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The family Costellariidae MACDONALD, 1860 (Gastropoda: Neogastropoda) from the lower Badenian (Middle Miocene) Lajta Limestone Formation of Letkés (Pannonian Basin, Hungary)

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A letkési alsó badeni (középső miocén) Lajtai Mészkő Formáció Costellariidae MACDONALD, 1860 (Gastropoda: Neogastropoda) együttese

Összefoglalás

Tanulmányunkban a Letkés (Börzsöny hegység) melletti Bagoly-hegy kora badeni (középső miocén) lelőhelyéről az elmúlt évtizedben begyűjtött gastropodafauna egy részét, a Costellariidae-családhoz tartozó fajokat mutatjuk be. A fosszíliaegyüttes a Lajtai Mészkő Formáció Pécsszabolcsi Tagozatát képviselő limonitos, agyagos-márgás homokból került elő. Az itt talált 17 faj a Középső-Paratethys más lelőhelyeihez viszonyítva a család legmagasabb diverzitású előfordulását jelenti. Hat faj, *Bellardithala boehmi* (BOETTGER, 1906), *B. lapugyensis* (HOERNES & AUINGER, 1880), *Ebenomitra pseudopyramidella* (BOETTGER, 1906), *Pusia avellanella* (BOETTGER, 1906), *P. paraleucozona* (BOETTGER, 1906) és *P. vexans* (BOETTGER, 1902) eddig nem volt ismert a hazai miocénból, mellettük négy faj új a tudományra nézve: *Bellardithala borzsonyensis* spec. nov., *Pusia pseudomoravica* spec. nov., *P. palmulleri* spec. nov. és *P. crassiornata* spec. nov. Leírunk továbbá két *Bellardithala* sp. példányt is, melyek valószínűleg szintén új fajt képviselnek, ám ennek bevezetése további gyűjtőmunkát igényel. Az itt tárgyalt Costellariidae-együttes vegyes összetételt mutat, sekély- és mélyvízi fajok egyaránt előfordulnak a lelőhelyen, tehát – hasonlóan a Bagoly-hegyről korábbi publikációkban már ismertetett korall- és más gastropodaegyüttesekhez – egy részük bizonyosan allochton példány.

Tárgyszavak: Costellariidae, miocén, badeni, Letkés, Magyarország, Középső-Paratethys

Abstract

Newly collected Middle Miocene Costellariidae gastropod material obtained from the northern margin of the Pannonian Basin (Central Paratethys) is studied. The specimens were found in the lower Badenian (Langhian) limonitic clayey-marly sands of the Lajta Limestone Formation exposed at the Bagoly Hill locality, Letkés (western edge of the Börzsöny Mts, Hungary). Altogether, 17 costellariid species were found, including *Bellardithala borzsonyensis* spec. nov., *Pusia pseudomoravica* spec. nov., *P. palmulleri* spec. nov., and *P. crassiornata* spec. nov. which are described as new species. *Bellardithala boehmi* (BOETTGER, 1906), *B. lapugyensis* (HOERNES & AUINGER, 1880), *Ebenomitra pseudopyramidella* (BOETTGER, 1906), *Pusia avellanella* (BOETTGER, 1906), *P. paraleucozona* (BOETTGER, 1906), and *P. vexans* (BOETTGER, 1902) are recorded for the first time from the Miocene of Hungary. The taxonomic status of *Bellardithala* sp. is discussed. As the taxonomic composition of the Costellariidae assemblage found at the locality suggests, a mixture of various shallow- and deeper-water species indicates the allochthonous origin of a portion of the association.

Keywords: Costellariidae, Miocene, Badenian, Letkés, Hungary, Central Paratethys

Introduction

Letkés as a fossiliferous Miocene site was mentioned for the first time in the literature 160 years ago (HAUER & STACHE 1865), then STACHE (1866) presented a small fauna list with 14 mollusc species from unknown localities in the vicinity of the village. HALAVÁTS mentioned Letkés in two papers (1881, 1884), and – now focusing only on the Costellariidae – in the second work, he recorded a costellariid species ("*Costellaria intermittens* R. HÖRN. & AU."). It was FRANZENAU (1886) who published the first study on the fossil assemblage of Letkés (91 invertebrate taxa are enumerated) based on a donation to the Hungarian National Museum. In that publication, the author cited only HALAVÁTS' costellariid record, but in his following paper (FRANZENAU 1897) – where 89 gastropods were listed – another costellariid appeared: "*Mitra ebenus* Lam." Almost 60 years later, in a comprehensive monograph of the Middle Miocene molluscs of Letkés and the neighboring fossiliferous site, Szob, CSEPREGHY-MEZNERICS (1956) added a third species to the costellariid fauna of the site: "*Vexillum* (*Vexillum*) *cupressinum* BROCCHI". However, the first photographs of Costellariidae species from Letkés did not appear until six years later (STRAUSZ 1962), and detailed descriptions were published even later (STRAUSZ 1966). Most recently, HARZHAUSER & LANDAU (2021) mentioned the presence of two species: *Ebenomitra leucozona* (ANDRZEJOWSKI, 1830) and *Vexillum szobbiensis* (HALAVÁTS, 1884) based on the material illustrated by STRAUSZ (1966).

The achievements in the publications mentioned above were based on sporadic field work and sampling. The gastropod assemblage studied in this paper is obtained from a single locality (Bagoly Hill); it was collected mainly by the second author and Zoltán VICIÁN in the past decade. All the superfamilies and families analyzed so far (Rissooidea, Tonnoidea, Muricoidea, Buccinoidea, Cancellariidae, Conoidea) are characterized by a large number of specimens and a high α-diversity (see KOVÁCS & VICIÁN 2023 and references therein). This material allows us to present a revised, rich costellariid fauna with 16 recognized species and one species-level unidentified taxon. Four new species, *Bellardithala borzsonyensis* spec. nov., *Pusia pseudomoravica* spec. nov., *P. palmulleri* spec. nov., and *P. crassiornata* spec. nov. are described.

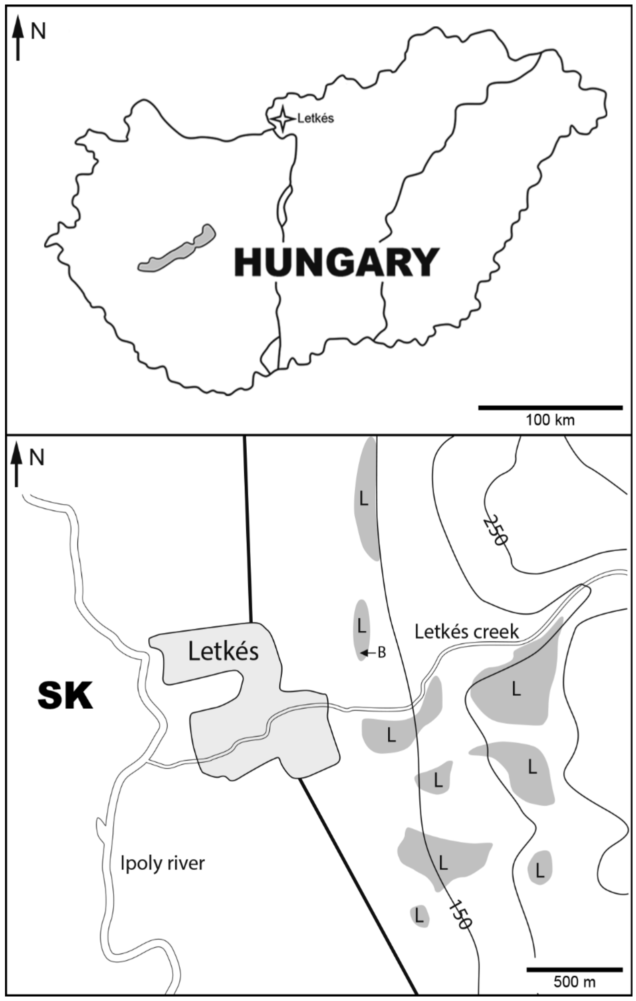

Figure 1. Location of Letkés in Hungary, and the Badenian marine deposits east of the village
L – Lajta Limestone Fm., B – Bagoly Hill locality

1. ábra. *Letkés és a falutól K-re található badeni üledékek*
L – Lajtai Mészkő F., B – a vizsgált bagoly-hegyi feltárás

Geological setting

Letkés is a well-known early Badenian (Langhian) fossiliferous site between the Ipoly River and the western hills of the Börzsöny Mts (N Hungary) (*Fig. 1*). Several sampling points were previously mentioned in the literature (CSEPREGHY-MEZNERICS 1956); the study locality is situated about 400 m eastward from the village on the western slope of the Bagoly Hill (N 47.888319°, E 18.784647°). The Börzsöny Mts (N Pannonian Basin) belongs to the Miocene Inner Carpathian Volcanic Chain in the Central Paratethys and consists of mainly andesite of about 1000 m thickness. At the margins, the volcanic rocks are overlain by shallow marine sedimentary formations belonging to the Lajta Limestone Formation (limestone, "schlier", different clayey, sandy and marly deposits) (SELMECZI et al. 2024: 84). The study locality mainly consists of resedimented, yellowish-brownish clayey-marly sand beds without clearly visible layers – the sediments represent the lower Badenian Pécsszabolcs Member of the Lajta Limestone Fm.

The subsurface thickness of the section is about 170 cm. The uppermost unit (40–60 cm) is characterized by marly sand with some bentonite, containing mainly coastal to nearshore mollusc shells. The next limonitic sandy unit (20–60 cm) contains fragmentary colonial coral blocks and various rock fragments of andesite and andesitic tuff, but some quartz pebbles also occur – the origin of this assemblage is probably related to earthquakes. The richest macrofauna came from this unit; well-preserved mollusc shells are frequent in "pockets" among rocks or coral blocks. The presumably resedimented third unit (20–30 cm) is of limonitic clayey sandy facies with similarly rich but poorly to moderately preserved mollusc remains. At the base of the section, there is a 10–20-cm-thick autochthonous light grey clay bed, which sporadically contains mollusc shells and solitary corals. This fourth unit is underlain by an unfossiliferous, greenish clay layer.

The marine macrofauna of the locality is remarkably rich in fossils of rocky intertidal and inner to outer neritic communities containing mainly scleractinians, bryozoans and molluscs. The preservation of mollusc shells is variable; the specimens were not preserved in their original environment, the bivalve shells are always disconnected, and the gastropod shells are often scratched or worn.

Material and methods

The Costellariidae specimens described and illustrated in this paper were collected by the second author at the Bagoly Hill locality of Letkés. The material (1001 specimens) comprises largely moderately preserved specimens in various stages of ontogeny, with the prevalence of adult exemplars. Some of the shells with preserved protoconch were detected. The type material and illustrated specimens are stored in the Hungarian Natural History Museum (HNHM, Budapest), and the rest of the conchological material is stored in the private collection of the second author (Coll. ZK). The paleontological collections of the HNHM and the Geological Survey of Hungary (SZTFH) (former Hungarian Geological Institute) were also revisited for this study.

In the synonymy list, only the type and the most relevant latest works – regarding the Paratethyan and primarily Hungarian occurrence of Costellariidae gastropods – are cited. For further discussion about the taxonomy, synonyms, and overall geographic and stratigraphic distribution of respective species, see LANDAU et al. (2013) and HARZHAUSER & LANDAU (2021). The taxonomic concept of the Costellariidae follows FEDOSOV et al. (2017) and HARZHAUSER & LANDAU (2021). The shell morphology, terminology and morphometric abbreviations are borrowed from HARZHAUSER & LANDAU (2021). Further morphometric data are given by statistical methods: mean and standard deviation. Morphometric abbreviations used in the text: SL = shell length, MD = maximum diameter, AA = apical angle, LWH = last whorl height, AH = aperture height, AL = aperture length, AW = aperture width, S = length of siphonal canal, n = number, μ = mean, σ = standard deviation.

Systematic paleontology

Superfamily Turbinelloidea RAFINESQUE, 1815
Family Costellariidae MACDONALD, 1860
Genus *Bellardithala* HARZHAUSER & LANDAU, 2021
Type species: *Voluta obsoleta* BROCCHI, 1814, by subsequent designation. Pliocene, Italy.

Bellardithala boehmi (BOETTGER, 1906)
(Plate I, Figs 1–2)

1906 *Mitra* (*Micromitra*) *boehmi* n. sp. – BOETTGER, p. 11.
2021 *Bellardithala boehmi* (BOETTGER, 1906) nov. comb. – HARZHAUSER & LANDAU, p. 16, figs 6A1–A2, B1–B2, C1–C2.

Material: 2 specimens.

Remarks: Two shells are available that morphologically correspond to the material from Coşteiu de Sus and Lăpugiu de Sus (Romania) (cf. ZILCH 1934, pl. 17, fig. 14; HARZHAUSER & LANDAU 2021, figs 6A–C). *Bellardithala boehmi* is a rare Paratethyan species, which until now was known only from the above-mentioned localities of the Făget Basin. Only two specimens are available in the examined material, which suggests extremely low species abundance in the assemblage. The specimens represent the first record from the Miocene of Hungary and the Pannonian Basin.

Stratigraphic and geographic distribution: Middle Miocene (Badenian): Central Paratethys (HARZHAUSER & LANDAU 2021). From Hungary, the species is known from the lower Badenian deposits of Letkés (this paper).

Bellardithala borzsonyensis spec. nov.
(Plate I, Figs 3–14)

Material: 67 specimens.

Type material: Holotype: HNHM PAL 2024.144.1., SL 5.85 mm, MD 2.10 mm (*Plate I/3–4*); Paratype 1: HNHM PAL 2024.146.1., SL 5.54 mm, MD 1.93 mm (*Plate I/5–6*); Paratype 2: HNHM PAL 2024.147.1., SL 5.50 mm, MD 1.90 mm (*Plate I/7–8*); Paratype 3: HNHM PAL 2024.148.1., SL 5.60 mm, MD 2.14 mm (*Plate I/9–10*); Paratype 4: HNHM PAL 2024.149.1., SL 5.26 mm, MD 2.10 mm (*Plate I/11–12*); Paratype 5: HNHM PAL 2024.150.1., SL 4.97 mm, MD 1.90 mm (*Plate I/13–14*).

Type locality: Letkés (Bagoly Hill), Börzsöny Mountains, Hungary.

Type stratum: Limonitic marly sand of the Pécsszabolcs Member (Lajta Limestone Formation), Middle Miocene, lower Badenian (= Langhian), lower Lagenidae Zone.

Etymology: Referring to the Börzsöny Mts, where the new species occurs.

Diagnosis: Shell small-sized, fusiform, moderately slender, spire high conical, weakly scalate, teleoconch of four to five slightly convex whorls. Axial ribs orthocline, prominent, densely spaced, bearing smoothened, attenuated beads, concave interspaces between axials with low, flattened spiral cords separated by incised furrows. Subsutural band prominent, swollen, beaded; siphonal fasciole with six convex, beaded spiral cords variable in thickness; aperture wide, columella with three well-developed columellar folds, fourth abapical fold indistinct, siphonal canal long.

Description: Shell small-sized, fusiform, moderately slender, with high conical, slightly scalate spire, apical angle 36–46°. Teleoconch of four to five slightly convex whorls, irregular in shape, separated by narrowly incised, weakly undulating suture, spire whorls reaching maximum whorl diameter in their abapical half; last whorl 60–64% of total shell height. Protoconch damaged in all specimens. Spire whorls with prominent, convex, orthocline axial ribs, separated by concave interspaces of similar width, crossed by considerably lowered, wide or only slightly convex spiral cords separated by narrowly incised furrows. In cross-sections of axial ribs and spiral cords forming attenuated, flattened beads, spherical to subquadrate in shape, regular in size. Beads in axial ribs sometimes densely spaced, connected, non-separated, forming continuous thickened node-chain-like ornamentation on ribs surface, often resulting in almost smoothened ribs appearance. Beads only exceptionally distinguishable, well-separated by narrow interspaces. Subsutural band distinct, swollen, placed close adapical suture, bearing row of slightly convex, suppressed nodules, abapically restricted by subsutural furrow. Initially, first teleoconch whorl of 14–

16 axial ribs and 3–4 spiral cords, increasing to 17–24 axials and 5–7 spirals on later teleoconch whorls. Last whorl slightly convex, decorated by nonuniform, densely spaced, rounded, often smooth, polished orthocline 18–25 axial ribs of equal strength, separated by concave interspaces mostly of same width; interspaces significantly narrower in some specimens. Spiral sculpture well-defined rather in interspaces between axial ribs, composed of 10–14 flattened, low spiral cords separated with narrow spiral furrows. In cross-sections of axial and spiral cords sometimes developed weak, strongly suppressed beads, spherical, subquadrate to subrectangular in shape, usually regular in size, weakly separated by barely visible, narrow interspaces. Prominent, swollen subsutural band close to adapical suture, in cross-sections with axials bearing subquadrate to slightly axially elongated nodules; subsutural band abapically well-delimited by subsutural groove. Last whorl abapically passing via faint concavity into slightly constricted base, decorated by well-defined, rounded beads, spherical to subquadrate in shape, equal in size, well-separated by narrow interspaces. Siphonal fasciole with six spiral cords variable in thickness; upper two cords prominent, broad, convex, beaded, separated by narrow furrows, third to sixth cord less pronounced, narrow, decorated by weakened beads. Aperture wide, with slightly developed anal sinus; columellar callus narrow, indistinct. Columella with four columellar folds; three adapical folds most prominent, only slightly weakening abapically, fourth abapical fold tiny, indistinct, hardly discernible. Outer lip slightly thickened, 5–7 small denticles placed within aperture. Siphonal canal long.

Shell measurements and ratios (based on type specimens): SL (n = 6): 4.97–5.85 mm, μ = 5.45 mm (σ = 0.27 mm); MD (n = 6): 1.90–2.14 mm, μ = 2.01 mm (σ = 0.10 mm); AA (n = 6): 36–46°, μ = 42.83° (σ = 3.23°); SL/MD (n = 6): 2.52–2.78, μ = 2.71 (σ = 0.14); AL/AW (n = 6): 3.33–3.94, μ = 3.72 (σ = 0.20); AH/S (n = 6): 1.51–1.76, μ = 1.62 (σ = 0.08).

Remarks: *Bellardithala obsoleta* (BROCCHI, 1814) is a similar costellariid widespread from the Middle Miocene to the Pliocene in the Proto-Mediterranean Sea (BELLARDI 1887; LANDAU et al. 2011, 2013; CHIRLI 2002; KOLOKOTRONIS 2021). Although some morphological similarities between this species and *B. borzsonyensis* spec. nov. are evident, the Proto-Mediterranean *B. obsoleta* differs mainly by its somewhat larger and more robust shell, protracted spire and last whorl, more prominent and stronger axial ribs, slightly suppressed spiral sculpture, and indistinct subsutural band (see CHIRLI 2002, pl. 28, figs 5–12; LANDAU et al. 2013, pl. 34, figs 18–19; KOLOKOTRONIS 2021, pl. 1, figs 1–2).

Bellardithala dacica HARZHAUSER & LANDAU, 2021, described from the Badenian of Ukraine and Romania (HARZHAUSER & LANDAU 2021), is distinguished by its larger size of the shell, wider spiral furrow running below adapical spiral band, higher and more protracted last whorl, more elongate and narrower aperture, and higher number of denticles placed in outer lip within the aperture. In addition, *B. dacica* features its coarse sculpture, characterized by sparsely arranged axials and spirals on early teleoconch whorls, changing to delicate ornamentation, composed of densely spaced, cancellate sculpture on the last whorl, which clearly separates it from the new species (cf. HARZHAUSER & LANDAU 2021, figs 8A–C).

Similarly, the specimens identified as *Bellardithala* cf. *dacica* HARZHAUSER & LANDAU, 2021 by those authors (see figs 7G–I) have a larger shell, higher and more elongated last adult whorl, narrower and more protracted aperture with a higher number of denticles within the outer lip. Also, the last whorl is decorated by a slightly attenuated sculpture, characterized by densely spaced and much more delicate spiral cords and axial ribs, distinguishing it from *B. borzsonyensis* spec. nov.

Bellardithala partschi (HÖRNES, 1852), the most abundant costellariid known from the Badenian of the Central Paratethys (HARZHAUSER & LANDAU 2021), is superficially similar species that differs from *B. borzsonyensis* spec. nov. in its larger size, fewer spiral cords and axial ribs, broader spirals and axials and wider interspaces between them, giving the overall shell ornamentation a coarser appearance. Moreover, the species has a narrower aperture and moderately long siphonal canal, and columellar folds more rapidly weaken abapically (cf. HARZHAUSER & LANDAU 2021, figs 9D–F).

Stratigraphic and geographic distribution: Middle Miocene (lower Badenian): Central Paratethys: Letkés (Pannonian Basin, Hungary).

Bellardithala lapugyensis (HOERNES & AUINGER, 1880)
(Plate I, Figs 15–16)

1880 *Mitra Lapugyensis* nov. form. – HOERNES & AUINGER (pars), p. 89, pl. 10, figs 21a–c [non pl. 10, figs 22a–c = *Bellardithala fedosovi* HARZHAUSER & LANDAU, 2021].

2021 *Bellardithala lapugyensis* (HOERNES & AUINGER, 1880) nov. comb. – HARZHAUSER & LANDAU, p. 25, figs 9A1–A2, B1–B2, C1–C2.

Material: 1 specimen.

Remarks: Only a single subadult specimen is available, which points to the very low abundance of the species in the studied Costellariidae assemblage. The shell morphology largely agrees with the type specimens from Lăpugiu de Sus (Romania) figured in HARZHAUSER & LANDAU (2021, figs 9A–C). The specimen represents the first finding of this costellariid in the Miocene of Hungary.

Stratigraphic and geographic distribution: Middle Miocene (Badenian): Central Paratethys (HARZHAUSER & LANDAU 2021). From Hungary, the species is known from the lower Badenian of Letkés (this paper).

Bellardithala sp.
(Plate I, Figs 17–20)

Material: 2 specimens.

Remarks: The shells are characterized by their slender fusiform shell shape, elongated adult whorl, narrow aperture, long siphonal canal, sparsely spaced axial ribs separated by wider interspaces on early teleoconch whorls, passing to densely spaced axials on the last adult whorl, with small, flattened beads developed on cross-sections of axials and spirals. These specimens are reminiscent of the Badenian Central Paratethyan *Bellardithala dacica* (cf. HARZHAUSER & LANDAU 2021, figs 8A–C). However, *B. dacica* slightly differs in its larger shell with a higher number of axial ribs separated by narrower interspaces and broader spiral cords on early teleoconch whorls; the axial sculpture on the last adult whorl is weakened and suppressed, whereas spiral cords are more prominent, and the spiral band running below the adapical suture is broader and is separated by a wider spiral groove (cf. HARZHAUSER & LANDAU 2021, figs 8A–C). Similar specimens identified as *Bellardithala* cf. *dacica* by HARZHAUSER & LANDAU (2021, figs 7G–I) also slightly differ from our *Bellardithala*, mainly in their larger shell size, more densely spaced axial ribs and their narrower interspaces on early and penultimate teleoconch whorls, and somewhat broader, less pronounced, slightly flattened spiral cords separated by narrower interspaces on the siphonal fasciole. The shells from Letkés are not conspecific with any Miocene Paratethyan or Mediterranean Costellariidae member and probably represent an undescribed species. Only two specimens were found; therefore, we propose leaving their nomenclature open for now. New material could clarify the taxonomic status of this enigmatic species.

Stratigraphic and geographic distribution: Middle Miocene (lower Badenian): Central Paratethys: Letkés (Pannonian Basin, Hungary).

Genus *Ebenomitra* MONTEROSATO, 1917

Type species: *Mitra ebenus* LAMARCK, 1811, by subsequent designation. Recent, Mediterranean Sea.

Ebenomitra leucozona (ANDRZEJOWSKI, 1830)
(Plate II, Figs 1–8)

1830 *Mitra leucozona* Nobis – ANDRZEJOWSKI, p. 98, pl. 4, figs 6a–b.
1954 *Mitra ebenus* – CSEPREGHY-MEZNERICS, p. 46, pl. 6, figs 6–7 (non LAMARCK, 1811).
1966 *Mitra* (*Pusia*) *ebenus* – STRAUSZ, p. 366, pl. 26, fig. 5, figs 3–5 (non LAMARCK, 1811).
2021 *Ebenomitra leucozona* (ANDRZEJOWSKI, 1830) nov. comb. – HARZHAUSER & LANDAU, p. 28, figs 4E, 10A–C, 11A (*cum syn.*).
2023 *Ebenomitra leucozona* (ANDRZEJOWSKI, 1830) – BISKUPIČ, p. 755, figs 12–23.

Material: 97 specimens.

Remarks: The examined specimens are featured by their very wide intraspecific variability in shell shape. We have detected specimens characterized by typically solid, broadly biconic fusiform shell shapes, but the specimens with extremely slender shell outlines were also observed, including several transitional forms. These slender shells are characterized by their unusually narrow fusiform shell shape, higher spire and last whorl, and narrower, elongated aperture, which partially differs from typical broadly to moderately slender specimens. Such varieties within the species are known from the literature only exceptionally (see FRIEDBERG 1911, pl. 1, fig. 12). Similar shells with slightly elongated spire and last whorl are relatively rare in the Central Paratethys and they are known from Austria (HÖRNES 1852, pl. 10, fig. 11; HARZHAUSER & LANDAU 2021, fig 10B), and Slovakia (BISKUPIČ 2023, figs 22–23).

An enormously wide spectrum of morphological variety within the genus *Ebenomitra* comparable to those from Letkés was also documented in shells of a modern European *E. ebenus* (LAMARCK, 1811), as reported by POPPE & GOTO (1991, pl. 34, figs 14–16), CHIRLI (2002, pl. 24, figs 9–12, pl. 25, figs 1–6) and online at https://conchology.be/?t=263&family=COSTELLARIIDAE&fullspecies=Pusia%20ebenus&shellID=3533, and http://www.idscaro.net/sci/04_med/class/fam3/species/pusia_ebenus1.htm.

Among the Costellariidae of the Central Paratethys Sea, *Ebenomitra leucozona* represents one of the most common species (HARZHAUSER & LANDAU 2021), which is partly demonstrated by its relatively common occurrence in the studied assemblage.

In several examined shells, poorly preserved residual color patterns in normal light were recognized, which are characterized by an orange-brown background with a well-defined pale band running above the mid-whorl on the last whorl and a somewhat weaker band developed along the abapical suture on the spire whorls and close the base. From the Central Paratethys, the findings of shells with residual colour patterns are rarely known (cf. HOERNES & AUINGER 1880, MIKUŽ 2009, HARZHAUSER & LANDAU 2021).

Stratigraphic and geographic distribution: Middle Miocene (Badenian): Central Paratethys (HARZHAUSER & LANDAU 2021). Early Badenian distribution in Hungary is known from Sámsonháza and Letkés, the late Badenian occurrence was reported from Budapest (Illés Street) (Pannonian Basin) (FRANZENAU 1897; CSEPREGHY-MEZNERICS 1954; STRAUSZ 1966; this paper).

Ebenomitra pseudopyramidella (BOETTGER, 1906)
(Plate II, Figs 9–12)

1906 *Mitra* (*Uromitra*) *ebenus* LMK. var. *pseudopyramidella* n. nom. – BOETTGER, p. 9 [*nov. nom. pro Mitra ebenus* HOERNES & AUINGER, 1880, pl. 7, fig. 13].
2021 *Ebenomitra pseudopyramidella* (BOETTGER, 1906) nov. comb. – HARZHAUSER & LANDAU, p. 31, figs 4F, 10D–F, 11B (*cum syn.*).
2023 *Ebenomitra pseudopyramidella* (BOETTGER, 1906) – BISKUPIČ, p. 755, figs 24–29.

Material: 4 specimens.

Remarks: The material from the Bagoly Hill is concordant with the specimens presented in the literature (e.g., EICHWALD 1829; HOERNES & AUINGER 1880; FRIEDBERG 1911) and agrees with the revised description and illustrations of HARZHAUSER & LANDAU (2021). Only four shells were found, which indicates a low abundance of the species in the studied area. The findings from Letkés represent the first confirmed occurrence in the Miocene of the Hungarian part of the Pannonian Basin.

Stratigraphic and geographic distribution: Middle Miocene (Badenian): Central Paratethys (HARZHAUSER & LANDAU 2021). From Hungary, the species is recorded from the early Badenian of Letkés (this paper).

Genus *Pusia* SWAINSON, 1840

Type species: *Mitra microzonias* LAMARCK, 1811, by monotypy. Recent, Indo-Pacific.

Pusia avellanella (BOETTGER, 1906)
(Plate II, figs 13–16)

1906 *Mitra* (*Uromitra*) *avellana* BELL. var. *avellanella* n. var. – BOETTGER, p. 9.

2021 *Pusia avellanella* (BOETTGER, 1906) nov. comb. – HARZHAUSER & LANDAU, p. 36, figs 4H, 13A–F (*cum syn.*).

2023 *Pusia avellanella* (BOETTGER, 1906) – BISKUPIČ, p. 757, figs 30–33.

Material: 31 specimens.

Remarks: The specimens examined herein are conspecific with the shells figured in the literature (HOERNES & AUINGER 1880, ZILCH 1934, FRIEDBERG 1911, BAŁUK 1997, HARZHAUSER & LANDAU 2021). Occurrence at Letkés represents the first evidence of the species from the Miocene of Hungary.

Stratigraphic and geographic distribution: Middle Miocene (Badenian): Central Paratethys (HARZHAUSER & LANDAU 2021). From the lower Badenian sediments of Hungary, the species is known from Letkés (this paper).

Pusia pseudomoravica spec. nov.
(Plate II, Figs 17–21)

Material: 8 specimens.

Type material: Holotype: HNHM PAL 2024. 157.1., SL 9.88 mm, MD 3.87 mm (*Plate II/18–19*); Paratype 1: HNHM PAL 2024.158.1., SL 10.30 mm, MD 3.91 mm (*Plate II/20–21*); Paratype 2: HNHM PAL 2024.156.1., SL 8.90 mm, MD 3.56 mm (*Plate II/17*).

Type locality: Letkés (Bagoly Hill), Börzsöny Mts, Hungary.

Type stratum: Limonitic marly sand of the Pécsszabolcs Member (Lajta Limestone Formation), Middle Miocene, lower Badenian (= Langhian), lower Lagenidae Zone.

Etymology: Combination of the Greek *pseudis* (ψευδής) = false and *moravica* = the name of the closely similar Badenian species *Pusia moravica* (HOERNES & AUINGER, 1880).

Diagnosis: Shell medium-sized, fusiform, moderately broad, spire conical, scalate, teleoconch of six slightly convex, subcylindrical whorls. Axial sculpture more prominent than spiral sculpture; axial ribs prosocline, convex, smooth, densely spaced, at least four weak spiral cords separated by incised furrows close adapical suture, spiral sculpture abapically attenuated, disappearing, strongly reduced; siphonal fasciole with five spiral cords variable in thickness; aperture moderately narrow, columella with four columellar folds, siphonal canal moderately short.

Description: Shell medium-sized, fusiform, moderately broad, with conical, scalate spire, apical angle 41–46°. Teleoconch consisting of six weakly convex, subcylindrical, nearly flat-sided whorls, with periphery below mid-whorl, well-separated by incised, weakly undulating suture, last whorl reaches 60–64% of total shell height. Protoconch not preserved. On teleoconch whorls, axial sculpture more prominent than spiral sculpture; spire whorls bearing uniformly arranged, convex, smooth, weakly prosocline axial ribs of equal strength, separated by narrow, concave interspaces of same width. First two teleoconch whorls of 15–20 axial ribs, increasing to 21–24 axial ribs on later teleoconch whorls. In first two teleoconch whorls, axial ribs initially opisthocline, changing to prosocline ribs on later teleoconch whorls. Two to four weak spiral cords placed close adapical suture, separated by narrowly incised furrows, weak in axials but well distinguishable in their interspaces, in cross-sections with axial ribs sometimes with barely visible, weak, flattened, polished nodes, subquadrate to subrectangular in shape. Additional spiral sculpture only rarely developed, composed of very fine spiral cords separated by indistinct furrows, strongly reduced and rapidly weakened abapically; in mid-whorl and abapical third of teleoconch whorls axial ribs and interspaces between them usually smooth, spiral sculpture often lacks. Last whorl subcylindrical, weakly convex, bearing uniformly arranged, convex, smooth, prosocline 22–24 axial ribs, separated by concave interspaces of same width or slightly widely spaced; of about three to five indistinct spiral cords and furrows running in adapical part of whorl close adapical suture, sometimes with weakly distinguishable, strongly suppressed, blunt nodes in their cross-sections; spiral sculpture rather well-defined in interspaces between axial ribs, abapically quickly disappearing, interspaces between axialls usually smooth. Axial ribs prominent, neatly arranged, stretched from adapical suture to siphonal fasciole, towards adapical suture becoming slightly more prominent, on base towards siphonal fasciole rapidly becoming thinner. Last whorl moderately constricted with moderately basal concavity. Siphonal fasciole with about five spiral cords, second cord pronounced, convex, other cords narrow, less prominent. Aperture moderately narrow, ovoid, with indistinct, narrow anal sinus. Columella with four strongly oblique columellar folds, first adapical fold most prominent, followed by three less pronounced abapical folds, rapidly weakened abapically. Outer lip thin, 6–10 delicate lirae within. Siphonal canal moderately short.

Shell measurements and ratios (based on type specimens): SL (n = 3): 8.90–10.30 mm, μ = 9.69 mm (σ = 0.58 mm); MD (n = 3): 3.56–3.91 mm, μ = 3.78 mm (σ = 0.15 mm); AA (n = 3): 41–46°, μ = 43° (σ = 2.16°); SL/MD (n = 3): 2.50–2.63, μ = 2.56 (σ = 0.05); AL/AW (n = 3): 3.55–3.75, μ = 4.64 (σ = 1.41); AH/S (n = 3): 2.60–2.90, μ = 2.72 (σ = 0.12).

Remarks: *Pusia moravica* (HOERNES & AUINGER, 1880) is a closely similar species, which is a little-known, extremely rare Paratethyan taxon, so far known only by two fragmentary specimens found in the Badenian basinal clays exposed at Rudice (Vienna Basin, Czechia) (HARZHAUSER & LANDAU 2021). In some aspects, the shells from Letkés partly agree with the revised description and specimens figured by HARZHAUSER & LANDAU (2021, figs 13I–J). Nevertheless, *Pusia moravica* differs from the new species in its larger shell (restored height about 13–16 mm), narrower apical angle (restored apical angle about 33°), higher last adult whorl, weakly gradate spire, fewer number of axial ribs on penultimate whorl (about 15 axials), subcylindrical outline of the penultimate whorl, trigonal shape of axial ribs, smooth siphonal fasciole lacking spiral cords, and less oblique columellar folds. It is obvious that the two species are morphologically very similar, which may indicate a possible phylogenetic relationship between them.

Stratigraphic and geographic distribution: Middle Miocene (early Badenian): Central Paratethys: Letkés (Pannonian Basin, Hungary).

Pusia paraleucozona (BOETTGER, 1906)
(Plate II, Figs 22–25)

1906 *Mitra* (*Uromitra*) *ebenus* LMK. var. *paraleucozona* n. var. – BOETTGER, p. 8.
2021 *Pusia paraleucozona* (BOETTGER, 1906) nov. comb. – HARZHAUSER & LANDAU, p. 41, figs 14A–B.

Material: 8 specimens.

Remarks: The collected specimens have a slightly broader shell shape, lower teleoconch whorls, somewhat more convex-sided and shorter last adult whorl, and gradate spire, which slightly differs from the shells illustrated by BAŁUK (1997, pl. 9, fig. 6), and HARZHAUSER & LANDAU (2021, figs 14A–B). These minor morphological differences can be explained due to intraspecific variability within the species. The findings from Letkés represent the first evidence of the species from the north Pannonian Basin of Hungary.

Stratigraphic and geographic distribution: Middle Miocene (Badenian): Central Paratethys (HARZHAUSER & LANDAU 2021). From Hungary, the species is recorded from the lower Badenian strata of Letkés (this paper).

Pusia palmulleri spec. nov.
(Plate III, Figs 1–12)

Material: 13 specimens.

Type material: Holotype: HNHM PAL 2024.145.1., SL 7.65 mm, MD 2.84 mm (*Plate III/1–2*); Paratype 1: HNHM PAL 2024.151.1., SL 7.16 mm, MD 2.80 mm (*Plate III/3–4*); Paratype 2: HNHM PAL 2024.152.1., SL 7.65 mm, MD 2.71 mm (*Plate III/5–6*); Paratype 3: HNHM PAL 2024.153.1., SL 6.33 mm, MD 2.35 mm (*Plate III/7–8*); Paratype 4: HNHM PAL 2024.154.1., SL 5.05 mm, MD 2.14 mm (*Plate III/9–10*); Paratype 5: HNHM PAL 2024.155.1., SL 6.96 mm, MD 2.48 mm (*Plate III/11–12*).

Type locality: Letkés (Bagoly Hill), Börzsöny Mts, Hungary.

Type stratum: Limonitic marly sand of the Pécsszabolcs Member (Lajta Limestone Formation), Middle Miocene, lower Badenian (= Langhian), lower Lagenidae Zone.

Etymology: Named in memory of Pál MÜLLER (1935–2015), Hungarian palaeontologist and prominent specialist on the Miocene decapod crustaceans of the Central Paratethys.

Diagnosis: Shell medium-sized, moderately broad, pupiform, spire high, weakly gradate, teleoconch of five slightly convex whorls; axial ribs broad, convex, slightly compressed, smooth, separated by wide interspaces, no spiral sculpture on spire whorls. Last whorl weakly convex, glossy, axial ribs rapidly weakened, subobsolete, strongly suppressed, aperture wide, siphonal canal long.

Description: Medium-sized *Pusia* species, shell pupiform, moderately broad, with high, weakly gradate spire, apical angle 41–51°. Protoconch not preserved. Teleoconch of five slightly to more convex-sided whorls, becoming rapidly elevated, separated by undulating, narrowly, deeply incised suture; last teleoconch whorl 60–63% of shell height. Teleoconch whorls bearing nonuniform axial sculpture extend from suture to suture, composed of widely spaced, prominent, broad, convex, slightly compressed, smooth orthocline to weakly opisthocyrt axial ribs, often irregular in thickness and arrangement, separated by interspaces of similar width, interspaces in some specimens more broadly developed; axials exceptionally opisthocline; 9–12 axial ribs on early teleoconch whorls, increasing to 14 axial ribs on penultimate whorl. Spiral sculpture on spire whorls lacks. Last whorl slightly convex to subcylindrical, glossy, with moderately constricted base, axial sculpture becoming subobsolete, axial ribs strongly suppressed, attenuated. Last adult whorl in some specimens smooth, with no visible axial ribbing. Siphonal fasciole usually with one or two, exceptionally with three smooth spiral cords, sometimes accompanied by few, very narrow spiral furrows; adapical one to two cords most prominent, broad, rounded, separated by broad interspaces, third abapical cord barely visible, narrow, faint. Aperture wide, ovoid, with indistinct anal canal, columellar callus poorly developed, faint. Columella with four oblique columellar folds weakening abapically, adapical two folds more prominent, third and fourth abapical folds weak, strongly suppressed. Outer lip thin, with 7–8 delicate lirae within. Siphonal canal long.

Shell measurements and ratios (based on type specimens): SL ($n = 6$): 5.05–7.65 mm, $\mu = 6.8$ mm ($\sigma = 0.90$ mm); MD ($n = 6$): 2.14–2.84 mm, $\mu = 2.55$ mm ($\sigma = 0.25$ mm); AA ($n = 6$): 41–51°, $\mu = 47.5°$ ($\sigma = 3.59°$); SL/MD ($n = 6$): 2.35–2.82, $\mu = 2.65$ ($\sigma = 0.16$); AL/AW ($n = 6$): 2.91–3.88, $\mu = 3.37$ ($\sigma = 0.31$); AH/S ($n = 6$): 1.53–2.01, $\mu = 1.78$ ($\sigma = 0.17$).

Remarks: The species features its pupiform spire, nonuniform, and coarse axial sculpture of broad, convex axial ribs separated by relatively wide interspaces, and strongly attenuated sculpture on the last whorl, which reliably separate it from other Cenozoic *Pusia* members known from the circum-Mediterranean region. *Pusia pseudorecticosta* (BOETTGER, 1906) is a similar Miocene costellariid distributed in the Central and Eastern Paratethys and the Proto-Mediterranean (HARZHAUSER & LANDAU 2021) that differs from the new species in its larger shell, somewhat slenderer fusiform spire, less convex whorls, and more delicate and densely spaced axial ribs separated by relatively narrower interspaces (see BAŁUK 1997, pl. 10, figs 3–7; HARZHAUSER & LANDAU 2021, figs 15A–D). From the Badenian reef deposits of Węglinek and Łychów (Poland), KRACH (1981, pl. 20, figs 1–5) reported shells identified as *Mitra* (*Vexillum*) *ebenus leucozona* (ANDRZEJOWSKI, 1830) [non *Ebenomitra leucozona* (ANDRZEJOWSKI, 1830)] . At first sight, these specimens seem conspecific with the new species but slightly differ in their larger shells (SL 13 mm, MD 3 mm), fusiform and more gradate spire, well-developed, almost sharpened, prominent and uniformly arranged axial ribs of equal strength, separated by deeper interspaces. These shells are most likely not identical with *P. palmulleri* spec. nov. and probably represent a distinct *Pusia* species.

The Proto-Mediterranean *Uromitra minuta* (BELLARDI, 1887) from the Lower Miocene (Burdigalian) of the Torino Hills (Italy) is strongly reminiscent of the new species in its overall shell morphology. Even though this Italian species was assigned to *Uromitra* by FERRERO MORTARA et al. (1981), it is not excluded that it represents *Pusia* based on its conchological features. Nevertheless, *Uromitra minuta* differs in its somewhat stocky appearance of the shell, slightly longer and broader last whorl, shorter spire, fewer number of axial ribs (of about 10 axials) on teleoconch whorls, fewer number and broader axials on the last whorl (cf. BELLARDI 1887: 66, pl. 6, fig. 34; FERRERO MORTARA et al. 1981, pl. 53, fig. 7).

Stratigraphic and geographic distribution: Middle Miocene (early Badenian): Central Paratethys: Letkés (Pannonian Basin, Hungary).

Pusia pseudorecticosta (BOETTGER, 1906)
(Plate III, Figs 13–20)

1906 *Mitra (Costellaria) pseudorecticosta* n. nom. – BOETTGER, p. 10.
1954 *Vexillum* (*Costellaria*) *vindobonense* FRIEDBERG – CSEPREGHY-MEZNERICS, p. 45, pl. 5, fig. 30.
2021 *Pusia pseudorecticosta* (BOETTGER, 1906) – HARZHAUSER & LANDAU, p. 42, figs 4J, 15A–D.
2023 *Pusia pseudorecticosta* (BOETTGER, 1906) – BISKUPIČ, p. 757, figs 36–41.

Material: 668 specimens.

Remarks: The studied specimens are featured by their highly variable and nonuniform shell shape, which points to extremely wide-ranging intraspecific variability of the species. In our material, commonly occurring shells with typically narrowly fusiform shape, high, slightly gradate spire, and slightly convex teleoconch whorls decorated by axial ribs separated by weakly narrower interspaces, which correspond to those figured in BAŁUK (1997, pl. 10, figs 3–7), LANDAU et al. (2013, pl. 34, figs 10–12), HARZHAUSER & LANDAU (2021, figs 15A–D) and BISKUPIČ (2023, figs 36–41). However, a part of the material comprises shells that slightly differ from typical forms in shell shape and ratio between the last whorl and spire. These peculiar specimens are characterized by their stout and somewhat broader shell outline; the spire is often slightly lower, teleoconch whorls are more stepped, and the last whorl is longer. The axial sculpture is more or less identical to those bearing typical slender forms. Moreover, we have detected numerous transitional forms between slender and stout forms, and thus, we consider these shells as just an extremely broad local morph. A similar wide spectrum of varieties within the species, ranging from slender shells with high spire to broadly fusiform shells, is also known from the Badenian of Korytnica, Poland (see BAŁUK 1997, pl. 10, figs 3–7).

This taxon is one of the most abundant Paratethyan species within the family Costellariidae, as reported by HARZHAUSER & LANDAU (2021), which agrees with its abundant occurrence at Letkés, where it predominates the Costellariidae assemblage. CSEPREGHY-MEZNERICS (1954) figured a specimen from Sámsonháza identified as *Vexillum* (*Costellaria*) *vindobonense* FRIEDBERG (see pl. 5, fig. 30), but the low quality of the shell illustration did not allow reliably confirm its affiliation to this species. The specimen was re-examined from the collection of HNHM, and its affiliation to *Pusia pseudorecticosta* was confirmed.

Stratigraphic and geographic distribution: Early–Middle Miocene (Ottnangian–Badenian): Central Paratethys; Middle Miocene (Tarkhanian): Eastern Paratethys; Middle Miocene (Serravallian): Proto-Mediterranean (HARZHAUSER & LANDAU 2021). From the early Badenian of Hungary, the species is known from Sámsonháza (CSEPREGHY-MEZNERICS 1954) and Letkés (this paper).

Pusia vexans (BOETTGER, 1902)
(Plate III, Figs 21–24)

1902 *Mitra* (*Costellaria*) *recticosta* BELL. var. *vexans* n. – BOETTGER, p. 13.
2021 *Pusia vexans* (BOETTGER, 1902) nov. comb. – HARZHAUSER & LANDAU, p. 46, figs 4L, 15I1–I2, J1–J2, K1–K2.

Material: 3 specimens.

Remarks: Only three shells, one juvenile and two adult specimens are available. The shells are concordant with the specimens from the type locality of Coşteiu de Sus (Romania) figured in ZILCH (1934, pl. 17, fig. 16) and HARZHAUSER & LANDAU (2021, figs 15I1–I2, J1–J2, K1– K2,) and the material from Korytnica (Poland) illustrated by BAŁUK (1997, pl. 10, figs 1–2). One of the specimens features somewhat weakly convex teleoconch whorls bearing fewer axial ribs, which slightly differs from the type material. In addition, the axials are more robust, and the shell and last whorl are somewhat more elongated (*Plate III/21–22*), which may relate to the intraspecific variability of the species.

Stratigraphic and geographic distribution: Middle Miocene (Badenian): Central Paratethys (HARZHAUSER & LANDAU 2021). In Hungary, the species occurs in the lower Badenian strata of Letkés (this paper).

Pusia crassiornata spec. nov.
(Plate III, Figs 25–28)

Material: 2 specimens.

Type material: Holotype: HNHM PAL 2025.2.1., SL 5.90 mm, MD 2.19 mm (*Plate III/25–26*); Paratype: HNHM PAL 2025.3.1., SL 5.10 mm, MD 1.91 mm (*Plate III/27–28*).

Type locality: Letkés (Bagoly Hill), Börzsöny Mts, Hungary.

Type stratum: Limonitic marly sand of the Pécsszabolcs Member (Lajta Limestone Formation), Middle Miocene, lower Badenian (= Langhian), lower Lagenidae Zone.

Etymology: Referring to the broad, prominent axial ribs that represent one of the features that characterize the species. Combination of the Latin *crassus* = dense, thick, solid and *ornatus* = decorated.

Diagnosis: Shell small, fusiform, moderately broad, spire high conical, teleoconch of four to five convex whorls; sculpture of prominent, strong, smoothened axial ribs, separated by deeply concave interspaces; spiral sculpture on spire whorls absent; siphonal fasciole with four convex spiral cords; aperture wide, columella with four columellar folds, siphonal canal moderately short.

Description: Shell small, fusiform, moderately broad, with high conical spire, apical angle 35°. Teleoconch composed of at most five convex, glossy whorls, with periphery at mid-whorl or slightly below, separated by slightly incised, undulating suture; last whorl 61–62% of total shell height. Protoconch damaged, incomplete. Teleoconch whorls decorated with prominent, rounded, swollen axial ribs, well-separated by deeply concave interspaces of same width. No spiral sculpture on spire whorls. Number of axial ribs varying from 9–10 on first teleoconch whorl, increasing to 11–13 axial ribs on last whorls. Last whorl convex, inflated, with relatively sparsely spaced, well-defined, convex, smooth, strong axial ribs nearby of equal strength, faintly obsolete towards siphonal fasciole, axials well-separated by concave interspaces almost of same width. Last whorl abapically passing via distinct concavity into strongly constricted base. Spiral sculpture lacks, except for four convex, slightly thickened spiral cords on siphonal fasciole; adapical two cords more prominent, separated by relatively wide interspaces, abapical third to fourth cords weakened, narrow, densely spaced. Aperture wide, ovoid, anal sinus weak, indistinct; columella with four oblique columellar folds rapidly weakening abapically, adapical fold most prominent, three abapical folds indistinct. Outer lip thin, three delicate lirae placed deep inside aperture. Siphonal canal moderately short.

Shell measurements and ratios (based on type specimens): SL (n = 2): 5.10–5.90 mm, μ = 5.50 mm (σ = 0.40 mm); MD (n = 2): 1.91–2.19 mm, μ = 2.05 mm (σ = 0.14 mm); AA (n = 2): 35°, μ = 35° (σ = 0°); SL/MD (n = 2): 2.67–2.69, μ = 2.68 (σ = 0.01); AL/AW (n = 2): 3.64–3.93, μ = 3.78 (σ = 0.14); AH/S (n = 2): 2.58, μ = 2.58 (σ = 0).

Remarks: *Pusia crassiornata* spec. nov. is distinguished by its high spire and moderately broad shell shape, convex teleoconch whorls, relatively short last whorl, and strong, broad, rounded axial ribs, which partly reminiscent *P. vexans*, known from the Middle Miocene (Badenian) of the Central Paratethys Sea (cf. HARZHAUSER & LANDAU 2021). Nevertheless, *Pusia vexans* differs in its slightly broader shell shape and somewhat narrower and densely spaced axial ribs (HARZHAUSER & LANDAU 2021, figs 15I1–I2, J1–J2, K1–K2). *Pusia pyrenaica* (PEYROT, 1928), described from the Upper Oligocene (Chattian) of the Adour Basin (France), resembles the specimens from Letkés mainly in its slender shell outline and high spire but differs in its larger shell size, weakly convex teleoconch whorls, indistinct angulation placed close the adapical suture on the last whorl, and somewhat stepped appearance of teleoconch whorls (cf. PEYROT 1928, pl. 8, figs 27–28; LOZOUET 2021, pl. 6, figs 1–6). Two closely related Proto-Mediterranean costellariids were described from the Early Miocene (Burdigalian) of the Torino Hills (Italy). Although they were placed in *Uromitra* by FERRERO MORTARA et al. (1981), they show some morphological features comparable to *Pusia*. *Uromitra crassicosta* (BELLARDI, 1850) differs from the new species in its larger shell (SL 7 mm, MD 3 mm), opisthocline axial ribs that are much broader and are separated by narrower interspaces, delicate axial striae on teleoconch whorls, and in having only three columellar folds (cf. BELLARDI 1850: 28, pl. 2, fig. 28, 1887, p. 63, pl 6, fig. 29; FERRERO MORTARA et al. 1981, pl. 53, fig. 14). The second one, *Uromitra decipiens* (BELLARDI, 1887), differs in its larger shell size (SL 6.5 mm, MD 2.5 mm), higher and less convex teleoconch whorls, weakly convex and somewhat narrower but robust last whorl, and higher number of inner lirae within the aperture (cf. BELLARDI 1887: 65, pl. 6, fig. 33; FERRERO MORTARA et al. 1981, pl. 53, fig. 12).

Stratigraphic and geographic distribution: Middle Miocene (early Badenian): Central Paratethys: Letkés (Pannonian Basin, Hungary).

Genus *Vexillum* RÖDING, 1798

Type species: *Vexillum plicatum* RÖDING, 1798 (= *Voluta plicarium* LINNAEUS, 1758), subsequent designation by WOODRING (1928: 244), Recent, Indo-West Pacific.

Vexillum badense (HOERNES & AUINGER, 1880)
(Plate IV, Figs 1–3)

1880 *Mitra* (*Costellaria*) *Badensis* nov. form. – HOERNES & AUINGER, p. 83.
1969 *Vexillum* (*Costellaria*) *badensie* [sic] HOERNES & AUINGER – CSEPREGHY-MEZNERICS, p. 93, pl. 5, figs 21, 29.
1972 *Vexillum* (*Costellaria*) *badense* HOERNES & AUINGER – CSEPREGHY-MEZNERICS, p. 30, pl. 14, figs 5–6.
2021 *Vexillum badense* (HOERNES & AUINGER, 1880) – HARZHAUSER & LANDAU, p. 48, figs 16A1–A2, B1–B2, C1–C2, D1–D2.

Material: 4 specimens.

Remarks: Although only four incomplete specimens were retrieved, the overall shell morphology allows their clear identification and placement to the species and agrees with the type material figured in HARZHAUSER & LANDAU (2021, figs 16A–D). *Vexillum badense* was a relatively rare component in the Badenian (Middle Miocene) gastropod assemblages of the Central Paratethys Sea, as suggested by the authors mentioned above, which is also reflected by its rare occurrence at Letkés.

Stratigraphic and geographic distribution: Middle Miocene (Badenian): Central Paratethys (HARZHAUSER & LANDAU 2021). From the Badenian of Hungary, this taxon was reported from Szokolya (Börzsöny Mts) by BÁLDI (1960) and from Borsodbóta (Bükk Mts) by CSEPREGHY-MEZNERICS (1969, 1972).

Vexillum harmati CSEPREGHY-MEZNERICS, 1954
(Plate IV, Figs 4–7)

1954 *Vexillum* (*Costellaria*) *harmati* n. sp. – CSEPREGHY-MEZNERICS, p. 45, pl. 5, figs 29, 31–33.
1966 *Mitra* (*Vexillum*) *harmati* CSEPREGHY-MEZNERICS, 1954 – STRAUSZ, p. 368, pl. 12, fig. 9.
2021 *Vexillum harmati* (CSEPREGHY-MEZNERICS, 1954) – HARZHAUSER & LANDAU, p. 50, figs 17A1–A2, B1–B2, C1–C2, D1–D2, E1–E2.

Material: 74 specimens.

Remarks: The presented material is concordant with specimens illustrated in the literature (CSEPREGHY-MEZNERICS 1954, STRAUSZ 1966, HARZHAUSER & LANDAU 2021). Several subadult specimens slightly differ in shell shape and axial sculpture. These shells are characterized by more convex teleoconch whorls, densely spaced axial ribs, and narrower interspaces between them. These specific features could be related to the intraspecific variability of the species. This rare Paratethyan taxon has only been recorded at the type locality of Sámsonháza in Hungary (CSEPREGHY-MEZNERICS 1954, STRAUSZ 1966, HARZHAUSER & LANDAU 2021). The studied specimens represent new evidence from Letkés and the second confirmed record from Hungary for the species.

Stratigraphic and geographic distribution: Middle Miocene (Badenian): Central Paratethys (HARZHAUSER & LANDAU 2021). From Hungary, the species was mentioned from the lower Badenian sediments of Sámsonháza (CSEPREGHY-MEZNERICS 1954, STRAUSZ 1966) and Letkés (this paper).

Vexillum intermittens (HOERNES & AUINGER, 1880)
(Plate IV, Figs 8–12)

1880 *Mitra* (*Costellaria*) *intermittens* n. form. – HOERNES & AUINGER, p. 85, pl. 10, figs 1–4.
1966 *Mitra* (*Vexillum*) *intermittens* HOERNES & AUINGER, 1880 – STRAUSZ, p. 368, pl. 25, figs 9–10.
2021 *Vexillum intermittens* (HOERNES & AUINGER, 1880) – HARZHAUSER & LANDAU, p. 51, figs 4M, 16E1–E2, F1–F2, G1–G2, H1–H2.

Material: 16 specimens.

Remarks: The specimens from the Bagoly Hill locality feature wide-ranging intraspecific variability, which is shown mainly in the axial sculpture. In most of the specimens, the axial ribs are usually well-developed in the early, penultimate and last teleoconch whorls, which agree with the sculpture of the species (HOERNES & AUINGER 1880, HARZHAUSER & LANDAU 2021). However, in some specimens, the axial ribbing almost completely disappeared on the entire teleoconch whorls surface, and the shells are nearly smooth, which partially differs from the material illustrated by the authors mentioned earlier. In shell size and shape, they are conspecific with the type material.

From Letkés, a single specimen was mentioned and figured by STRAUSZ (1966, pl. 25, figs 9–10). Although HARZHAUSER & LANDAU (2021) considered it as *Vexillum szobbiensis* (HALAVÁTS, 1884), the revision of the material suggests its clear affiliation to *V. intermittens (*see *Plate IV/8–9*).

Stratigraphic and geographic distribution: Middle Miocene (Badenian): Central Paratethys (HARZHAUSER & LANDAU 2021). From the early Badenian of Hungary, the species was mentioned by HALAVÁTS (1884) and STRAUSZ (1966) from Letkés.

Genus *Tosapusia* HABE, 1964
Type species. *Mitropifex isaoi* KURODA & SAKURAI in KURODA, 1959, by monotypy, Recent, Indo-West Pacific.

Tosapusia pseudocupressina (BAŁUK, 1997)
(Plate IV, Figs 13–14)

1956 *Vexillum* (*Vexillum*) *cupressinum* – CSEPREGHY-MEZNERICS, p. 414 [non BROCCHI, 1814].
1966 *Mitra* (*Vexillum*) *cupressina* – STRAUSZ, p. 369, pl. 25, figs 4–5 [non BROCCHI, 1814].
1972 *Vexillum* (*Vexillum*) *cupressinum* – CSEPREGHY-MEZNERICS, p. 30, pl. 14, fig. 7 [non BROCCHI, 1814].
1997 *Vexillum* (*Uromitra*) *pseudocupressinum* nom. n. – BAŁUK, p. 37, pl. 11, fig. 3.
2021 *Tosapusia pseudocupressina* (BAŁUK, 1997) nov. comb. – HARZHAUSER & LANDAU, p. 58, figs 4O, 19E1–E2, F1–F2, G1–G2, H1–H2.

Material: 1 specimen.

Remarks: The overall morphology of the shell is identical to the specimens figured, e.g., by BAŁUK (1997) and HARZHAUSER & LANDAU (2021). Only a single specimen was found, which indicates extremely low species abundance in the studied locality.

Stratigraphic and geographic distribution: Middle Miocene (Badenian): Central Paratethys (HARZHAUSER & LANDAU 2021). From the early Badenian of Hungary, the species is known from Szob (Börzsöny Mts) (STRAUSZ 1966), Borsodbóta (Bükk Mts) (CSEPREGHY-MEZNERICS 1972), and Letkés (Börzsöny Mts) (CSEPREGHY-MEZNERICS 1956; this paper).

Discussion and conclusion

During the Middle Miocene, the marine depositional paleoenvironments of the northern part of the Pannonian Basin were strongly influenced by the volcanic activity of the Inner Carpathian Volcanic Chain, which included the Börzsöny Mts (KARÁTSON et al. 2000, KARÁTSON & NÉMETH 2001). The proximity of volcanic formations (see KARÁTSON & NÉMETH 2001, SZÉKELY & KARÁTSON 2004) and their activity may have had an unfavorable impact on the adjacent marine habitats and respective faunal assemblages at that time, as the lithology and the preservation of the fossils at Letkés suggest (see KOVÁCS & VICIÁN 2014). The mixed, transported, and often damaged macrofauna found in redeposited sediments (probably as a result of seismic activity) is comprised mainly of elements referring to rocky intertidal, inner to outer neritic, and coral reef communities (KOVÁCS & VICIÁN 2023). The prevalence of shallow water molluscan taxa is significant and, together with hermatypic scleractinian corals, primarily point to shallow sublittoral marine habitats – as possible original paleoenvironments of the major part of the assemblage (KOVÁCS & VICIÁN 2017, 2023).

Based on costellariid gastropods, the paleoenvironmental settings defined in this study perfectly fit those proposed by the authors mentioned above. At the site, mixed Costellariidae species originating from distinct (shallow- to deeper-water marine) paleoenvironments co-occurred in the same deposits. The taxa preferring rather shallow water (inner neritic) paleoenvironments are considered the following species: *Ebenomitra leucozona*, *E. pseudopyramidella*, *Pusia avellanella*, *P. pseudorecticosta*, and *Vexillum harmati*, whereas typically deeper water (middle to outer neritic) costellariids are *Pusia paraleucozona*, *P. vexans*, *Vexillum badense*, *V. intermittens*, and *Tosapusia pseudocupressina* (cf. HARZHAUSER & LANDAU 2021; BISKUPIČ 2023). In addition, the most abundant species, *Pusia pseudorecticosta*, may indicate its assumed origin from inner neritic habitats with sea grass meadows, as suggested by its paleoecological preferences proposed by HARZHAUSER & LANDAU (2021) and BISKUPIČ (2023).

The studied Costellariidae assemblage reach high diversity, as indicated by the presence of 17 species found. *Bellardithala borzsonyensis* spec. nov., *Pusia pseudomoravica* spec. nov., *P. palmulleri* spec. nov., and *P. crassiornata* spec. nov. are established as new species, and a single taxon, *Bellardithala* sp., is left in open nomenclature. Six species represent the first confirmed records from Hungary: *Bellardithala boehmi*, *B. lapugyensis*, *Ebenomitra pseudopyramidella*, *Pusia avellanella*, *P. paraleucozona*, and *P. vexans*. In the Costellariidae association, *Pusia pseudorecticosta* (668 specimens) strongly dominates (66.7%), whereas *Bellardithala lapugyensis*, and *Tosapusia pseudocupressina* (1–1 specimen for each species) show an extremely low abundance (0.1%) (*Fig. 2*).

As follows from the above, the presented results point to a much higher species richness and abundance of this gastropod group at Letkés than referred to by the early authors. Surprisingly, the results also suggest that the studied association, composed of 17 species, belongs to the most diversified Costellariidae assemblage in the Badenian of the Central Paratethys Sea. Other coeval Paratethyan localities with the occurrence of Costellariidae reached considerably lower diversity than the assemblage from the Bagoly Hill. The most species-rich assemblages attaining the highest α-diversities of 14 and 12 species have so far been recorded from Lăpugiu de Sus (Romania) and Korytnica (Poland) (HARZHAUSER & LANDAU 2021). The high diversity of Costellariidae from Letkés corresponds to the Middle Miocene Climatic Optimum (~17–14 Ma), which was characterized by the increase of the Middle Miocene gastropod faunas in the Central Paratethys Sea (cf. HARZHAUSER et al. 2024). At that time, the costellariids reached the highest diversity (32 species) and belonged to one of the most speciose gastropod families (HARZHAUSER et al. 2024).

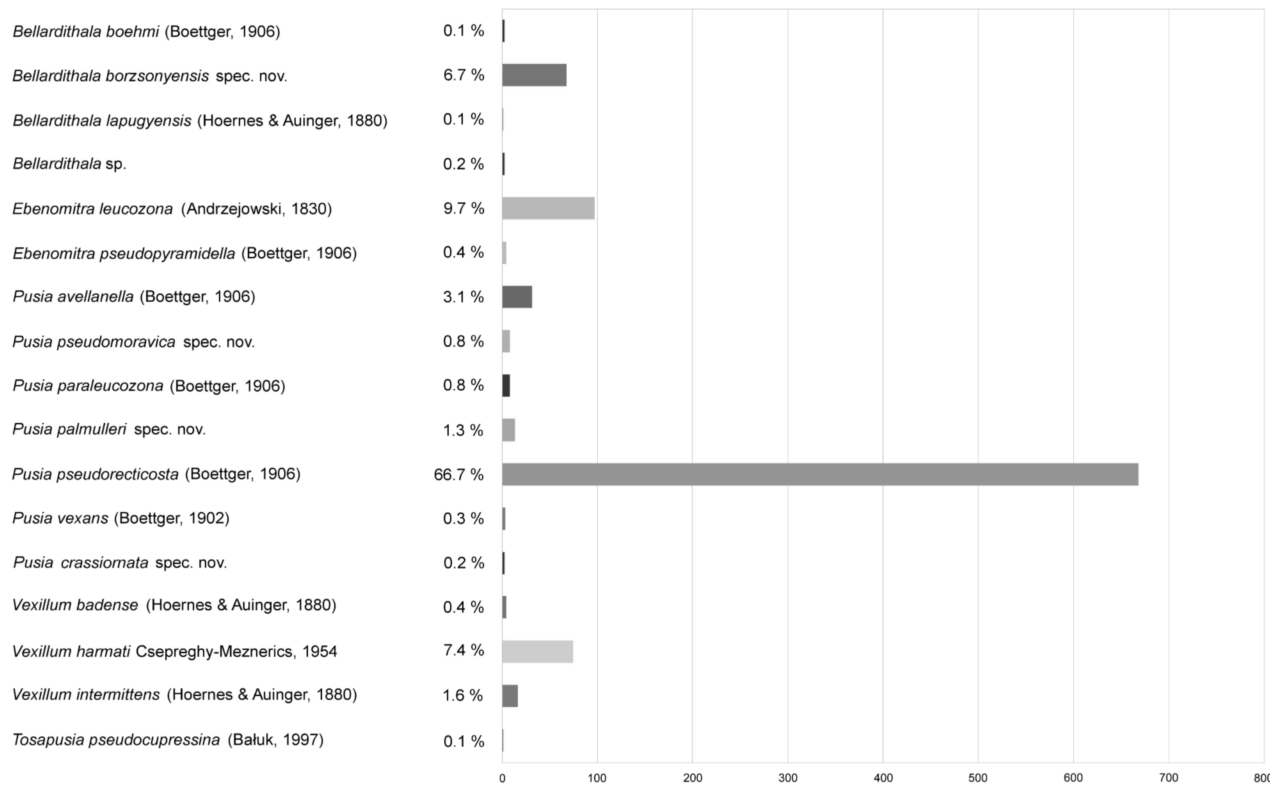

Figure 2. An overview and percentage representation of the studied Costellariidae species found in the lower Badenian sediments of the Bagoly Hill locality at Letkés.
2. ábra. *A vizsgált bagoly-hegyi (Letkés) alsó badeni üledékek Costellariidae-fajai, és az együttes százalékos összetétele.*

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Manuscript received: 4/12/2024

Plates – Táblák

Plate I – I. Tábla

Figs 1–2. *Bellardithala boehmi* (BOETTGER, 1906), SL 9.04 mm, MD 3.30 mm, Coll. ZK.

Figs 3–4. *Bellardithala borzsonyensis* spec. nov., holotype/*holotípus*, SL 5.85 mm, MD 2.10 mm, HNHM PAL 2024.144.1.

Figs 5–6. *Bellardithala borzsonyensis* spec. nov., paratype 1/*paratípus 1*, SL 5.54 mm, MD 1.93 mm, HNHM PAL 2024.146.1.

Figs 7–8. *Bellardithala borzsonyensis* spec. nov., paratype 2/*paratípus 2*, SL 5.50 mm, MD 1.90 mm, HNHM PAL 2024.147.1.

Figs 9–10. *Bellardithala borzsonyensis* spec. nov., paratype 3/*paratípus 3*, SL 5.60 mm, MD 2.14 mm, HNHM PAL 2024.148.1.

Figs 11–12. *Bellardithala borzsonyensis* spec. nov., paratype 4/*paratípus 4*, SL 5.26 mm, MD 2.10 mm, HNHM PAL 2024.149.1.

Figs 13–14. *Bellardithala borzsonyensis* spec. nov., paratype 5/*paratípus 5*, SL 4.97 mm, MD 1.90 mm, HNHM PAL 2024.150.1.
Figs 15–16. *Bellardithala lapugyensis* (HOERNES & AUINGER, 1880), SL 3.69 mm, MD 1.66 mm, Coll. ZK.
Figs 17–18. *Bellardithala* sp., SL 5.98 mm, MD 2.07 mm, Coll. ZK.
Figs 19–20. *Bellardithala* sp., SL 5.51 mm, MD 2.14 mm, Coll. ZK.
Scale bars/*méretvonalak*: 2 mm.

Plate II – II. Tábla

Figs 1–2. *Ebenomitra leucozona* (ANDRZEJOWSKI, 1830), SL 12.98 mm, MD 6.05 mm, Coll. ZK.
Figs 3–4. *Ebenomitra leucozona* (ANDRZEJOWSKI, 1830), SL 14.53 mm, MD 6.03 mm, Coll. ZK.
Fig. 5. *Ebenomitra leucozona* (ANDRZEJOWSKI, 1830), SL 16.10 mm, MD 6.29 mm, Coll. ZK.
Fig. 6. *Ebenomitra leucozona* (ANDRZEJOWSKI, 1830), SL 15.87 mm, MD 6.03 mm, Coll. ZK.
Figs 7–8. *Ebenomitra leucozona* (ANDRZEJOWSKI, 1830), SL 15.58 mm, MD 5.56 mm, Coll. ZK.
Figs 9–10. *Ebenomitra pseudopyramidella* (BOETTGER, 1906), SL 13.16 mm, MD 5.28 mm, Coll. ZK.
Figs 11–12. *Ebenomitra pseudopyramidella* (BOETTGER, 1906), SL 10 mm, MD 4.43 mm, Coll. ZK.
Figs 13–14. *Pusia avellanella* (BOETTGER, 1906), SL 8.34 mm, MD 3.73 mm, Coll. ZK.
Figs 15–16. *Pusia avellanella* (BOETTGER, 1906), SL 9.63 mm, MD 3.62 mm, Coll. ZK.
Fig. 17. *Pusia pseudomoravica* spec. nov., paratype 2/*paratípus 2*, SL 8.90 mm, MD 3.56 mm, HNHM PAL 2024.156.1.
Figs 18–19. *Pusia pseudomoravica* spec. nov., holotype/*holotípus*, SL 9.88 mm, MD 3.87 mm, HNHM PAL 2024. 157.1.
Figs 20–21. *Pusia pseudomoravica* spec. nov., paratype 1/*paratípus 1*, SL 10.30 mm, MD 3.91 mm, HNHM PAL 2024.158.1.
Figs 22–23. *Pusia paraleucozona* (BOETTGER, 1906), SL 7.21 mm, MD 3.31 mm, Coll. ZK.
Figs 24–25. *Pusia paraleucozona* (BOETTGER, 1906), SL 7.95 mm, MD 3.66 mm, Coll. ZK.
Scale bars/*méretvonalak*: 2 mm.

Plate III – III. Tábla

Figs 1–2. *Pusia palmulleri* spec. nov., holotype/*holotípus*, SL 7.65 mm, MD 2.84 mm, HNHM PAL 2024.145.1.
Figs 3–4. *Pusia palmulleri* spec. nov., paratype 1/*paratípus 1*, SL 7.16 mm, MD 2.80 mm, HNHM PAL 2024.151.1.
Figs 5–6. *Pusia palmulleri* spec. nov., paratype 2/ *paratípus 2*, SL 7.65 mm, MD 2.71 mm, HNHM PAL 2024.152.1.
Figs 7–8. *Pusia palmulleri* spec. nov., paratype 3/*paratípus 3*, SL 6.33 mm, MD 2.35 mm, HNHM PAL 2024.153.1.
Figs 9–10. *Pusia palmulleri* spec. nov., paratype 4/*paratípus 4*, SL 6.96 mm, MD 2.48 mm, HNHM PAL 2024.154.1.
Figs 11–12. *Pusia palmulleri* spec. nov., paratype 5/*paratípus 5*, SL 5.05 mm, MD 2.14 mm, HNHM PAL 2024.155.1.
Fig. 13. *Pusia pseudorecticosta* (BOETTGER, 1906), SL 9.38 mm, MD 4.11 mm, Coll. ZK.
Figs 14–15. *Pusia pseudorecticosta* (BOETTGER, 1906), SL 11.03 mm, MD 3.60 mm, Coll. ZK.
Fig. 16. *Pusia pseudorecticosta* (BOETTGER, 1906), SL 11.49 mm, MD 3.80 mm, Coll. ZK.
Fig. 17. *Pusia pseudorecticosta* (BOETTGER, 1906), SL 11.67 mm, MD 4.20 mm, Coll. ZK.
Fig. 18. *Pusia pseudorecticosta* (BOETTGER, 1906), SL 10.46 mm, MD 4.16 mm, Coll. ZK.
Figs 19–20. *Pusia pseudorecticosta* (BOETTGER, 1906), SL 10.93 mm, MD 4.23 mm, Coll. ZK.
Figs 21–22. *Pusia vexans* (BOETTGER, 1902), SL 6.54 mm, MD 2.24 mm, Coll. ZK.
Figs 23–24. *Pusia vexans* (BOETTGER, 1902), SL 5.10 mm, MD 2.18 mm, Coll. ZK.
Figs 25–26. *Pusia crassiornata* spec. nov., holotype/*holotípus*, SL 5.90 mm, MD 2.19 mm, HNHM PAL 2025.2.1.
Figs 27–28. *Pusia crassiornata* spec. nov., paratype/*paratípus*, SL 5.10 mm, MD 1.91 mm, HNHM PAL 2025.3.1.
Scale bars/*méretvonalak*: 2 mm.

Plate IV – IV. Tábla

Fig. 1. *Vexillum badense* (HOERNES & AUINGER, 1880), SL 15.18 mm, MD 5.46 mm, Coll. ZK.
Figs 2–3. *Vexillum badense* (HOERNES & AUINGER, 1880), SL 11.55 mm, MD 4.15 mm, Coll. ZK.
Figs 4–5. *Vexillum harmati* CSEPREGHY-MEZNERICS, 1954, SL 11.61 mm, MD 3.25 mm, Coll. ZK.
Fig. 6. *Vexillum harmati* CSEPREGHY-MEZNERICS, 1954, SL 10.58 mm, MD 3.16 mm, Coll. ZK.
Fig. 7. *Vexillum harmati* CSEPREGHY-MEZNERICS, 1954, SL 8.52 mm, MD 2.77 mm, Coll. ZK.
Figs 8–9. *Vexillum intermittens* (HOERNES & AUINGER, 1880). Refiguration of the specimen in STRAUSZ (1966, pl. 25, figs 9–10) from Letkés, unknown locality (SZTFH Földtani Szolgálat, Gyűjteményi Osztály), SL 13 mm, MD 4.20 mm.
Fig. 10. *Vexillum intermittens* (HOERNES & AUINGER, 1880), SL 13.26 mm, MD 4.26 mm, Coll. ZK.
Figs 11–12. *Vexillum intermittens* (HOERNES & AUINGER, 1880), SL 12.14 mm, MD 4.15 mm, Coll. ZK.
Figs 13–14. *Tosapusia pseudocupressina* (BAŁUK, 1997), SL 19.30 mm, MD 5.67 mm, Coll. ZK.
Scale bars/*méretvonalak*: 2 mm for Figs 1–12, 5 mm for Figs 13–14.

Plate I – I. Tábla

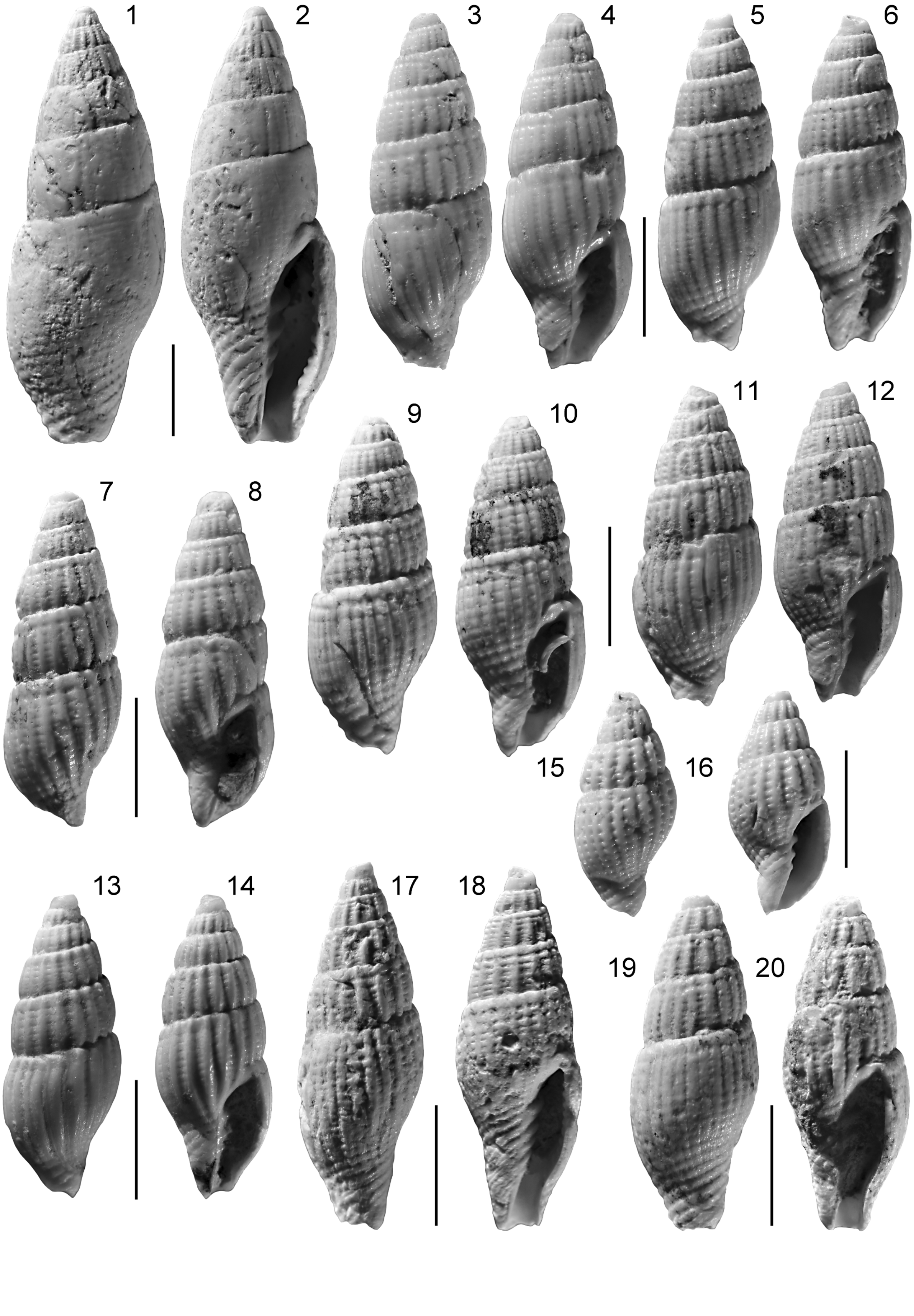

Plate II – II. Tábla

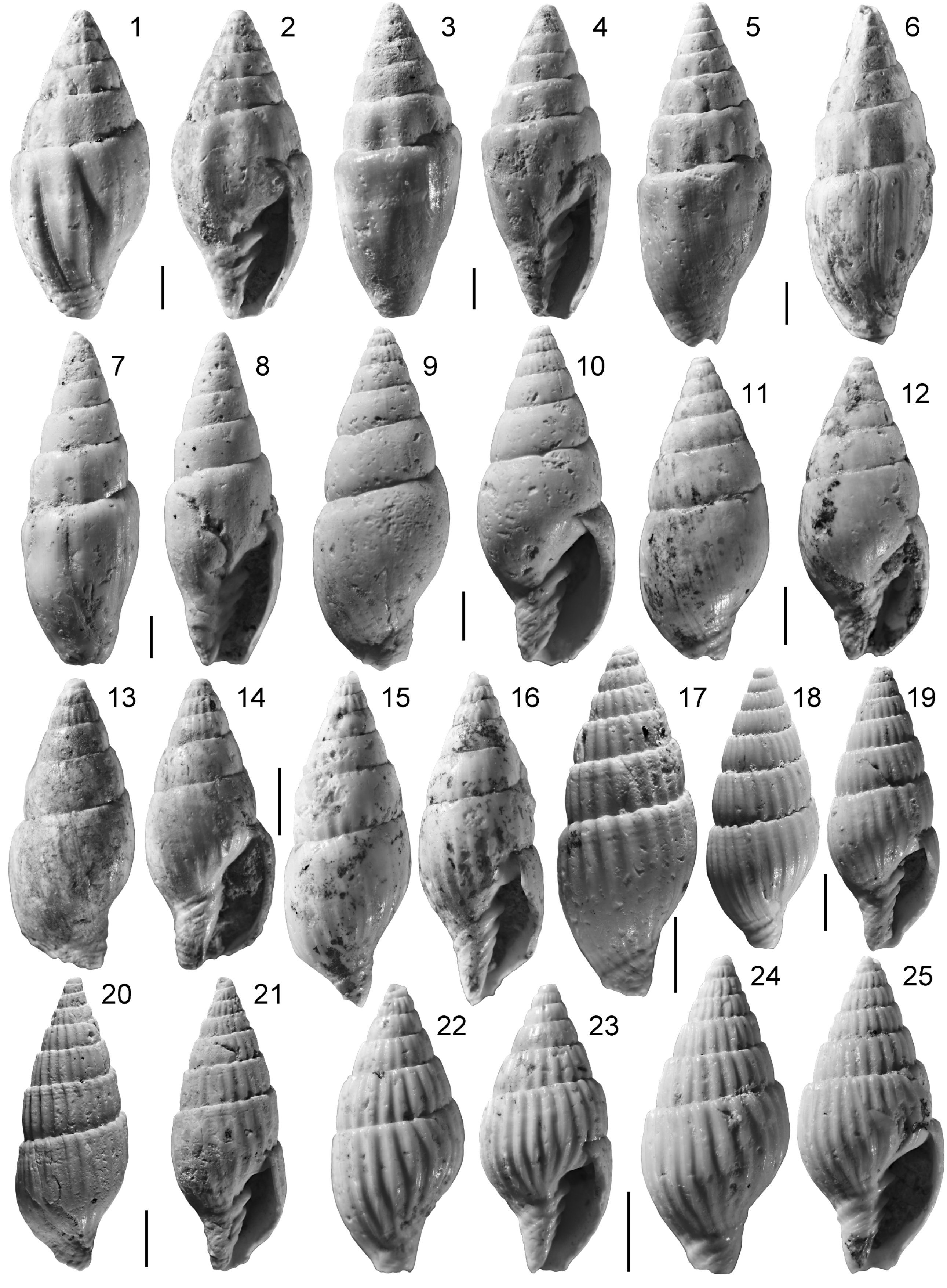

Plate III – III. Tábla

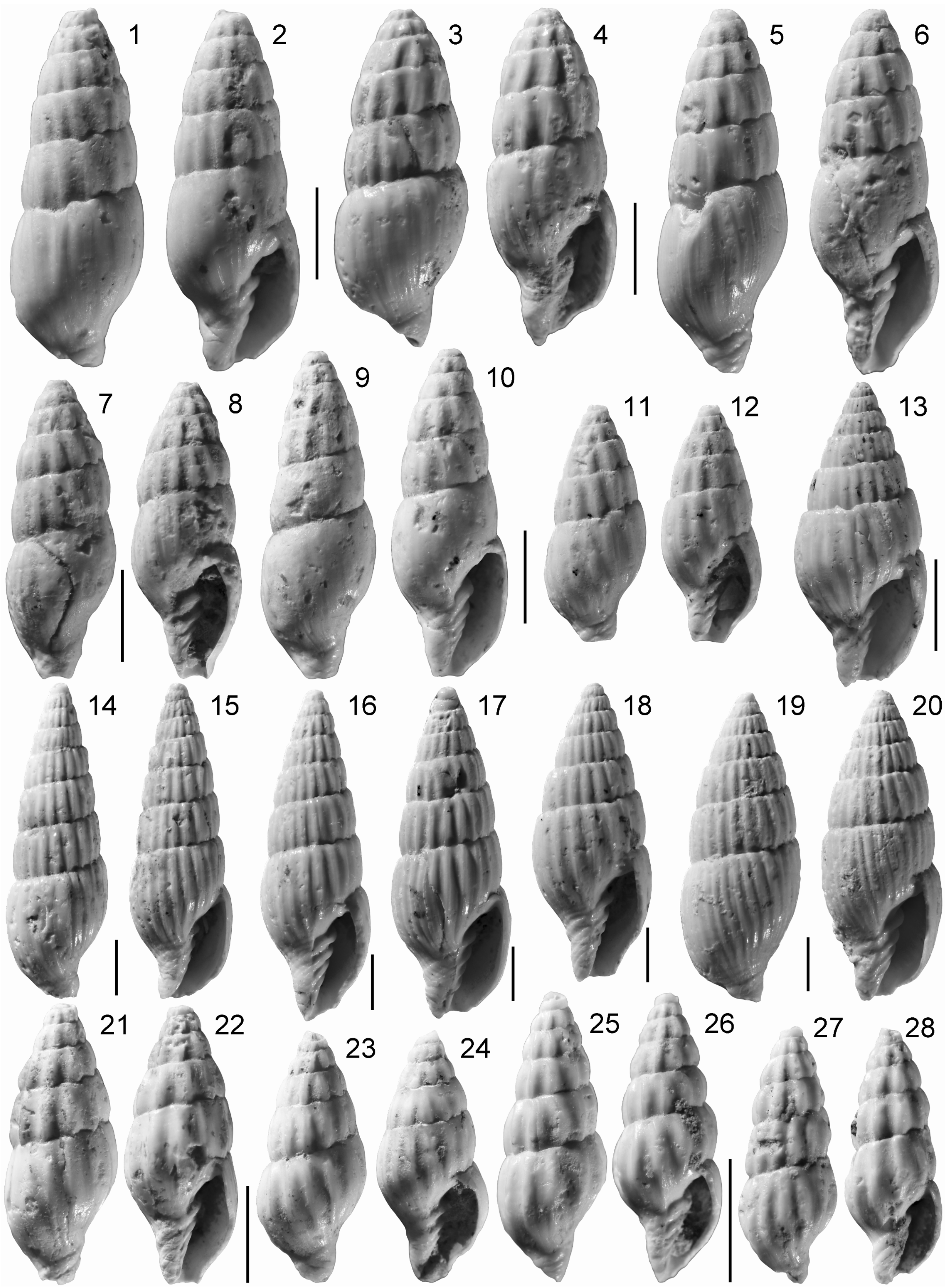

Plate IV – IV. Tábla