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Pannonian (late Miocene) ostracod fauna from Pécs-Danitzpuszta in Southern Hungary

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Pannóniai kagylósrák fauna Pécs-Danitzpusztáról

Összefoglalás

A pécs-danitzpusztai homokbányában, a kitermelt homok feküjében egy tektonikailag erősen kibillentett pannóniai márga rétegsor tárul fel. Az összlet vastagsága 65 m a szarmata–pannóniai határtól a fedő homokig. Ez a bányaudvar a pannóniai emelet aljának legjobb, rétegtanilag legteljesebb felszíni feltárása Magyarországon, ezért komplex őslénytani, rétegtani feldolgozása nemzetközi jelentőségű. Tanulmányunk a rétegsor kagylósrák-maradványainak vizsgálatáról szól. 45 preparált kőzetmintából 29 tartalmazott értékelhető, jó megtartású kagylósrák faunát, összesen 39 taxont, amelyek 9 nemet képviselnek.

A ma is élő, tengeri eredetű nemek (*Loxoconcha, Cyprideis, Amnicythere*) élőhelyeit figyelembe véve a vizsgált együttesek aránylag sekély, de hullámbázis alatti, alacsony energiájú, csendes környezetben, pliohalin (9–16‰) sótartalmú vízben élhettek. Az édesvízi eredetű bevándorlók közül a *Candona*-nem különböző alnemei nyilvánvalóan elviselték a brakkvizet is, ahogy azt a ma is élő *Typhlocypris* subgenus esetében látjuk. Ugyanez igaz lehetett arra a néhány *Cypria* fajra is, amelyek nagyon elterjedtek voltak a Pannon-tóban. A *Herpetocyprella*-nem, amelynek csak egyetlen élő faját ismerjük, de amely szintén igen elterjedt volt a Pannon-tóban, a bezáró kőzetek fáciesei alapján erősen tágtűrésű lehetett. A kihalt nemek (*Hemicytheria, Loxocorniculina, Amplocypris*) mind brakkvízi környezetben (a szarmata Paratethysben vagy brakkvízi tavakban) éltek.

Biosztratigráfiailag négy egységre osztottuk a rétegsort. Az intervallum zónák alját minden esetben egy-egy marker faj első előfordulása (vélelmezett első megjelenése) jelöli ki. A *Hemicytheria lorentheyi* zóna a pannóniai rétegsor alsó 5,5 méterét fogja át. A *Hemicytheria tenuistriata* zóna 29 m, a *Candona (Propontoniella) candeo* zóna 18 m vastag. Az *Amplocypris abscissa* zóna mintázott vastagsága 6,5 méter. A hasonló fáciesű, bár homogénebb beocsini rétegsorban, amely a Fruska Gorában található mintegy 150 km-re délkeletre Pécstől, magnetosztratigráfiai adatok alapján a szarmata-pannóniai határ kora 11,6 millió év, a *Hemicytheria tenuistriata* első megjelenésének kora 11,23 millió év, a Danitzpusztán az *Amplocypris abscissa* zónában megjelenő *Candona (Reticulocandona) reticulata* első előfordulásának kora pedig 10,2 millió év. Ezek alapján feltételezzük, hogy feltárásunkban a pannóniai márga rétegsor a 11,6 – 10 millió évek közti intervallumot képviseli.

A feltárás kagylósrák- és puhatestű zonációjának összevetése azt mutatja, hogy a *Hemicytheria lorentheyi* zóna egésze és a *H. tenuistriata* zóna legalsó része korrelálható a *Lymnocardium praeponticum – Radix croatica* zónával, míg a feltárás felső részén az *Amplocypris abscissa* zóna ad átfedést a *Lymnocardium schedelianum* zónával.

Keywords: késő Miocén, Pannon-tó, osztrakodák, őskörnyezet, biosztratigráfia, Mecsek

Abstract

The large outcrop at Pécs-Danitzpuszta, southern Hungary, exposes a 65-meter-thick succession of calcareous marls, clay marls and calcareous sands that were deposited during the early history of Lake Pannon, a vast, Caspian-type lake in Central Europe in the late Miocene. Within the framework of the complex stratigraphic investigation of this succession, well preserved, relatively diverse benthic ostracod assemblages containing 39 taxa were recovered from 29 samples (16 samples were barren). Palaeoecological interpretation of the ostracod genera suggests that deposition took place in a low-energy environment, in the shallow sublittoral zone of Lake Pannon, in pliohaline (9–16‰ salinity) water. The entire succession was divided into four interval zones based on the first occurrences of assumedly useful marker fossils: *Hemicytheria lorentheyi* Zone (from sample D29), *Hemicytheria tenuistriata* Zone (from sample D17), *Propontoniella candeo* Zone (from sample D115) and *Amplocypris abscissa* Zone (from sample D209). Based on comparison to the Beočin section 150 km to the SE, where a lithologically and stratigraphically similar section was dated magnetostratigraphically by an international team, we tentatively assume that the Pannonian marl succession of the Pécs-Danitzpuszta outcrop represents the time interval of 11.6 to ca. 10 Ma.

Keywords: late Miocene, Lake Pannon, ostracods, palaeoenvironment, biostratigraphy, Mecsek Mts

Introduction

In the large sand pit of Pécs-Danitzpuszta, which is famous for its unique middle to late Miocene reworked terrestrial and marine vertebrate remains (SZABÓ et al. this volume), a 65-meter-thick, tectonically tilted succession is exposed that consists of calcareous marls, clay marls and calcareous sands (SEBE et al. 2021). This Pannonian (upper Miocene, Tortonian) succession represents fairly continuous sedimentation from the Sarmatian/Pannonian boundary to the top of the marl. The marl is overlain by a thick sand body that is exploited in the pit. This succession, deposited in Lake Pannon, offers a unique opportunity to investigate various fossil groups and to establish correlation between the biostratigraphic systems.

This study focuses on the ostracod fauna of the Pannonian marls. The primary objective of this work is the documentation of the ostracod assemblages along the profile in order to determine their biostratigraphic and palaeoecological significance. Early Pannonian ostracod records are poorly known in SW Hungary (SZÉLES 1982; SZUROMI-KORECZ 1991, 1992), but they were extensively studied in other parts of the southern Pannonian Basin where the lithology and thus the inferred palaeoenvironment was similar to that in Danitzpuszta, such as the areas in the vicinity of Zagreb (SOKAČ 1972) and Belgrade (KRSTIĆ 1960, 1985; RUNDIĆ et al. 2011). Most recently, the ostracod record from the 120-meter-thick calcareous marl succession of Beočin (near Novi Sad, Serbia) was investigated and published by STOICA & RUNDIĆ in TER BORGH et al. (2013). The Beočin outcrop was also subject to magnetostratigraphic investigations, which dated the marl succession between 11.6 Ma (Sarmatian/Pannonian boundary) and ca. 9.9 Ma (TER BORGH et al. 2013). These papers, as well as some other modern, well-documented ostracod studies on thoroughly investigated lower Pannonian outcrops from the entire area of Lake Pannon (e.g., GROSS 2004, FILIPESCU et al. 2011, OLTEANU 2011, BOTKA et al. 2020) offer a good opportunity to place the Danitzpuszta ostracod record into a biostratigraphic and palaeoecological framework.

Geological setting and stratigraphy

The Pécs-Danitzpuszta sand pit is the best outcrop of the oldest Pannonian (upper Miocene) strata in the Mecsek area (KLEB 1973). The pit is located at the eastern boundary of Pécs, on the north side of Highway 6 (*Figure 1*). Sand has been produced here since the beginning of the 20th century.

The stratigraphically lower part of the exposed Pannonian succession belongs to the Endrőd Formation (*Figure 2*; SEBE et al. 2015; SEBE et al. 2020). It consists of massive, greyish white calcareous marls, clay marls, sand, and even fine gravel, altogether amounting to 65 meters of stratigraphic thickness. The marls contain plant remains, a rich mollusk fauna and vertebrate fossils. Plant remains indicate a thermophilous flora with taxa suggesting extensive lakeshore swamp forests (HABLY & SEBE 2016). Based on the mollusk fauna, the bottom of the succession belongs to the *Lymnocardium praeponticum* Zone, whereas the top of the marl is assigned into the *Lymnocardium schedelianum* Zone (11.6–11.4 Ma and 11–10.2 Ma respectively, according to MAGYAR & GEARY 2012, BOTKA et al. 2021). The overlying limonitic, coarse-grained sands contain reworked middle Miocene (Badenian and Sarmatian) and Pannonian aquatic and terrestrial vertebrate fossils (KAZÁR et al. 2001, 2007; KAZÁR 2003; CSERPÁK 2018; SZABÓ et al. 2021), where the youngest terrestrial mammals, including the early form of *Hippotherium primigenium,* indicate the MN9/10 mammal zones (Vallesian, 11.1–8.7 Ma; KORDOS in KAZÁR et al. 2001, 2007; KAZÁR 2003; GASPARIK in SEBE et al. 2015).

The marl succession and partly the overlying sand and gravel beds were tilted into a near-vertical position by structural movements (KONRÁD & SEBE 2010). We sampled the calcareous marl succession from two measured profiles. The upper part of the marl (D114 to D219) was sampled in 2015 in the eastern part of the northern wall of the sand pit, whereas the lower part (D35 to D1) was sampled in 2018, when a new trench was digged on the top of the northern wall across the almost vertical marl layers, exposing the oldest Pannonian, Sarmatian, and Badenian deposits (*Figures 1, 2*; SEBE et al. 2021).

Material and methods

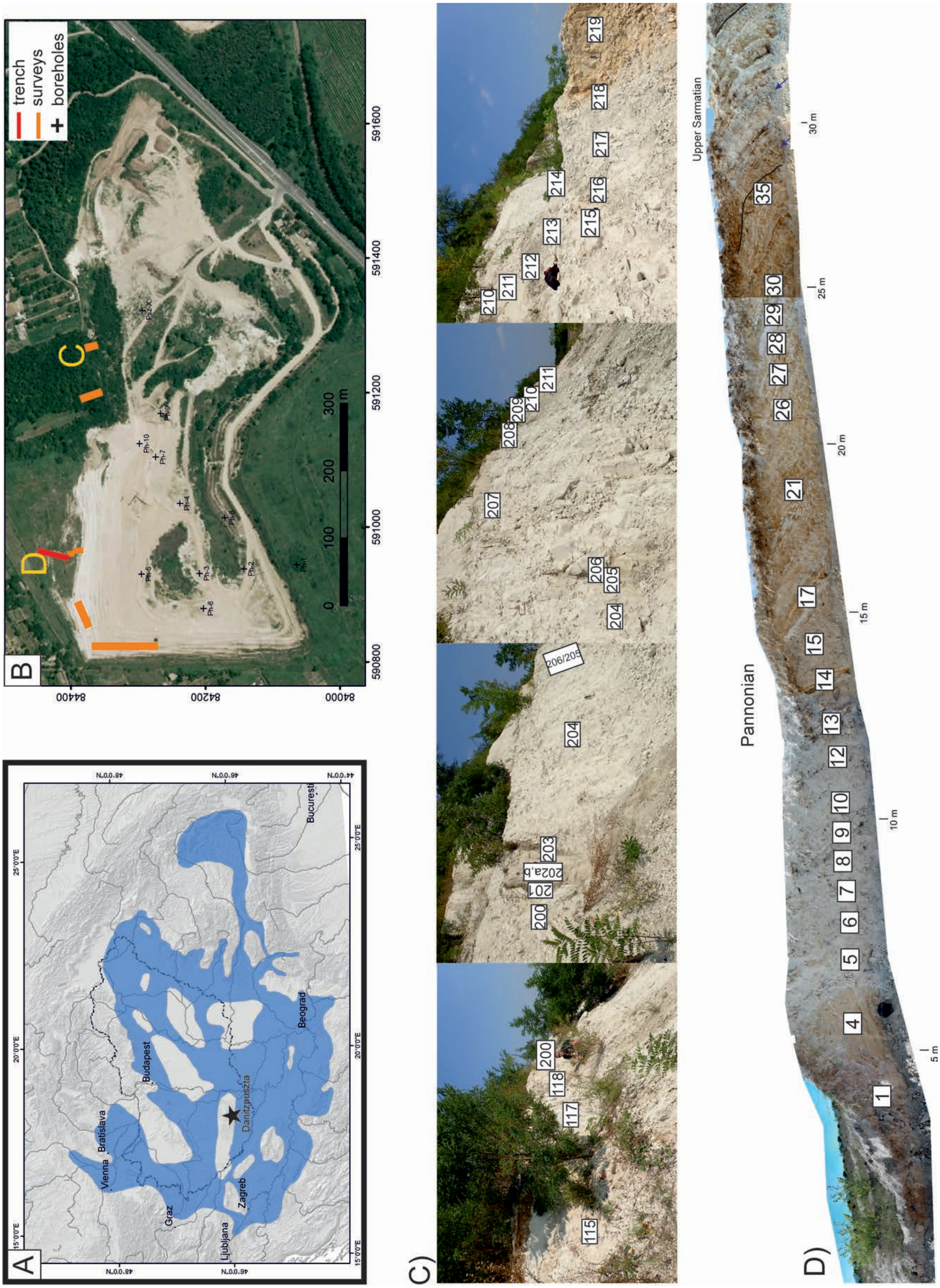
Forty-five samples were examined from the 65-meter-thick Pannonian marl succession: 20 from its lower part, exposed in the trench at the northern wall of the pit, and 25 from the upper part of the succession, in the eastern part of the outcrop (*Figure 1*). Twenty-nine samples contained ostracod carapaces and single valves, the others were free of ostracods (*Figure 3*). The carbonate skeletal microfauna was processed with hydrogen-peroxide (10%) from about 500 g of air-dried sediments. The ostracod valves were selected under stereomicroscope. Hitachi S-2600N scanning electron microscope was used for SEM investigation. SEM images were taken at the Department of Botany of the Hungarian Natural History Museum in Budapest.

Ostracod assemblages and palaeoenvironments

The Danitzpuszta succession yielded a relatively diverse benthic ostracod material made up of 39 taxa with generally well-preserved valves (*Appendix*). Shed valves of juvenile specimens and valves of dead individuals can be preserved depending on delicacy of the valves and "valve-remains transport" (ZHAI et al. 2015).

→ **Figure 1**. A) Lake Pannon within the Pannonian Basin at ca. 10.8 Ma (after MAGYAR et al. 1999). B) Aerial view of the Pécs-Danitzpuszta sand pit with the collection sites (C: pit, D: trench). C–D) Logged strata with the sample locations (C: pit, D: trench)

→ ***1. ábra.*** *A) A Pannon-tó kiterjedése a Pannon-medencében kb. 10,8 millió évvel ezelőtt (MAGYAR et al. 1999 alapján). B) A pécs-danitzpusztai homokbánya a gyűjtési helyekkel (C: bányafal, D: kutatóárok). C–D) A bányafal (C) és a kutatóárok (D) rétegsora a mintavételi helyekkel*


A
Vienna
Bratislava
Budapest
Graz
Ljubljana
Zagreb
Beograd
Bucuresti
Danitzpuszta
15°0'0"E
20°0'0"E
25°0'0"E
44°0'0"N
46°0'0"N
48°0'0"N
B
trench
surveys
boreholes
C
D
0
100
200
300
m
590800
591000
591200
591400
591600
84000
84200
84400
C)
115
117
118
200
201
202a,b
203
204
206/205
205
206
207
208
209
210
211
212
213
214
215
216
217
218
219
D)
Pannonian
Upper Sarmatian
5 m
10 m
15 m
20 m
25 m
30 m
1
4
5
6
7
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12
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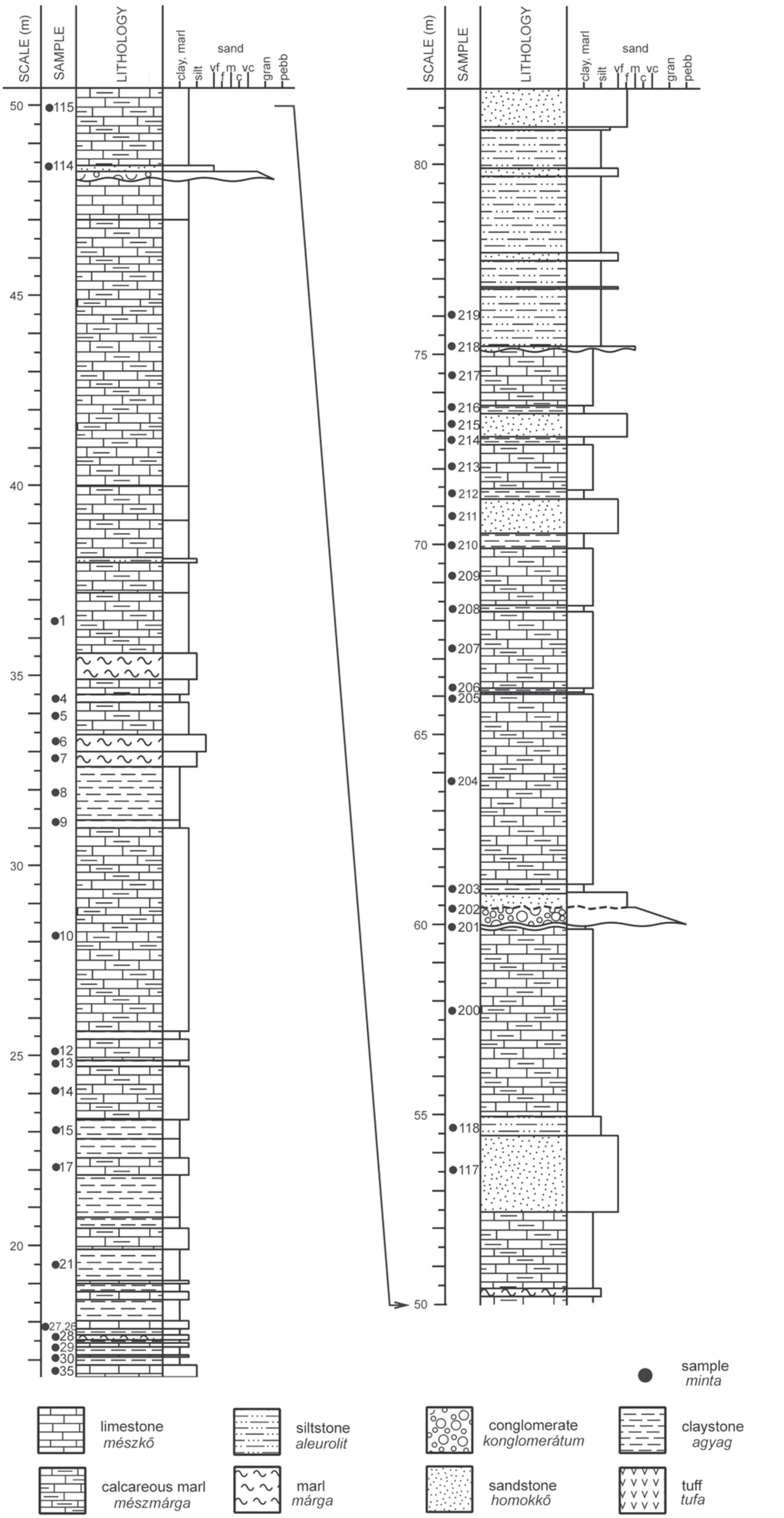
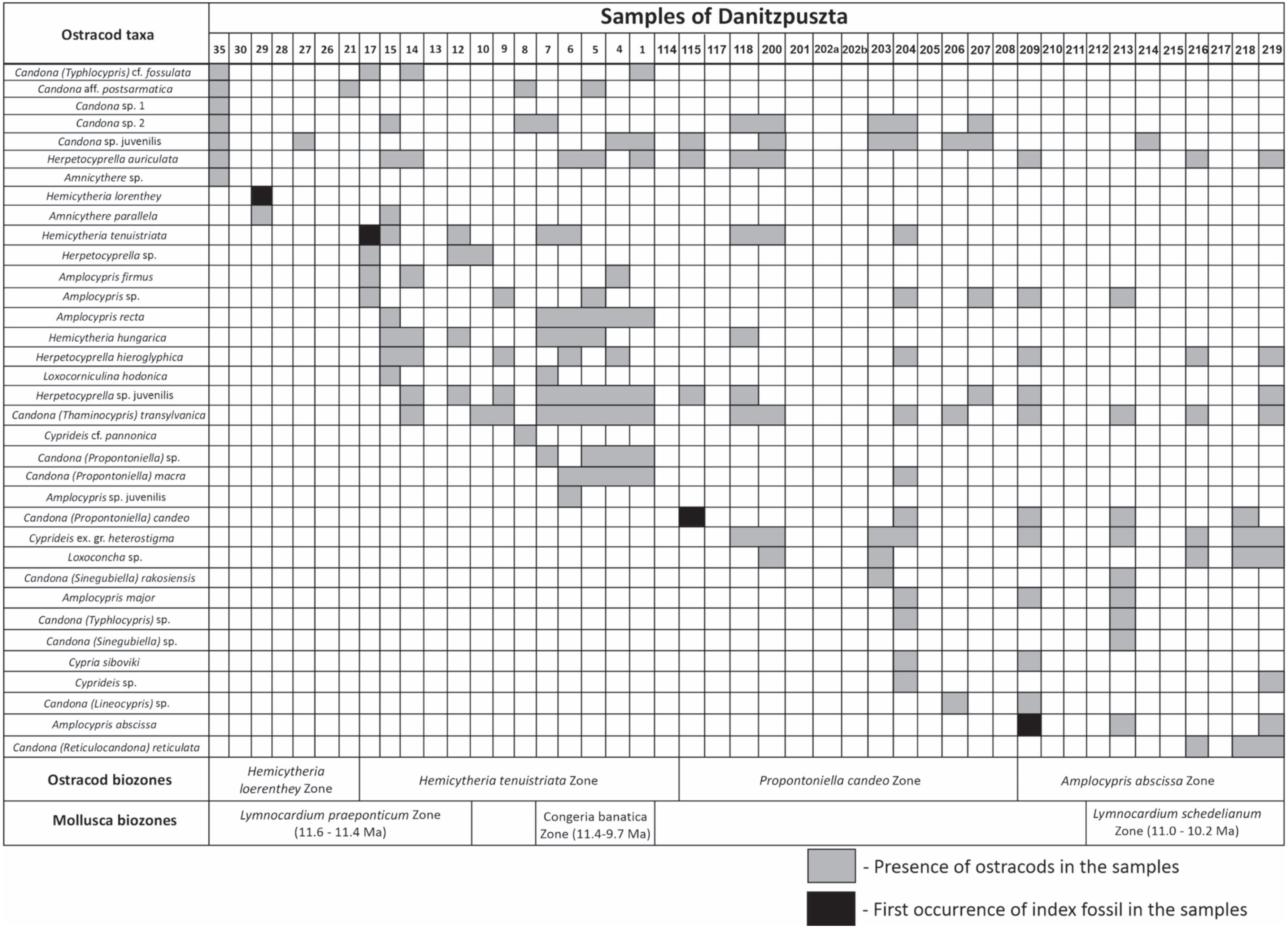


← **Figure 2.** Composite sedimentary log of the Pannonian marl with the sampled layers

← ***2. ábra.*** *A feltárt pannóniai rétegsor finomszemű (uralkodóan mészmárgából álló) részének kompozit szelvénye a mintázott rétegek számának feltüntetésével*

→ **Figure 3.** Distribution of Pannonian ostracod species across the investigated succession. First occurences of biostratigraphic marker species (according to KRSTIĆ 1985) in black. The mollusk biozones are from BOTKA et al., 2021

→ ***3. ábra.*** *A pannóniai kagylósrákok előfordulása a vizsgált szelvényben. Azoknak a fajoknak az első előfordulását, amelyeket KRSTIĆ (1985) biosztratigráfiai zónajelzőknek használt, fekete téglalapok jelzik. A puhatestű biozonációt BOTKA et al. (2021) alapján tüntettük fel*


Samples of Danitzpuszta
Ostracod taxa
35 30 29 28 27 26 21 17 15 14 13 12 10 9 8 7 6 5 4 1 114 115 117 118 200 201 202a 202b 203 204 205 206 207 208 209 210 211 212 213 214 215 216 217 218 219
Candona (Typhlocypris) cf. fossulata
Candona aff. postsarmatica
Candona sp. 1
Candona sp. 2
Candona sp. juvenilis
Herpetocyprella auriculata
Amnicythere sp.
Hemicytheria lorenthey
Amnicythere parallela
Hemicytheria tenuistriata
Herpetocyprella sp.
Amplocypris firmus
Amplocypris sp.
Amplocypris recta
Hemicytheria hungarica
Herpetocyprella hieroglyphica
Loxocorniculina hodonica
Herpetocyprella sp. juvenilis
Candona (Thaminocypris) transylvanica
Cyprideis cf. pannonica
Candona (Propontoniella) sp.
Candona (Propontoniella) macra
Amplocypris sp. juvenilis
Candona (Propontoniella) candeo
Cyprideis ex. gr. heterostigma
Loxoconcha sp.
Candona (Sinegubiella) rakosiensis
Amplocypris major
Candona (Typhlocypris) sp.
Candona (Sinegubiella) sp.
Cypria siboviki
Cyprideis sp.
Candona (Lineocypris) sp.
Amplocypris abscissa
Candona (Reticulocandona) reticulata
Ostracod biozones
Hemicytheria loerenthey Zone
Hemicytheria tenuistriata Zone
Propontoniella candeo Zone
Amplocypris abscissa Zone
Mollusca biozones
Lymnocardium praeponticum Zone (11.6 - 11.4 Ma)
Congeria banatica Zone (11.4-9.7 Ma)
Lymnocardium schedelianum Zone (11.0 - 10.2 Ma)
- Presence of ostracods in the samples
- First occurrence of index fossil in the samples

Sixteen samples were free of ostracods (*Figure 3*). No correlation was found between lithology and the barren samples; the presence or absence of benthic ostracods did not depend on the grain size of the sediments. Where ostracods were found, we did not see any indication of decreased oxygen levels. Changes in nutrient availability might have been a control on ostracod distribution, but this environmental factor is difficult to identify.

The composition of the ostracod fauna does not show any significant change across the section. Some of the identified genera (members of the Cytheroidea superfamily) are survivors of marine origin (*Amnicythere, Loxoconcha, Loxocorniculina, Cyprideis, Hemicytheria*), whereas others (members of the Cypridoidea superfamily) are considered freshwater and brackish immigrants (*Candona, Cypria, Herpetocyprella, Amplocypris*). In the following we briefly review the known habitat and (palaeo)ecological demand of each genus in order to create a basis for the environmental interpretation of our assemblages.

Amnicythere occurs in the lowermost part of the section (*Figure 3*). This genus appeared in the brackish marine Sarmatian and has radiated in the Paratethys. In addition to some sporadic occurrences in the Tortonian and lower Messinian of the Mediterranean, as many as 19 species were reported from the upper Messinian Lago-Mare deposits (GLIOZZI et al. 2005). The genus has 10 living representatives, all inhabiting fresh to oligo – mesohaline waters of the Black-Azov, Caspian and Aral Seas (GLIOZZI & GROSSI 2008, NAMIOTKO et al. 2011).

Representatives of genus *Loxoconcha* occur in the upper part of the section (*Figure 3*). This genus first appeared in the Cretaceous (MOORE 1961) or in the Palaeocene (MORKHOVEN 1963). According to SAVATENALINTON & MARTENS (2009), family Loxoconchidae includes 22 extant genera, most of them living in marine and brackish environments; only six species are known from freshwater ecosystems (KARANOVIC 2012). In the modern ostracod fauna of the Caspian Sea, *Loxoconcha* is the most eurytopic genus, hence its high density on the shelf of the South Caspian basin (GOFMAN 1966). It can be equally found on algae, on the bottom, or within the substrate (ELOFSON 1941, PURI et al. 1969). Some species dwell in the profundal zone of the Caspian (down to 875 m; BOOMER et al. 2005), but only a few species live in the agitated littoral zone with freshwater influence (GOFMAN 1966).

Loxocorniculina, an extinct genus of the family Loxoconchidae, was found in the lower part of the section (*Figure 3*). It is a typical Paratethyan form, which first appeared in the Sarmatian and spread into the Palaeo-Mediterranean during the late Messinian Lago-Mare event (FARANDA et al. 2007). The fossil *Loxocorniculina djafarovi* indicates oligohaline to mesohaline water of variable depth (IACCARINO et al. 2008).

Cyprideis occurs in the outcrop upsection from sample D8 (*Figure 3*). It first appeared at the end of the Palaeogene and spread across Eurasia and America in the Miocene. Its relatively few extant species can be found worldwide, especially in brackish and hypersaline (or otherwise chemically extreme), shallow-water environments (MORKHOVEN 1963, VAN HARTEN 1990). In the Caspian Sea, *Cyprideis torosa* was found in abundance in a sample from 13 m water depth, whereas it was completely missing from samples taken from 62 m depth and below (BOOMER et al. 2005). The phenotype (including size, shape, pores and ornaments of the valves) is influenced by environmental factors such as salinity (SANDBERG 1964; VAN HARTEN 1975, 2000; SCHWEITZER & LOHMANN 1990; BOWLES 2013). The widespread *Cyprideis pannonica*, occurring in sample D8, was observed to be characteristic for shallow, hypersaline or alkaline waters (BENSON 1973, 1978).

The extinct genus *Hemicytheria*, occurring throughout the outcrop (*Figure 3*), is mostly known from the Sarmatian and Pannonian layers of the Pannonian Basin System. It is interpreted to have lived in brackish (oligo- to pliohaline) waters, although less typically it has also been found in freshwater layers (SOKAČ 1972).

Of the genera that immigrated into Lake Pannon from freshwater and athalassic waterbodies, *Candona* is widespread throughout the outcrop (*Figure 3*). The nominal subgenus *Candona* is known to have populated freshwater lakes of the Northern Hemisphere since the Eocene (KRSTIĆ 1972b), although a few species tolerate oligo- and miohaline environments as well. BOOMER et al. (2005) reported specimens from 62 to 405 m water depth from the Caspian. Most *Candona (Candona)* species are infaunal (MORKHOVEN 1963). Subgenus *Propontoniella*, a probable ancestor of subgenus *Serbiella* (KRSTIĆ 1972b), is known exclusively from the older Pannonian deposits. The extant subgenus *Lineocypris* entered the palaeontological record in the Late Cretaceous. Today it lives in freshwater, especially in deep lakes (MORKHOVEN 1963). Subgenus *Reticulocandona* was originally endemic to Lake Pannon, but its fossils were recovered from the Pontian of Azerbaijan as well (KRSTIĆ 1972b). Subgenera *Sinegubiella* and *Thaminocypris* were endemic to Lake Pannon, although the latter was also found in the Mio-Pliocene of the Dacian basin. The first appearance of subgenus *Typhlocypris* was recorded in Lake Pannon. Its extant species are living in fresh- and athalassic waters of Europe (SOKAČ 1972).

The genus *Cypria* occurs in samples D204 and D209 (*Figure 3*). This genus is known from the Tertiary to the present day. Most of the extant species are active swimmers and prefer a freshwater, plant-rich environment (MORKHOVEN 1963; SOKAČ 1972). For instance, *Cypria ophtalmica* occurs in springs of five regions: Northern Italy, Eastern Iberia, Upper Danube, Southern Anatolia and Central and Western Europe (ROSATI et al. 2014).

The species *Herpetocyprella auriculata* and *H. hieroglyphica* occur throughout the succession (*Figure 3*). The only extant *Herpetocyprella* species, *H. mongolica* lives in the saline lake of Issyk-Kul, Kyrgyzstan (KARANOVIC 2012), while fossil species were reported from the freshwater Pliocene deposits of Central Asia (MANDELSHTAM & SHNEIDER 1963). Based on this distribution, DANIELOPOL et al. (2008) erected two hypotheses concerning the palaeoecology and palaeobiogeography of *Herpetocyprella*. According to the first hypothesis, it originally habitated shallow freshwaters, and its valves were transported into Lake Pannon. The second hypothesis claims that it was probably present in marginal environments of the Sarmatian Paratethys sea, and later it formed autochthonous populations in Lake Pannon. In the first case, adaptation of the originally freshwater genus to saline waters took place repeatedly and independently in Central Europe and later in Central Asia, whereas in the latter case a salt-tolerating species migrated from Lake Pannon to Central Asia in a stepping-stone manner, from lake to lake (DANIELOPOL et al. 2008). We think that the common occurrence and wide geographical distribution of *Herpetocyprella* in Lake Pannon deposits (see above), with our Danitzpuszta data added, favors the second model. RUNDIĆ (2006) found that *Herpetocyprella* species ("*Hungarocypris"* in that paper) were typical nearshore dwellers, preferring sandy substrates, and that they rarely occur in fine-grained sediments. In our material, however, both *Herpetocyprella* species were found in offshore clays and silts, similarly to the Transylvanian Basin samples of KOVÁCS et al. (2016) and BOTKA et al. (2020), and to the Kisalföld ("Danube") Basin samples of CZICZER et al. (2009). *Herpetocyprella auriculata* and *H. hieroglyphica* thus appear to have been rather ubiquitous species that inhabited the littoral to sublittoral and perhaps even the profundal zones of the early Lake Pannon.

The extinct genus *Amplocypris*, occurring throughout the section (*Figure 3*), is represented by at least four species in the outcrop. This genus was apparently endemic to Lake Pannon and later migrated to the Dacian Basin.

Based on the modern distribution and environmental demand of *Loxoconcha*, *Cyprideis* and *Amnicythere*, the investigated assemblages probably lived in relatively shallow but low-energy, pliohaline (9–16‰ salinity) waters in the sublittoral zone of Lake Pannon. Various subgenera of *Candona* obviously tolerated brackish water, as it is evidenced by the extant *Typhlocypris*. Probably the same applies to the few *Cypria* species that are widespread in the deposits of Lake Pannon. *Herpetocyprella* seems to have been a highly eurytopic genus. The other extinct genera, i.e., *Loxocorniculina, Hemicytheria* and *Amplocypris* were all brackish-water (oligo- to pliohaline) dwellers.

Biostratigraphy

Pannonian ostracod biostratigraphic systems are numerous (e.g. SOKAČ 1972, 1990; JIŘIČEK 1983, 1985; KRSTIĆ 1974, 1985, 1990; SZUROMI-KORECZ 1992; *Figure 4*). The most detailed, highest-resolution system was elaborated by KRSTIĆ (1985, 1990), based primarily on densely collected samples from outcrops in the area of the former Yugoslavia. Recently, however, several authors emphasized that the influence of the palaeoenvironmental changes on the distribution of ostracods had been underestimated, and that a reconsideration of the biozonation is needed (e.g., GROSS 2004, OLTEANU 2011, STOICA & RUNDIĆ in TER BORGH et al. 2013).

Keeping the difficulties and uncertainties of Pannonian ostracod biostratigraphy in mind, we based the evaluation of the Danitzpuszta material on the stratigraphic system of KRSTIĆ (1985). However, instead of her rather vaguely defined zones, we looked for first occurrences of species, and defined our zones as interval zones between those first occurrences. We also compared our results with the ostracod record from Beočin in Serbia (STOICA & RUNDIĆ in TER BORGH et al. 2013), where the lithology of the investigated succession and thus the inferred depositional environment is similar to that of Danitzpuszta, and where the first occurrences of ostracod species had been dated by magnetostratigraphic method (TER BORGH et al. 2013). (The correlation between the micropalaeontologically and the magnetostratigraphically investigated sections of the Beočin outcrop is missing from TER BORGH et al. 2013, but is available in the PhD thesis of TER BORGH 2013). We are confident that the relatively uniform lithology and depositional environment throughout the section lends credit to our biostratigraphic evaluation.

Based on consecutive first occurrences, we distinguished four stratigraphic intervals (interval zones) in the Danitzpuszta succession: *Hemicytheria lorentheyi* Zone (D35 to D21), *Hemicytheria tenuistriata* Zone (D17 to D114), *Propontoniella candeo* Zone (D115 to D208), and *Amplocypris abscissa* Zone (D209 to D219) (*Figure 3*).

Hemicytheria lorentheyi occurs in only one sample (D29), but this species is known to be characteristic of the lowermost Pannonian interval in other sections (e.g., MÉHES 1908, GROSS 2004). Other species occurring in the *Hemicytheria lorentheyi* Zone in our material include *Amnicythere parallela, Amnicythere* sp., *Herpetocyprella auriculata, Candona (Typhlocypris)* cf. *fossulata* and *C.* aff. *postsarmatica* (*Figure 3*). *Candona postsarmatica* is also considered a very basal Pannonian species, a contemporary of *Hemicytheria lorentheyi*; SZUROMI-KORECZ (1992) identified it in the Nagykozár–2 borehole, 4 km S of the Danitzpuszta outcrop, where it occurred in the lowermost Pannonian *Spiniferites pannonicus* Zone of the dinoflagellate biostratigraphy (SÜTŐNÉ SZENTAI 2012).

Hemicytheria tenuistriata first occurs in sample D17 (*Figure 3*). The stratigraphic range of this species is known to overlap with that of *Hemicytheria lorentheyi*, but it has not been reported so far from the lowermost Pannonian layers. In Beočin, *H. tenuistriata* first occurs in a reversed polarity interval, interpreted to be between C5r1n and C5r.2r-1n, and thus dated at 11.23 Ma (inferred by us from data available in TER BORGH 2013). The *Hemicytheria tenuistriata* Zone in Danitzpuszta contains the following species: *Amplocypris firmus, A. recta, Amplocypris* sp., *Candona (Thaminocypris) transylvanica, C. (Typhlocypris)* cf. *fossulata, C. (Propontoniella) macra, C. (Propontoniella)* sp., *C.* aff. *postsarmatica, Candona* sp., *Cyprideis* cf. *pannonica, Hemicytheria hungarica, Herpetocyprella*

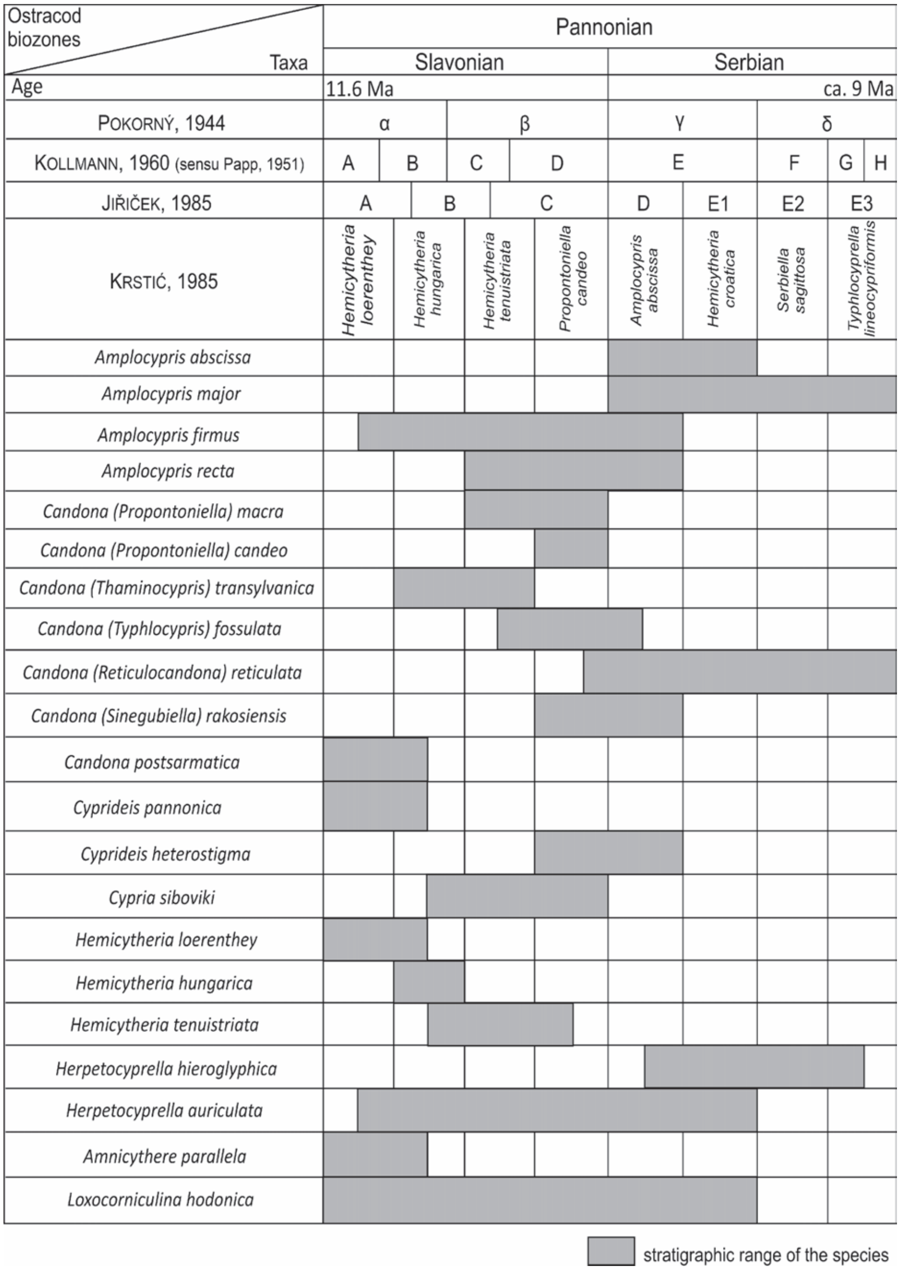


Figure 4. Literature-based stratigraphic distribution of the ostracod species identified in the Pécs-Danitzpuszta outcrop, according to POKORNY (1944), KOLLMANN (1960), JIŘIČEK (1985) and KRSTIĆ (1985). Compilation is based on KOVÁCS et al. (2016)

4. ábra. *A pécs-danitzpusztai feltárásban azonosított pannóniai kagylósrák fajok rétegtani elterjedése POKORNÝ (1944), KOLLMANN (1960), JIŘIČEK (1985) és KRSTIĆ (1985) alapján. A korreláció KOVÁCS et al. (2016) munkáját követi*

hieroglyphica, H. auriculata, Herpetocyprella sp., *Amnicythere parallela* and *Loxocorniculina hodonica* (*Figure 3*). *Amplocypris firmus* and *Loxocorniculina hodonica* share their first occurrence with *Hemicytheria tenuistriata* both in the Danitzpuszta and Beočin records.

Candona (Propontoniella) candeo first occurs in sample D115 (*Figure 3*). This species is missing from the Beočin record, but it was recorded in the stratigraphically thoroughly investigated succession of Guşteriţa (Sibiu, Transylvanian Basin, Romania; BOTKA et al. 2020). In that outcrop, the first occurrence of *Candona (Propontoniella) candeo* was coeval with the first occurrence of the dinoflagellate species *Pontiadinium pecsvaradense*, and the age of their first occurrence was speculated to be about 10.75 Ma. In the Danitzpuszta outcrop, however, an occurrence of *Pontiadinium pecsvaradense* is known from D1–3 (KRIZMANIĆ et al., 2021), 14–15 m below the first occurrence of *Candona (Propontoniella) candeo* in sample D115. (In fact, specimens of subgenus *Propontoniella* from samples D1, D4, D5 and D7 might belong to *Candona (Propontoniella) candeo*, but their poor preservation hindered species-level identification.) The following species occur in our *Candona*

(Propontoniella) candeo Zone: *Candona (Propontoniella) macra, C. (Sinegubiella) rakosiensis, C. (Thaminocypris) transylvanica, C. (Typhlocypris)* sp., *Cypria siboviki, Cyprideis* ex. gr. *heterostigma, Hemicytheria tenuistriata, H. hungarica, Herpetocyprella auriculata*, and *H. hieroglyphica* (*Figure 3*).

Amplocypris abscissa first occurs in sample D209 (*Figure 3*). This species was not recorded in Beočin (although a taxonomically questionable form designated „*Amplocypris* ex gr. *abscissa*" is present throughout the section, from the Sarmatian/Pannonian boundary up to the highest sample, covering the time interval of 11.6–9.9 Ma; TER BORGH et al. 2013). Other species in our *Amplocypris abscissa* Zone include *Amplocypris major, Candona (Propontoniella) candeo, C. (Reticulocandona) reticulata, C. (Sinegubiella) rakosiensis, C. (Thaminocypris) transylvanica, Cypria siboviki, Cyprideis* ex. gr. *heterostigma, Herpetocyprella auriculata, H. hieroglyphica* (*Figure 3*). *Candona (Reticulocandona) reticulata*, first occurring in sample D216, is one of the latest appearing species in the Beočin section as well; its first occurrence corresponds to ca. 10.25 Ma (assuming a constant depositional rate throughout C5n.2n in the Beočin succession).

Comparing the ostracod and mollusk zonations in the Danitzpuszta outcrop, we found that the *Hemicytheria lorentheyi* Zone and the lowermost part of the *Hemicytheria tenuistriata* Zone overlap with the *Lymnocardium praeponticum – Radix croatica* Zone. In the upper part of the section, the *Amplocypris abscissa* Zone overlaps with the *Lymnocardium schedelianum* Zone. This latter relationship is similar to that reported from the Hennersdorf section (cf., HARZHAUSER & MANDIC 2004 and DANIELOPOL et al. 2011).

Conclusions

The Pécs-Danitzpuszta outcrop yielded a characteristic limno-brackish Lake Pannon benthic ostracod fauna with well-preserved valves from 29 samples collected from the 65 meter thick Pannonian Endrőd Marl succession. Thirty-nine ostracod taxa, which belong to 9 genera, 8 families and 1 order (*Podocopida*), were identified.

Based on the ecology of extant genera and palaeoecological interpretation of the extinct ones, the studied ostracod assemblages probably lived in relatively shallow but low-energy, pliohaline (9–16‰ salinity) waters in the sublittoral zone of Lake Pannon.

Biostratigraphically, we divided the succession into four interval zones based on the first occurrence (supposed first appearance) of four species. The *Hemicytheria lorentheyi* Zone is 5.5 m thick, and represents the basal part of the Pannonian succession (from 11.6 Ma onwards). The overlying *Hemicytheria tenuistriata* Zone is 29 m thick; the first occurrence of *H. tenuistriata* in the Beočin outcrop was magnetostratigraphically dated as 11.23 Ma. The following *Candona (Propontoniella) candeo* Zone is 18 m thick. The overlying *Amplocypris abscissa* Zone was sampled in 6.5 m thickness. Because *Candona (Reticulocandona) reticulata,* first appearing in the Beočin succession at ca. 10.2 Ma, has its first occurrence in the upper part of this 6.5 m interval, we tentatively suggest that the age of the investigated Pannonian interval is 11.6–10 Ma.

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Plate I – I. tábla

The depicted specimens are adult individuals. LV = left valve, RV = right valve / *Az ábrákon felnőtt egyedek szerepelnek oldalnézetben. LV = bal teknő, RV = jobb teknő*

1 – *Amnicythere parallela* (MÉHES 1908), RV in lateral view, scale: 200 µm, D29

2 – *Cyprideis pannonica* (MÉHES 1908), RV in lateral view, scale: 500 µm, D8

3 – *Cyprideis* ex gr. *heterostigma* POKORNÝ 1952, RV in lateral view, scale: 500 µm, D219

4 – *Hemicytheria tenustriata* (MÉHES 1908), LV in lateral view, juvenile specimen, scale: 200 µm, D15.

5 – *Hemicytheria tenustriata* (MÉHES 1908), RV in lateral view, scale: 200 µm, D12

6 – *Hemicytheria lorenthey* (MÉHES 1908), RV in lateral view, scale: 500 µm, D29

7 – *Hemicytheria hungarica* (MÉHES 1908), LV in lateral view, scale: 200 µm, D15

8 – *Hemicytheria hungarica* (MÉHES 1908), RV in lateral view, scale: 250 µm, D7

9 – *Loxocorniculina hodonica* POKORNÝ 1952, RV in lateral view, scale: 250 µm, D15

10 – *Candona (Candona)* aff. *postsarmatica* KRSTIĆ 1972, LV in lateral view, scale: 500 µm, D8

11 – *Candona (Candona)* aff. *postsarmatica* KRSTIĆ 1972, RV in lateral view, scale: 500 µm, D8

12 – *Candona (Propontoniella) macra* KRSTIĆ 1972, RV in lateral view, scale: 250 µm, D4

13 – *Candona (Propontoniella) candeo* KRSTIĆ 1972, RV in lateral view, scale: 200 µm, D213

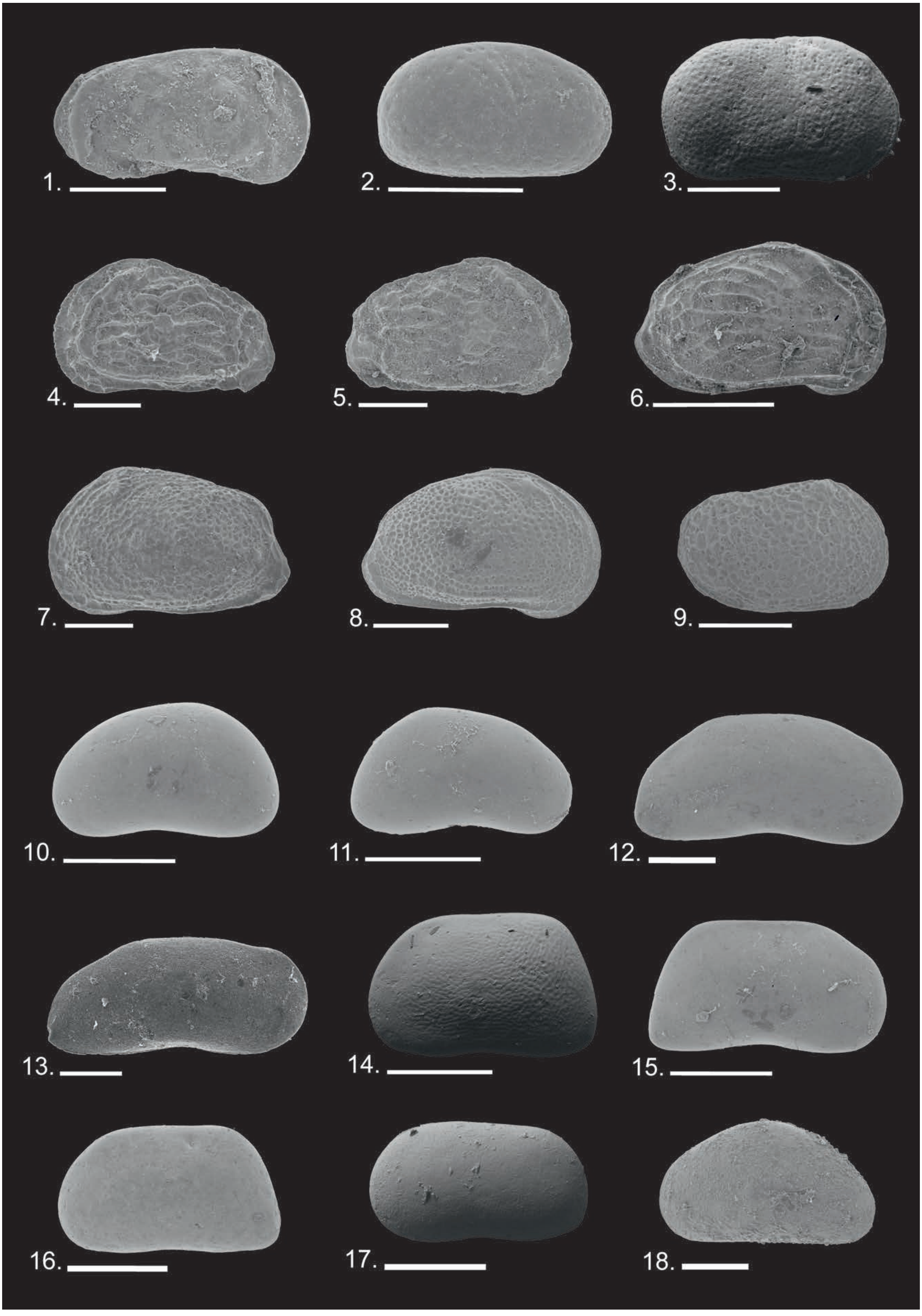
14 – *Candona (Reticulocandona) reticulata* (MÉHES 1908), LV in lateral view, scale: 500 µm, D216

15 – *Candona (Thaminocypris) transylvanica* (HÉJJAS 1894), RV in lateral view, scale: 500 µm, D4

16 – *Candona (Thaminocypris) transylvanica* (HÉJJAS 1894), LV in lateral view, scale: 500 µm, D7

17 – *Candona (Sinegubiella) rakosiensis* (MÉHES 1907), LV in lateral view, scale: 200 µm, D213

18 – *Candona (Thyphlocypris)* cf. *fossulata* POKORNÝ 1952, RV in lateral view, scale: 250 µm, D14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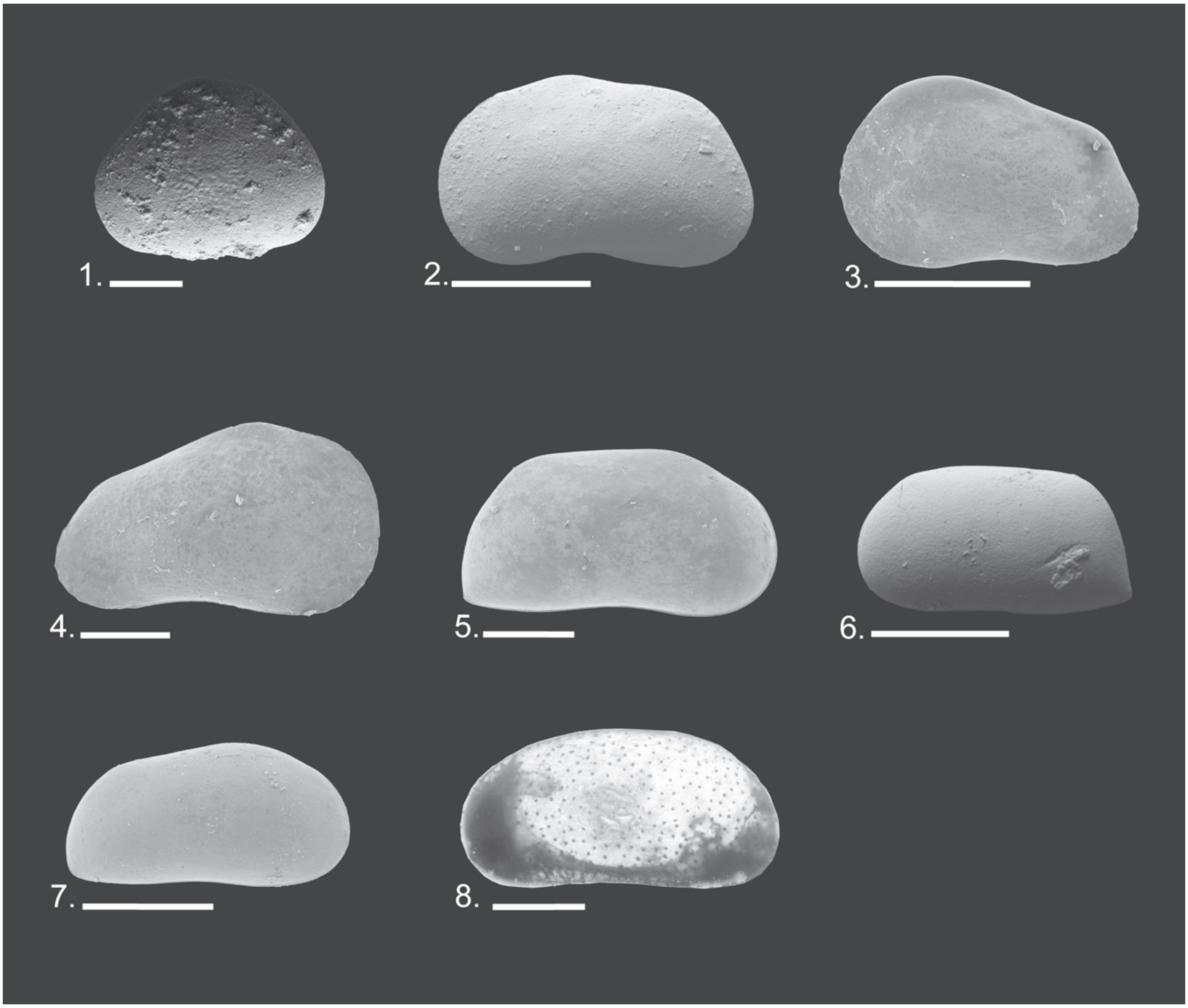

Plate II – II. tábla

Where not indicated otherwise, the depicted specimens are adult individuals. LV = left valve, RV = right valve / *A 3, 4, 6. ábrán juvenilis, a többin felnőtt egyedek szerepelnek oldalnézetben. LV = bal teknő, RV = jobb teknő*

1 – *Cypria siboviki* KRSTIĆ 1968, LV in lateral view, scale: 200 μm, D209

2 – *Herpetocyprella auriculata* (REUSS 1850), LV in lateral view, scale: 500 μm, D200

3 – *Herpetocyprella hieroglyphica* (MÉHES 1907), juvenile LV in lateral view, scale: 500 μm, D9

4 – *Herpetocyprella hieroglyphica* (MÉHES 1907), juvenile RV in lateral view, scale: 250 μm, D9

5 – *Amplocypris abscissa* (REUSS 1850), RV in lateral view, scale: 500 μm, D213

6 – *Amplocypris major* KRSTIĆ 1973, juvenile LV in lateral view, scale: 250 μm, D213

7 – *Amplocypris firmus* KRSTIĆ 1973, RV in lateral view, scale: 500 μm, D4

8 – *Amplocypris recta* (REUSS 1850), LV in lateral view, scale: 500 μm, D15

Appendix

Systematic Palaeontology

Here we follow the classification of HORNE et al. (2002) and HARTMANN & PURI (1974). The lists of synonyms and the *Stratigraphic range and geographic distribution* sections contain items which were published with proper illustrations of specimens. The Pécs-Danitzpuszta specimens are deposited in the Department of Palaeontology, Eötvös Loránd University, Budapest. Abbreviations: L: length, H: height.

Phylum Arthropoda SIEBOLD & STANNIUS 1845
Subphylum Crustacea PENNANT 1777
Class Ostracoda LATREILLE 1802
Order Podocopida MÜLLER 1894
Suborder Cytherocopina BAIRD, 1850
Superfamily Cytheroidea BAIRD, 1850
Family Leptocytheridae HANAI 1957
Genus *Amnicythere* DEVOTO 1965

Amnicythere parallela (MÉHES, 1908)
Plate I, fig. 1

1908 *Krithe parallela* n. sp. – MÉHES, pp. 550–551, pl. 10, figs 1–3.
1960 *Leptocythere parallela* (MÉHES) – KRSTIĆ, p. 279, pl. 1, figs 19–20; pl. 2, figs 22–33; pl. 3, figs 16–17; pl. 4, figs 6, 7, 10–16.
1972 *Leptocythere parallela* (MÉHES) – SOKAČ, p. 66, pl. 30, figs 4, 7–10.
1973a *Leptocythere* (*Amnicythere*) *parallela* (MÉHES) – KRSTIĆ, pp. 57–58, figs 4–11; pl. 5, figs 1–3; pl. 6, fig. 5.
1973a *Leptocythere* (*Amnicythere*) aff. *parallela* (MÉHES) – KRSTIĆ, pp. 58–59, figs 12–16; pl. 1, fig. 6.
1980 *Leptocythere parallela* (MÉHES) – IONESI & CHINTAUAN, pl. 1, fig. 3.
1982 *Leptocythere parallela* (MÉHES) – SZÉLES, p. 252, fig.12.
1985 *Leptocythere* (*Amnicythere*) aff. *parallela* (MÉHES) – KRSTIĆ, pl. 11, fig. 4.
1986 *Leptocythere parallela* (MÉHES) – IONESI & CHINTAUAN, pl. 1, fig. 8.

Material: Danitzpuszta trench (4 valves)

Dimensions: L = 485.930–583.422 µm, H = 242.577–288.425 µm, L/H = 2.003–2,23 µm

Stratigraphic range and geographic distribution: lower Sarmatian (Volhynian) and Maeotian of the Euxinian Basin and lower Pannonian of the Pannonian Basin: Sarmatian (upper Volhynian) of Southern Dobrogea (IONESI & CHINTAUAN 1986); Maeotian of Moldova (IONESI & CHINTAUAN, 1980); Pannonian of the Vienna Basin in the Czech Republic and Mt. Medvednica in Croatia (SOKAČ 1972), Sopron (Darufalva) (MÉHES 1908) and Tengelic (SZÉLES 1982) in Hungary, Prnjavor in Bosnia (KRSTIĆ 1985), and Malo Bučje, Velika Moštanica, Sibovik–5, Vrčin in Serbia (KRSTIĆ 1960, 1973a).

Family Cytherideidae SARS 1925
Subfamily Cytherideinae SARS 1925
Genus *Cyprideis* JONES 1857

Cyprideis pannonica (MÉHES, 1908)
Plate I, fig. 2

1908 *Cytheridea pannonica* n. sp. – MÉHES, pp. 553–555, pl. 11, figs 6–14.
1929 *Cytheridea pannonica* MÉHES – ZALÁNYI, p. 73, textfig 351: 10, 361: 6.
1944 *Cytheridea pannonica* MÉHES – ZALÁNYI, p. 90, p. 172.
1944 *Cyprideis pannonica* (MÉHES) – POKORNÝ, pp. 292–293, pl. 1, figs 3–4.
1960 *Cyprideis pannonica* (MÉHES) – KOLLMANN, p. 163, pl. 13, figs 1–4.
1959 *Cyprideis pannonica* (MÉHES) – ZALÁNYI, p. 213.
1963 *Cyprideis pannonica* (MÉHES) – SZÉLES, pl. 6, figs 1–2.
1966 *Cyprideis pannonica* (MÉHES) – HANGANU, pl. 40. fig. 2.
1968a. *Cyprideis* (*Cyprideis*) cf. *pannonica* (MÉHES) – KRSTIĆ, p. 111, pl. 1, figs 2–3.
1970 *Cyprideis pannonica* (MÉHES) – TRELEA et al. pp. 111–112, pl. 3, figs 10 a–c.
1973 *Cyprideis pannonica* (MÉHES) – BENSON, text–fig. 2, E–F.
1974 *Cyprideis pannonica* (MÉHES) – CERNAJSEK, pp. 473–474, pl. 2, fig. 5.
1975 *Cyprideis pannonica* (MÉHES) – IONESI & CHINTAUAN, pl. 1, fig. 3.
1976 *Cyprideis pannonica* (MÉHES) – CHINTAUAN & NICORICI, p. 12, pl. 1, figs 5–7.
1978 *Cyprideis pannonica* (MÉHES) – CARBONNEL, pl. 1, figs 11–13.
1978 *Cyprideis pannonica* (MÉHES) – BENSON, pl. 2, figs 4–8.
1979 *Cyprideis* (*Cyprideis*) *pannonica* (MÉHES) – BASSIOUNI, pp. 84–85, pl. 1, figs 1–6.
1980 *Cyprideis pannonica* (MÉHES) – IONESI & CHINTAUAN, pl. 1, fig. 2.
1983 *Cyprideis pannonica* (MÉHES) – JIŘIČEK, pl. 6, fig. 32.
1985 *Cyprideis pannonica* (MÉHES) – IONESI & CHINTAUAN, pl. 1, fig. 2.
1985 *Cyprideis pannonica* (MÉHES) – JIŘIČEK, p. 396, pl. 53, figs 1–4.
1990 *Cyprideis* (*Cyprideis*) ex. gr. *pannonica* – KRSTIĆ & STANCHEVA, pl. 9, fig. 10.

1996 *Cyprideis pannonica* (MÉHES) – ÜNAL, p. 92, pl. 1, fig. 9–11.
1998 *Cyprideis pannonica* (MÉHES) – KOVÁČ et al., pl. 4, figs 5–6.
2000 *Cyprideis pannonica* (MÉHES) – CHINTAUAN, pl. 1, fig. 7.
2001 *Cyprideis pannonica* (MÉHES) – TUNOĞLU & ÜNAL, p. 171, pl. 1, fig. 8.
2005 *Cyprideis pannonica* (MÉHES) – RADU & STOICA, pl. 2, figs 9–11.
2008 *Cyprideis pannonica* (MÉHES) – NAZIK et al., pl. 1, figs 8–9.
2008 *Cyprideis pannonica* (MÉHES) – BEKER et al., p. 9, pl. 1, figs 1–3.
2011 *Cyprideis pannonica* (MÉHES, 1908) – WITT, pl. 1, fig. 1.
2011 *Cyprideis pannonica* (MÉHES) – FILIPESCU et al., text-fig. 5, fig. 15.
2013 *Cyprideis pannonica* (MÉHES) – STOICA et al., pl. 2, fig. 1.

Material: Danitzpuszta trench (4 valves)
Dimensions: L = 851.243–875 µm H = 475.02–501.493 µm, L/H = 1.745–1.792
Stratigraphic range and geographic distribution: Sarmatian to Pannonian of the Pannonian Basin system, Sarmatian to Meotian of the Dacian Basin, Sarmatian of the Euxinian Basin, upper Miocene of the Aegean Basin, Messinian of the Eastern Mediterranean Basin, upper Miocene to Plio-Pleistocene of continental Turkey: Sarmatian in Nexing in Austria (CERNAJSEK 1974); Tusa (CHINTAUAN & NICORICI 1976), Livezile (CHINTAUAN 2000), and Oarba de Mureş (FILIPESCU et al. 2011) in Transylvania, Romania; Pannonian in Malacky M–16 borehole in Slovakia (KOVÁČ et al. 1998); Hodonín (POKORNÝ 1944; JIŘIČEK 1983, 1985) and Svatobořice–Mistřín (CARBONNEL 1978) in the Czech Republic; Drassburg in Austria (KOLLMANN 1960); Sopron, Peremarton, Budapest–Kőbánya, Tiszta berek, Duna–Tisza Interfluve (MÉHES, 1908, ZALÁNYI 1944, SZÉLES 1963) and Tihany (ZALÁNYI 1959) in Hungary; Badnjevac, Varovnica in Serbia (ZALÁNYI 1929, KRSTIĆ 1968a); Krško in Slovenia (KRSTIĆ & STANCHEVA 1990); Szócsán/Soceni in Transylvania, Romania (MÉHES 1908); Sarmatian in Hârlău (TRELEA et al. 1970, RADU & STOICA 2005), Siret and Moldova valleys (IONESI & CHINTAUAN 1975, 1980) in Romania; Meotian at Teleajen river, Prahova, Brăteşti (HANGANU 1966, IONESI & CHINTAUAN, 1980) and Rămnicu Sărat (STOICA et al. 2013) in Romania; Sarmatian in Pinarhisar in Turkey (WITT 2011) and Văleni (Dobrogea) in Romania (IONESI & CHINTAUAN 1985); ?upper Miocene („Pannonian and Pontian") in Gelibolu BE–18 in Turkey (ÜNAL 1996; TUNOĞLU & ÜNAL 2001); Messinian in DSDP Leg 42A, Site 376, Florence Rise, W of Cyprus (BENSON 1978) and DSDP Leg 13, Site 129, Hole 129A, Levantine Basin (BENSON 1973); upper Miocene in Arguvan, Malatya in Turkey (BASSIOUNI 1979; NAZIK et al. 2008); Plio-Pleistocene in Karapınar-Konya in Turkey (BEKER et al. 2008).

Cyprideis ex gr. *heterostigma* POKORNÝ, 1952
Plate I, fig. 3

Material: Danitzpuszta pit (256 valves, 1 carapace)
Dimensions: L = 570.382–1130 µm, H = 309.585–663 µm, L/H = 1.704–1.842
Remarks: The anterodorsal outline shows a variability in convexity, maybe due to sexual dimorphism. There is significant variability in the convexity of the valves as well; it is difficult to decide whether it reflects intraspecific variation or higher convexity is a diagnostic morphological character of another species. There are more adults than juveniles.

Family Hemicytheridae PURI 1953
Subfamily Hemicytherinae PURI 1953
Genus *Hemicytheria* POKORNÝ 1952

Hemicytheria tenuistriata (MÉHES, 1908)
Plate I, figs 4–5

1908 *Cythereis tenuistriata* n. sp. – MÉHES, pp. 559–561, text-figs 5–10.
1985 *Graptocythere (Hemicytheria) tenuistriata* (MÉHES) – KRSTIĆ, pl. 13, fig. 5.
2011 *Hemicytheria tenuistriata* (MÉHES) – OLTEANU, pl. 26, fig. 8.
2013 *Hemicytheria tenuistriata* (MÉHES) – TER BORGH et al., pl. 8, fig. 5.

Material: Danitzpuszta pit (13 valves); Danitzpuszta trench (19 valves)
Dimensions: L = 399–802.624 µm H = 247–476.447 µm, L/H = 1.615–1.685
Stratigraphic range and geographic distribution: lower Pannonian in the Pannonian Basin: Sopron in Hungary (MÉHES 1908); Velika Moštanica (KRSTIĆ 1985) and Beočin (TER BORGH et al. 2013) in Serbia.

Hemicytheria lorentheyi (MÉHES, 1908)
Plate I, fig. 6

1908 *Cythereis Lőrentheyi* n. sp. – MÉHES, pp. 561–562, pl. 8, figs 1–6.
1960 *Hemicytheria lőrentheyi* (MÉHES) – KRSTIĆ, p.280, pl. 1, fig. 23; pl. 3, fig. 20; pl. 4, fig. 5.
1969 *Hemicytheria* cf. *loerenthei* (MÉHES) – GRAMANN, pp. 501, pl. 35, fig. 4.
1972 *Hemicytheria lőrentheyi* (MÉHES) – IONESI & CHINTAUAN, pp. 101–102, pl. 5, fig. 4.
1983 *Hemicytheria lorentheyi* (MÉHES) – JIŘIČEK, pl. 6, fig. 31.
1985 *Hemicytheria lorentheyi* (MÉHES) – JIŘIČEK, p. 405, pl. 56, figs 4–6.
2004 *Hemicytheria lorentheyi* (MÉHES) – GROSS, p. 86, pl. 13, figs 5–6; pl. 14 fig. 9.

Material: Danitzpuszta trench (1 valve)
Dimensions: L = 1003.76 µm H = 591.47 µm, L/H = 1.697
Stratigraphic range and geographic distribution: Sarmatian of the Euxinian Basin, lower Pannonian of the Pannonian Basin, and Messinian (Meotian–Pontian) of the Aegean (Strymon) Basin: Sarmatian of Moldova (IONESI & CHINTAUAN, 1972); lower Pannonian of Sopron, Budapest–Kőbánya, Peremarton, Hungary (MÉHES 1908); Belgrade, Serbia (KRSTIĆ 1960); Mataschen, Austria (GROSS 2004); Bučany–48, Slovakia (JIŘIČEK 1983); Mutěnice, Czech Republic (JIŘIČEK, 1985); Messinian (Meotian–Pontian) of Strymon Basin (GRAMANN 1969).

Hemicytheria hungarica (Méhes, 1908)
Plate I. figs 7–8

1908 *Cythereis hungarica* n. sp. – Méhes, pp. 562–563, pl. 8, figs 7–9.
2009 *Hemicytheria hungarica* (Méhes) – Tóth, p. 89, pl. 5, figs 4–5 cum. syn.
2010 *Hemicytheria hungarica* (Méhes) – Zorn, p. 266, pl. 1, fig. 13.

Material: Danitzpuszta pit (6 valves); Danitzpuszta trench (27 valves)

Dimensions: L = 531.444–823.895 µm H = 301.321–483.859 µm, L/H =1.703–1.763

Stratigraphic range and geographic distribution: Sarmatian of the Euxinian Basin, Sarmatian and lower Pannonian of the Pannonian Basin system: Sarmatian of the Caucasus region (Schneider, 1953); Sarmatian of the Danube Basin, Slovakia (Dornič & Kheil 1963) and Csákvár, Hungary (Tóth 2009); lower Pannonian of Sopron (Darufalva) and Budapest–Kőbánya in Hungary (Méhes 1908); Prnjavor in Bosnia (Krstić 1985); Drassburg in Austria (Zorn 2010).

Family Loxoconchidae Sars 1925
Genus *Loxocorniculina* Krstić 1972

Loxocorniculina hodonica Pokorný, 1952
Plate I, fig. 9

1952 *Loxoconcha hodonica* n. sp. – Pokorný, pp. 308–309, pl. 5, figs 1, 2, 9, figs 36–37.
1960 *Loxoconcha hodonica* Pokorný – Krstić, p. 281, pl. 2, fig. 28.
1963 *Loxoconcha hodonica* Pokorný – Grekoff & molinari, p. 5, pl.2, figs 5–6.
1966 *Loxoconcha hodonica* Pokorný – Hanganu, pl. 43, fig. 3.
1969 *Loxoconcha* cf. *hodonica* Pokorný – Gramann, pp. 509–510, pl. 34, figs 1–2.
1972 *Loxoconcha hodonica* Pokorný – Sokač, pp. 84–85, pl. 44, figs 6–7.
1972a. *Loxoconcha* (*Loxocorniculina*) *hodonica* Pokorný – Krstić, p. 253, pl. 4, fig. 7; pl. 6, figs 4–6.
1972 *Loxoconcha hodonica* Pokorný – Sissingh, p. 133, pl. 10, figs 15–16.
1985 *Loxoconcha* (*Loxocorniculina*) *hodonica* Pokorný – Krstić, pl. 12, fig. 10.
2013 *Loxocorniculina hodonica* (Pokorný) – ter Borgh et al., text-fig. 8, 30.
2016 *Loxocorniculina hodonica* Pokorný – Kovács et al., pl. 3, figs 2–3.

Material: Danitzpuszta trench (4 valves)

Dimensions: L = 475–535.852 µm H = 322.242–325 µm, L/H= 1.474–1.648

Stratigraphic range and geographic distribution: lower Pannonian of the Pannonian Basin system, Meotian of the Dacian Basin, Messinian of the Mediterranean Basin: lower Pannonian of Hodonín in the Czech Republic (Pokorný 1952); Mt. Medvednica in Croatia (Sokač 1972); Velika Moštanica, Sibovik–2a, Velika Plana, Vrčin, Belgrade, Makiš, and Beočin in Serbia (Krstić 1960, 1972a, 1985; ter Borgh et al. 2013); Lopadea Veche and Gârbovița in Transylvania, Romania (Kovács et al. 2016); Maeotian of Teleajen River valley, Prahova in Romania (Hanganu 1966); Messinian (Meotian–Pontian) of the Strymon Basin (Gramann 1969); Messinian (?) of Crete (Sissingh 1972); Messinian of Reggio Emilia in Italy (Grekoff & Molinari 1963).

Superfamily Cypridoidea Baird 1845
Family Candonidae Kaufmann 1900
Subfamily Candoninae Kaufmann 1900
Genus *Candona* Baird 1845

Candona (Candona) aff. *postsarmatica* Krstić, 1972
Plate I, figs 10–11

1972b. *Candona* (*Candona*) *postsarmatica* n. sp. – Krstić, pp. 9–11, pl. 2, figs 4–6; p. 113.
1972b. *Candona* aff. *postsarmatica* n. sp. – Krstić, pl. 4, fig. 2.
1980a. *Candona (Candona)* aff. *postsarmatica* Krstić – Krstić, fig. 10.
1985 *Candona (Candona) postsarmatica* Krstić – Krstić, pl. 3, fig. 2.
2011 *Candona (Caspiocypris) postsarmatica* – Olteanu, pl. 2, fig. 1.
2013 *Candona (Caspiocypris) postsarmatica* – Mazzini et al., pl. 2, fig. e.

Material: Danitzpuszta trench (10 valves)

Dimensions: L = 971.880–1000.739 µm H = 511.266–554.633 µm, L/H = 1.804–1.9

Remark: In her original publication Krstić depicted only females, without giving their size. Our specimens have more rounded outline, but it is difficult to decide if this difference is due to sexual dimorphism, ontogenetic state, or our material represents a different species.

Stratigraphic range and geographic distribution of C. postsarmatica: lower Pannonian of the Pannonian Basin system, Tortonian of Turkey: lower Pannonian of Belgrade and Aleksinac in Serbia (Krstić 1972b, 1980a, 1985); Carand in Transylvania, Romania (Olteanu 2011); Tortonian of Çankiri Basin, Tuğlu, in Turkey (Mazzini et al. 2013).

Candona (Propontoniella) macra Krstić, 1972
Plate I, fig. 12

1972b. *Candona (Propontoniella) macra* – Krstić, pp. 35–36, pl. 11, figs 15–18, p. 123.
1985 *Candona (Propontoniella) macra* – Krstić, pl. 1, fig. 9.
2016 *Candona (Propontoniella) macra* Krstić – Kovács et al., pl. 2, figs 9–12.
2019 *Propontoniella macra* – Spadi et al., text–fig 3, I; text–fig 16, F–I.

Material: Danitzpuszta pit (2 valves); Danitzpuszta trench (15 valves)

Dimensions: L = 725–984.157 µm H = 350–442.223 µm, L/H = 2.071–2.225

Stratigraphic range and geographic distribution: lower Pannonian of the Pannonian Basin system: Vranović–1, Mt.

Krndija, Croatia (SPADI et al. 2019); Velika Moštanica, Sibovik (Belgrade) in Serbia (KRSTIĆ 1972b, 1985); Cunța in Transylvania, Romania (KOVÁCS et al. 2016).

Candona (Propontoniella) candeo KRSTIĆ, 1972
Plate I, fig. 13

1972b. *Candona (Propontoniella) candeo* – KRSTIĆ, pp. 36–37, pl. 4, fig. 10; pl. 11, figs 1–4, figs 29–32; p. 124.
1985 *Candona (Propontoniella) candeo* – KRSTIĆ, pl. 2, fig. 3–6.

Material: Danitzpuszta pit (29 valves)
Dimensions: L = 736.87–827.2 μm H = 339.65–359.49 μm L/H = 2.3–2.44
Stratigraphic range and geographic distribution: lower Pannonian of the Pannonian Basin: Velika Moštanica, Sibovik creek in Serbia (KRSTIĆ 1972b, 1985).

Candona (Reticulocandona) reticulata (MÉHES, 1907)
Plate I, fig. 14

1907 *Aglaia reticulata* n. sp. – MÉHES, pp. 442–443, pl. 3, figs 10–14.
1962 *Candona (Lineocypris) reticulata* (MÉHES) – SOKAČ, pl. 1, fig. 6.
1963 *Candona (Lineocypris) reticulata* MÉHES – SZÉLES, pl. 5, fig. 5.
1971 *Candona (Lineocypris) reticulata* (MÉHES) – OLTEANU, p. 91, pl. 3, fig. 3.
1972b. *Candona (Reticulocandona) reticulata* (MÉHES) – KRSTIĆ, pp. 59–60, pl. 17, figs 1–2, 6–7; pl. 24, fig. 7; figs 48–49.
1972 *Candona (Lineocypris) reticulata* (MÉHES) – SOKAČ, pp. 53–54, pl. 23, figs 12–16.
1980b. *Candona (Reticulocandona) reticulata* (MÉHES) – KRSTIĆ, pl. 2, figs 4–6.
1982 *Candona (Lineocypris) reticulata* MÉHES – SZÉLES, p. 241, pl. 4, figs 2, 4–5.
2011 *Candona (Reticulocandona) reticulata* (MÉHES) – OLTEANU, pl. 9, fig. 4.
2011 *Reticulocandona reticulata* (MÉHES) – RUNDIĆ et al., pl. 9, figs 9–10.

Material: Danitzpuszta pit (10 valves)
Dimensions: L = 476.585–530.056 μm, H = 276.246–333.957 μm, L/H = 1.587–1.725
Remark: Although the the posterodorsal rim is variable, each individual has a diagnostic fine reticulation on the valve surface.
Stratigraphic range and geographic distribution: Pannonian of the Pannonian Basin: Szócsán/Soceni in Transylvania, Romania (MÉHES 1907); Budapest–Kőbánya, Danube–Tisza Interfluve, Tengelic in Hungary (MÉHES 1907; SZÉLES 1963, 1982); Mt. Medvednica in Croatia (SOKAČ 1962, 1972); Beočin, Belgrade (ZV–3) in Serbia (KRSTIĆ 1972b, 1980b; RUNDIĆ et al. 2011); Groşi, Rieni in Transylvania, Romania (OLTEANU 1971, 2011).

Candona (Thaminocypris) transylvanica (HÉJJAS, 1894)
Plate I, figs 15–16

1894 *Candona reticulata* n. sp. – HÉJJAS, p. 63, pl. 4, figs 14 a, b, c.
1972b. *Candona* (*Thaminocypris*) cf. *transylvanica* (HÉJJAS) – KRSTIĆ, pp. 63–64, pl. 18, fig. 8.
2016 *Candona* (*Caspiocypris*) *transilvanica* (HÉJJAS) – KOVÁCS et al., pl. 2, figs 5–8, 13–15.

Material: Danitzpuszta pit (18 valves); Danitzpuszta trench (40 valves)
Dimensions: L = 1035.667–1128.067 μm H = 558.371–669.064 μm, L/H = 1.686–1.854
Stratigraphic range and geographic distribution: lower Pannonian of the Pannonian Basin: Belgrade ("London" C–2) in Serbia (KRSTIĆ 1972b); Târgu Mureş, Băgău, Miercurea Nirajului, Lopadea Veche, Gârbovița, Cunța in Transylvania, Romania (HÉJJAS 1894, KOVÁCS et al. 2016).

Candona (Sinegubiella) rakosiensis (MÉHES, 1907)
Plate I, fig. 17

1907 *Aglaia rákosiensis* n. sp. – MÉHES, pp. 513–514, pl. 6, figs 8–13.
1972b. *Candona* (*Sinegubiella*) *rakosiensis* (MÉHES) – KRSTIĆ, p. 80, pl. 25, figs 8–11, pl. 30, fig. 1.
1972 *Candona* (*Caspiocypris*) *rakosiensis* (MÉHES) – SOKAČ, p. 39, pl. 15, figs 1–3.

Material: Danitzpuszta pit (4 valves)
Dimensions: L = 440–549.131 μm H = 230–289.469 μm, L/H = 1.897–1.913
Stratigraphic range and geographic distribution: lower Pannonian of the Pannonian Basin: Sopron, Budapest–Kőbánya in Hungary (MÉHES 1907); Mt. Medvednica in Croatia (SOKAČ 1972); Đurinci in Serbia (KRSTIĆ 1972b).

Candona (Typhlocypris) cf. *fossulata* POKORNÝ, 1952
Plate I, fig. 18

1952 *Candona fossulata* n. sp. – POKORNÝ, pp. 264–266, text–fig. 11, 12; pl. 2 fig. 1.
1972 *Candona (Typhlocypris) fossulata* POKORNÝ – SOKAČ, pp. 59–60, pl. 28, fig. 1.
1972b. *Candona (Typhlocypris)* aff. *fossulata* POKORNÝ – KRSTIĆ, p. 84, pl. 24, fig. 12; pl. 27, figs 4–7.
1980 *Candona (Typhlocypris)* ex. gr. *fossulata* POKORNÝ – FREELS, pp. 63–64, pl. 9, figs 21–26.

Material: Danitzpuszta trench (10 valves)
Dimensions: L = 828.630–1025 μm H = 460.177–550 μm, L/H = 1.801–1.863
Remark: The postero-dorsal and the ventral margin is more rounded than in the holotype.
Stratigraphic range and geographic distribution of C. fossulata: lower Pannonian of the Pannonian Basin, upper Miocene of Turkey: lower Pannonian in Hodonín in Czech Republic (POKORNÝ 1952); Mt. Medvednica in Croatia (SOKAČ 1972); Karagača creek in Serbia (KRSTIĆ 1972b); upper Miocene of Denizli basin in Turkey (FREELS 1980).

Subfamily *Cyclocypridinae* KAUFMANN 1900
Genus *Cypria* FISCHER 1855

Cypria siboviki KRSTIĆ, 1968
Plate II, fig 1

1968b. *Cypria siboviki* n. sp. – KRSTIĆ, p. 247–248, pl. 66, figs 1–2.
1972 *Cypria siboviki* KRSTIĆ – SOKAČ, pp. 64, pl. 24, figs 15–16, 19.
1975 *Cypria siboviki* KRSTIĆ – KRSTIĆ, p. 195–196, pl. 1, figs 1–2.
1975 *Cypria* aff. *siboviki* KRSTIĆ – KRSTIĆ, pl. 1, fig. 3.

Material: Danitzpuszta pit (2 valves)

Dimensions: L = 485–500.1 µm, H = 350–373.215 µm, L/H = 1.340–1,386

Stratigraphic range and geographic distribution: lower Pannonian of the Pannonian Basin: Mt. Medvednica in Croatia (SOKAČ 1972); Velika Moštanica, Sibovik 7/2 in Serbia (KRSTIĆ 1968b, 1975).

Family *Cyprididae* BAIRD 1845
Genus *Herpetocyprella* DADAY 1909

Herpetocyprella auriculata (REUSS, 1850)
Plate II, fig. 2

1850 *Cypridina auriculata* n. sp. – REUSS, p. 51, pl. 8, fig. 8.
1991 *Hungarocypris auriculata* (REUSS) – SZUROMI-KORECZ, pp. 225–228, pl. 17, figs 1–8, cum syn.
2008 *Herpetocyprella auriculata* (REUSS) – DANIELOPOL et al., p. 152, text-figs 2 C, D; 3A, C; 4 A–C, 10 D, E.
2011 *Hungarocypris auriculata* (REUSS) – OLTEANU, pl. 1, figs 2, 4–7, 9–10.
2016 *Herpetocyprella auriculata* (REUSS) – KOVÁCS et al., pl. 1, figs 6–10.

Materials: Danitzpuszta pit (35 valves); Danitzpuszta trench (22 valves)

Dimensions: L = 1166–675 µm H = 646–875 µm, L/H = 1.805–1.914

Stratigraphic range and geographic distribution: Pannonian of the Pannonian Basin system: Vienna (REUSS 1850) and Sankt Margarethen (DANIELOPOL et al. 2008) in Austria; Muteniče, Svatoborice, Hodonín, Stavěšice in the Czech Republic (POKORNÝ 1944, 1952; JIŘIČEK 1983, 1985; DANIELOPOL et al. 2008); Sopron, Tengelic, Nagykozárd, Máriakéménd, Tisztaberek in Hungary (MÉHES 1907, ZALÁNYI 1944, SZÉLES 1982, SZUROMI-KORECZ 1991); Mt. Medvednica in Croatia (SOKAČ 1972); Belgrade, Velika Moštanica, Sibovik 9, Đurinci in Serbia (KRSTIĆ 1973b, 1985); Holod, Şoimi (OLTEANU 2011), Gârboviţa, and Cunţa (KOVÁCS et al. 2016) in Transylvania, Romania.

Herpetocyprella hieroglyphica (MÉHES, 1907)
Plate II, fig. 3–4

1907 *Cypris hieroglyphica* n. sp. – MÉHES, p. 508, pl. 3, figs 15–19.
1991 *Hungarocypris hieroglyphica* (MÉHES) – SZUROMI-KORECZ, pp. 228–230, pl. 18, figs 1–2, cum syn.
2008 *Herpetocyprella hieroglyphica* (MÉHES) – DANIELOPOL et al., p. 153, text-fig. 11.
2011 *Hungarocypris hieroglyphica* (MÉHES) – OLTEANU, pl. 1, figs 1, 3, 8.
2016 *Herpetocyprella hieroglyphica* (MÉHES) – KOVÁCS et al., pl. 1, figs 1–5.

Materials: Danitzpuszta pit (25 valves); Danitzpuszta trench (13 valves)

Dimensions: L = 950.438–1807.306 µm H = 561.818–909.175 µm, L/H = 1,691 –1,987

Stratigraphic range and geographic distribution: lower Pannonian of the Pannonian Basin system: Danube–Tisza Interfluve in Hungary (SZÉLES 1963); Hodonín (JIŘIČEK 1985) and Stavěšice (DANIELOPOL et al. 2008) in the Czech Republic; Mt. Medvednica in Croatia (SOKAČ 1967, 1972); Vrčin, Karagača creek in Serbia (KRSTIĆ 1960, 1973b, 1985); Szócsán/Soceni (MÉHES 1907, DANIELOPOL et al. 2008), Şoimi, Holod (OLTEANU 1971, 2011), Lopadea, Gârboviţa, Cunţa (KOVÁCS et al. 2016) in Transylvania, Romania.

Subfamily Cypridopsinae BRONSTEIN 1947
Genus *Amplocypris* ZALÁNYI 1944

Amplocypris abscissa (REUSS, 1850)
Plate II, fig. 5

1972 *Amplocypris abscissa* (REUSS) – SOKAČ, p. 36, pl. 11, figs 2, 4, 6; pl. 13, figs 2, 4, 5–6.
1973c. *Amplocypris abscissa* (REUSS) – KRSTIĆ, pp. 102–103, pl. 1 fig. 4; pl. 4, figs 3–4, pl. 8, fig. 1.
1983 *Amplocypris abscissa* (REUSS) – JIŘIČEK, pl. 6, fig. 36.
1985 *Amplocypris abscissa* (REUSS) – JIŘIČEK, p. 393, pl. 51, figs 13–15.
1989 *Amplocypris abscissa* (REUSS) – OLTEANU, pl. 1, fig. 16.
2011 *Amplocypris abscissa* (REUSS) – DANIELOPOL et al., text-figs 1 A–B, 2, 3, 7–10.
2011 *Amplocypris* aff. *abscissa* (REUSS) – OLTEANU, pl. 5, fig. 5; pl. 22, fig. 5.

Material: Danitzpuszta pit (22 valves)

Dimensions: L = 726.027–1082.241 µm H = 356.025–553.896 µm, L/H = 1.954–2.039

Stratigraphic range and geographic distribution: lower Pannonian of the Pannonian Basin: Hodonín in the Czech Republic (JIŘIČEK 1983, 1985); Sankt Margarethen, Hennersdorf in Austria (DANIELOPOL et al. 2011); Mt. Medvednica in Croatia (SOKAČ 1972); Belgrade in Serbia (KRSTIĆ 1973c); Sinteşti in Transylvania, Romania (OLTEANU 1989, 2011).

Amplocypris major KRSTIĆ, 1973
Plate II, fig. 6

1972 *Amplocypris major* KRSTIĆ – SOKAČ, p. 36, pl. 13, figs 1–3.
1973c. *Amplocypris major* – KRSTIĆ, pp. 100–102, figs 61–65; pl. 5, figs 1–2.
1985 *Amplocypris major* KRSTIĆ – KRSTIĆ, pl. 5, figs 6–8.
2011 *Amplocypris major* KRSTIĆ – OLTEANU, pl. 4, fig. 3.

Material: Danitzpuszta pit (5 valves)

Dimensions: L = 964.906–1331 µm H = 516.333–653 µm, L/H = 1.869–2.038

Stratigraphic range and geographic distribution: Pannonian of the Pannonian Basin: Mt. Medvednica in Croatia (SOKAČ 1972); Belgrade in Serbia (KRSTIĆ 1973c, 1985); Soceni in Transylvania, Romania (OLTEANU 2011).

Amplocypris firmus KRSTIĆ, 1973
Plate II, fig. 7

1973c. *Amplocypris firmus* n. sp. – KRSTIĆ, pp. 103–104, pl. 1, fig. 1; pl. 3, fig. 2; pl. 10 figs 1–3.
1973c. *Amplocypris* cf. *firmus* KRSTIĆ – KRSTIĆ, pl. 8, fig. 4.
1985 *Amplocypris firmus* – KRSTIĆ, pl. 6, fig. 4.
2013 *Amplocypris* ex. gr. *firmus* KRSTIĆ – TER BORGH et al., fig. 7/1.
2016 *Amplocypris firmus* KRSTIĆ – KOVÁCS et al., pl. 1, figs 15–19.

Material: Danitzpuszta trench (7 valves)

Dimensions: L = 825–1082.267 µm H = 375–540.935 µm, L/H = 2.001–2.2

Stratigraphic range and geographic distribution: lower Pannonian of the Pannonian Basin system: Velika Moštanica, Sibovik 7/2, Beočin, Đurinci in Serbia (KRSTIĆ 1973c; TER BORGH et al. 2013); Gârbovița, Cunța in Transylvania, Romania (KOVÁCS et al. 2016).

Amplocypris recta (REUSS, 1850)
Plate II, fig. 8

1850 *Cytherina recta* n. sp. – REUSS, p. 52, pl. 8, fig. 11.
1972 *Amplocypris recta* (REUSS) – SOKAČ, p. 35, pl. 11, figs 5, 7–8.
1973c. *Amplocypris recta* (RSS.) – KRSTIĆ, p. 113, pl. 3, fig. 1; pl. 16, figs 6–7.
1973c. *Amplocypris* ex. gr. *recta* (RSS.) – KRSTIĆ, p. 113, pl. 16 figs 4–5.
1982 *Amplocypris recta* REUSS – SZÉLES, p. 246, pl. 7, figs 4–5.
1982 *Amplocypris* aff. *recta* REUSS – SZÉLES, pp. 246–247, pl. 7, fig. 6; pl. 7, figs 1, 3.
1983 *Amplocypris recta* (REUSS) – JIŘIČEK, pl. 6, fig. 35.
1985 *Amplocypris* aff. *recta* (REUSS) – JIŘIČEK, p.392, pl. 51, figs 10–12.
1985 *Amplocypris recta* (REUSS) – KRSTIĆ, pl. 15, fig. 1.
1998 *Amplocypris recta* (REUSS) – KOVAČ et al., pl. 4, fig. 9.
1998 *Amplocypris recta* (REUSS) – PIPÍK & HOLEC, pl. 1, figs 1–2.
2004 *Amplocypris recta* (REUSS) – PIPÍK et al., pl. 1, fig. 14.
2011 *Amplocypris recta* – DANIELOPOL et al., fig. 4.
2011 *Amplocypris recta* (REUSS) – OLTEANU, pl. 22, fig. 7.

Materials: Danitzpuszta pit (3 valves); Danitzpuszta trench (34 valves)

Diemensions: L= 631,410 – 1717,526 µm, H= 331,675 – 867,911 µm, L/H= 1,904 –1,979

Stratigraphic range and geographic distribution: Pannonian of the Pannonian Basin system: Moosbrunn (REUSS 1850) and Sankt Margarethen (DANIELOPOL et al. 2011) in Austria; Studienka (PIPÍK et al. 2004), Borský Svätý Jur (PIPÍK & HOLEC 1998), and boreholes in the Vienna Basin (KOVAČ et al. 1998) in Slovakia; Hodonín in the Czech Republic (JIŘIČEK 1983, 1985); Tengelic in Hungary (SZÉLES 1982); Mt. Medvednica in Croatia (SOKAČ 1972); Đurinci in Serbia (KRSTIĆ 1973c, 1985); Şoimi in Transylvania, Romania (OLTEANU 2011).