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The Pannonian Palaeoecology and Biostratigraphy of Molluscs from Kostanjek - Medvednica Mt., Croatia

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Key words: Mollusca, *Cardiidae*, *Lymnocardiidae*, Phylogenetic series, Biozone, Pannonian, Pannonian basin, Medvednica Mt., Croatia.

Abstract

On the south-western slope of Medvednica Mt., an 83 m thick geological column Kostanjek-1, composed of strata representing the Sarmatian and Pannonian stages, was investigated in detail. Facies analysis allowed separation of five lithofacies units (A, AB, B, C and D) and the sedimentary mechanisms for particular successions were defined. A rich community of fossil molluscs (50 species) and ostracods (42 species) was sampled and determined. From these fossil determinations, the sediment age was defined, and biofacies analysis allowed the determination of three basic palaeobiocenosis types: 1) a community from Sarmatian brackish lagoons, 2) a community from an Early Pannonian littoral lake, and 3) a lake basin community in the Late Pannonian. The main "record" of the salinity crisis (drop) at the Sarmatian-Pannonian boundary influences in a selective way the majority of organisms, and is shown best in the evolutionary form changes of cardid bivalves, for which phylogenetic series were made. On the basis of dominant and characteristic forms in the entire association of Pannonian molluscs five biozones were separated: I) *Lymnocardium praeponticum* acrozone, II) *Radix croatica - Lymnocardium plicataeformis - Gyraulus praeponticus* cenozone, III) *Neodelminiella venusta - Lymnocardium cekusi* cenozone, IV) *Congeria banatica - Lymnocardium gorjanovici - Gyraulus tenuistriatus* cenozone and V) *Congeria czjzeki - Lymnocardium winkleri - Gyraulus tenuistriatus* cenozone. Many ostracod forms supply and test the stratigraphic value of molluscs and support zonality of Pannonian layers.

1. INTRODUCTION

At Podsused near Zagreb, in an abandoned surface excavation of cement marls, near Kostanjek (Fig. 1) an 83 m thick lithostratigraphical column was investigated comprising layers of Sarmatian and Pannonian age.

Five lithofacies units (A, AB, B, C, D) were separated on the basis of their structural-petrographic characteristics. From layers with greater concentrations of fossils, a rich community of molluscs, foraminifera and ostracods was sampled, from which three basic biofacies were distinguished and the sediment age was defined. In summary, 23 gastropod species (21 of Pannonian and 2 of Sarmatian age) and 27 bivalve species (24 of Pannonian and 3 of Sarmatian age) were determined. Within the mollusc association various forms were detected: from facies and zonal to transitional and endemic species, as well as species with opportune and equilibrium characteristics.

Without discussing the chronostratigraphic division of the younger Miocene layers, the interpretation of the Sarmatian stage was accepted according to SENEŠ & PAPP (1974), and the Pannonian (Table 1) partially according to PAPP (1951, 1953) and STEVANOVIĆ (1957, 1985), and mostly according to the division of Croatian geologists, used for the "Basic Geological Maps" (ŠIKIĆ et al., 1978, 1979).

In the middle of the Sarmatian (Bessarabian), the western areas of Paratethys were being separated by a natural barrier i.e. the Carpathian arch, from eastern Back-Carpathian parts, and a distinct sedimentary environment called the Pannonian basin, was being formed (STEVANOVIĆ, 1985). As the marine cycle of sedimentation continued into the eastern parts (Sarmatian *sensu lato*, according to Barbot de Marny) in the Pannonian basin, a considerable desalinization of the water occurred, under which regime, layers with separate lithological and faunistic content were being formed. These layers are defined as a separate stage, the Pannonian. The Early Pannonian substage approximately corresponds to the period of the upper part of the Middle and Late Sarmatian (*sensu lato*), while the Late Pannonian substage is equivalent to the Meotian stage of eastern areas (STEVANOVIĆ, 1985).

Among the numerous authors who wrote about the biostratigraphy of the Pannonian strata, Papp's research is significant. Thus, PAPP (1951, 1953) divided the Pannonian layers on the basis of molluscs into several biozones: A) gravel and sand with *Replidacna*, B) sand with *Melanopsis impressa* and *Congeria ornithopsis*, C) sand with *M. fossilis* and *C. partschi*, D) sand and gravel with *M. vindobonense* and *M. fossilis constricta*, and E) clay with *M. vindobonense* and *C. subglobosae*. Papp places biozones A, B, C and D to the "Lower-congerian layers", where zone A is similar to the Sarmatian series (A/B), and zone E represents the "Middle-congerian layers" (Table 2). Later, PAPP (1956) studied marls and gravels around Podsused and correlated them to the similar layers of the Vienna basin. The high content of a coarse-grained component in the Vienna basin layers determined the boundary facies in which river molluscs

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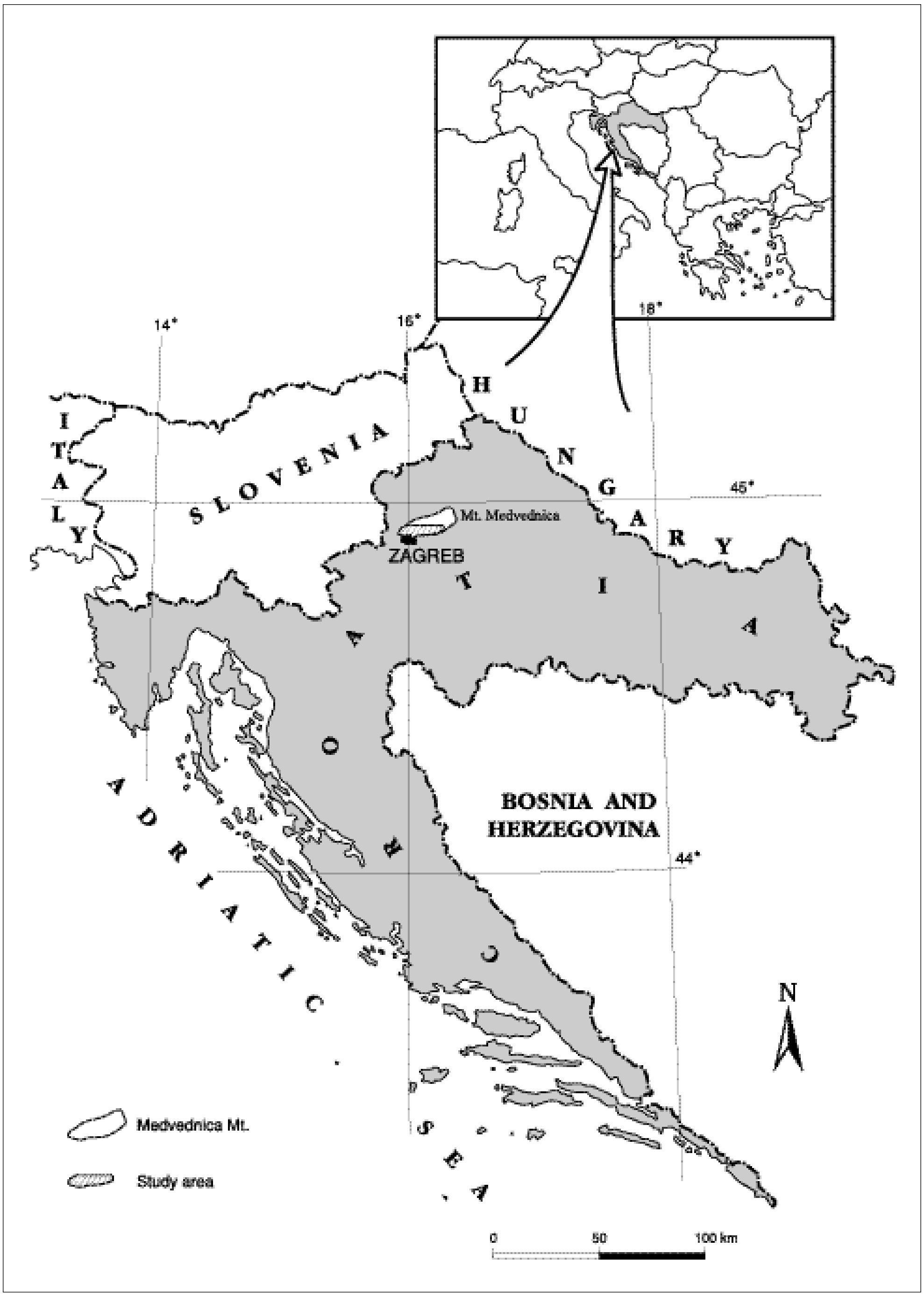


Fig. 1 Geographical location of the Kostanjek-1 column.

lived, while at the same time in the more distant area around Medvednica Mt. a lacustrine sedimentary regime was established, and therefore, according to their faunistic content, these sediments can be compared, but with reservations (VRSALJKO et al., 1995).

With his studies of the central parts of the Pannonian basin, STEVANOVIĆ (1985), completed previous divisions of the Pannonian layers, differentiating basin, transitional and littoral facies (Table 2), with their associated molluscan communities. This allowed further division of this stage into two substages: the Lower Pannonian (Slavonian: Early and Late) and the Upper Pannonian (Serbian).

In the areas of the Pannonian basin the layers are also zoned on the basis of their characteristic ostracod communities. The works of POKORNY (1946) and SOKAČ (1972, 1985) in this area are prominent. These authors, with small differences, both divide the Pannonian basin (Table 1) into the following biozones: α-zone with *Hemicitherya hungarica* and *Miliamina subvelatina*, and the β-*Erpetocypris abscisa* zone (Early Pannonian), and finally the γ-*Cyprideis pannonica* and δ-*Erpetocypris recta* zones (Late Pannonian).

As the location of the study area (Fig. 1) is palaeogeographically approximately half way between sites described by Papp and Stevanović, both results will be

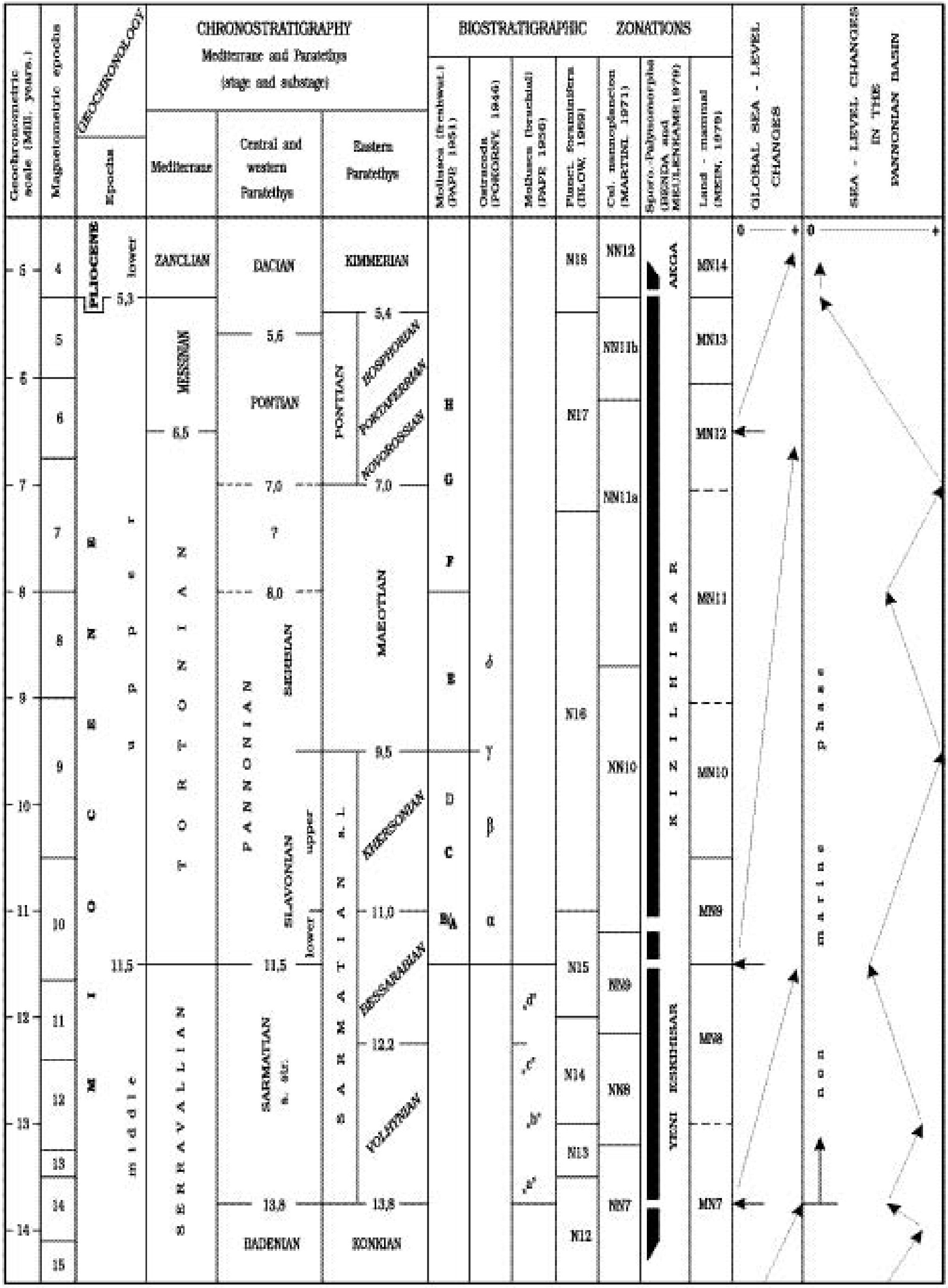


Table 1 A stratigraphic correlation scheme for the younger Miocene layers (compilation after SENEŠ & PAPP, 1974; STEININGER et al., 1985; NAGYMAROSY & MÜLLER, 1988).

used for comparison. Accepting earlier stratigraphic division of the Pannonian stage into substages (Early and Late), the results of Croatian geologists will be mostly used here (JENKO, 1944; OŽEGOVIĆ, 1944; KRANJEC et al., 1973; ŠIKIĆ et al., 1978, 1979).

		AUSTRIA	CROATIA								SERBIA			
Stage	Substage	PAPP (1951)	MOSS (1944)		OŽEGOVIĆ (1944)		JENKO (1944)		ŠIKIĆ et al. (1979)		STEVANOVIĆ (1985)			VRSALJKO (this paper)
											Basenian facies	Transit facies	Littoral facies	
PONTIAN	NOVOROSSIAN (ANDRUSOV, 1917)	F	Upper Pannonian	Zone with *Valencie-nnesia*	Upper Pannonian	Abichi layers	Upper Pannonian	Rhomboidea layers	Lower Pontian	Abichi layers	Upper - abichi layers with *Paradacna abichi*	*Congeria praerhomboidea*, *C. rumana*	*Congeria ungula caprae*	**PONTIAN**
														?
PANNONIAN	SERBIAN (STEVANOVIĆ, 1957)	E	Middle Pannonian	Zone with *Provalencie-nnesia*	Lower Pannonian	Prevalenciennesian layers ("white marls")	Lower Pannonian	Abichi layers (plus Banatica layers)	Upper Pannonian	Banatica layers	Lower - abichi layers with *Paradacna abichiformis*	*Congeria czjzeki*, *C. zsigmondyi*	*Congeria subglobosa* *Melanopsis vindobonensis*	*C. czjzeki* - *L. winkleri* - *G. tenuistriatus*
	SLAVONIAN (ANDRUSOV, 1923) Upper	D	Lower Pannonian	Zone with *Undulotheca*							"White marls" with *Congeria banatica*, *Undulotheca pancici*		*Congeria hoernesi*, *C. partschi*	*C. banatica* - *L. gorjanovici* - *G. tenuistriatus*
		C		Zone with *Velutinopsis*										*N. venusta* - *L. cekusi*
	Lower	B A		Zone with *Radix croatica*				Croatica layers	Lower Pann.	Croatica layers	Clay and marls with *Radix croatica*	*Congeria ornithopsis*, *Melanopsis impressa*	Oolitic limestone with *Nubecularia*	*R. croatica* - *L. plicataeformis* - *G. praeponticus* *L. praeponticum*
														SARMATIAN

Table 2 Biostratigraphic correlation of the Pannonian strata of central and western Paratethys.

2. MATERIAL AND METHODS

Samples were taken in succession from sand and marls of the Sarmatian and Pannonian layers for palaeontological, sedimentological, petrographical and geochemical analyses. Using the method of "directed dotted sample" a rich community of fossil molluscs (50 species, Table 5) and ostracods (42 species, Table 6) was collected from the Kostanjek-1 geological column. For definition of the structural-petrographic complex of certain layers, particle analyses of the light and heavy fractions, and measurements of granulometry, sphericity and grain roundness were used. Calcimetry, chemical and trace element analyses provided geochemical data.

Due to the large number of determined morphotypes (Table 5) detailed descriptions and synonyms were avoided - only the current systematic terminology has being used. After determination of the mollusc community, biofacies analyses (Figs. 4-6) of individual palaeobiocenoses and biostratigraphic zoning of the Pannonian layers was undertaken (Fig. 2).

3. DESCRIPTION AND INTERPRETATION OF THE KOSTANJEK-1 GEOLOGICAL COLUMN

3.1. LITHOFACIES

Five lithofacies units were separated in the succession (Fig. 2): A) *laminated silty marl*, AB) *laminated and layered marl and clay* , B) *layered clayey limestone and marl with sand layers* , C) *cross laminated gravel with sand lenses*, and D) *massive marl with clay layers.*

The *laminated silty marls* (A) comprise the basal lithofacies of the column, and are 1 m thick. The boundary with lithofacies AB is conformable and interfingered, marked by a 10 cm band of clay. The succession consists of rhythmical changes of very thin laminae (0.1-0.5 mm): dark laminae with a greater concentration of organic matter being alternated with light laminae with a greater proportion of carbonate minerals. The average carbonate content is 40-50 %, and the concentration of strontium (~700 ppm) and manganese (~1500 ppm) is relatively constant (Tables 3 and 4). The most frequent fossil material includes fish vertebrae and scales, ostracods, foraminifera and macroflora casts, and small gastropods and bivalves (Fig. 4).

The laminated marls were deposited in a relatively deep, calm and protected environment, where sedimentation was taking place from suspended flow under a regime of constant climate change (Fig. 7). The probable cause of the poor fossil content is the low level of aeration (BOTTJER & SAVRDA, 1990). Rare, small ervilia, ostracods and foraminifera of the *Miliolidae* group define the Sarmatian age and brackish character of the sedimentary environment.

The *laminated and layered marls and clay* (AB) conformably overlie lithofacies A, and pass continuously into platy limestone (B). This lithofacies is approximately 3 m in thickness. The marls are more silty and contain 70-80 % of the carbonate component, while clays are rich in organic detritus, granules of pyrite and limonite, and have a low carbonate content. Laminae are 0.2-0.5 cm thick and layers are 5-10 cm in thickness. Macrofauna remains are rare and frequently include fish fragments, while fossil grasses and continental flora also occur. Small, deformed bivalve forms of the *Lymnocardinae* subfamily, and small pond gastropods are the most frequent molluscs. Large ostracods of the *Amplocypris* group also occur.

The succession retains the structural complex of the Sarmatian layers, but with a new type (oligohaline - Fig. 3) of fossil community in the Early Pannonian substage, which shows the constant desalinization and shallowing of the environment (VRSALJKO, 1997). The cause of shallowing is most probably aggradational infilling of the Sarmatian lagoon and/or lifting of the sedimentary area. Disappearance of old inhabitants and their replacement by new faunistic elements is the result of the alterted water chemistry, which was closely related to regional events (SENEŠ & PAPP, 1974).

Layered clay-limestone and marls with sand layers (B) overlie the transitional sediments (AB) in the succession. The lower boundary is conformable while the upper contact has been eroded by deposition of lithofacies C. The total thickness is 31 m. Six large cycles are observed in the succession with the fining-upwards trends. Layered clay-limestone in the lower part of the cycle, passes gradually upwards into silty marl with poorly visible lamination and sand layers of variable thickness. The cycles are 2-7 m thick with a higher concentration of marl, while the sand layers (lenses) are 0.5-5.0 cm thick. The limestone layers have a higher concentration of carbonate (~95%), and marls have more siliciclastic component. The sands are loosely consolidated and poorly sorted with well-rounded grains up to 0.5 mm (exceptionally up to 0.5 cm) in diameter and in parts exhibit planar cross lamination. The light mineral fraction contains quartz (35 %), feldspate (20 %), rock fragments (40 %) and calcite (5 %). The heavy fraction most frequently contains limonite and magnetite (15 %), dolomite (15 %), epidote (6 %) and tourmaline (3 %). The manganese content is constant (~300 ppm), while the strontium content noticably decreases upwards, from 3,320-710 ppm. The fossil material contains a mollusc and ostracod community representing small number of specimens of many species, together with a similar distribution of fish remains, fossil grasses, continental macroflora and frequent bioturbation (Fig. 5). Mollusc shells are poorly preserved because of their original aragonite composition, and the most frequent samples are pulmonate gastropods and small limnocardids.

Deposition of the limestone occurred during periods of low input of terrigenous particles, in contrast to the silty marls deposited from suspension during periods of

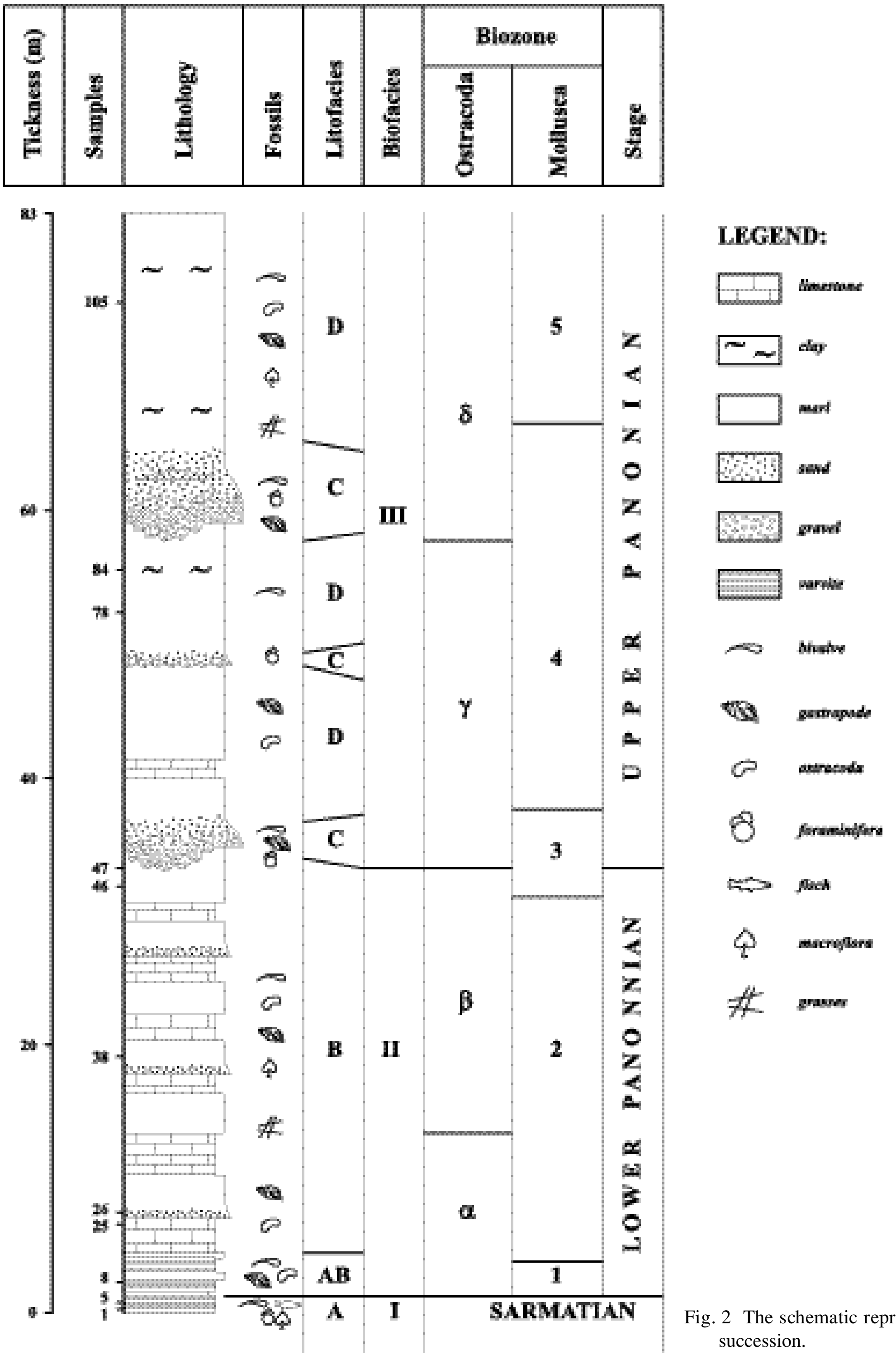


Fig. 2 The schematic representation of the Kostanjek-1 succession.

greater siliciclastic input from the continental hinterland (Fig. 8). ALLEN & COLLINSON (1986) reported similar results, in their research of the modern Littlefield Lake (Michigan, USA). The origin of sand layers relates to periods of the stronger influence of fluvial processes. The rhythmic sedimentation shows the permanent relationships between subsidence, eustatic processes and the transport of material from a denuded area. A broad photic zone and global temperature decrease in the Early Pannonian (STEVANOVIĆ, 1985) caused increased production of O_2 and CO_2, which resulted in favourable conditions for the comparatively rapid settlement of "new" organisms adapting to oligohaline waters. A high concentration of strontium is more likely to be explained by the increased portion of aragonite which is linked to, and probably resulted from the dissolution of mollusc shells, rather than by the increased salinity, as shown by KRANZ (1976) in Triassic carbonates.

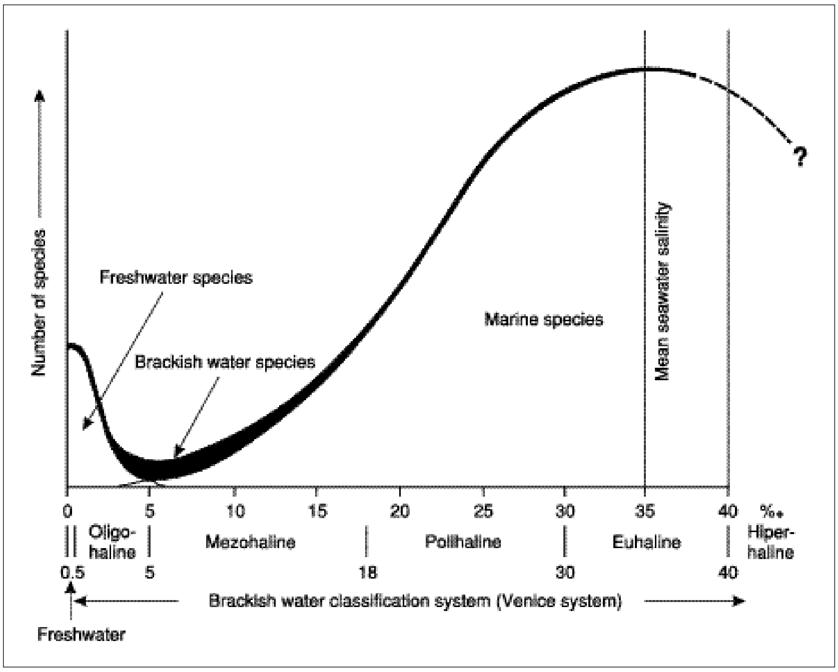
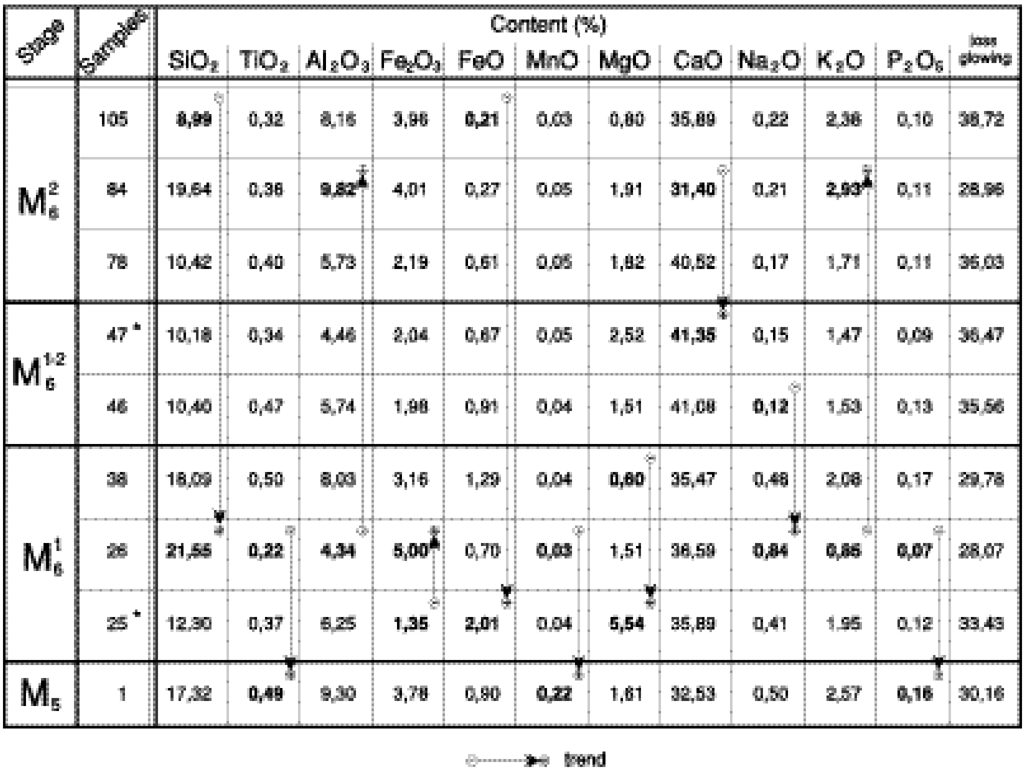


Fig. 3 A diagram representation of salinity and species diversity (from HUDSON, 1990).

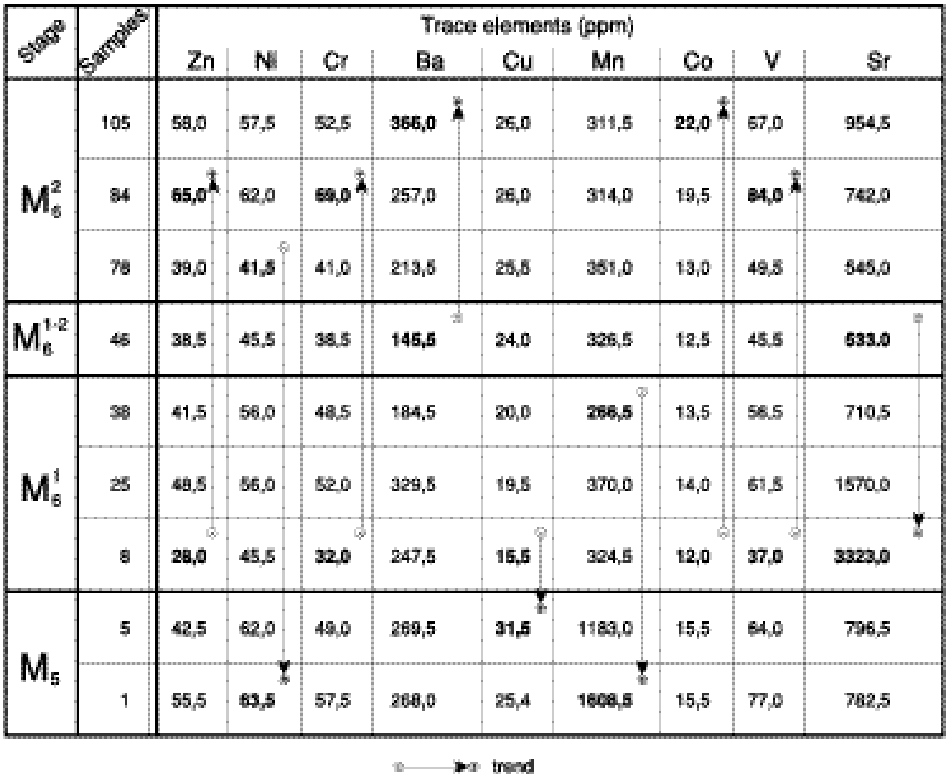


Stage	Samples	Content (%)											
		SiO_2	TiO_2	Al_2O_3	Fe_2O_3	FeO	MnO	MgO	CaO	Na_2O	K_2O	P_2O_5	loss glowing
M_6^2	105	**8,99**	0,32	8,16	3,96	**0,21**	0,03	0,80	35,89	0,22	2,36	0,10	38,72
	84	19,64	0,36	**9,82**	4,01	0,27	0,05	1,91	**31,40**	0,21	**2,93**	0,11	28,96
	78	10,42	0,40	5,73	2,19	0,61	0,05	1,82	40,52	0,17	1,71	0,11	36,03
M_6^{1-2}	47*	10,18	0,34	4,46	2,04	0,67	0,05	2,52	**41,35**	0,15	1,47	0,09	36,47
	46	10,40	0,47	5,74	1,98	0,91	0,04	1,51	41,08	**0,12**	1,53	0,13	35,56
M_6^1	38	18,09	0,50	8,03	3,16	1,29	0,04	**0,80**	35,47	0,48	2,08	0,17	29,78
	26	**21,55**	**0,22**	**4,34**	**5,00**	0,70	**0,03**	1,51	36,59	**0,84**	**0,86**	**0,07**	28,07
	25*	12,30	0,37	6,25	**1,35**	**2,01**	0,04	**5,54**	35,89	0,41	1,95	0,12	33,43
M_5	1	17,32	**0,49**	9,30	3,78	0,90	**0,22**	1,61	32,53	0,50	2,57	**0,16**	30,16

Table 3 Major element composition of the marl and sand (*) samples.

The *cross layered gravel with sand lenses* (C) comprises three horizons approximately 2 m, 0.3 m and 8 m thick from the base to the top of the lithofacies. The lower boundary is distinctly erosional, while the upper boundary with lithofacies D is gradational. This gravel is polymict, clast-supported, trough cross-layered and normally graded. Grain-size is commonly around 3 cm, exceptionally up to 15 cm. Grains are semi-rounded and well sorted, and marly clasts of larger dimensions are frequent. The content of the light and heavy fractions shows great similarity with the sands of previous facies. Well-rounded fragments of mollusc shells (melanopsids, congeria, cardids), occur together with algae and foraminifera that are reworked. On the basis of superpositional relationships and autochtonous molluscan community in underlying and overlying deposits of lithofacies D (*Congeria banatica* etc.) the sediment age is defined as Late Pannonian.

The chaotic appearance of the sediment and frequent large marl clasts indicate on the effects of sedi-



Stage	Samples	Zn	Ni	Cr	Ba	Cu	Mn	Co	V	Sr
M_6^2	105	58,0	57,5	52,5	**366,0**	26,0	311,5	**22,0**	67,0	954,5
	84	**65,0**	62,0	**69,0**	257,0	26,0	314,0	19,5	**84,0**	742,0
	78	39,0	**41,5**	41,0	213,5	25,5	351,0	13,0	49,5	545,0
M_6^{1-2}	46	38,5	45,5	38,5	**146,5**	24,0	326,5	12,5	45,5	**533,0**
M_6^1	38	41,5	56,0	48,5	184,5	20,0	**266,5**	13,5	56,5	710,5
	25	48,5	56,0	52,0	329,5	19,5	370,0	14,0	61,5	1570,0
	8	**28,0**	45,5	**32,0**	247,5	**15,5**	324,5	**12,0**	**37,0**	**3323,0**
M_5	5	42,5	62,0	49,0	269,5	**31,5**	1183,0	15,5	64,0	796,5
	1	55,5	**63,5**	57,5	268,0	25,4	**1608,5**	15,5	77,0	782,5

Table 4 Trace element composition of the marl samples.

ment slumping. The overlying mixed fossil community represents the allochthonous element in the given lacustrine ambient (VRSALJKO et al., 1995). The lens-shaped gravel bodies, structure of trough cross-bedding and gradual upward decrease in grain-size indicates a probably fluvial sedimentary origin (?fan delta). Considering the size and poor roundness and sorting of the clasts, the relative proximity of the source area (e.g. Medvednica Mt.) can be assumed. Considerable tectonic movements at the end of the Early Pannonian in the broad area of the Pannonian basin (ŠIKIĆ et al., 1979), were probably the trigger for the formation of these sediments, which resulted in the deepening of the lacustrine palaeoecosystem. This also increased the fluvial input of terrigenous material into the area.

Massive marls with clay layers (D) complete the succession continuously overlying the gravel of lithofacies C. This lithofacies is distinguished by the compactness of the marl layers which are more strongly bioturbated and rarely contain cm-thick clay layers. The carbonate content is constant (~65%). There is a rich community of deep-water lacustrine bivalves and numerous ostracod forms, which together show that the sediments belong to the Late Pannonian substage (Fig. 6).

The marls and clay were deposited slowly from suspension in the deeper, more distal parts of the lake (Fig. 9). Primary sedimentary structures are poorly preserved due to the increased destructive activity of a benthic infauna.

3.2. BIOFACIES

In view of other biotic and abiotic ecological factors which were prevalent during the life of the organisms and which were important parameters in environmental determination (DODD & STANTON, 1990), previously defined sedimentary models (Figs. 7-9) were applied to the fossil community. Therefore, one basic biofacies unit was separated for sediments of the Sarmatian stage, and two biofacies units for the younger, Pannonian stage.

Biofacies 1 is a **fossil community of brackish lagoons** (Fig. 4). A sparse molluscs, ostracods and foraminifera existed in the community in thin-laminated marls and clay of the Sarmatian age. The most common are molluscs *Ervilia* and *Cardium*, ostracods from the *Aurila* and *Loxoconcha* genera, and foraminifera from the *Miliolidae* and *Elphidium* groups. The remains of fish, macroflora and radiolarians are also common.

Seasonal surface suspension flows stratified the water column, weak vertical circulation and thermal stratification being formed due to differences in water density, which influenced the organic production and distribution of the biomass (DODD & STANTON, 1990). A warmer surface layer was created, aerated and of decreased salinity with increased concentrations of zoo- and phytoplankton. The colder, deeper layer was of increased salinity supporting benthic organisms which have anaerobic respiratory characteristics (similar to the modern environment in the Black Sea). The degree of fossilization of skeletal parts and frequent

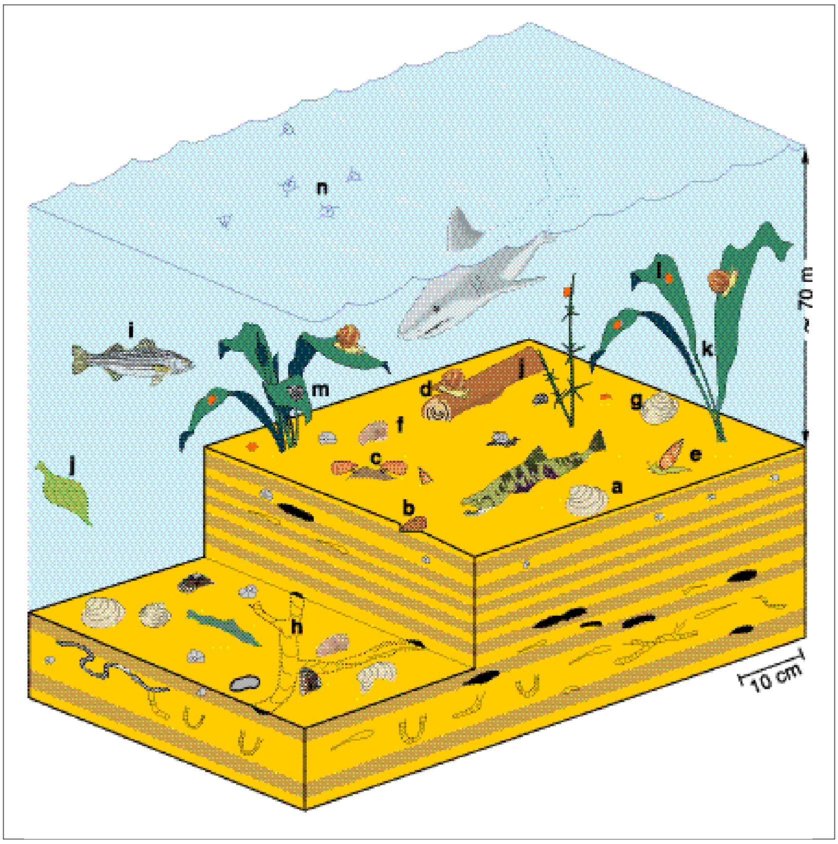


Fig. 4 The brackish Sarmatian lagoon community. Legend: a) *Ervilia dissita*; b) *Modiolus incrassatus*; c) *Musculus sarmaticus*; d) *Gibbula* sp.; e) *Hydrobia* sp.; f) *Cardium vindobonense*; g) *Mactra vitaliana*; h) ichnofossils; i) fish; j) macrophyta; k) grasses; l) ostracoda; m) foraminifera; n) radiolaria.

globules of authigenic pyrite, limited by the organic carbon concentration, dissolved phosphate and terrigenous Fe-minerals, illustrate a more reduced aquatic environment (ALLISON, 1990). The sparsity of certain biogenic structures and preservation of primary lamination (BOTTJER & SAVRDA, 1990), also indicate deposition in relatively deeper environment. Under the deep-water anoxic conditions in which clay and marl are layered, the calcitisation of aragonitic shells ceases due to the increased concentrations of organic matter, which increased the conservation of organism skeletons (BRETT & SPEYER, 1990).

Biofacies 2 is composed of a **littoral lacustrine community** (Fig. 5). The marls and limestones of the Lower Pannonian contain a specific, endemic association of molluscs and ostracods. Endemism which developed in certain groups of organisms occured due to the spatial isolation of the Pannonian basin (STEVANOVIĆ, 1985) from other parts of Paratethys during the Pannonian. Shallow carbonates of the Lower Pannonian supported an ostracod community which has numerous species, dominated by the *Hungarocypris*, *Amplocypris*, *Loxoconcha* and *Candona* genera (Table 6). Within the mollusc community, the most numerous and most frequent are pulmonate gastropods of *Radix* and *Gyraulus* genera and in smaller proportions representatives of *Lymnocardium*, *Micromelania*, *Valvata* and *Orygoceras* (Table 5). Bivalves of the *Lymnocardium* genus here represent the derived forms from their older cardid ancestors (GORJANOVIĆ-KRAMBERGER, 1890), that survived the salinity crisis at the end of the Sarmatian. Limonitised imprints of a continental flora, swamp grass and fish skeletons are also common, while gastropods and foraminifera rarely occur in sands.

Aeration of the shallow water column is the cause of the increased pH (PIRSON, 1985) and greater concentration of dissolved gasses which participate in the formation of carbonate mud. The rich community of swamp grass supported an epibenthos herbivorous gastropod and ostracod community. The use of dissolved aragonite for the skeletal formation of most molluscs was closely connected with its increased content in this shallow water area. A considerable presence of lacustrine gastropods which breathe with their lungs presupposes constant vertical (?daily) migration of these organisms. In some shells growths shaped like hollow needles have been noticed on their ribs, and were probably used for temperature regulation. Formation of secondary ribs in some shells (*Lymnocardium plicataeformis* and *L. praeponticum*) was connected with the extra strengthening of otherwise small and thin shells.

Biofacies 3 represents a **fossil community of a lacustrine basin** (Fig. 6). Sediments of this biofacies are represented by marls of a comparatively deeper lake. On many levels within these sediments lensoid gravel-sand bodies of fluvial origin occur. Marls contain a rich autochthonous community of fossil molluscs, in which bivalves of the *Congeria* and *Lymnocardium*

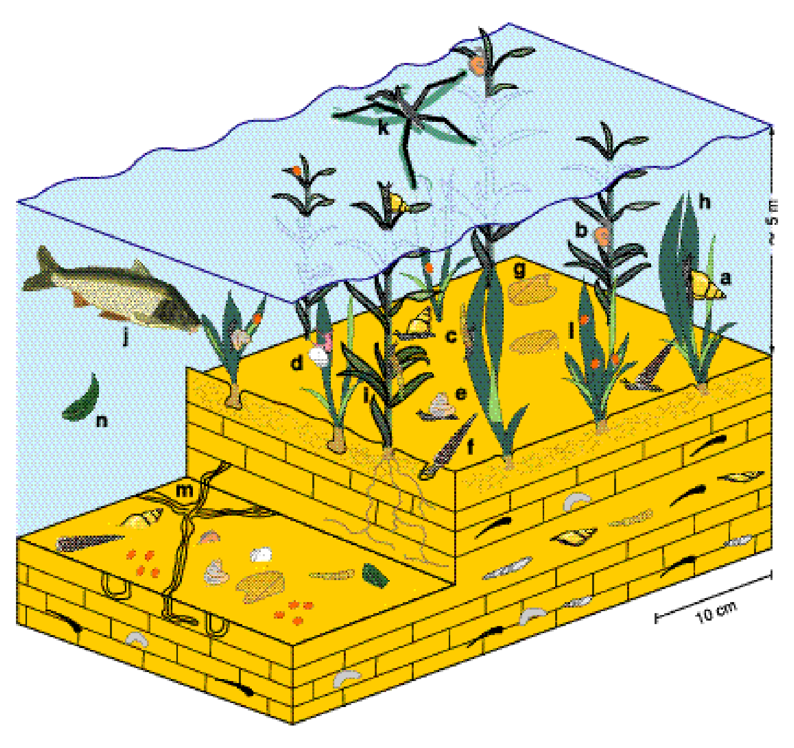


Fig. 5 The littoral lacustrine community of the Early Pannonian. Legend: a) *Radix croatica*; b) *Gyraulus praeponticus*; c) *Micromelania striata*; d) *Valvata* sp.; e) *Hydrobia* sp.; f) *Orygoceras laevis*; g) *Limnocardium praeponticum*; h) watered grasses; i)algae (?*Chara*); j) fish; k) insecta; l) ostracoda; m) ichnofossils; n) continental macroflora.

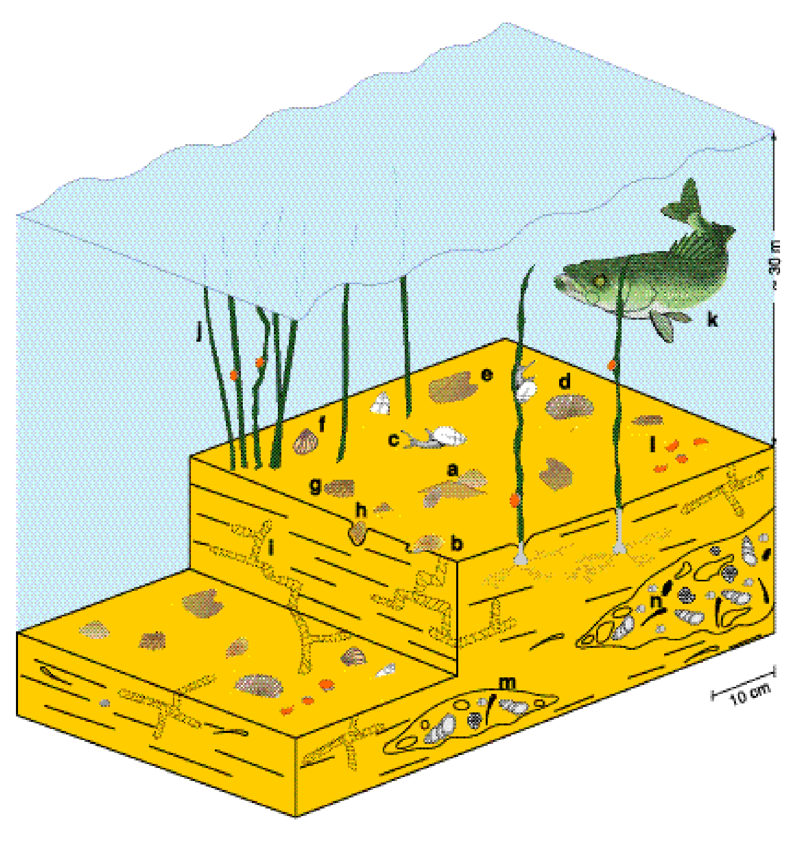


Fig. 6 The lacustrine basin community of the Late Pannonian. Legend: a) *Congeria banatica*; b) *Congeria czjzeki*; c) *Valenciennius* sp.; d) *Limnocardium winkleri*; e) *Limnocardium gorjanovici*; f) *Limnocardium cekusi*; g) *Paradacna syrmiense*; h) *Pisidium* sp.; i) ichnofossils; j) watered grasses; k) fish; l) ostracoda; m) *Melanopsidae*; n) foraminifera.

(*sensu lato*) genera dominate, and gastropods of the genera *Valenciennius*, *Gyraulus* and *Radix* are present in smaller numbers (Table 5). An abundant ostracod population contains different genera, of which in the lower parts of the column the most frequent were *Candona*, *Cypria*, *Hemicytheria* and *Cyprideis*, while close to the top of the column "new" representatives of the *Candona* subgenus were found (Table 6). The marls were almost completely reworked by extensive bioturbation of various orientations, and often contain the imprints of fish scales, continental macroflora and limonitised fossil grass.

In the gravel lenses there is a mixed type of allochthonous fossil community. The large, freshwater gastropods (BRUSINA, 1897; PAPP, 1956) of the *Melanopsidae* are numerous (Table 5), and are dispersed as bioclasts in sand. Apart from gastropods there are also individual examples of bivalves with thick shell membranes (*Congeria partschi*, *C. ornithopsis*), as well as *Ervilia*, *Mactra* and *Ostrea*, which are reworked from earlier Sarmatian and Badenian layers. Algae (?*Lithothamnium*) and foraminifera from older levels are also common in the sandy matrix. This resedimented fossil community does not have particular stratigraphic value, as in the Vienna basin (PAPP, 1953), but defines depositional processes.

The aforementioned process of the deepening of the depositional system at the end of the Early Pannonian is here represented by the changed style of sedimentation, as well as by evolutionary changes of the pulmonate gastropods (MOSS, 1944) and limnocardids (Fig. 10). The mollusc community (Table 5) and numerous ostracod species (Table 6) determine the high degree of adaptive radiation (adjustments and expansion) in new ecological environments. At the same time, the area of grass communities is decreased, and organisms adapt to a comparatively deeper, calcite-clay mud substrate. A highly oxygenated area is confirmed by the occurrence of imprints of water grasses, which need light for photosynthesis. The water grass grew distintly high and also stabilized the bottom, and herbivorous organisms fed on them. Mollusc skeletons are mainly well preserved, although they had a fragile structure as a result of their predominant calcitic composition and insignificant postmortal erosion. Small pyrite granules frequntly occur in marls, which may indicate a more reducing environment (ALLISON, 1990). However, these conditions were most probably present only close to the bottom. Faunistic diversity with the dominant *Congeria* and *Lymnocardium* genera in the upper parts of this facies might suggest slightly increased salinity to mesohaline (Fig. 10) by the end of the Pannonian, and this is supported by the occurrence of new bivalve genera (*Didacna*, *Paradacna*, *Caladacna*) and ostracod subgenera (*Lineocypris*, *Typhlocyprella*, *Sinegubiella*). Congerian forms belong to the Modioliformes and Subglobosae groups, which live attached by a byssus to a soft substrate (ANDRUSOV, 1923) and are good indicators of calm and brackish water.

3.3. RECONSTRUCTION OF LAYERED MECHANISMS

The Sarmatian clay and marls (Facies A) were deposited in comparatively deeper and more protected, semi-closed areas (lagoons, estuaries). The insufficiency of considerable fluvial flows and smaller amounts of planktonic foraminifera indicate the isolation of the depositional system. The depth of the depositional system is determined by the high content of reductive layered components (pyrite, manganese, phosphate), low biogenic content and degree of skeletal fossilization and by the preservation of primary mm-lamination and the low granulometric composition (DODD & STANTON, 1990). Facies A sediments ("varvite") were deposited from surface suspension flows and with frequent seasonal climate changes (Fig. 7) by changing the thermal gradient (thermocline) of a stratified water column. Light laminae were formed during periods of lower atmospheric temperatures, when the inflow of terrigenous material was decreased, while dark laminae were deposited during the increased inflow of siliciclastic and organic terrigenous material. A similar example was described by BOTTJER & SAVRDA (1990). Constant turbidity of the surface level and bottom currents, together with the probable vertical stratification of water salinity, had a selective influence on organic production (similar to the modern situation in Black Sea).

Characteristics of Sarmatian depositional system continued to the Early Pannonian as indicated by continuous sedimentation. This is expressed by deposition of the "transitional layers" of facies AB, characterized by structural-petrographic properties of the older, underlying deposits. The fossil association of small, degenerated cardids and pulmonate gastropods indicate partial "life discontinuity" towards the older deposits, as the consequence of shallowing, restriction and desalinization of the marine environment (VRSALJKO, 1997).

Limestone and marls of facies B were deposited in a shallow, "lake-pond" palaeoenvironment (Fig. 8), without considerable influence of a land area. Limestone beds were layered in the shallow littoral zone, and marls deposited from suspension were layered in slightly deeper lake areas (sublittoral), by combined physicochemical and biogenic processes. The basic model for the interpretation of the formation of these layers is a study by ALLEN & COLLINSON (1986). Periodic and comparatively poor inflow of terrigenous material is indicated by cm-thick interlayers of fine-grained sand, which have the form of bands or lenses, with planar cross-lamination (?ripple marks). The discovery of numerous "Seegrasswissenfauna" (pulmonate gastropods, small limnocardids and ostracods), which live on water grasses ("fossil reed" - KRANJEC et al., 1973) as epibionts, determine the high degree of aeration and desalinization of the lacustrine area. Frequent limonite granules indicate the oxidizing conditions of carbonate layering (ALLISON, 1990).

The gravels (C) and marls (D) were sedimented in a comparatively deeper palaeolacustrine environment (Fig. 9). Tectonic activity at the end of the Early Pannonian has been determined by boundary faults with considerable vertical movements in two directions (ŠIKIĆ et al., 1979). Coarse clastic sediments were transported from higher land areas to the depositional system by rivers and torrents, most probably forming a fan delta. In the upper half of the Kostanjek-1 column,

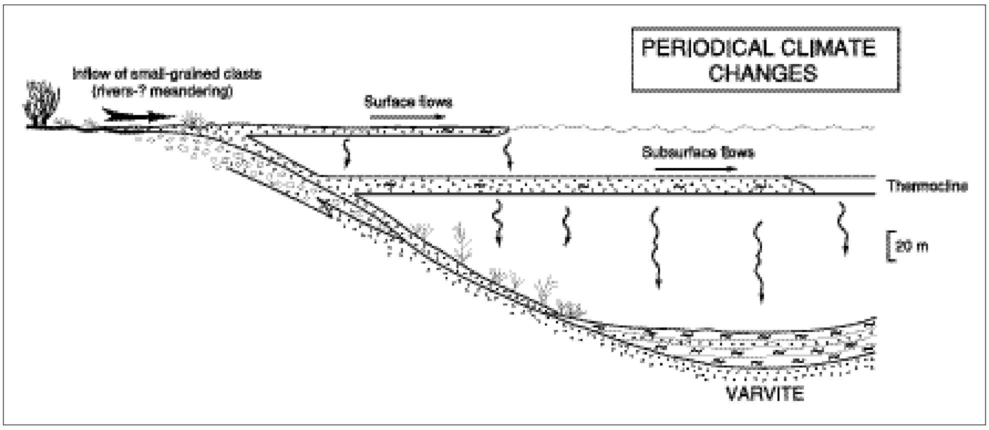


Fig. 7 Idealized depositional model for sedimentation of the Sarmatian clays.

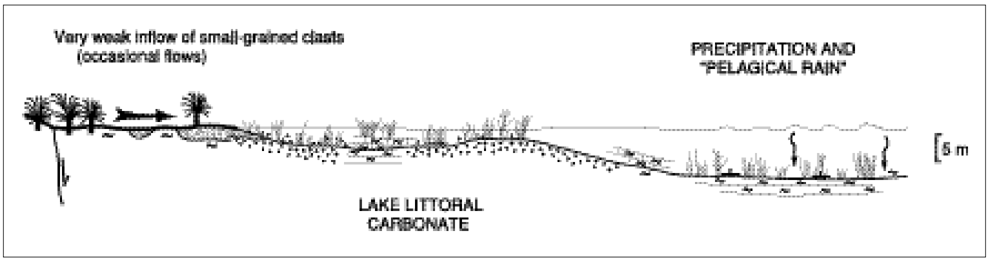


Fig. 8 Idealized depositional model for sedimentation of the Lower Pannonian carbonates.

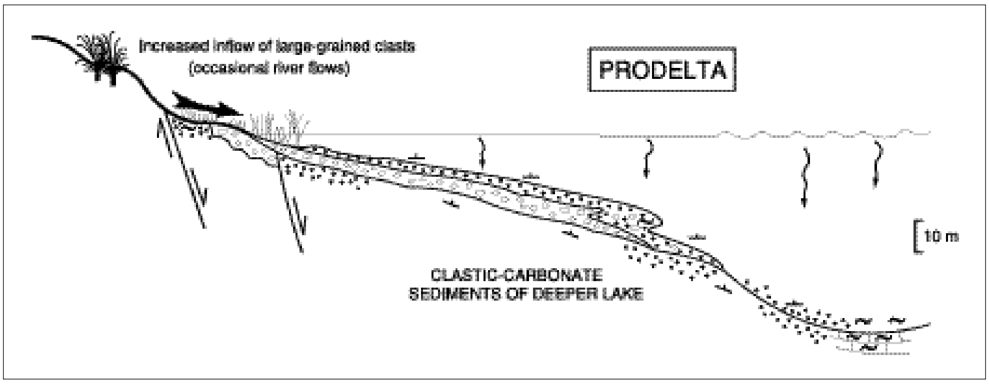


Fig. 9 Idealized depositional scenario allowing simultaneous deposition of coarse fluvial clastics and deep-water Upper Pannonian marls.

where the marl layers are dominant, three levels with gravel and sand were separated, so the instability, i.e. the occasional occurrence of significant rivers flows can be postulated. The discovery of a new limnocardid community and ostracods in the youngest part of the layers indicate the possible reestablishment of connections between these areas and the Paratethys area, as is proved by STEVANOVIĆ (1985).

3.4. EVOLUTIONARY SERIES OF THE *CARDIIDAE* FAMILY

Within the vertical sediment succession, lithological changes as well as faunistic changes have been detected, from the Sarmatian up to the Late Pannonian. Combined, sedimentological and palaeontological analysis allowed the definition of the formation, trends and characteristics of the layers. During the evolution of the depositional system (Figs. 7-9) the permanent desalinization of the water became evident, particularly as shown by the *Cardiidae* group of molluscs.

At the end of Badenian only some groups of organisms (SENEŠ & PAPP, 1974) survived the salinity crisis, while certain cardid species "continued" into the Sarmatian with considerable evolutionary changes. The change from mesohaline to polihaline conditions resulted in the cardid bivalves developing smaller and thinner shells with the reduction of teeth-hook apparatus. In the newly formed brackish Sarmatian environment, a cardid form can be found, which has been defined by some authors as a separate *Cerastoderma* subgenus (KOJUMDGIEVA, 1969), and by others as a *Cardium* genus (GORJANOVIĆ-KRAMBERGER, 1890). Here, the results from the later, more current study have been adapted.

The continuous salinity drop, which overlaps in the western and central Paratethys areas with the period of the formation of the Pannonian basin (lower part of the Middle Sarmatian), and its isolation from the eastern parts (STEVANOVIĆ, 1985), resulted in an evolutionary surge in the cardid group. For the majority of spe-

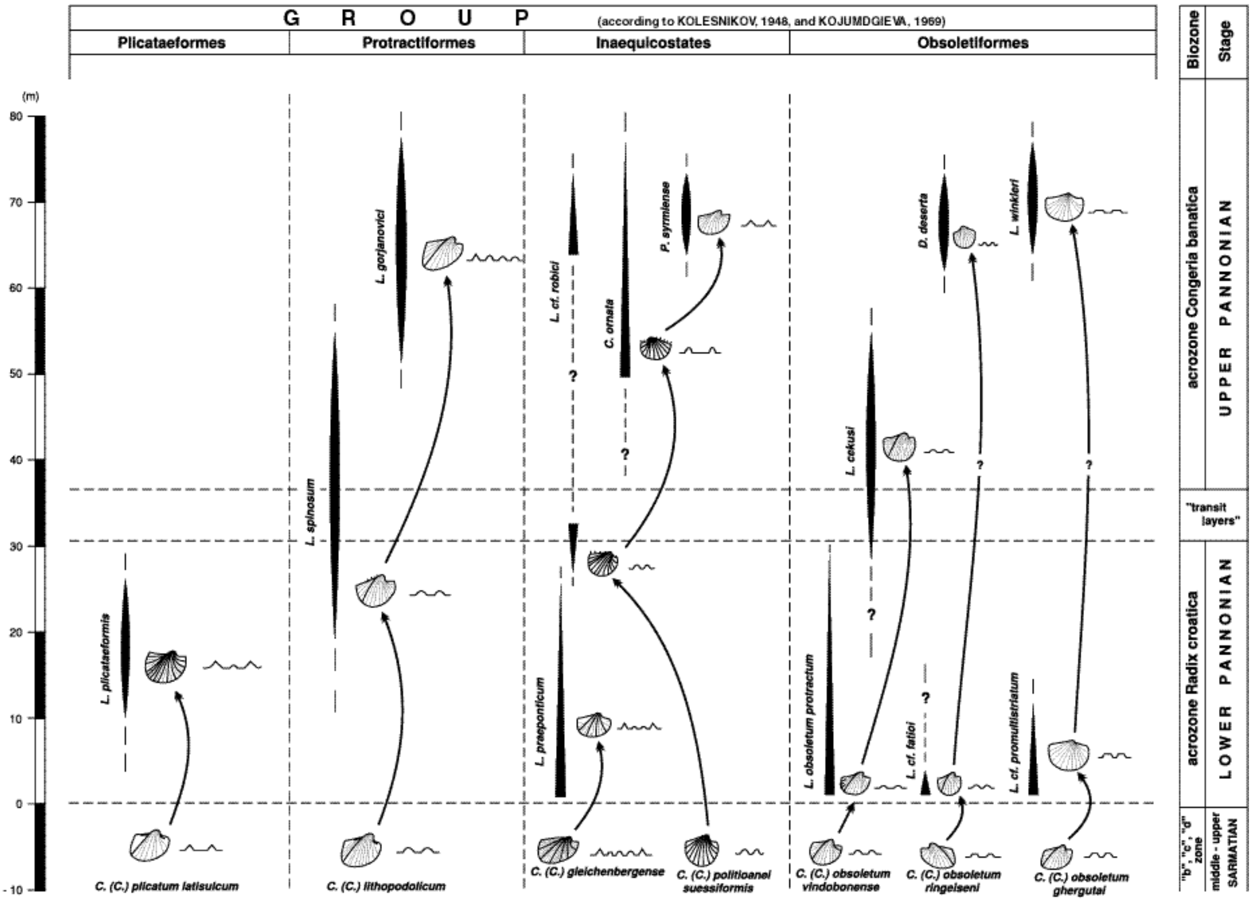


Fig. 10 The phylogeny of the *Cardiidae* family (according to basal diagnostic elements: number and type of ribs), and span of species occurrences in the sedimentary succession of the Sarmatian and Pannonian.

cies of Sarmatian cardids the salinity drop has a disastrous influence. Only a few species evolved and adapted to the new conditions. Evolutionary changes are expressed by their smaller dimensions, longer and thinner shells, the increased number and occurrence of secondary ribs, almost entire reduction of cardinal teeth hooks, and probably altered skeleton mineralization. Recently most authors separate and determine these Pannonian forms as a separate *Lymnocardium* genus (STEVANOVIĆ, 1957), which is also accepted in this paper.

Spatial isolation of the Pannonian basin was the cause of the occurrence of the variability and endemism in many species. The multiple mutations provide evolutionary material for the occurrence of new limnocardid species in a comparatively short period of time. The formation of new species of the *Lymnocardiinae* subfamily at the end of Pannonian (*Paradacna* , *Didacna*, *Caladacna*) marks the evolutionary maximum of this group. This maximum may have two interpretations: 1) the settlement (expansion) of "finished species" from the eastern parts (Dacian and Euxinian basin), due to a reestablished connection with the unique Paratethys area (STEVANOVIĆ, 1985), and/or 2) a mixture of newly settled "immature eastern species" with domiciliary forms, and comparatively accelerated evolutionary change up to the level of creation of new genera, which is more probable.

Starting from the fact that all Pannonian limnocardids (*sensu lato*) are evolutionary derived from the Sarmatian cardids (*sensu lato*), using morphological-functional scale analysis, and following the constructive morphological diagnostic characteristics (BASCH, 1990), their phylogenetic series were defined (Fig. 10). Phylogenetic relationships were produced according to the models of KOLESNIKOV (1948) and KOJUMDGIEVA (1969), who divided the cardid group into four basic groups: Obsoletiformes, Inaequicostates, Protractiformes and Plicataeformes.

The Plicataeformes group is the most poorly represented in the Pannonian strata of the Kostanjek-1 column. Not until the Lower Pannonian sediments is the *Lymnocardium plicataeformis* species found, which is probabaly an evolutionary descendant of the Sarmatian *Cardium* (*Cerastoderma*) *latisulcum* form. The new species is quite variable as indicated by the changeable number of ribs (13-15), that are sometimes decorated with pierce marks, and by the occurrence of weaker secondary ribs (3-4) in some samples.

The Protractiformes group has two representatives in the Pannonian layers: *Lymnocardium spinosum* which can be most frequently found in the zone of tran-

MOLLUSCA	LITOFACIES					BIOFACIES			BIOZONE (this paper)				
	A	AB	B	C	D	1	2	3	1	2	3	4	5
Radix (Radix) croatica			+				●			—			
Radix (Radix) extensa			+				●			—	—		
Radix (Radix) kobelti					+		○	●			—	—	—
Gyraulus (Gyraulus) praeponticus			+				●		—	—	—		
Gyraulus (Gyraulus) dubius			+				●	○		—	—		
Gyraulus (Gyraulus) tenuistriatus					+			●				—	—
Micromelania striata			+		+		●	●		—	—	—	—
Orygoceras laevis			+		+		●	○		—	—	—	—
Orygoceras cf. brusinai					+			○					—
Undulotheca halavatsi					+			○				—	—
Neodelminiella venusta					+			○			—		
Velutinopsis cf. pancici					+			○					—
Melanopsis fossilis				+	+			⊗			?	?	
Melanopsis bouei				+				⊗			?	?	
Melanopsis impresa				+				⊗			?	?	
Pseudamnicola (Pseudamnicola) minima		+					●		—	—			
Hydrobia (Hydrobia) frauenfeldi		+	+				●		—	—			
Hydrobia (Baglivia) cf. ambiqua			+				○		—	—			
Valvata (Valvata) cf. simplex			+				○			—			
Valvata (Cinncina) cf. obtusaeformis		+	+				●		—	—			
Caspia (Caspia) cf. latior		+	+				○		—	—			
Valvata sp.	+					●							
Hydrobia sp.	+					●							
Limnocardium praeponticum		+	+				●		—	—			
Limnocardium spinosum			+		+		●	●		—	—	—	
Limnocardium cf. promultistriatum			+				○		—	—			
Limnocardium winkleri					+			●					—
Limnocardium cf. fatioi			+				○		—	—			
Limnocardium cf. robici			+		+		○	●		—	—	—	
Limnocardium plicataeformis			+				●			—			
Limnocardium cekusi			+		+		●	●		—	—	—	
Limnocardium gorjanovici					+			●				—	—
Limnocardium obsoletum protractum		+	+				○		—	—			
Paradacna syrmiense					+			○					—
Caladacna ornata					+			●				—	—
Didacna deserta					+			○				—	—
Congeria banatica					+			●				—	—
Congeria sp. (*aff. banatica*)					+			○				—	—
Congeria czjzeki					+			●					—
Congeria martonfii				+	+			●				—	—
Congeria ornithopsis				+				⊗			?	?	
Congeria partschi				+				⊗			?	?	
Congeria zahalkai					+			○				—	—
Congeria sp. (? nov.)			+				○			—	—		
? Cerastoderma protracta			+		+		○	●		—	—	—	—
? Cerastoderma margaritacea					+			○				—	—
Pisidium sp.			+		+		○	●		—	—	—	—
Ervilia dissita dissita	+					●							
Cardium (Cerastoderma) vindobonense	+					○							
Cardium (Cerastoderma) gleichenbergense	+					○							

sitional layers (Lower - Upper Pannonian) and *Lymnocardium gorjanovici* which has been found in the upper part of the Upper Pannonian marls. The former is an indirect descendant (between the original form and *L. spinosum* a transitional form should be defined) from the Sarmatian *Cardium* (*Cer.*) *lithopodolicum* species, and differs from it by the considerably increased number of ribs, and significantly smaller shell size and finally by strengthening of the back hook edge with small pierce marks. The latter *L. gorjanovici* form is once again larger and distinguished by the occurrence of various rib types, from pointed to rounded.

In the Inaequicostates group, the Early Pannonian *Lymnocardium praeponticum* developed from the original Sarmatian *Cardium* (*Cer.*) *gleichenbergense* form, keeping the basic shell characteristics. Later forms: *Caladacna ornata* and *Paradacna syrmiense* occured in the Late Pannonian along with significant changes in the number and type of ribs, and greater elongation. *Lymnocardium robici* with apparent variability (changable relations between rib width and interribs parts) might be the transitional form among the majority of Pannonian limnocardids (*sensu lato*).

The most represented group is the Obsoletiformes, in which the evolutionary changes from the original Sarmatian cardids to the Pannonian limnocardids, can be clearly followed. Earlier Pannonian forms (*Lymnocardium obsoletum protractum*, *L. fatioi* and *L. promultistriatum*) originated directly from older brackish forms (GORJANOVIĆ-KRAMBERGER, 1890), with insignificant morphometric differences. It is possible that *L. cekusi*, which generally appears in the middle of the sedimentary column, is the transitional form to the Late Pannonian *Didacna deserta* and *L. winkleri* forms. GORJANOVIĆ-KRAMBERGER (1890) was the first to define the *L. cekusi* species in the lowest parts of Pannonian marls of Vrapče. However the author was not aware of the biostratigraphic condensation phenomenon, which necessitates revision of the stratigraphic position of this species (VRSALJKO, 1997).

The evaluation of the comparative significance of every limnocardid species throughout geological history cannot be completely understood without study of the adaptive (natural selection) and morphogenetic (growth processes) factors, which is not complete in this case. However, on the basis of the established development series, and some specific mollusc index fosssils, it is possible to suggest biostratigraphic zoning in the sediments of the Pannonian basin, which should be completed and tested by future research.

3.5. BIOZONES

Accepting earlier research, especially PAPP (1951, 1953, 1956) and STEVANOVIĆ (1951, 1953, 1957, 1985), on the stratigraphy of Pannonian basin, new solutions are proposed here (Fig. 2, Tables 2 and 5).

In the Kostanjek-1 geological column (Fig. 2), rare samples of *Ervilia dissita* and *Cardium* (*Cerastoderma*) *vindobonense* with a rare accessory foraminiferal community of *Miliolidae* and *Elphidium* group occur within the laminites (facies A), which collectively indicates zone “d” (SENEŠ & PAPP, 1974), i.e. N15 zone, which is of the Late Sarmatian age (*sensu stricto*).

Lower Pannonian marls and clays of facies AB contain ostracod samples, which represent an overture for the later explosion and divergence of species (HAJEK-TADESSE, pers. comm.). In this lowest part of the Pannonian there are also examples of small limnocardids.

Previous analysis of individual, characteristic mollusc species, resulted in the Pannonian layers of broader areas (KRANJEC et al., 1973; ŠIKIĆ et al., 1978, 1979) being divided into two acrozones (lower *Radix croatica* and the upper *Congeria banatica*), which are inadequate. Treating the entire fossil mollusc community by the method of characteristic associations (uniqueness of identical community) produced more detailed results. Therefore, in the entire Pannonian succession of the Kostanjek-1 column three zones and two subzones can be separated (Table 2, Fig. 2):

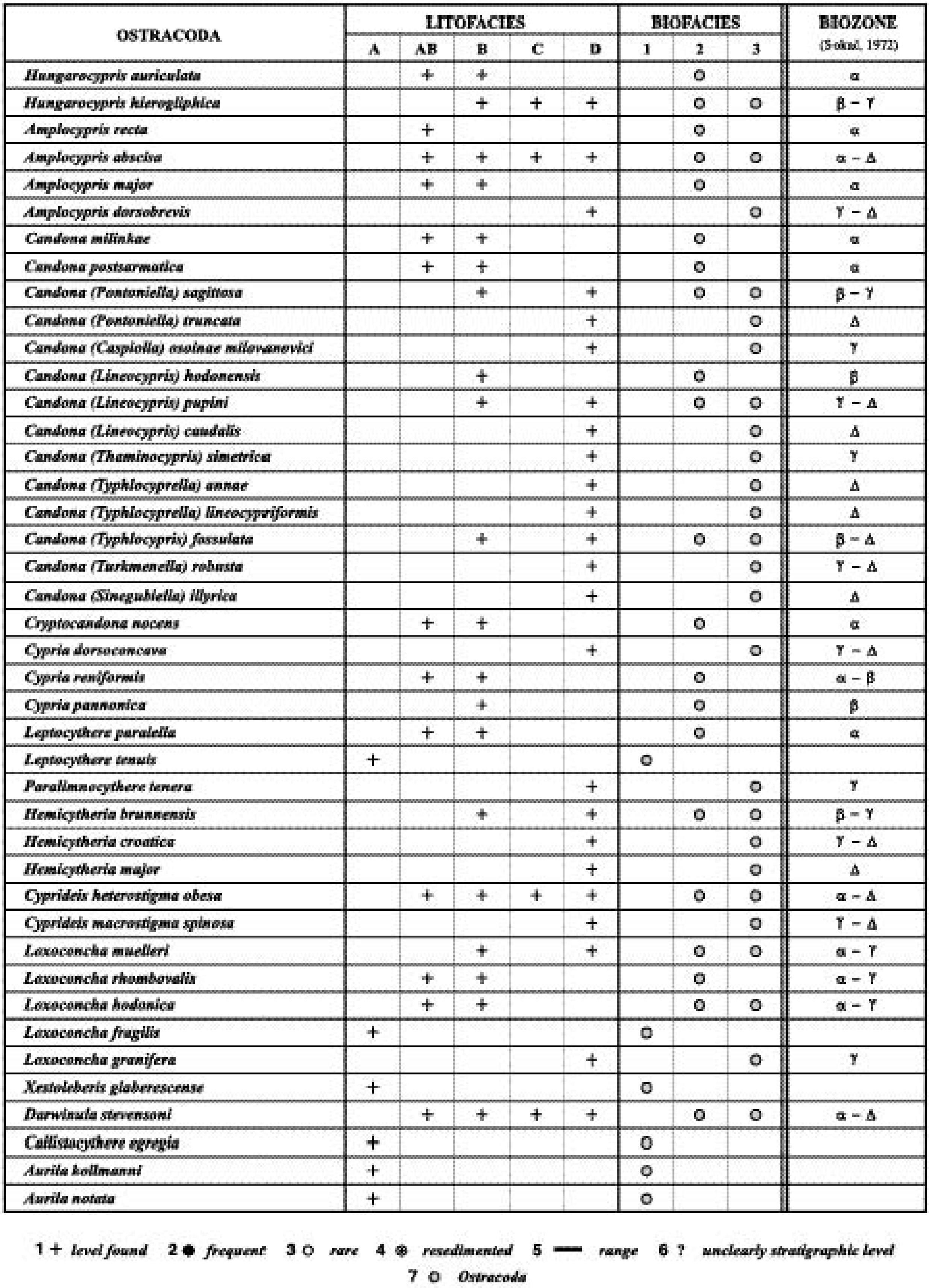
Subzone I (0-3 m thick): “poor zone of transitional layers” - *Lymnocardium praeponticum* acrozone. Fine-laminated clay and marl with rare samples of *L. praeponticum* and small gastropods of *Hydrobia* and the *Valvata* group. The lowest part of the Early Pannonian substage.

Zone II (3-27 m thick): Cenozone *Radix croatica* - *Lymnocardium plicataeformis* - *Gyraulus praeponticus*. Layered limestone and marl with frequent and numerous gastropods. Examples of *Radix croatica*, *R. extensa*, *Gyraulus praeponticus*, *G. dubius* and others, and bivalves of *Lymnocardium plicataeformis*, *L.* cf. *promultistriatum*, *L. praeponticum*, *L. obsoletum*, *Congeria* sp. ?nov. and other accessory forms, which entirely represent the Early Pannonian.

Subzone III (27-35 m thick): “transitional layers” - *Neodelminiella venusta* - *Lymnocardium cekusi* Cenozone. Silty marl with rare gastropod community including *Neodelminiella venusta*, *Radix kobelti*, *Gyraulus dubius*, *Undulotheca halavatsi* and others. Also bivalves of *Lymnocardium cekusi*, *L. spinosum*, *L.* cf. *robici*, ?*Cerastoderma protracta*, and other transitional species, determined (conditionally) as the Middle Pannonian.

Zone IV (35-65 m thick): *Congeria banatica* - *Lymnocardium gorjanovici* - *Gyraulus tenuistriatus* Cenozone. Massive marl with abundant bivalve community: *Congeria banatica*, *C. martonfii*, *C. zahalkai*, *Lymno*-

Table 5 List of molluscs from the Kostanjek-1 column.



OSTRACODA	**LITOFACIES**					**BIOFACIES**			**BIOZONE** (Sokač, 1972)
	A	**AB**	**B**	**C**	**D**	**1**	**2**	**3**	
Hungarocypris auriculata		+	+				○		α
Hungarocypris hierogliphica			+	+	+		○	○	β – γ
Amplocypris recta		+					○		α
Amplocypris abscisa		+	+	+	+		○	○	α – Δ
Amplocypris major		+	+				○		α
Amplocypris dorsobrevis					+			○	γ – Δ
Candona milinkae		+	+				○		α
Candona postsarmatica		+	+				○		α
Candona (Pontoniella) sagittosa			+		+		○	○	β – γ
Candona (Pontoniella) truncata					+			○	Δ
Candona (Caspiolla) ossoinae milovanovici					+			○	γ
Candona (Lineocypris) hodonensis			+				○		β
Candona (Lineocypris) pupini			+		+		○	○	γ – Δ
Candona (Lineocypris) caudalis					+			○	Δ
Candona (Thaminocypris) simetrica					+			○	γ
Candona (Typhlocyprella) annae					+			○	Δ
Candona (Typhlocyprella) lineocypriformis					+			○	Δ
Candona (Typhlocypris) fossulata			+		+		○	○	β – Δ
Candona (Turkmenella) robusta					+			○	γ – Δ
Candona (Sinegubiella) illyrica					+			○	Δ
Cryptocandona nocens		+	+				○		α
Cypria dorsoconcava					+			○	γ – Δ
Cypria reniformis		+	+				○		α – β
Cypria pannonica			+				○		β
Leptocythere paralella		+	+				○		α
Leptocythere tenuis	+					○			
Paralimnocythere tenera					+			○	γ
Hemicytheria brunnensis			+		+		○	○	β – γ
Hemicytheria croatica					+			○	γ – Δ
Hemicytheria major					+			○	Δ
Cyprideis heterostigma obesa		+	+	+	+		○	○	α – Δ
Cyprideis macrostigma spinosa					+			○	γ – Δ
Loxoconcha muelleri			+		+		○	○	α – γ
Loxoconcha rhombovalis		+	+				○		α – γ
Loxoconcha hodonica		+	+				○	○	α – γ
Loxoconcha fragilis	+					○			
Loxoconcha granifera					+			○	γ
Xestoleberis glaberescense	+					○			
Darwinula stevensoni		+	+	+	+		○	○	α – Δ
Callistocythere egregia	+					○			
Aurila kollmanni	+					○			
Aurila notata	+					○			

1 + ***level found*** **2 ●** ***frequent*** **3 ○** ***rare*** **4 ⊛** ***resedimented*** **5 —** ***range*** **6 ?** ***unclearly stratigraphic level***
7 ○ ***Ostracoda***

Table 6 List of ostracods from the Kostanjek-1 column.

cardium gorjanovici, *L. cekusi*, *L. spinosum*, *Caladacna ornata* and others. Gastropods *Gyraulus tenuistriatus*, *Orygoceras laevis*, *Micromelania striata* and other less important fossils also occur. Lower and central part of the Late Pannonian substage.

Zone V (65-83 m thick): *Congeria czjzeki - Lymnocardium winkleri - Gyraulus tenuistriatus* Cenozone. Massive marl and clay with evolved bivalve community including *Congeria czjzeki*, *C. banatica*, *Lymnocardium winkleri*, *L.* cf. *robici*, *Paradacna syrmiense* , *Didacna deserta*, *Pisidium* sp. Also contains gastropods *Orygoceras* cf. *brusinai*, *Velutinopsis* cf. *pancici*, *Gyraulus tenuistriatus* and others. Uppermost part of the Late Pannonian substage.

Due to the specific development and comparatively narrow regional spreading of "so-called Croatica layers" (JENKO, 1944), this locality in Podsused, among other possibilities, should serve as the stratotype for correlation in the western and central parts of the Pannonian basin (HOLLAND, 1990).

4. CONCLUSIONS

1) In the study area the formation of the Pannonian basin as a separate palaeogeographic province, which partly overlaps with the isolation of the western and central Paratethys from the eastern parts during the Middle Sarmatian (*sensu lato*), is expressed in the layering of fluvial-lacustrine Pannonian sediments with a unique endemic mollusc and ostracod fauna which have oligohaline characteristics.
2) The end of the Sarmatian (*sensu stricto*) sedimentation cycle in the study area is manifested as a continuity of sedimentation into the Pannonian, due to the significant desalinization of the water.
3) The salinity drop at the Sarmatian-Pannonian boundary is manifested by the disappearance of most Sarmatian organisms (especially gastropods and foraminifera), and the occurrence of new Pannonian mollusc and ostracod forms. It can be best followed through the evolutionary changes of the *Cardiidae* family.
4) Altered water chemistry in the Pannonian is reflected by changes in the style of sedimentation, and can be followed through geochemical parameters such as carbonate content and content of trace elements (especially strontium and manganese).
5) The great variability and weak diversity of taxonomic structures of organisms in the Early Pannonian substage is the consequence of basin isolation, and is manifested by the endemism of most fossil groups.
6) Gravel lenses of fluvial origin (fan delta system), situated in the Upper Pannonian deep-water marls, are the result of synsedimentary tectonics, which reflected regional tectonic movements.
7) Taxonomic diversity of the fossil community of the Late Pannonian is the consequence of optimum environmental conditions, and relates to the evolutionary maximum of most lacustrine organisms, and was probably the consequence of the introduction of new species from the Back-Carpathian area.
8) Layering of the Sarmatian laminites in reduced conditions with high contents of manganese and pyrite (comparable with the recent situation in the Black Sea), together with high periodic organic production, could indicate their potential as source rocks.
9) Phylogenetic analysis of the *Cardiidae* family should be complemenented with the analysis of adaptive and morphogenetic factors, to improve the qualitative estimation of their evolutionary and stratigraphic significance.

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