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DIPLOMARBEIT

Quantifying evolution – paleolake mollusks from the Dinaride Lake System (Middle Miocene, Sinj Basin, SE Croatia)

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Science may set limits to knowledge, but should not set limits to imagination.

—Bertrand Russell (1872 – 1970)

Abstract

The present investigation deals with the mollusk evolutionary patterns and environmental change in a lower Middle Miocene succession in the Sinj Basin (Dalmatia, SE Croatia) reflecting the depositional history of a long-lived freshwater lake. Despite its mature investigation stage, an analysis of a quantified mollusk record, providing insight into species contributions, taxonomic relationships and the nature of the morphologic changes, is completely missing up to now.

The taxonomic diversification of freshwater gastropods and its connection with morphologic disparity events are documented for a ca. 100-m-thick section representing the topmost infill of the Sinj Basin. Based on the available age model, these alterations occur extremely fast on a millennial scale, re-proving the significance of long-lived lakes for evolutionary research. Furthermore, the simultaneity of morphologic shifts in systematically independent taxa suggests them to be tightly linked to environmental changes. Most probably, climatic fluctuations leading to variations in lake-level and habitat types are the driving factors for these radiation events.

The study provides statistical treatment of quantified samples accompanied by a taxonomic revision of the taxa. Additionally, based on the mollusk distribution a paleoenvironmental interpretation is given, supported by sedimentological data and previous palynological analysis. Actually, it supports previous results of the section's division into two limestone-coal cycles, grading from shallow intermediate-energy settings with high freshwater input via fossil-poor transgressive limestones to shallow low-energy conditions, resulting finally in a total lake drought at the section top.

The discussion will focus on the evolutionary lineages of four species, two of *Melanopsis* and two of *Prososthenia* (chapter 4.5.). All four species appear almost continuously and can be divided into several morphotypes based on different sculpture features; in some cases also size plays a role. It will be demonstrated that the morphs occur sequentially, each more or less limited to a special interval. Moreover, the changes in morphology appear at the same time in different taxa.

Keywords: evolutionary lineages, radiation events, paleoecology, statistical analysis, Middle Miocene, Dinaride Lake System, Sinj Basin

1. Introduction

During the Early and Middle Miocene Southeastern Europe accommodated a series of long-living freshwater lakes, termed the Dinaride Lake System (DLS; KRSTIĆ et al, 2003; HARZHAUSER & MANDIC, 2008). These environments gave rise to an outstanding evolution of endemic mollusks.

Long-lived lakes provide excellent examples for evolutionary and diversification patterns of mollusks. Compared to short-term representatives the prolonged lake durations give much more possibilities for speciation processes, endemic evolutions and radiation events. Continuous lake successions are ideal places for studies on modes and tempo of evolution (MARTENS et al., 1994; MICHEL, 1994; amongst others).

The term “long-lived” applies to a lake that persists more than 100 000 years (GORTHNER, 1994). The number of extant representatives is comparatively low. Whereas most Recent lakes are short-term and result of the ice ages, long-lived lakes are mainly of tectonic origin (GORTHNER, 1994). As the term “ancient” can lead to confusion regarding relative longevity versus absolute age of origin, it will not be used here.

The Sinj Basin represents a classic area of fossil mollusk research, widely known as the freshwater Miocene of Dalmatia. The taxonomic frame was established already by the end of the 19th century in the line with numerous extensive monographic studies (NEUMAYR, 1869; BRUSINA, 1870, 1874, 1876, 1882a, b, 1884, 1885, 1892, 1897, 1902 and 1907). Subsequently, OLUJIĆ (1936, 1999) tried to describe evolutionary lineages. By reworking the same section this investigation provides a taxonomic revision for the studied mollusk fauna and a discussion of previous results of OLUJIĆ (1936, 1999).

It deals particularly with statistical

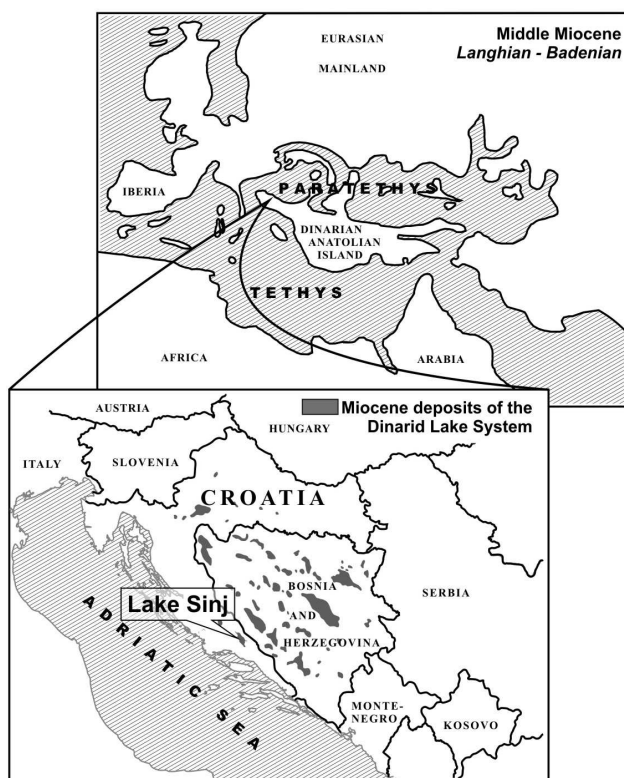


Fig. 1. Paleogeographic setting of Lake Sinj (after MANDIC et al., 2009).

analysis of the quantified taxonomic record, disparity events, evolutionary lineages, and the paleoecologic reconstruction of this freshwater environment, integrating previous studies on sedimentary facies (MANDIC et al., 2009) and palynology (JIMÉNEZ-MORENO et al., 2008)

2. Geological setting

The studied section Lučane is located in Dalmatia, SE Croatia (Fig. 1) and displays the upper part of the infill of the Sinj Basin. This basin is a NW-SE elongated pull-apart structure within the External Dinarides, measuring 38 x 9 km (MANDIC et al., 2009; fig. 2). Like other similar basins within the Dinarides it accommodated during the Early and Middle Miocene a long-lived freshwater lake. Together they form the so-called Dinaride Lake System (KRSTIĆ et al., 2003; HARZHAUSER & MANDIC, 2008). Based on ESRI® ARCGIS® 9 data the lake had an approximate surface area of 132 km². It was settled in a karst region made up by Mesozoic to Paleogene platform carbonates.

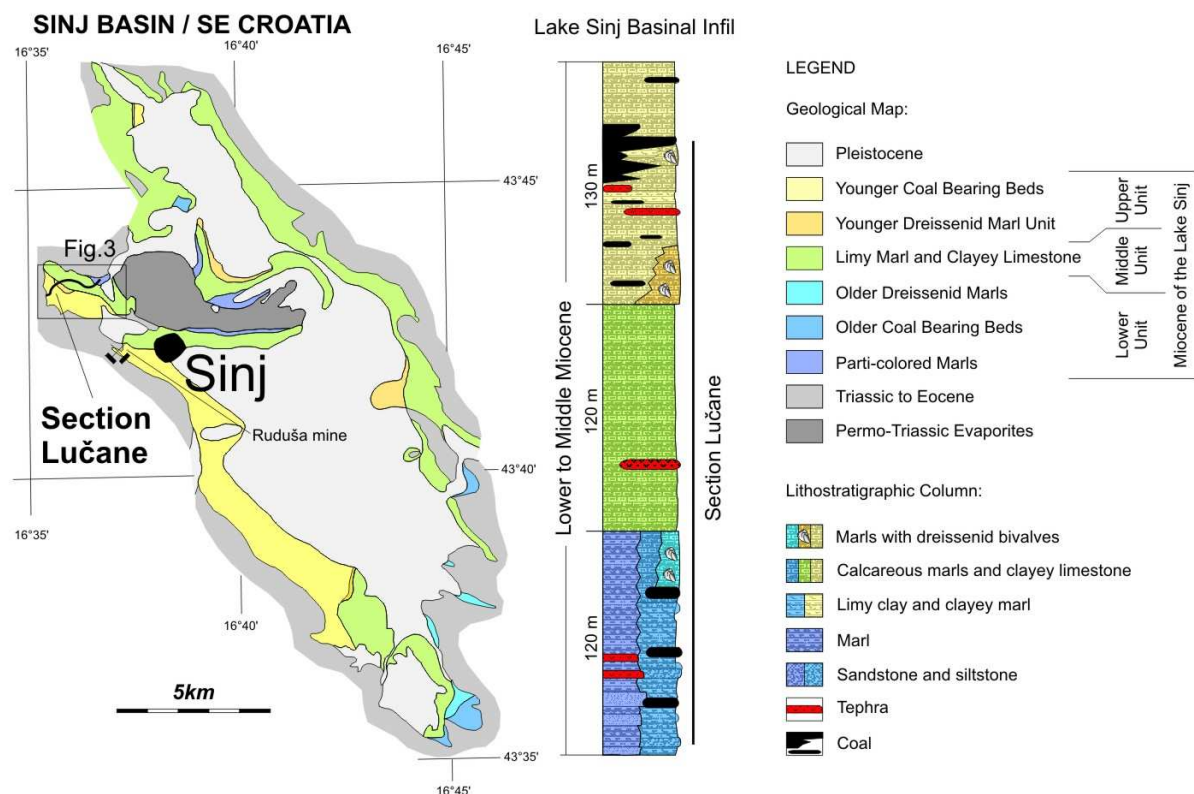


Fig. 2. Geological map of the Sinj Basin showing the classification and distribution of lithostratigraphic units of the Miocene infill (after DE LEEUW et al., 2010).

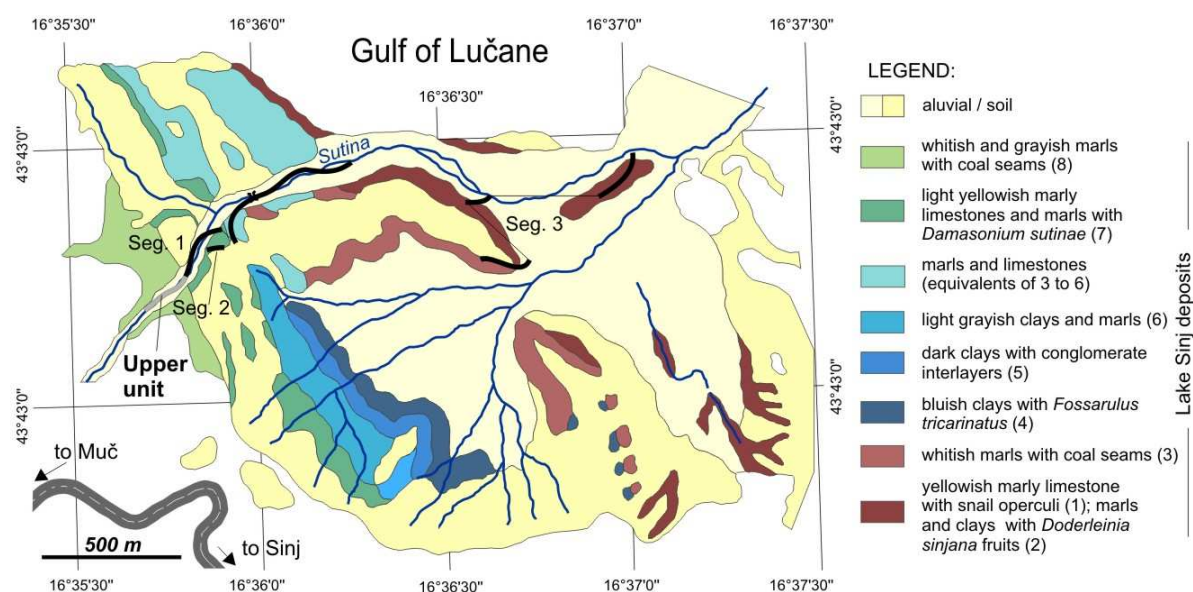


Fig. 3. Geological map of the Gulf of Lučane showing the position of the studied section, here marked as “upper unit” (after DE LEEUW et al., 2010).

The basin infills have been extensively studied by KERNER (1905 and 1916a, b), ŠUŠNJARA & ŠČAVNIČAR (1974), ŠUŠNJARA & SAKAČ (1988), MANDIC et al. (2009) and DE LEEUW et al. (2010).

The thickness of the basinal infill in the studied region attains more than 500 m (Fig. 3). This investigation deals with its topmost interval (“upper unit”) consisting of about 100 m thick fossiliferous coal-bearing limestone (Fig. 4), superposing limestones poor in fossils and organic matter. Previous sedimentological and palynological results on the same succession are presented by MANDIC et al. (2009) and JIMÉNEZ-MORENO et al. (2008).

According to these authors, the section comprises two large-scale, shallowing upward cycles, each starting with fossil poor limestones and passing into highly fossiliferous, coal-bearing beds. The two cycles can be subdivided into several intervals, which will be defined and characterized in detail in chapter 4.4. The studied partial section overlays volcanic ash intercalations (at ca. 40 m; fig. 4). The succession starts with ca. 10 m of limestone-coal interbeddings followed by 5 m of pure limestones. These are superposed by 10 m of highly fossiliferous beds with massive coal seams. Upsection, 40 m of mainly limestones follow, intercalated by few coal beds. The upper 30 m are again characterized by

► Fig. 4. Lučane section with position of studied samples, indicated by numbers and letters (compare tab. 1; modified after MANDIC et al., 2009).



limestone-coal interbeddings. Its topmost part includes a single 2-m-thick coal seam, representing the base of a 15-m-thick coal sequence currently covered by vegetation (OLUJIC,

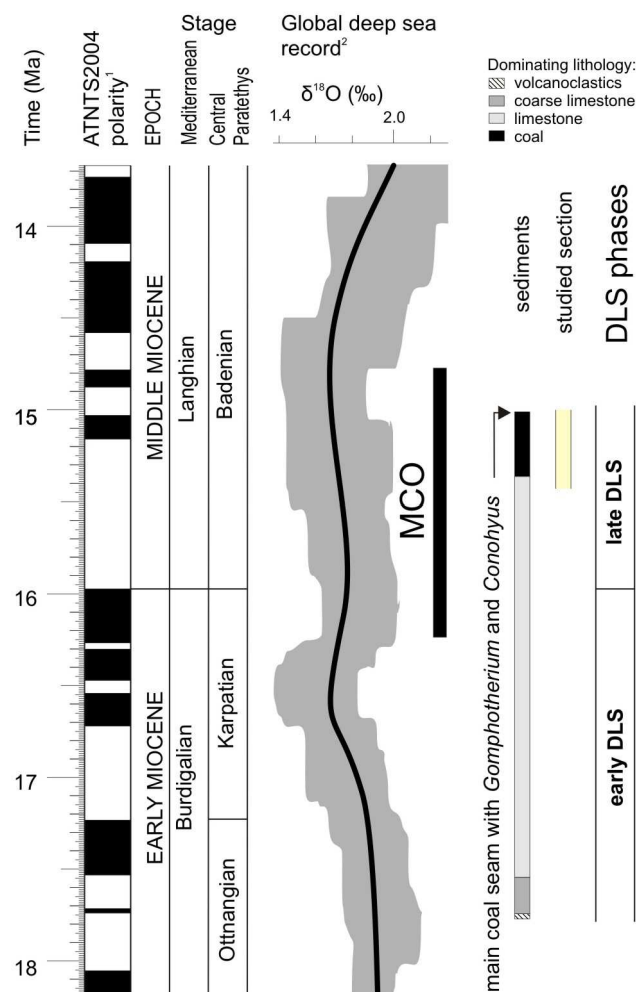


Fig. 5. Geochronologic timescale (modified after DE LEEUW et al., 2010; ¹LOURENS et al., 2004; ²ZACHOS et al., 2001)

conditions expected for the Middle Miocene investigated time interval (Fig. 5).

1999).

Few tephra layers intercalate the section. Recent integrative stratigraphic studies combining Ar/Ar geochronology and magnetostratigraphic results yielded a time span from 15.4 to 15.0 Ma for the studied 100 m interval correlating it to the Lower Langhian (DE LEEUW et al., 2010; fig. 5). The base of the section is marked by a 40-cm-thick tephra layer, dated with 15.43 ± 0.1 Ma (DE LEEUW et al., 2010).

The pollen record with high abundances of thermophilous and xeric plants indicates a generally subtropical climate (JIMÉNEZ-MORENO et al., 2008). It was subjected to minor and major fluctuations resulting in a varying flora that is reflected in the pollen record. These recurrent changes between dry and humid phases can be related to astronomical cycles. The overall warm climate detected corresponds well to

the Middle Miocene Climatic Optimum, coinciding with the

3. Material and methods

28 samples were treated by diluted H_2O_2 and afterwards sieved through a set of three sieves (250 μm , 125 μm and 63 μm). During this procedure a variable amount of sediment was washed, reaching from about 150 g to over 5 kg (Tab. 1). In some cases, complete specimens were picked out previously to prevent the fragile mollusks from damage while washing.

Only the residues of the coarse fraction (250 μm) were determined and counted using a binocular microscope. Hereby, each bivalve shell was treated as one individual. In most gastropods the part bearing the protoconch was counted, but in melanopsids and neritids the abapical part with the aperture was used showing more characteristic features.

To outline the relative fossil content of each sample the density was calculated as the amount of individuals divided by sample weight (Tab. 1).

Sample	n	Weight [kg]	Density
A	89	2.973	29.9
J	305	1.500	203.3
L	435	1.620	268.5
Lx	47	1.500	31.3
M2	266	1.500	177.3
O	90	1.000	90.0
T1	2159	1.500	1439.3
V	680	0.750	906.7
Y	467	1.500	311.3
Z	1494	0.750	1992.0
β	18	1.795	10.0
γ	257	1.798	142.9
θ	3	0.158	19.0
$\theta 1$	0	0.312	0.0
μ	7	0.248	28.3
ν	35	1.701	20.6
$\nu 1$	17	1.637	10.4
45	411	4.713	87.2
44	4845	4.980	972.9
43	368	4.648	79.2
42/41	38	2.283	16.6
37	287	4.390	65.4
33	1111	5.108	217.5
32	280	3.264	85.8
26	8	1.500	5.3
25	60	1.500	40.0
22	4	1.500	2.7
20	64	3.136	20.4

Tab. 1. Sample density.

For diversity indices and analysis only individuals determined to species level were included. The data bank using percentage values was set up in Microsoft Excel and transferred to PRIMER 6.1.10 (CLARKE & WARWICK, 1994). There the analysis was divided into two runs: first including the complete sample list, second excluding the small samples (<100 individuals) for being possibly not significant. By that the influence of potentially overrepresented taxa could be limited.

Before starting with the analysis the data were square root transformed to limit the contribution of most abundant taxa (CLARKE & WARWICK, 1994). In the following, this was analyzed using Bray-Curtis similarities to provide a cluster analysis to obtain average group similarities, including a SIMPROF check to test for evidence of structure (red lines; CLARKE

& WARWICK, 1994). Based on the same matrix a non-metric multidimensional scaling (nMDS) with a minimum stress of 0.01 was generated to visualize the “distances” (= relative similarities) of the samples. Based on both the cluster analysis and the nMDS, factors were defined to outline which species are responsible for the similarities or dissimilarities, respectively, between the single clusters (SIMPER analysis).

Two samples (91 and 9) were excluded from analysis because of statistically insignificant fossil content.

4. Results and discussion

4.1. Faunal composition – qualitative data

The counting of the samples yielded a total amount of 13,845 individuals comprising at least 18 gastropod species of 9 genera and 5 bivalve species of 2 genera (Tab. 2).

Generally, the section is characterized by the evolutionary lineages of *Melanopsis lyrata*, *Melanopsis lanzaeana*, *Prososthenia schwarzi* and *Prososthenia cincta*, each containing 3-4 morphotypes. For the lowermost part of the section smooth morphs are typical, whereas the upper part is characterized by half-ribbed and ribbed forms. The evolutionary traits of these four species will be discussed in chapter 4.5.

Mytilopsis jadrovi, *Theodoxus sinjanus*, *Orygoceras dentaliforme*, *Pseudamnicola torbariana* and *Pseudamnicola* n. sp. appear almost throughout the section. Within the interval between 60-70 m, these are accompanied by *Fossarulus fuchsi* and sculptured species of *Orygoceras*. *Unio*, *Ferrissia* and *Melanopsis* n. sp. occur here for a short interval as well. The uppermost part of the section bears *Prososthenia neutra*, *Fossarulus* cf. *armillatus* and pulmonate snails such as *Gyraulus* and *Lymnaea*. The middle part of the section yields only few poorly preserved samples, with *Mytilopsis aletici* as typical element.

Detailed systematic descriptions are provided in chapter 6 (systematic order after BOUCHET & ROCROI, 2005).

samples		20	22	25	26	32	33	37	42/41	43	44	45	v1	v	μ	θ1	θ	γ	β	Z	Y	V	T1	O	M2	Lx	L	J	A	Total	
Theodoxus sinjanus																															
Theodoxus cf. sinjanus		22		4	1	14	76	5	1	71	220	21	5	3				20	8	3	3	2	29	4	1					421	
Melanopsis lanzaeana morph lanzaeana				1																										96	
Melanopsis lanzaeana morph rugosa				1		23	106	21		28	261									40	1	4	4	1						486	
Melanopsis lanzaeana morph costata										21										94	1	2					11			129	
Melanopsis lanzaeana morph glabra																				52		52	28	5			85	10		232	
Melanopsis lyrata morph semicostata		5		30	1	93	390	150	8	70		2							1											749	
Melanopsis lyrata morph costata										1	397									17										399	
Melanopsis lyrata morph lyrata																			14	7	16			2		9				17	
Melanopsis n. sp.										4	6									1										48	
Prososthenia bicarinata																														10	
Prososthenia cincta morph primaeva																														1	
Prososthenia cincta morph semievoluta										5		27	1	3						79	9	4	30	4	12	3	11			36	
Prososthenia cincta morph cincta										2								1		360	12	27	187	14	43	6	23	6		155	
Prososthenia neutra																														678	
Prososthenia schwarzi morph transitans		10		5		12	73	4		96																		19	26	45	
Prososthenia schwarzi morph apleura						2				42	93	8								7										200	
Prososthenia schwarzi morph semicostata																			1	49	17	10	80	3	2	1	21	1		152	
Prososthenia schwarzi morph schwarzi												1						6	1	148	47	263	776	40	35	4	79	2		185	
Prososthenia sp. indet.		6		7		19	104	20	4	70	722	309	7	21				2	132	1	535	361	267	945	27	150	30	283		1402	
Pseudamnicola torbariana				5		18	19	4	1	4	75	2						1	9	1	13			3						4022	
Pseudamnicola n. sp.		2				2	16	23	16	50	2057							41	30	2	10	19					47			155	
Fossarulus cf. armillatus																														2315	
Fossarulus fuchsi						1	1	4																				28		28	
Fossarulus sp. indet.						14	45	18											3		1	1								6	
Lymnaea sp.						2	2												1								1	5		82	
Gyraulus geminus																											14			15	
Orygoceras cornucopiae						1	1	1																			1	4		4	
Orygoceras dentaliforme		1		1		47	18	9	1	81	2							26	22	9	23	7	16	1	4	104				372	
Orygoceras stenonemus						3	2	3	1	2	11								1			1		1	1	1	17			43	
Orygoceras sp. indet.												2	1	1				4												8	
Ferrissia illyrica										1																				1	
Mytilopsis aletici												14			1			5												20	
Mytilopsis cf. dvarensis																1														1	
Mytilopsis jadrovi		19	3	3	6	31	256	25	7	23	797	21	3	7	6			26	1	29	4	11	22	2	1	5	5	3		1316	
Unio cf. rackianus intermedius										1																				1	
Unio sp.										2	1																			3	
Total		64	4	60	8	280	1111	287	38	368	4845	411	17	35	7	0	3	257	18	1494	467	680	2159	90	266	47	435	305	89		13845

Tab. 2. Complete sample list. The dotted lines reflect the environmental intervals defined in 4.4.

4.2. Ecology of extant relatives

In order to provide information for a paleoecological reconstruction it is essential to know about the ecology of Recent species, genera or families. In the following, extant relatives of the recorded fossil species will be described as far as possible according to their preferred habitats, energy settings and diets. Additionally, this information is combined in table 3.

- a. *Theodoxus* is a typical inhabitant of lakes, marsh/fluviatile channels, estuaries (PLAZIAT & YOUNIS, 2005) and major rivers (PFLEGER, 1984), preferring increased water energy. There it lives on stones and graze on algae (GLÖER, 2002). Animals from brackish water populations tend to be smaller in size (GLÖER, 2002).
- b. Melanopsids are known today from freshwater rivers and ponds with high oxygen content (HARZHAUSER et al., submitted; PFLEGER, 1984), shallow lakes with inundated marshes and on mud/gravel intertidal shores of estuaries (PLAZIAT & YOUNIS, 2005), displaying their tolerance on a wide range of conditions, including brackish water (GEARY, 1990). PLAZIAT & YOUNIS (2005) worked on species from Iraq and discovered that melanopsids with nodular morphology are more common in freshwater environments, whereas the smoother morphs are more abundant in estuarine water. Concerning diet, *Melanopsis praemorsa* seems to be a generalist. It grazes on diverse plant food, detritus and carrion (GEARY, 1990; MOUAHID et al., 1996).
- c. *Prososthenia* is one of the most common taxa in this section. According to RUST (1997) hydrobiids prefer littoral mudplains, feeding on algae. Many extant Hydrobiidae are common in springs and brooks and in general in shallow inland coastal waters. Often they constitute mass occurrences including sympatric appearance of related taxa (GLÖER, 2002; BICK & ZETTLER, 1994).
Pseudamnicola is common on shallow mud grounds with low freshwater supply (GLÖER & ZETTLER, 2007). The related *Amnicola* GOULD & HALDEMAN, in HALDEMAN, 1840 is known to feed on algae today (DILLON, 2000).

Family	Genus	Ecology of recent relatives		References
		Habitat	Diet / Mode of Life	
Neritidae	<i>Theodoxus</i>	lakes, marsh or fluviatile channels, estuaries or major rivers, living attached to stones; elevated water energy; sometimes also appears in slightly brackish water	grazing on algal mats	GLÖER, 2002 PFLEGER, 1984 PLAZIAT & YOUNIS, 2005
Melanopsidae	<i>Melanopsis</i>	small rivers and ponds with high oxygen content, shallow freshwater lakes with inundated marshes, alternatively on mud/gravel intertidal shores of estuaries	diverse plant food, detritus and carrion	GEARY, 1990 MOUAHID et al., 1996 PFLEGER, 1984 PLAZIAT & YOUNIS, 2005
Hydrobiidae	<i>Prososthenia</i>	littoral mudplains	grazing on algal mats	RUST, 1997
	<i>Pseudamnicola</i>	shallow mud grounds with low freshwater supply	feeding on algae	GLÖER & ZETTLER, 2007
Bithyniidae	<i>Fossarulus</i>	slowly moving or stagnant water, rivers and springs, living attached to stones and wood		GLÖER, 2002 HARZHAUSER & TEMPFER, 2004 RUST, 1997
Lymnaeidae	<i>Lymnaea</i>	stagnant or slowly flowing water with dense vegetation, preferring high pH-values and carbonate-rich water	dried leaves, algae and carrion	DILLON, 2000 GLÖER, 2002 PFLEGER, 1984
Planorbidae	<i>Gyraulus</i>	stagnant or slowly moving waters, common in the subaquatic parts of the rooted vegetation of swamps and lakes and in muddy puddles	mainly detritus, little algae	DILLON, 2000 GLÖER, 2002 HARZHAUSER & TEMPFER, 2004 PFLEGER, 1984 PLAZIAT & YOUNIS, 2005
	<i>Orygoceras</i>	shallow eulittoral to middle sublittoral		HARZHAUSER et al., 2002
	<i>Ferrissia</i>	lentic or slowly running water and lives under leaves or twigs	grazing on algal mats	DILLON & HERMAN, 2009 GLÖER, 2002
Dreissenidae	<i>Mytilopsis</i>	nearshore environments of major rivers, freshwater or brackish lakes, estuaries, living attached to rocks or plants	byssate filter-feeding epibionts	HARZHAUSER, 2004 HARZHAUSER & MANDIC, 2009 PFLEGER, 1984
Unionidae	<i>Unio</i>	enhanced freshwater input and rather calm water; abundant in vicinity of lakes and ponds	filter-feeding especially on smaller particles	DILLON, 2000 PFLEGER, 1984

Tab. 3. Ecology of extant relatives regarding habitat, diet and mode of life.

- d. *Fossarulus* has no extant representatives. It is supposed to have preferred similar habitats like *Prososthenia* (HARZHAUSER et al., submitted). The morphologically and taxonomically related *Emmericia* inhabits rivers and springs, living attached to stones and wood (GLÖER, 2002; RUST, 1997). The fossil representatives were interpreted as a lacustrine element marking slowly moving or stagnant water (HARZHAUSER & TEMPFER, 2004).
- e. The Recent pulmonate *Lymnaea stagnalis* (LINNAEUS, 1758) is common in stagnant or slowly flowing water with dense vegetation, feeding on dried leaves, algae and also carrion. It prefers high pH-values, carbonate-rich waters and can even endure intermittent desiccations (PFLEGER, 1984; DILLON, 2000; GLÖER, 2002).
- f. *Gyraulus* prefers stagnant or only slowly moving waters and is common especially in the subaquatic parts of the rooted vegetation of swamps and lakes and in muddy puddles (HARZHAUSER & TEMPFER, 2004; PLAZIAT & YOUNIS, 2005; PFLEGER, 1984). *G. albus* (O.

F. MÜLLER, 1774) feeds mainly on detritus and sometimes on algae (GLÖER, 2002) whilst *Planorbis contortus* avoids algae (DILLON, 2000).

The extinct *Orygoceras* is classified with planorbid pulmonate snails (HARZHAUSER et al., 2002), suggesting restricted diving depth. In neighboring Lake Pannon they appear from shallow eulittoral to middle sublittoral zones (HARZHAUSER et al., 2002).

The Recent ancylid *Ferrissia wautieri* prefers lentic or slowly running water and lives under leaves or twigs (GLÖER, 2002), grazing on algal mats (DILLON & HERMAN, 2009).

- g. *Mytilopsis* belongs to the family Dreissenidae comprising byssate filter-feeding epibionts (HARZHAUSER & MANDIC, 2009) and occurring nowadays in major rivers, freshwater and brackish lakes and estuaries (PFLEGER, 1984). Former authors stated that *Mytilopsis* was most common in nearshore environments of Lake Pannon. Therein, some generalist species also occur in fluvial settings associated with Neritidae, Unionidae and Planorbidae (HARZHAUSER & TEMPFER, 2004) or live attached to rocks or plants (HARZHAUSER, 2004). Some species are suggested to prefer bottom-level conditions in deeper water (HARZHAUSER & MANDIC, 2009). *Mytilopsis aletici* is a common species in the middle part of the section. It is characterized by an extraordinary large sized, thin-walled shell and interpreted to have settled in sublittoral and littoral environments under low-energy regimes (MANDIC et al., 2009).
- h. Unionidae are known to be a clear signal for purely freshwater settings and rather calm water (PFLEGER, 1984). They are more often found in vicinity of lakes or ponds rather than in truly riverine habitats, filtrating there fine suspension particles (DILLON, 2000).

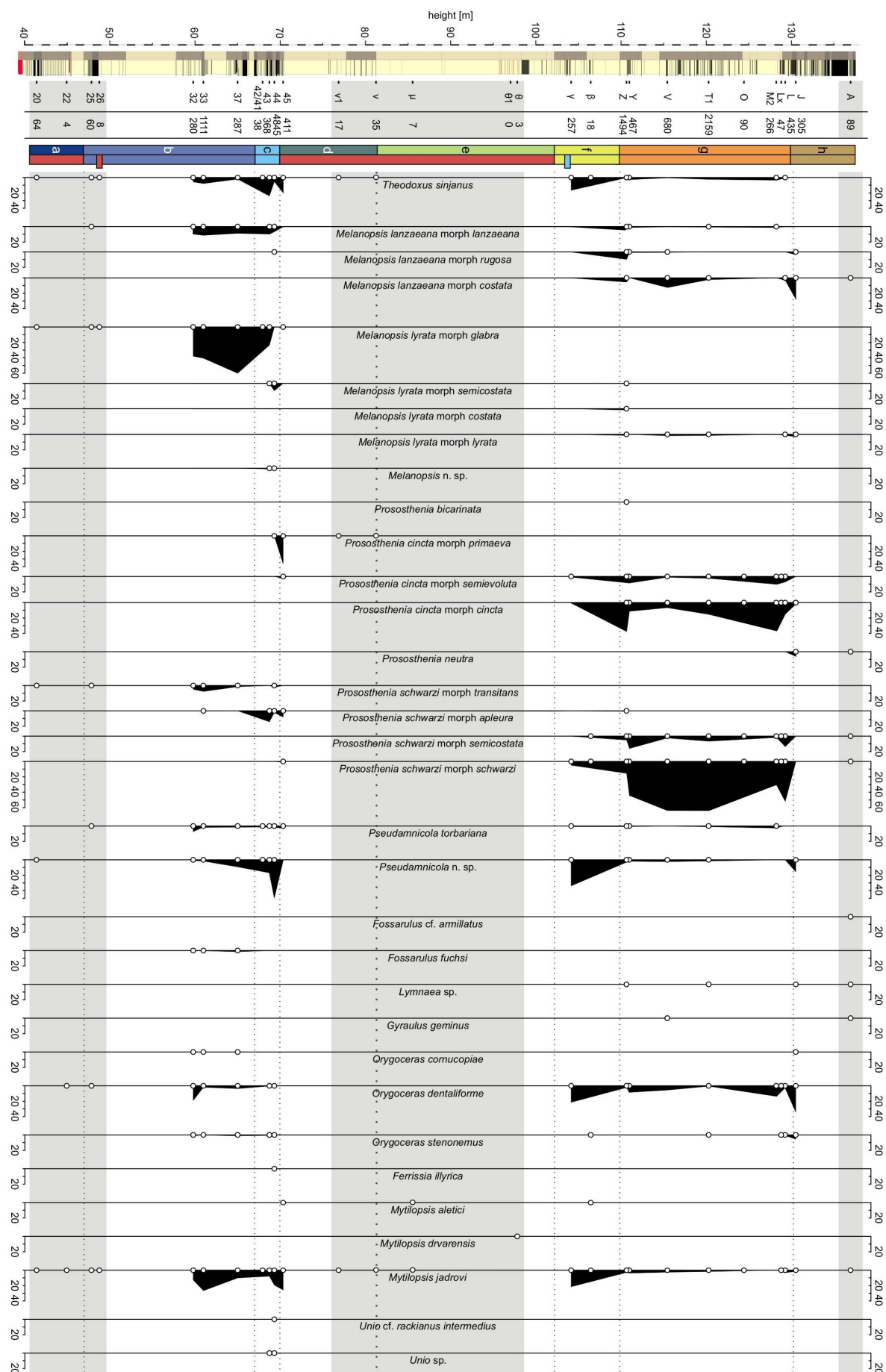
4.3. Statistical analysis – quantitative data

The lowermost section part (40-60 m; fig. 6) is defined by samples with poorly preserved fossils. The most abundant species are *Mytilopsis jadrovi* and *Theodoxus sinjanus*. Smooth morphotypes of *Melanopsis lyrata* prevail within the next 10 m along with smooth *Melanopsis lanzaeana* and *Prososthenia schwarzi*. At the end of this interval a morphologic shift is observed, resulting in half-ribbed and few ribbed morphs of *Melanopsis* and *Prososthenia*. Additionally, the new lineage of *Prososthenia cincta* appears and the very common *Pseudamnicola* n. sp. comes up with high abundances.

The next interval (70-100 m; fig. 6) is marked by fossil-poor samples. *Prososthenia* is common, followed by scattered shells of *Mytilopsis* and *Theodoxus* (Tab. 2). The shells of both species possibly are not that prone to fragmentation and therefore might be overrepresented.

Above, a faunal change occurs: *Mytilopsis*, *Theodoxus* and *Pseudamnicola* n. sp. retreat and are replaced by ribbed melanopsids and prosostheniids, accompanied by *Orygoceras*. The uppermost interval is characterized by the complete collapse of the melanopsid and prosostheniid assemblages and contains mainly pulmonates.

Bivalves are rare aside from the common bivalve *Mytilopsis jadrovi*. Hence, the section is predominated by gastropods, in number of species and individuals. This trend was also noted by MANDIC et al. (2009), who stated that gastropods prevail within coal layers, while bivalves are more abundant in massive limestones. Most of the latter species (e.g. *Mytilopsis aletici*) are poorly preserved and cannot be extracted from the limestones. Therefore, no quantitative data can be provided.



4.3.1. Diversity indices

Diversity patterns show a characteristic bimodal distribution with maxima around 60-70 m and 100-110 m (Fig. 7). An additional peak occurs at the topmost part (sample J, at 130 m). An extreme diversity minimum is recorded at 80-100 m.

The lowermost part shows a peak at sample 25, which marks the initial occurrence of *Melanopsis lanzaeana* and *Pseudamnicola torbariana*. The following bell-shaped curve with maxima at samples 32 and 43 denotes the most diverse section part including the first appearance of *Fossarulus*

Sample	Species	n	Richness	Shannon	Simpson
A	6	84	1.128	1.519	0.758
J	9	304	1.399	1.622	0.753
L	8	152	1.393	1.054	0.517
Lx	5	17	1.412	1.197	0.662
M2	6	116	1.052	1.243	0.658
O	3	63	0.483	0.728	0.459
T1	10	1212	1.268	1.018	0.467
V	9	412	1.329	1.191	0.535
Y	8	106	1.501	1.253	0.592
Z	10	955	1.312	1.490	0.702
β	4	12	1.207	0.983	0.561
γ	7	121	1.251	1.553	0.769
θ	0	0	***	0.000	***
θ1	0	0	***	0.000	***
μ	1	6	0.000	0.000	0.000
v	3	13	0.780	1.010	0.654
v1	3	9	0.910	0.937	0.639
45	7	86	1.347	1.554	0.763
44	12	4121	1.322	1.557	0.694
43	10	295	1.583	1.845	0.823
42/41	6	34	1.418	1.332	0.699
37	11	249	1.812	1.438	0.611
33	11	960	1.456	1.609	0.739
32	11	245	1.818	1.809	0.786
26	3	8	0.962	0.736	0.464
25	7	53	1.511	1.365	0.647
22	2	4	0.721	0.562	0.500
20	5	58	0.985	1.364	0.723

Tab. 4. Diversity indices.

fuchsi and sculptured *Orygoceras* species, *O. stenonemus* and *O. cornucopiae*.

Subsequently, a tremendous decrease in mollusk diversity is observed, lasting from about 80-100 m. Upsection, the second bell-shaped curve has its maximum at samples γ and Z. Within sample Z the only occurrence of *Prososthenia bicarinata* is reported.

The last peak at the section top suggests a faunal change, resulting in high frequencies of new elements such as *Prososthenia neutra*, *Gyraulus geminus* and *Fossarulus* cf. *armillatus*.

◀ Fig. 6. Abundance values (black graphs) connected with presence/absence data (circles) of all taxa. For the percentage values just samples with >100 individuals were plotted, so there is no data in certain intervals (gray bars). The colored bar to the left is split into two parts, regarding first the environmental intervals discussed in 4.4. (see also tab. 7) and second the grouping due to the analysis (see also fig. 8). The columns next to it mark sample positions and total individual number.

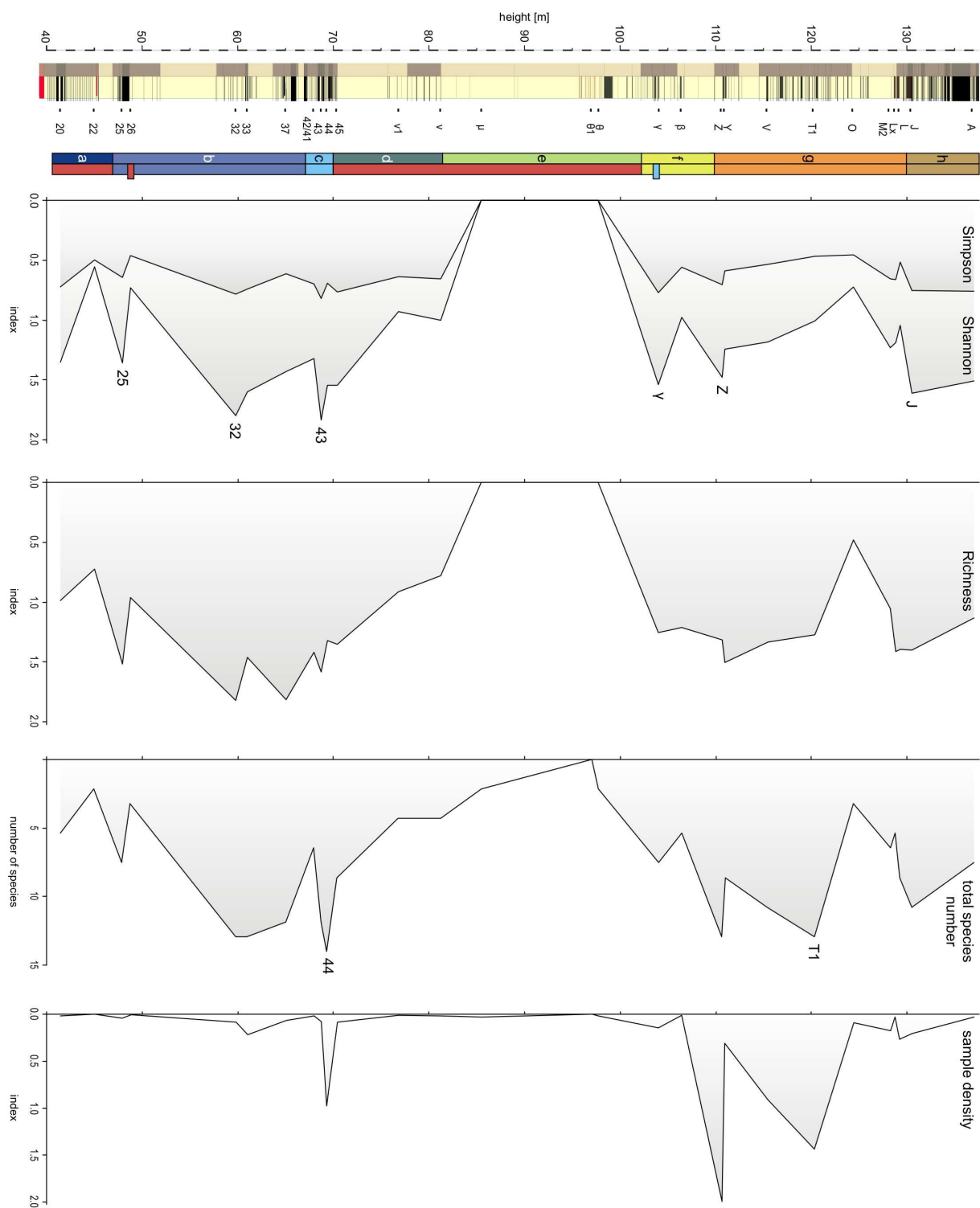


Fig. 7. Diversity indices including Shannon-Wiener-Index, Simpson Index and Richness. Additionally, total species number and sample density have been plotted for easy comparison. The numbers/letters next to the graphs refer to samples marking eye-catching peaks.

4.3.2. Statistical analysis

The statistical treatment of quantitative data was carried out, comprising a cluster analysis (Fig. 8a, b), an nMDS (Fig. 8c, d) and a SIMPER analysis (Tab. 5, 6), to reveal major similarity groups within the section and their substantial contributors. The analysis is divided into two runs, including in the first one all samples and in the second one just a reduced data set excluding small samples (<100 individuals), limiting the significance of overrepresented taxa.

4.3.2.1. First run

The cluster analysis arranged the samples in three main groups, apart from some outliers at about 40% of the Bray-Curtis similarity (Fig. 8a, c). The delimitation of the single clusters was very precise, so that the SIMPROF check (red lines) did not detect subclusters. For each group a factor used in a factor analysis was defined (SIMPER, Tab. 5) to reveal the contributions of the single species to the similarities, alternatively dissimilarities. Only the three main clusters were included; outliers were treated separately.

Cluster 1: includes samples 25, 32, 33, 37, 42/41, 43, 44 and γ ; comprising the lower section part with *Mytilopsis jadrovi*, *Theodoxus sinjanus*, the smooth morphotype of *Melanopsis lyrata* and *Pseudamnicola* n. sp. as typical elements.

Cluster 2: includes samples 20, 22, 26, 45, v1, v and μ ; set up by small sized samples from lower and middle section part; grouping due to preservation. Most abundant species are *Mytilopsis jadrovi* and *Theodoxus sinjanus*.

Cluster 3: includes samples Z, Y, V, T1, O, M2, Lx and L; uniform cluster of the upper section part with half-ribbed and ribbed morphotypes of melanopsids and especially prosostheniids as dominating species.

Outliers: β , J and A.

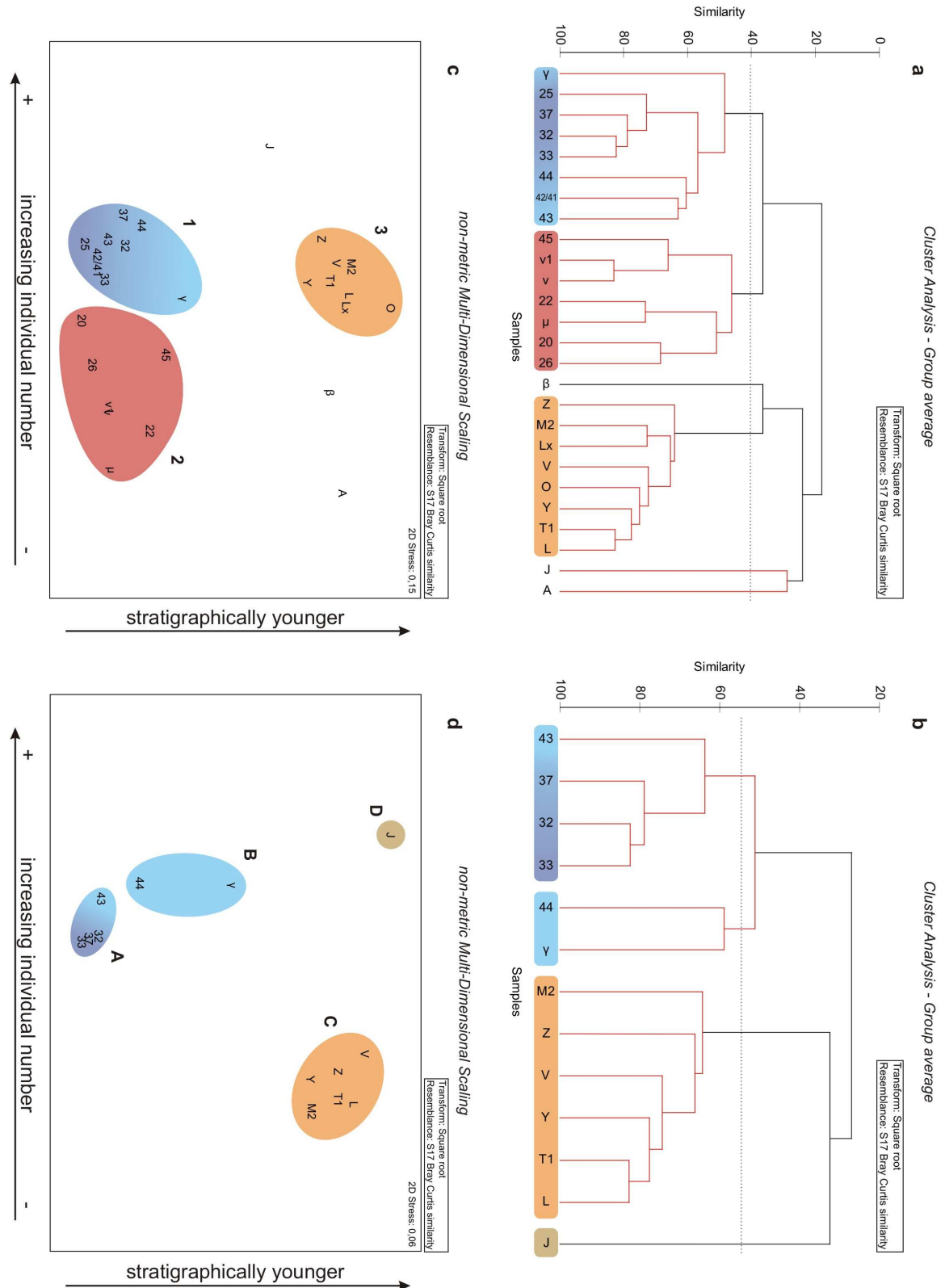


Fig. 8. Statistical analysis. a) Cluster analysis, including all samples; b) Cluster analysis, excluding samples of small size (<100 individuals); c) non-metric Multi-Dimensional Scaling, including all samples; d) non-metric Multi-Dimensional Scaling, excluding samples of small size (<100 individuals). The colors of the cluster analysis and the nMDS are corresponding and resemble the different section intervals defined below (Tab. 7).

In fact, these three groups are very consistent, each one more or less representing a certain part of the section. The most important pattern, especially noted within the SIMPER analysis provides the comparison between clusters 1 and 3. As noted above, cluster 2 is defined by poorly preserved small-sized samples and it will not be interpreted.

Clusters 1 and 3 reflect the two different faunas below and above the fossil-poor limestone interval. Cluster 1 is defined by seven species accounting 92.38%, comprising all the smooth morphs of *Melanopsis*, and cluster 3 by six species coming up with 90.00% of average similarity, including the half-ribbed and ribbed morphotypes of *Prososthenia* (Tab. 5).

Their disparity is reflected by an average dissimilarity between both of 77.49%. This approves the clear separation of the section into the two limestone-coal cycles proposed by MANDIC et al. (2009), indicated also by the nMDS, where both clusters are clearly isolated. Due to this grouping the x-axis is suggested to display the varying amount of species or individuals, respectively, per sample, whereas the largest samples arrange to the right. The y-axis is supposed to reflect the timescale and the evolutionary changes, becoming upwards stratigraphically younger. The two main clusters (1, 3) arrange clearly due to their morphologic disparity.

The grouping of sample γ is noteworthy. It assort somewhat apart in the cluster analysis and the nMDS. This reflects slight differences in the faunal composition, especially the higher abundance of (half-)ribbed morphs. Within the section, sample γ is separated from other samples of this cluster by 35 m of mainly massive limestones.

The most apparent outliers are the samples A and J. Although they group together in the cluster analysis the average similarity ranges only around 30%. The composition of the samples varies as well. Sample J represents a transitional fauna, which comprises elements of the preceding (characterized by strongly sculptured melanopsids and prosostheniids) and the upcoming interval (appearance of new taxa) displayed in sample A. This indicates a stepwise change in environment.

The small sized sample β clusters aside as well. Due to its limited fossil content the percentage values might be too high in some cases. Nevertheless, in the nMDS-plot it appears near the upper cluster. Within the section, sample β lies just 3 m below sample Z and contains several elements that are typical for this cluster (e.g. ribbed morphotypes of *Prososthenia*). The average similarity between both ranges only around 35%. Again, this sample might

represent a transition, starting already with sample γ , which also bears some few ribbed forms of *Prososthenia*.

SIMPER Analysis - first run

Cluster 1 (25, 32, 33, 37, 42/41, 43, 44, γ)						Clusters 2 & 1							
Average similarity: 59.35						Average dissimilarity = 63.67							
	Avg. Ab.	Av. Sim	Sim/SD	Contrib. %	Cum. %	Cl. 2 Avg. Ab.	Cl. 1 Avg. Ab.	Av. Diss	Diss/SD	Contrib. %	Cum. %		
Mytilopsis jadrovi	3.83	12.85	3.89	21.65	21.65	0.91	4.69	10.24	1.54	16.08	16.08		
Melanopsis lyrata m. glabra	4.69	11.72	1.03	19.74	41.39	7.40	3.83	8.97	1.64	14.08	30.16		
Theodoxus sinjanus	2.94	8.74	2.78	14.73	56.12	0.40	3.64	8.43	1.30	13.24	43.40		
Pseudamnicola n. sp.	3.64	7.83	0.95	13.19	69.31	3.39	2.94	5.71	1.46	8.96	52.36		
Pseudamnicola torbariana	1.70	5.04	3.36	8.49	77.80	0.95	1.96	4.86	1.19	7.64	60.00		
Melanopsis lanzaeana m. lanzaeana	2.03	4.71	0.98	7.93	85.73	0.00	2.03	4.73	1.54	7.43	67.42		
Orygoceras dentaliforme	1.96	3.95	1.09	6.65	92.38	2.03	0.04	4.53	0.85	7.12	74.54		
						0.81	1.35	4.15	1.13	6.51	81.05		
						0.23	1.70	3.78	1.79	5.94	86.99		
						0.41	0.72	2.12	0.70	3.33	90.32		

Cluster 2 (20, 22, 26, 45, v1, v, μ)						Clusters 2 & 3							
Average similarity: 53.02						Average dissimilarity = 85.14							
	Avg. Ab.	Av. Sim	Sim/SD	Contrib. %	Cum. %	Cl. 2 Avg. Ab.	Cl. 3 Avg. Ab.	Av. Diss	Diss/SD	Contrib. %	Cum. %		
Mytilopsis jadrovi	7.40	39.35	2.77	74.21	74.21	7.40	1.59	14.28	2.43	16.77	34.86		
Theodoxus sinjanus	3.39	9.71	0.91	18.32	92.53	0.00	4.58	10.91	3.28	12.81	47.67		
						3.39	0.89	6.99	1.48	8.21	55.88		
						0.00	2.50	5.94	2.78	6.98	62.86		
						0.23	2.62	5.84	2.15	6.86	69.72		
						0.95	1.91	4.69	1.45	5.50	75.22		
						2.03	0.00	4.48	0.83	5.26	80.48		
						0.00	1.15	2.64	0.88	3.10	83.58		
						0.40	0.74	2.11	1.04	2.47	86.05		
						0.91	0.00	2.10	0.61	2.46	88.52		
						0.81	0.00	1.74	0.40	2.04	90.56		

Cluster 3 (Z, Y, V, T1, O, M2, Lx, L)						Clusters 1 & 3							
Average similarity: 68.75						Average dissimilarity = 77.49							
	Avg. Ab.	Av. Sim	Sim/SD	Contrib. %	Cum. %	Cl. 1 Avg. Ab.	Cl. 3 Avg. Ab.	Av. Diss	Diss/SD	Contrib. %	Cum. %		
Prososthenia schwarzi m. schwarzi	6.51	22.20	3.25	32.29	32.29	0.28	6.51	12.43	3.31	16.04	16.04		
Prososthenia cincta m. cincta	4.58	14.76	3.50	21.47	53.76	4.69	0.00	9.29	1.59	11.98	28.03		
Prososthenia cincta m. semievoluta	2.62	8.02	2.56	11.66	65.42	0.00	4.58	9.04	3.52	11.66	39.69		
Prososthenia schwarzi m. semicostata	2.50	7.62	3.42	11.09	76.50	3.64	0.74	6.38	1.28	8.24	47.92		
Mytilopsis jadrovi	1.59	4.75	1.63	6.91	83.41	0.11	2.62	4.95	2.52	6.38	54.30		
Orygoceras dentaliforme	1.91	4.53	1.28	6.59	90.00	0.00	2.50	4.93	2.89	6.36	60.66		
						3.83	1.59	4.46	1.88	5.75	66.41		
						2.94	0.89	4.12	1.55	5.32	71.73		
						2.03	0.57	3.46	1.59	4.46	76.19		
						1.96	1.91	3.16	1.35	4.08	80.27		
						1.35	0.00	2.66	1.11	3.43	83.70		
						1.70	0.57	2.41	1.34	3.11	86.81		
						0.00	1.15	2.20	0.89	2.84	89.65		
						0.71	0.44	1.57	1.21	2.03	91.68		

Tab. 5. SIMPER analysis of first run with Bray-Curtis Similarities/Dissimilarities. The abbreviation “m.” means “morph”.

4.3.2.2. Second run

For the second run (Fig. 8b, d) all samples with less than 100 individuals were excluded to check the significance of the first run's grouping. At ca. 55% of the Bray-Curtis Similarity the clusters arrange as follows:

Cluster A: includes samples 32, 33, 37 and 43; lower part of the section, marked especially by smooth melanopsids, *Mytilopsis jadrovi* and *Theodoxus sinjanus*.

Cluster B: includes samples 44 and γ ; transition during transgression interval, with *Pseudamnicola* n. sp. and again *Mytilopsis* and *Theodoxus* as characteristic taxa.

Cluster C: includes samples Z, Y, V, T1, M2 and L; upper part of the section, again uniform cluster with half-ribbed and ribbed prosostheniids dominating.

Cluster D: includes sample J; uppermost part of section, treated as own cluster to reveal differences to Cluster C; ribbed melanopsids and *Orygoceras dentaliforme* prevail.

As in the first run, Cluster C, with eight species accounting 90.31% of average similarity, remained consistent and sample J is an outlier again, but clusters A and B split (Tab. 6). Whereas smooth melanopsids still dominate in cluster A, half-ribbed morphs gain more importance in cluster B. In addition *Pseudamnicola* n. sp. becomes a common element. Although the samples of Cluster B, 44 and γ , are isolated from each other by ca. 35 m, their grouping with 60% of average similarity is convincing. While Cluster A is defined by eight species making up 93.81% average similarity, B comprises just four species accounting almost the same value, namely 93.87%.

The strong delimitation between the lower and the upper part of the section is still clearly developed and expressed by average dissimilarities between clusters A and C with 75.80% and B and C with 68.20%, respectively (Tab. 6).

Hence, the second run displays an affirmation of the first one and, in some cases, states the results even more precisely.

SIMPER Analysis - second run

Cluster A (32, 33, 37, 43)						Cluster C (Z, Y, V, T1, M2, L)					
Average similarity: 71.82	Avg. Ab.	Av.Sim	Sim/SD	Contrib. %	Cum. %	Average similarity: 69.76	Avg. Ab.	Av.Sim	Sim/SD	Contrib. %	Cum. %
Melanopsis lyrata m. glabra	6.29	20.75	6.68	28.88	28.88	Prososthenia schwarzi m. schwarzi	6.55	21.14	3.35	30.31	30.31
Mytilopsis jadrovi	3.67	11.37	9.05	15.83	44.71	Prososthenia cincta m. cincta	4.33	12.82	3.99	18.38	48.69
Melanopsis lanzaeana m. lanzaeana	3.09	11.14	43.40	15.51	60.22	Prososthenia schwarzi m. semicostata	2.57	7.02	2.77	10.07	58.75
Theodoxus sinjanus	2.88	7.34	3.24	10.22	70.45	Prososthenia cincta m. semievoluta	2.38	6.88	2.36	9.86	68.61
Pseudamnicola n. sp.	2.34	5.19	1.66	7.23	77.68	Orygoceras dentaliforme	2.15	5.57	2.12	7.99	76.61
Pseudamnicola torbariana	1.64	4.63	11.65	6.44	84.12	Mytilopsis jadrovi	1.41	3.78	1.34	5.42	82.03
Orygoceras dentaliforme	2.06	3.99	1.87	5.55	89.67	Theodoxus sinjanus	1.19	3.22	2.01	4.62	86.65
Prososthenia schwarzi m. transitans	1.56	2.98	0.85	4.14	93.81	Melanopsis lanzaeana m. costata	1.54	2.55	0.78	3.66	90.31

Cluster B (44, y)					
Average similarity: 58.78	Avg. Ab.	Av.Sim	Sim/SD	Contrib. %	Cum. %
Pseudamnicola n. sp.	6.44	23.06	###	39.22	39.22
Mytilopsis jadrovi	4.52	17.42	###	29.63	68.86
Theodoxus sinjanus	3.19	9.15	###	15.57	84.43
Orygoceras dentaliforme	3.02	5.55	###	9.45	93.87

Clusters A & B							Clusters B & C						
Average dissimilarity = 48.89	Cl. A Avg. Ab.	Cl. B Avg. Ab.	Av.Diss	Diss/SD	Contrib. %	Cum. %	Average dissimilarity = 68.20	Cl. B Avg. Ab.	Cl. C Avg. Ab.	Av.Diss	Diss/SD	Contrib. %	Cum. %
Melanopsis lyrata m. glabra	6.29	0.00	12.14	5.14	24.83	24.83	Pseudamnicola n. sp.	6.44	0.99	10.49	5.14	15.38	15.38
Pseudamnicola n. sp.	2.34	6.44	7.86	2.77	16.07	40.89	Prososthenia schwarzi m. schwarzi	1.11	6.55	10.48	2.86	15.36	30.74
Melanopsis lanzaeana m. lanzaeana	3.09	1.26	3.63	1.32	7.42	48.31	Prososthenia cincta m. cincta	0.00	4.33	8.28	3.21	12.14	42.88
Orygoceras dentaliforme	2.06	3.02	3.57	1.14	7.31	55.62	Mytilopsis jadrovi	4.52	1.41	6.01	3.67	8.82	51.70
Melanopsis lyrata m. semicostata	0.15	1.55	2.88	1.02	5.89	61.51	Prososthenia schwarzi m. semicostata	0.00	2.57	4.93	2.43	7.23	58.93
Theodoxus sinjanus	2.88	3.19	2.55	1.39	5.21	66.72	Theodoxus sinjanus	3.19	1.19	3.88	1.81	5.69	64.62
Prososthenia schwarzi m. apleura	1.06	0.75	2.50	1.02	5.11	71.83	Prososthenia cincta m. semievoluta	0.45	2.38	3.64	2.03	5.34	69.95
Prososthenia schwarzi m. transitans	1.56	0.76	2.42	1.28	4.95	76.78	Orygoceras dentaliforme	3.02	2.15	3.38	1.39	4.95	74.90
Mytilopsis jadrovi	3.67	4.52	2.25	2.54	4.60	81.38	Melanopsis lanzaeana m. costata	0.00	1.54	2.93	1.15	4.30	79.20
Prososthenia schwarzi m. schwarzi	0.00	1.11	2.23	0.94	4.55	85.94	Melanopsis lyrata m. semicostata	1.55	0.05	2.87	0.98	4.21	83.41
Orygoceras stenonemus	0.87	0.26	1.22	1.64	2.50	88.44	Melanopsis lanzaeana m. lanzaeana	1.26	0.75	2.38	1.42	3.49	86.90
Pseudamnicola torbariana	1.64	1.13	1.11	0.89	2.26	90.71	Melanopsis lyrata m. lyrata	0.00	0.80	1.53	1.34	2.24	89.14
							Melanopsis lanzaeana m. rugosa	0.36	0.80	1.46	0.84	2.13	91.28

Clusters A & C							Clusters B & D						
Average dissimilarity = 75.80	Cl. A Avg. Ab.	Cl. C Avg. Ab.	Av.Diss	Diss/SD	Contrib. %	Cum. %	Average dissimilarity = 65.81	Cl. B Avg. Ab.	Cl. D Avg. Ab.	Av.Diss	Diss/SD	Contrib. %	Cum. %
Prososthenia schwarzi m. schwarzi	0.00	6.55	12.32	3.95	16.25	16.25	Melanopsis lanzaeana m. costata	0.00	5.29	10.17	18.02	15.46	15.46
Melanopsis lyrata m. glabra	6.29	0.00	11.76	5.29	15.52	31.77	Mytilopsis jadrovi	4.52	1.28	6.23	9.32	9.47	24.93
Prososthenia cincta m. cincta	0.00	4.33	8.03	3.30	10.59	42.36	Theodoxus sinjanus	3.19	0.00	6.20	2.27	9.42	34.35
Prososthenia schwarzi m. semicostata	0.00	2.57	4.78	2.49	6.31	48.66	Orygoceras dentaliforme	3.02	5.85	5.32	1.30	8.09	42.43
Melanopsis lanzaeana m. lanzaeana	3.09	0.75	4.42	2.98	5.83	54.50	Prososthenia neutra	0.00	2.50	4.81	18.02	7.31	49.74
Prososthenia cincta m. semievoluta	0.00	2.38	4.41	2.88	5.82	60.31	Pseudamnicola n. sp.	6.44	3.93	4.78	3.36	7.27	57.01
Mytilopsis jadrovi	3.67	1.41	4.26	1.87	5.61	65.93	Orygoceras stenonemus	0.26	2.36	4.07	4.39	6.19	63.20
Theodoxus sinjanus	2.88	1.19	3.24	1.36	4.27	70.20	Melanopsis lyrata m. lyrata	0.00	1.72	3.31	18.02	5.03	68.23
Pseudamnicola n. sp.	2.34	0.99	3.02	1.29	3.99	74.19	Melanopsis lanzaeana m. rugosa	0.36	1.90	3.00	2.64	4.56	72.79
Prososthenia schwarzi m. transitans	1.56	0.00	2.92	1.45	3.85	78.04	Melanopsis lyrata m. semicostata	1.55	0.00	2.87	0.71	4.36	77.15
Melanopsis lanzaeana m. costata	0.00	1.54	2.84	1.18	3.75	81.79	Prososthenia cincta m. cincta	0.00	1.40	2.70	18.02	4.11	81.25
Orygoceras dentaliforme	2.06	2.15	2.63	1.38	3.46	85.25	Melanopsis lanzaeana m. lanzaeana	1.26	0.00	2.33	0.71	3.53	84.79
Prososthenia schwarzi m. apleura	1.06	0.14	2.00	0.71	2.64	87.90	Prososthenia schwarzi m. schwarzi	1.11	0.00	2.23	0.71	3.38	88.17
Pseudamnicola torbariana	1.64	0.76	1.78	1.23	2.35	90.25	Pseudamnicola torbariana	1.13	0.00	2.16	4.51	3.28	91.45

Clusters A & D							Clusters C & D						
Average dissimilarity = 74.40	Cl. A Avg. Ab.	Cl. D Avg. Ab.	Av.Diss	Diss/SD	Contrib. %	Cum. %	Average dissimilarity = 67.69	Cl. C Avg. Ab.	Cl. D Avg. Ab.	Av.Diss	Diss/SD	Contrib. %	Cum. %
Melanopsis lyrata m. glabra	6.29	0.00	11.76	4.89	15.81	15.81	Prososthenia schwarzi m. schwarzi	6.55	0.00	12.31	3.69	18.19	18.19
Melanopsis lanzaeana m. costata	0.00	5.29	9.86	49.99	13.26	29.07	Melanopsis lanzaeana m. costata	1.54	5.29	7.02	2.60	10.37	28.56
Orygoceras dentaliforme	2.06	5.85	7.08	2.32	9.52	38.59	Orygoceras dentaliforme	2.15	5.85	6.87	3.51	10.15	38.71
Melanopsis lanzaeana m. lanzaeana	3.09	0.00	5.77	16.60	7.75	46.34	Pseudamnicola n. sp.	0.99	3.93	5.53	3.27	8.16	46.87
Theodoxus sinjanus	2.88	0.00	5.35	2.01	7.19	53.53	Prososthenia cincta m. cincta	4.33	1.40	5.40	2.05	7.98	54.85
Prososthenia neutra	0.00	2.50	4.66	49.99	6.27	59.80	Prososthenia schwarzi m. semicostata	2.57	0.00	4.78	2.33	7.06	61.91
Mytilopsis jadrovi	3.67	1.28	4.47	2.23	6.00	65.81	Prososthenia neutra	0.00	2.50	4.66	17.35	6.89	68.80
Melanopsis lanzaeana m. rugosa	0.00	1.90	3.55	49.99	4.77	70.57	Prososthenia cincta m. semievoluta	2.38	0.00	4.41	2.69	6.51	75.31
Melanopsis lyrata m. lyrata	0.00	1.72	3.21	49.99	4.31	74.89	Orygoceras stenonemus	0.18	2.36	4.06	6.69	6.00	81.31
Pseudamnicola n. sp.	2.34	3.93	3.15	1.24	4.23	79.12	Melanopsis lanzaeana m. rugosa	0.80	1.90	2.84	3.09	4.20	85.51
Pseudamnicola torbariana	1.64	0.00	3.04	2.34	4.09	83.21	Theodoxus sinjanus	1.19	0.00	2.25	2.02	3.32	88.83
Prososthenia schwarzi m. transitans	1.56	0.00	2.92	1.29	3.93	87.13	Melanopsis lyrata m. lyrata	0.80	1.72	1.73	1.44	2.55	91.38
Orygoceras stenonemus	0.87	2.36	2.79	4.71	3.75	90.88							

Tab. 6. SIMPER analysis of second run with Bray-Curtis Similarities/Dissimilarities. The abbreviation “m.” means “morph”.

Section intervals		most common taxa	Samples	Remarks	Environmental interpretations		current investigation
					lake ecology ¹	climate ²	
Second cycle							
h	Ready for shore (130.0 - 137.5 m)	<i>Melanopsis</i> ssp., <i>Pulmonata</i>	J, A	strong retreat of <i>Prososthenia</i>	shallowing, developing peat bog, up to complete desiccation	no data	shallowing, low-energy conditions, up to complete desiccation
g	A new reign (110.0 - 130.0 m)	<i>Prososthenia</i> ssp., <i>Orygoceras dentaliforme</i>	Z, Y, V, T1, V, O, M2, Lx, L	<i>Prososthenia</i> dominating, melanopsids stay to background	fluctuating conditions	generally warmer interval with intermediate cool subperiod	continuously shallowing, low- energy regime
f	A new dawn (102.0 - 110.0 m)	<i>Prososthenia</i> ssp., <i>Pseudamnicola</i> n. sp., <i>Orygoceras dentaliforme</i> , <i>Theodoxus sinjanus</i> , <i>Mytilopsis jadrovi</i>	Y, β	half-ribbed and ribbed morphotypes of <i>Prososthenia</i> start to emerge, no melanopsids	shallowing environment	enduring cooler period	shallow, low-energy setting without freshwater supply
e	Intermission (81.5 - 102.0 m)	<i>Mytilopsis aletici</i>	μ , θ 1, θ	poor fossil content, bad preservation	long-term transgression with short intermediate regressions	long-term cooler period	deeper water, low-energy conditions
First cycle							
d	The collapse (70.0 - 81.5 m)	<i>Mytilopsis aletici</i>	45, v1, v	poor fossil content, bad preservation	deeper water, low-energy environment	dry conditions	deeper water setting
c	(R)evolution (66.5 - 70.0 m)	<i>Melanopsis</i> spp., <i>Prososthenia</i> spp., <i>Pseudamnicola</i> n. sp., <i>Mytilopsis jadrovi</i>	42/41, 43, 44	great morphologic shift, development of half-ribbed and few ribbed morphotypes of <i>Melanopsis</i> and <i>Prososthenia</i>	marginal lake setting	climate becoming again warmer	shallow, low-energy regime, freshwater supply
b	The rise (45.5 - 66.5 m)	<i>Melanopsis</i> spp., <i>Mytilopsis jadrovi</i>	25, 26, 32, 33, 37	rise of melanopsids	from open lake to shallower conditions (coal seams)	generally cooler period	fluctuating water depth, shallow marginal conditions, intermediate water energy
a	A small start (40.0 - 45.5 m)	<i>Theodoxus sinjanus</i> , <i>Mytilopsis jadrovi</i>	20, 22	poor fossil content	shallow habitats near lake margins	arid conditions	nearshore environment with continuous freshwater input, intermediate water energy

Tab. 7. Section interval overview including paleoenvironmental interpretations of previous (¹MANDIC et al., 2009; ²JIMÉNEZ-MORENO et al., 2008) and current works. For reasons of correlation the arrangement follows the stratigraphic order.

4.4. The environmental history – paleoecology

Based on the statistical analysis, section intervals are defined (Tab. 7) for paleoenvironmental interpretation. In some cases the delimitations are not strictly defined but represent rather transitions.

This chapter integrates also previously published data on sedimentary facies (MANDIC et al., 2009) and palynology (JIMÉNEZ-MORENO et al., 2008).

4.4.1. First cycle – small and smooth

4.4.1.1. A small start – *Mytilopsis-Theodoxus*-assemblage (40-45.5 m)

The section base cannot be properly evaluated due to limited sample sizes resulting from bad fossil preservation. Consequently, the analysis unites these samples into clusters characterized by small sample size. Those bottommost samples are dominated by *Theodoxus sinjanus*, *Mytilopsis jadrovi* and *Prososthenia schwarzi*. High abundance values may also result from selective preservation of the thick-shelled *Theodoxus* and *Mytilopsis*. *Prososthenia* appears only with small smooth morphs.

The pollen record with high percentage values of thermophilous and xeric plants indicates rather arid conditions (JIMÉNEZ-MORENO et al., 2008). The lithological interpretation suggests shallow habitats near the lake margins (MANDIC et al., 2009). This is approved by the appearance of *Prososthenia*; as a hydrobiid it prefers marginal muddy settings. Furthermore, the co-occurrence of both *Theodoxus* and *Mytilopsis* implies a nearshore environment with continuous freshwater input under at least intermediate water energy.

4.4.1.2. The rise – *Melanopsis-Mytilopsis*-assemblage (45.5-66.5 m)

In sample 25, taken at 48 m, especially *Prososthenia* and *Theodoxus* decline and are replaced by smooth morphotypes of *Melanopsis lyrata* and *Pseudamnicola torbariana*. Sample 25 joins Cluster 1, arranging especially with samples 32, 33 and 37. This might hint towards a gradual shift of environmental conditions.

Above the coal (sample 26), a tremendous decrease of fossil content is noticed and the formation of limestone with few coal seams starts. This phase coincides with a decrease of

warm elements in the pollen spectra, indicating a cooler subperiod (Luc 2a in JIMÉNEZ-MORENO et al., 2008) with open lake conditions (MANDIC et al., 2009).

After this interval a notable peak in mollusk evolution is recorded. This coincides with the return to more arid conditions (MANDIC et al., 2009), documented in sample 32 at 60 m. Particularly the melanopsids start to flourish, whereas the hydrobiids (*Prososthenia*, *Pseudamnicola*) decline slightly. Nevertheless, a first change in morphology appears in *Prososthenia schwarzi* with first occurrence of the *apleura*-morph. *Orygoceras dentaliforme* also increases in number and the arrival of new species such as *Fossarulus fuchsi*, *Lymnaea* sp. and *Pseudamnicola* n. sp. is documented. *Theodoxus* becomes less important. This tendency maintains over the next samples (33, 37). Within this section part *Melanopsis lyrata* is the dominant species, accompanied by *Melanopsis lanzaeana* and *Mytilopsis jadrovi*.

The similarity of the three samples (32, 33 and 37) is also supported by the Cluster analysis. Especially the decline of *Theodoxus* and the appearance of *Lymnaea* are important: the faunal composition indicates a shallow, possibly highly vegetated nearshore environment. Hence, the mollusk record approves previous interpretations of the coal-bearing beds as shallowing environments (MANDIC et al., 2009).

4.4.1.3. (R)evolution (66.5-70.5 m)

Almost at the uppermost part of the first limestone-coal cycle reflected by the accumulation of many thick coal seams, new lineages start to evolve and diversify. This results in an evolutionary heyday in samples 43 and especially 44 at 69.5 m with a total diversity of 13 mollusk species. Moreover, the first great disparity of morphotypes in *Melanopsis* and *Prososthenia* is documented.

Within sample 44 *Pseudamnicola* n. sp. is highly abundant and contributes to ca. 50% of the total individual number. Its abundance may be a result of its high preservation potential due to its small size (ca. 2-3 mm) or because hydrobiids may form mass occurrences.

The ancyliid gastropod *Ferrissia illyrica*, although recorded with just one individual, signals rather lentic or slowly running water. Less energetic water conditions are also indicated by the retreat of *Theodoxus*. Additional information comes from pollen data: in this interval a strong increase of thermophilous plants is observed, even stronger as in preceding intervals. This is interpreted as a marginal lake environment with dry conditions (JIMÉNEZ-MORENO et al., 2008; MANDIC et al., 2009).

However, *Mytilopsis* contributes to nearly 20% of the fauna excluding fully stagnant bottom conditions. This is also indicated by the rare shells of *Unio*. Fluvial input might have been limited to occasional events which allowed also *Melanopsis* n. sp. to settle the lake. This elegant, high conical melanopsid is only recorded from samples 43 and 44 by not more than 10 individuals that display a high variety in shell size.

This interval, which is characterized by the accumulation of many coal seams, reflects a shallowing, low-energy environment with at least temporal fluvial input.

4.4.1.4. The collapse – Mytilopsis aletici-beds (70.5-81.5 m)

One meter above (sample 45) the shells are poorly preserved, but again the development of new half-ribbed and ribbed morphs is documented. Freshwater elements like *Unio* completely disappear. This change also becomes clear in connection with the cluster analysis: sample 45 either joins the “small sample group” or remains isolated. This replacement of certain morphotypes was most probably triggered by changes of the environmental conditions.

Within the next 10 m of mainly massive limestones, the samples (v1 and v) yield few and poorly preserved mollusks. The limestones are interpreted as deeper water deposits (MANDIC et al., 2009). This is supported by the occurrence of coquinas consisting of monospecific accumulations of *Mytilopsis aletici* which is considered to have preferred sublittoral, low-energy settings (MANDIC et al., 2009). In-situ conditions are indicated by many specimens with articulated valves which are oriented parallel to the bedding plane.

With the very beginning of this interval the pollen record suggests a rather warm climate with high abundances of thermophilous plants and few conifers (JIMÉNEZ-MORENO et al., 2008).

4.4.2. Second cycle – large and ribbed

4.4.2.1. Intermission (81.5-102 m)

At 81 m starts an interval of about 20 m of fossil-poor, massive limestones, containing mainly *Mytilopsis aletici*. After MANDIC et al. (2009) this is the beginning of the second limestone-coal cycle. The long series of pure limestones are again interpreted as transgression. Short intermediate zones with limestone-coal interbeddings are interpreted as short-term regressions, which become more common and extensive upwards. Furthermore, the interval from 81.5-110 m is interpreted as a slightly cooler period based on the high percentage of

conifers (JIMÉNEZ-MORENO et al., 2008). Within the interval from 81.5 to 102 m the studied samples (μ , $\vartheta 1$ and ϑ) show just few and mostly poorly preserved shells.

Surprisingly, melanopsids are missing in that limestone interval suggesting unfavorable conditions for this group. Again the abundance of *M. aletici* and the extremely reduced amount of other fossils approve the assumption of a somewhat deeper lake environment.

4.4.2.2. A new dawn (102-110 m)

Towards the end of this long-term cooler period the number of coal seams increases, indicating a beginning regression that represents the base of the highly fossiliferous beds of the second limestone-coal cycle proposed by MANDIC et al. (2009) (sample γ at 104 m). Herein no smooth morphotypes appear anymore. As sample γ groups always with samples from the lower part of the section, although it is about 35 m above, we suppose that the overall environmental conditions did not change fundamentally during the transgression.

This tendency is also expressed in sample β , which clusters aside but shows some similarities with the samples of the following interval (Cluster 3, with ca. 35% of average similarity) due to the disappearance of smooth morphotypes and the development of half-ribbed and ribbed morphs.

In summary, the interval reaching from 67-110 m displays a long-term transition resulting in the more or less complete replacement of morphotypes. Nevertheless, the continuous occurrence of most of the mollusk taxa during this period excludes a complete environmental perturbation. The only species that seems to flourish under these conditions is *Mytilopsis aletici* that disappears afterwards.

4.4.2.3. A new reign – *Prososthenia*-assemblage (110-130 m)

A strong shift is recorded in sample Z (110 m), where half-ribbed and ribbed forms, especially of *Prososthenia*, predominate, accompanied by *Pseudamnicola* and *Orygoceras*. Besides, *Lymnaea* sp. and *Prososthenia bicarinata* appear with one individual each. The hydrobiids *Prososthenia* and *Pseudamnicola* point to a shallower habitat. *Orygoceras* and *Lymnaea* as lung-breathing pulmonates support this interpretation. *Mytilopsis* and *Theodoxus* are subordinate. Both *Melanopsis* species re-occur, although generally in low numbers.

Prososthenia replaces *Melanopsis* as the predominant genus and highly sculptured morphotypes prevail. Because of the dominance of hydrobiids shallow water conditions with limited fluvial input and thus decreased water energy are suggested.

This turnover continues from sample Z onward over the next 20 m. Consequently, all samples within this interval (Z, Y, V, T1, O, M2, Lx and L) cluster together with a minimum average similarity of more than 60%.

The lithological and palynological records reveal fluctuations in climatic and environmental parameters (MANDIC et al., 2009; JIMÉNEZ-MORENO et al., 2008). These, however, were not strong enough to have major influence on the fauna.

4.4.2.4. Ready for shore (130-137.5 m)

After this somewhat conservative faunal interval again a radical change occurs. It starts with half a meter of coal at 130 m, grading into limestone-coal interbeddings with an increasing amount of large coal seams, interpreted as a developing peat bog (MANDIC et al., 2009). The change is recorded in sample J (130.5 m) with a decline of ribbed prosostheniids, an increase of *Melanopsis* and *Orygoceras* and even the new appearance of *Prososthenia neutra*. *Orygoceras* was probably an inhabitant of rather shallow environments with stagnant or slowly flowing water.

At the top of the section the coal beds become even thicker, represented by sample A (137 m). It consists of a high number of taxa such as *Gyraulus geminus*, *Lymnaea* sp. and *Fossarulus* cf. *armillatus*, which rarely occur in other samples. All other taxa become uncommon except for the hydrobiid *Prososthenia neutra*. This smooth species already appears in some layers beneath the studied section (MANDIC, pers. comm.). It is interpreted as pioneer species, which occurs shortly after major crisis, but soon after becomes replaced by more competitive taxa.

Combining these data with information from lithological and pollen records, a final aggradation at the section top is indicated and the lake desiccated (MANDIC et al., 2009; JIMÉNEZ-MORENO et al., 2008). Consequently, species typical for lotic or deeper lentic waters retreated and mollusks were restricted to small pools that seasonally dried out.

The isolated position of samples J and A is also reflected in the statistical analysis. Within the first run of the cluster analysis they seem to group together, but with an insignificant average similarity of only 30%. In this case the nMDS shows their separation even better.

4.5. Evolutionary patterns in Lake Sinj

A major aim of this integrative study was to correlate morphological changes and disparity events in the mollusk fauna with environmental shifts in Lake Sinj. The latter were previously studied by OLUJIĆ (1999), who worked on supposed evolutionary lineages of melanopsid and prosostheniid gastropods from the same section. He presented a morphotype classification, data on their stratigraphic ranges and considerations on possible trigger mechanisms for the observed morphologic variations. He noticed the simultaneity of shifts in evolution, regarding changes in sculpture and size, and tried to relate them to intrinsic and extrinsic parameters.

4.5.1. New results

4.5.1.1. Shell sculpture

In the studied section, the first changes in sculpture of *M. lyrata* and *Melanopsis lanzaeana* with half-ribbed morphotypes occur between 65-70 m. In some cases this shift begins in sample 43, in others not before sample 44. E.g. half-ribbed morphs of *Melanopsis lyrata* appear in sample 43 but increases in number in sample 44, whereas similar types of *M. lanzaeana* appear in sample 44 (Fig. 10). Half-ribbed morphs of *M. lyrata* completely replace the former smooth ones, whereas smooth *M. lanzaeana* still predominate.

No data are available from the following interval due to the low number of samples and the lack of faunas. The second major shift to ribbed morphs appears at ca. 110 m. The last great change spans the uppermost 10 m, displaying a strong collapse for melanopsids and especially prosostheniids.

Orygoceras displays similar tendencies. It occurs throughout the section with three species, one smooth and two sculptured forms. The two latter species are typically present in periods of high morphologic plasticity of other gastropod groups. Probably, they represent only short disparity events. Thus, they might also rather represent morphotypes of a single species. This assumption, however, cannot be proven without more material.

4.5.1.2. Shell size

A further eye-catching pattern is the change in shell size. In some cases the morphotypes do not differ in appearance or expression of sculpture but in dimensions. Examples are provided from both melanopsids and prosostheniids. The first changes within the prosostheniids appear at sample 33 even before the melanopsids. In this sample *P. schwarzi* morph *apleura* attains nearly the double size of *P. schwarzi* morph *transitans* (Fig. 9).

Another example is reported from ca. 110 m, where ribbed morphotypes start to prevail. In this case *M. lyrata* morph *lyrata* attains nearly the double size of *M. lyrata* morph *costata*.

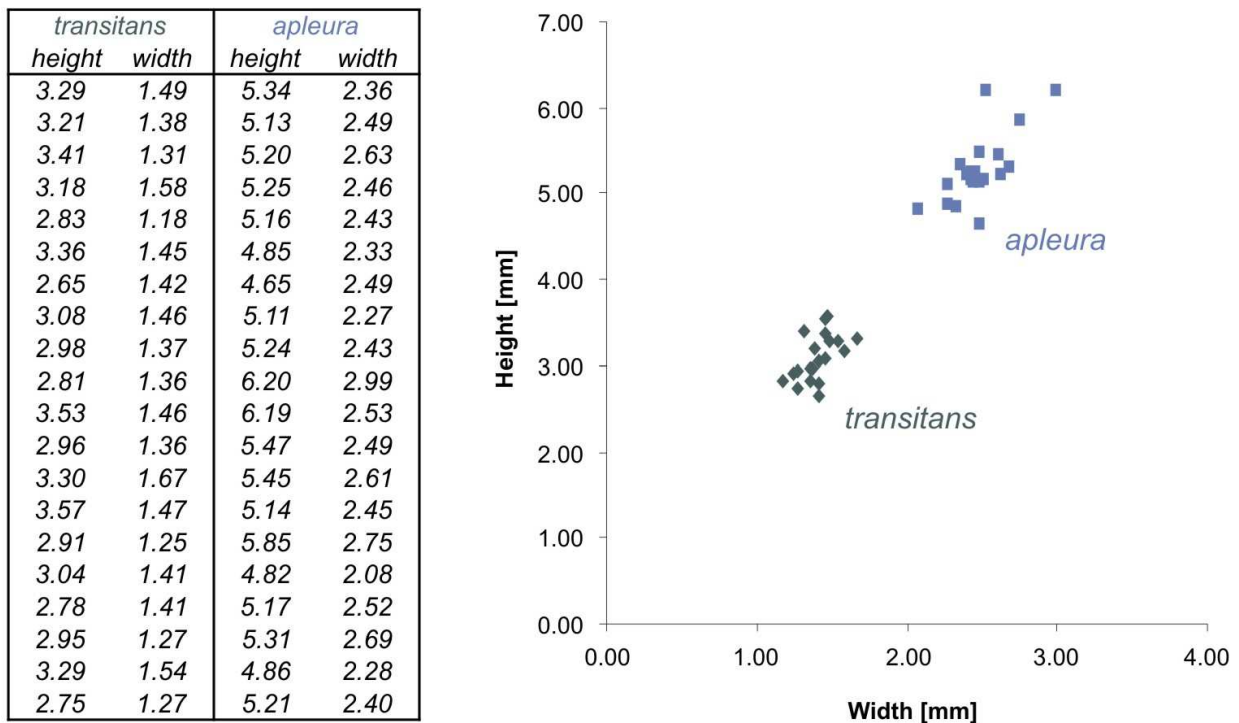


Fig. 9. Proportion of dimensions in two morphotypes of *Prososthenia schwarzi*. All specimens stem from sample 44 (69.5 m).

4.5.2. Comparing the results

OLUJIĆ (1999) presents a detailed diagram with the stratigraphic ranges of his morphotypes (Fig. 10). One grave problem emerged during the comparison of the results according the correlation with Olujić's data: he documents the greatest evolutionary shift and the greatest morphological disparity exactly within the fossil-poor interval around 95-105 m.

Although Olujić worked on the same section, he included also data from several further sections from this region, which he correlated to this one and integrated the fossil content (OLUJIĆ, 1999). This probably explains his comprehensive amount of data for the otherwise fossil-poor intervals. Therefore, it is not surprising that not all species/morphotypes described by OLUJIĆ (1999) were found. One "missing" species is *Prososthenia vojskavae* OLUJIĆ, 1999, a high conical hydrobiid with up to 6 straight-sided whorls and prominent last one.

Also *Prososthenia cincta* morph *ecostata* was not found, probably due to few and badly preserved samples within the corresponding interval. Even OLUJIĆ (1999), who worked on more material, detected just relatively few individuals.

Nevertheless, the concurrence of Olujić's and the newly established lineages is striking in many cases; although there are some major discrepancies, as well:

Especially in *Melanopsis lyrata* morph *costata* there are strong differences. No specimens could be detected in this study in the interval proposed by OLUJIĆ (1999) whilst the only record appears distinctly higher in the section (sample Z). His *costata*-lineage is rather congruent with that of *M. lyrata* morph *semicostata*.

Prososthenia schwarzi morph *semicostata* and *Prososthenia cincta* morph *semievoluta* display similar patterns. Again, within the interval from ca. 95-105 m no sufficient data can be presented due to the fossil-poor and badly preserved samples. Afterwards, these morphotypes occur in high numbers, although they are missing in Olujić's graph.

The lineages from *Prososthenia schwarzi* morph *semicostata* to *Prososthenia schwarzi* morph *schwarzi*, alternatively from *Prososthenia cincta* morph *semievoluta* to *Prososthenia cincta* morph *cincta* are congruent in most cases. Thus, the observed disparity seems to reflect only intraspecific variability.

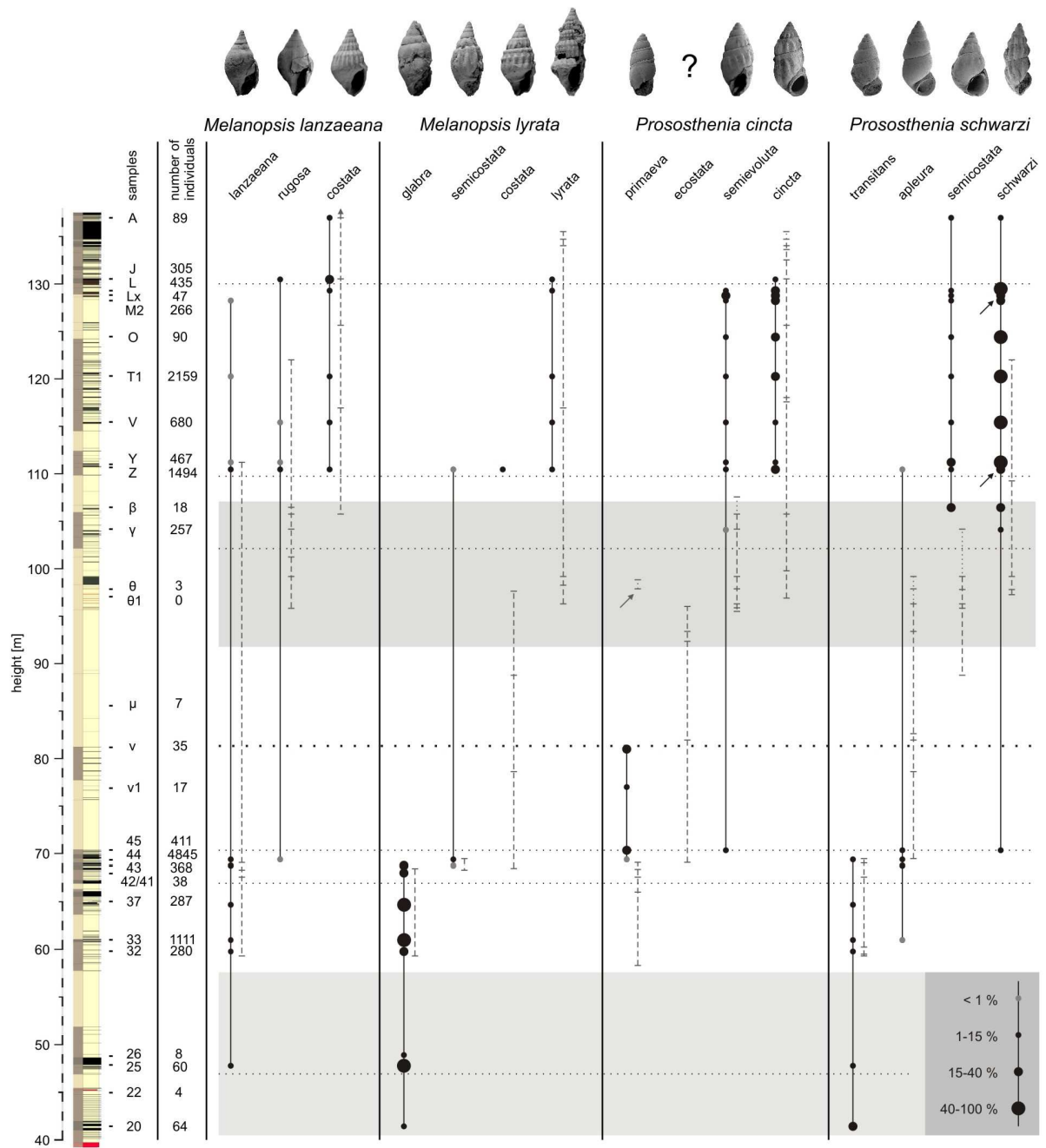


Fig. 10. Stratigraphic ranges with abundance values of evolutionary lineages of melanopsids and prosostheniids. The continuous lines display the results of this study, the dashed lines those from OLUJIC (1999). The dotted lines represent additional morphs by Olujić that were taxonomically revised and are thus added to the correct morphotypes (see systematic part for detailed discussion). Horizontal lines display the samples studied by OLUJIC (1999). The dark gray bar in the middle represents the major radiation event in his work. The interval marked by the light gray bar provides no data from OLUJIC (1999). The arrows label nearly covered dots/lines or outliers, that easily could be missed. The arrow at the line's head of *Melanopsis lanzaeana* morph *costata* means a continuing record in OLUJIC (1999), exceeding this scale. Concerning *Prososthenia cincta* morph *ecostata* just Olujić's data were plotted, because no specimens were found during this investigation. Therefore, the appropriate illustration is missing above (?). The pictures are not to scale.

However, *Prososthenia cincta* morph *primaeva*, stratigraphically clearly separated from following ones (as own “subspecies”), also appears outside the Olujić lineages. This may be rooted in the somewhat ambiguous taxonomic concept of Olujić as he united morphologically very different specimens in this morphotype (Pl. 5, figs. 52-55, 63; pl. 6, figs. 68, 72-74 in OLUJIĆ, 1999).

4.5.3. Diversity models

Comparing diversity indices and the number of species/morphs per sample (Fig. 11) it becomes apparent that especially the lineages of *Melanopsis lyrata*, *M. lanzaeana*, *Prososthenia schwarzi* and *P. cincta* contribute mostly to diversity peaks and the bimodal distribution.

It seems that those two peaks could be the tails of a single bell-shaped curve (dashed line in fig. 11) – only the midpoint is missing. This assumption is supported by the fact that some of the morphs that prevail in the upper part of the section already appear below (at around 70 m). The tremendous decrease in mollusk diversity in between might respond either to disadvantageous environmental conditions or to poor preservation or both.

Herein, however, another model for the bimodal distribution in the diversity curve is proposed. The two peaks are distinct and separate diversity maxima, whereas the “low tide” in between reflects an environmental crisis. This is strongly supported by the exactly congruent rhythm of the two limestone-coal cycles, suggesting a concomitant change in the hydrology of the lake (MANDIĆ et al., 2009).

The first occurrence of morphotypes in the lower cycle, which are otherwise typical for the second cycle is no contradiction: these taxa endured the crisis and re-appeared afterwards. Besides, the distribution diagram in OLUJIĆ (1999) does not respond to abundance values; it simply displays presence-absence data. Furthermore, OLUJIĆ (1999) stated that there are severe differences regarding abundances of distinct morphotypes within layers of same age but different locality. Hence, the co-occurrence of certain morphs seems to be strongly dependent on the paleoenvironment. In the studied section the crisis was probably more dramatic than in other lake areas.

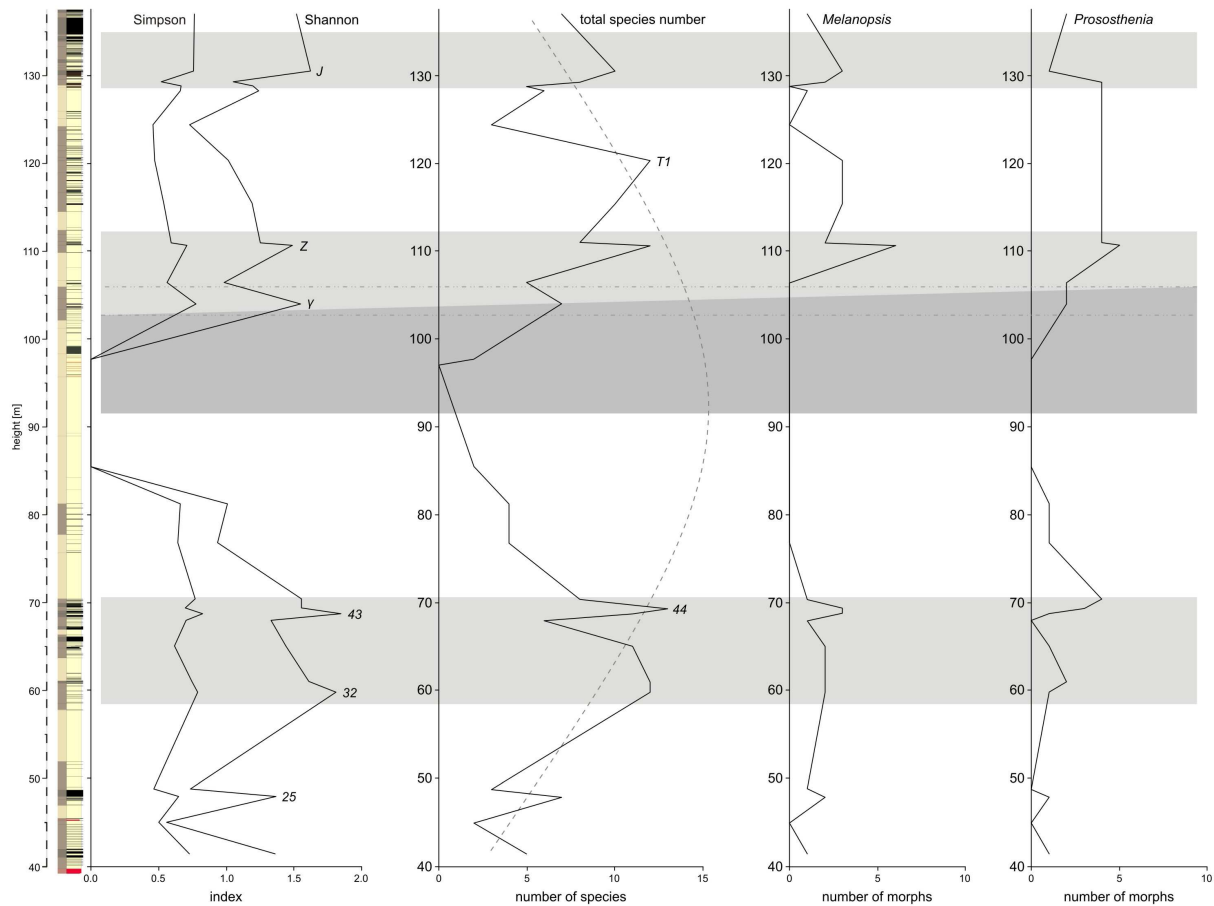


Fig. 11. Comparison of diversity indices, including Simpson and Shannon-Wiener Index, total species number species per sample and number of morphotypes per sample for each *Melanopsis* and *Prososthenia* (just including those species in evolutionary lineages). The light gray bars signal high diverse intervals. The dark gray bar displays the major radiation event in OLUJIC (1999); the dotted lines indicate an overlapping. The dashed bell-shaped curve refers to the first diversity model (see text). The numbers/letters next to the graphs refer to samples marking noticeable peaks.

There is another peak in the diversity diagram (Fig. 11) at the top of the section (sample J at 130 m). This might be based on the (re-)appearance of new species after an environmental crisis. The peak is absent Olujić's data because it is mainly based on species, which are not discussed in OLUJIC (1999), who focused on melanopsids and prosostheniids.

4.5.4. Modes of evolution – and driving factors

The most obvious questions are: why do these changes appear and why at certain times? Within the section several small-scale radiation events are observed. In general, they display on a large-scale view a more or less gradual evolution with intervals of lower and higher diversification and fluctuating evolution rates. The lithological record implies the latter to be highly dependent on environmental parameters: the greatest shifts happen during periods of

limestone-coal interbeddings. Nevertheless the question remains, whether the changes appear exactly within these coal-rich intervals or shortly before, within pure limestones.

Interestingly, in most cases the morphotypes do not replace each other completely. Thus, it does not suggest anagenetic evolution (GOULD & ELDREDGE, 1977) as, e.g., in some melanopsid lineages from Lake Pannon (GEARY et al., 2002).

Radiations may be triggered 1) by colonization of a new lake area with less competition or unoccupied ecological niches, 2) extinction of competitors or 3) replacement of competitors as result of a new adaptation (RIDLEY, 2004). The first scenario cannot be proven, because no data exist on the exact lake physiography and its interconnectivity with other lakes of the DLS. The second scenario is unlikely, due to the simultaneity of the morphological shifts in unrelated clades. Therefore, the third scenario might apply to Lake Sinj.

In fact, during periods of high disparity no extreme lake conditions are registered, such as desiccation. However, the environment has changed slowly but continuously and the mollusks were not forced to change their mode of life – not until a threshold was reached (MARTENS et al., 1994).

The parameters underlying intra-lacustrine radiation in both Recent (e.g. BERTHOLD, 1990; MARTENS et al., 1994; MICHEL et al., 1992; MICHEL, 1994; VON RINTELEN et al., 2004; GENNER et al., 2007) and fossil (e.g. GEARY, 1990; GEARY et al., 2002) long-lived (“ancient”) lakes have been extensively discussed on a broad spectrum of localities. Among the wide range of possible intrinsic and extrinsic factors, there are some recurring patterns, including escalation, i.e. the co-evolution of predator and prey, substrate conditions, depth tolerance, lake-level changes, hydrodynamic conditions, water chemistry, and reproduction mechanisms. By this, the simultaneity of evolution must be kept in mind, meaning that the changes must have been large-scale to have major impact on different systematic clades (e.g. GEARY, 1990).

- a. Escalation is frequently named as possible reason for evolution of sculpture (e.g. VERMEIJ & COVICH, 1978; BERTHOLD, 1990; MARTENS et al., 1994; WEST & COHEN, 1994; GEARY et al., 2002; VON RINTELEN et al., 2004; WILSON et al., 2004), particularly concerning the co-evolution of mollusks and crabs. Due to higher constructional stability sculptured shells resist better to enhanced predation than smooth ones. Decapods and predatory gastropods are unknown from Lake Sinj. Molluscivore fishes might have been present but

are undescribed so far. The low amount of feeding marks and repair scars, however, suggest little impact by fishes on mollusk evolution in the lake.

- b. Tectonically created lake basins provide diverse substrates along the shore line (MICHEL, 1994; HAUFFE et al., submitted), displaying dispersal barriers and thus diversification possibilities by ecological segregation, hence denoting congruence between substrate type and morphotype (MICHEL et al., 1992). Similar patterns were studied by PLAZIAT & YOUNIS (2005), who worked on melanopsids from Iraq and discovered that smooth morphs prevail in estuaries, whereas those with nodular morphology are more common in freshwater environments.

Even OLUJIĆ (1999) mentioned the higher abundance of ribbed forms in sand layers and nearshore environments.

On a larger geographic scale, HARZHAUSER et al. (submitted) generally suggest habitat segregation as one driving force for radiation in the Dinaride Lake System, based on isotope data from mollusk shells. Perhaps, the mode of substrate diversification, as the replacement of pure limestones by limestone-coal interbeddings, was rapid enough to exceed the ecologic threshold of several species leading to sudden diversification (MARTENS et al., 1994).

- c. MICHEL (1994) stated that diversification might be spurred through the interaction of depth tolerance and lake stability. Indeed, aside from lake-level fluctuations and minor climate changes, the lake environment is presumed to have been rather stable (MANDIC et al., 2009), also proved by the continuous occurrence of several species throughout the whole section. Possibly the discussed taxa or morphs, respectively, started to inhabit different depths. However, the most diverse periods are within limestone-coal interbeddings, which are interpreted as shallow settings, making this interpretation rather ambiguous.
- d. Lake-level changes may also support radiations. GEARY (1990) relates the shifts in melanopsid speciation to a water level rise in Lake Pannon, resulting in an increase of habitat availability. MARTENS et al. (1994) states generally that minor lake-level fluctuations create dynamic conditions in seemingly stable littoral communities.

The major changes in mollusk morphology occurred during limestone-coal interbeddings that formed in marginal lake environments. Additionally, these periods are characterized by increased records of thermophilous and xeric plants, pointing to warmer and rather arid conditions (JIMÉNEZ-MORENO et al., 2008). The oscillating lake level had an impact on the extension and development of vegetation belts fringing the lake. Of course, the nutrient supply and food source from vegetation will have differed strongly between periods of high lake level and pure limestone deposition and those of the coal swamp formation. Aside from habitat fragmentation during lake level low stands, this different nutrient supply might have played a major role for the observed radiations.

- e. OLUJIĆ (1999) related the observed disparity and morphological plasticity to changing water chemistry of the lake. Thus, in certain intervals the ion concentration must have been elevated and more carbonate available, speeding the evolution of sculpture or size. Indeed, the massive limestones in the section document intense chemosynthetically induced carbonate precipitation due to high photosynthetic activity (MANDIĆ et al., 2009). In respect to the basement, consisting of Mesozoic to Eocene carbonates, the availability of carbonate was probably never a limiting factor in the lake system.

5. Conclusion

Mollusks are valuable tools for paleoenvironmental and evolutionary research in long-lived lakes. The studied lower Middle Miocene section bears an outstanding example of mollusk radiation and allows estimates about the mode and tempo of morphologic change in certain gastropod lineages.

Several phases of successive replacement of morphotypes are observed. Typically assemblages with smooth morphotypes are gradually passing into assemblages with strongly sculptured shells. These events are limited to certain periods and occur nearly simultaneously in unrelated species-groups of the gastropods *Melanopsis* and *Prososthenia*. To describe these patterns, a quantified mollusk record was statistical analyzed. The base for this was a detailed taxonomic study and a revision of the taxa and a comparison with the ecological requirements of extant relatives.

Moreover, the mollusk distribution within the section was compared with previous sedimentological and palynological data.

Two distinct phases are evident which are also expressed in the lithology as two limestone-coal cycles. These represent shallow lake habitats which are separated by an intermediate limestone-dominated interval with few and poorly preserved mollusks that formed during a lake level high. The lower cycle is characterized by abundant melanopsids, neritids, mytilopsids and later on also unionids, reflecting an environment with continuous freshwater supply and elevated water energy. The upper cycle is predominated by hydrobiids and pulmonate gastropods suggesting a restricted low-energy setting.

The uppermost part of the second cycle is characterized by a retreat of both melanopsids and former prosostheniids, and the rise of pulmonates and new *Prososthenia neutra* which is considered to represent a pioneer species. This indicates an ongoing aggradation of lake sediments and a complete desiccation at the section top for the first time in the depositional history of the lake.

These diversity cycles are coinciding with disparity maxima in 4 distinct lineages: *Melanopsis lyrata*, *M. lanzaeana*, *P. schwarzi* and *P. cincta*. All these lineages tend to start with smooth shelled morphs which gradually pass into strongly sculptured morphs. The gradual replacement and the co-occurrence of morphotypes in several samples suggest an intra-specific variability which leads to higher morphologic disparity in certain phases. The coincidence of high disparity and overall diversity clearly points to a common trigger mechanism and optimum conditions for these lake mollusks. Both phases are restricted to lowered lake level and a rather arid climate. Therefore, extrinsic factors such as climatic shifts might be the main force for the radiations. The comparably lower lake level may have caused habitat segregation and might have influenced water chemistry. Clearly, substrate type was changing as well as indicated by deposits rich in plant debris. The changing vegetation will have had an impact on the food supply for the mainly herbivorous gastropods. All this might have boosted the formation of local populations. Why sculptured shells have been an advantage compared to smooth ones during these phases remains an unsolved question.

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6. Systematic part

Class Gastropoda CUVIER, 1797

Subclass Neritimorpha GOLIKOV & STAROBOGATOV, 1975

Superfamily Neritoidea RAFINESQUE, 1815

Family Neritidae RAFINESQUE, 1815

Subfamily Neritinae POEY, 1852

Genus *Theodoxus* MONTFORT, 1810

Type species: *Theodoxus lutetianus* MONTFORT, 1810 (= *Nerita fluviatilis* LINNAEUS, 1758), Recent, France.

***Theodoxus sinjanus* (BRUSINA, 1876)**

Pl. 5, figs. 5-7

1869 *Neritina Grateloupiana* FÉRUSAC – NEUMAYR, p. 365, pl. 12, figs. 16-17.

1876 *Neritina sinjana* BRUSINA – BRUSINA, p. 113.

1884 *Neritodonta sinjana* BRUSINA – BRUSINA, p. 82.

1897 *Neritodonta sinjana* BRUS. – BRUSINA, p. 28, pl. 15, figs. 10-21.

1929 *Theodoxus (Calvertia) sinjanus* (BRUSINA) – WENZ, p. 2980.

Material: 517 specimens from samples 20, 25, 26, 32, 33, 37, 42/41, 43, 44, 45, v1, v, γ, β, Z, Y, V, T1, M2, L.

Dimensions: Height: up to 6 mm, diameter: up to 8 mm.

Description: Protoconch conical, smooth, made up from about 2 whorls. Spire short and bulky, consists of up to 4 whorls. The last whorl forms a weak shoulder with a more or less straight ramp. Abapically from this shoulder a convex margin forms. The aperture is semilunar; the inner lip is nearly straight and the outer lip strongly convex. A broad columellar plate is moderately dentated to nearly smooth. Coloring is highly variable, including dense striation, zig-zag lines or mottled patterns. Mostly, it covers the whole shell; in some cases it is limited to regular bands.

Distribution: Endemic species from Dinaride Lake System and recorded from localities Sinj (Župića potok) (BRUSINA, 1882, 1897) and Lučane (41.5-129.5 m).

Remarks: It can be separated from *T. semidentatus* by the higher elevated spire of the latter species.

Already BRUSINA (1884) noticed that *Theodoxus grateloupiana* (NEUMAYR, 1869) is partly a synonym of *T. sinjanus*. Some specimens illustrated in NEUMAYR (1869; pl. 12, figs. 16-17) refer to this species because of their prominent and dentated columella plate, the semilunar aperture and the depressed spire.

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Subclass Caenogastropoda COX, 1959

Order Cerithiimorpha GOLIKOV & STAROBOGATOV, 1975

Superfamily Cerithioidea FLEMING, 1822

Family Melanopsidae H. & A. ADAMS, 1854

Genus *Melanopsis* FÉRUSAC, 1807

Type species: *Buccinum praemorsum* LINNAEUS, 1758, Recent, Spain.

***Melanopsis lanzaeana* BRUSINA, 1874**

Pl. 1, figs. 13-21

1869 *Melanopsis pygmaea* PARTSCH – NEUMAYR, p. 356, pl. 12, fig. 1 (non 1856 *Melanopsis pygmaea* HÖRNES).

1874 *Melanopsis Lanzaeana* BRUSINA – BRUSINA, p. 34.

1897 *Melanopsis Lanzaeana* BRUS. – BRUSINA, p. 12, pl. 5, figs. 7-8.

1897 *Melanopsis Lanzaeana rugosa* BRUS. n. for. – BRUSINA, p. 12, pl. 5, fig. 9.

1929 *Melanopsis lanzaeana lanzaeana* BRUSINA – WENZ, p. 2770.

1929 *Melanopsis lanzaeana rugosa* BRUSINA – WENZ, p. 2771.

1999 *Melanopsis lanzae* (BRUSINA) – OLUJIĆ, p. 21, 49.

1999 *Melanopsis lanzae lanzae* (BRUSINA) forma – OLUJIĆ, p. 21, 49, pl. 2, figs. 13-14, 21.

1999 *Melanopsis lanzae rugosa* (BRUSINA) forma – OLUJIĆ, p. 21, 49, pl. 2, figs. 15-18, 22-24, pl. 3, fig. 25.

1999 *Melanopsis lanzae costata* OLUJIĆ forma – OLUJIĆ, p. 21, 49, pl. 2, figs. 19-20, pl. 3, figs. 26-28.

Material: 847 specimens from samples 25, 32, 33, 37, 43, 44, Z, Y, V, T1, M2, L, J, A.

Dimensions: Height: 5-10 mm, diameter: 3-5 mm, spire angle: 50-70°.

Description: Protoconch conical, consisting of about 2 whorls. Spire conical and compact, consisting of up to 8 straight to slightly convex sided whorls. Because the whorls are strongly

addressed they form in profile a distinct coeloconoid outline. Only in *costata*-morphotype (after OLUJIĆ, 1999) early teleoconch whorls bear sculpture in the form of opisthocline axial ribs. These are of highly variable number and strength, reaching from weak to very prominent. On the last 2-4 whorls nodes occur on the ribs close to the upper suture, being arranged into one more or less prominent spiral row. These may form well defined knobs pointing towards the apex or indistinct, strongly axially elongate swellings. Both sculpture elements, nodes and ribs, may even be largely reduced (*rugosa*-morph in OLUJIĆ, 1999) or are completely missing (*lanzaeana*-morph in OLUJIĆ, 1999). The suture beyond the row of nodes is not incised (as it is in *M. lyrata*). The axial ribs grade into sigmoidal ribs which fade out on the base towards the siphonal canal. The last whorl shows a distinct shoulder and attains about 50-60% of the total height. The aperture is ovoid, elongate with narrow posterior angulation and wide convex posterior margin with short siphonal canal and convex outer lip. The inner lip is thickened, reaches to the base and shows a very prominent callus pad. The columella may rarely develop a weak convexity in the middle part of the aperture. This can result in an indistinct swelling but never shows a fold. Rarely, the original coloring is preserved as brown to yellow zigzag lines.

Distribution: *Melanopsis lanzaeana* is an endemic species of the Dinaride Lake System. It is recorded only from the localities Ribarić (BRUSINA, 1874, 1897) and Lučane (48-137 m).

Remarks: Like *M. lyrata*, *Melanopsis lanzaeana* is a quite variable species that also combines several morphotypes. Each of them does occur in distinct layers although their stratigraphic ranges may overlap sometimes. So 3 morphotypes (A-C), originally defined by OLUJIĆ (1999), can be separated.

1. *Melanopsis lanzaeana* morph A is characterized by a lack of sculpture and appears to be the “typical” *M. lanzaeana* defined by BRUSINA (1897). It appears within the samples 25, 32, 33, 37, 43, 44, Z, Y, T1, M2 with 486 specimens.

2. *Melanopsis lanzaeana* morph B shows beginning sculpture with weakly expressed ribs and nodes and corresponds to the subspecies *Melanopsis lanzaeana rugosa* BRUSINA, 1897 (*rugosa*-morph in OLUJIĆ, 1999). The nodes may cause large swellings. It is represented in samples 44, Z, Y, V, J with 129 specimens.

3. *Melanopsis lanzaeana* morph C bears a large number of prominent axial ribs and small distinct knobs and corresponds to the *costata*-morph in OLUJIĆ (1999). It occurs in samples Z, V, T1, L, J, A with 232 specimens.

Melanopsis lanzaeana differs from *Melanopsis lyrata* in its more compact habitus, the prominent callus pad, the mostly missing or weakly expressed columella fold and by having just one row of nodes (in sculptured specimens).

NEUMAYR (1869) misidentified this species as *Melanopsis pygmaea* HÖRNES, 1856, which is a much younger species in Lake Pannon (PAPP, 1953). *M. pygmaea* is much more slender and higher conical than *M. lanzaeana*.

***Melanopsis lyrata* NEUMAYR, 1869**

Pl. 1, figs. 1-9, 20

1869 *Melanopsis* (*Canthidomus*) *lyrata* nov. sp. – NEUMAYR, p. 358, pl. 11, figs. 8a-b.

1874 *Melanopsis lyrata* var. *cylindracea* BRUS. – BRUSINA, p. 45.

1897 *Melanopsis lyrata* NEUMAYR – BRUSINA, p. 10, pl., 4, figs. 6-7.

1929 *Melanopsis cylindracea* BRUSINA – WENZ, p. 2698.

1999 *Melanopsis lyrata* NEUMAYR – OLUJIĆ, p. 19, 47.

1999 *Melanoptychia lyrata glabra* OLUJIĆ forma – OLUJIĆ, p. 20, 48, pl. 1, figs. 1a-b.

1999 *Melanoptychia lyrata semicostata* OLUJIĆ forma – OLUJIĆ, p. 20, 48, pl. 1, figs. 2-4.

1999 *Melanoptychia lyrata costata* OLUJIĆ forma – OLUJIĆ, p. 20, 48, pl. 1, figs. 11-12.

1999 *Melanopsis lyrata lyrata* NEUMAYR forma – OLUJIĆ, p. 20, 48, pl. 1, fig. 7-10.

Material: 1213 specimens from samples 20, 25, 26, 32, 33, 37, 42/41, 43, 44, 45, Z, V, T1, L, J.

Dimensions: Height: 8-14 mm, diameter: 3-5 mm, spire angle: 40-60°.

Description: Protoconch conical, consisting of about 2 whorls. Spire high conical, consisting of up to 8 straight sided whorls. In profile the whorls are sub-parallel or may form a conical outline. In sculptured morphotypes early teleoconch whorls may bear prominent opisthocline axial ribs of highly variable number. They are equal in width or narrower than the interspaces between the ribs. On the last 2-4 whorls nodes occur on the ribs close to the upper suture, being arranged into two more or less prominent spiral rows. These nodes may form well defined knobs or strongly axially elongate swellings. Both sculpture elements, nodes and ribs, may even be largely reduced (*glabra*-morph in OLUJIĆ, 1999). If present, the two rows of nodes are separated by a slight concavity. The suture below the lower row of nodes is typically incised. The two rows of nodes persist on the last whorl which is nearly cylindrical in its upper half and contacts then gradually into the convex base. The axial ribs grade into

sigmoidal ribs which fade out on the base towards the siphonal canal. The height of the last whorl attains about 50-60% of the total height. The aperture is ovoid, elongate with narrow posterior angulation and wide concave posterior margin with short siphonal canal and convex outer lip. The canal is delimited by a narrow but well defined fold. The inner lip is weakly thickened, often weakly separated from the base and lacks a callus pad. The columella develops a pronounced convexity in the middle part of the aperture. This convexity may form an indistinct swelling or may near a very strong columellar fold perpendicular to the axis. A single but well developed fasciole appears on the base. Rarely, the original coloring is preserved as brown to yellow zigzag lines.

Distribution: *Melanopsis lyrata* is an endemic species of the Dinaride Lake System. It is recorded only from the localities Ribarić (NEUMAYR, 1869; BRUSINA, 1897), Miočić (BRUSINA, 1874) and Lučane (41.5-130.5 m).

Remarks: *Melanopsis lyrata* is a quite variable species. Whilst the holotype of NEUMAYR (1869) is a very slender shell with prominent nodes, OLUJIC (1999) illustrates much more bulky shells with predominant axial sculpture. OLUJIC (1999) introduced several new names for *Melanopsis lyrata*, affirmatively referred to in text as forms and therefore not representing the available subspecies names (ICZN IV, Article 16). Yet, as those names could be easily interpreted as available species-group names the additional arguments on their formal unavailability must be stressed out. Hence, as OLUJIC (1999) classified shells with columellar fold within the genus *Melanoptychia* NEUMAYR, 1880, all these subspecies were defined under the generic rank of *Melanoptychia*. This implies that the subspecies names were defined for a taxon without established nominal species. In any case, the validity of *Melanoptychia* is doubtful. Already JEKELIUS (1944) recognized that all *Melanoptychia* species (in the Late Miocene Lake Pannon) have counterparts within *Melanopsis*. The absence or presence of a columellar fold may thus be a mere intrageneric variation. If considered as *Melanopsis*, the proposed subspecies names *costata*, *semicostata* and *glabra* are partly preoccupied by *M. costata* NEUMAYR, 1869 (= *M. cosmanni* PALLARY, 1916), *Melanopsis costata* (OLIVIER, 1804) and *Melanopsis glabra* BRUSINA, 1874. Finally, OLUJIC (1999) did not define a holotype, either. In respect to the complex combination of nomenclatoric mistakes and formal lapses, the species group names introduced by OLUJIC (1999) should not be accepted as valid.

Despite those problems, the various morphotypes of *Melanopsis lyrata* do not co-occur randomly but appear in distinct layers. Based on this evidence 4 morphotypes, originally

defined by OLUJIĆ (1999), can be accepted, marking them however with letters A to D for more clear expression of their nomenclatural status:

1. *Melanopsis lyrata* morph A is characterized by reduced sculpture (*glabra*-morph in OLUJIĆ, 1999) – no ribs or nodes – and predominates in samples 20, 25, 26, 32, 33, 37, 42/41, 43, 45 with 749 specimens.
2. *Melanopsis lyrata* morph B comprises morphologies with few and blunt ribs (*semicostata*-morph in OLUJIĆ, 1999) that occur only in the last 2-3 whorls. It is represented in samples 43, 44, Z with 399 specimens.
3. The comparatively more stout and spiny shells of *Melanopsis lyrata* morph C, referred to as *costata* by OLUJIĆ, 1999, occur in sample Z with 17 specimens. The sculpture appears only in the last 2-3 whorls.
4. *Melanopsis lyrata* morph D is the more delicate morphotype, with numerous axial ribs and nodes starting even at the first few whorls, representing the typical *M. lyrata*. It appears in samples Z, V, T1, L, J with 48 specimens.

Melanopsis lyrata differs from *Melanopsis lanzaeana* BRUSINA, 1874 in its cylindrical last whorl, the elongate shape, the lack of a callus pad and by having two rows of nodes (in sculptured specimens). Generally, *Melanopsis lanzaeana* seems to develop only very rarely *Melanoptychia*-morphs with weak columellar fold.

BRUSINA (1874) describes a variety of this species, called *Melanopsis lyrata* var. *cylindracea*. Later on, it was elevated to species level (BRUSINA, 1876). It is more cylindrical and much larger (about 20 mm in height), but with regard to intraspecific variation it cannot be sufficiently separated from the nominal species.

***Melanopsis* n. sp.**

Pl. 1, figs. 10-12

Material: 10 specimens from samples 43, 44.

Holotype: NHMW Inv. 2010/0042/0001, height: 13 mm, diameter: 5 mm, spire angle: 35°; illustrated on pl. 1, figs. 10-12.

Paratype 1: NHMW Inv. 2010/0042/0002, height: 28 mm, diameter: 13 mm, spire angle: 35°; from sample 43 (68.5 m).

Paratype 2 (Coll. NHM Zagreb): Height: 10 mm, diameter: 4 mm, spire angle: 30°; from type stratum.

Paratype 3 (Coll. NHM Zagreb): Height: 16 mm, diameter: 6 mm, spire angle: 35°; from sample 43 (68.5 m).

Locus typicus: Sinj, Lučane Section.

Stratum typicum: Within lacustrine limestone-lignite interbeddings at the Lučane Section at 69.5 m (sample 44).

Age: Langhian, Middle Miocene.

Diagnosis: An elegant, high conical melanopsid with elevated spire, small last whorl and swelling below each suture.

Description: Protoconch conical, consisting of about 2 whorls. Spire high conical, consisting of about 8 straight to slightly convex sided whorls. Sutures weakly incised, resulting in profile in a more or less straight outline. Whorls become continuously larger, with a last whorl making up about 30% of the total height. Sculpture starting within the last 3-5 whorls, expressed by weak to prominent swellings below the sutures. Aperture ovoid, elongate and narrow, with relatively long siphonal canal and convex outer and inner lip. The latter is very weakly developed and lacks a callus pad. The columella shows about 5 weak fasciolar bands that start in the middle of the aperture and become stronger towards the neck.

Remarks: The species displays a high variability in size. One specimen appears to be about three times larger than the type species. Due to fragmentation no exact measurements can be taken, but it ranges around at least 35 mm in height and 15 mm in diameter.

Probably, the holotype, being the most complete specimen, is a juvenile specimen as suggested by the relatively long siphonal canal (~1/8 of total height). Unfortunately, it is never preserved in one of the larger (adult) specimens.

It differs from other morphologically similar species mostly in the presence (*M. visianiana* BRUSINA, 1874, *M. friedeli* BRUSINA, 1885, *M. astathmeta* BRUSINA, 1897, *M. filifera* NEUMAYR, 1880) or strength (*M. sinjana* BRUSINA, 1874) of the subsutural swelling, and the relation of the height of the last whorl to the entire teleoconch. Due to the high spire, the last whorl is much smaller in *Melanopsis* n. sp. than in *M. hranilovici* BRUSINA, 1897, *M. sinjana* BRUSINA, 1874, *M. visianiana* BRUSINA, 1874, *M. astathmeta* BRUSINA, 1897 and *M. filifera* NEUMAYR, 1880. Furthermore, most of the compared species occur in quite different regions: *M. hranilovici* BRUSINA, 1897 is known from Sarajevo region (BRUSINA, 1897), *M. friedeli* BRUSINA, 1885 is described from Podvornica (BRUSINA, 1897), *M. acicularis* FÉRUSSAC, 1823

from Repušnica, Western Slavonia (NEUMAYR, 1869) and *M. astathmeta* BRUSINA, 1897 occurs in Malino, Slavonia (BRUSINA, 1897). Hence, all species except *M. hranilovici* are Pliocene in age; the latter one is Miocene in age.

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Order Littorinimorpha GOLIKOV & STAROBOGATOV, 1975

Superfamily Rissooidea GRAY, 1847

Family Hydrobiidae STIMPSON, 1865

Subfamily Pyrgulinae BRUSINA, 1882

Genus *Prososthenia* NEUMAYR, 1869

Type species: *Prososthenia schwarzi* NEUMAYR, 1969, Miocene, Ribarić, Dalmatia/SE Croatia.

***Prososthenia bicarinata* OLUJIĆ, 1999**

Pl. 4, fig. 7

1999 *Prososthenia bicarinata* OLUJIĆ – OLUJIĆ, p. 28, 56, pl. 7, figs. 84-89.

Material: 1 specimen from sample Z.

Dimensions: Due to fragmentation no measurements can be taken, but the height is estimated to range around 6-7 mm.

Description: Only the last whorl lacking the aperture is preserved. The identification of the fragment is only based on the two keels. The first one is situated below the suture, the second one around the middle of the whorl, forming a concave profile in between.

Distribution: Endemic species of Lake Sinj, recorded from section Lučane and Orlov kuk (OLUJIĆ, 1999).

Remarks: According to the descriptions and illustrations from OLUJIĆ (1999) this form is usually extremely bulky and irregularly shaped. These features and the two keels suggest that *Prososthenia bicarinata* is a valid species.

***Prososthenia cincta* NEUMAYR, 1869**

Pl. 3, figs. 7-14, pl. 4, figs. 1-2, 5

- 1869 *Prososthenia cincta* nov. sp. – NEUMAYR, p. 361, pl. 12, fig. 6.
 1869 *Prososthenia Schwarzi* nov. sp. – NEUMAYR, p. 360, pl. 12, fig. 5.
 1874 *Prososthenia Schwarzi* var. *cingulata* BRUS. – BRUSINA, p. 50.
 1897 *Prososthenia cincta ecostata* BRUS. n. for. – BRUSINA, p. 18, pl. 8, fig. 26.
 1926 *Prososthenia cincta ecostata* BRUSINA – WENZ, p. 1989.
 1926 *Prososthenia cincta cincta* NEUMAYR – WENZ, p. 1989.
 1999 *Prososthenia cetinae eminens* OLUJIĆ forma – OLUJIĆ, p. 24, 52, pl. 4, fig. 51.
 1999 *Prososthenia cincta* NEUMAYR – OLUJIĆ, p. 24, 52.
 1999 *Prososthenia cincta primaeva* OLUJIĆ forma – OLUJIĆ, p. 25, 53, pl. 5, figs. 52-55.
 1999 *Prososthenia cincta ecostata* OLUJIĆ forma – OLUJIĆ, p. 25, 53, pl. 5, figs. 56, 64, pl. 6, fig. 75.
 1999 *Prososthenia cincta semievoluta* OLUJIĆ forma – OLUJIĆ, p. 25, 53, pl. 5, figs. 57-61, 65, pl. 6, fig. 69.
 1999 *Prososthenia cincta cincta* NEUMAYR forma – OLUJIĆ, p. 25, 53, pl. 5, figs. 62, 66-67, pl. 6, figs. 70-71.
 1999 *Prososthenia sutinae* OLUJIĆ – OLUJIĆ, p. 26, 53.
 1999 *Prososthenia sutinae lateralis* OLUJIĆ forma – OLUJIĆ, p. 26, 54, pl. 6, fig. 76.
 1999 *Prososthenia sutinae electa* OLUJIĆ forma – OLUJIĆ, p. 26, 54, pl. 6, figs. 77-78.
 1999 *Prososthenia sutinae pretiosa* OLUJIĆ forma – OLUJIĆ, p. 26, 54, pl. 6, fig. 79.

Material: 869 specimens from samples 44, 45, v1, v, γ, Z, Y, V, T1, O, M2, Lx, L, J.

Dimensions: Height: 2.5-5.5 mm, diameter: 1-2 mm, spire angle: 30-45°.

Description: Protoconch smooth, consisting of about 1.2 whorls. Spire conical, from slender to very bulky, consisting of up to 6 straight-sided to convex whorls with strongly incised sutures. The first 1-2 whorls are always smooth. Afterwards, in some morphotypes, weak to prominent axial ribs may occur. These are first perpendicular to the axis but become prosocyrts on the last whorl. Each of the last 2-3 whorls bears a more or less prominent subsutural swelling. If present, the ribs start below that swelling and reach to the lower suture. The last whorl sometimes appears to be very bulky and makes up about 40-60% of the total height. Aperture is ovoid, with convex outer lip and slightly convex to nearly straight inner lip.

Distribution: Endemic species of the Dinaride Lake System. It is recorded from the localities Ribarić (NEUMAYR, 1869) and Lučane (69.5-130.5 m).

Remarks: Comparable to already described taxa, problems of validity and variation arises. Four morphotypes can be distinguished:

1. *Prososthenia cincta* morph A is a small, smooth and in most cases more bulky form with a large last whorl. It was treated as *primaeva*-morph in OLUJIĆ (1999) and occurs in samples 44, 45, v1, v with 36 specimens. *Prososthenia sutinae lateralis* OLUJIĆ, 1999 should also be

treated as this morph. OLUJIĆ (1999) found this form within two layers only and even described this form as just slightly deviating from his *primaeva*-morph.

2. *Prososthenia cincta* morph B includes also smooth, but large forms. This *ecostata*-morph in OLUJIĆ, 1999 was already described by BRUSINA (1897). Although OLUJIĆ (1999) found some few individuals, in the course of this work not a single one could be detected.

3. *Prososthenia cincta* morph C comprises all weakly ribbed shells with subsutural swelling (*semievoluta*-morph in OLUJIĆ, 1999), including *Prososthenia sutinae electa* OLUJIĆ, 1999. It appears in samples 45, γ , Z, Y, V, T1, O, M2, Lx, L with 155 specimens.

4. *Prososthenia cincta* morph D is the typical *P. cincta*, already defined by NEUMAYR (1869), with prominent axial ribs and subsutural swelling, often bulky and irregularly shaped. Also *Prososthenia sutinae pretiosa* OLUJIĆ, 1999 and *Prososthenia cetinae eminens* OLUJIĆ, 1999 range within this morphotype. It occurs in samples Z, Y, V, T1, O, M2, Lx, L, J with 678 specimens.

P. cincta differs from *P. schwarzi* especially in the subsutural swelling and the usually more bulky shape. Some specimens treated by OLUJIĆ (1999) as *Prososthenia cincta* morph *primaeva* do not show the significant swelling, either, and could therefore not be classified as this species. These individuals represent *Prososthenia schwarzi* morph *transitans*.

***Prososthenia neutra* BRUSINA, 1897**

Pl. 4, figs. 3-4, 6, 12

1897 *Prososthenia? neutra* BRUS. n. sp. – BRUSINA, p. 19, pl. 9, figs. 3-4.

1926 ?*Prososthenia neutra* BRUSINA – WENZ, p. 1994.

1999 *Prososthenia superstes* OLUJIĆ – OLUJIĆ, p. 28, 56.

1999 *Prososthenia superstes praevia* OLUJIĆ forma – OLUJIĆ, p. 28, 56, pl. 7, fig. 82.

1999 *Prososthenia superstes intermedia* OLUJIĆ forma – OLUJIĆ, p. 28, 56, pl. 7, fig. 83.

Material: 45 specimens from samples J, A.

Dimensions: Height: 3-4 mm, diameter: 2.5-2 mm, spire angle: 40-50°.

Description: Protoconch conical, smooth and made up of about 1.25 whorls. Spire conical, slender and smooth, consisting of up to 6 convex sided whorls with incised sutures. In profile they form a cyrtconoid outline. It has a very constant morphology with whorls becoming

regularly larger towards last whorl that obtains about 50% of the total height. The aperture is ovoid to elliptically with a slightly convex inner lip and a prominent, strongly convex outer lip.

Distribution: Endemic species of the Dinaride Lake System; occurs in sections Miočić (BRUSINA, 1897) and Lučane (130.5-137 m), but also in Gacko Basin (MANDIC et al., submitted).

Remarks: In OLUJIĆ (1999) this species was erroneously introduced as new taxon *Prososthenia superstes*, including two morphs, namely *P. superstes praevia* and *P. superstes intermedia*.

This species can be separated from both *Prososthenia schwarzi* and *Prososthenia cincta* by their mainly bulky shape and sometimes irregular formed whorls. Another similar species described from this region is *Prososthenia eburnea* BRUSINA, 1884, which was not detected in this section. It is even more slender and usually consists of about 7 nearly straight-sided whorls.

***Prososthenia schwarzi* NEUMAYR, 1869**

Pl. 2, figs. 1-15, pl. 3, figs. 1-6

1869 *Prososthenia Schwarzi* nov. sp. – NEUMAYR, p. 360, pl. 12, fig. 4 (non fig. 5, = *Prososthenia cincta* NEUMAYR, 1869).

1874 *Prososthenia Schwarzi* var. *apleura* BRUS. – BRUSINA, p. 50, pl. 3, fig. 10.

1897 *Prososthenia Schwarzi* NEUM. – BRUSINA, p. 17, pl. 8, figs. 24, 25.

1926 *Prososthenia schwartzi apleura* BRUSINA – WENZ, p. 1998.

1926 *Prososthenia schwartzi schwartzi* NEUMAYR – WENZ, p. 1996.

1999 *Prososthenia schwartzi* NEUMAYR – OLUJIĆ, p. 22, 50.

1999 *Prososthenia schwartzi transitans* OLUJIĆ forma – OLUJIĆ, p. 23, 51, pl. 4, figs. 36-37.

1999 *Prososthenia schwartzi apleura* BRUSINA forma – OLUJIĆ, p. 23, 51, pl. 4, figs. 38-40.

1999 *Prososthenia schwartzi semicostata* OLUJIĆ forma – OLUJIĆ, p. 23, 51, pl. 4, figs. 41-43.

1999 *Prososthenia schwartzi schwartzi* NEUMAYR forma – OLUJIĆ, p. 23, 51, pl. 4, figs. 44-45.

1999 *Prososthenia cetinae increscens* OLUJIĆ forma – OLUJIĆ, p. 24, 52, pl. 4, fig. 48.

1999 *Prososthenia cetinae amplificata* OLUJIĆ forma – OLUJIĆ, p. 24, 52, pl. 4, fig. 49.

1999 *Prososthenia cetinae elegans* OLUJIĆ forma – OLUJIĆ, p. 24, 52, pl. 4, fig. 50.

Material: 1939 specimens from samples 20, 25, 32, 33, 37, 43, 44, 45, γ, β, Z, Y, V, T1, O, M2, Lx, L, A.

Dimensions: Height: 3-5.5 mm, diameter: 1-2 mm, spire angle: 30-45°.

Description: Protoconch smooth and consists of about 1.2 whorls. Spire high conical to cyrtconoid, consisting of up to 7 strongly convex whorls with strongly incised sutures. The first 2-3 whorls are always smooth; afterwards, sculpture is developed in some morphs, reaching from weak to prominent axial ribs. They may reach from one suture to the other or may be restricted to the middle part of the whorls – but never result in a subsutural swelling. In both cases the ribs are most prominent in the middle of each whorl. In some specimens they seem to be straight, in some others more or less opisthocylindrical. The last whorl attains about 40-50% of the total height. Aperture is ovoid, with slightly convex to nearly straight inner lip and sometimes very prominent convex outer lip.

Distribution: Endemic species of the Dinaride Lake System. It is recorded from the localities Ribarić (NEUMAYR, 1869) and Lučane (41.5-137 m).

Remarks: Here again the problem of validity of the many proposed subspecies arises. These are probably mere morpho-phenotypes. Moreover, the generally available species name *Prososthenia cetinae* OLUJIĆ, 1999 (including 4 morphotypes) represents a synonym of partly *P. schwarzi* and *P. cincta*. Thus, although the subspecies names introduced by OLUJIĆ (1999) are invalid, his 4 morphologies can be defined:

1. *Prososthenia schwarzi* morph A is a small and smooth form, rather ovoid shaped than conical and is referred to the *transitans*-morph in OLUJIĆ, 1999. *Prososthenia cetinae increscens* OLUJIĆ, 1999 is a variety of this morph. It appears within the samples 20, 25, 32, 33, 37, 44 with 200 specimens.
2. *Prososthenia schwarzi* morph B comprises another smooth but larger and more conical form. This *apleura*-morph in OLUJIĆ (1999) is represented in samples 33, 43, 44, 45, Z with 152 specimens. Also *Prososthenia cetinae amplificata* OLUJIĆ, 1999 corresponds to this morph.
3. *Prososthenia schwarzi* morph C is characterized by beginning sculpture on the last 2-3 whorls (*semicostata*-morph), but in habitus similar to morph B. *Prososthenia cetinae elegans* OLUJIĆ, 1999 ranges within this type. It occurs in samples β, Z, Y, V, T1, O, M2, Lx, L, A with 185 specimens.
4. *Prososthenia schwarzi* morph D appears to be the typical *P. schwarzi* defined by NEUMAYR (1869), a sculptured form with prominent axial ribs on the last 2-3 whorls. It is represented in the samples γ, β, Z, Y, V, T1, O, M2, Lx, L, J, A with 1402 specimens.

P. schwarzi differs from *Prososthenia cincta* NEUMAYR, 1869 mainly in the missing subsutural swelling. NEUMAYR (1969) separated *P. cincta* from this species by its distinct keel below the sutures whilst in *P. schwarzi* there is only a thin band, if developed at all. To avoid confusions, a more definite taxonomic concept is followed herein, separating both taxa by the presence of such sutural band or keel.

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Subfamily Pseudamnicolinae RADOMAN, 1977

Genus *Pseudamnicola* PAULUCCI, 1878

Type species: *Bythinia lucensis* ISSEL, 1866, Recent, Tuscany, Italy.

***Pseudamnicola torbariana* (BRUSINA, 1874)**

Pl. 4, figs. 8-11, 13

1874 *Amnicola Torbariana* BRUSINA – BRUSINA, p. 66, pl. 5, figs. 15-16.

1902 *Pseudoamnicola? Torbariana* BRUS. – BRUSINA, pl. 10, figs. 14-17.

1926 *Amnicola (Amnicola) torbariana* BRUSINA – WENZ, p. 2083.

Material: 155 specimens from samples 25, 32, 33, 37, 42/41, 43, 44, 45, γ, Z, Y, T1, M2.

Dimensions: Height: 1-3 mm, diameter: 1-1.5 mm, spire angle: 60-80°.

Description: Protoconch conical, comprises about 1.25 whorls and is consistently covered with distinct wrinkles; it is clearly separated from the teleoconch. Spire conical, plump and smooth, with up to 4 whorls, beginning very small but rapidly increasing in diameter. The whorls are convex with the maximum close to the incised adapical suture, resulting in a somewhat stepped outline; no ramp is developed. The last whorl obtains about 50-70% of the total height. Aperture is ovoid and thickened, with convex outer lip and rounded anterior tip. The inner lip starts concave, but becomes strongly convex towards the base, mostly pronounced at the middle of the aperture, right next to the umbilicus. The latter is very small and nearly covered by the inner lip; some specimens show traces of a funicular ridge.

Distribution: Endemic species of Lake Sinj, recorded from Miočić (BRUSINA, 1874) and Lučane (48-128 m).

Remarks: The typical protoconch ornamentation is also observed in *Pseudamnicola hoeckae* HARZHAUSER & BINDER, 2004 from the Vienna Basin (Upper Miocene), confirming the herein described forms as belonging to this genus, too. WENZ (1920) described one of his specimens as *Pseudamnicola* cf. *torbariana*, which differed from the type species in its less flattened sutural part of the whorls. As HARZHAUSER & BINDER (2004) mentioned, this might probably be *Pseudamnicola hoeckae* HARZHAUSER & BINDER, 2004.

WENZ (1926) placed this species into the genus *Amnicola* GOULD & HALDEMAN, in HALDEMAN, 1840, which was originally described from Northern America. Because of the obvious geographical isolation between Northern America and Europe, PAULUCCI (1878) introduced the new genus *Pseudamnicola* to separate the European genus from the American one.

Another species described from Dalmatia is *Pseudamnicola stosiciana* BRUSINA, 1884. This form is characterized by its relatively broad last whorl and more slender shape.

***Pseudamnicola* n. sp.**

Pl. 5, figs. 1-2, 8, 10

Material: 2315 specimens from samples 20, 32, 33, 37, 42/41, 43, 44, γ , Z, Y, V, T1, J.

Holotype: NHMW Inv. 2010/0042/0003, height: 2.0 mm, diameter: 0.9 mm, spire angle: 15°; illustrated on pl. 5, figs. 1-2, 8, 10.

Paratype 1: NHMW Inv. 2010/0042/0004, height: 2.5 mm, diameter: 0.9 mm, spire angle: 20°; from type stratum.

Paratype 2 (Coll. NHM Zagreb): Height: 2.2 mm, diameter: 1.0 mm, spire angle: 20°; from type stratum.

Paratype 3 (Coll. NHM Zagreb): Height: 2.4 mm, diameter: 1.0 mm, spire angle: 15°; from type stratum.

Locus typicus: Sinj, Lučane Section.

Stratum typicum: Within lacustrine limestone-lignite interbeddings at the Lučane Section at 69.5 m (sample 44).

Age: Langhian, Middle Miocene.

Diagnosis: A very small, smooth and slender form with wrinkled protoconch, incised sutures and slightly detached aperture.

Description: The protoconch is conical, comprising 1.25 whorls. It is densely covered with distinct wrinkles, classifying it clearly as Pseudamnicolinae. The ornamentation is strongest at the apex, then dissipates consistently and becomes almost smooth towards the transition to the teleoconch. The protoconch is clearly separated from the teleoconch.

The shell is slender elongate; in most cases the specimens are very slender, with whorls only slightly increasing in diameter towards the aperture, whereas some others are more bulky with a broader last whorl. The spire is smooth apart from fine prosocline growth lines and consists of about 5-6 whorls, each convex in profile and with strongly incised sutures. The last whorl takes up to 50% of the total height and ends up in a convex base that becomes almost straight towards the aperture. The latter is elliptical, inclined with an angle of about 30° to the axis and in most cases slightly detached from the base. The lips are equally thickened; in some specimens there is a very weak swelling below the umbilicus.

Remarks: Its protoconch sculpture defined this genus as belonging to the subfamily Pseudamnicolinae. Although there are some other hydrobiid species that show comparable surface patterns on their subadult shell the similarity with the *Pseudamnicola* protoconch is striking (see *P. torbariana* (Pl. 4, figs. 11, 13) and *P. hoeckae* HARZHAUSER & BINDER, 2004). Just in some Belgrandiinae species protoconch features are similar, e.g. in *Microprososthenia* KADOLSKY & PIECHOCKI, 2000. Yet, there is a continuous transition to the teleoconch and rarely a detached aperture. Generally, they are more bulky in shape. One genus that is reminiscent of the new species regarding its shape is *Martinietta* SCHLICKUM, 1974. Its protoconch, however, shows a slightly granular surface, but lacks the distinct wrinkles.

Also the Bithyniidae can be excluded due to their protoconch sculpture; e.g. in *Bithynia jurinaci* (BRUSINA, 1884) very weak spiral striation appears on the initial cap (HARZHAUSER & BINDER, 2004).

Although the shape is reminiscent of *Prososthenia*, the wrinkled protoconch allows a clear separation. The Late Miocene *Prososthenia radmanesti* (FUCHS, 1870) illustrated by BRUSINA (1902) would be similar in shape and size but differs in its larger shell and the less incised sutures. The columellar swelling of the Late Miocene *Odontohydrobia* PAVLOVIĆ, 1928, is more prominent.

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Family Bithyniidae GRAY, 1857

Genus *Fossarulus* NEUMAYR, 1869

Type species: *Fossarulus Stachei* NEUMAYR, 1869, Miocene, Miočić, Dalmatia/SE Croatia.

***Fossarulus* cf. *armillatus* BRUSINA, 1876**

Pl. 5, figs. 11-12, 14

1876 *Fossarulus armillatus* BRUSINA – BRUSINA, p. 112.

1897 *Fossarulus armillatus* BRUS. – BRUSINA, p. 21, pl. 8, figs. 1-2.

1926 *Fossarulus armillatus* BRUSINA – WENZ, p. 2201.

Material: 28 specimens from sample A.

Dimensions: No exact measurements can be performed due to the fragmentary preservation. Size ranges around 4 mm in height and 3 mm in diameter; spire angle: 40-50°.

Description: Protoconch is conical, completely smooth and consists of about 1.5 whorls. Spire is conical, quite bulky and bears delicate sculpture. Whorls are convex with maximum convexity in the adapical half and almost straight-sided towards lower suture. Right at the beginning of the teleoconch 2-3 thin and delicate keels with equal interspaces appear that quickly become more prominent; no sutural ramp is formed. Parallel to the keels extremely fine lines occur, about 6 within the interspaces and ca. 7 above the first keel. Due to pronounced fragmentation the lower whorls and therefore also the aperture are not preserved. After drawings by BRUSINA (1897) the last whorl makes up to 60% of the total height and bears 3 strong and thin keels with very weakly developed nodules. Below, 2-3 very weak keels appear along the aperture. The aperture is ovoid with elevated posterior margin, strongly convex outer and nearly straight to slightly convex inner lip. Both can be extremely thickened.

Distribution: Endemic species of the Dinaride Lake System, recorded from Miočić (BRUSINA, 1897) and section Lučane (137 m).

Remarks: No complete specimen is preserved. Hence, the determination is based on shape and the expression of the keels. It differs from *Fossarulus tricarinatus* BRUSINA, 1870 in its bulkier shape and the thinner keels. Moreover, in *F. tricarinatus* the keels appear not before the third whorl. *Fossarulus moniliferus* BRUSINA, 1876 is less bulky, too.

Although the lower part is missing in each specimen, the nodeless keels at the third whorl preclude a classification as one of the stronger sculptured species, e.g. *Fossarulus fuchsi*.

***Fossarulus fuchsi* BRUSINA, 1882**

Pl. 5, figs. 3-4, 9, 13

1882 *Fossarulus Fuchsi* BRUS. nov. spec. – BRUSINA, p. 38.

1897 *Fossarulus Fuchsi* BRUS. – BRUSINA, p. 21, pl. 7, figs. 27, 28.

1926 *Fossarulus fuchsi* BRUSINA – WENZ, p. 2203.

Material: 6 specimens from samples 32, 33, 37.

Dimensions: No exact measurements can be performed due to the fragmentary preservation. Size ranges around 4 mm in height and 3 mm in diameter; spire angle: 45-60°.

Description: Protoconch conical and smooth, consisting of about 1.5 whorls. Spire conical, bulky with rich sculpture, consisting of up to 4 whorls. Whorls are convex, strongest towards apex, and nearly straight towards lower suture. The first whorls are almost smooth aside from very weak traces of 2-3 keels. These start thin and delicate but become more prominent and increase in number towards the aperture, up to 6 on the last whorl. A concave furrow separates the keel and a narrow sutural ramp is developed above the upper keel. Furthermore, nodes appear on the keels very soon. They are small, round, prominent and numerous. On the last whorl, which makes up about half of the total height, the first two keels (with nodes) below the suture are most prominent. The others – towards the aperture – become indistinct and the lowermost keels do not bear nodes any more. The aperture is not preserved. Referring to the drawings of BRUSINA (1897) it is ovoid and has a strongly convex and thickened outer lip. The inner lip is nearly straight to slightly convex.

Distribution: Endemic species of Lake Sinj, recorded from the localities Potravljje (BRUSINA, 1897) and Lučane (60-65 m).

Remarks: This species is hard to separate from similar ones such as *F. stachei* NEUMAYR, 1869, *F. hoernesii* BRUSINA, 1882 and *F. auritus* BRUSINA, 1882.

These could be identified based on their different apertures, but in none of the specimens this part is preserved completely. Therefore, size and the development of keels and nodes, especially on the first few whorls are chosen as main criterion for identification. *F. hoernesii* and *F. auritus* are much larger, *F. stachei* is more bulky in shape and develops two distinct keels without nodes on the second whorl.

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Subclass Heterobranchia GRAY in TURTON, 1840

Order Pulmonata CUVIER, 1817

Superfamily Lymnaeoidea RAFINESQUE, 1815

Family Lymnaeidae RAFINESQUE, 1815

Subfamily Lymnaeinae RAFINESQUE, 1815

Genus *Lymnaea* LAMARCK, 1799

Type species: *Helix stagnalis* LINNAEUS, 1758, Recent.

***Lymnaea* sp.**

Pl. 6, figs. 1-2, 11

Material: 12 specimens from samples 32, 33, Z, T1, J, A.

Dimensions: No complete specimen preserved, just upper whorls; height: up to 5 mm, diameter: up to 3.5 mm.

Description: Protoconch smooth, with erect tip, consisting of about half a whorl. Spire smooth and high conical; the number of whorls cannot be determined, because no complete specimen exists. The whorls increase rapidly in dimensions and seem to be rhomboidal in profile – one outline convex with strongest curvature abapically, second one also convex but most bent adapically. Sutures moderately incised. No aperture is preserved.

Distribution: Recorded from section Lučane (60-132 m).

Remarks: There are just two *Lymnaea* species described from this region: *Lymnaea klaici* BRUSINA, 1884 is an elegant species, with high conical spire and conspicuous inner lip; *Lymnaea korlevici* BRUSINA, 1884 is broader and shows fewer whorls, whereas the last one is very prominent making up to 80% of the total height. The poor preservation does not allow any clear identification.

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Superfamily Planorboidea RAFINESQUE, 1815

Family Planorbidae RAFINESQUE, 1815

Subfamily Planorbinae RAFINESQUE, 1815

Genus *Gyraulus* AGASSIZ, 1837

Type species: *Planorbis albus* O. F. MÜLLER, 1774, Recent.

***Gyraulus geminus* (BRUSINA, 1897)**

Pl. 6, figs. 3, 10

1897 *Planorbis geminus* BRUS. n. sp. – BRUSINA, p. 5, pl. 2, figs. 11-16.

1923 *Gyraulus (Gyraulus) geminus* (BRUSINA) – WENZ, p. 1554.

Material: 15 specimens from samples V, A.

Dimensions: Height: about 0.5 mm, diameter: about 2 mm (up to 4 mm).

Description: Protoconch consists of about 1.25 whorls and shows the typical striae for the genus *Gyraulus* (RIEDEL, 1993). Shell thick-walled, discoidal, smooth and consists of up to 5 whorls. Whorls are planspiral, strongly rounded to slightly flatten in profile and increase rapidly in diameter; each whorl covers about 20% of the preceding one and is about twice as large in height. Last whorl attains about 25-35% of the total diameter. No distinct keel appears, but strongest curvature is in the middle of the whorl. The aperture is not preserved. The outer lip is elevated in the middle resulting in a more or less triangular shape; margins are convex. Surface is smooth, aside from weak prosocline growth lines.

Distribution: Recorded from localities Goručica, Miočić (BRUSINA, 1897) and Lučane (115.5 m, 137 m).

Remarks: *G. geminus* can be easily differed from *Gyraulus dalmaticus* (BRUSINA, 1884) by the keel and the relatively larger last whorl of the latter species. Another similar species is *Gyraulus pulici* (BRUSINA, 1897), which is larger and just recorded from Bosnia and Herzegovina.

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Genus *Orygoceras* BRUSINA, 1882

Type species: *Orygoceras dentaliforme* BRUSINA, 1882, Miocene, Ribarić, Dalmatia/SE Croatia.

***Orygoceras cornucopiae* BRUSINA, 1882**

Pl. 6, fig. 6

1882 *Orygoceras cornucopiae* nov. spec. – BRUSINA, p. 45, pl. 11, figs. 1-3.

1897 *Orygoceras cornucopiae* BRUS. – BRUSINA, p. 2, pl. 1, figs. 7-9.

1902 *Orygoceras cornucopiae* BRUS. – BRUSINA, pl. 2, figs. 15-16.

1928 *Orygoceras cornucopiae* BRUSINA – WENZ, p. 2485.

Material: 4 specimens from samples 32, 33, 37, J.

Dimensions: Due to fragmentary preservation no measurements could be taken; after BRUSINA (1882) the height reaches up to 7.8 mm and the diameter up to 1.4 mm.

Description: Protoconch consists of about 0.75 whorls and shows typical striae. Spire is uncoiled, dentaliform and long, attaining its largest diameter towards the aperture. Spire starting smooth, but soon prominent rings with narrow interspaces occur. These rings become more prominent towards the aperture.

Distribution: Endemic species of the Dinaride Lake System. It is recorded from the localities Parčić, Miočić (BRUSINA, 1882, 1897) and Lučane (60-130.5 m).

Remarks: Differs from *O. stenonemus* by the dense formation of rings.

***Orygoceras dentaliforme* BRUSINA, 1882**

Pl. 6, fig. 4

1882 *Orygoceras dentaliforme* nov. spec. – BRUSINA, p. 42, pl. 11, figs. 9-15.

1897 *Orygoceras dentaliforme* BRUS. – BRUSINA, p. 2, pl. 1, figs. 13-14.

1928 *Orygoceras dentaliforme* BRUSINA – WENZ, p. 2485.

Material: 372 specimens from samples 22, 25, 32, 33, 37, 43, 44, 45, γ, Z, Y, V, T1, M2, Lx, L, J.

Dimensions: Due to fragmentary preservation no measurements can be taken; after BRUSINA (1882) the height reaches up to 7 mm and the diameter up to 1.5 mm. The collected specimens fit within this range.

Description: Protoconch consists of about 0.75 whorls and shows typical striae, designating it as planorbid species (HARZHAUSER et al., 2002). Spire is uncoiled, dentaliform and long, attaining its largest diameter towards aperture. Shell usually smooth except for few large ring-like swellings formed by growth lines in few specimens. If present, they occur only in the abapical part of the shell. Rings are always regularly around spire, parallel to aperture.

Distribution: Endemic species of the Dinaride Lake System. It is recorded from the localities Parčić, Ribarić, Sinj (Župića potok) (BRUSINA, 1882, 1897) and Lučane (45-130.5 m).

Remarks: Differs from *O. stenonemus* and *O. cornucopiae* by being either smooth or bearing less prominent, fewer and far more abapically situated rings.

***Orygoceras stenonemus* BRUSINA, 1882**

Pl. 6, figs. 5, 9

1882 *Orygoceras stenonemus* nov. spec. – Brusina, p. 43, pl. 11, figs. 4-8.

1897 *Orygoceras stenonemus* BRUS. – BRUSINA, p. 2, pl. 1, figs. 10-12.

1928 *Orygoceras stenonema* BRUSINA – WENZ, p. 2490.

Material: 43 specimens from samples 32, 33, 37, 42/41, 43, 44, β, T1, Lx, L, J.

Dimensions: Due to fragmentary preservation no measurements could be taken; after BRUSINA (1882) the height ranges around 5 mm and the diameter is up to 1 mm. The specimens fit within this range.

Description: Protoconch consists of about 0.75 whorls and shows typical striae. The spire is uncoiled, dentaliform and long, attaining its largest diameter close to the aperture. Spire starting smooth, but soon prominent rings with wide interspaces occur. They become more prominent towards the aperture.

Distribution: Endemic species of the Dinaride Lake System. It is recorded from the localities Parčić, Ribarić, Sinj (Župića potok) (BRUSINA, 1882, 1897) and Lučane (60-130.5 m).

Remarks: Differs from *O. cornucopiae* by the wider interspaces between the rings.

Subfamily Bulininae P. FISCHER & CROSSE, 1880

Genus *Ferrissia* WALKER, 1903

Type species: *Ancylus rivularis* SAY, 1817, Recent, Eastern North America.

***Ferrissia illyrica* (NEUMAYR, 1880)**

Pl. 6, figs. 7-8, 12

1880 *Ancylus Illyricus* n.f. – NEUMAYR, p. 486, pl. 7, fig. 16.

1902 *Ancylus illyricus* NEUM. – BRUSINA, pl. 1, figs. 20-21.

1907 *Ancylus illyricus* NEUM. 1880 – BRUSINA, p. 195.

1923 *Pseudancylus illyricus* (NEUMAYR) – WENZ, p. 1698.

Material: 1 specimen from sample 44.

Dimensions: Height: 2.8 mm, diameter: 1.5 mm, convexity: 1 mm.

Description: Protoconch round, ranges around 400 µm and bears a “collar” of numerous and narrow spaced, thin radial ribs. At the uppermost part it is smooth and shows a small pit right in the center. The shell is ovoid and slightly broader anterior. The apex points slightly towards right. Moreover, distinct concentric growth lines appear. At the inside the radial ribs extend almost to the shell margins, whereas the growth lines are restricted to the outer surface.

Distribution: Recorded from Haptovac/Metokija (Gacko Basin, Bosnia and Hercegovina) (NEUMAYR, 1880), Parčić, Miočić (BRUSINA, 1902) and Lučane (69.5 m).

Remarks: WALKER (1903) separated the Eastern American ancylids into two “sections” (treated as subgenera), *Laevapex* with smooth apex and *Ferrissia* with radial ribs. The ribs and the pit at the protoconch identified this specimen unmistakable as *Ferrissia*. It is similar to *Ferrissia wittmanni* that is recorded from the Ottnangian of the Western Paratethys (KOWALKE & REICHENBACHER, 2005) and *Ferrissia* species from the Sarmatian of the Central Paratethys (HARZHAUSER & KOWALKE, 2002) and shows nearly the same protoconch features, but differs conspicuously in strong radial ribs reaching to the shell margins.

NEUMAYR (1880) described this species belonging to the genus *Ancylus* O. F. MÜLLER, 1774. As already mentioned by SCHLICKUM (1976), the shape of the shell of *Ferrissia* differs from *Ancylus* and also from *Acroloxus* BECK, 1838. *Ancylus* is characterized by a cap-like shape with a more rounded shell and a higher apex; *Acroloxus* is distinguished by its apex pointing to the left, whereas in *Ferrissia* it points towards the right.

SCHLICKUM (1976) also quoted erroneously that *Ferrissia illyrica* is also known from the Pontian stage (Upper Miocene), while NEUMAYR (1880) described this species from the Middle Miocene of Bosnia and Herzegovina (MANDIC et al., submitted).

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Class Bivalvia LINNAEUS, 1758

Superorder Heterodonta NEUMAYR, 1883

Order Veneroida H. & A. ADAMS, 1856

Family Dreissenidae GRAY in TURTON, 1840

Genus *Mytilopsis* CONRAD, 1858

Type species: *Mytilus leucophaetus* CONRAD, 1831, Recent, Eastern USA.

***Mytilopsis aletici* (BRUSINA, 1907)**

Pl. 7, fig. 8

1907 *Congerina aletici* n. sp. – BRUSINA, p. 206.

1978 *Congerina aletici* n. sp. – KOCHANSKY-DEVIDÉ in KOCHANSKY-DEVIDÉ & ŠLIŠKOVIĆ, p. 61-63, 94, pl. 11, figs. 10-15, pl. 12, figs. 1-2.

Material: 20 specimens from samples 45, μ , β .

Dimensions: The available specimens from the samples are poorly preserved. Therefore, the better preserved specimens collected from debris at the topmost part of the section have been measured. Length, height, convexity: 57 x 57 x 6 mm, 50 x 42 x 6 mm, 52 x 52 x 6 mm.

Description: Shell circular, large and flat, with straight dorsal margins and strongly convex anterior margin. Shell wall is thin. Furthermore, the shell bears prominent growth lines and usually a delicate but sharp and short keel, starting at the umbo and stretching across about one third of the shell.

Distribution: Endemic from Dinaride Lake System, recorded from Sinj Basin (BRUSINA, 1907) and Kupres Basin (KOCHANSKY-DEVIDÉ & ŠLIŠKOVIĆ, 1978). In section Lučane it appears between 70.5 and 107.5 m.

Remarks: Differs from both *M. frici* and *M. drvarensis* by its umbonal angle, which attains in both species c. 90°, whereas in *M. aletici* it measures c. 180°. Moreover, it differs from *M. drvarensis* in surface sculpture: *M. aletici* has a shorter keel, no radial ribs and is larger.

Because BRUSINA (1907) added no illustration to his description, KOCHANSKY-DEVIDÉ & ŠLIŠKOVIĆ (1978) described this form erroneously again as new species, although BRUSINA provided a valid description with exact statement of locality (Kalina at Košute, southern Sinj Basin).

***Mytilopsis cf. drvarensis* (TOULA, 1913)**

1913 *Congeria Drvarensis* n. f. – TOULA, p. 642, pl. 24, figs. 11-12.

1978 *Congeria drvarensis* TOULA 1913 – KOCHANSKY-DEVIDÉ in KOCHANSKY-DEVIDÉ & ŠLIŠKOVIĆ, p. 58, 93, pl. 9, figs. 16-28, pl. 10, figs. 1-12.

Material: 1 specimen from sample 9.

Dimensions: No exact measurements could be taken due to fragmentation. Estimated values: length, height, convexity: 40 x 45 x 5.6 mm, umbonal angle: ca. 90°.

Description: Shell large, moderately convex with convexity index (c/H) of about 0.12, rounded in outline. Dorsal margins, both anterior and posterior, are slightly concave to straight, and form an umbonal angle of c. 90°. The ventral margin is convexly rounded. Keel is prominent, stretching from umbo in ventral direction with length of about ¾ of total shell diameter. Hereby also distinct growth lines occur. No hinge is preserved.

Distribution: Endemic from Dinaride Lake System, recorded from following localities/regions: Drvar Basin, Sanski Most, Bihać Basin, Livno Basin, Mostar Basin, Gacko Basin, Sinj Basin (KOCHANSKY-DEVIDÉ & ŠLIŠKOVIĆ, 1978). In section Lučane it appears at 98 m.

Remarks: The preservation of available material is poor; the classification of the only specimen is based on the long keel, the size and the umbonal angle but it cannot be excluded that the specimen represents only a variation of *M. aletici*.

Generally, *M. drvarensis* differs from *M. aletici* in longer exterior surface keel and occasionally by the presence of weak radial ribs behind the keel.

***Mytilopsis jadrovi* (BRUSINA, 1892)**

Pl. 7, figs. 1-2, 9

1892 *Congeria Jadrovi* BRUSINA – BRUSINA, p. 195.

1897 *Congeria Jadrovi* BRUS. – BRUSINA, p. 30, pl. 17, figs. 12-14.

1902 *Congeria Jadrovi* BRUS. – BRUSINA, pl. 21, figs. 2-5.

1978 *Congeria jadrovi* BRUSINA 1897 – KOCHANSKY-DEVIDÉ in KOCHANSKY-DEVIDÉ & ŠLIŠKOVIĆ, p. 37-38, 87, pl. 1, figs. 26-39.

Material: 1316 specimens from samples 20, 22, 25, 26, 32, 33, 37, 42/41, 43, 44, 45, v1, v, μ , γ , β , Z, Y, V, T1, O, Lx, L, J, A.

Dimensions: Length, height, convexity of some specimens: 4.5 x 7.5 x 2 mm, 2 x 3.5 x 1 mm, 4 x 5.5 x 2 mm.

Description: Shell subtriangular, elongated, with two equally sized valves, measuring up to 8 mm in height and up to 5 mm in length. Umbo is pointed with an angle reaching from 40-75°. Dorsal posterior margin slightly convex to nearly straight. From this point, the margin bends strongly and becomes convex towards the ventral end. This is pointed but slightly rounded. Anterior margin is in most cases more or less straight with intention of a byssal notch. A prominent broad keel is present, slightly bent to nearly straight, reaching the ventral margin. In dorsoventral profile it forms a convex crest, most curved at about one third of the height. Divided by the keel two main fields can be distinguished: both the posterior and the anterior field appear to be nearly straight to slightly convex in profile, whereas the anterior field is far more inclined. The shell exterior surface is smooth. The hinge comprises an elongated posterior internal ligament band and a distinct apophysis, situated posterior from the pointed umbo, reaching from small to prominent and comprising a triangular shape, with an angle of about 90-130°. It bears an anterior byssal retractor muscle imprint that is positioned at the ventral part of the hinge plate and appears to be semilunar in shape. The anterior adductor muscle lies in the center of the hinge plate and forms a slightly curved incision, reaching from the posterior margin of the hinge plate to the apophysis. The shape of the posterior muscle

imprints could not be determined, being either very indistinctly or rarely preserved. The pallial line has no sinus.

Distribution: Endemic from Dinaride Lake System, recorded from following localities/regions: Sinj Basin (BRUSINA, 1897), Miočić, Biočić, Kadina glavica, Psunj, Utinja, Medvednica, Prijedor, Eminovo Selo, Zenica, Sarajevo, Konjic (KOCHANSKY-DEVIDÉ & ŠLIŠKOVIĆ, 1978). In section Lučane it appears between 41.5 and 137 m.

Remarks: Differs from *M. nitida* whose keel is more straight and blunt resulting in a reduction of the anterior external surface field; moreover it is more convex in shape. The distribution is almost the same, but it is even more prevalent than *M. jadrovi*. Another similar species is *M. neumayri*, but this one is by far larger and the keel is not that high. Furthermore, the anterior external surface field is strongly reduced. *M. neumayri* occurs also in the Pannonian Basin System, from the Karpatian to the Upper Pannonian.

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Superorder Palaeoheterodonta NEWELL, 1965

Order Unionida STOLICZKA, 1871

Family Unionidae RAFINESQUE, 1820

Genus *Unio* PHILIPSSON, 1788

Type species: *Mya pictorum* LINNAEUS, 1758, Recent.

***Unio cf. rackianus intermedius* ŽAGAR-SAKAČ, 1987**

Pl. 7, fig. 3

1874 *Unio Rackianus* BRUSINA – BRUSINA, p. 115, pl. 5, figs. 9-10.

1987 *Unio rackianus intermedius* n. ssp. ŽAGAR-SAKAČ – ŽAGAR-SAKAČ, p. 77, pl. 5, figs. 1-3.

Material: 1 specimen from samples 44.

Dimensions: Due to fragmentation the length could not be measured but just estimated. Length, height, convexity: 32 x 24 x 9 mm, umbonal angle: about 125°.

Description: Shell elliptically in shape, strongly convex, especially towards the middle of the shell height. On both sides of the umbo a slight depression occurs in outline before it merges

in its elliptical shape. Although the shell is damaged it shows an intention of two posterior radial keels. Also some weak growth lines appear. Because the shell sticks in the sediment umbo and inner features could not be described.

Distribution: Endemic from Dinaride Lake System, recorded from Muša, Panj/Hrvace (Sinj Basin), Miočić, Koljane (ŽAGAR-SAKAČ, 1987) and Lučane (69.5 m).

Remarks: Due to poor preservation the determination is based on the two radial keels and moreover on shape and size. Regarding these features, *U. rackianus intermedius* differs from other subspecies. The nominal subspecies *Unio rackianus rackianus* BRUSINA, 1874 is much larger and more elongated, whereas *Unio rackianus simplex* ŽAGAR-SAKAČ, 1987 is more compact; both show stronger keels.

Unio sp.

Pl. 7, figs. 4-7

Material: 2 adult specimens from sample 43, 1 juvenile from sample 44 (Pl. 7, figs. 4-7).

Dimensions: Length, height, convexity: 30 x 25 x 5 mm (estimated values; because of fragmentation no measurements could be taken); juvenile specimen: length, height, convexity: 2.8 x 1.9 x 0.8 mm.

Description: As far as the shape can be identified in adult specimens, the shell appears to be quite short. The surface consists of at least two strong posterior keels. Hinge and inner features are not sufficiently preserved.

The juvenile specimen is almost complete and ovoid to sub-rectangular shaped. The prodissoconch is raised, slightly acuminate and cap-like; it bears the embryonic shell that measures about 200 µm. The outer surface bears weak growth lines and a posterior field which is demarcated by a slight keel. The hinge consists of extremely prominent cardinal and elongated posterior teeth. Especially the cardinal tooth of the right valve is strongly broadened and extended. On both valves the hinge plate between cardinal and posterior teeth has an angle of about 150°. Muscle scars are small and rounded to ovoid, the pallial line is integripalliat.

Distribution: Recorded from section Lučane from 68.5-69.5 m.

Remarks: Due to pronounced fragmentation the adult individuals could not be identified on species level.

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Zusammenfassung

Quantifizierung von Evolution – fossile Süßwasser-Mollusken des Dinariden-Seensystems (Mittel-Miozän, Sinj-Becken, SO Kroatien)

Diese Untersuchung behandelt Evolutionsprozesse und Umweltveränderungen anhand eines mittel-miozänen Aufschlusses im Sinj-Becken (Dalmatien, SO Kroatien), das die Ablagerungsgeschichte eines langlebigen Süßwassersees widerspiegelt. Trotz einer weit reichenden Untersuchung fehlten bisher quantitative Daten, um Einsicht in Artenverteilungen, taxonomische Beziehungen und die Ursachen der morphologischen Veränderungen zu erhalten.

Die taxonomische Diversifikation der Süßwasser-Gastropoden in Verbindung mit morphologischen Disparitäts-Events wurde anhand eines ca. 100 m dicken Profils, das den obersten Teil der Beckenfüllung umfasst, dokumentiert. Basierend auf dem bestehenden Altersmodell passieren diese Änderungen in nur wenigen zehntausend Jahren, was erneut die Bedeutung langlebiger Seen für die Evolutionsforschung belegt. Des Weiteren lässt die Gleichzeitigkeit der morphologischen Abwandlungen bei voneinander systematisch unabhängigen Taxa auf einen engen Konnex zu Umweltveränderungen schließen. Höchstwahrscheinlich sind klimatische Fluktuationen, die zu Schwankungen des Seespiegels und der Habitattypen führte, treibende Faktoren für diese Radiationsevents.

Diese Studie beinhaltet die Anwendung statistischer Methoden auf quantifizierte Proben und eine taxonomische Revision der auftretenden Taxa. Anschließend folgt eine Interpretation des Paläoenvirons auf Basis der Molluskenverteilung. Dies wird unterstützt durch sedimentologische Daten und frühere palynologische Analysen. Tatsächlich wird das frühere Modell der Gliederung in zwei Kalkstein-Kohle-Zyklen bestätigt, die vom seichten Milieu mit mittlerer Wasserenergie und hohem Süßwassereintrag über fossilarme Transgressionskalksteine zu einem seichten, niedrigerenergetischen Setting reichen und zuletzt die komplette Austrocknung des Sees am Profiltop dokumentieren.

Die Diskussion setzt einen Schwerpunkt auf die Evolutionslinien von vier Arten, je zwei der Gattungen *Melanopsis* und *Prososthenia* (Kapitel 4.5.). Alle vier Arten kommen nahezu im ganzen Profil vor und können in mehrere Morphotypen untergliedert werden, basierend auf

ihrer Skulpturierung; in wenigen Fällen auch ob ihrer Größe. Es wird gezeigt, dass die Morphotypen sequentiell auftreten, jeder mehr oder weniger beschränkt auf einen bestimmten Abschnitt. Diese morphologischen Veränderungen passieren zeitgleich in unterschiedlichen Taxa.

Schlüsselwörter: Evolutionslinien, Radiationsevents, Paläoökologie, statistische Analyse, Mittel-Miozän, Dinariden-Seensystems, Sinj-Becken

- - -

Plates

Plate 1

- Figs. 1-3. *Melanopsis lyrata* NEUMAYR, 1869, morph B (= *semicostata* forma of OLUJIĆ, 1999). Scale bar corresponds to 0.5 cm; from sample 44.
- Figs. 4-6. *Melanopsis lyrata* NEUMAYR, 1869, morph C (= *costata* forma of OLUJIĆ, 1999). Scale bar corresponds to 0.5 cm; from sample Z.
- Figs. 7-9. *Melanopsis lyrata* NEUMAYR, 1869, morph D (= *lyrata* forma of OLUJIĆ, 1999). Scale bar corresponds to 0.5 cm; from sample V.
- Figs. 10-12. *Melanopsis* n. sp.
Holotype (NHMW Inv. 2010/0042/0001); scale bar corresponds to 1 cm; from sample 44.
- Figs. 13-15. *Melanopsis lanzaeana* BRUSINA, 1874, morph A (= *lanzaeana* forma of OLUJIĆ, 1999). Scale bar corresponds to 0.5 cm; from sample 44.
- Figs. 16-18. *Melanopsis lanzaeana* BRUSINA, 1874, morph B (= *rugosa* forma of OLUJIĆ, 1999). Scale bar corresponds to 1 mm; from sample Z.
- Figs. 19-21. *Melanopsis lanzaeana* BRUSINA, 1874, morph C (= *costata* forma of OLUJIĆ, 1999). Scale bar corresponds to 0.5 cm; from sample A.
- Fig. 22. *Melanopsis lyrata* NEUMAYR, 1869, morph A (= *glabra* forma of OLUJIĆ, 1999). Scale bar corresponds to 0.5 cm; from sample 33.

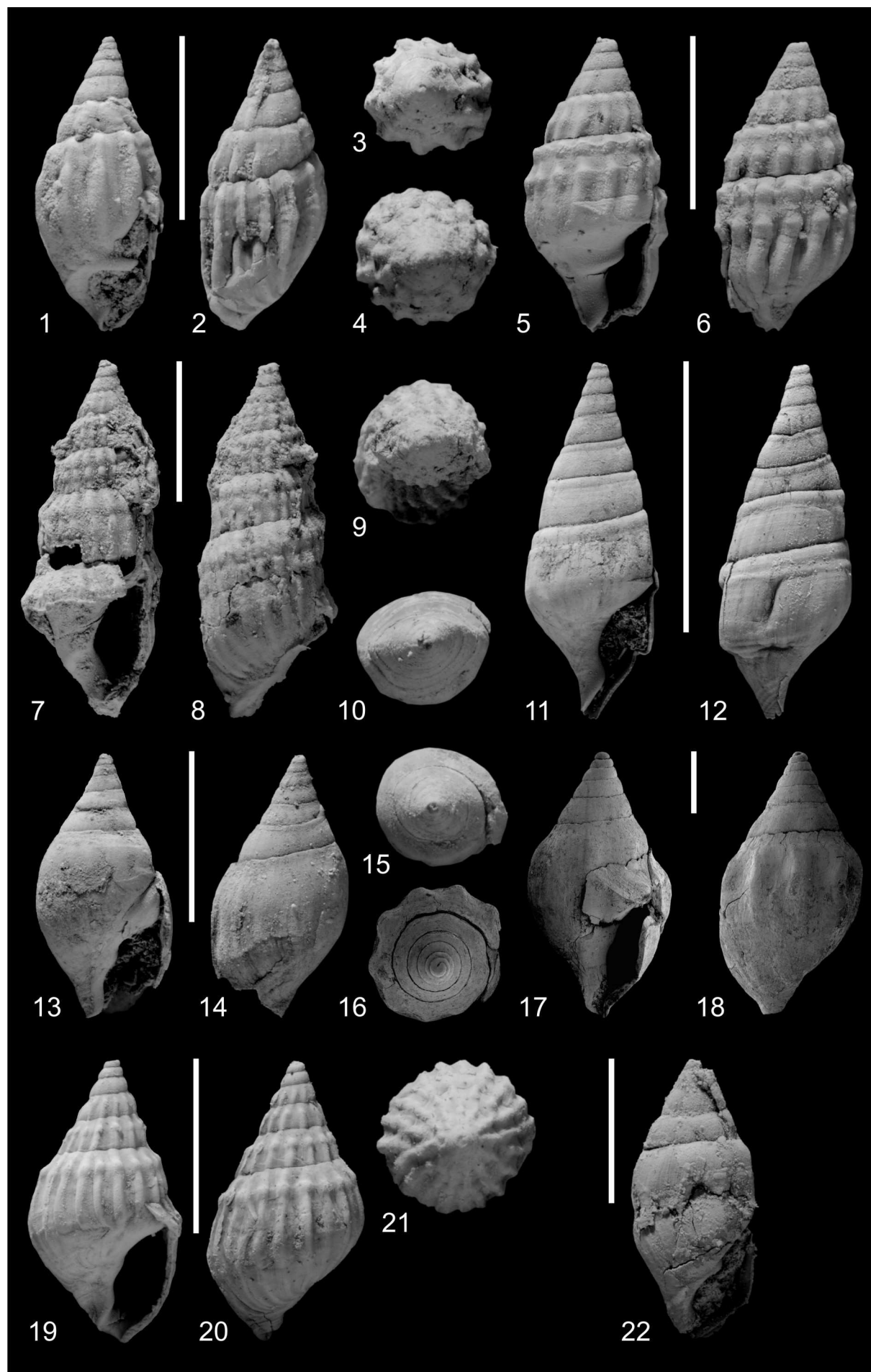


Plate 2

Scale bar corresponds to 1 mm

- Figs. 1-3, 7. *Prososthenia schwarzi* NEUMAYR, 1869, morph A (= *transitans* forma of OLUJIĆ, 1999). Fig. 7 shows protoconch of fig. 1; from sample 44.
- Figs. 4-6, 8. *Prososthenia schwarzi* NEUMAYR, 1869, morph A (= *transitans* forma of OLUJIĆ, 1999). Fig. 8 shows protoconch of fig. 5; from sample 44.
- Figs. 9-10, 13. *Prososthenia schwarzi* NEUMAYR, 1869, morph C (= *semicostata* forma of OLUJIĆ, 1999). From sample Z.
- Figs. 11-12, 14-15. *Prososthenia schwarzi* NEUMAYR, 1869, morph C (= *semicostata* forma of OLUJIĆ, 1999). Fig. 15 shows protoconch of fig. 11; from sample Z.

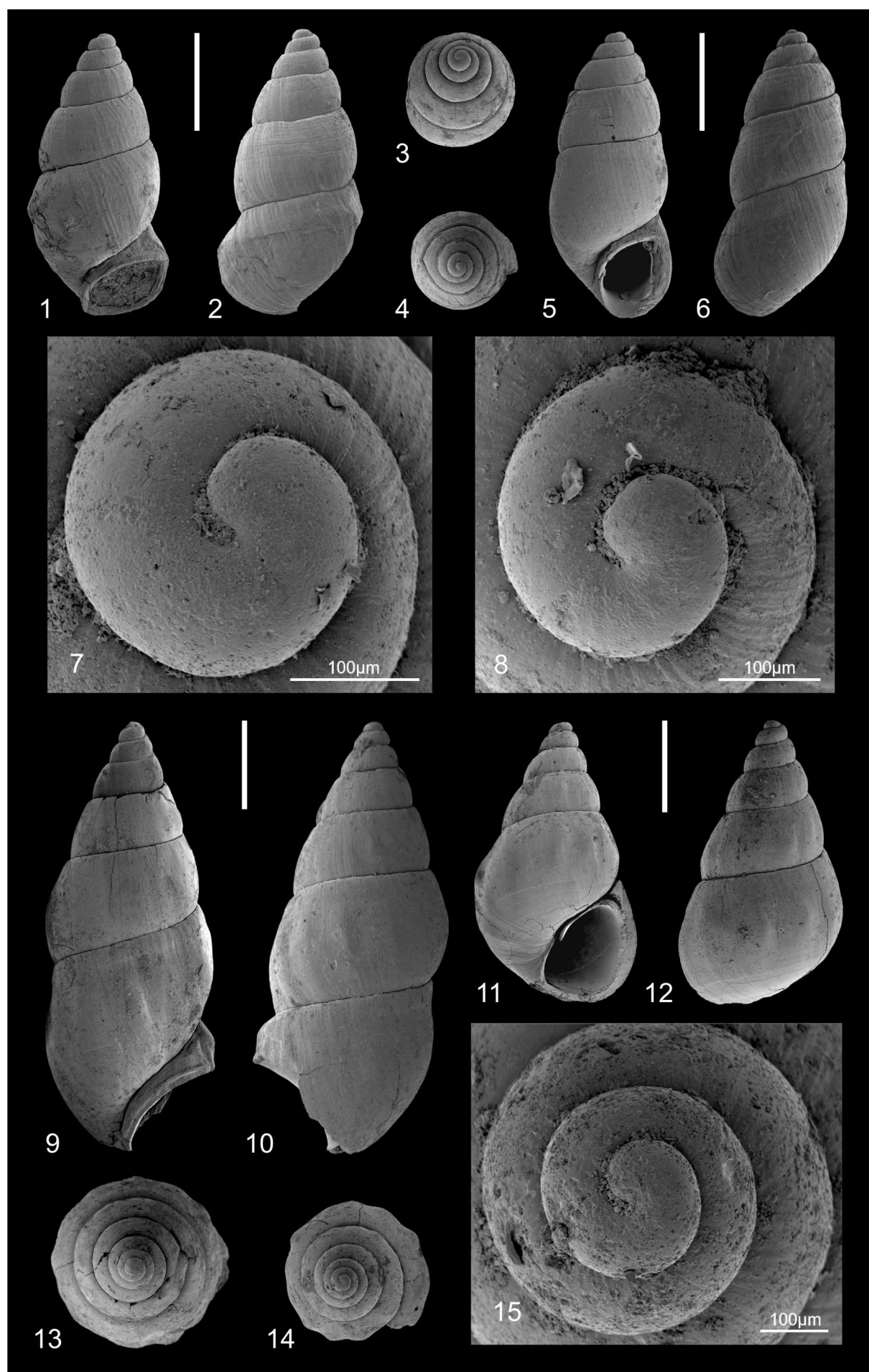


Plate 3

Scale bar corresponds to 1 mm

- Figs. 1-2, 5. *Prososthenia schwarzi* NEUMAYR, 1869, morph B (= *apleura* forma of OLUJIĆ, 1999). From sample 44.
- Figs. 3-4, 6. *Prososthenia schwarzi* NEUMAYR, 1869, morph D (= *schwarzi* forma of OLUJIĆ, 1999). From sample V.
- Figs. 7-9. *Prososthenia cincta* NEUMAYR, 1869, morph A (= *primaeva* forma of OLUJIĆ, 1999). From sample 44.
- Figs. 10, 13-14. *Prososthenia cincta* NEUMAYR, 1869, morph C (= *semievoluta* forma of OLUJIĆ, 1999). From sample Z.
- Figs. 11-12. *Prososthenia cincta* NEUMAYR, 1869, morph C (= *semievoluta* forma of OLUJIĆ, 1999). From sample Z.

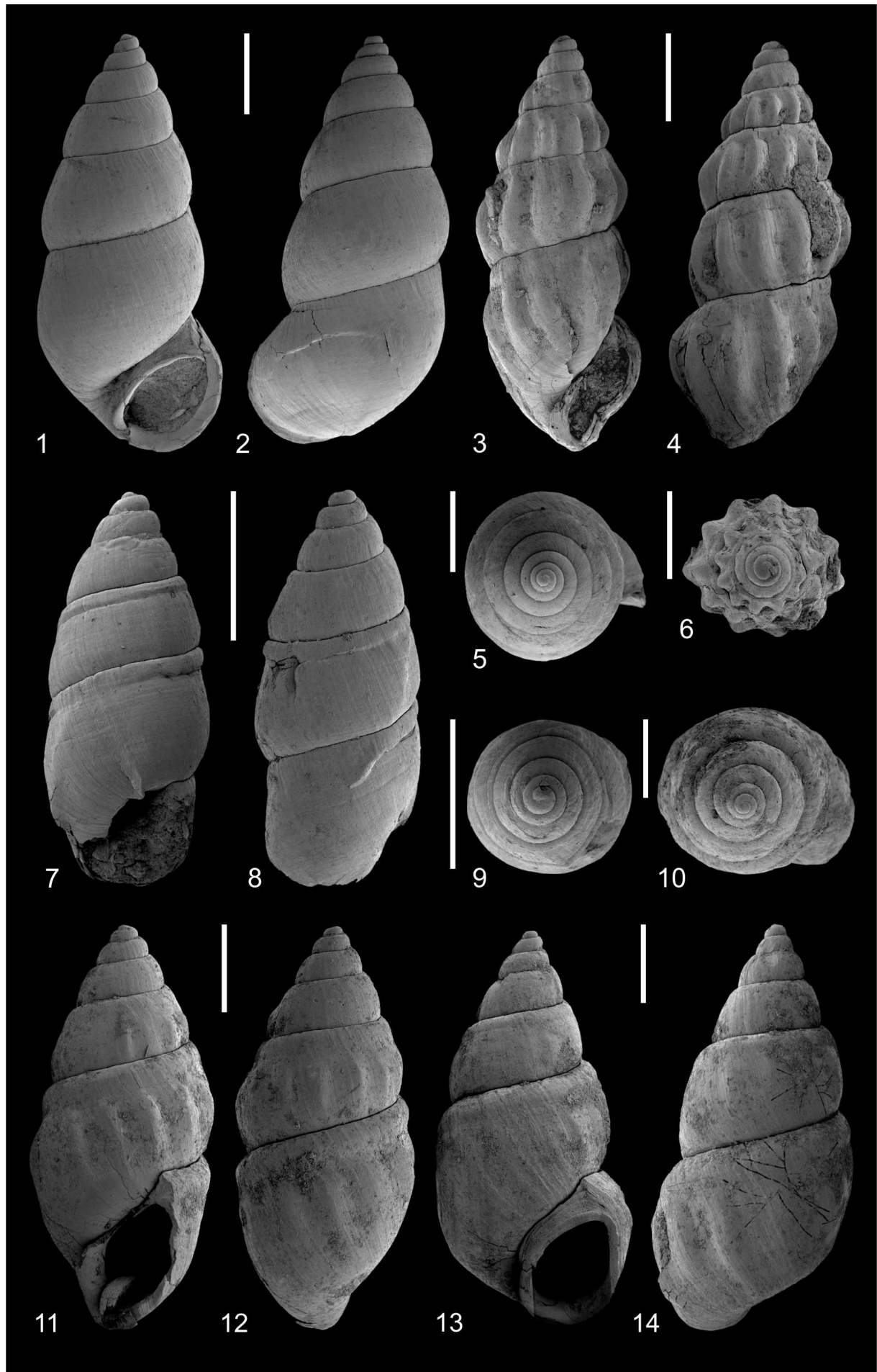


Plate 4

- Figs. 1-2, 5. *Prososthenia cincta* NEUMAYR, 1869, morph D (= *cincta* forma of OLUJIĆ, 1999). Scale bar corresponds to 1 mm; from sample Z.
- Figs. 3-4, 6, 12. *Prososthenia neutra* BRUSINA, 1897.
Scale bar corresponds to 1 mm; fig. 12 shows protoconch of fig. 3; from sample A.
- Fig. 7. *Prososthenia bicarinata* OLUJIĆ, 1999.
Scale bar corresponds to 1 mm; from sample Z.
- Figs. 8-11, 13. *Pseudamnicola torbariana* (BRUSINA, 1874).
From sample 44.
Specimen 1: 8) scale bar corresponds to 0.2 mm; 13) detail of fig. 8.
Specimen 2: 9-10) scale bar corresponds to 1 mm; 11) detail of fig. 9.

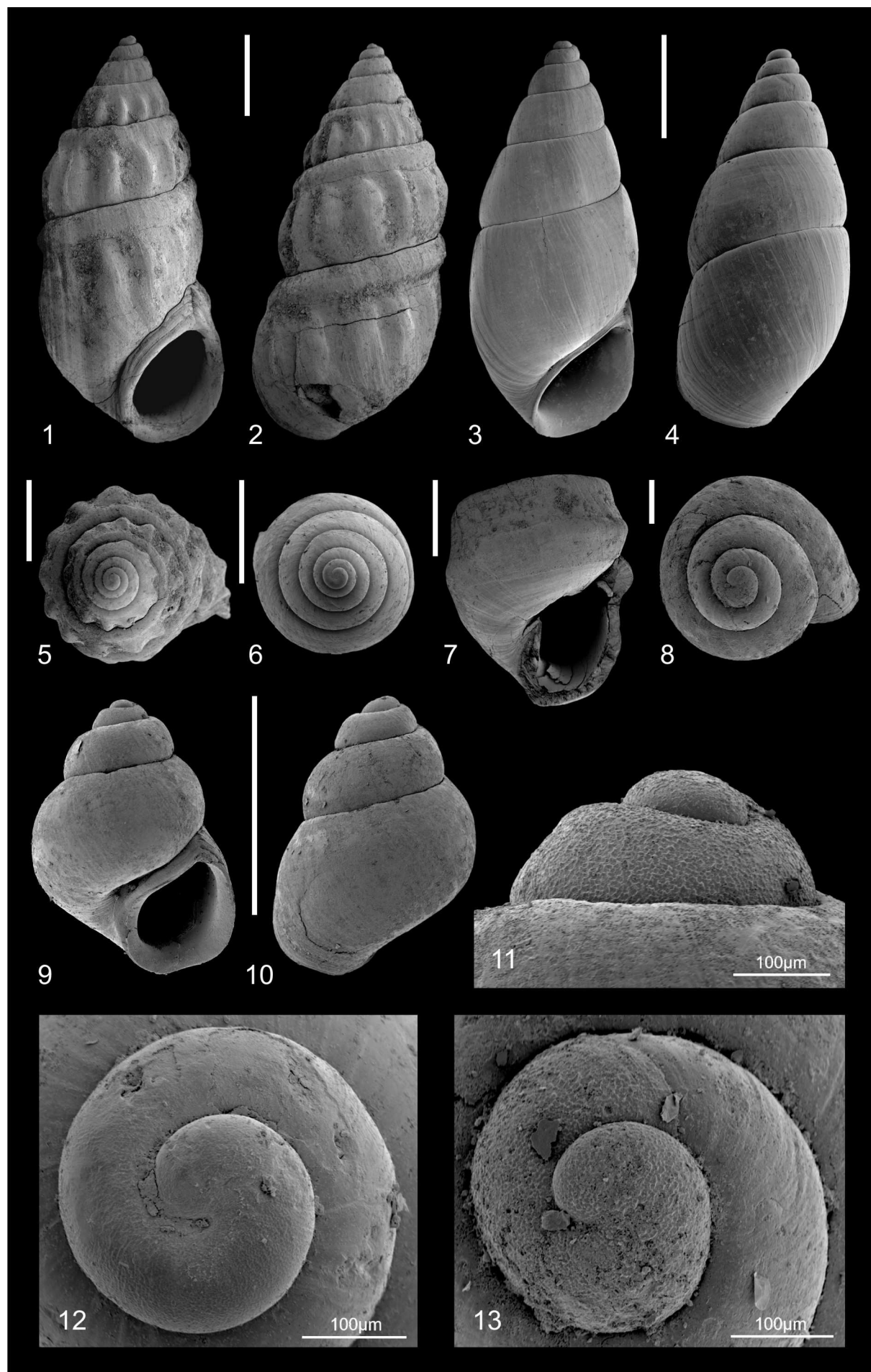


Plate 5

- Figs. 1-2, 8, 10. *Pseudamnicola* n. sp.
Holotype (NHMW Inv. 2010/0042/0003); 1-2) scale bar corresponds to 1 mm; 8) scale bar corresponds to 0.5 mm; fig. 10 shows protoconch of fig. 1; from sample 44.
- Figs. 3-4, 9, 13. *Fossarulus fuchsi* BRUSINA, 1882.
Scale bar corresponds to 1 mm; fig. 13 shows protoconch of fig. 3; from sample 33.
- Figs. 5-7. *Theodoxus sinjanus* (BRUSINA, 1876).
Scale bar corresponds to 1 mm; from sample 44.
- Figs. 11-12, 14. *Fossarulus* cf. *armillatus* BRUSINA, 1876.
Scale bar corresponds to 1 mm; fig. 14 shows protoconch of fig. 11; from sample A.

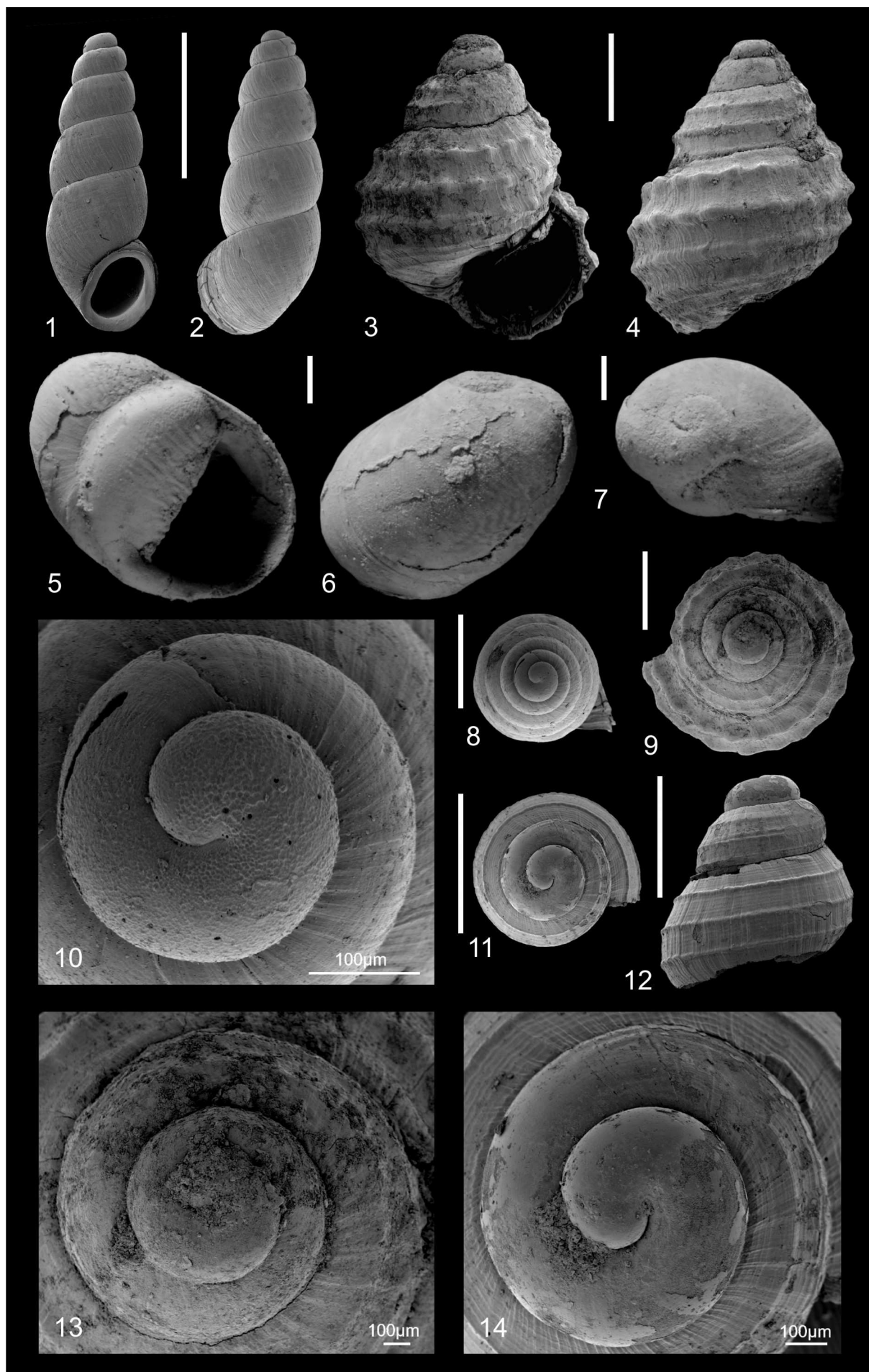
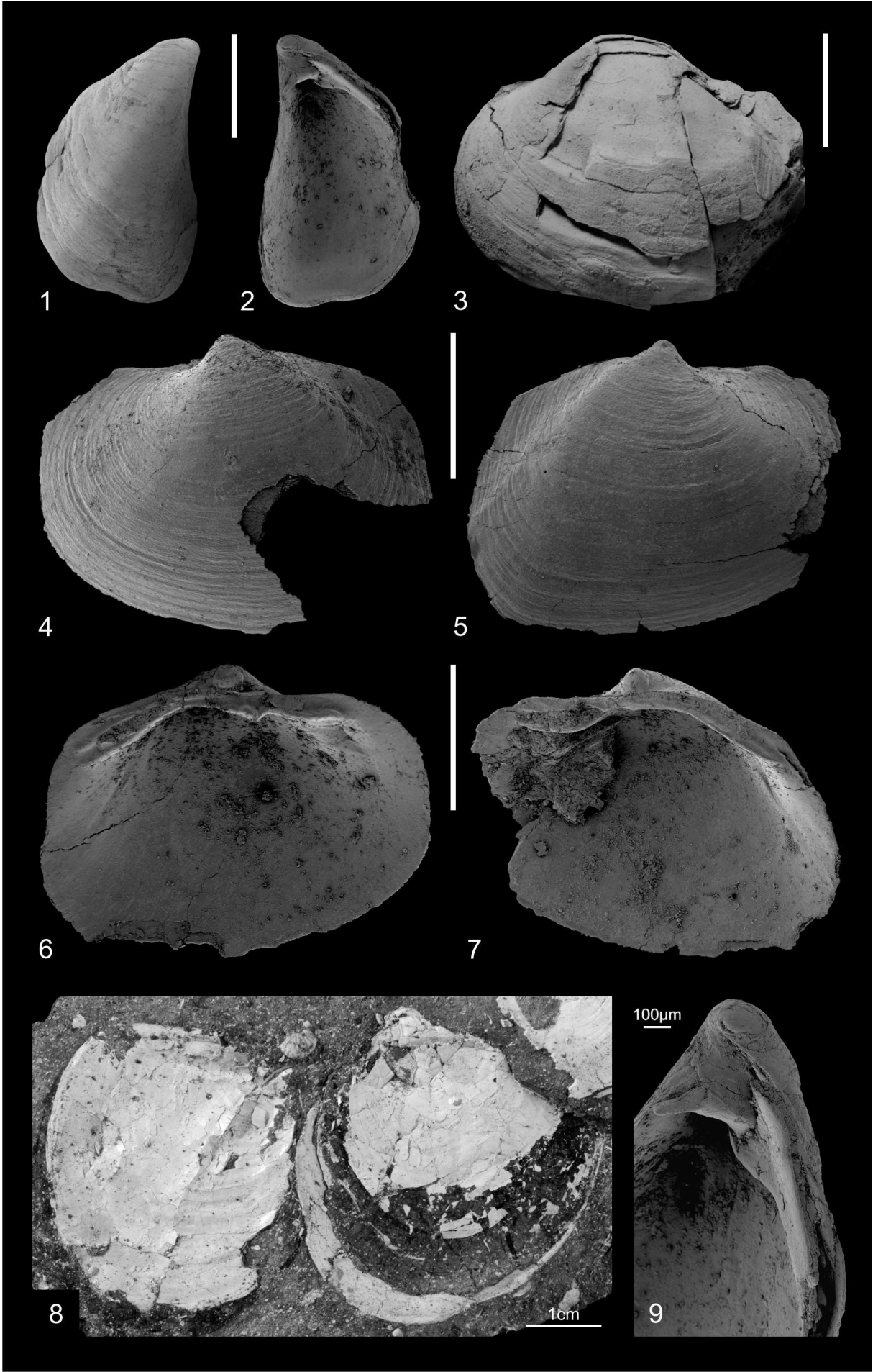


Plate 6

- Figs. 1-2, 11. *Lymnaea* sp.
Scale bar corresponds to 1 mm; fig. 11 shows protoconch of fig. 1; from sample A.
- Figs. 3, 10. *Gyraulus geminus* (BRUSINA, 1897).
Scale bar corresponds to 1 mm; fig. 10 shows protoconch of fig. 3; from sample A.
- Fig. 4. *Orygoceras dentaliforme* BRUSINA, 1882.
Scale bar corresponds to 1 mm; from sample J.
- Figs. 5, 9. *Orygoceras stenonemus* BRUSINA, 1882.
Specimen 1: 5) scale bar corresponds to 1 mm; from sample J.
Specimen 2: 9) protoconch; from sample 44.
- Fig. 6. *Orygoceras cornucopiae* BRUSINA, 1882.
Scale bar corresponds to 1 mm; from sample J.
- Figs. 7-8, 12. *Ferrissia illyrica* (NEUMAYR, 1880).
Scale bar corresponds to 1 mm; fig. 12 shows protoconch of fig. 7; from sample 44.

Plate 7

- Figs. 1-2, 9. *Mytilopsis jadrovi* (BRUSINA, 1892).
RV; scale bar corresponds to 1 mm; fig. 9 shows hinge of fig. 1;
from sample 44.
- Fig. 3. *Unio* cf. *rackianus intermedius* ŽAGAR-SAKAČ, 1987.
LV; scale bar corresponds to 1 cm; from sample 44.
- Figs. 4-7. *Unio* sp.
Juvenile specimen; 4, 6) LV; 5, 7) RV; scale bar corresponds to 1 mm;
from sample 44.
- Fig. 8. *Mytilopsis aletici* (BRUSINA, 1907).
From the collection of the NHMW.



Curriculum vitae

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1993-1997	Elementary school: VS Leonding, A-4060 Leonding
1997-2005	Secondary school: BRG Fadingerstraße 4, A-4020 Linz
2005	Graduation diploma
2005-2006	Civilian Service at the Retirement Home Hart-Leonding

Scientific career

2006	Matriculation of Biology at University of Vienna
2008	Specialization on Paleobiology
2008	Fieldwork at Hallstatt/Austria regarding biostratigraphy of Late Triassic ammonites.
2008	Participation in an excavation of a Burdigalian oyster-reef at Stetten in Korneuburg (Austria) under the leadership of the Natural History Museum Vienna.
2008	Excursion to selected Mesozoic and Cenozoic localities of Southern Germany with particular reference to faunal composition and regional geology.
2008-2009	Sample preparation and treatment at the Natural History Museum Vienna.
2008-2010	Digitalization and inventory of type material at the Natural History Museum Vienna.
2009	Excursion to several localities in the Western USA, with special emphasis on the mammal evolution of Northern America.
2009	Educational excavation of Pleistocene cave bears in the High Tatra, Slovakia.
2009	Fieldwork at Gbely in Slovakia with emphasis on Late Miocene freshwater systems.
Since 2009	Member of the Austrian Paleontological Society (ÖPG).
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- 2010 Excursion to the Red Sea with emphasis on the actuopaleontologic comparison of fossil and recent reefs.
- 2010 Excavation of ammonite sites in Southern Turkey with focus on Late Triassic biostratigraphy.
- 2010 Excavation of a Miocene mammal site in Northern Greece with emphasis on paleobiogeography and -diversity.
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Publications

- BASTL, K. A. & NEUBAUER, T. A. 2010. Tagungsbericht zum 37. Treffen des Arbeitskreises Wirbeltierpaläontologie in der Paläontologischen Gesellschaft in Wien. – GMit, 40: 62-64.

Vienna, September 10th, 2010

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