Austrian Journal of Earth Sciences | Vienna | 2015 | Volume 108/2 | 15 - 67 | DOI: 10.17738/ajes.2015.0013

The freshwater mollusk fauna of the Middle Miocene Lake Drniš (Dinaride Lake System, Croatia): a taxonomic and systematic revision

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KEYWORDS Gastropoda; Bivalvia; taxonomy; systematics; nomenclature; stratigraphy; paleobiogeography

Abstract

The present contribution displays a taxonomic and systematic revision of the exceptionally rich mollusk fauna of the Middle Miocene Lake Drniš, Southern Croatia. In total, 44 species of freshwater mollusks (36 freshwater gastropods, 8 bivalves) and 5 species of terrestrial gastropods are recorded. The assemblage is dominated by melanopsids and hydrobiids concerning number of species and individuals. Such a composition is typical among the coeval paleolakes of the Dinarides and is indicative of a perennial, moderately shallow setting. The fauna proves the highly endemic character of the Dinaride Lake System: 95.4 % of the freshwater species recorded for Lake Drniš only occur within this system. Moreover, the fauna shows a particularly strong relation-ship with that of nearby Lake Sinj (79.5 %). Only four freshwater species (9.1 %) are endemic to Lake Drniš. The present work ties the fauna to the stratigraphical framework established for the coeval Dinaride lakes Sinj, Kupres, and Gacko, and suggests an age of ca. 15.7–15.0 Ma, classifying the deposits into the early Middle Miocene (early Langhian).

Among the Hydrobiidae (Gastropoda: Truncatelloidea) the new genus *Kadolskya* Neubauer and Harzhauser nov. gen. is introduced. Among the Dreissenidae (Bivalvia: Veneroidea) the new subfamily Congeriinae Mandic and Harzhauser nov. subfam., the new genus *Illyricocongeria* Mandic nov. gen., and the new species *Illyricocongeria moirae* Mandic nov. sp. are described.

Der vorliegende Beitrag stellt eine taxonomische und systematische Revision der reichen Molluskenfauna des mittelmiozänen Drniš-Sees in Südkroatien dar. Insgesamt wurden 44 Arten von Süßwassermollusken (36 Süßwassergastropoden, 8 Bivalven) und 5 Arten von terrestrischen Gastropoden erfasst. Die Vergesellschaftung wird dominiert von Melanopsiden und Hydrobiiden betreffend der Anzahl der Arten ebenso wie der Individuen. Solch eine Zusammensetzung ist typisch unter den gleichzeitig existierenden Paläoseen der Dinariden und deutet auf einen perennierenden, vorherrschend seichten See hin. Die Fauna belegt den hoch endemischen Charakter des Dinariden-Seensystems: 95,4 % der Süßwasser-Arten, die im Drniš-See gefunden wurden, treten nur in diesem System auf. Darüber hinaus zeigt die Fauna eine besonders starke Beziehung zu dem nahegelegenen Sinj-See (79,5 %). Nur vier Süßwasser-Arten (9,1 %) sind auf den Drniš-See beschränkt. Die vorliegende Arbeit knüpft die Fauna an das bestehende stratigraphische Rahmenkonzept an, welches für die gleichzeitig auftretenden Seen Sinj, Kupres und Gacko etabliert wurde, und deutet ein Alter von etwa 15,7–15,0 Ma an, was die Ablagerungen als frühes Mittelmiozän (frühes Langhium) klassifiziert.

Unter den Hydrobiiden (Gastropoda: Truncatelloidea) wird die neue Gattung *Kadolskya* Neubauer and Harzhauser nov. gen. eingeführt. Für die Dreissenidae (Bivalvia: Veneroidea) werden die Unterfamilie Congeriinae Mandic und Harzhauser nov. subfam., die neue Gattung *Illyricocongeria* Mandic nov. gen. und die neue Art *Illyricocongeria moirae* Mandic nov. sp. beschrieben.

1. Introduction

During the second half of the 19th century, the mollusk fauna of the freshwater Miocene of the Dinarides was intensively studied. Numerous works documented the extremely rich fauna and described over hundred species-group taxa (Neumayr, 1869, 1880; Brusina, 1870, 1872, 1874, 1876, 1878, 1881, 1882, 1884, 1896, 1897, 1902, 1907; Bourguignat, 1880). Despite faunal differences and gradients within, the whole system tem showed a high degree of endemism in comparison to other coequal freshwater systems of Europe. Because of this, Krstić et al. (2003) invented the term "Dinaride Lake System" (DLS) as collective for the freshwater lakes present in many sedimentary basins during the Early and Middle Miocene (Harzhauser and Mandic, 2008; Neubauer et al., 2015a,b). Following the initial period of taxonomic descriptions, later studies mainly focused on distinct systematic groups (Jurišić-Polšak, 1979, 1984; Kochansky-Devidé and Slišković, 1978; Žagar-Sakač, 1981, 1986, 1987, 1990; Žagar-Sakač and Sakač, 1984; Harzhauser and Mandic, 2010; Neubauer et al., 2014b) or provided summaries of certain regions (Jurišić-Polšak and Slišković, 1988). Especially during the last few years again several taxonomic investigations have been published (Jurišić-Polšak et al., 1993; Bulić and Jurišić-Polšak, 2009; Neubauer et al., 2011, 2013a, b; Krstić et al., 2013). These studies showed the distinctiveness and high rate of endemism of the involved lakes, i.e., Lake Sinj, Lake Kupres, Lake Gacko, and Lake Pag.

The present study displays a taxonomic and systematic revision of Lake Drniš, faunistically one of the richest lakes among the Dinaride Lake System. Beginning with the earliest descriptions by Neumayr and Brusina, 61 species and subspecies of mollusks have been described so far (50 freshwater gastro-

pods, 4 terrestrial gastropods, 7 bivalves). Since then, the fauna has not been studied in detail anymore; only few single systematic groups have been treated (Jurišić-Polšak, 1979, 1984; Kochansky-Devidé and Slišković, 1978; Žagar-Sakač, 1981, 1986, 1987). The latest author to list the gastropod taxa was Wenz (1923–1930). Consequently, the taxonomic and systematic concept applied to this fauna is largely outdated. We provide a detailed taxonomic study based on available type material and updated systematics. Only confirmed records are treated, based on the available material or on illustrations in the literature.

2. Geological setting

The Miocene Drniš Basin is a 23.5 x 1.9 km large, NNW-SSE striking, crescent structure, stretching from the NW margin of the Kosovo Polje in the North, along the NE margin of the Petrovo Polje karstic plain in its central part, to the Vrba River valley in the South (Ivanović et al., 1977, 1978). It belongs to a series of intramontane sedimentary basins of the Dinaride Mountains (Mandic et al., 2009, 2011; De Leeuw et al., 2011, 2012; Vlahović et al., 2012), settled in the Outer Dinarides (Schmid et al., 2008; Korbar, 2009), providing a carbonate dominated basement made of Triassic-Middle Eocene platform carbonates, Middle Eocene Flysch successions, and Upper Eocene to Lower Oligocene Molasse coal-bearing deposits (Papeš et al., 1984; Raić et al., 1984; Babić and Zupanič, 2007; Zupanič and Babić, 2011; Vlahović et al., 2012). Miocene deposits, bearing occasionally layers with well-preserved freshwater lacustrine mollusks are dominated by marl and limestone, are inclined by ~15° to the Southwest.

The Drniš Basin belongs to the main Dinaride wrenching zone of the Karlovac-Split suture (Schmid et al., 2008), related to Miocene and/or Pliocene transpressional tectonics, resulting from northward oblique-slip motions of the underthrusting Adriatic block (Tari, 2002) and/or post-Messinian opening of the Albanian Foredeep (Picha, 2002). Extensional tectonics coinciding with a climate optimum during the Early to Middle Miocene produced a number of synchronous NW-SE striking long-lived lake basins within the Dinaride Mountain Chain collectively termed as Dinaride Lake System (Fig. 1; Krstić et al., 2003; Harzhauser and Mandic, 2008; Neubauer et al., 2011, 2013a, b, 2015a, b; De Leeuw et al., 2012). The deposits of these paleo-lakes cover large parts of today's Croatia, Bos-nia and Herzegovina, SW Serbia, and NW Montenegro. Many of these basins have been accurately studied lately and display important tie points in the regional continental stratigraphical framework. The present magnetostratigraphic, chronostratigraphic, and biostratigraphic data suggest a time frame of 18 to 13 Ma for the duration of the entire system (Jiménez-Moreno et al., 2008, 2009; Harzhauser and Mandic, 2008; De Leeuw et al., 2010, 2011, 2012; Mandic et al., 2011; Neubauer et al., 2011, 2013a, b), corresponding to middle Burdigalian to Early Serravallian.

Data about the sedimentary evolution of the Drniš Basin are only sparsely available and largely derive from geological maps (Kerner, 1896, 1901; Ivanović et al., 1977, 1978). Miocene lacustrine sediments with a mean thickness of 80 m cover a 0.1–1.9 km narrow, elongated area with a total sediment cover of ca. 10 km². Since large parts of the Kosovo Polje, Petrovo Polje and Vrba Valley are today overlain with Quaternary deposits, the original extent of Lake Drniš might have been somewhat larger. Beyond that, its presently crescent shape could also be a product of post-sedimentary compressive tectonics destroying sedimentary evidence of the connection with the neighboring Sinj Basin. Data on the age of the deposits are entirely missing. Based on faunal comparisons Neubauer et al. (2013a, b) suggested a similar age as for the Kupres and Gacko basins (ca. 15.8–15.2 Ma; Mandic et al., 2011). Discussing the biostratigraphical framework will be one focus of the present work.

The main locality in the Drniš Basin is Miočić, 7 km ENE of Drniš, which yielded several thousand mollusk shells (Neumayr, 1869; Brusina, 1874, 1884). The name "Miočić" referred to in the literature is broadly defined and usually also includes the nearby villages Biočić and Parčić, each ca. 1 km NNW and SSE of Miočić (Brusina, 1884; Kittl, 1895). Most of the taxa considered in the present study have been found or are first described from there. The locality is situated at the low hillsides marking the NE margin of the basin. The fossils derive from small outcrops or surface collections from water fissures and vineyards covering the hills. Additional material derives from the localities Vrba at the foot of Mt. Drvar, 2 km SE Kljake, and Kadina glavica, 2.5 km S Miočić (Fig. 1; Brusina, 1874, 1884; Kochansky-Devidé and Slišković, 1978).

Several authors indicate stratification of the sediments (Neumayr in Neumayr and Paul, 1875; Brusina, 1884), but only a single study provides a faunal list based on a section (Žagar-Sakač and Sakač, 1984). The 106.4 m-thick composite section "Liskovača" presented by latter authors is located at the southernmost tip of Petrovo Polje ca. 1.5 km SSE of Čavoglave (GPS/WGS84: 43°46'13" N, 16°20'34" E; Croatian Base Map M 1 : 5000), not far from Brusina's locality Vrba.

The succession starts with a 4 m-thick basal conglomerate superposing discordantly the Upper Cretaceous marine limestone. It is followed by a 28 m-thick interval of monotonous marl bearing melanopsid, emmericid, and dreissenid shell accumulations. Additionally, coal and clayey interbeds are present in the upper part of this interval. The section continues with 24 m-thick, weakly bedded, monotonous marls and clayey marls with common dreissenid, unionid, and melanopsid beds, together with clay, sand, coal and leaf remain intercalations. This is followed by a 10 m-thick marly interval with few dreissenid beds interbedded by thin conglomerate, coal and clay beds and lenses. Upsection a 27 m-thick interval follows, represented by gastropod-bearing marl with coal and clayey interbeds in the lower part, grading upwards to limy marl, and marly limestone on top. The succession ends in a 10 m-thick, weakly fossiliferous, thick-bedded limestone grading upwards into a 4 m-thick calcareous breccia marking the very top of the section.

The section documents evolution of the Lake Drniš within a single transgression-regression depositional cycle. Its rich mollusk record combined with dominating carbonate petrography indicates prevailing deposition in a littoral facies of a perennial carbonate lake (Mandic et al., 2009). The central part of the section with numerous coal and coaly clay interbeds, remains of swamp vegetation, and lenses of crushed mollusk shells marks a depositional phase of prevailing marginal, deltaic settings. This phase culminates in its middle part with conglomerate intercalations, which might mark the presence of clastic-channel facies of the nearby alluvial plain (Gierlowski-Kordesch et al., 1991). The breccia on top of the section suggests a tectonically induced end of the lacustrine deposition typical for many Dinaride Basins (De Leeuw et al., 2011, 2012; Vlahović et al., 2012).

Although the species list presented by Žagar-Sakač and Sakač (1984) portends a rich mollusk fauna, many determinations are very unreliable. Many of the mentioned taxa, partly only based on few fragments, have never been reported from the Drniš Basin or the DLS before. Since these alleged occurrences still need verification, we do not consider them in the present study.

3. Material and methods

For this work, we studied the available type material stored at the Croatian Natural History Museum in Zagreb (NHMZ), the National Museum in Sarajevo (NHMS), and the Austrian Geological Survey in Vienna (GBA). For several species, additional material is present from the localities Miočić, Biočić, Parčić, and Vrba in the rich collection of the Natural History Museum Vienna (NHMW; coll. no. 2014/0315). A part of that material was collected by Ernst Kittl and formed the base for the identifications in his excursion report (Kittl, 1895). A small number of specimens were collected by the authors from Miočić (locality "Miočić 1" in Figure 1; GPS/WGS84: 43° 52'17.9" N, 16°13'49.1" E). The SEM images of the types stored at the NHMZ were made with a Tescan TS5136MM; those of the types stored at the GBA were made with the FEI Inspect S at the Department of Paleontology of the University of Vienna. The SEM images of additional material of the NHMW were made with the on-site JEOL JSM-6610LV.

4. Systematic paleontology

The systematic arrangement follows Bouchet and Rocroi (2005), Wade et al. (2006), Jörger et al. (2010), Criscione and

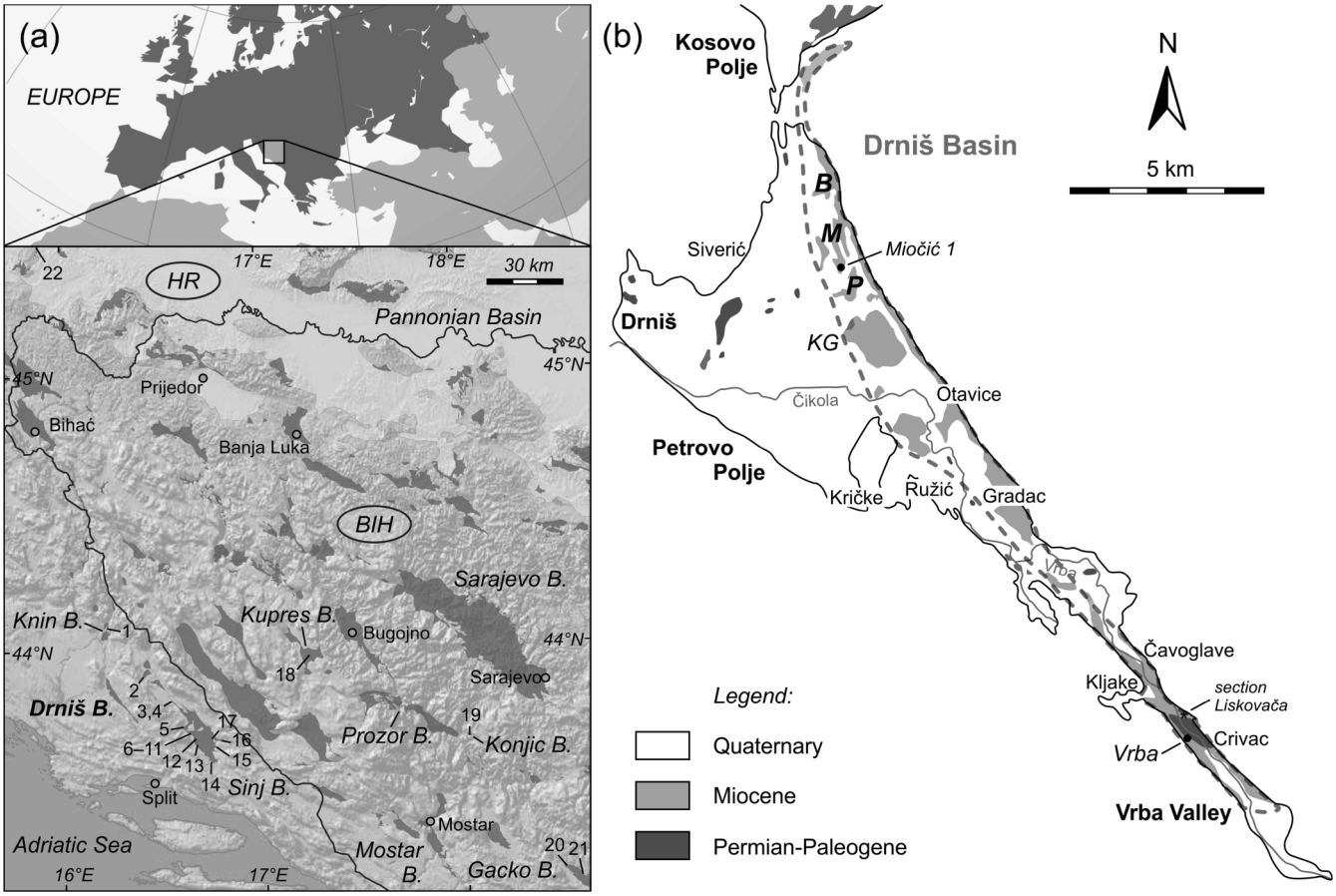


Figure 1: (a) Geographical overview of the southern part of the Dinaride Lake System with indication of most of the localities and basins mentioned in the text (modified after Harzhauser et al., 2012; Neubauer et al., 2013a): 1 – Golubić, 2 – Lemeš (exact position unknown), 3 – Ribarić, 4 – Potravlje, 5 – Lučane, 6 – Ruduša (= Goručica), 7 – Župića potok, 8 – Trnovača, 9 – Stuparuša, 10 – Čugurina glavica, 11 – "bunar", 12 – Bunarska Glavica, 13 – Turjaci (= Turiake), 14 – Strmendolac (Crveni klanac), 15 – Svinjača, 16 – Ruda, 17 – Otok, 18 – Fatelj, 19 – Džepi, 20 – Gračanica, 21 – Vrbica, 22 – Dugoselo. (b) Geological sketch of the Drniš Basin, showing the extent of the Miocene sediment cover and the fossiliferous localities (in italic). Localities: B – Biočić, M – Miočić, P – Parčić, KG – Kadina Glavica.

Ponder (2013), and the FreshGEN database (Neubauer et al., 2014a). The synonymy lists only include references where the species were described or illustrated, where a new combination was established or where taxa considered being junior synonyms were first described; additionally, references to the Fossilium Catalogus by Wenz (1923–1930) and the type catalogue of the Natural History Museum Zagreb (Milan et al., 1974) are given, if applicable. For complete synonymy lists see Wenz (1923–1930).

In the type catalogue of Milan et al. (1974) several nomenclatural mistakes occur, which are summarized and formalized here. First, they often wrongly refer to "holotypes". Generally, cases where they define a "holotype" from a series of syntypes actually display valid lectotype designations (ICZN, 1999, Art. 74.1 and 74.5). In other instances, they indicate a "holotype", although no holotype or lectotype was ever designated and the first description is based on more than one individual (not depending on whether there is only one illustration). In most cases, this "holotype" then actually refers to a syntype illustrated in the work of the first description or a later publication (e.g., Brusina, 1897, 1902 illustrated many of the specimens he used for previous species descriptions). Only where the first description is verifiably based on a single specimen, this individual (if preserved) is the holotype (by monotypy). The indication of "syntypes" (and the according collection numbers) often refers only to specimens illustrated by Brusina. However, all the other specimens Brusina had at hand for the first description are syntypes as well. For these, the collection numbers are unknown, though. None of the designations of "neotypes" fulfills the requirements stated by the Code (ICZN, 1999, Art. 75.3); they are all invalid as will be demonstrated below.

Abbreviations used for indications of dimensions: H – height; W – width; L – length; C – Valve convexity.

Class Gastropoda Cuvier, 1795
Subclass Heterobranchia Gray, 1840
Superfamily Valvatoidea Gray, 1840
Family Valvatidae Müller, 1774
Genus *Valvata* Müller, 1774

Type species: *Valvata cristata* Müller, 1774. Recent; Europe. Type by subsequent monotypy (see Welter-Schultes, 2012).

***Valvata*? *homalogyra* Brusina, 1874**
Figure 2A–C

* 1874 *Valvata homalogyra* Brusina – Brusina, p. 90.
1897 *Valvata homalogyra* Brus. – Brusina, p. 26, pl. 14, figs 7–9.
1928 *Valvata* (*Valvata*) *homalogyra* Brusina – Wenz, p. 2469 [cum syn.].
1974 *Valvata* (*Valvata*) *homalogyra* Brusina – Milan et al., p. 143.
? 2006 *Valvata homalogyra* Brusina, 1874 var. – Kókay, p. 32, pl. 3, figs 11–12.
2014 *Valvata homalogyra* Brusina, 1874 – Haszprunar, p. 52.

Material: 1 specimen (NHMZ 3120-766).
Type material: The syntype series includes 14 specimens (NHMZ 1613 and NHMZ 1625.1-13) from Goručica SW Sinj (= Ruduša) described by Brusina (1874) but not illustrated due to bad preservation. Brusina (1897) subsequently illustrated only one specimen from Miočić. This misled Milan et al. (1974) to regard Miočić as the type locality and the specimen, which was available for the present study, as the "holotype". Yet, surprisingly, the latter is apparently not even the specimen documented by Brusina (1897).
Dimensions (H x W): 1.03 x 1.79 mm.
Description: Small, low trochiform shell with up to 3 whorls that quickly and continuously increase in diameter. Protoconch unknown. Last whorl large, attains over 90 % of total shell height. Aperture near circular to slightly elliptical, with sharply edged peristome. Umbilicus rather narrow but deep, reaches up to protoconch.
Remarks: The only other valvatid recorded for the Dinaride lakes is *Valvata abdita* Brusina, 1902 from the Early/Middle Miocene of Dugoselo (Glina Basin, see Mandic et al., 2012 for the age constraints). This species clearly differs in its higher trochiform spire and the lower whorl expansion rate.

The systematic placement within *Valvata* is uncertain. A diagnostic feature of *Valvata* is the spiral striae on the protoconch, which is unknown in this species, due to preservation. The shape is also common among hydrobiids (e.g., Harzhauser et al., 2014a).
Distribution: Drniš Basin (Miočić), Sinj Basin (Ruduša, Župića potok, "bunar") (Brusina, 1874, 1884, 1907). The locality "bunar" is described in Brusina (1907) as a "large well [in Croatian 'veliki bunar'] beside Goručica bridge in Sinj on the main road to Split". This led Wenz (1929) to term the locality "Veliki Bunar". Here we follow the original term applied by Brusina (1907). The record from the late Early Miocene of Somlóvásárhely, Hungary, by Kókay (2006) needs verification.

Subclass Neritimorpha Golikov and Starobogatov, 1975
Order Cycloneritimorpha Frýda, 1998
Superfamily Neritoidea Rafinesque, 1815
Family Neritidae Rafinesque, 1815
Subfamily Neritininae Poey, 1852
Genus *Theodoxus* Montfort, 1810

Type species: *Theodoxus lutetianus* Montfort, 1810 [currently considered as a synonym of *Theodoxus fluviatilis* (Linnaeus, 1758)]. Recent; Europe. Type by original designation (Welter-Schultes, 2012).

***Theodoxus imbricatus* (Brusina, 1878)**
Figure 2M–O

* 1878 *Neritina imbricata*, Brusina – Brusina, p. 353.
1884 *Neritodonta imbricata* Brusina – Brusina, p. 76, pl. 2, figs 7–10.
1897 *Neritodonta imbricata* Brus. – Brusina, p. 27, pl. 14, figs

32–34, pl. 15, figs 1–2.
1907 *Neritodonta imbricata exarmata* n. f. – Brusina, p. 204.
1929 *Theodoxus* (Calvertia) *imbricatus imbricatus* (Brusina) – Wenz, p. 2958.
1929 *Theodoxus* (Calvertia) *imbricatus exarmatus* (Brusina) – Wenz, p. 2959.
1974 *Theodoxus* (Calvertia) *imbricatus exarmatus* (Brusina) – Milan et al., p. 107.
2013a *Theodoxus imbricatus* (Brusina, 1878) comb. nov. – Neubauer et al., p. 131, figs 3A–F.

Material: One specimen illustrated by Brusina (1897); 3 specimens from Miočić (NHMW 2014/0315/0002, NHMW 2014/0315/0067).

Type material: Details of type material unknown (type locality: Miočić, Drniš Basin).
It is uncertain whether the specimens illustrated by Brusina (1897) are part of the original material of Brusina (1878) or derive from newly collected material. The specimen illustrated by Brusina (1897, pl. 14, figs 33–34) is available in the NHMZ collection (NHMZ 3130-776), while the one illustrated on pl. 14, fig. 32 could not be found. Brusina (1897) stated that "the specimen is stored in the collection of the University Graz, no. 1421", but this could not be verified.
Dimensions (H x W): 4.6 x 4.6 mm (Brusina, 1897, pl. 14, figs 32–34); 9.25 x 9.49 mm (syntype of *T. i. exarmatus*; NHMZ 3131-777/1; Miočić, Drniš Basin; Brusina, 1897, pl. 15, fig. 1); 7.57 x 8.41 mm (syntype of *T. i. exarmatus*; NHMZ 3131-777/2;

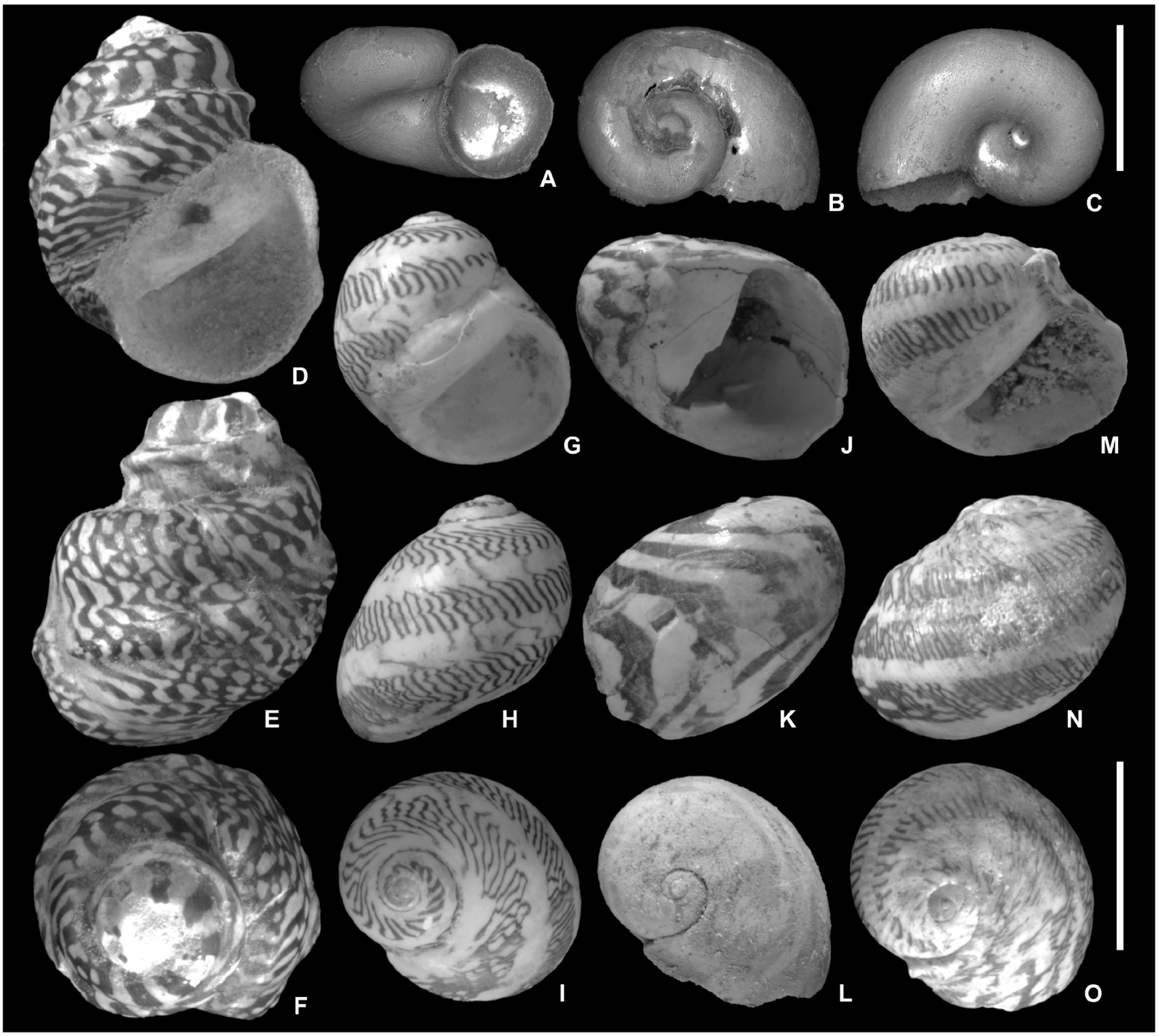


Figure 2: Valvatidae and Neritidae. (A–C) *Valvata*? *homalogyra* Brusina, 1874. Specimen erroneously considered as holotype by Milan et al. (1974) (NHMZ 3120-766), Miočić. (D–F) *Theodoxus lorkovici* (Brusina, 1878). Miočić (GBA 2014/008/0001). (G–I) *Theodoxus lorkovici* (Brusina, 1878). Miočić (GBA 2014/008/0002). (J–L) *Theodoxus sinjanus* (Brusina, 1876). Specimen illustrated by Neumayr (1869, pl. 12, fig. 16) as "*Neritina Grateloupana*" (GBA 1869/01/22/1), Miočić. (M–O) *Theodoxus imbricatus* (Brusina, 1878). Miočić (NHMW 2014/0315/0002). Scale bars correspond to 1 mm (A–C) and 5 mm (D–O).

Miočić, Drniš Basin; Brusina, 1897, pl. 15, fig. 2).

Description: Morphologically very variable species, comprising up to 3 whorls. Fully grown individuals attain 10 mm in both width and height. Protoconch smooth, consisting of ca. 1 whorl. Body whorl nearly fully overgrows preceding whorls, develops distinct shoulder near the upper suture, which produces narrow horizontal ramp adapically. Second rounded angle occurs between shoulder and base; whorl portion in between more or less flattened. Aperture regularly semilunar, inclined to axis with ca. 45°; massive callus pad present, sometimes bearing numerous, weak denticles. In some specimens, sculpture appears on last whorl, expressed as simple bulge at the shoulder up to strong, irregularly shaped tubercles, arranged in two spiral lines. Color pattern variable as well: brown or yellow; densely spaced irregular axial lines to wide-spaced zigzag lines; may cover entire shell or may be confined to certain spiral areas.

Remarks: Brusina (1907) split the bulk of specimens he originally determined as *Neritina imbricata* and introduced the new forma *Neritodonta imbricata exarmata* with the same angulated morphology but without the tubercles typical for *N. imbricata imbricata*. As shown already by Neubauer et al. (2013a) this feature is quite variable even in the same sample and apparently not diagnostic. Therefore, we consider both names synonymous. Despite its variability, the species cannot be confused with other Dinaride neritids, based on the shouldered to angled morphology. The only similar taxon is *Theodoxus reiseri* (Brusina, 1902) from Džepi (Prozor Basin), which has a comparable morphology and mode of sculpture. It can be distinguished by the irregularly shaped aperture and the partly elevated spire. Also the shoulder is weaker expressed.

Distribution: Drniš Basin (Miočić), Kupres Basin (Fatelj) (Brusina, 1878, 1897; Neubauer et al., 2013a). Alleged records from the Sinj Basin (Veliki Bunar, Župića potok) mentioned by Wenz (1929) are incorrect; none of the cited publications documented it from there.

***Theodoxus lorkovici* (Brusina, 1878)**

Figure 2D–I

* 1878 *Neritina Lorkovici*, Brusina – Brusina, p. 354.
1884 *Neritodonta Lorkovići* Brusina – Brusina, p. 78, pl. 2, figs 1–6.
1897 *Neritodonta Lorkovići* Brus. – Brusina, p. 27, pl. 15, figs 3–9.
1929 *Theodoxus* (*Calvertia*) *lorkovići* (Brusina) – Wenz, p. 2961.
1974 *Theodoxus* (*Calvertia*) *lorkovici* (Brusina) – Milan et al., p. 107.

Material: Specimens illustrated by Brusina (1897); 43 specimens from Miočić (NHMW 2014/0315/0068, NHMW 2014/0315/0086, NHMW 2014/0315/0195), 34 from Parčić (NHMW 2014/0315/0145, NHMW 2014/0315/0157); 23 from Miočić (GBA 2008/265/0130, GBA 2014/008/0001, GBA 2014/008/0002).

Type material: Details of type material unknown (type locality: Miočić, Drniš Basin). It is uncertain whether the specimens illustrated by Brusina (1897) and indicated as syntypes by Milan et al. (1974) (NHMZ 2719-365/1-3) are part of the original material of Brusina (1878) or derive from newly collected material.

Dimensions (H x W): 8.69 x 7.56 mm (Brusina, 1897, pl. 15, fig. 3); 10.39 x 7.29 mm (Brusina, 1897, pl. 14, figs 4–5); 7.64 x 7.45 mm (Brusina, 1897, pl. 14, fig. 6); 8.79 x 7.92 mm (Brusina, 1897, pl. 14, fig. 7); 9.54 x 7.31 mm (Brusina, 1897, pl. 14, fig. 8); 8.47 x 8.09 mm (Brusina, 1897, pl. 14, fig. 9). All specimens are from Miočić.

Description: High-coiled, rather slender neritid, consisting of 3.25 whorls. Protoconch unknown. Last whorl attains 85–90 % of total height; two very weak, rounded angulations occur: one near upper suture, second at transition to straight base; whorl portions above and below upper angulation low convex. Occasionally, marked bulges may form instead of angulations, producing irregular shape (Figs 2D–F). Aperture inclined with ca. 45°; thick callus pad present, bearing few, weak denticles in its center. Coloring variable, can be expressed as spirally arranged reticulate pattern, spirally arranged dark bands, dense axially undulating pattern, or dense, irregular axial lines.

Remarks: Despite its considerable morphological variability, this species can be distinguished from all other coeval neritids of Central and Southeastern Europe, based on ist slender, slightly angulated morphology.

Distribution: Only known from the Drniš Basin (Miočić, Parčić).

***Theodoxus sinjanus* (Brusina, 1876)**

Figure 2J–L

1869 *Neritina Grateloupana* [sic] Férussac – Neumayr, p. 365, pl. 12, figs 16–17 [partim; non *Neritina Grateloupiana* Férussac, 1823].
1874 *Neritina Grateloupana* [sic] Férussac – Brusina, p. 90 [non Férussac, 1823].
* 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 [cum syn.].
1974 *Theodoxus* (Calvertia) *sinjanus* (Brusina) – Milan et al., p. 110.
1979 *Theodoxus* (Neritaea) *sinjanus* (Brusina) – Jurišić-Polšak, p. 19, pl. 3, figs 4–11.
? 2006 *Theodoxus sinjanus* (Brusina), 1884 – Kókay, p. 30, pl. 2, figs 11–13.
2011 *Theodoxus sinjanus* (Brusina, 1876) – Neubauer et al., p. 204, pl. 5, figs 5–7.

Material: Specimens illustrated by Brusina (1897); 5 specimens from Miočić (NHMW 2014/0315/0116); 2 from Miočić (GBA 1869/01/22/1-2, illustrated in Neumayr 1869).

Type material: Milan et al. (1974) designated the specimen from Župića potok (Sinj Basin) illustrated by Brusina (1897, pl.

15, fig. 10) as lectotype (NHMZ 3134-780/1). Since it cannot be ascertained whether this specimen was among the material used by Brusina (1876) for the first description, this procedure is invalid.

Dimensions (H x W): 6.94 x 7.37 mm (Brusina, 1897, pl. 15, fig. 10); 7.55 x 8.44 mm (Brusina, 1897, pl. 15, fig. 11); 6.38 x 8.30 mm (Brusina, 1897, pl. 15, fig. 12).

Description: Protoconch flat and immersed, smooth, consisting of ca. 1 whorl. Shell comprises up to 4 whorls. Spire almost fully covered by last whorl, which markedly expands laterally, producing an about oval shape. This expansion is expressed by more or less straight ramp, formed by weak shoulder, and convex flanks. Aperture semicircular, with massive, distinctly demarcated callus pad, occasionally bearing numerous weak to prominent denticles. Coloring variable, including dense axial striation, spirally arranged reticulate patterns, axial zigzag lines, or mottled patterns.

Remarks: The species differs from *T. semidentatus* (Sandberger, 1875) from Ribarić (Sinj Basin), which exhibits an elevated spire and a distinct concavity near the upper suture of the last whorl. *Theodoxus grateloupianus* (Férussac, 1823), with which the species was confused by Neumayr (1869), was described from the Early Miocene of the Aquitaine Basin, France, and has a rather slender, high-coiled shell (cf. Lozouet et al., 2001).

Distribution: Drniš Basin (Miočić), Sinj Basin (Ribarić, Strmendolac-Crveni klanac, Župića potok, "bunar") (Neumayr, 1869; Brusina, 1884, 1897, 1907; Jurišić-Polšak et al., 2000). The record from the late Early Miocene of Nagygörbő, Hungary, by Kókay (2006) needs verification.

Subclass Caenogastropoda Cox, 1960
Superfamily Cerithioidea Fleming, 1822
Family Melanopsidae H. Adams and A. Adams, 1854
Subfamily Melanopsinae H. Adams and A. Adams, 1854
Genus *Melanopsis* Férussac in Férussac and Férussac, 1807

Type species: *Melania costata* Olivier, 1804. Recent; Europe. Type by subsequent designation by Gray (1847).

Melanopsis acanthica Neumayr, 1869

Figure 3A–B

* 1869 *Melanopsis* (*Canthidomus*) *acanthica* nov. sp. – Neumayr, p. 357, pl. 11, figs 6–7.
1874 *Melanopsis acanthica* Neumayr – Brusina, p. 43.
1929 *Melanopsis acanthica* Neumayr – Wenz, p. 2650.
? 1988 *Melanopsis acanthica* Neumayr – Jurišić-Polšak and Slišković, p. 170, pl. [1], figs 1–8.

Material: Several hundred specimens from Miočić (NHMW 2014/0315/0066, NHMW 2014/0315/0092, NHMW 2014/0315/0093, NHMW 2014/0315/0095, NHMW 2014/0315/0196), 2 from Biočić (2014/0315/0139); 34 from Miočić (GBA 2008/021/0246, GBA 2008/021/0253).

Type material: GBA 1869/01/4/1-2 (syntypes); Miočić, Drniš Basin (Neumayr, 1869, pl. 11, figs 6–7).

Dimensions (H x W): 35.0 x 16.6 mm (syntype; Neumayr, 1869, pl. 11, fig. 6); 24.8 x 14.7 mm (syntype; Neumayr, 1869, pl. 11, fig. 7).

Description: Shell conical, with up to 10 whorls. Sculpture already starts on early teleoconch with distinct ribs, which increase in strength during ontogeny. On 3rd teleoconch whorl, these ribs grade into small, axially elongated, spiky nodules, situated approximately in center of whorls. From 4th whorl onwards, second row of nodules is present near lower suture; on last whorl, third row is visible. Nodules always vertically aligned; nodules connected both vertically and horizontally via thin but distinct, concave ribs, what gives impression of near reticulate pattern on last whorl. Sutures not incised. Last whorl attains ca. 60 % of shell height. Thin, sharp fasciole present on neck. Aperture broadly lenticular; callus glossy, moderately thick. Outer lip destroyed in all available specimens.

Remarks: The species is similar to the co-occurring *M. zitteli* Neumayr, 1869 concerning shape and size, but differs in the mode of sculpture. In *M. zitteli*, densely arranged, slightly inclined ribs cover the entire shell. Like in *M. acanthica*, three rows of nodules are present on the last whorl, but these are much smaller and blunt. Since both taxa are endemic to the Drniš Basin and show considerable morphological similarities, they are probably closely related.

Distribution: Drniš Basin (Biočić, Miočić) (Neumayr, 1869; Brusina, 1874). Its presence in the Late Miocene white marl of Livno Basin (Čelebić-Jaruga, Šaćirovina) indicated by Jurišić-Polšak and Slišković (1988) needs verification (see also Kochansky-Devidé and Slišković, 1981 and De Leeuw et al., 2011 for the stratigraphic position).

Melanopsis geniculata Brusina, 1874

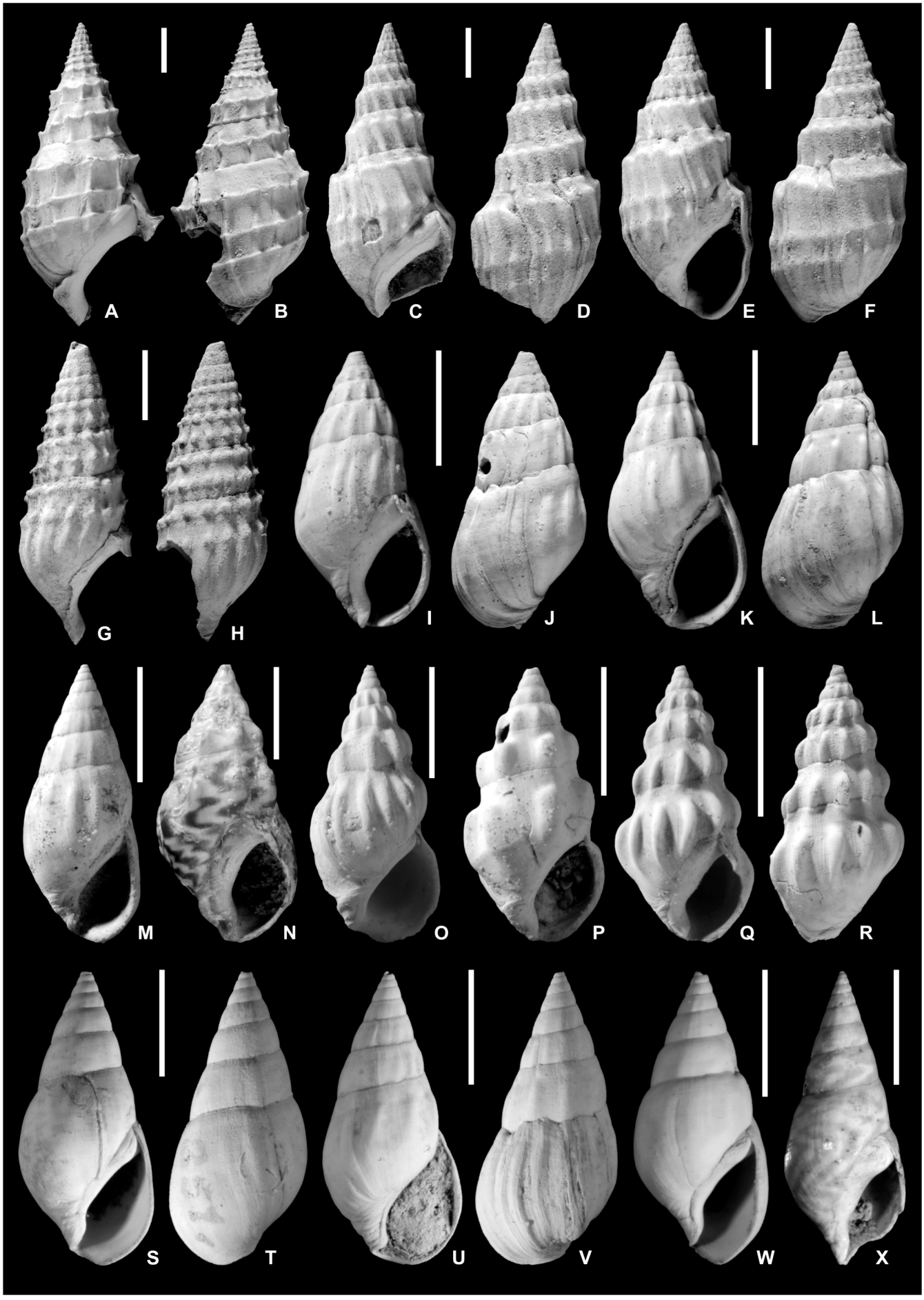
* 1874 M*elanopsis geniculata* Brusina – Brusina, p. 40, pl. 1, figs 9–10.
1897 *Melanopsis geniculata* Brus. – Brusina, p. 11, pl. 4, figs 21–26.
1902 *Melanopsis geniculata* Brus. – Brusina, pl. 6, fig. 55.
1929 *Melanopsis geniculata* Brusina – Wenz, p. 2734 [partim; excluding records of *M. g. enodota* [sic]].
1974 *Melanopsis geniculata* Brusina – Milan et al., p. 91.
2013a *Melanopsis geniculata* Brusina, 1874 – Neubauer et al., p. 134, figs 4C–D.

non 1912 *Melanopsis geniculata* – Fischer and Wenz, p. 511.
non 1917 *Melanopsis* cf. *geniculata* Brusina – Wenz, p. 59.
non 1921 *Melanopsis* cf. *geniculata* Brusina – Wenz, p. 191.
non 1922 *Melanopsis geniculata* – Wenz, p. 64.
non 1963 *Melanopsis* (*Canthidomus*) *geniculata geniculata* Brusina – Kühn, p. 380, pl. 2, figs 7a, b.

Material: Specimens illustrated by Brusina (1897).

Type material: NHMZ 3207-853 (syntype); Miočić, Drniš Basin.

Dimensions (H x W): 11.10 x 5.72 mm (syntype; Brusina, 1874,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pl. 1, figs 9–10); 11.07 x 6.09 mm (Brusina, 1897, pl. 4, fig. 21); 9.44 x 5.10 mm (Brusina, 1897, pl. 4, fig. 23); 11.97 x 5.15 mm (Brusina, 1897, pl. 4, fig. 24); 16.36 x 7.26 mm (Brusina, 1897, pl. 4, fig. 25); 9.02 x 4.05 mm (Brusina, 1897, pl. 4, fig. 26). All are syntypes from Miočić.

Remarks: The typical feature of this species is the presence of irregular tubercles on the last 2–3 whorls, resulting in an uneven shell shape. These excrescences emerge from regularly arranged ribs on earlier whorls. In some specimens, however, the sculpture is strongly reduced to irregular bulges. For a detailed description see Neubauer et al. (2013a). Records from the Early Miocene of the Mainz Basin by Fischer and Wenz (1912) and Wenz (1917, 1921, 1922) are misidentifications. Wenz (1929) synonymized these records with *Brotia escheri aquitanica* (Noulet, 1846). It is incomprehensible, how these authors could confuse these two species, which belong to different families and do not resemble each other at all. Since the aforementioned authors only cited the name without descriptions or illustrations, a clarification of the whole problem is infeasible. After latest revisions, *Brotia escheri aquitanica* should be treated as *Tinnyea aquitanica*. For discussions of this taxonomically as well as nomenclaturally problematic group see Harzhauser et al. (2002) and Kowalke (2004). The misidentification by Kühn (1963) for material from the Late Miocene of Greece was already rectified by Papp (1979), who synonymized the records with *M. freybergi* Kühn, 1951.

The status of the subspecies *Melanopsis geniculata enodata* Brusina, 1897 from Župića potok (Sinj Basin) is highly uncertain. Brusina (1897) introduced it as a subspecies of *M. geniculata*, but it has actually quite little in common with the present taxon. Despite of that, Wenz (1929) and Milan et al. (1974) considered both taxa synonymous. Unfortunately, Brusina only illustrated a single specimen from the backside, never described it, and only cited the name once more in a species list (Brusina, 1907). Still, the elongate shape with nearly straight-sided whorls and the presence of weak spiral bulges clearly distinguish it from *M. geniculata* as well as other Dinaride melanopsids. We consider the differences sufficient to separate both taxa on species level.

Distribution: Drniš Basin (Miočić), Sinj Basin (Župića potok), Kupres Basin (Fatelj) (Brusina, 1874, 1897; Neubauer et al., 2013a).

Figure 3: Melanopsidae. (A–B) *Melanopsis acanthica* (Neumayr, 1869). Syntype (GBA 1869/01/4/1), Miočić. (C–D) *Melanopsis zitteli* (Neumayr, 1869). Syntype (GBA 1869/01/5/1), Miočić. (E–F) *Melanopsis zitteli* (Neumayr, 1869). Syntype (GBA 1869/01/5/2), Miočić. (G–H) *Melanopsis lyrata* (Neumayr, 1869). Syntype (GBA 1869/01/6), Miočić. (I–J) *Melanopsis inconstans* (Neumayr, 1869). Syntype (GBA 1869/01/3/10), Miočić. (K–L) *Melanopsis inconstans* (Neumayr, 1869). Syntype (GBA 1869/01/3/9), Miočić. (M) *Melanopsis inconstans* (Neumayr, 1869). Syntype (GBA 1869/01/3/8), Miočić. (N) *Melanopsis inconstans* (Neumayr, 1869). Syntype (GBA 1869/01/3/5), Miočić. (O) *Melanopsis inconstans* (Neumayr, 1869). Syntype (GBA 1869/01/3/2), Miočić. (P) *Melanopsis inconstans* (Neumayr, 1869). Syntype (GBA 1869/01/3/1), Miočić. (Q–R) *Melanopsis inconstans* (Neumayr, 1869), "*plicatula*"-morphotype. Parčić (NHMW 2014/0315/0003). (S–T) *Melanopsis visianiana* Brusina, 1874. Syntype (NHMZ 3205-851), Miočić. (U–V) *Melanopsis visianiana* Brusina, 1874. Syntype of *M. visianiana costulata* (NHMZ 2981-627/2), Miočić. (W) *Melanopsis visianiana* Brusina, 1874. Miočić (NHMZ 2981-627/2). (X) *Melanopsis visianiana* Brusina, 1874. Miočić (NHMZ 2981-627/2). Scale bars correspond to 5 mm.

***Melanopsis inconstans* Neumayr, 1869**

Figure 3I–R

* 1869 *Melanopsis inconstans* nov. sp. – Neumayr, p. 356, pl. 11, figs 9–18.
1874 *Melanopsis inconstans* Neumayr – Brusina, p. 39.
1874 [*Melanopsis inconstans*] var. *costulata* Brus. – Brusina, p. 39.
1874 [*Melanopsis inconstans*] var. *nodulosa* Brus. – Brusina, p. 39.
1874 [*Melanopsis inconstans*] var. *plicatula* Brus. – Brusina, p. 39.
1876 *Melanopsis nodulosa*, Brusina – Brusina, p. 115.
1876 *M.*[*elanopsis*] *plicatula*, Brusina – Brusina, p. 115.
1897 *Melanopsis plicatula* Brus. – Brusina, p. 11, pl. 4, figs 17–18.
1897 *Melanopsis inconstans nodulosa* Brus. – Brusina, p. 11, pl. 4, figs 19–20.
1902 *Melanopsis plicatula* Brus. – Brusina, pl. 6, figs 51–52.
1929 *Melanopsis inconstans* Neumayr – Wenz, p. 2756 [cum syn.].
1929 *Melanopsis plicatula* Brusina – Wenz, p. 2805 [cum syn.].
1974 *Melanopsis inconstans* Neumayr – Milan et al., p. 92.
1974 *Melanopsis plicatula* Brusina – Milan et al., p. 96.

non 1873 *Melanopsis inconstans*? Neum. – Capellini, p. 543.

Material: Several hundred specimens from Miočić (NHMW 1883C/0008/4963, NHMW 1884D/0009/1135, NHMW 1884D/0009/1136, NHMW 2014/0315/0054, NHMW 2014/0315/0055, NHMW 2014/0315/0056, NHMW 2014/0315/0057, NHMW 2014/0315/0076, NHMW 2014/0315/0078, NHMW 2014/0315/0088, NHMW 2014/0315/0090, NHMW 2014/0315/0104, NHMW 2014/0315/0191, NHMW 2014/0315/0197, NHMW 2014/0315/0198); ca. 100 from Biočić (NHMW 2014/0315/0143); more than thousand from Parčić (NHMW 2014/0315/0003, NHMW 2014/0315/0164, NHMW 2014/0315/0165, NHMW 2014/0315/0166); 9 specimens from Miočić 1 (NHMW 2014/0315/0001); several hundred from Miočić (GBA 2008/021/0247, GBA 2008/021/0249, GBA 2008/021/0251, GBA 2008/021/0255).

Type material: GBA 1869/01/3/1-10 (syntypes); Miočić, Drniš Basin.

Dimensions (H x W): 11.2 x 6.5 mm (syntype; Neumayr, 1869, pl. 11, fig. 9); 13.1 x 6.1 mm (syntype; Neumayr, 1869, pl. 11, fig. 10); 14.9 x 6.8 mm (syntype; Neumayr, 1869, pl. 11, fig. 11); 13.6 x 6.2 mm (syntype; Neumayr, 1869, pl. 11, fig. 12); 15.7 x 8.0 mm (syntype; Neumayr, 1869, pl. 11, fig. 13); 14.4 x 7.3 mm (syntype; Neumayr, 1869, pl. 11, fig. 14); 15.5 x 7.7 mm (syntype; Neumayr, 1869, pl. 11, fig. 15); 12.4 x 5.6 mm (syntype; Neumayr, 1869, pl. 11, fig. 16); 12.3 x 7.8 mm (syntype; Neumayr, 1869, pl. 11, fig. 17); 12.6 x 6.5 mm (syntype; Neumayr, 1869, pl. 11, fig. 18); 9.11 x 4.34 mm (syntype of *M. plicatula*; NHMZ 2976-622/1; Miočić, Drniš Basin; Brusina, 1897, pl. 4, fig. 17); 11.09 x 5.02 mm (syntype of *M. plicatula*; NHMZ 2976-622/2; Miočić, Drniš Basin; Brusina, 1897, pl. 4, fig. 18).

Remarks: This species is morphologically extremely variable. The common feature of all specimens is the conical shell with up to 8 whorls, comparable dimensions, and the relative size of the last whorl (55–65 %). The main difference between specimens attributed to this taxon is the mode and strength of sculpture. This might be expressed as numerous, densely-spaced, weak, equally convex ribs up to widely-spaced, prominent, highly convex, almost knob-like crests – and every possible combination of intermediate forms. Naturally, the various expressions produce different outlines, reaching from almost straight-sided to stepped, from slender to broad. Brusina (1874) tried to categorize this morphological variability and introduced the variety "*costulata*" for specimens with numerous, weak ribs (Neumayr, 1869, pl. 11, figs 16–18) and the variety "*nodulosa*" for the remaining ones characterized by fewer but more prominent and more convex ribs (Neumayr, 1869, pl. 11, figs 9–15). Additionally, he described the variety "*plicatula*" for morphologies with sharp ribs, which was neither illustrated by Neumayr nor by himself at that time. Later he elevated it to species level (Brusina, 1876, 1897). From a nomenclatural view, this is not tenable, since he did not refer at all to a nominal form (*M. inconstans inconstans*). Similar to Brusina (1874) but apparently unaware of this work, Neumayr in Neumayr and Paul (1875; footnote on p. 38) suggested that the taxon has to be split into several species. From his own observations at the type locality (Miočić) he concluded that the specimens described and illustrated by him in 1869 belong to a series of chronologically successive forms. In default of sufficient material and stratified collections, which are not available for Miočić at all, he did not elaborate on the issue.

The many hundred specimens available to us, including the type material, demonstrate an extreme variability that cannot be reliably separated into taxonomic clusters. Therefore, we synonymize *M. plicatula* and the two varieties "*nodulosa*" and "*costulata*" of Brusina (1874) with *M. inconstans*.

The record of the Messinian of Castellina Marittima (Pisa, Italy) is based on a misidentification by Capellini (1873; see also Pantanelli, 1886, p. 82).

Distribution: Drniš Basin (Biočić, Miočić, Parčić), Sinj Basin (Otok, Trnovača, Turjaci, Župića potok), and Lemeš (Neumayr, 1869; Brusina, 1874, 1884, 1897; Kerner, 1906). Moreover, it is mentioned from the late Burdigalian to early Langhian Obrovac Basin (Bilišane), the Pliocene of Nona (= Nin) in NW Dalmatien, and the Sarmatian Čremušnica in NW Croatia (Brusina, 1874; Schubert, 1907, 1909a; Wenz, 1929). At least the latter two need verification by new material.

***Melanopsis lyrata* Neumayr, 1869**

Figure 3G–H

* 1869 *Melanopsis* (*Canthidomus*) *lyrata* nov. sp. – Neumayr, p. 358, pl. 11, fig. 8.
1874 *Melanopsis Pančićiana* Brusina – Brusina, p. 44, pl. 1, figs 11–12.
1874 *Melanopsis lyrata* Neumayr – Brusina, p. 44.
1874 [*Melanopsis lyrata*] var. *cylindracea* Brus. – Brusina, p. 45.
1874 [*Melanopsis lyrata*] var. *misera* Brus. – Brusina, p. 45.
1896 *Melanopsis Kišpatići* Brus. – Brusina, p. 123 [nomen nudum].
1897 *Melanopsis Pančićiana* Brus. – Brusina, p. 10, pl. 4, figs 3–4.
1897 *Melanopsis Kišpatići* Brus. – Brusina, p. 10, pl. 4, fig. 5.
1897 *Melanopsis lyrata* Neum. – Brusina, p. 10, pl. 4, figs 6–7.
1897 *Melanopsis misera* Brus. – Brusina, p. 10, pl. 4, fig. 8.
1929 *Melanopsis cylindracea* Brusina – Wenz, p. 2698 [cum syn.].
1929 *Melanopsis kišpatići* Brusina – Wenz, p. 2761 [cum syn.].
1929 *Melanopsis misera* Brusina – Wenz, p. 2781 [cum syn.].
1929 *Melanopsis pančićiana* Brusina – Wenz, p. 2800 [cum syn.].
1974 *Melanopsis kispatici* Brusina – Milan et al., p. 93.
1974 *Melanopsis misera* Brusina – Milan et al., p. 94.
1974 *Melanopsis panciciana* Brusina – Milan et al., p. 95.
2011 *Melanopsis lyrata* Neumayr, 1869 – Neubauer et al., p. 207, pl. 1, figs 1–9, 22 [cum syn.].
2013a *Melanopsis lyrata* Neumayr, 1869 – Neubauer et al., p. 135, figs 5G–H.
2013b *Melanopsis lyrata* Neumayr, 1869 – Neubauer et al., figs 5A–G.

Material: 21 specimens from Miočić (NHMW 1884D/0009/1137, NHMW 2014/0315/0058, NHMW 2014/0315/0059); 4 from Biočić (NHMW 2014/0315/0133); 1 from Miočić (GBA 2008/021/0250).

Type material: GBA 1869/01/6 (syntype); Ribarić, Sinj Basin.

Dimensions (H x W): 22.4 x 8.2 mm (syntype; Neumayr, 1869, pl. 11, fig. 8); 27.09 x 10.69 mm (syntype of *M. kispatici*; NHMZ 2970-616; Miočić, Drniš Basin; Brusina, 1897, pl. 4, fig. 5); 10.55 x 4.38 mm (syntype of *M. misera*; NHMZ 2972-618; Lučane, Sinj Basin; Brusina, 1897, pl. 4, fig. 8); 30.54 x 11.52 mm (syntype of *M. panciciana*; NHMZ 3660-1300/1-2; Ribarić, Sinj Basin; Brusina, 1874, pl. 1, figs 11–12).

Description: Detailed descriptions are provided by Neubauer et al. (2011, 2013a, b).

Remarks: This species exhibits considerable morphological variability, which led to the splitting into numerous species and subspecies by later authors (Brusina, 1874, 1897; Olujić, 1999). Partly, this was a result of local morphological differences. The typical specimens found in Ribarić (N Sinj Basin) are relatively small and show delicate riblets und nodules. Additionally, larger specimens occur, which exhibit similarly small riblets und nodules. For these, Brusina (1874) invented the name *M. panciciana* (unfortunately the specimen was poorly drawn). Brusina (1874) also described *M. lyrata* var. *cylindracea* for smaller, cylindrical specimens from Ribarić and *M. lyrata* var. *misera* for smaller, ovoid specimens from Vrba (Drniš basin) and Stuparuša and Turjaci (Sinj Basin). Later, Brusina (1897) noticed that *M. lyrata* var. *cylindracea* fully corresponds to *M. lyrata* and considered it a junior synonym. In contrast, he treated *Melanopsis misera* as separate species. Finally, Brusina (1897) introduced *M. kispatici* for large specimens from Miočić, which have a slightly smaller last whorl, but otherwise correspond to *M. lyrata*.

All these taxa differ only in details, mainly in size. While *M. cy-*

lindracea and *M. misera* were already synonymized by Neubauer et al. (2011), we considered also *M. panciciana* and *M. kispatici* junior synonyms of *M. lyrata*. For discussion about the morphotypes introduced by Olujić (1999) see Neubauer et al. (2011).

Wenz (1929) erroneously considered the name "*Melanopsis lyrata*" a primary homonym and, as not to introduce a replacement name, synonymized this species with *M. cylindracea* Brusina, 1874. However, the species Wenz referred to as senior homonym was clearly introduced as "*Melanopsis lirata*" by Gassies (1869). Wenz was correct about the priority issue, though: Gassies (1869) was published on January 1st, while Neumayr (1869) was published on June 30th.

Distribution: Drniš Basin (Biočić, Miočić, Vrba), Sinj Basin (Bunarska Glavica, Čugurina Glavica, Lučane, Ribarić, Stuparuša, Turjaci), Gacko Basin (Gračanica, Vrbica), Kupres Basin (Fatelj), Mostar Basin (Mostar) (Neumayr, 1869; Brusina, 1874, 1897, 1907; Kerner, 1906; Neubauer et al., 2011, 2013a, b).

***Melanopsis visianiana* Brusina, 1874**

Figure 3S–X

* 1874 *Melanopsis Visianiana* Brusina – Brusina, p. 37, pl. 1, figs 7–8.
1897 *Melanopsis Visianiana* Brus. – Brusina, p. 11, pl. 5, fig. 5.
1897 *Melanopsis Visianiana costulata* Brus. n. for. – Brusina, p. 12, pl. 5, fig. 6.
1929 *Melanopsis visiniana visiniana* [sic] Brusina – Wenz, p. 2851.
1929 *Melanopsis visiniana* [sic] *costulata* Brusina – Wenz, p. 2852.

non 2003 *Melanopsis visianiana costulata* Brusina – Papaianopol et al., p. 156.
non 2006 *Melanopsis visianiana* Brusina, 1874 – Kókay, p. 46, pl. 15, figs 5–7.

Material: Several hundred specimens from Miočić, inclusively "*costulata*"-phenotype (NHMW 2014/0315/0060, NHMW 2014/0315/0061, NHMW 2014/0315/0077, NHMW 2014/0315/0084, NHMW 2014/0315/0091, NHMW 2014/0315/0190, NHMW 2014/0315/0199); 11 from Biočić (NHMW 2014/0315/0138); 3 from Parčić (NHMW 2014/0315/0153); ca. 40 from Miočić 1 (NHMW 2014/0315/0001).

Type material: NHMZ 3205-851 (syntype); Miočić, Drniš Basin.

Dimensions (H x W): 13.84 x 5.96 mm (syntype; Brusina, 1874, pl. 1, figs 7–8); 11.61 x 5.20 mm (Brusina, 1897, pl. 5, fig. 5); 12.85 x 5.93 mm (syntype of *M. visianiana costulata*; NHMZ 2981-627/2; Miočić, Drniš Basin; Brusina, 1897, pl. 5, fig. 6).

Description: Slender, elongate shell with up to 10 whorls. Whorls weakly convex to almost straight in profile, creating near perfectly conical outline. Last whorl attaining 60–65 % of total shell height. Base slightly concave. Weak fasciole present on neck. Aperture broadly ovoid; callus moderately thickened. Coloring occasionally present as yellow zigzag lines (Fig. 3X). In some specimens, weak, widely-spaced ribs occur on last three whorls. These ribs form low, broad, convex crests; maximum convexity in whorl center, decreasing towards sutures.

Remarks: Direct comparison of the type material of each *M. visianiana visianiana* and *M. visianiana costulata* showed that both taxa are near identically shaped. They perfectly match concerning general dimensions, whorl outline, number of whorls, size of last whorl, and shape of aperture. The only difference is the presence of weak, widely spaced ribs in *M. visianiana costulata* (Figs 3U–V), which we consider to range within intraspecific variability. Moreover, the name "*costulata*" is pre-occupied by another variety described by Brusina (1874), *Melanopsis inconstans costulata* (see discussion of *M. inconstans*). Since we synonymize both varieties anyway, the introduction of a replacement name for this primary homonym would be pointless. The specimens from the late Early Miocene of Nagygörbő, Hungary, misidentified as *M. visianiana* by Kókay (2006), differ in their convex whorls and slightly ovoid shape. Likewise, the alleged record of *M. visianiana costulata* from the Pelendavian (Middle Romanian, Late Pliocene) of the Dacian Basin by Papaianopol et al. (2003) certainly represents a misidentification.

Distribution: Drniš Basin (Biočić, Miočić), Sinj Basin (Trnovača) (Brusina, 1874, 1897).

***Melanopsis zitteli* Neumayr, 1869**

Figure 3C–F

* 1869 *Melanopsis* (*Canthidomus*) *Zitteli* nov. sp. – Neumayr, p. 357, pl. 11, figs 4–5.
1874 *Melanopsis Zitteli* Neumayr – Brusina, p. 43.
1929 *Melanopsis Zitteli* Neumayr – Wenz, p. 2853.

Material: More than 100 specimens from Miočić (NHMW 2014/0315/0053, NHMW 2014/0315/0080, NHMW 2014/0315/0081, NHMW 2014/0315/0082, NHMW 2014/0315/0192, NHMW 2014/0315/0200); 1 from Biočić (NHMW 2014/0315/0141); 32 from Miočić (GBA 2008/021/0248, GBA 2008/021/0254).

Type material: GBA 1869/01/5/1-2 (syntypes); Miočić, Drniš Basin.

Dimensions (H x W): 30.9 x 13.5 mm (syntype; Neumayr, 1869, pl. 11, fig. 4); 25.2 x 11.6 mm (syntype; Neumayr, 1869, pl. 11, fig. 5).

Description: Shell conical, with up to 10 whorls. Sculpture already starts on early teleoconch with numerous thin but distinct ribs, which slightly increase in strength during ontogeny. From 3rd whorl onwards, small, blunt nodules are present on each rib near upper suture; these produces weakly stepped outline in later ontogeny. From 4th whorl onwards, ribs become distinctly inclined. On last whorl, two additional, weak rows of nodules are visible: one right in lateral extension of upper suture of previous whorl; second, even weaker row slightly below. On last whorl, ribs become weakly sigmoidal. Sutures not incised. Last whorl attains ca. 50–60 % of shell height. Weak fasciole present on neck. Aperture broadly lenticular; callus glossy, moderately thick.

Remarks: The species is similar to the co-occurring *M. acan-*

thica Neumayr, 1869 (for discussion see above). The specimen from Župića potok (Sinj Basin) illustrated as *M. dalmatina* Brusina, 1884 by Brusina (1897, pl. 5, fig. 11) resembles the present species regarding its size and the stepped, slender habitus and might be conspecific. More material of this locality is necessary to fully understand the morphological plasticity of *M. dalmatina* and help to clarify this issue.
Distribution: Endemic to the Drniš Basin (Biočić, Miočić).

Order Littorinimorpha Golikov and Starobogatov, 1975
Superfamily Truncatelloidea Gray, 1840
Family Bithyniidae Gray, 1857
Genus *Bithynia* Leach in Abel, 1818

Type species: *Helix tentaculata* Linnaeus, 1758. Recent; Europe. Type by subsequent designation by Herrmannsen (1846).

***Bithynia jurinaci* Brusina, 1884**
Figure 4A–B, P

1869 *Bythinia* [sic] *tentaculata* L. sp. – Neumayr, p. 363, pl. 12, fig. 8 [non *Helix tentaculata* Linnaeus, 1758].
1874 *Bythinia* [sic] *tentaculata* Linné – Brusina, p. 69 [non Linnaeus, 1758] [partim; only regarding DLS records].
* 1884 *Bythinia* [sic] *Jurinaci* Brusina – Brusina, p. 53.
1928 *Bulimus jurinaci* (Brusina) – Wenz, p. 2244 [partim; only regarding DLS records].
1974 *Bulimus* (*Bulimus*) *jurinaci* (Brusina) – Milan et al., p. 64, pl. 1, figs 6–7.
? 1988 *Bulimus jurinaci* (Brusina) – Jurišić-Polšak and Slišković, p. 170.
2013b *Bithynia jurinaci* Brusina, 1884 – Neubauer et al., figs 6G–H.

non 1925 *Bithynia jurinaci* Brusina – Fischer and Wenz, p. 229, pl. 7, figs 16–19.
non 2004 *Bithynia jurinaci* (Brusina, 1884) – Harzhauser and Binder, p. 7, pl. 2, figs 8–11.

Material: Many hundred specimens from Miočić (NHMW 2014/0315/0009, NHMW 2014/0315/0089, NHMW 2014/0315/0094, NHMW 2014/0315/0107, NHMW 2014/0315/0118, NHMW 2014/0315/0121, NHMW 2014/0315/0203, NHMW 2014/0315/0206); ca. 100 from Biočić (NHMW 2014/0315/0193); 3 from Parčić (NHMW 2014/0315/0147); 58 from Miočić 1 (NHMW 2014/0315/0001); 2 from Miočić (GBA 2008/008/0093, GBA 1869/01/14; the latter was illustrated in Neumayr, 1869).
Type material: The type material is lost; Milan et al. (1974) invalidly designated a neotype from material from the type locality Miočić (NHMZ 3853-1493), since he failed to fulfill the requirements of Art. 75.3 of the Code.
Dimensions (H x W): 7.14 x 4.84 mm; 6.34 x 4.10 mm. The largest specimen found attains 9.6 x 5.6 mm.
Description: For detailed description see Neubauer et al. (2013b: suppl. online material).
Remarks: This species is the only documented *Bithynia* from the Dinaride Lake System. Harzhauser and Binder (2004), following previous determinations by Lörenthey (1902), Halaváts (1903) and Troll (1907) for material from Lake Pannon, identified specimens from the Late Miocene of the Vienna Basin as *B. jurinaci*. Despite the similar morphology, the large stratigraphic gap of more than 5 Ma raises doubts about these identifications (Neubauer et al., 2013b). The same might be true for the Pliocene records from Slavonia by Neumayr (1869, p. 378), Brusina (1874), Herbich and Neumayr (1875), and Neumayr and Paul (1875). Likewise, the mention from Frankfurt-Praunheim (Praunheim Formation, middle-late Burdigalian) by Fischer and Wenz (1925) is very doubtful.
Distribution: Sinj Basin (Ruduša, Trnovača, Turjaci, Župića potok), Drniš Basin (Biočić, Miočić, Parčić), Gacko Basin (Gračanica, Vrbica) (Brusina, 1884; Neubauer et al., 2013b). Records from the Early/Middle Miocene of the Knin Basin (Golubić) and the Pliocene of Nona (= Nin) listed by Wenz (1928) together with the one from the Late Miocene of Livno Basin (Čelebić-Jaruga, Šaćirovina) by Jurišić-Polšak and Slišković (1988) need verification.

Family Emmericiidae Brusina, 1870
Genus *Emmericia* Brusina, 1870

Type species: *Paludina patula* Brumati, 1838. Recent; Croatia, France, Germany, Italy. Type by subsequent designation by Clessin (1880).

***Emmericia canaliculata* Brusina, 1870**
Figure 4C–E, Q

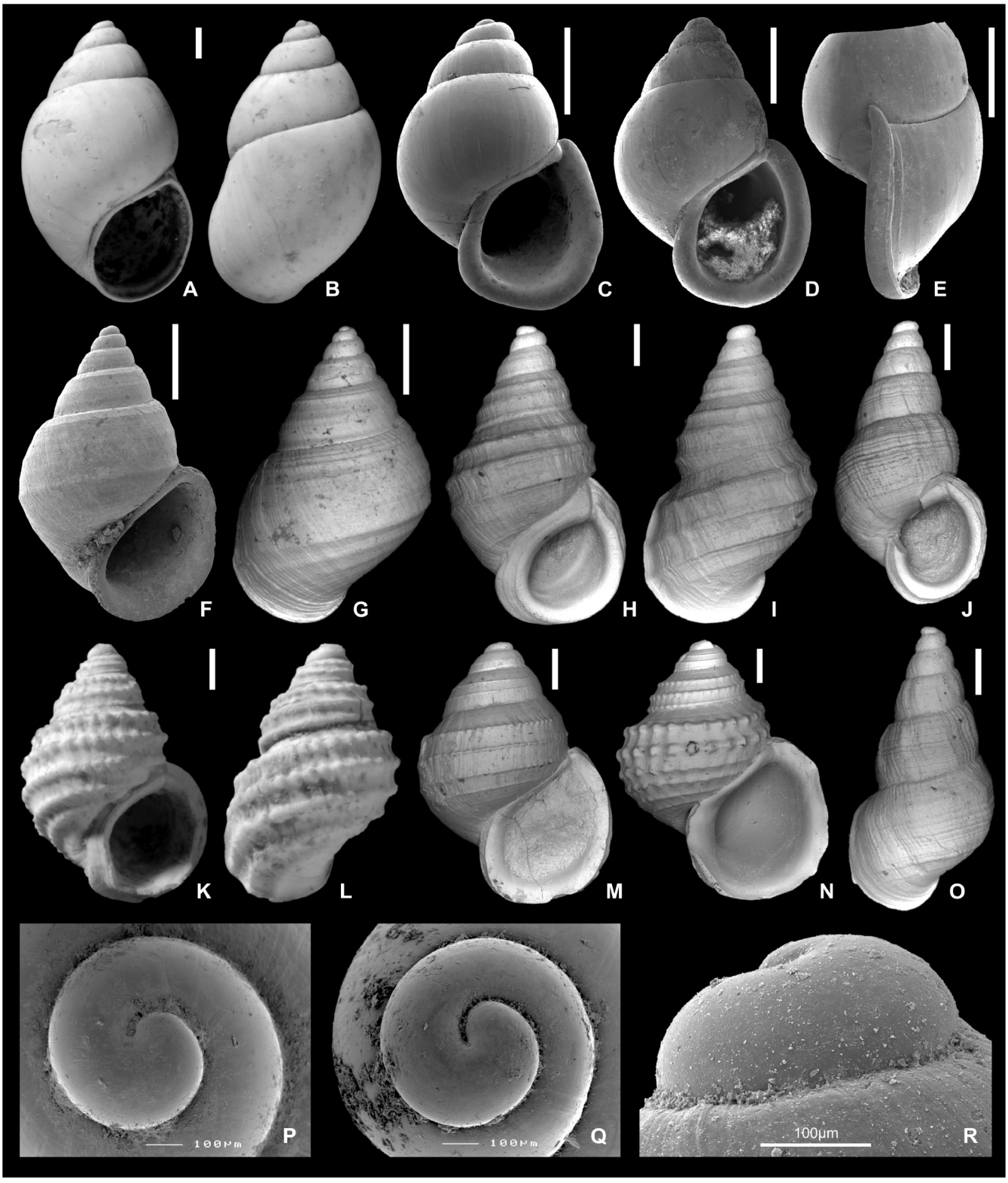
* 1870 *Emmericia canaliculata* Brus. – Brusina, p. 933.
1874 *Emmericia canaliculata* Brusina – Brusina, p. 58, pl. 4, figs 5–6.
1897 *Emmericia canaliculata* Brus. – Brusina, p. 21, pl. 7, figs 22–24.
1926 *Emmericia canaliculata* Brusina – Wenz, p. 2194 [partim; only regarding DLS records].

Figure 4: Bithyniidae and Emmericiidae. (A–B) *Bithynia jurinaci* Brusina, 1884. Specimen illustrated by Neumayr (1869) as "*Bithynia tentaculata*" (GBA 1869/01/14), Miočić. (C) *Emmericia canaliculata* Brusina, 1870. Miočić (NHMW 2014/0315/0004). (D) *Emmericia canaliculata* Brusina, 1870. Miočić (NHMW 2014/0315/0005). (E) *Emmericia canaliculata* Brusina, 1870. Miočić (NHMW 2014/0315/0006). (F, R) *Fossarulus crossei* Brusina, 1878. Miočić (NHMW 2014/0315/0008). (G) *Fossarulus crossei* Brusina, 1878. Specimen illustrated by Brusina (1897) (NHMZ 3033-679), Miočić. (H–I) *Fossarulus tricarinatus* Brusina, 1870. Syntype of *F. eginae* (NHMZ 3026-672), Vrba. (J, O) *Fossarulus moniliferus* Brusina, 1876. Syntype of *F. eginae ecarinata* (NHMZ 3027-673), Vrba. (K–L) *Fossarulus stachei* Neumayr, 1869. Syntype (GBA 1869/01/10), Miočić. (M) *Fossarulus stachei* Neumayr, 1869. Lectotype of *F. auritus* (NHMZ 3021-667), Miočić. (N) *Fossarulus stachei* Neumayr, 1869. Syntype (?) of *F. armillatus* (NHMZ 3023-669), Miočić. (P) *Bithynia jurinaci* Brusina, 1884. Miočić (NHMW 2014/0315/0009). (Q) *Emmericia canaliculata* Brusina, 1870. Miočić (NHMW 2014/0315/0007). Scale bars correspond to 1 mm if not stated otherwise.

1974 *Emmericia canaliculata* Brusina – Milan et al., p. 68.

non 1902 *Emmericia canaliculata* Brusina – Boistel, p. 665, 669, 670, textfig. 6.
non 1903 *Hydrobia* (*Emmericia*) *canaliculata* Brusina – Halaváts, p. 42, pl. 1, fig. 13.
non 1990 *Emmericia canaliculata* Brusina, 1870 – Stojaspal, p. 657, pl. 1, fig. 5.
non 2004 *Emmericia canaliculata* Brusina, 1870 – Harzhauser and Binder, p. 9, pl. 2, figs 18–20.

Material: ca. 40 specimens and fragments from Miočić (NHMW 1883C/0008/4969, NHMW 2014/0315/0004, NHMW 2014/0315/0005, NHMW 2014/0315/0006, NHMW 2014/0315/0007, NHMW



2014/0315/0049, NHMW 2014/0315/0106, NHMW 2014/0315/0205); 2 from Miočić (GBA 2008/010/0021).

Type material: Milan et al. (1974) stated that the type material of Brusina (1870, 1874) from Goručica (= Ruduša, Sinj Basin) is lost, so they designated a neotype from the material studied by Brusina (1897) from the locality Miočić (NHMZ 3016-662). This designation is invalid as it does not fulfill Art. 75.3 of the Code. Moreover, the specimen chosen by Milan et al. (1974) is quite untypical for *E. canaliculata*. It corresponds regarding overall morphology, so it is certainly conspecific with the syntype, but it lacks the characteristically reflected peristome. We illustrate an additional specimen from the NHMW collection from Miočić that shows this feature and better corresponds to the syntype from Ruduša.

Dimensions (H x W): 6.30 x 3.28 mm (NHMZ 3016-662).

Description: Sturdy, broadly conical, glossy, fragile shell, consisting of 4 convex whorls. Protoconch slightly depressed, with 1.1 smooth whorls passing over indistinct growth rim into teleoconch. Sutures weakly incised. Last whorl attains about three fourths of total height (including expanded peristome). Base straight to slightly convex. Aperture widely ovoid with typical but weakly concave notch at posterior part of inner lip. Posterior tip of aperture may be demarcated from preceding whorl, leaving slit-like incision. Inner lip thin, sheet-like. Outer lip strongly reflected, collar-like, so that final shell lamella grows into abapertural direction. In lateral view, course of outer lip is sigmoidal, showing two strong emarginations: below posterior tip and at anterior portion. About 1–3 mm (measured at outer lip) before peristome regularly elliptical constriction occurs inside shell, most distinct anteriorly (transition between outer lip and columellar region) and posteriorly (transition between outer and inner lip); constriction indistinct in between; not visible on outer surface. Umbilicus fully covered. Shell entirely smooth aside from weakly prosocline growth lines. In all examined specimens, both protoconch and reflected peristome are conspicuously lighter colored than spire.

Remarks: This species is the only recorded *Emmericia* from the DLS and can be easily distinguished from other members of the genus due to its eye-catching aperture. The roughly coeval *E. roetzeli* Harzhauser and Neubauer in Harzhauser et al., 2012 from the Aflenz Basin (Austria) exposes a straighter whorl outline and is distinctly larger. However, the high similarity of both forms might indicate a close relationship. The specimens from the Late Miocene of Austria and Hungary, erroneously identified as *E. canaliculata* by Halaváts (1903), Stojaspal (1990), and Harzhauser and Binder (2004), differ in the presence of the umbilicus and the thickened but poorly reflected aperture. The specimen illustrated as *E. canaliculata* by Boistel (1902) from the Late Miocene locality Confranchette in the Bresse graben, France, differs in its stepped spire. The Pliocene species *E. botici* Brusina, 1902, *E. damini* Brusina, 1896, and *E. schulzeriana* Brusina, 1882 from Slavonia and Serbia are all more slender; *E. krizanici* Brusina, 1902 and *E. zivkovici* Brusina, 1902 both form a distinct angle between upper part and base of the last whorl.

Distribution: Sinj Basin (Ruduša), Drniš Basin (Miočić) (Brusina, 1874, 1897).

Genus *Fossarulus* Neumayr, 1869

Type species: *Fossarulus Stachei* Neumayr, 1869. Miocene; Dalmatia. Type by monotypy.

Remarks: After the first description of the then monotypic genus *Fossarulus* by Neumayr (1869), Brusina (1870, 1874, 1876, 1878, 1897, 1907) introduced 11 further species and 3 subspecies within this genus from the DLS. All of these show small differences in shape and in the strength of the spiral sculpture. This, however, can be highly variable within a single species, especially for DLS taxa in general (e.g., Neumayr, 1869; Olujić, 1999; Neubauer et al., 2011, 2013a, b). Apparently this seems to be particularly true for *Fossarulus* species. Neubauer et al. (2013b) already synonymized the three taxa endemic for the Gacko Basin with *F. moniliferus* Brusina, 1876 from Ribarić (Sinj Basin), showing that the single taxa actually represent ecophenotypes (see also Mandic et al., 2011). There, sculpture ranged from weak traces of keels to prominent ridges with nodules. Similar tendencies are shown by the morphologies recorded for the Drniš and Sinj basins as well. Jurišić-Polšak (1984) demonstrated that in the Sinj Basin *F. tricarinatus* experiences morphological change over time. Even in the very same sample, morphologies vary considerably concerning general shape and strength of keels (own observations on material collected from Stuparuša, Sinj Basin). Also for a representative from outside the DLS, *F. srbici* of the Metohia Basin in the Kosovo, variability in the strength of the keels was documented (Milošević, 1972).

Given the extreme morphological plasticity of this genus, partly reflected in minor stratigraphical and local differences, it is exceedingly difficult to draw a line between taxonomic units in the DLS group. Currently, we consider only 5 species as accepted, i.e., *Fossarulus crossei* Brusina, 1878, *F. moniliferus* Brusina, 1876, *F. stachei* Neumayr, 1869, *F. tricarinatus* Brusina, 1870, and *F. pullus* Brusina, 1874.

The first four species were first described or mentioned from the Drniš Basin; for these see discussions below. In contrast, *Fossarulus pullus* Brusina, 1874 is recorded from Goručica (= Ruduša, Sinj Basin) and several Bosnian localities (cf. Neumayr, 1880). The status of this taxon has been very doubtful. Milan et al. (1974, p. 72) indicated that the holotype, "being the only specimen of that species", is lost. Brusina (1974), however, referred to 138 (incomplete) specimens when describing the species, but clearly mentioned that the figure is based on several fragments (Brusina, 1874, p. 56). Probably Milan et al. (1974) overlooked that and searched for a complete specimen, which was never found by Brusina. Consequently, the status of this species is entirely unresolved and the details of the type material are unknown, wich is why we refrain from a final judgment. From the description and the illustration it looks

similar to the "*moniliferus-group*". In case both are considered synonymous, *F. pullus* would gain priority.
The only other *Fossarulus* species documented from outside the DLS are *F. mariae* Pavlović, 1935, *F. praeponticus* Milošević, 1972, and *F. srbici* Milošević, 1972 from the Middle Miocene of the Metohia Basin, *F. tetracarinatus* Pavlović, 1903 from the Late Miocene to Early Pliocene of the Kosovo and Metohia basins (Pavlović, 1903, 1932; Atanacković, 1959), and *F. milessii* Papp, 1979 from the Late Miocene of Greece.

Fossarulus crossei Brusina, 1878

Figure 4F–G, R

* 1878 *Fossarulus Crossei*, Brusina – Brusina, p. 351.
1897 *Fossarulus Crossei* Brus. – Brusina, p. 22, pl. 8, figs 21–22.
1926 *Fossarulus crossei* Brusina – Wenz, p. 2202 [cum syn.].
1974 *Fossarulus crossei* Brusina – Milan et al., p. 70.
? 1988 *Fossarulus crossei* Brusina – Jurišić-Polšak and Slišković, p. 170.

Material: Specimen illustrated by Brusina (1897); 3 specimens from Miočić (NHMW 2014/0315/0008, NHMW 2014/0315/0178).
Type material: Details of type material unknown (type locality: Miočić, Drniš Basin). It is uncertain whether the specimen illustrated by Brusina (1897) and indicated as holotype by Milan et al. (1974) (NHMZ 3033-679) is part of the original material of Brusina (1878) or derives from newly collected material. No remarks are given as to that by Brusina (1878, 1897).
Dimensions (H x W): 4.29 x 2.81 mm (Brusina, 1897, pl. 8, figs 21–22).
Description: Shell broadly conical, deltoid, with ca. 5 straight-sided whorls. Sutures weakly incised. Protoconch unknown. On about antepenultimate whorl, 2 faint keels appear, one close to upper suture, one near lower suture. Keels initially obtuse, become stronger during ontogeny; they never bear nodes. Keels might be accompanied by numerous thin, fragile spiral lines that continue one base. Latter is straight to weakly convex. Aperture ovoid with posterior notch. Outer lip expanded, slightly reflected, almost covers umbilicus.
Remarks: *Fossarulus crossei* can be easily separated due to its distinctly deltoid shape with poorly convex whorls; this is never found in any other *Fossarulus* species.
Distribution: Drniš Basin (Miočić) (Brusina, 1878, 1897). Its presence in the Late Miocene white marl of Livno Basin (Čelebić-Jaruga, Šaćirovina) indicated by Jurišić-Polšak and Slišković (1988) needs verification.

Fossarulus moniliferus Brusina, 1876

Figure 4J, O

* 1876 *Fossarulus moniliferus*, Brusina – Brusina, p. 111.
1897 *Fossarulus moniliferus* Brus. – Brusina, p. 21, pl. 8, figs 3–6.
1897 *Fossarulus Eginae ecarinata* Brus n. for. – Brusina, p. 22, pl. 8, figs 9–10.
1897 *Fossarulus Buzolići* Brus. n. sp. – Brusina, p. 22, pl. 8, figs 14, 17–18.
1897 *Fossarulus Buzolići complanatus* Brus. n. for. – Brusina, p. 22, pl. 8, figs 15–16.
1897 *Fossarulus Bulići* Brus. n. sp. – Brusina, p. 22, pl. 8, figs 19–20.
1902 *Fossarulus Bulići* Brus. – Brusina, pl. 11, figs 40–43.
1926 *Fossarulus bulići* Brusina – Wenz, p. 2202.
1926 *Fossarulus buzolići buzolići* Brusina – Wenz, p. 2202.
1926 *Fossarulus buzolići complanatus* Brusina – Wenz, p. 2202.
1926 *Fossarulus eginae ecarinatus* Brusina – Wenz, p. 2203 [cum syn.].
1926 *Fossarulus moniliferus* Brusina – Wenz, p. 2204 [cum syn.].
1974 *Fossarulus bulici* Brusina – Milan et al., p. 70.
1974 *Fossarulus buzolici buzolici* Brusina – Milan et al., p. 70.
1974 *Fossarulus buzolici complanatus* Brusina – Milan et al., p. 70.
1974 *Fossarulus eginae ecarinata* Brusina – Milan et al., p. 71.
1974 *Fossarulus moniliferus* Brusina – Milan et al., p. 71.
2009 *Fossarulus tricarinatus* Brusina, 1870 – Krstić et al., p. 42, pl. 1, figs 1–2 [non *Fossarulus tricarinatus* Brusina, 1870].
2011 *Fossarulus bulici* Brusina – Mandic et al., fig. 5.6.
2011 *Fossarulus buzolici* Brusina – Mandic et al., fig. 5.7.
2011 *Fossarulus fuchsi* Brusina – Mandic et al., fig. 5.8 [non *Fossarulus fuchsi* Brusina, 1897].
2013b *Fossarulus moniliferus* Brusina, 1876 – Neubauer et al., figs 6A–F, I.

non? 1953 *Fossarulus bulici* Brusina – Papp, p. 124, pl. 3, fig. 23.

Material: Type material of Neumayr and Brusina only.
Type material: Details of type material unknown (type locality: Ribarić, Sinj Basin). It is uncertain whether the specimen illustrated by Brusina (1897) and indicated as holotype by Milan et al. (1974) (NHMZ 3024-670) is part of the original material of Brusina (1876) or derives from newly collected material. No remarks are given as to that by Brusina (1876, 1897).
Dimensions (H x W): 5.43 x 3.19 mm (Brusina, 1897, pl. 8, figs 3–4); 7.30 x 3.89 mm (syntype of *F. bulici*; Avtovac-Gacko, Gacko Basin; Brusina, 1897, pl. 8, figs 19–20; NHMZ 3032-678); 3.24 x 3.68 mm (broken; syntype of *F. buzolici*; Avtovac-Gacko, Gacko Basin; Brusina, 1897, pl. 8, fig. 14; NHMZ 3029-675); 6.29 x 3.79 mm (syntype of *F. buzolici*; Avtovac-Gacko, Gacko Basin; Brusina, 1897, pl. 8, figs 17–18; NHMZ 3029-677); 8.35 x 4.24 mm (syntype of *F. buzolici complanatus*; Avtovac-Gacko, Gacko Basin; Brusina, 1897, pl. 8, figs 15–16; NHMZ 3030-676); 6.28 x 3.33 mm (syntype of *F. eginae ecarinata*; Vrba, Drniš Basin; Brusina, 1897, pl. 8, figs 9–10; NHMZ 3027-673).
Description: Shell slender conical, consisting of 4–5 whorls. Protoconch entirely smooth, depressed, consisting of ca. 1 highly convex whorl that passes without growth rim into teleoconch. Early teleoconch covered with faint growth lines and numerous, thin, irregular, indistinct spiral lines. Whorl profile low to moderately convex; when sculpture is present convexity occasionally appears stronger. Spiral sculpture usually present from first to second teleoconch whorl onwards. Expression varies between almost fully reduced and promi-

nent with all kinds of intermediates: numerous weak spiral grooves, traces of 3 spiral keels, 3 sharp keels, 3 keels with numerous distinct nodules. On last whorl, additional, weaker keels are visible on base. With emergence of sculpture growth lines become stronger. In case of prominent keels, straight subsutural ramp is formed above uppermost keel. Last whorl attaining 65–70 % of total height; base straight. Aperture broadly drop-shaped, with posterior concave notch on inner lip; peristome always expanded (ranging from weakly to strongly), mostly reflected and often thickened; peristome uninterrupted apart from thin posterior canal.

Remarks: This taxon consists of very slender morphologies, usually with highly convex whorls and often with weak sculpture. It differs from both *F. stachei* and *F. tricarinatus*, which comprise stouter and thicker shells with less-convex whorls. The specimens identified as *F. fuchsi* and *F. tricarinatus* by Mandic et al. (2011) and Krstić et al. (2013) fully correspond to the present species. The same is true for *F. eginae ecarinatus* from Vrba. The subspecies *F. bulici turritus* introduced by Protzen (1932) for specimens from Pliocene Gottschee (= Kočevje, S Slovenia) matches with *F. moniliferus* as well but is stratigraphically distinctly younger. The record of *F. bulici* from the Late Miocene Pannonian Basin by Papp (1953) is doubtful and needs a more detailed re-evaluation.

Distribution: Drniš Basin (Vrba), Sinj Basin (Ribarić), Gacko Basin (Gacko, Gračanica, Vrbica), Kupres Basin (Kupres) (Brusina, 1876, 1884, 1897; Krstić et al., 2013; Neubauer et al., 2013b); its occurrence in the Pliocene of Kočevje (Protzen, 1932) needs verification.

***Fossarulus stachei* Neumayr, 1869**

Figure 4K–N

* 1869 *Fossarulus Stachei* nov. sp. – Neumayr, p. 361, pl. 12, fig. 7.
1874 *Fossarulus Stachei* Neumayr – Brusina, p. 53.
1876 *Fossarulus armillatus*, Brusina – Brusina, p. 112.
1882 [*Fossarulus*] *auritus* nov. spec. – Brusina, p. 38 [nomen nudum].
1882 [*Fossarulus*] *Fuchsi* nov. spec. – Brusina, p. 38 [nomen nudum].
1882 [*Fossarulus*] *Hoernesi* nov. spec. – Brusina, p. 38 [nomen nudum].
1897 *Fossarulus Fuchsi* Brus. – Brusina, p. 21, pl. 7, figs 27–28.
1897 *Fossarulus Hoernesi* Brus. – Brusina, p. 21, pl. 7, figs 29–30.
1897 *Fossarulus Stachei* Neum. – Brusina, p. 21, pl. 7, figs 25–26.
1897 *Fossarulus auritus* Brus. – Brusina, p. 21, pl. 7, figs 31–34.
1897 *Fossarulus armillatus* Brus. – Brusina, p. 21, pl. 8, figs 1–2.
1926 *Fossarulus armillatus* Brusina – Wenz, p. 2201 [cum syn.].
1926 *Fossarulus auritus* Brusina – Wenz, p. 2202 [cum syn.].
1926 *Fossarulus fuchsi* Brusina – Wenz, p. 2203 [cum syn.].
1926 *Fossarulus hoernesi* Brusina – Wenz, p. 2204 [cum syn.].
1926 *Fossarulus stachei* Neumayr– Wenz, p. 2205 [cum syn.].
1974 *Fossarulus armillatus* Brusina – Milan et al., p. 69.
1974 *Fossarulus auritus* Brusina – Milan et al., p. 70.
1974 *Fossarulus fuchsi* Brusina – Milan et al., p. 71.
1974 *Fossarulus hoernesi* Brusina – Milan et al., p. 71.
1984 *Fossarulus tricarinatus susnjarai* n. subsp. – Jurišić-Polšak, p. 200, 206, pl. 2, figs 1–2, pl. 3, fig. 2.
1984 *Fossarulus tricarinatus susnjarai* var. *nodosoaltus* n. var. – Jurišić-Polšak, p. 201, 207, pl. 2, figs 3–4.
2011 *Fossarulus fuchsi* Brusina, 1897 – Neubauer et al., p. 212, pl. 5, figs 3–4, 9, 13.
? 2013 *Fossarulus fuchsi* Brusina, 1897 – Krstić et al., p. 13, pl. 3, figs 3a–b.

Material: 1 specimen from Miočić (NHMW 2014/0315/0186); 1 from Biočić (NHMW 2014/0315/0183); 2 from Parčić (NHMW 2014/0315/0146); 1 fragment from Miočić 1 (NHMW 2014/0315/0001); 2 from Miočić (GBA 2008/010/0020).

Type material: GBA 1869/01/10 (syntype); Miočić, Drniš Basin.

Dimensions (H x W): 6.60 x 4.80 mm (syntype; Neumayr, 1869, pl. 12, fig. 7); 6.59 x 4.82 mm (syntype (?) of *F. armillatus*; NHMZ 3023-669; Miočić, Drniš Basin; Brusina, 1897, pl. 8, figs 1–2); 7.65 x 6.29 mm (lectotype of *F. auritus*, designated by Milan et al., 1974; NHMZ 3021-667; Miočić, Drniš Basin; Brusina, 1897, pl. 7, figs 31–32); 5.76 x 3.78 mm (syntype of *F. fuchsi*; NHMZ 3018-664; Potravlje, Sinj Basin; Brusina, 1897, pl. 7, figs 27–28); 9.41 x 6.29 mm (syntype of *F. hoernesi*; NHMZ 3019-665; Župića potok, Sinj Basin; Brusina, 1897, pl. 7, figs 29–30).

Description: Bulky, conical shell, consisting of up to 4.5 moderately convex whorls. Protoconch entirely smooth, depressed, consisting of ca. 1 highly convex whorl that passes without growth rim into teleoconch. Early teleoconch covered with faint growth lines and numerous, thin, irregular, indistinct spiral lines. Soon distinct keels appear with traces of small nodules. Expression of nodules in later ontogeny varies between weak and prominent. On penultimate whorl, 3 rows of nodules present; on last whorl, additional, weaker rows are visible on base. Last whorl attaining ca. 70–75 % of shell height. Aperture broadly drop-shaped, with posterior concave notch on inner lip; slightly to distinctly expanded, weakly reflected, weakly thickened.

Remarks: This taxon is characterized by rather bulky morphologies and remains so well-separated from the slenderer *F. tricarinatus* and the frail *F. moniliferus*. The types of *F. armillatus*, *F. auritus*, *F. fuchsi*, and *F. hoernesi* match with the syntype of *F. stachei*. The minor differences in apertural expansion and strength of nodules are considered to range within the common variability. *F. tricarinatus susnjarai* Jurišić-Polšak, 1984 closely resembles the syntype of *F. fuchsi* and thus ranges within the present species.

Distribution: Drniš Basin (Biočić, Miočić, Parčić), Sinj Basin (Otok, Ribarić, Potravlje, Strmendolac-Crveni klanac, Tabak, Trnovača, Turjaci, Župića potok) (Neumayr, 1869; Brusina, 1874, 1897; Kerner, 1906; Jurišić-Polšak, 1984; Jurišić-Polšak et al., 2000). The record from Kamengrad by Wenz (1926) needs verification. The fragment illustrated as *F. fuchsi* by Krstić et al. (2013) from the Kupres Basin does not allow a proper identification. More material is needed to verify this record.

***Fossarulus tricarinatus* Brusina, 1870**
Figure 4H–I

* 1870 *Fossarulus tricarinatus* Brus. – Brusina, p. 935.
1874 *Fossarulus tricarinatus* Brusina – Brusina, p. 54, pl. 3, figs 11–12.
1882 [*Fossarulus*] *Eginae* nov. spec. – Brusina, p. 38 [nomen nudum].
1897 *Fossarulus Eginae* Brus. – Brusina, p. 21, pl. 8, figs 7–8.
1897 *Fossarulus tricarinatus* Brus. – Brusina, p. 22, pl. 8, figs 11–13.
1907 *Fossarulus tricarinatus* gigas n. for. – Brusina, p. 226.
1926 *Fossarulus eginae eginae* Brusina – Wenz, p. 2203 [cum syn.].
1926 *Fossarulus tricarinatus tricarinatus* Brusina – Wenz, p. 2206 [cum syn.].
1926 *Fossarulus tricarinatus gigas* Brusina – Wenz, p. 2208.
1974 *Fossarulus eginae eginae* Brusina – Milan et al., p. 71.
1974 *Fossarulus tricarinatus tricarinatus* Brusina – Milan et al., p. 72.
1984 *Fossarulus tricarinatus tricarinatus* Brusina – Jurišić-Polšak, p. 198, 205, pl. 1, figs 1–2.
1984 *Fossarulus tricarinatus tricarinatus* var. *altus* n. var. – Jurišić-Polšak, p. 199, 205, pl. 1, figs 3–4, pl. 3, fig. 1.

non 1951 *Fossarulus tricarinatus* Pavlovic [sic] – Vitális, p. 45.
non 1963 *Fossarulus tricarinatus* Brusina – Kühn, p. 374, pl. 1, figs 1–2.

Material: Specimen illustrated by Brusina (1874); Several tens of specimens from Vrba (NHMW 1884D/0009/1162, NHMW 2014/0315/0181).
Type material: Details of type material unknown (type locality: Stuparuša, Sinj Basin). It is uncertain whether the specimen illustrated by Brusina (1874) and indicated as holotype by Milan et al. (1974) (NHMZ 3222-868) is part of the original material of Brusina (1870) or derives from newly collected material.
Dimensions (H x W): 8.56 x 4.94 mm (Brusina, 1897, pl. 8, figs 11–12); 7.39 x 4.56 mm (syntype of *F. eginae*; NHMZ 3026-672; Vrba, Drniš Basin; Brusina, 1897, pl. 8, figs 7–8).
Description: Stout, conical shells with up to 5 weakly convex whorls. Protoconch unknown. Soon, 3 distinct, broad, blunt keels emerge, gaining rapidly in strength. Keels most prominent on last whorl, sometimes creating irregular surface. Sutural ramp is formed by uppermost keel, producing stepped outline; on last whorl prominent shoulder is formed. Last whorl attains 65–70 % of total shell height. Aperture drop-shaped, strongly thickened, constricted, slightly reflected, with thin posterior canal.
Remarks: This species comprises rather stout, conical and thick-shelled individuals with poorly to moderately convex whorls and poorly incised sutures. The keels never bear any kind of nodules. *Fossarulus eginae* Brusina, 1897 fully corresponds to *F. tricarinatus*, while the subspecies *F. eginae ecarinatus* Brusina, 1897 rather ranges within the variability of *F. moniliferus*. *Fossarulus tricarinatus* can be distinguished from *F. stachei*, which has distinctly broader shells, and from *F. moniliferus*, which is more slender and has more convex whorls. The mention of *F. tricarinatus* from the Early Pannonian (Early Tortonian) of Piuszpuszta, Hungary, by Vitális (1951) is probably based on a misspelling. Since Vitális gave "Pavlović" as author, he supposedly wanted to refer to *Fossarulus tetracarinatus* Pavlović, 1903. Given the stratigraphical and paleogeographical gaps, it is unlikely that the Pannonian material represents either of both species.
The misidentification by Kühn (1963) for material from the Late Miocene of Greece was already rectified by Papp (1979), who introduced the new species *Fossarulus milessii* for these shells.
Distribution: Bihać Basin (Bosanska Krupa), Drniš Basin (Miočić, Vrba), Kamengrad Basin (Dabar), Prozor Basin (Konjic-Repovica), Mostar Basin (Mostar, Mukoš), Sarajevo Basin (Zenica), Sinj Basin (Lučane, Potravlje, Stuparuša, Svinjača, Ruda, Tabak, Župića potok) (Brusina, 1870, 1874, 1884, 1897, 1907; Neumayr, 1880; Kerner, 1906; Wenz, 1926; Jurišić-Polšak, 1984). Some of the records by Jurišić-Polšak (1984) from localities of the Sinj Basin need to be verified from the material.

Family Hydrobiidae Stimpson, 1865
Subfamily Belgrandiinae De Stefani, 1877
Genus *Cyclothyrella* Neubauer, Mandic, Harzhauser and Hrvatović, 2013

Type species: *Litorinella candidula* Neumayr, 1869. Middle Miocene; Dalmatia. Type by original designation.

***Cyclothyrella candidula* (Neumayr, 1869)**
Figure 5A–E

* 1869 *Litorinella candidula* nov. sp. – Neumayr, p. 364, pl. 12, fig. 15.
1926 *Prososthenia candidula* (Neumayr) – Wenz, p. 1988 [partim; only regarding DLS records].

Material: 3 specimens from Miočić (NHMW 2014/0315/0169); 6 specimens from Parčić (NHMW 2014/0315/0014, NHMW 2014/0315/0015, NHMW 2014/0315/0016, NHMW 2014/0315/0017, NHMW 2014/0315/0214).
Type material: The type material is said to be stored at the GBA, but the respective box in the collection is empty and the specimens not detectable (type locality: Ribarić, Sinj Basin).
Dimensions (H x W): 4.2 x 2.25 mm (Fig. 5A); 4.0 x 2.0 mm (Fig. 5B); 4.0 x 2.25 mm (Fig. 5C).
Description: Small, slender, drop-shaped shell with 5 convex whorls. Protoconch consisting of 1.2 whorls covered with typical reticulate pattern, which fades out towards teleoconch; transition marked by onset of prosocline growth lines. Last whorl attains ca. 55–60 % of total shell height; grades into straight base. Aperture elliptical to widely drop-shaped, expanded, with glossy peristome. Columella bears weak fold; in some specimens, fold is stronger, sharper inside shell (Fig. 5D). Umbilicus very narrow, slit-like.
Remarks: As shown by Neubauer et al. (2013a) this species

cannot be affiliated with *Prososthenia*, given the reticulate protoconch, the elliptical, expanded aperture, and the columellar fold, all of which are untypical for that genus. A very similar taxon is *C. klietmanni* (Neubauer in Neubauer et al., 2011) from Lučane in the Sinj Basin, which is more slender and distinctly smaller

Distribution: Drniš Basin (Miočić, Parčić), Sinj Basin (Ribarić) (Neumayr, 1869; Kittl, 1895). The records from the Pannonian of Hungary listed in Wenz (1926) certainly represent misidentifications.

***Cyclothyrella tryoniopsis* (Brusina, 1874)**

Figure 5G–K

* 1874 *Prososthenia tryoniopsis* Brusina – Brusina, p. 50, pl. 3, figs 5–6.

1902 [*Prososthenia*]? *humilis* [Brus.] – Brusina, pl. 8, figs 24–26.

1926 *Prososthenia humilis* Brusina – Wenz, p. 1993.

1926 *Prososthenia tryonopsis* [sic] Brusina – Wenz, p. 2003 [cum syn.].

1974 *Prososthenia tryoniopsis* Brusina – Milan et al., p. 130.

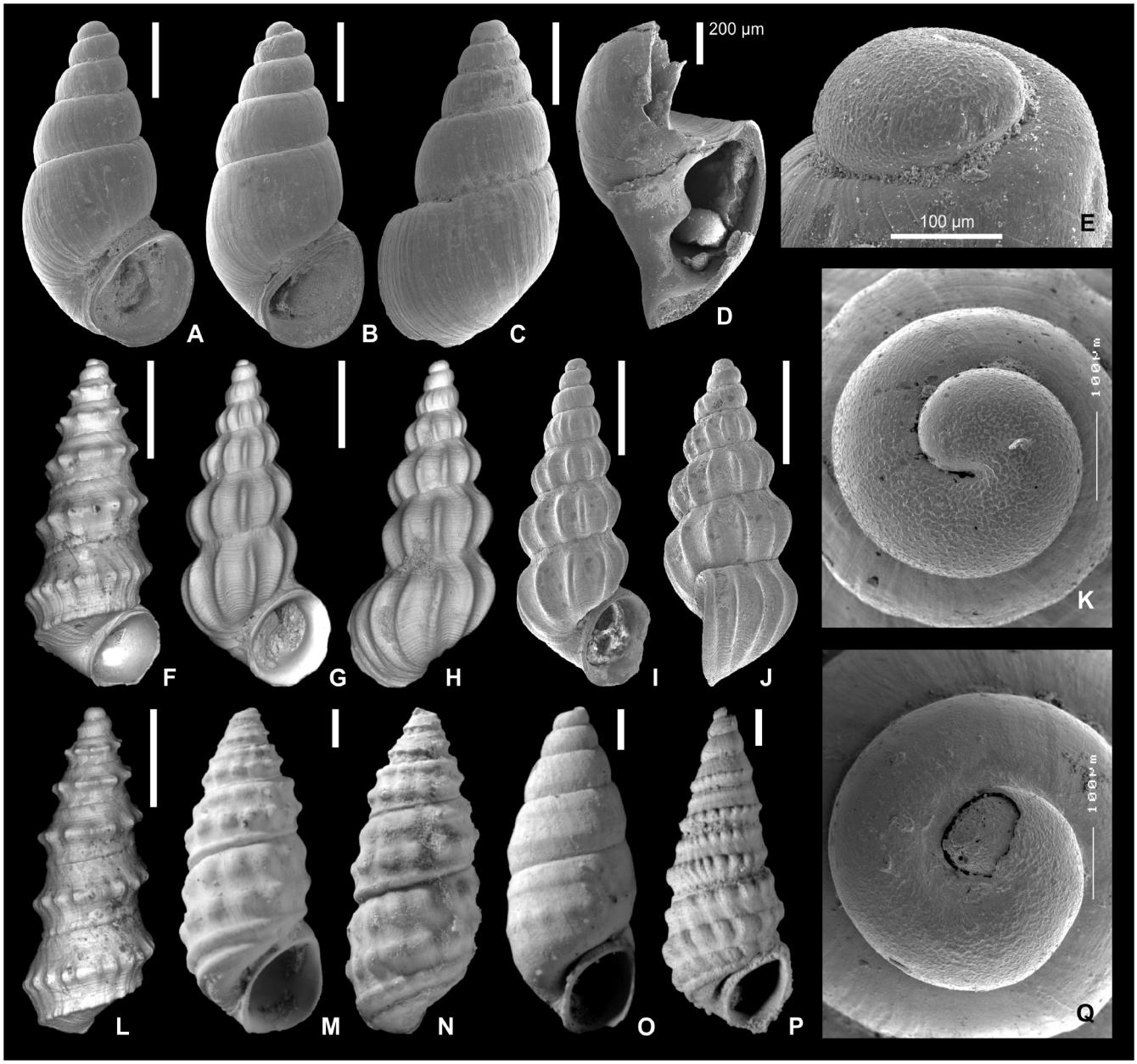


Figure 5: Hydrobiidae. (A) *Cyclothyrella candidula* (Neumayr, 1869). Parčić (NHMW 2014/0315/0014). (B, E) *Cyclothyrella candidula* (Neumayr, 1869). Parčić (NHMW 2014/0315/0015). (C) *Cyclothyrella candidula* (Neumayr, 1869). Parčić (NHMW 2014/0315/0016). (D) *Cyclothyrella candidula* (Neumayr, 1869). Parčić (NHMW 2014/0315/0017). (F, L) *Pyrgula dalmatina* Brusina, 1881. Specimen illustrated by Brusina (1897) (NHMZ 3078-724), Miočić-Parčić. (G–H) *Cyclothyrella tryoniopsis* (Brusina, 1874). Syntype (NHMZ 3218-864), Miočić. (I) *Cyclothyrella tryoniopsis* (Brusina, 1874). Miočić (NHMW 2014/0315/0018). (J) *Cyclothyrella tryoniopsis* (Brusina, 1874). Miočić (NHMW 2014/0315/0019). (K) *Cyclothyrella tryoniopsis* (Brusina, 1874). Miočić (NHMW 2014/0315/0020). (M–N) *Pseudodianella haueri* (Neumayr, 1869). Syntype (GBA 1869/01/12/1), Miočić. (O) *Pseudodianella haueri* (Neumayr, 1869). Syntype of *P. inermis* (GBA 1869/01/13), Miočić. (P) *Pseudodianella haueri* (Neumayr, 1869). Syntype (?) of *P. exilis* (NHMZ 2543-189/1), Miočić. (Q) *Pseudodianella haueri* (Neumayr, 1869). Miočić (NHMW 2014/0315/0035). Scale bars correspond to 1 mm if not stated otherwise.

1974 *Prososthenia humilis* Brusina – Milan et al., p. 128.
? 1988 *Prososthenia tryniopsis* [sic] Brusina – Jurišić-Polšak and Slišković, p. 171.
2013a *Cyclothyrella tryoniopsis* (Brusina, 1874) comb. nov. – Neubauer et al., p. 138, figs 6B, G, J.

Material: 24 specimens from Miočić (NHMW 2014/0315/0018, NHMW 2014/0315/0019, NHMW 2014/0315/0020, NHMW 2014/0315/0044, NHMW 2014/0315/0071, NHMW 2014/0315/0083); 8 from Parčić (NHMW 2014/0315/0152); 3 from Miočić (GBA 2008/008/0094).
Type material: NHMZ 3218-864 (syntype); Miočić, Drniš Basin.
Dimensions (H x W): 3.80 x 1.66 mm (syntype; Brusina, 1874, pl. 3, figs 5–6); 2.57 x 0.93 mm (syntype of *P. humilis*; NHMZ 2569-215/1-3; Džepi, Prozor Basin; Brusina, 1902, pl. 8, figs 24–26); 3.37 x 1.43 mm (Fig. 5I).
Description: A detailed description is provided by Neubauer et al. (2013a).
Remarks: Examination of protoconchs of specimens from Miočić confirmed the observations by Neubauer et al. (2013a) for material from the Kupres Basin. The wrinkled protoconch, as well as the near circular, non-thickened and expanded aperture, distinguish this species clearly from members of *Prososthenia* Neumayr, 1869. The synonymization of *Prososthenia*? *humilis* Brusina, 1902 from Džepi with the present species is based on near identical shape, sculpture and dimensions. The degree of lateral expansion of the aperture of *C. tryoniopsis* is quite variable among specimens from Miočić and thus cannot serve as separation criterion either; rather it seems dependent on individual age. The spiral lineation typical of *C. tryoniopsis* has not been documented for material from Džepi but it is considered to range within intraspecific variability.
Distribution: Drniš Basin (Miočić, Parčić), Prozor Basin (Džepi), Kupres Basin (Fatelj), Sinj Basin (Trnovača), (Brusina, 1874, 1902; Neubauer et al., 2013a). Its presence in the Late Miocene white marl of Tomislavgrad Basin (Šuica gaz) indicated by Jurišić-Polšak and Slišković (1988) needs verification (see also Kochansky-Devidé and Slišković, 1981 and De Leeuw et al., 2011 for the stratigraphic position).

Subfamily Pyrgulinae Brusina, 1881
Genus *Prososthenia* Neumayr, 1869

Type species: *Prososthenia schwartzi* Neumayr, 1869. Middle Miocene; Dalmatia. Type by subsequent designation (Clessin, 1880).

***Prososthenia dalmatina* (Neumayr, 1869)**
Figure 6G–H

* 1869 *Litorinella dalmatina* nov. sp. – Neumayr, p. 364, pl. 12, fig. 13.
1875 *Nematurella dalmatina* Neumayr sp. – Sandberger, p. 673, pl. 32, fig. 3.
1876 *Prososthenia decipiens*, Brusina – Brusina, p. 111.
1897 *Prososthenia dalmatina* (Neum.) – Brusina, p. 18, pl. 8, fig. 29.
1926 *Prososthenia dalmatina* (Neumayr) – Wenz, p. 1990 [cum syn.].

non 1925 *Prososthenia dalmatina* Neumayr – Fischer and Wenz, p. 228, pl. 7, fig. 11.

Material: 36 specimens from Miočić (NHM 2014/0315/0072, NHMW 2014/0315/0127, NHMW 2014/0315/0204); 1 from Biočić (NHMW); more than thousand from Parčić (NHMW 2014/0315/0022, NHMW 2014/0315/0144, NHMW 2014/0315/0167, NHMW 2014/0315/0188); ca. 50 from Miočić (GBA 2008/008/0084).
Type material: GBA 1869/01/19 (syntype); Miočić, Drniš Basin.
Dimensions (H x W): 7.90 x 2.90 mm (syntype; Neumayr, 1869, pl. 12, fig. 13); largest individuals found among the rich material of the NHMW collection attains 8.9 mm in height.
Description: Relatively large, slender drop-shaped shell, with 7 weakly convex, nearly straight-sided whorls. Protoconch contains ca. 0.8 whorls with irregular surface. Aside from regular, distinct prosocline growth lines teleoconch sometimes covered by high number of faint, densely spaced spiral grooves. In some specimens, weak bulge may occur at upper sutures. Last whorl makes up 50–60% of total shell height, grades without marked transition into slightly convex to straight base. Aperture roughly triangular to ovoid; not reflected. In lateral view, outer lip appears slightly sigmoidal; inner lip protrudes below posterior tip; broad emargination is formed at anterior portion. In latest ontogeny, whorl detaches from base, grows with angle of ca. 45° in anterior direction; this results in seemingly thickened posterior region. Umbilicus fully covered.
Remarks: Due to the posterior notch at the aperture Sandberger (1875) placed this species within the genus *Nematurella* Sandberger, 1875. However, *Nematurella* species exhibit a bulge behind the aperture, which is lacking here. Moreover, the posterior notch is also typical for *Prososthenia*. The elongated ovoid aperture with the thickened posterior tip indeed rather argues for *Prososthenia*. The high number of whorls, the slender shape, and the ornamentation distinguishes *P. dalmatina* from all other coeval hydrobiids of this region.
Brusina (1876) introduced *P. decipiens* as new species from Sinj, but apart from mentioning overall similarities with *P. dalmatina* he did not provide much further discussion. Unfortunately, he never illustrated it. Also the details of the type material are unknown. Later, Brusina (1884) revised himself stating that a taxonomic separation from *P. dalmatina* is untenable, which was followed by later authors (Wenz, 1926).
The specimens from Frankfurt-Praunheim (Praunheim Formation, middle-late Burdigalian) determined as *P. dalmatina* by Fischer and Wenz (1925) represent a different species. They differ in the more conical, more elongate shape, the presence of a distinct subsutural band and a thin keel below the whorl

center, and the rounder aperture.

Distribution: Drniš Basin (Biočić, Miočić, Parčić), Sinj Basin (Župića potok, "bunar", unnamed locality N Kovačević) (Neumayr, 1869; Brusina, 1884, 1907; Schubert, 1909a). It has been furthermore indicated from the locality Lemeš by Brusina (1884), claiming already its uncertain geographic position. Lemeš in Central Dalmatia is an upper Jurassic fossiliferous site at the col of the old road between Miočić and Vrlika (Schubert, 1909b). The record of "*Litorinella* aff. *dalmatina*" from Bilišane by Schubert (1909b) needs verification. The mention from Ruduša by Wenz (1926) could not be found in the literature.

***Prososthenia eburnea* Brusina, 1897**

Figure 6E–F, L–N, O

1869 *Litorinella ulvae* Pennant sp. – Neumayr, p. 363, pl. 12, figs 10–11 [non *Turbo ulvae* Pennant, 1777].

1884 *Prososthenia eburnea* Brusina – Brusina, p. 49 [nomen nudum].

* 1897 *Prososthenia eburnea* Brus. – Brusina, p. 18, pl. 8, figs 30–33, pl. 9, figs 1–2.

? 1897 *Prososthenia sepulcralis* (Partsch.) – Brusina, p. 18, pl. 9, figs 5–6 [partim; non *Paludina sepulcralis* Partsch in Czjžek, 1848].

1902 [*Nematurella*]? *eburnea* [Brus.] – Brusina, pl. 9, figs 10–12.

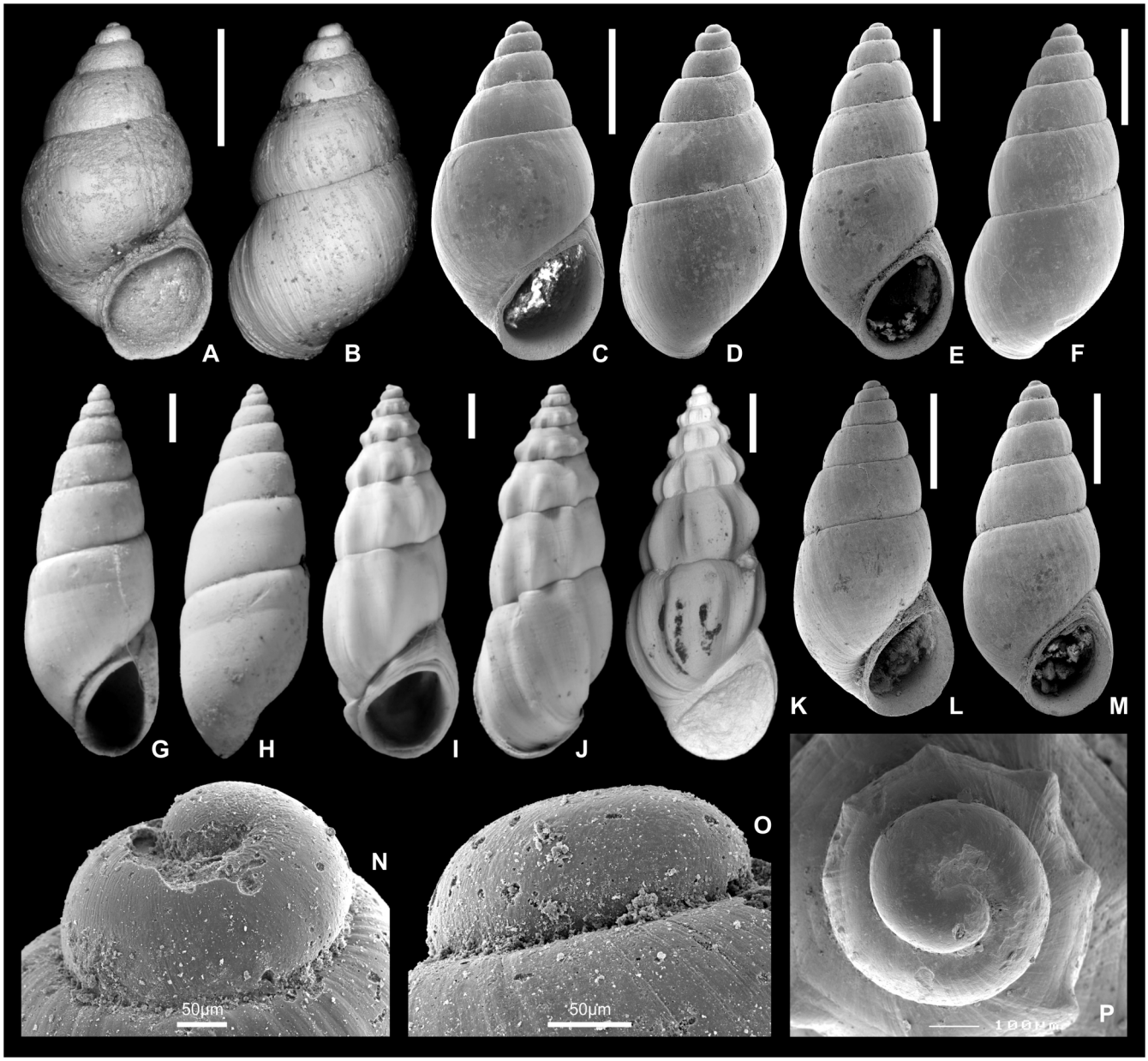


Figure 6: Hydrobiidae. (A–B) *Prososthenia neutra* Brusina, 1897. Specimen illustrated by Brusina (1897, pl. 9, figs 7–8; NHMZ 3041-687/2), Miočić. (C–D) *Prososthenia neutra* Brusina, 1897. Miočić (NHMW 2014/0315/0021). (E–F, N) *Prososthenia eburnea* Brusina, 1897. Miočić (NHMW 2014/0315/0023). (G–H) *Prososthenia dalmatina* (Neumayr, 1869). Parčić (NHMW 2014/0315/0022). (I–J) *Prososthenia tournoueri* (Neumayr, 1869). Miočić (NHMW 2014/0315/0026). (K) *Prososthenia tournoueri* (Neumayr, 1869). Syntype of *P. drobaciana* (NHMZ 3219-865), Miočić. (L, O) *Prososthenia eburnea* Brusina, 1897. Miočić (NHMW 2014/0315/0024). (M) *Prososthenia eburnea* Brusina, 1897. Miočić (NHMW 2014/0315/0025). (P) *Prososthenia tournoueri* (Neumayr, 1869). Miočić (NHMW 2014/0315/0027). Scale bars correspond to 1 mm if not stated otherwise.

1926 *Prososthenia eburnea* Brusina – Wenz, p. 1991 [cum syn.].
? 1926 *Prososthenia sepulcralis sepulcralis* (Partsch) – Wenz, p. 1998 [partim; only regarding DLS records; non Partsch in Čžjžek, 1848].
1974 *Prososthenia eburnea* Brusina – Milan et al., p. 104.
1999 *Prososthenia vojskavae* Olujić – Olujić, p. 27, 55.
1999 *Prososthenia vojskavae decens* Olujić – Olujić, p. 28, 56, pl. 80a, b.
1999 *Prososthenia vojskavae decens* Olujić – Olujić, p. 28, 56, pl. 81a, b.
? 2013b *Prososthenia neutra* Brusina, 1897 – Neubauer et al., figs 7C, E, H [partim; non figs 7A, B, D, F–G; non *Prososthenia neutra* Brusina, 1897].

non 1917 *Prososthenia eburnea* Brusina – Koch, p. 11.
non 1956 *Prososthenia eburnea*? Brusina – Bartha, p. 507.
non 2013a *Prososthenia eburnea* Brusina, 1884 – Neubauer et al., p. 143, figs 8C–D, G, I [partim].

Material: More than 150 specimens from Miočić (NHMW 2014/0315/0023, NHMW 2014/0315/0024, NHMW 2014/0315/0025, NHMW 2014/0315/0043, NHMW 2014/0315/0085, NHMW 2014/0315/0113); 3 from Miočić 1 (NHMW 2014/0315/0001); 28 from Miočić (GBA 2008/008/0085).
Type material: Milan et al. (1974) selected the specimen illustrated by Brusina (1897, pl. 8, figs 30–31) from Trnovača (Sinj Basin) as "holotype" (NHMZ 3039-658/1), which is nomenclaturally incorrect. Since all mentions of this species before 1897 are nomina nuda, Milan et al. (1974) actually selected the new type from the syntype series, corresponding to a valid lectotype designation (ICZN, 1999, Art. 74.1).
Dimensions (H x W): 3.97 x 1.75 mm (lectotype; Brusina, 1897, pl. 8, figs 30–31); largest specimen found measuring 5.1 mm in height.
Description: Slender drop-shaped shell, entirely smooth, consisting of 6 whorls. Protoconch weakly granular, comprising c. 0.8 whorls; passes without definite border into teleoconch. Whorls very weakly convex to straight-sided. Sutures weakly incised. Last whorl attains up to ca. 53–60 % of total height, producing blunt but distinct angulation between whorl flank and base. Aperture inclined, usually regularly ovoid, sometimes outer lip more expanded. In latest ontogeny, whorl detaches from base, grows with angle of ca. 45° in anterior direction; this results in seemingly thickened posterior region. In specimens with stronger detached aperture, slit-like umbilicus is visible. Peristome glossy, sometimes weakly thickened. In lateral view, outer lip slightly sigmoidal, with very weak indentation below posterior tip; inner lip slightly protruding below posterior tip. Orthocline, rarely weakly sigmoidal, growth lines cover shell.
Remarks: The present species displays a morphological link between the slender *P. dalmatina* (Neumayr, 1869) and the bulky *P. neutra* (Brusina, 1897). The former taxon differs in its larger size, the higher number of whorls, and the presence spiral striation. The latter species is not easily separated from *P. eburnea*. Most specimens of *P. eburnea* and *P. neutra* available to us show clear differences, justifying a taxonomic separation. However, a number of intermediate morphologies are present, which cannot be unambiguously affiliated to one of both names. Even the specimen illustrated by Brusina (1897, pl. 9, figs 3–4) as *P. neutra*, which was designated as lectotype by Milan et al. (1974), has similarities to *P. eburnea*.
The diagnostic differences between both species are the relatively higher and broader last whorl, the stronger convex whorls, and the smaller size of *P. neutra*. These characteristics produce the typically bulky appearance. Additionally, *P. eburnea* shows a stronger angulation between whorl flank of the last whorl and base. In this respect it resembles *Nematurella zuschini* Neubauer and Harzhauser in Harzhauser et al. (2012) from the coeval Aflenz Basin, Austria. That species develops an even stronger angulation, a conical outline, and a more distinctly detached aperture.
Especially the material from the Sinj and Gacko basins document the extreme morphological plasticity of *P. eburnea*, partly in the same sample. Variability regards conical vs. drop-shaped outline, profile of whorls, whorl expansion rate, inclination of aperture, and degree of detachment and thickening of aperture. This misled Neubauer et al. (2013b: Figs 7C, E, H) to identify a part of the material as *P. neutra*. The small, stout, ovoid morphotype from Fatelj, determined as *P. eburnea* by Neubauer et al. (2013a: fig. 8D), probably corresponds to a different, yet unidentified species.
The specimens described by Olujić (1999) under the new names *P. vojskavae decora* and *P. vojskavae decens* fully match with *P. eburnea*. Maybe also the specimens from Miočić determined as *P. sepulcralis* by Brusina (1884, 1897), which is a Late Miocene species of Lake Pannon, fall into the morphological range of *P. eburnea*.
Alleged records from the Late Pannonian (Late Tortonian-Messinian) of Tab, Hungary, by Bartha (1956) and from Prvonožina, Croatia (Viviparus beds, Pliocene), by Koch (1917) certainly reflect different species. The misidentification by Gillet and Geissert (1971) for material from Trílofon, Greece (Trilophos Formation, ?Messinian-Zanclean), was already corrected by Rust (1997), who synonymized the record with ?*Hydrobia* aff. *grandis*.
Distribution: Drniš Basin (Miočić), Gacko Basin (Gračanica, Vrbica), Glina Basin (Dugoselo), Sinj Basin (Potravlje, Trnovača, Turjaci) (Brusina, 1884, 1897, 1902; Neubauer et al., 2013b; own data).

***Prososthenia neutra* Brusina, 1897**

Figure 6A–D

* 1897 *Prososthenia*? *neutra* Brus. n. sp. – Brusina, p. 19, pl. 9, figs 3–4, 7–8.
1926 ?*Prososthenia neutra* Brusina – Wenz, p. 1994 [cum syn.].
1974 ?*Prososthenia neutra* Brusina – Milan et al., p. 128.
? 2009 *Prososthenia* sp. – Bulić and Jurišić-Polšak, p. 143, pl. 2, figs 11–12.

? 2011 *Prososthenia neutra* Brusina, 1897 – Neubauer et al., p. 209, pl. 4, figs 3–4, 6, 12.
? 2013b *Prososthenia neutra* Brusina, 1897 – Neubauer et al., figs 7B, D, G [partim; non figs 7A, C, E–F, H].

non 1925 *Prososthenia neutra* Neumayr – Fischer and Wenz, p. 229, pl. 7, figs 12–15.

Material: 37 specimens from Miočić (NHMW 2014/0315/0021, NHMW 2014/0315/0047, NHMW 2014/0315/0063, NHMW 2014/0315/0073, NHMW 2014/0315/0110, NHMW 2014/0315/0112); 1 from Miočić (GBA 2008/008/0095).
Type material: NHMZ 3041-687/1 (lectotype); Miočić, Drniš Basin. Although they referred to a "holotype", Milan et al (1974) validly designated a lectotype from Brusina's syntypes (Brusina, 1897, pl. 9, figs 3–4).
Dimensions (H x W): 3.27 x 1.67 mm (lectotype); 2.87 x 1.62 mm (Brusina, 1897, pl. 9, figs 7–8; NHMZ 3041-687/2).
Description: Broad, drop-shaped shells, consisting of 5 whorls. Protoconch weakly granular, comprising less than 1 whorl; passes without definite border into teleoconch. Whorls moderately to highly convex. Sutures weakly incised. Sometimes weak angulation is formed between flank of last whorl and base. Last whorl attains 60–70 % of total shell height. In latest ontogeny, whorl detaches from base, grows with angle of ca. 45° in anterior direction; this results in seemingly thickened posterior region. In specimens with stronger detached aperture, slit-like umbilicus is visible. Peristome glossy, sometimes weakly thickened, slightly expanded. In lateral view, outer lip slightly sigmoidal, with very weak indentation below posterior tip; inner lip slightly protruding below posterior tip.
Remarks: For similarities with co-occurring *P. eburnea* see discussion above. Specimens from Sinj and Gacko basins described as *P. neutra* by Neubauer et al. (2011; 2013b: Figs 7B, D) have untypically weakly convex whorls and are larger. They correspond in the large last whorl, separating them from *P. eburnea*. Maybe these specimens represent yet another species, distinct from both *P. neutra* and *P. eburnea*. Such morphologies have not been described from the Drniš Basin. They closely resemble the specimens from the Sinj Basin, for which Olujić (1999) introduced the new names *P. superstes praevia* and *P. superstes intermedia*. More material is needed to clarify this issue.
The specimens from Gacko illustrated by Neubauer et al. (2013b: Figs 7C, E) rather reflect *P. eburnea* and are synonymized accordingly. The specimen in Fig. 7A is probably another species, different from *P. neutra* and *P. eburnea*. The highly polymorphic character of all the taxa discussed here makes taxonomic delimitations very difficult.
Shells from Frankfurt-Praunheim and Ginnheim (Praunheim Formation, middle-late Burdigalian) determined as *P. neutra* by Fischer and Wenz (1925) represent a different species. The German specimens vary in the slender, irregular shape.
Distribution: Drniš Basin (Miočić); records from the Gacko Basin (Gračanica, Vrbica), Sinj Basin (Lučane), and Pag (Crnika) remain uncertain (Bulić and Jurišić-Polšak, 2009; Neubauer et al., 2011, 2013b).

***Prososthenia tournoueri* (Neumayr, 1869)**

Figure 6I–K, P

* 1869 *Pyrgidium Tournoueri* nov. sp. – Neumayr, p. 360, pl. 12, figs 2–3.
1874 *Prososthenia Drobaciana* Brusina – Brusina, p. 52, pl. 3, figs 7–8.
1874 *Prososthenia Tournoueri* Neumayr – Brusina, p. 52, pl. 3, fig. 9.
1875 *Tryonia Tournoueri* Neumayr sp. – Sandberger, p. 672, pl. 31, fig. 15.
1897 *Prososthenia Tournoueri* (Neum.) – Brusina, p. 17, pl. 8, fig. 23.
1926 *Prososthenia drobaciana* Brusina – Wenz, p. 1991 [cum syn.].
1926 *Prososthenia tournoueri* (Neumayr) – Wenz, p. 2002 [cum syn.].
1974 *Prososthenia drobaciana* Brusina – Milan et al., p. 128.
? 1988 *Prososthenia tournoueri* Neumayr – Jurišić-Polšak and Slišković, p. 170, 171.

Material: 82 specimens from Miočić (NHMW 1883C/0008/4966, NHMW 2014/0315/0026, NHMW 2014/0315/0027, NHMW 2014/0315/0070, NHMW 2014/0315/0074, NHMW 2014/0315/0202); 2 from Biočić (NHMW 2014/0315/0135); 4 from Miočić (GBA 2008/010/0014).
Type material: GBA 1869/01/7/1-3 (9 syntypes); Miočić, Drniš Basin.
Dimensions (H x W): 10.10 x 3.20 mm (syntype; Neumayr, 1869, pl. 12, fig. 2); 6.48 x 2.56 mm (syntype of *P. drobaciana*; NHMZ 3219-865; Miočić, Drniš Basin; Brusina, 1874, pl. 3, figs 7–8). Largest specimen found in NHMW collection with 10.2 mm in height.
Description: Slender shell with up to 8.5 whorls. Protoconch weakly granular, composed of about 1 whorl; transition to teleoconch invisible. Soon strong, widely spaced axial ribs occur; in first 3–5 whorls, upper portion of ribs slightly concave, lower portion weakly convex, producing spruce-like outline; strongest curvature of ribs below whorl center; ribs are sharp and short, not reaching to upper suture. This growth style changes on last 2–3 whorls, which are higher and more slender in relation to preceding ones. Ribs now totally cover whorls, become broader but less convex. Ribs are not aligned vertically across whorls. Additionally, faint and densely arranged spiral lines cover surface. Aperture roughly triangular to semi-lunar, strongly thickened all around, particularly in posterior region. Peristome weakly reflected, especially at left anterior tip; thin posterior canal present. Umbilicus fully covered. In lateral view, outer lip appears slightly sigmoidal; inner lip protrudes below posterior tip; broad emargination is formed at anterior portion.
Remarks: As Sandberger (1875) correctly mentioned, this species cannot be affiliated to *Pyrgidium* Tournouër, 1869, which

differs largely concerning aperture and sculpture. Sandberger's (1875) classification as *Tryonia* Stimpson, 1865, does not fit either, as this genus is restricted to North and South America (Kabat and Hershler, 1993). The later designation as *Prososthenia* by Brusina (1874, 1897) and Wenz (1926) fits perfectly regarding general shape, protoconch sculpture, and the thickened aperture. Co-occurring *P. drobaciana* Brusina, 1874 cannot be sufficiently separated from this species, corresponding in outline, the typically spruce-like sculpture, and the shape of aperture.

Distribution: Drniš Basin (Biočić, Miočić), Sinj Basin (Turjaci), (Neumayr, 1869; Brusina, 1874, 1884, 1897; Jurišić-Polšak and Slišković, 1988). The mention from Trnovača by Wenz (1926) could not be found in the literature; maybe he confused it with Turjaci. Its presence in the Late Miocene white marl of Tomislavgrad Basin (Šuica gaz) and Livno Basin (Čelebić-Jaruga, Šaćirovina) indicated by Jurišić-Polšak and Slišković (1988) needs verification.

Genus *Pseudodianella* Neubauer, Mandic, Harzhauser and Hrvatović, 2013

Type species: *Pyrgula haueri* Neumayr, 1869. Middle Miocene; Dalmatia. Type by original designation.

***Pseudodianella haueri* (Neumayr, 1869)**
Figure 5M–Q

* 1869 *Pyrgula Haueri* nov. sp. – Neumayr, p. 362, pl. 11, figs 1–2.
1869 *Pyrgula inermis* nov. sp. – Neumayr, p. 362, pl. 11, fig. 3.
1874 *Pyrgula Haueri* Neumayr – Brusina, p. 49.
1874 [*Pyrgula Haueri*] var. *exilis* Brus. – Brusina, p. 49.
1874 *Pyrgula inermis* Neumayr – Brusina, p. 49.
1902 *Diana Haueri* Neum. – Brusina, pl. 7, figs 33–35.
1902 [*Diana*] *exilis* Brus. – Brusina, pl. 7, figs 36–38.
1926 *Diana exilis* (Brusina) – Wenz, p. 2120 [cum syn.].
1926 *Diana haueri* (Neumayr) – Wenz, p. 2121 [cum syn.].
1926 *Diana inermis* (Neumayr) – Wenz, p. 2122 [cum syn.].
1974 *Diana exilis* (Brusina) – Milan et al., p. 68.
? 1988 *Diana haueri* (Neumayr) – Jurišić-Polšak and Slišković, p. 171.
2013a *Pseudodianella haueri* (Neumayr, 1869) comb. nov. – Neubauer et al., p. 144, figs 7B–D, H–J.

Material: 65 specimens from Miočić (NHMW 2014/0315/0035, NHMW 2014/0315/0087, NHMW 2014/0315/0168, NHMW 2014/0315/0201); more than hundred from Parčić (NHMW 2014/0315/0155, NHMW 2014/0315/0156, NHMW 2014/0315/0170, NHMW 2014/0315/0171, NHMW 2014/0315/0173); 6 from Biocic (NHMW 2014/0315/0175, NHMW 2014/0315/0176); 25 from Miočić (GBA 2008/010/0013).
Type material: GBA 1869/01/12/1-2 (syntypes); Miočić, Drniš Basin.
Dimensions (H x W): 8.90 x 4.00 mm (syntype; Neumayr, 1869, pl. 11, fig. 1); 8.30 x 3.50 mm (syntype; Neumayr, 1869, pl. 11, fig. 2); 8.40 x 3.50 mm (syntype of *P. inermis*; GBA 1869/01/13; Miočić, Drniš Basin; Neumayr, 1869, pl. 11, fig. 3); 8.98 x 3.49 mm (syntype (?) of *P. exilis*; NHMZ 2543-189/1; Miočić, Drniš Basin; Brusina, 1902, pl. 7, fig. 36); 7.62 x 3.15 mm (syntype (?) of *P. exilis*; NHMZ 2543-189/2; Miočić, Drniš Basin; Brusina, 1902, pl. 7, fig. 38); 8.98 x 3.38 mm (syntype (?) of *P. exilis*; NHMZ 2543-189/3; Miočić, Drniš Basin; Brusina, 1902, pl. 7, fig. 37).
Remarks: Detailed description and discussion are provided by Neubauer et al. (2013a). Only a small note on nomenclatural details shall be appended here: Wenz (1926) stated that *Diana Haueri* var. *exilis* Brusina, 1874 is a nomen nudum and the species was correctly introduced in Brusina (1876). This is not correct, since Brusina (1874) gave a short descriptive note and explicitly referred to a figure in Neumayr (1869) (indication sensu ICZN, 1999, Art. 12.2).
Distribution: Drniš Basin (Biočić, Miočić, Parčić), Kupres Basin (Fatelj), Sinj Basin (Trnovača, Župića potok) (Neumayr, 1869; Brusina, 1884, 1902; Kittl 1895; Neubauer et al., 2013a). The records from Prozor Basin (Podbor-Šćit) by Katzer (1903) and from the Late Miocene of Tomislavgrad Basin (Šuica gaz) by Jurišić-Polšak and Slišković (1988) need verification.

Genus *Pyrgula* De Cristofori and Jan, 1832

Type species: *Turbo annulatus* Linnaeus, 1758. Recent; Europe. Type by monotypy.

***Pyrgula dalmatina* Brusina, 1881**
Figure 5F, L

* 1881 *Pyrgula dalmatina* Brusina sp. n. – Brusina, p. 258.
1897 *Pyrgula dalmatina* Brus. – Brusina, p. 15, pl. 11, figs 22–23.
1926 *Pyrgula dalmatina* Brusina – Wenz, p. 2099 [cum syn.].
1974 *Pyrgula dalmatina* Brusina – Milan et al., p. 133.

Material: Specimen illustrated by Brusina (1897).
Type material: Details of type material unknown (type locality: Miočić-Parčić, Drniš Basin). It is uncertain whether the specimen illustrated by Brusina (1897) and indicated as holotype by Milan et al. (1974) (NHMZ 3078-724) is part of the original material of Brusina (1881) or derives from newly collected material.
Dimensions (H x W): 3.27 x 1.39 mm (Brusina, 1897, pl. 11, figs 22–23).
Description: Conical shell with up to 7 whorls. Protoconch highly convex, dome-shaped; surface unknown. Already on early teleoconch, small central crest of nodules is present; nodules reach from well-rounded knobs to distinct spikes. Depending on their expression weak to strong concavities are formed above and below nodules. Apart from central crest, whorls are straight-sided and separated by weakly incised sutures; thereby whorls continuously pass into each other. On last three whorls, two weak, narrow bands emerge, one below upper suture, second above lower suture; these bands

bear weak traces of nodules; lowermost band is most prominent, bearing small but distinct nodules and demarcates whorl flank from straight base. Last whorl attains 45 % of total height. Aperture widely ovoid; not thickened or reflected; slightly detached, leaving slit-like umbilicus. Shell surface covered by numerous, faint spiral grooves.
Remarks: This is the only species of *Pyrgula* described from the DLS. It strongly reminds of *P. tessellata* Brusina, 1897 from the Pliocene Viviparus beds of Glogovnica, Croatia. That species has stronger, more widely spaced, and laterally extended nodules, which almost form short, narrow ridges.
Distribution: Endemic to the Drniš Basin (Miočić-Parčić) (Brusina, 1881, 1884).

?Subfamily Pseudamnicolinae Radoman, 1977
Genus *Kadolskya* Neubauer and Harzhauser nov. gen.

Type species: *Lithoglyphus panicum* Neumayr, 1869. Middle Miocene, Langhian; Dalmatia.
Etymology: In honor of Dietrich Kadolsky (Beneath the Surface Geoconsultants Ltd., Sanderstead, Surrey, United Kingdom), a renowned specialist on Cenozoic Hydrobiidae.
Diagnosis: Tiny, globular shell with convex, slightly stepped whorls; protoconch consisting of 1 whorl, bearing distinct wrinkles, which fade out towards transition to teleoconch; last whorl large, inflated; aperture drop-shaped, thickened, detached in late ontogeny, forming shallow, wide groove on neck; growth lines distinct, prosocline.
Affiliated species: At present, only the type species is affiliated with the new genus (for description see below).
Remarks: As already discussed by Neubauer et al. (2013a), this species cannot be classified with *Lithoglyphus*, based on deviating protoconch sculpture. However, the classification as *Bania*, as proposed by Neubauer et al. (2013a), is disputed as well. Typical *Bania*, like the co-occurring species [including the type species *Bania prototypica* (Brusina, 1872)], have conical to ovoid shells with strongly convex whorls and a thin, occasionally expanded or reflected aperture. *Kadolskya* differs conspicuously in its globular shape and the extremely thickened aperture with the shallow groove on the neck. Some recent species of *Pseudamnicola* form similar shell shapes (e.g., Glöer et al., 2010), but they do not expose such thickened peristomes and differ in their granulated to grooved protoconch microsculpture (Falniowski and Szarowska, 1995; Szarowska et al., 2006; Delicado and Ramos, 2012). There is no other hydrobiid genus with a comparable combination of features known to us.
Today, hydrobiid systematics is largely based on molecular data and softpart anatomy, wich is why a systematic classification of *Kadolskya* with a distinct subfamily remains illusive. The protoconch microsculpture is no monophyletic criterion for a certain clade but found among many different hydrobiid as well as cochlicopid taxa (see summary in Neubauer et al., 2013a). Likewise, an apertural thickening is found among many different, not related hydrobiid species (e.g., Jekelius, 1932; Schlickum, 1978; Kadolsky and Piechocki, 2000; Neubauer et al., 2011, 2013a). Based on general shape, size, and the presence of prosocline growth lines, we preliminarily place the genus within the Pseudamnicolinae.
Distribution: Restricted to the Early to Middle Miocene Dinaride Lake System.

***Kadolskya panicum* (Neumayr, 1869) nov. comb.**
Figure 7A–C, K

* 1869 *Lithoglyphus panicum* nov. sp. – Neumayr, p. 364, pl. 12, fig. 9.
1897 *Lithoglyphus*? *panicum* Neum. – Brusina, p. 24, pl. 12, fig. 16.
1902 [*Lithoglyphus*]? *panicum* Neum. – Brusina, pl. 11, figs 72–74.
1928 *Lithoglyphus panicum* Neumayr – Wenz, p. 2278 [cum syn.].

non 1893 *Lithoglyphus panicum*, Neumayr – Locard, p. 204, pl. 10, fig. 9a–b.

Material: 2 specimens from Miočić (NHMW 2014/0315/0180); several hundred from Parčić (NHMW 2014/0315/0010, NHMW 2014/0315/0046, NHMW 2014/0315/0161); ca. 50 from Miočić (GBA 2008/011/0007).
Type material: GBA 1869/01/21 (syntype); Miočić, Drniš Basin.
Dimensions (H x W): 2.60 x 2.20 mm (syntype; Brusina, 1869, pl. 12, fig. 9).
Description: Almost spherical shell with 4 whorls. Protoconch densely covered with distinct wrinkles, comprising ca. 0.8 whorls. Sculpture fades out after 0.5 whorls; transition to teleoconch blurred. First teleoconch whorls small, expose slightly stepped architecture with strong convexity in adapical whorl portion. Last whorl extremely broad, well-rounded, attaining up to 90% of total height. Aperture drop-shaped, markedly thickened all around, with glossy peristome. Aperture nearly fused with base of last whorl; in latest ontogeny, aperture becomes constricted, leading to shift into abapical direction and detachment from base of last whorl. Thereby, many former growth lamellae become visible in many cases. In profile, aperture is inclined to axis with ca. 15°; lips almost perfectly parallel; sometimes anterior portion of inner lip slightly protruding. Umbilicus mostly covered; sometimes present but very small, slit-like. Because of apertural constriction, broad, shallow groove is present on neck (below mostly covered umbilicus) in several specimens with detached aperture. Whole shell covered with numerous weak spiral lines and distinct prosocline growth lines.
Remarks: The wrinkled protoconch precludes a classification as *Lithoglyphus* Pfeiffer, 1828, whose juvenile shell is smooth (Falniowski, 1990). The spherical shape together with the small size, the large last whorl, and the specially thickened lip prevents confusion with all other species. Despite the new combination, the gender of the species epithet remains unchanged as noun in apposition (ICZN, 1999, Art. 31.2.1). The putative record of this species from the Middle Miocene of Le Locle, Switzerland, by Locard (1893) refers to a different spe-

cies. The specimen illustrated by Locard (1893) differs from *K. panicum* in the slenderer, more stepped morphology and the non-thickened aperture.

Distribution: Drniš Basin (Miočić, Parčić) and Lemeš (Neumayr, 1869; Brusina, 1884). The record from the Bihać Basin (Bosanska Krupa) is uncertain (Neumayr, 1880, p. 465).

Subfamily unassigned
Genus *Bania* Brusina, 1896

Type species: *Stalioa prototypica* Brusina, 1872. Middle Miocene; Dalmatia. Type by monotypy (ICZN, 2001).

Remarks: For a detailed description and discussion of the genus and the difficulties of its systematic placement see Neubauer et al. (2013a). Discussions about the nomenclatural problems of *Bania* and *Stalioa* are provided by Kadolsky (1993, 1998) and ICZN (2001, Op. 1965).

***Bania prototypica* (Brusina, 1872)**

1869 *Amnicola immutata* Frauenfeld [sic] – Neumayr, p. 363, pl. 12, fig. 12 [non *Paludina immutata* Hörnes, 1856].
* 1872 *Stalioa prototypica* Brus. – Brusina, p. 144.
1896 *Bania prototypica* Brus. – Brusina, p. 130.
1926 *Bania prototypica* (Brusina) – Wenz, p. 2093 [partim; only regarding DLS records].
1974 *Bania prototypica* (Brusina) – Milan et al., p. 61, pl. 1, figs 4–5.

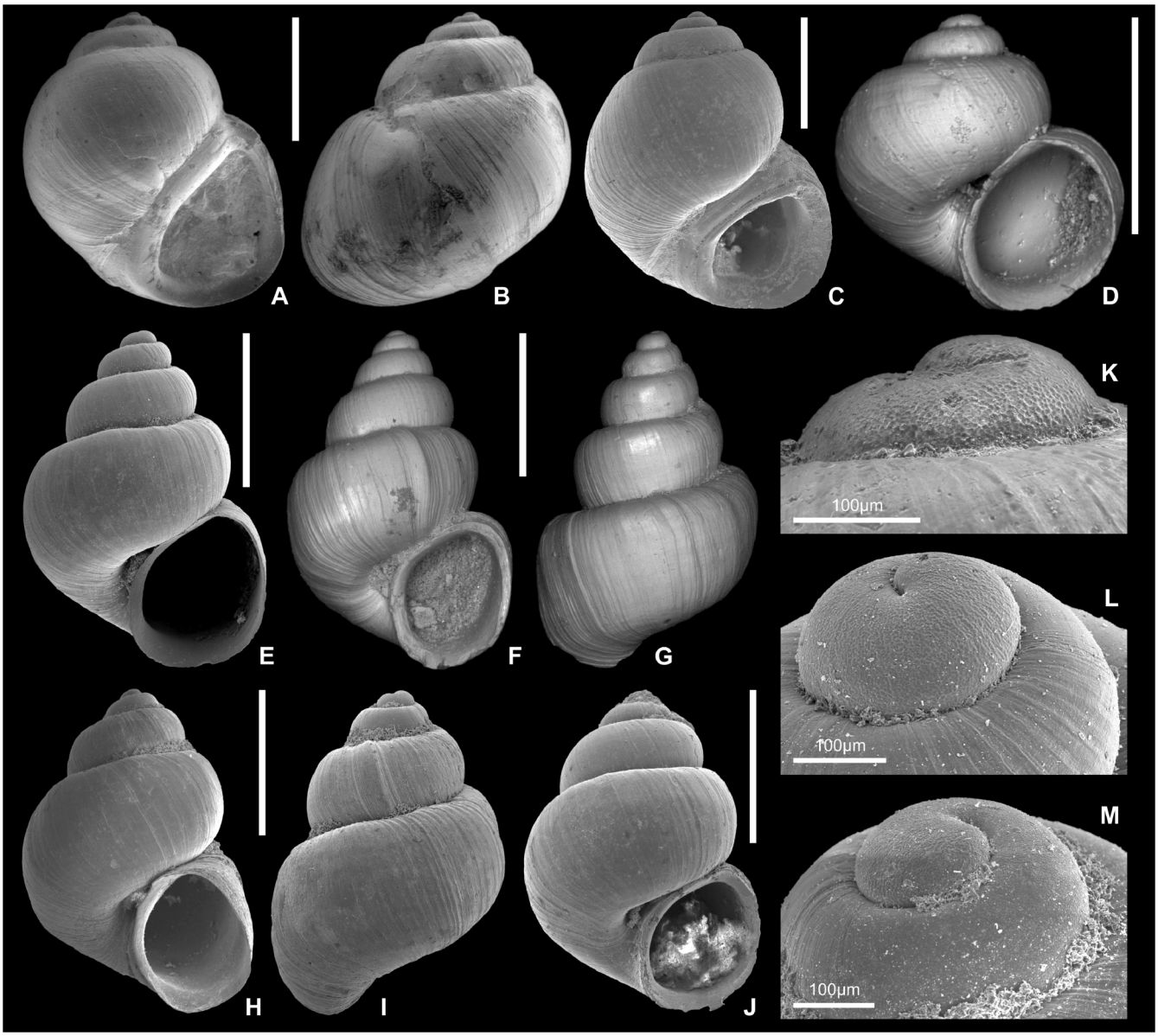


Figure 7: Hydrobiidae. (A–B, K) *Kadolskya panicum* (Neumayr, 1869). Syntype (GBA 1869/01/21), Miočić. (C) *Kadolskya panicum* (Neumayr, 1869). Parčić (NHMW 2014/0315/0010). (D) *Bania valvatoides* (Brusina). Specimen incorrectly designated as neotype by Milan et al. (1974) (NHMZ 3925-1565/1-3), Miočić. (E, L) *Bania stosiciana* (Brusina, 1874). Miočić (NHMW 2014/0315/0011). (F–G) *Bania stosiciana* (Brusina, 1874). Specimen illustrated by Brusina (1902) (NHMW 2615-261/1-3), Miočić. (H–I, M) *Bania torbariana* (Brusina, 1874). Miočić (NHMW 2014/0315/0012). (J) *Bania torbariana* (Brusina, 1874). Miočić (NHMW 2014/0315/0013). Scale bars correspond to 1 mm if not stated otherwise.

? 1993 *Pseudoamnicola* (*Bania*) cf. *prototypica* Brusina – Jurišić-Polšak et al., p. 216, pl. 2, figs 9–10.

non 1877 *Stalioa prototypica*, Brusina – De Stefani, p. 323, pl. 18, fig. 21.
non 2011 *Bania prototypica* (Brusina) – Mandic et al., fig. 5.14.
non 2013 *Bania prototypica* (Brusina) – Krstić et al., p. 13, pl. 3, figs 2a–b.

Material: Specimen invalidly designated as neotype by Milan et al. (1974).
Type material: The syntypes of *B. prototypica* are lost. Milan et al. (1974) invalidly designated a specimen from the type locality Goručica (= Ruduša) as neotype (NHMZ 3926-1566/1). However, the designation does not fulfill the criteria stated by the Code, since no discussion is provided (ICZN, 1999, Art. 75.3). As we do not have material from the type locality, we cannot define a neotype.
Dimensions (H x W): 2.0 x 1.4 mm (NHMZ 3926-1566/1).
Remarks: The taxonomic status of the members of the species-group including *Bania prototypica* (Brusina, 1872), *B. stosiciana* (Brusina, 1874), and *B. torbariana* (Brusina, 1874) is very intricate. The biggest problem is the lack of type material for *B. prototypica* and *B. torbariana* and the thereby emerging difficulties in defining the species. For those two taxa, Milan et al. (1974) invalidly introduced neotypes and "neosyntypes". Especially for *B. prototypica*, the type species of *Bania*, the situation is unclear. Apart from the short Latin description and illustration in Brusina (1874), there is no further affirmed reference to this species (apart from mentions in species lists). Moreover, Brusina (1874) only cited it from Goručica (= Ruduša) in the Sinj Basin, but later also listed it for Miočić (Brusina, 1884). The main reason to include *B. prototypica* in another genus than *B. stosiciana* and *B. torbariana* was the apertural thickening, which is, however, not developed in the specimen (invalidly) designated as "neotype" by Milan et al. (1974). In that specimen, two thickenings occur on the last whorl, but not directly at the peristome. Moreover, such thickenings are not uncommon and appear in variable expressions on many shells of *B. stosiciana* as well, including the available syntype. These growth rims are thus not diagnostic. The comparison of the illustration of *B. prototypica* in Brusina (1874) and the syntype of *B. stosiciana* still allows a preliminary differentiation of both species. *Bania prototypica* has one whorl less, a more ovoid shape and the aperture is not detached. This distinction remains tentative given the lack of sufficient material for *B. prototypica*.
For *B. torbariana*, the situation is less problematic. This species was described from Miočić and the material available to us as well as the "neosyntypes" defined by Milan et al. (1974) perfectly matches the description and illustrations in Brusina (1874, 1902). The species can be differentiated from *B. prototypica* and *B. stosiciana* because of its broader, ton-like shape. The record of "*Stalioa prototypica*" from the Pleistocene (late Villafranchian) of Italy by De Stefani (1877) is based on a misidentification. The Italian specimens have less convex whorls and a rather ovoid shell shape. The specimen identified as "*Bania prototypica*" by Krstić et al. (2013) does not correspond to the present species but rather matches with *B. torbariana*. The determinations of material from Gacko as "*Bania prototypica*" by Mandic et al. (2011) have been revised by Neubauer et al. (2013b) and synonymized with *B. valvatoides*.
Distribution: Drniš Basin (Miočić), Udbina Basin (Laudonov Gaj), Sinj Basin (Ruduša) (Brusina, 1874, 1884; Jurišić-Polšak et al., 1993).

Bania stosiciana **(Brusina, 1874)**

Figure 7E–G, L

* 1874 *Amnicola Stošićiana* Brusina – Brusina, p. 65.
1902 *Pseudoamnicola*? *Stošićiana* [Brus.] – Brusina, pl. 10, figs 11–13.
1926 *Amnicola* (*Amnicola*) *stošićiana stošićiana* Brusina – Wenz, p. 2081 [partim; only regarding DLS records].
1974 *Amnicola* (*Amnicola*) *stosiciana stosiciana* (Brusina) – Milan et al., p. 131.
2013 *Pseudamnicola* cf. *torbariana* Brusina – Krstić et al., p. 12, pl. 3, fig. 1 [non *Amnicola Torbariana* Brusina, 1874].

non 1888 [*Amnicola*] *Stosiciana* Brus. – Handmann, p. 60.
non 1989 *Pseudamnicola stošićiana* (Brusina) – Pană, p. 77, pl. 3, figs 15–16.
non 2013 *Pseudamnicola stosiciana* Brusina – Krstić et al., p. 12, pl. 3, figs 4a–b.

Material: Specimen illustrated by Brusina (1902); several hundred from Miočić and Biočić (NHMW 2014/0315/0011, NHMW 2014/0315/0179, NHMW 2014/0315/0184). It is difficult to distinguish juvenile specimens of *B. stosiciana* and *B. torbariana*, so it is impossible to provide more precise numbers.
Type material: Details of type material unknown (type locality: Miočić, Drniš Basin). It is uncertain whether the specimens illustrated by Brusina (1902) and indicated as syntypes by Milan et al. (1974) (NHMZ 2615-261/1-3) are part of the original material of Brusina (1874) or derive from newly collected material.
Dimensions (H x W): 2.36 x 1.48 mm (Brusina, 1902, pl. 10, fig. 11).
Description: Smooth shell with up to 5 whorls. Protoconch consists of ca. 1 whorl; surface highly granulated in its beginning, grading into weak, irregular spiral grooves near border to teleoconch. Sutures deeply incised. Whorls strongly convex in upper half of the whorls, resulting in step-like outline. Whorls regularly increase in height and diameter, producing conical shape. Last whorl attains up to two thirds of total height; grades into straight base. Aperture widely elliptical, rarely thickened; slightly detached, touching base of preceding whorl, leaving moderately wide umbilicus. Distinct prosocline growth lines cover surface. In late ontogeny, growth rims, expressed as marked thickenings, occasionally occur on outer surface.

Remarks: The main difference to the very similar, co-occurring *B. torbariana* (Brusina, 1874) is the regular conical outline. The stepped spire separates it from *B. tripaloi* (Brusina, 1884). *Bania stosiciana crassa* (Brusina, 1897) with convex-sided whorls and a slightly thickened aperture ranges within the morphological variability of *B. valvatoides* (Brusina, 1872) and was already synonymized by Neubauer et al. (2013b). That species differs from *B. stosiciana* in its very broad, bulky appearance.

The specimen identified and illustrated as "*Pseudamnicola* cf. *torbariana*" by Krstić et al. (2013) from Kupres matches with the present species. The specimen determined as "*Pseudamnicola stosiciana*" actually represents a spire fragment of a different hydrobiid (*Prososthenia*?). Certainly, also the mention of "*Amnicola stosiciana*" from the Late Miocene of the Vienna Basin by Handmann (1888) refers to a different species. Specimens from the Parscovian (Late Dacian, Early Pliocene) of the Dacian Basin, misidentified as *P. stosiciana* by Pană (1989), can be distinguished by their non-stepped, conical spire with weakly convex whorls.

Distribution: Drniš Basin (Biočić, Miočić), Kupres Basin (Kupres) (Brusina, 1874, 1884; Krstić et al., 2013).

***Bania torbariana* (Brusina, 1874)**

Figure 7H–J, M

* 1874 *Amnicola Torbariana* Brusina – Brusina, p. 66, pl. 5, figs 15–16.
1902 [*Pseudoamnicola*]? *Torbariana* [Brus.] – Brusina, pl. 10, figs 14–17.
1907 *Pseudamnicola*? *Pauluccii* n. sp. – Brusina, p. 218.
1926 *Amnicola* (*Amnicola*) *pauluccii* Brusina – Wenz, p. 2075.
1926 *Amnicola* (*Amnicola*) *torbariana* Brusina – Wenz, p. 2083 [partim; only regarding DLS records].
1974 *Amnicola* (*Amnicola*) *torbariana* (Brusina) – Milan et al., p. 57.
? 2011 *Pseudamnicola torbarianus* (Brusina, 1874) – Neubauer et al., p. 211, pl. 4, figs 8–11, 13.
2013 *Bania prototypica* (Brusina) – Krstić et al., p. 13, pl. 3, figs 2a–b [non *Stalioa prototypica* Brusina, 1872]

non 1888 [*Amnicola*] *Torbariana* Brus. – Handmann, p. 60.
non 2013 *Pseudamnicola* cf. *torbariana* Brusina – Krstić et al., p. 12, pl. 3, fig. 1.

Material: Several hundred from Miočić and Biočić (NHMW 1883C/0008/4972, NHMW 2014/0315/0012, NHMW 2014/0315/0013, NHMW 2014/0315/0051, NHMW 2014/0315/0052, NHMW 2014/0315/0111, NHMW 2014/0315/0124). It is difficult to distinguish juvenile specimens of *B. stosiciana* and *B. torbariana*, so it is impossible to provide more precise numbers.

Type material: The syntypes of *B. torbariana* are lost. Milan et al. (1974) designated specimens from the type locality Miočić as "neosyntypes" (NHMZ 2116-262/1-4), a term not available in nomenclature (ICZN, 1999). Also, designation of several specimens as equivalent types is not permitted; additionally, the designation does not fulfill the relevant criteria requested by the Code.

Dimensions (H x W): 2.86 x 1.93 mm ("neosyntype", Brusina, 1902, pl. 10, fig. 15); 2.25 x 1.60 mm (Fig. 7H–I, M).

Description: Smooth, fragile shell with up to 4 whorls. Protoconch consists of ca. 1 whorl; surface highly granulated in its beginning, grading into weak, irregular spiral grooves near border to teleoconch; latter is marked by onset of prosocline growth lines. Sutures deeply incised. Whorls strongly convex, sometimes producing step-like outline. Whorls usually increase more rapidly in height than in diameter, producing broadly ovoid, ton-like shape. Last whorl attains up to two thirds of total height; grades into straight base. Aperture widely elliptical, sharply terminated; slightly detached from base, touching base of preceding whorl, leaving moderately wide umbilicus. In late ontogeny, growth rims, expressed as marked thickenings, occasionally occur on outer surface.

Remarks: The diagnostic difference from *B. stosiciana* is the tonlike shape produced by the rapid whorl height increase. The color differences stated by Brusina (1874) could not be con-firmed: both species expose bright white shells in most of the samples.

Brusina (1907) introduced the new species *Pseudamnicola pauluccii* for specimens from the locality "bunar" in the city of Sinj. These specimens perfectly match with juveniles of *B. torbariana*; hence, we consider this species synonymous with *B. torbariana*. Individuals from Lučane (Sinj Basin) identified as "*Pseudamnicola torbarianus*" by Neubauer et al. (2011) expose untypically thickening apertures, leaving some doubts about the identification, but otherwise match with the present species. The specimen determined as "*Pseudamnicola* cf. *torbariana*" by Krstić et al. (2013) from Kupres rather matches with *B. stosiciana*. In contrast, the specimen identified as *B. prototypica* corresponds to the present species. Certainly, also the mention of "*Amnicola torbariana*" from the Late Miocene of the Vienna Basin by Handmann (1888) refers to a different species.

Distribution: Drniš Basin (Biočić, Miočić), Sinj Basin (Trnovača, "bunar") (Brusina, 1874, 1884, 1907).

***Bania valvatoides* (Brusina, 1874)**

Figure 7D

1872 *Stalioa valvatoides* Brus. – Brusina, p. 144 [nomen nudum].
* 1874 *Stalioa valvatoides* Brusina – Brusina, p. 61, pl. 4, figs 9–10.
1897 *Pseudoamnicola*? *Stošićiana crassa* Brus. n. for. – Brusina, p. 22, pl. 12, figs 17–18.
1926 *Bania valvatoides* (Brusina) – Wenz, p. 2093 [cum syn.].
1974 *Bania valvatoides* (Brusina) – Milan et al., p. 61, pl. 1, figs 2–3.
2009 *Pseudoamnicola* (*Staja*) *šoštarićiana* [sic] Brusina, 1974 – Krstić et al., p. 39, pl. 1, fig. 5.
2011 *Bania prototypica* (Brusina) – Mandic et al., fig. 5.14 [non *Stalioa prototypica* Brusina, 1874].

2013b *Bania valvatoides* (Brusina, 1874) – Neubauer et al., figs 8A–I.

Material: The specimen invalidly designated as neotype by Milan et al. (1974).
Type material: Syntypes from Goručica (= Ruduša) and Miočić lost; Milan et al. (1974) wrongly stated that Brusina (1874) preferred the specimen from Goručica (= Ruduša), which is lost. So they decided to designate a neotype (NHMZ 3925-1565/1-3) from additional material from Miočić. This is not valid according to the Code (Art. 75.3) and no type exists at present.
Dimensions (H x W): 1.5 x 1.3 mm ("neotype", Fig. 7D).
Remarks: For detailed description and discussion about morphological variability, similarities to other taxa and synonymizations see discussions above and Neubauer et al. (2013b: suppl. online material).
Distribution: Drniš Basin (Miočić), Gacko Basin (Gračanica, Vrbica), Sinj Basin (Ruduša) (Brusina, 1874, 1884; Neubauer et al., 2013b).

Clade Panpulmonata Jörger et al., 2010
Order Hygrophila Férussac, 1822
Superfamily Lymnaeoidea Rafinesque, 1815
Family Lymnaeidae Rafinesque, 1815
Subfamily Lymnaeinae Rafinesque, 1815

Genus *Lymnaea* Lamarck, 1799

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

***Lymnaea klaici* Brusina, 1884**
Figure 8A–C

1869 *Limnaea subpalustris* Thomae – Neumayr, p. 366, pl. 12, fig. 19 [non *Limnaeus subpalustris* Thomä, 1845]
* 1884 *Limnaea Klaići* Brusina – Brusina, p. 57.
1897 *Limnaea Klaići* Brus. – Brusina, p. 3, pl. 2, figs 4–5.
1923 *Lymnaea klaići* Brusina – Wenz, p. 1219 [cum syn.].
1974 *Lymnaea klaici* Brusina – Milan et al., p. 82.

Material: Specimens illustrated by Brusina (1897); 8 specimens from Biočić (NHMW 2014/0315/0136); 20 from Miočić (GBA 2008/148/0010, GBA 2008/148/0011, GBA 1869/01/25).
Type material: Details of type material unknown (type locality: Miočić, Drniš Basin). It is uncertain whether the specimen illustrated by Brusina (1897, pl. 2, fig. 4) and indicated as holotype by Milan et al. (1974) (NHMZ 2943-589) is part of the original material of Brusina (1884) or derives from newly collected material.
Dimensions (H x W): 40.28 x 20.69 mm (Brusina, 1897, pl. 2, fig. 4); 31.68 x 13.45 mm (Brusina, 1897, pl. 2, fig. 5).
Description: Large, slender shell with 6 moderately convex whorls. Sutures poorly incised. Whorls gain constantly in height and diameter; only last whorl slightly inflated. Last whorl attains 70 % of total shell height, grades into steep, straight base. Aperture reflected, with marked columellar fold, sheet-like inner lip, slightly expanded outer lip. Surface smooth apart from distinct orthocline growth lines.
Remarks: Brusina (1884) clearly stated that his species is not conspecific with "*Limnaea subpalustris*" recorded by Neumayr (1869). The specimen illustrated by Neumayr represents a juvenile and may indeed be conspecific. We follow Wenz (1923) who synonymized both. *Stagnicola subpalustris* (Thomä, 1845) from the Early Miocene of the Mainz Basin has a more inflated last whorl and a weaker columellar fold (see also Harzhauser et al., 2014b). The generic attribution of L. klaici is based on the pointy spire, the slightly inflated last whorl, and the large size.
Distribution: Drniš Basin (Biočić, Miočić), Sinj Basin (Ribarić, Ruduša, Strmendolac-Crveni klanac, Trnovača, Župića potok) (Brusina, 1884; Jurišić-Polšak et al., 2000). The uncertain record from the Late Miocene of Corni (= Cornii de Sus, Bacau, Dacian Basin), Romania, mentioned by Wenz (1923) is surely a misidentification.

Genus *Radix* Montfort, 1810

Type species: *Helix Auricularia* Linnaeus, 1758. Recent; Europe. Type by original designation (Welter-Schultes, 2012).

***Radix korlevici* (Brusina, 1884)**
Figure 8D–E

* 1884 *Limnaea Korlevići* Brusina – Brusina, p. 56.
1897 *Limnaea Korlevići* Brus. – Brusina, p. 3, pl. 2, figs 6–7.
1902 [*Lymnaea*] *hyaloleuca* [Brus.] – Brusina, pl. 1, figs 36–39.
1923 *Radix* (*Radix*) *hyaloleuca* (Brusina) – Wenz, p. 1250 [cum syn.].
1923 *Radix* (*Radix*) *korlevići* (Brusina) – Wenz, p. 1253 [cum syn.].
1974 *Radix* (*Radix*) *hyaloleuca* (Brusina) – Milan et al., p. 81.
1974 *Radix* (*Radix*) *korlevici* (Brusina) – Milan et al., p. 82.
? 2000 *Lymnaea* cf. *korlevići* Brusina – Dolić et al., p. 4, pl. 3, figs 18–19.
? 2000 *L.*[*ymnaea*] cf. *hyaloleuca* Brusina – Dolić et al., p. 4, pl. 3, fig. 20.
? 2006 *Radix hyaloleuca* (Brusina), 1902 – Kókay, p. 52, pl. 17, fig. 15.
2013b *Radix korlevici* (Brusina, 1884) – Neubauer et al., figs 9A–B, D [cum syn.].

non 1981 *Lymnaea hyaloleuca* Brusina, 1897 – Pană et al., p. 121, pl. 68, figs 4–6.
non 2004 *Limnaea korlevici* Brusina – Pătruțoiu, p. 343.

Material: Specimen illustrated by Brusina (1897); 2 poorly preserved molds from Miočić (GBA 2008/148/0009).
Type material: Details of type material unknown (type locality: Miočić, Drniš Basin). It is uncertain whether the specimen illustrated by Brusina (1897) and indicated as holotype by Milan et al. (1974) (NHMZ 2945-591) is part of the original mate-

rial of Brusina (1884) or derives from newly collected material.
Dimensions (H x W): 14.26 x 7.76 mm (Brusina, 1897, pl. 2, figs 6–7); 7.67 x 4.09 mm (lectotype of *L. hyaloleuca*, designated by Milan et al., 1974; NHMZ 2381-27; Avtovac-Gacko, Gacko Basin; Brusina, 1902, pl. 1, figs 36–37).
Remarks: For detailed description and discussion on synonymizations and generic classification see Neubauer et al. (2013b: suppl. online material). Kókay (2006) determined several juvenile specimens from the Sarmatian (late Serravallian) of Várpalota, Hungary, as *Radix hyaloleuca*. These shells are indeed very similar to the type of *R. hyaloleuca* and might be conspecific. However, it is hardly possible to clarify this based on juvenile shells only. The same applies for records from the Late Pontian-Dacian of the Dacian Basin by Pană et

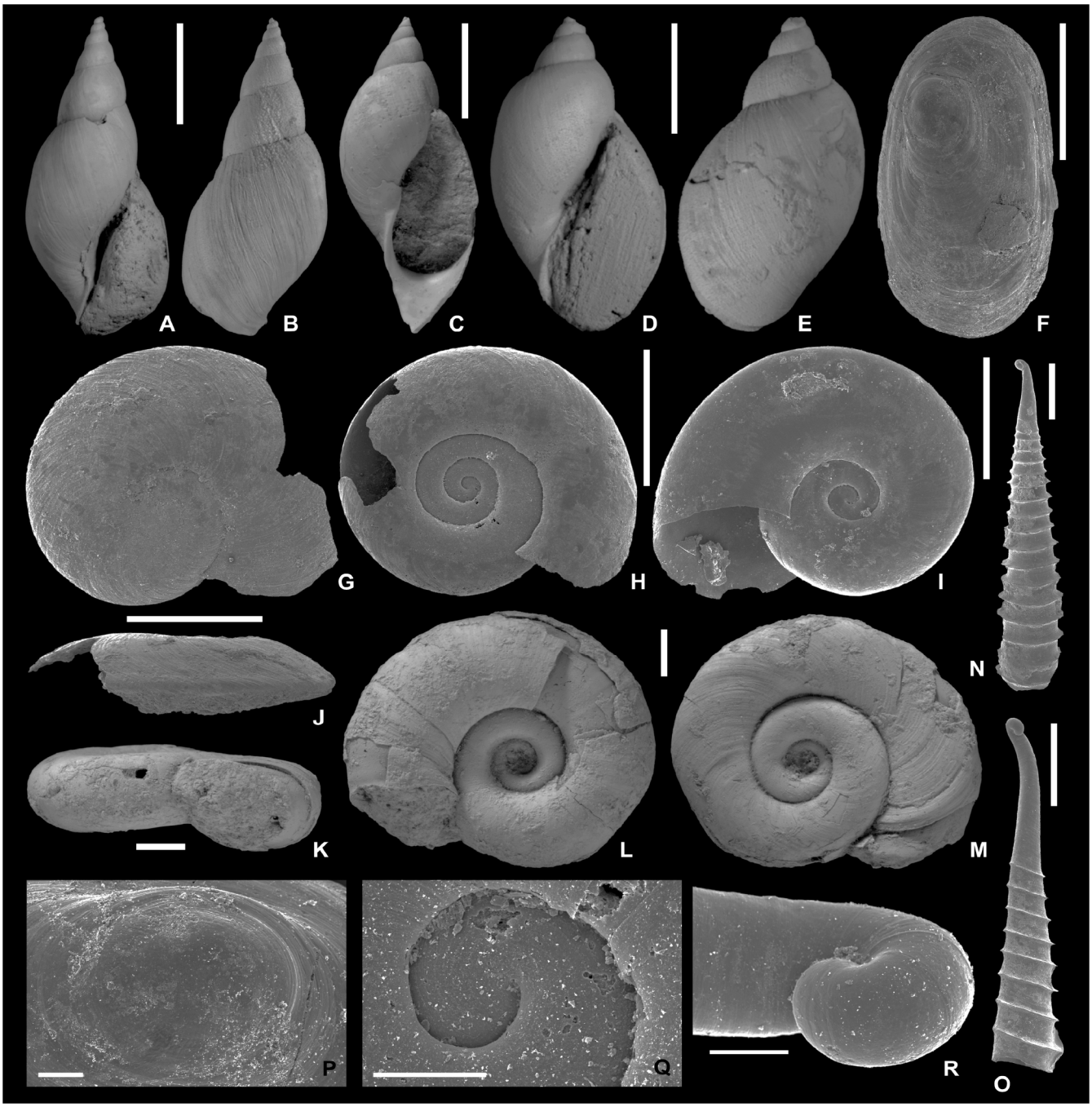


Figure 8: Pulmonate gastropods. (A–B) *Lymnaea klaici* Brusina, 1884. Specimen illustrated by Brusina (1897) (NHMZ 2943-589), Miočić. (C) *Lymnaea klaici* Brusina, 1884. Specimen illustrated by Neumayr (1869) as "*L. subpalustris*" (GBA 1869/01/25), Miočić. (D–E) *Radix korlevici* (Brusina, 1884). Specimen illustrated by Brusina (1897) (NHMZ 2945-591), Miočić. (F, P) *Ferrissia illyrica* (Neumayr, 1880). Parčić (NHMW 2014/0315/0028). (G, J). *Gyraulus dalmaticus* (Brusina, 1897). Miočić (NHMW 2014/0315/0029). (H, Q) *Gyraulus geminus* (Brusina, 1897). Miočić (NHMW 2014/0315/0030). (I) *Gyraulus geminus* (Brusina, 1897). Miočić (NHMW 2014/0315/0031). (K–M) *Planorbarius mantelli* (Dunker, 1848). Specimen illustrated by Neumayr (1869) as "*Planorbis cornu*" (GBA 1869/01/26), Miočić. (N) *Orygoceras dentaliforme* (Brusina, 1882), "*cornucopiae*"-morphotype. Parčić (NHMW 2014/0315/0032). (O, R) *Orygoceras dentaliforme* (Brusina, 1882), "*cornucopiae*"-morphotype. Parčić (NHMW 2014/0315/0033). Scale bars correspond to 10 mm (A–B), 5 mm (C–E, K–M), 1 mm (F–H, J, N–O), 500 µm (I), and 100 µm (P–R).

al. (1981) and Pătruțoiu (2004). Given the big stratigraphical and paleobiogeographical gap it is unlikely that those are conspecific with the present species. Likewise, it remains unresolved whether the records from the Early Miocene of Radoinja, Serbia, by Dolić et al. (2000) correspond to *R. korlevici*. The poorly preserved material does not allow a proper assessment.
Distribution: Drniš Basin (Miočić), Gacko Basin (Gračanica, Vrbica), Sinj Basin (Strmendolac-Crveni klanac) (Brusina, 1884, 1897, 1902; Jurišić-Polšak et al., 2000; Neubauer et al., 2013b).

Superfamily Planorboidea Rafinesque, 1815
Family Planorbidae Rafinesque, 1815

Genus *Ferrissia* Walker, 1903

Type species: *Ancylus rivularis* Say, 1817. Recent; North America. Type by original designation.

***Ferrissia illyrica* (Neumayr, 1880)**
Figure 8F, P

* 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 [partim; only regarding DLS records].
2011 *Ferrissia illyrica* (Neumayr, 1880) – Neubauer et al., p. 214, pl. 6, figs 8–9, 13.
2013b *Ferrissia illyrica* (Neumayr, 1880) – Neubauer et al., figs 11G–K [cum syn.].

non? 1973 *Ancylus illyricus* Neumayr – Schütt and Besenecker, p. 18, pl. 2, fig. 26.
non? 1975 *Ancylus illyricus* Brusina [sic] – Čtyroký, p. 155.
non? 1976 *Ferrissia illyrica* (Neumayr) – Schütt, p. 47, pl. 7, figs 26–28.

Material: 1 specimen from Parčić (NHMW 2014/0315/0028).
Type material: The type specimen from Avtovac-Gacko (Gacko Basin) is lost; no neotype or lectotype is defined.
Dimensions (L x W x H): 2.3 x 1.25 x 0.7 mm.
Remarks: For detailed descriptions and discussions see Neubauer et al. (2011, 2013b: suppl. online material).
Distribution: Gacko Basin (Avtovac-Gacko, Gračanica, Vrbica), Drniš Basin (Miočić, Parčić), Sinj Basin (Lučane, Ruduša, Strmendolac-Crveni klanac) (Neumayr, 1880; Brusina, 1884; Jurišić-Polšak et al., 2000; Neubauer et al., 2011, 2013b). The records from the Pannonian Basin (Wenz, 1923; Čtyroký, 1975) and from the late Middle to Late Miocene of Greece (Schütt and Besenecker, 1973; Schütt, 1976) probably represent different species.

Genus *Gyraulus* Charpentier, 1837

Type species: *Planorbis albus* Müller, 1774. Recent; Europe. Type by subsequent designation by Dall (1870).

***Gyraulus dalmaticus* (Brusina, 1884)**
Figure 8G, J

* 1884 *Planorbis dalmaticus* Brusina – Brusina, p. 56.
1897 *Planorbis dalmaticus* Brus. – Brusina, p. 6, pl. 2, figs 17–25.
1923 *Gyraulus* (*Gyraulus*) *dalmaticus* (Brusina) – Wenz, p. 1548 [cum syn.].
1974 *Gyraulus* (*Gyraulus*) *dalmaticus* (Brusina) – Milan et al., p. 118.

Material: Specimens illustrated by Brusina (1897); 1 specimen from Miočić (NHMW 2014/0315/0029).
Type material: Details of type material unknown (type locality: Trnovača, Sinj Basin). It is uncertain whether the specimens illustrated by Brusina (1897) are part of the original material of Brusina (1884) or derive from newly collected material. Therefore, the lectotype designation by Milan et al. (1974) (NHMZ 2949-595) is invalid.
Dimensions (H x W): 0.62 x 2.46 mm (Brusina, 1897, pl. 2, figs 17–19).
Description: Small, flattened, discoid, planispiral shell with 3 whorls, which increase rapidly and constantly in diameter. Apical depression slightly deeper than umbilical; both widely concave. Distinct, sharp angulation is developed above whorl center, producing slightly asymmetrical profile; never results in offset keel. Whorl portions above and below angulation weakly convex. Last whorl overgrows 18 % of preceding whorl. Aperture slightly asymmetrical, heart-shaped.
Remarks: The species differs from co-occurring *G. geminus* in ist distinct, subcentral angulation and the higher whorl expansion rate. The wide-spread *G. kleini* (Gottschick and Wenz, 1916) has a blunter angulation and less flattened shell.
Distribution: Drniš Basin (Miočić), Sinj Basin (Strmendolac-Crveni klanac, Trnovača) (Brusina, 1884, 1897; Jurišić-Polšak et al., 2000).

***Gyraulus geminus* (Brusina, 1897)**
Figure 8H–I, Q

1869 *Planorbis applanatus* Thomae – Neumayr, p. 368, pl. 12, fig. 22 [non *Planorbis applanatus* Thomä, 1845].
1874 *Planorbis applanatus* Thomae – Brusina, p. 101 [non Thomä, 1845].
* 1897 *Planorbis geminus* Brus. n. sp. – Brusina, p. 5, pl. 2, figs 11–16.
1923 *Gyraulus* (*Gyraulus*) *geminus* (Brusina) – Wenz, p. 1554 [partim; only regarding DLS records].
1974 *Gyraulus* (*Gyraulus*) *geminus* (Brusina) – Milan et al., p. 119.
? 2006 *Gyraulus geminus* (Brusina), 1897 – Kókay, p. 56.

non 2011 *Gyraulus geminus* (Brusina, 1897) – Neubauer et al., p. 213, pl. 6, figs 3–4, 11.

Material: 2 specimens from Miočić (NHMW 2014/0315/0030, NHMW 2014/0315/0031); 2 from Miočić (GBA 2008/150/0011, GBA 1869/01/27; the latter was illustrated in Neumayr, 1869).
Type material: NHMZ 2947-593 (lectotype, designated by

Milan et al., 1974); Goručica (= Ruduša), Sinj Basin.
Dimensions (H x W): 0.76 x 3.33 mm (lectotype; Brusina, 1897, pl. 2, figs 11–13).
Description: Small, discoid, planispiral shell with 4 weakly convex whorls, which increase slowly but constantly in diameter. Both apical and umbilical depressions equally widely and weakly concave. Blunt but distinct angulation is developed at whorl center; never results in offset keel. Whorl portions above and below angulation weakly convex. Last whorl overgrows 20 % of preceding whorl. Aperture symmetrical, heart-shaped.
Remarks: This species was introduced by Brusina (1897) for erroneous records of "*Planorbis applanatus*" from DLS deposits (Neumayr, 1869; Brusina, 1874, 1884). *Gyraulus applanatus* (Thomä, 1845) was described from Early Miocene deposits of the Mainz Basin and can be distinguished by ist typically pronounced basal keel (see also Harzhauser et al., 2014b). It differs from co-occurring *G. dalmaticus*, which has a prominent basal keel and a markedly higher whorl expansion rate. The record from Lučane by Neubauer et al. (2011) is based on a misidentification. The studied specimens differ from *G. geminus* in the distinctly higher whorl expansion rate and the relatively higher whorls; they rather correspond to *G. pulici* (Brusina, 1897) described from Gacko (Neubauer et al., 2013b).
Distribution: Drniš Basin (Miočić), Sinj Basin (Ruduša, Trnovača) (Brusina, 1884, 1897). The records from the Pannonian of Hungary by Wenz (1923) correspond to a different species. The mention from the Late Badenian (Early Serravallian) of Pusztamiske, Hungary, by Kókay (2006) is rather doubtful and needs verification.

Genus *Orygoceras* Brusina, 1882

Type species: *Orygoceras cornucopiae* Brusina, 1882 (currently considered as a synonym of *Orygoceras dentaliforme* Brusina, 1882). Middle Miocene; Dalmatia. Type by subsequent designation by Cossmann (1921).

***Orygoceras dentaliforme* Brusina, 1882**
Figure 8N–O, R

* 1882 *Orygoceras dentaliforme* nov. spec. – Brusina, p. 42, pl. 11, figs 9–15.
1882 *Orygoceras stenonemus* nov. spec. – Brusina, p. 43, pl. 11, figs 4–8.
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.
1897 *Orygoceras stenonemus* Brus. – Brusina, p. 2, pl. 1, figs 10–12.
1897 *Orygoceras dentaliforme* Brus. – Brusina, p. 2, pl. 1, figs 13–14.
1902 [*Orygoceras*] *curvum* [Brus.] – Brusina, pl. 2, figs 2–5.
1902 [*Orygoceras*] *bifrons* [Brus.] – Brusina, pl. 2, figs 6–14.
1902 [*Orygoceras*] *cornucopiae* [Brus.] – Brusina, pl. 2, figs 15–16.
1902 [*Orygoceras*] *euglyphum* [Brus.] – Brusina, pl. 2, figs 17–19.
1902 [*Orygoceras*] *leptonema* [Brus.] – Brusina, pl. 2, figs 20–22.
1907 *Orygoceras subula* n. sp. – Brusina, p. 219.
1928 *Orygoceras bifrons* Brusina – Wenz, p. 2484 [cum syn.].
1928 *Orygoceras cornucopiae* Brusina – Wenz, p. 2485 [cum syn.].
1928 *Orygoceras curvum* Brusina – Wenz, p. 2485 [cum syn.].
1928 *Orygoceras dentaliforme* Brusina – Wenz, p. 2485 [cum syn.].
1928 *Orygoceras euglyphum* Brusina – Wenz, p. 2486 [cum syn.].
1928 *Orygoceras leptonema* Brusina – Wenz, p. 2489 [cum syn.].
1928 *Orygoceras stenonema* Brusina – Wenz, p. 2490 [cum syn.].
1928 *Orygoceras subula* Brusina – Wenz, p. 2490 [cum syn.].
1974 *Orygoceras bifrons* Brusina – Milan et al., p. 113.
1974 *Orygoceras cornucopiae* Brusina – Milan et al., p. 113.
1974 *Orygoceras curvum* Brusina – Milan et al., p. 114.
1974 *Orygoceras dentaliforme* Brusina – Milan et al., p. 114.
1974 *Orygoceras euglyphum* Brusina – Milan et al., p. 114.
1974 *Orygoceras leptonema* Brusina – Milan et al., p. 115.
1974 *Orygoceras stenonema* Brusina – Milan et al., p. 115.
? 1988 *Orygoceras cornucopiae* Brusina – Jurišić-Polšak and Slišković, p. 170, 171.
2011 *Orygoceras cornucopiae* Brusina, 1882 – Neubauer et al., p. 213, pl. 6, fig. 7.
2011 *Orygoceras dentaliforme* Brusina, 1882 – Neubauer et al., p. 213, pl. 6, fig. 5.
2011 *Orygoceras stenonemus* Brusina, 1882 – Neubauer et al., p. 214, pl. 6, figs 6, 10.
2013a *Orygoceras dentaliforme* Brusina, 1882 – Neubauer et al., p. 146, figs 6D–E.
2013b *Orygoceras dentaliforme* Brusina, 1882 – Neubauer et al., fig. 10D.

non 1936 *Orygoceras cornucopiae* Brus. – Vitális, p. 637 (table).

Material: Several tens of largely fragmented specimens from each Miočić and Parčić (NHMW 2014/0315/0032, NHMW 2014/0315/0033, NHMW 2014/0315/0048, NHMW 2014/0315/0065, NHMW 2014/0315/0109, NHMW 2014/0315/0150, NHMW 2014/0315/0151, NHMW 2014/0315/0158, NHMW 2014/0315/0162, NHMW 2014/0315/0172, NHMW 2014/0315/0187, NHMW 2014/0315/0189, NHMW 2014/0315/0194); 1 fragment from Miočić 1 (NHMW 2014/0315/0001); 8 from Miočić (GBA 2008/006/036, GBA 2008/006/0037).
Type material: NHMZ 3574-1214/1a, NHMZ 3576-1216/1a (syntypes); both from Ribarić, Sinj Basin.
Dimensions (H x W): 6.90 x 1.25 mm (syntype; Brusina, 1882, pl. 11, figs 13–14); 4.72 x 0.72 mm (syntype; Brusina, 1882, pl. 11, figs 11–12); 7.51 x 1.24 mm (syntype of *O. cornucopiae*; NHMZ 2932-578; Miočić, Drniš Basin; Brusina, 1882, pl. 11, figs 1–3); 5.29 x 0.71 mm (syntype of *O. stenonemus*; NHMZ 3578-1218/1-2; Župića potok, Sinj Basin; Brusina, 1882, pl. 11, figs 4–5).
Description: Detailed descriptions are provided by Neubauer et al. (2011, 2013a, b).
Remarks: Following Neubauer et al. (2013a), we synonymize following species described from DLS deposits with *O. denta-*

liforme: *O. bifrons Brusina*, 1902, *O. cornucopiae* Brusina, 1882, *O. curvum* Brusina, 1902, *O. euglyphum* Brusina, 1902, *O. leptonema* Brusina, 1902, and *O. stenonemus* Brusina, 1882. Many of these are based on fragments and mostly minor differences in the expression of sculpture. After careful examination of the type material of all species, we consider them to be conspecific and the members to reflect local phenotypes. In the Drniš Basin, the phenotypes *dentaliforme* (smooth), *stenonemus* (with widely spaced rings), and *cornucopiae* (with densely spaced rings), latter of which is the most common, co-occur. *Orygoceras subula* Brusina, 1907 was overlooked by Neubauer et al. (2013a) and displays yet another phenotype, which was introduced for a part of the original material described and illustrated as *O. dentaliforme* by Brusina (1882); it is only known from Župića potok in the Sinj Basin.
The records from the Pannonian of Austria and Romania by Bittner (1888) and Vitális (1936) probably refer to different species.
Distribution: Drniš Basin (Miočić, Parčić), Gacko Basin (Gračanica, Vrbica), Glina Basin (Dugoselo), Prozor Basin (Džepi), Udbina Basin (Laudonov Gaj), Kupres Basin (Fatelj), Sinj Basin (Lučane, Ribarić, Strmendolac-Crveni klanac, Trnovača, Župića potok) (Brusina, 1882, 1884, 1897, 1902; Bittner, 1887; Jurišić-Polšak et al., 1993, 2000; Neubauer et al., 2013a, b). Its presence in the Late Miocene of Tomislavgrad Basin (Šuica gaz) and Livno Basin (Čelebić-Jaruga) indicated by Jurišić-Polšak and Slišković (1988) needs verification.

Genus *Planorbarius* Duméril, 1806

Type species: *Helix cornea* Linnaeus, 1758. Recent; Europe. Type by subsequent monotypy by Froriep (1806).

***Planorbarius mantelli* (Dunker, 1848)**
Figure 8K–M

* 1848 *Planorbis Mantelli*, Dkr. – Dunker, p. 159, pl. 21, figs 27–29.
1869 *Planorbis cornu* Brongniart – Neumayr, p. 366, pl. 12, fig. 21 [non *Planorbis cornu* Brongniart, 1810].
1874 *Planorbis cornu* Brongniart – Brusina, p. 100 [non Brongniart, 1810].
1923 *Coretus cornu mantelli* (Dunker) – Wenz, p. 1452.
? 2013b *Planorbarius* sp. – Neubauer et al., figs 11A–F.
2014a *Planorbarius mantelli* (Dunker 1848) – Harzhauser et al., p. 15, pl. 3, figs 5, 7–13, 15–16 [cum syn.].

Material: 6 specimens and several fragments from Miočić (NHMW 2014/0315/0079, NHMW 2014/0315/0099, NHMW 2014/0315/0100); 8 from Biočić (NHMW 2014/0315/0130); 18 from Miočić (GBA 2008/150/0009, GBA 2008/150/0010, GBA 1869/01/26; the latter was illustrated in Neumayr, 1869).
Type material: The details of the type material of Dunker (1848) are unknown.
Dimensions (H x W): 10.8 x 32.8 mm (specimen illustrated by Neumayr, 1869, pl. 12, fig. 21); diameter reaches up to 38 mm in specimens from Lake Rein (Harzhauser et al., 2014a).
Remarks: The specimen studied by Neumayr (1869) closely resembles *P. mantelli* described from other Middle Miocene localities (e.g., Harzhauser et al., 2014a). It fully matches regarding shape, whorl convexity, and size. The only difference is the absence of spiral striae in Neumayr's specimen, which could be a result of the moderate preservation. However, distinct striae are present on several of the juvenile specimens available from the same locality. Consequently, there is no doubt that the synonymization of "*Planorbis cornu*" as stated by Neumayr (1869) and Brusina (1874) with *P. mantelli* by Wenz (1923) is correct.
Maybe also the fragments from Gacko documented by Neubauer et al. (2013b) belong to this species. The characteristics are strikingly similar to typical *P. mantelli* (compare Harzhauser et al., 2014a).
Distribution: Within the DLS reported from the Drniš Basin (Biočić, Miočić) and the Sinj Basin (Ruduša) (Neumayr, 1869; Brusina, 1874, 1884). For the many other Miocene records see Wenz (1923) and Harzhauser et al. (2014a).

Superorder Eupulmonata Haszprunar and Huber, 1990
Infraorder Stylommatophora Schmidt, 1855
Non-achatinoid clade sensu Wade et al., 2006
Unassigned subclade Elasmognatha Mörch, 1864
Superfamily Succineoidea Beck, 1837
Family Succineidae Beck, 1837
Subfamily Succineinae Beck, 1837
Genus *Oxyloma* Westerlund, 1885

Type species: *Succinea hungarica* Hazay, 1880 [currently considered as a synonym of *Oxyloma dunkeri* (Pfeiffer, 1865)]. Recent; Hungary. Type by monotypy.

***Oxyloma drnisana* (Brusina, 1897) nov. comb.**
Figure 9M–N

1874 *Succinea elegans* Risso – Brusina, p. 95 [non *Succinea elegans* Risso, 1826].
1884 *Succinea drnisana* Brusina – Brusina, p. 59.
* 1897 *Succinea drnisana* Brus. – Brusina, p. 1, pl. 1, figs 5–6.
1923 *Succinea* (*Amphibina*) *drnišana* Brusina – Wenz, p. 891.
1974 *Succinea* (*Hydrotropa*) *drnisana* Brusina – Milan et al., p. 137.

Material: Type material only.
Type material: NHMZ 2931-577 (syntype); Miočić, Drniš Basin.
Dimensions (H x W): 9.33 x 4.77 mm (syntype, fragmentary; Brusina, 1897, pl. 1, figs 5–6; no complete specimen available).
Remarks: The species is based on insufficient, fragmentary material; more is needed to provide full descriptions and allow sound comparisons with other succineids. The difference to co-occurring *S. martinovici* is the conspicuously more slender morphology. The generic placement is provisional; the general shape fits well to *Oxyloma* as already indicated by previous authors, when placing it in *Amphibinia* and *Hydro-*

tropa, which are synonyms of *Oxyloma*.
The correct authorship of this species is "Brusina, 1897". Brusina (1884), when first applying the name to rectify a former misidentification, failed to provide a description or illustration. Hence, the 1884-work does not meet the requirements of Art. 12.1 of the Code, since the original discussion of this taxon (then misidentified as *S. elegans*) did not contain any description either. Brusina (1897) made the name available by providing illustrations.
Distribution: Endemic to the Drniš Basin (Miočić) (Brusina, 1884, 1897).

Genus *Succinella* Mabille, 1871

Type species: *Succinea oblonga* Draparnaud, 1801. Recent; Eurasia. Type by subsequent designation by Boettger (1947).

***Succinella martinovici* (Brusina, 1902) nov. comb.**
Figure 9O

1874 *Succinea oblonga* Draparnaud – Brusina, p. 95 [non *Succinea oblonga* Draparnaud, 1801].
1884 *Succinea Martinovići* Brusina – Brusina, p. 59.
* 1902 *Succinea Martinovići* [Brus.] – Brusina, pl. 1, fig. 4.
1923 *Succinea* (*Lucena*) *martinovići* Brusina – Wenz, p. 897.
1974 *Succinea* (*Hydrophyga*) *martinovici* Brusina – Milan et al., p. 137.

Material: Type material only.
Type material: NHMZ 2357-3 (syntype); Miočić, Drniš Basin.
Dimensions (H x W): 2.75 x 2.55 mm (syntype, fragmentary; Brusina, 1902, pl. 1, fig. 4; no complete specimen available).
Remarks: The species is based on insufficient, fragmentary

Figure 9: Terrestrial gastropods. (A–D) *Pseudochloritis schlosseriana* (Brusina, 1874). Specimen illustrated by Brusina (1897) (NHMZ 3569-1209/1), Miočić. (E–H) *Pseudochloritis schlosseriana* (Brusina, 1874). Miočić (NHMZ 576). (I–L) *Archaeozonites*? sp. Specimen invalidly designated as lectotype of *Megalotachea neumayri* (Brusina, 1878) by Milan et al. (1974) (NHMZ 3570-1210/3), Miočić. (M–N) *Oxyloma drnisana* (Brusina, 1897). Syntype (NHMZ 2931-577), Miočić. (O) *Succinella martinovici* (Brusina, 1902). Syntype (NHMZ 2357-3), Miočić. Scale bars correspond to 5 mm (A–L) and 1 mm (M–O).

material; more is needed to provide full descriptions and allow sound comparisons with other succineids. The generic placement is based on the bulbous spire whorls, which are rapidly increasing in width, thus being reminiscent of the extant *Succinella oblonga* (Draparnaud, 1801).
Here the same nomenclatural problem arises as for *O. drnisana* above. Brusina (1884) did not provide a description or illustration when first applying the name to rectify a former misidentification. Hence, the 1884-work does not meet the requirements of Art. 12.1 of the Code, since the original discussion of this taxon (then misidentified as *S. oblonga*) did not contain any description either. Brusina (1902) made the name available by providing illustrations.
Distribution: Drniš Basin (Miočić), Sinj Basin (Ruduša) (Brusina, 1884, 1902).

Unassigned "subclade" Limacoidea
Superfamily Zonitoidea Mörch, 1864
Family Zonitidae Mörch, 1864
Genus *Archaeozonites* Sandberger, 1875

Type species: *Archaeozonites subverticillus* Sandberger, 1875. Early Miocene; Germany. Type by subsequent designation, probably by Wenz and Zilch (1959) [Note: Wenz & Zilch (1959, p. 248) considered that the type is fixed by monotypy, but Sandberger (1875) clearly mentioned two species when introducing his new genus].

***Archaeozonites*? sp.**
Figure 9I–L

Material: Specimen invalidly designated as lectotype (NHMZ 3570-1210/3) of *Megalotachea neumayri* by Milan et al. (1974) (see below); 1 specimen from Biočić (NHMW 2014/0315/0129); 1 from Miočić 1 (NHMW 2014/0315/0001).
Dimensions (H x W): 10.41 x 16.07 mm (NHMZ 3570-1210/3); 9.97 x 16.97 mm (NHMZ 3570-1210/2).
Description: No complete shell exists, hindering a precise description. Shell low trochiform, consisting of ca. 4 weakly convex whorls. Sutures weakly incised. Last whorl exhibits pronounced angulation around mid-height, separating weakly convex upper and lower sides; latter grades into straight base; angulation never producing offset keel. Last whorl probably attains around 80 % of total height. Aperture not preserved. Umbilicus open but partly obscured by sediment. Whole shell covered with dense, distinct, rib-like prosocline growth lines.
Remarks: Sculpture and angulated outline fit well to *Archaeozonites* but the generic placement of this fragment and the relation to other species remain doubtful, due to the very poor preservation.

The late Early to Middle Miocene *Archaeozonites costatus* (Sandberger, 1875), as described by Gottschick and Wenz (1916) and Harzhauser et al. (2014a), lacks the strong angulation and has a wider umbilicus.
Distribution: Drniš Basin (Biočić, Miočić).

Unassigned subclade
Superfamily Helicoidea Rafinesque, 1815
Family Helicidae Rafinesque 1815
Genus *Megalotachea* Pfeffer, 1930

Type species: *Helix turonensis* Deshayes, 1831. Early Miocene; France. Type by subsequent designation by Truc (1971).

***Megalotachea neumayri* (Brusina, 1878) nov. comb.**
Figure 10A–C

1869 *Helix subcarinata* A. Braun – Neumayr, p. 365, pl. 12, fig. 20 [erroneously indicated as fig. 18 on plate captions] [non *Helix subcarinata* Menke, 1828].
1874 *Helix* [(*Macularia*)] *subcarinata* A. Braun – Brusina, p. 96 [non Menke, 1828].
* 1878 *Helix Neumayri*, Brusina – Brusina, p. 354.
1907 *Murella Neumayeri* [sic] Brus. 1878 – Brusina, p. 211.
1923 *Cepaea neumayri* (Brusina) – Wenz, p. 646 [partim].
1974 *Cepaea neumayri* (Brusina) – Milan et al., p. 104.
1980 [*Cepaea*] *neumayri* (Brusina, 1878) – Richardson, p. 282.

Material: None.
Type material: Milan et al. (1974) designated a lectotype (NHMZ 3570-1210/3) from the type locality Miočić. First, this procedure is not valid, since they did not refer to a specific syntype (maybe not even to a specimen from the original material of Brusina, 1878; see ICZN, 1999, Art. 74.5). Second, the specimen does not correspond to the illustration in Neumayr (1869), for which the name *Helix neumayri* was actually introduced (Brusina, 1878). It particularly differs in the presence of an umbilicus, which is indicated to be fully overgrown in the specimen illustrated in Neumayr (1869). The material of Neumayr (1869) is not available; the respective box in the GBA collection is empty and the specimen is not detectable.
Dimensions (H x W): 12.5 x 19.5 mm (estimated after illustrations in Neumayr, 1869).

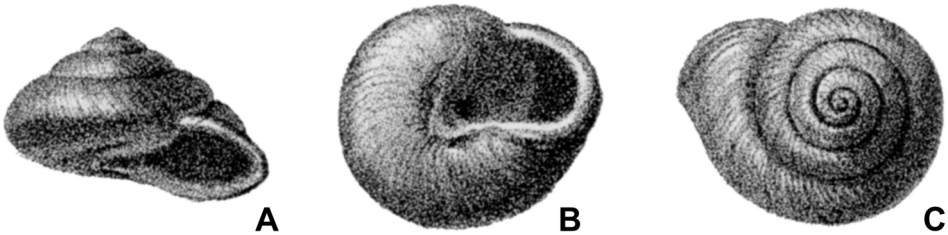


Figure 10: (A–C) Facsimile reproduction of "*Helix subcarinata* A. Braun" illustrated by Neumayr (1869, pl. 12, fig. 20) [= *Megalotachea neumayri* (Brusina, 1878)]. Mind the confusion of the figure captions for the plate. All figures are scaled to 1.5 times of their originally illustrated size, which reflected the actual size of the specimens.

Description: Medium-sized shell comprising ca. 4 teleoconch whorls with moderately high, conical spire and slightly angulated and low last whorl. Base weakly convex; last whorl distinctly widening close to markedly prosocline aperture, forming flaring peristome with well-defined outer lip. Umbilicus fully covered by thin but wide callus.
Remarks: The material illustrated by Neumayr (1869) seems to be lost and the description is based on the figures. According to these, the species seems to represent a *Megalotachea*. It is reminiscent of the Early Miocene *Megalotachea macrocheila* (Reuss in Reuss & Meyer, 1849), as described by Harzhauser et al. (2014b), concerning the flaring peristome and the thin but wide umbilical callus. A clear difference is the lower last whorl and the weak angulation of *M. neumayri*.
Lueger (1981) tentatively synonymized *M. neumayri* (Brusina, 1878) with the Pannonian "*Cepaea*" *etelkae* (Halaváts, 1925), based on the assumption that the former name is a nomen dubium. Lueger (1981) stated that no type was fixed and the definition and illustration by Neumayr (1869), which was used as basis for the introduction of *M. neumayri* by Brusina (1878), are insufficient. The species, however, is still valid since indicated and illustrated properly; and before 2000 the default of a type fixation was not a limiting criterion (ICZN, 1999, Art. 72.2). Moreover, the globular "*Cepaea*" *etelkae* has little in common with *M. neumayri* and the synonymization of Lueger (1981) is obviously wrong. "*Helix subcarinata* A. Braun" referred to by Neumayr and Brusina is a nomen nudum. Moreover, the name is a primary homonym of the recent Helix subcarinata Menke, 1828. Wenz (1923) lists the fossil species as synonym of "*Cepaea*" *subglobosa subsoluta* (Sandberger, 1858), which clearly differs from *M. neumayri* in its higher spire and the less flaring apertural margin. Wenz (1923) synonymized *Helix baconicus* Halaváts, 1903 from the late Pannonian of Hungary with *M. neumayri*. Aside from the stratigraphic gap of more than 5 Ma separating both species, the Hungarian shell differs in its more convex base, lower spire and weaker umbilical callus.
Distribution: Drniš Basin (Miočić), Sinj Basin (Ruduša) (Brusina, 1884).

Family Elonidae Gittenberger, 1979
Genus *Pseudochloritis* C. Boettger, 1909

Type species: *Helix inflexa* Klein, 1846. Miocene; Germany. Type by original designation.

***Pseudochloritis schlosseriana* (Brusina, 1874)**
Figure 9A–H

1869 *Helix* cf. *Turonensis* Deshayes – Neumayr, p. 365, pl. 12, fig. 18 [erroneously indicated as fig. 20 on plate captions].
* 1874 *Helix* [(*Macularia*)] *Schlosseriana* Brusina – Brusina, p. 97.
1897 *Helix* (*Chloritis*) *Schlosseriana* Brus. – Brusina, p. 1, pl. 1, figs 3–4.
1923 *Cyrtochilus schlosserianum* (Brusina) – Wenz, p. 502.
1974 *Trophidomphalus* (*Pseudochloritis*) *schlosseriana* (Brusina) – Milan et al., p. 67.
1980 [*Cyrtochilus*] *schosseriana* [sic] (Brusina, 1874) – Richardson, p. 47.

Material: Specimen illustrated by Brusina (1897) and a single specimen from Miočić (NHMZ 576).
Type material: Details of type material unknown (type locality: Miočić, Drniš Basin). It is uncertain whether the specimen illustrated by Brusina (1897) and indicated as holotype by Milan et al. (1974) (NHMZ 3569-1209/1) are part of the original material of Brusina (1874) or derive from newly collected material. The material of Neumayr (1869), for which the name was actually introduced, is not available; the respective box in the GBA collection is empty and the specimen is not detectable.
Dimensions (H x W): 17.34 x 24.88 mm (NHMZ 3569-1209/1); 19.42 x 25.36 mm (NHMZ 576; Brusina, 1897, pl. 1, figs 3–4).
Description: Low trochiform shell, consisting of 3.8 moderately convex whorls. Sutures moderately incised. Last whorl regularly convex, with whorl flank exposing a perfectly semicircular profile; attains 85 % of total height. Aperture strongly inclined, reflected, strongly thickened; outer lip semicircular, anteriorly broadly fused with base; umbilicus thereby fully covered.
Remarks: The species is reminiscent of *P. incrassatus* (Klein, 1853) from coeval deposits of Central Europe. *Pseudochloritis schlosseriana* differs in the stronger thickening and distinct reflection of the peristome, resulting in a full cover of the umbilicus. Also, shells are higher trochiform and have a higher, more rounded last whorl. We follow Binder (2008) and Harzhauser et al. (2014a), who treated *Pseudochloritis* as separate genus.
Distribution: Endemic to the Drniš Basin (Miočić) (Brusina, 1874, 1884, 1897).

Class Bivalvia Linnaeus, 1758
Superorder Heterodonta Neumayr, 1883
Order Venerida Gray, 1854
Family Dreissenidae Gray in Turton, 1840

Remarks: Recent molecular genetic studies (Stepien et al., 2003; Therriault et al., 2004; Albrecht et al., 2007; Bilandžija et al., 2013) challenge the evidence from the fossil record (Nuttall, 1990; Müller et al., 1999; Harzhauser and Mandic, 2010) and indicate that the absence of the apophysis is a plesiomorphic state. However, this might be true for the extant clades included in those phylogenetic studies, but does not apply to the entire family. For the extinct dreissenid subfamily Dreissenomyinae Harzhauser and Mandic (2004) documented the progressive, apophysis loss being a clear consequence of the adaptation to an infaunal mode of life. In the present study, we use the evidence for the monophyly of the apophysis-lacking epifaunal representatives (Stepien et al., 2001; Therriault et al., 2004) to redefine the subfamily Dreisseninae Gray in Turton, 1840 sensu Nuttall (1990). In particular, we exclude all apophysis-bearing dreissenids missing the mantle sinus from the

Dreisseninae and classify them within the new subfamily Congeriinae.

Subfamily Dreisseninae Gray in Turton, 1840

Genus *Dreissena* Van Beneden, 1835

Type species: *Mytilus polymorphus* Pallas, 1771. Recent; Caspian Sea (recently introduced to Western Europe and North America). Type by monotypy.

Remarks: The genus includes all mytiliform, epifaunal Dreisseninae. *Dreissena cymbula* Brusina, 1892 represents the oldest known member of the genus.

***Dreissena cymbula* Brusina, 1892**

Figure 11E–G

1874 *Dreissena* sp. – Brusina, p. 126.

* 1892 [*Dreissensia*] *cymbula* Brusina n. sp. Mss. – Brusina, p. 199.

1897 *Dreissensia cymbula* Brus. – Brusina, p. 31, pl. 17, figs 16–18.

? 1897 *Congeria* (?) *cymbula* Brus. – Andrusov, p. 233, pl. 36, figs 39–40.

1902 [*Dreissensia*] *cymbula* [Brus.] – Brusina, pl. 21, figs 82–85.

1974 *Dreissensia cymbula* Brusina – Milan et al., p. 34.

1993 *Dreissena cymbula* (Brusina) – Jurišić-Polšak et al., p. 216, pl. 4, figs 2–3.

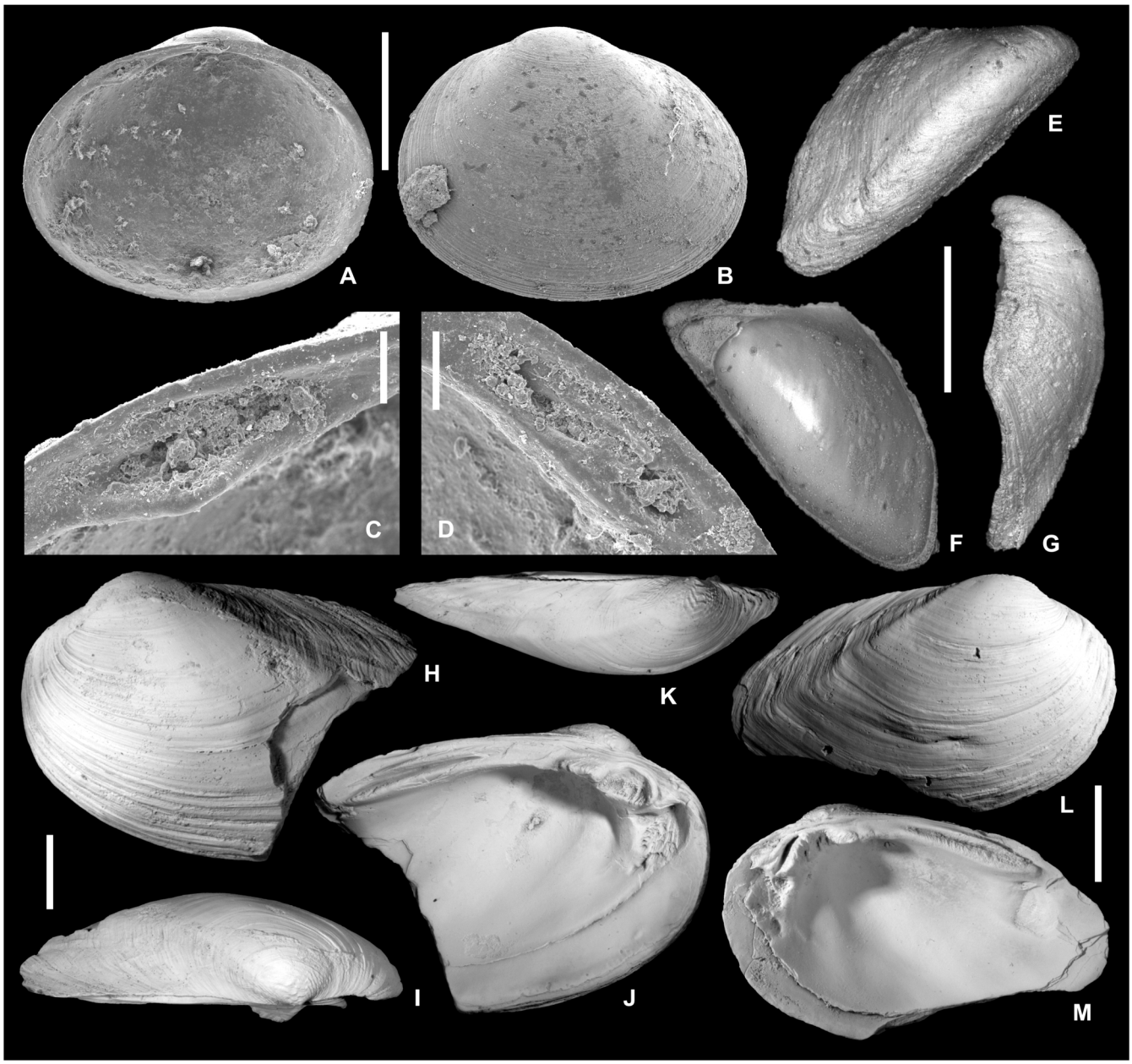


Figure 11: Sphaeriid, dreisseninae and unionid bivalves. (A–D) *Pisidium bellardii* Brusina, 1884. RV, Miočić (NHMW 2014/0315/0034). (E–G) *Dreissena cymbula* Brusina, 1892. Specimen illustrated by Brusina (1902) (NHMZ 2816-462/1-6), Miočić. (H–J) *Unio rackianus* Brusina, 1874. Syntype (Brusina, 1874, pl. 5, fig. 9; NHMZ 3232-878/1), Miočić. (K–M) *Unio rackianus* Brusina, 1874. Syntype (Brusina, 1874, pl. 5, fig. 10; NHMZ 3232-878/2), Miočić. Scale bars correspond to 10 mm (H–M), 1 mm (A–B, E–G), and 100 µm (C–D).

Material: 2 left valves from Miočić (NHMW 2014/0315/0207) and 1 previously not illustrated right valve from the collection of Brusina (1902) (NHMZ 2816-462/1-6).
Type material: Single left valve from Miočić illustrated by Brusina (1897, pl. 17, figs. 16–18; syntype, NHMZ 3152-798). However, it could not be located in the NHMZ type collection.
Dimensions (L x W): 2.49 x 1.21 mm (Fig. 11E–G; NHMZ 2816-462/1-6).
Description: Shell narrowly mytiliform, minute in size. Anterior margin straightened, dipping posteriorly by ~55°; ventral margin narrowly convex, pointing posteroventrally; posterior margin dorsally straightened, subparallel to anterior margin, then broadly convex in its ventral portion. Shell convexity moderate, with the summit shifted slightly into dorsal direction. In cross-section perpendicular to dorsal margin, it is subtrigonal with steep anterior and shallower posterior side. Central longitudinal keel slightly sigmoidal in exterior view. Shell exterior smooth except for growth lines slightly projecting at distal shell portion. Umbo prosogyrate, slightly ventrally bended. Proximal shell portion inflated, projecting slightly over hinge line. Septum large, attaining about 30 % of shell height.
Remarks: When describing the Pannonian fauna of the Zagreb area, Brusina (1892) also mentioned "*Dreissensia cymbula*" from Miočić as a new species. Although he referred to the illustrations of the then unpublished manuscript of his monograph (Brusina, 1897), he made the name available by providing a short description. *Dreissensia* Bronn, 1862 is an incorrect subsequent spelling of *Dreissena* (ICZN, 1955, Op. 351).
This species is the only certain *Dreissena* recorded for the DLS. The second one, *Dreissena*? *gasperinii* Brusina, 1907 (= *Dreissena* sp. Brusina 1874; NHMZ3271-911/1-3) from Čugurina glavica in Sinj, is based on molds only and the absence of the apophysis cannot be ascertained. The record of Andrusov (1897, 1898) remains uncertain since he noted the presence of an apophysis in specimens he originally investigated, but later became aware that Brusina (1897, 1907) considered this species to miss the apophysis, i.e., classified it as a real *Dreissena*.
Distribution: Drniš Basin (Miočić), Udbina Basin (Laudonov Gaj) (Brusina, 1892, 1897, 1902; Jurišić-Polšak et al., 1993).

Subfamily Congeriinae Mandic and Harzhauser nov. subfam.

Type genus: *Congeria* Partsch, 1836. Late Miocene; Central and Southeastern Europe.
Diagnosis: Dreissenidae with apophysis, but missing mantle sinus.
Remarks: The group ranges from the Eocene to Recent and includes all apophysis-bearing dreissenids without a mantle sinus. The Recent members encompass the North American *Mytilopsis* and the troglodytic ("*Congeria*" sensu Bilandžija et al., 2013) in SE Europe. The two main diversity peaks of the Congeriinae result from two main radiation events – the first in the Early to Middle Miocene Dinaride Lake System and the second in the Late Miocene Lake Pannon (Harzhauser and Mandic, 2010).
While the genus-level taxonomy of European Congeriinae is poorly constrained, all its American fossil and Recent members can be classified with *Mytilopsis*. The molecular clock analysis recently suggested *Mytilopsis* to be a sister group of the European Congeriinae with the divergence age ranging between 34.4 and 11.6 Ma (Bilandžija et al., 2013). Such a range can be interpreted in many different ways, but it coincides apparently well with the timing of their westwards migration, which is well constrained through oldest fossil representatives found in the Upper Oligocene deposits of Central and tropical South America (Nuttall, 1990). As a consequence, we consider the genus *Mytilopsis* to be restricted to the New World. Fossil European species previously attributed to this genus (Harzhauser and Mandic, 2010) have to be classified with Amygdalia Nevesskaja in Nevesskaja et al., 2013, *Andrusoviconcha* Starobogatov, 1970 (which has been lately treated as junior synonym of *Mytilopsis* by Nevesskaja et al., 2013).

Genus Andrusoviconcha Starobogatov, 1970

Type species: *Congeria modiolopsis* Andrusov, 1897 (currently considered as a synonym of *Congeria panticapaea* Andrusov, 1897 after Nevesskaja et al., 2013). Late Miocene, Maeotian; Crimean Peninsula. Type by original designation.

***Andrusoviconcha jadrovi* (Brusina, 1892) nov. comb.**
Figure 12Q–V

* 1892 [*Congeria*] *Jadrovi* Brusina n. sp. Mss. – Brusina, p. 197.
1897 *Congeria Jadrovi* Brus. – Brusina, p. 30, pl. 17, figs 12–14.
1902 [*Congeria*] *Jadrovi* [Brus.] – Brusina, pl. 21, figs 2–5.
1974 *Congeria jadrovi* Brusina – Milan et al., p. 28.
1978 *Congeria jadrovi* (Brusina, 1897) – Kochansky-Devidé and Slišković, p. 37, 87, pl. 1, figs 26–32, textfigs 3.1–3 [cum syn.].

Material: 1 articulated specimen and 1 fragment from Miočić (NHMW 2014/0315/0040, NHMW 2014/0315/0210), > 40 fragmented specimens from Parčić (brook) (NHMW 2014/0315/0042, NHMW 2014/0315/0208), > 50 fragmented specimens from Parčić (NHMW 2014/0315/0041, NHMW 2014/0315/0209).
Type material: Milan et al. (1974) designated the specimen illustrated by Brusina (1897, pl. 17, figs 12–13) from Trnovača (Sinj Basin) as lectotype (NHMZ 3150-796/1). However, the specimens stored under that collection number – one complete left valve from Trnovača indicated as lectotype and one anterior fragment of a left valve from Župica potok referred to the illustration in Brusina (1897, pl. 17, fig. 14) – do not correspond to the figures in Brusina (1897). Additional material has not been found in the collection.
Dimensions (L x H x C): 8.6 x 7.3 x 2.3 mm (LV of the articulated specimen on figs 12Q–R). The largest specimen was reported by Kochansky-Devidé and Slišković (1978) from the Drniš Basin (no locality indicated), attaining a size of 9.0 x 4.0 x 2.2 mm (note that their specimen was probably differently oriented, i.e., with the keel placed vertically).

Remarks: Similar to the situation of *Dreissena cymbula* above, Brusina (1892) mentioned "*Congeria Jadrovi*" from the Sinj Basin as new species. Although he referred to the illustrations of the then unpublished manuscript of his monograph (Brusina, 1897), he made the name available by providing a short description. More detailed descriptions and comparisons are provided by Kochansky-Devidé and Slišković (1978) and Neubauer et al. (2011, 2013b: suppl. online material).

A longitudinal ledge is mostly present and forms a sharply pointed ventral margin. This feature appears to provide the only straight-forward differentiation toward the ledge-less but otherwise highly similar *Andrusoviconcha neumayri* (An-

Figure 12: Congeriinae bivalves. (A–D) *Illyricocongeria moirae* nov. gen. nov. sp. Holotype, articulated specimen (NHMW 2014/0315/0036), Miočić. (E–K) *Illyricocongeria moirae* nov. gen. nov. sp. Paratype, anterior LV fragment (NHMW 2014/0315/0037), Miočić. (L) *Illyricocongeria aletici* (Brusina, 1907). Parčić (NHMW 2014/0315/0038). (M–N) *Illyricocongeria aletici* (Brusina, 1907). Parčić (NHMW 2014/0315/0122). (O) *Illyricocongeria aletici* (Brusina, 1907). Parčić (NHMW 2014/0315/0125). (P) *Illyricocongeria aletici* (Brusina, 1907). Parčić (NHMW 2014/0315/0128). (Q–R) *Andrusoviconcha jadrovi* (Brusina, 1892). Articulated specimen (NHMW 2014/0315/0040), Miočić. (S–T) *Andrusoviconcha jadrovi* (Brusina, 1892). RV fragment (NHMW 2014/0315/0041), Parčić. (U–V) *Andrusoviconcha jadrovi* (Brusina, 1892). RV fragment (NHMW 2014/0315/0042), Parčić (brook). Scale bar corresponds to 1 mm (A–I, L–N) and 0.1 mm (J–K, O–V).

drusov, 1897) from the Lower Miocene of Laa an der Thaya in NE Austria.

Distribution: Drniš Basin (Biočić, Kadina glavica, Miočić), Gacko Basin (Gračanica), Glina Basin (Utinja), Prozar Basin (Čelebići), Požega Basin (Rogoljica), Prijedor Basin (Marini, Mala/Velika Žuljevica), Sinj Basin (Bila glavica near Trilj, Lučane, Sveta Kata, Trnovača, Župića potok), Tomislavgrad Basin (Eminovo Selo), Zenica-Sarajevo Basin (Čajdraš, Blažuj) (Kochansky-Devidé and Slišković, 1978; Neubauer et al., 2011, 2013b).

Andrusoviconcha nitida (Kochansky-Devidé in Kochansky-Devidé and Slišković, 1978) nov. comb.

* 1978 *Congeria nitida* n. sp. – Kochansky-Devidé in Kochansky-Devidé and Slišković, p. 35, 87, pl. 1, figs 1–20, textfigs 3.6–8.

Material: None.

Type material: Mold of a left valve embedded in limestone (NHMS 3710); Vučipolje near Duvno (= Tomislavgrad), Tomislavgrad Basin.

Dimensions (L x H x C): 8.9 x 5.7 x ca. 1.2 mm (holotype; Kochansky-Devidé and Slišković, 1978, pl. 1, fig. 1); the largest specimen attains 12 mm in length (for more data see Kochansky-Devidé and Slišković, 1978).

Remarks: The species was described from the Tomislavgrad Basin, but stated to be widespread throughout the DLS. Kochansky-Devidé and Slišković (1978) also mentioned it from the "Petrovo polje" (= Drniš Basin), but without providing an exact locality. For a detailed description of the species see there. We have not detected it during this study, but list it as a matter of completeness.

Distribution: Kochansky-Devidé and Slišković (1978) list following basins (largely without indication of localities): Banja Luka, Derventa, Drniš, Drvar, Duvno (= Tomislavgrad), Glina (Utinja, Sjeničak), Hodovo (Rotimlja near Stolac), Konjic, Prnjavor, Sinj.

Genus *Illyricocongeria* Mandic nov. gen.

Type species: *Congeria aletici* Brusina, 1907. Middle Miocene, Langhian; Dalmatia.

Etymology: After the ancient Roman province Illyricum encompassing the territory of the taxon's geographic distribution.

Diagnosis: Congeriinae with the shell anteriorly protruded beyond the umbo and the exterior longitudinal projecting ledge present at least in early ontogeny.

Description: Strongly inequilateral, heteromyarian shell with more or less restricted anterior margin projecting always dorsally beyond umbo. Shell wall rather thin, outline modiolid, subtrapezoidal, rhomboidal or circular. Hinge apparatus toothless, with at least residual septum bearing anterior adductor scar and posteriorly from it at least rudimental apophysis with byssal protractor muscle scar. Umbo prosogyrate, smooth for first 0.5 mm. Thereafter, a more or less projecting fine longitudinal ledge appears, which may be restricted to early ontogeny or, more commonly, reaches posteroventral shell margin, dividing the shell into anterior and posterior area. Shell exterior smooth except for concentric undulations (growth rugae) and growth lines.

Affiliated species: *Illyricocongeria acuta* (Kochansky-Devidé in Kochansky-Devidé and Slišković, 1981), *I. aletici* (Brusina, 1907), *I. avis* (Kochansky-Devidé in Kochansky-Devidé and Slišković, 1981), *I. bosniaca* (Katzer, 1913), *I. bosniaca acuticostata* (Kochansky-Devidé in Kochansky-Devidé and Slišković, 1981), *I. clivunensis* (Kochansky-Devidé in Kochansky-Devidé and Slišković, 1981), *I. cor* (Kochansky-Devidé in Kochansky-Devidé and Slišković, 1978), *I. cvitanovici* (Brusina, 1907), *I. dalmatica* (Brusina, 1874), *I. drvarensis* (Toula, 1913), *I. frici* (Brusina, 1904), *I. fuchsi* (Pilar, 1873), *I. katzeri* (Kochansky-Devidé in Kochansky-Devidé and Slišković, 1978), *I. novica* (Kochansky-Devidé in Kochansky-Devidé and Slišković, 1978), *I. obliqua* (Kochansky-Devidé in Kochansky-Devidé and Slišković, 1978), *I. pernaeformis* (Andrusov, 1897), *I. pikijae* (Kochansky-Devidé, 1979), *I. scaphula* (Brusina in Andrusov, 1897), *I. stojcicae* (Kochansky-Devidé in Kochansky-Devidé and Slišković, 1978), *I. volucris* (Kochansky-Devidé in Kochansky-Devidé and Slišković, 1978), and tentatively also *I.*? *soklici* (Kochansky-Devidé in Kochansky-Devidé and Slišković, 1978).

Remarks: The type species of the genus has been previously placed together with two other species (*I.*? *soklici* and *I. frici*) by Kochansky-Devidé and Slišković (1978, 1981) into their Luciniformes species-group encompassing the low convex dreissenids of circular outline endemic to DLS. Whereas *I. frici* is a certain member of the genus, the combination of *Illyricocongeria*? *soklici* remains uncertain, because its hinge is not known at present and the proximal ledge seems to be absent.

Other members of *Illyricocongeria* according to the present taxonomic concept have been previously associated by Kochansky-Devidé and Slišković (1978, 1981) to the different species-groups of Andrusov (1897), i.e., Mytiliformes (*I. novica*), Modioliformes (*I. acuta*, *I. avis*, *I. clivunensis*), Subglobosae (*I. cvitanovici*, *I. dalmatica*, *I. drvarensis*, *I. fuchsi*, *I. katzeri*, *I. obliqua*, *I. pikijae*, *I. scaphula*), Rhomboideae (*I. pernaeformis*), and Eocaenae (*I. bosniaca*, *I. bosniaca acuticostata*, *I. cor*, *I. stojcicae*, *I. volucris*). Except for the Eocaenae, which include ancestral Paleogene members, the other species-groups were originally defined for classifying the Congeriinae after general shape and outline (Andrusov, 1897). However, it has been shown that these groups are largely polyphyletic, only uniting species with a common mode of life (Harzhauser and Mandic, 2004, 2010).

Illyricocongeria, in contrast, represents a monophyletic species-group reflecting the Early to Middle Miocene endemic radiation in the Dinaride Lake System (Harzhauser and Mandic, 2010; De Leeuw et al., 2012). Different shell shapes reflect different niches (life-styles) that have been accommodated during that radiation. Additionally to the endemic distribution, tentatively reflecting a restricted genetic pool, with most taxa predating the Lake Pannon radiation, we argue that the shared morphological features – particularly the anterior shell protru-

sion combined with the longitudinal projecting ledge, restricted to Miocene Dinaride basin species – allow a straightforward definition of the genus and provide reasonable evidence on the presumed monophyly.

The members of *Illyricocongeria* previously classified as "*Subglobosae*" might have given rise to the Late Miocene *Congeria* as postulated already by Andrusov (1897), but the actual fossil and stratigraphic evidence do not clearly favor a potential candidate for a direct ancestor. Both genera are morphologically and paleogeographically well separated. *Congeria* tentatively originated through invention of a chemosymbiontic mode of life resulting in extremely thickened shell-walls (Harzhauser and Mandic, 2004). In contrast, all *Illyrocongeria* are relatively thin-walled. Beyond that, *Congeria* has a completely reduced anterior shell margin never projecting dorsally beyond the umbo. Finally, *Congeria* is restricted to Lake Pannon, whereas *Illyricocongeria* was endemic to the Dinaride realm. Stratigraphically, the two genera co-existed in the Late Miocene. The youngest *Illyricocongeria* species (*I. avis*, *I. bosniaca acuticostata*, *I. brevisosta*, and *I. clivunensis*) were found in Upper Miocene deposits of the residual Dinaride basins of Livno and Tomislavgrad (Kochansky-Devidé and Slišković, 1981). They possibly lived there until the Pliocene desiccation event (De Leeuw et al., 2011). Yet, the troglodytic Congeriinae in the Recent Dinarides surviving this event (Bilandžija et al., 2013; Morton and Puljas, 2013) shows different morphological features than *Illyricocongeria* and *Congeria*. Therefore, their classification with any of them is unlikely. Possibly, we deal here with a new, still unnamed genus.

Distribution: Restricted to the Illyrian Region – Early to Middle Miocene Dinaride Lake System and the residual Late Miocene lakes of Livno and Tomislavgrad.

Illyricocongeria aletici (Brusina, 1907) nov. comb.

Figure 12L–P

1905 *Congeria Aletići* Brus. n. sp. – Brusina, p. 35 [nomen nudum].
*1907 *Congeria Aletići* n. sp. – Brusina, p. 222.
1978 *Congeria aletici* n. sp. – Kochansky-Devidé and Slišković, p. 61, pl. 11, figs 10–15, pl. 12, figs 1–2, text-fig. 8/1–3.
1981 *Congeria volucris bicostata* n.sp. – Kochansky-Devidé and Slišković, p. 12, 22, pl. 3, figs 11–19.
2011 *Mytilopsis aletici* (Brusina 1907) – Neubauer et al., p. 215, pl. 7, fig. 8.
2013a *Mytilopsis aletici* (Brusina, 1907) – Neubauer et al., p. 147, figs 9A–G.

Material: 5 fragments of the umbonal area of left valves from Parčić (NHMW 2014/0315/0038, NHMW 2014/0315/0211, NHMW 2014/0315/0122, NHMW 2014/0315/0125, NHMW 2014/0315/0128): one with complete umbonal ledge, two displaying the hinge area, and two with interior sides embedded in gray silty marl also bearing *Pseudodianella haueri*.

Type material: Brusina's (1907) syntypes from Kalina/Košute have not been found at NHMZ.

Dimensions: Only fragments are available; the largest one comprising the proximal left shell area is about 20 x 20 mm in size, the length of the projecting umbonal posteroventral ridge is 10 mm.

Remarks: Descriptions are provided in Brusina (1907), Kochansky-Devidé and Slišković (1978) and Neubauer et al. (2011, 2013a). Kochansky-Devidé and Slišković (1978) erroneously deemed the designation by Brusina (1907) to be invalid because of an absent figure. They provided a new species designation with a "holotype" coming presumably from the type stratum outcropped in the neighboring quarry Brnaze. As long as the syntypes are missing, those specimens available in the NHMZ provide the best reference for the feature complex included. We lean additionally our taxonomic concept on careful differential analyses provided by former authors, allowing reasonable differentiation toward closely related *I. frici*, *I. drvarensis*, and *I. dalmatica* (see also Neubauer et al., 2011, 2013a). Better preserved material is nevertheless urgently needed to shed more light on their actual relationships.

Our identification follows comparison of the available fragments with the material from Fatelj (Kupres Basin; Neubauer et al., 2013a) and is based on a short longitudinal umbonal ledge excluding its classification as *I. drvarensis*. In particular, the available umbonal shell portions reveal an anterior shell area much larger than in *I. frici* or in any other dreissenid except for the Late Miocene infaunal *Dreissenomya schroeckingeri* (Fuchs, 1870). The present record represents its first documentation in the Drniš Basin. However, considering the extraordinary similarity of the fauna with that of the Sinj Basin, its presence is not surprising.

Distribution: Drniš Basin (Miočić), Kupres Basin (Fatelj), Sinj Basin (Košute/Kalina, Brnaze, Lučane) (Kochansky-Devidé and Slišković, 1978; Neubauer et al., 2011, 2013a).

Illyricocongeria moirae Mandic nov. sp.

Figure 12A–K

Material: 16 valves from Miočić: one articulated specimen (holotype, NHMW 2014/0315/0036); one left and three right anterior valve fragments (NHMW 2014/0315/0212); three left (including paratype), one right anterior, and two posterior (probably right and left) valve fragments (NHMW 2014/0315/ 0213); four left and one right anterior valve fragment (NHMW 2014/0315/ 0045). > 11 valve fragments from Biočić: one mold of a left valve missing most of the anterior portion (NHMW 2014/0315/ 0102), more than 10 internal and external molds on four charophyte limestone specimens (NHMW 2014/0315/ 0103).

Type material: The holotype (Figs 12A–D) is one articulated specimen, NHMW 2014/0315/0036, 21.8 mm in length (anterior protrusion not preserved), 22.2 mm in height, and 12.9 mm in shell convexity. The paratype (Figs 12E–K) is a fragment of the anterior part of a left valve with the complete hinge apparatus preserved, NHMW 2014/0315/0037, 17.1 mm (fragmented) in length, 14.7 mm (fragmented) in height, and 7.0 mm shell convexity.

Dimensions (L x H): From the type locality, no complete specimens are available except for the holotype. From Biočić, the NHMW stocks samples of the charophyte stem and oogonian limestone with numerous juvenile and young adult specimens (NHMW 2014/0315/0103). Dimensions of largest complete specimens are 13.1 x 11.3 mm, 10.7 x 8.8 mm, and 7.7 x 8.7 mm.
Type locality: Miočić NE Drniš in Dalmatia (S Croatia).
Type stratum: Lower Langhian (lower Middle Miocene).
Etymology: The new species is named after Moira Mandic, the daughter of one of the authors.
Diagnosis: Small-sized, modiolid, proximally inflated, distally flattened *Illyricocongeria* with smooth exterior, steep convex anterior side, concave shallow, broadly rounded, wing-like protruding posterodorsal side, large septum, and thin resilium.
Description: Shell small, approximately as high as long, reaching 22.2 mm in length in largest specimen. Outline inequilateral, modiolid subtriangular to suboval, anterodorsally pointing, ventrally subvertical, broadly rounded, posteroventrally narrowly rounded, anteroventrally straightened with corresponding margin dipping at ~65°. Umbo pointed, distinctly prosogyrate. Proximal shell broadly inflated; distal shell portions flattened. In anterior view, shell moderately convex with inflation attaining 30% of height. Convexity inequilateral with maximum placed at ~30 % of height; dorsal shell projection over hinge line reaching ~4% of height. Anterior shell area convex, dorsally steep, ventrally flattening. Central shell area convex, oblique, with convexity maximum in anterior shell half. Posterior shell area dorsally concave, ventrally flattened. On every available left valve, fine, up to 5 mm long, very sharp, slightly projecting longitudinal ledge present, starting at ~0.5 mm of growth; on single right valve showing proximal portion it is absent (or not preserved). Distinct keel can continue distally from ledge by about 5 mm. Shell exterior smooth except for narrow concentric undulations (growth rugae) and fine growth lines. Growth lines projecting on the anteriormost shell area. Hinge apparatus large, deep, subtriangular, anteriorly pointed septum, enclosed by wall-like anterior shell margin; continuing lobe-like beneath dorsal shell margin. Space between dorsal shell margin and dorsal wall of septum, showing narrowly concave, anteriorly adjoining umbo, is ventrally gaping, adjoining dorsally very thin ventral margin of resilifer. Resilifer solid but narrow, distally elongated, slightly sagittally bended, with sharp anterior end adjoining dorsal shell margin at dorsal projection of apophysis. Latter is integrated in posterodorsal outer margin of septum and very slightly posteroventraly projecting. Byssal retractor scar large, deep, laterally elongated, starting posteriorly from adductor scar. Latter large-sized, deep, subtriangular, anteriorly pointing, with tip projecting anteriorly from umbo.
Remarks: The new species is closely related to *Illyricocongeria fuchsi* (Pilar, 1873) but has at least two times larger anterior adductor muscle scar and septum, respectively. Beyond that, it has much thinner resilifer (= apophysis) and narrower ligamental suture. Additionally, the angle between dorsal and anteroventral margins of the septum is obtuse in the investigated specimens of *I. fuchsi* from the type locality (Dugoselo, NHMZ 1037), while it is acute in *I. moirae*. The complete outline of *I. fuchsi* is unknown at present, but the posterodorsal area seems to be stronger wing-like protruded in *I. moirae*. The age of Dugoselo in the Glina Basin has been constrained through Ar/Ar dating by Mandic et al. (2012) to about 16 Ma, so slightly older than the Miočić deposits.
Other related species are *I. obliqua* (Kochansky-Devidé in Kochansky-Devidé and Slišković, 1978) from Lješljane (Prijedor Basin, NW Bosnia and Herzegovina) and *I. dalmatica* (Brusina, 1874) from Ribarić near Potravlje (Sinj Basin). They both differ in the anterodorsally elongated shape. Moreover, the former has a sharp longitudinal keel, whereas the latter possess a tiny but sharp longitudinal ledge up to the posteroventral shell margin.
Distribution: Drniš Basin (Miočić, Biočić).

Family Sphaeriidae Deshayes, 1854
Subfamily Sphaeriinae Baker, 1927

Genus *Pisidium* Pfeiffer, 1821

Type species: *Tellina amnica* Müller, 1774. Recent; Palearctic and E North America. Type fixed by the ICZN under the plenary powers.

***Pisidium bellardii* Brusina, 1884**
Figure 11A–D

* 1884 *Pisidium Bellardii* Brusina – Brusina, p. 48.
1897 *Pisidium Bellardii* Brus. – Brusina, p. 36, pl. 21, figs 43–45.
1974 *Pisidium bellardii* Brusina – Milan et al., p. 47.
2013b *Pisidium bellardii* Brusina, 1884 – Neubauer et al., figs 14J–L.

non 2006 *Pisidium bellardii* Brusina, 1897 – Kókay, p. 97, pl. 38, figs 4–5.

Material: Specimen illustrated by Brusina (1897); 1 single valve from Miočić (NHMW 2014/0315/0034).
Type material: Details of type material unknown (type locality: Trnovača, Sinj Basin). It is uncertain whether the specimen illustrated by Brusina (1897) and indicated as holotype by Milan et al. (1974) (NHMZ 3203-849) is part of the original material of Brusina (1884) or derives from newly collected material.
Dimensions (L x H): 1.87 x 1.51 mm (Brusina, 1897, pl. 21, figs 43–45).
Remarks: A detailed description and discussion is provided by Neubauer et al. (2013b). The specimens from the Late Badenian (Early Serravallian) of Herend, Hungary, identified as *P. bellardii* by Kókay (2006) correspond to a different species. They differ in their subtriangular, distinctly asymmetrical shape.
Distribution: Drniš Basin (Miočić), Gacko Basin (Gračanica, Vrbica), Sinj Basin (Ruduša, Trnovača) (Brusina, 1884, 1897; Neubauer et al., 2013b).

Superorder Palaeoheterodonta Newell, 1965
Order Unionida Stoliczka, 1871
Family Unionidae Rafinesque, 1820

Genus *Unio* Philipsson, 1788

Type species: *Mya pictorum* Linnaeus, 1758. Recent; Europe. Type fixed by the ICZN under the plenary powers.

***Unio katzeri* Brusina, 1904**

* 1904 *Unio Katzeri* Brus. n. for. – Brusina, p. 498, pl. 2, fig. 9a, pl. 3, fig. 9b.
1981 *Unio katzeri* Brusina 1906 – Žagar-Sakač, p. 16.
1986 *Unio katzeri katzeri* Brusina n. ssp. [sic] – Žagar-Sakač, p. 171, 177, pl. 1, figs 1–3, pl. 4, fig. 1, pl. 5, fig. 3.
1986 *Unio katzeri tricostatus* n. ssp. – Žagar-Sakač, p. 173, 178, pl. 2, figs 1–2, pl. 4, fig. 2, pl. 5, fig. 2.
1986 *Unio katzeri bicostatus* n. ssp. – Žagar-Sakač, p. 174, 178, pl. 3, figs 1–2, pl. 4, fig. 3, pl. 5, fig. 1.

Material: None.
Type material: NHMS 1436 (syntype); Šipovo, Šipovo Basin (Bosnia and Herzegovina).
Remarks: This species was not detected in the course of our investigations, but recorded from the Drniš Basin by Žagar-Sakač (1986). This author introduced two subspecies, based only on differences of the number of radial folds ("ribs"). They co-occur with the nominal subspecies in the Sinj Basin. Moreover, the same variability has been demonstrated by Brusina (1904) for the type material from Šipovo as well. Consequently, we consider the separation as biological subspecies not justified. These morphologies rather represent local phenotypes of a single polymorphic species.
Distribution: Obrovac Basin (Bilišane/Kuridža kuće), Drniš Basin (Kadina glavica, Liskovača), Sinj Basin (Borići, Brnaze, Hrvace, Jabuka, Kalina kuće, Košute, Lučane, Muša, Prčela, Turjaci, Strmendolac, Vedrine), Šipovo Basin (Šipovo).

***Unio rackianus* Brusina, 1874**
Figure 11H–M

* 1874 *Unio Račkianus* Brusina – Brusina, p. 115, pl. 5, figs 9–10.
1974 *Unio Rackianus* Brusina – Milan et al., p. 54.
2011 *Unio rackianus* Brusina 1874 – Neubauer et al., p. 216, pl. 7, figs 3–7.
2013b *Unio rackianus* Brusina, 1874 – Neubauer et al., figs 15A–G [cum syn.].

Material: 4 valves and fragments from Miočić (NHMW 2014/0315/0115, NHMW 2014/0315/0182); 2 from Biočić (NHMW 2014/0315/0120, NHMW 2014/0315/0186); several fragments from Parčić (NHMW 2014/0315/0039).
Type material: NHMZ 3232-878/1-2 (syntypes); Miočić, Drniš Basin; single left and right, posteriorly fragmented valves (illustrated by Brusina, 1874 and Žagar-Sakač, 1987).
Dimensions: Žagar-Sakač (1987) indicates a maximum shell length of 65 mm and a height of 50 mm; for more measurements see there.
Remarks: Detailed descriptions and discussions are provided by Žagar-Sakač (1987) and Neubauer et al. (2011, 2013b).
Distribution: Drniš Basin (Biočić, Miočić, Parčić), Gacko Basin (Gračanica), Sinj Basin (Koljane, Lučane, Muša, "bunar", Panj, Ribarić, Ruduša) (Brusina, 1874; Žagar-Sakač, 1987; Neubauer et al., 2011, 2013b).

5. Discussion

5.1 Faunal composition

Altogether the fauna of Lake Drniš comprises 49 mollusk species (36 freshwater gastropods, 5 terrestrial gastropods, 8 bivalves). There is evidence, however, that not all of these taxa settled the lake at the same time. Several authors indicated distinct stratigraphic successions in the Miocene freshwater sediments and faunal differences through time (Neumayr and Paul, 1875; Brusina, 1884; Kittl, 1895; Žagar-Sakač and Sakač, 1984). Brusina (1884) and Kittl (1895) provided an overview of the faunal differences between the single strata as well as the various localities in the northern part of the basin. In the area of Miočić, Kittl (1895) distinguished two layers of different age and faunal content. The largest part of the fauna obviously derives from the highly fossiliferous beds termed "Miočić a" by Kittl (1895), which seemingly forms the lowermost mollusk-bearing deposits of the basin. This bed can be traced to Biočić and comprises a very rich fauna of at least 40 freshwater species, dominated by melanopsids and hydrobiids in species and individual numbers (Tab. 1). Among the six species of melanopsids *Melanopsis inconstans*, *M. acanthica*, *M. visianiana*, and *M. zitteli* are most abundant. Hydrobiids are represented by 11 species, with very frequent *Bania torbariana* and common *Prososthenia eburnea*, *P. tournoueri*, and *Pseudodianella haueri*. Pulmonates and bivalves are rather rare elements in terms of individuals. The successive bed "Miočić b" corresponds to the "youngest deposits of the basin" given by Brusina (1884, p. 37) and Kittl (1895) and crop out west of Miočić, comprising abundant *Bithynia jurinaci*, *Emmericia canaliculata*, and *Bania torbariana*, and – more towards Siverić (Fig. 1) – also *Planorbarius mantelli*, *Lymnaea* sp., *Megalotachea neumayri*, and *Unio rackianus*.

The locality Parčić, in contrast, contains only 15 freshwater species. Apart from the rare occurrences of *Cyclothyrella candidula* and *Pyrgula dalmatica*, all other species are known from Miočić as well, but largely in deviating relative abundances. The fauna is dominated by *Melanopsis inconstans* (especially the *plicatula*-phenotype), *Prososthenia dalmatina*, and *Kadolskya panicum*, with co-occurring, less common *Pseudodianella haueri*, *Theodoxus lorkovici*, and *Orygoceras dentaliforme*. Probably the deposits from Parčić are of equal or similar age as "Miočić a"; the varied composition might reflect local ecological differences (or may be a result of collecting biases).

Taxon	Miočić	Biočić	Parčić	Vrba	endemic	Sinj Basin	Kupres Basin	Gacko Basin	outside DLS
Valvata? *homalogyra* Brusina, 1874	x					x			
Theodoxus imbricatus (Brusina, 1878)	x						x		
Theodoxus lorkovici (Brusina, 1878)	x		x		x				
Theodoxus sinjanus (Brusina, 1876)	x					x			
Melanopsis acanthica Neumayr, 1869	x	x	x						
Melanopsis geniculata Brusina, 1874	x					x	x		
Melanopsis inconstans Neumayr, 1869	x	x	x			x			x
Melanopsis lyrata Neumayr, 1869	x	x		x		x	x	x	
Melanopsis visianiana Brusina, 1874	x	x				x			
Melanopsis zitteli Neumayr, 1869	x	x			x				
Bithynia jurinaci Brusina, 1884	x	x	x			x		x	
Emmericia canaliculata Brusina, 1870	x					x			
Fossarulus crossei Brusina, 1878	x		x						
Fossarulus moniliferus Brusina, 1876				x		x	x	x	
Fossarulus stachei Neumayr, 1869	x	x	x			x			
Fossarulus tricarinatus Brusina, 1870	x			x		x			
Cyclothyrella candidula (Neumayr, 1869)	x		x			x			
Cyclothyrella tryoniopsis (Brusina, 1874)	x		x			x	x		
Prososthenia dalmatina (Neumayr, 1869)	x	x	x			x			
Prososthenia eburnea Brusina, 1884	x					x		x	
Prososthenia neutra Brusina, 1897	x					x		?	
Prososthenia tournoueri (Neumayr, 1869)	x	x				x			
Pseudodianella haueri (Neumayr, 1869)	x	x	x			x	x		
Pyrgula dalmatina Brusina, 1881			x		x				
Kadolskya panicum (Neumayr, 1869)	x		x			x			
Bania prototypica (Brusina, 1872)	x					x			
Bania stosiciana (Brusina, 1874)	x	x					x		
Bania torbariana (Brusina, 1874)	x	x				x			
Bania valvatoides (Brusina, 1872)	x					x		x	
Lymnaea klaici Brusina, 1884	x	x				x			
Radix korlevici (Brusina, 1884)	x					x		x	
Ferrissia illyrica (Neumayr, 1880)	x		x			x		x	
Gyraulus dalmaticus (Brusina, 1884)	x					x			
Gyraulus geminus (Brusina, 1897)	x					x			
Orygoceras dentaliforme Brusina, 1882	x		x			x	x	x	
Planorbarius mantelli (Dunker, 1848)	x	x				x			x
Oxyloma drnisana (Brusina, 1897)	x				x				
Succinella martinovici (Brusina, 1902)	x					x			
Archaeozonites? sp.	x	x			x				
Megalotachea neumayri (Brusina, 1878)	x					x			
Pseudochloritis schlosseriana (Brusina, 1874)	x				x				
Dreissena cymbula Brusina, 1892	x								
Andrusoviconcha jadrovi (Brusina, 1892)	x	x				x			
Andrusoviconcha nitida (Kochansky-Devidé and Slišković, 1978)	?					x			
Illyricocongeria aletici (Brusina, 1907)	x					x	x		
Illyricocongeria moirae Mandic nov. sp.	x	x			x				
Pisidium bellardii Brusina, 1884	x					x		x	
Unio katzeri Brusina, 1904						x			
Unio rackianus Brusina, 1874	x	x	x			x		x	
total	**46**	**18**	**15**	**3**	**7**	**37**	**9**	**11**	**2**

Table 1: Species list for Lake Drniš with indication of faunal relationships with other coeval lakes of the DLS. This compilation is based on verified literature records (Brusina, 1874, 1884, 1897; Kittl, 1895) and own data.

Fossil documentation from the southern, elongated part of the basin is rather poor. The locality Vrba yielded only the three species *Fossarulus moniliferus*, *F. tricarinatus* and rare *Melanopsis lyrata*. Žagar-Sakač and Sakač (1984) reported *Melanopsis inconstans*, *Orygoceras* sp., *Bulimus* [= *Bithynia*] sp., *Unio katzeri*, and a doubtful record of "*M. sinjanus*" [maybe a misidentified *M. visianiana*] from the nearby section "Liskovača". Additionally, they listed several doubtful names of dreissenids and unionid bivalves never reported from the basin or the DLS so far. Most of these are based on poor material and most likely represent misidentifications. More material is needed to verify these records.

5.2 Paleoecology

The melanopsid-truncatelloid assemblage typical for the northern part is very common among lakes of the DLS and has been documented for the lakes Sinj, Kupres, and Gacko (Neumayr, 1869; Brusina, 1874; Mandic et al., 2009, 2011; Neubauer et al., 2011, 2013a, b). Such a composition is indicative of a perennial, moderately shallow lake (Neubauer et al., 2013a,

b). A recently published study on the isotopic compositions of shell aragonites from the Sinj and Drniš basins mollusks demonstrated slightly alkaline freshwater conditions (Harzhauser et al., 2012). This study also showed that the faunal differences between the two stratigraphic layers of Miočić can be explained by deviating paleoecological conditions. The isotope signatures of species of the younger interval, i.e., *Bithynia jurinaci*, *Emmericia canaliculata*, *Bania torbariana*, and *Unio rackianus*, indicate considerably cooler annual mean temperatures. The occurrence of several pulmonate and terrestrial gastropods in that period (Brusina, 1884) likely reflects a shallowing and spatial restriction of the lake.

5.3 Paleobiogeography

With 44 freshwater species Lake Drniš is the second-richest lacustrine fauna among the Dinaride lakes, ranging behind Lake Sinj with its 58 species and subspecies (Neubauer et al., 2015b). The two lakes share a large percentage of their fauna; 35 of the 44 freshwater species recorded for Lake Drniš are also present in Lake Sinj (79.5 %). This high similarity suggests an at least temporal hydrological connection between both lakes, which are today separated by a high mountain ridge of 15 km width. Relevant relationships are also indicated with Lake Kupres (9 species; 20.4 %) and Lake Gacko (11 species; 25.0 %). Only four freshwater species (9.1 %) are only known from Lake Drniš. Apart from *Melanopsis inconstans* and *Planorbarius mantelli,* all species are endemic to the DLS (95.4 %). Among these, *Planorbarius mantelli* is the only species that occurs outside Croatia and Bosnia and Herzegovina. Wesselingh et al. (1999) suggested that for both Recent and fossil species of *Planorbarius* avian dispersal was an important factor controlling their distributions. This might explain why this very wide-spread species (Wenz, 1923), which probably evolved from its ancestor *P. cornu* (Brongniart, 1810) during the late Early Miocene in Central Europe, is the only one that could enter this region.

5.4 Stratigraphy

At present, there is no precise age estimate for the Miocene freshwater deposits of the Drniš Basin. Based on faunal comparisons, Neubauer et al. (2013a, b) suggested a similar age as for the Kupres and Gacko basins as well as for the upper interval of the Sinj Basin. For the Kupres Basin, the presence of the biostratigraphic indicator species *Illyricocongeria aletici* (Brusina, 1907) as well as the absence of its predecessor *I. drvarensis* (Toula, 1913) helped to tie the fauna to the biostratigraphic framework of the DLS. In the Sinj Basin, *I. drvarensis* occurs during the interval of 15.9–15.7 Ma, while *I. aletici* is documented for the interval of 15.25–15.0 Ma (De Leeuw et al., 2010). Accordingly, an approximate age of 15.5 ± 0.2 Ma (early Langhian) was suggested by Neubauer et al. (2013a) for the development of the Lake Kupres fauna. The facts that 1) *I. aletici* is present in the Drniš Basin and 2) the Drniš fauna (particularly the one from the lower beds) shows high similarities with those of lakes Sinj, Kupres, and Gacko, imply the same age as for Lake Kupres and Lake Sinj. Most likely, the fauna of Lake Drniš developed around 15.7 and continued up to 15.0 Ma, classifying it into the early Langhian.

Acknowledgments

We are grateful to Zlata Jurišić-Polšak and Maria Bošnjak (both Croatian Natural History Museum in Zagreb, NHMZ), Božena Čvorović (National Museum in Sarajevo, NHMS), and Irene Zorn (Austrian Geological Survey, GBA) for providing access to the type collections. Nives Borčić made the photographs, Hrvoje Posilović the SEM documentation of the type material stored at the NHMZ. Mladen Juračić and Zlatan Bajraktarević facilitated access to the SEM device at the Geological Department, Faculty of Science, University of Zagreb. We acknowledge permission by the NHMZ to publish this documentation. Alice Schumacher (NHMW) made the photographs of the type material stored at the GBA. Dietrich Kadolsky (Beneath the Surface Geoconsultants Ltd., Sanderstead, Surrey, UK) is thanked for helpful comments on hydrobiid taxonomy. We are grateful to Ewa Stworzewicz (Polish Academy of Sciences, Kraków) and Carmine D'Amico (Università degli Studi del Molise, Campobasso) for their constructive reviews. This work contributes to the projects "Freshwater systems in the Neogene and Quaternary of Europe: Gastropod biodiversity, provinciality, and faunal gradients" (Project no. P25365-B25) and "Mollusk evolution of the Miocene Dinaride Lake Systems" (Project no. P18519-B17) financed by the Austrian Science Fund FWF.

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Received: 22 August 2014
Accepted: 21 May 2015

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