

The family Architectonicidae J. E. Gray, 1850 (Gastropoda: Heterobranchia) from the lower Serravallian of Rohožník (Vienna Basin, Central Paratethys): new evidence and description of a new species

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Key words: Architectonicidae, Gastropoda, Serravallian, Badenian, Vienna Basin, Central Paratethys.

This work presents new records of the Architectonicidae from the middle Miocene of the Central Paratethys Sea. The shells were obtained from the lower Serravallian (upper Badenian) marine sediments revealed at the fossiliferous site Rohožník – Konopiská, situated in the eastern Vienna Basin (Slovakia). The herein surveyed architectonicids comprise two species, of which *Nipteraxis transmontanus* spec. nov. is established as new, and *Spirolaxis cornicula* (O. Boettger, 1902) is recorded for the first time from Slovakia, representing the first occurrence of the species in the upper Badenian of the Central Paratethys realm. Paleoecology of both taxa is shortly commented on and compared with the habitat preferences of similar species. In the benthic assemblages at Konopiská, the architectonicids were associated with ahermatypic scleractinian corals, which most probably represented their potential hosts.

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INTRODUCTION

Architectonicid gastropods are fossil and extant marine semi-infaunal predators (Bieler, 1993) and are distributed worldwide, mainly in subtropical and tropical waters

(Bieler, 1993; Bieler & Petit, 2005). They are characterised by a wide bathymetric range, usually distributed from the infralittoral to bathyal zones (e.g., Melone & Taviani, 1985; Poppe & Goto, 1991; Bieler, 1993; Solsona & Martinell, 1996; Bogi et al., 2002; Smriglio & Mariottini, 2002; Bieler & Petit, 2005; Tenório et al., 2011; Cavallari et al., 2014), but also occur in intertidal (Bieler & Petit, 2005) and abyssal depths (Melone & Taviani, 1985; Bieler & Petit, 2005).

In the Central Paratethys Sea, this gastropod group was widespread from the Ottnangian (lower Miocene) to the Badenian (middle Miocene), and the highest diversity was reached during the early/middle Badenian (Langhian) (Harzhauser & Landau, 2023). Altogether, 18 species were confirmed by the review of these authors.

From the Neogene Western Carpathian basins of Slovakia, the Miocene Architectonicidae are poorly known and were mentioned only in a few papers, usually in faunal lists without illustrations, taxonomic remarks, or distributional data. Their earliest stratigraphic occurrence from Slovakia is documented from the Eggenburgian (Burdigalian) sediments exposed at Lipovany (Novohrad-Nógrád Basin), including a single species, *Architectonica (A.) coracollata* (Lamarck, 1822) (Steininger et al., 1971; Ondrejčková, 1972). From the lower Badenian (Langhian) sediments exposed near Kosihovce (Novohrad-Nógrád Basin), *Simplexollata simplex* (Brocchi, 1831) was recognised by Hano (1950), and from the coeval locality, Chĺaba (Danube Basin), Ondrejčková (1978) reported *Pseudotorinia marthae* (O. Boettger, 1902) and *Architectonica* sp. in the faunal list. Ruman & Hudáčková (2015) mentioned from the upper Badenian (Serravallian) deposits of the eastern Vienna Basin two taxa: *Architectonica (Architectonica) monilifera* (Bronn, 1831) from Devínska Nová Ves and *Architectonica* sp. from Devínska Nová Ves and Kúty.

The abovementioned overview shows that the overall knowledge on this gastropod family from Slovakia is relatively meagre. From the surveyed locality Konopiská near

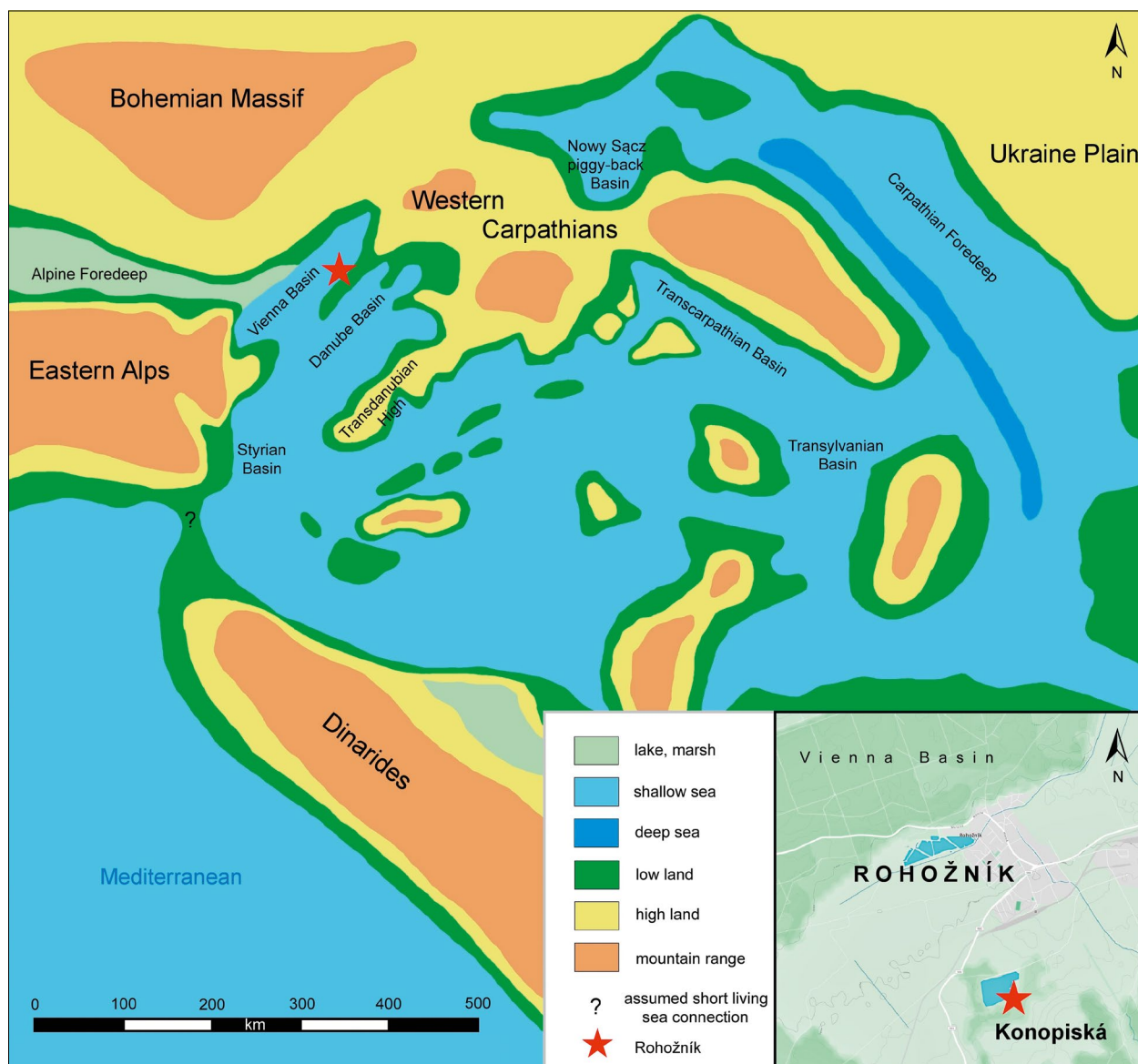


Fig. 1. Paleogeographical map of the Central Paratethys Sea during the late middle Miocene, Serravallian (late Badenian – Sarmatian) showing the assumed position of Rohožník within the Vienna Basin (modified from Kováč et al., 2017); and the current geographic position of the locality Konopiská near Rohožník.

Rohožník, the first evidence of Architectonicidae is given herein, representing the first, more thorough taxonomic study focusing on this gastropod group and their paleoecology from the Slovak part of the Western Carpathians.

GEOLOGICAL SETTINGS

The studied area (Fig. 1) is situated in the Vienna Basin, on the north-western margin of the Pannonian Basin System, which belonged to the epicontinental Central Paratethys Sea during the Miocene (Kováč et al., 2008; Lambert et al., 2008).

The Konopiská site is located near Rohožník village, on the eastern margin of the Slovak part of the Vienna Basin (Záhorská nížina Lowland), at the western edge of the Malé Karpaty Mountains. The site comprises an area of an old clay pit and its vicinity (48°26'39"N, 17°09'53"E). The middle Miocene shallow to deeper water marine strata (clays, organodetritic corallinacean marls and limestones, sandy clays, sands) belonging to the Badenian and Sarmatian regional stages were detected (e.g., Čierna, 1973; Kučerová, 1986; Hladilová, 1991; Fordinál et al., 2012). The studied architectonicid assemblages were found in the upper Badenian (= lower Serravallian) clayey sediments attributed to the Studienka Formation and the foraminiferal *Bulimi-*

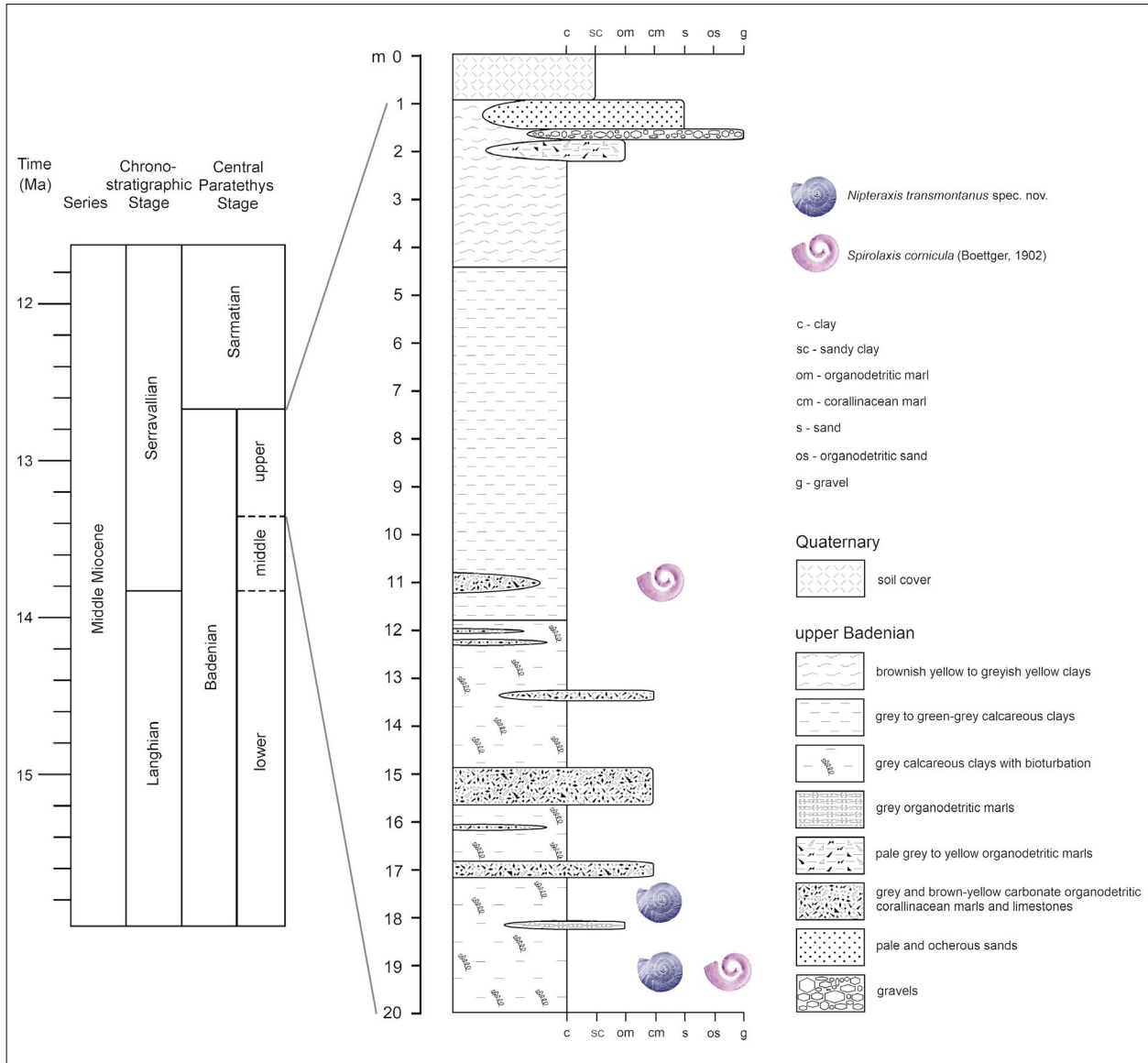


Fig. 2. Middle Miocene chronostratigraphy with regional Central Paratethyan stages and simplified schematic lithological profile of the upper Badenian (lower Serravallian) marine deposits exposed in the former clay pit (modified from Biskupič, 2023b) showing the occurrences of respective Architectonicidae species.

na-Bolivina Biozone (e.g., Kučerová, 1986; Hladilová, 1991; Lambert et al., 2008; Jamrich et al., 2024), that were exposed in the lower and middle parts of the section of the former clay pit (Fig. 2). Species-rich invertebrate and vertebrate faunas were reported, e.g., by Švagrovský (1971), Čierna (1973), Holec (1973, 1975), Kučerová (1986), Hladilová (1991), Lambert et al. (2008), Fuksi et al. (2011), Hyžný & Gašparič (2014), and Ruman & Hudáčková (2015). The most recent work, more comprehensively describing the lithology, paleoecology, and gastropod fauna, was provided by Biskupič (2020, 2021, 2023a,b).

MATERIAL AND METHODS

The collected material comprises six specimens of *Nipteraxis transmontanus* spec. nov., and two specimens of *Spirolaxis cornicula* (O. Boettger, 1902), which were found in a former clay pit at Konopiská near the Rohožník village in the 1980's by the fossil collector Štefan Meszároš (Bratislava, Slovakia), and between 1994 and 2004 by the author. This material is now stored in the collection of the Natural History Museum of the Slovak National Museum, Bratislava, Slovakia (SNM-PM).

Measurements of the protoconchs were made with a digital microscope, a Leica DVM6. The pictures were taken

with a Nikon D 5600 digital camera and a macro-objective AF-S Micro NIKKOR 60mm f/2.8G ED. The photos of small shells of *Spirolaxis* were documented using the additional help of extension tubes Kenko (12/20/36 mm).

The higher systematics of gastropods follow Bouchet et al. (2017) and Harzhauser & Landau (2023). The taxonomic arrangement of the family Architectonicidae J. E. Gray, 1850, proposed by Bieler (1985, 1993) and Harzhauser & Landau (2023), is accepted herein. The terminology of shell morphology and abbreviations was adopted from Bieler (1993) and Harzhauser & Landau (2023).

Abbreviations used in the text: SL = shell length, MD = maximum diameter, SSC = subsutural cord, MC(s) = mid-cord(s), UPC = upper peripheral cord, LPC = lower peripheral cord, IPC = infraperipheral cord, PUC = proxumbilical cord, UC = umbilical crenae, PG = parietal groove, CG = crenal groove.

SYSTEMATICS

Class Gastropoda Cuvier, 1795

Subclass Heterobranchia Burmeister, 1837

Superfamily Architectonicoidea J. E. Gray, 1850

Family Architectonicidae J. E. Gray, 1850

Genus *Nipteraxis* Cossmann, 1916

Type species (by original designation): *Solarium plicatum* Lamarck, 1804.

Nipteraxis transmontanus spec. nov.

Figs 3-7

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Material. — 6 specimens.

Type material and dimensions. — Holotype: Z 40758, SL: 6.27 mm, MD: 10.60 mm (Figs 3a-3c); Paratype 1: Z 40759, SL: 4.87 mm, MD: 8.60 mm (Figs 4a-4c); Paratype 2: Z 40760, SL: 6.24 mm, MD: 10.36 mm (Figs 5a-5c); Paratype 3: Z 40761, SL: 7.71 mm, MD: 11.42 mm (Figs 6a-6c); Paratype 4: Z 40762, SL: 4.18 mm, MD: 8.10 mm (Figs 7a-7c).

Additional material. — Z 40763, SL: 2.65 mm, MD: 5.26 mm.

Type locality. — Konopiská clay pit at Rohožník, Vienna Basin, Slovakia.

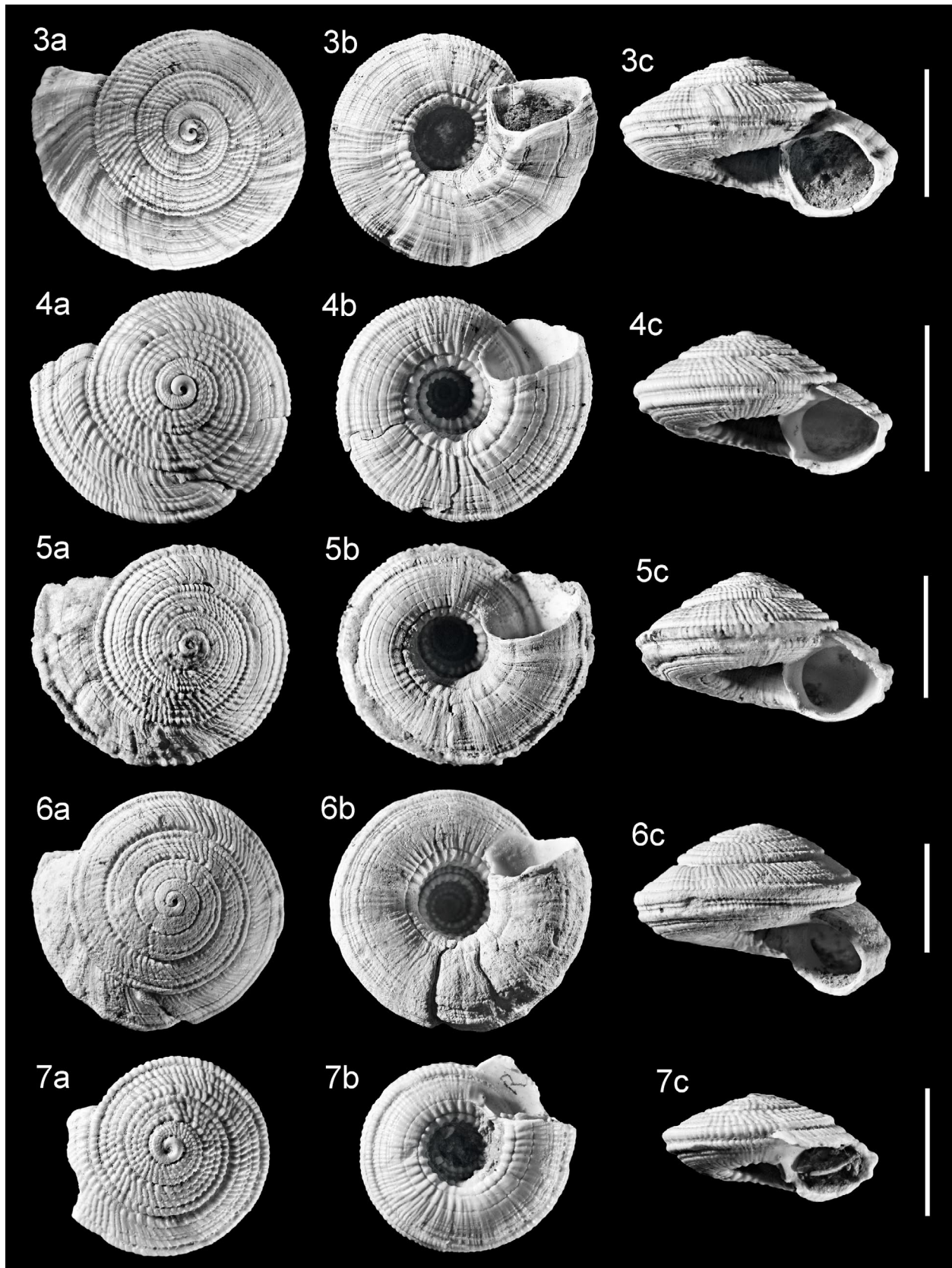
Type stratum. — Grey calcareous clays with bioturbation of the Studienka Formation, middle Miocene, upper Badenian (= lower Serravallian), *Bulimina-Bolivina* Biozone.

Etymology. — Referring to the historical Latin name of the Záhorie region (*Processus Transmontanus* = the area situated beyond the Malé Karpaty Mts.) where the fossils of

the new species occur.

Diagnosis. — Medium-sized, spherical-lenticular, solid shell with moderately elevated conical spire and angulated periphery with two rounded keels formed by more prominent LPC and slightly weaker IPC. Dorsal sculpture of spiral cords with axially elongated beads; LPC, SSC and UPC prominent, MCs somewhat weaker; sculpture on last whorl faintly obsolete, suppressed. Base with fine growth lines and flat, wide spiral cords, increasing in width towards wide umbilicus; PUC and UC with axial folds.

Description. — Shell spherical-lenticular, solid, medium-sized, reaching maximally 11.42 mm in MD, with moderately elevated conical spire and angulated periphery. Protoconch heterostrophic, medium-sized of about 1.2 smooth convex whorls with diameter ranging from 0.91 to 0.95 mm. Protoconch-teleoconch transition well-delimited by protoconch lip. Teleoconch composed of about 3.45 – 4.45 whorls, separated by narrowly incised, slightly undulated suture. First teleoconch whorl convex sided, initially bearing strong, dense growth lines, subsequently disappearing and replaced by slightly raised, prominent, beaded SSC, UPC and LPC; MC poorly defined, indistinct. Second and third teleoconch whorls nearly flat- to moderately convex-sided, sculptured with four to five spiral cords with well-defined beads resulting in chain-like appearance of cords. LPC, SSC and UPC most prominent, nearly same strength, with larger, distinctive beads; two MCs, occasionally one, both somewhat weak with less pronounced beads; spiral cords well separated by undulating, narrow spiral grooves. Beads well defined, rounded on upper surfaces, often non-uniform in shape and size, asymmetric, subquadratic to rectangular, rhomb-like or slightly axially oblong. Axially elongated beads cover spiral cord surfaces exceptionally making densely spaced, more or less prominent prosocline axial ribs in some specimens. Last whorl convex, with angulated periphery. Sculpture more uniform toward aperture, weakening, spiral cords becoming lower, flattened, broader, smoothish in some specimens; beads gradually weaken, become faintly obsolete, or disappear. Interspaces between spiral cords narrow, incised, or intercalated by a fine spiral row. Periphery characterised by two keels formed by LPC and IPC, both separated by a well-defined, moderately deep, wide spiral groove, intercalated by tiny, poorly defined spiral row, usually placed just below LPC; spiral groove crossed by fine, dense growth lines. LPC more prominent, slightly overhanging IPC, swollen, and convex; IPC moderately weaker; LPC and IPC covered by densely spaced, axially elongated beads. Base slightly convex, bearing delicate axial sculpture composed of densely growth lines and occasional folds. Basal field decorated by five to seven spiral cords. Three to four spiral cords close to periphery fine, and slightly convex, central one sometimes stronger, and flattened. Spiral cords separated by



Figs 3-7. *Nipteraxis transmontanus* spec. nov., Rohožník – Konopiská (clay pit), upper Badenian. **3a-c.** Holotype, Z 40758, **a** apical view, **b** umbilical view, **c** apertural view. **4a-c.** Paratype 1, Z 40759, **a** apical view, **b** umbilical view, **c** apertural view. **5a-c.** Paratype 2, Z 40760, **a** apical view, **b** umbilical view, **c** apertural view. **6a-c.** Paratype 3, Z 40761, **a** apical view, **b** umbilical view, **c** apertural view. **7a-c.** Paratype 4, Z 40762, **a** apical view, **b** umbilical view, **c** apertural view. Scale bars = 5 mm.

interspaces of variable width, ranging from narrow spiral grooves of almost equal strength to relatively wide, shallow spiral furrows, making spiral cords more widely spaced. Two to three band-like spiral cords close to umbilicus relatively broad, low, and flat, separated by narrowly incised spiral furrows, interspaces sometimes intercalated by fine, indistinct spiral thread. Spiral and axial sculpture towards aperture gradually weakening to indistinct, faintly obsolete. PUC broad, flat, and covered by axial folds or axially elongated beads. UC with conspicuous, prominent axial folds, strongly convex with rounded to slightly acute tops, separated by interspaces of same width. PUC and UC distinctly delimited by deeply incised, narrow furrow; UC well-distinguishable, protruding above wide, cylindrical umbilicus, reaching about 28–36% of maximum shell diameter. Aperture subcircular with very weak, narrow, shallow CG; PG lacking.

Remarks. — The new species is placed in the genus *Nipteraxis* based on its overall shell morphology characterised by medium-sized, solid, spherical-lenticular shell with moderately wide umbilicus, angulated periphery with two keels formed by a more prominent LPC and slightly weaker IPC, base sculptured by spiral cords increasing in width towards umbilicus, and UC with axial folds, as defined in the genus description given by Bieler (1985) and Harzhauser & Landau (2023).

Nipteraxis deformatus Harzhauser & Landau, 2023, is a closely similar Central Paratethyan species, described from the early/middle Badenian (Langhian) Baden Formation of the Vienna Basin, Austria (see Harzhauser & Landau, 2023; p. 32, figs 4E, 16A–D). This architectonicid differs from *N. transmontanus* spec. nov. in its larger shell, somewhat higher spire, slightly deformed teleoconch whorls decorated by slight swellings and bumps, somewhat more delicate beads on the spire, much narrower umbilicus, and in having a larger protoconch. In addition, the sculpture on the spire seems more uniform than in the new species. *N. exmoniliferus* (Sacco, 1892), known from the Badenian (Langhian–Serravallian) of the Central Paratethys Sea (see Harzhauser & Landau, 2023; p. 34, figs 4F, 17A–D), resembles *N. transmontanus* spec. nov. in overall shell morphology and size but is distinguished by its slightly higher spire, more dominant LPC forming a strong keel on the periphery giving the last whorl a more angulated profile, weaker IPC, less convex base bearing more densely spaced and better-defined beads and growth lines, narrower umbilicus, and larger protoconch. Furthermore, the beads are well-developed and evenly spaced on the entire surface of teleoconch whorls, including the last whorl on both the spire and base.

Paleoecology. — At the site, the species was detected in basal pelitic sediments. Its presence in grey calcareous clays with bioturbation referring to deeper sublittoral (cir-

calittoral) habitat with the muddy sea floor, influenced by unfavourable settings, such as lowered water circulation and possible episodic hypoxia near the sea bottom (e.g., Hladilová, 1991; Hladilová et al., 1998; Lambert et al., 2008; Biskupič, 2020, 2021, 2023a,b). According to Jamrich et al. (2024), sedimentation took place in open sea environments characterised by low oxygen levels and temperate warm waters. The habitat was characterised by the conditions of normal water salinity (Biskupič, 2020, 2021, 2023a,b).

Distribution at the locality. — Grey calcareous clays with bioturbation: 6 specimens.

Stratigraphic and geographic range. — Central Paratethys: upper Badenian (Serravallian) of Slovakia (Rohožník – Konopiská, Vienna Basin).

Genus *Spirolaxis* Monterosato, 1913

Type species (by monotypy): *Pseudomalaxis centrifuga* Monterosato, 1890.

Spirolaxis cornicula (O. Boettger, 1902)

Figs 8–9

Discohelix (*Pseudomalaxis*) *corniculum* O. Boettger, 1902: 116.

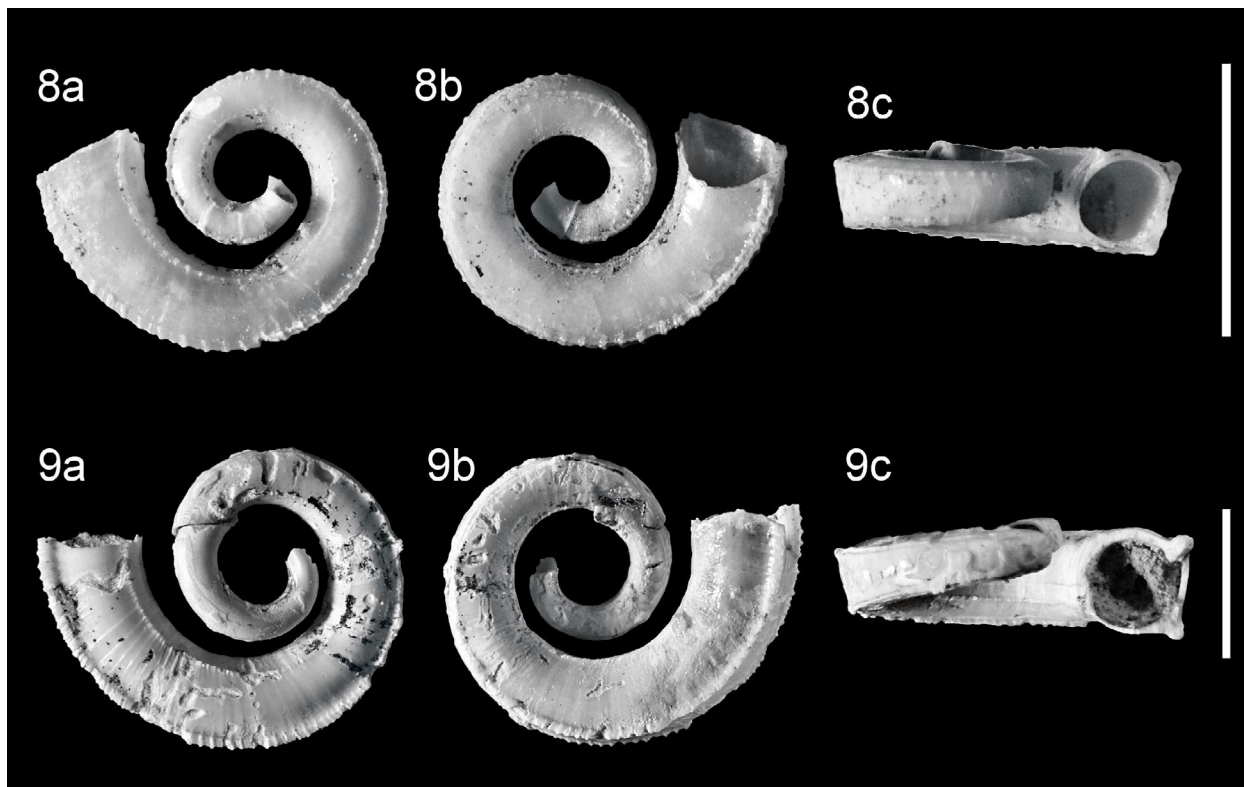
Spirolaxis cornicula (Boettger, 1902) – Harzhauser & Landau, 2023: 42, figs 21A–C (cum syn.).

Material. — 2 specimens.

Illustrated material and dimensions. — Z 40764, SL: 0.80 mm, MD: 2.60 mm (Figs 8a–8c); Z 40765, SL: 1.70 mm, MD: 4.84 mm (Figs 9a–9c).

Remarks. — The shells from Konopiská are identical to the type material from Coșteiu de Sus and Lăpușiu de Sus (Romania) figured by Zilch (1934; pl. 7, figs 19–21) and re-illustrated in Bieler (1984; pl. 3, figs 21–22), and Harzhauser & Landau (2023; figs 21A–C). *Spirolaxis cornicula* is an extremely rare Badenian species known only from a few localities of the Central Paratethys Sea (cf. Harzhauser & Landau, 2023). Only two exemplars were collected at Konopiská, which indicates a very low abundance of the species in the study area. These rare finds document its first evidence in the Miocene of the Vienna Basin and the Slovak part of the Western Carpathians, and also the first occurrence in the upper Badenian of the Central Paratethys.

Paleoecology. — The shells were found in two distinct marine sedimentary facies, which reflects the relatively wide habitat preference of the species. The occurrence in grey calcareous clays with bioturbation suggests deeper marine (circalittoral depths) paleoenvironment affected by sluggish water circulation, resulting in lowered oxygen content or occasional hypoxic events near the muddy sea bottom (e.g., Hladilová, 1991; Hladilová et al., 1998; Lam-



Figs 8-9. *Spirolaxis cornicula* (O. Boettger, 1902), Rohožník – Konopiská (clay pit), upper Badenian. **8a-c.** Z 40764, **a** apical view, **b** umbilical view, **c** apertural view; **9a-c.** Z 40765, **a** apical view, **b** umbilical view, **c** apertural view. Scale bars = 2 mm.

bert et al., 2008; Biskupič, 2020, 2021, 2023a,b). In contrast, its presence in intercalations of grey and brown-yellow carbonate organodetritic coralline marls and limestones of the Sandberg Formation points to shallow water (infralittoral) paleoenvironment characterised by higher water energy, nutrient-rich and well-aerated conditions, with sedimentation in nearshore, algae dominated habitat (Biskupič, 2020, 2023b). These interlayers were formed as a result of episodic redeposition of infralittoral facies by storm currents (Lambert et al., 2008) from the adjacent carbonate platforms or talus formed by coralline red algae along the paleo-coast of the Malé Karpaty Mts. (e.g., Baráth, 1994; Hladilová et al., 1998; Lambert et al., 2008; Jamrich et al., 2024). In both paleoenvironments, normal water salinity and warm water settings prevailed (Biskupič, 2020, 2023b).

Distribution at the locality. — Grey calcareous clays with bioturbation: 1 specimen; grey and brown-yellow carbonate organodetritic coralline marls and limestones: 1 specimen.

Stratigraphic and geographic range. — Central Paratethys: middle Badenian (Langhian) of Hungary and Romania (Harzhauser & Landau, 2023); upper Badenian (Serravallian) of Slovakia (this paper).

DISCUSSION

The members of the family Architectonicidae J. E. Gray, 1850 are predatory, semi-infaunal gastropods feeding on coelenterates (Bieler, 1993), showing various specialisations for feeding on hexacorallian coelenterates such as stony corals, sea anemones, and zoanths (e.g., Haszprunar, 1985; Bieler, 1993; Mifsud, 1997; Smriglio & Mariottini, 2002; Bieler & Petit, 2005; Schiaparelli et al., 2022). In addition, surprisingly, some architectonicids are commensalists with coelenterates (colonial sea anemones, actinarians, scleractinians), as reported by Robertson (1967, 1974) and summarised by Solsona & Martinell (1996).

The co-occurrence of Architectonicidae with abundant ahermatypic scleractinian corals in the same horizons at the Konopiská locality agrees and perfectly fits their specific prey and/or commensalism preferences, as previously suggested. In grey calcareous clays with bioturbation in which *Nipteraxis transmontanus* spec. nov., and *Spirolaxis cornicula* occur, the scleractinian assemblage comprises four solitary coral species: *Stephanophyllia elegans* (Bronn, 1837), *Caryophyllia (Caryophyllia) inops* Reuss, 1871, *C. (Acanthocyathus) verrucosa* Milne-Edwards & Haime, 1848, and *Flabellum roissyanum* Milne-Edwards & Haime, 1848. Also, in carbonate organodetritic coralline

marls and limestones with the rare occurrences of *Spirolaxis cornicula*, abundant small-sized Caryophylliidae corals were recorded. Rare scleractinians [*Siderastrea italica* (Defrance, 1826), *Plesiastraea (Palaeoplesiastraea) desmoulini* Milne-Edwards & Haime, 1851, Caryophylliidae indet., *Flabellum roissyanum*], as potential hosts of architectonicids, were also found in shallow water sandy and sandy-clayey facies exposed in the uppermost part of the section, but no shells of Architectonicidae were observed there.

In the eastern Vienna Basin, coeval pelitic sediments of the Studienka Formation that were deposited in similar deteriorated conditions (lowered water circulation, occasional hypoxia near the sea floor) were uncovered, namely at the Brickyard site near Devínska Nová Ves and several localities in the vicinity of Devín (southern slopes of Devínska Kobyla) (e.g., Hudáčková & Kováč, 1993; Tomašových, 1998; Hudáčková & Spezzaferri, 2002; Kováčová et al., 2009; Hyžný et al., 2012; Jamrich et al., 2024). However, no species of Architectonicidae have yet been reported from there, as shown by the works of Schaffer (1898), Toulá (1900, 1915), Seneš & Cicha (1973), Švagrovský (1981), Tomašových (1998), Hyžný et al. (2012), and Ruman & Hudáčková (2015). Also, as suggested by those authors, no data about the occurrence of scleractinian corals, as a possible prey of architectonicids, are known from these localities. Nevertheless, the shells of Architectonicidae were found at Kúty and Devínska Nová Ves – Útočnice, characterised by more favourable, shallow water settings (cf. Ruman & Hudáčková, 2015), with the occurrence of hermatypic scleractinian corals at Útočnice (cf. Biskupič, 2023c).

As follows from the above, the Architectonicidae were found only in a few localities. Their distribution was restricted and strictly associated with their potential hosts – the scleractinian anthozoans; they represented rare and species-poor elements in the gastropod faunas during the upper Badenian (lower Serravallian) in the eastern Vienna Basin. These conclusions correspond to the statement of Harzhauser & Landau (2023), who recorded a considerably decreased diversity of architectonicids in the Central Paratethys Sea from the middle Badenian to the late Badenian (Langhian/Serravallian) as a result of a distinct decline of Paratethyan cnidarian faunas due to the climatic cooling.

Representatives of the genus *Nipteraxis* are only known from the fossil record (Bieler, 1985, 1988; Bieler & Petit, 2005; MolluscaBase eds., 2023a; Harzhauser & Landau, 2023). Therefore, their habitat preferences are poorly known and were dealt with in detail only in a few papers (see Solsona & Martinell, 1996; Bogi et al., 2002; Harzhauser & Landau, 2023). As summarised by Harzhauser & Landau (2023), the middle Miocene Paratethyan *Nipteraxis* members occurred in various habitats; they were found in deposits indicating shallow marine inner neritic environments, sometimes with seagrass but also occurred in deeper water habitats, preferring fine silty-sandy to clayey bottoms. A species

very similar to *Nipteraxis transmontanus* spec. nov. from Rohožník, *N. deformatus* Harzhauser & Landau, 2023, was adapted to middle to outer neritic water depths (Harzhauser & Landau, 2023).

The genus *Spirolaxis* Monterosato, 1913 includes extinct and modern species (Bieler, 1984; Harzhauser & Landau, 2023; MolluscaBase eds., 2023b), showing considerable water depth range of modern representatives, inhabiting shallow water (sublittoral) but also bathyal depths on soft sandy and muddy sea bottom (Bieler, 1984, 1993; Melone & Taviani, 1985; Smriglio & Mariottini, 2002). According to Harzhauser & Landau (2023), *Spirolaxis cornicula* most probably preferred middle to outer neritic paleoenvironments, which partially coincides with the herein presented habitat preference of the species (infralittoral and circalittoral settings at Konopiská).

CONCLUSION

This paper discusses two rare species of the lower Serravallian (upper Badenian) Architectonicidae from the Central Paratethys Sea. From the basinal pelitic facies of the Studienka Formation exposed at the locality Rohožník – Konopiská (Vienna Basin, Slovakia), *Nipteraxis transmontanus* spec. nov. is described as a new taxon. The findings of *Spirolaxis cornicula* represent new rare records in the Central Paratethys Sea and the first evidence in the upper Badenian (lower Serravallian).

Nipteraxis transmontanus spec. nov. and *Spirolaxis cornicula* were collected in grey calcareous clays with bioturbation; the second also occurred in the intercalations of corallinacean marls. These architectonicids were adapted to the moderately deep sublittoral (circalittoral) settings, with normal water salinity, and affected by lowered water oxygenation and occasional hypoxic events near the clayey bottom, whereas *S. cornicula* also inhabited shallow marine (infralittoral) nearshore environment with the dominance of coralline red algae. In both paleoenvironments, they were connected with ahermatypic scleractinian corals, which represented probably their preferred prey.

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