

Stratigraphic and palaeogeographic significance of lacustrine molluscs from the Pliocene *Viviparus* beds in central Croatia



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ABSTRACT

The mollusc fauna from the Pliocene *Viviparus* beds of Vukomeričke Gorice hills in central Croatia was investigated at four sites in the region of Kravarsko, S of Zagreb. The region represents a Pleistocene horst-anticline at the southern margin of the Sava depression. Sediments are dominated by clay, bearing some sand, gravel and lignite intercalations. The molluscs, comprising 11 gastropod and 2 bivalve species, seven of which (76.9%) are endemic to the region, prove that the studied deposits were derived from the ancient Lake Slavonia. The taxonomic revisions include the introductions of *Viviparus kochanskyae* n. sp. for specimens from Lake Slavonia previously identified as *V. fuchsi* NEUMAYR, 1872 and *Prososthenia? praeslavonica* n. nom. replacing the primary homonym *Hydrobia vitrella* BRUSINA, 1897 non STEFANESCU, 1896. Recognized as an independent phase in the geodynamic evolution of the Pannonian Basin, the new regional stage Cernikian is introduced for the succession, defined by the complete depositional sequence of the *Viviparus* beds. Two stratigraphic horizons detected in the studied sites are constrained by the Lower Cernikian *Viviparus kochanskyae* and the Upper Cernikian *Viviparus hoernesii* zones and remain in good agreement with previous regional data. The historical timeline for Lake Slavonia is enabled through several zonal markers calibrated to the Geological Time Scale in the Dacian Basin. Accordingly, the Early Cernikian transgression dates to c. 4.3 Ma, the Late Cernikian transgression to c. 3.1 Ma, indicating strong alteration of the lacustrine depositional settings during the Pliocene, most likely related to changes in the regional climate. Interestingly, the second transgression of Lake Slavonia is marked by the evolution of strongly sculptured viviparid shells and coincides with the Pliocene Climate Optimum.

Keywords: Lake Slavonia, Pliocene, *Paludina* beds, mollusc taxonomy, stratigraphy

1. INTRODUCTION

The climatic and geodynamic settings during the Pliocene provided conditions facilitating extended lacustrine environments in southeastern Europe (NEUBAUER et al., 2015a, c). The resulting long-lived palaeo-lakes such as Lakes Slavonia, Metohia, Transylvania and Dacia were all characterized by explosive adaptive radiations of viviparid snails (HARZHAUSER & MANDIĆ, 2008; NEUBAUER et al., 2015a). This phenomenon allowed NEUMAYR & PAUL (1875) in

their famous, pioneering study on Lake Slavonian molluscs to establish a regional biostratigraphy, enabling an excellent stratigraphic control of those deposits stretching over more than 600 km along the southern margin of the Pannonian Basin.

The present investigation deals with the corresponding mollusc record of Lake Slavonia (Figure 1). The samples originate from the region of Kravarsko, which is the type locality of several species described by BRUSINA (1874a, b,



Figure 1: Map illustrating the reconstructed extent of the Pliocene Lake Slavonia (light blue) adapted from NEUBAUER et al. (2015a); *Viviparus* beds (dark blue) are redrawn from the geological map of the Croatian Geological Survey M 1:300,000; Pannonian basin infill (gray) is redrawn from the previous map and from the Yugoslavian geological map M 1:500,000; SRTM topographic model is the ArcGIS World Shaded Relief map by ESRI. White dots indicate studied localities and the type localities of the Cernikian defined in the present study.

1897, 1902). Situated in central Croatia, in the close vicinity of Zagreb, it represents the western most extent of the palaeo-lake. Freshwater deposits alternate therein with alluvial series, providing an approximately 400 m thick Pliocene continental succession (GALOVIĆ, 1952). The series is usually referred to in the literature as the “*Paludina* beds” (KRSTIĆ, 2003; POPOV et al., 2004). *Paludina* FÉRUSAC, 1812, however, is a junior synonym of *Viviparus* MONTFORT, 1810, which is why we use the term “*Viviparus* beds” in the present study. Note that this is only an informal lithostratigraphic unit according to the international stratigraphic code (SALVADOR, 1994).

The aim of the study is to investigate and document the taxonomic inventory of the region, to update the taxonomy of the identified species, and to evaluate the resulting biostratigraphic and palaeo biogeographic patterns for Lake Slavonia and the neighbouring palaeo-lakes. Additionally, the outdated Late Miocene to Pliocene stratigraphic nomenclature of the Sava depression sedimentary series is revised and a new stage name is introduced, constrained by the depositional duration of the *Viviparus* beds and Lake Slavonia, respectively.

2. SOUTHERN PANNONIAN BASIN AND SAVA DEPRESSION

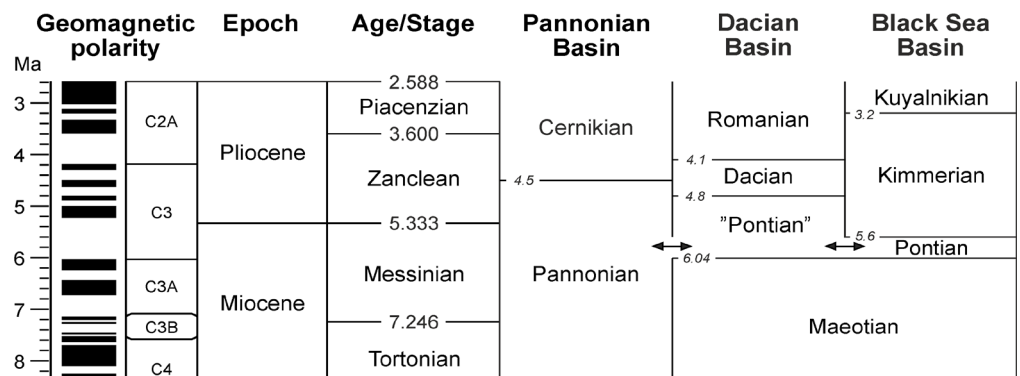
The Pannonian back-arc basin is a large Neogene extensional structure located between the Alpine, Dinaride and Carpathian fold-and-thrust belts in central and SE Europe (SCHMID et al., 2008; USTASZEWSKI et al., 2014). Its formation is bound to the rapid Miocene roll-back of the Carpathian (and probably Dinaride) slab attached to the European continent, and to the Adriatic microplate, respectively (MATENCO & RADIVOJEVIĆ, 2013). The initiation of the synrift phase is marked by the first alluvial and lacustrine deposition in its southern domain dated to ~18 Ma (Early Miocene). Its marine ingressions by the Central Paratethys clearly followed later at ~15 Ma in the Middle Miocene (ĆORIĆ et al., 2009; MANDIĆ et al., 2012) (Figure 2). In northeastern Croatia, the post-rift deposition had already begun at ~13.8 Ma in the late Badenian and continued throughout the middle-late Miocene (PAVELIĆ, 2001). The area of north Croatia experienced strong compressional uplifting in the Pliocene and Pleistocene that caused erosion and reworking of the Miocene deposits and exhumation of the pre-Miocene basement (PAVELIĆ, 2001).

By the end of the Middle Miocene, the Paratethys Sea retreated and the remaining brackish Lake Pannon gave rise to spectacular endemic mollusc radiation in the Late Miocene (MÜLLER et al., 1999; HARZHAUSER & MANDIĆ, 2008; NEUBAUER et al., 2015a, c). Isolation lasted up to 6.04 Ma when the connection with the Dacian Basin becomes established during the early Pontian (STOICA et al., 2013), followed by the migration of the endemic fauna into the Eastern Paratethys (STEVANOVIĆ et al., 1990). With the onset of the Pliocene, Lake Pannon was largely infilled by sediment due to the prograding river systems of the palaeo-Danube and palaeo-Tisza and became restricted in its ultimate phase to NE Croatia and N Serbia (MAGYAR et al., 1999, 2013; UHRIN & SZTANÓ, 2012). During a new period of isolation from the Dacian Basin in the late Dacian, it became replaced by the freshwater environment of Lake Slavonia (STEVANOVIĆ et al., 1990; MARINESCU & PAPAIANOPOL, 1995).

The initiation of Lake Slavonia is marked by a major extinction event of brackish water dwellers such as *Congerina rhomboidea* HÖRNES, 1870, *Phyllocardium planum* (DESHAYES, 1838) or *Prosodacnomya? vodopici* (BRUSINA, 1902) (NEUMAYR & PAUL, 1875; STEVANOVIĆ et al., 1990). The succession documenting the rapid endemic radiation of viviparid snails is consequently termed the *Viviparus* beds. The Lake Slavonia deposits extend from the studied region to westernmost Romania, infilling the Sava, Slavonian-Syrmian, Bačka and Banat depressions of the southern Pannonian Basin (Figure 1). The threefold stratigraphic classification into the lower, middle and upper *Viviparus* beds is well established throughout the region, supported by the biostratigraphic zonation of *Viviparus* species (NEUMAYR & PAUL, 1875; PENECKE, 1884; JENKO, 1944; OŽEGOVIĆ, 1944; TAKŠIĆ, 1954; MARINESCU & PAPAIANOPOL, 1995; LUBENESCU & LUBENESCU, 2008). The upper boundary is marked by the establishment of alluvial depositional settings marked by the Pleistocene *Corbicula* beds in the Slavonian-Syrmian, Bačka and Banat depressions, dated to ~2 Ma (GAUDENYI et al., 2013, 2015).

The investigated region (Figure 1) represents the southern margin of the Sava depression, a NW-SE striking extensional structure filled by more than 5 km of predominantly siliciclastic Neogene deposits (TROSKOT-ČORBIĆ et al., 2009). The sedimentary infill of the Sava depression (Figure

Figure 2: Chronostratigraphic correlation table for the late Neogene indicating the stratigraphic positions of the units referred to in the present study. Standard chronostratigraphy derives from HILGEN et al. (2012). Compilation of Paratethys regional stages is adapted from NEUBAUER et al. (2015b). Palaeogeographic connection events are marked by arrows. The Cernikian is a new Pannonian Basin stage defined in the present study.



3) shows three depositional megacycles separated by compressional phases dated to the late Middle Miocene, the Miocene-Pliocene transition and the early Pleistocene (SAFTIĆ et al., 2003). The first cycle comprises up to 2 km of Middle Miocene marine deposits of the Central Paratethys, the second cycle represents up to 2.5 km of Upper Miocene brackish water deposits of Lake Pannon, and the third cycle includes up to 0.9 m of freshwater deposits of the Pliocene Lake Slavonia (OŽEGOVIĆ, 1944; SAFTIĆ et al., 2003). Pleistocene to Holocene alluvial, marsh and aeolian deposits seal the succession.

3. REVISION OF THE STRATIGRAPHIC NOMENCLATURE AND THE NEW REGIONAL STAGE CERNIKIAN

In terms of regional stratigraphic nomenclature, the complete second megacycle of the Sava depression infill corresponds to the Pannonian stage (Figure 3). Its lower boundary corresponds to the formation of Lake Pannon, coinciding with the major extinction of Sarmatian marine species (Sarmatian–Pannonian extinction event of HARZHAUSER & PILLER, 2007). Its upper boundary is defined by the formation of Lake Slavonia. In the Sava depression, the Pannonian is four-fold, composed of the *Radix croatica*, *Congeria banatica*, *Paradacna abichi* and *Congeria rhomboidea* beds (JENKO, 1944; LUČIĆ et al., 2001). Hitherto, the *P. abichi* and the *C. rhomboidea* beds were correlated with the Pontian Eastern Paratethys stage (STEVANOVIĆ, 1951; STEVANOVIĆ et al., 1990; LUČIĆ et al., 2001). However, such correlation is shown to be incorrect. In the Pannonian Basin, volcanic ash on top of the lower “Pontian” deposits in the vicinity of Tihany (central Hungary), correlates with the top of the *P. abichi* beds, revealing an ⁴⁰Ar/³⁹Ar calibration point of 7.95 Ma (WIJBRANS et al., 2007; MAGYAR & GEARY, 2012; SZTANÓ et al., 2013). Such an age significantly predates the Pontian interval, which is constrained in the northern Black Sea Basin to 6.04–5.60 Ma (KRIJGSMAN et al., 2010). To avoid the pitfalls of erroneous correlations in the future and to stabilize the regional chronostratigraphic schemes, the usage of units defined outside the respective geodynamic complex should be rejected.

Yet, the third depositional megacycle of the Sava depression (Figure 3), marked by the deposition of

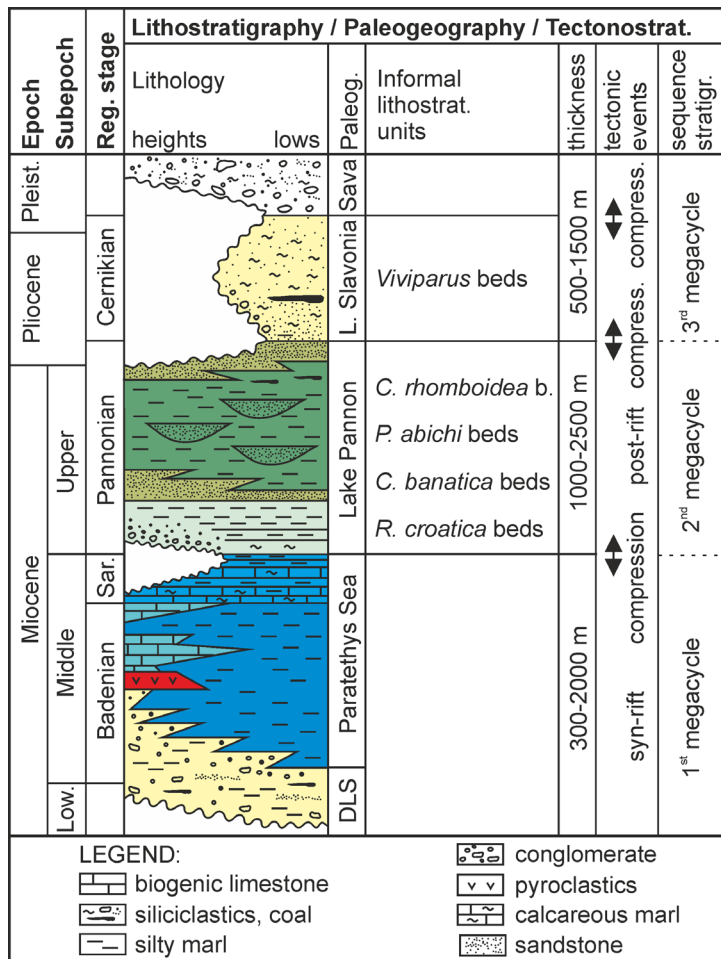


Figure 3: Revised regional stratigraphic scheme of the Sava Basin (modified after SAFTIĆ et al., 2003). Those authors place the synrift/posrift boundary at the transition of the middle to late Miocene. Yet, in the eastern Sava depression this boundary correlates with the middle Badenian as documented by PAVELIĆ (2001). MATENCU & RADIVOJEVIĆ (2012) demonstrated that the synrift phase continues in some regions of the southern Pannonian Basin well into the Pannonian, whereas the postift phase may start already in the early Badenian.

the *Viviparus* beds during the Pliocene and Pleistocene, has also been correlated with the Dacian and/or Romanian regional stages of the Dacian Basin (JENKO, 1944; LUČIĆ et al., 2001; POPOV et al., 2004; MALVIĆ, 2012). However, due to tectonic inversion, Lake Slavonia represents a fully independent palaeogeographic unit from the early Pliocene, showing depositional dynamics different to those of the Dacian Basin (SAFTIĆ et al., 2003; SZTANÓ et al., 2013; STOICA et al., 2013; VAN BAAK et al., 2015). Considering the enormous thickness of the *Viviparus* beds along with their well-established stratigraphic subdivision (e.g., PENECKE, 1884; JENKO, 1944; OŽEGOVIĆ, 1944; TAKŠIĆ, 1954), and following the example from the Dacian Basin (ANDREESCU & PAPAIANOPOL, 1975; ANDREESCU, 1975; PAPAIANOPOL et al., 2003), we recognize a practical need for the introduction of a new and independent chronostratigraphic unit.

Thus, we herewith introduce the Cernikian new regional stage (Figure 2). The stage name derives from the village of Cernik near the boundary stratotype, as defined below (Figure 1 and 3). The stratigraphic content of the new regional stage corresponds to the *Viviparus* beds as defined by NEUMAYR & PAUL (1875). Its duration equals their maximum depositional extent, i.e., it corresponds to the duration of Lake Slavonia. The stage is threefold as defined by its fossil content. Hence, the Lower Cernikian or Lower *Viviparus* beds include the *V. neumayri* and *V. kochanskyae* zones; the Middle Cernikian or Middle *Viviparus* beds comprise the *V. bifarcinatus*, *V. stricturatus* and *V. nothus* zones; and the Upper Cernikian or Upper *Viviparus* beds include the *V. sturi*, *V. hoernesi*, *V. zelebori* and *V. vukotinovici* zones.

The section NE of Cernik (Figure 1) is composed of marly clay with lignite seams bearing *V. neumayri*. It is superposed on the topmost Pannonian sand and is proposed as the boundary stratotype for the Cernikian (NEUMAYR & PAUL, 1875, p. 9, fig. 4). The most complete succession occurring in the valley N of Malino (Figure 1) including Lower, Middle and Upper *Viviparus* beds, described in detail in NEUMAYR & PAUL (1875, p. 10-11, fig. 6), represents the type section ("holostratotype"). A highly instructive, artificially outcropped section, showing a complete development of the *Viviparus* beds is described by OŽEGOVIĆ (1944) from the Gojlo anticline (Figure 1) E of Kutina in NE Croatia ("faciostratotype"). There, the 900-m-thick Cernikian interval is composed largely of greenish clay and fine-sand with abundant viviparids. The 200-m-thick Lower Cernikian and the 600-m-thick Upper Cernikian interval contain 0.1 to 2-m-thick coal seams.

4. VUKOMERIČKE GORICE HORST-ANTICLINE

The investigated samples are from a 12 km² area large, 7.8 km long, and NW-SE striking region around Kravarsko. This village and municipality is located 30 km S of Zagreb in Croatia (Figure 1). The region is located on the NE flank of slightly elevated, forested countryside termed Vukomeričke Gorice, representing a large-scale horst-anticline composed of several smaller anticlines, uplifted in the Pleistocene along parallel longitudinal faults (PIKIJA, 1987a). Its surface is composed of the *Viviparus* beds, which are partly overlain by periglacial

deposits at the northeastern margin (PIKIJA, 1987b). The basement, detected in wells at a depth of 863 m (Well Dubranec 2; GALOVIĆ, 1952), consists of Palaeozoic green quartz-chlorite schists and belongs to the Internal Dinaride Jadar-Kopaonik thrust sheet (SCHMID et al., 2008). It is directly overlain by Badenian biogene limestones. Upwards, the succession comprises Sarmatian marls and sandstones, Pannonian marls and Cernikian clays (Figure 3).

The Cernikian interval attains thicknesses of 200 to 450 m with inclinations of 2° to 12°. In the Kravarsko area, the Middle Cernikian was not discovered either by drilling or surface mapping (GALOVIĆ, 1952; GAGIĆ & SOKAČ, 1970; JURKOVIĆ, 1993). The Lower Cernikian, is represented here only by the *V. kochanskyae* zone, and is dominated by plastic clay, bearing some sand packages and up to 3.8 m thick coal seams consisting of reed- and wood-like plant material (STUR, 1863; FARKAŠ-VUKOTINOVIĆ, 1863; JURKOVIĆ, 1993; ŠEBEČIĆ, 2010). Above an indistinct unconformity, the Upper Cernikian shows an erosional contact with some faunal reworking. Sandy clays alternate and there are few lignite seams, and local coarse to fine grained gravel packages. The *V. sturi*, *V. hoernesi* and *V. vukotinovici* zones were detected in the Upper Cernikian.

The initial work on the mollusc fauna of the Vukomeričke Gorice hills was carried out by PILAR (1873) and BRUSINA (1874a, b, 1884, 1885, 1896, 1897, 1902). KOCH (1917) provided the last census of the fauna recording 41 species altogether, although his list lacked the Middle Cernikian zonal markers. GAGIĆ & SOKAČ (1970) studied the ostracods from the drill cores. The faunal composition suggested a vegetated lake bottom in shallow sublittoral water-depths of 10 m or less, and a Pliocene to Pleistocene age for the Cernikian deposits.

5. LOCALITIES AND SAMPLES

From each locality one sample was analyzed, coded as Kra-I, VGK-39, VGK-38 and VGK-35 (Figure 1).

Kra-I is located 1.73 km NW of the Holy Cross church in Kravarsko, SW of the houses termed Povoljnaki, at 192 m a.s.l., on the slope below the main road (45.595525°N 16.038053°E). The outcrop area is an active landslide laterally extending about 50 m. Except for a 3.4 m thick interval exposed at the northern limit of the landslide area, the bedding is largely disturbed. The former outcrop is dominated by a structure-less, grayish to yellowish clayey silt, with scattered plant remains. A 1.15 m thick unit of gray homogenous clay is intercalated in the lower part of the interval. The topmost 25% of this package displays fine-scale banding due to the intercalation of fine and medium grained sand. The sampled mollusc concentration occurs in the land-slide area, laterally to the outcrop, being strongly deformed and disjointed. It acted apparently as an inhomogeneity surface with the original stratigraphic position on top of the undisturbed interval (Figure 4).

VGK-39 is located within Kravarsko, 330 m NW of the Holy Cross church, at 215 m a.s.l. on the same slope as the

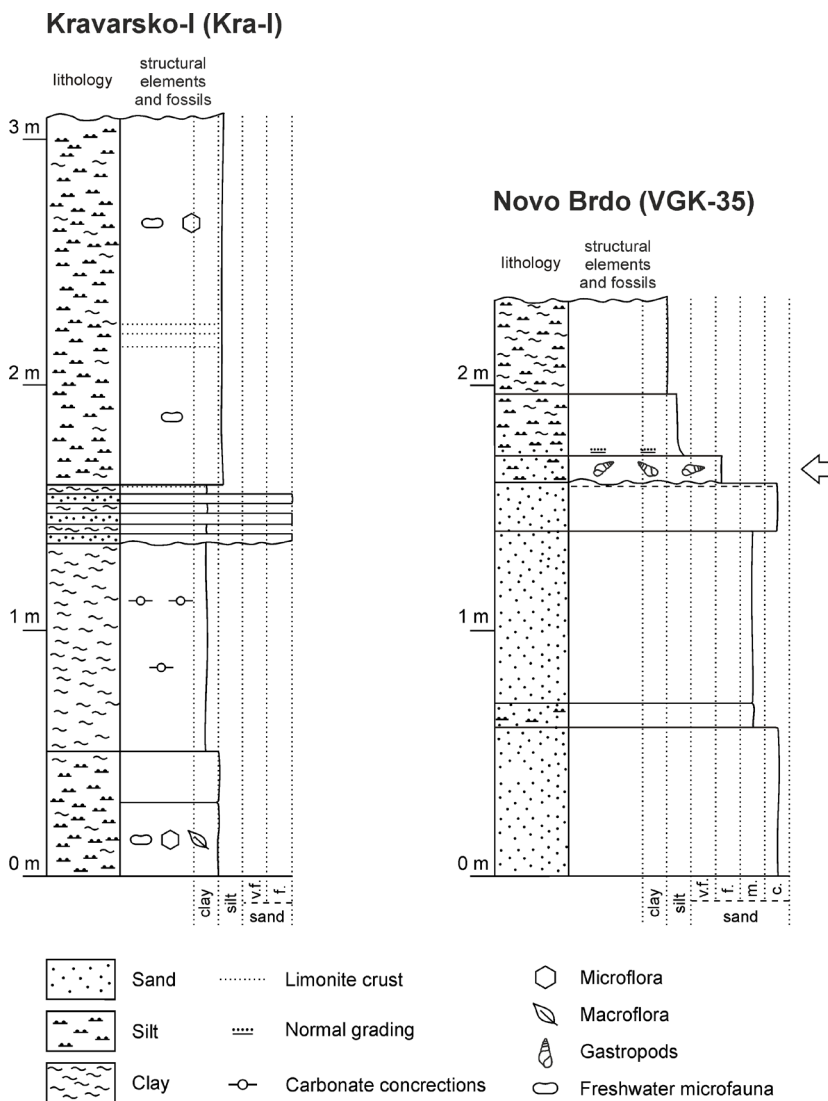


Figure 4: The studied sections. Arrow marks the mollusc sample.

previous locality, 80 m W of the road junction (45.588015°N 16.044973°E). This locality has no exposed section. The sample was taken from a shell accumulation entirely disturbed by the land-slide very similar to Kra-I.

VGK-38 is located 3 km NE of Donji Hruševac, 7.3 km SE of the previous sample point, in the Veliki Burdelj wood, 230 m NW of the path to Brenčići, in the trench of the NE flowing ephemeral stream at 152 m a.s.l. (45.551984°N 16.084993°E). The collected gastropod shell originated from debris accumulated by the stream. The shells derive from an unknown position within the Cernikian deposits exposed along the trench in upstream direction. The distance to the stream head of only 260 m makes longer transport improbable.

VGK-35 is located 2.7 km WSW of VGK-39, beside the path in the wood SWS of Novo Brdo at 165 m a.s.l. (45.582877°N 16.021478°E). The small outcrop exposes 1.6 m of yellowish macrofossil free sand in its lower part. A 0.8 m thick fining upward interval of sandy to clayey silt follows (with an erosive boundary) in the upper part of the section. The sample comes from the initial 10 cm of the latter inter-

val bearing poorly preserved, non-oriented mollusc shells suspended in a sandy silt matrix (Figure 4).

6. RESULTS AND DISCUSSION

6.1. Taxonomy, palaeoecology and stratigraphy

The taxonomic revision provides several updates for the fauna (Table 1). *Viviparus kochanskyae* is introduced as a new species for the zonal marker of the Lower Cernikian, a taxon formerly identified as *Viviparus fuchsi* (NEUMAYR, 1872), which, however, is restricted to the Pannonian Basin. Three species, *Microcolpia friedeli*, *Prososthenia? slavonica* and *Potomida seljani* are newly combined in agreement with modern systematics (see taxonomy below). The cross-checking of the literature allowed a precise stratigraphic and palaeo biogeographic evaluation of the record (Tables 2 to 3). Except for *Lithoglyphus decipiens*, *Bithynia vukotinovi* and *Theodoxus semiplicatus*, all other taxa are approved and appear to be restricted to Lake Slavonia (Table 3).

Altogether, the samples contain 13 lacustrine species, comprising 2 bivalve and 11 gastropod species (Table 1). As expected for the *Viviparus* beds, viviparids are the most diverse (4 species), followed by melanopsids and hydrobiids (2 species each). Further families (valvatids, ner-

Table 1: Species identified in the studied samples. The previously unknown species from central Croatia are marked by asterisks.

Class	Family	Species	Kra-I	VGK-39	VGK-38	VGK-35
Gastropoda	Valvatidae	<i>Valvata subcarinata</i>	x	x		
		<i>Theodoxus semiplicatus</i>	x	x		
	Viviparidae	<i>Viviparus kochanskyae</i> n. sp.	x	x		
		<i>Viviparus hoernesii</i>				x
		<i>Viviparus aulacophorus</i> *		x		
		<i>Viviparus dezmanianus</i>			x	
	Melanopsidae	<i>Melanopsis clavigera</i> *				x
<i>Microcolpia friedeli</i>		x	x			
Bythiniidae		<i>Bythinia vukotinovi</i>	x	x		
Hydrobiidae	<i>Prososthenia? slavonica</i> *		x			
	<i>Lithoglyphus decipiens</i> *	x	x			
Bivalvia	Sphaeriidae	<i>Pisidium solitarium</i> *		x		
	Unionidae	<i>Potomida seljani</i>		x		

Table 2: Stratigraphic distribution of the identified taxa in the revised Lake Slavonia chrono- and biostratigraphic scheme. Integrating results by NEUMAYR & PAUL (1875) and PENECKE (1884), the Lake Slavonia viviparid gastropod zones are defined here by the first appearance of the name-giving taxon. Except for *V. neumayri* and *V. stricturatus*, all are confined to their respective zones. Horizons identified in the studied region are marked in bold.

Substage	Lineage Zone <i>Viviparus</i>	<i>Valvata subcarinata</i>	<i>Theodoxus semiplicatus</i>	<i>Viviparus kochanskyae</i> n. sp.	<i>Viviparus hoernesii</i>	<i>Viviparus aulacophorus</i>	<i>Viviparus dezmanianus</i>	<i>Melanopsis clavigera</i>	<i>Microcolpia friedeli</i>	<i>Bythinia vukotinovici</i>	<i>Prososthenia? slavonica</i>	<i>Lithoglyphus decipiens</i>	<i>Pisidium solitarium</i>	<i>Potomida seljani</i>
Upper Cernikian	<i>vukotinovici</i>	?	x									x		x
	<i>zelebori</i>	?	x					x			x	x		l
	<i>hoernesii</i>	?	x		X		(X)	X			l	x		l
	<i>sturi</i>	?	x				x			?	x	x		l
Middle Cernikian	<i>notha</i>	?	x				x			?	x	x		l
	<i>stricturatus</i>	?	x				x			x	x	x		l
	<i>bifarcinatus</i>	?	x							?	x	x		l
Lower Cernikian	<i>kochanskyae</i>	X	X	X		X			X	X	X	X	X	X
	<i>neumayri</i>					x				?		x		

X: present study

x: literature data

?: literature data on *Valvata piscinalis* and *Bythinia tentaculata*

l: interpolated

Table 3: Stratigraphic (epoch) and geographic (palaeolake or region) distribution of the species identified in the studied samples; X - present, (-) - absent (previously misidentified), ? - identification uncertain.

Species	Miocene							Pliocene					Pleistocene					
	Bresse	Frankfurt	Dinarides	Metohia	Lake Pannon	Lake Dacia	Black Sea	Metohia	Brasov	NE Croatia	Lake Dacia	Black Sea	Aegean	Bresse	Rome	Pannon. B.	Black Sea	Aegean
<i>Valvata subcarinata</i>				(-)	(-)			(-)	X							(-)		
<i>Theodoxus semiplicatus</i>							(-)	X	X	X		(-)				(-)		
<i>Viviparus kochanskyae</i> n. sp.	(-)				(-)	(-)	(-)	(-)	X		(-)	(-)					(-)	(-)
<i>Viviparus hoernesii</i>									X	(-)								
<i>Viviparus aulacophorus</i>									X									
<i>Viviparus dezmanianus</i>									X	(-)	?							
<i>Melanopsis clavigera</i>									X			(-)						(-)
<i>Microcolpia friedeli</i>					(-)				X	(-)								
<i>Bythinia vukotinovici</i>									X	X	X							X
<i>Prososthenia? slavonica</i>		(-)			(-)			(-)	X				(-)	(-)	(-)			
<i>Lithoglyphus decipiens</i>			X		X	X	X	(-)	(-)	X	X	X				(-)		
<i>Pisidium solitarium</i>									X									
<i>Potomida seljani</i>																		

itids, bithyniids, unionids and sphaeriids) are represented by only one species each.

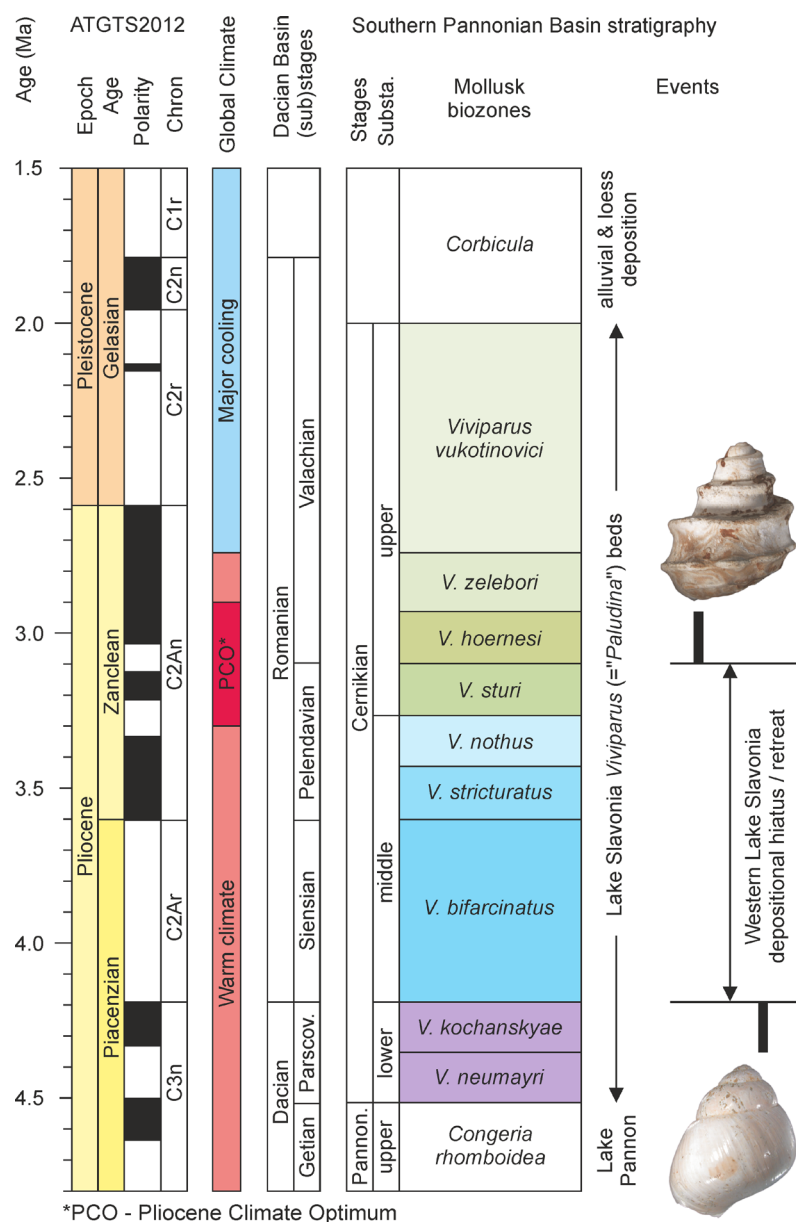
The highest number of species (10) is recorded from VGK-39, and they are also the best preserved. Material from sample Kra-I exhibits limonite colouring and partial leach-

ing and contains a smaller number of species (6), all present in the previous sample. The difference in composition is probably only a taphonomic feature. This is supported by the presence of *V. kochanskyae* in both samples, which is a zonal marker restricted to the upper part of the Lower Cernikian.

Figure 5: Stratigraphic correlation of the Lake Slavonia stratigraphic units with the Dacian Basin chronostratigraphy after VAN BAAK et al. (2015). Calibration of *Viviparus* biozones is based mainly on LUBENESCU & LUBENESCU (2008) and own data (see text). Standard chronostratigraphy follows HILGEN et al. (2012). Note the indicated position of the two stratigraphic levels identified in the studied sites and the one million year gap between them. This agrees with previously published results showing the absence of middle *Viviparus* beds in western Lake Slavonia. This implies a 1 myr long retreat of the Lake Slavonia eastwards with subsequent short-term flooding during the Pliocene Climate Optimum.

In sample VGK-39, the melanopsid *Microcolpia friedeli* is the most frequent species, followed by the hydrobiid *Prososthenia? slavonica*. Melanopsids are generalists occurring in lakes and rivers, tolerating even slightly brackish conditions (GLAUBRECHT, 1996; BANDEL, 2000). Hydrobiids are present in different types of environments, and are usually well adapted to littoral mud flat settings (GLÖER, 2002; NEUBAUER et al., 2013a, b). *Valvata piscinalis*, which may represent an ecological counterpart of *V. subcarinata*, prefers fresh- and hard-water lake settings with a rich vegetation cover (ØKLAND, 1990). *Theodoxus danubialis*, as a potential counterpart of *T. semiplicatus*, is most abundant in fluvial environments but is also found in lakes (JURIŠIĆ-POLŠAK, 1979; WELTER-SCHULTES, 2012). *Bythinia* is a generalist, living in stagnant and moderately running waters on detritus-rich substrates (GLÖER, 2002). Viviparids are pure freshwater dwellers (WELTER-SCHULTES, 2012). Some European species prefer rivers, others settle in lakes. In Lake Geneva, they are highly abundant in the shallow, littoral zone (GLÖER, 2002). With respect to the ecological requirements of the mollusc species, from the dominantly muddy sediment and the lignites, a calm, littoral setting of a freshwater lake can be inferred for the samples, which is in agreement with previous ostracod data (GAGIĆ & SOKAČ, 1970).

Due to the generally poor preservation, the sample from Novo brdo (VGK-35) revealed only two species (Table 1), both of which are absent in Kravarsko. *Viviparus hoernesii* is a zonal marker of the Upper Cernikian, *Melanopsis clavigera* is restricted to the *V. hoernesii* and *V. zelebori* zones (PENECKE, 1884). This suggests a stratigraphic position within the middle Upper Cernikian. *V. dezmani-anus*, identified as a single species from the Burdelj wood (VGK-38), could be of the same age. It has a long stratigraphic range (PENECKE, 1884), concurring among others also with *V. hoernesii*. This is in agreement with the results



*PCO - Pliocene Climate Optimum

of previous investigators reporting both viviparid species as constituents of the Upper Cernikian fauna of the Vukomeričke Gorice hills (GALOVIĆ, 1952; GAGIĆ & SOKAČ, 1970).

6.2. Calibration of the Cernikian to the GTS and the Pliocene Climate Optimum

Although representing an isolated lake, at least temporary southward outflow from the Pannonian Basin existed according to PAPAIANOPOL & MARINESCU (1995), allowing some species to migrate to the Dacian Basin (Figure 5 and 6). This facilitates a rough calibration of the Cernikian biostratigraphy to the Dacian and Romanian substages based on shared *Viviparus* zonal markers (Figure 6). This allows an indirect correlation to the Geological Time Scale (GTS) based on the magnetostratigraphic age model for the Pliocene of the Dacian Basin of VAN BAAK et al. (2015). This model calibrates the Upper Dacian (Parscovian) base to 4.5 Ma, the



Figure 6: Palaeogeographic map of the Pliocene after NEUBAUER et al. (2015a) indicating lakes from where the species observed at the Vukomeričke Gorice hills were previously reported. Note that most of these occurrences are proven to be erroneous after the present revision (see Table 3).

Lower Romanian (Sienian) base to 4.2 Ma, the Middle Romanian (Pelendavian) base to 3.6 Ma and the Upper Romanian (Valachian) base to 3.1 Ma.

The calibration presented in Figure 5 is based on a literature review: LUBENESCU & LUBENESCU (2008) showed *V. stricturatus* and *V. sturi* to be restricted to the Pelendavian of the Dacian Basin. ANDREESCU et al. (2013) presented *V. bifarcinatus* as a zonal marker of the same substage. VAN BAAK et al. (2015) used the first appearance of *V. stricturatus* as a marker of the base of the Pelendavian. LUBENESCU & LUBENESCU (2008) reported *V. pilari* and *V. rudis* as being restricted to the Valachian. The latter species are restricted in the Pannonian Basin to the *V. hoernesii* zone (PENECKE, 1884). The correlation of the Cernikian base with the base of the Parscovian follows PAPA- IANOPOL et al. (2003).

According to the presented correlation, the Cernikian spans the interval from 4.5 Ma to 2.0 Ma. The lower boundary of the Middle Cernikian is correlated to 4.2 Ma, the base of the Upper Cernikian corresponds to 3.3 Ma, approximately coinciding with the start of the Pliocene Climate Optimum (PCO). The period between 4.3 and 2.7 Ma represents a general warm phase during the Pliocene, culminating between 3.3 and 2.9 Ma. At that time, polar temperatures increased by up to 10°C, the ice caps melted rapidly and global sea level was about 25 m higher than today (FOLLAND et al., 1990; RAYMO et al., 1996; FEDOROV et al., 2013; WILLEIT et al., 2013). Interestingly, the increase of shell sculpture in lineages of the Lake Slavonia viviparids parallels the warming trend during the PCO (Figure 6). Thereafter, generally weaker sculptured species of the *V. vukotinovi* zone followed (NEUMAYR & PAUL, 1875).

6.3. Implications for the history of Lake Slavonia

The biostratigraphic framework described above allows correlation of the studied sites with the Lower and Upper Cernikian (Figure 5). This fully agrees with previous results by GALOVIĆ (1952) and GAGIĆ & SOKAČ (1970) confirming that the Middle Cernikian is missing in the Vukomeričke Gorice hills. Considering that the area represents the west-

ernmost extent of Lake Slavonia and in respect to the general eastward fluvial flow direction in the Pannonian Basin, important implications for the history of Lake Slavonia can be drawn.

In particular, the distribution pattern in the mollusc assemblages proved that two main flooding events of Lake Slavonia occurred in the investigated area, correlating with the *Viviparus kochanskyi* zone and the *Viviparus hoernesii* zone. The first flooding coincided with the start of relatively warm climate conditions in the region (Figure 6). Lake Slavonia had already at c. 4.3 Ma a distinctly larger surface than Lake Pannon in its final phase in the early Pliocene at c. 4.5 Ma (MAGYAR et al., 1999) (Figure 1). In contrast, the Middle Cernikian seems to represent a generally arid climate phase in the region, resulting in the retreat of Lake Slavonia from the Vukomeričke Gorice hills. The second ingression at c. 3.1 Ma coincided with the PCO (FEDOROV et al., 2013; WILLEIT et al., 2013), followed apparently by the re-establishment of humid conditions and a further increase in the size of Lake Slavonia (Figure 5).

MARINESCU & PAPA- IANOPOL (1995) reconstructed Lake Slavonia rather as a system of lakes connected by rivers. Such a scenario was certainly possible for the time of the Middle Cernikian arid spell reflected by a more than 1 Ma long interruption of lacustrine deposition in the Vukomeričke Gorice hills. The renewed rise of the lake indicates that Lake Slavonia was not simply filled from the west to the east like the Miocene Lake Pannon (MAGYAR et al., 2013). Instead, active subsidence in the southern Pannonian Basin provided accommodation space for terrestrial input and allowed the persistent existence of lacustrine conditions throughout the Pliocene and the earliest Pleistocene (SAFTIĆ et al., 2003). Previous authors (GALOVIĆ, 1952; GAGIĆ & SOKAČ, 1970) indicated the presence of the zonal marker *V. vukotinovi* in the Vukomeričke Gorice hills with FOD at ~2.5 Ma. Therefore, the tectonic inversion could not have started prior to that time.

A connection to the Dacian Basin as suggested by MARINESCU & PAPA- IANOPOL (1995) is corroborated by the high similarities between the mollusc faunas. Following the

synopsis of NEUBAUER et al. (2015a), 50 of the 163 species (30.7%) recorded for Lake Slavonia are also known from Lake Dacia (Figure 6). It is therefore likely that temporary one-way connections existed through outflow from the Pannonian Basin (MARINESCU & PAPAIANOPOL, 1995).

7. CONCLUSION

The Pliocene *Viviparus* beds of the Vukomeričke Gorice hills in central Croatia represent the topmost sequence-stratigraphic megacycle of the Sava depression sedimentary infill. This interval represents an independent phase of the geodynamic evolution of the Pannonian Basin. For that reason, a new regional stage termed the Cernikian is introduced here, defined by the depositional cycle comprising the *Viviparus* beds. The cycle is linked to the development of a freshwater lake termed Lake Slavonia. Its deposits transgressively overlie Pannonian brackish-water deposits of Lake Pannon, previously referred to the Pontian. The Pontian stage, however, is clearly older and was defined in a completely different geodynamic area. Therefore, regional stages such as the Pontian, Dacian and Romanian should only be used in the respective type areas and must not be applied to the southern Pannonian Basin.

The investigated mollusc fauna from the region of Kravarsko, including 13 freshwater lacustrine species, is dominated by gastropods (11 species). The taxonomic update of the fauna resulted in several revisions. The widely used name *Viviparus fuchsi* NEUMAYR, 1872 refers to a distinct species from Lake Pannon. Therefore, we introduce the new species *Viviparus kochanskyae* n. sp. for specimens from Lake Slavonia previously identified with *V. fuchsi*. The former “*Viviparus fuchsi* zone” is consequently re-named to the “*Viviparus kochanskyae* zone”. *Hydrobia slavonica vitrella* BRUSINA, 1897, from the Pannonian of Grgeteg in Syrmia is preoccupied by the Sarmatian species *Hydrobia vitrella* STEFANESCU, 1896. Therefore, we introduce *Prososthenia? praeslavonica* n. nom. Three species are newly combined: *Microcolpia friedeli* (BRUSINA, 1885), *Potomida seljani* (BRUSINA, 1902) and *Prososthenia? slavonica* (BRUSINA, 1874).

The fauna shows an excellent match with the *Viviparus* beds of NE Croatia proving it as a fully integrated constituent of the long-lived Lake Slavonia. The biostratigraphy of Lake Slavonia is well established, based on the rapid endemic evolution of viviparid gastropods. Two stratigraphic horizons detected in the studied sites support previous regional subdivisions. These are the Lower Cernikian *Viviparus kochanskyae* zone and the Upper Cernikian *Viviparus hoernesii* zone. The lack of the Middle Cernikian in the Vukomeričke Gorice hills indicates strong alteration of the lacustrine depositional settings in the Pliocene of the southern Pannonian Basin. Considering that the subsidence was constant within the respective megacycle, the inferred pattern is best explained by the Middle Cernikian arid spell reflected by back-stepping of the lake.

The timing of the latter event is enabled through several zonal markers calibrated to the Geological Time Scale in the

Dacian Basin, indicating where some species of Lake Slavonia migrated via rivers. Accordingly, the Early Cernikian lacustrine transgression dates to c. 4.3 Ma and the base of the Late Cernikian to c. 3.1 Ma, proving a more than 1 Ma long depositional hiatus for the region. Interestingly, the second lacustrine transgression of Lake Slavonia is marked by the evolution of strongly sculptured viviparid shells and coincides exactly with the Pliocene Climate Optimum.

8. SYSTEMATIC PALAEONTOLOGY

Gastropod systematics follows BOUCHET & ROCROI (2005) and the WoRMS database. Systematics of the bivalves follows BOUCHET & ROCROI (2010) and GRAF & CUMMING (2007, 2014).

Abbreviations:

- LVB – Lower *Viviparus* beds
- MVB – Middle *Viviparus* beds
- UVB – Upper *Viviparus* beds
- NHM – Natural History Museum
- GBA – Geological Survey Vienna, Austria

Class Gastropoda CUVIER, 1795

Subclass Heterobranchia GRAY, 1840

Superfamily Valvatoidea GRAY, 1840

Family Valvatidae GRAY, 1840

Genus *Valvata* O. F. MÜLLER, 1774

Type species: *Valvata cristata* O.F. MÜLLER, 1774; Recent, Europe; type by monotypy.

Valvata subcarinata BRUSINA, 1878

Figures 7.1-4

1869 *Valvata piscinalis* LAMARCK – NEUMAYR, p. 378, pl. 13, fig. 11 [pars; non *Nerita piscinalis* O. F. MÜLLER, 1774; non Vienna Basin occurrences].

1874a *Valvata piscinalis* MÜLLER – BRUSINA, p. 88-89 [pars; non *Nerita piscinalis* O. F. MÜLLER, 1774; non Vienna Basin occurrences].

1874b *Valvata piscinalis* MÜLLER – BRUSINA, p. 71 [pars; non *Nerita piscinalis* O. F. MÜLLER, 1774; non Vienna Basin occurrences].

1875 *Valvata piscinalis* MÜLLER – NEUMAYR & Paul, p. 78, pl. 9, fig. 18 [pars; non *Nerita piscinalis* O. F. MÜLLER, 1774; non Vienna Basin occurrences].

*1878 *Valvata subcarinata*, BRUSINA – BRUSINA, p. 352-353.

1884 *Valvata piscinalis* MÜLLER – PENECKE, p. 36 [pars; non *Nerita piscinalis* O. F. MÜLLER, 1774; non Vienna Basin occurrences].

1884 *Valvata subcarinata* BRUS. – PENECKE, p. 36.

1884 *Valvata Hörnesii* nov. form. – PENECKE, p. 38, pl. 10, fig. 3.

1897 *Valvata subcarinata* BRUS. – BRUSINA, p. 25, pl. 13, figs. 32-39.

1928 *Valvata (Cincinna) subcarinata* BRUSINA – WENZ, p. 2450 [pars; regarding only Slavonian occurrences].
non 1932 *Valvata (Cincinna) piscinalis subcarinata* BRUS. – JEKELIUS, p. 64, pl. 5, figs. 25-27.

1974 *Valvata (Cincinna) subcarinata* BRUSINA – MILAN et al., p. 145.

2014 *Valvata subcarinata* BRUSINA, 1878 – HASZPRUNAR, p. 100.

Material: VGK-39 (3 specimens from sample no. 16, 3 specimens from sample no. 36, and 11 specimens from sample no. 40), and Kra-I (3 specimens from sample no. 5, and 2 specimens from sample no. 26).

Dimensions: Height x width – 4.2 x 4.7 mm (Figs. 5.1-2); 4.4 x 4.7 mm (Figs. 5.3-4).

Description: Glossy, trochiform shell, slightly wider than high ($W/H=0.92$), with 4.5 rounded whorls rapidly and continuously increasing in diameter, delineated by deep sutures. Last whorl attains 87% of total shell height. Aperture is subcircular, weakly oblique, slightly angulated adapically at the contact with the last whorl. Peristome is sharply edged. Umbilicus narrow and deep. Shell covered with fine, non-projecting growth lines and fine axial undulations marking the growth stops. Protoconch low trochiform, attaining little more than one whorl, showing fine spiral microsculpture typical for valvatids.

Remarks: *Valvata subcarinata* BRUSINA, 1878 was introduced as a replacement name for *Valvata piscinalis* NEUMAYR, 1869 non MÜLLER, 1774 [although erroneously indicated as “non LAMARCK”] (HASZPRUNAR,

2014). The indication of a “holotype” of *V. subcarinata* by MILAN et al. (1974) for a specimen illustrated by BRUSINA (1897, pl. 13, figs. 32-34; Coll. NHM Zagreb Inv. No. 2117-763/1) from Čaplja is incorrect. The eleven specimens from Sv. Linart (= St. Leonhardt, church NW Cernik) studied by NEUMAYR (1869) are syntypes and no holotype or lectotype exists at present. To settle this issue, we herewith designate the specimen illustrated by NEUMAYR (1869, pl. 13, fig. 11; Coll. GBA Inv. No. 1869/001/0069) as the lectotype. NEUMAYR & PAUL (1875) assigned the locality to the LVB *V. fuchsi* [= *kochanskyae*] zone.

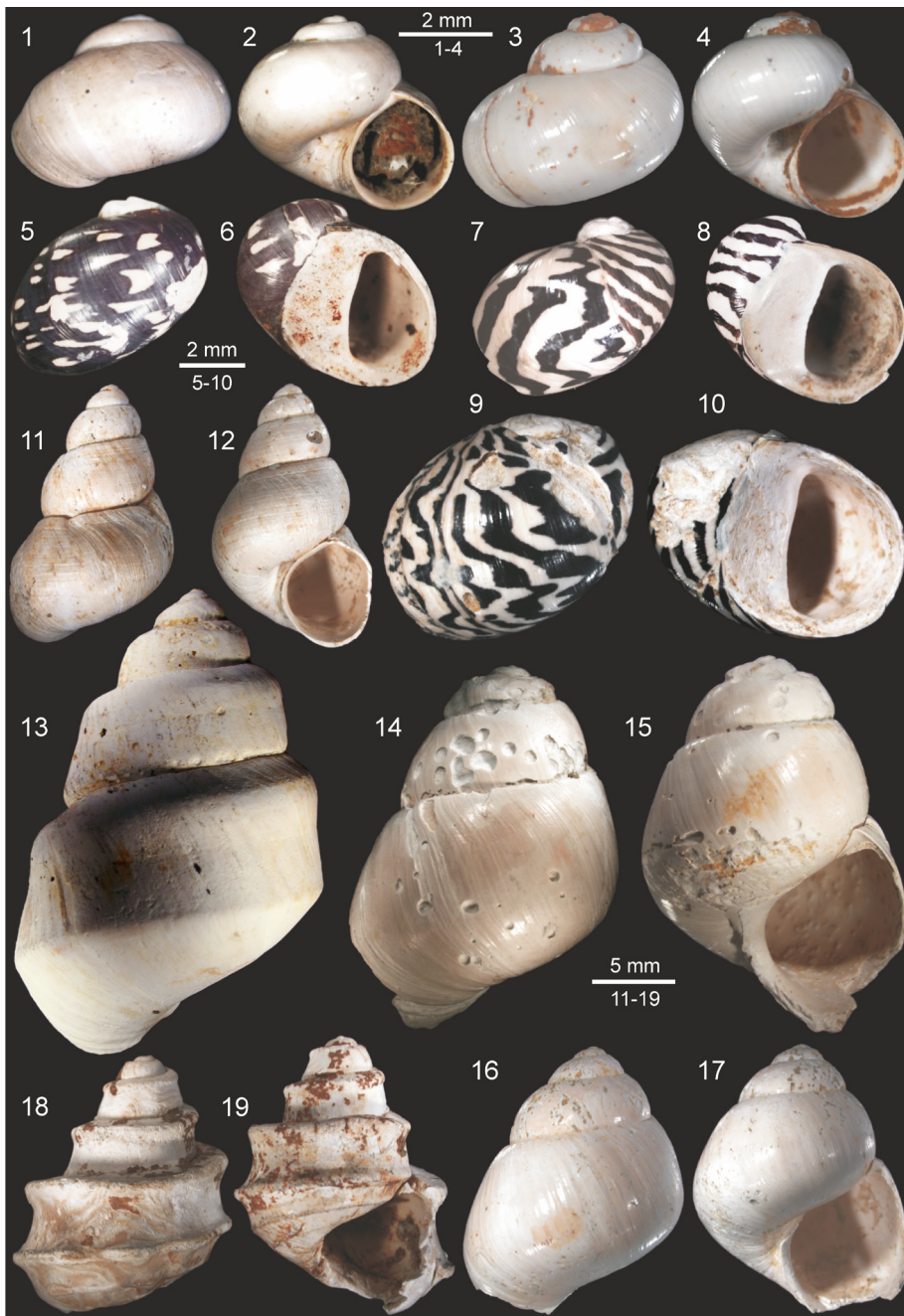


Figure 7: Pliocene lacustrine gastropods (Valvatidae, Neritidae and Viviparidae) from the Pliocene of the Kravarsko region. **1-4** – *Valvata subcarinata* BRUSINA, 1878; 1-2 – VGK-39 sample no. 36; 3-4 – Kra-I sample no. 26. **5-10** – *Theodoxus semiplicatus* (NEUMAYR in HERBICH & NEUMAYR, 1875); 5-6 – VGK-39 sample no. 34; 7-8 – VGK-39 sample no. 34; 9-10 – Kra-I sample no. 25. **11-12** – *Viviparus aulacophorus* BRUSINA, 1874; VGK-39 sample no. 31. **13** – *Viviparus dezmani* BRUSINA, 1874; 13 – VGK-38 sample no. 19. **14-17** – *Viviparus kochanskyae* n. sp.; 14-15 – VGK-39 sample no. 37; 16-17 – Kra-I sample no. 27. **18-19** – *Viviparus hoernesi* NEUMAYR, 1869; 18-19 – VGK-35 sample no. 29.

For a long time, this species was considered conspecific with specimens from the Pannonian of Moosbrunn in the Vienna Basin identified by HÖRNES (1856) as *Valvata piscinalis* MÜLLER, 1774 (NEUMAYR, 1869; BRUSINA, 1874a,b; NEUMAYR & PAUL, 1875). Even after BRUSINA (1878) introduced *V. subcarinata* as a new species restricted to Lake Slavonia sediments, this error was carried forward by WENZ (1928). PAPP (1953, pl. 5, fig. 2) was the first to recognize this mistake and related the distinctly older Austrian occurrence with the Pannonian species *Valvata obtusaeformis* LÖRENTHEY, 1906 stating its different outline due to a much slower increase of the spire's diameter. After BANDEL (2010), the latter species might be related to the valvatoid hydrobiid genus *Jekeliella* BANDEL, 2010.

The Recent *Valvata piscinalis* MÜLLER, 1774 differs in its lower spire, the wider umbilicus and the missing posterior notch at the aperture, which is well-developed in specimens from the type locality and the present material from Kravarsko. BRUSINA (1874a, b) mentioned "two to three" specimens out of 35 from Kravarsko that develop a sharp median spiral keel, restricted to the early whorls. This is not developed in our material. Though BRUSINA (1897) illustrated just those keeled specimens as representatives of *V. subcarinata*, he still considered the more frequent non-keeled morphotype as conspecific. We follow this approach and treat both morphologies as belonging to the same species.

PENECKE (1884), in contrast, used a different concept of *V. subcarinata* for his material. He restricted it to the keeled morphotype found in the LVB at Malino and Čaplja. For the keeled specimens from the UVB at Repušnica and Čaplja, he introduced *V. hoernesii* as new species, which later was considered a juvenile specimen of *V. subcarinata* by BRUSINA (1897). Consequently, he continued to identify the non-keeled morphologies with the Recent *Valvata piscinalis*, claiming its presence in all stratigraphic horizons of Lake Slavonia. He erroneously synonymized *V. sulekiana* BRUSINA, 1874 with *V. piscinalis*, which differs clearly in its strongly flattened spire.

The stratigraphically older specimens from the Late Miocene Metohia Basin in Kosovo, erroneously identified as *V. subcarinata* by MILOŠEVIĆ (1984), differ in a narrower spire and smaller aperture. Specimens from the Dacian of the Braşov Basin, referred to *V. subcarinata* by JEKELIUS (1932), expose several weak to prominent spiral keels and thus represent a different species.

Distribution: Restricted to the *Viviparus* beds of central Croatia (Prvonožina), NE Croatia (Ciglenik, Gromačnik, Malino, Novska, Repušnica, Bečić, Sv. Linart, Sibišnj, Čaplja). The occurrence of the present species in the Pliocene (?) of the Marija Gorica hills in NW Croatia is based on a record of *Valvata* cf. *piscinalis* in GORJANOVIĆ-KRAMBERGER (1892). This record was treated by BRUSINA (1902, pl. 13, fig. 34) as *Valvata* sp., which was apparently overlooked by WENZ (1926) who considered it as synonym of *V. subcarinata*.

Subclass Neritimorpha GOLIKOV & STAROBOGATOV, 1975

Order Cycloneritimorpha FRÝDA, 1998

Superfamily Neritoidea RAFINESQUE, 1815

Family Neritidae RAFINESQUE, 1815

Genus *Theodoxus* MONTFORT, 1810

Type species: *Theodoxus lutetianus* MONTFORT, 1810 (currently considered as a synonym of *Theodoxus fluviatilis* (LINNAEUS, 1758)); Recent, Europe; type by original designation.

Theodoxus semiplicatus (NEUMAYR in HERBICH & NEUMAYR, 1875)

Figures 7.5-10

- ? 1873 *N.[eritina] Danubialis*, PFR. – PILAR p. 112, 132, 176.
- 1874a *Neritina danubialis* var. *sagittifera* – BRUSINA, p. 91 [nomen nudum].
- 1874b *Neritina danubialis* var. *sagittifera* – BRUSINA, p. 73 [nomen nudum].
- ? 1874a *Neritina danubialis* C. PFEIFFER – BRUSINA, p. 90 [non C. PFEIFFER, 1828].
- ? 1874b *Neritina danubialis* C. PFEIFFER – BRUSINA, p. 72 [non C. PFEIFFER, 1828].
- *1875 *Neritina semiplicata* SANDB. – HERBICH & NEUMAYR, p. 412-413 [pars; excl. synonyms].
- 1875 *Neritina danubialis* var. *sagittifera* BRUS. – NEUMAYR & PAUL, p. 35 [nomen nudum].
- 1884 *Neritina sagittifera* BRUSINA – BRUSINA, p. 89-90.
- 1884 *Theodoxus semiplicatus* NEUMAYR – BRUSINA, p. 101-102.
- 1884 *Neritina semiplicata* SANDBERGER – PENECKE, p. 17, pl. 10, figs. 30-35.
- ? 1884 *Theodoxus danubialis* C. PFEIFFER – BRUSINA, p. 100-101.
- 1896 *Neritina (Theodoxus) semiplicata* NEUMAYR – STEFANESCU, p. 115-116, pl. 10, figs. 70-72.
- 1897 *Neritodonta sagittifera* BRUS. – BRUSINA, p. 26, pl. 14, figs. 23-24.
- 1902 *Neritodonta sagittifera* BRUS. – BRUSINA, pl. 15, figs. 39-40.
- 1902 *Theodoxus semiplicatus* (NEUM.) – BRUSINA, pl. 15, figs. 65-71.
- 1902 *Neritodonta* sp. – BRUSINA, pl. 15, figs. 59-61.
- ? 1902 *Theodoxus danubialis?* (C. PFEIFF.) – BRUSINA, p. 15, figs. 50-52.
- 1929b *Theodoxus (Calvertia) sagittiferus* (BRUSINA) – WENZ, p. 2976.
- 1929b *Theodoxus (Theodoxus) semiplicatus* (NEUMAYR) – WENZ, p. 3005-3006.
- ? 1929b *Theodoxus (Theodoxus) cf. danubialis* (C. PFEIFFER) – WENZ, p. 2993-2994.
- 1932 *Theodoxus semiplicatus* (NEUMAYR) – JEKELIUS, p. 56-58, pl. 1, figs. 1-60, pl. 2, figs. 1-65, pl. 3, figs. 1-50, pl. 23, figs. 1-14.

- 1944 *Theodoxus (Calvertia) sagittiferus* (BRUSINA) – JENKO, p. 114.
- 1974 *Theodoxus (Calvertia) sagittiferus* (BRUSINA) – MILAN et al., p. 110.
- 1979 *Theodoxus (Theodoxus) semiplicatus semiplicatus* (PENECKE) [sic] – JURIŠIĆ-POLŠAK, p. 27, pl. 9, figs. 5-8.
- ? 1979 *Theodoxus (Theodoxus) danubialis* (PFEIFFER) – JURIŠIĆ-POLŠAK, p. 29, pl. 9, figs. 3-4.
- 2008 *Theodoxus (Theodoxus) semiplicatus* NEUMAYR – LUBENESCU & LUBENESCU, p. 81, fig. 1.7-9.

Material: V GK-39 (3 specimens from sample no. 14, 9 specimens from samples no. 34), and Kra-I (3 specimen from sample no. 4, and 4 specimens from samples no. 25).

Dimensions: Height x width – 5.8 (first whorl broken) x 5.6 mm (Figs. 5.5-6), 6.2 x 5.4 mm (Figs. 5.7-8), 6.6 x 7.3 mm (Figs. 5.9-10).

Description: Solid shell, consisting of 2.75 whorls. Spire consists of two flattened whorls (always eroded in the present material). Depending on the shell's growth angle, the spire may be distinct or be fully covered by the last whorl. Last whorl increases strongly in diameter, producing an oval shape in outline. Aperture is semicircular, slightly inclined toward the columella, with sharp lateral margin. Callus pad is well demarcated, slightly concave, smooth, bearing very fine denticles at its adapertural edge. Colouring is dominantly expressed by black, axial zig-zag and wavy bands. In a few specimens the bands are fused, so that only a few lunate spots remain white.

Remarks: *T. semiplicatus* NEUMAYR in HERBICH & NEUMAYR, 1875 from Vârghiș and Araci (Dacian, Brașov Basin, W Romania) was made available through a *lapsus calami* for *T. semidentatus* SANDBERGER, 1875 (see footnote in HERBICH & NEUMAYR, 1875, p. 413). The latter species had been introduced for a misidentified species from the Middle Miocene of Ribarić in the Drniš Basin, SE Croatia. Not realizing that the Middle Miocene species is distinct from the Pliocene one, HERBICH & NEUMAYR (1875) mentioned "*T. semiplicatus*" (instead of *T. semidentatus*) also from the Dacian of the Brașov Basin. As they explicitly referred the misspelled species name to a different specimen, both names are valid. BRUSINA (1884) was the first to recognize that these two names refer to different species.

Although citing 57 syntypes from Čaplja near Podvinje in Slavonia (NE Croatia), BRUSINA (1874a) did not provide any description or illustration of his new subspecies *T. danubialis sagittiferus*. This species-group name is therefore a *nomen nudum*, a fact first recognized by JURIŠIĆ-POLŠAK (1979). Nevertheless, NEUMAYR & PAUL (1875) also found it at Čaplja, in beds belonging to the *V. hoernesii* zone, and accepted it as an available name. BRUSINA (1884) elevated the name to the species rank and provided a morphological description and therefore made it available.

PENECKE (1884) revised the neritid record of the central Lake Slavonia accepting only three species, i.e., *T. semi-*

plicatus NEUMAYR in HERBICH & NEUMAYR, 1875, *T. transversalis* PFEIFFER, 1828 and *T. militaris* NEUMAYR, 1869. While this was not followed by BRUSINA (1897, 1902) and WENZ (1928), JURIŠIĆ-POLŠAK (1979) confirmed PENECKE's classification in her revision of the Neogene Croatian neritids, detecting again only three species, although splitting them into eight subspecies. These are *T. transversalis* (incl. *T. t. transversalis*, *T. t. amethystinus*, *T. t. slavonicus*), *T. semiplicatus* (incl. *T. s. semiplicatus*, *T. s. capillaceus*), and *T. militaris* (*T. m. militaris*, *T. m. decostatus*, *T. m. oblongus*). In the corresponding deposits of Vukomeričke Gorice hills she detected only *T. danubialis* and *T. transversalis*. *T. militaris* clearly differs from the present species by its axial ribs. *T. transversalis* (sensu JURIŠIĆ-POLŠAK, 1979) is characterized by transverse colour-bands which are absent in our material.

T. semiplicatus is characterized by fine denticles on the callus pad, distinguishing it clearly from *T. danubialis*. A tooth beneath the muscle insertion can be absent or present in *T. semiplicatus* (JURIŠIĆ-POLŠAK, 1979). In our specimens it is completely absent, making them similar in this respect to *T. danubialis*. The fact that a faint dentation of the columellar pad can easily remain undetected, the previous *T. danubialis* records from the Vukomeričke Gorice hills by PILAR (1873), BRUSINA (1874a, b) and JURIŠIĆ-POLŠAK (1979) require closer inspection.

JEKELIUS (1932) provided an excellent description and illustrations of numerous specimens of *T. semiplicatus* from several localities of the Dacian of the Brașov Basin. In contrast, the record from the Pleistocene of SE Hungary by HALAVÁTS (1888), later referred to by WENZ (1929b), has been revised by KROLOPP (1976b) as *T. prevostianus* (PFEIFFER, 1828). The much older records from the Maeotian of SW Ukraine, SW Moldavia, and Romania by ROŠKA (1973), GOZHIK & PRYSJAZHNJUK (1978), GOZHIK & DATSENKO (2007), and STOICA et al. (2007) are possibly based on erroneous identifications.

The alleged occurrence in the "Pliocene" of Bresnica in Serbia mentioned by JURIŠIĆ-POLŠAK (1979) is most likely based on "*Neritodonta* sp." of BRUSINA (1902, pl. 15, figs. 53-55). The latter species was collected from lacustrine deposits at the Bresnica brook near Kragujevac, considered as Langhian (Middle Miocene) in age (PAVLOVIĆ, 1931; JOVANOVIĆ, 2012). The species actually represents *Theodoxus brusinae* (PAVLOVIĆ, 1931), differing from the present species in its more rounded outline. "*Neritina semiplicata*" sensu HOERNES (1877) from the Late Messinian (ÇAGATAY et al., 2006) or Early Pliocene (MELINTE-DOBRIANESCU et al., 2009) *Mastra* beds of İntepe in NW Turkey is a misidentification. *Theodoxus* sp. from the Miocene Lake Rein in Styria is similar but lacks the crenulation (HARZHAUSER et al., 2014).

Distribution: LVB to UVB of Lake Slavonia in central Croatia (Kravarsko – the present study); Northeastern Croatia (Čaplja, Cernik, Kindrovo, Sibirj, Malino, Gromačnik, Ciglenik, Duboki dol, Repušnica, Kovačevac), NW Serbia (Čerević) and W Romania (Giulvaz); Dacian of the Brașov Ba-

sin in central Romania (e.g., Araci (=Arpatac), Vârghiș) and of Lake Dacia (e.g., Breasta) (PENECKE, 1884; JEKELIUS, 1932; JURIŠIĆ-POLŠAK, 1979).

Subclass Caenogastropoda COX, 1959

Order Architaenioglossa HALLER, 1890

Superfamily Viviparoidea GRAY, 1847

Family Viviparidae GRAY, 1847

Subfamily Viviparinae GRAY, 1847

Genus *Viviparus* MONTFORT, 1810

Type species: *Viviparus fluviarium* MONTFORT, 1810 (currently considered as a synonym of *Viviparus viviparus* (LINNAEUS, 1758)); Recent, northern Eurasia, Europe, Anatolia and Northern America; type by original designation.

Viviparus aulacophorus BRUSINA, 1874

Figures 7.11-12

- *1874a *Vivipara aulacophora* BRUSINA – BRUSINA, p. 88, pl. 2, figs. 14-15.
- 1874b *Vivipara aulacophora* BRUSINA – BRUSINA, p. 70, pl. 2, figs. 14-15.
- 1875 *Vivipara aulacophora* BRUS. – NEUMAYR & PAUL, p. 66.
- 1884 *Vivipara Rudolphi* nov. form. – PENECKE, p. 29, pl. 9, fig. 14.
- 1897 *Vivipara aulacophora* BRUS. – BRUSINA, p. 24, pl. 12, figs. 23-24.
- 1902 *Vivipara aulacophora* BRUS. – BRUSINA, pl. 12, fig. 7.
- 1928 *Viviparus aulacophorus* (BRUSINA) – WENZ, p. 2293 [pars; excluding records of *Vivipara anthracophila* = *V. leiostracus*].
- 1974 *Viviparus aulacophorus* BRUSINA – MILAN et al., p. 148.

Material: VGK-39 (3 specimens from sample no. 10, and 3 specimens from sample no. 31).

Dimensions: Height x width – 16.4 x 9.8 mm (Figs. 5.11-12), 34.2 x 22.9 mm (specimen illustrated by BRUSINA, 1902).

Description: Slender shell, consisting of 5 convex whorls. Shell width attains about 60% of total height; suture not very deep but distinct. Last whorl attains 70% of total shell height. The junction between the whorls is irregular, slightly gaping. Protoconch is eroded, apex is blunt. Whorls increase more strongly in height than diameter, resulting in a drop-shaped shell outline. Aperture is oval to slightly drop-shaped, with a weak posterior notch. Peristome is sharp; umbilicus is narrow and slit-like. Shell surface is glossy, bearing numerous fine, weakly but irregularly undulated spiral grooves; crossed by growth lines they partially produce a fine reticulate pattern.

Remarks: When describing the species, BRUSINA (1874a) had only a single specimen from Cernik (Sv. Linart)

N of Nova Gradiška at hand. The specimen, with a height of 30 mm and a width of 20 mm, represents a holotype by monotypy (ICZN Art. 73.1.2) and is stored in the NHM Zagreb (Inv. No. 3215-861; MILAN et al., 1974). Following the detailed geological description of the area by NEUMAYR & PAUL (1875), the deposits at the type locality may be ascribed to the *V. neumayri* zone.

Viviparus rudolphi PENECKE, 1884 from the *V. kochanskya* zone of Malino was previously recognized by BRUSINA (1897) as a synonym of *V. aulacophorus*. WENZ (1926) erroneously synonymized the *nomen nudum* “*V. anthracophilus*” as given in NEUMAYR & PAUL (1875) with *V. aulacophorus*. He apparently overlooked the correction note in NEUMAYR & PAUL (1875, p. 106), where they clearly indicate it as an error pro *V. leiostracus*. Following ICZN Art. 32.4 and 32.5, the name *anthracophilus* clearly represents an inadvertent error and is thus unavailable.

The specimen given as “*Viviparus neumayri* trans *V. suessi*” in NEUMAYR & PAUL (1875, pl. 4, fig. 4) from the UVB of Novska seems to show a very fine spiral sculpture too, but has a much lower spire. *Viviparus pauli* BRUSINA, 1874 and *V. dautzenbergi* BRUSINA, 1902 are both larger than the present species and develop a much more prominent spiral sculpture (see also BRUSINA, 1897). *Viviparus pauli* has been listed from Kravarsko by BRUSINA (1874a, b) but could not be detected in the course of our investigation.

Distribution: Restricted to the LVB of Lake Slavonia from Kravarsko in the west via Nova Gradiška (Cernik/Sv. Linart, Rešetari/Jukićev jarak) up to Malino in the east (BRUSINA, 1874a, b; NEUMAYR & PAUL, 1875; PENECKE, 1884). It was previously unknown from Kravarsko (KOCH, 1917).

Viviparus dezmanianus BRUSINA, 1874

Figure 7.13

- 1869 *Vivipara rudis* nov. sp. – NEUMAYR, p. 375, pl. 14, fig. 11 [pars; non fig. 5].
- *1874a *Vivipara Dežmaniana* BRUSINA – BRUSINA, p. 81-82, pl. 2, figs. 7.
- 1874a [*Vivipara Dežmaniana*] var. *complanata* BRUS. – BRUSINA, p. 81-82, pl. 2, fig. 6.
- 1874b *Vivipara Dežmaniana* BRUSINA – BRUSINA, p. 64-65, pl. 2, figs. 7.
- 1874b [*Vivipara Dežmaniana*] var. *complanata* BRUS. – BRUSINA, p. 64-65, pl. 2, fig. 6.
- 1875 *Vivipara Dežmaniana* BRUS. – NEUMAYR & PAUL, p. 67, pl. 6, figs. 9-10, 16-18.
- 1884 *Vivipara Dežmanniana* [sic] BRUS. – PENECKE, p. 30.
- 1928 *Viviparus dezmanianus dezmanianus* (BRUSINA) – WENZ, p. 2312-2314.
- 1974 *Vivipara dezmanianus* (BRUSINA) – MILAN et al., p. 146, 148.

Material: VGK-38 (1 specimen from sample no. 19).

Dimensions: Height x width – 29.6 x 18.5 mm (Fig. 5.13).

Descriptions: Solid shell, large, broadly drop-shaped, comprising 5.25 whorls; width attains about 65% of height. Protoconch is not preserved. First three whorls are weakly convex and separated by shallow sutures, producing a pointed, conical apex. Thereafter whorls expand more strongly in height than width, resulting in an overall drop-shaped outline. From the third whorl onwards, whorls expose markedly stepped outlines with flanks sub-parallel to the axis, a narrow sutural ramp and incised, slightly gaping sutures. Angulation between ramp and flank starts rounded, but becomes progressively more strongly angled and sharper. Ramps dip by 30° to 60°. Flanks are initially slightly convex and then straight, up to slightly concave on the last whorl; a central spiral furrow emerges on the last two whorls. A second angulation is present at the transition between whorl flank and base; it becomes visible only on the last two whorls. Base of the last whorl is weakly convex. Last whorl attains about 80% of the total shell height. Aperture is fragmented, but obviously broadly drop-shaped, posteriorly slightly narrowed. Peristome is sharp in its preserved columellar part. Umbilicus is closed. Growth lines are distinct, opisthocline.

Remarks: BRUSINA (1874a) introduced this species including a specimen of the syntype series of *V. rudis* NEUMAYR, 1869. It is not clear from the discussion whether he considered *V. dezmanianus* as a replacement name of NEUMAYR's specimen or simply wanted to include it in the new species. Therefore, all specimens studied by BRUSINA (1874a) and the single specimen from NEUMAYR (1869) are syntypes of *V. dezmanianus*. The specification of a "holotype" by MILAN et al. (1974), referring to the specimen from Kovačevac (Coll. NHM Zagreb Inv. No. 4272-1912/1) that was illustrated in BRUSINA (1874a, b), is incorrect. To settle this issue we designate the same specimen herewith as a lectotype.

We follow NEUMAYR & PAUL (1875) and WENZ (1926) and consider *V. complanatus* BRUSINA, 1874 as conspecific with *V. dezmanianus*. Its type series comprises 127 specimens from Čaplja. It attains only 75% of the height of the typical morphotype and the keels are less pronounced, resulting in rather straight-sided whorl flanks (as in our specimens). These minor variations are considered to be within the range of intraspecific variability.

In their revision of the viviparids from the Pliocene of the Dacian Basin, LUBENESCU & ZAZULEAC (1985) rejected the presence of *V. dezmanianus* in Lake Dacia. They treated the identifications of COBĂLCESCU (1883) and WENZ (1942) as *V. pseudo dezmanianus* LUBENESCU & ZAZULEAC, 1985, whereas the specimens from the Sienian by PORUMBARU (1881), FONTANNES (1887) and STEFANESCU (1896) were referred to *V. dezmanianus dacicus* LUBENESCU & ZAZULEAC, 1985. As noticed by NEUBAUER et al. (2014a), the latter taxon is a junior synonym of *V. dezmanianus turburensis* FONTANNES, 1887. Whether or not *V. dezmanianus turburensis* is really related to *V. dezmanianus* needs a more detailed assessment of the type material.

According to TABOYAKOVA (1964), the record of *V. dezmanianus* from the late Pliocene to Pleistocene of the Rioni Bay in Georgia (e.g., WENZ, 1926) actually represents *Viviparus nataliae* MIKHAYLOVSKIY, 1913. The species is, however, still listed from that region by ANISTRATENKO & GOZHIK (1995). A more thorough taxonomic revision of those records is required to confirm or reject this claim.

Distribution: Restricted to the MVB and UVB of NE Croatia. This is its first record from central Croatia. NEUMAYR & PAUL (1875) restrict the species at Sibirj, Slobodnica, Gromačnik, Ciglenik, Podvinje-Čaplja trench, Repušnica and Novska to the *V. stricturatus* and *V. nothus* zones (as applicable). PENECKE (1884) in turn listed the species from the *V. stricturatus* to *V. hoernesii* zone at Ciglenik, Malino, Sibirj and Podvinje-Čaplja trench.

Viviparus hoernesii NEUMAYR, 1869

Figures 7.18-19

- *1869 *Vivipara Hörnesii* nov. sp. – NEUMAYR, p. 376, pl. 14, fig. 14 [pars; non fig. 13].
- 1874a *Vivipara Hörnesii* NEUMAYR – BRUSINA, p. 84-85.
- 1874b *Vivipara Hörnesii* NEUMAYR – BRUSINA, p. 67-68.
- 1875 *Vivipara Hörnesii* NEUM. nov. form. – NEUMAYR & PAUL, p. 56-57, pl. 4, fig. 21.
- 1884 *Vivipara Hörnesii* NEUM. – PENECKE, p. 28.
- 1896 *Vivipara Hörnesii* NEUM. – BRUSINA, p. 135.
- 1917 *Vivipara Hörnesii* NEUM. – KOCH, p. 12.
- 1928 *Viviparus hörnesii* (NEUMAYR) – WENZ, p. 2326-2328.

Material: VGK-35 (2 specimens from sample no. 9, 1 specimen from sample no. 18, and 2 specimens from sample no. 29).

Dimensions: Height x width (of fragmented specimen) – 17.0 x 13.3 mm (Figs. 5.18-19).

Description: Solid, glossy shell, conical, with 5 whorls, with the last whorl attaining about 80% of the total height. Protoconch is not preserved. Apex is blunt. On the second whorl a prominent angulation emerges, forming a straight, near horizontal subsutural ramp. Angulation successively passes into a marked, sharp keel. A second sharp keel bearing irregular, elongated nodes emerge at the transition between whorl flank and base and are visible only on the last whorl. Whorl flank between keels is regularly concave. Below the lower keel, 2 weak and thin keels cover the base of the last whorl. Base is straight. Aperture is not preserved but apparently sub-oval; umbilicus is completely covered.

Remarks: The type series includes a large number of specimens from the Bukovica valley N of Novska (as are all the illustrated specimens), Repušnica and Gradiška. We designate herewith the specimen illustrated in NEUMAYR (1869, pl. 14, fig. 14), stored in the collection of the GBA (Inv. No. 1869/001/0055), as the lectotype. The type stratum in Bukovica belongs to the *V. hoernesii* zone, which the species is restricted to.

NEUMAYR in NEUMAYR & PAUL (1875) separated the specimen of NEUMAYR (1869) illustrated on Pl. 14, fig. 13 as the new species *V. ornata*, based on the absence of nodes on the keels. PENECKE (1884) stated that these two species rather form a morphological continuum and a distinction is possible only between extreme morphotypes, which we do not follow.

WENZ (1928) also lists the species from Craiova in the Dacian Basin, which needs a careful re-examination. LUBENESCU & LUBENESCU (2008) did not list this species in their comparison between Dacian and Pannonian basin molluscs.

Distribution: Restricted to the UVB of Lake Slavonia – central Croatia (Farkašić, Hrastovica near Petrinja, Kravarsko), northeastern Croatia (Bečić, Brestača, Čaplja bei Podvinje, Bukovica, Giglenik, Gradiška, Gromačnik, Malino, Novska, Repušnica, and Sibirj), northwestern Serbia (Novi Sad – Petrovaradin) (NEUMAYR & PAUL, 1875; BRUSINA, 1874a, b; PENECKE, 1884; KOCH, 1917; WENZ, 1928).

***Viviparus kochanskyae* n. sp.**

Figures 7.14-17

- 1869 *Vivipara concinna* SOW. – NEUMAYR, p. 373, pl. 14, fig. 4 [non *Paludina concinna* SOWERBY, 1812; non *Paludina concinna* sensu HÖRNES, 1856].
- 1873 *Vivipara Fuchsi*, NEUMAYR – PILAR, p. 110 [non *Vivipara Fuchsi* NEUMAYR, 1872].
- 1874a *Vivipara Fuchsi* NEUMAYR – BRUSINA, p. 75 [non *Vivipara Fuchsi* NEUMAYR, 1872].
- 1874b *Vivipara Fuchsi* NEUMAYR – BRUSINA, p. 59 [non *Vivipara Fuchsi* NEUMAYR, 1872].
- 1875 *Paludina loxostoma* SANDBERGER – SANDBERGER, p. 691-692.
- 1875 *Vivipara Fuchsi* NEUMAYR – NEUMAYR & PAUL, p. 58, pl. 5, fig. 5 [non *Vivipara Fuchsi* NEUMAYR, 1872].
- 1884 *Vivipara Fuchsi* NEUM. – PENECKE, p. 29 [non *Vivipara Fuchsi* NEUMAYR, 1872].
- 1917 *Vivipara Fuchsi* NEUM. – KOCH, p. 12 [non *Vivipara Fuchsi* NEUMAYR, 1872].
- 1928 *Viviparus fuchsi* (NEUMAYR) – WENZ, p. 2318-2321 [non *Vivipara Fuchsi* NEUMAYR, 1872; pars; regarding only Slavonian occurrences].

Material: VGK-39 (2 specimens from sample no. 17, 1 specimen from sample no. 20, 1 specimen from sample no. 37) and Kra-I (3 specimens from sample no. 6, and 1 specimen from sample no. 27).

Etymology: In honour of the Croatian palaeontologist Vanda KOCHANSKY-DEVIDÉ (1915-1990) for her contribution to Neogene malacology.

Diagnosis: Broadly ovoid, solid shell of moderate size comprising 4-5 whorls, which expand more rapidly in height

than diameter, with flanks initially convex, then flattened on the last two whorls.

Type specimen: We designate the specimen illustrated by NEUMAYR (1869) as the holotype (Coll. NHM Vienna Inv. No. 1855/0035/0052). Type locality Nova Gradiška [=Cernik] was referred to LVB by NEUMAYR & PAUL (1875).

Dimensions: Height x width – 28.3 x 19.3 mm (largest specimen, last quarter of the last whorl is missing, VGK-39 sample no. 20), 23.2 x 15.8 mm (fragmented, Figs. 5.14-15), Height x width – 16.5 x 13.3 mm (fragmented, Figs. 5.16-17).

Description: Smooth, solid shell, broadly ovoid, with 4.75 whorls and narrow umbilicus. Shell width attains about 70% of its height. Protoconch not preserved in the present material. Whorls expand rapidly in height and diameter, with the last one attaining c. 75-80% of total height. Early whorls slightly convex, not stepped, separated by distinct but shallow suture. Flanks of the last two whorls flattened, passing into marked convexity below. Base is straight, inclined by about 45°. The latter is not fully preserved in our material; appears to be drop-shaped. Fine growth lines cover the shell.

Remarks: The alleged presence of “*Viviparus fuchsi*” in the *Viviparus* beds of Croatia traces back to a series of misidentifications and nomenclatural mistakes. It started with a misidentification of NEUMAYR (1869), who mentioned “*Vivipara concinna*” from Nova Gradiška in NE Croatia, apparently referring to the identification and illustrations from HÖRNES (1856, p. 581, pl. 47, fig. 17). That author, however, had described a much older species from the middle Pannonian of Moosbrunn in the Vienna Basin. Despite superficial similarities, the single Slavonian specimen differs in the less stepped spire and the characteristically flattened whorl flanks passing into the marked convexity towards the base. Beyond that, neither of these species is *Viviparus concinnus* (SOWERBY, 1812), which is yet another species from the Paleogene of southern England. Recognizing this, NEUMAYR (1872) introduced the new name *Viviparus fuchsi* in a short note on the *Viviparus* beds, yet explicitly referring it to “*V. concinna* HÖRNES non SOW.”. Despite his clear intention to introduce the name for the Slavonian species, *V. fuchsi* is still a replacement name for HÖRNES’ misidentified specimens from Moosbrunn and not for the Slavonian species.

Obviously unaware of NEUMAYR’s (1872) new name, SANDBERGER (1875) introduced “*Paludina loxostoma*” as replacement name for the species described by HÖRNES (1856). Although SANDBERGER (1875) also gives NEUMAYR’s record from the *Viviparus* beds in the synonymy list and mentions its occurrence in Nova Gradiška, it is entirely clear from the discussion that *P. loxostoma* was intended solely as a replacement for HÖRNES’ material. He even listed the record of *Viviparus fuchsi* by BRUSINA (1874a, b) in the synonymy list, but, for whatever reason, did not consider it a valid

name. *Paludina loxostoma* SANDBERGER, 1875 is therefore an objective junior synonym of *Viviparus fuchsi* NEUMAYR, 1872. It was later also considered synonymous by NEUMAYR & PAUL (1875) and WENZ (1928).

Based on illustrations of NEUMAYR & PAUL (1875), PAPP (1953) was the first to recognize the differences between the Pannonian and Slavonian species, but wrongly concluded that *V. fuchsi* is restricted to the *Viviparus* beds and *V. loxostomus* is the correct name of the Pannonian species. Therefore, *V. fuchsi* was not mentioned from the Pannonian Basin by later authors (e.g., STRAUSZ, 1942; BARTHA, 1977; STEVANOVIĆ et al., 1990; HARZHAUSER & BINDER, 2004).

In summary, *V. fuchsi* NEUMAYR, 1872 and *V. loxostomus* (SANDBERGER, 1875) refer to the same species from the Late Miocene of the Pannonian Basin, whereas the Slavonian species, usually referred to as “*Viviparus fuchsi*”, actually has no name. Therefore, we introduce *Viviparus kochanskyae* as a new species. Consequently, also the former “*Viviparus fuchsi* zone” has to be re-named the “*Viviparus kochanskyae* zone”.

“*Viviparus fuchsi*” from the Late Miocene Lake Bresse-Valence in SE France originates from a misidentification by DELAFOND & DEPÉRET (1893). The French specimens have well-rounded, convex whorls and correspond well to *Viviparus dresseli* (TOURNOUËR, 1875), described from the surroundings of Lyon, a species they give in the synonymy list of *V. fuchsi*. Specimens of “*Viviparus fuchsi*” identified from the Akchagylian (Late Pliocene) of the Syzran region in western Samara/Russia by PAVLOV (1925) and from the Pontian of the Danube delta region in SE Ukraine by GOZHNIK (2002) and GOZHNIK & DATSENKO (2007) have convex whorls instead of the typically flattened ones and represent other, yet undetermined species.

Viviparus kochanskyae seems to be absent in the Dacian Basin. It is not listed (as *V. fuchsi*) in the monograph on its viviparid snails by LUBENESCU & ZAZULEAC (1985). The Pontian record at Ploiești by WENZ (1928) dates back to a list of PILIDE (1877), reproduced also by STEFANESCU (1897, p. 61). *Viviparus fuchsi* identified by BEREGOV (1940) from the Maotian and Dacian of Bulgaria was shown by LUBENESCU & ZAZULEAC (1985) to represent *V. incertus* sensu MACAROVICI, 1940. The latter species name was recently recognized to be a primary homonym of *V. incertus* FUCHS, 1877 by NEUBAUER et al. (2014a), who introduced *V. wesselinghi* as a replacement name.

JEKELIUS (1932) reported *V. fuchsi* species from Dacian deposits of the Galat brook near Aita Seacă and Ebhát határ near Hăghig in the Brașov basin, but without providing any illustrations or description. This record still needs to be verified.

The alleged lineage leading from *Viviparus fuchsi* to *V. leiostacus* in the Pliocene of Kos as described by NEUMAYR (1880a) is based on misidentifications of *V. calverti* (WILLMANN, 1981, p. 151). The record of *V. fuchsi* from the Plio-Pleistocene of Patras, Greece, by OPPENHEIM (1894, p. 820), who did not provide description or illustrations, needs re-examination.

Distribution: Restricted to the LVB (W to E) of Vukomeričke Gorice S of Zagreb / central Croatia (Prvonožina, Dubranec, Kravarsko), Slavonia / NE Croatia (Repušnica W Kutina, Novska, Cernik N Nova Gradiška, Bečić, Malino, Sibinj, Podvinje – Čaplja N Slavonski Brod) and Strymian / NW Serbia (Čerević E Novi Sad) (BRUSINA, 1874a, b; NEUMAYR & PAUL, 1875; PENECKE, 1884; KOCH, 1917; WENZ, 1928).

Order unassigned

Superfamily Cerithioidea FLEMING, 1822

Family Melanopsidae ADAMS & ADAMS, 1854

Genus *Melanopsis* FÉRUSAC in FÉRUSAC & FÉRUSAC, 1807

Type species: *Melania costata* OLIVIER, 1804; Recent, Eastern Mediterranean and Middle East; type by subsequent designation by GRAY (1847).

Melanopsis clavigera NEUMAYR in NEUMAYR & PAUL, 1875

Figures 8.9-10

*1875 *Melanopsis clavigera* NEUM. nov. form – NEUMAYR & PAUL, p. 41, pl. 7, figs. 13-14.

1884 *Melanopsis clavigera* NEUM. – PENECKE, p. 22.

non 1890 *Melanopsis clavigera* NEUMAYR – OPPENHEIM, p. 591.

non 1891 *Melanopsis clavigera* NEUMAYR – OPPENHEIM, p. 466, pl. 26, fig. 4.

1897 *Melanopsis clavigera* NEUM. – BRUSINA, p. 7, pl. 5, fig. 19.

? 1897 *Melanopsis clavigera cesticillus* BRUS.n. for. – BRUSINA, p. 7, pl. 5, fig. 20.

? 1902 *Melanopsis clavigera cesticillus* BRUS. – BRUSINA, pl. 6, fig. 41.

1929a *Melanopsis clavigera clavigera* NEUMAYR – WENZ, p. 2694-2695 [pars; regarding only Slavonian records].

? 1929a *Melanopsis clavigera cesticillus* BRUSINA – WENZ, p. 2695-2696.

? 1974 *Melanopsis clavigera cesticillus* BRUSINA – MILAN et al., p. 88.

Material: VGK-35 (3 specimens from sample no. 8, and 2 specimens from sample no. 28).

Dimensions: Height x width (of fragmented specimen) – 20.8 x 10.1 mm (Figs. 6.9-10).

Descriptions: Solid shell with slender to bulky conical, coeloconoid to ovoid outline and up to 9 whorls. Shell width attains about 50% of height. Whorls are separated by narrow, irregular sutures. Protoconch unknown. Sculpture starts on the second teleoconch whorl, comprising about 8 slightly prosocline axial ribs, extending across entire whorl height. Number of ribs is roughly constant throughout ontogeny – ribs increase constantly in strength and are more or less continuous on successive whorls. On the last whorls, the ribs bear weak nodes near the upper suture. Nodes become successively stronger,

producing a markedly stepped shell outline for the last 3 whorls. Rib portions above and below nodes are concave. On the last 2-3 whorls, nodes are laterally connected via weak, concave keels. On the last whorl, ribs bear an additional elongate axial convexity marking the angulation between whorl flank and the straight base. In one specimen, each rib bears two nodes; in two other specimens, no nodes are developed at all. The last whorl attains about two thirds of the total shell height. The aperture is slender, elongated and has a thickened callus pad; it lacks a columellar fold. Peristome and siphonal canal are not fully preserved. Fine growth lines are visible at the exterior surface of the shell.

Remarks: BRUSINA (1897) introduced the new subspecies *Melanopsis clavigera cesticillus* for a specimen from

Kozarica near Novska, but did not provide a description or discussion. From the illustrations he provided, it seems he based the distinction on the absence of ribs and nodes on the last two whorls. A specimen of *M. clavigera cesticillus* from the same locality illustrated in BRUSINA (1902) shows a prominent keel, bearing irregular, bulbous knobs. As we are currently not aware of any morphotype representing a morphological transition to the typical *M. clavigera*, a taxonomic separation appears reasonable.

The record of *Melanopsis clavigera* by OPPENHEIM (1891) from the early Pliocene of Megara in Greece is clearly a misidentification. The Greek species is much more gracile and bears finer and sharper ribs with three rows of small nodes. Due to its weak spiral keel it does not show the stepped

morphology typical of *Melanopsis clavigera*. It is also very likely that the Pleistocene record from Stanná in W Greece by OPPENHEIM (1890), which lacks an illustration, can be ruled out as being conspecific with the present species.

Distribution: Pliocene UVB in Ciglenik, Gromačnik, Gromačnik-Sibinj road, Kovačevac E Nova Gradiška, Slavonki Brod (Čaplja and Čaplja-Podvinje trench). This is its first record from central Croatia.

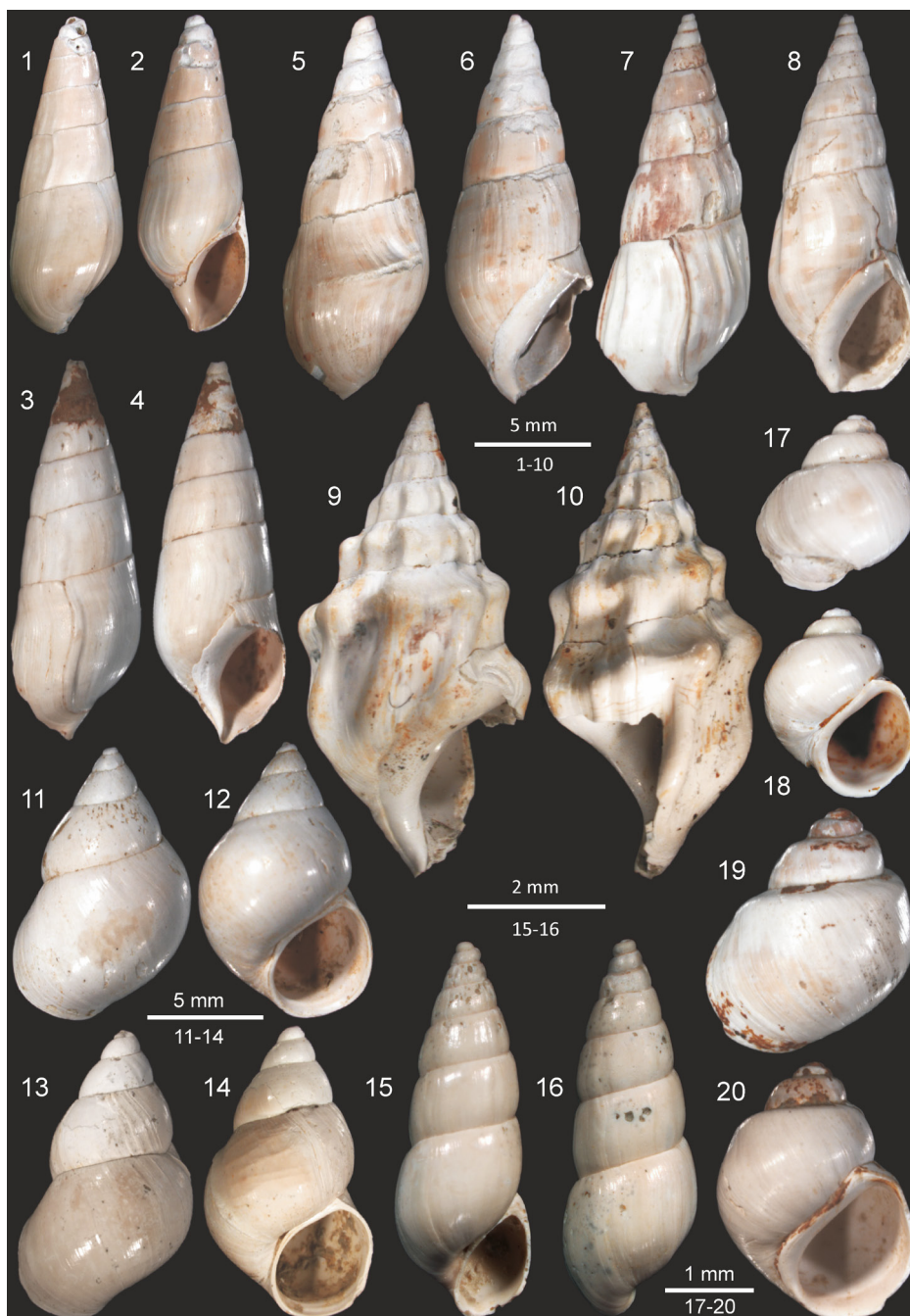


Figure 8: Pliocene lacustrine gastropods (Melanopsidae, Bithyniidae, Hydrobiidae and Lithoglyphidae) from the Pliocene of the Kravarsko region. **1-8** – *Microcolpia friedeli* (BRUSINA, 1885); 1-2 – VGK-39 sample no. 33; 3-4 – Kra-I sample no. 23; 5-6 – VGK-39 sample no. 33; 7-8 – Kra-I sample no. 24. **9-10** – *Melanopsis clavigera* NEUMAYR in NEUMAYR & PAUL, 1875; VGK-35 sample no. 28. **11-14** – *Bithynia vukotinovici* (BRUSINA, 1874); 11-12 – Kra-I sample no. 21; 13-14 – VGK-39 sample no. 30. **15-16** – *Prososthenia? slavnica* (BRUSINA, 1874); VGK-39 sample no. 38. **17-20** – *Lithoglyphus decipiens* BRUSINA, 1885; 17-18 – VGK-39 sample no. 32; 19-20 – Kra-I sample no. 22.

Genus *Microcolpia* BOURGUIGNAT, 1884

Type species: *Melanopsis acicularis* FÉRUSSAC, 1823; Recent, Europe; type by subsequent designation by COSSMANN (1909) [misspelt as “*Microcalpia*”].

***Microcolpia friedeli* (BRUSINA, 1885) n. comb.**

Figures 8.1-8

1869 *Melanopsis acicularis* FERUSSAC – NEUMAYR, p. 370, pl. 13, fig. 6 [non *Melanopsis acicularis* FÉRUSSAC, 1823].

1874a *Melanopsis acicularis* FÉRUSSAC – BRUSINA, p. 37 [pars; only regarding locality Kravarsko].

1874b *Melanopsis acicularis* FÉRUSSAC – BRUSINA, p. 24 [pars; only regarding locality Kravarsko].

1875 ?*Melanopsis acicularis* FER. – NEUMAYR & PAUL, p. 48-49 [non *Melanopsis acicularis* FÉRUSSAC, 1823].

*1885 *Melanopsis Friedeli* BRUS. – BRUSINA, p. 160.

1896 *Melanopsis Friedeli* BRUS. – BRUSINA, p. 120.

1897 *Melanopsis Friedeli* BRUS. – BRUSINA, p. 8, pl. 6, figs. 5-8.

1917 *Melanopsis Friedeli* BRUSINA – KOCH, p. 11.

1929a *Melanopsis friedeli* BRUSINA – WENZ, p. 2725-2726.

1974 *Melanopsis friedeli* BRUSINA – MILAN et al., p. 91. non 2003 *Melanopsis friedeli* BRUSINA, 1897 – PANĀ, p. 319, pl. 9, figs. 14-16.

Material: VGK-39 (3 specimens from sample no. 12, and 4 specimens from sample no. 33) and Kra-I (3 specimens from sample no. 3, 3 specimens from sample no. 23, and 5 specimens from sample no. 24).

Dimension: Height x width – 16.8 x 5.8 mm (Figs. 6.3-4), 17.4 x 6.7 mm (Figs. 6.7-8).

Description: Glossy, slender shell, elongate, with up to 9 whorls, and width attaining about 58% of height. Whorls are weakly convex to straight in cross-section; sutures are shallow; the resulting outline is almost perfectly conical. Shell base is slightly concave. Last whorl attains 55-60% of the total shell height. Some specimens with convex whorls develop weak, slender, irregularly spaced, opisthocyrt ribs on the last 3-4 whorls, with the point of maximum convexity in the middle. Ribs on the last whorl are sigmoidal, parallel with the growth lines. Aperture is oval, with moderately thickened callus. Colouring occasionally present as yellow to orange quadratic spots, arranged in a loose chequer-board like pattern.

Remarks: As already stated in BRUSINA (1885), this species might be closely related to *Microcolpia acicularis* (FÉRUSSAC, 1823), which is the type species of *Microcolpia* BOURGUIGNAT, 1884. The original description by BRUSINA (1885) was a rectification of erroneous identifications of specimens from Kravarsko and Podvornica with *M. acicularis* by BRUSINA (1874a, b). BRUSINA (1897) provided an excellent illustration of one complete specimen from the *Viviparus* beds of Podvornica, which was designated as a neotype by MILAN et al. (1974) (Coll. NHM Zagreb Inv. No. 2998-664). However, this designation is insufficient according to ICZN Art. 75.3. It is entirely unclear

whether the original type material of BRUSINA (1885) has been lost or was later illustrated by BRUSINA (1897). Therefore, no type exists at present.

The exact geographic position of the Podvornica locality is uncertain. MILAN et al. (1974) indicated it to be ESE of Kutina, while JURIŠIĆ-POLŠAK (1979) positioned it N of Kravarsko. Its actual position could not be verified from additional literature.

The partly enormous intraspecific variation of *Microcolpia* species has recently been demonstrated by morphometric analysis for a Late Pleistocene to Holocene *Microcolpia* species flock from the Pețe thermal spring in Romania (NEUBAUER et al., 2014b). *Melanopsis astathmeta* BRUSINA, 1897 from the LVB of Novska (= *M. decollata* sensu PENNECKE, 1884 non STOLICZKA, 1862) is very similar to the non-ribbed morphotype of *M. friedeli*. It is slightly broader, has a larger last whorl and a more expanded aperture (cf. BRUSINA, 1897). Nevertheless, it is clearly a specimen of *Microcolpia*. *Melanopsis sandbergeri* NEUMAYR, 1869 from the LVB (?) of Repušnica has a bulkier last whorl and a distinct fasciole on the neck. *M. recurrens* NEUMAYR in NEUMAYR & PAUL, 1875 (= *M. decollata* sensu NEUMAYR, 1869 non STOLICZKA, 1862) from Repušnica differs in its slightly stepped whorls with deeper sutures.

The identification of *Melanopsis* cf. *friedeli* from the Portaferrian (latest Pannonian) of Beočin (N Serbia) by KOCH (1902) has not recently been confirmed (STEVANOVIĆ et al., 1990) and remains doubtful. The record by PANĀ (2003) from the Sienisian of Valea Fântânei in the Dacian Basin is a misidentification. The illustrated specimens are shorter, have higher apical angles and more convex outlines.

Distribution: Lake Slavonia deposits in central Croatia at Podvornica, Kravarsko and Prvožina; occurrences in the LVB of northern Serbia (Krivci/Sremski Karlovci) could not be approved and need careful re-examination.

Order Littorinimorpha GOLIKOV & STAROBOGATOV, 1975

Superfamily Truncatelloidea Gray, 1840

Family Bithyniidae GRAY, 1857

Genus *Bithynia* LEACH in ABEL, 1818

Type species: *Helix tentaculata* LINNAEUS, 1758; Recent, Europe; type by subsequent designation by HERRMANNSEN (1846).

***Bithynia vukotinovići* BRUSINA, 1874**

Figures 8.11-14

1873 *B.[ythinia] Vukotinovići*, BRUS. – PILAR, p. 109, 176 [nomen nudum].

*1874a *Bythinia Vukotinovići* BRUSINA – BRUSINA, p. 69, pl. 5, figs. 13-14 [erroneously as “*Vukotiuovići*” in plate captions].

1874b *Bythinia Vukotinovići* BRUSINA – BRUSINA, p. 51-52, pl. 5, figs. 13-14 [erroneously as “*Vukotiuovići*” in plate captions].

- ? 1875 *Bythinia tentaculata* L. – NEUMAYR & PAUL, p. 73 [non *Helix tentaculata* LINNAEUS, 1758].
- 1875 *Bythinia Vukotinovići* BRUS. – NEUMAYR & Paul, p. 17, 74.
- ? 1881 *Bythinia Rumana*, PORUMBARU – PORUMBARU, p. 38, pl. 9, figs. 5-5a.
- ? 1881 *Bythinia Vukotinovići* (BRUS.) – PORUMBARU, p. 37, pl. 9, figs. 4-4a.
- 1883 *Bythinia tentaculata* LINNÉ – COBĂLCESCU, p. 140, pl. 13, figs. 14a-b [non *Helix tentaculata* LINNAEUS, 1758].
- 1885 *Bythinia Vukotinovići* BRUS. – BRUSINA, p. 162.
- ? 1884 *Bythinia tentaculata* LINNÉ – PENECKE, p. 33 [non *Helix tentaculata* LINNAEUS, 1758].
- 1896 *Bythinia Vucotinovići* [sic] STEFANESCU p. 108, pl. 10, figs. 22-27.
- 1917 *Bythinia Vukotinovići* BRUS. – KOCH, p. 15.
- 1928 *Bulimus vukotinovići vukotinovići* (BRUSINA) – WENZ, p. 2258-2259.
- 1932 *Bulimus vukotinovići* (BRUSINA) – KREJCI-GRAF & WENZ, p. 110.
- 1942 *Bulimus (Bulimus) vukotinovići* (BRUSINA) – WENZ, p. 52, pl. 16, figs. 243-248.
- 1961 *Bythinia vucotinovići* [sic] BRUS. – BOGACHEV, p. 304, pl. 49, pl. 16-19.
- 1972 *N. [eumayria] vukotinovići* (BRUSINA) – GIROTTI, p. 126-127, figs. 14-15.
- 1974 *Bulimus (Bulimus) vukotinovići* (BRUSINA) – MILAN et al., p. 64.
- 1997 *Bulimus (Bulimus) vukotinovići* (BRUSINA) – PAPA- IANOPOL & POPESCU, p. 200, 205, pl. 5, fig. 10.
- non 2003 *Bulimus (Bulimus) vukotinovići* (BRUSINA) 1874 – PANĂ, 312-313, pl. 8, fig. 1.
- 2003 *Bulimus (Bulimus) vukotinovići* (BRUSINA, 1874) – PAPA- IANOPOL & MARINESCU, p. 270-271, pl. 7, fig. 5.
- 2006 *Bulimus (Bulimus) vukotinovići* (BRUSINA) – PAPA- IANOPOL, p. 80, pl. 1, figs. 6-8.
- 2007 *Bithynia vucotinovići* [sic] BRUSINA – GOZHİK & DATSENKO, p. 83, pl. 75, figs. 2-5, pl. 76, figs. 1-2.

Material: VGK-39 (3 specimens from sample no. 30) and Kra-I (2 specimens from sample no. 1, and 1 specimen from sample no. 21).

Dimensions: Height x width – 12.6 x 8 mm (Figs. 5.11-12), 13.3 x 7.6 mm (Figs. 6.13-14).

Description: Glossy, solid shell, broad conical, with width attaining about 60% of height, consisting of 5 convex to near straight-sided whorls. Protoconch is not preserved; early whorls convex to angulated, separated by shallow sutures. Last whorl height attains about 75% of total shell height; grows more strongly in an anterior direction in adult specimens, the point of maximum convexity of the whorls shifting downwards and producing a deeper suture. Base is weakly convex to straight. Aperture is oblique, ovoid, rounded anteriorly, and more or less pointed posteriorly. Peristome slightly thickened, adjoined interiorly by a shallow furrow for the operculum. In

lateral view, aperture is inclined to the axis with about 10°. Umbilicus covered or narrowed, slit-like. Shell is covered by opisthocline to slightly opisthocyrt growth lines, which sometimes become stronger and form small riblets. Additionally, shell surface occasionally bears irregular spiral wrinkles.

Remarks: The syntype series of BRUSINA (1874a) comprises shells from the Pliocene of Kravarsko (church) in central Croatia and from Podvinje (Čaplja) in northeastern Croatia. Additionally, he had a few opercula from Bečić as well, which he assigned to the present species. MILAN et al. (1974) erroneously considered the syntype illustrated by BRUSINA (Coll. NHM Zagreb Inv. No. 3852-1492/1) as the holotype, which according to ICZN Art. 74.5 does not classify as a valid lectotype designation. Therefore, following the ICZN formal provisions of Art. 74.7, we designate this specimen, illustrated in BRUSINA (1874a, pl. 5, figs. 13-14), as the lectotype. Type locality is the slope beneath the church in Kravarsko; the type stratum belongs to the LVB *V. kochanskyae* zone.

The differences to *B. tentaculata* are the larger size and the shape of the whorls with maximum convexity in a more abapical position. PILAR (1873) discovered the present species in the wood between Dubranec and Dragošći together with *Theodoxus sagittiferus* [= *T. semiplicatus*], *Viviparus fuchsi* [= *V. kochanskyae*], and *Microcolpia friedeli* (among others), which could imply the same stratigraphic position as for Kravarsko. NEUMAYR & PAUL (1875) observed *N. vukotinovići* in the *V. stricturatus* zone of Gromačnik in NE Croatia and detected *B. tentaculata* in LVB (Cernik, Čaplja, Gornji Raić) and MPB (Gromačnik). PENECKE (1884) only distinguished *B. tentaculata* in the Pliocene of northeastern Croatia, particularly in the Čaplja trench (LVB, UVB), Malino (LVB-UVB) and Sibirj (MVB). Interestingly, BRUSINA (1885) doubted the presence of *B. tentaculata* in Slavonia, but (in contrast to WENZ, 1928) did not synonymize the respective identifications with *B. vukotinovići*. This is probably because the latter identifications were never documented by an illustration. A reinvestigation of the material from the Pliocene of northeastern Croatia is necessary to solve the species-level content of the Bithyniidae there. From central Croatia, KOCH (1917) reported only the presence of *B. vukotinovići* (Prvo- nožina, Dubranjec, and Kravarsko) and considered *B. tentaculata* to be absent there.

PORUMBARU (1881) was the first who identified *B. vukotinovići* from the Pliocene of Crețești and Podari in the Dacian Basin. From Crețești he also described the new species *Bithynia rumana*. His illustrations show quite bulky specimens indicating that neither identification represents *B. vukotinovići*. COBĂLCESCU (1883) only recognized *B. tentaculata* from the coeval deposits of Cărlig representing a quite slender phenotype. STEFANESCU (1896) subsequently discovered *B. vukotinovići* in the Pelendavian of Breasta and Bucovăț, illustrating slender specimens clearly resembling the lectotype. He synonymized *B. rumana* with *B. vukotinovići*, but did not include *B. tentaculata* of COBĂLCESCU (1883). WENZ (1928) was the first to synonymize the latter identification with *B. vukotinovići*, but still considered *B. rumana* as separate species. Note that GI-

ROTTI (1972) again synonymized the latter species with *B. vukotinovici*, which is followed herein.

Distribution: Lake Slavonia deposits of central Croatia (LVB of Kravarsko, LVB? of Dubranec and Prvonožina) and northeastern Croatia (LVB? of Podvinje/Čaplja, MVB of Gromačnik and other questionable localities as listed below); Pelendavian deposits of the Dacian Basin in Romania, Sienisian to Pelendavian equivalents (late Kimmerian) of SW Moldavia and of SW Ukraine.

WENZ (1942) discovered it was restricted to the Romanian ("Levantin") of the Dacian basin and illustrated specimens from Bucovăț, Valea Seacă and Valea Budurească. PAPAIAŃOPOL & POPESCU (1997) and PAPAIAŃOPOL et al. (2003) considered *B. vukotinovici* to be a biostratigraphic marker of the Pelendavian. Finally, PAPAIAŃOPOL & MACALEŢ (2006) confirmed the former stratigraphic range and illustrated additional specimens from Greaca, Podari, and Călugăreni. The record from the Sienisian of Carriere Rosia by PANĂ (2003) is based on a misidentification.

Except for Romania, the presence of *B. vukotinovici* in the Lake Dacia deposits was also listed from the "Levantin" of Giurgiulești in SW Moldavia by MACAROVICI (1940). Beyond that, GOZHIK & DATZENKO (2007) documented it from the adjacent SW Ukraine ranging there from the late Pliocene (uppermost Kimmerian) to the early Pleistocene. In the Pleistocene, the species concurs with *B. tentaculata*. Its presence in the Kuyalnikian of Odessa was documented by BOGACHEV (1961). Its record from the Pleistocene of the Taman Peninsula in SW Russia by VASSOEVIČ (1928) was not accompanied by an illustration and cannot be approved.

Family Hydrobiidae STIMPSON, 1865

Genus *Prososthenia* NEUMAYR, 1869

Type species: *Prososthenia schwartzi* NEUMAYR, 1869; Middle Miocene, Croatia; type by subsequent designation by CLESSIN (1880).

Remark: The present species closely resembles species from the Pliocene of Italy, which were treated as *Prososthenia* by SCHLICKUM (1972) and ESU & GIROTTI (1975). Most probably, these species do not represent *Prososthenia*, considering the morphological differences from its type species, which is smaller, bulkier and strongly sculptured. A revision of this group, however, is beyond the scope of the present study.

Prososthenia? slavonica (BRUSINA, 1874) n. comb.

Figure 8.15-16

*1874a *Hydrobia Slavonica* BRUSINA – BRUSINA, p. 65, pl. 4, figs. 13-14.

1874b *Hydrobia Slavonica* BRUSINA – BRUSINA, p. 48, pl. 4, figs. 13-14.

1875 *Hydrobia slavonica* BRUS. – NEUMAYR & PAUL, p. 77.

1884 *Hydrobia slavonica* BRUS. – PENECKE, p. 35.

1884 *Hydrobia tenuis* nov. form. – PENECKE, p. 35, pl. 10, figs. 4a-c.

non 1888 *Hydrobia slavonica*, BRUSINA – HALAVÁTS, p. 177-178, pl. 31, fig. 8.

non 1889 *Hydrobia slavonica* BRUS. – TUCCIMEI, p. 120, pl. 2, fig. 13.

non 1893 *Hydrobia slavonica* – DELAFOND & DEPÉRET, p. 130, 154, pl. 7, fig. 35, pl. 9, figs. 33-35.

1897 *Hydrobia? slavonica* BRUS. – BRUSINA, p. 19, pl. 9, figs. 22-23, 26-27.

1902 *Hydrobia? slavonica* – BRUSINA, pl. 9, figs. 1-2.

non 1914 *Hydrobia slavonica*, BRUS. – HALAVÁTS, p. 219.

non 1922 *Hydrobia* cf. *slavonica* – WENZ, p. 42-43, 64, pl. 3, fig. 24.

non 1925 *Hydrobia slavonica* BRUSINA – FISCHER & WENZ, p. 225-226, pl. 7, figs. 1-6.

1926 *Hydrobia slavonica* BRUSINA – WENZ, p. 1935-1936 [pars; excl. Hungarian, Romanian, German and Italian occurrences].

non 1977 *Hydrobia slavonica* BRUSINA – SCHLICKUM & PUISSÉGUR, p. 275, pl. 24, fig. 6.

non 1978 *Hydrobia slavonica* BRUSINA – SCHLICKUM & PUISSÉGUR, p. 5, pl. 1, fig. 7.

Material: VGK-39 (22 specimens from sample no. 38, 23 specimens from sample no. 41, and >30 specimens from sample P1).

Dimensions: height x width – 5.5 x 2.0 mm (largest specimen of sample 38, Figs. 6.15-16); 3.4 x 1.9 mm (largest specimen of sample 41).

Description: Glossy, slender drop-shaped shell, comprising up to 7 low convex whorls, and width attaining about 35% of shell height. Shell outline is variable in width, including wider and slender morphologies. Apex is slightly inflated, blunt, with highly convex initial two whorls. The following three whorls are weakly convex and form a regular conical outline; they are separated by distinct, moderately deep to shallow sutures. Shell height increases faster than the diameter, producing the typically drop-shaped appearance. In later ontogeny whorl flanks are sub-parallel to the axis, weakly convex, often centrally flattened, with slightly deeper sutures than before. The last whorl forms about 55% of the total shell height, is globose with a slightly convex shell base. Umbilicus is covered or very narrow. Aperture is ovate to drop-shaped, oblique. Posterior shell portion of the aperture is thickened and attached to the base of the preceding whorl. Shell is covered with orthocone growth lines. A weak subsutural band is present in a few specimens.

Remarks: BRUSINA (1874a, b) based this species on specimens from the localities of Bečić, Podvinje (Čaplja) and Sibinj in Slavonia (NE Croatia). We designate herewith the specimen from Čaplja illustrated by BRUSINA (1874a, pl. 4, figs. 13-14) and stored at the NHM Zagreb (Inv. No. 3051-697) as the lectotype. Its previous reference as "holotype" in MILAN et al. (1974) does not constitute a valid lectotype designation (ICZN Art. 74.5).

PENECKE (1884) stated that the typical *H. slavonica* is absent in his samples from Slavonia and separated shells with flattened whorls as the new species *Hydrobia tenuis*. This feature is quite variable in populations of *H. slavonica*, which is why *H. tenuis* was considered synonymous with *H. slavonica* by BRUSINA (1897) and WENZ (1922). The illustrated specimen derives from the *Viviparus stricturatus* zone of Sibinj.

Hydrobia cf. *slavonica* sensu WENZ (1922) and *Hydrobia slavonica* sensu FISCHER & WENZ (1925) from the late Burdigalian “*Prososthenia* beds” (= Praunheim Formation; KÜMMERLE & RADTKE, 2012) of Frankfurt am Main and Bommersheim in Germany (see also WENZ, 1926) superficially resemble the largest specimens from Lake Slavonia, but their spire is broader, the aperture is larger, whorls are convex and sutures are deeper.

Hydrobia slavonica sensu TUCCIMEI (1889) from the Plio-Pleistocene of Rocantica NE of Rome is a misidentification, being distinctly smaller with a height of only 2.3 mm and having a relatively larger last whorl. It was not mentioned in the census of the Plio-Pleistocene mollusc fauna from central Italy by ESU & GIROTTI (1975).

Hydrobia slavonica reported from the Pleistocene of Lake Bresse is also based on erroneous identifications. The specimen from the lower Pleistocene (MN 17 according to ESU, 1999) of Montagny-lès-Beaune illustrated by SCHLICKUM & PUISSÉGUR (1978) has a similar size but more convex whorls and deeper sutures. The same is true for specimens from Le Villard near Domsure and Bligny-sur-Ouche illustrated by DELAFOND & DEPERÉT (1893) and the single specimen reported by SCHLICKUM & PUISSÉGUR (1977) from the middle Pleistocene of Saint-Bernard.

The misidentifications from the Dacian of the Braşov Basin locality Vârghiş (HERBICH & NEUMAYR, 1875) and Bodoş (= Buduş) (ROTH, 1881) also reported in WENZ (1926) were synonymized by JEKELIUS (1932) with his new species *Hydrobia barzaviae*. Its presence in the Pleistocene *Viviparus boeckhi* zone of Szentes in SE Hungary reported by HALAVÁTS (1888, 1914) was revised by KROLOPP (1976a, p. 201). After KROLOPP (1976a), the *Hydrobia* species therein actually represents a new, as yet undescribed species.

BRUSINA (1897) introduced *Hydrobia slavonica vitrella* for specimens from the late Portaferrian (late Pontian) of Grgeteg in Syrmia (NW Serbia). This name is a primary homonym of *H. vitrella* STEFANESCU, 1896, a Sarmatian species from the Transylvanian Basin. Therefore, we propose *Prososthenia? praeslavonica* n. nom. as a replacement name for the Serbian species. The syntype from Grgeteg illustrated by BRUSINA is missing in the collection of the NHM Zagreb (MILAN et al., 1974); it may be stored in the Coll. STEVANOVIĆ at the NHM Belgrade (pers. comm. Zoran MARKOVIĆ, NHM Belgrade). *H. vitrella* STEFANESCU, 1896 differs from BRUSINA’s species in its larger last whorl. With a height of 3.1 mm *P. praeslavonica* is distinctly smaller than *P. slavonica*. While WENZ (1926) synonymized it with *P. slavonica*, STEVANOVIĆ (1951) treated it as an independent

subspecies, which he also reported from Sremski Karlovci. Because of the morphological and stratigraphical differences, we consider both taxa as separate species. *P. praeslavonica* is perhaps the phylogenetic ancestor of *P. slavonica*. The systematic position of both species within *Prososthenia* is still questionable, given the highly elongate shell and the thin peristome (cf. BRUSINA, 1897). Unfortunately, we lack material for *P. praeslavonica* and do not know about the more diagnostic features such as protoconch sculpture of either species, which is why a systematic revision would be based on weak ground and is therefore avoided here.

Distribution: It is restricted to Lake Slavonia deposits from Kravarsko in the West to Slavonski Brod (Bečić-Ciglenik [= Ciglenik], Malino, Sibinj, Slobodnica, and Čaplja) in the East. Its presence is ascertained for the MVB (Sibinj, Malino, Slobodnica) and the UVB (Bečić). The corresponding horizon at Čaplja remains unknown at present. Its occurrences further to the east at Bačko Novo Selo (NE Serbia; MVB and UVB) given by KRSTIĆ & KNEŽEVIĆ (2003) are questionable. Its presence at Kravarsko was previously unknown (KOCH, 1917).

The stratigraphic position of the type stratum at Čaplja was not specified by BRUSINA (1874a). According to NEUMAYR & PAUL (1875), this locality covers the *Viviparus fuchsi* [= *kochanskyae*], *V. hoernesi* and *V. zelebori* zones. Additionally, these authors list *H. slavonica* from the *V. stricturatus* zones at Slobodnica and the *V. sturi* zone at Bečić. Malino and Sibinj belong to the *V. bifarcinatus* zone (PENECKE, 1884).

Family Lithoglyphidae TRYON, 1866

Genus *Lithoglyphus* MENKE, 1830

Type species: *Paludina fusca* PFEIFFER, 1828; Recent, Europe; type by monotypy.

Lithoglyphus decipiens BRUSINA, 1885

Figures 8.17-20

1869 *Lithoglyphus naticoides* FERUSSAC sp. – NEUMAYR, p. 378, pl. 13, fig. 10 [non *Paludina naticoides* C. PFEIFFER, 1828].

1874a *Lithoglyphus fuscus* ZIEGLER – BRUSINA, p. 67-68 [non *Paludina fusca* C. PFEIFFER, 1828].

1874b *Lithoglyphus fuscus* ZIEGLER – BRUSINA, p. 49-50 [non *Paludina fusca* C. PFEIFFER, 1828].

1875 *Lithoglyphus fuscus* ZIEGLER – NEUMAYR & PAUL, p. 74-75 [non *Paludina fusca* C. PFEIFFER, 1828].

1881 *Lithoglyphus fuscus*, ZIEGLER – PORUMBARU, p. 39, pl. 9, figs. 9, 9a [non *Paludina fusca* C. PFEIFFER, 1828].

1883 *Lithoglyphus fuscus* ZIEGLER – COBĂLCESCU, p. 143-145, pl. 14, figs. 1-8 [non *Paludina fusca* C. PFEIFFER, 1828].

1884 *Lithoglyphus fuscus* ZIEGLER – PENECKE, p. 34 [non *Paludina fusca* C. PFEIFFER, 1828].

*1885 *L. [lithoglyphus] decipiens* BRUS. – BRUSINA, p. 162.

1894 *Lithoglyphus Kinkelini* – BRUSINA in ENGELHARDT, p. 171 [not seen].

- 1896 *Lithoglyphus Neumayri* BRUSINA – STEFANESCU, p. 111-112, pl. 10, figs. 52-53, 57.
- 1897 *Lithoglyphus decipiens* BRUS. – BRUSINA, p. 23, pl. 12, figs. 8-11.
- 1902 *Lithoglyphus Kinkelini* BRUS. – BRUSINA, pl. 11, figs. 59-61.
- 1928 *Lithoglyphus decipiens* BRUSINA – WENZ, p. 2272-2276.
- 1932 *Lithoglyphus acutus decipiens* BRUSINA – KREJCI-GRAF & WENZ, p. 114.
- 1940 *Lithoglyphus decipiens* BRUSINA – MACAROVICI, p. 325-326, pl. 5, figs. 91-93.
- 1942 *Lithoglyphus acutus decipiens* BRUSINA – WENZ, p. 48, pl. 15, figs. 200-205.
- 1973 *Lithoglyphus acutus decipiens* BRUSINA – ROSHKA, p. 190-191, pl. 30-31, figs. 442-447.
- 1974 *Lithoglyphus acutus decipiens* BRUSINA – MILAN et al., p. 79.
- 1995 *Lithoglyphus decipiens* BRUSINA – PAPAIANOPOL & MARINESCU, pl. 46, figs. 5-7.
- 2003 *Lithoglyphus acutus decipiens* (BRUSINA) – PANĀ, p. 310, pl. 6, figs. 5-6.

Material: VGK-39 (3 specimens from sample no. 11, 3 specimens from sample no. 32, and 17 specimens from sample no. 39), and Kra-I (1 specimen from sample no. 1, 3 specimens from sample no. 2, and 4 specimens from sample no. 22).

Dimensions: Height x width – 5.55 x 4.5 mm (Figs. 6.17-18), 7.5 x 5.75 mm (Figs. 6.19-20).

Descriptions: Small, solid, bulky shell with up to 4 whorls, and width attaining about 80% of shell height. Apex is blunt. Spire trochiform, stepped, with deep sutures, flattened, subhorizontal ramps and slightly convex flanks. Blunt angulation present between ramps and flanks. Last whorl large, attaining 83% of shell height, showing straightened, oblique shell base. Aperture is ovate- semicircular, inclined by 45° toward axis. Peristome thickened, slightly protruding anteriorly and posteriorly, forming a continuum with the callus pad. Umbilicus covered by the latter. Apertural plane posteriorly inclined. Dense opisthocline growth lines present on glossy exterior shell.

Remarks: NEUMAYR (1869) identified his specimen from the LVB of Cernik (Sv. Linart church; STUR, 1862; NEUMAYR & PAUL, 1875) erroneously with the Recent *Lithoglyphus naticoides* (PFEIFFER, 1828), which has a distinctly lower spire and a bulkier last whorl. The specimen he illustrated on pl. 13, fig. 10 (height x width = 8.0 x 5.3 mm) is stored in the collection of the GBA (Inv. No. 1869/001/0068). BRUSINA's (1874a) specimens derive from a number of localities from the central part of Lake Slavonia as well as from Vlaško Kostanjevlje (= Kostanjevec) in Kravarsko and Farkašić donated to him by Lj. v. FARKAŠ-VUKOTI-NOVIĆ. He claimed these are somewhat smaller in size than those from NE Croatia and identified them as Recent *L. fuscus* PFEIFFER, 1828, which was followed by NEUMAYR & PAUL (1875).

The introduction of *L. decipiens* BRUSINA, 1885 was a text-note referring to all specimens from Slavonia previ-

ously misidentified with *L. fuscus*. Later, BRUSINA (1897) provided synonymy to his new species and illustrated specimens from Kovačevac and Malino. The specimen from Kovačevac (NHM Zagreb Inv. No. 3090-736) was erroneously referred to as the "holotype" by MILAN et al. (1974). According to PENECKE (1884), the sediments at Kovačevac belong to the UVB *V. zelebori* zone.

From the LVB of Malino, NEUMAYR in NEUMAYR & PAUL (1875) described the new species *L. histrio* which he presumed to be an aberrant variation from *L. fuscus* sensu BRUSINA. It differs from the present species in its elongated, ovoid morphology.

L. kinkelini BRUSINA, 1894 from the Portaferrian of Kurd (SE Hungary) – illustrated for the first time in BRUSINA (1902) – was synonymized by WENZ (1928) with *L. decipiens*. WENZ (1928) also listed *Bithynia brusinae* HALAVÁTS, 1903 from the latest Pannonian of Kötöcs SE Balaton (Hungary) as well as *L. naticoides* sensu HALAVÁTS (1888) from the *V. boeckhi* zone (Pleistocene) of Szentes in SE Hungary as synonyms of the present species. However, KROLOPP (1976b) approved HALAVÁTS' original identification, pointing out that *L. decipiens* is absent in the Pleistocene of SE Hungary. The presence of *L. decipiens* at Kötöcs was confirmed by MÜLLER & MAGYAR (1992).

STEFANESCU (1896) erroneously introduced *Lithoglyphus neumayri* as a new name for the specimens from Slavonia and Romania identified previously with *L. fuscus*, apparently unaware of *L. decipiens*. He referred the authorship to BRUSINA, mentioning the corresponding collection label seen at the NHM Zagreb. Moreover, he was apparently unaware of introducing a primary homonym of *Lithoglyphus neumayri* SINZOV, 1877. Anyway, *L. neumayri* is an objective junior synonym of *L. decipiens*.

Distribution: The species occurs in numerous localities of Lake Slavonia, ranging from the LVB to the UVB (PENECKE, 1884) and Lake Dacia (see below). The oldest records are listed from the Portaferrian (late Pontian sensu STEVANOVIĆ et al., 1990) of Hungary (e.g., Kötöcs) and the late Maeotian of SW Ukraine (ROSHKA, 1973). Particularly the Ukrainian record extends the stratigraphic and geographic range of the species enormously, which is why a careful revision of ROSHKA's material is required.

In addition to numerous central Lake Slavonian occurrences (LVB to UVB), NEUMAYR & PAUL (1875) referred two specimens from the upper Portaferrian Lake Pannon deposits at Grgeteg and Sremski Karlovci (both NW Serbia) to this species.

WENZ (1942) documented specimens from the *Pyrgula eugeniae* beds (late Dacian; ANDREESCU et al., 2013) of the area around Iordăcheanu/Plavia/Valea Urloii and the late Romanian of Valea Seacă. He listed this species in the Dacian Basin from the middle Pontian to the late Romanian. PAPAIANOPOL & MARINESCU (1995) illustrated specimens from the Getian of Moreni in the Dacian Basin and Parscovian of Tudor Vladimirescu well at the Moesian platform (both Romania). PAPAIANOPOL et al. (1995) cited it from two additional – Getian and Parscovian – localities. Fi-

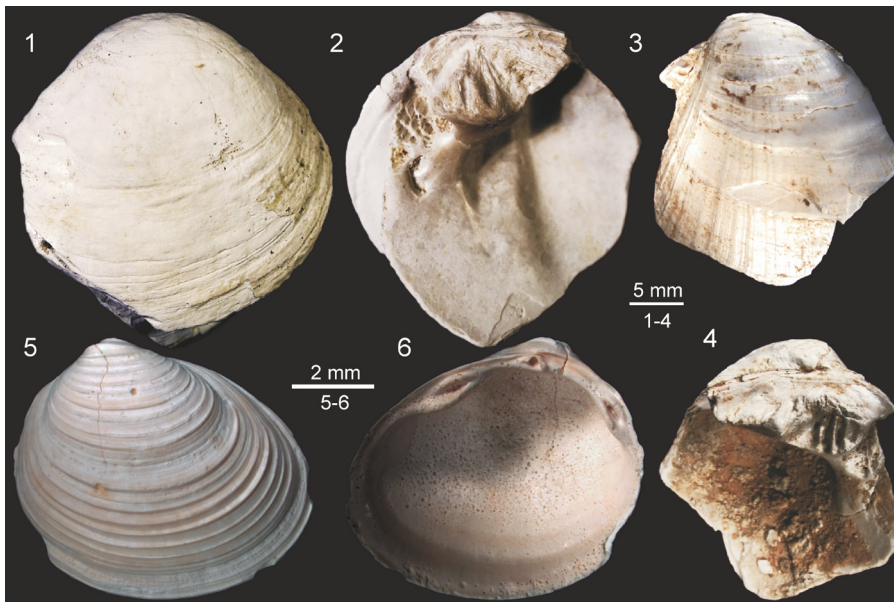


Figure 9: Pliocene lacustrine bivalves (Unionidae and Sphaeriidae) from the Pliocene of the Kravarsko region. 1-2 – *Potomida seljani* (BRUSINA, 1902); 1-2 – VGK-39 sample no. 35; 3-4 – VGK-39 sample no. 35. 5-6 – *Pisidium solitarium* NEUMAYR, 1875; 5-6 – VGK-39 sample no. 13.

nally, PANĂ (2003) illustrated specimens from the Pelendavian (middle Romanian) of Ploșoru (Olari) in the Dacian Basin. Additional localities in Romania, where this species was cited from but not more recently documented from, go back to WENZ (1928; Dacian and Romanian), KREJCI-GRAF & WENZ (1932; upper Pontian, Dacian, upper Romanian), and PAPAIANOPOL et al. (2003; late Dacian and Parscovian).

Records by WENZ (1928) that could not be confirmed are from (1) the Dacian of Araci (=Arpatac) in the Brașov basin, not confirmed by JEKELIUS (1932), (2) the Upper? Miocene from Sarajevo (Lukavica) based on “*Lithoglyphus* cf. *fuscus*” in NEUMAYR (1880b), an identification automatically related to *L. decipiens* by WENZ (1928), although it has never been recorded from the Dinarides (e.g., HARZHAUSER & MANDIC, 2008), and (3) the Pliocene of the area around Orahovac (Kosovo) based on “*Lithoglyphus fuscus*” in PAVLOVIĆ (1903). All these occurrences are highly dubious and have never been described or illustrated.

MACAROVICI (1940) illustrated specimens from the Dacian of Dmytrivka in SW Ukraine belonging palaeogeographically to the easternmost part of Lake Dacia. In addition, he recorded this species from numerous other Dacian localities in Moldova as well as in the SW Ukraine.

Class Bivalvia LINNAEUS, 1758

Superorder Palaeoheterodonta NEWELL, 1965

Superfamily Unionoidea RAFINESQUE, 1820

Family Unionidae RAFINESQUE, 1820

Subfamily Unioninae RAFINESQUE, 1820

Tribe Anodontini RAFINESQUE, 1820

Genus *Potomida* SWAINSON, 1840

Type species: *Mysca* (*Potomida*) *corrugata* SWAINSON, 1840 (currently considered a junior synonym of *Poto-*

mida littoralis (CUVIER, 1798)); Recent, Europe and Middle East; type by original designation.

Potomida seljani (BRUSINA, 1902) n. comb.

Figure 9.1-4

*1902 *Unio Seljani* BRUS. – BRUSINA, p. 9, pl. 25, figs. 7-8.

1958 *Unio seljani* BRUSINA – MODELL, p. 224, pl. 4, fig. 3.

1974 *Unio seljani* BRUSINA – MILAN et al., p. 55.

1981 *Unio* (*Wenziella*) *seljani* BRUSINA 1902 – ŽAGARSAKAČ, p. 18, pl. 2, figs. 5, 6, pl. 3, fig. 10.

Material: VGK-39 (3 specimens from sample no. 15 and 2 specimens from sample no. 35).

Dimensions: Height x length (fragment of the anterior shell) – 30.7 x 28.4 mm (Figs. 7.3-4; 32 x 50 mm reconstructed).

Descriptions: Shell thick, moderate in size and convexity, elongated with height (reconstructed) attaining about 65% of length. Outline is inequilateral with inflated, prosogyrate umbo shifted anteriorly and projecting over the hinge line. Anterior and ventral margins are rounded; posterior margin is not preserved, possibly sub-rectangular. Transverse keel is present posteroventrally. Shell wall is nacreous, lamellate, maximum of 4 mm thick. Exterior surface bears coarse, irregularly undulated to zigzag-patterned concentric lirae in the first 8 mm of ontogeny. Afterwards, the shell exterior is smooth, apart from projecting growth constrictions and very fine growth lines. Hinge comprises one massive, trigonal pseudocardinal on the right valve, subdivided by vertical grooves, adjoined by two elongated, pseudocardinals on the left valve. Anterior adductor scar is deep and rugose.

Remarks: The holotype by monotypy is one fragmented left valve from Kravarsko (Burdelj wood) with a missing posterior shell portion and centrally fragmented hinge (NHM

Zagreb Inv. No. 2846/493; height of 28.5 mm, length of 36.0 mm, convexity of 10.5 mm). Originally made available by illustration, ŽAGAR-SAKAČ (1981) provided a detailed description, recombining the species with the genus *Wenziella* MODELL, 1958. The latter is a junior synonym of *Potomida* SWAINSON, 1840 after GRAF & CUMMINGS (2014).

Distribution: Known only from the Pliocene of Kravarsko in central Croatia.

Superorder Heterodonta NEUMAYR, 1883

Order Venerida GRAY, 1854

Superfamily Sphaeroidea DESHAYES, 1855

Family Sphaeriidae DESHAYES, 1855

Subfamily Pisidiinae GRAY, 1857

Genus *Pisidium* PFEIFFER, 1821

Type species: *Tellina amnica* MÜLLER, 1774; Recent, Northern Hemisphere; type by subsequent designation by GRAY (1847).

Pisidium solitarium NEUMAYR in NEUMAYR & PAUL, 1875

Figure 9.5-6

*1875 *Pisidium solitarium* NEUM. nov. form. – NEUMAYR & PAUL, p. 26, pl. 8, fig. 35.

1884 *P[isidium]. solitarium* NEUM. – PENECKE, p. 16.

1897 *Pisidium solitarium* NEUM. – BRUSINA, p. 35, pl. 21, figs. 11-14.

Material: VGK-39 (3 specimens from sample no. 13, and 1 specimen from sample P1).

Dimensions: Height x length – 6.5 x 7.6 mm (Figs. 7.5-6).

Descriptions: Shell ovoid, fragile, inequilateral, posteroventrally elongated with length attaining 85% of height, with umbo shifted posteriorly, and the anterior part strongly protruded. Moderately convex, with convexity attaining 32% of total height, and with dorsally shifted point of maximum convexity. Opisthogyrate umbo is slightly projecting over the hinge line. Anterior margin strongly convex, other margins are weakly convex. Exterior shell surface bears regular, projecting sharp-topped commarginal lirae interrupted by concave growth constrictions (two in specimen on Figures 9.5-6). Adductor scars are of similar medium size but of different shapes. The posterior one is subcircular, anterior one narrowly ovate inclined toward the umbo. Pallial line is integripalliate. Right hinge has elongated lateral teeth, two massive anteriorly and two slender posteriorly. Cardinal teeth are much smaller but distinct, elongated, inclined, joined beneath the umbo, the posterior one longer than the anterior.

Remarks: Holotype by monotypy is a single left valve (height x length = 12.9 x 10.2 mm) from the *V. vukotinovici* zone of Novska illustrated by NEUMAYR & PAUL (1875) on pl. 8, fig. 35 and stored in the GBA (Inv. No. 1875/002/0028). BRUSINA (1897) illustrated for the first time a right

valve and additionally a hinge detail of the left valve of the species from the type locality.

Pisidium slavonicum NEUMAYR in NEUMAYR & PAUL, 1875 exhibits a similar shell sculpture but is larger, stronger postero-ventrally elongated, with a less robust and weaker arched hinge. Likewise, *P. clessini* NEUMAYR in NEUMAYR & PAUL, 1875 (MVB-UVB) has a comparable sculpture, but its hinge is not that robust and arched (e.g., BRUSINA, 1897, pl. 21, figs. 22-26).

The record of *P. solitarium* by CAPELLINI (1880) from the late Miocene of Italy is a misidentification and does not even match at the genus level, showing a completely different hinge type. Note that *Pisidium solitarium* sensu PRIME (1870) is a *nomen nudum* introduced in a synonymy list of “*Pisidium henslowianum*, Jenyns” (= *Pisidium henslowanum* (SHEPPARD, 1825)) and therefore no senior homonym.

Distribution: Pliocene *Viviparus* beds of northeastern (UVB of Novska; NEUMAYR & PAUL, 1875) and central Croatia (LVB of Kravarsko; this study).

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