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Late Miocene ostracodes of Serbia: morphologic and palaeoenvironmental considerations

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Abstract. About 11.5 million years ago, a tectonic uplift of the Eastern and Western Carpathians separated the Pannonian Basin from the rest of the Paratethys. This orogenesis event caused an unconformity between the Sarmatian brackish sediments and the Pannonian lake-sea deposits. More than 6 Ma later, in these parts of the Paratethys, changes in the geographic framework, hydrological conditions and brackish – caspibrackish water chemistry led to the disappearance of restricted marine forms of life. A few euryhaline and marginal marine species survived this environmental change. Among the ostracodes, some originally freshwater taxa, such as *Candoninae,* entered the lake-sea. Many lineages show gradual morphological changes. The older, low diversity ostracode fauna from the Lower Pannonian dispersed to the endemic species and genera during the Upper Pannonian. This interval is assigned as the "bloom time" for many ostracodes, both qualitatively and quantitatively. This time sequence is the last appearances of genera such as *Aurila, Cytheridea*, *Propontoniella,* etc. and simultaneously, the first appearances for many new genera, such as *Zalanyiella, Serbiella, Camptocypria, Sinegubiella* etc. During the Pontian, migration processes were present. Therefore, it can be supposed that many eastern Paratethyan forms have Pannonian origin.

Key words: Late Miocene, ostracodes, morphology, paleoenvironment, Serbia.

Апстракт. На прелазу између средњег и горњег миоцена, пре око 11,5 милиона година, тектонска издизања у Карпатима су довела до одвајања Панонског простора од остатка Паратетиса. То је резултирало дискорданцијом између сарматских, бракичних и панонских, каспибракичних наслага. Скоро 6 милиона година касније, промене географских прилика, хидролошких услова и формирање ослађене водене средине, довеле су до потпуног изумирања морских организама. Само неколико еврихалинских форми као и оних који су настањивали приобалне делове успело је да се прилагоди и преживи. Код остракода, слатководни облици попут кандонина, све више настањују такво велико језеро-море док неки филогенетски низови показују постепене измене. Старије панонска, слабије разноврсна остракодска фауна еволуира у неке ендемичне облике током млађег панона када долази и до правог процвата остракода, како по броју врста тако и по броју јединки. То је период последњег појављивања родова *Aurila, Cytheridea*, *Propontoniella* односно време првог појављивања родова *Zalanyiella, Serbiella, Camptocypria, Sinegubiella.* За време понта, запажени су миграциони процеси на овом простору и сматра се да многи облици који живе у источном Паратетису имају панонско порекло.

Кључне речи: млађи миоцен, остракоде, морфологија, палеоекологија, Србија.

Introduction

As a product of Alpine tectonics in the Late Oligocene and the Early Miocene, a few molasse basins were created along the northern foreland of the uplifting mountain ranges in middle and southeastern Europe (Fig. 1). Although, each basin has its own individual history, their developments display some common features; repeated cycles of isolation from the world oceans, as inferred from the barrenness of the fauna or the presence of endemic organisms, and evolution from fully marine through brackish to caspibrackish and fluvial depo-environments (Kovač & Marton, 1998; Pipík, 2000; Fordinal *et al.*, 2006;). Temporary isolation and filling of the western-central Paratethyan basins started from west to east. Firstly, the Alpine molasse

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basin was filled with sediments during the Middle Miocene, then the Pannonian Basin during the Late Miocene–Early Pliocene and, finally, the Dacian Basin during the Pliocene (HORVATH, 1990; MAGYAR *et al.*, 1999). Simultaneously, the eastern Paratethyan basins (Black Sea and Caspian) remained aquatic (SAFAK, 2002; TUNOGLU, 2001, 2002, 2003; WITT, 2003).

During the Late Miocene, most of Serbia belonged to the Pannonian Basin, while a small part of eastern Serbia corresponded to the Dacian area. During this time interval, there was a brief connection between them, but the most important period was during the existence of the so-called "Pannonian–Pontian lake-sea", a deposition area completely isolated and closed from the east by the Carpathian Mountains. Some authors when referring to the Pannonian and Pontian Stages used the name *Lake Pannon* (MAGYAR & GEARY, 1999; MAGYAR *et al.*, 1999; MÜLLER *et al.*, 1999; SZUROMI-KORECZ *et al.*, 2004). The above-mentioned connections between the basins established in the Pontian represented the last phase of the evolution of the western Paratethys. Subsequently, the Pannonian Basin disappeared as a lake-sea and transformed to a marshland environment. On the other side of the Carpathians Mt., the Dacian Basin still continued its existence during the early Pliocene.

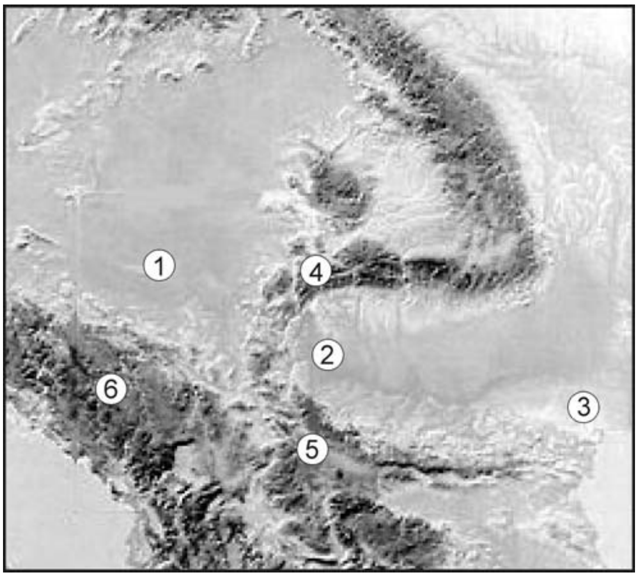


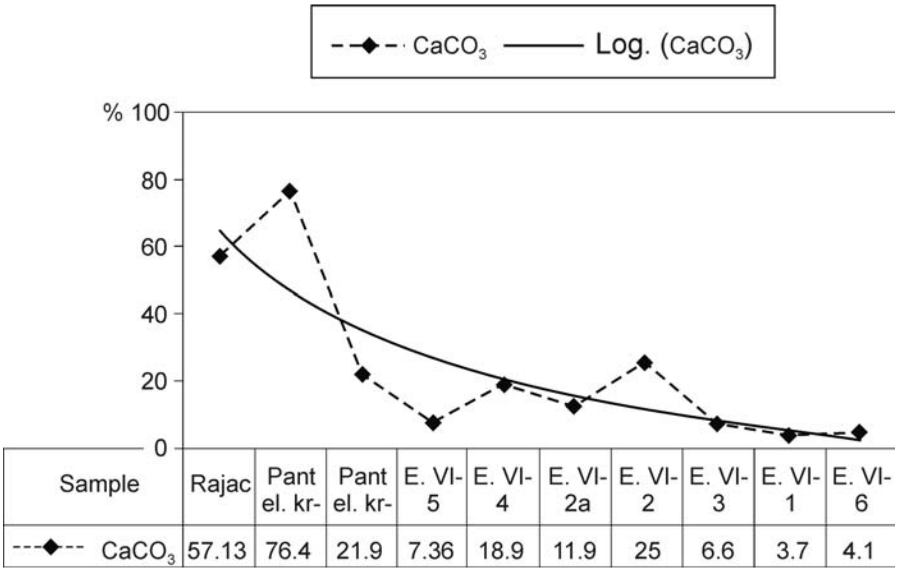
Fig. 1. The Late Miocene Paratethyan province: **1**, the Pannonian Basin; **2**, the Dacian Basin; and **3**, Euxinian Basin; **4**, the Carpathians Mt.; **5**, the Balkans Mt.; and **6**, the Dinarides.

Sedimentological studies have been limited to the investigation of main grain-size classes (rudites, arenites and lutites). Among forty samples, 42% of them are rudites (> 2mm), 38% are sand (0.63–2mm) and 20% are mud (< 0.63 mm). These deposits are slightly dominated by a coarse mean grain-size of gravel and sand (rudites, > 2mm). The distribution of the sedimentary material follows the expected general, fluvial lacustrine model: the coarsest deposits are distributed in the main channels, associated with a more dynamic water regime. On the contrary, the smaller particles occur in zones of low energy (OBRADOVIĆ & JOVANOVIĆ, 1987). Except in the opening of the main channel (the Kolubara Bay), where tidal currents and waves continuously generated high dynamic conditions throughout the year, the mean grain-size pattern does not correspond to a dynamic regime during the major part of the year.

Table 1. CO_2 and $CaCO_3$ content of the well Rgh-107.5, the Kolubara basin, western Serbia.

BOREHOLE Rgh-107.5	SAMPLES No.	Depth (m)	% CO_2	% $CaCO_3$
1	01	05.70–06.80	3.20	7.27
2	16	92.70–93.00	1.20	2.73
3	27	139.60–139.80	2.00	4.55
4	28	144.00–144.20	2.40	5.46
5	29	150.00–150.20	4.40	10.00
6	31	168.70–168.90	2.40	5.46
7	35	192.00–192.20	2.80	6.36
8	41	234.00–234.20	5.60	12.73
9	42	240.30–240.50	14.40	32.73
10	43	247.30–247.50	1.20	2.73
11	44	257.00–257.20	35.60	80.92
12	45	262.40–262.60	29.60	67.28
13	46	267.50–267.70	34.40	78.19

For example, in the well Rgh-107.5 (Kolubara Basin), there are rapid decreases of calcium carbonate from the bottom to the top of the investigated well (Table 1). More consolidated deposits, such as Sarmatian limestones and sandstones, contain up to 80% of $CaCO_3$. On the other hand, semi-consolidated Pannonian and Pontian marls and sands contain a low percent of carbonate, as well as of carbon dioxide. Sample No. 28 (144.00–144.20 m) corresponds to marly sands and marls (OBRADOVIĆ & JOVANOVIĆ, 1987). Sands have a symmetrical grain size distribution and good sorting. Sandy marls shown similar effects. It is concluded that there was multiple alteration in the profile of the fluvial and near shore lake-sea deposits. Fluvial flows dispersed silicoclastites to the near shore parts and temporary deposited them on the land or alluvial environment. Somewhat different cases were observed on the sandy-silts (maximum 21.46% sand) and silts (maximum 98.95% silt) from the Late Miocene sediments of eastern Serbia. These deposits were earlier investigated by KRSTIĆ *et al.* (1992, 1995, 1997) and MIHELČIĆ (1990, 1991). There is a clear trend of decreasing calcium carbonate toward the younger Miocene Stages (Fig. 2). Also, curves of sorting and grain-size values show that the sediments have middle to good sorting and dominantly an asymmetrical grain-size distribution. Some other characteristics, such as pH (7.7–7.9)



Sample	Rajac	Pant el. kr-	Pant el. kr-	E. VI-5	E. VI-4	E. VI-2a	E. VI-2	E. VI-3	E. VI-1	E. VI-6
CaCO$_3$	57.13	76.4	21.9	7.36	18.9	11.9	25	6.6	3.7	4.1

Fig. 2. Decreasing trend of CaCO$_3$ from the Bessarabian to the Pontian (sandy-silts and silts from some localities of the Dacian Basin of eastern Serbia, after DODIKOVIĆ, 2001).

and Eh (+26 to –20), indicate that these deposits are the products of a slightly alkaline and low reduction environment (DODIKOVIĆ, 2001).

Quantitative and qualitative diversity of ostracodes

In the western and central Serbia (an example of the Kolubara Basin), more than 36 genera with 206 ostracod species were identified in the Late Miocene (RUNDIĆ, 1997). The most abundant taxa are representatives of *Candoninae,* including genera such as *Camptocypria*, *Cryptocandona*, *Fabaeformiscandona*, *Hastacandona*, *Lineocypris*, *Pontoniella*, *Propontoniella*, *Serbiella*, *Sinegubiella*, *Thaminocypris* etc. with about 80 species. Among the more abundant genera are *Amplocypris* (25 species), *Cyprideis* (23), *Loxoconcha* (22), *Hemicytheria* (20) and *Amnicythere* (19), which represent together about 90% of the total number of specimens. The findings of *Cypria* (8 species), *Hungarocypris* (4), *Xestoleberis* (3), *Candona* (2), *Ilyocypris*, *Tyrrhenocythere*, *Mediocytherideis* and *Stenocypria* (all with one species) were scarce and they represent only 10% of the mentioned population. Most of them have been recognized as infra/sublittoral. A smaller number of taxa have been found in the intertidal zone. Individual abundance may exceed 400 individuals per sample. Species diversity increases appreciably from the Lower Pannonian and is maximal during the Upper Pannonian (Fig. 3). This basin is the most illustrative example of marginal deposition in the whole of western and central Serbia during the Late Miocene. Other areas have more-less similar characteristics, except the northern province of Serbia (Vojvodina), where there is carbonate development. The best example of this kind is on the Fruška Gora Mt., where the Upper Pannonian is represented by fine grained "cement marls", which correspond to the deeper part of the Pannonian Basin. The ostracod assemblages contain several genera, such as *Typhlocyprella,*

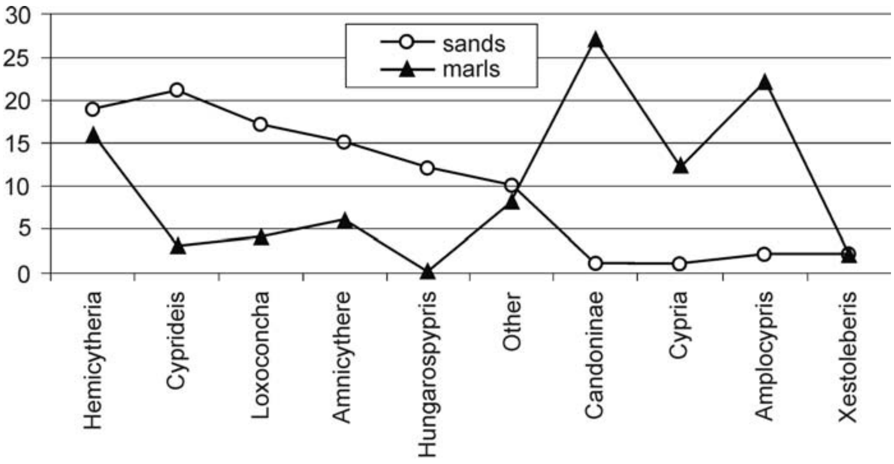


Fig. 3. Species number of main genera in relation to the sediments. The Lower Pannonian of the Kolubara Basin.

Zalanyiella, Camptocypria, *Serbiella*, *Amplocypris*, *Hemicytheria*, *and Cypria*. Apart from *Candoninae*, all other genera are represented by a few species only and their percentage contribution to the total population is small. The most abundant forms are different *Reticulocandona*, *Zalanyiella*, *Serbiella*, *Camptocypria*, etc. It seems that some representatives of *Candoninae* prefer more fine-grained deposits than the others.

In the eastern Serbia (Dacian Basin), there are certain similarities with the Pannonian basin but the ostracodes represent a different paleoenvironment, including a greater numbers and diversity of *Leptocytherinae* (Table 2). Conversely, the *Candoninae* are not as diversified as in the Pannonian Basin. During the Late Miocene (Late Bessarabian – Pontian), the ostracodes had the greatest diversity in the Maeotian and Pontian. The most abundant genera are representatives of *Leptocytherinae* (*Amnicythere*, *Euxinocythere*, *Maeotocythere*) on the one hand, and different forms of *Candoninae* on the other (> 80%). More than others, Dacian and Euxinian species, such as *Amnicythere sinegubi* KRSTIĆ, *A. alizadei* SHEIDAEVA, *A. palimpsesta* (LIVENTAL) *A. subcaspia* (LIVENTAL), *Maeotocythere prebaquana* (LIVENTAL*)*, *Euxinocythere immutata* STANCHEVA, *E. suzini* (SCHNEIDER) etc., have been found.

Among the *Candoninae*, *Candona* ex gr. *neglecta* Sars, *C. fagiolata* STANCHEVA, *Camptocypria ossoinensis* KRSTIĆ, *Camptocypria balcanica* ZALÁNYI, *Hastacandona pontica* AGALAROVA, *Bakunella guriana* (LIVENTAL*)*, *Reticulocandona orientalis* KRSTIĆ, *Pontoniella paracuminata* KRSTIĆ, have been identified. Genera such as *Loxoconcha, Aurila, and Xestoleberis* are present in Sarmatian with a small number of species and relatively abundant specimens. In the higher stratigraphic levels, in addition to representatives of *Candoninae* and *Leptocytherinae*, the rare *Darwinula*, *Getocytheria, Stanchevia, Mediocytherideis, Tyrrhenocythere* etc. have been found. Most interestingly, representatives of the genus *Cyprideis* have a very small frequency and are limited to a few species, unlike the Pannonian basin. There are also similar results regarding the Pontian ostracodes from the eastern Black Sea region of Turkey (TUNOGLU, 2001, 2002, 2003).

Generally, there is a high diversity in the ostracod assemblages of the Upper Pannonian, Chersonian and also Maeotian. What are the possible reasons for this? First of all, there are some external factors, such as tectonic events and geographical isolation, the consequences of which were relatively stable aquatic conditions and an adequate range of time. If the Sarmatian *s. str.* – Upper Pannonian time period (over 2 Ma) is considered, then it can be said that the time interval was sufficient for taxonomic adaptation. During the older Pannonian, the first 'shock' affects the ostracodes and other fauna. The already freshened and relatively well-adapted Sarmatian brackish forms could not tolerate more freshening. Some of genera are completely absent, for example: *Cytheridea*, *Miocyprideis*, *Cyamocytheridea*, *Aurila,* etc. However, some other representatives, such as *Loxoconcha*, *Leptocythere*, *Hemicytheria,* etc., managed to survive the critical point and later developed special features as result of the adaptation. Mesohaline to freshwater and river-marsh genera, such as different *Candona*, *Cypria*, *Amplocypris*, and *Hungarocypris*, played the most important role. They are the markers for the future new ostracod assemblages, which consequently occur at the beginning of the Upper Pannonian. The second important event in the ostracod development during the Pannonian was the first appearance of many new taxons, such as *Zalanyiella*, *Camptocypria*, *Serbiella*, *Lineocypris*, *and Thaminocypris,* etc. There was also an increase in the ostracod abundance and diversity. An individual abundance may exceed a few hundred individuals per sample. At the same time, there was a high rate of speciation, which was probably the result of some optimal conditions and natural factors, such as geographic isolation, lake-sea adaptation, reproductive mode and dispersal, sexual selection, etc. (MARTENS, 1997). According to these authors, the tempo and manner of speciation were very different in various ancient lake assemblages. An example of a high diversity phenomenon, considered by MAYBURY & WHATLEY (1988), was the Upper Pliocene faunas of Cornwall, England and northwest France. They concluded that "*the high diversity symbolize general result of many factors as favourable preservation, high abundance, competent niche exploitation, the mixing of brackish, marine, cold and warm water species and some degree of allopatric speciation due to partial isolation of faunas because of the incomplete transgression of the Armorican and Cornubian massifs*".

It seems that there are many similarities between these and the Upper Pannonian assemblages. It was the time of the highest development of the faunas of the Pannonian basin. Biostratigraphically, it was the acme zone for many species (an example, the genus *Hemicytheria* represent 75% of all individuals).

After the Pannonian, tectonic subsidence of the Carpathian belt resulted in the reconnection of the Pannonian and Dacian Basins during the Pontian for the last time. At the beginning, thanatocoenoses were slightly different with many transitional types. Later, these differences became more visible. The faunal assemblages had new elements, such as *Bakunella*, *Tyrrhenocythere,* etc. During the Upper Pontian in this widespread environment, there was a trend of decreasing biodiversity among the ostracodes, unlike the previous period. The habitat was more saline and it resulted in species reduction. Analogous ideas were presented by BODERGAT (BONADUCE & SGARRELLA, 1999). The samples have numerous specimens but with relative few species. On the other hand, the faunas show an eastwards migration trend as some genera occupied eastern provinces and finally the Dacian Basin. In my opinion, many of the ostracod genera from the Dacian area have a Pannonian origin. In the Dacian Basin, for example,

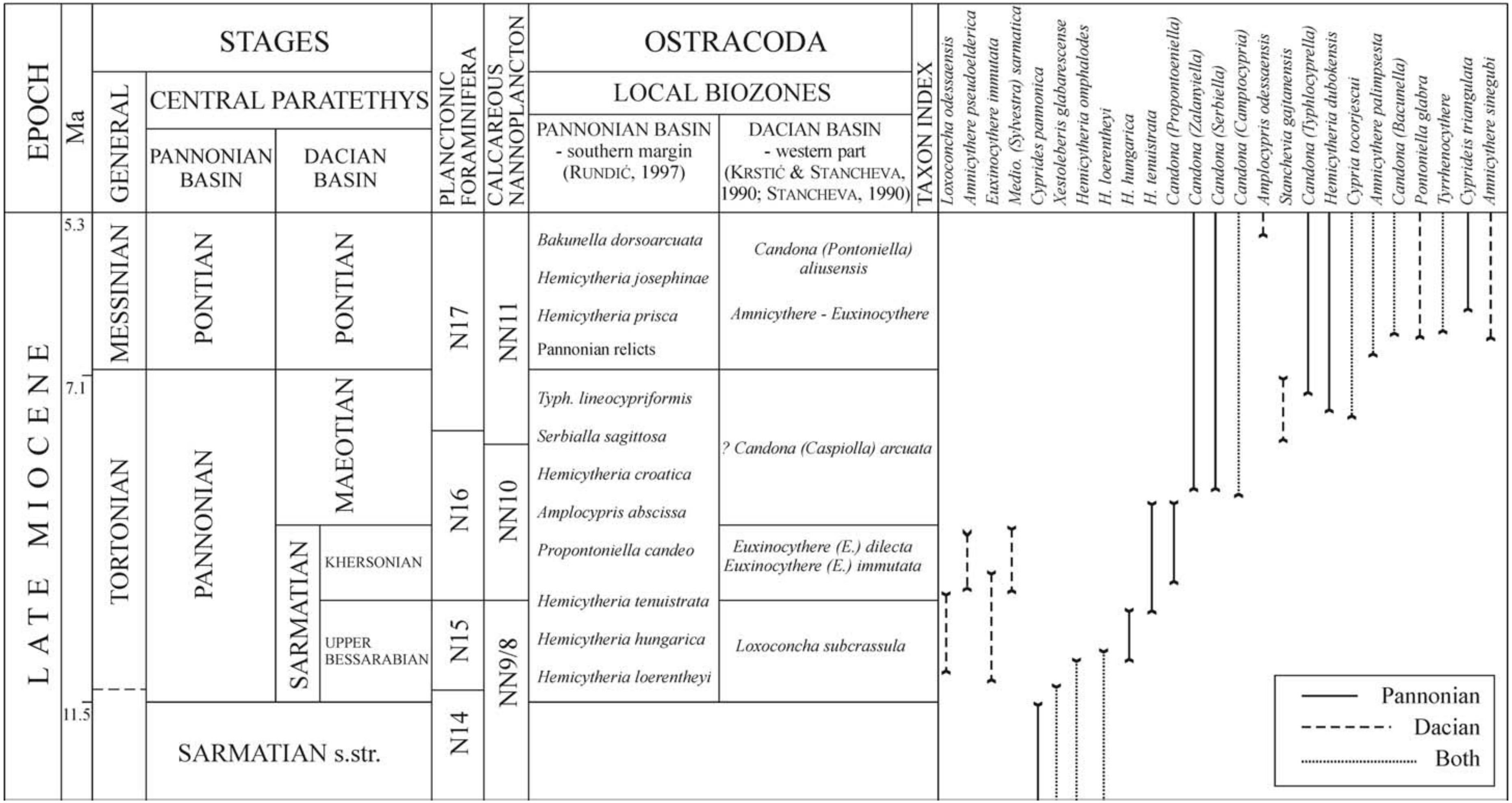


Table 2. The correlation chart of the Late Miocene of Central Paratethys of Serbia and local ostracodes biozonation.

there are very abundant and diversified associations with *Amnicythere, Pontoniella*, *Candona*, *Bakunella* and *Tyrrhenocythere* in the younger levels of Pliocene (OLTEANU, 1998, 2000). There are also similar results regarding some representatives of molluscs (MÜLLER *et al*., 1999).

Morphological and phyllogenetical relationships (an example of the genus *Hemicytheria*, POKORNY)

An attempt has been made to correlate morphological features with some phylogenetical and paleoecological characteristics of the genus *Hemicytheria*. In earlier ostracod references, there are many different considerations concerning the genus *Hemicytheria*. In some, it was considered as an independent genus like in the first Pokorny description (POKORNY, 1955; STANCHEVA, 1971; SOKAČ, 1972; OLTEANU & VEKUA, 1989; OLTEANU, 2001; RUNDIĆ, 2002). Others considered it to be one of the subgenus: *Heterocythereis* (*Hemicytheria*) and *Heterocythereis* (*Tyrrhenocythere*) – MORKHOVEN (1962); *Graptocythere* (*Hemicytheria*) or *Aurila* (*Hemicytheria*) – KRSTIĆ, 1985, 1990. STANCHEVA (1971) divided the genus *Hemicytheria* on the three subgenus: *Getocytheria*, *Hemicytheria s. str*. and *Tyrrhenocythere*. The main parameters for these taxonomic relationships were: carapace morphology, hinge structure, muscle scars pattern and type of marginal pore canals. The anatomy of the soft body of recent representatives of the subfamily *Hemicytherinae* were also explored (MCKENZIE & BONADUCE, 1993).

Based on paleontological standards, some of the characteristics of the fossil representatives of the genus *Hemicytheria* could be shown. Above all, based on the carapace morphology, there are two main groups of *Hemicytheria*: one with a pitted and the other with a reticulated sculpture. It is not possible to clearly determine the phylogenetic evolution of *Hemicytheria*. It can be assumed because of biostratigraphical results in Early Pannonian deposits, that there was a branching off of the phylogenetic lineage in the Lower Pannonian. SOKAČ (1972) believed it probably occurred in the Upper Pannonian. The older Pannonian forms have pitted sculptures [*Hemicytheria ampullata* (MEHES), *H. hungarica* (MEHES)] which presented descendant species for smooth branch (*H. marginata* SOKAČ) and reticulate branch (*H. reticulata* SOKAČ, *H. dubokensis* KRSTIĆ). SOKAČ also considered the smooth forms to be phylogenetically younger because the marginal pore canals can be straight as well as bifurcated, whilst the pitted forms have only straight pore canals. The oldest Pannonian species, *H. omphaloedes* (REUSS) and *H. loerentheyi* (MEHES), also have a reticulated surface. Therefore, it could be said that the branching off occurred during the Lower Pannonian because there are representatives with both types of sculptures (only if the oldest forms of *Hemicytheria* are considered as the independent subgenus – *Graptocythere*). During the Upper Pannonian, there are forms with both types of ornamentation. In the Pontian, only three reticulated species remained whilst the pitted ones had disappeared. The ascendant/descendant problems are impossible to solve at this moment, because of the necessity for a very detailed instars analysis. If the marginal pore canals are considered, SOKAČ (1972) correctly claimed that the younger forms have both straight and bifurcated pore canals while the oldest pitted *Hemicytheria* have only straight ones. Meanwhile, investigations have shown that all the older species have straight pore canals, both the pitted and reticulated morphotypes.

The carapace size can reveal some of the rules of the development of *Hemicytheria*. Diagrams of the mean value of length and the L/H ratio are correlated and they show the trend of ostracod carapace development. In these diagrams (Figs. 4, 5), two trends in shell development can be seen. The first one is the continuous tendency of the value to increase from the Lower Pannonian to the Upper Pannonian, when some of the *Hemicytheria* have a maximal value. The second one, the opposite trend is visible during the Pontian when the *Hemicytheria* species decreased in value and lost some of their features, while some species disappeared completely. Most of large Upper Pannonian hemicytherids died off. During the Lower Pontian, there are transitional Pannonian/Pontian forms but they are not of great significance and disappear afterwards. From the relatively numerous Pannonian hemicytherids, only a few species survived [*H. josephinae* (ZALÁNYI)*, H. portafericae* RUNDIĆ and *H. pejinovicensis* (ZALÁNYI)] in the Upper Pontian. Small forms represented only 5% of total number of species. There is gradual increase in value during the Pannonian. In the Late Pannonian, the ostracodes "bloom" and all of *Hemicytheria* species have maximal dimensions. Forms of 1 mm in length represented about 40% of the total species and they dominated throughout the Upper Pannonian. Some transitional Pannonian/Pontian types have large shells but later the carapace trends to decrease in size. The best examples are Late Pontian species, which have smaller dimensions. The five greatest forms, according to the size of their shells, represented about 25% of the total species and all of them occurred during the Upper Pannonian and Pontian, especially (*H. dubokensis* KRSTIĆ*, H. portafericae* RUNDIĆ – Figs. 3, 4).

It can be concluded that there was a gradual disappearance of hemicytherids during the Late Miocene in the Pannonian Basin, as well as during the Maeotian in the Dacian Basin. This was the result of an increasingly freshening environment, which led to a completely freshwater biotope at the beginning of the Pliocene. The low percentages of dissolved carbonates and low salinity tolerance were not sufficient for the existence of hemicytherids. Meanwhile, later in the Dacian Basin there were similar forms represented by the genus

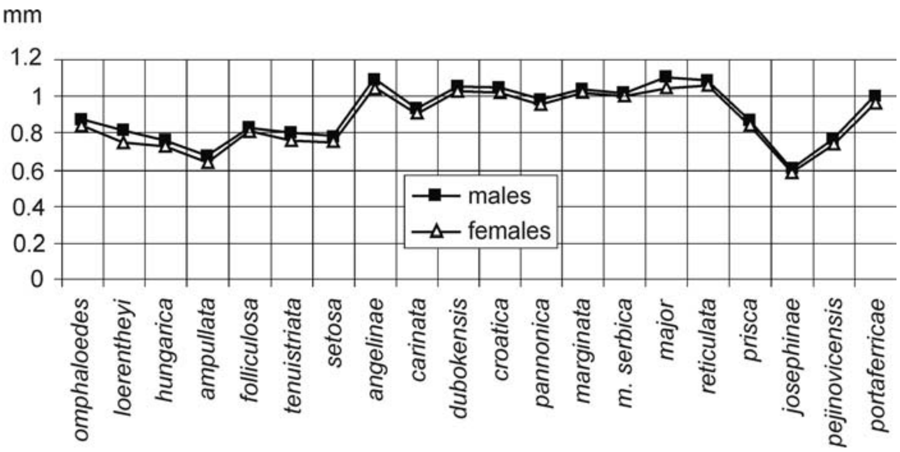
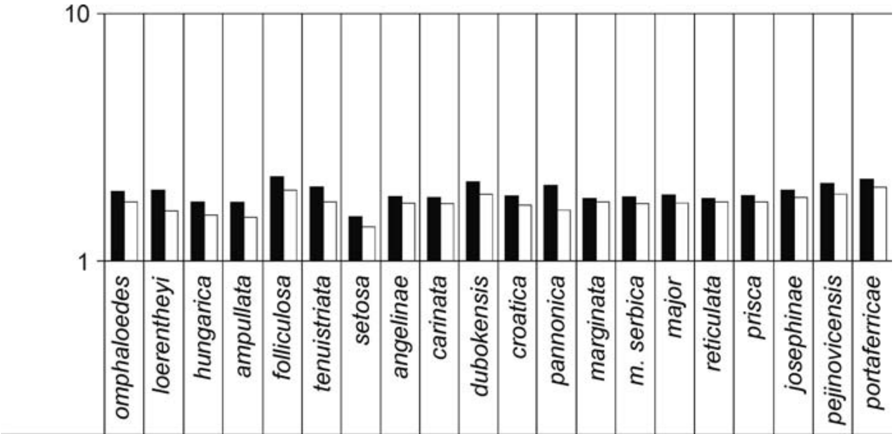


Fig. 4. The mean value of the length (mm) for the all of *Hemicytheria* species during the Pannonian and Pontian.



	omphaloedes	loerentheyi	hungarica	ampullata	folliculosa	tenuistriata	setosa	angelinae	carinata	dubokensis	croatica	pannonica	marginata	m. serbica	major	reticulata	prisca	josephinae	pejinovicensis	portaferricae
■ males	1.9	1.9	1.7	1.7	2.1	2	1.5	1.8	1.8	2.1	1.8	2	1.7	1.8	1.8	1.7	1.8	1.9	2	2.1
□ females	1.7	1.6	1.5	1.5	1.9	1.7	1.4	1.7	1.7	1.8	1.7	1.6	1.7	1.7	1.7	1.7	1.7	1.8	1.8	2

Fig. 5. Length/height ratio for some *Hemicytheria* species.

Tyrrhenocythere (Krstić, 1975; Krstić & Stancheva, 1990; Olteanu, 2000; Olteanu & Vekua, 1989; Stancheva, 1990). The genus *Tyrrhenocythere* has only been found in two wells in the Kolubara Basin during the Pontian (Rundić, 1997), despite the fact that more than 40 wells have been investigated in a diameter of about 30 km. The findings of the Pannonian realm from other locations are very limited. This could be explained by the fact that during the Pontian both basins communicated and migration processes between their inhabitants occurred for the last time. In addition, some other genera found in the Dacian Basin, such as *Bakunella, Pontoniella* and *Mediocytherideis* and probably many molluscs, have a western origin. After the Pontian, the Pannonian Basin finally disappeared.

Paleoenvironmental considerations

The main paleoenvironmental interpretations are based on the quantitative and qualitative analyses of ostracod assemblages and their morphological reflection to the main physico-chemical parameters of the habitat, including temperature, oxygen content, ionic concentration, salinity, etc.

According to Peypouquet (1979) and Rundić (1998), there is a connection between the sculpture and the Mg/Ca ratio of the carbonate of carapaces. Calcite crystals, constituting the hard layer of the carapace, are built perpendicular to the cuticle and their thickness is proportional to the Mg content of the crystal network. Frequently, the most gradated types are found in seawater conditions, the Mg content of which is higher than in freshwater conditions. As stated by Smith & Horne (2002), in nonmarine aquatic systems, the calcite mineral branch point represents an important step in determining the major ion composition of natural waters. In dilute water, below approximately 0.3 g/l, the most common major ions are bicarbonate, calcium and magnesium. With increasing salinity, these ionic concentrations rise, until calcite saturation is attained and calcite precipitates, at a total ionic concentration of approximately 0.3 g/l. This is the calcite branch point, the first mineral branch point in natural waters. Beyond this point, at about 1.4 g/l, the water becomes depleted in calcium and enriched in bicarbonates, or vice versa, resulting in a solute path towards bicarbonate enriched, calcium depleted saline water, or bicarbonate depleted, calcium enriched saline water. Ultimately, other mineral branch points are attained (gypsum, for example) and further changes in the major ion composition occurs [EUGSTER & JONES (1979), *in*: SMITH & HORNES, 2002]. However, some authors consider that this hypothesis is not sufficient. Namely, studies of the New Caledonia area have shown that, despite a high Mg/Ca ratio, the morphotypes are not more gradated than in others sites, and certainly less than the specimens living in seawaters where this ratio has only standard values. Other parameters, such as calcium content of the available food, pH and Redox potential (HOIBIAN *et al.*, 2000), may have a contributing effect on carapace calcification. Ornamentation of many ostracod shells is affected by the Mg/Ca ratio of lake water: with Mg/Ca >1, the carapaces are heavily reticulate and the opposite ratio favors smooth ostracod valves. For example, CHIVAS *et al.* (1983) noted the connection between the thickness and ornamentation of an ostracod carapace and the water depth for fossil material obtained from Lake Buchanan in Queensland. They found that ostracodes belonging to the genus *Paracypris* associated with charophytes had a thick shell with a rarely visible reticulation and commonly no spines. Assemblage with charophytes indicates shallow water (up to 2 m), since this is the preferred habitat of these algae. In the same core, specimens of *Reticypris* with reticulated and often spinose shells are thought to indicate deeper water (> 2 m), since remains of shallow-water charophytes are absent (CARBONEL *et al.*, 1988).

Essential in paleoenvironmental studies of the Serbian Late Miocene ostracod assemblages are 1) geographical position and 2) time range. It must be realised that there are extensive erosion and unconformity between Sarmatian restricted marine sediments and younger, caspibrackish deposits (RUNDIĆ, 1995, RUNDIĆ & MITROVIĆ,1998). This, by mountains enclosed system, was affected by continental water, which resulted in a brackish lake-sea and the nearly total extermination of marine biota. Only a few ostracod genera were able to survive these environmental changes (*Aurila*, *Loxoconcha*, *and Xestoleberis*). The newly formed habitats and gradually expanding lake-sea created a kind of "ecological gap", and stimulated the rapid evolution of survivors and the immigration of freshwater dwellers from the marshes, ponds and rivers (most of *Candona*, *Darwinula, Ilyocypris,* etc.). As with other fossils and in a still existing *long living lake* (MÜLLER *et al.*, 1999), the originally low diversity fauna radiated into a large number of related endemic species and genera in the expanding and ecologically unoccupied lake-sea. The best examples for this are the many genera of Candonids, which had a radiated development during the Pannonian Stage. From the small number of species and genera during the Lower Pannonian (such as *Propontoniella* and *Cryptocandona*), in the Upper Pannonian there was an expansive evolution of these lineages (*Serbiella, Zalanyiella, Camptocypria, Sirmiella, Lineocypris, Typhlocyprella,* etc.) in both species and specimens. They are immigration forms from the marginal rivers and swamps, but most of them are the result of time resolution. Most of them are endemic species and lived only in this realm, such as *Hungarocypris*, which is a typical near shore dweller, preferring a sandier type of stratum. It is scarce in associations from fine-grained sediments. Its large and massive carapace must be the result of a rich ionic concentration, as well as living in warm, oxygenated and clear water (RUNDIĆ, 1991). However, the fossil record includes only three species of *Hungarocypris* with numerous individuals during the Pannonian–Pontian. The genus *Amplocypris* shows similar characteristics. The appearance of corpulent forms, strong carapaces and clear ornamentation give evidence for a shallow-water basin type with mobile flow and an important donation of land material. In normal oxygenated habitats, increasing ionic concentrations led to an increase in the number of sculptured morphotypes. The best examples are representatives of the family Cytherideidae (*Hemicytheria*, *Loxoconcha*, *Leptocythere*, and *Cyprideis*) with mostly ornamented forms. Analyses of the genus *Hemicytheria* in both Pannonian and Pontian deposits show that more than 90% of the species have ornamented shells. Taphonomic analysis of fossil associations, particularly the numerous specimens of *Hemicytheria setosa* RUNDIĆ, shows that during the Late Miocene, salinity was not the principal influence on the occurrence of valves and the type of ornamentation. This ornamented form lived on coastal and mobile parts of the Pannonian lake-sea and its ornamentation is a reaction to the adaptation. On the other hand, the Upper Pontian nodose forms lived in environments with decreased salinity and increased organic matter and silica (*Leptocythere*, *Ilyocypris*). In the Kolubara coal basin, these forms were discovered in sediments with a rich organic content. Based on sedimentological studies, data concerning transport and depositional mechanisms, which appear with intermittent alteration between fluvial and coastal deposition, are obtained. Fluvial flows brought and deposited more silicoclastics in the coastal regions, but in the alluvial part of the land, this occurrence was only periodic (well Rgh-107.5). MÜLLER *et al.* (1999), suggesting that the Pannonian–Pontian lake-sea continuously shrank in the north, due to the prograding deltas. They stated that the more southerly shores were much less affected by progradation. The shoreline remained in more or less the same position for a longer period of time. Along these shores, successions of paralic lignite beds were formed (STEVANOVIĆ *et al.*, 1990). In phases of highstand, the lake-sea enlarged in some areas in the south and the shoreline became simpler as large islands became flooded. Coarse-grained clastic rims formed around the islands. From the very beginning of the lake-sea, these coarse clastics were often capped by white calcareous marl or limestone in the southern part of the basin, in locations far from the river mouths.

Modern analogues of Pannonian–Pontian ostracodes from the modern Ponto-Caspian regions have been used to estimate the paleosalinity of the lake-sea. These comparisons suggest that the average salinity of the Pannonian–Pontian lake-sea may have been approximately 10–12 ‰, but that significant local differences existed in shallow parts, such as the southern "shelf" dominated by river deltas. Natural water examination gives data similar to the results of the paleoecological approach. Down from the lacustrine prodelta silt, which is a regional stamp in the basin, inborn waters have salt in an amount approximately, or sometimes even higher, than that of normal marine salinity. Innate waters from above the silt, however, are diluted because of mixing with meteoric water, as shown by the diagenetic carbonates. The salinity of these diluted waters is about 5 ‰, which sets the lower limit for the original lake-sea salinity (MÜLLER *et al.*, 1999).

Conclusions

According to qualitative and quantitative analysis of the ostracodes, the results of a factor analysis applied to the most frequent species to the population structures, it is possible to distinguish several different assemblages based on salinity:

- *Stenocypria, Cyprinotus, Cypridopsis, Ilyocypris, Darwinula* and *Candona* characterize the oligohaline environments (0.5–8 ‰ of NaCl) and indicate a shallow, coastal part of river mouths or in swamps. They occurred in the lowest parts of the Pannonian and in the Upper Pontian.
- *Hungarocypris, Thaminocypris, Propontoniella, Cypria, Serbiella, Camptocypria, Zalanyiella, Typhlocyprella, Pontoleberis,* etc. represent the dominant group of the caspibrackish–mesohaline habitats (8–18 ‰). All of them are related to the entire Pannonian–Pontian and lived in shallow infralittoral environments covered by water plants.
- Assemblages with *Cyprideis, Amplocypris, Leptocythere*, *Hemicytheria, Loxoconcha* and *Xestoleberis* represents more meso- to polyhaline (18–30 ‰) habitats and these associations occupied most of the southern Pannonian estuary (the Kolubara Basin, the Velika Morava Bay, eastern Serbia). Estuaries are semi-enclosed coastal waterbodies in which there is a salinity gradient from fully marine (35 ‰) to fresh water. The salinity varies due to tidal and seasonal influences.
- Ornamented forms of ostracodes lived in the coastal parts and the sculpture is a reaction to adaptation.
- Increases of ionic concentrations resulted in increased diversity (for ex. mostly of Upper Pannonian ostracodes)
- A deficiency of oxygen and a low Mg/Ca ratio in the water can eliminate sculptured morphotypes.
- Nodose ostracodes from the Upper Pontian (*Amnicythere, Ilyocypris*) lived under conditions of low salinity and increased organic matter.

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Резиме

Млађе миоценске остракоде Србије: морфолошка и палеоеколошка разматрања

Пре око 11,5 милиона година, тектонска издизања у Карпатима су довела до одвајања Панонског простора од остатка Паратетиса. То је резултирало дискорданцијом између сарматских, бракичних и панонских, каспибракичних наслага. Почетком плиоцена, промене географских прилика, хидролошких услова и формирање ослађене водене средине, довеле су до потпуног изумирања морских организама. Само неколико еврихалинских форми као и оних који су настањивали приобалне делове успело је да се прилагоди и преживи. Код остракода, слатководни облици попут кандонина, све више настањују такво велико језеро-море док неки филогенетски низови показују постепене измене. Старије панонска, слабије разноврсна остракодска фауна еволуира у неке ендемичне облике током млађег панона. Горњи панон је време процвата остракода, како по броју врста тако и по броју јединки. То је период последњег појављивања родова *Aurila, Cytheridea*, *Propontoniella* односно време првог појављивања родова *Zalanyiella, Serbiella, Camptocypria, Sinegubiella*. За време понта, запажени су миграциони процеси на овом простору и сматра се да многи облици који живе у источном Паратетису имају панонско порекло.

Остракоде које су настањивале Панонску провинцију, а посебно њене маргиналне делове, делимично су се разликовале од оних које су живеле у Дакијској провинцији. Основни разлози леже у чињеници да су те две провинције у појединим етапама током старијег горњег миоцена – панона, биле међусобно одвојене. Свака биопровинција је имала своје посебне карактеристике. Панонска је била више изолована и формирала је временом специфичну остракодску заједницу. Старије асоцијације су биле сиромашније јер су егзистовале у једној новој средини у односу на дотадашње услове. То се посебно добро види на примеру из Колубарског басена. Млађе панонске асоцијације су много више разноврсне и имају много више јединки. Основни разлог је довољно дуго време адаптације и касније повољни животни услови. Појављују се потпуно нови родови као одговор на већ консолидоване животне услове. Током горњег панона десиће се прави процват у еволуцији остракода на панонском простору. То се посебно односи на неке таксоне као што су кандониде и хемицитериде које доживљавају експанзију. С друге стране, у Дакијској провинцији која је у исто време више комуницирала са црноморским басеном, присутне су друге групе остракода које указују на ту везу, а посебно лептоцитерине. Такође, има и потпуно другачијих таксона којих нема у Панонском басену (*Getocytheria*, *Stanchevia*). Интересантно је рећи да род *Cyprideis* има врло малу заступљеност за разлику од Панонске провинције где је један од руководећих облика.

Посебно је добро проучен род *Hemicytheria* са свим својим врстама (20) и који показује све поменуте трендове у развоју остракодске фауне који су владали током панона и понта.

Са палеоеколошког аспекта посматрано, током млађег миоцена на простору обе провинције, егзистовало је неколико различитих типова средине у којима је живела остракодска заједница. Прву карактерише присуство родова који насељавају олигохалинске (< 8 ‰), плитке обалске делове речних ушћа и мочвара: *Stenocypria, Cyprinotus, Cypridopsis, Ilyocypris, Darwinula, Candona*. Присутне су током старијег панона и млађег понта. Друга, доминантна заједница (*Hungarocypris, Thaminocypris, Propontoniella, Cypria, Serbiella, Camptocypria, Zalanyiella, Typhlocyprella, Pontoleberis*) представља каспибракичну, мезохалинску средину (< 18 ‰) односно инфралиторал обрастао воденом вегетацијом. Трећа остракодска асоцијација у којој су представници *Cyprideis, Amplocypris, Leptocythere*, *Hemicytheria, Loxoconcha* и *Xestoleberis* (> 18 ‰) одговара мезо и полихалинском биотопу односно најчешће већини тадашњих панонских и дакијских естуара (Колубарски басен, Великоморавски залив, и други заливи у источној Србији).

У вези са претходним, могуће је донекле успоставити међусобну зависност биотопских услова са изгледом и саставом остракодске љуштуре. Примећено је да, на пример, нодозне форме настањују средине које имају низак ниво растворене соли односно повећан проценат органске материје (родови *Ilyocypris* и *Amnicythere* у Колубарском басену). Сматра се и да смањен ниво кисеоника односно низак однос Mg/Ca у води, може довести до елиминације орнаментисаних форми остракода.