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Sarmatian and Pannonian mollusks from Pécs-Danitzpuszta, southern Hungary: a unique local faunal succession

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Szarmata és pannóniai puhatestű faunák különleges helyi sorrendje Pécs-Danitzpusztáról

Összefoglalás

A pannóniai puhatestűek közel két évszázados kutatása során kiderült, hogy a különböző faunák földrajzi elterjedése szabályos mintázatot mutat. Mivel a Pannon-tó medre oldalirányban épülő üledékcsomagokkal töltődött fel, a medencének a behordástól távoli részén kondenzált üledékképződés folyt, a peremektől a medence közepe felé pedig egyre fiatalabb sekélyvízi üledékek rakódtak le. A medencéből kiemelkedő aljzati magaslatok környékén, amennyiben ezek üledékforrásként szolgáltak, megtörik ez a szabályos trend. A késő miocén korai szakaszában a Mecsek is ilyen kiemelkedés volt. A Pécs-Danitzpusztán feltárt 200 méter vastag szarmata–pannóniai rétegsor képződését a helyi szerkezeti és üledékképződési viszonyok időben úgy alakították, hogy a különböző puhatestű faunák egyedi, másutt eddig nem tapasztalt sorrendben követik egymást.

A rétegsor alján található szarmata tengeri faunát egy édesvízi vagy oligohalin (alacsony sótartalmat elviselő) együttes követi, amely a mikrofauna alapján még szintén szarmata korú. Bár a kövületek megtartási állapota nem teszi lehetővé biztos következtetések levonását, úgy tűnik, hogy az együttes fajai – elsősorban a tüdőscsigák – a legidősebb pannóniai fauna őseit képviselik.

A következő ősmaradvány-tartalmú rétegekben egy „törpe" faunát találunk: a kis méretű, de változékony, „szarmata típusú" szívkagylók tömege sok helyről ismerős a Pannon-medencében a szarmata–pannóniai határ közeléből. Ezeknek a kagylóknak az alapos taxonómiai vizsgálata a jövő feladata; minden bizonnyal megtalálhatók köztük a jól ismert szarmata és pannóniai formákat összekötő, mindeddig ismeretlen formák.

A rétegsor következő, jelentős részét a Pannon-medence déli felében nagy elterjedést mutató „fehér márgák" teszik ki. Ezek a Pannon-tó szublitorális és profundális zónájában halmozódtak fel, faunájuk alapján pedig két egységre bonthatók ugyanúgy, mint Horvátországban vagy Szerbiában: a *Lymnocardium praeponticum* Zónára (vagy *Radix croatica* Zónára), melynek becsült kora 11,6–11,4 millió év, és a *Congeria banatica* Zónára, amely 11,4 és 9,7 millió év között képződött a Pannon-medencében.

A fehér márga lerakódása azonban Pécs-Danitzpusztán ennél hamarabb véget ért. Kőzetliszt ülepedése váltotta fel, amelynek gazdag szublitorális puhatestű faunája a *Lymnocardium schedelianum* Zónába tartozik; korát 10,5–10,2 millió évre tehetjük. Ez a fauna gyakori a Bécsi-medencében, a Dél-Bánságban és a Pannon-medence egyéb peremi területein, de sehol nem találták meg a fehér márgák fedőjében. Horvátországban és Szerbiában a mélyvízi márgák képződése ebben az időben is zajlott és tovább folytatódott.

A pécs-danitzpusztai rétegsort végül egy vastag, limonitos homoktest fedi. A homokból kagylók és csigák lenyomatai és kőbelei kerültek elő. A fauna tipikus sekélyvízi, litorális környezetre utal, rétegtanilag a *Lymnocardium conjungens* Zóna felső részébe tartozik, kora 10,2–10,0 millió évre becsülhető. Hasonló faunák ismertek Burgenlandból, Szerbiából, a Partiumból, de ezeken a helyeken soha nem a *L. schedelianum* Zóna közvetlen fedőjéből, mint Danitzpusztán.

Pécs-Danitzpusztán tehát olyan faunák egymáshoz való rétegtani viszonyát lehet tanulmányozni, amelyek eddig nem voltak megfigyelhetők egyetlen szukcesszióban vagy akár egymáshoz nagyon közeli földrajzi pozícióban sem.

Kulcsszavak: miocén, Pannon-tó, puhatestűek, biosztratigráfia, paleoökológia, Mecsek, szarmata–pannóniai határ

Abstract

As the almost 200-year palaeontological research revealed, the geographical distribution of various fossil mollusk faunas in deposits of the late Neogene Lake Pannon displays a regular pattern. The lake basin was filled by lateral accretion of sediments, resulting in condensed sedimentary successions in the distal parts of the basin and successively

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younger shallow-water deposits from the margins towards the basin center. Exposed intra-basin basement highs, however, broke this strict pattern when they acted as sediment sources during the lake's lifetime. The Mecsek Mts in southern Hungary was such an island in Lake Pannon during the early late Miocene. Deposition of the 200 m thick Sarmatian–Pannonian sedimentary succession in Pécs-Danitzpuszta at the foot of the Mecsek Mts was thus controlled by local tectonic and sedimentary processes, resulting in a unique succession of facies and mollusk faunas. A typical, restricted marine Sarmatian fauna is followed by a distinct freshwater or oligohaline interval, which, according to micropalaeontological evidence, still belongs to the Sarmatian. Although poor preservation of fossils does not allow firm conclusions, it seems that freshwater Sarmatian snails were the ancestors of the brackish-water-adapted early Pannonian pulmonate snail taxa. The successive "Sarmatian-type" dwarfed cockle fauna is similar to those widely reported from the Sarmatian–Pannonian boundary in various parts of the Pannonian Basin; however, a thorough taxonomic study of its species is still lacking. The bulk of the sedimentary succession corresponds to the sublittoral to profundal "white marls," which are widespread in the southern Pannonian Basin. In Croatia and Serbia, they are divided into the *Lymnocardium praeponticum* or *Radix croatica* Zone (11.6–11.4 Ma) below, and the *Congeria banatica* Zone (11.4–9.7 Ma) above; this division can be applied to the Pécs-Danitzpuszta succession as well. Sedimentation of the calcareous marl, however, ceased at Pécs-Danitzpuszta at about 10.5–10.2 Ma ago (during the younger part of the *Lymnocardium schedelianum* Chron), when silt was deposited with a diverse sublittoral mollusk fauna. Similar faunas are known from the Vienna Basin, southern Banat, and other marginal parts of the Pannonian Basin System, but not from Croatia and Serbia, where deposition of the deep-water white marls continued during this time. Finally, the Pécs-Danitzpuszta succession was capped with a thick, coarse-grained sand series that contains mollusk molds and casts representing a typical littoral assemblage. This littoral fauna is well-known from easternmost Austria, northern Serbia, and northwestern Romania, but never directly from above the sublittoral *L. schedelianum* Zone. The fauna is characteristic for the upper part of the *Lymnocardium conjungens* Zone and has an inferred age of ca. 10.2–10.0 Ma. The Pécs-Danitzpuszta succession thus allows to establish the chronostratigraphic relationship between mollusk faunas that have not been observed in one succession nor in close proximity to each other in other parts of the Pannonian Basin.

Keywords: Miocene, Lake Pannon, mollusks, biostratigraphy, palaeoecology, Mecsek Mts, Sarmatian–Pannonian boundary

Introduction

The upper Miocene (Pannonian) lacustrine to deltaic basin fill of the Pannonian Basin in Central Europe is exposed along the basin margins and around the intrabasinal basement highs (today hills or mountains) as a consequence of a Pliocene to Recent basin inversion (RUSZKICZAY-RÜDIGER et al. 2020 and references therein). The lacustrine layers exposed in the Pécs-Danitzpuszta sand pit in South Hungary at the foot of the Mecsek Mts (*Figure 1A*) first gained fame as a textbook example of intra-Pannonian tectonic processes that tilted the lacustrine white marls and the lower part of the overlying limonite-stained sands into a vertical position (VADÁSZ 1953; BARTHA 1966; KLEB 1968, 1973). In these reports, the dislocated layers were interpreted as "lower Pannonian", whereas the overlying, almost horizontal sand layers were identified as "upper Pannonian". These assignments, however, were poorly supported with biostratigraphic evidence. Only faint, poor-quality pictures of "*Congeria* sp. and *Lymnocardium* sp. in a calcareous marl layer", "*Melanopsis*-bearing calcarenite", and "*Congeria balatonica*" from the sand were published to support this interpretation (BARTHA 1966, KLEB 1973). Based on the lithological features, the white marl of the outcrop was correlated with the *Congeria banatica*-bearing white marls of Croatia and Serbia ("Slavonian" or "Beočin-type" beds and fauna), whereas the overlying limonitic sand was tentatively correlated with the *Congeria balatonica*- and *Lymnocardium schmidti*-bearing, 7–8 million-year-old sand apron that covers the southern foothills of the Mecsek Mts (BARTHA 1964, 1966; KLEB 1968, 1973; KAZÁR et al. 2007).

Later the outcrop also became famous as a palaeontological site. The marl is the type locality of some endemic Pannonian calcareous nannofossils (BÓNA & GÁL 1985, 1987), and the overlying sand layers were discovered to be a Mecca for vertebrate palaeontologists and amateur collectors by yielding an amazing amount and variety of reworked Miocene vertebrate fossils (SZABÓ et al. 2021, and references therein). The biostratigraphic position and age of the fossiliferous Pannonian lacustrine sediments, however, remained obscure. In the last two decades, however, large amounts of mollusk fossils were collected from the outcrop. In addition, a trench was excavated in 2018 on top of the tilted beds to expose the layers that underlie the marl (*Figure 1B*); this trench revealed a Badenian to Sarmatian to Pannonian (middle to upper Miocene) succession with several fossiliferous layers (*Figure 2*).

In this study, we present the mollusk record of the Sarmatian–Pannonian succession of the outcrop (its Badenian fossils are discussed in DULAI et al. 2021) and evaluate the mollusk fauna from biostratigraphic and palaeoecological points of view. We compare the assemblages with other well-known faunas. For a detailed geological context and description of the succession, the reader is referred to SEBE et al. (2021).

Material and methods

The studied material includes fossils recently collected layer-by-layer from both the trench (Layers D50 to D1) and along a section on the northern wall of the pit (Layers D212 to D227; *Figures 1B, 2*), as well as specimens collected earlier by Krisztina SEBE and her students from the University

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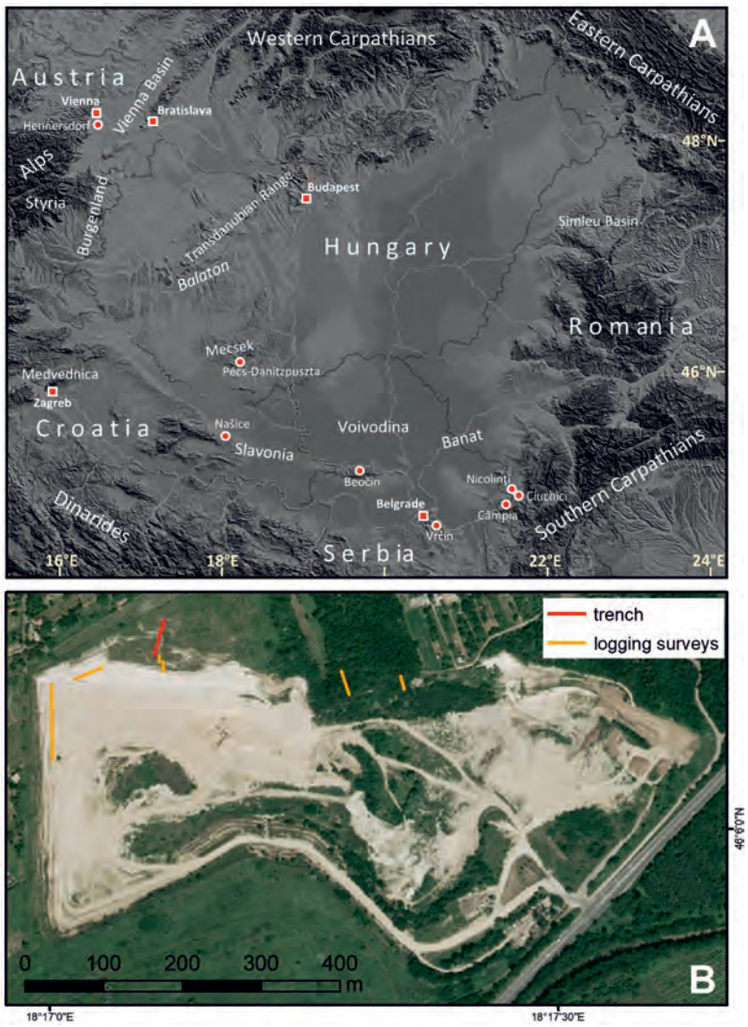

Figure 1. A: Location map of the Pannonian Basin surrounded by the Alps, Western, Eastern and Southern Carpathians and Dinarides with the geographical names referred to in the text. B: Satellite photo of the sand pit with the location of the exploratory trench and the logged surveys (SEBE et al. 2021)

1. ábra. *A: Az Alpokkal, Kárpátokkal és Dinaridákkal körülvett Pannon-medence a szövegben hivatkozott földrajzi nevekkel. B: Műholdas felvétel a pécs-danitzpusztai bányáról a kutatóárok és a vizsgált szelvények jelölésével (SEBE et al. 2021)*

of Pécs, László KANIZSAI, a private collector, István CZICZER (University of Szeged), Imre MAGYAR, and others, from various parts of the Pannonian succession during the last two decades. The investigated fossils are reposited in the Natural History Museum, Budapest; Local History and Natural History Museum Collection, Komló; and Mining and Geological Survey of Hungary, Budapest. The fossils collected by the authors were cleaned and prepared in the laboratory of the Department of Palaeontology at the Eötvös Loránd University, Budapest, and in the Natural History Museum, Budapest. Polyvinyl acetate was used for solidifying fragile fossils. For mollusk determination, a Zeiss SteREO Discovery.V12 modular binocular stereo microscope was used in the Laboratory of MOL Plc., Budapest. Thin sections were prepared in the Laboratory of MOL Plc.,and they were investigated with a Zeiss Axio Imager.A1 polarizing microscope. Photos were taken by two cameras (macroscopic images: Canon EOS 40D digital camera with Canon EF 100 mm f/2.8L IS USM macro lens; microscopic images: Zeiss AxioCam MRc 5 camera mounted on the Zeiss microscopes with the help of the AxioVision 40×64 v.4.9.1.0 software). Some of the borrowed museum specimens were photographed in the Bakony Museum of the Hungarian Natural History Museum, Zirc.

Comparison of our specimens with the type materials reposited in the Natural History Museum Vienna (NHMW), Geological Survey of Austria, Vienna (GBA), Croatian Natural History Museum, Zagreb (HPM) and Mining and Geological Survey of Hungary, Budapest (MBFSZ) led to some clarification of taxonomic identities and uncertainties that are important for correct age determination (see in Appendix). At the genus level we followed a conservative approach. All dreissenids possessing an apophysis (an appendix that served as pedal retractor catchment) are attributed here to *Congeria*, because subdivision of this large group into monophyletic flocks, supported by compelling morphological and stratigraphical arguments, has not happened so far. We use the genus *Lymnocardium* collectively for all Lake Pannon cardiids that have not been separated into clearly established genera, but put it into a quotation mark where morphological dissimilarity to the type of *Lymnocardium* argues for a different – as yet undecided – generic placement.

Mollusk assemblages and depositional environments

The Sarmatian–Pannonian succession of the Pécs-Danitzpuszta section can be divided into several intervals based on the mollusk fauna. In this chapter, a brief description of each interval is given with its typical fossil mollusk content, its characteristic lithology, and the inferred depositional environment. The full list of the identified taxa for each layer is given in the digital annex of this paper.

Unit 1. Layers D55 to D47 yield moulds ("steinkerns") of poorly preserved restricted marine species, such as *Ervilia* sp. (a fragment), Lymnocardiinae sp. (*Plate I, figures 2–3*), and Dreissenidae sp. (*Plate I, figure 1*).

Unit 2. The overlying layers (D43–D37), consisting of marl, tuffaceous sand and limestone, contain a poorly preserved gastropod fauna with freshwater forms, such as lymnaeids [*Radix* cf. *croatica* (*Plate I, figures 5–6*), ?*Lymnaea* sp. (*Plate I, figures 4, 7, 10*)], planorbids (*Plate I, figure 8*), hydrobiids (*Plate I, figures 11, 13*), and the neritid *Theo-*

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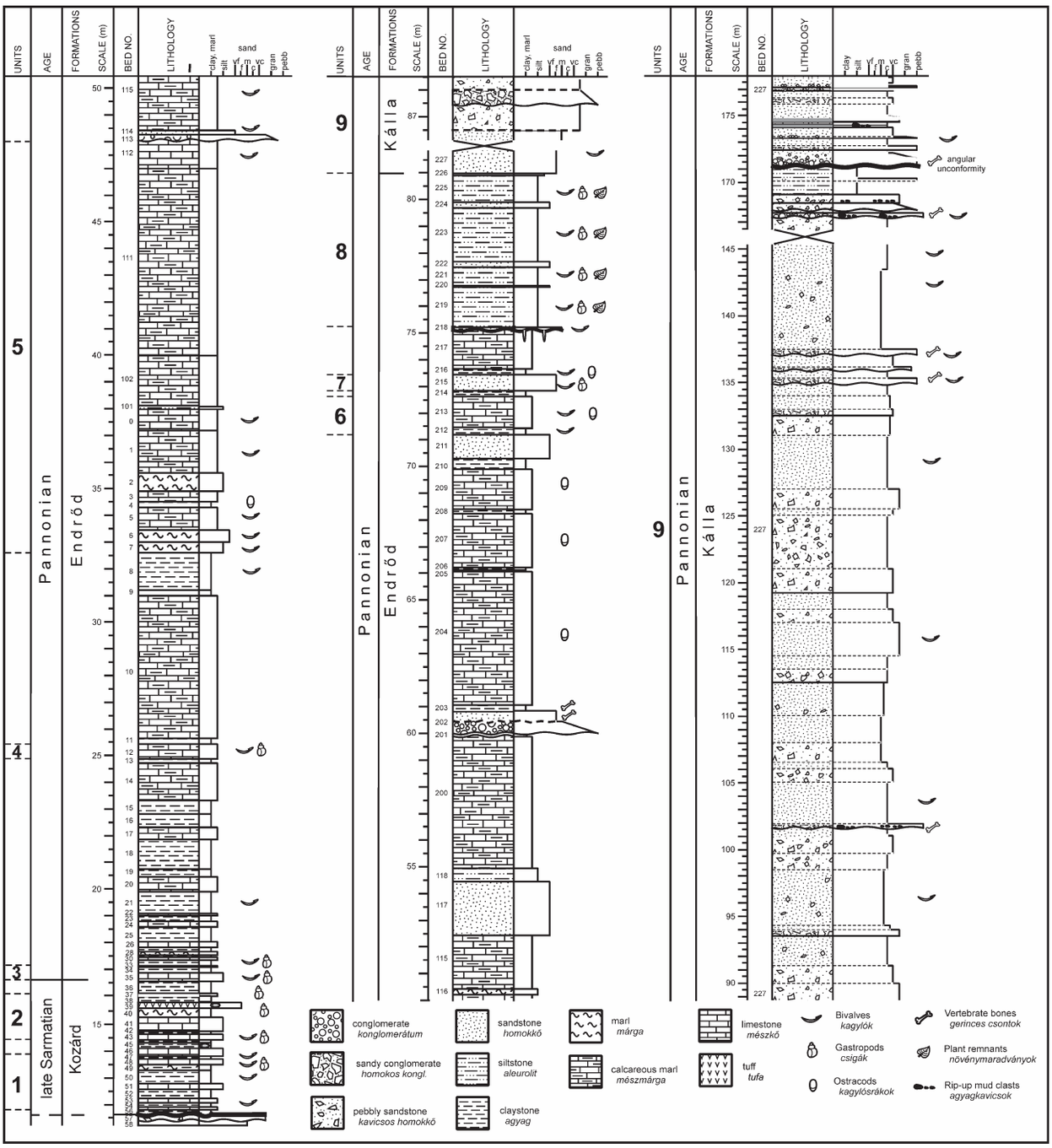

Figure 2. Lithologic log of the pécs-Danitzpuszta succession, with sample locations and layer and unit numbers. Faunal intervals are discussed in the text. (SEBE et al. 2021)

2. ábra. *A Pécs-danitzpusztai homokbánya középső-késő miocén szelvénye a vizsgált minták helyével és a fauna biosztratigráfiai és paleoökológiai értékelése alapján elkülönített intervallumokkal. (SEBE et al. 2021)*

doxus sp. (*Plate I, figure 9*). A land snail also occurred, whereas bivalves are completely missing from these layers.

Unit 3. The limestone layers D35 and D33 are densely packed with moulds of small cardiids and a few hydrobiids (*Plate II, figures 1–20*). The cardiids show very high variability in terms of outline, convexity, and rib pattern. Many of them are similar to various Sarmatian and Pannonian taxa, such as *Inaequicostata pia* (*Plate II, figures 1–2*), *I. nigra* (*Plate II, figures 11–12*), *Obsoletiformes fischeriformis (Plate II, figure 9*), *O. kaudensis* (*Plate II, figures 5, 10*), *Plicatiformes plicatus*, *Planacardium* sp. (*Plate II, figure 3*), "*Lymnocardium*" *praeponticum* (*Plate II, figure 4*) and others (*Plate II, figures 6–8*). Due to their extreme variability and poor preservation, we are not confident about

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these identifications (see *Digital annex*). Similar cardiid faunas have been described from various parts of the Pannonian Basin, but the identification of the species remains ambiguous even when the preservation of the shells is good (e.g., JEKELIUS 1944). These assemblages, which undoubtedly include so far unknown links between the Sarmatian restricted marine and Pannonian brackish lacustrine cardiids, deserve a thorough study in the future.

Unit 4. The fauna embedded into the calcareous marl of Layer D12 consists of cardiids ["*Lymnocardium*" cf. *praeponticum* (*Plate III, figures 11–12*), "*L.*" cf. *plicataeformis* (*Plate III, figure 15*), *Lymnocardium* sp. (*Plate III, figures 13–14*)], dreissenids [*Congeria* cf. *banatica* (*Plate III, figures 1–4*), *C.* cf. *martonfii* (*Plate III, figure 5*), *C.* cf. *ramphophora* (*Plate III, figure 9*), *C.* cf. *neumayri* (*Plate III, figure 10*), and *Congeria* div. sp. (*Plate III, figures 6–8*)], planorbids (*Gyraulus tenuistriatus* and *Orygoceras fuchsi*), lymnaeid (*Radix croatica; Plate III, figures 17–19*) and hydrobiid (*Prososthenia sundecici* and *Micromelania striata*) snails. This fauna is widespread in the southern Pannonian Basin and its embedding layers are distinguished as "Croatica formation" in Croatia. The environmental interpretation of the fauna is controversial; usually it is interpreted to represent shallow, strongly freshened water, but there are arguments for a sublittoral or even profundal habitat (for a detailed discussion see SEBE et al. 2020).

Unit 5. The marl, calcareous marl and limestone layers between D7 and D112 yielded small, thin-shelled cardiids [*Paradacna* cf. *syrmiensis, P. abichi* (*Plate IV, figures 1–5*), "*Lymnocardium*" *margaritaceum* (*Plate IV, figures 10–11*), and Lymnocardiinae sp. (*Plate IV, figures 6–9*)], dreissenids (*Congeria czjzeki* and *C. banatica*) and snails [Hydrobiidae sp., *Micromelania striata* (*Plate IV, figure 13*), *Velutinopsis* sp. (*Plate IV, figure 12*), *Gyraulus* sp., *Orygoceras fuchsi*, and *O. brusinai* (*Plate IV, figure 14*)]. This fauna is also well-known in the southern Pannonian Basin under the names "Slavonian" or "Beočin-type" or "Banatica" fauna, and it is widespread in the white marls of Voivodina (Serbia), Slavonia and Medvednica Mts. (Croatia), and southern Burgenland and eastern Styria (Austria) (e.g., GORJANOVIĆ-KRAMBERGER 1899, SAUERZOPF 1952, SREMAC 1981, STEVANOVIĆ & PAPP 1985, VRSALJKO 1999, VASILIEV et al. 2007, GANIĆ et al. 2010, RUNDIĆ et al. 2011, TER BORGH et al. 2013). It is characterized by small-sized and thin-shelled mollusks, commonly cardiids, some dreissenids, and mostly pulmonate snails. These mollusks are interpreted to have lived in the sublittoral to profundal depth of Lake Pannon.

Unit 6. The soft clay of D212 and white marl of D213 contain scattered specimens of *Congeria partschi firmocarinata*. This species lived in the sublittoral zone of Lake Pannon (e.g., HARZHAUSER & MANDIC 2004).

Unit 7. The fossil fauna of Layer D215, a 60 cm thick quartz sandstone, is unique within the marl succession. It contains compressed molds of *Melanopsis fossilis* (*Plate IV, figure 16*), *M.* cf. *vindobonensis*, *Unio* cf. *atavus* (*Plate IV, figure 15*), *Congeria* sp., and *Lymnocardium* sp. The large *Melanopsis* species and *Unio atavus* were typical shallow-water, littoral dwellers in Lake Pannon (e.g., HARZHAUSER et al. 2007). As both the under- and overlying, fine-grained layers contain sublittoral fauna, the littoral shells and sand of D215 were probably transported into the sublittoral zone by gravity flows.

Unit 8. The uppermost ca. 6 m of the fine-grained succession, consisting of yellow silty marl and clayey siltstone (D219–D226), contains the most diverse mollusk assemblage of the entire section. Preservation is variable: fresh and dissolved shells, imprints as well as moulds were found. The fauna includes *Congeria partschi firmocarinata* (*Plate V, figure 1*), *C. zsigmondyi* (*Plate V, figures 2–3*), *Dreissenomya primiformis* (*Plate V, figures 4–7*), *Lymnocardium schedelianum* (*Plate VI, figures 1–2*), *L. winkleri* (*Plate V, figures 12–15*), *L.* aff. *boeckhi* (*Plate V, figures 8–11*), „*L.*" *carnuntinum* (*Plate VI, figures 3–4*), "*L.*" *tegulatum* (*Plate VI, figures 5–7*), "*L.*" cf. *asperocostatum* (*Plate VI, figure 12*), "*L.*" aff. *danicici* (*Plate VI, figure 8*), "*Lymnocardium*" cf. *proximum* (*Plate VI, figure 9*), "*Pontalmyra*" *otiophora* (*Plate VI, figure 13*), *Caladacna* aff. *steindachneri* (*Plate VI, figure 19*), *Paradacna* sp. (*Plate VI, figures 10–11*), ?*Parvidacna* sp., ?*Pseudocatillus* sp. (*Plate VI, figure 15*), ?*Phyllocardium* sp. (*Plate VI, figure 20*), Lymnocardiinae sp. (*Plate VI, figures 14, 16–18*), *Orygoceras fuchsi*, *O. brusinai*, *Gyraulus tenuistriatus* (*Plate VI, figure 22*), *Melanopsis fossilis*, *M. austriaca* (*Plate VI, figure 21*), and ?*Micromelania* sp. This assemblage shares a number of species (*C. partschi firmocarinata*, *C. zsigmondyi*, *D. primiformis*, *L. schedelianum*, and "*L.*" *carnuntinum*) with the fauna of Hennersdorf (near Vienna; PAPP 1953, 1985; HARZHAUSER & MANDIC 2004) and also with the fauna of Câmpia (Langenfeld) and Nicolinți (Nikolincz) in southern Banat, at the foothills of the Southern Carpathians, Romania (*C. zsigmondyi*, *L. winkleri*, "*L.*" *carnuntinum* (=*L. pseudosuessi*), and "*L.*" *tegulatum*) (HALAVÁTS 1882, 1886). Most of these mollusks are known to have lived in sublittoral environment (e.g., HARZHAUSER & MANDIC 2004, CZICZER et al. 2009). *Parvidacna, Pseudocatillus*, and *Phyllocardium* are littoral dwellers (e.g., MÜLLER & SZÓNOKY 1990), but they are represented by few specimens only, with incomplete preservation and/or in early ontogenetic stage, which makes their identification uncertain. The few specimens of the shallow-water *Melanopsis* could have been re-deposited from a littoral environment.

Unit 9. In the limonite-stained sand (D227) that overlies the marl succession, the aragonitic. shells were completely dissolved, leaving behind cavities between the imprints of the inner and outer shell surfaces. In most cases, only the cemented internal mold ("steinkern") was preserved and collected. As the mollusks are scattered in the sand, most specimens were collected from the heaps left behind by the industrial sieving of the sand. Thus, the exact stratigraphic position of the fossils within the sand body was impossible to reconstruct. In spite of this, three stratigraphic units could be distinguished: the lowermost part, the bulk of the sand, and the uppermost part separated from the bulk of the sand by a well-established unconformity surface.

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From the lowermost part of the sand, *Congeria partschi* (*Plate VII, figure 6*) and *Lymnocardium schedelianum* were identified. The former species occurred in abundance in some samples (*Plate VIII, figure 5*). Species from the bulk of the sand include *Congeria ungulacaprae* (*Plate VII, figure 4–5*), *C. hemiptycha* (*Plate VII, figures 1–3*), *C. partschi* (*Plate VIII, figure 2–3*), *C. balatonica* (*Plate VIII, figure 1*), *Lymnocardium schedelianum* (*Plate VIII, figure 10*), *L.* cf. *conjungens* (*Plate VIII, figure 9*), *L.* cf. *tucani* (*Plate VIII, figures 6–8*), *L.* cf. *proximum*, "*L.*" *carnuntinum*, "*L.*" aff. *danicici* (*Plate VIII, figure 5*), *Phyllocardium complanatum* (*Plate VIII, figure 11*), and *Melanopsis* cf. *fossilis.* The following species were collected from the top of the sand: *Congeria ungulacaprae*, *Dreissenomya dactylus* (*Plate VIII, figure 4*), *Lymnocardium* cf. *conjungens*, *L.* cf. *hantkeni*, *Lymnocardium* sp., and *Melanopsis vindobonensis.*

The composition of the entire fauna recovered from the sand is very similar to that of the classical Vrčin, Karagača creek site in Serbia (PAVLOVIĆ 1927, 1928) and to the littoral Pannonian faunas of Burgenland, Austria (SAUERZOPF 1952, LUEGER 1980, MAGYAR et al. 1999), Medvednica Mts., Croatia (BRUSINA 1892), and Şimleu Basin, Romania (CHIVU et al. 1966, NICORICI & KARÁCSONYI 1983, BARTHA et al. 2021). All the identified species are known from, and most of them are restricted to, littoral sandy deposits. The common occurrence of articulated valves excludes long post-mortem transport of the shells in the shoreface. Gravitational re-deposition of the shells together with the embedding sand from the littoral zone to a deeper depositional environment, however, is conceivable (e.g., BRETT & BAIRD 1986).

Biostratigraphy and age

Unit 1. The marginal marine mollusk fauna of layers D55 to D47 indicates Sarmatian age (*Figure 3*).

Unit 2. The age of the freshwater fauna from D43–D37 is difficult to assess. *Radix croatica* is a marker fossil of the lowermost Pannonian in the white marls of Croatia and Serbia (e.g., VRSALJKO 1999, VASILIEV et al. 2007, SEBE et al. 2020), but *Radix* cf. *croatica* occurs here with other freshwater forms but without brackish cardiids. The preservation of the mollusks from these layers does not allow a detailed morphological comparison with their well-established Pannonian counterparts. As the microfauna indicates Sarmatian age (SZUROMI-KORECZ et al. 2021), we assume that these mollusks represent a freshwater Sarmatian fauna, with the probable ancestors of the early Pannonian forms.

Unit 3. The mass occurrence of small, mostly "Sarmatian-type" cardiids (D35–D33) at the Sarmatian–Pannonian boundary is a commonly reported phenomenon in the Pannonian Basin, and it is alternately assigned into the uppermost Sarmatian or lowermost Pannonian in the literature (*Figure 3*).

Unit 4. The fauna from layer D12 is attributed to the basal Pannonian "*Lymnocardium*" *praeponticum* Zone, which was interpreted to have an age of 11.6–11.4 Ma (MAGYAR & GEARY 2012; *Figure 3*).

Unit 5. Interval D7–D112 can be correlated with the *C. banatica* Zone, although *Congeria banatica* itself occurs only sporadically. Some of the identified taxa were first described from similar *C. banatica*-bearing white marls in Slavonia (GORJANOVIĆ-KRAMBERGER 1899). The age of the

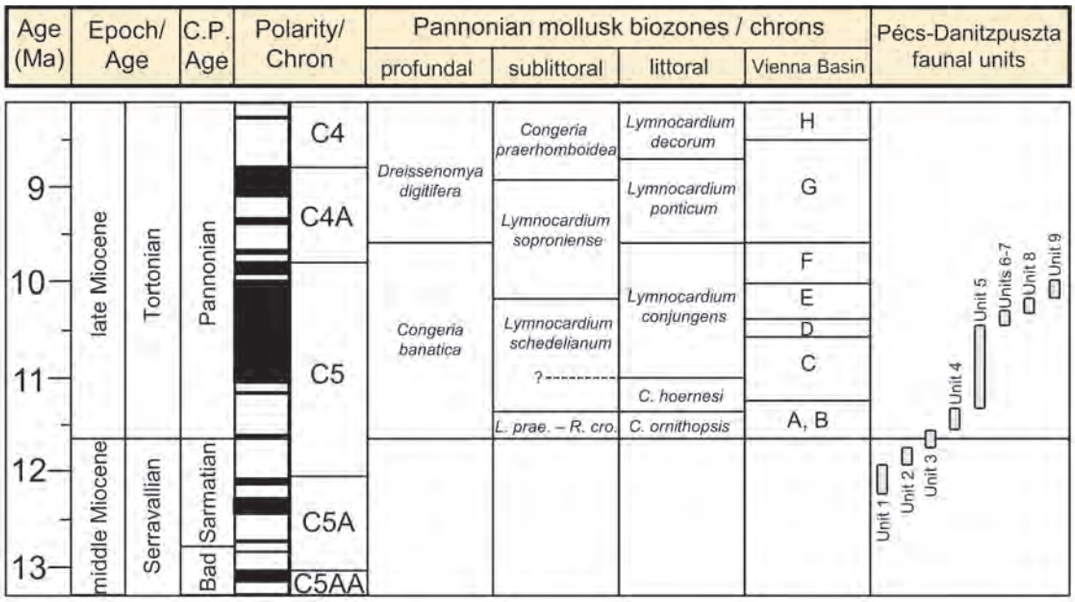

Figure 3. Stratigraphic chart for the late middle Miocene to early late Miocene with the mollusk zones of the Pannonian (according to MAGYAR & GEARY 2012 and HARZHAUSER et al. 2004) and with the biochronostratigraphic interpretation of the Pécs-Danitzpuszta faunal units.
C. P.: Central Paratethys; Bad: Badenian; *L. prae.* – *R. cro.*: *"Lymnocardium" praeponticum* – *Radix croatica*; *C.*: *Congeria*

3. ábra. *A pécs-danitzpusztai feltárásban azonosított puhatestű faunák biosztratigráfiai helyzetének és korának értelmezése. A rétegtani táblázat MAGYAR & GEARY (2012) és HARZHAUSER et al. (2004) alapján készült.*
Rövidítések: C. P.: Középső-Paratethys; Bad: badeni; L. prae. – R. cro.: "Lymnocardium" praeponticum – Radix croatica; C.: Congeria

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C. banatica Zone is estimated between 11.4–9.7 Ma (MAGYAR & GEARY 2012; *Figure 3*).

Units 6 and 7. The interval D212–D215 contains species (*Congeria partschi firmocarinata* and *Unio atavus*) that were interpreted as markers of "Zone E" by PAPP (1951, 1953), similarly to some species of the overlying Unit 8 (*Figure 3*).

Unit 8. The mollusk assemblage from D219 to D226 belongs to the *Lymnocardium schedelianum* Zone, the age of which was constrained between 11.0 and 10.2 Ma by MAGYAR & GEARY (2012). The diverse fauna of this interval resembles the fauna of Hennersdorf in the Vienna Basin (PAPP 1953) and that of Câmpia and Nicolinți in southern Banat (HALAVÁTS 1882, 1886). Based on astronomically tuned logs, the age of the carefully studied Hennersdorf outcrop was given as 10.4–10.3 or 10.5–10.4 Ma ("Zone E;" HARZHAUSER et al. 2004 and HARZHAUSER et al. 2013, respectively). As to the age of the Câmpia and Nicolinți faunas, they are placed stratigraphically above the *Valenciennius*-bearing Ciuchici ("Csukics") outcrop (HALAVÁTS 1886, MARINESCU et al. 1977); therefore, they must be younger than the first appearance datum of *Valenciennius* (9.6–9.7 Ma or slightly older; see CZICZER et al. 2009). There are two lines of evidence, however, which suggest that the Pécs-Danitzpuszta fauna should be older than the Câmpia and Nicolinți mollusks. First, *L.* aff. *boeckhi* from Pécs-Danitzpuszta strongly resembles *L. boeckhi* from Câmpia, but the pentagonal rib cross-section and the straight anterior edge of the valve are less pronounced and less stable patterns in the former. Considering the mode of evolution in several cardiid lineages in Lake Pannon (MÜLLER & MAGYAR 1992, GEARY et al. 2010), it seems reasonable to suppose that the Pécs-Danitzpuszta form might represent the ancestral, less developed state of *L. boeckhi*. Second, the ostracod assemblages from Câmpia contain a lot of newly appearing, "Pontian-type" species (OLTEANU 1989, 2011), whereas the Pécs-Danitzpuszta fauna seems to belong to the older *Amplocypris abscissa* Zone (CSOMA et al. 2021), similarly to the Hennersdorf locality (DANIELOPOL et al. 2011). Considering the above arguments, the age of Unit 8 most probably falls between 10.5 and 10.2 Ma (*Figure 3*).

Unit 9. The littoral fauna of the overlying sand is very similar to the fauna that PAVLOVIĆ (1927, 1928) described from Serbia and to the Pannonian faunas of Burgenland, Austria, both belonging to the upper part of the *Lymnocardium conjungens* Zone (ca. 10.2–9.6 Ma; MAGYAR & GEARY 2012). Considering that the sand directly overlies the at least 10.2 Ma old marl succession, the best estimate for the age of the sand body is 10.2–10.0 Ma (*Figure 3*). The only species in the sand whose known stratigraphic range is not conform with this interpretation is *Dreissenomya dactylus*; it was described from the *"Congeria balatonica* Beds" (*L. decorum* Zone; *Figure* 3) of Lake Balaton, with a first known appearance in the *L. ponticum* Zone. The specimens from Pécs-Danitzpuszta reveal, however, that this form is identical with *D. lithodomiformis* PAVLOVIĆ (1927) from Vrčin; thus, the known life span of *D. dactylus* has to be extended to ca. 10.2–8.1 Ma (see Appendix).

Discussion

There are two peculiarities in the facies order and timing in the Pécs-Danitzpuszta outcrop that make this succession unique: the occurrence of a freshwater fauna close to the top of the Sarmatian, and the timing and development of siliciclastic sedimentation and faunal change in the upper part of the succession.

In the upper part of the Sarmatian stage, a freshwater unit (Unit 2) overlies restricted marine (Unit 1) deposits. This 3-m-thick freshwater interval contains pulmonate snails (lymnaeids and planorbids), hydrobiids, and neritids. No marine or brackish-water forms occur in these layers. The next fossiliferous unit (Unit 3), however, is almost completely devoid of snails (apart from a few hydrobiids), and contains an abundance of various small cardiids. Cardiids have marine origin and they occur in freshwater only extremely rarely. Thus, Unit 3 can be interpreted as having deposited in brackish water. The fauna of Unit 4 contains both pulmonate snails, similar to (and partly identical with?) the species of Unit 2, and some small cardiids, again similar to the species in Unit 3. The common occurrence of originally freshwater pulmonates (lymnaeids and planorbids) and brackish-water cardiids in these lowermost Pannonian layers is a source of controversy in environmental interpretation (SEBE et al. 2020). A possible scenario is that the salinity of the Sarmatian seawater decreased to such an extent that it exerted stress on marine cardiids and, at the same time, allowed freshwater pulmonates to enter the brackish lake. The cardiids responded by adopting r-strategy (e.g., MONTES et al. 2020), whereas the pulmonates took advantage of their ability to survive in waters of up to 10–11 psu salinity (*Stagnicola palustris*, *Radix ovata*, and *Lymnaea stagnalis* are recent examples from the bays of the Åland Islands in the Baltic Sea; CARLSSON 2006). All these faunal changes from Unit 1 to 4 took place under relatively stable conditions in the depositional environment, where clay and limestone layers formed alternately.

The bulk of the Pécs-Danitzpuszta section consists of white or light grey calcareous marls with mollusks that are widespread in the southern part of the Pannonian Basin and can be studied in surface outcrops in the Croatian and Serbian parts of the basin. These marls were deposited in the profundal zone of Lake Pannon, away from the entry points of intense clastic input, under slow sedimentation rates. Deposition of these marls lasted as long as favorable conditions prevailed. The top of the marl was subsequently eroded in the outcrops of Beočin, Serbia (TER BORGH et al. 2013) and Našice, Croatia (VASILIEV et al. 2007); the age of the uppermost layers preserved below the unconformity is 9.9 Ma in Beočin based on magnetostratigraphy (TER BORGH et al. 2013) and less than 8 Ma in Našice based on dinoflagellate stratigraphy (BARANYI, pers. comm.). In contrast, in Pécs-Danitzpuszta, the marl is capped with the 10.5–10.2 Ma old sublittoral *Lymnocardi-*

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um schedelianum Zone (Unit 8); the deposition of the distal marls thus ended here much earlier than in the Croatian and Serbian localities. Finally, the overlying littoral fauna that represents the upper part of the *Lymnocardium conjungens* Zone has been known elsewhere from above the sublittoral *Lymnocardium soproniense* Zone (10.2–8.9 Ma; in Burgenland, MAGYAR et al. (1999) and in the Şimleu Basin, BARTHA et al. 2021), or directly from above pre-Neogene basement (PAVLOVIĆ 1927, 1928), but never from above the *L. schedelianum* Zone. The Pécs-Danitzpuszta faunal succession thus testifies a temporal overlap between the *Congeria banatica* Zone deposited in the profundal depth of Lake Pannon, the *Lymnocardium schedelianum* Zone representing sublittoral sedimentation, and the upper part of the *Lymnocardium conjungens* Zone that formed in shallow, littoral waters of the lake.

Conclusions

Deposition of the Sarmatian–Pannonian succession at the foot of an intrabasinal basement high, the Mecsek Mts, was controlled by local tectonic and sedimentary processes that overprinted the regional trends. As a consequence, this succession offers a unique opportunity to correlate various mollusk assemblages that do not usually occur in a single vertical succession or in close proximity to each other in other parts of the Pannonian Basin.

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Plate I – I. tábla

Sarmatian mollusks from the Pécs-Danitzpuszta exploratory trench (D55 to D37 interval, Units 1 and 2). 1: Dreissenidae sp., D55; 2: Lymnocardiinae sp., D55; 3: Lymnocardiinae sp., D47; 4: ?*Lymnaea* sp., D43; 5: *Radix* cf. *croatica*, D43; 6: *Radix* cf. *croatica*, D40; 7: ?*Lymnaea* sp., D39; 8: Planorbidae sp., D37; 9: *Theodoxus* sp., D37; 10: ?*Lymnaea* sp., thin section, 1N, D39; 11: Limestone densely packed with gastropods, mostly hydrobiids, D43; 12: Gastropod and ostracod segments, thin section, 1N, D40; 13: Hydrobiid snail and ostracod segments, thin section, 1N, D39

*Szarmata puhatestűek a pécs-danitzpusztai kutatóárokból (D55–D37, 1. és 2. szakasz). 1: Dreissenidae sp., D55; 2: Lymnocardiinae sp., D55; 3: Lymnocardiinae sp., D47; 4: ?*Lymnaea *sp., D43; 5:* Radix *cf.* croatica*, D43; 6:* Radix *cf.* croatica*, D40; 7: ?*Lymnaea *sp., D39; 8: Planorbidae sp., D37; 9:* Theodoxus *sp., D37; 10: ?*Lymnaea *sp., vékonycsiszolat, 1N, D39; 11: Csigás mészkő, főként Hydrobia-félékkel, D43; 12: Csiga- és kagylósrák-metszetek, vékonycsiszolat, 1N, D40; 13: Hydrobia-féle csiga- és kagylósrák-metszetek, vékonycsiszolat, 1N, D39*

Plate II – II. tábla

Sarmatian-type mollusks of layer D35 (Unit 3), Pécs-Danitzpuszta, exploratory trench. 1–2: *Inaequicostata* cf. *pia*; 3: ?*Planacardium* sp.; 4: "*Lymnocardium*" cf. *praeponticum*; 5 and 10: *Obsoletiformes* cf. *kaudensis*; 6–8: Lymnocardiinae sp.; 9: *Obsoletiformes* cf. *fischeriformis*; 11–12: *Inaequicostata* cf. *nigra*; 13–15: Cardiid bivalves in thin sections, 1N; 16–20: Hydrobiid snails in thin sections, 1N

Szarmata típusú puhatestűek a D35-ös rétegből (3. szakasz), Pécs-Danitzpuszta, kutatóárok. 1–2: Inaequicostata *cf.* pia*; 3: ?*Planacardium *sp.; 4: "*Lymnocardium*" cf.* praeponticum*; 5 és 10:* Obsoletiformes *cf.* kaudensis*; 6–8: Lymnocardiinae sp.; 9:* Obsoletiformes *cf.* fischeriformis*; 11–12:* Inaequicostata *cf.* nigra*; 13–15: Cardium-féle kagylók vékonycsiszolatokban, 1N; 16–20: Hydrobia-féle csigák vékonycsiszolatokban, 1N*

Plate III – III. tábla

Pannonian mollusks of layer D12 (Unit 4), Pécs-Danitzpuszta, exploratory trench. 1–4: *Congeria* cf. *banatica*; 5: *Congeria* cf. *martonfii*; 6–8: *Congeria* div. sp.; 9: *Congeria* cf. *ramphophora*; 10: *Congeria* cf. *neumayri*; 11–12: "*Lymnocardium*" cf. *praeponticum*; 13–14: *Lymnocardium* sp.; 15: "*Lymnocardium*" cf. *plicataeformis*; 16: Ostracod valve and quartz grains in thin section, 1N; 17–19: *Radix croatica*; 20: Hydrobiidae? sp.

Pannóniai puhatestűek a D12-es rétegből (4. szakasz), Pécs-Danitzpuszta, kutatóárok. 1–4: Congeria *cf.* banatica*; 5:* Congeria *cf.* martonfii*; 6–8:* Congeria *div. sp.; 9:* Congeria *cf.* ramphophora*; 10:* Congeria *cf.* neumayri*; 11–12: "*Lymnocardium*" cf.* praeponticum*; 13–14:* Lymnocardium *sp.; 15: "*Lymnocardium*" cf.* plicataeformis*; 16: Kagylósrák teknő és kvarcszemcsék vékonycsiszolatban, 1N; 17–19:* Radix croatica*; 20: Hydrobiidae? sp.*

Plate IV – IV. tábla

Pannonian mollusks of the white marls (D7 to D215 interval, Units 5–7), Pécs-Danitzpuszta sand pit. 1–5: *Paradacna abichi*; 6–9: Lymnocardiinae sp.; 10–11: *"Lymnocardium" margaritaceum*; 12: *Velutinopsis* sp.; 13: *Micromelania striata; 14: Orygoceras brusinai; 15: Unio* cf. *atavus; 16: Melanopsis fossilis*

Pannóniai puhatestűek a fehér márgából (D7–D215, 5–7. szakasz), pécs-danitzpusztai homokbánya. 1–5: Paradacna abichi*; 6–9: Lymnocardiinae sp.; 10–11:* "Lymnocardium" margaritaceum*; 12:* Velutinopsis *sp.; 13:* Micromelania striata*; 14:* Orygoceras brusinai*; 15:* Unio *cf.* atavus*; 16:* Melanopsis fossilis

Plate V – V. tábla

Pannonian mollusks of the silts (D219 to D226 interval, Unit 8), Pécs-Danitzpuszta sand pit. 1: *Congeria partschi firmocarinata*; 2–3: *Congeria zsigmondyi*; 4–7: *Dreissenomya primiformis*; 8–11: *Lymnocardium* aff. *boeckhi*; 12–15: *Lymnocardium winkleri*

Pannóniai puhatestűek az aleurolitból (D219–D226, 8. szakasz), pécs-danitzpusztai homokbánya. 1: Congeria partschi firmocarinata*; 2–3:* Congeria zsigmondyi*; 4–7:* Dreissenomya primiformis*; 8–11:* Lymnocardium *aff.* boeckhi*; 12–15:* Lymnocardium winkleri

Plate VI – VI. tábla

Pannonian mollusks of the silts (D219 to D226 interval, Unit 8), Pécs-Danitzpuszta sand pit. 1–2: *Lymnocardium schedelianum*; 3–4: "*Lymnocardium*" *carnuntinum*; 5–7: "*Lymnocardium*" *tegulatum*; 8: "*Lymnocardium*" aff. *danicici*; 9: "*Lymnocardium*" cf. *proximum*; 10–11: *Paradacna* sp.; 12: "*Lymnocardium*" cf. *asperocostatum*; 13: "*Pontalmyra*" *otiophora*; 14 and 16–18: Lymnocardiinae sp.; 15: ?*Pseudocatillus* sp.; 19: *Caladacna* aff. *steindachneri*; 20: ?*Phyllocardium* sp.; 21: *Melanopsis austriaca*; 22: *Gyraulus tenuistriatus*

Pannóniai puhatestűek az aleurolitból (D219–D226, 8. szakasz), pécs-danitzpusztai homokbánya. 1–2: Lymnocardium schedelianum*; 3–4: "*Lymnocardium*"* carnuntinum*; 5–7:* "Lymnocardium" tegulatum*; 8:* "Lymnocardium" *aff.* danicici*; 9:* "Lymnocardium" *cf.* proximum*; 10–11:* Paradacna *sp.; 12:* "Lymnocardium" *cf.* asperocostatum*; 13:* "Pontalmyra" otiophora*; 14 and 16–18: Lymnocardiinae sp.; 15: ?*Pseudocatillus *sp.; 19:* Caladacna *aff.* steindachneri*; 20: ?*Phyllocardium *sp.; 21:* Melanopsis austriaca*; 22:* Gyraulus tenuistriatus

Plate VII – VII. tábla

Pannonian mollusks of the limonitic sand (Layer D227, Unit 9), Pécs-Danitzpuszta sand pit. 1–3: *Congeria hemiptycha*; 4–5: *Congeria ungulacaprae*; 6: *Congeria partschi*

Pannóniai puhatestűek a limonitos homokból (D227-es réteg, 9. szakasz), pécs-danitzpusztai homokbánya. 1–3: Congeria hemiptycha*; 4–5:* Congeria ungulacaprae*; 6:* Congeria partschi

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Plate VIII – VIII. tábla

Pannonian mollusks of the limonitic sand (Layer D227, Unit 9), Pécs-Danitzpuszta sand pit. 1: *Congeria balatonica*; 2–3: *Congeria partschi*; 4: *Dreissenomya dactylus*; 5: "*Lymnocardium*" aff. *danicici*; 6–8: *Lymnocardium* cf. *tucani*; 9: *Lymnocardium* cf. *conjungens*; 10: *Lymnocardium schedelianum*; 11: *Phyllocardium complanatum*

Pannóniai puhatestűek a limonitos homokból (D227-es réteg, 9. szakasz), pécs-danitzpusztai homokbánya. 1: Congeria balatonica; *2–3:* Congeria partschi; *4:* Dreissenomya dactylus; *5:* "Lymnocardium" *aff.* danicici; *6–8:* Lymnocardium *cf.* tucani; *9:* Lymnocardium *cf.* conjungens; *10:* Lymnocardium schedelianum; *11:* Phyllocardium complanatum

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Plate I – I. tábla

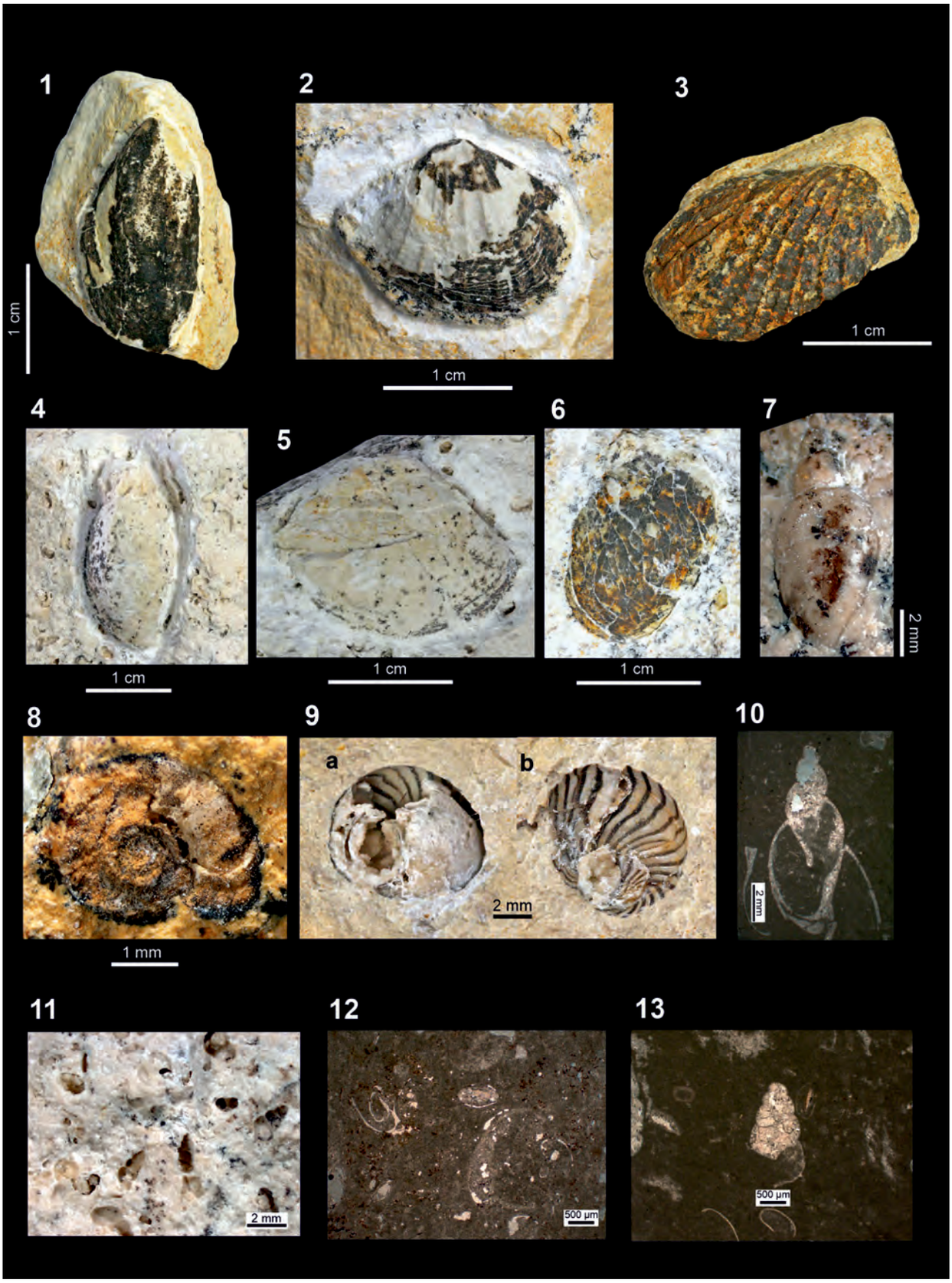

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Plate II – II. tábla

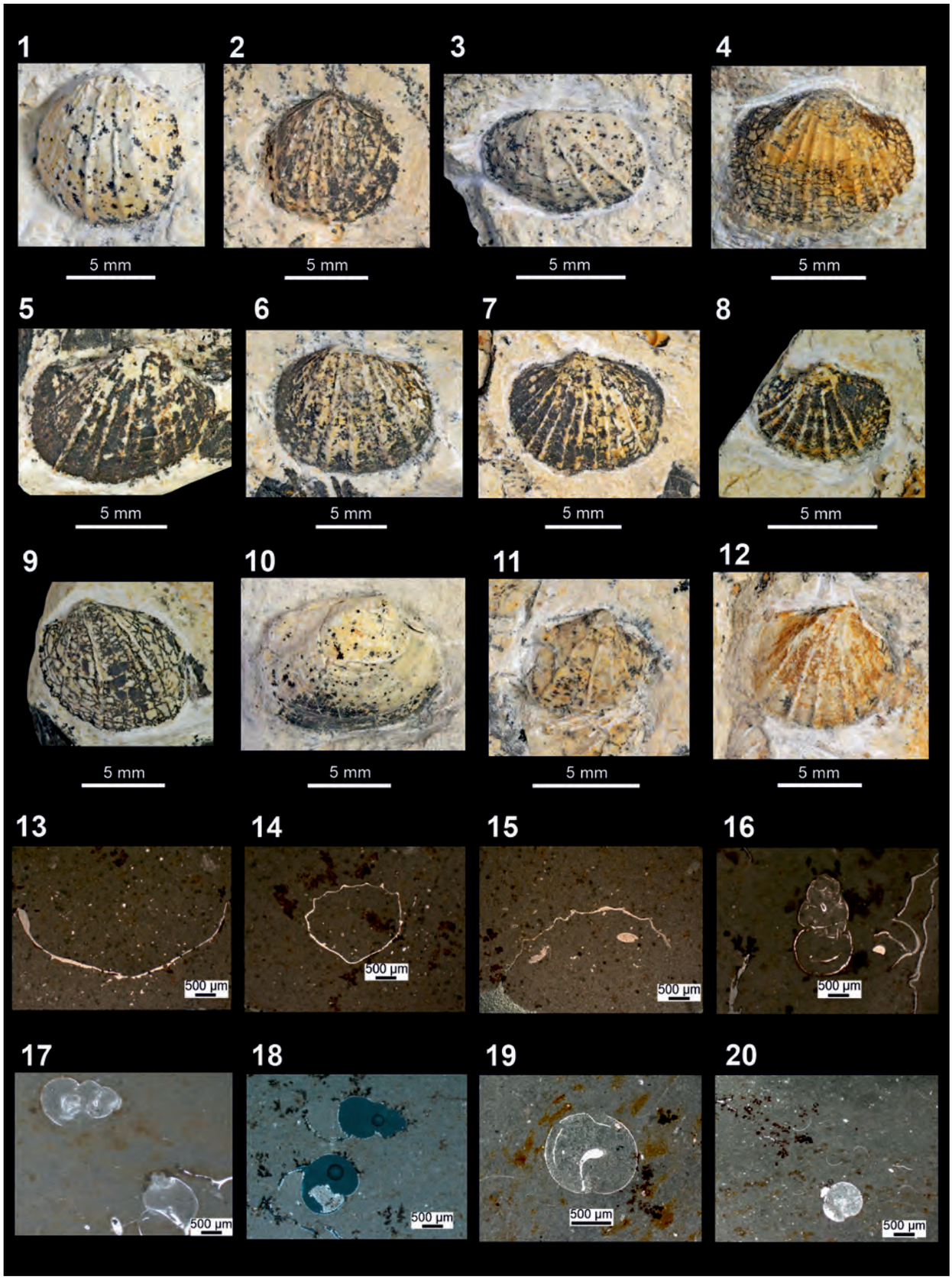

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Plate III – III. tábla

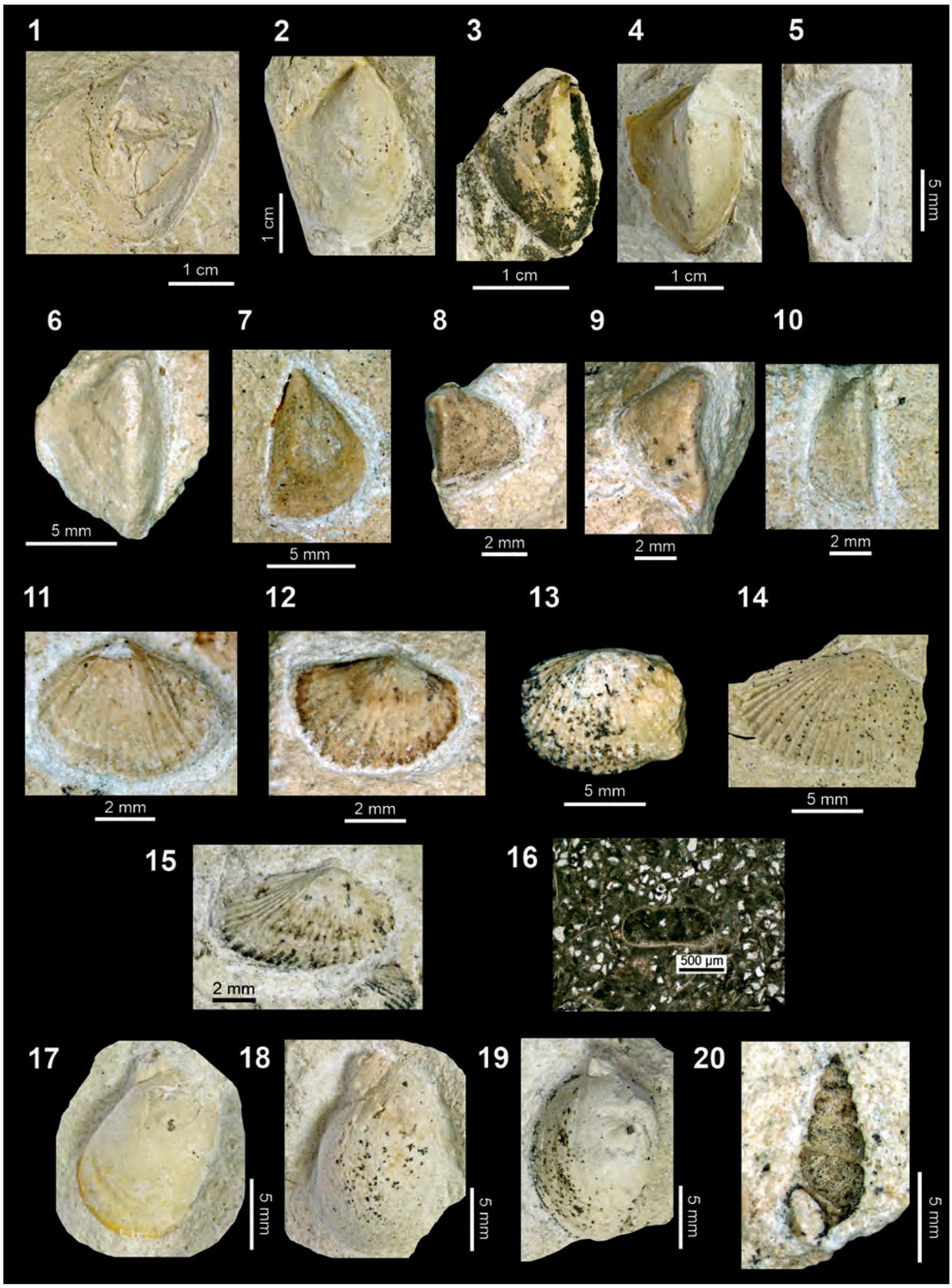

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Plate IV – IV. tábla

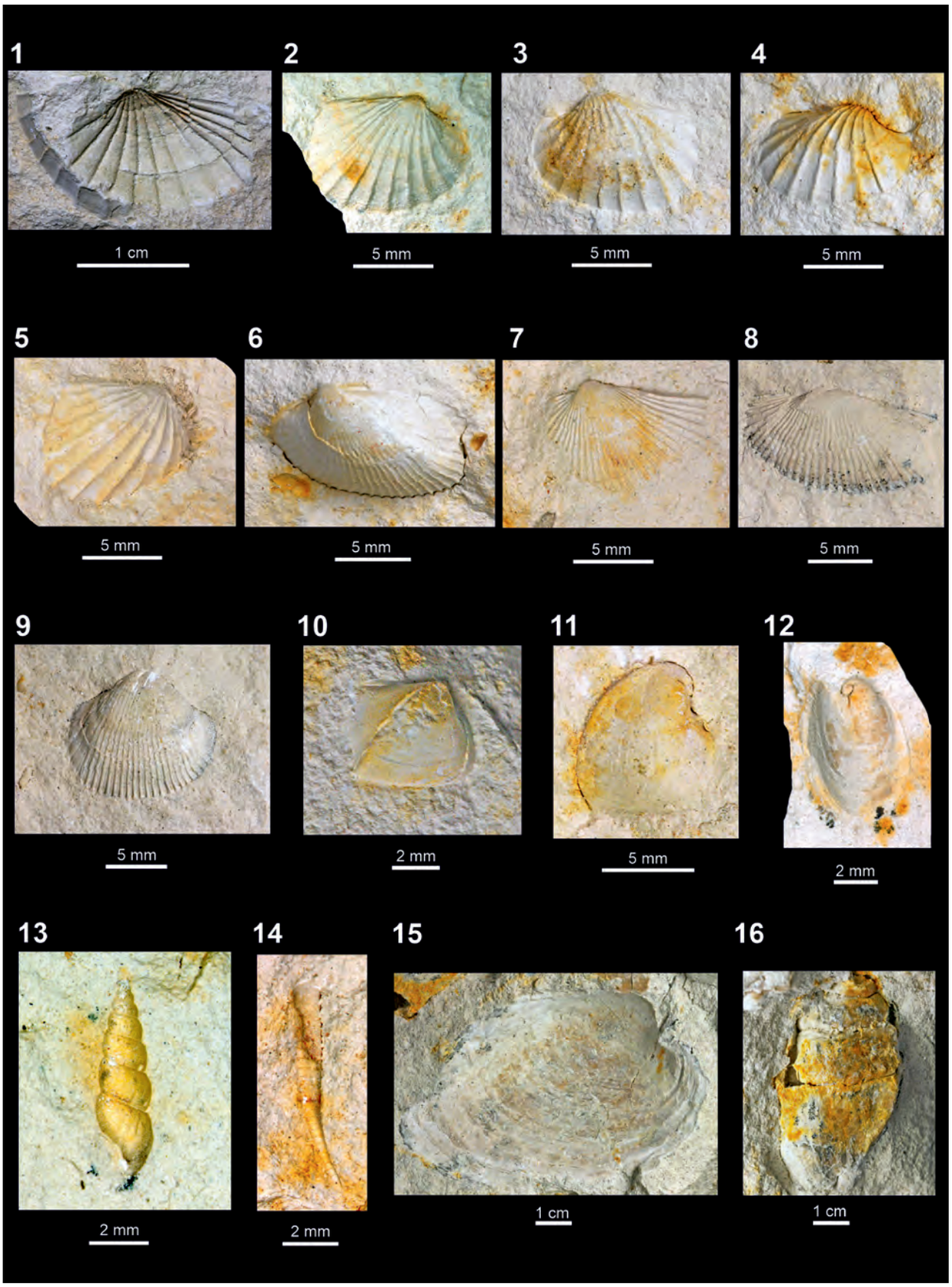

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Plate V – V. tábla

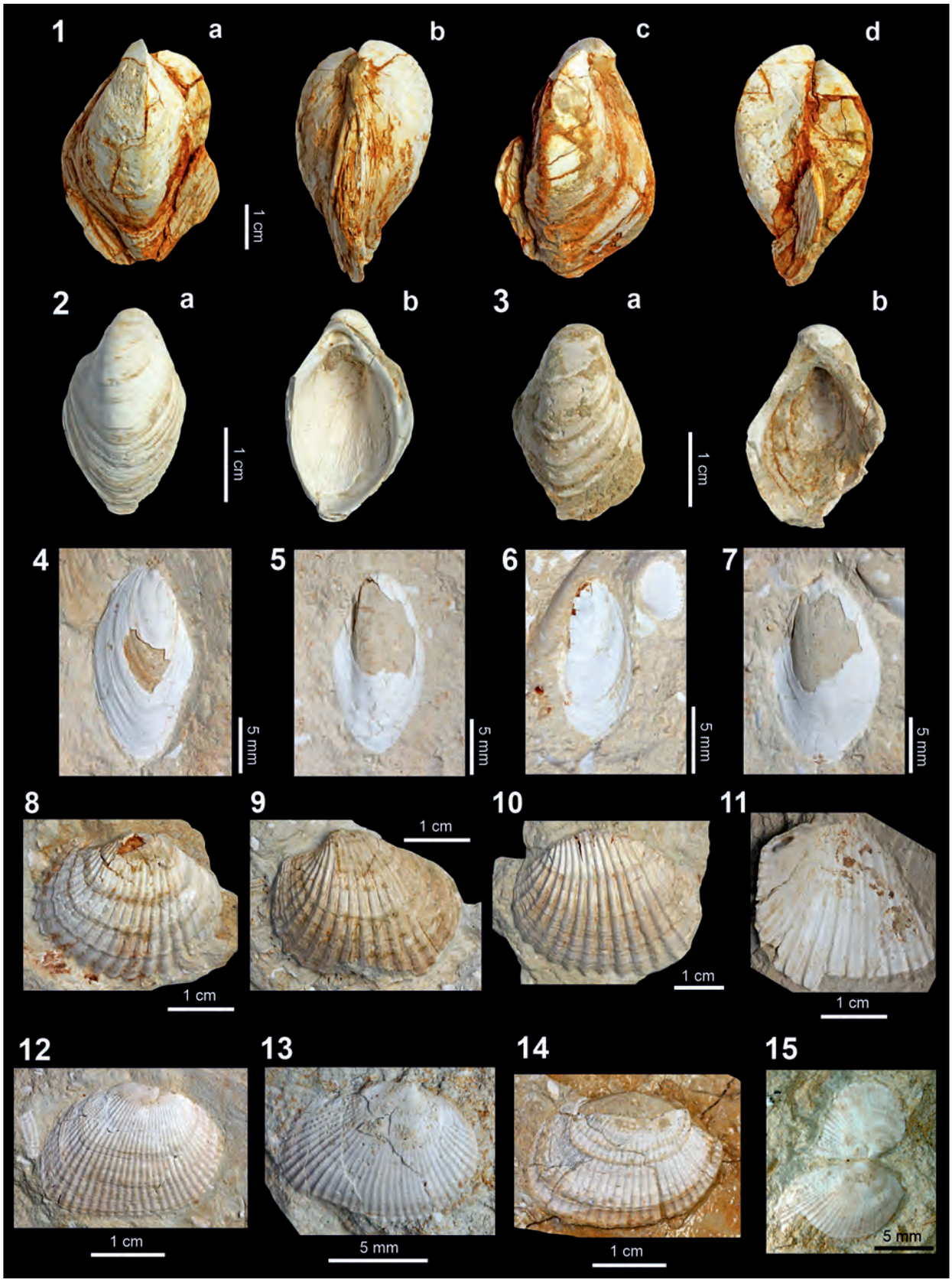

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Plate VI – VI. tábla

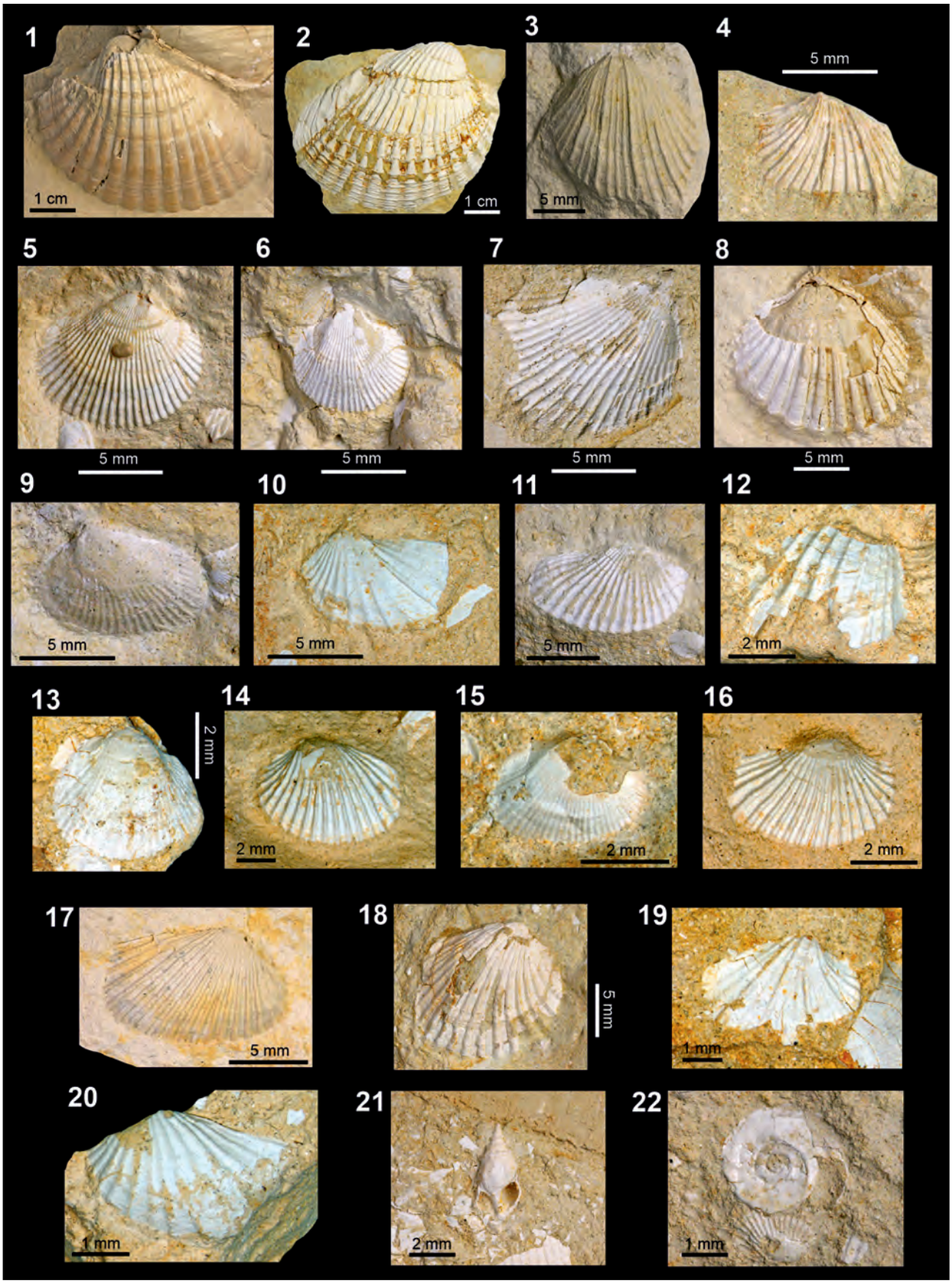

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Plate VII – VII. tábla

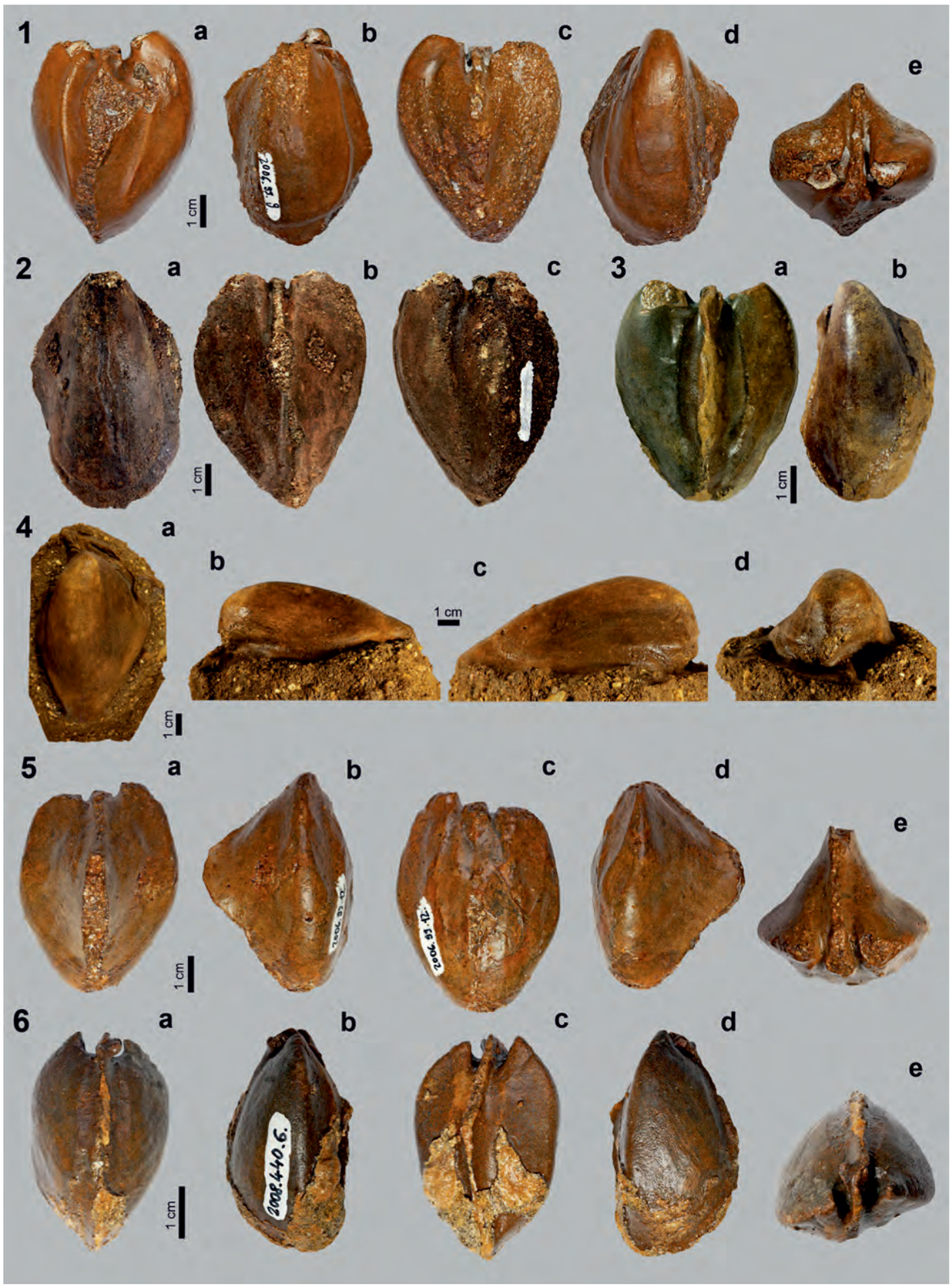

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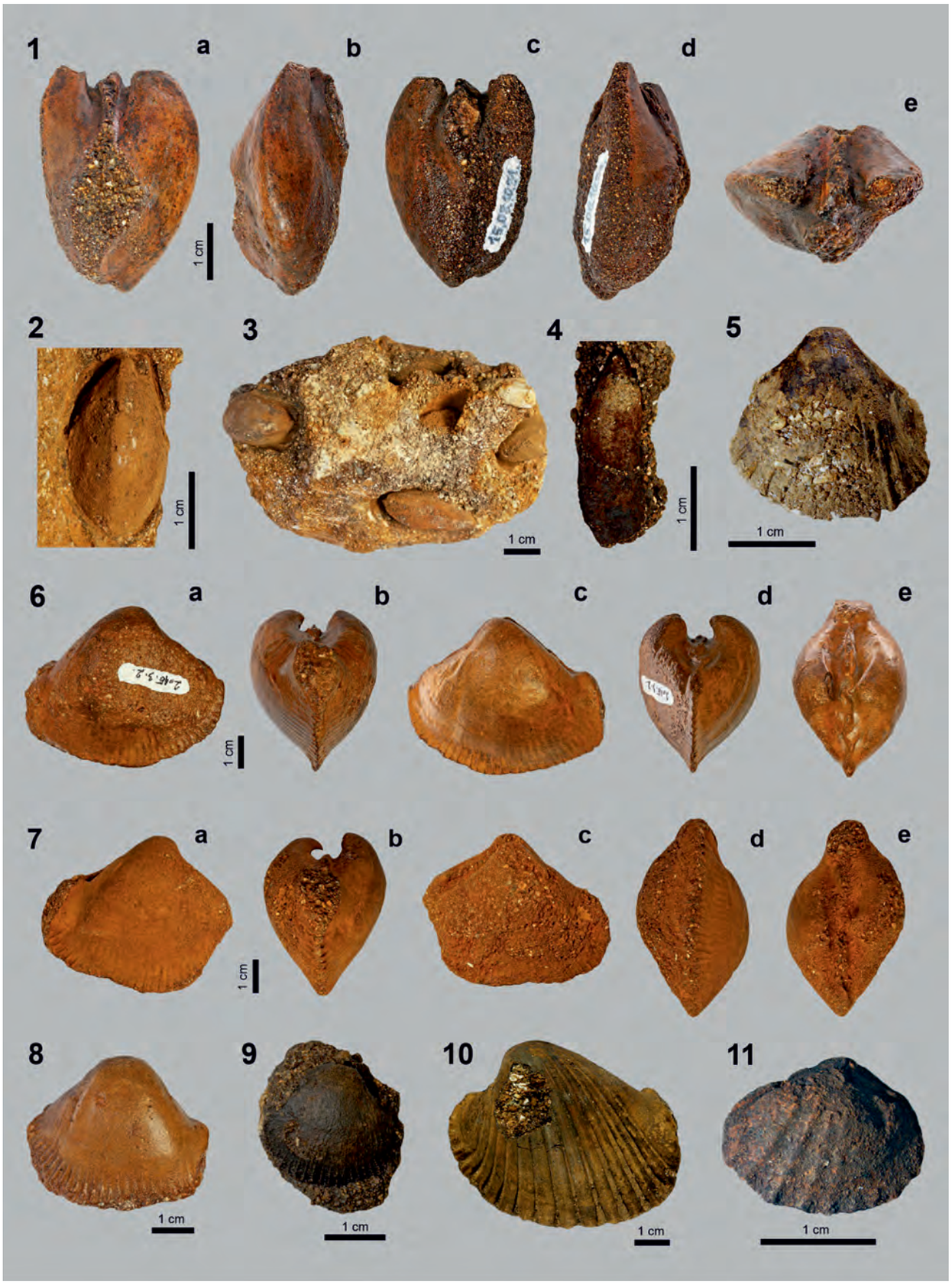
Plate VIII – VIII. tábla



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Appendix

Systematic Palaeontology

Our approach to taxonomic identifications is outlined in chapter *Material and methods*.

Bivalvia LINNAEUS, 1758
Cardiidae LAMARCK, 1809
Lymnocardiinae STOLICZKA, 1870
Genus *Lymnocardium* STOLICZKA, 1870
Type species: *Cardium haueri* M. HÖRNES, 1862; original designation

"*Lymnocardium*" *carnuntinum* (M. HÖRNES, 1862) (Plate VI, figs 3–4)

*1862 *Cardium Carnuntinum* M. HÖRNES, p. 204, pl. 30, fig. 2.
1882 *Cardium* (*Adacna*) *Suessi* BARB. – HALAVÁTS, p. 150, pl. 14, figs 6–8.
1886a *Cardium* (*Adacna*) *pseudo-Suessi* HALAVÁTS, p. 127, pl. 6, figs 1–5. [new synonym]
1886b *Cardium* (*Adacna*) *pseudo-Suessi* HAL. – HALAVÁTS, p. 128, pl. 25, figs 3–4.
non 1899 *Limnocardium pseudo-Suessi* HÁL. – GORJANOVIĆ-KRAMBERGER, p. 236.
1953 *Limnocardium carnuntinum* (PARTSCH, HOERNES) – PAPP, p. 199, pl. 23, figs 17–19; pl. 24, Fig. 5.
1959 *Limnocardium pseudosuessi* HALAVÁTS – MILETIĆ-SPAJIĆ, pl. 8, figs 9–10.
1966 *Limnocardium carnuntinum* PARTSCH – CHIVU et al., p. 246, pl. 2, fig. 5.
?1968 *Limnocardium pseudosuessi* HALAVÁTS – SAGATOVICI, pl. 14, fig. 4.
1983 *Limnocardium pseudosuessi* (HALAV.) – KORPÁS-HÓDI, p. 145, pl. 1, fig. 3.
1985 *Limnocardium pseudosuessi* (HALAVÁTS) – KORPÁS-HÓDI in JÁMBOR et al., p. 227, pl. 19, fig. 2.
1985 *Limnocardium carnuntinum* (PARTSCH) – PAPP, p. 307, pl. 42, figs 8–10.
2003 *Lymnocardium* (*Lymnocardium*) *carnuntinum* (HÖRNES) – SCHULTZ, p. 616, pl. 87, figs 9–10; pl. 88, fig. 7.
2008 *Lymnocardium pseudosuessi* (HALAVÁTS) – CZICZER et al., pl. 30 figs 5a–b.

Type locality: Vienna, 10th district (Inzersdorf, Wienerberg)
Type material: Syntypes: NHMW, 1851/II/158
Remarks: Neither the description nor the illustrations by HÖRNES (1862) refer to the distinct primary and secondary radial ribs of this species. HALAVÁTS (1886) recognized *L. pseudosuessi* as a new species based on this characteristic rib pattern. A comparison of the syntypes of *L. pseudosuessi* with those of *L. carnuntinum*, however, unanimously shows that they represent the same species.

L. carnuntinum is widely known from the marginal parts of the Pannonian Basin System, such as the Vienna Basin in Austria, the Avala Mts. and Morava Valley in Serbia, the southern Banat, Oaş, and Şimleu Basins in western Romania, and in the margins of the Transdanubian Range in Hungary.

Stratigraphic range and age: The oldest known dated occurrence of the species was reported from borehole Lajoskomárom (Lk)–1, 585.3–572 m (KORPÁS-HÓDI in JÁMBOR et al. 1985), from the *Spiniferites oblongus* Zone (SÜTŐ-SZENTAI in JÁMBOR et al. 1985), which is thought to be ca. 11.2–10.8 Ma (MAGYAR & GEARY 2012). The latest occurrences are known from the northwestern foreland of the Transdanubian Range, dated as 9.4–8.9 Ma (Szák Fm.; KORPÁS-HÓDI 1983; CZICZER et al. 2009).

Lymnocardium schedelianum (FUCHS, 1870) (Plate VI, figs 1–2; Plate VIII, fig. 10)

1862 *Cardium apertum* MÜNSTER – M. HÖRNES, p. 201, pl. 29, figs 5–6.
*1870 *Cardium Schedelianum* FUCHS, p. 354.
non 1884 *Adacna Schedeliana* PARTSCH – BRUSINA, p. 151, pl. 28, fig. 43.
1903 *Limnocardium Schedelianum* PARTSCH – ANDRUSOV, p. 39, pl. 3, figs 18–21.
non 1943 *Limnocardium schedelianum* PARTSCH – GILLET, p. 58, pl. 5, fig. 11.
?1943 *Limnocardium schedelianum* PARTSCH var. *sarbiense* Gillet, p. 59, pl. 5, fig. 12.
1953 *Limnocardium schedelianum* (PARTSCH) – PAPP, p. 198, pl. 24, fig. 3.
?1966 *Limnocardium schedelianum* PARTSCH – CHIVU et al., p. 246, pl. 2, fig. 7.
1967 *Limnocardium schedelianum* (PARTSCH) – SPAJIĆ, p. 115, pl. 2, figs 1–5.
1980 *Limnocardium schedelianum* PARTSCH – STEVANOVIĆ, pl. 4, fig. 13.
1980 *Limnocardium schedelianum* (PARTSCH) – LUEGER, pl. 3, fig. 1.
1983 *Limnocardium schedelianum* (PARTSCH) – NICORICI & KARÁCSONYI, pl. 3, fig. 2.
1985 *Limnocardium schedelianum* (PARTSCH) – PAPP, p. 307, pl. 42, fig. 11.
1988 *Lymnocardium* cf. *soproniense* VITÁLIS – MAGYAR, p. 212, pl. 1, fig. 4.
1995 *Lymnocardium schedelianum* (BRUSINA) – FORDINÁL, p. 32, pl. 5, fig. 2.

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1999 *Lymnocardium schedelianum* (PARTSCH) – MAGYAR et al., p. 672, pl. 1, fig. E.
2003 *Lymnocardium* (*Lymnocardium*) *schedelianum* (FUCHS) – SCHULTZ, p. 626, pl. 89, figs 10, 12.

Type locality: Brunn am Gebirge (FUCHS 1870)
Type material: Syntypes: NHMW, 1846/37/668

Remarks: In the 19th century, this species was confused with *Lymnocardium apertum* (MÜNSTER) (see HÖRNES 1862; FUCHS 1870). A possible source of this confusion was that a typical *L. schedelianum* specimen was labelled in the old collection of the Natural History Museum Vienna as coming from Tihany, where *L. apertum* is a common species. As the recent revision of *L. schedelianum* (see SCHULTZ 2003) maintained the notion of HÖRNES (1862), FUCHS (1870), and ANDRUSOV (1903) that this species occurs in Tihany, we find it important to emphasize that repeated exhaustive collections in Tihany (HALAVÁTS 1902, LŐRENTHEY 1905, VITÁLIS 1908, BARTHA 1959, MÜLLER & SZÓNOKY 1990, SZTANÓ et al. 2013) failed to yield *L. schedelianum* specimens from any outcrop of the region. To our best understanding, this species evolved into other forms and thus went extinct by the time when the Tihany beds were deposited (MAGYAR et al. 2016). Therefore, we argue that the Tihany specimen of *L. schedelianum* in the Vienna museum collection was mislabeled.

In fact, *L. schedelianum* can be easily distinguished from *L. apertum* by its more elongated outline, higher number of ribs, and significantly larger size. It shows, however, very close resemblance to *L. soproniense* VITÁLIS and *L. variocostatum* VITÁLIS, which can be considered as its descendants (MAGYAR et al. 2016).

Lymnocardium schedelianum is a widely distributed species in the Pannonian Basin: it occurs in the Vienna Basin in Austria and the Czech Republic, in the Danube Basin in Austria, Slovakia, and Hungary, in the northern and eastern margins of the Great Hungarian Plain in Hungary and Romania, south of the Danube and the Sava in Serbia and Bosnia, along the Sava in Slovenia, and in Burgenland in Austria. *Lymnocardium schedelianum* is recovered from both sublittoral clay layers and littoral sand deposits.

Stratigraphic range: Lymnocardium schedelianum and *L. conjungens* Zones (?11.0–9.6 Ma). According to PAPP (1953), the oldest occurrences of the species belong to "Zone D" in the Vienna Basin (10.6–10.4 Ma according to HARZHAUSER et al. 2004). The youngest specimens in the sublittoral deposits are ca. 10.2 Ma and ca. 9.6 Ma old in the littoral deposits (MAGYAR et al. 2016).

Lymnocardium winkleri (HALAVÁTS, 1882) (Plate V, figs 12–15)

*1882 *Cardium* (*Adacna*) *Winkleri* nov. form. HALAVÁTS, p. 153, pl. 15, figs 3–4.
1883 *Cardium* (*Adacna*) *Winkleri* nov. form. HALAVÁTS, p. 169, pl. 15, figs 3–4.
1959 *Limnocardium winkleri* HALAVÁTS – MILETIĆ-SPAJIĆ, pl. 8, fig. 14.
?1962 *Limnocardium winkleri* HALAVÁTS – SZÉLES, p. 56, pl. 3, fig. 4.
?1971 *Limnocardium winkleri* HALAVÁTS – SZÉLES, p. 327, pl. 1, fig. 8.
(?)1977 *Pseudocatillus* sp. – V. LUBENESCU & D. LUBENESCU, pl. 3, figs 17–18.
(?)1977 (?) *Pseudocatillus* sp. – V. LUBENESCU & D. LUBENESCU, pl. 4, fig. 8.
1978 *Limnocardium lukae* STEV. – STEVANOVIĆ, p. 341.
1980 *Limnocardium Winkleri lukae* n. subsp. STEVANOVIĆ, p. 128, 139, pl. 3, figs 19–22. [new synonym]
?1980 *Limnocardium winkleri* HAL. – STEVANOVIĆ, pl. 4, fig. 11.
?1983 *Limnocardium winkleri* (HALAV.) – KORPÁS-HÓDI, p. 145, pl. 1, fig. 4.
?1985 *Limnocardium winkleri lukae* STEV. – KORPÁS-HÓDI in JÁMBOR et al., p. 227, pl. 19, fig. 3.
1987 *Limnocardium winkleri lukae* STEVANOVIĆ – JÁMBOR et al., pl. 4, fig. 3.
?1992 *Limnocardium winkleri lukae* STEV. – KORPÁS-HÓDI, pl. 1, fig. 4.
?1995 *Lymnocardium* aff. *winkleri* (HALAVÁTS) – MAGYAR, fig. 4F.

Type locality: Câmpia (Langenfeld, Néramező) (HALAVÁTS 1882)
Type material: Syntypes: MBFSZ, Pl. 6379

Remarks: Lymnocardium winkleri represents the early stage of the probably anagenetic evolutionary lineage that leads to *L. majeri* (HÖRNES) then to *L. peregrinum* (in the Eastern Paratethys). For this lineage EBERZIN (1947) erected the subgenus *Arpadicardium*. Distinction of the subspecies *L. winkleri lukae* (STEVANOVIĆ, 1980) is probably not justified, because neither the description nor the illustration of this subspecies contained any obvious diagnostic feature by which it could be distinguished from *L. winkleri*. Therefore, here we treat *L. winkleri lukae* as a junior synonym of *L. winkleri*.

Stratigraphic range: The stratigraphic range of the species is weakly constrained. The oldest dated occurrence is known from the Lajoskomárom (Lk)–1 borehole, 577.6 m, belonging to the *Spiniferites oblongus* Zone (ca. 10.8–11.2 Ma) (JÁMBOR et al. 1985). Stratigraphically upward, the transition to *L. majeri* is gradual, and no criterion has been suggested so far for the distinction between the two chronospecies.

Dreissenidae GRAY, 1840
Genus *Congeria* PARTSCH, 1835
Type species: *Congeria subglobosa* PARTSCH, 1835; subsequent designation, STOLICZKA, 1870

Congeria hemiptycha BRUSINA, 1902 (Plate VII, figs 1–3)

1892 *Congeria subglobosa* PARTSCH – BRUSINA, p. 180.
v *1902 *Congeria subglobosa hemiptycha* BRUS. – BRUSINA, pl. 20, figs 1–3.
1927 *Congeria Pančići* nov. spec. PAVLOVIĆ, p. 16, pl. 2, figs 5–7; pl. 3, figs 1–3. [new synonym]
1928 *Congeria Pančići* nov. spec. PAVLOVIĆ, p. 11, pl. 2, figs 5–7; pl. 3, figs 1–3.
1939 *Congeria subglobosa hemiptycha* BRUS. – KOLLMANN, p. 55.
1944 *Congeria hemiptycha* BRUSINA – JEKELIUS, p. 146, pl. 62, fig. 4.
1952 *Congeria pancici pancici* PAVLOVIĆ – SAUERZOPF, p. 4.
1952 *Congeria pancici hemiptycha* BRUSINA – SAUERZOPF, p. 4.
1952 *Congeria pancici longiconcha* n. ssp. SAUERZOPF, p. 11, pl. 1, figs 3–4. [new synonym]

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1953 *Congeria pancici pancici* PAVLOVIĆ – PAPP, p. 176, pl. 17, figs 1–2.
1959 *Congeria subglobosa mlavica* n. ssp. MILETIĆ-SPAJIĆ, p. 108, 121, pl. 5, fig. 1. [new synonym]
1959 *Congeria* cf. *pancici* PAVLOVIĆ – MILETIĆ-SPAJIĆ, pl. 5, fig. 2.
1968 *Congeria subglobosa longitesta* PAPP – SAGATOVICI, pl. 12, fig. 27; pl. 13, figs 1–2.
1974 *Congeria hemiptycha* BRUSINA – MILAN et al., p. 32.
1980 *Congeria pancici* – LUEGER, pl. 2, fig. 1.
1980 *Congeria* sp. – LUEGER, p. 111, pl. 2, fig. 4.
1981 *Congeria pancici pancici* PAVLOVIĆ – V. LUBENESCU, p. 167, pl. 10, fig. 1.
1981 *Congeria subglobosa hemiptycha* BRUSINA – V. LUBENESCU, p. 170–171, pl. 10, fig. 3.
1983 *Congeria pancici pancici* PAVLOVIĆ – NICORICI & KARÁCSONYI, p. 231, pl. 1, figs 1–2.
1985 *Congeria pancici* PAVLOVIĆ – PAPP, p. 301, pl. 39, figs 1–2.
v 1988 *Congeria* sp. – MAGYAR, p. 212, pl. 1, fig. 1.
2003 *Congeria pancici pancici* PAVLOVIĆ – SCHULTZ, p. 811, pl. 110, figs 1–3.
2003 *Congeria pancici longiconcha* SAUERZOPF – SCHULTZ, p. 812, fig. 20.

Type locality: Zagreb–Markuševec (BRUSINA 1902)

Type material: Syntypes: HPM, 2787-433, 392.1-4, 393.I-II

Remarks: The "holotype" designation by MILAN et al. (1974) cannot be accepted as valid lectotype designation according to ICZN Article 74.5. The "stratum typicum" is also erroneously given by MILAN et al. (1974) as "marls;" the species occurred in sand (see BRUSINA 1892).

The only difference between the type specimens of *C. hemiptycha* BRUSINA and *C. pancici* PAVLOVIĆ is that the former has a corrugated posterior field. The presence and degree of corrugation, however, is highly variable among the specimens, and can hardly be considered a diagnostic feature.

Congeria hemiptycha occurs in littoral sands in the Vienna Basin (Austria), Kál Basin (Hungary), Oaş and Şimleu Basins, Banat region and Transylvanian Basin (Romania), Avala Mts. (Serbia), Medvednica Mts. (Croatia), and several locations in Burgenland (Austria).

Stratigraphic range and age: According to PAPP (1985), this species occurs in "Zone D" (very rarely) and "Zone E" (common and typical). SCHULTZ (2003), however, listed a lot of localities belonging to "Zone D" and some even to "Zone C". Following the age model of HARZHAUSER et al. (2004), *C. hemiptycha* was already present at ca. 10.6 Ma (beginning of "Chron D"), but its first appearance and ancestry remains vague. The youngest occurrences belong to the upper part of the *Lymnocardium conjungens* Zone and thus can be as young as ca. 9.6 Ma. After that, *C. hemiptycha* disappeared from the fossil record so the lineage probably went extinct.

Congeria partschi firmocarinata PAPP, 1953
(Plate V, fig. 1)

*1953 *Congeria partschi firmocarinata* n. ssp. PAPP, p. 174, pl. 16, fig. 7.
1977 *Congeria partschi firmocarinata* PAPP – V. LUBENESCU & D. LUBENESCU, pl. 2, figs 6–7.
? 1980 *Congeria partschi firmocarinata* PAPP – LUEGER, p. 118, 121, pl. 2, figs 2–3.
1985 *Congeria partschi firmocarinata* – PAPP, p. 296, pl. 38, fig. 3.
2005 *Congeria partschi firmocarinata* PAPP – SCHULTZ, p. 815, pl. 110, figs 4–5; pl. 111, fig. 4.

Type locality: Hennersdorf (PAPP 1953)

Type material: Holotype: NHMW, 787/1969, Coll. PAPP 632

Remarks: Although our specimens were heavily deformed by lithostatic pressure, it can be established that the Pécs-Danitzpuszta and Hennersdorf specimens are morphologically indistinguishable.

Stratigraphic range and age: According to PAPP (1953, 1985), this species is restricted to "Zone E", dated as 10.4–10.1 Ma by HARZHAUSER et al. (2004).

Congeria zsigmondyi HALAVÁTS, 1882
(Plate V, figs 2–3)

*1882 *Congeria Zsigmondyi* n. form. HALAVÁTS, p. 154, pl. 15, figs 7–10.
1883 *Congeria Zsigmondyi* n. form. HALAVÁTS, p. 171, pl. 15, figs 7–10.
1897 *Congeria zsigmondyi* – ANDRUSOV, p. 214, pl. 11, figs 21–26.
1944 *Congeria zsigmondyi* HALAVÁTS – JEKELIUS, p. 144, pl. 60, figs 4–7, excl. f. 8.
1953 *Congeria zsigmondyi* HALAVÁTS – PAPP, p. 175, pl. 16, figs 5–6.
1966 *Congeria zsigmondyi* HAL. – BARTHA, pl. 3, figs 1–3.
?1971 *Congeria szigmondyi* [sic!] HALAVÁTS – GRÄF et al., text-fig. 3: 3, pl. 1, figs 2–6, 10–11.
1971 *Congeria zsigmondyi* HALAVÁTS – BARTHA in GÓCZÁN & BENKŐ, pl. 25, figs 1–3.
?1981 *Congeria zsigmondyi* HALAVÁTS – V. LUBENESCU, pp. 164–165, pl. 9, fig. 5.
1985 *Congeria zsigmondyi* HALAVÁTS – PAPP, p. 297, pl. 38, figs 7–10.
1999 *Congeria zsigmondyi* – MAGYAR, p. 11, fig. 2.
2001 *Congeria zsigmondyi* HALAVÁTS – GULYÁS, fig. 7.
2004 *Congeria zsigmondyi* – HARZHAUSER & MANDIC, p. 342, fig. 9/2.
2005 *Congeria zsigmondyi* HALAVÁTS 1882 – SCHULTZ, p. 828, pl. 113, figs 2–3.

Type locality: Câmpia (Langenfeld, Néramező) (HALAVÁTS 1882)

Type material: Syntypes: MBFSZ, Pl. 1

Remarks: This species is commonly reported from various parts of the Pannonian region: Vienna Basin in Austria, NW Romania, Transylvanian Basin, southern Banat, and Mecsek Mts in Hungary.

Stratigraphic range and age: According to PAPP (1985), this species is restricted to clays of "Zone E." SCHULTZ (2005), however, lists a few localities conditionally assigned to "Zone D." The Soceni locality is also considered older than Zone "E," but the occurrence of *C. zsigmondyi* in Soceni is questionable, because three of the four depicted specimens in JEKELIUS (1944) are from Câmpia, and the only specimen depicted from Soceni probably represents another species. On the other hand, the type locality of the species is most probably somewhat

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younger than "Zone E" in the Vienna Basin. Thus, the age interval of *C. zsigmondyi* can be estimated as 10.6–9.6 Ma.

Genus *Dreissenomya* FUCHS, 1870
Type species: *Congeria schroeckingeri* FUCHS, 1870; original designation

Dreissenomya (Sinucongeria) dactylus (BRUSINA, 1894) (Plate VIII, fig. 4)

1894 *Congeria dactylus* n. sp. BRUSINA, p. 243.
1900 *Congeria dactylus* BRUSINA – ANDRUSOV, p. 80, 125.
1902 *Congeria dactylus* BRUS. – BRUSINA, pl. 20, figs 9–13 (14–17?).
1915 *Dreyssensiomya* [sic!] *dactylus* BRUS – VITÁLIS, p. 334, pl. 2, figs 2–3.
1927 *Dreissensiomya lithodomiformis* nov. spec. PAVLOVIĆ, p. 24, pl. 4, figs 1–2. [new synonym]
1928 *Dreissensiomya lithodomiformis* nov. spec. PAVLOVIĆ, p. 17, pl. 4, figs 1–2.
1974 *Congeria dactylus* BRUSINA – MILAN et al., p. 26.
1990 *Congeria dactylus* BRUSINA – BASCH, p. 555, pl. 3, fig. 3.
1992 *Dreissenomya* (*Sinucongeria*) *dactyla* (BRUSINA) – BASCH & ŽAGAR-SAKAČ, p. 27, pl. 17, figs 3–6.
2005 *Mytilopsis* cf. *scrobiculata scrobiculata* (ANDRUSOV) – SCHULTZ, p. 798, pl. 105, figs 9–10.
2015 *Dreissenomya dactylus* (BRUSINA) – KATONA et al., p. 149, pl. 11, fig. 8.

Type locality: "between Balatonkenese and Siófok" (BRUSINA 1894), i.e., south of Balatonkenese

Type material: Lectotype: HPM, 2789-435 (subsequently designated by MILAN et al. 1974)

Remarks: BRUSINA (1894) characterized his new species as "presenting the appearance of a *Lithodomus,*" but he did not give further description. In our view, his remark can be considered a valid diagnosis because *D. dactylus* is the only dreissenid that resembles the marine mytilid boring bivalve "*Lithodomus*" (*Lithophaga*), also known as date mussel. PAVLOVIĆ (1927, 1928) also noted this similarity, hence the name *lithodomiformis*. The species was illustrated from Balatonkenese (BRUSINA 1902), Tihany (VITÁLIS 1915), Vrčin-Karagača creek (PAVLOVIĆ 1927, 1928), Jagnjedovec (BASCH 1990, BASCH & ŽAGAR-SAKAČ 1992), Vösendorf (SCHULTZ 2005), and Balatonalmádi (KATONA et al. 2015).

Stratigraphic range and age: The oldest known occurrence, Vösendorf, is assigned to "Zone E" of PAPP (1951, 1953), dated as 10.4–10.1 Ma (HARZHAUSER et al. 2004). The occurrences in Tihany, Balatonalmádi and Balatonkenese belong to the *Lymnocardium decorum* Zone, 8.7–8.0 Ma (MAGYAR & GEARY 2012), whereas the biostratigraphic position and age of the Jagnjedovec material (BASCH 1990) is unknown to us.

Gastropoda CUVIER, 1795
Hydrobiidae STIMPSON, 1865
Genus *Micromelania* BRUSINA, 1874
Type species: Micromelania cerithiopsis BRUSINA, 1874; subsequent designation, DOLLFUS, 1912

Micromelania striata GORJANOVIĆ-KRAMBERGER, 1890 (Plate IV, fig. 13)

v *1890 *Micromelania striata* KRAMB.-GORJ. – GORJANOVIĆ-KRAMBERGER, p. 157, pl. 6, figs 9–9a.
(?)1893 *Micromelania lapadensis* nov. form. LŐRENTHEY, p. 311, pl. 4, fig. 14b. [new synonym?]
1985 *Micromelania striata* GORJ.-KRAMB. – JÁMBOR et al., pl. 23, figs 5–6.
1987 *Micromelania striata* GORJ.-KRAMB. – JÁMBOR et al., pl. 8, figs 5–6.
2013 *Micromelania* sp. – TER BORGH et al., fig. 9:20.

Type locality: Zagreb–Vrapče (GORJANOVIĆ-KRAMBERGER 1890)

Type material: Syntypes: HPM, 5165-330/1-2 (MILAN et al. 1974); GBA

Remarks: In addition to the syntypes reposited in HPM, a specimen collected by the author of the species is also available in the type collection of GBA.

The shell has 9–11 whorls with fine parallel growth lines and longitudinal striae, resulting in a square grid ornamentation. This can only be observed on well-preserved shells or sometimes on imprints. *Micromelania lapadensis* described by LŐRENTHEY (1893) is probably a junior synonym of *M. striata*, but the figure of LŐRENTHEY does not allow precise comparison.

Stratigraphic range and age: This species was described and mentioned from old Pannonian offshore (sublittoral and profundal) marls all over the Pannonian Basin proper (Vrapče, Medvednica Mts., Croatia – GORJANOVIĆ-KRAMBERGER 1890; Lopadea Veche, Transylvanian Basin, Romania – LŐRENTHEY 1893; Lajoskomárom-1 borehole, Hungary – JÁMBOR et al. 1985, 1987; Beočin, Fruška Gora Mts., Serbia – TER BORGH et al. 2013). It is a common species in the *Lymnocardium praeponticum*, *Congeria czjzeki* and *Congeria banatica* Zones (from 11.6 to 9.5 Ma).

Lymnaidae RAFINESQUE, 1815
Genus *Radix* MONTFORT, 1810
Type species: *Radix auriculatus* MONTFORT, 1810; original designation

Radix croatica (GORJANOVIĆ-KRAMBERGER, 1890) (Plate III, figs 17–19)

v *1890 *Limnaea croatica* KRAMB.-GORJ. – GORJANOVIĆ-KRAMBERGER, p. 154, pl. 6, figs 1–3.
?v 1890 *Limnaea extensa* KRAMB.-GORJ. – GORJANOVIĆ-KRAMBERGER, p. 155, pl. 6, fig. 4. [new synonym?]
1944 *Radix* (*Limnaea*) *croatica* KR.-G. – MOOS, p. 344.
1956 *Radix kobelti* BRUSINA – PAPP, p. 71.
1967 *Radix croatica* (GORJANOVIĆ-KRAMBERGER) – TAKTAKISHVILI, text-fig. 7a.
1985 *Radix croatica* (GORJ.-KRAMB.) – JÁMBOR et al., pl. 23, fig. 4.
1985 *Radix kobelti* REUSS – STEVANOVIĆ & PAPP, pl. 27, fig. 11.
1987 *Radix croatica* (GORJ.-KRAMB.) – JÁMBOR et al., pl. 8, fig. 4.
2013 *Radix kobelti* REUSS – TER BORGH et al., fig. 9:19.

Type locality: Zagreb–Vrapče (GORJANOVIĆ-KRAMBERGER 1890)

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Type material: Syntypes: HPM 5178-343–5180-345 (MILAN et al. 1974), GBA

Remarks: In addition to the syntypes reposited in HPM, a specimen collected by the author of the species is also available in the type collection of GBA, subsequently labelled as "syntype."

Fine growth lines, four whorls (in most cases, just three whorls can be seen, the last whorl covers the third one), and a strongly widening last whorl with an oval and rimmed aperture characterize this species. Protoconch can be observed only in well-preserved specimens. *Limnaea extensa* species of GORJANOVIĆ-KRAMBERGER is probably a steinkern of a *R. croatica* specimen and shows the internal structure and ornamentation and all the four whorls of *R. croatica*. *Radix kobelti* is not a synonym of *R. croatica*, but it is frequently confused with *R. croatica*. *Radix kobelti* is a shallow-water species of young Pannonian ("Pontian") sands, whereas *R. croatica* is a typical member of old Pannonian marls and limestones.

Stratigraphic range and age: This species was described and mentioned from old Pannonian offshore (sublittoral and profundal) marls all over the Pannonian Basin (Vrapče, Medvednica Mts., Croatia – GORJANOVIĆ-KRAMBERGER 1890; Kostanjek/Podsused, Medvednica Mts., Croatia – PAPP 1956, VRSALJKO 1999; Gojlo-4 and Bujavica-9 boreholes, Sava Basin, Croatia – MOOS 1944; Lajoskomárom–1 borehole, Hungary – JÁMBOR et al. 1985, 1987; Beočin, Fruška Gora Mts., Serbia – STEVANOVIĆ & PAPP 1985, TER BORGH et al. 2013). *Lymnocardium praeponticum* mollusk biozone = "Croatica Beds" in Croatia (from 11.6 to 11.45 Ma). It is a common member of the *L. praeponticum – R. croatica* dwarf fauna.

Planorbidae RAFINESQUE, 1815

Genus *Gyraulus* CHARPENTIER, 1837

Type species: *Planorbis albus* O. F. MÜLLER, 1774; subsequent designation, DALL, 1870

Gyraulus tenuistriatus (GORJANOVIĆ-KRAMBERGER, 1899) (Plate VI, fig. 22)

v *1899 *Planorbis tenuistriatus* KRAMB.-GORJ. – GORJANOVIĆ-KRAMBERGER, p. 129, pl. V fig. 7.

1956 *Planorbis* (*Gyraulus*) cf. *tenuistriatus* GORJ.-KRAMBG. – PAPP, p. 70.

1977 *Planorbis tenuistriatum* [sic!] GORJ.-KRAMB. – V. LUBENESCU & D. LUBENESCU, pl. 2 fig. 5.

1984 *Gyraulus* sp. – V. LUBENESCU & POPESCU, pl. 1 fig. 8.

1985 *Gyraulus tenuistriatus* (GORJ.-KRAMB.) – JÁMBOR et al., pl. 23 fig. 3.

1987 *Gyraulus tenuistriatus* (GORJ.-KRAMB.) – JÁMBOR et al., pl. 8 fig. 3.

2009 „*Gyraulus*" *tenuistriatus* (GORJANOVIĆ-KRAMBERGER) – CZICZER et al., fig. 6o.

2010 „*Gyraulus*" *tenuistriatus* (GORJANOVIĆ-KRAMBERGER) – MAGYAR, fig. 11.

2013 *Gyraulus praeponticus* (GORJ.-KRAMB.) – TER BORGH et al., fig. 9: 17–18.

2016 *Gyraulus* sp. – MANDIC et al., fig. 17.

2016 *Planorbi* [sic!] sp. – WANEK, p. 29, fig. 5.

2019 *Gyraulus tenuistriatus* (GORJANOVIĆ-KRAMBERGER) – BOTKA et al., fig. 3: f.

Type locality: Babindol, south of Londžica (Gorjanović-Kramberger 1899)

Type material: Syntype: HPM 5457-607

Remarks: According to ICZN Article 74.5, the "holotype" designation by MILAN et al. (1974) cannot be accepted as valid lectotype designation.

This species has a planispiral shell with four whorls and fine growth lines, which can be thickened forming a slightly bulging ornamentation. Width of the aperture is ca. 1/3 of the shell width. It clearly differs from *G. praeponticus* GORJANOVIĆ-KRAMBERGER, which has only three whorls and wider aperture.

Stratigraphic range and age: This species was described and mentioned from old Pannonian offshore (sublittoral and profundal) marls all over the Pannonian Basin (Londžica, Krndija Mts., Croatia – GORJANOVIĆ-KRAMBERGER 1899; Kostanjek/Podsused, Medvednica Mts., Croatia – PAPP 1956; Lajoskomárom–1 borehole, Hungary – JÁMBOR et al. 1985, 1987; localities of the northern foreground of the Transdanubian Range, Hungary – CZICZER et al. 2009; Beočin, Fruška Gora Mts., Serbia – TER BORGH et al. 2013; various localities from the Transylvanian Basin, Romania – V. LUBENESCU & D. LUBENESCU 1977, LUBENESCU 1981, LUBENESCU & POPESCU 1984, MAGYAR 2010, WANEK 2016, BOTKA et al. 2019). It is a common species in the *Lymnocardium praeponticum*, *Congeria czjzeki* and *Congeria banatica* Zones (from 11.6 to 9.5 Ma).

Genus *Orygoceras* BRUSINA, 1882

Type species: *Orygoceras cornucopiae* BRUSINA, 1882; subsequent designation, COSSMANN, 1921

Orygoceras fuchsi (KITTL, 1886)

*1886 *Creseis Fuchsi* n. f. KITTL, p. 50, pl. 2, figs 1–3.

v 1890 *Orygoceras levis* KRAMB.-GORJ. – GORJANOVIĆ-KRAMBERGER, p. 158, pl. 6, fig. 11. [new synonym]

v 1892 *Orygoceras corniculum* BRUSINA n. sp. – BRUSINA, pp. 169–171.

1893 *Orygoceras levis* Kramb.-Gorj. ? – Lőrenthey, pp. 310–311.

1902 *Orygoceras corniculum* BRUSINA – BRUSINA, pl. 2, figs 34–37.

1902 *Orygoceras corniculum* BRUS. – LŐRENTHEY, pp. 194–196, pl. 11, figs 20–22; pl. 12, fig. 11.

1944 *Orygoceras fuchsi* KITTL – JEKELIUS, p. 118, pl. 43, figs 22–23.

1956 *Orygoceras fuchsi fuchsi* (KITTL) – PAPP, p. 70.

1985 *Orygoceras laevis* [sic!] GORJ.-KRAMB. – JÁMBOR et al., pl. 23, figs 7–8.

1985 *Orygoceras fuchsi fuchsi* (KITTL) – PAPP, p. 288, text-figs 38–39:1–2c.

1987 *Orygoceras laevis* [sic!] GORJ.-KRAMB. – JÁMBOR et al., pl. 8, figs 7–8.

1999 *Orygoceras fuchsi* KITTL – LENNERT et al., pl. 5, figs 10–11.

2010 *Orygoceras levis* GORJANOVIĆ-KRAMBERGER – MAGYAR, fig. 29b:E.

2019 *Orygoceras levis* GORJANOVIĆ-KRAMBERGER – BOTKA et al., fig. 3:g.

Type locality: Forchtenstein (KITTL 1886). According to LŐRENTHEY (1903), the type locality is not correct, the specimens described and figured by KITTL (1886) must have originated from the Sopron area, where old Pannonian layers are exposed.

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Type material: unknown

Remarks: The species has a thin, smooth, dentaliform shell. Growth lines can sometimes be seen. Protoconch is a half smooth whorl. According to LŐRENTHEY (1903), *O. corniculum* is a junior synonym of *O. fuchsi*. We share this opinion and add that the same applies to *O. levis*.

Stratigraphic range and age: This species was described and mentioned from old Pannonian offshore (sublittoral and profundal) marls all over the Pannonian Basin (?Forchtenstein, Eisenstadt–Sopron Basin, Austria – KITTL 1886; Vrapče, Medvednica Mts., Croatia – GORJANOVIĆ-KRAMBERGER 1890; Lopadea Veche, Transylvanian Basin, Romania – LŐRENTHEY 1893; Markuševec, Medvednica Mts., Croatia – BRUSINA 1892, 1902; Ripanj, Šumadija Hills, Serbia – BRUSINA 1902; Budapest-Kőbánya, Pannonian Basin and Tinnye, Zsámbék Basin, Hungary – LŐRENTHEY 1902; Soceni, Pannonian Basin, Romania – JEKELIUS 1944; Lajoskomárom–1 borehole, Hungary – JÁMBOR et al. 1985, 1987; Kostanjek/Podsused, Medvednica Mts., Croatia – PAPP 1956; Leobersdorf, Vienna Basin, Austria – PAPP 1985; Oarba de Mureş and Guşteriţa, Transylvanian Basin, Romania – MAGYAR 2010, BOTKA et al. 2019). It is a common species in the *Lymnocardium praeponticum*, *Congeria czjzeki*, and *Congeria banatica* Zones (from 11.6 to 9.5 Ma). Sporadic occurrences were reported from the much younger *Congeria rhomboidea* Zone (from 8 to ?5 Ma) as well.

Orygoceras brusinai GORJANOVIĆ-KRAMBERGER, 1890 (Plate IV, fig. 14)

v *1890 *Orygoceras Brusinai* KRAMB.-GORJ. – GORJANOVIĆ-KRAMBERGER, p. 158, pl. 6, figs 10–10a.
v 1892 *Orygoceras filocinctum* BRUSINA n. sp. – BRUSINA, p. 171. [new synonym]
v 1892 *Orygoceras cultratum* BRUSINA n. sp. – BRUSINA, p. 171. [new synonym]
1902 *Orygoceras filocinctum* BRUSINA – BRUSINA, pl. 2, figs 23–28.
1902 *Orygoceras cultratum* BRUSINA – BRUSINA, pl. 2, figs 29–33.
1902 *Orygoceras cultratum* BRUS. – LŐRENTHEY, p. 196, pl. 12, fig. 13; pl. 13, figs 2–5.
1902 *Orygoceras filocinctum* BRUS. – LŐRENTHEY, p. 197, pl. 11, fig. 23; pl. 12, fig. 12; pl. 13, fig. 1.
1944 *Orygoceras fuchsi filocinctum* BRUSINA – JEKELIUS, p. 118, pl. 43, figs 24–25.
1944 *Orygoceras fuchsi cultratum* BRUSINA – JEKELIUS, p. 118, pl. 43, figs 26–28.
1956 *Orygoceras fuchsi brusinai* GORJ.-KRAMBG. – PAPP, p. 70.
1985 *Orygoceras fuchsi filocinctum* BRUSINA – PAPP, p. 288, text-fig. 40:3a–b.
2010 *Orygoceras brusinai* GORJANOVIĆ-KRAMBERGER – MAGYAR, fig. 29b:D.

Type locality: Zagreb–Vrapče (GORJANOVIĆ-KRAMBERGER 1890)

Type material: Syntype: HPM 5162-327

Remarks: This species has thin dentaliform shell, ornamented with rings on the upper part. Growth lines can sometimes be seen on well-preserved specimens. Protoconch is a half smooth whorl. *Orygoceras brusinai*, *O. filocinctum*, and *O. cultratum* are probably junior synonyms. *Orygoceras cultratum* bears less rings, which are far from each other, while *O. filocinctum* has more, closer spaced rings. However, this observation might be a matter of the preservation state or intraspecific variability.

Stratigraphic range and age: This species was described and mentioned from old Pannonian offshore (sublittoral and profundal) marls all over the Pannonian Basin (Vrapče, Medvednica Mts., Croatia – GORJANOVIĆ-KRAMBERGER 1890; Markuševec, Medvednica Mts., Croatia – BRUSINA 1892, 1902; Budapest-Kőbánya, Pannonian Basin and Tinnye, Zsámbék Basin, Hungary – LŐRENTHEY 1902; Soceni, Pannonian Basin, Romania – JEKELIUS 1944; Kostanjek/Podsused, Medvednica Mts., Croatia – PAPP 1956; Leobersdorf, Vienna Basin, Austria – PAPP 1985; Oarba de Mureş, Transylvanian Basin, Romania – MAGYAR 2010). *Orygoceras brusinai* is less common than *O. fuchsi* in the *Lymnocardium praeponticum*, *Congeria czjzeki* and *Congeria banatica* Zones (from 11.6 to 9.5 Ma).

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