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Middle Miocene freshwater mollusks from Lake Sinj (Dinaride Lake System, SE Croatia; Langhian)

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Abstract

This study provides the first assemblage-based taxonomic revision of the mollusk fauna of the Middle Miocene Dinaride Lake System (DLS). The assemblage, consisting of more than 13.000 specimens, was sampled from a 100-m-thick Lower Langhian interval of the Lučane section in the Sinj Basin (Croatia). 18 gastropod species and 3 bivalve species are detected from the succession. All are endemic to the Dinaride Lake System. Within that system, the described fauna of Lake Sinj displays strong similarities with the coeval and geographically close fauna of Lake Drniš. Reduced faunistic relations to other lakes of the DLS are discussed to result from slightly different stratigraphic ages and deviating paleoecologic settings. Many melanopsid and prososthenid gastropod taxa in the literature are considered to be mere morphotypes of few polymorphic species resulting in nomenclatorial rectifications.

Melanopsis lucanensis Neubauer n. sp. and *Belgrandia klietmanni* Neubauer n. sp. are introduced as new species.

Key words: Miocene, freshwater, gastropods, bivalves, taxonomy, new species, variability.

Kurzfassung

Diese Arbeit präsentiert die erste taxonomische Revision der mittelmiozänen Molluskenfauna des Dinariden-Seen-Systems (DLS) basierend auf der quantitativen Analyse einer distinkten Vergesellschaftung. Die Vergesellschaftung aus mehr als 13.000 Individuen stammt aus einem 100 m mächtigen Intervall des unteren Langhiums des Lučane Profils im Sinj Becken (Kroatien). 18 Gastropoden- und 3 Bivalvenarten wurden in der Abfolge nachgewiesen. Alle davon sind endemisch für das DLS. Innerhalb des Seen-Systems zeigt die beschriebene Fauna große Übereinstimmungen mit der des gleich alten und geographisch nahe gelegenen Drniš-Sees. Deutlich geringere faunistische Beziehungen zu anderen Seen des DLS dürften auf etwas unterschiedliche stratigraphische Alter und unterschiedliche paläoökologische Bedingungen zurückzuführen sein. Viele Melanopsiden- und Prososthenien-Taxa der Literatur werden lediglich als Morphotypen einiger weniger polymorpher Arten betrachtet, was zu zahlreichen nomenklatorischen Berichtigungen führt.

Melanopsis lucanensis Neubauer n. sp. und *Belgrandia klietmanni* Neubauer n. sp. werden als neue Arten eingeführt.

Schlüsselwörter: Miozän, Süßwasser, Gastropoden, Bivalven, Taxonomie, neue Arten, Variabilität.

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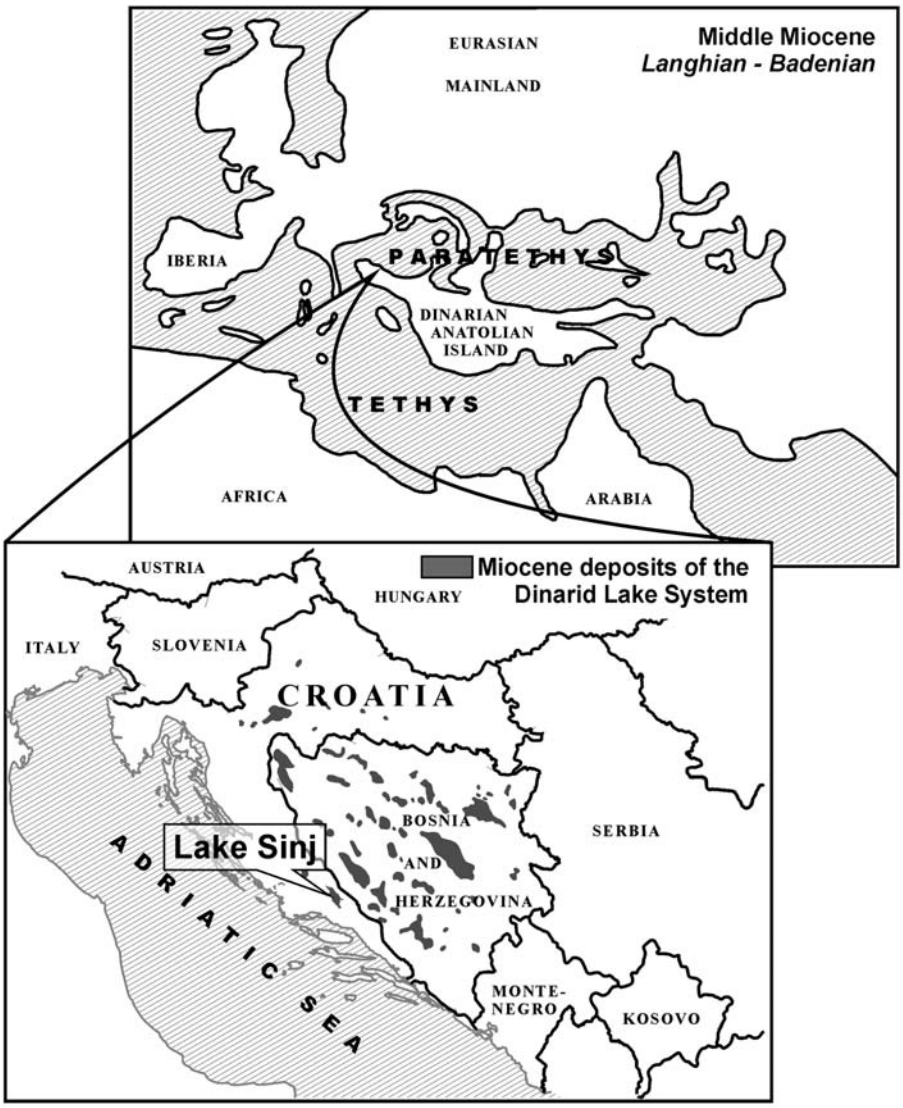
Introduction

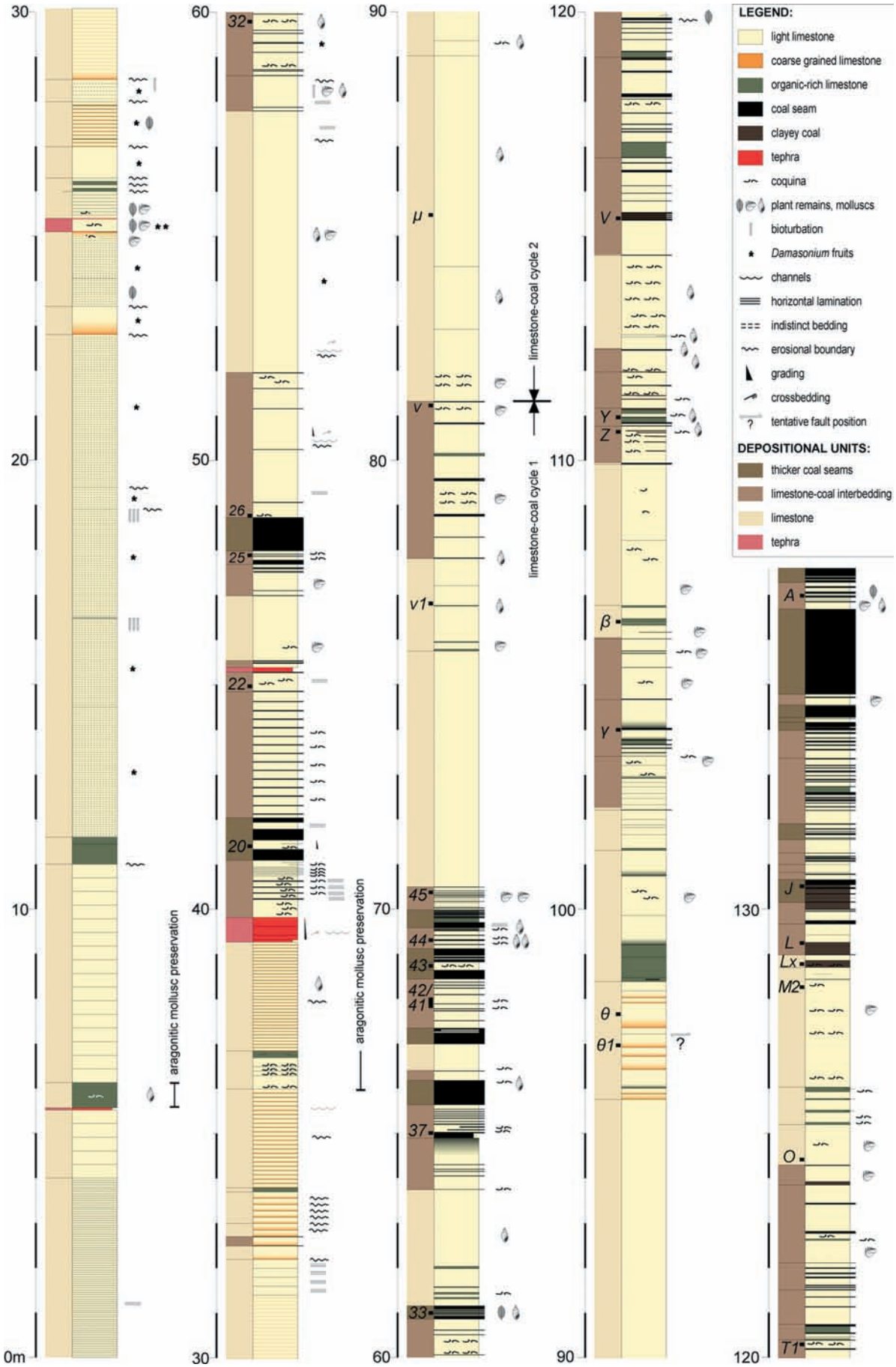
During the Early and Middle Miocene Southeastern Europe accommodated a series of long-lived freshwater lakes, termed the Dinaride Lake System (DLS; Fig. 1; KRSTIĆ et al. 2003, HARZHAUSER & MANDIC 2008). This system comprised a series of more or less interconnected individual lakes which are usually termed according to the geological basin in which the related sediments are preserved. Due to erosion, the connections between these basins are unknown and it cannot be categorically excluded that the DLS existed as huge lake, covering c. 75,000 km^2 during short episodes (HARZHAUSER & MANDIC 2008). The different stratigraphic ages of several basins, however, point to a succession of lakes in time of very variable extension spanning the time between ~18 and ~13 Ma. The stratigraphic data are available from Lake Gacko (MANDIC et al. 2011a), Southern Pannonian Basin (MANDIC et al. 2011b), Lake Pag (JIMÉNEZ-MORENO et al. 2009), Lake Livno (DE LEEUW et al. 2011) and Lake Sinj (DE LEEUW et al. 2010). Lake Drniš (NEUMAYR 1869, BRUSINA 1874, 1897) and Lake Kupres (BRUSINA 1902, KOCHANSKY-DEVIDÉ & SLIŠKOVIĆ 1981) provide further mollusk-rich faunas which are still poorly dated.

Aside from new stratigraphic data only the taxonomic analysis gives hints to the connectivity and faunistic similarities between these basins. The Sinj Basin, which was covered by Lake Sinj, represents a classic area of research on Miocene mollusks. The taxonomic frame was established already by the end of the 19th century in nu-



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

► Fig. 2. Lučane section with position of studied samples, indicated by numbers and letters (modified after MANDIC et al. 2009).


LEGEND:
light limestone
coarse grained limestone
organic-rich limestone
coal seam
clayey coal
tephra
coquina
plant remains, molluscs
bioturbation
Damasonium fruits
channels
horizontal lamination
indistinct bedding
erosional boundary
grading
crossbedding
tentative fault position
DEPOSITIONAL UNITS:
thicker coal seams
limestone-coal interbedding
limestone
tephra
limestone-coal cycle 2
limestone-coal cycle 1
aragonitic mollusc preservation
aragonitic mollusc preservation
0m
10
20
30
40
50
60
70
80
90
100
110
120
130
32
26
25
22
20
45
44
43
42/
41
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μ
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Lx
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O
T1

merous extensive monographic studies (Neumayr 1869, Brusina 1870, 1874, 1876, 1881, 1882, 1884, 1892, 1897, 1902 and 1907). Subsequently, Olujić (1936, 1999) tried to describe evolutionary lineages of prososthenid and melanopsid gastropods. More recent investigations dealt with the taxonomy and regional distribution of Dreissenidae (Kochansky-Devidé & Slišković 1978, Harzhauser & Mandic 2010), Unionidae (Žagar-Sakač 1981, 1986, 1987, 1990, Žagar-Sakač & Sakač 1984), Neritidae (Jurišić-Polšak 1979) and certain *Fossarulus* species (Jurišić-Polšak 1984). A synthesis of the literature data on the gastropod fauna of the DLS is provided by Harzhauser & Mandic (2008) and an analysis of the stable isotope patterns of several mollusk species from the DLS is presented by Harzhauser et al. (2011).

Geological setting

The studied Lučane section 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 tectonic depression within the External Dinarides, measuring 38 × 9 km (Mandic et al. 2009). Calculated from ESRI© ArcGis® 9 data the lake sediments today preserved cover an area of 132 km² within a karst region made up of Mesozoic to Paleogene platform carbonates (Korbar 2009). The sedimentary succession has been studied by Kerner (1905 and 1916a, b), Šušnjara & Šćavničar (1974) and Šušnjara & Sakač (1988). Recently, Mandic et al. (2009) and De Leeuw et al. (2010) provided a detailed sedimentological analysis and an age model, which is based on Ar/Ar dating of volcanic ashes and magnetostratigraphy. According to these papers, the thickness of the basinal infill in the studied region reaches more than 500 m. This investigation deals with its topmost interval consisting of c. 100-m-thick coal-bearing limestones (Fig. 2) which were deposited between 15.4 and 15.0 Ma (Early Langhian); the base of the section 39.5 m is marked by a 40-cm-thick tephra layer, dated at 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). Recurrent changes between dry and humid phases have been related to astronomical cycles (Mandic et al. 2009). The overall warm climate corresponds to the conditions expected for the Middle Miocene Climatic Optimum. Latest isotope analyses of mollusks shells yielded a mean surface water temperature around 19–21°C (Harzhauser et al. 2011). Moreover, isotope values were similar to those from coeval layers from the Drniš Basin. This, and a high number of co-occurring taxa (e.g., Brusina 1874, 1882, 1897; Neumayr 1869), might indicate hydrological interconnection between both lakes, whereas a possible influence of the proximate proto-Mediterranean Sea can be excluded (Harzhauser et al. 2011).

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. In some cases, complete specimens were picked out before sieving to prevent the fragile mollusks from damage while washing. Only the residues of the coarse fraction (250 µm) were determined and counted. 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. In bivalves for each species the number of the most abundant valve was counted.

Systematics

The systematic order follows largely Bouchet & Rocroi (2005, 2010). For planorbid phylogeny insights of recent studies on molecular data were adopted (Albrecht et al. 2007). All specimens are stored in the collection of the Natural History Museum Vienna under the prefix NHMW 2010/0042. Type materials from Brusina (1874, 1876, 1882 and 1897), Neumayr (1869 and 1880) and Olujić (1999) and material from the collection of the NHMW have been studied.

Class Gastropoda Cuvier 1797

Subclass Neritimorpha Golikov & Starobogatov 1975

Superfamily Neritoidea Rafinesque 1815

Family Neritidae Rafinesque 1815

Subfamily Neritininae 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 Grateloupana* [sic] Férussac – Neumayr: 365, pl. 12, figs. 16–17 (partim) [non *Neritina Grateloupiana* Férussac 1823].

1876 *Neritina sinjana* Brusina: 113.

1884 *Neritodonta sinjana* Brusina – Brusina: 82.
1897 *Neritodonta sinjana* Brus. – Brusina: 28, pl. 15, figs. 10–21.
1929 *Theodoxus* (*Calvertia*) *sinjanus* (Brusina) – Wenz: 2980.
1974 *Theodoxus* (*Calvertia*) *sinjanus* (Brusina) – Milan et al.: 110.
1979 *Theodoxus* (*Neritaea*) *sinjanus* (Brusina) – Jurišić-Polšak: 19, pl. 3, figs. 4–11.

Material: 486 specimens from samples 20, 25, 26, 32, 33, 37, 42/41, 43, 44, 45, ν1, ν, γ, β, Z, Y, V, T1, M2, L.

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

Description: Protoconch flat and immersed, smooth, consisting of c. 1 whorl. Spire short and bulky, consisting of up to 4 whorls. The last whorl forms a weak shoulder with a more or less straight ramp and convex flanks. The aperture is semicircular; the inner lip is nearly straight and the outer lip strongly convex. The broad columellar plate is moderately dentated with the maximum sculpture in its middle part. Coloring is highly variable, including dense striation, zigzag lines or mottled patterns. Usually, this pattern covers the entire shell; in some cases it is limited to regular bands.

Remarks: It is separated from the DLS species *T. semidentatus* (Sandberger 1875) by the distinctly lower spire and it lacks the slight concavity within the adapical third of the whorls. *Theodoxus crenulatus* (Klein 1853) is widespread in coeval deposits of the freshwater systems fringing the Paratethys Sea (~15–12 Ma; Zwiefaltendorf/Germany, Soceni/Romania and the Vienna Basin; Harzhauser & Mandic 2008). A main difference between *T. crenulatus* and *T. sinjanus* is that in the latter the wrinkles and folds of the columellar pad are most prominent in its middle part and reach there far to the base, thus covering a more or less trigonal area of the pad. The Early Miocene *Theodoxus grateloupianus* (Férussac 1823) sensu Lozouet et al. (2001) develops a deep suture between last whorl and spire and its callus pad is well demarcated from the base.

Distribution: Endemic species of the Dinaride Lake System (DLS), known from Lake Sinj and Lake Drniš (Brusina 1884, 1897, 1907; Jurišić-Polšak 1979; Jurišić-Polšak et al. 2000). It is recorded from the localities Sinj (Župića potok / type locality, Novi bunar), Lučane (41.5–129.5 m), Brnaze (well NB-1), Crveni klanac and Miočić.

Subclass Caenogastropoda Cox 1959

Order Cerithiimorpha Golikov & Starobogatov 1975

Superfamily Cerithioidea Fleming 1822

Family Melanopsidae H. & A. Adams 1854

Genus ***Melanopsis*** Férussac 1807

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

Melanopsis lanzaeana Brusina 1874

Pl. 1, Figs. 13–21

1869 *Melanopsis pygmaea* "Partsch" – Neumayr: 356, pl. 12, fig. 1 [non *Melanopsis pygmaea* Hörnes 1856].
1874 *Melanopsis Lanzaeana* Brusina: 34.
1884 *Melanopsis Trstenjaki* Brusina: 55.
1897 *Melanopsis Lanzaeana* Brus. – Brusina: 12, pl. 5, figs. 7–8.
1897 *Melanopsis Lanzaeana rugosa* Brusina: 12, pl. 5, fig. 9 [non *Melanopsis rugosa* Handmann 1887].
1897 *Melanopsis Trstenjaki* Brus. – Brusina: 15, pl. 4, fig. 9.
1929 *Melanopsis lanzaeana lanzaeana* Brusina – Wenz: 2770.
1929 *Melanopsis lanzaeana rugosa* Brusina – Wenz: 2771.
1999 *Melanopsis lanzae lanzae* (Brusina) – Olujić: 21, 49, pl. 2, figs. 13–14, 21.
1999 *Melanopsis lanzae rugosa* (Brusina) – Olujić: 21, 49, pl. 2, figs. 15–18, 22–24, pl. 3, fig. 25.
1999 *Melanopsis lanzae costata* Olujić: 21, 49, pl. 2, figs. 19–20, pl. 3, figs. 26–28 [non *Melanopsis costata* (Olivier 1804), non *Melanopsis costata* Neumayr 1869].
1999 *Melanopsis trstenjaki* Brusina – Olujić: 21, 50, pl. 3, fig. 29.
1999 *Melanopsis lanzae senilis* Olujić: 22, 50, pl. 3, figs. 30–32, 34.

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 and smooth, consisting of about 1 whorl. Spire conical and compact, consisting of up to 8 straight to slightly convex-sided whorls. The strongly adpressed whorls form a coeloconoid outline. Only few specimens develop sculpture of opisthocline axial ribs on early teleoconch whorls (= *costata*-morphotype in Olujić 1999). These are of highly variable number and strength. Nodes occur on the ribs close to the upper suture on the last 2–4 whorls, being arranged into a more or less prominent spiral row. The nodes 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* Brusina 1897) or are completely missing (= *lanzaeana* Brusina 1874 s.str.). The suture below the row of nodes is only weakly incised. The axial ribs grade into sigmoidal ribs which fade out on the base towards the siphonal canal. The last whorl develops 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 without forming a fold. Rarely, the original coloring is preserved as brown to yellow zigzag lines.

R e m a r k s : *Melanopsis lanzaeana* is a morphologically very variable species with numerous morphotypes. Although their stratigraphic ranges may overlap, most of the morphotypes tend to be confined largely to certain stratigraphic levels. Three morphotypes are especially distinct:

1. *Melanopsis lanzaeana* (s.str.) morphotype A is characterized by a lack of sculpture and represents the *M. lanzaeana* as defined by BRUSINA (1874). It appears within the samples 25, 32, 33, 37, 43, 44, Z, Y, T1, M2 with 486 specimens.

2. *Melanopsis lanzaeana* morphotype B develops weak sculpture consisting of weak ribs and nodes, which may cause large swellings. It is represented in samples 44, Z, Y, V, J with 129 specimens. This morphotype was described as *Melanopsis lanzaeana rugosa* by BRUSINA (1897). According to ICZN 53.3 this name, however, is unavailable as a primary homonym of *Melanopsis rugosa* HANDMANN 1887 which was established for a Late Miocene species from the Vienna Basin.

3. *Melanopsis lanzaeana* morphotype C bears a large number of prominent axial ribs and small distinct knobs. It occurs in samples Z, V, T1, L, J, A with 232 specimens. OLUJIĆ (1999) introduced the name *Melanopsis lanzae costata* for this morphotype. According to ICZN 53.3 this name is unavailable as a primary homonym of *Melanopsis costata* NEUMAYR 1869 (= *Melanopsis cosmanni* PALLARY 1916) which is an Early Pliocene species from Slavonia. Moreover, it is a secondary homonym of *Melania costata* OLIVIER 1804, which is an extant species in the Eastern Mediterranean region.

Apart from these 3 morphotypes, OLUJIĆ (1999) considered two other taxa from stratigraphically younger deposits as members of the *lanzaeana*-lineage: *M. trstenjaki* BRUSINA 1884 and *M. lanzae senilis* OLUJIĆ 1999. *M. trstenjaki* from Potravlje (Sinj Basin), is similar to *M. lanzaeana* morph C but has more wide-spaced ribs and the nodes are more spiny and pointing upwards. *M. l. senilis* has a strongly reduced sculpture with traces of both axial ribs and a single row of nodes. These two taxa indeed seem to represent morphological entities within the phylogenetic lineage of *M. lanzaeana* and should be treated as morphotypes D and E.

Melanopsis lanzaeana differs from *Melanopsis lyrata* in its more compact habitus, the prominent callus pad, the mostly missing or weakly expressed columellar 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 from Lake Pannon (PAPP 1953, HARZHAUSER & MANDIC 2008). Aside from the huge stratigraphic gap between both species, *Melanopsis pygmaea* differs in its much more slender and higher conical shell from *M. lanzaeana*.

D i s t r i b u t i o n : *Melanopsis lanzaeana* is an endemic DLS species known exclusively from Lake Sinj (Lučane section, 48–137 m, Ribarić section, BRUSINA 1874, 1897).

Melanopsis lucanensis NEUBAUER n. sp.

Pl. 1, Figs. 10–12

M a t e r i a l : 9 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: NHMW Inv. 2010/0042/0035, height: 10 mm, diameter: 4 mm, spire angle: 30°; from type stratum; Paratype 3: NHMW Inv. 2010/0042/0036, height: 16 mm, diameter: 6 mm, spire angle: 35°; from sample 43 (68.5 m).

D e r i v a t i o n o m i n i s : Named after the section.

L o c u s t y p i c u s : Sinj, Lučane Section.

S t r a t u m t y p i c u m : Within lacustrine limestone-lignite interbeddings at the Lučane Section at 69.5 m (sample 44).

A g e : Early Langhian, Middle Miocene.

D i a g n o s i s : A slender, high conical melanopsid with elevated spire, relatively short last whorl and a subsutural swelling.

D e s c r i p t i o n : Protoconch conical, consisting of about 1 whorl. 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 starts within the last 3–5 whorls, expressed by weak to prominent swellings below the sutures. Aperture ovoid, elongate and narrow, with 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. The species displays a high variability in size. One specimen appears to be about two to three times larger than the other type attaining c. 35 mm in height and 15 mm in diameter. The holotype, being the most complete specimen, is a subadult specimen as suggested by the relatively long siphonal canal (~⅛ of total height).

R e m a r k s : *Melanopsis lucanensis* differs from other morphologically similar species (*M. visianiana* BRUSINA 1874, *M. friedeli* BRUSINA 1885, *M. astathmeta* BRUSINA 1897, *M. filifera* NEUMAYR 1880) mostly by the presence of the subsutural swelling or by the strength of that feature (*M. sinjana* BRUSINA 1874). Due to the high spire, the last whorl is much smaller in *M. lucanensis* 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 these 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.

Melanopsis enodata Brusina 1897 is slightly reminiscent species of the new species. It was originally introduced as subspecies of *Melanopsis geniculata* Brusina 1874 from Župića potok (Sinj Basin). It corresponds to *M. lucanensis* in its rather slender shape and the delicate swelling below the sutures but is smaller and has an elliptical outline. In addition, it bears conspicuous bulges beneath the swellings and remnants of weak axial ribs on the last whorl.

Distribution: Known so far only from Lake Sinj (Lučane section, 68.5–69.5 m).

Melanopsis lyrata Neumayr 1869

Pl. 1, Figs. 1–9, 2

1869 *Melanopsis (Canthidomus) lyrata* Neumayr: 358, pl. 11, figs. 8a–b.
1874 *Melanopsis lyrata* Neumayr – Brusina: 44–45.
1874 *Melanopsis lyrata* var. *cylindracea* Brusina: 45.
1874 *Melanopsis lyrata* var. *misera* Brusina: 45.
1876 *Melanopsis cylindracea* Brusina – Brusina: 115.
1897 *Melanopsis lyrata* Neumayr – Brusina: 10, pl., 4, figs. 6–7.
1897 *Melanopsis misera* Brus. – Brusina: 10, pl. 4, fig. 8.
1929 *Melanopsis cylindracea* Brusina – Wenz: 2698.
1999 *Melanoptychia lyrata glabra* Olujić: 20, 48, pl. 1, figs. 1a–b [non *Melanopsis glabra* Brusina 1874].
1999 *Melanoptychia lyrata semicostata* Olujić: 20, 48, pl. 1, figs. 2–4.
1999 *Melanoptychia lyrata costata* Olujić: 20, 48, pl. 1, figs. 5–12 [non *Melanopsis costata* (Olivier 1804), non *Melanopsis costata* Neumayr 1869].
1999 *Melanopsis lyrata lyrata* Neumayr – Olujić: 20, 48, pl. 1, figs. 7–10.

Material: 1210 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 smooth and conical, consisting of about 1 whorl. Spire high conical, consisting of up to 8 slightly convex 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 (*costata*-morphotype in Olujić 1999) or strongly axially elongate swellings (*semicostata*-morphotype in Olujić 1999). Both sculpture elements, nodes and ribs, may even be largely reduced (*glabra*-morphotype 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 then passes 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.

Remarks: *Melanopsis lyrata* is a quite variable species. Whilst the holotype of Neumayr (1869) is a very slender shell with prominent nodes, Olujić (1999) illustrates much more bulky shells with predominant axial sculpture. Olujić (1999) introduced several new infraspecific names in the *Melanopsis lyrata* complex, referred to in text as forms and therefore not representing available subspecies names (ICZN 1999: Article 15.2). Olujić (1999) classified shells with columellar fold within the genus *Melanoptychia* Neumayr 1880. Therefore, all the newly established 'subspecies' of *M. lyrata* were defined as belonging to *Melanoptychia*, while the nominal form *M. lyrata* s.str. was classified as *Melanopsis*. Apart from this being an invalid and taxonomically nonsensical procedure, the taxonomic 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 intraspecific variation or influenced by hybridization (Bandel 2000). If placed into *Melanopsis* (as we do), the names *costata* and *glabra* are preoccupied by *M. costata* Neumayr 1869 (= *M. cosmanni* Pallary 1916), *Melanopsis costata* (Olivier 1804) and *Melanopsis glabra* Brusina 1874. Furthermore, Olujić (1999) did not define holotypes, either. In conclusion, the new species group names introduced by Olujić (1999) are neither taxonomically nor nomenclaturally valid.

Despite those problems, the various morphotypes of *Melanopsis lyrata* do not co-occur randomly but appear in distinct stratigraphic layers. Based on this evidence 4 morphotypes can be defined, marking them with letters A to D for more clear expression of their nomenclatural status:

1. *Melanopsis lyrata* morphotype A is characterized by reduced sculpture (*glabra*-morph in Olujić 1999) – no ribs or nodes – and occurs in samples 20, 25, 26, 32, 33, 37, 42/41, 43, 45 with 746 specimens.

2. *Melanopsis lyrata* morphotype B comprises morphologies with few and blunt ribs (*semicostata*-morph in

OLUJIĆ 1999) that occur only on 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* morphotype C, referred to as "*costata*" by OLUJIĆ 1999, occur in sample Z with 17 specimens. Sculpture appears only on the last 2–3 whorls.

4. *Melanopsis lyrata* morphotype 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*. Subsequently, it was elevated to species level (BRUSINA 1876) without illustration. 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. Likewise, *Melanopsis misera* BRUSINA 1874, originally treated as variety of *M. lyrata,* was later treated as distinct species by BOURGUIGNAT (1880) and BRUSINA (1884). It is smaller, more conical and bears axial ribs with two distinct rows of spiny nodes. Herein, we consider tentatively this taxon as another morphotype of *M. lyrata,* following the original concept of BRUSINA (1874). Similarly, the validity of *Melanopsis panciciana* BRUSINA 1874 and *Melanopsis kispatici* BRUSINA 1897 appears to be rather doubtful regarding the similarity of shape and sculpture with *M. lyrata*.

Distribution: *Melanopsis lyrata* is an endemic DLS species known from Lake Drniš (Miočić, BRUSINA 1874, 1897), Lake Sinj (Ribarić, NEUMAYR 1869, Lučane section, 41.5–130.5 m) and Lake Gacko (Unit D in Vrbica and Gračanica opencast coalmines, MANDIC et al. 2011a).

Order Littorinimorpha GOLIKOV & STAROBOGATOV 1975

Superfamily Rissooidea GRAY 1847

Family Hydrobiidae STIMPSON 1865

Subfamily Pyrgulinae BRUSINA 1881

Genus ***Prososthenia*** NEUMAYR 1869

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

Prososthenia bicarinata OLUJIĆ 1999

Pl. 4, Fig. 7

1999 *Prososthenia bicarinata* OLUJIĆ: 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 based on the sculpture consisting of two keels. The first one is situated below the suture, the second one around the middle of the whorl, forming a concave interspace.

Remarks: According to the type material described by OLUJIĆ (1999) this species is extremely bulky and irregularly shaped, which allows a clear separation from all other representatives of the genus.

Distribution: An endemic DLS species known so far only from Lake Sinj (Orlov kuk section, OLUJIĆ 1999, Lučane section, 110 m).

Prososthenia cincta NEUMAYR 1869

Pl. 3, Figs. 7–14, Pl. 4, Figs. 1–2, 5

1869 *Prososthenia cincta* nov. sp. NEUMAYR: 361, pl. 12, fig. 5 [plate legend gives erroneously Fig. 5 as *P. Schwartzi*, and Fig. 6 as *P. cincta*. See HERBICH & NEUMAYR (1875: 422) for correction].
1874 *Prososthenia Schwarzi* [sic] var. *cingulata* BRUSINA: 50.
1897 *Prososthenia cincta ecostata* BRUSINA: 18, pl. 8, fig. 26.
1926 *Prososthenia cincta ecostata* BRUSINA – WENZ: 1989.
1926 *Prososthenia cincta cincta* NEUMAYR – WENZ: 1989.
1999 *Prososthenia cetinae* OLUJIĆ: 23, 51, pl. 4, fig. 51 [partim].
1999 *Prososthenia cetinae eminens* OLUJIĆ: 24, 52, pl. 4, fig. 51.
1999 *Prososthenia cincta primaeva* OLUJIĆ: 25, 53, pl. 5, figs. 52–55 [partim].
1999 *Prososthenia cincta ecostata* BRUSINA – OLUJIĆ: 25, 53, pl. 5, figs. 56, 64, pl. 6, fig. 75.
1999 *Prososthenia cincta semievoluta* OLUJIĆ: 25, 53, pl. 5, figs. 57–61, 65, pl. 6, fig. 69.
1999 *Prososthenia cincta cincta* NEUMAYR – OLUJIĆ: 25, 53, pl. 5, figs. 62, 66–67, pl. 6, figs. 70–71.
1999 *Prososthenia sutinae* OLUJIĆ: 26, 53, pl. 6, figs. 76–79.
1999 *Prososthenia sutinae lateralis* OLUJIĆ: 26, 54, pl. 6, fig. 76.
1999 *Prososthenia sutinae electa* OLUJIĆ: 26, 54, pl. 6, figs. 77–78.
1999 *Prososthenia sutinae pretiosa* OLUJIĆ: 26, 54, pl. 6, fig. 79.

Material: 869 specimens from samples 44, 45, ν1, ν, 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 slightly granular, consisting of about 1 broad trochiform whorl. 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. After-

wards, in some morphotypes, weak to prominent axial ribs may occur. These are first perpendicular to the axis but become prosocyrt 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 inner lip.

Remarks: The morphological plasticity resulted in the description of numerous taxa which we consider as synonyms of *Prososthenia cincta*. Generally, four morphotypes occur:

1. *Prososthenia cincta* morphotype A is small, smooth except from the subsutural swelling and in most cases very bulky with a large last whorl. It was introduced as "*primaeva*" in Olujić (1999) and occurs in samples 44, 45, ν1, ν with 36 specimens. *Prososthenia sutinae lateralis* Olujić 1999 falls also within the range of this morphotype. Even Olujić (1999) mentioned that it is very close to his "*primaeva*".

2. *Prososthenia cincta* morphotype B includes also smooth, but large forms. This morphotype was treated as subspecies *ecostata* by Brusina (1897). This rare morphotype was not detected again.

3. *Prososthenia cincta* morphotype C comprises all weakly ribbed shells with subsutural swelling ("*semievoluta*" 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* morphotype D is the typical *P. cincta* as 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. schwartzi* 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 and should be treated as *Prososthenia schwartzi* Neumayr 1869.

Distribution: *Prososthenia cincta* is an endemic DLS species known from Lake Sinj (Lučane section, 69.5–130.5 m and Ribarić section, Neumayr 1869) and Lake Kupres (Jurišić-Polšak & Sliškovic 1988).

Prososthenia neutra Brusina 1897

Pl. 4, Figs. 3–4, 6, 12

1897 *Prososthenia? neutra* Brusina: 19, pl. 9, figs. 3–4.
1926 *?Prososthenia neutra* Brusina – Wenz: 1994.
1999 *Prososthenia superstes* Olujić: 28, 56, pl. 7, figs. 82–83.
1999 *Prososthenia superstes praevia* Olujić: 28, 56, pl. 7, fig. 82.
1999 *Prososthenia superstes intermedia* Olujić: 28, 56, pl. 7, fig. 83.

Material: 45 specimens from samples J, A.

Dimensions: Height: 3–4 mm, diameter: 1.5–2 mm, spire angle: 40–50°.

Description: Protoconch broad trochiform, with granular surface 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 cyrtoconoid outline. It has a very constant morphology with whorls becoming regularly larger towards the last whorl which comprises 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.

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

This species can be separated from both *Prososthenia schwartzi* 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.

Distribution: Endemic species of the Dinaride Lake System, occurs in Lake Drniš (Miočić, Brusina 1897), Lake Sinj (Lučane section, 130.5–137 m) and in Lake Gacko (Unit A and D in Gračanica opencast coalmine and Unit D in Vrbica opencast coalmine, Mandic et al. 2011a).

Prososthenia schwartzi Neumayr 1869

Pl. 2, Figs. 1–15, Pl. 3, Figs. 1–6

1869 *Prososthenia Schwartzi* Neumayr: 360, pl. 12, fig. 4, 6 [plate legend gives erroneously Fig. 5 as *P. Schwartzi*, and Fig. 6 as *P. cincta*. See Herbich & Neumayr (1875: 422) for correction].
1874 *Prososthenia Schwarzi* [sic] *apleura* Brusina: 50, pl. 3, fig. 10.
1897 *Prososthenia Schwarzi* [sic] Neum. – Brusina: 17, pl. 8, figs. 24–25.
1926 *Prososthenia schwartzi apleura* Brusina – Wenz: 1998.
1926 *Prososthenia schwartzi schwartzi* Neumayr – Wenz: 1996.
1999 *Prososthenia cetinae* Olujić: 23, 51, pl. 4, figs. 48–50 [partim].
1999 *Prososthenia cetinae increscens* Olujić: 24, 52, pl. 4, fig. 48.
1999 *Prososthenia cetinae amplificata* Olujić: 24, 52, pl. 4, fig. 49.
1999 *Prososthenia cetinae elegans* Olujić: 24, 52, pl. 4, fig. 50.
1999 *Prososthenia cincta primaeva* Olujić: 25, 53, pl. 5, figs. 72–74 [partim; non *Prososthenia cincta* Neumayr 1869].
1999 *Prososthenia schwartzi transitans* Olujić: 23, 51, pl. 4, figs. 36–37.
1999 *Prososthenia schwartzi apleura* Brusina – Olujić: 23, 51, pl. 4, figs. 38–40.
1999 *Prososthenia schwartzi semicostata* Olujić: 23, 51, pl. 4, figs. 41–43.

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

Material: 1935 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 weakly granular, consisting of about 1 low trochiform whorl. Spire high conical to cyrtoconoid, consisting of up to 7 strongly convex whorls with strongly incised sutures. The first 2–3 whorls are always smooth; afterwards, sculpture of weak to prominent axial ribs may be developed in some morphotypes. These may reach from one suture to the other or may be restricted to the middle part of the whorls – but never form 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 opisthocyrt. The last whorl attains about 40–50% of the total height. Aperture is ovoid, with slightly convex inner lip and sometimes very prominent convex outer lip.

Remarks: Here again the problem of validity of the many proposed taxa arises. These are probably mere morpho-phenotypes. Moreover, the available species name *Prososthenia cetinae* OLUJIĆ 1999 (including 4 morphotypes) represents a synonym of partly *P. schwartzi* and *P. cincta.* The simultaneously introduced "forma" names are unavailable. Four morphotypes predominate:

1. *Prososthenia schwartzi* morphotype A is a small and smooth form, rather ovoid than conical and is referred to as "*transitans*" in OLUJIĆ 1999. *Prososthenia cetinae increscens* OLUJIĆ 1999 is a further variety. It appears within the samples 20, 25, 32, 33, 37, 44 with 198 specimens.

2. *Prososthenia schwartzi* morphotype B comprises another smooth but larger and more conical morphotype (= *apleura* in BRUSINA 1897 and *Prososthenia cetinae amplificata* OLUJIĆ 1999). It is represented in samples 33, 43, 44, 45, Z with 150 specimens.

3. *Prososthenia schwartzi* morphotype C is characterized by the development of weak axial ribs on the last 2–3 teleoconch whorls ("*semicostata*" in OLUJIĆ 1999 and *Prososthenia cetinae elegans* OLUJIĆ 1999), but is otherwise identical in habitus with morphotype B. It occurs in samples β, Z, Y, V, T1, O, M2, Lx, L, A with 185 specimens.

4. *Prososthenia schwartzi* morphotype D represents the typical *P. schwartzi* as defined by NEUMAYR (1869). It comprises sculptured shells with prominent axial ribs on the last 2–3 whorls and occurs in samples γ, β, Z, Y, V, T1, O, M2, Lx, L, J, A with 1402 specimens.

P. schwartzi differs from *Prososthenia cincta* NEUMAYR 1869 mainly in the absence of the subsutural swelling. NEUMAYR (1969) separated *P. cincta* from this species by its distinct keel below the sutures whilst in *P. schwartzi* 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.

Distribution: Endemic DLS species, known so far from Lake Sinj (Lučane section, 41.5–137 m, Ribarić, NEUMAYR 1869) and Lake Kupres (JURIŠIĆ-POLŠAK & SLIŠKOVIĆ 1988).

Subfamily Belgrandiinae DE STEFANI 1877

Genus ***Belgrandia*** BOURGUIGNAT 1869

Belgrandia klietmanni NEUBAUER n. sp.

Pl. 5, Figs. 1–2, 8, 10

Type species: *Cyclostoma gibbum* DRAPARNAUD 1805, by subsequent designation (KOBELT 1878), Recent, Southern France.

Material: 2315 specimens from samples 20, 32, 33, 37, 42/41, 43, 44, γ, Z, Y, V, T1, J; voucher specimens SMF 337002.

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: NHMW Inv. 2010/0042/0037, height: 2.2 mm, diameter: 1.0 mm, spire angle: 20°; from type stratum; Paratype 3: NHMW Inv. 2010/0042/0038, height: 2.4 mm, diameter: 1.0 mm, spire angle: 15°; from type stratum.

Derivatio nominis: Named after Johannes Klietmann (Department of Paleontology, University of Vienna).

Locus typicus: Sinj, Lučane Section.

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

Age: Early Langhian, Middle Miocene.

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

Description: The protoconch is broad and low trochiform, comprising 1 whorl. It is densely covered with distinct wrinkles. This ornamentation is strongest at the apex, then becomes gradually weaker and is almost smooth towards the transition to the teleoconch. The protoconch is clearly separated from the teleoconch.

The shell is slender elongate with whorls only slightly increasing in diameter towards the aperture. The spire is covered with faint spiral grooves and distinct prosocline growth lines and consists of about 5–6 whorls, each convex in profile and with moderately incised sutures. The last whorl takes up to 50% of the total height and ends up in a steep and fairly straight base. The aperture is elliptical, inclined with an angle of about 30° to the axis and in most cases slightly detached. The lips are equally thickened. In some specimens there is a very weak swelling below the umbilicus.

Remarks: The generic affiliation of this species is still problematic. The wrinkled protoconch surface is common in many species among the Hydrobiidae (e.g. Hershler & Ponder 1998). It is found in several species of the Belgrandiinae, e.g. *Belgrandia* Bourguignat 1869, *Microprososthenia* Kadolsky & Piechocki 2000, and *Belgrandiella* Wagner 1928. Also the similarity with the *Pseudamnicola* protoconch is striking (see *P. torbarianus,* pl. 4, figs. 11, 13, and *P. hoeckae* Harzhauser & Binder 2004). However, such a slender shape is unknown from *Pseudamnicola.*

Belgrandia corresponds in the slender shape, the strong convexity of the whorls and the detached aperture. Though, the typical distinct bulge behind the peristome is missing in *B. klietmanni.* Another 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.

Maybe the generic affiliation will have to be reconsidered in a more fundamental taxonomic revision by integrating more information from other hydrobiid taxa.

This species strongly reminds of "*Litorinella" candidula* Neumayr 1869, which is similar in size and number of whorls. However, it is rather drop-shaped and never develops a detached aperture.

Distribution: Endemic DLS species, known so far from Lake Sinj (Lučane section 41.5–130.5 m).

Subfamily Pseudamnicolinae Radoman 1977

Genus ***Pseudamnicola*** Paulucci 1878

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

Pseudamnicola torbarianus (Brusina 1874)

Pl. 4, Figs. 8–11, 13

1874 *Amnicola Torbariana* Brusina: 66, pl. 5, figs. 15–16.
1902 *Pseudoamnicola? Torbariana* Brus. – Brusina: pl. 10, figs. 14–17.
1926 *Amnicola* (*Amnicola*) *torbariana* Brusina – Wenz: 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 low trochiform with slightly inflated initial part, comprising 1 whorl fully covered with distinct wrinkles; it is clearly separated from the teleoconch. Shell ovoid, stocky 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 sometimes thickened, with convex outer lip and rounded anterior tip. The inner lip forms a distinct posterior notch. The umbilicus is very small and nearly covered by the inner lip; some specimens show traces of a funicular ridge.

Remarks: The typical protoconch ornamentation is also observed in *Pseudamnicola hoeckae* Harzhauser & Binder 2004 from the Vienna Basin (Upper Miocene), confirming the generic affiliation. Wenz (1920) described one of his specimens from the Late Miocene of the Vienna Basin as '*Pseudamnicola* cf. *torbariana'*, which differed from the type species in its less flattened sutural part of the whorls. This Lake Pannon species should be treated as *Pseudamnicola hoeckae* Harzhauser & Binder 2004. *Pseudamnicola stosicianus* Brusina 1884 from Dalmatia is characterized by its relatively broad last whorl but otherwise more slender shape.

Concerning the gender of *Pseudamnicola*, which is currently under discussion, we follow Falkner et al. (2002) who suggested the grammatical gender of *Pseudamnicola* to be masculine.

Distribution: Endemic DLS species, recorded from Lake Sinj (Lučane section, 48–128 m) and Lake Drniš (Miočić, Brusina 1874).

Family Emmericiidae Brusina 1870

Genus ***Fossarulus*** Neumayr 1869

Type species: *Fossarulus stachei* Neumayr 1869, Miocene, Dalmatia/SE Croatia.

Fossarulus cf. ***armillatus*** Brusina 1876

Pl. 5, Figs. 11–12, 14

1876 *Fossarulus armillatus* Brusina: 112.
1897 *Fossarulus armillatus* Brus. – Brusina: 21, pl. 8, figs. 1–2.
1926 *Fossarulus armillatus* Brusina – Wenz: 2201.

Material: 28 specimens from sample A.

Dimensions: No exact measurements can be performed due to the fragmentary preservation. After Brusina (1897) size is around 7 mm in height and 5 mm in diameter; spire angle: 40–50°.

Description: Low trochiform protoconch with immersed initial part, consisting of c. 1.2 entirely smooth whorls. Teleoconch conical and bulky. Whorls are convex with maximum convexity in the adapical half and almost straight-sided towards the lower suture; no sutural ramp is developed. Two to three thin and delicate keels with equal interspaces appear on the earliest teleoconch whorls. These keels become more prominent quickly and are accompanied by about 6 spiral threads within the interspaces and by c. 7 threads above the first keel. The lower whorls and the aperture are not preserved due to fragmentation. The illustrations in Brusina (1897)

suggest that the last whorl makes up about 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; outer lip strongly convex, inner lip with distinct posterior notch; both can be extremely thickened.

Remarks: No complete specimen is preserved. Hence, the determination is based on the general shape and the morphology of the keels. It differs from *Fossarulus tricarinatus* Brusina 1870 and *Fossarulus moniliferus* Brusina 1876 in its bulkier shape and the thinner keels. Moreover, the keels appear not before the third whorl in *F. tricarinatus*. The node-less keels of the third whorl exclude identification as one of the stronger sculptured species, such as *Fossarulus fuchsi* Brusina 1897.

The family status of *Fossarulus* is still controversial. Wenz (1939) placed *Fossarulus* within the Emmericiinae among the Micromelaniidae. Due to the largely deviating shape, the affiliation to this family is doubtful. Bouchet & Rocroi (2005) classified *Fossarulus* as Bithyniidae, in isolated position from *Emmericia*. Comparable protoconch and aperture morphologies indeed suggest a strong relationship. Thus, the original classification from Brusina (1870) is followed herein.

Distribution: Endemic DLS species recorded from Lake Sinj (Lučane section, 137 m) and Lake Drniš (Miočić, Brusina 1897).

Fossarulus fuchsi Brusina 1897

Pl. 5, Figs. 3–4, 9, 13

1882 *Fossarulus Fuchsi* Brusina: 38 [nomen nudum].
1897 *Fossarulus Fuchsi* Brus. – Brusina: 21, pl. 7, figs. 27–28.
1926 *Fossarulus fuchsi* Brusina – Wenz: 2203.

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

Dimensions: No complete specimen is preserved. Size ranges around 7 mm in height and 5 mm in diameter (Brusina 1897); spire angle: 45–60°.

Description: Protoconch trochiform and smooth, consisting of about 1.2 whorls. Teleoconch conical, bulky with rich sculpture, consisting of up to 4 whorls. Whorls are convex with maximum convexity in the adapical part and nearly straight towards the lower suture. The first whorls are almost smooth except for 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 appear on the last whorl. A concave furrow separates the keels 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 two thirds 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. According 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; a weak posterior angulation may be developed.

Remarks: This species is difficult to distinguish from similar ones, such as *F. stachei* Neumayr 1869, *F. hoernesi* Brusina 1897 and *F. auritus* Brusina 1897 without the aperture preserved. Therefore, size and the development of keels and nodes, especially on the first few whorls are chosen as main criteria for the identification. *F. hoernesi* and *F. auritus* are much larger; *F. stachei* is more bulky in shape and develops two distinct keels without nodes on the second whorl. All four species (including *F. fuchsi*) might represent phenotypes of a single polymorphic species. Our material, however, does not allow a clarification.

Distribution: Endemic DLS species of Lake Sinj (Potravlje, Brusina 1897, Lučane, 60–65 m) and Lake Gacko (Unit D in Vrbica opencast coalmine, Mandic et al. 2011a).

Subclass Pulmonata Cuvier in Blainville 1814

Supraorder Basommatophora Keferstein 1864

Order Hygrophila Férussac 1822

Suborder Branchiopulmonata Morton 1955

Superfamily Lymnaeoidea Rafinesque 1815

Family Lymnaeidae Rafinesque 1815

Genus ***Lymnaea*** Lamarck 1799

Type species: *Helix stagnalis* Linnaeus 1758, Recent, Europe.

"***Lymnaea***" sp.

Pl. 6, Figs. 1–2, 12

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

Dimensions: No complete specimen is preserved; height of spire fragments: up to 5 mm, diameter: up to 3.5 mm.

Description: Protoconch smooth, with erect tip; transition to the teleoconch indistinct. Spire smooth and high conical; the number of whorls cannot be determined, because no complete specimen exists. The whorls increase rapidly in diameter and are rhomboidal in profile. Sutures moderately incised. No aperture is preserved.

Remarks: There are just two *Lymnaea* species described from this region: *Lymnaea klaici* Brusina 1884 exposes a 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 preserva-

tion does not allow any clear identification, but the rather broad shape is reminiscent of *L. korlevici.*

Distribution: Recorded from Lake Sinj (Lučane section, 60–132 m).

Superfamily Planorboidea Rafinesque 1815

Family Planorbidae Rafinesque 1815

Subfamily Planorbinae Rafinesque 1815

Genus ***Gyraulus*** Charpentier 1837

Type species: *Planorbis albus* Müller 1774, Recent, Europe.

Gyraulus geminus (Brusina 1897)

Pl. 6, Figs. 3–4, 11

1897 *Planorbis geminus* Brusina: 5, pl. 2, figs. 11–16.
1923 *Gyraulus (Gyraulus) geminus* (Brusina) – Wenz: 1554.

Material: 15 specimens from samples V, A.

Dimensions: Height: c. 0.5 mm, diameter: c. 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). Teleoconch thick-walled, discoidal, smooth, consisting of up to 5 whorls. Whorls are planispiral, strongly rounded to slightly flattened 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 the 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, apart from weak prosocline growth lines.

Remarks: *G. geminus* can be easily distinguished 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 relatively broader and known so far only from Bosnia and Herzegovina.

Distribution: Endemic DLS species recorded from Lake Sinj (Goručica, Brusina 1897, Lučane section, 115.5–137 m) and Lake Drniš (Miočić, Brusina 1897).

Genus ***Orygoceras*** Brusina 1882

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

Orygoceras cornucopiae Brusina 1882

Pl. 6, Fig. 7

1882 *Orygoceras cornucopiae* Brusina: 45, pl. 11, figs. 1–3.
1897 *Orygoceras cornucopiae* Brus. – Brusina: 2, pl. 1, figs. 7–9.
1902 *Orygoceras cornucopiae* Brus. – Brusina: pl. 2, figs. 15–16.
1928 *Orygoceras cornucopiae* Brusina – Wenz: 2485.

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

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

Description: The protoconch consists of about 0.75 whorls. The teleoconch is uncoiled, dentaliform and long, attaining its largest diameter close to the aperture. Early teleoconch smooth except for growth lines. Soon, prominent, narrow-situated ribs are intercalated separated by concave interspaces. These ribs may grade into sharp rings and become more prominent and slightly crowded towards the aperture and are usually oblique to the axis. The shell is elliptical in cross-section. Aperture is not preserved.

Remarks: Differs from *O. stenone*mus Brusina 1882 by the densely spaced ribs. The protoconch sculpture is very poorly preserved and even hardly detectable in SEM pictures but indicates the presence of striae as typical for many planorbids (Riedel 1993).

Distribution: Endemic species of the DLS. It is recorded from Lake Sinj (Lučane, 60–130.5 m) and Lake Drniš (Parčić, Coll. NHM Vienna, Miočić, Brusina 1882, 1897). It seems to re-appear also in the Late Miocene Lake Livno and Lake Tomislavgrad (= Duvno, = Županjac) (Jurišić-Polšak & Sliković 1988; De Leeuw et al. 2011).

Orygoceras dentaliforme Brusina 1882

Pl. 6, Fig. 5

1882 *Orygoceras dentaliforme* Brusina: 42, pl. 11, figs. 14–15 [partim].
1897 *Orygoceras dentaliforme* Brus. – Brusina: 2, pl. 1, figs. 13–14.
1928 *Orygoceras dentaliforme* Brusina – Wenz: 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 the fragmentary preservation no measurements can be taken; according to 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: The protoconch comprises ca. 0.75 whorls and bears faint spiral striae. The teleoconch is uncoiled, dentaliform and long, attaining its largest diameter close to the aperture, which is not preserved. In cross-section the teleoconch has an elliptical shape. The shell is usually smooth except for delicate growth lines.

Remarks: BRUSINA (1882) united a broad range of morphologically quite variable specimens reaching from completely smooth and straight shells to sparsely ribbed and curved specimens. Herein we treat only straight and smooth specimens as *Orygoceras dentaliforme*. It differs from *O. stenonemus* BRUSINA 1882 and *O. cornucopiae* BRUSINA 1882 in the strongly reduced sculpture.

Orygoceras fuchsi (KITTL 1886) from the Late Miocene of Lake Pannon is reminiscent of *O. dentaliforme* but the teleoconch is much more curved and the striae on the protoconch are more distinct (HARZHAUSER et al. 2002).

Distribution: An endemic DLS species which is recorded from Lake Sinj (Lučane, 45–130.5 m, Župića potok, Ribarić, BRUSINA 1882, 1897), Lake Drniš (Parčić, Coll. NHM Vienna), and Lake Gacko (Unit D in Vrbica opencast coalmine, MANDIC et al. 2011a).

Orygoceras stenonemus BRUSINA 1882

Pl. 6, Figs. 6, 10

1882 *Orygoceras stenonemus* BRUSINA: 43, pl. 11, figs. 4–8.
1897 *Orygoceras stenonemus* BRUS. – BRUSINA: 2, pl. 1, figs. 10–12.
1928 *Orygoceras stenonema* BRUSINA – WENZ: 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 can be performed; after BRUSINA (1882) the height ranges around 5 mm and the diameter attains c. 1 mm. The newly collected specimens fit well within that range.

Description: The protoconch consists of about 0.75 whorls and bears very weak spiral striae (pl. 6, fig. 10). The teleoconch is uncoiled, dentaliform and long, attaining its largest diameter close to the aperture. Early teleoconch smooth except for delicate growth lines. Soon after, wide-spaced narrow ribs with convex interspaces are intercalated. These ribs are only slightly oblique and become more prominent towards the aperture. The teleoconch is elliptical to slightly semilunar in cross-section.

Remarks: Differs from *O. cornucopiae* by the wider interspaces between the ribs. These are narrower and less oblique relative to the axis of the shell. Nevertheless, both species have the same geographic and stratigraphic distribution and it might turn out that both taxa are only morphotypes of a single species.

The species name *stenonemus* is a latinized Greek compound noun meaning "narrow thread" and is of masculine gender.

Distribution: Endemic DLS species which is recorded from Lake Sinj (Lučane, 60–130.5 m, Župića potok, Ribarić, BRUSINA 1882, 1897) and Lake Drniš (Parčić, Coll. NHM Vienna). JURIŠIĆ-POLŠAK & SLIŠKOVIĆ (1988) mentioned it also from Lake Kupres.

Subfamily Ancylinae RAFINESQUE 1815

Genus ***Ferrissia*** WALKER 1903

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

Ferrissia illyrica (NEUMAYR 1880)

Pl. 6, Figs. 8–9, 13

1880 *Ancylus Illyricus* NEUMAYR: 486, pl. 7, fig. 16.
1902 *Ancylus illyricus* NEUM. – BRUSINA: pl. 1, figs. 20–21.
1907 *Ancylus illyricus* NEUM. 1880 – BRUSINA: 195.
1923 *Pseudancylus illyricus* (NEUMAYR) – WENZ: 1698.

Material: 1 specimen from sample 44.

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

Description: Protoconch cap-like, convex, ranging around 400 µm. The smooth cap bears a small pit in its center and is fringed by numerous and narrow spaced, thin radial threads. The teleoconch is ovoid and slightly broader in the anterior part, with an apex pointing slightly towards right. It is smooth apart from concentrical growth lines on the outer surface, whereas the radial threads extend almost to the shell margins along the inner shell surface.

Remarks: The shell is reminiscent of *Ferrissia wittmanni* (SCHLICKUM 1964) from the Early Miocene of the Western Paratethys (KOWALKE & REICHENBACHER 2005) and to a *Ferrissia* species from the Sarmatian of the Central Paratethys (HARZHAUSER & KOWALKE 2002), which shows nearly the same protoconch features, but differs conspicuously in their strong radial ribs on the outer shell surface reaching to the shell margins. SCHLICKUM (1976) erroneously mentioned *Ferrissia illyrica* also from the Late Miocene.

Current investigations on planorbid phylogeny inferred from molecular data (ALBRECHT et al. 2007) indicate a strong of relationship of *Ferrissia* with *Ancylus* MÜLLER 1774 and rejected earlier studies based on morphological characters which placed *Ferrissia* within the Bulininae (BOUCHET & ROCROI 2005).

Distribution: Endemic DLS species, recorded from Lake Gacko (Unit B in Gračanica opencast coalmine and Unit D in Vrbica opencast coalmine at Avtovac (= Haptovac) near Gacko (= Metokija), MANDIC et al. 2011a), Lake Sinj (Lučane section, 69.5 m) and from Lake Drniš (Parčić, Coll. NHM Vienna, Miočić, BRUSINA 1902).

Class Bivalvia LINNAEUS 1758

Superorder Heterodonta NEUMAYR 1883

Order Venerida GRAY 1854

Family Dreissenidae GRAY in TURTON 1840

Genus ***Mytilopsis*** CONRAD 1857

Type species: *Mytilus leucophaeatus* Conrad 1831, Recent, Eastern USA.

Mytilopsis aletici (Brusina 1907)

Pl. 7, Fig. 8

1905 *Congeria Aletići* Brusina: 35 [nomen nudum].
1907 *Congeria Aletići* Brusina: 206.
1978 *Congeria aletici* n. sp. [sic] – Kochansky-Devidé in Kochansky-Devidé & Sliškovic: 61–63, 94, pl. 11, figs. 10–15, pl. 12, figs. 1–2.

Material: 21 specimens from samples 45, μ, β.

Dimensions: Length, height, convexity of some specimens: 57 × 57 × 6 mm, 50 × 42 × 6 mm, 52 × 52 × 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 a delicate but sharp and short keel, starting at the umbo and stretching across about one third of the shell. Inner features are not preserved or covered with sediment.

Remarks: Differs from both *Mytilopsis frici* (Brusina 1904) and *M. drvarensis* (Toula 1913) 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 its surface sculpture: *M. aletici* has a shorter keel, no radial ribs and is larger and flatter. Because Brusina (1907) added no illustration to his description, Kochansky-Devidé & Sliškovic (1978) considered its original description by Brusina as invalid species-designation and redescribed it again. The description of Brusina (1907), however, is clearly valid (ICZN, 1999: Article 12).

Distribution: Endemic species of the DLS, known so far only from Lake Sinj (Lučane section, 70.5–107.5 m, Kalina/Košute, Brnaze/Sinj, Grab, Brusina 1907, Kochansky-Devidé & Sliškovic 1978), Lake Kupres (Fatelj hill, Kochansky-Devidé & Sliškovic 1981) and Lake Hodovo (Hodovo, Kochansky-Devidé & Sliškovic 1981).

Mytilopsis jadrovi (Brusina 1892)

Pl. 7, Figs. 1–2, 9

1892 *Congeria Jadrovi* Brusina: 195.
1897 *Congeria Jadrovi* Brus. – Brusina: 30, pl. 17, figs. 12–14.
1902 *Congeria Jadrovi* Brus. – Brusina: pl. 21, figs. 2–5.
1978 *Congeria jadrovi* Brusina 1897 – Kochansky-Devidé & Sliškovic: 37–38, 87, pl. 1, figs. 26–39.

Material: 690 specimens from samples 20, 22, 25, 26, 32, 33, 37, 42/41, 43, 44, 45, ν1, ν, μ, γ, β, Z, Y, V, T1, O, Lx, L, J, A.

Dimensions: Length, height, convexity of some specimens: 4.5 × 7.5 × 2 mm, 2 × 3.5 × 1 mm, 4 × 5.5 × 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 ranging from 40 to 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 indication 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; the anterior field is far more inclined than the posterior field. 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, ranging from small to prominent and is of 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.

Remarks: *Mytilopsis nitida* (Kochansky-Devidé in Kochansky-Devidé & Sliškovic 1978) develops a straight and blunt keel resulting in a reduction of the anterior external surface field; moreover it is more convex in shape.

Another morphological similar species is *M. neumayri* (Andrusov 1897), which is larger and has a lower keel. 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.

Distribution: An endemic DLS species recorded from Lake Sinj (Lučane section, 41.5–137 m, Trnovača and Župića potok in Sinj, St. Kata, Bila glavica near Trilj), Lake Drniš (Miočić, Biočić, Kadina glavica), Lake Livno (Eminovo Selo), Lake Sarajevo (Čajdraš and Blažuj) and Lake Konjic (Čelebići). Further it is known from the Southern Pannonian Basin (Mt. Psunj, Rogoljica; Karlovac subdepression, Utinja; Prijedor basin, Marini, Mala/Velika Žuljevica) (Brusina 1897, Kochansky-Devidé & Sliškovic 1978, Mandic et al. 2011a).

Superorder Palaeoheterodonta Newell 1965

Order Unionida Gray 1854

Family Unionidae Rafinesque 1820

Genus ***Unio*** Philipsson 1788

Type species: *Mya pictorum* Linnaeus 1758, Recent, Europe.

Unio rackianus Brusina 1874

Pl. 7, Fig. 3–7

1874 *Unio Račkianus* Brusina: 115, pl. 5, figs. 9–10.
1907 *Unio Račkianus* Brus. 1874 – Brusina: 208.
1974 *Unio rackianus* Brusina – Milan et al.: 54.
1981 *Unio rackianus* Brusina – Žagar-Sakač: 16.
1987 *Unio rackianus rackianus* Brusina – Žagar-Sakač: 72, pl. 1, figs. 1–2, pl. 2, figs. 1–2, pl. 3, figs. 1–2, pl. 9, fig. C.
1987 *Unio rackianus simplex* n. ssp. Žagar-Sakač: 76, pl. 4, figs. 1–3, pl. 9, fig. A.
1987 *Unio rackianus intermedius* n. ssp. Žagar-Sakač: 77, pl. 5, figs. 1–3, pl. 9, fig. B.

Material: 3 adult specimens from samples 43, 44, 1 juvenile from sample 44.

Dimensions: Estimated dimensions (length × height × convexity) of adult specimen illustrated on fig. 3: 32 × 24 × 9 mm, umbonal angle: about 125°, and juvenile specimen illustrated on figs. 4–7: 2.8 × 1.9 × 0.8 mm.

Description: Shell of illustrated adult specimen elliptically in shape, strongly convex, especially towards the middle of the shell height. On both sides of the umbo a slight depression occurs. The second individual is only partially preserved. Though damaged both shells show intentions of two posterior radial keels. Weak growth lines appear. Umbo and inner features are covered by sediment or are not preserved.

The juvenile specimen is almost complete and elliptical 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.

Remarks: Žagar-Sakač (1987, 1990) proposed a phylogenetic lineage from *Unio rackianus simplex* via *U. r. intermedius* to *U. r. rackianus*, coinciding with a trend towards more complex umbonal ornamentation. Herein, we treat *Unio rackianus* as a rather polymorphic species and consider the subspecies as mere morphotypes. Based on the development of two radial keels, the small size and the rounded shape the specimens range within the *intermedius* morphotype. The nominal morphotype is larger and more elongate, whereas the *simplex* morphotype of Žagar-Sakač (1987) is more compact and lacks the strong keels. The single juvenile right valve is attributed only tentatively to *Unio rackianus*.

Unio cubranovici Brusina 1902 might represent an independent phylogenetic lineage which developed at c. 16 Ma and is restricted to the Glina subdepression of the Southern Pannonian Basin System (Mandic et al. 2011b). The separation of *Unio katzeri* Brusina 1904 from Lake Šipovo is less distinct. It was discussed to be a predecessor of *Unio rackianus* by Žagar-Sakač & Sakač (1984). Nevertheless, it co-occurs in Lake Sinj at several localities together with *U. rackianus,* whilst *U. rackianus* appears in Lake Gacko in distinctly older strata where *U. katzeri* is absent (Mandic et al. 2011a). Maybe, both taxa are also only variations of a single species. In this case, the name *Unio rackianus* would gain priority.

Distribution: Endemic species of the DLS. It is recorded from Lake Sinj (Lučane section, 68.5–69.5 m, Muša/Sinj polje, Panj/Hrvace, Novi Bunar/Sinj, Koljane, Ribarić) and Lake Drniš (Miočić) (Brusina 1907, Žagar-Sakač 1987).

Discussion

The counting of the samples yielded a total amount of 13,180 individuals comprising at least 18 gastropod species of 10 genera and 3 bivalve species of 2 genera, all of which are typical freshwater taxa (Tab. 1). This is confirmed by isotope data, which characterize Lake Sinj as pure freshwater setting (Harzhauser et al. 2011). Bivalves comprise about 10% of all counted individuals, almost exclusively represented by minute *Mytilopsis jadrovi. M. aletici*, the large-sized producer of monospecific shell accumulations, and the thick walled, massive *Unio rackianus* are extremely rare. 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 shallow paleoenvironments (e.g. coal layers) whereas bivalves are more abundant in the massive limestones which formed during lake high-stands.

The average size of the species is small, reaching from the minute *Belgrandia klietmanni* with about 2–3 mm in height to *Melanopsis lyrata* with about 8–14 mm; just the dimensionally highly variable but rare *M. lucanensis* attains in some cases nearly 3 cm in height. Larger taxa are only represented by the bivalves *Mytilopsis aletici* and *Unio rackianus* attaining c. 6 cm in length. Generally, the section is characterized by the dominance of *Melanopsis lyrata, Melanopsis lanzaeana, Prososthenia*

Tab. 1. Vertical distribution of occurring taxa in section Lučane with quantified samples. The asterisk marks large bivalve taxa, which are not found in sieved samples (apart from 1 juvenile unionid in Sample 44). Thus, these counts do not reflect comparable percentage values.

Height in section [m]	41.41	44.97	47.89	48.77	59.79	61.00	65.01	67.91	68.73	69.31	70.37	76.81	81.22	85.47	97.00	98.00	104.00	106.41	110.64	110.97	115.40	120.29	124.43	128.26	128.78	129.24	130.51	136.98	
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	3		8	1	14	76	5	1	71	220	15	5	3				20	2	3	3	2	29		4		1			**486**
Melanopsis lanzaeana morph A			1		23	106	21		28	261									40	1		4		1					**486**
Melanopsis lanzaeana morph B										21									94	1	2						11		**129**
Melanopsis lanzaeana morph C																			52		52	28				5	85	10	**232**
Melanopsis lucanensis n. sp.									3	6																			**9**
Melanopsis lyrata morph A	2		30	1	93	390	150	8	70		2																		**746**
Melanopsis lyrata morph B									1	397									1										**399**
Melanopsis lyrata morph C																			17										**17**
Melanopsis lyrata morph D																			14		7	16				2	9		**48**
Prososthenia bicarinata																			1										**1**
Prososthenia cincta morph A										5	27	1	3																**36**
Prososthenia cincta morph C											2						1		79	9	4	30	4	12	3	11			**155**
Prososthenia cincta morph D																			360	12	27	187	14	43	6	23	6		**678**
Prososthenia neutra																											19	26	**45**
Prososthenia schwarzi morph A	8		5		12	73	4			96																			**198**
Prososthenia schwarzi morph B						2			42	93	6								7										**150**
Prososthenia schwarzi morph C																		1	49	17	10	80	3	2	1	21		1	**185**
Prososthenia schwarzi morph D											1						6	1	148	47	263	776	40	35	4	79		2	**1402**
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			**4022**
Belgrandia klietmanni n. sp.	2				2	16	23	16	50	2057							41		30	2	10	19					47		**2315**
Pseudamnicola torbarianus			5		18	19	4	1	4	75	2						1		9	1		13		3					**155**
Fossarulus cf. *armillatus*																												28	**28**
Fossarulus fuchsi					1	1	4																						**6**
Fossarulus sp. indet.					14	45	18												3		1	1							**82**
Lymnaea sp.					2	2													1			1					1	5	**12**
Gyraulus geminus																					1							14	**15**
Orygoceras cornucopiae					1	1	1																				1		**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	17		**43**
Orygoceras sp. indet.											2	1	1				4												**8**
Ferrissia illyrica										1																			**1**
*Mytilopsis aletici**											14			1		1		5											**21**
Mytilopsis jadrovi	8	2	2	4	18	127	17	5	14	398	11	3	5	6			14	1	18	3	7	13	2		1	4	5	2	**690**
*Unio rackianus**									2	2																			**4**
Total	**29**	**3**	**59**	**6**	**267**	**982**	**279**	**36**	**358**	**4446**	**393**	**17**	**33**	**7**	**0**	**3**	**245**	**12**	**1483**	**466**	**676**	**2150**	**90**	**266**	**47**	**434**	**305**	**88**	**13180**

schwartzi and *Prososthenia cincta*, each developing 3–4 morphotypes. In this study we refer to these forms as morphotypes rather than chronosubspecies. The forms are suggested to represent morphological varieties of the single species, probably a dependence of morphology and environment. Introducing chronosubspecies would imply a beginning speciation which is not considered herein.

For the lowermost part of the section smooth morphs are typical, whereas the upper part is dominated by half-ribbed and ribbed forms. Basically, *Mytilopsis jadrovi*, *Theodoxus sinjanus, Orygoceras dentaliforme, Pseudamnicola torbarianus* and *Belgrandia klietmanni* appear almost throughout the section. The lower section interval comprises high abundances of *M. jadrovi* and *T. sinjanus*, indicating at least intermediate water-energy (Pfleger 1984, Plaziat & Younis 2005). Within the interval between 60–70 m these are accompanied by *Fossarulus fuchsi* and sculptured species of *Orygoceras. Unio, Ferrissia* and *Melanopsis lucanensis* occur here as well. Especially the appearance of unionids indicates enhanced fluvial input (Pfleger 1984). The middle part of the section, comprising about 40 m of more or less pure limestones, yields only few poorly preserved samples with poorly preserved shells. There, *Mytilopsis aletici* is the only common element, reflecting probably a deeper eulittoral to sublittoral environment (Mandic et al. 2009). The uppermost part of the section bears *Prososthenia neutra*, *Fossarulus* cf. *armillatus* and pulmonate snails such as *Gyraulus* and *Lymnaea*. As air-breathing gastropods, pulmonates are mostly restricted to the upper parts of the littoral zone, thus implying shallow water conditions. Thick coal seams at the section top, representing high-lying mires, support this interpretation. Finally, this resulted in an emersion phase for the first time of the 2-Ma-long depositional history of Lake Sinj (Mandic et al. 2009, De Leeuw et al. 2010).

Based on the literature survey given in Harzhauser & Mandic (2008), the entire gastropod fauna of Lake Sinj comprises 80 species-level taxa whilst 110 taxa are recorded from the entire DLS fauna. The quantitative samples from the Lučane section revealed only 18 gastropod species. This suggests a comparatively high contribution of rare species in the total Lake Sinj fauna. Moreover, this relatively low number of species might point to a restricted spectrum of paleoenvironments that has been covered by our samples or might be an effect of the narrow time-window covered by the section comprising only 400 kyr.

The mollusk fauna of Lake Sinj and the DLS in general experienced major radiation events of certain mollusk taxa. The high endemicity of c. 98% of the gastropod fauna of the DLS is clearly linked to these local radiations (Harzhauser & Mandic 2008). These rapid radiations are mirrored by the difficulties to apply clear taxonomic concepts to the very polymorphic melanopsids and prososthenids. These problems are also evident in the Late Miocene faunas of Lake Pannon (Harzhauser et al. 2002, Geary et al. 2002). Hence, the number of species-level data in the literature is probably strongly inflated due to the outdated taxonomic concept of early workers. This inflation of names is obvious from the synonymy lists in the systematic chapter. Thus, a total revision of the fauna would probably reduce the species number significantly.

About 55% of described taxa including *Theodoxus sinjanus*, *Melanopsis lyrata*, *Prososthenia neutra*, *Pseudamnicola torbarianus*, *Fossarulus armillatus*, *Orygoceras cornucopiae*, *O. dentaliforme*, *O. stenonemus*, *Ferrissia illyrica*, *Mytilopsis jadrovi* and *Unio rackianus* are also known from the geographically very close Lake Drniš. The absence of some species, such as *Prososthenia schwartzi* and *Mytilopsis aletici* from Lake Drniš might be related to its only slightly older age.

Lake Gacko was situated in a distance of c. 150 km, and its mollusk fauna is slightly older (15.2–15.8 Ma (Mandic et al. 2011a). Nevertheless, it displays also surprisingly high species-level congruence (35%) with Lake Sinj. Species which occur in both lakes are: *Melanopsis lyrata*, *Prososthenia neutra*, *Fossarulus fuchsi*, *Orygoceras dentaliforme*, *Ferrissia illyrica*, *Mytilopsis jadrovi,* and *Unio rackianus*. All these species, except for *F. fuchsi*, are present also in the Lake Drniš deposits. Thus, these taxa are either very mobile and widespread in the DLS and/or are characterized by longer stratigraphic life-spans. The poor faunistic relations with Lake Pag (Bulić & Jurišić-Polšak 2009) are clearly linked to the much older age of its mollusk assemblage which developed during 17.2–16.7 Ma (Jiménez-Moreno et al. 2009).

Conclusion

This is the first quantified analysis of a section- and sample-based mollusk assemblage from the Miocene Dinaride Lake System. All taxa derive from a single section representing the sedimentary infill of Lake Sinj, which was one of numerous lakes of the DLS. Most of the species have not been illustrated since the 19th century and modern systematic revisions are largely missing. The mollusk fauna is indicative of a freshwater system, which was predominated by melanopsid and hydrobiid gastropods in shallow water settings and by dreissenid bivalves in "offshore" settings concerning individual numbers. Fluviolacustrine taxa, such as *Ferrissia* and *Unio* are rare and

confined to few layers. The literature-based biodiversity is strongly overestimated due to the numerous superfluous taxa, which have been introduced for mere morphotypes.

The high faunistic similarities with the coeval or slightly older and geographically close-by Lake Drniš but also with the more distanced Lake Gacko suggest either direct aquatic connections or very good faunistic exchange. The taxonomic similarities with other DLS lakes, such as Lake Pag are distinctly lower. This is evident due to different stratigraphic ages of the faunas.

The DLS faunas are still poorly resolved concerning stratigraphic ages of individual assemblages and in respect to their occurrence in certain lakes of the DLS. This contribution is thus the first step to resolve the taxonomy, biogeography and stratigraphy of one of the most diverse Miocene freshwater systems of Europe.

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Plates

Plate 1
All figures by T. Neubauer, NHMW.

Figs. 1–3. *Melanopsis lyrata* Neumayr 1869 (morphotype B).
NHMW Inv. 2010/0042/0011; scale bar corresponds to 5 mm; sample 44.

Figs. 4–6. *Melanopsis lyrata* Neumayr 1869 (morphotype C).
NHMW Inv. 2010/0042/0012; scale bar corresponds to 5 mm; sample Z.

Figs. 7–9. *Melanopsis lyrata* Neumayr 1869 (morphotype D).
NHMW Inv. 2010/0042/0013; scale bar corresponds to 5 mm; sample V.

Figs. 10–12. *Melanopsis lucanensis* Neubauer n. sp.
Holotype NHMW Inv. 2010/0042/0001; scale bar corresponds to 10 mm; sample 44.

Figs. 13–15. *Melanopsis lanzaeana* Brusina 1874 (morphotype A).
NHMW Inv. 2010/0042/0007; scale bar corresponds to 5 mm; sample 44.

Figs. 16–18. *Melanopsis lanzaeana* Brusina 1874 (morphotype B).
NHMW Inv. 2010/0042/0008; scale bar corresponds to 1 mm; sample Z.

Figs. 19–21. *Melanopsis lanzaeana* Brusina 1874 (morphotype C).
NHMW Inv. 2010/0042/0009; scale bar corresponds to 5 mm; sample A.

Fig. 22. *Melanopsis lyrata* Neumayr 1869 (morphotype A).
NHMW Inv. 2010/0042/0010; scale bar corresponds to 5 mm; sample 33.

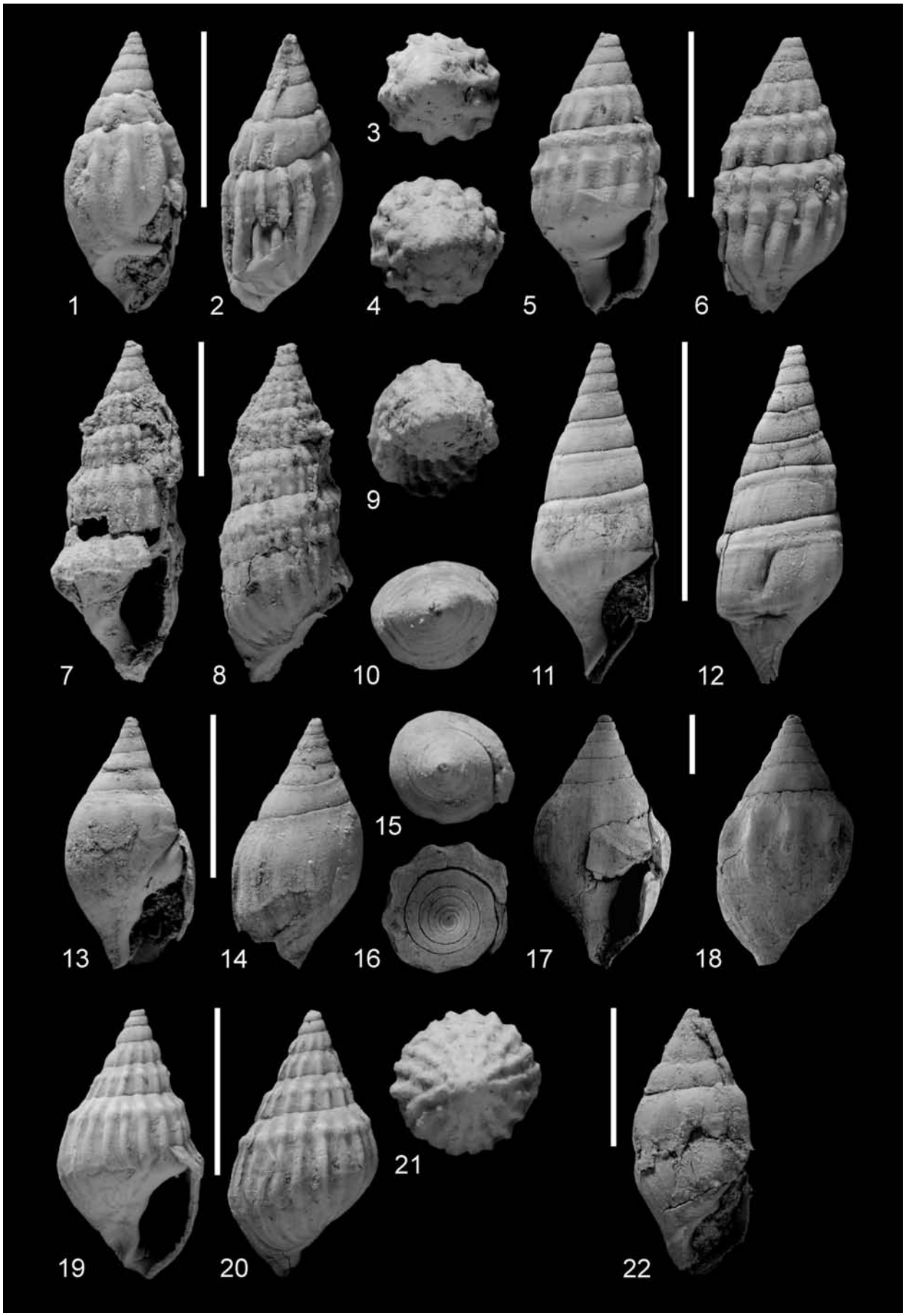
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Plate 2
All figures by T. Neubauer, NHMW, scale bar corresponds to 1 mm.

Figs. 1–8. *Prososthenia schwartzi* Neumayr 1869 (morphotype A).
Figs. 1–3, 7: Fig. 7 shows protoconch of Fig. 1; sample 44, NHMW Inv. 2010/0042/0014.
Figs. 4–6, 8: another specimen; Fig. 8 shows protoconch of Fig. 5; sample 44, NHMW Inv. 2010/0042/0014.

Figs. 9–15. *Prososthenia schwartzi* Neumayr 1869 (morphotype C).
Figs. 9–10, 13: sample Z, Figs. 11–12, 14–15: another specimen; Fig. 15 shows protoconch of Fig. 11; sample Z, NHMW Inv. 2010/0042/0016.

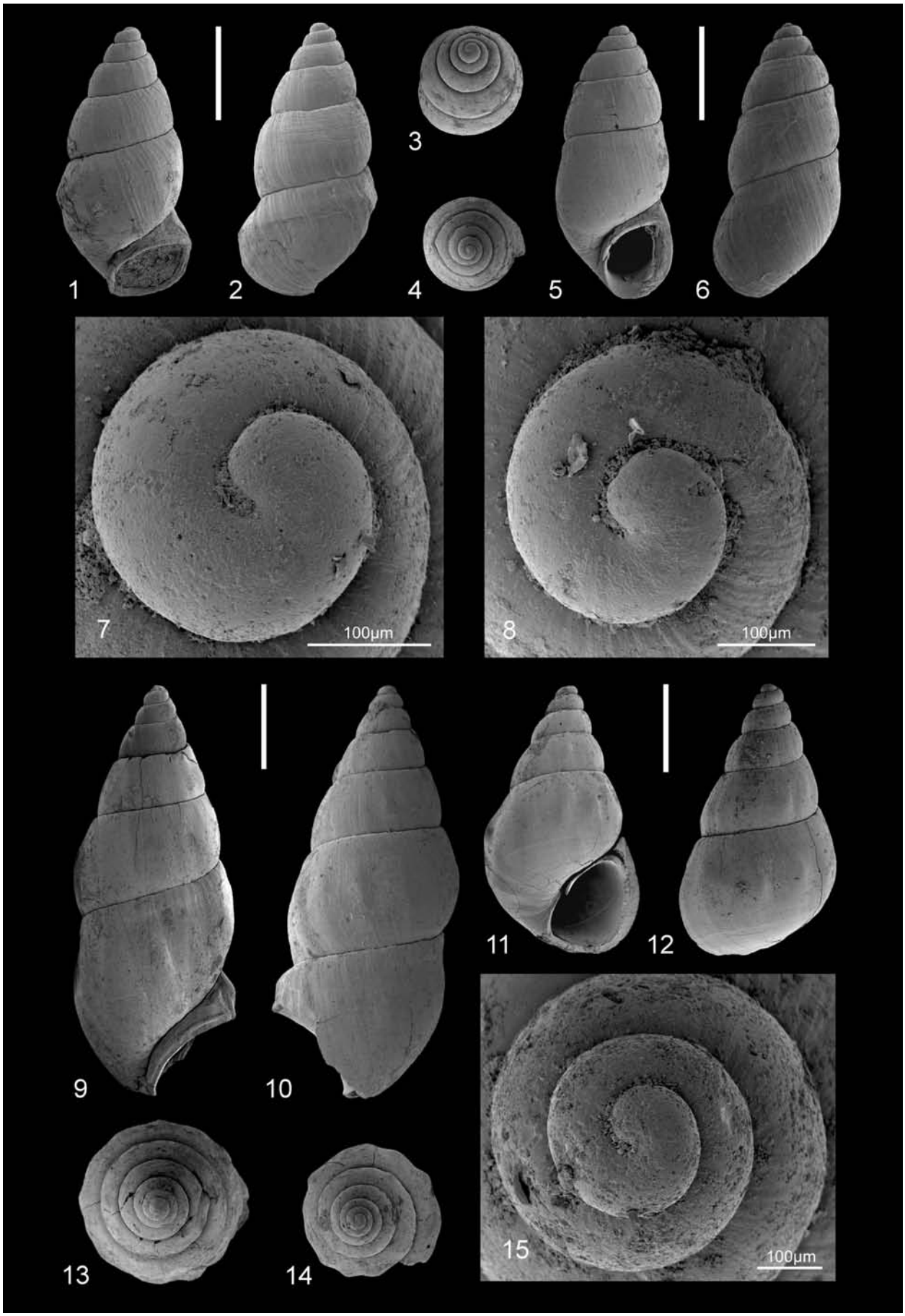
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Plate 3
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Figs. 1–2, 5. *Prososthenia schwartzi* Neumayr 1869 (morphotype B).
NHMW Inv. 2010/0042/0015; sample 44.

Figs. 3–4, 6. *Prososthenia schwartzi* Neumayr 1869 (morphotype D).
NHMW Inv. 2010/0042/0017; sample V.

Figs. 7–9. *Prososthenia cincta* Neumayr 1869 (morphotype A).
NHMW Inv. 2010/0042/0018; sample 44.

Figs. 10–14. *Prososthenia cincta* Neumayr 1869 (morphotype C).
Figs. 10, 13–14: sample Z, NHMW Inv. 2010/0042/0019.
Figs. 11–12: another specimen; sample Z, NHMW Inv. 2010/0042/0019.

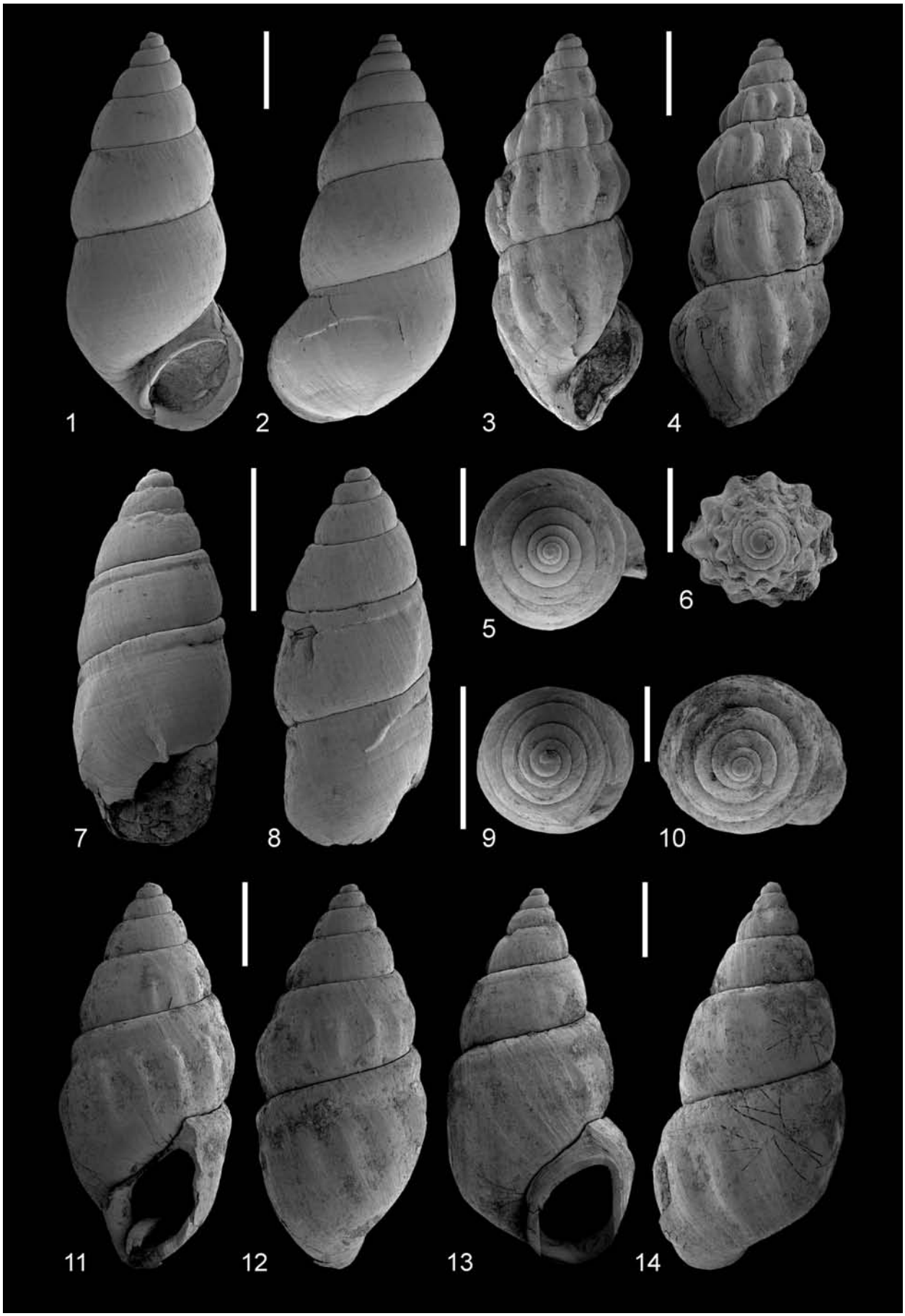
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Plate 4
All figures by T. Neubauer, NHMW.

Figs. 1–2, 5. *Prososthenia cincta* Neumayr 1869 (morphotype D).
NHMW Inv. 2010/0042/0020; scale bar corresponds to 1 mm; sample Z.

Figs. 3–4, 6, 12. *Prososthenia neutra* Brusina 1897.
NHMW Inv. 2010/0042/0021; scale bar corresponds to 1 mm; Fig. 12 shows protoconch of Fig. 3; sample A.

Fig. 7. *Prososthenia bicarinata* Olujić 1999.
NHMW Inv. 2010/0042/0022; scale bar corresponds to 1 mm; sample Z.

Figs. 8–11, 13. *Pseudamnicola torbarianus* (Brusina 1874).
Figs. 8, 13: scale bar in Fig. 8 corresponds to 0.2 mm; Fig. 13 shows detail of Fig. 8; sample 44 NHMW Inv. 2010/0042/0023.
Figs. 9–11: another specimen; scale bar in Figs. 9–10 corresponds to 1 mm; Fig. 11 shows detail of Fig. 9; sample 44 NHMW Inv. 2010/0042/0023.

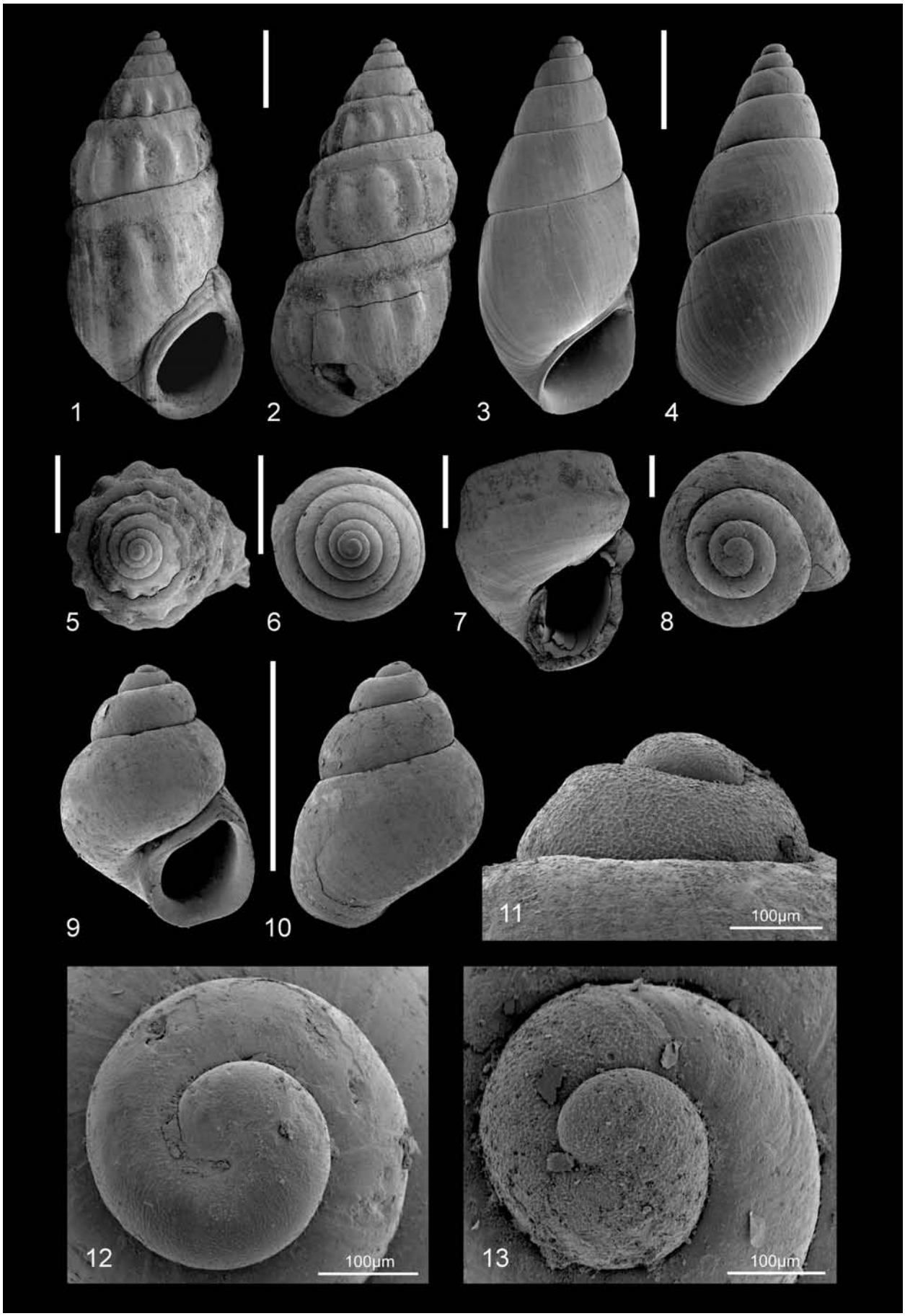
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Plate 5
All figures by T. Neubauer, NHMW.

Figs. 1–2, 8, 10. *Belgrandia klietmanni* Neubauer n. sp.
Holotype NHMW Inv. 2010/0042/0003.
Figs. 1–2: scale bar corresponds to 1 mm; Fig. 8 scale bar corresponds to 0.5 mm; Fig. 10 shows protoconch of Fig. 1; sample 44.

Figs. 3–4, 9, 13. *Fossarulus fuchsi* Brusina 1882.
NHMW Inv. 2010/0042/0024; scale bar corresponds to 1 mm; Fig. 13 shows protoconch of Fig. 3; sample 33.

Figs. 5–7. *Theodoxus sinjanus* (Brusina 1876).
NHMW Inv. 2010/0042/0026; scale bar corresponds to 1 mm; sample 44.

Figs. 11–12, 14. *Fossarulus* cf. *armillatus* Brusina 1876.
NHMW Inv. 2010/0042/0025; scale bar corresponds to 1 mm; Fig. 14 shows protoconch of Fig. 11; sample A.

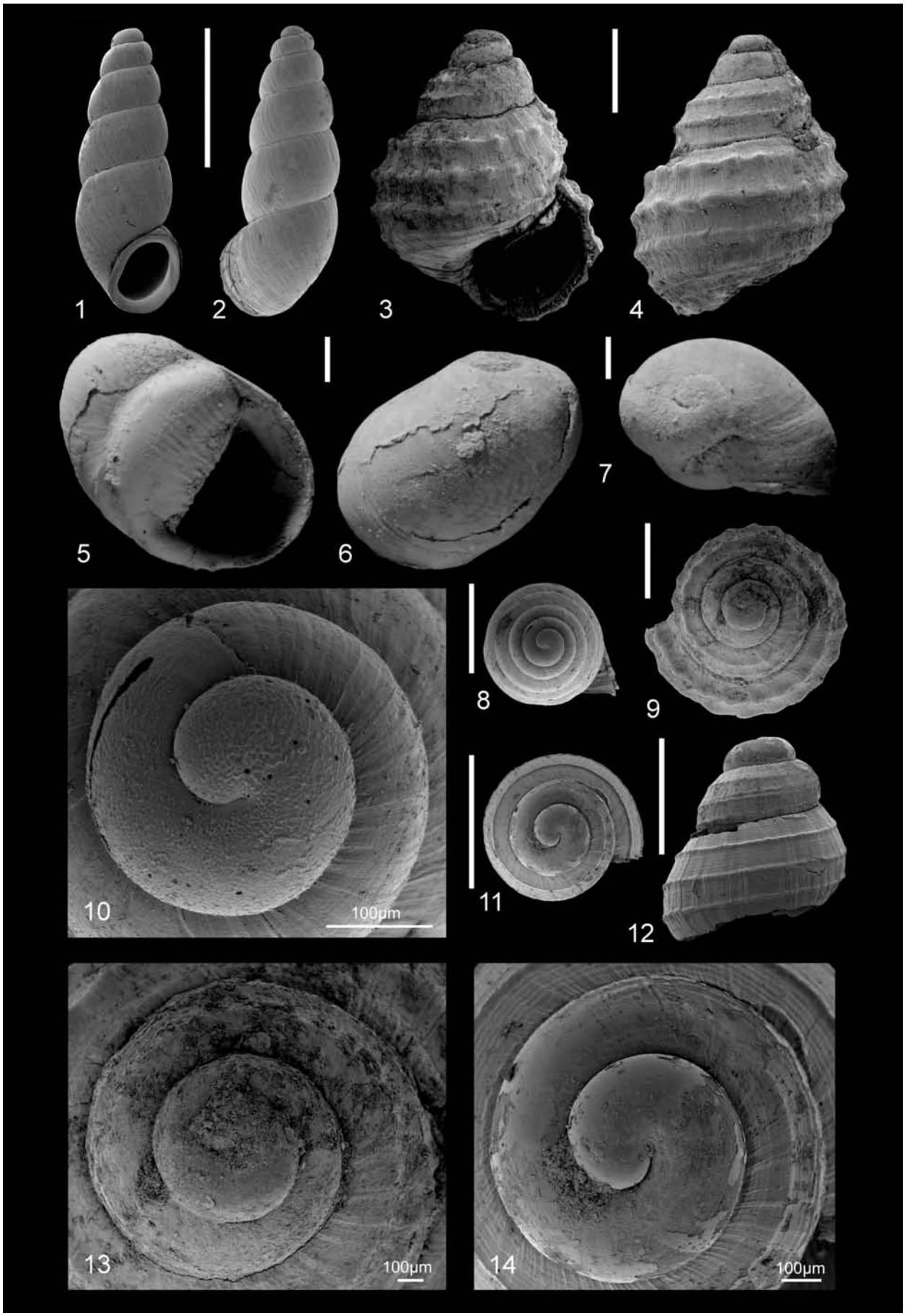
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Plate 6
All figures by T. Neubauer, NHMW.

Figs. 1–2, 12. *Lymnaea* sp.
NHMW Inv. 2010/0042/0027; scale bar corresponds to 1 mm;
Fig. 12 shows protoconch of Fig. 1; sample A.

Figs. 3–4, 11. *Gyraulus geminus* (Brusina 1897).
NHMW Inv. 2010/0042/0028; scale bar corresponds to 1 mm;
Fig. 11 shows protoconch of Fig. 4; sample A.

Fig. 5. *Orygoceras dentaliforme* Brusina 1882.
NHMW Inv. 2010/0042/0029; scale bar corresponds to 1 mm;
sample J.

Figs. 6, 10. *Orygoceras stenonemus* Brusina 1882.
NHMW Inv. 2010/0042/0031; Fig. 6, scale bar corresponds to 1 mm; sample J.
Fig. 10: protoconch of a second specimen; sample 44.

Fig. 7. *Orygoceras cornucopiae* Brusina 1882.
NHMW Inv. 2010/0042/0030; scale bar corresponds to 1 mm;
sample J.

Figs. 8–9, 13. *Ferrissia illyrica* (Neumayr 1880).
NHMW Inv. 2010/0042/0032; scale bar corresponds to 1 mm;
Fig. 13 shows protoconch of Fig. 8; sample 44.

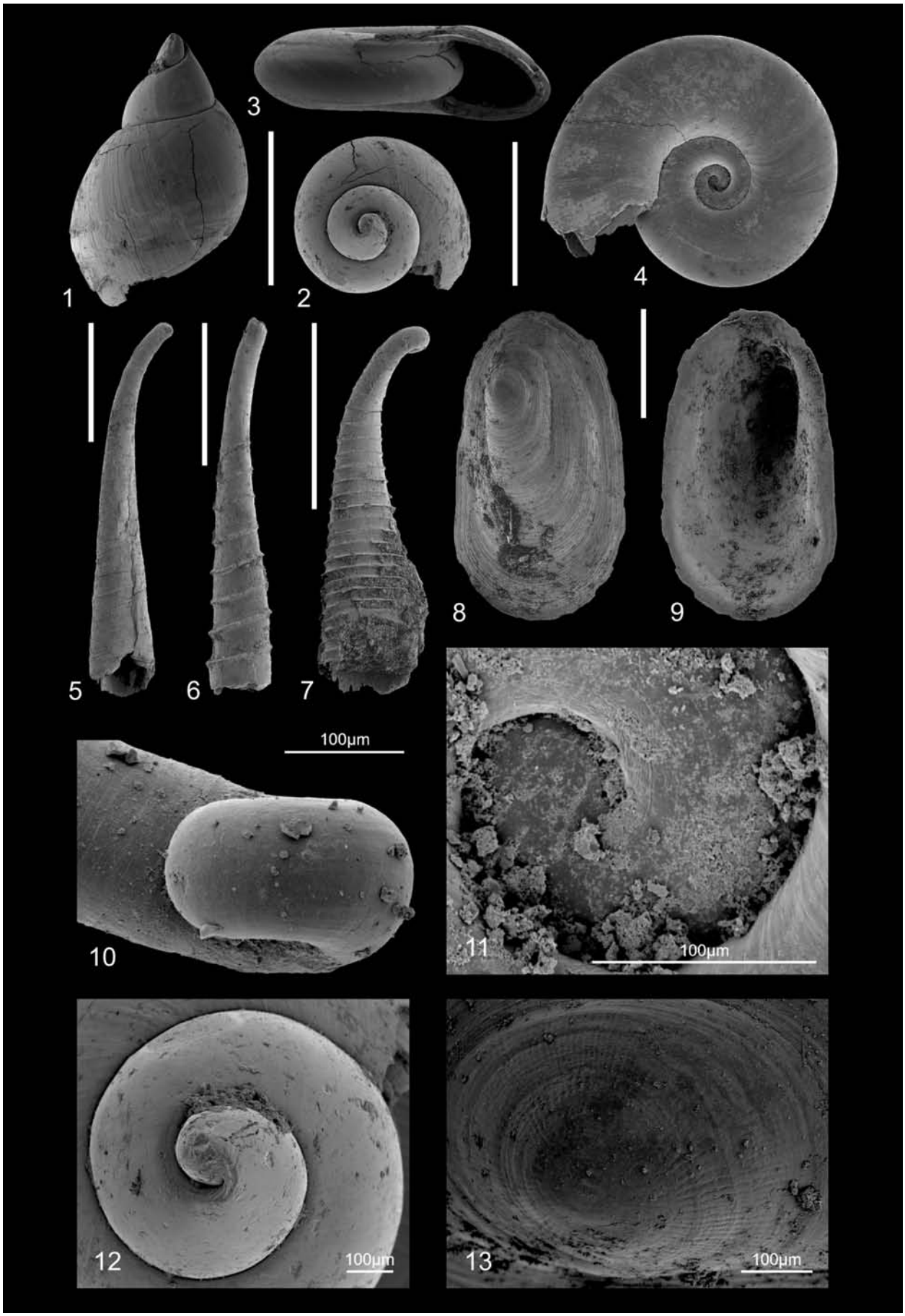
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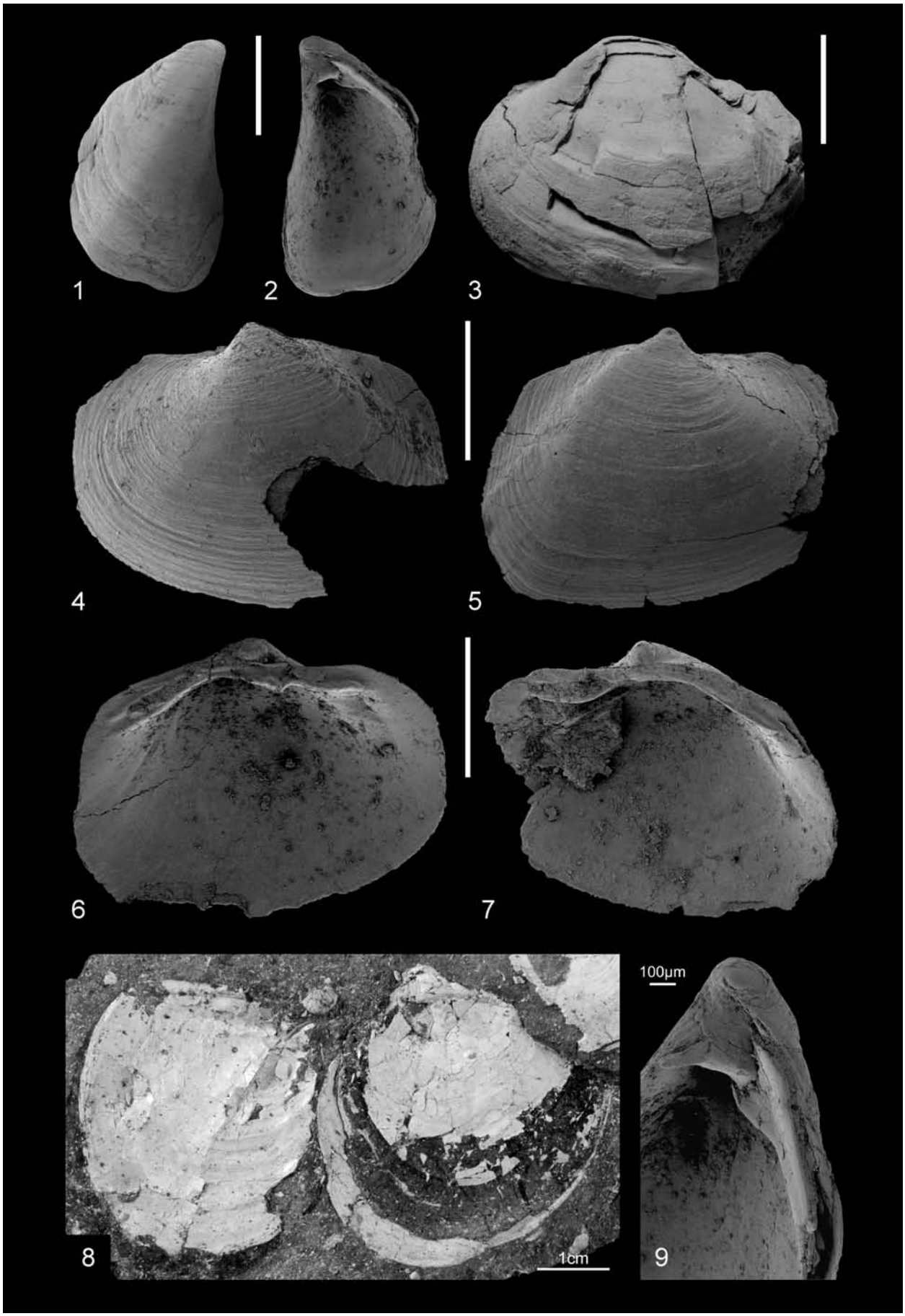
Plate 7
All figures by T. Neubauer and A. Schumacher, NHMW.

Figs. 1–2, 9. *Mytilopsis jadrovi* (Brusina 1892).
NHMW Inv. 2010/0042/0033, RV; scale bar corresponds to 1 mm; Fig. 9 shows hinge of Fig. 1; sample 44.

Fig. 3–7. *Unio rackianus* Brusina 1874.
NHMW Inv. 2010/0042/0034; Fig. 3: LV; scale bar corresponds to 1 cm; sample 44.
Figs. 4–7: juvenile specimen; Figs. 4, 6: LV; Figs. 5, 7: RV; scale bar corresponds to 1 mm; sample 44.

Fig. 8. *Mytilopsis aletici* (Brusina 1907).
Left specimen: RV.
Right specimen: articulated shell with fragmented LV on top; scale bar corresponds to 1 cm; Sutina, Sinj Basin (Coll. NHMW).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