Palaeontology The Palaeontological Association www.palass.org

[Palaeontology, Vol. 56, Part 1, 2013, pp. 129–156]

A NEW MIOCENE LACUSTRINE MOLLUSC FAUNA OF THE DINARIDE LAKE SYSTEM AND ITS PALAEOBIOGEOGRAPHIC, PALAEOECOLOGIC AND TAXONOMIC IMPLICATIONS

by THOMAS A. NEUBAUER[1]*, OLEG MANDIC[1], MATHIAS HARZHAUSER[1] *and* HAZIM HRVATOVIĆ[2]

[1]Department of Geology and Palaeontology, The Natural History Museum Vienna, Burgring 7, 1010 Wien, Austria; e-mails: thomas.neubauer@nhm-wien.ac.at, oleg.mandic@nhm-wien.ac.at, mathias.harzhauser@nhm-wien.ac.at
[2]Federal Institute for Geology – Sarajevo, Ustanička 11, 71210 Ilidža, Bosnia and Herzegovina; e-mail: hharish@bih.net.ba
*Corresponding author.

Typescript received 4 July 2011; accepted in revised form 22 February 2012

Abstract: The Dinaride Lake System, as one of the largest freshwater systems in the Neogene of Europe, is widely known for its exceptional mollusc fauna. During the Early and Middle Miocene, it displayed a major evolutionary hotspot resulting in a high level of endemicity. Despite advanced investigations in that region, comprehensive knowledge on the mollusc fauna of the Kupres basin is largely lacking. The herein presented results give insight into this outstandingly preserved fauna and are the base for a systematic revision of several supraspecific taxa among the Hydrobiidae. Because their phylogeny is poorly known, this study may serve as starting point for an overall systematic revision of this highly diverse family. Moreover, the faunal composition allows inferences on palaeobiogeography and hydrological connections within the Dinaride Lake System during the early Middle Miocene. About one-third of the described taxa are restricted to the Kupres basin. The other taxa document faunistic relations to the coeval faunas of the Sinj, Drniš and Džepi basins. Phases of hydrological isolation, indicated by carbonate dominated lithology, coincide with a high frequency of sculptured morphologies within the gastropods. Phases of increased aridity led to high evaporation, a lowered lake level and enhanced carbonate production which seem to have promoted strongly calcified shells. The stratigraphic ranges of the species imply a depositional age of 15.5 ± 0.2 Ma (earliest Middle Miocene; Langhian). Among the Hydrobiidae *Cyclothyrella* gen. nov. and *Pseudodianella* gen. nov. are introduced as new genera. *Bania obliquaecostata* sp. nov., *Melanopsis corici* sp. nov., *Nematurella vrabaci* sp. nov., *Prososthenia diaphoros* sp. nov. and *Prososthenia undocostata* sp. nov. are described as new species. For the secondary homonym *Melanopsis bittneri* (Neumayr, 1880), the new name *Melanopsis medinae* nom. nov. is proposed.

Key words: molluscs, Dinaride Lake System, Bosnia and Herzegovina, Middle Miocene, taxonomy, palaeoecology.

THE Dinaride Lake System (Krstić *et al.* 2003) is a complex Miocene continental environment in SE Europe, formed within a palaeogeographic barrier between the Paratethys and the Mediterranean seas. Known for its exceptional mollusc fauna (Harzhauser and Mandic 2008, 2010), it became a target of intensive integrated research resolving its stratigraphic setting and palaeoenvironmental history (Jiménez-Moreno *et al.* 2008, 2009; Mandic *et al.* 2009, 2011; De Leeuw *et al.* 2010, 2011). Except for the Sinj basin, from where a detailed taxonomic revision is already available (Neubauer *et al.* 2011), our knowledge on the mollusc fauna from other basins is still fragmentary (Kochansky-Devidé and Slišković 1978, 1981) or out-dated (Neumayr 1880; Brusina 1902, 1905). A major problem for taxonomic revisions was the complex geographic and geologic setting with numerous basins. Therefore, most authors were unable to assign the already described taxa and localities in the literature to discrete basins and palaeo-lakes. Even the latest synopsis by Harzhauser and Mandic (2008) treated the Dinaride Lake System fauna as an entity. The faunistic interrelations between the various basin faunas, however, can only be evaluated after a revision of the single assemblages.

The Fatelj mollusc fauna (Kupres basin, S Bosnia and Herzegovina) was initially studied by Brusina (1902) from scarce debris collections resulting in descriptions of several rather large-sized gastropod taxa. Subsequently, Kochansky-Devidé and Slišković (1981) studied its dreissenid bivalves, yet without detailed documentation of all species identified therein. Finally, Jurišić-Polšak and Slišković (1988) provided a preliminary list of species. Thus, although belonging to the few exceptionally well-preserved faunas of the Dinaride Lake System, the taxonomic frame of the Fatelj fauna is entirely missing.

The present investigation will fill this gap to increase our knowledge on taxonomic content and palaeoenvironmental settings of the Dinaride Lake System. Beyond that, the implications drawn from the presented data will have significant impact on supraspecific systematics of the Hydrobiidae from the European lacustrine Neogene. Currently, the status of the family Hydrobiidae, its monophyly, family rank and included groups, is still under discussion (Wilke *et al.* 2001; Anistratenko 2008). This debate is, however, beyond the scope of this paper, and we thus refer to Bouchet and Rocroi (2005).

GEOLOGICAL SETTING AND SECTION

The Kupres basin is an about 95 km^2 large, NW–SE striking karst plane (polje) in southern Bosnia and Herzegovina (Fig. 1). It is the highest plane in that part of the Dinarides comprising the water shed between the Adriatic and Black seas fluvial systems. The basement represents the northern margin of the External Dinarides and consists predominantly of Mesozoic marine platform carbonates (Hrvatović 2006). The basin was initiated during the Early Miocene, reflecting the extensional tectonic regime originating from back arc rifting of the Pannonian basin (Ilić and Neubauer 2005). The sedimentary thickness of the lacustrine, predominantly carbonate deposits, is unknown because the lack of coal deposits did not favour explorational drillings (Đerković 1964). They are exposed on an area of only about 23 km^2, yet with a possible extension below the Pleistocene-Holocene cover of up to 80 km^2 (Papeš 1972, 1975; Vujnović *et al.* 1975; Vujnović 1981).

The stratigraphical position of the Kupres basin is still under discussion. Đerković (1964) considered the deposits as Upper Miocene based on the fossil record. Papeš (1975) suggested a Miocene age without precise differentiation. Finally, Kochansky-Devidé and Slišković (1981) proposed a Late Miocene age based on dreissenid bivalves.

The investigated locality (WGS84: 43°58′17.2″N, 017°14′06.9″E, 1140 m) is placed at the NW slope of a small hill termed Fatelj (Fig. 1). It was artificially outcropped at a distance of about 5 m on the west side of a

FIG. 1. Palaeogeographic map (sediment distribution) of the Dinaride Lake System with position of the studied section Fatelj and localities mentioned in the text: (1) Dugo Selo, (2) Biočić, (3) Miočić, (4) Parčić, (5) Vrba, (6) Ribarić, (7) Lučane, (8) Stuparuša, (9) Župića, (10) Trnovača, (11) Turjaci, (12) Brnaze, (13) Košute, (14) Grab, (15) Džepi, (16) Hodovo/Stolac, (17) Vrbica, (18) Gračanica/Gacko. Dinaride Lake System sediments are dark, Paratethys deposits of Pannonian basin are light shaded. Compiled after geologic maps of former Yugoslavia 1:100 000 and 1:500 000 and ESRI ArcGIS base maps.

small path leading to the main road (Bugojno-Livno). The path leaves the road about 3.8 km S of Kupres and heads to the WNW along the northern side of the Fatelj hill. The site is distanced about 1 km from the road close to the bank of the rivulet Mrtvica.

The section is about 3 m long and comprises three lithological units delimited by transitional boundaries (Fig. 2). No formation name is established for these deposits in the literature. The beds are dipping with 15 degrees to the NNE (015 degrees). Unit 1 is about 1 m thick and made up by greenish limestone and marly limestone with a clay component ranging between 3 and 7 per cent. Small to medium-sized dreissenid bivalves

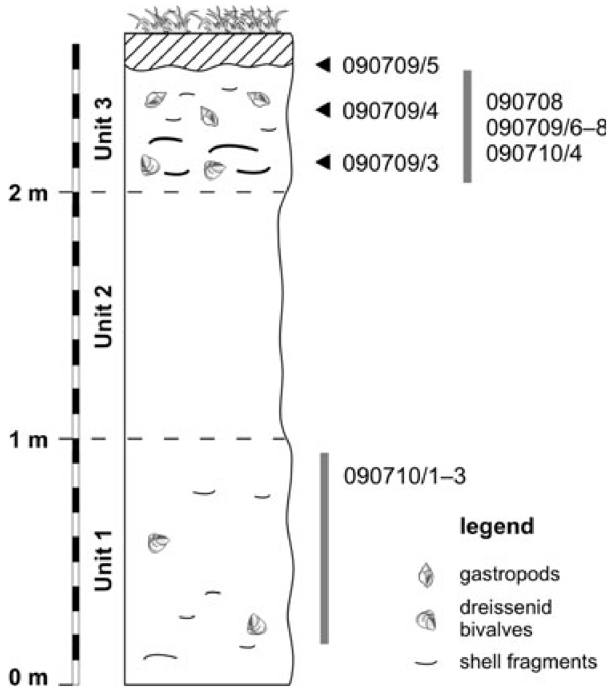

FIG. 2. Fatelj section with sedimentary Units 1–3 as defined in the text. The arrows mark the positions of stratified samples, while the bars represent nonstratified, unit-related samples.

and gastropods are floating in the sediment. Additionally, fish bone remains are present. Aragonite shells are largely leached. The about 1-m-thick Unit 2 is lithologically similar to the previous unit but barren of macrofossils. Unit 3 is about 0.5 m thick and comprises beige to whitish-grey marly limestones with large dreissenid shells in its lower part grading into the gastropod-dominated upper part of the unit. It is a moderately dense shell accumulation with horizontally oriented bivalve shells and nonoriented gastropod shells in the upper part. The aragonite preservation is moderate to excellent. At about 2.5 m, Unit 3 grades into an about 30-cm-thick soil horizon rich in gastropods that are reworked from the underlying horizon.

MATERIALS AND METHODS

Eleven mollusc samples (Fig. 2) have been taken for detailed taxonomic evaluation of the fauna – three in Unit 1 (090710/1–3), one in the dreissenid coquina of Unit 3 (090709/3), two in the gastropod coquina of the same unit (090709/8 and 090710/4), one in the boundary interval to the soil horizon appearing rich in micromolluscs (090709/5) and three in debris of Unit 3 (090708, 090709/6–7). One additional sample (090709/4) was taken in the gastropod coquina of the Unit 3 that appeared suitable for sieving and quantitative evaluation of abundances.

Samples 090709/4 and 5 were treated with diluted hydrogen peroxide and washed through 2 and 0.5 mm sieves. To preclude double counting, only the adapical/umbonal part was included.

SYSTEMATIC PALAEONTOLOGY

Remarks. Systematics follows Bouchet and Rocroi (2005, 2010) and Jörger *et al.* (2010) for Pulmonata. For additional synonyms, see Brusina (1907), Wenz (1923–1930) and Milan *et al.* (1974).

Repository. Unless noted differently, all specimens and samples are stored in the collection of the Natural History Museum of Vienna under the prefix NHMW 2011/0138.

Class GASTROPODA Cuvier, 1797
Subclass NERITIMORPHA Golikov and Starobogatov, 1975
Superfamily NERITOIDEA Rafinesque, 1815
Family NERITIDAE Rafinesque, 1815
Subfamily NERITININAE Poey, 1852

Genus THEODOXUS Montfort, 1810

Type species. Theodoxus lutetianus Montfort, 1810 (= *Nerita fluviatilis* Linnaeus, 1758); Recent; France.

Theodoxus imbricatus (Brusina, 1878) comb. nov.
Figure 3A–F

1878 *Neritina imbricata* Brusina, p. 352.
1884 *Neritodonta imbricata* 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.

Material. Four specimens from Samples 090709/4; 18 from debris collections.

Description. Morphologically quite variable species with up to three whorls. Fully grown individuals attain 10 mm in width and height. The protoconch is smooth and comprises about one whorl. The body whorl nearly fully overgrows the preceding whorls and develops a distinct shoulder near the upper suture. This results in a narrow horizontal ramp. The aperture is regularly semilunar and with *c.* 45 degrees inclined to the axis. A large and massive callus pad is formed, sometimes with weak denticles in the centre of the adapertural margin. In some specimens, sculpture appears in late ontogeny, reaching from a simple bulge at the shoulder up to irregular excrescences, which are arranged in two spiral lines. Also the brown or yellow colouring is highly variable, ranging from densely spaced irregular axial

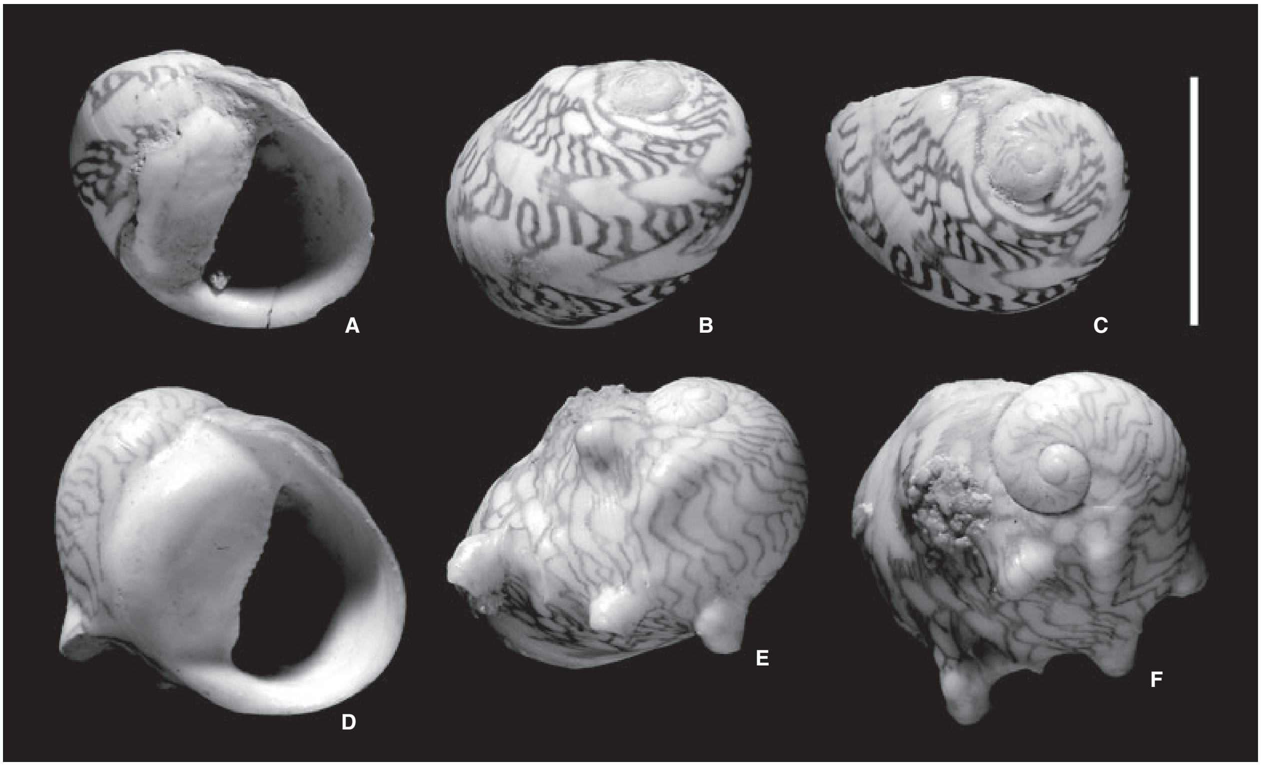

FIG. 3. Neritidae, each in front, back and apical view. A–C, *Theodoxus imbricatus* (Brusina, 1878); NHMW 2011/0138/0098; smooth phenotype with distinctly developed shoulder. D–F, *Theodoxus imbricatus* (Brusina, 1878); NHMW 2011/0138/0098; shell with vast excrescences. Both specimens are from debris of Unit 3. Scale bar represents 5 mm.

lines to wide-spaced zigzag lines. The pattern may cover the entire shell or may be confined to spiral areas.

Remarks. The type material was described by Brusina (1878) and illustrated later in Brusina (1884). This species is characterised by its distinct shoulder and (if present) by the aberrant sculpture, both of which exclude confusion with other species. *Theodoxus reiseri* (Brusina, 1902) from Džepi exhibits an analogue mode of sculpture but has an angulated last whorl, which may even result in a distinct keel. Moreover, its aperture lacks any denticles.

Distribution. Middle Miocene of the Kupres basin and Drniš basin (Miočić).

Subclass CAENOGASTROPODA Cox, 1959
Order CERITHIIMORPHA Golikov and Starobogatov, 1975
Superfamily CERITHIOIDEA Fleming, 1822
Family MELANOPSIDAE Adams and Adams, 1854

Genus MELANOPSIS Férussac, 1807

Type species. Buccinum praemorsum Linnaeus, 1758; Recent; Spain.

Melanopsis angulata Neumayr, 1880
Figure 4A–B

1880 *Melanopsis angulata* n.f. Neumayr, p. 479, pl. 7, fig. 8.

Material. Three specimens from debris collections (Unit 3).

Description. Sturdy small shell, somewhat more than 10 mm in height and 7 mm in width, with up to seven strongly adpressed whorls. Protoconch unknown. The early teleoconch develops an axial sculpture with weak nodes near the lower suture. On the last three whorls, an additional row of more distinct nodes may occur below the upper suture. There, the axial ribs are very weakly expressed. On the last whorl, the nodes grade into distinct spines. At the upper suture, distinct notches are formed by the axial ribs. The last whorl attains about three quarters in height. The aperture is wide and simple, without notable thickenings.

Remarks. This species is highly reminiscent of *Melanopsis defensa* Fuchs, 1870 from the Late Miocene of Romania. However, as the latter species is restricted to the middle to late Pannonian (= Tortonian) of Lake Pannon (Harzhauser and Mandic 2008), it is very unlikely that they are conspecific. A single specimen of *Melanopsis angulata* Neumayr, 1880 from Džepi shows only a single row of

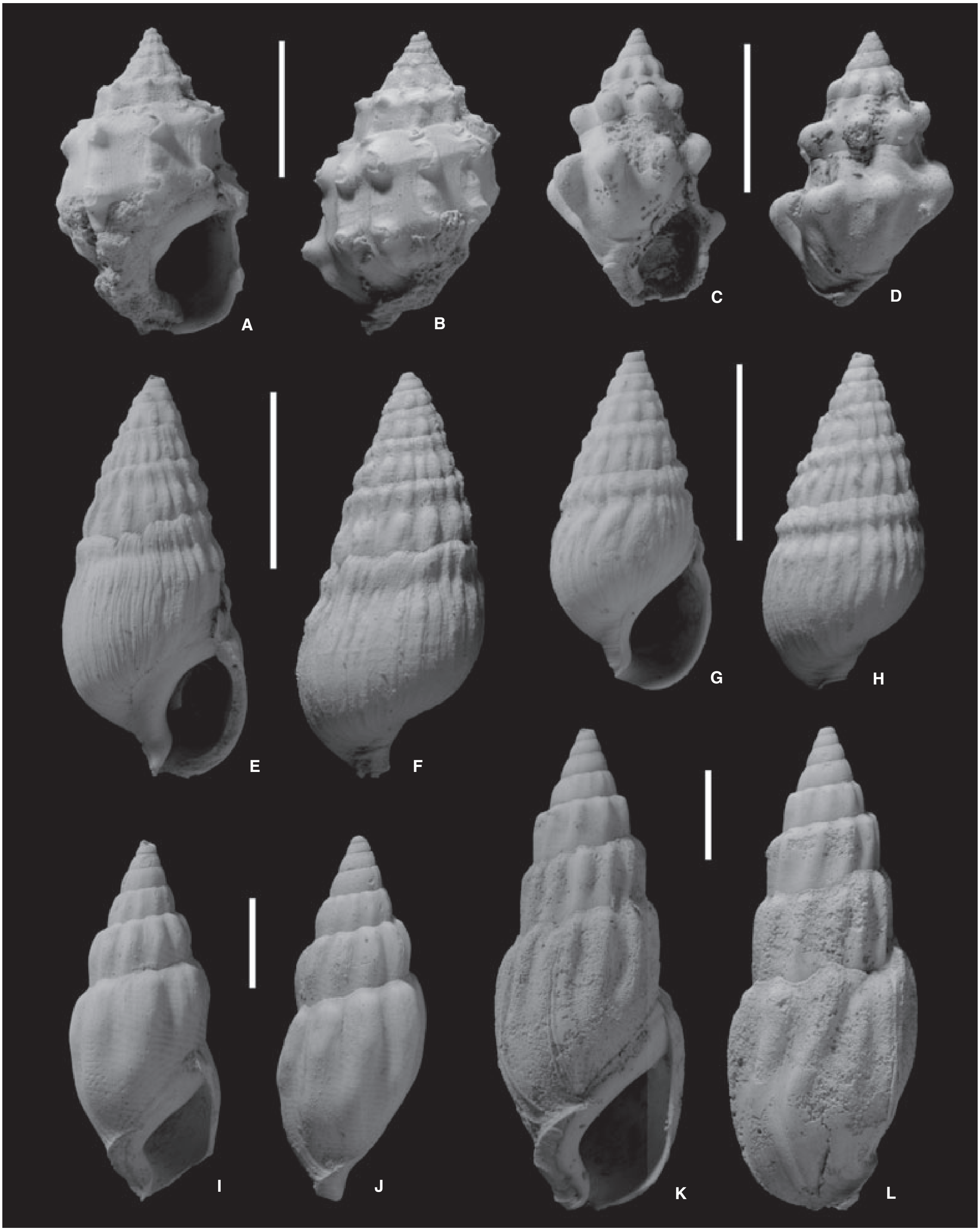

FIG. 4. Melanopsidae, in front and rear view. A–B, *Melanopsis angulata* Neumayr, 1880; NHMW 2011/0138/0099; C–D, *Melanopsis geniculata* Brusina, 1874; NHMW 2011/0138/0104; E–F, *Melanopsis corici* sp. nov.; Paratype 1, NHMW 2011/0138/0101; G–H, *Melanopsis corici* sp. nov.; Holotype, NHMW 2011/0138/0100; I–J, *Melanopsis cvijici* Brusina, 1902; NHMW 2011/0138/0103; K–L, *Melanopsis cvijici* Brusina, 1902; NHMW 2011/0138/0103. All specimens are from debris of Unit 3. Scale bars represent 5 mm.

nodes. As all other features are coinciding, we consider the different number of rows in that species as intraspecific variability.

Distribution. Middle Miocene of the Kupres and Džepi basins.

Melanopsis corici sp. nov.
Figure 4E–H

Derivation of name. In honour of the geologist and palaeontologist Stjepan Ćorić (Geological Survey Vienna) for his valuable help during our Dinaride Lake System studies.

Holotype. NHMW 2011/0138/0100 (Fig. 4G–H).

Paratypes. NHMW 2011/0138/0101 (Fig. 4E–F); NHMW 2011/0138/0102; both from debris collection.

Type locality. Fatelj section, Kupres basin, Bosnia and Herzegovina.

Type horizon. Langhian, Lower Middle Miocene; debris of Unit 3.

Material. 105 specimens from debris collection (Unit 3); a few fragments from Sample 090709/5.

Diagnosis. Rather small melanopsid with faint sculpture consisting of a subsutural band and subjacent elongate swellings to short ribs.

Description. Conical to slightly ovoid shell, consisting of 7–9 whorls. The largest specimen attains 15 mm in height and 7 mm in diameter. Protoconch unknown. Early teleoconch smooth with weakly convex whorls. Soon a subsutural band emerges, accompanied by a single row of elongate swellings in the middle of the whorl. The band usually bears weak densely spaced nodes. In some specimens, sculpture may be stronger with distinct nodes on the band and stronger ribs below. In any case, between the band and the subjacent swellings/ribs, a concave furrow is developed. Even in stronger ornamented individuals, the swellings or ribs fade out towards the base of the last whorl, which attains about 60 per cent of shell height. The rather wide aperture exposes a slightly thickened inner lip and a strongly convex to slightly angulated outer lip; this sometimes results in a roughly triangular shape. Distinct growth lines cover the entire surface.

Remarks. The combination of ribs and nodes is highly reminiscent of *Melanopsis lyrata* Neumayr, 1869, while shape and size rather reminds of *M. astrapaea* Brusina, 1876. Both species, however, lack the subsutural band. The wide and simple aperture without any swelling or fasciole distinguishes this species from other species.

Distribution. Middle Miocene of the Kupres basin.

Melanopsis cvijici Brusina, 1902
Figure 4I–L

1902 *Melanopsis Bittneri* Brus.; Brusina, pl. 7, figs 18–21 (non *Melanopsis Bittneri* Fuchs, 1877).
1902 *Melanopsis Cvijici* Brus.; Brusina, pl. 29, figs 19–22.

Material. Several hundred specimens from debris collection (Unit 3); single occurrences from samples 090709/4 and 090709/5.

Description. Large-sized slender species, up to 30 mm in height and 12 mm in width, with up to nine whorls. Protoconch unknown. Early teleoconch whorls start smooth, but soon distinct axial ribs occur, which are most prominent near the upper suture. This results in a distinctly stepped morphology. The last whorl makes up 50–70 per cent of the total shell height. The aperture exhibits a strong callus pad without any columellar fold. The anterior part of the aperture including the canal is somewhat recurved. In some specimens, colouring of densely spaced, faint, brown, zigzag lines is preserved (Fig. 4I–J).

Remarks. *Melanopsis cvijici* Brusina, 1902 differs from *Melanopsis bittneri sensu* Brusina (1902) from Džepi only in its slightly less stepped spire. This slight difference seems to be a poor base for a separation on the species level, and therefore, both taxa are considered to be conspecific. Moreover, that name is a primary homonym of *Melanopsis bittneri* Fuchs, 1877, which was introduced for a Pliocene species from Greece, and thus is not available.

Distribution. Middle Miocene of the Kupres and Džepi basins.

Melanopsis geniculata Brusina, 1874
Figure 4C–D

1874 *Melanopsis geniculata* Brusina p. 40, pl. 1, figs 9–10.
1897 *Melanopsis geniculata* Brus.; Brusina, p. 11, pl. 4, figs 21–26.
1897 *Melanopsis geniculata enodata* Brus. n. for.; Brusina, p. 11, pl. 4, fig. 27.
1902 *Melanopsis geniculata* Brus; Brusina, pl. 6, fig. 55.

Material. Five specimens from debris collection (Unit 3).

Description. Conical shell with 6–7 whorls, attaining 16 mm in height and 7 mm in width. Protoconch unknown. Weak axial swellings occur in the middle of the antepenultimate whorl, grading soon into prominent, slightly axially elongated globular knobs. Whilst the whorl diameter increases continuously, the number of nodes remains the same, resulting in an almost regular axial arrangement. The sutures are weakly incised. The last whorl attains about two-thirds in height and grades into a steep and slightly concave base. The aperture is largely destroyed in all specimens. A weak callus pad with intentions of a columellar swelling can be distinguished. The outer lip is simple and sharp.

Remarks. The globular knobs allow a clear identification of this species. The polymorphic *Melanopsis inconstans* Neumayr, 1869 and *M. plicatula* Brusina, 1876, both from Miočić and both showing comparable morphologies in some specimens, are larger and display short and sharp ribs rather than nodes.

Distribution. Middle Miocene of the Kupres basin, Drniš basin (Miočić), and Sinj basin (Župića brook/Sinj).

Melanopsis lyrata Neumayr, 1869
Figure 5G–H

1869 *Melanopsis (Canthidomus) lyrata* nov. sp. Neumayr, p. 358, pl. 11, fig. 8.
1874 *Melanopsis Pančićiana* Brusina, p. 44, pl. 1, figs 11–12.
1896 *Melanopsis Kišpatići* Brus.; Brusina, p. 123 (*nomen nudum*).
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.
1897 *Melanopsis Pančićiana* Brus.; Brusina, p. 10, pl. 4, figs 3–4.
2011 *Melanopsis lyrata* Neumayr 1869; Neubauer *et al.*, p. 207 (*cum syn.*), pl. 1, figs 1–9, 22.

Material. Two specimens from debris of Unit 3.

Description. Slender ovoid to conical shell, up to 23 mm in height and 9 mm in diameter (in *kispatici*- and *panciciana*-morphs up to 30 mm in height and 15 mm in diameter), with up to nine whorls. Protoconch unknown. Whorls soon bear ribs with two rows of distinct nodes. These may vary from round knobs to small spines. The ribs remain rather weak throughout ontogeny. The last whorl makes up more than 50 per cent of the height. The aperture is narrow and exposes a weakly thickened, glossy columella. A weak columellar swelling may occur. A single fasciole with a sharp posterior margin reaches from the central part of the columella down to the anterior canal.

Remarks. Brusina (1874, 1896, 1897) introduced several new species: *Melanopsis panciciana* Brusina, 1874 from Ribarić, *M. kispatici* Brusina, 1897 from Miočić, and *M. misera* Brusina, 1874 from Lučane, all of which correspond with *M. lyrata* in sculpture. The only separating criterion seems to be size and only slight deviations in shape (Brusina 1874, 1897). However, these features seem to be insufficient to separate these taxa on the species level. Therefore, they are treated herein as synonyms of *Melanopsis lyrata* Neumayr, 1869.

Distribution. Middle Miocene of the Kupres basin, Drniš basin (Miočić), Vrba, and Sinj basin (Ribarić, Lučane, Stuparuša, Turjaci).

Melanopsis medinae nom. nov.
Figure 5A–D

1880 *Melanoptychia Bittneri* n. f. Neumayr, p. 480, pl. 7, fig. 11.
1902 *Melanoptychia Bittneri* Neum.; Brusina, pl. 29, figs 27–28.
non 1877 *Melanopsis Bittneri*; Fuchs, p. 40, pl. 4, figs 12–17.
non 1902 *Melanopsis Bittneri* Brus.; Brusina, pl. 7, figs 18–21 (= *Melanopsis cvijici* Brusina, 1902).

Derivation of name. Named after Medina Mandic (Vienna) for her valuable assistance during field studies and careful collection of now presented material.

Material. Several hundred specimens from debris collection of Unit 3; three specimens from Sample 090709/5.

Description. Conical to ovoid, highly sculptured shell, consisting of up to nine whorls. Maximum dimensions among available specimens are 21 mm in height and 10 mm in diameter. General shape ranges from bulky and almost globose to fairly slender. Protoconch unknown. Whorl outline is roughly rectangular to slightly trapezoid, resulting in a step-like arrangement. This is enhanced by the ornamentation, which includes axial ribs with two rows of small rounded nodes below the upper suture. In some specimens, the lower row of nodes is reduced. The last whorl attains about two-thirds in height. The aperture has a thickened callus pad with a sharp and distinct columellar fold. In contrast, the outer lip is sharp and simple. The siphonal canal is short and recurved towards the neck.

Remarks. Initially, *Melanopsis bittneri* was introduced by Fuchs (1877) for a species from the Pliocene of Livonates near Corinth in Greece (Papp 1959). Later, this species name was used by Neumayr (1880) for a Miocene species from Džepi and by Brusina (1902) for another Miocene species from Fatelj. While the latter name is a primary homonym of *Melanopsis Bittneri* Fuchs, 1877, the other species is a secondary homonym. It was introduced as *Melanoptychia* Neumayr, 1880, which is now regarded as invalid genus and synonym of *Melanopsis* (Jekelius 1944; Bandel 2000; Neubauer *et al.* 2011). *Melanopsis bittneri* Brusina, 1902 is a synonym of *M. cvijici* Brusina, 1902 (see above). Therefore, a new name had only to be introduced for the species of Neumayr (1880).

The mode of sculpture is reminiscent of *M. lyrata* (Neumayr, 1869), which lacks the stepped spire architecture and is more slender. It differs from *M. cvijici* Brusina, 1902 in its smaller size, the presence of nodes and the columellar fold.

Distribution. Middle Miocene of the Kupres and Džepi basins.

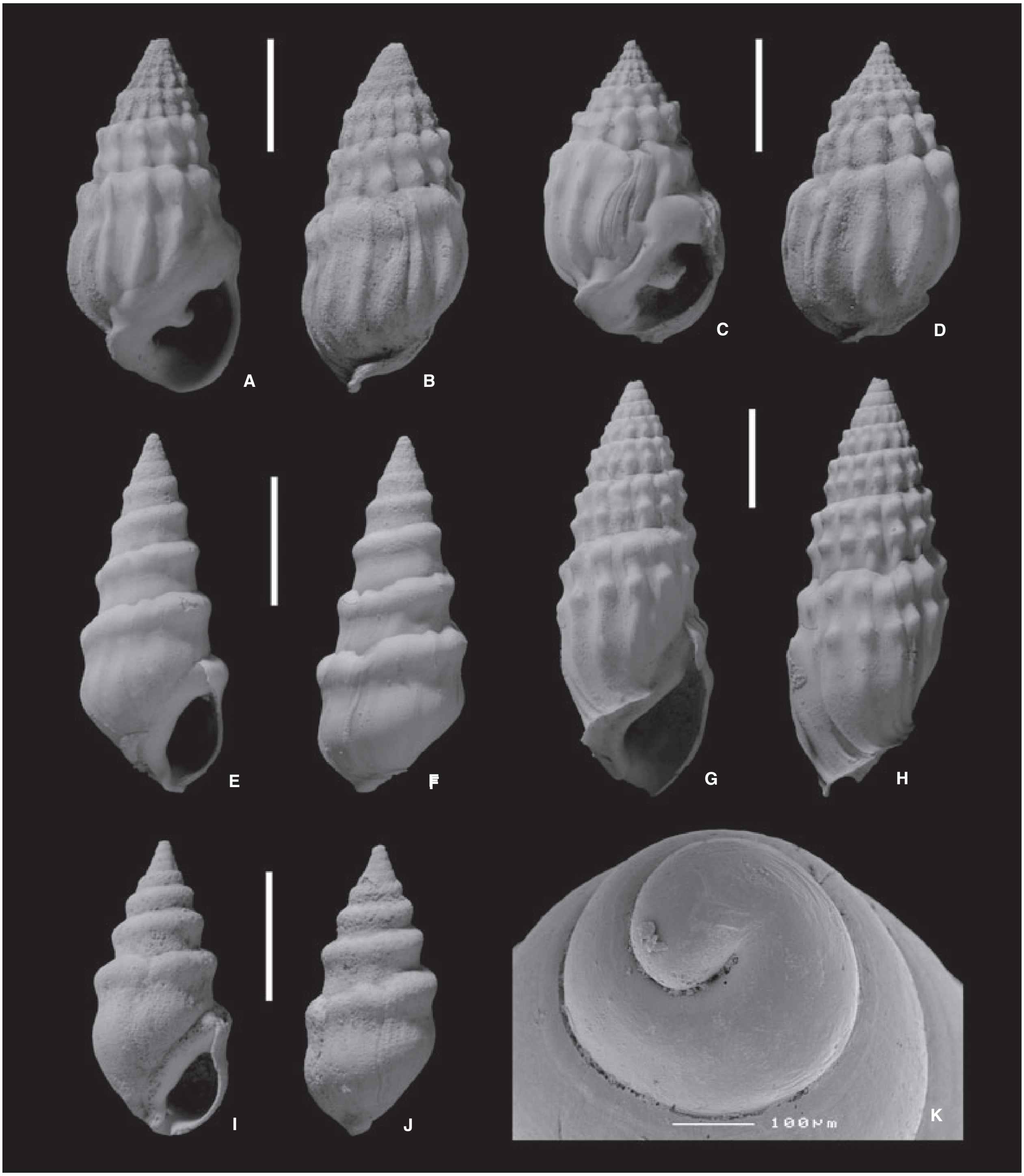

FIG. 5. Melanopsidae, in front and rear view. A–B, *Melanopsis medinae* nom. nov.; NHMW 2011/0138/0106; C–D, *Melanopsis medinae* nom. nov.; NHMW 2011/0138/0106; E–F, *Melanopsis mojsisovicsi* (Neumayr, 1880); NHMW 2011/0138/0107; G–H, *Melanopsis lyrata* Neumayr, 1869; NHMW 2011/0138/0105; I–J, *Melanopsis mojsisovicsi* (Neumayr, 1880); NHMW 2011/0138/0107; K, *Melanopsis mojsisovicsi* (Neumayr, 1880); NHMW 2011/0138/0107; protoconch. All specimens are from debris of Unit 3. Scale bars represent 5 mm (A–J).

Melanopsis mojsisovicsi (Neumayr, 1880) comb. nov.
Figure 5E–F, I–K

1880 *Melanoptychia Mojsisovicsi* n.f. Neumayr, p. 481, pl. 7, figs 9–10.
1902 *Melanopsis* sp. Brusina, pl. 29, figs 23–26.

Material. Several hundred specimens from debris collection of Unit 3; 20 from Sample 090709/4; a single specimen from Sample 090709/5.

Description. Slender shell attaining up to 15 mm in height and 6 mm in diameter, with up to 7–10 whorls. The protoconch is dome-shaped with smooth surface and consists of less than one whorl. This species develops a stepped spire. Instead of axial ribs, it bears two broad bulges of which the lower one is seen only on the last whorl, which makes up *c.* 60 per cent of the total height. These bulges are separated by a wide concave furrow. The lower bulge coincides with a distinct angulation of *c.* 45 degrees, marking the transition into the straight base. The aperture is narrow with a sharp outer lip and a weak callus pad. Rarely colouring is preserved with wide-spaced, narrow, yellow axial bands.

Remarks. This species could be confused with *Melanopsis filifera* Neumayr, 1880 from Drvar (W Bosnia and Herzegovina), which may also exhibit weak bulges. This species lacks the stepped morphology and has a broader last whorl. *M. lanzaeana* Brusina, 1874 may also form weak bulges but has a distinctly wider aperture and a fairly straight whorl outline as documented by Neubauer *et al.* (2011) from Lučane in the Croatian Sinj basin.

Distribution. Middle Miocene of the Kupres and Džepi basins.

Order LITTORINIMORPHA Golikov and Starobogatov, 1975
Superfamily RISSOOIDEA Gray, 1847
Family HYDROBIIDAE Stimpson, 1865
Subfamily BELGRANDIINAE de Stefani, 1877

Genus CYCLOTHYRELLA gen. nov.

Type species. Litorinella candidula Neumayr, 1869; Middle Miocene; Dalmatia.

Derivation of name. Derived from Greek κὺκλος (kyklos; circle) and θὺρα (thyra; door, gate), referring to the almost round aperture.

Included species. Litorinella candidula Neumayr, 1869; *Prososthenia tryoniopsis* Brusina, 1874 (= *Prososthenia*? *humilis* Brusina, 1902); *Belgrandia klietmanni* Neubauer *in* Neubauer *et al.*, 2011.

Diagnosis. Ovoid to conical shell, with large and wrinkled protoconch and well-rounded, slightly everted, and detached aperture.

Description. This genus comprises slender species with up to seven strongly convex whorls. The protoconch is about 250–300 μm in size and comprises somewhat less than one whorl. It is low trochiform with slightly immersed initial part. The surface is covered with distinct wrinkles, which start to fade out at *c.* 0.75 whorls. There, irregular thin spiral threads may occur. The transition to the teleoconch is mostly continuous. In some species, prominent ribs occur. Apart from the protoconch, the most characteristic feature is the detached, sharply edged, slightly everted and widely elliptical to almost round aperture. A narrow umbilicus is developed.

Remarks. The affiliation of the new genus with the subfamily Belgrandiinae is preliminary. Among the eight subfamilies of Hydrobiidae, listed by Bouchet and Rocroi (2005), several genera have comparable protoconch surfaces. Clenchiellinae Taylor, 1966, which are endemic to North America and the Tateinae Thiele, 1925, which are confined to Australia and New Zealand are unlikely candidates because of their biogeographic separation and thus are not discussed.

Among the Hydrobiinae wrinkled protoconch surface is found in *Hydrobia* Hartmann, 1821. However, it additionally develops regular faint spiral striae, which are never observed in the Dinaride species. Similarly, *Islamia* Radoman, 1973, as representative of the Islamiinae Radoman, 1973, has a strongly reticulate surface, but differs largely in its valvatoid growth style and the peristome with sharp edges. Irregular wrinkles are found in *Nymphophilus* Taylor, 1966 (Nymphophilinae Taylor, 1966), which, however, is endemic to North America and beyond that differs in shape (Thompson 1979). An affiliation with the Pseudamnicolinae Radoman, 1977 is unlikely due to the smooth protoconch of *Pseudamnicola* Paulucci, 1878 (see also discussion of *Bania*). Some species included in *Cyclothyrella* were formerly classified as *Prososthenia* Neumayr, 1869, which belongs to the Pyrgulinae Brusina, 1881. This genus, however, lacks a detached and sub-circular aperture and its protoconch lacks wrinkles.

In contrast, several genera of the Belgrandiinae de Stefani, 1877 develop comparable surface patterns: *Belgrandiella* Wagner, 1928, *Daphniola* Radoman, 1973, *Graziana* Radoman, 1975 (Szarowska 2006) and *Belgrandia* Bourguignat, 1869 (Haase 2000). Also growth style, whorl convexity and detached aperture of *Belgrandia* correspond quite well to *Cyclothyrella*; only the strong opercular ridge is missing.

Therefore, a position of *Cyclothyrella* within the Belgrandiinae is proposed herein. The remarkably similar protoconch features of *Cyclothyrella* and *Bania* might indicate a close relation of both genera within the same subfamily. Nevertheless, protoconch features are not necessarily (sub)family-specific (Szarowska 2006).

Wrinkled textures on the embryonic shells are common also in the Cochliopidae Tryon, 1866, which are largely confined to Northern and Southern America (Hershler and Thompson 1992; Wesselingh 2006). Comparable patterns are observed among several genera, e.g. *Coahuilix* Taylor, 1966, *Heleobia* Stimpson, 1865, *Paludiscala* Taylor, 1966, *Phreatoceras* Hershler and Longley, 1987, *Sioliella* Haas, 1949, and *Stygopyrgus* Hershler and Longley, 1986 (Hershler and Thompson 1992; Wesselingh 2006). Of these only *Heleobia* occurs also in extant European freshwater systems. The considered patterns on embryonic shells probably developed several times independently (Hershler and Ponder 1998). The conical to bulbous shape common in *Heleobia* is not found in *Cyclothyrella*. As cochliopids and hydrobiids are today classified based on soft-part anatomy or molecular data, a distinct separation by shell features is simply impossible. Following, a relationship with the Cochliopidae cannot be fully excluded, but the high degree of morphologic similarity with the Belgrandiinae argues for a systematic classification therein.

Cyclothyrella tryoniopsis (Brusina, 1874) comb. nov.
Figure 6B, G, J

1874 *Prososthenia tryoniopsis* Brusina, p. 50, pl. 3, figs 5–6.
1902 *Prososthenia? humilis* Brus.; Brusina, pl. 8, figs 24–26.

Material. 144 specimens from Samples 090709/4; 26 from Sample 090709/5; a few from debris.

Description. Very slender conical shell with up to seven strongly convex whorls. Shell up to 4 mm in height and 1.5 mm in width. Protoconch large with *c.* 300 μm maximum diameter, consisting of about one whorl, without distinct separation from the teleoconch. Its initial part is strongly inflated (*c.* 40 per cent of protoconch diameter). The protoconch is coated with distinct wrinkles, which fade out after *c.* 0.75 whorls and pass into faint irregular spiral threads. The wrinkles are spiky and rather wide-spaced, sometimes even isolated from each other. The teleoconch sculpture comprises sharp and strongly curved axial ribs, which may develop a slight concavity in their adapical half. While ribs become stronger during ontogeny, their number per whorl stays nearly constant (10–14). The last whorl attains about 45–50 per cent of total height and passes into a rather straight base. The aperture is sub-circular, slightly everted and has sharp terminations. Moreover, it is weakly detached, forming a narrow umbilicus. In some specimens, the whole surface is covered with numerous densely spaced spiral lines. In lateral view, a weak indentation occurs in the adapical part of the outer lip.

Remarks. Protoconch features and the sub-circular and nonthickened aperture distinguish this species from *Prososthenia* Neumayr, 1869. In particular, it differs from *Prososthenia schwartzi* Neumayr, 1869 in the rather ovoid shape, the stronger ribs and the everted nonthickened aperture. The strongly ribbed *P. drobaciana* Brusina, 1874 has an ovoid to triangular aperture and a larger last whorl.

Prososthenia? *humilis* Brusina, 1902 was erroneously introduced from Džepi as new species by Brusina (1902). It is a synonym of *C. tryoniopsis*, being almost identical in shape, sculpture and dimensions. The presence of spiral lineation ranges within the typical intraspecific variability.

Distribution. Middle Miocene of the Kupres basin, Drniš basin (Miočić), Sinj basin (Trnovača/Sinj), and Džepi basin.

Subfamily HYDROBIINAE Stimpson, 1865

Genus NEMATURELLA Sandberger, 1875

Type species. Nematurella flexilabris Sandberger, 1875; Middle Miocene; Tramelan, Switzerland.

Nematurella vrabaci sp. nov.
Figure 6A, F, I

1902 *Nematurella*? sp. Brusina, pl. 29, figs 29–30.

Derivation of name. Named in honour of Sejfudin Vrabac, professor of geology and palaeontology at the University of Tuzla in Bosnia and Herzegovina and expert in regional stratigraphy and palaeogeography.

Holotype. NHMW 2011/0138/0108 (Fig. 6A, I).

Paratypes. NHMW 2011/0138/0109; NHMW 2011/0138/0110; both from same sample.

Type locality. Fatelj section, Kupres basin, Bosnia and Herzegovina.

Type horizon. Langhian, Lower Middle Miocene; Unit 3 (Sample 090709/4).

Material. Thirty-three specimens from Sample 090709/4; 48 from debris collections (Unit 3).

Diagnosis. Glossy ovoid shell with largely convex whorls and widely ovoid, detached aperture.

Description. Drop-shaped, smooth shell with up to seven whorls. Shell height attains up to 7 mm; width 3.5 mm. The protoconch is broad trochiform with immersed initial part and comprises *c.* 1 highly convex whorl with granular surface and a maximum diameter of 250 μm. No distinct border to the teleoconch is

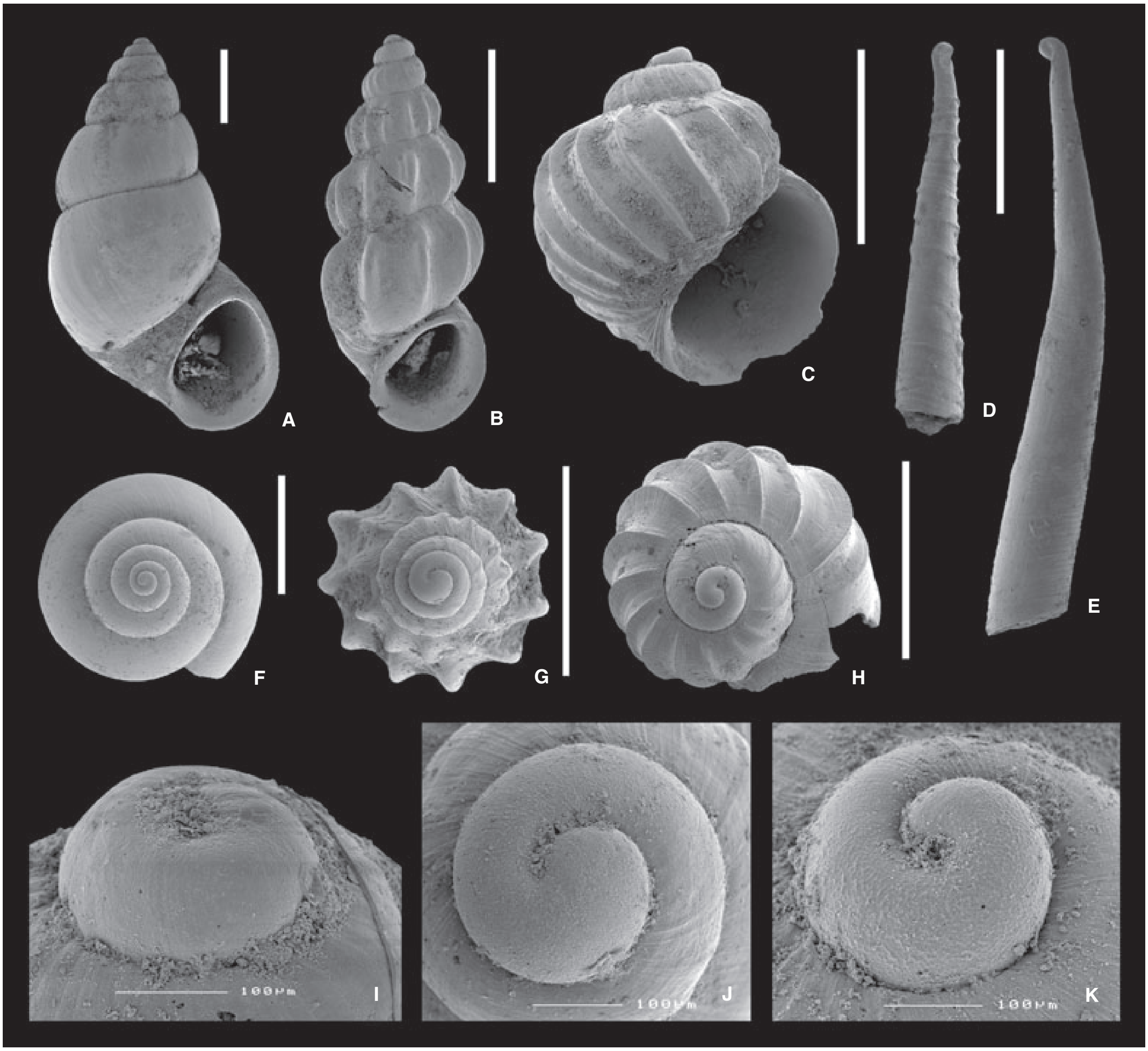

FIG. 6. Hydrobiidae and Planorbidae. A, I, *Nematurella vrabaci* sp. nov.; Holotype, Sample 090709/4, NHMW 2011/0138/0108; front view with detached aperture (A) and detail picture of the apex (I); B, *Cyclothyrella tryoniopsis* (Brusina, 1874); Sample 090709/4, NHMW 2011/0138/0116; front view with everted aperture; C, K, *Bania obliquaecostata* sp. nov.; Holotype, Sample 090709/4, NHMW 2011/0138/0112; front view (C) and magnification of protoconch (K); D, *Orygoceras dentaliforme* Brusina, 1882; Sample 090709/5, NHMW 2011/0138/0127; sculptured morphotype (fractured) exhibiting widely spaced and weak rings; E, *Orygoceras dentaliforme* Brusina, 1882; Sample 090709/5, NHMW 2011/0138/0127; smooth phenotype; F, *Nematurella vrabaci* sp. nov.; from debris of Unit 3, NHMW 2011/0138/0111; apical view; G, J, *Cyclothyrella tryoniopsis* (Brusina, 1874); Sample 090709/4, NHMW 2011/0138/0116; apical view (G) with detail picture of juvenile shell; H, *Bania obliquaecostata* sp. nov.; Sample 090709/4, NHMW 2011/0138/0115. Scale bars represent 1 mm (A–H).

developed. Usually whorls are regularly convex; in some individuals, they may exhibit a more stepped architecture. The sutures are moderately incised. The last whorl grades into a slightly convex base and makes up somewhat more than half of shell height. The aperture is regularly and widely ovoid. In some specimens, it may begin to detach early resulting in a stronger inclined growth direction of the last whorl (Fig. 6A). In either case, it usually becomes detached in fully grown specimens, forming a wide umbilicus. The outer lip is sharply edged and slightly everted in latest ontogeny. In lateral view, it displays two emarginations (anterior and posterior) producing a sinusoidal profile.

Remarks. The wide and detached aperture that lacks thickened lips prevents confusion with any Dinaride species. The similarly sized *Nematurella kadimai* Brusina, 1902 from Lovča in Croatia never displays a detached aperture and has a more distinctly stepped spire. *Prososthenia eburnea* Brusina, 1884 (regarded as *Nematurella* Sandberger, 1875 by Brusina 1902) is more slender and has less convex whorls; the aperture is not detached. The Middle Miocene species *N. flexilabris* Sandberger, 1875 from Switzerland and *N. mediocris* (Ludwig, 1865) from Central Germany expose comparable outlines and degrees of whorl convexity but a nondetached aperture with a distinct rim behind the peristome (Schlickum 1960). *Nematurella pappi* Schlickum, 1960 and *N. scholli* Schlickum, 1960 are more ovoid and also lack the detached aperture.

Subfamily PYRGULINAE Brusina, 1881

Genus MARTICIA Brusina, 1897

Type species. Hydrobia tietzei Neumayr, 1880; Middle Miocene; Bosnia and Herzegovina.

Marticia hidalgoi Brusina, 1902
Figure 7A, E–G

1902 *Marticia Hidalgoi* Brus.; Brusina, pl. 29, figs 31–32.

Material. More than 1000 individuals from Sample 090709/4 and debris collections.

Description. Broad trochiform shell with up to seven whorls. Dimensions usually range around 6 mm in height (max. 7.5 mm) and 3 mm in width (max. 4 mm). The protoconch is high trochiform with weakly immersed initial part and comprises *c.* 1 whorl with strongly granular surface sculpture. It is not clearly separated from the teleoconch. Whorls soon expose a stepped outline with flanks parallel to the axis, a narrow sutural ramp and weakly incised sutures. In most specimens, two keels are formed of which the strongest appears near the upper suture, forming the border between flank and sutural ramp. The second one is formed close to the lower suture. The keels range from weak to prominent, from thin blade-like flanges to broad bulges. In addition, the whorls bear faint spiral grooves. In some individuals, the sculpture is strongly reduced to sutural ramp and spiral lines, without keels. The detachment of the whorls already starts soon resulting in a stronger inclined growth direction of the last whorl, which attains about half of shell height. A distinct angulation appears between the whorl and the rather straight base. The aperture is small and ovoid to subcircular. As it is always detached from the base, it forms a wide umbilicus. The lips have sharp terminations and are almost parallel in lateral view; sometimes, a weak posterior indentation occurs.

Remarks. Differs from *Marticia tietzei* (Neumayr, 1880) from Džepi in the broad shape and the stepped whorl outline. Maybe both taxa represent only local morphotypes of a single species.

Distribution. Restricted to the Kupres basin (Fatelj, Middle Miocene).

Genus PROSOSTHENIA Neumayr, 1869

Type species. Prososthenia schwartzi Neumayr, 1869; Middle Miocene; Dalmatia.

Prososthenia diaphoros sp. nov.
Figure 8E, J

Derivation of name. Derived from Greek διάφορος (diáphoros; different, varying), referring to the axial ribs that do not run parallel with the growth lines.

Holotype. NHMW 2011/0138/0118 (Fig. 8E).

Paratypes. NHMW 2011/0138/0119; NHMW 2011/0138/0120; both from same sample.

Type locality. Fatelj section, Kupres basin, Bosnia and Herzegovina.

Type horizon. Langhian, Lower Middle Miocene; Unit 3 (Sample 090709/4).

Material. Several hundred specimens from Sample 090709/4; a few from debris (Unit 3).

Diagnosis. Slender, fragile and ovoid shell, with a strongly granular protoconch and a thin, roughly semilunar aperture. The last few whorls bear subtle ribs, which are not parallel to the growth lines.

Description. Exceptionally slender shell, with 4.5 mm height and 1.5 mm width, consisting of six whorls. The protoconch measures *c.* 300 μm in diameter and is composed of one low trochiform whorl with strongly granular surface. Its initial part is distinctly inflated and attains about 40 per cent of the total diameter. A distinct rim occurs at the transition to the teleoconch. The maximum convexity of the whorls appears slightly below their middle, forming an almost straight adapical part. In some individuals, this architecture becomes more distinct and results in a spruce-like outline. Densely spaced, delicate ribs occur on the antepenultimate whorl, reaching from suture to suture. Prosocline growth lines cover the surface, whereas the ribs are slightly sigmoidal to orthocline. The last whorl attains about the half of shell height and forms a steep and straight base. The aperture is regularly ovoid to semilunar and develops a thin, continuous peristome. Rarely a narrow umbilicus is developed. In lateral view, two distinct anterior and posterior emarginations are formed on the outer lip.

Remarks. This species is reminiscent of *Prososthenia serbica* Brusina, 1892 from the roughly coeval Lake

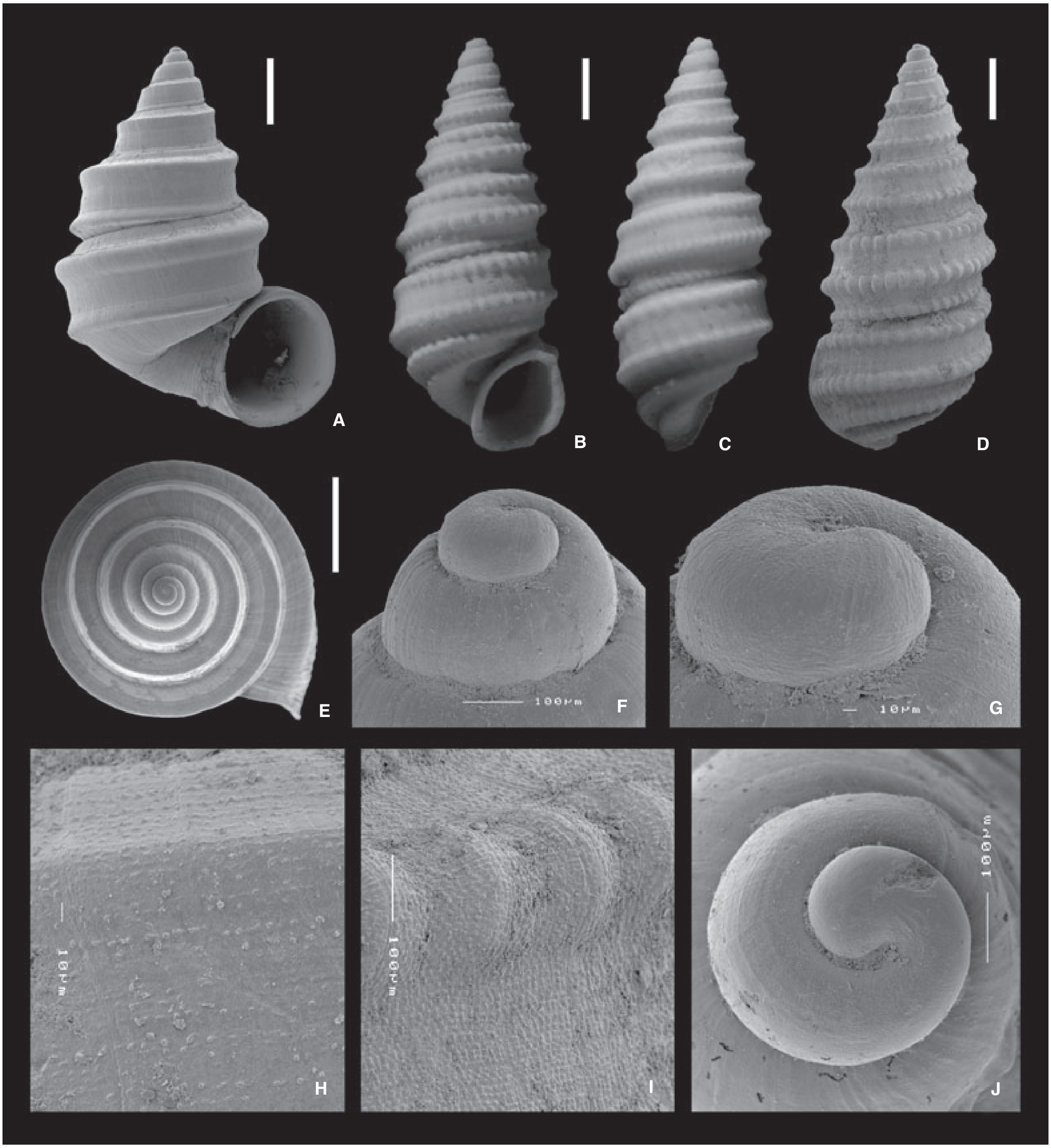

FIG. 7. Pyrgulinae (Hydrobiidae). A, F–G, *Marticia hidalgoi* Brusina, 1902; NHMW 2011/0138/0117; highly keeled specimen in apertural view (A) with magnification of apical region (F) and protoconch (G); B–C, *Pseudodianella haueri* (Neumayr, 1869); NHMW 2011/0138/0126; front and back view; D, H–J, *Pseudodianella haueri* (Neumayr, 1869); NHMW 2011/0138/0126; back view (D), teleoconch sculpture on the third whorl with scattered elongated nodules (H) and on the sixth whorl with a dense pattern of merely quadrate nodules (I), and apical region (J); E, *Marticia hidalgoi* Brusina, 1902; NHMW 2011/0138/0117; apical view. All specimens are from debris of Unit 3. Scale bars represent 1 mm (A–E).

Serbia at Zvezdan near Zaječar in E Serbia (not part of the Dinaride Lake System), corresponding well in whorl outline and apertural emarginations. However, a weak subsutural band is present in the Serbian species, and the columellar lip exhibits a distinct angulation in its centre. Moreover, the herein described species is less conical and exposes a conspicuously larger last whorl.

FIG. 8. *Prososthenia* species (Hydrobiidae). A, F, *P. undocostata* sp. nov.; holotype, from debris of Unit 3, NHMW 2011/0138/0123; front view exposing the thickened aperture (A) and detail of apex (F); B, H, *P. undocostata* sp. nov.; paratype 1, from debris of Unit 3, NHMW 2011/0138/0124; apical view (B) with magnification of protoconch (H); C, I, *P. eburnea* Brusina, 1884; Sample 090709/5, NHMW 2011/0138/0122; apical view (C) with magnification of protoconch (I); D, G, *P. eburnea* Brusina, 1884; Sample 090709/5, NHMW 2011/0138/0122; apertural view (D) and detail of apical region (G); E, *P. diaphoros* sp. nov.; Holotype, Sample 090709/4, NHMW 2011/0138/0118; apertural view; J, *P. diaphoros* sp. nov.; Sample 090709/4, NHMW 2011/0138/0121; apical region. Scale bars represent 1 mm (A–E).

Distribution. Restricted to the Kupres basin (Fatelj, Middle Miocene).

Prososthenia eburnea Brusina, 1884
Figure 8C–D, G, I

1869 *Litorinella ulvae* Pennant sp.; Neumayr, p. 363, pl. 12, figs 10–11 (non *Turbo ulvae* Pennant, 1777).
1874 *Hydrobia stagnalis* Basterot [*sic*]; Brusina, p. 62 (non *Hydrobia stagnalis* Baster, 1765 = *Heleobia stagnorum* (Gmelin, 1791)).
1884 *Prososthenia eburnea* Brusina, p. 49.
1897 *Prososthenia*? *eburnea* Brus.; Brusina, p. 18, pl. 8, figs 30–33, pl. 9, figs 1–2.
1902 *Nematurella*? *eburnea* Brus.; Brusina, pl. 9, figs 10–12.

Material. Several hundred shells from Sample 090709/5; 10 specimens from Sample 090709/4.

Description. Small, slender and fairly ovoid shell. The protoconch exhibits a granular surface and comprises about one depressed whorl. The embryonic cap is immersed. The transition to the teleoconch is marked by a more or less distinct rim. This species is represented by phenotypes of several size classes, whereas the largest (max. 5 mm in height and 2 mm in width) attains about the double size of the smallest class (height: 2.5 mm; width: 1 mm). Intermediate forms occur as well. Depending on size, the specimens have 5–7 whorls, which are weakly convex. Especially in small specimens, this often results in an adpressed architecture forming a regular ovoid to elliptical outline. The last whorl makes up to 50–70 per cent of shell height, whereas smaller individuals usually have a larger body whorl. The aperture is ovoid to semilunar, simple and leaves no umbilicus. Weak growth lines and numerous faint spiral grooves cover the surface.

Remarks. Brusina (1884) introduced *Prososthenia eburnea* as a new species from Miočić and Trnovača at Sinj. Previously, Neumayr (1869) reported *Litorinella ulvae* from the former locality. The Extant European *Hydrobia ulvae* (Pennant, 1777) differs from the Dinaride species clearly in its conical shape and the angulated last whorl. The reinvestigation of the specimens collected by Neumayr (1869) at the Austrian Geological Survey (Vienna) proved that they are conspecific with *P. eburnea*. Similarly, any relation with the Extant European cochliopid *Heleobia stagnorum* (Gmelin, 1791) (= *Hydrobia stagnalis* Baster, 1765) is ruled out based on its distinctly more convex whorls.

This species can be distinguished from *Prososthenia neutra* Brusina, 1897 in its weaker convexity of the whorls and the generally more slender shape.

Distribution. Middle Miocene of the Kupres basin, Drniš basin (Miočić), Sinj basin (Trnovača/Sinj, Turjaci), and Glina subdepression in the southern Pannonian basin (Dugo Selo/Lasinja).

Prososthenia undocostata sp. nov.
Figure 8A–B, F, H

Derivation of name. Derived from Latin *unda* (wave) and *costatus* (ribbed) referring to the wavy pattern formed by the ribs at the upper sutures.

Holotype. NHMW 2011/0138/0123 (Fig. 8A–B).

Paratypes. NHMW 2011/0138/0124; NHMW 2011/0138/0125; both from debris.

Type locality. Fatelj section, Kupres basin, Bosnia and Herzegovina.

Type horizon. Langhian, Lower Middle Miocene; debris of Unit 3.

Material. Twenty-two specimens from debris collection (Unit 3).

Diagnosis. Conical shell with weak axial ribs and distinctly thickened ovoid aperture.

Description. Conical shell with 6 weakly convex whorls. Maximum dimensions range around 5.5 mm in height and 2.5 mm in width. The protoconch measures about 300 μm and consists of about one high trochiform whorl. It displays a granular sculpture and a continuous transition into the teleoconch. Early teleoconch whorls are smooth except for weak growth lines. The last few whorls exhibit weak axial ribs, which form slight convexities at the upper suture. This results in the eponymous undulated pattern. The last whorl encompasses somewhat more than 50 per cent and forms a convex base. The ribs are strongest in its adapical part and tend to fade out towards the base. The aperture is ovoid and notably thickened, especially in its posterior part. No umbilicus is developed. In lateral view, a weak posterior emargination occurs on the outer lip.

Remarks. The granular protoconch sculpture and the ovoid and thickened aperture suggest an affiliation with *Prososthenia* Neumayr, 1869. It differs from *Prososthenia schwartzi* Neumayr, 1869 in its broader conical shape and the weaker ribs. The slender *P. drobaciana* Brusina, 1874 exhibits a similarly thickened aperture but has stronger ribs. *Robicia pyramidella* Brusina, 1897 from the Pliocene of Slavonia is comparable in size and shape but has no thickened aperture. The ribs cover almost the entire teleoconch. In none of these species, an undulated pattern is observed.

Genus PSEUDODIANELLA gen. nov.

Type species. Pyrgula haueri Neumayr, 1869; Middle Miocene; Dalmatia.

Derivation of name. Referring to the similarities with the extant *Dianella* Gude, 1913.

Included species. Pyrgula haueri Neumayr, 1869 (=*Pyrgula inermis* Neumayr, 1869 = *Pyrgula exilis* Brusina, 1876); *Diana amplior* Pavlović, 1903; *Diana petkovici* Pavlović, 1903; *Pyrgula tricarinata* Fuchs, 1877; *Pyrgula brusinai* Tournouër, 1875.

Diagnosis. Ovoid to conical shell, with granular sculpture and faint striae on the protoconch, weakly convex whorls, and distinct basal emargination at the rather small aperture.

Description. The protoconch is slightly granular and shows traces of several weak spiral striae; it comprises about one high trochiform whorl. In some individuals, the transition to the teleoconch is marked by a distinct rim. Whorls are weakly convex with moderately incised sutures. The sculpture consists of spiral keels or spiral rows of nodes, occasionally depending on ontogenetic stage. The aperture is small, ovoid, and somewhat detached with slightly everted and nonthickened lips. In lateral view, a weak posterior indentation appears, whereas a broad emargination is formed at its basal part.

Remarks. Already Brusina (1902) noticed, that several Dinaride taxa cannot be affiliated with the genus *Pyrgula* Cristofori and Jan, 1832. This has a regular conical shape and a distinctly smaller last whorl. The same criteria are mentioned by Clessin (1878) to separate the 'usual *Pyrgula*' from his (extant) species, for which he introduced the new subgenus *Diana*, not knowing, that the name was preoccupied for a fish genus (Risso 1826). Because of this primary homonym, Gude (1913) suggested the new name *Dianella* for all *Diana* species. The protoconch ornamentation, however, clearly distinguishes the Dinaride species from the extant *Dianella thiesseana* (Clessin, 1878), which has a smooth protoconch with numerous small pores (Falniowski and Szarowska 1995*b*; Anistratenko 2008). It differs also from *Pyrgula annulata* (Linnaeus, 1758), which shows a wrinkled to malleate surface (Riedel *et al.* 2001). Nevertheless, the overall shape and the often occurring spiral sculpture suggest a relationship to *Pyrgula* and *Dianella*.

Although their protoconchs are unknown, the Late Miocene '*Diana*' *amplior* Pavlović, 1903 and '*Diana*' *petkovici* Pavlović, 1903 from Skopje basin are included herein in *Pseudodianella* based on their shape and the prominent keels. '*Diana*' *gracilis* Pavlović, 1903 from the same basin does not fit within this concept as it has strongly rounded whorls, a small last whorl and a concave base; it ranges rather within *Micromelania* Brusina, 1874. Brusina (1881) and Wenz (1926) also placed the four species from Burgerstein (1877) from Skopje basin in '*Diana*' or *Dianella*, respectively, which were originally described as *Prososthenia suessi*, *P. crassa*, *P. nodosa*, and *P. reticulata*. However, the axial sculpture, the convex whorls and the posterior thickened aperture separate these taxa clearly from *Pseudodianella*.

Also the Pliocene *Pyrgula tricarinata* Fuchs, 1877, from Livonates near Korinth and *Pyrgula brusinai* Tournouër, 1875 from Kos in Greece, correspond well in outline, spiral sculpture and aperture and thus are regarded as congeneric. This extends the stratigraphic range of the genus *Pseudodianella* at least into the Pliocene.

Pseudodianella haueri (Neumayr, 1869) comb. nov.
Figure 7B–D, H–J

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 var. *exilis* Brus.; Brusina, p. 49.
1875 *Pyrgula Haueri* Neumayr; Sandberger, p. 671, pl. 31, fig. 14.
1876 *Pyrgula exilis* Brusina; Brusina, p. 115.
1902 *Diana exilis* Brus.; Brusina, pl. 7, figs 36–38.
1902 *Diana Haueri* (Neum.); Brusina, pl. 7, figs 33–35.

Material. Thirty-eight specimens from Samples 090709/4; 84 from Sample 090709/5; 127 from debris collections.

Description. Shell regularly ovate with up to eight whorls. Maximum height 9 mm, width 4.5 mm. The protoconch consists of about one whorl that is high trochiform with convex adapical and nearly straight abapical part. In initial stages, it is slightly granular to almost smooth. Later in ontogeny, the granulation becomes more distinct and is accompanied by weak spiral striae. The border to the teleoconch is marked by a distinct rim. The early teleoconch whorls develop two prominent keels. The lower one occurs slightly below the middle of the whorl and causes an angulation. The second one is weaker and occurs directly below the upper suture. These spiral keels soon grade into rows of nodes, which vary from numerous delicate knobs to few broad nodes. A third very weak keel appears on the penultimate whorl close to the lower suture producing there a weak bulge. This keel continues to the base of the last whorl, where it becomes stronger and may bear nodes. There, it is accompanied by another subjacent, weaker keel. In few specimens, sculpture may be reduced to mere intentions. Whorls are generally weakly convex and have moderately incised sutures. The last whorl attains about the half of the total height. The aperture is small and ovoid and with 40 degrees inclined to the axis. The columellar lip is moderately convex and slightly detached from the base, leaving a slit-like umbilicus. The outer lip is well rounded and has sharp terminations. In lateral view, it protrudes centrally (around the second row of nodes), while it is conspicuously indented on the base.

In exceptionally well-preserved specimens, teleoconch microsculpture occurs in the form of spirally arranged lines of pustules (Fig. 8H–I). Its expression is highly depending on ontogeny. In the early stages, the pustules are elongate (*c.* 5 μm in length) and rather scattered. The density increases continuously and grades into a pattern of quadrate pustules nearly without any interspaces on the last whorl.

Remarks. This species exposes a wide spectrum of morphological variations, reaching from highly sculptured to almost smooth forms. Because of this, Neumayr (1869) introduced *Pyrgula inermis* based on only one specimen from Miočić as new species, differing from *P. haueri* in the largely reduced sculpture and the straighter whorl outline. Anyway, it cannot be separated sufficiently and should be treated as a morphological variety of *Pseudodianella haueri*. Likewise, *Pyrgula exilis* Brusina, 1876 was originally described as variety of *P. haueri* by Brusina (1874) referring to type material of Neumayr (1869). It was established based on the slightly different alignment and expression of the nodes: these are smaller and more densely arranged. This, however, cannot serve as specific feature as intraspecific variability tends to be high in this species. Thus, these three taxa (*haueri*, *inermis*, and *exilis*) are treated as phenotypes of a single species.

Distribution. Middle Miocene of the Kupres basin, Drniš basin (Miočić, Biočić, Parčić), and Sinj basin (Trnovača/Sinj, Župića brook/Sinj).

Subfamily INCERTE SEDIS

Genus BANIA Brusina, 1896

Type species. Bania prototypica Brusina, 1872 by monotypy (ICZN 2001); Middle Miocene; Dalmatia/SE Croatia.

Included species

Dinaride Lake System species. Amnicola stosiciana Brusina, 1874 (together with *Pseudoamnicola stosiciana crassa* Brusina, 1897); *Amnicola torbariana* Brusina, 1874; *Bythinella? dokici* Brusina, 1902; *Bythinella? pachychila* Brusina, 1902; *Lithoglyphus panicum* Neumayr, 1869; *Lithoglyphus tripaloi* Brusina, 1884; *Pseudamnicola? pauluccii* Brusina, 1907; *Stalioa prototypica* Brusina, 1872; *Stalioa valvatoides* Brusina, 1874.

*From other regions/*ages. *Paludestrina pseudoglobulus* d'Orbigny, 1852 from the Late Langhian – Early Serravallian of the Steinheim basin (Finger 1998); *Paludina immutata* von Frauenfeld *in* Hörnes, 1856 from the Serravallian of the Eisenstadt-Sopron basin (*sensu* Harzhauser and Kowalke 2002); *Pseudamnicola hoeckae* Harzhauser and Binder, 2004 from the Tortonian of the Vienna basin; *Pseudamnicola*? *spreta* Brusina, 1897 from the Pliocene of Slavonia.

Diagnosis. Comprising small and rather sturdy species, always with reticulate protoconch and convex to step-like whorls.

Description. Minute shells, usually not exceeding 3.5 mm in height. The protoconch is always wrinkled (reticulate), usually with strongest expression in early ontogeny and fading out towards the mostly indistinct transition to the teleoconch; it consists of somewhat more than one whorl. More or less prominent, prosocline growth lines cover the teleoconch. The shell consists of up to five whorls, which are usually strongly convex and sometimes form a stepped spire. In most cases, the last whorl makes up more than two-thirds of shell height. The aperture is ovoid, usually everted and sometimes conspicuously detached from the base. Occasionally, it may be particularly thickened. An umbilicus may occur depending on grade of detachment, thickening and growth style.

Remarks. The reticulate protoconch clearly unites the affiliated species. After the studies of the protoconchs of type material from Neumayr (1869), Brusina (1872, 1874, 1884, 1897, 1907) and Harzhauser and Binder (2004) and material from Finger (1998) and Harzhauser and Kowalke (2002), several taxa formerly or currently classified under the genera *Amnicola* Gould and Haldeman in Haldeman, 1840, *Pseudamnicola* Paulucci, 1878 or *Lithoglyphus* Pfeiffer, 1828 are now referred to *Bania* Brusina, 1896. Data on embryonic shells of *Bythinella*? *dokici* Brusina, 1902, *Bythinella*? *pachychila* Brusina, 1902, and *Pseudamnicola*? *spreta* Brusina, 1897 are still not available. They are thus only preliminary placed herein based on similarities in shell morphology. Because of the wide temporal and geographical distribution (see above), it can be assumed that many of the roughly coeval Neogene European species currently assigned to *Amnicola* or *Pseudamnicola* (Wenz 1926) actually represent species of *Bania*.

An affiliation with *Pseudamnicola* is rejected because of the smooth protoconch of the latter taxon (Falniowski and Szarowska 1995*a*; pers. obs. on type species *Pseudamnicola lucensis* (Issel, 1866), NHMW Malacological Collection, Inv. no. 32906). Likewise, a classification as *Lithoglyphus* Pfeiffer, 1828 is ruled out, as it has a largely smooth to weakly granular protoconch (Falniowski 1990; Szarowska 2006). A detailed discussion of the nomenclatorial problems concerning *Stalioa* Brusina, 1870 and *Bania* Brusina, 1896 was provided by Kadolsky (1993, 1998) and in the subsequent decision of the ICZN, Opinion 1965 (2001). Following, the next available genus name to unite the considered species is *Bania* Brusina, 1896.

Bania prototypica was initially placed within the Emmericiinae because of the apertural thickening (Brusina 1870). However, the embryonic shells found in Emmericiinae usually attain about the double size and are smooth or covered with small pits (Szarowska 2006; Harzhauser *et al.* 2012; Neubauer *et al.* 2011). Also apertures are mainly larger and distinctly curved in lateral view. Protoconch sculpture and shape also exclude a systematic position within the Pseudamnicolinae Radoman, 1977 or the Lithoglyphidae Tryon, 1866.

However, no clear family affiliation can be presented so far. As the reticulate pattern on the protoconch is also frequent in Belgrandiinae (see discussion of *Cyclothyrella* gen. nov.), a phylogenetic position therein might be possible. *Bania* would also fit within the broad spectrum of forms known among the Belgrandiinae concerning its shape.

Bania obliquaecostata sp. nov.
Figure 6C, H, K

Derivation of name. Derived from Latin *obliquus* (inclined) and *costatus* (ribbed), referring to the teleoconch sculpture.

Holotype. NHMW 2011/0138/0112 (Fig. 6C, K).

Paratypes. NHMW 2011/0138/0113; NHMW 2011/0138/0114; both from same sample.

Type locality. Fatelj section, Kupres basin, Bosnia and Herzegovina.

Type horizon. Langhian, Lower Middle Miocene; Unit 3 (Sample 090709/4).

Material. Twenty-one specimens from Sample 090709/4; three from debris (Unit 3); mainly fractured.

Diagnosis. Minute, globose shell with reticulate protoconch, distinct oblique ribs, and large, sharply edged aperture.

Description. Minute fragile shell with up to four strongly convex whorls. The sturdy to globose shell attains about 2.5 mm in height and 2 mm in diameter. The protoconch comprises somewhat less than one whorl; its microsculpture is reticulate, fading out after about half a whorl. The sutures are strongly incised. The whorl convexity has its maximum in the upper half, resulting in a slightly stepped spire. The early teleoconch is smooth apart from densely spaced prosocline growth lines. Soon, weak axial ribs appear which rapidly increase in strength. They are strongly inclined and form distinct and sharp triangular crests in profile. Additionally, in some specimens, weak and irregular spiral grooves and threads cover the surface. The last whorl attains about 80 per cent of the total shell height and grades into a straight base. The aperture is large, strongly inclined and parallel to the axial ribs. The outer lip is simple, neither thickened nor everted. No umbilicus is developed.

Remarks. This species is easily identified based on its peculiar sculpture displaying strongly inclined ribs. Such a pattern has not been found in any other Dinaride taxon. Such extremely bulky shapes are generally untypical among hydrobiids. Slightly reminiscent taxa are found in *Sadleriana* Clessin, 1890 and some pseudamnicolid species, both of which have an entirely smooth protoconch (Falniowski and Szarowska 1995*a*; Szarowska 2006). Also some species of *Zagrabica* Brusina, 1884 may form globular shells. Their protoconchs are unknown so far. However, this genus is known only from the Late Miocene to Pliocene of South-Eastern Europe (Brusina 1897; Macaleţ 2005). Moreover, *Zagrabica* species are usually distinctly larger.

Clade PANPULMONATA Jörger *et al*., 2010
Order HYGROPHILA Férussac, 1822
Suborder BRANCHIOPULMONATA Morton, 1955
Family PLANORBIDAE Gray, 1840

Genus ORYGOCERAS Brusina, 1882

Type species. Orygoceras dentaliforme Brusina, 1882; Middle Miocene; Dalmatia, SE Croatia.

Orygoceras dentaliforme Brusina, 1882
Figure 6D–E

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 dentaliforme* Brus.; Brusina, p. 2, pl. 1, figs 13–14.
1897 *Orygoceras euglyphum* Brus. n. sp.; Brusina, p. XV (*nomen nudum*).
1897 *Orygoceras leptonema* Brus. n. sp.; Brusina, p. XV (*nomen nudum*).
1897 *Orygoceras stenonemus* Brus.; Brusina, p. 2, pl. 1, figs 10–12.
1902 *Orygoceras bifrons* Brus.; Brusina, pl. 2, figs 6–14.
1902 *Orygoceras cornucopiae* Brus.; Brusina, pl. 2, figs 15–16.
1902 *Orygoceras curvum* Brus.; Brusina, pl. 2, figs 2–5.
1902 *Orygoceras euglyphum* Brus.; Brusina, pl. 2, figs 17–19.
1902 *Orygoceras leptonema* Brus.; Brusina, pl. 2, figs 20–22.
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.
2011 *Orygoceras cornucopiae* Brusina 1882; Neubauer *et al*., p. 213, pl. 6, fig. 7.

Material. Thirty-seven specimens from Sample 090709/4; *c.* 100 from Sample 090709/5; mainly fractured.

Description. Uncoiled, dentaliform shell with max. length of 8 mm and max. width of 1.5 mm. The planispirally coiled protoconch comprises less than one whorl and bears faint spiral striae. The teleoconch exposes a great variety of growth and sculpture patterns. It may be straight to slightly angulated (Fig. 6E), smooth to highly ornamented. The sculpture ranges from faint rings to distinct blades, both with variable spacing and inclination. Also the position of these rings varies. In profile, the shell is ovoid to slightly semilunar. The aperture is inclined and often exposes a ring directly behind the opening, even in otherwise smooth specimens.

Remarks. Beginning in 1882, Brusina (1882, 1897, 1902) introduced almost 10 species of this enigmatic genus within the Dinaride Lake System, most of which differ only in sculpture. This, however, may diverge largely between different environments, e.g., depending on varying carbonate availability (see discussion below). The co-occurrence of *Orygoceras dentaliforme* Brusina, 1882, *O. stenonemus* Brusina, 1882, and *O. cornucopiae* Brusina, 1882 in several localities suggests them to be morphotypes of one species rather than biological species. Likewise, also *O. euglyphum* Brusina, 1897 and *O. leptonema* Brusina, 1897 from Dugo Selo, and *O. bifrons* Brusina, 1902 from Džepi range within that variability. The curved *O. curvum* Brusina, 1902 from Džepi corresponds in sculpture (if present) and whorl profile also well with *Orygoceras dentaliforme* and is regarded as further phenotype.

Only *Orygoceras tropidophorum* Brusina, 1902 from Džepi may represent a separate species based on its two distinct spiral keels and the contorted teleoconch.

Distribution. Middle Miocene of the Kupres basin, Džepi basin, Drniš basin (Miočić, Parčić), Sinj basin (Ribarić, Lučane, Trnovača, Župića potok), Gacko basin (Vrbica/Avtovac, Gračanica), and Glina subdepression in the southern Pannonian basin (Dugo Selo/Lasinja).

Class BIVALVIA Linnaeus, 1758
Superorder HETERODONTA Neumayr, 1883
Order VENERIDA Gray, 1854
Family DREISSENIDAE Gray *in* Turton, 1840

Genus MYTILOPSIS Conrad, 1857

Type species. Mytilus leucophaeatus Conrad, 1831; Recent; Eastern USA.

Mytilopsis aletici (Brusina, 1907)
Figure 9A–G

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.

Material. One articulated specimen, 14 right valves, 6 left valves and numerous fragmented specimens from Samples 090709/3–8 and 090710/1–4.

Description. Shell up to 45 mm in size, as high as long, thin shelled, low convex and strongly inflated in the initial *c.* 20 mm of growth, afterwards flattened. Outline with straight dorsal margin and rounded ventral margin, inequilateral with strongly reduced anterior shell portion; a sinus-like inlet might be present posteroventrally in adult individuals. The anterodorsal shell margin forms an acute, ear-like protrusion. The umbo projects over the dorsal margin. A sharp transversal keel is present proximally becoming more or less suppressed at a length of about 12 mm. It might be formed as weak radial undulation of the shell joining distally the posteroventral sinus. An additional proximal keel can occur dorsally of it. Outer shell surface is shiny with fine growth lines bundled to growth rugae resulting in a wavy outer shell surface. The anterior part of the dorsal margin is shortened, reaching maximally 25 per cent of anterior length. The hinge plate is narrow and concave with reduced, granular apophysis, which is slightly projecting posteroventrally (Fig. 9B). A fine, distally thinning ligament ridge strikes parallel to the posterior dorsal margin.

Remarks. The type locality of this species is Košute in the Sinj basin. Unfortunately, the type specimens are lost (Kochansky-Devidé and Slišković 1978). These authors considered it to be endemic for the Sinj basin but closely related to *Mytilopsis frici* (Brusina, 1906) from the Šipovo basin. Based on the regional stratigraphic position and the high grade of evolutionary adaptation of both species, they were discussed as stratigraphic markers for the youngest deposits of the Dinaride Lake System by Kochansky-Devidé and Slišković (1978). The stratigraphic range of *M. aletici* was currently constrained by integrated Ar/Ar geochronology and magnetostratigraphy to the time interval from 15.3 to 15.0 Ma (De Leeuw *et al.* 2010).

Its presence in Fatelj and in Hodovo, SE of Mostar was reported by Kochansky-Devidé and Slišković (1981). In both localities, they were identified together with *M. volucris bicostata* (Kochansky-Devidé and Slišković, 1981) and *M.* cf. *katzeri* (Kochansky-Devidé and Slišković, 1978).

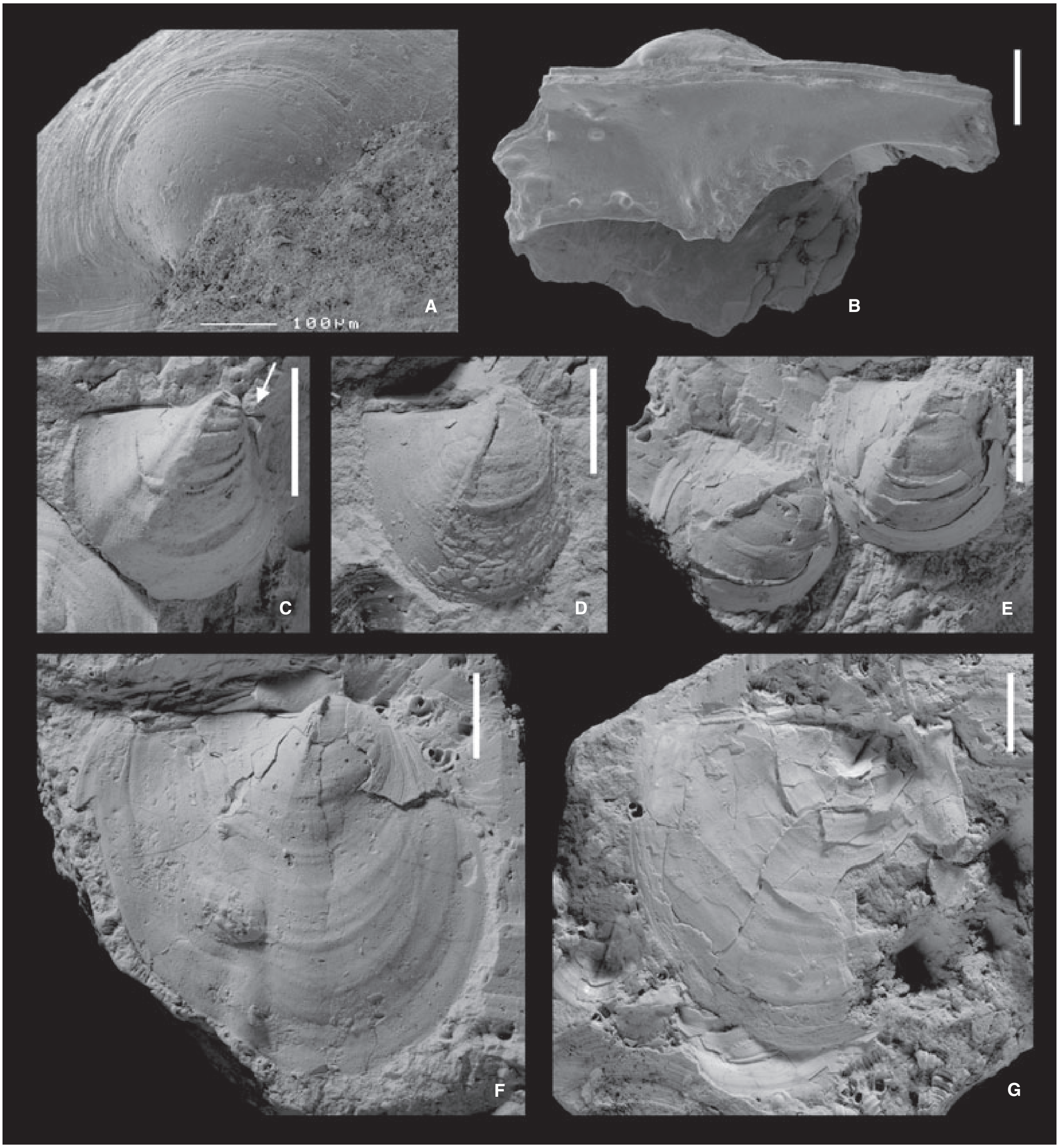

FIG. 9. *Mytilopsis aletici* (Brusina, 1907; Bivalvia: Dreissenidae). A–B, NHMW 2011/0138/0128; right valve with view of protodissoconch (A) and hinge plate with apophysis (B); C, NHMW 2011/0138/0049; right valve of a subadult morphotype with two weak keels (the arrow signals the anterodorsal protrusion); D, NHMW 2011/0138/0053; right valve of a subadult specimen; E, NHMW 2011/0138/0047; right valves of two subadult individuals; F, NHMW 2011/0138/0066; right valve of a fully grown specimen; G, NHMW 2011/0138/0066; articulated adult specimen with fragmented right valve and view on the interior side of the left valve. All specimens are from debris collections of Unit 3, except for C and D (Unit 1). Scale bars represent 1 mm (B) and 1 cm (C–G), respectively.

Contrasting previous results, the present study implies that in Fatelj only one single species occurs, whereas the other two names represent erroneous identifications of younger ontogenetic stages of *M. aletici*. In particular, it could be verified that all collected specimens have an anterodorsal shell protrusion that is typically present in

M. aletici but absent in *M. katzeri* and *M. volucris*. Such protrusion is apparently missing in *M. frici* as well, allowing objective distinction of that otherwise very similar species.

Distribution. Middle Miocene of the Kupres basin, Sinj basin (Lučane, Košute, Brnaze, Grab) and Hodovo-Rotimlja basin (Hodovo).

DISCUSSION

Palaeoecology

The section represents a shallowing upward interval. The very fine marl and the dominance of moderately sized dreissenid bivalves in Unit 1 can be interpreted as somewhat deeper littoral settings (Harzhauser and Mandic 2004, 2010). Unit 2 is barren of fossils and may represent a phase of unsuitable conditions for settlement of benthic fauna. The accumulation of large-sized *Mytilopsis aletici* shells at the base of Unit 3 points already to a slightly shallower, but still lentic depositional setting and might represent tempestitic layers. Finally, the gastropod coquina on top marks a very calm littoral setting. Particularly, Hydrobiidae are the dominating group within that unit: in Sample 090709/4, they attain 94.6 per cent of the total individual number. The most abundant taxa are *Marticia hidalgoi* Brusina, 1902 and *Prososthenia diaphoros* sp. nov., followed by *Cyclothyrella tryoniopsis* (Brusina, 1874), together accounting for 85.7 per cent (Fig. 10). Interestingly, most of the taxa are fairly small (<1 cm). Also the few occurring melanopsids are represented largely by the rather small *Melanopsis mojsisovicsi* (Neumayr, 1880). Pulmonates are represented by one species only (*Orygoceras dentaliforme* Brusina, 1882). In many other Dinaride lakes, they are usually more diverse (e.g. Sinj, Drniš, and Gacko basins). Such a composition of mollusc assemblage points to a perennial long-lived lake with a shallow littoral mud flat setting (Bick and Zettler 1994; Glöer 2002).

A noteworthy aspect in the faunal composition is the overall high diversity of melanopsids and hydrobiids. This is in contrast to patterns observed in many extant long-lived lakes showing exclusive radiations in one of these families (Michel 1994). This author supposed that if both hydrobiids and ‘thiarids’ are represented in a lake system, only one or the other clade shows high rates of endemic evolution. Obviously, this hypothesis cannot be applied in general, as species richness in the Kupres basin is comparable in both families (Melanopsidae: 7, Hydrobiidae: 8).

Patterns of morphological evolution

The most striking feature of the presented fauna is its high percentage of sculptured taxa. Of the 17 gastropod taxa, 13 always display ornamentation encompassing a great variety of patterns. Only *Nematurella vrabaci* sp. nov. and *Prososthenia eburnea* Brusina, 1884 lack any macrosculpture. Two further species, *Theodoxus imbricatus* (Brusina, 1878) and *Orygoceras dentaliforme* Brusina, 1882 expose sculpture only in few specimens (in *Orygoceras c.* 40 per cent in Sample 090709/4).

In Sample 090709/4, the amount of sculptured individuals attains 94.0 per cent. The percentage of sculptured

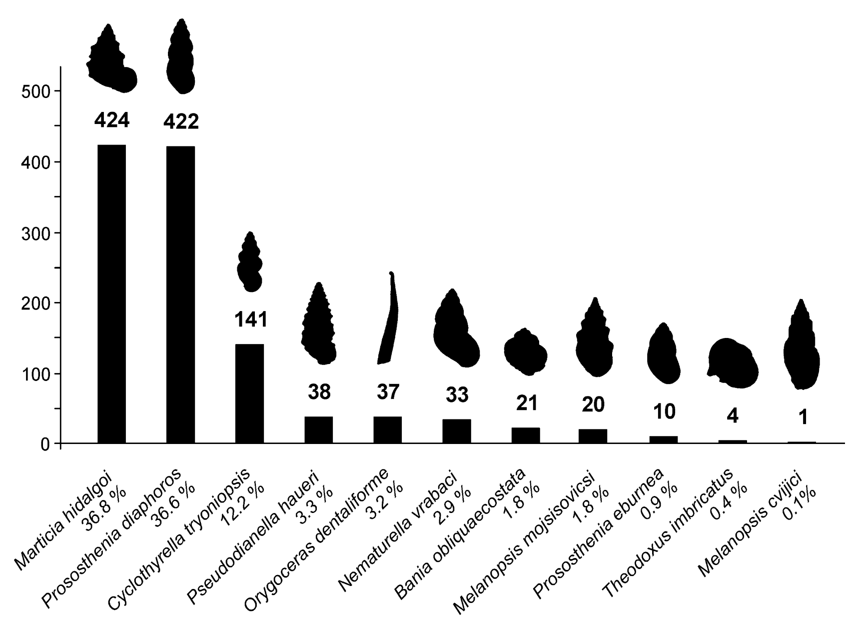

FIG. 10. Abundances of molluscs in Sample 090709/4, exhibiting the clear domination of *Marticia hidalgoi* Brusina, 1902 and *Prososthenia diaphoros* sp. nov., followed by *Cyclothyrella tryoniopsis* (Brusina, 1874). The mollusc images are not to scale.

specimens varies largely between Samples 4 and 5. Although no quantitative data exist for Sample 090709/5 smooth *Prososthenia eburnea* Brusina, 1884 obviously dominates. Also among *Orygoceras* a distinctly lower proportion of sculptured morphotypes is recorded.

The high degree of ornamentation in unrelated taxa points to an extrinsic trigger mechanism. Common explanation models favour escalation, i.e. the co-evolution of predator and prey, to result in thicker and highly sculptured phenotypes (Vermeij and Covich 1978; West and Cohen 1994; Wilson *et al.* 2004). Indeed, especially among melanopsids, the number of repair marks is striking (Figs 4K, 5B–C, F, H). The hypothesis is supported by some findings of fish remains, indicating potential predators. However, hydrobiids almost lack any scars or repair marks. Thus, escalation as selection pressure maintaining sculptured phenotypes can be largely excluded, especially regarding the dominating hydrobiids. At least an influence of predation on gastropod population structure can be assumed.

There is no allochthonous clastic material recorded from the section, pointing to negligible fluvial influx and minor sediment transport into the lake. This supported the establishment of rather restricted lake environments during phases of lowered lake level with enhanced carbonate precipitation because of increased water temperature (Cohen 2003). Indeed, the tendency to strongly sculptured morphologies is comparable to the pattern observed in Lake Sinj. There, aridity associated with falling lake level, higher evaporation and enhanced carbonate availability are considered to have favoured the formation of larger and ornamented shells (Neubauer *et al.* 2011, unpublished data). As the development of the Kupres basin is widely unknown and the depositional interval of Fatelj section is too short, no distinct evolutionary trend can be identified. Nevertheless, a high degree of carbonate production is obvious as Sample 090709/4 consists by about 90 per cent from authigenic carbonate material. The carbonate saturated and alkaline lake water might have favoured excessive shell accretion. This might also explain the enigmatic teleoconch microsculpture in *Pseudodianella haueri* (Neumayr, 1869), which in general is rarely found in hydrobiids (Hershler and Ponder 1998). As an additional effect, the mechanically robust shells might have provided a good defence against molluscivore fish predators.

Palaeobiogeography

The studied fauna of the Kupres basin is part of the endemic Dinaride Lake System fauna. Within that system, it displays an endemicity of 30 per cent. This confirms that autochthonous evolution within the single palaeo-lakes played an important role in diversification of the fauna. Such a pattern is recorded also from the Sinj basin (Neubauer *et al.* 2011, unpublished data) and shows that the Dinaride Lake System fauna should not be treated as entity as done in Harzhauser and Mandic (2008).

The palaeogeographic distribution of widespread taxa implies that faunal exchange was strongly correlated with geographic distance. That is evidenced in the high faunal similarity of the Kupres basin with the close by Sinj and Drniš basins (38.9 per cent) and the Džepi basin (33.3 per cent; Table 1). The distribution of shared taxa in the three regions implies the transitional character of the Kupres basin within the Dinaride Lake System. The first two basins share mostly the same species whilst the third one has largely other faunal elements in common with the Kupres basin, documenting a strong East-West gradient. In particular, except for *Theodoxus imbricatus* (Brusina, 1878) and *Mytilopsis aletici* (Brusina, 1907), the Drniš and the Sinj basin share all other species that they have in common with the Lake Kupres fauna (*Melanopsis geniculata* Brusina, 1874, *Melanopsis lyrata* Neumayr, 1869, *Cyclothyrella tryoniopsis* (Brusina, 1874), *Prososthenia eburnea* Brusina, 1884, *Pseudodianella* gen. nov. *haueri* (Neumayr, 1869), and *Orygoceras dentaliforme* Brusina, 1882). In contrast, despite its high similarity to Fatelj, the Džepi fauna shows distinctly decreased relations to the Sinj and Drniš faunas, having only two species in common (*C. tryoniopsis* and *O. dentaliforme*). The fact that closer basins share larger percentages of the faunal content confirms that the

TABLE 1. Mollusc taxa from Fatelj shared with Sinj basin, Drniš basin and Džepi basin.

Taxon	Sinj basin	Drniš basin	Džepi basin
Theodoxus imbricatus (Brusina, 1878)		×	
Melanopsis angulata Neumayr, 1880			×
Melanopsis corici sp. nov.			
Melanopsis cvijici Brusina, 1902			×
Melanopsis geniculata Brusina, 1874	×	×	
Melanopsis lyrata Neumayr, 1869	×	×	
Melanopsis medinae nom. nov.			×
Melanopsis mojsisovicsi (Neumayr, 1880)			×
Cyclothyrella tryoniopsis (Brusina, 1874)	×	×	×
Nematurella vrabaci sp. nov.			
Marticia hidalgoi Brusina, 1902			
Prososthenia diaphoros sp. nov			
Prososthenia eburnea Brusina, 1884	×	×	
Prososthenia undocostata sp. nov.			
Pseudodianella haueri (Neumayr, 1869)	×	×	
Bania obliquaecostata sp. nov.			
Orygoceras dentaliforme Brusina, 1882	×	×	×
Mytilopsis aletici (Brusina, 1907)	×		

Dinaride Lake System also primary consisted of largely isolated lacustrine environments getting only occasionally and locally into contact. Such events could occur during humid climate periods when the regional lake levels increased. Such climate intervals, paced to 400 and 100 kyr eccentricity maxima, were currently recognised also as triggers of the immigration of DLS elements into the Gacko basin (Mandic *et al.* 2011).

Biostratigraphy

The high endemicity of the fauna excludes a biostratigraphic correlation outside the Dinaride Lake System. In particular, no coeval freshwater system in Europe shows any elements found herein (Harzhauser and Mandic 2008, 2010; Harzhauser *et al.* 2012). Beyond that, their regional correlation is challenged by the evolutionary island character of the fauna within the various palaeolakes of the Dinaride Lake System, as demonstrated above. Nevertheless, the faunistic relations of the Fatelj fauna with the assemblages from the Sinj, Drniš and Džepi basins imply some exchange and document that all these assemblages were roughly coeval.

Comparing similarities between single localities (and not basins), the described fauna displays the strongest affinities with Miočić of the Drniš basin (Fig. 1; Table 1). Seven species occur in both sections (Neumayr 1869; Brusina 1874, 1897, 1902). In contrast, Lučane in the Sinj basin, which shares the biostratigraphic marker species *Mytilopsis aletici* with Fatelj, has only two other taxa in common with it (*Melanopsis lyrata* and *Orygoceras dentaliforme*; Neubauer *et al.* 2011). Lučane shares 48 per cent of taxa with Miočić (Neubauer *et al.* 2011) but lacks *M. aletici* that has never been found in the Drniš basin (Kochansky-Devidé and Slišković 1978, 1981). Its phylogenetic predecessor *M. drvarensis* is frequent in that basin (Žagar-Sakač and Sakač 1984) but absent in Miočić. Based on these patterns, a rough age correlation between the three localities can be proposed. The fauna from Fatelj seems to be slightly younger than the highly similar Miočić fauna, which precedes the FOD of *M. aletici*. In contrast, it is slightly older than the Lučane fauna, which includes already the strati-

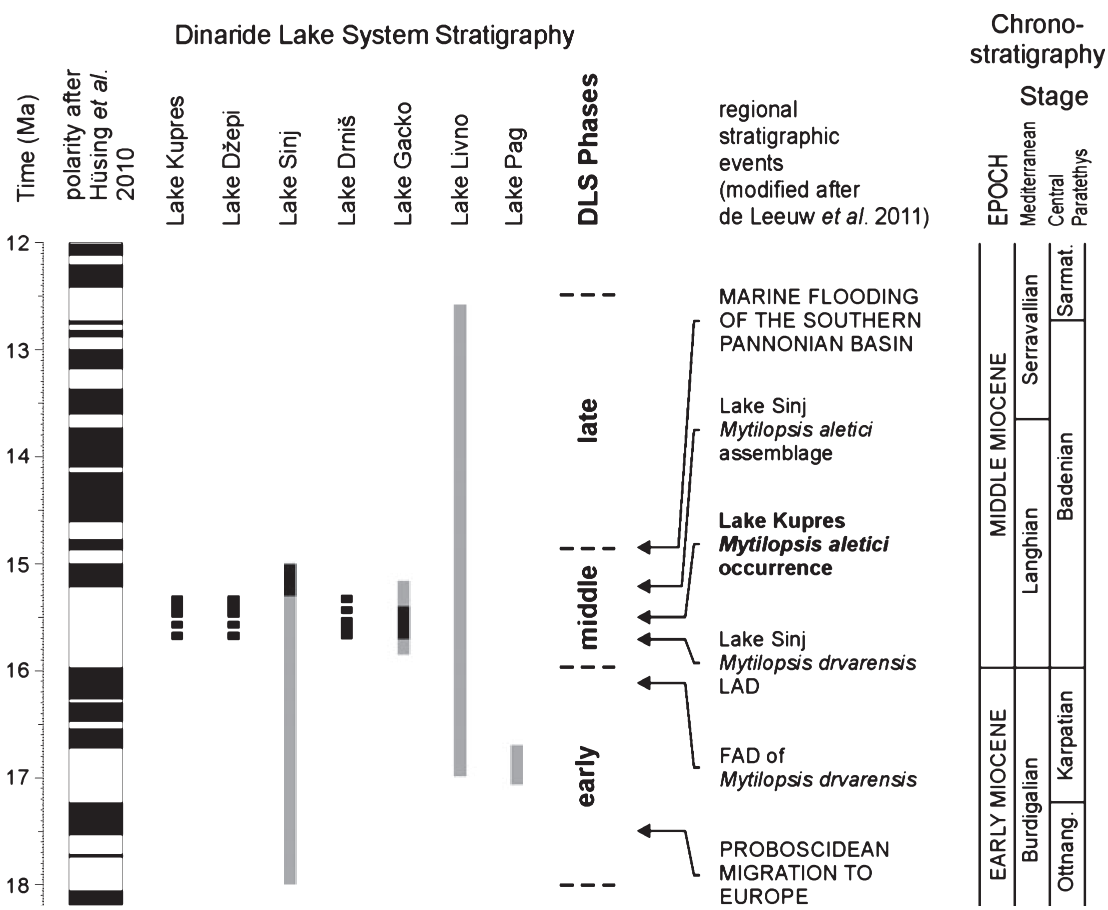

FIG. 11. Time-frame of the Dinaride Lake System with stratigraphic ranges of certain basins referred to in the discussion. The grey bars reflect the total (dated) stratigraphic range of a basin; the black bars correspond to intervals of faunal overlap with the Kupres basin, whereas the dashed parts signal biostratigraphic uncertainties.

graphic marker *M. aletici*. The stratigraphic range of the older *M. drvarensis* at the Lučane section spans a time interval between 15.9 and 15.7 Ma and that of *Mytilopsis aletici* covers an interval of 15.3 and 15.0 Ma (De Leeuw *et al.* 2010). Therefore, the fauna of Fatelj seems to have developed around 15.5 ± 0.2 Ma (Langhian, early Middle Miocene; Fig. 11). The high similarity with the up to know undated Džepi fauna suggests that it is approximately of the same age.

Hence, the presented stratigraphic concept, which is rooted in recent age models for the DLS (Jiménez-Moreno *et al.* 2009; De Leeuw *et al.* 2010, 2011; Mandic *et al.* 2011), represents an important milestone in understanding the origin and evolution of the Dinaride Lake System as palaeogeographic barrier between the Paratethys and the Mediterranean Sea.

Implications for hydrobiid taxonomy

This study provides a discussion of several supraspecific taxa among the Hydrobiidae. The newly described and revised genera not only comprise species endemic to the DLS but have influence on taxonomy throughout the Neogene of Europe. Hence, *Bania* is by far no endemic taxon but is known at least from the Middle Miocene to Pliocene of the Pannonian basin, the Vienna basin and the Steinheim basin in Southern Germany (Brusina 1897; Finger 1998; Harzhauser and Kowalke 2002; Harzhauser and Binder 2004). Likewise, *Pseudodianella* gen. nov. is known from the Late Miocene of the Skopje basin and the Pliocene of Greece (Fuchs 1877; Pavlović 1903). Only *Cyclothyrella* gen. nov. is documented so far only from the DLS.

On a broader scale, this investigation might be a useful contribution for the taxonomic revision of lacustrine hydrobioids of the Neogene of Europe, whose systematics is actually poorly known. Especially on family and subfamily level, many current classifications follow largely outdated concepts of the late nineteenth and early twentieth century (Wenz 1923–1930, 1938–1944) based on macromorphological characters. In future, more attention has to be directed to early ontogenetic stages of gastropods to increase our toolkit in reconstructing fossil biodiversity.

Acknowledgements. Our sincere thanks go to Medina Mandic (Vienna) for the assistance with the field work, Alice Schumacher (NHMW) for the photographs, and Reinhard Zetter (University of Vienna) allowing the SEM documentation at the Department of Palaeontology. Daniela Esu (University of Rome) and Frank P. Wesselingh (NCB Naturalis) are thanked for their constructive reviews. The study was financed by the FWF Project P18519-B17: 'Mollusc Evolution of the Neogene Dinaride Lake System'.

Editor. Svend Stouge

REFERENCES

ADAMS, H. and ADAMS, A. 1853–1858. *The genera of Recent Mollusca arranged according to their organizations*. Van Voorst, London, 2 vol. of text (661 pp.), 1 vol. of plates.

ANISTRATENKO, V. V. 2008. Evolutionary trends and relationships in hydrobiids (Mollusca, Caenogastropoda) of the Azov-Black Sea basin in the light of their comparative morphology and paleozoogeography. *Zoosystematics and Evolution*, **84** (2), 129–142.

BANDEL, K. 2000. Speciation among the Melanopsidae (Caenogastropoda). Special emphasis to the Melanopsidae of the Pannonian Lake at Pontian time (Late Miocene) and the Pleistocene and Recent of Jordan. *Mitteilungen aus dem Geologisch-Paläontologischen Instituts der Universität Hamburg*, **84**, 131–208.

BASTER, J. 1765. *Opuscula subseciva, observationes miscellaneas de animalculis et plantis quibusdam marinis, eorumque ovariis et seminibus continentia. Tomus II. Liber II.* Bosch, Harlemi, 53–99.

BICK, A. and ZETTLER, M. L. 1994. The Distribution of Hydrobiids and the Effect of Sediment Characteristics on the Population Dynamics of *Hydrobia ventrosa* in a Coastal Region of the Southern Baltic. *International Review of Hydrobiology*, **79** (3), 325–336.

BOUCHET, P. and ROCROI, J.-P. 2005. Classification and Nomenclator of Gastropod Families. *Malacologia*, **47**, 1–397.

—— —— 2010. Nomenclator of Bivalve Families; with a classification of bivalve families by R. BIELER, J. G. CARTER, and E. V. COAN. *Malacologia*, **52**, 1–184.

BOURGUIGNAT, J. R. 1869. *Catalogue des mollusques terrestres et fluviatiles des environs de Paris à l'Époche Quaternaire. Annexe de l'ouvrage âges antéhistoriques*. Paris, 33 pp.

BRUSINA, S. 1870. Monographie der Gattungen *Emmericia* und *Fossarulus*. *Verhandlungen der Kaiserlichen und Königlichen Zoologisch-Botanischen Gesellschaft in Wien*, **20**, 925–938.

—— 1872. Naravoslovne crtice sa sjevero-istočne obale Jadranskoga mora. Dio prvi. Putopis. *Rad Jugoslavenske Akademije Znanosti i Umjetnosti*, **19**, 105–177.

—— 1874. *Fossile Binnen-Mollusken aus Dalmatien, Kroatien und Slavonien nebst einem Anhange*. Actienbuchdruckerei, Agram, 138 pp.

—— 1876. Decription d'espèces nouvelles, provenant des terrains tertiaires de Dalmatie. *Journal of Conchology*, **24**, 109–116.

—— 1878. Molluscorum fossilium species novae et emendatae in tellure tertiaria Dalmatiae, Croatiae et Slavoniae inventae. *Journal de Conchyliologie*, **21**, 347–356.

—— 1881. Le Pyrgulinae dell'Europa orientale. *Bollettino della Società Malacologica Italiana*, **7** (13–19), 229–292.

—— 1882. *Orygoceras*. Eine neue Gasteropodengattung der Melanopsiden-Mergel Dalmatiens. *Beitrage zur Paläontologie Österreich-Ungarns und des Orients*, **2**, 33–46.

—— 1884. Die Neritodonta Dalmatiens und Slavoniens nebst allerlei malakologischen Bemerkungen. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft*, **11**, 17–120.

—— 1892. Fauna fossile terziaria di Markuševec in Croazia. Con un elenco delle Dreissensidae della Dalmazia, Croazia e Slavonia. *Glasnik Hrvatskog Naravoslovnog Društa*, **7**, 113–210.

—— 1896. Neogenska zbirka iz Ugarske, Hrvatske, Slavonije i Dalmacije na Budimpeštanskoj izložbi. *Hrvatsko Naravoslovno Družtvo*, **9**, 98–150.

—— 1897. Gragja za neogensku malakološku faunu Dalmacije, Hrvatske i Slavonije uz neke vrste iz Bosne i Hercegovine i Srbije. *Djela Jugoslavenske Akademije Znanosti i Umjetnosti*, **18**, 1–43.

—— 1902. *Iconographia molluscorum fossilium in tellure tertiaria hungariae, croatiae, slavoniae, dalmatiae, bosniae, herzegovinae, serbiae and bulgariae inventorum*. Officina Soc. Typographicae, Agram, 30 pl.

—— 1905. Naravoslovne crtice sa sjevero-istočne obale Jadranskoga mora. Dio treći. Putopis. *Rad Jugoslavenske Akademije Znanosti i Umjetnosti*, **163**, 1–40.

—— 1906. Šipovo i njegova tercijarna fauna. *Glasnik Zemaljskog Muzeja Bosne i Hercegovine*, **16**, 493–498.

—— 1907. Naravoslovne crtice sa sjevero-istočne obale Jadranskoga mora. Dio četvrti i posljednji. Specijalni. *Rad Jugoslavenske Akademije Znanosti i Umjetnosti*, **169**, 195–251.

BURGERSTEIN, L. 1877. Beitrag zur Kenntniss des Jungtertiären Süsswasser-Depots bei Ueskueb. *Jahrbuch der Kaiserlichen und Königlichen Geologischen Reichsanstalt*, **27**, 243–250.

CLESSIN, S. 1878. Aus meiner Novitäten-Mappe. *Malakozoologische Blätter*, **25**, 122–129.

—— 1890. *Die Molluskenfauna Österreich-Ungarns und der Schweiz*. Bauer & Raspe, Nürnberg, 858 pp.

COHEN, A. S. 2003. *Paleolimnology: the history and evolution of Lake Systems*. Oxford University Press, Oxford, 500 pp.

CONRAD, T. A. 1831. Description of fifteen new species of Recent and three of Fossil shells, chiefly from the coast of the United States. *Journal of the Academy of Natural Sciences of Philadelphia*, **6**, 256–268.

—— 1857. Description of a new genus of the family Dreissenidae. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **9**, 167.

COX, L. R. 1959. Thoughts on the classification of the Gastropoda. *Proceedings of the Malacological Society of London*, **33**, 239–261.

CRISTOFORI, G. D. and JAN, G. 1832. *Catalogus in IV sectiones divisus rerum naturalium in Museo exstantium Josephi de Cristofori et Georgii Jan plurium Acad. Scient. et Societ. Nat. Cur. Sodalium complectens adumbrationem oryctognosiae et geognosiae atque prodrumum faunae et floriae Italiae Superioris. Section II, Conchyliologia. Mantissa in Secundam Partem Catalogi Testaceorum*. Carmignani, Parmae, 8 pp.

CUVIER, G. 1797. *Tableau élémentaire de l'histoire naturelle des animaux*. Beaudouin, Paris, 710 pp.

D'ORBIGNY, A. 1850–1852. *Prodrome de Paléontologie. Stratigraphique universelle des animaux mollusques et rayonnés faisant suitre au cours élémentaire de paléontologie et de géologie stratigraphique*. Masson, Paris, Tome I: 394 pp. (1850); Tome II: 427 pp. (1850); Tome III: 194 pp. (1852).

DE LEEUW, A., MANDIC, O., VRANJKOVIĆ, A., PAVELIĆ, D., HARZHAUSER, M., KRIJGSMAN, W. and KUIPER, K. F. 2010. Chronology and integrated stratigraphy of the Miocene Sinj basin (Dinaride Lake System, Croatia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **292**, 155–167.

—— —— KRIJGSMAN, W., KUIPER, K. and HRVATOVIĆ, H. 2011. A chronostratigraphy for the Dinaride Lake System deposits of the Livno-Tomislavgrad Basin: the rise and fall of a long-lived lacustrine environment. *Stratigraphy*, **8** (1), 29–43.

ĐERKOVIĆ, B. 1964. Geološke karakteristike Kupreškog polja i mogućnost gradnje mikroakumulacija. *Geološki Glasnik*, **10**, 121–137.

FALNIOWSKI, A. 1990. Anatomical characters and SEM structure of radula and shell in the species-level taxonomy of freshwater prosobranchs (Mollusca: Gastropoda: Prosobranchia): a comparative usefulness study. *Folia Malacologica*, **4**, 53–142.

—— and SZAROWSKA, M. 1995*a*. Shell SEM outer and inner structure and rissoacean phylogeny V: *Pseudamnicola* cf. *moussoni* (CALCARA) (Gastropoda: Prosobranchia: Rissoacea: Hydrobiidae). *Malakologische Abhandlungen. Staatliches Museum für Tierkunde Dresden*, **17** (15), 173–180.

—— —— 1995*b*. Shell SEM outer and inner structure and rissoacean phylogeny V: *Dianella thiesseana* (KOBELT) (Gastropoda: Prosobranchia: Rissoacea: Hydrobiidae). *Malakologische Abhandlungen. Staatliches Museum für Tierkunde Dresden*, **17** (16), 181–189.

FÉRUSSAC, A. E. J. P. J. F. D'. A. DE. 1807. *Essai d'une méthode conchyliologique appliquée aux mollusques fluviatiles et terrestres d'après la considération de l'animal et de son test. Nouvelle édition augmentée d'une synonymie des espèces les plus remarquables, d'une table de concordance systématique de celles qui ont été décrites par Géoffroy, Poiret et Draparnaud, avec Müller et Linné, et terminée par un catalogue d'espèces observées en divers lieux de la France*. Delance, Paris, xvi + 142 pp.

—— 1822. *Tableaux systématiques des animaux mollusques classés en familles naturelles, dans lesquels on a établi la concordance de tous les systèmes; suivis d'un prodrome général pour tous les mollusques terrestres ou fluviatiles, vivants ou fossiles*. Bertrand Sowerby, Paris, Londres, 110 pp.

FINGER, I. 1998. Gastropoden der *kleini*-Schichten des Steinheimer Beckens (Miozän, Süddeutschland). *Stuttgarter Beiträge zur Naturkunde (B)*, **259**, 1–51.

FLEMING, J. 1822. *The philosophy of zoology, a general view of the structure, functions and classification of animals, 2*. Constable & Co., Edinburgh, 618 pp.

FUCHS, T. 1870. Beiträge zur Kenntniss fossiler Binnenfaunen. Die Fauna der Congerienschichten von Radmanest im Banate. *Jahrbuch der Kaiserlichen und Königlichen Geologischen Reichsanstalt*, **20**, 343–364.

—— 1877. Studien über die jüngeren Tertiärbildungen Griechenlands. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe*, **37** (2), 1–42.

GLÖER, P. 2002. *Die Tierwelt Deutschlands, 73. Teil: Die Süßwassergastropoden Nord- und Mitteleuropas. Bestimmungsschlüssel, Lebensweise, Verbreitung*. ConchBooks, Hackenheim, 327 pp.

GMELIN, J. F. 1791. *Caroli a Linné, systema naturae. Tomus I. Pars VI*. Beer, Lipsiae, 3021–3910.

GOLIKOV, A. N. and STAROBOGATOV, Y. I. 1975. Systematics of prosobranch gastropods. *Malacologia*, **15** (1), 185–232.

GRAY, J. E. 1840. Shells of molluscous animals. 105–152. *Synopsis of the contents of the British Museum*, Forty-second edition. G. Woodfall, London.

—— 1847. A list of the genera of recent Mollusca, their synonyma and types. *Proceedings of the Zoological Society of London*, **15**, 129–242.

—— 1854. A revision of the arrangement of the families of bivalve shells (Conchifera). *Annals and Magazine of Natural History (Series 2)*, **13** (77), 408–418.

GUDE, G. K. 1913. On some preoccupied molluscan names (generic and specific). *Proceedings of the Malacological Society of London*, **10**, 292–293.

HAAS, F. 1949. On fresh water mollusks from the Amazonian Region. *Anales del Instituto de Biologia, Mexico*, **20**, 107–132.

HAASE, M. 2000. A revision of the genus *Belgrandia*, with the description of a new species from France (Caenogastropoda: Hydrobiidae). *Malacologia*, **41** (1), 171–201.

HALDEMAN, S. S. 1840. *A monograph of the Limniades and other freshwater univalve shells of Northern America*. J. Dobson, Philadelphia, 16 pp.

HARTMANN, W. 1821. System der Erd- und Flußschnecken der Schweiz. Mit vergleichender Aufzählung aller auch in den benachbarten Ländern, Deutschland, Frankreich und Italien sich vorfindenden Arten. *Neue Alpina*, **1**, 194–268.

HARZHAUSER, M. and BINDER, H. 2004. Synopsis of the Late Miocene mollusc fauna of the classical sections Richardhof and Eichkogel in the Vienna basin (Austria, Pannonian, MN 9–MN11). *Archiv für Molluskenkunde*, **133** (1–2), 1–57.

—— and KOWALKE, T. 2002. Sarmatian (Late Middle Miocene) Gastropod Assemblages of the Central Paratethys. *Facies*, **46**, 57–82.

—— and MANDIC, O. 2004. The muddy bottom of Lake Pannon – a challenge for dreissenid settlement (Late Miocene; Bivalvia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **204**, 331–352.

—— —— 2008. Neogene lake systems of Central and South-Eastern Europe: faunal diversity, gradients and interrelations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **260**, 417–434.

—— —— 2010. Neogene dreissenids in Central Europe: evolutionary shifts and diversity changes. 11–29. *In* VAN DER VELDE, G., RAJAGOPAL, S. and BIJ DE VAATE, A. (eds). *The zebra mussel in Europe*. Backhuys Publishers, Leiden/Margraf Publishers, Weikersheim, 555 pp.

—— NEUBAUER, T. A., MANDIC, O., ZUSCHIN, M. and ĆORIĆ, S. 2012. A Middle Miocene endemic freshwater mollusc assemblage from an intramontane Alpine lake (Aflenz Basin, Eastern Alps, Austria). *Paläontologische Zeitschrift*, **86**, 23–41, doi: 10.1007/s12542-011-0117-x.

HERSHLER, R. and LONGLEY, G. 1986. Phreatic hydrobiids (Gastropoda: Prososbranchia) from the Edwards (Balcones Fault Zone) Aquifer Region, south-central Texas. *Malacologia*, **27**, 127–172.

—— —— 1987. Phreatoceras, a new name for Hadoceras Hershler & Longley, 1986 (Gastropoda) Non Strand, 1934 (Cephalopoda). *Proceedings of the Biological Society of Washington*, **100**, 402.

—— and PONDER, W. F. 1998. A Review of Morphological Characters of Hydrobioid Snails. *Smithsonian Contributions to Zoology*, **600**, 1–55.

—— and THOMPSON, F. G. 1992. A review of the aquatic gastropod subfamily Cochliopinae (Prosobranchia: Hydrobiidae). *Malacological Review (Supplement)*, **5**, 1–140.

HÖRNES, M. 1856. Die fossilen Mollusken des Tertiär-Beckens von Wien. I. Band. Univalven. *Abhandlungen der Geologischen Reichsanstalt*, **3** (10. Lieferung), 461–736.

HRVATOVIĆ, H. 2006. *Geological guidebook through Bosnia and Herzegovina*. Geological Survey of Federation BiH, Sarajevo, 172 pp.

HÜSING, S. K., CASCELLA, A., HILGEN, F. J., KRIJGSMAN, W., KUIPER, K. F., TURCO, E. and WILSON, D. 2010. Astrochronology of the Mediterranean Langhian between 15.29 and 14.17 Ma. *Earth and Planetary Science Letters*, **290**, 254–269.

ICZN 2001. Opinion 1965: *Euchilus* Sandberger, 1870 And *Stalioa* Brusina, 1870 (Mollusca: Gastropoda): *Bithinia deschiensiana* Deshayes, 1862 And *Paludina Desmarestii* Prévost, 1821 Designated As The Respective Type Species, With The Conservation Of *Bania* Brusina, 1896. *Bulletin of Zoological Nomenclature*, **58** (1), 63–65.

ILIĆ, A. and NEUBAUER, F. 2005. Tertiary to recent oblique convergence and wrenching of the Central Dinarides: constraints from a palaeostress study. *Tectonophysics*, **410**, 465–484.

ISSEL, A. 1866. Dei molluschi raccolti nella provincia di Pisa. *Memorie della Societa Italiana di Scienze Naturali*, **2** (1), 1–38.

JEKELIUS, E. 1944. Sarmat und Pont von Soceni (Banat). *Memorille Institutului geologic al Romaniei*, **5**, 1–167.

JIMÉNEZ-MORENO, G., MANDIC, O., HARZHAUSER, M., PAVELIĆ, D. and VRANJKOVIĆ, A. 2008. Vegetation and climate dynamics during the early Middle Miocene from Lake Sinj (Dinaride Lake System, SE Croatia). *Review of Palaeobotany and Palynology*, **152**, 237–245.

—— DE LEEUW, A., MANDIC, O., HARZHAUSER, M., PAVELIĆ, D., KRIJGSMAN, W. and VRANJKOVIĆ, A. 2009. Integrated stratigraphy of the early Miocene lacustrine deposits of Pag Island (SW Croatia): palaeovegetation and environmental changes in the Dinaride Lake System. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **280**, 193–206.

JÖRGER, K. M., STÖGER, I., KANO, Y., FUKUDA, H., KNEBELSBERGER, T. and SCHRÖDL, M. 2010. On the origin of Acochlidia and other enigmatic euthyneuran gastropods, with implications for the systematics of Heterobranchia. *BMC Evolutionary Biology*, **10**, 323.

JURIŠIĆ-POLŠAK, Z. and SLIŠKOVIĆ, T. 1988. Slatkovodni gastropodi neogenskih naslaga jugozapadne Bosne, 164–174. *Zbornik referata naučnog skupa "Minerali, stijene, izumrli i živi svijet BIH", Zemaljski Muzej Bosne i Hercegovine, Sarajevo, 7–8 Oktobar 1988.*

KADOLSKY, D. 1993. Der Gattung *Nystia* zugeordnete Arten im Tertiär des mittleren und westlichen Europas (Gastropoda: Rissooidea). *Archiv für Molluskenkunde*, **122**, 335–402.

—— 1998. *Euchilus* Sandberger, 1870 and *Stalioa* Brusina, 1870 (Mollusca, Gastropoda): proposed designation of *Bithinia* *deschiensiana* Deshayes, 1862 and *Paludina desmarestii* Prévost, 1821 as the respective type species, with the conservation of *Bania* Brusina, 1896. *Bulletin of Zoological Nomenclature*, **55** (2), 82–86.

KOCHANSKY-DEVIDÉ, V. and SLIŠKOVIĆ, T. 1978. Miocenske kongerije Hrvatske, Bosne i Hercegovine. *Palaeontologia jugoslavica*, **19**, 1–98.

—— —— 1981. Mlade miocenske kongerije Livanjskog, Duvanjskog i Kupreškog polja u jugozapadnoj Bosni i Hodova u Hercegovini. *Palaeontologia jugoslavica*, **25**, 1–25.

KRSTIĆ, N., SAVIĆ, L., JOVANOVIĆ, G. and BODOR, E. 2003. Lower Miocene lakes of the Balkan Land. *Acta Geologica Hungarica*, **46**, 291–299.

LINNAEUS, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis locis*. Tomus 1, Tenth edition. Laurentius Salvius, Holmiae, iii + 824 pp.

LUDWIG, R. 1865. Fossile Conchylien aus den tertiären Süsswasser- und Meerwasser-Ablagerungen in Kurhessen, Grossherzogtum Hessen und der Bayer'schen Rhön. *Palaeontographica Abteilung A*, **14**, 40–97.

MACALEŢ, R. 2005. Biostratigraphic value of the taxa *Zagrabica, Radix* and *Melanoides* identified in the Neogene deposits from the Dacic Basin. *Acta Palaeontologica Romaniae*, **5**, 299–302.

MANDIC, O., PAVELIĆ, D., HARZHAUSER, M., ZUPANIČ, J., REISCHENBACHER, D., SACHSENHOFER, R. F., TADEJ, N. and VRANJKOVIĆ, A. 2009. Depositional history of the Miocene Lake Sinj (Dinaride Lake System, Croatia): a long-lived hard-water lake in a pull-apart tectonic setting. *Journal of Paleolimnology*, **41**, 431–452.

—— DE LEEUW, A., VUKOVIĆ, B., KRIJGSMAN, W., HARZHAUSER, M. and KUIPER, K. F. 2011. Palaeoenvironmental evolution of Lake Gacko (Southern Bosnia and Herzegovina): impact of the Middle Miocene Climatic Optimum on the Dinaride Lake System. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **299**, 475–492.

MICHEL, E. 1994. Why snails radiate: a review of gastropod evolution in long-lived lakes, both recent and fossil. *Archiv für Hydrobiologie – Beiheft: Ergebnisse der Limnologie*, **44**, 285–317.

MILAN, A., SAKAČ, K. and ŽAGAR-SAKAČ, A. 1974. *Katalog originala tipova vrsta pohranjenih u Geološko-paleontološkom muzeju u Zagrebu*. Geološko-paleontološki muzej u Zagrebu, Zagreb, 186 pp.

MONTFORT, D. DE. 1810. *Conchyliologie systématique, et classification méthodique des coquilles; offrant leurs figures, leur arrangement générique, leurs descriptions caractéristiques, leurs noms; ainsi que leur synonymie en plusieurs langues. Ouvrage destiné à faciliter l'étude des coquilles, ainsi que leur disposition dans les cabinets d'histoire naturelle. Coquilles univalves, non cloisonnées. 2*. Schoell, Paris, 676 pp.

MORTON, J. E. 1955. The Functional Morphology of the British Ellobiidae (Gastropoda Pulmonata) with Special Reference to the Digestive and Reproductive System. *Philosophical Transactions of the Royal Society of London*, **B239**, 89–160.

NEUBAUER, T. A., MANDIC, O. and HARZHAUSER, M. 2011. Middle Miocene Freshwater Mollusks from Lake Sinj (Dinaride Lake System, SE Croatia; Langhian). *Archiv für Molluskenkunde*, **140** (2), 201–237.

NEUMAYR, M. 1869. II. Beiträge zur Kenntniss fossiler Binnenfaunen. *Jahrbuch der Kaiserlichen und Königlichen Geologischen Reichsanstalt*, **19**, 355–382.

—— 1880. V. Tertiäre Binnenmollusken aus Bosnien und der Hercegovina. *Jahrbuch der Kaiserlichen und Königlichen Geologischen Reichsanstalt*, **30** (2), 463–486.

—— 1883. Zur Morphologie des Bivalvenschlosses. *Sitzungsberichte der Akademie der Wissenschaften Wien*, **88**, 385–419.

PAPEŠ, J. 1972. *List Livno. SFR Jugoslavija. Osnovna Geološka Karta 1:100.000*. Savezni geološki zavod, Beograd.

—— 1975. *Tumač za list Livno. SFR Jugoslavija. Osnovna Geološka Karta 1:100.000*. Savezni geološki zavod, Beograd, 63 pp.

PAPP, A. 1959. *Handbuch der stratigraphischen Geologie, 3. Band: Tertiär. Erster Teil, Grundzüge regionaler Stratigraphie*. Ferdinand Enke Verlag, Stuttgart, 411 pp.

PAULUCCI, M. 1878. *Matériaux pour servir à l'étude de la faune malacologique terrestre et fluviatile de l'Italie et de ses îles*. Savy, Paris, 54 pp.

PAVLOVIĆ, P. S. 1903. Građia za poznavanje tercijara u Staroj Srbiji. *Annales Géologiques de la Péninsule Balkanique*, **6** (1), 155–189.

PENNANT, T. 1777. *British zoology. Vol. IV. Crustacea. Mollusca. Testacea*. White, London, viii + 154 pp.

PFEIFFER, C. 1828. *Naturgeschichte deutscher Land- und Süsswasser-Mollusken. Dritte Abtheilung*. Landes-Industrie-Comptoir, Weimar, vi + 84 pp.

POEY, F. 1852. Introduccion a los Ciclostomas con generalidades sobre los moluscos gastropodos y particularmente sobre los terrestres operculados. *Memorias Sobre la Historia Natural de Cuba*, **1** (8), 77–96.

RADOMAN, P. 1973. New classification of fresh and brackish water Prosobranchia from the Balkans and Asia Minor. *Prirodnjački Muzej u Beogradu, Posebna Izdanja*, **32**, 3–30.

—— 1975. Specijacija u okviru roda *Belgrandiella* i njemu srodnih rodova na balkanskom polustvu. *Bulletin du Museum d'Histoire Naturelle de Belgrade, Série B*, **30**, 29–69.

—— 1977. Hydrobiidae auf der Balkanhalbinsel und in Kleinasien. *Archiv für Molluskenkunde*, **107** (416), 203–223.

RAFINESQUE, C. S. 1815. *Analyse de la nature ou tableau de l'univers et des corps organisés*. Privately published, Palerme, 223 pp.

RIEDEL, F., HEALY, J. M., RÖPSDORF, P. and SITNIKOVA, T. Y. A. 2001. Ecology, Shell Morphology, Anatomy and Sperm Ultrastructure of Caenogastropod *Pyrgula annulata*, with a Discussion of the Relations between the 'Pyrgulidae' and Caspian and Baikalian Rissooideans. *Limnologica*, **31**, 289–302.

RISSO, A. 1826. *Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes, 4*. Levrault, Paris, 438 pp.

SANDBERGER, F. 1870–1875. *Die Land- und Süßwasser-Conchylien der Vorwelt*. Kreidel, Wiesbaden, livr. 11: 353–1000 (1875) pp.

SCHLICKUM, W. R. 1960. Die Gattung *Nematurella* Sandberger. *Archiv für Molluskenkunde*, **89**, 203–214.

STEFANI, C. DE. 1877. Molluschi continentali fino ad ora notati in ltalia nei terreni pliocenici, ed ordinamento di questi ultimi. *Atti della Società Toscana di Scienze Naturali Residente in Pisa*, **3** (2), 274–325.

STIMPSON, W. 1865. Researches upon the Hydrobiinae and allied forms: chiefly made from materials in the Museum of the Smithsonian Institution. *Smithsonian Miscellaneous Collections*, **7**, 1–59.

SZAROWSKA, M. 2006. Molecular phylogeny, systematics and morphological character evolution in the Balkan Rissooidea (Caenogastropoda). *Folia Malacologica*, **14** (3), 99–168.

TAYLOR, D. W. 1966. A remarkable snail fauna from Coahuila, México. *The Veliger*, **9** (2), 152–228.

THIELE, J. 1925–1926. Mollusca = Weichtiere. 15–266. *In* KÜKENTHAL, W. and KRUMBACH, T. (eds). *Handbuch der Zoologie*. De Gruyter, Berlin & Leipzig.

THOMPSON, F. G. 1979. The systematic relationships of the hydrobioid snail genus *Nymphophilus* Taylor 1966 and the status of the subfamily Nymphophilinae. *Malacological Review*, **12**, 41–49.

TOURNOUËR, R. 1875. Diagnose d'une coquille fossile des terrains tertiaires supérieurs d'eau douce de l'île de Cos. *Journal de Conchyliologie*, **23**, 167.

TRYON, G. W. 1866. [Book review of] Researches upon the Hydrobiinae and allied forms by Dr. Wm. Stimpson, 8 vol. Smithsonian Institution, Washington DC, August 1865, 58 p. *American Journal of Conchology*, **2** (2), 152–158.

TURTON, W. 1840. *A manual of the land and freshwater shells of the British Islands with figures of each of the kinds. A new edition, thoroughly revised and much enlarged, by John Edward Gray*. Longman, Orme, Brown, Green, and Longmans Paternoster Row, London, 324 pp.

VERMEIJ, G. J. and COVICH, A. P. 1978. Coevolution of freshwater gastropods and their predators. *The American Naturalist*, **112**, 833–843.

VUJNOVIĆ, L. 1981. *Tumač za list Bugojno. SFR Jugoslavija. Osnovna Geološka Karta 1:100.000*. Savezni geološki zavod, Beograd, 54 pp.

—— VRHOVČIĆ, J., JOVANOVIĆ, R., ŽIVANOVIĆ, M., SOFILJ, J., AHAC, A., ANDIJASEVIĆ, M., GOVEDARICA, M., JOVIĆ, R., VELJOVIĆ, R. and MITROVIĆ, P. 1975. *List Bugojno. SFR Jugoslavija. Osnovna Geološka Karta 1:100.000*. Savezni geološki zavod, Beograd.

WAGNER, A. J. 1928. Studien zur Molluskenfauna der Balkanhalbinsel mit besonderer Berücksichtigung Bulgariens und Thraziens, nebst monographischer Bearbeitung einzelner Gruppen. *Annales Zoologici Musei Polonici Historiae Naturalis*, **6** (4), 263–399.

WENZ, W. 1923–1930. *Fossilium Catalogus I: Animalia. Gastropoda extramarina tertiaria*. W. Junk, Berlin, 3387 pp.

—— 1938–1944. Gastropoda. Teil 1: Allgemeiner Teil und Prosobranchia. *In* SCHINDEWOLF, O. H. (ed.). *Handbuch der Paläozoologie, Band 6*. Verlag Gebrüder Bornträger, Berlin, 1639 pp.

WESSELINGH, F. P. 2006. Molluscs from the Miocene Pebas Formation of Peruvian and Colombian Amazonia. *Scripta Geologica*, **133**, 19–290.

WEST, K. and COHEN, A. 1994. Predator-prey coevolution as a model for the unusual morphologies of the crabs and gastropods of Lake Tanganyika. *Archiv für Hydrobiologie – Beiheft: Ergebnisse der Limnologie*, **44**, 267–283.

WILKE, T., DAVIS, G. M., FALNIOWSKI, A., GIUSTI, F., BODON, M. and SZAROWSKA, M. 2001. Molecular systematics of Hydrobiidae (Mollusca: Gastropoda: Rissooidea): testing monophyly and phylogenetic relationships. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **151**, 1–21.

WILSON, A. B., GLAUBRECHT, M. and MEYER, A. 2004. Ancient lakes as evolutionary reservoirs: evidence from the thalassoid gastropods of Lake Tanganyika. *Proceedings of the Royal Society*, **B271**, 529–536.

ŽAGAR-SAKAČ, A. and SAKAČ, K. 1984. Nalazišta unionacejske faune neogenskih (miocenskih) naslaga Dalmacije (južna Hrvatska). *Rad Jugoslavenske Akademije Znanosti i Umjetnosti*, **411**, 209–230.