Stagnicola armaniacensis*, *Gyraulus dealbatus*, *Planorbarius* cf. *mantelli*, and *Pisidium* s.l. sp. Previous authors (Rolle 1862; Wenz 1932; Csepreghy-Meznerics 1950; Kókay 1967, 2006) described a number of additional taxa to the ones detected herein. Few of these taxa or records have been revised properly, which is why we briefly discuss their status here, in order to enable us to provide a revised list of non-marine species known from Hidas (Tab. 2).

Rolle (1862) described a single planorbid species, *Planorbis alienus*, from Hidas. The species, nowadays placed in the *Gyraulus*, is easily distinguished from all other known planorbids. Seven decades later, Wenz (1932) added the subspecies *Brotia escheri inornata*, forming monospecific assemblages in clays/lignitic clays, to the list of non-marine taxa. Today the taxon is classified in the pachychilid genus *Tinnyea*, which is believed to have dwelled primarily in fluviatile habitats (Kowalke 2004). In the first comprehensive taxonomic study of Hidas mollusks, Csepreghy-Meznerics (1950) identified seven additional freshwater to oligohaline species (in addition to numerous marine and brackish-water species). Most of her records, however, contain no description or illustration and sometimes no discussion, making it impossible to verify them. Among them are

Table 1. Material list of the taxa retrieved from late Middle Miocene deposits at Hidas in this study.

Species	Family	No. specimens	ecology
Vitta tuberculata (Schréter *in* Horusitzky, 1915)	Neritidae	5	brackish
Hydrobiidae gen. et sp. indet.	Hydrobiidae	7	brackish
Tritia? *schoenni* (Hoernes & Auinger, 1882)	Nassariidae	2	brackish
Pustulosia submitralis (Eichwald, 1851)	Batillariidae	12	brackish
Tiaracerithium pictum (Basterot, 1825)	Batillariidae	10	brackish
Terebralia duboisi (Hörnes, 1855)	Potamididae	1	brackish
Gibborissoia cf. *varicosa* (Basterot, 1825)	Litiopidae	30	brackish
Stagnicola armaniacensis (Noulet, 1857)	Lymnaeidae	70	freshwater
Gyraulus dealbatus (Braun *in* Walchner, 1851)	Planorbidae	467	freshwater
Gyraulus sp.	Planorbidae	2	freshwater
Planorbarius cf. *mantelli* (Dunker, 1848)	Planorbidae	116	freshwater
Carychium gibbum Sandberger, 1875	Ellobiidae	21	terrestrial
Strobilops costatus (Clessin, 1877)	Strobilopsidae	2	terrestrial
Vertigo diversidens Sandberger, 1872	Vertiginidae	7	terrestrial
Gastrocopta nouletiana (Dupuy, 1850)	Gastrocoptidae	7	terrestrial
Discus solarioides (Sandberger, 1872)	Discidae	1	terrestrial
Zonitoides cf. *suevicus* (Jooss, 1918)	Gastrodontidae	1	terrestrial
?Eloninae gen. et. sp. indet.	Elonidae	2	terrestrial
Pisidium s.l. sp.	Sphaeriidae	2	freshwater
Total		765	

the widespread neritid species *Neritina grateloupiana* [= *Theodoxus grateloupianus* (Férussac, 1823)] and *Neritina picta* [= *Vitta picta* (Férussac, 1823)] and the hydrobiids *Hydrobia frauenfeldi* [= *Sarmata frauenfeldi* (Hörnes, 1856)], *Hydrobia hoernesi* Friedberg, 1923, and *Hydrobia punctum* (Eichwald, 1850) (see also Strausz 1966). Her record of *Hydrobia frauenfeldi* may represent our Hydrobiidae gen. et sp. indet. *Hydrobia hoernesi* has an ovoid, slightly stepped shell (Friedberg, 1923), and *Hydrobia punctum* is small and globular (Eichwald 1853), neither of which we found in our material. In addition, she listed and illustrated the species *Hydrobia pupa* (Sacco, 1895b), which was originally placed in the marine genus *Pisinna* (Anabathridae) and was later again placed there by Moisescu (1986). She also described the new lymnaeid species *Myxas hidasensis* Csepreghy-Meznerics, 1950, showing a species with strongly inflated last whorl, which is superficially reminiscent of the early members of the Pannonian evolutionary lineage leading to the huge, limpet-shaped Valencienniinae (*e.g.*, Taktakishvili 1967). Csepreghy-Meznerics (1950) as well as Strausz (1966) considered it more likely that this species may derive from Pannonian strata, so it is not included here in the list of Middle Miocene species from Hidas.

Among the bivalves, she listed an unidentified species of *Unio* (Unionidae) from freshwater strata and two dreissenids, *Congeria basteroti* (Deshayes, 1836) and *Congeria sandbergeri* [sic] (Andrusov, 1890), from strata containing primarily marine taxa. The dreissenids may represent brackish-water dwellers. The classifications of these species have not been properly revised so far, but following the systematic work of Andrusov (1897), who established informal groupings, many of which were later formalized by Starobogatov (1970), these species should be classified in the genera *Andrusoviconcha* and *Coelogonia*.

Kókay (1967) described additionally *Valvata hidasensis*, which he later referred to the truncatellid genus *Sandbergerina* Kadolsky, 1993 (Kókay 2006). However, the illustrations of Kókay (1967) suggest that the species

has nothing to do with *Sandbergerina* or Truncatellidae, which are characterized by a decollate apex. Rather, the species may belong in a group of pseudamnicoline-type hydrobiids such as *Bania*. Further research is needed to verify the identity and classification of this species.

In a monograph focusing primarily on the marine mollusks of the Mecsek Mountains, Bohn-Havas (1973) added the record of *Valvata simplex* Fuchs, 1870 to the list of species from Hidas. She did not describe or illustrate that species or refer to Kókay's (1967) on *Valvata hidasensis*. *Valvata simplex* is a Pannonian species, its occurrence in late Badenian strata is unlikely, which is why it is not included in the list here. On a nomenclatural note, Fuchs' name is a junior homonym of *V. simplex* Gould, 1841; nowadays it is classified as *Muellerpalia octonaria haszprunari* Neubauer, Harzhauser, Kroh, Georgopoulou & Mandic, 2014.

Kókay (2006) further reported "*Nematurella aquensis* [...] var.", summarizing a variety of shells that might not all be conspecific. The kind of morphology, showing a small, ovoid shell with approximately four whorls, is not found in our material. He also mentioned *Ferrissia wittmanni* (Schlickum, 1964) from Hidas, but again this identification is uncertain. The shell from Várpalota illustrated by Kókay (2006, pl. 20, fig. 14) shows a regularly elliptical shell, while the original of Schlickum (1964, pl. 2, figs 36–38) is distinctly more slender and tapered towards the apex (see also Kowalke & Reichenbacher 2005). Kókay's specimens may rather represent the common Middle Miocene species *Ferrissia deperdita* (Desmarest, 1814) as illustrated by Harzhauser *et al.* (2014a) and Salvador *et al.* (2016c).

In addition, Wenz (1923–1930) listed a number of species from upper Pannonian ("Pontian") strata from

Table 2. Revised list of freshwater and terrestrial mollusk species recorded from Hidas. The table only contains taxa that we either treated in our revision or at least consider likely to form distinct species. Taxa that could not be verified due to the lack of descriptions and/or illustrations and which could potentially represent misidentifications of other listed taxa were excluded. See Discussion for more details.

Species	Family	Sources
Freshwater taxa		
Tinnyea inornata (Wenz, 1932)	Pachychilidae	Wenz (1932), Csepreghy-Meznerics (1950), Strausz (1966), Bohn-Havas (1973)
"*Sandbergerina*" *hidasensis* (Kókay, 1967)	Hydrobiidae?	Kókay (1967, 2006)
Stagnicola armaniacensis (Noulet, 1857)	Lymnaeidae	this study
Ferrissia cf. *deperdita* (Desmarest, 1814)	Planorbidae	Kókay (2006)
Gyraulus alienus (Rolle, 1862)	Planorbidae	Rolle (1862), Strausz (1966), Kókay (2006)
Gyraulus dealbatus (Braun *in* Walchner, 1851)	Planorbidae	this study
Gyraulus sp.	Planorbidae	this study
Planorbarius cf. *mantelli* (Dunker, 1848)	Planorbidae	this study
Unio sp.	Unionidae	Csepreghy-Meznerics (1950)
Pisidium s.l. sp.	Sphaeriidae	this study
Terrestrial taxa		
Carychium gibbum Sandberger, 1875	Ellobiidae	this study
Strobilops costatus (Clessin, 1877)	Strobilopsidae	this study
Vertigo diversidens Sandberger, 1872	Vertiginidae	this study
Gastrocopta nouletiana (Dupuy, 1850)	Gastrocoptidae	this study
Discus solarioides (Sandberger, 1872)	Discidae	this study
Zonitoides cf. *suevicus* (Jooss, 1918)	Gastrodontidae	this study
?Eloninae gen. et. sp. indet.	Elonidae	this study
Megalotachea turonensis (Deshayes, 1832)	Helicidae	Strausz (1966)

Hidas, which are listed here for the sake of completeness: *Viviparus sadleri* (Neumayr, 1869), *Viviparus achatinoides* (Deshayes, 1838) (Viviparidae), and *Zagrabica maceki* Brusina, 1884 (currently considered to belong in Lithoglyphidae; Neubauer *et al.* 2021). Wenz (1923) also considered *Gyraulus alienus* to derive from Pontian strata, but Rolle (1862) had stated explicitly that the specimens were collected from strata that contain only freshwater taxa in between marl and lignite layers, matching the here studied Middle Miocene succession. Moreover, according to Rolle, *G. alienus* co-occurs with "*Hydrobia ventrosa* Mont." [= *Ecrobia ventrosa* (Montagu, 1803)] in some layers. That extant species is remarkably similar to and may represent our Hydrobiidae gen. et sp. indet. Consequently, it is more likely that *G. alienus* comes from late Badenian rather than Pannonian strata (see also Strausz 1966, p. 487; Kókay 2006, p. 54).

The only terrestrial gastropod species reported from Hidas so far is the record of "*Helix* (*Cepaea*) *eversa larteti* Boissy, 1840" by Strausz (1966). This species was originally described from the Langhian of Sansan (France) and is today considered a junior synonym of *Megalotachea turonensis* (Deshayes, 1832) according to Höltke & Rasser (2016). The terrestrial species we identified herein are all new for Hidas.

Biostratigraphy

The microvertebrates, specifically the occurrences of *Albanensia albanensis*, *Forsythia gaudryi* (both Sciuridae), and *Democricetodon freisingensis* (Cricetidae), recently described from the same deposits, suggest an early Serravallian (late Badenian) age of the assemblage (*c*. 13.5–13.3 Ma; Hír *et al.* 2024). This age is in line with our findings. Of all taxa we encountered only *Vitta tuberculata* is constrained to the late Badenian (Papp 1952; Švagrovský 1960, 1964; Harzhauser *et al.* 2018). *Tritia*? *schoenni* is in the Central Paratethys known from Karpatian to Badenian strata (Harzhauser & Kowalke 2004). The freshwater taxa *Stagnicola armaniacensis*, *Gyraulus dealbatus*, and *Planorbarius* cf. *mantelli*, as well as the mudwhelk species (*Pustulosia submitralis*, *Tiaracerithium pictum*, *Terebralia duboisi*), all fit well to a Middle Miocene age (Harzhauser *et al.* 2014a, 2023a, b; Neubauer *et al.* 2017; Höltke *et al.* 2018), but do not further constrain the age. The three freshwater taxa actually have a longer range and occur also in the Early Miocene (*e.g.*, Salvador *et al.* 2016c). The terrestrial gastropod species are all typical Middle Miocene species, known from the Langhian as well as the Serravallian (Wenz 1923, Hír & Kókay 2004, Kókay 2006, Stworzewicz *et al.* 2013, Harzhauser *et al.* 2014a, Neubauer *et al.* 2017, Harzhauser & Neubauer 2018).

Paleoecology

The here recovered assemblage is a mixture of elements from different types of paleoenvironments. Six species (*Vitta tuberculata*, *Tritia*? *schoenni*, *Pustulosia submitralis*, *Tiaracerithium pictum*, *Terebralia duboisi*, *Gibborissoia* cf. *varicosa*) are typical polyhaline to normal-marine dwellers, five species (*Stagnicola armaniacensis*, *Gyraulus dealbatus*, *Gyraulus* sp., *Planorbarius* cf. *mantelli*, *Pisidium* s.l. sp.) lived in fresh waters, and seven species (*Carychium gibbum*, *Strobilops costatus*, *Vertigo diversidens*, *Gastrocopta nouletiana*, *Discus solarioides*, *Zonitoides* cf. *suevicus*, Eloninae? gen. et. sp. indet.) are terrestrial. The ecology of the unidentified Hydrobiidae gen. et sp. indet. is unknown, but it resembles species belonging to a group of brackish-water species that was common across the Paratethys Sea during the Middle Miocene.

The brackish-water part of the assemblage, including neritids, mudwhelks (potamidids, batillariids), and nassariids, is typical of coastal swamp, mangrove, and mudflat environments (Harzhauser & Kowalke 2002, Harzhauser *et al.* 2023b). Similar taxonomic compositions have been reported from the Karpatian (late Early Miocene) of the Korneuburg Basin and from middle–late Badenian (Middle Miocene) coal deposits in the Vienna Basin (Harzhauser *et al.* 2018), as well as from modern tropical–subtropical ecosystems (Reid *et al.* 2008, Candri *et al.* 2020). The generally relatively high diversity of mudwhelks at Hidas, reported by us as well as by Csepreghy-Meznerics (1950), especially the genus *Terebralia*, indicate the potential presence of mangrove environments (Harzhauser *et al.* 2023b). *Pustulosia* is often found associated with *Terebralia* in mudflat deposits and may have also lived on mangroves (Harzhauser *et al.* 2023a, b). *Terebralia* points to winter sea-surface temperatures of at least 20 °C (Thivaiou *et al.* 2023). Other groups commonly associated with mangroves, such as Ellobiidae (excluding Carychiinae) or Assimineidae (Reid *et al.* 2008, Candri *et al.* 2020, Harzhauser *et al.* 2023c), have not been found at Hidas or other localities in the Mecsek Mountains so far.

The freshwater taxa with abundant pulmonate species (Planorbidae, Lymnaeidae), both in terms of relative number of species and individual abundance, point to a lentic or slowly moving, probably highly vegetated environment, such as a lake or pond (Welter-Schultes 2012). The type of composition is typical of geologically short-lived environments, such as many present-day European lake faunas.

The terrestrial gastropods indicate a moist-adapted community, in line with the vicinity to a water body. Species of *Carychium* thrive in consistently humid environments, often found beneath leaf litter or between

stones in meadows, swamps, and forests near water bodies (Welter-Schultes 2012). Similarly, extant *Strobilops* species, as noted by Pilsbry (1927–1935), inhabit decaying logs and dead leaves in moderately humid forests. The genus *Vertigo* displays a broad modern distribution, occurring in diverse habitats, with European species predominantly found in wetland and mesic environments and rarely in xeric conditions (Horsák *et al.* 2024). *Gastrocopta*, a widely distributed and species-rich genus, occupies habitats from arid to wet, including forests, shrublands, grasslands, and floodplains, often within leaf litter, under logs or stones, or on bedrock outcrops (Nekola & Coles 2010). *Discus* is typical of shaded, humid, and often mountainous regions, residing in leaf litter, soil, humus, or beneath rotting wood and stones, and occasionally in damp, shady open habitats (Welter-Schultes 2012). European species of *Zonitoides* prefer woodlands and moist environments, such as meadows, riparian woods, and swamps, emphasizing the adaptability of land snails to a wide range of ecological conditions (Welter-Schultes 2012).

In terms of relative abundance, the freshwater taxa make up the majority of the assemblage (85.9%), which is especially on account of the most common species (*Gyraulus dealbatus*). The brackish (8.8%) and terrestrial (5.4%) components are comparatively rare, despite the high number of species they contribute (both 36.8% relative to the total number of species). Species with large shells, such as *Planorbarius*, *Stagnicola*, *Tritia* or the mudwhelks, are only present as fragments or juveniles. Also some of the individuals of smaller-shelled brackish species (*Gibborissoia*, *Vitta*) are partly fragmented, *e.g.*, lack the aperture or the apex (Fig. 2). Among the small freshwater and terrestrial species, most specimens are well preserved, only a few show signs of transportation or reworking (*e.g.*, blue color, eroded surfaces, sediment infills differing from matrix).

In summary, these data suggest that the assemblage was washed together and deposited in a low-energy setting, perhaps a pond or oxbow lake or (mangrove) backwater swamp, most certainly in close proximity to the shoreline. Brackish-water taxa were transported from a nearby mudflat/mangrove environment, perhaps during an overspill or flooding event. Considering the fragmentation of larger pulmonates, probably even the freshwater fauna was transported, at least a short distance. Since most shells are generally well-preserved, it is unlikely that the assemblage was repeatedly reworked, *e.g.*, by storms. These results are in accordance with environmental reconstructions of Hír *et al.* (2024), who suggested the presence of a shallow pond or paludal environment surrounded by humid arboreal vegetation under a mild paleoclimate.

Acknowledgments

We are grateful to János Hír for sharing the material; to Bernard M. Landau, Aleksandr Guzhov, Jeff Nekola, and Michal Horsák for sharing thoughts on taxonomic matters; to Ronald Janssen for sending land snail specimens for comparison; to Holger Gebhardt, Fritz Geller-Grimm, Martin Gross, Martin Košťák, Imre Magyar, Martin Mazuch, and Jan Sklenář for searching the scientific collections under their care for type materials; to Martin Gross and Aleksandr Guzhov for providing photographs of type material; to Zoltán Kovács for supplying relevant Hungarian literature; to Zoltán Kovács and Adam Tomašových for reviewing an earlier draft of the manuscript. This paper contributes to National Research, Development and Innovation Office project NKFIH 148576.

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